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HANDBOOK OF AVIAN ANATOMY:

NOMINA ANATOMICA AVIUM

Second Edition

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HANDBOOK OF AVIAN ANATOMY

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—J. J. B.

INTRODUCTION

ANTHONY S. KING

HISTORICAL BACKGROUND

The International Committee on Avian Anatomical Nomenclature (ICAAN) was founded by the World Association of Veterinary Anatomists (WAVA) in 1971. The details of the background to this event were summarized in the General Introduction to the first edition of the *Nomina Anatomica Avium* (NAA) (1979). The first General Chairman was Alfred M. Lucas; it was his untiring devotion to the advancement of avian morphology that led to the formation of ICAAN. Under his active leadership the membership was rapidly augmented to include about 70 international authorities, representing all branches of avian morphology. Within two years draft lists for all the systems of the body had been prepared, and these were considered in 1973 at the First General Meeting of ICAAN in Omaha, Nebraska. At this meeting A. M. Lucas relinquished the post of General Chairman, and was replaced by A. S. King. In 1974 ICAAN received provisional lists at its Second General Meeting in Liverpool, England. At this meeting A. S. King resigned from the General Chairmanship and J. J. Baumel was elected General Chairman, an office he has held to the present. After meetings of the Editorial Committee in Liverpool in 1976 and in Ithaca, New York in 1977, the first edition of the *Nomina Anatomica Avium* was published in 1979.

The nomenclatures of mammalian anatomy (human, *Nomina Anatomica,* NA; veterinary, *Nomina Anatomica Veterinaria,* NAV; histology, *Nomina Histologica,* NH; and embryology, *Nomina Embryologica,* NE) have all been revised periodically. Regular updating is even more necessary for the NAA than the other *Nomina,* because it contains extensive reviews of the literature. Consequently, at a meeting of ICAAN in 1985 at the Royal Veterinary College, London, in association with the XIIth International Congress of Anatomy, plans for the preparation of a second edition of the NAA were initiated. At that meeting it was decided to harmonize the NAA with the NAV for anatomical terms and with the NH for histological terms. A great many of the terms were already the same. Obviously, some terms in the NAA relate to structures which are strictly avian, and these will always constitute differences between the NAA and the other *Nomina.* Some other terms in the NAA are synonyms of NAV and NH terms, but were selected because they

are in common use in avian literature. Also some minor differences arose through the manner in which Latin terms are constructed (see below, Variations in Latin Usage in the Various *Nomina*). Such terms have been brought into line with the NAV in the second edition of the NAA.

ICAAN next met (1986) at the Zoologisch Laboratorium of the University of Leiden. There it was proposed that the second edition of the NAA should be ready by mid-1989 and that it would have to be largely rewritten, with expansion of the text by about 15%, 25 to 30 additional illustrations, and several more pages of references.

Since the understanding of structure requires the integration of all its aspects, it was resolved to complete the histological terms for the visceral systems (Splanchnologia), but not to include the terms for the cell or basic tissues since these are likely to be standard for vertebrates and covered by the NH. An important goal was to keep the price of the book as low as possible in order that it would be readily available to the individual worker.

In his search for a publisher, the General Chairman of ICAAN, Julian Baumel, approached the Smithsonian Institution, which declared its interest in publishing the book for an affordable price, but only if a substantial subvention of was received. This would be similar to the subvention provided by the National Library of Health toward the publication by Academic Press for the first edition. The search for a subvention for the second edition now became urgent.

ICAAN met again in August 1987 in Montreal, in association with the International Congress of the World Veterinary Association (WAVA). The meeting was largely occupied by financial problems. Despite favorable assessments of the academic value of the NAA by several university publishing houses, progress was at a standstill from lack of supporting funds if the price of the book were to be moderate. Private publication by desktop methods was rejected as not doing justice to the work. An interest free loan was offered by the WAVA, but the cost of publication and uncertainties about repaying the loan discouraged acceptance. The search for funds was extended to other foundations and scientific societies in the US and UK.

In early 1989, with the assistance of George Clark of the University of Connecticut, the General Chairman approached the Nuttall Ornithological Club (NOC). At the end of that year the Publications Committee of the NOC authorized Raymond A. Paynter, Jr., editor of the Nuttall Ornithological Club Publications, to accept the second edition of the NAA for publication in its series.

In the light of this welcome decision, ICAAN convened in Antwerp in August 1989, at the Prince Leopold Institute of Tropical Medicine, to finalize the objectives and format of the new edition. In August of the following year, the subcommittee chairmen of ICAAN met at Tufts University, Boston, and in discussion with the NOC, agreed to complete a manuscript by April 1991.

The preparation of the 16 chapters of the new edition has been primarily the work of the individual subcommittee chairmen, as indicated in the preamble to each chapter. The final collation and integration of the lists of terms, annotations, and illustrations of all chapters, the unification of the bibliography, and the preparation of the index, have been the work of the General Chairman.

GENERAL OBJECTIVES OF *NOMINA ANATOMICA AVIUM*

The principal objective of the second edition of the *Nomina Anatomica Avium* is the same as that of the first, namely to promote international scientific communication by establishing an agreed terminology in a universally accepted language. Other general objectives are to survey the literature and to provide a bibliography and illustrations. Thus the *Nomina Anatomica Avium* is unique among the several *Nomina* by being not only a list of terms but also an anatomical reference book. In practice, achieving the objective of standardizing the nomenclature for avian anatomy involved choosing one term where two or more were in use, replacing terms that were obviously defective, and devising new terms in Latin when none existed.

In selecting terms the following principles, which are common to the other *Nomina*, were followed: (1) as few changes as possible should be made in well established terms; (2) with few exceptions, each structure should bear only one name; (3) each term should be in Latin; (4) each term should be as short and simple as possible; (5) each term should be easy to remember, and should above all be informative; (6) eponyms should not be used; (7) every minor structure need not be named.

THE SECOND EDITION

Readership. The work is designed for all biologists who teach or research with normal or pathological avian material. However, it cannot meet the needs of those who lack a general grounding in vertebrate morphology, since limitations of space preclude the definition of many basic structures (e.g.,

Carpometacarpus, Mesencephalon). The annotations do define structures requiring specialized knowledge (e.g. Corpus vasculare phalli), but for full descriptive details the standard works on avian anatomy and physiology, and/or the original papers cited in the annotations, are required.

Title. The title of the book has been changed to *Handbook of Avian Anatomy: Nomina Anatomica Avium,* 2nd Edition, in order better to represent its contents. "Handbook" is used in the sense of a reference book concisely covering the important features of a whole field of knowledge. The relationship between the title and the subtitle of the first edition reflected the historical origin of the work. *Nomina Anatomica Avium* (anatomical names of birds) was conceived as a list of names of anatomical parts like the other (mammalian) *Nomina,* but gradually annotations, references, and illustrations were developed. The previous subtitle, "An Annotated Anatomical Dictionary of Birds", sought to include such accessions but was somewhat misleading since the contents were not comprehensive or in alphabetical order. The updating and augmentation of the annotations in the new edition enhance its significance as a source book of information on avian morphology. Therefore, the title and subtitle have now been reversed, giving priority to the more general title of *Handbook of Avian Anatomy.*

Terminology. One change already mentioned is the harmonization of the terms with those of the NAV and NH. Errors in the Latin in the first edition have been corrected. Histological terms have been systematically added to the visceral systems and included in some other systems (e.g., Integument, Systema lymphaticum). Some groups of terms that were fragmentary in the first edition (e.g., Juncturae laryngis) have been completed. Rarely (e.g., nephron, phallus) a set of terms has been replaced by fresh terms based on new knowledge. In general, as few terms as possible have been changed. Terms in brackets following the primary recommended terms are secondary official alternatives. Italicized terms are ontogenetic.

Variations in Latin usage in the various Nomina. In the Introduction to the fourth edition of the *Nomina Anatomica* (NA) (1977:8) the International Committee on Anatomical Nomenclature (IANC) advocated a liberal approach to the use of Latin in anatomy, in an attempt to simplify complex or unfamiliar terms. Several conservative usages were discussed, such as the insistence on a*n*ulus; this was replaced in the fourth edition of the NA by a*nn*ulus, thus agreeing with the familiar "annular" and "annulaire", though the NH in the same volume still used a*n*ulus in the Spermatozoon. It was also pointed out that in the newer *Nomina Embryologica* and *Nomina Histologica,* adjectives rather than genitives were preferred in many of the newly Latinized embryological and histological terms, and that some existing terms in the NA itself were similarly altered. For example, "renal cortex" can be presented as Cortex renis, as in the Paris *Nomina Anatomica* of 1955, and

this usage has been retained in the NAV (1983). However, "renal cortex" can also be directly translated into Cortex renalis, and this term was adopted by the fourth edition of the NA and the first edition of the NH (published together in 1977); this has been retained in the sixth edition of the NA and the third edition of the NH (published together in 1989). Other new adjectival forms occurred in the fourth and sixth editions of the NA, usually as official alternatives [in brackets]; examples are Ossa cranii [cranialia] and Ossa carpi [carpalia], and others appeared in the sixth edition such as Cavitas thoracis [thoracica]. The NH (1989) went somewhat further, for example, with Cavitas oris [oralis] whereas the NA retained Cavitas oris.

It was further argued in the fourth edition of the *Nomina Anatomica* (p.A8) and the first edition of the *Nomina Anatomica Avium* (pp.x-xi) that the more a Latin term resembles its vernacular equivalent, the easier it is to interpret it. This can be illustrated by the term *Cavum* nasi of the Basle *Nomina Anatomica* of 1895 (BNA), the Jena *Nomina Anatomica* of 1936 (JNA), and the Paris Nomina Anatomica of 1955 (PNA). In the fourth edition of the NA in 1977 this became *Cavitas* nasi, and has finally yielded to *Cavitas* nasi [*nasalis*] in the sixth edition of the NA (1989). The 1983 edition of the NAV has retained Cavum nasi. Cavitas nasalis closely resembles "nasal cavity" of English, and "cavité nasale", "cavità nasale", and "cavidad nasal" of the Romance languages. This similarity helps biologists, such as those from Arabic, African, or Asian nations, who may have little or no knowledge of Latin but use English or a Romance language as a second language. This substitution of Cavitas for Cavum was evidently initiated by the NH. In its footnote 99, the fourth edition of the NA (1977) noted that it had "followed the Histology Subcommittee in substituting Cavitas for Cavum throughout this section" (Splanchnologia), thus changing 12 terms, these changes being carried forward into the sixth edition of the NA (1989). The NAV (1983) retained Cavum throughout Splanchnologia.

One reason for defending old terms is that they belong to classical Latin, new terms being resisted because they are late Latin or even recent Latin neologisms. For example, it is possible to object to Cavitas because it is new Latin, whereas Cavum is classical Latin. But linguistic arguments can be difficult to sustain. For example, the third edition of the NAV requires Arbor bronch*a*lis, without the familiar i, and justifies it in annotation 219 by claiming that this is the correct Latin spelling. However, the Latin Dictionary of Lewis and Short (1969) and the Oxford Dictionary derive bronch*ia* from βρογχια—Greek, with an *iota* before the alpha. Another reason for resisting changes of old into new terms is that this infringes the first of the seven principles for selecting terms (mentioned above), i.e., that as few changes as possible should be made in well established terms. The authors of standard anatomical textbooks naturally object particularly strongly to changes in ter-

minology. On the other hand, new terms may well satisfy the fifth and sixth principles, in being more simple and informative.

In general, the second edition of the NAA continues to support the attitude of the IANC, reaffirming the view expressed in the first edition that Latin should be "the servant and not the master of anatomists" (NAA, 1979:xi). Despite this, however, in the second edition of the NAA the NAV terms are given priority, in the interests of harmonization. Nevertheless, some of the NA and NH terms are given as official alternatives. In this way the second edition of the NAA forms a bridge between the NA and NH on the one hand and the NAV on the other. The wind of change is detectable in anatomical terminology, but the trend is slow. Further evolution must be left to future editions of the various *Nomina*.

Annotations. As in the first edition, annotations are indicated in the lists of terms by a superscript number and follow the lists in each chapter. Because of the increased importance of the annotations, their objectives were thoroughly reconsidered and defined as follows: (1) to list synonyms, citing the first and other major sources; (2) to analyse homologies; (3) to justify the choice of a term; (4) to provide an anatomical definition or illustration of any term that might not be readily understood; (5) to summarize (within obvious limitations of space) the essentials of the site, organization, and function of complex structures; (6) to cite major descriptive and review articles published since the first edition; and (7) to rectify omissions and errors of the first edition.

Some reviewers of the first edition found the Latin difficult. For example, a nonanatomist might not know that the kidney is Ren and the liver Hepar. Where the English form of a term is not easily recognizable from the Latin (e.g., Palpebra ventralis) the annotations usually now give the English form (lower eyelid) at least once. It is generally accepted that biologists may translate the official Latin terms of the various *Nomina* into their own vernacular. However, it is recommended that the Latin version be used when the term is first introduced into a publication. Economy of space precludes the systematic conversion into languages in addition to English.

Bibliography. As in the first edition, the references show the authorities for the selection of a term and for the anatomical data in the annotations. Newly added references remedy omissions from the first edition; they also include citations of major review articles, as well as papers presenting new findings, published after the first edition.

Illustrations. The main objective of the illustrations remains unchanged, i.e., to clarify complex structures and identify their parts. However, lesser structures that are not the prime purpose of a figure are sometimes included in order to substitute for a textual definition or to elucidate an annotation. Measurements are not given, as is standard procedure in classical reference works on vertebrate morphology (for example, see Goodrich, 1958; Marshall, 1962; Romer, 1962). Some figures have been redrawn or relabeled, and many new illustrations have been added.

Index. In the first edition the index included many English versions of terms, but without doing so consistently. Therefore, it was sometimes difficult for nonanatomists, unfamiliar with Latin, to find the name of a particular structure. The new index contains the Latin terms, the English equivalents of terms not readily recognizable from the similarity of the Latin to the English, and many of the commonly used synonyms of the recommended terms.

INFORMATION ON USING *NOMINA ANATOMICA AVIUM*

Taxonomic nomenclature. Most of the anatomical structures that are listed are common to birds generally, but important structures or variations of features peculiar to individual species or larger taxa are included if the necessary anatomical facts are known. The scientific taxonomic nomenclature is that of Morony, Bock, and Farrand (1975); common names in English have been selected from widely used field guides and faunal references; the common names have been standardized throughout the volume. In certain instances both the common name and the scientific name of a bird is given. When published works are cited, often only the generic name is given; the full binomial name of the species (if known) may be obtained from the cited references. Scientific names of orders and families are often converted into their informal equivalents (e.g., gruids for Gruidae, or passeriforms for Passeriformes). The common names of the ordinary laboratory and domestic forms always refer to the species of genera indicated below. It is recognized that the derivation of these birds has not, in fact, always been conclusively established, but for convenience the relationships are assumed to be as stated:

Duck:	forms of *Anas platyrhynchos*
Goose:	forms of *Anser anser*
Pigeon:	forms of *Columba livia*
Turkey:	forms of *Meleagris gallopavo*
Chicken:	forms of *Gallus gallus*
Quail:	forms of *Coturnix*
Canary:	forms of *Serinus canarius*
Guinea Fowl:	forms of *Numida meleagris*
Budgerigar:	forms of *Melopsittacus undulatus*

Abbreviations. For each of the General Abbreviations the first is singular and the second (in parenthesis) is plural. Thus "A." stands for the nominative singular Arteria, and "Aa." stands for the nominative plural Arteriae. Then the nominative and genitive singular forms of the term are given in full, e.g., Arteria, arteriae, followed (for nouns only) by the nominative and genitive plural cases, e.g., arteriae, arteriarum. For an explanation of nominative and genitive, singular and plural, see Appendix A, Latin Grammar. The abbreviations in the Key to Main Headings represent the titles of the major subdivisions of the terminology, e.g., Myol. represents Myologia.

General Abbreviations

A. (Aa.)	=Arteria, arteriae; arteriae, arteriarum
Anast. (Anastt.)	=Anastomosis, anastomosis; anastomoses, anastomosium
Annot. (Annott.)	=Annotation(s)
Ant.	=Anterior
Apt. (Aptt.)	=Apterium, apterii; apteria, apteriorum
Artc. (Artcc.)	=Articulatio, articulationis; articulationes, articulationum
Caps. (Capss.)	=Capsula, capsulae; capsulae, capsularum
Cart. (Cartt.)	=Cartilago, cartilaginis; cartilagines, cartilaginorum
Caud.	=Caudalis
Corp. (Corpp.)	=Corpus, corporis; corpora, corporum
Cran.	=Cranialis
Decuss. (Decuss.)	=Decussatio, decussationis; decussationes, decussationum
Fac. (Facc.)	=Facies, faciei; facies, facium
Fasc. (Fascc.)	=Fasciculus, fasciculi; fasciculi, fasciculorum
For. (Forr.)	=Foramen, foraminis; foramina, foraminum
G. (Gg.)	=Ganglion, ganglii; ganglia, gangliorum
Gl. (Gll.)	=Glandula, glandulae; glandulae, glandularum
Lat.	=Lateralis
Lig. (Ligg.)	=Ligamentum, ligamenti; ligamenta, ligamentorum
M. (Mm.)	=Musculus, musculi; musculi, musculorum
Maj.	=Major
Med.	=Medialis
Mem. (Memm.)	=Membrana, membranae; membranae, membranarum
Min.	=Minor
N. (Nn.)	=Nervus, nervi; nervi, nervorum
Nuc. (Nucc.)	=Nucleus, nuclei; nuclei, nucleorum

Pedunc. (Peduncc.)	=Pedunculus, pedunculi; pedunculi, pedunculorum
Plx. (Plxx.)	=Plexus, plexus; plexus, plexuum
Post.	=Posterior
Pt. (Ptt.)	=Pteryla, pterylae; pterylae, pterylarum
Proc. (Procc.)	=Processus, processus; processus, processuum
Prof.	=Profundus
R. (Rr.)	=Ramus, rami; rami, ramorum
Rdx. (Rdxx.)	=Radix, radicis; radices, radicum
Rec. (Recc.)	=Rectrix, rectricis; rectrices, rectricum
Reg. (Regg.)	=Regio, regionis; regiones, regionum
Rostr.	=Rostralis
Rmx. (Rmxx.)	=Remex, remigis; remiges, remigum
Superf.	=Superficialis
Sut. (Sutt.)	=Sutura, suturae; suturae, suturarum
Sync. (Syncc.)	=Synchondrosis, synchondrosis; synchondroses, synchondrosium
Synd. (Syndd.)	=Syndesmosis, syndesmosis; syndesmoses, syndesmosium
Synos. (Synoss.)	=Synostosis, synostosis; synostoses, synostosium
Tec. (Tecc.)	=Tectrix, tectricis; tectrices, tectricum
Tr. (Trr.)	=Tractus, tractus; tractus, tractuum
V. (Vv.)	=Vena, venae; venae, venarum
Vas l. (Vasa l.)	=Vas lymphaticum, vasis lymphatici; vasa lymphatica, vasorum lymphaticorum
Ventr.	=Ventralis

Key to Main Headings

Art.	=Arteriae
Arthr.	=Arthrologia
Cardvas.	=Systema cardiovasculare
Cloaca	=Cloaca
CNS	=Systema nervosum centrale
Cor	=Cor
Diges.	=Apparatus digestorius [Systema digestorium]
Endoc.	=Glandulae endocrinae
Fem.	=Organa genitalia feminina
Integ.	=Integumentum commune
Lym.	=Systema lymphaticum et Splen [Lien]
Masc.	=Organa genitalia masculina
Myol.	=Myologia
Osteo.	=Osteologia

Pericar.	=Pericardium, Pleura, et Peritoneum
PNS	=Systema nervosum periphericum
Resp.	=Apparatus respiratorius [Systema respiratorium]
Sens.	=Organa sensuum [Organa sensoria]
Term. sit.	=Termini situm et directionem indicantes—Termini generales
Topog.	=Anatomia topographica externa
UG.	=Apparatus urogenitalis [Systema urogenitale]
Urin.	=Organa urinaria
Ven.	=Venae

Recommended Form of Citations

1) Book citation in body of text:
   Baumel, *et al.* (1993)
2) Chapter citation in body of text:
   Evans (1993)
3) Book citation in bibliography:
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Authors are requested to employ the Latin terms in scientific articles and books, at least on the first occasion when a term is used.

ORGANIZATION OF ICAAN

General. The International Committee for Avian Anatomical Nomenclature (ICAAN) comprises: General Chairman, Vice-chairman, Secretary General, Chairmen of subcommittees, Consultant for Avian Taxonomy, Consultant for Classical Languages. The Committee is organized into subcommittees related to the body systems, each subcommittee having its own Chairman (and in some instances, Vice-chairman). The Executive Committee consists of the General Chairman and Vice-chairman, and Secretary General of ICAAN, subcommittee Chairmen, and the Editorial Committee.

At the time of publication of the second edition of the *Nomina Anatomica Avium* the holders of these offices were: General Chairman, J. J. Baumel; Vice-chairman, M. Yasuda; Secretary General , A. S. King; Consultant for Avian Taxonomy, R. L. Zusi; Consultant for Classical Languages, L. Malinovský. The Chairman of the Editorial Committee is J. J. Baumel; its members are J. E. Breazile, H. E. Evans, A. S. King, and J. C. Vanden Berge.

The Subcommittee Chairmen are:

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J. J. Baumel and R. J. Raikow (Arthrologia).
J. J. Baumel (Systema cardiovasculare).
J. E. Breazile and W. J. Kuenzel (Systema nervosum centrale).
G. A. Clark (Termini situm et directionem indicantes, Termini generales; Anatomia topographica externa; Integumentum commune).
J. L. Dubbeldam (Systema nervosum periphericum).
A. Epple (Glandulae endocrinae).
H. E. Evans and G. R. Martin (Organa sensuum).
A. S. King (Apparatus respiratorius; Apparatus urogenitalis).
J. McLelland (Pericardium, pleura et peritoneum; Apparatus digestorius).
D. Berens von Rautenfeld (Systema lymphaticum).
J. C. Vanden Berge and G. A. Zweers (Myologia).

Functions of General Chairman and Secretary General. The General Chairman and Secretary General work together to manage the general policy of ICAAN, to select subcommittee chairmen and members of subcommittees, to organize general meetings of ICAAN, meetings of the Executive Committee, and meetings of the Editorial Committee, to arrange for the production of lists of terms, and to settle controversial terms (see below).

Although the General Chairman is responsible for the approval of additional subcommittee members, any member of a committee may propose new subcommittee members. Such a proposal is sent to the General Chairman. The General Chairman consults the subcommittee Chairman in the appropriate field. If the subcommittee chairman approves of the proposal, the General Chairman obtains from the proposed new subcommittee member a curriculum vitae and a list of his avian publications. If the General Chairman now approves of the proposal, he notifies the new member of his decision and sends him the relevant documents.

Functions of subcommittee chairmen and subcommittee members. The subcommittees are responsible for the various anatomical systems. It is the duty of the chairman of each subcommittee to prepare the list of terms for that system, with the help of his subcommittee members.

Functions of the Executive Committee. The Executive Committee formulates and implements ICAAN policy (see above for composition of this Committee).

Functions of the Editorial Committee. The Editorial Committee is responsible for the publication of the *Nomina Anatomica Avium* (see above for composition of this Committee).

Controversial Terms. In general, controversial terms are settled through discussion at General Meetings of ICAAN. However, in difficult cases the decision rests with the best qualified person, i.e., the subcommittee chairman, after appropriate discussion at a General Meeting. If all else fails, the decision is made by the General Chairman in consultation with the Secretary General.

1

TERMINI SITUM ET DIRECTIONEM PARTIUM CORPORIS INDICANTES

GEORGE A. CLARK, JR.

With contributions by subcommittee members: J. J. Baumel and A. S. King.

The following account is an expansion of that in NAA (1979). We are greatly indebted to A. M. Lucas, V. Komárek, and V. Simic for their contribution in the previous edition. We appreciatively acknowledge M. J. Spring who prepared the figures for this chapter.

Terms of orientation. Cranial and caudal are used throughout the *Handbook of Avian Anatomy*, except that rostral replaces cranial within the head from the level of the occipital condyles. Superior and inferior are entirely avoided, but the prefixes supra- and infra- are retained for convenience and because of long usage, e.g., Nervus infraorbitalis. Anterior and posterior are used only in the eye and ear (see **Organa Sensoria**), but again the prefix post- has occasionally been used in terms which are well established, such as Ligamentum postorbitale. The prefix pro- has generally been preferred to pre-, although both have been used. That some anatomists strongly prefer anterior and posterior as general alternatives to cranial and caudal is recognized, because these are time-honored terms in the literature of vertebrate morphology. However, these terms can be confused through their entirely different meaning in human anatomy, where they refer to ventral and dorsal. Anyone not convinced of this potential confusion should examine the anatomical writings of the eminent nineteenth century prosectors of the Zoological Society of London, W. A. Forbes, A. H. Garrod, and F. E. Beddard. Although writing as zoologists in zoological journals, these authors commonly used anterior and posterior in the human sense. Sometimes the usage of human anatomy and the zoological usage were both employed in the same paper (e.g., Beddard, 1896). Even so, it is not realistic to expect the instant and universal adoption of cranial and caudal; nevertheless, it is hope that eventually this will be achieved.

Anatomical position of a bird. In order to apply adjectives to designate the relative positions of body parts, their locations, or relationships, or to designate

planes, axes, or surfaces, it is necessary to specify the standard anatomical position of a bird. This position is arbitrarily defined as one in which: (1) the bird stands erect with femorotibial and intertarsal joints slightly flexed, (2) the wings are outstretched laterally, and (3) the neck is fully extended rather than in the S-shaped curve of the living bird (NAA, 1979).

The upper surface of the wing, regardless of its position, is designated as dorsal, even when it is folded against the side of the trunk; its lower surface is termed ventral. Moreover, the wing has cranial and caudal margins. In the pelvic limb, caudal and cranial surfaces apply proximal to the intertarsal joint, and dorsal and plantar surfaces are used in the foot distal to that joint. See Figs. 1.1, 1.2, and **Introduction.** Terms of orientation.

TERMINI GENERALES[48]

Aboralis[1]
Afferens[2]
Ascendens[3]
Caudalis [Posterior][4]
Centralis[5]
Centrifugalis[6]
Centripetalis[6]
Coronalis[7]
Cranialis [Anterior][8]
Descendens[9]
Dexter[10]
Distalis[11]
Dorsalis[12]
Efferens[13]
Externus[14]
Fibularis[15]
Frontalis[16]
Horizontalis[17]
Intermedius[18]
Internus[19]
Lateralis[20]
Longitudinalis[21]
Medialis[22]
Medianus[23]
Medius[24]
Occipitalis[25]
Oralis[26]
Paramedianus [Sagittalis][27]
Plantaris[28]
Periphericus, Peripheralis[29]
Perpendiculus[30]
Profundus[31]
Proximalis[32]
Radialis[33]
Rostralis[34]
Sinister[35]
Superficialis[36]
Tibialis[37]
Transversalis, Transversus[38]
Ulnaris[39]
Ventralis[40]
Verticalis[41]

AXES, LINEAE ET PLANA

Axis rostrocaudalis[42]
Axis proximodistalis[43]
Linea mediania dorsalis[44]
Linea mediania ventralis[44]
Planum medianum[45]
Plana paramediana [P. sagittalia][27 45]
Plana transversalia[46]
Plana dorsalia[47]

ANNOTATIONS

(1) **Aboralis.** Aboral, away from the mouth. Contrast with Oralis.

(2) **Afferens.** Afferent, to bring or carry toward a structure or point. Contrast with Efferens.

(3) **Ascendens.** Ascending, directed cranially. Contrast with Descendens. (See **Cardvas.** Intro.).

(4) **Caudalis [Posterior].** Caudal, of, or in the direction of, the tail (Fig. 1.2). Contrast with Cranialis. The term Posterior is used in the eye and ear (see **Intro.** Terms of orientation).

(5) **Centralis.** Central. In, at, near, or towards the center. Contrast with Peripheralis.

(6) **Centrifugalis.** Centrifugal, departing or turning away from the center or axis. **Centripetalis.** Centripetal, approaching or turning toward the center or axis.

(7) **Coronalis.** Coronal, pertaining to the crown (Corona).

(8) **Cranialis [Anterior].** Cranial, of, or in the direction of the head (Fig. 1.2). Contrast with Caudalis. The term Anterior is used in the eye (see **Intro.** Terms of orientation).

(9) **Descendens.** Descending, directed downwards or caudally. Contrast with Ascendens. See **Cardvas.** Intro.

(10) **Dexter.** On, or pertaining to, the right. Contrast with Sinister.

(11) **Distalis.** Distal. Distant or farthest from a central point, plane (Fig. 1.2). For limbs the trunk is the reference point; for example, the manus is distal to the antebrachium. With arteries the heart is the ultimate site of reference. Contrast with Proximalis.

(12) **Dorsalis.** Dorsal. Toward or near the back (Figs. 1.1, 2) (see **Intro.** Terms of orientation). Contrast with Ventralis.

(13) **Efferens.** Efferent, conducting or carrying away from or outward. Contrast with Afferens.

(14) **Externus.** External, or outward. Contrast with Internus.

(15) **Fibularis.** Fibular, pertaining to the fibula, a bone on the lateral or fibular side of the limb. Contrast with Tibialis.

(16) **Frontalis.** Frontal, designating the forehead or Frons (**Topog.** Annot. 5.).

(17) **Horizontalis.** Horizontal, pertaining to the planes parallel to the back or dorsal surface of the body and lying at right angles to both median and transverse planes.

(18) **Intermedius.** Intermediate, situated between two points, parts, or planes of reference.

(19) **Internus.** Internal, inner or inward. Contrast with Externus.

(20) **Lateralis.** Lateral, pertaining to the side (Fig. 1.1). Contrast with Medialis.

(21) **Longitudinalis.** Longitudinal, along the long axis of the body or a part.

(22) **Medialis.** Medial, toward the middle; situated closer to the midline of the body or a part. Contrast with Lateralis.

(23) **Medianus.** Situated or extending in the axial plane; located in the middle of the body or of a structure (e.g. a limb).

(24) **Medius, Media, Medium.** Middle, e.g., the middle item of three related structures (e.g. A. renalis media).

(25) **Occipitalis.** Occipital, pertaining to the occipital complex of bones at the back of the head. (**Topog.** Annot. 7).

(26) **Oralis.** Oral, pertaining to, or directed toward, the mouth. Contrast with Aboralis.

(27) **Paramedianus [Sagittalis]; Plana paramediana [P. sagittalia].** Synonymy: Parasagittalis. These terms designate positions or planes lateral and parallel to the median plane of the body. Any plane to the side of, and parallel to the median sagittal (interparietal) suture (plane) of the skull.

(28) **Plantaris.** Plantar, designating the sole of the Pes (foot). In most birds when standing the metatarsal part of the Pes is elevated, but in some, such as podicipediforms, the entire plantar surface of the Pes rests on the ground. See Figs. 1.1, 2).

(29) **Periphericus, Peripheralis.** Peripheral. Distant from the center; near the circumference. Contrast with Centralis.

(30) **Perpendicularis.** Perpendicular, pertaining to lines or planes running at right angles to other lines or planes.

(31) **Profundus.** Deep. Contrast with Superficialis.

(32) **Proximalis.** Proximal, toward or nearer a central point, plane, or point of origin. For limbs the trunk is the reference point; for example, the humerus is proximal to the ulna. Contrast with Distalis.

(33) **Radialis.** Radial, pertaining to the radius, hence indicating the leading edge of the antebrachium (forearm) or other parts of the thoracic limb (wing). Contrast with Ulnaris.

(34) **Rostralis.** Rostral means directed towards the tip of the Rostrum (beak), and is used in the head in place of Cranialis. See Fig. 1.2.

(35) **Sinister.** On or pertaining to the left. Contrast with Dexter.

(36) **Superficialis.** Superficial; pertaining to the surface. Contrast with Profundus.

(37) **Tibialis.** Tibial, pertaining to the tibia, hence indicating the medial side of the limb. Contrast with Fibularis.

(38) **Transversalis, Transversus.** Transversal or transverse. Lying across the long axis of the body or a part.

(39) **Ulnaris.** Ulnar, pertaining to the ulnar side or trailing edge of the thoracic limb. Contrast with Radialis.

(40) **Ventralis.** Ventral. Pertaining to the belly or lower side of the abdomen (Figs. 1.1, 1.2). (See Terms of orientation.) Contrast with Dorsalis.

(41) **Verticalis.** Vertical, designating any line or plane that passes vertically through the body.

(42) **Axis rostrocaudalis.** Rostrocaudal axis. The longitudinal axis of the body from the tip of the rostrum to the tip of the tail.

(43) **Axis proximodistalis.** Proximodistal axis. The longitudinal axis of a limb from the center of the shoulder to the tip of the Digitus major of the Manus or from the center of the hip joint to the claw of Digitus III of the Pes.

(44) **Linea mediana dorsalis/ventralis.** Middorsal and midventral lines. Lines projected onto the dorsal and ventral surfaces, respectively, of the body representing the surface edges of Planum medianum.

(45) **Planum medianum.** Median plane, the middle dorsoventral plane that bisects the body longitudinally into right and left halves.

(46) **Plana transversalia.** Planes that cut across the body from side to side, at right angles to the rostrocaudal axis of the body. Transverse planes of limbs or other appendages are at right angles to the proximodistal axes.

(47) **Plana dorsalia.** Synonymy: horizontal planes, frontal planes. Dorsal planes are parallel to the dorsal surface of the body and perpendicular to the median and transverse planes.

(48) **Termini generales.** Comprehensive lists of general terms are found in the human *Nomina Anatomica* (NA, 1989) and the *Nomina Anatomica Veterinaria* (NAV, 1983). Word roots among these terms have been used to construct anatomical names for all vertebrates including birds. In the present volume, several of the sections on avian organ systems are preceded by brief lists of general terms.

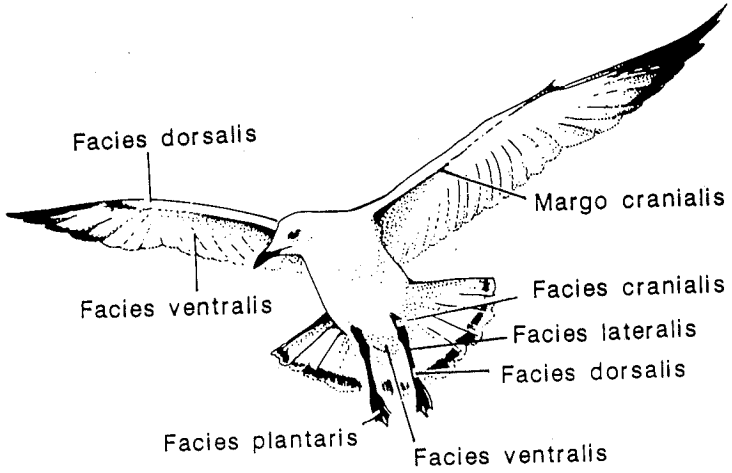

Fig. 1.1. General nomenclature for body surfaces. (See Anatomical position of a bird.)

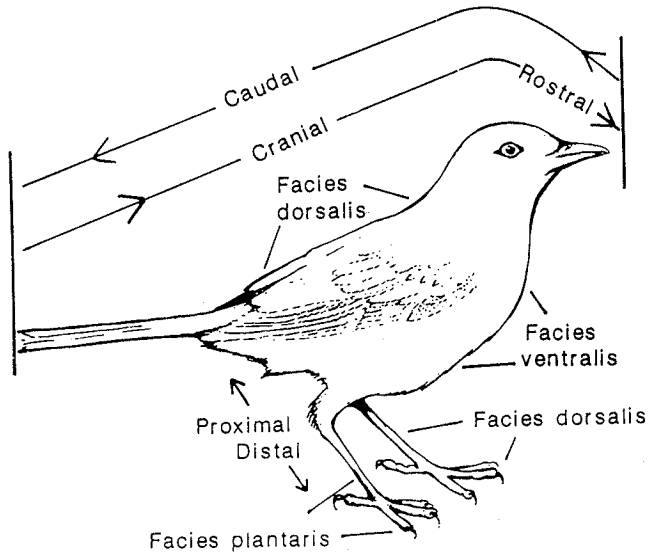

Fig. 1.2. Terms of position and direction for a bird. The term rostral refers to the direction towards the tip of the beak and is used in the head only. (See Terms of orientation.)

2

ANATOMIA TOPOGRAPHICA EXTERNA

GEORGE A. CLARK, JR.

With contributions from subcommittee members: E. H. Burtt, Jr.; M. H. Clench; D. W. Johnston; Vl. Komárek; P. Stettenheim. Helpful suggestions and/or information have been given by J. J. Baumel, H. Berkhoudt, H. E. Evans, Gy. Fehér, A. S. King, A. M. Lucas, J. McLelland, G. Michel, and G. A. Zweers. M. J. Spring prepared the figures. This chapter is contribution number 681 of the New York State Science Service.

This chapter on external topographic anatomy provides names for the parts and regions, and combines coverage traditionally separated in anatomical nomenclatures as Partes Corporis and Regiones Corporis (e.g., in NAV, 1983). The name of a part can be used to designate a region that is an external surface area having arbitrary boundaries. Names given in the subsequent chapters on Integumentum Commune, Osteologia, and other systems may also be useful in describing aspects of external topography. Internal structures are not visible externally; nonetheless, for certain purposes external regions may be designated most usefully in terms of underlying structures such as bones. Although coining of new names may be necessary at times, efforts should be made to determine whether suitable terms exist already in the published literature.

In the following list, terms recommended for mammals in the NAV (1983) are used for birds where such use does not severely contradict current ideas on homology. A goal here is to provide terms applicable over a wide range of taxa. Unfortunately, it is not possible to list all available terms in this necessarily brief account. In selecting specialized terms useful for only a limited range of bird taxa, we have emphasized terms applicable to widely encountered birds, including poultry. Coues (1872) extensively reviewed avian topographic anatomy including details for many terms used here. Additional terms are available in the exceptionally thorough presentations of external topographic anatomy for particular species by Komárek (1958, 1979) on the chicken and goose and by Lucas and Stettenheim (1972) for the chicken, turkey, quail, duck, and pigeon. Campbell and Lack (1985) provided a general summary of the major taxonomic groups of birds of the world, including many differences in external topographic anatomy.

TERMINOLOGY

FACIES ET MARGINES[1]

Facies/Margo dorsalis
  Facies dorsalis alae[2]
Facies/Margo ventralis
  Facies ventralis alae[2]
Facies/Margo lateralis
Facies/Margo medialis
Facies/Margo cranialis
Facies/Margo caudalis
Facies/Margo rostralis
Facies plantaris

CAPUT[3]

Regio cranialis [Cranium][3]
  Pileum[4]
    Frons [Regio frontalis][5]
    Corona [Vertex][6]
    Occiput [Regio occipitalis][7]
  Crista pennae[8]
  Regio auricularis[9]
    Apertura auris externae[9]
Angulus craniofacialis [A. frontonasalis][3]
Regio facialis [Facies][3]
Regio oralis
  Os[10]
  Rima oris [Apertura oris][10]
  Angulus oris[11]
Rostrum[3 12]
  Rostrum maxillare[12]
    Culmen[13]
    Tomium maxillare[14]
    Unguis maxillaris (**Integ.** Annot. 82)
  Rostrum mandibulare[12]
    Gonys[13]
    Tomium mandibulare[14]
    Unguis mandibularis (**Integ.** Annot. 82)
      Lamellae rostri[15]
Regio malaris [Mala][16]
  Rictus[17]
    Pars maxillaris
    Pars mandibularis
Regio interramalis[18]
  Mentum[19]
  Regio gularis [R. submalaris][20]
Regio nasalis
  Naris[21]
    Operculum nasale[21]
  Cera[22]
Lorum[23]
Regio orbitalis
  Oculus[24]
  Palpebra dorsalis[24]
  Palpebra ventralis[24]
  Membrana nictitans [Palpebra tertia][25]
Projectio pennarum[26]
Saccus protrudens[27]

COLLUM[28]

Nucha[28]
Jugulum[28]
Regio ingluvialis[29]

TRUNCUS[30]

Regio omalis [Omus][31]
  Axilla[32]
Dorsum trunci[33]
  Dorsum[33]
  Pyga[33]
Latus trunci[33]
  Axilla[32]
  Ilia[33]
Ventrum trunci
  Regio ingluvialis[29]
  Pectus[34]
  Venter[34]
    Pars infrapubica
    Pars suprapubica
    Facies subcaudalis
  Ventus cloacae[35]
    Eminentia venti[35]
  Crissum[35]

CAUDA[36]

Dorsum caudae[36]
Ventrum caudae[36]
Rectrices[36]
Uropygium[36]
Bulbus rectricium[36]
Glandula uropygialis (**Integ.** Annot. 13)

ALA [MEMBRUM THORACICUM][37]

Regio omalis [Omus][31]
Axilla[32]
Brachium[37]
Cubitus[37]
Antebrachium[37]
Carpus[37]
Manus[37]
Alula[37]
Calcar alae (**Integ.** Annot. 88)

MEMBRUM PELVICUM[38]

Coxa[38]
Femur[38]
Genu[38]
Crus[38]
Articulatio intertarsalis[38]
Pes[38]
Tarsometatarsus[38 39]
Junctura metatarsophalangealis[38]
Calcar metatarsale (Fig. 2.4; **Integ.** (Annot. 89; **Osteo.** Annot. 296)

(continued)

MEMBRUM PELVICUM [38] (cont.)

Pulvinus hypotarsalis (**Integ.** Annot. 85)
Pulvinus metatarsalis[40]
Plica metatarsalis[40]
Digiti[38,41]
  Digitus pedis I [Hallux][41]
  Digiti pedis II-IV[41]
Phalanges
Pulvinus digitalis (Fig. 2.4; **Integ.** Annot. 86)
Unguis digiti pedis[41]
Juncturae interphalangeales[38]
Tela interdigitalis[42]

ANNOTATIONS

(1) **Facies et Margines.** The listed terms for the surfaces and margins of the head, trunk, limbs, and other appendages suffice for many descriptions. Synonymous terms may be substituted, e.g., tibial and fibular or radial and ulnar as borders or surfaces of a limb. Thus surfaces and margins can often be named for prominent underlying structures.

(2) **Facies dorsalis alae; Facies ventralis alae.** Dorsal (upper) and ventral (lower) surfaces of the wing. Facies ventralis alae is also referred to as Facies volaris or F. palmaris.

(3) **Caput.** The head is arbitrarily divided into the **Regio cranialis** (cranial region, an upper part; synonymy: Cranium), **Regio facialis** (sides and throat; synonymy: Facies), and **Rostra** (jaws; Annot. 12; see also **Osteo.** Annot. 40, 53 for definitions of upper and lower jaws and parts of jaws).

Angulus craniofacialis [A. frontonasalis]. The angle at the junction of the culmen with the slope of the frontal region. See **Arthr.** Zonae flexoriae of the skull.

(4) **Pileum.** The forehead, crown, and occiput together (Thomson, 1964: 827).

(5) **Frons** (Fig. 2.1). The forehead extends from the bill to about the transverse level of the nasal (rostral) margin of the eye.

(6) **Corona** (Fig. 2.1). The crown extends over the top of the head (**Caput**) from the **Frons** to the **Occiput** (Annot. 7). A boundary between the crown and occiput is sometimes distinguishable by feather coloration, but is more often indefinite.

(7) **Occiput** (Fig. 2.1). A region on the rear of the head, between the crown (**Corona**) and the nuchal region. Some writers have considered the occiput to be the rear part of the crown.

(8) **Crista pennae.** A crest or tuft of lengthened feathers on the head (Van Tyne and Berger, 1959). This definition, unlike that of Newton and Gadow (1896), does not include the fleshy combs of chickens and the horny casques in hornbills and cassowaries.

(9) **Regio auricularis.** The ear region about the auditory aperture (**Apertura auris externae**) is typically caudal and slightly ventral to the eye (Fig. 2.1). It is sometimes marked by distinctive auricular feathering. See **Org. Sens.** Annot. 55, 56.

(10) **Os.** The mouth.

Rima oris. (Komárek, 1958). Synonymy: Apertura oris (NAA, 1979). Rima, L. cleft or fissure. The opening of the mouth is frequently called the "gape" in ornithological literature.

(11) **Angulus oris.** Synonymy: commissural point or rictal commissure. The corner or angle of the mouth.

(12) **Rostrum.** The beak or bill (Fig. 2.2). Skeletal parts of the upper jaw or maxilla (**Rostrum maxillare**) and lower jaw or mandible (**Rostrum mandibulare**) are covered by the integumental Rhamphotheca (**Integ.** Annot. 81). See **Osteo.** Annot. 40, 53 for closely related terms.

(13) **Culmen.** The middorsal ridge of the Rostrum maxillare extending from the tip of the bill to the base of the feathers on the forehead at or near the craniofacial angle.

Gonys. The midventral ridge of rhamphotheca lying superficial to the Rostrum [Symphysis] mandibulae (**Osteo.** Annot. 40, 53; **Arthr.** Annot. 21). Coues (1872) reviewed the history of this term and suggested that the proper term should have been Genys, meaning lower jaw or chin, but "Gonys" (which correctly refers to the knee) has been so widely used in the ornithological literature that a change seems impractical.

(14) **Tomium maxillare; Tomium mandibulare.** The cutting edge of the rhamphotheca on each ramus of the upper and lower jaws (Fig. 2.2). The tomia form the borders of the forward part of the opening of the mouth (**Rima oris;** Annot. 10, 12).

(15) **Lamellae rostri.** A series of small, closely set vertical ridges of rhamphotheca along the outer margin of the lower tomia and/or the inner margin of the upper tomia used for straining or grasping food as in the phoenicopterids (flamingos) and anatids.

(16) **Regio malaris [Mala].** The malar region ("cheek") lies on the side of the head and superficially covers the caudal end of the jaws (Fig. 2.1). The malar region is ventral to the auricular region (Annot. 9) and dorsal to the throat (Annot. 20).

(17) **Rictus.** A fleshy border of the mouth (Os) from its corner or angle (**Angulus oris**) grading rostrally into the maxillary and mandibular tomia (Coues, 1872). This definition is more restricted than one that considers the rictus to be the Rima oris (commissural line) along which the mandibles close (Fig. 2.2).

(18) **Regio interramalis.** Synonymy: Regio intermandibularis. This triangular area lies between the two mandibular rami caudal to the Rostrum [Symphysis] mandibulae (gonys). See Annot. 12.

(19) **Mentum.** The Mentum is the soft rostral part of the interramal region (Annot. 18) caudal to the Gonys (Annot. 13) and hard interramal space (Coues, 1872). The Mentum is caudally continuous with the gular (submalar) region. The Mentum is thus the area, usually feathered between the exposed mandibular rami, i.e., the rostral part of the interramal region in the fork on the underside of the bill.

(20) **Regio gularis [R. submalaris].** The gular region, the caudal part of the interramal region, forms the throat and extends from the mentum caudally to an imaginary line between the caudal ends of the mandibles (**Osteo.** Annot. 43).

(21) **Naris.** Synonymy: nostril or external nasal aperture. The nares, commonly round or elongate in shape, penetrate the bone and rhamphotheca of the maxilla usually near its caudal end (Fig. 2.2; **Resp.** Annot. 1). A projecting shelf termed the **Operculum nasale** (operculum, L.lid or cover) partially or completely covers the naris in some birds including chickens, pigeons, and starlings (*Sturnus vulgaris*). See Fig. 2.2; **Resp.** Annot. 2.

(22) **Cera.** The cere, a thickened part of the integument, either naked or feathered, straddles or encircles the base of the nasal region as in accipitrids, falconids, columbids, psittacids, and strigids. (**Integ.** Annot. 81).

(23) **Lorum.** (L. a strap). The lore (pl. lores; adj. loral) is the area between the eye and the upper jaw (Coues, 1872) (Fig. 2.1).

(24) **Oculus.** The eye.

Palpebra dorsalis; Palpebra ventralis. In birds the dorsal eyelid is typically immobile and the ventral one mobile (Newton and Gadow, 1896: 234), but in certain owls, part or all of the upper eyelid can move (Lucas and Stettenheim, 1972: 14, 31). (Fig. 2.2; **Sens.** Annot. 34).

(25) **Membrana nictitans [Palpebra tertia].** When drawn caudally from its folded position at the medial angle of the eye, the translucent or opaque nictitating membrane protectively moistens and covers the eye (**Sens.** Annot. 40).

(26) **Projectio pennarum.** This new term designates a projection of feathers on the head and neck as illustrated by the crests (Annot. 8) in many birds, hackles on the dorsal side of the neck, and "ear" tufts in certain owls.

(27) **Saccus protrudens.** This new term designates a variety of diverticula that when inflated protrude externally from the head or neck and originate from either the digestive or respiratory tract. Examples of such diverticula occur in the gular region of frigate birds (Fregatidae), in the respiratory tract in the Marabou Stork (*Leptoptilos crumeniferus*), and along the esophagus of the Sage Grouse (*Centrocercus urophasianus*) and bustards (Otididae). These diverticula are covered with bare or feathered skin (**Resp.** Annot. 21; **Digest.** Annot. 3, 27, 29-30).

(28) **Collum.** Synonymy: Cervix. On the neck (**Collum**), the dorsal region adjacent to the skull is termed the **Nucha** (nape of the neck or nuchal region). Caudally the root of the neck lying between the shoulders has been termed the "interscapular" portion. The **Jugulum** is the ventral side of the neck (Fig. 2.1).

(29) **Regio ingluvialis.** In those avian species that possess a crop this term designates the region of the crop at the front of the breast and thoracic inlet at the root or the base of the neck.

(30) **Truncus.** The trunk is the entire body between neck and tail excluding the limbs.

(31) **Regio omalis [Omus].** The shoulder is the arbitrarily delimited region of junction of the wing and trunk. The Greek term Omos is used (**Osteo.** Annot. 164) in its Latin transliteration, Omus.

(32) **Axilla.** The armpit, an arbitrarily delimited region on the underside of the wing and immediately adjacent trunk. The so-called "axillary" feathers are attached on the ventral surface of the upper arm (Lucas and Stettenheim, 1972: 80). See Fig. 2.3.

(33) **Dorsum trunci.** Synonymy: Notaeum (Coues, 1872: 15). The term **Dorsum trunci** designates the entire upper part of the trunk of a bird including the back and rump.

Dorsum. The back, not including the rump (Fig. 2.1).

Pyga. The rump, the caudal part of the Dorsum trunci together with the base of the uropygium, externally differentiated only by feathering ("rump patch") of contrasting color or texture. The pyga does not include most of the uropygium (Fig. 2.1).

Latus trunci. The side of the trunk includes cranial and caudal areas. Cranially, the Latus trunci merges with the neck (Collum). The caudal boundary of the Latus trunci follows the cranial border of the preacetabular ilium and the cranial margin of the thigh. Most of the caudal part of the trunk is located deep to the thigh which covers all except a small area next to the tail (see Annot. 34). Dorsal and ventral boundaries for the Latus trunci are arbitrarily delimited.

Ilia (Fig. 2.3). The flank lies between the caudal part of the abdomen and the rump. The ilia is not the same as the ilium. See **Osteo.** Annot 245.

(34) **Pectus.** The breast (Figs. 2.1, 3).

Venter. The abdomen or belly. The boundary between the breast and the abdomen roughly coincides with the caudal border of the sternum and the last rib (Figs. 2.1, 3)

Venter, Pars infrapubica/suprapubica. Facies subcaudalis. The uropygium and caudal vertebrae form the moveable *dorsal* wall of the rearmost part of the abdomen; the skin covering the part of the dorsal wall directly under the uropygium is referred to as the subcaudal surface of the abdomen. The suprapubic part of the *lateral* abdominal wall wall extends from the uropygium to the pubis and upper border of the rear half of the ischium. The infrapubic part of the abdominal wall is partially lateral and partially ventral, and extends from pubis to the last rib and caudal border of the sternum. See Baumel (1988; 1990).

(35) **Crissum.** The term crissum designates the region surrounding the **Ventus cloacae** (opening of the cloaca) (**Cloaca** Annot. 18; Figs. 2.1, 2.3)

Eminentia venti (Baumel, 1988). The protruding elevation bearing the vent (orifice of the cloaca). See **Masc.** Annot. 27, Promontorium cloacale.

(36) **Cauda.** The tail, including its dorsal side (**Dorsum caudae**), ventral side (**Ventrum caudae**), the tail flight feathers (**Rectrices**), their coverts (**Tectrices caudales**), and the **Uropygium,** the fleshy tail mass (Baumel, 1988: 5). See **Integ.** Annot. 62.

Bulbus rectricium. The paired rectricial bulbs are major components of the Uropygium. Each bulb is a fibro-adipose structure which has a partially surrounding capsule of striated muscle in which are embedded the calami of the rectrices and their major coverts (Campbell and Lack, 1985: 579; Baumel, 1988). A rectricial bulb lies on each side of the pygostyle to which it is loosely attached.

(37) **Ala (Membrum thoracicum).** The wing includes the upper arm (**Brachium**), elbow (**Cubitus**), forearm (**Antebrachium**), wrist (**Carpus**), hand (**Manus**), (carpometacarpus, feathered forefinger (**Alula**), and major and minor digits) (See **Integ.** Annot. 65).

(38) **Membrum pelvicum.** The pelvic limb includes the hip (**Coxa**), thigh (**Femur**), knee (**Genu**), shank or leg (**Crus**), intertarsal joint (**Artc. intertarsalis**), and foot (**Pes**). The last includes the **Tarsometatarsus,** metatarsophalangeal joints (**Juncturae metatarsophalangeales**), the toes (**Digiti**), and toe joints (**Juncturae interphalangeales**). See **Arthr.** Annot. 182, 183.

(39) **Tarsometatarsus.** The part of the limb enclosing the tarsometatarsal bones is commonly called the "tarsus" in the ornithological literature and erroneously referred to as the shank (Coues, 1927). The shank or crus in mammals and birds lies between the knee and the ankle (see **Osteo.** Annot. 284).

(40) **Pulvinus metatarsalis.** The metatarsal pad is a fat body covered with podotheca at the distal end of the Tarsometatarsus on its plantar surface and on the bases of digits II to IV. (Fig. 2.4; **Integ.** Annot. 16; **Arthr.** Annot. 179).

Plica metatarsalis. A narrow transverse fold in the skin between the first digit and metatarsal pad.

(41) **Digiti.** Synonymy: Hallux [I] = Digitus primus; I-IV = Digitus secundus/tertius/quartus. The four toes of most birds correspond to digits I-IV in ancestral vertebrates. Some birds have undergone evolutionary reduction in number of toes with the Ostrich having the extreme of only 2 toes. In most birds the terminal phalanx in each toe is a claw (**Unguis**) having a bony core and an integumental rhamphothecal cover (**Integ.** Annot. 87). In typical birds **Digitus I** is the hind toe or hallux. **Digiti II** through **IV** are most commonly forwardly directed and are numbered from medial to lateral (Van Tyne and Berger, 1959: 50.). See Figs. 2.1, 4; and **Osteo.** Annot. 299, 300, numbering of phalanges.

(42) **Tela interdigitalis.** See Fig. 2.4. The skin webbing between the toes, the extent of which differs considerably among different kinds of birds. Many species lack such webbing.

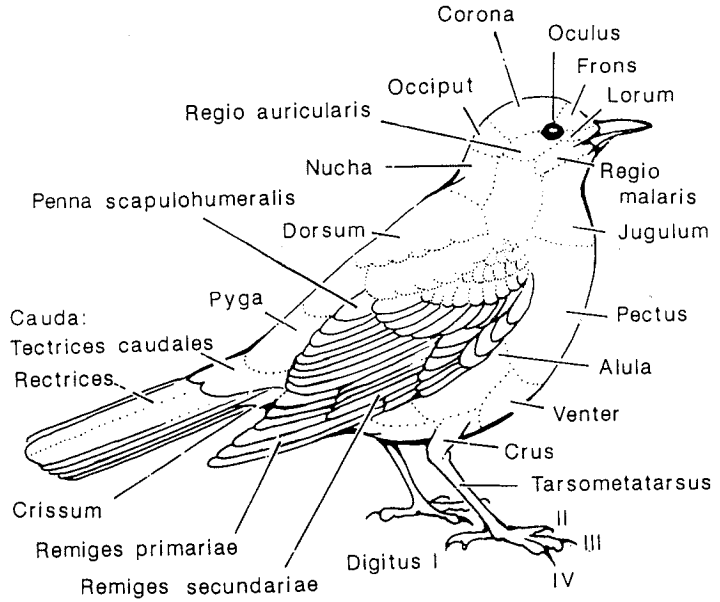

Fig. 2.1. External topography of a bird in lateral view.

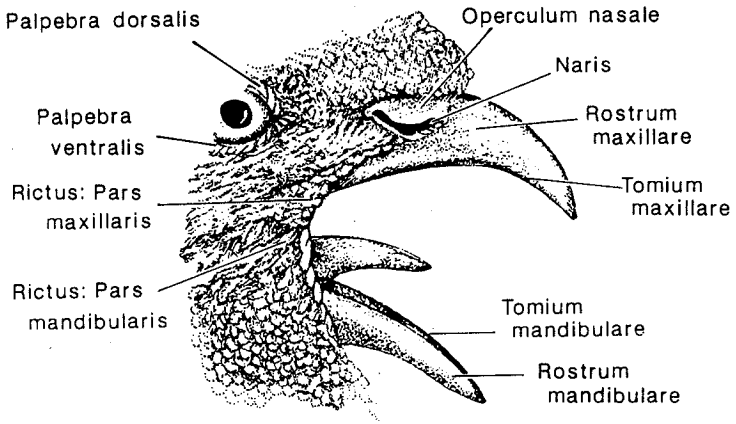

Fig. 2.2. Rostral part of the head of a single comb White Leghorn chicken (*Gallus gallus*); right lateral view. After Lucas and Stettenheim, 1972.

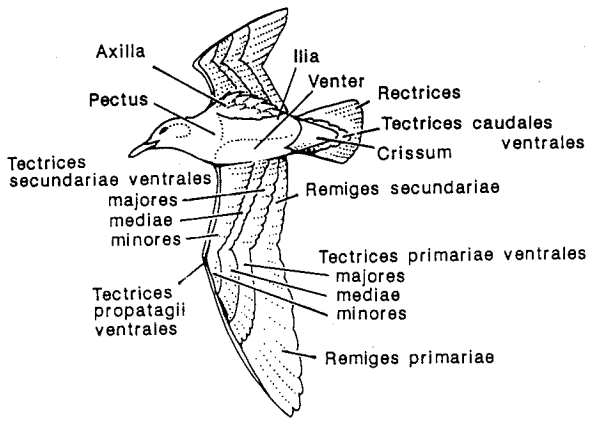

Fig. 2.3. External topography of the underparts of a bird in flight (Modified after P. Grant, 1986, *Gulls, a Guide to Identification*, 2nd ed., with permission of Academic Press, London).

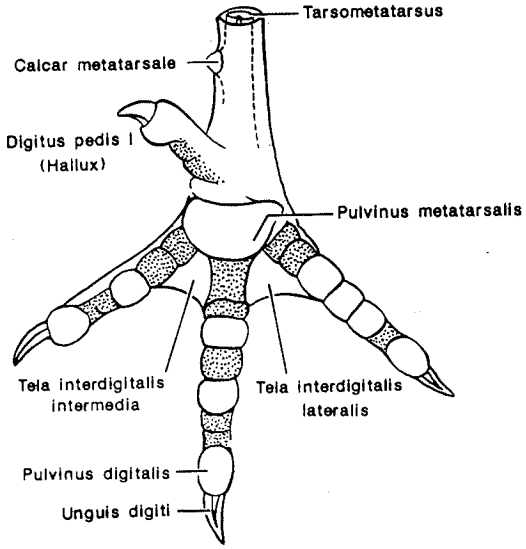

Fig. 2.4. Foot of a single comb White Leghorn chicken (*Gallus gallus*); plantar view, right side.

3

INTEGUMENTUM COMMUNE

GEORGE A. CLARK, JR.

With contributions from subcommittee members: E. H. Burtt, Jr.; M. H. Clench; D. W. Johnston; Vl. Komárek; M. Morlion; R. I. C. Spearman; P. Stettenheim. Helpful suggestions and/or information have been given by J. J. Baumel, H. Berkhoudt, R. E. Brown, A. H. Brush, H. E. Evans, Gy. Fehér, A. S. King, A. M. Lucas, J. McLelland, G. Michel, and G. A. Zweers. M. J. Spring prepared the figures. This chapter is contribution number 682 of the New York State Science Service.

Good general introductions to the literature on the integument can be found in Lucas and Stettenheim (1972), Stettenheim (1972), Spearman (1983), and Spearman and Hardy (1985). In the following account, the terminology of the feathers is in three sections: (1) parts of a feather, (2) structural kinds of feathers, and (3) names of feathers, individually or collectively, on different parts of the body. The subject of molt is not covered here, but Palmer (1972) has provided a useful introduction.

TERMINOLOGY

CUTIS[1]

Epidermis[2]
- Stratum corneum[3]
- Stratum intermedium[4]
- Stratum basale[5]
- Membrana basalis[6]

Dermis [Corium][7]
- Stratum superficiale[8]
- Stratum profundum[9]
  - Stratum compactum[9]
  - Stratum laxum[9]
- Lamina elastica[10]

Mm. nonstriati dermatis[11]
- Mm. pennarum[11]
  - Tendo elastica[11]
- Mm. apteriales[11]

Folliculus[11]
- Collum folliculi[11]
- Paries folliculi[11]
- Mm. pennarum
- Tendo elastica[11]

Glandulae auriculares[12]

Glandula uropygialis[13]
- Lobus glandulae uropygialis
- Septum interlobare

(continued)

CUTIS[1] (cont.)

Capsula glandulae uropygialis
Papilla uropygialis
  Ductus glandulae uropygialis
  Porus ductus glandulae uropygialis
    Circulus uropygialis[13 62]
Glandulae externae labii venti[14]
Area incubationis[15]

TELA SUBCUTANEA [SUBCUTIS]

Mm. pterylarum[11]
Corpora adiposa [Panniculus adiposus][16]
Corpus adiposum abdominale laterale
Corpus adiposum abdominale transversum
Corpus adiposum abdominale medioventrale
Corpus adiposum coracoclaviculare
Corpus adiposum dorsocervicale
Corpus adiposum femorale craniale
Corpus adiposum femorale caudale
Corpus adiposum iliocaudale [C. a. caudofemorale]
Corpus adiposum ischiopubicum
Corpus adiposum laterocervicale
Corpus adiposum mesenteriale[16]
Corpus adiposum orbitae
Corpus adiposum ophthalmicum
Corpus adiposum pectorale
Corpus adiposum paracloacale[16]
Corpus adiposum plantare profundum[16]
Corpus adiposum plantare superficiale[16]
Corpus adiposum spinale
Corpus adiposum subalare
Corpus adiposum synsacrale
Corpus adiposum thoracicum laterale
Corpus adiposum tracheale

PARTES PENNAE[17]

Folliculus[11]
  Collum[11]
  Paries[11]
Vagina pennae[18]
Scapus pennae[19]
  Calamus pennae[19 20]
    Umbilicus proximalis[20]
    Umbilicus distalis[20]
    Galerus pulposus[21]
  Hypopenna[43]
    Hyporhachis[43]
    Hypovexillum[43]
    Barbae umbilicales[43]
  Rhachis pennae[19]
    Cortex[22]

PARTES PENNAE[17] (cont.)

Medulla[22]
Sulcus ventralis[23]

Vexillum pennae[24]
  Vexillum internum[24]
  Vexillum externum[24]
  Pars plumacea[25]
  Pars pennacea[25]

  Barba pennae[26]
    Ramus[26]
      Cortex[22]
      Medulla[22]
      Petiolus[27]
      Incisura rami[27]
      Crista dorsalis[28]
      Crista ventralis[28]
        Tegmen[28]
          Villi[28]
      Ruga proximalis[29]
      Ruga distalis[29]
    Vexillum barbae[30]
      Vexillum barbae proximale
      Vexillum barbae distale
    Barbula rami[31]
      Barbula proximalis[31]
      Barbula distalis[31]
      Barbula rhachidialis[32]
      Barbula stylosa[33]
      Barbicella[34]
      Basis barbulae[35]
        Arcus dorsalis[36]
        Dens ventralis[36]
        Stylus dorsalis[36]
        Flexura[37]
    Pennula[38]
      Nodus[38]
      Internodus[38]
      Dens nodosus[38]
      Cilium dorsale[39]
      Cilium ventrale[39]
      Hamulus[39]
Apex[40]
Margo[40]
  Incisura vexilli[41]
Zona impendens[42]

PENNAE[44]

Pluma[45]
  Plumula[45]
  Neossoptilus[45]
  Prepenna[45]
  Preplumula[45]
Semipluma[46]
Penna contorna[47]
  Penna volatus[47 48]
    Remex[48]
    Rectrix[48]
    Tectrix[63]
Pennae contornae generales[47]
Pulvipenna [Pulvipluma][49]
Seta[50]
Semiseta[50]
Filopluma[51]

(continued)

PLICA ET PATAGIA CUTIS[52]

- Patagia alae[52]
  - Propatagium[53]
    - Patagium alulae[55]
    - Patagium cervicale [Plica cervicalis][52]
- Postpatagium[54]
- Metapatagium[53]
- Tela interdigitalis[86]

PTERYLAE[56]

- Pteryla capitalis[57]
- Pteryla dorsalis[58]
  - Pars cervicalis
  - Pars interscapularis
  - Pars spinalis
  - Pars pelvica
  - Circulus uropygialis[59]
- Pteryla lateralis[60]
- Pteryla ventralis[61]
  - Pars cervicalis
  - Pars pectoralis
  - Pars axillaris
  - Pars sternalis
  - Pars abdominalis
  - Pars venti[61]
- Pteryla caudalis[62]
  - Rectrices[48 62]
  - Tectrices caudae[63]
    - Tectrices dorsales caudae[63]
      - Tectrices caudales dorsales majores[63]
      - Tectrices caudales dorsales minores
    - Tectrices ventrales caudae[63]
      - Tectrices caudales ventrales majores[63]
      - Tectrices caudales ventrales minores
- Pteryla scapulohumeralis[64]
- Pteryla alae[65]
  - Remiges
    - Remiges primarii[66]
    - Remiges secundarii[67]
      - Diastema remigum secundarium[67]
    - Remiges tertiarii [R. humerales][68]
    - Remex carpalis[69]
    - Remiges alulae [R. alulares][70]
- Tectrices alae[63 71]
  - Tectrices marginales manus[71]
  - Tectrices marginales propatagii[71]
  - Tectrices dorsales
    - Tectrices dorsales alulae
    - Tectrices dorsales propatagii[71]
    - Tectrices primariae dorsales majores
    - Tectrices primariae dorsales mediae
    - Tectrices primariae dorsales minores
    - Tectrix carpalis dorsalis
    - Tectrices secundariae dorsales majores
    - Tectrices secundariae dorsales mediae
    - Tectrices secundariae dorsales minores
    - Tectrices tertiariae dorsales
  - Tectrices ventrales

PTERYLAE[56] (cont.)

- Tectrices primariae ventrales majores
- Tectrices primariae ventrales mediae
- Tectrices primariae ventrales minores
- Tectrices secundariae ventrales majores
- Tectrices secundariae ventrales mediae
- Tectrices secundariae ventrales minores
- Tectrices ventrales propatagii
- Tectrices tertiariae ventrales
- Pteryla membri pelvici[72]
  - Pars femoralis
  - Pars cruralis
  - Pars tarsometatarsalis
  - Pars digitalis

APTERIA[56 73]

- Apteria capitalia[74]
- Apteria dorsalia[75]
  - Apterium scapulare
  - Apterium spinale
- Apteria lateralia[76]
  - Apterium cervicale laterale
  - Apterium truncale laterale
- Apterium ventrale[77]
  - Pars cervicalis ventralis
  - Pars sternalis
  - Pars pectoralis
  - Pars abdominalis mediana
  - Pars abdominalis lateralis
- Apterium caudale[78]
- Apteria alae[79]
  - Apterium humerale
  - Apterium subhumerale
  - Apterium antebrachiale ventrale
  - Apterium propatagiale ventrale
- Apterium membri pelvici[80]

INTEGUMENTUM SPECIALE

- Rhamphotheca[81]
  - Cera[81]
  - Unguis maxillaris[82]
  - Unguis mandibularis[82]
- Podotheca[83]
  - Scuta[84]
  - Scutella[84]
- Acrotarsium[84]
- Acropodium[84]
- Pulvinus hypotarsalis[85]
- Pulvinus metatarsalis (**Topog.** Annot. 40)
- Pulvinus digitalis[86]
  - Pulvinus ungualis[86]

(continued)

INTEGUMENTUM SPECIALE

Areae interpulvinares[86]
Tela interdigitalis[86]
Ungues
  Unguis digiti manus[87]
    Unguis digiti alulae
    Unguis digiti majoris
  Unguis digiti pedis[87]
    Scutum dorsale
      Processus pectinatus
    Scutum plantare
Calcaria
  Calcar alae[88]
  Calcar metatarsale[89]

ANNOTATIONS

(1) The terminology for the layers of the **Cutis** (skin) was extensively reviewed by Lucas and Stettenheim (1972: 485-489 and Figs. 338, 367, 375, 381). Spearman (1983) and Sawyer, et al.(1986) have summarized studies on skin keratinization.

(2) **Epidermis.** Outermost, nonvascular, epithelial layer of the skin (Spearman and Hardy, 1985). See Fig. 3.1.

(3) **Stratum corneum.** This outer horny layer of nonliving cells, produced by the underlying living cells, provides a protective barrier between the environment and the body. As the laminae of the Stratum corneum are pushed to the surface, the bonding between the laminae weakens (dehiscence), and the outermost cells are sloughed off (desquamation). The Stratum lucidum of mammals cannot be distinguished in birds (Hodges, 1974).

(4) **Stratum intermedium.** A middle epidermal layer of generally polyhedral cells with signs of keratinization and vacuolization (Fig. 3.1). Stratum granulosum, a name applied in mammals, could be used to designate a thin outer layer of the avian Stratum intermedium, but it does not occur in plantar skin and is elsewhere reported to be distinguishable only with electron micrographs (Hodges, 1974). The term Stratum transitivum has also been applied to this thin layer in birds, but Sawyer, et al. (1986) on the basis of their studies of scales, included this layer as the superficial part of the Stratum intermedium. The term Stratum intermedium is preferred to "Stratum spinosum" which is used for mammals. In birds the "spiny cells" are not limited to the intermediate layer. In mammalian epidermal histogenesis the term "Stratum intermedium" has been used to designate a "middle" layer that eventually becomes the spiny layer (Sengel, 1976: 11).

(5) **Stratum basale.** The deepest epidermal layer (Fig. 3.1), usually only one cell thick and containing cuboidal or columnar cells which are dividing and unkeratinized.

(6) **Membrana basalis.** The basement membrane lies between the plasma membrane of the basal cells and the dermis (Fig. 3.1). Electron microscopy reveals at least two layers and a space. Lucas and Stettenheim (1972: 486, 491, 495) reviewed terms that have been applied to this structure.

(7) **Dermis [Corium].** This inner layer of the skin is composed mainly of connective tissue. Avian dermis typically lacks the papillary superficial layer and reticulate inner layer that characterize mammalian dermis; hence different names are used for layers of the dermis in birds. The appearance of the avian dermal layers is highly varied, depending on species, location, and age (Stettenheim, 1972). See Figs. 3.1, 2.

(8) **Stratum superficiale.** This outer layer of dermis contains collagenic connective tissue and is generally less dense than that of the underlying Stratum compactum.

(9) **Stratum profundum.** This deep layer of the dermis contains a **Stratum compactum,** which is an outer dense feltwork of elastic fibers and collagenic fiber bundles, and a looser deeper **Stratum laxum** which includes smooth muscles and the bases of the follicles of the contour feathers.

(10) **Lamina elastica.** This very thin dermal layer of elastic fibers forming a horizontal lattice sometimes separates dermis from subcutis. Feather follicles lie superficial to the Lamina elastica and hence within the dermis, whereas the basal ends of hair follicles are generally described as located in the subcutis.

(11) **Musculi nonstriati dermatis.** These smooth muscles in the dermal layer consist of two types: feather muscles and apterial muscles. See **Myol.** Annot. 4.

Musculi pennarum. These nonstriated feather muscles are attached at each end to an elastic tendon (**Tendo elastica**) which is fastened to the connective tissues of the external follicle walls of contour, semiplume, bristle, and body down feathers. See Lucas and Stettenheim (1972) for illustrations of the arrangements of feather muscles.

Mm. apteriales. Lange (1931) designated the apterial muscles as the "Stratum musculo-elasticum", but these muscles are part of the loose layer (Stratum laxum) and not a distinct layer of dermis. Where apterial muscles are contiguous with feather muscles, elastic bundles connect the two types.

Musculi pterylarum. Dermal slips of striated skeletal muscles that move or tense an entire feather tract (Petry, 1951). See **Myol.** Annot. 4.

Folliculus. The follicle is a cutaneous tubular invagination surrounding a cavity within which a feather develops and remains seated. The follicular wall contains epidermal and dermal layers, and thus the epidermis of the contained feather faces the epidermis of the follicle (Lucas and Stettenheim, 1972: Figs. 239, 306, 307). Parts of the follicle include the neck (**Collum**) and the wall (**Paries**). Associated with the follicle are numerous blood vessels, a complex innervation, and nonstriated feather muscles (**Mm. pennarum**), each of which is attached to the follicle by an elastic tendon (see Annot. 11.

(12) **Glandulae auriculares.** Numerous small holocrine auricular glands in the wall of the external acoustic canal (Meatus acusticus externus) occur in at least some birds, and consist in the chicken of sac-shaped organs that open by short ducts directly into the canal of the outer ear (Lucas and Stettenheim, 1972; Menon and Salinukul, 1989).

(13) **Glandula uropygialis.** Uropygial gland (Fig. 3.3). Synonymy: oil gland, preen gland. This subcutaneous, holocrine gland on the uropygium occurs in most birds (Jacob and Ziswiler, 1982; see Johnston, 1988, for an extensive comparative survey of this gland). The lobes (singular: **Lobus glandulae uropygialis**) are separated by an interlobar septum (**Septum interlobare**) and covered by an external capsule (**Capsula glandulae uropygialis**). A caudally or dorsocaudally projecting gland papilla (**Papilla uropygialis**) contains one or two ducts. Each duct (**Ductus glandulae uropygialis**) terminates at an exterior opening (**Porus ductus glandulae**

uropygialis). In many birds the papilla bears a tuft of feathers (**Circulus uropygialis** (see Annot. 59).

(14) **Glandulae externae labii venti.** Mucus secreting glands open on the external surface of the labia of the vent and surrounding featherless skin in certain species of birds including at least some charadriiforms and passeriforms (Quay, 1967). See **Cloaca.** Annot. 21.

(15) **Area incubationis.** Synonymy: brood patch. An incubation patch is a modification of ventral skin around the time of incubation, marked by a loss of feathers and increased vascularity of the skin (Kern and Coruzzi, 1979). Used for warming of eggs (Drent, 1975), the patch is single in most species, but paired or even triple in some. It occurs in either or both sexes, associated with incubation habits. The most widespread pattern among the taxonomic orders is that both sexes share the incubation with each sex developing an incubation patch (Drent, 1975), e.g., in the podicipedi-, procellari-, grui-, charadrii-, pici-, most columbi-, some of the falconi- and passeriforms.

(16) **Corpora adiposa [Panniculus adiposus].** Subcutaneous fat bodies, organ-like structures holding lipid reserves. Fat bodies are not part of the integument or any other commonly recognized organ system, but are arbitrarily included here, because many of them are near the skin (Fig. 3.4). Subcutaneous fat deposits are patchy in distribution. Names for 16 fat bodies in the chicken embryo were provided by Liebelt and Eastlick (1954) and used by King and Farner (1965) for the White-crowned Sparrow (*Zonotrichia leucophrys*) (Fig. 3.4). Latin versions of fat body names were provided in NAA (1979). Additional fat bodies have been observed in birds: (1) in the orbit (H. E. Evans, pers. comm.), (2) between the postacetabular ilium and tail (iliofemoral), (3) both superficially and deep in the sole of the foot, and (4) extraperitoneally (J. J. Baumel, 1988 and pers. comm.). English names for the fat bodies listed with Latin names are, in the same sequence, orbital, ophthalmic, dorsocervical, laterocervical, tracheal, claviculo-coracoid, spinal, synsacral, iliocaudal (the caudofemoral of Baumel, 1988: 7), lateral thoracic, lateral abdominal, pectoral, transverse abdominal, medioventral abdominal, ischio-pubic, subalar, cranial femoral (synonym: sartorial), caudofemoral (synonym: femoral), deep plantar, superficial plantar, mesenteric, and paracloacal. The mesenteric is incorporated in the posthepatic septum, while the paracloacal lies on each side of the cloaca (Baumel, 1988).

(17) **Partes pennae** (Figs. 3.5, 6, 7). In designating the position of parts on a feather of the trunk, "dorsal" signifies the external (outer) side of the feather, and ventral specifies the internal (inner) side. See Lucas and Stettenheim (1972: Chaps. 5, 6, 7) for details and illustrations of feather parts.

(18) **Vagina pennae** (new term). This is the sheath that encloses a newly formed and growing natal or regenerating feather. Composed of epidermal cells derived from the outer layer of a feather blastema, it is lost by flaking and splitting as the feather matures.

(19) **Scapus.** The central shaft of a typical feather has two parts, the proximal **Calamus,** which is tubular and embedded in the follicle, and the more distal **Rhachis,** which is essentially a solid extension of the wall of the calamus on the dorsal side (Lucas and Stettenheim, 1972: 237-238). The rachis is that portion of the shaft which bears barbs, if any are present, and which is above the skin. The Greek term Rhachis is usually spelled as rachis in English. See Figs. 3.5, 6.

(20) **Umbilicus proximalis; Umbilicus distalis.** The proximal umbilicus (synonym: inferior umbilicus) is a pit on the basal end of the calamus and is the remnant of the opening through which the pulp core entered a developing feather. The distal umbilicus (synonym: superior umbilicus) is a pit on the ventral side of the calamus at the level where the vanes begin and is the remnant of the upper opening through which the pulp core passed from inside the wrapped up vanes of a developing feather into the calamus. The distal umbilicus marks the distal end of the calamus (Fig. 3.5).

(21) **Galerus pulposus.** Pulp cap. Within the cavity of the calamus of a mature feather the pulp caps are a continuous series of downward (proximally) opening cups, stacked to form a thin-walled tube with transverse partitions. Pulp caps developmentally first appear alongside the rachis and then later are formed through the distal umbilicus into the calamus (Lucas and Stettenheim, 1972: 236-337, 381-383; Fig. 159).

(22) **Cortex; Medulla.** The rachis is largely solid and contains a dense outer layer, the **Cortex,** resembling the wall of the calamus and a pithy core, the **Medulla.** The terms cortex and medulla are general and applied to a variety of structures including the ramus of a barb (Fig. 3.7).

Medulla. Synonymy: Substantia medullaris (Purslow and Vincent, 1978).

(23) **Sulcus ventralis.** A groove on the ventral side of the rachis is most prominent in large flight feathers of the wing and tail, less distinct in coverts and contour feathers on the body, and faint or absent in other feathers.

(24) **Vexillum; Vexillum internum; Vexillum externum.** Vexilla are vanes of contour feathers and semiplumes. Vexilla consist of more or less flexible sheets on opposite sides of the rachis, composed of narrow, flattened, parallel, and closely spaced plates called barbs. For flight feathers the terms Vexillum internum (inner vane) and Vexillum externum (outer vane) refer, respectively, to vanes on the medial and lateral sides of the rachis of the rectrices (with tail folded) and the secondaries and proximal primary rectrices (with wing extended). For the distal primaries that are oriented parallel to the longitudinal axis of the wing (wing extended), the Vexillum externum is on the cranial edge of the rachis. In many flight feathers the outer vane is narrower with a more acute angle between its barbs and the rachis (see Feduccia and Tordoff, 1979; Baumel, 1988: 47).

(25) **Pars plumacea; Pars pennacea.** The fluffy or plumaceous zone of a contour or semiplume feather is near the basal end, whereas the pennaceous zone is in the relatively flat, distal portion of the vane. In the Pars pennacea the barbs are flat, parallel, and interlocking, whereas in the Pars plumacea they are downy and noninterlocking (Fig. 3.5).

(26) **Barba pennae.** (Chandler, 1916). A barb is an inclusive term for a primary branch (**Ramus**) of the rachis plus the secondary branches (**Barbulae**) of that ramus. Some authors have used the term barb as a synonym of ramus. Pennaceous barbs are cohesive or interlocking, whereas plumaceous barbs are not. (Figs. 3.6, 7)

(27) **Petiolus; Incisura rami.** The petiole is the base of a ramus of a pennaceous barb in which the base is narrower than the portion immediately distal. A notch, if present, in the ventral margin of the ramus immediately distal to the petiole is called the **Incisura rami.**

(28) **Crista dorsalis; Crista ventralis.** (Figs. 3.7, 8). Synonymy: dorsal and ventral ridges (Chandler, 1916). Dorsal and ventral crests of the long, laterally compressed,

filamentous, ramus of a pennaceous barb. The Crista dorsalis rises above the level of the roots of the barbules. The ventral crest in the wing feathers of many nonpasserines is expanded and curved to form a thin shelf known as the **Tegmen** (pl. tegmina), which projects almost parallel to the distal barbules (Fig. 3.8). The **Villi** are a fringe of projections on the edge of the tegmen (Gladstone, 1918; Lucas and Stettenheim, 1972: 258-259).

(29) **Ruga proximalis; Ruga distalis.** A proximal and distal series of ridges (rugae) on each side of the ramus of a pennaceous barb at the attachment of the barbules (Lucas and Stettenheim, 1972: 245-246 and Fig. 164).

(30) **Vexillum barbae.** The vanule is a vane composed of interlocking barbules on one side of a pennaceous barb. Vexillum barbae proximale is the vanule pointing towards the base of the feather, while the Vexillum barbae distale points towards the apex of the feather.

(31) **Barbula rami.** A barbule is a secondary branch of the rachis of a feather and is generally an offshoot of a ramus. It is a long slender projection, even a filament. Barbules are of two major types: plumaceous (noninterlocking) and pennaceous (interlocking). Plumaceous-type barbules are alike on both sides of a barb, whereas pennaceous-type barbules are different on proximal and distal sides of a barb.

Barbula proximalis is a barbule on the proximal side of the ramus and thus points towards the base of the feather (Fig. 3.7).

Barbula distalis is a barbule pointing towards the apex of the feather (Figs. 3.6, 7).

(32) **Barbula rhachidialis.** (new term). This designates a rachidial barbule that attaches to the side of the rachis between the attachments of pennaceous-type rami. Rachidial barbules form a continuous row with those on the proximal side of each ramus but they are much simpler in structure.

(33) **Barbula stylosa.** A stylet barbule on a ramus is a small, stiff, slender barbule with a simple shape, i.e. few or no projections.

(34) **Barbicella.** A latinized form of barbicel, a specialized process of a barbule. (Synonymy: Processus barbulae (NAA, 1979)).

(35) **Basis barbulae.** The base (basal plate) of a barbule is its narrow strap- or plate-like proximal portion with few or no projections (Fig. 3.7).

(36) **Arcus dorsalis.** The dorsal flange. This lip along the dorsal border of the base of a proximal pennaceous-type barbule projects toward the ramus. This flange engages the hooklets of the pennula of a distal barbule so as to unite barbs and hold together the surface of the vane of the feather (Fig. 3.7).

Dens ventralis. The ventral tooth is a long, triangular projection from the apical end of the base of a pennaceous-type barbule. The Dens is more elaborate in distal barbules than in proximal barbules, especially on the flight feathers. (Fig. 3.7)

Stylus dorsalis. The dorsal spine is any of 3 to 5 low triangular projections at the free end of the dorsal border of the base of a proximal pennaceous-type barbule.

(37) **Flexura.** Flexules (Chandler, 1916) are special, distally curved, fiber-like processes that arise from the dorsal border of the Basis, in place of dorsal spines, in pennaceous-type barbules of the body contour feathers of many water birds.

(38) **Pennula.** The slender, distal, part of a barbule formed of jointed segments, termed cells, each of which is often furnished with projections at its distal end. The term "pennulum", although used by several authors, is incorrect, having no basis in Latin (Fig. 3.7).

Nodus. A swelling or node at the distal portion of a cell (Annot. 38) along the pennula of a plumaceous barbule (Lucas and Stettenheim, 1972: 244).

Internodus. The main portion of a cell in the pennula of a plumaceous barbule.

Dens nodosus. A nodal prong (dens, L.tooth) is a rounded or conical projection from a node; 2 to 4 commonly occur. The size and shape of the prongs vary along the pennula of a downy barbule. The character of the prongs is fairly consistent throughout downy feathers from different parts of a bird yet differs among kinds of birds (Chandler, 1916). Nodal prongs are hence the most useful microscopic feature for taxonomic identification of feathers (Day, 1966).

(39) **Cilium dorsale.** A dorsal cilium is a spine-like barbicel on the external side of the pennula of a pennaceous-type barbule. One or more such projections are usually present on distal barbules, but rarely present on proximal barbules (Fig. 3.7).

Cilium ventrale. A ventral cilium is a straight or gently recurved barbicel on the ventral side of the pennula of a pennaceous-type barbule. Several such projections are present on distal barbules, but they are short or absent on proximal barbules (Fig. 3.7).

Hamulus (pl.: hamuli). A hooklet (Hamulus) is a barbicel with a hooked tip on the distal ventral side of the proximal portion of the pennula; it arises from a distal barbule. In a series of projections along a barbule, the hooklets are immediately behind the ventral teeth (Dens ventrale) and they grade into the ventral cilia. The number of hooklets varies from 2 to 9, depending on the kind of bird and the location of feathers on the body (Fig. 3.7).

(40) **Apex; Margo.** The apex is the distal tip of the feather, whereas the margin is the edge of the vane (Fig. 3.5).

(41) **Incisura vexilli.** Synonymy: emargination. An indentation in the margin may be present on either or both the inner or outer vanes of the primaries. The commonly used term "notch" may be misleading in possibly suggesting that the vane width is similar on either side of the indentation.

(42) **Zona impendens.** A friction zone is a special region of the inner vane, within areas of overlap of adjacent flight feathers of the wing and tail, which helps to prevent these feathers from slipping too far apart (Lucas and Stettenheim, 1972: 260-261). Within this zone, the distal barbules have enlarged dorsal barbicels, which rub against the barbs and rachides of the overlying feathers.

(43) **Hypopenna.** (Fig. 13.5). Synonymy: afterfeather, aftershaft, hypoptile, accessory plume. The term afterfeather designates any group of structures attached to the rim (Ora) of the distal umbilicus on the underside of a feather. The term includes barbs arising directly from the rim (**Barbae umbilicales**) as well as tufts and feather-like structures with barbs attached to a median shaft, the **Hyporhachis.** The term Hyporhachis (also spelled hyporachis) and its equivalent, aftershaft, should not be used to designate the Hypopenna as a whole; **Hypovexillum** designates a vane of the Hypopenna.

(44) **Pennae.** A general term for feathers of all kinds.

(45) **Pluma.** A down feather has completely fluffy (plumaceous) vanes, with its rachis, if any, shorter than its longest barbs. In many birds, body downs (**Plumulae**) arise from a set of follicles independent of those that produce contour feathers (Golliez, 1967; Lucas and Stettenheim, 1972: 266). The body downs of wing, tail, and vent are arranged in distinct, organized patterns, and names are available for these regions (Lucas and Stettenheim, 1972: Figs. 119, 20). However, on other regions of the body, the body downs are more variable and less well arranged, and thus far no names have been suggested.

A different category of downs, the natal down (**Neossoptilus;** synonymy: neossoptile, neoptile) occurs at hatching to some extent in nearly all avian orders. Natal downs include (1) **Preplumulae,** downs that are predecessors of the adult body downs, and (2) **Prepennae,** downs that arise from follicles that subsequently produce adult semiplumes and pennaceous feathers. The feathers (Pennae and Plumulae) of the adult plumage are termed teleoptiles (singular: Teleoptilus).

(46) **Semipluma.** A semiplume feather possesses completely plumaceous barbs; the length of its rachis exceeds that of its longest barbs (Lucas and Stettenheim, 1972: 263). Because downs, semiplumes, and contour feathers intergrade, it is sometimes difficult to classify intermediate forms.

(47) **Penna contorna.** A contour feather has relatively flat, closely knit (pennaceous) vanes, although the basal part of the vanes can be variably plumaceous. The main types of contour feathers are the flight feathers of the wing and tail (**Pennae volatus**), the coverts (**Tectrices**) of wing and tail, and the common, ordinary, relatively pennaceous feathers of the head, neck, trunk, and limbs (**Pennae contornae generales**).

(48) **Penna volatus.** (Fig. 3.9). The flight feather include the remiges (sing. **Remex**) of the wing and the rectrices (sing. **Rectrix**) of the tail. These feathers are ordinarily the largest on the wing and tail (**Osteo.** Annot. 205; **Arthr.** Annot. 189).

(49) **Pulvipenna [Pulvipluma].** Synonymy: powder down. Powder feathers are modified to produce an extremely fine white powder. Powder feathers are highly varied in both structure and pterylography (Schüz, 1927; Eiselen, 1939; Lucas and Stettenheim, 1972). Examples of birds with marked development of powder feathers include tinamids, ardeids, and columbids. The term powder feather is a more general term than "powder down" because powder-shedding feathers can have the basic structure of contour feathers, semiplumes, or downs in different kinds of birds.

(50) **Seta.** A bristle is a feather generally having a stiff tapered rachis with barbs, if any, only at the base. A bristle is almost invariably heavily melanic in part (Stettenheim, 1974). Bristles most commonly occur around the mouth and eyes (compare Annot. 51.

Semiseta. A semibristle, a feather intermediate between a bristle and a contour feather. Because these feather types intergrade, their classification may sometimes be difficult.

(51) **Filopluma.** A filoplume is a slender, often hair-like, feather that typically possesses barbs, if any, only at the distal end. In contrast, another hair-like kind of feather, the bristle, has its barbs at the proximal end of the rachis. Although the follicle of a filoplume is always near that of a contour feather or body down, a filoplume is a distinct feather and not part of another feather. Unlike contour feathers and body downs, filoplumes lack feather muscles. Filoplumes are believed to serve a sensory function (Necker, 1985).

(52) **Patagium.** Membranous expansion of skin, supported by ligaments and muscles, that span a joint in the wing. Patagia are covered with feathers, forming a smooth contoured airfoil when the wing is extended, yet allow the wing to be freely flexed in its folded position.

Plica. A skin fold. See Tela interdigitalis of the podotheca (Annot. 86).

Patagium cervicale. (Synonymy: Plica cervicalis). The fold of skin extending laterally from the base of the neck to the leading edge of the Propatagium. Where present, as in psittaciform, piciform, and passeriform birds, it appears to be the cranio-medial extension of the Propatgium and is supported by the M. cucullaris, pars propatagialis, with its insertion upon the Lig. propatagiale (**Arthr.** Annot. 141; **Myol.** Annot. 9.

(53) **Propatagium.** A broad fold of skin filling in the angle between arm and forearm of the avian wing from the shoulder to the carpus, forming the cranial (leading) edge and camber of the wing. Between the two layers of skin of the propatagium are the Lig. propatagiale in the leading edge, the Lig. limitans cubiti (see **Arthr.** Annot. 141), propatagial parts of several muscles in different birds (see **Myol.**), as well as nerves and vessels.

Metapatagium. A triangular skin fold reaching from the side of the trunk to the caudal margin of the brachium.

(54) **Postpatagium.** A double thickness of skin projecting caudally from the antebrachium and manus, extending the length of the wing from the elbow to the tip of the manus. The calami of the secondary and primary remiges are embedded in, and are aligned and partially supported by, the Postpatagium.

(55) **Patagium alulae.** A fold of skin connecting the Digitus alularis to the cranial border of the Digitus major. (**Topog.** Annot. 37)

(56) **Pterylae; Apteria.** Pterylae are feather tracts, areas of skin bearing contour feathers. Birds have their feathers grouped into pterylae which are usually separated by mainly featherless spaces, **Apteria** (see Clench, 1970). Down feathers can occur among the contour feathers as in many waterbirds, but an area bearing only down feathers or no contour feathers is considered to be an apterium. An apterium may bear occasional semiplumes.

It is doubtful that any one nomenclatural system for pterylosis can adequately cover all kinds of birds. The objective here is to provide general terms that can be applied to a great variety of birds, but adjustments may be necessary for application to particular species.

Lucas and Stettenheim (1972) and others have used the term "tracts" in the plural for major feather groups and the singular "tract" for individual components. In contrast, Nitzsch (1867), Clench (1970), Komárek, et al. (1982), and others have referred to each of the major feather groups as a "tract" (**Pteryla**) and individual components of a tract have been designated differently by different authors using terms such as "regions", "elements", or parts (**Pars**). Because the term "regions" is commonly used to designate external topographic portions of the body that do not correspond with the pterylosis, it seems best, as recommended by Lucas and Stettenheim (1972: 74), not to use the term regions for the parts of the pterylae. Komárek, et al. (1982) avoided such possible confusion by referring to a subdivision of a pteryla or apterium as a part ("pars"). Their usage is followed here; this account therefore

differs from NAA (1979), which followed Lucas and Stettenheim (1972). See also Annot. 73.

(57) **Pteryla capitalis** (Fig. 3.9). Capital tract, the inclusive term for the arrangement of feathers on the head. As many as 12 parts of the capital tract have been distinguished, but such parts have often been arbitrarily delimited on the basis of their locations or the relative abundance and types of feathers rather than a clear separation by apteria (Lucas and Stettenheim, 1972: 76-77).

(58) **Pteryla dorsalis.** The dorsal tract (Clench, 1970) extends from the base of the head caudally to the level of the caudal end of the pelvis, just caudal to the uropygial gland. The dorsal tract may be subdivided as follows: a cervical part on the neck, an interscapular part between the wings, a spinal part on the back, and in some birds a separate pelvic part (Fig. 3.9).

(59) **Circulus uropygialis.** The uropygial tuft, a group of small feathers on the tip of the uropygial gland (Johnston, 1988).

(60) **Pteryla lateralis.** This paired tract, particularly notable in many nonpasserines, lies on the side of the body ventral to the axillary region.

(61) **Pteryla ventralis.** The ventral tract reaches from the head to the base of the uropygium and may be subdivided, often rather arbitrarily, as follows: a cervical part on the neck, a pectoral part on the breast, a paired axillary part extending from the caudolateral corner of the pectoral part to the axilla, a sternal part on either side of the keel, and a paired abdominal part behind the caudal margin of the sternum. (Fig. 3.9)

Pars venti. The part of the ventral feather tract in the region of the vent of the cloaca.

(62) **Pteryla caudalis.** Feathers of the tail and their coverts (**Tectrices caudae**). The most conspicuous feathers of the caudal tract are usually the major tail feathers, the **Rectrices** (sing. **Rectrix**). These are numbered from medial to lateral starting at the midline. The rectrices are overlapped both above and below by rows of major coverts (**Tectrices caudales majores**). The major coverts are cranially overlapped by one or more rows of minor coverts (**Tectrices caudales minores**) (Annot. 63; **Arthr.** Annot. 198).

(63) **Tectrix.** Synonymy: covert; deck feather. A covert is usually a small feather overlying the base of a flight feather (remex or rectrix) or located between the base of a remex and the cranial edge of the wing. Coverts overlying, dorsally or ventrally, the bases of remiges or rectrices may be aligned in several rows and are named according to their placement (dorsal [superior]/ventral [inferior]), their row (greater [major], median [middle], lesser [minor], and the feathers they cover (e.g. primary, secondary, rectrix). The major dorsal and ventral caudal tectrices are implanted in the Bulbus rectricium, whereas the minor ones are in the skin (Baumel, 1988). See Annot. 71; **Topog.** Annot. 36.

(64) **Pteryla scapulohumeralis.** The scapulohumeral tract covers the shoulder and base of the wing. It includes the feathers termed scapulars which originate above the dorsal side of the shoulder and the proximal part of the humerus (Fig. 3.9).

(65) **Pteryla alae.** The alar tract includes the remiges and the dorsal and ventral coverts of the wing (Annot. 48, 63, 67, 71).

(66) **Remiges primarii.** Primary remiges are attached to the caudodorsal side of the manus. Primaries are numbered from the wrist to the wingtip (Morlion, 1971) (**Topog.** Figs. 2.1, 3; 3.10, 11).

(67) **Remiges secundarii.** Synonymy: Remiges cubitales. The secondary remiges are flight feathers along the caudal edge of the forearm (antebrachium) including the region of the elbow. Secondaries are numbered from the wrist to the elbow (**Topog.** Figs. 2.1, 2,3; Figs. 3.10, 11).

Diastema remigum secundarium. In some genera and families of birds an extra wide space or gap occurs between the 4th secondary remex and the next secondary proximal to it (Stephan, 1970; Lucas and Stettenheim, 1972; Jeikowski, 1974). When a gap is present the wing is termed diastataxic, as exemplified by an anatid. A wing without a gap is eutaxic, as in most galliforms and all passerines.

(68) **Remiges tertiarii [R. humerales].** Synonymy: tertials, tertiaries, posthumeral quills. Tertiary or humeral remiges are flight feathers overlying the humerus as found in some large, long-winged birds such as the Andean Condor (*Vultur gryphus*) (Van Tyne and Berger, 1959). These flight feathers are not aligned in series with the primaries and secondaries (Lucas and Stettenheim, 1972: 80-83). Sometimes distinct-appearing proximal secondaries have incorrectly been called "tertials".

(69) **Remex carpalis.** A relatively small flight feather which, if present, is located on the dorsal surface of the wing in the gap on the wrist between the primaries and secondaries.

(70) **Remiges alulae.** An alular quill, usually relatively small, borne on the alular digit (**Osteo.** Annot. 216). The alular quills have been numbered from proximal to distal (e.g., in Van Tyne and Berger, 1959) and in the opposite direction (e.g., in Lucas and Stettenheim, 1972). Lucas and Stettenheim (1972: 89-90) summarized some of the arguments in favor of each of these methods of counting, but there is not yet a standard method.

(71) **Tectrices alae.** Coverts (**Tectrices**) overlap the remiges on both the dorsal and ventral surfaces of the wing. Rows of coverts are numbered to coincide with those of the remiges. Where three or more rows of coverts adjoin the remiges, the coverts in the row immediately adjacent to the remiges are termed the greater (major) coverts, the next row constitutes the middle (median) coverts, and the remaining row or rows are the lesser (minor) coverts. Some rows of wing coverts can be partially (**Tectrices primariae ventrales mediae**) or completely (**Tectrices secundariae ventrales majores**) absent (Morlion, 1971). The feathers termed "axillaries" originate from the undersurface of the wing immediately distal to the axilla and are part of the **Tectrices tertiariae ventrales.** The **Tectrices marginales manus/propatagii** are exceedingly dense on the leading edge of the manus and propatagium with their follicles embedded in the connective tissue surrounding Lig. propatagiale (R. E. Brown, pers. comm.). Other tectrices (**Tectrices dorsales manus/propatagii**) cover the remaining area of the upper surface of the manus and propatagium and are less densely arrayed. Most of the lower surface of the propagagium is usually an apterium (Annot. 79); however certain birds exhibit some irregular ventral propatagial tectrices (R. E. Brown, pers. comm.). Lucas and Stettenheim (1972) designate all of the upper and lower propatagial tectrices as "marginal". See Figs. 3.10, 11.

(72) **Pteryla membri pelvici.** The tract of the pelvic limb contains a femoral part including all the feathering on the thigh, a crural part, and a tarsometatarsal part for the distal part of the limb. A digital part occurs only in those birds with feathering extending distally onto the toes, e.g. in ptarmigans (*Lagopus*).

(73) **Apteria.** An apterium is an area of skin lacking pennaceous feathers. An apterium can occur between and within the feather tracts. Apteria, whether bare or covered with down feathers (Annot. 56), are named according to their position on the body or by their relationship with the pterylae. Arbitrary decisions must sometimes be made as to whether a gap in feathering constitutes an apterium or simply exceptional spacing between feather rows. Throughout birds as a whole, major differences occur in the arrangement of apteria, but no comprehensive survey of the taxonomic differences is available. Consequently, the names provided here are general ones that may be applicable in a broad range of taxa. Lucas and Stettenheim (1972: 93) provided a more extensive list of potential terms. See Annot. 56.

(74) **Apteria capitalia.** Apteria on the head.

(75) **Apteria dorsalia.** Apteria on or near the middorsal line (Clench, 1970; Morlion, 1971; Lucas and Stettenheim, 1972). Dorsal apteria can be located bilaterally rather than in the midline as in the case of the Apterium scapulare which, when present, lies between the interscapular part of the dorsal tract and the scapulohumeral tract (Fig. 3.9).

(76) **Apteria lateralia.** Apteria on the side of the neck (A. cervicale) or trunk (A. truncale).

(77) **Apterium ventrale.** Parts of the ventral apterium can occur both in a midventral space and bilaterally, the latter in association with bilateral feather tracts. A cervical part occurs on the underside of the neck. The sternal part is the space covering the keel, whereas the pectoral parts lie bilaterally on the breast. Abdominal parts may occur medially and bilaterally (Fig. 3.9).

(78) **Apterium caudale.** A caudal apterium includes any nonfeathered area of or near the uropygium. Special parts may be designated for particular taxa.

(79) **Apteria alae.** Among apteria of the wing, the humeral apterium lies between the scapulohumeral tract and the feathers on the propatagium. The subhumeral apterium lies on the ventral side of the brachium. The propatagial apterium lies in a triangular space between the lesser ventral ("under") secondary coverts and the ventral coverts of the propatagium (see Annot. 71).

(80) **Apterium membri pelvici.** The apterium of the pelvic limb may be subdivided into parts as necessary for different species.

(81) **Rhamphotheca.** The horny covering of the beak, both inside and outside surfaces of the bones of the jaws. The rhamphotheca is hard in most birds, but leathery, for example, at the tip (nail) in flamingos and anatids. The shape of the rhamphotheca is basically that of the underlying bone, but modified by outgrowths and local thickenings (**Topog.** Annot. 12-15). **Cera.** A soft, thick portion of the rhamphotheca at the proximal end of the upper bill in certain birds including falconiforms, some cracids, columbids, psittacids, and strigiforms (**Topog.** Annot. 22).

(82) **Unguis maxillaris; Unguis mandibularis.** The thickened areas of rhamphotheca, "nails", at the tips of the maxillary and mandibular rostra and delimited by a difference in color or by a groove in procellariiform, most pelecaniform, and anseriform birds.

(83) **Podotheca.** The nonfeathered, scale-covered integument of the avian ankle, tarsometatarsus, and digits (see Annot. 84).

(84) **Scutum.** A scale is a flat, rounded, or conical raised area of highly keratinized epidermis, separated from other scales by inward folds of thinner, less keratinized epidermis. Scales vary in size, shape, amount of overlap, and degree of fusion, even on parts of the same foot.

Scutella (sing. **Scutellum**) are small scales of the podotheca including the reticulate scales on the soles of the feet.

Acrotarsium; Acropodium. Scaly covering (part of the podotheca) of the dorsal side of the tarsometatarsus and digits, respectively.

(85) **Pulvinus hypotarsalis.** Synonymy: Pulvinus calcaneus. A thick heel pad on the plantar surface of the hypotarsus (**Osteo.** Annot. 288) just distal to the intertarsal joint in the nestlings of certain hole-nesting birds such as alcedinids, bucerotids and picids. **Pulvinus metatarsalis** (**Topog.** Annot. 40).

(86) **Pulvinus digitalis.** A toe pad (see Lennerstedt, 1975, for detailed structure of digital pads).

Pulvinus ungualis. The digital pad that lies under the base of the unguis and distal interphalangeal joint. Quinn and Baumel (1990) have discussed the function of this pad.

Areae interpulvinares. Regions on the plantar surface of a toe between the pads.

Tela interdigitalis. Webbing between toes occurs in many birds (e.g. sphenisci-, pelecani-, anseri-, and charadriiforms). The interdigital tela is continuous with the podotheca of the digits (**Topog.** Annot. 42).

(87) **Unguis digiti manus.** The horny part of the claw at the tip of a digit that encloses the terminal phalanx. The Hoatzin (*Opisthocomus*) is a notable example of a bird with claws on the wing; many other birds bear inconspicuous alular claws. (**Osteo.** Annot. 224; **Arthr.** Annot. 137.)

Unguis digiti pedis. A claw on a toe (pedal digit). See **Osteo.** Annot. 300. **Processus pectinatus.** A comb-like expansion of the **Scutum dorsale** on the medial edge of digit III in ardeids, caprimulgids, and other birds (Coues, 1927: 138).

Scutum plantare. The plantar podothecal portion of a claw on a toe.

(88) **Calcar alae** (new term). This term designates wing spurs in general. A horny sheath invests a bony core which is a part of the skeleton other than a digit (Coues, 1872), specifically on the radial side of the carpus or carpometacarpus. Birds with wing spurs include cassowaries, screamers, jacanas, sheathbills, and certain geese and plovers; the sites of the spurs differ among these birds.

(89) **Calcar metatarsale.** A metatarsal spur, consisting of a pointed horny sheath over a bony core, occurs on the caudal or medial surface of the tarsometatarsus in males of certain galliform species and is usually reduced or absent in females (Lucas and Stettenheim, 1972: 609-612) (**Topog.** Fig. 2.4; **Osteo.** Annot. 296).

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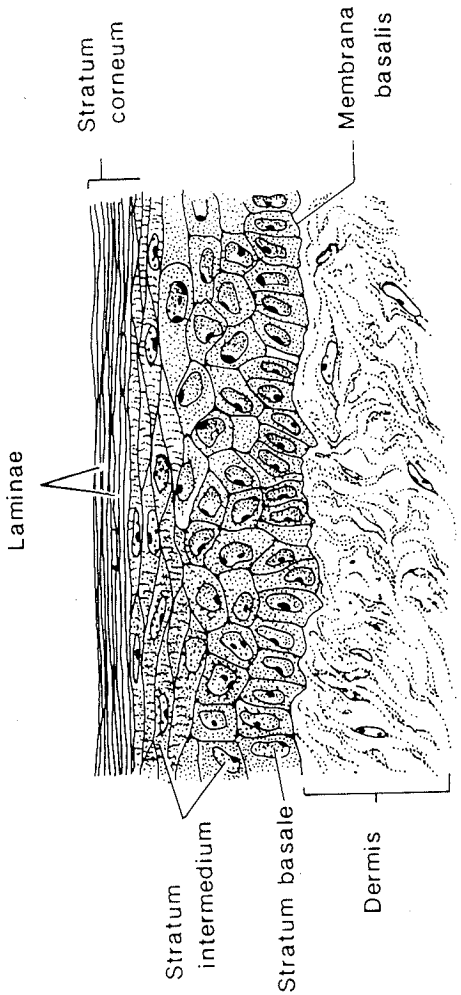

Fig. 3.1. Microscopic section of the epidermis of a chicken (*Gallus gallus*). From Lucas and Stettenheim, 1972.

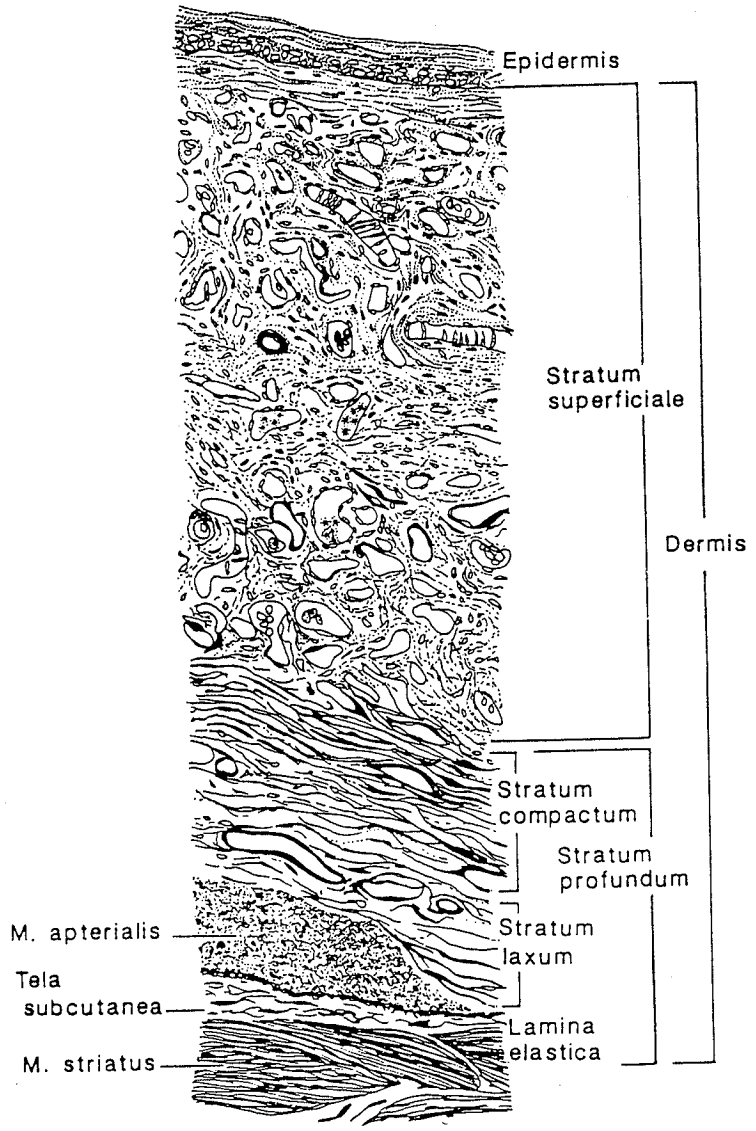

Fig. 3.2. Microscopic section of the skin and subjacent tissues of a chicken (*Gallus gallus*). From Lucas and Stettenheim, 1972.

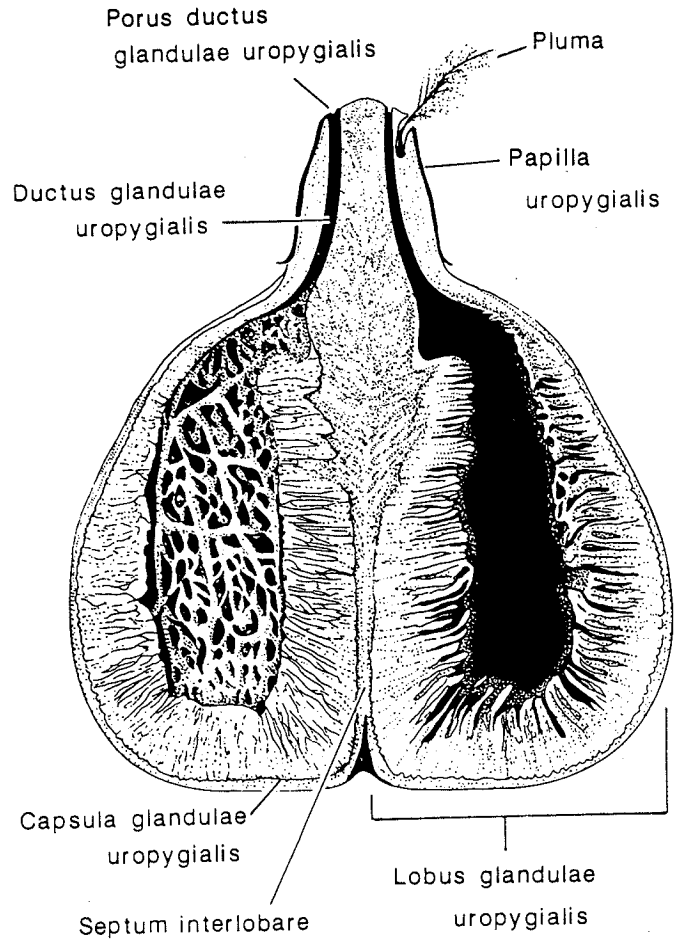

Fig. 3.3. Schematic frontal section of the uropygial gland of a chicken (*Gallus gallus*). The section is parallel to the long axis of the gland; the accumulated secretion has been removed from the left lobe. Note that only one feather has been illustrated from the tuft on the papilla. Modified from Lucas and Stettenheim, 1972.

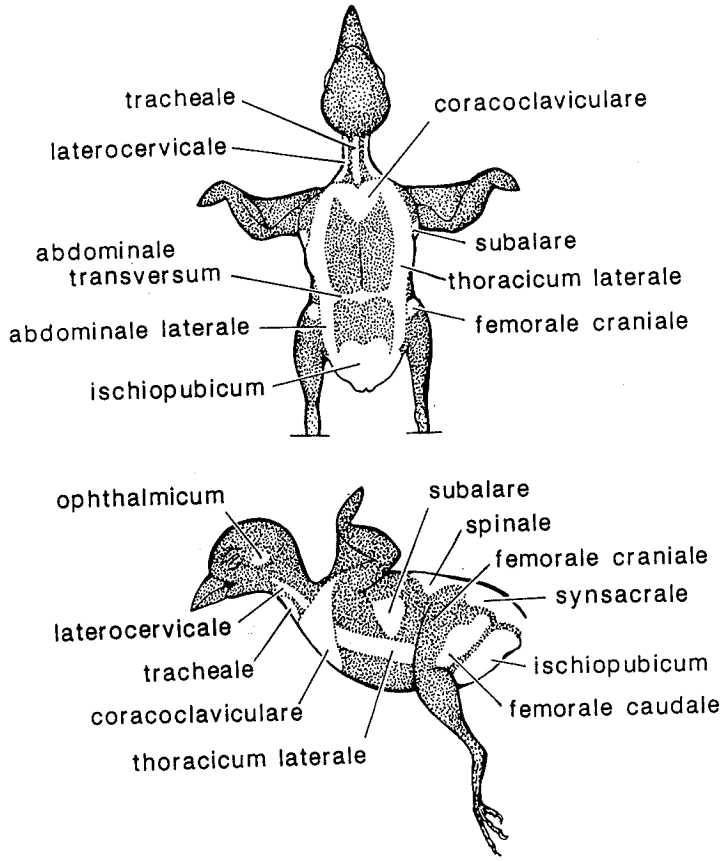

Fig. 3.4. Major subcutaneous fat bodies (Corpora adiposa) in the White-crowned Sparrow (*Zonotrichia leucophrys*). Top: ventral view; bottom: lateral view. From J. R. King and D. S. Farner, 1965, Ann. N. Y. Acad. Sci. **131**: 429; used with permission of the publisher, New York Academy of Sciences.

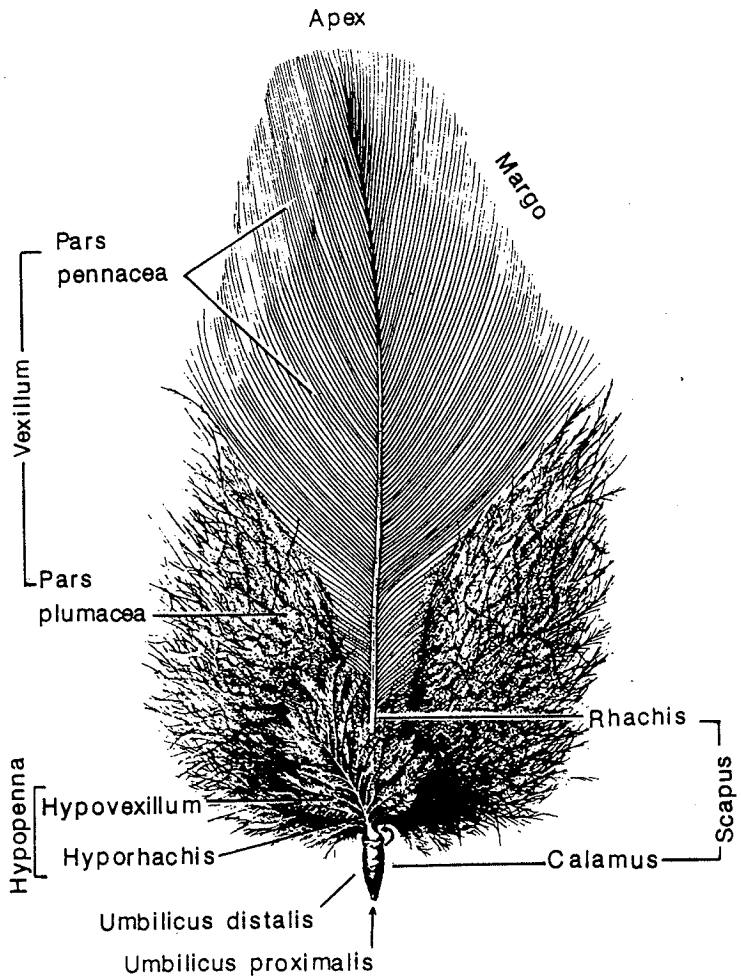

Fig. 3.5. Ventral view of parts of a contour feather of a chicken (*Gallus gallus*). From Lucas and Stettenheim, 1972.

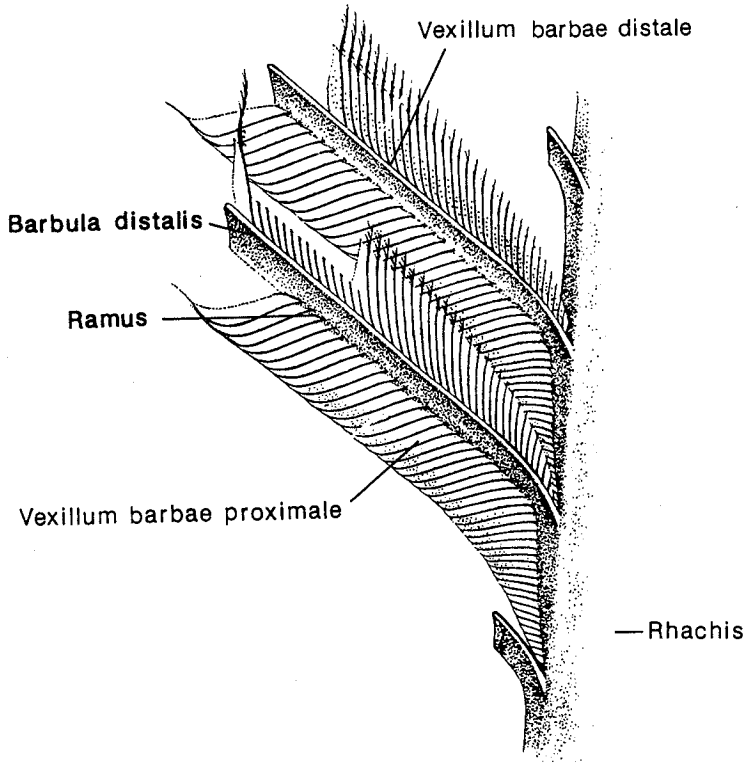

Fig. 3.6. Diagrammatic representation of the barbs attached to the rachis of a feather. After R. Nickel, A. Schummer, and E. Seiferle, 1977, *Anatomy of Domestic Birds*. Used with permission of the publisher, Verlag Paul Parey, Berlin.

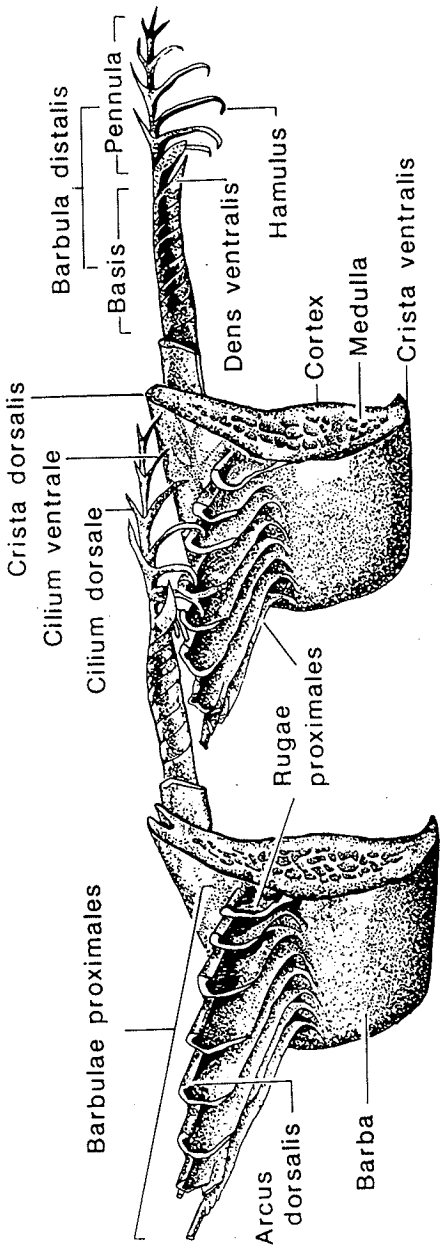

Fig. 3.7. Microscopic detail of the barbs and barbules of a flight feather. Short portions of two barbs from the pennaceous part of the vane of the remex of a chicken (*Gallus gallus*) showing the interlocking of the proximal and distal barbules. From Lucas and Stettenheim, 1972 with permission of the author.

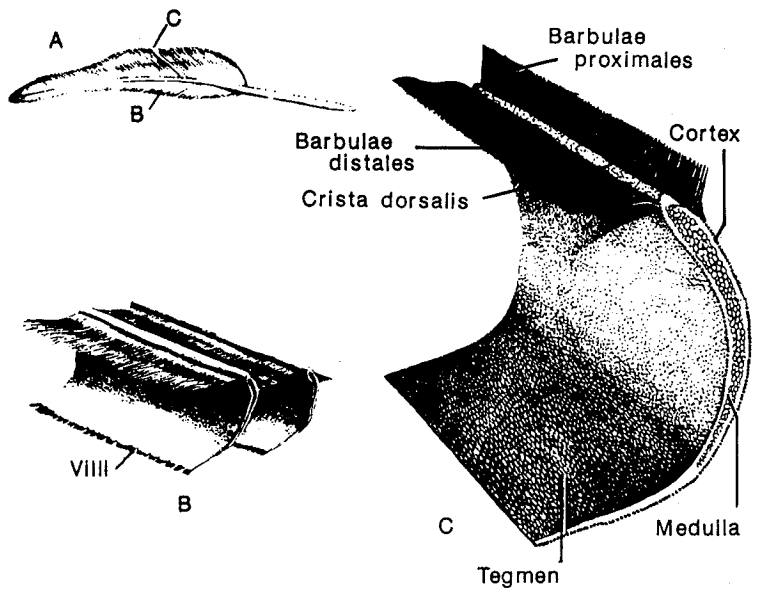

Fig. 3.8. Tegmen (expanded ventral ridge) on the pennaceous barbs of a primary remex from a Mute Swan (*Cygnus olor*). A, Whole feather, indicating location of barbs; B, section of barb from the inner vane with plain tegmen, in oblique view of distal side; C, sections of two barbs from outer vane with fringed tegmen, in oblique view of distal side. After Lucas and Stettenheim, 1972 with permission of author.

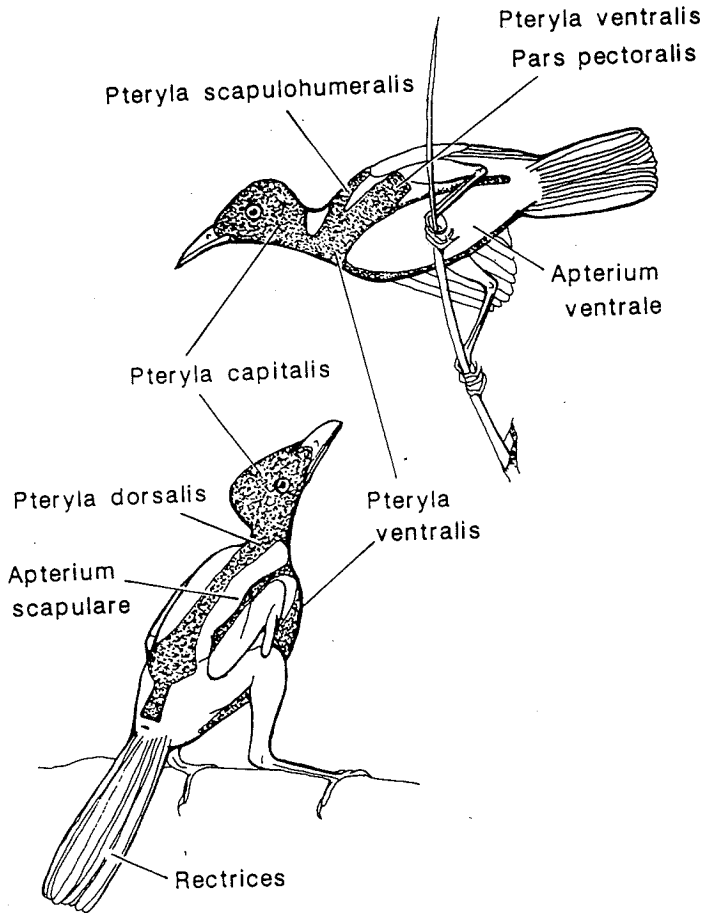

Fig. 3.9. Diagrammatic positions of pterylae on the trunk of a generalized passerine bird. Note that pterylae of the wings and legs are not shown. After Ames, et al.1968.

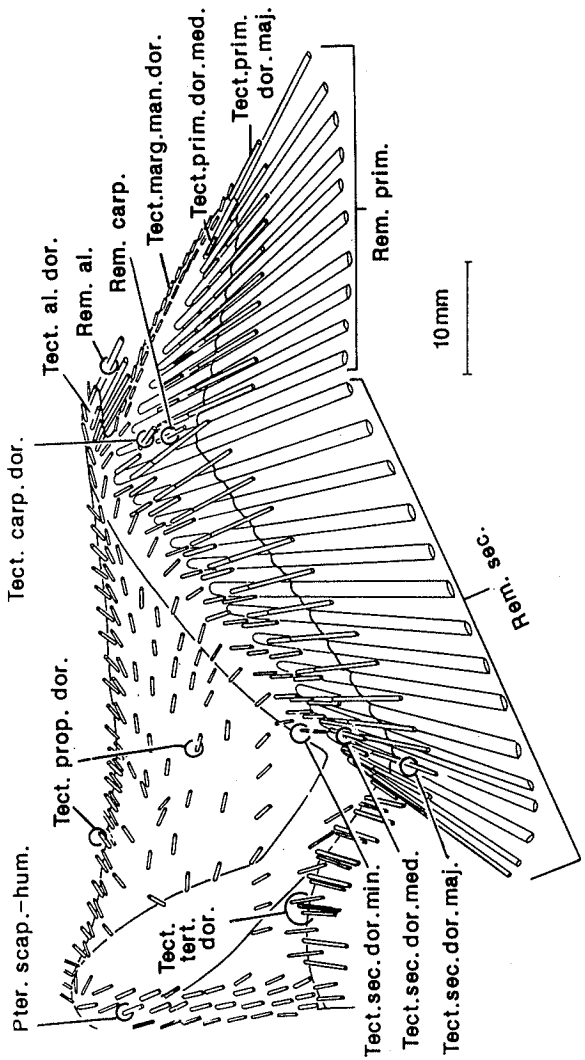

Fig. 3.10. Dorsal view of the pteryla of the wing in the Red-throated Bee-eater (*Merops bulocki*). Full names for abbreviated terms listed here in alphabetical order: Pteryla scapulohumeralis, Remex carpalis, Remiges alulae, Remiges primarii, Remiges secundarii, Tectrices dorsales alulae, Tectrices dorsales propatagii, Tectrices marginales dorsales manus, Tectrices primariae dorsales majores/mediae, Tectrices secundariae dorsales majores/mediae/minores; Tectrices tertiariae dorsales, Tectrix carpalis dorsalis. After an original illustration by M. L. Morlion.

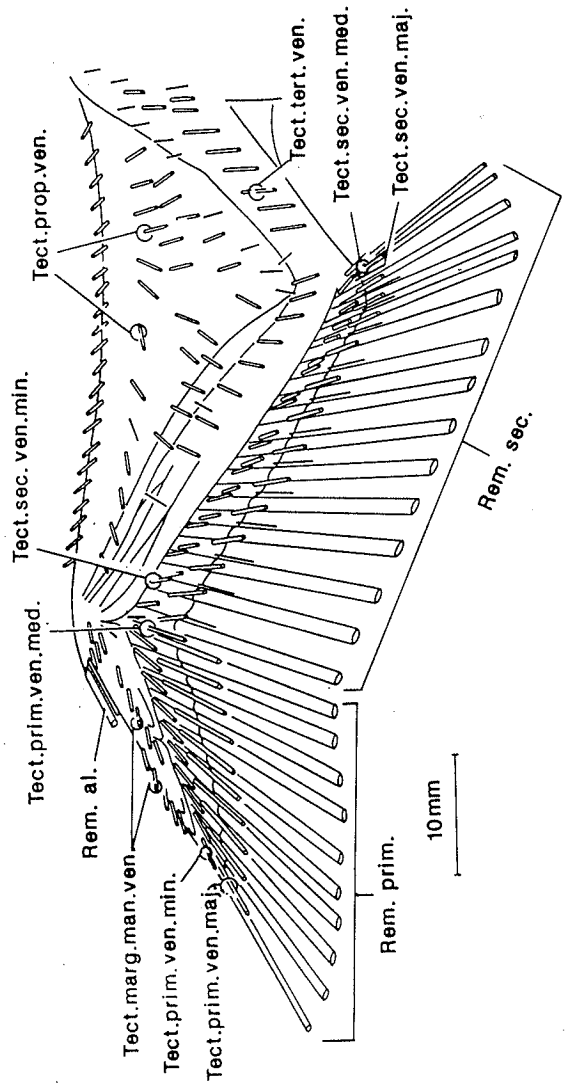

Fig. 3.11. Ventral view of the pteryla of the wing in the Red-throated Bee-eater (*Merops bulocki*). Full names for abbreviated terms listed here in alphabetical order: Remiges alulae, Remiges primarii/secundarii, Tectrices marginales manus, Tectrices primariae ventrales majores, Tectrices secundariae ventrales majores/minores, Tectrices tertiariae ventrales, Tectrices ventrales propatagii, Tectrix primaria ventralis media. After an original illustration by M. L. Morlion.

4

OSTEOLOGIA

JULIAN J. BAUMEL
and
LAWRENCE M. WITMER

With contributions from subcommittee members: P. Ballmann, D. Hogg, V. Komárek, R. Landolt, R. J. Raikow, E. I. Saiff, R. W. Storer, J. C. Vanden Berge, R. L. Zusi, G. Zweers.

Among contemporary workers in avian osteology, Peter Ballmann for years has been concerned with standardization of anatomical terminology. His scholarly and painstaking assistance in the compilation of the postcranial osteological terminology is most commendable. In the first and second editions of *Nomina Anatomica* (**NAA**, 1979) R. L. Zusi, J. Vanden Berge, and R. Landolt have made important contributions in codifying the nomenclature of the skull and vertebral column. The dissertation of Butendieck (1980) provided a worthy review and critique of the osteology terminology of the NAA (1979).

The highly detailed nomenclature of the skeleton of birds presented here will be particularly useful to avian paleontologists, myologists, arthrologists, and systematists who use osteological characters. In the compilation of terms the major works most heavily drawn upon were those of Fürbringer (1888), Lambrecht (1933), and Ballmann (1969a) for the limb bones; Barkow (1856), Boas (1929, 1933), Komárek (1970, 1979), Landolt and Zweers (1985), and Zweers, et al. (1987) for the vertebral column; Hofer (1945, 1949, 1955) and Müller (1963) for the skull.

Nomenclature of digits of wing. The matter of homologies of the digits of the avian thoracic limb has long been a debatable point among avian morphologists. There is still no indisputable evidence for deciding if the elements of the avian manus represent digits I, II, III or II, III, IV. Berger (1966) summarized the controversy on the subject, citing the principal literature up to that time. Seichert and Rychter (1972) discussed and further reviewed the literature on this topic. Recently Hinchliffe (1985) and Müller and Alberch (1990), using more precise techniques than the older embryo-staining methods, have determined that the persisting digits in one species of modern birds

(chicken) are II, III, and IV. On the other hand, most workers regard birds as derivatives of theropod dinosaurs; in these dinosaurs, the evolutionary sequence clearly points to the presence of digits I-II-III as being the components of the tridactyl manus (Ostrom, 1976). Thus the problem is still unresolved.

Rather than perpetuate names of the skeleton and musculature of the manus based on the controversial numbering of the digits by arbitrarily choosing one of the systems in use, an alternative, less equivocal scheme was adopted in the first edition of the NAA (1979): P. Brodkorb originally suggested reviving the proposal of Milne-Edwards (1867-71), designating the digits and their skeletal elements by the descriptive names: Digitus alularis (the so-called pollex), Digitus major, and Digitus minor; Os metacarpale alulare, Os metacarpale majus, and Os metacarpale minus. This terminology has been well accepted, and continues in the present edition. See Annot. 214 and **Myol.** Intro.

Format for listing terms. The skeletal parts that are listed and described are mostly those of the *dried bones of mature individuals* from which the cartilaginous and ligamentous structures have been removed. Most of the anatomical names for skeletal features are listed under the name of the individual bone of which they are parts. For example, Foramen n. ophthalmici and Proc. postorbitalis are parts of Os laterosphenoidale.

On the other hand, numerous features of the skull, pelvis, and vertebral column are not limited to a single bone, but extend over two or more different, adjacent bones (e.g., crests, fissures, fossae, etc.). Extensive fusion of individual bones of the adult avian skeleton often makes it difficult or impossible to identify adjacent bones from one another; however, many of them can be readily distinguished in immature skeletons.

Names of such *compound shared features* in the mature skull involving more than one bone are listed under the headings **Facies** and **Cranium;** subheadings are Cavum nasi, Orbita, Cavum tympanicum, Cavitas cranialis, and Mandibula. In the adult skull *features confined to individual bones* are to be found under the headings: **Ossa faciei** and **Ossa cranii;** in some instances the same term may be listed in more than one place.

In the postcranial skeleton, other complexes of shared elements are: the Notarium and Synsacrum (parts of Columna vertebralis), the Carpometacarpus, Os coxae, Tibiotarsus, and Tarsometatarsus; these receive treatment similar to that of Facies and Cranium.

TERMINOLOGY

TERMINI GENERALES

Aditus	Angulus	Antrum
Ala	Anulus [Annulus]	Apertura

TERMINI GENERALES (cont.)

Apex	Excavatio	Os compactum
Apophysis	Extremitas	Os spongiosum[6]
Arcus	Facies	Os medullare[6]
Area	Facies articularis	Os pneumaticum
Basis	Fenestra	Os sesamoideum
Calvaria	Fissura	Ostium
Canalis	Fonticulus	Phalanx
Canalis nutriens	Foramen	Pila[4]
Canaliculus	Foramen nutriens	Porus
Caput	Foramen pneumaticum[3]	Pori pneumatici[3]
Cellulae	Fossa	Processus
Cervix	Fossula	Radix
Collum	Fovea	Ramus
Cartilago epiphysialis[2]	Foveola	Recessus
Cavitas	Hiatus	Rostrum
Cavum medullare	Incisura	Scapus[5]
[Cavitas medullaris][6]	Impressio	Septum
Carina	Intumescentia	Sinus
Concavitas	Jugum	Spina
Condylus	Labium	Squama
Corpus	Labrum	Stylus
Cortex	Lacuna	Synostosis
Cornu	Lamina	Torus
Cotyla[1]	Linea	Trabeculae ossis
Crista	Meatus	Trochanter
Crus	Margo	Trochlea
Diaphysis[2]	Medulla	Tuber
Discus	Metaphysis[2]	Tuberculum
Diverticulum	Orificium	Tuberositas[7]
Eminentia	Os, ossis	Zona flexoria (**Arthr.**)
Epicondylus	Os planum	Zona elastica (**Arthr.**)
Epiphysis[2]	Os longum	Zygapophysis

SKELETON AXIALE

CRANIUM[8]

Zona flexoria [Ginglymus] craniofacialis (**Arthr.** Annot. 46)

CALVARIA[16] (Figs. 4.1, 2, 5, 6)

Lamina externa	Depressio frontalis[14]
Frons	Fossa temporalis[104]

(continued)

CALVARIA[16] (Figs. 4.1, 2, 5, 6) (cont.)

Meatus acusticus externus[19]
Fossa glandulae nasalis[15]
Occiput
Prominentia cerebellaris[16]
Crista [Linea] nuchalis sagittalis[17]
Crista [Linea] nuchalis transversa[17]
Facies nuchalis
Foramen rami occipitalis ophthalmicae externae
Lamina interna
  Crista vallecularis[106]
  Crista frontalis interna[14]
Tuberculum pineale[37]
Fossa cerebelli[36]
  Crista maginalis[36]
  Impressio eminentiae sagittalis[106]
  Sulcus sinus sagittalis dorsalis (**Ven.** Annot. 31)
Cellulae pneumaticae[6]

BASIS CRANII EXTERNA[28] (see Figs. 4.4) and Ossa cranii)

Lamina parasphenoidalis [L. basitemporalis][96]
  Ala parasphenoidalis
  Basis rostri parasphenoidali
    Proc. basipterygoideus[93]
Proc. lateralis parasphenoidalis[97]
Proc. medialis parasphenoidalis[97]
Os basioccipitale
Canales n. hypoglossi
  Condylus occipitalis[83]
  Tuberculum basilare[83]
Os exoccipitale
  Fossa parabasalis[86]
    Crista fossae parabasalis[86]
Proc. paroccipitalis [P. paroticus][85]
Foramen magnum[18]
Os laterosphenoidale [O. pleurosphenoidale][88]

CAVUM CRANII [CAVITAS CRANIALIS] (see Fig. 4.6; Cranium and Ossa cranii for additional terminology)

BASIS CRANII INTERNA

Eminentia aqueductus vestibuli
Fossa cranii caudalis
  Canales n. hypoglossi
  Eminentia canalis semicircularis
  Foramen magnum[18]
  Fossa acustica interna[101]
  Fossa medullae oblongatae
  Fovea ganglii vagoglossopharyngealis[39]
Fossa cranii media[35]
  Fossa tecti mesencephali (**CNS**)
    Fossa ganglii trigemini
    Crista tentorialis
Fossa cranii rostralis
  Crista frontalis interna[14]
  Foramen ethmoidale[34]
  Foramen n. olfactorii
  Foramen opticum[32]
  Fossa bulbi olfactorii
    Septum osseum fossae bulbi[33]
Fossa cerebelli[36]
  Crista marginalis[36]
  Fossa auriculae cerebelli[38]
  Sulcus v. semicircularis

OSSA CRANII[8] (see **Intro.** Figs. 4.1-6)

Os basioccipitale
  Condylus occipitalis[83]
    Incisura mediana condyli[83]
    Tuberculum basilare[83]
  Facies externa
  Facies medullae oblongatae
  Fossa subcondylaris
  Fovea ganglii vagoglossopharyngealis[39]
Os exoccipitale
  Canalis semicircularis posterior
  Facies cerebralis
  Facies externa (see Cav. cran.)
  Fossa parabasalis[86]
    Crista fossae parabasalis[86]
    Foramen n. glossopharyngealis[39]
    Foramen n. vagi[39]
    Ostium canalis carotici
    Ostium canalis ophthalmici externi[27 86]
  Incisura foraminis magni
  Proc. condylaris[83]
    Canales n. hypoglossi
  Proc. paroccipitalis [P. paroticus][85 20]
Os supraoccipitale
  Crista [Linea] nuchalis transversa[17]
  Facies cerebellaris (see Cav. cran.)
  Facies nuchalis
  Fonticulus occipitalis[87]
  Foramen v. occipitalis externae
Os laterosphenoidale [Os pleurosphenoidale][88]
  Facies orbitalis
    Area muscularis aspera[89]
    Proc. postorbitalis[30a]
  Facies cerebralis
    Canalis n. maxillomandibularis[90]
    Foramen n. maxillomandibularis[90]
    Foramen n. abducentis
    Foramen n. oculomotorii
    Foramen n. trochlearis
    Foramen n. ophthalmici[90]
    Incisura n. optici
  Facies tecti mesencephali
    Fossa ganglii trigemini
    Sulcus n. ophthalmici
    Sulcus n. trochlearis
  Facies temporalis
Os basisphenoidale (Fig. 4.6)
  Facies cerebralis
    Canalis n. abducentis
    Sella turcica[91] (Fig. 4.6)
      Dorsum sellae[91]
      Fossa hypophysialis
      Foramen ophthalmicum internum[91]
      Ostium canalis carotici (Canalis craniopharyngealis)[92]
Os parasphenoidale (Figs. 4.4, 5)
  Rostrum parasphenoidale [R. sphenoidale][96]
    Canalis orbitalis[95]
    Facies articularis palatina
    Facies articularis pterygoidea
    Facies articularis vomeralis
    Basis rostri parasphenoidalis[94]
    Proc. basipterygoideus[93]
    Canalis orbitalis[95]
  Lamina parasphenoidalis [L. basitemporalis][96]
    Ala parasphenoidalis[84 20]
    Proc. lateralis parasphenoidalis[97]
    Proc. medialis parasphenoidalis[97 49]
    Canalis caroticus cranialis[99 121]
    Crista basilaris transversa
    Crista fossae parabasalis[86]
  Tuba auditiva [pharyngotympanica] communis[94 98]

(continued)

OSSA CRANII[8] (see Intro. Figs. 4.1-6) (cont.)

Tuba auditiva [pharyngotympanica][98]
Ostium pharyngeale
Ostium tympanicum
Os squamosum [Squamosum][102]
Facies cerebralis
Facies externa
Cotyla quadratica squamosi[100]
Fossa temporalis[104]
Crista temporalis[104]
Fossa subtemporalis[104]
Proc. postorbitalis[30]
Proc. suprameaticus[103]
Proc. zygomaticus[102]
Ossa otica[105] (see Cav. tymp.)
Os epioticum
Os opisthoticum
Os prooticum[24]
Os metoticum
Cotyla quadratica otici[24]
Pila otica[24]
Proc. paroccipitalis [P. parotica][85]
Vestibulum
Canales semicirculares ossei (Sens. Intro.)
Canalis semicircularis anterior
Canalis v. semicircularis anterioris (Ven. Annot. 32, 36)
Canalis semicircularis lateralis
Canalis v. semicircularis lateralis (Ven. Annot. 32, 36)
Canalis semicircularis posterior
Cochlea (Sens. Annot. 40-43)
Lagena (Sens. Annot. 55)
Fossa acustica interna[101]
Foramen n. ampullaris caudalis
Foramen n. ampullaris lateralis
Foramen n. ampullaris rostralis
Foramen n. cochlearis
Foramen n. facialis
Os parietale
Crista [Linea] nuchalis transversa[17]
Facies externa
Facies interna
Os frontale[14]
Facies cerebralis
Crista vallecularis[106]
Impressio eminentiae sagittalis (CNS Annot. 78)
Crista frontalis interna[14]
Sulcus sinus sagittalis dorsalis (Ven. Annot. 31)
Facies dorsalis
Fossa glandulae nasalis[15]
Foramina neurovascularia
Facies orbitalis
Impressio glandulae nasalis
Margo supraorbitalis
Proc. lacrimalis [P. prefrontalis][107]
Os mesethmoidale[108]
Lamina dorsalis[108]
Septum nasale osseum[55 108]
Sulcus n. olfactorii[31]
Os ectethmoidale [Os latero-ethmoidale][109]
Facies nasalis
Facies orbitalis
Os lacrimale [Os prefrontale][110]
Facies articularis frontonasalis[111]
Incisura ductus nasolacrimalis (Sens. Annot. 38)
Proc. orbitalis
Proc. supraorbitalis

CAVUM TYMPANICUM [CAVITAS TYMPANICA][21 19]

Canalis ophthalmicus externus[27 86]
Cotylae quadratica otici[24 100]
Cotyla quadratica squamosi[24 100]
Ostium canalis tubae auditivae [pharyngotympanicae]
Columella (Sens. Annot. 55)
Foramen m. columellae
Hiatus subtympanicus[20]
Pila otica [P. prootica][24]
Recessus columellae [R. antevestibularis][22]
Fenestra vestibuli[22]
Fenestra cochleae [F. pseudorotunda][22]
Recessus pneumatici paratympanici[23 49]
Recessus tympanicus caudalis[26]
Foramen pneumaticum caudale
Recessus tympanicus dorsalis[25]
Foramen pneumaticum dorsale
Recessus tympanicus rostralis[26]
Foramen pneumaticum rostrale
Cellulae pneumaticae
Siphonium[49]

ORBITA[29] (Figs. 4.1, 2)

Paries caudalis orbitae
Os laterosphenoidale [Os pleurosphenoidale][88]
Proc. postorbitalis[30a]
Paries dorsalis orbitae
Impressio gl. nasalis[15]
Os frontale
Paries medialis orbitae
Septum interorbitale[29]
Paries rostralis orbitae[109]
Os ectethmoidale[109]
Fonticuli interorbitales[29]
Fonticuli orbitocraniales[29]
Foramen n. maxillomandibularis[90]
Foramen n. olfactorii
Foramen n. ophthalmici[90]
Foramen opticum[32] (see Os lat. sphen.)
Foramen orbitonasale laterale[31]
Foramen orbitonasale mediale[31]
Margo supraorbitalis
Margo infraorbitalis
Arcus suborbitalis[30b]
Sulcus n. olfactorii[31]

FACIES[8]

MAXILLA (see Ossa max. et palati) (Fig. 4.4)

Fenestra antorbitalis [F. orbitonasalis][9]
Hiatus craniofacialis septi[10]
Arcus jugalis[11]
Arcus suborbitalis[30]
Rostrum maxillae[40]
Palatum osseum
Concavitas palati
Fissura interpalatina
Fenestra palatina[13]

(continued)

MAXILLA (see Ossa max. et palati) (Fig. 4.4) (cont.)

Canalis neurovascularis maxillae[57]
Canaliculi neurovasculares[57]
Foramina neurovascularia[57]
Foveae corpusculorum nervosorum[41]
Dentes[82]

CAVUM NASI [CAVITAS NASALIS]

Apertura nasi [nasalis] ossea[12]
Pila supranasalis[12]
Septum nasi [nasale] osseum[55]
Conchae nasales[55] (**Resp.**)
Recessus pneumatici paranasales (**Resp.**)
Fossa antorbitalis[9]
Os ectethmoidale[109]

MANDIBULA (see Ossa mand.) (Figs. 4.1, 2)

Rostrum [Symphysis] mandibulae[40]
Ramus mandibulae
- Pars caudalis[42]
- Pars intermedia[42]
- Pars symphysialis[42]
- Angulus mandibulae[43]
- Crista tomialis[56]
- Facies lateralis
- Facies medialis
- Proc. coronoideus[44]
- Proc. lateralis mandibulae[49d 84 96]
- Proc. medialis mandibulae[49d 84 96]
  - Facies articularis parasphenoidalis[49d]
- Fenestra caudalis mandibulae[46]
- Fenestra rostralis mandibulae[46]
- Fossa aditus canalis neurovascularis[48]
- Fossa lateralis mandibulae[48]
- Canalis neurovascularis mandibulae[47]
  - Canaliculi neurovasculares[57]
  - Foramina neurovascularia[57]
  - Foveae corpusculorum nervosorum[41 57]

Tuberculum pseudotemporale[45]
Fossa articularis quadratica[49a]
- Cotylae fossae articularis[49a]
  - Cotyla caudalis
  - Cotyla lateralis[72]
    - Cotyla rostralis[72]
  - Cotyla medialis (see Quadr.)
  - Sulcus intercotylaris[49a]
  - Tuberculum intercotylare [Crista intercotylaris][49a]
  - Foramen pneumaticum articulare[49c]

Proc. retroarticularis[49b]
Incisura retroarticularis[49b]
Fossa caudalis[51]
- Crista transversa fossae[51]

Recessus conicalis[50]
Dentes[82]

OSSA FACIEI[8] (Intro.)

OSSA MAXILLAE ET PALATI (Figs. 4.4, 7)

Os nasale
- Proc. frontalis
- Proc. maxillaris[54]
- Proc. premaxillaris[54]

Os premaxillare
- Corpus ossis premaxillare
  - Proc. frontalis
  - Proc. maxillaris[54]
  - Proc. palatinus
  - Crista tomialis[56]
  - Canalis neurovascularis maxillae[57]
    - Canaliculi neurovasculares
    - Foramina neurovascularia[57]
    - Foveae corpusculorum nervosorum[41]
  - Rostrum maxillae[40]

Os maxillare[53]
- Crista tomialis[56]
- Proc. jugalis[59 11]
- Proc. nasalis
- Proc. maxillopalatinus [P. palatinus][58]
- Proc. premaxillaris
- Canalis neurovascularis[57]
  - Canaliculi neurovasculares
  - Foramina neurovascularia[57]
  - Foveae corpusculorum nervosorum[41]

Os palatinum [Os pterygopalatinum][60]
- Pars choanalis[60]
  - Angulus caudomedialis[64]
  - Crista dorsolateralis[62]
  - Crista medialis[62]
  - Crista ventralis[64]
  - Facies articularis parasphenoidalis[62]
  - Facies articularis vomeralis
  - Fossa choanalis[60]
  - Lamella choanalis[64]
  - Lamella dorsalis[62]
  - Proc. caudomedialis[64]
  - Proc. rostralis[63]
- Pars lateralis [Lamella caudolateralis][60]
  - Angulus caudolateralis[66]
  - Crista lateralis[65]
  - Facies articularis pterygoidea
  - Fossa ventralis[67]
  - Proc. maxillaris[60]
  - Proc. pterygoideus[60 61]

Vomer[68 69]
- Corpus vomeris
- Facies articularis palatina[68 69]
- Facies articularis parasphenoidalis[69]
- Facies articularis pterygoidea[68 69]
- Facies articularis maxillaris[68 69]
- Facies articularis premaxillaris[68 69]
- Proc. pterygoideus

Os pterygoideum[61] (Figs. 4.2, 4)
- Facies articularis basipterygoidea[93]
- Facies articularis quadratica
- Pes pterygoidei[69]
  - Facies articularis palatina[69]
  - Facies articularis parasphenoidalis[69]
  - Pars palatina[61]
- Proc. dorsalis[70]
- Proc. quadraticus

Os jugale
- Tuberculum lacrimale [T. prefrontale] (**Arthr.** Annot. 19)

Os quadratojugale[11]
- Condylus quadraticus[73]

(continued)

OSSA MAXILLAE ET PALATI (Figs. 4.4, 7) (cont.)

Os quadratum [Quadratum][71]
  Corpus ossis quadrati
  Facies tympanica
    Crista tympanica[19]
    Foramen pneumaticum
    Sulcus pneumaticus
  Proc. mandibularis[72]
    Condylus caudalis[72]
    Condylus lateralis
      Cotyla quadratojugalis[73]
      Condylus rostralis[72]
    Condylus medialis
    Condylus pterygoideus
    Sulcus intercondylaris
  Proc. orbitalis
  Proc. oticus[71 24]
    Capitulum [Condylus] oticum[24]
    Capitulum [Condylus] squamosum[71]
    Crista tympanica[19]
    Incisura intercapitularis[71]
    Sulcus pneumaticus

OSSA MANDIBULAE (see also Mand.)

Os dentale[52]
  Pars dorsalis
  Pars ventralis
  Pars symphysialis
Os angulare[49b]
  Proc. retroarticularis
Os articulare[49c]
  Foramen pneumaticum articulare[49]
  Proc. medialis mandibulae[49d 84 96]
Os coronoideum[52]
Os prearticulare[52]
Os spleniale[52]
Os supra-angulare[52]
  Proc. lateralis mandibulae[49d 84 99]

OSSA ACCESSORIA CRANII[75]

Anulus [Annulus] tympanicus[77]
Os nuchale[76]
Ossa sclerae (**Sens.** Annot. 8)
Os siphonium [Siphonium][49c]
Os suprajugale
Ossa supraorbitalia[74]
Os lacrimopalatinum
Ossa suturarum[78]
Os uncinatum[78]

LARYNX

Skeleton laryngis (**Resp.** Larynx)

SYRINX

Skeleton syringis (**Resp.** Syrinx)

APPARATUS HYOBRANCHIALIS [A. HYOLINGUALIS][79]

Paraglossum[80]
  Cornua
Basihyale [Basibranchiale rostrale][81]
  Crista dorsalis
  Proc. parahyalis[81]
  Arcus parahyalis[81]
Urohyale [Basibranchiale caudale][81]
Cornu branchiale
  Ceratobranchiale
  Epibranchiale
  Pharyngobranchiale

COLUMNA VERTEBRALIS[112 113 129 139 141]

PARTES VERTEBRAE[113] (Figs. 4.8, 9)

Corpus vertebrae[113]
  Facies articularis caudalis
  Facies articularis cranialis
  Facies lateralis corporis
    Concavitas lateralis
    Sulcus lateralis[115]
    Eminentia costolateralis[116]
      Fovea costalis[117]
    Proc. costalis[118]
    Tuberositas lig. collateralis (**Arthr.** Annot. 60)
    Foramina pneumatica
  Facies ventralis corporis
    Proc. postlateralis[121]
    Proc. caroticus[121]
    Sulcus caroticus[121]
    Crista [Proc.] ventralis corporis[119]
      Alae cristae ventralis[120]
      Crista ventrolateralis[122]
    Fovea cranioventralis[114]
  Facies dorsalis corporis[113]
Arcus vertebrae [A. neuralis][127a]
  Lamina lateralis arcus [Pediculus arcus][127a]
    Incisura cranialis arcus[128a]
    Incisura caudalis arcus[128a]
  Lamina dorsalis arcus[127a]
    Area lig. elastici[126]
    Proc. spinosus [arcus]
Proc. transversus vertebrae[123 127a]
  Facies dorsalis
  Facies ventralis
  Fovea costalis[117]
Zygapophysis [Proc. articularis] caudalis[132]
  Crista transverso-obliqua[124]
  Facies articularis
  Torus dorsalis[125]
Zygapophysis [Proc. articularis] cranialis[132]
  Facies articularis
Ansa costotransversaria[135]
  Foramen transversarium[134a 138]
  Tuberculum ansae[135]
  Cristae laterales ansae[135]
  Proc. costalis
Lamina arcocostalis[127b 134a]
  Foramen laterale arcus
Lamina corporocostalis[127c]
Foramen vertebrale[113]
Canalis vertebralis[113]
Canalis caroticus cervicalis[121]
Hiatus interarcualis[128b]
  Lacuna interzygapophysialis[128c]
Foramen intervertebrale[128a]
Foramen transversarium[134a]
Canalis vertebrarterialis[134b]

VERTEBRAE CERVICALES SPECIALES[129] (see above for parts of a generalized free vertebra)

Atlas[130] (Fig. 4.8)
- Corpus atlantis
  - Facies articularis axialis
  - Fossa condyloidea[131]
  - Facies articularis dentalis
  - Foramen fossae[130]
  - Incisura fossae[130]
  - Tuberositas lig. transversi
  - Proc. ventralis corporis
- Arcus atlantis
  - Ansa costotransversaria[135]
  - Foramen transversarium[134a]
  - Incisura caudalis arcus[136a]
  - Zygapophysis [Proc. articularis] caudalis[132]
    - Facies articularis
  - Proc. spinosus [P. dorsalis]

Axis[130] (Fig. 4.8)
- Corpus axis
  - Dens[136b]
    - Fovea aspera
    - Facies articularis atlantica
    - Fovea lig. collateralis atlantoaxialis (**Arthr.**)
  - Proc. ventralis corporis[119]
- Arcus axis
  - Lamina dorsalis arcus
  - Ansa costotransversaria[135]
    - Foramen transversarium[134 138]
  - Proc. costalis axis[138]
  - Proc. spinosus [P. dorsalis][137]
  - Lacuna interzygapophysialis[128c]
  - Lamina lateralis arcus[127a]
    - Incisura caudalis arcus[128a]
    - Incisura cranialis arcus[128a]
  - Zygapophysis [Proc. articularis] caudalis[132]
    - Facies articularis
  - Zygapophysis [Proc. articularis] cranialis[132]
    - Facies articularis

VERTEBRAE THORACICAE, [LUMBICALES], ET SACRALES[139 141b]

(see above for parts of a typical free vertebra)

NOTARIUM [Os dorsale][140a] (Fig. 4.9)

- Canalis notarii [C. vertebralis][140b]
- Crista spinosa [dorsalis] notarii[140b]
- Lamina transversa notarii[141c]
  - Fenestrae intertransversariae[141c]
- Corpus notarii[142a]
  - Crista ventralis notarii[119]
    - Fenestrae intercristales[119]
  - Foramina intervertebralia[128 143]
  - Eminentia costolateralis[116]

VERTEBRAE SYNSACRALES[141a] (Fig. 4.9)

SYNSACRUM[141a] (see Os coxae)

- Canalis synsacri [C. vertebralis][143b]
- Extremitas cranialis synsacri
- Facies dorsalis synsacri
  - Crista spinosa [C. dorsalis] synsacri[142c]
  - Lamina transversa synsacri[141c]

SYNSACRUM[141a] (see Os coxae) (cont.)

- Margo lateralis laminae transversae[141c]
- Fenestrae intertransversariae[141c]
- Facies lateralis synsacri
  - Foramina intervertebralia[143a 128a]
  - Eminentia costolateralis[116]
- Facies visceralis synsacri[142b]
  - Corpus synsacri[142a]
    - Crista ventralis synsacri[119]
    - Sulcus ventralis corporis
  - Vertebra acetabularis[141b]
- Proc. costalis
- Proc. transversus
- Fossae renales (see Pelvis)
- Extremitas caudalis synsacri

VERTEBRAE CAUDALES (Figs. 4.9, 15) (see above for parts of a typical vertebra)

- Vertebrae caudales stabiles[141a]
- Vertebrae caudales liberae[144]
  - Proc. haemalis[144]
- Pygostylus [Coccyx][145]
  - Apex pygostyli
  - Basis pygostyli[146]
  - Corpus pygostyli
    - Crista ventralis
    - Facies articularis cranialis
    - Proc. haemalis[144]
    - Canalis vascularis
  - Lamina pygostyli[146]
    - Proc. transversus[146]
    - Canalis pygostyli [C. vertebralis]
  - Margo cranialis
  - Margo caudalis
    - Discus pygostyli[146]

CAVUM THORACIS [CAVITAS THORACICA]

- Apertura thoracica caudalis
- Apertura thoracica cranialis
- Facies visceralis sterni (see Sternum)
- Spatium intercostale
- Sulcus pulmonalis[148] (**Resp.** Annot. 49)

COSTAE[147] (see Cav. thor.)

- Costa vertebralis
  - Extremitas dorsalis costae
    - Capitulum costae[116]
    - Collum costae
    - Tuberculum costae[117]
    - Incisura capitulotubercularis[148]
    - Angulus costae
  - Corpus costae
    - Facies medialis [F. pulmonalis]
    - Facies lateralis
    - Margo caudalis
    - Margo cranialis
    - Proc. uncinatus[148] (Fig. 4.9)
  - Extremitas ventralis costae
    - Facies articularis intercostalis (**Arthr.** Annot. 81)
- Costa sternalis
  - Extremitas dorsalis costae

(continued)

COSTAE[147] (see Cav. thor.) (cont.)

Facies articularis intercostalis (**Arthr.** Annot. 81)

Extremitas ventralis costae
Facies articularis sternalis[157]

SKELETON APPENDICULARE

OSSA CINGULI MEMBRI THORACICI

STERNUM[149] (Fig. 4.11)

Corpus sterni[149]
Facies muscularis sterni[152]
Linea intermuscularis[153]
Planum postcarinale[154]
Facies visceralis sterni[152]
Pars cardiaca
Pars hepatica
Foramen pneumaticum
Pori pneumatici
Sulcus medianus sterni
Margo costalis [lateralis] sterni[157]
Incisurae costales[157]
Loculus costalis[157]
Pila costalis[155]
Proc. articularis sternocostalis[157]
Facies articularis costalis[157]
Margo cranialis sterni
Pila coracoidea[158]
Sulcus articularis coracoideus[156 175a]
Labrum externum
Tuberculum labri externi (**Arthr.** 89, 90)
Labrum internum
Proc. craniolateralis sterni[150]
Impressio m. sternocoracoidei
Rostrum sterni[159] (**Arthr.** Annot. 86)
Foramen rostri[160]
Spina externa rostri[159]
Alae spinae sternae
Spina interna rostri[159]
Spina communis[159]
Septum interarticulare[159]
Spatium intercoracoidale[160]
Margo caudalis sterni[157]
Fenestra lateralis[151]
Fenestra medialis[151]
Incisura lateralis[151]
Incisura medialis[151]
Trabecula intermedia[151]
Trabecula lateralis[151]
Trabecula mediana[151]
Proc. caudolateralis sterni[150]
Carina sterni[161] (Fig. 4.11)
Apex carinae
Facies articularis furculae
Tuberositas lig. sternoclavicularis (**Arthr.** Annot. 85)
Facies lateralis carinae
Linea intermuscularis[153]
Margo cranialis carinae
Crista lateralis carinae[161]
Crista mediana carinae
Pila carinae[161]
Sulcus carinae[161]
Margo ventralis carinae

CLAVICULA [FURCULA][162] (Fig. 4.10)

Extremitas omalis claviculae [Epicleideum][164]
Proc. acrocoracoideus claviculae[165]
Facies articularis acrocoracoidea
Proc. acromialis claviculae[165]
Facies articularis acromialis
Extremitas sternalis claviculae
Apophysis furculae [Hypocleideum][163]
Scapus [Corpus] claviculae
Proc. interclavicularis[163]

SCAPULA[166] (Fig. 4.10)

Extremitas cranialis [Caput] scapulae
Acromion[166]
Crista lig. acrocoracoacromiali[166]
Facies articularis clavicularis
Sulcus supracoracoideus[172]
Proc. glenoidalis scapulae[167b]
Facies articularis humeralis[167a]
Labrum glenoidale
Facies articularis coracoidea[168 173a]
Tuberculum coracoideum[168 173a]
Collum scapulae[170]
Corpus scapulae[170]
Facies medialis [F. costalis][166]
Facies lateralis[166]
Margo dorsalis [M. vertebralis]
Margo ventralis
Tuberculum m. scapulotricipitis[169]
Extremitas caudalis [Spina] scapulae

CORACOIDEUM [OS CORACOIDEUM] (Fig. 4.10)

Extremitas omalis coracoidei[171a]
Proc. acrocoracoideus[171a]
Facies articularis clavicularis
Impressio lig. acrocoracohumeralis
Tuberculum brachiale[171b]
Proc. glenoidalis coracoidei[167b]
Facies articularis humeralis[167a]
Labrum glenoidale
Facies articularis scapularis[173a]
Cotyla scapularis[173b]
Proc. procoracoideus[172]
Facies articularis scapularis[173a]
Sulcus supracoracoideus[172 177]
Corpus coracoidei
Facies dorsalis
Cotyla scapularis[173b]
Facies ventralis
Margo lateralis
Margo medialis
Foramen [Incisura] n. supracoracoidei
Linea intermuscularis ventralis[174]
Extremitas sternalis coracoidei
Crista articularis sternalis[175a]
Facies externa
Crista intermedia
Facies interna
Facies articularis intercoracoidea[175b]
Angulus medialis
Proc. lateralis[176]
Angulus lateralis
Margo supra-angularis[176]
Impressio m. sternocoracoidei
Canalis triosseus[177]
Cavitas glenoidalis[167]

OSSA ALAE [MEMBRI THORACICI][178]

SKELETON BRACHII

HUMERUS[178] (Fig. 4.12)

Extremitas proximalis humeri
- Caput humeri[178 179]
  - Incisura capitis humeri[180]
  - Crista incisurae capitis
  - Tuberculum dorsale[182]
- Crista deltopectoralis[184]
  - Angulus cristae
  - Impressio m. pectoralis
  - Crista m. supracoracoidei[183]
- Tuberculum ventrale[187]
  - Crista bicipitalis[184]
- Fossa pneumotricipitalis [F. tricipitalis][188]
  - Foramen pneumaticum[189]
  - Crus dorsale fossae[188]
  - Crus ventrale fossae[188]
  - Margo caudalis[188]
- Planum intertuberculare[181]
  - Sulcus [Canalis] n. coracobrachialis[181]
  - Intumescentia humeri[190]
- Sulcus transversus[185]
- Impressio coracobrachialis[186]

Corpus humeri
- Facies caudalis[178]
  - Margo caudalis[188]
- Facies cranialis[178]
  - Margo caudalis[188]
  - Margo dorsalis
  - Margo ventralis
    - Linea m. latissimi dorsi
    - Sulcus n. radialis[191]

Extremitas distalis humeri
- Condylus dorsalis humeri[192]
- Condylus ventralis humeri[192]
- Incisura intercondylaris[193]
- Fossa m. brachialis
- Epicondylus dorsalis [Ectepicondylus][194 178]
- Epicondylus ventralis [Entepicondylus][194 178]
- Proc. flexorius[195]
- Tuberculum supracondylare dorsale[196]
  - Proc. supracondylaris dorsalis[196]
- Tuberculum supracondylare ventrale[196]
- Fossa olecrani
  - Sulcus scapulotricipitalis[200]
  - Sulcus humerotricipitalis[200]
  - Os sesamoideum m. scapulotricipitis[202]

SKELETON ANTEBRACHII (Fig. 4.13)

ULNA[198] (Fig. 4.13)

Extremitas proximalis ulnae
- Proc. cotylaris dorsalis[197]
  - Cotyla dorsalis[198]
  - Cotyla ventralis[198]
  - Crista intercotylaris
- Impressio m. brachialis
- Impressio m. scapulotricipitis
- Incisura radialis[199]
- Olecranon[201]
- Sulcus tendinosus[203]
- Tuberculum bicipitale ulnae[210]
- Tuberculum lig. collateralis ventralis[203]

Corpus ulnae
- Facies caudodorsalis[204]
- Facies caudoventralis[204]
- Facies cranialis[204]
- Lineae intermusculares
- Margo caudalis
- Margo dorsalis
- Margo interosseus [M. cranialis]
- Papillae remigales caudales[205]
- Papillae remigales ventrales[205]

Extremitas distalis ulnae
- Trochlea carpalis[206]
  - Condylus dorsalis ulnae[206]
    - Labrum condyli dorsalis
  - Condylus ventralis ulnae[206]
  - Sulcus intercondylaris[206]
- Tuberculum carpale[207]
  - Incisura tuberculi carpalis[207]
- Depressio radialis[208]
- Incisura tendinosa[209]

ULNA[198] (Fig. 4.13) (cont.)

RADIUS (Fig. 4.13)

Extremitas proximalis radii
- Caput radii
  - Cotyla humeralis
- Facies articularis ulnaris
- Tuberculum bicipitale radii[210]

Corpus radii
- Lineae intermusculares
- Margo dorsalis
- Margo interosseus [caudalis]
- Margo ventralis

Extremitas distalis radii
- Facies articularis radiocarpalis[211]
- Facies articularis ulnaris[211]
- Depressio ligamentosa[212]
- Sulcus tendinosus[211]
- Tuberculum aponeurosis ventralis[213]

SKELETON MANUS

OSSA CARPI[214] (Fig. 4.14)

(Ossa carpi proximalia)[214]
(Ossa carpi centralia)[214]
(Ossa carpi distalia)[214]
Os carpi radiale[215]
- Facies articularis metacarpalis[215]
- Facies articularis radialis
- Facies articularis ulnaris

Os carpi ulnare[215]
- Corpus
- Crus longum[215]
- Crus breve[215]
- Incisura metacarpalis[215]
- Proc. muscularis[215]
- Facies articularis ulnaris
- Facies articularis metacarpalis[215]

Os prominens[216]

CARPOMETACARPUS (Fig. 4.14) (Osteo. Intro.; Arthr. Annot. 128)

Extremitas proximalis carpometacarpi
- Os metacarpale alulare[216]
- Proc. alularis
  - Facies articularis alularis
  - Proc. extensorius
- Trochlea carpalis[215]
  - Facies articularis radiocarpalis
  - Facies articularis ulnocarpalis
- Fossa infratrochlearis[218]
- Fossa supratrochlearis[219]
- Fovea carpalis caudalis[217]
- Fovea carpalis cranialis[217]
- Proc. pisiformis[220]

Corpus carpometacarpi
- Facies dorsalis
- Facies ventralis
- Margo caudalis
- Margo cranialis
- Os metacarpale majus
  - Sulcus tendinosus
  - Proc. intermetacarpalis[221]
  - Protuberantia metacarpalis[221]
- Os metacarpale minus
- Spatium intermetacarpale

Extremitas distalis carpometacarpi
- Symphysis metacarpalis distalis[222]
  - Sulcus interosseus[223]
- Facies articularis digitalis major
- Facies articularis digitalis minor

OSSA DIGITORUM MANUS[224] (Osteo. Intro.)

Phalanx digiti alulae

Phalanx proximalis digiti majoris
- Facies articularis metacarpalis
- Facies articularis phalangealis
- Fossa dorsalis
- Fossa ventralis
- Pila cranialis phalangis[225]

Phalanx distalis digiti majoris
- Facies articularis metacarpalis

Phalanx digiti minoris

OSSA CINGULI MEMBRI PELVICI

PELVIS ET OS COXAE[226] (Figs. 4.9, 15) (For synsacrum see Columna vertebrale; see below for elements of Os coxae).

Acetabulum[226]
- Foramen acetabuli[226]

Antitrochanter[232]

Canalis [Sulcus] iliosynsacralis[234]

Crista iliosynsacralis[233]

Concavitas infracristalis[235]

Fenestra ischiopubica[229 227]

Foramen ilioischiadicum[230]

Foramen obturatum[227 252]

Fossa renalis[237 250]
- Pars ischiadica fossae[237]
- Pars pudenda fossae[237]
- Recessus caudalis fossae[250]

Incisura caudalis pelvis[238]

Incisura marginis caudalis[231]

Proc. marginis caudalis[231]

OS COXAE[226] (Figs. 4.9, 15)

ILIUM (Figs. 4.9, 15)

Ala [Pars] preacetabularis ilii[245]
- Facies dorsalis
  - Fossa iliaca dorsalis
  - Crista iliaca dorsalis[245]
  - Crista iliaca lateralis[247]
- Facies ventralis
  - Areae articulares vertebrales[246]
  - Margo cranialis
  - Margo lateralis
  - Margo medialis [M. vertebralis]

Ala [Pars] postacetabularis ilii[245]
- Facies dorsalis
  - Fossa iliocaudalis[249]
  - Crista dorsolateralis ilii[248]
  - Spina dorsolateralis ilii[248]
- Facies lateralis[235]
  - Crista dorsolateralis ilii[248]
  - Lamina infracristalis ilii[251 235]
    - Concavitas infracristalis[235]
    - Margo foraminis ilioischiadici
- Facies ventralis
- Facies renalis ilii
- Crista caudalis fossae renalis
- Margo caudalis[238]
- Margo lateralis[247]
- Pila postrenalis[241]
- Recessus caudalis fossae[250]
- Spina dorsolateralis ilii[248]

Corpus ilii[239]
- Crista iliaca obliqua[242]
- Pila ilioischiadica[236]
- Crista iliaca intermedia[243]
- Facies renalis ilii
- Incisura acetabularis[240]
- Antitrochanter[232]
  - Facies articularis femoralis
  - Sulcus antitrochantericus[232]
- Tuberculum preacetabulare [Proc. pectinealis][244]

ISCHIUM (Figs. 4.9, 15)

Corpus ischii
- Incisura acetabularis[240]
- Margo [Incisura] foraminis ilioischiadici
- Incisura foraminis obturatorii
- Margo ventralis [M. pubica]
- Pila ilioischiadica[236]
- Proc. antitrochantericus[232]
  - Facies articularis femoralis
- Proc. obturatorius[252]

Ala ischii
- Facies lateralis
- Facies medialis (**Arthr.** Annot. 150)
- Margo ventralis [M. pubica]
- Proc. terminalis ischii[253]
- Sulcus obturatorius[228]

PUBIS[254] (see Os coxae)

Corpus pubis
- Incisura acetabularis
- Tuberculum preacetabulare [Proc. pectinealis][244]
- Scapus pubis[5 254]
- Apex pubis (**Arthr.** Annot. 149)

OSSA MEMBRI PELVICI

FEMUR [OS FEMORIS] (Fig. 4.16)

Extremitas proximalis femoris
- Caput femoris
  - Facies articularis acetabularis
  - Fovea lig. capitis
- Collum femoris
  - Facies articularis antitrochanterica[255]
- Trochanter femoris[256]
  - Crista trochanteris
  - Fossa trochanteris
  - Impressiones musculares trochanteris[257]
  - Impressiones ligamentosae trochanteris[257]

Corpus femoris[258]
- Facies caudalis
  - Linea intermuscularis
- Facies cranialis
  - Linea intermuscularis
- Facies lateralis
- Facies medialis

Extremitas distalis femoris
- Condylus lateralis[259 261]
  - Fovea tendinis m. tibialis cranialis
  - Impressio lig. cruciati caudalis[263]
  - Impressio lig. cruciati cranialis[263]
  - Trochlea fibularis[261]
  - Crista tibiofibularis[262]
  - Crista supracondylaris lateralis
    - Tuberculum m. gastrocnemialis lateralis
- Condylus medialis[259 264]
  - Crista supracondylaris medialis[264]
    - Tuberculum m. gastrocnemialis medialis
- Epicondylus lateralis
  - Impressio lig. collateralis lateralis
- Epicondylus medialis
  - Impressio lig. collateralis medialis
- Fossa poplitea
- Impressiones ansae m. iliofibularis[260]
- Sulcus intercondylaris
  - Impressio lig. cruciati cranialis
- Sulcus patellaris[259]
  - Facies articularis patellaris
  - Crista lateralis sulci patellaris[259]
  - Crista medialis sulci patellaris[259]

Patella[265]
- Facies articularis femoralis
- Facies cranialis
- Sulcus [Canalis] m. ambientis[265]

TIBIOTARSUS (Fig. 4.17) (**Arthr.** Annot. 167)

Extremitas proximalis tibiotarsi
- Caput tibiae[266]
  - Area interarticularis
  - Crista cnemialis cranialis[269 270]
  - Crista cnemialis lateralis
  - Crista patellaris[269]
  - Facies articularis lateralis[266]
  - Facies articularis medialis[266]
  - Facies articularis fibularis[267]
  - Facies gastrocnemialis[271]

TIBIOTARSUS (Fig. 4.17) (**Arthr.** Annot. 167) **(cont.)**

- Fossa flexoria[274]
- Fossa retropatellaris[268]
- Impressio lig. collateralis medialis
- Incisura tibialis[273]
- Sulcus intercnemialis[272]

Corpus tibiotarsi[275]
- Crista fibularis (**Arthr.** Annot. 162)
- Facies caudalis
- Facies cranialis
- Facies medialis
- Linea extensoria[276]
- Lineae m. fibularis [peronei]
- Margo lateralis [M. fibularis]
- Margo medialis
- Tuberositas poplitea[274]

Extremitas distalis tibiotarsi
- Condylus lateralis[280]
- Condylus medialis[280]
- Epicondylus lateralis
  - Depressio epicondylaris lateralis[281]
- Epicondylus medialis
  - Depressio epicondylaris medialis[281]
- Incisura intercondylaris
  - Area intercondylaris (**Arthr.** Annot. 171)
    - Impressio lig. intercondylaris
- Sulcus m. fibularis [peronei][282]
- Trochlea cartilaginis tibialis[279]
  - Cristae trochleae[279]
  - Tuberculum retinaculi m. fibularis [peronei][282]
  - Sulcus extensorius
  - Tuberositas retinaculi extensori[278] (**Arthr.** Annot. 187)
  - Pons supratendineus[277]
  - Canalis extensorius[278]

FIBULA (Fig. 4.17)

Caput fibulae[261]
- Facies articularis femoralis
- Facies articularis tibialis[267]
- Fovea m. poplitei
- Tuberositas lig. collateralis lateralis

Corpus fibulae
- Crista articularis tibialis (**Arthr.** Annot. 161, 162)
- Tuberculum m. iliofibularis

Spina fibulae

Os sesamoideum intertarsale (**Arthr.** Annot. 164)

OSSA PEDIS

OSSA TARSI[283]

Ossa proximalia tarsi
- Tibiale [Astragalus][283]
- Fibulare [Calcaneum][283]

Os tarsi distale[283]

OSSA METATARSALIA (Fig. 4.18) (**Arthr.** Annot. 173, 174)

Os metatarsale I [primum] [hallucis] (**Arthr.** Fig. 5.9)
- Proc. articularis tarsometatarsalis
- Trochlea metatarsi I [primi] [hallucis]
  - Tuberculum laterale
  - Tuberculum mediale

Os metatarsale II [secundum]
Os metatarsale III [tertium]
Os metatarsale IV [quartum]

TARSOMETATARSUS[284] (Fig. 4.18) **Arthr.** Annot. 173, 174)

Extremitas proximalis tarsometatarsi
- Area intercotylaris[285]
  - Fovea menisci lateralis
- Sulcus ligamentosus[286]
- Cotyla lateralis
- Cotyla medialis
  - Eminentia intercotylaris (**Arthr.** Annot. 171)
- Impressio lig. collateralis lateralis
- Impressiones retinaculi extensorii
- Sulcus m. fibularis [peronei] longus
  - Tuberculum m. fibularis [peronei] brevis

Hypotarsus[288] (Fig. 4.18)
- Canales hypotarsi[288]
- Crista lateralis hypotarsi[289]
- Crista intermedia hypotarsi[289]
- Crista medialis hypotarsi[289]
- Fossa parahypotarsalis lateralis
- Fossa parahypotarsalis medialis
- Sulci hypotarsi[288]

Corpus tarsometatarsi
- Facies dorsalis[292]
- Facies plantaris[292]
- Crista medianoplantaris[290]
- Facies subcutanea lateralis[293]
- Facies subcutanea medialis[293]
- Fossa metatarsi I [hallucis] (**Arthr.** Annot. 174, 175, 180)
- Proc. calcaris[296]
- Fossa infracotylaris dorsalis[291]
- Foramen vasculare proximale (**Art.** Annot. 79)
- Tuberositas m. tibialis cranialis[291]
- Sulcus extensorius[295]
  - Arcus extensorius[287]
  - Impressiones retinaculi extensorii
  - Tuberositas m. tibialis cranialis
  - Sulcus flexorius[294]
    - Crista plantaris lateralis[294]
    - Crista plantaris medialis[294]

Extremitas distalis tarsometatarsi
- Canalis interosseus distalis[298]
- Foramen vasculare distale[298]
- Fossa supratrochlearis plantaris
- Incisura intertrochlearis lateralis
- Incisura intertrochlearis medialis
- Trochlea metatarsi II [secundi]
  - Foveae ligg. collateralium
- Trochlea metatarsi III [tertii]
  - Foveae ligg. collateralium
- Trochlea metatarsi IV [quarti]
  - Foveae ligg. collateralium
- Trochlea accessoria[297]
- Os cuneatum (**Arthr.** Annot. 182)

OSSA DIGITORUM PEDIS[299]

Phalanges proximales et intermediae
- Basis phalangis
  - Cotyla articularis
- Corpus phalangis
  - Facies dorsalis
  - Facies plantaris
- Capitulum phalangis
  - Trochlea articularis
  - Fovea lig. collateralis

Phalanx ungualis [terminalis][300]
- Basis phalangis
  - Cotyla articularis
  - Tuberculum extensorium (**Arthr.** Annot. 183)
  - Tuberculum flexorium (**Arthr.** Annot. 182)
- Corpus phalangis
  - Sulcus neurovascularis[300]
- Apex phalangis

ANNOTATIONS

(1) **Cotyla.** (Cotyla, Gk. cup). In this work "cotyla" is used for a shallow concave articular surface (Howard, 1929; Lambrecht, 1933).

(2) **Cartilago epiphysialis; Epiphysis; Diaphysis; Metaphysis.** During development and growth of a long bone, ossification begins in the middle of the shaft (Diaphysis), and extends proximally and distally by growth of ossifying zones (Metaphysis) into the cartilaginous end (Epiphysis). The epiphyses of birds, unlike mammals, do not ossify endochondrally from separate centers of ossification, but only by extension from the metaphysial centers.

(3) **Os pneumaticum.** Bone invaded by air sacs; the sacs are outgrowths of the lungs, tympanic cavity, or nasal cavity.

Foramen pneumaticum; Pori pneumatici. In the paleontological literature the foramina are commonly known as "pneumatopores". The skull, vertebrae, and bones of limb girdles are usually pneumatic; limb bones are variably pneumatic in different taxa of birds. Pneumaticity usually involves only the proximal elements of the limb, but in some forms may extend into its distal extremity. Since pneumaticity is so widespread in the skeleton, the foramina and smaller pores are listed only for the bones in which they form especially distinctive features. See Annot. 6 and **Resp.** Annot. 70, 75-77.

(4) **Pila** (L. pillar or column). Pila refers to a reinforcing element of a bone that may form a distinct, prominent bar, or may be a thickening that blends almost imperceptibly into the bone of which it is a part.

(5) **Scapus** (L. shaft, stem). Used in this work to refer to a slender, attenuated bone or part of a bone in the instances that "corpus" (body) is not applicable (e.g., clavicle, pubis). See **Integ.** Partes pennae for another usage of Scapus.

(6) **Os medullare.** Female birds are unique in possessing a special system of highly labile, secondary (medullary) bone within the marrow cavities of much of the skeleton during the reproductive period. This bone grows as spicules into the medullary cavity from the endosteal surface, serving as a labile reserve of mineral that can be mobilized to provide calcium for egg shell formation. Taylor, et al. (1971) present an extensive review of medullary bone (see also Hodges, 1974).

Os spongiosum. Spongy bone (also known as trabecular or cancellous bone) is found throughout the avian skeleton. In early postnatal life the spongy bone of the Calvaria (**Diploë**), vertebrae, limb bones, etc. is filled with red marrow (see Hodges, 1974). Later the red marrow is replaced by fatty marrow or by pneumatic mucosal diverticula invading the bones from the nasal or tympanic cavities (Stork, 1972; Warnke and Stork, 1977; Witmer, 1990) or lungs and air sacs.

The **Cellulae pneumaticae** are cavities or spaces, lined with mucosa, that are smooth-walled, e.g., long bones and skulls of nestlings, or highly strutted as in the skulls of adult birds. See Annot. 189; **Resp.** Annot. 21, 70, 72, 75-77.

(7) **Tuberositas.** (L. tuberosus, full of lumps). In anatomical usage "Tuberositas" usually refers to a roughened or knobby area of bone for attachment of tendons or ligaments (Donath and Crawford, 1969).

(8a) **Facies; Cranium.** Following the *Nomina Anatomica Veterinaria* (ICVGAN, 1983), "Facies" is used in this work for the facial skeleton ("splanchnocranium"), and "Cranium" refers to the part of the head skeleton enclosing the brain ("neurocranium").

(8b) **Ginglymus craniofacialis [G. nasofrontalis].** This term is treated with the flexible zones of the skull in **Arthr.** Annot. 46.

(9) **Fenestra antorbitalis** (Heilmann, 1926). Synonymy: antorbital vacuity (Shufeldt, 1909); Hiatus orbitonasalis (NAA, 1979). When the skull is viewed from the side, this is the pronounced gap, often triangular, bounded by the nasal process of the maxillary bone, the maxillary process of the nasal bone, the jugal and lacrimal bones, closed by skin laterally (Fig. 4.1). It represents the antorbital vacuity of archosaurian reptiles (Witmer, 1987).

Fossa antorbitalis [F. infraorbitalis]. The antorbital fossa is the space medial or deep to the Fenestra antorbitalis which houses the Sinus antorbitalis [Sinus infraorbitalis] (see **Resp.** Annot. 17), an evagination of the nasal cavity. The osseous walls of the Fossa are variable; often the palatine process of the maxilla, the palatine bone, and the ectethmoid contribute to its walls (Witmer, 1987). Witmer maintains that the antorbital fenestra and fossa are completely homologous with those of non-avian archosaurs. Fossa infraorbitalis is retained as an alternative term because of its widespread use.

(10) **Hiatus craniofacialis septi.** Synonymy: Fissura craniofacialis (Hofer, 1955). In the dried skull, the hiatus is the interval between the rostral edge of the interorbital septum and the caudal border of the osseous nasal septum in birds having such a septum (e.g., *Anser*). The hiatus is completed by a septum of cartilage in intact specimens (Butendieck, 1980). Bühler, et al. (1988) state that this hiatus is characteristic of all modern prokinetic birds as well as many neognathine rhynchokinetic birds. Paleognathines have a continuous nasal/interorbital septum. See Annot. 55.

(11) **Arcus jugalis.** Synonymy: Arcus zygomaticus. The jugal arch is a slender, generally straight, bar that connects the upper jaw with the quadrate bone (Figs. 4.2, 4); exceptions include a strongly sigmoid shape in some penguins and a laterally bowed shape in *Nyctibeus* and *Caprimulgus*. The arch consists of three ankylosed elements: Proc. jugalis of Os maxillare, Os jugale proper, and Os quadratojugale. See **Arthr.** Intro.

(12) **Apertura nasi [nasale] ossea.** Synonymy: Naris. The shape of the nasal aperture (schizorhinal, holorhinal) is related to kinesis of the upper jaw (see Garrod, 1873; Hofer, 1955; Bock, 1964; Yudin, 1965; the reviews of Bühler 1981 and Zusi 1984). Some pelecaniform, sphenisciform, and other birds have paired, minute osseous apertures of the nasal cavity. See **Resp.** Annot. 1; **Arthr.** Zonae flexoriae.

Pila supranasalis. The median column of bone making up the dorsal border of the external nares; formed by processes of the nasal and premaxillary bones. See **Arthr.** Fig. 2.

(13) **Fenestra palatina.** Synonymy: Fonticulus palatinus (Hofer, 1949). Oval or elongate opening in the rostral part of the bony palate between the two premaxillae. In birds such as *Strix, Gallinula,* and anseriforms, the fenestra is set off distinctly from the more caudal **Fissura interpalatina.** The two are confluent in, e.g., *Diomedea, Cathartes,* and *Larus.*

(14) **Depressio frontalis.** The frontal region (forehead) of the skull in some birds (e.g., *Ardea, Anser*) is indented by this shallow, longitudinal concavity (Fig. 4.6); in other birds the frontal region may be flat or dorsally convex.

Crista frontalis interna. Median crest on the interior of the vault of the calvaria extending from the fossa of the olfactory bulb to the upper end of the cerebellar fossa.

(15) **Fossa glandulae nasalis.** In certain birds the Glandula nasalis (so-called "salt gland") occupies a pronounced depression on the dorsal aspect of the supraorbital margin of the orbit, involving mostly the frontal bone (e.g., penguins, albatrosses loons, gulls). In others (e.g., pelecaniforms, grebes) the gland is intraorbital, i.e., ventral to the supraorbital wall of the orbit there occupying the shallow **Impressio gl. nasalis** (see Siegel-Causey (1990).

(16) **Calvaria.** The so-called cap or dome of the skull.

Prominentia cerebellaris (Shufeldt, 1909). The external, median convexity of Os supraoccipitale and Os parietale in the nuchal region of the skull dorsal to the Foramen magnum (Figs. 4.4, 5). The prominence overlies the dorsum of the Cerebellum, reflecting its contour externally, e.g., *Buteo, Columba, Corvus,* and trochilids. See Annot. 17.

(17) **Crista [Linea] nuchalis sagittalis.** This median crest is dorsal to the Foramen magnum, and provides attachment for the sheet of deep fascia separating the right and left columns of dorsal neck muscles. The Crista surmounts the Prominentia cerebellaris in some forms (e.g., *Gavia, Morus*).

Crista [Linea] nuchalis transversa. Synonymy: Crista temporalis (Hofer, 1945); Crista occipitalis (Davids, 1952). Arched, usually distinct, crest separating the nuchal plane of the supraoccipital bone (for attachment of the neck muscles) from the smoother part of the calvaria (parietal and squamosal bones) farther rostrally (Figs. 4.1, 5). This crest may extend caudolaterad to reach Proc. paroccipitalis (Annot. 85) (Figs. 4.2, 3).

(18) **Foramen magnum.** Synonymy: Foramen occipitale magnum. The opening in the base of the skull that transmits the spinal cord and its meninges; it is bounded by the supra-, ex-, and basioccipital bones. Duijm (1951) reviewed the position and plane of the Foramen magnum in the major skull types of birds.

(19) **Meatus acusticus externus.** Synonymy: Fossa auricularis cutanea (Freund, 1926). The wall of the Meatus is formed mostly by cutaneous, fibrous, and cartilaginous tissues. The osseous wall of the Meatus is formed by the parasphenoid ala (Annot. 20), lateral margin of the paroccipital process, and **Crista tympanica** of the body of the quadrate bone (see **Arthr.** Annot. 37).

(20) **Hiatus subtympanicus.** Synonymy: Hiatus alae tympanicae (NAA, 1979). Deficiency (notch or fenestra) in the junctional area between the Ala parasphenoidalis and the margin of Proc. paroccipitalis that partially bounds the external acoustic meatus. See Annot. 19, 84.

(21) **Cavum tympanicum [Cavitas tympanica].** The middle ear cavity consists of a shallow, open concavity in the dried skull. Owing to the placement of Membrana tympanica, only the ventral part of the osseous concavity is tympanic cavity proper; the caudodorsal part is Meatus acusticus externus (Freund, 1926). See Annot. 19.

(22) **Recessus columellae** (new term). **[Recessus antevestibularis]** (NAA, 1979); Synonymy: Antivestibulum (Magnus, 1870); Recessus cavi tympani (Hasse, 1871); Recessus stapedialis (Stresemann, 1934). "Recessus columellae" replaces Recessus antevestibularis which is retained as an alternative. "Recessus columellae" is a more descriptive memory aid since this evagination of the tympanic cavity houses the basal portion of the ear ossicle (**Columella**) (Fig. 4.3) in the complex of otic bones. Fenestra vestibuli, Fenestra cochleae, and Recessus tympanicus caudalis open into the recess of the columella (see Annot. 26); the recess is lacking in certain birds, e.g., diomedeids, Mesozoic birds (Witmer, 1990); shallow in *Larus*, but relatively deep in others (e.g., *Gallinula, Gallus, Strix, Ceryle*).

Fenestra cochleae [F. pseudorotunda]. Synonymy: Fenestra rotunda. Opening within Os opisthoticum (Fig. 4.3), closed in life by Membrana tympanica secundaria. The avian and mammalian fenestrae are considered nonhomologous (de Beer, 1937); hence the term Fenestra pseudorotunda.

Fenestra vestibuli. Synonymy: Fenestra ovalis. This opening into the vestibule of the osseous labyrinth is occupied by the footplate (base) of the Columella (see **Sens.** Fig. 16.7).

(23) **Recessus pneumatici paratympanici (Resp.** Annot. 21). Collective term for the three major, consistently occurring, air filled evaginations of the tympanic cavity into the surrounding bones; namely, the rostral, caudal, and dorsal tympanic recesses. The openings or ostia by which the sinuses communicate with the tympanic cavity are called **Foramina pneumatica** (see Witmer, 1990). Among the several putative functions of the pneumatization of the skull of birds, Warnke and Stork (1977) suggest thermoregulation and insulation.

(24) **Pila otica** (new term). Synonymy: opisthotic columella (Lowe, 1926); Pila prootica (NAA, 1979). This usually short pillar of bone articulates with the quadrate bone (see below); since it ossifies with varying contributions from the opisthotic and prootic bones, its name has been simplified to Pila otica. The pila intervenes between the foramen of the dorsal tympanic recess and Recessus columellae (Fig. 4.3; Annot. 22).

Cotyla quadratica otici. Cup-shaped surface of the otic complex for articulation with the otic capitulum of the quadrate bone (Fig. 4.3). The cotyla is largely prootic in most birds with some contribution from the opisthotic. In some birds, the cotyla is partly located on the free end of the Pila otica. See paragraph above and Annot. 100.

(25) **Recessus tympanicus dorsalis (Resp.** Annot. 21). Synonymy: Recessus tympanicus superior (Suschkin, 1899; Pycraft, 1902;, Müller, 1963); Antrum pneumaticum dorsale (NAA, 1979). The **Foramen pneumaticum dorsale** leading to the dorsal tympanic recess is located near the squamosal and otic articular facets for the quadrate bone (Fig. 4.3). Diverticula from this recess invade the prootic, squamosal, parietal and occipital bones.

(26a) **Recessus tympanicus rostralis (Resp.** Annot. 21). Synonymy: Recessus tympanicus anterior (Parker, 1869; Suschkin, 1899; Pycraft, 1902; Müller, 1963); presphenoid sinus (Saiff, 1974); Antrum pneumaticum rostrale (NAA, 1979).

Foramen pneumaticum rostrale of the rostral recess is located in the rostroventral part of the tympanic cavity, dorsal to the ostium of the auditory tube, and dorsolateral to the bony Canalis caroticus cranialis (see Figs. 4.2, 3, 5; Annot. 99). Diverticula from this recess invade the base of the skull (parasphenoid bone).

(26b) **Recessus tympanicus caudalis. (Resp.** Annot. 21) Synonymy: Recessus tympanicus inferior (Müller, 1963); Antrum pneumaticum caudale (NAA, 1979). The **Foramen pneumaticum caudale** connects this recess with the columellar recess or the caudal part of the tympanic cavity. The Recess is ventrolateral to the rostral semicircular canal, and sends diverticula into the exoccipital bone.

(27) **Canalis ophthalmicus externus.** Synonymy: Canalis facialis; Canalis stapedialis. The canal conducts the A. et V. ophthalmica externa, and in some forms, the Chorda tympani of N. facialis. The caudal ostium of the canal is located in the Fossa parabasalis on the external skull base (Figs. 4, 5). The canal arches dorsal to the Columella then rostrally; its lateral wall may project in relief into the tympanic cavity, or may be incompletely ossified so that the lumen of the canal is visible in the dried skull. The rostral opening of the canal is medial to the otic process of the quadrate, lateral to Foramen n. maxillomandibularis.

(28) **Basis cranii externa.** Synonymy: basicranium. In this work "Basis cranii externa" is defined as limited to the exterior aspect of the bones forming the floor of the cranial cavity proper; thus Basis interna and externa of the cranium are opposites that correspond in area to one another. In some birds the cerebral surface of the base of the cranium is widely separated from the external surface by pneumatic spaces, evaginations of the tympanic cavity.

(29) **Orbita.** The osseous orbit of birds is bounded mainly by cranial bones. In most birds the floor of the orbit is not bone, but consists mainly of jaw muscles. Exceptions are the snipes and woodcocks (Scolapacidae) in which the orbit is almost completely enclosed by bone (Hofer, 1955). See Annot. 30.

Fonticuli interorbitales; Fonticuli orbitocraniales. Synonymy: Fonticuli orbitales, Barkow (1856); Foramina obturata orbitalia. In the dried skull these are unpaired deficiencies in the bone of the interorbital septum or paired ones in the caudal wall of the orbit; the latter communicate with the cranial cavity (Figs. 2, 3, 6). In intact specimens the fonticuli are closed by fibrous membranes.

(30a) **Proc. postorbitalis.** Synonymy: Proc. orbitalis posterior; Proc. postfrontalis. In most carinate birds, and the ratite *Rhea*, the postorbital process is formed largely by Os laterosphenoidale; Os squamosal (e.g., some galliforms) or Os frontale (*Struthio*) contribute to the base of the Proc. postorbitalis. Consult Müller (1963: 81) for discussion of the postorbital process.

The postorbital process commonly forms the caudoventral border of the orbit (Figs. 4.2, 5); however, in certain birds (e.g., anseriforms) it projects rostrally and contributes to the ventral margin of the orbit (see below, Arcus suborbitalis). The tips of Proc. postorbitalis and Proc. zygomaticus are joined in some birds (e.g., psittaciforms and galliforms). See below and Annot. 108.

(30b) **Arcus suborbitalis** (Portmann, 1950). A complete osseous arch bounds the orbit ventrally in some psittaciforms, scolopacids (Gadow and Selenka, 1891), and the anatid, *Dendrocygna* (Shufeldt, 1909). This arch is formed by junction of a lengthy caudal extension of Os lacrimale and the rostral extension of the Proc. postorbitalis or the postorbital/zygomatic complex; in other birds these structures form an arch connected by Lig. suborbitale (**Arthr.** Annot. 30).

(31) **Foramen orbitonasale laterale/mediale.** Longitudinal opening(s) between the orbital surface of Os frontale and the dorsal border of Os ectethmoidale. A single slit-like foramen is present in some birds (e.g., *Ardea, Aythya*); both medial and lateral foramina are found in other birds (e.g., *Columba, Gallus, Coragyps, Corvus.*) The medial foramen (Fig. 4.1) conducts N. olfactorius and the medial ramus of N. ophthalmicus from orbit to nasal cavity; the lateral foramen conducts the lateral ramus of N. ophthalmicus and duct(s) of Glandula nasalis.

Sulcus n. olfactorii. Longitudinal groove for the olfactory nerve and ethmoid artery; located in the angle between the upper part of the interorbital septum and the Lamina dorsalis of Os mesethmoidalis which is applied to the roof of the orbit (see Fig. 4, 1; Annot. 108).

(32) **Foramen opticum.** Located in the boundary zone between the caudal edge of the interorbital septum and the caudal wall of the orbit (Figs. 6, 2, 3). The foramen in carinates is usually a single opening inside the cranial cavity, but the foramen is divided by the relatively thin interorbital septum into a pair of closely related foramina, one in each orbit. In some psittaciforms (pers. obs.) and cardueline finches (Zusi, 1978) the two optic foramina are widely separated from one another by a thick septum. In other birds the optic foramina may be continuous with the Fonticuli orbitocraniales and other foramina (Annot. 29, 88).

(33) **Septum osseum fossae bulbi.** The fossa for the olfactory bulb is divided by a bony septum in *Apteryx* (Starck, 1955) and in the albatross (*Diomedea* sp.) and psittacids.

(34) **Foramen ethmoidale.** Transmits A. et V. ethmoidalis into the orbit from the cranial cavity; separate openings for the artery and vein are present in some birds. See Annot. 31.

(35) **Fossa cranii media.** Synonymy: Fossa mesencephalica. The middle cranial fossa houses the Diencephalon and Chiasma opticum medially and the Tectum mesencephali on each side. The Fossa is not homologous with the middle cranial fossa of mammals. See Os basisphenoidale and Os laterosphenoidale for additional terms.

(36) **Crista marginalis.** This crest separates each side of the **Fossa cerebelli** from the general chamber of the vault of the calvaria that houses the telencephalic hemispheres of the brain.

(37) **Tuberculum pineale.** On the internal surface of the Calvaria the Tuberculum pineale is a triangular eminence at the junction of Crista frontalis interna with the marginal crests of the cerebellar fossa. The dorsal expanded end of the body of Glandula pinealis is closely related to the Tuberculum.

(38) **Fossa auriculae cerebelli.** Synonymy: Fovea hemispherii cerebelli; Fossa subarcuata. The fossa in birds contains the cerebellar auricle (Fig. 4, 6). "Subarcuate fossa" is inappropriate, since in mammals it lodges the endolymphatic sac; therefore the avian and mammalian fossae are non-homologous. See **Ven.** Annot. 35.

(39) **Fovea ganglii vagoglossopharyngealis.** In the floor of the caudal fossa of the cranium, the fovea (pit) is located in the suture between the exoccipital and opisthotic bones; the fovea houses the combined proximal [root] ganglia of the X and IX cranial nerves (Fig. 4.6). Separate foramina for each nerve are found in the bottom of the fovea that lead to the parabasal fossa on the external skull base (Figs. 4.4, 5). See Annot. 86; and **PNS.**

(40) **Rostrum [Symphysis] mandibulae** (new term). (Rostrum, L. beak or prow). The rostrum is the pointed, apical region of the mandible formed by the union of the symphysial segments of the right and left mandibular rami. Although this region of ankylosis of the mandibular rami is commonly called the "mandibular symphysis", in the strict sense, the symphysis is the actual joint connecting the two. See Annot. 42; **Arthr.** Annot. 21. and **Topog.** Annot. 12.

Rostrum maxillae (new term, R. Zusi, pers. comm.). This is the pointed, apical region of the upper jaw formed by the ankylosis of the bodies of right and left premaxillary bones that corresponds to the Rostrum mandibulae (Fig. 4.2). See **Topog.** Annot 12.

(41) **Foveae corpusculorum nervosorum.** In the bones of the maxilla and mandible these small pits deep to the rhamphotheca house sensory corpuscles (Fig. 4.2); the foveae are especially numerous and conspicuous in the rostra of the upper and lower jaws of *Apteryx,* ibis and spoonbills, anseriforms, and sandpipers and snipes (Scolopacidae). See Annot. 57 and **Sens.** Annot. 66.

(42) **Pars symphysialis/intermedia/caudalis** (Lebedinsky, 1920). The symphysial part of the mandibular ramus is the rostral segment that unites with the opposite ramus at the Symphysis mandibularis (see Annot. 40 and **Arthr.** Annot. 21 and Fig. 4.4). Pars intermedia extends caudally to Zona flexoria intramandibularis caudalis which is often marked by the **Fenestra rostralis mandibulae.** Pars caudalis extends from the caudal flexion zone to the retroarticular process, and includes the area of attachment of the jaw muscles, facets for articulation with Os quadratum, and Fenestra caudalis mandibulae in birds that have dual fenestrae on each side (Annot. 46). See **Arthr.** Annot. 46-48.

The Ramus mandibulae is peculiar in caprimulgids in that the rostral, attenuated one-third is set off by an oblique, moveable syndesmotic joint from the bowed, stronger rear two-thirds.

(43) **Angulus mandibulae.** This is the point on the dorsal border of the Ramus mandibulae where the ramus becomes angulated or curved ventrally (e.g., charadriiforms, caprimulgiforms, columbiforms, falconiforms, and passerines). See Annot. 56. The angle marks the caudal extent of the rhamphothecal sheath covering the exposed part of the mandible.

(44) **Proc. coronoideus.** Synonymy: Proc. pseudocoronoideus; Proc. m. adductoris mandibulae. Any process of Pars caudalis of the mandible to which is attached the strong "aponeurosis" of M. adductor mandibulae externus, pars rostralis (**Myol.** Annot. 18). In different birds it is commonly found on the dorsal margin of the mandible, often coincident with the Angulus mandibulae (Johnson, 1984); it may, however, be located on the lateral surface of the mandible as in anseriforms (Zweers, 1974). See Figs. 4.1, 2.

In finches, processes for the insertion of aponeuroses of M. adductor mandibulae externus "profundus" also occur caudal to Proc. coronoideus (Richards and Bock, 1973) (see **Myol.** Annot. 18).

(45) **Tuberculum pseudotemporale.** Synonymy: Proc. pseudotemporalis. The pseudotemporal tubercle which is located slightly rostral to the quadratomandibular joint near the base of Proc. medialis mandibulae (Fig. 4.1) is the point of insertion of the tendon of M. pseudotemporalis superficialis (**Myol.** Annot. 19). The tubercle is prominent in heavy-billed finches.

(46) **Fenestrae mandibulae.** Synonymy: Foramen mandibulare anterior; Foramen mandibulare posterior (Lebedinsky, 1920); Foramen ovale; interangular vacuity or fenestra (Shufeldt, 1909). **Fenestra rostralis mandibulae** is found in the region of the caudal intramandibular flexion zone (**Arthr.** Fig. 2); **Fenestra caudalis mandibulae** occurs in Pars caudalis of the mandibular ramus (see Annot. 42, 48). The fenestrae may be completely lacking in some taxa. Other birds may possess only one of the fenestrae (e.g., *Columba*). Two fenestrae occur in certain birds (e.g., some charadriiforms, gruiforms, psittaciforms, and strigiforms). Consult Lebedinsky (1920) for details.

(47) **Canalis neurovascularis mandibulae.** Synonymy: The canal conducts vessels and the intramandibular ramus of the mandibular nerve from the region of the coronoid process to the symphysial region of Ramus mandibulae. See Annot. 48.

(48) **Fossa aditus canalis neurovascularis.** Synonymy: Fossa medialis mandibulae (Johnson, 1984). Depression on the internal aspect of Pars caudalis of the mandibular ramus that leads to the aditus or opening of the mandibular canal. The floor of the fossa often consists of thin bone, and may exhibit an opening(s), Fenestra caudalis mandibulae. The fossa is pronounced and extensive in many birds (e.g., *Pygoscelis, Gavia, Cathartes, Anser*).

Fossa lateralis mandibulae (Johnson, 1984). Shallow depression on the lateral aspect of the mandibular ramus at or near its rostral fenestra, e.g., *Diomedea, Larus.*

(49a) **Fossa articularis quadratica.** Area of the mandible for articulation with the condyles of Proc. mandibularis of Os quadratum (see Fig. 4.3; Annot. 72).

Cotylae fossae articularis. These are the facets for articulation with the condyles of the Os quadratum. The medial cotyla is separated from the others (see below); however, the lateral and caudal cotylae are merged into a common articular surface in some birds (e.g., *Larus*); distinct in others (e.g., *Ardea, Morus*).

Sulcus intercotylaris; Tuberculum intercotylare (Johnson, 1984); **[Crista intercotylaris]** (Zusi, 1987). The groove, boss of bone, or bony crest in the articular fossa of the mandible of different birds; these structures separate the medial and lateral cotylae (Fig. 4.3). The tuberculum is especially prominent in psittacids.

(49b) **Proc. retroarticularis.** Synonymy: Proc. mandibularis posterior (Lebedinsky, 1920); Proc. angularis posterior (Hofer, 1945); postarticular process. This process projects caudally past the articular fossa of the mandible; formed mainly by the **Os angulare** to the rear of Proc. lateralis mandibulae. Weakly developed, pointed, or stubby in most birds, the retroarticular process is prominent, e.g., in galliforms, ciconiiforms, psittaciforms, anseriforms and phoenicopterids (**Arthr.** Fig. 5.2D); in the last two taxa the process is attenuated and blade-like. The Proc. retroarticularis is also well developed in birds that forcefully open the jaws while foraging, probing into flowers or fruit (Zusi, 1967). Well developed in *Aechmophorus*, but not in other grebes (R. W. Storer, pers. comm.). See Annot. 50, 51.

Incisura retroarticularis (Johnson, 1984). In lateral view of the caudal segment of the mandibular ramus, this is a notch between the Proc. lateralis mandibulae and the retroarticular process; the incisure is the notched edge of the lateral cotyla.

(49c) **Foramen pneumaticum articulare.** An opening in the upper surface of Proc. medialis mandibulae (formed by **Os articulare**) that leads to pneumatic spaces in the caudal segment of the mandibular ramus (Figs. 4.1, 3); the lower jaw of some birds is extensively pneumatic (e.g., flamingos, hornbills, toucans).

The **Siphonium** is a connective tissue tube, ossified in some birds (e.g., *Corvus*), that connects the pneumatic foramen of Os articulare with the mandibular diverticulum of the tympanic cavity. See Cavum tympanicum; and Witmer (1990).

(49d) **Proc. medialis/lateralis mandibulae.** Both of these are processes of Pars caudalis of the mandible (mainly Os articulare); Proc. medialis mandibulae (Figs. 4.1, 3) is much the stronger of the two; it projects medially with its tip curved dorsally (exception: psittaciforms)(see below). The weak lateral process forms part of the cotyla for the lateral condyle of the quadrate bone; in some birds it is the attachment of Lig. postorbitale (**Arthr.** Annot. 42). See also **Arthr.** Annot. 32.

Facies articularis parasphenoidalis. In certain birds this articular surface near the tip of the Proc. medialis mandibulae forms a joint with the lateral or medial parasphenoidal process of Lamina parasphenoidalis of the external base of the skull (see Annot. 96 and **Arthr.** Annot. 32).

(50) **Recessus conicalis**. Synonymy: Fossa conicalis (Shufeldt, 1909). Recessus posterior (Lebedinsky, 1920); Cavum mandibulare (Zweers, 1974). In anseriform birds this is an unusual, deep recess ventral to the medial cotyla of the quadratomandibular joint. Its opening is located between the blade-like Proc. retroarticularis and Proc. medialis mandibulae. A somewhat similar deep recess is present in certain psittaciforms, however its opening faces dorsally rather than caudally. See Annot. 51.

(51) **Fossa caudalis.** Synonymy: Fossa posterior (Lebidinsky, 1920); postarticular surface (Milne-Edwards, 1867-71). In birds of many different taxa this term refers to the shallow concavity of the caudal surface of Proc. mandibulae medialis, located medial to the retroarticular process (Fig. 4.1). This is the area for insertion of M. depressor mandibulae (**Myol.** Annot. 24); (**Arthr.** Annot. 37). See Lebidinsky (1920) for a detailed, comparative account of Fossa caudalis in numerous avian taxa.

Crista transversa fossae (new term). This distinct transverse crest extends from the Proc. medialis mandibulae to Proc. lateralis mandibulae Fig. 4.3). The crest separates two different fossae; it forms the caudal wall of the articular fossa for Os quadratum, and its rear surface is the upper part of Fossa caudalis (see above). The crest, which exhibits a distinct tubercle in some birds, is an attachment of Membrana postmeatica and Lig. occipitomandibulare. See **Arthr.** Annot. 37.

(52) **Ossa mandibulae.** Each ramus of the mandible is considered to consist of seven separate bones. Different names for the various elements abound in the literature. The tabular synonymy compiled by Müller (1963) is summarized below; terms selected by him are followed in this present terminology with one exception. Os coronoideum is not ordinarily present in birds.

Os dentale. Synonymy: dentary; dentosplenial; mentomandibulare. This is the principal element of each mandibular ramus (Fig. 4.1); it articulates with the supra-angular and splenial elements by squamous sutures at the junction of intermediate and caudal segments of the ramus. **Os articulare** forms most of Fossa articularis quadratica. See Lebedinsky (1920) and Jollie (1957) dealing with the mandible of carinates, and Müller (1963) regarding the ratite mandible.

Os prearticulare. Synonymy: Os goniale; **Os coronoideum,** Synonymy: Os complementare; **Os spleniale,** Synonymy: Os operculare; **Os supra-angulare,** Synon-

ymy: surangulare. **Os mentomandibulare.** According to Romanoff (1960:995) paired mentomandibular elements replace the cartilage at the mandibular symphysis, then ankylose with one another.

(53) **Os maxillare; Maxilla.** As an individual bone, Os maxillare is one of the components of the avian upper jaw. As a general term, "Maxilla" refers to the entire complex of structures that make up the upper jaw; i.e., the opposite of "Mandibula", the lower jaw (see Annot. 40 and **Topog.** Annot. 8).

(54) **Proc. maxillaris** Synonymy: Proc. postnarialis or P. subnarialis. **Proc. premaxillaris.** Synonymy: Proc. dorsonarialis. Process of the nasal bone.

(55) **Septum nasi [nasale] osseum; Conchae nasales.** These structures may be supported in part by the vomer, maxilla, and ectethmoid bones. The rostral part of the nasal septum and nasal conchae in the caudal part of the nasal cavity vary in the extent that they ossify in different birds, usually remaining more or less cartilaginous. These structures characteristically ossify extensively in, for example, *Diomedea*, some parrots, birds of prey (*Buteo, Strix*), herons and ibis (*Ardea, Eudocimus*), pelecaniforms, trochilids, *Coccyzis*, some coraciiforms, and passeriforms. See Annot. 10; **Resp.** Annot. 6-9.

(56) **Crista tomialis.** Synonymy: tomial shelf (Johnson, 1984). The paired sharp edges of the upper and lower jaws (Figs. 4.2, 4). Hard keratinized rhamphotheca invests the crests from the tips of the rostra of mandible and maxilla caudally to the level of the Angulus mandibulae. See Annot. 43, 44; **Integ.**

(57) **Canalis neurovascularis maxillae.** Paired longitudinal canal that conducts the terminal branch of N. ophthalmicus and accompanying vessels from the rostral end of the nasal cavity into the Rostrum maxillae (Annot. 40) of the upper jaw (mainly in Os premaxillae). The canal is relatively long, e.g., in a heron or duck, quite short in a gull or vulture.

In birds with large maxillary bones (e.g., *Anas, Anser, Larus*, and *Hesperornis*) a separate neurovascular canal enters the maxilla near its junction with the jugal arch; this canal conducts parts of the nasopalatine branch of N. maxillaris to openings on both medial and lateral sides of the caudolateral maxillary tomial crest and adjacent palate (see below).

Foramina [Pori] neurovascularia. The ramifications of the branches of the ophthalmic and nasopalatine nerves (and companion vessels) leave their neurovascular canals (Fig. 4.2) via smaller **Canaliculi neurovasculares** that open on the surface of the bone of the upper jaw via foramina (pores) deep to the rhamphotheca (especially in the Rostrum maxillae). The foramina often open into **Foveae corpusculorum nervorsorum,** pits or hollows beneath the rhamphotheca which house sensory corpuscles; the foveae are remarkably abundant in *Capella*. See Annot. 41; and **Sens.** Annot. 70.

(58) **Proc. maxillopalatinus [Proc. palatinus].** This process of Os maxillare in many birds arises from the maxilla near its junction with Proc. maxillaris of Os palatinum (Figs. 4.1, 4; Annot. 64). The maxillopalatine process of different birds exhibits a variety of orientations and configurations largely due to variation in the form of the maxillary diverticulum of the antorbital sinus (Witmer, 1990); it contributes to the formation of the nasal cavity in most birds and to the palate in the birds such as anseriforms, ciconiiforms, and passeriforms (see Hofer, 1949). In anseriforms the right and left maxillopalatines are synostosed in the median plane.

(59) **Proc. jugalis.** This process of Os maxillare has also been called Proc. labialis (see Annot. 11).

(60) **Os palatinum** [Os pterygopalatinum] (see Annot. 61 and Fig. 4.4, 7). Four features of the palatine bone are common to most birds: **Pars choanalis** which is associated with the Fossa choanalis (see below, this annot.); (2) **Pars lateralis** (see next paragraph) which is generally lateral to Pars choanalis, is associated mainly with the attachment of M. pterygoideus; (3) **Proc. maxillaris** (synonymy: Proc. premaxillaris, NAA, 1979; prepalatine, Parker, 1879), connected to the maxilla, is usually a slender bar which, in all neognathines, has a bending zone (Zona flexoria palatina, see **Arthr.**); (4) **Proc. pterygoideus** (synonymy: postpalatine, Parker, 1879) connects the palatine with the pterygoid bone, and may include a fused portion of Os pterygoideus (see Annot. 61). Certain features listed under Pars choanalis and Pars lateralis are absent in some birds; Parker (1879), Hofer (1945), and Richards and Bock (1979) discuss the variety of shapes and relationships of palatine bones in different avian taxa, and include other palatine features not presented in this terminology. Ziswiler (1985) provides a concise summary on types of avian palates; see Witmer and Martin (1987) for a critique of palatal typology.

Pars lateralis (Fig. 4.7) in part replaces the term "Lamella caudolateralis" of the NAA (1979), a term derived from Proc. posterolateralis of (Beddard, 1898; Hofer, 1945; and Bühler, 1970); **Lamella caudolateralis** is retained as an alternative (bracketed) term in the present edition. Pars lateralis is usually a flared plate facing ventrally in some birds, obliquely ventromedially in others, and medially as in psittacids (Beddard, 1898). Pars lateralis is convoluted in *Fulica*, and extremely expanded laterally in caprimulgids.

Fossa choanalis (Fig. 4.7). Synonymy: Fossa medialis (NAA, 1979). Paired, shallow furrow between the medial and ventral crests of **Pars choanalis** of Os palatinum (Fig. 4.4); the furrow faces medially, forming the lateral wall of the chamber of the Choana which connects nasal cavity with oropharynx (see Annot. 64; and **Resp.** Annot. 5).

(61) **Os pterygoideum** (Figs. 4.4, 2, 5). **Pars palatina** of Os pterygoideum that joins Os palatinum (Annot. 60) is also known as the antero-, hemi-, or mesopterygoid (Parker, 1879; Pycraft, 1900; Jollie, 1957). Bühler, et al. (1988) indicate that most modern prokinetic neognathines have this palatal ontogeny wherein an "intrapterygoid" joint forms between Pars palatina and the rest of the pterygoid bone from which it was detached in early postnatal life (see **Arthr.** Annot. 17). In paleognathine birds and some neognaths, no part of the pterygoid splits off (Jollie, 1957). According to Hofer (1945) Os pterygoideum may be arched (e.g., *Mergus*), bent (e.g., *Vanellus*), or extended (e.g., *Ardea*). See Annots. 69, 70, 93.

(62) **Facies articularis parasphenoidalis.** The surface at the zone of contact between the palatine bone and parasphenoid rostrum. Such contact and articulation are absent in some birds. In some passerines and a few other taxa, a winglike portion of the parasphenoid facies, the **Lamella dorsalis** (synonymy: palatine hasp, Richards and Bock, 1973), extends up alongside the lateral surface of the rostrum; the edge of Lamella dorsalis is **Crista dorsolateralis** (synonymy: Cr. dorsalis, NAA, 1979).

Crista medialis (Fig. 4.7). This is the medial edge of the border of the surface of Pars choanalis that articulates with the Rostrum parasphenoidale. In some birds the right and left medial crests fuse in the midline on the lower surface of the parasphenoid rostrum and exhibit an unpaired median crest (most pelecaniforms, *Capella, Steatornis, Podargus*).

(63) **Proc. rostralis** (Jollie, 1958). Synonymy: Proc. choanalis rostralis (Bühler, 1970; NAA, 1979); ethmo-palatine bar (Parker, 1879). This is a rostral extension of the Crista medialis or Lamella dorsalis of Pars choanalis of the palatine bone for articulation with the Vomer; well exemplified in *Anser, Ardea, Caprimulgus, Corvus*).

(64) **Lamella choanalis** (Fig. 4.7). Synonymy: wall of palatine trough (Richards and Bock, 1973). A curved plate, often deeply concave, of Pars choanalis forming the lateral and dorsal wall of the Fossa choanalis of each palatine bone. In caprimulgids, the dorsal part of the lamella is curved medially and fused with its counterpart in the midline ventral to the parasphenoid rostrum, forming a palatine roof of the Pars caudalis of the choana (see **Resp.** Annot. 5). In some birds the plate is extended vertically ventrally forming the **Crista ventralis** which deepens the caudal part of the choana, pronounced, e.g., in *Larus* and *Diomedea*. In birds whose palatines are apposed or fused in the median plane, the right and left Cristae ventrales together form an unpaired, median ventral palatine crest (e.g., *Morus*).

Angulus caudomedialis. The angle formed by the caudal border of Lamella choanalis with its Crista ventralis.

Proc. caudomedialis. Synonymy: mediopalatine process (Richards and Bock, 1973). A caudal projection of Crista ventralis of some birds.

(65) **Crista lateralis.** The thickened lateral edge of the Pars lateralis of the palatine bone to which the aponeurosis of M. pterygoideus is attached.

(66) **Angulus caudolateralis.** Angle at the intersection of caudal and lateral margins of Pars lateralis of the palatine bone. In some forms (some passerines and a few other taxa) the angle is prolonged caudally as a pointed process which has been called the "transpalatine process", not an apt descriptive term.

(67) **Fossa ventralis.** Synonymy: Fossa muscularis. A usually shallow excavation on the ventral surface of Pars lateralis of the palatine bone between its Crista lateralis and Crista ventralis for attachment of part of M. pterygoideus. The fossa is deep in birds with prominent ventral crests of, e.g., *Diomedea, Cathartes, Larus, Capella.*

(68) **Vomer.** Synonymy: Prevomer. Paired elements, in adults most often fused into a single median structure that typically articulates with the parasphenoid rostrum and/or the Pars choanalis of the palatine bone (see below, this paragraph); not present in all birds; weakly developed in galliforms. The (fused) vomer varies in shape, ranging from a horizontally flattened plate, strongly V-shaped in cross section, to a laterally compressed, vertical plate. In passerine birds the vomer extends into the "ethmoid tissue" (Fig. 4.4), a condition unique to this group (see Hofer, 1949). In palaeognaths the vomer and pterygoids exclude the paired palatines from contact with one another and with the parasphenoid rostrum. In paleognaths the vomer has articular surfaces for pterygoid, palatine, maxillary, and premaxillary bones in addition to the Rostrum parasphenoidale.

(69) **Facies articularis parasphenoidalis.** In many neognathine birds the pterygoid, palatine bones, and the Vomer have surfaces for articulation with Rostrum parasphenoidale (**Arthr.** Annot. 29, 15, 16, 23).

Pes pterygoidei (Johnson, 1984). The "foot of the pterygoid", i.e., the expanded rostral end of the pterygoid bone (Fig. 4.4) that has articular surfaces for the parasphenoid rostrum and the palatine bone.

(70) **Proc. dorsalis.** Dorsal muscular process of Os pterygoideum of many birds, especially prominent in woodpeckers (Picidae) (Hofer, 1945). See **Myol.** Annot. 21.

(71) **Os quadratum.** Synonymy: Quadratum. Walker (1888) presented a comparative description (1888) of the variable form of the avian quadrate bone. **Proc. oticus** of the quadrate articulates with the prootic/opisthotic and squamosal (and sometimes laterosphenoid) elements by means of often separate otic and squamosal capitula. In some birds (e.g., *Hesperornis,* ratites, some neognaths; Witmer, 1990) the **Incisura intercapitularis** is indistinct and the capitula merge, lending the appearance of being "single-headed". See Annot. 24, 100; and Figs. 4.2, 3, 5).

Facies tympanica. The tympanic surface of the otic process and upper body of the quadrate bone forms with Ala parasphenoidea the rostral wall of the tympanic cavity; the tympanic membrane is attached to the crest of this surface. See Annot. 19.

(72) **Condylus caudalis.** Synonymy: Proc. postmandibularis. The **Proc. mandibularis** of the quadrate bone of most taxa of birds possess three condyles (see Bock, 1960; and **Arthr.** Annot. 35). The three condyles are arranged in a somewhat triangular configuration, the caudal condyle projecting toward the rear.

Condylus pterygoideus. In most birds the condyle of Os quadratum for articulation with the lateral end of Os pterygoideum has a rounded, convex articular facet (Fig. 4.3). In ratites, tinamous, and the hesperornithiforms the facet is broad and flattened (Witmer, 1990).

Condylus lateralis. In most birds the lateral condyle of the quadrate bears only the articular facet on its ventral surface for the **Cotyla lateralis** of the mandible (Fig. 4.5); however, most endemic New World jays (e.g., *Aphelocoma*) possess an additional condyle (**Condylus rostralis**) on the rostral surface of the lateral condyle of the quadrate. This condyle fits into a caudally-facing **Cotyla rostralis** on the mandible directly above the lateral cotyla. This forms the "buttress complex" (Zusi, 1987), anchoring the mandible to the quadrate when the open lower jaw is used in pounding.

(73) **Cotyla quadratojugalis.** The cotyla of the quadrate bone for articulation with the **Condylus quadraticus** of Os quadratojugale is located on the root of the lateral condyle of the mandibular process of Os quadratum.

(74) **Ossa supraorbitalia** (Beddard, 1898). Synonymy: Os supraciliare.

(75) **Ossa accessoria cranii.** See Jollie (1957) for a discussion of the accessory bones of the avian head.

(76) **Os nuchale.** Synonymy: Stylus postoccipitalis. Apparently unique to cormorants (*Phalacrocorax*) and the Anhinga in which it forms a moveable joint with a rounded protuberance of the occipital region of the skull (Dullemeijer, 1951).

(77) **Anulus [Annulus] tympanicus.** An osseous ring to which the periphery of the tympanic membrane is attached occurs in strigiforms and *Gallus* (Stellbogen, 1930). The ring is formed by parts of the exoccipital and parasphenoid bones (Kühne and Lewis, 1985).

(78) **Ossa suturarum.** Supernumerary bones developed in sutures between cranial bones; seen readily in young turkeys and ducks.

Os uncinatum (Burton, 1970). Located between the ventral end of Os lacrimale and the jugal bar in examples of musophagids.

(79) **Apparatus hyobranchialis** (Goodrich, 1958). Synonymy: Apparatus hyolingualis (consult **Myol.** Annot. 25); Apparatus hyoideus. The avian "tongue skeleton" is made up principally of elements from the hyoid arch and other more caudal branchial arches. The terminology adopted is that of McLelland (1968). Müller (1963:56)

provides a comprehensive synonymy. Zweers (1974, 1982) described the hyobranchial apparatus in *Anas* and *Columba;* he noted that the hyobranchial elements are commonly cartilage rather than bone.

(80) **Paraglossum.** Synonymy: Entoglossum. The paraglossum of most birds has the shape of an arrow head, bearing short, caudolaterally directed cornua. Psittaciforms possess a wide, flat paraglossum with a central foramen, or, more commonly, paired paraglossals united rostrally by a cartilaginous or bony isthmus (Beddard, 1898). In *Psittacus* (Homberger, 1986) each of the paired paraglossals is bifurcate rostrally.

(81) **Basihyale.** Synonymy: Basibranchiale rostrale; Basihyoideum; Pars basihyalis copulae; Copula I (Müller, 1963). This element is a derivative of the hyoid arch. See below.

Proc. parahyalis; Arcus parahyalis. In parrots (Mivart, 1895; Homberger, 1986) the Basihyale possesses a caudal enlargement from which the dorsolateral Proc. parahyalis arises on each side. These processes unite mid-dorsally to form the paraglossal arch in several Australian and Indopacific genera (*Melopsittacus, Eos, Vini, Lorius,* and *Nestor*).

Urohyale. [Basibranchiale caudale]; Synonymy: Urohyoideum; Pars urohyalis copulae; Basibranchiale I; copula II (Müller, 1963). The Basihyale and Urohyale are separate in young birds, but fused to one another in adults.

(82) **Dentes.** True teeth are known only from the fossil birds *Archaeopteryx, Parahesperornis, Hesperornis,* and *Ichthyornis* (Gingerich, 1972; Martin, 1984). Martin, et al. (1980) reviewed the morphology of avian dentitions. In *Osteodontornis* (Pseudodontornithidae) and its relatives the "teeth" are bony projections of the jaws, covered by rhamphotheca (Howard, 1957).

(83) **Condylus occipitalis.** The main part of the condyle is formed by Os basioccipitale; lateral contributions are from Os exoccipitale on each side. For a comprehensive comparative study of the avian occipital condyle see Goedbloed (1958).

Incisura mediana condyli. This is the median notch, usually present on the dorsum of the occipital condyle (Fig. 4.5); the tip of the Dens of the Axis rides in the incisure during dorsiflexion of the atlanto-occipital joint (Landolt and Zweers, 1985; Weisgram and Zweers, 1987). See **Arthr.** Annot. 64.

Tuberculum basilare. Synonymy: mamillary proc. (Pycraft, 1902; Saiff, 1974; Witmer, 1990). The basal tubercles originate as paired swellings at the rostral corners of the basioccipital bone; in later development they become sheathed ventrally by Lamina parasphenoidalis (Fig. 4.3). The tubercles serve for insertion of cervical muscles, principally M. rectus capitis dorsalis. They are best developed in long-skulled birds, e.g., *Morus, Hesperornis.* In some cases, the tubercles may coincide with Proc. medialis parasphenoidalis (see Annot. 97). Tuberculum basilare is an appropriate name in that it is clearly homologous with the "basal tubera" of nonavian archosaurs.

(84) **Ala parasphenoidalis.** Synonymy: Ala tympanica (NAA, 1979); alaparasphenoidalis (Jollie, 1957). Although this part appears to be a lateral extension of Lamina parasphenoidalis (Erdmann, 1940), it is actually formed as a separate center of ossification that merges with the lamina in certain birds, remaining separate in others (Figs. 4.4). In some birds the Ala parasphenoidalis is flared and wing-like, forming part of the margin of the external acoustic meatus (Annot. 20). In others the ala is not wing-like, but a boss of bone, the Proc. lateralis parasphenoidalis (Annot. 97) that

forms a joint with the Proc. medialis mandibulae (as in *Diomedea, Morus,* and *Larus*). See **Arthr.** Annot. 32.

(85) **Proc. paroccipitalis** (Shufeldt, 1909) **[P. paroticus]** (NAA, 1979). Synonymy: Ala posttympanica; Proc. occipitalis lateralis (Davids, 1952); Proc. opisthoticus (Zusi, 1962). Proc. exoccipitalis (Richards and Bock, 1973; Johnson, 1984). The paraoccipital process forms the caudal wall of Cavum tympanicum and Meatus acusticus, and provides attachment for Lig. occipitomandibularis (**Arthr.** Annot. 37) and M. depressor mandibulae (Figs. 4.4, 3, 5). The paroccipital processes of Mesozoic birds are directed more or less laterally (Witmer, 1990, whereas those of most neornithine birds project ventrolaterally. These processes are especially prominent in *Gavia, Pelecanus, Anser,* and *Caprimulgus.*

The paroccipital process is a compound bone formed by three elements: (1) the opisthotic medially; (2) the metotic laterally (see Annot. 105); and (3) the exoccipital which forms a caudal sheath of variable lateral extent.

(86) **Fossa parabasalis** (Kesteven, 1925). Synonymy: Fossa jugularis. Depression on the exterior of the skull base, just medial to the ventral margin of the tympanic cavity. Canals for cranial nerves VII, IX, X, (X), the cerebral carotid and the external ophthalmic arteries open into the fossa (Fig. 4.5). Not present in all birds.

Crista fossae parabasalis. This crest forms the prominent raised medial margin of the parabasal fossa as in examples of anseriforms and phoenicopterids (flamingos).

(87) **Fonticulus occipitalis.** Synonymy: Fonticulus occipitalis lateralis (Barkow, 1829); occipital fontanelle. Large paired openings lateral or dorsolateral to the Foramen magnum as in the anseriforms, some alcids, scolopacids, gruids and aramids, threskiornithids, and phoenicopterids (Beddard, 1898). These openings, like the orbital fonticuli (Annot. 29), are closed by fibrous membranes in intact specimens. Olson and Feduccia (1980) discuss the taxonomic significance of the fonticuli.

(88) **Os laterosphenoidale [Os pleurosphenoidale]).** Synonymy: Os orbitosphenoidale (NAA, 1979); Os alisphenoidale. This bone forms much of the ventral part of the caudal wall of the orbit, and extends from the interorbital septum (where it is notched or perforated for cranial nerves II, III, IV, and VI) laterally to the temporal fossa and the postorbital process (see Annot. 30) and tympanic cavity; it forms part of the margin of Foramen n. maxillomandibularis (Lang, 1956). In addition to the large laterosphenoid ossification, there is often a separate late-appearing ossification, the orbitosphenoid, a dorsomedial element that fuses with its counterpart and the mesethmoid (Hogg, 1978; Goodrich, 1958; and Müller, 1963).

(89) **Area muscularis aspera.** The orbital surface of Os laterosphenoidale of many large birds exhibits a roughened area for attachment of the jaw muscles; extremely pronounced in *Phoenicopterus* (**Myol.** Annot. 19).

(90) **Foramen n. maxillomandibularis.** Synonymy: Foramen prooticum spurium (Müller, 1963). Single opening between the prootic and laterosphenoid bones in birds and other archosaurs that transmits the N. maxillomandibularis (Figs. 4.1, 3, 6). Apparently only a small proportion of birds possesses separate foramina for the maxillary and mandibular nerves, e.g., *Tyto, Buteo, Cathartes* (Barnikol, 1953), *Columba,* some *Gallus* (pers. obs.).

Canalis n. maxillomandibularis. In some forms (e.g., *Columba*) the maxillomandibular nerve traverses a relatively lengthy canal to exit the cranial cavity, whereas in others (e.g., *Corvus*) the opening is simply a hole in thin bone, a foramen.

Foramen n. ophthalmici. Synonymy: Foramen rami profundi V. This foramen is located between the laterosphenoid and the basisphenoid/parasphenoid/interorbital septum complex.

(91) **Sella turcica; Dorsum sellae.** Consult Jollie (1957) and Hogg (1978) for the development of the base of the skull in the chicken; Müller (1963) in *Rhea*. For the anatomy of the Sella turcica in different birds see Wingstrand (1951), Starck (1955), and Baumel (1968). The Sella houses the hypophysis. The rostral end of the cranial carotid canal is an opening in the rear wall of the Sella, the Dorsum sellae, which is completely osseous in some birds, fibrous in others (Baumel, 1968).

Foramen ophthalmicum internum. Conducts the internal ophthalmic vessels into the orbit from the Sella turcica.

(92) **(Canalis craniopharyngealis).** This vestige of the embryonic Rathke's pouch may be seen in a median section of the skull base. The canal connects the Sella turcica to a median foramen on the Basis cranii externa (Wingstrand, 1951; Müller, 1963; Witmer, 1990).

(93) **Proc. basipterygoideus.** Synonymy: Proc. pterygoideus. A process on each side of Rostrum parasphenoidale (see Annot. 96) for articulation with the pterygoid bone. Occurs in ratites, procellariiforms, anseriforms, and galliforms; many charadriiforms and cathartid vultures; some caprimulgiforms and strigiforms; and trogoniforms (see Beddard, 1898). The homologies of the basipterygoids in extant birds, Cretaceous fossil birds, as well as non-avian archosaurs are discussed by Witmer and Martin (1987) and Olson and Feduccia (1980).

(94) **Tuba auditiva [pharyngotympanica] communis.** In most birds, the common auditory tube or chamber is formed by the confluence of the right and left tubes (see Annot. 98 for exceptions). The common tube is located on the ventral aspect of the base of Rostrum parasphenoidale (Fig. 4.4) (**Basis rostri parasphenoidalis**), where it is well delineated (e.g., in *Anser*). The common tube opens into the Infundibulum tubarum, a chamber which itself passes through a median slit in the roof of the oropharynx. See Annot. 98; and **Digest.** Annot. 19.

(95) **Canalis orbitalis.** This short canal opens on each side of the base of Rostrum parasphenoidale (Fig. 4.3); it is an offshoot of the cranial carotid canal that transmits the carotid branch, A. sphenoidea (**Art.** Annot. 18).

(96) **Lamina parasphenoidalis [L. basitemporalis].** Synonymy: basitemporal plate; Lamina basiparasphenoidalis (NAA, 1979). On the Basis cranii externa, this lamina is located rostral to the area where the ventral neck muscles insert on the basioccipital bone in front of the occipital condyle (Figs. 4.4, 5). The lamina assumes markedly different configurations in various birds (see Annot. 98), moreover, the lamina of certain birds exhibits processes (see below) that articulate with the medial process of the mandible, forming the so-called "mandibular brace" of Bock (1960). See Annot. 83 regarding Tuberculum basilare and **Arthr.** Annot. 32.

"Basitemporal" is inappropriate since the Lamina is not related to a "temporal" bone (see synonymy of Os squamosum) or region; it is retained as a bracketed alternative term because of its widespread use. "Lamina parasphenoidalis" is an abbreviated form that does not reflect its origin from the basiparasphenoid center of ossification.

Rostrum parasphenoidale [R. sphnoidale]. Synonymy: sphenoidal rostrum (Shufeldt, 1909; Os rostroparasphenoidale). Attenuated prolongation of the Basis cranii externa to which the lower border of the interorbital septum is joined and with which the pterygoid and palatine bones articulate. See Figs. 4.6, 3, 5.

(97) **Proc. lateralis parasphenoidalis; Proc. medialis parasphenoidalis.** Synonymy: medial and lateral basitemporal processes (Bock, 1960). Bock has described these processes of the parasphenoid lamina in detail for representatives of numerous avian taxa; Kozlova (1961) described them in alcids. See **Arthr.** Annot. 32 for particulars; see also Annot. 83 concerning Tuberculum basilare.

(98) **Tuba auditiva [T. pharyngotympanica].** Synonymy: Eustachian tube. This paired osseous tube is lined with mucosa continuous with that of the tympanic cavity and the oropharynx. The tube parallels the usually oblique, rostrolateral border of Lamina parasphenoidalis (nearly transverse in *Phoenicopterus*). The tube extends from the tympanic cavity to the base of Rostrum parasphenoidale, and most often joins the opposite tube (Annot. 94). The rostral openings of the tubes in ratites and the Cretaceous hesperornithiforms (Witmer, 1990) are widely separated. In some birds (e.g., albatrosses, flamingos) the lateral osseous wall is lacking, completed by connective tissue (Saiff, 1974).

(99) **Canalis caroticus cranialis.** Synonymy: parabasal canal (Müller, 1963, p. 76); vidian or basipterygoid canal (Goodrich, 1930); carotid canal (Shufeldt, 1909:283). Here it is qualified as the "cranial carotid canal" to distinguish it from the cervical carotid canal (Annot. 121). The cranial carotid canal extends from the parabasal fossa through the skull base medial to the auditory tube, then into the Sella turcica (Annot. 91); not only does it conduct the carotid vessels, but branches of cranial nerve VII. See Wingstrand (1951), Jollie (1957), Müller (1963: 76); and Baumel (1968) for particulars.

(100) **Cotyla quadratica squamosi.** Cup-shaped surface of Os squamosum for articulation with the squamosal capitulum of the quadrate bone (see Fig. 4.3; Annot. 24, 103). In some birds (e.g., *Anas*) the laterosphenoid bone makes a substantial contribution to the squamosal coytyla.

(101) **Fossa acustica interna.** Located on the lateral wall of the caudal fossa of the cranial cavity near the fossa for the auricle of the cerebellum, this depression contains the exit foramina for the branches of the vestibulocochlear and facial nerves. See Ossa cranii for more terms.

(102) **Os squamosum [Squamosum].** Synonymy: Os temporale.

Proc. zygomaticus Synonymy: Proc. lateralis. This process of Os squamosum is situated ventral to the postorbital process and is strongly developed in some birds, e.g., ratites, gaviiforms, galliforms, piciforms, and passeriforms (Figs. 4.4, 5). The tip of Proc. zygomaticus is fused with the postorbital process in some birds (e.g., galliforms). See Annot. 30b.

(103) **Proc. suprameaticus.** This process of Os squamosum forms part of the cotyla for the squamosal capitulum of the quadrate bone; and contributes to the upper boundary of the external acoustic meatus.

(104) **Fossa temporalis.** Excavation on the lateral aspect of the cranium dorsal to the external acoustic meatus and caudal to the postorbital process (Figs. 4.1, 5). In some birds (e.g., larids and ardeids) the fossa is strongly etched into the cranium (mainly Os squamosum). In some birds its sharp border, **Crista temporalis** nearly

reaches the median plane dorsally (Fig. 4.5). A tough fibrous membrane invests the the jaw muscles occupying the fossa (**Arthr.** Annot. 31).

Fossa subtemporalis. In some birds (e.g., *Morus, Gallus, Haematopus, Ardea, Fulica*) this is a shallow concavity between the caudal margin of the temporal fossa and the lateral part of the transverse nuchal crest (Fig. 4.1; Annot. 17).

(105) **Ossa otica.** In early postnatal development the three major otic elements (**Os prooticum, Os epioticum, Os opisthoticum**) coalesce with one another and adjacent surrounding bones. This complex contains the osseous labyrinth of the inner ear (Sandoval, 1963; Hogg, 1978). **Os metoticum** is an additional element lateral to the auditory capsule and forms much of the paroccipital process (see Toerien, 1971; and Annot. 85). The metotic cartilage is a neomorph of embryonic birds, and perhaps other archosaurs, that attaches to the basal plate, occipital arch, and auditory capsule (de Beer and Barrington, 1934). See Cavum tympanicum.

(106) **Crista vallecularis.** Crest of bone on the inner aspect of the calvaria that marks the lateral border of the **Eminentia sagittalis** of the cerebrum (**CNS** Annot. 78). The crest occupies the longitudinal groove in the brain surface known as the Vallecula telencephali.

(107) **Proc. lacrimalis [P. prefrontalis].** Lateral flared projection of the lateral margin of the frontal bone immediately caudal to its articulation with Os lacrimale; present, e.g., in *Larus, Morus, Cathartes.* See Annot. 110.

(108) **Os mesethemoidale.** This bone forms much of the rostral osseous part of the interorbital septum and, in some birds, part of the nasal septum (Fig. 4.1); it also forms the Lamina dorsalis (see below).

Lamina dorsalis (Shufeldt, 1909). The transverse plate of Os mesethmoidale that lies perpendicular to the interorbital septum. The Lamina articulates with the ventral surface of the frontal bone; prior to fusion of these two elements it is seen readily in skulls of young chickens and ducks (e.g., *Aythya*). In rhynchokinetic skulls the Lamina dorsalis extends rostrad to the level of the craniofacial flexion zone. See **Arthr.** Sut. front. eth.

(109) **Os ectethmoidale. [Os lateroethmoidale];** Synonymy: Proc. or (Planum) antorbitalis(e); Aliethmoid and Pars plana (Shufeldt, 1909). Vertical, transverse plate of bone forming part of the rostral wall of the orbit, separating it from the nasal cavity (Figs. 4.1, 2). In certain birds the lacrimal is fused with the ectethmoid forming the lacrimal-ectethmoid complex (Cracraft, 1968), e.g., in some charadriiforms (*Larus, Haematopus*) (Johnson, 1984).

(110) **Os lacrimale [Os prefrontale].** Müller (1963) reviewed the controversy over the homology of the lacrimal/prefrontal bone. Witmer notes that most evidence points to the homology of the lacrimal bone of birds with that of the nonavian archosaurs: (1) the lacrimal always forms the caudal margin of the antorbital fenestra in all archosaurs, including birds; and (2) in the dinosaurs leading to birds the prefrontal is progressively reduced in size and the lacrimal is enlarged. See Cracraft (1968) for a comprehensive review on variation of the lacrimal bone. See Annot. 107, 111.

(111) **Facies articularis frontonasalis.** This is the surface of Os lacrimale that articulates with both Os frontale and Os nasale; in some birds the lacrimal bone articulates medially with the ectethmoid and occasionally with Os jugale. See **Arthr.** Fig. 5.2.

(112) **Columna vertebralis.** The total number of vertebrae as well as the number of regional vertebrae varies in different avian taxa. The total number ranges from 39-64 (pygostyle counted as one vertebra). Fewest vertebrae occur in passerine birds; most occur in the swans and ratites. Most interspecific variation in numbers occurs in the cervical series of vertebrae (see Annot. 129). Individual variation in number of vertebrae within taxa is common.

(113) **Partes vertebrae.** See the review papers of Komárek (1970), and Zweers, et al. (1987) for a detailed treatment of the nomenclature of the features of avian vertebrae. Following Boas (1929) the names of the parts of a vertebra listed herein are based mainly on a hypothetical "typical" cervical vertebra of Boas' Segment II (see Annot. 129); however, the cervical vertebrae lack distinct, prominent transverse processes such as possessed by the thoracic, synsacral, and caudal vertebrae.

Dorsally each vertebra consists of an arch (Arcus vertebrae) and a ventral body (Corpus vertebrae). The opening enclosed by the two is the **Foramen vertebrale.** Collectively the entire series of the vertebral foramina produce the **Canalis vertebralis** that houses the spinal cord, its meninges, and the internal vertebral venous sinus (**Ven.** Annot. 46). The arch and body bear several processes which are lever arms for muscle attachment or articular surfaces connecting vertebrae (see Annot. 127a; and **Arthr.** Annot. 60).

Corpus vertebrae. The Corpus of typical cervical and thoracic vertebrae has expanded cranial and caudal ends, with a constricted midsection, the **Concavitas lateralis.** The **Facies dorsalis corporis** (the spinal cord surface of the vertebral body) is not flat, but forms a longitudinal sulcus.

Birds are the only vertebrate animals in which most of the intercorporal articular surfaces are heterocoelus or saddle-shaped (Fig. 4.8). Of infrequent occurence (e.g., penguins, auks, gulls) the vertebrae in the thoracic region are opisthocoelous, having concave caudal articular surfaces (Beddard, 1898). Martin (1987) notes that certain modern birds (e.g., charadriiforms) still retain amphicoelous vertebrae in the region "just anterior to the sacrum" (see **Arthr.** Annot. 60). The vertebrae of *Archaeopteryx* and *Ichthyornis* are amphicoelous, although hesperornithiformes are heterocoelous.

(114) **Fovea cranioventralis.** Synonymy: Fovea anteroventralis (Boas, 1929). This pit (Fig. 4.8) accomodates the ventral lip of the articular surface of the body of the vertebra cranial to it upon ventral flexion of the neck.

(115) **Sulcus lateralis.** The groove on the side of the body of a cervical vertebra (Facies lateralis) accommodating the ascending vertebral artery and vein.

Tuberositas lig. collateralis. Synonymy: Tuberositas lateralis corporis (Landolt and Zweers, 1985). The caudal end of each vertebral body exhibits on its lateral side a distinct marking for attachment of Lig. collaterale. See **Arthr.** Annot. 60.

(116) **Eminentia costolateralis.** Synonymy: Proc. costolateralis (Boas, 1929); parapophysis; Tuberculum costarium (Komárek, 1979). The costolateral eminence is a small prominence of the lateral surface of the bodies of thoracic vertebrae that bears an articular facet, Fovea costalis, for the head of a rib, **Capitulum costae.** The fovea occurs on free thoracic vertebrae as well as those of the notarium and synsacrum. Replacement of Komárek's term "tuberculum costarium" avoids confusion with the tuberculum of a rib (see below, Annot. 117 and **Arthr.** Annot. 79.

(117) **Fovea costalis.** Articular surface on the lateral end of a transverse process of a vertebra for the tubercle of the rib, **Tuberculum costae.** The costal fovea also occurs on the Eminentia costolateralis (see Annot. 116; and **Arthr.** 79).

(118) **Proc. costalis.** Synonymy: Spina laminae ventralis (Komárek, 1970); Pleurapophysis. A rudimentary rib with its proximal end ankylosed to the Corpus and Proc. transversus of a cervical vertebra, its free caudal end forming an attenuated style or spine (Fig. 4.8). See Annot. 141b regarding the costal processes of sacral vertebrae.

(119) **Crista [Proc.] ventralis corporis.** Synonymy: Hypapophysis; Proc. latus (Boas, 1929); Crista ventralis (Komárek, 1979). These median, ventral crests (processes) display interspecific variablity in shape and relative development. "Crest" is descriptively apt for laterally compressed, plate-like processes. The crests are present on the ventral side of the bodies of the cranial and caudal series of cervical vertebrae, but lacking in the intermediate series (see Annot. 129). The size of the ventral crest on the Atlas of different avian taxa is variable; that of the Axis is quite strong in many birds (see Boas, 1929).

Ventral crests are most strongly developed on the cranial series of thoracic vertebrae and the cervicothoracic transitional vertebrae of spheniscids, *Gavia*, alcids, and some anseriforms (Beddard, 1898). They are considered adaptations for powerful underwater use of the neck (Kuroda, 1954). See below Annot. 122; and **Arthr.** Annot. 72. The paired ventral longus colli muscles are attached to the crests (**Myol.** Annot. 56).

Fenestrae intercristales. Synonymy: Foramina intercristales (Komárek, 1979). The ventral crests of cranial thoracic vertebrae (including those of the Notarium) of some taxa are ankylosed to one another. The fenestrae are windows (openings) of variable size and shape where the ventral intercristal ligaments are incompletely ossified, in other words, incomplete fusion of adjacent ventral crests (see Annot. 140); **Arthr.** Annot. 63).

(120) **Alae cristae ventralis.** Paired wing-like lateral extensions of the ventral edge of the Crista ventralis; seen in the cranial series of thoracic vertebrae of certain diving birds, e.g., *Gavia* (Kuroda, 1954); slightly developed in *Anas* (Landolt and Zweers, 1985) and alcids (Strauch, 1985). According to R. W. Storer (pers. comm.) the alae are best developed in the loons, next in some penguins (*Aptenodytes*), present in all alcids, and fairly well developed in the larger alcid species (*Alca, Uria, Pinguinus, Fratercula*) and the diving ducks (e.g., *Clangula*).

(121) **Proc. caroticus.** Synonymy: Catapophysis (Beddard, 1898); Proc. sublateralis (Boas, 1929); Proc. hemalis (Komárek, 1970a). Paired incurved processes on the ventral side of vertebral bodies of the intermediate group of cervical vertebrae (Fig. 4.8B; Annot. 129). The carotid processes are not homologous with the haemal processes of the tail region of birds and other vertebrates (Annot. 144).

Each of the carotid processes forms the lateral wall of the **Sulcus caroticus.** Slips of M. longus colli ventralis (**Myol.** Annot. 56) are attached to the carotid processes.

In most birds the free ends of a pair of carotid processes are connected by a ligamentous bridge producing a short canal. In certain birds, e.g., *Pelecanus, Ardea, Dendrocopos*, the paired processes become ankylosed, forming a complete osseous canal (see below). Fused processes are thought to be convergent features in species having the ability to throw the head forward (Jenni, 1981). In *Dendrocopos* the fused carotid processes are equipped with a ventral median crest; Jenni (1981) considers that the crests are adaptations for drilling and drumming (see Annot. 119).

Canalis caroticus cervicalis. Synonymy: subvertebral canal. On the ventral surface of the intermediate segment of the cervical vertebral column the internal carotid arteries course in this osseo-fibrous canal that is partially formed by the carotid processes (Annot. 121a, 99). See **Art.** Annot. 15.

Proc. postlateralis (Zusi and Storer, 1969). Synonymy: Proc. inferolateralis (Boas, 1929); Proc. ventrolateralis (Landolt and Zweers, 1985). Seen in ventral view of cervical vertebrae, this process in grebes is a paired caudolateral projection of the vertebral body; for attachment of M. longus colli ventrales (Zusi and Storer, 1969). Present also in *Morus* and *Phoenicopterus*.

(122) **Crista ventrolateralis.** Synonymy: Proc. inferolateralis (Boas, 1929); Proc. ventrolateralis (NAA, 1979). Ventrolaterally oriented, paired projections attached to the ventrolateral border of the body of certain thoracic vertebra; the ventrolateral crests flank the Crista ventralis on each side; present, e.g., in *Larus*, and the owls, *Strix, Nyctea*. See Fig. 4.8A.

(123) **Proc. transversus vertebrae.** Synonymy: Diapophysis. Paired process that projects laterally from each side of the vertebral arch. During postnatal maturation of the skeleton the transverse processes of cervical vertebrae become fused with cervical ribs (see Annot. 134, 138). The transverse process of most of the cervical vertebrae is not a pronounced feature as in the thoracic, synsacral, and caudal regions (see Annot. 134, 135); it is often indistinguishable from the Ansa costotransversaria of cervical vertebrae in mature birds (Annot. 135).

(124) **Crista transverso-obliqua** (Boas, 1929). The cervical vertebrae of long-necked birds best exhibit this crest on the dorsal surface of the vertebral arch. The crest of each side extends obliquely caudolaterally onto its caudal zygapophysis.

(125) **Torus dorsalis.** Synonymy: Hyperapophysis (Beddard, 1898); Processus dorsalis (Boas, 1929). This boss of bone is found on the Crista transverso-obliqua of the dorsum of the caudal zygapophysis (Fig. 4.8D); for attachment of Mm. ascendentes (see **Myol.** Annot. 46-49). The location of the torus varies from the base to near the tip of the zygapophysis; it is strongly developed on cervical vertebrae of some forms (e.g., *Alca, Haliaëtus, Morus*). The use of "Torus" is preferable since it avoids confusion with the spinous [dorsal] process of the vertebral arch.

(126) **Area lig. elastici.** Synonymy: Facies lig. elastici (Komárek, 1970). Interlaminar and interspinous elastic ligaments are usually attached cranially and caudally on the dorsal lamina of the vertebral arch at the base of Proc. spinosus [dorsalis]. Bony markings of the ligaments are variously developed as roughened tuberosities, facies, fossae, or foveae that are here designated generically as "areae". See **Arthr.** Annot. 63.

(127a) **Arcus vertebrae.** Each end of the vertebral arch is attached to the dorsolateral border of its vertebral body; the arch forms the lateral wall (Lamina lateralis arcus) and the dorsal wall (Lamina dorsalis arcus) of the vertebral canal (see below). The transverse process is a lateral projection of the arch; its base marks the dividing line between lateral lamina and dorsal lamina, best exhibited in thoracic vertebrae since cervical vertebrae lack prominent transverse processes. The level of the zygapophyses indicates the dividing line between dorsal and lateral laminae in cervical vertebrae.

Lamina lateralis arcus [Pediculus arcus]. Lamina lateralis is a substitute name for the mammalian "Pediculus". In birds the lateral part of the vertebral arch is plate-like rather than a constricted stalk (pedicle) as in mammals; this lamina is especially expansive in the "long vertebrae" of birds (Komárek, 1970a). See Annot. 128a.

Lamina dorsalis arcus is the segment of the vertebral arch that extends from the base of the transverse process of one side to that of the opposite side; it bears the Proc. spinosus on the midline of its dorsal aspect. See Annot. 128 b, c.

(127b) **Lamina arcocostalis** (Landolt and Zweers, 1985). This lamina is a thin shelf of bone continuous with the caudal margin of Ansa costotransversaria (Fig. 4.8D); the lamina extends lateroventrad from the vertebral arch often over the entire length of the spine of the costal process in anserids and anatids. In *Gallus* and *Phoenicopterus* the arcocostal lamina is less extensive, not reaching the tip of the costal process. The lamina may be considered as an extension of the Ansa which forms the dorsolateral wall of a craniocaudally-attenuated transverse foramen whereby the foramen becomes converted into a canal (see Annot. 127c).

(127c) **Lamina corporocostalis** (new term; well illlustrated, but not named by Komárek, 1979:106). In conjunction with the occurrence of the arcocostal lamina, another lamina, the corporocostal lamina, extends medially from the costal spine to the vertebral body. It forms the ventral floor of the attenuated transverse foramen (canal) in the birds noted in the paragraph above. Both the arco- and corporocostal laminae are derived by ossification of intermuscular aponeuroses or fascial sheaths (see **Myol.**).

(128a) **Incisura caudalis/cranialis arcus.** Synonymy: Incisura vertebralis (Komárek, 1979). These are notches in the cranial and caudal borders of the Lamina lateralis arcus. The cranial notch of one vertebra and the caudal notch of the vertebra in front of it together form the boundaries of a **Foramen intervertebrale** for passage of the spinal nerve and vessels into and out of the vertebral canal. The caudal incisure is generally markedly the deeper of the two (Annot. 143a).

(128b) **Hiatus interarcualis.** The opening or gap between the dorsal laminae of the arches of adjacent (articulated) vertebrae as seen in dorsal view (see Zusi, 1962; Komárek, 1979). The hiatus is closed by the interlaminar elastic ligaments and membranes (see **Arthr.**). The hiatus is bounded by the Lacunae interzygapophysiales of the dorsal laminae of the arches of two adjoining vertebrae (see below), most pronounced in the cervical region (see below).

(128c) **Lacuna interzygapophysialis** (new term). "Incisura arcualis" (Komárek, 1970), has been replaced to avoid confusion with the Incisurae cranialis/caudalis arcus (of Lamina lateralis) that are boundaries of the intervertebral foramina. The Lacuna is the V-shaped or often broadly U-shaped indentation of the Lamina dorsalis of the vertebral arch, located between the right and left zygapophyses (Fig. 4.8C) at each end of a vertebra (see paragraph above); two adjoining lacunae form the cranial and caudal boundaries of the Hiatus interarcualis.

(129) **Vertebrae cervicales.** The greatest number of cervical vertebrae are found in ratites (ca. 20) and in swans (23-25); fewest in coraciiforms and passeriforms. Boas (1929) characterized the cervical vertebral column as consisting of three morphologically and functionally distinct sections: Segment I, the most cranial series, Segment II, the intermediate series, and Segment III, the most caudal series. Zusi (1962) noted that the joints within and between the segments permit I and III to be flexed ventrally, but Segment II can be flexed only dorsally; this arrangement allows the neck to be held in its characteristic S-shaped retracted position.

In birds generally, most of the cervical vertebrae are invaded by diverticula of the cervical system of air sacs (see below); however Boas (1929) reported that all of the cervical vertebrae were apneumatic in the following diving birds: *Colymbus (Gavia), Plotus (Anhinga), Podiceps, Alca,* and *Spheniscus.*

(130) **Atlas; Axis.** These are the specialized first and second cervical vertebrae, respectively. The Axis is also known as Epistropheus. The Atlas is apneumatic in all birds examined, the Axis being apneumatic in many birds (Boas, 1929).

(131) **Fossa condyloidea.** Synonymy: ventral semi-ring (Boas, 1929). Cupped-shaped or semicircular concave surface of the Atlas for articulation with the occipital condyle of the base of the skull.

Incisura fossae; Foramen fossae. The condyloid fossa on the cranial aspect of the Atlas may be perforated (Foramen fossae) or have an open dorsal notch (Incisura fossae) in which the apex of the dens rides. See **Arthr.** Fibrocartilago atlantis.

(132) **Zygapophysis caudalis [Proc. articularis caudalis].** Synonymy: postzygapophysis. **Zygapophysis cranialis [Proc. articularis cranialis.** Synonymy: prezygapophysis. The zygapophysis is one of four processes of each vertebra that project from the vertebral arch or the base of the transverse process. The pair of cranial zygapophyses of one vertebra and the pair of caudal zygapophyses of the vertebra in front form freely moveable synovial joints on each side. The free caudal vertebrae of most birds lack zygapophyses; exception: the albatross *Diomedea* (see Annot. 128c; **Arthr.** Annot. 65).

Caudal zygapophyses are present on the Atlas of most birds studied by Boas (1929), thus paired atlantoaxial zygapophysial articulations exist. See **Arthr.** Annot. 68.

(133) **Proc. costalis atlantis.** A rudimentary rib is not evident on the Atlas of most birds (Boas, 1929); therefore the Atlas of relatively few birds exhibits transverse foramina (see Annot. 134, 135). Boas (1929) depicted well developed, complete transverse foramina of the Atlas in *Rhea* and *Cygnus,* incomplete ones in other forms. See Annot. 118, 123, 134, 138.

(134a) **Foramen transversarium.** Synonymy: Foramen costotransversarium. The transverse foramen characterizes most of the cervical vertebrae of birds (for exception, see Annot. 133). Even though the avian transverse foramina may have considerable length and might be referred to as canals (Annot. 127b, c), the term "Foramen transversarium" is retained for consistency with the mammalian nomenclatures. See below, Annot. 135 for the fetal derivation of the foramen.

(134b) **Canalis vertebrarterialis** (Boas, 1929). On each side of the cervical vertebral column the series of transverse foramina forms this canal that extends the length of the cervical column and conducts the ascending vertebral artery and companion vein(s) (**Art.** Annot. 11).

The cervical transverse foramen is the equivalent of the opening formed in the angle between the tuberculum and capitulum of each rib and the transverse process of a thoracic vertebra (see Fig. 4.8A, B; Annot. 148). Thus the series of thoracic costovertebral openings is morphologically equivalent to the cervical vertebrarterial canal; moreover, it carries the descending vertebral vessels (**Art.** Annot. 11) as well as loops of the paravertebral autonomic nerve trunk.

(135) **Ansa costotransversaria** (Boas, 1929). Synonymy: Lamina ventralis (Komárek, 1970). The Ansa (L. loop) is formed by postnatal ankylosis of the rudimentary cervical rib (Costa cervicalis) with the transverse process and vertebral body of a vertebra. Thus the ansa represents part of the external wall of a transverse foramen, and the body (and lateral lamina of the vertebral arch) form the medial wall (Fig. 4.8B) The ansa demonstrates surface features: a knob-like **Tuberculum ansae** (Knopffortsatz, Boas, 1929) and a series of linear **Cristae laterales** (Langskanten,

Boas, 1929). These features mark the attachment of tendons of lateral cervical musculature (**Myol.** Annot. 53, 54).

(136a) **Incisura caudalis arcus.** The caudal notch of the arch of the Atlas forms the rostral boundary of the atlanto-axial intervertebral foramen for the second cervical spinal nerve (see Annot. 128a).

(136b) **Dens axis.** Synonymy: Proc. odontoideus. The joints between the avian Axis and Atlas differ from those of mammals: in addition to the articulation of the Dens with the Atlas, an Artc. intercorporea and paired zygapophysial articulations are present. The atlas and axis are ankylosed in adult hornbills (Bucerotidae) (Kemp, 1985).

(137) **Proc. spinosus [P. dorsalis] axis.** Although commonly present, the spinous process is lacking from the Axis of some forms (e.g., the scolapacid, *Gallinago delicata*).

(138) **Proc. costalis axis.** The rudiment of a rib is present on the Axis of many, but not all, birds that have been studied; occasionally weak projecting tips of the costal processes are found (Boas, 1929). When present, Proc. costalis forms an arch and completes the transverse foramen. See Annot. 133, 135.

(139) **Vertebrae thoracicae.** Synonymy: Vertebrae dorsales. The first thoracic vertebra is defined as the cranialmost vertebra with a complete rib (i.e., having vertebral and sternal segments) that articulates directly or indirectly with the sternum (see Annot. 147). The vertebrae at the root of the neck that bear moveable ribs, not reaching the sternum, have been called "Vertebrae cervicodorsales" (Newton, 1896; Zusi, 1962); these are transitional in configuration between cervical and thoracic vertebrae. See Annot. 141a; and **Arthr.** Fig. 5.10).

(140a) **Notarium.** Synonymy: Os dorsale. The Notarium (Gk. noton, back) is a unit of several (2-6) (Barkow, 1856; Storer, 1982) thoracic vertebrae that are coalesced rather completely in adults, but not fused with the synsacrum (see **Arthr.** for significance of the joint between the notarium and synsacrum). The Notarium (Fig. 4.9) is characteristically present in at least 17 families of birds, occasional in several others: tinamous, *Pelecanus*, threskiornithids (ibis and spoonbills), galliforms, columbiforms, as well as all podicipediforms and most falconids (Storer, 1982). The Mesozoic birds *Archaeopteryx* and *Gobipteryx* possess several "fused anterior dorsal (thoracic) vertebrae" (Martin, 1987).

In certain birds (e.g., larids, rhynchopids, gruids, *Branta* and *Anser*) consolidation of the thoracic vertebral column is achieved by ossification or calcification of the epaxial muscle tendons that interdigitate and may fuse to one another and to the transverse and spinous processes of adjacent vertebrae. This sort of consolidation as well as the rather complete synostotic coalescence (above) are both found in some groups (e.g., grebes and cranes; R. W. Storer, pers. comm.). See **Arthr.** Annot. 71.

(140b) **Canalis notarii.** The segment of the vertebral canal that traverses the Notarium (see Annot. 144). **Crista spinosa [dorsalis] notarii.** Synonymy: Crista dorsalis notarii (NAA, 1979). Crest formed by the ankylosed spinus processes.

(141a) **Synsacrum.** Synonymy: Os lumbosacrale; Os pelvicum. A rigid unit consisting of ankylosed vertebrae in mature birds (Figs. 4.9, 11). The preacetabular part of the Synsacrum incorporates one or several thoracic vertebrae and the "lumbar series" (synsacral segment II of Boas, 1933) that are attached to the preacetabular ilium; the proper sacral vertebrae are opposite the acetabulum (see below); several more of the proximal caudal vertebrae caudales (urocaudals, Parker, 1888) comprise

the postacetabular series. Interspecific variation exists in the number of vertebrae forming the synsacrum. See Barkow (1856), Boas, (1933), and van Oort (1905) for detailed comparative studies of the synsacrum in different taxa.

The synsacrum is synostosed on each side with the Os coxae, the three elements forming the bony pelvis; the pelvis and uropygium (**Topog.** Annot. 36) together form the dorsal abdominal wall (Baumel, 1988). See **Arthr.** Artcc. synsacri.

(141b) **Vertebrae sacrales.** One or two "true" sacral vertebrae (Segment III vertebrae of Boas, 1933) are identified by their conspicuous costal processes, lacking in the vertebrae to the front and rear of them. In some birds the costal processes of the sacral vertebra(e) extend laterally to the hip bone near the acetabulum, thus the name, **Vertebra acetetabularis** (Du Toit, 1912-13; Komárek, 1979; Radu, 1975) which is well exemplified in the pelvis of *Larus, Strix, Gallinula.* See Fig. 4.9.

(141c) **Lamina transversa notarii/synsacri.** During skeletal maturation the transverse processes of the notarial and synsacral vertebrae become coalesced, producing on each side a continuous transverse lamina. In mature birds the lateral border of each Lamina of the synsacrum becomes firmly ankylosed with the hip bone (Os coxae) of its side. In instances where the fusion between the transverse processes is incomplete, the persistent windows are known as **Fenestrae intertransversariae.** The fenestrae as well as smaller foramina are traversed by nerves and vessels. See Figs. 4.9, 11.

(142a) **Corpus notarii/synsacri.** This is the unit of consolidated vertebral bodies (corpora) that form the median, ventral column of bone of the notarium and that of the synsacrum.

(142b) **Facies visceralis synsacri.** Synonymy: Facies abdominalis. See Barkow (1856) and Boas (1933) for features of this ventral (internal) surface of the synsacrum which is in contact with abdominal organs (viscera).

(142c) **Crista spinosa [dorsalis] synsacri.** The crest formed by the ankylosed spinous processes of the synsacral vertebrae.

(143a) **Foramina intervertebralia.** Dual intervertebral foramina may exist in some birds over part of the length of the synsacrum, especially immature ones; these are separate openings for the dorsal and ventral roots of the spinal nerve, the roots uniting external to the vertebral canal (e.g., *Struthio, Rhea, Somateria, Porphyrio, Alca, Corvus*) (Boas, 1933).

(143b) **Canalis synsacri [vertebralis].** See Annot. 140b. The part of the vertebral canal of the synsacrum. The canal is enlarged along the middle of its length; the enlarged chamber contains the lumbosacral intumescence of the spinal cord which is known as the Cranium inferior (or ischiadicus) by older authors (Barkow, 1856).

(144) **Proc. haemalis.** Synonymy: intercentrum; chevron bones. Found only on the rear three or so caudal vertebrae on their ventral surfaces, including the pygostyle. Prominent in large birds (e.g., albatross, penguin, heron, pelican) and in some smaller forms (e.g., *Crotophaga, Dendrocopos*); inconspicuous and vestigial, e.g., in the pigeon and chicken. The haemal processes are usually ankylosed to the cranial ends of the vertebral bodies, projecting ventrocranially and underlying the intervertebral discs and rear of the vertebra ahead. In *Crotophaga* the processes are fused at their bases with the vertebral body, and also articulate firmly with the body of the vertebra cranial to it.

In some mature birds certain of the haemal processes occur as distinct nodular elements attached by ligaments to the discs and/or to the vertebral bodies (*Diomedea* sp.). The haemal processes are persistent intercentra (Piiper, 1928), an element of embryonic vertebrae; absent in other vertebral regions except the atlas and axis. Archosaurs closest to birds lack intercentra in the vertebral column except in the tail and C1, C2. See Annot. 121 for comparison with cervical carotid processes.

(145) **Pygostylus.** Synonymy: Urostylus; Coccyx. Compound bone formed by postnatal ankylosis of 3-6, commonly 5-6, of the terminal free caudal vertebrae. The fetal development of the pygostyle is reviewed by Steiner (1938) and van Oort (1905). Holmgren (1955) contended that the Ostrich pygostyle is not homologous with that of carinate birds, a claim refuted by de Beer (1956). See Baumel (1988) for the structures attached to the pygostyle, its relationships, and remarks on its evolutionary significance.

(146) **Basis pygostyli.** Derived from fusion of the several vertebral bodies incorporated into the pygostyle. **Lamina pygostyli.** Blade-like portion of pygostyle derived from vertebral spinous processes and arches. Rudimentary transverse processes are present on the pygostyle of certain piciforms (Burt, 1930: 478). **Discus pygostyli:** In woodpeckers (piciforms) especially, and other scansorial birds, the pygostyle is distinguished by a strong transverse, shield-like disc on its caudal margin (Burt, 1930), the disc serving as an expanded area of attachment for the extraordinarily well developed muscles that depress the tail.

(147) **Costae.** The freely moveable ribs of different avian taxa vary in number. Ribs of the cervicothoracic transitional region of the vertebral column are short "floating ribs" that fail to reach the sternum (Costae incompletae). The so-called "true ribs" (Costae completae verae) consist of vertebral and sternal elements; the sternal segments articulate with Margo costalis sterni (see Annot. 157). In some instances the sternal part of one or more of the ribs do not articulate directly with the sternum (Costae completae spuriae), but with the sternal parts of true complete ribs cranial to them. Caudal to the true ribs a variable number of floating vertebral ribs may occur; the last of the series of true ribs often articulates with the ventral side of the preacetabular ilium in various birds (**Arthr.** Annot. 80).

(148) **Proc. uncinatus.** Synonymy: Appendix epipleuralis (Shufeldt, 1890). Dorsocaudally oriented process attached to the caudal border of the vertebral ribs. Screamers (Anhimidae) and megapodids lack uncinate processes (R. W. Storer, pers. comm.). See **Myol.** Annot. 59.

Incisura capitulotubercularis. The neck region (collum) of a vertebral rib exhibits this notch between its capitulum and tubercle. The interval between the neck and the transverse process of the vertebral rib corresponds to the transverse foramen of the cervical vertebrae. See Fig. 4.9; Annot. 134.

Sulcus pulmonalis. The elongated sulcus between the dorsal parts of adjacent ribs. The sulcus is occupied by lung tissue, the **Torus intercostalis** (**Resp.** Annot. 49); each Torus is in contact with the ribs cranial and caudal to it, as well as with the intercostal muscles and parietal pleura.

(149) **Sternum.** See Fürbringer (1888) for a detailed synonymy for the parts of the avian sternum. He distinguished a cranial part, the "Costosternum", to which the ribs are attached, and a caudal part, the "Xiphosternum", also referred to as Metasternum.

Corpus sterni. Synonymy: Tabula sterni.

(150) **Proc. craniolateralis sterni.** Synonymy: Proc. sternocoracoideus; Proc. precostalis.

Proc. caudolateralis sterni. Synonymy: Proc. posterior lateralis sterni or Proc. xiphoideus lateralis sterni (Fürbringer, 1888). Fürbringer noted that some galliforms possess this distinctive, extraordinarily elongated, lateral process of the sternum that branches into strong lateral and medial trabeculae. See Annot. 151.

(151) **Incisurae et fenestrae sterni.** The caudal part of the sternum is notched (incisurae) or perforated (fenestrae) in a variety of ways in different avian taxa (Fig. 4.11). Bars of bone between incisurae/fenestrae are referred to as "trabeculae"; the openings in the sternum are closed by fibrous membranes. See Fürbringer (1888) for illustrations of the various patterns.

(152) **Facies muscularis sterni.** Synonymy: Facies ventralis or externa. The surface of Corpus sterni lateral to the base of the carina to which the pectoralis and supracoracoid muscles are attached.

Facies visceralis sterni. Synonymy: Facies dorsalis or interna. Inner surface of sternum related to heart and liver.

(153) **Linea intermuscularis.** M. supracoracoideus is attached to the ventral surface of the Corpus sterni and to the adjacent lateral aspect of the Carina sterni (**Myol.** Annot. 76). The intermuscular lines on each surface mark the bony attachment of the dense fascia that invests the muscle and separates it from M. pectoralis.

(154) **Planum postcarinale.** Synonym: Planum postpectorale (Fürbringer, 1902). The Carina sterni does not reach the caudal margin of the sternum in some forms (e.g., pelecaniforms). The planum is therefore the continuous bilateral flat surface of Facies muscularis of the sternum caudal to the carina.

(155) **Pila costalis.** The column of bone that reinforces the costal margin of the sternum, prolonged onto the Trabecula lateralis in some birds (Fig. 4.11).

(156) **Sulcus articularis coracoideus.** Synonymy: coracoid groove or depression. Located at the cranial margin of the Corpus sterni, this is the surface for articulation with the coracoid. The sulcus is a narrow, attenuated, curved groove on each side of the sternum; it extends from the base of the craniolateral process medially to the side of Rostrum sterni or onto its dorsal surface (e.g., *Larus, Branta*). In some birds the Sulcus is directed caudolaterally from the midline Rostrum; however in others it is oriented nearly transversely (e.g., *Gallus, Coccyzus, Dendrocopos, Progne*). In several groups the coracoidal sulci overlap in the median plane (see **Arthr.** Annot. 89, 90). Commonly the length of the Sulcus is nearly perpendicular to the median plane, but its lateral end is depressed or elevated in some birds. See Fig. 4.11.

(157) The **Margo costalis sterni,** when viewed from the side, exhibits a series of notches (**Incisurae costales**) separated from one another by partitions, each known as a **Proc. articularis sternocostalis** (Komárek, 1979). Between two adjacent processes is a small compartment called the **Loculus costalis** (new term); the head of the sternal rib partly occupies a locule, and articulates with the caudal surface of a sternocostal articular process, **Facies articularis costalis.** In some avian taxa dual articular facets exist for the corresponding facets on the dual-headed sternal ribs (see **Arthr.** Annot. 83).

Margo caudalis sterni. The caudal margin of the sternum is highly variable in shape; it may be squared, rounded, intact, or notched. See Fürbringer (1888) for characteristic shapes of sterna of numerous taxa.

(158) **Pila coracoidea.** The transversely oriented, curved pillar of bone along the cranial margin of the Corpus sterni (Fig. 4.11) that strengthens the articular sulcus for Os coracoideum.

(159) **Rostrum sterni.** Synonymy: Manubrium sterni; Spina intercoracoidea sterni (see Fürbringer, 1888, for complete synonymy and descriptions and summary of variation of the Rostrum). Serves as an attachment of parts of Membrana sternocoracoclavicularis (**Arthr.** Annot. 86). The spines of the Rostrum are designated **Spina externa** and **Spina interna** because of their continuity with the external and internal labra of the Sulcus articularis coracoideus. Spina externa is usually present; in some psittacines, picids, and most passerines, including the Menurae, the external spine is forked, its processes are called the **Alae spinae externae.** The Spina interna is of much less frequent occurrence (occurring in, e.g., galliforms, cuculids, meropids, upupids, and bucerotids), and is frequently represented by a tubercle(s) between the two Labra interna of the coracoidal articular sulcus. The external and internal spines may coalesce producing the **Spina communis** (see Fig. 4.11; Annot. 160).

(160) **Foramen rostri.** Synonymy: Foramen interspinale. The foramen is an opening at the base of the ankylosed external and internal spines of the sternal rostrum (e.g., galliform and coraciiform birds). In some birds the **Septum interarticulare** connects the external and internal spines, and separates the right and left coracoidal sulci in the midline by bone or membrane; in birds having side-to-side or overlapping contact between the two coracoids the **Spatium intercoracoidale** is open (**Arthr.** Annot. 90).

(161) **Carina sterni.** Synonymy: Crista sterni (Fürbringer, 1888); (Carina, L. keel). The vertical plate of bone attached to the median line of the Corpus sterni found in most birds (thus "carinate birds"). In the psittaciform, *Strigops,* the carina is lacking. Ratites generally lack a distinct, well developed carina, e.g., *Struthio.* The sternum of *Apteryx, Casuarius,* and *Rhea* exhibits a slight crest (Beddard, 1898).

Crista lateralis carinae. A paired crest on each side of the dorsal, thick part of the cranial margin of the carina (e.g., *Gallus, Cathartes*). The **Sulcus carinae** is the shallow groove between the two lateral crests; the Sulcus is an elongated triangle in *Gallus.* The **Pila carinae** (Fig. 4.11) is the thick reinforcing pillar of bone of the cranial margin of the carina.

(162) **Clavicula [Furcula].** (Fig. 4.10. (Furcula, L. fork). Furcula refers to the united, paired clavicles. When not ankylosed at their ventral ends, the clavicles may be joined by cartilage or fibrous tissue (many parrots, owls, *Buceros, Alcedo;* Newton, 1896). Glenny and Friedmann (1954) discussed the reduction or suppression of the clavicle in various birds (e.g., Australian parrots). According to Austin (1961) the scrub bird *Atrichornis* is the only passerine with noncoalesced clavicles (see Rich, et al., 1985). The clavicles are absent in all ratites except for the emu (Elzanowski, 1989).

Fürbringer (1888) describes subcoracoid, acrocoracoid, and supracoracoid segments of the clavicle, the last extending to the scapula, and presented a summary of the form of the clavicle. See Stegmann (1964) for the functional implications of the configuration of the clavicle. Jenkins, et al. (1988) have observed cineradiographically movements of the clavicle during flight. See **Arthr.** Annot. 85.

(163) **Apophysis furculae [Hypocleideum].** Synonymy: Lamina interclavicularis. In most birds the ventral part of the Furcula is drawn out into a median projecting blade, rod, or knob that is attached to the Apex carinae directly or indirectly (see **Arthr.** Annot. 85). Fürbringer (1888) describes three varieties of the **Proc. interclavicularis,** one of which projects proximally into the angle formed by the junction of the two furcular rami.

(164) **Extremitas omalis claviculae [Epicleidium].** Synonymy: Extremitas scapularis. (Omos, Gk. shoulder). This is the dorsal expanded end of each clavicle at the shoulder (see below, Annot. 165; and **Topog.** Annot. 32).

(165) **Proc. acromialis claviculae; Proc. acrocoracoideus claviculae.** Clavicles of certain birds possess distinct processes for articulation with the cranial tip of the scapula (Proc. acromialis) and the upper, pointed end of the coracoid bone (Proc. acrocoracoideus). In diomedeids, ciconiiforms, and falconiforms only the caudally directed Proc. acromialis of the clavicle is well developed. Both processes are present, e.g., in *Alcedo, Merops, Ramphastos,* and *Sturnus* (Fürbringer, 1888).

(166) **Scapula.** See Fürbringer (1888) for additional terms and comparative descriptions of the avian scapula not listed here. His illustrations depict the range of shapes of avian scapulae. **Facies lateralis.** Synonymy: Facies externa or dorsolateralis of the scapula. **Facies medialis [costalis].** Synonymy: Facies interna or ventromedialis of the scapula.

Acromion. (Omion, Gk. small shoulder). The pointed cranial end of the scapula, near its glenoid process. In *Menura* and *Atrichornis* (passerine suborder Menurae) the acromion is bifurcate, having two blunt knob-like processes (Rich, et al., 1985).

Crista lig. acrocoracoacromiali. In some birds this short crest on the dorsum of the acromion is continuous with the dorsal margin of the scapula; for attachment of the acrocoracoacromiale ligament (Fig. 4.10; **Arthr.** Annot. 95). The crest is pronounced, e.g., in *Cathartes, Ardea, Branta, Phoenicopterus,* and *Columba.*

(167a) **Facies articularis humeralis.** Synonymy: Pars scapulae fossae glenoidalis; Pars coracoidea fossae glenoidalis (Fürbringer, 1888). The humeral articular facet of the glenoid process of the scapula adjoins the humeral articular facet of the glenoid process of the coracoid, the two surfaces together forming the **Cavitas glenoidalis** for articulation with the head of the humerus. The coracoid generally contributes much the larger area to the humeral articular surface (e.g., *Strix varia*). The slightly concave articular facets of both bones are invested with the thick elastic cartilage (J. Baumel and R. Brown, pers. obs.), Lig. coracoscapulare interosseum, with which the humerus actually articulates; the elevated margins (labra) of this ligament deepen the shallow glenoid cavity (**Arthr.** Annot. 93).

(167b) **Proc. glenoidalis scapulae.** Set off somewhat perpendicular to the body of the scapula, the glenoid process of the scapula bears the surface for articulation with the head of the humerus; the glenoid process in certain birds also articulates directly with the procoracoid process of the coracoid. See Fig. 4.10.

Proc. glenoidalis coracoidei. This is the low, lateral offset of the shaft of the coracoid bone that bears the humeral articular surface, usually continuous with the base of the procoracoid process.

(168) **Facies articularis coracoidea.** Linear articular surface on the cranial extremity of the scapula extending between the acromion and the glenoid process; forms a joint with the procoracoid and adjacent glenoid process of the coracoid bone.

Tuberculum coracoideum. Some birds (e.g., *Ardea, Larus, Branta*) possess this convex spherical or ellipsoidal boss of the cranial surface of the Proc. glenoidalis of the scapula; the Tuberculum fits into a cupped surface on the coracoid together forming the coracoscapular joint (see Fig. 4.10; and below, Annot. 173b). The

coracoscapular joint surfaces in most birds are less elaborate than those just described (see above paragraph).

(169) **Tuberculum m. scapulotricipitis.** In some birds this distinct tubercle for attachment of the scapulotriceps muscle is located on the ventral border of the scapula directly caudal to its Proc. glenoidalis (Fig. 4.10).

(170) **Corpus scapulae.** The neck **(Collum scapulae)** and cranial half of the body (Corpus) of the scapula is generally a rounded cylinder in cross section; its caudal half is flattened and usually blade-like, straight, or curved. The caudal half of the atypical scapula of penguins (spheniscids) is a wide paddle-shape.

(171a) **Extremitas omalis coracoidei.** The shoulder or dorsal end of the coracoid bone (Omos, Gk. shoulder).

Proc. acrocoracoideus. (Acro-, Gk. combining form, an extremity or highest point of a structure). This is the dorsal end of the coracoid bone that projects past its glenoid process.

(171b) **Tuberculum brachiale.** Synonymy: Tuber brachialis (Ballmann, 1969a); Tuberositas brachialis (Lambrecht, 1933; Howard, 1929); Tuberositas humeralis. This term refers to the low projection on the medial side of the acrocoracoid process of the coracoid of some forms which is directed ventrally, overhanging the supracoracoid sulcus to some degree. In the birds in which it exists, the tuberculum is the attachment of the acrocoraco-acromial ligament which forms part of the medial wall of the triosseal canal (Annot. 177) in some birds. Although "Tuberculum brachialis" (sic) is used frequently in avian paleontology, it is not descriptively apt, as the tubercle has no direct relationship to the brachium or humerus.

(172) **Proc. procoracoideus** (Sabatier, 1880). Synonymy: see Fürbringer (1888: 41). This is a projection of the medial border of the coracoid, its upper edge roughly perpendicular to the coracoid shaft, its medial border gradually merging with the shaft ventrally. In some birds its tip is curved abruptly dorsally forming the medial boundary of the smoothly curved Sulcus supracoracoideus. See **Arthr.** Annot. 87, 97.

Sulcus supracoracoideus (Ballmann, 1969a). Groove for the tendon of M. supracoracoideus on the base of Proc. procoracoideus and adjacent part of the upper shaft of the coracoid bone that forms a pulley for the tendon of M. supracoracoideus (Fig. 4.10).

(173a) **Facies articularis scapularis.** In some birds this narrow, linear facet is on the internal surface of the upper edge of the procoracoid process, and is prolonged laterally onto the base of Proc. glenoidalis (Annot. 168); the continuous surface makes contact with a corresponding surface on the scapula, producing a simple coracoscapular joint (**Arthr.** Annot. 93). Other birds possess a more complicated joint (see Annot. 173b).

(173b) **Cotyla scapularis.** Synonymy: Facies scapularis (Ballmann, 1969a). Occurring in some birds (e.g., *Ardea, Larus, Branta*), this is the spherical or ellipsoidal concavity on the glenoid process/procoracoid process of Os coracoideum adjacent to its glenoid facet (Fig. 4.10). The cotyla receives the corresponding Tuberculum coracoideum of the scapula, the two forming the coracoscapular joint (**Arthr.** Annot. 93). In most birds the joint surfaces of the coracoscapular joint are less elaborate than those described here (see Annot. 168 and 173a). The Cretaceous birds *Ambiortus* and *Apatornis* exhibit the Cotyla/Tuberculum type of coracoscapular joint that Martin (1987) considers primitive for modern birds.

(174) **Linea intermuscularis ventralis** (Lambrecht, 1933). Synonymy: anterior intermuscular line (Fisher, 1945). These intermuscular lines on the coracoid are illustrated by Ballmann (1969a). See **Myol.** Annot. 74, 76.

(175a) **Crista articularis sternalis.** This surface of the coracoid for articulation with the sternum is divided into ventral and dorsal facets (**Facies externa and F. interna**). In some birds (e.g., *Ardea, Columba, Corvus*) they are not continuous with one another. The margins of each of the facets are sharply defined where they meet the superficial and deep surfaces of the coracoid. The external and internal articular facets are set off from one another by a slightly curved ridge **(Crista intermedia)** that articulates with a corresponding groove at the bottom of the coracoidal articular sulcus of the sternum. In some birds the sternal articular facets of the coracoid are subdivided into medial and lateral parts by a non-articular segment. See **Arthr.** Annot. 89, 90.

(175b) **Facies articularis intercoracoidea.** Articular facet located on the medial angle of the sternal end of the coracoid in birds whose coracoids articulate with one another in the median plane. See Annot. 160; **Arthr.** Annot. 90.

(176) **Proc. lateralis.** Synonymy: Proc. lateralis posterior; Proc. externus; Proc. sternocoracoideus. In many birds this process of the sternal end of the coracoid is drawn out into a point, the **Angulus lateralis.** The upper border of the lateral process is known as the **Margo supra-angularis** (E. N. Kurochkin, pers. comm.).

(177) **Canalis triosseus.** Synonymy: Foramen triosseum; Canalis supracoracoideus (Fürbringer, 1888). The canal transmits, and serves as a pulley for, the tendon of M. supracoracoideus. In some birds the canal is produced by only two bones, the procoracoid process of the coracoid and the scapula, with no contribution from the clavicle; the canal may be formed completely by the coracoid alone in birds having an ossified bridge connecting the acrocoracoid and procoracoid processes (e.g., Musophagidae, Meropidae, Upupidae, Bucerotidae, *Columba livia,* and trochilids). See **Arthr.** Annot. 87, 95, 171.

(178) **Ossa alae [Ossa membri thoracici].** Bones of the wing or thoracic limb. Terms of direction of the wing bones are based on the defined anatomical position of the avian wing, i.e., extended and abducted (see **Gen. Intro.**). In this anatomical position the extensor (dorsal) aspect of the humerus faces caudally and the flexor (ventral or palmar) aspect faces cranially. The long axis of the ellipsoidal articular surface of the Caput humeri is nearly vertical with the wing outstretched (Fürbringer, 1888); the epicondyles at the distal end of the humerus are situated dorsally and ventrally.

Of special interest to paleontologists is the work of Ballmann (1969a) which contains a comprehensive terminology for all the skeletal elements of the wing, including attachments of ligaments and muscles. See also Komárek (1979).

Humerus. Consult Fürbringer (1888) for a synonomy of terms on parts of the humerus. **Facies caudalis** of the humerus is also known as its anconal surface; **Facies cranialis** is also known as its volar or palmar surface.

(179) **Caput humeri.** Synonymy: Caput articulare humeri (Fürbringer, 1888). The head of the proximal end of the humerus, specifically its articular surface.

(180) **Incisura capitis humeri.** Synonymy: capital groove (Howard, 1929); Incisura collaris. The pronounced notch of the head of the humerus, located between the articular surface of the Caput humeri and Tuberculum ventrale (Fig. 4.12A). With the

wing folded against the trunk, the incisure accommodates the scapular labrum of Cavitas glenoidalis.

Crista incisurae capitis. The crest or ridge of bone that connects the head of the humerus with the ventral tubercle; the crest separates the proximal end of the incisure of the head of the humerus from the Sulcus transversus (see Annot. 185).

(181) **Planum intertuberculare** (Fürbringer, 1888). Synonymy: Planum [Facies] bicipitale. The intertubercular plane refers to much of the cranial surface of the expanded proximal end of the humerus distal to its Caput, i.e., the area between the dorsal and ventral tubercles and part of the surface between the bicipital and deltopectoral crests. Features included in this plane are: Sulcus transversus, Impressio coracobrachialis, and Intumescentia humeri. The Planum in most birds is covered by the tendon and aponeurosis of origin of M. biceps brachii.

Sulcus [Canalis] n. coracobrachialis. In many different birds this is a shallow transverse groove at the distal margin of the intertubercular plane of the humerus (see above) which conducts N. coracobrachialis from the distal end of the bicipital crest to the ventral border of the Impressio coracobrachialis (Fig. 4.12).

Characteristic of charadriiforms (Ballmann, 1979), the nerve is transmitted by an osseous canal deep to the distal part of the surface of the Intumescentia humeri.

(182) **Tuberculum dorsale.** Synonymy: Tuberculum minus or laterale; Tuberculum m. supracoracoidei. Located at the proximal end of the deltopectoral crest, for insertion of the principal part of the tendon of M. supracoracoideus. See Fig. 4.12; Annot. 183.

(183) **Crista m. supracoracoidei** (Fürbringer, 1888). This crest is an accessory insertion of the tendon of the supracoracoideus muscle, its main insertion being the Tuberculum dorsale. The crest extends distally from the Tuberculum to the base of Crista deltopectoralis. Well displayed in examples of phasianids, alcids, psittacids, and columbids. See Annot. 182.

(184) **Crista deltopectoralis.** Synonymy: Crista deltoidea; Crista pectoralis; Crista tuberculi minoris, or lateralis, or dorsalis. "Crista deltopectoralis" is used in the paleontological literature (e.g., Ostrom, 1979), and is a reasonable name inasmuch as both M. pectoralis and the cranial head of M. deltoideus major are attached to opposite surfaces of the crest.

Crista bicipitalis. Synonymy: Crista tuberculi majoris, or medialis, or ventralis. Origin of the aponeurosis of the humeral head of M. biceps brachii.

(185) **Sulcus transversus** (Lambrecht, 1933). Synonymy: Ligamental furrow (Howard, 1929). Located on the cranial surface of the humerus just distal to Caput humeri (Fig. 4.12); for attachment of the Lig. acrocoracohumerale. The sulcus is strongly defined in, e.g., *Larus*.

(186) **Impressio coracobrachialis.** An impression for insertion of M. coracobrachialis cranialis. The impression is a fairly distinct shallow excavation in many birds, e.g., *Branta, Chordeiles, Aegolius, Crotophaga;* a deeply etched triangular fossa in larids and charadriids (Fürbringer, 1888).

(187) **Tuberculum ventrale.** Synonymy: Tuberculum mediale or majus (Fürbringer, 1888). The ventral tubercle of the humerus is continuous with the proximal end of Crista bicipitalis (Fig. 4.12), and is much stronger than Tuberculum dorsale. The ventral tubercle is extraordinarily prominent in ratite birds (Fürbringer, 1888); it is a common point of insertion of several of the short muscles of the shoulder region arising from the scapula and coracoid.

(188) **Fossa pneumotricipitalis [Fossa tricipitalis].** Synonymy: Fossa pneumoanconaea (Fürbringer, 1888); Fossa pneumatica. This excavation in the proximal humerus varies in its form and development in different avian groups. Its name indicates that parts of the triceps muscle complex and the pneumatic foramen of the humerus are housed in the fossa. The name M. triceps brachii has replaced the term M. anconaeus, requiring a change in Fürbringer's name of the fossa. The humerus is hardly, or not at all, pneumatic in some avian groups (Fürbringer, 1888) (e.g., *Gavia, Pygoscelis, Alca*); in the forms having apneumatic humeri the fossa is present nonetheless, thus "Fossa tricipitalis" is appropriate as suggested by Fürbringer's term, Fossa anconaea.

Well developed pneumotricipital fossae extend into the Caput humeri and Tuberculum ventrale (e.g., *Larus*). In most birds the fossa is a single continuous excavation, bounded ventrally and dorsally by **Crus ventrale fossae** and **Crus dorsale fossae** (Fig. 4.12) which converge on the apex of the ventral tubercle. The single fossa is occupied by both heads of M. humerotriceps, the insertion of M. scapulohumeralis cranialis and the pneumatic foramen. See **Myol.** 71-74, 82).

In other birds (also well exemplified by *Larus*) a second or additional fossa is formed between the Crus dorsalis fossae (medial bar of Bock (1962); Crista coracoidea of Komárek (1979) and the Caput humeri. This second fossa is bounded dorsally by the **Margo caudalis** of the humerus (Fig. 4.12) that extends from the Caput distally onto the caudal aspect of the shaft of the humerus; the Margo caudalis is a pronounced ridge in many birds, lacking in others. The second fossa is occupied by the dorsal head of M. humerotriceps. Consult Bock (1962) for a comprehensive treatment of this topic in passerine birds; see below, Annot. 189.

(189) **Foramen pneumaticum.** When present, this foramen (or multiple foramina) is located in the Fossa pneumotricipitalis of the humerus (Annot. 188). The pneumatic foramen is not found in the humeri of all birds; humeri of birds with dual fossae generally are not pneumatised. The pneumatic foramen is lacking in: penguins, procellariiforms (except albatrosses), loons, grebes, cormorants and anhingas, several tribes of ducks (mainly the diving ones); most charadriiforms, rallids, and many oscine passerines (S. Olson, P. Ballmann, pers. comms.).

(190) **Intumescentia humeri.** Term used by Fürbringer (1888) and Buri (1900) for the convex, smooth swelling distal to, and continuous with, the intertubercular plane (Annot. 181) of the cranial aspect of the proximal end of the humerus; the intumescence is directly opposite Fossa pneumotricipitalis on the caudal side (see Fig. 4.12).

(191) **Sulcus n. radialis.** A distinct sulcus on the dorsal surface of the shaft of the humerus for N. radialis occurs only rarely: *Casuarius,* hummingbirds and swifts (Apodiformes).

(192) **Condylus dorsalis humeri.** Synonymy: Condylus [Trochlea] radialis, or medialis, or internus. With the limb in the anatomical position this condyle on the dorsal (radial) side of the distal end of the humerus articulates with both Radius and Ulna. **Condylus ventralis humeri.** Synonymy: Condylus [Trochlea] ulnaris, medialis, or internus; this condyle articulates only with the ulna (see **Arthr.** Fig. 5.4).

(193) **Incisura intercondylaris.** Synonymy: Vallis intertrochlearis (Fürbringer, 1888); Vallis intercondylica (Ballmann, 1969a). Notch separating the dorsal and ventral condyles of the humerus.

(194) **Epicondylus dorsalis. [Ectepicondylus];** Epicondylus radialis, or lateralis, or externus. **Epicondylus ventralis. [Entepicondylaris];** Epicondylaris ulnaris, or medialis, or internus (see Fig. 4.12; Annot. 178; **Myol.** Annot. 91, 92).

(195) **Proc. flexorius.** Process at distal end of humerus, ventral to Condylus ventralis of the distal humerus for attachment of the tendinous head of M. flexor carpi ulnaris (Ballmann, 1969a). See Fig. 4.12; **Arthr.** Annot. 110 (Trochlea humeroulnaris).

(196) **Tuberculum supracondylare dorsale.** Synonymy: Eminentia m. extensoris metacarpi radialis (E. N. Kurochkin, pers. comm). Most birds possess a relatively compact tubercle on the dorsal border of the distal humerus, a short distance from the dorsal epicondyle (Fig. 4.12) for the origin of M. extensor carpi [metacarpi] radialis (see **Myol.** Annot. 87). In some birds the Tuberculum is displaced distally, thus so close to the dorsal epicondyle that the two are nearly indistinguishable. In some birds (e.g., diomedids, charadriiforms, passeriforms) the muscle is attached to a stout, pointed **Proc. supracondylaris dorsalis.** Swifts and hummingbirds are unusual in having the tubercle for M. extensor carpi [metacarpi] radialis displaced far proximally on the humeral shaft (Zusi and Bentz, 1982). See **Arthr.** Annot. 141; **Myol.** Annot. 77, 78.

Tuberculum supracondylare ventrale. Attachment of Lig. collaterale ventrale of the elbow joint (**Arthr.** Annot. 105).

(197) **Proc. cotylaris dorsalis.** Prominent dorsal extension of the proximal Ulna that bears the Cotyla dorsalis on its cranial surface and Impressio m. scapulotriceps on its dorsal surface.

(198) **Cotyla dorsalis; Cotyla ventralis.** Synonymy: Cotyla externa/interna (Lambrecht, 1933); Facies glenoidalis externa et interna (Ballmann, 1969a). The concave articular surfaces of the ulna for the dorsal and ventral condyles of the humerus. The ventral cotyla is the larger of the two, and is located at the base of the Olecranon (see above and Fig. 4.13).

(199) **Incisura radialis.** Synonymy: Depressio radialis proximalis (Howard, 1929; Ballmann, 1969a). The concave facet on the proximal ulna for articulation with Caput radii; situated just past the distal margin of Cotyla dorsalis (Fig. 4.12).

(200) **Sulcus scapulotricipitalis.** Synonymy: Sulcus m. scapulotricipitis; Sulcus dorsalis m. tricipitis. **Sulcus humerotricipitalis.** Synonymy: Sulcus m. humerotricipitis; Sulcus ventralis m. tricipitis. Located on the dorsal aspect of the distal humerus, the sulci for the two tendons of the triceps brachii complex are separated by a low ridge; the Sulcus humerotricipitalis is the larger of the two.

(201) **Olecranon.** Synonymy: Proc. coronoideus ulnaris (Lambrecht, 1933). Strong, pointed process of the proximal end of the ulna for attachment of M. humerotriceps and Trochlea humeroulnaris (**Arthr.** Annot. 110). Barnett and Lewis (1958) note that the olecranon is lacking in some birds, e.g., the swift *Micropus,* the penguin *Aptenodytes;* however this process appears to be replaced by sesamoid bones in the tendons of the triceps muscles in these forms. See Annot. 202.

(202) **Os sesamoideum m. scapulotricipitis.** Synonymy: Patella ulnaris (Fürbringer, 1888). This is a sesamoid bone in the tendon of M. scapulotriceps of some species; unusually well developed in the hummingbirds (Zusi and Bentz, 1984) and in spheniscids.

(203) **Tuberculum lig. collateralis ventralis** (Fig. 9). Synonymy: Facies lig. interni (Ballmann, 1969a). Point of attachment to the ulna of the ventral collateral ligament of the elbow joint (see Fig. 4.13).

Sulcus tendinosus. In some birds this sulcus is a well delineated feature on the ventral surface of the proximal Ulna, located between the Olecranon and the edge of the ventral cotyla; the tendon of M. flexor carpi ulnaris glides in this sulcus, separated from the sulcus by part of Trochlea humeroulnaris (see **Arthr.** Fig. 5.4).

(204) **Facies corporis ulnae.** Of the three surfaces of the body of the ulna, **Facies caudodorsalis** is subcutaneous; the caudodorsal surface is separated from **Facies caudoventralis** by the row of Papillae remigiales caudales (Annot. 205). **Facies cranialis** is shallowly concave; its proximal half exhibits pronounced intermuscular crests in some of the larger birds. The flattened ulna (and radius) in spheniscids possesses only dorsal and ventral surfaces.

(205) **Papillae remigales caudales; Papillae remigales ventrales.** Synonymy: Papillae ulnares anconales (Lambrecht, 1933); quill knobs (Edington and Miller, 1941). Markings on the ulna for attachment of the ligaments of the follicles of the secondary flight feathers. See Fig. 4.13; and **Arthr.** Annot. 199, 204.

(206) **Condylus dorsalis ulnae.** Synonymy: Condylus externus or caudalis. **Condylus ventralis ulnae.** Synonymy: Condylus internus, or cranialis, or metacarpalis. As a result of the torsion of the ulnar shaft, the dorsal condyle is located somewhat more caudally than the ventral condyle. At the distal end of the ulna the two condyles and the groove between them form the **Trochlea carpalis.** On the ventral surface of the distal ulna the trochlea is markedly deepened in some birds (e.g., *Phoenicopterus*) forming the **Sulcus intercondylaris** (Fig. 4.13) between the two condyles. Os carpi radiale and Meniscus intercarpalis articulate with both condyles; Os carpi ulnare articulates mainly with the dorsal condyle. See **Arthr.** Annot. 117-119.

(207) **Tuberculum carpale.** Synonymy: Tuberositas carpalis (Lambrecht, 1933). The carpal tubercle is a conspicuous, in some birds pointed, process (e.g., *Larus*) on the ventral aspect of the distal end of the ulna, closely related to the ventral condyle of its trochlea, for the attachment of the Lig. ulno-ulnocarpale distale and Lig. ulnometacarpale ventrale (see Fig. 4.13).

Incisura tuberculi carpalis (new term). This notch between the ventral condyle of the ulna and the Tuberculum carpale is pronounced in some forms (e.g., the vultures *Cathartes* and *Coragyps*); in these forms the notch contains pneumatic pores. The deep part of Lig. ulno-ulnocarpale distale occupies much of the incisura (*Columba*).

(208) **Depressio radialis.** Synonymy: Depressio radialis distalis (Lambrecht, 1933; Ballmann, 1969a); Sulcus radialis (NAA, 1979). This surface of the distal end of the ulna is involved in the distal radioulnar joint, the counterpart of the proximal radioulnar joint. Located on the dorsal surface of the ulna near the carpal tubercle, this surface is the ulnar attachment of Lig. interosseum radioulnare which prevents direct contact of the two bones; the radius glides against the ligament in flexion and extension of the wrist joints. See Fig. 4.12; **Arthr.** Annot. 116.

(209) **Incisura tendinosa** (Lambrecht, 1933; Ballmann, 1969a). Situated on the distal end of the ulna near its dorsal condyle, the curved Incisura acts as a pulley for the tendons of Mm. extensor metacarpi ulnaris and extensor digitorum communis as they change direction and enter the manus. The tendons are held in the incisure by a fibrous retinaculum (ossified in *Gavia*). See Fig. 4.13.

(210) **Tuberculum bicipitale radii** (Howard, 1929). Synonymy: Tuberculum externum (Lambrecht, 1933). Tubercle on the proximal radius for insertion of M. biceps brachii. In most birds the tendon of M. biceps brachii bifurcates, the main branch inserting on the proximal end of the radius, the other to the proximal ulna **Tuberculum bicipitale ulnae** (Berger, 1966). In the higher passeriforms the radial tendon of the biceps inserts into a fovea (pit), considered by Ballmann (1969a) to be a diagnostic feature. See Fig. 4.13.

(211) **Facies articularis radiocarpalis.** Synonymy: Articulatio scapholunaris (Lambrecht, 1933). Surface on the distal radius for articulation with Os carpi radiale. **Facies articularis ulnaris.** The distal ends of radius and ulna do not directly articulate; the two are closely related but separated by Lig. radioulnare interosseum (see Annot. 208; and **Arthr.** Annot. 116).

Sulcus tendinosus. A single wide groove, or two parallel grooves (e.g., gaviiforms, McKitrick, 1991), on the dorsum of the distal end of the radius occupied by tendons of extensor muscles of the wrist joint passing across the carpus into the hand.

(212) **Depressio ligamentosa.** Synonymy: ulnar depression (Howard, 1929). Located on the caudal surface of the distal radius this depression is occupied by the Lig. interosseum radioulnare distale (see Annot. 208; and **Arthr.** Annot. 116).

(213) **Tuberculum aponeurosis ventralis.** Synonymy: Ligamental process (Howard, 1929). The Tuberculum is located on the distal end of the radius ventral to the articular surface for Os carpi radiale. The tubercle serves as the attachment of the Aponeurosis ventralis that fans out onto the remiges in the wrist region (**Arthr.** Annot. 113 and Fig. 4.13).

(214) **Ossa carpi.** Recently Hinchliffe (1985) has restudied the embryological development of the carpal bones and metacarpals in *Gallus*, using more precise techniques than those of earlier works. He contends that of the five embryonic carpal elements, the "radiale" becomes the definitive Os carpi radiale. The embryonic "ulnare" regresses and disappears; it is replaced by carpal 'x'. The "pisiform", however, becomes Os carpi ulnare, the definitive adult proximal carpal bone; the latter name is retained because of familiarity.

In early postnatal life the three remaining carpals become incorporated with the proximal ends of the metacarpals, forming the compound bone, the Carpometacarpus. For details of the development of the avian wrist and hand and homologies of the digits see Steiner (1922), Montagna (1945), Holmgren (1955), Romanoff (1960), Berger (1966), Seichert and Richter (1972), and Hinchliffe (1985). See **Osteo.** Intro. "Nomenclature of digits of wing"; and **Arthr.** Annot. 112, 122, 128.

(215) **Os carpi ulnare** (**Arthr.** Annot. 112, 122). Synonymy: Os cuneiform (Lambrecht, 1933); ulnare. U-shaped carpal bone in the caudal angle of the wrist region; unusual triangular-shaped in spheniscids. **Crus longum et Crus breve.** These are the two limbs of Os carpi ulnare; Crus longum is situated ventrally, Crus breve dorsally. **Proc. muscularis.** At the proximal end of the Os carpi ulnare the muscular process projects from the body of the ulnare that connects its two crura; M. flexor carpi ulnaris, Retinaculum ulnocaroremigiale and Lig. humerocarpale attach to the muscular process. See **Myol.** Annot. 85.

Incisura metacarpalis is the U-shaped notch between the two crura of Os carpi ulnare which clasp the proximal end of the Carpometacarpus. **Facies articularis metacarpalis** is the surface of the Os carpi ulnare that articulates with the caudal part of the Trochlea carpalis of the Carpometacarpus.

Os carpi radiale. Synonymy: Os scapholunare (Lambrecht, 1933). On the cranial aspect of the wrist, the radial carpal bone articulates with the distal end of the radius, carpal trochlea of the distal ulna, and the **Trochlea carpalis** of the Carpometacarpus (see **Arthr.** Annot. 112, 122).

(216) **Os metacarpale alulare.** Synonymy: Metacarpus pollicis; Proc. metacarpalis pollicis [digiti I or II]. See **Osteo.** Intro. for remarks on the nomenclature of digits of the manus.

Extremitas proximalis carpometacarpi. The proximal end of this compound bone is formed by ankylosis of some of the distal carpal bones with the fused proximal ends of the three metacarpal bones (see Annot. 214).

Os prominens. Sesamoid bone in the propatagial ligament (see **Arthr.** Annot. 141) near its attachment to the extensor process of the carpometacarpus; it is *not* a carpal bone, but is listed with the carpals because of its topographic proximity to them. Os prominens occurs, e.g., in buteos, falconids, and strigids.

(217) **Fovea carpalis caudalis.** Synonymy: Fossa carpalis posterior; **Fovea carpalis cranialis.** Fossa carpalis anterior (Ballmann, 1969a). The foveae are located at the cranial and caudal ends of the articular surfaces of Trochlea carpalis of the Carpometacarpus (Fig. 4.14). With the wrist joint in extension, the edge of the Os carpi radiale fits into the Fovea cranialis; with the joint flexed the Fovea caudalis accommodates the distal edge of the Os carpi ulnare.

(218) **Fossa infratrochlearis.** Synonymy: Fossa carpalis interna (Ballmann, 1969a). The depressed area of attachment of the Lig. radiocarpo-metacarpale ventrale at the proximal end of the ventral side of the Carpometacarpus. See Fig. 4.14; and **Arthr.** Fig. 5.5.

(219) **Fossa supratrochlearis.** Synonymy: Facies ligamentalis externa (Ballmann, 1969a). At the proximal end of the dorsal side of the Carpometacarpus this is the depression for attachment of the dorsal ulnocarpo-metacarpal ligament. See Fig. 4.14; and **Arthr.** Fig. 5.5.

(220) **Proc. pisiformis.** Synonymy: Apophysis pisiformis (Lambrecht, 1933). Stubby process of the ventral surface of the proximal end of the Carpometacarpus (Fig. 4.14); serves for attachment of the Retinaculum flexorum, and as a pulley changing the direction of the tendon of M. flexor digitorum profundus.

(221) **Proc. intermetacarpalis** (Milne-Edwards, 1867-71). Synonymy: Tuberositas muscularis (Ballmann, 1969a). This is a process of the major metacarpal bone that projects caudally overlapping, and often fusing with, the dorsum of the minor metacarpal bone (Fig. 4.14); it receives the insertion of M. extensor metacarpi ulnaris. Not present in all birds, it occurs in examples of galli-, pici-, coracii-, and passeriform birds, as well as coliiforms (Ballmann, pers. comm.).

Protuberantia metacarpalis (new term). Synonymy: carpometacarpal process (Harrison, 1968); carpometacarpal protuberance (Feduccia and Olson, 1982). In certain birds the cranial border of the major metacarpal bone bears this hump-like process at about its middle, e.g., in the oscine passerines *Menura* and *Chlamydera*

(Feduccia and Olson, 1982); in yet other passerines, *Progne* and *Sturnus* (pers. obs.), the protuberance is situated farther distally than the above examples.

(222) **Symphysis metacarpalis proximalis/distalis** (Lambrecht, 1933; Ballmann, 1969a). The regions of ankylosis of the proximal and distal ends of the major and minor metacarpal bones to one another in early postnatal maturation. These so-called "symphyses" are in reality synchondroses which when ankylosed become synostoses. See **Arthr.** Annot. 129.

(223) **Sulcus interosseus.** Longitudinal groove on the dorsal aspect of the region of the distal metacarpal symphysis (Fig. 4.14); the sulcus is occupied by tendons of Mm. interossei.

(224) **Ossa digitorum manus.** The most common phalangeal formula of birds: one alular phalanx, two phalanges of Digitus major, and one phalanx of Digitus minor. In a number of avian orders the alular digit possesses two phalanges, the terminal phalanx often bearing a claw (hoatzins and turacos, R. W. Storer, pers. comm.); Digitus major often has a third phalanx in anatids (R. W. Storer, pers. comm). See **Integ.** Annot. 87 for comment on supernumerary digital claws (phalanges); **Arthr.** Annot. 137.

(225) **Pila cranialis phalangis.** This is the thickened leading edge of the large proximal phalanx of Digitus major that forms a strong reinforcing bar of bone (Fig. 4.14). The caudal border of the phalanx is thin and fenestrate in some avian taxa.

(226) **Os coxae** (Coxa, L. hip). Each hip bone is formed by the postnatal ankylosis of Ilium, Ischium, and Pubis. The **Pelvis** is formed by consolidation of the two hip bones with the synsacrum (see **Arthr.**).

Acetabulum. The socket in the Os coxae into which the head of the femur fits. **Foramen acetabuli.** The opening in the floor of the Acetabulum varies in size in different birds. See **Arthr.** Annot. 151.

(227) **Foramen obturatum.** This oval opening situated caudoventral to the Acetabulum transmits the tendon of M. obturatorius medialis and N. obturatorius. The foramen is the detached cranial part of Fenestra ischiopubica (Boas, 1933). See Fig. 4.15; Annot. 252.

(228) **Sulcus obturatorius.** Long, wide, shallow groove on the medial surface of Ala ischii. M. obturatorius medialis lies in the Sulcus as well as on the adjacent medial surface of the pubis and Membrana ischiopubica.

(229) **Fenestra ischiopubica.** Synonymy: Foramen obturatorium, pars caudalis; Foramen oblongum. This gap between the shaft of the pubis and the ischium is of variable shape: from slit-like to elongated oval or triangular; very wide in some forms, e.g., *Gavia, Diomedea, Dendrocopus;* it is open at its caudal end in *Apteryx.*

(230) **Foramen ilioischiadicum.** Situated just caudal to the acetabulum, the foramen is bounded dorsally by the ilium and ventrally by the ischium (Fig. 4.15). The foramen transmits the ischiadic nerves and vessels (**Arthr.** Mem. ilio. isch.). Generally round or short oval shape; at its caudal end the foramen is incompletely enclosed by bone in tinamous and *Apteryx,* and extends caudally most of the length of the postacetabular ilium in *Rhea, Struthio,* and *Casuarius.*

(231) **Incisura marginis caudalis** (Fig. 4.9). In lateral view the caudal border of the hip bone (Os coxae) of many birds is indented between Spina dorsolateralis ilii and the tip of Proc. terminalis ischii; this notch is in the region of the ilioischiadic synostosis (see Annot. 230; and **Arthr.** 148).

Proc. marginis caudalis. Synonymy: Spina iliocaudalis (Boas, 1933). This projection of the caudal margin of the Os coxae of the pelvis between Spina dorsolateralis ilii and the Proc. terminalis ischii is present in some birds (e.g., *Gallus, Ardea*); not to be confused with the Spina dorsolateralis ilii itself (see Annot. 249).

(232) **Antitrochanter.** Located caudodorsal to the Acetabulum, this projection of Os coxae bears an articular surface which is in contact with the neck and trochanter of the Femur; formed mainly by the ischium and to a lesser degree by the ilium.

Sulcus antitrochantericus (Fig. 4.15). Usually a relatively narrow groove dorsal to the Antitrochanter which is the caudal prolongation of the extensive, shallow Fossa iliaca dorsalis of the preacetabular ilium. The sulcus is especially prominent in loons (R. W. Storer, pers. comm).

(233) **Crista iliosynsacralis.** A median ridge formed by fusion of the right and left dorsal iliac crests with the Crista dorsalis of the synsacrum (see Annot. 143, and below, Annot. 234).

(234) **Sulcus iliosynsacralis.** In birds in which the dorsal synsacral crest and the dorsal iliac crests remain separate a furrow, the iliosynsacral sulcus, is present on each side of the synsacral crest; the Sulcus contains epaxial muscles. This condition is seen for example in *Columba, Ceryle, Corvus.*

Canalis iliosynsacralis (Fig. 4.15). Synonymy: Canalis iliosacralis (Nauk, 1938); subiliac space (Howard, 1929); canalis ilioneuralis (Shufeldt, 1888). Paired canals occur in the pelvis of birds having an iliosynsacral crest (Annot. 233) (see Komárek, 1979, for illustrations). The paired canals are separated by the dorsal synsacral crest; each is roofed dorsally by the Ala preacetabularis of the ilium; the ventral wall of each canal is the Lamina transversa of the synsacrum (Annot. 141). The canal contains epaxial muscles, occurring, e.g., in *Diomedea, Cathartes, Strix, Gallus, Branta, Phoenicopterus.*

(235) **Concavitas infracristalis.** The shallow, wide depression on the lateral surface of the pelvis caudal to the ilioischiadic foramen in many birds; formed largely by the infracristal lamina of the ilium (Annot. 251). The depth of the concavity is exaggerated by the overhanging Crista dorsolateralis ilii (Fig. 4.15). M. ischiofemoralis arises from this surface. Consult Boas (1933).

(236) **Pila ilioischiadica.** This is the reinforcing pillar of bone along the ventral border of each side of the pelvis extending from the level of the cranial end of the Fossa renalis toward Proc. terminalis ischii. The cranial part of the Pila forms Crista iliaca obliqua (Annot. 242); caudally it contributes to the ventral acetabular wall and ilioischiadic foramen, merging with Ala ischii. See Fig. 4.9.

(237) **Fossa renalis** (Fig. 4.9). The Fossa renalis is the paired deep fossa on each side of the Corpus synsacri which accommodates the kidney; formed partly by the Synsacrum and partly by the Os coxae (mainly ilium). In general, the cranial division of the kidney is not housed in the fossa, but occupies the shallow depression on the ventral surface of the preacetabular ilium.

Pars ischiadica fossae is the smaller cranial part of the Fossa renalis that contains the middle division of the kidney and the ischiadic (lumbosacral) nerve plexus; the acetabular foramen is an opening in the side of Pars ischiadica.

Pars pudenda fossae is the larger, wider caudal part of the renal fossa that contains the caudal division of the kidney and the pudendal nerve plexus; the ilioischiadic foramen is an opening in the lateral wall of Pars pudenda. See Annot. 250; consult Radu (1975) for comparison of Fossa renalis in galliforms and anseriforms.

(238) **Incisura caudalis pelvis.** When viewed from its dorsal or ventral aspect, the intact bony pelvis of many birds demonstrates just past its Margo caudalis a wide, semilunar, or rectangular indentation, bounded on each side by the Spina dorsolateralis ilii (Annot. 248). The incisure is notably deep in falconiform, ciconiiform and strigiform pelves; its middle part is occupied by the basal part of the free caudal vertebral column; laterally it is completed by the iliocaudal membrane (**Arthr.** Annot. 185).

(239) **Corpus ilii.** This is the strongly developed central part of the Ilium, cranial and dorsal to the Acetabulum, from which its pre- and postacetabular alae (wings) emanate.

(240) **Incisura acetabularis.** The body of each of the three elements (ilium, ischium, and pubis) of the Os coxae contributes a segment of the circumference of the acetabulum; each part thus displays a C-shaped Incisura acetabularis prior to synostosis of the three elements (see **Arthr.** Annot. 146).

(241) **Pila postrenalis.** The transverse pillar of bone that strengthens the caudal border of the pudendal part of the renal fossa. Well exemplified in *Strix*, *Larus*, and *Columba*. See Annot. 250.

(242) **Crista iliaca obliqua** (Boas, 1933). The heavy oblique bar of bone that forms the ventrolateral border of Pars ischiadica of Fossa renalis; the Crista extends between the ventral surface of Ala preacetabularis ilii to the ventral wall of the Acetabulum (see Fig. 4.9; Annot. 236).

(243) **Crista iliaca intermedia** (Boas, 1933; synsacral strut, Strauch, 1985). Slightly developed in most birds. In some birds this transverse crest is formed on the ventral surface of Ala postacetabularis ilii, within the renal fossa, at the level of the acetabular foramen. The costal process(es) of the so-called true sacral or "acetabular" vertebrae (see Fig. 4.9 and Annot. 141) articulate with the medial end of the crest. The crest is well developed in most charadriiforms (Strauch, 1985); exhibited also, e.g., in *Morus*, *Cathartes*, and *Columba*. See **Arthr.** Annot. 76.

(244) **Tuberculum preacetabulare [Proc. pectinealis].** Synonymy: Proc. preacetabularis; Proc. prepubica. The name, Tuberculum preacetabulare (Boas, 1933), indicates its location at the ventrocranial margin of the acetabulum. It serves as the rear attachment of the Lig. inguinale (**Arthr.** Annot. 184) which bounds the neurovascular lacuna for the the external iliac vessels and branches of the lumbar nerve plexus. In most birds the Tuberculum is formed by the ilium, in ratites primarily by the pubis (Beddard, 1898). The Tuberculum preacetabulare is generally a stubby torus of bone; however, it is an elongated process in *Struthio*, tinamous, galliforms (Beddard, 1898), and the cuculiform *Geococcyx* (Larson, 1930). See Fig. 4.15.

(245) **Ala [Pars] preacetabularis ilii; Ala [Pars] postacetabularis ilii.** Synonymy: pre-ilium; post-ilium (Parker, 1888).

Crista iliaca dorsalis. Synonymy: Crista iliaca superior (Milne Edwards, 1867-71); Linea iliodorsalis (Lambrecht, 1933). The dorsal (or dorsomedial) border of the preacetabular ilium (see Fig. 4.15 and Annot. 234).

(246) **Areae articulares vertebrales.** Several areas of the ventral surface of the preacetabular ilium that articulate with the transverse processes of the cranialmost series of synsacral vertebrae. These areas can be seen only in immature birds in which the synsacrum and ilium may be disarticulated (see illustrations in Boas, 1933); most frequently the synsacrum and ilium are ankylosed (synostoses) in mature individuals.

(247) **Crista iliaca lateralis** (Milne-Edwards, 1867-71). **[Margo lateralis]** (NAA, 1979). In dorsal view this is the lateral free edge of the preacetabular ilium that in some birds forms a pronounced ledge (Fig. 4.9) (see Annot. 245).

(248) **Crista dorsolateralis ilii.** Synonymy: Crista dorsolateralis (Boas, 1933); Linea iliolateralis (Lambrecht, 1933); Crista iliaca dorsolateralis (NAA, 1979). Lateral ledge of the postacetabular ilium that marks the boundary between its dorsal and lateral surfaces; indistinct or lacking in some birds, e.g., in the pelecaniforms (*Morus*, *Pelecanus*) and anseriforms (*Branta*, *Athyia*). The crest serves as an attachment of the aponeurosis of origin of M. iliotibialis (see Fig. 4.15 and **Myol.** Annot 100).

Spina dorsolateralis ilii. Synonymy: Proc. iliolateralis (Boas, 1933); Spina iliaca dorsalis (NAA, 1979). This is the caudal prolongation of the Crista dorsolateralis ilii (Fig. 4.15). In *Columba* (Baumel, 1988) the base of the spine forms part of the pulley for change of direction of M. caudofemoralis as the latter enters the lower surface of the uropygium.

(249) **Fossa iliocaudalis.** This depression on the dorsal surface of the caudal part of the postacetabular ilium on either side of the caudal end of the synsacrum serves as a point of attachment of M. levator caudae (Fig. 4.15).

(250) **Recessus caudalis fossae.** Synonymy: Recessus iliacus (Boas, 1933); obturator depression (Harvey, et al., 1968). This is the recess of the renal fossa that invaginates the caudalmost junctional region of the postacetabular ilium and ischium. The recess is deep in *Gallus* and *Meleagris*, some strigids and gruiforms (e.g., *Gallinula*); it does not enclose part of the kidney, but is filled by the origin of M. obturator medialis (Butendieck, 1980). See Fig. 4.9 and Annot. 237.

(251) **Lamina infracristalis ilii** (Fig. 4.15). Synonymy: Superficies infracrista (Boas, 1933); Lamina ischiadica ilii (NAA, 1979). The vertical lamina of the postacetabular ilium just ventral to Crista dorsolateralis ilii; the lower margin of the Lamina ankyloses with the Ala ischii caudal to the Foramen ilioischiadica (exception: some ratites). See Annot. 235.

(252) **Proc. obturatorius** (Fig. 4.15). Synonymy: Proc. ventralis. This ventrally directed process of the ischium separates the obturator foramen from the ischiopubic fenestra; formed by ossification of Lig. ischiopubicum.

(253) **Proc. terminalis ischii.** Synonymy: Proc. terminalis ischiadicus (Boas, 1933); Angulus ischiadicus (Lambrecht, 1933). This process is the most caudal extent of the ischium, often pointed; its lower border articulates with the pubis (Fig. 4.15). See Annot. 231.

(254) **Pubis.** The shaft (**Scapus pubis**) of the rather delicate pubis of most birds closely parallels the ventral border of Ala ischii. The two are separated by the obturator foramen and the ischiopubic fenestra (see Fig. 4.15; Annot. 229). In some birds the free ends of the pubes curve inward and closely approximate one another.

(255) **Facies articularis antitrochanterica.** Synonymy: Articulatio iliacalis (Lambrecht, 1933); Facies glenoidea proximalis (Ballmann, 1969b). Articular surfaces located on the dorsal aspect of the Collum femoris and the medial surface of the Trochanter femoris. See Fig. 4.16; Annot. 232, 262; **Arthr.** Annot. 152.

(256) **Trochanter femoris.** Synonymy: Trochanter major. On the proximal end of the femur this structure is the elevated, expanded part of the femur continuous with its neck (Annot. 257). Ametov (1971) observed that certain saltatorial birds (e.g., *Passer domesticus, Parus major,* and *Sitta europaea*), birds that progress by leaping, lack the femoral trochanter. See Fig. 4.16; **Arthr.** Annot. 182.

Fossa trochanteris. The concavity of the medial surface of the elevated trochanter of the femur; often deepened by the overhang of the **Crista trochanteris** (e.g., *Larus, Gallus, Phoenicopterus*).

(257) **Impressiones mm. trochanteris; Impressiones ligg. trochanteris** (Fig. 4.16). Markings on the lateral aspect of the Trochanter femoris for the obturator and iliotrochanteric muscles and certain ligaments which are detailed by Ballmann (1969b).

(258) **Corpus femoris.** The body or shaft of the avian femur is commonly circular in cross section; no sharply defined borders are present except in atypical femora (e.g., *Gavia*) which has a laterally compressed, truncated femur, somewhat quadrate in cross section.

(259) **Sulcus patellaris** (Fig. 4.16). Synonymy: Fossa patellaris (Lambrecht, 1933); rotular groove (Howard, 1929). Articular groove for the Patella at the distal end of the femur.

Crista lateralis/medialis sulci patellaris. The crests of the patellar sulcus are sharply defined in some taxa.

Condylus medialis; Condylus lateralis. These articular condyles of the distal femur are also known as Condylus internus and Condylus externus. See Annot. 261.

(260) **Impressiones ansae m. iliofibularis.** Synonymy: impressions of the biceps loop. The ligamentous ansa (L. loop) for M. iliofibularis has two femoral attachments: one on the caudal surface of the distal femur just proximal to the lateral condyle, the other a distinct scar on the cranial surface of the femur proximal to the lateral crest of the patellar sulcus; a third attachment is the fibula just distal to its neck. See Berger (1966); **Myol.** Annot. 102; **Arthr.** Annot. 186.

(261) **Trochlea fibularis** (Fig. 4.16). Synonymy: Sulcus fibularis. The spool-shaped joint surface on the lateral femoral condyle for articulation with the **Caput fibulae.** See **Arthr.** Fig. 5.7.

(262) **Crista tibiofibularis** (Howard, 1929). Synonymy: Crista peroneo-tibialis (Ballmann, 1969b). Crest on the lateral condyle of the femur that separates its tibial articular surface from that for the fibula; the Crista forms the medial wall of the Trochlea fibularis (see Annot. 261; and **Arthr.** Fig. 5.7; Annot. 154). See Fig. 4.16.

(263) **Impressio lig. cruciati caudalis/cranialis.** The impression for the caudal cruciate ligament is located on the caudal aspect of the distal end of the femur just proximal to the lateral condyle; the impression for the cranial cruciate ligament is farther distal, in the intercondylar sulcus (see Fig. 4.16 and **Arthr.** Fig. 5.7).

(264) **Crista supracondylaris medialis.** Synonymy: Adductor crest. This sharp crest extends proximally from the medial condyle of the femur, and is continuous with the caudal intermuscular line of the Corpus femoris (see Fig. 4.16).

(265) **Patella.** Sesamoid bone in the common tendon of the Mm. femorotibiales and M. iliotibialis. Barnett and Lewis (1958) contend that the elongated patellar crest of some birds (e.g., the common diving petrel *Pelecanoides urinatrix*) represents fusion of the patella with the patellar crest of the tibiotarsus to which the patellar ligament is attached in most birds (see Annot. 269).

Sulcus [Canalis] m. ambientis. Generally the tendon of M. ambiens perforates or grooves the patellar ligament; in a few birds it perforates or grooves the patella (see Berger, 1966).

(266) **Facies articularis medialis/lateralis** (Fig. 4.17B). Neither of these articular facets on **caput tibiae** of the proximal end of the Tibiotarsus is concave; therefore, "cotyla" or "glenoid fossa" are inappropriate; however, well developed intra-articular menisci intervene between the femur and head of the tibia, deepening the surfaces in contact with the femoral condyles (see **Arthr.** Artcc. genus). The smaller lateral facet faces laterodorsally (see Annot. 262); the larger medial facet lies in a nearly transverse plane.

(267) **Facies articularis tibialis.** Just distal to its surface for articulation with the femur, the medial surface of the Caput fibulae bears another surface that articulates with the lateral surface (**Facies articularis fibularis**) of the proximal tibiotarsus. See Fig. 4.17B; Annot. 262, 263; and **Arthr.** Annot. 157, 159.

(268) **Fossa retropatellaris** (Fig. 4.17). Synonymy: Fossae synoviales (Ballmann, 1969a); Fossa retrocristalis (NAA, 1979). The retropatellar fossa is situated between the Crista patellaris and the femoral articular facets on the proximal surface of the head of the Tibiotarsus. The Fossa in certain birds appears to be subdivided by a low ridge. In the intact joint the fossa contains the retropatellar fat body (**Arthr.** Annot. 158). See Ballmann, 1969a.

(269) **Crista patellaris** (Lambrecht, 1933). Synonymy: Crista rotularis (Milne-Edwards, 1867-71; Howard, 1929). Crest connecting the proximal ends of the two cnemial crests of the Tibiotarsus. The patellar crest varies in different birds from transverse to oblique depending on the elevation of the cranial cnemial crest above the articular plane of the head of the tibiotarsus; the Lig. patellae is attached to the crest. See Fig. 4.17; Annot. 265; and **Arthr.** Annot. 158.

(270) **Crista cnemialis cranialis** (Fig. 4.17). Synonymy: Crista cnemialis anterior (Ballmann, 1969a); Crista cnemialis interna or medialis (Cnemial, Gk. tibial). The cranial cnemial crest is elevated well above the level of the knee joint in some aquatic birds (R. W. Storer, pers. comm.) e.g., grebes, herons, flamingos, the diving petrels (Pelecanoididae), and shearwaters (*Puffinus*); enormously long in the loons. In foot-propelled diving birds the elongation of the crest is associated with shortening of the femur (R. W. Storer, pers. comm.)

(271) **Facies gastrocnemialis** (Ballmann, 1969a). The medial surface of Crista cnemialis cranialis and the area of the Tibiotarsus caudal to the crest (Fig. 4.17); origin of the medial head of M. gastrocnemius.

(272) **Sulcus intercnemialis** (Kolda and Komárek, 1958). Synonymy: Sulcus intercristalis (NAA, 1979). Wide longitudinally-oriented sulcus between the cranial and lateral cnemial crests (Fig. 4.17); for origin of M. extensor digitorum longus.

(273) **Incisura tibialis.** (Fig. 4.17). Seen from proximal or lateral view, this is the groove between the caudal surface of the lateral cnemial process and the Facies articularis fibularis of the Tibiotarsus; for passage of the tendon of the Caput femorale of M. tibialis cranialis (Ballmann, 1969a).

(274) **Fossa flexoria** (Fig. 4.17A). Synonymy: Fossa flexoris digitorum longi (Ballmann, 1969a). Depression on the caudal aspect of the proximal end of the Tibiotarsus distal to Facies articularis lateralis extending to the proximal edge of the fibular crest; serves as origin for M. flexor digitorum longus.

Tuberositas poplitea (Fig. 4.17). Linear scar on the caudal surface of the tibial shaft just distal to Fossa flexoria; for attachment of M. popliteus (P. Ballmann, pers. comm.). The tuberosity is pronounced in larger birds, e.g., *Ardea, Branta, Phoenicopterus.*

(275) **Corpus tibiotarsi.** The proximal two-thirds of the shaft of the Tibiotarsus is for the most part three-sided, with cranial, medial, and caudal surfaces (Ballmann, 1969a).

(276) **Linea extensoria** (Ballmann, 1969a). The intermuscular line of the cranial surface of the Tibiotarsus is prolonged from Crista cnemialis cranialis along the length of the shaft of the bone; continuous with the medial margin of Sulcus extensorius.

(277) **Pons supratendineus** (Fig. 4.17D). Synonymy: supratendinal bridge (Howard, 1929); Lig. transversum ossificatum (Lambrecht, 1933). (Pons, L. bridge). The supratendinal bridge is located at the distal end of the cranial surface of the Tibiotarsus proximal to its condyles. The bridge is ligamentous in *Bubo, Otus* (Berger, 1966), parrots, and ratites (Martin, 1987). See below, Annot. 278.

(278) **Canalis extensorius** (Fig. 4.17D). The passage deep to the Pons supratendineus at the distal end of the Tibiotarsus that transmits the tendon of M. extensor digitorum longus. See **Arthr.** Annot. 164.

Tuberositas retinaculi extensoris. Scar at each margin of the Sulcus extensorius of the distal tibiotarsus just proximal to Pons supratendineus (Annot. 277); for attachment of the extensor retinaculum (**Arthr.** Annot. 187). Since the retinaculum is oriented obliquely the two scars are at different levels.

(279) **Trochlea cartilaginis tibialis** (Fig. 4.17A). The trochlea is the wide furrow on the caudal surface of the distal end of the Tibiotarsus, serving as the articular surface for Cartilago tibialis. The sharp **Cristae** on either side of the trochlea are continuous with the tibiotarsal condyles (see Annot. 280; and **Arthr.** Annot. 164).

(280) **Condylus lateralis/medialis tibiotarsi.** The surfaces of these condyles of the Tibiotarsus that articulate with the Tarsometatarsus face cranially and distally, and caudally are continuous with the crests of the trochlea for the tibial cartilage (see Annot. 279).

(281) **Depressio epicondylaris lateralis/medialis.** Shallow depression on both lateral and medial sides of the lower end of the tibiotarsus just proximal to the distal articular surfaces of its condyles.

(282) **Tuberculum retinaculi m. fibularis [peronei].** On the cranial surface of the distal tibiotarsus the Tuberculum is separated from the proximal part of the lateral condyle by the **Sulcus m. fibularis [peronei]** (Fig. 4.17C); the tuberculum is the upper point of attachment of the retinaculum which bridges the sulcus and restrains the tendon of M. fibularis brevis in the Sulcus.

(283) **Ossa tarsi.** The proximal tarsals consist of two elements, the **Tibiale [Astragulus]** and the **Fibulare [Calcaneum],** which fuse to each other and to the tibia, producing the condyles of the distal end of the compound bone, the tibiotarsus. "Tibiale" is preferred over Astragalus because in fetal birds there is only one condensation (Cartilago tibiale) that articulates medially with the tibia, whereas the Astragulus of other amniotes is a compound element composed of additional elements (e.g., intermedium and centralia) that have been lost in birds (Müller and Alberch, 1990). The fibulare does not ossify in most ratites and tinamous; in the exceptions (*Struthio* and some *Dromaius*) the cartilaginous lateral condyle ossifies with the tibiale.

The avian ankle is characterized by an additional element, "Os pretibiale", that McGowan (1985) maintains is associated with the tibiale, whereas Martin and Stewart (1985) associate it with both tibiale and fibulare condensations (although more so with the latter). The pretibiale begins ossifying before either tibiale or fibulare; as a result, it is very unlikely that the pretibiale is homologous to the intermedium of other tetrapods (G. Müller, pers. comm.).

The single distal tarsal bone **(Os tarsi distale)** fuses with the metatarsals forming the proximal end, including the Hypotarsus, (Annot. 288) of the compound bone, the Tarsometatarsus. Although some workers (see Romanoff, 1960) identified up to four distal tarsals in birds, most recent workers have been able to identify only one (Hinchliffe, 1977; McGowan, 1985; Müller and Alberch, 1990). See **Arthr.** Annot. 167.

(284) **Tarsometatarsus.** Metatarsal bones II, III, IV of modern birds ankylose extensively with one another and the distal tarsal bone, forming the definitive Tarsometatarsus. Os metatarsale I is not involved in the ankylosis; instead it has a ligamentous junction with the medial border of the Tarsometatarsus. See Annot. 283; **Topog.** Annot. 43; and **Arthr.** Fig. 5.9 & Annot. 167, 173, 174.

(285) **Area intercotylaris** (Fig. 4.18D). This is the relatively flat area between the plantar parts of the two cotylae of the proximal tarsometatarsus, in other words, the area between the Eminentia intercotylaris and the Hypotarsus. See **Arthr.** Annot. 171.

(286) **Sulcus ligamentosus.** In some birds (e.g., *Pelecanus,* and the vulture *Catharte*s) this is a transverse groove at the junction of the proximal Hypotarsus and Area intercotylaris; the ligament from the distal end of Cartilago tibialis is attached in the groove. See Fig. 4.18; and **Arthr.** Annot. 166.

(287) **Arcus extensorius.** In certain birds an osseous arch is found on the cranial aspect of the proximal Tarsometatarsus that restrains, and acts as a pulley for, the tendon of M. extensor digitorum longus (e.g., strigids, picids, rallids, *Fulica, Chaetura,* et al.) (see Berger, 1966). The arch is in fact the ossified ligamentous Retinaculum extensorium tarsometatarsi of most birds. See Annot. 277, 295; and **Arthr.** Annot. 188.

(288) **Hypotarsus** (Fig. 4.18). Synonymy: Calcaneus. This process on the plantar aspect of the proximal Tarsometatarsus is formed mostly by the distal tarsal element (Annot. 283) capping the proximal end of Os metatarsale III. The Hypotarsus is simple in some birds, consisting of a wide sulcus between low crests (e.g., falconiforms, strigids). In most birds it is complex, having sulci and high crests, and perforated by one or more canals (Newton, 1896). The Sulci and Canales hypotarsi conduct flexor tendons of the pedal digits; consult Berger (1966), Simpson and Cracraft (1981), and Strauch (1985) for details in different taxa. See Fig. 4.18; **Integ.** Annot. 68; and **Arthr.** Fig. 8.

(289) **Cristae hypotarsi** (Fig. 4.18). Synonymy: Crista externa/interna hypotarsi (Ballmann, 1969a; Crista ecto-/entogastrocnemialis, (Lambrecht, 1933); calcaneal ridges (Howard, 1929). Lateral, intermediate, and medial crests of hypotarsus.

(290) **Crista medianoplantaris** (Fig. 4.18). Synonymy: Crista plantaris (Neugebauer, 1845); Crista plantaris mediana (NAA, 1979); hypotarsal ridge. Median, curved crest that forms a buttress from the middle of the Hypotarsus, gradually merging distally into the plantar shaft of the tarsometatarsus. The tendon of the gastrocnemius muscle extends past its main attachment on the hypotarsus to blend with the superficial border of the Crista (see Annot. 294 and **Myol.** Annot. 126), creating a septum. The septum forms the medial wall of an osseo-fibrous compartment enveloping the bundle of long flexor tendons for the digits (see **Arthr.** Annot. 176, Canalis flexorius metatarsi).

(291) **Fossa infracotylaris dorsalis** (Fig. 4.18A). Synonymy: Depressio antinterosealis (Lambrecht, 1933); Fossa anterior (Ballmann, 1969a). An excavation on the dorsum of the proximal end of the tarsometatarsus immediately distal to its cotylae. The Foramina vascularia proximalia open into the Fossa (**Art.** Annot. 79); the tuberosity for insertion of M. tibialis cranialis in some birds is situated in the distal part of the Fossa, or in the upper part of Sulcus extensorius of those birds lacking a distinct Fossa.

(292) **Facies corporis tarsometatarsi.** The surfaces of the shaft of the Tarsometatarsus vary in their configurations in different taxa. In cross section the shaft may be: (1) rectangular, laterally compressed (e.g., *Gavia*); (2) rectangular, compressed in its dorsoplantar dimension (e.g., *Coragyps*); (3) triangular, **Facies plantaris** flat (e.g., *Ardea*); (4) triangular, **Facies dorsalis** flat (e.g., *Pelecanus*); U-shaped, concave plantar surface (e.g., *Strix*) (Annot. 294).

(293) **Facies subcutanea lateralis/medialis** (Fig. 4.18A). Generally the medial and lateral surfaces (see Annot. 295) of the Tarsometatarsus are covered only with the scaly Podotheca (see **Integ**). By contrast, the plantar and dorsal surfaces of the Tarsometatarsus have bundles of flexor and extensor tendons interposed between podotheca and bone (Ballmann, 1969a).

(294) **Sulcus flexorius** (Fig. 4.18C). Synonymy: Sulcus longitudinalis plantaris. In certain birds (e.g., *Buteo, Aquila, Strix*) the plantar (flexor) surface of the Tarsometatarsus is strongly grooved longitudinally by the Sulcus flexorius which is bounded by the prominent, sharp **Crista plantaris medialis** and **Crista plantaris lateralis** (Fig. 4.18C). The sulcus forms the floor of the Canalis flexorius metatarsi that accommodates the bundle of tendons of the flexor muscles of the digits (**Arthr.** Annot. 178).

(295) **Sulcus extensorius** (Fig. 4.18A). Synonymy: Sulcus longitudinalis dorsalis. In some taxa a shallow, longitudinal sulcus indents the dorsal (extensor) surface of the Tarsometatarsus, and contains the intrinsic extensor muscles of the digits (see Annot. 287, 290, 294).

(296) **Proc. calcaris** (Komárek, 1979). This is the osseous core of the metatarsal spur (Calcar metatarsale). The Proc. calcaris is ankylosed to the medial or caudal aspect of the tarsometatarsus in males of some galliform birds. See **Integ.** Annot. 89.

(297) **Trochlea accessoria.** In piciform, cuculiform, and psittaciform birds the trochlea of the metatarsal bone of the fourth digit possesses an accessory trochlea (Milne-Edwards, 1867-71; Steinbacher, 1935). See Ballmann (1969a) for diagrams of atypical forms of the tarsometatarsal trochleae in several major taxa of birds including those listed above as well as coliiforms.

(298) **Canalis interosseus distalis.** Synonymy: Canalis m. add. dig. ext. (Lambrecht, 1933). Longitudinally oriented canal that conducts the tendon of M. extensor brevis digiti IV and vessels into the lateral intertrochlear incisure. The upper end of the canal (Fig. 4.18C) is continuous with the **Foramen vasculare distale** (**Art.** Annot. 79); in some birds the canal is replaced by a groove.

(299) **Ossa digitorum pedis.** The general avian phalangeal formula is: Hallux, two phalanges; Digitus secundus, three phalanges; Digitus tertius, four phalanges; Digitus quartus, five phalanges. (The hallux is lacking in most ratites).

The recommended scheme of numbering the phalanges is that of Berger (1966) and Lucas and Stettenheim (1972). This consists of designating: the most proximal phalanx of a digit as number 1, the next most distal number 2, etc.; in digit IV with five phalanges, the most distal (ungual) phalanx is number 5. The paper of Quinn and Baumel (1990), on the tendon-locking mechanism of the avian foot, follows their scheme. The scheme of Lennerstedt (1975) who designates the ungual phalanx as number 1, the next most proximal phalanx as number 2, etc. is less satisfactory.

(300) **Phalanx ungualis.** Synonymy: Phalanx terminalis or distalis. This usually claw-shaped phalanx (flattened in grebes, R. W. Storer pers. comm.) forms the bony core of the heavily keratinized claw (Unguis). See **Arthr.** Annot. 182, 183.

Sulcus neurovascularis (new term). The curved groove on each side of the Corpus of the ungual phalanx that carries nerves and vessels; located just beneath the podotheca of the claw.

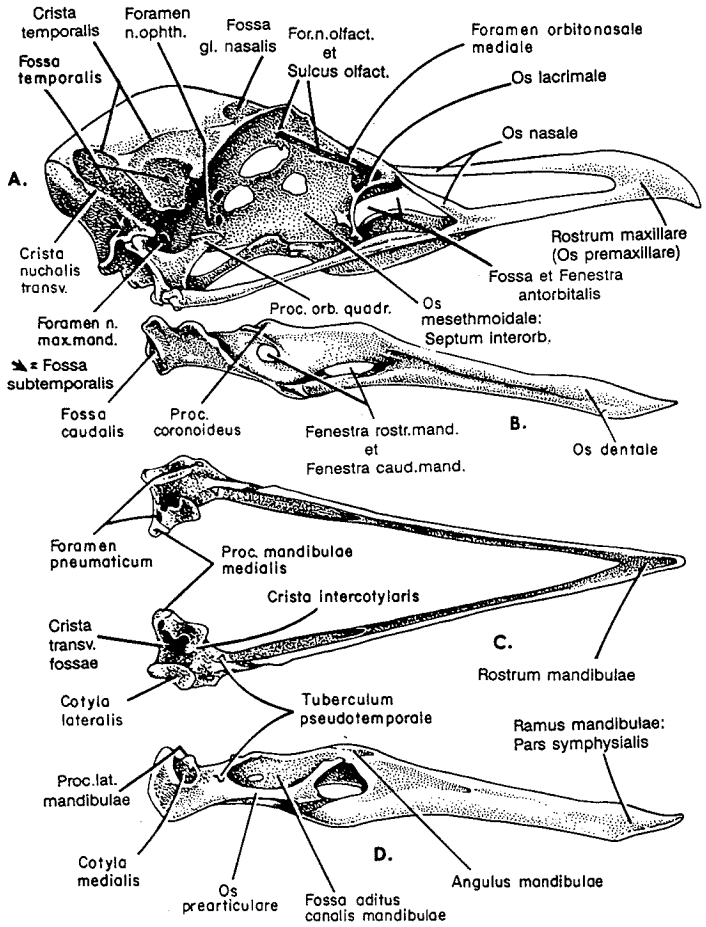

Fig. 4.1. Cranium and mandible of the gull *Larus argentatus*. Drawing by Wm. P. Hamilton. A, cranium, right lateral aspect; B, ramus of mandible, right lateral aspect; C, mandible, dorsal aspect; D, left ramus of mandible, medial aspect. Observe that: (1) the Fossa temporalis of this form is subdivided by a pronounced crest (Annot. 104); (2) in the dried skeleton of gulls the region of the Fenestra rostralis mandibulae often demonstrates several of the individual components that form the mandible (see Annot. 52, Ossa mandibulae; **Arthr.** Annot. 48); (3) Proc. retroarticularis is not a prominent feature in gulls (see **Arthr.** Fig. 5.2D, mandible of *Anas*); however the Fossa caudalis is distinct; (4) Crista transversa fossae is the partition separating the caudal fossa from the articular fossa. With permission of Academic Press.

Abbreviations: mand., mandibulae; max. mand., maxillomandibularis; ophth., ophthalmici; orb., orbitalis; quad., quadrati; transv., transversa.

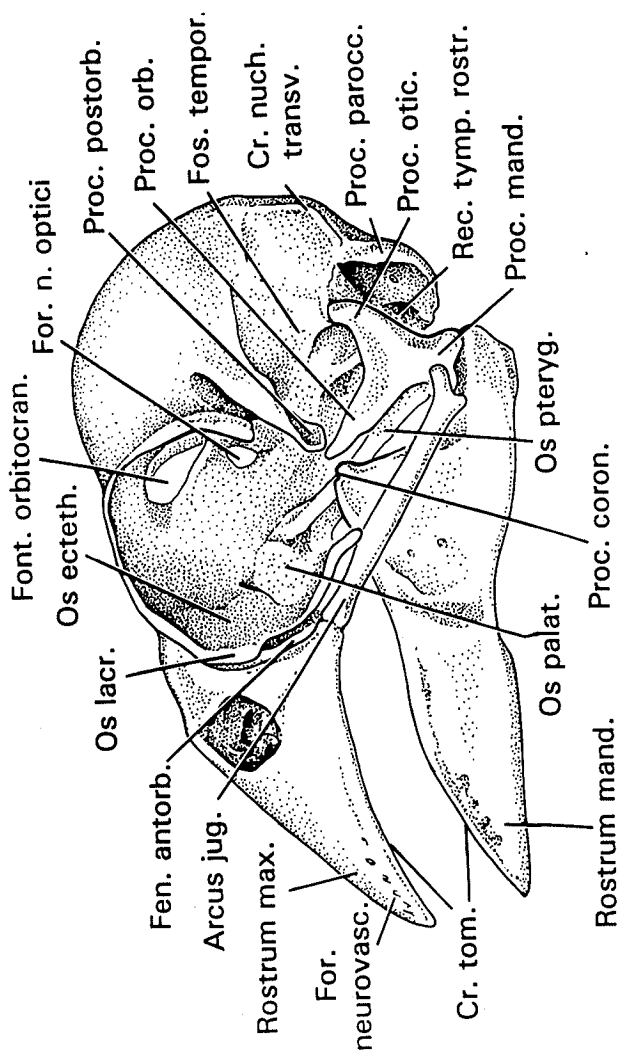

Fig. 4.2. Craniofacial skeleton and mandible of the Evening Grosbeak, *Coccothraustes vespertina*; left lateral view. Modified with permission from Witmer and Rose (1991).

Abbreviations: coron., coronoideus; Cr. nuch. transv., Crista nuchalis transversa; Cr. tom., Crista tomialis.; Fen. antorb., Fenestra antorbitalis; For., foramen; lacr., lacrimale; parocc., paroccipitalis; Rec., Recessus.

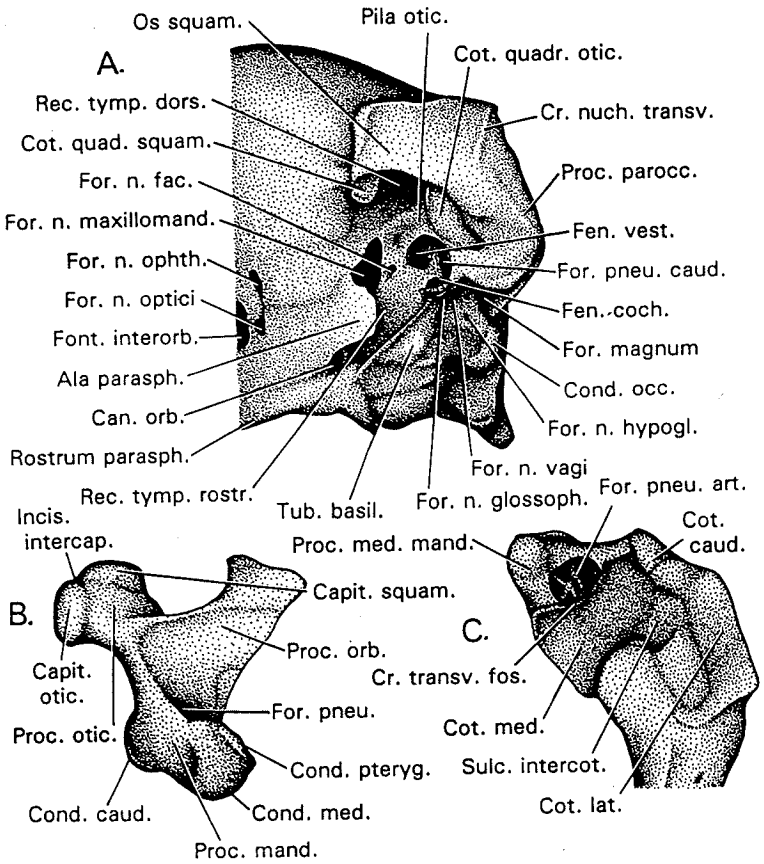

Fig. 4.3. Closeups of parts of the skull of a Greater Frigatebird, *Fregata minor.* A, Ear region and adjacent base of the cranium; left ventrolateral view. B, Quadratum, left side, medial view. C, Pars caudalis of left ramus of the mandible, dorsal view. Modified with permission from Witmer (1990).

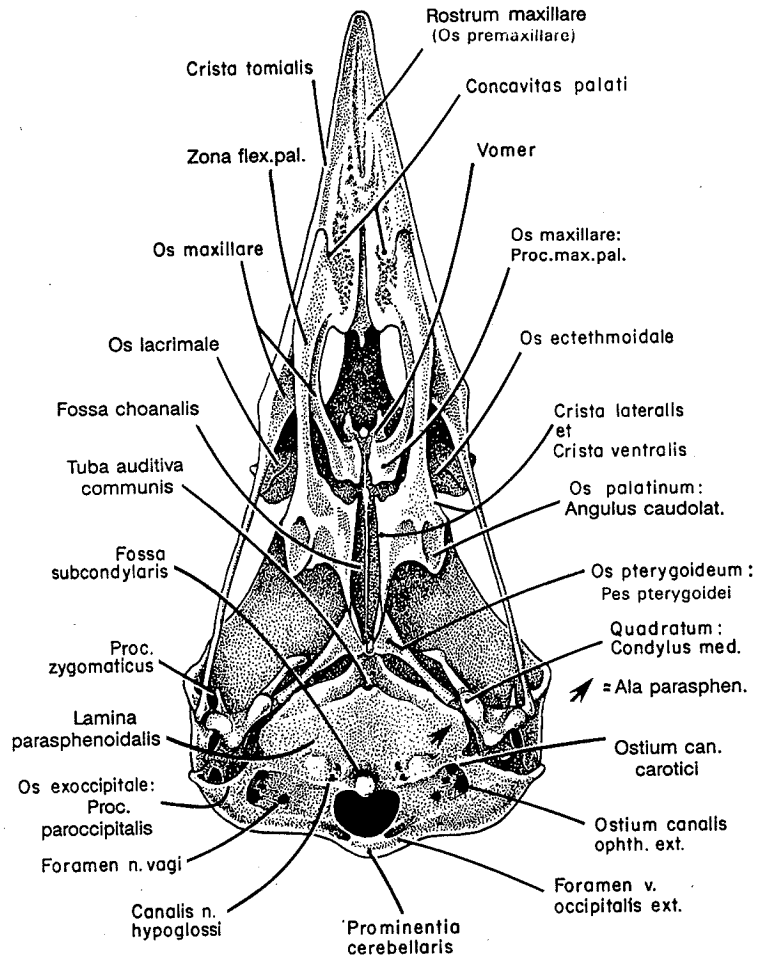

Fig. 4.4. Base of the skull, palate, and maxillary jaw of the Crow, *Corvus brachyrhynchos;* ventral aspect. Redrawn from Bock (1964). The leader for Lamina parasphenoidalis crosses the Proc. oticus of the quadrate bone. The depression in which the openings for the A. carotis cerebralis and A. ophthalmica externa are located is the Fossa parabasalis. The Foramen n. glossopharyngealis is just caudomedial to the Ostium canalis carotici. Tip of arrow rests on Ala parasphenoidalis.

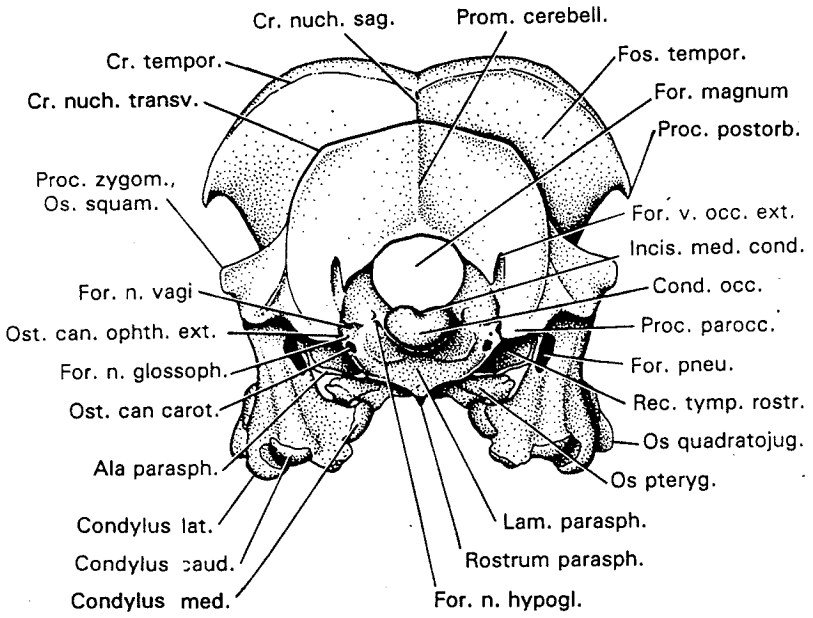

Fig. 4.5. Occipital region of skull of the Great Blue Heron, *Ardea herodias;* caudal (occipital) view. Original drawing of L. M. Witmer.

Abbreviations: Cond. occ., Condylus occipitalis; Cr. nuc. sag./transv., Crista nuchalis sagittalis/transversus; For. n. hypogl./vagi, Foramen n. hypoglossi/vagi; For. pneu., Foramen pneumaticum; Incis. med. cond., Incisura mediana condyli; Lam., Lamina; Ost. can. carot., Ostium canalis carotici; Prom., Prominentia; Rec., Recessus.

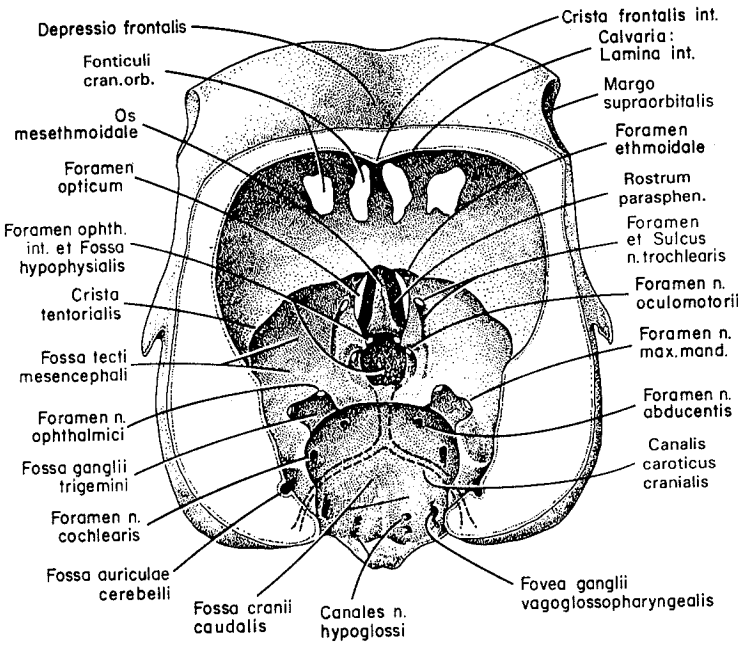

Fig. 4.6. Cranial cavity of the pigeon, *Columba livia.* Caudal view; transverse section through the Foramen magnum, plane of section inclined rostrally. Redrawn from Baumel (1968). Observe: (1) the Fossa cranii rostralis (perforated by Fonticuli cranio-orbitales) houses the telencephalic hemispheres; (2) at its ventral end the carotid canal opens into Fossa parabasalis on the base of the skull and at its rostral end into Fossa hypophysialis (Annot. 99); (3) the proximal ganglia of cranial nerves X and IX occupy a common depression, Fovea ganglii vagoglossopharyngealis, in the floor of Fossa cranii caudalis (Annot. 39). With permission of Academic Press.

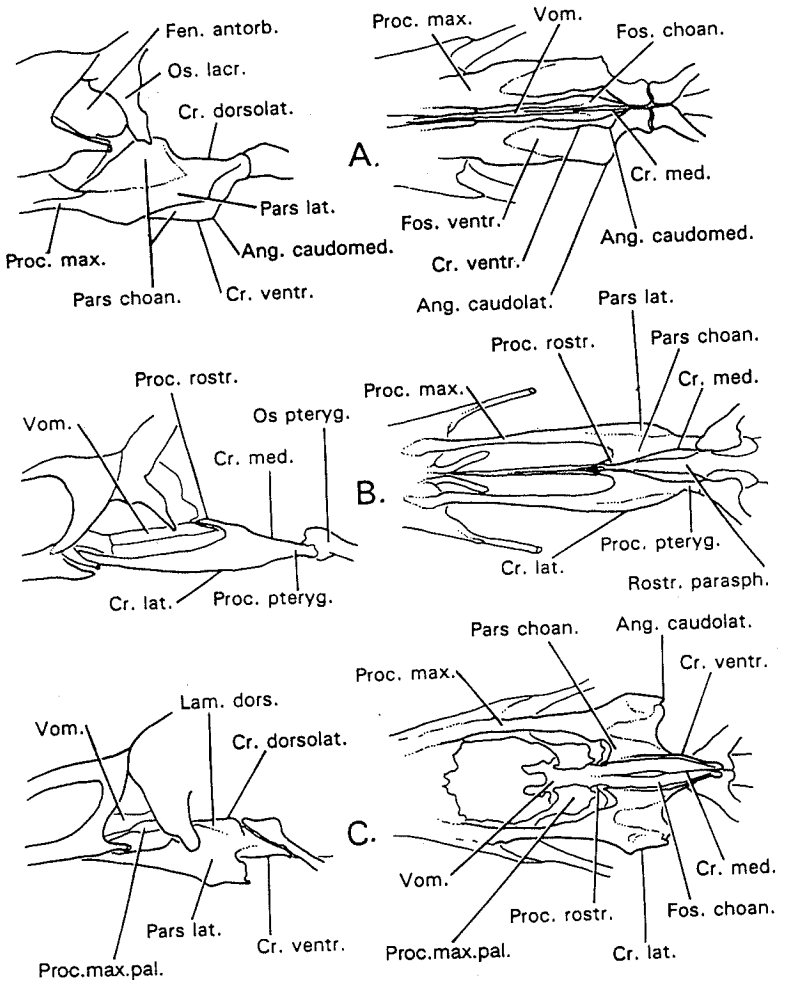

Fig. 4.7. Principal features of Os palatinum. A, *Diomedea nigripes;* B, *Crax fasciolata;* C, *Corvus brachyrhynchos.* Two views of each example are presented: the three figures in the left column depict the lateral view of the palatine bone; those in the right column are ventral views. See also Fig. 4.4 (maxillary jaw, palate, and skull base of the crow, *Corvus*).

Abbreviations: Ang., Angulus; Cr.; Crista; Fen., Fenestra; Fos., Fossa. Redrawn from originals of R. L. Zusi with permission.

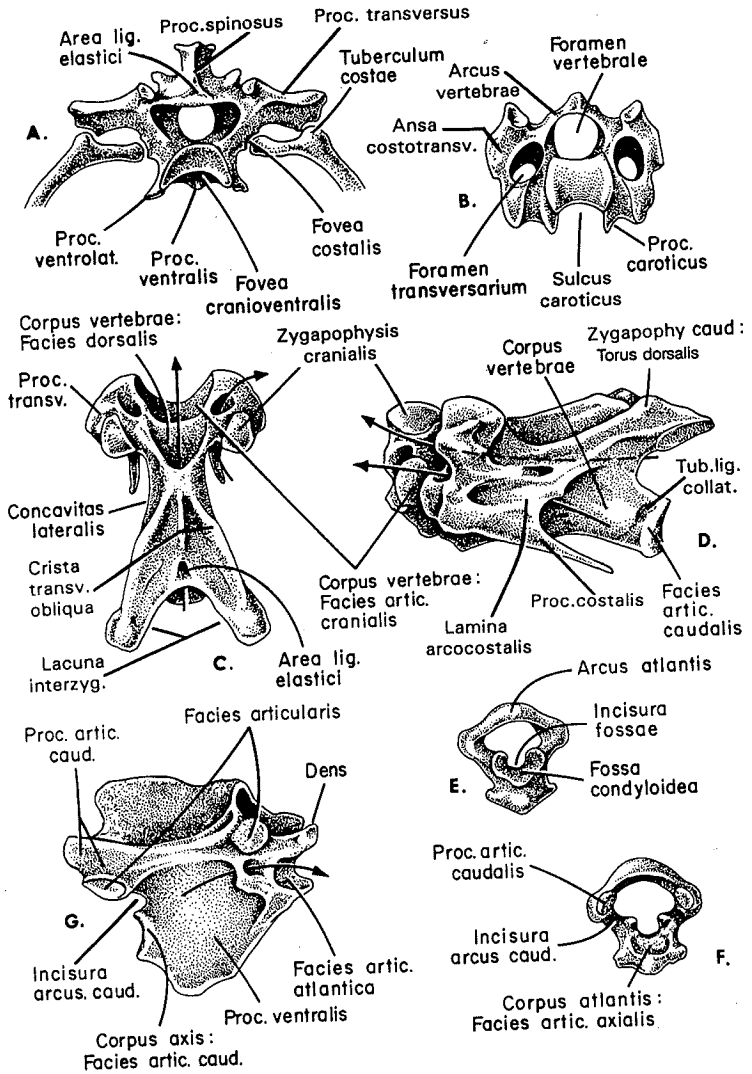

Fig. 4.8. Features of the cervical and thoracic vertebrae (see Figs. 4.9, 15 for notarial, synsacral, and caudal vertebrae).

A, Thoracic vertebra 2, *Larus,* cranial aspect; redrawn from Boas (1929).

B, Cervical vertebra 9, *Gavia,* cranial aspect; redrawn from Boas (1929).

(continued)

Fig. 4.8. *(cont.)*

C, Cervical vertebra 9, *Meleagris*, dorsal aspect; redrawn from Ghetie, et al. (1976).

D, Generalized cervical vertebra, craniolateral oblique view, left side. Redrawn from Ghetie, et al. (1976).

E, Atlas, *Meleagris;* cranial aspect; redrawn from Harvey, et al. (1968).

F, Atlas, *Meleagris;* caudal aspect; redrawn from Harvey, et al. (1968).

G, Axis, *Meleagris;* right lateral aspect; redrawn from Ghetie, et al. (1979). Arrows in C, D and G traverse the vertebral and transverse foramina. With permission of Academic Press.

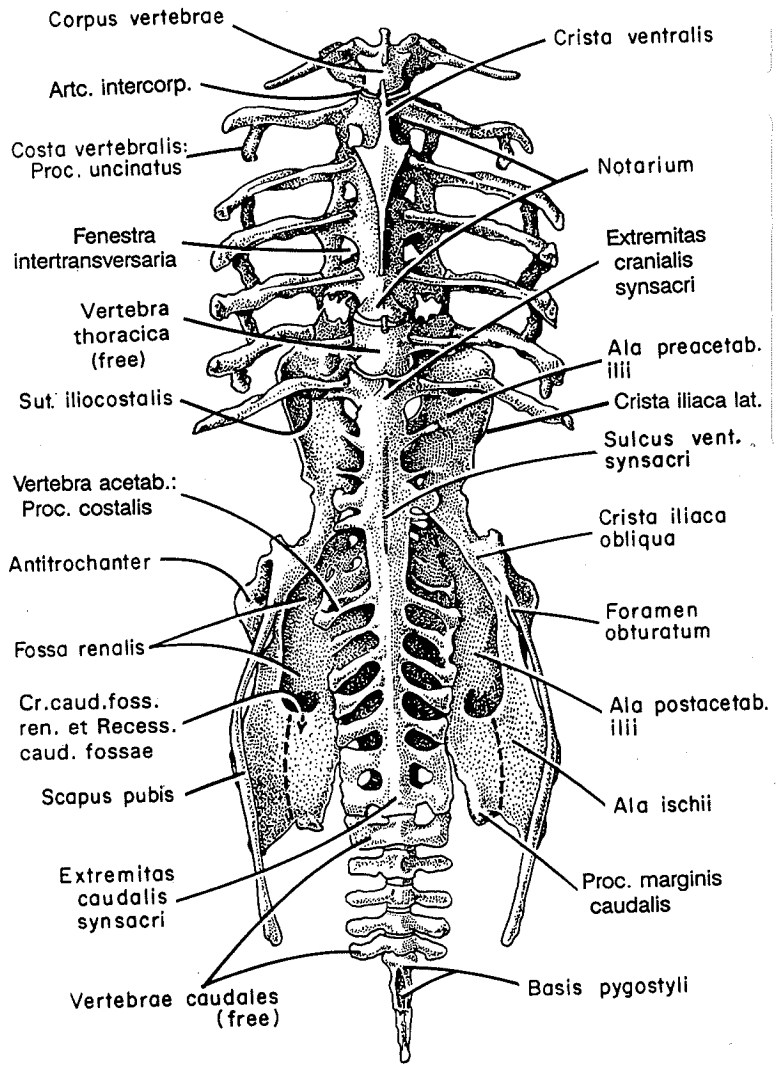

Fig. 4.9. Notarium, Synsacrum, and Os coxae of the turkey, *Meleagris gallapavo;* ventral view. Redrawn from Harvey, et al. (1968). The dashed lines represent the Sync. ilioischiadica (see Fig. 4.15. On the left side of the figure the arrow inserted into Recessus caudalis fossae passes dorsal to the ledge of bone, Pila postrenalis (**Annot.** 241). With permission of Academic Press.

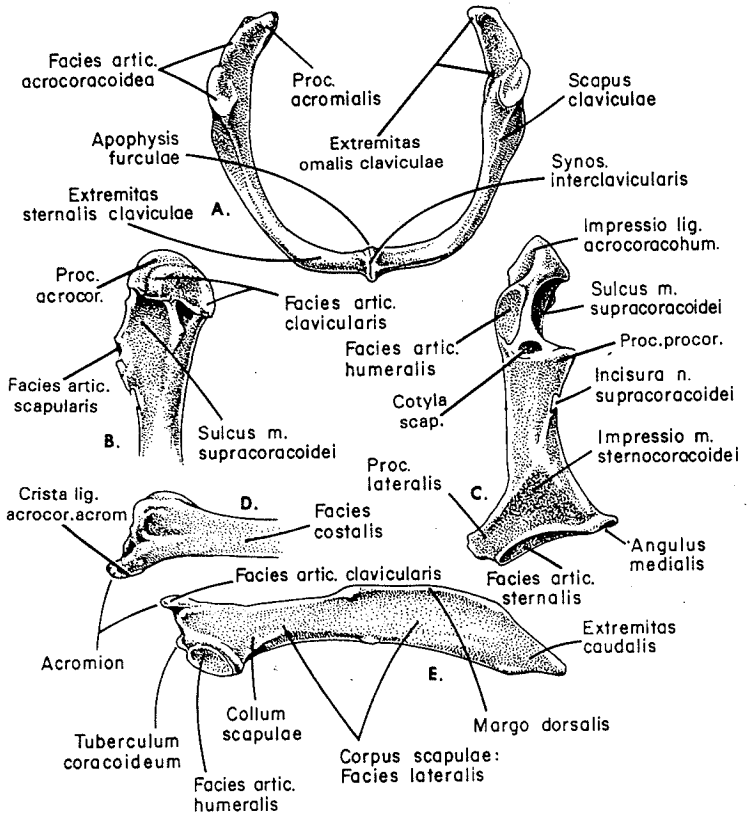

Fig. 4.10. Bones of the girdle of the thoracic limb of the eagle, *Aquila chrysaetos*. Redrawn from Howard (1929). A, Clavicula, caudal aspect; B, Coracoideum, left shoulder extremity, medial aspect. C, Coracoideum, left dorsal surface; D, Scapula, left cranial extremity, medial (costal) surface; E, Scapula, left lateral surface. The ankylosed left and right clavicles form the Furcula (see Annot. 162). With permission of Academic Press.

Abbreviations: acrocor., acrocoracoideus; acrocoracohum., acrocoracohumeralis; acrocor. acrom., acrocoracoacromiali; artic., articularis; glen. scap., glenoidalis scapulae; procor., procoracoideus.

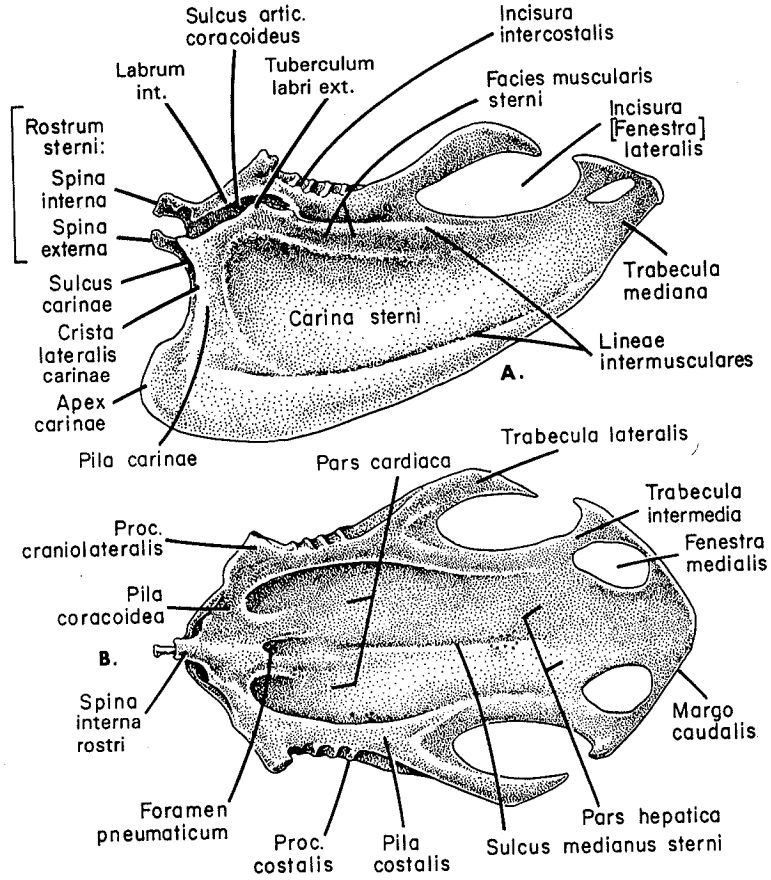

Fig. 4.11. Sternum of the pigeon, *Columba livia*. Redrawn from original of J. J. Baumel. A. left lateral aspect; B. visceral (dorsal) aspect. Abbreviation: artic., articularis. With permission of Academic Press.

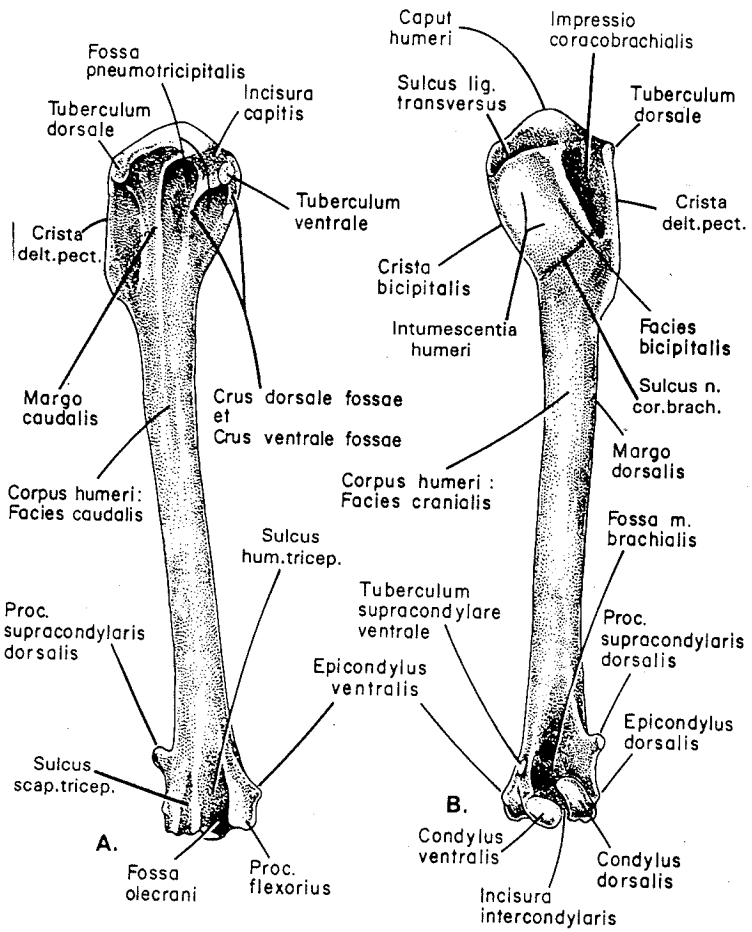

Fig. 4.12. Humerus of the gull, *Larus argentatus*. Original drawing of Wm. P. Hamilton. A. caudal surface; B. cranial surface. In *Larus* the impression for M. coracobrachialis cranialis is strongly etched and the pneumotricipital fossa is the dual type, non-pneumatic (see Annot. 188, 189).

Abbreviations: cor. brach., coracobrachialis; delt. pect., deltopectoralis; hum. tricep., humerotricipitalis; scap. tricep., scapulotricipitalis. With permission of Academic Press.

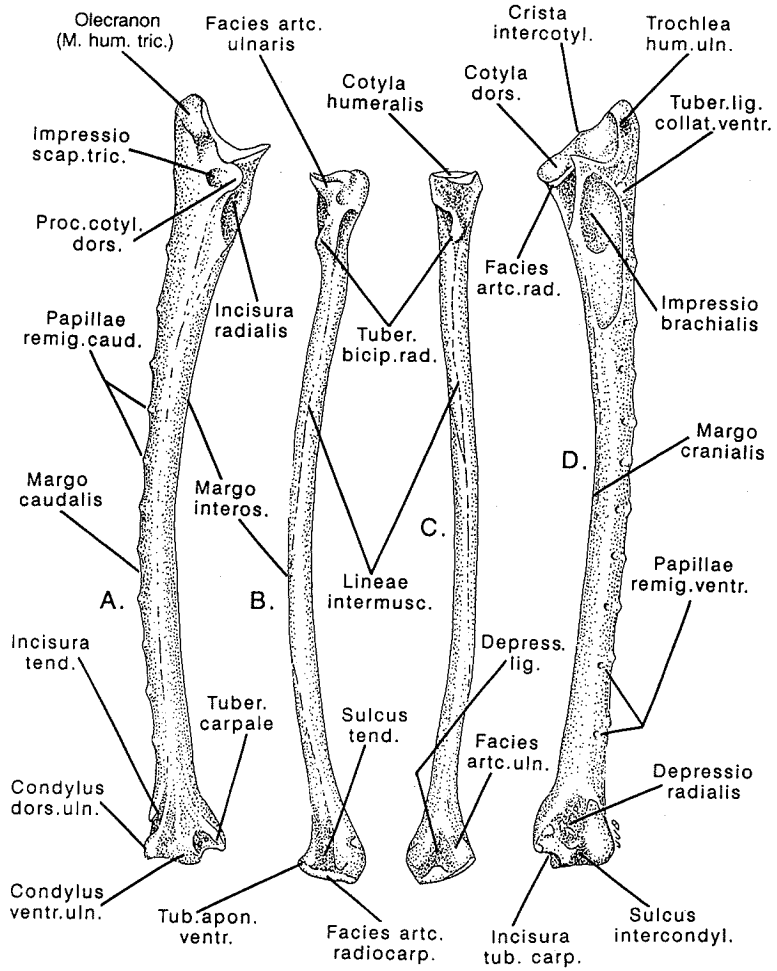

Fig. 4.13. Radius and Ulna of the vulture, *Cathartes aura;* right side. A. Ulna, dorsal aspect; B. Radius, dorsal aspect; C. Radius, ventral aspect; D. Ulna, ventral aspect. Original drawing of J. J. Baumel. Note that the terminology of these bones is based on the wing in the anatomical position (see Annot. 178 and **Gen. Intro.**).

Abbreviations: apon., aponeurosis; artc., articularis; bicep., bicipitale; collat., collateralis; cotyl., cotylaris; interos., interosseus; lig. ligamenti(-osa); remig., remigalis; tend., tendinosa(-us); tub. (tuber.), tuberculum(-i); uln., ulnaris.

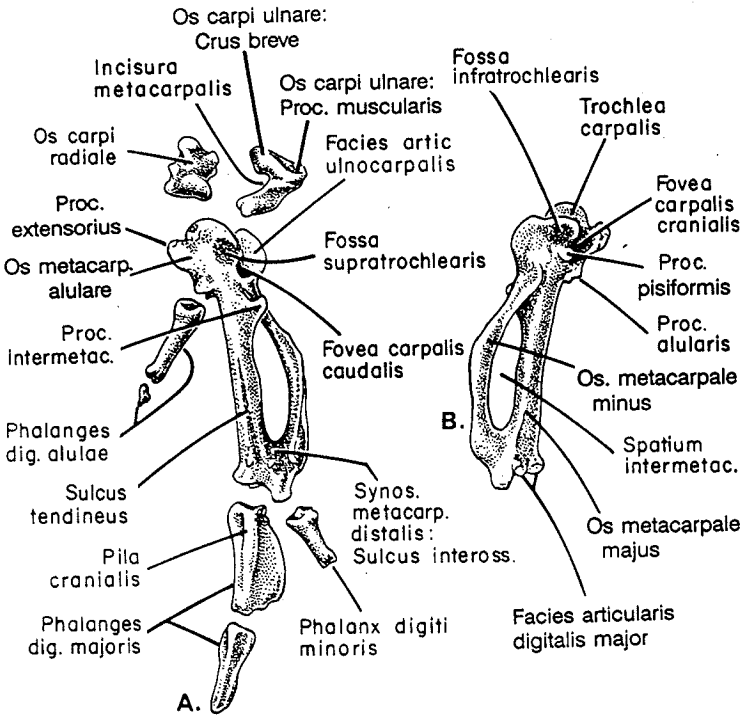

Fig. 4.14. Carpal and metacarpal bones, and phalanges of the turkey, *Meleagris gallapavo;* from left wing. Redrawn from Ghetie, et al. (1976). A. Dorsal aspect; B. ventral aspect. Note that the alular digit of the turkey has two phalanges (see Annot. 224). With permission of Academic Press.

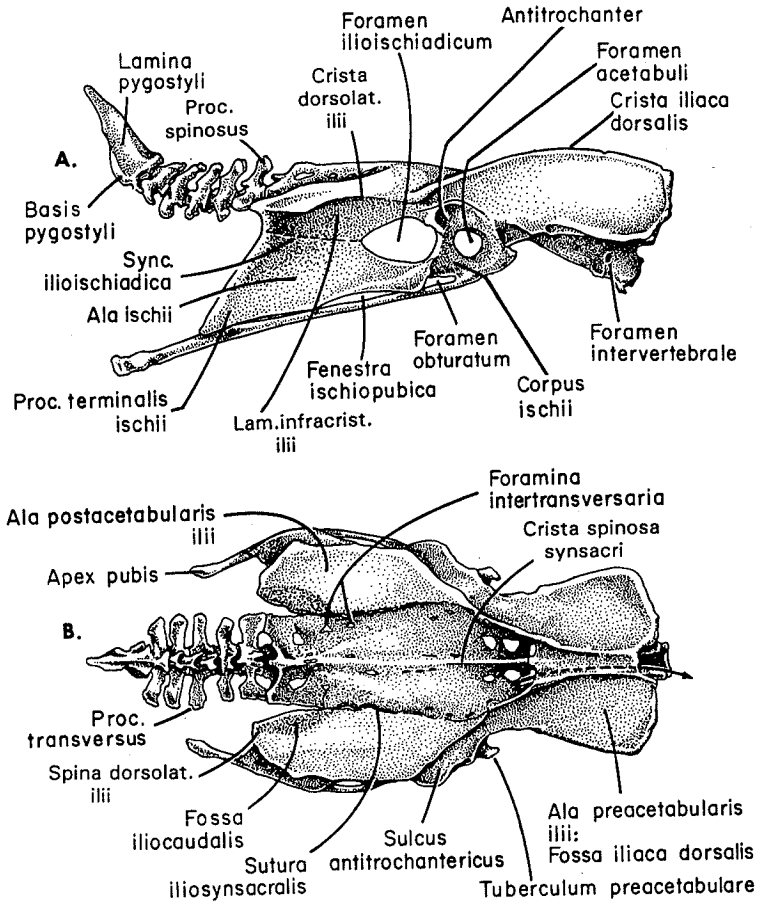

Fig. 4.15. Pelvis (Os coxae + Synsacrum) and caudal vertebrae of the turkey, *Meleagris gallapavo.* Redrawn from Harvey, et al. (1968). A. lateral aspect, right side; B. dorsal aspect. In B the arrow traverses Canalis iliosynsacralis (Annot. 234.). In A notice the dual intervertebral foramina in the synsacral part of the vertebral column (see Annot. 144). With permission of Academic Press.

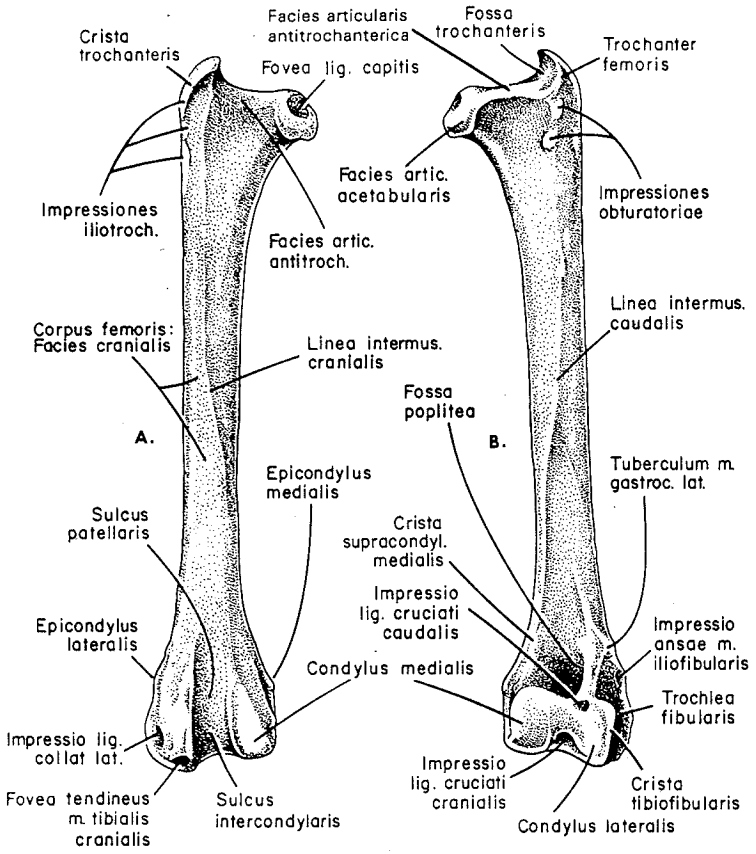

Fig. 4.16. Femur of the gull, *Larus argentatus;* right side. Original drawing of Wm. P. Hamilton. A. cranial aspect; B. caudal aspect. With permission of Academic Press.

Abbreviations: antitroch., antitrochanterica; artic., articularis; gastroc., gastrocnemialis; iliotroch., iliotrochantericae; intermus., intermuscularis.

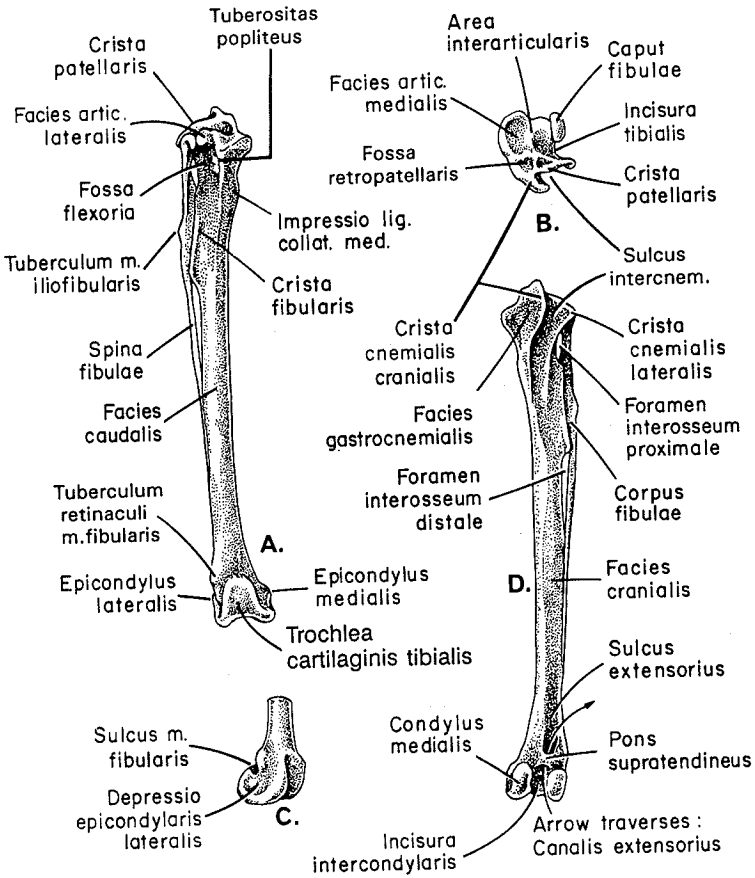

Fig. 4.17. Tibiotarsus and Fibula of the goose, *Branta canadensis;* left side. Original drawing of Wm. P. Hamilton. A. caudal aspect; B. proximal articular surfaces of both bones; C. distal extremity of tibiotarsus, lateral aspect; D. cranial aspect. With permission of Academic Press.

Abbreviations: artic., articularis; collat., collateralis.

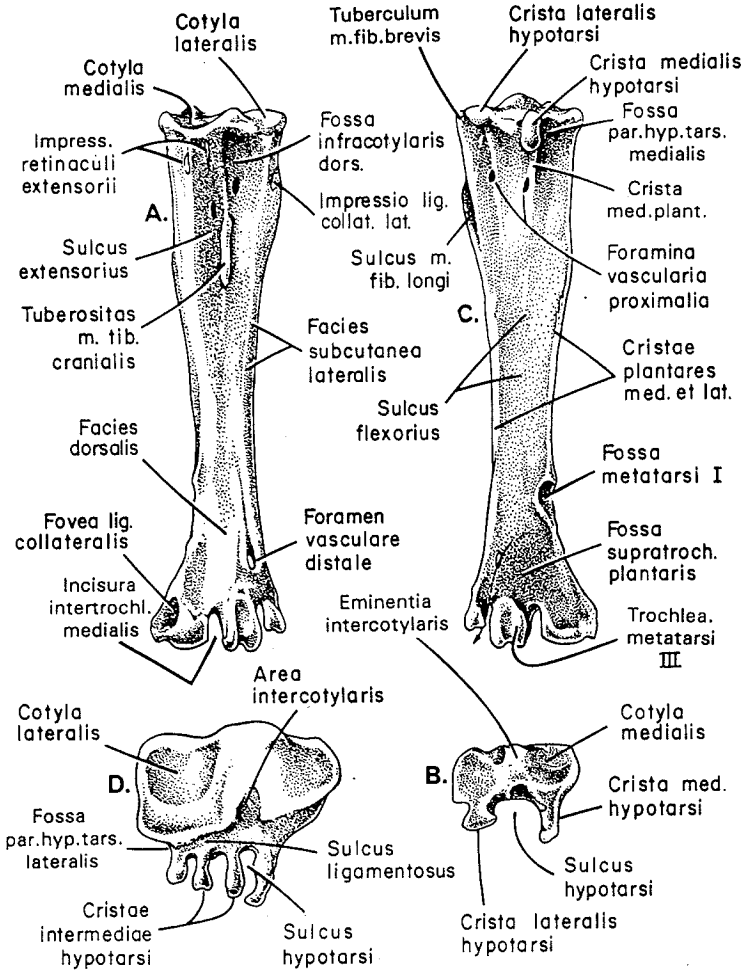

Fig. 4.18. Features of the Tarsometatarsus of the eagle, *Aquila chrysaetos* (A-C) and the goose, *Anser caerulescens (Chen hyperborea)* (D); all bones from the left limb. Redrawn from Howard (1929). A, dorsal aspect; B, proximal end; C, plantar aspect; D. proximal end. At the distal end of C, the arrow traverses Canalis interosseus distalis (not labelled) (see Annot. 298) which conducts the tendon of M. ext. digiti IV. The Eminentia intercotylaris in the articulated intertarsal joint projects between the tibiotarsal condyles and is the distal attachment of Lig. intercondylare tibiometatarsale (**Arthr.** Annot. 171). With permission of Academic Press.

Abbreviations: impress., impressiones; intertroch., intertrochlearis; med. plant., medianoplantaris; par. hyp. tars., parahypotarsalis.

5

ARTHROLOGIA

JULIAN J. BAUMEL
and
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With contributions from subcommittee members: P. Ballman, P. Bühler, D. A. Hogg, J. Kaman, P. Stettenheim, J. Vanden Berge, R. L. Zusi, G. A. Zweers.

This section in the first edition of NAA (1979) is entitled Arthrologia rather than Syndesmologia, the heading used in both the older editions of the human *Nomina Anatomica* (NA) (IANC, 1966) and *Nomina Anatomica Veterinaria* (NAV) (ICVGAN, 1973). The more recent editions of NA and NAV (IANC, 1983; ICVGAN, 1983) have also adopted the designation, Arthrologia. Trotter and Peterson (1966) pointed out that "Syndesmology" means the study of ligaments and, in the literal sense, is less comprehensive than the term "Arthrology", which encompasses the consideration of all joint structures and functions. They commented that anatomical terminology includes numerous structures in the body called ligaments (e.g., atrophied fetal blood vessels, thickenings of mesenteries, meninges, etc.) that are excluded from the category of syndesmology.

Feather ligaments. Avian arthrological terminology differs in a major respect from that of mammals owing to the presence of feathers. The large flight feathers of wing and tail constitute an exoskeleton of sorts. An elaborate system of ligaments connect these feathers to one another and to the bony skeleton. Not only do these ligaments anchor the feathers, but some are so disposed as to produce (passively) movements of opening and closing of the flight feathers (see Annot. 113, 115, 189-200 and terms under Ligamenta pennarum).

Flexion zones of the jaw apparatus (Fig. 2.). Avian skulls are characterized by several types of cranial kinesis that involve bending zones (**Zonae flexoria**) within bony elements. These are included here rather than with Osteologia for the sake of convenience. Strictly speaking, these features are not joints (Juncturae) in the usual sense because they are specialized regions within individual elements rather than places where separate elements are

conjoined. For this reason they are classified as Zonae rather than Juncturae (see Annot. 46).

The term "flexoria" replaces "elastica" of the NAA, 1979. Elasticity is a mechanical term used when elastic energy or resilience is involved, especially if an extension is directly proportional to a force or load. While these principles seem to play a role in the bendable bars of the avian skull, they are not necessarily a critical feature of these zones. Zona flexoria more accurately conveys the bending nature of the mechanism.

Naming of ligaments and joints; Hyphenation of names. Ligaments are named generally by indicating their osseous attachments (e.g., Lig. iliofemorale) or some aspect of their topography relative to the joint (e.g., Lig. collaterale ventrale).

Joints are often named by the bones or parts of bones that are united at the joint (e.g., Sut. vomeropalatina). In order to make clear what osseous elements are involved in the joint, some anatomical names must be hyphenated (e.g., Artc. quadrato-quadratojugalis, a term in which the hyphen clarifies that the joint connects Os quadratum with Os quadratojugale.

Juncturae ossium; Articulationes. Junctura(e) ossium (literally: junction of bones) is adopted in this work as the general term for all joints, i.e., fibrous, cartilaginous, osseous, and synovial. This term was used in the *Basle Nomina Anatomica* (BNA, 1895) and *Jena Nomina Anatomica* (JNA, 1936) terminologies (see **Intro.**). This usage, however, disagrees with the contemporary NA (IANC, 1983) and the NAV (ICVGAN, 1983); in both of these nomenclatures the former terms, "Diarthrosis", "Articulus", and "Junctura synovialis" are set aside, and "Articulationis" was adopted as the general term for all sorts of joints. In practice, however, the human and veterinary terminologies use "Articulationis" primarily to refer to synovial joints; this practice has been continued in this present NAA-2. See Annot. 1.

Types of joints. See Annot. 1 for a discussion of categories of joints. Cartilaginous, fibrous, and synovial joints are the only types of joints listed in the *Nomina Anatomica Veterinaria* (ICVGAN, 1983). A number of bones in the avian skeleton that are connected by means of cartilage and fibrous tissue in early postnatal life become secondarily united in later life by osseous fusion (ankylosis). In this work some of these modified primary joints in mature, adult birds are listed as "synostoses" in order to direct particular attention to them, since certain of them are important structural specializations peculiar to birds. For example, in such distinctively avian (among extant archosaurian forms) structures such as the notarium, synsacrum, pygostyle, furcula, carpometacarpus, and tarsometatarsus. These are of functional and evolutionary significance in avian structural design. Synchondroses refer to joints that were primarily cartilaginous, later modified, or that persist as cartilaginous joints in adult, mature birds.

Simplification of terms. In a number of instances the combining form of the names of various skeletal elements has been abbreviated in order to simplify and make more manageable the anatomical names of articulations and ligaments, and to clearly differentiate terms having a degree of similarity. For example, terms involving articulations between Radius and Ulna with Os carpi radiale and Os carpi ulnare (see Annot. 111) must be distinguished.

In the limbs, owing to the incorporation of carpal and tarsal bones with the bones of the hand, crus, and foot, compound names have been given to the skeletal elements. In order to avoid at least some of the cumbersome arthrological terms, abbreviated combining forms are used. For example, "tibio-" for "tibiotarso-" (see Annot. 155); "radiocarpo-" and "ulnocarpo-" for Os carpi radialis and Os carpi ulnaris (see Annot. 112).

In the literature the existing names for the various wrist (carpal) joints and their ligaments are confusing, difficult to learn and remember. The nomenclatural precepts of making anatomical names descriptive, meaningful, and an aid to memory were applied in developing the terminology of the wrist joints in the previous and present editions of the NAA. This terminology may be employed for birds generally, notwithstanding interspecific variation in the occurrence, attachments, and configuration of the ligaments of the wrist region. See Annot. 112.

In the head the combining form "jugo-" refers to any part of the jugal arch, not necessarily Os jugale proper (see Annot. 38, 40). The form "rostro-" refers to the Rostrum parasphenoidale (see Annot. 22, 23); "otico-" is used to refer to the otic complex of bones (see Annot. 9).

TERMINOLOGY

TERMINI GENERALES

Aponeurosis
Articulatio[1] **(Intro.)**
Bursa synovialis
Cartilago
Discus
Fibrocartilago
Zona flexoria ossea[45]
Junctura fibrosa[1]
Syndesmosis
Sutura
  Sutura serrata
  Sutura squamosa
  Sutura foliata
  Sutura plana
Gomphosis[2]
Junctura cartilaginea[4] **(Intro.)**
  Synchondrosis
  Symphysis
Juncturae ossium[1]
  Synostosis
Junctura synovialis **(Intro.)**
  Articulatio simplex
  Articulatio composita
  Articulatio plana

(continued)

TERMINI GENERALES (cont.)

Articulatio spheroidea
Articulatio ellipsoidea
Articulatio condylaris
Articulatio trochoidea
Articulatio sellaris[2]
Ginglymus[46]
Cartilago articularis
Cavitas articularis
Discus articularis
Meniscus articularis
Capsula articularis
Membrana fibrosa
Membrana synovialis
Plica synovialis
Villi synoviales
Synovia
Vasa articularia
Nervi articulares
Ligamenta
Ligamentum collaterale
Ligamentum interosseum
Ligamentum extracapsulare
Ligamentum intracapsulare
Ligamentum elasticum[3]
Membrana
Retinaculum[114 144 165]

JUNCTURAE OSSIUM [1]

(see Intro.)

JUNCTURAE CAPITIS [4] (Osteo. Figs. 4.1-6)

SUTURAE CRANII [4]

Sut. supraoccipitoparietalis[5]
Sut. interparietalis[6]
Sut. interfrontalis[7]
Sut. frontoparietalis[8]
Sut. exoccipitosquamosa
Sut. parietosquamosa
Sut. frontosquamosa
Sut. laterospheno-squamosa
Sut. laterospheno-frontalis
Sut. oticosquamosa
Sut. oticoparietalis
Sut. supraoccipitosquamosa

SYNCHONDROSES CRANII [4]

Syncc. interoticae[9]
Sync. exoccipito-prootica
Sync. supraoccipito-exoccipitalis
Sync. prootico-laterosphenoidalis
Sync. otico-supraoccipitalis
Sync. prootico-basioccipitalis
Sync. basioccipito-parasphenoidalis
Sync. basioccipito-exoccipitalis
Sync. exoccipito-parasphenoidalis
Sync. otico-parasphenoidalis
Sync. laterospheno-parasphenoidalis
Sync. basiparaspheno-rostroparasphenoidalis
Sync. basispheno-parasphenoidalis
Sync. basispheno-rostroparasphenoidalis
Sync. mesethmo-laterosphenoidalis (**Osteo.** Annot. 88)
Sync. [Artc.] interlaterosphenoidalis[10]

SUTURAE FACIEI MAXILLARIS [4 11]

Sutt. faciei maxillaris[11 4]
Sut. frontopremaxillaris
Sut. frontonasalis
Sut. frontomesethmoidalis[12]
Sut. fronto-ectethmoidalis
Sut. lacrimo-ectethmoidalis[13]
Sut. lacrimofrontalis
Sut. lacrimonasalis
Sut. mesethmonasalis
Sut. mesethmoparasphenoidalis
Sut. mesethmopremaxillaris
Sut. nasopremaxillaris
Sut. nasomaxillaris
Sut. internasalis[14]
Sut. intermaxillaris
Sut. interpremaxillaris
Sut. maxillopremaxillaris
Sut. vomeropalatina[15 23]
Sut. vomeromaxillaris[16]
Sut. palatomaxillaris
Sut. rostromaxillaris (**Intro.**)
Sut. palatopremaxillaris
Sut. interpterygoidea[17]
Sut. interpalatina[17]
Sut. pterygopalatina[17]
Sut. intervomeralis[18]
Sut. jugomaxillaris
Sut. jugolacrimalis[19]
Sut. jugo-quadratojugalis

SUTURAE FACIEI MANDIBULARIS (Osteo. Annot. 40, 42)

Sut. angulosplenialis
Sut. angulosuprangularis
Sut. articuloangularis
Sut. articulo-prearticulo-angularis
Sut. articulo-prearticulo-supraangularis
Sut. articulosupraangularis
Sut. articuloprearticularis
Sut. dentosplenialis
Sut. dentoangularis
Sut. dentosupraangularis
Sut. supraangulosplenialis
Symphysis mandibularis[21]

SYNCHONDROSES FACIEI

Sync. rostromesethmoidalis[22]
Sync. mesethmo-ectethmoidalis

ARTICULATIONES MAXILLAE ET PALATI [11] (Fig. 5.1; Osteo. Figs. 4.1, 4, 7)

Artc. jugolacrimalis[19]
Lig. jugolacrimale[20]
Artc. vomerorostralis[23]
Lig. mesethmovomerale [L. vomerale][23]
Artc. quadrato-quadratojugalis[24]
Lig. interosseum[24]
Artc. quadrato-squamoso-otica[25]
Lig. quadratosphenoidale[25]
Lig. quadratotemporale[25]
Artc. quadratopterygoidea[26]
Artc. palatorostralis[29 23]

(continued)

ARTICULATIONES MAXILLAE ET PALATI[11] (Fig. 5.1; Osteo. Figs. 4.1, 4, 7) (cont.)

Artc. pterygorostralis[27 23]
Artc. pterygobasipterygoidea[27]
Artc. pterygopalatina[28]
Lig. mesethmopalatinum [L. orbitale][29]
Lig. palatomaxillare[47]
Lig. palatolacrimale
Lig. suborbitale[30]
Lig. maxillomandibulare[30]
Membrana circumorbitalis[31]
Septum orbitale[31]
Membrana temporalis[31]

ARTICULATIONES MANDIBULI ET OSSIS QUADRATI (see Sutt. faciei mand.)

Artc. [Synd.] mandibulosphenoidalis[32]
Lig. mandibulosphenoidale[32]
Lig. occipitomandibulare[37]
Membrana postmeatica[37]
Lig. intramandibulare[34]
Synd. mandibulo-occipitalis[33]
Lig. mandibulo-occipitale[33]
Lig. postorbitale[42]
Lig. orbitoquadratum[42]
Lig. zygomaticomandibulare[43]
Artc. ectethmomandibularis[44]
Artc. quadratomandibularis[35]
Lig. quadratomandibulare caudale[36]
Lig. quadratomandibulare rostrale[36]
Lig. quadratomandibulare laterale[36]
Lig. jugomandibulare mediale[38]
Lig. jugomandibulare laterale[40]
Lig. lacrimomandibulare[41]
Lig. laterospheno-jugale[34]
Meniscus articularis[39]
Ligamenta columellae (Sens. Auris media)

ZONAE FLEXORIAE OSSIUM FACIEI[45] (Fig. 5.2)

Zona flexoria craniofacialis[46]
Zona flexoria craniofacialis lateralis[46]
Zona flexoria craniofacialis medialis[46]
Zonae flexoriae maxillares[47 11]
Zona flexoria rostrodorsalis[47]
Zona flexoria rostroventralis[47]
Zona flexoria dorsomedialis[47]
Zona flexoria nasalis dorsalis[46]
Zona flexoria nasalis ventralis[46]
Zona flexoria arcus jugalis[47]
Zona flexoria palatina[47]
Lig. palatomaxillare[47]

(continued)

ZONAE FLEXORIAE OSSIUM FACIEI[45] (Fig. 5.2) (cont.)

Zonae flexoriae mandibulares[48]
Zona flexoria intramandibularis rostralis[48]
Zona flexoria intramandibularis caudalis[48]
Synd. intramandibularis caudalis[49]
Lig. intramandibulare

JUNCTURAE APPARATUS HYOBRANCHIALIS [HYOLINGUALIS][50] (see Myol. Fig. 2b; and Annot. 25)

Synd. interparaglossalis[51]
Artc. paraglosso-basihyalis[51]
Lig. paraglosso-basihyale ventrale
Lig. paraglosso-basihyale dorsale
Sync. [Artc.] basihyo-urohyalis[52]
Artc. cerato-basihyalis[53]
Sync. [Artc.] epi-ceratobranchialis[54]
Synd. urohyocricoidea[57]
Lig. arytenoparaglossale[58]

JUNCTURAE LARYNGIS[55] (see Resp. Larynx and Figs. 8.2-7)

JUNCTURAE COLUMNAE VERTEBRALIS[59]

JUNCTURAE INTERVERTEBRALES GENERALES (Fig. 5.10)

Artc. intercorporalis[60]
Capsula articularis
Lig. collaterale[60]
Meniscus intervertebralis[61]
Fenestra centralis
Anulus [Annulus] fibrosus[61]
Discus intervertebralis[62]
(Lig. suspensorium corporum vertebralium)[62]
Ligg. dorsalia vertebrae
Lig. elasticum interspinale
Lig. elasticum interlaminare[63]
Lig. elasticum obliquum
Lig. elasticum transversum
Membrana interlaminaris
Lig. interspinosum
Ligg. lateralia vertebrae
Lig. laterodorsale
Lig. interansale[63]
Ligg. ventralia vertebrae
Lig. ventrolaterale[63]
Lig. intercristale ventrale[63]
Artc. zygapophysialis[65]
Capsula articularis
Meniscus articularis[66]

JUNCTURAE SPECIALES REGIONIS CERVICALIS Osteo. (Fig. 4.8)

Artc. atlanto-occipitalis[64]
Membrana atlanto-occipitalis ventralis[67]
Membrana atlanto-occipitalis dorsalis[67]
Fibrocartilago atlantis[64]

(continued)

JUNCTURAE SPECIALES REGIONIS CERVICALIS Osteo. (Fig. 4.8) (cont.)

Artcc. atlantoaxiales[68]
Artc. atlantodentalis[68]
Artc. intercorporea[68]
Artc. zygapophysialis[65]
Membrana atlantoaxialis
Lig. apicis dentis
Lig. transversum atlantis[69]
Lig. collaterale atlantoaxiale[69]
Synos. costotransversaria[70]
Artc. costotransversaria[70]

JUNCTURAE NOTARII[71] (Osteo. Fig. 4.9)

Synos. intercorporalis
Synos. intertransversaria
Synos. [Sut.] interspinalis
Lig. intercristale ventrale[72]
Artc. notariosynsacralis[71]

JUNCTURAE SYNSACRI[73] (Osteo. Fig. 4.9)

Synos. intercorporalis[74]
Synos. intertransversaria
Synos. interspinalis[74]
Symphysis postsynsacralis[75]
Sut. [Synos.] iliosynsacralis[76]
Ligg. iliosynsacralia[76]
Synos. interiliospinalis[77]

JUNCTURAE CAUDAE[75] (Osteo. Figs. 4.9, 15)

Lig. intertransversarium
Synoss. pygostyli[78]
Artc. propygostylaris[75]
Symphysis postsynsacralis

JUNCTURAE COSTARUM[79] (Osteo. Figs. 4.8, 9)

Sync. capitis costae[79]
Lig. collaterale[79]
Artc. costotransversaria[79]
Sut. iliocostalis[80]
Sync. intercostalis[81] (Fig. 4.9)
Sut. costouncinata[82]
Lig. triangulare[82]
Artc. sternocostalis[83]

JUNCTURAE CINGULI MEMBRI THORACICI

JUNCTURAE STERNI (Osteo. Fig. 4.11)

Membranae incisurarum [fenestrarum] sterni[84]
Lig. corpus claviculae[85]
Synd. sternoclavicularis[85]

(continued)

JUNCTURAE STERNI (Osteo. Fig. 4.11) (cont.)

Lig. sternoclaviculare
Synos. interclavicularis (Osteo. Annot. 162-163)
Membrana sternocoracoclavicularis[86]
Lig. sternoprocoracoideum[86]
Lig. sternocoracoideum mediale[86]
Lig. intercoracoideum[86]
Lig. sternocoracoideum longum[86]
Lig. sterno-acrocoracoideum[86]
Lig. sternoclaviculare longum[86]
Lig. sternoacromiale[86]
Lig. coracoideum[86]
Lig. acrocoraco-procoracoideum[87]
Membrana cristoclavicularis[88]
Artc. sternocoracoidea[89]
Capsula articularis
Artc. intercoracoidea[90]
Ligg. collateralia sternocoracoidea[91]
Lig. sternocoracoideum internum
Lig. sternocoracoideum externum[91 89]
Lig. sternocoracoideum laterale[92 89]

JUNCTURAE REGIONIS OMALIS (Fig. 5.3)

Synd. [Artc.] coracoscapularis[93]
Cavitas glenoidalis[93 100]
Lig. coracoscapulare interosseum[93]
Labra cavitatis glenoidalis[93]
Labrum coracoideum
Labrum scapulare
Lig. coracoscapulare dorsale[94]
Lig. coracoscapulare ventrale[94]
Lig. acrocoraco-acromiale[95]
Synd. [Artc.] acrocoracoclavicularis[96]
Lig. acrocoracoclaviculare superficiale
Lig. acrocoracoclaviculare profundum
Synd. procoracoclavicularis[97]
Lig. procoracoclaviculare[97]
Synd. acromioclavicularis[98]
Lig. acromioclaviculare
Lig. scapuloclaviculare dorsale[99]

JUNCTURAE ALAE (Figs. 5.3-5)

ARTICULATIO OMALIS [Artc. coraco-scapulo-humeralis][100] (see Symph. coracoscap.; and Osteo. Annot. 167-171)

Capsula articularis
Cavitas glenoidalis
Lig. coracoscapulare interosseum[93]
Fibrocartilago humeroscapularis[100]
Lig. acrocoracohumerale[101]
Bursa acrocoracoidea[101]
Lig. coracohumerale dorsale[102]
Lig. scapulohumerale dorsale[102]
Lig. scapulohumerale caudale
Lig. scapulohumerale laterale
Lig. humeroscapulare transversum
Bursa supracoracoidea[101]

(continued)

ARTICULATIO OMALIS [Artc. coraco-scapulo-humeralis][100] (see Symph. coracoscap.; and **Osteo.** Annot. 167-171) **(cont.)**

Plicae synoviales et Ligg. intracapsularia[103]
Plica synovialis coracoidea
Plica synovialis scapularis
Plica synovialis transversa
Lig. intracapsulare coracoideum craniale
Lig. intracapsulare coracoideum caudale

JUNCTURAE CUBITI[104] (see Fig. 5.4 and Ligg. acces. alae)

Artc. humeroulnaris[104]
Artc. humeroradialis[104]
Artc. radioulnaris proximalis[104]
Capsula articularis
Lig. collaterale ventrale[105]
Lig. collaterale dorsale[106]
Lig. craniale cubiti[107]
Lig. limitans cubiti[141]
Lig. radioulnare transversum[109]
Meniscus radioulnaris[108]
Trochlea humeroulnaris[110] (Fig. 5.4)
Pars humeralis[110]
Pars ulnaris[110]
Pars humeralis accessoria[110]
Lig. tricipitale[111]

JUNCTURAE CARPI ET MANUS[112] (Fig. 5.5)

Aponeurosis ventralis[113-115]
Retinaculum flexorium[114]
Aponeurosis ulnocarporemigalis[115]
Digitationes remigales[196]
Synd. radioulnaris distalis
Lig. radioulnare interosseum[116]
Artcc. ulnocarpalis et radiocarpalis[112]
Artc. ulnocarpalis
Lig. ulno-ulnocarpale proximale[117]
Lig. ulno-ulnocarpale distale[117]
Lig. ulno-radiocarpale ventrale[118]
Lig. ulno-radiocarpale interosseum[119]
Lig. ulno-metacarpale ventrale[120]
Artc. radiocarpalis[121]
Lig. radio-radiocarpale craniale
Lig. radio-radiocarpale ventrale
Lig. radio-radiocarpale dorsale[121]
Artcc. intercarpales (**Osteo.** Annot. 214)
Meniscus intercarpalis[122]
(Syncc. intercarpales)[123]
Lig. menisco-metacarpale
Artcc. carpo-carpometacarpales[124 112]
Lig. radiocarpo-metacarpale craniale
Lig. radiocarpo-metacarpale dorsale
Lig. radiocarpo-metacarpale ventrale[125]
Lig. ulnocarpo-metacarpale ventrale[126]
Lig. ulnocarpo-metacarpale dorsale[127]

(continued)

JUNCTURAE CARPI ET MANUS[112] (Fig. 5.5) **(cont.)**

Juncturae carpometacarpi
Synoss. carpometacarpales[128]
Synos. intermetacarpalis proximalis[129]
Synos. intermetacarpalis distalis[129]
Artcc. metacarpophalangeales[130]
Artc. metacarpophalangealis alulae[131]
Lig. obliquum alulae[131]
Lig. collaterale caudale
Artc. metacarpophalangealis digiti majoris
Lig. collaterale ventrale[132]
Lig. collaterale caudale[133]
Lig. obliquum intra-articulare[134]
Meniscus articularis[135]
Artc. metacarpophalangealis digiti minoris
Lig. collaterale ventrale
Lig. collaterale dorsale
Juncturae interphalangeales manus
Artc. interphalangealis lateralis[136]
Lig. interosseum
Artc. interphalangealis digiti majoris[137]
Lig. collaterale ventrale
Lig. collaterale craniale
Lig. collaterale caudale[138]
Meniscus articularis
Lig. interphalango-remigale[139 113]

LIGAMENTA ACCESSORIA ALAE[140]

Aponeurosis ventralis carpalis[113-115]
Aponeurosis dorsalis antebrachii[194]
Digitationes remigales[194]
Aponeurosis ventralis antebrachii[194]
Lig. propatagiale[141]
Pars elastica[141]
Lig. limitans cubiti[141]
Lig. humerocarpale[143 195]
Lig. m. extensoris longi digiti majoris[145]
Lig. m. ulnometacarpalis dorsalis[145]
Lig. m. extensoris metacarpi ulnaris[145]
Membrana interossea antebrachii
Retinaculum m. scapulo-tricipitis[142 111]
Retinaculum m. extensoris metacarpi ulnaris[144]
Septum humerocarpale[195]
Trochlea humeralis (see Junct. cubiti)

JUNCTURAE CINGULI MEMBRI PELVICI[146] (see Juncturae synsacri)

JUNCTURAE OSSIS COXAE (**Osteo.** Fig. 4.15)

Sut. iliosynsacralis[73]
Sync. ischiopubica
Sut. ischiopubica[147]
Membrana ischiopubica[147]
Lig. ischiopubicum[147]
Sync. ilioischiadica[148]

(continued)

JUNCTURAE OSSIS COXAE (Osteo. Fig. 4.15) (cont.)

Membrana ilioischiadica[148]
Sync. iliopubica
(Symphysis pubica)[149]
(Symphysis ischiadica)[150]
Membrana acetabuli[151]

JUNCTURAE MEMBRI PELVICI

JUNCTURA COXAE[152] (Fig. 5.6)

Artc. coxocapitalis[152]
Artc. coxotrochanterica[152]
  Capsula articularis
  Labrum acetabulare
Lig. iliofemorale[153]
Lig. pubofemorale
Lig. ischiofemorale[153]
Lig. capitis femoris

JUNCTURAE GENUS[154] (Fig. 5.7)

Artc. femorotibialis[155]
Artc. femorofibularis[156]
Artc. femoropatellaris
  Capsula articularis
  Lig. patellae[158]
  Retinacula patellae
  Lig. collaterale mediale
  Lig. collaterale laterale
  Corpus adiposum retropatellare[158]
Meniscus medialis
  Cornu craniale
  Cornu caudale
  Lig. meniscotibiale caudale
  Lig. meniscofemorale
Meniscus lateralis[159]
  Lig. meniscotibiale craniale
  Lig. meniscofibulare caudale
  Lig. meniscocollaterale[160]
  Lig. meniscofemorale
Lig. transversum genus
Lig. cruciatum craniale
Lig. cruciatum caudale

JUNCTURAE ET LIGAMENTA INTRACRURALES
(see Artc. tib-fib.)

Artc. tibiofibularis[157]
Lig. tibiofibulare craniale[157]
Lig. tibiofibulare obliquum[157]
Synd. tibiofibularis
Lig. tibiofibulare interosseum[161]
Foramen interosseum proximale[162]
Foramen interosseum distale[162]
Membrana interossea cruris
Retinaculum extensorium tibiotarsi[187]

JUNCTURAE TARSI ET PEDIS (Figs. 5.8, 9)

Artc. cartilago-tibiotarsalis[163]
Cartilago tibialis[164]
Os sesamoideum intertarsale[166]
Lig. cartilago-sesamoideum

(continued)

JUNCTURAE TARSI ET PEDIS (Figs. 5.8, 9) (cont.)

Retinaculum flexorium[165]
Retinaculum laterale[165]
Retinaculum mediale[165]
Lig. metatarso-sesamoideum[166 169]
Lig. cartilago-metatarsale[166 169]
Articulatio intertarsalis[167]
  Capsula articularis[165]
  Meniscus medialis[168]
    Cornu craniale
    Cornu caudale
  Meniscus lateralis[168]
    Cornu craniale
    Cornu caudale
  Lig. meniscosesamoideum[169 166]
  Lig. meniscotibiale[170 168]
    Crus mediale
    Crus laterale
  Lig. tibiometatarsale intercondylare[171]
  Lig. intercondylare transversum
  Lig. collaterale mediale[172]
  Lig. collaterale laterale[172]
  Lig. accessorium[172]

JUNCTURAE TARSOMETATARSALES ET INTERMETATARSALES[173]

Synos. tarsometatarsalis[173]
Synos. intermetatarsalis[173]
Synos. intermetatarsalis hallucis[174]
Lig. interosseum[175]
Lig. elasticum metatarsi I[175]
Lig. transversum metatarsale[176]
Canalis flexorius metatarsi[178]
Vagina fibrosa flexoria[178]
Canalis flexorius plantae[178]
Artcc. metatarso-phalangeales[180 182 179]
Aponeurosis plantaris[179]
Corpus adiposum plantare profundum[179]
Corpus adiposum plantare superficiale[179]
Lig. collaterale[181]
Lig. plantare[182] (Fig. 9)
Vagina fibrosa[182]
Os cuneatum[182]
Lig. obliquum hallucis[177]
Lig. rectum hallucis
Artcc. interphalangeales
  Lig. collaterale
  Lig. plantare[182]
  Vagina fibrosa[182]
  Lig. elasticum extensorium unguis[183]
  Lig. elasticum tendinis flexoris[183]

LIGAMENTA ACCESSORIA MEMBRI PELVICI

Ansa m. iliofibularis[186]
  Pars femoralis distalis
  Pars femoralis proximalis
  Pars fibularis
Lig. inguinale[184]
Membrana iliocaudalis[185]
Retinaculum m. fibularis [peronei][188]
Retinaculum extensorium tibiotarsi[187]
Retinaculum extensorium tarsometatarsi[188]

LIGAMENTA PENNARUM[189]

Ligg. remigium primariorum
- Lig. elasticum interremgale major[190]
- Aponeurosis ventralis[113]
- Retinaculum flexorium[114]
- Aponeurosis ulnocarpo-remigalis[115] [113]
  - Digitationes remigales
- Retinacula ulnocarpo-remigalia[191]
- Aponeurosis interphalango-remigalis[192] [139]
  - Digitationes remigales
- Lig. interphalango-remigale[139] [192]
- Ligg. phalangoremigalia distalia[193]
  - Lig. elasticum intertectricale
  - Lig. elasticum intertectricale carpale[198]

Ligg. remigium secondariorum
- Aponeurosis ventralis antebrachii[194]
  - Digitationes remigales
- Aponeurosis dorsalis antebrachii[194]
  - Digitationes remigales
- Lig. elasticum interremigale major[190]
- Lig. elasticum interremigale minor[197]
  - Digitationes remigales
- Septum humerocarpale[195] [143]
  - Digitationes remigales[196]
- Lig. cubiti[199]
- Trochlea humeroulnaris[110] (see Artc. cubiti)
  - Pars humeralis[110]
  - Pars ulnaris[110]
  - Pars humeralis accessoria[110]

Ligg. rectricium
- Lig. elasticum interrectricale[200]

ANNOTATIONS

(1) **Juncturae ossium; Junctura(e); Articulatio(nes).** "Juncturae ossium" is the general term for all types of joints between bones. Some of the flexion zones of the skull are located between bones, others within bones (see Annot. 45 ff.). As a part of a heading for a group of joints the simple, shortened form "Juncturae" is used (e.g., Juncturae columnae vertebralis). The term "Junctura ossea" (literally "bony joint") refers in the strict sense to a synostosis or the nonmoveable fusion of bones to one another. "Articulatio" refers to a freely moveable synovial joint. See **Arthr. Intro.** and Annot. 4 for a discussion of these terms.

(2) **Gomphosis.** Examples of the peg and socket joint in birds are the Artc. quadrato-quadratojugalis and Artc. ectethmomandibularis. See Annot. 24, 25.

Artc. sellaris. This is a synovial joint whose articular surfaces have the configuration of a saddle. Each of the two apposing bones making up the joint has two surfaces at right angles to each other, one concave, the other convex. See, for example, intercorporal joints of cervical vertebrae.

(3) **Lig. elasticum.** Elastic ligaments are found in many parts of the avian body; e.g., in the propatagial skin fold, vertebral column, phallus (**Masc.** Annot. 46), and pedal digits, in certain joint capsules and ligaments of limb joints, as well as those connecting the flight feathers of both wing and tail. See Annot. 93, 141, 183, 190, 197, 198, 200.

(4) **Juncturae capitis; Suturae et Synchondroses cranii.** The avian skull is characterized by a high degree of fusion (synostosis) of its separate elements that occurs in early life; most often the fibrous joints (suturae and syndesmoses) and cartilaginous joints (synchondroses) of many parts of the skull, in particular, and other parts of the postcranial skeleton (see **Intro.**), become ankylosed, often so completely, that traces of the joints are obliterated in mature individuals.

(5) **Sut. supraoccipitoparietalis.** Synonymy: Sutura lambdoidea. A pronounced Crista nuchalis transversa occurs along this suture in certain birds (e.g., *Gavia, Morus, Ardea, Anser, Ceryle.*) See **Osteo.** Annot.17.

(6) **Sut. interparietalis.** Synonymy: Sutura sagittalis.

(7) **Sut. interfrontalis.** Synonymy: Sutura metopica.

(8) **Sut. frontoparietalis.** Synonymy: Sutura coronalis.

(9) **Syncc. interoticae.** The so-called "periotic" complex of otic bones (Os prootica, Os epiotica, and Os opisthotica) coalesce into a unit that contains most of the inner ear structures. See Jollie (1957); Sandoval (1963); Müller (1963); **Osteo.** Annot. 105.

(10) **Sync. interlaterosphenoidalis.** In addition to the joint between the paired laterosphenoid bones, other paired "sphenoid" elements of the base of the fetal skull are connected by cartilage in earlier development; therefore several different "Syncc. intersphenoidales" exist (Jollie, 1957; Müller, 1963) that later become ankylosed. See **Osteo.** Annot. 88.

(11) **Sut. faciei maxillaris; Artcc. maxillae et palati; Zonae flexoriae maxillae.** "Maxillary" in this sense refers to the entire upper jaw/palatal skeleton (**Osteo.** Annot. 35).

(12) **Sut. frontomesethmoidalis.** The rostral end of the mesethmoid plate possesses a horizontal Lamina dorsalis, perpendicular to the interorbital septum, that articulates broadly with the ventral surface of the frontal bones, just caudal to the craniofacial hinge (seen readily in, for example, *Cathartes, Gallus, Anser, Ardea*) (Annot. 46; and **Osteo.** Annot. 109).

(13) **Sut. lacrimo-ectethmoidalis.** Synonymy: Sut. prefronto-ectethmoidalis. The lacrimal and ectethmoid bones are joined along much of their dorsoventral extents in some birds (e.g., *Columba, Corvus, Crotophaga);* whereas only their ventral ends are joined in such forms as *Larus delawarensis* and *Buteo lineatus.* See Newton (1896: 876) and **Osteo.** Annot. 110, 111 regarding the use of "lacrimal/prefrontal".

(14) **Sut. internasalis.** The side-to-side apposition of the nasal bones in the median plane is apparently of rare occurrence. An internasal suture does occur in *Falco tinnunculus* near the craniofacial hinge (Suschkin, 1899) and in the spoonbill, *Platalea* (Hofer, 1945).

(15) **Sut. vomeropalatina.** In neognathous birds the vomer is commonly fused to the rostral end of Os palatinum which rides along the ventrum of Rostrum parasphenoidale; e.g., *Larus,* anseriforms (see Hofer, 1949). Actually the part of the palatine with which the vomer articulates is the so-called antepterygoid (Jollie, 1957; Bock, 1964) which is incorporated into the palatine in adult neognathous birds. See Annot. 17, 28 for vomeropalatine relationships of paleognathous birds; and **Osteo.** Annot. 60.

(16) **Sut. vomeromaxillaris.** This paired joint is located between the maxillopalatine process of the maxilla and the vomer as in passerine and ciconiiform birds. See **Osteo.** Fig. 4.4.

(17) **Sut. interpalatina.** Located between the choanal parts of the right and left palatine bones in the region where they articulate with the parasphenoid rostrum (e.g., *Gavia, Anser,* and *Corvus*). The interpalatine suture becomes ankylosed in some neognathine birds (e.g., *Eudocimus, Morus, Caprimulgus*); in most ratites the palatines are separated from one another by the vomer and the pterygoids. See Hofer (1945, 1954) and Bock (1963) for different palatal configurations. See also Annot. 28 and **Osteo.** Figs. 4.4, 7. Sut.pterygopalatina.

Sut. interpterygoidea. At their articulations with the parasphenoid rostrum, the paired pterygoid bones also articulate with one another in certain birds, e.g., psittacids.

(18) **Sut. intervomeralis.** In mature birds in which the vomer is present it is a single midline structure related to the distal part of the parasphenoid rostrum; however, in fetal life the vomers are paired. The right and left vomers ultimately fuse except in woodpeckers (e.g., *Picus minor;* Coues, 1927) in which they persist as separate elements on either side of the mesethmoid septum. In mature dried skulls of forms such as *Gallinago, Larus,* and *Corvus* some evidence of the original paired elements can be distinguished in the form of a notch or cleft at either the rostral or caudal end of the vomer. See **Osteo.** Annot. 68, 69.

Sut. intrapterygoidea; Sut. pterygopalatina. See **Osteo.** Annot. 60, 61 for discussion of these terms.

(19) **Artc. jugolacrimalis; Sut. jugolacrimalis.** Synonymy: Sut. [Artc.] jugoprefrontalis. The lacrimal bone is firmly anchored by ligaments (occasionally synostosed) to the jugal arch in some forms: penguins (Zusi, 1974), *Pelecanus, Balaeniceps;* however, this does not hinder kinesis since the lacrimal moves with the arch as an integral part of the upper jaw (Bühler, 1970). In other birds (e.g., *Cathartes, Pelecanus, Corvus*) the lacrimal articulates with the jugal arch via a lengthy ligament (Annot. 20) that allows movement between the two bones, hence a syndesmosis rather than a suture. The ligament is attached to the prominent Tuberculum lacrimale on the jugal arch in, e.g., *Pelecanus, Rhamphastos.* In other taxa the joint between lacrimal and jugal arch is a synovial articulation (e.g., *Gavia, Morus,* and tinamous; Beddard, 1898). See **Osteo.** Annot. 111; Davids (1952).

(20) **Lig. jugolacrimale** (Zweers, 1974). Synonymy: Lig. jugoprefrontale (NAA, 1979). Connects Tuberculum lacrimale of Arcus jugalis (**Osteo.** Annot. 11) with the ventral tip of Os lacrimale (e.g., anseriform birds). Ghetie, et al. (1976) describe Membrana lacrimomaxillaris rostral to Lig. jugolacrimale in *Anser;* the membrane should be called Membrana jugolacrimale.

(21) **Symphysis mandibularis.** Synonymy: Sut. intermandibularis; Sut. interdentalis. This is actually a synchondrosis between the right and left Ossa dentalia; these bones have overgrown and covered the cartilaginous joint of earlier development. Ultimately the symphysis is ossified, producing a synostosis in adults of most birds. See **Osteo.** Fig. 4.1.

(22) **Sync. rostromesethmoidalis.** Synonymy: Sync. mesethmo-rostroparasphenoidalis. Originally a cartilaginous joint between the parasphenoid rostrum and the mesethmoid plate which later become synostosed.

(23) **Artc. vomerorostralis.** Synonymy: Artc. vomero-rostroparasphenoidalis (NAA, 1979). All birds that have been studied so far show a movable articulation between the vomer and the ventral edge of Rostrum parasphenoidale. See Hofer (1949) for discussion of articulations of the vomer in different taxa.

In many birds the palatine and pterygoid bones as well as the vomer contact the parasphenoid rostrum; such contact takes the form of a sliding joint that is part of the kinetic mechanism of the skull.

Lig. mesethmovomerale [Lig. vomerale] (Fig. 5.1). Extends from ventrocranial edge of the interorbital septum to the vomer; occurs in anseriforms (Fisher and Goodman, 1962; Zweers, 1974).

(24) **Artc. quadrato-quadratojugalis.** Often a synovial joint in which a peg or condyle of Os quadratojugale fits into a cotyla in the lateral aspect of the quadrate bone. In *Sturnus* (De Kock, 1955) and in *Caprimulgus* (Bühler, 1970) this joint is a syndesmosis, not a synovial joint. See **Osteo.** Fig. 4.4.

Lig. interosseum. This is a strong ligament connecting the condyle of the quadratojugal to the bottom of its socket in the quadrate bone (e.g., *Anser, Cairina*).

(25) **Artc. quadrato-squamoso-otica.** In certain avian taxa each of the two condyles of Proc. oticus of the Quadratum articulates independently of the other; therefore, two separate joint cavities are present: Art. quadratosquamosa and Artc. quadrato-otica (e.g., *Columba*). In other taxa both condyles of the quadrate and their receiving surfaces on the otic and squamosal bones are enclosed within one common articular capsule (e.g., *Gallus, Corvus*).

Lig. quadratosphenoidale. In the pigeon this is a short, broad ligament which connects the caudomedial side of the quadrate to the Os parasphenoidale at the point where the latter forms the rostrodorsal border of the tympanic cavity (van Gennip, 1986).

Lig. quadratotemporale. Lig. quadratotemporale connects Proc. suprameaticus to the caudal border of the otic process of the quadrate of the pigeon (van Gennip, 1986).

(26) **Artc. quadratopterygoidea.** A common configuration of this joint among birds is a single cotyla of the proximal end of Os pterygoideum articulating with the Condylus pterygoideus near the mandibular process of the quadrate bone. The pterygoid articulates via two facets in the grouse, *Tympanuchus,* and the pheasant, *Phasianus;* located between the two facets is the pneumatic foramen of the Os quadratum in *Tympanuchus*. See Hofer (1945) for differences in this joint related to the degree of kinesis of the upper jaw. See **Osteo.** Annot. 72.

(27) **Artc. pterygorostralis; Artc. pterygobasipterygoidea.** Synonymy: Artc. pterygo-rostroparasphenoidalis. (1) In some avian forms (e.g., *Ardea, Fulica, Thalasseus, Coccyzus, Corvus*) the rostral end of Os pterygoideum (Pes pterygoidii) articulates with the palatine bone (see Annot. 28) and Rostrum parasphenoidale (**Osteo.** Annot. 69, 96.). (2) In other birds (e.g., *Cathartes, Gallinago, Caprimulgus, Columba*) the middle of the length of Os pterygoideum also articulates with the Proc. basipterygoideus of Rostrum parasphenoidale. (3) In *Rhea* the basipterygoid process articulates with the caudal end of Os pterygoideum (Bock, 1963). (4) In the anseriforms *Anser* and *Cairina* the basipterygoid process is located rostrally near the pterygopalatine articulation, and is the only articulation of Os pterygoideum with the Rostrum. See Annot. 23; **Osteo.** Fig. 4.4 and Annot. 60.

(28) **Artc. pterygopalatina.** Synonymy: Sut. intrapterygoidea. The pterygopalatine synovial joint is actually the Sutura intrapterygoidea in many neognathous birds in which a rostral part of the developing fetal Os pterygoideum ("antepterygoid") unites with the caudal end of Os palatinum; the "postpterygoid" remains as the definitive

Os pterygoideum (Jollie, 1957); this division and reattachment of part of the pterygoid does not occur in *Rhea* (Müller, 1963). In ratites the palatine is united to the lateral side of the pterygoid (**Synd. pterygopalatina**) instead of its rostral end as in neognaths (Bock, 1963). See Annot. 15 and 29; and **Osteo.** Fig. 4.4 and Annot. 60-61.

(29) **Artc. palatorostralis.** In neognathous birds this is the synovial joint between the palatine bone and the lower border of the parasphenoid rostrum (see **Osteo.** Annot. 62). In ratites the pterygoid is interposed between the rostrum and the palatine bone. See Annot. 28, 23.

Lig. mesethmopalatinum [L. orbitale]. Passes from the interorbital septum to the articulation between pterygoid and palatine bones as in anseriforms (Fisher and Goodman, 1962; Zweers, 1974).

(30) **Lig. suborbitale** (Fig. 5.1). Synonymy: Lig. suboculare (Bock, 1964). This thin fascial/ligamentous band stretches from the ventral tip of Os lacrimale to Proc. postorbitalis and the upper end of Lig. postorbitale. The suborbital ligament participates in the formation of the ventrolateral wall of the orbit. See Fig. 5.1; and **Osteo.** Annot. 30.

Lig. maxillomandibulare. Located at the corner of the mouth, it extends from the rostral end of the jugal bar to the upper border of the mandible near its coronoid process. This ligament is known only in caprimulgids (Bühler, 1981); it functions to prevent excessive opening of the mouth.

(31) **Membrana circumorbitalis.** The thickened fibrous rim of the orbit is attached to its supraorbital margin, the Os lacrimale, the jugal arch, and suborbital ligament; the membrane may be continuous with the orbital septum (Elzanowski, 1987).

Septum orbitale. The attenuated, thin extension of Membrana circumorbitalis that forms the connective tissue framework of the eyelids (palpebrae).

Membrana temporalis. Synonymy: Lig. temporale (Bas, 1955). Spans the temporal fossa, and serves as partial origin of the underlying muscles that fill the fossa (Bas, 1955; Zusi, 1975). See **Osteo.** Fig. 4.1 and Annot. 104; **Myol.** Annot. 18.

(32) **Artc. [Synd.] mandibulosphenoidalis.** Synonymy: Artc. mandibulo-parasphenoidalis; Artc. articulo-parasphenoidalis; Artc. articulo-basitemporalis. The mandible of some birds possesses these direct articulations of the mandible with the parasphenoid bone of the base of the skull in addition to its indirect articulation via the quadrate bone. In these mandibulosphenoid joints, each Proc. mandibularis medialis abuts a process of the parasphenoid lamina forming the so-called "medial brace" of the mandible (Bock, 1960). In birds having the brace (e.g., *Rynchops nigra*, *Pygoscelis adeliae*) the medial process of the mandible articulates with either the medial or lateral parasphenoid (basitemporal) processes of the lamina (varying in different taxa; **Osteo.** Annot. 96-97). Bock contends that the brace supports the open mandible, preventing its caudal dislocation in birds wherein the condyles of the quadrate and the receiving cotylae of the mandible do not form a strongly interlocked joint, a viewpoint with which Zusi (1967) disagrees. See Bock and Morioka (1971) for a discussion of the functional properties of the mandibulosphenoid joint. See Annot. 33 and **Osteo.** Annot. 84.

Lig. mandibulosphenoidale. Synonymy: Lig. mandibulo-basiparasphenoidale. This ligament strengthens the mandibulosphenoid joint which is a syndesmosis in some species (e.g., *Charadrius*, Bock, 1960), a synovial joint in others (e.g., *Rynchops*).

(33) **Synd. mandibulo-occipitalis.** Synonymy: Synd. occipito-mandibularis (NAA, 1979). Caprimulgids exhibit this unusual incidence of a direct junction of the mandible with the braincase; this syndesmosis connects the paraoccipital process of the exoccipital with the Proc. medialis mandibulae (Bühler, 1981) by means of the **Lig. mandibulo-occipitale.** The name of the ligament has been changed to avoid confusing it with the omnipresent occipitomandibular ligament in the retroarticular region (see Annot. 37).

(34) **Lig. intramandibulare.** Connects the two elements of the oblique hinged flexion zone of the Ramus mandibulae at the junction of its rostral and middle thirds in *Caprimulgus* (Bühler, 1970). See Zonae flex. mand.; Fig. 5.2; and **Osteo.** R. mandibulae.

Lig. laterospheno-jugale. In hornbills (Bucerotidae) this ligament connects the postorbital process of Os laterosphenoidale with the jugal bar (Starck, 1940).

(35) **Artc. quadratomandibularis.** Synonymy: Artc. quadrato-articularis. See Zusi (1967) for a thorough discussion of the avian quadratomandibular joint. The quadrate bone articulates mostly with Os articulare of the mandible usually by means of three articular condyles (Bock, 1960), four in the New World jays (Zusi, 1987). See **Osteo.** Annot. 72.

(36) **Lig. quadratomandibulare caudale.** This ligament extends from Proc. pterygoideus of the quadrate to the mandible near the base of its medial process. The ligament is stretched during opening of the jaws; relaxation of M. depressor mandibulae causes the jaws to snap shut by elastic recoil of the ligament (Bock and Morony, 1972). Present in most passerines; particularly well developed in tyrannid flycatchers.

Lig. quadratomandibulare rostrale (Elzanowski, 1987). This ligament is fastened to the rostral surface of the body of Os quadratum between its pterygoid and quadratojugal articular facets, and is attached to the mandible just forward of its quadrate cotylae. Lig. quadratomandibular rostrale is elastic in *Columba* and *Tinamus*, nonelastic in bucerotids (Elzanowski, 1987); present also in passerines (Bock and Morony, 1972).

Lig. quadratomandibulare temporale. This ligament in the pigeon connects the Proc. supramеaticus to the quadrate on its edge between the dorsal and caudolateral surfaces. It restricts medially directed movements of the quadrate, relative to the cranium (van Gennip, 1986).

Lig. quadratomandibulare laterale. In the pigeon this broad, short ligament is attached to the Proc. lateralis mandibulae just caudal to the Lig. postorbitale and extends to the Proc. mandibularis of the quadrate (van Gennip, 1986).

(37) **Lig. occipitomandibulare** (Bock, 1964). Synonymy: Lig. exoccipitomandibulare; Lig. depressor mandibulae (Rooth, 1953); Lig. neurocranio-mandibulare (Fuchs, 1955; Davids, 1952). The band-like occipitomandibular ligament is continuous with the medial edge of Membrana postmeatica (see below); it spans the quadratomandibular and quadrato-squamoso-otic joints, and connects the medial part of the Crista transversa fossae (**Osteo.** Annot 51) of the mandible to the Proc. paroccipitalis that partially bounds the tympanic cavity. The superficial surface of the ligament serves as partial origin of the deep part of M. depressor mandibulae (**Myol.** Annot. 24) and contributes to the caudoventral wall of the Meatus acusticus externus. See Fig. 5.1; and **Osteo.** Annot. 19, 21.

Membrana postmeatica (Elzanowski, 1987). Thick, fibrous sheet attached to the dorsal, ventral, and caudal margins of the osseous external acoustic meatus; also

attached to the lateral border of the Lig. occipitomandibulare and the lateral part of the Crista transversa fossae (**Osteo.** Annot. 51) of the mandible (**Osteo.** Annot. 51). The membrane forms much of the caudoventral wall of the acoustic meatus (see above) where it is lined with skin; it is covered caudally by M. depressor mandibulae. See **Osteo.** Annot. 19, 21, 51, 85.

(38) **Lig. jugomandibulare mediale.** Synonymy: Lig. jugomandibular internum; Lig. jugale (Fuchs, 1955); Lig. jugo-mandibulare caudale (Bas, 1955); Lig. quadratojugo-mandibulare mediale. This ligament actually connects the quadratojugal part of the jugal arch with the caudal end of the mandible; the ligament is attached near the apex of the medial process of the mandible (see Lebedinsky, 1921, who discusses the medial point of attachment of this ligament). Two medial jugomandibular ligaments are present in the hornbill, *Tockus* (Rawal and Bhatt, 1973); the ligament is absent in *Rynchops* (Zusi, 1962) and in tinamous (Elzanowski, 1987). See **Intro.** Annot. 39, 40 and Fig. 5.1.

(39) **Meniscus articularis.** In anseriforms (Hofer, 1945; Zweers, 1974) this distinct wedge-shaped meniscus is found in the caudal part of the quadratomandibular joint where it is attached to the internal aspect of the transverse part of the Lig. jugomandibulare mediale.

(40) **Lig. jugomandibulare laterale.** Synonymy: Lig. jugo-mandibulare rostrale (Bas, 1955); Lig. quadratojugo-mandibulare laterale. This short ligament is attached to the caudolateral end of the jugal arch just opposite the quadratojugo-quadrate joint, and extends to the lateral process of the mandible. See **Intro.** Annot. 38 and Fig. 5.1.

(41) **Lig. lacrimomandibulare** (Davids, 1952; Goodman and Fisher, 1962). Synonymy: Lig. prefrontomomandibulare (NAA, 1979). Typical of anseriforms, this subcutaneous ligament extends caudoventrad from the ventral tip of Os lacrimale, passes lateral to the quadratojugal bone, and is attached to the rostrodorsal tip of the Proc. mandibularis lateralis. According to Davids (1952) this ligament resists retraction of the mandible upon contraction of its adductor muscles. In *Anser* it forms a distinct wide band that contributes to the rostroventral wall of the orbit; in *Mergus* it is absent (Goodman and Fisher, 1962). See Fig. 5.1; **Osteo.** Annot. 110, 111; and illustration in Zweers (1974).

(42) **Lig. postorbitale.** The term, Lig. postorbitale is almost universally employed, the term reflecting one of its attachments, namely, the apex of Proc. postorbitalis of Os laterosphenoidale (**Osteo.** Annot. 30). At its ventral end the ligament is affixed to the Proc. lateralis mandibulae or to a tubercle somewhat rostral to Proc. lateralis (*Diomedea, Larus*). In some birds, where the ligament crosses the caudal end of the jugal arch, it produces a notch. In others Lig. postorbitale may have different attachments: in tinamous (Elzanowski, 1987) and *Balaeniceps* it is fastened to the Arcus jugalis; in *Podilymbus* the zygomatic process is an accessory attachment (Zusi and Storer, 1969). Lig. postorbitale assists in supporting the quadratojugo-quadrate articulation, and plays a role in kinesis of the upper jaw (Bock, 1964; Zusi, 1967). See Osteo. Annot. 30.

Lig. orbitoquadratum (Elzanowski, 1987). Unique to tinamous, this ligament extends from the orbital process of Os quadratum to the dorsal wall of the orbit, dorsal and rostral to the Foramen n. maxillomandibulare.

(43) **Lig. zygomaticomandibulare.** Synonymy: Lig. squamosomandibulare (Lebedinsky, 1921). This ligament connects the zygomatic process of Os squamosum to the coronoid process of the mandible.

(44) **Artc. ectethmomandibularis.** Bock and Morioka (1971) described this unusual peg and socket synovial joint between the dorsal border of the mandible and the ventral tip of Os ectethmoidale in the meliphagids.

(45) **Zonae flexoriae ossium faciei (Arthr** Intro). Substitute term for the "Zonae elasticae ossium faciei" (NAA, 1979). These are bending zones of the bones of the facial skeleton. See Bock (1964), Zusi (1967, 1984), and Bühler (1981) for reviews dealing with kinesis of the avian skull.

(46) **Zona flexoria craniofacialis** (Fig. 5.2). Synonymy: Ginglymus craniofacialis or frontonasalis (see Bühler, 1970 for comments on the usage of these terms); Zona elastica craniofacialis (NAA, 1979). In birds the bending zone between neurocranium and the facial skeleton is a transverse band of limited rostrocaudal extent consisting of thinned parts of the Proc. premaxillaris of Os nasale and the Proc. frontalis of Os premaxillare at their junction with the rostral ends of Os frontale and Lamina dorsalis of Os mesethmoidale. The cranio-facial connection occurs only rarely as a syndesmosis or as a synovial joint (large parrots, e.g., *Ara*).

The craniofacial flexion zone has been commonly known in the literature as the craniofacial or frontonasal hinge. Although "ginglymus" (Ginglymos, Gk. hinge) is descriptively apt, in widespread use, and easily understood, there has been objection to its use. In a general sense a hinge may be jointed or flexible; however, in its anatomical sense ginglymus pertains strictly to a hinge-type, synovial articulation. Another reason for adoption of "Zona flexoria craniofacialis" is for the sake of consistency with the names of the other flexion zones of the facial skeleton.

The craniofacial flexion zone is a transverse axis of bending that permits movements of elevation and depression of the upper jaw (kinesis) (see Annot. 23). The zone may be undifferentiated in dorsal view, it may be visible as a narrow, flat, transverse band, or it may be sharply diffentiated caudally by inflated bone of the cranium and rostrally by inflation of the maxilla. In some birds the zone is a long, indefinite region; in others it is marked dorsally by a distinct, transverse sulcus floored by thin bone (*Morus, Rynchops, Strix, Cacatua, Ceryle*). In other forms, the flexion zone is a narrow, transverse seam flush with the dorsal surfaces of bones rostral and caudal to it (*Gavia, Cathartes, Ardea, Aix, Coccyzus*).

The craniofacial zone is short (in its rostro-caudal dimension) in birds with holorhinal nostrils; the entire upper jaw rotates (elevation-depression) as a unit about the zone at the base of the upper jaw; this is the prokinetic condition common to most birds. See Hofer (1954), Bühler (1981), and Zusi (1984) for discussions of the different types of craniofacial flexion zones.

Zona flexoria craniofacialis lateralis; Zona flexoria craniofacialis medialis. Schizorhinal birds with long attenuated nostrils have two craniofacial axes of the craniofacial bending zone (Fig. 5.2). The two axes are some distance apart, the axis of the lateral zone located more caudally than the axis of the medial zone (e.g., *Larus, Pluvialis*). Zona lateralis is formed by the lateral portions of the nasal bones near their fusion with the frontal bones. The other, Zona medialis, consists of the frontal processes of the premaxillary bones and, with a few exceptions, the medial portions of the nasals (Zusi, 1984). See Fig. 5.2.

(47) **Zonae flexoriae maxillares.** (see Fig. 5.2; Annot. 11; **Osteo.** Annot. 53). Synonymy: Zonae elastica maxillares (NAA, 1979). These are the flexion zones of the upper jaw exclusive of the craniofacial hinge. In rhynchokinetic birds, which are usually schizorhinal, kinetic movements include bending of the upper jaw at one or more locations other than the craniofacial zone (e.g., the paleognaths, some

gruiforms, some charadriiforms, pigeons, and a few other birds) (see Fig. 5.2); and Zusi (1967, 1984), Bock (1964), Bühler (1981).

Zona flexoria rostrodorsalis (Fig. 5.2). Synonymy: Zona elastica premaxillonasalis distalis (NAA, 1979). A bending zone just caudal to the maxillary rostrum (**Osteo.** Annot. 40) on the dorsal bar of the upper jaw. **Zona flexoria rostroventralis.** Synonym: Zona elastica premaxillomaxillaris (NAA, 1979). A bending zone (sometimes extensive) caudal to the maxillary rostrum **Osteo.** Annot. 40) on the ventral bars of the upper jaw.

Zona flexoria dorsomedialis (Fig. 5.2). Synonymy: Zona elastica premaxillonasalis proximalis (NAA, 1979). A bending zone near the middle of the length of the dorsal bar of the upper jaw, typical of ratites.

Zona flexoria arcus jugalis. The flattened flexion zone at the thinned rostral end of the jugal arch (Fig. 5.2) has become specialized into a syndesmosis in cardueline finches.

Zona flexoria palatina (Fig. 5.2). The flexion zone of the premaxillary process of Os palatinum is represented by a syndesmosis in parrots. Upward bending of this zone in *Columba* is limited by **Lig. palatomaxillare** (van Gennip, 1986).

(48) **Zonae flexoriae mandibulares** (Fig. 5.2). Certain birds, especially those that swallow large food items (sphenisci-, procellari-, pelecani-, ciconii-, anseri-, and charadriiforms) possess two zones of bending in each ramus of the mandible that permit widening of the interramal distance.

Zona flexoria intramandibularis rostralis. Synonymy: Zona elastica intramandibularis distalis. The rostral intramandibular zone is near Rostrum mandibulae (**Osteo. Annot. 40). Zona flexoria intramandibularis caudalis.** Synonymy: Zona elastica intramandibularis proximalis. In general the caudal intramandibular zone is situated at the junction of the middle and caudal thirds of the ramus of the mandible in the vicinity of the rostral mandibular fenestra; the caudal zone is elongated in *Pelecanus*. See **Osteo.** Annot. 42, 46. Consult Yudin (1961), Zusi (1962, 1974), and Bühler (1981).

(49) **Synd. intramandibularis caudalis.** In *Caprimulgus* (and probably in Nyctibiidae) the bending zone of the mandible is developed as a distinct, oblique, mobile, syndesmotic joint situated between the rostral and intermediate thirds of the length of the mandibular ramus (Bühler, 1970). See **Osteo.** Ramus mandibulae, Fig. 4.1.

(50) **Juncturae apparatus hyobranchialis [hyolingualis].** Names for these joints are based mostly on the terminology that McLelland (1968) adopted for the elements of the hyobranchial apparatus. Zweers (1974, *Anas*) and Homberger (1986, *Psittacus*) designate several ligaments associated with joints between the basihyal, urohyal, and ceratobranchial elements that are mainly capsular ligaments rather than discrete collateral ligaments. See **Osteo.** Annot. 79.

(51) **Synd. interparaglossalis.** The paired paraglossal elements in some parrots are joined by cartilage rostrally and a fibrous connection caudally (Beddard, 1898; Homberger, 1986).

Artc. paraglosso-basihyalis. Synonymy: Artc. basihyoentoglossalis; Artc. basihyoparaglossalis; Artc. entoglosso-basibranchialis (NAA, 1979). This is a saddle-type joint (Artc. sellaris; Annot. 2) in *Anas* (Zweers, 1974). For the most part only side to side movements are permitted in others: e.g., *Columba, Fulica*).

(52) **Sync. [Artc.] basihyo-urohyalis.** Synonymy: Sync. basihyobasibranchialis; Sync. [Artc.] intrabasibranchialis (NAA, 1979). Usually a cartilaginous joint between the rostral and caudal basibranchial elements in *Gallus* (McLelland, 1968); and *Columba* (Zweers, 1982). The rostral element represents the basihyal and the caudal element represents basibranchiale I. See **Osteo.** Annot. 81.

(53) **Artc. ceratobasihyalis.** Synonymy: Artc. basihyoceratobranchialis; Artc. ceratobasibranchialis (NAA, 1979). Os ceratobranchiale is the proximal element of the branchial cornu; in certain birds the ceratobranchial articulates with both the basihyal and the urohyal. See Homberger (1986).

(54) **Sync. [Artc.] Epi-ceratobranchialis.** Synonymy: Artc. ceratohyo-epibranchialis; Sync. intracornualis (NAA, 1979).

(55) (56) These annotations have been withdrawn. See **Resp.** Juncturae laryngis.

(57) **Synd. urohyocricoidea.** Synonymy: Synd. cricobasibranchialis (NAA, 1979). In some birds (*Columba, Strix*) the caudal basibranchial element is connected by fibrous tissue to the ventral surface of the body of Cartilago cricoidea of the larynx.

(58) **Lig. arytenoparaglossale.** Paired cords of elastic tissue in *Gallus* that connect the rostral processes of the arytenoids with the cornua of the paraglossal bones. The ligaments are longer and thicker in males than in females (White, 1975).

(59) **Juncturae columnae vertebralis.** Consult Barkow (1856) for an extensive review of interspecific variation in the arthrology of the avian vertebral column. See Fig. 5.10 and **Osteo.** Fig. 4.15.

(60) **Artc. intercorporalis** (Barkow, 1856). The joints between adjacent vertebral bodies in the cervical region and the cranial part of the thoracic region are synovial joints, some with intra-articular menisci (see Annot. 61-64, 71, 74, 78). In the caudal thoracic region of some taxa, and the synsacral region universally, these joints become ankylosed, forming synostoses; the joints between the bodies of the free caudal vertebrae are symphyses (*Columba*, Baumel, 1988) or synovial joints (*Gallus*, du Toit, 1912-13).

In birds generally, the intercorporal joints throughout the length of the presynsacral vertebral column are mostly Artcc. sellares (Annot. 2) (heterocoelous; saddle-shaped) (Beddard, 1898). The vertebral bodies of the thoracic vertebrae are opisthocoelous in penguins, in Charadrii, and in some parrots (Parker, 1888). See **Osteo.** Annot. 113b; Figs. 4.8, 9.

Lig. collaterale (Fig. 5.10). This strong paired collateral ligament connects vertebral bodies; it is continuous with the articular capsule of the intercorporal joints. The caudal end of the lateral surface of each vertebral body exhibits a distinct tuberosity for attachment of this ligament (**Osteo.** Fig. 4, 8D) (see Barkow, 1856).

(61) **Meniscus intervertebralis.** Synonymy: Fibrocartilago intercalaris corpum vertebralium (Jäger, 1858). The synovial joints between bodies of cervical vertebrae are incompletely divided by intra-articular menisci, attached at their periphery to the inner aspect of the articular capsule (e.g., the ibis *Eudocimus* and the owl *Strix* (pers.

obs.); *Anas* (Landolt and Zweers, 1985); *Gallus*, (Zweers, et al., 1987). The menisci are thin toward their centers, having openings, (**Fenestrae centrales,** (Landolt and Zweers, 1985) of variable shape (Jäger, 1858). According to Jäger in *Anas* the menisci in the thoracic region are attached to the margins of adjacent vertebral bodies as well as to articular capsules.

Anulus [Annulus] fibrosus. In certain birds (e.g., *Columba, Gallus*) instead of a proper meniscus the intervertebral connective tissue consists merely of a thickened ring attached to the inner surface of the articular capsule. In *Anas* the Anulus fibrosus is variably attached to the circumference of adjacent vertebral bodies and to the articular capsule (Jäger, 1858).

(62) **Discus intervertebralis.** A complete articular disc connects the bodies of the free caudal vertebrae. Lacking a synovial cavity, these joints are symphyses (Barkow, 1856), consisting in large birds (*Meleagris, Branta*) of elastic cartilage (J. Baumel and R. E. Brown, pers. obs.).

(**Lig. suspensorium corporum vertebralium**). Vestige of the notochord that persists in some adult birds (Jäger, 1858). In *Anas* with vertebrae separated, the point of attachment of the suspensory ligament to the center of the articular surfaces of adjacent vertebral bodies is marked by small, rough indentations (Zweers, 1974); Landolt and Zweers, 1985).

(63) **Lig. elasticum interlaminare** (Fig. 5.10). Synonymy: Lig. flavum; Lig. interarcuale. Present mostly in cervical and thoracic regions; these ligaments are unpaired narrow bundles that connect laminae of adjacent vertebrae (see **Osteo.** Annot. 126 for bony attachments; and Boas, 1929). Boas notes that the ligaments are strongest in the caudal cervical region.

Lig. elasticum interspinale. Boas (1929) described an additional system of elastic ligaments spanning the dorsal concavity of the root of the neck in *Rhea;* these are the Ligg. elasticae interspinales profunda et superficiales of Barkow (1856). Landolt and Zweers (1985) describe elastic tissue connections between the spinous processes of the caudalmost cervical and cranial thoracic vertebrae in *Anas* and *Gallus* as well as those between the axis and the third cervical vertebra. An elastic ligament connects the cranial margin of the pygostyle with the caudal vertebra cranial to it in *Columba* (Baumel, 1988).

Lig. interansale. Synonymy: Lig. laterale (Zweers, et al., 1987). A serial ligament found over the length of the cervical vertebral column connecting the caudal edge of the Ansa costotransversaria (**Osteo.** 4.8) with the cranial border of the Ansa of the next most caudal vertebra (Zweers, et al., 1987).

Lig. ventrolaterale. In *Anas* this ligament connects the Proc. caroticus (**Osteo.** 4.8B) of one vertebra with the Crista ventrolateralis of the vertebra cranial to it (Zweers, et al., 1987). See **Osteo.** Annot. 121.

Lig. intercristale ventrale. Synonymy: Lig. interspinale ventrale (Zweers, et al., 1987). In *Anas* this ligament connects the ventral crests (processes) of cervical vertebrae 12–16 with one another in *Anas* (Zweers, et al., 1987), and is well developed in the thoracic vertebrae of other birds. See **Osteo.** Annot. 119.

(64) **Artc. atlanto-occipitalis; Fibrocartilago atlantis.** The occipital condyle fits into Fossa condyloidea of the Atlas. In some taxa the fossa is a complete osseous cup; in others it is an osseous semiring ventrally, completed dorsally by Fibrocartilago atlantis (intercartilago atlantis, Boas, 1929). The floor of the fossa is perforated by a foramen that transmits the Lig. apicis dentis (see Goedbloed, 1958 and **Osteo.** Fig. 4.8E).

(65) **Artc. zygapophysialis** (see **Osteo.** Columna vertebralis). In order to remain consistent with the human and veterinary nomenclatures, "Proc. articularis" is designated as an alternative term for the osseous Proc. zygapophysialis (**Osteo.** Annot. 132). "Artc. zygapophysialis" is widely used in comparative vertebrate anatomy as a term applying only to the synovial joints between zygapophyses of adjacent vertebrae, whereas "processus articularis" is nonspecific as to its location and confusing when referring to joints.

(66) **Meniscus articularis.** According to Barnett (1954b) the zygapophysial joints of the cervical vertebral column of *Columba palumbus* possess thin, fibrous menisci containing scattered cartilage cells.

(67) **Membrana atlanto-occipitalis.** Synonymy: Lig. capsularis atlanto-occipitalis (Goedbloed, 1958). The continuity between the ventral and dorsal membranes (connecting the atlas with the margin of the foramen magnum) is interrupted on each side by the exit from the cranial cavity of the huge V. occipitalis interna.

(68) **Artcc. atlantoaxiales.** In certain avian taxa the atlas and axis articulate by means of two separate synovial joints, one between the Dens and the Corpus atlantis and the second between Corpus atlantis and Corpus axis. In most birds two additional zygapophysial synovial joints connect the vertebral arch of the atlas with that of the axis. See Boas (1929), Goedbloed (1958), and Weisgram and Zweers (1987) for details of the atlantoaxial joints and several other ligaments in **Anas; Osteo.** Annot. 130-133.

(69) **Lig. transversum atlantis.** Ossified in some birds (e.g., *Phalacrocorax, Numenius,* and *Corvus,* Goedbloed, 1958), this transverse ligament of the atlas holds the dens of the Axis against Facies articularis dentalis of the Atlas. Weisgram and Zweers (1987) describe the nonossified ligament in *Anas.*

Lig. medianum atlantoaxiale. Boas (1929) describes this ligament that extends from the ventral surface of the root of the Dens to the dorsal aspect of Corpus atlantis at a point just caudal to the Artc. atlantodentalis.

Lig. collaterale atlantoaxiale. Strong paired ligaments corresponding to the alar ligaments of mammals in that they limit rotatory movements between atlas and axis; these ligaments extend transversely from foveae on each side of the root of the dens to impressions on the inner surface of the atlas lateral to Facies articularis dentalis. Each Lig. collaterale is fused with the ventral surface of Lig. transversum atlantis.

(70) **Synos. costotransversaria; Artc. costotransversaria.** With the exception of the atlas, most cervical vertebrae of adult birds have costal processes ankylosed to transverse processes and to vertebral bodies; The Foramen transversarium (for the vertebral artery) is partly bounded by the costal process (Boas, 1929) (see **Osteo.** Annot. 134, 135, Ansa costotransversa). In the root of the neck a variable number of short, movable cervical ribs are found in most birds.

(71) **Juncturae notarii.** The Notarium is a rigid, consolidated unit of vertebrae formed by ankylosis of the bodies and the transverse and spinous processes of the intermediate group of thoracic vertebrae. In some taxa lacking the Notarium some rigidity is brought about by mortising of adjacent vertebral spines. Some stiffening of the thoracic vertebral column is produced in other birds (e.g., pelecaniforms, charadriiforms, and anseriforms) by ossification of the tendons of epaxial muscles that ankylose with the transverse processes and spinous processes of the vertebrae. See **Osteo.** Annot. 73, 140 and Fig. 4.9.

Artc. notariosynsacralis. In taxa possessing the notarium one or two freely moveable synovial (or cartilaginous) joints are present between the notarium and the synsacrum (exception: *Pelecanus* Barkow, 1856). Baumel, et al. (1990) have determined that ventilatory movements of the entire pelvis (plus uropygium) occur at the notarial/synsacral joint(s) (**Osteo.** Fig. 4.9).

(72) **Lig. intercristale ventrale.** The series of thoracic and cervical vertebrae at the root of the neck are characterized by prominent ventral crests that are connected by these unpaired longitudinal ligaments. In some adult birds Ligg. intercristalia are partially ossified. See **Osteo.** Annot. 119.

(73) **Juncturae synsacri.** The Synsacrum is formed by a variable number of the caudalmost thoracic vertebrae, the lumbar, sacral, and the cranialmost series of caudal vertebrae that are ankylosed in varying degree in different taxa. The synsacrum becomes united with the pelvic girdles on each side (see Annot. 76). This topic is covered for large comparative series of birds by Barkow (1856) and Boas (1933). See **Osteo.** Annot. 141a and Fig. 4.9.

(74) **Synos. intercorporalis.** In postnatal life the fibrocartilaginous joints connecting bodies (corpora) of the synsacral vertebrae are completely converted to synostoses in adults. Along the middle of its length the ventral surface of the consolidated unit of synsacral vertebral bodies demonstrates a fusiform enlargement. The enlargement reflects externally the lumbosacral intumescence (swelling) of the spinal cord occupying that part of the vertebral canal. Seen in longitudinal section, the vertebral bodies opposite the intumescence are dorsoventrally compressed compared to those cranial and caudal to them. See **Osteo.** Fig. 4.9 and Annot. 142A, Corpus synsacri).

Synos. interspinalis. The synostosed spinous processes of the synsacral vertebrae form a continuous crest, Crista spinosa synsacri, that extends either the partial or full length of the synsacrum. See **Osteo.** Annot. 134, 143 and Fig. 4.15.

(75) **Symphysis postsynsacralis.** This is the joint between the last element of the synsacrum with the first free caudal vertebra (see Annot. 60).

Artc. propygostylaris. Joint between the last free caudal vertebra and the Pygostylus. In *Columba* (Baumel, 1988) this is usually a synovial joint; functionally it is primarily a hinge joint allowing cranial and caudal rocking of the pygostyle. The transverse hemicylinder of the last typical caudal vertebra fits into the matching concave notch of the pygostyle. An elastic ligament connects the cranial border of the pygostyle with the spinous process of the vertebra ahead of it.

Juncturae caudae. In *Columba* the joints between the free caudal vertebrae are symphyses, the elastico-fibrocartilaginous disks uniting adjacent vertebral bodies. See Annot. 63.

(76) **Sut. [Synos.] iliosynsacralis; Ligg. iliosynsacralia.** The lateral ends of the transverse processes of the synsacral vertebrae fuse with the medial border of the acetabular and postacetabular ilium by an elongated linear suture. Cranial to Fossa renalis of the pelvis the transverse processes of the synsacral vertebrae ankylose extensively with Facies ventralis of the preactabular ilium. In some taxa (e.g., *Morus, Buteo, Eudocimus, Thalasseus*) the costal processes of the "sacral" vertebrae opposite the acetabulum form prominent lateral bracing struts that articulate with the side wall of the pelvis. See **Osteo.** Annot. 243 and Fig. 4.15.

(77) **Synos. interiliospinalis.** In certain birds (e.g., *Morus, Eudocimus, Buteo, Gallus, Aythya*) the cranial end of the Crista spinosa of the synsacrum is fused with the paired dorsal crests of the adjacent preacetabular ilia producing the Crista iliosynsacralis; this produces iliosynsacral sulci or canals that contain epaxial muscles on each side of the crest of the spines and ventral to the preacetabular ilia. See **Osteo.** Annot. 233-234 and Fig. 4.15.

(78) **Synoss. pygostyli.** The pygostyle is formed by ankylosis of several terminal caudal vertebrae: *Columba* (6), *Fulica, Cygnus, Strix* (5) (Steiner, 1938). See **Osteo.** Annot. 146.

(79) **Juncturae costarum.** The junction of the Capitulum costae with the Corpus vertebrae (**Sync. capitis costae**) is a cartilaginous joint, i.e., a persistent synchondrosis. On the ventrocranial aspect of this joint is a thickening of the perichondrium which forms a collateral ligament. The joint connecting Proc. transversus and the Tuberculum costae is the synovial type (**Artc. costotransversaria**). See Fig. 5.10 and **Osteo.** Fig. 4.8.

(80) **Sut. iliocostalis.** In some birds the cranial synsacral (thoracic) vertebrae possess ribs. Each of these ribs (the part of the rib just distal to its Tuberculum) often forms a fibrous joint with the ventral surface of the preacetabular ilium (e.g., *Morus, Aythya, Rynchops, Corvus*). In other birds these ribs synostose with this part of the ilium (*Gavia, Ardea*). See **Osteo.** Fig. 4.9.

(81) **Sync. intercostalis.** The junction between each vertebral and sternal rib is a persistent cartilaginous joint (e.g., in *Columba, Gallus*).

(82) **Sut. costouncinata; Lig. triangulare.** In some birds the joint between the vertebral rib and its uncinate process is a synostosis. Ghetie, et al. (1976) illustrate a triangular ligament in the angle between the upper border of uncinate process and adjacent caudal border of its rib.

(83) **Artc. sternocostalis.** The joint between the sternal rib and its articular facet on the costal margin of the sternum is a synovial joint. The articular facets are single in some birds (e.g., *Gallus*) and double in others (e.g., *Gavia, Aythya, Buteo,* and *Corvus*). See **Osteo.** Annot. 157 and Fig. 4.11.

(84) **Membranae incisurarum [fenestrarum] sterni.** Synonymy: Membrane intertrabeculares (Fürbringer, 1902). The notches and fenestrae of the sternum are separated by trabeculae; these openings are spanned by strong fibrous membranes which are continuous with the periosteum of both surfaces of the Corpus sterni. See **Osteo.** Annot. 151 and Fig. 4.11.

(85) **Lig. corpus claviculae.** In birds exhibiting a reduced clavicle this is the ligamentous vestige of its shaft. The ligament may be thread-like or a strong ligamentous cord; the persistent bony part of the clavicle consists of only the Extremitas omalis [Epicleideum] (See Glenny and Friedmann, 1954).

Synd. sternoclavicularis. The apex of Carina sterni is usually situated near the Apophysis furculae, joined to it by the sternoclavicular ligament of variable length. In some species the union is transformed into a synovial joint (several procellariiforms and most pelecaniforms, e.g., *Morus;* in extreme cases the joint is synostosed (e.g., *Pelecanus, Sagittarius* (Fürbringer, 1888, *Fregata*). See **Osteo.** Annot. 161, 163.

(86) **Membrana sternocoracoclavicularis.** Synonymy: Lamina lateralis; membrana coracoclavicularis (Fürbringer, 1888). Stretches between the inner border of the clavicle, the medioventral border of the coracoid, and the sternum dorsal to Carina sterni (see Fig. 5.3). Many variations in the form and development of its parts occur throughout Aves.

A number of specialized thickenings of the Membrana sternocoracoclavicularis have been described as ligaments in different taxa; these extend from the cranial border (especially Rostrum sterni) of the sternum to various parts of the coracoid, to the clavicles, to the scapula; some connect right and left coracoids, etc. In the list of terms the most important of these (Fürbringer, 1888) are listed as subordinate items under Membrana sternocoracoclavicularis, one of which is defined below.

Lig. sternoprocoracoideum. Thickened, distinct band of Memb. sternocoracoclavicularis that extends from the Rostrum sterni to the ventral border of Proc. procoracoideus of the coracoid (e.g., *Columba*) (Fig. 5.3). Part of this ligament in some birds (e.g., *Meleagris, Branta*) is attached along the medial border of the coracoid, extending between the medial angle of the coracoid to the procoracoid.

(87) **Lig. acrocoraco-procoracoideum.** In birds that lack a distinct Proc. procoracoideus, Membrana sternocoracoclavicularis continues uninterruptedly toward the shoulder where it is attached to Proc. acrocoracoideus of the coracoid bone.

(88) **Membrana cristoclavicularis.** Synonymy: Lig. cristoclaviculare; Lig. sternoclaviculare; Lamina mediana or Laminae laterales of Membrana sternocoracoclavicularis; Crista membranacea (Fürbringer, 1888). This median bilaminar membrane is formed by the side-to-side adhesion of the ventral ends of the paired Membranae sternocoracoclaviculares; it connects the ventral end (Apophysis) of the furcula to the Apex and Crista mediana of the cranial margin of Carina sterni, extending dorsally to the level of Rostrum sterni (**Osteo.** Fig. 4.11). M. supracoracoideus and M. pectoralis arise from each side of Memb. cristoclavicularis. The most cranial part of the membrane is a band-like ligament rather than a membrane. Sy (1936) illustrates Memb. cristoclavicularis in the anatid, *Bucephala.*

(89) **Artc. sternocoracoidea.** An elongated saddle-type (Artc. sellaris) synovial joint that permits combinations of hinge-type movements and mediolateral gliding between the ventral end of the coracoid and the generally obliquely disposed, horizontal Sulcus articularis coracoideum of the sternum.

The sternal end of the coracoid is concave on its deep aspect, the concavity articulates with the convex Sulcus articularis coracoideus of the sternum (**Osteo.** Fig. 4.11); the articular surfaces of both elements in some birds are subdivided into medial and lateral parts. The sulcus is concavo-convex, i.e., concave in the dorso-ventral dimension with a short radius of curvature; the sulcus is convex in its medio-lateral dimension, having a long radius of curvature. See Fürbringer (1888: 185) for discussion of the variation in configuration of this joint. See also **Osteo.** Annot. 156.

(90) **Artc. intercoracoidea.** In most birds the medial borders of the sternal ends of the coracoids lie closely adjacent (but separate) to one another. In fact, the two sternocoracoid joints of certain birds abut or overlap one another forming synovial joints; in Ardeidae and Musophagidae the right coracoid in part lies ventral to the left one (Fürbringer, 1888). The overlapping also occurs in some procellariiforms (Kuroda, 1954), and in *Buteo,* falconids, *Bubo,* and *Ichthyornis.*

(91) **Ligg. collateralia sternocoracoidea.** Synonymy: Ligg. accessoria sternocoracoidea (Fürbringer, 1888). Fürbringer described collateral ligaments, of varying configuration and position, in different taxa that connect the base and shaft of the coracoid with the internal and external labra of Sulcus articularis coracoideus of the sternum. The external sternocoracoid ligament in some birds is attached to the Tuberculum labri externum of the coracoid sulcus of the sternum (**Osteo.** Fig. 4.11A).

(92) **Lig. sternocoracoideum laterale.** A fascia-like ligament in *Casuarius, Tinamus,* and galliforms (Fürbringer, 1888) that extends from the lateral edge of Proc. craniolateralis of the sternum to the lateral border of Proc. lateralis of the sternal end of the coracoid.

(93) **Synd. [Artc.] coracoscapularis; Lig. coracoscapulare interosseum.** The coracoid and scapula are united mainly by the Lig. coracoscapulare interosseum consisting of elastic cartilage (J. Baumel and R. E. Brown, pers. obs) (see next paragraph). The ligament itself forms the articular surface **(Cavitas glenoidalis)** that receives the head of the humerus (see Annot. 100).

The coracoscapular interosseous ligament and articular capsules also connect the two bones: The glenoid process and acromion of the scapula join the base of the procoracoid process and adjacent shaft of the coracoid bone. In some birds the joints are simple syndesmoses connecting irregular surfaces by short ligaments that permit little movement between the bones. In other birds (e.g., *Branta, Pelecanus*) the joints are elaborate, partially synovial, partially syndesmotic. The synovial parts are spheroidal/ellipsoidal articulations that are more mobile than the simple syndesmoses (**Osteo.** Annot. 167a, b). In the elaborate joints the coracoid possesses the concave receiving surface (Cotyla) and the scapula bears the convex Tuberculum (**Osteo.** Annot. 173a, b). In the ratite birds, *Struthio, Rhea,* and *Apteryx,* the coracoid and scapula are fused (Feduccia, 1985). See **Osteo.** Annot. 167a, 168.

(94) **Lig. coracoscapulare dorsale.** Synonymy: Lig. coracoscapulare accessorium dorsale (Fürbringer, 1888). This ligament occurs in certain large birds in which the Lig. acrocoraco-acromiale is not strongly developed (e.g., *Ciconia, Egretta, Cathartes, Haliaeetus,* Fürbringer, 1888).

Lig. coracoscapulare ventrale. Synonymy: Lig. coracoscapulare accessorium internum (Fürbringer, 1888). This ligament is conspicuous in *Egretta, Haliaeetus,* and others; however it is not as well developed as Lig. coracoscapulare dorsale.

Both the above ligaments are accessory to Lig. coracoscapulare interosseum, which is the strongest ligament uniting the scapula and coracoid. Lig. coracoscapulare dorsale connects the cranial surface of the scapular glenoid process with the adjacent coracoid in the floor of the triosseal canal. Lig. coracoscapulare ventrale connects the ventral border of the scapular glenoid process with the inner surface of the neck of the coracoid.

(95) **Lig. acrocoraco-acromiale.** Forms the fibrous medial wall of the Canalis triosseus, extending from the Tuberculum brachiale (**Osteo.** Annot. 171b) of the acrocoracoid ventrally to Crista lig. acrocoraco-acromiali (**Osteo.** Annot. 166). See Fürbringer (1888) for discussion of the relative development of this ligament in different birds. See **Osteo.** Annot. 177, 166.

(96) **Synd. [Artc.] acrocoracoclavicularis.** The shoulder extremity of the clavicle is attached principally to the medial surface of Proc. acrocoracoideus of the coracoid bone. In some species Proc. acromialis of the clavicle is prolonged caudally, and articulates also with the Acromion of the scapula (see Annot. 98; and **Osteo.** Annot. 165).

The acrocoracoclavicular joint is a syndesmosis, modified as a symphysis in some forms of birds. In other avian groups the junction is a typical synovial joint

(*Spheniscus, Alca, Pelecanus, Ciconia, Haliaeëtus, Buceros*). In *Fregata* this joint is a synostosis (see Fürbringer, 1888).

(97) **Synd. procoracoclavicularis.** Occurs in birds whose coracoid bones possess well developed procoracoid processes (e.g., *Buteo, Columba*).

(98) **Synd. acromioclavicularis.** The dorsal end of the clavicle does not directly join the acromion of the scapula in some birds; instead the two are connected by a long Lig. acromioclaviculare. A synovial joint connects the two elements in *Picus and Ramphastos;* a symphysis is present in some taxa (Fürbringer, 1888). See **Osteo.** Annot. 165.

(99) **Lig. scapuloclaviculare dorsale.** This distinct collateral ligament of the scapuloclavicular joint occurs in podicipediforms and anseriforms; it is more or less distinct from Lig. acromioclaviculare.

(100) **Artc. omalis.** Synonymy: Artc. coraco-scapulo-humeralis; Artc. humeralis. The avian (synovial) shoulder joint differs from the mammalian since the humerus articulates not only with the scapula, but with scapula and coracoid bones, both of which contribute to the osseous Cavitas glenoidalis. In fact, the head of the humerus articulates not with the so-called humeral articular facets of the glenoid processes of scapula and coracoid, but with the Lig. coracoscapulare interosseum which invests both these facets, and forms **Cavitas glenoidalis.** Sy (1936) notes that the floor of the cavity is deformable, its shape changing in response to contact with different aspects of Caput humeri as the latter rotates about its long axis. See Annot. 93; and **Osteo.** 167, 168.

Fibrocartilago humerocapsularis. Synonymy: Os humeroscapulare (Jäger, 1857). A fibrocartilaginous or osseous mass developed in the dorsal part of the articular capsule of the shoulder joint in certain avian taxa, deep to the origin of M. deltoideus major, pars cranialis (**Myol.** Annot. 79) (see Fürbringer, 1888; Jäger, 1857).

(101) **Lig. acrocoracohumerale** (Fig. 5.3). This is the principal collateral ligament of the shoulder joint, and usually quite independent of the articular capsule (Sy, 1936). The ligament extends from the apex and lateral surface of the acrocoracoid process of the coracoid to the Sulcus transversus of the cranial surface of the proximal extremity of the humerus. Sy discusses the function of this ligament. See **Osteo.** Annot. 185; and Fig. 4.12.

Bursa acrocoracoidea; Bursa supracoracoidea. These synovial bursae between Lig. acrocoracohumerale and the underlying bone and that deep to the tendon of M. supracoracoideus are usually in open communication with the general cavity of the shoulder joint.

(102) **Lig. coracohumerale dorsale.** Fürbringer (1888) noted that the dorsal coracohumeral ligament is lacking in many birds, but is very strongly developed in others. In columbiforms, particularly, the ligament is independent of the capsule, and is grooved where it is crossed by the overlying tendon of M. supracoracoideus.

Lig. scapulohumerale dorsale. Varies in its relative development in different taxa, but is only rarely lacking.

(103) **Plicae synoviales et Ligg. intracapsularia.** Fürbringer (1888) describes the interspecific variation in occurrence and strength of these intra-articular structures of the shoulder joint. In general the synovial folds and the ligaments are attached proximally to the scapular and coracoid labra of the glenoid cavity and distally to the humerus, articular capsule, or other ligaments. See Fig. 5.3.

(104) **Juncturae cubiti** (Fig. 5.4). The parts of Junctura cubiti (elbow joint) are named with the wing in the defined avian anatomical position: abducted and fully extended laterally (see **Intro.** and **Osteo.** Annot. 178); in the older literature descriptive terms were based on the wing in the folded position against the side of the trunk. The surface of the distal end of the humerus to which the M. triceps brachii is applied is its morphological dorsal or extensor (formerly "anconal") surface.

The compound elbow joint consists of three articulations: (1) radius and ulna with the humeral condyles and (2) the proximal radioulnar joint; the ulna of birds articulates with both humeral condyles. The synovial cavities of all three communicate.

(105) **Lig. collaterale ventrale.** This distinct, prominent triangular ligament connects the Tuberculum supracondylare ventrale of the humerus with the ventral aspect of ulna near the margin of its Cotyla ventralis. See Fig. 5.4; and **Osteo.** Annot. 203 and Fig. 4.13D.

(106) **Lig. collaterale dorsale.** Variable in its strength and extent in different avian taxa this dorsal collateral ligament of the elbow may be attached directly onto the humerus or to tendons near the Epicondylus dorsalis of the humerus; its distal attachment is onto the caudal border of the ulna near the proximal remigeal papillae (Stettenheim, 1959). See Fig. 5.4.

(107) **Lig. craniale cubiti** (Fig. 5.4A). This strong, poorly defined cranial part (flexor aspect) of the articular capsule of the elbow is attached to the intercondylar region of the humerus. Lig. craniale cubiti appears to consist partly of elastic tissue (*Gallus, Columba*) that may assist in the first stage of flexion of the fully extended elbow joint.

(108) **Meniscus radioulnaris.** The common synonym, Lig. anulare radii, is not an apt descriptive term; following Alix (1874) and Sy (1936) this distinct, intracapsular ligament is called a meniscus. The meniscus unites the proximal ends of radius and ulna (Fig. 5.4). The thick dorsal edge of the meniscus is not attached to the joint capsule; the thin deep portion of the meniscus is partly interposed between the dorsal humeral condyle and the cotyla of the ulna.

(109) **Lig. radioulnare transversum.** The common synonym, Lig. teres cubiti, is not appropriate for this flat, band-like ligament located on the dorsal aspect of the elbow (see Fig. 5.4).

(110) **Trochlea humeroulnaris** (Shufeldt, 1890) (Fig. 5.4). The comparative study of Bentz and Zusi (1982) of this ligamentous pulley examined examples of forty avian families. The pulley crosses the ventral aspect of the elbow joint, changing the direction of pull of the tendon of M. flexor carpi ulnaris (FCU) (Myol. Annot. 85, 88). They described a generalized form of the pulley and variants of the basic plan from which parts are deleted or modified. The names of the parts of the trochlea in the NAA (1979) have been replaced by the terms set down below.

The basic ancestral humeroulnar pulley consists of three main parts: (1) **Pars humeralis** arises from the dorsal surface of the medial epicondyle of the humerus; it descends across the superficial aspect of the FCU tendon; (2) **Pars ulnaris** is the continuation of Pars humeralis, which spirals over the cranial border of the tendon and passes to its deep surface where it becomes affixed to the proximal ulna; and (3) **Pars humeralis accessoria** extends distally from the ventral aspect of the medial epicondyle to join the main part of the pulley between its ulnar and humeral parts. In some forms (e.g., tinamous and trochilids) Pars humeralis is completely lacking.

(111) **Lig. tricipitale** (Stettenheim, 1959). Anchors the ventral edge of the tendon of M. scapulotriceps to the ventral margin of Sulcus m. humerotricipitis on the distal end of the humerus (**Osteo.** Fig. 4.12). The ligament is intracapsular, lying deep to the tendon of M. humerotriceps.

(112) **Juncturae carpi et manus.** The complicated arrangements and configurations of the articulating elements at the carpus add to the problems of applying meaningful descriptive names for the various ligaments by providing topographical connotations and/or indicating the bones connected by the ligaments. In order to avoid confusion of the names, the following usage has been adopted: (1) **"metacarpo-"** is the combining form used for Carpometacarpus; (2) **"radiocarpo-"** and **"ulnocarpo-"** refer to the carpal bones, Os carpi radiale and Os carpi ulnare; (3) the conventional combining forms, **"ulno-"** and **"radio-"** are used in referring to the long bones of the antebrachium, Ulna and Radius; (4) **hyphenation** is used in certain names to avoid confusion concerning the bones involved in formulation of the names of the ligaments; (5) names are applied so that terms of position and direction refer to the limb in its anatomical position (see Annot. 104, 155). See also **Arthr.** Intro.

Most of the terms on the wrist and hand articulations are based on dissections of *Gallus* and *Columba* that closely agree with the accounts of Stettenheim (1959) in several charadriiform birds and that of Sy (1936) in *Corvus* and other species. See Ghetie, et al. (1976) for illustrations of these joints in *Meleagris.*

(113) **Aponeurosis ventralis** (Pelissier, 1923). Synonymy: Lig. radiale metacarpi (Stettenheim, 1959); Lig. ulni metacarpale mediale (Kolda and Komarek, 1958). A fibrous fan-like structure, with its handle attached to the distal end of the radius, its main part radiating from the Os carpi ulnare to the metacarpus and the follicles of the primary flight feathers (remiges). Its proximal edge is continuous with the ventral antebrachial aponeurosis and its distal edge with the dense fascia investing the ventral (palmar) muscles of the manus; its two main parts are described below (Annot. 114, 115). See Figs. 5.5, 11; **Osteo.** Annot. 213.

(114) **Retinaculum flexorium.** This band-like, transverse "handle"-segment of Aponeurosis ventralis restrains the tendons of the flexor muscles (**Myol.** Annot. 86) passing deep to it, and is anchored to underlying ligaments and Os carpi radiale. The retinaculum extends caudally from the distal, ventral end of the radius (**Osteo.** Fig. 4.13) to the Crus longum of Os carpi ulnare where it blends with the distal end of the humerocarpal ligament (*Columba, Buteo,* pers. obs), and is continuous with the fan of the Aponeurosis in the angle of the wrist. See **Osteo.** Annot. 213.

(115) **Aponeurosis ulnocarporemigalis.** This is the distal radiate segment of Aponeurosis ventralis carpalis (see Annot. 114) that crosses ventral to the Crus longum of Os carpi ulnare and fans out in the area caudal to the angle of the wrist and along the caudal border of Os metacarpale minus. It is rather slightly attached to the Crus longum, and may have a synovial bursa between it and the Os carpi ulnare. The ulnocarporemigal aponeurosis radiates, sending digitations to the follicles of the proximal series of the primary remiges. Its proximal half flares toward the follicles of the distalmost two or three secondary remiges and to the carpal segment of the elastic interremigal ligament (*Columba, Gallus, Buteo*); the superficial collagenous bundles cross Os carpi ulnare and are continuous with Retinaculum flexorium (Annot. 114, 191; and Fig. 5.11).

(116) **Lig. radioulnare interosseum.** This is the only ligament that directly connects the distal ends of radius and ulna; it is interposed between the radius and the ulna, preventing their direct contact, and is continuous with Lig. ulno-radiocarpale interosseum. Lig. radioulnare interosseum is situated so that it limits distal movement of the radius relative to the ulna as in folding the wing. See Fig. 5.5B Annot. 119.

(117) **Lig. ulno-ulnocarpale proximale.** Synonymy: Lig. posticum ulnare carpi ulnaris (Stettenheim, 1959). **Lig. ulno-ulnocarpale distale.** Synonymy: Lig. obliquum carpi ulnaris. Both these ligaments are distinct in *Gallus* and *Columba;* in *Corvus* (Sy, 1936), and in several charadriiforms (Stettenheim, 1959). Both are situated on the ventral side of the joint, in part deep to the Aponeurosis ventralis. In *Pteroglossus,* a piciform, these two ligaments are represented by a single ligament. See Fig. 5.5B.

(118) **Lig. ulno-radiocarpale ventrale.** Thickened part of Capsula articularis of the ulno-radiocarpal joint (Fig. 5.5B).

(119) **Lig. ulno-radiocarpale interosseum.** Synonymy: Lig. ulnare carpi radialis. This intra-articular ligament extends ventrally from the Sulcus intercondylaris of the ulna to the Os carpi radiale. It is the major ligament connecting the ulna to the carpals; it limits distal movement of the radius. See Fig. 5.5B and Annot. 116.

(120) **Lig. ulno-metacarpale ventrale.** Synonymy: Lig. ulnare internum metacarpi (Stettenheim, 1959). This ligament is independent of Lig. radiocarpo-metacarpale ventrale in certain charadriiforms (Stettenheim, 1959) and *Columba;* in *Gallus* the two ligaments are combined distally (Fig. 5.5B).

(121) **Lig. radio-radiocarpale dorsale** (Fig. 5.5A). Synonymy: Lig. radiale externum carpi radialis (Stettenheim, 1959). In *Gallus* two digitations from the radius merge to form this ligament that is attached to the dorsal surface of Os carpi radiale.

(122) **Meniscus intercarpalis.** Synonymy: Lig. carpi interni. The intercarpal meniscus connects Os carpi ulnare with Os carpi radiale; it is said to represent the embryonic carpal, centrale III (Romanoff, 1960). Attachments of the meniscus to Os carpi ulnare are only at dorsal and ventral points; the intervening thin caudal border of the meniscus next to Os carpi ulnare is free. The slit-like opening between the free border and the ulnar carpal permits communication between the joint cavities proximal and distal to the meniscus. Its cranial attachment to the caudal, sharp border of Os carpi radiale forms the thick dorsal part of the wedge-like meniscus. See Fig. 5.5A; and **Osteo.** Annot. 214.

(123) **Syncc. intercarpales.** Each of the definitive carpal bones is formed during fetal development by coalescence of several carpal anlagen (Romanoff, 1960; Hinchliffe, 1985). See **Osteo.** Annot. 214.

(124) **Artcc. carpo-carpometacarpales.** The ulna and radius do not articulate directly with the Carpometacarpus; carpal bones and Meniscus intercarpalis are interposed. See Annot. 128 for an explanation of the development of the Os carpometacarpale and formation of the "intercarpal" joints.

(125) **Lig. radiocarpo-metacarpale ventrale.** Synonymy: Lig. internum ossis carpi radialis et metacarpi (Annot. 120; Fig. 5.5).

(126) **Lig. ulnocarpo-metacarpale ventrale.** Synonymy: Lig. internum ossis carpi ulnaris et metacarpi. Consists of two separate parts in *Gallus* (Fig. 5.5).

(127) **Lig. ulnocarpo-metacarpale dorsale.** Synonymy: Lig. externum ossis carpi ulnaris et metacarpi (Fig. 5.5).

(128) **Synoss. carpo-metacarpales.** The carpo-carpometacarpal articulations, as indicated by their names, are actually synovial joints between both of the free carpal bones and those carpals that coalesced with the proximal ends of the fused alular, major, and minor metacarpal bones in fetal and postnatal life (Hogg, 1982), forming the compound bone, Os carpometacarpale; therefore, the joints between the carpometacarpus and free carpals are actually intercarpal articulations. Compare with the ankle (intertarsal) joint: Annot. 167, 173. See **Osteo.** Annot. 214.

(129) **Synos. intermetacarpalis proximalis/distalis.** In postnatal life the three metacarpal elements are originally joined by cartilage, and in late postnatal maturation become ankylosed with one another. At their proximal ends the metacarpals also undergo synostosis with the carpals (see Annot. 128 and **Osteo.** Fig. 4.14). Distally the major and minor metacarpals fuse (see **Osteo.** Annot. 222). Romanoff (1960) points out how the development of the manus in ratites and penguins differs from the general avian pattern (consult Hinchliffe, 1985). See **Osteo.** Annot. 222.

(130) **Artcc. metacarpophalangeales.** Ligaments of the metacarpophalangeal synovial joints participate in guiding and limiting movements as well as strengthening the distal part of the wing, since the primary remiges are attached to the Carpometacarpus and phalanges. In general the ligaments of the ventral side of the joints are stronger than those of the dorsal side since they must resist more powerful forces against the ventral surface of the wing during flight.

(131) **Lig. obliquum alulae** (Fig. 5.5B). Synonymy: Lig. pollicare. Extends from distal edge of Proc. extensorius of the alular metacarpal to the base of the ventral surface of the alular phalanx.

Artc. metacarpophalangealis alulae. In most birds this is a synovial joint; however, in the penguin (*Pygoscelis adeliae*) the alular phalanx is fused (synostosed) at its base with the Os metacarpale alulare and the cranial margin of Os metacarpale major (see **Integ.** Annot. 70).

(132) **Lig. collaterale ventrale.** On the ventral side of the metacarpophalangeal joint of the major digit, this ligament consists of a broad, flat part and an elongate, cord-like part. The cord-like part is attached along the caudal crest of the proximal phalanx of Digitus major.

(133) **Lig. collaterale caudale.** The caudal collateral ligament of the metacarpophalangeal joint of Digitus major is variable in occurrence in different taxa, e.g., present in *Columba*, absent in *Gallus*.

(134) **Lig. obliquum intra-articulare.** This ligament of the metacarpophalangeal joint of Digitus major is present in *Columba* and *Gallus;* it appears to limit rotation about the long axis of Digitus major brought about by elevation of the caudal border of the wing.

(135) **Meniscus articularis.** Loosely organized fatty-fibrous intra-articular structure located in the dorsal part of the cavity of the metacarpophalangeal joint of Digitus major, attached to the inner surface of the joint.

(136) **Juncturae interphalangeales manus.** The phalanx of Digitus minor is attached along most of its length to the caudal edge of the proximal phalanx of Digitus major by an interosseous ligament (Pelissier, 1923); therefore, movements of the minor digit follow those of the major digit. Each of the two digits has an individual synovial cavity at its articulation with the Carpometacarpus.

In the penguin (*Pygoscelis adeliae*) the alular phalanx is fused with the cranial margin of Os metacarpale major and at its base with Os metacarpale alulare (**Synos. metacarpophalangealis alulae**). See **Integ.** Annot. 70.

(137) **Artc. interphalangealis digiti majoris.** The Digitus major of most birds usually possesses two phalanges; therefore, only one interphalangeal joint is present. In some groups of birds supernumerary phalanges in the form of inconstantly or regularly occurring wing claws are found on the alular and major digits (Fisher, 1940); Digitus major has three phalanges in certain birds, e.g., *Gavia* and the anatids (Berger, 1966); members of several avian orders possess two alular phalanges (see **Osteo.** Annot. 224; **Integ.** Annot. 70; and **Topog.** Annot. 40).

(138) **Lig. collaterale caudale.** The caudal collateral ligament of the interphalangeal articulation of Digitus major is a strong, but poorly defined, part of its articular capsule in *Gallus* and *Columba*.

(139) **Lig. interphalango-remigale.** This is a part of Aponeurosis interphalango-remigalis consisting of a tough ligamentous band; it strengthens the ventral side of Artc. interphalangealis of Digitus major. Distally the ligament is attached to the follicle of a remex rather than to bone (see Annot. 192).

(140) **Ligg. accessoria alae.** The accessory ligaments of the wings are those ligaments not associated with articulations of bones with one another per se, but with tendons or feathers (cf., retinacula of Cartilago tibialis). See Annot. 145.

(141) **Lig. propatagiale** (Fig. 5.11). Synonymy: Lig. elasticum propatagiale (NAA, 1979); elastic tendon of M. tensor propatagialis (Berger, 1966). The structure of the propatagium and its ligaments has been elucidated in recent comparative studies (R. E. Brown, 1991, pers. comm.; Brown, et al., 1989). The propatagial ligament is found in the cranial free edge of the propatagial skin fold; in different birds its proximal attachment is commonly from one or a combination of: (1) deltopectoral crest of the humerus, (2) tendons of insertion of Mm. pectoralis or deltoideus major near the crest, (3) fascia of M. pectoralis. Distally the ligament is attached to the extensor process of Os carpometacarpale and Digitus alularis. Although the propatagial ligament has been considered as the tendon of Caput craniale of M. deltoideus, pars propatagialis (M. tensor propatagialis), this muscle in fact inserts into the medial part of the ligament.

The structure of the propatagial ligament is variable. For example, in some birds (e.g., passeriforms) Lig. propatagiale is constructed of collagenous tissue in its medial and lateral segments with an intermediate segment of elastic tissue (**Pars elastica**). In *Diomedea* the ligament is almost entirely collagenous tissue. In some falconiforms the entire length of the ligament is made of a slender continuous collagenous band paralleled by an elastic band spanning its intermediate two-thirds. See **Myol.** Annot. 78-80.

Lig. limitans cubiti (R. E. Brown, 1991, pers. comm). Synonymy: tendon of M. propatagis brevis. This is the ligament in the propatagium that limits extension of the elbow joint, determining the maximum degree of its extension. It may share completely or partially the proximal attachment of Lig. propatagiale, or it may be

totally separate as in passeriforms. In different birds its distal attachments are: dorsal antebrachial fascia of the proximal forearm (Annot. 194), tendon of origin of M. extensor metacarpi radialis, dorsal capsule of elbow joint, etc. The elbow-limiting ligament varies in its form: single band, two ligamentous bands, a broad fascial sheet. The Caput caudale of M. deltoideus (so-called M. propatagialis brevis) inserts on the proximal part of this ligament (Annot. 194; see also **Myol.** Annot. 78-80 regarding propatagtial muscles.

(142) **Retinaculum m. scapulotricipitis.** A flat, wide ligamentous band that anchors the cranial edge of M. scapulotriceps to the proximal shaft of the humerus. This condition occurs widely among birds (Berger, 1966). See Annot. 111.

(143) **Lig. humerocarpale** (Fig. 5.11). Alix (1874) and Pelissier (1923) referred to this distinct, band-like ligament as "Lig. du petit palmaire"; it extends from the Epicondylus ventralis of the Humerus to the wrist region where it is attached to Crus longum of Os carpi ulnare. Berger (1966) equates the ligament with the entire ventral antebrachial aponeurosis; in fact, the humerocarpal ligament is generally independent of the more superficial Aponeurosis ventralis antebrachii. Lig. humerocarpale is closely related to M. flexor digitorum superficialis and Septum humerocarpale (see legend of Fig. 5.11 and Annot. 195, 114).

(144) **Retinaculum m. extensoris metacarpi ulnaris.** Berger (1966) discusses the occurrence of this retinaculum ("ulnar anchor") that holds the proximal tendon of M. extensor metacarpi ulnaris against the ulna. See Bentz and Zusi (1982) for the relationship of the retinaculum to the humeroulnar pulley.

(145) **Ligg. accessoria musculi.** On the dorsal side of the wrist (carpal) region these accessory ligaments are connected proximally to the distal end of the ulna, and join or envelop certain tendons of muscles (**Myol.** Annot. 88, 90) that cross the joints of the wrist. The accessory ligaments are arranged mechanically so that they passively contribute to the actions produced by the muscles with which they are associated (*Columba*, Berger, 1966).

(146) **Juncturae cinguli membri pelvici** (see Artcc. synsacri). The joints of the pelvic limb girdle include those of the hip bone (Os coxae) which is formed by coalescence of ilium, ischium, and pubis, as well as the joints between the synsacrum and Os coxae. These elements develop embryologically as separate cartilaginous anlagen in the acetabular region, subsequently undergoing complete ossification in postnatal life, and ultimate synostosis. All three elements contribute to the formation of the acetabulum. See Annot. 148.

(147) **Sut. ischiopubica.** In many carinate birds the caudal end of the ischium (Proc. terminalis ischii) (**Osteo.** Fig. 4.15) articulates by sutural ligaments with the dorsal border of the shaft of the pubis. In some passeriforms and piciforms this joint is ankylosed (Boas, 1933). In the dried skeleton of ratites the end of the ischium is synostosed to the pubis; however, the ilium does not join the ischium caudally. In tinamous and the Emu (*Dromaius*) there is no bony union of the caudal ends of the pubis, ischium, and ilium. See **Osteo.** Fig. 4.15.

Membrana ischiopubica. This membrane closes off the elongate Fenestra ischiopubica. See **Osteo.** Annot. 227, 229 and Fig. 4.15.

Lig. ischiopubicum. Extends from Proc. obturatorius of the ischium to the pubis, and forms the caudal border of the Foramen obturatum; in some avian taxa this ligament becomes ossified (Boas, 1933). See **Osteo.** Annot. 227 and Fig. 4.15.

(148) **Sync. ilioischiadica.** The ilium and ischium articulate at the acetabulum in all birds. In young carinate birds the postacetabular ilium and ischium are also joined by cartilage that ossifies caudal to the Fenestra ilioischiadica in older birds. In some ratites they remain separated or joined incompletely (Nauck, 1938). See Annot. 147 and **Osteo.** Annot. 231, 251 and Fig. 4.15.

Membrana ilioischiadica. This connective tissue sheet stretches across the caudal two-thirds of the Fenestra ilioischiadica. Muscles are attached to its superficial and deep surfaces; nerves and vessels traverse only the cranial part of the fenestra.

(149) **Symphysis pubica.** The two hip bones of the bony pelvis are connected to one another by junction of right and left pubes only in *Struthio* and *Archaeopteryx* (Heilmann, 1926) by the junction of right and left pubes.

(150) **Symphysis ischiadica.** Union of the right and left ischial bones occurs only in *Rhea;* the two ischia meet in a long median symphysis ventral to the synsacrum and kidneys; this partition separates these structures from the abdominal viscera (Barkow, 1856; Newton and Gadow, 1896).

(151) **Membrana acetabuli.** Closes the Foramen acetabuli in the deepest part of the Acetabulum; its ventral part blends with the acetabular attachment of Lig. capitis femoris (Fig. 5.6). See **Osteo.** Annot. 226.

(152) **Juncturae coxae.** Two distinct articulations are included within the single synovial cavity of the hip joint: (1) **Artc. coxocapitalis,** the articulation of Caput femoris with the Acetabulum; (2) **Artc. coxotrochanterica,** the articulation of the Trochanter and dorsal surface of the femoral neck with the Antitrochanter of Os coxae. See Fig. 5.6; and **Osteo.** Annot. 255.

(153) **Lig. iliofemorale** (Fig. 5.6). On the cranial aspect of the hip joint, the thick dorsal edge of the iliofemoral ligament is distinct from the thin dorsal part of the joint capsule.

Lig. ischiofemorale. Proximally this ligament is attached to the cranial border of the ilioischiadic foramen and the caudal border of the Antitrochanter; it extends distally to the caudal part of the trochanteric crest of the femur (see Fig. 5.6).

(154) **Junctura genus** (Fig. 5.7). The knee joint is formed of four separate articulations whose synovial cavities all intercommunicate: (1) the medial femoral condyle articulates with the medial meniscus and the tibiotarsus; (2) the lateral femoral condyle articulates with the lateral meniscus and fibula; (3) the femoral patellar sulcus articulates with the patella; (4) the proximal tibiotarsus articulates with the head of the fibula. The lateral femoral condyle has little direct articulation with the tibiotarsus since the lateral meniscus is interposed between them. The proximal tibiofibular articulation is a synovial joint (see Annot. 161).

(155) **Artc. femorotibialis.** The major bone of the crus is the Tibiotarsus, the distal end of the tibia being capped by tarsal elements (Annot. 167). For simplification of the terminology of the knee region, the combining form "tibio-" instead of "tibiotarso-" is used. See Annot. 156-157.

(156) **Artc. femorofibularis** (Fig. 5.7). The proximal and medial articular facets of the Caput fibulae articulate with the Trochlea fibularis of the lateral condyle of the femur (see Annot. 154).

(157) **Artc. tibiofibularis.** The Caput fibulae articulates directly with the lateral surface of the tibiotarsus just distal to the point of attachment of the lateral meniscus

to Caput fibulae laterally (see Annot. 159) and to the tibial plateau medially. At this level the fibula is also fastened to the tibiotarsus by two ligaments: (1) the obliquely disposed extracapsular **Lig. tibiofibulare obliquum** (*Meleagris*, Ghetie, 1976; and *Columba*, pers. obs.) which forms the upper boundary of the proximal tibiofibular foramen; and (2) the nearly transverse, intracapsular **Lig. tibiofibulare craniale** which is located just beneath, and adherent to, the Lig. transversum genus (see Fig. 5.7 and Annot. 154, 162).

(158) **Lig. patellae.** This so-called ligament is actually the tendon of Mm. femorotibiales that extends from the distal border of the Patella to Crista patellaris of the Tibiotarsus. Lig. patellae forms much of the cranial wall of the articular cavity of Artc. femorotibialis.

Corpus adiposum retropatellare. Intracapsular fat body of the knee joint located behind the patella. See **Osteo.** Annot. 268.

(159) **Meniscus lateralis** (Fig. 5.7). Synomymy: Femoro-fibular disc (Haines, 1942). This meniscus is an oblong disc attached at its medial end to the interarticular area of the head of the tibia. The lateral end of this meniscus is affixed to the inner surface of the Caput fibulae. The lateral menicus separates the lateral condyle of the femur from the lateral articular facet of the tibia. During flexion/extension of the knee joint the head of the fibula protracts and retracts alongside the tibia, pivoting about the attachment of the medial end of the meniscus.

Meniscus medialis. This C-shaped meniscus has an open central part that permits direct articulation of the medial femoral condyle with the tibiotarsus. See Fig. 5.7.

(160) **Lig. meniscocollaterale** (Fig. 5.7). Connects the cranial edge of Meniscus lateralis with the cranial border of Lig. collaterale laterale of the knee (Haines, 1942; Cracraft, 1971).

(161) **Synd. tibiofibularis; Lig. tibiofibulare interosseum** (Fig. 5.7). This slightly moveable joint connects the Crista fibularis of the proximal shaft of the Tibiotarsus with Corpus fibulae and Spina fibulae. See Müller and Streicher (1989) for a discussion of the ontogeny of the Synd. tibiofibularis, as well as interspecific variation and biomechanics of this joint.

(162) **Foramen interosseum proximale; Foramen interosseum distale.** These are openings between the Tibiotarsus and the Fibula proximal and distal to Synd. tibiofibularis (see above). The foramina transmit nerve and vessels that pass between the flexor and extensor compartments of the crus. See **Osteo.** Fig. 4.17; **Art.** Annot. 76; and **Ven.** Annot. 71.

(163) **Artc. cartilago-tibiotarsalis.** Cartilago tibialis articulates with Trochlea cartilaginis tibialis on the caudal surface of the distal end of the Tibiotarsus; the joint cavity of this articulation is continuous with that of the intertarsal joint. Cartilago tibialis forms the caudal wall of Artc. intertarsalis (see Fig. 5.8; and **Osteo.** Annot. 279).

(164) **Cartilago tibialis** (Fig. 5.8). Synonymy: Cartilago semilunaris; Sustentaculum (Fujioka, 1962); Sustentaculum tarsi (Komárek, 1979). Shufeldt (1890) described the tibial cartilage as the fibrocartilaginous block that lies on the caudal aspect of the Trochlea cartilaginis tibialis at the distal end of the Tibiotarsus. The tendons of M. gastrocnemius and superficial flexors ride in the wide sulcus on the superficial surface of Cartilago tibialis, and the deep flexor tendons of the pedal digits glide through canals within it. Hudson (1937) noted the presence of Cartilago tibialis in many different avian taxa. See **Osteo.** Annot. 279.

(165) **Retinaculum mediale; Retinaculum laterale** (Barnett, 1954a). Tough, ligamentous sheets that bind the sides of Cartilago tibialis to the tibiotarsal epicondyles caudal to the collateral ligaments of the intertarsal joint; the retinacula contribute to the articular capsule (Fig. 5.8; and Annot. 164). The tendinous expansion of M. fibularis longus is also fastened to the lateral border of the cartilage.

Retinaculum flexorium. This transverse fibrous arch is attached to the curved lateral and medial margins of Cartilago tibialis; it restrains tendons (mainly M. gastrocnemius) that lie in the sulcus on the caudal surface of Cartilago tibialis.

(166) **Os sesamoideum intertarsale.** In certain birds the mediodistal angle of Cartilago tibialis forms this distinct ossified process (Cracraft, 1971); this sesamoid articulates extensively with the Tarsometatarsus.

Lig. metatarso-sesamoideum. The strong Lig. metatarso-sesamoideum connects Os sesamoideum intertarsale with the Tarsometatarsus distal to the rim of its medial cotyla, caudal to the attachment of Lig. collaterale mediale of the intertarsal joint; in some birds it is continuous with the medial collateral ligament itself (e.g., *Columba*, Cracraft, 1971; *Gallus*). See Annot. 169.

Lig. cartilago-metatarsale. Unites the middle of the distal end of Cartilago tibialis to Sulcus ligamentosus on the proximal surface of the Tarsometatarsus just caudal to its articular cotylae. See Annot. 164, 169; and **Osteo.** Annot. 286.

(167) **Artc. intertarsalis.** Synonymy: Artc. tibiotarso-tarsometatarsalis; Artc. mesotarsalis. The joint between the proximal and distal rows of tarsal bones, found in birds, dinosaurs, and pterosaurs (McGowan, 1985). This joint is not homologous to the mammalian ankle joint (Artc. tarsocruralis). The Fibula does not take part in the formation of the avian intertarsal joint. No independent tarsal elements are found in adult birds, since during fetal and postnatal development the proximal row of tarsal elements cap the distal end of the tibia, forming its condyles, the distal element fusing with the metatarsals (Hogg, 1980). See Annot. 163, 164 and **Osteo.** Annot. 283 for literature citations.

(168) **Meniscus medialis; Meniscus lateralis.** According to the comparative study of Stolpe (1932) only the lateral meniscus of the intertarsal joint is well developed. The medial meniscus is absent or poorly developed in some taxa: *Gallus, Acryllium* (Stolpe, 1932); *Columba, Cyanocitta, Asio;* well developed in *Ara* (Stolpe, 1932) and *Meleagris* (Barnett, 1954a). Meniscus lateralis is strongly attached to Lig. collaterale laterale in many birds. Both menisci are absent in flamingos (phoenicopterids); two complete menisci exist in psittaciforms (Stolpe, 1932). See Fig. 5.8 and Annot. 169, 170.

(169) **Lig. meniscosesamoideum.** Connects Cornu caudalis of Meniscus lateralis with the intertarsal sesamoid (*Columba, Gallus*). See Annot. 166.

(170) **Lig. meniscotibiale.** Synonymy: Kreuzband (Stolpe, 1932). Attached to the intercondylar incisure of the the Tibiotarsus proximocranial to the attachment of Lig. tibiometatarsale intercondylare. Distally the meniscotibial ligament bifurcates, its medial crus usually better developed than the lateral one. The crura become continuous with the cranial edges of the menisci (see Stolpe, 1932: 171). See Fig. 5.8 and Annot. 168).

(171) **Lig. tibiometatarsale intercondylare.** Synonymy: Lig. anticum (Gadow and Selenka, 1890; Stolpe, 1932); Lig. tibiometatarseum mediale (Ghetie, et al., 1976). This strong intracapsular ligament extends upward from Eminentia intercondylaris of the Tarsometatarsus to a distinct impression on Incisura intercondylaris of the distal

end of the Tibiotarsus. This ligament appears to be twisted on itself; its proximal part may be blended with ligamentous bands from the menisci of the joint (see Fig. 5.8; and Annot. 170).

(172) **Lig. collaterale mediale/laterale** (Fig. 5.8). Stolpe (1932) stated that one collateral ligament on each side of the intertarsal joint is the usual avian condition, however, he mentions that the flamingo has two clear-cut collateral ligaments on each side of the joint: one short, one long. Barnett (1954a) described an accessory band of Lig. collaterale in *Meleagris*.

(173) **Juncturae tarsometatarsales et intermetatarsales.** Metatarsal bones II, III, and IV ossify separately perichondrally, then ankylose with each other near the middle of their length. The distal tarsal elements form the "hypotarsal cap" that fuses with the common metatarsal bone, producing the definitive Tarsometatarsus of the adult (Hamilton, 1952). Persistent markings on the tarsometatarsus of adult birds of different taxa provide evidence of the fusion of the separate metatarsal bones. See Annot. 167; and **Osteo.** Annot. 284, 288.

(174) **Synd. intermetatarsalis hallucis.** This slightly moveable joint between metatarsal I and the shallow, elongate depression on metatarsal II shows no evidence of a synovial cavity in *Gallus* or *Columba*. See Annot. 175 and Fig. 5.9; **Osteo.** Fig. 14.

(175) **Lig. interosseum.** At its proximal end the articular surface of Os metatarsale I is held in the Fossa metatarsi I on metatarsal bone II by the Lig. interosseum. In the dried Tarsometatarsus conspicuous roughened areas at each end of the fossa indicate the attachment of the proximal and distal thickened parts of this ligament (*Columba, Gallus*) (see below).

Lig. elasticum metatarsi I. This ligament extends from the distal part of Os metatarsale I to the medial aspect of the distal end of Os metatarsale II near its trochlea. This elastic ligament permits the distal end of Os metatarsale I to be drawn away from the plantar surface of the Tarsometatarsus and assists in its return movement. See Fig. 5.9.

(176) **Lig. transversum metatarsale.** Synonymy: Lig. a (Cracraft, 1971). The transverse metatarsal ligament unites Tuberositas lateralis of the distal end of Os metatarsale I and the adjoining proximal phalanx of the hallux with the lateral epicondyle of Os metatarsale IV (*Columba, Gallus*) (see Fig. 5.9). The ligament spans the plantar flexor canal (Annot. 178), acting as a retinaculum to hold the flexor tendons of the digits against the plantar surface of the Tarsometatarsus.

(177) **Lig. obliquum hallucis.** Synonymy: Lig. c (Cracraft, 1971). The oblique ligament of the hallux extends from the plantar side of the base of the proximal phalanx of the Hallux distad to the medial side of the base of the proximal phalanx of Digitus II (*Columba, Gallus*); it appears to limit hyperextension of the hallux. See Fig. 5.9.

(178) **Canalis flexorius metatarsi** (new term). This is an osseo-fibrous tunnel that contains the compact bundle of tendons of the long flexor muscles of the digits and the bellies of short intrinsic muscles of the hallux. The bundle is enveloped and held in place against the plantar surface of the body of the tarsometatarsus (see **Osteo.** Annot. 292, 294) by the fibrous flexor sheath, **Vagina fibrosa flexoria,** which is attached to the medial and lateral borders of the tarsometatarsus. The canal extends from the distal end of the hypotarsus to the level of the metatarsophalangeal joints where the long flexor tendons enter the flexor canal of the sole (see below).

Canalis flexorius plantae (see legend of Fig. 5.9). This is the flexor canal of the sole (L. planta) of the foot. Tendons of the flexor muscles of the toes pass through this short passageway into the distal foot where they splay out to the individual digits. The plantar aspect of the canal is formed by Lig. transversum metatarsale and Tuberositas lateralis of Os metatarsale I; the dorsal aspect of the canal is formed by the surface of the Tarsometatarsus just proximal to its trochleae (Fossa supratrochlearis plantaris). See **Osteo.** Fig. 4.18).

(179) **Aponeurosis plantaris.** Synonymy: Lig. b. (Cracraft, 1971). Consists of a distal, tough connective tissue sheet that covers the plantar aspect of metatarsophalangeal joints II, III, and IV. The strongest attachments of the aponeurosis are to the bases of the proximal phalanges of digit II (medial), digit III and digit IV (lateral). The proximal thin part of the Aponeurosis plantaris is attached mainly to Lig. transversum metatarsale and to the lateral border of Os metatarsale I. See Fig. 5.9.

Corpus adiposum plantare profundum. An organized fat pad occupies the compartment deep to Aponeurosis plantaris, cushioning the more deeply situated tendons and joints.

Corpus adiposum plantare superficiale. This fat body lies superficial to Aponeurosis plantaris, forming much of the mass of Pulvinus metatarsalis (**Topog.** Annot. 46).

(180) **Artcc. metatarsophalangeales.** In most birds the hallux is rotated so that its plantar surface opposes the plantar surfaces of digits II, III, IV; however, in piciforms, cuculiforms, and psittaciforms the lateral digit (IV) is reversed, its plantar surface facing forward. Modifications of the metatarsophalangeal joint of digit IV in these groups are not included in this present terminology (see Steinbacher, 1935).

Birds which possess an "elevated" hallux wherein the metatarsophalangeal joint of the Hallux is situated more proximally than the metatarsophalangeal joints of the other digits are unable to use the hallux in grasping a perch or prey.

In some taxa, the hallux is rudimentary or lacking. See Coues (1927), and Campbell and Lack (1985) for thorough accounts of the feet of birds; and **Osteo.** Annot. 297.

(181) **Lig. collaterale.** Proximally the collateral ligaments of the metatarsophalangeal joints are attached bilaterally to a Fovea lig. collaterale (**Osteo.** Fig. 4.14A) of the metatarsal trochleae and distally to the base of the proximal phalanx and to Lig. plantare (Fig. 5.9). See Annot. 182.

(182) **Lig. plantare.** Synonymy: Lig. subarticulare (Cracraft, 1971). A well-developed fibrocartilaginous plantar ligament forms the plantar wall of each of the metatarso-phalangeal articulations, and is firmly attached to the bases of the proximal phalanges and the collateral ligaments of the joints. A deep sulcus in the plantar surface of each plantar ligament transmits the flexor tendons which are held against the plantar ligament by the fibrous flexor sheath (**Vagina fibrosa**) that stretches across the sulcus. The plantar ligament of the metatarsophalangeal joint of the hallux is poorly developed by comparison with the others (*Columba, Gallus*) (**Myol.** Annot. 3, 121).

Plantar ligaments also occur at all interphalangeal joints except those that involve the ungual phalanges. See Annot. 181 and Fig. 5.9; **Osteo.** Ossa digitorum pedis.

Os cuneatum (Ametov, 1971). These wedge-shaped cuneate bones occupy the metatarsophalangeal (MP) joint cavities of digits II, III, and IV of certain birds that progress by leaping or hopping (e.g., *Passer domesticus, Parus major, Sitta europaea*) rather than walking with alternating strides. Each joint contains a dorsal and a

plantar cuneate bone, each articulating with the proximal phalanx and trochlea of its metatarsal bone. On both sides of the joint each cuneate bone is connected to the proximal phalanx and the metatarsal bone by four oblique collateral ligaments, independent of the principal MP collateral ligaments. See **Osteo.** Annot. 256.

(183) **Lig. elasticum extensorium unguis** (new term: Quinn and Baumel, 1990). Hudson (1937), Berger (1952) have described in *Corvus* and in cuculids elastic extensor ligaments on the dorsal aspects of the pedal digits that are attached to the distal ends of the penultimate phalanges and the bases of the distal (ungual) phalanges; these elastic ligaments extend the distal interphalangeal joints automatically when not resisted by contraction of M. flexor digitorum/hallucis longus. See **Osteo.** Ossa digitorum pedis.

Lig. elasticum tendinis flexoris (new term: Quinn and Baumel, 1990). The elastic ligaments of the flexor tendons were noted by Schaffer (1903); Cracraft (1971). They are located within the digital flexor tendon sheath between the plantar surface of the phalanges and the dorsal surfaces of the tendons of M. flexor digitorum/hallucis longus. Proximally the bundle(s) of each elastic ligament is continuous with the collagenous bundles of the tendon itself. Distally each ligament is attached mainly to the plantar ligament of the interphalangeal joint. In those birds in which the elastic ligament has been studied, it is found opposite the next-to-last phalanx of each digit; in some birds additional ligaments are present at more proximal levels (e.g., *Corvus* and penguins in which they are strongly developed). See Quinn and Baumel (1990) for the function of these ligaments.

(184) **Lig. inguinale.** This fibrous band (quite distinct in larger birds) stretches caudally from the lateral margin of the preacetabular ilium to the Tuberculum preacetabulare (**Osteo.** Fig. 4.15B). Lig. inguinale forms the ventral boundary of the neurovascular hiatus for passage of the femoral nerve and vessels; abdominal muscles arise from its ventral convex edge.

(185) **Membrana iliocaudalis** (Baumel, 1988). Fibrous sheet connecting the transverse processes of free caudal vertebrae on each side with the dorsolateral process of the ilium and the caudal margin of Os coxae. The paired membranes help to form the dorsal wall of the abdominal cavity (**Osteo.** Annot. 231 and Fig. 4.15B).

(186) **Ansa m. iliofibularis** (Ansa, L. loop). Synonymy: Ansa bicipitalis. The Ansa has two femoral bands and one fibular band; caudal to the knee the ansa acts as a fibrous pulley for the tendon of M. iliofibularis (M. biceps femoris). See **Myol.** Annot. 102; consult Zusi and Bentz (1984) and Raikow (1985).

(187) **Retinaculum extensorium tibiotarsi.** Synonymy: Lig. transversum. The tendon of M. tibialis cranialis is restrained by this tough fibrous arch that is located on the distal end of cranial surface of Tibiotarsus just proximal to the osseous Pons supratendineus. The tibiotarsal retinaculum is obliquely disposed, not transversely as its older name indicates. On a deeper level the tendon of M. extensor digitorum longus also passes deep to this retinaculum. See Fig. 5.8B; **Myol.** Fig. 6.17; and **Osteo.** Annot. 278.

(188) **Retinaculum extensorium tarsometatarsi.** Located on the dorsal (cranial) aspect of the proximal Tarsometatarsus, this fibrous arch holds the tendon of M. extensor digitorum longus against the bone and acts as its pulley. The Retinaculum is an osseous arch in certain avian taxa (see Fig. 5.8B; and **Osteo.** Annot. 287).

Retinaculum m. fibularis [peronei]. Fibrous band that spans the sulcus for the tendon of M. fibularis brevis on the lateral condyle of the distal tibiotarsus (see **Osteo.** Annot. 282).

(189) **Ligg. pennarum.** Specialized ligamentous connections of wing and tail flight feathers other than the general connective tissue attachment of the follicles of remiges, rectrices, and major tectrices to bones, integument, and fascias. The ligaments interconnect adjacent flight feathers, others passing from parts of the skeleton to the feathers, either concerned with their movements or their stabilization. See Pelissier (1923) for a comparative study of the feather ligaments of the wing; see also Robin and Chabray (1884), Stettenheim (1959), and Raikow (1985).

(190) **Lig. elasticum interremigale major.** Synonymy: Grand ligament palmaire superieur (Alix, 1874); grand ligament marginale (Pelissier, 1923); interremigeal lig. (Stettenheim, 1959); Lig. elasticum interremigiale (NAA, 1979). This elastic ligament is found in the free caudal edge of the postpatagial skin fold between adjacent remiges. The part of the ligament between feathers splits and passes around each feather follicle on its dorsal and ventral aspects (*Astur*, Pelissier, 1923). Sy (1936) illustrates differences in form and relationship of the ligament to the follicles of the remiges in representatives of five different orders. The elastic ligament of the primary remiges is continuous with that of the secondary remiges in the carpal region (see Annot. 197; and Fig. 5.11).

(191) **Retinacula ulnocarpo-remigalia.** Variable bands from Os carpi ulnare or from Aponeurosis ventralis that extend to follicles of the remiges and major ventral tectrices (coverts) of the carpal region (see Pelissier, 1923). See Annot. 113, 115; and Fig. 5.11.

(192) **Aponeurosis interphalango-remigalis** (Fig. 5.11). Located on the ventral side of Digitus major. The Aponeurosis is attached to the skeleton in the region of interphalangeal joint of the major digit; it radiates to the follicles of several adjacent remiges.

(193) **Ligg. phalangoremigalia distalia.** Individual ligamentous slips from the ventral surface of the terminal phalanx of Digitus major to several of the most distal primary remiges.

(194) **Aponeurosis ventralis antebrachii** (see Annot. 143); **Aponeurosis dorsalis antebrachii** (Pelissier, 1923). Dense fascial sheets covering the flexor and extensor muscles of the forearm. The Lig. limitans cubiti (see Annot. 141) blends with the proximal end of the Aponeurosis dorsalis antebrachii to a variable degree in birds of different taxa.

Digitationes remigales from the caudal margin of dorsal antebrachial aponeurosis pass to the follicles of the secondary remiges.

(195) **Septum humerocarpale.** This well defined intermuscular fascial sheet passes dorsally from the humerocarpal ligament to the ventral aspects of the secondary remiges. The septum is described in detail by Alix (1874) and Pelissier (1923). See Annot. 143, Lig. humerocarpale; and Fig. 5.11.

(196) **Digitationes remigales.** Synonymy: Ligg. sous-remigien (Pelissier, 1923). These ligamentous slips from Septum humerocarpale and from the elastic ligament of M. flexor carpi ulnaris are attached to the follicles of the secondary remiges. See Annot. 197; and Fig. 5.11.

(197) **Lig. elasticum interremigale minor.** Synonymy: Lig. elasticum m. flexoris carpi (NAA, 1979). This continuous elastic ligament stretching the length of the antebrachium is cranial to, and parallels, the major elastic interremigal ligament which is found in the margin of the postpatagium (see Annot. 190); not present in the manus. The minor interremigal ligament receives the insertion of Pars remigalis [caudalis] of M. flexor carpi ulnaris (Fig. 5.11). Alix (1874) noted the elastic structure of this ligament, and referred to the part of the muscle inserting on it as "rotateur des remiges" inasmuch as it sends digitations to each secondary feather. Pelissier (1923) called it the "lig. du cubital anterieur", noting that it is not continuous in the coraciiform bird, *Tockus* (formerly *Lophoceros*), but consists of a series of individual digitations to the secondaries.

(198) **Lig. elasticum intertectricale.** Synonymy: intercovertal lig. (Stettenheim, 1959). Connects adjacent major ventral tectrices (covert feathers) (see **Integ.** of the antebrachium, carpus, and manus. Lig. elasticum intertectricale is strongest and best developed in the carpal region **(Lig. elasticum intertectricale carpale),** e.g., *Columba* and charadriiforms (Stettenheim, 1959) and tapers proximally and distally in the wing. See Fig. 5.11.

(199) **Ligg. cubiti** (Pelissier, 1923). Short ligaments that run from the follicles of the secondary remiges to the series of Papillae remigales caudales of the shaft of the Ulna; the ligaments are not attached to the apices of the follicles, but slightly distal to them.

(200) **Lig. elasticum interrectricale.** Synonymy: "lig. elastique souscaudal ou inferior" (Robin and Chabry, 1884). This elastic ligament is placed just deep to the fold of integument that connects the collars of follicles of the rectrices where they protrude from the rectrical bulbs. The form of this ligament varies markedly between different birds, e.g., in *Columba* it consists of a thin, wide transverse band stretching between the follicles of the rectrices on their dorsal and ventral aspects (Baumel, 1988); in *Gallus* the ligament consists of strong separate segments in the spaces between adjacent retrices; and in *Larus* the ligament consists of a cylindrical elastic bar dorsal to the rectrices, a flat band ventrally with no elements of the ligament in the interrectrical spaces. See Baumel (1988) Figs. 10, 14.

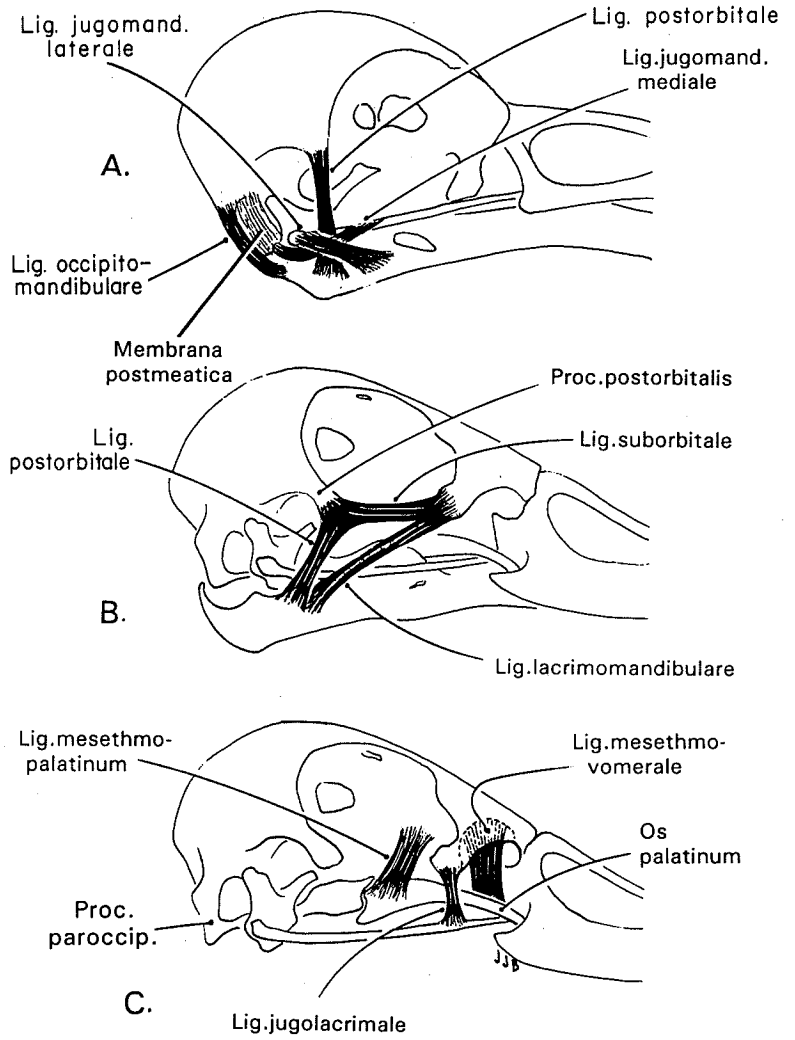

Fig. 5.1. Ligaments of the skull. A, *Corvus;* lateral view, right side of the skull showing the superficial ligaments; B and C, *Anser,* lateral view, right side of the skull. In B the superficial ligaments are shown; the more deeply disposed ligaments are shown in C. Redrawn from Bock (1964). With permission of Academic Press.
Abbreviation: paroccip., paroccipital.

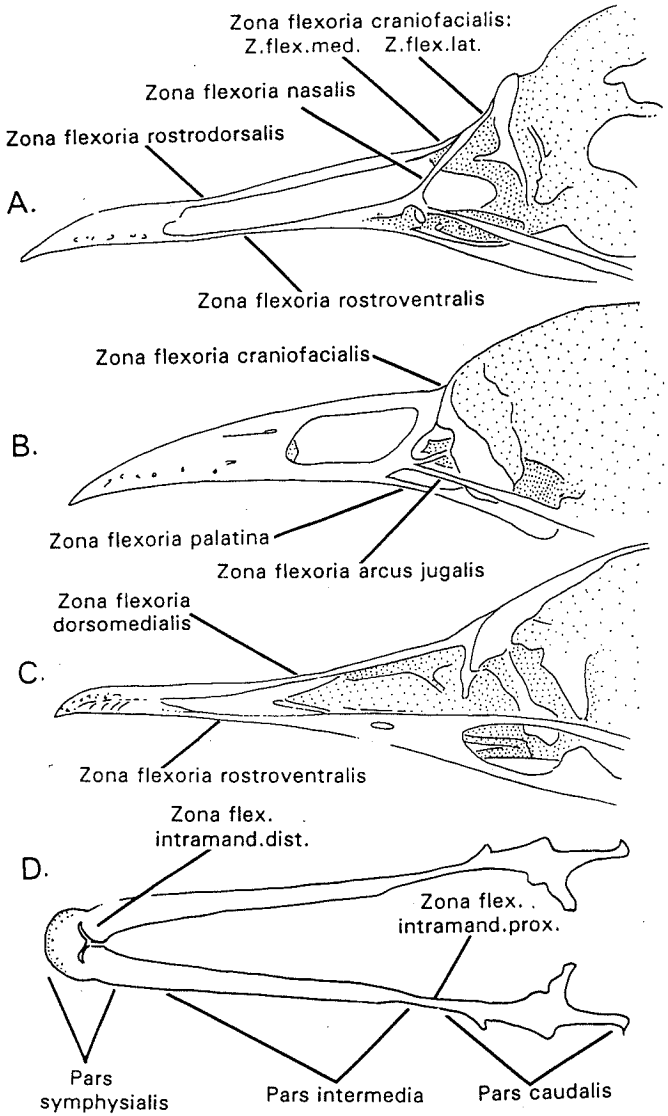

Fig. 5.2. Flexion (bending) zones of the avian skull; examples of the major types. A, B, and C: upper (maxillary) jaw bending zones, redrawn from Zusi (1984); D, lower (mandibular) jaw bending zones, after Komárek (1979). Note: not all of the different flexion zones shown appear in any one species.

A, the plover, *Pluvialis squatarola.* Rhynchokinetic skull, schizorhinal nostril (charadriiform type). B, the jay, *Cyanocitta stelleri;* Prokinetic skull, holorhinal nostril. C, the Ostrich, *Struthio camelus;* Rhynchokinetic skull, schizorhinal nostril (ratite type). D, the duck, *Anas platyrhynchos;* Mandible. Each mandibular ramus of this form demonstrates both rostral and caudal intramandibular flexion zones. See **Osteo.** Fig. 4.1 for lateral view of the caudal intramandibular zone of the mandibular ramus of a gull (*Larus*).

Abbreviation: intermand., intermandibularis.

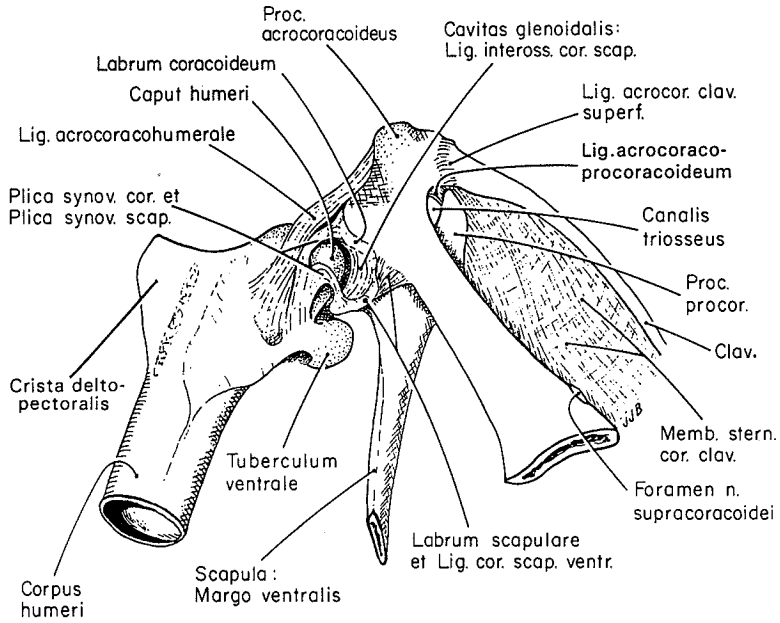

Fig. 5.3. The shoulder joint (Artc. omalis) of the pigeon, *Columba livia.* Right shoulder, ventral aspect; the general articular capsule is not depicted. Original drawing, J. J. Baumel. With permission of Academic Press.

Abbreviations: acrocor.clav., acrocoraco-claviculare; acrocor. procor., acrocoraco-procoracoideum; cor. scap., coracoscapulare; inteross. cor. scap., interosseum coracoscapulare; procor., procoracoideus.

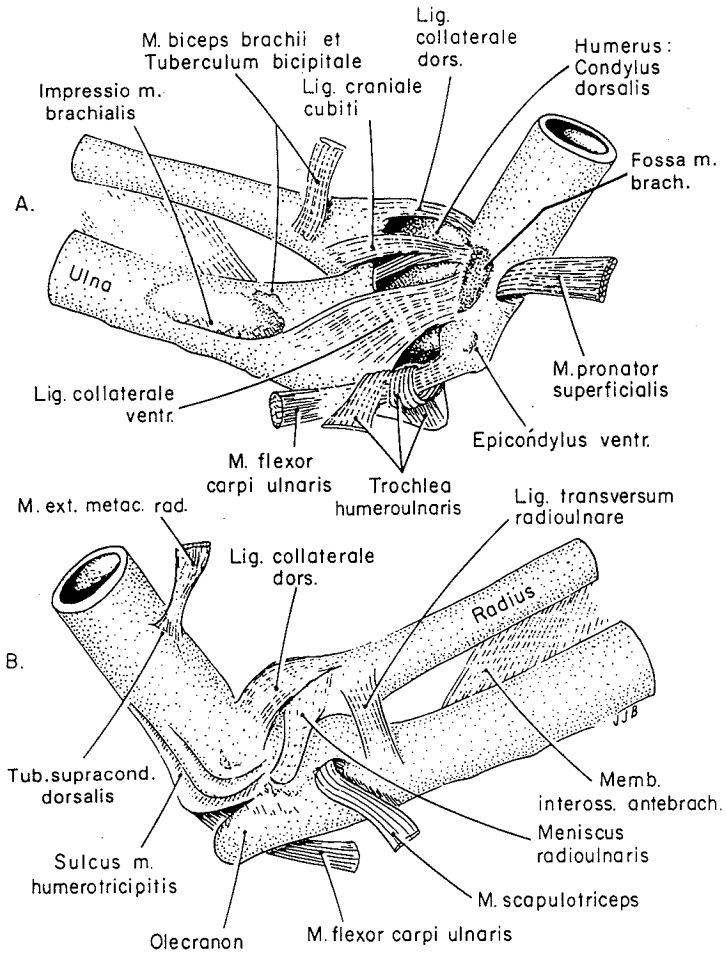

Fig. 5.4. The elbow joint (Junctura cubiti) of the pigeon, *Columba livia;* Right side. Original drawing, J. J. Baumel. A, ventral aspect; B, dorsal aspect. Note: (1) Lig. craniale cubiti splits into two slips, one attached to the radius, the other attached to the ulna; the latter intervenes between the two bones. (2) in A the well developed articular capsule has been removed between the three distinct ligaments. (3) in B the articular capsule is quite delicate (not shown). (4) the Meniscus radioulnaris has strong attachments to radius and ulna. (5) the dorsal and caudal aspects of the humeroulnar joint are strengthened by the tendons of the triceps muscles and possess no collateral ligaments. With permission of Academic Press.

Abbreviations: M. ext. metac. rad., M. extensor metacarpi radialis; Memb. inteross. antebrach., Membrana interossea antebrachialis; Tub. supracondy., Tuberculum supracondylare.

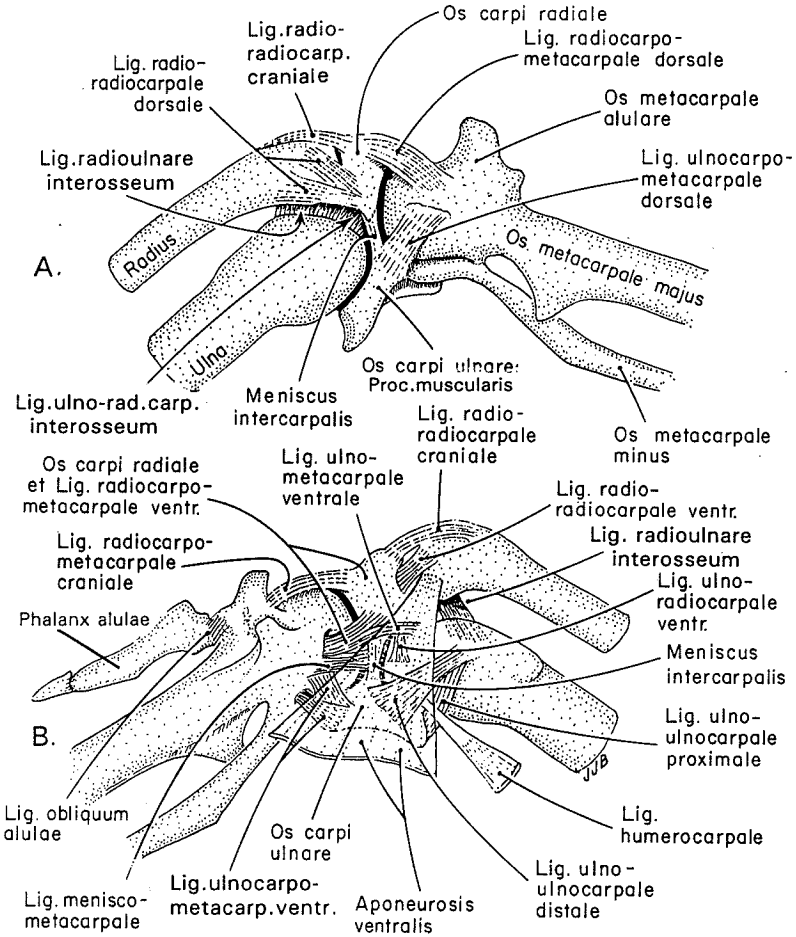

Fig. 5.5. The joints of the wrist (Juncturae carpi) of the chicken, *Gallus gallus.* Original drawing, J. J. Baumel. A, dorsal aspect; B, ventral aspect. Note: (1) The bones are drawn apart slightly to demonstrate the interosseous ligaments and meniscus; the joint spaces are depicted in solid black. (2) The Lig. interosseum radiolnare and Lig. ulno-radiocarpale interosseum are continuous with one another. (3) the Aponeurosis ventralis is superficial to many of the ventral ligaments of the joint; the main part of the aponeurosis is depicted (see Annot. 114, 115 and Fig. 5.11). (4) the Lig. radioulnare interosseum is interposed between the distal extremities of the radius and ulna, so that the two bones articulate directly with one another only slightly, if at all. With permission of Academic Press.

Abbreviations: Lig. ulno-rad. carp, Lig. ulno-radiocarpale.

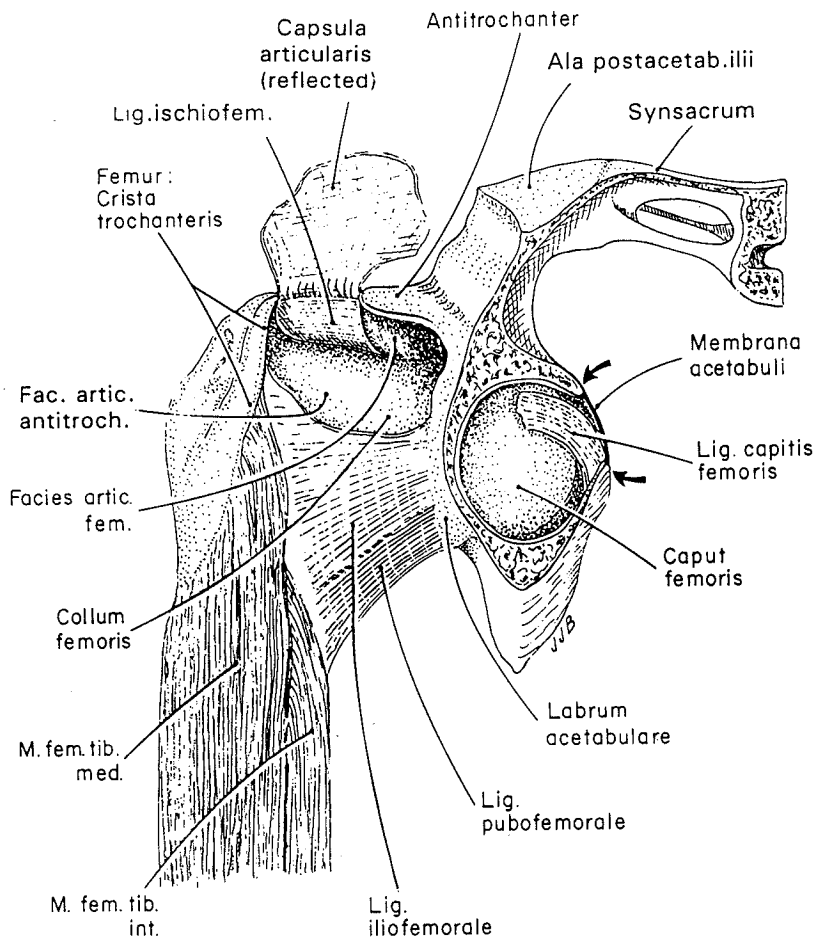

Fig. 5.6. The hip joint (Junctura coxae) of the pigeon, *Columba livia*. Right side, cranial aspect. Original drawing, J. J. Baumel. The pelvis is sectioned approximately transversely, opening a window into the Acetabulum and exposing the head of the femur and its ligament. The femur is rotated laterally and withdrawn slightly from the Acetabulum. The two arrows indicate the upper and lower margins of Foramen acetabuli.

Note: (1) the cranial and dorsal parts of the articular capsule are delicate; the remainder of the capsule consists of the strong, thick ilio-, pubo-, and ischiofemoral ligaments (see Annot. 153). (2) the joint between the neck of the Femur and the Antitrochanter (Artc. coxotrochanterica) in addition to those of the head of the femur with the acetabulum (Artc. coxocapitalis). Modified with permission of Academic Press.

Abbreviations: antitroch., antitrochanterica; M. fem. tib., M. femorotibialis.

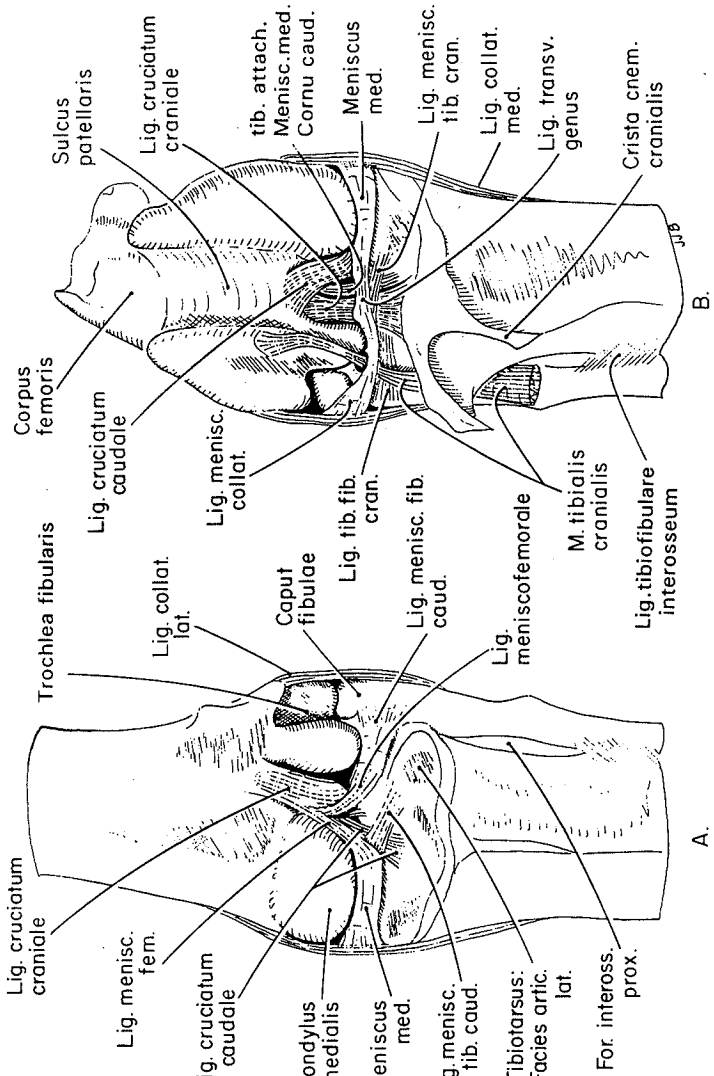

Fig. 5.7. The joint of the knee (Junctura genus) of the pigeon, *Columba livia*. Original drawing, J. J. Baumel. A, caudal aspect of right knee, hyperextended. B, cranial aspect of right knee; fully flexed. Note: (1) the tendon of M. tibialis cranialis perforates the Meniscus lateralis. (2) in B, that Meniscus lateralis sends a dorsal extension between Caput fibulae and the lateral surface of the lateral condyle of the femur. (3) the attachment of both menisci to collateral ligaments of the joint. With permission of Academic Press.

Abbreviations: For. inteross. prox., Foramen interosseum proximale; menisc. collat., meniscocollaterale; menisc. fem., meniscofemorale; menisc. fib. caud., meniscofibulare caudale; menisc. tib., meniscotibiale.

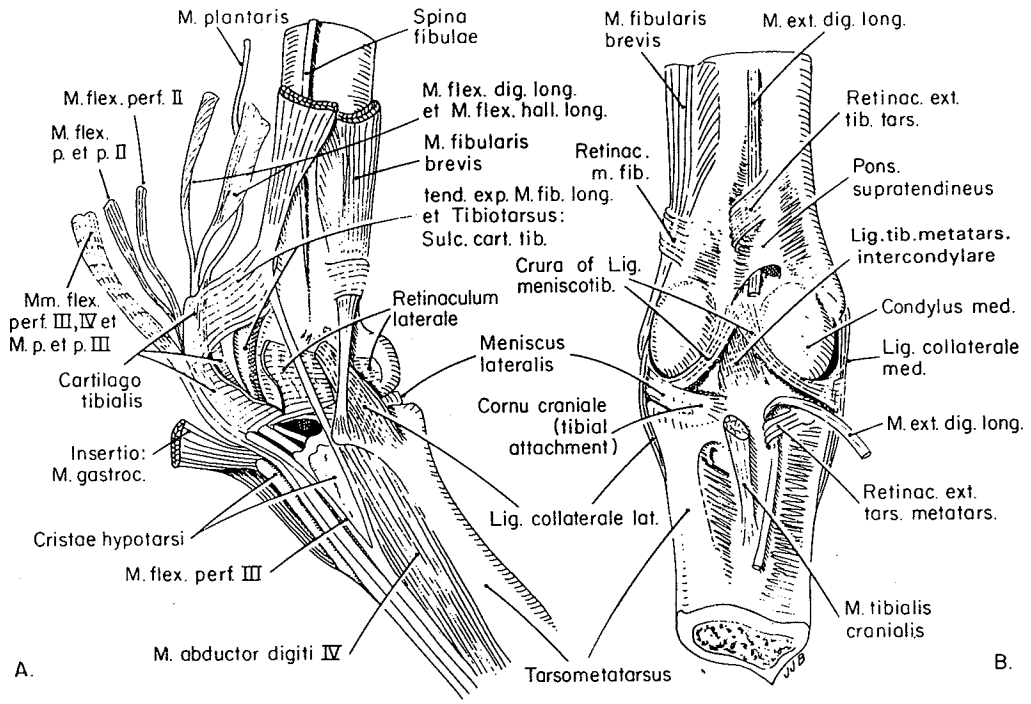

Fig. 5.8. The joints of the ankle (Juncturae intertarsales) of the pigeon, *Columba livia*. Original drawing, J. J. Baumel. A, lateral aspect, right limb; B, cranial aspect, right limb.

Note: (1) in A, the attachments of M. plantaris and M. fibularis longus to Cartilago tibialis. (2) in A, the tibial cartilage drawn caudally out of its articular sulcus on the distal extremity of the Tibiotarsus. (3) the Artc. cartilago-tibiotarsalis communicating with the Artc. intertarsalis. (4) in A, the distal part of the Retinaculum laterale serving as the articular capsule of the intertarsal joint. (5) the tendon of M. tibialis cranialis (cut) traverses the Retinaculum extensorium tibiotarsi. (6) the medial crus of Lig. meniscotibiale is attached to the margin of the medial cotyla of the Tarsometatarsus since no medial meniscus is present (see Annot. 168). With permission of Academic Press.

Abbreviations: intercondy. tib. metatars., intercondylare tibiometatarsale; meniscotib., meniscotibialis; M. flex. perf. II, III, IV; M. flexor perforatus digiti II, III or IV; M. flex. p. et p. dig. II, III, M. flexor perforans et perforatus digiti II or III; Retinac. ext. tars. metatars., Retinaculum extensorium tarsometatarsi; Retinac. ext. tib. tars., Retinaculum extensorium tibiotarsi; Sulc. cart. tib., Sulcus cartilaginis tibialis; tend. exp., tendinous expansion.

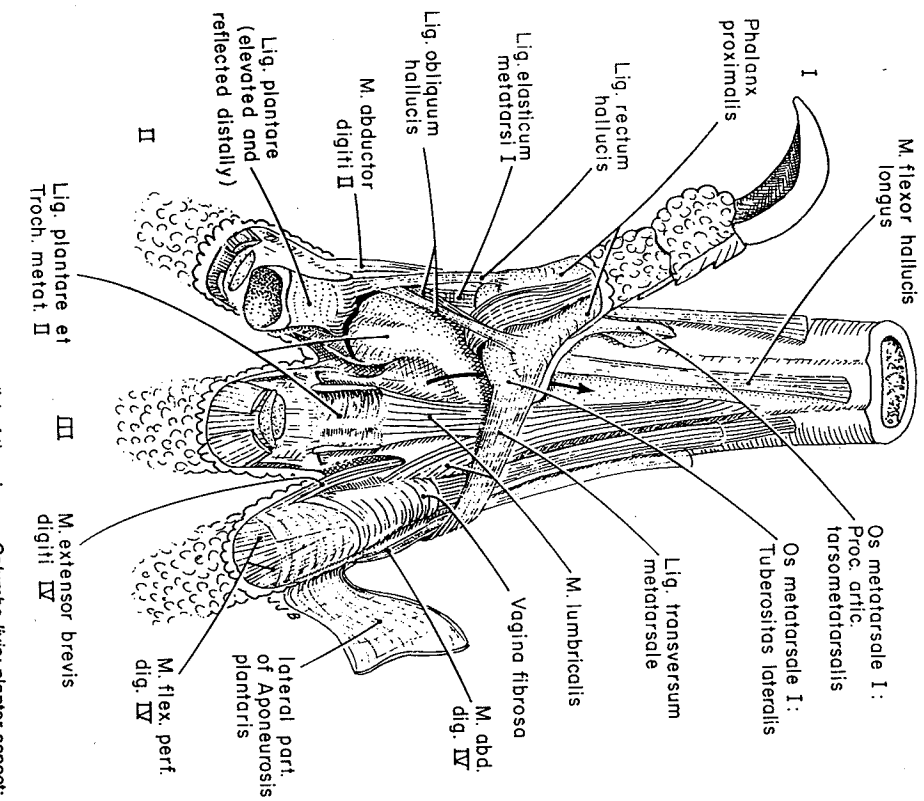

Fig. 5.9. Joints of the foot (Juncturae pedis) of the pigeon, *Columba livia*; plantar aspect; right foot. Original drawing of J. J. Baumel. Digitus I [Hallux] is hyperextended and drawn medially; the arrow is situated in Canalis flexorius plantaris through which pass the long flexor tendons to the digits. With permission of Academic Press.

Note: (1) the deep part of the Lig. obliquum hallucis is attached to the medial aspect of the trochlea of metatarsal II; its superficial part is attached to the proximal phalanx of Digitus II. (2) on the fourth digit the Vagina fibrosa is intact, attached to the margins of the plantar ligament and to the proximal phalanx. On the third digit the flexor sheath and tendons are removed showing the plantar ligament and its attachment to the base of the proximal phalanx. On the second digit the plantar ligament is elevated from its trochlea and reflected distally showing its dorsal surface. (3) a strong part of Aponeurosis plantaris (only partially depicted) extends transversely across the metatarsophalangeal joints; a thin portion (not shown) extends proximally to become continuous with the transverse metatarsal ligament and the lateral tuberosity of the first metatarsal bone.

Abbreviations: M. abd. dig. IV, M. abductor digiti IV; M. flex. perf. dig. IV, M. flexor perforatus digiti IV.

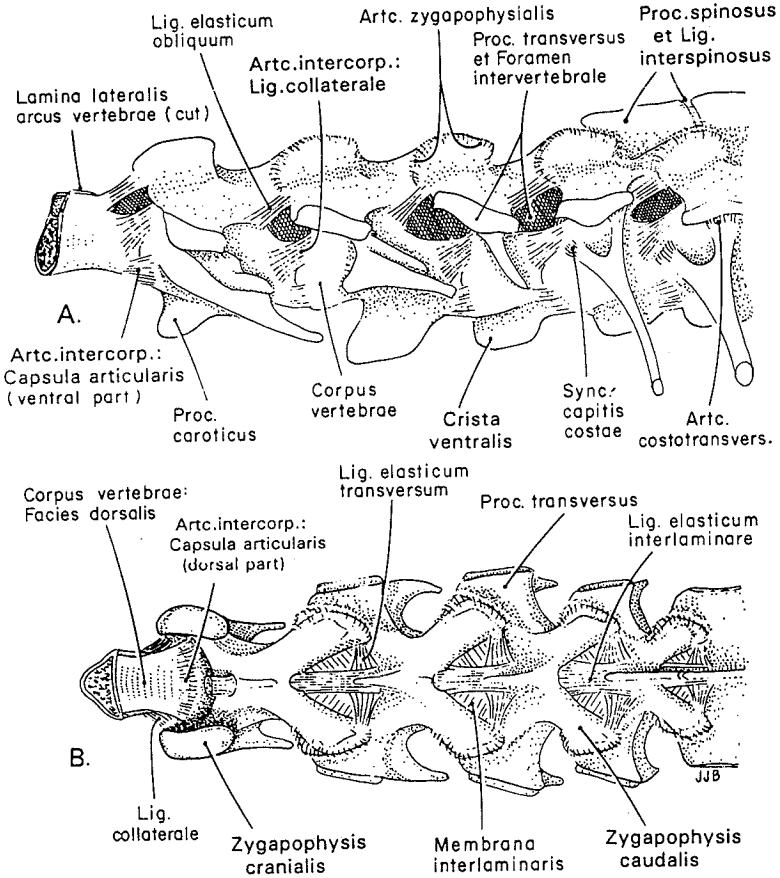

Fig. 5.10. Ligaments of the joints of the vertebral column (Juncturae columnae vertebralis) of the pigeon, *Columbia livia.* This segment of the column is from the cervicothoracic transitional region at the root of the neck. A, lateral view, left side; B, dorsal view. Original drawing, J. J. Baumel. With permission of Academic Press.

Note: (1) the arch of the cranialmost vertebra in both A and B is cut away. (2) only the lateral margin of Lig. elasticum obliquum is depicted, the deeper part of the ligament being situated on the ventral surface of Proc. articularis caudalis of the vertebra which forms the cranial attachment of the ligament. (3) Lig. elasticum obliquum assists Lig. elasticum interlaminare in maintaining the dorsal concavity of this part of the neck. (4) both the transverse and the oblique elastic ligaments of one side are tensed when the vertebral column is flexed to the contralateral side. (5) most of the joints between vertebral bodies are synovial joints having a meniscus. (6) the exceptionally large intervertebral foramina of this vertebral segment transmit the roots of the brachial plexus and huge veins.

Abbreviation: intercorp., intercorporalis.

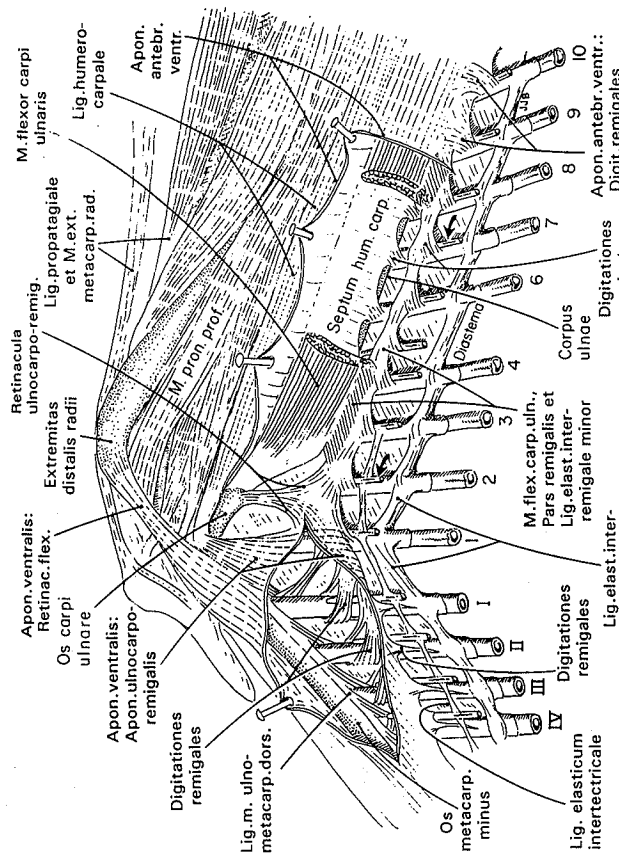

Fig. 5.11. Ligaments of the feathers (Ligg. pennarum) of the wing of the pigeon, *Columba livia;* ventral aspect, right wing. Original drawing, J. J. Baumel. Arrows indicate lower major coverts of the secondary remiges (Tectrices secundariae ventrales majores); Roman numerals indicate Remiges primarii; Arabic numerals indicate Remiges secundarii. With permission of Academic Press.

Note: (1) the Diastema or hiatus in the series of secondary remiges (see **Integ.** Annot. 53). (2) the digitations to the remiges from the ventral antebrachial aponeurosis, from the Lig. elasticum interremigale minor and from the Septum humerocarpale. (3) the Lig. humerocarpale spliting to enclose M. flex. dig. superf., the cranial and caudal laminae blending on the dorsal side of the muscle and becoming continuous with the Septum humerocarpale. (4) the space deep to the reflected parts of Aponeurosis ventralis that houses the belly of M. ulnometacarpalis dorsalis (removed to display the calami of the primary feathers).

Abbreviations: Apon. antebr. ventr., Aponeurosis antebrachialis ventralis; Apon. ventr. carp., Aponeurosis ventralis carpalis; Lig. m. ulnometac. dors., Lig. m. ulnometacarpalis dorsalis; Lig. elast. m. flex. carp. uln., Lig. elasticum m. flexoris carpi ulnaris; Lig. elast. propatag., Lig. propatagiale, pars elastica; M. ext. metac. rad., M. extensor metacarpi radialis; M. flex. carp. uln., M. flexor carpi ulnaris; M. pron. prof., M. pronator profundus; Retin. flex., Retinaculum flexorum; Septum hum. carp., Septum humerocarpale.

6

MYOLOGIA

JAMES C. VANDEN BERGE
and
GART A. ZWEERS

With contributions from subcommittee members: J. J. Baumel, B. Bhattacharyya, T. Fujioka, E. Kurochkin, R. J. Raikow, R. L. Zusi.

Comments on nomenclature and homology. The subcommittee acknowledges the continuing inherent difficulties in adopting a standardized nomenclature for the musculature when a proposed term may imply a homology between muscles in different taxa for which the homology is unknown. In the same manner, a different term may imply nonhomology between muscles whose nonhomology is also unknown. Raikow and his co-workers (1975, 1979), Vanden Berge (1970, 1979, 1982), Hall (1984), Homberger (1986), and Schroeter and Tosney (1990) have commented on this common problem in comparative anatomy. In most cases this difficulty may not present a major concern for most systematic studies, except for those dealing with higher taxa.

In this revision, the subcommittee has continued to cite references to original comprehensive works presented in the NAA, 1979, to cite comprehensive tables of synonymy in more recent literature (e.g., Zweers, 1982; Homberger, 1986; Baumel, 1988; Homberger and Meyers, 1989), and to propose new terms only when such structures were considered to be well described and clearly representative of recently discovered musculoskeletal relationships of functional, evolutionary, or systematic significance. Previous annotations have been expanded for selected structures; new annotations have been added as needed for clarification of originally proposed terms as well as for new terms. Zusi and Bentz (1984) presented a list of abbreviations for the musculature in birds, based on the standardized terminology of the previous edition (NAA, 1979). We have continued the use of a descriptive nomenclature for the musculature of the avian wing without enumeration of the digits (see **Osteo.** Intro. Nomenclature of digits of wing). Similarly, we have continued the use of the nomenclature for the musculature of the avian hip and thigh as previously adopted, even though we are aware of related studies of the reptilian musculoskeletal system (Walker, 1977; Rowe, 1986) which have

suggested a different terminology for certain muscles. In all instances we have attempted to follow the criteria which we established in compilation of the first edition (see NAA, 1979).

Muscles of the pelvic limb and the Garrod formula. In the previous edition (NAA, 1979:176-177) we have discussed and listed the so-called "formula muscles of Garrod" which constitute a set of anatomical variations in the musculature of the pelvic limb once thought to be characteristic of major taxa of birds. There is considerable doubt that the "formula" muscles of the pelvic limb are of any value, phylogenetically or taxonomically, in view of numerous other character variations in the musculature which are now known in birds. For this reason, in this edition we have eliminated all reference to the muscle symbols in the annotations and refer the reader to the NAA, 1979 edition.

TERMINI GENERALES

Musculus skeleti[1]
Origo[1]
Caput
Venter
Fascia
Epimysium
Insertio[1]
Perimysium
Fasciculus muscularis
Musculus subcutaneus[4]
Musculus striatus[1]
Musculus nonstriatus[1]
Musculus unipennatus
Musculus bipennatus
Musculus multipennatus
Musculus fusiformis
Musculus planus
Musculus quadratus
Musculus abductor
Musculus adductor
Musculus articularis
Musculus constrictor
Musculus depressor
Musculus dilator
Musculus expansor
Musculus extensor
Musculus flexor
Musculus levator
Musculus protractor
Musculus retractor
Musculus rotator
Musculus pronator
Musculus supinator
Musculus sphincter
Musculus tensor
Tendo
  Aponeurosis
  Area tuberculata tendinis[124]
Intersectio tendinea[2]
Manica flexoria[121]
Vagina tendinis[3 121 124]
  Plica vagina tendinis[124]
Vincula tendinum
  Vinculum breve
  Vinculum longum
Bursa synovialis
Tendo ossificans[1]

TERMINOLOGY

MUSCULI NONSTRIATI DERMATIS [4]

M. adductor retricium[67]
M. expansor secundariorum[5]
Mm. pennarum[4]
Tendo elastica[4]
Mm. apteriales[4]
M. orbicularis palpebrarum[15]

MUSCULI PTERYLARUM [SUBCUTANEI] [4]

M. constrictor colli[6]
  Pars intermandibularis
M. cucullaris
  M. cucullaris capitis[7]
    Pars interscapularis[8]
    Pars propatagialis[9]
    Pars clavicularis[10]
  M. cucullaris cervicis[7]
    Pars nuchalis
    Pars clavicularis[10]
M. latissimus dorsi
  Pars interscapularis[8 77]
  Pars metapatagialis[77]
  Pars scapulohumeralis[11 77]
M. serratus superficialis
  Pars metapatagialis[70]
  Pars scapulohumeralis[11 70]
M. pectoralis
  Pars subcutanea thoracica[12 75]
  Pars subcutanea abdominalis[12 75]
  Pars propatagialis[9 75]
M. biceps brachii
  Pars propatagialis[9 83]
M. deltoideus
  Pars propatagialis[79]

MUSCULI CAPITIS

MUSCULI BULBI OCULII [13]

M. rectus dorsalis
M. rectus ventralis
M. rectus lateralis
M. rectus medialis
M. obliquus dorsalis
M. obliquus ventralis
Musculi membranae nictitantis[14]
  M. quadratus membranae nictitantis
    Vagina tendinis
  M. pyramidalis membranae nictitantis
    Tendo m. pyramidalis
Musculi palpebrarum et periorbitae[15]
  M. levator palpebrae dorsalis
  M. depressor palpebrae ventralis
  M. tensor periorbitae
M. columellae[16]

MUSCULI MANDIBULAE [17]

M. adductor mandibulae externus[18]
  Pars rostralis [temporalis]
  Pars ventralis [medialis]
  Pars profunda
M. pseudotemporalis superficialis[19]
M. pseudotemporalis profundus[20]
M. adductor mandibulae ossis quadrati [caudalis][20]
M. pterygoideus[21]
M. ethmomandibularis[22]
M. protractor pterygoidei et quadrati[23]
M. depressor mandibulae[24]

MUSCULI APPARATUS HYOBRANCHIALIS [HYOLINGUALIS][25]

M. intermandibularis ventralis[26]
  Pars rostralis
  Pars caudalis
M. intermandibularis dorsalis[26]
M. serpihyoideus[27]
M. stylohyoideus[28]
M. branchiomandibularis[29]
  Pars rostralis
  Pars caudalis
M. interceratobranchialis [ceratohyoideus][30]
M. ceratoglossus[31]
M. hyoglossus rostralis [medialis][32]
M. hyoglossus transversus[34]
M. mesoglossus[34]
M. hyoglossus obliquus [lateralis][33]
M. supraglossus[34]
M. genioglossus[35]

MUSCULI LARYNGIS [LARYNGEALES] [37] (see Resp.)

M. constrictor glottidis[38]
M. dilator glottidis[38]
M. cleidohyoideus
M. cricohyoideus dorsalis[36]
M. cricohyoideus ventralis[36]
M. hyovalvularis[36]
M. tracheolateralis
M. tracheovalvularis[36]

MUSCULI TRACHEALES [37] (see Resp.)

M. cleidotrachealis
M. cleidohyoideus
M. sternotrachealis
M. tracheolateralis

MUSCULI SYRINGEALES [39] (see Resp.)

M. obliquus ventralis
M. obliquus lateralis
Mm. syringeales
M. syringealis dorsalis
M. syringealis ventralis
M. syringealis superficialis

(continued)

MUSCULI SYRINGEALES [39] (see Resp.) (cont.)

M. syringealis profundus
M. syringealis caudalis
M. tracheobronchialis dorsalis
M. tracheobronchialis brevis
M. tracheobronchialis ventralis
M. vocalis dorsalis
M. vocalis ventralis

MUSCULI VERTEBRALES [40]

Aponeurosis transversa[40]
M. biventer cervicis[41]
  Pars cranialis
  Pars caudalis
Mm. craniocervicales[40]
  M. complexus[42]
  M. splenius capitis[43]
  M. rectus capitis dorsalis[44]
  M. rectus capitis lateralis[44]
  M. rectus capitis ventralis[44]
    Pars lateralis
    Pars medialis
Mm. cervicales dorsales[40]
  M. longus colli dorsalis[47]
    Pars cranialis[48]
    Pars caudalis[49]
      Tendo axialis[48 49]
      Pars profunda[50]
      Pars thoracica[51]
Mm. ascendentes
  M. ascendens cervicalis[4046]
  M. ascendens thoracicus[46]
M. intercristalis[52]
Mm. interspinales[52]
Mm. iliocostalis et longissimus dorsi[45]
Mm. cervicales laterales[40]
  Mm. intertransversarii[53]
  Mm. inclusi[54]
    Mm. inclusi dorsales
    Mm. inclusi ventrales
Mm. cervicales ventrales[40]
  M. flexor colli lateralis [brevis][55]
  M. flexor colli medialis [profundus][55]
  M. longus colli ventralis[56]
    Pars cranialis
    Pars caudalis

MUSCULI TRUNCI ET REGIONIS CAUDALIS

MUSCULI TRUNCI [57]

M. scalenus[58]
Mm. levatores costarum[58]
Mm. intercostales externi[59]
Mm. intercostales interni[59]
M. costosternalis[60]
  Pars major
  Pars minor
M. costoseptalis[61]
M. sternocoracoideus[62]
M. rectus abdominis[63]
M. obliquus externus abdominis[63]
M. obliquus internus abdominis[63]
M. transversus abdominis[63]

MUSCULI CAUDAE ET CLOACAE[64]

M. bulbi rectricium[67]
  Tendo centralis
M. adductor rectricium[67]
M. levator caudae[65]
  Pars vertebralis
  Pars rectricalis
M. depressor caudae[65]
  Aponeurosis cruciata[65]
  Pars proximalis
  Pars distalis
  Pars profunda
M. lateralis caudae[65]
M. caudofemoralis[66 110]
  Pars caudalis
M. pubocaudalis externus[66]
M. pubocaudalis internus[66]
  Pars pelvica
  Pars caudalis
Mm. cloacales[68]
  M. sphincter cloacae
    Septum supracloacale[68]
  M. transversus cloacae
  M. contractor cloacae
  M. depressor anguli venti
  M. levator cloacae [M. retractor phalli caudalis]
  M. dilator cloacae [M. retractor phalli cranialis]

MUSCULI ALAE [MEMBRI THORACICI]

M. rhomboideus superficialis[69]
M. rhomboideus profundus[69]
M. serratus superficialis[70]
  Pars cranialis
  Pars caudalis
  Pars metapatagialis[70]
M. serratus profundus[70]
M. scapulohumeralis cranialis[71]
M. scapulohumeralis caudalis[71]
Mm. subcoracoscapulares[72]
  M. subscapularis[73]
    Caput laterale
    Caput mediale
  M. subcoracoideus
M. coracobrachialis cranialis[74]
M. coracobrachialis caudalis[74]
M. pectoralis[75]
  Pars propatagialis[9]
  Pars sternobrachialis
  Pars costobrachialis
  Aponeurosis [Membrana] intramuscularis[75]
M. supracoracoideus[76]
M. latissimus dorsi[77]
  Pars cranialis
  Pars caudalis
  Pars metapatagialis
M. deltoideus [Complexus m. deltoideus][78]
  Pars propatagialis [M. propatagialis][79]
    Caput craniale [Pars longa]
    Caput caudale [Pars brevis]
  Pars major [M. deltoideus major][80]
    Caput craniale
    Caput caudale
    Caput proximale
  Pars minor [M. deltoideus minor][80]
    Caput dorsale
    Caput ventrale
M. triceps brachii
  M. scapulotriceps[81]
  M. humerotriceps[82]
  M. coracotriceps[82]

(continued)

MUSCULI ALAE [MEMBRI THORACICI] (cont.)

M. biceps brachii[83]
  Caput coracoideum
  Caput humerale
  Pars propatagialis[9]
M. expansor secundariorum[5]
M. brachialis (Figs. 6.11, 12)
M. pronator superficialis[84]
M. pronator profundus[84]
M. flexor carpi ulnaris[85]
  Pars remigalis[85]
M. flexor digitorum superficialis[86]
M. flexor digitorum profundus[86]
M. extensor carpi radialis[87]
  Caput dorsale
  Caput ventrale
M. extensor carpi ulnaris[88]
M. extensor digitorum communis[88 90]
M. extensor longus alulae[90]
M. extensor longus digiti majoris[90]
  Pars proximalis
  Pars distalis
M. supinator (Fig. 6.11)
M. ectepicondylo-ulnaris[91]
M. entepicondylo-ulnaris[92]
M. ulnometacarpalis dorsalis[89]
M. ulnometacarpalis ventralis[89]
M. interosseus dorsalis[93]
M. interosseus ventralis[93]
M. extensor brevis alulae[94]
M. abductor alulae[95]
M. flexor alulae[96]
M. adductor alulae[97]
M. abductor digiti majoris[98]
M. flexor digiti minoris[99]

MUSCULI MEMBRI PELVICI

Mm. iliotibiales[100]
  M. iliotibialis cranialis[101]
  M. iliotibialis lateralis[101]
    Pars preacetabularis
    Pars postacetabularis
    Hiatus acetabularis[101]
  M. iliotibialis medialis[101]
M. iliofibularis[102]
  Ansa m. iliofibularis (**Arthr.** Annot. 186)
M. ambiens[103]
Mm. iliotrochanterici[104]
  M. iliotrochantericus caudalis
  M. iliotrochantericus cranialis
  M. iliotrochantericus medius
M. iliofemoralis externus[105]
M. iliofemoralis internus[106]
Mm. femorotibiales[107]
  M. femorotibialis lateralis [externus]
  M. femorotibialis intermedius [medius]
  M. femorotibialis medialis [internus]
M. flexor cruris lateralis[108]
  Pars pelvica
  Pars accessoria
M. flexor cruris medialis[109]
M. caudofemoralis[110]
  Pars caudalis (see Mm. caudae)
  Pars pelvica
M. ischiofemoralis (Fig. 6.16)
M. obturatorius lateralis[111 112]
  Pars dorsalis
  Pars ventralis
M. obturatorius medialis[111]
M. pubo-ischio-femoralis[113]
  Pars lateralis [cranialis]
  Pars medialis [caudalis]
  Pars accessoria

(continued)

MUSCULI MEMBRI PELVICI (cont.)

M. tibialis cranialis[114]
  Caput femorale
  Caput tibiale
M. extensor digitorum longus[115]
M. fibularis [peroneus] longus[116]
M. fibularis [peroneus] brevis[117]
  Caput fibulare
  Caput tibiale
M. gastrocnemius[118]
  Pars lateralis [externa]
  Pars intermedia
  Pars medialis [interna]
  Pars supramedialis
M. plantaris[119]
M. popliteus[120]
M. flexor perforans et perforatus digiti II[121]
M. flexor perforans et perforatus digiti III[121]
M. flexor perforatus digiti II[121]
M. flexor perforatus digiti III[121]
  Vinculum tendinum flexorum[122]
M. flexor perforatus digiti IV[121]
M. flexor hallucis longus[123]
M. flexor digitorum longus[123]
  Vinculum tendinum flexorum[122]
  Area tuberculata tendinis[124]
  Plicae vaginae tendinis[124]
  Lig. elasticum tendinis flexoris[124]
M. extensor hallucis longus[125]
  Pars proximalis
  Pars distalis
  Lig. elasticum extensorium unguis[124]
M. flexor hallucis brevis[126]
M. abductor digiti II[127]
M. adductor digiti II[127]
M. extensor proprius digiti III[128]
M. extensor brevis digiti III
M. extensor proprius digiti IV[129]
M. extensor brevis digiti IV[129]
M. abductor digiti IV[130]
M. adductor digiti IV[130]
M. lumbricalis

ANNOTATIONS

(1) **Musculus skeleti.** At present considerable evidence supports the development of the avian skeletal muscle fibers from somites. The basis for patterning of skeletal and connective tissues resides within the neural crest cell population in the head and in the somatopleure of the body wall (Chevallier, 1979; Jacob, et al. 1979; Christ, et al., 1983; Noden, 1983; McClearn and Noden, 1988).

Musculus striatus; M. nonstriatus. "Striated" and "nonstriated" refer to the histological profile of the respective muscle cell types (NAV, 1983:H12). Since a striated profile is also characteristic of myocardium, use of "M. striatus" as a synonym for M. skeleti is not recommended; however, M. nonstriatus is equivalent to smooth muscle.

Tendo ossificans. In some avian taxa, the long tendons of the wing and leg muscles, and some of the flattened aponeuroses and long tendons of the muscles of the vertebral column (see **Osteo.** Annot. 140a) develop ossified areas *within* tendon. These areas are discrete and nonpathologic, characterized by the appearance of a new intratendinous cell population, increased vascularization, initial mineralization of the intercellular matrix, and later ossification.

The terms **Origo** [Synonymy: Insertio proximale, Punctum fixum; NA, 1977:A37, footnote 78] and **Insertio** [Synonymy: Insertio distale, Terminatio, Punctum mobile] have not been problematical in the avian literature in contrast to other Nomina (IANC; NA, 1977:A26, footnote 34). Although some skeletal muscles have no well-defined skeletal attachments, descriptive, and/or functional relationships are usually sufficient for adequate identification of these muscles, e.g., M. supraglossus and M. mesoglossus in psittacine birds (Annot. 34; see Homberger, 1986).

(2) **Intersectio tendinea.** Synonymy: Inscriptio tendinea. A complete tendinous band between two or more parts of the same muscle (Annot. 66), or between different muscles (Annot. 8), generally without continuity of the fleshy bundles. In some muscles (Annot. 42), however, short muscle fibers attach on incomplete bands within a single belly, but other longer muscle fibers extend through the tendinous band.

(3) **Vagina tendinis.** Schaffer (1903) was apparently the first to accurately describe the general structure and structural adaptations of the fibrous/synovial sheath of the avian pedal digital tendon. Recently, these were more fully characterized by Quinn and Baumel (1990); see also Annot. 121 and 124; Frewein (1967) and Greenlee, et al. (1975).

(4) **Musculi nonstriati dermatis** is a collective term for smooth muscles within the dermis (as defined by Lucas and Stettenheim, 1972:483, Fig. 294). These muscles consist of two principal types: feather muscles and apterial muscles.

Feather muscles (**Musculi pennarum;** Synonymy: Mm. pennales (NAA, 1979) are attached at each end by an elastic tendon (**Tendo elastica**) to the connective tissues of the external wall of follicles of contour, semiplume, bristle, and body down feathers (Lucas and Stettenheim, 1972, Chap. 8). Filoplumes lack feather muscles. Basically, feather muscles have a simple to complex parallelogram arrangement and function as erectors, depressors, retractors, and rotators (Langley, 1904:242). See Fig. 6.1.

Lange (1931) designated the apterial muscles (**Mm. apteriales**) as a "Stratum musculo-elasticum"; these muscles lie within loose connective tissue of the dermis (Stratum laxum), but do not form a distinct layer. In *Gallus,* they are most abundant in the following apteria: scapular (caudal part), pectoral, and lateral areas of the trunk, pelvis, and tail. Elastic tendons also connect apterial muscles with feather muscles.

Musculi pterylarum [subcutanei]. Synonymy: Musculi cutanei, after NAV, 1983:A41; "dermal muscles" (Lucas and Stettenheim, 1972:505). After Petry (1951), they are named "muscles of the feather tracts". Thin sheets or narrow bands of striated muscle lie in both the transverse (circular) and longitudinal planes of the neck within the superficial fascia (Tela subcutanea). They lie adjacent to or beneath large cervical feather tracts (e.g., M. constrictor colli, Annot. 6; M. cucullaris, Annot. 7, 8, 10) and abdominal feather tracts (Pars subcutanea, M. pectoralis, Annot. 12). Others may attach on the innermost lamina of a feather tract itself (Pars scapulohumeralis of Mm. latissimus dorsi and serratus superficialis, Annot. 11), but not to individual feather follicles. They position one feather tract relative to an adjacent tract, smoothing out the surface contour of the body (Osborne, 1968).

(5) **M. expansor secundariorum.** Synonymy: M. dermo-ulnaris (Owen, 1842). This nonstriated muscle may consist of a proximal tendon, and an intermediate fan-shaped belly associated with a distal tendon. **Tendo proximalis** is variably inserts onto muscle fascia (especially M. scapulohumeralis caudalis), or directly onto the scapula and coracoid, extending as far as the sternocoracoidal articulation in some taxa. In other taxa the tendon extends distally into the wing beneath the subhumeral

apterium, being continuous with attachments of the scapulohumeral slips from Mm. serratus superficialis and latissimus dorsi (Annot. 11).

Tendo distalis (T. humeralis) is attached to the ventral epicondyle of the humerus or to the Trochlea humeroulnaris (**Arthr.** Annot. 110), and directly on the follicles of two to six of the most proximal secondaries in the elbow region. See Fig. 6.12; and descriptions of Berger (1966), and Vanden Berge (1970).

(6) **M. constrictor colli** (Fig. 6.3). Synonymy: M. cutaneus colli (Fujioka, 1963; Zweers, 1982); M. dermohyoideus (Zweers, 1982); M. dermodorsalis (Burt, 1930); see also Homberger and Meyers (1989). M. constrictor colli is the most superficial of the muscles underlying the cervical pterylae, and is typically a thin sheet of muscle, oriented circumferentially, usually opposite the cranial half or less of the neck, in some taxa more extensive caudally. Separated muscle bundles are best organized ventrally where they attach to each side of a median ventral raphe, but more widely spaced dorsally and caudally where they end in superficial fascia and a dorsal median raphe. The most rostral bundles may be attached to the cranium, especially on the caudal and dorsal rim of the external acoustic meatus where they blend with the attachment of M. cucullaris capitis (Annot. 7). The entire muscle receives its innervation from R. cervicalis, N. hyomandibularis of the facial nerve (PNS Annot. 24).

M. constrictor colli, pars intermandibularis (Figs. 6.3, 7). Synonymy: M. basibranchialis mandibularis, pars superficialis (Vanden Berge, 1975); M. intermandibularis ventralis, pars caudalis (Zweers, 1974, 1982); see Homberger and Meyers (1989). Two major variations of this muscular slip occur. One is a fleshy band or sheet of muscle, forming the rostralmost bundles of the constrictor colli. In another the slip is attached to the lateral surface of Proc. retroarticularis of the mandible (**Osteo.** Annot. 49). In either case, it meets its counterpart in a midventral raphe, united with the caudal edge of M. intermandibularis ventralis (Annot. 26) and/or with the deeper hyobranchial muscles (Annot. 26, 27). Pars intermandibularis should be used for either variant based on evidence that the craniocervical part of M. constrictor colli, M. serpihyoideus, and M. stylohyoideus have a common basis in development (Noden, 1983) and innervation (N. facialis).

(7) **M. cucullaris capitis** (Fig. 6.3) Cucullus, L. hood or cowl. Synonymy: M. dermotemporalis (Homberger and Meyers, 1989). An extensive sheet of fasciculi oriented longitudinally between M. constrictor colli and M. cucullaris cervicis, deep to the lateral cervical apterium, resembling a hood over the caudal aspect of the head and neck. The cranial attachments include: Membrana temporalis (**Arthr.** Annot. 31; **Osteo.** Annot. 104), the rim of Meatus acusticus externus (**Osteo.** Annot. 19) and Os squamosum, dorsal to these; the caudal extension of the belly typically consists of a middorsal and midventral raphe and three slips, **Pars interscapularis, Pars propatagialis,** and **Pars clavicularis** (Annot. 8-10); innervation from accessory nerve via its external ramus (PNS Annot. 27). See Vanden Berge (1975).

M. cucullaris cervicis. Pars nuchalis typically consists of three to six widely spaced, oblique, ribbon-like fasciculi, some of which attach on Proc. costalis of the most caudal series of cervical vertebrae (**Osteo.** Annot. 118). **Pars clavicularis** is a more or less separate sheet of muscle attached to the clavicle. Both parts are attached to Pars interscapularis of the Pteryla dorsalis (**Integ.** Annot. 58) intermingling with the interscapular parts of M. cucullaris and M. latissimus dorsi (Annot. 8).

(8) **M. cucullaris capitis, pars interscapularis.** Synonymy: M. dermospinalis (Owen, 1842). Dorsal terminal part of M. cucullaris capitis inserting into Pars interscapularis of the Pteryla dorsalis (**Integ.** Annot. 58) where it may overlap, or unite by means of a tendinous intersection (Annot. 2), with **M. latissimus dorsi, pars interscapularis,** and M. cucullaris cervicis (Annot. 7; Berger, 1966; Osborne, 1968).

(9) **Pars propatagialis: M. cucullaris capitis, M. pectoralis, and M. biceps brachii.** All three are fleshy slips which insert, together with **Pars propatagialis, M. deltoideus** (Annot. 78), on Lig. propatagiale (**Arthr.** Annot. 141). The propatagial slip of M. cucullaris capitis is well developed in psittacines, picids, and passerines. That of M. biceps brachii also inserts on Lig. limitans cubiti (**Arthr.** Annot. 141). In other avian taxa, muscle bundles from M. cucullaris capitis ("Pars omocutaneus", Osborne, 1968) insert on Pars scapulohumeralis of the Pteryla alaris (**Integ.** Annot. 64, 65) and one or more of the slips may attach on dense fascia of the shoulder. In some taxa these slips may be partly aponeurotic or even absent (see, e.g., "biceps slip", Hudson and Lanzillotti, 1964; Vanden Berge, 1970).

For other patagial muscles see M. serratus superficialis, M. latissimus dorsi. See also Annot. 70, 75, 77 and 83; and Fig. 6.13

(10) **M. cucullaris capitis, pars clavicularis.** Synonymy: Mm. claviculohyoideus and claviculoglandularis mandibularis externus anterior (Zweers, 1982). A ventral terminal part of cucullaris capitis inserts principally on the clavicle. In those birds which have a pendulant crop (Ingluvies, **Digest.** Annot. 24), e.g., tinamous, galliforms, hoatzin, sandgrouse, pigeons/doves, and psittacines, Pars clavicularis may form superficial and deep sheets which ensheath this organ and support it in a sling-like fashion ("M. levator ingluviei", Fürbringer, 1888).

(11) **Pars scapulohumeralis** ("dermo-iliacus", "dermo-costalis", Owen, 1842) is a fleshy slip from **M. latissimus dorsi** and **M. serratus superficialis,** respectively. Both slips attach to the caudal end of Pteryla scapulohumeralis (**Integ.** Annot. 61) where they merge with the interscapular slip of M. cucullaris capitis. The slip from M. serratus superficialis is the more common of the two and typically the larger (see Vanden Berge, 1970). In certain taxa (*Gavia, Colaptes,* and some passerines, Berger, 1966), the attachment on the scapulohumeral feather tract is prolonged as a fibroelastic tendon which ends on the tendon of M. expansor secundariorum (Annot. 5). See Fig. 6.11.

(12) **M. pectoralis, pars subcutanea thoracica/abdominalis.** Synonymy: the principal name, after Osborne, 1968; M. dermohumeralis (Owen, 1842); M. pectoralis abdominalis (Vanden Berge, 1970). **P. subcutanea thoracica** attaches on the tendon of insertion of M. pectoralis to the humerus, and extends caudad beneath the lateral body apterium, ending beneath the caudal rows of Pars axillaris [pectoralis] of the Pteryla ventralis (**Integ.** Annot. 60). **Pars subcutanea abdominalis** is connected to the thoracic slip by an intermediate tendon, but extends farther caudally over the pectoral apterium, lateral to Pars sternalis and Pars abdominalis of the ventral feather tract, and terminates on the fascial sheath over M. obliquus externus abdominis at its pubic attachment. See Annot. 75, Osborne (1968), and Vanden Berge (1970) for examples of variation.

(13) **Musculi bulbi oculi.** There are six extrinsic muscles of the avian eyeball, arranged as three opposing pairs: **Mm. rectus dorsalis/ventralis; Mm. rectus lateralis/; Mm. obliquus dorsalis/ventralis.** All six muscles arise from the Septum interorbitale, and insert on the Sclera. They are innervated like their mammalian

counterparts (**PNS** Fig. 15.2; Bubien-Waluszewska, 1981) and function in direct movements (positioning) of the eyeball. Although no trochlea is associated with it, **M. obliquus dorsalis** is probably a homologue of the mammalian M. obliquus superior. See Fig. 6.2.

For a review of eye muscles in several birds, see Abraham and Stammer (1966), Zusi and Bentz (1984), Elzanowski (1987); McVean, et al. (1987) describe their fiber types in *Columba*.

(14) **Musculi membranae nictitantis.** Two muscles concerned with movement of the nictitating membrane originate from the eyeball. The aponeurosis of **M. quadratus membranae nictitantis** is reflected on itself to form a fibrous sheath (Vagina tendinis) for passage of the tendon of **M. pyramidalis membranae nictitantis** as the latter arches over N. opticus (Slonaker, 1918; Simic and Jablan-Pantic, 1959; Elzanowski, 1987). The innervation of these muscles from N. abducens is reviewed by Bubien-Waluszewska (1981); see **PNS** Annot. 16; **PNS** Fig. 15.2; and Martin (1985).

(15) **Musculi palpebrarum et periorbitae.** In addition to the six extrinsic eye muscles (Annot. 14) the interorbital septum serves as origin of a striated muscle for the upper and lower eyelids and one of the floor of the orbit. **M. levator palpebrae dorsalis** inserts in the Plicae marginales dorsales (**Sens.** Annot. 36) of the upper eyelid; its innervation is the dorsal ramus of the oculomotor nerve (**PNS** Fig. 15.2; Bubien-Waluszewska, 1981). **M. depressor palpebrae ventralis** inserts on the proximal edge of the fibrous tarsus of the lower eyelid. **M. tensor periorbitae** forms a muscular sling separating the orbital contents from the jaw muscles (Elzanowski, 1987). The latter two muscles are innervated by the mandibular nerve (Bubien-Waluszewska, 1981). Nonstriated muscle fibers arranged approximately parallel to the free margins of the eyelids form **M. orbicularis palpebrarum.**

(16) **M. columellae.** This is the only muscle of the avian middle ear (see **Sens.** Annot. 52). See **Sens.** Fig. 16.3.

(17) **Musculi mandibulae.** A collective term for those muscles which are involved in opening and closing the jaws (Fig. 6.4; Bhattacharyya, 1982); individual muscles are named after Lakjer (1926). These have been described in several ways: (1) on the arrangement of their fasciculi to their constituent aponeuroses (after Gans and Bock, 1965); (2) on their position relative to the facial and craniofacial articulations (Bock, 1968), and (3) on their causal role in kinetics of the avian skull (Bock, 1964; Zweers, 1974) (Fig. 6.5). With the exception of M. depressor mandibulae (Annot. 24), they are derived from the mandibular arch muscle primordium (McClearn and Noden, 1988), innervated by N. mandibularis (**PNS** Annot. 13).

(18) **M. adductor mandibulae externus** (Fig. 6.5). Synonymy: M. masseter superficialis, medius and profundus (Fujioka, 1963). This muscle complex consists of several aponeuroses attached to the cranium, and another series of aponeuroses attached to the mandible (Zweers, 1974; van Gennip, 1986). Three main subdivisions are described, one or more of which may also be subdivided. The muscle functions to elevate the lower jaw (Bühler, 1981).

Pars rostralis [temporalis]. Synonymy: Pars superficialis, (Lakjer, 1926); P. superficialis or lateralis (Dzerzhinsky and Yudin, 1982). This part of M. add. mand. ext. is often described as having temporal and orbital origins. The temporal subdivision is the more extensive and attaches to Proc. zygomaticus and areas caudal and dorsal to it (see Fossa temp. **Osteo.** Annot. 102, 104; Memb. temp. **Arthr.** Annot. 31). In some taxa (e.g., *Phalacrocorax, Anhinga*) this subdivision is hypertrophied,

and has an occipital attachment (Crista nuchalis transversa (**Osteo.** Annot. 17) with a separately derived head, Caput nuchale, attached to the upper dorsal cervical region by a fibrous septum in which is embedded the Os nuchale (**Osteo.** Annot. 76; Dullemeijer, 1951; Owre, 1967).

The orbital subdivision extends rostrad to the caudal wall of the orbit (**Osteo.** Annot. 29; van Gennip, 1986). Pars rostralis inserts on Proc. coronoideus (**Osteo.** Annot. 44) of the mandible.

Pars ventralis [medialis, Lakjer, 1926] is the "central" and, in some cases the largest, division of M. add. mand. ext. A complex aponeurosis of origin attaches on Proc. postorbitalis, as well as on Lig. postorbitale and Proc. zygomaticus. Pars ventralis inserts on the caudolateral face of the mandible (van Gennip, 1986).

Pars profunda [caudalis] (Lakjer, 1926; "profundus", including "caudalis," Dzerzhinsky and Yudin, 1982) is typically the smallest division, variable in development (e.g., Zusi and Bentz, 1984). When present as a separate division (McClearn and Noden, 1988), it attaches to the body and otic process of the quadrate, lateral to attachments of M. add. mand. caud. except for a fibrous gap through which passes Ramus pterygoideus of the mandibular nerve (**PNS** Annot. 13; Lakjer, 1926; Barnikol, 1953). The insertion of Pars profunda on the mandible, between Fossa articularis quadrati and Proc. coronoideus (**Osteo.** Annot. 44), is independent of the insertion of M. adductor mandibulae caudalis (Annot. 20).

(19) **M. pseudotemporalis superficialis.** Synonymy: M. temporalis (Fujioka, 1963; Watanabe and Yasuda, 1970). This muscle has been considered the most lateral (at its origin) of the so-called "adductor mandibulae internus" subsystem of muscles (including Mm. pseudotemporalis profundus, adductor mandibulae caudalis, pterygoideus and ethmomandibularis, Annot. 20-22). In some taxa M. pseudotemporalis superficialis attaches primarily on Area muscularis aspera (**Osteo.** Annot. 89) of Os laterosphenoidale. It is separated from M. adductor mandibulae externus, pars rost. by N. maxillaris and Rete ophthalmicum (Dzerzhinsky and Yudin, 1982) and, in part, also by R. pterygoideus (**PNS** Annot. 13) of N. mandibularis (van Gennip, 1986). The muscle inserts on Tuberculum pseudotemporale (**Osteo.** Annot. 45). See Fig. 6.5.

(20) **M. pseudotemporalis profundus.** Synonymy: M. quadratomandibularis (Hofer, 1950), Fujioka (1963). **M. adductor mandibulae caudalis.** Synonymy: M. pseudotemporalis (Dubale, 1969; Rawal, 1971). M. adductor mandibulae "posterior" of many authors; not to be confused with pars profunda of M. adductor mandibulae externus (Annot. 18). These two muscles form a "quadrate" portion of an "adductor mandibulae internus" muscle subsystem.

The relative development of M. pseudotemporalis profundus is proportional to that of Proc. orbitalis quadrati on which it has a primary attachment (Hofer, 1950). The quadrate attachment is rostral to that of M. adductor mandibulae caudalis from which it is separated by a fibrous gap through which passes the pterygoid ramus of the mandibular nerve (**PNS** Annot. 13; Lakjer, 1926; Barnikol, 1953). The attachment on the mandible is rostral to Proc. coronoideus and to the attachments of the other jaw muscles (*Columba*, van Gennip, 1986); see Burton (1974c) and Bhattacharyya (1989) for other taxa.

M. adductor mandibulae ossis quadrati [caudalis] has a primary attachment on the body of the quadrate, rostral and deep to the attachments of M. add. mand. ext, pars prof. (see Annot. 18). The mandibular attachment lies between Tuberculum pseudotemporale (**Osteo.** Annot. 45), laterally, and M. pterygoideus medially (Annot. 21).

M. pseudotemporalis profundus should be considered functionally independent from M. adductor mandibulae caudalis (see Annot. 21; Bock, 1964; Bühler, 1981) (Fig. 6.5).

(21) **M. pterygoideus** (Fig. 6.5). Synonymy: M. adductor mandibulae internus (Hofer, 1950). M. pterygoideus is the "palatopterygoid" portion of an "adductor mandibulae internus" subsystem, i.e., defined by its attachments on the palatine and pterygoid bones (see **Osteo.** 61, 67). Various subdivisions have been described: (1) pars dorsalis and pars ventralis, each of which has lateral and medial subdivisions (Lakjer, 1926); (2) three principal aponeuroses and pars lateralis, pars centralis medialis, pars dorsalis medialis (Zusi, 1962; Burton, 1974a, c), or (3) pars centralis, pars dorsalis lateralis, pars dorsalis medialis, and pars retractor, the latter a separate slip which attaches on the braincase (Richards and Bock, 1973). In many taxa Pars dorsalis medialis (Zusi and Bentz, 1984), which is also described as pars dorsalis rostralis (van Gennip, 1986), is the only portion which seems well defined. The muscle inserts primarily on the caudomedial aspect of the mandible and Proc. medialis mandibulae. See Fig. 6.5.

M. pterygoideus and M. pseudotemporalis profundus (Annot. 20) simultaneously close both the upper and lower jaws, functioning via the force lever arm of the quadrate/pterygoid/palatine/jugal bar axis, in addition to other functions (Bühler, 1981).

(22) **M. ethmomandibularis.** Derived from M. pterygoideus and characteristic of psittaciforms, it has an extensive attachment on the interorbital septum and on the medial face of the mandible. It is important in generating biting forces during elevation of the lower jaw, as well as chewing forces by forward translation of the lower jaw, distinctive of the feeding system of psittacines (Hofer, 1950; Burton, 1974c; Homberger, 1980, 1986).

(23) **M. protractor pterygoidei et quadrati.** Synonymy: M. craniopterygoquadratus (Fujioka, 1963); M. sphenopterygoquadratus (Dubale, 1969; Rawal, 1971). Although Lakjer (1926) described two muscles, M. protractor pterygoidei sensu stricto and M. protractor quadrati, both attached to the base of the interorbital septum; these are best considered as one muscle with two parts, defined by their insertions to Os pterygoideum and Quadratum (Figs. 6.4, 5). The muscle forces are exerted on the "palatoquadrate bridge" to protract and elevate the upper jaw (Bühler, 1981; see Bock, 1966 for the configuration in woodpeckers). See Figs. 6.4, 5.

(24) **M. depressor mandibulae** (Figs. 6.4, 5, 6). Synonymy: M. occipitomandibularis (Fujioka, 1963); M. digastricus (Berger, 1966). The cranial attachment largely fills the Fossa subtemporalis (**Osteo.** Annot. 104) between Crista nuchalis transversa and Fossa temporalis above the ear opening. It extends ventrally over the lateral surface of Proc. paroccipitalis. The muscle also has an extensive attachment on Memb. postmeatica and Lig. occipitomandibulare. The muscle inserts in Fossa caudalis of the mandible (**Osteo.** Annot. 51), including Fossa conicalis and Proc. retroarticularis in birds having these features. It may consist of distinct parts, with different functions (Bock, 1964; Zusi, 1967; Zweers, 1974). Bühler (1970, and pers. comm.) suggests that in caprimulgids an internal head, fused with Lig. occipitomandibulare (**Arthr.** Annot. 37 may not be part of this muscle set. The muscle is innervated by the hyomandibular branch of the facial nerve (**PNS** Annot. 23). See Figs. 6.4, 5, 6.

(25) **Musculi apparatus hyobranchialis [hyolingualis].** The new alternative term "hyolingualis" (Richards and Bock, 1973; Bhattacharyya, 1982) is more indicative of the functional role of this musculature in support and movement of the tongue and hyoid apparatus in feeding, food and water transport, and related movements (see Zweers, 1982).

Several subgroups of hyolingual musculature are described (Zweers, 1982; Homberger, 1986; Homberger and Meyers, 1989). One, the "external hyolingual muscles" (Annot. 6, 26), consists of subcutaneous cervical and "gular" muscles which connect hyolingual elements, other than bones, with nonlingual elements. These muscles, which typically lie between the tip of the beak and the floor of the pharynx, may extend caudally as far as the trachea and pectoral girdle. They have a major influence on positioning food in the floor of the mouth.

A second, the "extrinsic hyolingual muscles" (Annot. 27, 28, 29, 35, and 37), connects skeletal elements of the hyoid apparatus with nonhyobranchial structures (e.g., mandible, larynx, trachea, clavicle), and directly influences positioning of the lingual apparatus, glottis, and pharyngeal valves. A third, the "intrinsic hyolingual muscles" (Annot. 30, 34), connect two or more elements within the hyolingual apparatus and directly influence positional changes of hyobranchial elements relative to each other.

See Homberger (1986), as well as Homberger and Meyers (1989), for recent descriptions of laminae and attendant fascial musculoskeletal and/or glandular compartments, associated with the hyolingual apparatus in *Psittacus* and *Gallus*, respectively.

(26) **Mm. intermandibulares.** May be single or two independent muscles that differentiate by day 12 of development (*Coturnix;* McClearn and Noden, 1988). The muscles arise from the medial surface of Pars caudalis of the mandible, and insert on a midventral raphe which may extend from the level of the Rostrum mandibulae (M. intermand. ventr.) to the level of Os urohyale of the hyoid apparatus (M. intermand. dors.). Both muscles are innervated by R. intermandibularis of N. mandibularis.

M. intermandibularis ventralis. Synonymy: M. mylohyoideus (in many studies, see Homberger and Meyers, 1989). The ventral intermandibular muscle is the more superficial and rostral of the two muscles (Fig. 6.7). **Pars rostralis** is oriented rostromedially toward a midventral raphe, and only its most caudal bundles are transversely oriented. **Pars caudalis** is oriented caudomedially toward a midventral raphe. It may insert directly on Os urohyale (**Osteo.** Annot. 81) or on a nodule ("sesamoid plate", Evans, 1969, Figs. 5-9; "nodulus", Homberger, 1986) which articulates with the hyobranchial skeleton. Pars rostralis and Pars caudalis may be continuous with one another at the attachment on the mandible.

M. intermandibularis dorsalis. Synonymy: M. mylohyoideus anterior, "anterior" belly (Mudge, 1903); M. hyomandibularis transversus (Kallius, 1905); M. suspensor hyoideus (Ghetie and Atanasiu, 1962). M. intermandibularis dorsalis is independently developed in some taxa (*Anser* and *Anas;* Ghetie and Atanasiu, 1962; Zweers, 1974) but absent in others (e.g., *Columba;* Zweers, 1982). It is apparently derived from a horizontal splitting of the muscle primordium associated with the mandibular arch (Kallius, 1905) and lies dorsocaudal to M. intermandibularis ventralis, in part or entirely covered superficially by the latter. This muscle also inserts with its counterpart on a median raphe, separate from that of M. intermand. ventr.

(27) **M. serpihyoideus** Synonymy: M. basibranchialis mandibularis, pars medialis (Vanden Berge, 1975; see Homberger and Meyers, 1989). The prefix "serpi" appears to be derived from the Latin serpo, "to creep", "serpiginous" pertaining to a "creeping eruption" that extends with an arciform border. "Serpi-" may refer to: (1) the topographic position of this muscle as it develops by a medial invagination between M. intermand., M. interceratobranchialis, and the hyolingual musculature or (2) its variable proximal attachments (including Pars caudalis of the mandible, extending medially to Lamina parasphenoidalis in some taxa; see Berger, 1966, Richards and Bock, 1972, and Burton, 1974, for examples) or (3) its arciform rostral border in some taxa. The name has been in common use for many years (Figs. 6.6, 7).

M. serpihyoideus is innervated by R. hyoideus of N. facialis (**PNS** Annot. 23; Baumel, 1975); it inserts on a median raphe ventral to the Urohyale, concerned with support of the gular region. It is part of the "external hyolingual musculature" (Zweers, 1982).

(28) **M. stylohyoideus** (Figs. 6.6, 7). Synonymy: M. basibranchialis mandibularis, pars lateralis (Vanden Berge, 1975; see Homberger and Meyers, 1989). Its development from the muscle primordium associated with the hyoid arch; Kallius (1905) indicated its homology with the same muscle in mammals, and its innervation by R. hyoideus of N. facialis (**PNS** Annot. 24). By way of (1) origin on the lateral and ventral aspects of Pars caudalis of the mandible, including Proc. retroarticularis, and (2) insertion on the hyolingual apparatus (Os basihyale), M. stylohyoideus is functionally an "extrinsic hyolingual muscle" (Zweers, 1982).

(29) **M. branchiomandibularis.** Synonymy: M. mandibularis epibranchialis (Vanden Berge, 1975; see Homberger and Meyers, 1989). A complex muscle in psittaciforms (Homberger, 1986); derived from the primordium of the third pharyngeal arch, and innervated by N. glossopharyngeus (**PNS** Annot. 60). **Pars rostralis** and **Pars caudalis** are both present in many taxa. Bhattacharyya (pers. comm.) reports that an attachment on the lateral aspect of the ramus of the mandible, though less common, occurs in a number of passerines as well as nonpasserines. Both parts ensheath the horn branchial on which they insert.

(30) **M. interceratobranchialis [ceratohyoideus].** Considered to be derived from the mandibular muscle primordium (Kallius, 1905, but see McClearn and Noden, 1988); although topographically distinct from M. intermandibularis, it is associated primarily with the hyolingual musculature. It is innervated by R. intermandibularis of N. mandibularis (**PNS** Annot. 14; Baumel, 1975a). Although Zweers (1982) considered the muscle to be part of the functional "external hyolingual musculature," it may be an element of the "intrinsic" musculature, connecting the branchial horns (Cornua) to each other by way of a midline raphe.

(31) **M. ceratoglossus.** This muscle connects the ceratobranchiale with the Paraglossum (Fig. 6.8). Homberger (1986) completely describes this muscle in the psittacines and discusses its synonymy. See Homberger and Meyers (1989).

(32) **M. hyoglossus rostralis [medialis]** (Fig. 6.8). Synonymy: M. paraglossobasibranchialis medialis (Vanden Berge, 1975). An intrinsic hyolingual muscle attached to most of the ventral surface of the Paraglossum and Os basihyale (**Osteo.** Annot. 80, 81) just caudal to the paraglossum. "Rostralis" or "medialis" refers to its position relative to M. hyoglossus obliquus (Annot. 33).

(33) **M. hyoglossus obliquus [lateralis].** Synonymy: M. paraglossobasibranchialis lateralis (Vanden Berge, 1975). The obliquity of its muscle fasciculi extending from Os basihyale to the cornua of the paraglossum (**Osteo.** Annot. 80) is the basis for the term "obliquus" (Fig. 6.8); "lateralis" refers to the position of the muscle relative to M. hyoglossus rostralis [medialis] (Annot. 33).

(34) **M. hyoglossus transversus; M. mesoglossus; M. supraglossus.** Considered unique to psittaciforms, these muscles have been described and characterized by Homberger (1986). She suggests a derivation of M. hyoglossus ("hypoglossus") transversus and M. mesoglossus from M. hyoglossus rostralis ("anterior") and derivation of M. supraglossus from M. hyoglossus obliquus.

(35) **M. genioglossus.** M. genioglossus has one attachment on Rostrum mandibulae, but its other attachment varies: (1) on the hyobranchial skeleton or the fascia of associated muscle ("geniohyoideus") (Fig. 6.8) and (2) on the connective tissue underlying the oral mucosa lateral to the tongue ("genioglossus" and "geniopharyngealis"; Zweers, 1982). The insertion may extend as far caudally as the cricoid cartilage. Zweers (1982) considers the muscle a protractor of the hyolingual apparatus and part of the "external hyolingual musculature". Absent in adult *Gallus* (Homberger and Meyers, 1989), it is said to be present in the foetus (Noden, 1983).

(36) **M. cricohyoideus dorsalis; M. cricohyoideus ventralis.** These muscles are described in **Resp.** Annot. 45; they connect Os basihyale with Cartilago cricoidea. With **M. hyovalvularis** and **M. tracheovalvularis,** they are integrated into the functional apparatus directly governing movements of the "ventral pharyngeal valves" and "pharyngeal scrapers", independent of lingual, glottal and beak movements (*Columba;* Zweers, 1982; Zweers and Berkhoudt, 1987; Heidweiller and Zweers, 1990).

(37) **Musculi laryngis [laryngeales]; Musculi tracheales.** Differences in the construction of the passeriform larynx (*Corvus* sp.) from that of the nonpasseriform larynx (*Columba livia*), and the attendant kinematic possibilities, suggest that there are at least two different types of operational laryngeal systems in birds (Zweers, et al., 1981; Zweers and Berkhoudt, 1987). The mechanism of the larynx of *Columba* has been incorporated into elements of the feeding system (Zweers, 1982). For description of both of these muscle systems see **Resp.** Annot. 30, 45.

(38) **M. dilator glottidis; M. constrictor glottidis.** The attachments, functional role, and related terminology for these two muscles is fully described in **Resp.** Annot. 30. See, also, **Resp.** Annot. 25, 27, 28, 29, and 45; **PNS** Annot. 53.

(39) **Musculi syringeales.** For an extensive review of the variation in the syringeal muscles in passerine and nonpasserine birds, see **Resp.** Annot. 45, 46; for innervation, see **PNS** Annot. 30, 31, 63.

(40) **Musculi vertebrales.** Most studies of the intrinsic cervical musculature of birds (Palmgren, 1949; Zusi, 1962; Burton, 1971, 1974a, b; Jenni, 198; Zusi and Bentz, 1984) adopt the terminology of Boas (1929) although Kuroda (1962) used a slightly different set of names. Zusi and Storer (1969) suggested that in complex serially arranged muscles, the functional units ("unit criterion" of Landolt and Zweers, 1985), are those fasciculi inserting on a given vertebra rather than those originating from a vertebra. Their suggestions are adopted here. According to Zweers, et al. (1987), four subsystems are recognized as follows:

Musculi craniocervicales. This subsystem of muscles positions the head relative to the cranial end of the cervical column. All muscles in this subsystem have a primary attachment on the more cranial series of cervical vertebrae ("first division" of Boas, 1929; see **Osteo.** Annot. 129) but frequently extend caudally over additional cervical vertebrae. All insert on the cranium.

Mm. cervicales dorsales, laterales, and ventrales. These three subsystems position the cranial end of the cervical column relative to the trunk region of the body. The dorsal and lateral subsystems are continuous caudally with a large muscle mass often known as Mm. iliocostalis et longissimus dorsi (Annot. 45). The ventral subsystem consists of a cranial set of short flexors of the head and neck and a very long and complex series of muscle units collectively known as M. longus colli ventralis (Annot. 56).

Aponeurosis transversa (Landolt and Zweers, 1985). The muscles of the craniocervical system, and those of the first part of the dorsal and lateral cervical

systems, often are attached to this common aponeurosis. According to Landolt and Zweers (1985) it is attached to low crests on the dorsal edge of the Ansa costotransversaria (**Osteo.** Annot. 123, 127b, 135) and adjacent base of the cranial zygapophysis, and may extend to the caudal zygapophysis of the first series of cervical vertebrae. On the 2-3 cervical vertebrae caudal to the Axis, the aponeurosis is attached to the bony pillar which connects the cranial and caudal zygapophysis of each vertebra (see Boas, 1929, Tab. 3, Figs. 1, 3). Muscles attached to this aponeurosis include M. complexus (Annot. 42), M. rectus capitis dorsalis (Annot. 44), and M. ascendens cervicalis (Annot. 46). See **Arthr.**

(41) **M. biventer cervicis.** The only muscle of the cervical vertebral column which connects Notarium (**Osteo.** Annot. 140) with the Cranium (see Landolt and Zweers, 1985; Zweers, et al., 1987); it is well separated from other epaxial muscles within a separate fascial sheath (Kuroda, 1962) (Fig. 6.9). Typically two bellies are present, the caudal belly longest, extending from Notarium to the seventh (*Gallus*) or eighth (*Anas*) cervical vertebra; the cranial belly is short, typically extending from the level of the third cervical vertebra to its cranial attachment (Crista nuchalis transversa, **Osteo.** Annot. 17). An intermediate tendon connects the two bellies; a single, elongated, fleshy belly exists in the penguin *Pygoscelis* (Kuroda, 1962). According to Boas (1929) and Kuroda (1962) the muscle is absent in some taxa (e.g., *Anhinga, Nannopterum, Ardea*).

(42) **M. complexus.** (Fig. 6.9). Synonymy: "hatching muscle" (Fisher, 1966). "M. complexus" is an unfortunate term, referring to the obsolete name for the mammalian M. semispinalis capitis considered homologous with the avian complexus. Its contractile properties and other internal changes may not be directly related to the actual "pipping" of the shell (Bock and Hikida, 1968, 1969; Brooks and Garrett, 1970; Hayes and Hikida, 1976). Two or so fleshy slips are attached to Apon. transversa (Annot. 40) beginning on cervical vertebra 3; the 2-3 tendinous intersections, corresponding to the fusion of the slips, are incomplete. Either the medial or lateral bundles of the common belly extend the length of the muscle to the cranium (Crista nuchalis transversa; (**Osteo.** Annot. 17).

(43) **M. splenius capitis.** Synonymy: M. obliquus capitis cranialis or M. rectus capitis dorsalis major, or both (Fujioka, 1963). Description, variability, and general occurrence of this muscle in many taxa of birds are summarized by Burton (1971). Decussation of the attachments of the muscle from either side on Proc. spinosus of the Axis has been described in several birds (Burton, 1971; Zusi and Bentz, 1984; Landolt and Zweers, 1985; Zweers, et al., 1987; Fritsch and Schuchmann, 1988) and may be more common in other taxa than presently known. See Fig. 6.9.

(44) **M. rectus capitis dorsalis.** Synonymy: M. rectus capitis superior (Boas, 1929); M. trachelomastoideus (Fujoika, 1963). A series of fleshy slips (five in *Anas;* Landolt and Zweers, 1985) arise from the ventral surface of Aponeurosis transversa, and extend to the occipital bone near M. rectus capitis ventralis.

M. rectus capitis lateralis and **M. rectus capitis ventralis** attach by a series of fleshy slips on Crista ventralis corporis (**Osteo.** Annot. 119) of the first series of cervical vertebrae. **Pars lateralis** and **Pars medialis** of **M. rectus capitis ventralis** have been described in *Anas platyrhynchos* (Landolt and Zweers, 1985). M. rectus capitis lateralis is attached to the ventral-lateral part of Crista nuchalis transversa (**Osteo.** Annot. 17) extending onto the caudal border of Proc. paroccipitalis. M. rectus capitis ventralis is attached to the basioccipital bone near M. rectus capitis dorsalis. See Fig. 6.9.

(45) **M. longissimus dorsi.** In mammals the equivalent muscle system consists of two sets of muscle, "iliocostalis" and "longissimus", typically separable from each other on the basis of attachments; in birds such a separation is not so readily apparent. The caudalmost fleshy attachments of M. longus colli dorsalis, pars thoracica, and Mm. intercristales presumably form a "longissimus dorsi"; M. ascendens thoracicus and Mm. intertransversarii, an "iliocostalis" (Zusi and Bentz, 1984), but it seems best to consider the muscle system as a single unit awaiting further clarification. According to Baumel, et al. (1990), the longissimus is functionally inspiratory during ventilation of the lungs since it elevates the pelvis at the notarial-synsacral articulation (**Arthr.** Annot. 71), increasing the volume of the thoracoabdominal cavity.

(46) **M. ascendens cervicalis; M. ascendens thoracicus** (Fig. 6.9). Synonymy: Mm. ascendentes; M. obliquus colli (Gadow and Selenka, 1891; Kuroda, 1962); Mm. obliquotransversales (Shufeldt, 1890; Harvey, et al., 1968). A single structural/functional unit (see Annot. 41) consists of numerous, serially arranged, fleshy slips attached near the base of the Zygapophysis cranialis (**Osteo.** Annot. 132) and Ansa costotransversaria (**Osteo.** Annot. 123, 134, 135), the first slips also attaching on Aponeurosis transversa. A structural unit of this muscle is formed typically from two to four slips from the second through fourth cervical vertebrae, caudal to the terminal aponeurosis (on Crista transverso-obliqua and/or Torus dorsalis, **Osteo.** Annot. 124, 125). R. dorsalis of each cervical spinal nerve enters the muscle on its medial side.

(47) **M. longus colli dorsalis.** At least four separate muscle units form this muscle complex which appears to be the avian equivalent of the spinalis muscle system in mammals. Kuroda (1962) described it as one muscle complex, M. longus colli posticus. The several parts are variously joined and/or interdigitate with other cervical muscles, particularly M. ascendens cervicalis and Mm. intercristales.

(48) **M. longus colli dorsalis, pars cranialis.** Synonymy: pars anterior (Kuroda, 1962); M. splenius colli, including "splenius capitis" and "splenius accessorius" (Boas, 1929). The primary unit consists of multiple fleshy slips, varying in relative size and length, but characterized by their attachments on Proc. spinosus (**Osteo.** Annot. 137) of several cervical vertebrae of the most cranial series. All slips converge on a single long tendon (**Tendo axialis**), in common with the longest slip of Pars caudalis, and attach to Torus dorsalis of the Axis. This long tendon ascends in a sulcus on the lateral aspect of the Torus dorsalis of a few cervical vertebrae just caudal to the Axis.

Boas (1929) also described a deeper series of similar, but "accessory", fleshy slips as "splenius anticus" if attaching on Torus dorsalis of the Atlas, and "splenius accessorius" if attached to Torus dorsalis of cervical vertebrae just caudal to the Axis (Fig. 6.9). Landolt and Zweers (1985) review the occurrence of the unit which connects Proc. spinosus of the third cervical vertebra to the Atlas, perhaps the most frequent of the accessory slips to have been described. In this edition of the NAA, all unit slips defined by the above criteria are elements of this muscle system (Landolt and Zweers, 1985; Zweers, et al., 1987).

(49) **M. longus colli dorsalis, pars caudalis** (Fig. 6.9). Synonymy: pars posterior (Kuroda, 1962); M. spinalis cervicis (Boas, 1929). Several fleshy slips attach on an aponeurosis from the notarium (Zweers, et al., 1987) and spinous processes of the most caudal cervical vertebra. The more lateral slips end as tendons inserting on Torus dorsalis of neck vertebrae of the second and third series (Boas, 1929); the longest slip, medial to the others, ends as a tendon (**Tendo axialis**) attached to Torus dorsalis of the Axis with slips of Pars cranialis (Annot. 48).

(50) **M. longus colli dorsalis, pars profunda.** Synonymy: M. dorsales pygmaei (Boas, 1929); M. profundus colli posticus (Kuroda, 1962). Of inconstant occurrence in avian taxa generally (see Zusi and Storer, 1969); when present consists of a series of fleshy slips similar to M. longus colli, pars caudalis but attached to the caudal series of cervical vertebrae.

(51) **M. longus colli dorsalis, pars thoracica.** Synonymy: M. spinalis thoracis (Boas, 1929). Not always separable from other muscles in the subsystem; includes those fleshy slips inserting on the arches of thoracic vertebrae similar to the attachments of other parts of the longus colli dorsalis system; see Annot. 45.

(52) **Mm. intercristales and Mm. interspinales.** Mm. intercristales are intersegmental muscles which typically extend craniad from the Crista transverso-obliqua (**Osteo.** Annot. 124) of one cervical vertebra to that of the next cervical vertebra in the series. In the most cranial series of cervical vertebrae, Mm. intercristales are sometimes difficult to separate from the fleshy slips known as "splenius accessorius" (M. longus colli dorsalis, pars cranialis, Annot. 48). Dorsal rami of spinal nerves enter the epaxial muscles between M. ascendens cervicalis (laterally) and M. intercristalis (medially).

More or less discrete medial slips connecting adjacent spinous processes of vertebrae are considered to be **Mm. interspinales.** The latter are not as clearly developed as Mm. intercristales.

(53) **Mm. intertransversarii.** Synonymy: M. colli lateralis (Kuroda, 1962). Mm. intertransversarii and Mm. inclusi (Annot. 54) constitute the lateral subsystem of cervical muscles. The intertransverse muscles consist of a series of intersegmental, multipennate muscles, attached by flat aponeuroses on Tuberculum ansae and Cristae laterales of Ansa costotransversaria (**Osteo.** Annot. 135) of one cervical vertebra to these features next in the series, forming the principal lateral musculature of the neck (Zusi and Storer, 1969; Landolt and Zweers, 1985).

(54) **Mm. inclusi.** Inclusi are usually considered derivatives of Mm. intertransversarii, but form a muscle system uniting Lamina lateralis arcus (**Osteo.** Annot. 127) with Proc. costalis.

Mm. inclusi dorsales unite Corpus vertebrae with the Proc. costalis. **Mm. inclusi ventrales** in some taxa these ventral fleshy slips form the muscular "floor" of Canalis vertebrarterialis between successive transverse foramina (**Osteo.** Annot. 134; Landolt and Zweers, 1985).

(55) **M. flexor colli lateralis/medialis** (Fig. 6.9). Synonymy: "lateralis" and "medialis" are somewhat more descriptive than the alternate terms "brevis" and "profundus", respectively (Boas, 1929).

M. flexor colli lateralis lies ventrolateral to, and partly concealed by, M. rectus capitis dorsalis (Annot. 44), with which it shares attachments on the cranial series of cervical vertebrae. A serial arrangement of fleshy slips inserts as a tendon on Proc. costalis of the Atlas.

M. flexor colli medialis appears to be the continuation of certain more cranial elements of M. longus colli ventralis (Annot. 56; Zusi and Storer, 1969). Usually described as an independent muscle consisting of fleshy slips extending from Proc. caroticus (**Osteo.** Annot. 121) and the attenuated spine of Proc. costalis of the more caudal series of vertebrae that insert as a tendon on Crista ventralis corporis (**Osteo.** Annot. 119) of a more cranial series of cervical vertebrae. Each slip typically spans at least two intercorporeal articulations between attachments (Zweers, Vanden Berge, and Koppendraier, 1987).

(56) **M. longus colli ventralis** (Fig. 6.9). The major muscle mass consists of a series of muscular slips attached to Crista ventralis corporis (**Osteo.** Annot. 119) of the most caudal series of cervical vertebrae and to Proc. caroticus (**Osteo.** Annot. 121) of the intermediate series. The terminal tendon of each unit is attached to the attenuated spine of Proc. costalis of the vertebra immediately cranial to the last fleshy slip. This subsystem lies between the two sets of Mm. intertransversarii (Annot. 53); attachments on the first series of cervical vertebrae interdigitate with similar attachments of M. flexor colli lateralis and M. flexor colli medialis (Annot. 55). For additional information on the slips, see Landolt and Zweers (1985) and Zweers, Vanden Berge, and Koppendraier (1987).

(57) **Musculi trunci.** Collective term for the muscles of the thoracic and abdominal walls. See Fedde (1987) for a recent review on the descriptive morphology and innervation of the trunk muscles; George and Berger (1966), Zusi and Bentz (1984), and Baumel (1988) illustrate the abdominal musculature.

M. quadratus lumborum was described in *Rhea americana* by Gadow and Selenka (1891), but this muscle is apparently greatly reduced (vestigal) or absent in birds generally.

(58) **M. scalenus.** Fedde (1987) describes a pars cranialis and pars caudalis in *Gallus*, both slips attaching cranially on the transverse processes of the lowest one or two cervical vertebrae; each slip inserts caudally, and separately, on the lateral surface of the first and second vertebral rib (**Osteo.** Annot. 147).

Mm. levatores costarum. These fleshy slips have the same basic attachments as the scalenus muscle, i.e., from the transverse process of a vertebra to the vertebral rib of the next caudal vertebra caudal, dorsal to the uncinate process of that rib. These two muscle sets form a continuous series, the scalenus lying most cranial to all vertebral ribs and the first levator inserts to the first vertebral rib with an uncinate process. The levators are accessory muscles of ventilatory inspiration.

(59) **Mm. intercostales externi.** The fleshy bellies of the external intercostal muscles are most prominent in the more cranial intercostal spaces while those of **Mm. intercostales interni,** reciprocally, are most prominent in the more caudal series (Fedde, 1987). These muscles lie ventral to the uncinate processes in the intercostal space, attached to the ventral half of each vertebral rib, the fleshy part giving way to an aponeurosis, at the level of the uncinate process, extending dorsad toward the vertebral column. Kirby (1980) described the fleshy slips of external intercostals dorsal to the uncinates of the first two vertebral ribs in some piciforms, but these appear to correspond to the scalene-levator costarum series (Annot. 58).

Attachments of fleshy parts of external intercostal muscles to uncinate processes are (**Osteo.** Annot. 148) sometimes extensive, and may appear as separate "appendicocostales" muscles (Shufeldt, 1890; "intercostales superficiales" of Harvey, 1968).

Fedde (1987) postulates that the length of the uncinate proc. is proportional to effectiveness of the external intercostal muscle to set the rib into motion. Attachments of the muscles on the ventromedial surface of an uncinate process improve the mechanical advantage in cranial shift of the ribs (Sync. intercostalis, **Arthr.** Annot. 81, 82), increasing coelomic volume. The external intercostal muscles are generally inspiratory in function, the internal intercostals expiratory (Fedde, 1987).

(60) **M. costosternalis.** Synonymy: M. subcostalis; M. "triangularis sterni"; M. transversus thoracis. This muscle is attached to Proc. craniolateralis sterni and by fleshy slips on one or more sternal ribs, ventral to the intercostal muscles (Annot. 59). The intercostals extend ventrally to the joint between sternal and vertebral ribs; therefore the costosternalis slips are visible through the thin aponeurosis of the overlying intercostal muscles. The costosternalis may represent a discontinuous innermost intercostal muscle. According to de Wet, et al. (1967) and Fedde (1987) in *Gallus* Pars major is functionally distinct from Pars minor, viz., inspiratory vs. expiratory, respectively.

(61) **M. costoseptalis.** Synonymy: M. costopulmonaris (de Wet, et al. 1967). This muscle consists of four striated intrathoracic slips attached to the medial surface of sternal ribs 3-6 opposite Sync. intercostalis, and insert on the lateral margin of Septum horizontale (**Pericar.** Annot. 2, 3; King, 1966, 1975) that separates the pleural cavity from the remainder of the thoracoabdominal cavity (*Gallus*, deWet, et al., 1967).

(62) **M. sternocoracoideus.** This muscle is usually described with muscles of the thoracic limb. It has no known function in ventilation (Fedde, 1987) and none beyond the obvious positioning of the coracoid relative to the sternum. For further information, see **Arthr.** Annot. 89, 91.

(63) **M. obliquus externus abdominis; M. obliquus internus abdominis; M. transversus abdominis.** These ventrolateral subpubic abdominal muscles are the primary muscles of expiratory ventilation (Fedde, 1987). Attachments of the external oblique muscle include the uncinate processes and lateral surface of vertebral rib elements, and the ventral border of the shaft of the pubis, Lig. inguinale (**Arthr.** Annot. 184), and Tuberculum preacetabulare (**Osteo.** Annot. 244); it inserts on the sternum and a ventral median raphe. The internal abdominal oblique extends cranioventrad from the ventral border of the pubis and ilium to the caudal border of the last rib.

M. rectus abdominis. The rectus abdominis is attached to to the ventral border of Scapus pubis (**Osteo.** Annot. 254) and to the trabeculae of the sternum (**Osteo.** Annot. 150, 151). The fasciculi that parallel those of the internal oblique and rectus abdominis make up the so-called "anterior" belly of the internal oblique (Fedde, 1987). The aponeuroses of the oblique and transverse abdominal muscles do not form a rectus sheath such as that of mammals. What has been called a tendinous intersection opposite the last ribs is actually a vestige of yolk sac resorption.

(64) **Musculi caudae.** Baumel (1988) presents a comprehensive, topographical description of the entire tail apparatus in *Columba livia*, which includes a functional analysis of the movements of the entire tail (uropygium) and its appended flight feathers. Other descriptive material is given in Vanden Berge (1975); Bentz (1983); Zusi and Bentz (1984); and Raikow (1985a).

(65) **M. levator caudae; M. lateralis caudae.** M. levator caudae may consist of a **Pars vertebralis** and **Pars rectricalis,** differentiated on the basis of insertion. The proximal fasciculi insert on Proc. spinosus of the most caudal vertebrae; the distal

fasciculi attach to the rectricial bulb, including the follicles of the major coverts and rectrices. **M. lateralis caudae** inserts on the superior and lateral surfaces of the collar of the follicle of the outermost rectrix (rectrix 6 in *Columba livia*, Baumel, 1988). See Fig. 6.10A.

M. depressor caudae (Fig. 6.10B). M. depressor caudae is the ventral counterpart of M. levator caudae in general structure, position, and function. Three separate subdivisions, Pars proximalis, P. distalis, P. profunda, are described in *Columba livia* (Baumel, 1988). A large proportion of the flattened tendon of **Pars proximalis** from each side decussate obliquely to form an interwoven construction, the **Aponeurosis cruciata** (Baumel, 1988) This aponeurosis is an attachment for some of the ventral, extrinsic muscles of the tail, M. pubocaudalis internus (Annot. 66) and M. caudofemoralis, Pars caudalis (Annot. 110). **Pars distalis** is attached in part to the cruciate aponeurosis and partly to the rectricial bulb (Annot. 67). **Pars profunda** inserts on the most caudal vertebrae and pygostyle. The hypaxial depressor caudae is more complex than its epaxial counterpart.

(66) **M. pubocaudalis externus; M. pubocaudalis internus; M. caudofemoralis, pars caudalis** (Fig. 6.10). These (Annot. 110) are the extrinsic ventral muscles of the uropygium. The pubocaudalis muscles originate from the pubis and adjacent ischium and insert on tail structures. Both are structural components of the suprapubic lateral abdominal wall and are plastered together in their lower parts. All three muscles are functionally expiratory during ventilation (Baumel, et al., 1990).

M. pubocaudalis internus is digastric, consisting of **Pars pelvica** and **Pars caudalis,** the two parts separated by a tendinous intersection, each part having an independent innervation. Fascia of pubocaudalis internus is continuous with Membrana iliocaudalis (**Arthr.** Annot. 185) and Septum supracloacale (Annot. 68).

(67) **M. bulbi rectricium; M. adductor rectricium.** M. bulbi rectricium is a striated muscle which ensheaths a well organized fibro-adipose mass known as the rectricial bulb, concerned with spreading the rectrices. M. adductor rectricium, on the other hand, is a nonstriated muscle associated primarily with the inner aspect of the ventral elastic ligament of the rectrices; it connects adjacent rectricial follicles. For a detailed description of both muscles see Baumel (1988). See Fig. 6.10A.

(68) **Musculi cloacales** (Fig. 6.10A). A collective term for those muscles which interdigitate in the wall of the proctodeum and the eminence of the vent. See **Cloaca.** Annot. 26, and Baumel (1988) for description of their functional roles.

M. sphincter cloacae (**Cloaca.** Annot. 27) is an intrinsic striated muscle of the cloacal wall, extending into the dorsal and ventral lips bordering the external opening or vent, its fascia continuous with Septum supracloacale. The dorsal sheetlike portion bridges the space between the tendinous intersections of M. pubocaudalis internus, better developed than the subcutaneous ventral portion. M. sphincter cloacae is the hypertrophied muscular element of the phalloid organ in the Buffalo Weaver, *Bubalornis albirostris* (Bentz, 1983).

M. transversus cloacae (**Cloaca** Annot. 28) consists of one or two separate heads of origin and/or separate bellies in some taxa, e.g., apodiforms (Zusi, pers. comm.; Vanden Berge, pers. obs.). It originates mainly from fascia of the caudal border of the thigh muscles, ischium, pubis, and iliocaudal membrane (**Arthr.** Annot. 185) (Baumel, 1988; Zusi and Bentz, 1984). It inserts into the fascia of M. sphincter cloacae above and below the vent of the cloaca. The muscle lies superficial to M. pubocaudalis ext. and M. pubocaudalis int. to which it is closely related both

topographically and functionally; it is an important expiratory muscle (Baumel, et al., 1990). See Fig. 6.10A.

Septum supracloacale (Baumel, 1988). This membranous partition separates the dorsal wall of the cloaca, duct of the cloacal bursa, and the dorsum of the bursa from the lower surface of the uropygium. It is prolonged cranially from sphincter cloacae, and is attached to the tendinous intersection of M. pubocaudalis internus (Annot. 66) on each side.

For additional information on other cloacal muscles, see **M. contractor cloacae (Cloaca.** Annot. 29); **M. depressor anguli venti (Cloaca.** Annot. 30); **M. levator cloacae [M. retractor phalli caudalis] (Cloaca.** Annot. 31; **Masc.** Annot. 51); **M. dilator cloacae [M. retractor phalli cranialis] (Cloaca.** Annot. 32; **Masc.** Annot. 51).

(69) **M. rhomboideus superficialis; M. rhomboideus profundus.** Fürbringer (1886; 1902) suggested that Mm. rhomboideus superficialis, rhomboideus profundus, and serratus profundus (Annot. 70) are derived from the same muscle primordium; they are innervated by Plexus brachialis accessorius (**PNS** Annot. 36). These two muscle sheets originate from spinous processes of the last few cervical vertebrae and the thoracic vertebrae, extending in some taxa as far caudally as the cranial margin of the pelvis. Both muscles attach on the vertebral margin and medial surface of the scapula, the superficial sheet sometimes extending as far as the adjacent shaft of the clavicle. See Fig. 6.12.

(70) **M. serratus superficialis.** Synonymy: M. serratus ventralis cranialis et caudalis (Nagamura, Nishida, and Nomura, 1974). Pars cranialis and Pars caudalis are typically present, often contiguous at their origins from the ribs at the level of the uncinate processes; each part has a separate fleshy insertion on the ventral margin of the scapula, separated by a common aponeurosis. Its innervation is independent of that of M. serratus profundus (**PNS** Fig. 4). **Pars scapulohumeralis** of M. serr. superf. is a separate, striated, subcutaneous slip (see Annot. 11; Hikida, 1972; Hikida and Bock, 1974, 1976) (Fig. 6.12).

Pars metapatagialis is a slip of M. serratus superficialis in the metapatagial fold of skin (**Integ.**) that inserts into the caudal end of the humeral feather tract. Present in most birds that have been examined, Pars metapatagialis is sometimes associated with a short, thin band of elastic tissue in the metapatagial fold (R. E. Brown, pers. comm.).

M. serratus profundus. Usually consists of one to several fasciculi which originate on the caudalmost cervical vertebrae and the cervical ribs, and one or more of the succeeding thoracic ribs, inserting along a continuous line on the medial surface of the scapula. Fedde (1987) indicates that this is an accessory muscle of ventilatory inspiration in contrast to M. serratus superficialis which is an accessory expiratory muscle.

(71) **M. scapulohumeralis cranialis.** Synonymy: M. dorsalis scapulae (Nagamura, Nishida, and Nomura, 1974); M. proscapulohumeralis (Berger, 1966, 1968). **M. scapulohumeralis caudalis.** Synonymy: M. teres major et infraspinatus (Fujioka, 1959; Sullivan, 1962); M. dorsalis scapulae (Berger, 1966; Nagamura, Nishida, and Nomura, 1974). M. scap. hum. cran. is absent in some birds; when present, it is attached to the neck (Collum) of the scapula, immediately behind the glenoid process, and cranial to the attachment of M. scapulohumeralis caudalis (on the lateral face of the body of the scapula). M. scap. hum. cran. is usually deep to a retinaculum which attaches M. scapulotriceps (Annot. 81) to the neck and body of the scapula; it inserts in Fossa pneumotricipitale (**Osteo.** Annot. 18) near the distal end of Crus dorsale fossae. M. scapulohumeralis caudalis inserts on the terminal end of Crus ventrale fossae. See Fig. 6.12.

(72) **Mm. subcoracoscapulares.** A collective name for a muscle set which attaches on the medial face of the cranial end of the scapula, extending to the medial face of the coracoid. In many taxa, four heads are described (Fürbringer, 1888, 1902). Most recent authors describe two separate muscles, **M. subscapularis,** typically having two heads, and **M. subcoracoideus** which may be two-headed (Berger, 1966). The muscle complex is innervated by the N. subcoracoscapularis (**PNS** Fig. 15.4).

(73) **M. subscapularis.** The well defined heads, **Caput laterale** ("Pars externa") and **Caput mediale** ("Pars interna", Hudson and Lanzillotti, 1964) form a common tendon that inserts on Tuberculum ventrale (**Osteo.** Annot. 187) of the proximal humerus along with M. subcoracoideus.

(74) **M. coracobrachialis cranialis.** This muscle originates on Proc. acrocoracoideus (**Osteo.** Annot. 171a) of the coracoid, and inserts in a distinct fossa on the Planum intertuberculare of the humerus (in some taxa). See **Osteo.** Annot. 181. .

M. coracobrachialis caudalis. Synonymy: M. flexor coracobrachialis (Simic and Andrejevic, 1964). Attached proximally to the shaft of the coracoid, it contributes to formation of Linea intermuscularis ventralis (**Osteo.** Annot. 174; see Annot. 76). It inserts on Tuberculum ventr. (**Osteo.** Annot. 187) of humerus, dorsal to insertions of Mm. subcoracoscapulares (Annot. 72).

(75) **M. pectoralis.** Simic and Andrejevic (1963, 1964) recognize Pars sternobrachialis and Pars. costo ("thoraco-") brachialis with separate proximal attachments on the sternum and thoracic ribs, respectively, but a common insertion on Crista deltopectoralis (**Osteo.** Annot. 184). Other studies of these parts indicate different fiber orientations and innervation patterns by two distinct branches from the ventral cord of the brachial plexus (see Rosser and George, 1986; Dial, et al., 1987; Kaplan and Goslow, 1989; Sokoloff, et al., 1989).

Aponeurosis (Membrana) intramuscularis is an intramuscular extension of the aponeurosis of insertion; muscle fasciculi from Pars costobrachialis attach to it. See Fisher (1946), Kuroda, (1960; 1961a, b) and Vanden Berge (1970) for further description.

Pars propatagialis, and **Partes subcutanea thoracica et abdominalis** are fleshy slips of M. pectoralis which are listed and annotated under Mm. pterylarum (see Annot. 9, 12; Fig. 6.11).

(76) **M. supracoracoideus.** Synonymy: "deep head" of M. supracoracoideus. This muscle is most probably a derivative of M. deltoideus minor (Annot. 80) as originally suggested by Fürbringer (1902; M. deltoideus minor, pars ventralis) and substantiated by Sullivan (1962; "M. coracobrachialis anterior, pars ventralis"). Deep to the origins of M. pectoralis, M. supracoracoideus is attached to the sternocoracoclavicular membrane, sternum (**Osteo.** Annot. 153) and coracoid (**Osteo.** Annot. 174), resulting in the formation of discrete linear scars on the bones. The tendon lies in Sulcus supracoracoideus (**Osteo.** Annot. 172) on the base of the Proc. procoracoideus and traverses the Canalis triosseus (**Osteo.** Annot. 177). Insertion is on Tuberculum dorsale of the humerus (**Osteo.** Annot. 182, 183). N. supracoracoideus perforates Memb. sternocoracoclavicularis (**Arthr.** Annot. 86, 88) or the body of the coracoid (**Osteo.** Annot. 172), entering the deep face of the muscle.

(77) **M. latissimus dorsi. Pars cranialis** and **Pars caudalis,** as well as the two parts attaching on feather tracts (**Pars interscapularis,** Annot. 8; **Pars scapulohumeralis,** Annot. 11), arise by cleavage in a single muscle primordium (Sullivan, 1962). Pars cranialis and Pars caudalis have separate insertions on the humerus (Fig. 6.12). In

penguins, the tendons of both parts pass over a fibrous loop (Retinaculum m. scapulotricipitis, **Arthr.** Annot. 142) on which is also attached M. scapulotriceps (Schreiweis, 1982, Fig. 8). Variation exists with respect to the presence or absence of one or the other of the slips to the humerus, as well as in either or both of the slips to the feather tracts in avian taxa generally (Berger, 1966, 1969).

Pars metapatagialis of M. latissimus is of uncommon occurrence. In certain birds it inserts into the caudal end of the humeral feather tract with Pars metapatagialis of M. serratus superficialis (R. E. Brown, pers. comm.) (see Annot. 70).

(78) **M. deltoideus [Complexus m. deltoidei].** Buri (1900) in his comprehensive study of the musculature of the shoulder joint in birds, and more recent studies of Brown, et al. (1989) on the Propatagium (**Arthr.** Annot. 141) indicate that this muscle complex consists of three principal sudivisions, based on distal attachments: (1) Pars propatagialis which attaches to Lig. propatagiale and Lig. limitans cubiti; (2) Pars major which attaches to Crista deltopectoralis; and (3) Pars minor which attaches to Tuberculum dorsale of the humerus. All three subdivisions attach proximally to bones of the shoulder. See Figs. 6.11-13 and Annots. 79-80.

(79) **M. deltoideus, pars propatagialis [M. propatagialis].** Synonymy: M. tensor propatagialis, Pars longa/brevis (NAA, 1979). This subdivision of the deltoid complex can occur in three forms: (1) a single muscle having a single head of origin, a single belly, and two insertions: Lig. propatagiale and Lig. limitans cubiti, respectively; (2) two heads of origin with a single belly, having the same two insertions; and (3) two anatomically separate parts, **Pars cranialis** (formerly M. propatagialis brevis), on Lig. propatagiale, and **Pars caudalis** (formerly M. tensor propatagialis brevis), on Lig. limitans cubiti. Associated with one or both parts are fleshy propatagial slips derived from other muscles, including M. cucullaris capitis, M. pectoralis, and M. biceps brachii (Annot. 9). Variations in the morphology and attachments of Pars caudalis on M. extensor carpi radialis (Annot. 87) and the dorsal antebrachial fascia at the elbow, have been described in several taxa (Fürbringer, 1888; Buri, 1900; Berger, 1966; Hudson, et al. 1969; Vanden Berge, 1970; Zusi and Bentz, 1982; Brown, et al. (1989). See Fig. 6.11.

M. deltoideus, pars major [M. deltoideus major]. Caput craniale, attaching on Fibrocartilago humerocapsularis (**Arthr.** Annot. 100), and **Caput caudale,** attaching on bones of the shoulder joint, but only a single belly with a suggestion of internal division is present in others (Fig. 6.12; also Berger, 1966, 1969; Raikow, 1977). Raikow (1985b, Fig. 4) has described and illustrated a third separate head **Caput proximale** in *Atrichornis* and *Menura.* Variation occurs in the number of heads present and their relative development, presence or absence of a "scapular anchor" (retinaculum) (Fig. 6.12), and extent of insertion on Crista deltopectoralis (humerus) (**Osteo.** Annot. 184). In some taxa, Pars major is reduced while Pars propatagialis is markedly more developed (R. E. Brown, pers. comm.).

(80) **M. deltoideus, pars minor [M. deltoideus minor].** Synonymy: M. coracobrachialis anterior (Sullivan, 1962). **Caput ventrale** is a separate slip arising from Membrana sternocoracoclavicularis (**Arthr.** Annot. 86), inserting more or less in common with **Caput dorsale** on the proximal end of Crista deltopectoralis, often overlapping the insertion of M. supracoracoideus (Annot. 76) on Tuberculum dorsale of the humerus. (Hudson and Lanzillotti, 1964; Berger, 1966; Hudson, et al., 1969; Vanden Berge, 1970, and Raikow, 1978). See Fig. 6.12.

(81) **M. scapulotriceps** (Fig. 6.11). This muscle arise from the scapula (**Osteo.** Annot. 169) by a retinaculum superficial to M. scapulohumeralis cranialis (Annot. 71), and from the humerus (Retinaculum m. scapulotricipitis, **Arthr.** Annot. 142; Hudson, Schreiweis, and ChenWang, 1972). In penguins, these attachments unite into a single fibrous band (Retinaculum scapulohumerale) which extends from the scapula to the humerus, and over which pass the tendons of M. latissimus dorsi (Annot. 77; Schreiweis, 1982). Distally, the muscle has an additional attachment on the humerus (Lig. tricipitale, **Arthr.** Annot. 111). A large **Os sesamoideum m. scapulotricipitis** (**Osteo.** Annot. 202) is present in the tendon of insertion of some taxa (Schreiweis, 1982; Zusi and Bentz, 1984). Its insertion is on the dorsal aspect of Proc. cotylaris dorsalis of the ulna (**Osteo.** Annot. 198)

(82) **M. humerotriceps.** The proximal origin on the humerus may be partially subdivided into "caput mediale", "caput posticum" and "caput breve" by the insertions of other muscles (M. scapulohumeralis cranialis; M. scapulohumeralis caudalis; M. latissimus dorsi) near the Fossa pneumotricipitalis (**Osteo.** Annot. 188; Buri, 1900), but these are not usually considered important subdivisions. The insertion is on the Olecranon of the ulna (**Osteo.** Annot. 201).

M. coracotriceps. Synonymy: Caput coracoideum m. anconei (Fürbringer, 1886); M. anconeus coracoideus (Berger, 1966). It has been assumed that this muscle is "vestigial" in birds generally (NAA, 1979; Berger, 1966; in ciconiiforms, Vanden Berge, 1970). Rosser and George (1985) suggest that in *Columba* the histochemical characteristics of the extrafusal fibers and density of muscle spindles indicate that the muscle is tonic in function, serving as an active and sensitive mechanoreceptor, capable of slow and sustained contraction, i.e., a "kinesiological monitor" of the state of contraction in M. triceps brachii (Annot. 81, 82), and/or M. expansor secundariorum.

(83) **M. biceps brachii** (Figs. 6.11, 13). This muscle corresponds to the biceps brachii in mammals. The avian biceps lacks a scapular head, its heads arising from the coracoid and humerus, producing an aponeurosis that covers the intumescence of the humerus (**Osteo.** Annot. 190). The humeral head from Crista bicipitalis (**Osteo.** Annot. 184) is the larger and more conspicuous. Variation includes a single belly and tendon (*Baleniceps*) or two bellies and two tendons of insertion (herons), Vanden Berge, 1970), variation in radial and ulnar insertions (**Osteo.** Annot. 210), and variation in the propatagial slip (Annot. 9). In *Chaetura* and other swifts the muscle is absent (Berger, 1966).

(84) **M. pronator superficialis; M. pronator profundus** (Fig. 6.13). Synonymy: "brevis" = superficialis and "longus" = profundus do not necessarily apply since the so-called "pronator longus" is not always the longer of the two muscles. Both muscles arise from the humerus, M. pronator superf. on Tuberculum supracondylare ventrale (**Osteo.** Annot. 196) and M. pronator profundus on Epicondylus ventralis (**Osteo.** Annot. 178, 194 in common with the attachment of M. entepicondyo-ulnaris (Annot. 92). See Berger (1966); Raikow (1978), and Bentz (1979) for variation.

(85) **M. flexor carpi ulnaris.** Its tendon of origin passes from Proc. flexorius of the humerus (**Osteo.** Annot. 195), glides through Sulcus tendinosus (**Osteo.** Annot. 203) on the proximal ulna, and crosses the Trochlea humeroulnaris (Bentz and Zusi, 1982; **Arthr.** Annot. 110); the tendon may enclose a sesamoid. The fusiform belly is invested by the intermuscular Septum humerocarpale (**Arthr.** Annot. 143, 195). **Pars remigalis** (new term) consists of a series of fleshy slips obliquely oriented to their insertion on Lig. elasticum interremigale minor (**Arthr.** Annot. 197). The principal part of the muscle inserts on Proc. muscularis of Os carpi ulnare (**Osteo.** Annot. 215).

The muscle has at least two functions: (1) flexion of the wrist via Lig. ulnocarpometacarpale ventrale (**Arthr.** Annot. 120) on Proc. pisiformis (**Osteo.** Annot. 215a)

of the carpometacarpus, and (2) movement and positioning of the flight feathers by way of the attachments of Pars remigalis to the elastic ligament and indirectly, distally, to the Retinacula ulnocarpo-remigalia and/or Aponeurosis ulnocarporemigalis (**Arthr.** Fig. 5.11 and Annot. 115), both of which attach on Os carpi ulnare. See Buri (1900) and Berger (1966) for examples of variation. See Fig. 6.13.

(86) **M. flexor digitorum superficialis.** Synonymy: M. flexor digitorum sublimis. **M. flexor digitorum profundus.** Both muscles develop from a common muscle primordium from which is also derived M. flexor carpi ulnaris (Annot. 85; Sullivan, 1962; Shellswell and Wolpert, 1977). The superficial flexor is separated from the other two muscles by Septum humerocarpale (**Arthr.** Annot. 195). See Fig. 6.13.

M. flexor digitorum superficialis varies in birds generally. At its origin, it is related to Lig. humerocarpale (**Arthr.** Annot. 143), and may show a reciprocal development relative to that of the ligament (see review in Berger, 1966). The tendons of M. flexor digitorum superficialis and profundus pass under the Retinaculum flexorium (Fig. 6.12; and **Arthr.** Annot. 114) in a common sheath on the ventral side of Os carpi ulnare. The tendon of the deep flexor passes about Proc. pisiformis (**Osteo.** Annot. 215a), which acts as a pulley, the tendon terminating on Phalanx distalis digiti majoris. The tendon of the superficial flexor inserts on Phalanx proximalis. A vinculum between the tendons is described in melanerpine woodpeckers and sapsuckers (Goodge, 1972).

(87) **M. extensor carpi radialis.** Synonymy: M. extensor metacarpi radialis. The name "extensor carpi" for both the radial and ulnar extensor muscles is more appropriate than "extensor metacarpi" since these muscles extend the carpal *joints* at the wrist. Typically present are dorsal and ventral heads of origin (Berger, 1966), in some taxa, from different areas of the humerus (see Zusi and Bentz, 1982), receiving one or more attachments from Lig. limitans cubiti (see M. deltoideus, Pars propatagialis, Annot. 79; **Arthr.** Annot. 141). One or two tendons insert on Proc. extensorius of Os metacarpale alulare. See Fig. 6.12

(88) **M. extensor carpi ulnaris.** Synonymy: M. extensor metacarpi ulnaris (NAA, 1979); M. flexor metacarpi ulnaris (Stegmann, 1978), but see Annot. 87 and Berger (1966). Two proximal attachments of this muscle are: (1) the distal end of the humerus (Epicondylus dorsalis, **Osteo.** Annot. 178, 194), and (2) the proximal end of the ulna ("ulnar anchor", Retinaculum m. extensoris carpi ulnaris, **Arthr.** Annot. 144). In hummingbirds, swifts, and suboscines Bentz and Zusi (1982) describe a second retinaculum-like structure, containing a large sesamoid continuous with Trochlea humeroulnaris (**Arthr.** Annot. 110).

The distal tendon of extensor carpi ulnaris, with that of **M. extensor digitorum communis,** lies in a fibro-osseous canal (Incisura tendinosa, **Osteo.** Annot. 209) on the distal end of the ulna. On the dorsum of the wrist the tendons pass under a retinaculum (Lig. m. extensoris carpi ulnaris, **Arthr.** Annot. 144; Lig. digitometacarpale, Stegmann, 1978; Lig. ossis metacarpi et primae phalangis digiti secundi, Stettenheim, 1959) which redirects the force of the tendons toward their attachments: M. extensor carpalis ulnaris on Proc. intermetacarpalis (**Osteo.** Annot. 221), and M. extensor digitorum communis on the cranial aspect of Phalanx proximalis digiti majoris. See Fig. 6.12.

(89) **M. ulnometacarpalis dorsalis** arises from the ulna (Lig. m. ulnometacarpalis dorsalis, **Arthr.** Annot. 145) and overlies Incisura tendinosa (**Osteo.** Annot. 209) and its extensor tendons (Mm. extensor carpi ulnaris and extensor dig. communis, Annot. 88). The insertion on Os metacarpale minor is sometimes divided by proximal fasciculi of M. flexor digiti minoris (Annot. 99) (Fig. 6.12). The tendon of **M. ulnometacarpalis ventralis** traverses a sulcus between Tuberculum carpale and Condylus ventralis on the distal ulna (**Osteo.** Annot. 206, 207; Butendieck, 1980, Fig.40) and ventrad over Os carpi radiale ("Sulcus tendineus", Butendieck, 1980; Fig. 42), deep to the tendons of M. extensor carpi radialis (Annot. 87), proximal to its insertion on the dorsal face of the base of Proc. extensorius, Os metacarpale alulare. See Fig. 6.12.

(90) **M. extensor longus alulae.** Synonymy: M. extensor pollicis longus; M. extensor longus digiti II. An ulnar and a radial head of origin have been described (Rosser, 1980).

M. extensor longus digiti majoris. Synonymy: M. extensor indicis longus; M. extensor longus digiti III. **Pars distalis** is topographically located in the manus proper and unites with the tendon of **Pars proximalis.** This distal head has been designated M. flexor metacarpi brevis (Fisher and Goodman, 1955; Berger, 1966) but, according to Sullivan (1962), Pars distalis ("M. extensor medius brevis") is derived from M. extensor longus digiti majoris ("M. extensor medius longus") in which case it would represent "M. extensor brevis digiti majoris". The tendon inserts on the distal phalanx of the major digit; the corresponding tendon of **M. extensor digitorum communis** inserts on the proximal phalanx.

(91) **M. ectepicondylo-ulnaris** (Fig. 6.12). Synonymy: M. anconeus (Berger, et al., 1966). The muscle has its origin on the Epicondylus dorsalis ("ectepicondyle", **Osteo.** Annot. 194) of the humerus; its origin is opposite that of M. entepicondylo-ulnaris (Annot. 92). Although "M. anconeus" has been widely used for this muscle, "anconeus" also has been used for M. triceps brachii.

(92) **M. entepicondylo-ulnaris.** Synonymy: M. anconeus medialis (Fujioka, 1959); known to many avian anatomists as the "gallinaceous muscle." It has been described only in the Kiwi (*Apteryx*), in Tinamiformes (Hudson, et al., 1972), in Galliformes (Hudson and Lanzillotti, 1964), and in some Anatidae (Sy, 1936; Zusi and Bentz, 1978). Beddard (1884) described an "anconeus internus" in *Scopus* which suggests M. entepicondylo-ulnaris, but this has never been substantiated. This muscle arises from Epicondylus ventralis of the humerus, in common with the origin of M. pronator profundus (Annot. 84); see also Butendieck (1980, Fig. 36, "Fossa muscularis"). It inserts on the proximal caudoventral face of the ulna.

(93) **M. interosseous dorsalis; M. interosseous ventralis.** Synonymy: "ventralis" also known as "palmaris" or "volaris". The two muscles largely fill the intermetacarpal space; the M. interosseous ventralis is sometimes unipennate (Vanden Berge, 1970).

(94) **M. extensor brevis alulae.** Synonymy: M. extensor pollicis brevis; M. extensor brevis digiti II.

M. levator alulae. Livezey (pers. comm.) has described and illustrated this small muscle on the dorsum of the alula in the Galapagos Cormorant, *Compsohelieus harrisi.* It has not been described in other taxa.

(95) **M. abductor alulae.** Synonymy: M. abductor pollicis; M. abductor digiti II.

(96) **M. flexor alulae.** Synonymy: M. flexor pollicis; M. flexor digiti II.

(97) **M. adductor alulae.** Synonymy: M. adductor pollicis; M. adductor digiti II.

(98) **M. abductor digiti majoris.** Synonymy: M. abductor indicis; M. abductor digiti III.

(99) **M. flexor digiti minoris.** Synonymy: M. flexor digiti III or IV.

(100) **Mm. iliotibiales.** The developmental studies in *Gallus* (Schroeter and Tosney, MS.) indicate that the iliotibialis group of muscles consists of M. iliotibialis cranialis and lateralis, M. ambiens (Annot. 103), and M. iliofibularis. M. iliotibialis medialis is most probably a derivative of this group.

(101) **M. iliotibialis cranialis.** Synonymy: M. sartorius (Hudson, 1937); M. extensor iliotibialis anterior (Fisher, 1946). Variation exists in the proximal attachments of this muscle to the caudal thoracic vertebrae, synsacrum, and preacetabular ilium. More than one head may be present (see review in Berger, 1966; Vanden Berge, 1975; and others). See Fig. 6.14.

M. iliotibialis lateralis. This muscle is attached along the lateral margin of Ala preacetabularis and Ala postacetabularis of the ilium. Two subdivisions, **Pars preacetabularis** and **Pars postacetabularis** are recognized. The two parts may be essentially continuous, or there may be an intermediate gap, **Hiatus acetabularis.** The hiatus is a derived state resulting from the loss of the central portion of the muscle (Raikow, 1987).

M. iliotibialis medialis. A separate muscle, lying deep to the preacetabular part of the iliotibialis lateralis, has been described in the flamingos (Vanden Berge, 1970), and in the stilt, *Cladorhynchus leucocephalus* (Olson and Feduccia, 1980).

All three muscles terminate distally with Mm. femorotibiales (Annot. 107) in a common tendon (Lig. patellae, **Arthr.** Annot. 158; **Osteo.** Annot. 265; **PNS** Annot. 46) on the patellar crest.

(102) **M. iliofibularis.** Synonymy: M. biceps femoralis. M. iliofibularis, together with Mm. flexor cruris lateralis and flexor cruris medialis (Annot. 108, 109), have been considered homologs of the mammalian "hamstring" muscles. Which of these three, if any, is the counterpart of which mammalian muscle is unclear (for synonymy, see Vanden Berge, 1975). M. iliofibularis is apparently derived from the iliotibialis muscle group, independent from the other two muscles (Schroeter and Tosney, MS.). The tendon of insertion passes through a fibrous loop (**Ansa m. iliofibularis, Arthr.** Annot. 186), with N. paraperoneus and N. peroneus (**PNS** Annot. 51), and inserts on Tuberculum m. iliofibularis, Corpus fibulae. See Figs. 6.15, 16.

(103) **M. ambiens** (Fig. 6.17) arises on Tuberculum preacetabulare (**Osteo.** Annot. 244) on the body of the ilium. The distal tendon merely grooves or sometimes perforates the patellar ligament or patella (**Osteo.** Annot. 265), then inserting on the proximal aponeurosis of the digital flexor muscles in the popliteal fossa.

(104) **Mm. iliotrochanterici.** Synonymy: Gadow and Selenka (1891) considered this muscle group to be peculiar to birds, without homology in mammals, but others, following Fisher (1946), refer to **M. iliotrochantericus caudalis** as "gluteus profundus", **M. iliotrochantericus cranialis** as "iliacus", and retain the name **M. iliotrochantericus medius.** Recently, Rowe (1986) has suggested homology with a similar set of muscles in reptiles but with differing views in the associated terminology. The three muscles derive from a deep proximal group of thigh muscles, including also M. iliofemoralis externus (Annot. 105) and M. iliofemoralis internus (Annot. 106) (Schroeter and Tosney, MS.). All three muscles originate on the preacetabular ilium and insert on the lateral aspect of Trochanter femoris; details in Ballmann, 1969b). According to Vanden Berge (1982), statements about the presence/absence of M. iliotrochantericus medius, as a distinct muscle element in the avian thigh, should also characterize the passage of a neurovascular bundle (N. coxalis cranialis; A. cranialis coxae, see **Art.** Annot. 70) proximally between Mm. iliotrochantericus medialis and cranialis (Rosser, et al., 1982, and Schulin, 1987). See Figs. 6.15, 16).

(105) **M. iliofemoralis externus** (Gadow and Selenka, 1891). Synonymy: M. gluteus medius et minimus (Hudson, 1937); M. piriformis (Fisher, 1946). This muscle originates on a caudal prolongation of the Fossa iliaca dorsalis of the preacetabular ilium (**Osteo.** Annot. 232), and inserts on the lateral surface of the Trochanter femoris. The degree of separation of this muscle from M. iliotrochantericus caudalis (Annot. 104) is variable (Fig. 6.15); the muscle is absent in some taxa, but reappears as a developmental anomaly or even as a re-established feature (Raikow, et al., 1979).

(106) **M. iliofemoralis internus** (Gadow and Selenka, 1891). Synonymy: M. iliacus; M. psoas. Originates on the ilium, deep to the origin of the iliotrochantericus medius, and inserts on the caudomedial surface of the proximal end of the femur (Fig. 6.17).

(107) **Mm. femorotibiales.** The chief variations in **M. femorotibialis lateralis [externus]** pertain to the origin of Pars proximalis and the presence or absence of a discrete Pars distalis (Berger, 1966). The proximal part inserts on Lig. patellae (**Arthr.** Annot. 158); the distal part, on Crista cnemialis lateralis of the tibia. The three subdivisions, Mm. femorotibialis lateralis [externus]/intermedius/and medialis [internus], form a common tendon (in which the patella develops) on which Mm. iliotibiales insert (Annot. 101).

(108) **M. flexor cruris lateralis** (Fisher, 1946). Synonymy: M. caudilioflexorius (Gadow, 1891); M. semitendinosus (Hudson, 1937). Two parts have been long recognized: **Pars pelvica,** the main belly which is attached to the caudal end of the pelvis and Membrana iliocaudalis (**Arthr.** Annot. 185), and **Pars accessoria** (pars femoralis, or "accessory semitendinosus") which is attached to the distal femur. The latter, however, is part of the insertion, not a second head of origin; it joins with the pelvic part in a distal raphe with additional tendinous variations in certain groups (McKitrick, 1986; Raikow, 1987). See Fig. 6.16.

Among the variants: Pars pelvica may be present without pars accessoria, but the latter apparently is never present alone. In some major avian taxa, both parts are absent (e.g., in accipiter hawks and owls; see Berger, 1966 and Hoff, 1966).

(109) **M. flexor cruris medialis** (Fisher, 1946). Synonymy: M. ischioflexorius; M. semimembranosus. This muscle is deep to M. flexor cruris lateralis, its origin typically on the lateral surface of the ischium. The tendon of insertion may attach directly on the proximal portion of the tibia, or it may form a common aponeurosis with the tendon of M. flexor cruris lateralis (Annot. 108) and the proximal aponeurosis of M. gastrocnemius, Pars intermedia (Annot. 118. See examples in Goodge, 1972; Swierczewski and Raikow, 1981; Schulin, 1987). See Fig. 6.17.

(110) **M. caudofemoralis.** Synonymy: M. piriformis. This is a homolog of the coccygeofemorales muscle system in reptiles (Romer, 1927). Differentiation of the muscle during development (*Gallus*) (Schroeter and Tosney, MS.), suggests that it is a single muscle having two parts, **Pars caudalis** and **Pars pelvica,** rather than two independent muscles (NAA, 1979; Vanden Berge, 1982). Pars caudalis is the part most frequently described, rarely absent in the presence of Pars pelvica. Both parts may be absent (see Table IX. 2, Berger, 1966). See Fig. 6.16.

During avian evolution the relative length of the skeleton of the tail became reduced, however, the **Pars caudalis** (formerly M. caudofemoralis, NAA, 1979) persists and has a strong insertion on the uropygium. Pars caudalis produces movements

of the uropygium rather than acting on the pelvic limb; it also acts as an expiratory ventilatory muscle in the pigeon (Baumel, et al., 1990).

Pars pelvica (formerly M. iliofemoralis, NAA, 1979) is a secondarily derived belly which is attached chiefly to the ilium, but to the ischium in some taxa. Pars caudalis and Pars pelvica may have a common femoral tendon of insertion, without continuity of their respective fleshy parts, but in some taxa (e.g., ratites) their femoral attachments are separate.

(111) **Mm. obturatorius lateralis and medialis.** *Lateralis* is sometimes known as "externus"; *medialis*, as "internus". According to Romer (1927), the obturator muscles differentiate from a common primordium which appears to be equivalent to the obturatorius externus in mammals, not obturator internus. Substitution of the terms *lateralis* and *medialis* are consistent with the positional relationships between them.

(112) **M. obturatorius lateralis. Pars dorsalis** and **Pars ventralis** are clearly defined parts of this muscle in passerines (Raikow, 1976; 1978, Fig. 5; 1987) and some other avian taxa (Berger, 1966, 1969).

(113) **M. pubo-ischio-femoralis.** The synonym "M. adductor", with several qualifying terms ("longus et brevis", "superficialis et profundus", "longus et magnus") has been in common use. Cracraft (1971) indicated that the muscle probably has no significant functional role in adduction of the femur, but is more likely a postural muscle (Helmi and Cracraft, 1977). The term of Gadow and Selenka (1891), "M. pubo-ischio-femoralis", is descriptive in terms of the origin (pubis and/or ischium) and insertion (femur) of this muscle. In nonpasserines, its two subdivisions are **Pars lateralis** and **Pars medialis;** in passerines, **Pars cranialis** is equivalent to the lateral subdivision and **Pars caudalis** to the medial subdivision (Raikow, 1976). The two main subdivisions are separable by the orientation of their respective fasciculi and/or by the passage of a branch of N. obturatorius between them. In the mousebirds (Coliiformes), a third part, **Pars accessoria,** is attached distally on the tibiotarsus (Berman and Raikow, 1982); it may be unique to this group of birds. See Fig. 6.16.

(114) **M. tibialis cranialis** (Fig. 6.15). In strigid owls **Caput femorale** and **Caput tibiale** may remain independent, forming two bellies and two tendons of insertion (Hoff, 1966). The proximal tendon of Caput femorale arises from Condylus lateralis of the femur, perforates or grooves Meniscus lateralis (**Arthr.** Annot. 159), and passes distally across Incisura tibialis (**Osteo.** Annot. 273). Crossing the knee, the tendon is restrained by a retinaculum in some birds (Berman and Raikow, 1982); its tendon of insertion traverses Retinaculum extensorium tibiotarsi (**Arthr.** Annot. 187), and inserts on the tarsometatarsus (Tuberositas m. tibialis cranialis (see **Osteo.** Annot. 291). In some taxa, a neurovascular bundle passes under the bifurcation of the tendon at its insertion (Vanden Berge, 1970; see Midtgård, 1982).

(115) **M. extensor digitorum longus.** The proximal attachment is in Sulcus intercnemialis of the tibiotarsus (**Osteo.** Annot. 272); the distal tendon is restrained, along with with that of M. tibialis cranialis (Annot. 114) by the fibrous Retinaculum extensorium tibiotarsi (**Arthr.** Annot. 187). Distally, the tendon enters Canalis extensorius (**Osteo.** Annot. 278) and passes beneath the osseous Pons supratendineus (**Osteo.** Annot. 277), crosses the intertarsal joint, then passes beneath the fibrous Retinaculum extensorium tarsometatarsi (**Arthr.** Annot. 188) (**Osteo.** Annot. 287). The tendon typically gives rise to branchings to the second, third, and fourth toes, and rarely to the hallux (for exceptions, see Berman and Raikow, 1982 and Berman, 1984).

(116) **M. fibularis [peroneus] longus.** Variation in the Mm. fibularis longus and brevis in many taxa was described by Mitchell (1913). Hudson (1937) and Berger (1966) did not consider the wide variation in relative development of the two muscles significant in terms of avian systematics; for a differing opinion, cf., Kurochkin (1968). See Fig. 6.16.

Typically, the tendon inserts on the tibial cartilage by an aponeurosis, grooves the proximal end of the Tarsometatarsus (Sulcus m. fibularis [peronei] longus) between the insertion of M. fibularis brevis (Annot. 117; Tuberculum retinaculi m. fibularis, **Osteo.** Annot. 282) and the attachment of Lig. collaterale laterale (**Arthr.** Annot. 172), and terminates on the tendon of M. flexor perforatus digiti III (Annot. 121).

(117) **M. fibularis [peroneus] brevis.** This muscle varies among avian taxa. In New World nine-primaried oscine passeriforms, a derivative head, **Caput tibiale,** distinct from the primary head, **Caput fibulare,** is said to be an important taxonomic character (Kurochkin, 1968; Raikow, 1976, 1978). The tendon lies in a sulcus on the distal end of the tibiotarsus where it is restrained by a retinaculum **Osteo.** Annot. 282). Insertion is on the proximal tarsometatarsus (Tuberculum m. fibularis brevis), plantar to the sulcus for M. fibularis longus (Annot. 116).

(118) **M. gastrocnemius.** Typically consists of three parts: **Pars lateralis** (= externa), **Pars intermedia,** and **Pars medialis** (=interna). A separate fourth part, **Pars supramedialis,** has been described in some species of the suboscine passerine families Eurylaimidae and Philepittidae (Raikow, 1987). These subdivisions are referred to as "Pars" rather than "Caput" since they may have separate bellies, sharing in the formation of a common tendon of insertion. The presence or absence of accessory heads associated with Pars lateralis (Vanden Berge, 1970) or Pars medialis (Raikow, 1970, 1978, 1987) may serve as taxonomic characters.

(119) **M. plantaris.** No homology with the mammalian plantaris has been established. Its presence or absence was once a part of the technical taxonomic diagnosis of avian taxa. Raikow (pers. comm.) indicated that the tendon of insertion in dendrocolaptid passerines is regularly in common with that of M. gastrocnemius, Pars intermedia. A similar insertion has been described in other birds (Vanden Berge, 1970). See **Arthr.** Fig. 5.8.

(120) **M. popliteus.** Homology with the mammalian popliteus is not established. The muscle originates in Fossa flexoria (**Osteo.** Annot. 274) of the proximal tibia, near the origin of M. flexor digitorum longus, resembling the site of the popliteus muscle in mammals. It inserts on the caudal surface of Caput fibuli.

(121) **Mm. flexores perforantes et perforati digiti II et III.** (Figs. 6.16, 19). Synonymy: M. flexor digitorum medius (Frewein, 1967). **Mm. flexores perforati digiti II, III, et IV.** Synonymy: M. flexor digitorum superficialis (Frewein, 1967). **M. flexor hallucis longus; M. flexor digitorum longus.** Synonymy: M. flexor digitorum profundus (Frewein, 1967). See **Topog.** for numbering and names of pedal digits.

A "perforans" (perforating) tendon is one which passes between the decussating medial and lateral phalangeal insertions of the "perforatus" (perforated) tendon at metatarsophalangeal and/or interphalangeal joints. The "sleeve" formed by the so-called "bifurcation" of each perforated tendon around the perforating tendon, is known as **Manica flexoria** (ICVGAN, 1983). In the avian foot, the second and third toes typically have three sets of flexor tendons, one of which is both perforating as well as perforated. Therefore, these two toes each have one "proximal" flexor tendon

(M. flexor perforatus digiti II or III) perforated by two others, one of which ("intermediate" M. flexor perforans et perforatus digiti II or III) is itself perforated by the "distal" digital flexor tendon (M. flexor digitorum longus). In some taxa, M. flexor perforatus digiti II attaches on both the medial and lateral side of Phalanx proximalis and is perforated by the tendons of M. flexor perforans et perforatus digiti II and M. flexor digitorum longus (for examples see Schreiweis, 1982; Vanden Berge, 1970; and Zusi and Bentz, 1984). In many other taxa, the same tendon has been described as "not perforated", but the descriptions do not necessarily indicate that the tendon is inserting *only* on the lateral, or *only* on the medial aspect of the phalanx in a *primary*, i.e., "non-perforated" state. See Berman and Raikow, 1982; Schreiweis, 1982; McKitrick, 1985; and Raikow, 1987, for descriptions of this relationship.

The hallux typically has a "superficial" flexor tendon (M. flexor hallucis brevis, Annot. 126) which is perforated by the tendon of the "deep" M. flexor hallucis longus. A "superficial" (M. flexor perforatus digiti IV) of digit four is perforated by the tendon of M. flexor dig. long.

Most of these long flexor tendons also pass through Cartilago tibialis (**Arthr.** Annot. 164) and Hypotarsus (**Osteo.** Annot. 288) to enter Sulcus flexorius on the plantar aspect of the foot. The position of these long tendons, and their positional relationships to one another, are usually definite for different taxa (see Hudson, 1937, and Vanden Berge, 1970). The tendons also pass through Canalis flexorius plantae (**Arthr.** Annot. 178) and sulci on the plantar surfaces of the Ligg. plantare (**Arthr.** Annot. 182, and Fig. 9) of the metatarsophalangeal and interphalangeal (except the terminal one) joints of the toes.

Mm. flexores perforantes et perforati digiti II et III are considered "intermediate" flexors in the sense that their tendons "perforate" those of the "superficial" flexors (Mm. flexores perforati digiti II et III), but are, in turn, perforated by corresponding digital tendons of M. flexor digitorum longus.

Mm. flexores perforati digiti II, III, et IV. One or more of these three muscles may have two proximal attachments or "heads". The long flexors of the second and fourth toes arise on the aponeurosis of M. flexor perforatus digiti III (see Cracraft, 1971) which is attached to Fossa poplitea of the femur. A second, lateral, or "fibular" attachment may be continuous with the tendon of M. ambiens (Annot. 103) when present. Raikow (1987) described variations in the heads and tendon(s) of M. flexor perforatus digiti IV in several passerines. A M. flexor perforans et perforatus digiti IV has never been described.

(122) **Vinculum tendinum flexorum.** The fibroelastic band (Fig. 6.19) which connects the tendons of M. flexor perforans et perforatus digiti III and M. flexor perforatus digiti III in the foot is highly variable among birds generally (Hudson, 1937). A second fibroelastic band unites the tendons of Mm. flexor hallucis longus and flexor digitorum longus in some birds. The tendons of these muscles may be totally independent in some birds, partially or completely fused in others. Raikow (1985a, 1987) has reviewed the various degrees and patterns of fusion and interconnections between the deep digital flexors in association with different functional and adaptive specializations of the feet (Raikow, 1985a, Tables V, VII, VIII).

(123) **M. flexor hallucis longus; M. flexor digitorum longus.** Origins of M. flexor hallucis longus are distinctly separate from those of M. flexor digitorum longus. There may be multiple heads of origin, one or more of which may have a variable relationship to the tendon of insertion of M. iliofibularis (Annot. 102; Raikow and Cracraft, 1983; McKitrick, 1985; Raikow, 1987). The relationship between these two deep flexor muscles and their tendons, distally, has been classified into at least eight

different types, including subtypes in certain groups. Raikow (1985a, Tables V, VII, VIII) discusses and illustrates these types, and presents in tabulated form a concise summary of the distribution of each type among avian groups, related to the foot type and relative development of the hallux. The tendons insert on Tuberculum flexorium of each ungual phalanx.

(124) **Area tuberculata tendinis; Plicae vaginae tendinis; Lig. elasticum tendinis flexoris; Lig. elasticum extensorium unguis.** These terms are fully described and illustrated in Quinn and Baumel (1990); see **Arthr.** Annot. 183.

Area tuberculata tendinis. Roughened patches on the digital plantar surface of tendons of Mm. flexor hallucis longus and flexor digitorum longus opposite transverse semicircular folds (**Plicae vaginae tendinis**) (see Annot. 3) on the apposing surface of the tendon sheath. The sheath plicae when pressed against the tuberculate areas form a locking mechanism holding the distal interphalangeal joints in the flexed position. First thought to be an adaptation peculiar to "perching" birds (Schaffer, 1903), this "tendon-locking mechanism" occurs in birds of many foot types (e.g., *Gavia, Pelecanus, Ardea, Larus, Cygnus, Buteo, Upupa*). It is differentiated in the 15 day fetal *Gallus*.

(125) **M. extensor hallucis longus. Pars proximalis** and **Pars distalis** are well defined in some taxa (Hudson, Lanzillotti and Edwards, 1959), but the entire muscle is one of the more variable of the group of short muscles of the toes (Berger, 1966; Raikow, 1976; Berman and Raikow, 1982; Berman, 1984). Since there is but one short extensor of the hallux, the use of the qualifier, "longus", may seem unnecessary. However, Pars proximalis may represent the "long" extensor and Pars distalis, the short ("brevis"). In addition, there may be an additional head present (pars accessoria; Berman and Raikow, 1982).

(126) **M. flexor hallucis brevis.** The muscle is attached on the shaft of the tarsometatarsus (Fossa parahypotarsalis medialis) and is separated from Sulcus flexorius (**Osteo.** Annot. 294) by a ligamentous intermuscular septum extending distally from Crista medianoplantaris (**Osteo.** Annot. 290) in some taxa (e.g., *Larus*). Distally, the tendon is perforated by the tendon of M. flexor hallucis longus (Annot. 121).

(127) **M. abductor digiti II; M. adductor digiti II.** M. abductor digiti II probably functions as an extensor (Cracraft, 1971); it arises from the medial side of the distal half of the tarsometatarsus and inserts on the base of the proximal phalanx (Fig. 6.18). **M. adductor digiti II** is attached in the Sulcus flexorius, deep to the flexor tendons, and inserts on the lateral face of the base of the first phalanx; absent in some taxa (e.g., Tetraonidae; Hudson, et al., 1959; Berger, 1966).

(128) **M. extensor proprius digiti III.** In most taxa of birds, this muscle is of rare and irregular occurrence (Fig. 6.18). Hudson, Schreiweis, and ChenWang (1972) state that it has been seen in five living genera of ratites and tinamiforms. Berman (1984) describes accessory muscle slips in *Amazona*. See Holmes (1962).

(129) **M. extensor proprius digiti IV; M. extensor brevis digiti IV.** The tendon of insertion of M. extensor brevis digiti IV passes through Canalis interosseus tendineus (**Osteo.** Annot. 295, 298). A second short toe muscle, M. extensor proprius digiti IV, is described and illustrated by Berman and Raikow (1982, Fig. 8A). See also Trochlea accessoria, **Osteo.** Annot. 297.

(130) **M. abductor digiti IV.** Present in most groups of birds (Berger, 1966), but often minute and identified only by staining techniques (Bock and Shear, 1972).

M. adductor digiti IV has been described (Gadow and Selenka, 1891), Hudson (1937), but is insignificant and extremely rare in occurrence.

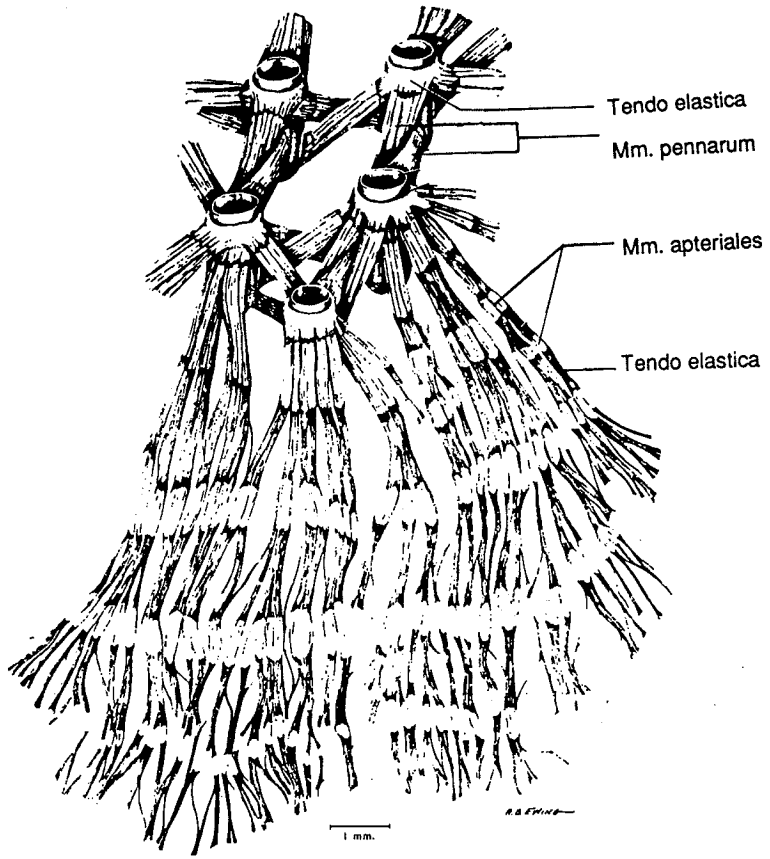

Fig. 6.1. Musculi nonstriati dermatis in the chicken, *Gallus gallus:* muscles of feather follicles and of the apterium. From Lucas and Stettenheim (1972:483).

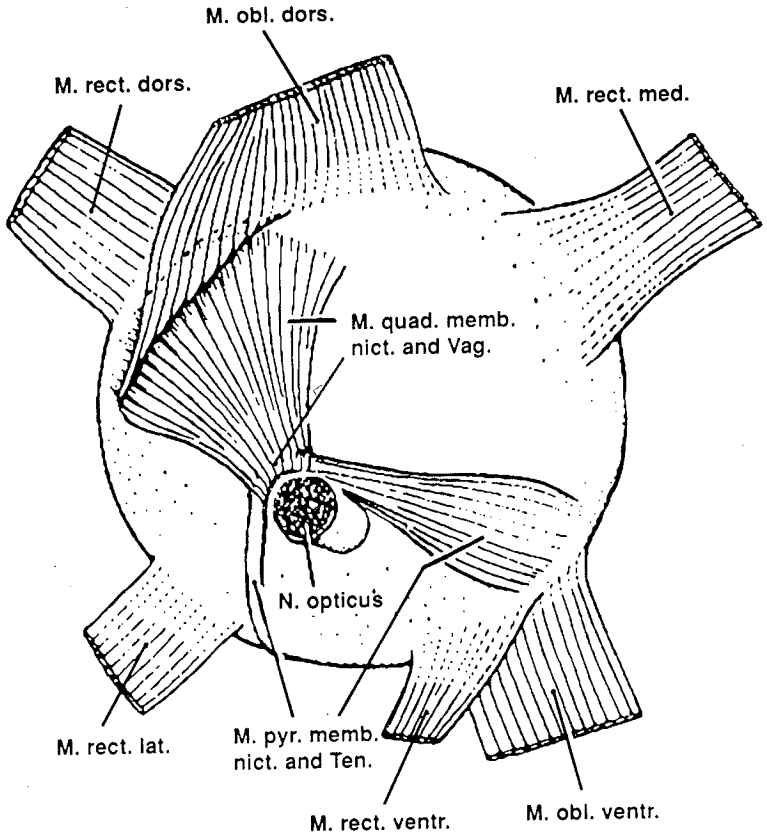

Fig. 6.2. Generalized pattern of attachment of Mm. bulbi oculi et Membrana nictitantis on the eyeball. (Redrawn with modification after Elzanowski (1987).

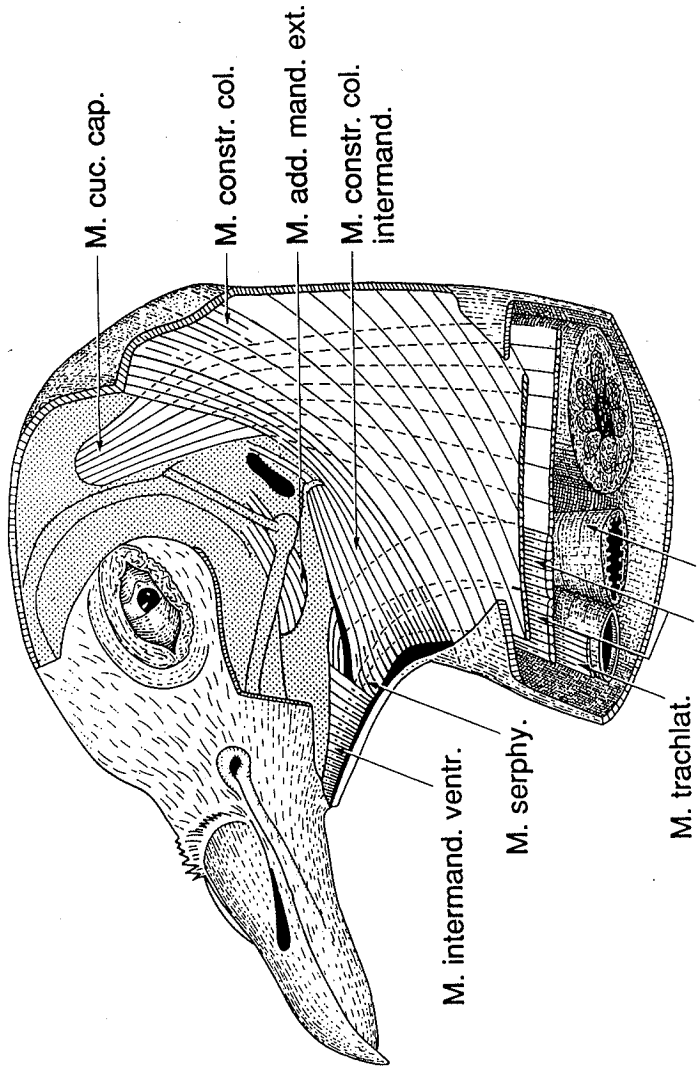

Fig. 6.3. Musculi subcutanei, lateral view in the pigeon, *Columba livia*. From Zweers (1982).

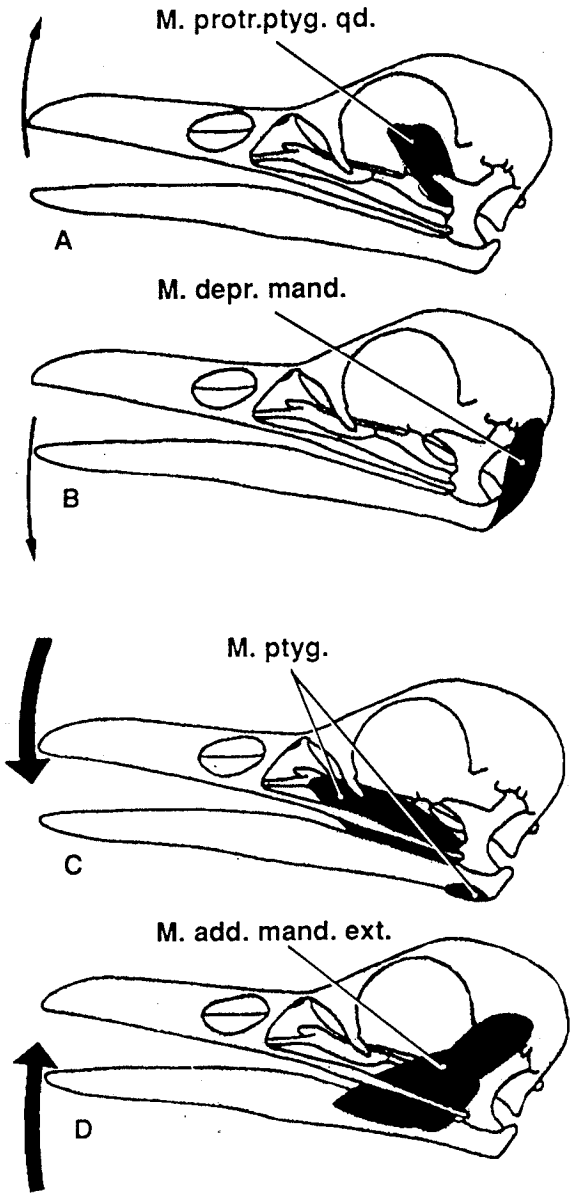

Fig. 6.4. Generalized pattern of selected Musculi mandibulae. From Bühler (1981). Thin arrows indicate bill opening; thicker arrows, bill closing.

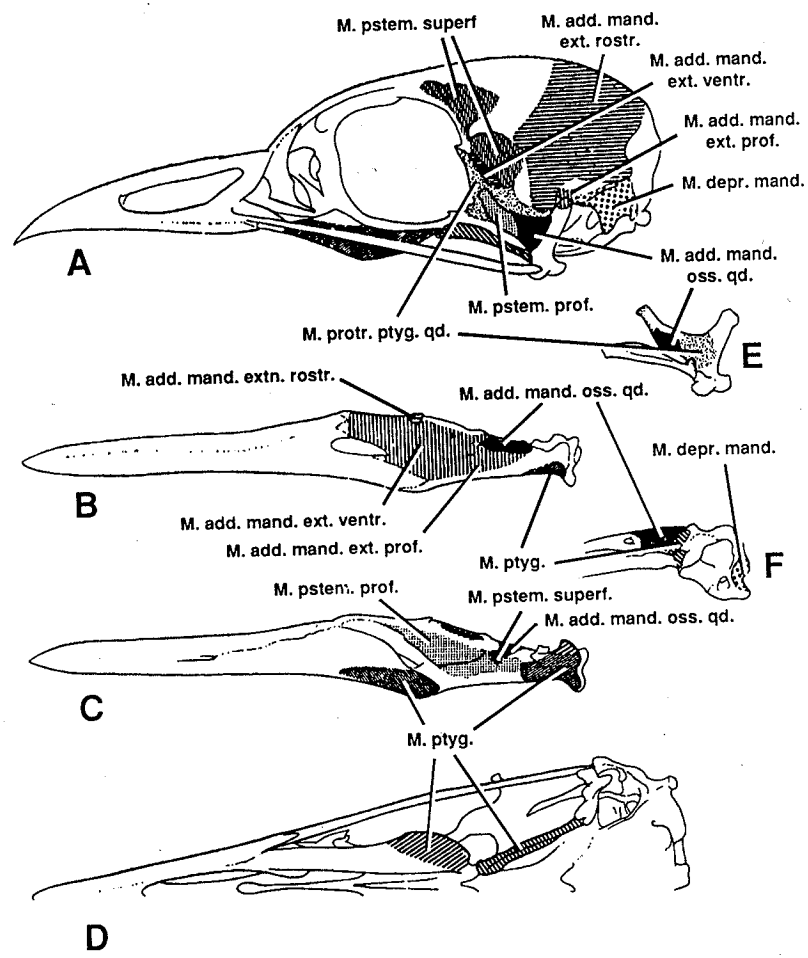

Fig. 6.5. Schematic of the attachments of jaw muscles in a grebe, *Podilymbus podiceps*. From Zusi and Storer (1969).

A. Lateral view of the skull; B. Lateral view of mandible; C. Medial view of mandible; D. Ventral view of skull; E. medial view of the quadrate bone; F. Dorsal view of the caudal end of the mandible.

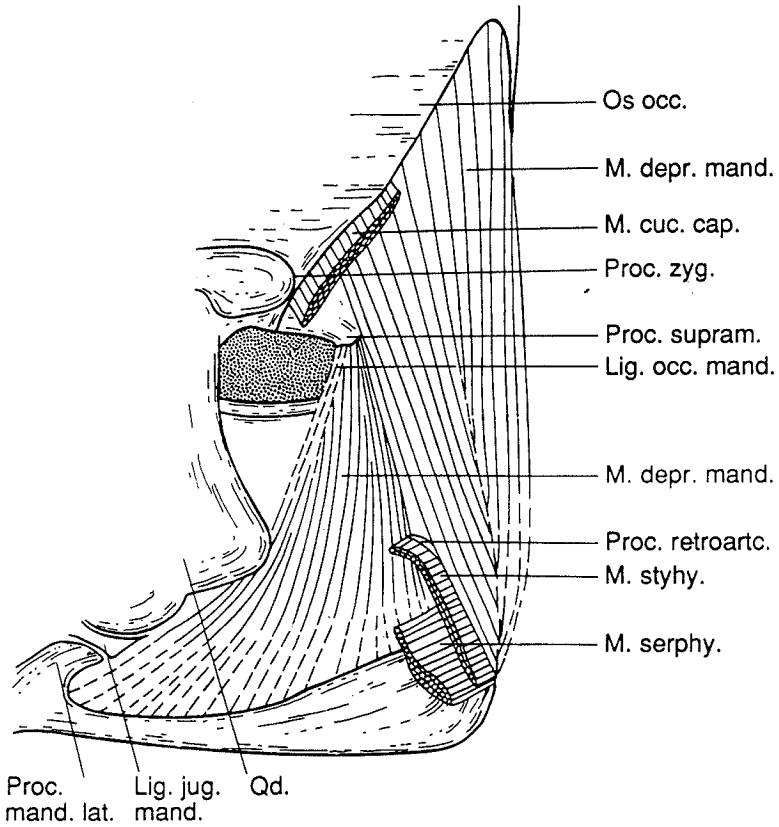

Fig. 6.6. M. depressor mandibulae in the Mallard, *Anas platyrhynchos*. From Zweers (1974); redrawn with permission.

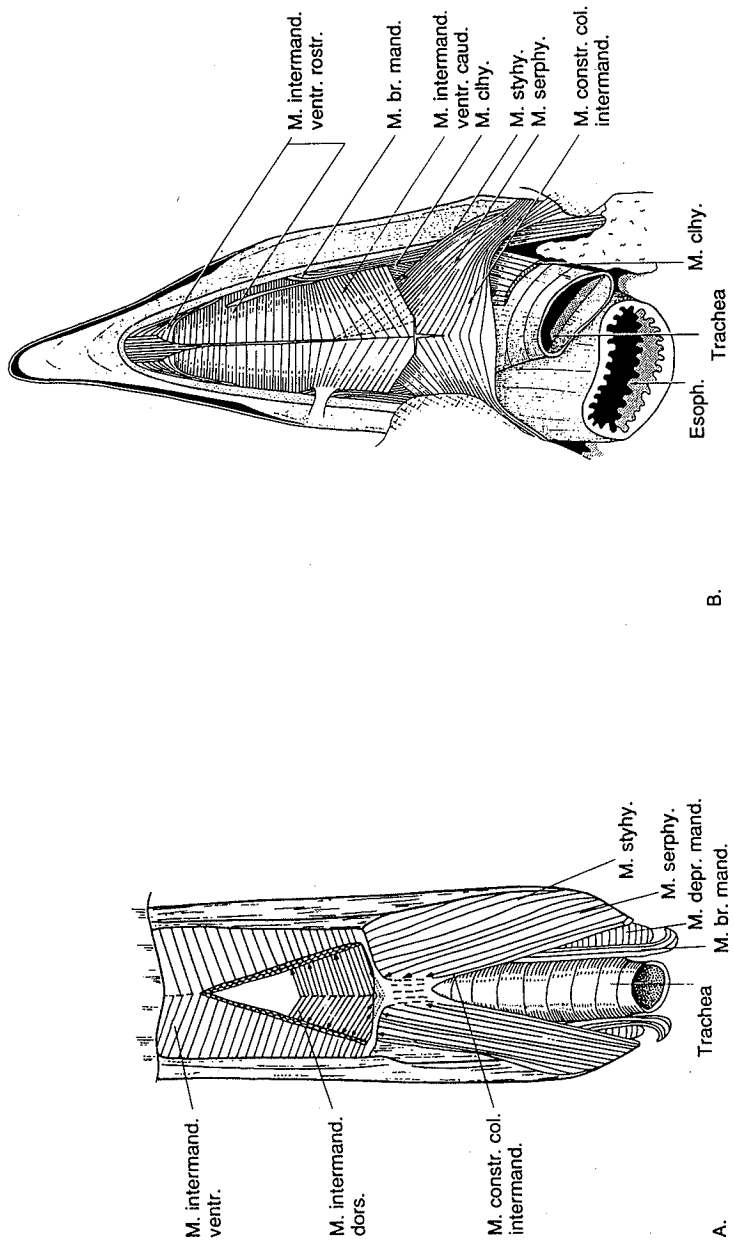

Fig. 6.7. Superficial ventral view of the hyobranchial musculature. A. the Mallard, *Anas platyrhynchos* (Zweers, 1974); B, the pigeon, *Columba livia* (Zweers, 1982). Redrawn with permission of the author.

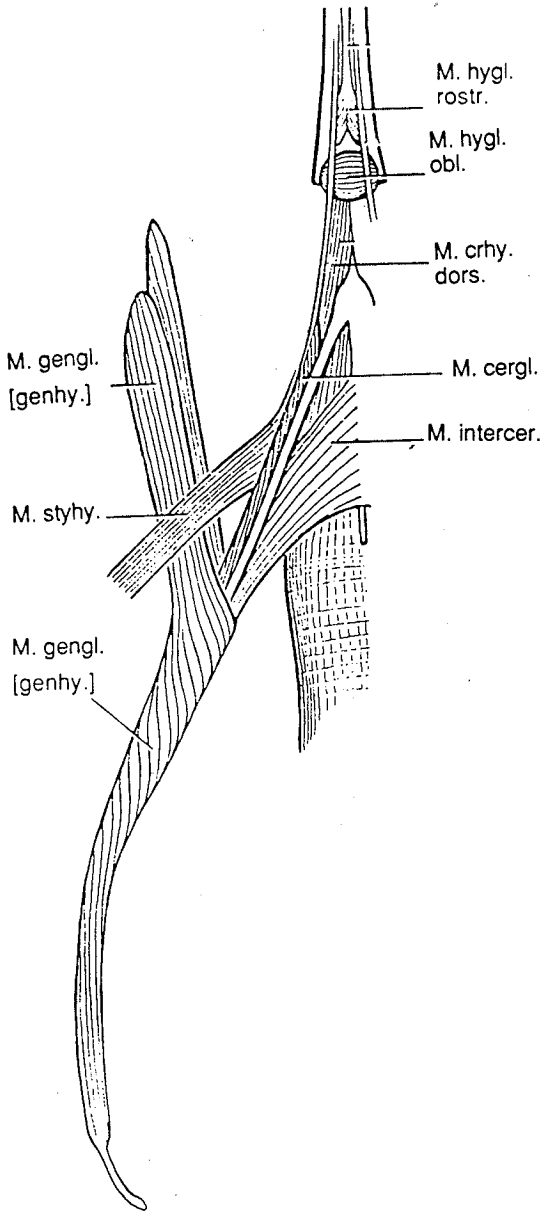

Fig. 6.8. Hyoid musculature in a sandpiper, *Tringa totanus*. Adapted from Burton (1974).

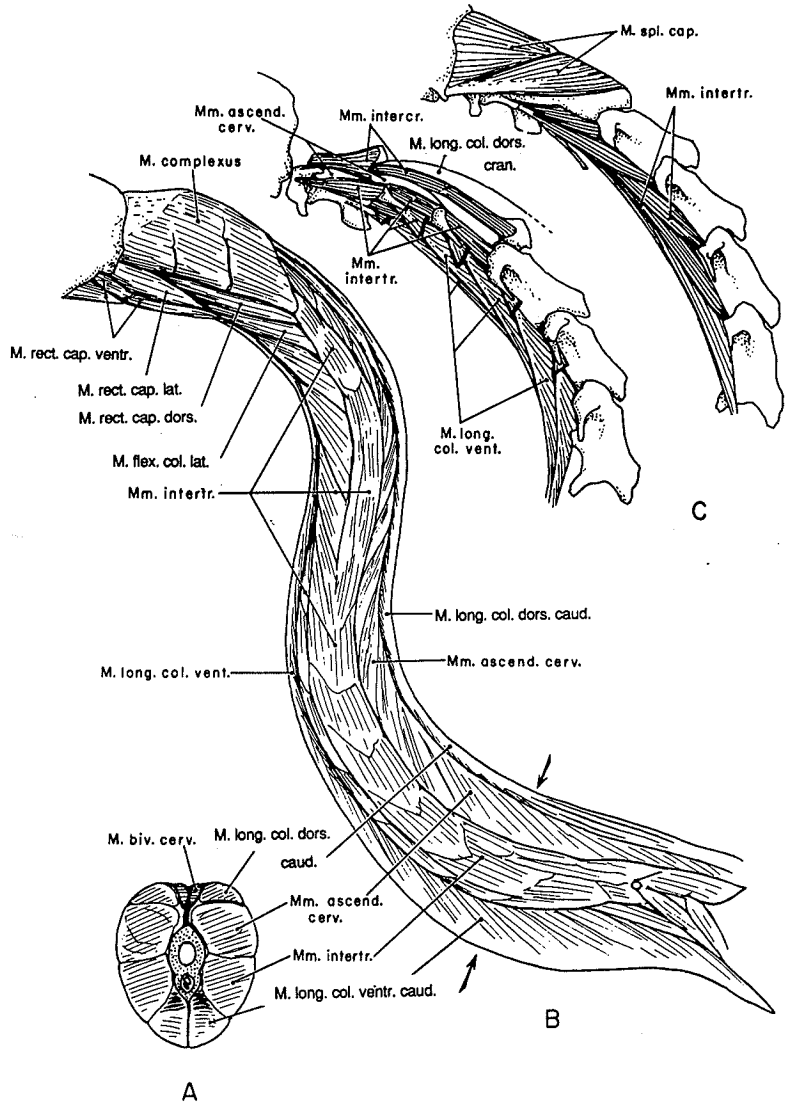

Fig. 6.9. Lateral view of the cervical muscles in a grebe, *Podilymbus podiceps*. Redrawn from Zusi and Storer (1969), with permission.

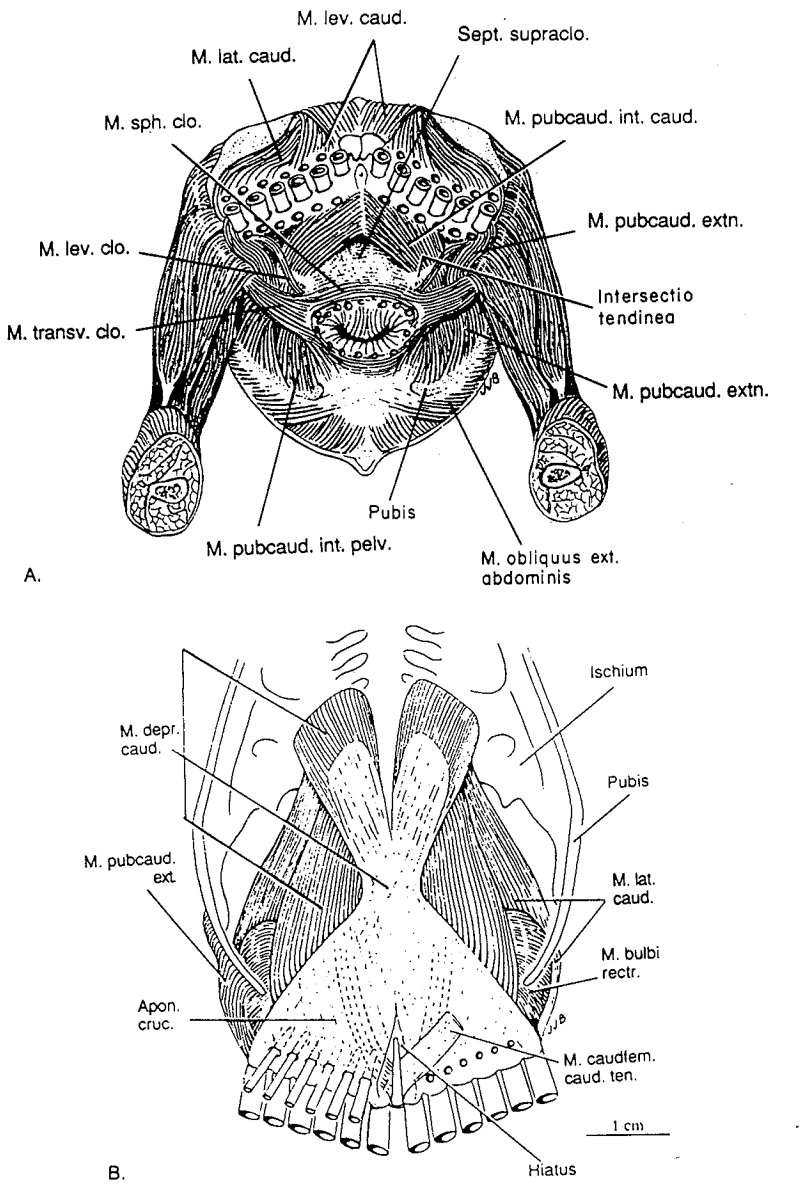

Fig. 6.10. Muscles of the tail in the pigeon, *Columba livia*. From Baumel (1988). A. caudal view. B. ventral view. Note the M. depressor caudae and Aponeurosis cruciata. With permission of Springer-Verlag, Heidelberg.

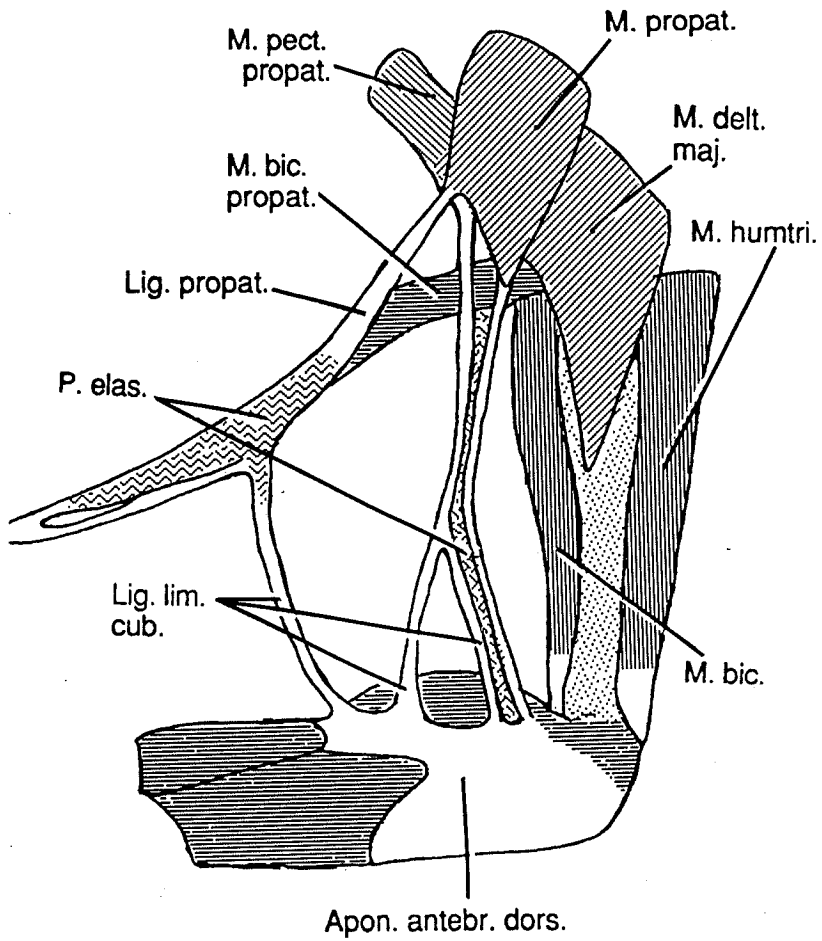

Fig. 6.11. Propatagial muscles and Lig. propatagiale of ibis, *Eudocimus albus*. Original drawings (J. C. Vanden Berge).

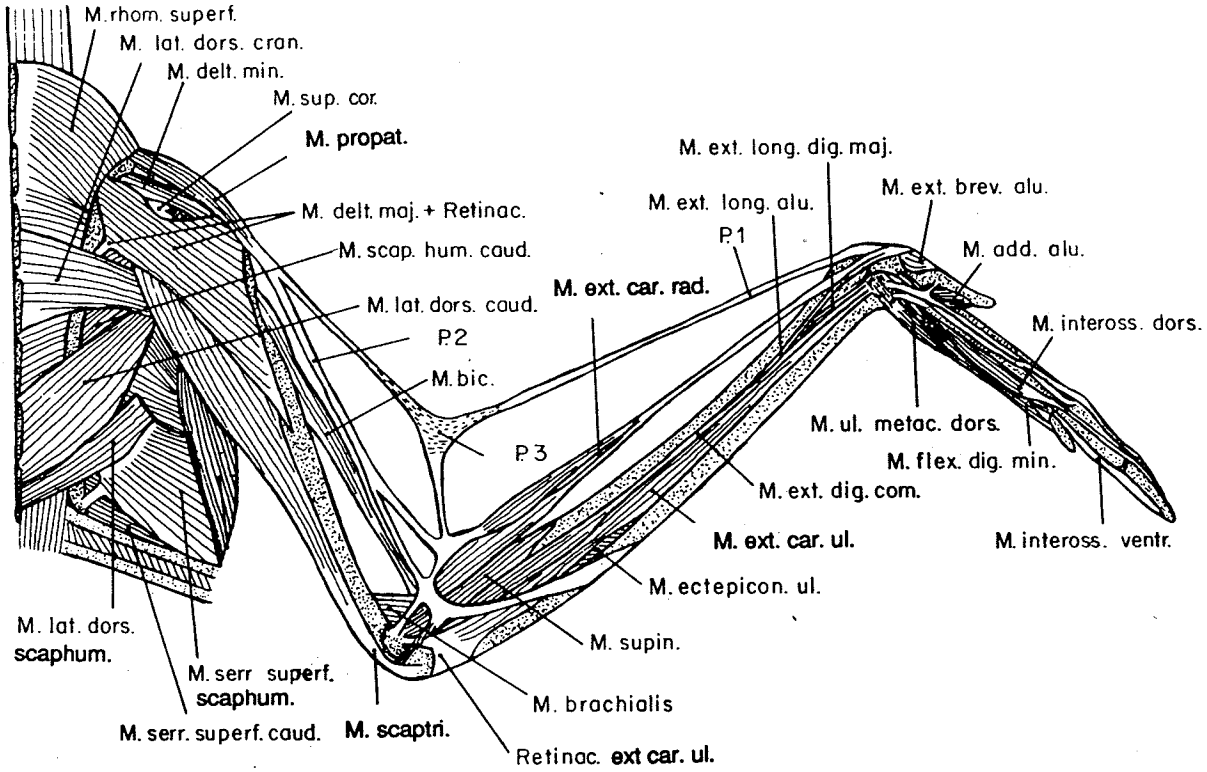

Fig. 6.12. Muscles of the wing in the night heron, *Nycticorax nycticorax;* dorsal view. From Nomina Anatomica Avium (1979), with permission of Academic Press.

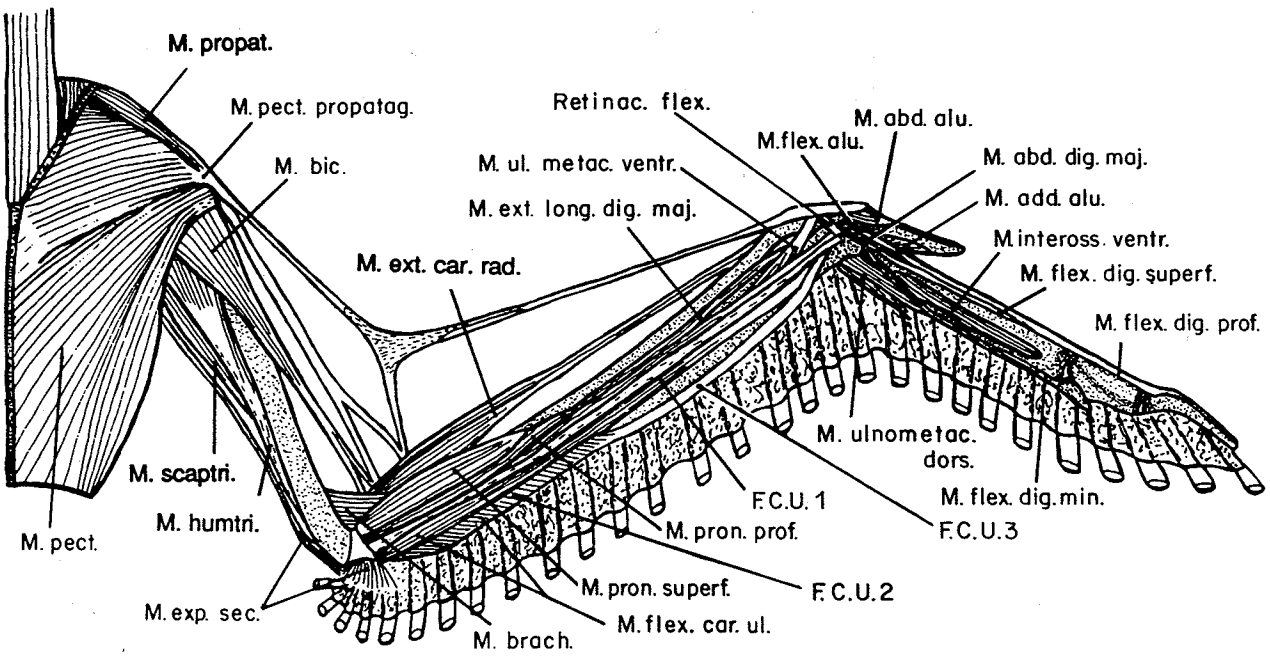

Fig. 6.13. Muscles of the wing in the night heron, *Nycticorax nycticorax,* ventral view. From Nomina Anatomica Avium (1979), with permission of Academic Press.

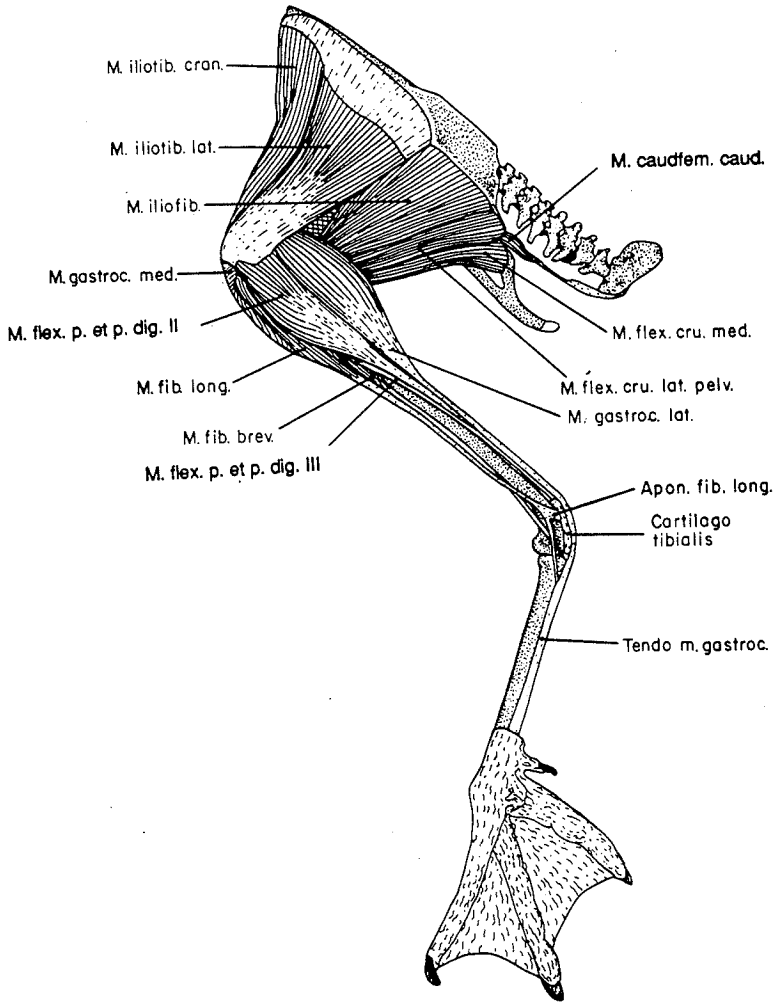

Fig. 6.14. Muscles of the pelvic limb of the gull, *Larus delawarensis*. Lateral view, superficial layer. After Hudson, et al. (1969). From Nomina Anatomica Avium (1979), with permission of Academic Press.

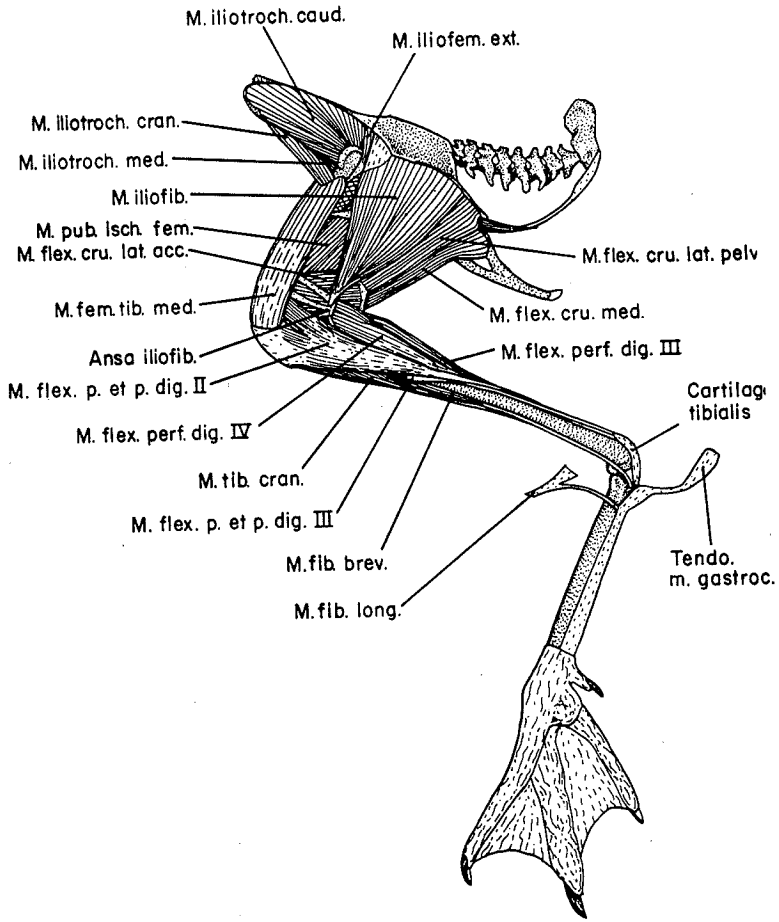

Fig. 6.15. Muscles of the pelvic limb of the gull, *Larus delawarensis*, second layer, lateral view. After Hudson, et al. (1969). From Nomina Anatomica Avium (1979), with permission of Academic Press.

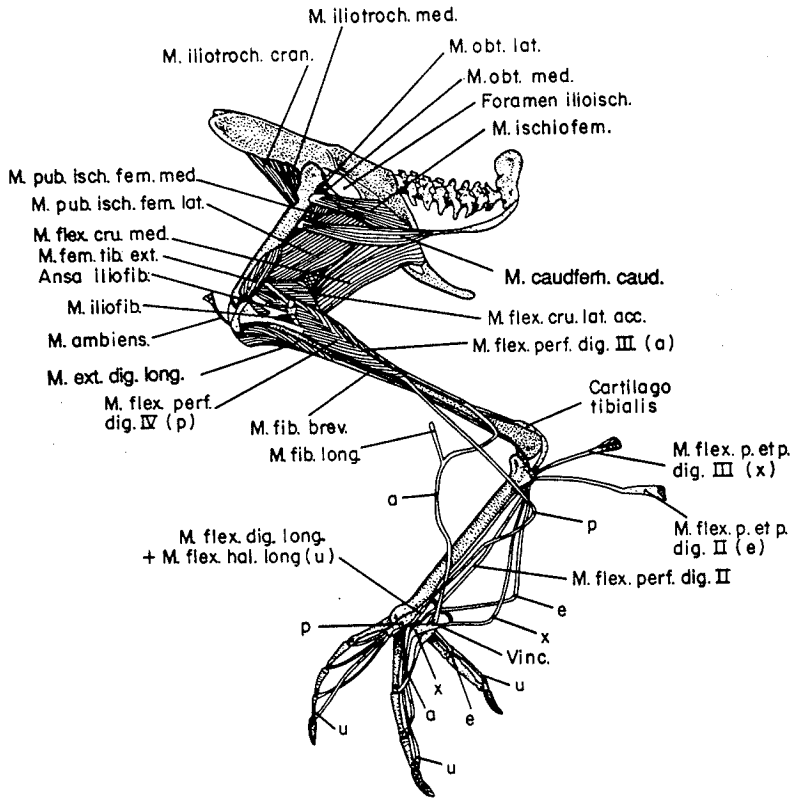

Fig. 6.16. Muscles of the pelvic limb of the gull, *Larus delawarensis*. Lateral view, third layer. After Hudson, et al. (1969). From Nomina Anatomica Avium (1979), with permission of Academic Press.

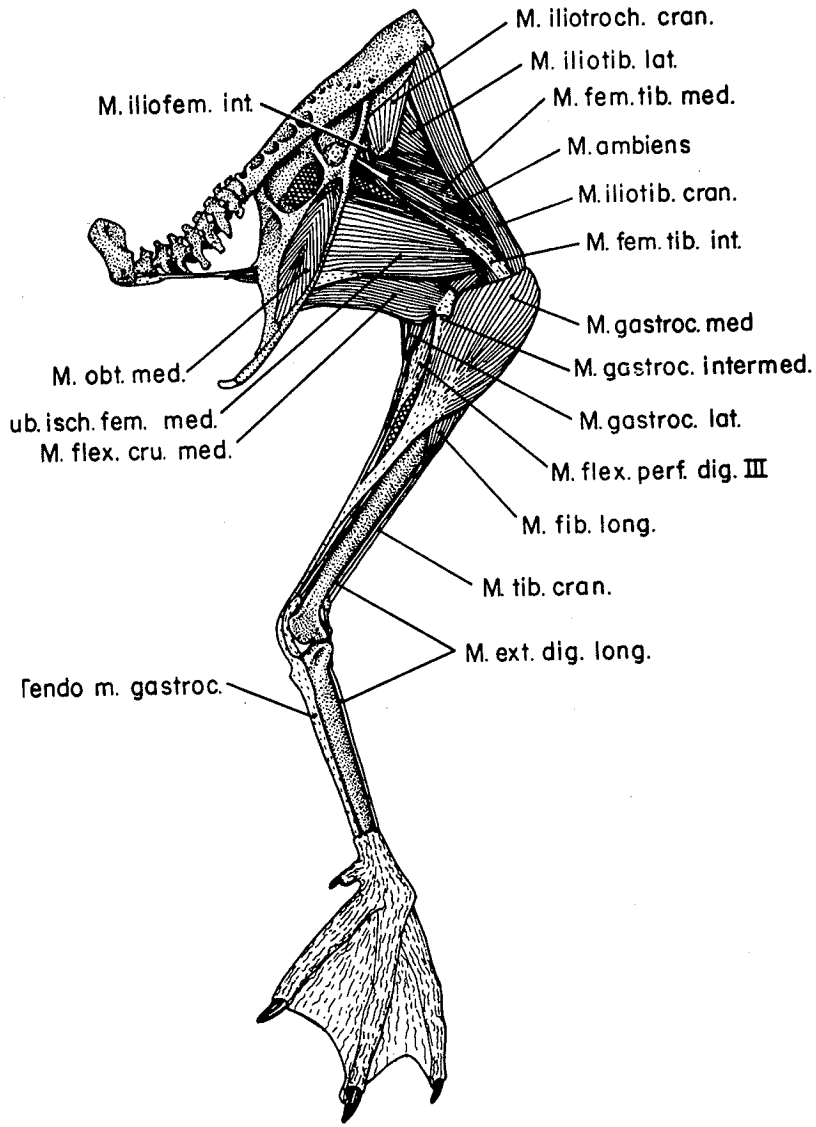

Fig. 6.17. Muscles of the pelvic limb of the gull, *Larus delawarensis*, medial view. After Hudson, et al. (1969). From Nomina Anatomica Avium (1979), with permission of Academic Press.

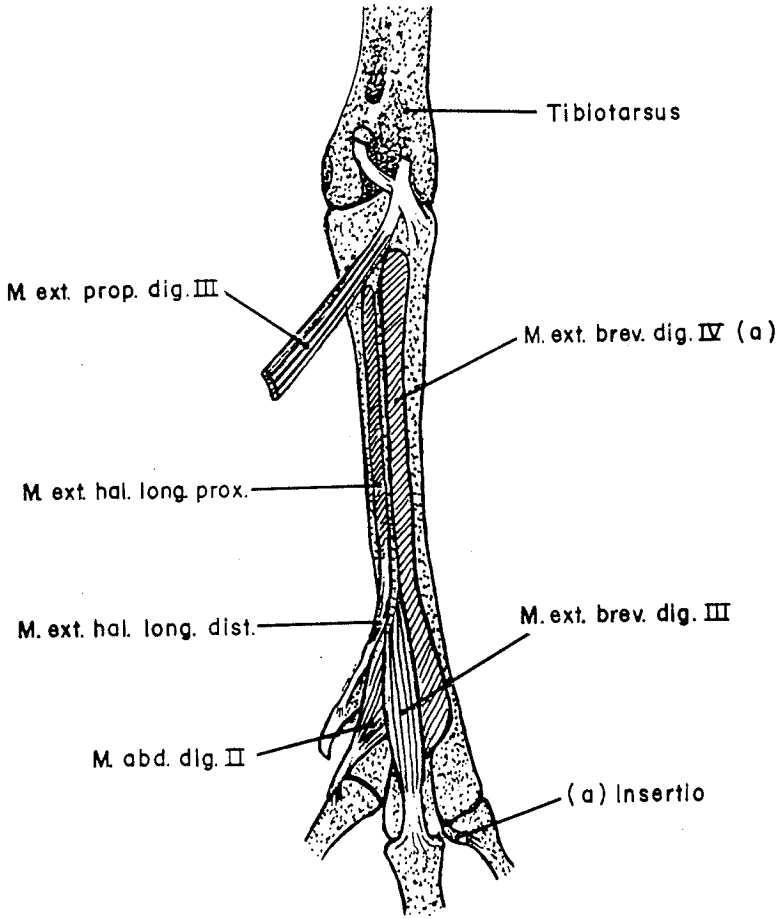

Fig. 6.18. Muscles of the foot of a tinamou, *Crypturellus tataupa*. Dorsal view. After Hudson, et al. (1972). From Nomina Anatomica Avium (1979), with permission of Academic Press.

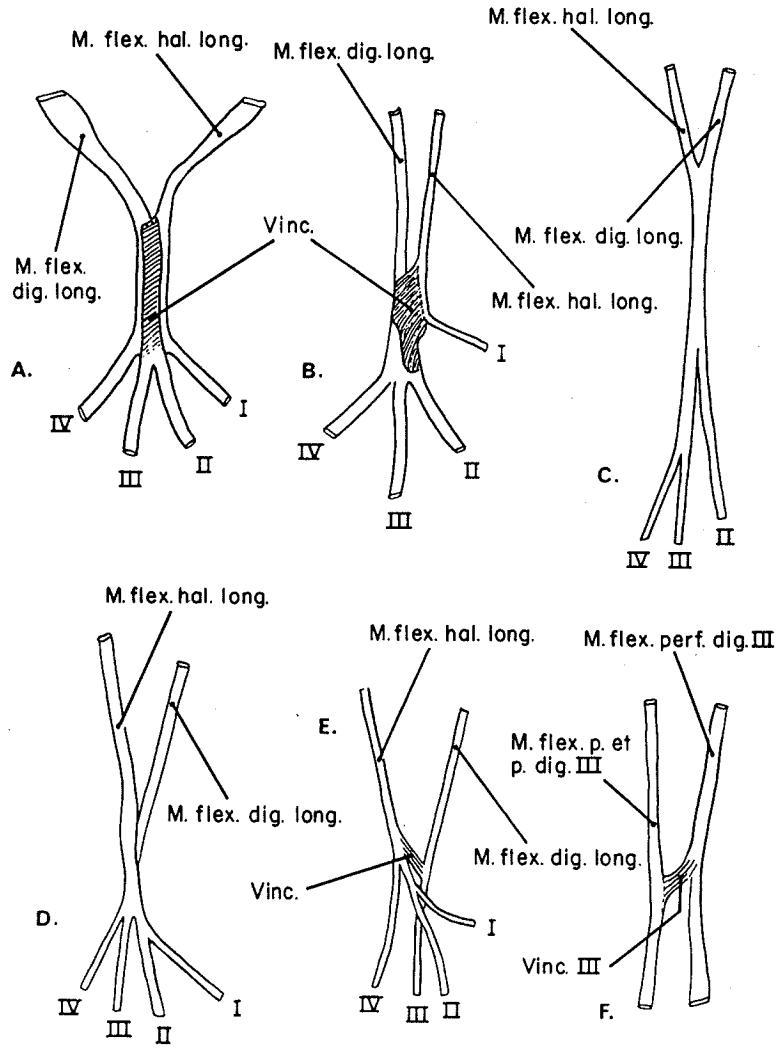

Fig. 6.19. Major types of arrangement of the deep plantar tendons in birds. After Hudson (1937). From Nomina Anatomica Avium (1979), with permission of Academic Press.

List of Abbreviations for Muscles

Abbreviation	Muscle
M. abd. alu.	M. abductor alulae
M. abd. dig. II	M. abductor digiti II
M. abd. dig. maj.	M. abductor digiti majoris
M. add. alu.	M. adductor alulae
M. add. mand. ext. rostr. ext. ventr. ext. prof.	M. adductor mandibulae externus, Pars rostralis [temporalis], Pars ventralis [medialis], and Pars profunda
M. add. mand. oss. qd.	M. adductor mandibulae ossis quadrati [caudale or posterior]
M. ascend. cerv.	M. ascendens cervicalis
M. bic./bic. propat.	M. biceps brachii/Pars propatagialis
M. biv. cerv.	M. biventer cervicis
M. brach.	M. brachialis
M. br. mand.	M. branchiomandibularis
M. bulbi rectr.	M. bulbi rectricium
M. caudofem. caud.	M. caudofemoralis, Pars caudalis
M. cergi.	M. ceratoglossus
M. clhy.	M. cleidohyoideus
M. constr. col. constr. col. intermand.	M. constrictor colli, including Pars intermandibularis
M. cuc. cap.	M. cucullaris capitis
M. delt. maj./delt. min.	M. deltoideus complex, Pars major/ Pars minor
M. depr. caud.	M. depressor caudae
M. depr. mand.	M. depressor mandibulae
M. ectepicon.	M. ectepicondyloulnaris
M. exp. sec.	M. expansor secundariorum
M. ext. brev. alu.	M. extensor brevis alulae
M. ext. brev. dig. III, IV	M. extensor brevis digiti III or IV.
M. ext. dig. com.	M. extensor digitorum communis
M. ext. dig. long.	M. extensor digitorum longus
M. ext. long. alu.	M. extensor longus alulae
M. ext. long. dig. maj.	M. extensor longus digiti majoris, Pars proximalis
M. ext. car. rad.	M. extensor carpi radialis
M. ext. car. ul., Retinac.	M. extensor carpi ulnaris, including the retinaculum
M. ext. hal. long. prox./dist.	M. extensor hallucis longus, Pars proximalis or distalis, respectively

Abbreviation	Muscle
M. ext. prop. dig. III	M. extensor proprius digiti III
M. fem. tib. lat./intermed., med.	M. femorotibialis lateralis, intermedius and medialis
M. fib. brev./fib. long.	M. fibularis brevis and M. fibularis longus, respectively
M. flex. alu.	M. flexor alulae
M. flex. car. ul.	M. flexor carpi ulnaris
M. flex. cru. lat. acc./lat.peiv.	M. flexor cruris lateralis, Pars accessoria and Pars pelvica
M. flex. cru. med.	M. flexor cruris medians
M. flex. col. lat.	M. flexor colli lateralis
M. flex. dig. long.	M. flexor digitorum longus
M. flex. dig. min.	M. flexor digiti minoris
M. flex. dig. prof.	M. flexor digitorum profundus
M. flex. dig. superf.	M. flexor digitorum superficialis
M. flex. hal. brev.,hal. long.	M. flexor hallucis brevis and flexor hallucis longus
M. flex. p. et p. dig. II, III	M. flexor perforans et perforatus digiti II and III
M. flex. perf. dig. II, III, IV	M. flexor perforatus digiti II, III and IV
M. gastroc. intermed./lat./med.	M. gastrocnemius, Pars intermedia/ Pars lateralis/Pars mediana
M. humtri.	M. humerotriceps
M. hygl. obl.	M. hyoglossus obliquus
M. hygl. rostr.	M. hyoglossus rostralis
M. iliofem. ext./int.	M. iliofemoralis externus/internus,
M. iliofib.	M. iliofibularis
M. iliotib. cran./lat.	M. iliotibialis cranialis/lateralis,
M. iliotroc. caud./cran./med.	M. iliotrochantericus caudalis/ cranialis, and medialis
M. intercr.	M. intercristalis
M. intermand. dors.,	M. intermandibularis dorsalis/ ventralis/Pars rostralis and Pars caudalis
M. inteross. dors./ventr.	M. interosseus dorsalis/ventralis,
M. intertr.	M. intertransversarius
M. ischiofem.	M. ischiofemoralis
M. lat. caud.	M. lateralis caudae
M. lat. dors. cran./caud./scaphum.	M. latissimus dorsi, Pars cranialis, Pars caudalis, Pars scapulohumeralis

Abbreviation	Muscle
M. lev. caud.	M. levator caudae
M. lev. clo.	M. levator cloacae
M. long. col. dors. cran., dors. caud.	M. longus colli dorsalis, Pars cranialis/Pars caudalis
M. long. col. ventr.	M. longus colli ventralis
M. obl. ext. abd.	M. obliquus externus abdominis
M. obl. dors., vent.	M. obliquus dorsalis and ventralis
M. obt. lat., med.	M. obturatorius lateralis and medialis, respectively
M. pect., pect. propat.	M. pectoralis/Pars propatagialis,
M. pron. superf.	M. pronator superficialis
M. propat. P.1, P.2, P.3	M. deltoideus complex, Pars propatagialis. Three portions of Lig. propatagiale, including Pars elastica
M. protr. ptyg. qd.	M. protractor pterygoidei et quadrati
M. pstem. superf./prof.	M. pseudotemporalis superficialis/ profundus
M. ptyg.	M. pterygoideus
M. pubcaud. extn.	M. pubocaudalis externus
M. pubcaud. int./caud./pelv.	M. pubocaudalis internus, Pars caudalis and Pars pelvica
M. pub. isch. fem. lat., med.,	M. pubo-ischio-femoralis lateralis/medialis
M. pyr. memb. nict. & Ten.,	M. pyramidalis membranae nictitantis and tendon of insertion
M. quad. memb. nict. & Vag.	M. quadratus membranae nictitantis and Vagina tendinis
M. rect. cap. dors., lat. ventr.	M. rectus capitis dorsalis, lateralis, and ventralis, respectively
M. rect. dors./lat./med./ventr.	M. rectus dorsalis, lateralis, medialis and ventralis
M. rhom. superf.	M. rhomboideus superficialis
M. scap. hum. caud.	M. scapulohumeralis caudalis
M. scaptri.	M. scapulotriceps
M. serr. superf. caud./scaphum.	M. serratus superficialis, Pars caudalis/Pars scapulohumeralis
M. serphy.	M. serpihyoideus
M. sph. clo.	M. sphincter cloacae
M. spl. cap.	M. splenius capitis
M. styhy.	M. stylohyoideus

Abbreviation	Muscle
M. sup. cor.	M. supracoracoideus
M. supin.	M. supinator
M. tib. cran.	M. tibialis cranialis
M. trachlat.	M. tracheolateralis
M. transv. clo.	M. transversus cloacae
M. tri. hum.	M. humerotriceps
M. ul. metac. dors.	M. ulnometacarpalis dorsalis

List of Abbreviations for Other Structures

Abbreviations	Structures
Apon. cruc.	Aponeurosis cruciata, M. depressor caudae
Apon. antebr. dors.	Aponeurosis antebrachialis dorsalis
Apon. fib. long.	Aponeurosis m. fibularis longi
Ansa iliofib.	Ansa m. iliofibularis
Esoph.	Esophagus
For. ilioisch.	Foramen ilioischiadicum
Lig. jug. mand.	Lig. jugomandibulare
Lig. lim. cub.	Lig. limitans cubiti
Lig. propat., P. elas.	Lig. propatagiale and Pars elastica
Os occ.	Os occipitale
Proc. mand. lat.	Proc. lateralis mandibulae
Proc. retroartc.	Proc. retroarticularis
Proc. supram.	Proc. suprameaticus, Os squamosum
Lig. occ. mand.	Lig. occipitomandibulare
Proc. zyg.	Proc. zygomaticus, Os squamosum
Qd.	Os quadratum
Retinac. flex.	Retinaculum flexorium
Sept. supracl.	Septum supracloacale
Vag.	Vagina tendinis or tendon sheath
Vinc.	Vinculum

7

PERICARDIUM, PLEURA ET PERITONEUM

JOHN MCLELLAND

With contributions from subcommittee members: H.-R. Duncker and A. S. King.

TERMINOLOGY

PERICARDIUM

Basis pericardii[1]
Pericardium fibrosum
  Lig. hepatopericardiacum[1]
Pericardium serosum
  Lamina parietalis
  Lamina visceralis
Cavum pericardii [Cavitas pericardialis]
  Sinus transversus pericardii

PLEURA

Pleura parietalis (Fig. 7.1)
  Septum horizontale[2]
  Mm. costoseptales[3]
Pleura visceralis [P. pulmonalis]
Cavum pleurae [Cavitas pleuralis][4]

PERITONEUM

Tunica serosa
Tela subserosa
Peritoneum parietale
  Septum obliquum[2]
  M. septi obliqui[5]
Peritoneum viscerale (Figs. 7.1, 2)
  Cavum peritonei [Cavitas peritonealis]
Cavum hepaticum peritonei [Cavitas peritonealis hepatica][6]
Cavum hepaticum ventrale peritonei [Cavitas peritonealis hepatica ventralis][6]
Cavum hepaticum dorsale peritonei [Cavitas peritonealis hepatica dorsalis][6]

(continued)

PERITONEUM (cont.)

Cavum intestinale peritonei [Cavitas peritonealis intestinalis][6]
- Lig. hepaticum[7]

Septum posthepaticum[8] (Fig. 7.2)

Mesenterium dorsale (Fig. 7.2)
- Radix mesenterii
- Mesoduodenum
- Lig. gastroduodenale[9]
- Lig. duodenohepaticum[10]
- Lig. duodenocecale[11]
- Mesojejunum
- Mesoileum
- Lig. ileocecale[12]
- Mesorectum

Mesenterium ventrale (Figs. 7.1, 2)
- Lig. falciforme hepatis
- Lig. ileodiverticulare[13]

Mesorchium

Mesovarium (Fig. 7.2)

Mesoviductus
- Lig. dorsale oviductus (**Fem.** Annot. 32)
- Lig. ventrale oviductus (**Fem.** Annot. 32)

Funiculus musculosus

ANNOTATIONS

(1) **Basis pericardii; Lig. hepatopericardiacum.** The pericardial base is the surface of the pericardial sac that rests dorsally against the bifurcation of the trachea, the esophagus, and the horizontal septum on each side. The hepatopericardial ligament is the caudal part of the fibrous pericardium which is drawn out into a pointed bilaminar sheet that becomes continuous with the part of the ventral mesentery between the hepatic lobes (*Gallus, Columba*). Wolf (1967) describes lateral pericardial ligaments that attach to the abdominal wall at the level of the caudal border of the liver.

(2) **Septum horizontale; Septum obliquum.** During development two gross partitions, one dorsal and the other ventral, are formed on each side of the body by penetration of the cranial and caudal thoracic air sacs into the pulmonary fold. The Septum horizontale (Fig. 7.1), the dorsal partition, is composed of parietal pleura. Among the many different names by which it has been referred are: diaphragme pulmonaire (Sappey, 1847:21-26); diaphragmite anterieur (Milne-Edwards, 1865); pulmonary aponeurosis (Huxley, 1882; Butler, 1889; Goodrich, 1930:633; Goodchild, 1970); horizontal septum (Beddard, 1896; 1898:37; Poole, 1909; Duncker, 1971, 1979); horizontal diaphragm (Juillet, 1912); septum pulmonale (Kern, 1963:50); bronchopleural membrane (McLelland and King, 1970); saccopleural membrane (McLelland and King, 1975).

The Septum obliquum (Fig. 7.1), the ventral partition, which consists of parietal peritoneum, has been known by various names: diaphragme-thoracoabdominal (Sappey, 1847:21-26; Juillet, 1912); diaphragmite thoracoabdominal (Milne-Edwards, 1865); oblique septum (Huxley, 1882; Beddard, 1885; 1888; 1896; 1898:38; Butler, 1889; Goodrich, 1930:633; Goodchild, 1970; Duncker, 1971, 1979); septum thoraco-abdominale (Kern, 1963:50; abdominal diaphragm (Salt and Zeuthen, 1960); bronchoperitoneal membrane (McLelland and King, 1970); saccoperitoneal membrane (McLelland and King, 1975).

Much ambiguity surrounds the terms applied to these dorsal and ventral partitions since only a few authors defined their terms precisely, e.g., Duncker (1971, 1979) restricted his terms to the serosal component of each partition; Juillet (1912) and McLelland and King (1970, 1975) explicitly included both the serosal component and the air sac component in their terms. The terms Septum horizontale and Septum obliquum are now restricted to the *serosal derivatives* in each of the two partitions, the horizontal septum being derived from the parietal pleura of the dorsal partition, and the oblique septum being derived from the parietal peritoneum of the ventral partition. The term "saccopleural membrane" has recently been used in the literature by Cook, et al. (1986a).

(3) **Mm. costoseptales.** The striated costoseptal muscles (Fig. 7.1) insert into the lateral part of the horizontal septum (Fedde, et al., 1964). See **Myol.** Annot. 61.

(4) **Cavum pleurae [Cavitas pleuralis].** A fully developed pleural cavity only occurs in early ontogeny (Duncker, 1979), and it seems likely that in all birds a certain amount of obliteration, sometimes total, of the cavity takes place during embryonic development. Nevertheless, extensive areas of cavity are known to persist in the adult in a number of taxa including *Gallus* (Groebbels, 1932:45; Kern, 1963:49-50; McLelland and King, 1975). In *Gallus* the pleural cavity is best developed on the dorsolateral aspect of the lung (Fig. 7.1) where the filaments uniting the parietal pleura to the visceral pleura are relatively delicate; in contrast the parietal and visceral pleurae on the ventromedial surface of the lung are extensively fused together.

(5) **M. septi obliqui.** The muscle of the oblique septum is nonstriated (smooth), and lies in the medial part of the oblique septum (Fig. 7.1). It is absent in certain taxa, e.g., *Apteryx* (Huxley, 1882).

(6) **Cavum hepaticum peritonei [Cavitas peritonealis hepatica]; Cavum hepaticum dorsale/ventrale peritonei [Cavitas peritonealis hepatica dorsalis/ventralis]; Cavum intestinale peritonei [Cavitas peritonealis intestinalis].** The terminology for the subdivisions of the peritoneal cavity is based on Grau (1943a). The four hepatic peritoneal cavities (Figs. 7.1, 2), right and left dorsal and right and left ventral, lie cranial and lateral to the posthepatic septum (Annot. 8).

Synonymy of the right and left dorsal hepatic cavities: pulmohepatic recesses (Butler, 1889:43; Beddard, 1889; Poole, 1909); dorsalen Bauchfellhohlen (Bittner, 1925); pulmonary recesses (Goodrich, 1930:636); Goodchild, 1970); dorsalen Leberbauchfellsacken (Kern, 1963:29). Synonymy of the right and left ventral hepatic cavities: ventral liver sacs (Butler, 1889; Poole, 1909); ventralen Bauchfellhohlen (Bittner, 1925); liver sacs (Goodrich, 1930:636); compartiments abdominaux inferieurs (Petit, 1933); ventralen Leberbauchfellsacken (Kern, 1963:29). In almost half the domestic fowl examined by Kajigaya, et al. (1987) a tunnel was present between the right and left dorsal hepatic peritoneal cavities.

Synonomy of the Cavum intestinale peritonei: posthepatic intestinal cavity (Poole, 1909); intestinal coelomic chamber (Goodrich, 1930:636; Goodchild, 1970); compartiment abdominal superieur (Petit, 1933); Eingeweidebauchfellsack (Kern, 1963:50). The intestinal peritoneal cavity (Fig. 7.2) is a midline space lying between the left and right partitions of the posthepatic septum (see Annot. 8). The left dorsal hepatic peritoneal cavity and intestinal peritoneal cavity connect with each other, but otherwise the peritoneal cavities are blind.

(7) **Lig. hepaticum.** Synonymy: pulmohepatic ligament (Butler, 1889); horizontal hepatic ligament (Goodrich, 1930:636; Goodchild, 1970; McLelland and King, 1975). Right and left hepatic ligaments (Fig. 7.1) extend between the oblique septum and the visceral peritoneum of the liver and separate the dorsal and ventral hepatic peritoneal cavities.

(8) **Septum posthepaticum.** The term posthepatic septum was used by Butler (1889) for the right and left double-layered partitions (Fig. 7.2) separating the intestinal peritoneal cavity from the hepatic peritoneal cavities. The left partition extends between the dorsolateral parietal peritoneum and the left surface of the Ventriculus (gizzard). The right partition extends between the dorsolateral parietal peritoneum and the right surface of the Ventriculus.

(9) **Lig. gastroduodenale.** A short gastroduodenal peritoneal ligament extends between the proximal part of the mesoduodenum and the posthepatic septum on the right face of the ventriculus (gizzard) (Bittner, 1924; Pilz, 1937; Grau, 1943a; Kern, 1963:17; McLelland, 1990).

(10) **Lig. duodenohepaticum.** The short duodenohepatic perjtoneal ligament extends between the proximal part of the mesoduodenum and the peritoneum on the visceral surface of the liver close to the Porta hepatis (**Digest.** Annot. 94) (Bittner, 1924; Pilz, 1937; Kern, 1963:18; McLelland (1990).

(11) **Lig. duodenocecale.** The short duodenocecal peritoneal ligament extends between the proximal part of the mesoduodenum and the mesentery near the base and body of the left cecum (McLelland, 1990).

(12) **Lig. ileocecale.** The ileocecal peritoneal ligament extends between the ileum and the mesentery close to the right cecum (McLelland, 1990).

(13) **Lig. ileodiverticulare.** The short ileodiverticular peritoneal ligament extends between the vitelline diverticulum and the ileum.

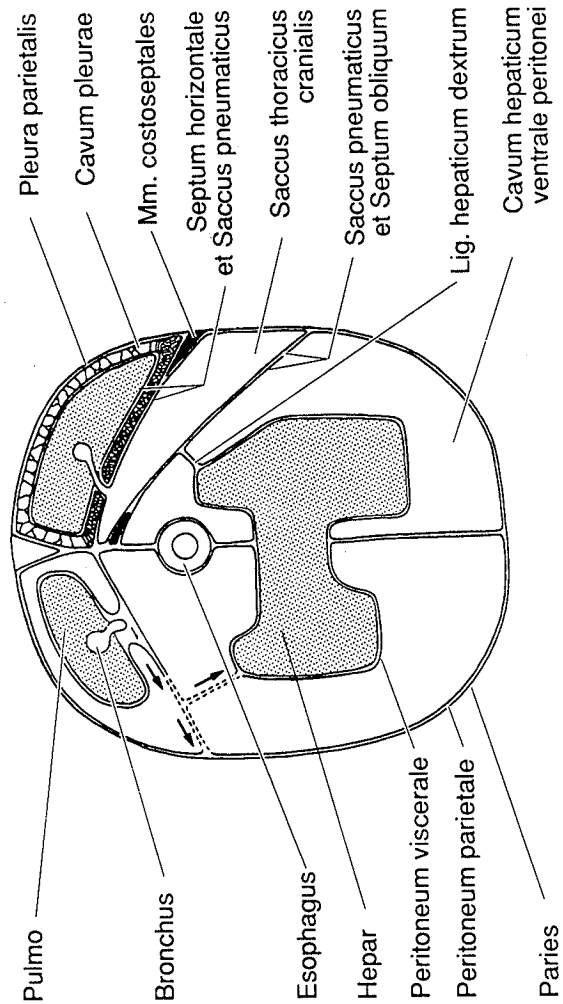

Fig. 7.1. Pleural and peritoneal cavities of *Gallus*. Schematic transverse sections through the trunk at the level of the lungs and liver (Hepar). From McLelland and King (1970), reproduced by permission of Gustav Fischer Verlag, Jena.

The left side of the figure (based on Goodrich, 1930) shows how the pleural cavity is separated from the peritoneal cavity in the embryo by extension of the pulmonary fold ventrolaterally to the lateral body wall and to the liver (dashed lines); the three *large arrows* indicate the direction in which these extensions grow. The single small arrow near the ventral end of the bronchus indicates the subsequent penetration by the air sacs. The leader labelled "Saccus pneumaticus et Septum obliquum" indicates a two layered structure: the cranial thoracic air sac plastered to the oblique septum itself (see Annot. 2). "Paries" refers to the body wall which is lined with the parietal peritoneum.

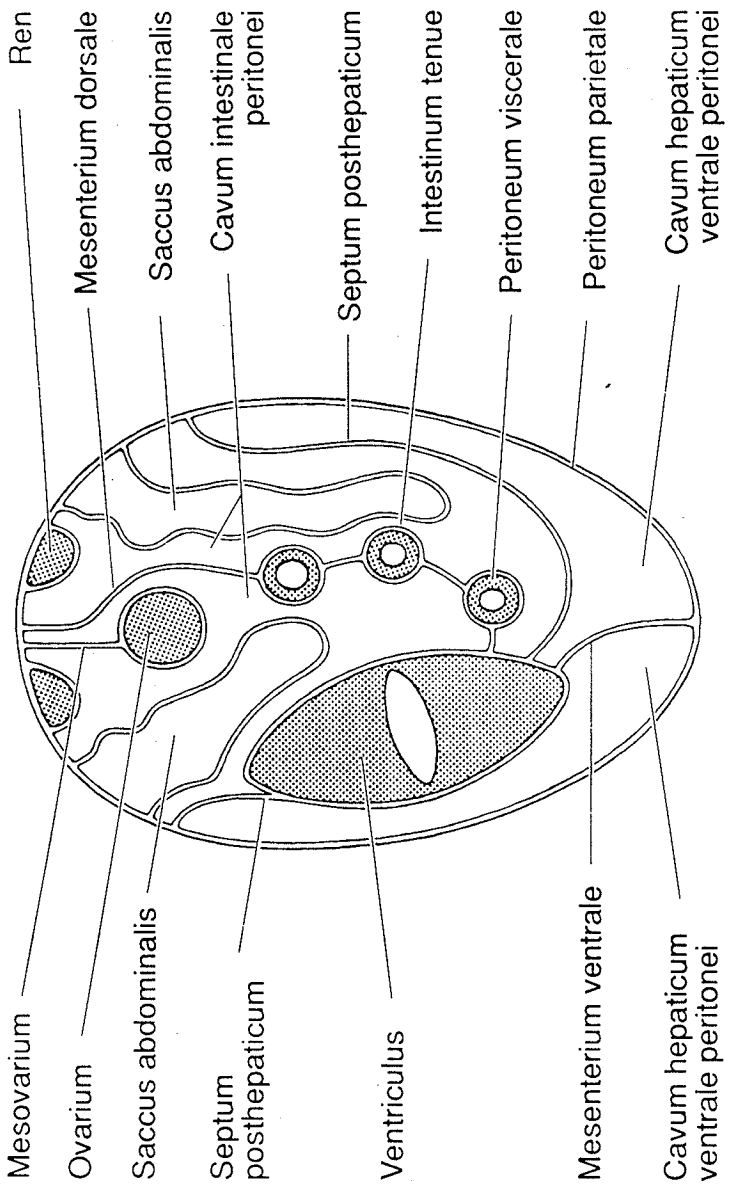

Fig. 7.2. Subdivisions of the peritoneal cavity of *Gallus*. Schematic transverse section through the trunk at the level of the ovary and Ventriculus (muscular stomach). From McLelland and King (1970), reproduced by permission of Gustav Fischer Verlag, Jena.

8

APPARATUS RESPIRATORIUS [SYSTEMA RESPIRATORIUM]

ANTHONY S. KING

With contributions from subcommittee members: A. S. Gaunt, J. N. Maina, and G. A. Zweers.

The main developments in the terminology and annotations for the Apparatus Respiratorius in this second edition of the *Nomina Anatomica Avium* relate to the muscles and joints of the Larynx, and the muscles, cartilages, and membranes of the Syrinx, by far the most difficult aspect being the muscles of these organs. This progress has been made possible by extensive original research on the larynx published during the last decade, and reviews in Vol. 4 of *Form and Function in Birds* of studies on the syrinx published during the 19th and 20th centuries. G. A. Zweers and A. S. Gaunt have made outstanding contributions on the larynx and syrinx, respectively, through both their numerous original publications and their invaluable advice and criticism during the preparation of my drafts; Zweers drafted the material on laryngeal arthrology. My thanks are due to J. N. Maina for his careful survey of the drafts. Any factual errors remaining in the Annotations are my responsibility.

Other advances in this new chapter include the completion of the terms for mesoscopic and microscopic structures, the systematic listing of vessels and nerves, and the inclusion of components of the air sacs.

I gratefully acknowledge the help of Steve Walsh, whose computer expertise made possible my operation of the word processor without which this work would not have been produced.

TERMINOLOGY

CAVUM NASI [CAVITAS NASALIS]

Naris[1]
- Operculum nasale[2]
- Lamella verticalis naris[3]

Choana (**Diges.** Fig. 1)
- Pars rostralis[4]
- Pars caudalis[5]

(continued)

CAVUM NASI [CAVITAS NASALIS] (cont.)

- Septum nasale (**Osteo.** Annot. 55)
- Concha nasalis rostralis[6]
- Concha nasalis media[7]
- Concha nasalis caudalis[8]
- Concha nasalis septalis[9]
- Meatus nasalis[10]
- Valvula nasalis[11]
- Crista nasalis[12]
- Regio vestibularis[13]
  - Epithelium stratificatum squamosum noncornificatum
- Regio respiratoria[14]
  - Tunica mucosa respiratoria[38]
    - Epithelium pseudostratificatum columnare ciliatum
      - Epitheliocytus ciliatus
      - Exocrinocytus caliciformis[38]
      - Epitheliocytus basalis
      - Glandulae mucosae
- Regio olfactoria[15]
  - Epithelium olfactorium
    - Epitheliocytus neurosensorius olfactorius
      - Dendritum
      - Cilium
      - Axon
    - Epitheliocytus sustenans
    - Epitheliocytus basalis
  - Glandula olfactoria
- Cisterna vestibularis[16]
- Sinus septalis[16]
- Sinus infraorbitalis [Sinus antorbitalis][17]
  - Sinus conchoinfraorbitalis [S. conchoantorbitalis][18]
  - Apertura sinus infraorbitalis [A.s. antorbitalis][19]
- Ostium ductus nasolacrimalis
- Glandula nasalis[20]
  - Lobus medialis[20]
    - Ductus lobi medialis
  - Lobus lateralis[20]
    - Ductus lobi lateralis
- Diverticula cervicocephalica[21]
  - Recessus pneumatici paratympanici
  - Recessus pneumatici paranasales

LARYNX

- Mons laryngealis[22]
- Cavum laryngis [Cavitas laryngealis]
  - Glottis[23]
    - Sulcus laryngealis[24]
  - Crista ventralis[26]
- Tunica mucosa respiratoria[38]
  - Epithelium pseudostratificatum columnare ciliatum
    - Epitheliocytus ciliatus
    - Exocrinocytus caliciformis[38]
    - Epitheliocytus basalis
    - Glandulae mucosae
- Cartt. laryngis [Cartt.laryngeales]
  - Cart. cricoidea
    - Proc. rostralis[25]
    - Corpus[25]
    - Ala[27]
    - Cart. cricoidea dorsalis[27]
  - Cart. procricoidea[28]
    - Corpus[28]
    - Cauda[28]
  - Cart. arytenoidea
    - Corpus
    - Proc. rostralis
    - Proc. caudalis[29]

(continued)

LARYNX (cont.)

- Juncturae laryngis [J. laryngeales][30]
  - Juncturae procricoideae[31]
    - Artc. procrico-cricoidea[31]
      - Lig. procrico-cricoideum[31]
    - Artc. procrico-cricoidea dorsalis[31]
      - Lig. procrico-cricoideum dorsale[31]
    - Artc. procrico-arytenoidea[31]
  - Juncturae arytenoideae[32]
    - Synd. aryteno-cricoidea[32]
      - Lig. aryteno-cricoideum[32]
    - Synd. aryteno-cricoidea dorsalis[32]
      - Lig. aryteno-cricoideum dorsale[32]
    - Synd. intra-arytenoidea[32]
    - Synd. interarytenoidea[32]
      - Lig. interarytenoideum caudale[32]
      - Lig. interarytenoideum rostrale[32]
  - Juncturae cricoideae[33]
    - Artc. crico-cricoidea dorsalis[33]
    - Synd. crico-cricoidea dorsalis[33]
      - Lig. crico-cricoideum dorsale[33]
    - Synd. intercricoidea[33]
    - Artc. intercricoidea dorsalis[33]
      - Lig. intercricoideum dorsale[33]
    - Lig. tracheo-cricoideum[34]
    - Lig. tracheo-cricoideum dorsale[34]
    - Synd. cricobasibranchialis[34]
      - Lig. cricobasihyale[34]
      - Lig. arytenoglossale[34]
- Mm. laryngis [Mm. laryngeales]
  - M. dilator glottidis[35]
  - M. constrictor glottidis[35]
  - M. cleidohyoideus[50]
  - M. tracheolateralis[50]
  - M. cricohyoideus dorsalis[50]
  - M. cricohyoideus ventralis[50]
  - M. tracheovalvularis[50]
  - M. hyovalvularis[50]
- Vasa Sanguinea et Nervi Laryngis
  - Aa. hyobranchiales
    - A. laryngea propria (**Art.** Annot. 33)
  - V. mandibularis
    - V. lingualis
      - V. laryngea
- N. glossopharyngeus
  - N. laryngopharyngealis (**PNS** Annot. 63)
  - N. laryngealis
    - Rr. musculares (**PNS** Annot. 63)
    - Rr. laryngotracheales (**PNS** Annot. 63)

TRACHEA

- Cartt. tracheales[36]
- Tunica mucosa respiratoria[38]
  - Epithelium pseudostratificatum columnare ciliatum
    - Epitheliocytus ciliatus
    - Exocrinocytus caliciformis[38]
    - Epitheliocytus microvillosus[38]
    - Epitheliocytus basalis
    - Endocrinocytus respiratorius[38]
    - Glandulae mucosae
- Ansa trachealis[36]
- Saccus trachealis[36]
- Bulbus trachealis[36]
- Mm. tracheales[50]
  - M. sternotrachealis[50]
  - M. tracheolateralis[50]
  - M. cleidotrachealis[50]
  - M. cleidohyoideus[50]

(continued)

TRACHEA (cont.)

Vasa Sanguinea et Nervi Tracheae
- A. carotis communis
  - A. esophagotracheobronchialis
    - R. trachealis
- A. carotis externa
  - A. trachealis descendens
- V. esophagotrachealis
  - V. trachealis descendens
- V. jugularis
  - V. trachealis descendens
  - Vv. tracheales
  - V. trachealis ascendens

N. glossopharyngeus
- N. laryngealis
  - Rr. tracheales

N. vagus
- N. recurrens
  - Rr. musculorum tracheae

N. hypoglosscervicalis
- R. cervicalis descendens (**PNS** Annot. 30)
- R. tracheosyringealis
  - Rr. tracheales (**PNS** Annot. 31)

SYRINX[37]

Cavum syringis [Cavitas syringealis]
- Tunica mucosa respiratoria[38]
  - Epithelium pseudostratificatum columnare ciliatum
    - Epitheliocytus ciliatus
    - Exocrinocytus caliciformis[38]
    - Epitheliocytus basalis
    - Glandulae mucosae
  - Epithelium simplex columnare ciliatum
  - Epithelium stratificatum squamosum noncornificatum
  - Epithelium simplex squamosum

Tympanum[39]
Bulla syringealis[40]
Cartt. syringeales
- Cartt. tracheosyringeales[41]
- Cartt. bronchosyringeales[42]
- Pessulus[43]
  - Mem. semilunaris[44]
- Cartt. accessoriae[45]
  - Cartt. membranosae
    - Cart. membranosa dorsalis[45]
    - Cart. membranosa ventralis[45]
  - Proc. vocalis[45]

Lig. interbronchiale[46]
- Foramen interbronchiale[46]

Lig. syringeale[46]
Mem. tympaniformis lateralis[47]
Mem. tracheosyringealis[47]
Mem. tympaniformis medialis[48]
Labium laterale[49]
Labium mediale[49]
Valvula syringealis[49]
Mm. syringeales[50 51]
- M. tracheobronchialis dorsalis[51]
- M. tracheobronchialis brevis[51]
- M. tracheobronchialis ventralis[51]
- M. syringealis dorsalis[51]
- M. syringealis ventralis[51]
- M. vocalis dorsalis[51]
- M. vocalis ventralis[51]
- M. obliquus ventralis[51]
- M. obliquus lateralis[51]
- M. syringealis superficialis[51]
- M. syringealis profundus[51]
- M. syringealis caudalis[51]
- M. syringealis[51]

Vasa Sanguinea et Nervi Syringis
- A. carotis communis

(continued)

SYRINX[37] (cont.)

- A. esophagotracheobronchialis
  - R. syringealis
- V. jugularis
  - V. esophagotracheobronchialis
    - Vv. syringeales

N. hypoglossocervicalis
- R. tracheosyringealis (**PNS** Annot. 31)
- R. syringealis (**PNS** Annot. 31 32)

BRONCHUS PRIMARIUS, PARS EXTRAPULMONALIS[52]

Cartt. bronchiales[52]
- Memm. interanulares[52]

Lig. bronchiale mediale[52]
Tunica mucosa respiratoria[38]
- Epithelium pseudostratificatum columnare ciliatum
  - Epitheliocytus ciliatus
  - Exocrinocytus caliciformis[38]
  - Epitheliocytus basalis
  - Endocrinocytus respiratorius[38]
  - Glandulae mucosae

PULMO

Neopulmo[57]
Paleopulmo[57]
Facies costalis[53]
Facies vertebralis[53]
Facies septalis[53]
Sulci costales[54]
Tori pulmonales[54]
- Tori intercostales[54]
- Tori marginales[54]
  - Torus marginalis cranialis
  - Torus marginalis caudalis

Margo costovertebralis[55]
Margo costoseptalis[55]
Margo vertebroseptalis[55]
Margo cranialis[55]
Margo caudalis[55]
Angulus craniodorsalis[55]
Angulus caudodorsalis[55]
Angulus cranioventralis[55]
Angulus caudoventralis[55]
Hilus pulmonalis
Planum anastomoticum[56]
- Linea anastomotica[56]

BRONCHUS PRIMARIUS, PARS INTRAPULMONALIS[58]

Tunica mucosa respiratoria[38]
- Epithelium pseudostratificatum columnare ciliatum
  - Epitheliocytus ciliatus
  - Exocrinocytus caliciformis[38]
  - Epitheliocytus basalis
  - Endocrinocytus respiratorius[38]
  - Glandulae mucosae

Bronchi secundarii[59]
- Bronchi medioventrales[60]
- Bronchi mediodorsales[61]
- Bronchi lateroventrales[62]
- Bronchi laterodorsales[63]
  - Epitheliocytus cuboideus[38]
  - Epitheliocytus squamosus[38]

(continued)

BRONCHUS PRIMARIUS, PARS INTRAPULMONALIS[58] (cont.)

Parabronchus[64]
  Epitheliocytus squamosus[38]
Atrium[65]
  Epitheliocytus squamosus[38]
  Epitheliocytus granularis[69]
  M. atrialis[66]
  Septum interatriale[67]
Infundibulum[68]
  Epitheliocytus squamosus[38]
Pneumocapillaris[71] (Fig. 22)
  Epitheliocytus respiratorius[72]
Septum interparabronchiale[70]
Ostium[73]

  Saccobronchus[74]
Vasa Sanguinea et Lymphatica et Nervi Pulmonis
  Arteria pulmonalis (**Art.**)
    Rr. cranialis/caudomedialis/caudolateralis/accessorius
      Aa. interparabronchiales[75]
        Arteriolae intraparabronchiales[75]
  A. carotis communis
    A. esophagotracheobronchialis
      R. bronchialis[75]
  V. pulmonalis (**Ven.**)
  Rdxx. cranialis/caudomedialis/caudolateralis
    Vv. interparabronchiales[75]
      Vv. intraparabronchiales[75]
        Vv. atriales[75]
        Venulae septales[75]
        Venulae intraparabronchiales[75]
      Vv. bronchiales[75]
      V. esophagotrachealis
        V. esophagealis
        Vv. bronchiales[75]
Truncus thoracoabdominalis
  Vasa l. thoracica interna (**Lym.** Annot. 27)
    Vasa l. pulmonalia superficialia
  Vas l. pulmonale commune (**Lym.** Annot. 29)
    Vas l. pulmonale profundum dextrum
    Vas l. pulmonale profundum sinistrum
N. vagus
  Rr. pulmonales (**PNS** Annot. 70)
  N. recurrens
    Rr. bronchiales
    N. pulmoesophagealis (**PNS** Annot. 79)
      R. pulmonalis
        Plexus pulmonalis

SACCI PNEUMATICI[76]

Saccus cervicalis[77]
  Diverticula vertebralia[78]
  Diverticula intermuscularia[79]
  Diverticula subcutanea[80]
Saccus clavicularis[81]
  Pars medialis[82]
  Pars lateralis[82]
Diverticula intrathoracica[83]
  Diverticula cardiaca[83]
  Diverticula sternalia[83]
Diverticula extrathoracica[84]
  Diverticulum subscapulare[84]
    Diverticula subcutanea[84]
  Diverticulum axillare[84]

(continued)

SACCI PNEUMATICI[76] (cont.)

    Diverticulum humerale
    Diverticula subcutanea
  Diverticulum subpectorale
    Diverticula subcutanea
  Diverticulum suprahumerale
Saccus thoracicus cranialis[85]
Saccus thoracicus caudalis[85]
Saccus abdominalis[86]
  Diverticula perirenalia[87]
  Diverticula femoralia[87]
Ossa pneumatica[88] (**Osteo.** Annot. 23 88)
  Foramen pneumaticum[89]
  Pori pneumatici[89]

ANNOTATIONS

(1) **Naris.** The external aperture of the Cavum nasi. Terms for the form of the nostril are: Nares gymnorhinales, exposed nares; Nares perviae, open nares as in most birds; Nares imperviae, nares closed secondarily by growth of the horny beak as in some pelecaniforms, though these species breathe by secondary nares at the angle of the mouth (MacDonald, 1960). In sulids even the bony aperture is closed (Thompson, 1964:505; **Topog.** Annot. 21). Terms for the shape of the bony aperture (taxonomically significant) are: holorhinal, caudal margin rounded; schizorhinal, caudal margin a slit; amphirhinal, two bony openings on each side.

(2) **Operculum nasale.** The nasal operculum (Fig. 8.1a) is a horny flap dorsal to the nares in *Gallus* and some other species (Bang, 1971), and ventral to the nares in wrynecks (*Jynx*) (Bang and Wenzel, 1985:200) (**Topog.** Annot. 21).

(3) **Lamella verticalis naris.** Synonymy: Atrial concha (Bang, 1971). The vertical lamella of the nostril (Fig. 8.1a) is a cartilaginous sheet arising from the ventral border of the Naris in *Gallus* (Bang, 1971; King, 1975:1886) and a few other species e.g., members of Apodiformes and *Turnix* (Bang, 1971).

(4) **Choana, Pars rostralis.** A narrow rostral slit, possibly homologous to the median palatine suture of mammals (Heidrich, 1908).

(5) **Choana, Pars caudalis.** Synonymy: interpalatine cleft, Choana I (Lucas and Stettenheim, 1972: Fig. 362). The triangular opening, caudal to the maxillopalatine processes, between the palatine bones, and divided dorsally in the midline by the Vomer and Septum nasale (see **Osteo.** Fig. 4.7). Possibly homologous to the mammalian Choanae.

(6) **Concha nasalis rostralis.** Synonymy: Concha ventralis. Rostralis is preferred because in birds with a long nasal cavity (e.g., *Hydrophasianus;* Bang, 1971), there is no room for a ventrodorsal relationship between the conchae. The rostral nasal concha (Fig. 8.1a) varies in form and is sometimes absent as in Sulidae (Bang, 1971).

(7) **Concha nasalis media.** Synonymy: maxillary concha (Bang, 1971); maxilloturbinal (Bellairs and Jenkin, 1960:285). Maxillary implies homology to the maxillary concha of mammals and other vertebrates, but this is uncertain and, therefore, the topographical term, middle nasal concha, is preferred. Its form varies (Fig. 8.1b). It is absent in very few birds, among them certain phalacrocoracids (Bang and Wenzel, 1985:203).

(8) **Concha nasalis caudalis.** Probably homologous with the single Concha of most reptiles (Bellairs and Jenkin, 1960:285). Very variable in form (Fig. 8.1c). In *Gallus* the caudal nasal concha is a hollow dome, its only exit being to the infraorbital [antorbital] sinus. It is typically covered with olfactory epithelium, and has a relatively great surface area in the highly olfactory *Apteryx* and *Pagodroma.* It is absent in only a few taxa, e.g., *Sula,* and *Collocalia* (Bang, 1971), and *Psittacus* (Pohlmeyer and Kummerfeld, 1989). In *Collocalia* the roof of the nasal cavity has an extensive olfactory epithelium (Bang and Wenzel, 1985; **Osteo.** Fig. 4.11).

(9) **Concha nasalis septalis.** Unique to petrels (e.g., *Pagodroma*), the septal nasal concha arises from the Septum nasale and interdigitates with the Concha nasalis caudalis (Fig. 8.1c), its epithelium being olfactory (Bang, 1971).

(10) **Meatus nasalis.** The airway between the Conchae and the nasal walls (Figs. 8.1b, c). Since the three Conchae nasales lie in a rostrocaudal series, the mammalian terms, Meatus nasi dorsalis, medius, and ventralis are inapplicable.

(11) **Valvula nasalis.** The nasal valve is a paired crescentic mucosal fold attached to the Septum nasale or to the adjoining roof of the nasal cavity, level with the caudal end of the Concha media. Occurs in all water-feeding and diving birds with patent nostrils except *Cinclus,* and in a few land species. It is forced into position by water pressure and then passively deflects water from the Regio olfactoria (Bang and Wenzel, 1985:205).

(12) **Crista nasalis.** Synonymy: Schwelle. The nasal crest is a ridge between the vestibular and respiratory regions in birds generally, but reduced or lacking in some species (Bang, 1971). It directs inspired air to the most rostral extension of the olfactory membrane (Bang and Wenzel, 1985:201).

(13) **Regio vestibularis.** Synonymy: nasal vestibule (Bang, 1971); vestibular zone, anterior zone (Sandoval, 1964). The vestibular region contains the Concha nasalis rostralis when this concha is present; it is lined by stratified squamous epithelium, and receives the secretion of the Glandula nasalis. It warms and humidifies the inspired air (Bang and Wenzel, 1985:200).

(14) **Regio respiratoria.** Synonymy: middle or respiratory area of Bang (1971) and Sandoval (1964). The respiratory region of the nasal cavity contains the Concha nasalis media. Its mucociliary epithelium is the primary defence against infection of the lower respiratory tract (Bang and Wenzel, 1985:203).

(15) **Regio olfactoria.** Synonymy: olfactory chamber (Bang, 1971); inner zone (Sandoval, 1964). The olfactory region contains the Concha nasalis caudalis and is lined by olfactory epithelium.

(16) **Cisterna vestibularis.** The vestibular cistern is a trough on the floor of the Regio vestibularis in many species. It catches secretion of the Glandula nasalis, thus humidifying the inspired air (Bang and Wenzel, 1985:200).

Sinus septalis. The septal sinus (Fig. 8.1b) consists of bony spaces in the Septum nasale which are continuous with the nasal cavity, occurring in a few species such as *Rhea* (Bang, 1971).

(17) **Sinus infraorbitalis [Sinus antorbitalis].** Synonymy: orbital sac; subocular sac (Romanoff, 1960:537; Bellairs and Jenkin, 1960:290); maxillary sinus (Bang, 1971). The term "infraorbital sinus" is widely used in veterinary literature, the sinus being often infected. In *Cacatua Ara,* and *Amazona* the sinus has a capacious

extension into the upper beak, a transverse canal connecting the left and right sinuses, and a paired blind-ending cervical diverticulum (Pohlmeyer and Kummerfeld, 1989). The alternative term, Sinus antorbitalis, arises from homology with archosaurian reptiles and is widely used in paleontology (**Osteo.** Annot. 9).

(18) **Sinus conchoinfraorbitalis [S. conchoantorbitalis].** The conchoinfraorbital sinus occurs in the many species (e.g., *Gallus)* in which the Sinus infraorbitalis connects with the interior of the Concha nasalis caudalis (Bang, 1971).

(19) **Apertura sinus infraorbitalis [A.s antorbitalis].** The opening of the Sinus infraorbitalis into the Cavum nasi.

(20) **Glandula nasalis; Lobus medialis; Lobus lateralis.** Synonymy: supraorbital gland (Beddard, 1898); salt gland. The nasal gland secretes salt in marine birds and in some desert species and raptors, but not in the large majority of terrestrial species (Peaker and Linzell, 1975:220). Therefore salt gland is not appropriate in birds generally. Typically there is an independent Lobus lateralis and medialis (Technau, 1936). In *Gallus,* and closely related forms, only the Lobus medialis is present (Marples, 1932). See **Osteo.** Annot. 15.

(21) **Diverticula cervicocephalica.** Diverticula pneumatizing the skull, and sometimes other parts of the head and neck (Bignon, 1889; Groebbels, 1932:59; Coe, 1960; Bellairs and Jenkins, 1960:290; Romanoff, 1960:537; King, 1966:217). The cervicocephalic diverticula that invade the skull come from both the tympanic cavity and the nasal cavity (**Osteo.** Annot. 23,25). The cervical diverticulum of the psittacid infraorbital sinus (Annot. 17) is included; this extends as paired sacs nearly enclosing the vertebral column, surrounding the crop, and resting like a saddle over the shoulders (Walsh and Mays, 1984). In some birds, e.g., *Leptoptilos,* there are apparently major connexions between the nasal cavity and the air pouches of the neck (Coe, 1960; Akester, et al., 1973) (which are examples of Sacci protrudentes (**Topog.** Annot. 28), and **Osteo.** Annot. 9, 23.

(22) **Mons laryngealis.** The conspicuous laryngeal mound carrying the opening into the larynx (Fig. 9.1).

(23) **Glottis.** The slit-like opening into the Cavum laryngis (Fig. 9.1). There were many synonyms in the early literature (White, 1970:7), but this term is now used in amphibians and reptiles as well as birds (e.g., Marshall, 1962:403, 478, 585; Bock, 1978).

(24) **Sulcus laryngealis.** The prominent laryngeal sulcus, continuing the glottis caudally. Present in *Anser* and *Gallus* (White, 1970:8; 1975:1891), and *Corvus brachrhynchos* (Bock, 1978).

(25) **Proc. rostralis; Corpus.** The rostral process and body of the cricoid cartilage (Fig. 8.3). Incomplete, fused tracheal cartilages are attached ventrocaudally to the body in *Columba* (Zweers, et al., 1981) and *Corvus* (Bock, 1978; White, pers. comm.).

(26) **Crista ventralis.** Synonymy: Proc. cricoideus medianus (Zweers and Berkhoudt, 1987). A median ossified ridge projecting dorsally from the Corpus of the Cart. cricoidea in *Apteryx,* Spheniscidae, *Anas, Gallus,* and *Corvus* (White, 1975:1892; Zweers and Berkhoudt, 1987; McLelland, 1989:72).

(27) **Ala; Cart. cricoidea dorsalis.** In Accipitridae and *Gallus* (Fig. 8.3) each paired Ala (cricoid wing) is a cartilaginous plate attached dorsolaterally to the Corpus of the Cart. cricoidea by a strip of flexible cartilage; in *Fulica* and *Pica* attachment is

by a bony suture (see McLelland, 1989:72). In *Corvus corax, C. orru and C. brachyrhynchos* (Shufeldt, 1890:Fig. 10; White, pers. comm.; Bock, 1978) the Ala is represented by a separate, fully ossified, rod-like Cart. cricoidea dorsalis (Figs. 8.4, 7). In *Corvus corone* and *C. monedula* the dorsal cricoid cartilage is not totally separate, but rostrally has a small cartilaginous connexion to the rest of the cricoid cartilage (Zweers and Berkhoudt, 1987). The partial or complete separation of the dorsal cricoid cartilage may make the passeriform larynx more mobile, justifying a functional distinction between passeriform and non-passeriform larynges (Zweers and Berkhoudt, 1987).

(28) **Cart. procricoidea.** The small median procricoid cartilage intervenes between the two arytenoids, and between the two cricoid alae (Figs. 8.3, 6) or between the two dorsal cricoid cartilages (Figs. 8.4, 7). In *Gallus* (White, 1970; 1975:1892) and *Columba* (Zweers, et al., 1981) it is comma-shaped with a bony body (corpus) and a cartilaginous tail (cauda) (Fig. 8.2). In *Corvus* species (Fig. 8.4) it has no tail and is cuboidal (Bock, 1978; White, pers. comm.) or almost spherical (Zweers and Berkhoudt, 1987). According to White (1970:12) the term Cart. procricoidea was adopted by most earlier authors, but others regarded it as a part of the cricoid cartilage.

(29) **Proc. caudalis.** Synonymy: dorsal arytenoid (Bock, 1978). The caudal process of the arytenoid cartilage is variable, or even absent as in ratites and penguins (see McLelland, 1989:74). It forms a separate dorsal arytenoid cartilage in *Corvus brachyrhynchos* (Bock, 1978) as shown on the left side of Fig. 8.7, but not in *Corvus orru* and *C. corax* (White, pers. comm.) or in *C. monedula* and *C. corone* (Zweers and Berkhoudt, 1987).

(30) **Juncturae laryngis [J. laryngeales].** There are four groups of articular structures of the larynx: (1) procricoid joints; (2) arytenoid joints; (3) cricoid joints; and (4) extrinsic structures. Most of the laryngeal joints occur in all species studied, but in passerines the independent Cart. cricoidea dorsalis produces six additional joints (Zweers and Berkhoudt, 1987), all with names ending in "dorsalis". The terms are hyphenated to distinguish the two osteological constituents. For review see McLelland (1989:72-76).

(31) **Juncturae procricoideae.** The Cart. procricoidea articulates with the Cart. cricoidea and Cart. arytenoidea.

Artc. procrico-cricoidea. Synonymy: Artc. cricoprocricoidea (Zweers, et al., 1981). A synovial procrico-cricoid joint (Fig. 8.2) appears to be typical in nonpasserine species (spheniscids, Watson, 1883:201; *Eudocimus albus*, Baumel, pers. comm.; *Gallus*, White, 1975), but in *Columba* it is a syndesmosis, the elements connected by the **Lig. procrico-cricoideum** (Fig. 8.6). **Artc. procrico-cricoidea dorsalis.** This synovial joint (Fig. 8.4) occurs in corvids between the procricoid and the dorsal cricoid cartilage (Bock, 1978; Zweers and Berkhoudt, 1987), being the homologue of the nonpasserine Artc. procrico-cricoidea. The joint is supported by the **Lig. procrico-cricoideum dorsale** (Fig. 8.7).

Artc. procrico-arytenoidea. Synonymy: Artc. arytaenoprocricoidea (Zweers and Berkhoudt, 1987). A synovial procrico-arytenoid joint (Figs. 8.2, 4, 6, 7) occurs in spheniscids (Watson, 1883:202), *Gallus* (White, 1975:1893), *Columba* (Zweers, et al., 1981), and several corvids (Bock, 1978; Zweers and Berkhoudt, 1987).

(32) **Juncturae arytenoideae.** The Cart. arytenoidea articulates with the Cart. procricoidea (Annot. 31), with the Ala of the Cart. cricoidea or with the homologous Cart. cricoidea dorsalis, and within its own components.

Synd. aryteno-cricoidea. Synonymy: Artc. arytaenocricoidea (Zweers and Berkhoudt, 1987); Artc. cricoarytenoidea (NAA, 1979; McLelland, 1989:73). An aryteno-cricoid syndesmosis is formed in nonpasserines (spheniscids, Watson, 1883:202; *Gallus*, White, 1975:1892; *Columba*, Zweers, et al., 1981; *Strix*, Baumel, pers. comm.), and corvids (Zweers and Berkhoudt, 1987), where the body of the arytenoid lies along the body and (in nonpasserines) the wing of the cricoid cartilage. The two cartilages are held together by the **Lig. aryteno-cricoideum** (Figs. 8.6, 7).

Synd. aryteno-cricoidea dorsalis. In corvids, the preceding syndesmosis is continued caudally by this additional syndesmosis, which is formed between the body of the arytenoid cartilage and the dorsal cricoid cartilage by the **Lig. aryteno-cricoideum dorsale** (Fig. 8.7) (Zweers and Berkhoudt, 1987).

Synd. intra-arytenoidea. The intra-arytenoid syndesmosis (Fig. 8.7) is a fibrous joint between the body and caudal process of the arytenoid cartilage in *Corvus brachyrhynchos* (Bock, 1978), but not in *C. corax* and *C. orru* (S. S. White, pers comm.) or *C. corone* and *C. monedula* (Zweers and Berkhoudt, 1987). See Annot. 29.

Synd. interarytenoidea. In *Strix varia* the caudal ends of the left and right Corpora arytenoidea articulate directly by fibrous tissue (see next paragraph), the interarytenoid syndesmosis (Baumel, pers. comm.).

Lig. interarytenoideum caudale. Synonym: arytenoarytenoid ligament (White, 1975:1893). In *Gallus* (White, 1975) and *Columba* a strong unpaired caudal interarytenoid ligament (Fig. 8.6) joins the caudal ends of the left and right arytenoid cartilages (Zweers, et al., 1981). Presumably this ligament is the homologue of the fibrous tissue of the Synd. interarytenoidea.

Lig. interarytenoideum rostrale. Synonymy: Lig. intracricoideum rostrale (Zweers and Berkhoudt, 1987). In certain corvids the rostral tips of the arytenoid cartilages are connected (Fig. 8.7) by a sheet of elastic fibres (Zweers and Berkhoudt, 1987).

(33) **Juncturae cricoideae.** The Cart. cricoidea articulates with the Cart. arytenoidea (Annot. 32), with the Cart. cricoidea dorsalis in passerines, and within its own components.

Art. crico-cricoidea dorsalis. Synonymy: Artc. intracricoidea (Bock, 1978; NAA, 1979; McLelland, 1979:72). The term Art. crico-cricoidea dorsalis comes from Zweers and Berkhoudt (1987). Since it specifies the two components (Fig. 8.7), it is preferred to the synonym. This synovial joint was recorded in several corvids (Bock, 1978; White, pers. comm.; Zweers and Berkhoudt, 1987), but note the direct cartilaginous connection mentioned in Annot. 27.

Synd. crico-cricoidea dorsalis. A syndesmosis in corvids between the caudal end of the body of the cricoid cartilage and the dorsal cricoid cartilage, formed by the **Lig. crico-cricoideum dorsale** (Fig. 8.7) (Zweers and Berkhoudt, 1987).

Synd. intercricoidea. In *Strix varia* (Baumel, pers. comm.), though not *Columba* (Zweers, et al., 1981), the caudal tips of the left and right Alae cricoideae articulate directly in the midline.

Artc. intercricoidea dorsalis. A synovial joint in corvids formed by contact in the midline of the caudal tips of the dorsal cricoid cartilages, bound by a strong **Lig. intercricoideum dorsale** (Fig. 8.7) (Zweers and Berkhoudt, 1987). This joint is the homologue of the preceding joint.

(34) **Lig. tracheo-cricoideum; Lig. tracheo-cricoideum dorsale; Synd. cricobasibranchialis; Lig. cricobasihyale; Lig. arytenoglossale.** The Ligg. tracheocricoideum and tracheo-cricoideum dorsale (synonym: Ligg. annulo trachealis cricoideum and annulo trachealis cricoideum dorsale, Zweers and Berkhoudt, 1987) connect the first three tracheal cartilages with the caudal border of the cricoid and dorsal cricoid cartilages in corvids (Fig. 8.6) (Zweers and Berkhoudt, 1987). In *Columba* and *Strix varia* the urohyal element of the hyoid bone is connected to the ventral surface of the body of the cricoid cartilage by fibrous tissue, forming the Synd. cricobasibranchialis (Baumel, 1979:145). In some corvids an (elastic) cricobasihyal ligament (Lig. cricobasihyale, synonym: Lig. hyocricoideum of Zweers and Berkhoudt, 1987) connects the Crista dorsalis of the basihyal to the dorsal surface of the cricoid cartilage. The Lig. arytenoglossale is a paired cord of elastic tissue in *Gallus*, connecting the rostral process of the arytenoid cartilage with the cornu of the paraglossal bone (White, 1975:1894).

(35) **M. dilator glottidis; M. constrictor glottidis.** The dilator and constrictor muscles of the glottis are the intrinsic muscles of the larynx (Annot. 50). In *Gallus* (White, 1975:1894) and birds generally (Yarrell, 1833; Gadow and Selenka, 1891; Groebbels, 1932; White, pers. comm.) the dilator of the glottis is lateral and superficial, running essentially from the wing and body of the cricoid to the arytenoid cartilage (Fig. 8.5). The constrictor runs from the caudal midline of the larynx (typically from the procricoid cartilage) to the arytenoid and cricoid cartilages (Fig. 8.5), and has several divisions. In *Gallus* White (1975) distinguished three, i.e., medial, lateral, and middle divisions, though their fibres intermingle.

In *Columba* the fibres of the constrictor muscle are attached not to the procricoid but to the interarytenoid ligament (immediately dorsal to the procricoid) (Zweers, et al., 1981). Bock (1978) distinguished three parts in the constrictor complex of *Corvus brachyrhynchos*, and Zweers, et al. (1981) analysed the homologies of Bock's three parts to the three divisions in *Gallus* of White (1975). Zweers, et al. (1981), and Zweers and Berkhoudt (1987) identified five discrete muscles within the constrictor complex of *Columba* (Fig. 8.5) and *Corvus* species, and established their homologies within these two genera and in *Gallus*. In so doing, they suggested ten different names for these two sets of five muscles.

These new studies of the two intrinsic laryngeal muscles have not altered the original interpretation of their function, which had been shown by electrical stimulation in *Gallus* to dilate and constrict the glottis respectively (White and Chubb, 1967). These functions have been confirmed cinematographically and electromyographically in other species by Zweers, et al. (1981). Therefore it is proposed to retain dilation/constriction of the glottis as the basis of the nomenclature. With detailed knowledge of these muscles in a wider range of species it may become advantageous to name the individual components of the constrictor muscle (see **Myol.** Annot. 38).

(36) **Cartt. tracheales.** The tracheal cartilages are complete rings, closely interlocked, with minimal intervals between them (McLelland, 1965), and therefore the Ligg. anularia of mammals are lacking; also there is no counterpart of the M. trachealis of mammals. In sphenisciforms the trachea is divided into left and right channels by a median septum containing cartilaginous bars which are continuous with the tracheal rings (Watson, 1883; Zeek, 1951). A septum also occurs in certain procellariiforms (Beddard, 1898:439, 499). A longitudinal dorsal ridge resembling an incomplete septum, occurs in *Casuarius* sp. (Forbes, 1981).

Ansa trachealis. A tracheal loop or coil. One or several such loops occupy an excavation in the sternum in *Cygnus* and gruids (see Johnsgard, 1961, for anseriforms, and McLelland, 1989:83, for review). In some other taxa the coils lie between the skin and pectoral muscles, as in *Platalea, Anseranas, Crax*, and *Aramus*. Among passerine birds, a coiled trachea occurs in the paradisaeid *Manucodia* (Ames, 1971:137) and *Phonygammus* (Rüppell, 1933; Clench, 1978).

Saccus trachealis. In a few birds such as *Dromaius* (Murie, 1867) and *Oxyura jamaicensis* (Wetmore, 1918) a tracheal sac opens from the trachea (McLelland, 1989:87).

Bulbus trachealis. An expansion of the trachea, the tracheal bulb, occurs a short distance rostral to the syrinx in the males of many anseriform species. A second tracheal bulb occurs just caudal to the larynx in *Melanitta fusca* (see McLelland, 1989:88, for review).

(37) **Syrinx.** Huxley (1877) introduced this term to replace "upper" and "lower" larynx. Three types of syrinx, tracheobronchial, tracheal, and bronchial, were recognized by nineteenth century anatomists, according to the gross anatomical (not embryological) distinction between the tracheal and the bronchial elements (Gadow, 1896:940; King, 1989:109). The tracheal elements are the direct continuation of the trachea, and therefore lie in the *midline* and *cranial to the bifurcation of the airway;* their skeletal components, i.e., the tracheosyringeal cartilages, typically are complete rings. The bronchial elements lie *caudal to the bifurcation of the airway* and are therefore *paired;* their skeletal components, i.e., the bronchosyringeal cartilages, constitute the skeleton of the most cranial part of the left and right primary bronchi and are typically C-shaped half-rings.

The *tracheobronchial syrinx* (Fig. 8.8) has both tracheal and bronchial elements. It occurs in the great majority of birds (Fürbringer, 1888:1088; Gadow, 1896:941; Beddard, 1898:61; King, 1989:110). In the *tracheal syrinx*, specialization of the tracheal elements dominates, as in the suboscine superfamily Furnarioidea. In this taxon the wall of the tracheal part of the syrinx is largely membranous, the tracheosyringeal cartilages being reduced to thin circlets embedded in the tracheosyringeal membrane (Fig. 8.17) or absent (Fig. 8.18). Tracheal forms of syrinx occur in other orders (King, 1989:112). In the *bronchial syrinx* the bronchial elements are modified, the syrinx of *Steatornis* being an extreme form (Fig. 8.9). Bronchial types of syrinx also occur in spheniscifom and strigiform species (King, 1989:115).

Ames (1971:14) classified the passeriform syringeal cartilages into "A" and "B" types according to their shape. This system has proved its value in passeriform taxonomy (e.g., Ames, 1971; Lanyon and Lanyon, 1989), but does not lend itself to the general anatomical analysis of syrinxes. Although flawed (King, 1989:117), the historical method offers a simple anatomical basis for classifying the syrinx of many, if not all, birds.

(38) **Tunica mucosa respiratoria.** The epithelial lining of the airways was reviewed by King (1966), King and Molony (1971), Duncker (1971), Hodges (1974), Bang and Wenzel (1985), and McLelland (1989). The nasal cavity (except the Regio vestibularis), larynx, trachea, syrinx, extrapulmonary primary bronchus, and intrapulmonary primary bronchus have a basically similar respiratory epithelium, i.e., pseudostratified with ciliated columnar cells, goblet cells (**Exocrinocyti calciformes**), basal cells, and simple alveolar mucous glands embedded in the epithelium. The trachea also possesses a non-ciliated columnar cell characterised by microvilli (Epitheliocytus microvillosus) (McLelland, 1989:93), and in a few species the mucous glands penetrate beneath the epithelium (Duncker, 1971:96). Where there is

contact between membranes or movement, as in the larynx and syrinx, the epithelium is modified. Thus, in the passerine syrinx (Setterwall, 1901), it changes to cuboidal or stratified squamous on the lateral labium and simple squamous on the medial tympaniform membrane (the primary vibrating membrane). In the roots of the secondary bronchi the typical respiratory epithelium of the primary bronchus changes abruptly to a cuboidal epithelium without mucous elements, and then almost immediately to a simple squamous epithelium which continues into the parabronchi.

Endocrinocyti respiratorii. Synonymy: neurite-receptor cell complex, Cook and King, 1969; granular cell, King, et al., 1974; granule-containing cell, McLelland and Molony, 1983; neuroendocrine cell, Smith, et al., 1986; neuroepithelial cell, Cook, et al., 1986a). Respiratory endocrine cells occur in the trachea and primary bronchus. They contain membrane-bound dense-cored granules suggesting amine-handling characteristics, and sometimes form synapses with presumptive afferent axonal endings; they may therefore have a dual endocrine and receptor function (Cook and King, 1969; King, et al., 1974; McLelland and MacFarlane, 1986; Cook, et al., 1986a). In the intrapulmonary primary bronchus of *Streptopelia risoria* (McLelland and MacFarlane, 1986), but not *Gallus* (King, et al., 1977), the endocrine cells form large clusters resembling the pulmonary neuroepithelial bodies of other vertebrate classes.

(39) **Tympanum.** Synonymy: Trommel (Wunderlich, 1884); tracheal box (Gadow, 1896:941; Forbes, 1881; Beddard, 1898:289); drum (Ames, 1971:15); tympanic box or tympanic chamber (Warner, 1972b). The tympanum (King, 1989:125) is the rigid cylinder formed by the close apposition or fusion of tracheosyringeal cartilages. Typically its diameter exceeds that of the trachea. The Tympanum is a characteristic of the tracheobronchial type of syrinx (Fig. 8.8). In most birds the most cranial cartilage of the tympanum forms the cranial limit of the syrinx (Haecker, 1900). A tympanum is also present in some tracheal types of syrinx (Figs. 8.17, 18). In the most specialized bronchial types of syrinx, as in *Steatornis*, the Tympanum is absent (Fig. 8.9).

(40) **Bulla syringealis.** Synonymy: Bulla tympanica. The typical syringeal bulla is an asymmetrical dilation of the *left* side of the tympanum (Figs. 8.12, 13) in males of the subfamily Anatinae, except the Oxyurini (Johnsgard, 1961); in *Tadorna tadorna* the dilation is greater on the right side (Gadow and Selenka, 1891:727; King, 1989:133). In the males of most Anatini the bulla is largely or entirely osseous, but in all Aythyini (Fig. 8.13) and most Mergini it is partly or extensively membranous (Johnsgard, 1961; Warner, 1971).

(41) **Cartt. tracheosyringeales.** The most cranial of the tracheosyringeal cartilages usually form the Tympanum. In a few taxa the cartilages become incomplete dorsally and/or ventrally, as in Columbidae (Fig. 8.14), Psittacidae (Fig. 8.15), and Furnarioidea (Figs. 8.17, 8.18) (King, 1989:128). Gaps thus created in the syringeal wall are closed by Memm. tracheosyringeales.

(42) **Cartt. bronchosyringeales.** Synonymy: intermediary bars (Owen, 1866:331; Miskimen, 1951); Halbringe. The bronchosyringeal cartilages are usually paired and C-shaped. Compared with the true bronchial cartilages which follow them caudally, they are broader, more irregular with expanded ends, and of greater diameter, but the transition is gradual (King, 1989:138). Their free ends typically support the Mem. tympaniformis medialis. In a few species bronchosyringeal cartilages immediately caudal to the trachea are complete rings (King, 1989:138). The latter occur especially in the bronchial type of syrinx, where 10 or more complete bronchosyringeal rings

may follow the bifurcation of the trachea, as *Steatornis* (Fig. 8.9) (King, 1989:138); the complete rings are followed by several C-shaped cartilages bearing the Mem. tympaniformis medialis.

(43) **Pessulus.** Synonymy: Steg (Haecker, 1900). This median cartilage (Fig. 8.11) splits the airway of the syrinx in most birds. It is absent in various taxa (King, 1989:141), including the oscine Alaudidae (Mayr, 1931), this being one of the two significant deviations in the homogeneous structure of the oscine syrinx (Ames, 1971:148).

(44) **Mem. semilunaris.** A projection of the mucosa (Fig. 8.11) extending the Pessulus cranially. Although often regarded as a component of the basic syrinx, the semilunar membrane is erratically absent in both passeriform and non-passeriform species (King, 1989:165).

(45) **Cartt. accessoriae.** The accessory cartilages are small paired structures attached to the medial tympaniform membrane or the tracheosyringeal and bronchosyringeal cartilages.

Cart. membranosa dorsalis; Cart. membranosa ventralis. Synonymy: Cartt. arytenoideae (Müller, 1878; Owen, 1866:223); Cartt. tensores (Wunderlich, 1884); Stellknorpel (Haecker, 1900); internal cartilages (Ames, 1971:104, 144; Lanyon, 1984). These thin, paired, membrane cartilages of irregular shape nearly always lie in the left and right medial tympaniform membranes, especially in Tyrannidae (Ames, 1971:104, 144). Haecker (1900) illustrated a dorsal cartilage in the oscine *Pica* (Fig. 8.10). Köditz (1925) believed that the ventral cartilage occurs in all oscines, a dorsal cartilage being present in only some. A dorsal membrane cartilage was illustrated by Müller (1878:Plate V) in *Anthracothorax dominicus* (Trochilidae); Beddard (1898:191) described one at the ventral aspect of the first and second bronchosyringeal cartilages of ramphastid species. These appear to be the only reports outside the Passeriformes.

Proc. vocalis. This rather obscure term originated from Müller (1878:33), was adopted by Garrod (1877) and Beddard (1898:69, 423), and reestablished by Ames (1971:143). The term refers to a small paired cartilage rod or plate (Figs. 8.17, 18) that appears to occur almost exclusively in the Furnarioidea (Garrod, 1877; Ames, 1971:143). It gives attachment to M. sternotrachealis, and in some genera also to M. tracheolateralis and to the M. vocalis ventralis and/or dorsalis. Beddard (1898:69, 423) described a rudimentary Proc. vocalis in two species of Ciconiidae.

(46) **Lig. interbronchiale.** Synonymy: Bronchidesmus (Garrod, 1879; Myers, 1917). The term used by Wunderlich (1884) for the connective tissue bridge (Fig. 8.11) joining the left and right primary bronchi. The interbronchial ligament is present in most but not all birds (King, 1989:166).

Foramen interbronchiale. Synonymy: Subpessular air space (Warner, 1971, 1972a). The space between the bifurcation of the trachea and the Lig. interbronchiale (Figs. 8.8, 11).

Lig. syringeale. The syringeal ligament is a loose fascial sheath originating from the strong septum between the clavicles in *Gallus* (Youngren, et al., 1974; Gaunt and Gaunt, 1977). Contraction of the sternotrachealis muscle tenses the ligament and rotates the pessulus, thus modifying the tension in the lateral tympaniform membrane (Gaunt and Gaunt, 1977; Brackenbury, 1989:196).

(47) **Mem. tympaniformis lateralis.** Synonymy: Mem. tympaniformis externa (Gadow, 1896:937; Greenewalt, 1968:27). One of the most difficult components of the syrinx to define, the lateral tympaniform membrane is a membrane or series of membranes between the lateral aspects of either the last tracheosyringeal cartilages (Fig. 8.14) or the most cranial bronchosyringeal cartilages (Fig. 8.8b). Variants are shown in Figs. 8.9, 16. In a few species such as *Gallus* it is well developed and a major source of sound production. It appears to be absent in about as many nonpasseriform species as it is present (King, 1989:153). In oscines it is supposed to be the region indicated in Fig. 8.11, but this is particularly controversial (King, 1989:150-159). Although authors have named this region the lateral tympaniform membrane, Ames (1971:16) and Warner (1972b) considered there to be *no* true membranous areas in the lateral wall of the passeriform syrinx. Gaunt, et al. (1973) pointed out the proximity of the membrane to the lateral labium (Fig. 8.11); both components consist of a thickened area of loose connective tissue in the lateral wall, so the anatomical distinction between them is almost negligible (King, 1989:157, 165).

Mem. tracheosyringealis. The tracheosyringeal membrane or membranes contribute to the dorsal and/or ventral wall of the tracheal element of the syrinx. They are always associated with thinning or loss of tracheosyringeal cartilages in the midline. They occur especially in Columbidae (Fig. 8.14), Psittacidae (Fig. 8.15), and Furnarioidea (Figs. 8.17, 8.18) (King, 1989:160).

(48) **Mem. tympaniformis medialis.** Synonymy: Mem. tympaniformis interna (Gadow, 1896:937; Ames, 1971:16; Warner, 1972b). The paired medial tympaniform membrane (Figs. 8a, 11, 12, 14) seems to be present in the great majority of species, being without question the primary vibrating membrane in many taxa (Greenewalt, 1968:28). The membrane is suspended between the free ends of the bronchosyringeal cartilages. It is apparently absent in those few ciconiiform species which have a tracheal type of syrinx wherein the bronchial rings are complete (King, 1989:144). Its presence in some psittacids has been questioned (Nottebohm, 1976; Gaunt and Gaunt, 1985), but it is present in *Ara ararauna* (King, 1989:144).

(49) **Labium laterale; Labium mediale.** Synonymy: labium externum, internum (Haecker, 1900); "inner and outer vocal cords", Setterwall, 1901; Stimmpolster or Stimmlippen (Rüppell, 1933). Paired connective tissue pads, projecting respectively from the lateral and medial wall into the airway of the oscine syrinx (Fig. 8.11). The lateral labium is one of the three "invariable features of the songbird syrinx", the other two being the medial tympaniform membrane and perhaps the membrane cartilages (Greenewalt, 1968). It is virtually indistinguishable from the lateral tympaniform membrane (Annot. 47). Non-passerine species in general lack the lateral labium (King, 1989:164). The medial labium seems to occur only in passeriforms (King, 1989:165).

Valvula syringealis. A crescentic syringeal valve projecting caudally from the lateral wall of the right side of the tympanum in *Anas* (King, 1989:149) and *Aythya fuligula* (Fig. 8.12) (Warner, 1971). A paired syringeal valve projects into the narrowest part of the syringeal airway in *Myiopsitta monachus* (A. S. Gaunt, pers. comm.).

(50) **Mm. laryngeales; Mm. tracheales; Mm. syringeales.** The muscles of the airway between the larynx and lung are usually categorised as laryngeal, tracheal, and syringeal muscles. A muscle that has extensive contact with the trachea could reasonably be called a tracheal muscle; by pulling on the trachea such a muscle will almost certainly act indirectly on the larynx at one end and on the syrinx at the other, and could therefore be regarded also as a laryngeal or a syringeal muscle. Sometimes the

muscles of the larynx, trachea, and syrinx are classified as extrinsic and intrinsic muscles. An extrinsic muscle should have an attachment *beyond* the organ concerned, whereas an intrinsic muscle should have *all* its attachments *on* the organ itself. This distinction can be upheld for the larynx, the dilator and constrictor muscles being clearly intrinsic and any other muscles extrinsic. However, in many species there can be no truly intrinsic tracheal muscles, and unequivocal intrinsic syringeal muscles are uncommon even in passeriforms (King, 1989:168, 172).

In the literature of the last two centuries many muscles have been associated with the upper airways of birds. The same name has often been applied to nonhomologous muscles, and different names have been applied to homologous muscles (George and Berger, 1966:262). The basic problems are the small size of many of these muscles and the occurrence of detailed interspecific variations. It can be difficult to decide whether a fascicle of muscle fibres is a new muscle, a minor variant of a muscle previously known, or a dissection artefact.

M. cleidohyoideus. In the NAA (1979), this muscle was named M. sternohyoideus. Zweers (1982) established from the literature that, in birds examined so far, there is a muscle that attaches to the *clavicle* at its caudal end, runs cranially in close relationship to the *skin* of the neck and the *trachea* (though not directly attached to the trachea), and attaches at its cranial end to the *larynx* or in some species the *hyoid bone;* this is well attested in *Tetrao urogallus* by Yarrell (1833) (his furculo-tracheal muscle), in *Grus* by Fisher and Goodman(1955) (their M. tracheohyoideus), in *Nucifraga* by Bock, et al. (1973) (their M. tracheohyoideus), in Calidridinae by Burton (1974) (his M. cleidohyoideus), in *Gallus* by Gaunt and Gaunt (1977) (their M. tracheohyoideus), and in *Columba livia* by Zweers (1982) (his M. claviculohyoideus). The term M. sternohyoideus, as in the first edition of the NAA, is a misnomer for this muscle, because it has no attachment to the sternum. M. tracheohyoideus is equally a misnomer, because it is not known to arise from the trachea in any species of bird. Gaunt and Gaunt (1977) suggested that the best name would be M. cleidohyoideus, which expresses the correct caudal attachment. An alternative would be M. cleidolaryngeus, which would also describe the correct cranial attachment not only in *Gallus* but in passeriforms as well (so far as is known). However, workers on the passeriform larynx (e.g., Bock and his coworkers) have hitherto been content with the suffix "-hyoideus" when naming this muscle. The adoption of M. cleidohyoideus rather than cleidolaryngeus will therefore minimize disturbance among established terms.

M. sternohyoideus. Gadow and Selenka (1891:307) used the expression "System des m. sterno-hyoideus" to cover a list of about 10 muscles. Most of these appear to be synonyms for one muscle, but their use of "System" implied that some of these names might relate to separate muscles. They then stated (p. 308) that a true M. sterno-hyoideus, as seen in its primitive condition in reptiles, does still occur in *Apteryx*. They also suggested (pp. 310, 730) that parrots possess a similar "sternohyoid" muscle (except that it fails to reach the sternum). M. sternohyoideus will not be listed in the NAA until its existence in birds is confirmed.

M. tracheohyoideus. The M. tracheohyoideus was not formally listed in the NAA (1979), but Vanden Berge included it in his Table 1. Zweers (1982) pointed out that the M. tracheohyoideus of Fisher and Goodman (1955) in *Grus americana* and of Bock, et al. (1973) in *Nucifraga* are the same muscle as the cleidohyoideus of Burton (1974) in charadriiforms and his own M. claviculohyoideus in *Columba livia;* thus these muscles are in fact the M. cleidohyoideus discussed two paragraphs above. Zweers (1982) also revealed that at least one other group of recent authors has applied the term tracheohyoideus to the M. tracheolateralis. M. tracheohyoideus will not be listed in this edition of the NAA.

M. cricohyoideus. Zweers (1982) reported this muscle in *Columba livia* as running between the cricoid and the hyoid bone; presumably it is an extrinsic laryngeal muscle (McLelland, 1989:76). In *C. livia* it consists of a small dorsal and a large ventral component, the **M. cricohyoideus dorsalis** and **ventralis,** which arise respectively from the dorsal and ventral aspects of the Os basibranchiale and insert together on the ventral and ventrolateral aspect of the cricoid cartilage. Zweers interpreted the dorsal component as representing the M. thyrohyoideus of George and Berger (1966:262) in birds generally, of Fisher and Goodman (1955) in *Grus,* and of Bock, et al., (1973) in *Nucifraga,* and representing the M. thyreohyoideus of Burton (1974) in *Charadrii* and of Zweers et al. (1977) in *Anas.* In other species, apparently only one component is present. Thus the dorsal component of this muscle, but not the ventral, was found by Zweers and Berkhoudt (1987) in *Corvus corone* and *C. monedula,* and by Heidweiller and Zweers (1990) in the estrildids *Poephila guttata* and *Lonchura striata;* in these species the authors referred to it as either "M. cricohyoideus", or "M. cricohyoideus (dorsalis)". Homberger and Meyers (1989) also used the term M. cricohyoideus in *Gallus.* However, they interpreted their muscle as representing the combined M. cricohyoideus ventralis and M. hyovalvularis of Zweers (1982) in *Columba.* In a Table of synonymies and homologies, Homberger and Myers identified in the literature nine other names that had been applied to their M. cricohyoideus. This illustrates the difficulty of codifying the terminology for such muscles with justice to all authors. Moreover, the terminology is still in active evolution—see, e.g., the use of M. thyreohyoideus in *Anas* by Zweers, et al. (1977), followed by the substitution of M. cricohyoideus dorsalis for an apparently homologous muscle in *Columba* by Zweers (1982). The selection of names in the NAA must inevitably be arbitrary, and subsequent changes will probably be necessary as further knowledge becomes available. For the pharyngeal functions of these muscles see **Myol.** Annot. 36.

M. tracheovalvularis. A very small muscle in *Columba livia* passing between the first tracheal rings and the pharyngeal wall, and represented by Bock's (1978) cricohyoideus posterior in *Corvus,* (Zweers, et al., 1981); an extrinsic laryngeal muscle (McLelland, 1989:76).

M. hyovalvularis. A muscle in *Columba livia* running along the dorsolateral aspect of the larynx, between the hyoid bone and the pharyngeal wall (Zweers, et al., 1981), and also present in *Poephila guttata* and *Lonchura striata* (Heidweiller and Zweers, 1990). Interpreted by Zweers (1982) as represented by the M. dermoglossus and M. thyrohyoideus of *Grus* (Fisher and Goodman, 1955), the M. cricohyoideus superior of *Nucifraga* (Bock, et al., 1973), and the M. thyreohyoideus superior of *Loxops* (Richards and Bock, 1973). Homberger and Meyers (1989) regard it as part of their M. cricohyoideus in *Gallus;* this is an extrinsic laryngeal muscle (McLelland, 1989:76). See **Myol.** Annot. 36.

M. sternotrachealis (Fig. 8.6). Owen (1886:224) regarded this as "the most constant of all the muscles affecting the lower larynx", and George and Berger (1966:263) believed that it "has apparently been found in all birds studied". Ames (1971:109) confirmed that it occurs in passerines generally. Beddard (1898:258) claimed its absence in some psittaciforms, but Gaunt and Gaunt (1985) and King (1989:168) found it in six psittacid species; feeble in oscines (Ames, 1975; Warner, 1972b).

M. cleidotrachealis (Fig. 8.13). Synonymy: M. ypsilotrachealis (Gadow and Selenka, 1891:730; Rüppell, 1933; Lockner and Youngren, 1976). This synonym has been very widely employed, but M. cleidotrachealis has also been used for a long time (e.g., Beddard, 1898:292). German veterinary anatomists have applied M. ypsilotrachealis to the M. sternotrachealis; this term has therefore been used for two entirely different muscles, and for this reason M. cleidotrachealis is preferred. This

muscle has been described in many members of the Anseriformes (Gadow, 1896:938; Beddard, 1898:464; Rüppell, 1933; Lockner and Youngren, 1976; King, 1989:168). It has also been reported in representatives of four other orders, e.g., *Crypturellus, Crax,* and *Tockus* by Beddard (1898:222, 292, 487), and sphenisciforms by Watson (1883). The essential characteristics of this muscle are its origin from the clavicle and its direct insertion on the trachea, cranial to the insertion of M. sternotrachealis.

M. tracheolateralis (Fig. 8.8). Synonymy: M. contractor tracheae (Watson, 1883); M. tracheobronchialis (Haecker, 1900); M. laryngosyringeus (Köditz, 1925); M. bronchotrachealis (Rüppell, 1933); M. trachealis lateralis (Zweers, 1982); M. cricotrachealis lateralis (Zweers and Berkhoudt, 1987). This paired muscle occurs in the great majority of avian orders, if not all (Fürbringer, 1888:1089; Beddard, 1898:62; Gadow, 1896:938; Ames, 1971:105, 133). Complete loss of this muscle has been claimed in some ratites, most ciconiids and cathartids, and some galliforms, but sometimes the loss is "complete" only in the sense that the muscle ends well cranial to the syrinx (King, 1989:169). Typically it attaches caudally to the syrinx, forms a lateral band along the whole of the trachea, and attaches cranially to the larynx. It is sometimes divided into a dorsal and a ventral part, the former attaching cranially to the larynx and the latter to the hyoid (respectively, M. trachealis lateralis, pars cricoidea and pars hyoidea of Zweers, 1982); or both parts attach to the larynx (the M. cricotrachealis lateralis of Zweers and Berkhoudt, 1987). For further discussion see McLelland (1989:98) and King (1989:169).

(51) **Mm. syringeales.** The principal sources on the passeriform syringeal muscles are Ames (1971, 1975) and Warner (1972b), with contributions from Miskimen (1951). The anatomy of the syringeal muscles in subpasseriforms is less well known. However, the 19th century literature contains much information on the muscles of subpasseriforms (see Fürbringer, 1888:1087; Gadow, 1896:937; and particularly Beddard, 1898). For review see King (1989:169).

The syringeal muscles are very small, and not always sharply distinguished from each other anatomically. This no doubt accounts for the different numbers of syringeal muscles claimed by various authors in oscines, even though this taxon is noted for the anatomical uniformity of these muscles (Ames, 1971:94; 1975); for example, the maximum total number of paired muscles (excluding M. sternotrachealis and M. tracheolateralis) is four according to Ames (1971:89), five according to Warner (1972b), seven according to Fürbringer (1888:1091), and eight according to Köditz (1925).

As noted by George and Berger (1966:268), Ames (1971:10), and Warner (1972b), the nomenclature most commonly used for the passeriform syringeal muscles originated with Owen (1866:223); Ames employed this terminology. Fürbringer's (1888) nomenclature, however, was adopted by Gadow (1896:939) and Haecker (1900), and has been closely followed by Warner (1972b) also. Among other major terminologies are those of Wunderlich (1884), Setterwall (1901), and Köditz (1925). Synonymy was worked out by Köditz (1925), Ames (1971:90), and Warner (1972b), essentially as in Table 8.1. The terminology adopted here is based on that of Fürbringer (1888).

M. tracheobronchialis dorsalis/brevis/ventralis; M. syringealis dorsalis and ventralis. Synonyms: see Table 8.1. These syringeal muscles are present in oscines as in Fig. 8.20. Ames (1971:89-94) interpreted the M. tracheobronchialis dorsalis and brevis as two parts of the same muscle, and considered the M. syringealis

ventralis to consist of medial and lateral parts (Fig. 8.18). The M. tracheobronchialis dorsalis and ventralis, and the M. syringealis dorsalis also occur in the suborder Menurae (Ames, 1971:85, 87).

M. vocalis dorsalis and ventralis; M. obliquus ventralis and lateralis. These occur in suboscine passeriforms as in Figs. 8.15, 16 and 17 (Ames, 1971:20-79).

M. syringealis superficialis/profundus; M. syringealis caudalis; M. syringealis. The non-passeriform groups usually have no intrinsic syringeal muscles and only a single paired (clearly) *extrinsic* syringeal muscle, the M. tracheolateralis, which typically inserts on the tracheal or bronchial elements of the syrinx. This is the basic tracheobronchial syrinx which is generally agreed to occur in the majority of nonpasserine orders (Fürbringer, 1888:1089; Gadow, 1896:938; Beddard, 1898:61; Ames, 1971:133; King, 1989:175); it also occurs in several families of suboscine Passeriformes as in *Psarisomus* (Eurylaimidae) (Ames, 1971:133). However, there are certainly two pairs of short syringeal muscles in some psittacids (Gadow, 1896; Evans, 1969:70; Nottebohm, 1976; Gaunt and Gaunt, 1985; King, 1989:176); it is proposed to name these according to their topographical position, i.e., M. syringealis superficialis and M. syringealis profundus (Figs. 8.15, 16). There is also a fully authenticated single pair of true syringeal muscles in *Steatornis caripensis* (Suthers and Hector, 1985, their M. broncholateralis), which can reasonably be distinguished by the term M. syringealis caudalis because of its unique position caudal to the division of the airway (Fig. 8.7). The presence of one additional pair of short specialized syringeal muscles in *Gallinago* and *Falco* was mentioned by Wunderlich (1884), Fürbringer (1888:1089), and Gadow (1896:939), but without full documentation. Forbes (1881) reported with an illustration a very convincing single pair of true syringeal muscles in *Rhea*. Any such single pairs of muscles would now be called simply M. syringealis, until authenticated details of their topography and attachments justify adding a descriptive adjective to the name. Hasty commitment to homologies or functions should be avoided.

(52) **Bronchus primarius, Pars extrapulmonalis; Cartt. bronchiales; Memm. interanulares; Lig. bronchiale mediale.** The term Bronchus primarius was introduced by Juillet (1912). The extrapulmonary part of the primary bronchus lies between the syrinx and the lung. Its bronchial cartilages are C-shaped, except in Hirundinidae where they are complete rings (Warner, 1972b). The thin interannular membranes connect adjacent bronchosyringeal and/or bronchial cartilages (Figs. 8.8b, 10). The thicker medial bronchial ligament completes the gap between the ends of the bronchial cartilages (Fig. 8a) (King, 1989:23).

(53) **Facies costalis; Facies vertebralis; Facies septalis.** The costal surface of the lung adjoins the thoracic wall, its vertebral surface relates to the vertebrae, and its septal surface faces the Septum horizontale (see Chap. 7).

(54) **Sulci costales; Tori pulmonales; Tori intercostales; Tori marginales.** The ribs make costal sulci on the costal and vertebral surfaces of the lung. Between two Sulci costales (Fig. 8.22) there is a Torus intercostalis (Quitzow, 1970) an approximately transverse strip of lung tissue. Together, the intercostal and marginal tori constitute the Tori pulmonales. The term Torus pulmonis was used by Schulze (1908) and Groebbels (1932:44).

(55) **Margo costovertebralis; Margo costoseptalis; Margo vertebroseptalis; Margo cranialis; Margo caudalis; Angulus craniodorsalis; Angulus caudodorsalis; Angulus cranioventralis; Angulus caudoventralis.** Figure 8.21 shows the relationships between the borders, angles, and surfaces (Quitzow, 1970) of the essentially

quadrilateral lung of most birds. In primitive species with a poorly developed Neopulmo (Annot. 57) the cranioventral and the caudoventral angles are indistinct, making the lung triangular with the apex pointing ventrally (Duncker, 1972).

(56) **Planum anastomoticum; Linea anastomotica.** Terms introduced by Locy and Larsell (1916a). Synonymy: Linea serpta, Quitzow, 1970. The anastomotic plane and its superficial Linea are caused mainly by the terminal anastomoses of the Parabronchi of: (a) the medioventral and mediodorsal secondary bronchi (Figs. 8.22, 23), and (b) the medioventral and lateroventral secondary bronchi (Fig. 8.23). The line is visible on the surface (Fig. 8.21).

(57) **Paleopulmo; Neopulmo.** Terms proposed by Duncker (1971), to indicate a phylogenetic relationship between the two main components of the lung. The Paleopulmo is present in all birds. It consists (Fig. 8.23) of: (a) Bronchi medioventrales and mediodorsales, and their Parabronchi; (b) the large Bronchus lateroventralis which connects directly to the Saccus thoracicus caudalis; and (c) two or three intermediate-sized Bronchi lateroventrales, which medially form Parabronchi joining Parabronchi from the fourth Bronchus medioventralis at the Planum anastomoticum. In supposedly primitive birds (e.g., sphenisciform species) the Paleopulmo forms the whole of the lung.

In most birds the Neopulmo forms about one tenth of the lung. It is a network (Fig. 8.23) of anastomosing bronchi consisting of: (a) the Bronchi laterodorsales and their Parabronchi; (b) laterally directed Parabronchi of the Bronchi lateroventrales; and (c) the connexions of this network to the caudal air sacs. It was named the reseau anastomotique by Campana (1875) and Locy and Larsell (1916a). McLelland (1989:234-236) has summarized the progressive development of the neopulmo in various taxa.

(58) **Bronchus primarius, Pars intrapulmonalis.** The part of the primary bronchus that lies within the lung is its intrapulmonary part (Juillet, 1912). It ends caudally by opening into the Saccus abdominalis (Fig. 8.22). A dilated mid-region, the "Vestibulum" was described by Huxley (1882) and mentioned by many others, but is not present in *Gallus* (Juillet, 1912; Payne and King, 1959; Akester, 1960; Quitzow, 1970) or in *Anas* and *Columba* (Akester, 1960). The term Vestibulum has also been applied to the region of the Bronchus primarius where the Bronchi medioventrales arise (Juillet, 1912; Groebbels, 1932:7), and even to the region of the Bronchus primarius which is *devoid* of branchings (Duncker, 1971). The term Mesobronchus was used by Huxley (1882) and a number of later authors for the region of the Bronchus primarius which lies caudal to the supposed Vestibulum. In view of its uncertain characteristics the term Vestibulum should not be used.

(59) **Bronchi secundarii.** These are the bronchi of the second order, and therefore include all those that arise from the primary bronchus (Campana, 1875:31; Locy and Larsell, 1916a). The earlier authors (e.g., Campana, 1875; Schulze, 1908) named them according to either the orientation of their origin from the primary bronchus, or their subsequent direction, or both their origin and their direction. At that time, both their orientation and their direction had been erroneously described (see Annot. 57 of NAA, 1979), and so the resulting terminology was misleading. A further complication has been the use of the same term for two or more different groups of secondary bronchi, as with "ventrobronchi", "dorsobronchi", and "laterobronchi" (Table 8.2). The resulting confusion pervaded the literature on the anatomy and physiology of the avian lung. The NAA (1979) produced a new terminology, on the two following principles: (1) all terms for the Bronchi secundarii should be based on the lung territory which they supply, as in Figure 8.23 (a relatively neglected precept,

Quitzow, 1970); (2) Terms which have already been in use, but with various meanings, should be avoided. The following new terms for the secondary bronchi resulted: Bronchi medioventrales, mediodorsales, lateroventrales, and laterodorsales. In the decade following the NAA (1979) these terms have been widely adopted by anatomists and physiologists. The same terms are listed here.

(60) **Bronchi medioventrales.** Synonymy: See Table 8.2. The medioventral bronchi are the four (or five) secondary bronchi which supply the medial and ventral regions of the lung (Fig. 8.23). They arise from the dorsomedial wall of the cranial region of the Bronchus primarius (Fig. 8.22) (Fischer, 1905; King, 1966:181; Quitzow, 1970). Many of their main branches pass in the medial direction over the Facies septalis to end by turning dorsally onto the Facies vertebralis.

(61) **Bronchi mediodorsales.** Synonymy: Table 8.2. The mediodorsal secondary bronchi supply the medial and dorsal regions of the lung (Fig. 8.23). They arise from the dorsal wall of the caudal part of the Bronchus primarius (Fig. 8.22), and then travel dorsally (Duncker, 1971).

(62) **Bronchi lateroventrales.** Synonymy: Table 8.2. The lateroventral secondary bronchi supply the lateral and ventral regions of the lung (Fig. 8.23). Their origins are directly opposite to those of the Bronchi mediodorsales (Fig. 8.22), i.e., from the ventral wall of the caudal part of the Bronchus primarius, and their course is ventral or caudoventral (Payne and King, 1960; King, 1966:181; Quitzow, 1970; Duncker, 1971). In birds generally, the large first or second bronchus connects with the Saccus thoracicus caudalis. The subsequent two or three intermediate sized bronchi contribute parabronchi to the Paleopulmo in all species; in species in which the Neopulmo is developed these intermediate sized Bronchi lateroventrales, and yet other more caudal and smaller ones, contribute parabronchi to the Neopulmo (Fig. 8.23).

(63) **Bronchi laterodorsales.** Synonymy: Table 8.2. These supply the lateral and dorsal regions of the lung (Fig. 8.23). They form a large part of the Neopulmo; since the degree of development of the Neopulmo varies greatly, the position, diameter, and number of the Bronchi laterodorsales also vary (Campana, 1875; Locy and Larsell, 1916a; Groebbels, 1932; King, 1966; Quitzow, 1970). They arise from the lateral wall of the caudal part of the Bronchus primarius and extend mainly laterally. The first two or three are of large diameter (certainly in *Gallus*, see King, 1966:182, and in *Cygnus*, see Fig. 30b of Duncker, 1971). The more caudal of these secondary bronchi are similar in diameter to Parabronchi; because of this, some authors (e.g., Akester, 1960; Duncker, 1971) excluded the whole of this group of bronchi from those of the Bronchi secundarii and classified them as Parabronchi.

(64) **Parabronchus.** Synonymy: Bronchus tertiarius (Campana, 1875; Akester, 1960; King, 1966; Lasiewski, 1972); Lungenpfeife (Krause, 1922); Bronchi fistularii (Quitzow, 1970; Gerisch, 1971). The Parabronchi are bronchi of the third or subsequent orders of branching, i.e., they arise from the Bronchi secundarii or from the subdivisions of the Bronchi secundarii (Fig. 8.22). The term Parabronchus is long established, having been introduced by Huxley (1882), and is now in general use by anatomists and physiologists. It includes both the parabronchial airway and the mantle of exchange tissue which surrounds that airway; the boundary of the Parabronchus is the Septum interparabronchiale (Annot. 70).

(65) **Atrium.** Synonymy: bronchiolus, vestibulum, fossa (see King, 1966:195; Gerisch, 1971:6). The term atrium was introduced by Krause (1922:295). The atria are the polygonal chambers (Fig. 8.24) leading towards the air capillaries from the

Parabronchi and from many secondary bronchi. The term is in general use, the many alternatives having fallen into disuse. For species variations see Annot. 70.

(66) **M. atrialis.** The atrial muscles form a network of smooth muscle bundles (Fig. 8.24) around the openings into the atria (King and Cowie, 1969; Gerisch and Schwarz, 1972; West, et al., 1977; McLelland, 1989:237). See Annot. 70.

(67) **Septum interatriale.** The thin interatrial septa (Fig. 8.24) are the atrial walls, separating adjacent atria (Gerisch, 1971). See also Annot. 70.

(68) **Infundibulum.** The term Infundibulum apparently originated from Krause (1922:292). It refers to the funnel-shaped ducts that open from the floor of an Atrium (Fig. 8.24) and lead to air capillaries. According to Gerisch (1971) the infundibula also give rise to Rami respiratorii, which are intermediate in size between Infundibulum and Pneumocapillaris.

(69) **Epitheliocytus granularis.** Synonymy: Epitheliocytus magnus, Cellula granularis (NAA, 1979; McLelland, 1989:246). The granular epithelial cell lines the Atrium and contains osmiophilic laminated bodies (for review see King and Molony, 1971:119). It is probably homologous to the the septal cell, great alveolar cell, type 2 epithelial cell, or granular pneumocyte of mammals.

(70) **Septum interparabronchiale.** The interparabronchial septa separate the exchange tissue of adjacent Parabronchi. According to Duncker (1971), these septa, and also the Atria and the Mm. atriales, are best developed in birds which fly poorly or not at all. Maina, et al. (1982) found that all these structures are well developed in anseriforms, galliforms, and charadriiforms, and poorly developed in columbiforms, psittaciforms, cuculiforms, and passeriforms, the septa often being entirely lost. See McLelland (1989:236) for review.

(71) **Pneumocapillaris.** Synonymy: Tubulus respiratorius, Ductulus respiratorius. The term air capillary or Luftkapillaren has been widely used since the beginning of the 20th century. Gerisch (1971) suggested Ductulus respiratorius, because he believed that anastomoses are not sufficiently common to justify the term air capillary. Smith, et al. (1986) proposed "respiratory labyrinth" because anastomoses are so profuse, but this term would be inapplicable to the *individual* tubules within the complex. The profuse anastomoses and fluctuating calibres of the air capillaries, and their interlocking relationships with the narrower and more uniform blood capillaries, were established by Maina (1982, 1988), with observations also by West, et al. (1977) and Fujii, et al. (1981). The quantitative morphology of the blood gas barrier and many other pulmonary components has been reviewed by Maina (1989:307-368) and Maina, et al. (1989).

(72) **Epitheliocytus respiratorius.** The respiratory epithelial cell which lines the Pneumocapillaris is homologous to the similar cell in the mammalian alveolar wall (the small alveolar cell, or type 1 epithelial cell), but it is much thinner than in mammals and is also the only cell lining the barrier, thus minimizing barrier thickness (Maina and King, 1982).

(73) **Ostium.** A term widely used but seldom defined. Muller (1908) and Schulze (1908) applied it to the general zone of attachment of the air sac to the lung, enclosing one or several actual orifices which open into the bronchi; King (1966:224) defined it explicitly in this way. Campana (1875:27) used Infundibulum for this general zone. Quitzow (1970) introduced the term "Area saccopulmonalis" for the same region; like Groebbels (1932) she restricted the term Ostium to the single opening from an air

sac into a secondary (or the primary) bronchus. The older meaning of Muller (1908) and Schulze (1908) was adopted in the NAA (1979), and is retained here (Fig. 8.22).

Within an Ostium there are two types of opening: (1) "Indirect connexion" which connects the air sac to Parabronchi (the Bronchi recurrentes of Schulze, 1910; Juillet, 1912; and other authors, and the indirect connexions of King, 1966:223), and (2) "Direct connexion" which connects the air sac to a secondary, or to the primary, bronchus (the "bronche directe" and "orifice direct" of Juillet, 1912; the "direkt Bronchen" and "direct Ostien" of Groebbels, 1932, and the "direct connexion" of King, 1966:223). Terms that indicate the direction of air flow in these connexions should be avoided, in view of the actual complexity of the flow (see Scheid and Piiper, 1989:376-381 for review). This excludes Bronchi recurrentes, and probably also the Bronchi pulmosaccales and saccopulmonales of Quitzow (1970). The terms "direct" and "indirect connexions" do not suggest direction of flow, and have been established for a long time. They are recommended for descriptive purposes, but not listed as official terms. For a review of the Ostia and their connexions see McLelland (1989:265-269).

(74) **Saccobronchus.** This is an old term adapted to a new meaning by Duncker (1971). It now refers to a single large funnel-like bronchus which collects many parabronchi and connects with an air sac. The old meaning was applied (e.g., by Schulze, 1910) to the many small parabronchial connexions of an air sac, the term thus being synonymous with Bronchus recurrens; this older usage was retained by some more recent authors (e.g., Quitzow, 1970).

A Saccobronchus (in the new sense) occurs only in the Saccus abdominalis and Saccus thoracicus caudalis. The Saccus abdominalis has been found to possess one such Saccobronchus in birds generally, except in Dromaiidae and Spheniscidae (Duncker, 1971). A Saccobronchus is particularly well developed in both the Saccus abdominalis and the Saccus thoracicus caudalis of *Ciconia, Anas,* and *Pluvialis* (Duncker, 1971: Figs. 24-26, 32).

(75) **Aa. interparabronchiales; Arteriolae intraparabronchiales.** The general architecture of the pulmonary circulation was established by Abdalla and King (1975). The microanatomy of the vasculature and the terminal airways was described by Maina (1982, 1988) and West, et al. (1981), with contributions by Akester (1974) and Fujii, et al. (1981). Radu and Radu (1971) provided information on the rami of the left and right pulmonary arteries (**Art.** Annot. 2).

Each ramus of the pulmonary artery gives rise to many interparabronchial arteries. These lie in the interparabronchial septa, and give off intraparabronchial arterioles which give rise to blood capillaries (Fig. 8.24). The blood capillaries form an anastomosing network interlocking with the network of air capillaries. The deoxygenated blood from the pulmonary trunk is delivered at right angles to the long axis of each parabronchus, causing a cross-current relationship between bulk parabronchial gas flow and blood flow (Scheid and Piiper, 1970).

Vv. interparabronchiales; Vv. intraparabronchiales; Vv. atriales; Venulae septales; Venulae intraparabronchiales. Some of the blood capillaries drain into septal venules and then via atrial veins into intraparabronchial veins; most of them empty via intraparabronchial venules into intraparabronchial veins, and thence into interparabronchial veins (Fig. 8.24). See **Ven.** Annot. 1, 2). There is no anatomical evidence for arteriovenous anastomoses in the avian lung (Abdalla and King, 1976a).

R. bronchialis; Vv. bronchiales. The paired bronchial rami arise from the A. esophagotracheobronchialis (Abdalla and King, 1976b, 1977). In anseriform, galliform, and columbiform species the bronchial veins of the extrapulmonary part of the primary bronchus drain via esophageal veins into the V. esophagotrachealis and thence into the cranial vena cava; the intrapulmonary part, and in *Gallus* the caudal region of the extrapulmonary part, drain into the pulmonary vein. For reviews of the pulmonary and bronchial circulation see West, et al. (1981:287-298) and Abdalla (1989:281-306).

(76) **Sacci pneumatici.** In all birds air sacs arise from the lungs. The literature on their anatomy is vast, much of it from the 19th century and not all of it reliable. Good general surveys were made by Baer (1896), Schulze (1910), and especially Groebbels (1932:54-76). More recent reviews are by King (1966:207-221) and McLelland (1989:258-271). There are six primordial pairs of sacs, but in nearly all birds two pairs fuse to form the median clavicular sac. The anatomy of the sacs varies greatly between species.

(77) **Saccus cervicalis.** Synonymy: superior-posterior sac, Campana (1875); thoracocervical sac, McLeod and Wagers (1939). The cervical sac consists of a pair of main chambers and diverticula. The main chambers fuse to form a median compartment in several orders (King, 1966:209), and rarely (e.g., *Meleagris,* King and Atherton, 1970) also fuse with the Pars lateralis of the clavicular sac to form a cervicoclavicular sac. The sac is absent in Gavidae and Podicipedidae (Gier, 1952; Duncker, 1971).

(78) **Diverticula vertebralia.** The vertebral diverticula of the Saccus cervicalis pass cranially and caudally along the vertebral column in birds generally (Groebbels, 1932:56; King, 1966:209; Duncker, 1971:50).

(79) **Diverticula intermuscularia.** In some birds intermuscular diverticula of the Saccus cervicalis penetrate between the cervical muscles and accompany branches of the brachial plexus (Duncker, 1971:50).

(80) **Diverticula subcutanea.** Extensive subcutaneous diverticula of the Saccus cervicalis have been reported in Pelecaniformes and a few other species from other orders (Groebbels, 1932:62-64; King, 1966:211) probably including *Leptoptilos* (Akester, et al., 1973).

(81) **Saccus clavicularis.** Synonymy: thoracic sac (Sappey, 1847; superior-anterior sac (Campana, 1875); ant. thoracic sac (McLeod and Wagers, 1939). The rival terms Saccus clavicularis (Schulze, 1910) and Saccus interclavicularis (Juillet, 1912) have had similar usage, but the shorter S. clavicularis is preferred.

(82) **Pars medialis; Pars lateralis.** The Pars medialis and Pars lateralis of the Saccus clavicularis are the primordial paired medial and lateral components of Locy and Larsell (1916a, b). These four primordial sacs fuse in most species, to form a single unpaired Saccus clavicularis. In *Meleagris* the Pars medialis persists as a pair of very small separate sacs (King and Atherton, 1970) (see also Annot. 77). It has been claimed that among the Ciconiiformes and Laridae the paired Pars medialis and Pars lateralis remain separate, giving four separate Sacci claviculares in the adult (King, 1966:214).

(83) **Diverticula intrathoracica.** The intrathoracic diverticula of the Saccus clavicularis extend variably around the heart (several **Diverticula cardiaca**) and along the sternum (several **Diverticula sternalia**) (Groebbels, 1932:57, 74-76; King, 1966: 212; Duncker, 1971; King, 1975:1910).

(84) **Diverticula extrathoracica.** The extrathoracic diverticula of the clavicular sac spread around the thoracic (pectoral) girdle (Groebbels, 1932:58, 74; King, 1966:212; Duncker, 1971; King, 1975:1911). Groebbels (1932:58) recognized four main extrathoracic diverticula: **Diverticulum subscapulare,** between the scapula and the thoracic cage; **Diverticulum axillare,** between the muscles around the shoulder region, and forming the **Diverticulum humerale** that invades the humerus in many species (**Osteo. Annot. 188, 189**); **Diverticulum subpectorale,** under the pectoral muscles; **Diverticulum suprahumerale,** covering the head of the humerus. Extensive subcutaneous diverticula have been reported in pelecaniforms, ciconiiforms, and coraciiforms (King, 1966:213). There is no agreement in the literature about the terminology for these diverticula; very little is known about species variations, so revision may be needed later.

(85) **Saccus thoracicus cranialis/caudalis.** Synonymy: ant./post. diaphragmatic sacs (Sappey, 1847; Juillet, 1912; Groebbels, 1935); middle-superior, middle-inferior sacs (Campana, 1875); ant., post. intermediate sacs (Locy and Larsell, 1916a, b); pre-postthoracic sacs (Schulze, 1910; Stresemann, 1934); ant., post. thoracic sacs (Akester, 1960). The thoracic sacs (paired) are essentially intrathoracic. The cranial sac is typically about one third the volume of the caudal sac, as in passeriforms; in this group the cranial sac connects with the clavicular (Duncker, 1971). The caudal thoracic sac is absent in *Meleagris* (King and Atherton, 1970). The thoracic sacs typically have no diverticula, but in phalacrocoracids diverticula of the cranial thoracic sac extend along the esophagus (Duncker, 1971).

(86) **Saccus abdominalis.** Synonymy: inferior sac (Campana, 1875); greater abdominal sac, McLeod and Wagers, 1939). The abdominal sac typically lies in the dorsocaudal region of the coelom. In many taxa (e.g., *Fratercula*) it is the largest sac, but in others (e.g., the closely related *Fulica*, and particularly *Apteryx* and sphenicids) it is one of the smallest (for reviews see King, 1966:216, and McLelland, 1989:264).

(87) **Diverticula perirenalia; Diverticula femoralia.** In many birds, the abdominal sacs give off several perirenal diverticula that extend along the kidneys, invading the adjacent vertebrae and pelvic girdle. Several femoral diverticula invade the bones and muscles of the pelvic limb (Groebbels, 1932:59; King, 1966:216; Duncker, 1971; King, 1975:1912).

(88) **Ossa pneumatica.** The air sacs invade the postcranial skeleton in most species, but the extent is extremely variable between species and even within species. Moreover, it is difficult to prove that a bone is not pneumatic at all, and errors have occcurred in the voluminous literature (King, 1966:223). In general the cervical sac pneumatizes the vertebral ribs, and cervical and thoracic vertebrae; the clavicular sac aerates the sternum, sternal ribs, thoracic girdle, and wing bones; and the abdominal sac aerates the pelvis, synsacrum, and bones of the pelvic limb (King, 1966:222). No bones are pneumatized by the thoracic sacs. The pneumatic bones of the postcranial skeleton of *Gallus* have been thoroughly reinvestigated (Hogg, 1984), but the facts for other species remain uncertain.

(89) **Foramen pneumaticum; Pori pneumatici.** The air sacs invade the skeleton through either a large pneumatic foramen or small pneumatic pores.

Table 8.1. Synonyms of syringeal muscles in oscine species Based on the text of Fürbringer (1886:p1091), and the Tables of Köditz (1925:140), Ames (1971:90), and Warner (1972b).

NAA	Owen, 1866 Shufeldt, 1890 Miskimen, 1951	Ames, 1971	Fürbringer, 1888 Gadow, 1896 Haecker, 1900
Mm. tracheolateralis	tracheo-lateralis	tracheolateralis	tracheobronchialis or trachealis
Mm. tracheobronchialis dorsalis	bronchotrachealis posticus	bronchotrachealis posticus	tracheobronchialis dorsalis
Mm. tracheobronchialis brevis	bronchotrachealis brevis	part of bronchotrachealis posticus	tracheobronchialis dorsalis brevis
Mm. tracheobronchialis ventralis	bronchotrachealis anticus	bronchotrachealis anticus	tracheobronchialis ventralis
Mm. syringealis dorsalis	bronchialis posticus	bronchialis posticus	syringeus dorsalis
Mm. syringealis ventralis	bronchialis anticus	bronchialis anticus, pars medialis and pars lateralis	syringeus ventralis
Mm.			syringeus ventrolateralis
Mm.			tracheobronchialis obliquus*
Mm.			
Mm.			

Table 8.1. Synonyms of syringeal muscles in oscine species (cont.)

Warner, 1972b	Köditz, 1925	Wunderlich, 1884	Setterwall, 1901
tracheolateralis	laryngosyringeus		
tracheobronchialis dorsalis	laryngosyringeus dorsolateralis	levator longus posterior arcus secundi	dorsolateralis longus
tracheobronchialis brevis	laryngosyringeus dorsalis (longus)	tensor mem. tympaniformis internae	dorsalis longus
tracheobronchialis ventralis	laryngosyringeus ventralis (longus)	levator longus anterior arcus secundi	ventralis longus
syringeus obliquus	syringeus dorsolateralis	levator brevis posterior arcus secundi	dorsolateralis brevis
syringeus ventralis	syringeus ventralis (brevis)	levator brevis anterior arcus secundi	ventralis brevis
	syringeus ventrilateralis internus (brevis)	laxator mem. tympaniformis externae	ventrilateralis brevis internus
	laryngosyringeus ventrilateralis (longus)*	rotator arcus tertii*	ventrilateralis brevis externus and ventrilateralis longus*
	syringeus dorsalis*		dorsalis brevis*
	syringeus ventrilateralis externus*		

*Synonomy uncertain.

Table 8.2. Some of the synonyms for the Bronchi secundarii.

Source	Bronchi medioventrales	Bronchi mediodorsales	Bronchi lateroventrales	Bronchi laterodorsales
Campana (1875)	Divergent	Internal	External	Posterior or dorsal
Huxley (1882)	Entobronchia	Ectobronchia		
Schulze (1908)	Ventral	Dorsal	Lateral	Intermediate
Juillet (1912)	Entobronchi	Ectobronchi		
Locy and Larsell (1916a, b)	Entobronchi	Ectobronchi	*Laterobronchi*	*Dorsobronchi*
Groebbels (1932)	Ventral	Dorsal	Lateribronchi	Dorsolateral
Vos (1934)	*Ventrobronchi*	*Dorsobronchi*	*Laterobronchi*	
McLeod and Wagers (1939)	*Ventrobronchi*	Dorsomedial	Dorsolateral	Dorsal
Grau (1943)	*Ventrobronchi*	*Dorsobronchi*		
Akester (1960)	Anterior dorsal	Posterior dorsal	Posterior ventral	
King (1966)	Craniomedial	Caudodorsal	Caudoventral	Caudolateral
Quitzow (1970)	Mediobronchi	*Dorsobronchi*	*Ventrobronchi*	*Laterobronchi*
Duncker (1971)	*Ventrobronchi*	*Dorsobronchi*	*Laterobronchi*	

Terms in italics have different meanings to different authors.

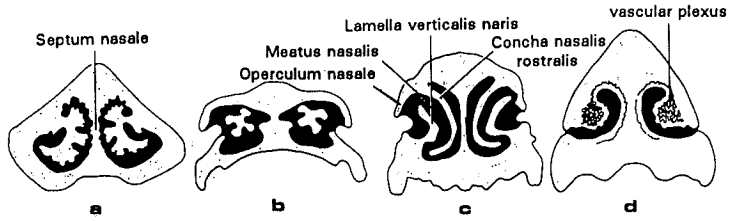

Fig. 8.1a. Transverse sections through the Concha nasalis rostralis of: (a) *Merops orientalis,* (b) *Nectarinia zeylonica,* (c) *Gallus gallus (domesticus),* and (d) *Steatornis caripensis.* Main airways black. The rich vascular plexus under the epithelium of the concha is shown in (d) only. Not to scale. From Bang and Wenzel (1985), with permission of the authors and Academic Press, London.

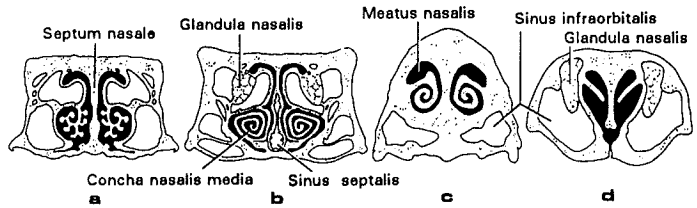

Fig. 8.1b. Transverse sections through the Concha nasalis media of (a) *Dromaius novaehollandiae,* (b) *Rhea americana,* (c) *Gallus gallus (domesticus),* and (d) *Fregata magnificens.* The concha in (c) typifies birds generally. Main airway black, other air spaces unshaded. Not to scale. From Bang and Wenzel (1985), with permission of the authors and Academic Press, London.

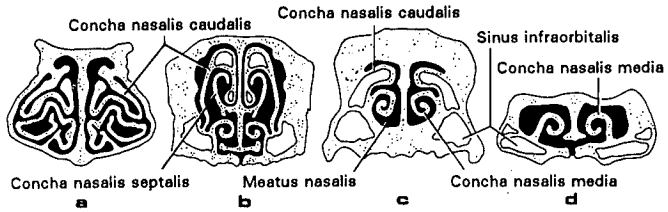

Fig. 8.1c. Transverse sections through the Concha nasalis caudalis of (a) *Apteryx australis,* (b) *Pagodroma nivea,* and (c) *Gallus gallus (domesticus),* and through the comparable region in (d) *Collocalia esculenta.* This concha has a relatively great surface area in the highly olfactory *Apteryx* and *Pagodroma.* The concha is absent in *Collocalia,* but the roof of the nasal cavity has olfactory epithelium. Nasal meatus black, other air spaces unshaded. Not to scale. From Bang and Wenzel (1985), with permission of the authors and Academic Press, London.

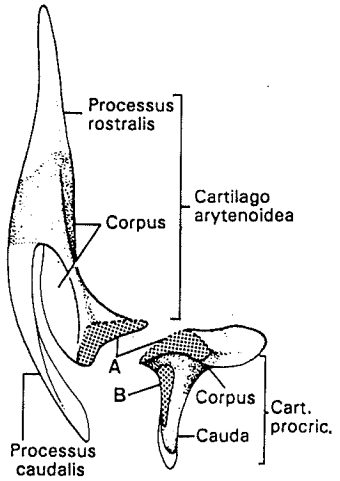

Fig. 8.2. Dorsal view of the left Cart. arytenoidea and the Cart. procricoidea of *Gallus*, rotated to display the surfaces of the Artc. procrico-arytenoidea (A) and a facet of the Artc. procrico-cricoidea (B). From White (1975), with permission of the author and Saunders, Philadelphia.

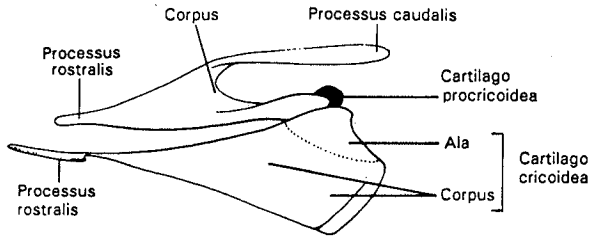

Fig. 8.3. Cartilagines laryngis of *Gallus*, left lateral view. From White (1975), with permission of the author and Saunders, Philadelphia.

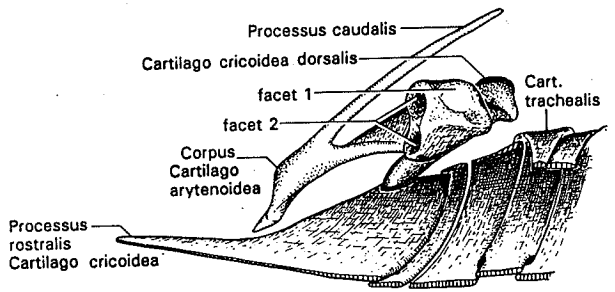

Fig. 8.4. Cartilagines laryngis of *Corvus corone* or *C. monedula*, medial view of the right half. The Ala of the Cart. cricoidea (Fig. 8.3) is represented in *Corvus* by the Cart. cricoidea dorsalis. Facet 1 on Cart. procricoidea is for Cart. cricoideus dorsalis, forming the Artc. procrico-cricoidea dorsalis; facet 2, two facets on Cart. procricoidea for Cart. arytenoidea, forming the Artc. procrico-arytenoidea. From Zweers and Berkhoudt (1987), with permission of the authors and Netherlands Journal of Zoology.

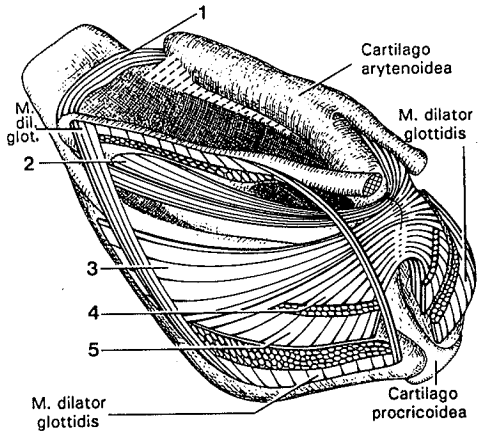

Fig. 8.5. The intrinsic laryngeal muscles of *Columba livia*, dorsocaudolateral view. Beneath the M. dilator glottidis, five components (1-5) of the M. constrictor glottidis are exposed. From Zweers, et al. (1981), with permission of the authors and Springer-Verlag.

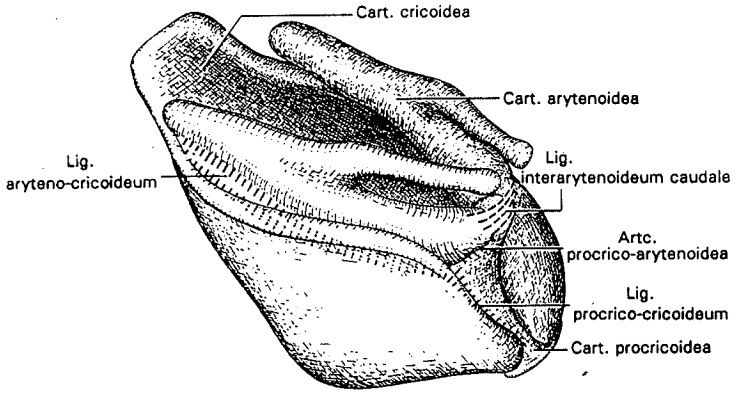

Fig. 8.6. Juncturae laryngis of *Columba livia*, dorsocaudolateral view. From Zweers, et al. (1981), with permission of the authors and Springer-Verlag.

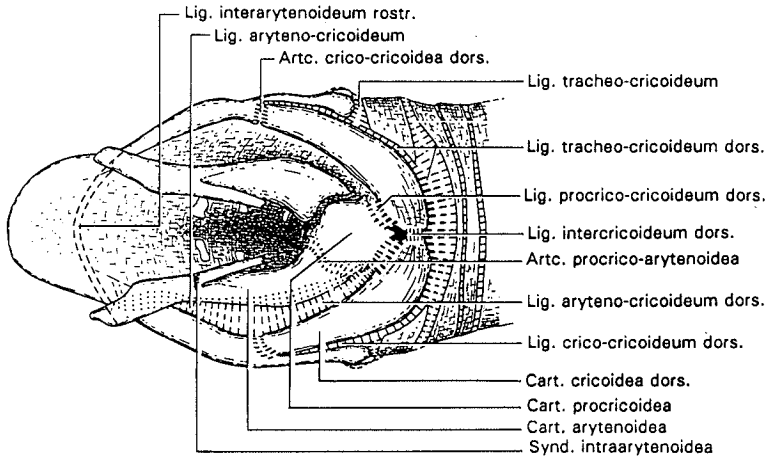

Fig. 8.7. Juncturae laryngis of corvid species, dorsal view. The left half shows the Synd. intra-arytenoidea between the body and caudal process of the arytenoid cartilage, found in *Corvus brachyrhynchos* only. The right half represents other corvids.

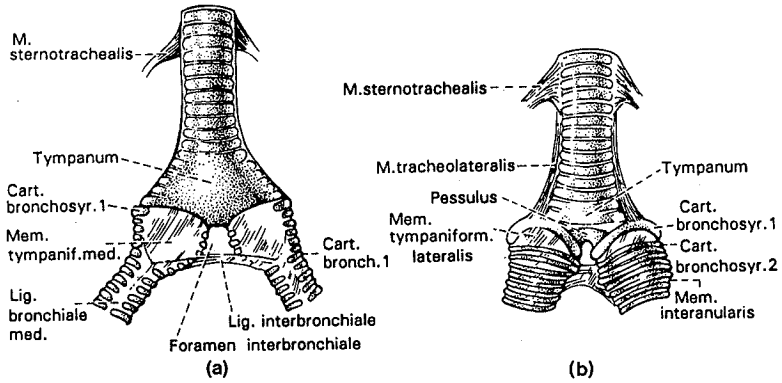

Fig. 8.8. Syrinx of female gull, *Larus argentatus*, (a) dorsal view; (b) ventral view. This is a typical, basic syrinx, of the tracheobronchial type. Five or six Cartt. tracheosyringeales are fused dorsally to form the Tympanum. There is a fairly distinct Mem. tympaniformis lateralis; Cart. bronchosyr. 1 is the most cranial bronchosyringeal cartilage; Cart. bronch. 1 is the first true bronchial cartilage; Mem. tympanif. med. is the medial tympaniform membrane. From King (1989), with permission of Academic Press, London.

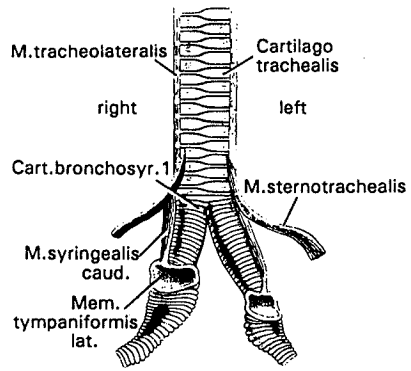

Fig. 8.9. Syrinx of the caprimulgiform *Steatornis caripensis*, ventral view. This is an extreme bronchial type of syrinx; having no Tympanum, the cranial boundary of the syrinx is the bifurcation of the airway. Both the left and the right elements of the syrinx carry a lateral (Mem. tympaniformis lat.) and a medial tympaniform membrane (latter not visible here). The syrinx is asymmetrical, with several more bronchosyringeal cartilages (Cart. bronchosyr.) on the left side than on the right. A single (paired) true syringeal muscle, M. syringealis caudalis, is present. From Garrod (1873).

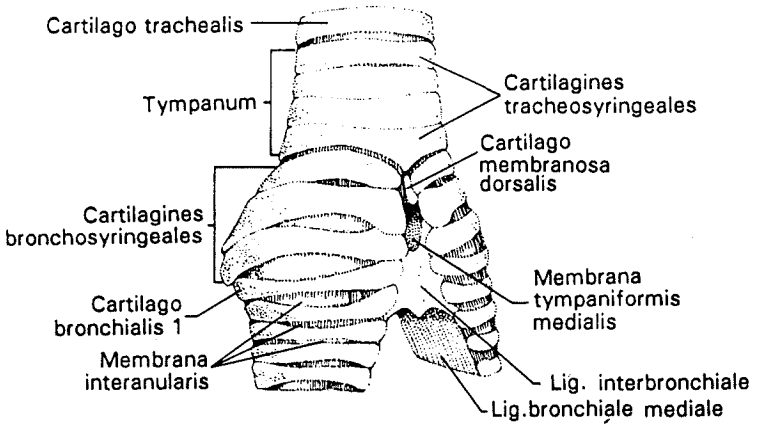

Fig. 8.10. Syringeal cartilages of the oscine *Pica pica*, dorsal view. The four Cartt. tracheosyringeales are fused to form the Tympanum. From Haecker (1900).

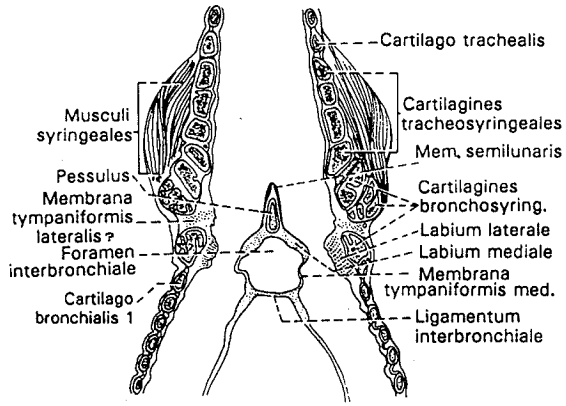

Fig. 8.11. Syrinx of the oscine *Turdus merula*, section in horizontal plane. The (stippled) soft tissue labelled "Mem. tympaniformis lateralis?" was so named by Haecker and others, but is too thick to be a true membrane; note its virtual continuity with the Labium laterale (also stippled). The four Cartt. tracheosyringeales form the Tympanum. From Haecker (1900).

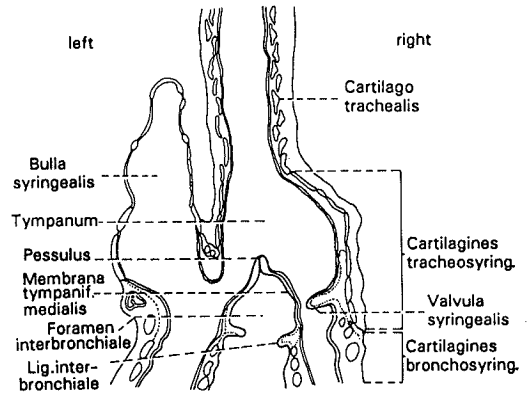

Fig. 8.12. Syrinx of a male anatid *Aythya fuligula*, section in horizontal plane. Abbreviations: bronchosyr., bronchosyringeales; tracheosyring., tracheosyringeales; tympanif., tympaniformis. From Warner (1971), with permission of the author and the Zoological Society of London.

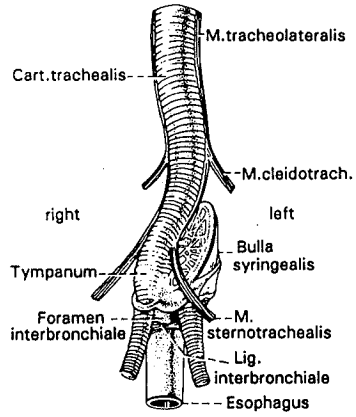

Fig. 8.13. Syrinx of a male anatid *Aythya fuligula*, ventral view. The Bulla syringealis is fenestrated by many irregular membranes. The M. cleidotrachealis is typical of anseriforms. From King (1989), with permission of Academic Press, London.

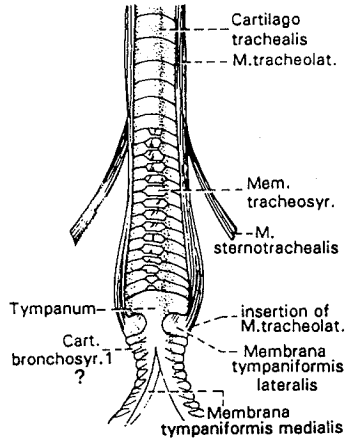

Fig. 8.14. Syrinx of the columbid *Streptopelia capicola*, dorsomedial view. The Cartt. tracheosyringeales (14 in this specimen) are reduced dorsally to thin bracelets embedded in the narrow elongated Mem. tracheosyringealis. As in columbids generally, the lateral wall of the Tympanum is completed by Mem. tympaniformis lateralis; M. tracheolateralis inserts directly on this membrane. Cart. bronchosyr. 1?, presumably is the most cranial Cart. bronchosyringealis. Redrawn from Rüppell (1933).

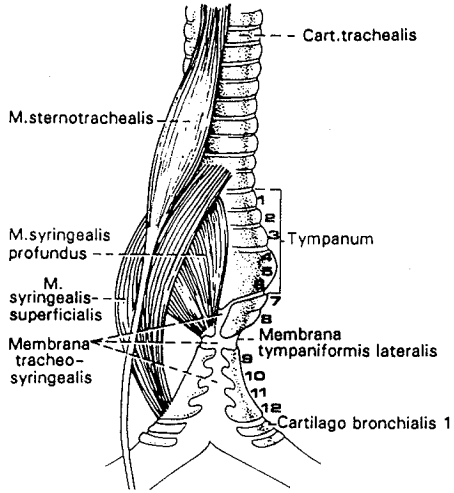

Fig. 8.15. Syrinx of the psittacid *Myiopsitta monachus*, ventral view. Cartilages 1 to 12 lie cranial to the bifurcation of the airway, and are therefore Cartt. tracheosyringeales. The increased diameter of rings 1, 2, and 3 shows that they are part of the Tympanum. The next cartilage, which also forms part of the Tympanum, is interpreted as three fused cartilage rings (4, 5, 6). Cartilages 7, 8, and 9-12 are paired, the median gap between them being closed by Mem. tracheosyringealis which is continuous laterally with the Mem. tympaniformis lateralis. There are two pairs of syringeal muscles, M. syringealis superficialis/profundus. From Gaunt and Gaunt (1985), with permission of the authors and Springer-Verlag.

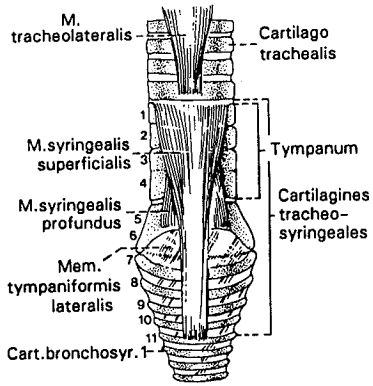

Fig. 8.16. Syrinx of the psittacid *Ara ararauna;* lateral view. Of the eleven Cartt. tracheosyringeales (1-11) 1 to 4 are fused to form the Tympanum. Cartilage 5-6 is paired and interpreted as two fused elements. Five more paired elements (7-11) occur cranial to bifurcation of the airway. The three cartilages immediately caudal to the bifurcation are C-shaped Cartt. bronchosyringeales (the first being Cart. bronchosyr. 1), supporting between them a Mem. tympaniformis medialis (not visible here); they form the entire skeleton of the Pars extrapulmonalis of the Bronchus primarius, which is therefore very short. From King (1989), with permission of Academic Press, London.

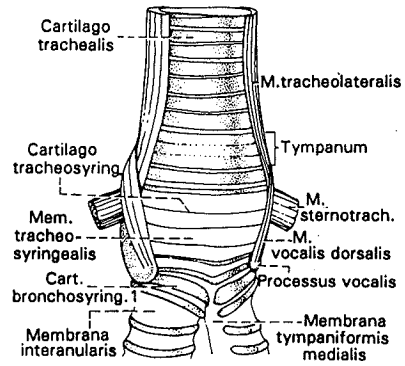

Fig. 8.17. Syrinx of the suboscine *Melanopareia maximiliani* (Rhinocryptidae), ventrolateral view. About 10 Cartt. tracheosyringeales altogether are present, the first three being fused ventrally to form the Tympanum (stippled). The three single lines which cross the (unstippled) Mem. tracheosyringealis are Cartt. tracheosyringeales reduced to delicate bracelets. One pair of syringeal muscles, M. vocalis dorsalis, is present. Cart. bronchosyr. 1 is the first bronchosyringeal cartilage. From Ames (1971), with permission of the author and the Peabody Museum of Natural History.

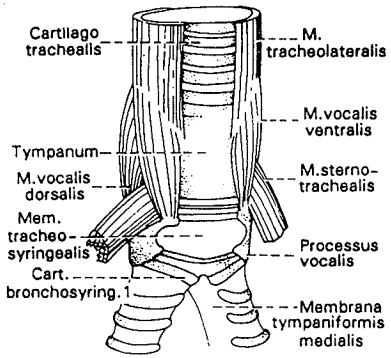

Fig. 8.18. Syrinx of the suboscine *Campylorhamphus trochilirostris* (Dendrocolaptidae), ventrolateral view. The Tympanum is formed from about nine fused Cartt. tracheosyringeales. The unstippled area caudal to the Tympanum is the Mem. tracheosyringealis, crossed cranially by three delicate Cartt. tracheosyringeales. Two pairs of syringeal muscles: M. vocalis dorsalis and ventralis. From Ames (1971), with permission of the author and the Peabody Museum of Natural History.

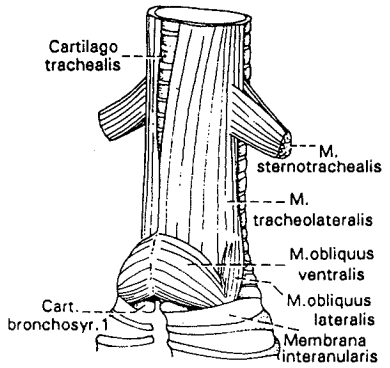

Fig. 8.19. Syrinx of the suboscine *Nuttalornis borealis* (Tyrannidae), ventrolateral view. This syrinx has virtually no Tympanum, having minimal fusion of Cartt. tracheosyringeales. Present are two pairs of syringeal muscles, M. obliquus ventralis/lateralis. From Ames (1971), with permission of the author and the Peabody Museum of Natural History.

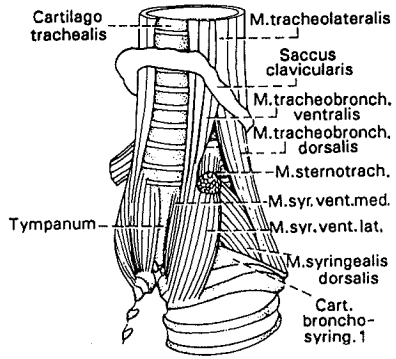

Fig. 8.20. Syrinx of the oscine *Corvus brachyrhynchos,* ventrolateral view. The Tympanum (visible in the midline) is formed from four fused Cartt. tracheosyringeales. Of the five pairs of syringeal muscles four are shown, M. tracheobronchialis ventralis/dorsalis, and M. syringealis ventralis/dorsalis. Ames (1971) interpreted M. syringealis ventralis as comprising a medial and lateral component (as shown). M. tracheobronchialis brevis is not illustrated. Abreviations: syr., syringealis. From Ames (1971), with permission of the author and the Peabody Museum of Natural History.

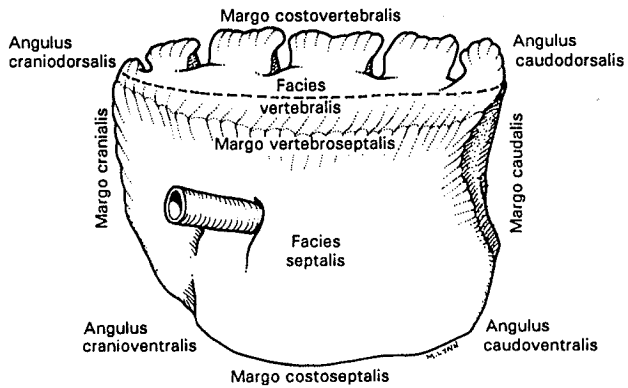

Fig. 8.21. Semidiagrammatic medial view of the right lung of *Gallus.* The broken line along the Facies vertebralis represents the Linea anastomotica. The Pars extrapulmonalis of the Bronchus primarius projects cranially from the Facies septalis. From King (1979), with permission of Academic Press, London.

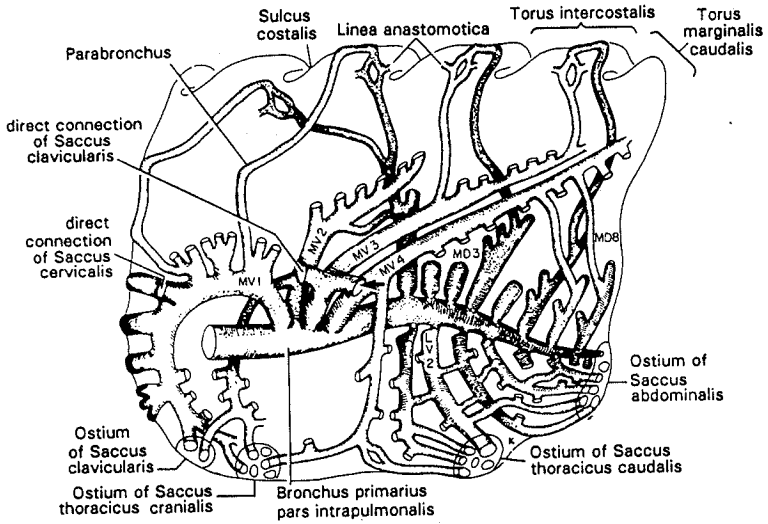

Fig. 8.22. Medial view of the right lung of *Gallus*, drawn as though transparent to show the main bronchi. Abbreviations: MV, Bronchi medioventrales; MD, Bronchi mediodorsales; LV, Bronchi lateroventrales. The four Ostia along the Margo costoseptalis are indicated by rings. *Arrow*, direct connection of Saccus thoracicus cranialis to bronchus MV3. From King (1966), with permission of Academic Press, London.

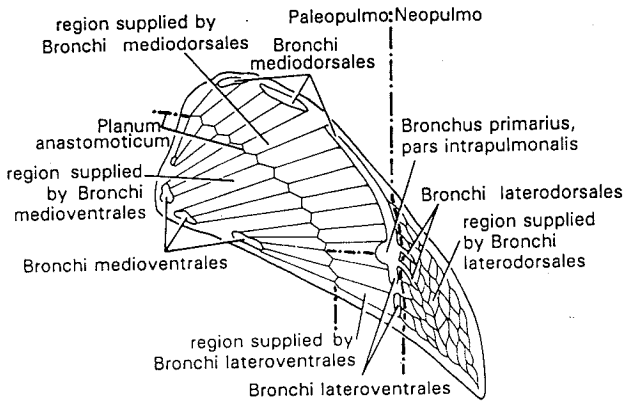

Fig. 8.23. Caudal view of a diagrammatic transverse section of the right lung of a bird with a well developed Neopulmo (e.g., *Gallus*), showing the approximate regions supplied by the four groups of Bronchi secundarii. From H.-R. Duncker, unpublished.

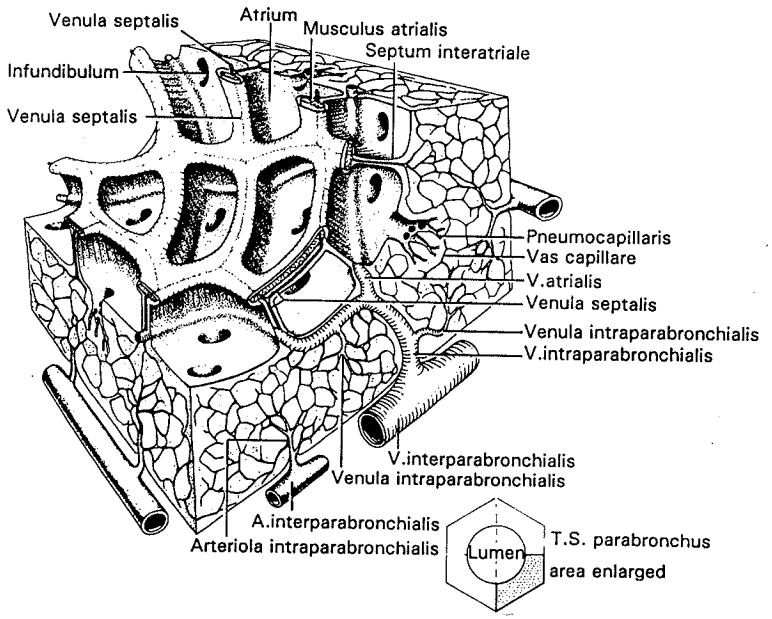

Fig. 8.24. Diagram of part of a Parabronchus (*Gallus*), showing the architecture of the wall of the Parabronchus and its blood vessels. For orientation see inset of transverse section of a Parabronchus. From King (1979), with permission of Academic Press, London.

9

APPARATUS DIGESTORIUS [SYSTEMA ALIMENTARIUM]

JOHN MCLELLAND

With contributions from subcommittee members: M. H. Clench, G. Duke, Gy. Fehér, Vl. Komárek, R. Landolt, G. Michel, T. Nishida, E. Pastea, U. M. Rawal, V. Simic, V. Ziswiler, G. Zweers.

I should like to take the opportunity of thanking the members of the Sub-Committee for their contributions to this chapter. In particular, I express my gratitude to Ruth Landolt who spent considerable time reviewing the Terminology and text and who made many valuable suggestions, and to Gart Zweers for his suggestions on the terminology of the oral cavity and and pharnyx and for making available Fig. 9.1.

TERMINOLOGY

CAVUM ORIS [CAVITAS ORALIS][1]

OS (Topog. Annot. 10)

- Bucca
- Rostrum (**Topog.** Annot. 12)
  - Rostrum maxillare (**Osteo.** Annot. 40)
  - Rostrum mandibulare (**Osteo.** Annot. 40)
- Dentes (**Osteo.** Annot. 82)
- Rima oris (**Topog.** Annot. 10)
- Angulus oris
- Palatum
  - Pars rostralis (**Resp.** Annot. 6)
  - Pars caudalis (**Resp.** Annot. 5)
  - Choana (Fig. 9.1)
  - Saccus oris[3]
  - Torus palatinus[22]
- Tunica mucosa oris (see Tun. muc. ling.)
  - Papillae palatinae[4]
  - Rugae palatinae[5]
    - Rugae palatinae laterales[5]
    - Rugae palatinae intermediales[5]
    - Ruga palatina mediana[5]
    - Ruga palatina transversalis[5]
  - Sulci palatini[6]
    - Sulci palatini laterales[6]

(continued)

OS (Topog. Annot. 10) (cont.)

- Sulcus palatinus medianus[6]
- Epithelium stratificatum squamosum[7]
- Caliculus gustatorius [Gemma gustatoria] (**Sens.** Annot. 6)
- Tela submucosa oris
- Corpus cavernosum palatae[8]

Glandulae oris[90]

- Gl. maxillaris[10]
- Gll. palatinae[11]
- Gl. anguli oris
- Gll. mandibulares rostrales[12]
- Gll. mandibulares caudales[13]
- Gll. mandibulares externae[14]
- Gll. mandibulares intermediae[14]
- Gll. mandibulares internae[14]
- Gll. linguales[15]
- Ductuli glandularum oralium[16]

LINGUA[17]

- Alae linguae[18]
- Apex linguae
- Corpus linguae
- Dorsum linguae
- Torus linguae[19]
- Margo linguae
- Radix linguae
- Ventrum linguae
- Frenulum linguae [F. lingualis]
- Papillae linguales[4]
- Papillae linguae caudales[4]

Sulci linguae[20]

- Rugae linguae
- Tunica mucosae linguae
  - Epithelium stratificatum squamosum[7]
  - Cuticula cornificata linguae[21]
  - Tela submucosa linguae
- Corpus cavernosum linguae[8]
- Musculi linguae (see **Myol.**)

APPARATUS HYOBRANCHIALIS [A. HYOLINGUALIS] (see Osteo. Arthr. Myol.)

PHARYNX[1]

- Cavum pharyngis [Cavitas pharyngealis]
- Infundibulum[22]
  - Rima infundibuli[22]
  - Sulcus medianus infundibuli
  - Sulcus lateralis infundibuli
  - Plica infundibuli
- Tuba auditiva (**Osteo.** Annot. 98)
- Tuba auditiva communis[22] (**Osteo.** Annot. 94)
- Ostium infundibulare tubae auditivae
- Glottis (Fig. 9.1)
- Tunica mucosa pharyngis
  - Papillae choanales[4]
  - Papillae pharyngis[4]
  - Papillae pharyngis caudoventrales[4]
  - Papillae pharyngis caudodorsales[4]
  - Plicae pharyngis[23]
  - Lymphonoduli pharyngis [Tonsilla pharyngea]
  - Epithelium stratificatum squamosum[7]

(continued)

PHARYNX[1] (cont.)

- Mons laryngealis (**Resp.** Annot. 22)
- Caliculus gustatorius [Gemma gustatoria] (**Sens.** Annot. 60)
- Tela submucosa pharyngis
- Tunica muscularis pharyngis

Glandulae pharyngis[9] (see Gll. oris)

- Gll. sphenopterygoideae[24]
- Gll. mandibulares caudales[13]
- Gll. cricoarytenoideae[25]
- Ductuli glandularium pharyngealium[26]

CANALIS ALIMENTARIUS

ESOPHAGUS [OESOPHAGUS]

- Pars thoracica
- Pars cervicalis
- Saccus esophagi[27]
- Ingluvies[28]
  - Ostium ingluviei
  - Fundus ingluviei
  - Diverticulum dextrum ingluviei[29]
  - Diverticulum sinistrum ingluviei[29]
  - Diverticulum medianum ingluviei[29]
- Tunica adventitia[30]
- Tunica muscularis
- Stratum longitudinale[31]
- Stratum circulare
- Tela submucosa
- Tunica mucosae ingluviei
  - Lamina muscularis mucosae
  - Plicae esophagi[32]
  - Plicae ingluviei[32]
  - Rugae ingluviei[33]
  - Epitheliocytus squamosus
- Gll. esophageae [Gll. esophageales][34]
  - Gll. ingluviei[35]
  - Mucocytus
  - Lymphonoduli esophageales[36]

Junctura esophagoproventricularis[37]

GASTER[37]

PROVENTRICULUS GASTRIS [PARS GLANDULARIS][38]

- Regio glandularis[39]
- Diverticulum proventriculi[39]
- Tunica serosa
- Tela subserosa
- Tunica muscularis
  - Stratum longitudinale
  - Stratum circulare
- Tela submucosa
- Tunica mucosa proventriculi
  - Plicae proventriculi[40]
  - Papillae proventriculi[41]
  - Rugae proventriculi[42]
  - Sulci proventriculi[42]
  - Mucocytus
  - Endocrinocytus gastrointestinalis[43]
- Gll. proventriculares superficiales[44]
- Gll. proventriculares profundae[41]
  - Mucocytus[45]

(continued)

PROVENTRICULUS GASTRIS [PARS GLANDULARIS][38] (cont.)

- Epitheliocytus columnaris[45]
- Epitheliocytus oxynticopepticus[46]
- Endocrinocytus gastrointestinalis[43]
- Lamina muscularis mucosae[47]
- Zona intermedia gastris[48]
- Isthmus gastris[48]

VENTRICULUS GASTRIS [PARS MUSCULARIS][49]

- Facies tendinea[50]
- Facies anularis [annularis][51]
- Curvatura minor[52]
- Incisura angularis[53]
- Curvatura major[52]
- Corpus ventriculi[54]
  - Saccus cranialis[54]
  - Saccus caudalis[54]
  - Sulcus cranialis[55]
  - Sulcus caudalis[55]
  - Plica angularis[56]
- Tunica serosa
- Tela subserosa
- Tunica muscularis
  - Stratum longitudinale[57]
  - Stratum circulare[58]
  - M. crassus cranioventralis[59]
  - M. crassus caudodorsalis[59]
  - M. tenuis craniodorsalis[59]
  - M. tenuis caudoventralis[59]
  - Centrum tendineum[60]
- Tela submucosa
- Tunica mucosae ventriculi
  - Lamina muscularis mucosae[61]
  - Plicae ventriculi[62]
  - Rugae ventriculi[63]
  - Sulci ventriculi[63]
  - Exocrinocytus columnaris[64]
  - Endocrinocytus gastrointestinalis[43]
  - Gll. ventriculares
  - Epitheliocytus nondifferentiatus
  - Exocrinocytus columnaris[64]
  - Cuticula gastris[65]
    - Procc. conicales[66]
    - Procc. dentales[66]
- Ostium ventriculopyloricum (Figs. 9.7, 9)

PARS PYLORICA GASTRIS[67]

- Bulbus pyloricus[68]
- Torus pyrloricus[69]
- Pylorus
- Tunica serosa
- Tela subserosa
- Tunica muscularis
  - Stratum longitudinale
  - Stratum circulare
  - Tela submucosa
- Tunica mucosa
  - Plicae pyloricae[71]
  - Exocrinocytus columnaris
  - Endocrinocytus gastrointestinalis[43]
  - Gll. pyloricae
  - Exocrinocytus columnaris
  - Cuticula gastris[65]
  - Papillae filiformes pyloricae[72]
- Ostium pyloricoduodenale[70]

INTESTINUM

INTESTINUM TENUE[73]

- Duodenum
  - Ansa duodeni[74]
    - Pars descendens
    - Flexura duodeni
    - Pars ascendens
    - Flexura duodenojejunalis
    - Papilla duodeni [Papilla duodenalis][75]
  - Gll. duodeni[90]
- Jejunum[76]
  - Ansae jejuni[77]
  - Ansa axialis[77]
  - Diverticulum vitellinum[78]
    - Saccus vitellinus
    - Ductus vitellinus
    - Papilla ductus vitellini[79]
    - M. sphincter diverticuli vitellini[87]
- Ileum[76]
  - Ansae ilei[77]
  - Ansa supraduodenalis[77]
  - Ansa supracecalis[77]
  - Papilla ilealis[80]
  - M. sphincter ilei[88]
  - Ostium ileocecale

INTESTINUM CRASSUM

- Cecum[81]
  - Basis ceci[82]
  - Corpus ceci[82]
  - Apex ceci[82]
  - Diverticula ceci[83]
  - Haustra ceci[83]
  - Ruga spiralis[83]
  - Ostium ceci[84]
  - M. sphincter ceci[88]
- Rectum [Colon][85]
  - Tunica serosa
  - Tela subserosa
  - Tunica muscularis
    - Stratum longitudinale
    - Stratum circulare
    - Pars externa[86]
    - Pars interna[86]
    - M. sphincter rectocoprodei[89]
  - Tela submucosa
    - Tunica mucosa
      - Lamina muscularis mucosae
      - Villi intestinales[91]
      - Plicae intestinales villosae[91]
      - Plicae intestinales submucosae[91]
      - Epitheliocytus columnaris
      - Exocrinocytus caliciformis
      - Endocrinocytus gastrointestinalis[43]
      - Gll. [Cryptae] intestinales[91]
      - Epitheliocytus nondifferentiatus
      - Epitheliocytus columnaris
      - Exocrinocytus caliciformis
      - Exocrinocytus cum granulis acidophilicis[92]
    - Lymphonoduli solitarii (see **Lym.**)
    - Lymphonoduli cecales (see **Lym.**)
    - Lymphonoduli rectales (see **Lym.**)
    - Anuli [Annuli] lymphatici jejunales (see **Lym.**)
    - Anuli [Annuli] lymphatici ileales
- M. sphincter rectocoprodei[89] (see **Cloaca**

CLOACA (see **Urogen.** Section on Cloaca)

HEPAR

Facies parietalis
Facies visceralis
Margo cranialis (Fig. 9.13)
Margo caudalis
Porta hepatis[94]
Fossa vesicae biliaris [F. v. felleae]
Impressio cardiaca
Impressio proventricularis
Impressio ventricularis (Fig. 9.13)
Impressio duodenalis[95]
Impressio jejunalis
Impressio splenalis
Impressio testicularis[96]
Incisura cranialis[97]
Incisura interlobaris[97]
Incisura caudalis[97]
Margo dexter (Fig. 9.13)
Margo sinister
Margo cranialis (Fig. 9.13)
Margo caudalis
Lobus dexter hepatis (Fig. 9.13)
  Proc. dorsalis dexter[98]
Lobus sinister hepatis (Fig. 9.13)
  Incisura lobaris[99]
  Pars lateralis[100]
  Pars medialis[100]
  Proc. dorsalis sinister[98]
  Proc. papillaris[101]
Pars interlobaris (Fig. 9.13)
  Proc. ventralis dexter[101]
  Proc. ventralis medius[101]
  Proc. cranialis[101]
Canales portales[102]
Capsula fibrosa perivascularis[102]
Trias hepatica[102]
Tunica fibrosa[93]
Tunica serosa[93]
Aa. interlobulares[102] (see **Art.**)
Vv. interlobulares[102] (see **Ven.**)
Ductuli interlobulares[102]
Lobuli hepatis[103]
  Lamina hepatica[104]
  Epitheliocytus hepatis [Hepatocytus]
  Canaliculi biliferes[104]
  Lacuna hepatis[105]
  Vasa sinusoidea[106]
  Macrophagocytus stellatus[106]
  Spatium perisinusoideum[106]
  Lipocytus perisinusoideus[106]
  Vv. centrales[106] (see **Ven.**)
  Vv. sublobulares[106]
Ductuli biliferes[107]
Ductus hepaticus dexter[107]
Ductus hepaticus sinister[107]
Ductus hepatocysticus[107]
Ductus hepatoentericus dexter[107]
Ductus hepatoentericus communis[107]
Ductus hepatoentericus accessorius[107]
Vesica biliaris [V. fellea][108]
  Ductus cysticoentericus[109]
  Tunica serosa
  Tela subserosa
  Tunica muscularis
  Tela submucosa
  Tunica mucosa vesicae
    Plicae tunicae mucosae
    Exocrinocytus columnaris

PANCREAS[110] (see **Endoc.** Annot.[7])

Lobus pancreatis dorsalis
Lobus pancreatis ventralis
Lobus pancreatis tertius
Lobus pancreatis splenalis

(continued)

PANCREAS[110] (see **Endoc.** Annot.[7]) **(cont.)**

Ductus pancreaticus dorsalis
Ductus pancreaticus ventralis[110]
Ductus pancreaticus tertius[110]
Tunica adventitia
Tunica mucosa
Tunica muscularis
M. sphincter ductus pancreatici[111]
Pars exocrina pancreatis
  Acini pancreatici
  Lobuli pancreatici
  Septa interlobularia
  Exocrinocytus pancreaticus
  Epitheliocytus centroacinosus
  Ducti intercalati
  Ducti intralobulares
  Ducti interlobulares
Pars endocrina pancreatis (**Endoc.** Annot. 7)

ANNOTATIONS

(1) **Cavum oris; Pharynx; Cavum pharyngis; Esophagus [Oesophagus].** Synonomy for Cavum oris and Cavum pharyngis: Cavitas oralis and Cavitas pharyngealis. Because in most birds there is no soft palate or oropharyngeal isthmus, the oral and pharyngeal cavities of birds together form a common chamber often referred to as the "oropharynx" (Fig. 9.1). On the basis of the embryology of the visceral arches, Lucas and Stettenheim (1972: 18) proposed that the dorsal transverse boundary between the oral and pharyngeal cavities lies between the Choana and the Rima infundibuli, extending laterally to the angles of the jaws. They suggested that the ventral transverse boundary between the two cavities lies between the paraglossal and basihyal bones (see **Osteo.**). In relation to surface features Zweers, et al. (1977) described the boundary in *Anas* as occurring at the level of the caudal lingual papillae (Fig. 9.1). Similarly they placed the junction of the pharynx and esophagus at the level of the caudodorsal and caudoventral pharyngeal papillae (Fig. 9.1).

(2) **Torus palatinus.** This term covers a variety of swellings of the palate like the highly vascular palatal cushion or pad of many psittacids (Evans, 1969) and the relatively broad elevations on the palate of many anseriform and passeriform (Fig. 9.1) species (Ziswiler, 1965; Kooloos, et al., 1989).

(3) **Saccus oris.** This term refers to the inflatable type of oral sac of some bustards (Otididae) (Fig. 9.2) described by Murie (1868, 1869) and Garrod (1874a, b) which is used during courtship for display or as a resonating chamber, as well as the various forms of food-carrying oral sacs such as the paired pouches of the Rosy Finch (*Leucosticte arctoa*) (Miller, 1941).

(4) **Papillae palatinae; Papillae linguales; Papillae linguae caudales; Papillae pharyngis; Papillae choanales; Papillae pharyngis caudoventrales; Papillae pharyngis caudodorsales.** The papillae of the palate, tongue, and pharynx (Fig. 9.1) show a wide range of interspecific differences in their shape and distribution. Because of the enormous variation in the anatomy of the oropharynx, attempts in the literature to name individual papillae according to their position have in general not proved

successful. However, most birds have a transverse row of lingual papillae at the base of the tongue (Papillae linguae caudales) (Fig. 9.1) and rows of pharyngeal papillae at the margin of the choana (Papillae choanales) (Fig. 9.1) caudal to the larynx (Fig. 9.1) (Papillae pharyngis caudoventrales) (Fig. 9.1) and caudal to the Rima infundibuli (Papillae pharyngis caudodorsales) (Zweers, et al., 1977; Zweers, 1982; Zweers and Berkhoudt, 1987; Kooloos, et al., 1989; Heidweiller and Zweers, 1990). Unlike in mammals, there has been little attempt to name papillae according to their shape, although Komárek, et al. (1982) in domestic birds were able to distinguish lenticular papillae and major and minor conical papillae.

(5) **Rugae palatinae; Rugae palatinae laterales; Ruga palatinae intermediales; Ruga palatina mediana; Ruga palatina transversalis.** Ridging of the palate (Fig. 9.1) is widespread in birds. Individual ridges may be named according to their position on the palate and whether they arise directly from the roof or indirectly from another ridge. A lateral palatine ridge on each side of the choana appears to be relatively common in birds (Göppert, 1903). In some species, e.g. *Gallus* and *Anser*, there is also a median ridge. Lateral, intermediate, and median palatine ridges occur in granivorous passerines, a variable number of secondary and tertiary ridges arising from the sides of the intermediate and lateral ridges (Ziswiler, 1965; Heidweiller and Zweers, 1990). In *Anas* Zweers, et al. (1977) described a transverse palatine ridge at the rostral part of the choana.

(6) **Sulci palatini; Sulci palatini laterales; Sulcus palatinus medianus.** Palatine grooves (Fig. 9.1) have been described in many species and may be individually named according to their position or orientation. For example, in most seed-eating passerines a lateral groove occurs between the lateral palatine ridge and the Tomium (**Topog.** Annot. 14) of the beak (Ziswiler, 1965), while a median transversely-oriented V-shaped groove is present in the palate of the Budgerigar (*Melopsittacus*) (Feder, 1969).

(7) **Epithelium stratificatum squamosum.** The stratified squamous epithelium of the oral cavity and pharynx is keratinized in areas subject to abrasion.

(8) **Corpus cavernosum palatae; Corpus cavernosum linguae.** Corpora cavernosa of the palate and tongue have been described in the Zebra Finch (*Poephila guttata*) by Heidweiller and Zweers (1990).

(9) **Gll. oris; Gll. pharyngis.** The terminology for the oral and pharyngeal salivary glands does not cover the subdivisions of the glands which show many interspecific variations (see Antony, 1920; Groebbels, 1932; Farenholz, 1937; McLelland, 1979; Homberger and Meyers, 1989; and Fig. 9.3). See Annot. 15, Gll. linguales.

(10) **Gl. maxillaris.** Synonymy: Gll. palatine maxillares (Antony, 1920). The maxillary gland is present in the rostral part of the palate (Fig. 9.3).

(11) **Gll. palatinae.** Synonymy: Gll. palatinae posteriores (Antony, 1920). In *Gallus* there are Gll. palatinae mediales and Gll. palatinae laterales (Saito, 1966). In *Columba* Zweers (1982) observed posterior external and internal palatine glands.

(12) **Gll. mandibulares rostrales.** Synonymy: Gll. inframaxillares (Cholodkowski, 1892); Gll. submaxillares anteriores (Heidrich, 1908); Gl. sublingualis (Homberger and Meyer, 1989). See Fig. 9.3. In *Caprimulgus* the rostral and caudal mandibular glands are represented by a single group of glands, the submandibular glands of Antony (1920).

(13) **Gll. mandibulares caudales.** Synonymy: Gll. submaxillares posteriores (Heidrich, 1908); Gll. mandibulares posteriores (Antony, 1920); Gl. mandibularis (Homberger and Meyer, 1989). The part of the Gll. mandibulares caudales in woodpeckers (Picidae), which produces the extremely sticky fluid that coats the tongue, is called the Gl. picorum by Antony (1920). In *Gallus* (Fig. 9.3) the caudal mandibular glands consist of medial, intermediate, and lateral groups (Saito, 1966). See Annot. 12.

(14) **Gll. mandibulares externae; Gll. mandibulares intermediae; Gll. mandibulares internae.** In many granivores and insectivores the mandibular glands consist of external, intermediate, and internal groups (Antony, 1920; Foelix, 1970).

(15) **Gll. linguales.** Rostral and caudal lingual glands (Fig. 9.3) occur in *Gallus* (Saito, 1966). Homberger and Meyer (1989) named the rostral gland Gl. lingualis rostralis and the caudal gland Gl. praeglottalis. In *Columba* Zweers (1982) observed inferior, anterior superior and posterior superior lingual glands.

(16) **Ductuli glandularum oralium.** The palatine, rostral mandibular, and lingual salivary glands have numerous openings, whereas the maxillary gland and the Gl. anguli oris have generally one opening each.

(17) **Lingua.** The nomenclature of the tongue is general and does not cover detailed interspecific variations (see Lucas, 1897; Gardner, 1926; McLelland, 1979; and Fig. 9.1).

(18) **Alae linguae.** The wings of the tongue are the bilateral caudally directed projections which occur at the root of the tongue in a number of taxa. See Heidweiller and Zweers (1990).

(19) **Torus linguae.** The lingual torus is the raised caudal part of the tongue in anatids.

(20) **Sulci linguae.** Grooves on the dorsal surface of the tongue have been described in many species and may be individually named according to their position (Fig. 9.1).

(21) **Cuticula cornificata linguae.** The heavily keratinized epithelium forming the nail-like plate on the ventral surface of the tongue of some species, e.g. *Gallus* (Susi, 1969).

(22) **Infundibulum; Rima infundibuli; Tuba auditiva communis.** The paired auditory tubes join one another at their median ends within the Basis cranii near the base of the Rostrum parasphenoidale. Here they form the Tuba auditiva communis; rostrally the common tube (e.g., in *Gallus* and *Columba*) opens into the dorsocaudal part of the Infundibulum, a laterally compressed, median chamber located caudal to the nasal cavity. A common tube is not present in ratites. The expanded, ventral end of the Infundibulum is connected with the pharynx via a short median cleft, the Rima infundibuli, located just caudal to the Pars caudalis of the Choana. See Fig. 9.4 and consult Heidrich (1908) for details of the Infundibulum. See also **Osteo.** Os parasphenoidalis and Annot. 94, 98.

(23) **Plicae pharyngis.** Both transverse and longitudinal pharyngeal folds have been described (see, e.g., Zweers and Berkhoudt, 1987).

(24) **Gll. sphenopterygoideae.** Synonymy: Gll. pterygoideae (Antony, 1920). The sphenopterygoid glands are distributed in the roof of the oral and pharyngeal cavities around the choanal and infundibular openings (Fig. 9.3).

(25) **Gll. cricoarytenoideae.** Synonymy: Gll. laryngeales (Homberger and Meyer, 1989). The cricoarytenoid glands are distributed in the laryngeal mound (Fig. 9.3).

(26) **Ductuli glandularium pharyngealium.** All the pharyngeal salivary glands have numerous multiple openings.

(27) **Saccus esophagi.** The esophageal sac is an inflatable enlargement of the cervical esophagus (Fig. 9.2) which functions during the breeding season in "showing off", or as a resonating chamber for the production of mating calls. Among the species possessing this sac are the Sage Grouse (*Centrocercus urophasianus*) (Clarke, et al., 1942; Honess and Allred, 1942), the Australian Bustard (*Ardiotis australis*) (Garrod, 1874a, b), and the Painted Snipe (*Rostratula benghalensis*) (Niethammer, 1966).

(28) **Ingluvies.** The Ingluvies or crop (Fig. 9.5) is in many taxa an expansible portion of the esophagus in which food is stored. Usually situated in the neck, it may be spindle-shaped as in *Casuarius*, *Anas*, and *Otis* and the emberizids and fringillids, or pendulant and sac-like as in tinamiform, falconiform, galliform, columbiform, and psittaciform species (Gadow, 1879a, b; 1891a: 671); Swenander, 1899, 1902; Niethammer, 1933; Ziswiler, 1967). The crop of *Opisthocomus* is unusual in consisting of both cervical and thoracic parts (Gadow, 1891; Boker, 1929). In addition to its storage function the crop of pigeons and doves (Columbidae) produces the nutritive "crop milk", while in *Opisthocomus*, in which the stomach is very reduced, the crop plays a unique role in the processing and bacterial fermentation of tough plant material (Grajal, et al., 1989). Among forms without a crop are penguins (Spheniscidae) and gulls (Laridae).

(29) **Diverticulum dextrum/sinistrum ingluviei; Diverticulum medianum ingluviei.** Right, left, and median diverticula occur in the crop of the columbids (Fig. 9.5d) (see Landolt, 1987a).

(30) **Tunica adventitia.** In the adventitial tunic of the pendulant type of crop like that of galliform species, striated muscle fibres of the M. cucullaris capitis, pars clavicularis may be present (see **Myol.** Annot. 9).

(31) **Stratum longitudinale.** A longitudinal layer of muscle is found in the esophagus of species of only a small number of families (Swenander, 1902; Hanke, 1957). Among pigeons it occurs in only a few species and is restricted to the thoracic part of the esophagus (Landolt, 1987a).

(32) **Plicae esophagi; Plicae ingluviei.** Longitudinal esophageal folds are present when the esophagus is contracted and disappear when the tube dilates. Similar ingluvial folds occur in the crop, although they are less regularly arranged (Landolt, 1987a).

(33) **Rugae ingluviei.** The mucous membrane of the exceptionally large crop of *Opisthocomus hoazin* is raised into approximately 20 roughly parallel ridges (Gadow, 1891; Boker, 1929). In columbiforms the caudal part of the crop has two to six ridges which are packed with glands (Landolt, 1987a).

(34) **Gll. esophageae [Gll. esophageales].** Wide variations in the structure and density of the esophageal glands occur in different species (Ziswiler, 1967; Landolt, 1987a). In *Melopsittacus* glands are totally absent from the cervical esophagus (Feder, 1969).

(35) **Gll. ingluviei.** The ingluvial glands are limited in number in the more sac-like forms of crop (Swenander, 1902).

(36) **Lymphonoduli esophageales.** Synonymy: Tonsilla esophagealis. Nodules of lymphoid tissue are frequently associated with the esophageal glands in the wall of the esophagus (Hodges, 1974: 46). See **Lym.** Annot. 18.

(37) **Gaster.** Synonymy: Ventriculus (Schummer, 1973: 48). The stomach consists basically of three compartments which may or may not be extremely distinguishable from each other. The cranial chamber is the Proventriculus which is continuous cranially with the Esophagus **(Junctura esophagoproventricularis)** and secretes gastric juice. The caudal chamber is the Ventriculus which in many species is the organ of mechnical digestion. Arising from the side of the Ventriculus is the small Pars pylorica gastris which connects the Ventriculus with the Duodenum.

Two basic types of stomach can usually be distinguished depending on whether the organ is adapted primarily for storage or has an important role in the physical preparation of food (McLelland, 1979). The first type characteristic of fish- and meat-eaters is a relatively undifferentiated, poorly-muscled sac-like structure (see Figs. 9.8, 10), the junction between the Proventriculus and Ventriculus being difficult to identify externally. In the second type, characteristic of omnivores, insectivores, herbivores, and granivores the Proventriculus and Ventriculus are clearly distinguishable from each other, the muscle tunic of the Ventriculus being massively developed (see Fig. 9.6). The form of the stomach in many birds, e.g. testacivores, is intermediate to these two types.

(38) **Proventriculus gastris [Pars glandularis].** Synonymy: Vormagen, Infundibulum, cardiac cavity, ventricule pepsique, ventricle succenturie, jabot (Schepelmann, 1906). See Figs. 9.6-10.

(39) **Regio glandularis; Diverticulum proventriculi.** The deep glands of the proventriculus (Annot. 41) are not distributed uniformly throughout the Proventriculus in some taxa, but are restricted to certain glandular regions (Fig. 9.8) as in *Buteo* and *Grus* (Swenander, 1902), *Struthio* (Cazin, 1887), *Chauna* (Mitchell, 1895), and *Eudyptula* (Pernkopf and Lehner, 1937), or to a diverticulum of the proventriculus as in *Anhinga* (Garrod, 1876) (Fig. 9.9).

(40) **Plicae proventriculi.** In some species, e.g., fish- and meat-eaters, proventricular folds serve to increase the storage capacity of the organ (Cazin, 1887; Swenander, 1902; Magnan, 1912). In certain procellariiforms, however, the folding of the proventricular wall has been described as an arrangement which allows an increase in the number of deep glands (Matthews, 1949).

(41) **Papillae proventriculi; Gll. proventriculares profundae.** In some species e.g., *Gallus* the inner surface of the proventriculus has numerous papilla-like elevations of the mucous membrane. The deep proventricular compound glands, which are the source of gastric juice, open on the apices of the papillae. For a description of the glands in *Anas* and *Gallus* see Michel (1971) and Hodges (1974: 51).

(42) **Rugae proventriculi; Sulci proventriculi.** The low merging ridges and grooves between the openings of the deep proventricular glands. In columbids the ridges form species-specific surface relief patterns, which are flattened when the proventricular wall dilates (Landolt, 1987a).

(43) **Endocrinocytus gastrointestinalis.** Gastrointestinal endocrine cells are scattered throughout the stomach and gut epithelium. They appear to be most concentrated in the pyloric part of the stomach. For a review see Hodges (1981) and **Endoc.** Annot. 6.

(44) **Gll. proventriculares superficiales.** Some taxa, e.g. *Gallus,* columbiforms, and *Melopsittacus* are reported to have no true superficial proventricular glands (Joos, 1941; Hodges, 1974; Landolt, 1987a).

(45) **Mucocytus; Epitheliocytus columnaris.** Although the ducts of the deep proventricular glands are lined by columnar epithelium, in *Gallus* only the cells of the largest ducts contain mucous granules.

(46) **Epitheliocytus oxynticopepticus.** In birds one cell type of the proventriculus combines the functions of the mammalian chief and parietal cells, and secretes both hydrochloric acid and pepsinogen.

(47) **Lamina muscularis mucosae.** In the proventriculus the muscularis mucosae is split by the deep glands into inner and outer layers.

(48) **Zona intermedia gastris; Isthmus gastris.** Synonymy for Zona intermedia gastris: cardia, Schalstück, Zwischenschlund (Schepelmann, 1906). The intermediate zone is the variably developed region (Figs. 9.7, 10) between the Proventriculus and Ventriculus which has histological features intermediate between the two. The zone sometimes marked off from the Proventriculus by a constricted Isthmus (Fig. 9.6).

(49) **Ventriculus gastris [Pars muscularis].** Synonymy: Kaumagen, Reibmagen, Pylorusraum, estomac proprement dit, ventricule charnu (Schepelmann, 1906) (Figs. 9.6-10). The common English name for this part of the stomach is "gizzard".

(50) **Facies tendinea.** Synonymy: Facies parietalis and Facies visceralis (Komárek, et al., 1982). The term used by Groebbels (1932: 472) for paired, relatively flat surfaces of the Ventriculus each of which contains a tendinous centre (Annot. 60 and Fig. 9.6). In the well-muscled Ventriculus, e.g., the chicken, the surfaces clearly face to the left and right.

(51) **Facies anularis [F. annularis].** Synonymy: Margo dorsalis, Margo ventralis, Margo cranialis and Margo caudalis (Komárek et al. 1982). The annular facies are the two relatively narrow surfaces of the well-muscled type of stomach which dorsally and ventrally unite the left and right tendinous surfaces (Fig. 9.6).

(52) **Curvatura minor; Curvatura major.** The lesser and greater curvatures are the short and long lengths of the circumference of the ventriculus between Proventriculus and Duodenum (Fig. 9.8).

(53) **Incisura angularis.** In some birds with a sac-like stomach e.g., *Phalacrocorax carbo* and *Ardea cinerea,* the lesser curvature of the Ventriculus is strongly angled (Pernkopf and Lehner, 1937).

(54) **Corpus ventriculi; Saccus cranialis; Saccus caudalis.** Synonymy for Saccus cranialis/caudalis of the ventriculus: superior/inferior sac (Garrod, 1872); poche superieur and cul-de-sac inferieur (Cazin, 1887); craniodorsal/caudoventral sac (Dziuk and Duke, 1972); kranialer/kaudaler Blindsack (Schummer, 1973: 54). The body (Corpus), cranial sac, and caudal sac (Fig. 9.7) can be identified in the well-muscled type of Ventriculus, but cannot be distinguished in the less developed types like those of most fish- and meat-eaters.

(55) **Sulcus cranialis; Sulcus caudalis.** Synonymy: sillon antero-superieur and sillon postero-inferieur (Cazin, 1887). The transverse grooves between the cranial and caudal sacs and the body of the Ventriculus (Fig. 9.6).

(56) **Plica angularis.** The openings of the ventriculus to the Proventriculus and Pars pylorica in certain birds, e.g., *Apteryx* and *Podiceps cristatus* appear to be separated by this angular fold (Pernkopf and Lehner, 1937).

(57) **Stratum longitudinale.** According to Pernkopf (1930) a longitudinal layer of muscle is usually absent in the Ventriculus except at the minor curvature. However, in the columbiform species examined by Landolt (1987a) the layer is totally absent except in *Treron* and *Phapitreron* in which it is restricted to the region of the craniodorsal thin muscle (see Annot. 59).

(58) **Stratum circulare.** In the well-muscled type of stomach as well as in the better developed intermediate forms of stomach, the circular muscle layer of the Ventriculus is clearly differentiated into four semi-autonomous masses (see Annot. 59 and Figs. 9.6, 7.

(59) **M. crassus cranioventralis, M. crassus caudodorsalis; M. tenuis craniodorsalis; M. tenuis caudoventralis.** Synonymy: vorderer/hinterer Hauptmuskel; oberer/unterer Zwischenmuskel (Groebbels, 1932: 472); M. lateralis dorsalis/ventralis, M. intermedius caudalis/cranialis (Schummer, 1973: 51). The terminology of the semi-autonomous smooth thick (crassus) and thin (tenuis) muscles of the Ventriculus (Figs. 9.6, 7) is that suggested by Dziuk and Duke (1972). In some fruit-eating pigeons including *Ptilinopus* and *Drepanoptila* the thick muscles form four rounded pads which narrow the gizzard lumen, an adaptation for separating fruit flesh from seeds and stones (Landolt, 1985, 1987a). In the small forms of *Ducula* there are 12-16 pads.

(60) **Centrum tendineum.** Synonymy: Operculum (Newton and Gadow, 1896: 917); Tendo intermuscularis (Komárek, et al., 1982). The tendinous centres on each side of the ventriculus (Fig. 9.6) provide the attachments of the circular muscle (see Annot. 50).

(61) **Lamina muscularis mucosae.** While a Lamina muscularis mucosae is absent in the Ventriculus of most taxa, Landolt (1987a) observed its presence in thirty-two columbiform species in the region of the thin muscles (Annot. 59).

(62) **Plicae ventriculi.** When the primary function of the Ventriculus is that of a storage organ for large items of food as in fish- and meat-eaters, its inner surface is strongly folded (Fig. 9.8), the folds usually disappearing when the chamber dilates with food (Swenander, 1902).

(63) **Rugae ventriculi; Sulci ventriculi.** The permanent mucosal ridges and grooves of the well-muscled type of Ventriculus.

(64) **Exocrinocytus columnaris.** The columnar exocrine cells of the surface epithelium and glands secrete the Cuticula which lines the inner surface of the gizzard. See Annot. 65.

(65) **Cuticula gastris.** Synonymy: couche cornee, revetement coriace (Cazin, 1887); keratinoid layer (Hedonius, 1892); koilin (Hofmann and Pregl, 1907). The gastric cuticle (Fig. 9.7) is the variably developed internal lining of the Ventriculus and the Pars pylorica, consisting of a carbohydrate/protein complex secreted by the ventricular and pyloric glands. In the well-muscled type of stomach the cuticle is

made up of clusters of hard vertical rods separated by softer horizontal matrix. For a recent description of the structure of the cuticle in *Gallus* see Akester (1986). In the poorly-muscled type of Ventriculus the cuticle is relatively soft and has much less internal organization (Groebbels, 1932: 492).

(66) **Procc. conicales; Procc. dentales.** The ventricular cuticle in certain fruit-eating pigeons, e.g., large forms of *Ducula,* is raised into a number of hard pointed conical processes (Garrod, 1878a; Wood, 1924; Cadow, 1933; Landolt, 1985). Since the cones alternate longitudinally, during contraction they meet like a toothed wheel which acts to peel off the flesh from seeds and stones. In some fruit-eating pigeons, e.g., *Treron* and *Phapitreron,* the cuticle over the enlarged craniodorsal thin muscle (Annot. 59) is raised into horizontal rows of tooth-like processes (Landolt, 1985).

(67) **Pars pylorica gastris.** Synonymy: Nebenmagen, Endstuck (Pernkopf and Lehner, 1937). The pyloric part of the stomach (Figs. 9.6, 8-10) is the variably developed portion between the Ventriculus and Duodenum which forms a distinct chamber in some taxa, e.g., *Struthio, Anhinga, Phalacrocorax, Ardea,* and *Botauris,* but in domestic birds is very reduced (Hodges, 1974: 63; Larsson, et al., 1974).

(68) **Bulbus pyloricus.** In *Ardea cinerea* a constriction divides the pyloric part of the stomach into proximal and distal portions, the smaller distal portion was named "pyloric bulb" by Pernkopf and Lehner (1937).

(69) **Torus pyloricus.** This pyloric torus is the conical protuberance in the pyloric part of the stomach of *Anhinga rufa* (Garrod, 1878b).

(70) **Ostium pyloricoduodenale.** The opening of the Pars pylorica of the stomach into the Duodenum.

(71) **Plicae pyloricae.** Frequently, as in many birds of prey, the mucosa of the pyloric part is strongly folded (Pernkopf and Lehner, 1937). In some taxa, annular folds of the mucosa subdivide the pyloric part as in *Ardea cinerea* (Cazin, 1887), or separate it from adjacent regions of the digestive tract as in *Pelecanus* (Pernkopf and Lehner, 1937).

(72) **Papillae filiformes pyloricae** (Fig. 9.9). The hair-like cuticular papillae project into the pyloric part of the stomach in darters (Anhingidae) (Garrod, 1876; Cazin, 1887) (Fig. 9.9).

(73) **Intestinum tenue.** Different patterns of arrangement of the convolutions and coiling of the small intestine are described by Gadow (1889) and have been used in taxonomy (see Annot. 74, 77).

(74) **Ansa duodeni.** The duodenal loop (Figs. 9.11, 16) is a "closed" loop of intestine as described by Gadow (1889) with both of its limbs held closely together by mesentery. In a few birds, e.g., *Spheniscus demersus,* the primary duodenal loop is thrown into a series of secondary folds, while in *Morus bassanus* it is compound (Mitchell, 1901). A duodenal loop is reported to be absent in certain fruit-eating pigeons (Beddard, 1911).

(75) **Papilla duodeni [P. duodenalis].** The duodenal papilla protrudes into the lumen of the duodenum, and carries the openings of the pancreatic and bile ducts into the duodenum and has been described in domestic birds by Batojeva and Batojev (1972) and Paik, et al. (1974).

(76) **Jejunum; Ileum.** While there is no morphological justification in birds for adopting the terms Jejunum and Ileum, they have still been retained for descriptive purposes such as for the naming of blood vessels etc., the junction between the two regions being at the Diverticulum vitellinum. See **Art.** Annot. 60.

(77) **Ansae jejuni; Ansa axialis; Ansae ilei; Ansa supraduodenalis; Ansa supracecalis.** The jejunum and ileum in most taxa are arranged in one or more closed jejunal and ileal loops (see Annot. 74) (Fig. 9.11). The axial loop (Mitchell, 1901) (Fig. 9.11) carries the Diverticulum vitellinum and therefore has both jejunal and ileal components. The supraduodenal loop (Mitchell, 1901) is usually the most distal loop of the Ileum (Fig. 9.11). In a relatively small number of taxa, one or more supracecal loops are present distal to the supraduodenal loop (Beddard, 1911).

(78) **Diverticulum vitellinum.** Synonymy: Meckel's diverticulum. The vitelline diverticulum (Fig. 9.11) is the permanent remnant of the yolk stalk which contributes in *Gallus* to extramedullary myelopoiesis after hatching (Olah and Glick, 1984) and for which a lymphoepithelial function has been suggested (Olah, et al., 1984). It is reported to be consistently absent in some species (Mitchell, 1901). According to Branton, et al. (1988) the position of the diverticulum in *Gallus* is constant (Annot. 76).

(79) **Papilla ductus vitellini.** The small papilla described in *Gallus* by Fehér and Gyuru (1971) on the inner wall of the gut which carries the opening of the yolk sac duct.

(80) **Papilla ilealis.** The ileal papilla is the protrusion of the terminal part of the ileum into the rectal lumen which occurs in some taxa including *Gallus, Meleagris* and *Anas* (Mahdi and McLelland, 1987). The term replaces "valva ileorectalis" of the NAA(1979) which may imply a flap-like closure.

(81) **Cecum.** In most groups of birds right and left ceca (Fig. 9.11) open into the cranial part of the Rectum. Ceca are absent in some species from at least seven orders including the Piciformes, Apodiformes, Coraciiformes, Columbiformes, Coliiformes, Cuculiformes, and Psittaciformes. A single unpaired cecum occurs in many herons and bitterns (Ardeidae) (Corti, 1923). Two pairs of ceca have been reported in the Secretary Bird (*Saggitarius serpentarius*) (Maumus, 1902). For a classification of ceca see McLelland (1989).

(82) **Basis ceci; Corpus ceci; Apex ceci.** These terms refer to the regions which can be identified externally in the well-developed type of ceca found in anseriform and galliform species. Typically there is a short, narrow, proximal zone or base in which the villi are especially well-developed, a long relatively wide, middle zone or body, and short distal zone or apex (McLelland, 1989).

(83) **Diverticula ceci; Haustra ceci; Ruga spiralis.** Outpouchings are present in the ceca of a small number of taxa including some ratites (*Struthio, Rhea,* and *Apteryx*), the tinamous (*Rhynchotus* and *Eudromia*), the loon (*Gavia*), screamers (Anhimidae), *Tragopan,* the bustard (*Otis*), and the sandgrouse (*Pterocles*). For a review see McLelland (1989). In the tinamou, *Eudromia elegans,* the ceca exhibit numerous

minute papilliform outgrowths or diverticula (Fig. 9.12) which correspond internally to a network of ridges like those of the ruminant reticulum (Beddard, 1890). By contrast, in *Struthio* the ceca have haustra-like outpouchings which are arranged in a helical manner and which correspond internally to a spiral valve-like ridge (Bezuidenhout, 1986).

(84) **Ostium ceci.** Usually the right and left ceca open separately into the rectum, but in *Struthio* and the sandgrouse (*Pterocles*) they share a common cecal orifice (Jacobshagen, 1937).

(85) **Rectum [Colon];** Haustra recti. The rectum or colon (Fig. 9.11) is the straight portion of the intestinal tract between the Ileum and the Cloaca. In *Struthio* the rectum is enormously elongated and can be divided into a proximal thin-walled portion with sacculations or haustra and a distal thick-walled portion free of haustra (Bezuidenhout, 1986).

(86) **Pars externa; Pars interna.** The circular muscle tunic of the small intestine in *Gallus* (Gabella, 1985) and *Anas* (Mahdi and McLelland, 1987) is clearly divisible into a thick outer portion and a thin inner portion.

(87) **M. sphincter diverticuli vitellini.** This sphincter was described in *Gallus* by Olah and Glick (1984) at the base of the diverticulum.

(88) **M. sphincter ilei; M. sphincter ceci.** Mahdi and McLelland (1987) found in *Anas* an ileal sphincter at the base of the Papilla ilealis and a cecal sphincter at the opening of each cecum.

(89) **M. sphincter rectocoprodei.** The presence of a rectocoprodeal sphincter 1-2 mm cranial to the junction of the rectum and coprodeum was described in *Anas* by Mahdi and McLelland (1989). See also **Cloaca.** Annot. 3.

(90) **Gll. duodeni.** The avian equivalent of Brunner's glands of mammals. Evidence for duodenal glands at the junction of the ventriculus (gizzard) and small intestine is provided by Clara (1934) and Patzelt (1936) in examples of a number of species.

(91) **Villi intestinales; Plicae intestinales villosae; Plicae intestinales submucosae; Gll. [Cryptae] intestinales.** The intestinal mucosa is arranged into villi or folds which show great interspecific variations (Muller, 1922; Ziswiler, 1967). The term Plicae intestinales submucosae refers to the relatively uncommon type of intestinal fold which is based on a core of submucosa (Muller, 1922; Jacobshagen, 1937; Fenna and Boag, 1974; Johnson and Skadhauge, 1975; Landolt, 1987b). The intestinal glands extend down into the mucous membrane between the villi. For accounts of the intestinal epithelial cells see Michel and Gutte (1971), Michael and Hodges (1973) and Hodges and Michael (1975).

(92) **Exocrinocytus cum granulis acidophilicis.** Formerly called the Paneth cell, there is only limited evidence for this type of cell in the intestinal glands of birds (Ziswiler, 1967).

(93) **Tunica serosa; Tunica fibrosa.** Most of the surface of the liver is invested with a single layer of serosal mesothelial cells below which is a layer of dense fibrous connective tissue (Glisson's capsule) which is relatively much thinner than that of mammals.

(94) **Porta hepatis.** Synonymy: Fossa transversa (Komárek, et al., 1982). See Fig. 9.13. The hepatic porta (L. gate or entrance) is the transverse groove stretching across the visceral surface of both liver lobes where the hepatic arteries and portal veins enter the liver and the hepatic ducts emerge.

(95) **Impressio duodenalis.** The descending and ascending parts of the duodenal loop make separate impressions (Fig. 9.13) on the visceral surface of the liver.

(96) **Impressio testicularis.** The impression formed on the liver by the right testis.

(97) **Incisura cranialis; Incisura interlobaris; Incisura caudalis.** These terms refer to deep notches in the liver. See Fig. 9.13. They were used by Komárek, et al. (1982), and replace Incisura interlobaris cranialis and Incisura interlobaris caudalis of the NAA (1979).

(98) **Proc. dorsalis dexter/sinister.** These terms were used by Komárek, et al. (1982) and replace "Proc. intermedius dexter/sinister" of the NAA (1979). See Figs. 9.13, 14a, c. Among the domestic birds the left process only occurs in *Gallus* and *Meleagris*. Both processes are absent in *Columba*.

(99) **Incisura lobaris.** Synonymy: Incisura intralobaris (Komárek et al. 1982). See Fig. 9.13.

(100) **Pars lateralis; Pars medialis.** These parts of the left lobe of the liver were used by Komárek et al. (1982), and replace "Pars caudodorsalis/caudoventralis" of the NAA (1979). In many taxa one or both of the liver lobes are partly subdivided. Among domestic species the division of the left lobe into two parts by a deep incision extending cranially from the caudal margin occurs only in *Gallus* and *Meleagris* (Fig. 9.13).

(101) **Proc. papillaris; Proc. ventralis dexter; Proc. ventralis medius; Proc. cranialis.** The presence of these processes of the left lobe and Pars interlobaris of the liver shows great intraspecific variation. The terminology is that adopted by Komárek, et al. (1982). Amongst domestic species Proc. papillaris (Fig. 9.14a) has been described in *Anas;* Proc. ventralis dexter (Fig. 9.14b) in *Anser* and *Gallus;* and Proc. cranialis (Fig. 9.14c) in *Anser.* The Proc. ventralis medius arises from the caudal margin of the parietal surface of the Pars interlobaris and has been described in *Anas, Anser,* and *Meleagris.*

(102) **Canales portales; Capsula fibrosa perivascularis; Trias hepatica; Arteriae interlobulares; Venae interlobulares; Ductuli interlobulares.** At some sites the liver lobules are demarcated by portal canals of connective tissue containing blood vessels and bile ducts. The connective tissue or perivascular fibrous capsule is continuous with the fibrous capsule of the liver and supports the hepatic triads. Each triad contains an interlobular artery which is a branch of the hepatic artery, an interlobular vein which is a branch of the portal vein, and an interlobular bile ductule.

(103) **Lobuli hepatis.** Classic hepatic lobules (see Annot. 102) are difficult to identify in birds except near the Porta hepatis.

(104) **Lamina hepatica; Canaliculi biliferes.** Abdelwahab (1987) has shown with the scanning electron microscope that the sheets of hepatocytes in *Anas* are in the form of branching cords, each cord consisting of 4-6 cells arranged around a central bile canaliculus. The bile canaliculi join at the periphery of the hepatic lobule to form interlobular bile ductules.

(105) **Lacuna hepatis.** Between the hepatic laminae are spaces or lacunae containing venous sinusoids.

(106) **Vasa sinusoidea; Macrophagocytus stellatus; Spatium perisinusoideum; Lipocytus perisinusoideus; Venae centrales; Venae sublobulares.** The sinusoids of the laminae drain into the central vein of the hepatic lobule. The sinusoids are lined by a flattened endothelial cell and a protuberant phagocytic cell, the stellate macrophage (Purton, 1969). They are separated from the sheets of hepatocytes by the perisinusoidal space. Within this space lie the perisinusoidal fat cells (Purton, 1976). Central veins of adjacent lobules anastomose to form sublobular veins which join to form hepatic veins.

(107) **Ductuli biliferes; Ductus hepaticus dexter/sinister; Ductus hepatocysticus; Ductus hepatoentericus dexter; Ductus hepatoentericus communis; Ductus hepatoentericus accessorius.** Synonomy for Ductus hepatocysticus and Ductus hepatoentericus: Ductus cysticus and Ductus choledochus (Komárek, et al. 1982). In *Gallus,* bile ductules (Fig. 9.15) from the right lobe of the liver are drained by the right hepatic duct, and those from the left lobe by the left hepatic duct (Miyaki, 1973). The hepatocystic duct (Fig. 9.15) branches from the right hepatic duct and enters the gall bladder. In birds, e.g., *Columba,* which have no gall bladder, the branch from the right hepatic duct, the right hepatoenteric duct, opens directly into the duodenum. This duct is absent in *Struthio* (Newton and Gadow, 1896: 299). In the majority of birds the right and left hepatic ducts unite on the visceral surface of the right lobe of the liver to form a common hepatoenteric duct (Figs. 9.13, 15, 16) which opens into the duodenum. An accessory hepatoenteric duct formed by the right and left hepatic ducts, and additional to the common hepatoenteric duct, was observed in cracids by Gadow (1891: 683) and in *Anser* by Simic and Jankovic (1959).

(108) **Vesica biliaris [V. fellea].** The gall bladder (Figs. 9.13, 14) is absent in some birds (Gorham and Ivy, 1938) (see Annot. 107 and **Art.** Annot. 58).

(109) **Ductus cysticoentericus.** The cysticoenteric duct (Figs. 9.13, 15, 16) connects the gall bladder with the duodenum. In contrast to mammals, a common bile duct is absent in birds.

(110) **Pancreas.** The terminology of the lobes of the Pancreas (Fig. 9.16) is that used for *Coturnix* and *Gallus* by Mikami and Ono (1962) and Mikami, et al. (1985), and replaces the nomenclature of the NAA (1979). The accessory pancreatic duct of the NAA (1979) has been renamed **Ductus pancreaticus tertius.** The major change is the division of the ventral lobe of Paik, et al. (1974) into the **Lobus pancreatis ventralis** and the **Lobus pancreatis tertius** on the basis of the distribution of the islets (see **Endoc.** Annot. 7). The gross morphology of the pancreatic lobes shows considerable interspecific variation. The number of pancreatic ducts varies from one to three depending on the species (Groebbels, 1932: 487).

(111) **M. sphincter ductus pancreatici.** Sphincter-like arrangements of the muscle at the openings of the pancreatic ducts into the intestine were described by Fehér and Fancsi (1971).

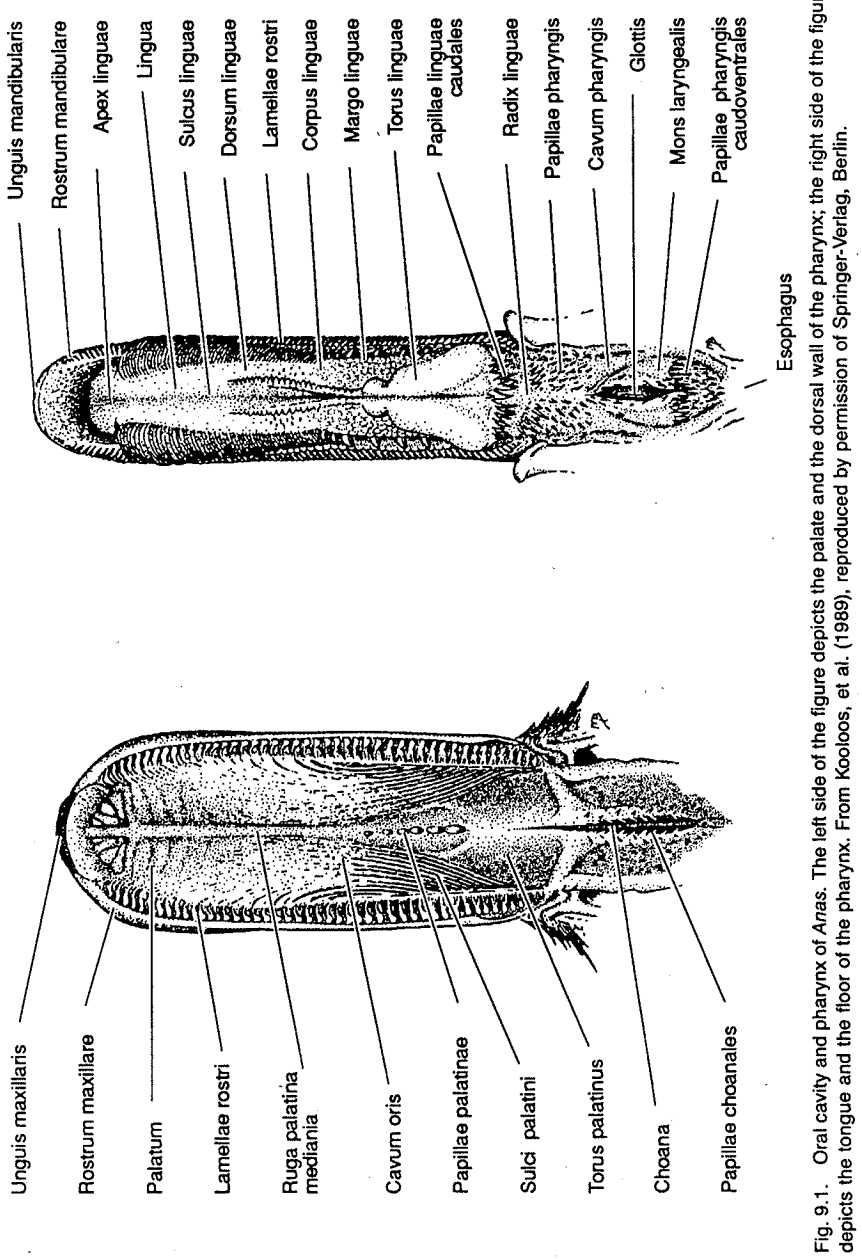

Fig. 9.1. Oral cavity and pharynx of *Anas.* The left side of the figure depicts the palate and the dorsal wall of the pharynx; the right side of the figure depicts the tongue and the floor of the pharynx. From Kooloos, et al. (1989), reproduced by permission of Springer-Verlag, Berlin.

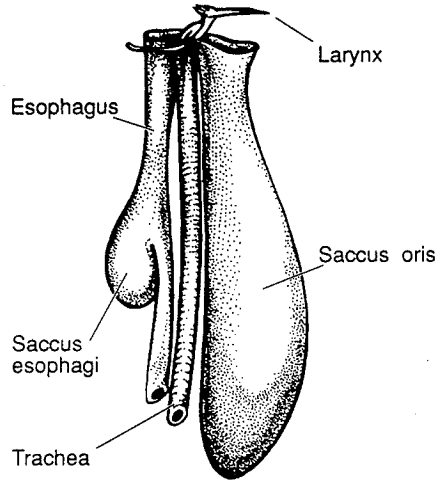

Fig. 9.2. Lateral view of the oral and esophageal sacs in the adult male Great Bustard (*Otis tarda*). From Garrod (1874a).

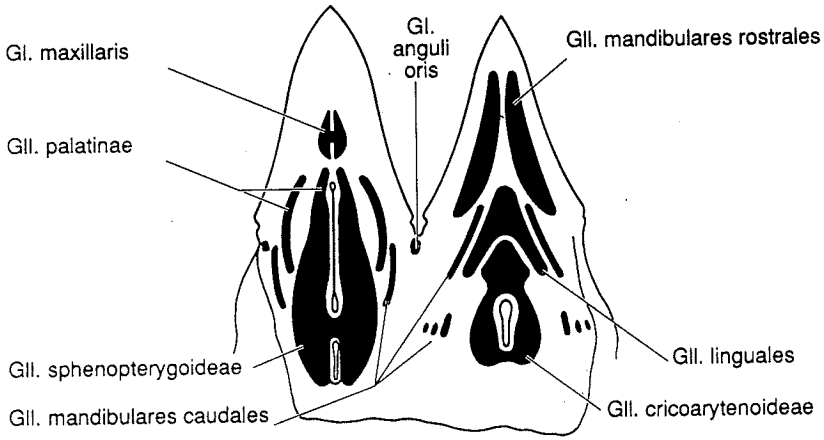

Fig. 9.3. Salivary glands of the oral cavity and pharynx of *Gallus*. The left side of the figure depicts the salivary glands of the palate and dorsal wall of the pharynx; the right side of the figure depicts the glands of the tongue, of the ventral wall of the oral cavity, and of the pharynx. From Saito (1966), reproduced by permission of the University of Miyazaki.

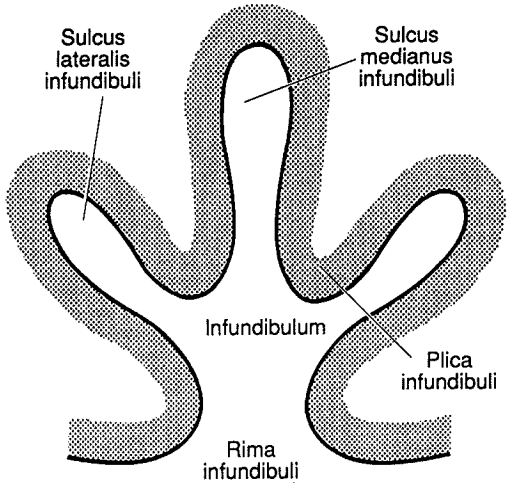

Fig. 9.4. Transverse section through the Infundibulum of *Gallus*. From Heidrich (1908). The bottom of the figure represents the dorsal wall of the pharynx, with its opening into the chamber called the Infundibulum. In its caudodorsal part the Infundibulum communicates with the auditory tubes and ventrally communicates with the Pharynx via a slit, the Rima infundibuli.

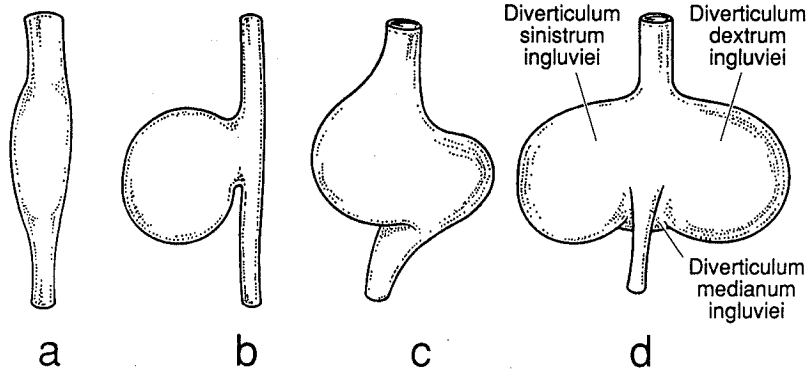

Fig. 9.5. Examples of the crop (Ingluvies). (a) Great Cormorant (*Phalacrocorax carbo*); (b) Peafowl (*Pavo cristatus*); (c) Budgerigar (*Melopsittacus undulatus*); and (d) *Columba*. Ventral views except (d) which is a dorsal view. (a) and (b) from Pernkopf and Lehner (1937); (c) and (d) from McLelland (1979), reproduced by permission of Academic Press, London and New York.

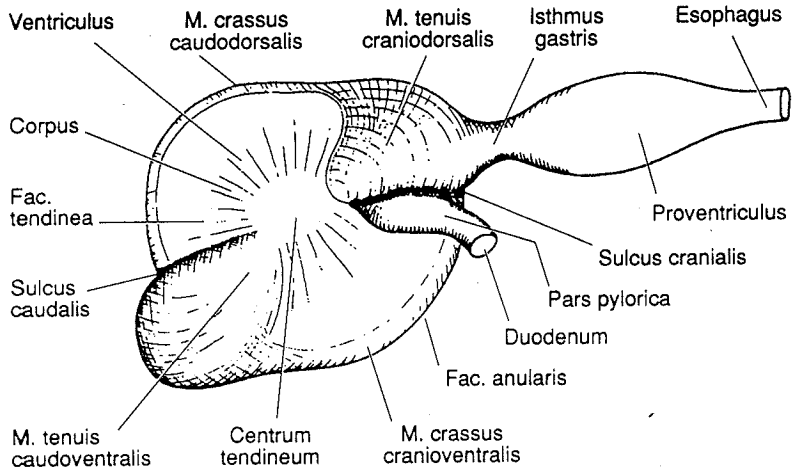

Fig. 9.6. Exterior of the Gaster (stomach) of *Gallus*. Lateral aspect, right side. In this species the Ventriculus is well-muscled. From McLelland (1975a), reproduced by permission of W. B. Saunders Company, Philadelphia.

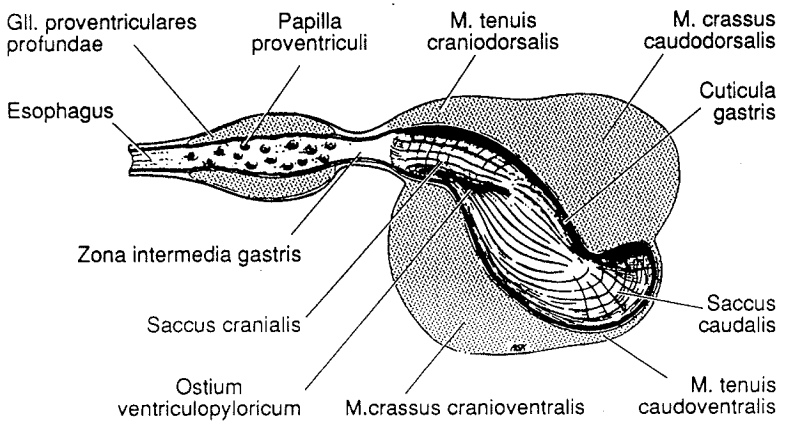

Fig. 9.7. Interior of the Gaster (stomach) of *Gallus*. Right side. From McLelland (1975a), reproduced by permission of W. B. Saunders Company, Philadelphia.

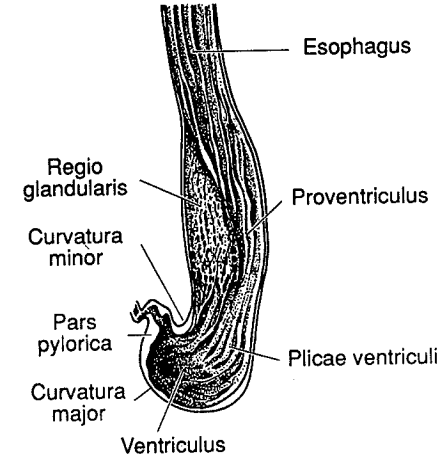

Fig. 9.8. Interior of the Gaster (stomach) of the Little Blue Penguin (*Eudyptula minor*). In this species the Proventriculus has a Regio glandularis and the Ventriculus is a poorly-muscled sac-like structure. From Pernkopf and Lehner (1937).

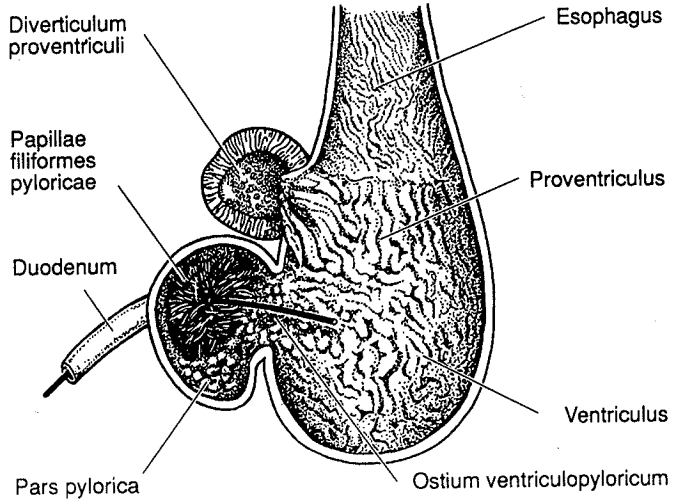

Fig. 9.9. Interior of the Gaster (stomach) of *Anhinga anhinga*. From Garrod (1876). This species possesses a Diverticulum proventriculi (see Annot. 38 for the significance of this structure) and a well developed Pars pylorica gastris (see Annot. 66). Note the probe passing from the Ventriculus through the Pars pylorica and into the duodenum.

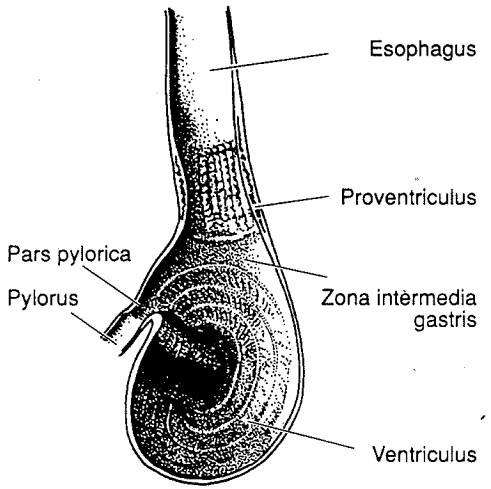

Fig. 9.10. The interior of the Gaster (stomach) of the Little Owl (*Athene noctua*). In this species the Ventriculus is a poorly-muscled sac-like structure. From Pernkopf and Lehner (1937).

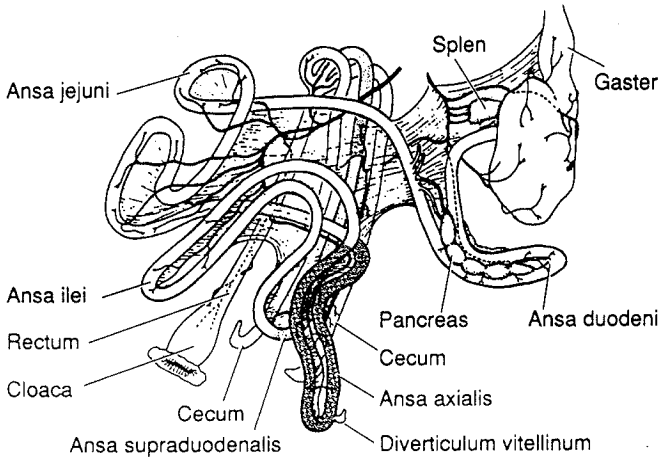

Fig. 9.11. Ventral view of the gastrointestinal tract of *Anser*. From McLelland (1975a) after Grau (1943b), reproduced by permission of W. B. Saunders Company, Philadelphia.

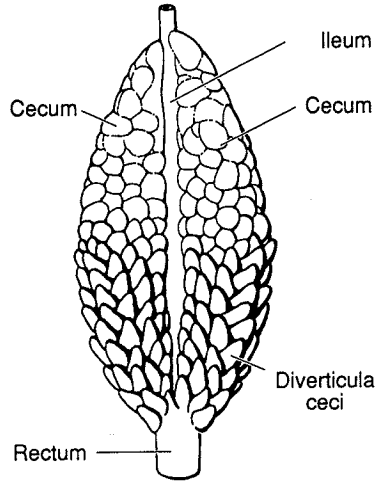

Fig. 9.12. Ceca of the Elegant Crested Tinamou (*Eudromia elegans*). The walls of the ceca consist of numerous small diverticula. From Beddard (1890).

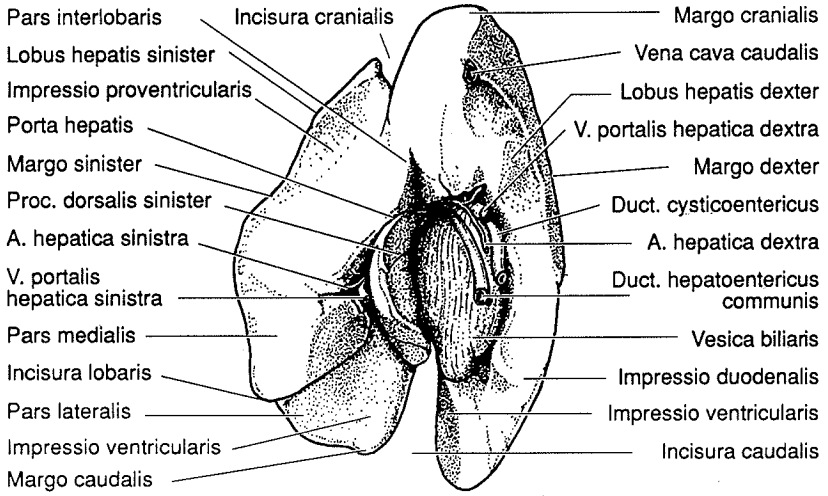

Fig. 9.13. Liver (Hepar) of *Gallus*, caudal view. From McLelland (1979), reproduced by permission of Academic Press, London and New York.

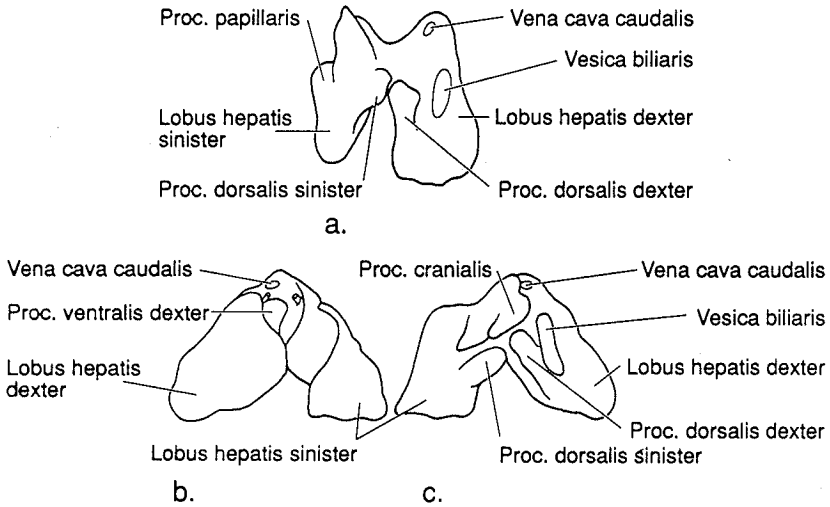

Fig. 9.14. Views of the liver (Hepar) of anatids: (a) *Anas*, caudal view; (b) *Anser*, cranial view; and (c) *Anser*, caudal view. Redrawn from Komárek, et al. (1982), reproduced by permission of Piroda, Bratislava.

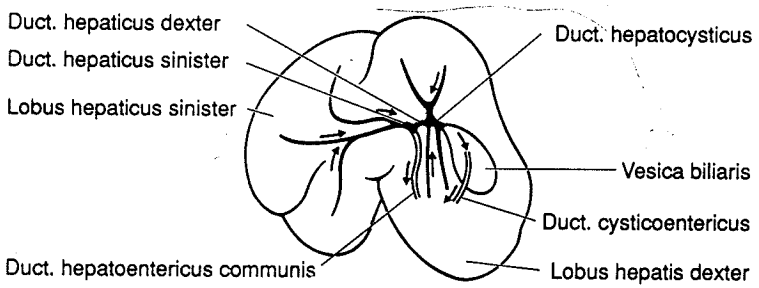

Fig. 9.15. Biliary system of *Gallus*. Caudal view of the liver showing the major intra- and extra-hepatic bile passages. From Miyaki (1973), reproduced by permission of the Japanese Society of Veterinary Science.

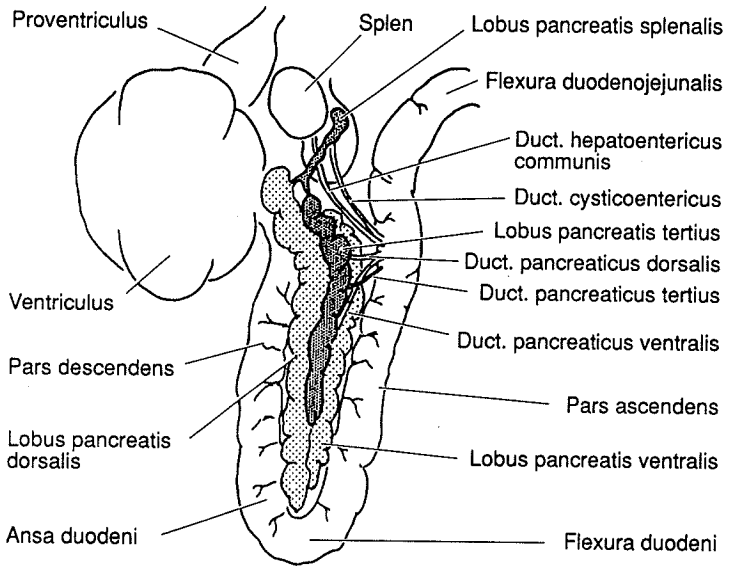

Fig. 9.16. Ventral view of the pancreas of the Japanese Quail (*Coturnix japonica*). From Mikami, et al. (1985), reproduced by permission of the Japanese Society of Veterinary Science.

10

APPARATUS UROGENITALIS [SYSTEMA UROGENITALE]

ANTHONY S. KING

With contributions from subcommittee members: M. R. Bakst, D. Berens v. Rautenfeld, K.-D. Budras, Gy Fehér, V. Komárek, P. E. Lake, T. Nishida, M. D. Tingari, R. F. Wideman, Jr., M. Yasuda.

As in the first edition of the NAA (1979), this part has four sections, namely Organa urinaria, Organa genitalia masculina, Organa genitalia feminina, and Cloaca. All four have undergone similar general developments, i.e., microscopic structures have been included, the terminology has been brought into line with the NAV (1983) and NH (1989) wherever appropriate, and the annotations have been revised to include important references omitted in the first edition and papers published since 1979. In the first three sections there have been some major changes in the terminology, which are summarized immediately below. Because of retirements and changing research interests, several of the original subcommittee members have withdrawn, but new members (see above) have replaced them. Any factual errors in the annotations must be attributed to me, not to them.

The literature on the macro-, meso-, and microscopic anatomy of the Organa urinaria in many avian species has been thoroughly reviewed by Siller (1971), Hodges (1974), Johnson (1979), Siller (1983), and Wideman (1988); all of these authors added many original observations. These reviews provide the general basis for the Annotations on the urinary organs. Notable developments in knowledge of nephronal microarchitecture have come during the last decade from the reconstructions by Wideman and Morild and coworkers; these have made it possible to evolve a new terminology for the components of the nephron which portrays the fundamental differences between the nephrons of birds and mammals. I am greatly indebted to Robert F. Wideman, Jr. for his assistance in the preparation of this and all other aspects of the list for Organa urinaria.

The principal changes in the section on the Organa genitalia masculina lie in the Nomina for the spermatozoon, the duct system of the testis, and the components of the phallus. The general revision of the Annotations has

drawn extensively on the review by Lake (1981). Generous assistance in the preparation of the manuscript, and particularly in the development of the Terminology and Annotations on the spermatozoon, was given by P. E. Lake (now retired from the Agricultural Research Council's Poultry Research Centre, Roslin, Midlothian, Scotland), M. D. Tingari (presently Vice-Chancellor of the University of Khartoum, Sudan), and Murray R. Bakst. I am particularly grateful to K.-D. Budras, Freie Universität Berlin, for his assistance with the Nomina and Annotations for the duct system of the testis and his valuable criticisms on testicular structure in general. The Terminology and Annotations on the phallus have been have been completely redesigned (the most difficult task in the entire chapter) in collaboration with Berens von Rautenfeld, Medizinische Hochschule Hannover. Helpful comments on the phallic musculature were received from Takao Nishida, University of Tokyo.

The general revision of the Annotations on the Organa genitalia feminina has been based mainly on the extensive review and researches by Gilbert (1979). Some new developments have been introduced in the terminology for the shelled egg and the shell itself. Valuable advice on the Nomina and Annotations, and especially those relating to microscopic anatomy, has been given by K.-D. Budras and Murray R. Bakst.

I am grateful to Berens von Rautenfeld for assistance with the revision of the Nomina and Annotations for the Cloaca.

The elegant artwork in Figs. 10.2, 5, 7, 10, 11, 12, 15, and 19 was executed by Alan Bannister, University of Liverpool, and for this I record my sincere gratitude. I also thank the following for generously allowing me to use their resplendent drawings: Robert F. Wideman Jr., Figs. 10.3 and 4; K.-D. Budras, Fig. 10.8; and V. Komárek, Figs. 10.13 and 14.

TERMINOLOGY

ORGANA URINARIA

REN

- Margo lateralis[1]
- Margo medialis[2]
- Facies ventralis[3]
- Facies dorsalis
- Extremitas cranialis
- Extremitas caudalis
- Divisio renalis cranialis[4]
- Divisio renalis media[4]
- Divisio renalis caudalis[4]
- Lobus renalis[5]
  - Lobulus renalis[6]
    - Regio lobuli corticalis[6]
    - Regio lobuli medullaris[6]
- Cortex renis [renalis][7]
- Medulla renis [renalis][7]

CORPUSCULUM RENALE

- Polus vascularis
- Polus tubularis
- Glomerulus[8]
  - Rete capillare glomerulare[8]
  - Vas capillare glomerulare
    - Endotheliocytus fenestratus
      - Membrana basilaris
  - Mesangium intraglomerulare[8]
    - Mesangiocytus intraglomerularis[8]
- Capsula glomerularis
  - Paries externus
  - Paries internus
  - Podocytus[9]
    - Cytotrabecula[9]
    - Cytopodium[9]
  - Lumen capsulae

TUBULUS RENALIS

- Nephron[10]
  - Nephron corticale[10]
  - Nephron juxtamedullare[10]
- Nephron corticale[11]
  - Tubulus proximalis[12]
    - Epitheliocytus microvillosus[12]
  - Tubulus intermedius[13]
  - Tubulus distalis[14]
    - Epithelium simplex cuboideum[14]
  - Macula densa[29]
- Nephron juxtamedullare[15]
  - Tubulus contortus proximalis[16]
  - Tubulus rectus proximalis[17]
    - Epitheliocytus microvillosus[18]
  - Tubulus attenuatus[19]
    - Epithelium simplex cuboideum[20]
  - Tubulus rectus distalis[21]
    - Epithelium simplex cuboideum[21]
    - Macula densa[29]
  - Ansa nephrica[22]
  - Tubulus contortus distalis[23]
- Tubulus conjungens[24]
  - Epithelium simplex cuboideum[24]
- Tubulus colligens[25] [Tubulus renalis colligens]
- Tubulus colligens corticalis[26]
  - Epithelium simplex cuboideum[26]
- Tubulus colligens medullaris[26]
  - Epithelium simplex cuboideum/columnare[26]
- Ductus colligens[27,43]
  - Epithelium stratificatum cuboideum/pseudostratificatum columnare[27]

COMPLEXUS JUXTAGLOMERULARIS[28]

- Macula densa[29]
  - Epitheliocytus maculae densae
- Tunica media arteriolae glomerularis
  - Endocrinocytus myoideus [Juxtaglomerularocytus][30]
- Mesangium extraglomerulare [Insula juxtavascularis][31]
  - Mesangiocytus extraglomerularis[31]

VASA et NERVI RENIS

A. renalis cranialis[32]
A. renalis media[32]
A. renalis caudalis[32]

Aa. intralobulares[33]
  Arteriola glomerularis afferens[34]
    Rete capillare glomerulare[8]
  Arteriola glomerularis efferens[35]
    Arteriolae rectae[36]

Systema portale renale (**Ven.** Annot. 59)
  Circulus venosus portalis
    V. portalis renalis cranialis[37]
    V. portalis renalis caudalis[37]
      Rr. renales afferentes[37]
        Vv. interlobulares[37]
          Rete capillare peritubulare corticale[38]
          Vas capillare sinusoideum[39]
  Valva portalis renalis[40]
Vv. renales craniales[37] (**Ven.** Annot. 58)
V. renalis caudalis[37] (**Ven.** Annot. 58)
  Rdxx. renales efferentes[37]
    Vv. intralobulares[37]
      Venulae rectae[41]

Truncus thoracoabdominalis
  Vasa l. renalia (**Lym.** Fig. 13.6)

Plexus aorticus (**PNS** Annot. 81)
  Plexus adrenalis
    Gg. adrenalia
    Plexus renales

URETER

Pars renalis[42]
  Rr. ureterici primarii[43]
    Rr. ureterici secundarii[43]
      Rr. ureterici tertiarii[43]
Pars pelvica[42]
Ostium cloacale ureteris (**Cloaca**)

Tunica mucosa[44]
  Epithelium pseudostratificatum columnare
  Lamina propria mucosae[44]
Tunica muscularis[44]
  Stratum longitudinale internum
  Stratum circulare
  Stratum longitudinale externum
Tunica adventitia
Tunica serosa

Vasa et Nervi Ureteris
  A. renalis cranialis
    Rr. ureterodeferentiales craniales
  A. ischiadica
    Rr. ureterodeferentiales medii
  A. pudenda
    Rr. ureterodeferentiales caudales
  Vv. testiculares
    Vv. ureterodeferentiales craniales
  V. renalis caudalis
    Vv. ureterodeferentiales mediae
  V. pudenda
    Vv. ureterodeferentiales caudales

Truncus thoracoabdominalis
  Vasa l. ureterodeferentialia (**Lym.** Figs. 13.6, 7)
N. pudendus
  Rr. ureterales

ANNOTATIONS

(1) **Margo lateralis.** The lateral border of the kidney (Ren) is deeply indented by major blood vessels (e.g., A. iliaca externa, A. ischiadica) (Fig. 10.1).

(2) **Margo medialis.** In many taxa the left and right kidneys fuse along the medial border, particularly in the Divisio caudalis (Johnson, 1968).

(3) **Facies ventralis.** The ventral surface has deep grooves caused by the vessels that cross it (Fig. 10.1). Varying depths of these grooves probably account for claims of more than three divisions in some species (Annot. 4).

(4) **Divisio renalis cranialis/media/caudalis** (Fig. 10.1). The cranial, middle, and caudal divisions are typical, being supplied respectively by the cranial, middle, and caudal renal arteries (as in *Gallus*), although the relative sizes of the divisions vary greatly with the species (Johnson, 1968). Boundaries are: between the cranial and middle divisions, A. and V. iliaca externa; between the middle and caudal divisions, A. and V. ischiadica (King, 1975: 1919; Johnson, 1979: 186). The three divisions are not homologous to the lobes of the mammalian kidney (Goodchild, 1956) and should not be called "lobes". Four divisions have been reported in Ciconiiformes and Charadrii and five in *Apteryx* (Francis, 1964), but the boundaries may be illusory (Annot. 3) (Johnson, 1979: 186). There are also reports of two entirely separate divisions (Das, 1924; Van Tyne and Berger, 1959; Feinstein, 1962); Johnson (1979: 186) confirmed this in Bucerotidae, but attributed other accounts to overlooking thin connections between the divisions.

(5) **Lobus renalis.** Medullary cones (Annot. 6) belonging to several adjacent lobules become grouped together, enclosed by a connective tissue sheath (Fig. 10.2). Typically the collecting ducts (Ductus colligentes) of the group converge into a secondary branch of the ureter (Fig. 10.2). The avian renal lobe is defined as such a group of medullary cones draining into a secondary branch of the ureter, plus the cortex that is associated with these cones (Johnson, 1979: 197). In teased preparations, a group of medullary cones is visible to the naked eye as a ragged tuft attached to a secondary branch of the ureter, as in Fig. 10.1 (see Lindgren, 1868; Goodchild, 1956; Siller, 1971: 202; Johnson, 1974). The group of medullary cones is probably homologous to the mammalian medullary pyramid; the avian renal lobe is probably homologous to the lobe of the multilobar type of mammalian kidney (King, 1975: p. 1922).

(6) **Lobulus renalis; Regio lobuli medullaris/corticalis.** In histological sections (Spanner, 1925; Feldotto, 1929; von Möllendorff, 1930: Fig. 201; Sperber, 1960: 470-478) the lobule is often pear-shaped (Fig. 10.2). It is enclosed by the (afferent) Vv. interlobulares (Fig. 10.3). The tapering part of the pear contains collecting tubules, and also the medullary loops (Ansae nephricae) of the juxtamedullary nephrons, all these being enclosed by a connective tissue capsule thus forming the medullary region of the lobule (Fig. 10.2); being cone-shaped, the medullary region of the lobule was named the "medullary cone" by Johnson (1979: 189), a term widely adopted (e.g., Siller, 1983: 92; Goldstein and Braun, 1989). The Tubuli colligentes typically empty into a single Ductus colligens (Fig. 10.2) which emerges from the lobule as the stalk of the pear. The wide part of the pear is the cortical region of the lobule (Fig. 10.2), containing cortical and juxtamedullary nephrons (except for the Ansae of the juxtamedullary nephrons). Three-dimensional studies by Johnson and

his co-workers in many species have shown that the cortical region of the lobule is not really pear-shaped, but more like an elongated loaf of bread (Johnson, et al., 1972; Johnson, 1974). This elongated cortical region typically contributes Tubuli colligentes to several independent medullary regions (Fig. 10.2); moreover any one medullary region may receive Tubuli colligentes from several independent cortical regions. Since a Lobulus renalis shares its drainage with its neighbours it can be argued that the term Lobulus is not strictly applicable; nevertheless the Lobulus renalis is a convenient structural concept.

(7) **Cortex renis; Medulla renis.** The renal cortex is formed by the cortical regions of the Lobuli renales, and the renal medulla by the medullary regions (medullary cones) (Annots. 5, 6). However, the Lobuli are embedded at varying depths in the kidney, so that the Cortex and Medulla do not form the continuous strata which typify most mammalian kidneys. The avian kidney does resemble the extreme renculus type of Cetaceae (Sperber, 1944: 401), with many lobes at varying depths. The cortex forms about 77% and the medulla 10% of the kidney volume of birds, depending on the order, body size, and habitat (Warui, 1989).

(8) **Glomerulus; Rete capillare glomerulare; Mesangium intraglomerulare; Mesangiocytus intraglomerularis.** Siller (1971: 203) and Johnson (1979: 203) reviewed these structures. The glomeruli of cortical and juxtamedullary nephrons are similar but the former are smaller. The glomerular capillary rete is much simpler in birds than in mammals, ranging from several simple capillary loops to a single loop. The intraglomerular mesangium forms the supporting framework of the capillary rete; in mammals the intraglomerular mesangiocytes are scattered between the capillary loops, but in birds they form a compact mass in the centre of the glomerulus (contrast the polar disposition of the Mesangiocyti *extra*glomerulares, Annot. 31). Avian glomeruli are much smaller than mammalian, but their greater number and the tubular secretion of urates compensate functionally.

(9) **Podocytus; Cytotrabecula; Cytopodium.** The podocyte is similar in birds and mammals. The cell body gives rise to long branching primary processes, the trabeculae (Cytotrabeculae). These form numerous pedicels (Cytopodia) which interdigitate with the pedicels of adjacent podocytes. Podocytes and intraglomerular mesangiocytes change their shape with fluctuations in water supply (Schwarz and Radke, 1981).

(10) **Nephron.** The structural and functional unit of the kidney. The kidney possesses two types of nephron. The Nephron corticale is restricted to the cortex and has no Ansa nephrica (Fig. 10.3). The Nephron juxtamedullare (Fig. 10.3) lies deep in the cortex adjacent to the medullary part of the lobule, and has an Ansa nephrica which descends into the medulla. The cortical nephron is regarded as reptilian in type, and the juxtamedullary as mammalian. However, ontogeny (in *Gallus*) fails to recapitulate the presumed phylogeny, since the "mammalian" type develops before the "reptilian" (Wideman, 1989). Intermediate types of nephron with very short loops have been reported (Huber, 1917; Feldotto, 1929; Sperber, 1960; Braun and Dantzler, 1972). In birds generally the great majority of nephrons are cortical (Huber, 1917; Feldotto, 1929; von Möllendorff, 1930; Sperber, 1960: 470-474; Siller, 1971: 203; Johnson, 1979: 199). A survey of seven species revealed no significant relationship between the proportion of juxtamedullary nephrons and urinary concentrating ability although the proportion of juxtamedullary nephrons ranged as widely as 7 to 30% (Goldstein and Braun, 1989), but other evidence from xeric and marine birds suggests that such a relationship may exist (Johnson and Ohmart, 1973; Goldstein and Braun, 1986; Braun, 1984).

(11) **Nephron corticale.** Synonym: reptilian type of nephron. Reconstructions of cortical nephrons of *Gallus* by Morild, et al. (1985a) showed the absence of a proximal convoluted part. Since they also lack an Ansa nephrica they cannot have any straight part either. Therefore the mammalian terms (Tubulus contortus proximalis, rectus proximalis, and rectus distalis) are inappropriate. Consequently Morild, et al. followed Wideman, et al. (1981) in using two general terms for the avian Nephron corticale, i.e., Tubulus proximalis and Tubulus distalis, and these have been adopted here. The proximal and distal tubules form four basic bends (Fig. 10.5), but additional loops and coils may occur particularly at bend 1.

(12) **Tubulus proximalis.** The NAA (1979) listed Pars tenuis (small diameter part) and Pars crassa (large diameter part) as components of the proximal tubule of the cortical nephron. This was based on reports (Siller, 1971: 210; Johnson, 1979: 204) that the proximal part of the proximal tubule is relatively thin, and the distal part relatively thick; these parts were supposed to correspond respectively to the convoluted and straight parts of the mammalian proximal tubule. However, Wideman, et al. (1981) found no such variations in tubular diameter or cell height. Nevertheless, Morild, et al. (1985a) did note conspicuous changes in diameter at all levels of the cortical nephrons. Pars tenuis and crassa have now been withdrawn, pending clarification.

The whole length of the Tubulus proximalis is lined by Epitheliocyti microvillosi (with brush border, etc., Annot. 18), like the mammalian proximal convoluted tubule (Siller, 1971: 210; Hodges, 1974: 513).

(13) **Tubulus intermedius.** A short and often ill-defined intermediate tubule, between the Tubulus proximalis and distalis in most cortical nephrons (Fig. 10.5), was described by Huber (1917), Feldotto (1929), Marshall (1934), Sperber (1960), and Oelofsen (1973). Johnson (1979: 208) interpreted it as probably a primitive nephronal loop. Siller (1971: 217) reported that some proximal tubules definitely end abruptly in a short narrow tubule with a low epithelium and no brush border, though these are difficult to identify. Siller (1983: 99) added nothing new on this subject. Wideman, et al. (1981) observed no intermediate tubule, but Morild, et al. (1985a) reported that the junction of the proximal and distal tubule is usually but not always abrupt. The evidence indicates a short but variable Tubulus intermedius.

(14) **Tubulus distalis.** Morild, et al. (1985a) showed that, basically, the distal tubule of the Nephron corticale begins at the surface of the cortex (after bend 3, in Fig. 10.5), travels to the V. intralobularis, and then returns towards the cortex to continue into a Tubulus colligens corticalis. However, it is extremely variable, ranging from a U-shaped loop (as just described) to a labyrinth of folds concentrated mainly around the V. intralobularis (Siller, 1971: 220). Its external diameter is about half that of the Tubulus proximalis (Morild, et al., 1985a).

The Tubulus distalis is lined by an Epithelium simplex cuboideum (Hodges, 1974: 517). Since the cells lack both a brush border and mucopolysaccharide granules they are easily distinguished from those of the Tubulus proximalis and Tubulus colligens respectively (Siller, 1971: 220). Regional variations have been observed in the height and shape (Morild, et al., 1985a) and ultrastructure and histochemistry (Nicholson, 1982) of this epithelium.

(15) **Nephron juxtamedullare.** Synonym: medullary nephron, mammalian type of nephron. The conformation of the juxtamedullary nephron of birds has not been precisely established (Wideman, 1988: 140). However, it does have convoluted and straight components, and a definite Ansa nephrica, and therefore a common terminology for mammals (NH, 1989) and birds is adopted here.

(16) **Tubulus contortus proximalis.** The proximal convoluted tubule is coiled (Morild, et al., 1985a), in the cortex of the lobule.

(17) **Tubulus rectus proximalis.** The transition between the Tubulus contortus proximalis and the Tubulus rectus proximalis occurs in the juxtamedullary cortex (Johnson, 1979: 205) or some way into the medulla (Siller, 1971: 211). The proximal straight tubule descends into the medulla (Fig. 10.5). In various species (Berger, 1966), but not *Anas* and *Gallus* (Michel and Junge, 1972), its cells seem to decrease progressively in size and the nuclei elongate (possibly artifacts, Johnson, 1979: 205). However, the external diameter certainly gets gradually smaller in histological preparations, obscuring the precise junction with the Tubulus attenuatus (Siller, 1971: 215). See Annot. 19.

(18) **Epitheliocytus microvillosus.** The whole length of the Tubulus contortus proximalis and Tubulus rectus proximalis is lined by these columnar to cuboidal cells. The brush border, terminal web, and apical tubules are present even in the cuboidal epithelium of the narrow part of the Tubulus rectus proximalis (Siller, 1971: 215).

(19) **Tubulus attenuatus.** Synonymy: thin segment of medullary loop; Pars descendens ansae of Segmentum intermedium (NAA, 1979). Once formed (Annot. 17), the Tubulus attenuatus (thin tubule) continues with uniform diameter (Johnson, 1979: 206). It connects Tubulus rectus proximalis to Tubulus rectus distalis (Fig. 10.5). In the mammalian *juxtamedullary* nephron the Tubulus attenuatus has a Pars descendens and a Pars ascendens; these terms are not appropriate here because in birds the loop turns in the Tubulus rectus distalis, the thin tubule having no Pars ascendens (Fig. 10.5). At the transition of the Tubulus attenuatus into the Tubulus rectus distalis in birds there is generally an abrupt increase in external diameter (Fig. 10.5) (Johnson, 1979: 206), but in *Gallus* the transition is gradual (Siller, 1971: 215). The loop of the *cortical* type of nephron in mammals (about 80% of all nephrons, Krstic, 1984), turns in the Tubulus rectus distalis, as in birds. See Annot. 22.

(20) **Epithelium simplex cuboideum.** The epithelium of the Tubulus attenuatus is much thicker in birds than in mammals, being simple cuboidal or low cuboidal instead of simple squamous, with brush border, apical tubules, and terminal web, but no folding of the basal and lateral membranes (Siller, 1971: 215; Johnson, 1979: 207).

(21) **Tubulus rectus distalis.** Synonymy: thick segment of medullary loop; Pars ascendens ansae (NAA, 1979). The distal straight tubule begins at the end of the Tubulus attenuatus (Fig. 10.5), continues to descend through the medulla, turns at the bottom of the Ansa nephrica, ascends the medulla, and enters the cortex to make contact with its parent juxtamedullary glomerulus, where it forms the Macula densa (Johnson, 1979: 207). Distal to the Macula densa, it becomes the Tubulus contortus distalis.

The distal straight tubule is lined by an Epithelium simplex cuboideum (Hodges, 1974: 517), with few or no microvilli but increasingly complex basal folds (Siller, 1971: 216).

(22) **Ansa nephrica.** Synonymy: medullary loop; loop of Henle; Ansa nephroni (NH, 1983; NAA, 1979). The descending limb of the avian medullary loop (Fig. 10.5) comprises the Tubulus rectus proximalis, the Tubulus attenuatus, and the first part of the Tubulus rectus distalis. The ascending limb is formed by the remainder of the Tubulus rectus distalis. The loop turns in the Tubulus rectus distalis. For the detailed disposition of the loops in the medulla of various avian taxa, see Johnson (1979: 209).

(23) **Tubulus contortus distalis.** The distal convoluted tubule begins immediately distal to the Macula densa. It is narrower and shorter than the Tubulus contortus proximalis. It runs towards the V. intralobularis, makes a few convolutions, and then turns abruptly to the periphery of the cortex to empty into the Tubulus conjungens (Fig. 10.5) (Johnson, 1979: 207). The cells of the Epithelium simplex cuboideum lack a brush border, but have deep lateral and basal folds (Siller, 1971: 220). Ultrastructural and histochemical variations have been observed along the distal convoluted tubule (Nicholson, 1982). Previously the Macula densa in both mammals and birds (Siller, 1971: 221; Johnson, 1979: 207) was generally considered to belong to the beginning of the distal convoluted tubule, but see Annot. 29.

(24) **Tubulus conjungens.** Synonmy: junctional tubule (Huber, 1917); initial collecting duct (Sperber, 1960); collecting tubule (Siller, 1971: 221); pars conjungens of Tubulus convolutus distalis (NAA, 1979); connecting tubule (Wideman, 1988). The Tubulus conjungens (connecting tubule) lies in the periphery of the cortex, and connects the distal end of both the cortical and the juxtamedullary type of nephron with the Tubulus colligens corticalis (Fig. 10.5) (Wideman, et al., 1981). Siller (1971: 221) regarded it as a part of the nephron, but this depends on embryological evidence which is lacking (Johnson, 1979: 199).

The cells of its Epithelium simplex cuboideum (sometimes low columnar) contain mucopolysaccharide granules (Hodges, 1974: 519) and are therefore clearly distinguishable from those of the Tubulus contortus distalis. Mucin is characteristic of collecting ducts but not the nephron. As Johnson (1979: 208) pointed out, this indicates a developmental origin from the metanephric diverticulum (like collecting tubules in general) and not from the Blastema metanephrogenicum (like nephrons). The avian Tubulus conjungens would presumably then be homologous to the mammalian Tubulus renalis arcuatus, which joins the distal convoluted tubule to the Tubulus colligens rectus in the medullary ray.

(25) **Tubulus colligens.** The collecting tubules of birds are named according to their site. The Tubulus colligens corticalis lies in the cortex (Fig. 10.4), and is continued in the medulla by the Tubulus colligens medullaris (Fig. 10.3).

(26) **Tubulus colligens corticalis.** Cortical collecting tubules lie a short distance below the surface of the cortex (Figs. 10.3, 4) (Wideman, et al., 1981). Each tubule drains a number of nephrons (Siller, 1971: 225; Wideman, 1988: Fig. 5A). The cortical type of nephron has no Ansa nephrica and therefore lacks the capacity for countercurrent multiplication for concentrating urine; however, the urine in the collecting tubules is concentrated by the medullary concentration gradient in the medullary cones (Wideman, et al. 1981). The **Epithelium simplex cuboideum** is characterized by mucopolysaccharide granules (Hodges, 1974: 519).

Tubulus colligens medullaris. The medullary collecting tubules descend through the medullary region of the Lobulus renalis, fusing to form progressively larger tubules (Fig. 10.3) (Wideman, 1988: Fig. 5A). They are a major constituent of

the medullary cone (Annot. 6), with species variations (Johnson, 1979: 209). As the tubules become larger, their lining changes from **Epithelium simplex cuboideum** to **Epithelium simplex columnare,** but all these cells are characterized by mucopolysaccharide granules (Hodges, 1974: 519).

(27) **Ductus colligens.** At the apex of the medullary part of the renal lobule (medullary cone), the collecting tubules typically converge into a single collecting duct, the Ductus colligens (Fig. 10.3); this represents the third order of branching of the ureter (Fig. 10.2) (see Annot. 43 for termination of ducts). The epithelium becomes more complex as the collecting tubules converge, ranging from **Epithelium stratificatum cuboideum to Epithelium pseudostratificatum columnare,** with mucopolysaccharide granules throughout (Johnson, 1979: 219).

(28) **Complexus juxtaglomerularis.** Despite doubts (Ogawa and Sokabe, 1971; Sokabe and Ogawa, 1974; Wideman, et al. 1981), evidence assembled by Johnson (1979: 208), Siller (1983: 96), and Wideman (1988: 155) established that the juxtaglomerular complex is present in birds, comprising the Macula densa, Endocrinocyti myoidei, and Mesangium extraglomerulare. The complex is complete in both cortical and juxtamedullary nephrons (Morild, et al., 1985b).

(29) **Macula densa** (Fig. 10.5). Always present in birds, in both Nephrona corticalia and Nephrona juxtamedullaria (Morild, et al. 1985a). The Macula densa is histologically similar to that of mammals (Siller, 1971: 221), but ultrastructural differences may exist (Siller, 1983: 96). Also it varies greatly in development (height, crowding of cells) even within the same kidney (for review see Wideman, 1988: 155). The *Nomina Histologica* (1983, 1989) regards the mammalian Macula densa as belonging to the Tubulus rectus distalis, and this has been adopted here for the avian Nephron juxtamedullare. In the avian Nephron corticale the Macula densa belongs to the Tubulus distalis, occurring after a short preglomerular segment (Fig. 10.5) (Morild, et al., 1985a).

(30) **Endocrinocytus myoideus [Juxtaglomerularocytus].** Synonymy: granular epithelioid cell (Ogawa and Sokabe, 1971; JG cell. The myoid endocrine cell is the renin-secreting, modified myocyte of the tunica media of the afferent glomerular arteriole at the vascular pole of the glomerulus. Siller (1971: 210) found the granules that typify these cells in mammals to be very difficult to demonstrate, but their presence has been confirmed electron microscopically (Ogawa and Sokabe, 1971; Morild, et al., 1985b).

(31) **Mesangium extraglomerulare [Insula juxtavascularis]; Mesangiocytus extraglomerularis.** The extraglomerular mesangiocyte is also known as the Polkissen, Goormaghtigh, or Lacis cell. The extraglomerular mesangium is formed by an aggregation of extraglomerular mesangiocytes at the vascular pole of the glomerulus. Ogawa and Sokabe (1971) failed to find these cells by either light or electron microscopy, but Siller (1971: 210) and Johnson (1979: 209) established their presence. See Annot. 8.

(32) **A. renalis cranialis/media/caudalis.** The cranial renal artery arises from the aorta, whereas the middle and caudal arteries arise from the A. ischiadica (Fig. 10.6) often by a common trunk (Goodchild, 1956; Siller and Hindle, 1969; Kurihara and Yasuda, 1975). The cranial artery distributes three or four primary branches to the Divisio cranialis of the kidney, the middle artery sends two to the middle division, and the caudal artery four or five to the caudal division (Kurihara and Yasuda, 1975). Despite the generalization that the A. iliaca externa supplies the kidney (Spanner, 1925; Sperber, 1960), Siller and Hindle (1969) showed from the very old literature that only an *Ardea* species gets blood from that source.

(33) **Aa. intralobulares.** The interlobular arteries arise from branches of the renal arteries. Siller and Hindle (1969) believed that Aa. interlobares have not yet been identified, but see Kurihara and Yasuda (1975) though their definition of "lobe" may differ from that used here. There are many intralobular arteries in each renal lobule (Fig. 10.4). They run parallel with each other and with the lateral border of the lobule, only slightly deeper than the glomeruli that they supply (Fig. 10.3) (Kurihara and Yasuda, 1975; Siller, 1983). They form afferent glomerular arterioles. Various authors reported that other arterioles arise from the intralobular arteries and connect directly with, e.g., the Vv. interlobulares or intralobulares, thus providing arteriovenous shunts (West, et al., 1981: 299), but Wideman, et al. (1981) were unable to find them.

(34) **Arteriola glomerularis afferens.** Because the Aa. intralobulares lie only a little deeper than the Glomeruli, the afferent glomerular arterioles are very short (Fig. 10.3) (Siller and Hindle, 1969; Kurihara and Yasuda, 1975).

(35) **Arteriola glomerularis efferens.** The efferent glomerular arteriole is longer than the afferent (Kurihara and Yasuda, 1975). It runs towards the periphery of the lobule and gives off two to five terminal branches that empty abruptly into Vasa capillaria sinusoidea of the Rete capillare peritubulare corticale, thus forming portal-arterial anastomoses (Fig. 10.4) (Kurihara and Yasuda, 1975; Wideman, et al., 1981).

(36) **Arteriolae rectae.** The arteriolae rectae descend in the medullary region (cone) of each lobule (Fig. 10.3). They arise near the medulla as in mammals (Siller and Hindle, 1969), being derived solely from efferent arterioles belonging to the juxtamedullary type of nephron (Wideman, et al., 1981). They open into a rich capillary network extending throughout the medullary cone (Johnson, 1979: 217).

(37) **Rr. renales afferentes; Vv. interlobulares; Rdxx. renales efferentes; Vv. intralobulares.** The afferent renal venous rami are the branches of the Vv. portalis renalis cranialis and caudalis; they end by forming the Vv. interlobulares. The efferent renal venous radices are formed by union of the Vv. intralobulares, and they discharge into the Vv. renales craniales and the V. renalis caudalis (Fig. 10.6). For the main channels of portal flow see **Ven.** Annot. 59.

(38) **Rete capillare peritubulare corticale.** The richly anastomosing cortical peritubular capillary network, which ramifies among the renal tubules within the cortex of each lobule. At the periphery of the lobule the rete receives venous blood from the venules of the Vv. interlobulares and arterial blood from the Arteriolae efferentes (Fig. 10.4). Wideman, et al. (1981) established that all renal tubules have access to this mixture of portal and arterial blood, except for the Ansae nephricae of the juxtamedullary nephrons. For other possible arteriovenous shunts see Annot. 33.

(39) **Vas capillare sinusoideum.** The vessels of the Rete capillare peritubulare corticale are not true capillaries but sinusoidal capillaries similar to those in the liver (Wideman, et al., 1981).

(40) **Valva portalis renalis.** The renal portal valve appears to be unique in being the only vascular valve containing innervated smooth muscle fibres in any vertebrate (Oelofsen, 1977). Essentially the valve is cone-shaped, with its the apex opening into the V. iliaca communis (Fig. 10.6) (Akester, 1964). In some species such as *Gallus* the valve has a single orifice, but in others it has multiple openings (Sperber, 1949).

In *Struthio camelus* there are evidently three cone shaped valves, side by side, at the usual site (Oelofsen, 1977). The valve is regulated by contraction of innervated smooth muscle cells at its base (Gilbert, 1961; Akester and Mann, 1969) or swelling of epithelioid cells at its apex (Spanner, 1939), the former perhaps for coarse and the latter for fine adjustment (Schwarz, et al., 1981).

(41) **Venulae rectae.** Presumably these drain the blood from the medullary cone of each lobule (Fig. 10.3). However, the Venulae rectae seem to be indistinguishable histologically from the Arteriolae rectae in birds, in contrast to those of mammals (Johnson, 1979: 217), and their drainage has not yet been established (Wideman, 1988: 140). The Venulae rectae and Arteriolae rectae together constitute the Vasa recta.

(42) **Pars renalis;** Pars pelvica. These terms were introduced by Goodchild (1956) and King (1975: p1925). The renal part of the ureter is the segment related to the kidney (Fig. 10.1). The pelvic part runs from the Extremitas caudalis of the kidney to the Urodeum.

(43) **Rr. ureterici primarii/secundarii/tertiarii.** The primary rami of the ureter are the direct tributaries of the ureter (Fig. 10.1). A secondary ramus of the ureter drains a group of collecting ducts and their medullary cones (Fig. 10.2), thus forming the basis of a Lobus renalis (Annot. 5). Each Ductus colligens is equivalent to a tertiary ramus of the ureter; it drains a single medullary cone and forms the basis of a Lobulus renalis (Fig. 10.2). Species variations in the numbers and patterns of primary rami were reviewed by Johnson (1979: 217).

(44) **Tunica mucosa; Tunica muscularis.** According to the reviews and original observations of Hodges (1974: 519) and Johnson (1979: 219) in a wide range of species, the epithelium of the ureter is a tall columnar pseudostratified type in which lie many vacuoles filled with mucopolysaccharides (Annot. 27). Columnar, bistratified, and transitional variants have been reported by other authors. Beneath the epithelium is a thick, gland-free Lamina propria mucosae. The Tunica muscularis contains three layers, the middle circular layer being much the best developed.

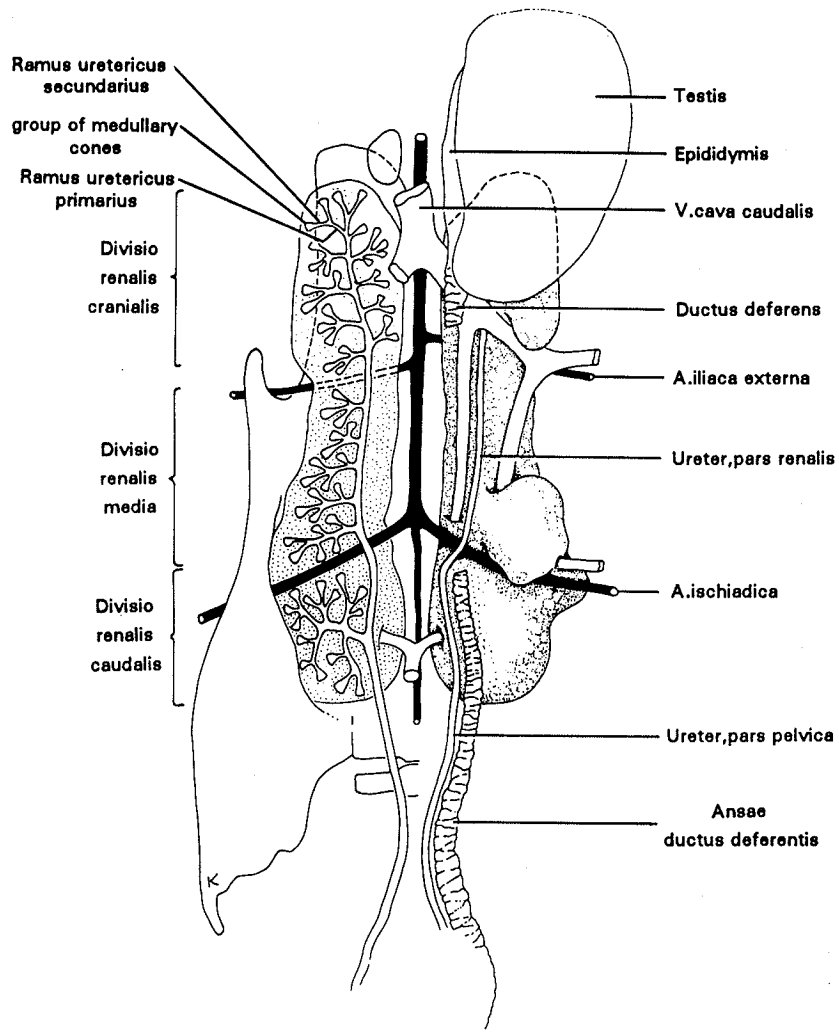

Fig. 10.1. Ventral view of the male urogenital system of *Gallus*. The right kidney is drawn as though transparent to show the primary and secondary rami of the ureter. Most of the cranial half of the left Ductus deferens has been removed. From King (1975), with permission from W. B. Saunders, Philadelphia.

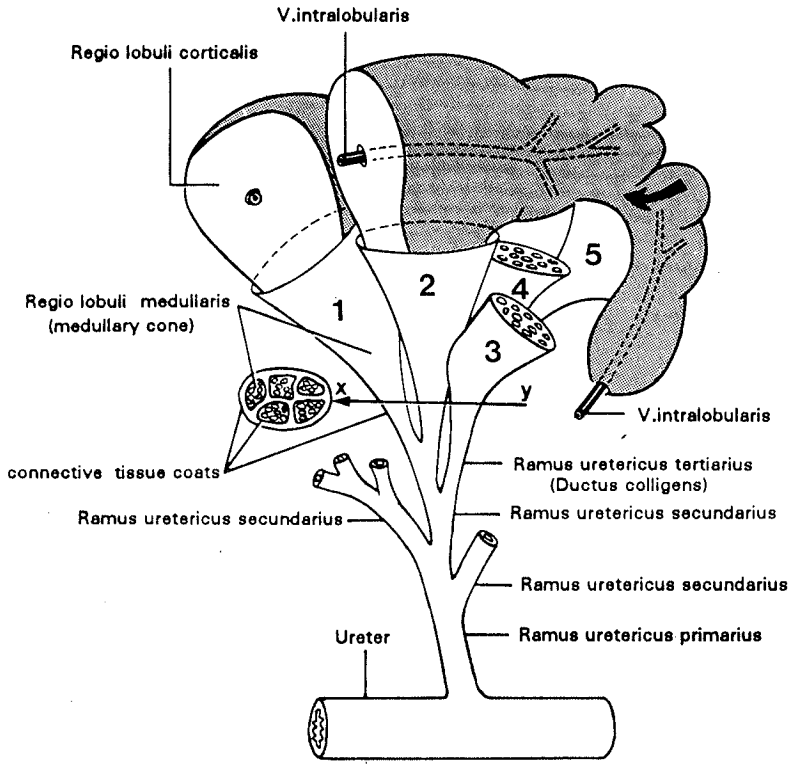

Fig. 10.2. Schematic diagram of the lobar and lobular architecture of the avian kidney. The Lobus renalis is based on a secondary ramus of the ureter. The diagram shows a secondary ramus draining a group of five Lobuli renales, 1-5, together constituting one renal lobe. Each of these five lobules is drained by its own collecting duct (Ductus colligens), which is equivalent to a tertiary ramus of the ureter. The five collecting ducts are enclosed in a common connective tissue coat (cut transversely at X-Y).

A renal lobule has a cortical region and a medullary region. The cortical region has an intralobular vein at its center. The medullary region of a lobule is also known as a medullary cone. It contains collecting tubules (Tubuli colligentes), transected in Lobuli 3 and 4 as small circles. The medullary region of each lobule is surrounded by its own connective tissue sheath, which blends with the connective tissue coat transected at X-Y. The cortical region of a lobule is not bounded by connective tissue, and therefore the cortex of adjacent lobules is blended. However, the lobules lie at irregular depths in the kidney, and consequently neither the cortex nor the medulla forms a uniform stratum. A given medullary region often drains the cortical regions associated with adjacent Vv. intralobulares. For example, two independent cortical regions blend at the arrow; medullary region 5 would receive collecting tubules from both of these cortical regions. Not drawn to scale. Based on Johnson (1974).

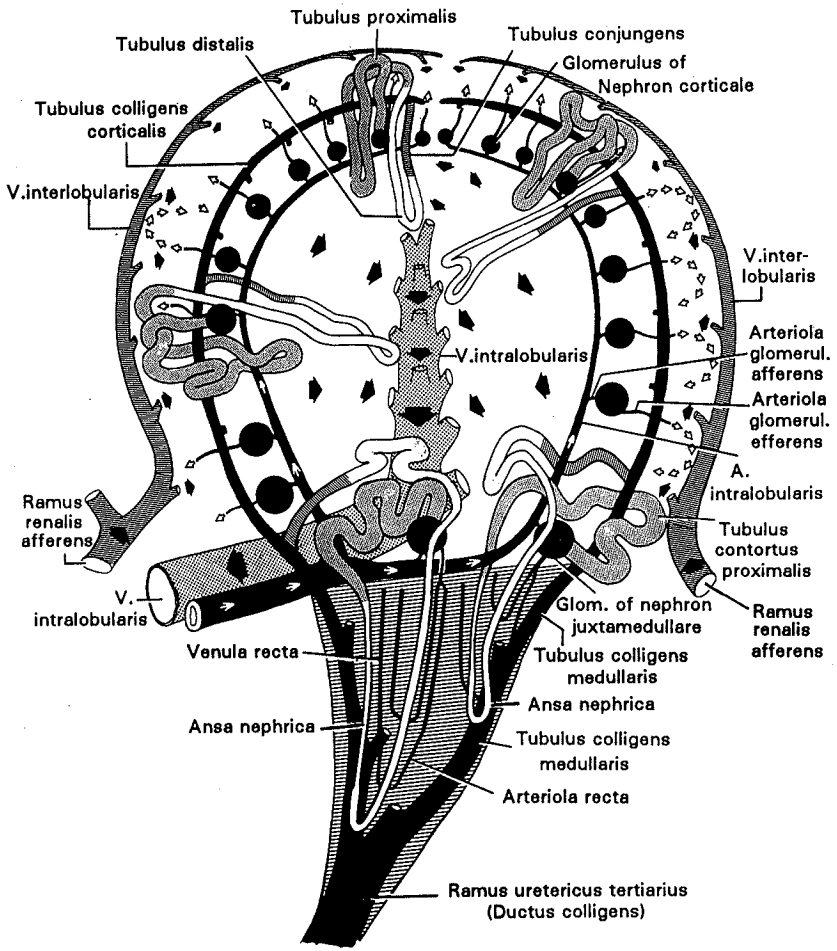

Fig. 10.3. Schematic longitudinal section through an avian renal lobule. Renal portal blood arrives (black arrows) in the afferent renal rami (R. renalis afferens) and thence interlobular veins (V. interlobularis). Arterial blood (white arrows) arrives in the intralobular arteries (A. intralobularis). Relatively small cortical glomeruli lie in a semicircle in the more superficial (upper) part of the cortical region of the lobule, and larger juxtamedullary glomeruli (Glom.) lie in the deeper part. The Arteriola glomerula afferens are very short. Efferent glomerular arterioles end by discharging (small open arrows) into the cortical peritubular capillary rete (not shown). In the centre of the lobule, blood from the rete (black arrows) drains into the V. intralobularis. Three cortical nephrons are shown in the upper part of the lobule; two juxtamedullary nephrons, each with an Ansa nephrica, lie in the lower part. The Tubulus conjungens is hatched. The Venula recta is speculative. From Wideman (1988) with permision of the author and CRC Press.

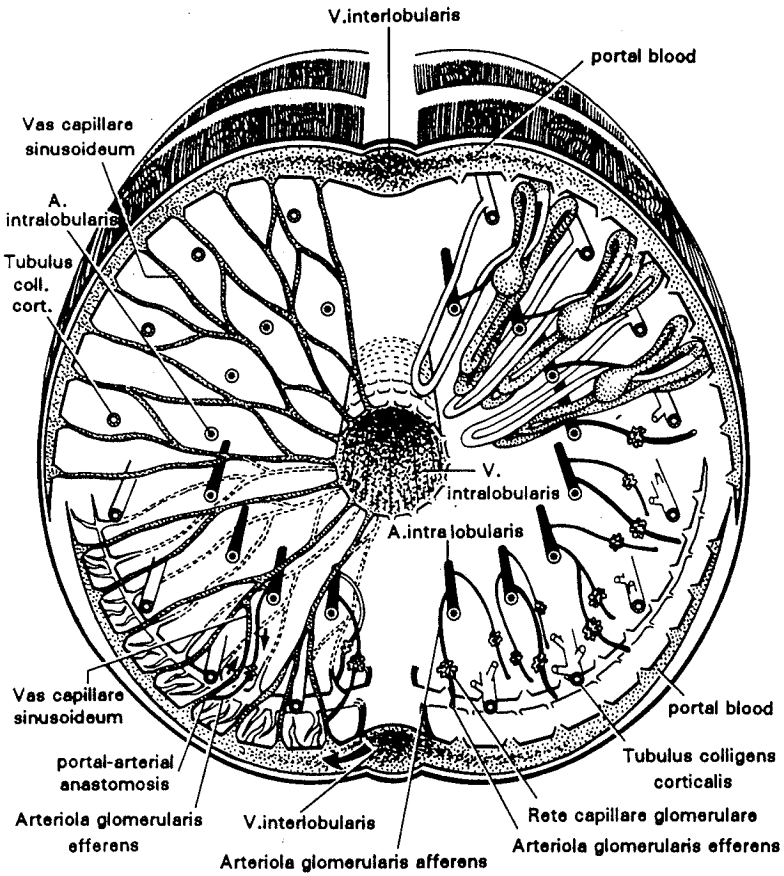

Fig. 10.4. Schematic transverse section through the cortical region of an avian renal lobule. Renal portal blood (arrow) arrives in the interlobular veins (Vv. interlobulares), passes through the Vasa capillaria sinusoidea, and drains out via the centrally placed intralobular vein (V. intralobularis). The sinusoidal capillaries form a profusely anastomosing network of vessels surrounding the nephronal tubules, the Rete capillare peritubulare corticale, much more extensive than shown here. The Aa. intralobulares should be slightly more peripheral in the lobule than shown, being only a little deeper than the glomeruli that they supply; the Arteriolae glomerulares afferentes are therefore shorter than shown. The Arteriolae glomerulares efferentes discharge into the sinusoidal capillaries at the periphery of the lobule, forming portal-arterial anastomoses. The cortical collecting tubules (Tubulus coll. cort.) lie a short distance below the interlobular veins, thus leaving room at the surface of the lobule for the most peripheral loops of the nephronal tubules. From Wideman, et al. (1981) with permission of the authors and the Journal of Morphology.

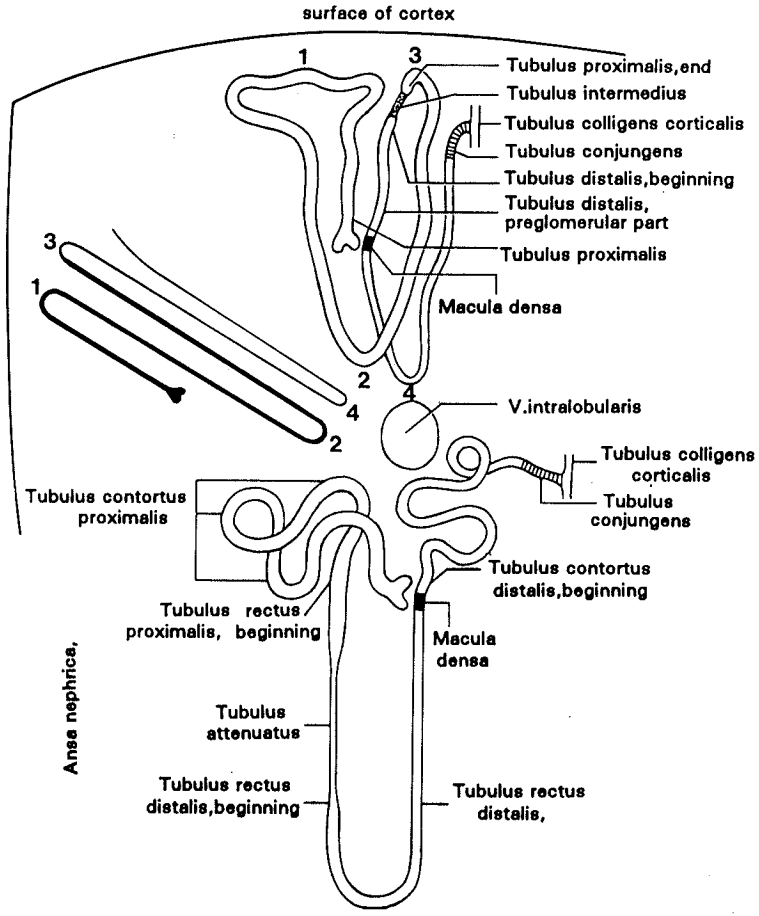

Fig. 10.5. Diagrams showing the main parts of two avian Nephrona corticalia (top), and one Nephron juxtamedullare (bottom); not drawn to scale. The arrangement of the two cortical nephrons is based on Morild, et al. (1985a), and shows four basic bends (1-4). Extra loops and coils may occur, particularly at bend 1 lying parallel with the surface of the lobule. In the highly schematic diagram at top left, the four bends and the loops connecting them have been separated to show the basic pattern more clearly. The Tubulus intermedius may be absent or difficult to see. The disposition of the juxtamedullary nephron is based on Wideman (1988: 140).

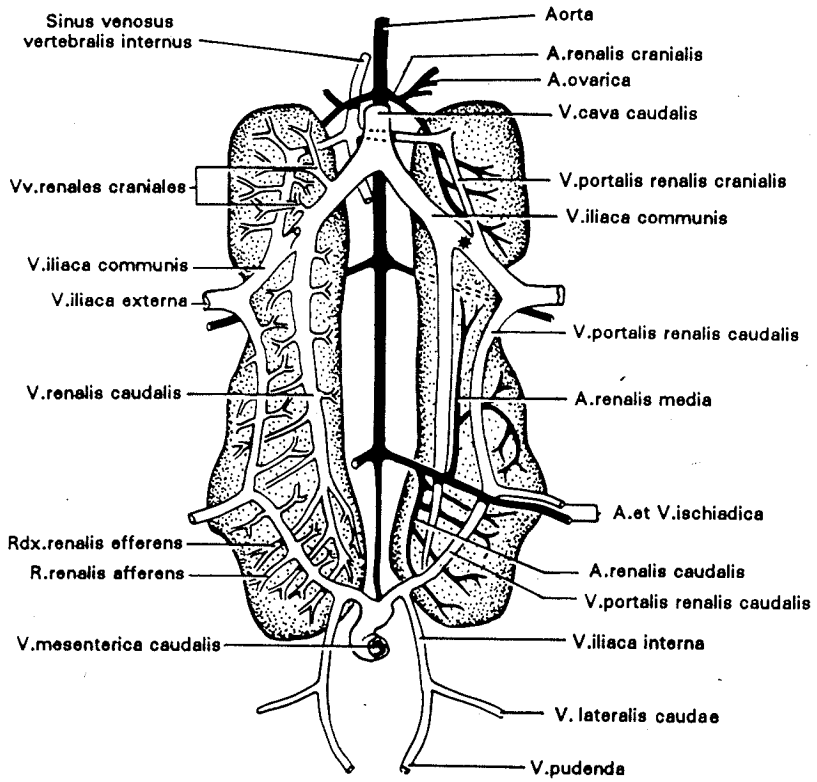

Fig. 10.6. Semidiagrammatic ventral view of the kidneys of *Gallus*, drawn as though transparent to show their blood vessels. *, site of Valva portalis renalis. Redrawn from King (1975), with permission from W. B. Saunders, Philadelphia.

TERMINOLOGY

ORGANA GENITALIA MASCULINA

TESTIS

Extremitas cranialis
Extremitas caudalis
Facies lateralis
Facies medialis
Margo liber
Margo epididymalis
Mesorchium

Tunica albuginea[1]
Interstitium testis
  Endocrinocytus interstitialis
Parenchyma testis
  Tubulus seminifer convolutus[2]
    Epithelium spermatogenicum
      Epitheliocytus sustenans[3]
      Cellulae spermatogenicae
    Lamina limitans[3]
      Membrana basalis[3]
      Stratum fibrosum[3]
      Stratum myoideum[3]
  Tubulus seminifer rectus[2]

Rete testis[4]
  Cisterna intracapsularis[4]
  Cisterna intratesticularis[4]
  Cisterna extratesticularis[4]

Vasa sanguinea et nervi testis
  A. testicularis[5]
  Vv. testiculares[5]
  Truncus thoracicoabdominalis
    Vasa l. testicularis (**Lym.** Fig. 13.6)
  Plexus aorticus (**PNS** Annot. 81)
    Plexus adrenalis
      Gg. adrenalia
        Plexus testicularis
Spermatogonium[6]
Spermatocytus primarius
Spermatocytus secundarius
Spermatidium
  Proacrosoma[7]
    Vesicula proacrosomatica[7]
    Granulum proacrosomaticum[7]
  Acrosoma[8]
    Membrana acrosomatica externa[12]
    Membrana acrosomatica interna[12]
    Substantia acrosomatica[8]
  Perforatorium[7,12]
  Corpusculum chromatoideum[9]
  Flagellum[10]
  Vagina cytoplasmatica

Spermatozoon[11]
  Caput[11]
    Acrosoma[12]
      Membrana acrosomatica externa[12]
      Membrana acrosomatica interna[12]
      Substantia acrosomatica[12]
    Perforatorium[12]
    Substantia subacrosomatica[12]
    Substantia postacrosomatica[12]
    Nucleus
    Fossula articularis[13]
  Flagellum[11,14]
    Pars conjungens[14]
      Capitulum[14]
      Centriolum proximale[14]

(continued)

TESTIS (cont.)

Pars intermedia[14]
Centriolum distale[14]
Axonema[15]
Microtubulus centralis[15]
Diplomicrotubulus periphericus[15]
Vagina mitochondrialis[16]
Anulus [Annulus][17]
Pars principalis[14]
Axonema[15]
Vagina amorpha[18]
Pars terminalis[14]
Axonema[15]

EPIDIDYMIS

Extremitas cranialis[19]
Extremitas caudalis[19]
Ductulus efferens proximalis testis[20]
Ductulus efferens distalis testis[20]
Ductulus conjungens[21]
(Ductulus paradidymidis)[22]
(Appendix epididymidis)[22]
(Ductus aberrans)[22]
(Ductulus aberrans)[22]
Ductus epididymidis[21]

A. testicularis
Rr. epididymales

DUCTUS DEFERENS

Ansae ductus deferentis[23]
Pars recta ductus deferentis[24]
Receptaculum ductus deferentis[25]
Papilla ductus deferentis[26]
Ostium ductus deferentis[26]
Glomus seminale[27]
Promontorium cloacale[27]

Vasa sanguinea et lymphatica et nervi ductus deferentis
A. renalis cranialis
Rr. ureterodeferentiales craniales
A. ischiadica
Rr. ureterodeferentiales medii
A. pudenda
Rr. ureterodeferentiales caudales
Vv. testiculares
Rr. ureterodeferentiales craniales
V. renalis caudalis
Vv. ureterodeferentiales mediae
V. pudenda
Vv. ureterodeferentiales caudales
Truncus thoracoabdominalis
Vasa l. ureterodeferentialia
N. pudendus
Rr. ductus deferentis
Plexus aorticus (PNS Annot. 81) (Lym.)
Plexus adrenalis
Gg. adrenalia
Rr. ductus deferentis

APPARATUS COPULATIONIS

Phallus masculinus[28]
Phallus nonprotrudens[29]
Corpus phallicum medianum[30]
Corpus phallicum laterale[30]

(continued)

APPARATUS COPULATIONIS (cont.)

Plicae lymphaticae[31]
Fossa ejaculatoria[32]
Sulcus ejaculatorius[32]
Lymphobulbus phalli dexter/sinister[33]
Corpus vasculare phalli[33]
Glomera corporis vascularis phalli[33]
Sinus lymphatici[33]
Vasa l. cloacalia[34]
Phallus protrudens[35]
Basis phalli[36]
Corpus fibrocartilagineum[37]
Lymphobulbus phalli[38]
Corpus vasculare phalli[38]
Glomera corporis vascularis phalli[38]
Sinus lymphaticus[38]
Cisterna lymphatica basis phalli[39]
Vasa l. cloacalia[40]
Corpus phalli[36]
Sulcus phalli[41]
Labium sulci phalli dextrum/sinistrum[42]
Rugae phalli[43]
Cisterna lymphatica corporis phalli[44]
Flexura phalli nonerecti/Apex phalli erecti[45]
Sacci phalli[36,46]
Saccus cutaneus phalli[46]
Ostium sacci cutanei phalli[46]
Rugae phalli[43]
Lamina epithelialis[47]
Lamina propria[47]
Saccus glandularis phalli[46]
Ostium sacci glandularis phalli[46]
Lamina epithelialis[47]
Lamina propria[47]
Lig. elasticum phalli[48]
Suspensorium phalli[49]
Involucrum phalli[36]
Fossa ejaculatoria[50]
Sulcus ejaculatorius[50]

M. retractor phalli caudalis [M. levator cloacae][51]
M. retractor phalli cranialis [M. dilator cloacae][51]

VASA et NERVI APPARATI COPULATIONIS

(see Vasa et Nn. cloacae and **Cloaca** Annots. 22-25)

ANNOTATIONS

(1) **Tunica albuginea.** An extremely thin fibrous layer covering the testis (Lake, 1981: 12) (Fig. 10.8). Septula testis and mediastinum testis are absent in birds (Tingari, 1971; Budras and Sauer, 1975; Budras and Schmidt, 1976).

(2) **Tubulus seminifer convolutus; Tubulus seminifer rectus.** The convoluted seminiferous tubule (Fig. 10.8) is equivalent to the Tubulus seminifer contortus of the NAV (1983) and the Tubulus seminifer convolutus of the NH (1989).

Tubulus seminifer rectus. The absence (Tingari, 1971) or presence (Osman, 1980) of the straight seminiferous tubule in birds was reviewed by Budras and Meier (1981). A dispute arises in defining where a Tubulus seminifer ends and the Rete testis begins. This is largely because the junction between the two is much shorter in birds than in mammals (Lake, 1981: 23). In the rat, the Tubulus seminifer convolutus is usually a closed loop which opens at both ends into a Tubulus seminifer rectus, and thence into the rete testis (generally accepted for man also (Williams and Warwick, 1980: 1411). In man the first part of the Tubulus seminifer rectus is lined by modified Epitheliocyti sustenantes and the rest by simple cuboidal epithelial cells with irregular microvilli and occasional cilia, the entire tubule being surrounded by a dense connective tissue sheath (Krstic, 1984: 431). The Tubulus seminifer rectus is said to be present in domestic mammals (e.g., Nickel, et al., 1973: 305; Banks, 1981: 478), but Trautmann and Fiebiger (1957: 260) state that the mammalian Tubuli seminiferi convoluti may open directly into the Rete testis. In birds the end of the Tubulus seminifer convolutus changes abruptly (Fig. 10.8) giving a short length of tubule that is lined by modified Epitheliocyti sustenantes; this short segment has been classically named the "Tubulus rectus" (e.g., Lake, 1957; Budras and Schmidt, 1976; NAA, 1979; Barker and Kendall, 1984; see Lake, 1981: 24 for review of the earlier literature). Budras and Meier (1981) argued that, because this short segment is lined by modified Epitheliocyti sustenantes, it belongs to the terminal segment of the Tubulus seminifer convolutus. They proposed to call it simply the terminal segment of the Tubulus seminifer convolutus. A further complication is that this terminal segment runs directly into a short duct that becomes an intratesticular cistern of the Rete testis (Annot. 4) (Fig. 10.8). This short duct has been named Tubulus rectus by some authors (e.g., Aire, 1979a). Its epithelium, however, is low cuboidal or simple squamous, i.e., identical to that of the Rete testis in most birds (Lake, 1981: 24; Budras and Meier, 1981), and therefore it can reasonably be regarded simply as an initial segment of the Rete testis (Budras, pers. comm., 1990).

(3) **Epitheliocytus sustenans; Lamina limitans; Membrana basalis; Stratum fibrosum; Stratum myoideum.** The Epitheliocytus sustenans (sustentacular cell) was formerly known as the Sertoli cell. Its intercellular junctions form a blood-testis barrier which prevents foreign proteins, produced by haploid germ cells, from reaching the blood and provoking an autoimmune reaction. The Lamina limitans has been regarded as part of this barrier. Its structure is similar to that of mammals (Rothwell and Tingari, 1973). The Membrana basalis is a classic basement membrane. The Stratum fibrosum comprises typical fibroblasts and collagen fibrils. The Stratum myoideum produces the rhythmic contractions that force the spermatozoa towards the epididymis.

(4) **Rete testis; Cisterna intracapsularis; Cisterna intratesticularis; Cisterna extratesticularis.** The rete testis has been found in species of several avian orders (Alverdes, 1924; Gray, 1937; Bailey, 1953; Stoll and Maraud, 1955; Tingari, 1971; Budras and Schmidt, 1976; Aire, 1979a; Budras and Meier, 1981; Tetzlaff, 1983; Barker and Kendall, 1984; Nasu, et al., 1985). In the domestic form of *Gallus gallus* its main component is a longitudinal intracapsular cistern which is embedded in the Tunica albuginea. This connects with transversely orientated intratesticular and extratesticular cisterns (Fig. 10.8) (Budras and Schmidt, 1976). The concept of a major intracapsular component and minor intratesticular and extratesticular components of the rete in *Gallus* was also supported by Stoll and Maraud (1955) and Aire (1979a), but Tingari (1971) and Nasu, et al. (1985) believed the main component in *Gallus* to be extratesticular. It is possible that the Rete testis may not be a universal feature of birds (Traciuc, 1967, 1969; Lake, 1981: 23).

(5) **A. testicularis; Vv. testiculares.** The A. testicularis arises from the cranial renal artery, and an accessory testicular artery occasionally arises from the aorta. The several testicular veins drain into the caudal vena cava (Nishida, 1964). See **Art.** Annot. 66; **Ven.** Annot. 56.

(6) **Spermatogonium.** Lin, et al. (1990) distinguished three types of spermatogonia in *Coturnix*, classifying them into dark type A, pale type A, and Type B, according to the mammalian terminology.

(7) **Proacrosoma; Vesicula proacrosomatica; Granulum proacrosomaticum; Perforatorium.** In the spermatid the proacrosome is the precursor of the acrosome. It is first seen as an elliptical body, the proacrosomatic vesicle, formed from the Golgi complex of the spermatid. This body then becomes attached to the nuclear membrane of the early spermatid (Tingari, 1973). The proacrosomatic granule is a small dense granule that arises in the proximal nuclear invagination of the early spermatid (Nagano, 1962). It then develops rapidly (Tingari, 1973) into the Perforatorium.

(8) **Acrosoma; Substantia acrosomatica.** At the late stage of development of the spermatid of the domestic fowl, when the nucleus elongates and condenses, the acrosome already shows the shape that characterizes the ejaculated spermatozoon (unlike mammals). The acrosomatic substance develops as an electron-lucent homogeneous material attached to the nucleolemma of the early spermatid (Tingari, 1973).

(9) **Corpusculum chromatoideum.** The chromatoid body is an electron-dense granule close to the nucleus of the spermatid, visible in histological preparations. It is evidently the "alveolar body" or "membrane body" of electron microscopy, which is an aggregate of proteinaceous vacuoles and granular material (Gunawardana and Scott, 1977; Xia, et al., 1986).

(10) **Flagellum.** The entire Flagellum of the spermatid is enclosed within a loose plasmalemma, and contains nine doublets and a central pair of microtubules (McIntosh and Porter, 1967; Tingari, 1973).

(11) **Spermatozoon.** The Spermatozoon consists of a Caput (head) and a Flagellum (tail). Reviews of the literature by McFarlane (1969) and Lake (1981: 40) established two general types of spermatozoon in birds. The simpler type (Fig. 10.7) is relatively short and plain, occurs throughout the non-passerine orders (except some charadriiforms), and resembles that of reptilia; the passerine type is relatively much longer, typically having a complex spiral shape which is considered to indicate higher evolutionary development (McFarlane, 1969).

(12) **Acrosoma; Substantia acrosomatica; Membrana acrosomatica externa/interna; Perforatorium; Substantia subacrosomatica; Substantia postacrosomatica.** The acrosome fits like a cone over the proximal end of the head of the spermatozoon (Fig. 10.7). It comprises the acrosomatic substance enclosed between the external and internal acrosomatic membranes (Bakst and Howarth, 1975) (Fig. 10.7). The Substantia acrosomatica, which is presumed to contain the enzymes that hydrolyse the path through the Lamina perivitellina, appears homogeneous (Lake, et al., 1968) and thus lacks the regional differences into the acrosomal cap and collar of mammals (Bakst and Howarth, 1975). The Perforatorium (synonymy: Spina acrosomae, NAA, 1979; acrosomal spine, Lake, et al., 1968; Tingari, 1973) is homogeneous and not membrane-bound (Bakst and Howarth, 1975) but is embedded in the

subacrosomatic substance (Fig. 10.7). The latter is a fine granular homogeneous material appearing confluent with the similar material of the postacrosomatic substance (Tingari, 1973). Since the Perforatorium is outside the acrosomatic membranes it is not strictly a part of the acrosome, and therefore the term Perforatorium is preferred to the Spina acrosomae of NAA (1979). However, the avian "acrosomal spine" differs from the mammalian perforatorium in the timing of its development (Tingari, 1973) and its definitive structure (Lake, 1981: 40). The homology of these structures is uncertain, and the use of "perforatorium" in birds should therefore be kept under review.

(13) **Fossula articularis.** The articular fossa is an irregular invagination of the head (Fig. 10.7), shaped to receive the articular facet(s) of the Capitulum (Thurston and Hess, 1987).

(14) **Flagellum.** The tail of the flagellum is divided into the Pars conjungens, Pars intermedia, Pars principalis, and Pars terminalis (Fig. 10.7) (Lake, et al., 1968).

Pars conjungens. Synonymy: Collum spermatozoi, NAA, 1979; neck. Separate masses of dense material arise in the space between the Centriolum proximale and the nuclear membrane (Nucleolemma) (Fig. 10.7). These fuse with dense material of the proximal centriole to form the several articular facets of the Capitulum (Lake, et al., 1968; Tingari, 1973; Bakst and Howarth, 1975).

Pars intermedia. Synonymy: Pars media (NAA, 1979); middle piece. The proximal boundary of the middle piece (Fig. 10.7) is formed by the line of fusion of the Centriolum proximale with the Centriolum distale (Bakst and Howarth, 1975). In mammals the distal centriole is a component of the Pars conjungens; in birds it forms part of the middle piece (Fig. 10.7), lying axially within the Vagina mitochondrialis (Lake, 1981: 45).

Pars principalis. The lengthy principal piece of the flagellum (Fig. 10.7) begins at the Anulus.

Pars terminalis. The short end piece of the flagellum (Fig. 10.7) consists only of the axonemal complex surrounded by the plasmalemma (Lake, et al., 1968; Thurston and Hess, 1987).

(15) **Axonema; Microtubulus centralis; Diplomicrotubulus peripheric us.** The Axonema is the axial filament complex, extending throughout the Pars principalis and Pars terminalis of the flagellum (Fig. 10.7). It consists of two central single "fibres" or microtubules, the central microtubules, which are surrounded by nine doublet "fibres" or microtubules known as the Diplomicrotubuli peripherici (peripheral diplomicrotubules) (Nagano, 1962; Lake, et al., 1968; Tingari, 1973). The term "fibre" is unsuitable, as each of these structures possesses a dense rim and lighter interior thus resembling a microtubule.

(16) **Vagina mitochondrialis.** In the Pars intermedia of the flagellum, the Axonema is surrounded by the mitochondrial sheath (Fig. 10.7). This consists of mitochondria arranged as roughly rectangular plates curved along the longitudinal axis (Lake, et al., 1968). In passerine spermatozoa, the mitochondria according to Fawcett, et al. (1971) are arranged in a spiral series, but according to McFarlane (1971: 20) and Humphreys (1972) there is typically only a single elongated mitochondrion which winds spirally around the Pars intermedia.

(17) **Anulus [Annulus].** The anulus is formed at an indentation of the plasmalemma at the distal end of the Vagina mitochondrialis (Fig. 10.7). Electron-dense material is deposited here on the inner surface of the plasmalemma, thus thickening the plasmalemma where it directly invests the escaping Axonema (Nagano, 1962; Lake, et al., 1968; Tingari, 1973).

(18) **Vagina amorpha.** A sheath of amorphous material surrounding the Axonema distal to the Vagina mitochondrialis. It becomes thinner towards the end of the Pars principalis (Lake, et al., 1968; Tingari, 1973; Thurston and Hess, 1987), and is absent from the Pars terminalis (Lake, 1981: 48) (Fig. 10.7).

(19) **Extremitas cranialis; Extremitas caudalis.** These terms replace the mammalian Caput, Corpus, and Cauda epididymidis, which are inappropriate in birds since the Ductuli efferentes testis occur throughout the whole length of the epididymis (Fig. 10.8).

(20) **Ductulus efferens proximalis/distalis testis.** The proximal ductules in *Gallus* and ratite species (Budras and Sauer, 1975; Budras and Meier, 1981) are generally much wider than the distal (Fig. 10.8). Both are lined by ciliated cells and cells with a brush border (microvilli). The proximal ductules arise from the glomerular capsules of the mesonephros, and the distal from the proximal and distal tubules and intermediate segments of the mesonephros (Budras and Sauer, 1975).

(21) **Ductulus conjungens; Ductus epididymidis.** Connecting ductules (Fig. 10.8) have been reported in ratites (Budras and Meier, 1981), *Anas* (Tetzlaff, 1983), and galliform species (Budras and Schmidt, 1976; Aire, 1979a, b). They are initially narrower than the Ductuli efferentes testis, but as they approach the Ductus epididymidis they join one another and become wider. The Ductuli conjungentes end by joining the Ductus epididymidis. Their epithelial lining is the same as the Ductus epididymidis. In the embryo they arise from the collecting tubules of the mesonephros (Budras and Sauer, 1975).

(22) **Ductulus paradidymidis: Appendix epididymidis; Ductus aberrans; Ductulus aberrans.** These vestigial structures are present in *Gallus* (Stoll and Maraud, 1955; Tingari, 1971). The paradidymal ductules, blind at both ends, are rare, but can be found in all parts of the epididymis. The Appendix epididymidis of *Gallus* is a cranial continuation of the epididymis (Fig. 10.8), and is attached to the adrenal gland (Budras and Sauer, 1975). It consists of the Ductus aberrans which develops from the mesonephric duct, and of Ductuli aberrantes which arise from the mesonephric tubules. The aberrant ductules open into the aberrant duct. Most of them are in the appendix of the epididymis, a few also in the main part of the epididymis.

(23) **Ansae ductus deferentis.** The sinuous curves of the main part of the Ductus deferens (Fig. 10.1).

(24) **Pars recta ductus deferentis.** The short straight caudal end of the Ductus deferens (Marvan, 1969).

(25) **Receptaculum ductus deferentis.** Synonymy: Ampulla ductus deferentis (Marvan, 1969; Kudo, et al., 1975). The receptaculum is the spindle-shaped terminal dilation of the deferent duct. The term Ampulla is descriptively accurate, but incorrectly suggests homology to the mammalian ampulla.

(26) **Papilla ductus deferentis; Ostium ductus deferentis.** Each Ductus deferens opens into the Urodeum via the Ostium of the caudally pointed papilla of the deferent duct (Figs. 10.2, 13, 14). *Cloaca* Annot. 6.

(27) **Glomus seminale.** Synonymy: seminal vesicle, seminal sac. **Promontorium cloacale.** The seminal glomus comprises knot-like convolutions of the caudal end of the Ductus deferens in passerines (Wolfson, 1952, 1954; Bailey, 1953; Middleton, 1972) and in the psittaciform *Melopsittacus undulatus* (Samour, et al., 1986). During the resting phase it is small, but in the breeding phase it enlarges and may enable storage and maturation of sperm. In passerines the enlargement causes the external body wall adjacent to the vent to bulge caudoventrally as the cloacal promontory, enabling the male to be sexed (Wolfson, 1952; Salt, 1954), but in some passerines a similar bulge occurs in the female in the nuptial phase (Nakamura, 1990). In *M. undulatus* the promontory is relatively inconspicuous but can be palpated (Samour, et al., 1986).

(28) **Phallus masculinus.** Synonomy: penis, Kopulationsorgane. The term Phallus for the vertebrate copulatory organ was proposed by comparative anatomists of the nineteenth century, and adopted by Gerhardt (1933: 297). The avjan phallus is not homologous to the mammalian penis (King and McLelland, 1984: 198); the mechanism of erection is lymphatic in birds and blood vascular in mammals; the semen travels by the external surface of the organ in birds and the internal urethra in mammals; and the phallus is solely reproductive in birds and both urinary and reproductive in mammals. The copulatory organs of birds and mammals should therefore have different names. The term masculinus differentiates the male organ from its female homologue.

(29) **Phallus nonprotrudens.** The non-intromittent type of avian phallus has been extensively studied in domestic galliform species. The nineteenth century literature repeatedly mentions an apparently similar semi-vestigial phallus in Ciconiiformes, Cracidae, Otidae, and "manche Sumpfvögel", but the sources of this information are lost. Wolfson (1954) described phallic structures, possibly similar to those of the domestic fowl, in passerines, especially Emberizidae. See King (1981: 138) for a review. According to Berens v. Rautenfeld and Budras (1978) there is no copulatory erectile body at all in *Fulica atra* and the "pigeon".

(30) (Phallus nonprotrudens): **Corpus phallicum medianum.** Synonymy: White body (Nishiyama, 1955; Lake, 1971: 1420); Colliculus phalli (Berens v. Rautenfeld, 1973). The median phallic body is a single midline structure (Fig. 10.9). It enlarges somewhat in erection, thus contributing to the distended phallic region that overhangs the ventral lip of the vent during ejaculation (see King, 1981: 130). According to Burrows and Quinn (1937), *Meleagris* has a paired median phallic body, but this structure is totally absent (Komárek, 1970; Feder, 1970; King, 1981: 133; Bakst and Cecil, 1983, 1986; Knight, et al., 1984).

Corpus phallicum laterale. Synonymy: Round folds (Nishiyama, 1955; Lake, 1971: 1420); Crus phalli (Berens v. Rautenfeld, 1973). Crus phalli suggests homology with the mammalian Crus penis; but the Crus contains blood vascular erectile tissue and is anchored to the ischium, whereas the avian lateral phallic body contains lymphatic erectile tissue and is not attached to bone. During ejaculation in *Gallus* and *Meleagris* the enlarged left and right lateral phallic bodies meet in the midline, thus contributing to the Sulcus ejaculatorius.

(31) **Plicae lymphaticae** (of Phallus protrudens). Synonymy: Lymph folds (Nishiyama, 1955; Lake, 1971: p1420; Plicae lymfaceae (Komárek, 1970). In *Gallus* and *Meleagris* the lymphatic folds lie on the ventrolateral floor of the proctodeum (Fig. 10.9). They consist of a connective tissue core with lymphatic channels (Knight, 1967: 89). In erection the folds contribute to the Sulcus ejaculatorius. Nishiyama and coworkers proposed that the folds add fluid to the semen of *Gallus* during ejaculation. Berens v. Rautenfeld and Budras (1978) confirmed active transudation from lymph formed by the Corpus vasculare phalli. Transudation also occurs from the urodeal wall in *Anas, Fulica atra,* and *Columba,* directly from the capillary beds of the A. pudenda (Fujihara and Nishiyama, 1976; Berens v. Rautenfeld and Budras, 1978; Berens v. Rautenfeld, 1985). Transudation zones in the urodeal wall in *Meleagris* and *Numida,* and their possible significance in avian morphology, were discussed by Fujihara, et al. (1986, 1988).

(32) **Fossa ejaculatoria; Sulcus ejaculatorius** (of Phallus nonprotrudens). The ejaculatory fossa is the region of the proctodeal floor in *Gallus* and *Meleagris* into which the papillae of the deferent ducts are directed (Komárek, 1970). In the erect phallus, the ejaculatory sulcus is the median groove between the enlarged left and right Corpora phallica lateralia and left and right Plicae lymphaticae, conveying semen from the ejaculatory fossa to the exterior of the vent (King, 1981: 128, 132, 133; Knight, et al., 1984). The Sulcus ejaculatorius of the Phallus nonprotrudens may well be homologous to that of the avian Phallus protrudens (Annot. 50) and that of the chelonian and crocodilian phallus (see King, 1981: 140-141 for review).

(33) **Lymphobulbus phalli dexter/sinister; Corpus vasculare phalli; Glomera corporis vascularis phalli; Sinus lymphatici** (of Phallus nonprotrudens). Synonymy of Lymphobulbus phalli: Corpus cavernosum, Tannenberg's body, vascular body, Gefässkörper, gefässreicher Körper (for historical review see Berens v. Rautenfeld, 1973; NAA, 1979). Corpus vasculare paracloacale. The term Gefässkorper (vascular body) originated from J. Müller's classic paper of 1836, and has been widely used. Consequently it was adopted by the NAA (1979). Berens v. Rautenfeld (1973) introduced the term Lymphobulbus phalli; in his usage, the vascular body itelf is no longer named, but is simply an integral part of the Lymphobulbus phalli. Schalkház, et al. (1982) suggested the term Lymphobulbus cloacae, but retained the term Corpus vasculare and also named the Sinus lymphaticus within which the Corpus vasculare is contained. Schalkház, et al. based these terms on the anseriform phallus, but the structures are similar enough in *Gallus* and *Anas* for the same terms to be used. The terms in this edition of the NAA combine the suggestions of Berens v. Rautenfeld and Schalkház, et al. (1982). Lymphobulbus phalli is preferred to Lymphobulbus cloacae, since this structure is primarily associated with the lymphatic erection of the phallus.

The Corpus vasculare phalli (vascular body of the phallus) of *Gallus* (Fig. 10.9) and *Meleagris* is an obvious red oval structure, 7-12 mm long (Nishiyama, 1955; Kudo, et al., 1975; Knight, et al., 1984). It consists of tufts of arterial capillaries, the Glomera corporis vascularis phalli (glomera of the vascular body of the phallus), enmeshed within a network of lymphatic capillaries (Knight, 1970; Sugimura, et al., 1975; Knight, et al., 1984). The lymphatic capillaries empty into subcapsular lymphatic sinuses enclosing the surface of the Corpus vasculare phalli. In *Gallus* and *Meleagris* these sinuses are not a single continuous subcapsular sinus as in *Anas* (Annot. 38), but a network of channels (Nishiyama, 1955; Knight, 1970; Sugimura, et al., 1975; Knight, et al., 1984). Corpus vasculare phalli receives blood from the A. pudenda. Many of the blood capillaries of the Glomera of *Gallus* have

ultrastructural adaptations for the transudation of lymph into the lymphatic capillaries (Berens v. Rautenfeld and Budras, 1975; Sasaki, et al., 1984).

The Corpus vasculare phalli is known to produce lymph for erection in *Gallus* and *Meleagris* (Nishiyama, 1950, 1955; Knight, 1970; Feder, 1970; Kudo, et al., 1975; Sugimura, et al., 1975; Berens v. Rautenfeld and Budras, 1975), and presumably in birds generally (King, 1981: 138, 142) (for anseriform and ratite species see Annot. 38); however, note the view of Berens v. Rautenfeld and Budras (1978) that there is no copulatory erectile body in *Fulica atra* and the pigeon (Annot. 29). In *Gallus* the lymph is collected into the subcapsular lymphatic sinuses on the surface of the vascular body, and is carried thence into the lymphatic spaces of the phallic bodies and lymphatic folds by a network of small lymphatic channels (Knight, 1970; Knight, et al., 1984); the component that is delivered to the lymphatic folds also contributes fluid (by transudation) to the semen in *Gallus* (Annot. 31). (See King, 1981: 129 for a review of controversies on these subcapsular and drainage channels, and p. 134 for other structural details.) See also **Cloaca** Annots. 22-24.

(34) **Vasa l. cloacalia** (of Phallus nonprotrudens). In *Gallus* all the lymphatics of the cloaca, including the phallus and its left and right Lymphobulbi phalli, drain into the Vas iliacum internum (**Lym.** Fig. 13.7) via a complex of Vasa l. pudenda accompanying the pudendal artery (Knight, 1970; Knight, et al., 1984). See **Cloaca** Annot. 24.

(35) **Phallus protrudens.** The true intromittent copulatory organ of the ratites, tinamids, and anseriforms (King, 1981: 112).

(36) **Basis phalli; Corpus phalli; Sacci phalli; Involucrum phalli** of Phallus protrudens. The Phallus protrudens has four basic components, i.e., the base of the phallus, the body of the phallus (Corpus phalli), the phallic sacs, and the phallic pouch (Involucrum phalli). The Basis phalli forms part of the ventral wall of the cloaca, in *Anas* much of it being enclosed by the Corpus fibrocartilagineum (Fig. 10.10). The Corpus phalli is invaginated in detumescence (Figs. 10.10, 11) but becomes the shaft of the phallus during erection (tumescence) (Fig. 10.12). The Sacci phalli form the hollow interior of the resting (detumescent) phallus, like an inverted finger of a glove (see Annot. 46). The Involucrum phalli is the connective tissue wrap enclosing the resting phallus (Figs. 10.10, 12).

(37) **Corpus fibrocartilagineum** (of Phallus protrudens). The fibrocartilaginous body is a gutter-shaped plate of fibrocartilage in *Anas* (Fig. 10.10) (Liebe, 1914; Guzsal, 1974; Berens v. Rautenfeld et al., 1974; Fujihara, et al., 1976). Its floor strengthens the ventral wall of the urodeum and proctodeum, and its wings reinforce the lateral walls. Dorsally it supports the unpaired Cisterna lymphatica basis phalli (Fig. 10.10). The Lig. elasticum (Annot. 48, Fig. 10.10) is attached to it ventrally (Berens v. Rautenfeld, et al., 1974). The blind end of the Saccus glandularis phalli is also attached to it ventrally (Fig. 10.10) (Guzsal, 1974), and this prevents evagination of the glandular sac during erection.

(38) **Lymphobulbus phalli; Corpus vasculare phalli; Glomera corporis vasculare phalli; Sinus lymphaticus** of Phallus protrudens. Synonomy of Sinus lymphaticus: Cavitas lymphatica (NAA, 1979). For other synonyms, see Annot. 33. In *Anas*, the Lymphobulbus phalli (dexter/sinister) consists of paired elongated sacs (Fig. 10.10) about 4 x 1 cm in the erect phallus, the left being larger than the right; they lie along each side of the urodeum between the cloacal sphincter and the urodeal wall (Müller, 1908; Liebe, 1914; Guzsal, 1974). Caudally the Sinus lymphaticus (lymphatic sinus) of each Lymphobulbus phalli opens directly into the median Cisterna lymphatica basis phalli (Fig. 10.10) (Liebe, 1914; Berens v. Rautenfeld, et al., 1974), this being the channel for erecting the phallus. Schalkház, et al. (1982) suggested Lymphobulbus cloacae, but phalli is preferred because the structure is essentially phallic rather than cloacal. The Corpus vasculare phalli (vascular body of the phallus) (Fig. 10.10) is plum-shaped, red, compact, and about 2 x 1 cm in *Anas* (Guzsal, 1974). The Glomera corporis vascularis phalli (glomera of the vascular body) consist of tufts of small arteries and arterioles forming dense networks of blood capillaries (Guzsal, 1974). The surface of the Corpus vascularis phalli is surrounded by the Sinus lymphaticus, which (in contrast to *Gallus*, Annot. 33) is a single continuous subcapsular space although the lumen is traversed by many thin elastic trabeculae (Eckhard, 1876; Müller, 1908; Liebe, 1914; Guzsal, 1974).

In erection in *Anas* the lymph comes from the vascular body of the phallus (Eckhard, 1876; Müller, 1908; Liebe, 1914; Berens v. Rautenfeld, et al., 1974). On anatomical grounds Grimpe (1930) suggested that erection is lymphatic in *Struthio* (confirmed in ratites by Berens von Rautenfeld, 1989, pers. comm.).

(39) **Cisterna lymphatica basis phalli** of Phallus protrudens. Synonomy: Crus phalli (Berens v. Rautenfeld, et al., 1974); sinus lymphaticus (Guzsal, 1974); Cavitas lymphatica (NAA, 1979); the base (caudal part) of the (paired) Corpus fibrolymphaticum (King, 1981: 123). The lymphatic cistern of the base of the phallus is a median lymphatic chamber, lying on the dorsal aspect of the Corpus fibrocartilagineum (Fig. 10.10). A dorsal median septum partly divides it into left and right compartments, but these connect freely with each other ventrally (Fig. 10.10); caudally they continue directly into the Cisterna lymphatica corporis phalli (Figs. 10.10, 12). Cranially, the Cisterna lymphatica basis phalli connects with the Sinus lymphaticus of the left and right Lymphobulbus phalli (Fig. 10.10).

(40) **Vasa lymphatica cloacalia** (of Phallus protrudens). During detumescence in anseriforms, and apparently also in ratites, each Lymphobulbus phalli drains cranially via Vasa l. cloacalia (Fig. 10.10) into the Vas l. iliacum internum (Budras and Berens v. Rautenfeld, 1984). In these species a paired lymph heart (Cor lymphaticum) propels lymph (10 ml in *Anas*) from the detumescent phallus to the venous system (Berens v. Rautenfeld and Budras, 1981; Budras, et al., 1987). See **Lym** Fig. 13.7; Annot. 6.

(41) **Sulcus phalli** (of Phallus protrudens). Synonomy: Sulcus ejaculatorius. The phallic sulcus lies on the external surface of the erect Corpus phalli (Fig. 10.12). In *Rhea* (Müller, 1836) and *Anas*, and more feebly in *Struthio* (Grimpe, 1930), it winds spirally around the whole length of the erect phallus (Fig. 10.13). In the detumescent (invaginated) phallus the sulcus lies on the *internal* surface of the Saccus cutaneus phalli (Annot. 46). "Sulcus ejaculatorius" implies that it carries semen; Berens v. Rautenfeld, et al. (1974) and King (1981: 124) questioned this.

(42) **Labium sulci phalli dextrum/sinistrum** (of Phallus protrudens. Synonymy: rechte Basalwulst or Rinnenwulst, linke Basalwulst or Hauptwulst (Liebe, 1914). The right and left labia of the phallic sulcus form the boundaries of the sulcus throughout its whole length. The left Labium is larger than the right, especially at the base of the erect phallus, and this gave rise to the earlier term "Hauptwulst" (Liebe, 1914). The NAA (1979) adopted the term Corpus fibrolymphaticum (left and right), but the simpler term, Labium, is now preferred.

(43) **Rugae phalli** (of Phallus protrudens). Ridges on the external surface of the erect phallus (Figs. 10.12, 13, 15b). In the invaginated phallus they project into the lumen of the Saccus cutaneus phalli (Figs. 10.10, 11, 15a). In *Anser* various papillae are associated with the Labia sulci phalli and Rugae phalli (Schalkház, et al., 1982).

(44) **Cisterna lymphatica corporis phalli** (of Phallus protrudens). Synonomy: fibröse Körper (Müller, 1836); cavernae penis (Guzsal, 1974); Cavitas lymphatica (NAA, 1979); the peripheral part of the corpora fibrolymphatica (King, 1981: 123). The lymphatic cistern of the body of the phallus extends throughout the whole length of the erect organ (Fig. 10.12). In the invaginated phallus the cistern surrounds the Saccus cutaneus phalli (Figs. 10.10, 11). At the base of the phallus it is directly continuous with the Cisterna lymphatica basis phalli (Fig. 10.11).

(45) **Flexura phalli non-erecti/Apex phalli erecti** (of Phallus protrudens). The flexure of the non-erect phallus occurs at the junction of the Saccus glandularis phalli with the Saccus cutaneus phalli (Figs. 10.10, 11), and is strongly curved when the phallus is invaginated (Fig. 10.14) (Komárek, 1969). In erection it becomes the Apex of the phallus (Fig. 10.13); here the Saccus glandularis phalli becomes continuous with the (now everted) Saccus cutaneus phalli, via the Ostium sacci glandularis phalli (Fig. 15b) (Komárek, 1969). The Apex penis of Guzsal (1974) is the deeply invaginated "root" of the phallus, and is not the Apex phalli here.

(46) **Sacci phalli; Saccus cutaneus phalli; Saccus glandularis phalli; Ostium sacci cutanei phalli; Ostium sacci glandularis phalli** (of Phallus protrudens). Synonomy: in the NAA (1979) the first four of these terms were respectively, Cavitas phalli, Pars cutanea phalli, Pars glandularis phalli, and Aditus ad cavitatem phalli. The body of the *resting* (detumescent) phallus of *Rhea, Casuarius, Dromaius* and anseriforms, resembles the invaginated finger of a glove (King, 1981: 118-125). Thus it consists of a tube, which ends blindly at the deep end and opens at the superficial end on the proctodeal floor (via the Ostium sacci cutanei phalli) (Figs. 10.10, 11). The two phallic sacs form the interior of this tube; the Saccus cutaneus phalli and Saccus glandularis phalli (the cutaneous and glandular sacs of the phallus) are of about equal length and in series with each other via the Ostium sacci glandularis phalli (Fig. 10.15a).

The glandular sac secretes mucus which presumably makes the phallus slippery when erect (Liebe, 1914), but the sac is devoid of erectile lymphatic tissue (Figs. 10.10, 11) (Komárek and Marvan, 1969; Guzsal, 1974). The cutaneous sac is lined by a non-secretory keratinized epithelium, and is backed by the erectile spaces of the Cisterna lymphatica corporis phalli (Figs. 10.10, 11, 12). Where the glandular sac continues into the cutaneous sac of the invaginated phallus (at the Flexura phalli) there is an abrupt increase in the diameter of the tube (Fig. 10.11) (Berens v. Rautenfeld, et al., 1974). The internal surface of the Saccus cutaneus of the invaginated phallus carries the Rugae phalli (Figs. 10.11, 15a) and a deep groove, the phallic sulcus; the groove runs to the Ostium sacci cutanei phalli on the proctodeal floor (Fig. 10.10), where it becomes continuous with the Sulcus ejaculatorius (Fig. 10.14).

When the phallus is erect the Saccus cutaneus phalli is everted, just as the invaginated finger of a glove can be everted. But the Saccus glandularis is prevented from everting by its anchorage to the Corpus fibrocartilagineum (Fig. 10.10). Therefore the detumescent phallus of *Rhea, Casuarius, Dromaius*, and *Anas* resembles the *totally* invaginated finger of a glove, but in the erect phallus only *half* of the finger has been evaginated. Although a Phallus protrudens also occurs in *Struthio*, apterygids, and tinamids, the Sacci phalli are absent; the phallus is intromittent but more primitive, resembling that of Chelonia and Crocodilia (King, 1981: 113).

In *Anser* Schalkház, et al. (1982) found that in the detumescent phallus the Ostium sacci glandularis phalli projected a short distance into the Saccus cutaneus phalli. They therefore suggested the term Praeputium phalli in place of Sacci phalli, but the lack of homology with the mammalian prepuce argues against this proposal. They also proposed "Ductus excretorius communis" for the tubular lumen of the Saccus glandularius, but this suggests that this tube has an excretory function.

(47) **Lamina epithelialis; Lamina propria** (of Phallus protrudens). The Saccus cutaneus phalli and Saccus glandularis phalli have an epithelial lining (Lamina epithelialis) supported by a connective tissue layer (Lamina propria) (Berens v. Rautenfeld, et al., 1974).

(48) **Ligamentum elasticum phalli** (of Phallus protrudens). A strong elastic ligament in all birds with the Phallus protrudens except *Apteryx* and tinamids (Gerhardt, 1933: 305-311), which runs axially throughout the length of the erect Phallus (Fig. 10.12). In *Anas* it is attached at one end to the Corpus fibrocartilagineum and at the other to Flexura phalli nonerecti (Figs. 10.10, 11). It helps to invaginate the detumescent phallus.

(49) **Suspensorium phalli** (of Phallus protrudens). In the non-erect phallus, this sleeve of elastic and collagenous connective tissue (Komárek, 1969) encloses the Saccus glandularis phalli (Fig. 10.15a); embedded in it is the Lig. elasticum phalli (Fig. 10.10). In the erect phallus it still encloses the whole length of the Saccus glandularis phalli (Fig. 10.15b); it is now itself largely enclosed by the Cisterna lymphatica corporis phalli (Figs. 10.12, 15b), with the Lig. elasticum phalli still embedded in it but fully extended (Fig. 10.12). During detumescence, the Lig. elasticum phalli and the elastic tissue of the Suspensorium phalli retract the Corpus phalli into its invaginated condition (Fig. 10.10). This is essentially the same as invaginating the finger of a glove by means of two elastic bands, both of which are inside the glove.

(50) **Fossa ejaculatoria; Sulcus ejaculatorius** (of Phallus protrudens). Synonomy: ejaculatory groove (Fujihara, et al. 1976). The ejaculatory fossa (in *Anas*) is a broad depression in the proctodeal floor, into which the openings of the papillae of the left and right deferent ducts are directed (Fig. 10.14). It leads to the narrow ejaculatory sulcus, a median groove in the proctodeal floor, which becomes continuous with the Sulcus phalli in both the resting (Fig. 10.14) and the erect phallus (Fig. 10.13). In the nonerect state the boundary between the Sulcus ejaculatorius and the Sulcus phalli occurs at the Ostium sacci cutanei phalli (Fig. 10.14).

(51) **M. retractor phalli caudalis; M. retractor phalli cranialis.** These muscles occur in males of *Struthio* (Müller, 1836: 146; Gadow and Selenka, 1891: 857), *Anas* (Liebe, 1914; Guzsal, 1974; Berens v. Rautenfeld, et al., 1974), and *Gallus* (Nishiyama, 1950, 1955). All these authors named them retractor phalli (or retractor penis), because both muscles attach to the *ventral* lip of the vent, close to or actually on the phallus, and they pull this attachment dorsocranially.

Two similar muscles have been described by other authors in *Gallus* (e.g., Knight, 1967: 61-62) and *Columba* (Baumel, 1988: 28) under the names M. levator cloacae and M. dilator cloacae. It has been assumed (Vanden Berge, 1979: 198; King, 1981: 98) that the M. levator cloacae is the same as M. retractor phalli caudalis (though with a trace of hesitation); (see **Cloaca** Annot. 31), and that M. dilator cloacae is the same as M. retractor phalli cranialis (less doubtful, since each is a

slender band of *non-striated* muscle (see **Cloaca** Annot. 32). Because the terms M. retractor phalli caudalis and cranialis have been used since the 19th century, and have been the subject of increasingly active research throughout this century, these names should be retained. However, they are only meaningful in the male bird. In the female, M. levator cloacae and dilator cloacae are more suitable. Moreover M. levator cloacae has been widely used (e.g., George and Berger, 1966: 283; Vanden Berge, 1979: 181; Baumel, 1988: 28). Consequently both sets of terms are retained as official alternates, giving priority to the phallic names under **Masc.** and the cloacal names under **Cloaca.**

The NAA (1979: 181, 332) listed only the M. retractor phalli, not specifying cranialis and caudalis. This omission has now been rectified. Müller (1836) also described in ratites a levator of the phallus (Heber der Ruthe), but its existence has not been confirmed; it is therefore omitted.

M. retractor phalli caudalis [M. levator cloacae]. Synonomy: M. retractor penis posterior (Nishiyama, 1950, 1955; Komárek, 1969; Guzsal, 1974); caudal retractor of the penis (King, 1975: 1932). The caudal retractor of the phallus is a slender paired muscle, stronger than the cranial retractor, arising from the dermis of the ventral aspect of the tail in *Anas* (Liebe, 1914). It inserts on the median phallic body in *Gallus* (Nishiyama, 1950, 1955), on the ventral aspect of the lateral phallic body in *Meleagris* (Knight, et al. 1984), and near the ventral surface of the Corpus fibrocartilagineum in *Anas* (Liebe, 1914; Komárek, 1969; Guzsal, 1974). In *Anas* it is a striated muscle (Komárek, 1969; Berens v. Rautenfeld, et al., 1974). For further details of attachments see **Cloaca** Annot. 31.

M. retractor phalli cranialis [M. dilator cloacae]. Synonymy: M. retractor penis anterior, Nishiyama (1950, 1955); cranial retractor of the penis (King, 1975: p1932). The cranial retractor of the phallus is a very slender paired band of smooth muscle (Berens v. Rautenfeld, et al., 1974; Nishida, et al., 1987; Ohsawa, et al., 1989). It inserts on the lateral aspect of the *ventral* lip of the vent close to the phallus in *Gallus* (Nishiyama, 1950, 1955), and on the Corpus fibrocartilagineum and Basis phalli in *Anas* (Liebe, 1914). In *Anas* it helps to invaginate the detumescent phalli (Liebe, 1914; Guzsal, 1974). For further details of attachments see **Cloaca** Annot. 32.

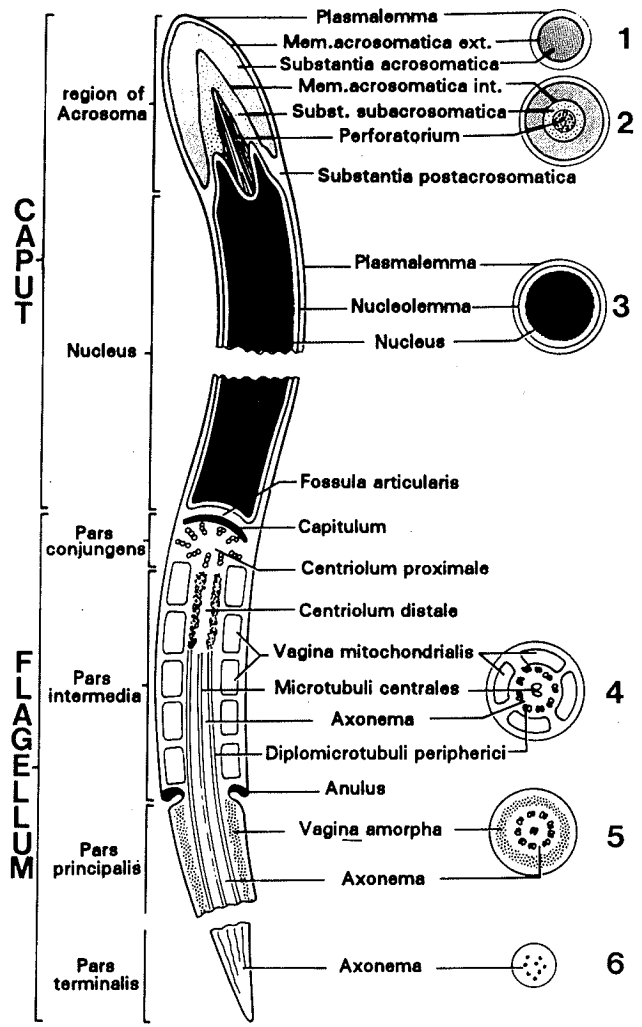

Fig. 10.7. Diagrams of a non-passerine spermatozoan in longitudinal section, with transverse sections at levels 1 to 6, to show the basic structural components.

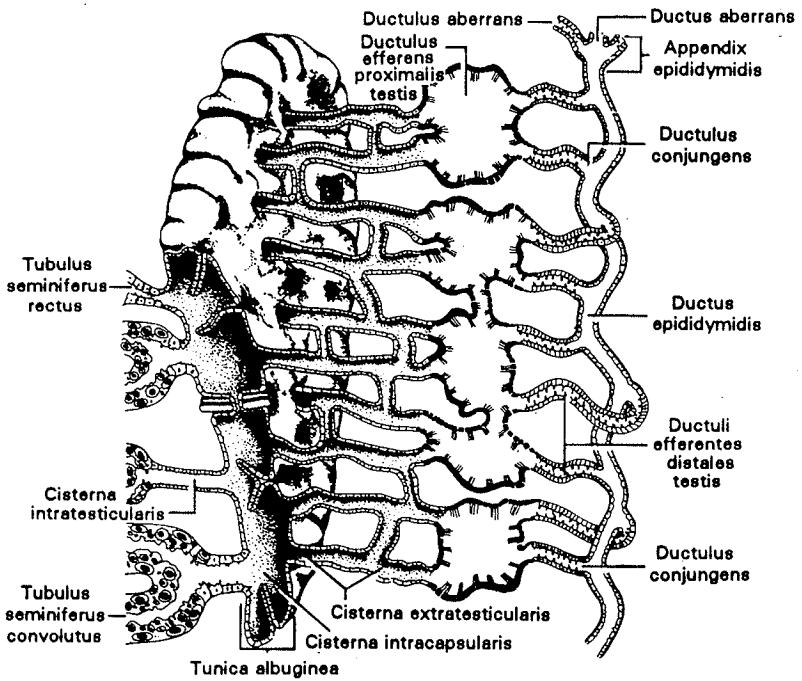

Fig. 10.8. Diagram of the Rete testis and its connections with the Epididimys and Testis in a sexually mature male *Gallus*. The main component of the Rete testis is the longitudinally orientated Cisterna intracapsularis, embedded in the Tunica albuginea. This connects with transversely orientated intra- and extratesticular cisterns. The junction of Tubuli seminiferi with the Rete testis is so abrupt that the Tubuli recti are almost indistinguishable from the intratesticular cisterns. From Budras and Schmidt (1976), with permission of the authors and Verlag Paul Parey, Berlin.

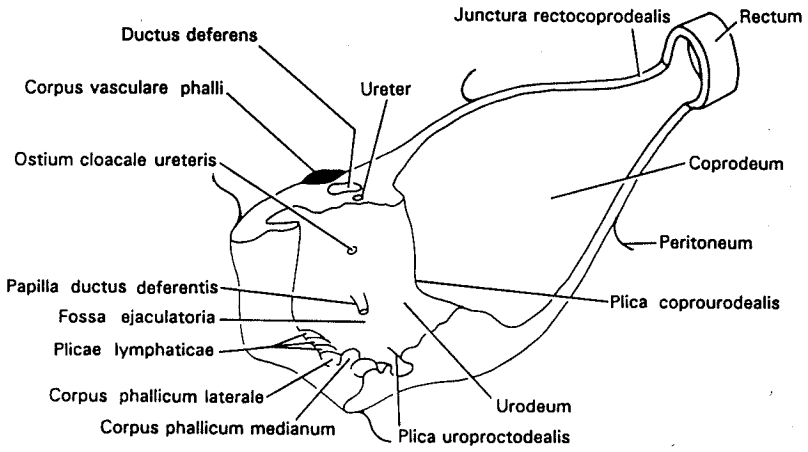

Fig. 10.9. Diagram of the interior of the left ventral quarter of the cloaca and vent of male *Gallus;* caudodorsal view; showing the cloacal compartments and the components of the non-erect Phallus nonprotrudens. From King (1975) with permission of W. B. Saunders, Philadelphia.

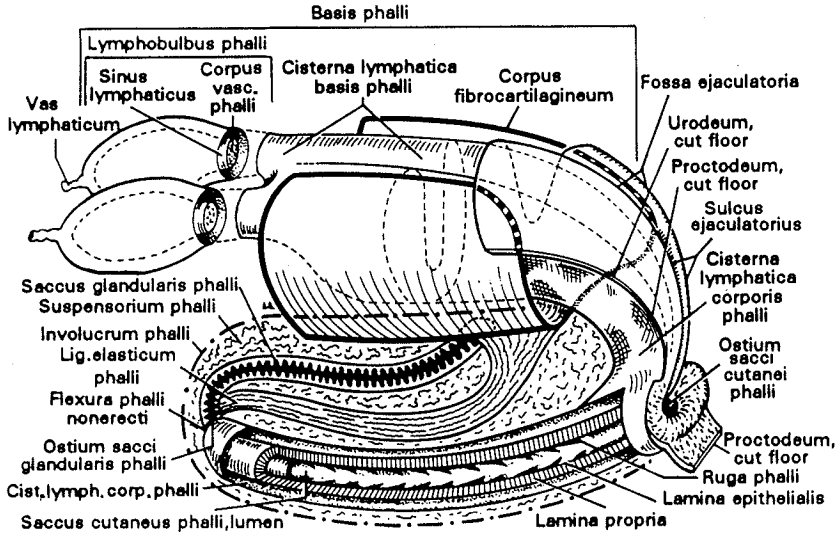

Fig. 10.10. Diagram of the left side of the non-erect Phallus protrudens of *Anas;* caudo-lateral view. The body of the phallus (Corpus phalli) is within its connective tissue envelope (Involucrum phalli) along with the Suspensorium phalli, consisting of elastic connective tissue, and the Lig. elasticum. The spiral form of the Corpus phalli is not shown (cf., Fig. 10.11). The left side of the two Sacci phalli has been opened, showing their lumen, Lamina epithelialis, and Lamina propria, and the lymphatic erectile space (Cisterna lymphatica corporis phalli) of the Saccus cutaneus phalli. In the erect Phallus the Flexura phalli non-erecti becomes the Apex phalli erecti (Fig. 10.12). The Basis phalli is supported by the trough-shaped Corpus fibrocartilagineum, which is embedded in the ventral wall of the urodeum and proctodeum. During erection, each Corpus vasculare phalli discharges lymph into the surrounding Sinus lymphaticus of the (paired) Lymphobulbus phalli. From there the lymph flows into the (unpaired) Cisterna lymphatica basis phalli, thence into the Cisterna lymphatica corporis phalli. The left Lymphobulbus phalli is larger than the right (not shown). In detumescence, the lymph drains from the Sinus lymphaticus of the Lymphobulbus phalli into Vasa lymphatica cloacalia (represented by Vas lymphaticum), and thence into the general lymphatic circulation. Based on Fig. 2A of Berens v. Rautenfeld, et al. (1974).

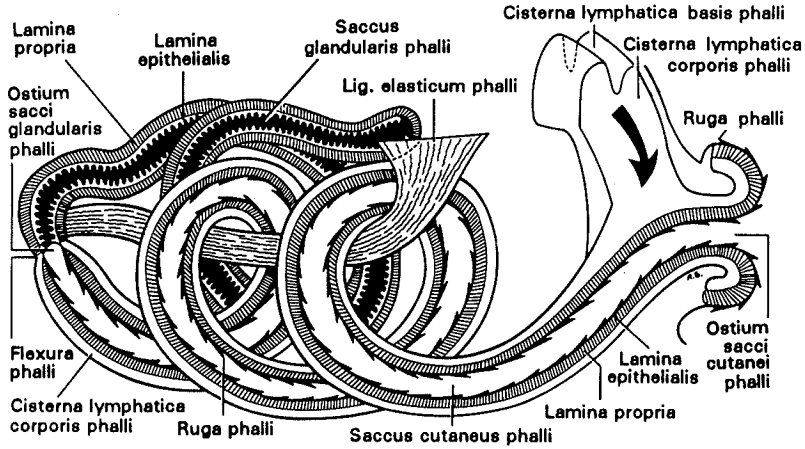

Fig. 10.11. Highly schematic left lateral view of the Corpus phalli of the non-erect Phallus protrudens of *Anas,* to show its spiral arrangement. The Saccus glandularis phalli and Saccus cutaneus phalli are shown as though cut in longitudinal section, thus revealing their internal lumen, Lamina epithelialis, and Lamina propria, and the lymphatic erectile space (Cisterna lymphatica corporis phalli) which encloses the Saccus cutaneus phalli. During erection, this space is filled with lymph flowing from the Cisterna lymphatica basis phalli (arrow). Erection has just started, since the Saccus cutaneus phalli has begun to evert through the Ostium sacci cutanei phalli, thus causing two or three Rugae phalli to appear outside the Ostium. Flexura phalli = Flexura phalli nonerecti. Based on Fig. 2B of Berens v. Rautenfeld, et al. (1974).

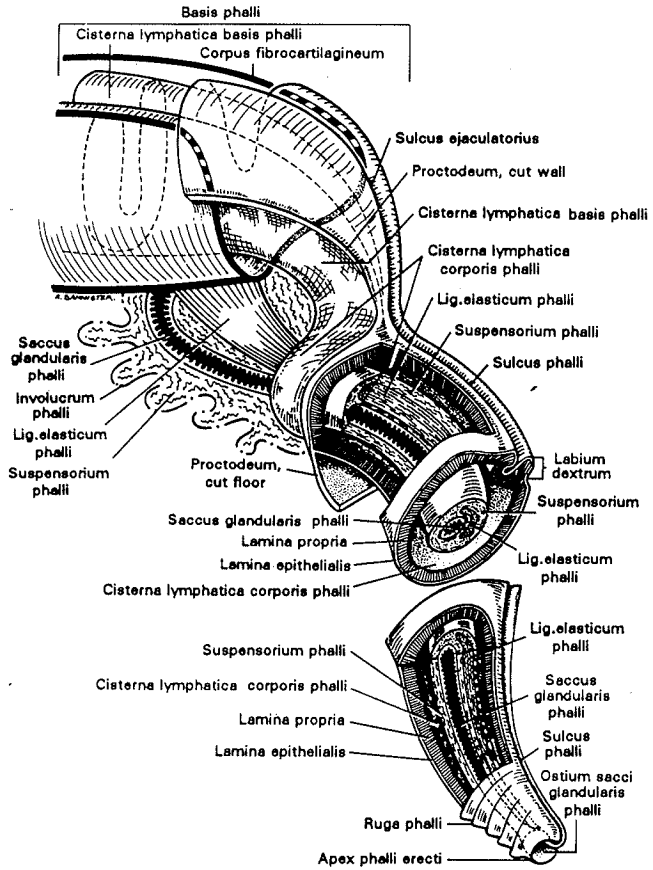

Fig. 10.12. Diagram of the erect Phallus protrudens of *Anas;* caudolateral view; left side. Flow of lymph from the Cisterna lymphatica basis phalli into the Cisterna lymphatica corporis phalli has everted the Corpus phalli from its Involucrum phalli. The Saccus cutaneus phalli is entirely externalized, so that its Rugae phalli cover the outer surface of the Corpus phalli. The left wall of the Corpus phalli has been partly removed. This shows the lumen of the Saccus glandularis phalli alongside the Ligamentum elasticum and the elastic connective tissue of the Suspensorium phalli, both of which are fully stretched from the Corpus fibrocartilagineum to the Apex phalli erecti. Fine trabeculae (not shown) span the lumen of the Cisterna lymphatica corporis phalli. The Labium sinistrum is relatively large, and overhangs the right Labium (not shown). Redrawn from Fig. 2C of Berens v. Rautenfeld, et al. (1974).

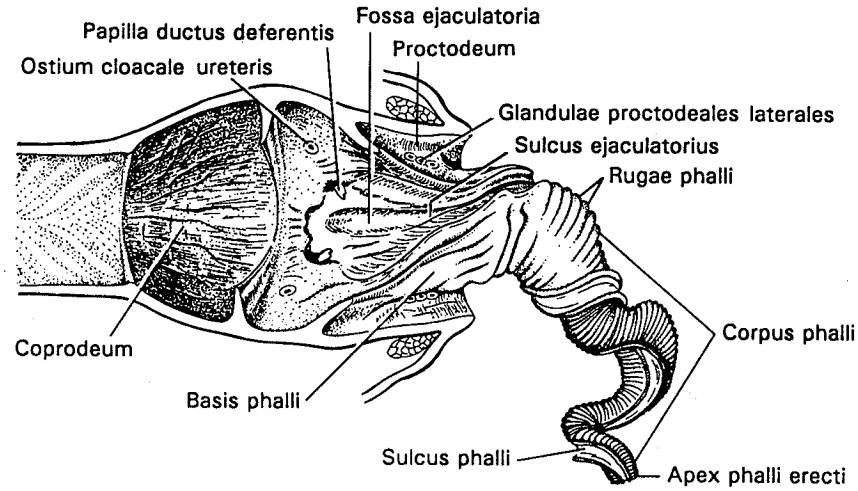

Fig. 10.13. Interior of the ventral half of the Cloaca of *Anas,* with erect Phallus; dorsal view. From Komárek (1969), with permission of the author and Anatomischer Anzeiger.

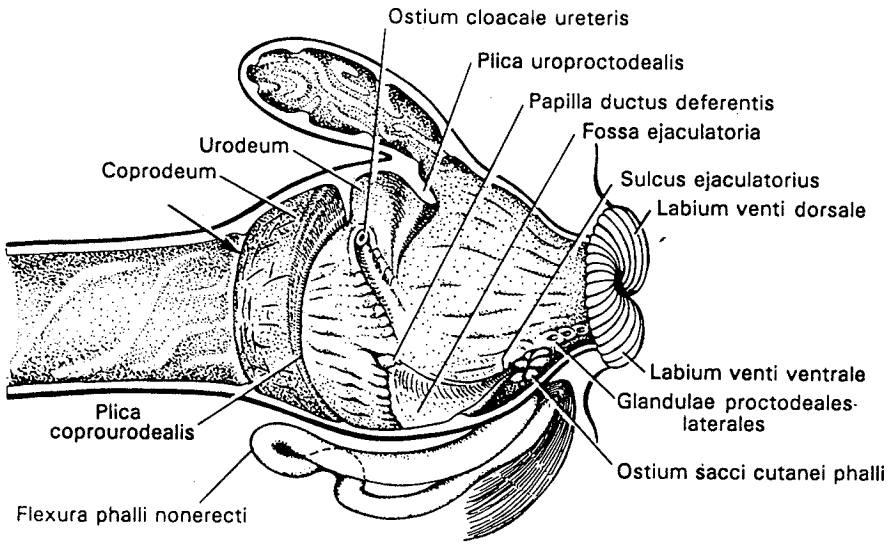

Fig. 10.14. Interior of the right half of the Cloaca of *Anser*, with non-erect phallus; left lateral view. This figure suggests the presence of a Plica rectocoprodealis (*arrow*) at the junction of the rectum and coprodeum, but a true rectocoprodeal fold is known to occur only in *Struthio*. However, in anseriforms generally there is an abrupt and conspicuous change in the mucosa at this point. From Komárek (1969), with permission of the author and Anatomischer Anzeiger.

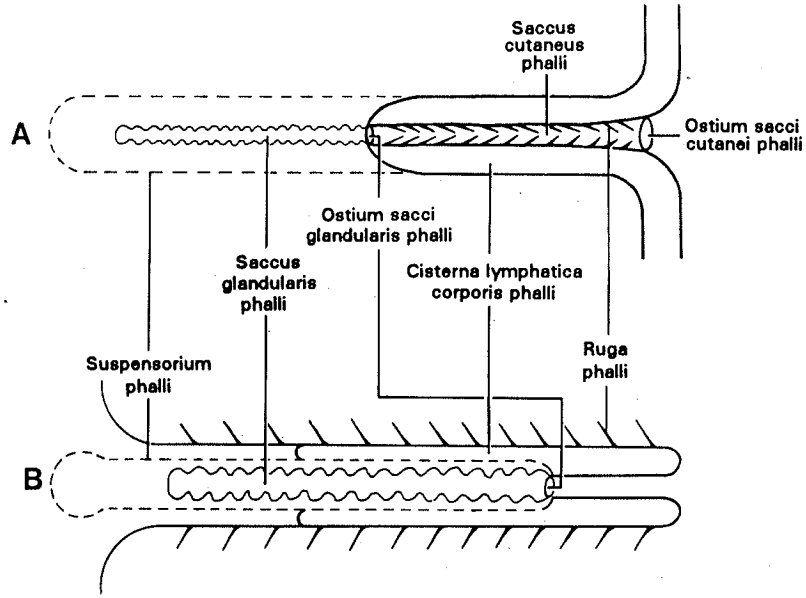

Fig. 10.15. Diagrams showing the relationships of the Saccus glandularis phalli and Saccus cutaneus phalli in (A) the resting, non-erect state, and (B) the erect state. In (A) both of the sacs are invaginated. In (B) the cutaneous sac is totally evaginated through the Ostium sacci cutanei phalli, thus externalizing the Rugae phalli. Therefore in the resting Phallus, the two Sacci resemble the totally invaginated finger of a glove; in the erect Phallus, half of the invaginated finger (the Saccus cutaneus phalli) has been evaginated, but the other half (the Saccus glandularis phalli) remains invaginated.

TERMINOLOGY

ORGANA GENITALIA FEMININA

OVARIUM SINISTRUM

Lobi ovarii[1]
Facies dorsalis[1]
  Hilus ovarii[2]
Facies ventralis[1]
Extremitas cranialis[1]
Extremitas caudalis[1]
Margo lateralis[1]
Margo medialis[1]
Mesovarium[3]
Epithelium superficiale[4]
  Mesotheliocytus cuboideus
Tunica albuginea[4]
Cortex ovarii[4]
Zonae parenchymatosae[4]
Medulla ovarii[4]
Zonae vasculosae[4]
Endocrinocytus interstitialis[5]

FOLLICULUS OVARICUS[6]

Pedunculus folliculi[7]
  Musculi pedunculares[7]
Plasmalemma ovocyti[8]
Zona radiata[8,9]
Lamina perivitellina[8,11]
Stratum granulosum[10]
  Cellulae strati granulosi[10]
Lamina basalis folliculi[12]
Thecae folliculi
  Theca interna[13]
  Theca externa[13]
    Cellulae thecales[13]
Tunica superficialis[14]
  Musculi intramurales[7]
Epithelium superficiale[4]
Stigma folliculare[14]
Folliculus postovulatorius[15]
Folliculus atreticus[16]
Corpus aureum[16]

Epoöphoron[17]
  Ductus epoöphorontis longitudinalis[17]
    Ductuli epoöphorontis transversi[17]
Paroöphoron[17]

Ovogonium
Ovocytus primarius
Ovocytus secundarius
Polocytus primarius
Polocytus secundarius
Ovum[18]
Vasa et Nervi Ovarii Sinistri
  Arteriae ovaricae[19]
    Aa. contortae[19]
      Aa. pedunculares[19]
        Aa. intramurales[19]
          Rete capillare terminale[19]
  Venae ovaricae[20]
    Vv. pedunculares[20]
      Vv. intramurales externae[20]
      Vv. intramurales mediae[20]
      Vv. intramurales internae[20]
  Truncus thoracoabdominalis
    Vasa l. ovarica[21]

(continued)

FOLLICULUS OVARICUS[6] (cont.)

Plexus aorticus (**PNS** Annot. 81)
  Plexus adrenalis
    Gg. adrenalia
      Plexus ovaricus[22]
      Nn. ovarici[22]
        Nn. folliculares[22]
          Nn. pedunculares[22]
          Nn. intramurales[22]

GONADUM DEXTRUM[23]
OVIDUCTUS SINISTER[24]

Tunica mucosa[25]
  Plicae primariae[25]
    Plicae secundariae[25]
  Epitheliocytus ciliatus[25]
  Exocrinocytus caliciformis[25]
  Lamina propria mucosae[25]
Tela submucosa[25]
Tunica muscularis
  Stratum circulare[25]
  Tela intermuscularis[25]
  Stratum longitudinale[25]
Tunica serosa[25]
  Mesothelium
  Lamina propria serosae

Infundibulum[26]
  Ostium infundibulare[26]
    Fimbriae infundibulares[26]
  Tubus infundibularis[26]
    Fossae glandulares infundibuli[26]
    Glandulae tubi infundibularis[26]
Magnum[27]
  Glandulae magni[27]
Isthmus[28]
  Pars translucens isthmi[28]
  Glandulae isthmi[28]
Uterus[29]
  Pars cranialis uteri[29]
  Pars major uteri[29]
  Recessus uterinus[29]
  Glandulae uterinae
  Lamellae uterinae[29]
Vagina[30]
  M. sphincter vaginae[30]
  Tubuli spermatici[31]
Ostium cloacale oviductus sinistri (**Cloaca** Annot. 7)
Lig. dorsale oviductus[32]
Lig. ventrale oviductus[32]
  Funiculus musculosus[32]

Vasa Sanguinea Oviductus
  Aa. oviductales[33]
    A. oviductalis cranialis[34]
      A. anastomotica[35]
      A. oviductalis marginalis ventralis[35]
      A. oviductalis marginalis dorsalis[35]
        Aa. infundibuli[34]
        Aa. magni[34]
    A. oviductalis cranialis accessoria[34]
      A. anastomotica[35]
      A. oviductalis marginalis ventralis[35]
      A. oviductalis marginalis dorsalis[35]

(continued)

OVIDUCTUS SINISTER (cont.)

- Aa. magni[35]
- Aa. isthmi[35]
- Aa. uteri[35,37,39]
  - A. uterina medialis[38]
  - A. uterina lateralis[38]
- A. oviductalis caudalis[39]
  - A. oviductalis marginalis ventralis[35]
  - A. oviductalis marginalis dorsalis[35]
    - Aa. uteri[37]
- A. vaginalis[40]
  - Aa. infundibuli[35]
  - Aa. magni[35]
- A. oviductalis media[36]
  - A. anastomotica[35]
  - A. oviductalis marginalis ventralis[35]
  - A. oviductalis marginalis dorsalis[35]
- Venae oviductales[41]
  - V. oviductalis cranialis
  - V. oviductalis marginalis ventralis
    - V. oviductalis marginalis dorsalis
      - Vv. infundibuli
      - Vv. magni
  - V. oviductalis media[41]
    - Vv. magni
    - Vv. isthmi
    - Vv. uteri
      - V. uterina lateralis
      - V. uterina medialis
  - V. oviductalis caudalis
    - Vv. uteri
    - V. vaginalis
- Nervi Oviductus[42]
  - Plexus aorticus (PNS 81)
  - Plexus adrenalis
    - Gg. adrenalia
      - Plexus renales
      - Plexus ovaricus
      - Plexus oviductales
  - N. pudendus
    - Rr. uterini
    - Rr. vaginales

OVIDUCTUS DEXTER[43]

OVUM TESTACEUM[44]

- Polus acutus[65]
- Polus obtusus[65]
- Discus germinalis[45]
- Membranae vitelli[46]
  - Plasmalemma ovocyti[47]
  - Lamina perivitellina[48]
  - Lamina continua[49]
  - Lamina extravitellina[50]
- Vitellus[51]
  - Vitellus albus[52]
    - Latebra[52]
      - Centrum latebrae[52]
      - Collum latebrae[52]
      - Discus latebrae[52]
    - Vitellus aureus[53]
- Albumen[54]
  - Stratum chalaziferum[55]
    - Chalaza[55]
  - Albumen rarum[56]
    - Stratum internum[56]
    - Stratum externum[56]
  - Albumen densum[57]
    - Albumen polare[57]

(continued)

OVUM TESTACEUM (cont.)

- Membranae testae[58]
  - Membrana testae externa[58]
  - Membrana testae interna[58]
  - Cella aeria[58]
- Testa[59]
  - Stratum mamillarium[60]
    - Mamilla[60]
      - Nucleus mamillae[60]
      - Galerum basale mamillae[60]
      - Conus mamillae[60]
  - Stratum spongiosum[61]
    - Stratum vallatum[61]
  - Stratum superficiale[62]
  - Cuticula[63]
  - Porus testae[64]
  - Canaliculus testae[64]

ANNOTATIONS

(1) **Lobi ovarii; Facies dorsalis; Facies ventralis; Extremitas cranialis; Extremitas caudalis; Margo lateralis; Margo medialis.** These terms can be applied to the immature ovary. Until the onset of laying, in *Gallus* the ventral surface is divided into ovarian lobes by 7 or 8 deep transverse fissures in the cortex (Procházková and Komárek, 1970; Oribe, 1983). These lobes may be recognisable in the sexually active ovary (Oribe, 1976), but the extremities, surfaces, and borders are not clear. However, in seasonal birds the ovary becomes small and compact during the eclipse period (Witschi, 1961), and these terms again become meaningful.

(2) **Hilus ovarii.** Synonymy: Ovarian stalk (Gilbert, 1969). The broad and ill-defined area of entry of the ovarian blood vessels and nerves into the Facies dorsalis.

(3) **Mesovarium.** The peritoneal fold attaching the Facies dorsalis of the immature ovary to the dorsal wall of the coelom (King, 1975: p1937). At maturity the Mesovarium is greatly reinforced by connective tissue, smooth muscle, and the blood vessels and nerves of the Hilus ovarii.

(4) **Epithelium superficiale; Tunica albuginea; Cortex ovarii; Zonae parenchymatosae; Medulla ovarii; Zonae vasculosae.** In the immature ovary a distinct ovarian cortex covers the whole of the separate ovarian medulla except at the Hilus (Benoit, 1950; Marshall, 1961; Gilbert, 1979: 273). Oögonia and Oöcyti are confined to the cortex. The medulla consists mainly of connective tissue with blood vessels, nerves, and smooth muscle (Gilbert, 1971a). During sexual activity the cortex and medulla are not distinct strata but are replaced by irregular areas: (1) Zonae parenchymatosae containing mainly oöcytes and developing follicles; (2) Zonae vasculosae containing primary sex cords, blood vessels, nerves, smooth muscle, and Endocrinocyti interstitiales (Procházková and Komárek, 1970; Gilbert, 1979: 273).

The "primary" Tunica albuginea is a thin layer of connective tissue, separating the outer covering of cuboidal Epithelium superficiale from the primary sex cords; it disappears during the second half of incubation (Romanoff, 1960: 833). The "defini-

tive" Tunica albuginea is a connective tissue layer that forms beneath the superficial epithelium, persisting in the mature ovary (Hodges, 1974: 330). The superficial epithelium covers all of the mature ovary, including each Folliculus ovaricus (Fig. 10.17) where it becomes flatter (Guzsal, 1966; Fujii, et al., 1980).

(5) **Endocrinocytus interstitialis.** Ovarian interstitial endocrine cells are large, round or polygonal, steroidogenic cells (Gilbert, 1979: 266). "Medullary" interstitial cells may arise from the primary (medullary) sex cords (Benoit, 1926; 1950: 391; Budras and Preuss, 1973). "Cortical" interstitial cells may come from the secondary (cortical) sex cords (Benoit, 1950: 391), or fibroblasts (Dahl, 1971; Budras and Preuss, 1973). "Thecal" interstitial cells occur within the Theca interna and externa of developing follicles (Marshall, 1961: 194; Hodges, 1974: 342), as "thecal glands" (Dahl, 1970; Gilbert, 1979: 286). Since these cells may be only different stages of the same cell (Narbaitz and De Robertis, 1968), it is inadvisable to name each individually.

(6) **Folliculus ovaricus.** The ovarian follicle supplies the oöcyte with yolk material from the liver, supports it as it grows, and releases it at ovulation.

(7) **Pedunculus folliculi; Musculi pedunculares; Musculi intramurales.** The growing follicle extrudes from the ovarian surface, forming the peduncle (pedicle, stalk) of the follicle. The peduncle carries small "parasitic" follicles. Peduncular arteries, veins, lymphatics, and nerves are drawn into the developing stalk (Nalbandov and James, 1949; Oribe, 1976; Gilbert, 1965). The peduncle also contains bundles of smooth muscle, the Musculi pedunculares (peduncular muscles), which enter the Tunica superficialis and Theca externa (Guzsal, 1966), thus forming the Musculi intramurales (intramural muscle bundles). Contrary to earlier views, Guzsal (1966) and Fujii, et al. (1980) found them only in the peduncular hemisphere of the follicle.

(8) **Plasmalemma ovocyti; Zona radiata; Lamina perivitellina.** The older and very confused terminology for these innermost layers of the wall of the follicle was evolved with the light microscope, but some layers are only distinguishable with the electron microscope (King, 1975: 1939). The terms listed here are based on ultrastructural observations (e.g., Perry, et al., 1978a, b, and for review, Gilbert, 1979: 279).

As recommended by Wyburn, et al. (1965), the classification of egg "membranes" of Boyd and Hamilton (1952) is adopted here: a primary egg membrane is formed by the cytoplasm of the Ovocytus, and a secondary by the cells of the Stratum granulosum (Annot. 11, 48); a tertiary egg membrane is added by the cells of the Oviductus (Annot. 49, 40). The Plasmalemma ovocyti (oöcyte plasmalemma) (Fig. 10.16) is a primary egg membrane.

(9) **Zona radiata.** Interdigitations (Fig. 10.16) between the Plasmolemma ovocyti and the Cellulae strati granulosi (Wyburn, et al., 1965; Wyburn and Baillie, 1966; Gilbert, 1971b; Rothwell and Solomon, 1977), in *Gallus* first appearing when the follicle is somewhat enlarged and disappearing at a diameter of about 15 mm (Gilbert, 1979: 281). Birds have no homologue of the mammalian corona radiata (Gilbert, 1979: 281).

(10) **Stratum granulosum** (synonym: Epithelium folliculare, Bellairs, 1965; Guzsal, 1966; Hodges, 1974; Nickel, et al., 1977); **Cellulae strati granulosi.** The mammalian term, follicular epithelium, is confusing in birds, since the avian follicle is also covered by the Epithelium superficiale (Gilbert, 1979: 285). The term Stratum granulosum was used by the NAA (1979) and by Rothwell and Solomon (1977), Perry, et al. (1978a), and Gilbert (1979). Apical processes of the Cellulae strati granulosi (granulosa cells) interdigitate with the oöcyte (Fig. 10.16); lateral processes

establish contacts between adjacent granulosa cells (Perry, et al. 1978a). The precise functions of the granulosa cells in the deposition of yolk is unknown, but they may transport (and perhaps modify) materials into the oöcyte (see Gilbert, 1979: 286, for review).

(11) **Lamina perivitellina.** Synonomy: vitelline membrane (Bellairs, 1965); vitelline layer (Bain and Hall, 1969); perivitelline membrane (King, 1975). The term Lamina perivitellina was used by the NAA (1979), and by Rothwell and Solomon (1977), Perry, et al. (1978a), and Gilbert (1979). The perivitelline lamina (or layer) is a narrow zone, between the Ovocytus and Stratum granulosum (Fig. 10.16), of ground substance and electron dense aggregates which finally form a meshwork of electron dense rods. It is almost certainly secreted by the Cellulae strati granulosi (Wyburn, et al. 1965), and is then a secondary membrane. It is analogous (Bakst and Howarth, 1977b) or even homologous (King, 1975: p1940) to the mammalian Zona pellucida. See also Annot. 48.

(12) **Lamina basalis folliculi.** A distinct boundary (Figs. 10.16, 17) between the Stratum granulosum and Theca interna (Wyburn, et al. 1965; Aitken, 1966). Atypical of a true basal lamina are its exceptional thickness, uncertainty whether it arises from the cells of the Stratum granulosum or from some other source, and its physical properties (NAA, 1979). For example, it allows the passage of complex lipoprotein particles, unlike typical basal laminae (Gilbert, 1979: 286).

(13) **Theca interna.** Forms about 25% of the Thecae folliculi (Fig. 10.17). It comprises a narrow inner layer of collagen fibres, a middle layer mainly of fibroblasts (Wyburn, et al., 1965; Aitken, 1966), and an outer layer of vacuolated cells (presumably Endocrinocyti interstitiales, Hodges, 1974: 336; Annot. 5). The structure varies with the size of the follicle (Hodges, 1974: 336). Perry, et al. (1978a) found many loosely packed fibroblast-like cells in a single discontinuous layer over the Lamina basalis folliculi; the spaces between the cells were filled by collagen fibres and a fine granular material that might be yolk going to the oocyte. It is very vascular (Annot. 19).

Theca externa. This layer (Fig. 10.17) consists of concentric alternating layers of collagen fibres and fibroblasts (Aitken, 1966) with a few elastic fibres (Guzsal, 1966; Hodges, 1974: 335). There are probably some smooth muscle fibres (Musculi intramurales) (for review see Hodges, 1974: 335, and Gilbert, 1979: 287). Endocrinocyti interstitiales are present (Annot. 5).

Cellulae thecales. Thecal cells include the fibroblast-like cells of the Theca interna and the fibroblasts of the Theca externa, but not the Endocrinocyti interstitiales of the two Thecae.

(14) **Tunica superficialis.** The whole follicle except the stigma (Guzsal, 1966; Fujii and Yoshimura, 1979; Fujii, et al., 1980) is enclosed by this superficial tunic of loose connective tissue, itself continuously covered by the Epithelium superficiale (Fig. 10.17). The Musculi intramurales lie mainly in this layer.

Stigma folliculare. The follicular stigma in *Gallus*, a relatively avascular white meridional line, is formed by fusion of the Epithelium superficiale with the Theca externa (Fujii and Yoshimura, 1979). Shortly before ovulation, the stigma thins by disintegration of the Stratum granulosum and Thecae folliculi, becomes transparent, and then splits (Yoshimura and Fujii, 1979; Fujii, et al., 1980). Pressure caused by the Mm. intramurales in the pedicular hemisphere of the follicle may help the splitting (Guzsal, 1966; Fujii, et al., 1980). In some species there is no stigma (Kern, 1963). For reviews see King (1975a: 1941) and Gilbert (1979: 289).

(15) **Folliculus postovulatorius.** The postovulatory follicle is the cup shaped remnant of a follicle after ovulation. Gilbert (1979: 292) has reviewed its structure and function. In *Gallus*, and most other species examined, regression is rapid (7-10 days). Cellulae granulosae and Endocrinocyti interstitiales persist during this period, and may be functional. In *Gallus* the postovulatory follicle affects the timing of oviposition of the egg derived from that follicle, and nesting behaviour. Such activity lasts for only 24 h, estrogen, progesterone, and prostaglandins being possibly involved.

(16) **Folliculus atreticus.** The elimination of follicles (atresia) has been reviewed by Gilbert (1979: 295). Atretic follicles occur in all investigated avian species, up to five types being described. "Bursting atresia", in which the Thecae folliculi rupture and release the yolk into the ovary or body cavity, is widespread in birds and lower vertebrates, yet is the least common form of atresia in birds. "Invasion atresia", mainly affecting smaller less yolky follicles, is the other well known variant; granulosa or thecal cells invade the follicle and the yolk is reabsorbed *in situ*.

Corpus aureum. The "yellow bodies", scattered throughout the ovary (Aitken, 1966), which may be late stages of regressing postovulatory follicles or remnants of atretic follicles.

(17) **Epoöphoron; Ductus epoöphorontis longitudinalis; Ductuli epoöphorontis transversi; Paroöphoron.** The Epoöphoron (synonym, Nebeneierstock) is the homologue of the Epididymis. The Ductus epoöphorontis longitudinalis (longitudinal epoöphoront duct) develops from the mesonephric duct and is the homologue of the Ductus deferens. The Ductuli epoöphorontis transversi (transverse epoöphoront ductules) develop from the tubules and intermediate segments of the mesonephros, and are firmly attached to the adrenal gland by connective tissue. Parts of the mesonephros and its vestiges form steroidogenic cells of the gonads and adrenal gland (Budras, 1972; Carlson, et al., 1983; Busse, 1985). The Paroöphoron is a rudiment of the nonsexual part of the mesonephros, between the ovary and kidney in the lateral part of the mesovarium (Hamilton, 1952: 497).

(18) **Ovum.** The Ovum is the female gamete, resulting from the second maturation division. The same term is traditionally used for the shelled egg, but see Annot. 44. For a review of oögenesis, progressing through Ovogonium, Ovocyti, Polocyti, and Ovum, see Gilbert (1979: 277).

(19) **Arteriae ovaricae.** In *Gallus* there are typically 2 to 4 ovarian arteries (Oribe, 1977). These arise: (a) quite often from the left cranial renal artery only (**Art.** Fig. 12.8) (Dang-quan-Dien, 1951); or (b) from both the cranial renal artery and the aorta (Fig. 10.18) (Mauger, 1941; Westphal, 1961), much the most common pattern (Oribe, 1977); or (c) directly from the aorta (Nalbandov and James, 1949), the rarest form (Oribe, 1977). In *Anas* and *Meleagris* they arise directly from the left renal artery (Hodges, 1965). The ovarian arteries form many Aa. contortae, strongly undulating or spiral in the immature but straightening in the mature ovary (Oribe, 1976). These give rise to the Aa. pedunculares, which form the Aa. intramurales (Fig. 10.17) in the Tunica superficialis of the ovarian follicle (Nalbandov and James, 1949; Nishida, et al., 1977; Oribe, 1980). Other smaller intramural arteries (Oribe, 1980) form the Rete capillare terminale (Fig. 10.17), adjacent to the Lamina basalis folliculi, thus contributing to the great vascularity of the Theca interna (Nishida, et al., 1977). See **Art.** Annot. 66.

(20) **Venae ovaricae.** In *Gallus* (Nalbandov and James, 1949) the cranial ovarian veins join the left adrenal vein and enter the caudal vena cava, and the caudal veins

drain into the caudal vena cava, or may first join the cranial oviductal vein (**Ven.** Fig. 12.16). The ovarian veins are formed by the Vv. pedunculares. These drain the external, middle, and internal Vv. intramurales (Fig. 10.17) (Fujii and Yoshimura, 1979; Oribe, 1981), the internal intramural veins being sinusoidal (Nishida, et al., 1977).

(21) **Vasa lymphatica ovarica.** In *Gallus* many lymphatics, with mural lymphoreticular formations, lie in the Zonae vasculosae along the main veins, but there are only a few in the Zonae parenchymatosae (Oribe, 1985). Drainage is directly into the Truncus thoracoabdominalis (see **Lym**).

(22) **Nervi ovarici.** The left ovary of adult *Gallus* is profusely innervated, particularly the mature follicles (Johnson, 1925; Mauger, 1941; Hsieh, 1951; Gilbert, 1965, 1969; Freedman, 1968; Bennett and Malmfors, 1970; Oribe and Fujii, 1978; for reviews, King, 1975: 1944; Gilbert, 1979: 273, 289). The sympathetic supply is derived from the Plexus ovaricus on the Hilus ovarii, and a parasympathetic contribution is suspected. From several large ganglia in the plexus, about 10 Nn. ovarici (ovarian nerves) supply the ovary. Nn. folliculares innervate a mature follicle, entering as Nn. pedunculares and continuing as Nn. intramurales in the Tunica superficialis, with branches into all layers external to the Lamina basalis folliculi. There are many ganglion cells in the follicular wall; functions of the intramural nerves are unknown, but most of them relate to blood vessels.

(23) **Gonadum dextrum.** In the genetic female of birds generally, the term Ovarium dextrum is not appropriate for the right gonad, which is usually arrested at a testis-like stage of development (Romanoff, 1960: 835). Only in *Apteryx* is a fully functional Ovarium dextrum regularly present (Kinsky, 1971). According to Brode (1928), in the normal mature female *Gallus* the right gonad is an ill-defined strip of tissue about 5 mm long and 1 mm wide, on the right ventral aspect of the caudal vena cava. If the adult left ovary is destroyed the right gonad develops into a testis or ovotestis (see King, 1975: 1945; Gilbert, 1979: 303).

(24) **Oviductus sinister.** The left oviduct is divided into infundibulum, magnum, isthmus, uterus, and vagina, these terms now being in almost universal use. Reviews by King (1975) and Gilbert (1979) of the extensive literature supply much of the following account. The structure of the left oviduct is singularly uniform throughout Aves (Marshall, 1961: 203), with only minor differences of largely unknown functional significance (Gilbert, 1979: 305). On functional grounds, Schwarz (1969) suggested abandoning the five classical subdivisions, substituting simply a cranial and a caudal region, the boundary at junction of magnum and isthmus.

(25) The wall of the oviduct consists of seven main layers, with minimal regional variations (Hodges, 1974: 348; King, 1975: p1946). (1) The Tunica mucosa, lined by more or less alternating Exocrinocyti caliciformes (goblet cells, possibly of several functional types) and Epitheliocyti ciliati (Aitken and Johnston, 1963; Fujii, et al., 1965; Guzsal, 1966; Draper, et al., 1968; Fujii, 1975). The mucosa has longitudinal spiral Plicae primariae carrying Plicae secundariae. The size of the Plicae varies with the regions of the oviduct (Surface, 1912; Blom, 1973). In sexually inactive hens the population of ciliated cells is greatly reduced (Fujii, 1981). (2) The Lamina propria mucosae, the loose connective tissue immediately underlying the epithelium and containing glands in most regions of the oviduct. (3) The Tela submucosa, a layer of well

vascularized and innervated connective tissue separating the mucosa from the muscular tunic. (4) The Stratum circulare of smooth muscle. (5) The connective tissue Tela intermuscularis between the two muscle layers, containing the larger blood vessels. (6) The Stratum longitudinale of smooth muscle. (7) The peritoneal Tunica serosa.

(26) **Infundibulum.** Synonym: Trichter. Comprises a funnel followed by a tubular region. The funnel opens by an elongated slit, the **Ostium infundibulare,** with thin flared lips, the **Fimbriae infundibulares** which are lined by ciliated cells only (Bakst and Howarth, 1975; Fujii, 1981). The **Tubus infundibularis** is the narrow tubular region (synonym: chalaziferous region, Richardson, 1935); its **Glandulae tubi infundibularis** secrete the Stratum chalaziferum and Chalazae of the shelled egg. **Fossae glandulares infundibuli** (glandular grooves) occur in the infundibular tube only (Surface, 1912; Aitken and Johnston, 1963); some spermatozoa may be stored here, constituting the "infundibular sperm host glands" (Drimmelen, 1946; Lorenz, 1964; Koyanagi and Nishiyama, 1981) (see Annot. 31). The role of the smooth muscle, vascularity, and innervation of the Infundibulum in capturing the ovulated secondary oöcyte were considered by Fujii, et al. (1981).

(27) **Magnum.** Synonym: Eiweissteil. The longest part of the oviduct. The **Glandulae magni,** crammed into the massive Plicae primariae, secrete the Stratum internum of the Albumen rarum. The region of the Magnum immediately preceding the Isthmus has a different glandular structure (Richardson, 1935; Aitken, 1971) and secretes the Albumen densum. The cells responsible for the many albumen proteins have not been identified with certainty (Gilbert, 1979: 321; Solomon, 1983: 389). See Annot. 54-57.

(28) **Isthmus.** A short region, with a slightly smaller calibre and weaker Plicae than the Magnum. The Pars translucens isthmi is a macroscopically distinct, constricted (1-3 mm wide), glandless zone at the beginning of the Isthmus. The **Glandulae isthmi** form the Membranae testae, and add some protein and water to the Albumen. Despite earlier controversy, it appears that the first deposits of calcium (but not calcium carbonate) occur in the Isthmus.

(29) **Uterus.** Synonymy: Schalendrüse, Eihälter, Kalkkammer, Camera calciferra, shell gland. The term "uterus" has been much criticised for implying an unjustifiable homology with the mammalian structure (e.g., Richardson, 1935; Marshall, 1961: 204; Gilbert, 1979: 305), "shell-gland" being preferred. However, "uterus" has been widely used in avian anatomy for over 150 years (e.g., Barkow, 1829: 444). Moreover "uterus" is extensively used throughout Amniota (e.g., Romer, 1962) and in Selachia (Marshall, 1962: 277), and even in Invertebrata as in Platyhelminthes (Llewellyn, 1972: 219) and the arthropod *Peripatus* (Ettershank, 1972: 406). Several criteria have influenced the choice of "uterus" in these animals. One has been the embryonic source of the oviduct; "uterus" is not applied to the teleost oviduct, which is not derived from the paramesonephric (Müllerian) duct, whereas the selachian oviduct is (Marshall, 1962: 349). Since all female tetrapods possess the paramesonephric duct (Goodrich, 1958: 696), the use of "uterus" in birds is no more offensive to homology than is its use in selachians. Another criterion is the fusion of two oviducts in the midline as in many mammals. The absence of this feature in reptiles apparently deterred Bellairs and Attridge (1975: 51) from using "uterus" in Reptilia. On the other hand the platyhelminths have only one oviduct, and *Peripatus* has two unfused oviducts, yet "uterus" is used. Marshall (1961: 204) realistically concluded that the term "uterus" in birds is "possibly irredeemably entrenched". Certainly any substitute term converting shell-gland into Latin (e.g., Camera calciferra) would

stand little chance of adoption. Moreover the single term "uterus" is convenient when applied to the vessels, nerves, etc. of the oviduct.

Pars cranialis uteri (synonym: red region) is the initial short, relatively tubular, portion (Johnston, et al., 1963) of the uterus. According to Solomon (1983: 396) "red region" is misleading, since it only applies during the phase of calcium transfer when the uterine vasculature is engorged. That this be regarded as part of the Isthmus (Davidson, et al., 1968; Draper, et al., 1972) was rejected by Aitken (1971) because its glands are characteristically uterine. The first deposit of calcium carbonate occurs here. **Pars major uteri** is the pouch-like portion of the Uterus that holds the egg during most of the period of shell formation (Johnston, et al., 1963). **Recessus uterinus** is the funnel-shaped, caudal region with a distinctive pink or greyish white colour and abundant cholesterin ester lipids in the ciliated cells (Fujii, 1963). The longitudinal primary folds of the uterus are intersected by transverse or oblique furrows, forming leaf-like **Lamellae uterinae** (Blom, 1973; Bakst, 1978a; King, 1979: 1948). Tunica muscularis extends into these transverse folds, helping to expel the egg (Schwarz, 1969).

(30) **Vagina.** A short muscular S-shaped tube connecting the uterus to the cloaca. M. sphincter vaginae is a thickening of Tunica muscularis of the first segment of the Vagina, though Aitken (1971) questioned the existence of a true sphincter.

(31) **Tubuli spermatici.** Synonymy: Fossulae spermaticae (NAA, 1979); sperm nests (Drimmelen, 1946); utero-vaginal glands (Bobr, et al. 1964); sperm-host glands (Pal, 1977); utero-vaginal sperm host glands (Friess, et al., 1978); sperm glands (Koyanagi and Nishiyama, 1981); sperm-storage tubules (Bakst, 1987); sperm-storage glands (Shugart, 1988). The term proposed by the NAA (1979) has not been adopted in the subsequent literature, possibly because the meaning of Fossula (L. little ditch) is not obvious or apposite. "Tubuli spermatici" is more informative; "tubuli" is preferred to "glandulae", since these may not be true glands (Hatch, 1983; Bakst, 1987). These structures are branched, or in some taxa unbranched, tubules definitely vaginal, being confined to the region of M. sphincter vaginae (Fujii, 1963; Shugart, 1988), and lined by tall columnar epithelial cells. They are the main storage site for spermatozoa in the oviduct (Bobr, et al., 1964) (see Annot. 26). They have been found in galli-, anseri-, and columbiform species by various authors, and more recently in charadriform, passerine, and probably falconiform species (Hatch, 1983; Bakst and Bird, 1987; Shugart, 1988). Evidence of secretory activity has been found in *Gallus* and *Anas* (Pal, 1977; Friess, et al., 1978; Gilbert, 1979: 331). How spermatozoa enter and survive in the tubules, and when and how they are released is still unknown. Deterioration in the fecundity of turkey hens could not be related to any microscopic changes in the tubules (Schuppin, et al., 1984).

(32) **Lig. dorsale oviductus; Lig. ventrale oviductus; Funiculus musculosus.** The dorsal oviductal ligament suspends the oviduct and continues ventrally as the fan-like ventral oviductal ligament, the free edge of which is reinforced by smooth muscle; caudally the latter increases to a muscular cord, the Funiculus musculosus, attaching to the Uterus and Vagina (Curtis, 1910; Kar, 1947).

(33) **Aa. oviductales.** The blood vessels of the left oviduct (Fig. 10.18 and **Art.** Fig. 12.8) have been studied in *Gallus, Meleagris,* and *Anas,* by Freedman and Sturkie (1963) and Hodges (1965), in *Anser* by Gertner (1969), and in *Columba* by Baumel (pers. comm.). See King (1975: p1950, 1958) and Baumel (1975: p1973) for details of these vessels in domestic species. It is not known how far these patterns apply to birds generally. See also **Art.** Annot. 67.

(34) **A. oviductalis cranialis; A. oviductalis cranialis accessoria.** The cranial oviductal artery arises from the left A. renalis cranialis; the accessory cranial oviductal artery arises from the left A. iliaca externa. In *Gallus* (Fig. 10.18) the cranial oviductal is typically present, and sometimes also the accessory (Hodges, 1965). *Meleagris* and *Anas* usually possess only the accessory (Hodges, 1965). In *Anser* both the cranial and the accessory are usually present (Gertner, 1969, respectively his R. infundibularis of the A. renovarica, and the A. oviductalis cranialis). In general, these two oviductal arteries supply the infundibulum and the cranial end of the magnum. In *Columba* (Baumel, pers. comm.) sometimes neither of them is present, and then the A. oviductalis media takes over the cranial part of the oviduct.

(35) **A. anastomotica; A. oviductalis marginalis ventralis/dorsalis; Aa. infundibuli; Aa. magni; Aa. uteri.** The anastomotic artery joins the A. oviductalis cranialis to the A. oviductalis cranialis accessoria and A. media in *Gallus* (Fig. 10.18), but is absent in *Meleagris* and *Anas*. In *Gallus* it contributes to the dorsal and ventral marginal oviductal arteries (**Art.** Annot. 72), which form Aa. infundibuli, magni, and uteri.

(36) **A. oviductalis media.** Synonymy: hypogastric artery (Freedman and Sturkie, 1963; Hodges, 1965). The middle oviductal artery arises from the left A. ischiadica or from the left A. renalis media, and supplies the caudal end of the magnum, the isthmus, and the uterus (Fig. 10.18). In *Columba* it is occasionally the only oviductal artery, and then supplies also the cranial end of the magnum and the infundibulum (Annot. 34).

(37) **Aa. uteri.** The uterine arteries arise from the middle and caudal oviductal arteries, via Aa. oviductales marginales dorsalis/ventralis. The vessels are better developed on the lateral (left) side of the uterus than the medial (right).

(38) **A. uterina medialis; A. uterina lateralis.** The medial and lateral uterine arteries arise from the middle and caudal oviductal arteries and supply the two sides of the uterus (Fig. 10.18). (They were respectively named the right lateral uterine artery and left lateral uterine artery by King, 1975a: 1950, and the medial lateral uterine artery and lateral lateral uterine artery by Hodges, 1965.) Although they are relatively large and constant, their origins, courses, and branches vary even within the same species. The many other medium-sized uterine arteries are so variable that they are not named here, but owing to their physiological importance attempts have been made to name them as follows. The A. uterina cranialis (left and right) of King (1975: 1950) is the anterior uterine artery (lateral and medial) of Freedman and Sturkie (1963) and Hodges (1965). The A. uterina ventralis of King (1975) is the inferior uterine artery of Freedman and Sturkie (1963) and Hodges (1965); this artery prolongs the A. oviductalis marginalis ventralis. The A. uterina dorsalis of King (1975) is the superior uterine artery of Freedman and Sturkie (1963) and Hodges (1965). The right and left caudal uterine aa. of King (1975a: 1950) are the middle uterine aa. of Freedman and Sturkie (1963) and the medial and lateral posterior uterine aa. of Hodges (1965).

(39) **A. oviductalis caudalis.** Synonymy: the intestinal branch of the internal pudendal (Westpfahl, 1961); the pelvic branch of the internal iliac (Freedman and Sturkie, 1963; Hodges, 1965). The caudal oviductal a. is a branch of the left pudendal a. (Figs. 10.18); see also **Art.** Annot. 67 and Fig. 12.8. It supplies variable Aa. uteri to both sides of the caudal part of the uterus, and may also supply the vagina (Baumel, 1975c: 1993).

(40) **A. vaginalis.** In *Gallus* the vaginal artery may arise as a separate branch of the left A. pudenda (Fig. 10.18), or be incorporated into the A. oviductalis caudalis as vaginal rami (Baumel, 1975c: 1993). When present as a separate artery it supplies both sides of the vagina; its branches are the vaginal arteries of Hodges (1965), and apparently also the posterior uterine aa. of Freedman and Sturkie (1963).

(41) **Vv. oviductales; V. oviductalis media.** With a few exceptions (King, 1975a: 1950), the oviductal veins (**Ven.** Fig. 12.16) are satellites of the arteries. See **Ven.** Annot. 61. The middle oviductal vein drains the region supplied by the A. oviductalis media, but the two vessels do not typically run in parallel and the vein is much more elaborate than the artery. In *Gallus* it generally drains into the left caudal renal vein (Baumel, 1975c: 2008).

(42) **Nervi oviductus.** The nerves of the oviduct have not been thoroughly investigated, except those of the uterus by Freedman and Sturkie (1963). The following data are based on reviews by Hodges (1974: 350), King (1975a: 1951), and Baumel (1975c: 2052). The sympathetic supply is from the left Plexus subvertebralis synsacralis, via its aortic plexus and thence the subsidiary renal, ovarian, and oviductal plexuses, using the oviductal arteries as roadways. The oviductal plexus associated with the middle oviductal artery (the hypogastric plexus of Freedman and Sturkie, 1963) especially supplies the magnum, isthmus, amd uterus. The term "adrenal" ganglia is misleading, since they are mainly concerned with reproductive structures (Baumel, 1975c: 2059). The parasympathetic supply is from the pudendal nerve, using particularly the caudal oviductal and vaginal arteries to reach the uterus.

(43) **Oviductus dexter.** The presence of a right oviduct as well as a left has been reported in various orders, particularly Falconiformes. It is usually only vestigial, even in *Apteryx* where the Gonadum dextrum is a functional ovary (Kinsky, 1971). In *Gallus* rudiments of the right oviduct can generally be found at the Cloaca (Webster, 1948; Winter, 1958; Williamson, 1965), usually resembling the Magnum histologically (Winter, 1958). Occasionally a full-sized right oviduct occurs in *Gallus*. None of the earlier accounts proved such oviducts fully functional (Sell, 1959), but Bickford (1965) and Gilbert (1975: 337) reported fully functional right and left oviducts in *Gallus*. The histological structure of the Oviductus dexter is not constant enough to warrant a list of components.

(44) **Ovum testaceum.** The term Ovum has long been applied to both the cell which arises solely from the ovary via the second reduction division (see Annot. 18) and the shelled egg which is derived from both the ovary and the oviduct (to the Romans, who usually began their meals with eggs, "ovum" meant the shelled egg). This double definition was used in the NAA (1979), and subsequently critized. The shelled egg is now Ovum testaceum. Although bird's eggs vary greatly in size, shape, and colour their basic structure is remarkably similar.

(45) **Discus germinalis.** In the laid egg, the germinal disc (Fig. 10.19) is a greyish area about 3 mm in diameter, just beneath the Cytolemma ovocyti; it contains the oöcyte nucleus (also called the germinal vesicle), and cytoplasm forming a thin layer covering the entire surface of the yolk. It may be called the blastoderm if fertilized, and blastodisc if unfertilized (Gilbert, 1971b).

(46) **Membranae vitelli.** King (1975a: 1953) proposed this term, yolk membranes, for the four layers that together separate the yolk from the albumen. This convenient concept was adopted by Hodges (1974: 393) and Gilbert (1979: 247). However, it must be distinguished from an older, similar term, "vitelline membrane". The new term, yolk membranes (Membran*ae* vitelli), is in the plural: the old term, "vitelline membrane" (singular), was in general use by light microscopists (e.g., Romanoff and Romanoff, 1949: 135), who could not resolve the structural components. Electron microscopists continued to use the same term, but applied it to several different components. Consequently the term "vitelline membrane" had many different meanings and caused unacceptable confusion; it has rightly fallen into disuse, and should not be revived.

(47) **Plasmalemma ovocyti.** The plasmalemma of the oöcyte becomes discontinuous just before ovulation (Bellairs, 1965), except at the Discus germinalis (Bakst and Howarth, 1977a).

(48) **Lamina perivitellina.** Synonymy: inner layer of vitelline membrane (Bellairs, et al., 1963). Shortly before ovulation the electron dense rods of the perivitelline lamina (Annot. 11; Fig. 10.16) change rapidly into a meshwork of collagen-like fibres with intervening pores (Bellairs, et al., 1963; Fujii, 1976; Bakst and Howarth, 1977a; Bakst, 1978b; Perry, et al., 1978b).

(49) **Lamina continua.** The continuous layer first appears in oviductal eggs, and is therefore a tertiary egg membrane (Annot. 8). It is a narrow granular layer about 50 to 100 nm thick (Bellairs, et al., 1963).

(50) **Lamina extravitellina.** Synonymy: outer layer of vitelline membrane (Bellairs, et al., 1963); outer perivitelline layer (Bakst and Howarth, 1977b). The extravitelline layer, 3-8 µm thick, consists of many layers of fine fibrils, again, a tertiary egg membrane.

(51) **Vitellus.** The yolk. There are two types: Vitellus albus containing about twice as much protein as fat, and Vitellus aureus containing about twice as much fat as protein (Boyd and Hamilton, 1952).

(52) **Vitellus albus.** The mass of white yolk (**Latebra**) (Fig. 10.19) consists of a central ball, the **Centrum latebrae** (Latebra, L. a hidden recess), which connects by a neck, the **Collum latebrae,** to the disc of the latebra, **Discus latebrae** (synonym: Nucleus of Pander). Romanoff and Romanoff (1949: 207) regarded the Latebra as the migration path of the nucleus from the centre of the oöcyte to the periphery during the final stage of rapid accumulation of yolk.

(53) **Vitellus aureus.** The yellow yolk (Fig. 10.19), consisting essentially of yolk spheres tightly packed within an aqueous continuous phase (Gilbert, 1979: 250). Sometimes about six concentric wide dark strata alternate with narrow pale strata. This is an artifact depending on the diet, the pale strata being deficient in carotinoid pigment. True stratification of the Vitellus aureus has been found in several species (Grau, 1976), but little is known about its structural basis. (For review, see Gilbert, 1979: 250.) The structure and arrangement of the yolk spheres was studied by Perry and Gilbert (1985).

(54) **Albumen.** Unlike the yolk, the albumen has little intrinsic structure, but is nevertheless divided into three main components with different amounts of water and ovomucin (Gilbert, 1979: 251).

(55) **Stratum chalaziferum; Chalaza.** The chalaziferous layer is the thin innermost layer of dense albumen (Fig. 10.19). Rotation of the egg as it descends the oviduct twists some of the strands of fibrous ovomucin of the Stratum chalaziferum, forming two Chalazae at the sharp end and one at the blunt end of the egg (Fig. 10.19). (From chalaza, Gk. a hail stone or tubercle, an obscure etymology.) Chalazae are absent in reptilian eggs (Bellairs and Attridge, 1975: 52).

(56) **Albumen rarum.** Commonly called the liquid albumen, but renamed the thin albumen (hence rarum, L. thin) by Gilbert (1971b). It consists of a structureless fluid, apparently free of fibres but containing mucin, in an inner and outer layer (Stratum internum, Stratum externum) (Fig. 10.19).

(57) **Albumen densum; albumen polare.** Synonym: thick white (Gilbert, 1971b). The dense albumen contains relatively more ovomucin than the thin albumen. At each end of the egg the Albumen densum is strongly connected to the Membrana testae interna by the Albumen polare (Fig. 10.19), polar albumen (synonym: ligament of the dense albumen).

(58) **Membranae testae.** Reviews by Simons (1971), Hodges (1974: 297), and Gilbert (1979: 251) provide the following account. The **Membrana testae interna** (internal shell membrane) lies on the surface of the Albumen (Fig. 10.19). It is penetrated by mucin fibres of the Albumen (Fig. 10.20), especially of the Albumen polare. It may be composed of three layers of fibres, alternating at right angles. The more complex **Membrana testae externa** may have six alternating layers of fibres in *Gallus* (Fig. 10.20). In galliforms there may be a very thin third layer adjacent to the Albumen. As the egg cools after laying, the internal membrane separates from the external at the Polus obtusus, forming the **Cella aeria** (Fig. 10.20), under which the head of the embryo lies. It is absent in reptiles (Bellairs and Attridge, 1975: 52).

(59) **Testa.** Since the first description of the structure of the Testa (egg shell) by Purkinje in 1830 (Simons, 1971: 10) two sets of terms have been developed from its two basic parts: (1) the organic matrix, and (2) the interstitial inorganic mass deposited throughout the organic matrix. The architecture of the organic part is mirrored by that of the inorganic part. The nomenclature can be based on the organic part (e.g., Gilbert, 1979: 253), the inorganic part (Simons, 1971: 13), or partly on the organic and partly on the inorganic part (Hodges, 1974: 402). The nomenclature adopted here is based on the organic part (Stratum mamillarium and Stratum spongiosum), since this is the primary biological element. The reviews of the literature, with original observations, by Romanoff and Romanoff (1949: 159), Simons (1971), Hodges (1974: 402), and Gilbert (1979: 253) supply the following account.

(60) **Stratum mamillarium.** The mamillary layer is formed by cone-shaped **Mamillae,** each mamilla consisting of a meshwork of very fine fibres (Fig. 10.20). The apices of the mamillae are embedded in the Membrana testae externa; their bases fuse together (except at the Canaliculi testae). Each Mamilla contains a small protein mass, the Nucleus mamillae (Romanoff and Romanoff, 1963: 164; synonym, mamillary core, Gilbert, 1979; Hodges, 1974), which receives fibres from the Membrana testae externa (Fig. 10.20). A cap-like deposit of calcite crystals, the **Galerum basale mamillae** (mamillary basal cap), infiltrates the apex of each Mamilla (Fig. 10.20). The **Conus mamillae** (mamillary cone) is an infiltration of similar crystals into the remainder of the Mamilla (Fig. 10.20).

(61) **Stratum spongiosum.** The spongy layer forms about two thirds of the shell. It consists of fibres running parallel with the surface (Fig. 10.20). Its inorganic component, the **Stratum vallatum** or palisade layer (synonym: column layer), is formed by calcite crystals arising at the Nucleus mamillarum and lying perpendicular to the surface.

(62) **Stratum superficiale.** Synonym: surface crystal layer. Descriptions emphasise the calcite crystals of this thin (3-8 μm) superficial layer, but a rich organic matrix has been reported (Simons, 1971: 19).

(63) **Cuticula** (Fig. 10.20). The cuticle is organic. It is sometimes called the true cuticle, to distinguish it from a powdery calcified deposit (the "cover") on the outer surface of the cuticle in some species. In other species the cover lies deep to the cuticle. Such profound species variations indicate that the outermost layer of the shell may not be homologous throughout birds, so that additional terms may become necessary (Gilbert, 1979: 257). "Shell accessory materials" has been suggested (Board, 1982).

(64) **Porus testae; Canaliculus testae.** In most taxa (exception: casuariiforms) small funnel-shaped pores open on the shell surface, covered only by the Cuticula (Fig. 10.20). The pores are plugged with material resembling that of the Cuticula, but cracks in this material allow diffusion of respiratory gases and water vapor; in some species the pores are not plugged (Board, 1982). Each pore continues into a **Canaliculus testae** which leads between adjacent Mamillae testae to the outer surface of the Memb. testae ext. (Fig. 10.20).

(65) **Polus acutus; Polus obtusus.** Respectively, the "sharp" and "blunt" ends of eggs of pyriform shape. In some taxa the egg is spherical (e.g., certain strigiforms), and in others (e.g., Pteroclididae and Podicipedidae) the two ends have a similar curvature (Pitman, 1964: 238-240).

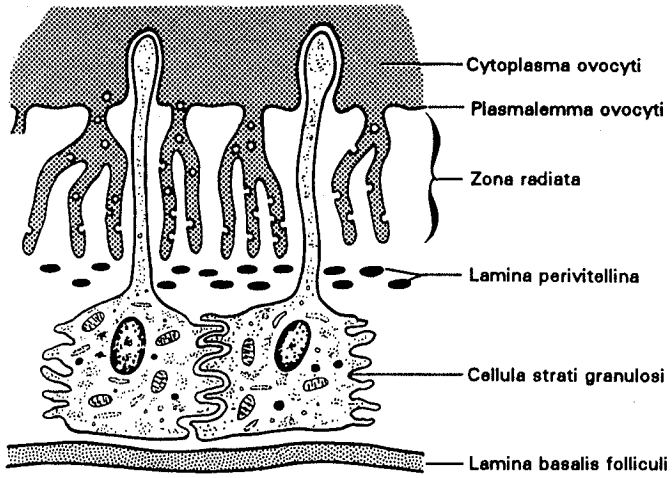

Fig. 10.16. Diagrammatic section through the innermost layer of the wall of the follicle of *Gallus*, at the square inset in Fig. 10.17. Redrawn from King (1975), with permission of W. B. Saunders, Philadelphia.

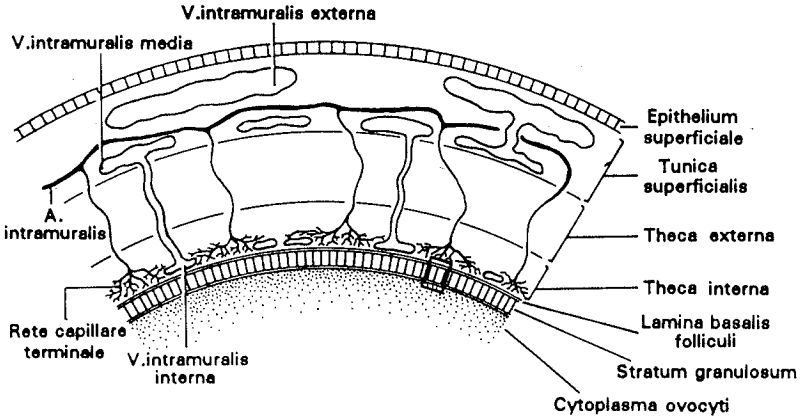

Fig. 10.17. Diagrammatic section through the wall of a follicle of *Gallus*, showing its layers and blood supply, based on Nalbandov and James (1949). Redrawn from King (1975), with permission of W. B. Saunders, Philadelphia.

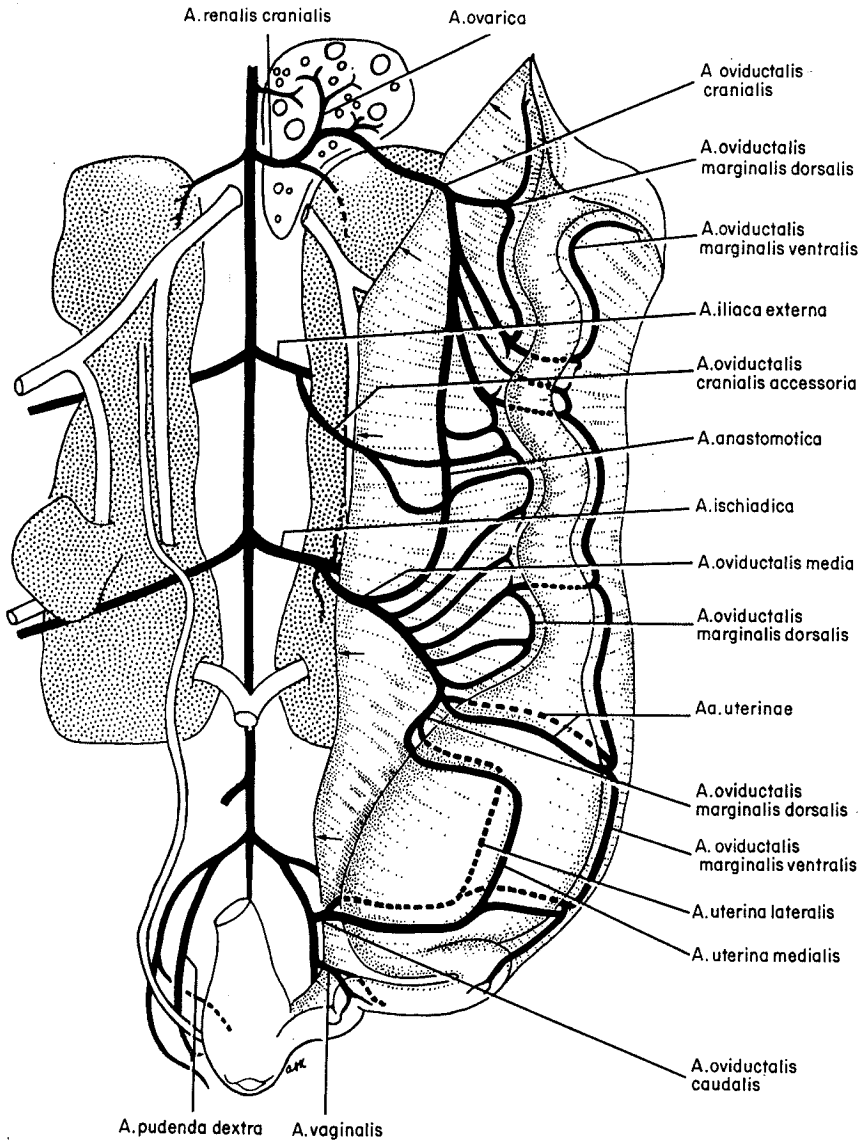

Fig. 10.18. Ventral view diagram of the arteries to the ovary and the main arteries to the oviduct of *Gallus*. Two to four Aa. ovaricae arise from the A. renalis cranialis and/or aorta (Annot. 19). The A. oviductalis cranialis accessoria is not always present in this species (Annot. 34). Redrawn from King (1975), with permission of W. B. Saunders, Philadelphia.

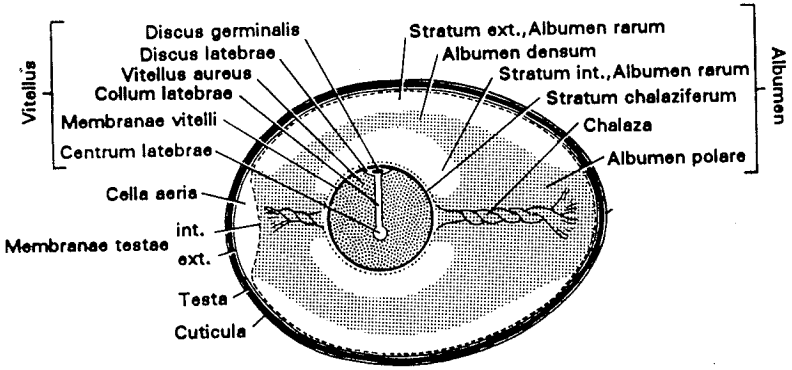

Fig. 10.19. Diagrammatic longitudinal section of an egg. From King and McLelland (1975), with permission of Bailliere Tindall, London.

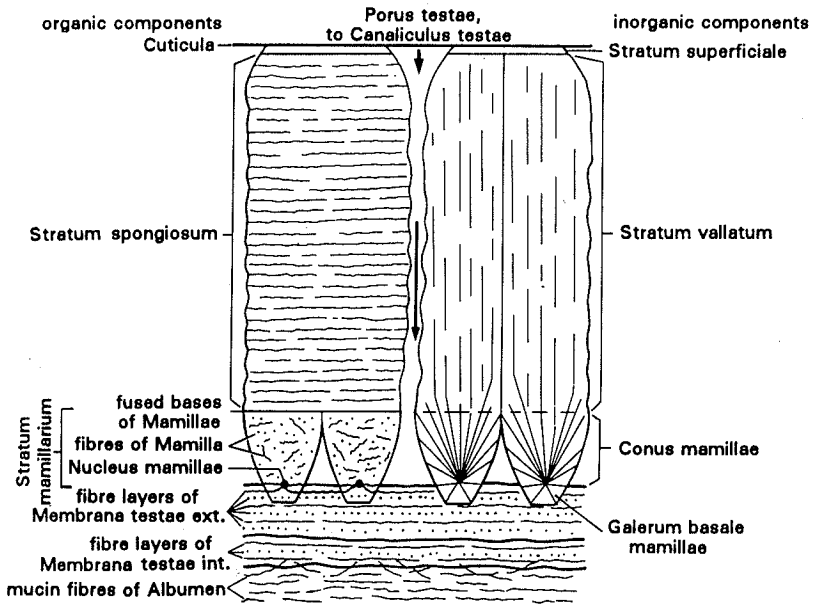

Fig. 10.20. Diagrammatic section through the egg shell (Testa) and shell membranes (Membranae testae) of *Gallus*. The left half shows the organic components of the shell, i.e., Stratum spongiosum and Stratum mamillarium, and the right shows the inorganic components. Mucin fibres of the Albumen penetrate the Membrana testae interna. The lines and dots in the Membrana testae interna and externa represent, respectively, three and six possible layers of fibres, alternating at right angles to each other. Fibres of the Membrana testae externa penetrate the apex of each Mamilla and become associated with the protein of the Nucleus mamillae.

The lines and dots in the Mamillae and Stratum spongiosum represent fibres; the lines in the right half of the diagram represent the long axes of calcite crystals. Crystals infiltrating the apex of each Mamilla form the cap-like Galerum basale mamillae; those infiltrating the rest of each Mamilla form the Conus mamillae. Crystals infiltrating the Stratum spongiosum form the Stratum vallatum (palisade layer). The thin Stratum superficiale has organic and inorganic constituents. The Porus testae (short arrow) is covered only by the organic Cuticula and leads into the Canaliculus testae (long arrow). Based on Hodges (1974, Fig. 165) and Gilbert (1979, Fig. 5.6a).

TERMINOLOGY

CLOACA

COPRODEUM[1]

Plica rectocoprodealis[2]
Junctura rectocoprodealis[3]

URODEUM[1]

Plica coprourodealis[4]
Ostium cloacale ureteris[5]
Papilla ductus deferentis[6]
  Ostium ductus deferentis[6]
Corpus vasculare phalli (**Masc.** Annot. 33, 38)
Ostium cloacale oviductus sinistri[7]
Ostium cloacale oviductus dextri[8]
Fossa oviductalis[8]
Plica uroproctodealis[9]
Corpus para-ampullare[10]

PROCTODEUM[1]

Bursa cloacalis[11]
  Collum bursae cloacalis[12]
  Ostium bursae cloacalis[13]
Glandula proctodealis dorsalis[14]
Glandulae proctodeales laterales[15]
Plicae lymphaticae (**Masc.** Annot. 32)
Plicae proctodeales[16]
Sinus proctodeales[16]
Phallus masculinus (**Masc.** Annot. 28)
  Phallus nonprotrudens (**Masc.** Annot. 29)
  Phallus protrudens (**Masc.** Annot. 35)
    Ostium sacci cutanei phalli (**Masc.** Annot. 50)
Phallus femininus[17]
Fossa ejaculatoria (**Masc.** Annot. 50)
Sulcus ejaculatorius (**Masc.** Annot. 50)

VENTUS[18]

Eminentia venti[18]
Labia venti
  Commissurae venti[19]
  Labium venti dorsale[19]
  Labium venti ventrale[19]
    Pars rugosa[20]
    Pars plana[20]
    Glandulae externae labii venti (**Integ.** Annot. 14)
    Glandulae internae labii venti[21]
Orificium venti
Promontorium cloacale (**Masc.** Annot. 27)
Vasa Cloacae
  A. pudenda
    Aa. cloacales[22]
      Rr. corporis vascularis phalli
    A. bursocloacalis[22]
      Rr. bursales
      Rr. cloacales[22]

(continued)

VENTUS[18] (cont.)

A. mesenterica caudalis[22]
  R. caudalis[22]
    Rr. cloacales[22]
    Rr. bursocloacales[22]
V. pudenda
  V. bursocloacalis
    Vv. bursales
    Vv. cloacales[23]
V. mesenterica caudalis
  V. bursalis
  Vv. cloacales[23]
Vas l. iliacum internum
  Vasa l. cloacalia[24]
Vas l. sacrale medianum
  Vasa l. bursae cloacalis[24]
Nervi Cloacae[25]
  Plexus pudendus
    N. lateralis caudae
      Rr. venti[25] (**PNS** Fig. 15.6)
      Rr. musculares[25] (**PNS** Fig. 15.6)
  N. pudendus (PNS)
    Gg. cloacalia[25]
      Plexus cloacalis[25]
        Nn. cloacales[25]
          Rr. cloacales
          Rr. bursae cloacalis
          Rr. vaginales
          Rr. corporis vascularis phalli

MUSCULI CLOACALES[26]

M. sphincter cloacae[27]
M. transversus cloacae[28]
M. contractor cloacae[29]
M. depressor anguli venti[30]
M. levator cloacae [M. retractor phalli caudalis][31]
M. dilator cloacae [M. retractor phalli cranialis][32]
Tunica mucosa[33]
  Plica cloacalis[33]
  Villi cloacalis[33]
  Epithelium[33]
    Epitheliocytus columnaris
    Exocrinocytus caliciformis[33]
    Glandula [Crypta] intestinalis[33]
  Lamina propria mucosae
  Lamina muscularis mucosae[34]
Tela submucosa
Tunica muscularis[34]
  Stratum circulare
  Stratum longitudinale
Tunica fibrosa[35]
Tela subserosa
Tunica serosa[35]
  Lamina propria serosae
  Mesothelium

ANNOTATIONS

(1) **Coprodeum; Urodeum; Proctodeum.** Gadow (1887) described the Cloaca (L. sewer or drain) of reptiles and birds as divided by folds of mucous membrane into these three compartments, but conceded that, especially in birds, ". . . the determination of the various chambers is beset with difficulties because of the extreme variability of the separating folds." In fact neither the folds nor the compartments are always distinct (Gerhardt, 1933: 277-280; King, 1981: 63-70). Nevertheless, Gadow's compartments and terminology are the foundation of cloacal morphology.

(2) **Plica rectoproctodealis.** Gadow (1887) proposed that the interior of the Coprodeum is separated from the Rectum by a macroscopically distinct annular rectocoprodeal fold containing a circular sphincter muscle. Such a fold has often been illustrated and described in *Gallus*, but it is not present (Jolly, 1915; Lillie, 1952: 388; Komárek, 1970; King, 1975a: 1960). Among the ratites the fold is well developed in *Struthio*, doubtful in *Casuarius* and *Rhea*, and absent in *Dromaius* (King, 1981: 71); in carinates it is very rare, having been reliably reported in *Falco tinnunculus* only (King, 1981: 75). In anseriforms including *Anas* (Komárek, 1969) a distinct fold has often been indicated (Fig. 10.14), but there is only a slight ridge where the epithelium changes to stratified squamous (King, 1981: 72).

(3) **Junctura rectocoprodealis.** In birds generally the rectocoprodeal junction is marked macroscopically solely by the beginning of the bell-shaped enlargement (Fig. 10.9) of the Coprodeum (King, 1981: 75). In anseriforms the junction is also macroscopically obvious at the abrupt change from the reddish rectal to the white (stratified squamous) cloacal mucosa. There is histological and radiographic evidence of a muscular sphincter at the junction in *Gallus* (King, 1981: 73). In *Anas* a sphincter occurs in the rectal wall 1-2 mm cranial to the mucosal change (**Diges.** Annot. 89).

(4) **Plica coprourodealis.** The coprourodeal fold is a prominent annular ridge between Coprodeum and Urodeum in most birds, but absent in some (King, 1981: 79). When well developed as in *Gallus* and *Anas* (Figs. 10.9, 14) it enables feces to be delivered directly through the vent, and prevents defecation during egg laying and ejaculation (Komárek, 1970; King, 1981: 79).

(5) **Ostium cloacale ureteris.** The claim that the Ureter opens on a papilla (Pilz, 1937) has been confirmed for only a few species e.g., *Struthio*, some sphenisciforms, *Columba livia*, and anseriforms (Figs. 10.13, 14) (King, 1981: 81). It is certainly incorrect for *Gallus* (Fig. 10.9) (King, 1975: p1962).

(6) **Papilla ductus deferentis; Ostium ductus deferentis.** In the adult male of all investigated birds the ductus deferens ends caudally on the ventrolateral wall of the urodeum at the conical papilla of the ductus deferens (Figs. 10.9, 13, 14), opening via its Ostium. In the juvenile female a very small homologous papilla has been found on both sides in spheniscids (Sladen, 1978) and anseriforms (Komárek, 1971), consistent with the claim (Witschi, 1961: 124; Fig. 21) that the ductus deferens persists in adult female birds and enlarges during the nuptial phase.

(7) **Ostium cloacale oviductus sinistri.** The opening of the left oviduct into the urodeum. In immature anseriforms and *Gallus* the ostium is closed by a membrane which breaks down at the onset of sexual maturity (see Gilbert, 1979: 307, and King, 1981: 85).

(8) **Ostium cloacale oviductus dextri; Fossa oviductalis.** In adult female birds the right oviduct occasionally has a true cloacal opening, the ostium of the right oviduct, but in the domestic anseriforms and galliforms there is usually only a pit-like depression, the oviductal fossa (Komárek, 1971). See King, 1975: 1952, and 1981: 85.

(9) **Plica uroproctodealis.** In all of the many avian species so far examined the urodeum is separated from the proctodeum by a distinct semicircular fold, which is best developed dorsally and fades out ventrally (Figs. 10.9, 14) (King, 1981: 86).

(10) **Corpus para-ampullare.** A globular, fluid-containing, structure about 2 mm diameter embedded near the Papilla ductus deferentis in about 2 per cent of male *Gallus*, usually on one side only. Considered to be a remnant of the Ductus paramesonephricus (Marvan, 1969).

(11) **Bursa cloacalis.** Synonymy: Bursa Fabricii. A pouch-like median dorsal diverticulum of the proctodeum. Involutes by the time of sexual maturity and except in ratites (Annot. 13) disappears entirely. Shape and internal structure vary (King, 1981: 87). See **Lym.** Annot. 12.

(12) **Collum bursae cloacalis.** The stalk of the Bursa cloacalis, running cranially along the dorsal wall of the urodeum to which it is attached. In *Struthio, Dromaius*, and *Rhea* the bursa is so far incorporated into the proctodeal wall that it lacks the stalk (Berens v. Rautenfeld and Budras, 1982).

(13) **Ostium bursae cloacalis.** The opening of the Bursa cloacalis through the dorsal wall of the Proctodeum. In nearly all birds studied this is a transverse slit close to the Plica uroproctodealis. In *Struthio* and *Dromaius* the lumen of the proctodeum and Bursa together form a single large cavity (Berens v. Rautenfeld and Budras, 1982) which in the early literature was mistaken for a true urinary bladder (King, 1981: 89). In the male *Struthio* the huge Phallus masculinus occupies this cavity, which persists after the lymphoid tissue in the bursal wall has involuted (Berens v. Rautenfeld and Budras, 1982).

(14) **Glandula proctodealis dorsalis.** Synonymy: bourrelet lympho-glandulaire (Jolly, 1915); foam gland, cloacal gland, paracloacal gland (see Klemm, et al., 1973); triangular fold (Fujihara, et al., 1985a). In *Coturnix coturnix* (Coil and Wetherbee, 1959; Klemm, et al., 1973) the dorsal proctodeal gland forms a prominent mound-like projection from the dorsal midline of the male and female Proctodeum. It comprises an encapsulated aggregation of glandular units, partly embedded in the M. sphincter cloacae. A similar glandular aggregation, though heavily infiltrated with lymphoid tissue, occurs in *Gallus* (Jolly, 1915; Komárek, 1970) and in males of *Meleagris* where it probably secretes a mucosubstance (Bakst and Cecil, 1985), and is presumably homologous to the gland in *Coturnix*. In *Coturnix* the secretion, which is a mucosubstance, is evidently squeezed from the gland by contraction of the M. sphincter cloacae. In the male it is released from the vent during coitus as a white froth (Tamura and Fujii, 1967; McFarland, et al., 1968). The froth also mixes with feces, and is therefore not restricted to sexual activity (Klemm, et al., 1973). Very small quantities of froth are also ejected from the Glandula proctodealis dorsalis by males of *Gallus* and *Meleagris* during ejaculation (Fujihara and Nishiyama, 1984; Fujihara, et al., 1985b; Bakst and Cecil, 1985). The effects of the froth on the fertilizing capacity and storage of sperm were surveyed by Fujihara, et al. (1987). Berens v. Rautenfeld (pers. comm.) doubts whether the glandular structure in *Coturnix* is homologous with the lymphoid structures in other species, and interprets the latter as a "dorsal proctodeal tonsil".

(15) **Glandulae proctodeales laterales.** Synonymy: tonsillae proctodeales (Berens v. Rautenfeld and Budras, 1982). The lateral proctodeal glands lie in the ventrolateral wall of the cloaca in both sexes of many birds (Forbes, 1877; Gadow, 1887; Komárek, 1970, 1971). In ratites, anseriforms (Figs. 10.13, 14), and the turkey the three to six

openings on each side are large and pore-like. In *Gallus* the openings are inconspicuous and much more numerous (see King 1981: 90, for review). The histology of these glands has not been reported, but Berens v. Rautenfeld and Budras (1982) claim that the term Tonsillae proctodeales would be more correct thus suggesting histological evidence for non-glandular tubes with lymphoid infiltration.

(16) **Plicae proctodeales; Sinus proctodeales.** The Plicae proctodeales are craniocaudal folds of the mucosa of the proctodeum in *Gallus* and *Meleagris*, but not *Anas* and *Anser*, the proctodeal sinuses being depressions between the folds (Komárek, 1970, 1971).

(17) **Phallus femininus.** A prominent structure on the proctodeal floor of female ratites, but weakly developed in anseriforms (King, 1981); also visible in females of taxa with Phallus nonprotrudens including *Gallus* and *Meleagris* (Komárek, 1971), especially in immature birds. In *Gallus* all the main components (Corpus vasculare phalli, Corpus phallicum medianum/laterale, and Plicae lymphaticae) are recognisable in the female (Preuss and Berens v. Rautenfeld, 1974).

(18) **Ventus.** The vent is the external opening of the cloaca (Gadow, 1896: 90; Berger, 1961: 300; Marshall, 1962: 585; King, 1975: 1963). The term anus has often been used in birds, but strictly should be confined to the external opening of the alimentary tract when separate from the urogenital openings (Berger, 1961: 300; Romer, 1962: 4), as in *Amphioxus*, Teleostei, and the higher mammals. Seen from the outside, the closed vent is not circular like the mammalian anus but a horizontal slit. For review see King (1981: 92).

Eminentia venti. The protrusion on which the vent is mounted in both sexes (**Topog.** Annot. 35).

(19) **Labium venti dorsale/ventrale; Commissurae venti.** The vent is closed by a dorsal and ventral lip (Fig. 10.14). At the left and right commissures of the vent the junction of the dorsal and ventral lips is deeply invaginated. The dorsal lip is smaller, but overhangs the ventral lip externally (Bakst, 1986).

(20) **Pars rugosa.** Synonymy: Pars externa (Komárek, 1970). The region of each Labium that is externally visible when the vent is closed. A cutaneous zone devoid of feathers but marked by numerous radial furrows (hence "rugosa", corrugated) (King, 1981: 92). The furrows enable the vent to dilate during defecation and copulation (Komárek, 1970).

Pars plana. Synonymy: Pars interna (Komárek, 1970). The mucous zone of each labium, only slightly furrowed (hence "plana", flat). The caudal (external) surface of the Labium ventrale has a Pars rugosa ventrally, which transforms dorsally into the Pars plana (overlaid by the Labium dorsale); the Pars plana continues over the rim of the lip to line the cranial (internal) surface. The caudal (external) surface of the Labium dorsale consists almost entirely of Pars rugosa; the Pars plana forms only a narrow ventral zone, which continues over the rim to line the cranial (internal) surface. The Pars plana is a stratified squamous cutaneous epithelium. When the proctodeum is lined mainly by a columnar epithelium (as in *Gallus*), the transition from stratified squamous into columnar epithelium occurs at the base of the inner surface of each Labium (Calhoun, 1954: 70). In other taxa the stratified squamous epithelium typically extends over the whole of the proctodeum (Annot. 33).

(21) **Glandulae internae labii venti.** The internal, mucus secreting, glands of the labia of the vent opening on the internal surfaces of the Labia, in most of 72 species but not anatids and phasianids (Quay, 1967). See **Topog.** Annot. 14.

(22) **Aa. cloacales.** In *Gallus* (Pintea, et al., 1967; Knight, 1970; Baumel, 1975c: p1997) and *Meleagris* (Knight, et al., 1984) the main arterial supply to the cloaca is from the A. pudenda. In *Columba* some Rr. cloacales and Rr. bursocloacales also arise from the R. caudalis of the A. mesenterica caudalis (**Art.** Annot. 80), but the main supply is from the visceral branch of the A. pudenda by the A. bursocloacalis (Baumel, 1988: 62).

(23) **Vv. cloacales.** The venous drainage of the cloaca of *Gallus* is mainly into the V. pudenda, but a few venules also drain into the V. mesenterica caudalis (Pintea, et al., 1967). *Columba* has both of these pathways (Baumel, 1988: 66), but the flow through the V. mesenterica caudalis is larger (**Ven.** Annot. 63).

(24) **Vasa l. cloacalia; Vasa l. bursae cloacalis.** The cloacal lymphatic vessels (**Lym.** Fig. 13.7), including those draining the entire phallic complex, empty into the Vas l. iliacum internum (Budras and Berens v. Rautenfeld, 1984). See **Masc.** Annot. 34, 40). The lymphatic vessels of the Bursa cloacalis drain into the Vas l. sacrale medianum (**Lym.** Fig. 13.7).

(25) **Nn. cloacae.** The gross anatomy of the cloacal nerves was established in *Gallus* by Hsieh (1951: 108), Pintea, et al., (1967), Knight (1970), Watanabe (1972), and Baumel (1975c: 2052, 2059), and in *Columba* by Baumel (1988: 49), and was reviewed by King (1981: 96). The basic source of cloacal nerves is the pudendal plexus.

The somatic pathways to the cloaca from the N. lateralis caudae include Rr. venti to the vent and Rr. musculares to the cloacal muscles. Degeneration studies suggested that some of these axons to the cloacal muscles may actually come from the N. tibialis via the Connexus caudalis (**PNS** Annot. 41). The N. pudendus may also provide some somatic cloacal fibres, presumably afferent, via many delicate rami to the cloacal wall (Knight, 1970: 68).

In *Gallus* the visceral cloacal fibres of the craniosacral system travel in the N. pudendus to the one large and several small Gg. cloacalia (synonymy: pelvic ganglion, Freedman and Sturkie, 1963; bursocloacal ganglion, Pintea, et al., 1967) that are formed on the pudendal nerve, on the dorsolateral aspect of the cloaca. These ganglia, with their connections to those of the opposite side and to the rectal ganglia, comprise the Plexus cloacalis. The cloacal plexus gives rise to small cloacal nerves (Nn. cloacales) supplying branches to all parts of the cloaca. The cloacal ganglia connect via the rectal ganglia with the N. intestinalis, which in turn connects with the Divisio thoracolumbaris of the visceral nervous system; therefore there are many routes for visceral fibres from both the thoracolumbar and the craniosacral system to reach the cloaca (Bennett, 1974: 37). In *Meleagris*, peripheral to the main G. cloacale, the N. pudendus also forms a G. paracloacale, which lies on and innervates the Corporis vasculare phalli (Knight, et al., 1984).

(26) **Mm. cloacales.** Earlier studies of these six, essentially extrinsic, cloacal muscles (**Myol.** Annot. 68) have been enhanced by Baumel's (1988: 25) observations on *Columba*, and his terminology is used here. The first four muscles (Annots. 27-30) are no longer difficult, but the last two are complicated by having two different sets of names. See King (1981:98, 125, 131) for a review of the earlier literature.

(27) **M. sphincter cloacae.** Synonymy: M. sphincter ani (Gadow and Selenka, 1891: 848). The cloacal sphincter is a striated muscle encircling the vent and proctodeum, much thicker dorsally than ventrally (Knight, 1967: 59; Baumel, 1988: 25).

(28) **M. transversus cloacae.** Synonymy: M. transversus perinei (Shufeldt, 1890: 312; Harvey, et al., 1968); M. transversoanalis (Beddard, 1898: 108; Gadow and Selenka, 1891: 129; George and Berger, 1966: 284); M. retractor ani (Ghetie, et al., 1976). This striated muscle arises from the caudal margin of the pelvis and inserts into the ventrolateral aspect of the cloacal sphincter (Knight, 1967: 60; Baumel, 1988: 26). In some taxa (e.g., Apodiformes) it may have two origins and bellies (Vanden Berge, 1979: 198). It has a ventilatory function, compressing the thoracoabdominal cavity at expiration (Baumel, 1990) and presumably also the cloaca. In *Anas* it may direct the erect phallus cranioventrally at coitus (Liebe, 1914).

(29) **M. contractor cloacae.** Synonymy: M. transversus perinei (Harvey, et al., 1968; Ghetie, et al., 1976). Vanden Berge (1979: 198) interpreted this infrequently-occurring striated muscle as a slip of M. pubocaudalis internus. Baumel (1988: 27) confirmed its absence as a discrete muscle in *Columba*, but observed corresponding bundles in M. pubocaudalis internus and M. sphincter cloacae. In *Gallus* it is a small but distinct muscle passing transversely across the craniodorsal aspect of M. sphincter cloacae, between the caudal ends of the pubic bones (Knight, 1967: 60).

(30) **M. depressor anguli venti.** This muscle has been described only by Baumel (1988: 27) in *Columba*, where it arises from the ventral midline beneath the vent and diverges dorsally on each side of the vent to insert into the M. transversus cloacae.

(31) **M. levator cloacae [M. retractor phalli caudalis].** Synonymy: M. levator ani (Gadow and Selenka, 1891: 848; Ghetie, et al., 1976); M. eversor urodeum (Harvey, et al., 1968). In *Gallus* this is a long narrow muscle arising from the ventral surface of the tail, inserting in the *ventral* midline on the phallus (Knight, 1967: 61). In *Columba* it is a long slender bundle running from the follicle of the outermost rectrix of the tail, splitting to insert both on the *dorsal* lip of the vent and on the phallic bodies on the *ventral* lip (Baumel, 1988). The M. levator ani (Müller, 1836; Gadow and Selenka, 1891: 848) inserts on the *dorsal* lip. The M. retractor phalli caudalis (**Masc.** Annot. 51) is a slender band inserting on the phallus (i.e., the *ventral* lip of the vent) in *Gallus, Meleagris*, and *Anas*. On the basis of their own observations on several ratite species and *Anas* and *Cygnus*, Gadow and Selenka (1891: 848, 857) described both M. levator ani *and* the two pairs of retractor muscles of the phallus; this, and the dorsal and ventral discrepancies in the insertions, raise the disturbing possibility that these might not all be the same muscle, but it is supposed that they probably are (**Masc.** Annot. 51). This conclusion is particularly supported by the observations of Liebe (1914) who described the pelvic musculature very thoroughly in *Anas;* he included the cranial and caudal retractor muscles of the phallus, but made no mention of a levator cloacae or levator ani muscle.

(32) **M. dilator cloacae [M. retractor phalli cranialis].** Synonymy: M. dialator cloacae (Knight, 1967: 62). A less known muscle than the levator cloacae, not formally listed in NAA, 1979 but mentioned in **Myol.** Annot. 68 of NAA, 1979. It has been clearly described in *Gallus* and *Columba;* in both it is a very delicate band. In *Gallus* (Knight, 1967: 62) it arises from the ischium and inserts on the *ventrolateral* aspect of the vent, and was distinguished by its light brown colour (smooth muscle?). In *Columba* (Baumel, 1988: 28) this nonstriated muscle arises from the the M. pubocaudalis internus and inserts on the *dorsal* lip of the vent. The M. retractor phalli cranialis (**Masc.** Annot. 51) inserts essentially on the *ventral* lip of the vent, and is nonstriated muscle. The differences in the insertions are again disquieting, but the

M. dilator cloacae and the M. retractor phalli cranialis are presumed to be the same muscle.

(33) **Tunica mucosa.** In most birds the mucosa of the coprodeum resembles that of the rectum, but is more or less elaborate depending on the species, probably reflecting water resorption (Johnson and Skadhauge, 1975). Many circular **Plicae cloacales** (cloacal folds) carrying Villi cloacales (cloacal villi) occur in the coprodeum of *Dromaius*. The xerophilic passerine *Poephila* has no folds but abundant tall, dense villi. *Gallus* also has many finger-like villi (Calhoun, 1954: 70). The columbid *Streptopelia* has some low broad villi and flat areas without villi. The coraciiform *Dacelo* and psittaciform *Eolophus* have no villi. In all these taxa (Johnson and Skadhauge, 1975; Hodges, 1974: 86) the coprodeal epithelium is simple columnar with goblet cells (Exocrinocyti caliciformes), and intestinal crypts (Cryptae intestinales) open between the villi or on the flat surfaces devoid of villi. In *Anas* and *Anser* the entire cloaca is lined by stratified squamous epithelium (Komárek and Marvan, 1969). The urodeal mucosa varies, being simple columnar with small villi in *Gallus* (Calhoun, 1954: 70), and a mixture of simple columnar and various compound epithelia without villi in other species (see King, 1981: 86 for review). The lining of the proctodeum is stratified squamous epithelium without villi in all taxa so far examined, except *Gallus* where the inner aspects of the labia of the vent are stratified squamous (Annot. 21), the lining of the rest of proctodeum columnar (King, 1981: 91).

(34) **Lamina muscularis mucosae; Tunica muscularis.** The muscularis mucosae and muscle tunic are recognisable in the cranial regions of the cloaca, but indistinct caudally where the extrinsic cloacal muscles predominate.

(35) **Tunica fibrosa; Tunica serosa.** The cranial part of the coprodeum is peritoneal (Fig. 10.8), having a serous coat. The rest of the cloaca is intrapelvic and has a fibrous coat.

11

GLANDULAE ENDOCRINAE

AUGUST EPPLE

TERMINOLOGY

GLANDULA THYROIDEA[1]

Capsula thyroidea
Colloidum thyroideum
Folliculus thyroideus
Parenchyma thyroidea
Stroma thyroidea

GLANDULA PARATHYROIDEA[2]

Capsula parathyroidea
Parenchyma parathyroidea
Stroma parathyroidea
Gll. parathyroideae accessoriae[3]

GLANDULA ULTIMOBRANCHIALIS[4]

Parenchyma ultimobranchialis
Stroma ultimobranchialis
Vesiculae ultimobranchiales

GLANDULA PINEALIS[5]

Corpus gl. pinealis
  Parenchyma pinealis
Pedunculus gl. pinealis[5]

SYSTEMA ENDOCRINUM MUCOSAE DIGESTORIUM[6]

Cellulae endocrinae mucosae digestorium

INSULAE PANCREATICAE[7]

Parenchyma insularum
Cellulae insularum[7]
  Cellulae A
  Cellulae B
  Cellulae D
  Cellulae F

GLANDULA ADRENALIS[8]

Capsula adrenalis
Partes corticales gl. adrenalis
Partes medullares gl. adrenalis
Glandulae adrenales accessoriae[9]
Paraganglia[10]

HYPOPHYSIS [GLANDULA PITUITARIA][11]

Adenohypophysis[12]
  Pars tuberalis
  Pars distalis[12]
    Zona rostralis partis distalis
    Zona caudalis partis distalis
Neurohypophysis[13] (CNS)
  Sulcus tuberoinfundibularis[14]
Eminentia mediana[14 15]
  Zona rostralis eminentiae medianae[15]
  Zona caudalis eminentiae medianae[15]
Infundibulum
Lobus nervosus
  Recessus neurophypophysialis[16]
  Tractus hypothalamohypophysialis

VASA SANGUINEA HYPOPHYSIS

A. carotis cerebralis[18]
  A. infundibularis[18]
    A. neurohypophysialis
Anastomosis intercarotica[18]
A. hypophysialis caudalis[17]
A. eminentiae rostralis
A. eminentiae caudalis
A. retrochiasmatica

(continued)

VASA SANGUINEA HYPOPHYSIS (cont.)

Aa. hypothalamicae ventrales[18]
R. rostralis a. carotis cerebralis
  A. cerebralis rostralis
  Aa. preopticae[19]
Systema portale hypophysiale[20]
  Vv. portales caudales[21]
Vasa sinusoidea portalia[22]
Vv. portales rostrales[21]
  Vasa sinusoidea portalia
Sinus cavernosus[23]
  Vv. adenohypophysiales[24]

ANNOTATIONS

(1) **Glandula thyroidea.** The avian thyroid tissue develops in the usual vertebrate pattern from pharyngeal endoderm (Romanoff, 1960). In contrast to mammals, all birds seem to have two separate glands (one on each side) that lie usually close to the common carotid artery and the jugular vein (Astier, 1980). The **Parenchyma thyroidea** of many birds seems to be of the follicular type only; however, parathyroid tissue and C cells (see Annot. 4) invade the glands of some species (see below). The connective tissue capsule is thin. The histophysiological variations of the follicular epithelium seem to be the same as in other vertebrates (Astier, 1980).

(2) **Glandula parathyroidea.** Birds have a total of two to four parathyroids which are typically located along the jugular vein between the thyroid and the ultimobranchial glands (Forsyth, 1908; Bargmann, 1939). It is assumed that the cranial and caudal parathyroids develop from the third and fourth pharyngeal pouches, respectively. In some taxa, e.g., *Gallus*, the capsules of two parathyroids are attached to each other, or the parenchyma is even fused within the same capsule (Abdel-Magied and King, 1978). In a number of species, the carotid body is either located close to, or embedded in the parathyroid (Watzka, 1933; DeKock, 1959). At least in some species, the parenchyma contains two types of chief cells; however, in contrast to mammals, oxyphil cells are absent. The strong innervation of the glands is mainly, but not exclusively, associated with blood vessels (Clark, et al., 1986).

(3) **Glandulae parathyroideae accessoriae.** These structures are not universally present in birds, or, if so, have not been identified. However, positive identification within the ultimobranchial gland has been made in several species, such as *Gallus* (Hodges, 1974: 444), *Corvus*, Strigidae, and *Columba* (Watzka, 1933). Their occasional presence outside the ultimobranchial gland, in thymus tissue and the thyroid gland has been described in the fowl by Nonidez and Goodale (1927).

(4) **Glandula ultimobranchialis.** The avian ultimobranchial gland develops from two different components: (1) endodermal, pharyngeal outpocketings, which (2) are invaded by calcitonin-producing C cells of neural crest origin (Le Douarin, et al., 1974). The resulting picture varies with the species (Watzka, 1933; Hodges, 1979), and mingling of both components with adjacent structures adds to the difficulties of defining the organ. Hence, the synonym "ultimobranchial body" appears to be misleading. In columbids, C cells have been found in the thyroid, which resembles the mammalian situation (Stoeckel and Porte, 1970). Immunocytochemistry may be the safest way to identify the C cells (Kameda, 1984), which in turn represent two subtypes (cf., Robertson, 1986). It remains to be seen if, or to what extent,

"parenchymal" and "vesicular" components can be related to endocrine and non-endocrine functions.

(5) **Glandula pinealis.** Synonymy: Corpus pineale; Epiphysis cerebri. The avian pineal is an endocrine organ that shows great species variations (Quay and Renzoni, 1967; Hartwig, 1980; Collin and Oksche, 1981; Binkley, 1989). Its predominent cell types are modified photoreceptors that produce the hormone melatonin. There are also glia- or ependyma-related supportive elements, and intrinsic neurons that project via the pineal tract to hypothalamic regions (Korf, et al., 1982). The intrinsic neurons tend to concentrate in the proximal (stalk) region of the pineal (**Pedunculus gl. pinealis**); according to Sato and Wake (1983), their number varies in adult birds from zero in the chicken to about 360 in the Golden Pheasant (*Chrysolophus pictus*). The avian pineal receives sympathetic innervation from the superior cervical ganglion (see **PNS**); this innervation is also subject to considerable interspecific variation (Ueck, 1979).

(6) **Systema endocrinum mucosae digestorium.** As in all vertebrates, the mucosal epithelium of the avian gut contains a large variety of endocrine cells. In birds, they are scattered from proventriculus to rectum. Immuno-cytochemically, there are at least ten different types, but it is likely that their number is larger. Morphologically, these cells can be assigned to two different categories: (l) "open cells" that seem to receive chemical stimuli from the gut lumen via apical microvilli; and (2) "closed-cells" that seem to occur mainly or exclusively in the Proventriculus. Closed cells seem to respond to humoral messages and or pressure. The limited data so far available show already many differences between birds and mammals, as well as between different avian species (Yamada, et al., 1983; Rawdon, 1988). The endocrine cells of the avian respiratory tract (McLelland and Macfarlane, 1986) can be considered phylogenetically as descendents of the mucosal endocrines of the gut.

(7) **Insulae pancreaticae: Cellulae insularum.** The bulk of the avian pancreas is located in a loop of the duodenum, but a fine extension, the splenic lobe, is always present near the spleen. In many species, the bulk of the pancreas consists of a dorsal and a ventral lobe; however, in phasianids there is an additional third lobe (see **Digest. Annot. 110**). In the chicken, the splenic and third lobe develop from the dorsal pancreas primordium, the dorsal lobe from the right and the ventral lobe from the left ventral primordium; intermingling of ventral and third lobe material occurs during the development (Ono, 1967). This terminology is confusing since in non-phasianids the large accumulation of islet tissue in the dorsal and splenic lobe (Guha and Ghosh, 1978) suggests that these pancreas regions of the birds are of dorsal primordium origin.

There are four major cell types: A cells, B cells, D cells, and F cells (**Cellulae A, B, D, F**)), producing the respective hormones glucagon, insulin, somatostatin and pancreatic polypeptide (Andrew, 1984; Rawdon, 1988; Hazelwood, 1989). However, birds are unique in that their islets occur largely in two different forms: large A islets (also called "dark" islets), consisting mainly of A and D cells; and smaller B islets (also called "light" islets), consisting mainly of B and D cells. At least in some species, including the chicken, there are also "mixed" islets, containing mainly A, B, and D cells (Iwanaga et al. 1983). F cells are scattered over the whole pancreas, either as single elements or as small groups; they tend to be more common in the derivatives of the ventral primordia (Andrew, 1984; Tomita, et al., 1985). On the other hand, A islets tend to be more common in the derivatives of the dorsal primordium, which is particularly obvious in the phasianids (Iwanaga, et al., 1983; Mikami, et al., 1985; Tomita et al. 1985). The highest concentration of islet tissue occurs always in the splenic lobe. Due to its small size and variability, the latter may have been overlooked in earlier pancreatectomies, which might explain differing results of the operation (Mialhe, 1958).

(8) **Glandula adrenalis.** Synonymy: Suprarenal gland. Birds have usually two discrete adrenals. These glands are often bilaterally asymmetric, both in size and shape; and in a few species, the glands are fused in the midline (Bachmann, 1954). The adrenals develop from two different germ layers: the steroidogenic "inter-renal" tissue (the equivalent of the mammalian cortex) from mesoderm, and the catecholaminergic, chromaffine tissue (the equivalent of the mammalian medulla) from neural crest cells. Both components intermingle greatly, and the chromaffin tissue occurs usually as islets between cords of steroidogenic cells. However, in some birds the chromaffin tissue tends to concentrate towards the outer region of the glands (Hartman and Brownell, 1949). In the duck (*Anas*), the cortex shows cytological differences which have led to the suggestion that, similar to mammals, an outer zone produces aldosterone, and an inner zone corticosterone (Holmes and Cronshaw, 1984). The chromaffine cells can be divided histochemically into norepinephrine and epinephrine cells. As in mammals, the percentage of these cell types varies greatly with the species; e.g., the cormorant (*Phalacrocorax niger*) has 100% norepinephrine cells, while some passeriforms have 95% epinephrine cells (Ghosh, 1980). See **Art. Ven.** for adrenal vessels.

(9) **Glandulae adrenales accessoriae.** In the Jackdaw (*Corvus monedula*) 1-3 accessory adrenal glands are embedded in the epididymis (Tracuic, 1969), but information on other taxa is lacking. The accessory glands should not be regarded as paraganglia; only tissue masses shown to contain chromaffin material should be termed paraganglia.

(10) **Paraganglia.** Extra-adrenal chromaffin tissue has been identified in various species in various locations. For several reasons, the carotid bodies also may be considered paraganglia (Böck, 1982).

(11) **Hypophysis cerebri [Glandula pituitaria].** The nomenclature for the components of this organ is clouded by doubtful anatomical distinctions, a wealth of alternative names for the same structure, and the fact that physiological function often overlaps more than one anatomically-distinct area. Structurally and functionally, it is difficult to consider the "hypophysis" separately from the aldehyde fuchsin-positive and aldehyde fuchsin-negative neurosecretory systems of the diencephalon. Since this chapter only considers the classical neurohypophysis and adenohypophysis, the reader is referred to key references which cover much of the literature on the nuclei that give rise to the axons terminating in the neurohypophysis: For aldehyde fuchsin-positive systems (producing mesotocin and vasotocin) see Blähser (1981) and Tolivia, et al. (1987); for the other systems that can be identified more or less by immunocytology only (i.e., the producers of releasing and inhibiting hormones of the adenohpophysial secretions), see Mikami and Yamada (1983) and Blähser (1984). Unfortunately, most of the avian hypothalamic nuclei are inhomogeneous entities, and their structure is as confusing as some of the terminologies (Oksche, 1983; Korf, 1984; Blähser, 1988).

(12) **Adenohypophysis; Pars distalis.** Synonymy: Pars anterior. The two distinct regions of the avian Pars distalis of the hypophysis (Zona rostralis and Zona caudalis) are commonly called cephalic and caudal lobes, respectively. They are characterized by different cell populations (Mikami, 1983; Mikami and Yamada, 1984).

(13) **Neurohypophysis.** Synonymy: Lobus posterior. The term "posterior lobes" of the hypophysis in birds differs from that in mammals because birds lack a Pars intermedia; this may lead to misunderstanding. The complex structural organization of the avian neurohypophysis has been reviewed by Mikami (1980) and Oksche (1980). See **CNS,** Sectiones hypothalami.

(14) **Sulcus tuberoinfundibularis.** This furrow, particularly in species with a strongly thickened median eminence, delineates the **Eminentia mediana** from the surrounding hypothalamus (Wingstrand, 1966). The term was defined for mammals by Spatz, et al. (1948), though Sulcus hypothalamo-hypophyseus was used by Kuhlenbeck and Haymaker (1949). See **CNS,** Annot. 94.

(15) **Zona rostralis eminentiae medianae; Zona caudalis eminentiae medianae.** The two zones of the avian median eminence of the neurohypophysis differ in innervation, histological/histochemical properties that reflect different secretions, and drainage via the hypophysial portal system (Annot. 20). Both zones secrete hypophysiotropic hormones. The rostral zone supplies the cephalic lobe of the Pars distalis, and it usually contains also many aldehyde-positive neurosecretory terminals that secrete vasotocin; the caudal zone supplies the caudal lobe of the Pars distalis (Mikami, 1980; Oksche, 1980; Blähser, 1981).

(16) **Recessus neurohypophysialis.** This is the extension of the third ventricle into the neurohypophysis.

(17) **A. hypophysialis caudalis.** In some birds, such as the pigeon *Columba*, caudal hyophysial arteries from the intercarotid anastomosis supply the neurohypophysis; in others the neurohypophysis is supplied by a branch of the infundibular artery, the A. neurohypophysialis.

(18) **A. infundibularis.** A. infundibularis is usually a branch of A. carotis cerebralis rostral to the **Anastomosis intercarotica (Art.** Annot. 17), near its bifurcation into the Rami rostralis and caudalis. Vitums, et al. (1964) state, "Each infundibular artery (right and left) usually originates as a single artery from the anterior ramus just rostral to the origin of the posterior ramus. In a few cases, the infundibular artery originates directly from the carotid artery at the point just caudal to the origin of the posterior ramus". Wingstrand (1951: 274) states that the blood supply to the primary plexus of the median eminence comes exclusively from the infundibular arteries. The vessels are fairly small and variable, but always start from the A. carotis cerebralis somewhere between the Diaphragma sellae (**CNS** Meninges) and its point of division into rostral and caudal rami. Because Wingstrand discussed 25-30 different species, his description should be accepted as the usual condition.

Aa. hypothalamicae ventrales. The hypothalamohypophysial tract is supplied by these arteries (Vitums, et al., 1964).

(19) **Aa. preopticae.** These arteries supply the supraoptic and paraventricular (neurosecretory) hypopthalamic nuclei (Vitums et al. 1964).

(20) **Systema portale hypophysiale.** The system starts from capillary beds in the median eminence and ends in the adenohypophysis. In *Zonotrichia, Columba,* and other birds Vv. portales form the sole afferent blood supply to the adenohypophysis (Vitums, et al., 1964; Wingstrand, 1951). In *Gallus* (Hasegawa, 1956) and *Anas* (Assenmacher, 1953) the Pars distalis also receives a limited part of its supply from caudal and rostral hypophysial arteries (Vitums, et al., 1964).

(21) **Vv. portales rostrales: Vv. portales caudales.** The rostral and caudal groups of veins are derived from capillary plexuses of the rostal and caudal zones of the median eminence, respectively (Vitums, et al., 1964; Singh and Dominic, 1970; Sharp and Follett, 1969) (see Annot. 16).

(22) **Vasa sinusoidea portalia.** According to Mikami, et al. (1970), these sinusoids in the portal zone of Pars distalis have a structure resembling postcapillary venules.

(23) **Sinus cavernosus.** The cavernous sinus of birds is a complicated structure subdivided into several separate components. It has not been determined that the separate components have interconnections and consequently the portal drainage from the neurohypophysis may be entirely separate from adenohypophysial drainage. See **Ven.** Annot. 18.

(24) **Vv. adenohypophysiales.** In *Zonotrichia* three main groups of veins drain from the portal sinusoids of the adenohypophysis into different parts of the cavernous sinus (Vitums, et al., 1964). A similar drainage occurs in the chicken (Green, 1951).

12

SYSTEMA CARDIOVASCULARE

JULIAN J. BAUMEL

With contributions from subcommittee members: A. J. Bezuidenhout, J. Kaman, A. S. King, L. Malinovský, U. Midtgård, T. Miyaki, T. Nishida.

The efforts of Jiri Kaman and Takao Nishida in formulating the original cardiovascular terminology in the first edition of the *Nomina Anatomica Avium* (NAA, 1979) deserve acknowledgement. In preparing this edition we have relied heavily on Dr. Midtgård's extensive series of papers on the vasculature of the pelvic limb of the past 10 years.

In the NAA (1979) "Systema Cardiovasculare" was adopted as a more meaningful heading for this section rather than "Angiologia". Systema Cardiovasculare is a more inclusive term, since Angiologia literally connotes vessels only. More recent editions of the *Nomina Histologica,* 2nd ed. (IANC, 1983) and the human *Nomina Anatomica,* 6th ed. (IANC, 1989) have followed the lead of the NAA (1979); however the *Nomina Anatomica Veterinaria,* 3d ed. (ICVGAN, 1983) still retains Angiologia.

Intrinsic vessels of viscera. Blood vessel terminology is found in chapters other than this cardiovascular chapter. In general, the names of vessels of macroscopic dimensions that supply or drain viscera are presented here. Vessels that make up the meso- and microscopic, intrinsic angioarchitecture of the major viscera are named elsewhere: consult Apparatus respiratorius, Apparatus urogenitalis, and Apparatus digestorius for intrapulmonary, intrarenal, and intrahepatic vessels and Glandulae Endocrinae for hypophysial blood vessels.

Spinal cord vasculature is presented in this chapter; neither of the mammalian nomenclatures includes this terminology.

Heart. The terminology of the avian heart differs from the mammalian nomenclatures in that the names of the parts of the atrial myocardium and ventricular myocardium are presented here.

The 6th edition of the human *Nomina Anatomica* (IANC, 1989) has been followed in naming the veins of the heart. Both "cor" (L.) and "cardia" (Gk.) are used to refer to the heart in anatomical terminology. Instead of the genitive form "cordis" the adjectival form "cardiaca" has been adopted, thus: V. cardiaca sinistra instead of V. cordis sinistra. By using the term "cardiac" the vessel terminology is consistent with that of the heart nerves, N. cardiacus and Plexus cardiacus, as well as Pericardium, Myocardium, Impressio cardiaca of the liver, etc.

Nomenclature of branches of A. celiaca and associated venous radices. The terminology for the celiac artery recommended by Malinovský (1965) has been adopted. In this scheme "proventricular" refers to the glandular stomach and "gastric" refers to the muscular stomach (ventriculus, gizzard). Malinovský defined various surfaces, margins, and parts of the muscular stomach on which the names of vessels are based in the definitive, adult individuals; he also presents recommendations on the reconciliation of vessel terminology of branches of A. celiaca in various species of several avian orders.

Nishida, Paik, and Yasuda (1969) based their terms on "muscular" and "glandular" stomach (example: A. gastrica glandularis sinistra). These authors name the primary subdivisions of A. celiaca as A. gastrica dextra and A. gastrica sinistra. Malinovský pointed out the difficulties in using this nomenclature in that the stomach is only one of several major organs supplied by A. celiaca.

Splenic-lienal. Nomina Anatomica Avium follows the human *Nomina Anatomica* (IANC, 1989) in adopting Splen for the spleen rather than Lien which has been retained as an official alternative name. This requires that the vessels be named accordingly; therefore, Aa. et Vv. splenicae.

Ascending-descending. Usage of the adjectives "ascendens" and "descendens" with respect to names of blood vessels require definition. These terms refer to the direction of blood flow in arteries. For example, blood in A. vertebralis ascendens flows cranially; that in A. vertebralis descendens flows caudally. The companion vein(s) of an artery designated ascendens takes the same name as its artery even though its blood drains caudally. For example, V. cutanea cervicalis ascendens parallels A. cutanea cervicalis ascendens (see Baumel, et al., 1983).

TERMINOLOGY

TERMINI GENERALES

(See *Nomina Histologica* IANC, 1989 for a more extensive list of general terms for the heart and vessels.)

Arteria
Arteriola
Anastomosis arterioarteriosa
Anastomosis arteriovenosa
Anastomosis venovenosa
Anastomosis lymphovenosa
Arcus arteriosus
Arcus venosus
Capillaris
Circulus arteriosus
Circulus venosus
Cisterna
Lumen vasis
Plexus arteriosus
Plexus vascularis
Plexus venosus
Lympha
Pulvinar luminalis
Rete venosum
Sanguis
Valvula venosa
Valvula lymphatica
Vas anastomoticum
Vas afferens [advehens]
Vas deferens [rehevens]
Vas capillare
Vas collaterale
Vas lymphaticum
Vasa nervorum
Vasa vasorum
Vena
Vena comitans
Venula
Rete arteriosum
Rete mirabile

COR (see Chapter Introduction) (Figs. 12.1, 2)

Basis cordis [Facies pulmonalis][1]
Facies sternalis [Facies ventrocranialis][1]
Facies hepatica [Facies dorsocaudalis][1]
Apex cordis
Fovea apicis cordis
Sulcus interventricularis paraconalis[2]
Sulcus interventricularis subsinuosus[2]
Sulcus coronarius [S. atrioventricularis]
Septum interatriale[3] (see Annot. 15)
Perforationes interatriales[3]
Pars cavopulmonalis[3]
Septum interventriculare
Chordae tendineae
Mm. papillares[4]
Trigona fibrosa[5]
Anulus [Annulus] fibrosus[5]

EPICARDIUM (see Pericardium)

MYOCARDIUM (see *Nom. Hist.*, 1989)

Mm. atriales[6]
Arcus longitudinalis dorsalis[6]
  Arcus transversus dexter[6]
  Arcus transversus sinister[6]
    (Fig. 12.2)
Mm. pectinati[6]
M. basianularis atrii[6] (Fig. 12.2)
Mm. ventriculares[7]
  Lamina superficialis[7]
  M. longitudinalis ventriculi sinistri[7]
  M. longitudinalis ventriculi dextri[7]
  M. valvae atrioventricularis dextrae[7]
  M. sinuspiralis
  M. bulbospiralis
    Pars superficialis
    Pars profunda
Trabeculae carneae
Mm. papillares

ENDOCARDIUM

SYSTEMA CONDUCENS CARDIACUM[8] (Fig. 12.3)

Nodus sinuatrialis[9 10]
  Rr. nodi sinuatrialis[10]
  Rr. myofibrarum conducentes atrii
  Rr. subepicardiales atriales[8]
  Rr. periarteriales atriales
  Rr. subendocardiales atriales
Nodus atrioventricularis[11]
Fasciculus [Truncus] atrioventricularis[11]
  Connexus cum fasciculo truncobulbari[12]
  Crus dextrum fasciculi
  Crus sinistrum fasciculi
    Rr. cruris[10]
    Rr. myofibrarum conducentes ventriculi[8]
    Rr. periarteriales
    Rr. subendocardiales ventriculares
    Rr. subepicardiales ventriculares[8]
Pars accessoria systematis conducentis
  Anulus [Annulus] atrioventricularis dexter[12]
  Nodus truncobulbaris[12]
  Fasciculus truncobulbaris[12]
  Connexus cum fasciculo atrioventriculari

SINUS VENOSUS[13]

Valva sinuatrialis[13]
  Valvula sinuatrialis dextra
  Valvula sinuatrialis sinistra
  M. pectinati valvae[14]
Septum sinus venosi[17]
Ostium venae cavae caudalis[13]

(continued)

SINUS VENOSUS[13] (cont.)

Ostium venae cavae cranialis dextrae[13]
Ostium venae cavae cranialis sinistrae[13]

ATRIUM DEXTRUM (Fig. 12.2)

Auricula dextra
Cavitas atrii dextri
Recessus sinister atrii dextri[15]
Ostium sinus venosi[13]
Ostium venae cavae cranialis sinistrae
Ostium venae proventricularis cranialis[16]
Ostia venarum cardiacarum
Foramina venarum minimarum[25]
Septum sinus venosi[17]

VENTRICULUS DEXTER (Fig. 12.2)

Cavitas ventriculi dextri
Ostium atrioventriculare dextrum
Valva atrioventricularis dextra[18]
Conus arteriosus [Infundibulum]
Ostium trunci pulmonalis
Valva trunci pulmonalis[19]
  Valvula semilunaris sinistra
  Valvula semilunaris dextra
  Valvula semilunaris dorsalis
  Foramina venarum minimarum[25]

ATRIUM SINISTRUM (Fig. 12.2)

Auricula sinistra
Cavitas atrii sinistri
Ostium venae pulmonalis dextrae[20]
Ostium venae pulmonalis sinistrae[20]
Camera pulmonalis[21]
Valva venae pulmonalis[22]
Foramina venarum minimarum[25]

VENTRICULUS SINISTER (Fig. 12.2)

Cavitas ventriculi sinistri
Ostium atrioventriculare sinistrum
Valva atrioventricularis sinistra[23]
  Cuspis sinistra
  Cuspis dextra[23]
  Cuspis dorsalis
Vestibulum aortae
Ostium aortae
Bulbus aortae[24]
Valva aortae[24]
  Valvula semilunaris sinistra
  Valvula semilunaris dextra ventralis
  Valvula semilunaris dextra dorsalis

ANNOTATIONS

(1) **Basis cordis [Facies pulmonalis].** The base of the heart is defined as its dorsal or pulmonary surface that consists mostly of the walls of the left and right atria. Pericardium intervening, the dorsal surface of the heart is related to the trachea, bronchi, and proventriculus (near the midline) and the ventral surface of the Septum horizontale (**Pericar.** Annot. 2) on each side of the median plane.

Facies sternalis; Facies hepatica. Synonymy: Facies ventralis and Facies ventrocranialis; Facies dorsalis and Facies dorsocaudalis. The sternal and hepatic surfaces of the heart are terms of Baum (1930), and indicate structures in contact with the heart (enclosed by its pericardial sac). These terms pertain no matter what the orientation of the sternum. The dorsal or visceral surface of the sternum in most birds is nearly parallel with the vertebral column, whereas the sternum of the Ostrich (*Struthio*) has a vertical segment (Bezuidenhout, 1981).

(2) **Sulci interventriculares.** Synonymy: right and left longitudinal sulci. In the avian heart the indistinct interventricular sulci are obliquely disposed, and do not parallel the axis of the heart. The terms adopted here follow the *Nomina Anatomica Veterinaria* (ICVGAN, 1983). The adjectives **"paraconalis"** and **"subsinuosus"** refer to the interventricular sulci that are related to the Conus arteriosus and Sinus venosus, respectively (Fig. 12.1).

(3) **Septum interatriale.** Only the cranioventral part of the adult interatrial septum represents the foetal septum; this part separates the left atrium from the Recessus sinister atrii dextri (Annot. 14), and was pierced by multiple **Perforationes interatriales** during foetal and neonatal life. The caudodorsal part (Pars cavopulmonalis) of the adult interatrial septum is formed by contributions from the embryonic pulmonary veins and the left cranial vena cava which become incorporated into the definitive left atrium and interatrial septum (Quiring, 1933-34). Functionally, the perforations correspond to the mammalian foetal Foramen ovale; in birds there is no vestigial adult equivalent of the mammalian fossa ovalis (Annot. 15).

(4) **Mm. papillares.** Papillary muscles are columns of myocardium projecting into the ventricular chamber to which are connected to the **Chordae tendinae** which anchor the cusps of the atrioventricular valve. Found only in the left ventricle of the avian heart; in the hearts of smaller birds they are poorly differentiated from the general myocardium, distinguished only as the point of attachment of the Chordae tendineae.

(5) **Anulus [Annulus] fibrosus; Trigona fibrosa.** The fibrous rings are elements of the "skeleton" of the heart; they support the attachment of the cusps of the four heart valves. The annuli are best developed about the left atrioventricular ostium and root of the aorta. The fibrous rings of the pulmonary trunk and the right atrioventricular ostium are relatively weakly developed except in large birds. The right fibrous trigone is the thickest, most rigid part of the heart skeleton, located directly dorsal to the root of the aorta. The left trigone is between the left side of the aortic annulus and the ventromedial part of the left atrioventricular annulus.

(6) **Mm. atriales.** Avian atrial musculature has distinctive parts. Most of the terminology is that of Quiring (1933-34). The muscular arches break up into definite, internally prominent fascicles, the **Mm. pectinati,** that merge into **M. basianularis** (Fig. 12.2) (Baumel, 1975c:1970), which is the circular layer of muscle around the bases of the atria that bounds the coronary sulcus and rests in contact with the ventricles.

Arcus longitudinalis dorsalis. (Fig. 12.2) Synonymy: median dorsal arch (Quiring, 1933-34). In some galliforms this a prominent arch of the atrial musculature that appears to be derived from M. basianularis just dorsal to the roots of the pulmonary trunk and aorta; the arch sweeps dorsally somewhat parallel to the cranial attachment of the interatrial septum, and subdivides on approaching the ostia of the pulmonary veins (Baumel, 1975c). The arch is doubled in the Ostrich heart (Bezuidenhout, pers. comm.).

Arcus transversus dexter/sinister. These are stout lateral offshoots of the longitudinal arch in the roof of the right and left atria; laterally each transverse arches splits, becoming continuous with the general pectinate muscles.

(7) **Mm. ventriculares.** Names of the parts of the ventricular myocardium are mostly based on the terms of Shaner (1923).

Lamina superficialis (Baumel, 1975c) is a thin superficial sheet of muscle just beneath the epicardium that invests the deeper ventricular musculature in the chicken (Baumel, 1975c) and Ostrich (*Struthio*) heart (Bezuidenhout, 1981).

M. longitudinalis ventriculi sinistri. Bezuidenhout (1981) noted that in the Ostrich (*Struthio*) heart this muscle plays a major role in the formation of the left ventricular wall, making little contribution to the wall of the right ventricle.

M. valvae atrioventricularis dextrae. (Fig. 12.2) This muscular right atrioventricular valve in the chicken (*Gallus*) and Ostrich (*Struthio*) heart was shown by Bezuidenhout (1983) to be formed by the cranial part of the **M. longitudinalis ventriculi dextri.**

(8) **Systema conducens cardiacum.** (Fig. 12.3) The cardiac impulse generating and conduction system is formed from modified cardiac muscle cells: Myocytus nodalis and Myocytus conducens cardiaca (purkinjiensis); a series of myocytes juxtaposed end-to-end are known as a Myofibrum (*Nomina Histologica,* IANC, 1989). The terminal ramifications of the subepicardial, subendocardial, and periarterial conducting tissue are also known as Myofibra purkinjiensis (*Nomina Histologia,* IANC, 1989); these make contact with typical cardiac muscle cells in the atria and ventricles.

Rr. subepicardiales. The presence of these ramifications of conducting tissue were noted in the Ostrich by Bezuidenhout (1981) immediately deep to the the epicardial serous membrane on the surface of the heart. See West, et al. (1981) for a review of the conducting system.

(9) **Nodus sinuatrialis.** Contemporary consensus holds that a discrete sinuatrial (S-A) node does exist in the avian heart, verified in *Gallus* by Kim and Yasuda (1979) and, more recently by Murakami, et al. (1981, 1985) in procellariid, ciconiid, anatid, falconid, columbid, gruid, psittacid, and passerine birds Both groups of the above authors remark that there are no direct conducting-tissue connections between the S-A and atrioventricular (A-V) nodes. The S-A node lies between the right atrial myocardium and epicardium at the right caudal region of the orifice of the right cranial vena cava (Fig. 12.3), where the caudal ends of the two valvules of the sinuatrial valve meet one another or actually occur within the valvules and sinus septum.

(10) **Rr. nodi sinuatrialis; Rr. cruris.** These are ramifications of nodal myofibers and myofibers of the A-V fasciculus and its main limbs (crura). In addition to the subendocardial and subepicardial ramifications, parts of the conducting tissue penetrate the myocardium. Some of these are distributed as cords within the periarterial connective tissue of the coronary arteries; in some instances the cords form circular

"muffs" of conducting cells (**Rr. periarteriales**) that surround the intramyocardial rami of Aa. coronariae (Davies, 1930; Chiodi and Bortolami, 1967).

(11) **Nodus atrioventricularis; Fasciculus [Truncus] atrioventricularis.** (Fig. 12.3) The atrioventricular part of the impulse conducting system has been investigated in representatives of twelve or more avian orders. Most recently the comparative study of Murakami, et al. (1985) presents a thorough review of the literature. Generally the A-V node is embedded in the connective tissue between the right atrial myocardium and and the right fibrous trigone on the caudodorsal part of the interventricular septum near the ostium of the left cranial vena cava (Kim and Yasuda, 1979). The A-V bundle (fasciculus) is prolonged from the A-V node deep in the interventricular (I-V) septum. One quarter of the distance to the apex, the bundle divides into right and left crura. As each crus descends in the septum it gradually surfaces under the endocardium on each side of the I-V septum; there its branches spread out as the subendocardial ramifications. The avian A-V bundle is relatively longer than the mammalian bundle which divides abruptly near its A-V node (Murakami, et al. 1985). This account does not agree with that of Chiodi and Bortolami, 1967) who contended that an A-V trunk is lacking in the hearts of some birds, the trunk being represented by multiple crura which depart directly from the A-V-node.

(12) **Anulus [Annulus] atrioventriculus dexter.** This ring-like component of the conducting system was first described in the bird by Ohmori (1928) and confirmed by Davies (1930). The right A-V annulus passes about the right A-V ostium between the two muscular components of the right A-V valve (Annot. 18), and is concerned with the contraction of the valve.

Nodus truncobulbaris; Fasciculus truncobulbaris. (Fig. 12.3) Synonymy for T-B fasciculus: recurrent branch of A-V bundle (Davies, 1930). Kim and Yasuda (1979) were the first to describe in detail the truncobulbar conducting system (*Gallus*) (see also Murakami, et al., 1985). The T-B node lies close to the left side wall of the aortic root, under the origin of the left coronary artery. The T-B node becomes attenuated as the T-B fasciculus; this bundle runs ventrally through the aortic Anulus fibrosus, and turns caudally to the right in the septal myocardium, finally ending by joining the A-V fasciculus at its point of bifurcation. Kim and Yasuda recognized the reciprocal relationship in size between the A-V and T-B nodes in different individuals, i.e., when the T-B node is large the A-V node is poorly developed, and vice versa.

(13) **Sinus venosus.** Synonymy: Sinus venarum cavarum. The Sinus venosus is a chamber of the heart that appears in certain birds; in different taxa of birds it is variously incorporated into the right atrium (Gasch, 1888). A distinct Sinus venosus is present in the heart of *Apteryx* (Adams, 1937), *Gallus* (Quiring, 1933-34), *Corvus*, *Struthio*, and others (Romanoff, 1960); its right boundary is usually set off from the right atrium by a prominent external groove. Internally it is demarcated from the right atrium by the sinuatrial valve.

Valva sinuatrialis. (Fig. 12.2) See Murakami, et al. (1978) for a comparative review of the opening between the two valvules of the sinuatrial valve (**Ostium sinus venosi**). The ostium of the sinus venosus is partially subdivided in some forms: one part serves as the opening to transmit blood from the right cranial vena cava and the caudal vena cava; blood from the the left cranial vena cava usually flows into the cavity of the right atrium via an opening separated from the cranial part of the ostium of the Sinus venosus by the **Septum sinus venosi** (see Annot. 17).

(14) **Mm. pectinati valvae.** Certain of the pectinate muscles are continuous with the bases of the valvules of the sinuatrial valve (Kolda and Komárek, 1958).

(15) **Recessus sinister atrii dextri.** Typical of the avian heart is this tubular "left recess of the right atrium" that extends to the left past the median plane of the heart and dorsal to the aortic bulb in the "duck" (Rigdon and Frolich, 1970); and in the chicken (Kern, 1926). This recess is separated from the left atrium by a part of the interatrial septum that represents the remnant of the foetal septum (Annot. 3).

(16) **Ostium venae proventricularis cranialis.** V. proventricularis cranialis (Fig. 12.17) drains venous blood from the glandular stomach; the vein may join the left cranial vena cava near its termination (Malinovský, 1965) or empty into the right atrium directly via this ostium (**Ven.** Annot. 51).

(17) **Septum sinus venosi.** Birds in which the left cranial vena cava opens directly into the right atrium possess the Septum sinus venosi, a muscular sheet that separates the orifice of the left cranial vena cava from the opening of the main part of the sinuatrial valve (see Annot. 13).

(18) **Valva atrioventricularis dextra.** (Fig. 12.2) This *muscular* valve closes the right atrioventricular ostium during ventricular contraction. It is formed of both atrial and ventricular musculature. A distinct band of M. sinuspiralis makes up the thicker external lamina of the valve; a fibrous layer separates the external lamina from the thinner internal lamina that is derived from an invagination of right atrial musculature (Shaner, 1923). At its thicker cranial border this valve contains the right fibrous annulus of the cardiac skeleton (see Annot. 5).

(19) **Valva trunci pulmonalis.** This valve of the pulmonary trunk is listed with the names of the parts of the right ventricle even though it is located in the root of the trunk of the pulmonary artery and not in the heart proper. This follows the convention of the mammalian **NA**(1989) and **NAV**(1983) anatomical nomenclatures (see **Art.** Annot. 1).

(20) **Ostium venae pulmonalis dextrae/sinistrae.** In some avian forms the right and left pulmonary veins empty into the left atrium via separate ostia (e.g., *Columba*, *Gallus*, *Anas*); in others the two pulmonary veins become confluent outside the heart, and produce a common pulmonary vein (*Melopsittacus*, Szabo, 1958). See **Ven.** Vv. pulmonales.

(21) **Camera pulmonalis.** (Fig. 12.2) On entering the left atrium, the pulmonary veins coalesce into a single, short vessel; this vessel invaginates the left atrium, extending to the left atrioventricular ostium (Quiring, 1933-34). The invaginated vein is called the pulmonary chamber (camera) which forms a subcavity of the left atrium. The left side of the subcavity has a free margin that directs blood into the left ventricle and separates the Camera from the general cavity of the left atrium (Annot. 22).

(22) **Valva venae pulmonalis.** (Fig. 12.2) The valve of the pulmonary vein is the left free margin of the Camera pulmonalis that seems to have a flap-valve action preventing regurgitation of blood from the left atrium into the Camera (Annot. 21).

(23) **Valva atrioventricularis sinistra.** Certain authors have called this the "tricuspid" valve of the avian heart. Although this valve possesses three cusps in some birds (two in others), the term should not be used with the bird heart in order to avoid confusion with the *right* atrioventricular valve (Valva tricuspidalis, NAV, 1983) of the mammalian heart.

Cuspis dextra. This cusp of the left A-V valve has been referred to in the literature as its "septal cusp".

(24) . **Valva aortae.** The aortic valve is located in the root of the ascending aorta, its position is marked externally by the **Bulbus aortae,** the expanded proximal part of the ascending aorta that houses the aortic valve. The valve and its parts are listed with the terms of the left ventricle instead of those of the aorta following the convention of the mammalian anatomical nomenclatures (see Annot. 19). The ostia of the coronary arteries are dealt with in **Art.** Annot. 4.

(25) **Foramina venarum minimarum.** See **Ven.** Annot. 9 for comments on these openings of the Vv. cardiacae minimae.

TERMINOLOGY

ARTERIAE

TRUNCUS PULMONALIS[2] (Fig. 12.1C)

Bulbus trunci pulmonalis
- Sinus trunci pulmonalis[1]
- Valva trunci pulmonalis (**Cor.** Annot. 19)

Bifurcatio trunci pulmonalis[2]
- Arteria pulmonalis[2]
  - R. cranialis[1]
  - R. caudomedialis[1]
  - R. caudolateralis[1]
  - R. accessorius[2]
    - Aa. interparabronchiales[3]

Lig. arteriosum[50]

AORTA (Figs. 12.6, 8)

AORTA ASCENDENS (Figs. 12.1, 8

Bulbus aortae (**Cor.** Annot. 24)
- Sinus aortae[4] (Fig. 12.8)
  - Sinus sinister[4]
  - Sinus dexter ventralis[4]
  - Sinus dexter dorsalis[4]

Valva aortae (**Cor.** Annot. 24)

Corpora para-aortica[5]

ARTERIAE CORONARIAE (Cor Fig. 12.1C)

A. coronaria sinistra[4]
- R. interatrialis
- R. atrialis dextra
- R. atrialis sinistra
- R. superficialis
  - R. interventricularis paraconalis[4]
  - Rr. conales
  - Rr. ventriculares
- R. circumflexus
  - Rr. atriales
  - Rr. ventriculares
- R. profundus
  - Rr. septales
  - Rr. ventriculares

(continued)

ARTERIAE CORONARIAE (cont.)

A. coronaria dextra[4] (Fig. 12.1C)
- R. superficialis
  - R. interventricularis subsinuosis[4]
  - Rr. ventriculares
- R. circumflexus
  - Rr. atriales
  - Rr. ventriculares
- R. profundus
  - Rr. septales
  - Rr. ventriculares

ARCUS AORTAE (Figs. 12.6, 8)

TRUNCUS BRACHIOCEPHALICUS[6] (Fig. 12.8)

ARTERIA CAROTIS COMMUNIS[7]

Sinus caroticus[7]

A. esophagotracheobronchialis[8]
- R. esophagealis
- R. trachealis
- R. syringealis
- R. bronchialis[2] (**Resp.** Annot. 70)

Aa. thyroideae[9]

A. esophagealis ascendens[10]

Truncus vertebralis (Fig. 12.6)
- A. vertebralis ascendens[11]
  - Aa. segmentales cervicales[51 65]
    - R. ventralis
    - R. dorsalis[84]
      - A. vertebromedullaris[84]
  - Anastomoses cum arteria carotis interna[11]
  - Anastomosis cum arteria occipitali
  - A. vertebralis descendens[11]
    - Aa. segmentales truncales
    - A. intercostalis dorsalis[52]
      - R. dorsalis[84]
        - A. vertebromedullaris[84]

A. comes nervi vagi[12] (Fig. 12.6)
- Aa. ingluviales[12]
- A. suprascapularis[13]
- A. esophagealis ascendens[10]
- A. transversa colli
- R. acromialis
- Rr. cutanei colli
- Rr. thymici
- A. cutanea cervicalis ascendens (**Ven.** Annot. 41b)

Glomus caroticum[14]

ARTERIA CAROTIS INTERNA[15] (Figs. 12.4, 6)

Anastomoses cum arteria vertebrali ascendenti[11]

A. occipitalis[16 12]

A. occipitalis profunda[11]

A. occipitalis superficialis

A. CAROTIS CEREBRALIS[17] (Figs. 12.4, 5)

A. sphenoidea[18]
- R. palatinus[18]
- R. sphenomaxillaris[18]

Anastomosis intercarotica[17]

(continued)

A. CAROTIS CEREBRALIS[17] (cont.)

A. hypophysialis caudalis (**Endoc.** Annot. 18)
A. ophthalmica interna[19]
A. infundibularis (**Endoc.** Annot. 19)
Ramus rostralis a. carotidis cerebralis (Fig. 12.5)
A. ventralis tecti mesencephali
A. cerebroethmoidalis
A. cerebralis rostralis
Aa. preopticae
A. ethmoidalis[18]
Anastomosis cum arteria supraorbitali
Anastomosis cum arteria ophthalmotemporali
Rr. orbitales
Rr. nasales
Rr. glandulae nasalis[18]
A. cerebralis media (Fig. 12.5)
Rr. laterales hemispherici
A. cerebralis caudalis
A. dorsalis cerebelli
Aa. dorsales tecti mesencephali
Rr. ventrales hemispherici
Rr. occipitales hemispherici
Rr. dorsales diencephali
A. choroidea ventriculi lateralis et tertii[20]
A. interhemispherica[20]
Rr. dorsales hemispherici
A. meningealis caudalis
R. pinealis
Ramus caudalis a. carotidis cerebralis
A. trigeminalis
Rr. medullares
A. interpeduncularis
A. basilaris[21] (Fig. 12.5)
A. ventralis cerebelli[22]
A. lateralis medullae oblongatae
Rete medullae oblongatae[22]
A. caudalis labyrinthi[23]
A. rostralis labyrinthi[23]
A. choroidea ventriculi quarti

ARTERIA OPHTHALMICA EXTERNA [A. STAPEDIA][24] (Fig. 12.4)

A. occipitalis[16]
A. occipitalis profunda[11]
A. occipitalis superficialis
Rete ophthalmicum[24]
A. temporalis
A. intramandibularis[25]
Rr. mentales
A. supraorbitalis
Rr. glandulae nasalis[18]
Aa. palpebrales dorsotemporales
Aa. ciliares anteriores[26]
A. infraorbitalis
Aa. palpebrales ventrales
A. ophthalmotemporalis[27](Fig. 1) (Fig. 12.4)
A. ciliaris posterior longa temporalis[26 28]
Rr. choroidei[29]
Aa. parallelae choroideae[28]
A. ciliaris posterior longa nasalis[26 28]
Rr. choroidei[29]
Aa. parallelae choroideae[28]
Circulus iridicus[28] (**Sens.** Fig. 16.2)
Circulus ciliaris[28]

(continued)

ARTERIA OPHTHALMICA EXTERNA [A. STAPEDIA][24] (cont.)

Anastomosis cum circulo iridico
Aa. ciliares posteriores breves[26]
Rr. choroidei
Aa. musculares bulbi oculi
Aa. glandulae membranae nictitantis (see **Sens.**)
A. pectinis oculi[29]
Anastomosis cum a. ethmoidali
Anastomosis cum a. ophthalmica interna

ARTERIA CAROTIS EXTERNA[30 12] (Figs. 12.4, 6)

A. cutanea cervicalis descendens (**Ven.** Annot. 41b)
A. comes nervi vagi[12]
A. occipitalis[16]
A. occipitalis profunda[11]
A. occipitalis superficialis
A. auricularis caudalis[31]
A. auricularis rostralis[31]
A. mandibularis[32]
A. esophagealis descendens
A. trachealis descendens
Aa. hyobranchiales [Aa. hyoideae]
A. laryngea[33]
Rr. pharyngeales
A. lingualis
A. lingualis propria
A. sublingualis[34]
A. submandibularis superficialis[35]
A. submandibularis profunda
A. maxillaris[38] (Fig. 12.4)
A. palatina[38]
R. palatinus lateralis
R. palatinus medialis
A. palatina mediana[38]
A. pterygopharyngealis
Rr. pharyngeales
Plexus pterygoideus[36]
R. nasalis
A. facialis (Fig. 12.4)
Rr. palpebrales ventrales
Rr. frontales
A. palpebralis dorsonasalis
R. nasalis[37]
A. pterygoidea dorsalis

ARTERIA SUBCLAVIA (Figs. 12.6, 8)

A. sternoclavicularis[39]
A. sternalis interna[40]
A. clavicularis
A. sternalis externa
A. coracoidea dorsalis[41]
A. esophagotrachealis[42]
A. thoracica interna
R. ventralis
R. dorsalis
Aa. intercostales ventrales[53]
Truncus pectoralis[43] (Fig. 12.8)
A. pectoralis cranialis
A. pectoralis media[44]
A. pectoralis caudalis
A. infrascapularis
A. cutanea thoracoabdominalis[44]

ARTERIA AXILLARIS (Figs. 12.6, 8)

A. subscapularis
A. supracoracoidea[45]
A. brachialis
  A. profunda brachii
  A. circumflexa dorsalis humeri
  A. antebrachialis dorsalis cranialis
A. bicipitalis[46]
  Rr. propatagiales
A. circumflexa ventralis humeri
A. nutricia humeri
A. collateralis radialis
A. collateralis ulnaris

ARTERIA RADIALIS[47] (Fig. 12.7)

A. recurrens radialis
A. cubitalis dorsalis
A. radialis profunda
  Aa. interosseae dorsales[48]
A. antebrachialis dorsalis caudalis
  Rr. postpatagiales
  A. postpagagialis marginalis
Rr. carpales dorsales
Rr. carpales ventrales
Rr. metacarpales dorsales
Rr. alulares
Rr. digitales dorsales
A. radialis superficialis
  Rr. propatagiales

ARTERIA ULNARIS (Fig. 12.7)

A. cutanea brachialis
A. recurrens ulnaris
A. cubitalis ventralis
A. ulnaris profunda[49]
  Rr. metacarpales ventrales
  A. postpatagialis marginalis
Rr. digitales dorsales
A. ulnaris superficialis
  A. metacarpalis interossea
  Rr. postpatagiales
  A. postpatagialis marginalis
  Rr. digitales ventrales

AORTA DESCENDENS (Figs. 12.8, 6)

Lig. arteriosum[50]
Lig. aortae[50]
Aa. segmentales truncales[51]
  Aa. intercostales dorsales[52]
Rr. dorsales
A. esophagealis[54]
A. musculorum colli

ARTERIA CELIACA [COELIACA] (see Chap. Intro.)

A. esophagealis[54]
A. proventriculus dorsalis[55]
Rr. esophageales
A. gastrica dorsalis[55]

(continued)

ARTERIA CELIACA [COELIACA] (cont.)

Ramus sinister arteriae celicae (Fig. 12.9)
  A. proventricularis ventralis
  A. gastrica sinistra[63]
  Rr. sacci[55]
  A. gastrica ventralis
  A. hepatica sinistra[56]
  A. gastroduodenalis[60]
Ramus dexter arteriae celicae (Fig. 12.9)
  Aa. splenicae [Aa. lienales][59]
  A. hepatica dextra[56]
  A. vesicae biliaris [A.v. felleae][58]
  A. ileocecalis[61]
  A. pancreaticoduodenalis[62]
  A. duodenojejunalis[60]
  A. gastrica dextra dorsalis[63]
  A. gastrica dextra ventralis[63]
  Rr. sacci[55]
Anastomosis arteriarum hepaticarum[57]
  Rr. mediani[57]

ARTERIA MESENTERICA CRANIALIS

A. duodenojejunalis
Aa. jejunales[60]
Aa. ileae[60]
A. ileocecalis[61]
A. marginalis intestini tenuis[64]
Aa. segmentales synsacrales[65 51]
  R. ventralis
  R. dorsalis
    A. vertebromedullaris[84]

ARTERIA RENALIS CRANIALIS (Fig. 12.8)

Aa. intralobulares (**Urin.** Annot. 33)
A. testicularis[66]
  Rr. epididymales
A. ovarica[66]
A. adrenalis [A. pararenalis]
Rr. ureterodeferentiales craniales (**Ven.** Annot. 57)
Rr. ureterici craniales
A. oviductalis cranialis[67 72]
  Rr. ovarii
  Aa. infundibuli
  Aa. magni

ARTERIA ILIACA EXTERNA[68] (Fig. 12.8)

A. oviductalis cranialis accessoria[67]
A. pubica[68]
  A. umbilicalis[68]
A. femoralis (Figs. 12.8, 10)
  A. cranialis coxae[70]
  A. femoralis medialis
  A. femoralis caudalis[73]
  A. circumflexa femoris[71]
  A. femoralis cranialis
  A. cutanea femoralis cranialis
Anastomosis ischiofemoralis[69]

ARTERIA ISCHIADICA (Figs. 12.8, 10)

A. renalis media (**Urin.** Annot 32)
  Aa. intralobulares (**Urin.** Annot. 33)
A. renalis caudalis (**Urin.** Annot. 32)
  Aa. intralobulares (**Urin.** Annot. 33)
  Rr. ureterodeferentiales medii
  Rr. ureterici medii
A. oviductalis media[67 72] (Fig. 12.8)
  A. magni
  Aa. isthmi
  Aa. uterinae (**Fem.** Annot. 37)
A. oviductalis marginalis ventralis[72]
A. oviductalis marginalis dorsalis[72]
A. caudalis coxae[70]
A. obturatoria
A. trochanterica
A. circumflexa femoris[71]
A. femoralis caudalis[73]
A. nutricia proximalis femoris
A. cutanea femoralis caudalis
A. suralis[74] (Fig. 12.10)
  A. suralis medialis
  A. suralis lateralis
  A. cutanea femoralis lateralis
  A. cutanea cruralis caudalis

ARTERIA POPLITEA[75] (Fig. 12.10)

A. genicularis lateralis
A. nutricia distalis femoris
A. tibialis medialis
A. genicularis medialis
A. cruralis medialis
A. tibialis caudalis
  A. fibularis [A. peronea]
    R. fibularis [peroneus] superficialis[78 77]
    R. fibularis [peroneus] profundus[78 77]
  Rete tibiotarsale[77]
A. tibialis cranialis[76] (Fig. 12.10)
  A. nutricia tibiae
  A. recurrens tibialis cranialis
  A. interossea
  Rete tibiotarsale[77]
A. epicondylaris medialis
A. epicondylaris lateralis
A. metatarsalis dorsalis communis[79]
  Aa. intermetatarsales plantares[79]
  Aa. tarsales plantares[79]
  A. metatarsalis plantaris medialis[79]
  A. metatarsalis plantaris lateralis[79]
    Arcus plantaris
    Rr. pulvinares
    Rr. digitales[79]
  A. metatarsalis dorsalis I[79]
  A. metatarsalis dorsalis II[79]
  A. metatarsalis dorsalis III[79]
    Aa. digitales[79]

PARS SYNSACRALIS AORTAE[51] (Fig. 12.11)

Aa. segmentales synsacri[51 65]
  R. ventralis
R. dorsalis
  A. vertebromedullaris[84]

ARTERIA MESENTERICA CAUDALIS (Fig. 12.8, 11)

R. cranialis
  Rr. ilei[61]
R. caudalis (Fig. 12.11)
  Rr. rectales
Rr. cloacales (**Cloaca** Annot. 22)
Rr. bursocloacales[80](**Cloaca** Annot. 22)

ARTERIA ILIACA INTERNA[81 68] (Figs. 12.8, 11)

A. pudenda[82]
  A. ventralis bulbi rectricium
  Aa. oviductales caudales[67 72]
  Aa. uterinae (**Fem.** Annot. 37)
  A. vaginalis (**Fem.** Annot. 40)
  Aa. cloacales (**Cloaca** Annot. 22)
    Rr. corporis vascularis phalli (**Cloaca**)
  A. bursocloacalis[80]
    Rr. bursales
Rr. cloacales (**Cloaca** Annot. 22)
R. ureterodeferentiales
A. lateralis caudae[83]
A. lateralis venti (Fig. 12.11)
  A. superficialis dorsalis bulbi rectricium
  A. cutanea dorsolateralis caudae[83]
  A. cutanea abdominalis[44]

ARTERIA MEDIANA CAUDAE (Fig. 12.11)

Aa. segmentales caudales[51]
  R. ventralis
  R. dorsalis
    A. cutanea dorsomedialis caudae[83]
A. profunda dorsalis bulbi [rectricium][83]
A. glandulae uropygialis[83]
A. vertebromedullaris[84]

ARTERIAE MEDULLAE SPINALIS

Aa. segmentales (**Ven.** Annot. 60)
  R. ventralis
  R. dorsalis
    A. vertebromedullaris[84]
      A. radicularis ventralis
      A. spinalis ventralis[85]
      Rr. marginales[86]
Rr. sulci
Rr. sulcocommissurales
A. radicularis dorsalis
Aa. spinales dorsales
Aa. dorsolaterales[85]
Rr. marginales[86]
Rr. fissurae

ANNOTATIONS

(1) **Sinus trunci pulmonalis.** Pulmonary sinuses are less well developed and thinner-walled than the aortic sinuses (see Annot. 4). Names of sinuses are based on their positions *in situ*.

(2) **Truncus pulmonalis; Bifurcatio trunci pulmonalis.** The pulmonary trunk bifurcates into right and left pulmonary arteries; the intrapulmonary branching patterns of the paired pulmonary arteries are similar. Rami of **A. pulmonalis** closely correspond to tributaries of V. pulmonalis; neither arteries nor veins correspond in their intrapulmonary branching pattern to that of the bronchial tree. Rr. caudomedialis and caudolateralis of the artery are generally dorsal to the two caudal venous radices. R. cranialis of the artery is lateral to the cranial radix of V. pulmonalis; this is based on the observations of Radu and Radu (1971) and Abdalla and King (1975) in *Gallus, Meleagris, Anser,* and in *Columba.* See **Resp.**

R. accessorius. In *Gallus* the medial aspect of each undivided pulmonary artery releases a distinct R. accessorius that supplies lung tissue cranial and medial to the hilus of the lung.

(3) **Aa. interparabronchiales.** Interparabronchial arteries are branches of each of the main rami of A. pulmonalis. See **Resp.** Vasa sanguinea intrapulmonalia for terminology of the microvasculature of the lung. For details of intrapulmonary architecture see Abdalla and King (1975). See **Resp.** Annot. 70.

(4) **Aorta.** The avian aorta is derived from the embryonic right fourth aortic arch. See Annot. 50 for comment on the vestigial remnant of the left fourth aortic arch.

Sinus aortae. Each of the three aortic sinuses is an evaginated, bulging segment of the bulb of the aorta at the root of the ascending aorta (**Cor.** Annot. 24). Each of the sinuses is occupied by a cusp of the aortic valve during ejection of blood (systole). Names of the sinuses are based on their *in situ* positions. Two of the sinuses, Sinus sinister and Sinus dexter ventralis, are "coronary"; i.e., they contain ostia of the coronary arteries.

Aa. coronariae. Each coronary artery commonly branches into superficial and deep rami near its origin (Figs. 12.1, 8). Differing from the mammalian condition, most of the blood supply to the avian heart is distributed to the myocardium from deep rather than surface arteries (see Baumel, 1975c, for details of distribution in *Gallus*). The superficial ramus of A. coronaria sinistra or other aberrant coronary artery may arise from the right dorsal sinus. See Petren (1926) and Lindsay and Smith (1965) for coronary aa. of *Gallus;* Bezuidenhout (1984) Ostrich *Struthio;* and Murakami, et al. (1986) for coronary aa. of representatives of nine different avian orders.

R. interventricularis paraconalis/subsinualis (see Fig. 12.1A, B and **Cor.** Annot. 2).

(5) **Corpora para-aortica.** Synonymy: Glomera aortica; Glomera pulmonalia (NAA, 1979). Intramural baroreceptors have been identified physiologically (Jones, 1969; West, et al., 1981: 262) and ultrastructurally (Taha, et al. (1983) in the wall of the avian aortic arch and pulmonary trunk. Groups of granular cells lie in the wall of these great arteries and in discrete encapsulated aggregations between the vascular trunks. The cells have innervation and secretory characteristics like the cells of the carotid body, therefore are probably chemoreceptors, thus constituting para-aortic bodies (Taha, et al. (1986).

(6) **Truncus brachiocephalicus.** Both right and left brachiocephalic trunks arise from the left side of the Aorta ascendens; each trunk divides into the subclavian and common carotid arteries. See Fig. 12.8.

(7) **A. carotis communis.** (Fig. 12.6) The common carotid artery is a short vessel that breaks up in the root of the neck into A. carotis interna, Truncus vertebralis, and A. comes n. vagi (Annot. 12). Variation of the arteries in the heart region in most orders of birds is thoroughly treated in the series of papers of Glenny cited in the bibliography of his monograph (Glenny, 1955).

Sinus caroticus. In mammals the baroreceptor zone of the carotid sinus is well known. As pointed out by earlier workers, a homologue of the mammalian carotid sinus ought to be located in the region of the avian common carotid artery; in fact, its presence at the level of the esophagotracheobronchial artery has been confirmed ultrastructurally in *Gallus* by Abdel-Magied, et al. (1982).

(8) **A. esophagotracheobronchialis.** (Fig. 12.6) Synonymy: A. syringotracheobronchialis (Bhaduri, et al., 1957); ductus shawi (Glenny, 1955). An artery or complex of arteries usually arising from: (1) the medial side of the common carotid artery (*Gavia, Larus, Phoenicopterus, Gallus, Branta, Trogon, Alcedo*); (2) the vertebral trunk (*Perisoreus*); or (3) the common carotid of one side and the contralateral vertebral trunk (*Spheniscus, Corvus*). The general distribution of A. esophagotracheobronchialis is to the caudal trachea and its bifurcation (syrinx), main bronchi (see **Resp.** Annot. 70), pericardium, Septum horizontale dorsal to the heart, and esophagus from the origin of the artery caudally to the esophago-proventricular junction. In some species the artery supplies the thyroid, parathyroid and ultimobranchial glands (see **Endoc.**) and the carotid bodies (see Annot. 42). Consult West, et al. (1981) and Hodges (1981) for further information.

(9) **Aa. thyroideae.** The arterial supply of the thyroid gland varies both in number of arteries to the gland and the site of origin of the thyroid arteries. From a review of the numerous papers of Glenny (cited in Glenny, 1955) in which he systematically surveyed the main arteries in the region of the heart, it appears that the majority of species have but a single artery to each gland (e.g., *Rhea, Spheniscus, Gavia, Podiceps, Cygnus, Fulica, Apus, Trogon,* and *Corvus*).

Two thyroid arteries to the gland are found in several columbid species, several galliform species, *Larus,* and *Phoenicopterus;* three thyroid arteries supply the thyroid gland of ducks (Anatidae) according to Assenmacher (1953). Usually the origin of single thyroid arteries and the caudal thyroid artery of the dual-artery condition is directly from the common carotid artery. Other sites of origin are: A. vertebralis, proximal part of A. esophagotracheobronchialis, A. comes n. vagi, terminal part of brachiocephalic trunk, or subclavian artery. Cranial thyroid arteries arise from A. comes n. vagi, common carotid, or ascending esophageal artery. Aa. thyroideae also supply the carotid body, parathyroid and ultimobranchial glands, and the distal ganglion of the vagus nerve (see Abdel-Magied and King, 1978; and Hodges, 1981).

(10) **A. esophagealis ascendens.** (Fig. 12.6) In certain species of unicarotid birds (Annot. 15), the artery that corresponds to the single persistent carotid of the other side is a superficial artery, modified to serve as the A. esophagealis ascendens in *Rhea, Apteryx, Casuarius,* some coraciiforms, *Trogon,* piciforms, and passeriforms (Glenny, 1955).

In *Phoenicopterus,* an unicarotid form having the single internal carotid fed by both common carotids, the A. esoph. asc. springs from the proximal part of A. comes

n. vagi (Bhaduri, et al., 1965). In bicarotid forms the ascending esophageal artery arises from the common carotids (*Grus*), or from the vertebral trunk (*Alcedo*) (Glenny, 1955), or from A. comes n. vagi.

(11) **Truncus vertebralis.** (Fig. 12.6) Synonymy: A. cervicovertebralis (Glenny, 1955). This is a short branch of A. carotis communis arising in the root of the neck that abruptly divides into the **Aa. vertebrales ascendens et descendens.** These branches of the Truncus vertebralis travel in the vertebrarterial canal (see **Osteo.** Annot. 134b), and supply the vertebral column, axial muscles, and the cervical spinal cord. The ascending vertebral artery anastomoses with the cervical parts of A. carotis interna and A. occipitalis profunda (Baumel, 1964). The descending vertebral artery anastomoses with the dorsal intercostal branches of the aortic system (Annot. 52).

(12) **A. comes nervi vagi** (Fig. 12.6). Synonymy: A. cervicalis superficialis (Glenny, 1955). This companion artery of the vagus nerve artery is usually a direct branch of A. carotis communis arising in the root of the neck, or may share a common stem with the vertebral trunk. A. comes n. vagi is the adult vessel derived from the foetal A. carotis externa; the definitive adult external carotid is a branch of the internal carotid arising near the base of the skull.

At its origin from the terminal part of the common carotid, the A. comes n. vagi courses craniad in a bundle with N. vagus and V. jugularis, and anastomoses with a branch(es) of the external carotid or occipital arteries in the upper neck.

Aa. ingluviales. These branches of A. comes n. vagi supply the region of the esophagus that is expanded to form the crop (see **Digest.**).

(13) **A. suprascapularis** (Fig. 12.6). Synonymy: A. cephalica humeri (Neugebauer, 1845; Bodrossy, 1938). This branch of the A. comes n. vagi supplies muscles and integument of the dorsal shoulder region and proximal brachium.

(14) **Glomus caroticum.** Synonymy: carotid body. Hodges (1981: 167) and West, et al. (1981: 262) reviewed the literature on the structure and function of the Glomus caroticum, a chemoreceptor sensitive to blood gas concentrations. De Kock (1958) surveyed the location of the carotid body and distribution of disseminated carotid body tissue in examples of passeriform, charadriiform, anseriform, and podicepediform birds. Some of the disseminated tissues were probably Corpora para-aortica (Abdel-Magied and King, 1978)(Annot. 5), but aberrant carotid body tissue definitely does occur in *Gallus* (Abdel-Magied and King, 1984). The carotid body proper lies between the terminal division of the Truncus brachiocephalicus and the thyroid gland, and is closely related to the parathyroid and ultimobranchial glands and vagus nerve, and supplied by local arteries. Its topographical anatomy, innervation, and blood supply in *Gallus* were established by Abdel-Magied and King (1978).

(15) **A. carotis interna.** Most birds are bicarotid; the two internal carotids ascend the neck side-by-side in the middle segment of the neck (Fig. 12.6) where they pass through an osseomuscular canal, **Canalis caroticus cervicalis** (new term) on the ventral aspect of the cervical vertebral column (**Osteo.** Annot. 121a, b). In most unicarotid forms the left carotid persists as the principal artery to the head. In certain unicarotid forms the single vessel represents the fused or conjugate right and left carotids; in some of these birds the basal portion of both carotids remains, while in others only the basal part of one of the conjugate vessels is present (Glenny, 1955). No matter how it be formed, the single carotid divides into right and left internal carotids near the base of the skull. In some unicarotid birds the fetal carotid that does not persist as a definitive carotid simply regresses, becoming a ligamentous vestige or

a small regional artery; in others it becomes modified into a superficial vessel of the neck. See Annot. 17 and 10.

(16) **A. occipitalis.** Near the base of the skull A. occipitalis generally rises from the external carotid (e.g., *Gallus, Columba, Larus*) or from the internal carotid (*Sturnus*. Cralley, 1965). Its deep branch communicates with A. vertebralis.

R. occipitalis of **A. ophthalmica** externa arises in the tympanic region, takes an intraosseous course caudally and emerges from an opening in the occipital bone near the nuchal crest. This occipital ramus is of widespread occurrence in fossil and recent birds (Elzanowski and Galton, 1991, J. vert. Paleont. 11 (1): 90-107). See Figs. 1, 2 of Midtgård (1984a).

(17) **A. carotis cerebralis.** This is the prolongation of the A. carotis interna past the origin of A. ophthalmica externa; in other words, it consists of the intrasphenoid segment of the internal carotid in its canal in the base of the cranium plus its intracranial segment (Stresemann, 1927-34; Kitoh, 1962).

Anastomosis intercarotica. This is the communication between the intracranial segments of the right and left cerebral carotids by means of a transverse connecting vessel or a side-to-side anastomosis (Fig. 12.4) (Wingstrand, 1951; Baumel and Gerchman, (1968). Functionally, this anastomosis is the equivalent of the mammalian Circulus arteriosus cerebri (Circle of Willis). The earliest mention of the intercarotid anastomosis in the literature is that of Barkow (1829) who described it in *Podiceps subcristatus, Fulica atra,* and *Ciconia alba.*

The intercarotid anastomosis gives off the principal arteries to the hypophysis (see **Endoc.** Annot. 17-19).

(18) **A. sphenoidea** (Fig. 12.4). This artery springs from the intrasphenoid part of the cerebral carotid artery found in the Canalis caroticus cranialis (see **Osteo.** Annot. 99) of the base of the skull; it leaves the canal via Foramen orbitale at the side of Rostrum parasphenoidale. In some forms the sphenoid artery is represented by R. palatinus and R. sphenomaxillaris that arise from the internal carotid as independent arteries. **Rr. glandulae nasales.** The arterial supply to the nasal (salt) gland is usually derived from A. supraorbitalis. In the duck, *Anas platyrhynchos*, the rami are mainly derived from the A. ethmoidalis as the latter course in the roof of the orbit (Hossler and Olson, 1984).

(19) **A. ophthalmica interna.** Arises from the segment of A. carotis cerebralis that lies at the side of the hypophysis within the Sella turcica, and passes into the orbit; this artery does not persist as a substantial vessel in the adults of some avian taxa (Wingstrand, 1951).

(20) **A. cerebralis caudalis** (Fig. 12.5). Synonymy: A. cerebri posterior.

A. choroidea ventriculi lateralis et tertii. Synonymy: A. choroidea anterior (Ariens-Kappers, 1933).

A. interhemispherica (Baumel, 1967). Synonymy: A. cerebri posterior communis. A. interhemispherica is usually an unpaired asymmetrical artery that arises from either the left or right A. cerebralis caudalis, and is distributed to both cerebral hemispheres (Baumel, 1967).

(21) **A. basilaris** (Fig. 12.5). A. basilaris is usually the prolongation of the R. caudalis of either the left or right A. carotis cerebralis; its counterpart persists as a vestigial local vessel. In a few taxa both Rr. caudales anastomose to form A. basilaris (e.g., galliforms, falconiforms, and strigiforms (Baumel and Gerchman, 1968; Kitoh, 1962). The smaller terminal branches of A. basilaris anastomose with branches of A. occipitalis profunda, A. spinalis ventralis, and A. vertebralis ascendens (T. Nishida, pers. comm.) (see Annot. 11).

(22) **A. ventralis cerebelli.** (Fig. 12.5) Represented on each side by two separate ventral cerebellar arteries in *Gallus* (Kitoh, 1962). In the passerine *Zonotrichia* the single stem of the ventral cerebellar artery divides into rostral and caudal branches (Vitums, et al., 1965). See also Baumel (1967) for a discussion of the relative territories of distribution of dorsal and ventral cerebellar arteries in different species of birds.

Rete medullae oblongatae. Synonymy: Rete mirabile medullae (Freedman and Kriebel, 1990). In the chicken this is a dense plexus of parallel arterioles in the subarachnoid space at the lateral surface of the medulla oblongata near the fossa for the combined ganglia of the IX and X cranial nerves. The rete is fed by the lateral artery of the medulla, a branch of the ventral cerebellar artery (Freedman and Kreibel, 1990).

(23) **Aa. labyrinthi.** Rostral and caudal labyrinthine arteries (Schmidt, 1964) spring directly from A. cerebellaris ventralis or A. lateralis medullae oblongatae (*Columba*), and enter the inner ear region via foramina that conduct branches of N. vestibulocochlearis (**Osteo.** Fossa acustica interna).

(24) **A. ophthalmica externa [A. stapedia].** (Fig. 12.4) Homologue of A. stapedia of other vertebrates (Hafferl, 1933; Goodrich, 1930).

Rete ophthalmicum. Synonymy: Rete mirabile ophthalmicum or temporale. For sake of brevity, it has been suggested by Midtgård (pers. comm.) that "Rete ophthalmicum" only be used. The rete actually consists of two components: arterial and venous retia enmeshed with one another. The numerous small arteries that form the arterial rete arise from the A. ophth. ext itself or from its branches. See West, et al. (1981) for diagrams of the ophthalmic rete in representatives of five different avian orders. It has been established that the Rete ophthalmicum is a countercurrent heat exchanger concerned with cooling of the arterial blood to the brain and the eye, and with reducing heat loss from the relatively large eyes of birds (Midtgård, 1984b). See Annot. 77 for more on retia.

(25) **A. intramandibularis.** Term provided as a substitute for A. alveolaris inferior, a mammalian term inappropriate in modern birds, all of which lack teeth. See **Osteo.** Annot. 82 regarding teeth in fossil birds).

(26) **Aa. ciliares anteriores et posteriores.** Following usage in the human *Nomina Anatomica* (IANC, 1989) and *Nomina Anatomica Veterinaria* (ICVGAN, 1983) the poles of the Bulbus oculi are arbitrarily defined as anterior and posterior even though in most birds the Axis bulbi is directed rostrolaterally rather than rostrally. Aa. ciliares are named according to the region of the eye that they enter. Other terms of direction and position with respect to the eye and orbit are: dorsal/ventral and nasal/temporal (see **Sens.** Intro.).

Aa. ciliares posteriores breves are direct branches of the A. ophthalmotemporalis; they enter the eyeball near the optic nerve. Aa. ciliares anteriores are branches of the palpebral arteries. In *Columba* (pers. obs.) and in *Anas platyrhynchos* (Hossler and Olson, 1984) the A. ciliaris posterior longa temporalis arises from the A. ophthalmotemporalis near the Rete ophthalmicum; the prolongation of A. ophthalmotemporalis on the medial aspect of the eyeball becomes a distinct **A. ciliaris posterior longa nasalis** in both forms.

Aa. parallelae choroideae. This is the term of Hossler and Olson (1984). These arteries are the multiple closely packed branches of the long posterior ciliary arteries that course parallel to one another and to similar parallel radices of the dorsal and ventral ciliary veins in the vascular tunic of the eye.

(27) **A. ophthalmotemporalis.** (Fig. 12.4) Following Wingstrand and Munk (1965) this artery is regarded as the main continuation of A. ophthalmica externa, and is the principal artery of supply to the Bulbus oculi. In the caudomedial region of the orbit around the optic nerve, a rich, plexiform system of anastomoses occurs between branches of A. ophth. ext., A. ophth. int., and A. ethmoidalis. (Fig. 12.5). See Annot. 26.

(28) **Circulus iridicus** (Oehme, 1969a). Formed mainly by A. ciliaris posterior longa temporalis that bifurcates on reaching the peripheral margin of the iris; the Circulus also receives branches of A. infraorbitalis and A. ethmoidalis (Hossler and Olson, 1984).

Circulus ciliaris (Oehme, 1969a). The ciliary arterial circle is peripheral to the iridial circle. In *Anas* (Hossler and Olson, 1984) the ciliary circle receives its blood primarily from ciliary branches of the infraorbital and ethmoidal arteries.

(29) **A. pectinis oculi.** Birds do not possess an artery comparable to the A. centralis retinae of mammals. The Pecten oculi is a vascular body that projects from the interior of the floor of the eye into the chamber of the vitreous humor (see **Sens.**). According to Wingstrand and Munk (1965), the Pecten supplies nutrients to the inner retinal layers; the Rr. choroidei of the Aa. ciliares longae et breves supply the capillary bed of the Lamina choriocapillaris that nourishes the external retinal layers. See Annot. 26.

(30) **A. carotis externa.** The external carotid is a branch of the internal carotid arising near the rear of the mandible. The pattern of branching of the external carotid demonstrates interspecific variation; the listed branches are consistently present in one configuration or another in all examples of taxa of birds that have been studied with any degree of completeness (see Fig. 12.4 and Annot. 12).

(31) **Aa. auriculares.** The origin of these arteries in the region of the external ear is variable; in different forms they arise from A. carotis externa, A. maxillaris, or A. mandibularis.

(32) **A. mandibularis.** (Fig. 12.4) Synonymy: A. lingualis; A. facialis externa.

(33) **A. laryngea.** Synonymy: A. laryngea propria. In the literature this artery has been qualified as "superior" to distinguish it from the artery to the syrinx, erroneously referred to as the "inferior larynx". The term "A. laryngea" has been used for the common stem of A. esophagealis, A. trachealis descendens, Rr. pharyngeales, and the laryngeal artery itself.

(34) **A. sublingualis.** (Fig. 12.4) A branch of A. lingualis in certain birds (see Annot. 32).

(35) **A. submandibularis superficialis.** (Fig. 12.4) This artery is especially strong in *Gallus* which possess highly vascularized skin appendages (such as wattles) in the intermandibular region.

(36) **Plexus pterygoideus.** This plexus is located on both ventral and dorsal aspects of the pterygoid bone and its attached muscles in the caudal part of the floor of the orbit. The plexus is formed by anastomoses among rami of A. sphenoidea, A. maxillaris, and A. palatina.

(37) **R. nasalis.** An extensive system of anastomoses connect nasal rami of A ethmoidalis, A. maxillaris, and A. palatina.

(38) **A. palatina.** (Fig. 12.4) This is the rostral prolongation of **A. maxillaris.** Right and left **Rr. palatini mediales** flank the nasal choana, and are confluent rostral to the choana, forming the unpaired **A. palatina mediana.** See **Ven.** Annot. 13, 14.

(39) **A. sternoclavicularis.** Synonymy: A. coracoidea (Glenny, 1951). See Fig. 12.6.

(40) **A. sternalis interna.** Often this artery is unpaired, arising from the A. sternoclavicularis of one side; it courses on the visceral aspect of the sternum near its median line.

(41) **A. coracoidea dorsalis.** Synonymy: A. acromialis. The A. coracoidea dorsalis is a branch of A. sternoclavicularis that parallels the dorsal (inner) aspect of Os coracoideum, and extends to the caudal part of the shoulder joint.

(42) **A. esophagotrachealis.** In galliform birds this artery springs directly from A. subclavia, sending branches craniad that supplement esophageal and tracheal branches from A. esophagotracheobronchialis (Glenny, 1951). In the turkey, *Meleagris*, A. esophagotrachealis gives off Rr. pericardii. See Annot. 8.

(43) **Truncus pectoralis.** (Fig. 12.6) Synonymy: A. thoracica externa. Both the *Nomina Anatomica* (IANC, 1983) and the *Nomina Anatomica Veterinaria* (ICVGAN, 1983) use "pectoral" for nerves and vessels (Pectus, L. breast). Usually bifurcates into cranial and caudal branches; most of its distribution is the pectoralis and supracoracoideus muscles (see Annot. 44 for other branches).

(44) **A. pectoralis media.** Present in some forms (e.g., *Columba*); absent in others (e.g., *Gallus*).

A. cutanea thoracoabdominalis. Synonymy: A. abdominopectoralis (Neugebauer, 1845). In *Gallus* this artery replaces A. pectoralis media; it supplies the skin of the caudal breast region and adjacent abdomen, and is the principal artery to the incubation (brood) patch. **A. cutanea abdominalis** from A. lateralis caudae also contributes to the supply of the incubation patch. See **Ven.** Annot. 49, 65.

(45) **A. supracoracoidea.** In some forms this artery shares a common stem with A. subscapularis. The A. supracoracoidea (and vein) accompanies N. supracoracoideus, both piercing the Membrana sternocoracoclavicularis (**Arthr.**) to enter M. supracoracoideus.

(46) **A. bicipitalis.** Accompanies N. bicipitalis into the M. biceps brachii, from there continuing into the Propatagium (see **Integ.**).

(47) **A. radialis.** For the most part this artery supplies structures in the antebrachium; it has little or no distribution in the wrist and hand (see Fig. 12.7).

(48) **Aa. interosseae dorsales** (Fig. 12.7). These arteries pass dorsad through the radio-ulnar interosseous space, and supply the extensor muscles and dorsal integument of the antebrachium.

(49) **A. ulnaris profunda.** (Fig. 12.7) This is the companion artery of the V. ulnaris profunda, a consistently prominent, subcutaneous vein on the ventral surface of the elbow region, commonly used for venipuncture. The deep ulnar artery is substantial in some birds, but is a minor artery in *Gallus* and *Columba.*

(50) **Lig. aortae.** (Fig. 12.6) The aortic end of this vestige of the foetal left Radix aortae (left dorsal aorta) is readily found and often partly patent in adult birds. Its aortic attachment is located just cranial to the origin of A. celiaca from the aorta.

Lig. arteriosum. Synonymy: Lig. botalli. This is the vestige of the right foetal ductus arteriosus that shunts blood from the pulmonary artery to the aorta.

(51) **Pars synsacralis aortae.** This is the part of the aorta generally between the origins of the external and internal iliac arteries, approximating the extent of the Synsacrum.

Aa. segmentales. Synonymy: Aa. intersegmentales. These paired somatic arteries for purposes of convenience are called "segmental". Actually they are intersegmental in their embryonic placement between adjacent somites. The segmentals occur over the entire length of the vertebral column, and are designated regionally: Aa. segmentales cervicales/truncales/synsacrales and caudales. The parent arteries of the segmentals are Aa. vertebrales ascendens et descendens, Aorta descendens, and A. mediana caudae (see Annot. 65).

(52) **A. intercostalis dorsalis.** The dorsal intercostal arteries are derived from the Rr. ventrales of the segmental arteries (see Annot. 53). Segmental branches of A. vertebralis descendens give off the dorsal intercostal arteries to the cranialmost intercostal spaces; farther caudally the dorsal intercostals are offshoots of segmental branches of the Aorta.

(53) **A. intercostalis ventralis.** These branches of A. thoracica interna supply the lower (sternal) parts of the intercostal spaces.

(54) **A. esophagealis.** (Fig. 12.9) This artery is a branch of A. celiaca (*Gallus* and *Columba*), a direct branch of the aorta (*Buteo*), or a branch of A. proventricularis dorsalis (*Larus, Pteroglossus*). In *Coturnix* esophageal arteries arise from both the aorta and the celiac artery. The A. esophagealis supplies the caudal part of the esophagus, sharing this role with Rr. esophageales of A. esophagotracheobronchialis and the dorsal proventricular artery.

(55) **A. gastrica dorsalis.** The dorsal gastric artery is the prolongation of **A. proventricularis dorsalis** onto the Ventriculus (muscular stomach). (Fig. 12.9)

Rr. sacci. In different species the arterial supply to the Sacci cranialis et caudalis of the Ventriculus is variably derived from the several gastric arteries.

(56) **Aa. hepaticae.** The left lobe of the liver often receives multiple left hepatic arteries from different branches of the left ramus of A. celiaca; more often the right hepatic artery tends to be a single branch of the right ramus of the A. celiaca (Malinovský, 1965; Malinovský, et al., 1973; and Malinovský and Visnanska, 1975). The hepatic arteries enter the Porta hepatis in company with the hepatic portal veins (**Ven.** Annot. 75, 76, 80). See Pavaux and Jolly (1968) and Miyaki (1978) for descriptions of the intrahepatic vessels of birds; and **Digest.** Hepar.

(57) **Anastomosis arteriarum hepaticarum.** Synonymy: R. communicans (Miyaki, 1973). This is the intrahepatic anastomosis that connects the right and left hepatic arteries. It runs along with the left ramus of the right hepatic portal vein (*Columba* and *Gallus*, Miyaki, 1973). **Rr. mediani** are branches of the Anastomosis that supply the dorsal interlobar liver substance.

(58) **A. vesicae biliaris [A. cystica].** (Fig. 12.9) Synonymy: A. vesicae felleae. The latest editions of the human *Nomina Anatomica* (IANC, 1989) and the *Nomina Histologica* (IANC, 1989) adopt the term Vesica biliaris for the gall bladder; the *Nomina Anatomica Veterinaria* (ICVGAN, 1983) retains Vesica fellea. The NA and the NAV continue to use A. cystica for the artery to the gall bladder, here listed as as a secondary, alternative name. The gall bladder is present in most orders of birds (**Digest.** Annot. 107, 108; its artery is usually a branch of the right hepatic artery.

(59) **Aa. splenicae.** (Fig. 12.9) Synonymy: Aa. lienales (see **Cardvas.** Intro.). The splenic arteries usually originate from the right ramus of A. coeliaca, occasionally from the undivided trunk of A. coeliaca (e.g., *Sturnus*, Cralley, 1965). For variability of Aa. splenicae see Malinovský (1965) (*Buteo*); Malinovský, et al., (1973) (*Anas*); Malinovský and Visnanska (1975) (*Anser*); Fukuta, et al. (1969a) (*Gallus*), who also describe accessory splenic arteries.

(60) **Aa. duodenales, jejunales, ileae.** The duodenum is the only differentiated part of the avian small intestine; "jejunal" and "ileal" in birds are arbitrary terms used in a regional sense only. The avian jejunum and ileum do not possess distinct morphological characteristics as in mammals; they correspond to the intermediate and terminal segments of the mammalian small intestine. The use of these terms facilitates the naming of vessels for these parts of the gut. See **Digest.** Annot. 76).

(61) **Aa. ileae; Aa. ileocecales.** Ileal branches of the right ramus of A. celiaca rather than ileocecal branches of this artery are present in species of birds that lack long caeca paralleling the terminal ileum (see **Digest.**). The ileum is also vascularized by branches of both the cranial and caudal mesenteric arteries.

A. ileocecalis. Both. A. celiaca and A. mesenterica cranialis send ileal branches to the suproduodenal loop of the ileum. Anastomoses between the cranial and caudal mesenteric arterial systems are found in the ileorectal junctional region where the roots of the intestinal cecae are located. See Fig. 12.11.

(62) **A. pancreaticoduodenalis.** (Fig. 12.9) This artery is usually the principal continuation of the right ramus of A. celiaca. Some species of birds possess long, parallel left and right Aa. pancreaticoduodenales. Rr. pancreatici are collaterals of rami that pass to the duodenum.

(63) **Aa. gastricae.** (Fig. 12.9) Several gastric arteries supply the muscular stomach (see **Intro.**). The arterial supply to the thick muscular body as well as to the thin Sacci cranialis et caudalis and the pyloric region are served in a variable fashion in different birds by these several gastric arteries and branches of the gastroduodenal artery. Nishida, et al. (1969) offered the generality (based on *Gallus*) that the main gastric arteries to the muscular stomach perforate the left and right tendinous surfaces, whereas the venous radicles from the muscular stomach emanate from the annular (marginal) surfaces. See **Cardvas.** Intro.

(64) **A. marginalis intestini tenuis.** This prominent, irregular "marginal artery" of the small intestine consists of a chain of anastomosing arteries that extends along the mesenteric border of the small intestine from the duodenal ansa (loop) to the supraduodenal ansa. The marginal artery is fed proximally from branches of the celiac system and distally from the system of the cranial mesenteric artery.

(65) **Aa. segmentales synsacrales.** (Fig. 12.8) A variable number of paired somatic branches of the aorta and its caudal extension arise from the level of the root of A. mesenterica cranialis to the caudal end of the synsacrum. The lumbar, sacral, and caudal vertebral elements that coalesce to make up the synsacrum are not clearly defined (Boas, 1929); therefore, the more general term, synsacral segmental arteries, seems preferable to attempting to apply more specific regional terms. See Annot. 51; **Osteo.** Annot. 141; and **PNS** Annot. 38.

(66) **A. ovarica; A. testicularis.** (Fig. 12.8) The ovarian artery occurs on the left side only in most avian species (see **Fem.** Annot. 19). Accessory ovarian arteries and testicular arteries (**Masc.** Annot. 5) may stem directly from the aorta or other adjacent arteries (Nishida, 1964). The ovarian vessels undergo enormous hypertrophy during egg-laying (**Fem.** Annot. 19; **Masc.** Annot. 5).

(67) **Aa. oviductales.** (Fig. 12.8) Oviductal arteries occur on the left side only, and, like the ovarian vessels, hypertrophy during egg-laying. As with most elongate viscera the oviduct acquires its blood supply from several arteries along its length. Longitudinal anastomoses occur between branches of these arteries near, or on, the oviduct similar to anastomoses along the intestine. See Annot. 72 and **Fem.** Annot. 35-42, 45.

The origin of the oviductal arteries varies between the different taxa that have been studied; individual variation within the same species is also exhibited by these arteries. In general **A. oviductalis cranialis** (**Fem.** Annot. 34) springs from the left cranial renal artery, directly from the aorta, or from A. iliaca externa. **A. oviductalis media** (**Fem.** Annot. 36) arises from the left A. ischiadica or its branch, A. renalis media. **Aa. oviductales caudales** spring from the left A. iliaca interna and A. pudenda. One of the major oviductal arteries may be absent, being replaced by branches from adjacent oviductal arteries in the series.

(68) **A. iliaca externa.** (Fig. 12.8) On leaving the pelvis and entering the thigh the name of this artery changes to A. femoralis. A common iliac artery is not present in birds; A. iliaca interna et A.i. externa spring independently from the aorta (Annot. 81).

A. pubica (Baumel, 1975c). Synonymy: A. epigastrica (Neugebauer, 1845); A. pelvica interna (Gadow and Selenka, 1891); A. umbilicalis (Hafferl, 1933; Nishida, 1963). The term, A. pubica, has topographic significance; i.e., the artery arises from the ext. iliac. a., courses with its companion vein and nerve along the ventral border of the pubis, sending rami into the ventral abdominal muscles and peritoneum. See Fig. 12.10 and Midtgård (1982).

A. umbilicalis. The proper umbilical artery branches off the A. pubica, and courses in the extraperitoneal fat of the ventral abdominal wall to the umbilical scar. See **Ven.** Annot. 74).

(69) **A. femoralis.** (Fig. 12.10) (Synonym: A. cruralis); **A. ischiadica.** (Synonym: A. sciatica). The ischiadic artery constitutes the main supply to the pelvic limb in most birds; this artery is known to be reduced only in the penguins, turacos (*Musophaga, Gallirex, Tauroco*) and in members of the passerine families Pipridae and Cotingidae. In these birds the limb is supplied instead by the femoral artery, the blood being diverted from the femoral to the ischiadic/popliteal artery by the highly developed A. femoralis medialis and the Anastomosis ischiofemoralis (Midtgård, 1982).

Anastomosis ischiofemoralis. Synonomy: Anastomosis arteriosa ischiofemoralis (Midtgård, 1982). The anastomotic segment connecting the femoral artery with the ischiadic artery (see above) represents the arterial counterpart of the similar venous anastomosis (Midtgård, 1982). See **Ven.** Annot. 66; Fig. 12.18.

(70) **A. cranialis coxae; A. caudalis coxae** (Baumel, 1975c). These names replace "Aa. gluteae cranialis et caudalis"; the coxal arteries supply muscles and integument over the pre- and postacetabular parts of the ilium. The adjective "gluteal" (Gr.) refers to the buttock. The postacetabular ilium is not comparable at all to the mammalian gluteal region; no gluteal region is described for birds, only a "coxal" region (Coxa, L. hip). Contemporary avian myologists do not use "gluteal" for muscles of the hip region. See Fig. 12.10; and **Myol.** Annot. 104.

(71) **A. circumflexa femoris.** This artery is a transverse branch of the femoral **or** ischiadic artery that "bends around" the proximal part of the femur as in mammals. Midtgård (1982) has studied the variable origin of this artery in different birds.

This term has been used erroneously for the longitudinal, spiral continuation of A. femoralis toward the knee within M. femorotibialis (Grzimek, 1963; Westpfahl, 1961), and also for a cranial branch of the proximal part of the femoral artery (Cralley, 1965).

(72) **Aa. oviductales marginales.** The ventral and dorsal marginal arteries of the oviduct are channels produced by anastomoses between asc- and descending rami of major branches of the three regional arteries of the oviduct. The longitudinally oriented marginal arteries parallel the oviduct and are located within the ventral and dorsal ligaments of the oviduct, generally accompanied by satellite veins. See **Fem.** Annot 34.

(73) **A. femoralis caudalis.** Synonymy: A. profunda femoris (Westfahl, 1961; Nishida, 1963); A. fem. proximocaudalis (NAA, 1979). This is a substitute name for A. prof. fem.; the latter term has been avoided to do away with comparison with the mammalian A. prof. fem., a branch of the femoral artery which courses longitudinally in the limb. Midtgård (1982) found only single caudal femoral arteries in his series, commonly arising from A. ischiadica; in most chararadriiforms and passeriforms, plus *Picus, Falco,* and *Fulica* the caudal femoral a. originates from A. femoralis medialis of the femoral artery system.

(74) **A. suralis** (Barkow, 1829). The use of the term "sural" (Sura, L. calf of the leg) for the nerves and vessels of the upper crus simplifies the terminology of the flexor compartment by limiting the number of terms using "tibialis" in this region. Branches of the sural artery and vein accompany the sural rami of N. tibialis to muscles of the distal thigh and proximal calf and the overlying integument (Midtgård, 1982). See Fig. 12.10.

(75) **A. poplitea.** (Fig. 12.10) This vessel is the continuation of A. ischiadica in the popliteal region behind the knee; its extent is from the level of the root of A. suralis to the point of origin of A. fibularis. Midtgård (1982) treats the variable relationship of the popliteal a. to M. popliteus in different birds.

(76) **A. tibialis cranialis.** (Fig. 12.10) This artery is the prolongation of A. poplitea distal to the origin of A. fibularis. A. tibialis cranialis leaves the flexor compartment of the crus via the distal interosseous foramen (**Arthr.** Annot. 162) and enters the extensor compartment. The course of the A. tibialis cranialis at the distal end of the tibiotarsus shows much interspecific variation; in the typical arrangement (e.g., *Tringa*) A. tib. cran. gives off a small superficial ramus and a deep ramus; the latter passes under the extensor retinaculum (**Arthr.** Annot. 187) in company with N. fibularis profundus. Consult Midtgård (1982) for a complete account of this artery.

(77) **Rete tibiotarsale** (Midtgård, 1981). Synonymy: Rete mirabile tibiotarsale (Hyrtl, 1864). Many taxa of birds possess the Rete tibiotarsale, a mixed network of arteries and veins on the cranial aspect of the tibiotarsus usually extending distally to the level of its extensor retinaculum. The network forms a countercurrent system involved in temperature regulation. The following summary is extracted from the comprehensive study of Midtgård (1981):

The tibiotarsal rete may be derived from the fibular artery, cranial tibial artery, or both, and may vary in complexity from simple to elaborate: Simple retia generally have 4-5 collateral arteries in contact with a larger number of veins; these are characteristic of the gruiform species investigated. Others occur in the gannet *Morus,* the penguin *Spheniscus,* the stork *Ciconia,* the tinamou *Crypturellus,* and the owl *Asio.* Elaborate retia consist of as many as 15-19 small arteries enmeshed with a larger number of veins, occurring in some pelecaniforms, anseriforms, galliforms, ciconiiforms, and the flamingo *Phoenicopterus.* See Annot. 24, Rete ophth.

(78) **Rr. fibulares.** (Fig. 12.10) The superficial and deep fibular rami of A. fibularis accompany the superficial and deep fibular [peroneal] nerves; near the intertarsal joint the two rami usually anastomose with the cranial tibial artery (Midtgård, 1982).

(79) **A. metatarsalis dorsalis communis.** In most groups of birds this artery is the prolongation of the deep ramus of A. tibialis cranialis that passes deep to the extensor retinaculum (**Arthr.** Annot. 188) and then into the foot where it divides (Annot. 77).

Aa. intermetatarsales plantares. These two arteries arise from the common dorsal metatarsal artery and pass from the dorsal surface to the plantar aspect of the foot by traversing the Foramina vascularia proximales of the Tarsometatarsus. There each of these arteries divides into a proximally directed (recurrent) A. tarsalis plantaris and the distally directed A. metatarsalis plantaris. (Fig. 12.10) A metatarsalis plantaris lateralis is usually dominant to its medial counterpart (Midtgård, 1982).

Aa. metatarsales dorsales. In his series of 43 avian species Midtgård (1982) found that the dorsal metatarsal aa. varied in number from one to three. In most species the A. metatars. dors. III is the only large artery of the foot; usually A. metatarsalis dorsalis II is present as a slender companion artery of the dorsal metatarsal nerve. All three arteries were present only in *Columba* and *Asio* of his series. The Foramen vasculare distale (**Osteo.** Fig. 4.18) of the Tarsometatarsus transmits either the entire A. metatarsalis dorsalis III or a branch of the latter to the plantar aspect of the foot. See Annot. **Osteo.** Annot. 298.

Aa. digitales. The digital arteries may arise from the plantar aspect of the foot or as the direct prolongation of the dorsal metatarsal arteries. Midtgård (1982) notes that each toe has a digital artery on both sides; however one member of each pair is prominent, the other much smaller. In all species studied the main digital arteries are: Digit I, medial; Digit II, lateral; Digit III, lateral; Digit IV, medial. Digital arteries may arise from plantar or dorsal metatarsal arteries as summarized by Midtgård. See **Ven.** Annot. 70 for the venous patterns of digital veins and the reciprocal asymmetry in their size to that of the arteries.

(80) **R. bursalis; A. bursocloacalis.** (Fig. 12.11) In *Columba* one of the arteries the cloacal bursa originates from R. caudalis of A. mesenterica caudalis; the blood supply of the bursa is also partly derived from A. bursocloacalis that springs from A. pudenda (Baumel, 1988). See Pintea, et al. (1967) and Zamojska (1975) for the pattern in *Gallus.* See also **Cloaca.** Annot. 22.

(81) **A. iliaca interna.** (Fig. 12.11) Synonymy: A. pudenda communis (Gadow and Selenka, 1891); A. hypogastrica (Barkow, 1829). In birds and other higher vertebrates the A. iliaca interna is distributed to the terminal parts of the digestive tract, reproductive tract, and urinary system (Annot. 68).

(82) **A. pudenda.** Synonymy: A. pudenda interna (Barkow, 1829). See below: Annot. 83, Aa. bulbi rectricium.

(83) **A. lateralis caudae.** (Fig. 12.11) Synonymy: A. musculocutanea caudae lateralis (Neugebauer, 1845); A. pudenda externa (Gadow and Selenka, 1891). "A. lateralis caudae" is a simplification of the term of Neugebauer, descriptive of its distribution, and that of its companion vein and nerve (**PNS** Annot. 74), to the dorsolateral tail region where it supplies the bulb of the rectrices, the muscles, and integument of the uropygium. Consult du Toit (1912-13) and Baumel (1988) for descriptions of the vessels of the uropygium and the adjacent structures. See Fig. 12.11.

Aa. bulbi rectricium. (Fig. 12.11) Arteries to the bulb of the rectrices (Baumel, 1988) are derived from several sources (see branches of the A. pudenda, A. lateralis caudae, and A. mediana caudae). Baumel described the relative hypertrophy of dorsal rami of two pairs of segmental branches of a. mediana caudae in the pigeon *Columba livia*. These vessels are the **A. profunda dorsalis bulbi [rectricium]** and the **A. cutanea dorsomedialis caudae;** they course between vertebral transverse processes to reach the rectricial bulb and skin on the dorsum of the uropygium. The extraordinary enlargement of certain of the caudal segmental arteries for supply of the uropygium was first noted by Barkow (1829) in the curlew *Bhurinus oedicnemius*.

A. glandulae uropygialis. In the pigeon (Baumel, 1988) the artery to the uropygial gland is an unpaired, enlarged dorsal ramus of a caudal segmental artery. See Zamojska (1975) for vascularization of the gland in the chicken.

(84) **Aa. vertebromedullares** (Sterzi, 1903). Synonymy: Aa. spinales (Kitoh, 1964); Aa. nervomedullares (Lob, 1967). These arteries are derived regionally from dorsal rami of segmental branches of the Aa. vertebrales, most of the length of Aorta descendens, and A. mediana caudae. The use of the name "A. spinalis" for the vertebromedullary arteries leads to confusion with the dorsal and ventral spinal arteries on the spinal cord (Medulla spinalis) itself (see Annot. 85).

See "Aa. medullae spinalis" for names of branches of the Aa. vertebromedullares (mostly after Lob, 1967). Vertebromedullary arteries supply spinal nerve roots, dorsal root ganglia and paravertebral ganglia, spinal dura mater, the spinal cord, the vertebrae, and the ligaments and joint capsules of the vertebral column.

(85) **A. spinalis ventralis; Aa. spinales dorsales; Aa. dorsolaterales.** Longitudinal arteries on the spinal cord that are formed by anastomoses between asc- and descending rami of Aa. radiculares ventrales et dorsales. At the foramen magnum A. spinalis ventralis communicates by means of weak anastomoses with terminal rami of A. basilaris (Annot. 21).

(86) **Rr. marginales.** Synonymy: Aa. perphericae (Sterzi, 1903). These rami form an irregular surface network of arteries that send radially penetrating branches into the lateral funiculi of the spinal cord, reaching the gray matter. Rr. marginales supply that part of the spinal cord not served by vessels entering the ventral and dorsal sulci of the cord (see Lob, 1967).

TERMINOLOGY

VENAE

VENAE PULMONALES[1] (see **Resp.**)

V. pulmonalis communis
  V. pulmonalis
    Rdx. cranialis[1]
Rdx. caudomedialis
Rdx. caudolateralis
Vv. interparabronchiales[2]

VENAE CARDIACAE[3] (**Cor.** Fig. 12.1A, B)

V. cardiaca sinistra[4 3]
  Pars basilaris[4]
  Pars interventricularis[4]
  Vv. conales (**Cor.** Annot. 2)
  Vv. septales[5]
  Vv. atriales
    V. interatrialis
  Vv. ventriculares
V. cardiaca circumflexa sinistra[6 4 3]
  Vv. atriales
  Vv. ventriculares
V. cardiaca media [dorsalis][7 3]
  Vv. apicis cordis[7]
  Vv. septales[5]
  Vv. ventriculares
Vv. cardiacae dextrae [ventrales][8]
  Vv. conales (**Cor.** Annot. 2)
  Vv. atriales
  Vv. ventriculares
  V. cardiaca circumflexa dextra[6]
Vv. cardiacae minimae[9]
  V. proventriculus cranialis[51]

VENA CAVA CRANIALIS[10] (Fig. 12.14)

VENA CEPHALICA ROSTRALIS[12 13] (Fig. 12.12)

V. maxillaris[13] (Fig. 12.12)
  V. palatina lateralis[14]
    V. nasalis ventralis[15]
    V. nasalis caudalis
    V. nasalis dorsalis[15]
    V. mandibularis interna
    V. mandibularis externa
    Anastomosis maxillofacialis[21]
    Anastomosis cum rete ophthalmico
V. ophthalmica (Fig. 12.12)
  V. ethmoidalis
    V. nasalis lateralis[15]
    V. nasalis medialis[15]
  Vv. frontales[16]
    V. frontalis profunda
    V. frontalis superficialis
  V. palpebralis dorsonasalis[23]
  V. anastomotica cum sinu olfactorio[31]
  V. ciliaris dorsalis (see V. facialis)
    Vv. choroideae
      Vv. parallelae choroideae (**Art.** Annot. 29)
V. ophthalmotemporalis[39]
  V. supraorbitalis[39]

(continued)

VENA CEPHALICA ROSTRALIS[12] (Fig. 12.12) (cont.)

V. infraorbitalis
V. ophthalmica interna
R. anastomoticus cum rete ophthalmico
Vv. musculares bulbi oculi
Vv. ciliares ventrales (see V. facialis)
Vv. choroideae
Vv. parallelae choroideae (**Art.** Annot. 29)
V. pectinis oculi
Vv. glandulae membranae nictitantis
Anastomosis cum sinu cavernoso[18]
Vv. comitantes a. maxillaris[13]
V. palatina medialis[14]
V. palatina mediana[19]
V. submandibularis[20]
V. submandibularis superficialis
V. submandibularis profunda
Rete pterygopharyngeale
V. pterygopharyngealis
V. facialis[21] (Fig. 12.12)
V. nasalis dorsalis[15]
V. nasalis lateralis[15]
Vv. frontales[16]
V. intermandibularis
V. palpebralis dorsonasalis[23]
Vv. ciliares anteriores
Sinus venosus sclerae[17]
Anastomosis maxillofacialis[21]
Vv. mandibulares caudales
V. palpebralis communis[22]
V. palpebralis ventralis[23]
Vv. ciliares anteriores
Sinus venosus sclerae[17]
V. palpebralis dorsotemporalis[23]
Vv. ciliares anteriores
Sinus venosus sclerae[17]
V. intramandibularis[24]
Vv. temporales
Anastomosis cum v. ophthalmica externa
Rete quadratopterygoideum
V. intramandibularis[24]
Vv. temporales
V. mandibularis[25] (Fig. 12.12)
V. lingualis
V. lingualis propria
V. sublingualis
V. laryngea
V. pharyngealis
V. esophagotrachealis
V. esophagealis descendens
V. trachealis descendens
Vv. hyobranchiales [hyoideae]
Rete palatopharyngeale[26]
Anastomosis interjugularis[27]
Vv. pharyngeales dorsales
Vv. musculares ventrales colli
V. occipitalis ventromediana[28]

VENA CEPHALICA CAUDALIS[29] (Fig. 12.12)

VENAE ENCEPHALICAE ET SINUS DURAE MATRIS[30] (Fig. 12.13)

Sinus olfactorius
V. cerebralis dorsorostralis
Sinus sagittalis olfactorius
V. rostralis diencephali
Sinus sagittalis dorsalis[31]
V. emissaria mediana

(continued)

VENAE ENCEPHALICAE ET SINUS DURAE MATRIS[30] (Fig. 12.13) (cont.)

V. cerebralis dorsomedialis
V. cerebralis dorsocaudalis
V. cerebralis interna
V. choroidea ventriculi lateralis
V. cerebralis magna
V. cerebralis caudalis
Sinus transversus
V. lateralis diencephali
Sinus sphenotemporalis
V. cerebralis media
V. cerebralis rostralis
V. lateralis corporis striati
V. lateralis tecti mesencephali
Sinus petrosus rostralis
V. intercruralis
V. caudalis tecti mesencephali
V. rostralis tecti mesencephali
V. ventralis tecti mesencephali
V. nervi trigemini
V. cerebralis basilaris
V. myelencephali basilaris
V. rostralis cruris cerebellaris
V. cerebellaris rostromediana
V. cerebellaris rostroventralis
V. rostrodorsalis myelencephali
Sinus cavernosus[18] (Fig. 12.12)
V. carotis cerebralis
Vv. adenohypophysiales[18]
V. choroidea ventriculi tertii
Sinus petrosus caudalis[32]
V. dorsalis tecti mesencephali
V. semicircularis rostralis[32]
Sinus occipitalis (Fig. 12.13)
Vv. meningeales
Vv. dorsales cerebelli
V. dorsalis labyrinthi[33]
V. occipitalis dorsomediana[34]
Sinus foraminis magni[46]
Sinus fossae auriculae cerebelli[35]
V. choroidea ventriculi quarti
V. nervi glossopharyngealis
Vv. dorsales myelencephali
V. cerebellaris lateralis
V. semicircularis lateralis[36]
V. occipitalis communis[37]
V. occipitalis interna[28 37]
V. occipitalis externa[32 37]
V. vertebralis ascendens[38]
V. occipitocollaris[38]
V. occipitalis profunda[41a]
V. occipitalis superficialis[41a]
V. cutanea cervicalis descendens[41b]
V. carotis cerebralis
V. sphenoidea (**Art.** Annot. 18)
V. palatina
V. sphenomaxillaris
V. ventralis labyrinthi[33]
V. ophthalmica externa[39] (**Art.** Annot. 24)
V. cutanea cervicalis descendens[41b]
Rete ophthalmicum[39] (**Art.** Annot. 24)
Anastomosis cum v. faciali[21]
V. auricularis rostralis[40]
V. auricularis caudalis[40]
Anastomosis cum v. faciali[21]

VENA JUGULARIS[11 27] (Figs. 12.12, 13)

V. occipitalis profunda[41a]
V. occipitalis superficialis[41a]
V. mandibularis[25]
Vv. musculares craniales colli

(continued)

VENA JUGULARIS[11 27] (cont.)

Vv. cutaneae colli
V. trachealis descendens
V. esophagealis ascendens
V. esophagealis descendens
Vv. ingluviales
  Rdxx. esophageales
Vv. tracheales
Vv. esophageales
V. cutanea cervicalis ascendens[41b]
V. cutanea cervicalis descendens[41b]
Plexus subcutaneus collaris[41b]
V. transversa colli
V. suprascapularis[42]
Vv. thyroidea
V. vertebralis communis[43 38]
  V. vertebralis ascendens[43]
  V. vertebralis descendens[43]
    Vv. vertebromedullares
    Vv. intercostales dorsales[44]
V. esophagotracheobronchialis[45]
V. trachealis ascendens
Vv. musculares caudales colli

SINUS [VENOSUS] VERTEBRALIS INTERNUS [PARS CERVICOTHORACICA][46 82] (Fig. 12.14)

Vv. segmentales cervicales/truncales[82]
  Vv. intercostales dorsales
    Vv. vertebromedulares
  Anastomosis cum sinu foraminis magni
  Anastomosis cum v. occipitali interna
Anastomoses sinujugulares[43]
Anastomoses sinurenales[46]
Anastomosis cum v. portali renali craniali[46] (**Urin.** Fig. 5)
Anastomosis cum v. portali renali caudali[46]
Anastomosis cum v. iliaca interna

VENA SUBCLAVIA (Fig. 12.14)

Truncus pectoralis[47] (Figs. 12.14, 15)
  V. pectoralis cranialis
  V. pectoralis media[47]
  V. pectoralis caudalis
V. thoracica interna[48 44] (Fig. 12.13)
  Rdx. dorsalis
  Rdx. ventralis
  V. sternalis interna
Vv. intercostales ventrales[48]
V. sternoclavicularis
  V. clavicularis
  V. coracoidea dorsalis
  V. sternalis externa
V. subscapularis
  V. supracoracoidea

VENA AXILLARIS (Figs. 12.14, 15)

V. cutanea thoracoabdominalis[49]
V. infrascapularis
Vv. brachiales[50]
V. bicipitalis

(continued)

VENA AXILLARIS (cont.)

V. circumflexa humeri ventralis
V. cutanea brachialis
V. profunda brachii
  V. circumflexa humeri dorsalis
  V. collateralis ulnaris
  V. collateralis radialis
V. basilica (Fig. 12.15)
  V. radialis
    V. cutanea propatagialis
      V. antebrachialis dorsalis cranialis
    V. radialis profunda
      Vv. interosseae dorsales
        V. cubitalis dorsalis
      V. antebrachialis dorsalis caudalis
        Rdxx. postpatagiales
    V. radialis superficialis
      V. cutanea propatagialis
      V. propatagialis marginalis
  V. ulnaris (Fig. 12.15)
    V. cubitalis ventralis
    V. ulnaris superficialis[50]
      V. ulnaris recurrens
    V. ulnaris profunda[50]
      Rdxx. postpatagiales
      Anastomosis cum v. ulnari superficiali
      Vv. carpales dorsales
      Vv. carpales ventrales
      Vv. metacarpales dorsales
      Vv. metacarpales ventrales
      V. metacarpalis interossea
        Vv. digitales dorsales
        Vv. digitales ventrales
      V. postpatagialis marginalis

VENA CAVA CAUDALIS[52] (Figs. 12.16, 17)

V. hepatica dextra[52] (Fig. 12.17)
  Rdx. dorsocaudalis
  Rdx. dorsocranialis
  Rdx. ventralis
    Vv. sublobulares
      Vv. centrales[53]
Vv. hepaticae medianae[53]
V. hepatica sinistra[53] (Fig. 12.17)
  Rdx. dorsocaudalis
  Rdx. dorsocranialis
  Rdx. ventralis
V. umbilicalis
V. hepatica accessoria[54]
V. adrenalis (Fig. 12.16)
  Vv. portales adrenales[55]
Vv. ovaricae[56] (Fig. 12.16)
  Vv. contortae
  Vv. pedunculares
    Vv. intramurales
Vv. testiculares
  Vv. ureterodeferentiales craniales[57]
  Vv. uretericae

VENA ILIACA COMMUNIS (Fig. 12.16)

Valva portalis renalis[59]
Vv. renales craniales[58]
  Rdxx. renales efferentes[58 59]
Vv. intralobulares[58]
V. oviductalis cranialis[61]
  Vv. ovaricae[56]

(continued)

VENA ILIACA COMMUNIS (cont.)

Vv. infundibuli
Vv. magni
V. renalis caudalis[58] (Fig. 12.16)
Vv. segmentales synsacrales[60]
Vv. intervertebrales[60]
Rdxx. renales efferentes
Vv. intralobulares[58]
V. oviductalis media[61] (Fig. 12.16)
Vv. magni
Vv. isthmi
Vv. uterinae (**Fem.**)
Vv. ureterodeferentiales mediae
Vv. uretericae

VENA ILIACA INTERNA[62] (Figs. 12.11, 16)

Anastomosis interiliaca[59 62]
Anastomosis cum v. mesenterica caudali
V. pudenda[63] (Fig. 12.11)
Vv. ureterodeferentiales caudales
Vv. uretericae
V. oviductalis caudalis[61]
Vv. uterinae (**Fem.**)
V. vaginalis
V. oviductalis marginalis dorsalis[61]
V. oviductalis marginalis ventralis[61]
V. bursocloacalis[63]
Vv. bursales
Vv. cloacales (**Cloaca** Annot. 26)
V. ventralis bulbi [rectricium][65]
V. lateralis caudae[64] (Fig. 12.11)
V. cutanea abdominalis[65 49]
V. cutanea dorsolateralis caudae
V. dorsalis superficialis bulbi [rectricium][65]
V. lateralis venti
V. efferens sinus vertebralis interni
V. mediana caudae[62] (Fig. 12.11)
V. cutanea dorsomedialis caudae
V. dorsalis profunda bulbi [rectricium][65]
V. uropygialis
Vv. segmentales caudales[60]
Vv. intervertebrales[60]
Vv. efferentes sinus vertebralis interni[82]

SINUS [VENOSUS] VERTEBRALIS INTERNUS, [PARS CAUDALIS][46 82] (Fig. 12.19)

Vv. segmentales
Vv. vertebromedullares
V. profunda dorsalis bulbi [rectricium]
Vv. efferentes sinus vertebralis interni
Vv. afferentes sinus vertebralis interni
V. supraspinosa
Vv. interspinosae

VENA ILIACA EXTERNA (Fig. 12.16)

V. pubica[74]
V. femoralis (see V. isch.)
V. coxae cranialis[67]
V. femoralis cranialis
V. cutanea femoralis cranialis
Anastomosis ischiofemoralis[66]

SYSTEMA PORTALE RENIS[59] (Fig. 12.16) (Urin.)

Circulus [venosus] portalis renalis[59]
Vena iliaca communis
V. portalis renalis cranialis
Rr. renales afferentes[59]
Anastomoses sinurenales [Anastomosis cum sinu vertebrali interno][46]
Vv. renales craniales
V. renalis caudalis
Vena iliaca interna[62] (Fig. 12.16)
V. portalis renalis caudalis[62]
Anastomosis interiliaca[59 62]
V. ischiadica[66]
Rr. renales afferentes[59]
Anastomoses sinurenales [Anastomoses cum sinu vertebrali interno][46]
Vv. segmentales caudales[60]
Vv. segmentales synsacrales[60]

VENA ISCHIADICA[66] (Figs. 12.16, 18)

V. coxae caudalis[67]
V. femoralis medialis
V. circumflexa femoris medialis
V. circumflexa femoris lateralis[68]
Anastomosis ischiofemoralis[66]
V. femoralis caudalis[68]
V. nutricia femoris proximalis
V. suralis[69]
V. cutanea femoralis caudalis
V. cutanea femoralis lateralis
V. cutanea cruralis caudalis
V. suralis lateralis
V. suralis medialis
V. poplitea[66 71] (Fig. 12.18)
V. lateralis genus
V. nutricia femoris distalis
V. tibialis medialis
V. medialis genus
V. cruralis medialis
V. tibialis caudalis[71] (Fig. 12.18)
Vv. tarsales plantares
Vv. metatarsales plantares[70]
V. metatarsalis plantaris superficialis medialis[70]
V. metatarsalis plantaris superficialis lateralis[70]
V. metatarsalis plantaris profunda
Arcus plantaris superficialis[70]
Vv. pulvinarum (see **Integ**).
Vv. digitales
V. fibularis [peronea][73]
V. proximalis genus
V. fibularis [peronea] superficialis[73]
V. fibularis [peronea] profunda[73]
Rete tibiotarsale[72]
V. tibialis cranialis[71] (Fig. 12.18)

(continued)

VENA ISCHIADICA[66] (Figs. 12.16, 18) (cont.)

V. metatarsalis dorsalis communis[70]
V. metatarsalis dorsalis medialis
V. metatarsalis dorsalis lateralis
Vv. pulvinarum
Vv. digitales

SYSTEMA PORTALE HEPATIS[75] (Fig. 12.17)

VENA PORTAE DEXTRAE HEPATIS[76] (Fig. 12.17)

V. mesenterica communis[78]
  V. mesenterica cranialis[78]
    Vv. jejunales
    Vv. ileae
    V. ileocecalis
  V. mesenterica caudalis [V. coccygomesenterica][78 62]
  Rdx. cranialis
    Vv. ileocecales
  Rdx. caudalis
    Vv. rectales
    V. bursalis[63](**Cloaca** Annot. 23)
    Vv. cloacales (**Cloaca** Annot. 23)
    Anastomosis cum anastomose interiliaca[78 62]
  V. marginalis intestini tenuis (**Art.** Annot. 64)
  V. proventriculosplenica[79]
    V. proventricularis dorsalis[79 51]
    V. gastrica dorsalis (**Art.** Annot. 63)
V. proventricularis dextra[79 51]
Vv. splenicae[79]
V. gastropancreaticoduodenalis
  V. duodenojejunalis
V. gastrica dextra (**Art.** Annot. 63)
  Vv. sacci caudalis
  V. sacci cranialis
  V. pylorica
V. pancreaticoduodenalis
  V. ileocecalis
  Vv. duodenales
  Vv. pancreaticae
Rr. intrahepatici v. portae dextrae
  Ramus dexter v. portae dextrae[76]
    Rr. dorsales
    Rr. ventrales
  Ramus sinister v. portae dextrae
    Pars transversa[77]
      Rr. mediani dorsales
      Rr. mediani ventrales
    Pars anastomotica

VENA PORTAE SINISTRAE HEPATIS[80] (Fig. 12.17)

Vv. proventriculares caudales[79]
V. proventricularis ventralis[79]
V. gastrica sinistra (**Art.** Annot. 63)
Vv. sacci caudalis
Vv. sacci cranialis
V. gastrica ventralis (**Art.** Annot. 63)

(continued)

VENA PORTAE SINISTRAE HEPATIS[80] (cont.)

V. pylorica
Rr. intrahepatici v. portae sinistrae
  Rr. dorsales
  Rr. ventrales
Vv. portales hepaticae propriae[81]

VENAE COLUMNAE VERTEBRALIS ET MEDULLAE SPINALIS

Sinus [venosus] vertebralis internus[46 82]
Vv. segmentales[82]
  Rdx. ventralis
    Rdx. dorsalis
      V. vertebromedullaris[83]
      Vv. radiculares dorsales[88]
      Vv. radiculares propriae
      Vv. radiculares ventrales[88]
      Vv. radiculares propriae
    V. spinalis ventralis[84]
      Vv. sulci[85]
      Vv. sulcocommissurales
      Vv. marginales[86]
      Vv. ventrolaterales[87]
    V. spinalis dorsalis[89]
      Vv. dorsolaterales[90]
      Vv. fissurae[91]

ANNOTATIONS

(1) **Vv. pulmonales.** The intrapulmonary tributaries of each V. pulmonalis correspond closely to the intrapulmonary rami of A. pulmonalis. The two caudal radices and their larger radicles lie generally ventral to corresponding rami of A. pulmonalis; the cranial radix is medial to its artery, e.g., *Gallus*, *Columba* (**Cor.** Annot. 20).

(2) **Vv. interparabronchiales.** These veins are tributaries of each of the three main radices of V. pulmonalis. Consult Radu and Radu (1971) for patterns of intrapulmonary vessels in several avian species, and Abdalla and King (1975) for angioarchitectural detail in *Gallus*. See **Resp.** Annot. 70 for tributaries.

(3) **Vv. cardiacae.** Synonymy: Vv. cordis. Generally cardiac veins are not satellites of coronary arteries and their rami; veins are commonly located subepicardially (exception: Vv. septales and the terminal segment of Pars basilaris of the left cardiac vein). The terminology of the cardiac veins is based mainly on the works of Lindsay (1967) in *Gallus* and Bezuidenhout (1984) in *Struthio*. Their studies indicate that many of the cardiac veins empty independently into the right atrium, therefore differing from the mammalian condition in this respect. Bezuidenhout (1984) notes that in the *Struthio* V. cardiaca sinistra, V. cardiaca circumflexa sinistra, and V. cardiaca media flow into a common sinus which opens into the right atrium near the ostium of the left cranial vena cava. See remarks regarding cardiac veins in **Cardvas.** Intro. and Fig. 12.1.

(4) **V. cardiaca sinistra.** Synonymy: V. cordis magna. The left cardiac vein of birds is usually not the largest of Vv. cardiacae; therefore the synonym, V. cordis magna, is

a misnomer. Lindsay (1967) describes two parts of this vein in *Gallus:* **Pars interventricularis** and **Pars basilaris** (see Annot. 6). In *Struthio* Pars basilaris passes to the right in the interval between the left auricle and the pulmonary trunk/aorta, receives septal veins from the dorsal part of the interventricular septum, penetrates the floor of the left recess of the right atrium and empties into the common sinus mentioned in Annot. 3 (Bezuidenhout, 1984).

(5) **Vv. septales.** In *Gallus,* the cranial part of Septum interventriculare is sometimes drained by left and right Vv. septales that empty into V. cardiaca sinistra and Vv. cardiacae ventrales, respectively (Lindsay, 1967) (see Annot. 4).

(6) **V. cardiaca circumflexa sinistra.** In *Gallus* Pars interventricularis of V. cardiaca sinistra occasionally continues directly as V. cardiaca circumflexa sinistra. Ordinarily the left circumflex cardiac vein is an independent vein (Lindsay, 1967) (Fig. 12.1B).

V. cardiaca circumflexa dextra. This vein is present in the Ostrich; it accompanies the circumflex branch of the right cornary artery (Bezuidenhout, 1984).

(7) **V. cardiaca media [dorsalis].** Synonymy: V. cordis media; V. cardiaca dorsalis. Usually the largest of the cardiac veins, the cranial segment (Lindsay, 1967) of the middle cardiac vein lies in Sulcus interventricularis subsinuosus [dorsalis]. It is formed by tributaries (**Vv. apicis cordis**) which spiral about the apex of the heart, one or more of which may anastomose with tributaries of the left circumflex cardiac vein. The V. cardiaca media receives septal veins from the interventricular septum, both ventricles, the right atrioventricular valve and right atrium.

(8) **Vv. cardiacae dextrae [ventrales].** (Fig. 12.1A) Synonymy: Vv. cordis minores; Vv. cardiacae ventrales. The system of right cardiac veins is located mostly in the subepicardial tissues of the ventral wall of Ventriculus dexter; the two or three main tributaries of the system span the coronary sulcus, and empty directly into Auricula dextra via separate ostia.

(9) **Vv. cardiacae minimae.** Synonymy: Vv. luminalia; Vv. thebesii. Vv. minimae drain blood from the myocardium directly into the heart chambers. The foramina of these veins are abundant in the right and left atria and right ventricle; in the left ventricle they occur infrequently (Uchiyama, 1929).

(10) **V. cava cranialis.** (Fig. 12.14) V. subclavia, V. jugularis, and Truncus pectoralis all converge to form V. cava cranialis of each side; consequently a V. brachiocephalica is not present in birds.

(11) **V. jugularis.** (Fig. 12.14) The paired jugular vein is formed by the confluence of V. cephalica rostralis and V. cephalica caudalis. In most birds V. jugularis dextra is significantly larger in caliber than V. jugularis sinistra. In certain taxa the **Anastomosis interjugularis** (Annot. 27) is obliquely disposed; it appears that part of the venous blood from the left side of the head is shunted to the right jugular system. Neugebauer (1845) discussed the anastomosis and asymmetry of jugular veins in different avian taxa. Wade (1876) noted that the left jugular is atrophied and nonfunctional in several passerine species. See Annot. 46, 82.

(12) **V. cephalica rostralis.** (Fig. 12.12) Synonymy: V. cephalica anterior; V. facialis communis (Neugebauer, 1845). See below (Annot. 13) concerning the origin of the rostral cephalic vein.

(13) **V. maxillaris.** (Fig. 12.12) Synonymy: V. facialis interna. V. maxillaris does not accompany A. maxillaris; the artery courses in the roof of the pharynx just deep to the mucosa, flanked by small paired or plexiform **Vv. comitantes a. maxillaris.** The prominent V. maxillaris courses in the floor of the orbit, turns ventrad between the caudal wall of the orbit and Os pterygoideum, and reaches the roof of the pharynx where its name changes to V. cephalica rostralis.

(14) **V. palatina medialis; V. palatina lateralis.** The medial palatine vein drains into the system of V. maxillaris; it may also have connections with the Vv. comitantes a. maxillaris, the lateral palatine vein, and Rete palatopharyngeum. In different species V. palatina lateralis is a tributary of either V. maxillaris or V. facialis.

(15) **Vv. nasales.** In different species the nasal veins may be tributaries of V. facialis, V. ethmoidalis, or both. In *Gallus* the medial and lateral nasal veins are confluent, forming a common nasal vein that drains into V. ethmoidalis. In *Columba* blood from V. nasalis lateralis flows into the system of V. facialis.

(16) **Vv. frontales.** The frontal veins are quite large in birds having prominent fleshy crests (e.g., galliforms); they drain either into the system of V. facialis or that of V. ethmoidalis.

(17) **Sinus venosus sclerae.** Synonymy: Canal of Schlemm. This sinus receives excess aqueous humor from the anterior chamber of the eye, and is drained by the several Vv. ciliares anteriores. See **Sens.** Annot. 11, 12.

(18) **Sinus cavernosus.** (Fig. 12.12) Synonymy: Sinus anuli basilaris (Kaku, 1959); Sinus perihypophysialis (Hasegawa, 1956). The paired cavernous sinuses are situated on either side of the Fossa hypophysialis in the floor of the cranial cavity; the two sinuses communicate with one another rostral and caudal to the fossa, forming a circular sinus (see synonyms above). The cavernous sinuses receive venous blood from the base of the hypothalamic region and hypopyhysis from the hypophysial portal system (**Vv. adenohypophysiales**) (see **Endoc.** Annot. 20-24). The cavernous sinus also has communications with V. carotis cerebralis, V. ophthalmotemporalis, and V. ophthalmica interna (Wingstrand, 1965). Consult Vitums, et al. (1964) for a detailed account of the blood supply and venous drainage of hypophysis. See **Endoc.** Annot. 20-23 for comments on systema portale hypophysiale.

(19) **V. palatina mediana.** Rostral to the nasal choana in the roof of the oral cavity this is an unpaired vein; reaching the choana it splits into paired Vv. palatinae mediales that flank the choana.

(20) **V. submandibularis.** Generally this vein is a tributary of V. cephalica rostralis; however in some birds it is a tributary of V. mandibularis.

(21) **V. facialis.** Common synonym: V. facialis externa. For the most part the facial vein is situated subcutaneously. Its terminal part courses medially just rostral to the external acoustic meatus, where in different birds it empties either into V. cephalica rostralis, the terminal part of V. cephalica caudalis, or into V. mandibularis.

(22) **V. palpebralis communis; V. palpebralis dorsotemporalis** (V. palpebralis dorsocaudalis (NAA, 1979)), joins **V. palpebralis ventralis** to form the common palpebral vein in some birds (Neugebauer, 1845). Not only do Vv. palpebrales drain blood from the eyelids (palpebrae) but they receive anterior ciliary veins and venous radicles from the nictitating membrane, bulbar conjunctiva, and the iridial region of the Bulbus oculi.

(23) **V. palpebralis dorsonasalis.** Synonymy: V. palpebralis dorsorostralis (NAA, 1979). The dorsonasal palpebral vein may drain into the ethmoid system of veins as in *Gallus* or into the system of V. facialis (e.g., *Columba*).

(24) **V. intramandibularis.** This vein courses in the neurovascular canal of the mandible with A. intramandibularis and the prolongation of N. mandibularis. See **Art.** Annot. 25.

(25) **V. mandibularis.** (Fig. 12.12) Synonymy: V. lingualis. V. mandibularis is the main vein from the region of the lower jaw; it empties into V. cephalica rostralis near the Anastomosis interjugularis (e.g., *Gallus*), further caudally as in *Columba* and *Milvus* (Neugebauer, 1845) near the junction of the rostral and caudal cephalic veins, or into V. jugularis itself.

(26) **Rete palatopharyngeale.** Synonymy: Rete mirabile basilaris (Neugebauer, 1845). A rich meshwork of interconnecting veins in the submucosa of the roof of the oropharynx.

(27) **Anastomosis interjugularis.** This name is a substitute name for Anastomosis venarum cephalicarum anteriorum (Neugebauer, 1845). Other synonyms: Ramus communicans pharyngicus (Bodrossy, 1938); and V. transversa (Matsumoto, 1955). The interjugular anastomosis actually joins the two rostral cephalic veins rather than the jugular veins themselves (see Figs. 12.12, 14 and Annot. 11).

(28) **V. occipitalis ventromediana** (Richards, 1968) (Fig. 12.12). The name of this vein is shorter and more descriptive than its synonym: R. anticus annuli venosi occipitalis (Neugebauer, 1845). The ventromedian occipital vein emanates from the right and left columns of the ventral neck musculature, passes rostroventrad and empties into the interjugular anastomosis. Within the neck musculature its right and left radicles anastomose with the cranial ends of the vertebral veins and the internal occipital veins as the latter emerge from the atlanto-occipital interval.

(29) **V. cephalica caudalis.** (Fig. 12.12) The caudal cephalic vein drains blood mostly from the veins of the brain via the cranial dural sinuses and from the inner ear and suboccipital regions (Neugebauer, 1845; Matsumoto, 1955; Richards, 1968). Most of the dural sinuses send blood dorsocaudally to sinuses in the occipital region; the latter flow into the common occipital veins, thence to the caudal cephalic vein as well as to the internal vertebral sinus (see Annot. 37). V. cephalica caudalis is not well developed in *Gallus* and *Meleagris;* in these forms it appears to be partly replaced by the large V. occipitalis ventromediana (Annot. 28).

(30) **Sinus durae matris; Vv. encephalicae.** (Fig. 12.13) The dural venous sinuses and the veins of the brain are named mostly according to Kaku (1959); for synonyms, see Neugebauer (1845) and Matsumoto (1955). Only the principal tributaries of the dural sinuses are listed; minor named radicles are not included.

(31) **Sinus sagittalis dorsalis.** Synonymy: Sinus longitudinalis. In some birds blood in the dorsal sagittal sinus flows predominantly caudad into Sinus occipitalis; in others it flows rostrad into Sinus olfactorius then via ethmoid veins into the ophthalmic veins in the orbit.

(32) **Sinus petrosus caudalis.** The caudal petrosal sinus is prolonged as V. semicircularis rostralis; the latter courses in its osseous canal along the rostral semicircular canal of the osseous labyrinth, and emerges from the occipital region of the skull via a foramen lateral to the Foramen magnum where it becomes designated as V. occipitalis externa.

V. semicircularis rostralis. A term substituting for Sinus semicircularis or Sinus petrosus posterior (Neugebauer, 1845). For details of relationships of veins that parallel the semicircular canals see Neugebauer (1845) and Ewald (1892). See also Annot. 36; and **Sens.** Labyrinthus osseus.

(33) **V. dorsalis labyrinthi; V. ventralis labyrinthi.** Named following Schmidt (1964). These veins of the inner ear drain into V. dorsalis cerebelli and V. occipitalis communis.

(34) **V. occipitalis dorsomediana.** This extracranial vein communicates with Sinus foraminis magni by way of an emissary foramen. In *Columba livia* a single foramen in the skull, just dorsal to the Foramen magnum, transmits the emissary vein. The veins are paired and situated near one another on each side of the median plane in certain birds (e.g., *Ceryle alcyon, Progne subis*). See **Osteo.** Annot. 87.

(35) **Sinus fossae auriculae cerebelli.** (Fig. 12.13) This term is more meaningful than its synonym, Sinus foveae hemispherii cerebelli (Neugebauer, 1845; Matsumoto, 1955; Kaku, 1959). See (**Osteo.** Annot. 38). **Sinus occipitalis** is situated over the dorsum of the cerebellum (Fig. 12.13).

(36) **V. semicircularis lateralis.** Synonymy: V. auris interna (Neugebauer, 1845). This vein courses in a bony tube attached to the osseous lateral semicircular canal; dorsal to the external acoustic meatus it joins V. ophthalmica externa.

(37) **V. occipitalis communis.** A substitute term for V. occipitalis lateralis (Neugebauer, 1845); this vessel is formed by the confluence of Vv. occipitalis interna et externa and leaves the cranial cavity via the atlanto-occipital interval. The common occipital vein should be considered the commencement of V. cephalica caudalis (Annot. 29). According to Romanoff (1960), V. occipitalis communis [lateralis] is believed to represent the true (primitive) jugular vein of embryonic birds.

(38) **V. vertebralis ascendens; V. occipitocollaris.** (Fig. 12.12) Just below the base of the skull the cranialmost ends of both these veins anastomose with V. occipitalis communis. V. occipitocollaris receives muscular and cutaneous radicles from the upper neck where it communicates with V. cephalica caudalis, V. vertebralis ascendens, V. jugularis, and Sinus vertebralis internus. Consult Neugebauer (1845), and see Annot. 43.

(39) **V. ophthalmica externa.** (Fig. 12.12) Synonymy: V. stapedia. The venous part of Rete ophthalmicum appears able to drain caudally into the external ophthalmic vein or rostrally into **V. ophthalmotemporalis** in the orbit. V. ophthalmotemporalis itself, although listed as a tributary of V. maxillaris, could be treated as a tributary of V. ophthalmica externa (see V. ophthalmica).

Rete ophthalmicum. Synonymy: Rete mirabile ophthalmicum or temporale. Arterial and venous ophthalmic retia are enmeshed with one another, forming a vascular heat exchange system that is important in cooling the brain (Kilgore, et al., 1979), and in reducing heat loss from the eye (Midtgård, 1984) (see **Art.** Annot. 24). The mixed rete is located in the caudal wall of the orbit between the quadrate and laterosphenoid bones (see above), and communicates with V. opthalmica externa caudally and V. ophthalmotemporalis rostrally. See Fig. 12.12.

(40) **Vv. auriculares.** In *Columba* the rostral and caudal auricular veins (and occasionally a ventral auricular vein) are tributaries of V. cephalica caudalis. In *Gallus* the auricular veins are tributaries of the V. facialis as depicted in Fig. 12.12.

(41a) **V. occipitalis profunda; V. occipitalis superficialis.** Both of these veins are companion veins of the same named arteries (see A. carotis externa). The termination of these veins is variable, emptying either into V. cephalica caudalis or V. jugularis.

(41b) **Plexus subcutaneus collaris** (Baumel, et al., 1983). In the subcutis of the neck of columbiform birds this extremely dense network of veins is drained by the **Vv. cutanea cervicalis ascendens/descendens** that empty into the jugulars. These erectile veins are similar to those of the avian and mammalian nasal cavity and external genitalia of mammals, and are capable of rapid engorgement, being filled via arteriovenous anastomoses. The plexus is involved in evaporative heat dissipation by gular flutter and panting.

(42) **V. suprascapularis.** Synonymy: V. cephalica humeri (Bodrossy, 1938; Szabo, 1958). Conducts venous blood from the dorsal shoulder region and proximal brachium into V. jugularis. According to Szabo this is a particularly strong vein in *Melopsittacus*.

(43) **V. vertebralis ascendens; V. vertebralis descendens.** The asc- and descending vertebral veins form longitudinal chains that are connected with Vv. segmentales at each level in the neck and cranial thoracic regions. In *Gallus* at the root of the neck the asc- and descending veins of each side flow together, forming the **V. vertebralis communis** (actually an enlarged segmental vein) that discharges into its jugular; smaller segmental veins may also serve as accessory channels conducting blood from the vertebral veins to the jugular. In *Columba* the asc- and descending vertebrals do not form a common trunk, but empty individually into two or three greatly enlarged, transversely oriented Vv. segmentales that connect V. jugularis with the Sinus vertebralis internus; these **Anastomoses sinujugulares** (new term) conduct blood from the Sinus into the jugulars, then to the cranial caval veins. See Fig. 12.14 and Annot. 38.

(44) **Vv. intercostales dorsales.** Two or three of the cranialmost dorsal intercostal veins anastomose with V. vertebralis descendens and with Sinus vertebralis internus. The more caudal series of dorsal intercostal veins drain into Sinus vertebralis internus. See V. thoracica interna and Annot. 48.

(45) **V. esophagotracheobronchalis.** This vein empties into the most caudal portion of the jugular vein. The companion artery of this vein is discussed in **Art.** Annot. 8.

(46) **Sinus [venosus] vertebralis internus.** Synonymy: Sinus columnae vertebralis (Szabo, 1958); epidural sinus (plexus). The internal vertebral sinus is present on the dorsal aspect of most of the length of the cervical, thoracic, and caudal spinal cord; (Figs. 12.14, 19); it is lacking in the region of the lumbar enlargement of the cord in the synsacral part of the vertebral canal, but present in the caudal vertebral canal (Fig. 12.19) (Baumel, 1988).

At all levels where it is located, the Sinus vertebralis internus *receives* blood from the intervertebral veins. Most of this blood from the neck and trunk regions is collected by the Sinus and flows toward the root of the neck mainly into the jugular veins (Annot. 43; Fig. 12.14), thence into the system of the cranial venae cavae. The segment of the Sinus in the caudal region drains ultimately into the internal iliac system of veins (Baumel, 1988). In other words the jugulars and caudal vena cava do not receive venous blood directly from segmental intervertebral veins (Baumel, 1975a). Other communications of the internal vertebral sinus are with the Sinus foraminis magni at the Foramen magnum (Fig. 12.13); the Vv. vertebrales; Vv. portalis renalis cranialis et caudalis (Mouchett and Cuypers (1959), V. renalis caudalis, V. iliaca interna, and V. mediana caudae. See Annot. 43, 52, 60, 82, Fig. 12.16; and **Urin.** Fig. 10.6.

Anastomoses sinurenales (new term). These are the connections between the internal vertebral sinus and the renal/renal portal veins (see Annot. 43 and Kurihara and Yasuda, 1975).

(47) **Truncus pectoralis.** Synonymy: V. thoracica externa. A common pectoral vein is lacking in some birds; in these instances the Vv. pectorales, instead of joining one another, empty individually into V. subclavia, e.g., *Melopsittacus* (Szabo, 1958).

V. pectoralis media is not present in all species.

(48) **Vv. thoracicae internae.** These veins course on the inner surface of the sternal ribs where they receive the Vv. intercostales ventrales; the internal thoracic veins flow craniad into V. axillaris, Vena cava cranialis, or both.

(49) **V. cutanea thoracoabdominalis** (Neugebauer, 1845). Drains the integument of the ventrolateral breast and abdomen, particularly the incubation (brood) patch (see **Integ.**) where it communicates with radicles of V. cutanea abdominalis, a tributary of V. lateralis caudae. Its companion, A. cutanea thoracoabdominalis, is a branch of the pectoral artery; however the vein empties into V. axillaris rather than into pectoral veins. See Annot. 65; and **Art.** Annot. 44.

(50) **Vv. brachiales.** (Fig. 12.15) Paired (or plexiform) satellite veins of A. brachialis that anastomose with each other and with radial and ulnar veins in the cubital region.

V. ulnaris superficialis. This vein frequently consists of paired venae comitantes that flank the strong, subcutaneous A. ulnaris superficialis.

V. ulnaris profunda is the largest of the veins draining the manus, carpus, and antebrachium; it accompanies the weak A. ulnaris profunda (**Art.** Annot. 49). The artery and vein course distally on a plane deep to M. flexor carpi ulnaris (Fig. 12.15).

(51) **V. proventricularis cranialis.** Nishida and Mochizuki (1976) compared the cranial proventricular vein of *Anas* with that of *Gallus;* Malinovský (1965) described this vein in *Columba.* Blood from the cranial segment of the proventriculus drains directly toward the heart rather than caudally into the hepatic portal system, and discharges into the right atrium or left cranial vena cava (Miyaki, 1978, Fig. 8). See Fig. 12.17 and **Cór.** Annot. 16.

(52) **Vena cava caudalis.** The short trunk of this vein does not parallel the vertebral column, but passes in a cranioventral direction to reach the right atrium of the heart; consequently the caudal vena cava does not receive dorsal intercostal or other segmental body wall veins (see Annot. 48, 58, 60; Figs. 12.16, 17).

(53) **Vv. hepaticae.** Intrahepatic radices of Vv. hepaticae have been named on the basis of dissections in *Gallus.* Miyaki (1973) designated the main radices of the left lobe of the liver, but not those of the right lobe. In *Anser* the larger radices of left and right hepatic veins are more numerous than in *Gallus;* they were not named by Pavaux and Jolly (1968). Vv. hepaticae medianae drain blood from Pars interlobaris of the liver; these have been observed in *Anser, Gallus,* and *Columba* (Pavaux and Jolly, 1968). The microscopic **Vv. centrales** collect blood from the liver sinusoids and themselves drain into **Vv. sublobulares;** the central and sublobular veins are tributaries of all the intrahepatic radices of the hepatic veins. See Fig. 12.17.

(54) **V. hepatica accessoria.** Miyaki (1973) describes in *Gallus* one or more accessory hepatic veins that drain the cranial part of the right lobe of the liver directly into the caudal vena cava.

(55) **Vv. portales adrenales.** (Fig. 12.16) Synonymy: Vv. adrenales afferentes. An adrenal portal system does exist in birds (Neugebauer, 1845; Szabo, 1958; Goodchild, 1969). Blood collected in body wall veins passes to the adrenal gland and through its system of microscopic portal venules; the latter reform into efferent adrenal venules that flow together to form **V. adrenalis** that discharges into the caudal vena cava.

(56) **Vv. ovaricae; (Fig. 12.16) Vv. testiculares.** These gonadal veins may form a common stem with the adrenal vein. Multiple left ovarian veins may exist; one or more ovarian veins may drain into V. oviductalis cranialis (*Gallus*); small right ovarian veins return venous blood from the rudimentary right ovary.

(57) **Vv. ureterodeferentiales.** Term introduced by Nishida (1964). These veins drain the ureter and Ductus deferens which closely accompany one another as they course toward the cloaca.

(58) **Vv. renales.** (Fig. 12.16) Vv. renales craniales are efferent from the cranial division of the kidney; blood from the middle and caudal divisions of the kidney drains into V. renalis caudalis. Several **Vv. intralobulares** of the kidney may become confluent to form one **Rdx. renalis efferens** or a single V. intralobularis may be a direct tributary of the proper V. renalis (Johnson et al., 1972). See **Urin.** Fig. 10.16).

(59) **Systema portale renis; V. portalis renalis caudalis/ cranialis.** The presence of a functional renal portal system is a basic feature of the avian kidney of importance in excretion of uric acid by tubular secretion (Johnson, 1978). The principal right and left renal portal veins of the system communicate, forming a venous ring designated the **Circulus [venosus] portalis renalis** by Kurihara and Yasuda (1975b). The components of this ring are: (1) cranial and caudal renal portal veins; (2) anastomoses of the cranial renal portal veins with the internal vertebral sinus, and (3) the interiliac anastomosis (**Urin.** Fig. 5).

According to Akester (1967), blood from V. iliaca interna and V. mesenterica caudalis may flow craniad in V. portalis renalis caudalis directly into V. iliaca communis, thence into Vena cava caudalis. Alternatively, venous blood from the pelvic limb may be diverted from V. iliaca externa by **Valva portalis renalis** into V. portalis renalis caudalis, then into V. mesenterica caudalis that leads to the hepatic portal system; Miyaki (1978) also calls attention to this communication of the two systems. Blood diverted by the renal portal vein also may flow craniad in the V. portalis renalis cranialis via its communications with the Sinus vertebralis internus (Fig. 12.16).

Rr. renales afferentes; Rdxx. renales efferentes. Rr. renales afferentes of Vv. portales renales may conduct venous blood into the kidney parenchyma, and mix there with arterial blood in the peritubular network of capillary sinuses (Siller, 1971); this mixed blood then drains into Rdxx. renales efferentes that empty into Vv. renales, leading ultimately into the system of V. cava caudalis. See **Urin.** Vasa sang. intraren.; Annot. 19; and Fig. 10.6.

(60) **Vv. segmentales synsacrales.** In the tail region local veins from the ventral surface of the uropygium empty on each side into the paired Vv. medianae caudae that flank the A. mediana caudae. Some of the tail segmental veins pass via afferent **Vv. intervertebrales** into the internal vertebral sinus, pars caudalis; more cranially

the sinus empties into the median caudal veins or interiliac anastomosis via efferent Vv. intervertebrales (Baumel, 1988). Cranial to this level efferent intervertebral veins from the sinus empty into the trunk of V. renalis caudalis that is located just lateral to the vertebral column (*Gallus*) or into the caudal renal portal vein (*Columba*). See Annot. 46 regarding internal vertebral sinus; Annot. 52 regarding V. cava caudalis; Annot. 62 regarding V. med. caud. and **Art.** Annot. 51).

(61) **Vv. oviductales marginales ventralis et dorsalis.** These marginal veins consist of longitudinal anastomoses between ascending and descending radices of the cranial, middle, and caudal oviductal veins. The marginal oviductal veins course in the ventral and dorsal ligaments of the oviduct with companion arteries., see **Art.** Annot. 67; and **Fem.** Annot. 35-44.

(62) **V. iliaca interna** (Neugebauer, 1845); **V. portalis renalis caudalis** (Fig. 12.16). Synonymy: V. hypogastrica; V. pudenda communis. The embryonic V. iliaca interna (Miller, 1903; Hamilton, 1952; Romanoff, 1960) is derived from the posterior cardinal vein. In the adult bird, *the caudal renal portal vein is defined as the segment of V. iliaca interna cranial to the interiliac anastomosis* (embryonic postcardinal anastomosis).

Anastomosis interiliaca. Synonymy: Arcus hypogastrica (Neugebauer, 1845) (see above and Figs. 12.11, 16).

V. mediana caudae. (Fig. 12.11) May be single or dual, flanking the A. mediana caudae. The medial caudal vein(s) may discharge into the interiliaac anastomosis (*Columba*) or join the V. pudenda (*Gallus*).

(63) **V. pudenda** (Neugebauer, 1845). The drainage territory of this vein from terminal parts of the urogenital and gastrointestinal tracts corresponds closely to that of the mammalian V. pudenda interna. The term, **V. bursocloacalis,** is taken from the study of Pintea, et al., 1967). Most of the venous drainage from the cloacal bursa in *Columba* is via V. bursalis of the V. mesenterica caudalis. See Fig. 12.11.

(64) **V. lateralis caudae.** (Fig. 12.11) Synonymy: V. musculocutanea caudae lateralis (Neugebauer, 1845); V. pudenda externa. V. lateralis caudae is a concise version of Neugebauer's term. This vein drains blood from the rectricial bulb (Baumel, 1988), its associated muscles, and integument of the dorsum of the uropygium; the vein (and its companion artery) passes cranioventrad, piercing the iliocaudal membrane behind the bony pelvis to enter the pelvic cavity.

V. cutanea abdominalis. (Bodrossy, 1938). This tributary of V. lateralis caudae partly drains the incubation patch (see Annot. 49) in *Columba.* In *Gallus* and *Meleagris* blood carried by V. cutanea abdominalis flows into V. femoralis caudalis, usually a tributary of V. ischiadica (see Fig. 12.18).

(65) **Vv. bulbi rectricium.** (Fig. 12.11) The three principal arteries to the bulb of the rectrices (tail flight quills) are accompanied by three veins: **V. dorsalis superficialis bulbi, V. dorsalis profunda bulbi, and V. ventralis bulbi.** These veins empty into the V. mediana caudae and V. lateralis caudae.

(66) **V. ischiadica.** (Figs. 12.16, 18) Caudal to the knee **V. poplitea** is the continuation of the caudal tibial vein; the popliteal vein is joined by the cranial tibial and fibular arteries. The prolongation proximally of the popliteal vein as it courses behind the femur is known as V. ischiadica. Just distal to the hip joint most of the blood from V. ischiadica is diverted to V. femoralis via the **Anastomosis ischiofemoralis** (Fig. 12.18) (Anastomosis venosa ischiofemoralis (Midtgård, 1982) which joins the femoral vein in the extensor compartment of the thigh. Consequently most of the venous

return from the hind limb enters the pelvis via the external iliac vein. Proximal to the ischiofemoral anastomosis the reduced part of V. ischiadica extends into the pelvis via the ilio-ischiadic foramen along with A. ischiadica, and terminates in V. portalis renalis caudalis. According to Midtgård (1982) this plan of venous drainage is present in most birds he has examined. See Fig. 12.18.

(67) **Vv. coxae.** These "veins of the hip" are substitute names for Vv. gluteae cranialis et caudalis. The cranial coxal vein empties into V. iliaca externa, the caudal coxal vein into V. ischiadica. See **Art.** Annot. 70.

(68) **V. femoralis caudalis.** A substitute term for V. profunda femoris (see **Ven.** Annot 65). This tributary of the ischiadic vein in the flexor musculature of the thigh is usually single in most species examined (Midtgård, pers. comm.) Consult **Art.** Annot. 71 for remarks relating to V. circumflexa femoris lateralis. See Fig. 12.18.

(69) **V. suralis.** (Fig. 12.18) Term of Neugebauer (1845) and Bodrossy (1938). Discussion of use of "sural" for vessels of the crus is found in **Art.** Annot. 74.

(70) **Vv. metatarsales.** Terminology of the vessels of the foot is from the comprehensive comparative studies of Midtgård (1978;1982) and the highly detailed work of Volmerhaus and Hegner (1963). The main digital veins drain into the **Arcus plantaris superficialis** in nearly all birds that have been studied. Like the arteries, the main digital veins may pass the metatarsal trochleae on either the dorsal or plantar side of the foot. Two superficial metatarsal veins (**V. metatarsalis plantaris superficialis (medialis/lateralis)**) extend up the tarsus from the plantar arch; usually the medial vein is much more prominent, and continues up the crus as V. tibialis caudalis (see Annot. 71). (The medial superficial vein is the V. metatarsea interna or magna of Neugebauer, 1845). The lateral vein joins the caudal tibial vein above the intertarsal joint. See **Art.** Annot. 79.

The **V. metatarsalis plantaris profunda** travels with its artery, and traverses the vascular foramen at the proximal end of the tarsometatarsus to join the cranial tibial vein.

The small **Vv. dorsales metatarsales** are companion veins of the dorsal metatarsal arteries. In *Gallus* they drain into the **V. metatarsalis dorsalis communis** which itself empties into the medial superficial plantar metatarsal vein (Volmerhaus and Hegner, 1963).

(71) **V. tibialis cranialis.** The cranial tibial vein does not accompany A. tibialis cranialis through the distal tibio-fibular interosseous foramen, but runs with A. fibularis through the proximal interosseous foramen where it joins V. tibialis caudalis just distal to the knee joint (see **Arthr.** Fig. 5.7).

V. tibialis caudalis. This vein carries most of the venous blood of the foot and leg centrally; in the knee region the caudal tibial vein changes its name to **V. poplitea** which itself becomes the V. ischiadica in the lower thigh (Annot. 66) (see Midtgård, 1978).

(72) **Rete tibiotarsale.** Synonymy: Rete mirabile tibiotarsale. In many different birds this is a network of anastomosing veins that parallels the cranial tibial artery opposite the cranial surface of the distal tibiotarsal, tarsal, and proximal metatarsal regions. The venous rete is intermingled with an arterial rete derived from multiple small branches of the fibular and cranial tibial arteries. The mixed rete varies from simple to elaborate in different taxa, and functions as a counter-current mechanism concerned with heat retention or dissipation (Midtgård, 1981; **Art.** Annot. 24, 77).

(73) **Vv. fibulares [peroneae] superficialis/profunda.** These fibular veins derive their names from the fact that they accompany the superficial and deep rami of the fibular nerve and their companion branches of the fibular artery (Baumel, 1975c; Midtgård, 1982). Multiple, plexiform counter-current veins that contribute to the Rete tibiotarsale are derived from fibular and cranial tibial veins (Midtgård, 1981).

(74) **V. pubica** (Baumel, 1975c). This tributary of the femoral vein courses within the attachments of the abdominal muscles to the pubis; they parallel the ventral border of the pubis. For synonymy see **Art.** Annot. 69. See Fig. 12.18.

(75) **Systema portale hepatis.** Inasmuch as birds also possess renal, adrenal, and hypophysial portal systems, the designation "hepatic portal" must be employed for the afferent veins conducting venous blood to the liver from the digestive viscera (proventriculus to rectum) and the spleen. Not only does the liver have afferent veins (most birds have a major right portal vein and a lesser left portal vein), but also receives arterial blood from the hepatic arteries, mainly via branches of the celiac artery. Veins that drain blood from the liver into the caudal vena cava are referred to simply as "hepatic veins" (see **Digest.** Annot. 106).

(76) **V. portae dextrae hepatis.** This "vein of the right entrance of the liver" is formed by the confluence of the common mesenteric vein with the gastropancreaticoduodenal and pancreaticosplenic veins. In *Buteo* (Malinovský, 1965) and *Gallus* (Miyaki, 1978) a common intrahepatic distribution of the short trunk of this vein is to the lateral part of the right lobe of the liver and via branches of an elongated, transverse left ramus to the medial region of the right liver lobe (see Annot. 77). This left ramus in some individuals extends to the left lobe to which it may contribute. In the junctional region of left and right lobes the left ramus anastomoses with V. portae sinistrae hepatis. Each ramus gives off three principal branches to its lobe. See **Digest.** Annot. 94.

(77) **Pars transversa.** This transverse part of Ramus sinister of the right hepatic portal vein yields numerous smaller dorsal and ventral rami and one or more substantial **Rr. mediani dorsales et ventrales** into Pars interlobaris of the liver (Pavaux and Jolly, 1968; Miyaki, 1973, 1978).

(78) **Vv. mesentericae cranialis/caudalis; [V. coccygomesenterica].** "V. coccygomesenterica" is firmly established in the literature, and is retained as an alternative term for **V. mesentérica caudalis.** The radices of this vein accompany the rami of A. mesenterica caudalis, and require the corresponding names. Near the junction of its cranial and caudal radices, V. mesenterica caudalis is confluent with Anastomosis interiliaca (see Figs. 12.11, 16).

Near the liver V. mesenterica caudalis joins **V. mesenterica cranialis** forming the **V. mesenterica communis.**

(79) **Vv. proventriculares.** These veins join Vv. splenicae in *Buteo* and *Gallus* (Malinovský, 1965), and produce the **V. proventriculosplenica,** a substantial tributary of V. portalis hepatica dextra; in other birds (e.g., *Columba*) proper Vv. splenicae drain directly into V. portalis hepatica dextra (see Annot. 51).

(80) **V. portae sinistrae hepatis.** A small, distinct V. portalis hepatica sinistra is formed by confluence of V. proventricularis caudalis, V. proventricularis ventralis, V. gastrica ventralis, and V. gastrica sinistra in *Buteo* (Malinovský, 1965) and *Gallus* (Miyaki, 1978). In other taxa, e.g., *Sturnus* (Cralley, 1965) and *Melopsittacus*) (Szabo, 1958), the gastric and proventricular veins empty individually into Ramus

sinister of the right hepatic portal vein. In *Gallus* V. portae sinistrae hepatis is distributed into the entire the left lobe, or a portion of it, in about one-fourth of the series investigated by Miyaki (1978); in the remainder of the series the left hepatic portal vein joins the R. sinister of the right hepatic portal or one of its branches. See Fig. 12.17 and **Digest.** Annot. 94.

(81) **Vv. portales hepaticae propriae** (Neugebauer, 1845). These small veins convey blood from the abdominal air sacs and adjacent peritoneum, and enter the ipsilateral lobe of the liver independent of Vv. portalis hepatica sinistra or dextra (Pavaux and Jolly, 1968; Miyaki, 1978); Miyaki suggested that these afferent veins be referred to as air sac veins rather than hepatic portal veins.

(82) **Vv. segmentales.** Vv. segmentales of neck, trunk, and tail drain to a great extent into Sinus vertebralis internus. For other connections of Vv. segmentales see **Ven.** Annot. 46, 52, 60. In the region of the lumbar intumescence of the spinal cord Sinus vertebralis internus is lacking; in this region Vv. segmentales empty into Vv. renales. Some of the segmental veins in the caudal region also flow via intervertebral veins into the internal vertebral sinus (*Columba*, Baumel, 1988) which then drains via **Vv. efferentes sinus vertebralis interni** (Annot. 82) into V. iliaca interna (Fig. 12.19)

(83) **Vv. vertebromedullares.** Synonymy: Vv. spinales. The alternate term, Vv. vertebromedullares, was introduced by Sterzi (1903); names for the tributaries of Vv. vertebromedullares follow the terminology of Lob (1967) in *Gallus;* as the name indicates, these veins drain venous blood from the spinal cord, meninges, bone, and joints of the vertebral column itself. See **Art.** Annot. 84.

(84) **V. spinalis ventralis.** The ventral spinal artery on the spinal cord is doubled along part(s) of the its length. Both V. spinalis ventralis and V. radicularis ventralis are best developed opposite the Corpus gelatinosum of the lumbar intumescence of the spinal cord (Medulla spinalis).

(85) **Vv. sulci.** These veins in the ventral sulcus of the spinal cord receive drainage from the ventral commissure and most of the gray matter of the cord (Lob, 1967).

(86) **Vv. marginales.** Synonymy: Vv. periphericae (Sterzi, 1903). Drain via short radial radicles into surface veins (vasocorona) that receive blood from the dorsolateral white matter of the spinal cord to the level of the apposition of white and gray matter (Lob, 1967).

(87) **Vv. ventrolaterales.** Weakly developed longitudinal veins along the line of attachment of the ventral nerve rootlets to the spinal cord.

(88) **Vv. radiculares ventrales.** Stronger than Vv. radiculares dorsales (Lob, 1967).

(89) **V. spinalis dorsalis.** This longitudinal vein courses in the median dorsal sulcus of the spinal cord, and is somewhat weaker than its ventral counterpart.

(90) **Vv. dorsolaterales.** These longitudinal veins course along the line of attachment of the dorsal nerve rootlets to the spinal cord.

(91) **Vv. fissurae.** These veins drain into Vv. dorsolaterales; Vv. fissurae drain blood from the white matter located dorsal to the dorsal commissure of the gray matter of the spinal cord.

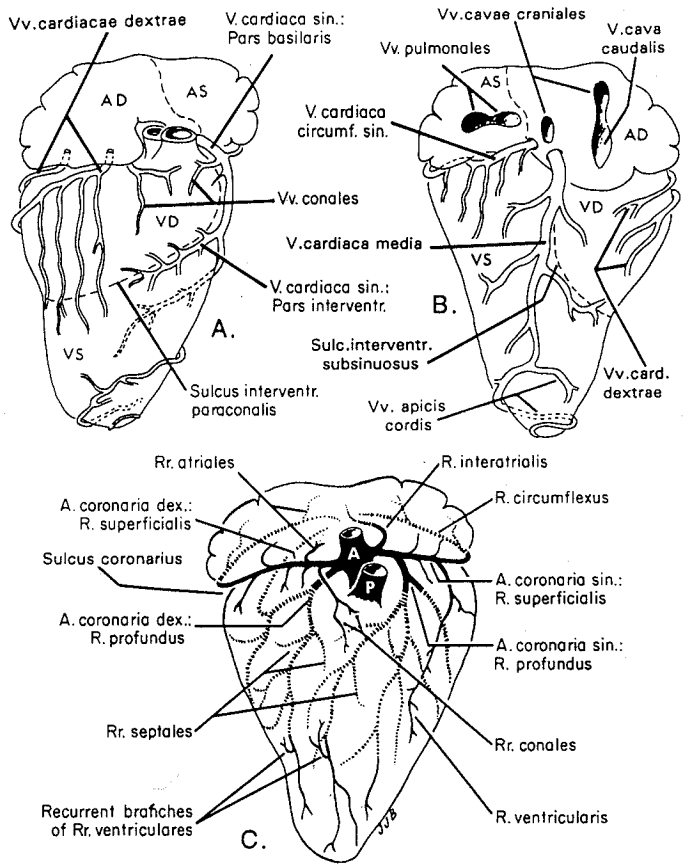

Fig. 12.1. Heart, coronary arteries, and cardiac veins; *Gallus*. A, B redrawn from Baumel (1975) after Lindsay (1967); C, redrawn from Baumel (1975c). A, Facies ventrocranialis of heart; B. Facies dorsocaudalis; C, Facies ventrocranialis. In the ventricles the cross-hatched lines represent the parts of the deep rami of the coronary arteries that are embedded in the myocardium of the ventral and right side of the Septum interventriculare. With permission of Academic Press.

Abbreviations: A, Aorta ascendens; AD, Atrium dextrum; AS, Atrium sinistrum; circumf., circumflexa; dex., dextra; interventr., interventricularis; P, Truncus pulmonalis; sin., sinistra; VD, Ventriculus dexter; VS, Ventriculus sinister.

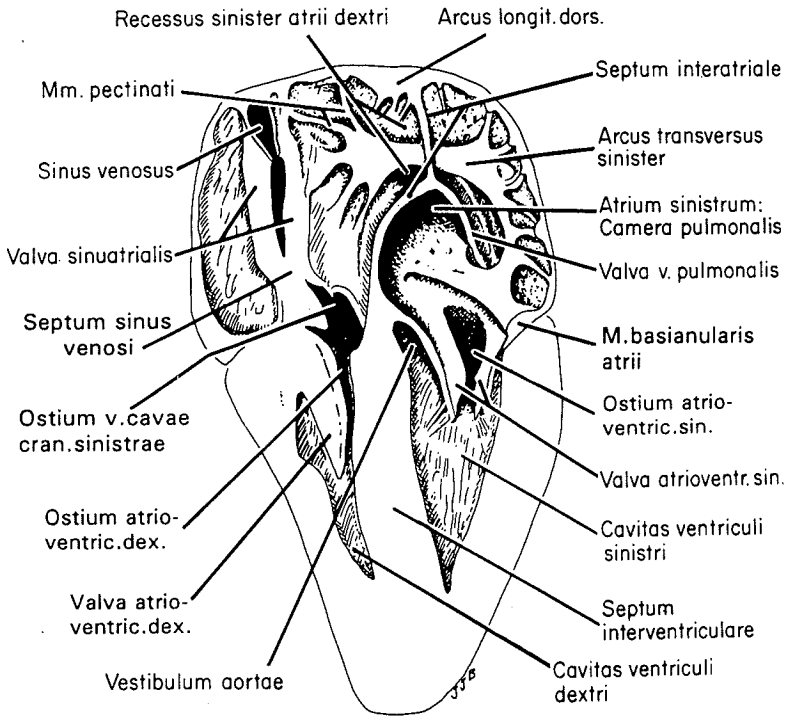

Fig. 12.2. Interior features of heart; *Gallus*. Heart sectioned in the dorsal plane; ventrocranial view. Redrawn from Baumel (1975c) after Quiring (1933-34). With permission of Academic Press.

Abbreviations: atrioventr., atrioventricularis (arum); dex., dextra(um); longit., longitudinalis; sin., sinistra(um).

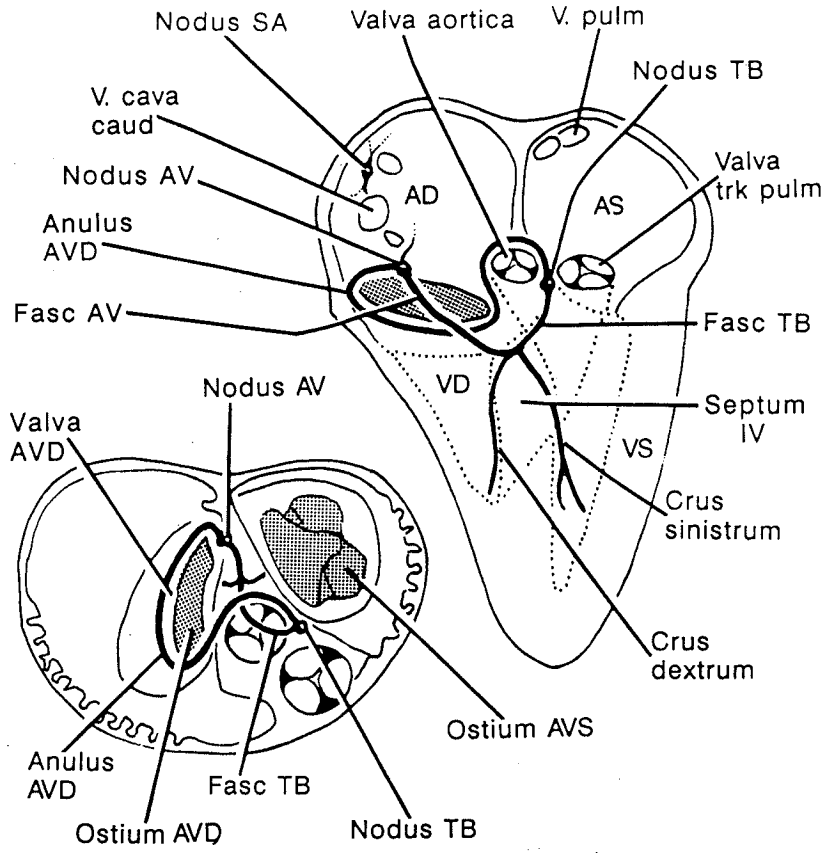

Fig. 12.3. Cardiac impulse conducting system of the avian heart. Adapted from Kim and Yasuda (1979). *Bottom left,* cranial view, atria removed; *Top right,* longitudinal section in a dorsal plane with the cranioventral part of the heart removed.

Abbreviations: AVD, atrioventriculare dextrum; AVS, atrioventricularis sinistra; IV, interventriculus; V. pulm., V. pulmonalis; TB, truncobulbaris; trc. pulm., trunci pulmonalis.

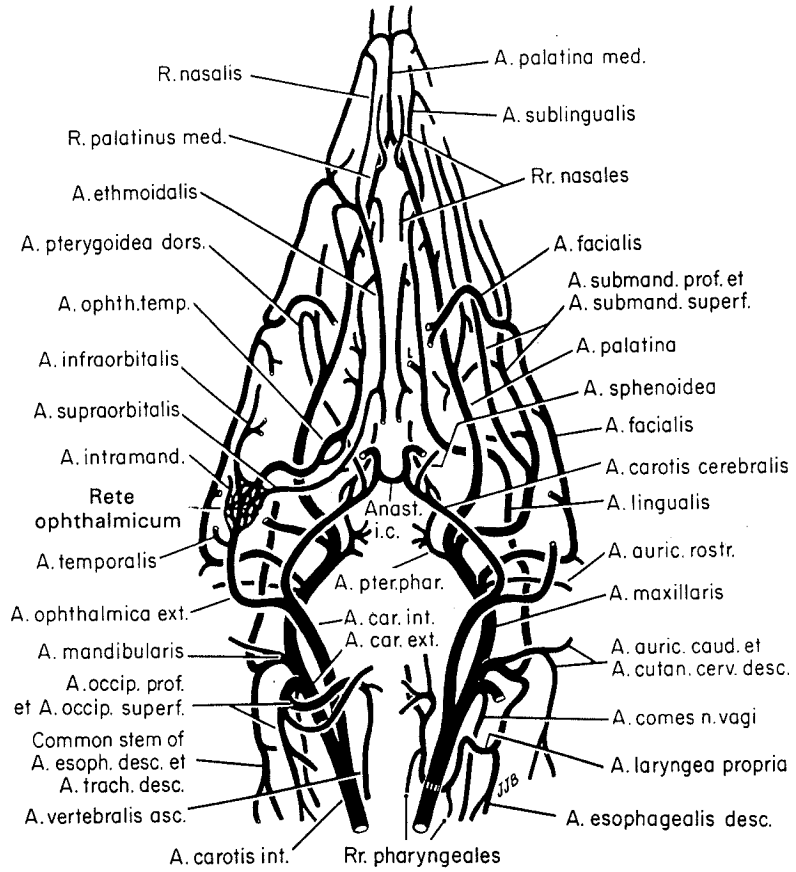

Fig. 12.4. Arteries of head, extracranial; *Gallus*. Dorsal view. Redrawn from Baumel (1975c). The right side of the drawing emphasizes the details of the more ventrally situated arteries, while the left side features the more dorsally situated arteries. With permission of Academic Press.

Abbreviations: Anast. i.c., Anastomosis intercarotica; auric., auricularis; car., carotis; cutan., cutanea; esoph., esophagealis; intramand., intramandibularis; L., A. lingualis propria; occip., occipitalis; prof., profunda; pter. phar., pterygopharyngealis; Rete ophth., Rete ophthalmica; submand., submandibularis; superf., superficialis; trach., trachealis.

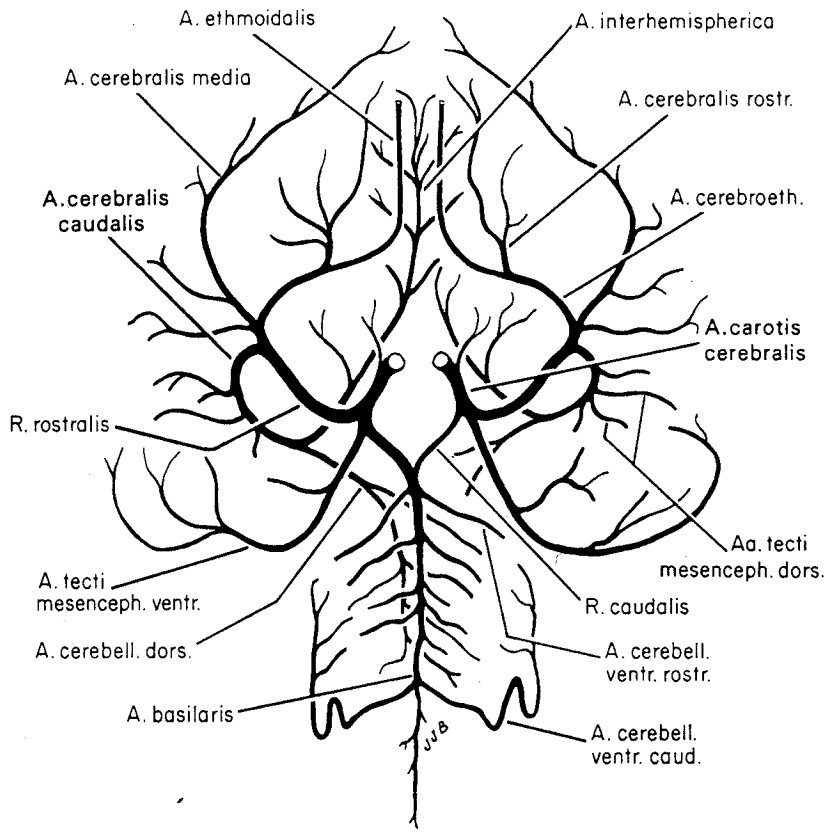

Fig. 12.5. Encephalic arteries; *Gallus*. Ventral view. Redrawn from Baumel (1975c) after Shiina and Miyata (1932). Note the asymmetry in: (1) the roots of A. basilaris; (2) A. interhemispherica; and (3) A. cerebellaris dorsalis. See **Art.** Annot. 20, 21 for details. With permission of Academic Press.

Abbreviations: cerebell., cerebellaris; mesenceph., mesencephali.

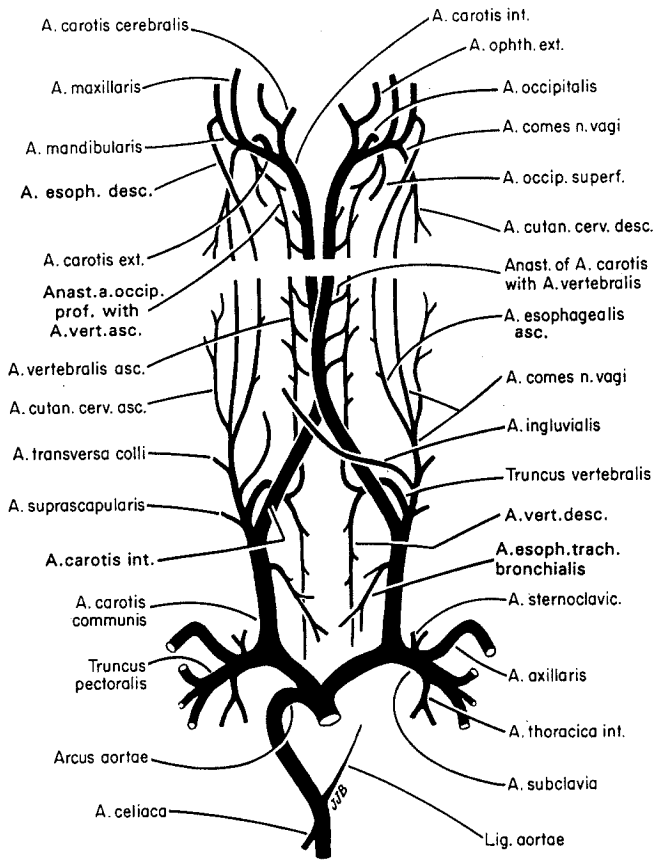

Fig. 12.6. Arteries of cervical region; *Columba livia*. Ventral view; foreshortening indicated by the white transverse band across the figure. Redrawn from Baumel (1964) and Bhaduri and Biswas (1954). With permission of Academic Press.

A. carotis communis consists of a short trunk in the root of the neck; its principal branch is A. carotis interna. A. carotis externa branches from the cranial end of A. carotis interna in adult birds; see **Art.** Annot. 15) regarding the foetal condition.

In many bicarotid birds (**Art.** Annot. 15) the two internal carotids converge as they ascend cranially; they course side by side in the Canalis caroticus cervicalis (**Osteo.** Annot. 121) of the middle segment of the neck.

Note the hexagonal configuration produced by the brachiocephalic arteries, the common carotids and the proximal parts of the internal carotids (Bhaduri and Biswas, 1954).

Abbreviations: cutan., cutanea; cerv., cervicalis; esoph. trach. bronch., esophagotracheobronchialis; occip., occipitalis; ophth., ophthalmica; vert., vertebralis.

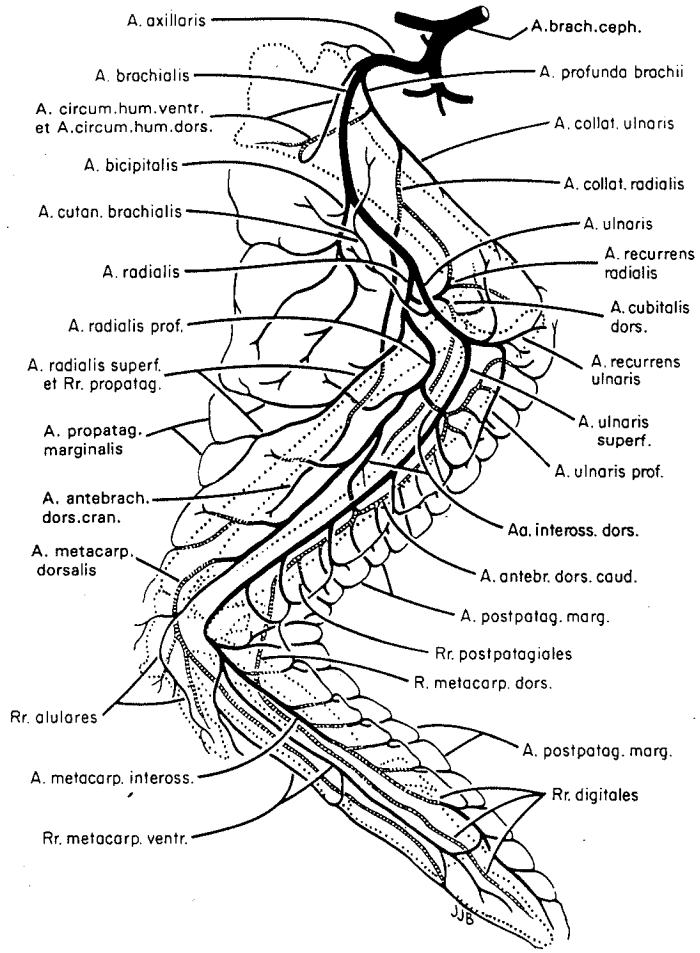

Fig. 12.7. Arteries of wing, ; *Columba livia*. Right side, ventral view. Original drawing, J. J. Baumel. Broken lines represent vessels dorsal to the skeleton. With permission of Academic Press.

Abbreviations: antebr., antebrachialis; circumf., circumflexa; collat., collateralis; cutan., cutanea; hum., humeri; inteross., interossea; marg., marginalis; metacarp., metacarpalis; postpatag., postpatagialis(es); propatag., propatagialis(es).

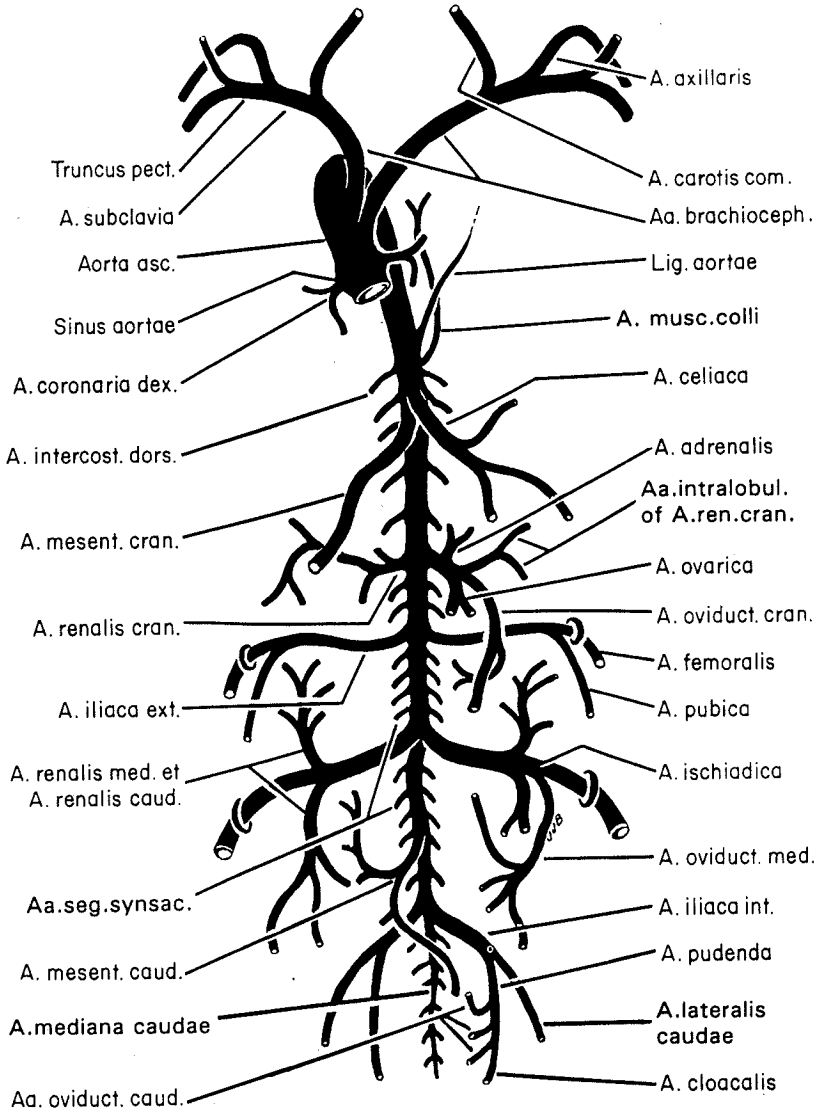

Fig. 12.8. Main branches of Aorta; *Gallus*, female; ventral view. Note on left side of specimen the prominent ovarian and oviductal arteries springing from A. renalis cranialis, A. ischiadica, and A. iliaca interna (see **Art.** Annot. 66, 67, 72 for details). With permission of Academic Press.

Abbreviations: dex., dextra; intercost., intercostalis; seg., segmentales; mesent., mesenterica; oviduct., oviductalis(es).

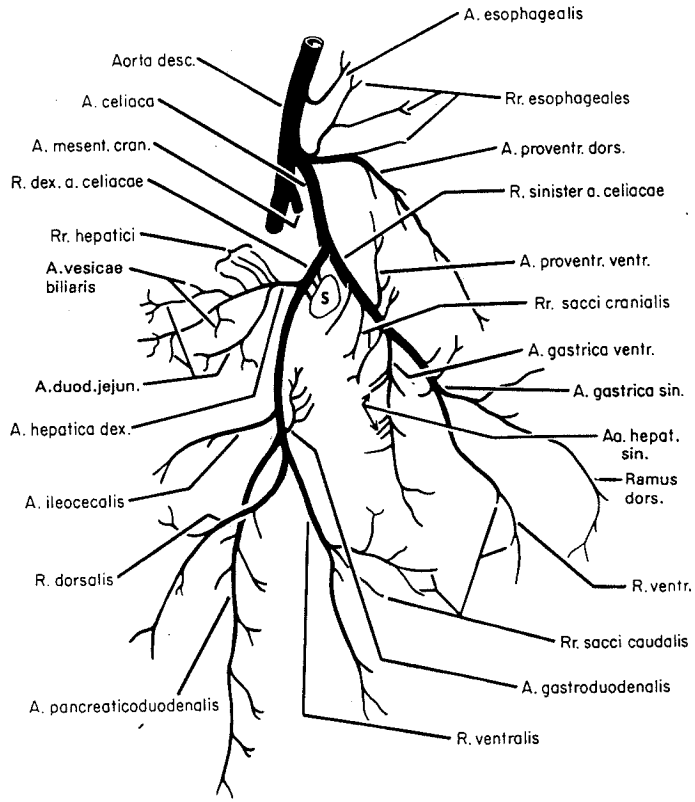

Fig. 12.9. Pattern of branching of A. celiaca in the goose, *Anser anser;* ventral view. Redrawn from Malinovský and Visnanska (1975). The A. celiaca supplies the glandular and muscular stomachs, liver, pancreas, spleen and small intestine (see **Art.** Annot. 54-64). With permission of Academic Press.

Abbreviations: dex., dextra(er); duodenojejun., duodenojejunalis; proventr., proventricularis; sin., sinistra(e).

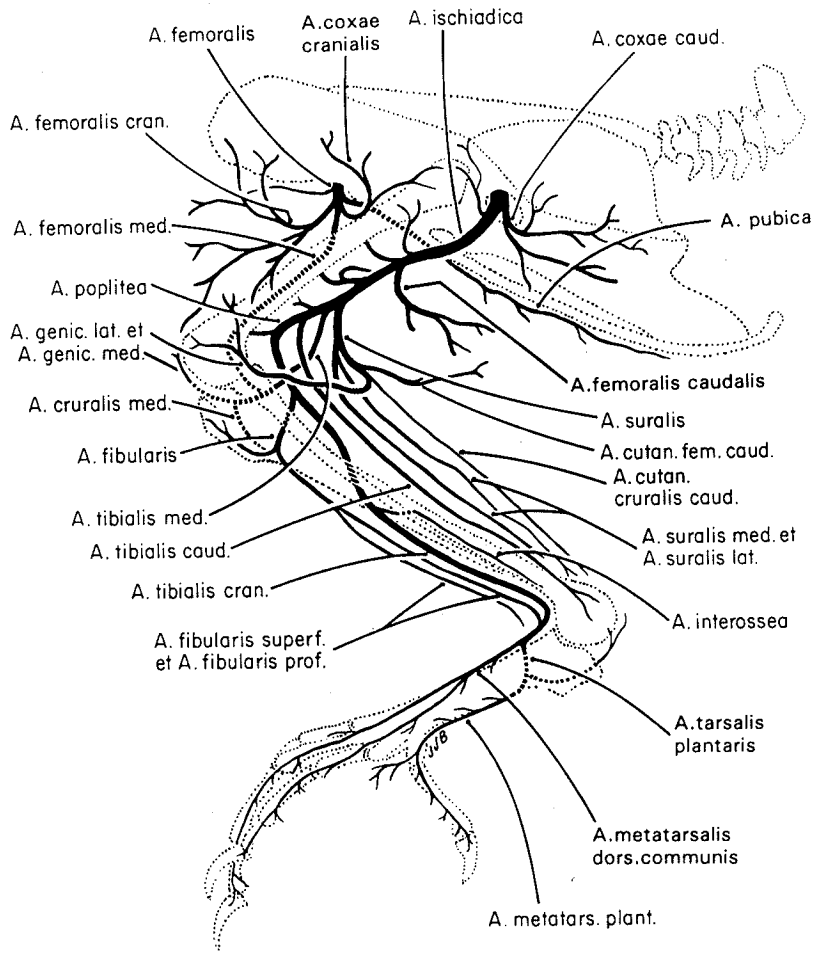

Fig. 12.10. Arteries of pelvic limb; *Columba livia*. Left side, lateral view. Original drawing, J. J. Baumel. With permission of Academic Press.

Abbreviations: cutan., cutanea; dist. caud., distocaudalis; fem., femoralis; genic., genicularis; metatars., metatarsalis; plant., plantaris; prof., profunda; prox. caud., proximocaudalis; superf., superficialis.

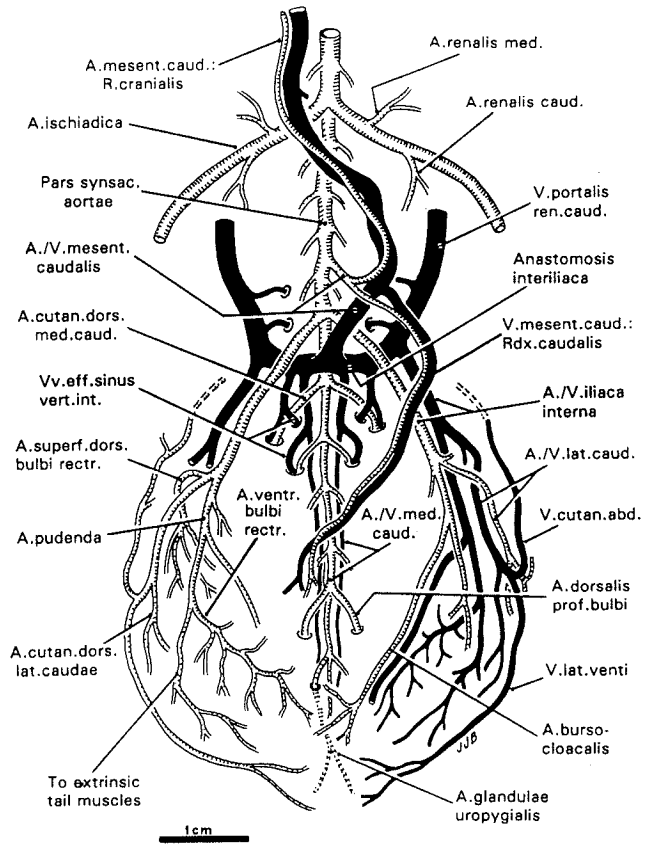

Fig. 12.11. Arteries and veins of tail region, *Columba livia;* ventral view. From Baumel (1975c). By courtesy of Springer-Verlag.

Tributaries of V. iliaca interna are shown on the *right side* of the figure; branches of A. iliaca interna on the *left side*. Arteries *hatched;* veins *solid black*. Note: (1) communication of V. mesenterica caudalis with the transverse Anastomosis interiliaca; (2) the prolongation of the internal iliac vein cranially past the anastomosis courses within kidney substance, this part being designated the caudal renal portal vein (see **Ven.** Annot. 62).

Abbreviations: abd., abdominalis; cutan., cutanea; eff., efferentes; mesent., mesenterica; rectr., rectricium; synsac., synsacralis.

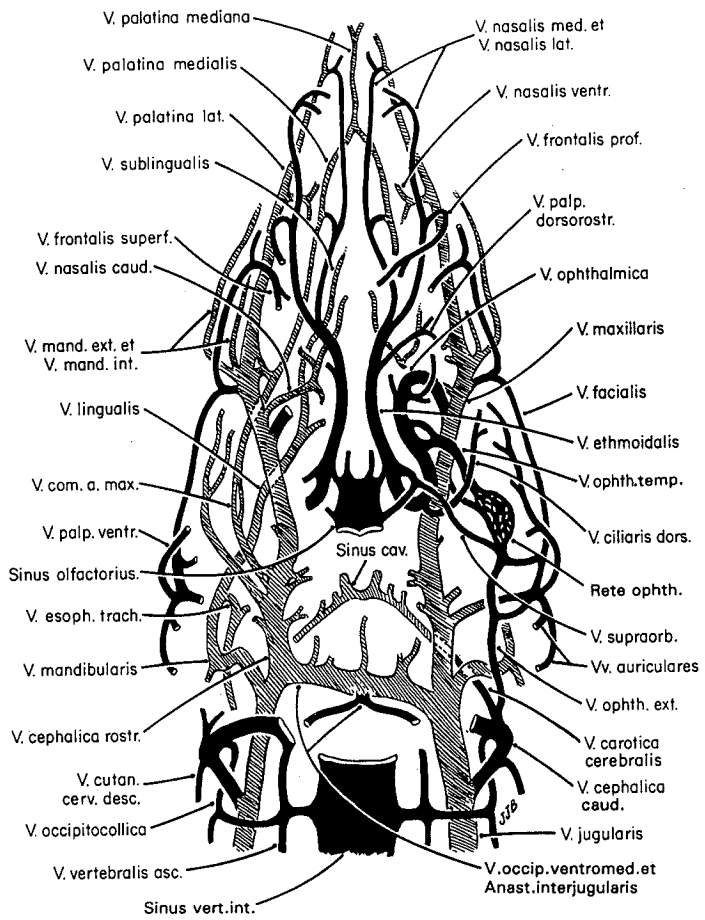

Fig. 12.12. Veins of head, extracranial; *Gallus.* Dorsal view. Redrawn from Baumel (1975). Black veins are located *closer* to the viewer (more dorsally) than the *more distant* hatched veins. With permission of Academic Press.

Abbreviations: ophth., ophthalmica; palp., palpebralis; Rete ophth., Rete ophthalmicum; Sinus cav., Sinus cavernosus; vert., vertebralis.

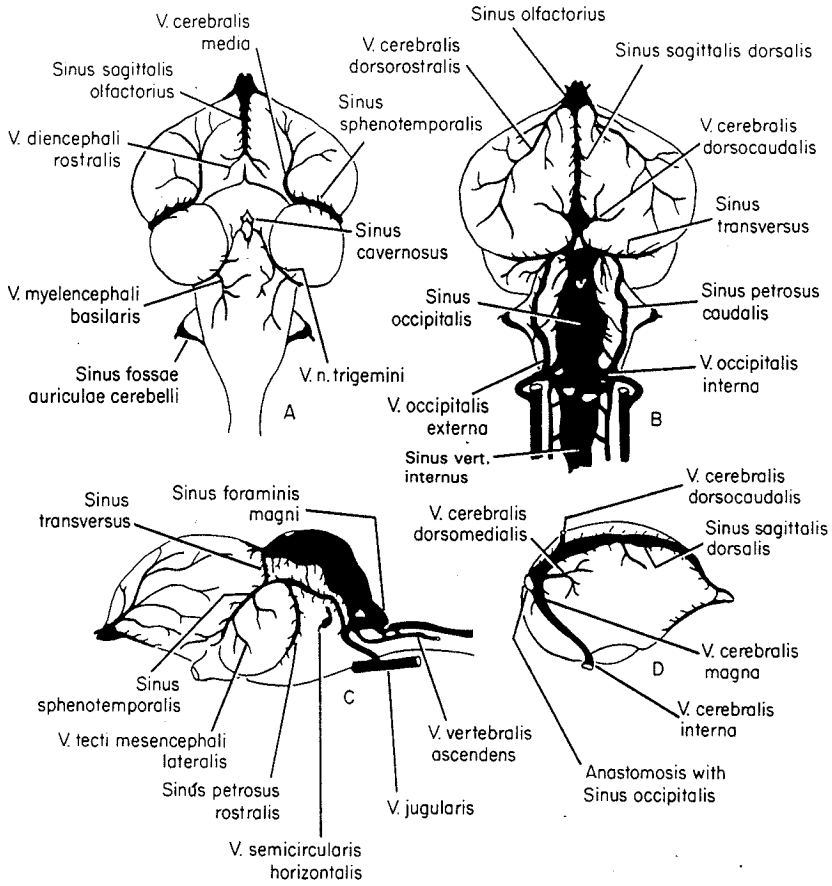

Fig. 12.13. Dural venous sinuses and encephalic veins; *Gallus.* A., ventral aspect of the brain; B., dorsal aspect of brain; C., left lateral aspect of brain; D., medial aspect of left telencephalic hemisphere. Redrawn from Kaku (1959) with modifications. With permission of Academic Press.

Most of the encephalic venous blood leaves the cranial cavity via, or in the vicinity of, the Foramen magnum where the dural sinuses empty into the jugular veins and the internal vertebral sinus. See Fig. 12.12; consult Baumel (1975c) for a brief account of the dural sinuses and the veins of brain.

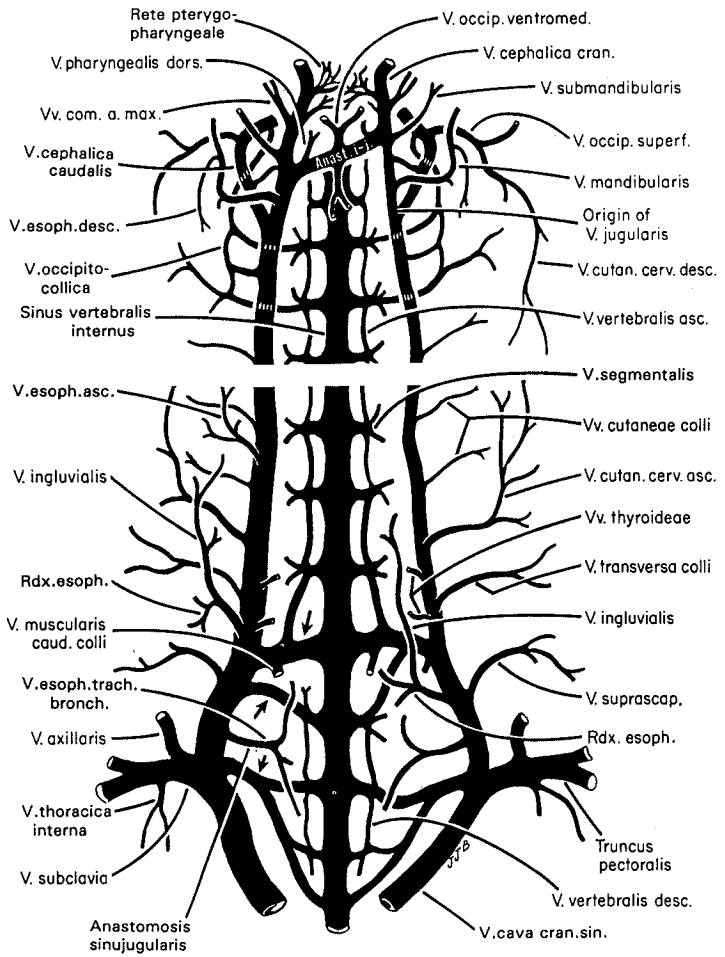

Fig. 12.14. Venous channels of cervical region; *Gallus*. Ventral view; foreshortening indicated by the white transverse band across the figure. Original drawing of J. J. Baumel. With permission of Academic Press.

Three longitudinal venous channels drain venous blood of the head and neck. Note the asymmetry of the jugular veins, the right jugular vein larger than the left one. The Anastomosis interjugularis actually connects the two cranial cephalic veins, not the jugulars per se. Sinus vertebralis internus communicates with the cranial dural sinuses via the Foramen magnum (see Fig. 12.13); the sinus drains at the root of the neck into the jugular veins on each side via several Anastomoses sinujugulares (*arrows*). The sinus lies in the epidural space of the vertebral canal dorsal to the spinal cord (see Baumel, 1975c).

Abbreviations: Anast. i-j., Anastomosis interjugularis; cerv., cervicalis; com., comitantes; cutan., cutanea; max., maxillaris; occip., occipitalis; Rete pteryg. pharyng., Rete pterygopharyngeale; esoph. trach. bronch., esophagotracheobronchialis; vert., vertebralis.

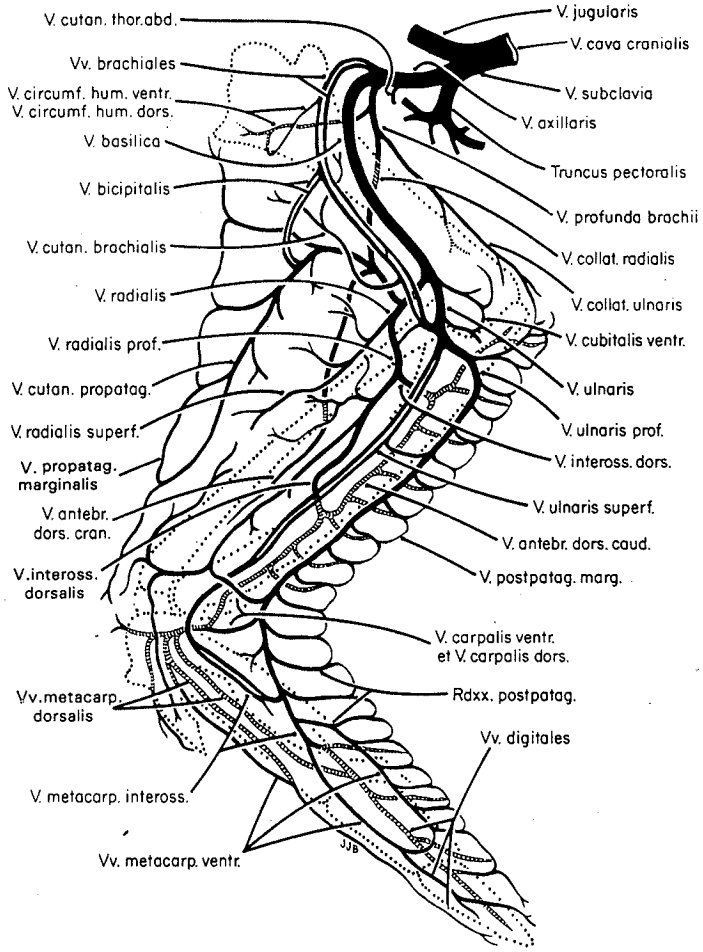

Fig. 12.15. Veins of wing; *Columba livia*. Right side, ventral view. Broken lines represent vessels dorsal to the skeleton of the wing. Note that: (1) V. ulnaris profunda is the strongest antebrachial vein, whereas its corresponding artery is rather weak; (2) V. basilica is the main vein of the brachium; (3) the confluence of V. subclavia and V. jugularis and Truncus pectoralis produces V. cava cranialis on each side (Fig. 12.14); hence brachiocephalic veins are not present in birds. With permission of Academic Press.

Abbreviations: antebr., antebrachialis; circumf., circumflexa; collat., collateralis; cutan., cutanea; hum., humeri; inteross., interossea; marg., marginalis; metacarp., metacarpalis; postpatag., postpatagialis(es); propatag., propatagialis; thor. abd., thoracoabdominalis.

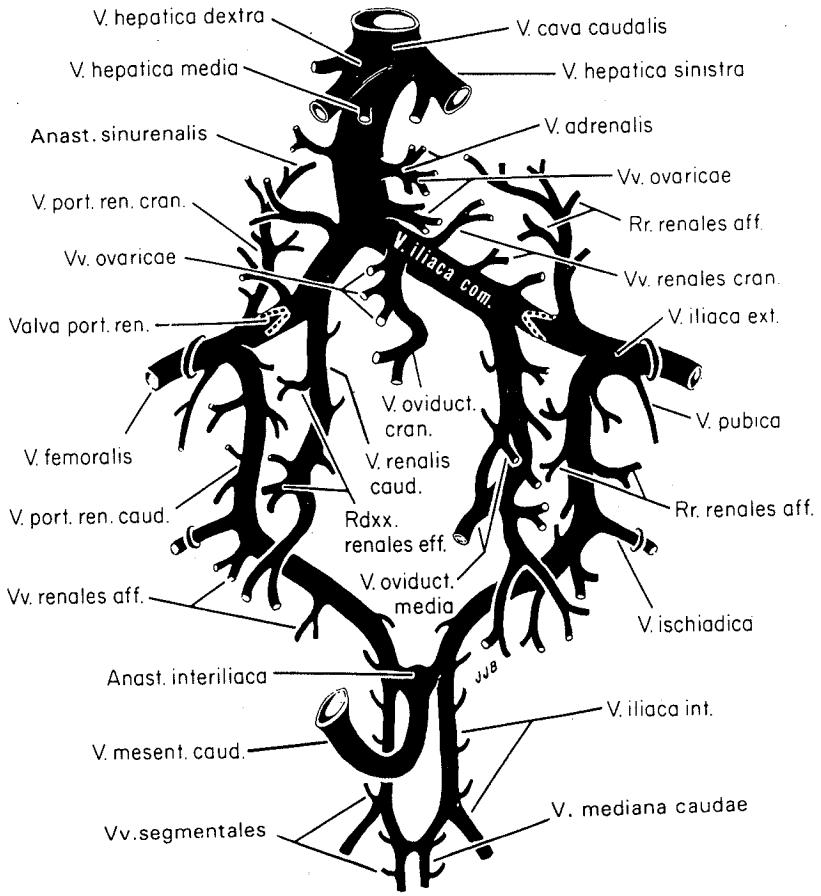

Fig. 12.16. Caudal vena cava and renal portal system of veins; *Gallus*. Ventral view. Redrawn from Baumel (1975c). See **Ven.** Annot. 62 that deals with the development of V. iliaca interna and explains the apparent inconsistency in the naming of V. iliaca communis. See also **Urogen.** Fig. 10.6. With permission of Academic Press.

Abbreviations: Aff., afferentes; anast., anastomosis; com., communis; eff., efferentes; mesent., mesenterica; oviduct., oviductalis; port., portalis; ren., renalis; ven., venosus; vert., vertebralis.

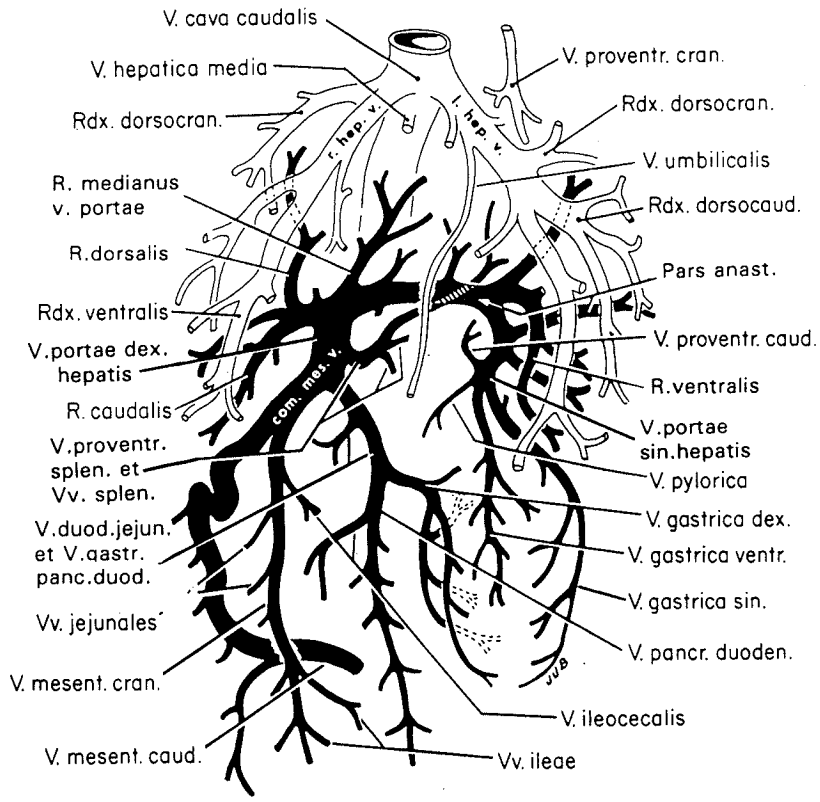

Fig. 12.17. Hepatic portal system and hepatic veins; *Gallus*. Ventral view. Redrawn from Baumel (1975c). At upper right of drawing observe V. proventricularis cranialis which is not a tributary of Systema portale hepatis; see **Ven.** Annot. 51 for details. With permission of Academic Press.

Abbreviations: com. mes. v., V. mesenterica communis; dex., dextra; duod(en)., duodenalis; gastr. pancr. duoden., gastopancreaticoduodenalis; hep., hepatica; jejun., jejunalis; l. hep. v., V. hepatica sinistra; mesent., mesenterica; pancr. duoden., pancreaticoduodenalis; port., portae; proventr., proventricularis; sin., sinistra.

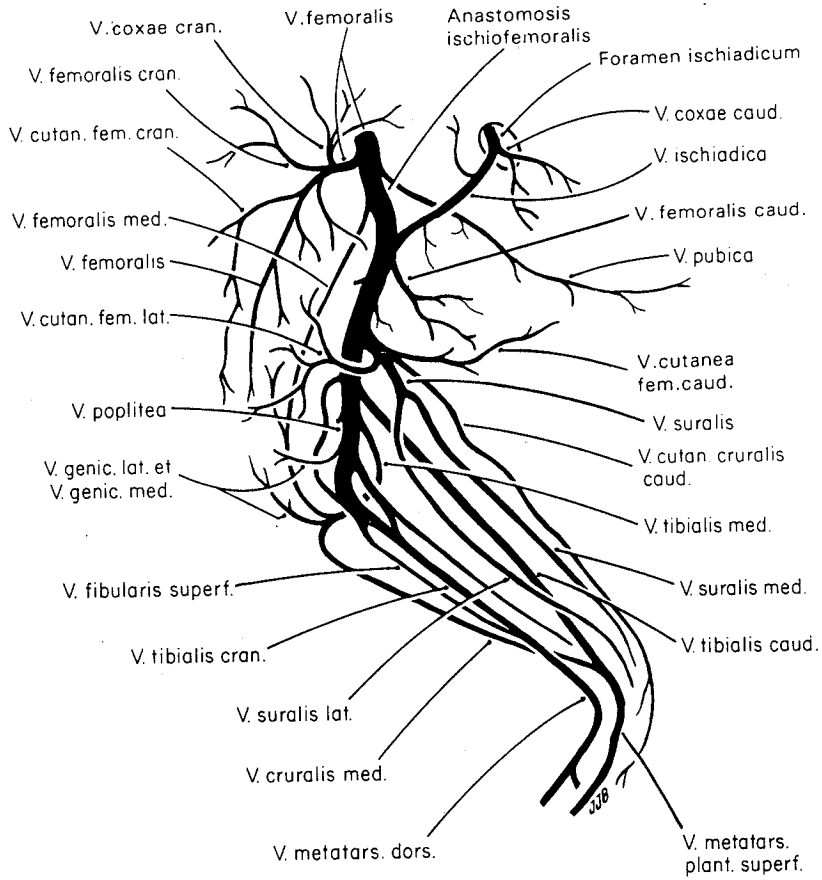

Fig. 12.18. Veins of pelvic limb; *Columba livia.* Left side, lateral view. Original drawing, J. J. Baumel. Although V. ischiadica is the main vein of the pelvic limb, most of the blood from the territory drained by V. ischiadica enters the pelvis via V. femoralis. This is accomplished by means of the huge Anastomosis ischiofemoralis (**Ven.** Annot. 66) on the medial side of the femur connecting the two veins at a level slightly distal to the hip joint. With permission of Academic Press.

Abbreviations: cutan., cutanea; fem., femoralis; genic., genicularis; metatars., metatarsalis; plant., plantaris; prof., profunda; superf., superficialis.

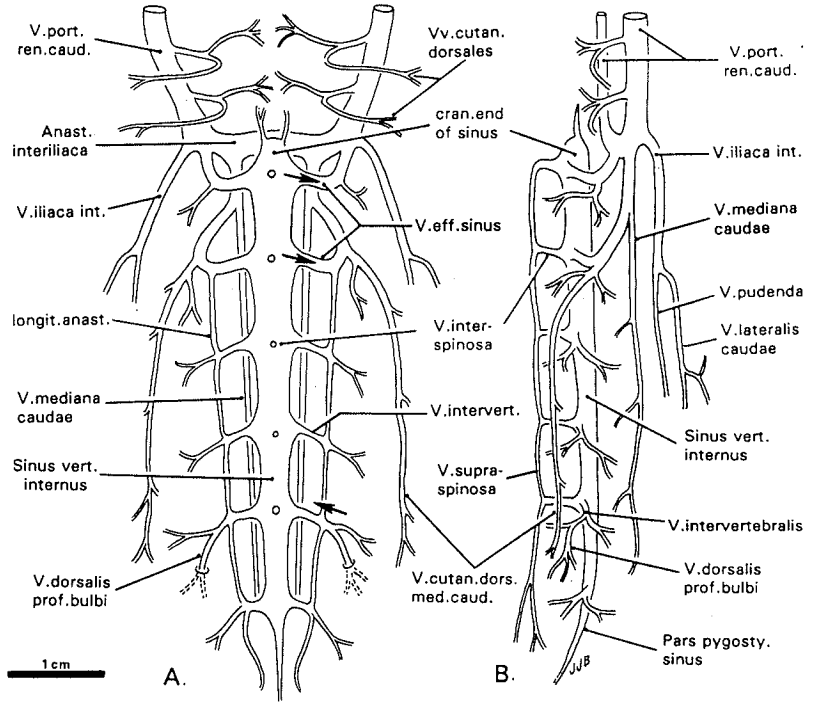

Fig. 12.19. Tail segment of the internal vertebral (epidural) sinus and its venous communications in the pigeon. A Dorsal view; B right lateral view. From Baumel (1988). With permission of Springer-Verlag.

The caudal part of the internal vertebral sinus is located on the dorsum of the spinal cord, within the vertebral canal of the tail; its cranial extremity is near the rear end of the synsacrum. The sinus is lacking in most of the synsacral part of the vertebral canal. See **Ven.** Annot. 46, 82 for remarks on the thoracic and cervical segments of the sinus.

Much of the venous blood from the dorsal side of the uropygium drains via afferent (intervertebral) veins into the caudal part of the sinus; the blood flows forward in the sinus, leaving the sinus via efferent sinus (intervertebral) veins which themselves empty into the main veins on the ventral side of the uropygium. *Arrows* alongside, or on, the afferent and efferent veins indicate the direction of blood flow. The supraspinous vein is not shown on A; the interspinous veins are indicated by small circles on the dorsum of the sinus in A. The longitudinal anastomosing veins that connect adjacent intervertebral veins are not depicted on B.

Abbreviations: anast., anastomosis; cutan., cutaneae; eff. efferens; intervert., intervertebralis; longit., longitudinal; port, portalis; pygosty., pygostylaris; ren, renalis; vert., vertebral.

13

SYSTEMA LYMPHATICUM ET SPLEN

D. BERENS V. RAUTENFELD

With contributions from subcommittee members: I. Bázantová, G. Fehér, W. Lippert-Burmester, L. N. Payne, K. Pohlmeyer, J. Schlüns.

TERMINOLOGY

Rete lymphaticum initiale
Vas lymphaticum initiale[1]
Sinus lymphaticus initialis [Vas lymphocapillare][2]
  Fibrae basilares[3]
  Fibrae fixationes[3]
  Accessus interendothelialis[3]
  Ponticulus endothelialis[3]
Vas l. precolligens [Vas l. precollectorium][4]
Vas l. fibrotypicum[4]
  Valvula lymphatica
  Fibrae basilares[3]
  Fibrae fixatiónes[3]
  Accessus interendothelialis
  Ponticulus endothelialis[3]
  Trabecula fibroendothelialis[4]
Vas l. colligens [Vas l. collectorium][5]
  Vas l. colligens superficiale[5]
  Vas l. colligens profundum[5]
Vas l. myotypicum[5]
  Valvula lymphatica
  Plexus lymphaticus colligens
Cor lymphaticum[6]
  Trabecula myofibroendothelialis[6, 4]
Lymphonodulus solitarius [Nodulus lymphaticus solitarius][7]
  Centrum germinale[7]
Lymphonodulus aggregatus [Nodulus lymphaticus aggregatus]
Lymphonodus [Nodus lymphaticus][8]
  Vas l. afferens[8]
  Capsula[8]
  Sinus lymphaticus intranodalis[8]
  Chorda lymphoreticularis[8]
  Lymphonodulus solitarius
  Venula postcapillaris[8]
  Vas l. efferens[8]
Formatio lymphoreticularis muralis interna[9]
Formatio lymphoreticularis muralis externa[9]
  Sinus lymphaticus intramuralis[9]
  Venula postcapillaris[9]
Formatio lymphoreticularis parenchymatosa[10]
  Venula postcapillaris

THYMUS

Lobus thymicus
  Capsula thymica
  Septum interlobulare thymicum
  Trabecula thymica
    Lobulus thymici
    Cortex thymicus
    Medulla thymica
    Corpuscula thymica[11]

BURSA CLOACALIS[12]

Tunica serosa bursalis
Tunica muscularis bursalis
Tunica mucosa bursalis[13]
  Plica bursalis[13]
    Lobulus bursalis[14]
      Pars lymphoepithelialis[14]
      Pars lymphoreticularis[14]
        Venula postcapillaris
      Lamina epithelialis interlobaris[14]

SPLEN[16]

Tunica serosa splenica
Capsula splenica
Trabeculae splenicae
Hilum splenicum
Pulpa splenica rubra
Pulpa splenica alba
  Lymphonoduli splenici
  Vagina periarterialis lymphatica[15]
  Vagina periellipsoidea[16]
Aa. splenicae (**Art.** Annot. 59)
  A. trabecularis
    A. centralis
      Vasa capillaria penicillaria[16]
      Vasa capillaria pre-ellipsoidea[16]
      Vasa capillaria ellipsoidea[16]
      Vasa capillaria terminalia[16]
Vv. splenicae (**Ven.** Annot. 79)
  V. trabecularis
    V. colligens
      Vasa venosa primordalia
Splen accessorius[17]

LYMPHONODULI AGGREGATI APPARATUS DIGESTORII

Lymphonoduli pharyngeales[18]
Lymphonoduli esophageales[18]
Lymphonoduli cecales[18]
Anuli [Annuli] lymphatici jejunales[19]
Anuli [Annuli] lymphatici ileales[19]

LYMPHONODUS[8]

Lymphonodus cervicothoracicus[8]
Lymphonodus lumbaris[8]

VASA LYMPHATICA COLLIGENTIA [COLLECTORIA][5 20]

Truncus thoracoabdominalis[21]
  Vas l. celiacum[22]
  Vas l. mesentericum craniale[23]
  Vas l. adrenale (Fig. 13.6)
  Vasa l. ovarica (**Fem.** Annot. 21)
  Vasa l. testicularia (Fig. 13.6)
  Vasa l. renalia (Fig. 13.6)
  Vasa l. ureterodeferentialia
  Vas l. iliacum externum
  Vas l. femorale
  Vas l. ischiadicum (Fig. 13.6)
  Plexus lymphaticus cordis lymphatici
  Cor lymphaticum (Fig. 13.7)
    Vasa l. afferentia
      Vas l. iliacum internum
      Vasa l. cloacalia (**Cloaca** Annot. 24)
    Vasa l. efferentia
      Vas l. mesentericum caudale[24]
      Vas l. sacrale medianum (Fig. 13.7)
        Vasa l. bursae cloacalis (**Cloaca** Annot. 24)
  Vas lymphaticum jugulare[25]
    Vas l. caroticum commune
      Vas l. vertebrale
      Vas l. thyroideum (Fig. 13.6)
      Vasa l. ingluvialia (Fig. 13.6)
      Vasa l. esophagealia (Fig. 13.6)
      Vas l. esophagotracheale
      Vas l. cephalicum caudale
      Vas l. cephalicum rostrale
  Vas lymphaticum subclavium[26]
    Vas l. axillare
    Vas l. sternoclaviculare
    Vas l. pectorale commune
    Vas l. brachiale profundum
    Vas l. basilicum
      Vas l. radiale
      Vas l. ulnare
Vasa lymphatica thoracica interna[27]
  Vasa l. pulmonalia superficialia
Vas l. cardiacum commune[28]
  Vas l. cardiacum dextrum
  Vas l. cardiacum sinistrum
Vas l. pulmonale commune[29]
  Vas l. pulmonale profundum dextrum
  Vas l. pulmonale profundum sinistrum
Vas l. proventriculare[30]

ANNOTATIONS

(1) **Vas lymphaticum initiale** (Fig. 13.1). Initial lymphatics always lie within organs and may be sinuses (lymph capillaries) or precollectors (see Annot. 4) (Konitz, et al., 1985; Berens v. Rautenfeld, et al., 1987a).

(2) **Sinus lymphaticus initialis [Vas lymphocapillare].** The term "initial lymph sinus" (Fig. 13.1) characterizes this section of the initial lymphatics better than "lymph capillary" (Berens v. Rautenfeld, et al., 1987a; Castenholz and Berens v. Rautenfeld, 1987).

(3) **Fibrae basilares; Fibrae fixationes; Accessus interendothelialis; Ponticulus endothelialis.** These structures are components of the "opening apparatus" (Fig. 13.2) of the initial lymphatics which permit the influx of fluids from the interstitial space into the lumen of the initial lymph sinus. All of these components also occur in "precollectors" (Vas l. precollectorium) (Berens v. Rautenfeld and Wenzel-Hora, 1985; Berens v. Rautenfeld, et al., 1987a). Except for the Fibrae fixationes, the elements in the heading of this annotation (Fig. 13.2) are not listed by the *Nomina Histologica* (NH) (1989). The components of the opening apparatus in birds, and amniotes generally, are: (1) a wide-meshed subendothelial network of reticulin fibres (Fibrae basilares); (2) anchoring filaments (Fibrae fixationes); (3) interendothelial openings (Accessus interendotheliales); (4) and endothelial bridges (Ponticuli interendotheliales) (Berens v. Rautenfeld, et al., 1976; Berens v. Rautenfeld, et al., 1983a; Berens v. Rautenfeld, et al., 1987a; and Berens v. Rautenfeld, et al., 1987b). Three transformation types of interendothelial openings exist (Berens v. Rautenfeld and Castenholz, 1987).

(4) **Vas lymphaticum precolligens [Vas l. precollectorium]; Vas lymphaticum fibrotypicum; Trabecula fibroendothelialis.** Precollectors (Fig. 13.1) form the first postsinusoidal section of the lymphatics equipped with valves and still situated within the organs (Berens v. Rautenfeld and Wenzel-Hora, 1985). **Vas lymphaticum fibrotypicum** (*Nomina Histologica*, 1989) has a subendothelial mantle of connective tissue fibres, but only occasionally has any smooth muscle cells (Berens v. Rautenfeld, et al., 1987a). Characteristic structural elements of the precollectors are connective tissue trabeculae (Trabeculae fibroendotheliales) (see Annot. 6) (Berens v. Rautenfeld, et al. 1983a; Berens v. Rautenfeld, et al. 1987a).

(5) **Vas lymphaticum colligens [Vas l. collectorium]; Vas lymphaticum myotypicum; Vas lymphaticum colligens superficiale; Vas lymphaticum colligens profundum.** All lymphatics vessels leading away from the organs (Fig. 13.1) are called "collectors" (Vas l. collectorium) (Berens v. Rautenfeld, et al., 1987a). Collectors are Vasa lymphatica myotypica (Fig. 13.3), i.e., the media of these vessels possesses several layers of nonstriated muscle (Berens v. Rautenfeld, et al., 1984). Only short segments of epifascial collectors (Vasa lymphatica colligentia superficialia) exist in avian skin (Berens v. Rautenfeld, et al., 1983b). In the limbs, subfascial collectors (Vasa lymphatica colligentia profunda) form the main lymphovascular route for lymph travelling centrally (Fig. 13.1).

(6) **Cor lymphaticum; Trabecula myofibroendothelialis.** Lymph hearts may be present only embryonally, e.g., in *Gallus* (Romanoff, 1960), but also postembryonally in certain ratites, Anserinae, and Laridae (Baum, 1930). Budras and Berens v. Rautenfeld (1982), Budras and Berens v. Rautenfeld (1984), and Budras, et al. (1987) deal with the functional and topographical anatomy of the lymph hearts in different birds. Lymph hearts remove lymph from the Phallus protrudens (**Masc.** Annot. 40).

Lymph from the lymph hearts drains into the internal vertebral venous sinus (a lymphovenous connection) **Ven.** Annot. 46, 82) (Budras and Berens v. Rautenfeld, 1984). Like collectors, lymph hearts have subendothelial smooth muscle cells, and a possibly unique type of striated muscle cell (Berens v. Rautenfeld and Budras, 1981; Budras and Berens v. Rautenfeld, 1983; Budras, et al., 1987). Their muscle-connective tissue trabeculae (Trabeculae myofibroendotheliales) contain striated muscle cells.

(7) **Lymphonodulus solitarius [Nodulus lymphaticus solitarius]; Centrum germinale.** Solitary lymph nodules occur in most organs and tissues of the chicken. "Mural lymphoreticular formations" (in the wall of the lymphatics) can be distinguished from parenchymal lymphoreticular formations (in the parenchymas), and tonsils (see Annot. 10). Solitary lymphoid nodules do not appear to be structurally comparable with the mammalian primary or secondary nodules of the *Nomina Histologica* (NH) (1989). Avian nodules consist of thymus-derived lymphoid tissue, and often include bursa-derived avian germinal centres. Numerous synonyms exist (cf. Payne, 1971, and Rose, 1981).

Avian germinal centres have a characteristic covering network of reticular cells (Olah and Glick, 1979), as well as blood capillaries; postcapillary venules with recirculating lymphocytes are always found outside avian germinal centers close to the reticular cells (Berens v. Rautenfeld and Budras, 1980; Berens v. Rautenfeld and Budras, 1983). The antigen-dependent formation of avian germinal centers in the spleen has been described by White, et al. (1975).

(8) **Lymphonodus [Nodus lymphaticus]; Vas lymphaticum afferens; Capsula; Sinus lymphaticus intranodalis; Chorda lymphoreticularis; Venula postcapillaris; Vas lymphaticum efferens.** Avian lymph nodes occur as cervicothoracic and lumbar lymph nodes in Anseriformes and certain other birds (Jolly, 1909-1910; Fürther, 1913), but not in *Gallus* (Baum, 1930). For reviews see Lindner (1961) and Rose (1981). Avian lymph nodes consist of a subordinate system of lymph sinuses, lymphoreticular cords and a thin capsule (Fig. 13.3) (Berens v. Rautenfeld, et al., 1981; Berens v. Rautenfeld and Budras, 1983; Berens v. Rautenfeld, et al., 1983a; Berens v. Rautenfeld, 1985), and lack trabeculae and an uniform hilum (Lindner, 1961; Berens v. Rautenfeld and Budras, 1983). The system of lymph sinuses cannot be subdivided into special sections (e.g., marginal sinuses). The afferent and efferent lymphatics reaching far into the parenchyma of the node display valves (Fig. 13.3) and a smooth muscle media (Berens v. Rautenfeld and Budras, 1983), and may mimic the presence of a central lymph sinus (Rose, 1981). The lymphoreticular cords display B- and T-lymphocyte areas (Sugimura, et al., 1977), postcapillary venules with recirculating lymphocytes, and a pool of free macrophages (Berens v. Rautenfeld and Budras, 1983). In anatids involution often begins even before sexual maturity (Berens v. Rautenfeld and Budras, 1983).

(9) **Formatio lymphoreticularis muralis interna; Formatio lymphoreticularis muralis externa.** Synonymy: Lymphonodulus muralis, NAA (1979); Sinus lymphaticus intramuralis; Venula postcapillaris. Mural lymphoreticular formations have been demonstrated in the wall of the lymphatics of many avian species (Kondo, 1937a; Kondo, 1937b; Biggs, 1957) including all so far examined (Berens v. Rautenfeld, et al., 1983b). For reviews see Payne (1971) and Rose (1981).

The new term "Formatio" was chosen because "lymphonodulus" (NAA, 1979) is a general term describing the structure of the secondary lymphatic tissue and is already in use. Mural formations also occur in reptiles (Kampmeier, 1969). In the bird a distinction must be made between internal and external variants (Fig. 13.4), i.e., in the intima and externa of the lymphatics (Berens v. Rautenfeld, et al., 1983a; Berens v. Rautenfeld, 1985). Only the external mural lymphoreticular formations have lymph sinuses (Fig. 13.4), which are connected to the lumen of the lymphatic vessel (Berens v. Rautenfeld et al., 1981; Berens v. Rautenfeld, et al., 1983b).

Internal formations also occur in the wall of lymph hearts (Berens v. Rautenfeld, et al., 1981). According to Berens v. Rautenfeld (1985), mural lymphoreticular for-

mations are avian lymph nodes which have developed postembryonally, since their induction is antigen-dependent. Mural formations can display all the structural features of the T- and B-lymphocyte areas of nodes (McCorkle, et al., 1979), postcapillary venules with recirculating lymphocytes, and lymph sinuses (Berens v. Rautenfeld, 1985).

(10) **Formatio lymphoreticularis parenchymatosa.** Parenchymal lymphoreticular formations have been described in the literature as "ectopic lymphoid areas, lymphatic nodes, lymphoid follicles, focal lymphoid areas, secondary nodules, nodular lymphatic tissue" etc. (Payne, 1971). They are not listed in NAA (1979), but are categorised as "aggregated nodules". See Annot. 9 for the choice of the term "Formatio"; this term covers the general collections of lymphoid tissue scattered throughout the body (Rose, 1981). It includes secondary lymphoid tissue in the oculonasal region, liver, gall bladder, peripheral nerves, and skin (Rose, 1981), endocrine glands (Payne and Breneman, 1952; Cogburn and Glick, 1981), but not the lymphoid tissue proper in the digestive tract (see below). Parenchymal formations display postcapillary venules with recirculating lymphocytes (cf., Cogburn and Glick, 1981).

(11) **Corpuscula thymica.** Synonymy: Hassal's corpuscles. The characteristics of these corpuscles in the chicken have been reviewed by Hodges (1974: 217-221).

(12) **Bursa cloacalis.** Synonymy: Bursa Fabricii (see **Cloaca** Annot. 11-13). The bursa is an appendage organ of the proctodeum in most birds (e.g., *Gallus*), but a mural organ in ratites (Berens v. Rautenfeld and Budras, 1982). For reviews of the structure and function of the bursa see Payne (1971) and Rose (1981); for the ontogenesis of the bursa in ratites see Müller (1985), and for involution of the bursa in *Gallus* and ratites see Berens v. Rautenfeld and Budras (1982).

(13) **Tunica mucosa bursalis; Plica bursalis.** The arrangement and number of folds in the mucosa of the cloacal bursa varies with the species. Primary, secondary and tertiary folds can be distinguished (Berens v. Rautenfeld and Budras, 1982).

(14) **Lobulus bursalis; Pars lymphoepithelialis; Pars lymphoreticularis; Lamina epithelialis interlobaris.** The term "folliculus" in the NAA (1979) has been replaced by the term "lobulus" (Fig. 13.5), because in the bursa of most of the avian species examined, the lobuli (Fig. 13.5) project into the lumen (e.g., in ratites) (Mathis, 1938; Berens v. Rautenfeld and Budras, 1982).

The term "folliculus" is characterized by mesenchymal structures. The term Pars lymphoepithelialis and Pars lymphoreticularis replace "medulla" and "cortex", respectively (Fig. 13.5). The notion of a central cortex and a peripheral medulla in the bursa of birds with projecting lobuli is misleading. The Pars lymphoepitheliales is comparable with the follicle-associated epithelium of other lymphoepithelial organs (Holbrook, et al., 1974; Glick, et al., 1977).

Lamina epithelialis interlobularis is the epithelium between the Partes lymphoepitheliales of the bursal lobuli (Holbrook, et al., 1974). The term Septum interfolliculare (NAA 1979) is omitted since this structure cannot be related to the projecting lobuli. For a review of the literature on avian species displaying projecting lobuli or invaginated lobuli (e.g., *Gallus*) see Berens v. Rautenfeld and Budras (1982). The projecting Lobulus may be developmentally primitive, since it is demonstrable only in the embryo of the chicken (Holbrook, et al., 1974) and duck (*Anas*) (Märk, 1944).

(15) **Vagina periarterialis lymphatica.** Synonymy: "Periarterial lymphatic sheath".

(16) **Splen.** Synonymy: Lien. Several new terms are introduced for lymphoid tissue of the white pulp and the terminal vasculature. These terms are: **Vagina periellipsoidea, Vasa capillaria penicillaria, Vasa capillaria pre-ellipsoidea, Vasa capillaria ellipsoidea, Vasa capillaria terminalia.**

See Fukuta, et al. (1969a, b), and Olah and Glick (1982) for a review of the literature.

(17) **Splen accessorius.** One or more small accessory spleens may occur near the spleen, weighing from 4 to 45 mg in 69 of 144 chickens (*Gallus*) (Glick and Sato, 1964).

(18) **Lymphonoduli pharyngeales/esophageales/cecales.** Synonymy: pharyngeal, esophageal, cecal tonsils. Lymphoid tissues occur in the lamina propria and (or) submucosa of the alimentary tract from Pharynx to Cloaca. The identification of B- and T-dependent areas in the cecal tonsils are described by Hoshi and Mori (1973). The term "gut associated lymphoid tissue" (GALT) has been widely used. The tonsils are Lymphonoduli aggregati of relatively constant occurrence and relatively large size. The existence of Lymphonoduli esophageales, however, is somewhat dubious, but were described by Zietschmann (1911), Schauder (1923), and Kovacs (1928).

(19) **Anuli [Annuli] lymphatici jejunales/ileales.** Cranial and caudal bands of lymphoid tissue have been recorded in both the jejunum and ileum of *Anas* (Leibovitz, 1968), but not in *Gallus*.

(20) **Vasa lymphatica colligentia [collectoria]** (see Annot. 5). Dransfield (1944, 1945) provided the most detailed account of the distribution of lymphatic vessels in *Gallus*, but without naming them; Baum (1930) and Kondo (1937a) named the major vessels. Previously unnamed lymphatic vessels are named herein according to the blood vessels which they follow or the organs from which they drain lymph; some previously named vessels have been similarly renamed. Most lymphatic vessels consist of two or more parallel trunks with frequent anastomoses between them (Dransfield, 1944, 1945). For a topographical summary see King (1975: 2010-13).

(21) **Truncus thoracoabdominalis.** Usually right and left trunks are present, with frequent anastomoses connecting them; sometimes present is a single vessel which may bifurcate near its termination (Figs. 13.6, 13.7). In *Gallus* the trunk or trunks always terminate in the Venae cavae craniales (Miyaki and Yasuda, 1977). Thoracic and lumbar parts of the thoracoabdominal trunk are distinguished by Baum (1930). Dransfield (1944, 1945) restricted the term thoracic duct to the lymphatics cranial to the celiac lymphatic plexus, and did not name the caudal part.

(22) **Vas lymphaticum celiacum.** The celiac lymphatic vessel (Fig. 13.6) receives tributaries from the thoracic esophagus, proventriculus, gizzard, duodenum, ileum, ceca, spleen, pancreas, and liver (Dransfield, 1944, 1945).

(23) **Vas lymphaticum mesentericum craniale.** The cranial mesenteric lymphatic vessel (Fig. 13.6) receives branches from the jejunum, ileum, ceca, testis, ovary, and the cranial part of the oviduct (Dransfield, 1944, 1945).

(24) **Vas lymphaticum mesentericum caudale** (Fig. 13.7). The caudal mesenteric vessel drains lymph from the rectum (Dransfield, 1944, 1945).

(25) **Vas lymphaticum jugulare.** Lymph carried by the jugular lymphatic vessel empties into the Vena jugularis (Fig. 13.6) near the junction of the latter with Vena subclavia (Dransfield, 1944, 1945), or into either the Truncus thoracoabdominalis or the Venae cavae craniales (Miyaki and Yasuda, 1977).

(26) **Vas lymphaticum subclavium.** The subclavian lymphatic vessel unites with the Vena subclavia near the junction of the latter with the Vena jugularis (Fig. 13.6) (Dransfield, 1944, 1945), or with the Truncus thoracoabdominalis or Vas lymphaticum jugulare (Miyaki and Yasuda, 1977).

(27) **Vasa lymphatica thoracica interna.** The internal thoracic lymphatics accompany the Vv. thoracicae internae (see **Ven.** Annot.47), receive drainage from the superficial lymphatics of the lung (Fig. 13.6) and abdominal muscles, and join the Vena cava cranialis close to its origin (Dransfield, 1944, 1945).

(28) **Vas lymphaticum cardiacum commune.** The common cardiac lymphatic is a single vessel (Fig. 13.6) which empties into the right Vena cava cranialis close to its termination at the right atrium, its tributaries being independent of the coronary arteries and veins (Dransfield, 1944, 1945).

(29) **Vas lymphaticum pulmonale commune.** The tributaries of the common vessel receive lymph from the deep pulmonary lymphatics and travel along the left and right pulmonary veins (Dransfield, 1944, 1945). The common pulmonary lymphatic is a single vessel which joins the left Vena cava cranialis close to, or with, the Truncus thoracoabdominalis (Fig. 13.6).

(30) **Vas lymphaticum proventriculare.** The proventricular lymphatic follows the cranial proventricular vein (see **Ven.** Annot. 12), and joins the left Vena cava cranialis close to, or in common with, the left Truncus thoracoabdominalis (Dransfield, 1944, 1945).

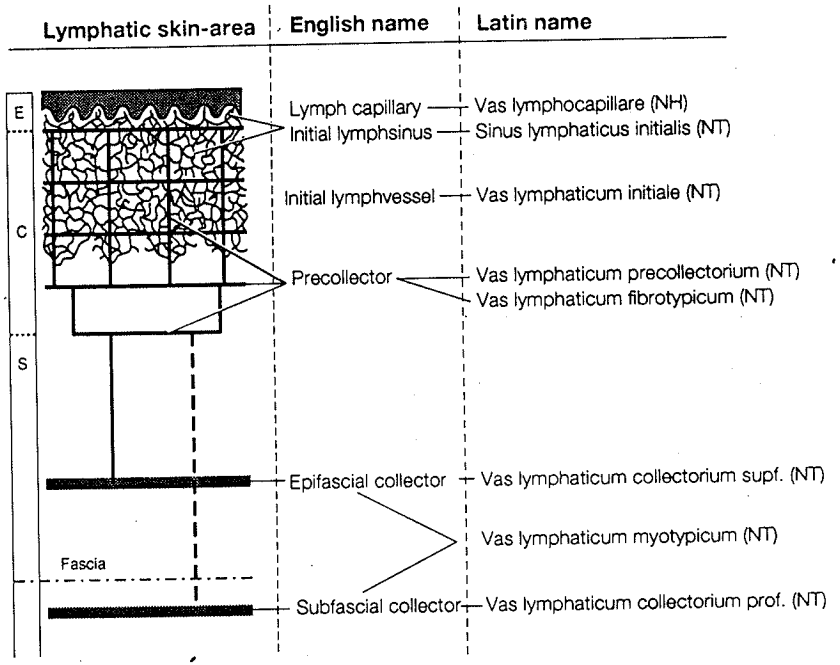

Fig. 13.1. Schematic representation of initial segments of lymph vessels in the skin, subcutis, and underlying skeletal muscle. New terms (NT) and terms of the *Nomina Histologia* (NH) (1989) are presented in their English and Latin forms. Note that the Vas l. precollectorium [precolligens] is a fibrotype vessel; the Vas l. collectorium [colligens] is a myotype vessel (see Annot. 4).

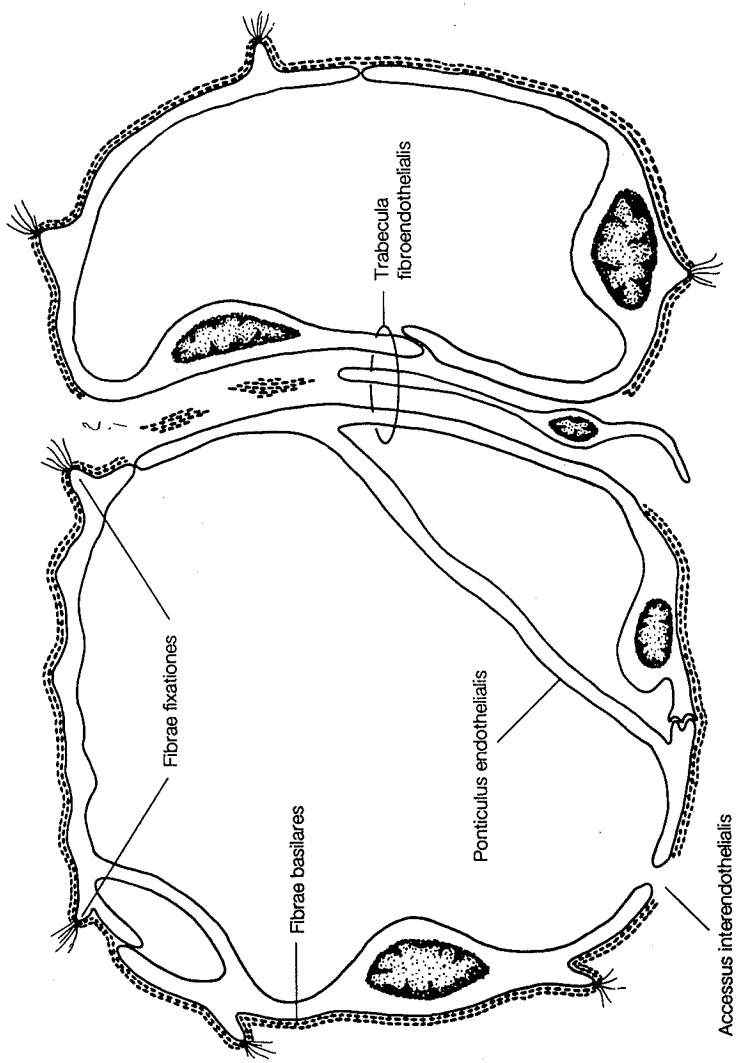

Fig. 13.2. Inital lymph vessel in transverse section, demonstrating its structural components. See Annot. 3.

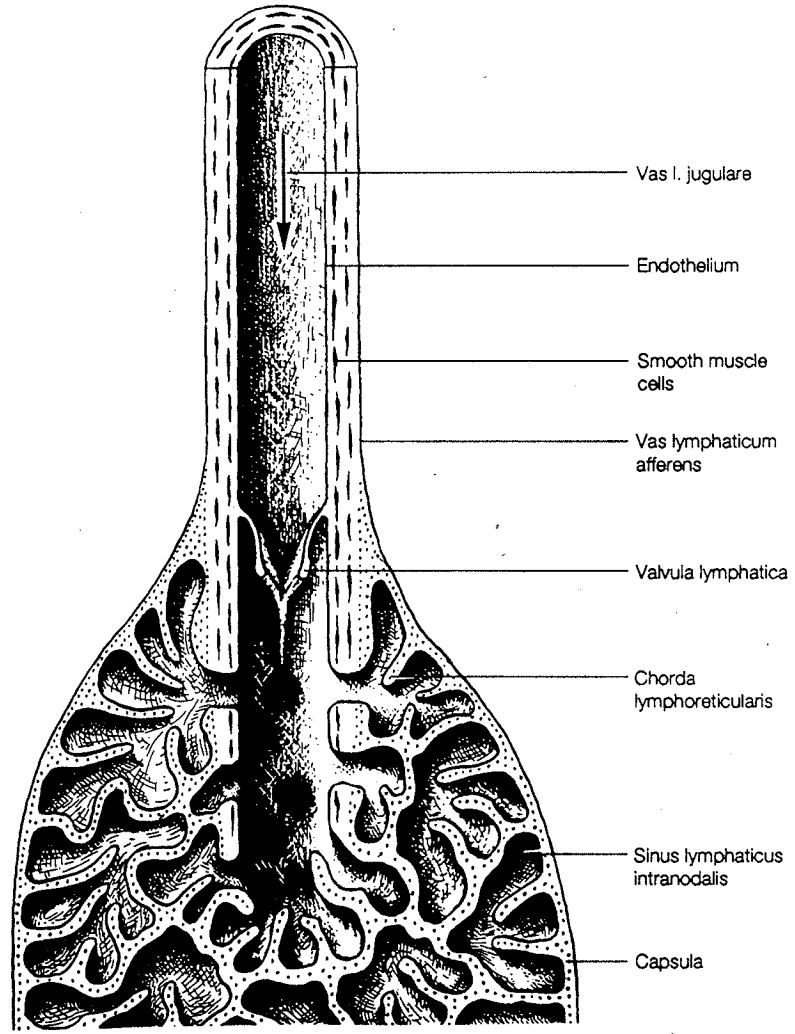

Fig. 13.3. Structure of the cranial part of a Lymphonodus cervicothoracicus of *Anas*. A subdivision into cortex, paracortex and medulla or different sinus segments is not possible. The afferent jugular trunk continues as a Vas. l. myotypicum far inside the node. See Annot. 8.

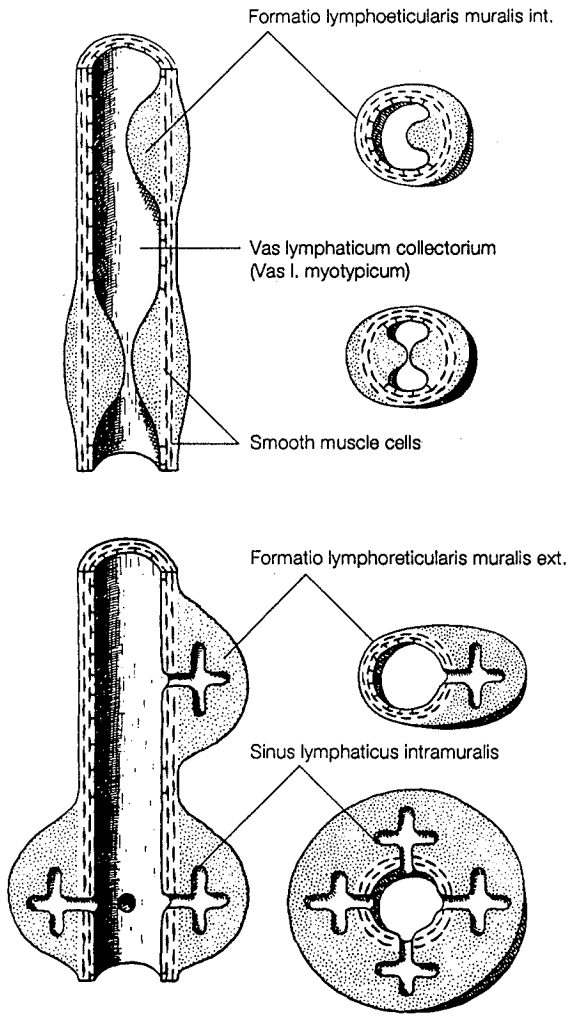

Fig. 13.4. Internal (above) and external (below) lymphoreticular formations of a Vas l. myotypicum. See Annot. 9.

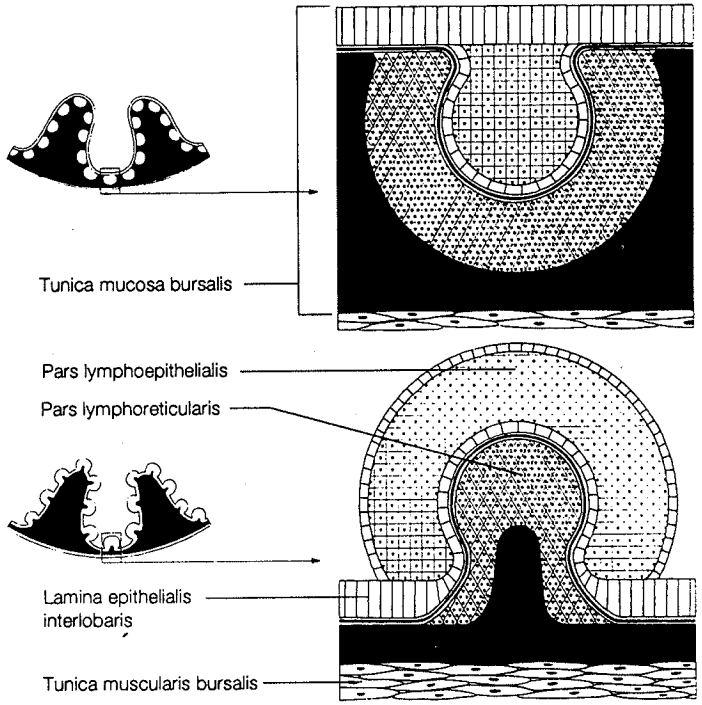

Fig. 13.5. Two types of Lobulus bursalis in the cloacal bursa: (above) the type found in *Gallus;* (below) the ratite type.

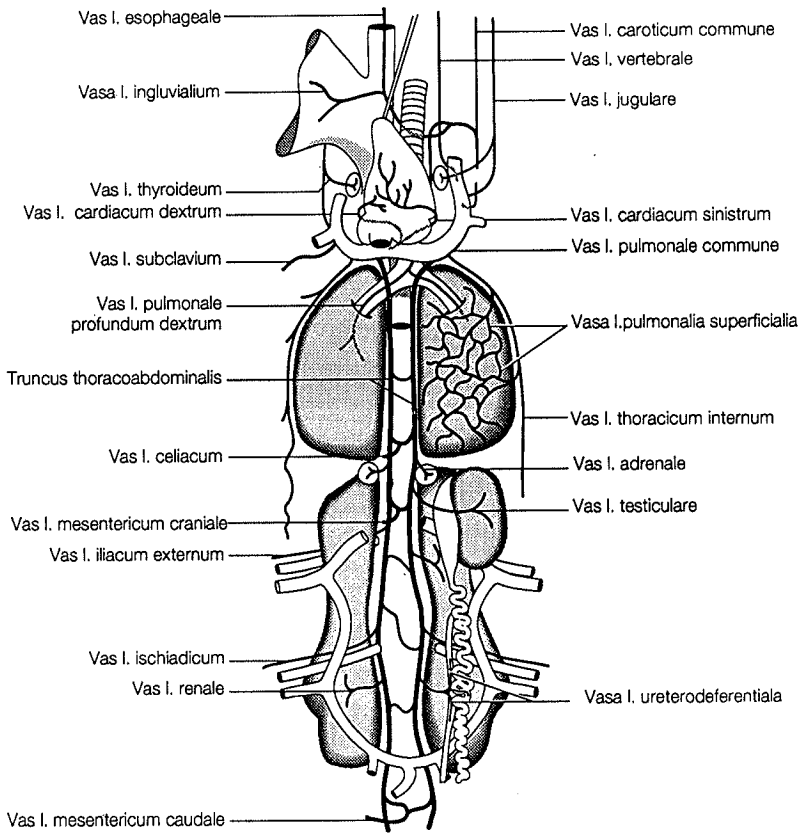

Fig. 13.6. Diagram of the lymphatic vessels of the trunk in *Gallus;* ventral view. Based on Baum (1930) and Dransfield (1944). Notice the termination (lymphovenous connections) of Truncus thoracoabdominalis and other lymph vessels into the cranial caval veins and jugular veins. See Fig. 13.7 for lymphovenous connections of the lymph hearts.

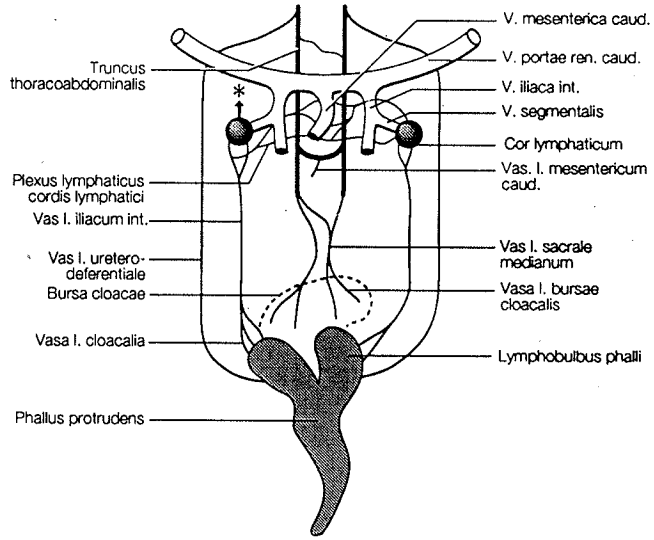

Fig. 13.7. Diagram of the lymphatic vessels of the caudal trunk area in male *Anas;* ventral view. Based on lymphography (pers. obs. of Berens v. Rautenfeld). Arrows in the area of the right lymph heart show Vasa l. efferentia to the venous system (based on studies of Budras and Berens v. Rautenfeld, 1984). The arrow with asterisk represents the lymphovenous connection to the "internal vertebral (epidural) venous sinus" (see **Ven.** Annot. 46, 82) and internal iliac veins.

14

SYSTEMA NERVOSUM CENTRALE

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This chapter on the central nervous system (CNS) is divided into three parts: terminology (employing the internationally accepted language of Latin), explanatory annotations, and figures with legends. In an attempt to make the chapter as useful as possible, we recommend that the reader first consult Fig. 1 which is a side view of the brain partitioned into regions in the order in which the anatomical terms are listed.

Terms presented first are those of features located within the spinal cord (Medulla spinalis) followed by those in the Medulla oblongata or Myelencephalon. The next region is the Metencephalon (includes the Pons and Cerebellum). The Pons and Medulla oblongata are traditionally combined into the more inclusive term, Rhombencephalon. Anatomical structures found within the Mesencephalon or midbrain are then listed. The most rostral sections are those located in the Prosencephalon (Diencephalon and Telencephalon).

Detailed annotations form the second section of the chapter. Numerical superscripts found throughout the list of terms refer to the annotations. Annotations include brief descriptions and English equivalents of terms, relevant references, controversial terms, and/or synonyms that historically have been used to identify the same neural structure.

Finally, a set of figures is included at the end of the chapter. Most of the terms presented in the terminology are identified on schematic plates of the CNS of the two-week old chick (*Gallus gallus*), adapted and redrawn from the stereotaxis atlas of the chick brain of Kuenzel and Masson (1988) with permission of Johns Hopkins University Press.

It is important to realize that the nomenclature found herein is not immutable. It is anticipated that many discoveries will occur during the decade of the nineties and turn of the century that will result in significant changes and additions to neural anatomical terminology of the avian CNS. The authors

apologize for the inevitable omission of studies from the literature which have been overlooked. Those who use this nomenclature are urged to submit suggestions for revision to the authors of this chapter or to individual subcommittee members.

The authors are greatly indebted to Manju Masson who prepared the final drawings of all the figures of the chapter. Supported in part from USDA Grant #90-37240-5506. Scientific Article No. A6203, Contribution No. 8372 of the Maryland Agricultural Experiment Station (Department of Poultry Science).

TERMINOLOGY

MEDULLA SPINALIS (see Figs. 14.1, 3, 5, 6; and PNS Intro. Spinal nerves)

- Fissura mediana [ventralis]
  - Funiculi medullae spinalis
  - Funiculus dorsalis
  - Funiculus lateralis
  - Funiculus ventralis
- Pars cervicalis
  - Intumescentia cervicalis[1]
- Pars thoracica
- Pars synsacralis[2]
  - Intumescentia lumbosacralis[1]
  - Corpus gelatinosum[3]
  - Fossa rhomboidea spinalis[3]
  - Lobi accessorii[4 7]
- Pars caudalis
- Sulcus medianus dorsalis
- Sulcus dorsolateralis
- Sulcus ventrolateralis
- Rdx. dorsalis n. spinalis
- Rdx. ventralis n. spinalis
- Rdx. n. accessorii

SECTIONES MEDULLAE SPINALIS (Figs. 14.1, 5, 6)

- Canalis centralis[3]
- Commissura alba[5]
- Commissura grisea
- Septum dorsale medianum
- Substantia grisea[6]
  - Cornu dorsale
    - Apex cornus dorsalis
  - Cornu ventrale
  - Nuc. substantiae gelatinosae
  - Nuc. dorsolateralis
  - Nuc. marginalis[4 7]
  - Nuc. proprius[8]
- Substantia intermedia[9]
  - Nuc. intermediolateralis[9]
    - Pars thoracolumbalis
      - Pars sacralis
  - Nuc. cervicalis lateralis[10]
  - Nuc. motorius
    - Nuc. motorius lateralis[11]
      - Pars thoracolumbalis
      - Pars sacralis
    - Nuc. motorius medialis[12]
  - Nuc. n. accessorii[36]
  - Nuc. tr. descendentis n. trigemini[13]
    - Subnuc. caudalis
      - Pars marginalis

(continued)

SECTIONES MEDULLAE SPINALIS (Figs. 14.1, 5, 6) (cont.)

- Pars gelatinosa
- Pars magnocellularis
- Substantia gelatinosa centralis
  - Nuc. cornucommissuralis
- Substantia alba
  - Funiculus dorsalis
    - Fasc. gracilis
    - Fasc. cuneatus
    - Fasc. proprius
  - Funiculus lateralis
    - Tr. hypothalamospinalis[14]
    - Tr. spinocerebellaris dorsalis[15]
    - Tr. spinocerebellaris ventralis[15]
    - Tr. spinocerebellaris rostralis[15]
    - Tr. occipitomesencephalicus[16 45 78 88 99]
    - Tr. reticulospinalis lateralis
    - Tr. rubrospinalis[77]
    - Tr. septomesencephalicus[78]
    - Tr. spino-olivaris
    - Tr. spinoreticularis[5]
    - Tr. spinothalamicus[5 17]
    - Tr. spinotectalis[5]
    - Fasc. proprius
    - Fasc. dorsolateralis[18]
    - Tr. descendens n. trigemini[37]
  - Funiculus ventralis
    - Tr. vestibulospinalis [lateralis]
    - Fasc. longitudinalis medialis[27]
      - Tr. interstitiospinalis[19]
      - Tr. vestibulospinalis [ventralis]
      - Tr. reticulospinalis medialis
    - Fasc. proprius

ENCEPHALON[21]

PARTES EXTERNAE ENCEPHALI (Figs. 14.2, 3)

- Bulbus olfactorius
- Cerebellum
  - Auricula cerebelli
  - Fissura cerebelli
  - Folia cerebelli
  - Hemispherium cerebelli
- Cerebrum [Hemispherium telencephali]
  - Eminentia sagittalis[104]
  - Fovea limbica
  - Pars occipitalis
  - Pars frontalis
  - Pars parietalis
  - Tuber ventrolaterale
  - Tuber ventromediale
  - Tuber ventrofrontale
  - Vallecula telencephali
- Chiasma opticum
- Fissura cerebellotectalis
- Fissura cerebrocerebellaris
- Fissura interhemispherica
- Fissura subhemispherica
- Glandula pinealis
- Hypophysis cerebri [Gl. pituitaria]
- Medulla oblongata
- Pons
- Tectum mesencephali
- Tr. opticus

RHOMBENCEPHALON[22]

MEDULLA OBLONGATA [MYELENCEPHALON][22 28]

(Figs. 14.1, 4A, 7-11)

Canalis centralis
Fibrae arcuatae superficiales
Fissura mediana [ventralis]
Fossa rhomboidea[24]
Calamus scriptorius
Funiculus dorsalis
  Fasc. cuneatus
  Fasc. gracilis
Funiculus ventralis
N. abducens
N. facialis
N. vestibulocochlearis
  Pars cochlearis
  Pars vestibularis
N. glossopharyngeus
N. vagus
N. accessorius
N. hypoglossus[32]
Pedunc. cerebellaris caudalis[15 23]
Corpus juxtarestiforme
Corpus restiforme
Sulcus lateralis
Sulcus ventrolateralis
Ventriculus quartus[24]
  Obex
  Plexus choroideus ventriculi quarti
  Recessus lateralis
  Sulcus intermedius dorsalis
  Sulcus limitans
  Sulcus medianus [dorsalis]
  Taenia ventriculi quarti
  Velum medullare caudale
Ventriculus cerebelli

SECTIONES MEDULLAE OBLONGATAE

Area postrema[22 25]
Commissura alba
Commissura infima
Commissura grisea
Complexus olivaris caudalis[26 72]
  Nuc. olivaris accessorius medialis
    Pars dorsalis
    Pars intermedia
    Pars ventralis
  Nuc. olivaris accessorius dorsalis
    Pars lateralis
    Pars medialis
  Nuc. olivaris principalis
    Pars lateralis
    Pars medialis
Decuss. cochlearis dorsalis
Fibrae arcuatae internae
Fibrae arcuatae externae
Fasc. longitudinalis medialis[27]
Fasc. uncinatus
Funiculus dorsalis
  Fasc. gracilis
  Fasc. cuneatus
Funiculus lateralis
Funiculus ventralis
Lemniscus lateralis[47]
Lemniscus medialis[28]
Lemniscus spinalis
  Tr. spinotectalis
  Tr. spinothalamicus
N. trigeminus
N. facialis
N. vestibulocochlearis
  Pars cochlearis

(continued)

SECTIONES MEDULLAE OBLONGATAE (cont.)

  Pars vestibularis
N. glossopharyngeus
N. vagus
N. accessorius
N. hypoglossus
Nuc. ambiguus[29]
Nuc. angularis[30 33 46]
Nuc. centralis medullae oblongatae
  Pars dorsalis
  Pars ventralis
Nuc. cuneatus[28 45 71 78 88]
Nuc. cuneatus accessorius [lateralis][31]
Nuc. commissuralis
Nuc. gracilis[28 45 71 88]
Nuc. intercalatus
Nuc. intermedius medullae oblongatae[32]
Nuc. intrafascicularis n. hypoglossi
Nuc. laminaris[33 46 47]
Nuc. magnocellularis cochlearis[34 46]
Nuc. motorius dorsalis n. vagi[35]
  Pars caudalis [posterior]
  Pars rostralis [anterior]
  Subnuc. lateralis ventralis
Nuc. n. accessorii[36]
Nuc. motorius n. glossopharyngei[35]
Nuc. sensorius n. glossopharyngei
Nuc. n. hypoglossi[32]
  Pars tracheo-syringealis
  Pars lingualis
Nuc. prepositus hypoglossi
Nuc. raphae magnae[39]
Nuc. raphae obscurae[39]
Nuc. raphae pallidae[39]
Nuc. reticularis gigantocellularis
Nuc. reticularis lateralis
  Subnuc. magnocellularis
  Subnuc. parvocellularis
  Subnuc. subtrigeminalis
Nuc. reticularis paragigantocellularis lateralis
Nuc. reticularis paramedianus[40]
Nuc. reticularis parvocellularis
Nuc. retroambiguus
Nuc. sensorius n. glossopharyngei
Nuc. supraspinalis[41]
  Pars dorsalis
  Pars ventralis
Nuc. tr. ascendentis n. glossopharyngei[37]
Nuc. tr. solitarii[42]
  Subnuc. medialis
    Pars superficialis
    Pars dorsalis
    Pars parasolitaria
    Pars ventralis
    Pars ventralis rostralis
    Pars lateralis
  Subnuc. lateralis
    Pars dorsalis [sulcalis]
    Pars superficialis
    Pars parasolitaria
  Subnuc. taeniae choroideae
Nuc. tr. descendentis n. trigemini[37 43 45]
  Subnuc. caudalis
    Pars marginalis
    Pars substantia gelatinosa
    Pars magnocellularis
  Subnuc. interpolaris
  Subnuc. oralis
Nuclei vestibulares[44]
  Nuc. vestibularis descendens
  Nuc. vestibularis lateralis dorsalis
  Nuc. vestibularis medialis
  Nuc. vestibularis rostralis [superior]
  Nuc. vestibularis tangentialis[44]
  Nuc. vestibularis lateralis ventralis

(continued)

SECTIONES MEDULLAE OBLONGATAE (cont.)

Organum postremum[25]
Rdx n. accessorii
Rdx. n. faciali
Rdx. n. glossopharyngei
Rdx. n. vestibulocochlearis
Rdx. n. vagi
  Pars ascendens
  Pars descendens
Rdx. caudalis n. hypoglossi
Rdx. rostralis n. hypoglossi
Tr. arcuatus superficialis dorsalis
Tr. ascendens n. glossopharyngei[37]
Tr. ascendens n. trigemini
Tr. bulbotectalis
Tr. bulbothalamicus
Tr. laminocerebellaris
Tr. lamino-olivaris
Tr. occipitomesencephalicus[16 45 78 88 99]
Tr. olivocerebellaris[26]
Tr. reticulospinalis lateralis
Tr. reticulospinalis ventralis
Tr. rubrospinalis[77]
Tr. solitarius
Tr. descendens n. trigemini[43]
Tr. spinocerebellaris dorsalis[15]
Tr. spinocerebellaris ventralis[15]
Tr. spinocerebellaris rostralis[15]
Tr. tectobulbaris dorsalis
Tr. tectospinalis
Tr. vestibulocerebellaris
Tr. vestibulomesencephalicus
Tr. vestibulospinalis lateralis
Tr. vestibulospinalis ventralis

METENCEPHALON

PONS[22] (Figs. 14.1, 4A, 11, 12)

Pedunc. cerebellaris intermedius[23]
Velum medullare rostrale
Organum subtrochleare

SECTIONES PONTIS

Corpus trapezoideum[46]
Decuss. n. trochlearis
Fasc. longitudinalis medialis[27]
Fasc. uncinatus
Lemniscus lateralis[47]
Lemniscus medialis[28]
Lemniscus spinalis
  Tr. spinotectalis
  Tr. spinothalamicus[17]
Nuc. accessorius n. abducentis[51]
Nuc. ceruleus[45 49 105]
Nuc. corporis trapezoidei[46]
  Pars dorsalis
  Pars intermedia[48]
  Pars ventralis
Nuc. lateralis pontis[45 50 72 78]
  Pars caudalis
  Pars rostralis
Nuc. lemnisci lateralis[47]
Nuc. medialis pontis[50 78]
  Pars caudalis
  Pars rostralis

(continued)

SECTIONES PONTIS (cont.)

Nuc. motorius n. facialis[52]
  Pars dorsalis[52]
  Pars intermedia
  Pars ventralis
Nuc. motorius n. trigemini[53]
  Pars principalis[52 53]
  Pars medialis[53]
  Pars ventralis
Nuc. n. abducentis[51]
Nuc. olivaris superior
Nuc. retrofacialis[56]
Nuc. papillioformis[72]
Nuc. parabrachialis[38]
  Pars dorsolateralis
  Pars medialis
  Pars superficialis lateralis
  Pars ventrolateralis
Nuc. raphae pontis[39]
Nuc. reticularis parvocellularis[45]
Nuc. reticularis pontis caudalis
  Pars gigantocellularis
Nuc. reticularis pontis rostralis
Nuc. salivatorius n. facialis[55]
Nuc. sensorius n. facialis[54]
Nuc. sensorius principalis n. trigemini[37 57 58]
  Pars dorsalis
  Pars ventralis
Nuc subceruleus dorsalis[45]
Nuc. subceruleus ventralis[45]
Nuc. tr. descendentis n. trigemini[43]
Rdx. ascendens n. trigemini
Rdx. mesencephalica n. trigemini
Rdx. n. abducentis
Tr. occipitomesencephalicus[16 45 78 88 99]
Tr. quintofrontalis[57 58 107]
Tr. rubrospinalis[77]
Tr. descendens n. trigemini[43]
Tr. spinocerebellaris dorsalis[15]
Tr. spinocerebellaris ventralis[15]
Tr. spinocerebellaris rostralis[15]
Tr. tectobulbaris dorsalis

CEREBELLUM[21 72 74] (Figs. 14.1, 4B, 11, 12)

Corpus cerebelli
Fissura prima
Fissura secunda
Fissura uvulonodularis
Folia cerebelli
Lobus caudalis
Lobus flocculonodularis
Lobus rostralis
Ventriculus cerebelli
Paraflocculus
  Paraflocculus dorsalis
  Paraflocculus ventralis
Flocculus
  Pedunc. flocculi
Hemispherium cerebelli
Sulci cerebelli
Vallecula cerebelli
Vermis cerebelli (Fig. 14.4B)
Lobulus I ------[Lobulus lingularis]
Lobulus IIa -----[Lobulus centralis]
Lobulus IIb
  Lobulus IIIa
  Lobulus IIIb
Lobulus IVa
Lobulus IVb --[Lobulus culminus]
Lobulus Va
Lobulus Vb
  Fissura prima
Lobulus VIa
Lobulus VIb ----------[Declive]

(continued)

CEREBELLUM[21 72 74] (Figs. 14.1, 4B, 11, 12) (cont.)

Lobulus VIc
Lobulus VIIa ------[Folium vermis]
Lobulus VIIb -------[Tuber vermis]
Lobulus VIIIa [Lobulus pyramidis]
Lobulus VIIIb
Fissura secunda
Lobulus IXa
Lobulus IXb ----[Lobulus uvularis]
Lobulus IXc
Lobulus X -----[Lobulus nodularis]

SECTIONES CEREBELLI[59 74]

Arbor vitae cerebelli
Commissura cerebellaris
Cortex cerebelli
  Stratum moleculare
  Stratum ganglionare
  Stratum granulosum
Decuss. tr. cerebellobulbaris
Fasc. uncinatus
Fissura precentralis
Fissura prepyramidalis
Fissura prima
Fissura secunda
Fissura uvulonodularis
Nuc. cerebellaris medialis [Nuc. fastigii][60 88]
Nuc. cerebellaris intermedius[60 88]
Nuc. cerebellaris lateralis[60 71 88]
Pedunc. cerebellaris caudalis [Corpus restiformis][23]
Pedunc. cerebellaris intermedius [Brachium pontis][23]
Pedunc. cerebellaris rostralis [Brachium conjunctivum][15 23]
Tr. dentato-rubro-thalamicus
Tr. cerebellobulbaris
Tr. laminocerebellaris
Tr. olivocerebellaris
Tr. pontocerebellaris
Tr. spinocerebellaris dorsalis[15]
Tr. spinocerebellaris ventralis[15]
Tr. spinocerebellaris rostralis[15]
Tr. vestibulocerebellaris
Ventriculus cerebelli

MESENCEPHALON (Figs. 14.1, 4A, 12-14)

Aqueductus mesencephali
Brachium colliculi mesencephali[63]
Colliculus mesencephali[45 62]
Commissura caudalis [posterior]
Commissura tectalis
Lamina tecti mesencephali
N. oculomotorius
N. trochlearis
Organum subcommissurale
Tectum mesencephali[61 62 76 86]
Tegmentum mesencephali
Ventriculus tecti mesencephli

SECTIONES MESENCEPHALI[64]

Aqueductus mesencephali
Area ventralis (of Tsai)
Colliculus mesencephali[62 63 65 71 78]
Stratum album centrale
Stratum griseum periventriculare
Stratum griseum centrale[45]
  Pars profunda

(continued)

SECTIONES MESENCEPHALI[64] (cont.)

  Pars intermedia
  Pars superficialis
Stratum griseum et fibrosum superficiale
Stratum opticum
Commissura caudalis [posterior]
  Pars pretectalis
  Pars medullaris
Commissura tectalis
Complexus isthmi[65]
  Nuc. magnocellularis isthmi
  Nuc. parvocellularis isthmi
  Nuc. isthmo-opticus[66]
  Nuc. semilunaris mesencephali
Decuss. n. oculomotorii[67]
Decuss. trochlearis
Decuss. pedunculi cerebellaris rostralis
Decuss. tr. rubrospinalis
Decuss. tr. tectospinalis
Fasc. longitudinalis medialis[27]
Fasc. tegmentalis[68]
Formatio reticularis lateralis mesencephali
Formatio reticularis medialis mesencephali
Griseum tectale[76]
  Pars compacta
  Pars dorsalis
  Pars ventralis
Lemniscus lateralis[47]
Lemniscus medialis[28]
Lemniscus spinalis
Tr. spinotectalis
Tr. spinothalamicus[17]
Nuc. centralis superior[39]
Nuc. commissuralis caudalis [posterior][69]
  Pars diffusa parvocellularis
Nuc. interstitialis commissurae caudalis
Nuc. fasciculi longitudinalis medialis
Nuc. intercollicularis[45 71]
Nuc. interpeduncularis
Nuc. lemnisci lateralis[47]
  Pars dorsalis
  Pars intermedia[48]
  Pars ventralis
Nuc. lentiformis mesencephali[72]
  Pars lateralis [P. parvocellularis]
  Pars medialis [P. magnocellularis]
Nuc. linearis caudalis[39]
Nuc. linearis intermedius[39]
Nuc. linearis rostralis[39]
Nuc. mesencephalicus lateralis
  Pars dorsalis[73 47 63]
  Pars ventralis
Nuc. mesencephalicus n. trigemini[74]
Nuc. mesencephalicus profundus[72]
Nuc. tegmenti pedunculopontini[79 105]
  Pars disseminata
  Pars compacta dorsalis
Pars compacta ventralis
Nuc. n. oculomotorii[75]
  Subnuc. accessorius[67]
  Subnuc. dorsomedialis
  Subnuc. dorsolateralis
  Subnuc. ventralis[67]
  Subnuc. centralis
Nuc. n. trochlearis
Nuc. pretectalis[78]
  Pars lateralis
  Pars medialis
  Pars principalis
Nuc. radicis opticae basalis[70 72]
  Pars dorsalis

(continued)

SECTIONES MESENCEPHALI[64] (cont.)

Pars ventralis
Nuc. ruber[28 78]
Nuc. semilunaris mesencephali
Nuc. subpretectalis
Nuc. dorsalis tegmenti
Nuc. ventralis tegmenti
Pedunc. cerebellaris rostralis [Brachium conjunctivum][15 23]
Pars ascendens
Pars descendens
Rdx. mesencephalica n. trigemini
Rdx. n. oculomotorii
Rdx. n. trochlearis
Rdx. optica basalis[70]
Substantia grisea centralis
Tegmentum mesencephali
Tr. bulbotectalis
Tr. bulbothalamicus
Tr. geniculotectalis
Tr. habenulo-interpeduncularis
Pars lateralis
Pars medialis
Tr. interstitiospinalis
Tr. isthmo-mesencephalicus
Tr. isthmo-opticus[66]
Tr. occipito-mesencephalicus[16 45 78 88 99]
Tr. opticus
Pars lateralis
Pars medialis
Tr. pretecto-subpretectalis
Tr. quinto-frontalis[58 107]
Tr. rubrospinalis[77]
Tr. septomesencephalicus[78]
Tr. tectobulbaris dorsalis
Tr. tectobulbaris ventralis
Tr. tectorotundus
Tr. tectospinalis
Tr. tectothalamicus
Tr. vestibulomesencephalicus

PROSENCEPHALON

DIENCEPHALON (Figs. 14.4A, 14-18)

THALAMUS

Commissura caudalis [C. posterior]
Foramen interventriculare
Plexus choroideus ventriculi tertii
Sulcus subhabenularis
Ventriculus tertius

SECTIONES THALAMI

Ansa lenticularis[79]
Area pretectalis
Area pretectalis diffusa
Area ventralis thalami[105]
Brachium colliculi mesencephali[63]
Complexus opticus principalis thalami[76 84]
Nuc. dorsolateralis rostralis [anterior] thalami[84]
Pars lateralis
Pars medialis [magnocellularis]
Nuc. lateralis rostralis [anterior] thalami[84]
Complexus spiriformis[88]

(continued)

SECTIONES THALAMI (cont.)

Nuc. spiriformis lateralis[79 88]
Nuc. spiriformis medialis[45 78 88]
Nuc. principalis precommissuralis[45 88]
Nuc. dorsolateralis caudalis [posterior] thalami[17 28 80 88]
Nuc. dorsolateralis intermedius thalami[88]
Nuc. dorsointermedius caudalis [posterior] thalami[79]
Nuc. dorsomedialis thalami[81]
Pars rostralis [anterior]
Pars caudalis [posterior]
Nuc. entopeduncularis ventralis rostralis[82]
Nuc. geniculatus lateralis[78]
Pars dorsalis [P. principalis]
Pars intercalatus
Pars ventralis[76 78 83 84]
Nuc. geniculatus ventralis
Nuc. interstitialis thalami
Nuc. intercalatus thalami[17 28 76 78 80]
Nuc. interstitio-pretecto-subpretectalis
Nuc. ovoidalis[85]
Nuc. periventricularis thalami
Pars magnocellularis
Pars parvocellularis
Nuc. reticularis thalami
Pars dorsalis
Pars ventralis
Nuc. rotundus[86 63]
Nuc. semilunaris thalami[87]
Nuc. subrotundus[45]
Nuc. superficialis parvocellularis thalami[80]
Nuc. triangularis
Nuc. ventrolateralis thalami
Rdx. optica basalis[70]
Stratum cellulare externum
Sulcus subhabenularis
Tr. bulbothalamicus
Tr. frontothalamicus
Tr. isthmo-opticus[66]
Tr. nuc. ovoidalis[63 87]
Tr. opticus
Pars lateralis
Pars medialis
Tr. occipitomesencephalicus[16 45 78 88 99]
Pars hypothalamica
Tr. quintofrontalis[58 107]
Tr. tectothalamicus
Tr. thalamofrontalis
Tr. thalamostriaticus

HYPOTHALAMUS

Chiasma opticum
Hypophysis cerebri [Gl. pituitaria] (see **Endoc.**)
Recessus neurohypophysialis [R. infundibuli]
Tr. opticus
Pars lateralis
Pars medialis
Tuber cinereum
Eminentia mediana[94]
Pars rostralis (P. para-infundibularis tuberis)
Pars caudalis (P. caudalis tuberis)
Ventriculus tertius

SECTIONES HYPOTHALAMI[90]

Ansa lenticularis[79]
Decuss. supraoptica
Pars dorsalis
Pars ventralis

(continued)

SECTIONES HYPOTHALAMI[90] (cont.)

Decuss. supramammillaris
Decuss. tr. infundibularis
Fasc. lateralis prosencephali
  Tr. quintofrontalis[58 107]
  Tr. frontothalamicus
  Tr. thalamostriaticus
  Tr. thalamofrontalis
Fasc. medialis prosencephali
  Tr. striohypothalamicus medialis
Regio caudalis [mammillaris] hypothalami
  Nuc. intercalatus hypothalami
  Nuc. mammillaris lateralis[14]
  Nuc. mammillaris medialis
  Nuc. premammillaris hypothalami
  Nuc. supramammillaris interstitialis
  Nuc. periventricularis hypothalami
Regio lateralis hypothalami
  Tr. hypothalamohypophysialis
  Tr. paraventriculohypophysialis
  Tr. supra-opticohypophysialis
  Tr. suprachiasmatico-hypophysialis
  Tr. infundibularis[95]
  Tr. opticus
    Pars lateralis
    Pars medialis
  Tr. hypothalamospinalis
  Tr. retinohypothalamicus[96]
Regio medialis [tuberalis] hypothalami
  Nuc. periventricularis hypothalami[14]
  Nuc. paraventricularis hypothalami[92]
  Nuc. dorsomedialis hypothalami[16]
  Nuc. ventromedialis hypothalami[16 93]
  Nuc. inferioris hypothalami
  Nuc. infundibuli hypothalami
  Eminentia mediana[94]
    Pars caudalis
    Pars rostralis
Regio pre-optica [R. rostralis] hypothalami[91]
  Nuc. preopticus periventricularis
  Nuc. magnocellularis preopticus
    Pars dorsalis
    Pars medialis
    Pars ventralis
  Nuc. rostralis [anterior] medialis hypothalami
  Nuc. decussationis supra-opticae[20]
    Pars dorsalis
    Pars ventralis[20]
  Nuc. supra-opticus
    Pars externus
    Pars ventralis
  Nuc. suprachiasmaticus
    Pars medialis[20]
  Nuc. preopticus medialis
  Nuc. preopticus medianus[102]
  Nuc. preopticus dorsolateralis
  Rdx. optica basalis[70]

EPITHALAMUS

Glandula pinealis (Fig. 14.4A; **Endoc.** Annot. 6)

SECTIONES EPITHALAMI

Commissura habenularis
Nuc. habenularis lateralis[105]
Nuc. habenularis medialis
Nuc. subhabenularis lateralis
Nuc. subhabenularis medialis
Stria medullaris [S. habenularis]
  Tr. archistriato-habenularis et precommissuralis
  Tr. hypothalamohabenularis
  Tr. olfactohabenularis
  Tr. septohabenularis
  Tr. taeniae habenularis
Tr. habenulo-interpeduncularis
  Pars lateralis
  Pars medialis

TELENCEPHALON (Figs. 14.1, 4A 14-20)

Bulbus olfactorius[97]
  Ventriculus olfactorius
Cerebrum [Hemispherium telencephali]
  Eminentia sagittalis[104]
  Fissura interhemispherica
  Fovea limbica
  Pars frontalis
  Pars occipitalis
  Pars parietalis
  Tuber ventrofrontale
  Tuber ventrolaterale
  Tuber ventromediale
  Vallecula telencephali
  Ventriculus lateralis
    Plexus choroideus ventriculi lateralis

SECTIONES TELENCEPHALI

Archistriatum[16 99 101 108]
  Archistriatum caudale
  Archistriatum intermedium
    Pars dorsalis
    Pars ventralis
  Archistriatum mediale[16 99]
  Archistriatum rostrale[16 99]
    Nuc. robustus[99]
    Nuc. taeniae
  Area coracoidea dorsolateralis
  Area parahippocampalis
  Area septalis
    Nuc. septalis lateralis
    Nuc. septalis medialis
    Nuc. accumbens[100]
    Nuc. interstitialis striae terminalis
  Area temporoparieto-occipitalis
  Bulbus olfactorius[97]
    Fila olfactoria
    Lamina glomerulosa
    Lamina granularis externa
    Lamina molecularis externa
    Lamina mitralis
    Lamina molecularis interna
    Lamina ependymalis
    Ventriculus olfactorius
  Capsula interna occipitalis
  Cingulum periectostriaticum[78]
  Commissura rostralis [anterior][100]
    Pars bulbaris[100]
    Pars temporalis[100]
  Commissura pallii
  Complexus paleostriaticus[101 79 100]

(continued)

SECTIONES TELENCEPHALI (cont.)

Nuc. intrapeduncularis[79 101]
Paleostriatum augmentatum[101]
Paleostriatum primitivum[79 82]
Paleostriatum ventrale[101]
Cortex prepiriformis
Cortex piriformis[100]
Ectostriatum[101]
Fasc. diagonalis (of Broca)
Fasc. lateralis prosencephali[82 100]
Ansa lenticularis
Fasc. medialis prosencephali[81]
Ager L (Field L)
Foramen interventriculare
Fornix
Hippocampus[103]
Hyperstriatum accessorium[104 78 81 101]
Hyperstriatum dorsale[81 104]
Hyperstriatum intercalatum supremum[80 100 101]
Lamina externa
Lamina interna
Hyperstriatum ventrale[101]
Pars dorsalis
Pars ventralis
Lamina archistriatica dorsalis
Lamina frontalis superior[104]
Lamina frontalis suprema[104]
Lamina hyperstriatica
Lamina medullaris dorsalis
Lamina medullaris ventralis
Lobus parolfactorius[100 101 105]
Neostriatum[78 101 107]
Pars caudalis[80]
Pars intermedia
Pars rostralis [frontalis][108]
Nuc. ansae lenticularis caudalis [posterior][106 79]
Nuc. ansae lenticularis rostralis [anterior][106 79]
Nuc. basalis [Nuc. trigeminalis] prosencephali[107 58]
Nuc. interstitialis commissurae pallii
Nuc. olfactorius rostralis [anterior]
Nuc. tr. diagonalis
Nuc. tr. septomesencephali
Organum paraventriculare
Organum vasculosum laminae terminalis
Organum laterale septi
Organum subseptale [O. interventriculare]
Plexus choroideus ventriculi lateralis
Substantia grisea periventricularis lateralis
Tr. cortico-habenularis et cortico-septalis
Tr. dorso-archistriaticus
Tr. fronto-archistriaticus[100 108]
Tr. frontothalamicus
Tr. occipitomesencephalicus[16 45 78 88 99]
Pars hypothalami[16]
Tr. quintofrontalis[58 107]
Tr. septomesencephalicus[78]
Tr. striomesencephalicus[105]
Tr. thalamofrontalis
Tr. thalamostriaticus
Tuberculum olfactorium[100]

MENINGES

Dura mater spinalis[110]
Dura mater encephali[109 110]
Dura mater propria
Lamina periostealis

(continued)

MENINGES (cont.)

Plica tentorialis[111]
Diaphragma sellae
Arachnoidea spinalis
Arachnoidea encephali
Cavum subarachnoideum [Cavitas subarachnoidea]
Liquor cerebrospinalis
Cisterneae subarachnoideae
Pia mater spinalis
Lig. denticulatum[112]
Lig. ventromedianum[112]
Septum ventromedianum
Lig. suspensorium transversum[112]
Pia mater encephali

ANNOTATIONS

(1) **Intumescentia cervicalis; Intumescentia lumbosacralis.** Enlargements of the region of the spinal cord from which the brachial and lumbosacral plexus arise; **Intumescentia cervicalis** is usually larger than the lumbosacral intumescence, in flying birds. In flightless birds, especially the Ostrich (*Struthio camelus*), **Intumescentia lumbosacralis** is larger in size (Kuhlenbeck, 1975). See **Osteo.** Annot. 145.

(2) **Pars synsacralis.** Since the synsacrum contains one or more thoracic vertebrae in addition to the lumbar, sacral, and some of the caudal vertebrae, pars synsacralis of the spinal cord seems more appropriate than pars lumbosacralis. (See **Osteo.** Annot. 141, 145).

(3) **Corpus gelatinosum.** A specialized glial structure which lies within the **Fossa rhomboidea spinalis** (see Annot. 24). Due to its high glycogen content the Corpus is often called the "glycogen body" (Gage, 1917; Terni, 1924). Lyser (1973) and Welsch and Wachtler (1969), utilizing electron microscopy, demonstrated that its structural elements are glycogen-laden glial cells; Moller (1978) has affirmed that the cells are astrocytes. The glial elements are innervated by nonmyelinated axons and receive a rich blood supply (Paul, 1971; 1973). The Corpus consists of dorsal and ventral parts connected by a constriction bounded by pia mater. The ventral portion encloses the **Canalis centralis** of the spinal cord (Hodges, 1974). Benzo, et al. (1975) have suggested a metabolic function of these cells related to myelination, while Azciotia, et al. (1985) suggest a secretory function. Sansone (1977) and Sansone and Lebeda (1976) described the distribution of glycogen contained within the spinal cord of the chicken. Uehara and Ueshima (1982) describe the development of these cells in the chick.

(4) **Lobi accessorii.** Most evident in the lumbosacral levels of the spinal cord; the lobes contain neurons of **Nuc. marginalis.** These lobes have been referred to as lobes of Lachi and as the nuclei of Hoffmann-von Kolliker (Ariëns Kappers, et al., 1936; De Genaro and Benzo, 1976). See **Annot.** 7.

(5) **Commissura alba.** Both dorsal and ventral white commissures are present in birds. The dorsal white commissure contains collaterals of dorsal root fibers and axons of cell bodies located within the grey matter. The ventral white commissure contains axons which cross the midline to form the spinoreticular, spinothalamic, and spinotectal tracts of the spinal cord.

(6) **Substantia grisea.** The dorsal horn of birds is laminated similar to the scheme originally developed in the cat by Rexed (1952; 1954). In chickens (*Gallus*) lamina III lies medial rather than ventral to lamina II (Brinkman and Martin, 1973; Martin, 1979) while in pigeons (Columbidae) a typical dorsoventral lamination pattern occurs (Leonard and Cohen, 1975). The two schemes shown in Fig. 5 represent at least two different types of dorsal horn lamination patterns in avian species. The novel "chicken" pattern appears to be widespread among various taxonomic groups. The type of pattern found in a given species has thus far been shown to be consistent across successively higher taxonomic categories. In other words, the pattern is conserved at the specific, generic, familial and ordinal taxonomic levels (Woodbury, 1989).

(7) **Nuc. marginalis.** This nucleus lies within the white matter of the spinal cord, usually near the surface. It is also represented by scattered cell bodies, often referred to as "paragriseal" neurons. Nuc. marginalis is also known as the nucleus of Hoffmann–von Kolliker. The marginal nucleus is particularly well developed in the synsacral levels where it protrudes from the spinal cord as the Lobi accessorii (See **Annot.** 4) near the attachment of the Lig. denticulatum.

(8) **Nuc. proprius.** Synonymy: Dorsal magnocellular column of the spinal cord grey matter (Jungherr, 1969; Bolton, 1971).

(9) **Substantia intermedia; Nuc. intermediolateralis.** Synonymy: Column of Terni. The dorsal commissural portion of Substantia intermedia within the thoraco-lumbar levels of the spinal cord has been demonstrated to contain autonomic preganglionic nerve cell bodies and to be the avian homologue of the mammalian intermediolateral cell column (Nuc. intermediolateralis) (Terni, 1923; MacDonald and Cohen, 1970; Ohmori, et al., 1984a). The nucleus has commonly been referred to as the column of Terni. Division of the nucleus into Pars thoraco-lumbaris and Pars sacralis corresponds to the locations of the "sympathetic" and "parasympathetic" (see **PNS**) preganglionic neurons, respectively (Ohmori, et al., 1984a).

(10) **Nuc. cervicalis lateralis.** Although no literature references are available to document the presence or homology of Nuc. cervicalis lateralis of mammals, cell accumulations are present in a comparable position in birds. Whether these represent a continuation of Nuc. marginalis, of the paragriseal system of the spinal cord of birds, or are separate entities is not known. See **Annot.** 7.

(11) **Nuc. motorius lateralis.** This nucleus lies only within lamina IX (Brinkman and Martin, 1973; Martin, 1979) of the cervical and lumbosacral enlargements and contains neurons supplying the thoracic and pelvic limb muscles (Ohmori, et al., 1982; 1984b). The nucleus is divided into two parts. Axons of motor neurons of Pars lateralis pass through Fasciculus dorsalis of peripheral nerves and innervate muscles of the extensor surface of the limbs, while axons of Pars medialis pass through Fasciculus ventralis and supply muscles of the flexor surfaces. See also Addens (1933).

(12) **Nuc. motorius medialis.** The nucleus lies within the ventral horn throughout the length of the spinal cord. In the enlargements it is located within lamina VIII (Brinkman and Martin, 1973; Martin, 1979). See **Annot.** 1.

(13) **Nuc. tr. descendentis n. trigemini.** The trigeminal nuclear complex extends into the cervical spinal cord as in mammals. The nucleus merges with the dorsal horn of the spinal cord gray matter. Dubbeldam and Karten (1978) describe the central projections of the trigeminal ganglion in the pigeon (*Columba livia*). Dubbeldam and Veenman (1978) and Dubbeldam (1980) describe the somatotopy of the trigeminal

system in the Mallard (*Anas platyrhynchus*). Dubbeldam, et al. (1979) describe the central projections of the glossopharyngeal and vagus ganglia in the Mallard. Dubbeldam (1984) relates the afferents of the glossopharyngeal and facial nerves in the pigeon to feeding behavior.

(14) **Tr. hypothalamospinalis.** This tract has been described in the pigeon by Cabot, et al. (1982). The tract arises from **Nuc. periventricularis hypothalami, Nuc. mammillaris lateralis** and **Nuc. suprachiasmaticus** of the hypothalamus. These findings have been supported by Gross and Oppenheim (1985).

(15) **Tr. spinocerebellaris ventralis; Tr. spinocerebellaris dorsalis; Tr. spinocerebellaris rostralis.** The presence of dorsal and ventral spinocerebellar tracts in birds has been demonstrated by Friedlander (1898), Sanders (1929), Ariëns Kappers, et al. (1936), Larsell (1948), and Whitlock (1952). Oscarsson, et al. (1963) studied these tracts in the duck and verified their existence, but indicated that the dorsal spinocerebellar tract may function in a somewhat different capacity than in mammals. The dorsal spinocerebellar tract axons originate from the cervical intumesence of the spinal cord, comparing well with Tr. spinocerebellaris rostralis of the cat (Lundberg and Oscarsson, 1962). The dorsal portion of the tract passes to the cerebellum via the caudal cerebellar peduncle and ventral portion joins the ventral spinocerebellar tract to enter the rostral cerebellar peduncle (Van Den Akker, 1970).

(16) **Tr. occipitomesencephalicus; Pars hypothalamica.** The occipitomesencephalic tract arises from the rostral two-thirds of the **Archistriatum** and is distributed contralaterally to the first few cervical segments of the spinal cord. Haartsen and Verhaart (1967) and Zeier and Karten (1971) indicate that this may be an avian homologue to Bagley's bundle of the goat. Pars hypothalamica arises from the **Archistriatum caudale** and the **Archistriatum mediale,** which appears to be homologous to the mammalian amygdaloid complex (Zeier and Karten, 1971). The fibers of this tract terminate with both medial and lateral hypothalamic regions in a manner similar to that of the amygdalofugal fibers of mammals (Zeier and Karten, 1971; Cohen and Karten, 1974). The most dense terminations of this tract are within the **Nuc. ventromedialis hypothalami** and **Nuc. dorsomedialis hypothalami.** (See **Annot.** 78).

(17) **Tr. spinothalamicus.** The spinothalamic tract of birds resembles that of mammals in its origin from the dorsal horn of the spinal grey, its decussation at segmental levels and its contribution to the lateral funiculus (Van Den Akker, 1970; Oscarsson, et al., 1963). The terminations of this tract within the thalamus have been studied by Karten and Revzin (1966) and Delius and Bennetto (1972). These investigators indicate terminations in **Nuc. intercalatus thalami, Nuc. dorsolateralis caudalis thalami** and **Nuc. superficialis parvocellularis thalami.** The tract is presumed to serve tactile, pain and thermal sensory systems, but electrophysiological evidence is limited to the tactile system (Delius and Bennetto, 1972).

(18) **Fasciculus dorsolateralis.** This is a well developed fasciculus in birds, located in part in the dorsal and lateral funiculi and corresponds to Lissaur's tract of mammals (Van Den Akker, 1970). It has been suggested that Fasciculus dorsolateralis contains long contralateral ascending pathways, forming a spinal lemniscus system (or a spino-bulbo-tectothalamic tract) (Kuhlenbeck, 1975).

(19) **Tr. interstitiospinalis.** Synonymy: Tr. tegmentospinalis (Kuhlenbeck, 1975). There is both an interstitiospinalis tract and a separate tegmentospinalis **tract** within the fasciculus longitudinalis medialis of mammals, both originating from the

tegmentum of the midbrain. Whether a tegmentospinal tract exists in birds has not been demonstrated.

(20) **Nuc. suprachiasmaticus, Pars medialis.** There is little agreement regarding the location of a retinorecipient nucleus that plays a role in circadian rhythms comparable to the suprachiasmatic nucleus of mammals. A retinal projection to the medial, anterior hypothalamus has been reported in the House Sparrow (*Passer domesticus*) (Hartwig, 1974) and Java Sparrow (*Padda oryzivora*) (Ebihara and Kawamura, 1981). In Fig. 14.18 it is shown as the SCNm. More evidence has accumulated that supports a more lateral hypothalamic nucleus as the avian equivalent of the SCN. It was first described by Repèrant (1973) as the **Nuc. decussationis supraopticae, Pars ventralis** (see DSv in Fig. 14.17) and several studies show it to be a retinorecipient nucleus (Cooper, et al., 1983; Cassone and Moore, 1987; Ehrlich and Mark, 1984; Meier, 1973) as well as one that demonstrates circadian variations (Cassone, 1988). It has been suggested that the nucleus be termed the "lateral hypothalamic retinorecipient nucleus" (Norgren and Silver, 1989).

(21) **Encephalon.** The Encephalon is the brain. It includes the cerebrum, cerebellum, and the brain stem. See Figs. 1, 2, 3 for surface features and parts of the brain.

(22) **Rhombencephalon.** The Rhombencephalon includes the **Pons** and the **Medulla oblongata.** Bläser (1981) described the localization of somatostatin and enkephalin immunoreactive neurons in the caudal brain stem of the domestic chicken (*Gallus*). Bohme (1970 described the organization of the fourth ventricle in *Gallus*. Brandis (1894) described the origin of cranial nerves from the medulla oblongata. Cabot, et al. (1982) described bulbospinal tracts in birds. Cohen and Schnall (1970) and Cohen et al. (1970) described the medullary cells of origin of vagal cardioinhibitory fibers in the pigeon. Hirunagi and Yasuda (1979) described the fine structure of the ependymal cells of the **Area postrema** in domestic fowl. Moll and Hilvering (1951) describe the Area in other birds.

(23) **Pedunculus cerebellaris caudalis, Pedunculus cerebellaris intermedius, Pedunculus cerebellaris rostralis.** The cerebellar peduncles are commonly referred to as Corpus restiforme (Peduncularis cerebellaris caudalis), Brachium pontis (Pedunculus cerebellaris intermedius) and Brachium conjunctivum (Pedunculus cerebellaris rostralis). For purposes of simplicity, the topographical terms, caudalis, intermedius, and rostralis have been adopted. This terminology allows the inclusion of Corpus juxtarestiformis and Corpus restiforme within the caudal peduncle.

(24) **Ventriculus quartus.** The fourth ventricle includes the **Fossa rhomboidea** (see Annot. 3) of the caudal pons and rostral medulla and is continuous dorsally with the **Ventriculus cerebelli.** The ventricle is bounded laterally by the caudal, intermediate and rostral cerebellar peduncles.

(25) **Area postrema, Organum postremum.** Area postrema represents an area on either side of the obex. Organum postremum represents a neuroglial circumventricular organ (Leonhardt, 1980). In domestic fowl (*Gallus*) and the pigeon (*Columba livia*), the organ has histological characteristics similar to those of mammals (Pessacq, 1967). The area is characterized by an ependymal layer, neuroglial parenchyma, and a high vascularity (Bohme, 1970). Kirunogi and Yasuda (1979) have described the organization of these structures in the chicken. See **Annot.** 22.

(26) **Complexus olivaris caudalis.** Synonymy: Complex. oliv. inferior. There is much variation in the description of the nuclei of the avian caudal olivary complex. The number of nuclei of the complex named by investigators varies from only two (Kooy, 1915; 1917) to as many as seven (Vogt-Nilsen, 1954). Yashimura (1909) provides a comparative study of this complex in birds. Furber (1983; 1984) indicates that the dorsal lamella of the complex is homologous, from lateral to medial, with the dorsal accessory, the principal, and a small part of the ventral accessory nuclei of the mammalian caudal olivary complex. The ventral lamina represents the remainder of the mammalian complex. Furber (1983) also provides a description of **Tr. olivocerebellaris** of birds. Armstrong and Clarke (1979) describe the development of the complex in the chick.

(27) **Fasciculus longitudinalis medialis.** This is the oldest and most constant longitudinal fiber system in the central nervous system of vertebrates. It is large in all vertebrates and exhibits a relative larger size in more primitive animals. The medial longitudinal fasciculus of birds appears to be homologous to that of other vertebrates (Sarnat and Netsky, 1974).

(28) **Lemniscus medialis.** The medial lemniscus of birds resembles that of mammals: in its origin from **Nuc. gracilis** and **Nuc. cuneatus** (Van Den Akker, 1970; Friedlander, 1898), its decussation within the **Medulla oblongata** and its ascent within the ventromedial portion of the brain stem. It terminates within the mesencephalon, ventral hypothalamus, **Nuc. ruber, Nuc. intercalatus thalami** and **Nuc. dorsolateralis caudalis thalami** (Wallenberg, 1904; Delius and Bennetto, 1972).

(29) **Nuc. ambiguus.** Synonymy: Nuc. motorius ventralis n. vagi (Bolton, 1971).

(30) **Nuc. angularis.** In the pigeon (*Columba livia*) this nucleus is divisible into three parts: (1) Pars lateralis, consisting of large cells; (2) Pars medialis containing small cells, resembling the adjacent Nuc. magnocellularis;and (3) Pars ventralis. The ventral part receives afferents from both the cochlear and lagenar nerves, whereas the medial and lateral parts receive afferents from the cochlear nerve (Boord and Rasmussen, 1963). The distribution of these afferents appear to maintain a tonotopic distribution within the nucleus, similar to that of the cochlear nuclei of mammals. It was suggested by Boord and Rasmussen (1963) that **Pars lateralis** and **Pars ventralis** are homologues of the caudal division of the dorsal cochlear nucleus of mammals. The medial part of the nucleus, along with the medial and lateral parts of Nuc. magnocellularis, appear to correspond to the ventral cochlear nucleus of mammals. Cajal (1908) describes the brain stem terminations of the cochlear nerve in birds. Correia, et al. (1982) describe the organization of the ascending auditory pathways in the pigeon.

(31) **Nuc. cuneatus accessorius [lateralis].** This nucleus corresponds to Nuc. cuneatus externus of Dubbeldam and Karten (1978). In birds it receives afferents from the **Ganglion trigeminale** and from the proximal ganglia of Nn. IX and X.

(32) **Nuc. intermedius medullae oblongatae.** This nucleus is said in some birds to contain both vagal and hypoglossal motor neurons, and in others to be entirely vagal or entirely hypoglossal in its composition. Based on retrograde degeneration studies (Watanabe, 1968; Watanabe, et al., 1975), the motor nucleus of the syrinx appears to be a part of this nucleus. Youngren and Phillips (1983) in the chicken (*Gallus*) and Manogue and Nottebohm (1982) in the budgerigar (*Melopsittacus undulatus*), describe the location of motor neurons supplying some tongue muscles, the trachea and the syrinx.

Nuc. n. hypoglossi. Synonymy: Nuc. n. cervicalis medialis (Watanabe, et al., 1975). This nucleus may be equivalent to the Nuc. intermedius of the medulla oblongata (see above paragraph). It was described by Nottebohm, Stokes and Leonard (1976), and includes a **Pars tracheo-syringealis** and **Pars lingualis** (see Figs. 14.7, 8).

(33) **Nuc. laminaris.** It has been suggested that Nuc. laminaris represents a primary auditory nucleus. Cochlear and lagenar fibers, however, do not terminate within the nucleus. Boord (1968), showed that the nucleus receives afferents from **Nuc. angularis,** and suggests that it is an avian homologue of the medial nucleus of the rostral olivary complex of mammals, representing a secondary nucleus of the auditory sensory system. Scheich et al. (1979) described the functional organization of some auditory nuclei in the guinea fowl. Parks (1979; 1981), Parks and Rubel (1975; 1978), Parks, et al. (1983), Smith (1981), and Smith and Rubel (1979) describe the development and organization of the brain stem auditory nuclei of the chicken (*Gallus*).

(34) **Nuc. magnocellularis cochlearis.** On the basis of cell morphology and fibrillar architecture the nucleus can be divided into three subnuclei (Boord and Rasmussen, 1963). Two divisions have been described by a number of investigators (Brandis, 1894; Holmes, 1903; Cajal, 1908; Sanders, 1929; Craigie, 1930). Jhavari and Morest (1982a, b) presented the architecture and some developmental aspects of this nucleus. Boord and Rasmussen (1963) demonstrated that the ventrolateral portion of the nucleus receives mixed afferents from both the cochlear and lagenar components of the vestibulocochlear nerve, whereas the remainder of the nucleus receives afferents only from the cochlear component. They suggest that the Nuc. magnocellularis cochlearis is an avian homologue of the rostral part of the ventral cochlear nucleus of mammals. The medial part of Nuc. magnocellularis appears to be the avian equivalent of region III while the lateral part of Nuc. magnocellularis is the equivalent of region I of the mammalian rostro-ventral cochlear nucleus of Harrison and Irving (1965).

(35) **Nuc. motorius dorsalis n. vagi; Nuc. motorius n. glossopharyngei.** Nuc. motorius dorsalis n. vagi has been referred to as the ventrolateral nucleus of the vagus nerve by those who classify **Nuc. intercalatus** as Nuc. dorsomedialis n. vagi. Craigie (1930) identified the Nuc. motorius dorsalis n. vagi as a combination nucleus of the glossopharyngeal nerve and vagus nerve. Nuc. motorius n. glossopharyngei is a rostral extension of **Nuc. motorius dorsalis n. vagi.** Katz and Karten (1983a, b) described 11 subnuclei within Nuc. motorius dorsalis n. vagi. Note that the rules established for this nomenclature have been altered in this case to accommodate both directional terms, caudalis and posterior, in order that they might be included as separate nuclei. Cohen and Schnall (1970) and Cohen, et al. (1970) have described the location of cardioinhibitory neurons within Nuc. motorius dorsalis n. vagi.

(36) **Nuc. n. accessorii.** Synonymy: column of Lenhossek. Although located mostly within the Medulla oblongata, Nuc. n. accessorii is principally a cervical spinal cord nucleus, representing the motor neurons supplying M. cutaneus colli lateralis (M. cucullaris capitis, **Myol.** Annot. 7). It has been argued that this muscle is the avian counterpart of the trapezius muscle of mammals (Watanabe, 1961). Huber (1936) describes a column of cells in the pigeon that occupy a position in the lateral part of the grey matter at about the level of the central canal and extending over the upper three or four cervical segments of the spinal cord, the "column of Lenhossek". Huber notes that the cells of this column are probably the cells of origin of fibers representing the spinal portion of the accessory nerve in mammals. Hildebrand (1975), however, found retrograde changes only in the dorsocentral motor column of Beccari after interruption of N. accessorius. His illustrations, however, do not provide a clear location of this cell group. See **Annot.** 32.

(37) **Nuc. tractus ascendentis n. glossopharyngei; Tr. ascendens n. glossopharyngei.** Nuc. tr. ascendens n. glossopharyngei represents that portion of the Nuc. n. glossopharyngei that lies adjacent to, and receives afferents from, the ascending tract of the glossopharyngeal nerve. **Tractus ascendens n. glossopharyngei** ascends medially along **Tr. descendentis n. trigemini.** It terminates in **Nuc. sensorius n. glossopharyngei** and sends collaterals into **Nuc. tr. ascendentis n. glossopharyngei** and into the medial zone of **Nuc. tr. descendens n. trigemini** (Dubbeldam et al. 1979). The tract may also contain vagal and/or hypoglossal fibers, with terminations in **Nuc. sensorius principalis n. trigemini** (Wild, 1981; Bottjer and Arnold, 1982).

(38) The **Nuc. parabrachialis** has been divided into four subnuclei in the pigeon: **Pars dorsolateralis, medialis, superficialis lateralis** and **ventrolateralis** (Arends, et al., 1988).

(39) **Nuclei raphae.** The raphae nuclei form a continuous series of nuclei within the brain stem raphae, extending from the caudal limits of the medulla oblongata to the rostral mesencephalon. These nuclei have many functions, and functionally are generally considered to be a part of the brain stem reticular formation. The nuclei included in this group from caudal to rostral are: **Nuc. raphae pallidae, Nuc. raphae obscurae, Nuc. raphae magnae, Nuc. raphae pontis, Nuc. centralis superior, Nuc. linearis caudalis, Nuc. linearis intermedius** and **Nuc. linearis rostralis.** These nuclei have been described in many mammals (see Taber, et al., 1960, for description in the cat), and are clearly present in birds (Breazile and Hartwig, 1989); however their function in birds has not been investigated.

(40) **Nuc. reticularis paramedianus.** Petrovicky (1966) indicated that the paramedian reticular nucleus is absent in birds, however it appears present in the chicken (*Gallus*), turkey (*Meleagris*), Java dove (*Streptopelia*) and pigeon (*Columba*). The stereotaxic atlas of the pigeon brain of Karten and Hodos (1967) indicates the presence of this nucleus made up of cell nests lying between the root fibers of the hypoglossal nerve and the midline raphe of the medulla oblongata. The cells are medium sized, darkly-staining.

(41) **Nuc. supraspinalis.** This nucleus contains neurons that supply motor innervation to some of the upper neck muscles (Wild and Zeigler, 1980; Gross, 1985). On the basis of cytologic organization, the nucleus is divisible into a pars dorsalis and a pars ventralis. Retrograde degeneration studies of Watanabe (1968) and Watanabe, et al. (1975) and unpublished HRP studies of Watanabe show that the Nuc. n. hypoglossi also innervates cervical muscles. See **PNS.** Annot. 30.

(42) **Nuc. tr. solitarii.** Facial, glossopharyngal and vagus nerves have projections to the Nuc. tr. solitarii. Contrary to previous reports (Kuhlenbeck, 1975), the facial nerve contains afferent fibers involved in taste (Berkhoudt, 1985). Based on the projections of nerves into the nucleus, a number of subnuclei have been described in the Mallard (*Anas platyrhynchos*) (Dubbeldam, 1979), the pigeon (Dubbeldam, 1984) and the chicken (*Gallus*) (Ganchrow, et al., 1986). The cytoarchitectonic study of the nucleus in the pigeon of Katz and Karten (1983) is the basis for the nomenclature presented here.

(43) **Nuc. tr. descendentis n. trigemini.** The nucleus represents a large dorsolateral nucleus in the caudal pons and the medulla. It extends into and is a component of the dorsal horn of the spinal grey matter. The subnuclear organization is similar to that of mammals. The caudal extent of the nucleus has not been determined in birds, but the adjacent **Tr. descendens n. trigemini** appears to extend to about the third cervical segment of the cord. Arends, et al. (1984) describe the efferent projections of this nucleus in the duck (*Anas platyrhynchos*).

(44) **Nuclei vestibulares.** The nomenclature of the vestibular nuclei adopted in this work is derived from Sanders (1929). For comparisons with other terminologies consult Larsell (1967) and Kuhlenbeck (1975). Eden and Corriea (1982) and Schwarz, et al. (1981) described the vestibular efferents from these nuclei in the pigeon (*Columba*). Vollrath and Delius (1976) describe the vestibular nuclear projections to the thalamus in the pigeon. Boord and Karten (1974) describe the efferent terminations of the vestibular component of the eighth nerve. Wold (1975; 1976; 1978a, b) describes the nuclear organization in relationship to both afferents and efferents. Peusner and Morest (1977a, b, c) describe the development and organization of **Nuc. vestibularis tangentialis** in the chick. Through the use of tracer methods, Eden and Correia (1982) identified multiple groups of efferent vestibular neurons.

(45) **Tr. occipitomesencephalicus.** Zeier and Karten (1971) have demonstrated that the occipitomesencephalic tract originates from the rostral two-thirds of the **Archistriatum** and is distributed ipsilaterally to the following structures: lateral part of **Nuc. spiriformis medialis, Nuc. subrotundus, Nuc. principalis precommissuralis** and lateral mesencephalic reticular formation, **Nuc. intercollicularis, Stratum griseum centrale** of **Colliculus mesencephali, Nuc. ceruleus, Nuc. subceruleus dorsalis** and **ventralis** and **Nuc. lateralis pontis.** Caudal to this level the tract is distributed bilaterally to **Nuc. reticularis parvocellularis, Nuc. subtrigeminalis, Nuc. tr. descendentis n. trigemini,** and **Nuc. gracilis** and **Nuc. cuneatus.** The contralateral component continues into the spinal cord to end within the upper cervical segments, overlapping somewhat with the termination of the septomesencephalic tract. See Annot. 16, 99.

(46) **Corpus trapezoideum; Nuc. corporis trapezoidei.** The trapezoid body is composed of third order axons from cells of **Nuc. laminaris** and second order axons from cells of the medial part of **Nuc. angularis** and the lateral part of **Nuc. magnocellularis cochlearis** (Boord, 1968; 1969). As these nuclei are considered to represent avian homologues of the dorsal and ventral cochlear nuclei and the medial nucleus of the rostral olivary complex of mammals, it appears that the **Corpus trapezoideum** of birds is homologous to that of mammals. Many of the axons of the Corpus trapezoideum terminate within **Nuc. corporis trapezoidei.** Knudsen (1980) described mechanisms of sound localization in owls (strigiforms).

(47) **Lemniscus lateralis.** The lateral lemniscus has been demonstrated to serve as the major afferent pathway to **Nuc. lemnisci lateralis** and **Nuc. mesencephalicus lateralis, Pars dorsalis** in the pigeon (*Columba*) (Boord, 1968), and contains efferents from the avian homologues of the mammalian cochlear nuclei and **Nuc. laminaris,** an avian counterpart of the medial nucleus of the rostral olivary complex (Cajal, 1908; Stotler, 1905). Owing to these relationships the lateral lemniscus of birds can be considered to be homologous to that of mammals. Correia, et al. (1982) describe the organization of ascending auditory pathways in the pigeon.

(48) **Nuc. lateralis lemnisci, Pars intermedia.** Synonymy: Pars lateroventralis (Boord, 1969). Boord equates **Pars intermedia** of the lateral lemniscus with **Nuc. ventralis lemnisci lateralis** of Karten and Hodos (1967).

(49) **Nuc. ceruleus.** Synonymy: Locus ceruleus. Shimizu et al. (1974) describe the distribution of efferents from this nucleus in the budgerigar. Gugliemone and Panzica (1982) describe the nucleus and its development in the chick.

(50) **Nuc. medialis pontis.** Brodal, et al. (1950) describe the avian homologues of the pontine grey of mammals. Armstrong and Clarke (1979) describe the development of the pontine nuclei in the chick.

(51) **Nuc. accessorius n. abducentis.** This nucleus is found in numerous taxa of birds as a small mass located ventrolateral to **Nuc. n. abducentis.** Kuhlenbeck (1975) indicated that it innervates muscles of the nictitating membrane (**PNS.** Annot. 16).

(52) **Nuc. motorius n. facialis, Pars dorsalis.** This nucleus innervates M. depressor mandibulae. It lies close to the dorsomedial part of **Nuc. motorius n. trigemini, Pars principalis.** This proximity is considered to reflect the functional association of these nuclei in the control of beak movements (Wild and Zeigler, 1980).

(53) **Nuc. motorius n. trigemini.** The relationships of the subdivisions of **Pars principalis** of this nucleus to jaw muscles have been clarified in the pigeon by Wild and Zeigler (1980). **Pars medialis** is the source of fibers innervating the M. depressor palpebrae ventralis in the pigeon and the duck. The ontogeny and migration of the trigeminal motor nucleus and the developmental relationships between these neurons and trigeminal afferents have been investigated by Heaton and Moody (1980) and Moody and Heaton (1983a, b, c).

(54) **Nuc. sensorius n. facialis.** This cell group has been described as Nuc. n. VII in the duck (*Anas*) (Dubbeldam, et al., 1976), but has also been recognized in the pigeon and the chicken (Ganchrow et al. 1986).

(55) **Nuc. salivatorius n. facialis.** The nucleus has been described in the duck (*Anas*) (Bout and Dubbeldam, 1985) and in the chicken (Ganchrow, et al., 1986). The role of this nucleus as a salivatory motor nucleus is uncertain.

(56) **Nuc. retrofacialis.** See Wild (1982) for a description of this nucleus which innervates one of the tongue muscles.

(57) **Nuc. sensorius principalis n. trigemini.** The size of this nucleus varies greatly in different taxa, correlating well with the size of the beak (Stingelin, 1961). The nucleus receives a topographically organized projection from the trigeminal ganglion and serves as the origin of the **Tr. quintofrontalis** (Wallenberg, 1904; Woodburne, 1936; Zeigler and Karten, 1973; Witkovsky, et al., 1973). The nucleus is clearly divisible into dorsal and ventral components (Woodburn, 1936). Studies of afferents and efferents with the aid of tracer methods in the pigeon and Mallard by have been conducted by Dubbeldam and Veenman (1978), Dubbeldam, (1980), Dubbeldam, et al., (1981) and Berkhoudt, et al., (1981).

(58) **Tr. quintofrontalis.** This tract arises from both dorsal and ventral divisions of **Nuc. sensorius principalis n. trigemini,** undergoes partial decussation, and terminates in **Nuc. basalis prosencephali.** It appears to represent a lemniscal pathway in birds (Wallenberg, 1903; Dubbeldam and Veenman, 1978; Dubbeldam, 1980; Dubbeldam, et al., 1981; Berkhoudt, et al., 1981).

(59) **Sectiones cerebelli.** Anatomical evidence for the existence of Tr. isthmocerebellaris, Tr. cerebello-motorius and Tr. tectocerebellaris in birds is lacking. For this reason they have not been included here in the list of terms. Nieuwenhuys (1967) presents a comparative anatomy of the cerebellum, including birds. Larsell (1948) describes the development and subdivisions of the cerebellum of birds. Feirabend, et al. (1978) describe the longitudinal organization of afferents and efferents of the cerebellar cortex in the chicken (*Gallus*). (Feirabend and Voogd (1986) describe the organization of the white matter of the cerebellum of the domestic chicken. Goodman, et al. (1964) describe the functional localization of the cerebellar surface of the chicken. Whitlock (1952) presents the sensory receptive areas in the chicken. Paula-Barbosa and Sobrinho-Simoes (1976) describe the ultrastructural organization of mossy fiber endings of the afferents in the cerebellum of the pigeon (*Columba*), rat (*Rattus*), and man (*Homo*). Clark (1977) describes visual and other connections to the cerebellum of birds. Schwarz and Schwarz (1983) and Renggli (1967) provide comparative studies of the relationship of the vestibular nuclei and the cerebellum in birds. Freedman (1977) describes climbing fibers of the avian cerebellum. Bortolami, et al. (1972) describe the relationship of the Nuc. mesencephalicus n. trigemini and the cerebellum in the duck (*Anas*). Brauth (1977) describes a direct accessory optic projection to the vestibulocerebellum.

(60) **Nuc. cerebellaris medialis [Nuc. fastigii]; Nuc. cerebellaris intermedius; Nuc. cerebellaris lateralis.** Comparative studies of representatives of 18 avian orders have demonstrated numerous differences in the number and structure of the deep cerebellar nuclei. In some falconids, psittaciforms, piciformes, meropids, trochilids and passeriforms there is a folding of the nuclei produced by concentrations of cells within the nuclei. These folds appear to be genetically fixed, like the fissures of the cerebellar cortex (Renggli, 1967). In general organization, in all orders examined, there are three identifiable nuclei or groups. These groups relate well to afferent and efferent projections from the overlying vermis, paravermis and hemispheric portions of the cerebellar cortex (Goodman, et al., 1964). Karten (1964) describes the efferent projections of these nuclei in the pigeon. Arends (1985) presents the corticonuclear and olivocerebellar organization in the pigeon. Nieuwenhuys (1967) presents a review of afferent and efferent organization of the cerebellum of birds.

(61) **Tectum mesencephali.** Synonymy: Lobus opticus; Tectum opticum. As a gross brain feature, the tectum mesencephali has been considered to be a primary visual center. Cohen and Karten (1974) summarizing information concerning this structure indicate that the term "optic lobe" is a misnomer, as only a limited portion of the lobe is actually related to the visual system. Since the midbrain tectum functions in other spheres of activity it is prudent to avoid a name with a functional connotation.

(62) **Colliculus mesencephali.** Synonymy: Tectum opticum. Failure to recognize the fundamental distinction between the optic lobe and the Tectum opticum has led to confusion, particularly regarding the comparative relationships of avian and mammalian brains (Cohen and Karten, 1974). The so-called optic lobe of birds is equivalent to the rostral colliculus of mammals and the optic tectum of birds is considered to be equivalent to the superficial cap of the mammalian rostral colliculus (Acheson, et al., 1980). Hunt and Kunzel (1976) studied the surface layers of the colliculus. The designation, Colliculus mesencephali, provides a topographic rather than a functional basis for the name. McGraw and McLaughlin (1980a, b) describe the synaptic organization of the colliculus in the chick (*Gallus*). Reperant and Angaut (1977) and Acheson, et al. (1980) describe its retinotectal projections in pigeons (*Columba*). Mestres and Delius (1982) also describe some mesencephatic tectum afferents in the pigeon. Rager (1980a, b) describes these projections in the chicken. Domesick and Morest (1977a, b) describe the development of the Colliculus mesencephali in the chick. Duff, et al. (1981) describe the retinal receptive areas in the pigeon. Bravo and Pettigrew (1981) describe the distribution of neurons projecting from the retina to telencephalic structures in the Barn Owl (*Tyto alba*) and the Burrowing Owl (*Athene cunicularia*). In general, the superficial layers of the tectum mesencephali receive retinal afferents and deeper layers receive other afferents and serve as the efferent layers of the colliculus. See Annot. 61.

(63) **Brachium colliculi mesencephali.** The mammalian brachium of the caudal colliculus is represented in birds as the **Tr. nuc. ovoidalis.** This tract contains axons with cell bodies of origin in **Nuc. mesencephalicus lateralis, Pars dorsalis,** the avian counterpart of the mammalian caudal colliculus (Karten, 1967). **Tr. nuc. ovoidalis** terminates primarily within **Nuc. ovoidalis,** the avian counterpart of the mammalian ventral division of the medial geniculate (Karten, 1967). Brachium colliculi mesencephali refers specifically to the "tectofugal" fibers projecting from the **Colliculus mesencephali** to **Nuc. rotundus,** the avian counterpart of the mammalian Nuc. lateralis caudalis of the thalamus (Karten and Revzin, 1966; Karten and Hodos, 1970; Benowitz and Karten, 1976b; Reiner and Karten, 1982; Revzin and Karten, 1966). See **Annot.** 62.

(64) **Sectiones mesencephali.** Bertler, et al. (1964) describes adrenergic connections between the mesencephalon and the telencephalon. Graef (1973a, b, c, d, e) describes the cytoarchitecture and myeloarchitecture of the mesencephalon of the chicken (*Gallus*). Verhaart (1972) provides a review of the fiber systems of the avian mesencephalon. Blähser and Dubois (1980) described the met-enkephalin containing neurons of the brain of domestic fowl. Blähser and Heinrichs (1982) similarly demonstrated the immunoreactive neuropeptide systems in domestic Mallard (*Anas platyrhynchos*), domestic fowl and Japanese Quail (*Coturnix coturnix*). These descriptions involve the mesencephalon to a great degree. Jungherr (1945) described a number of mesencephalic nuclei in the chicken.

(65) **Complexus isthmi.** The isthmal complex receives an intense and topographically organized input from the **Colliculus mesencephali** (Cohen and Karten, 1974). Clarke (1982a, b) described the development of the isthmic complex in the chick (*Gallus*).

(66) **Nuc. isthmo-opticus.** Synonymy: Ganglion opticum dorsale (Bellonci, 1888; Jelgersma, 1896), Nuc. opticus medialis (Perlia, 1889), Ganglion isthmi (Edinger and Wallenberg, 1899) and Nucleus of the isthmo-optic tract (Craigie, 1928). This nucleus has been demonstrated to give rise to a definite efferent tract (**Tr. isthmo-opticus**) which projects to the retina (Cowan and Powell, 1963; Holden, 1966; Ogden, 1967; Cowan and Wenger, 1968; Crossland and Hughes, 1978; Crossland and Uchwat, 1979; Cowan, 1970; 1982; Hayes and Holden, 1983). See Angaut and Reperant (1978) for a description of the nucleus. Sohal and Narayanan (1974) describe the development of the nucleus in the chick (*Gallus*).

(67) **Decuss. n. oculomotorii.** Some of the fibers from the ventral part of the oculomotor nuclear complex decussate proximal to the emergence of the oculomotor nerve (Kuhlenbeck, 1975). Niimi, et al. (1958) described a crossing component associated with the **Subnuc. accessorius** (considered to be the avian homologue of the Edinger-

Westphal nucleus of mammals). Heaton and Wayne (1983) indicate that a portion of the fibers from **Subnuc. ventralis** also decussate. Puelles (1978) describes the development of the crossing fibers in the chicken (*Gallus*).

(68) **Fasc. tegmentalis.** Several fiber bundles traversing the tegmentum in a mediolateral or lateromedial direction have been recognized (Zweers, 1971). The origin and termination of these fibers is not known.

(69) **Nuc. commissuralis caudalis.** Synonymy: Nuc. commissuralis posterior. This nucleus appears to be homologous with the nucleus of the caudal commissure of mammals.

(70) **Nuc. radicis opticae basalis [Nuc. ectomamillaris].** This nucleus in birds appears to be homologous to at least a portion of the nucleus of the basal optic tract of mammals (Brecha, et al., 1980). Rio (1979) described the organization of the nucleus in the pigeon and Rio, et al. (1983) describe the efferent projections to telencephalic structures. Reiner, et al. (1979) describe the afferents to the nucleus. Karten, et al. (1977) describe the accessory optic system in the pigeon.

(71) **Nuc. intercollicularis.** This nucleus receives afferents from the spinal cord, **Nuc. lateralis cerebelli, Colliculus mesencephali, Nuc. gracilis** and **Nuc. cuneatus** (Karten, 1963, 1965, 1967), and has been demonstrated to play an important role in song vocalization in birds. It may be involved in respiration rather than vocalization. Its homology with mammalian brain structures is not known.

(72) **Nuc. lentiformis mesencephali, Pars lateralis/medialis.** Gamlin and Cohen (1988) point out that the usual division of this nucleus into Pars magnocellularis and Pars parvocellularis, as described by Ehrlich and Mark (1984) and Gottlieb and McKenna (1986), has caused much confusion. The entire nucleus is in fact comprised of a mixture of large and small cells. Gamlin and Cohen (1988) suggest that Nuc. lentiformis mesencephali is comparable to the nucleus of the optic tract of mammals. Both Pars lateralis and Pars medialis have connections to **Complexus olivaris caudale, cerebellum, lateral pontine nucleus, Nuc. papillioformis, Nuc. radicis opticae basalis** and **Nuc. mesencephalicus profundus.** See also Clarke (1977), Brauth and Karten (1977), Brecha, et al. (1980), Brecha (1978) and Azevedo, et al. (1983) for descriptions of these nuclei.

(73) **Nuc. mesencephalicus lateralis, Pars dorsalis.** This nucleus appears to be an avian homologue of the caudal colliculus of mammals (Correia, et al., 1982). Referred to as the Ganglion laterale, it has been proposed to be the pneumotaxic center of birds. The latter conclusion is unlikely, as the nucleus is clearly a mesencephalic structure and the pneumotaxic center of mammals is Nuc. parabrachialis medialis. The term "torus semicircularis" has been applied to this nucleus, but does not apply well to birds; if used, it should be limited to reptiles and amphibians. Cobb (1964) compared the size of this nucleus with the size of the mesencephalic tectum in a variety of birds. Karten (1967) describes the diencephalic projections of the nucleus in the pigeon.

(74) **Nuc. mesencephalicus n. trigemini.** Rogers and Cowan (1973) describe the development of this nucleus in the chick. For a description of the relationships of this nucleus and the **Cerebellum** in birds (see Bortalami, et al. (1972). Manni, et al. (1965) demonstrate the relationship between jaw muscle afferents and Nuc. mesencephalicus n. trigemini in birds.

(75) **Nuc. n. oculomotorii.** The oculomotor complex in birds has been characterized in several taxa. Niimi, et al. (1958) and Heaton and Wayne (1983) describe it in the chick, Sohal (1977) in the duck and Heaton (1981) in *Coturnix*. The nomenclature used here is that of Heaton and Wayne (1983). Isomura (1973) has contributed to the study of this nucleus in the chicken (*Gallus*).

(76) **Griseum tectale.** Synonymy: Substantia grisea tecti. Described by Gamlin and Cohen (1988) as a pretectal nucleus, although associated with the mesencephalic tectum. They divide the area into a rostral retino-recipient region and a caudal, non-retino-recipient zone, referring to the latter as **Pars compacta.** Griseum tectale projects efferents to **Nuc. intercalatus thalami, Nuc. supraopticae pars ventralis, Nuc. geniculatus lateralis, pars ventralis** and **Complexus opticus principalis thalami.** The area also projects into the layers of **Tectum mesencephali.**

(77) **Tr. rubrospinalis.** Wild, et al. (1979) describe this tract in the pigeon. The tract decussates within the mesencephalon, immediately caudal to the nucleus and descends to lumbosacral levels of the spinal cord (Cabot, et al., 1982).

(78) **Tr. septomesencephalicus.** This tract arises from the dorsal telencephalon, predominantly from the **Hyperstriatum accessorium** and projects to the lateral **Neostriatum, Cingulum periectostriaticum,** internal lamella of the ventral geniculate nuc., **Nuc. pretectalis, Colliculus mesencephali, Nuc. intercalatus thalami, Nuc. spiriformis medialis, Nuc. ruber,** the medial reticular formation, pontine nuclei and **Nuc. cuneatus.** The system continues contralaterally into the spinal cord, terminating within the dorsal horn of the spinal grey where it overlaps with the terminations of **Tr. occipitomesencephalicus** (Adamo, 1967; Karten, 1969; Zecha, 1962).

(79) **Ansa lenticularis.** The Ansa lenticularis arises exclusively from the **Paleostriatum primitivum/Nuc. intrapeduncularis** component of the **Complexus paleostriaticus.** Ansa lenticularis terminates in **Nuc. ansae lenticularis rostralis, Nuc. ansae lenticularis caudalis, Nuc. dorsointermedius caudalis thalami, Nuc. spiriformis lateralis** and **Nuc. tegmenti pedunculopontini.** On the basis of anatomic and histochemical studies by Karten and Dubbeldam (1973) it appears that the avian Ansa lenticularis is an avian counterpart to that of mammals.

(80) **Nuc. dorsolateralis caudalis thalami; Nuc. superficialis parvocellularis thalami; Nuc. intercalatus thalami.** These nuclei represent thalamic relay nuclei for the cutaneous sensory information in birds (Delius and Bennetto, 1972). It has been demonstrated that Nuc. dorsolateralis caudalis thalami and Nuc. superficialis parvocellularis thalami projects to telencephalic structures, namely, **Hyperstriatum intercalatus supremum** and **Neostriatum caudalis, Pars rostralis et medialis** (Erulkar, 1955; Delius and Bennetto, 1972). The homologies of these nuclei with thalamic nuclei in mammals are not clear at present, but the possibility is evident that at least a portion of the nuclei involved, most likely **Nuc. dorsolateralis caudalis thalami** and **Nuc. superficialis parvocellularis thalami,** are avian counterparts of the ventrobasilar complex of mammals.

(81) **Nuc. dorsomedialis thalami, Pars rostralis.** This nucleus gives rise to a fiber system that accompanies **Fasc. medialis prosencephali** rostrally to terminate within the medial division of the **Hyperstriatum dorsale** and the immediately adjacent dorsomedial portion of **Hyperstriatum accessorium** (Zeier and Karten, 1971). No functional significance has been alleged to these structures, but it is speculated that Nuc. dorsomedialis, Pars rostralis may be comparable to the mammalian anterior

thalamic complex and its projection field in **Hyperstriatum dorsale** and **Hyperstriatum accessorium** may represent a homologue of part of the mammalian "limbic" system (Karten, et al., 1973). This speculation is strengthened by the proximity of the telencephalic region involved in this projection to the region of the avian brain that traditionally is considered to represent the hippocampal formation of mammals (Karten, et al., 1973).

(82) **Nuc. entopeduncularis ventralis rostralis.** This nucleus is considered to be an avian homologue of the subthalamic nucleus of mammals. It is referred to as the entopeduncular nuclear group by Craigie (1929) and is represented by nerve cell bodies scattered along **Fasc. prosencephali lateralis.** The cells resemble those of **Paleostriatum primitivum.** This nucleus includes the following nuclei as described by Rendahl (1924): (1) Nuc. dorsalis supraopticum, (2) Bed nucleus of Tr. thalamofrontalis anterior, and (3) Nuc. parastriatus.

(83) **Nuc. geniculatus lateralis, Pars ventralis.** Crossland and Uchwat (1979) describe the afferents to this nucleus.

(84) **Complexus opticus principalis thalami. Nuc. dorsolateralis rostralis thalami, Pars lateralis, Pars medialis** (also known as Pars magnocellularis) and **Nuc. lateralis rostralis thalami** are collectively considered to be Complexus opticus principalis thalami (Karten, et al., 1973; Bravo and Pettigrew, 1981; Ehrlich and Mark, 1984). Meier, et al. (1974) describe the thalamic organization of the retino-thalamo-hyperstriatal pathway in the pigeon. The complex appears to be an avian homologue of the dorsal nucleus of the lateral geniculate of mammals. These nuclei represent a primary thalamic termination of the optic tract in birds and remain quite distinct from **Nuc. geniculatus lateralis, Pars ventralis** and from **pretectal nuclei.** Karten and Nauta (1968) described the retinothalamic projections in the pigeon and owl. See Emmerton (1983) for a review of the avian visual system.

(85) **Nuc. ovoidalis.** Synonymy: Nuc. B (Rendahl, 1924); Nuc. anterior ventralis (Edinger and Wallenberg, 1899). Nuc. ovoidalis represents the thalamic relay nucleus of the auditory system. Karten (1967) shows that this nucleus is the avian homologue of the ventral portion of the mammalian medial geniculate body. Karten (1968) describes the telencephalic projection of the nucleus. Bonke, et al. (1979) describe the connections of the auditory forebrain nuclei of the guinea fowl (*Numida meleagris*).

(86) **Nuc. rotundus.** Anatomic, electrophysiologic and behavioral studies indicate that Nuc. rotundus represents a major thalamic relay for the visual sysetm of birds (Cowan, et al., 1961; Karten and Revzin, 1966; Revzin and Karten, 1966). Afferents to the nucleus arise in Tectum mesencephali and efferents project to the "tectofugal pathway" of the avian visual system (Karten, et al., 1973). Nuc. rotundus appears to be the avian counterpart of the Nuc. lateralis caudalis of mammals.

(87) **Nuc. semilunaris thalami.** Synonymy: Nuc. semilunaris parovoidalis. This nucleus lies adjacent to the ventrolateral aspect of Nuc. ovoidalis and receives a significant number of afferent fibers from that nucleus (Karten, 1967).

(88) **Complexus spiriformis.** This complex is considered to include Nuc. spiriformis lateralis, Nuc. spiriformis medialis, Nuc. principalis precommissuralis, Nuc. dorsolateralis caudalis and Nuc. dorsolateralis intermedius of the thalamus (Karten and Dubbeldam, 1973). The afferents to this region of the thalamus include those from the spinal cord, cerebellar nuclei, basal ganglia homologues (See **Annot.** 101),

Tr. occipitomesencephalicus and possibly a small projection from **Nuc. cuneatus** and **Nuc. gracilis.** Each of these afferent systems overlap to some degree. These observations suggest that Complexus spiriformis may correspond, at least in part, to the ventral tier of nuclei of the mammalian thalamus (Karten and Dubbeldam, 1973).

(89) **Nuc. triangularis.** Synonymy: Nuc. tr. habenulopeduncularis (Huber and Crosby, 1926; Craigie, 1930).

(90) **Sectiones Hypothalami.** Kuenzel and van Tienhoven (1982) provided an excellent description of the hypothalamic nuclei of the chicken (*Gallus*). The nomenclature provided here primarily represents their proposed organization. Crosby and Showers (1969) describe the organization of the hypothalammic nuclei in the sparrow. Goosens, et al. (1977) describe the immunochemistry of the hypothalamo-neurohypophyseal system in birds.

(91) **Regio preoptica [R. rostralis] hypothalami.** Panzica and Viglietti-Panzica (1980) describe the preoptic area in the chicken (*Gallus*). Berk and Butler (1981) describe the efferent projections of the medial preoptic and medial hypothalamus of the pigeon (*Columba*).

(92) **Nuc. paraventricularis hypothalami.** Schober, et al. (1977) have described hypothalamo-medullary connections from the region of this nucleus in the pigeon (*Columba*). Panzica and Viglietti-Panzica (1982; 1983) describe the parvocellular component and synaptology of neurosecretory neurons in this nucleus of the chicken (*Gallus*), as they relate to regulation of salt and water balance. Berk, et al. (1982) describe the localization of vasotocin and neurophysin-containing neurons in the diencephalon of the pigeon. Blähser, et al. (1978) and Blähser (1980) describe the localization of somatostatin containing neurons in the hypothalamus of the domestic Mallard (*Anas platyrhychos*) and chicken. Dubois, et al. (1974) describe the distribution of somatostatin in the median eminence of mammals, birds, and amphibians. Bons, (1976; 1980) and Bons, et al. (1978a, b) describe the topography of the mesotocin, vasotocin, and luteinizing hormone releasing hormone (LHRH) neuroendocrine systems and connections with the hippocampal area in the brain of the domestic Mallard and Japanese Quail (*Coturnix coturnix*). Jozsa and Mess (1982), Sterling and Sharp (1982), Mikami et al. (1988) and Kuenzel and Blähser (1991) localized LHRH containing neurons in the brain of domestic fowl. Korf, et al. (1982; 1983) describe the afferents to the nucleus in the Mallard and demonstrate that some of the neurons make contact with cerebrospinal fluid of the third ventricle. Viglietti-Panzica and Contenti (1983) describe the development of the nucleus in the chick.

(93) **Nuc. ventromedialis hypothalami.** Synonymy: Nuc. posterior medialis hypothalami (Bouille, et al., 1977). These investigators describe the hippocampal and septal connections to this nucleus.

(94) **Eminentia mediana.** There occur in *Zonotrichia leucophrys* anatomically distinct divisions of the median eminence that may be drained by separate rostral and caudal groups of hypophysial portal vessels (Vitums, et al., 1964).

(95) **Tr. infundibularis.** Benowitz and Karten (1976a) describe this and other tracts in the region of the infundibulum.

(96) **Tr. retinohypothalamicus.** Meier (1973) describes this tract in the chicken (*Gallus*), Bons (1974; 1976) in the duck (*Anas*), and Hartwig (1974) in the sparrow.

(97) **Bulbus olfactorius.** Ricke and Wenzel (1978) describe the projections of the olfactory bulb to the forebrain of the pigeon (*Columba*).

(98) **Fissura subhemispherica.** Synonymy: Transverse cerebral fissure (Baumel, 1967). The cleft between the ventral surface of one telencephalic hemisphere and the dorsal surface of the mesencephalic tectum.

(99) **Archistriatum.** Consideration of its cytoarchitectural organization and hodologic relationships makes it apparent that the Archistriatum is more complex than has been previously assumed (Zeier and Karten, 1971, 1973). Some of the associated subdivisions of the Archistriatum are included in this nomenclature. It should be emphasized, however that the subdivisions listed are by no means all the cytoarchitectonic components. By way of simplification of structural relationships of the Archistriatum, based upon investigations of Zeier and Karten (1973), it appears that its caudal one-third and most medial parts (**Archistriatum caudale** and **Archistriatum mediale**) represent "limbic" components of the Telencephalon. These regions project to the hypothalamus via **Pars hypothalamica of Tr. occipitomesencephalicus,** and may represent an avian counterpart of the mammalian amygdala (Zeier and Karten, 1971) (See **Annot.** 16). The rostral two-thirds (**Archistriatum rostrale** and **Archistriatum intermedium**) give rise to the nonhypothalamic component of **Tr. occipitomesencephalicus** and appear to function in a "somatic" rather and a visceroendocrine effector system. A nucleus, called **Nuc. robustus** can be recognized within this part of the Archistriatum of singing birds and the budgerigar, as part of the "vocalization circuit" (Paton, et al., 1981). This area of the Archistriatum compares with the pericentral cortex of the goat and the sensorimotor cortex of primates (Zeier and Karten, 1971).

(100) **Commissura rostralis [anterior].** Synonymy: Commissura interarchistriatica (Ariens Kappers, et al., 1936). On crossing the midline, this commissure divides into two major fascicles; a relatively diffuse rostromedial branch (Pars bulbaris) and a more compact, laterally directed, caudal branch (Pars temporalis). Pars bulbaris passes rostromedially to **Fasc. lateralis prosencephali** and terminates in an area ventral and lateral to **Lobus parolfactorius,** including **Nuc. accumbens,** the dorsal portion of the **Tuberculum olfactorium** and limited areas of the medial edge of **Paleostriatum intercalatum supremum.** A portion of Pars temporalis ends in the rostral one-third of the Archistriatum and continues by two paths: a dorsolateral projection to the temporo-parieto-occipital area as it continues rostrolaterally to the **Hyperstriatum intercalatum supremum** and a ventrolateral projection paralleling **Tr. frontoarchistriaticus** to terminate in the deep layers of the **Cortex piriformis** (Zeier and Karten, 1973).

(101) **Complexus paleostriaticus.** Several investigators have suggested that the paleostriate complex, consisting of the Paleostriatum augmentatum, Paleostriatum primitivum and Nuc. intrapeduncularis, represent the equivalent of the mammalian "basal ganglia" (caudate, putamen, and globus pallidus), whereas the overlying striatal masses of **Neostriatum, Ectostriatum, Hyperstriaticum ventrale, dorsale, et accessorium** are representative of the mammalian neocortex (Karten, 1969; Nauta and Karten, 1970; Zeier and Karten, 1971; Juorio and Vogt, 1967; Scheich, 1983; Dubbeldam and Vissner, 1987). These assumptions have been supported by Karten and Dubbeldam (1973) utilizing histochemical and neuroanatomic methods. **Paleostriatum augmentatum** and **Lobus parolfactorius** together are considered to be the equivalent of the mammalian caudate-putamen and Nuc. accumbens, respectively

(Reiner, et al., 1983). **Paleostriatum primitivum** and **Nuc. intrapeduncularis** appear to correspond to the outer and inner laminae of the globus pallidus of mammals (Karten and Dubbeldam, 1973). Moreover, a **Paleostriatum ventrale** has been recognized in the pigeon (Kitt and Brauth, 1981) and the duck. The latter is a small-celled area ventral to the **Lobus parolfactorius** and medial to **Fasc. lateralis prosencephali.** It receives afferents from **Lobus parolfactorius** and other prosencephalic structures (Brauth, et al., 1978) and may have connections with the **Archistriatum** and the reticular formation of the brain stem.

(102) **Nuc. preopticus medianus.** This sexually dimorphic nucleus within the preoptic hypothalamic area of the *Coturnix* quail was recently described and named by Adkins-Regan and Watson (1990). This nucleus was originally reported by Viglietti-Panzica, et al. (1986) as sexually dimorphic in *Coturnix;* they used the term Nuc. preopticus medialis (POM). The POM as presented in the pigeon (*Columba*) stereotaxic brain atlas (Karten and Hodos, 1967) does not accurately represent its anatomical position. It is suggested that the Nuc. preopticus medianus be applied to the nucleus within the preoptic area shown to be larger in males, involved in sexual behavior, and found to contain aromatase receptors (Balthazart, et al., 1990).

(103) **Hippocampus,** Bons, et al. (1976) describe the projections of the hippocampus of the pigeon to the hypothalamus.

(104) **Hyperstriatum accessorium.** Hyperstriatum accessorium makes up a major part of the gross brain structure. It is evidenced on the dorsal surface of the telencephalic hemisphere as the **Eminentia sagittalis** or "Wulst" (Fig. 14.2). The sagittal eminence may include (depending upon the author) **Hyperstriatum accessorium** and a variable subpial molecular layer, **Lamina frontalis superior, Lamina frontalis suprema, Hyperstriatum dorsale** and **Hyperstriatum intercalatus supremum.** Medially the sagittal eminence grades into the parahippocampal and hippocampal areas (Karten, et al., 1973). Nixdorf and Bischof (1982) describe the afferent connections to Eminentia sagittalis in the Zebra Finch; Bagnoli and Burkhalter (1983) present a similar study in the chicken. Watanabe, et al. (1983) describe the cytoarchitecture of the visual receptive cells of this region.

(105) **Lobus parolfactorius.** The Lobus can be divided into lateral and medial portions (Reiner, et al., 1983). The lateral portion, together with the **Complexus paleostriatum,** is the source of **Tr. striomesencephalicus.** This tract projects to **Nuc. habenularis lateralis, Area ventralis thalami, Nuc. tegmenti pedunculopontini** and **Nuc. ceruleus** (Kitt and Brauth, 1981).

(106) **Nuc. ansae lenticularis caudalis; Nuc. ansae lenticularis rostralis.** Synonymy: nucleus of the dorsal supraoptic decussation (Huber and Crosby, 1929); Nuc. entopeduncularis postero-superior (Kuhlenbeck, 1937). Nuc. ansae lenticularis corresponds to the entopeduncular nucleus of the alligator (*Alligator mississippiensis*) (Huber and Crosby, 1926) and a cell group believed by Papez (1935) to be comparable to the mammalian subthalamic nucleus. Powell and Cowan (1961) referred to the nucleus as the Nuc. posteroventralis and Baker-Cohen (1968) identified it as the entopeduncular nucleus. These nuclei have been referred to as the avian equivalent of the internal segment of the Globus pallidus or Substantia nigra. Karten and Dubbeldam (1973), however, indicate that on the basis of current information these assumptions are not justified, but that Nuc. ansae lenticularis rostralis/ caudalis may be more correctly considered to represent the avian counterpart of the mammalian subthalamic nucleus, nuclei of the field of Forel and other cell groups that receive

afferents from the Ansa lenticularis. To emphasize: the mammalian homologue of these nuclei is not definitively established.

(107) **Nuc. basalis [Nuc. trigeminalis] prosencephali.** The synonym indicates that this nucleus is primarily related to the termination of ascending fibers from the principal sensory nucleus of the trigeminal nerve. It may in fact represent a thalamic relay nucleus somewhat remote from the thalamus proper. It is not clear, however, that Nuc. basalis exclusively serves this function (Wallenberg, 1903; Woodburne, 1936; Witkovsky, et al., 1973). The name, Nuc. basalis is retained in the present terminology because of this contingency and the fact that the term is well established in the literature. Stingelin (1961) noted that the relative size of Nuc. basalis is proportional to the size of the principal sensory nucleus of the trigeminal nuclear complex. Physiological studies indicate that the principal sensory nucleus of the trigeminal complex is linked to Nuc. basalis by way of a direct monosynaptic pathway, the **Tr. quintofrontalis** (Witkovsky, et al., 1973). Dubbeldam, et al. (1981) and Berkhoudt, et al. (1981) describe the somatotopy of tactile representation in Nuc. basalis. Dubbeldam and Visser (1987) describe the efferents of Nuc. basalis and the interrelationships between Nuc. basalis and the **Neostriatum** in the Mallard.

(108) **Tr. fronto-archistriaticus.** This tract originates from Neostriatum, Pars rostralis and terminates in Archistriatum and the overlying lateral part of the Neostriatum (Wild, et al., 1985).

(109) **Meninges.** Early workers were able to identify only a pia-arachnoid lamina, and a Dura mater encephali, with little or no development of a **cavum subarachnoideum** in birds (see Hodges, 1974; Baumel, 1975 for reviews). Bohme (1970) and Jones and Dolman (1978), using light and electron microscopy, have demonstrated distinct **Pia** and **Arachnoid** layers, a subarachnoid cavity and arachnoid granulations in the pigeon (*Columba*) and the chicken (*Gallus*).

(110) **Dura mater spinalis; Dura mater encephali.** The internal vertebral venous sinus lies in the epidural space between the Dura mater spinalis and the periosteum of the vertebral canal. The dura mater encephali consists of two layers closely adherent, but separable from one another. Cranial dural venous sinuses are located in the plane between the two layers; both layers are vascularized by rami of the cerebral arteries.

(111) **Plica tentorialis.** This is a transverse fold of Dura mater encephali that lies in the Fissura subhemispherica between the caudoventral surface of the telencephalic hemispheres and the mesencephalic colliculus. The fold is attached to and extends the Crista tentorialis, an osseous ledge on the inner surface of the cranial cavity (See **Osteo.** Fig. 4.6).

(112) **Lig. suspensoria transversa.** Ligamentous bands of the Pia mater that stretch from **Lig. denticulatum** to **Lig. ventromedianum** and on to the opposite Lig. denticulatum, forming a hammock-like structure for the lumbosacral intumescence (**Annot.** 1) of the spinal cord (Dingler, 1965).

Sequence of sections. The sequence of brain sections are presented from caudal to rostral, beginning in the spinal cord, then Medulla oblongata, ending with the Telencephalon. In individual figures with multiple sections the uppermost section is most rostral, the bottom one is most caudal (see Fig. 14.1). The figures were adapted and redrawn from the atlas of Kuenzel and Masson (1988) with the permission of Johns Hopkins Press.

Abbreviations. In some instances the abbreviations for features on the sections of the brain do not agree completely with their recommended names as presented in the list of terms. In many of these, the abbreviation is not only followed by the recommended term but followed by parenthetical word or words. For example: CBI, Nuc. cerebellaris medialis (internus). The "internus" is not an alternate term but a non-recommended synonym which helps to explain why the abbreviation is CBI instead of CBM. On the other hand, parts of names in square brackets that follow the primary term, as explained in the general introduction, are "official", recommended, secondary alternative terms.

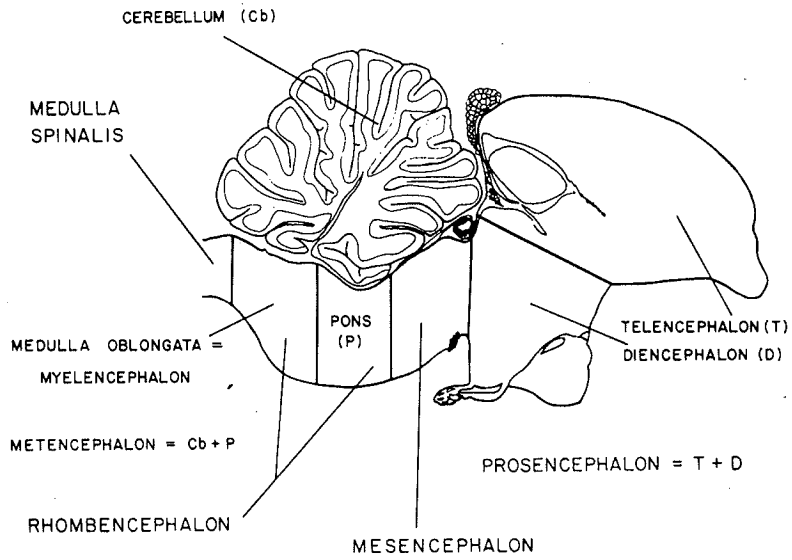


Fig. 14.1. Median-sagittal view of chick brain showing anatomical regions used in text.

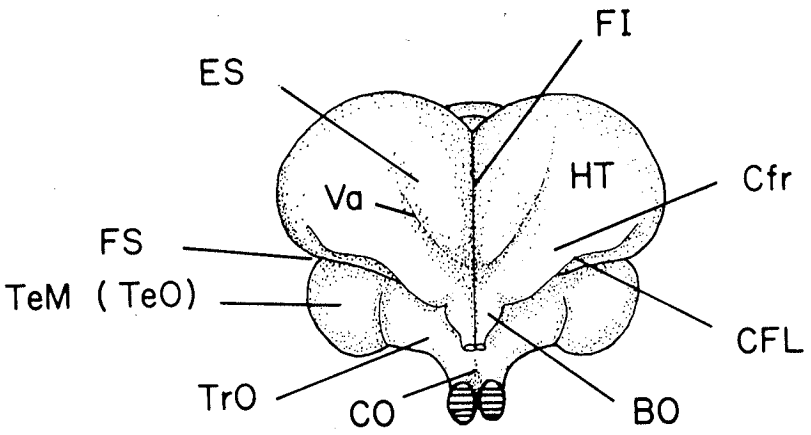


Fig. 14.2. Frontal aspect of the brain of the pigeon.

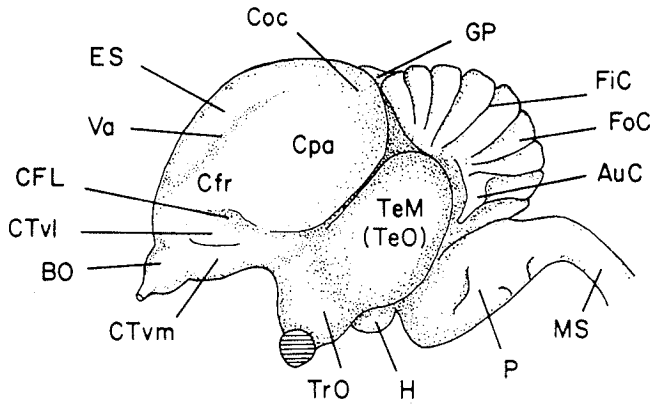


Fig. 14.3. Lateral aspect of the brain of the pigeon. Abbreviations for Figs. 14.1, 2, 3:

AUC	Auricula cerebelli
BO	Bulbus olfactorius
CFL	Cerebrum, Fovea limbica
Cfr	Cerebrum, Pars frontalis
Coc	Cerebrum, Pars occipitalis
Cpa	Cerebrum, Pars parietalis
CTvl	Cerebrum, Tuber ventrolaterale
CTvm	Cerebrum, Tuber ventromediale
CO	Chiasma opticum
ES	Eminentia sagittalis
FiC	Fissura cerebelli
FI	Fissura interhemispherica
FS	Fissura subhemispherica
FoC	Folia cerebelli
GP	Glandula pinealis
H	Hypophysis
HT	Hemispherium telencephali
MS	Medulla spinalis
P	Pons
TeM	Tectum mesencephali
TeO	Tectum opticum
TrO	Tr. opticus
Va	Vallecula telencephali

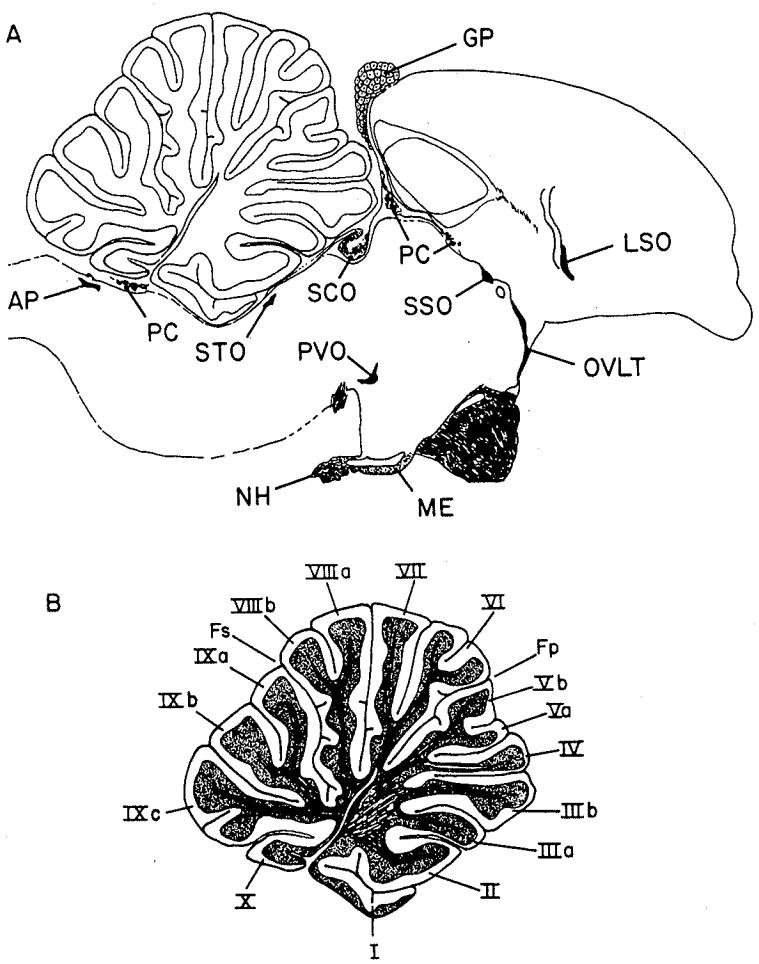


Fig. 14.4A. Mid-sagittal view of chick brain showing the location of circumventricular organs.

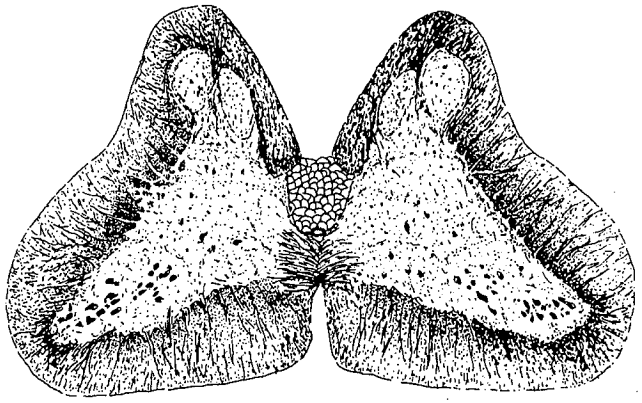
Fig. 14.4B. Sagittal view of cerebellum showing a numbering system for the many lobules of the structure. Note that the anatomical scheme will vary from species to species. Redrawn from Kuenzel and Masson (1988) with permission of Johns Hopkins Press.

Abbreviations for Fig. 14.4 A & B:

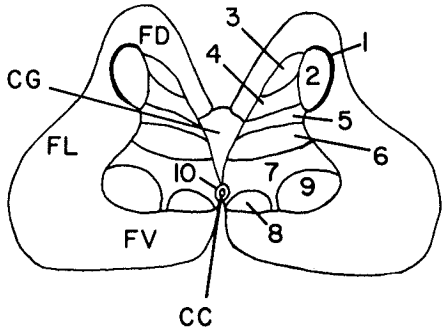
AP	Area postrema
GP	Glandula pinealis
LSO	Organum laterali septi
ME	Eminentia mediana
NH	Neurohypophysis
OVLT	Organum vasculosum laminae terminalis
PC	Plexus choroideus

PVO	Organum paraventriculare
SCo	Organum subcommissurale
SSO	Organum subseptale (O. interventriculare)
STO	Organum subtrochleare
Fp	Fissura prima
Fs	Fissura secunda

A. CHICK



B. CHICK



C. PIGEON

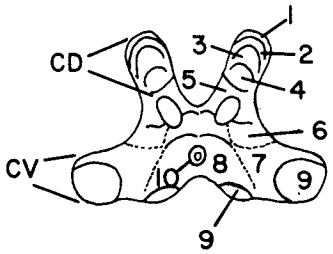
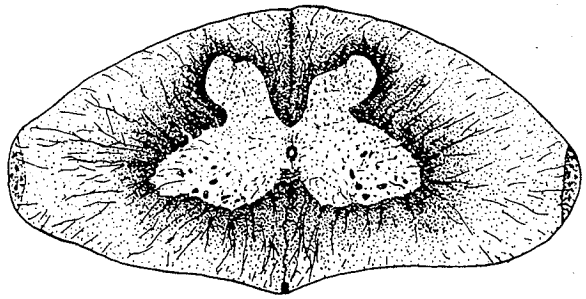


Fig. 14.5 A, B and C. Transverse sections of the avian spinal cord in the synsacral region. The Sinus rhomboidalis is apparent in the lumbosacral swelling of the cord and contains the gelatinous body. The dorsal horn is laminated in birds similar to other vertebrates. In chickens (Fig. 14.5A, 5B) lamina 3 lies medial rather than ventral to lamina 2 (Brinkman and Martin, 1973; Martin, 1979) while in pigeons (Fig. 14.5C) a typical dorsoventral lamination pattern occurs (Leonard and Cohen, 1975). The two schemes shown represent at least two different types of dorsal horn lamination patterns in avian species. The "chicken" pattern appears to be widespread among various avian taxa. The type of pattern found in a given species has thus far been shown to be consistent across successively higher taxa. In other words, the pattern is conserved at the specific, generic, familial and ordinal taxonomic levels (Woodbury, 1989).



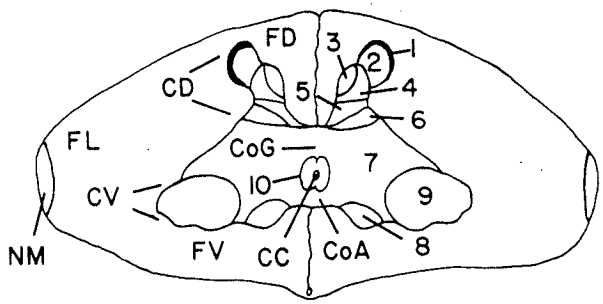
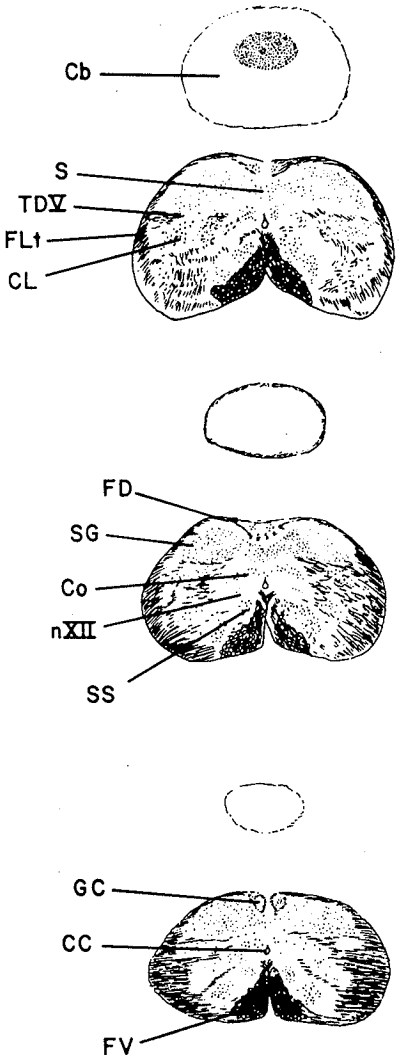


Fig. 14.6. A transverse section of the spinal cord of the chick in the cervicothoracic transitional region of the vertebral column. This is the level of the cervical intumescence of the cord from which the brachial plexus arises. The laminar pattern shown is that developed by Brinkman and Martin (1973).

Abbreviations for Figs. 14.5 and 6:

CC	Canalis centralis
CoA	Commissura alba
CoG	Commissura grisea
CG	Corpus gelatinosum
CD	Cornu dorsale
CV	Cornu ventrale
FD	Funiculus dorsalis
FL	Funiculus lateralis
FV	Funiculus ventralis
NM	Nuc. marginalis



Figs. 14.7, 8, 9. Transverse sections of the Medulla oblongata of the chick. Levels of sections (see Fig. 14.1). The most caudal section is at the bottom of each group of three. Redrawn from Kuenzel and Masson (1988) with permission of Johns Hopkins Press.

Abbreviations:

APa	Area postrema
Cb	Cerebellum
CC	Canalis centralis
CE	Nuc. cuneatus accessorius [lateralis]

(continued p. 535)

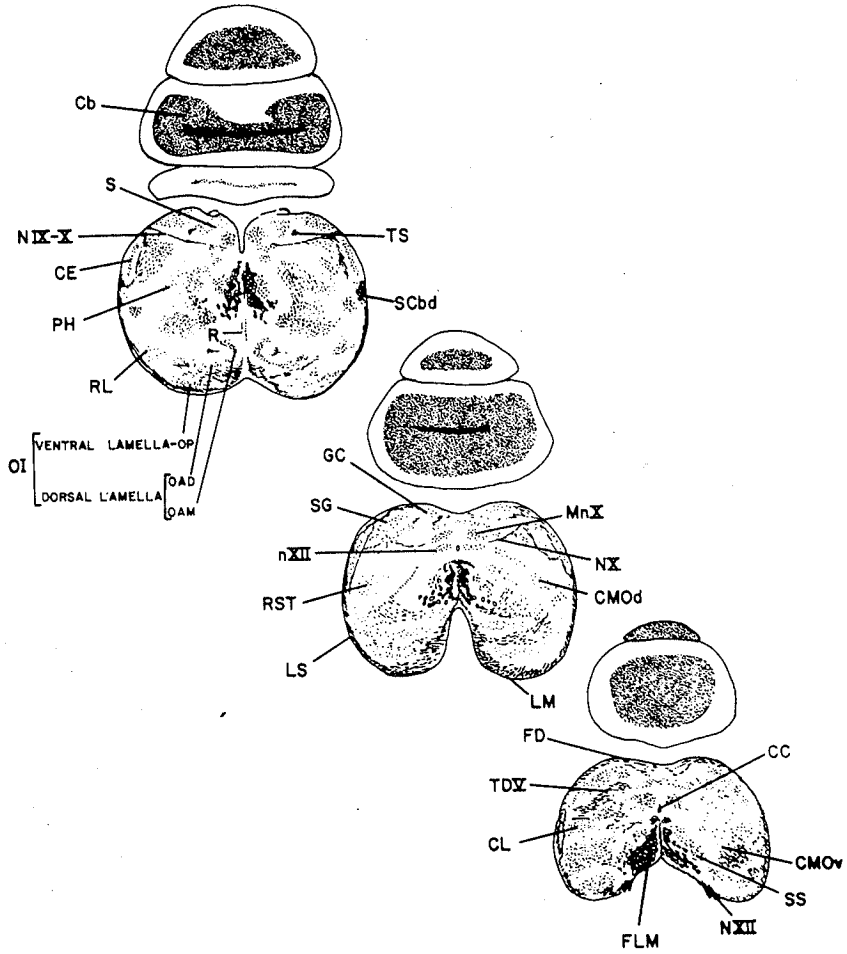


Fig. 14.8

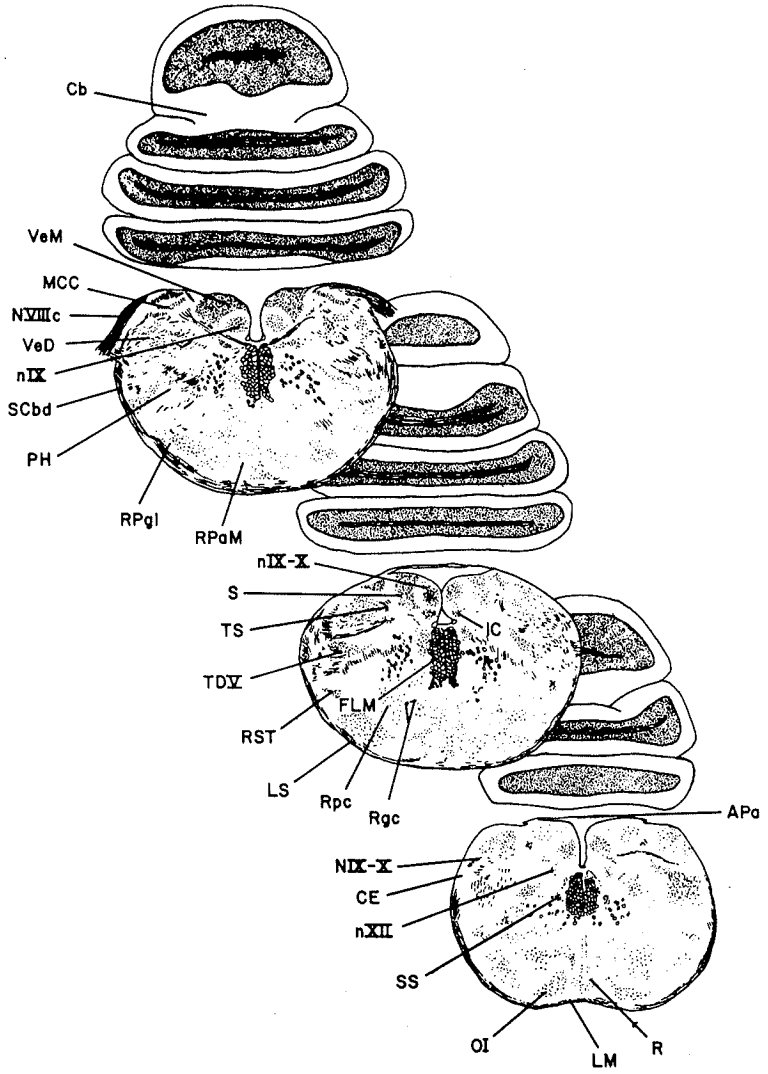
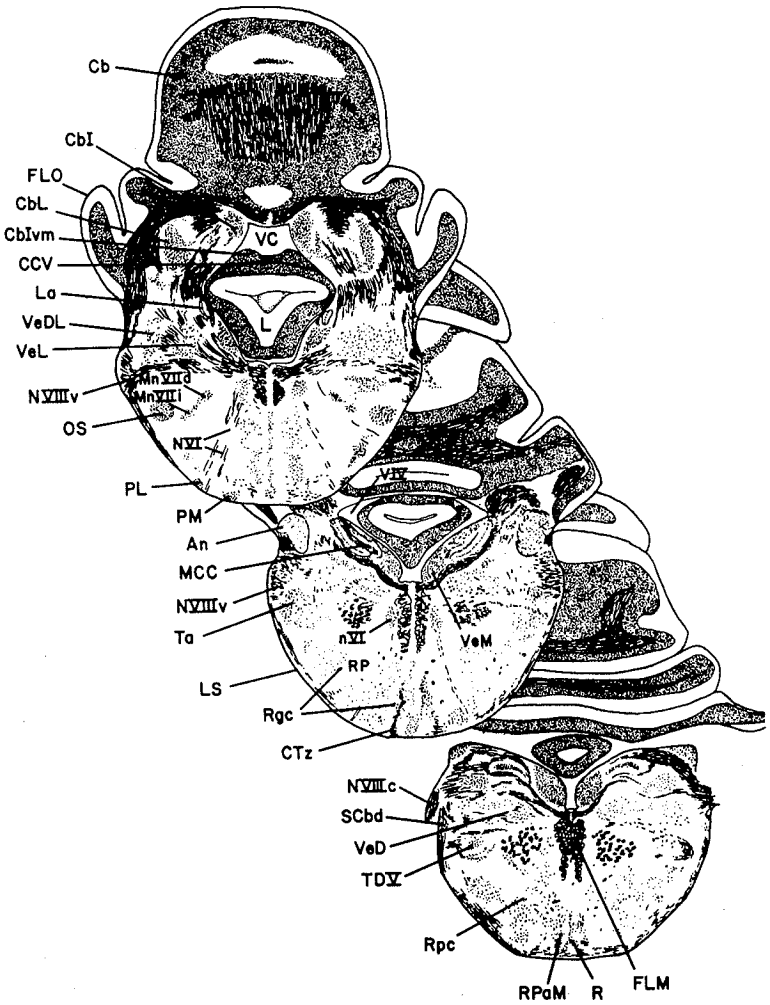


Fig. 14.9

(continued from p. 532)

CL	Nuc. cervicalis lateralis
CMOd	Nuc. centralis medullae oblongatae, Pars dorsalis
CMOv	Nuc. centralis medullae oblongatae, Pars ventralis
Co	Nuc. commissuralis
FD	Funiculus dorsalis
FLM	Fasc. longitudinalis medialis
FLt	Funiculus lateralis
FV	Funiculus ventralis
GC	Nuclei gracilis et cuneatus
IC	Nuc. intercalatus
LM	Lemniscus medialis
LS	Lemniscus spinalis
MCC	Nuc. magnocellularis cochlearis
MnX	Nuc. motorius dorsalis n. vagi
nIX	Nuc. motorius n. glossopharyngei
nIX-X	Nuc. n. glossopharyngei et Nuc. motorius dorsalis n. vagi
nXII	Nuc. n. hypoglossi
NVIIIc	N. vestibulocochlearis, Pars cochlearis
NIX-X	Nn. glossopharyngeus et vagus
NX	N. vagus
NXII	N. hypoglossus
OI	Complexus olivaris caudalis (components of OI include: OAD, OAM, and OP)
OAD	Nuc. olivaris accessorius dorsalis
OAM	Nuc. olivaris accessorius medialis
OP	Nuc. olivaris principalis
PH	(Plexus of Horsley)
R	Nuc. raphae
Rgc	Nuc. reticularis gigantocellularis
RL	Nuc. reticularis lateralis
Rpc	Nuc. reticularis parvocellularis
RPaM	Nuc. reticularis paramedianus
RPgl	Nuc. reticularis paragiganto-cellularis lateralis;
RST	Nuc. reticularis subtrigeminalis
S	Nuc. tractus solitarii
SCbd	Tr. spinocerebellaris dorsalis
SG	Pars substantia gelatinosa, Nuc. tr. descend. n. trigem.
SS	Nuc. supraspinalis
TDV	Nuc. tr. descendentis n. trigemini
TS	Tr. solitarius
VeD	Nuc. vestibularis descendens
VeM	Nuc. vestibularis medialis



Figs. 14.10, 11. Transverse sections of the Pons and rostral part of the Medulla oblongata of the chick. The most caudal section is at the bottom of each group of three. Redrawn from Kuenzel and Masson (1988) with permission of Johns Hopkins Press.

Abbreviations:

An	Nuc. angularis
BC	Pedunc. cerebellaris rostralis [Brachium conjunctivum]
Cb	Cerebellum

(continued p. 538)

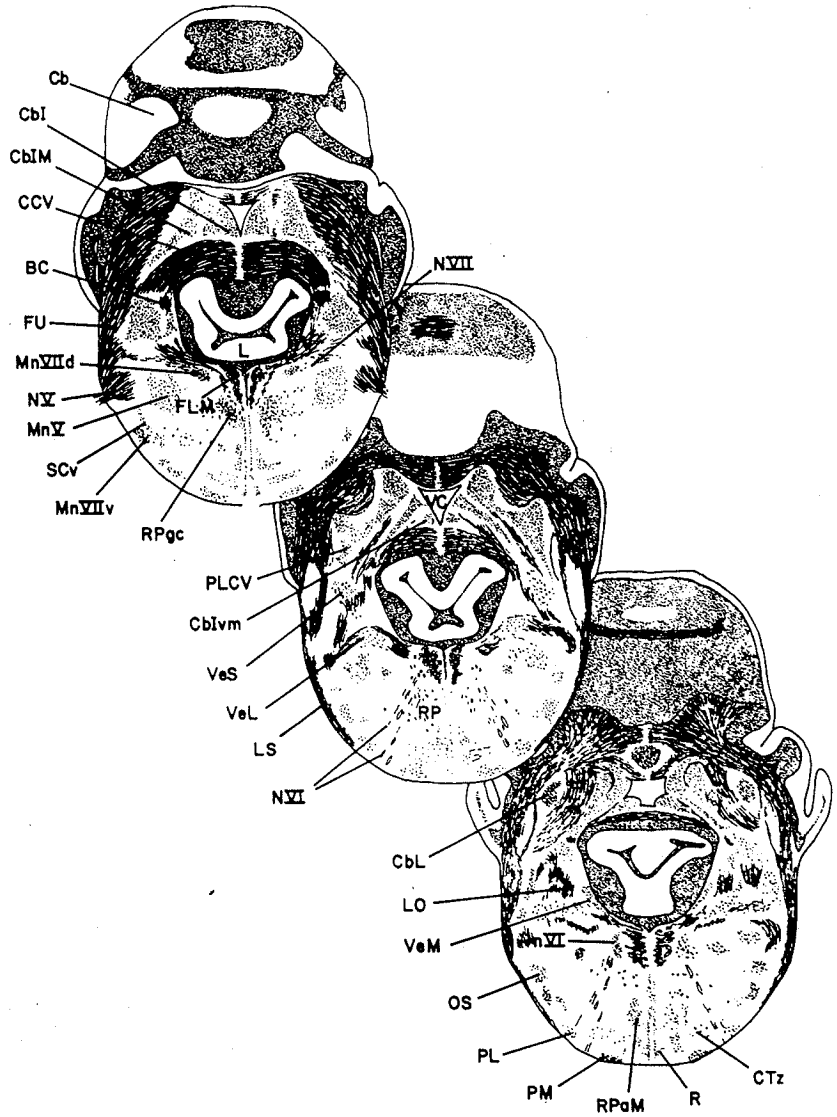
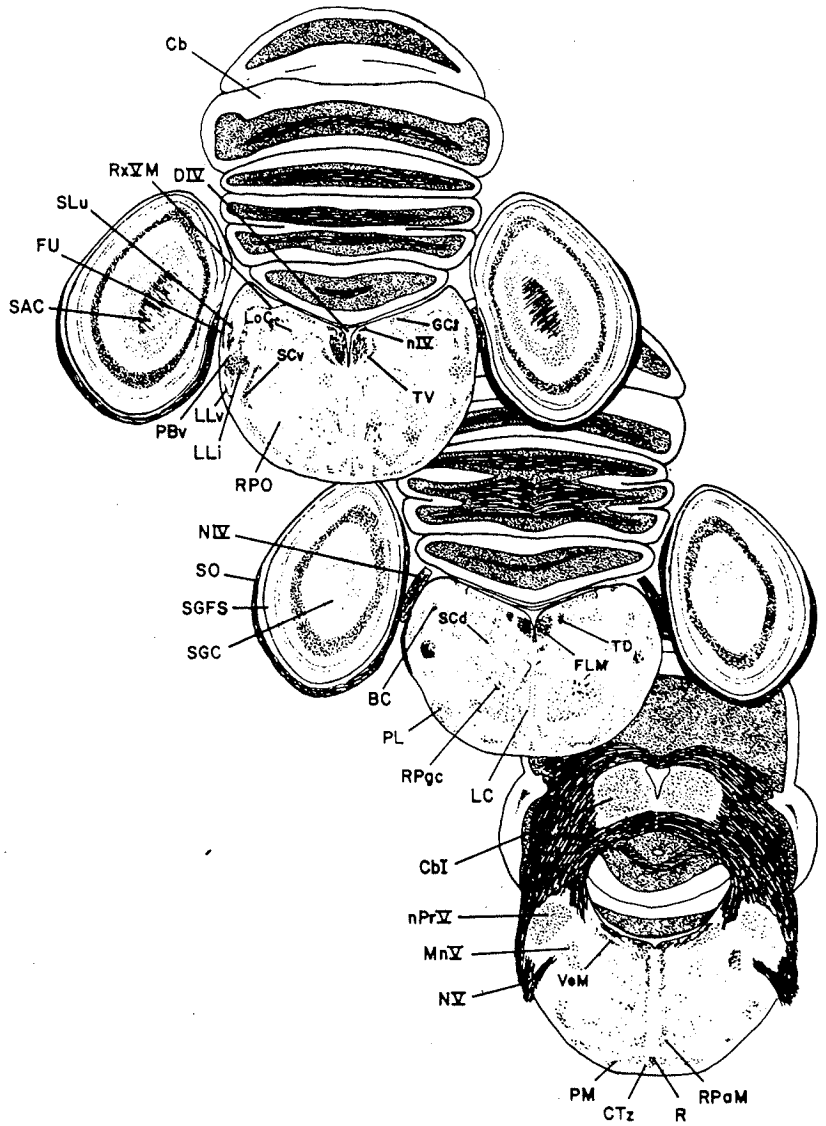


Fig. 14.11

(continued from p. 536)

CbI	Nuc. cerebellaris medialis (internus)
CbIM	Nuc. cerebellaris intermedius
CbIvm	Nuc. cerebellaris lateralis (internus, pars ventromedialis)
CbL	Nuc. cerebellaris lateralis
CCV	Commissura cerebellaris ventralis
CTz	Corpus trapezoideum
FLM	Fasc. longitudinalis medialis
FLO	Flocculus
FU	Fasc. uncinatus
L	Lobulus lingulae (Lingula)
La	Nuc. laminaris
LO	Tr. lamino-olivaris
La	Nuc. laminaris
LS	Lemniscus spinalis
MCC	Nuc. magnocellularis cochlearis
MnV	Nuc. motorius n. trigemini
MnVIId	Nuc. motorius n. facialis, Pars dorsalis
MnVIIi	Nuc. motorius n. facialis, Pars intermedia
MnVIIv	Nuc. motorius n. facialis, Pars ventralis
nVI	Nuc. n. abducentis
N V	N. trigeminus
N VI	N. abducens
N VII	N. facialis
N VIIIc	N. vestibulocochlearis, Pars cochlearis
N VIIIv	N. vestibulocochlearis, Pars vestibularis
OS	Nuc. olivaris superior
PL	Nuc. lateralis pontis
PLCV	Proc. lateralis cerebello-vestibularis
PM	Nuc. medialis pontis
R	Nuc. raphae
Rgc	Nuc. reticularis gigantocellularis
RP	Nuc. reticularis pontis caudalis
Rpc	Nuc. reticularis parvocellularis
RPaM	Nuc. reticularis paramedianus
RPgc	Nuc. reticularis pontis caudalis, Pars gigantocell.
SCbd	Tr. spinocerebellaris dorsalis
SCv	Nuc. subceruleus ventralis
Ta	Nuc. vestibularis tangentialis
TD V	Nuc. tr. descendentis n. trigemini
V IV	Ventriculus quartus
VC	Ventriculus cerebelli
VeD	Nuc. vestibularis descendens
VeDL	Nuc. vestibularis dorsolateralis
VeL	Nuc. vestibularis lateralis
VeM	Nuc. vestibularis medialis
VeS	Nuc. vestibularis rostralis (superior)



Figs. 14.12, 13. Transverse sections of the Mesencephalon and rostral part of the Pons in the chick. The most caudal section is at the bottom of each group of three. Redrawn from Kuenzel and Masson (1988) with permission of Johns Hopkins Press.

Abbreviations:

AVT	Area ventralis (Tsai)
BC	Pedunc. cerebellaris rostralis [Brachium conjunctivum] (continued p. 541)

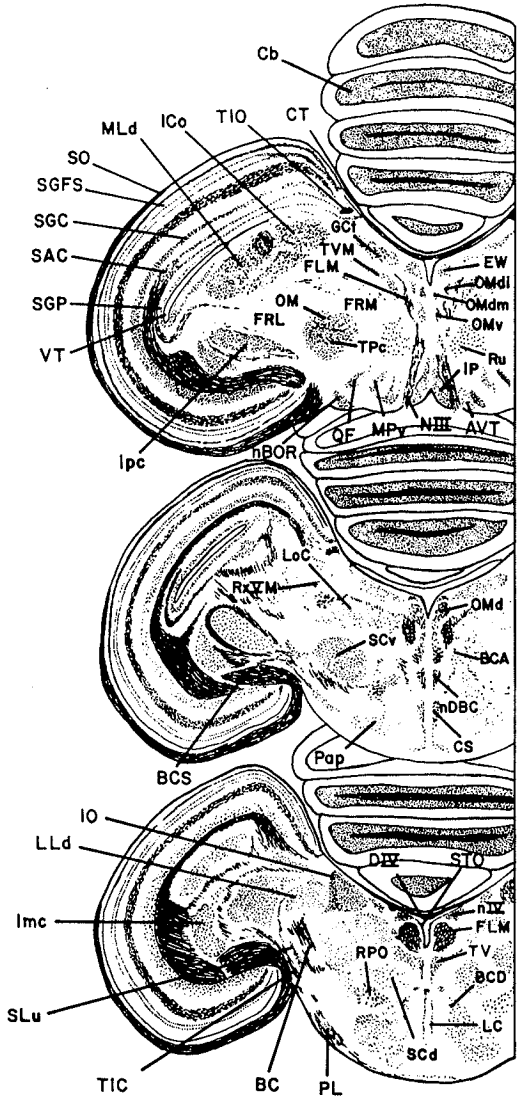


Fig. 14.13

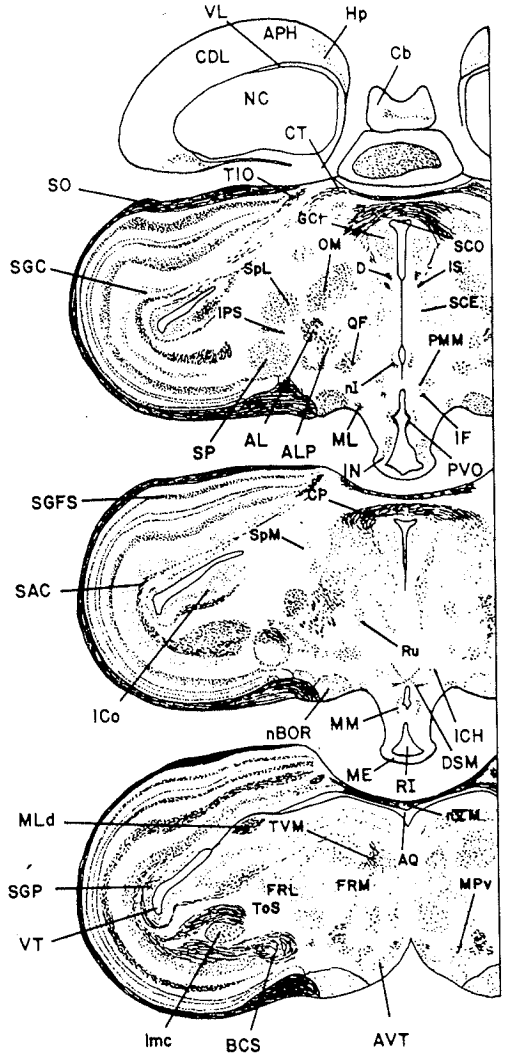
(continued from p. 539)

BCA	(Brachium conjunctivum ascendens)
BCD	(Brachium conjunctivum descendens)
BCS	Brachium colliculi mesencephali (superioris)
Cb	Cerebellum
Cbl	Nuc. cerebellaris internus
CS	Nuc. centralis superior
CT	Commissura tectalis
CTz	Corpus trapezoideum
D IV	Decuss. nervi trochlearis
EW	Nuc. n. oculomotorii (nuc. of Edinger-Westphal)
FLM	Fasc. longitudinalis medialis
FRL	Formatio reticularis lateralis mesencephali
FRM	Formatio reticularis medialis mesencephali
FUs	Fasc. uncinatus
GCt	Substantia grisea centralis
ICo	Nuc. intercollicularis
Imc	Complexus isthmi, Nuc. magnocell. isthmi
IOs	Nuc. isthmo-opticus
IPs	Nuc. interpeduncularis
Ipc	Nuc. parvocellularis isthmi
LCs	Nuc. linearis caudalis
LLd	Nuc. lemnisci lateralis, Pars dorsalis
LLi	Nuc. lemnisci lateralis, Pars intermedia
LLv	Nuc. lemnisci lateralis, Pars ventralis
LoC	Nuc. ceruleus (Locus ceruleus)
MLd	Nuc. mesencephalicus lateralis, Pars dorsalis
MnV	Nuc. motorius n. trigemini
MPv	Nuc. mesencephalicus profundus
nIV	Nuc. n. trochlearis
nBOR	Nuc. radicis opticae basalis
nDBC	Nuc. decussationis brachiorum conjunctivorum
nPrV	Nuc. sensorius principalis n. trigemini
N III	N. oculomotorius
N IV	N. trochlearis
N V	N. trigeminus
OM	Tr. occipitomesencephalicus
OMdl	Nuc. n. oculomotorii, Subnuc. dorsolateralis
OMdm	Nuc. n. oculomotorii, Subnuc. dorsomedialis
OMv	Nuc. n. oculomotorii, Subnuc. ventralis
Pap	Nuc. papillioformis
PBv	Nuc. parabrachialis, Pars ventrolateralis
PL	Nuc. lateralis pontis
PM	Nuc. medialis pontis
QF	Tr. quintofrontalis
R	Nuc. raphae
RPgc	Nuc. reticularis pontis caudalis, Pars gigantocellularis
RPO	Nuc. reticularis pontis rostralis (oralis)
Rus	Nuc. ruber
RxVM	Rdx. mesencephalica n. trigemini
SAC	Stratum album centrale
SCd	Nuc. subceruleus dorsalis

(continued p. 542)

(continued from p. 541)

SCv	Nuc. subceruleus ventralis
SGC	Stratum griseum centrale
SGFS	Stratum griseum et fibrosum superficiale
SGP	Stratum griseum periventriculare
SLu	Nuc. semilunaris mesencephali
SO	Stratum opticum
STO	Organum subtrochleare
TD	Nuc. tegmenti dorsalis
TIC	Tr. isthmocerebellaris
TIO	Tr. isthmo-opticus
TPc	Nuc. tegmenti pedunculo-pontinus, Pars compacta
TV	Nuc. tegmenti ventralis
TVM	Tr. vestibulomesencephalicus
VeM	Nuc. vestibularis medialis
VT	Ventriculus tecti mesencephali



Figs. 14.14, 15. Transverse sections of the caudal part of the Telencephalon, the caudal part of the Diencephalon, and Mesencephalon of the chick. The most caudal section is at the bottom of each group of three. For clarification from which brain region the schematic drawings are taken see Fig. 1. Redrawn from Kuenzel and Masson (1988) with permission of Johns Hopkins Press.

Abbreviations:

AL	Ansa lenticularis

(continued p. 545)

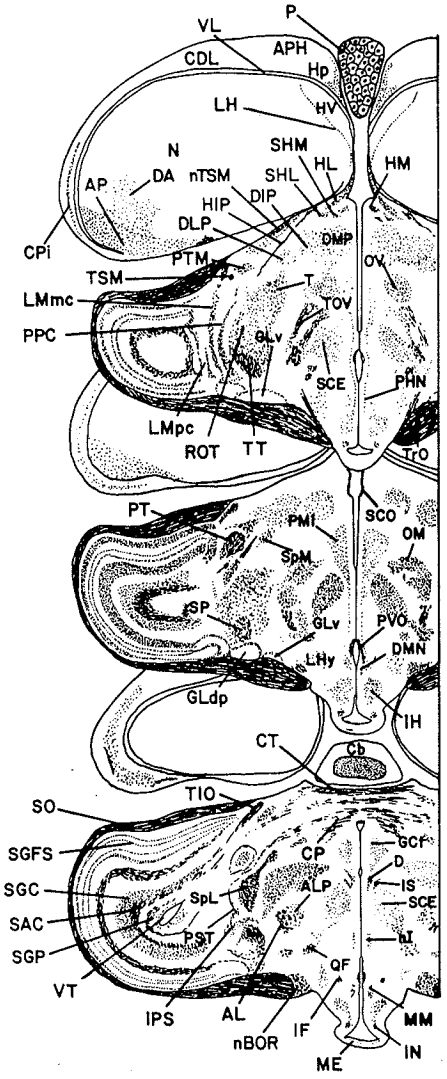


Fig. 14.15

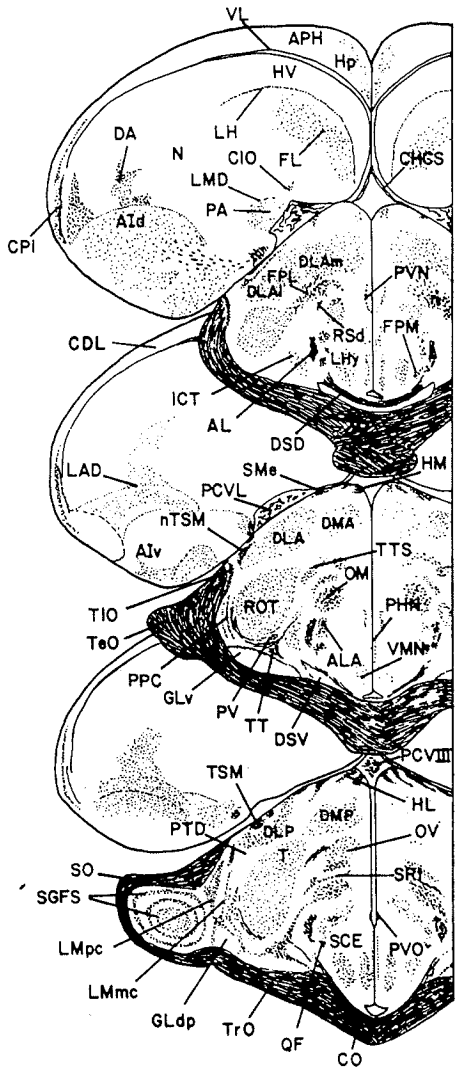
(continued from p. 543)

ALP	Nuc. ansae lenticularis caudalis (posterior)
AP	Area pretectalis
APH	Area parahippocampalis
AQ	Aqueductus mesencephali
AVT	Area ventralis (Tsai)
BCS	Brachium colliculi mesencephali (superioris)
Cb	Cerebellum
CDL	Area corticoidea dorsolateralis
CP	Commissura caudalis (posterior)
CPi	Cortex piriformis
CT	Commissura tectalis
D	Nuc. paragriseal is centralis mesencephali (Nuc. of Darkschewitsch)
DA	Tr. dorso-archistriaticus
DIP	Nuc. dorsointermedius caudalis (posterior) thalami;
DLP	Nuc. dorsolateralis caudalis (posterior) thalami
DMN	Nuc. dorsomedialis hypothalami
DMP	Nuc. dorsomedialis caudalis (posterior) thalami
DSM	Decuss. supramamillaris
FRL	Formatio reticularis lateralis mesencephali
FRM	Formatio reticularis medialis mesencephali
GCt	Substantia grisea centralis
GLdp	Nuc. geniculatus lateralis, Pars dorsalis (principalis)
GLv	Nuc. geniculatus lateralis, Pars ventralis
HIP	Tr. habenulo-interpeduncularis
HL	Nuc. habenularis lateralis
HM	Nuc. habenularis medialis
Hp	Hippocampus
HV	Hyperstriatum ventrale
ICH	Nuc. intercalatus hypothalami
ICo	Nuc. intercollicularis
IF	Tr. infundibularis
IHT	Nuc. inferioris hypothalami
Imc	Complexus isthmi, Nuc. magnocell. isthmi
IN	Nuc. infundibuli hypothalami
IPS	Nuc. interstitio-pretecto-subpretectalis
IS	Nuc. interstitialis thalami
LH	Lamina hyperstriatica
LHy	Regio lateralis hypothalami
LMmc	Nuc. lentiformis mesencephali, Pars medialis [P. magnocellularis]
LMpc	Nuc. lentiformis mesencephali, Pars lateralis [P. parvocellularis]
ME	Eminentia mediana
ML	Nuc. mamillaris lateralis
MM	Nuc. mamillaris medialis
MLd	Nuc. mesencephalicus lateralis, Pars dorsalis
MPv	Nuc. mesencephalicus profundus, Pars ventralis
nI	Nuc. intramedialis (nuc. c)
nV M	Nuc. mesencephalicus n. trigemini
nBOR	Nuc. radicis opticae basalis
nTSM	Nuc. tractus septomesencephalicus (Nuc. superficialis parvocellularis)

(continued p. 546)

(continued from p. 545)

N	Neostriatum
NC	Neostriatum, Pars caudalis
OM	Tr. occipitomesencephalicus
OV	Nuc. ovoidalis
P	Glandula pinealis
PHN	Nuc. periventricularis hypothalami
PMI	Nuc. paramedianus internus thalami
PMM	Nuc. premamillaris hypothalami
PPC	Nuc. principalis precommissuralis
PST	Tr. pretecto-subpretectalis
PT	Nuc. pretectalis
PTM	Nuc. pretectalis, Pars medialis
PVO	Organum paraventriculare
QF	Tr. quintofrontalis
RI	Recessus neurohypophysialis [Recessus infundibuli]
ROT	Nuc. rotundus
RSd	Nuc. reticularis thalami (superior, pars dorsalis)
Ru	Nuc. ruber
SAC	Stratum album centrale
SCE	Stratum cellulare externum
SCO	Organum subcommissurale
SGC	Stratum griseum centrale
SGFS	Stratum griseum et fibrosum superficiale
SGP	Stratum griseum periventriculare
SHL	Nuc. subhabenularis lateralis
SHM	Nuc. subhabenularis medialis
SO	Stratum opticum
SP	Nuc. subpretectalis
SpL	Nuc. spiriformis lateralis
SpM	Nuc. spiriformis medialis
T	Nuc. triangularis
TIO	Tr. isthmo-opticus
ToS	(Torus semicircularis)(See Annot. 73)
TOV	Tr. nuc. ovoidalis
TrO	Tr. opticus
TSM	Tr. septomesencephalicus
TT	Tr. tectothalamicus
TVM	Tr. vestibulomesencephalicus
VL	Ventriculus lateralis
VT	Ventriculus tecti mesencephali



Figs. 14.16, 17, 18. Transverse sections of the caudal part of the Telencephalon and the rostral part of the Diencephalon of the chick. The most caudal section is at the bottom of each group of three. Redrawn from Kuenzel and Masson (1988) with permission of Johns Hopkins Press.

Abbreviations:

AA	Archistriatum rostralis (anterior)
Ac	Nuc. accumbens
AId	Archistriatum intermedium, Pars dorsalis

(continued p. 550)

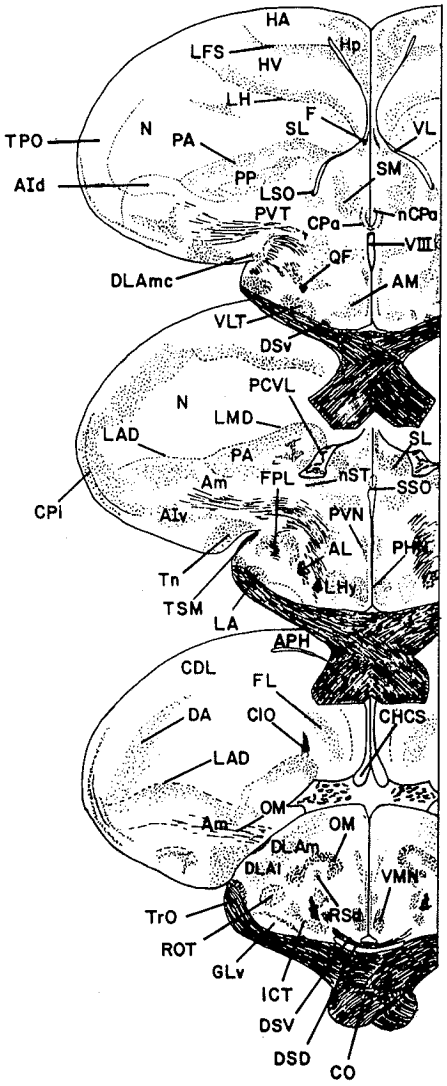


Fig. 14.17

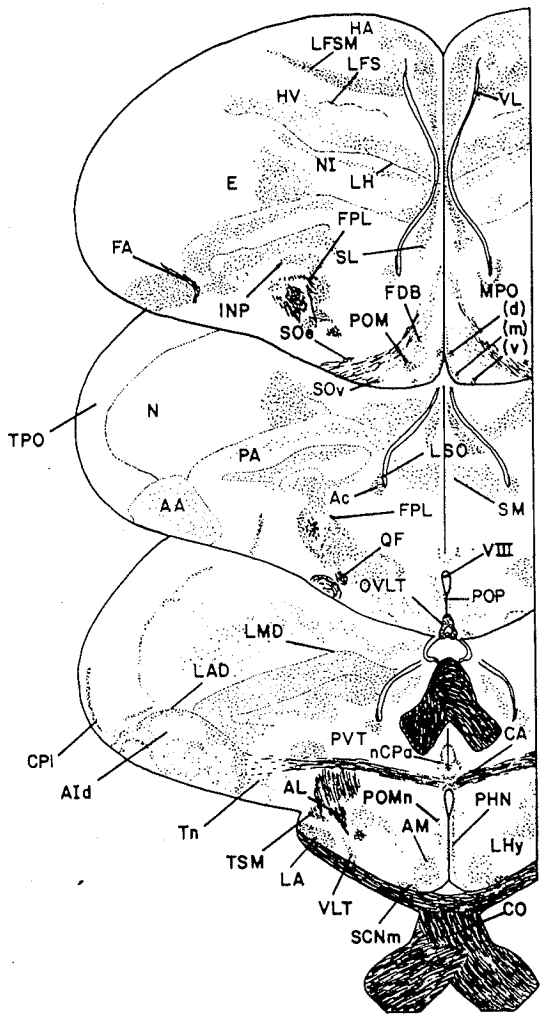


Fig. 14.18

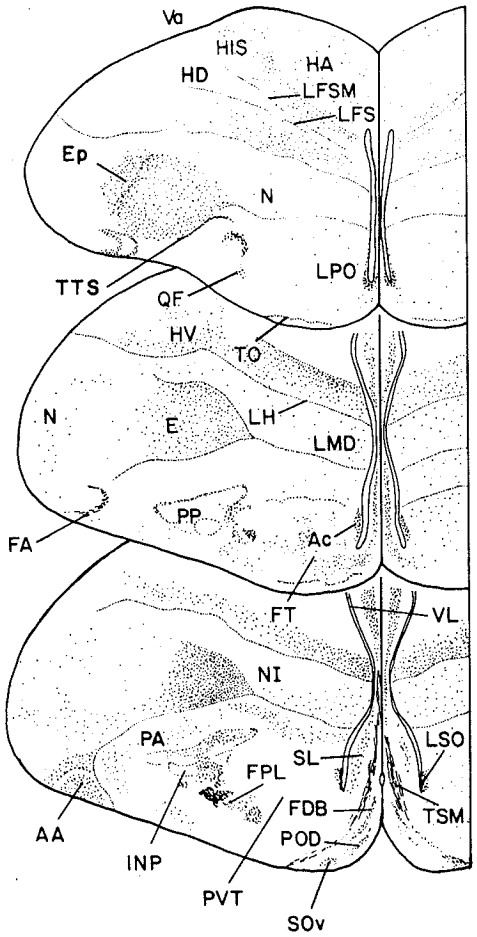
(continued from p. 547)

AIv	Archistriatum intermedium, Pars ventralis
AL	Ansa lenticularis
ALA	Nuc. ansae lenticularis rostralis (anterior)
Am	Archistriatum mediale
AM	Nuc. rostralis (anterior) medialis hypothalami
APH	Area parahippocampalis
CA	Commissura rostralis (anterior)
CDL	Area corticoidea dorsolateralis
CHCS	Tr. cortico-habenularis et cortico-septalis
CIO	Capsula interna occipitalis
CO	Chiasma opticum
CPa	Commissura pallii
CPi	Cortex piriformis
DA	Tr. dorso-archistriaticus
DLA	Nuc. dorsolateralis rostralis thalami
DLAl	Nuc. dorsolateralis rostralis thalami, Pars lateralis
DLAm	Nuc. dorsolateralis rostralis thalami, Pars medialis
DLAmc	Nuc. dorsolateralis rostralis thalami, Pars magnocellularis
DLP	Nuc. dorsolateralis caudalis thalami
DMA	Nuc. dorsomedialis rostralis thalami
DMP	Nuc. dorsomedialis caudalis thalami
DSD	Decuss. supraoptica, Pars dorsalis
DSV	Decuss. supraoptica, Pars ventralis
E	Ectostriatum
F	Fornix
FA	Tr. fronto-archistriaticus
FDB	Fasc. diagonalis (of Broca)
FL	Ager L (Field L)
FPL	Fasc. prosencephali lateralis
FPM	Fasc. prosencephali medialis
GLdp	Nuc. geniculatus lateralis, Pars dorsalis [principalis]
GLv	Nuc. geniculatus lateralis, Pars ventralis
HA	Hyperstriatum accessorium
HL	Nuc. habenularis lateralis
HM	Nuc. habenularis medialis
Hp	Hippocampus
HV	Hyperstriatum ventrale
ICT	Nuc. intercalatus thalami
INP	Nuc. intrapeduncularis
LA	Nuc. lateralis rostralis thalami
LAD	Lamina archistriatica dorsalis
LFS	Lamina frontalis superior
LFSM	Lamina frontalis suprema
LH	Lamina hyperstriatica
LHy	Regio lateralis hypothalami
LMD	Lamina medullaris dorsalis
LMmc	Nuc. lentiformis mesencephali, Pars medialis [P. magnocellularis]
LMpc	Nuc. lentiformis mesencephali, Pars lateralis [P. parvocellularis]
LSO	Organum laterale septi
MPOd	Nuc. magnocellularis preopticus, Pars dorsalis
MPOm	Nuc. magnocellularis preopticus, Pars medialis

(continued p. 551)

(continued from p. 550)

MPOv	Nuc. magnocellularis preopticus, Pars ventralis
nCPa	Nuc. interstitialis commissurae pallii
nST	Nuc. interstitialis striae terminalis
nTSM	Nuc. tr. septomesencephalicus
N	Neostriatum
NI	Neostriatum, Pars intermedia
OM	Tr. occipitomesencephalicus
OV	Nuc. ovoidalis
OVLT	Organum vasculosum laminae terminalis
PA	Paleostriatum augmentatum
PCVIII	Plexus choroideus ventriculi tertii
PCVL	Plexus choroideus ventriculi lateralis
PHN	Nuc. periventricularis hypothalami
POM	Nuc. preopticus medialis
POMn	Nuc. preopticus medianus
POP	Nuc. preopticus periventricularis
PP	Paleostriatum primitivum
PPC	Nuc. principalis precommissuralis
PTD	Nuc. pretectalis diffusus
PV	Nuc. posteroventralis thalami
PVN	Nuc. paraventricularis hypothalami
PVO	Organum paraventriculare
PVT	Paleostriatum ventrale
QF	Tr. quintofrontalis
ROT	Nuc. rotundus
RSd	Nuc. reticularis superior, Pars dorsalis
SCE	Stratum cellulare externum
SCNm	Nuc. suprachiasmaticus, Pars medialis
SGFS	Stratum griseum et fibrosum superficiale
SL	Nuc. septalis lateralis
SM	Nuc. septalis medialis
SMe	Stria medullaris
SO	Stratum opticum
SOe	Nuc. supraopticus, Pars externa
SOv	Nuc. supraopticus, Pars ventralis
SRt	Nuc. subrotundus
SSO	Organum subseptale
T	Nuc. triangularis
TeM	Tectum mesencephali
TeO	Tectum opticum
TIO	Tr. isthmo-opticus
Tn	Nuc. taeniae
TPO	Area temporo-parieto-occipitalis
TrO	Tr. opticus
TSM	Tr. septomesencephalicus
TT	Tr. tectothalamicus
TTS	Tr. thalamostriaticus
V III	Ventriculus tertius
VLs	Ventriculus lateralis
VLT	Nuc. ventrolateralis thalami
VMN	Nuc. ventromedialis hypothalami



Figs. 14.19, 20. Transverse sections of the rostral part of the Telencephalon of the chick. The most caudal section is at the bottom of each group of three. The top schematic diagram shows the bulbus olfactorius. Redrawn from Kuenzel and Masson (1988).

Abbreviations:

AA	Archistriatum rostrale
Ac	Nuc. accumbens
Bas	Nuc. basalis
BO	Bulbus olfactorius
CPP	Cortex prepiriformis
E	Ectostriatum
Ep	Cingulum periectostriaticum

(continued p. 554)

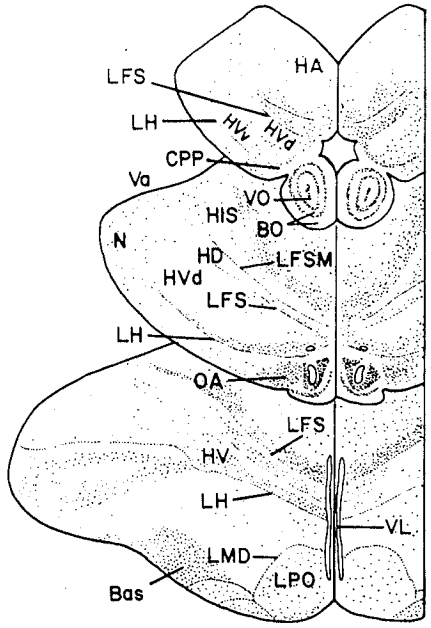


Fig. 14.20

(continued from p. 552)

FA	Tr. fronto-archistriaticus
FDB	Fasc. diagonalis (of Broca)
FPL	Fasc. lateralis prosencephali
FT	Tr. frontothalamicus et tractus thalamofrontalis
HA	Hyperstriatum accessorium
HD	Hyperstriatum dorsale
HIS	Hyperstriatum intercalatum supremum
HV	Hyperstriatum ventrale
HVd	Hyperstriatum ventrale, Pars dorsalis
HVv	Hyperstriatum ventrale, Pars ventralis
INP	Nuc. intrapeduncularis
LFS	Lamina frontalis superior
LFSM	Lamina frontalis suprema
LH	Lamina hyperstriatica
LMD	Lamina medullaris dorsalis
LPO	Lobus parolfactorius
LSO	Organum laterale septi
N	Neostriatum
NI	Neostriatum, Pars intermedia
OA	Nuc. olfactorius rostralis (anterior)
PA	Paleostriatum augmentatum
POD	Nuc. preopticus dorsolateralis
PP	Paleostriatum primitivum
PVT	Paleostriatum ventrale
QF	Tr. quintofrontalis
SL	Nuc. septalis lateralis
SOv	Nuc. supraopticus, Pars ventralis
TO	Tuberculum olfactorium
TSM	Tr. septomesencephalicus
TTS	Tr. thalamostriaticus
Va	Vallecula telencephali
VL	Ventriculus lateralis
VO	Ventriculus olfactorius

15

SYSTEMA NERVOSUM PERIPHERICUM

JACOB L. DUBBELDAM

With contributions from subcommittee members: J. J. Baumel, H. Berkhoudt, G. A. Clark, Jr., A. S. King, L. Malinovský, Y. Ohmori, T. Watanabe, M. Yasuda. The figures were redrawn by Martin Brittijn.

Since the first edition of *Nomina Anatomica Avium* (NAA, 1979), only a few terms have been added or changed in this chapter. However, some parts of the terminology have been rearranged and many new data from the literature have been inserted in the annotations. Two recent reviews (Bubien-Waluszewska, 1981, 1985), using predominantly the nomenclature of NAA (1979), offer an excellent introduction to the anatomy of the cranial nerves and the somatic peripheral nervous system. Much work, however, relates to the anatomy of the fowl or the pigeon, and interspecific differences are still sources of a number of ambiguities.

Cranial nerves. The extensive communications between the cranial nerves IX-XII cause problems in the interpretation of the origin and target of the various components of this complex. Tracing studies have helped solve some of the complications.

Spinal nerves. The spinal nerves are organized similarly to those of mammals, thus the numbering and naming of these nerves seems to offer no problem. However, the variable number of vertebrae between species results in differences in the contributions of certain nerves to the various regions (review in Bubien-Waluszewska, 1985), as well as within a given species (e.g., Kaiser, 1923). Moreover, the definition of the different regions (cervical, thoracic, etc.) is problematical. It is possible to use the terms cervical or thoracic nerves in a regional sense, but in a transitional zone it may be risky to ascribe a particular nerve to one or the other region. The nerves of the pelvic region are named collectively as Nn. synsacrales, which obviates the problem of the regional vertebrae incorporated in the Synsacrum (**Osteo.** Annot. 141a). The best method of designating spinal nerves is to number them, starting at the base of the cranium and proceeding caudally (Huber,

1936; Baumel, 1975a). The innervation of the tail region was described recently in the pigeon by Baumel (1988).

Connexus/Ramus communicans. The term "Connexus" is employed instead of "Ramus communicans" as in other anatomical nomenclatures, except for the "Rami communicantes" that connect the spinal nerves with the Truncus paravertebralis. Thus confusion between these specifically-defined communicating rami and other nerve communications is avoided. The term "anastomosis" is not used at all in reference to communications between nerves; as the term indicates, it refers to connections between tubular structures (vessels). One should be aware that for each listing of a connexus there will be a second listing of the same connexus, with the names of the structures involved indicated in reversed order.

Visceral nerves. The autonomic nervous system is often classified as a purely visceral efferent (motor) system. In the present terminology Pars visceralis of Systema Nervosum Peripheric um is *not* the equivalent of the autonomic nervous system, since the nerves making up Pars visceralis contain both visceral afferent and efferent neuronal processes. The terminology of Pars visceralis makes no reference to the autonomic "sympathetic" and "parasympathetic" divisions, nor to cholinergic or adrenergic systems, inasmuch as these have functional rather than anatomical connotations. The names of the neural elements are organized into craniosacral and thoracolumbar divisions for purposes of convenience.

The term "Plexus subvertebralis" is synonymous with the mammalian non-official terms "Plexus prevertebralis" or "Plexus collateralis". This terminology relates to the bipedal anatomical position of the birds compared to the upright anatomical position of man (see **Gen. Intro.:** terms of orientation; and **Topog.**). Neither the *Nomina Anatomica Veterinaria* (NAV; ICVGAN, 1983) nor the 6th Edition of the human *Nomina Anatomica* (IANC, 1989) has an inclusive term equivalent to the avian Plexus subvertebralis, but instead use general regional terms: Plexus aorticus thoracicus/abdominalis, Plexus hypogastricus superior.

The distribution of N. glossopharyngeus and N. vagus is visceral for the most part; therefore, these nerves are treated in detail in Pars visceralis, but only briefly in Pars somatica. Each major named autonomic ganglion of the head is listed with the cranial nerve which provides the so-called "motor root" of the ganglion. This practice was adopted in the 4th Edition of *Nomina Anatomica* (IANC, 1977) and continued in the 5th and 6th editions, but the last two editions of *Nomina Anatomica Veterinaria* (ICVGAN, 1973, 1983) are inconsistent in this regard.

TERMINOLOGY

PARS SOMATICA

NERVI CRANIALES

N. olfactorius[1]
- R. dorsalis
- R. ventralis

N. terminalis[1]

N. opticus[2] (**Osteo.** Annot. 32)
- Chiasma opticum

N. oculomotorius (Fig. 15.2; and Pars visc.)
- R. dorsalis
  - Rr. musculares
- R. ventralis
  - R. ganglionaris ciliaris[3]
  - Rr. musculares
- **Ganglion ciliare**[4]
  - Connexus cum n. abducenti
  - Connexus cum n. oculomotorio[3]
  - Connexus cum n. ophthalmico
  - Nn. choroidales[5]
  - N. iridociliaris[5 6 7]
    - Rdx. ganglionaris[6]
    - Rdx. ophthalmica[6]
    - Plexus anularis ciliaris[7]
      - Rr. ciliares[7]
    - Plexus anularis iridicus[7]
      - Rr. iridici[7]

N. trochlearis (Fig. 15.2; Fig. 4.3)
- R. muscularis
- Connexus cum n. ophthalmico

N. trigeminus (Fig. 15.1)
- Rdx. motoria
- Rdx. sensoria
- Ganglion trigeminale[8]

N. ophthalmicus[9]
- Connexus cum n. trochleari
- Rdx. iridociliaris[6] (see N. oculomot.)
- Connexus cum g. ethmoidali[10]
- Connexus cum g. ciliari
- Rr. glandulae nasalis[10] (see Pars visc. N. pal.)
- R. lateralis (**Osteo.** Annot. 31)
  - Rr. glandulae nasalis
  - Rr. frontales
    - Rr. cristales[11]
  - Rr. palpebrales dorsonasales[11]
  - Rr. nasales interni
- R. medialis (**Osteo.** Annot. 31)
  - Rr. nasales interni
  - R. premaxillaris dorsalis
    - Rr. rostri maxillaris[11]
  - R. premaxillaris ventralis
    - Connexus cum n. palatino[12]
    - Rr. palatini
    - Rr. rostri maxillaris[11]
    - Rr. glandularum palatinarum (**Digest.** Annot. 10)

N. maxillaris (Fig. 15.1)
- Connexus cum n. facialis[2]
- N. supraorbitalis[9]
  - Rr. cristales[11]
  - Rr. frontales
  - Rr. auriculares
  - Rr. glandulares lacrimales
  - R. palpebralis dorsotemporalis[11]
  - R. palpebralis ventrotemporalis[11]
  - N. infraorbitalis

(continued)

NERVI CRANIALES (cont.)

- Rr. palpebrales ventronasales[11]
- N. nasopalatinus
  - R. palatinus
  - R. nasalis
    - Rr. nasales externi
    - Rr. nasales interni
  - Connexus cum n. palatino[12]
  - Connexus cum g. ethmoidali
- N. mandibularis (Fig. 15.1)
  - Rr. musculares[13]
    - R. pterygoideus[13]
    - R. externus[13]
  - Rr. artc. quadratomandibularis
  - R. anguli oris
    - Rr. glandulares
    - Rr. palatini
    - Rr. cutanei
  - R. mandibularis externus
  - R. intermandibularis[14]
    - R. muscularis
    - Rr. cutanei
  - N. intramandibularis[15]
    - Connexus cum chorda tympani[21]
    - R. sublingualis[15]
      - Rr. glandulares
      - Rr. rostri mandibularis[11]
- **N. abducens** (Fig. 15.2)
  - Connexus cum g. ciliari
  - R. dorsalis[16]
  - R. ventralis[16]
- **N. facialis** (Fig. 15.1; see Pars visc.)
  - Geniculum n. facialis
  - Ganglion geniculi[17]
  - N. intermedius[19]
  - Chorda tympani[20] (see Pars visc.)
- N. palatinus[18] (see Pars visc.)
  - Ganglion sphenopalatinum[18] (see Pars visc.)
  - Ganglion ethmoidale[18] (see Pars visc.)
- N. hyomandibularis [R. caudalis]
  - R. auricularis
  - N. m. depressoris mandibulae[23]
  - R. hyoideus[24]
  - R. cervicalis[24]
  - Connexus cum g. cervicali craniali
  - Connexus cum n. glossopharyngeo (Fig. 15.3)
  - Connexus cum n. cervicali
- **N. vestibulocochlearis**[25] (see **Sens.**)
  - Pars vestibularis
    - Ganglion vestibulare[26]
    - R. rostralis
      - N. ampullaris anterior
      - N. ampullaris lateralis [horizontalis]
      - N. utricularis
    - R. caudalis
      - N. ampullaris posterior
        - N. cristae neglectae
      - N. saccularis
  - Pars cochlearis
    - Ganglion cochleare[26]
      - N. cochlearis
    - Ganglion lagenare[26]
      - N. lagenaris
- **N. glossopharyngeus** (Fig. 15.3; see Pars visc.)
  - N. laryngopharyngealis[63]
    - N. laryngealis[63]
    - Rr. musculares[63]
- **N. vagus**[73] (see Pars visc.)

(continued)

NERVI CRANIALES (cont.)

- **N. accessorius** (Fig. 15.3)
  - Rdxx. craniales
  - Rdxx. spinales
  - Connexus cum n. vago
  - R. externus[27] (see N. vagus)
- **N. hypoglossus** (Fig. 15.3)
  - Rdx. rostralis
  - Rdx. caudalis
  - Connexus cum g. cervicali craniali
  - Connexus cum n. cervicali primo[28]
- **N. hypoglossocervicalis**[29]
  - Connexus cum n. vago
  - Connexus cum n. glossopharyngeo
  - Connexus cum n. cervicali secundo
    - R. cervicalis descendens[30]
  - R. laryngolingualis[31]
    - Rr. linguales[31]
  - R. tracheosyringealis[31]
    - Rr. tracheales[31]
    - R. syringealis[31 32]

NERVI SPINALES[33] (see **PNS** Intro.)

- Fila radicularia
- Rdx. dorsalis
  - Ganglion spinale [G. radiculare dorsale]
- Rdx. ventralis
- N. spinalis
  - R. dorsalis
  - R. ventralis
  - Rr. communicantes (**PNS** Intro.)
  - R. meningeus

NN. CERVICALES (Figs. 15.3, 4; **PNS** Intro.)

- Rr. dorsales
  - Rr. articulares
  - Rr. musculares
  - Nn. cutanei cervicales dorsales[33]
  - Plexus cervicalis dorsalis[34]
- Rr. ventrales
  - Rr. musculares
  - Nn. cutanei cervicales ventrales[33]
  - Connexus cum n. faciali[35]
    - N. cutaneus colli[35]
  - Connexus cum n. hypoglosso[29]

PLEXUS BRACHIALIS[36]

- Radices plexus[37]
  - Rr. musculares[38]
- Trunci plexus
- Fasciculi plexus[39]
  - Fasc. dorsalis[40]
    - N. subscapularis
    - N. subcoracoscapularis
    - N. anconealis

(continued)

PLEXUS BRACHIALIS[36] (cont.)

- N. axillaris
  - Rr. musculares
  - N. cutaneus axillaris
- N. radialis
  - Rr. musculares
  - N. cutaneus brachialis dorsalis
  - N. propatagialis dorsalis
  - N. cutaneus antebrachialis dorsalis
  - R. superficialis
    - Rr. postpatagiales
  - R. profundus
    - Rr. carpales dorsales
    - R. alularis
    - Nn. metacarpales dorsales
      - Rr. postpatagiales
      - Rr. digitales
- Fasc. ventralis[40]
  - N. supracoracoideus (**Myol.** Annot. 76)
  - N. bicipitalis
    - Rr. propatagiales
  - N. medianoulnaris
    - N. cutaneus brachialis ventralis
    - N. medianus
      - Rr. musculares
      - N. propatagialis ventralis
      - R. superficialis
      - R. profundus
      - Rr. carpales ventrales
        - R. alularis
        - Nn. metacarpales ventrales
          - Rr. postpatagiales
          - Rr. digitales
      - N. cutaneus antebrachialis ventralis
    - N. ulnaris
      - Rr. musculares
      - N. cutaneus cubiti
      - R. caudalis
      - R. cranialis
      - Rr. postpatagiales
      - Rr. metacarpales ventrales
        - Rr. digitales
    - N. pectoralis
      - N. pectoralis cranialis
        - Rr. musculares
        - Nn. cutanei pectorales
      - N. pectoralis caudalis
        - Rr. musculares
        - Nn. cutanei abdominales (**Integ.** Annot. 15)

PLEXUS BRACHIALIS ACCESSORIUS[38]

- N. cutaneus omalis[38]
- Rr. musculares[38]

NN. THORACICI (PNS Intro.)

- Rr. dorsales
  - Rr. articulares
  - Rr. cutanei
  - Rr. musculares
- Rr. ventrales
  - Nn. intercostales
  - Rr. articulares
  - Rr. cutanei
  - Rr. musculares[41]
  - Rr. peritoneales

NN. SYNSACRALES[42] (PNS Intro.)

- Plexus lumbosacralis[43]
  - Radices plexus
  - Trunci plexus
  - Fasc. dorsalis[46]
  - Fasc. ventralis[46]
  - Plexus lumbalis[43] (Figs. 15.6)
    - R. cutaneus femoralis lateralis
    - R. cutaneus femoralis medialis[48]
    - N. cutaneus cruralis cranialis
    - N. pubicus[49]
    - N. femoralis (Figs. 15.6, 7)
      - N. cutaneus femoralis cranialis
      - N. coxalis cranialis (**Art.** Annot. 70; **Myol.** Annot. 104)
      - Rr. musculares[46]
    - N. obturatorius[48]
      - R. medialis
      - R. lateralis
  - Plexus sacralis[41]
    - Fasc. dorsalis[46]
    - Fasc. ventralis[46]
    - N. coxalis caudalis (**Art.** Annot. 70)
    - N. cutaneus femoralis caudalis
    - Rr. musculares[46]
    - Connexus caudalis[47]
    - N. ischiadicus[46] (Figs. 15.6, 7)
      - N. tibialis[46]
      - N. suralis lateralis
        - N. suralis medialis
          - N. plantaris medialis[50]
            - N. metatarsalis plantaris
          - N. interosseus
        - N. cutaneus suralis
        - N. paraperoneus [N. parafibularis][51]
          - N. plantaris lateralis[52]
            - N. metatarsalis plantaris
              - R. digitalis
          - Rr. musculares[46]
        - N. peroneus [N. fibularis][46]
          - Rr. musculares[46]
          - N. peroneus superficialis
            - Nn. metatarsales dorsales
              - Rr. digitales
          - N. peroneus profundus
            - Nn. metatarsales dorsales
            - Rr. digitales
  - N. furcalis[44]
- Plexus pudendus[44] (Fig. 15.6, 8)
  - Rr. cutanei
  - N. lateralis caudae[74]
    - Rr. venti
    - Rr. musculares
    - Rr. cutanei
    - Connexus caudalis[47]
  - N. intermedius caudae[74]
    - Rr. muscularis[74]
    - Rr. cutanei[74]
  - N. pudendus[74] (see Pars visceralis)
- N. bigeminus[45]

NN. CAUDALES (see PNS. Intro.) (Fig. 15.9)

- Plexus caudalis[53]
  - Ansae plexus caudalis
    - N. medialis caudae[54]
    - N. dorsalis bulbi rectricium[55]
    - N. accessorius dorsalis bulbi[55]
    - N. accessorius ventralis bulbi[55]
    - Nn. ventrales bulbi rectricium[55]
    - Rr. musculares[56]
    - Rr. cutanei
    - Rr. glandulae uropygialis

PARS VISCERALIS[57] (see **PNS** Intro.)

DIVISIO CRANIOSACRALIS

N. oculomotorius (Fig. 15.2; cf. Pars somatica)
- Ganglion ciliare[4]
  - Connexus cum n. oculomotorio
  - Connexus cum n. ophthalmico
  - Connexus cum n. abducenti
  - N. iridociliaris[5]
    - Rdx. ganglionaris[6]
    - Rdx. ophthalmica[6]
    - Plexus anularis ciliaris[7]
      - Rr. ciliares[7]
    - Plexus anularis iridicus[7]
      - Rr. iridici[7]

N. facialis (Fig. 15.1; Pars somatica)
- Ganglion geniculi[17]
- N. intermedius[19]
- Chorda tympani[20 21]
  - Connexus cum n. mandibulari[21]
  - Ganglia mandibularia[21]
    - Rr. glandulares (see **Digest.**)
  - Connexus cum n. maxillari[22]
    - Rr. glandulares lacrimales see N. max.)
- N. palatinus [R. rostralis][18] (see N. hyomand.)
  - Connexus cum n. glossopharyngeo
- R. ventralis
  - Connexus cum n. infraorbitali
  - Connexus cum g. sphenopalatino
  - Ganglion sphenopalatinum[58] (Fig. 1)
    - Rr. glandulae membranae nictitantis[18]
    - Connexus cum n. nasopalatino[18]
- R. dorsalis
  - Connexus cum g. ethmoidali
  - Ganglion ethmoidale[58]
    - Connexus cum n. ophthalmico[59]
    - Rr. glandulae nasalis[18]
    - Connexus cum g. sphenopalatino

N. glossopharyngeus (Fig. 15.3)
- Ganglion proximale[60]
- Ganglion distale[60]
  - Connexus cum n. palatino
  - Connexus cum n. hyomandibulari
  - Connexus cum g. cervicali craniali
- N. subcaroticus [N. precaroticus][68]
- N. lingualis[61]
  - Rr. pharyngeales
  - Rr. mm. hyobranchialium[60]
  - Rr. glandulares
  - Rr. gustatorii
- Connexus vagoglossopharyngealis[62 73]
- N. laryngopharyngealis[63]
  - N. laryngealis[63]
    - Rr. musculares[63]
    - Rr. laryngotracheales[63]
  - N. pharyngealis[64]
    - Rr. pharyngeales[64]
    - Rr. esophageales[64]
  - R. muscularis[64]
  - Connexus cum n. hypoglossocervicali
- N. esophagealis descendens[65]

(continued)

DIVISIO CRANIOSACRALIS (cont.)

- Rr. esophageales
- Rr. ingluviales
- Rr. tracheales
- Connexus cum n. vago

N. vagus[73] (Figs. 15.3, 9)
- Ganglion proximale[66]
  - Connexus cum n. accessorio
  - Connexus cum g. cervicali craniali
- R. externus[27]
- Connexus vagoglossopharyngealis[62]
- Connexus cum n. hypoglossocervicali
- Ganglion distale[66]
  - Rr. glandulares[67]
  - R. glomi carotici[68]
- N. cardiacus cranialis[69]
  - N. aorticus[69]
- N. recurrens
  - Rr. bronchiales
  - Rr. esophageales
  - N. pulmoesophagealis[70]
    - R. pulmonalis[70]
      - Plexus pulmonalis[70]
    - R. esophagealis
  - R. descendens
    - Rr. esophageales
    - Connexus cum plexu celiaco
  - R. ascendens
    - Rr. esophageales
    - Rr. ingluviales
    - Rr. tracheales
    - Rr. musculorum tracheae[71]
  - Rr. pulmonales[70]
  - Nn. cardiaci caudales[69 79]
- Rr. septi obliqui[72]
- Truncus communis n. vagi[73]
  - Rr. proventriculares
  - Rr. viscerales abdominales [Nn. gastrici][73]
  - Rr. proventriculares
  - Connexus cum plexu celiaco (Fig. 15.10)
  - Rr. ventriculares
  - Rr. pylorici
  - Rr. duodenales
  - Rr. pancreatici
  - Rr. hepatici

Plexus pudendus (Pars somatica)
- N. pudendus[74]
- Rr. ureterales (**Ren**)
- Rr. oviductales (**Fem**)
- Rr. vaginales (**Fem**)
- Rr. ductus deferentis (**Masc**)
- Ganglia cloacalia (**Cloaca** Annot. 25)
  - Plexus cloacalis (**Cloaca** Annot. 25)
  - Nn. cloacales (**Cloaca** Annot. 25)
    - Rr. cloacales
    - Rr. bursae cloacalis
    - Rr. corporis vascularis phalli
- Ganglion paracloacale (**Cloaca** Annot. 25)
- Ganglia rectalia[75] (**Cloaca** Annot. 25)
- Ganglion uterovaginale[75]
- N. intestinalis[76] (Fig. 15.10)
  - Ganglia n. intestinalis[76]

DIVISIO THORACOLUMBALIS

Truncus paravertebralis[83] (**PNS** Intro.)
- Ganglia paravertebralia (Figs. 15.3, 6, 9)

(continued)

DIVISIO THORACOLUMBALIS (cont.)

Rr. communicantes (**PNS** Intro.)
Connexus interganglionares
Ansae connexuum interganglionarum[77]
Plexus subvertebralis[78] (**PNS** Intro.)
Ganglia subvertebralia
Truncus paravertebralis cervicalis[77] (Fig. 15.10)
Ganglion cervicale craniale[77]
N. ophthalmicus externus[78]
Connexus cum n. trigemino
N. caroticus externus[78]
N. caroticus cerebralis[78]
Connexus cum n. faciali
Connexus cum n. glossopharyngeo
Connexus cum n. vago
Connexus cum n. hypoglosso
Truncus subvertebralis[78]
Plexus subvertebralis cervicalis[68 78]
Truncus paravertebralis thoracicus
N. cardiacus[79]
Rr. pulmonales[70]
Plexus pulmonalis
Nn. splanchnici thoracici[79]
Plexus subvertebralis thoracicus[79]
Ganglion celiacum
Ganglia mesenterica cranialia
Plexus celiacus[80] (Fig. 15.10)
Plexus splenicus[80]
Plexus hepaticus[80]
Plexus pancreaticoduodenalis[80]
Plexus proventricularis[80]
Plexus gastricus[80]
Plexus mesentericus cranialis[80]
Truncus paravertebralis synsacralis (Fig. 15.10)
Nn. splanchnici synsacrales[79]
Plexus subvertebralis synsacralis
Plexus aorticus[81]
Plexus adrenalis[81]
Ganglia adrenalia[81] (Fig. 15.10)
N. hepaticus[82]
Plexus renales[81] (**Ren**)
Plexus testicularis[81] (**Masc**)
Plexus ovaricus[81] (**Fem**)
Plexus oviductales[81] (**Fem**)
Plexus mesentericus caudalis[80]
Plexus iliacus internus
Truncus paravertebralis caudalis[83]
Nn. splanchnici caudales
Ganglia imparia[83] (Fig. 15.10)
Plexus pelvici
N. intestinalis[76] (see N. vagus)
Ganglia n. intestinalis[76]

ANNOTATIONS

(1) **N. olfactorius.** Consult Baumel (1975a) and Watanabe and Yasuda (1968) for descriptions of the peripheral course and relationships of the olfactory nerve. The latter authors refer to R. dorsalis as R. externus and to R. ventralis as R. internus.

N. terminalis. Wirsig-Wiechmann (1990) described cell bodies and fibers in *Gallus* forming a N. terminalis along the N. olfactorius; see also von Bartheld, et al. (1987).

(2) **N. opticus** (Fig. 15.2). See O'Flaherty (1971) for a study of the fiber size distribution of the optic nerve of *Anas platyrhynchos*. Duff and Scott (1979) described a gradient in mean fiber size from ventronasal to dorsotemporal in the optic nerve in the pigeon.

(3) **R. ganglionaris ciliaris** (Fig. 15.2). Synonymy: Rdx. brevis. This branch is also known as the oculomotor root of the ciliary ganglion [Connexus cum n. oculomotorio].

(4) **G. ciliare** (Fig. 15.2). The paper of Oehme (1968) reviews the literature pertaining to the avian ciliary ganglion and thoroughly treats the connections and "branches" of the ganglion as well as its components in several species of Corvidae. See Annot. 5, 6, 7.

(5) **N. iridociliaris** (Fig. 15.2). Synonymy: N. ciliaris major (Cords, 1904); N. ciliaris longus. See Annot. 6, 7.

Nn. choroidales (Fig. 15.2). Synonymy: Nn. ciliares breves. Oehme (1968) discusses the nomenclatural difficulties in applying mammalian names to the nerves "branching" from G. ciliare that pass to the Bulbus oculi. The terms, N. irido-ciliaris and Nn. choroidales, were proposed by Oehme (1968). Watanabe, et al. (1967) described the formation and distribution of these nerves in *Gallus*. There is some uncertainty concerning whether the N. iridociliaris supplies autonomic fibers to the iridial muscle of birds (Isomura, 1973; Oehme, 1969b; Holtzmann, 1896; Schwalbe, 1879), but it has been demonstrated to supply the fundus and the ciliary body (Oehme, 1968).

(6) **Rdx. ganglionaris; Rdx. ophthalmica** (Fig. 15.2). N. iridociliaris is formed by the union of two roots, viz., the Rdx. ophthalmica from N. ophthalmicus (often consisting of multiple rootlets) and the Rdx. ganglionaris from Ganglion ciliare (Bubien-Waluszewska, 1981). Oehme (1968) contends that Rdx. ophthalmica contributes sensory and sympathetic nerve fibers and that Rdx. ganglionaris contributes postganglionic "parasympathetic" fibers to Bulbus oculi. See Watanabe, et al. (1967) for an overview of synonyms used by older authors.

(7) **Plexus anularis ciliaris; Plexus anularis iridicus; Rami iridici** (Fig. 15.2). Synonymy: Plexus ciliaris (Watanabe, et al., 1967). N. iridociliaris courses rostrally within the eye bulb between the scleral and choroidal layers and ramifies into several branches. At the periphery of the ciliary muscle the branches form a circular ciliary plexus within the muscle (see **Sens**). One or more rami of the ciliary annular plexus form the iridial ring of nerves which in turn gives rise to Rr. iridici that supply the iris (Oehme, 1968).

(8) **G. trigeminale** (Fig. 15.1). Synonymy: G. semilunare, G. Gasseri. The trigeminal ganglion of some birds (e.g., *Gallus*, *Anser*) is partially divided into a smaller ophthalmic part and a larger maxillomandibular part. The extent of this division is reflected in the configuration of the Fossa ganglii trigemini of the interior of the floor of the cranial cavity in the dried skull (**Osteo.** Fig. 4.3).

(9) **N. ophthalmicus** (Figs 15.1, 2). The ophthalmic nerve is the principal afferent nerve of the upper jaw (Rostrum maxillare, see **Osteo.** Annot. 57). This nerve has been known as N. ophthalmicus profundus; the use of this term is confusing since in the older literature N. ophthalmicus superficialis refers to the supraorbital branch of N. maxillaris.

(10) **Rr. glandulae nasalis** (Fig. 15.1). Secretomotor nerve fibers to Gl. nasalis (salt gland) course via Connexus cum g. ethmoidali to N. ophthalmicus and are distributed via glandular rami (see N. facialis). The innervation of Gl. nasalis is treated by Ash, et al. (1969).

(11) **Rr. cristales** (Fig. 15.1). These branches of the opthalmic and maxillary nerve innervate the comb in *Gallus* (Bubien-Waluszewska, 1981).

Rr. palpebrales/dorsonasales/dorsotemporalis/ventrotemporalis/ventronasales. Synonymy: Rr. palpebrales rostrodorsales/caudodorsalis/caudoventralis/rostroventrales. Consult Bubien-Waluszewska (1981); see Fig. 15.1.

Rr. rostri maxillaris/mandibularis (Fig. 15.1). These afferent rami of N. ophthalmicus and N. mandibularis carry impulses centrally from the various sensory corpuscles and discs deep to the Rhamphotheca of the upper and lower jaws. These endings have been extensively studied in different birds (see Malinovský and Zemanek, 1969, for a concise review of the literature; for other citations see Gottschaldt, 1985); **Osteo.** Annot. 41; **Sens.** Annot. 62-64.

(12) **Connexus cum n. palatino.** Branches of the N. palatinus (VII) form a plexus with branches of N. ophthalmicus and N. maxillaris. Apparently facial fibers join trigeminal branches on their way to taste buds in the upper beak of the Mallard, *Anas platyrhynchos* (Krol and Dubbeldam, 1979).

(13) **Rr. musculares.** These rami of N. mandibularis supply the M. depressor palpebrae ventralis and the various parts of the jaw muscles, but not the M. depressor mandibulae. Certain of the Rr. musculares have been given specific names by Barnikol (1953): R. pterygoideus and R. externus. See **Myol.** Annot. 16, 17.

(14) **R. intermandibularis** (Fig. 15.1). Synonymy: R. circumflexus. Innervates skin between the mandibular rami as well as Mm. intermandibulares (**Myol.** Annot. 26).

(15) **N. intramandibularis** (Fig. 15.1). This is the main trunk of the mandibular nerve and lies in the mandibular neurovascular canal. See **Osteo.** Annot. 47; **Art.** Annot. 25; **Ven.** Annot. 24.

R. sublingualis (Fig. 15.1) (Cords, 1904). This branch of N. mandibularis has been referred to as N. or R. lingualis in the literature. The sublingual ramus does not have a lingual distribution proper, but is distributed to the mucosa of the floor of the oral cavity (see N. glossopharyngeus and N. hypoglossus).

(16) **R. dorsalis; R. ventralis.** The dorsal ramus of the abducent nerve corresponds to the combined dorsolateral and ascending rami of Baumel (1975a), and supplies M. rectus lateralis and M. quadratus membranae nictitantis. The ventral ramus corresponds to Baumel's R. descendens, and is distributed to M. pyramidalis of the Membrana nictitans.

(17) **G. geniculi** (Fig. 15.1). In a study of the sensory ganglion of N. facialis, Yntema and Hammond (1954) recognized a G. radicis and a G. geniculi, the former arising from the neural crest and the latter of placodal origin. It has been suggested that in the adult bird the G. radicis is incorporated in the vestibular ganglion (G. vestibulare et radicis facialis), but there is no definite proof (d'Amico-Martel and Noden, 1983).

(18) **N. palatinus [R. rostralis]** (Fig. 15.1). Synonymy: N. nasopalatinus (Bonsdorf, 1852). This ramus of N. facialis is considered by Santamaria-Arnáiz (1962) to be the homologue of the greater superficial petrosal or Vidian nerve of mammals. The nerve conducts parasympathetic fibers to **G. ethmoidale** and **G. sphenopalatinum** (see Pars visceralis). The ultimate distribution of this pathway presumably includes the Gl. nasalis, Gl. membranae nictitantis, Gl. lacrimalis, the palatine glands and glands of the nasal mucosa (Akester, 1979). These last communications are effected through Connexus cum n. nasopalatino. Viscero-sensory fibers innervate taste buds (Annot. 12).

(19) **N. intermedius.** The common stem of Chorda tympani and Connexus cum n. maxillaris is sometimes called the intermedial nerve (Schummer, 1973). It carries special and general visceral afferent fibers and general visceral efferent fibers (Bubien-Waluszewska, 1981). See Annot. 21.

(20) **Chorda tympani** (Fig. 15.1). Smith (1904-1905) describes two configurations of the Chorda tympani. In *Columba* and *Sturnus vulgaris*, the Chorda springs from N. hyomandibularis near its exit from the Basis cranii, enters the caudal portion of the tympanic cavity, crosses dorsal to Cartilago extracolumellaris, traverses the cavity with Lig. columello-squamosum (see **Sens.**), and leaves the cavity near the articulation of Quadratum with the squamous and otic bones. Crompton (1953) notes the same relationships of Chorda tympani in *Spheniscus demersus*. In *Gallus*, on the other hand, the Chorda tympani arises from the region of G. geniculi of N. facialis and arches above the tympanic cavity within the canal of the external ophthalmic vessels, entering the orbit with these vessels. Kuratani, et al. (1988b) find the Chorda tympani in the chick to be predominantly prespiracular, this in contrast to other vertebrates where it is postspiracular.

(21) **Connexus cum n. mandibulari; Connexus cum chorda tympani.** Cords (1904) reviewed the earlier literature regarding the existence and connections of the avian Chorda tympani. Cords and more recently Hsieh (1951) indicate that the Chorda joins either the intramandibular segment of N. mandibularis or its R. sublingualis (see Fig. 15, 1). Chorda tympani fibers innervate mandibular taste buds in the chicken (Ganchrow, et al., 1986).

Gg. mandibularia. These autonomic ganglia consist of scattered ganglion cells or small ganglia within the Chorda tympani. The efferent fibers supply the mandibular salivary gland (Akester, 1979).

(22) **Connexus cum chorda tympani; Connexus cum n. maxillari.** This connection of the chorda tympani with the maxillary nerve is the lesser superficial petrosal nerve of Hsieh (1951), who described it as forming a common stem with the Chorda tympani. The nerve becomes distinct from the Chorda within the canal of the external ophthalmic vessels, communicates with the perivascular sympathetic nerves, and joins the maxillary nerve just medial to the Rete mirabile ophthalmicum. According to Hsieh some of the facial nerve fibers that join N. maxillaris are distributed to the lacrimal gland (Annot. 18). If, however, this connection is to be considered an homologue of the mammalian lesser superficial petrosal nerve, its origin should be from the N. glossopharyngeus.

(23) **N. m. depressoris mandibulae** (Fig. 15.1). Synonymy: N. digastricus. Branch of the hyomandibular nerve to M. depressor mandibulae.

(24) **R. hyoideus** (Fig. 15.1). The hyoid ramus of N. hyomandibularis of the facial nerve innervates M. stylohyoideus and M. serpihyoideus (**Myol.** Annot. 27, 28).

R. cervicalis (Fig. 15.1). The cervical branch innervates the M. constrictor colli (**Myol.** Annot. 5).

(25) **N. vestibulocochlearis.** Terminology of the branches of the vestibulocochlear nerve are based primarily on the works of Ewald (1892) and Boord (1969).

(26) **G. vestibulare.** This afferent ganglion occupies the Fossa acustica interna of the caudal fossa of the cranial cavity.

G. cochleare; G. lagenare. These afferent ganglia extend along the basilar membrane of the cochlea beneath the Habenula perforata (**Sens.** Fig. 16.9) and the papilla of the Lagena, respectively. See **Sens.** Annot. 42; Smith (1985).

(27) **R. externus** (Fig. 15.3). The external ramus of the accessory nerve is distributed to the craniolateral portion of the cucullaris muscle (Baumel, 1975a). It appears to be a branch of the vagus nerve, but consists of fibers from N. accessorius that join and travel with the vagus nerve for a distance (Baumel, 1975a).

(28) **Connexus cum n. cervicali primo** (Fig. 15.3). Synonymy: Plexus hypoglossocervicalis and Plexus cervicalis (Nishi, 1938). See Annot. 29.

(29) **N. hypoglossocervicalis** (Fig. 15.3). This nerve is formed by the combination of the ventral elements of the hypoglossal nerve and the first cervical nerve. Kuratani, et al. (1988a) recently described the development of the hypoglossal nerve and associated structures in the chick embryo.

(30) **R. cervicalis descendens.** This branch of the hypoglossocervical nerve supplies M. sternotrachealis (Watanabe, 1964). The Nuc. intermedius is source of its fibers (Youngren and Phillips, 1983). See **Myol.** Annot. 37.

(31) **R. laryngolingualis.** Synonymy: R. rostralis (NAA, 1979); R. lingualis ventralis (Manogue and Nottebohm, 1982). This laryngolingual branch forms **Rr. linguales** (lingual rami) that supply motor fibers to several of the tongue muscles (Bubien-Waluszewska, 1981).

R. tracheosyringealis. Synonymy: R. trachealis or R. caudalis (NAA, 1979); R. trachealis (Bubien-Waluszewska, 1981). This nerve gives off **Rr. tracheales** that supply motor fibers to tracheal muscles. It also forms the **R. syringealis** (Annot. 32).

(32) **R. syringealis.** The syringeal ramus of the hypoglosso-cervical nerve is believed to be the motor supply to the intrinsic syringeal muscles. Nottebohm and Nottebohm (1976) contended that the fibers in this Ramus come from the hypoglossal nerve. See also Bubien-Waluszewska (1981) and Brackenbury (1989) for reviews. It has often been suggested that the vagus nerve, too, innervates syringeal nerves, either by direct branches or via the N. recurrens, but any such vagal fibers are likely to either have a visceral function in the syrinx or to be destined for the crop. Brackenbury (1989) reviewed the distribution of the right and left syringeal branches to the syringeal muscles, with reference to left hypoglossocervical dominance and the existence of two independent acoustic sources in the syrinx. **Resp.** Annot. 46.

(33) **Nn. spinales.** The naming of spinal nerves is somewhat difficult because of the problem of distinguishing between regions of vertebrae (see **PNS** Intro.). See Yasuda (1964) for a detailed terminology of cutaneous nerves of *Gallus*. Kaiser (1923) proved the segmental innervation of the skin in *Columba*.

(34) **Plexus cervicalis dorsalis** (Yasuda, 1964). Synonymy: Plexus suboccipitalis (Nishi, 1938). The dorsal cervical plexus is formed by the medial branches of the first three cervical dorsal rami (cf. Waluszewska-Bubien, 1985).

(35) **N. cutaneus colli.** This nerve is formed by a communication of N. facialis and the ventral rami of the third cervical nerve (Yasuda, 1964).

(36) **Plexus brachialis** (Figs. 15.4, 9). The terminal branches of this plexus have been classed into the following four divisions by Fürbringer (1879): (1) Nn. thoracici superiores; (2) Nn. brachiales superiores; (3) Nn. brachiales inferiores and (4) Nn. thoracici inferiores. These terms were used by Buri (1900), Baumel (1958), and Yasuda (1960). On the other hand the present nomenclature emphasizes the intrinsic organization of the plexus by the use of the terms Radices, Trunci, and Fasciculi (see Baumel, 1958, 1975). Bubien-Waluszewska (1985) surveys which nerves contribute to the brachial plexus in a number of birds.

(37) **Rdxx. plexus.** The radices (roots) of the brachial plexus are supported by an apparatus of long and short suspensory ligaments (Baumel, 1985) in several major taxa of birds. Rami to the ventral vertebral musculature arise from roots of the plexus.

(38) **Plexus brachialis accessorius** (Fig. 15.4). Synonymy: Nebenplexus (Fürbringer, 1879). This plexus is separable into two entities in the passeriform *Progne subis* (Baumel, 1958). **N. cutaneus omalis** supplies the skin of the shoulder region. **Rr. musculares** supply the rhomboid and serratus muscles.

(39) **Fasciculi plexus.** Nerve cords formed by junction of divisions of the trunks of the brachial plexus (Fig. 15.4).

(40) **Fasciculus dorsalis; Fasciculus ventralis** (Figs. 15.4, 5). The origin of the Fasciculus dorsalis, which supplies the dorsal forelimb muscles derived from the dorsal muscle mass, is situated laterally in the lamina 9; that of the Fasciculus ventralis which supplies the ventral muscles is located in the medial part of lamina 9 of the spinal grey (Ohmori, et al., 1982).

(41) **Rr. musculares.** These thoracic nerve branches include those to intercostal muscles (deWet, et al., 1967) and to Mm. costoseptales. (**Myol.** Annot. 61).

(42) **Nn. synsacrales.** These nerves include the caudal thoracic, lumbar, sacral and several caudal nerves, which are associated with the Synsacrum. (**Osteo.** Annot. 141, 145). See **PNS** Intro.

(43) **Plexus lumbosacralis** (Fig. 15.6; Annot. 43) This term does not indicate all the spinal nerves that contribute to the plexus, but is commonly employed. Boas (1933) used the term in the most definitive work available on the description of this plexus. Yasuda (1961) described the plexus as consisting of a Plexus cruralis, Plexus sacralis (ischiadicus) and Plexus pudendus.

Plexus lumbalis; Plexus sacralis (Figs. 15.6, 8). Branches of the lumbar plexus leave the Pelvis cranial to the hip joint (see **Arthr.** Annot 184); branches of the sacral plexus exit the Pelvis via the ischiadic foramen caudal to the hip.

(44) **N. furcalis.** This nerve bifurcates and contributes a cranial branch to Plexus lumbalis, a caudal branch to Plexus sacralis. It is the 25th spinal nerve in *Gallus* (Baumel, 1975a) and spinal nerve 22 or 23 in *Columba* (Kaiser, 1923), but cannot always be recognized.

Plexus pudendus (Figs. 15.8, 6). See Baumel (1988) for details of branching of the pudendal plexus.

N. intermedius caudae. Synonymy: N. cutaneus caudae (du Toit, 1912-13).

(45) **N. bigeminus** (Fig. 15.8). This is the ventral ramus of spinal nerve 30 in *Gallus* (Baumel, 1975a) and 25, 26 or 27 in *Columba*. It contributes to both Plexus sacralis and Plexus pudendus, but cannot always be recognized.

(46) **Rr. musculares.** The muscular branches of the femoral nerve (Fig. 15.7) are distributed primarily to the extensor muscles of the knee. The direct muscular branches of the sacral plexus, exclusive of tibial and peroneal nerve distribution, supply primarily the M. iliotibialis and M. iliofibularis.

N. ischiadicus, N. tibialis, N. peroneus [N. fibularis] (Figs. 15.6, 7). The ischiadic (sciatic) nerve is actually the combined tibial and the peroneal nerves in a common epineurial sheath with little or no communication of fibers between them; the two nerves are easily separable. Ohmori, et al. (1984a) showed that the tibial and peroneal nerves are derived from different fasciculi of the plexus: the N. peroneus and Rr. musculares from **Fasc. dorsalis,** the tibial nerve and remaining branches of the Plexus sacralis from the **Fasc. ventralis.**

(47) **Connexus caudalis** (Fig. 15.6). Synonymy: R. communicans caudalis (Buchholz, 1959-1960). This nerve connects N. lateralis caudae with a branch of N. coxalis caudalis; it contains motor fibers derived from the N. coxalis caudalis (Ohmori, et al., 1984), the distribution of the fibers is unknown.

(48) **N. cutaneus femoralis medialis** (Fig. 15.7). Synonymy: N. saphenus. See Buchholz (1959-1960) and Yasuda (1964) for the distribution of this nerve.

N. obturatorius (Fig. 15.7). N. cutaneus femoralis medialis and N. obturatorius are part of the Fasc. ventralis of the Plexus lumbalis (Ohmori, et al., 1984a). The remaining nerves are derived from the Fasc. dorsalis (Annot. 46).

(49) **N. pubicus.** Synonymy: N. ilioinguinalis (Buchholz, 1959-1960). Arises from the lumbar plexus or the intrapelvic part of the medial femoral cutaneous nerve, parallels the pubis, and sends muscular rami to abdominal muscles (Baumel, 1975a).

(50) **N. plantaris medialis** (Fig. 15.7). This nerve ends in the integument of the medial aspect of the ankle joint. The proximal part of the nerve corresponds to R. tibialis profundus and the distal part corresponds to R. cutaneus tarsalis medialis of Buchholz (1959-1960).

(51) **N. paraperoneus [N. parafibularis]** (Fig. 15.7). This is the term of Holmes (1963); Yasuda (1961) referred to it as the tibial plantar nerve, and Buchholz (1959-1960) referred to it as the tertiary fibular nerve. The paraperoneal nerve is a branch of the tibial nerve that accompanies N. peroneus through the Ansa m. iliofibularis and extends into the foot as N. plantaris lateralis (Annot. 52). See **Arthr.** Annot. 186.

(52) **N. plantaris lateralis** (Fig. 15.7). Synonymy: N. metatarsalis profundus plantaris (Buchholz, 1959-1960) (Annot. 51).

(53) **Plexus caudalis** (Figs. 15.8, 9). In the pigeon this plexus is formed by the ventral rami of the last 6 or 7 spinal nerves. The caudal plexus supplies ventral axial

muscles of the tail, M. bulbi rectricium, the dorsal integument of the uropygium and uropygial gland (Baumel, 1988). See Annot. 56. The dorsal axial muscles and integument of the uropygium are supplied by dorsal rami of the nerves that form the caudal plexus.

(54) **N. medialis caudae.** Synonymy: N. caudalis (du Toit, 1912-13).

(55) **N. dorsalis bulbi rectricium; Nn. ventrales bulbi rectricium; Nn. accessorii bulbi** (Fig. 15.8). See Baumel (1988) for the description of these nerves.

(56) **Rr. musculares.** The muscular rami of the caudal plexus can be specified after the muscles they innervate (see Fig. 15.8).

(57) **Pars visceralis.** This portion of the peripheral nervous system includes both visceral efferent and visceral afferent components. See **PNS** Intro.

(58) **G. sphenopalatinum** (Fig. 15.1). Synonymy: Ventral pterygopalatine ganglion. For connections of this ganglion see Schrader (1970); Watanabe and Yasuda (1970); Baumel (1975b) and Akester (1979). See Annot. 18

G. ethmoidale (Fig. 15.1). Synonymy: G. orbitonasale; dorsal pterygopalatine ganglion. For connections of this ganglion see Schrader (1970); Watanabe and Yasuda (1970); Baumel (1975b) and Akester (1979). See Annot. 18.

(59) **Connexus cum n. ophthalmico.** Krol and Dubbeldam (1979) describe a plexus of facial and trigeminal branches in the Mallard *Anas platyrhynchos*. See Annot. 12.

(60) **Ganglion proximale** (Fig. 15.3). Synonymy: G. jugulare; G. radicis. In general this afferent ganglion of the glossopharyngeal nerve is closely related or actually joined to G. proximale of N. vagus in a fossa of the base of the skull (**Osteo.** Annot. 39).

Ganglion distale. The distal afferent ganglion of N. glossopharyngeus is closely adjacent to the G. cervicale craniale of the paravertebral trunk (Fig. 15.3).

Rr. mm. hyobranchialium. The rami of the N. lingualis of the glossopharyngeal nerve innervate some of the branchiomandibular muscles (**Myol.** Annot. 29).

(61) **N. lingualis** (Fig. 15.3). Synonymy: N. lingualis dorsalis (Manogue and Nottebohm, 1982). See Annot. 31.

(62) **Connexus vagoglossopharyngealis** (Fig. 15.3). Synonymy: Anastomosis of Staderini. The variability of this connection in *Gallus* is described by Waluszewska-Bubien (1972). Similar variability occurs in *Anas*, in which the connection may be represented by two or three nerves (Dubbeldam, unpubl.).

(63) **N. laryngopharyngealis** (Fig. 15.3). Synonymy: N. pharyngolaryngealis (Manogue and Nottebohm, 1982). The laryngopharyngeal branch of the IXth nerve and its two main branches were reviewed by Baumel (1975b) and Bubien-Waluszewska (1981). One branch, the **N. laryngealis** innervates the intrinsic laryngeal muscles (**Resp.** Annot. 30) via its Rr. musculares, these being branchial efferent fibers from the Nuc. ambiguus; it also sends visceral efferent fibers to glands in the laryngeal mucosa (these may be vagal in origin, Annot. 62). The **Rr. laryngotracheales** supply visceral afferent and efferent fibers to the mucous membrane and glands of the larynx and the cranial part of the trachea.

(64) **N. pharyngealis.** This pharyngeal branch of the laryngopharyngeal nerve supplies the smooth muscle and mucosa of the Pharynx via its **Rr. pharyngeales** and of the cranial part of the Esophagus via its **Rr. esophageales.** Its **R. muscularis** is a small twig innervating the M. genioglossus.

(65) **N. esophagealis descendens.** The fibers that make up this nerve to the Esophagus and the Ingluvies are very likely of vagal origin (Baumel, 1975b: 2034; Watanabe, 1968).

(66) **Ganglion proximale.** Synonymy: G. jugulare; G. radicis. This afferent ganglion of the vagus nerve is located in Fovea vagoglossopharyngea in the floor of the caudal cranial fossa of the cranium. See Annot. 60; and **Osteo.** Annot. 39

Ganglion distale. Synonymy: G. trunci; G. courvreuri; G. thoracicum; G. nodosum. The distal vagal ganglion has been shown histologically and physiologically to contain exclusively afferent cell bodies, although many efferent fibers pass through it (Wakley and Bower, 1981). This ganglion is located in the root of the neck at the thoracic inlet.

(67) **Rr. glandulares.** These rami split off below the G. distale and probably innervate blood vessels in the ultimobranchial, parathyroid and thyroid glands.

(68) **Rr. glomi carotici.** The topography has recently been revised by Abdel-Magied and King (1978); see also **Art.** Annot. 14. The carotid body in *Gallus* is supplied by a single branch from the G. distale. Abdel-Magied and King (1982) and Taha and King (1983) showed that nearly all the axons in the carotid body (probably over 90%) are afferent with their cell bodies in the distal ganglion. The **N. subcaroticus** (subcarotid or precarotid nerve) is primarily a "sympathetic" nerve, but was claimed by Terni (1929) to carry fibers of the N. glossopharyngeus to the carotid body; it accompanies the A. carotis interna in the neck, but it does not reach the carotid body (Jones and Purves, 1970; Abdel-Magied and King, 1978; review in Bubien-Waluszewska, 1981)

(69) **N. cardiacus cranialis; Nn. cardiaci caudales.** The cranial cardiac nerves contain predominantly afferent nerve fibers from the heart, whereas the caudal cardiac nerves contain the only significant "parasympathetic" branches to the heart (Fedde et al. 1963) (Annot. 79).

N. aorticus. The aortic nerve is found more readily on the right side, as a branch of the cranial cardiac nerve, or of the distal vagal ganglion. It sends twigs to the aortic arch, where there is a baroreceptor zone (Taha, et al., 1983). The physiology and anatomy of the aortic nerve are reviewed by West, et al., (1981) and Bubien-Waluszewska (1981).

(70) **N. pulmoesophagalis; Rr. pulmonales.** For a description of these structures see Fedde et al. (1963) and Fedde (1970); King and Molony (1971); McLelland and Abdalla (1972). The **R. pulmonalis** of the N. pulmoesophagealis combines with the Rr. pulmonales of the N. vagus to form the **Plexus pulmonalis,** which distributes afferent fibers to the lung. For a review, see Bubien-Waluszewska (1981).

(71) **Rami musculorum tracheae.** The motoneurons of these nerves are found in the caudal part of the Nuc. intermedius medullae oblongatae (**CNS** Annot. 27).

(72) **Rami septi obliqui.** These branches provide partial innervation to the muscle of the oblique septum (Annot. 41; and **Pericar.** Annot. 5).

(73) **Nervus vagus.** Fiber spectrum studies by Abdalla and King (1979a, b; 1982) showed that the cervical trunk of the vagus contains about 16, 000 nerve fibers, the ratio of myelinated to unmyelinated being about 1.3:1. The myelinated fibers are afferent and efferent in roughly equal proportions. About 90% of the afferent myelinated fibers have their cell bodies in the G. distale n. vagi, the rest are in the G. proximale n. vagi or G. distale n. glossopharyngei. About 70% of the unmyelinated fibers are afferent. The numbers of afferent and efferent fibers were also established in the Connexus vagoglossopharyngealis and the recurrent, cranial cardiac, and pulmoesophageal nerves. See Figs. 15.3, 9.

Truncus communis n. vagi (Fig. 15.9). Synonymy: N. vagus impar. The right and left vagi unite on the Proventriculus to form this nerve; there appears to be some interchange of nerve fibers in this junction (Watanabe, 1960). A common vagal trunk is not always formed in the chicken (Waluszewska-Bubien, 1972). When present the common trunk divides at the caudal extremity of the Proventriculus into right and left vagus nerves or **Rr. viscerales abdominales [Nn. gastrici]** (Baumel, 1975: 2035-2036); (Fig. 9). For details on the innervation of the stomach, see Malinovský (1963).

(74) **N. lateralis caudae** (Fig. 15.6). Synonymy: external pudendal nerve (du Toit, 1912-1913). See **Art.** Annot. 83 for origin of this term.

The lateral and the intermediate nerves of the tail are the main somatic branches of the Plexus pudendus (**Cloaca** Annot. 25), both of them supplying **Rr. musculares** to the muscles of the tail and **Rr. cutanei** to the skin in the region of the vent and the tail (Baumel, 1988).

N. pudendus (Figs. 15.6, 9). Synonymy: N. pelvinus (Freedman and Sturkie, 1963); N. pelvicus, pelvic splanchnic nerve. The pudendal is the visceral branch of the Plexus pudendus. It contains sacral "parasympathetic" fibers innervating the reproductive organs and cloaca, but no somatomotor fibers (Ohmori, et al., 1984b).

N. intermedius caudae (Baumel, 1988) (Fig. 15.6, 8). Synonymy: N. cutaneus caudae (du Toit, 1912-1913). This branch of the pudendal plexus is distributed mostly to the ventral tail muscles.

(75) **Ganglion rectale** (Fig. 15.10). Synonymy: G. coli (Watanabe, 1972).

Ganglion uterovaginale. The uterovaginal ganglion of the chicken is located proximal to the cloacal ganglia, not as large as the latter (S. Freedman, pers. comm.).

(76) **N. intestinalis** (Fig. 15.10). Synonymy: nerve of Remak. For review of the structure and proposed function of this nerve see Pusstilnik (1937), Hsieh (1951), Watanabe (1972), Bennett (1974), and Akester (1979). N. intestinalis courses near the mesenteric border of the gut from the end of the rectum to the duodenum; numerous ganglia occur along its length. See **Cloaca,** Annot. 25.

(77) **Truncus paravertebralis cervicalis.** Synonymy: sympathetic trunk; N. vertebralis (Fig. 15.3). The cervical paravertebral trunk is the avian counterpart of the cervical sympathetic trunk of mammals. In birds this nerve passes through the Foramina transversaria from the thoracic inlet to the cranial cervical ganglion (Thebault, 1898) at the base of the skull.

Ganglion cervicale craniale. The cranial cervical ganglion of the avian paravertebral trunk is formed by fusion of the first two cervical ganglia. Individual ganglia are associated with the remainder of the cervical nerves (Hsieh, 1951).

Ansae connexuum interganglionarum (Fig. 15.10). The ansae are a series of anastomosing interganglionic connections looping ventral to the costal processes of the cervical vertebrae that form the ventral wall of each transverse foramen.

(78) **Plexus subvertebralis.** Synonymy: common carotid plexus (Hsieh, 1951). See **Intro.** Visceral nerves.

Truncus subvertebralis [N. caroticus cervicalis]. Synonymy: retrocarotid trunk (Terni, 1929). The trunk arises from the cranial cervical ganglion, and courses caudally along the cervical part of the internal carotid artery in the cervical carotid canal (**Osteo.** Annot. 121) on the ventral aspect of the vertebral column.

N. ophthalmicus externus; N. caroticus externus; N. caroticus cerebralis. Each of these nerves forms a periarterial plexus on the corresponding arteries. See **Art.** Annot. 17.

(79) **N. cardiacus** (Fig. 15.9). This is the so-called sympathetic cardiac nerve. This nerve along with other cardiac nerves has been described in detail by Hsieh (1951). The plexuses formed by these nerves are described by Ssinelnikow (1928); Thebault (1898) and Hsieh (1951) (Annot. 69).

Nn. splanchnici thoracici, Nn. splanchnici synsacrales (Fig. 15.10). In *Gallus* preganglionic fibers from thoracic ganglia 2-5 converge on the origin of the celiac artery and form with vagal fibers the **Plexus subvertebralis thoracicus.** Splanchnic fibers from thoracic ganglia 6-7 and synsacral ganglia 1-3, together with vagal fibers form an extensive plexus along the aorta (Akester, 1979).

(80) **Plexus celiacus; Plexus mesentericus cranialis/caudalis** (Fig. 15.10). For a description of these structures see Watanabe and Paik (1973) and Baumel (1975). The celiac plexus and its subsidiaries form a vascular plexus around the celiac artery and its branches to the viscera of each region (Akester, 1979).

(81) **Plexus aorticus.** The aortic plexus and its subsidiary plexuses have been reviewed by Baumel (1975). It lies on the aorta between the cranial mesenteric and ischiadic arteries. The paired **Plexus adrenalis** contains two or three large **Ganglia adrenalia** (Fig. 15.10), which contribute to the renal, gonadal, and oviductal plexuses. All subsidiary plexuses are distributed periarterially over the arteries of the different regions.

(82) **N. hepaticus** (Fig. 15.10). The distribution of nerves to the liver are described by Staderini (1889), Cords (1904), Marage (1889), Thebault (1898), and Hsieh (1951). The hepatic nerve is derived from a ganglion in the right adrenal plexus and from the cranial mesenteric plexus (Hsieh, 1951).

(83) **Gg. imparia** (Fig. 15.10). Several unpaired ganglia occur in the tail region where the paravertebral trunks converge and form a single trunk (*Columba*, Baumel, pers. comm).

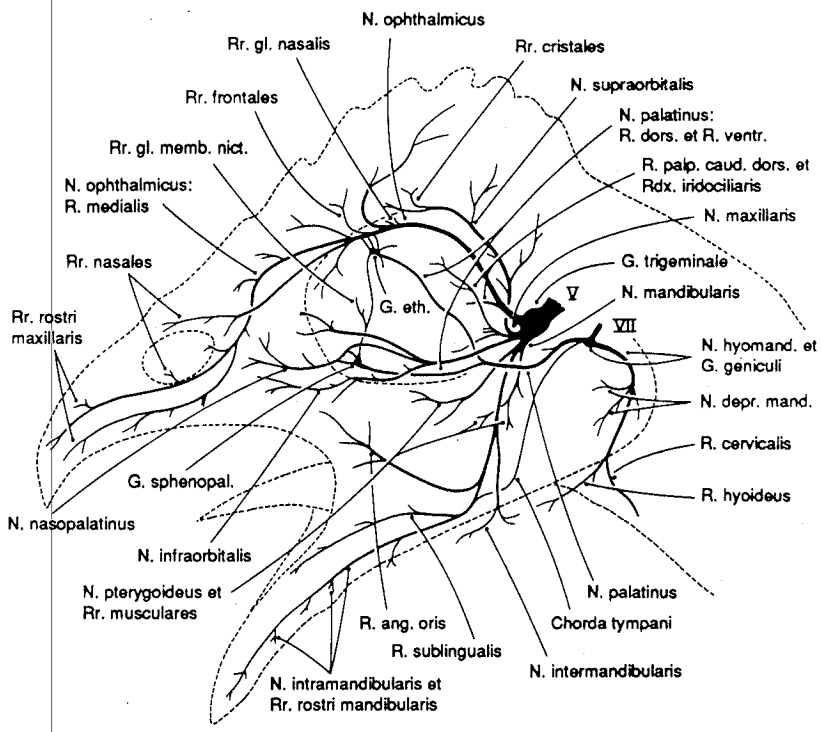


Fig. 15.1. The distribution of the trigeminal and facial nerves in the chicken, *Gallus gallus*. Lateral view of head, left side. Redrawn from Watanabe and Yasuda (1970) and Schrader (1970).

Abbreviations: G. eth., G. ethmoidale; G. sphenopal., G. sphenopalatinum; N. depr. mand., N. m. depressoris mandibulae; N. hyomand., N. hyomandibularis; Rr. gl. memb. nict., Rr. glandulae membranae nictitantis; R. ang. oris, R. anguli oris; R. palp. caud. dors., R. palpebralis caudodorsalis; V, N. trigeminus; VII, N. facialis.

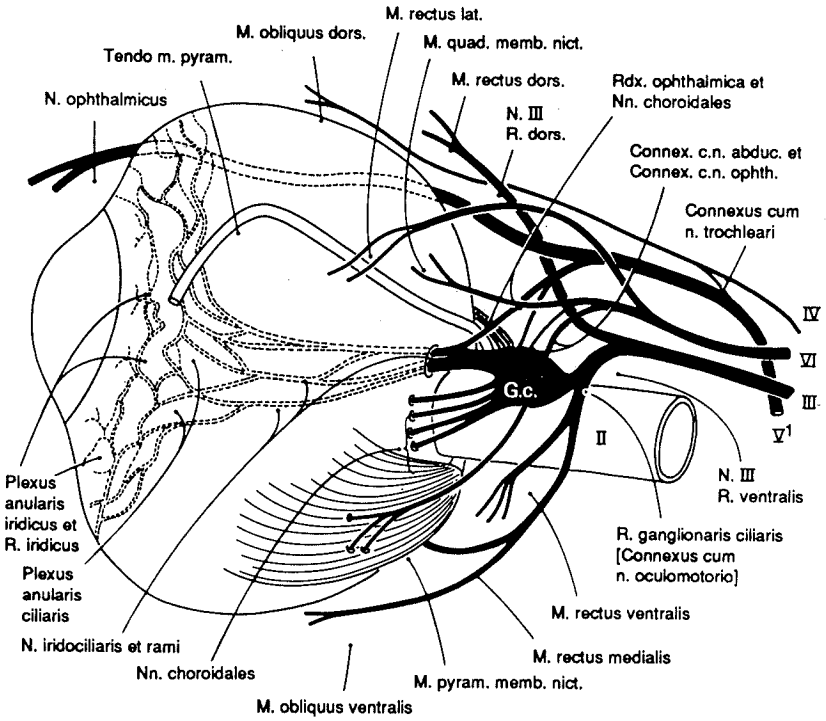


Fig. 15.2. Innervation of the eye of the chicken, *Gallus gallus*. Lateral view of the left eye. Redrawn from Watanabe, et al. (1967). Each of the nerves to the extrinsic eye muscles, including those of the nictating membrane is indicated by the name of the muscle.

Abbreviations: Connex. c. n. abduc., Connexus cum n. abducenti; Connex. c. n. ophth., Connexus cum n. ophthalmico; G. C., Ganglion ciliare; M. quad. memb. nict., M. quadratus membranae nictitantis; M. pyram. memb. nict., M. pyramidalis membranae nictitantis; II, N. opticus; III, N. oculomotorius; IV, N. trochlearis; V^1, N. ophthalmicus; VI, N. abducens; Tendo. m. pyram., Tendo m. pyramidalis membranae nictitantis.

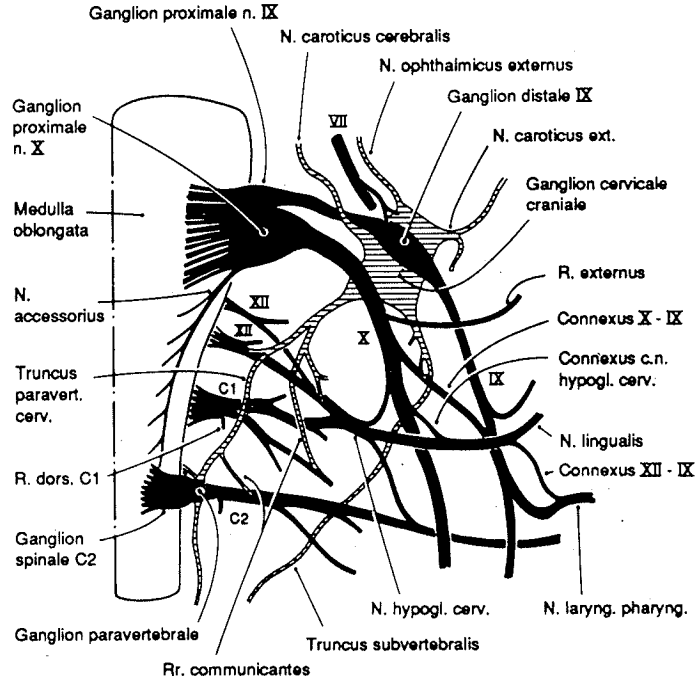


Fig. 15.3. Communications of the nerves at the base of the skull in the chicken, *Gallus gallus*. Dorsal aspect, right side, of the upper cervical spinal cord and Medulla oblongata. Redrawn from Baumel (1975a). Plexiform communications between the last four cranial nerves, the upper cervical nerves and the cranial end of the paravertebral autonomic nerve trunk occur intracranially and immediately below the base of the skull.

Note: (1) The three nerves springing from the upper end of G. cervicale craniale accompany arteries of similar names; (2) the proximal ganglia of cranial nerves IX and X are fused with one another and occupy a fossa in the base of the skull (Annot. 66); (3) the first cervical nerve (C1) differs from most of the other spinal nerves in lacking a dorsal root ganglion and no paravertebral ganglion attached to it; (4) the several connections of nerve C1 with nerves XII and X.

Abbreviations: C1, C2, Nn. cervicales 1 and 2; Connexus X-IX, Connexus vagoglossopharyngealis; Connexus c. n. hypogl. cerv., Connexus cum n. hypoglossocervicali; N. hypogl. cerv., N. hypoglossocervicalis; N. laryng. pharyng., N. laryngopharyngealis; Truncus paravert. cerv., Truncus paravertebralis cervicalis; VII, connexus of N. hyomandibularis of n. VII with G. distalis of N. glossopharyngeus and G. cervicale craniale; IX, N. glossopharyngeus; X, N. vagus; XII, N. hypoglossus.

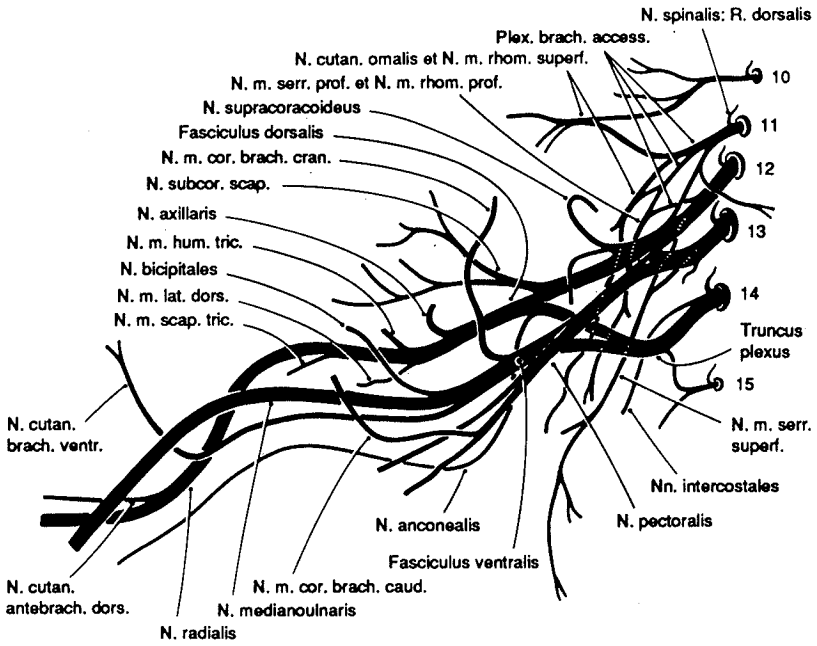


Fig. 15.4. Brachial plexus of the pigeon, *Columba livia*. Ventral view, right side. Redrawn from Baumel (1979). Numerals identify the spinal nerves that contribute to the formation of the plexus; the roots (Rdxx. plexus) of the plexus are the ventral rami of the spinal nerves (see the smaller Rr. dorsales). The proximal half (the viewer's right half) of the plexus is located within the thoracic cavity.

Abbreviations: N. cutan. antebrach. dors./ventr., N. cutaneus antebrachialis; N. m. cor. brach. caud./cran., N. m. coracobrachialis; N. m. hum. tric., N. m. humerotricipitis; N. m. lat. dors., N. m. latissimi dorsi; N. m. rhom. prof./superf., N. m. rhomboidei; N. m. serr. prof./superf., N. m. serrati profundi/superficialis; N. m. scap. tric., N. m. scapulotricipitis; N. subcor. scap., N. subcoracoscapularis; Plex. brach. access., Plexus brachialis accessorius.

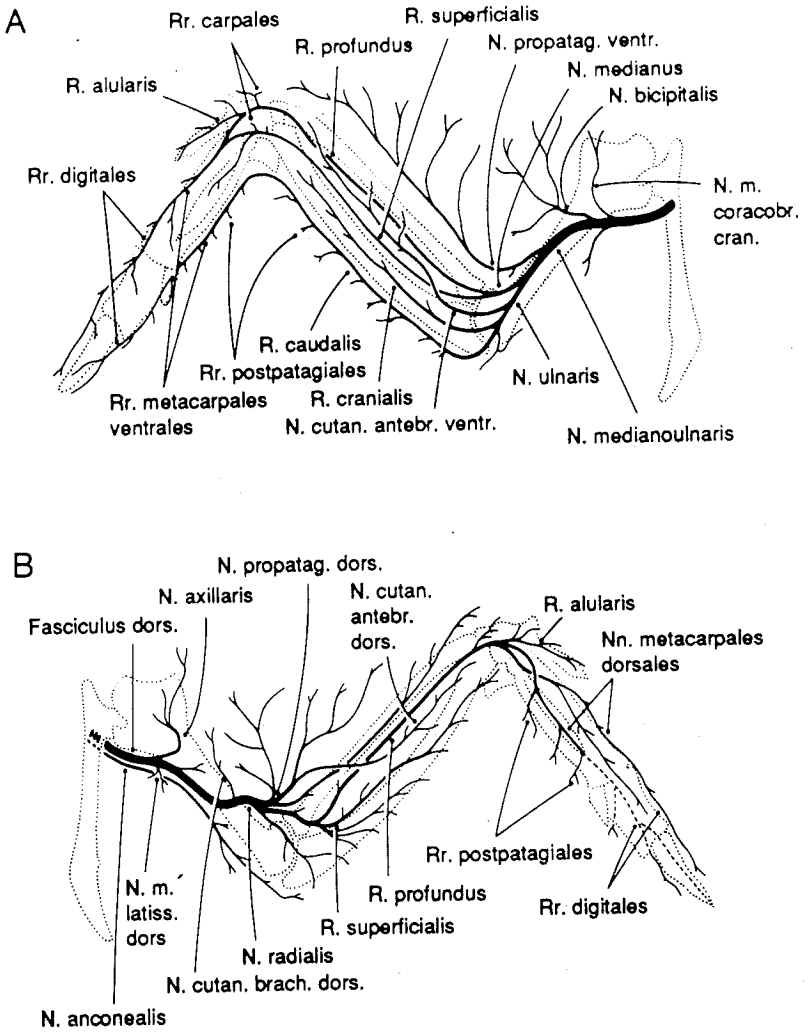


Fig. 15.5. Innervation of the wing of the pigeon, *Columba livia*. Right side: A. ventral nerves; B. dorsal nerves. Redrawn from Baumel (1979).

Note: (1) only a few of the muscular rami are identified; (2) the propatagial and postpatagial nerves are mostly cutaneous in their distribution; the postpatagial rami innervate the follicles of the large flight feathers; (3) see Fig. 15.4 for the origins of the radial and medianoulnar nerves from the brachial plexus.

Abbreviations: N. cutan. antebrach., N. cutaneus antebrachialis; N. cutan. brach. N. cutaneus brachialis; N. m. coracobr. cran., N. m. coracobrachialis cranialis; N. m. latiss. dors., N. m. latissimi dorsi; N. propatag., N. propatagialis.

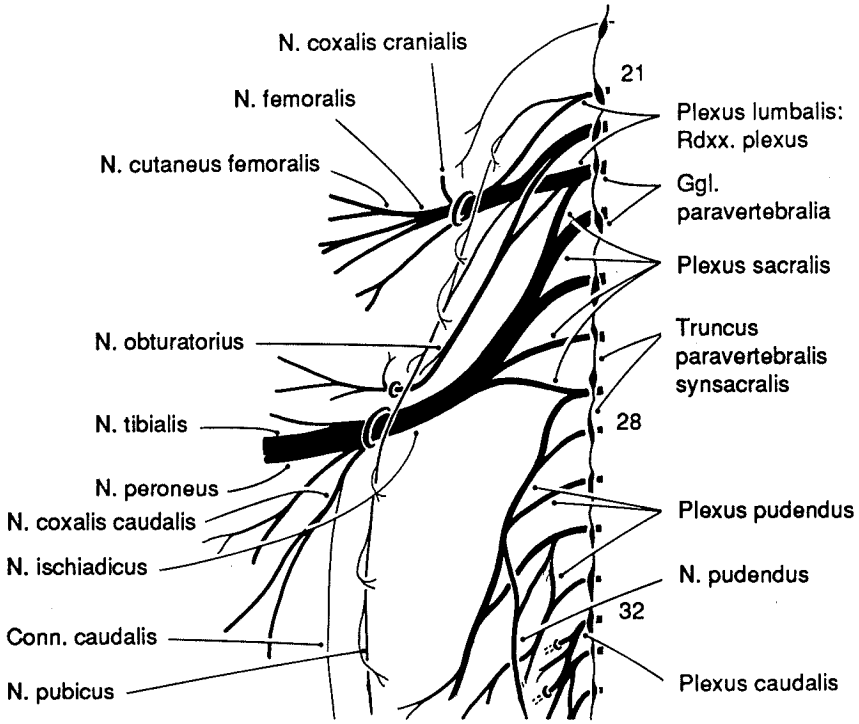


Fig. 15.6. Lumbosacral plexus of the pigeon, *Columba livia.* Ventral view, right side. Redrawn from Baumel (1979). Numerals indicate the nerves usually involved in the formation of the two subplexuses of the plexus. The Plexus lumbalis is formed by the ventral rami of spinal nerves 21-23; the Plexus sacralis is formed by nerves 23-27. Note that the 27th nerve contributes to both plexuses. See Fig. 15.7 and Annot. 46 relating to the distribution of the femoral, tibial, and peroneal nerves, the principal branches of the plexuses.

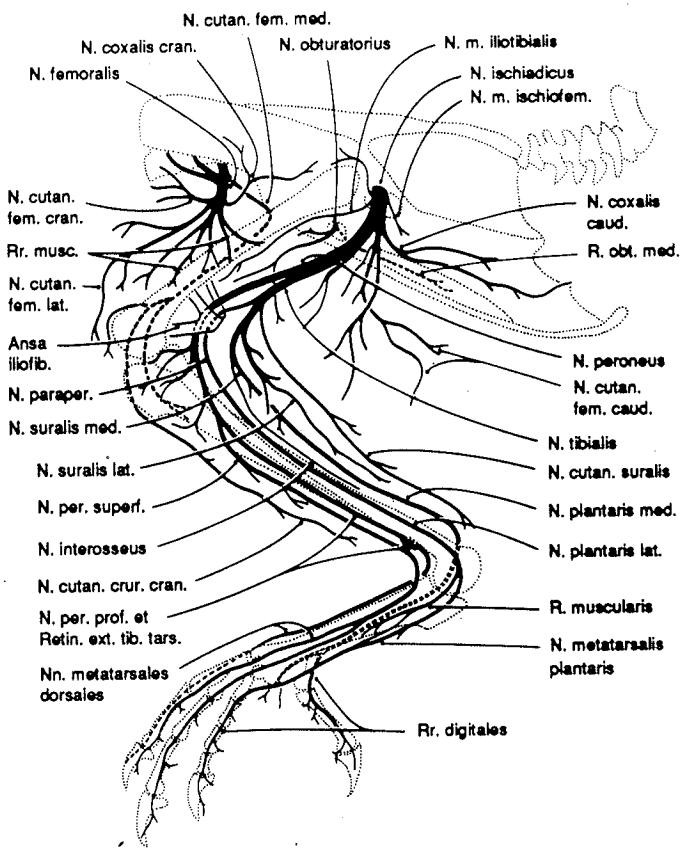


Fig. 15.7. Innervation of the pelvic limb of the pigeon, *Columba livia.* Lateral view, left side. Redrawn from Baumel (1979). Note: (1) most muscular nerves are unnamed; (2) N. plantaris medialis is the prolongation of N. suralis medialis; (3) N. plantaris lateralis is the continuation of N. paraperoneus. N. paraperoneus is actually adherent to N. peroneus as the two traverse the Ansa m. iliofibularis; (4) see **Art.** Annot. 74 and **Ven.** Annot. 69 concerning the sural nerves and related vessels.

Abbreviations: Ansa iliofib., Ansa m. iliofibularis; N. cutan. fem., N. cutaneus femoralis; N. cutan. crur. cran., N. cutaneus cruralis cranialis; N. m. ischiofem., N. m. ischiofemoralis; N. paraper., N. paraperoneus; N. per. prof./superf., N. peroneus profundus/superficialis; R. musc., R. muscularis; R. obt. med., R. medialis N. obturatorii; Retin. ext. tib. tars., Retinaculum extensorium tibiotarsi.

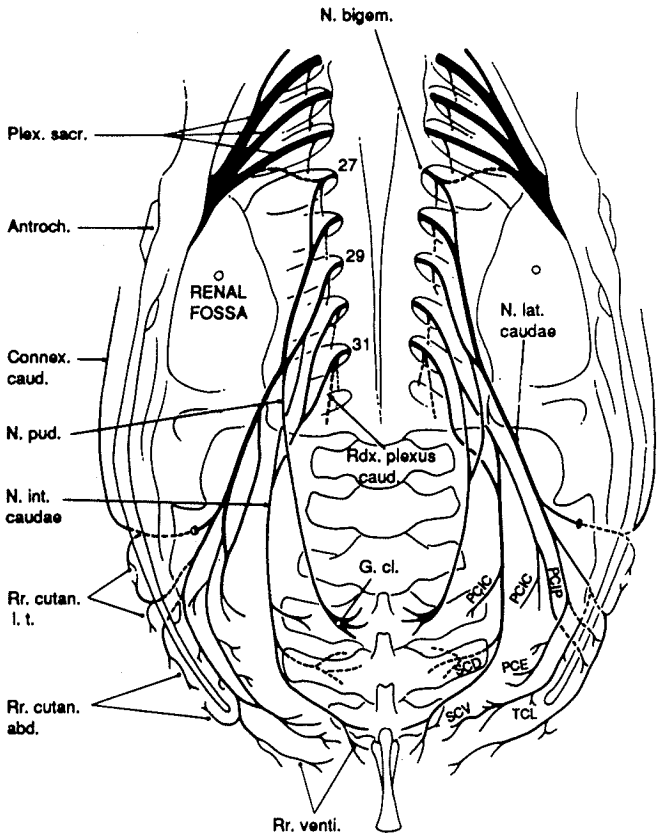


Fig. 15.8. Plexus pudendus and its nerves in the pigeon *Columba livia*, Lateral view, left side. Redrawn from Baumel (1979). Some variation occurs in the formation of the plexus and its pattern of branching. Numerals identify the spinal nerves that contribute to the plexus. The ventral ramus of spinal nerve 27 contributes to both sacral and pudendal plexuses (see Annot. 45).

Abbreviations: Antroch., Antitrochanter; Connex. caud., Connexus caudalis; G. cl., G. cloacale; N. bigem., N. bigeminus; N. int. caudae, N. intermedius caudae; N. isch., N. ischiadicus; N. lat. caudae, N. lateralis caudae; N. pud., N. pudendus; Plex. sacr., Plexus sacralis; Rr. cutan. abd./l. t., R. cutanei of the abdomen/lateral tail. In the right half a number of muscles innervated by the Rr. musculares are indicated: PCIC and PCIP, the caudal and pelvic parts of M. pubocaudalis; PCE, M. pubocaudalis externus; SCD, SCV, dorsal and ventral parts of M. sphincter cloacae; TCL, M. transversus cloacae.

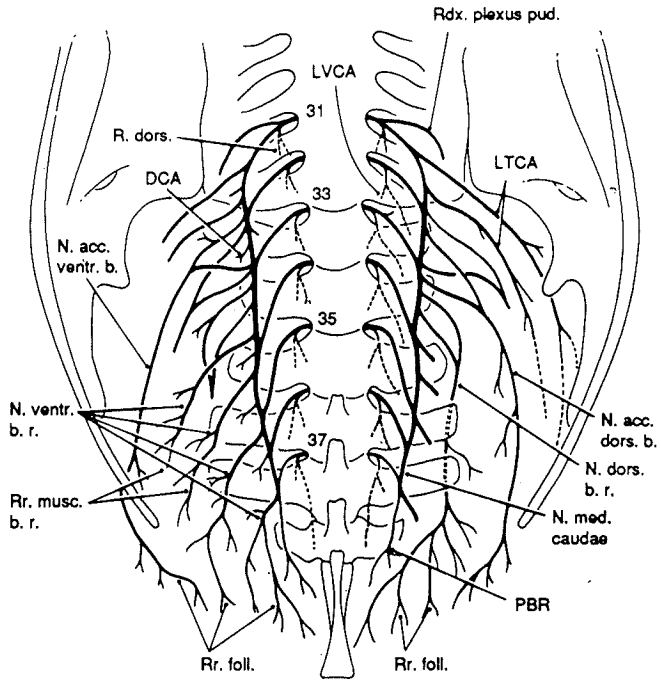


Fig. 15.9. Plexus caudalis and its branches in the pigeon, *Columba livia*. Ventral view; redrawn after Baumel (1988). The roots of the caudal plexus (ventral rami of spinal nerves 32-37(38) are nearly as large as those forming the pudendal plexus, a reflection of the abundant innervation required by the bulbs of the rectrices and the well-developed elevator and depressor muscles and integument of the uropygium, including the afferent innervation of the follicles of the flight feathers and their coverts and filoplumes. Note that the roots of the plexus are connected to one another by loops (ansae) that form a longitudinal chain, the N. medialis caudae.

Abbreviations: N. acc. dors./ventr. b., N. accessorius dorsalis/ventralis bulbi; N. dors./ventr. b.r., N. dorsalis/ventralis bulbi rectricium; R. dors., R. dorsalis nervi spinalis 31; Rr. foll., follicular branches; Rdx. plex. pud., last root of Plexus pudendus; Rr. musc. b.r., Rr. musculares bulbi rectricium. Rr. musculares innervate muscles of the tail region: DCA, M. depressor caudae; LTCA, M. lateralis caudae; LVCA, M. levator caudae.

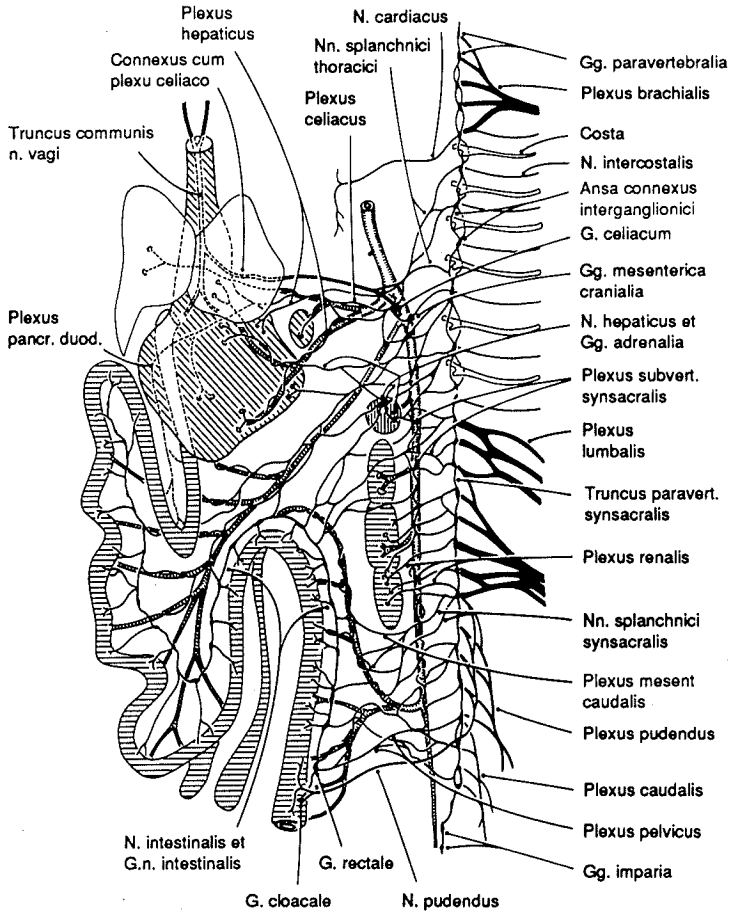


Fig. 15.10. Thoracoabdominal visceral nerves of the chicken, *Gallus gallus*. Redrawn from Baumel (1975b; after Stiemens, 1934). Ventrolateral view of the spinal nerves and paravertebral trunk of the left side showing the various splanchnic nerves forming the subvertebral plexuses (see Chap. Intro.) on the aorta and on the roots of its visceral branches.

Note: (1) the connection between the vagus nerve and the celiac plexus and the relation of the pudendal nerve to the Plexus pelvicus; (2) the rectal, ileal, and jejunal segments of N. intestinalis; (3) N. cardiacus provides pulmonary rami (not shown) as well as cardiac rami; (4) the loops (ansae) of the paravertebral trunk in the cervical, thoracic, and caudal regions; (5) the Gg. imparia which represent the fusion of the right and left paravertebral trunks in the caudal region.

Abbreviations: A, Gl. adrenalis; C, Cecum; D, Duodenum; H, Hepar; I, Ileum; J, Jejunum; K, Ren; P, Proventriculus; Plex. mesent. caud., Plexus mesentericus caudalis; Plex. pancr. duod., Plexus pancreaticoduodenalis; R, Rectum; S, Splen; V, Ventriculus.

16

ORGANA SENSUUM [ORGANA SENSORIA]

HOWARD E. EVANS
and
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With contributions from subcommittee members: J. J. Baumel, H. Berkhoudt, R. B. Chiasson, V. Ilyichev, A. S. King, L. Malinovský, C. J. Murphy.

The structure of many organs in birds differs significantly from that of reptiles or mammals and requires different descriptive terms. In the present list an effort has been made to use the same terms as appear in *Nomina Anatomica Veterinaria* (NAV; ICVGAN, 1983) for domestic mammals, *Nomina Anatomica* (NA; IANC, 1989) for humans, and *Nomina Histologica* (IANC, 1989) for both, when appropriate.

There are still unanswered questions in regard to all sensory organs involved in orientation, navigation, foraging and daily life, and many areas of controversy concerning the role of different sensory capacities. Tactile and taste sensitivity within the bill seem particularly important in the foraging of both waterfowl (Anseriformes) and shorebirds (Charadriiformes) (Berkhoudt, 1985a; Gottschaldt, 1985). There is good evidence that olfaction is particularly important in the foraging of kiwis (Apterygidae) and in pelagic seabirds (Procellariiformes) (Wenzel, 1971; Bang and Wenzel, 1985). In the latter group olfaction may also serve as an aid to navigation and homing, a role also ascribed to this sense in the pigeon (Wiltschko and Wiltschko, 1989).

Migration. Migrating or homing birds may utilise a range of sensory cues, perhaps in a redundant manner. There is evidence that birds can detect the coordinates of the earth's magnetic field (Wiltschko & Wiltschko, 1988) and we know that they can orient to stellar rotation (Emlen, 1975) as well as perceive small changes in barometric pressure which could aid the determination of flight altitude Keeton (1979). Information on the plane of polarization of light (Kreithen and Keeton, 1974; Helbig and Wiltschko, 1989) may be available to some birds, although this has been called into question recently and reviewed by Martin (1991). There is also evidence that in many

birds visual sensitivity extends throughout the visible spectrum and into the ultraviolet (Kreithen and Eisner, 1978; Emmerton and Delius, 1980). This ultraviolet sensitivity may be used to guide birds in their foraging as well as their orientation (Goldsmith, 1980).

Echolocation. Some cave nesting birds echolocate with poor acuity (compared with bats) by using sounds of relatively low frequency—in the range of 1.5–2.5 kHz in the oilbird, *Steatornis* (Konishi and Knudsen, 1979), and 4.5–7.5 kHz in the cave swiftlets, Apodidae (Griffin and Suthers, 1970). It has been suggested that pigeons (*Columba livia*) may also perceive low frequency infrasound and use this as an orientation cue (Kreithen and Quine, 1979). No birds have yet been recorded with sensitivity above 12kHz; greatest sensitivity lies in the range 1–5 kHz (Dooling, 1982) and the lowest auditory threshold in the most sensitive birds (the owls, Strigiformes) is similar to that of humans (Martin, 1990: 167).

Eye. The eye of the bird is distinctive for many of its features. It varies greatly in shape from near spherical to tubular and the axis may be directed rostrally (owl), laterally (finch), or caudally (woodcock). The poles of the bulb are designated "anterior" and "posterior" for consistency with the human *Nomina Anatomica* (IANC, 1989) and *Nomina Anatomica Veterinaria* (ICVGAN, 1983). The part of the eye nearest the beak is designated as "nasal" and that nearest the ear as "temporal". The field of binocular vision in front of or behind a bird varies greatly between species (see Martin, 1986, and Martin and Brooke, 1991, for comparisons between five species).

The lens of the bird eye has an annular pad or band, Pulvinus anularis lentis, that is not present in any other animal eye (Fig. 16.2; Annot. 32). This annular pad is wrapped around a hydrostatic "vesicular chamber" which in turn surrounds the "central core" of the lens. The refractive properties of the bird eye are influenced by this unique arrangement.

Unlike mammals, the ciliary processes of the bird's eye are in contact with the lens and usually attach to it. The ciliary muscle is attached to the inner surface of the sclera, extends across the inner surface of the scleral ring, and inserts at the scleral venous sinus and the sclerocorneal junction. The ciliary muscle appears capable of dilating the scleral venous sinus and the filtration angle of the ciliioscleral sinus (Annot. 11) (Fig. 16.2). Both lenticular and corneal accommodation have been demonstrated in birds (pigeon and chicken, Martin, 1987) but the actual mechanisms by which the ciliary muscles bring about these refractive changes are not understood. The mechanics of accommodation differ between bird and mammal. One hypothesis is that the avian bulb functions as a hydrostatic unit in which deformation of the shape and position of the lens and cornea is brought about by changes of

pressure within the bulb (Suburo and Marcantoni, 1983). In amphibious species, where a large range of accommodation is necessary to compensate for immersion, the curvature of the central core of the lens may be increased by forcing the lens through a constricted iris opening (Levy and Sivak, 1980).

At the point where the optic nerve exits from the bulb, the choroid and non-sensory retina project into the vitreous body as a highly vascular structure, the Pecten (Annot. 30).

Ear. The ear of the bird, which can be isolated *in situ* without great difficulty because of the pneumatic structure of the bone that surrounds it, is a model of simplicity with several distinctive features (Kuhne and Lewis, 1985): (1) a canal which connects the Scala tympani with the Scala vestibuli at the base of the Cochlea; (2) a Lagena at the end of the Cochlear duct; (3) a single, elongate ear ossicle, the columella, with processes attached to the tympanic membrane.

In the arrangement of terms for the ear the structures of the membranous labyrinth have been separated from those of the osseous labyrinth in order to clarify their relationships. Carelessness in the use of the terms "canal" and "duct" in past and current literature has led to confusion concerning the difference between the membranous and osseous labyrinths. The membranous labyrinth is the progenitor of the sensory structures of the inner ear and is filled with endolymph. The osseous labyrinth forms secondarily around the membranous labyrinth, contains perilymph, and is not in open communication with the endolymphatic spaces. For example, the Scala vestibuli and Scala tympani are creations of the osseous labyrinth, whereas the Ductus cochlearis (sometimes called the Scala media) and Lagena are terminal portions of the membranous labyrinth. Just as the semicircular "ducts" signify the membranous component versus the semicircular "canals" for the osseous portion, so should the other "ducts" and "canals" agree. Thus, the so-called Ductus brevis, which joins the basal portions of the Scala tympani and the Scala vestibuli, is herein named the Canalis interscalaris basalis, while the connection of the two scalae at the "apex" of the Cochlea (Helicotrema) is called the Canalis interscalaris apicalis. The latter is an appropriate term since in the bird the connection between the two scalae has length rather than being a simple hole or trema (Fig. 16.8).

Other special senses. The structures which mediate the detection of magnetic fields, infrasound, and heat detection in the beak or tongue are unknown. Furthermore, the structures underlying many sensory modalities are little understood. In particular these include olfaction, taste, and tactile sensitivity. Therefore a continuing mission is the identification of avian sensory transducers and an elucidation of their structure and function.

TERMINOLOGY

ORGANUM VISUS [OCULUS]

BULBUS OCULI[1] (Fig. 16.1 Term. Sit. Annot. 1; and Intro.)

- Polus anterior
- Polus posterior
- Equator[2]
- Bulbs oculi anterior
- Bulbus oculi posterior
- Meridiani bulbi[3]
- Axis bulbi [A. opticus][4]
- Axis visualis [A. visus][5]
  - Axis visualis temporalis
  - Axis visualis centralis
- Fundus oculi[6]

TUNICA FIBROSA BULBI[7]

- Sclera[7]
  - Anulus [Annularis] ossicularis sclerae[8]
  - Ossiculum sclerae
  - Ossicula posteriora sclerae[9]
  - Os nervi optici[10]
  - Sinus ciliosclerales[11]
  - Sinus venosus sclerae[12]
  - Lamina cartilaginea sclerae[13]
- Junctura corneoscleralis[15]
- Cornea[14]
  - Anulus [Annulus] corneae[15]
  - Limbus corneae
  - Facies anterior
  - Facies posterior
  - Epithelium corneae externum[14]
  - Lamina limitans superficialis[14]
  - Substantia propria corneae[14]
  - Lamina limitans profunda[14]
  - Epithelium corneae internum[14]

TUNICA VASCULOSA BULBI[16]

- Choroidea[17]
- Lamina suprachoroidea [L. fusca][17]
- Spatium perichoroideale[17]
- Lamina vasculosa[17]
- Lamina choroidocapillaris[17]
- Lamina basalis[17]
- Corpus ciliare[18]
- Corona ciliaris
- Processus ciliares[19]
- Plicae ciliares
- Zonula ciliaris[20]
  - Fibrae zonulares[20]
  - Spatia zonularia
- Musculus ciliaris[21]
  - M. ciliaris anterior[21]
  - M. ciliaris posterior[21]
  - Fibrae radiales[21]

IRIS[22]

- Facies anterior
- Facies posterior
- Margo pupillaris[22]
- Margo ciliaris[22]
- Anulus [Annulus] iridis
- Plicae iridis[22]
- Pupilla[22]
  - M. sphincter striatus pupillae[23]
  - M. sphincter myoepithelialis pupillae[23]
  - M. dilator striatus pupillae[23]
  - M. dilator myoepithelialis pupillae
- Stroma iridis[22]
- Tapetum lucidum iridis[24]
- Corpus iridocytorum[24]
- Iridocyti[24]
- Epithelium anterium iridis[22]
- Stratum pigmentum iridis[22]
- Angulus iridocornealis[32]
  - Reticulum trabeculare [Ligamentum pectinatum][32]
  - Spatia anguli iridocornealis[32]
- Circulus arteriosus iridis[23]
- Circulus arteriosus ciliaris[23]

TUNICA INTERNA BULBI[25]

- Retina[26] (CNS Annot. 42, 43)
  - Pars optica retinae
  - Stratum nervosum retinae[26]
  - Stratum neuroepitheliale[26]
  - Epitheliocytus bacillifer
  - Epitheliocytus conifer
  - Stratum bipolare[26]
  - Stratum ganglionaris[26]
  - Stratum neurofibrarum[26]
  - Nervus opticus[26]
  - Areae et foveae retinae[27]
    - Area centralis rotunda[27]
    - Area centralis horizontalis[27]
    - Fovea centralis[27]
    - Area temporalis[27]
    - Fovea temporalis[27]
  - Ora serrata[28]
  - Pars ciliaris retinae
  - Pars iridica retinae
  - Pars optica retinae
  - Stratum pigmentosum retinae[26]
  - Tapetum lucidum retinae[29]
  - Pecten oculi[30]
    - Pecten conicus oculi[30]
    - Pecten plicatus oculi[30]
    - Pecten vanellus oculi[30]
    - Pons pectinis[30]
    - Lamina basalis pectinis[30]

CAMERA ANTERIOR BULBI[31]

- Humor aquosus[31]
- Angulus iridocornealis[32]
- Reticulum trabeculare [Lig. pectinatum][32]
- Spatia anguli iridocornealis[32]

CAMERA POSTERIOR BULBI[31]

Humor aquosus

CAMERA VITREA BULBI[33]

Corpus vitreum[33]
Membrana vitrea[33]
Stroma vitreum[33]
Humor vitreus[33]

LENS[34] (Fig. 16.2)

Aqua vesiculae lentis
Axis lentis
Capsula lentis
Fibrae lentis
Corpus centrale lentis[34]
Equator lentis
Facies anterior lentis
Facies posterior lentis
Polus anterior lentis
Polus posterior lentis
Pulvinus anularis [annularis] lentis[34]
Radii lentis
Substantia lentis
Vesicula lentis[34]

ORGANA OCULI ACCESSORIA

Musculi bulbi[35] (Fig. 16.3)
- M. rectus dorsalis
- M. rectus ventralis
- M. rectus nasalis
- M. rectus temporalis
- M. obliquus dorsalis
- M. obliquus ventralis
- M. quadratus membranae nictitantis[37]
- M. pyramidalis membranae nictitantis[37]

Vagina bulbi
Spatium episclerale
Corpus adiposum orbitae
M. tensor periorbita
M. orbicularis oculi
Palpebrae[36]
- Facies cutanea
- Facies conjunctivalis
- Palpebra dorsalis[36]
- Palpebra ventralis[36]
- M. levator palpebrae dorsalis
- M. depressor palpebrae ventralis
- Limbus palpebralis[36]
- Plicae marginales[36]
- Cilia palpebralia (**Integ.** Annot. 40)
- Rima palpebrarum
- Tarsus palpebralis[36]
- Commissura palpebrarum temporalis
- Commissura palpebrarum nasalis
- Angulus oculi temporalis
- Angulus oculi nasalis

Membrana nictitans [Palpebra tertia][37]

(continued)

ORGANA OCULI ACCESSORIA (cont.)

Plica marginalis[37]
M. quadratus membranae nictitantis[37]
- Vagina fibrosa tendinis [Trochlea] (Fig. 16.3)

M. pyramidalis membranae nictitantis[37]
- Tendo m. pyramidalis

Conjunctiva
- Tunica conjunctiva bulbi
- Tunica conjunctiva palpebrarum
- Tunica conjunctiva membranae nictitantis
- Saccus conjunctivae
  - Fornix conjunctivae dorsalis
  - Fornix conjunctivae ventralis
  - Fornix conjunctivae membranae nictitantis

Apparatus lacrimalis[38] (Fig. 16.4)
- Glandula lacrimalis[38]
- Ductus gl. lacrimalis[38]
- Glandula membranae nictitantis[38]
- Ductus gl. membranae nictitantis
- Ductus nasolacrimalis[38]
- Canaliculus lacrimalis[38]
- Ostium canaliculi lacrimalis[38]

ORGANUM VESTIBULOCOCHLEARE [AURIS]

AURIS INTERNA

LABYRINTHUS MEMBRANACEUS (See Chap. Intro.)

Labyrinthus vestibularis[39] (Fig. 16.6)
- Endolympha
- Utriculus[40]
- Macula utriculi[40]
  - Cotilus[40]
  - Striola[40]
  - Rampa[40]
  - Statoconia[40]
  - Reticulum gelatinosum
  - Neuroepithelium

Ductus semicirculares[41]
- Ductus semicircularis anterior[41]
- Ductus semicircularis posterior[41]
- Ductus semicircularis lateralis[41]
- Epithelium ductus semicircularis
- Crus membranaceum commune[41]
- Crus membranaceum simplex
- Crus membranaceum ampullaria
- Ampullae membranaceae
  - Ampulla membranacea anterior
  - Crista ampullaris anterior
  - Ampulla membranacea posterior
  - Crista ampullaris posterior
  - Ampulla membranacea lateralis
  - Crista ampullaris lateralis
  - Crista neglecta[42]
  - Septum cruciatum[43]
  - Cupula gelatinosa
- Ductus utriculosaccularis[44]
- Sacculus[44]
  - Macula sacculi[44]
  - Statoconia
  - Reticulum gelatinosum
  - Neuroepithelium
- Saccus endolymphaticus[44]
- Ductus endolymphaticus[44]
- Ductus sacculocochlearis [D. reuniens][45]

Labyrinthus cochlearis

(continued)

LABYRINTHUS MEMBRANACEUS (cont.)

- Ductus cochlearis[45]
  - Spatium endolymphaticum
  - Tegmentum vasculosum[46]
  - Papilla basilaris[45]
  - Membrana tectoria
  - Lamina basilaris
  - Neuroepithelium
  - Kinocilia
  - Terminationes nervorum
  - Fibrocartilago ventralis
  - Fibrocartilago dorsalis
  - Ganglion cochleare
  - Habenula perforata
  - Lagena[45]
    - Macula lagenae
    - Statoconia
    - Reticulum gelatinosum
    - Neuroepithelium

LABYRINTHUS OSSEUS (Fig. 16.7B)

- Perilympha
- Spatium perilymphaticum
- Cochlea[47]
  - Apex cochleae
  - Basis cochleae
  - Canaliculus cochleae[50]
  - Canalis interscalaris basalis[48]
  - Canalis interscalaris apicalis [Helicotrema][49]
  - Cisterna scalae vestibuli
  - Fossa scalae vestibuli
  - Recessus scalae tympani
  - Scala tympani[45 48]
  - Scala vestibuli[45 48]
  - Vestibulum
- Canales semicirculares ossei
  - Canalis semicircularis anterior
  - Canalis semicircularis posterior
  - Canalis semicircularis lateralis
  - Crus osseum simplex[41]
  - Crus osseum ampullaria[41]
  - Crus osseum commune[41]
  - Ampullae osseae
    - Ampulla ossea anterior
    - Ampulla ossea posterior
    - Ampulla ossea lateralis

AURIS MEDIA (Fig. 16.7)

CAVUM TYMPANICUM [CAVITAS TYMPANICA]

- Recessus pneumaticus paratympanicus (**Osteo.** Annot. 23, 25, 26)
- Ostium tympanicum tubae auditivae (**Osteo.** Annot. 98; **Digest.** Annot. 19)
- Recessus columellae (**Osteo.** Annot. 22)
- Fenestra vestibuli
- Ligamentum anulare [annulare] columellae[51]
- Fenestra cochleae
  - Membrana tympanica secundaria
- Membrana tympanica
  - Margo fibroelastica[52]
  - Sinus pneumaticus marginalis[52]
  - Columella[53]
    - Scapus columellae

(continued)

CAVUM TYMPANICUM [CAVITAS TYMPANICA] (cont.)

- Basis columellae
- Lig. columellosquamosum
- Cartilago extracolumellaris[54]
  - Proc. anterior
  - Proc. posterior
  - Proc. ventralis
- Foramen m. columellae[55]
- M. columellae[56]
- Organum paratympanicum[57]

AURIS EXTERNA[58] (Fig. 16.7B)

- Apertura auris externae
- Meatus acusticus externus (**Osteo.** Annot. 19, 21)
- Pennae auriculares[59]
- Plumae auriculares rostrales
- Plumae auriculares caudales
- Operculum auris[60] (**Topog.** Annot. 5)
- Plica cavernosa[58]
- Glandulae auriculares (**Integ.** Annot. 24)

ORGANUM OLFACTORIUM [O. OLFACTUS][61]

- Concha nasalis caudalis (**Resp.** Annot. 5)
- Concha septalis (**Resp.** Annot. 9)
- Regio olfactoria (**Resp.** Annot. 15)
- Epithelium olfactorium
- Epitheliocytus neurosensorius olfactorius

ORGANUM GUSTATORIUM

- Caliculus gustatorius [Gemma gustatoria][62]
- Porus gustatorius
- Neurofibra gustatoria

TERMINATIONES NEURALES[63]

ORGANA SOMATOSENSORIA

- Organa sensoria integumenti
  - Terminatio neuralis libera[64]
  - Terminationes nervorum plumae et filopumae[65]
  - Terminationes dendriticae nervorum[66]
- Corpusculum nervosum terminale
  - Corpusculum lamellosum avium[67]
  - Corpusculum discoidale multicellulare[68]
  - Meniscus tactus[69]
- Terminationes sensorium apicis rostri[70]
- Organa sensoria musculi

(continued)

ORGANA SOMATOSENSORIA (cont.)

Fusus neuromuscularis
Organum nervosum terminale musculotendineum[71]
Terminationes dendriticae nervorum[66]
Organa sensoria tendinis
Fusus neurotendineus
Terminatio neuralis libera
Organum nervosum terminale musculotendineum
Terminationes dendriticae nervorum
Organa sensoria articulationis
Corpusculum nervosum terminale
Corpusculum lamellosum avium

ORGANA SENSORIA VISCERALIA[72]

Organa sensoria cardiovascularia
Corpora para-aortica (**Art.** Annot. 5)
Sinus caroticus (**Art.** Annot. 7)
Glomus caroticum (**Art.** Annot. 14)

ANNOTATIONS

(1) **Bulbus oculi.** (Fig. 16.1) The avian eye varies greatly in the shape of the bulb from near spherical, as in the chicken, through to tubular, as in owls (Strigiformes). The shape is maintained in part by the scleral ring (Annot. 8) rather than by intraocular pressure. No bird eye is flat (planus) or spherical (globose) although these shapes are often cited as two of the three classical types of avian eye (Walls, 1942). For development of the eye and its accessory structures see Slonaker (1922); for a comparison of the eyes of falconiform and passeriform birds see Lord (1956).

(2) **Equator.** (Fig. 16.1) The greatest circumference of the eyeball. Usually approximately perpendicular to the **Axis bulbi** (Annot. 4). All avian eyes studied to date show complex asymmetry with respect to the axis bulbi. The equator always lies posterior to the scleral ossicles, typically near, or coincident with, the limit **Ora serrata** of the nervous retina (Annot. 27).

(3) **Meridiani bulbi.** Lines surrounding the surface of the eyeball which pass through both anterior and posterior poles.

(4) **Axis bulbi [A. opticus].** (Fig. 16.1) A line passing through the central point of the cornea and the center of the lens. This is not an axis of symmetry for the bulb and thus does not usually pass through the posterior pole. It is usually an axis of symmetry for the optical system and hence was previously referred to as the optic axis. [This term avoids the Latin and Greek combination of Axis (L.) and opticus(G.)].

(5) **Axis visualis [A. visus].** (Fig. 16.1) A line passing from the center of a fovea through the center of the lens. It is assumed that such a line defines a direction of high spatial resolution within the visual field. Distinction should be drawn between **Axis visuale centralis** and **Axis visuale temporalis** whose presence depends upon the position (central or temporal) of the **Fovea** (Annot. 27) in the retina. In some species

both visual axes are present: kingfisher (*Alcedo*); bittern (*Botaurus*); kestrel (*Falco*). and tern (*Sterna*).

(6) **Fundus oculi** (Fig. 16.4). Common term in ophthalmology, referring to the internal surface or deepest portion of the posterior half of the eyeball. It is typically used to refer to the entire retinal surface, and is thus terminated by the **Ora serrata** (Annot. 28).

(7) **Tunica fibrosa bulbi.** (Fig. 16.2) The outer fibrous case of the eyeball formed by the opaque **Sclera** and clear **Cornea** which meet at the Junctura corneoscleralis (Annot. 15). There are few living cells in the sclera and cornea thus the metabolism of the **Tunica fibrosa bulbi** is low, as a consequence of no direct vascular supply.

(8) **Anulus [Annulus] ossicularis sclerae.** (Fig. 16.2 and Fig. 16.7A) The ring of bony ossicles which lies within the sclera anterior to the equator. It provides support for the shape of the bulb. There may be between 10 and 18 (the majority of species have 14 or 15) of the overlapping plate-like scleral ossicles (Curtis and Miller, 1938). The shape of the individual ossicles varies from flat or slightly convex to concave according to the shape of the eye.

(9) **Ossicula posteriora sclerae.** Ossifications in the sclera posterior to the equator, distinct from the scleral ring. When the ossicle forms around the optic nerve it is called the **Os nervi optici** (Annot. 10).

(10) **Os nervi optici.** The cartilage surrounding the optic nerve may ossify and form a complete ring or horseshoe-shaped bone. Formerly known as "Gemmingers ossicle" and "Os opticus", it has been recorded in over 200 species (Tiemeier, 1950, 1953). No satisfactory explanation of its presence has been published.

(11) **Sinus ciliosclerales.** (Fig. 16.2) A medial extension of the anterior chamber in the region of the iridiocorneal angle. Aqueous humour from the chamber drains into this sinus via the **Reticulum trabeculare** and then into the Sinus venosus sclerae (see Annot. 12, 32).

(12) **Sinus venosus sclerae.** (Fig. 16.2) Synonymy: Canal of Schlemm. A venous annulus near the iridiocorneal angle which drains aqueous humor from the ciliosclerał sinus. There may be two venous sinuses of the sclera depending upon the course of an annular artery **Circulus arteriosus ciliaris** which sometimes divides the chamber. (See Annot. 11, 32; **Ven.** Annot. 17, and **Art.** Annot. 28)

(13) **Lamina cartilaginea sclerae.** A cartilaginous cup within the sclera that is continuous with the scleral ring.

(14) **Cornea.** The avian cornea is considered to be similar to that of other vertebrates. Five layers are recognized: (1) the anterior epithelium **Epithelium corneae externum,** (2) the anterior limiting membrane **Lamina limitans superficialis,** a very thin layer formerly known as Bowman's membrane, (3) the substantia propria **Substantia propria corneae,** a layer of connective tissue which accounts for about 90% of the corneal thickness, (4) the posterior limiting membrane **Lamina limitans profunda,** a thin, homogeneous layer formerly known as Descemet's membrane, and (5) the posterior epithelium **Epithelium corneae internum.**

(15) **Anulus [Annulus] corneae.** The zone of transition between the opaque sclera and the transparent cornea is marked by a pigmented ring and referred to as the corneoscleral junction (**Junctura corneoscleralis**).

(16) **Tunica vasculosa bulbi.** (Fig. 16.1) The vascular layer of the eyeball internal to the **Sclera,** also referred to as the uveal tract or uvea. It is divided into three principal components: the **Choroidea** (Annot. 17), **Corpus ciliare** (Annot. 18), and **Iris** (Annot. 22).

(17) **Choroidea.** The choroid consists of blood vessels, bound in connective tissue, which provide the primary blood supply to the retina. The choroid is thickest in the fundus and has a prominent capillary bed. Five layers are recognized in the choroid: (1) **Lamina suprachoroidea,** which is thin, heavily pigmented and loosely attached to the sclera, (2) the **Spatium perichoroideale,** (3) the **Lamina vasculosa** whose blood vessels appear to be mostly arteries (see **Art.** Annot. 26), (4) the **Lamina choroidocapillaris,** and (5) the **Lamina basalis,** a thin basal layer which is loosely attached to the retina. The Spatium perichoroideale appears rather empty in prepared slides but there are striated and non-striated fiber bundles and cords of connective tissue which pass radially through it. The function of these muscle bundles has not been established. Duke-Elder (1958: 405) proposed that they may regulate blood flow in the choroid, while Walls (1942: 645) thought they may form part of the accommodatory mechanism. In the latter, the contraction and relaxation of the muscles, might alter the position of the retinal surface to adjust fine focus. In the flicker (*Colaptes*) the choroid is not empty-looking since it contains a thick mass of mucoid tissue which may have been developed as a cushion to prevent detachment of the retina during "woodpecking" (Walls, 1942: 645).

(18) **Corpus ciliare.** (Figs. 16.1, 2). The ciliary body of the bird is a concept rather than a unitary structure. It includes structures around the scleral venous sinus and consists principally of striated muscle fibers which are concerned with accommodative mechanisms. In birds both lenticular and corneal accommodation have been demonstrated (Troilo and Wallman, 1987; Martin, 1987). The mechanisms of accommodation are not understood completely (see Intro.).

(19) **Processus ciliares.** (Fig. 16.2) Unlike mammals, the ciliary processes of birds are numerous and irregular and may fuse with one another. Attached directly to the lens capsule and usually heavily pigmented, they are composed of non-sensory retina (Annot. 26).

(20) **Zonula ciliaris.** (Fig. 16.2) The ciliary zonule consists of zonular fibers **Fibrae zonulares,** with spaces in between, which pass from the ciliary processes, plicae, and adjacent areas to the lens capsule. In the bird they do not appear to be tensed at any time and probably do not function as in the mammal. Owing to the contact and fusion of ciliary processes with the lens, the zonular fibers in this region are short or fused in the contact zone.

(21) **Musculus ciliaris.** (Fig. 16.2) Synonymy: Musculus sclerocornealis. The ciliary muscle is the principal muscle bundle of the ciliary body (Annot. 18). There are considerable interspecific differences in size and fasciculation. The muscle attaches posteriorly to the inner surface of the sclera, and extends from the optic cup across the width of the scleral ring to the corneoscleral junction where it ends on the limbus of the cornea or on the Sinus venosus sclerae (Fig. 16.2). The ciliary muscle may appear as one muscle or may appear to be divided into two, three, or four muscles. Usually two muscles are distinguished, the **M. ciliaris anterior** or Crampton's muscle, and the **M. ciliaris posterior** or Brucke's muscle. The anterior and posterior muscles overlap in the region of the scleral ossicles. The M. ciliaris anterior is largest in hawks and owls, smallest in aquatic birds and absent in the cormorant (*Phalacrocorax*). The M. ciliaris posterior is large in the cormorant and gannet (*Morus*). The status of the **Fibrae radiales** (Müller's muscle) is uncertain. In some birds it is seen as a subdivision of Crampton's muscle while in others as a subdivision of Brucke's muscle. Rochon-Duvigneaud (1950: 228) regards Muller's muscle simply as fibers which pass between Crampton's and Brucke's muscles which do not merit a designation.

(22) **Iris.** (Fig. 16.2) The iris controls its aperture, the pupil, **Pupilla,** which in turn determines the brightness and quality of the retinal image (Martin, 1985: 322). The iris is thin at its ciliary border **Margo ciliaris** where it is attached to the ciliary body **Corpus ciliare** (Annot. 18) at the **Angulus iridocornealis** (Annot. 32). It thickens towards its midpoint, and then thins again towards the pupillary border **Margo pupillaris.** The pupillary border is in contact with the anterior surface of the lens. The margin of the pupil is folded **Plicae iridis.** The anterior surface of the iris is lined by a single layer of flattened epithelia cells **Epithelium anterium iridis.** The posterior surface is lined by layers of darkly pigmented cells **Stratum pigmentum iridis** derived from non-nervous retinal tissue (Annot. 26). Between the epithelial layers are connective tissue stroma **Stroma iridis** and two layers of muscles (Annot. 22). The anterior surface **Facies anterior** of the iris is typically heavily pigmented; both lipochrome and guanine are present (Duke-Elder, 1958; Oliphant, 1981). The color of the iris varies over the spectrum, and can be influenced by season, sex, emotional state, and diet (Mann, 1931).

(23) **M. sphincter pupillae; M. dilator pupillae.** Iris movement and size are under the control of two layers of muscles, sphincter and dilator, which are generally considered to be striated. It is these striated muscles which are responsible for the rapidity of the avian pupillary response (Oliphant, et al., 1983). In a number of avian species a second dilator system, in which muscle fibres are non-striated (myoepithelial), have also been described (Walls, 1942: 647; Oehme, 1969; Pilar and Vaughan, 1971). However, striated fibres are always more numerous than unstriated. The blood supply to the iris is from the ciliary artery (**Circulus arteriosus ciliaris**) (**Art.** Annot. 28). This divides at the margin of the iris to form an arterial circle **Circulus arteriosus iridis** which passes circumferentially within the iris (**Art.** Annot. 28).

(24) **Tapetum lucidum iridis.** This structure reported in the iris of columbiform birds consists of reflective cells **iridocyti** which are visible in histological sections under transmitted or polarized light. Chiasson and Ferris (1968) described two types of cells in the Inca Dove (*Scardafella inca*): cells with large reflecting platelets scattered in the superficial layer of the iris and deeper cells with smaller platelets forming a more discrete iridocyte body **Corpus iridocytorum.**

(25) **Tunica interna bulbi.** The innermost layer of the eyeball [formerly Tunica nervosa bulbi].

(26) **Retina.** Within the fundus (Annot. 6) the retina consists of two principal layers, an outer pigmented layer (**Stratum pigmentosum retinae**) adjacent to the choroid (Annot. 16) and an inner nervous layer (**Stratum nervosum retinae**). Within the inner nervous layer four main divisions are recognized: (1) The neuroepithelial layer (**Stratum neuroepitheliale**) lies between the pigmented epithelium and the external limiting membrane. It contains the visual cell outer segments and nuclei; (2) The bipolar layer **Stratum bipolare** which is further subdivided into an outer plexiform layer with visual cell synaptic terminals; an inner nuclear layer containing nuclei of the horizontal, bipolar, amacrine, and Müller cells; and an inner plexiform layer; (3) The ganglion cell layer **Stratum ganglionaris;** and (4) The optic fiber layer

Stratum neurofibrarum which forms the optic nerve on its exit from the globe. The site of exit of these fibers is linear rather than circular, as in mammals, and the pecten (Annot. 30) attaches on the internal aspect of the linear band. The external and internal limiting membranes are formed by the terminal bars of the fibres of adjacent Müller cells. These fibres pass radially through the retina and surround most neurons. Müller cells provide the primary mechanical support of the retina. Of all vertebrate retinae the bird's retina has the greatest regularity of differentiated layers. There is considerable interspecific variation in the relative thickness of the layers (Martin, 1985: 336). Outside the fundus, anterior to the **Ora serrata** (Annot. 28), the **Stratum pigmentosum retinae** continues as a layer of pigmented non-nervous tissue. It forms the **Processus ciliares** (Annot. 19), and where the retina extends over the posterior surface of the iris it becomes the **Stratum pigmentum iridis** (Annot. 22). Non-nervous retina also extends over the pecten (Annot. 30).

(27) **Areae et foveae retinae.** An **Area** is a clearly defined portion of the sensory retina characterized by cell types showing particular features such as increased density, specific size, or regular arrangement. Areae are thought to be associated with specific visual abilities, such as high spatial resolution or the detection of movement, in localized regions of the visual field. Most areae have photoreceptor cells which are longer, thinner, and more tightly packed than elsewhere in the retina, although there are also areae which contain specific types of ganglion cells (Hayes, et al., 1991). Areae are a common feature of the avian retina and show marked interspecific variability in their number, shape, and position. Three main types are recognized: (1) **Area centralis rotunda,** a circular area located in the central region of the fundus dorsal and nasal to the pecten, (2) **Area temporalis,** a circular area often located lateral to the central area in the temporal retina, and (3) **Area centralis horizontalis,** a linear area which may extend across the retina in an approximately horzontal plane, sometimes joining the central and temporal areas. The **Fovea centralis** and **Fovea temporalis** are each a circular depression in the retina which results from the radial displacement of more internal layers. It may be of variable depth, size and shape, but always occurs within a central or temporal area. No more than two foveae have been reported in any species. (See Meyer (1977) and Martin (1985) for interspecific differences and functional interpetations).

(28) **Ora serrata.** (Fig. 16.1) Synonymy: Ora terminalis. The anterior limit of the sensory retina which defines the boundary of the fundus (Annot. 6). Although, in the majority of avian taxa this margin is a ring of transition and better called "terminal" than "toothed", Ora serrata is retained because of its widespread use.

(29) **Tapetum lucidum retinae.** A reflective structure in the pigmented layer recorded in birds only in the retinae of goatsuckers (Caprimulgidae) by Nicol and Arnott (1974). In mammals, tapeta are common in the choroid, but no such tapetum has been reported in any bird (Martin, 1985: 348).

(30) **Pecten oculi.** (Figs. 16.1, 5) The pecten is a vascular structure, devoid of muscle or nervous tissue and covered by non-sensory retina (Annot. 26), which projects into the vitreous body **Corpus vitreum** (Annot. 33) from the exit of the optic nerve. Three types of pecten are recognized: (1) **Pecten oculi conicus,** found only in kiwis (Apterygidae), and similar in appearance to the conus papillaris of lizards, (2) **Pecten oculi vanellus,** found in the other extant Struthioniformes (ostrich, rheas, emu, and cassowaries) and the tinamous (Tinamiformes); in transverse section this pecten exhibits a central lamina with vanes radiating from it., (3) **Pecten oculi pliactus,** found in all other birds, transverse sections revealing a plicated structure with the

folds held in place by a bridge of tissue, the **Pons pectinis.** There is a basal membrane (**Lamina basalis pectinis**) upon which the pleats sit. The arterial supply to the pecten is completely separate from that of the choroid (**Art.** Annot. 29). The capillaries of the pecten form an extensive anastomotic network and their ultrastructure suggests that there is active transcellular transport through the capillary endothelial cells. Wood (1917) illustrated (in color) the gross appearance of the pecten for many species. The pecten usually has numerous pigment granules which give it a jet-black appearance. In the Humboldt Penguin (*Spheniscus humboldti*) and some procellariiform seabirds the pecten is unpigmented, except for the Pons pectinis. Wingstrand and Munk (1965) concluded that the pecten is a nutritive organ necessary for the maintenance of the inner retinal layers, a viewpoint supported by Dieterich and Pfautsch (1973). Brach (1975, 1977) suggested that the pecten is related primarily to intraocular pH regulation. Other explanations of how the pecten functions are those of Meyer (1977) Martin (1985), and See Wood (1917) Meyer (1977), Martin and Young (1984), and Martin (1985: 538) for descriptions of the pecten in a range of birds.

(31) **Camera anterior bulbi.** (Fig. 16.1) The anterior chamber of the eye is bounded by the cornea, lens and iris and iridocorneal angle peripherally. The chamber is filled by the aqueous humour **Humor aquosus** which usually has a density and refractive index similar to water. However, in the owl *Strix aluco* the aqueous humour is reported to be a viscous, mucinous substance (Barany, et al., 1957). Between the iris and the anterior lens surface another smaller chamber **Camera posterior bulbi** is present.

(32) **Angulus iridocornealis.** (Fig. 16.2) The iridocorneal angle lies within the anterior chamber where the base of the iris meets the cornea. Within this angle is the **Reticulum trabeculare [Ligamentum pectinatum]** and **Spatia anguli iridocornealis** (spaces of Fontana). These interstices between the trabeculae allow for drainage of aqueous fluid into the Sinus venosus sclerae (see Annots. 11, 12).

(33) **Camera vitrea bulbi.** (Fig. 16.1) The vitreous chamber of the eye is bounded by the retinal surface, lens and **Fibrae zonulares** (Annot. 21). The chamber is filled by the vitreous humour **(Humor vitreus)** which is viscous and has a density and refractive index higher than water. It can often be removed as a single body, the **Corpus vitreum.** The **Membrana vitrea** separates the vitreous body and the zonal fibres.

(34) **Lens.** (Fig. 16.2) The avian lens differs from that of mammals because it has an annular pad **Pulvinus anularis [Annulus] lentis,** also known as the ringwulst or borrelet, around its central core **Corpus centrale lentis.** This pad is separated from the central core by a fluid filled chamber **(Vesicula lentis).** This arrangement may be a hydrostatic mechanism for transmitting pressure from the ciliary muscles to the central core for accomodation. Marked interspecific differences in the size of the annular pad relative to the central portion of the lens have been noted. It is large in swifts (*Apus*) but relatively small in the Ostrich (*Struthio*).

(35) **Musculi bulbi.** (Fig. 16.3) The eyes of birds fit tightly within the orbits and the six extraocular muscles are reduced to thin bands. The opposing muscles are: (1) **M. rectus nasalis** and **M. rectus temporalis** around a vertical axis, (2) **M. rectus dorsalis** and **M. rectus ventralis** around a mediolateral axis, (3) **M. obliquus dorsalis** and **M. obliquus ventralis** around the anteroposterior axis. Eye movements, which are of small amplitude, can be described as: (1) impulses and oscillations; (2) tremors; (3) flicks; and (4) drifts (Nye, 1969; Pettigrew, et al., 1990). Amplitudes

vary in different meridians and movements are non-conjugate (Martin, 1986) as in reptiles.

(36) **Palpebrae.** The upper lid **Palpebra dorsalis** is short and thick whereas the lower lid **Palpebra ventralis** is longer, thinner and very moveable. They may be feathered or unfeathered. Closure of the eye is due mainly to the movement of the lower lid which has a fibrous **Tarsus.** Four muscles are involved in lid movement. When the lids are closed they meet as a slight arch above the level of the pupil. The lid margin (**Limbus palpebralis**) is thickened and segmented into a variable number of folds (**Plicae marginales**) to allow for stretching in closure. In the sparrow (*Passer domesticus*) there are 17 to 19 folds (Slonaker, 1918). At hatching bird's eyes may be open (precocial, nidifugous species such as anseriforms), or the lids may remain closed for a number of days (altricial, nidicolous species such as passeriforms). **Myol.** Annot. 16; and **Topog.** Annot. 24.

(37) **Membrana nictitans [Palpebra tertia].** The nictitating membrane or third-eyelid lies in the dorsonasal quadrant of the conjunctival sac. It is elastic and is moved rapidly (except in owls, strigiforms) over the surface of the cornea. All birds have a functional nictitating membrane that serves to protect, moisten and clean the cornea. The two muscles responsible for its movement are the **M. quadratus membranae nictitantis** and **M. pyramidalis membranae nictitantis** (Fig. 16.3; **Myol.** Annot. 15). The free margin of the membrane, the **Plica marginalis,** is thickened and folded under to act as a sweep to draw fluids and detritus from the corneal surface to the **Ostium canaliculi lacrimalis** (Annot. 38) at the nasal commissure of the lids. The cornea is kept moist primarily by secretions of the gland of the nictitating membrane and also by secretions from the lacrimal gland (Annot. 38). The nictitating membrane may be transparent, translucent, or opaque white as in dippers (*Cinclus*) and owls (Goodge, 1960). Descriptions of the nictitating membrane can be found in Slonaker (1918) for the House Sparrow (*Passer domesticus*), or in Simic and Jablan-Plantic (1959) for the chicken. In mammals the Plica semilunaris is a rudiment of the Membrana nictitans, and a comparison of birds and mammals is given by Stibbe (1928).

(38) **Apparatus lacrimalis.** (Figs. 16.4, 5). Two glands moisten, nourish, and lubricate the cornea: **Gl. membranae nictitantis,** the gland of the nictitating membrane, also known as the gland of the third eyelid, and **Gl. lacrimalis.** The gland of the nictitating membrane lies in the ventronasal quadrant of the orbit near inter-orbital septum, and secretes via its duct into the conjunctival space between the nictitating membrane and the cornea. The lacrimal gland lies in the ventrotemporal part of the orbit and its secretion via multiple ducts **Ductus gl. lacrimalis** enters the conjunctival space beneath the lower lid. Lacrimal fluid from both glands drains into dorsal and ventral lacrimal canals **Canaliculi lacrimales** at the nasal commissure of the lids and into the **Ostium canaliculi lacrimalis.** These canals join, forming **Ductus nasolacrimalis** which enters the nasal cavity. Marked interspecific differences occur in the relative size of the lacrimal gland (Wood, 1915; Martin, 1985: 334).

(39) **Labyrinthus vestibularis** (Figs. 16.5, 6). The avian vestibular organ is composed of three principal structures; **Utriculus** (Annot. 40), **Sacculus** (Annot. 44), and the **Ductus semicirculares** (Annot. 41). The function of the vestibular labyrinth as a whole is that of equilibration and this is mediated by sensory structures which are responsive to angular and linear acceleration and positional changes. However, the functions of the different receptors in the utricle, saccule and semicircular ducts are probably not totally separated (Smith, 1985).

(40) **Utriculus** (Fig. 16.6). The utricle is a chamber of the membranous labyrinth that gives rise to the semicircular ducts (Annot. 41). The sensory end organ is the **Macula utriculi** which is generally thought to be responsive to linear acceleration and gravity. The macula consists of hair cells, supporting cells and basal cells covered by a gelatinous meshwork in which numerous tiny calcareous crystals or **Statoconia** are embedded. The **Macula utriculi** has three main parts: (1) a central **Cotilus** which anteriorly and laterally is separated from the (2) **Rampa** by (3) a **Striola.** These regions are characterized by their types of hair cells. Jorgensen (1989) has examined the utricles of 20 bird species belonging to 13 families and described two types of hair cells and their distribution: bouton-innervated hair cells and calyceal hair cells.

(41) **Ductus semicirculares** (Fig. 16.6). The three semicircular ducts **Ductus semicircularis anterior/posterior/lateralis** are thin-walled membranous tubes which arise from the utricle. One end of each tube (**Crus m. ampullaris**) is enlarged forming the membranous ampulla **Ampulla membranacea** (Crus m. ampullaria) which contains a neuroepithelium, the **Crista ampullaris.** The ducts form approximately two-thirds of a circle and end at the side of the utricle opposite to that on which their ampullae are located (**Crus m. simplex**). The horizontal (lateral) duct terminates between the common crus and the caudal ampulla. The two vertical ducts (the anterior and posterior) join above the vestibule to form the **Crus membranaceum commune** which opens into the utricle. It is generally considered that the semicircular ducts are sensitive to angular acceleration (Smith, 1985: 299).

(42) **Crista [Papilla] neglecta.** This small sensory area on the floor of the Utriculus close to the **Crista ampullaris posterior** (Fig. 16.5) is often present in mammals as part of the Crista ampullaris caudalis (Boord, 1969; Jorgensen, 1970).

(43) **Septum cruciatum.** Synonomy: Eminentia cruciata; Septum cruciforme. A horizontal fold on the **Cupula** within the Ampullae of the anterior and posterior semicircular ducts (Igarashi and Yoshinobu, 1966; Smith, 1985).

(44) **Sacculus.** (Fig. 16.6) The saccule is thought to be responsive to linear acceleration and gravity. It is located in a bony recess on the wall of the vestibule caudal to the vestibular window (**Fenestra vestibuli**). The **Macula sacculi** forms one wall of the saccule and is attached to the bone; the macula is oval in shape and composed of a compact group of hair cells and supporting cells located over a connective tissue base through which the capillaries and myelinated nerve fibres course. Arising caudally from the saccule and adjacent to the utriculosaccular duct (**Ductus utriculosaccularis**) is the endolymphatic duct **Ductus endolymphaticus.** It traverses the vestibular aqueduct to end in an enlargement, the endolymphatic sac (**Saccus endolymphaticus**) within the cranial cavity.

(45) **Ductus cochlearis** (Figs. 16.7B, 8). Synonomy: Scala media. An outgrowth of the **Sacculus** filled with **Endolymph** and connected with it by the **Ductus sacculocochlearis [D. reuniens].** The blind end of the **Ductus cochlearis** is the **Lagena.** On each side of the cochlear duct are perilymphatic spaces: the **Scala vestibuli** (see Annot. 46) and **Scala tympani** (Amerlinck, 1923; Schwartzkopff and Winter, 1960; Jorgensen, 1970). Within the cochlear duct is the elongate **Papilla basilaris** with its various types of sensory cells (Takasaka and Smith, 1971).

(46) **Tegmentum vasculosum** (Fig. 16.8). A thick folded epithelium occupying a large part of the cochlear duct and compressing the **Scala vestibuli** so as to occlude the lumen (Amerlinck, 1923; Schwartzkopff, 1973; Smith, 1985).

(47) **Cochlea** (Figs. 16.7B, 8). The thin walled osseus tube enclosing the **Scala vestibuli, Scala tympani,** and **Ductus cochlearis** with its terminal **Lagena.** The **Cochlea** of birds is slightly curved rather than a coil as in mammals.

(48) **Canalis interscalaris basalis** (Fig. 16.8). Synonymy: **Ductus brevis.** An osseous connection at the base of the cochlea between the **Scala vestibuli** and the **Scala tympani.** "Ductus brevis" is an inappropriate synonym because this is a part of the bony labyrinth not the membranous labyrinth. See chapter Intro.

(49) **Canalis interscalaris apicalis [Helicotrema]** (Fig. 16.8). This is the apical osseous connection between the **Scala vestibuli** and the **Scala tympani.** An inappropriate synonym is "Ductus scalae" tympani. The term "Ductus" for structures in the inner ear should be restricted to parts of the membranous labyrinth.

(50) **Canaliculus cochleae.** Synonymy: Aqueductus cochlea; Canaliculus perilymphaticus. A connection between the Scala tympani and the subarachnoid space.

(51) **Lig. anulare [annulare] columellae.** A ring of fibrous tissue attaching the footplate of the **Columella** to the rim of the vestibular window.

(52) **Margo fibroelastica.** The thickened margin of the tympanic membrane. In its rostroventral attachment area it includes an air sinus, the **Sinus pneumaticus marginalis** of Pohlman (1921: 239)

(53) **Columella.** (Fig. 16.7B) Synonymy: **Columella auris.** The only auditory ossicle in the middle ear of a bird. It is of hyoid arch origin and extends from the tympanic membrane to the vestibular window. At the tympanic or distal end there is a tripartite extracolumellar cartilage and at the proximal or vestibular end there is an expanded basis or foot-plate occluding the vestibular window (for the Ostrich, *Struthio,* see Saiff, 1981 and **Osteo.** Annot. 22). See Müller (1963) for a detailed synonymy of parts of the avian columella.

(54) **Cartilago extracolumellaris.** (Fig. 16.7B, C) A tripod-like cartilage on the distal end of the columella fused to the tympanic membrane. Also referred to by the synonym: Pars extrastapedialis of the Columella. See Müller (1963) for a detailed synonymy for parts of the avian columella.

(55) **Foramen m. columellae** (Fig. 16.7A, C). An opening in the region of the subtympanic hiatus for the passage of the muscle of the columella (M. columellae) (Annot. 56) into the middle ear cavity.

(56) **M. columellae** (Fig. 16.7C). This muscle has its origin on the surface of the skull, passes into the middle ear cavity under the edge of the tympanic membrane and attaches to the extra-columellar cartilage, thus regulating the movement of the columella (Fig. 16.7C) by tensing it and the tympanic membrane to which it is attached indirectly. It has been synonymised with both the M. tensor tympani and the M. stapedius, and was called the M. occipito-tympanicus by Edgeworth (1935). Since it is innervated by the facial nerve (Pohlman 1921) and is associated with a derivative of the second or hyoid branchial arch (hyomandibular =columella =stapes) it is homologous to the M. stapedius muscle of mammals. This new term clearly associates the muscle with the columella, the only ear ossicle in the bird.

(57) **Organum paratympanicum.** A vesicular remnant of pharyngeal pouches noted by Vitali (1912) and reinvestigated by Federici (1927). The organ is of variable form, embedded in connective tissue caudodorsal to the quadrato-otic articulation. It is also called the organ of Vitali (Maderson and Jaskoll, 1976; Romanoff, 1960).

(58) **Auris externa.** (Fig. 16.7B) The external ear of birds may have ear flaps (Annot. 60) or specialized feathers (Annot. 59) associated with it. Diving birds have the narrowest lumen, while parrots, passerines, and falconiforms have wide ear openings. The external ear openings are asymmetrical in several genera of owls (Strigidae and Tytonidae), one being more dorsal and/or larger than the other (Ilyichev, 1961; Kelso, 1940). This asymmetry is associated with accurate sound localization in the frontal-vertical plane (Norberg, 1968, 1978; Knudsen and Konishi, 1979). Counter and Tsao (1986) described an additional membrane within the external acoustic meatus of the gull (*Larus*), rostral to the tympanic membrane, which appeared to be a collecting parabolic chamber. Perhaps this additional membrane is the same as the semicircular erectile fold (**Plica cavernosa**) described and illustrated by Pohlman (1921) and Evans (1982) deep in the external acoustic meatus close to the tympanic membrane (Fig. 16.7B). The base of this fold is separated by a bursa from the wall of the external acoustic meatus. For a discussion of the external and middle ear of birds see Kuhne and Lewis (1985). See also **Osteo.** Annot. 19, 21.

(59) **Pennae auriculares.** Feathers associated with the opening to the external ear. In some birds the rostral shielding feathers (**Plumae auriculares rostrales**) are rather open-spaced whereas in others (owls, Strigidae and Tytonidae; harriers, *Circus*) they form a facial disc. The caudal feathers **Plumae auriculares caudales** are often very dense and probably serve to reflect and amplify sound especially in those birds with a prominent facial ruff such as owls, harriers, and the nightjar *Caprimulgus* (Konishi, 1973; Ilyichev, 1961, 1975). In diving birds the feathers of the external ear may overlap and cover the meatus (Ilyichev, 1961; Lucus and Stettenheim, 1972: 99). See Annot. 56.

(60) **Operculum auris.** Skin folds capable of covering the ear opening may be rostral and/or caudal to the external acoustic meatus and may contain muscle. They are present in some owls (*Asio otis*), sandgrouse (Pteroclidae) and others. In the Budgerigar (*Melopsittacus*) there is one prominent dermo-osseous muscle capable of pulling a rostral skin fold over the ear opening (Evans, 1982). Norberg (1978) illustrates four external ear muscles in the Boreal Owl (*Aegolius funereus*), one acting on a preaural flap and three muscles acting on a postaural flap.

(61) **Organum olfactorium.** The literature on the avian olfactory system is not voluminous and the general impression is that birds are not very "olfactory" in their behaviour. However, there are birds in which olfaction has been demonstrated to be used in foraging and/or orientation. Taxa in which olfaction seems to be of considerable importance include the kiwis (Apterygidae), albatrosses and petrels (Procellariiformes), the Turkey Vulture (*Cathartes aura*), and the Oilbird (*Steatornis caripensis*) (Bang and Wenzel, 1985). Kiwis are the only birds with nostrils at the extremity of the bill and they have been shown capable of locating food by olfactory cues alone (Wenzel, 1971). The size of the nasal cavity and of the olfactory lobes of the brain show marked interspecific variation which is probably correlated with olfactory prowess (see Bang and Wenzel, 1985, for review).

(62) **Caliculus gustatorius [Gemma gustatoria].** Taste buds in birds are much less numerous than the thousands found in mammals. The greatest number (400-500) are

found in parrots and lesser numbers (100-200) in chickens. However, the gustatory ability of birds does not appear to be closely correlated with the numbers of taste buds observed (Kare and Mason, 1986) because investigators have concentrated on the tongue where they are scarce (Moore and Elliot, 1946; Gentle, 1971; Wenzel, 1983). Taste buds are found in several locations within the oral cavity. They may be in the non-keratinized oral mucosa of the rostral floor of the mouth adjacent to the tongue; on the palate; or on the dorsum of the tongue, commonly in association with the openings of salivary glands. (Botezat, 1904; Bath, 1906; Berkhoudt, 1977; 1985a). Taste buds are ovoid structures, with central neurosensory cells, which extend from the dermis to the superficial surface of the epidermis. Opening at the surface is a taste bud pore which may be elongated and terminate as one or several canals. (Kurosawa, et al., 1983; Berkhoudt, 1985a; Ganchrow and Ganchrow, 1985, 1989). In the Mallard (*Anas platyrhynchos*), tastebuds contain 20-30 intragemmel sensory fibers. The nerves responsible for the innervation of taste buds in the Mallard have been described by Krol and Dubbeldam (1979) and Gentle (1987). The topographic location of taste buds in relation to food-positioning while feeding has been studied by Berkhoudt (1977; 1985b) in the Mallard.

(63) **Terminationes neurales.** This inclusive heading, used in *Nomina Histologica* (IACN, 1989) covers all types of sensory structures in skin, muscles, joints, tendons, and visceral organs. In response to several requests urging the conservation of well known eponyms for terms with no satisfactory substitutes, the eponyms have been listed as synonyms in the annotations. In several cases similar looking cells described in birds and mammals differ physiologically and may ultimately be given different names Gottschaldt (1985). Alternate schemes of classification for nerve endings have been proposed and illustrated by Malinovský (1986a, b; 1989a, b; 1990).

(64) **Terminatio neuralis libera.** Free nerve endings, myelinated or not, are found in various tissues of the body. These endings may be associated with general or specific chemical, electrical, or mechanical sensations. They have been described in both the epidermis and dermis. Their function is not clear but they appear to be multimodal, slowly adapting mechanoreceptors (Malinovský pers. comm.) or thermoreceptors and nociceptors (Necker, 1983; Gottschaldt, 1985).

(65) **Terminationes nervorum plumae et filoplumae.** These sensory structures on feather follicles function as do mammalian sinus hairs. [For filopluma see Andres and von During (1984); Clark and deCruz (1989), and for pluma see Gewecke and Woike (1978); and Malinovský (1986b).]

(66) **Terminationes dendriticae nervorum.** Synonymy: Ruffini endings. The afferent axon arborizes and entwines the receptor but has no distinct outer capsule as in mammals, according to Gottschaldt (1985). Malinovský (pers. comm., 1990) says Ruffini formations always have a capsule. These dendritic endings have been described in articular capsules and joint ligaments (Iggo and Andres, 1982; Gottschaldt, 1985: 426). Similar endings have been seen in the beak of the goose (Gottschaldt, et al., 1982) and pigeon (Berkhoudt, 1985a). They function as slowly adapting, type II, mechanoreceptors, detecting the amplitude component of mechanical stimuli (Gottshaldt, 1985).

(67) **Corpusculum lamellosum avium.** Synonymy: Herbst corpuscle; Corpusculum herbsti. A lamellated, Pacinian-like receptor of birds, showing several specializations of non-nervous elements around its afferent nerve fibers. These corpuscles have: (1) an inner core formed by specialized Schwann cells, (2) an outer zone or subcapsular space which contains a collagen fiber system and surrounds the lamellated structure of the inner core, and (3) an outer capsule derived from the perineurium (Malinovský and Pac, 1985; Malinovský and Malinovský, 1985). These corpuscles are believed to function as a rapidly adapting mechanoreceptor, sensitive to acceleration components in mechanical stimuli, and optimally activated by vibrational stimuli. For reviews see Saxod, 1978; Iggo and Andres, 1982; Necker, 1983; Gottschaldt, 1985.

(68) **Corpusculum discoidale multicellulare.** Synonymy: Grandry corpuscles; Corpusculum Grandri (Halata, 1971; Pac and Malinovský, 1985; Gottschaldt, 1985). The former NAA (1979) term for this corpuscle, C. bicellulare, was not satisfactory because only a small percentage of all corpuscles have two cells. This is an encapsulated receptor, described mainly in anseriforms (Berkhoudt, 1980), consisting of 2 to 7 large, stacked cells with disc-like nerve terminals between them. This corpuscle functions as a rapidly adapting mechanoreceptor detecting velocity components in mechanical stimuli. Several confusions exist in the literature. Ziswiler and Trnka (1972) used the term "Grandry corpuscles" for what Botezat in 1906 called "Merkel corpuscles".

(69) **Meniscus tactus.** Synonymy: Complexus Merkeli. These small end-organs which appear to be groups of Merkel cells were described by Andersen and Nafstad (1968), Saxod (1978), Iggo and Andres (1982), Pac (1982), and Nafstad (1986). Gottschaldt (1985) referred to them as "terminal column receptors". The same endings have been seen in the pigeon palate by Berkhoudt (1985a). The *Nomina Histologica* (IANC 1989) calls the Merkel cell "Epithelioidocytus tactus". Ide and Munger (1978) describe "Merkel corpuscles" in the toe skin of the chicken and called them Grandry corpuscles

(70) **Terminationes sensorium apicis rostri.** The "bill-tip organ" is not really an "organ" but rather an aggregation of sensory structures (Grandy and Herbst-type cells) in the bill, best developed in charadriiforms and anseriforms. It has been seen in shorebirds such as snipe (Bolze, 1968; Goglia, 1964) and sandpipers (Gerritsen, 1988), and studied extensively in ducks and geese. In ducks the organ consists of a series of perpendicular connective tissue papillae within the horny nail of the upper and lower bill. Each papilla has a blood vessel loop within it and contains touch and vibration sensitive corpuscles of Herbst **Corpusculum lamellosum avium** proximally, and Grandry **Corpusculum discoidale multicellulare** distally, in a particular spatial arrangement (Gottschaldt and Laussmann, 1974; Zweers, et al., 1977; Saxod, 1978; Berkhoudt, 1976, 1980, 1985a; Gottschaldt, 1985). Goujon (1869) described an "apparatus" of tactile corpuscles in the beak of parrots. The bill-tip organ of the chicken was studied by Gentle and Breward (1986). Leitner and Roumy (1974a, b) described thermosensitive and mechanosensitive units in the upper bill of the duck. See **Osteo.** Annot. 41.

(71) **Organum nervosum terminale musculotendineum.** Synonymy: Golgi organ. This term coined by Berkhoudt (1980) is a Latin transliteration of the original Italian term used by Golgi in 1880 viz., "Organo nervosa terminale musculo-tendineo", for the structures he saw. It functions as a slowly adapting stretch receptor (Gottschaldt, 1985).

(72) **Organa sensoria visceralia.** These enteroceptors include sensory structures of the heart, great vessels, lungs and other organs (**Art.** Annot. 5, 7, 14).

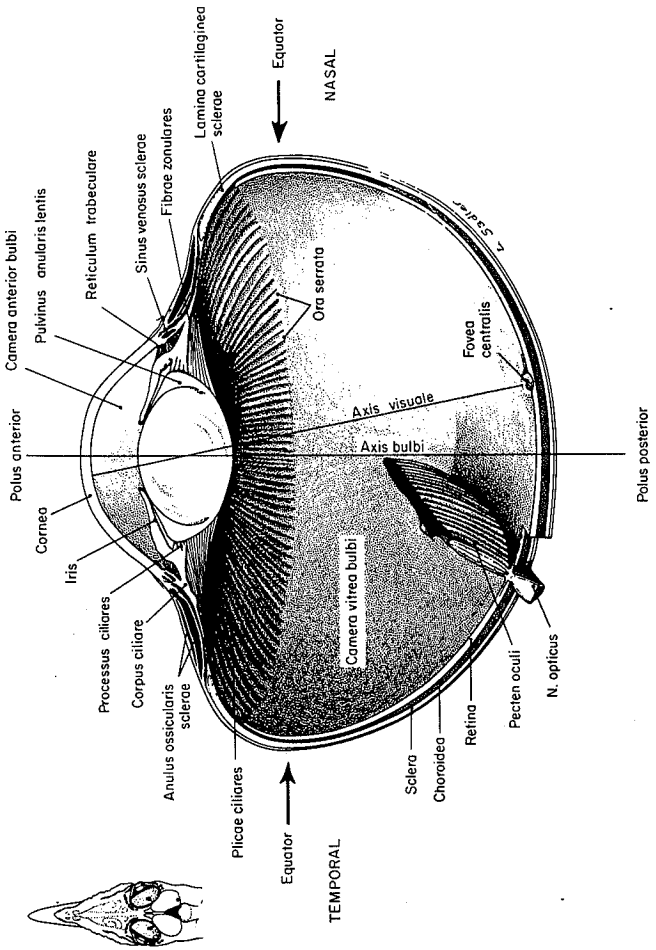

Fig. 16.1. Schematic dorsal section (inset A) through the eye of a chicken (*Gallus*). The view is of the interior of the ventral half of the bulb (from Evans, 1982). With permission of Academic Press.

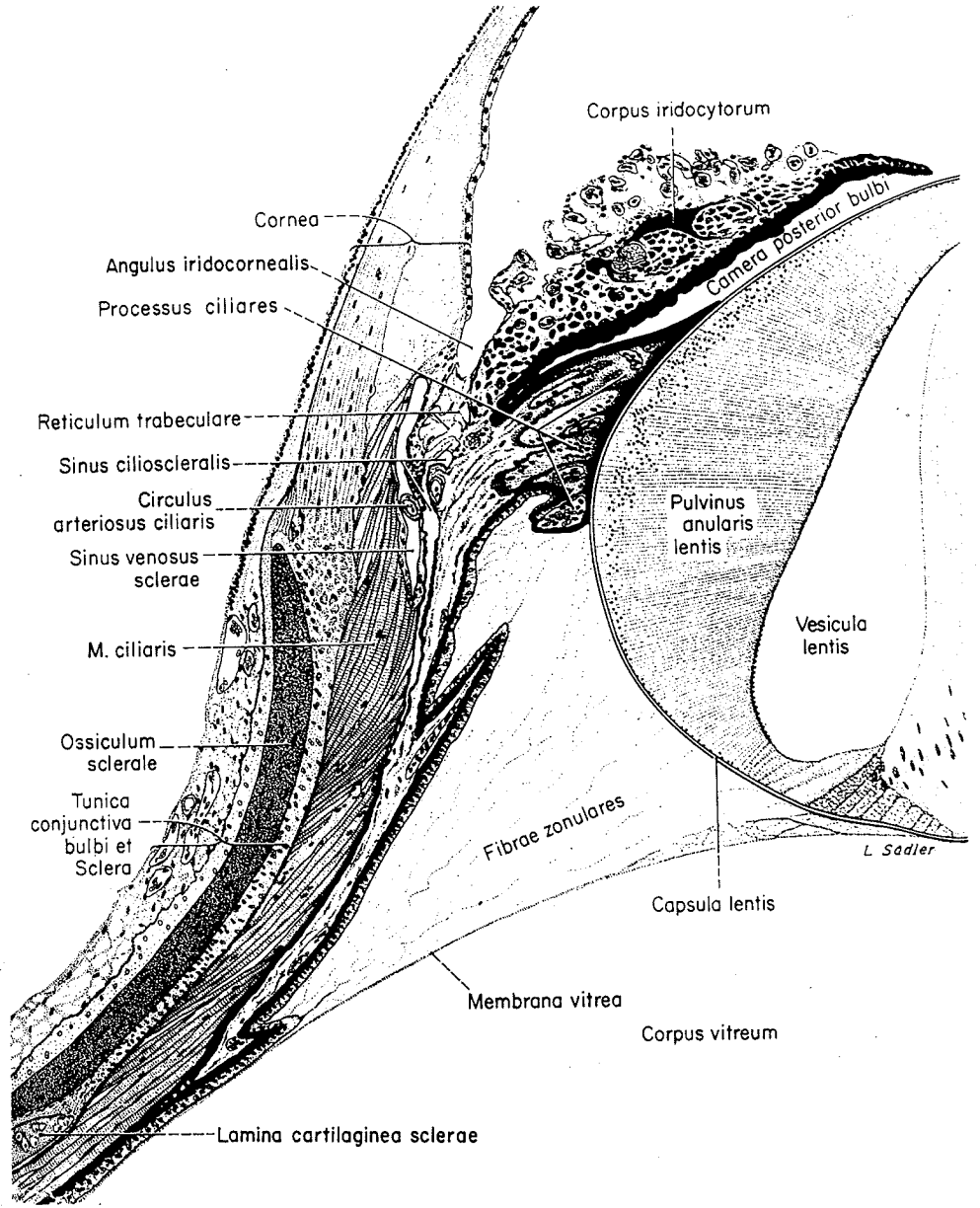

Fig. 16.2. Part of a schematic meridional section of the eye through the corneoscleral junction, ciliary region, and lens of the Inca Dove (*Scardafella inca*). Drawn from histological slides courtesy of R. B. Chiasson (from Evans, 1982). With permission of Academic Press.

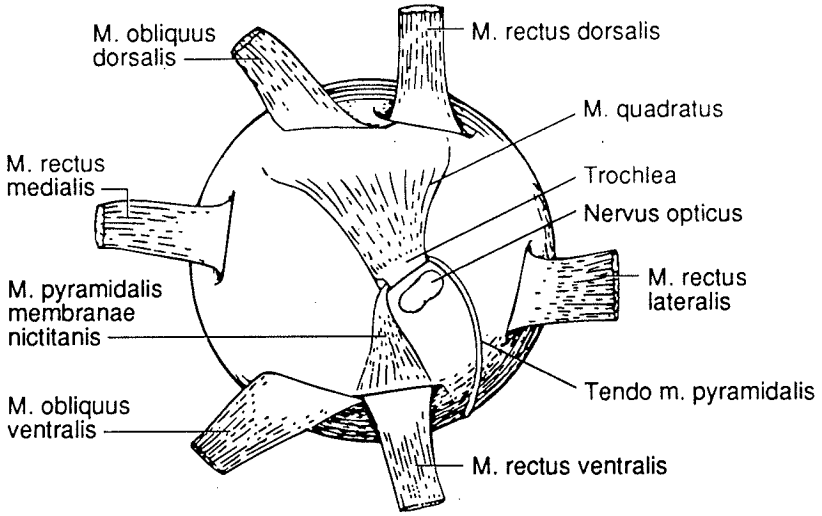

Fig. 16.3. Posterior view of the right eye of a House Sparrow (*Passer domesticus*) to show the extrinsic muscles of the bulb and nictitating membrane (from Evans, 1982). With permission of Academic Press.

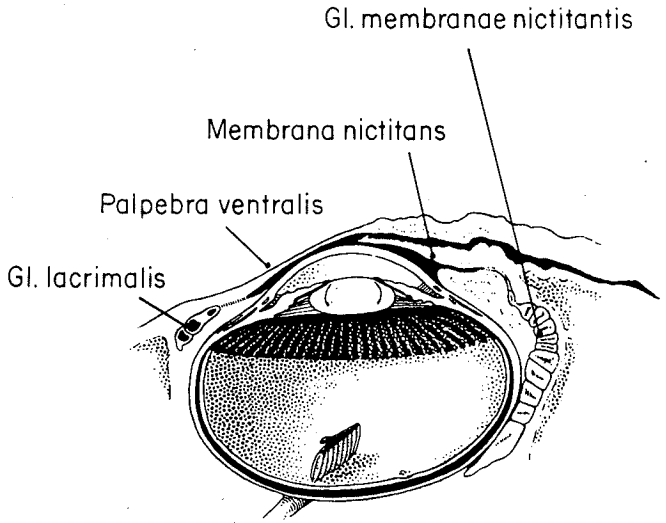

Fig. 16.4. Schematic dorsal section through the lower lid and orbit of a chicken eye to show the position of the lacrimal gland and the gland of the nictitating membrane (from Evans, 1982). With permission of Academic Press.

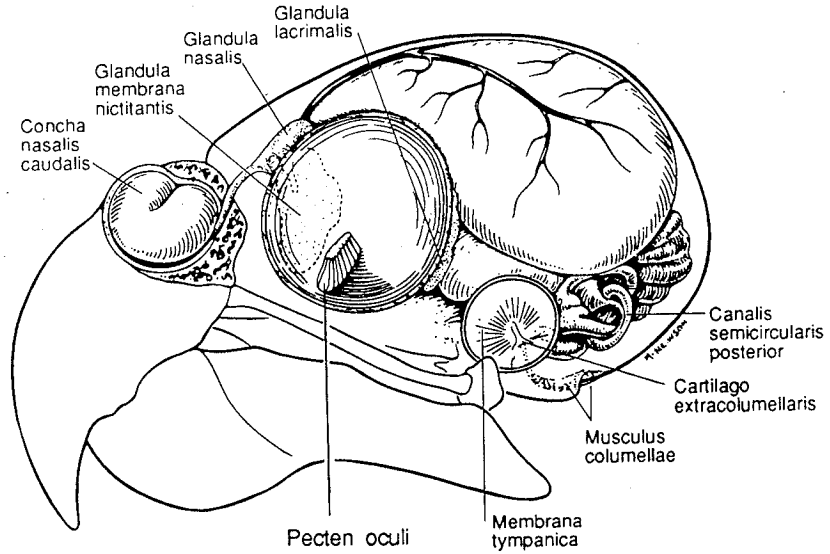

Fig. 16.5. Schematic lateral view of the head of a Budgerigar (*Melopsittacus undulatus*) with the skull roof and anterior portion of the eye removed. The nasal cavity and osseous labyrinth are exposed (from Evans, 1969).

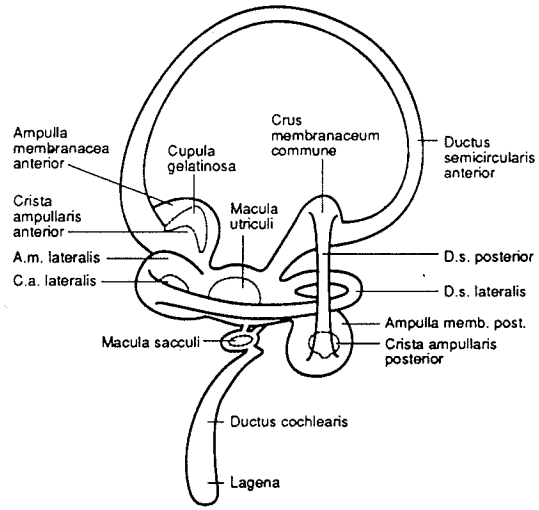

Fig. 16.6. Schematic lateral view of the left membranous labyrinth of a bird (after Smith, 1985).

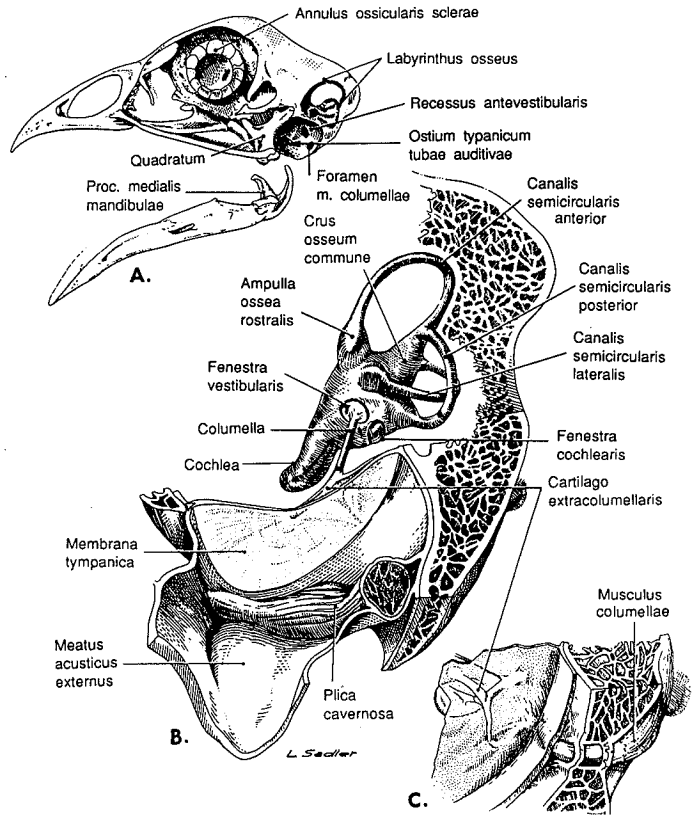

Fig. 16.7. The ear of the chicken (*Gallus*). A. Lateral view of the skull. The Membrana tympanica and Columella are removed to expose the middle ear cavity. B. Dorsolateral view of the left ear sculptured to show the osseous labyrinth and the floor of the external acoustic meatus. C. Lateral view of the caudoventral quadrant of the left ear. The processes of the extracolumellar cartilage show through the tympanic membrane. The tendon of M. columellae which originates on the external surface of the skull, passes through a foramen and enters the middle ear cavity where it attaches to the extracolumella (from Evans, 1982).

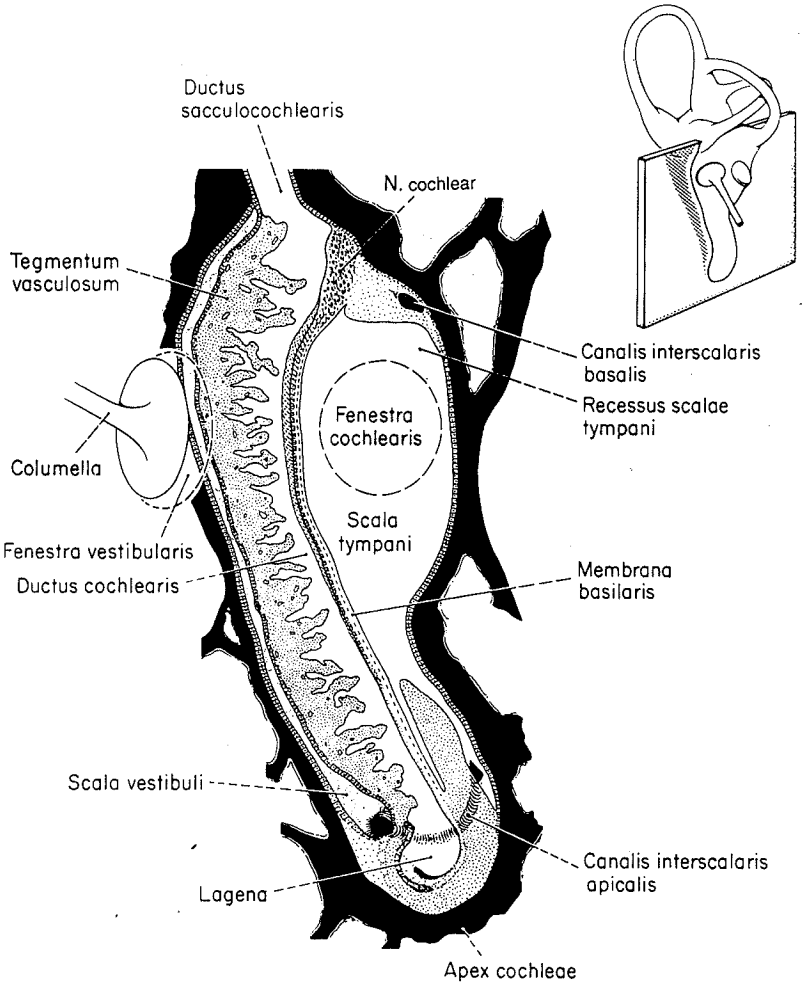

Fig. 16.8. Schematic longitudinal section of the chicken (*Gallus*) cochlea. Inset shows the plane of section. Note that the footplate of the columella covers the vestibular window on the Scala vestibuli (from Evans, 1982). With permission of Academic Press.

APPENDIX A

LATIN GRAMMAR

ANTHONY S. KING

Unlike English, Latin is an inflected language, which means that the form of a word may change and the changes may indicate its relation to other words. The anatomist is only concerned with the inflexions of nouns and adjectives, which are known as declensions. Declensions are based on numbers and cases. There are two numbers, singular and plural, and six cases.

Cases. The Nominative case indicates the *subject;* the Vocative is the case of *address;* the Accusative indicates the *object;* the Genitive indicates *possession;* the Dative names the *receiver* or *indirect object,* the Ablative indicates *from, by, on,* or *in,* and (in anatomy) *with.*

EXAMPLES:

Nominative	Arteria dividit	The artery divides
Vocative	Arteria	O artery!
Accusative	Arteriam seco	I cut the artery
Genitive	Arteriae ramus	The branch of the artery
Dative	Arteriae ligatura additur	A ligature is added to the artery
Ablative	Arteria sanguis fluit	Blood flows from the artery

In anatomy, the nominative and genitive (both singular and plural) are the only cases that are in constant use; the accusative and ablative are used occasionally in association with prepositions (see below, Prepositions); the accusative is used, though even more rarely, without a preposition (e.g., Termini situm et directionem indicantes, means "terms indicating position and direction", and, therefore, situm and directionem are accusative singular); the vocative and dative can for all practical purposes be ignored.

Gender. Nouns and adjectives have grammatical gender, distinguishing masculine (m.), feminine (f.), and neuter (n.). The gender of nouns can often be identified by the nominative singular. If this ends in -a, the gender (of anatomical nouns, e.g., Vena) will nearly always be feminine (among the few exceptions, are Chiasma, Soma, Stoma, Stroma, and Systema, all of which are neuter and of Greek derivation); if a noun ends in -us it will nearly always be masculine, but there are important anatomical exceptions (e.g., Manus is feminine, and Corpus, Glomus, and Viscus are neuter); and if it ends in -um it can be assumed to be neuter.

Nouns. There are five declensions of nouns. The genitive singular distinguishes each declension.

First declension. The nominative singular generally ends in -a, as in many anatomical terms such as Vena. The genitive singular ends in -ae, e.g., Venae. The nominative plural ends in -ae (Venae), and the genitive plural in -arum (Venarum). These nouns are feminine. The classical pronunciation of the diphthong -ae, as in Vertebrae, is *ai* as in aisle (Mountford, 1973) (which is similar to -ie as in pie); English-speaking anatomists generally mispronounce it -ee as in bee.

Second declension. The nominative singular commonly ends in -us, as in many anatomical terms such as Nervus. The genitive singular ends in -i, e.g., Nervi. These nouns are masculine. The nominative singular of some second declension nouns ends in -um (Labium); the genitive singular again ends in -i (Labii). Such nouns are neuter. Forms with the nominative singular ending in -us have the nominative plural ending in -i (Nervi) and genitive plural ending in -orum (Nervorum). Forms such as Labium have a nominative plural ending in -a (Labia) and genitive plural ending in -orum (Labiorum). The classical pronunciation of the ending -i ,as in Nervi, is long -i as in machine (Mountford, 1973); English-speaking anatomists commonly mispronounce it -ie as in pie. Thus the pronunciations of endings in -ae and -i by most English-speaking anatomists have been virtually reversed.

Other second declension nouns have a nominative singular ending in -er (e.g., Puer, a boy). These play no great part in anatomical nomenclature, but reappear in the declension of adjectives (see below). Their genitive singular, nominative plural, and genitive plural endings are the same as those of nouns with the nominative singular ending in -us.

Third declension. The nominative singular ends variously, but the genitive singular always ends in -is. The gender is variable. Among the many examples from anatomy are: Radix, radicis, f. root; Pes, pedis, m. foot; Cor, cordis, n. heart; Caput, capitis, n. head; Vas, vasis, n. vessel; Crus, cruris, n. leg; Mater, matris, f. mother; Nomen, nominis, n. name; Avis, avis, f. bird; Pons, pontis, m. bridge; Rete, retis, n. net.

Masculine and feminine nouns of the third declension have a nominative plural ending in -es (Radices, Pedes, Matres, Aves, Pontes) and genitive plural ending in -um (Radicum, Pedum, Matrum) or -ium (Avium, Pontium). Neuter nouns of the third declension have a nominative plural ending in -a (Corda, Capita, Vasa, Nomina) or -ia (Retia); the genitive plural again ends in -um (Cordum, Capitum, Nominum), or -ium (Retium). Vas is an irregular noun, mainly third declension but partly second declension: its genitive plural (Vasorum, as in Vasa vasorum) is typical of the second declension.

The Greek nouns mentioned above, Chiasma, Soma, Stoma, Stroma, and Systema, fit uneasily into the Latin third declension. The ending of the nominative singular in -a is itself atypical of the third declension. Stroma appears to be the only one of these with any claims to a classical Latin usage, its Greek endings being Latinized during the late Roman era as in the third declension (genitive singular, Stromatis; nominative plural, Stromata; genitive plural, Stromatum). The others, all of them new Latin, are declined similarly.

Fourth declension. The nominative singular ends in -us as in quite numerous anatomical terms such as Manus (f.), Plexus (m.), and Tractus (m.), or -u (e.g., Genu, n.). The genitive singular also ends in -us (Manus, Plexus, Tractus, Genus), but the vowel u is short in the nominative and long in the genitive, i.e., pronounced "oo" as in took in the singular, and "oo" as in shoot in the genitive; in Latin, s is always pronounced "ss" as in mass, not "s" as in was (Mountford, 1973). Fourth declension nouns ending in -us are either masculine or feminine; those ending in -u are neuter. The nominative plural also ends in -us (long u). The genitive plural ends in -uum (Manuum, Plexuum, Tractuum, Genuum) the first -u being long and the second -u being short. Nouns with the nominative singular ending in -us tend to cause difficulty to anatomists who are not familiar with Latin, because they may belong to the second (e.g., Nervus), third (e.g., Crus), or fourth (e.g., Manus) declension. In anatomical terms genitives are often used, and to make the genitive forms of these nouns correctly it is necessary to know to which declension they belong. For example, "a branch of a nerve" is translated into "Ramus nervi" (or nervi ramus, see below, Word Order), but "the skeleton of the crus" is translated into Skeleton cr*uris* and "the bones of the hand" into "Ossa man*us*". Fortunately the problem is easily solved because Latin Dictionaries give both the nominative and the genitive singular cases of nouns.

Fifth declension. The nominative singular ends in -es. The genitive singular ends in -ei. Two examples in anatomical terminology are Facies (genitive singular, faciei), and Ingluvies (Ingluvei). Both of these nouns are feminine. The nominative plural is the same as the nominative singular (Facies, Ingluvies), and the genitive plural ends in -erum (Facierum, Ingluvierum).

Adjectives. Adjectives agree with their nouns in number, case, and gender. There are two groups: adjectives of the first and second declensions, and adjectives of the third declension. Their endings respectively resemble the first two declensions of nouns, and the third declension of nouns.

First and second declensions. Adjectives of the first and second declensions end in -us (m.), -a (f.), -um (n.), or -er, -ra, -rum. In those ending in -us, -a, -um, the masculine is declined like Nervus, the feminine like Vena, and the neuter like Labium. Thus the nominative singular of Internus is Internus, Interna, Internum; hence Ramus internus, Capsula interna, and Labium internum. The genitive singular forms are Rami interni (of the internal ramus), Capsulae internae (of the internal capsule), and Labii interni (of the internal labium). The nominative plurals are Rami interni, Capsulae internae, and Labia interna; the genitive plurals are Ramorum internorum, Capsularum internarum, and Labiorum internorum.

Adjectives of the first and second declension ending in -er, -ra, -rum decline like Dexter (right). The nominative singular is Dexter (m.), Dextra (f.), Dextrum (n.); genitive singular, Dextri, Dextrae, Dextri; nominative plural, Dextri, Dextrae, Dextra; genitive plural, Dextrorum, Dextrarum, Dextrorum. Hence when dexter qualifies a masculine noun such as Ramus, the cases are Ramus dexter (the right branch), Rami dextri (of the right branch), Rami dextri (the right branches), and Ramorum dextrorum (of the right branches). When dexter qualifies a feminine noun, e.g., Crista, the corresponding cases are Crista dextra (the right crest), Cristae dextrae (of the right crest), Cristae dextrae (the right crests), and Cristarum dextrarum (of the right crests). When dexter qualifies the neuter Labium, the same four cases are Labium dextrum, Labii dextri, Labia dextra, and Labiorum dextrorum.

Third declension. Adjectives of the third declension with the nominative singular ending in -is decline like Dorsalis. The nominative singular is Dorsalis (m. and f.), and Dorsale (n.); genitive singular, Dorsalis (m., f., n.); nominative plural, Dorsales (m., f.), Dorsalia (n.); genitive plural, Dorsalium (m., f., n.). Hence Arteria dorsalis (the dorsal artery), and Vas dorsale (the dorsal vessel); Arteriae dorsalis (of the dorsal artery) and Vasis dorsalis (of the dorsal vessel); Arteriae dorsales (the dorsal arteries), Vasa dorsalia (the dorsal vessels); and Arteriarum dorsalium (of the dorsal arteries), Vasorum dorsalium (of the dorsal vessels).

Adjectives of the third declension with the nominative singular ending -or decline like Inferior. The nominative singular is Inferior (m., f.), Inferius (n.); genitive singular, Inferioris (m., f., n.); nominative plural, Inferiores (m., f.), Inferiora (n.); genitive plural, Inferiorum (m., f., n.).

Some adjectives of the third declension have the nominative singular ending in -ens. The present participles of verbs also end in -ens, or in -ans (e.g., afferens, derived from the present participle of the verb adfero, I carry to, i.e., adferens, carrying to; communicans, communicating, derived from communico, I communicate). Several other present participles are commonly used in anatomical Latin, including efferens, recurrens, ascendens, descendens, perforans. Present participles decline like adjectives. The nominative singular forms are afferens and communicans (m., f., n.); genitive singular afferentis and communicantis (m., f., n.); nominative plural afferentes and communicantes (m., f.) and afferentia and communicantia (n.); and genitive plural afferentium and communicantium (m., f., n.).

Prepositions. Only two prepositions are routinely used in anatomical terms, ad (to) and cum (with). Ad takes the accusative case. An example (from the NAV, 1983) is Ramus ad sulcum cranialem (branch to the cranial sulcus). Sulcus is a second declension masculine noun, and Cranialis a third declension adjective (resembling Dorsalis). The accusative singular of such second declension nouns ends in -um (hence Sulcum); the accusative singular of third declension adjectives like dorsalis ends in -em when masculine (hence cranialem) or feminine, and -e when neuter.

Cum takes the ablative. An example from the NAV (1983) is Ramus anastomoticus cum plexu ophthalmico (anastomotic branch with the ophthalmic plexus). The ablative singular of the fourth declension noun Plexus (m.) ends in -u, and the masculine ablative singular of the first and second declension adjective ophthalmicus ends in -o (feminine -a, neuter -o). An example from this edition of the NAA is Connexus cum nervo faciali (connection with the facial nerve). Here the ablative singular of the second declension noun Nervus (m.) ends in -o; the masculine, feminine, and neuter ablative singular cases of the third declension adjective Facialis end in -i.

Word order and formation of new terms. Fortunately for anatomists Latin is not strict about the order in which words are combined. For example "a branch of a nerve" can be translated into ramus nervi or nervi ramus. In anatomical Latin, however, the nominative noun always goes first, e.g., Venae cordis (the veins of the heart).

Before devising a composite term consisting of several nouns and adjectives, the anatomist should decide what he is trying to say in his own vernacular. Suppose he wants to say "greater curvature of the stomach". Clearly the adjective "greater" qualifies "curvature", not "stomach". Therefore the number, case, and gender of major (greater) must agree with Curvatura (singular, nominative, feminine), hence Curvatura major; "of the stomach" requires the genitive singular of (second declension, masculine) Ventriculus,

i.e., Ventriculi. These three terms can be written as in English, i.e., Major curvatura ventriculi, but in Latin the adjective is often placed after its noun. This is the rule in anatomical Latin, and indeed the first word in an anatomical term seems never to be an adjective; therefore, Curvatura major ventriculi would be acceptable. An alternative is to put the genitive noun in the middle instead of at the end, i.e., Curvatura ventriculi major, which is the form adopted by the NAV (1983) for this particular term; this may be stylistically better, since it resembles the word order in classical Greek, which influences classical Latin. However, the NAV and NH use both of these forms. For example, the NAV has Tunica mucosa oris in which the genitive noun is at the end, as it is in Tunica interna bulbi of the NH (1989). On the other hand, the NH also has Organa oculi accessoria, in which the genitive noun is in the middle. Where a term contains two nouns, one nominative and the other genitive and each of them is qualified by an adjective, the genitive noun followed by its genitive adjective can go at the end; an example is Crus rostrale capsulae internae (the rostral crus of the internal capsule) as in the NAV (1983).

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