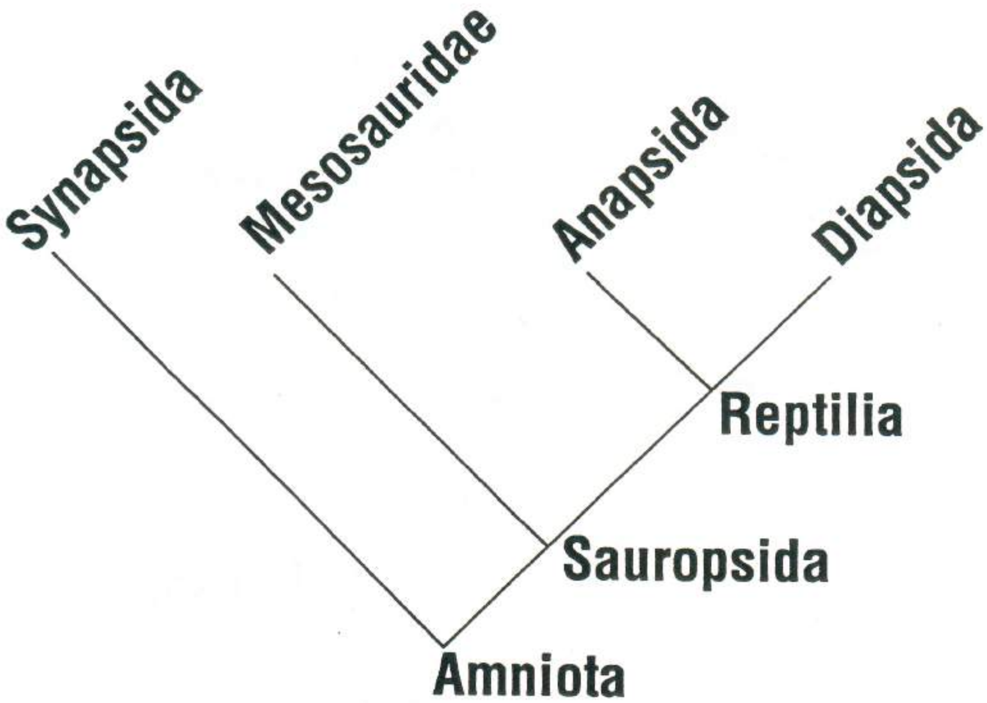
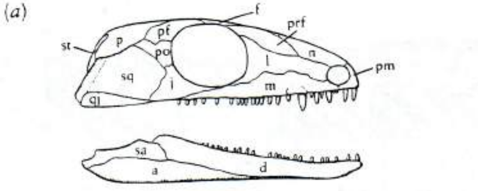
Pelycosauria y Therapsida

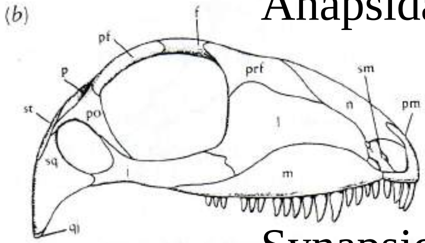
Los amniotos pueden dividirse en dos líneas principales: Los synapsidos (de quienes provienen los mamíferos) y los Sauropsidos (de quienes provienen “reptiles” y aves).

Los **Synápsidos** poseen una apertura (fenestra) en el cráneo, detrás del ojo, debajo de la unión entre los huesos postorbital y escamoso. Comparten un ancestro en común más reciente con un mamífero que con una lagartija. Filogenéticamente, no pertenecen a reptilia, pero a la mayoría se les conoce como “reptiles semejantes a mamíferos”

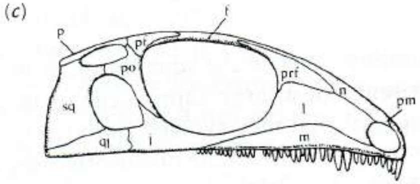




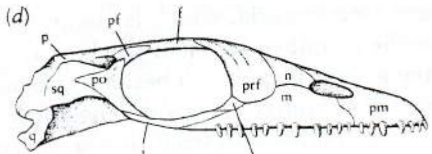
Anapsida



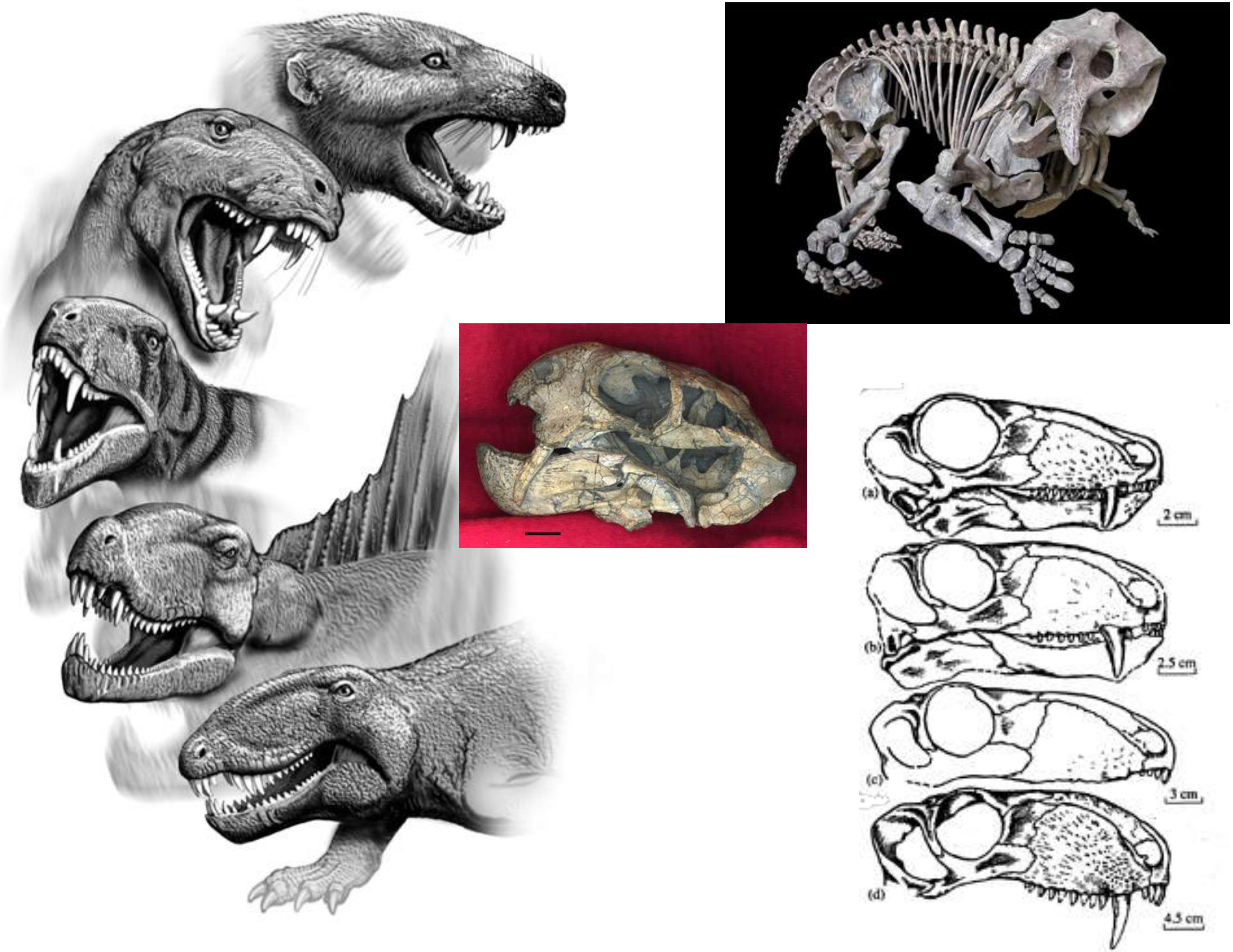
Synapsida



Diapsida



“Parapsida” o “Euryapsida”
(Diapsida modificados)


(a)
2 cm
(b)
2.5 cm
(c)
3 cm
(d)
4.5 cm

SYNAPSIDA:

-COMPARTEN UN ACMR CON MAMÍFEROS QUE CON REPTILES

-FENESTRA TEMPORAL, BAJO POSTORBITAL-ESCAMOSO

-REGION OCCIPITAL POSTERIORMENTE INCLINADA (NO VERTICAL)

-SUPRATEMPORAL SE CONECTA AL POSTORBITAL

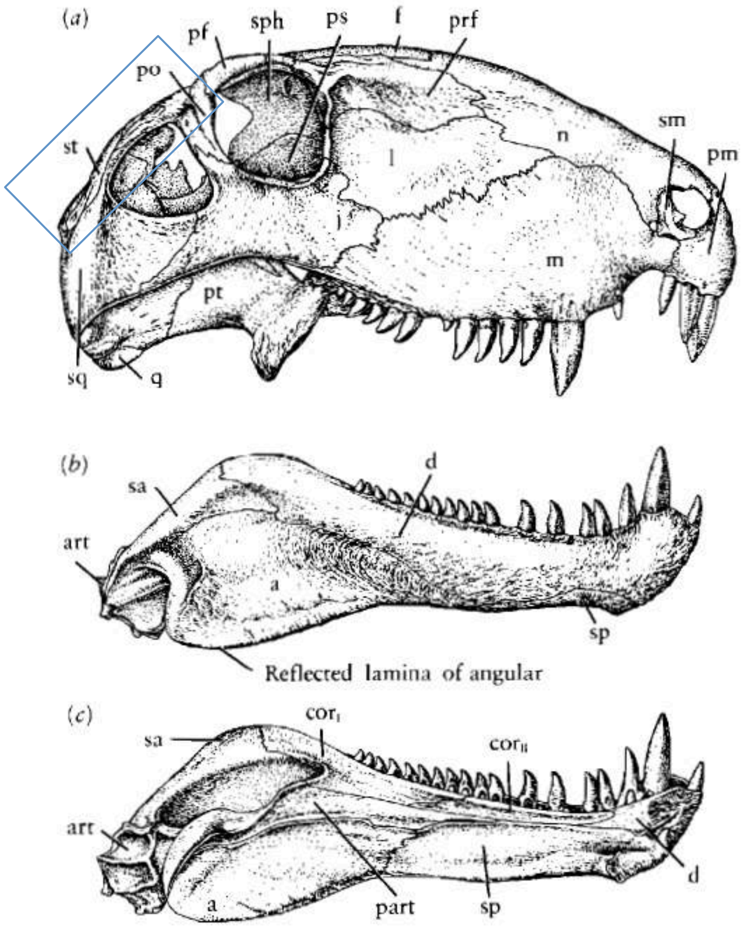
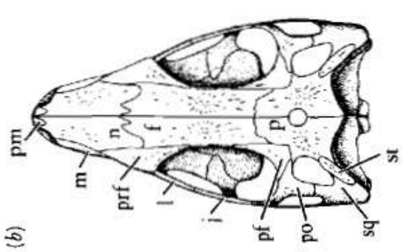
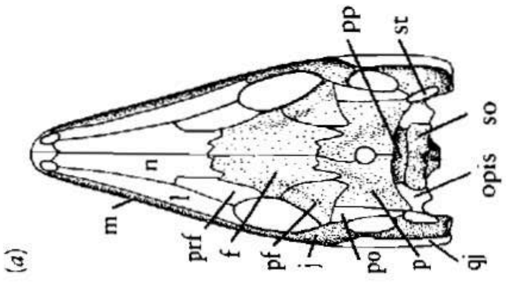


Figure 17-6. (*a*) Skull of *Dimetrodon*, in lateral view. (*b*) Lateral and (*c*) medial views of the lower jaw, ×¼. Abbreviations as in Figure 8-3. *From Romer and Price, 1940.*

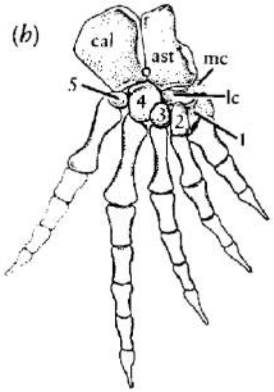
-PRESENCIA DE DOS HUESOS CORONOIDES (LADO MEDIAL MANDÍBULA)



PETROLACOSAURUS

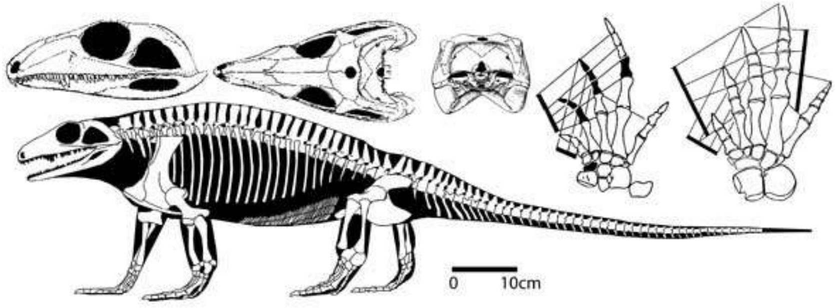


ARCHAEOTHYRIS (synapsida)

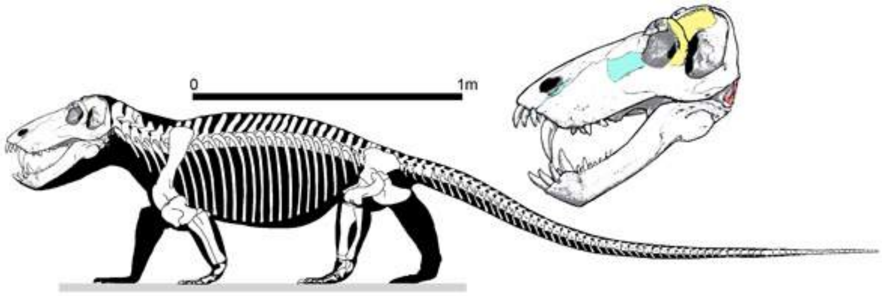


-CENTRALE MEDIAL (MC) BIEN DESARROLLADO EN EL TARSO

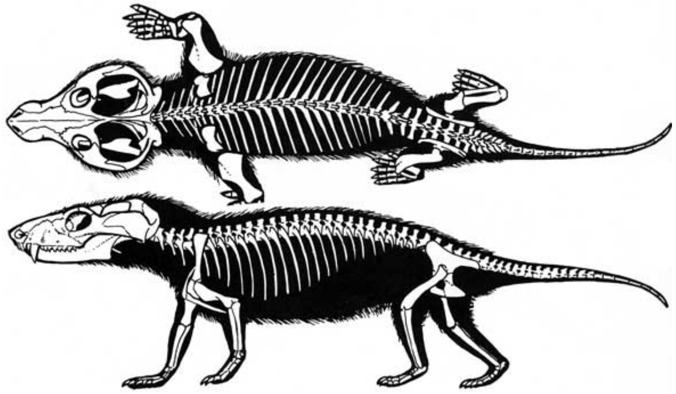
Tradicionalmente se discuten cuatro “tipos fundamnetales” de synapsidos, que en efecto son grupos sucesivamente sucesivamente anidados



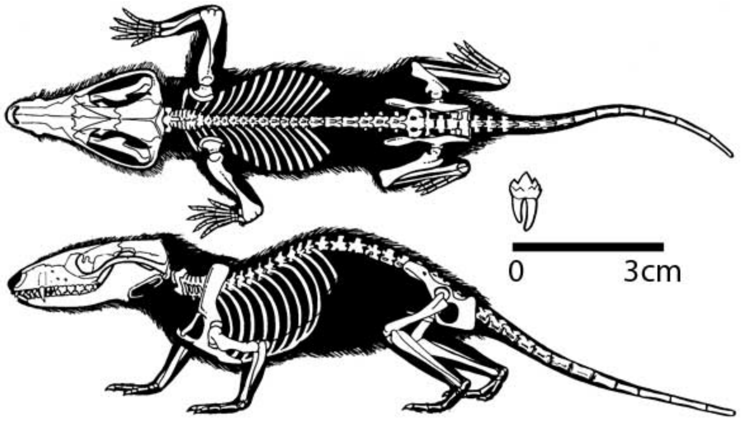
“Pelycosaurios” (parafilético, se usa para hablar de synapsidos basales) Carbonífero Superior-Pérmico. Muy “reptilianos” aún



Terápsidos. Pérmico-Triásico
Modificaciones craneales y posturales importantes



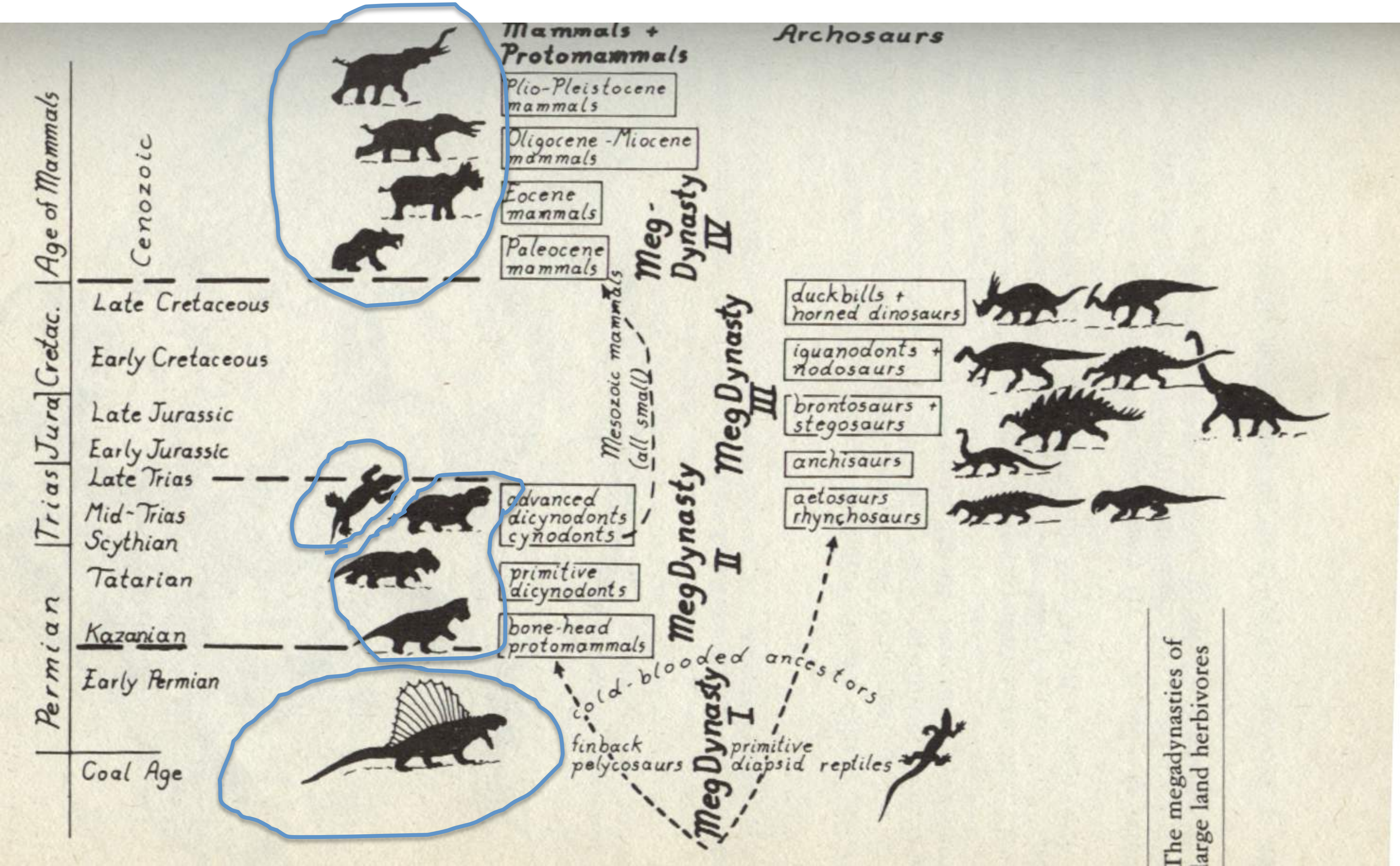
Cynodontes. Pérmico superior, Triásico
Muy similares a mamíferos



Mamíferos. Triásico
Oído interno tres huesos

Dinastías synapsidas

Meg Dynasty 1: Pelicosaurios del Pérmico inferior
Meg Dynasty 2: Terápsidos del Pérmico superior-Triásico inferior
Meg Dynasty 3: Mamíferos del Cenozoico



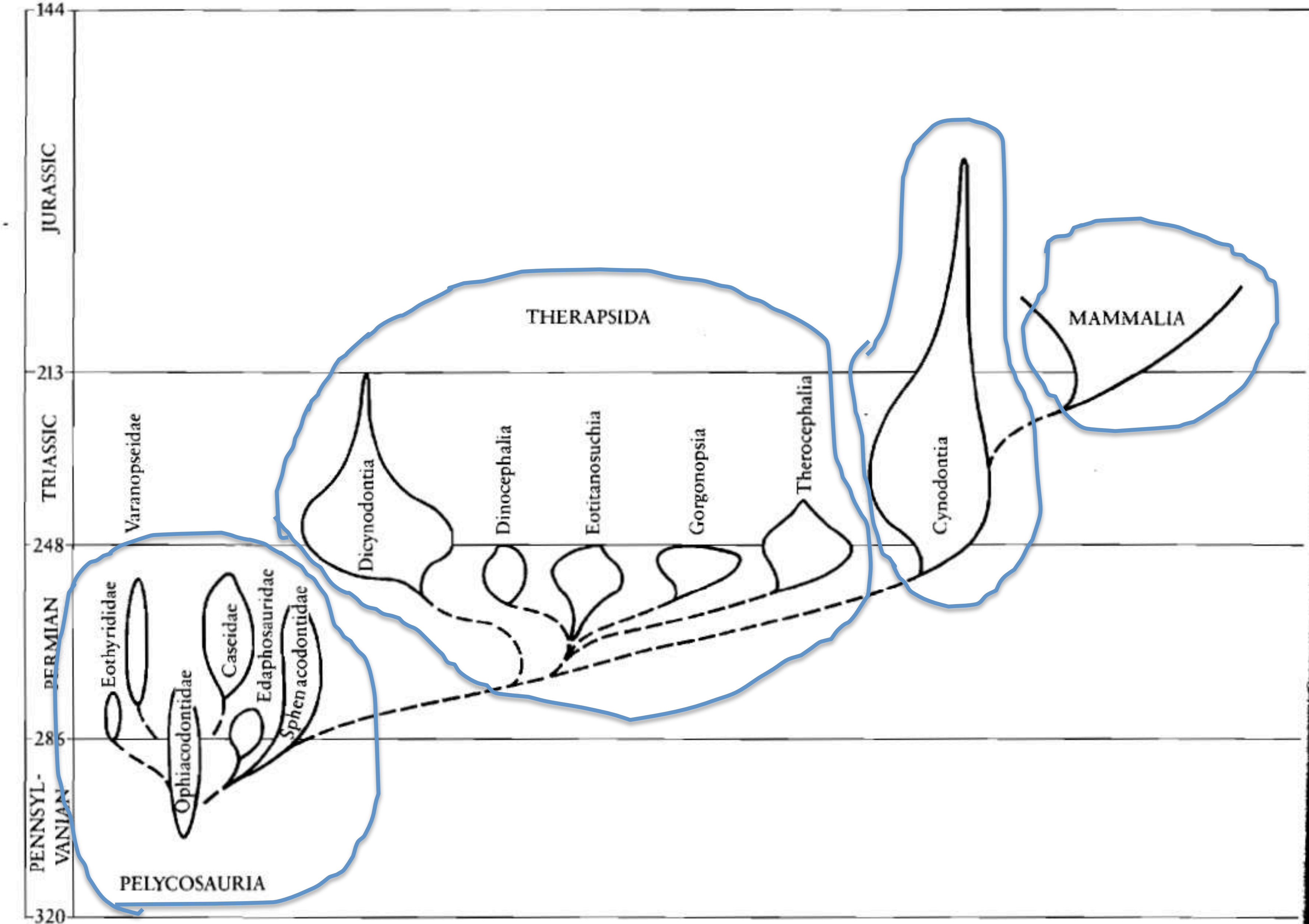


Figure 17-1. STRATIGRAPHIC RANGES OF THE MAJOR GROUPS OF MAMMAL-LIKE REPTILES.

Los primeros synápsidos (basales) se conocen colectivamente como un grupo “parafilético”, los Pelycosaurios (P en la figura) que excluyen a sus descendientes Terápsidos. Los pelycosaurios presentan abundantes dientes en el paladar.

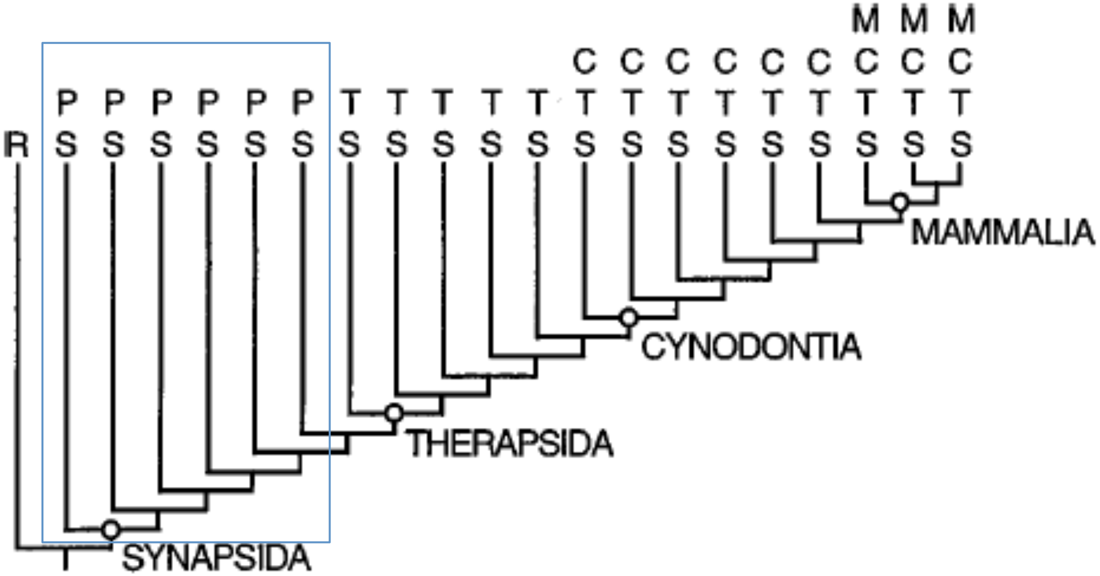
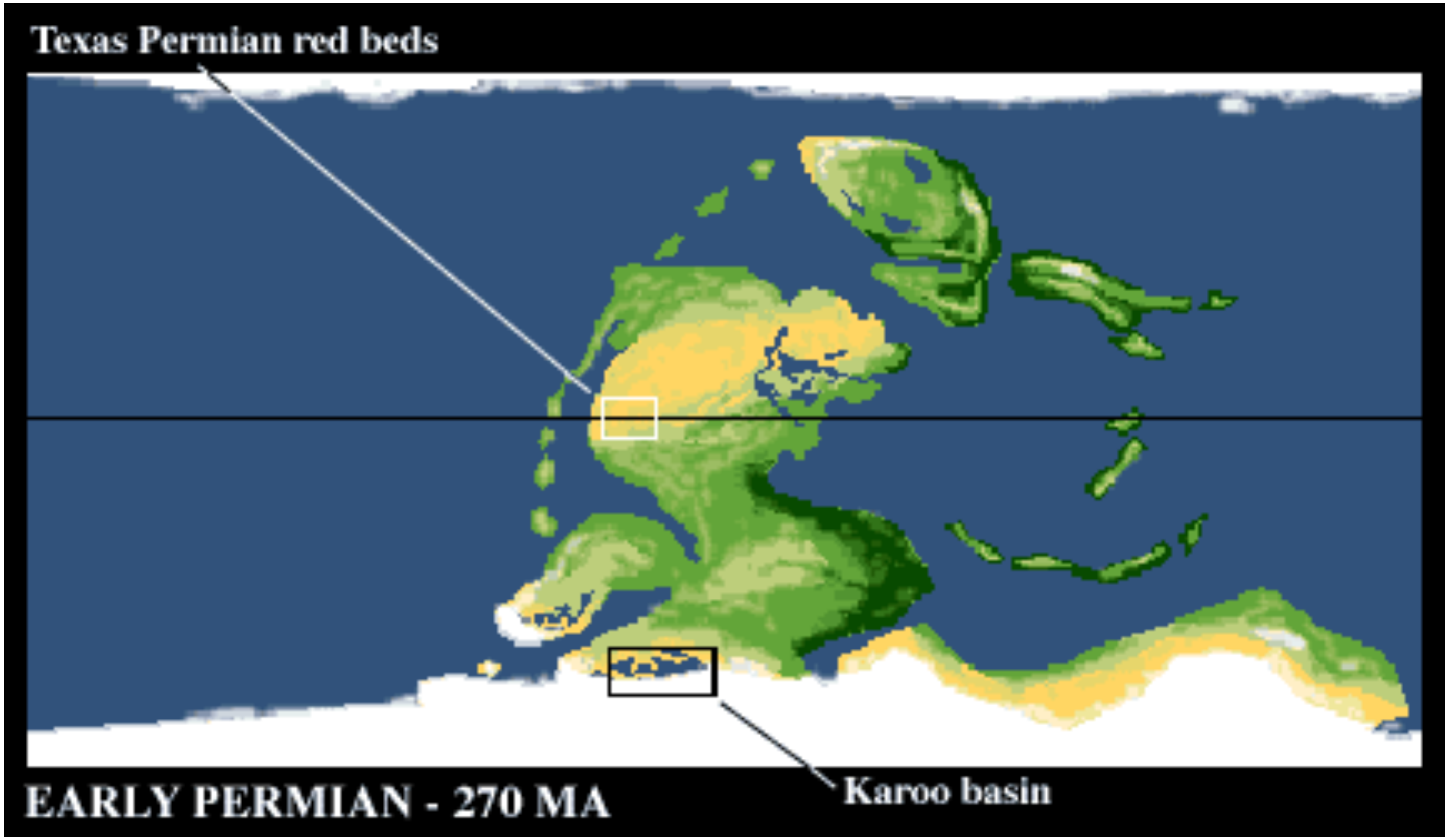
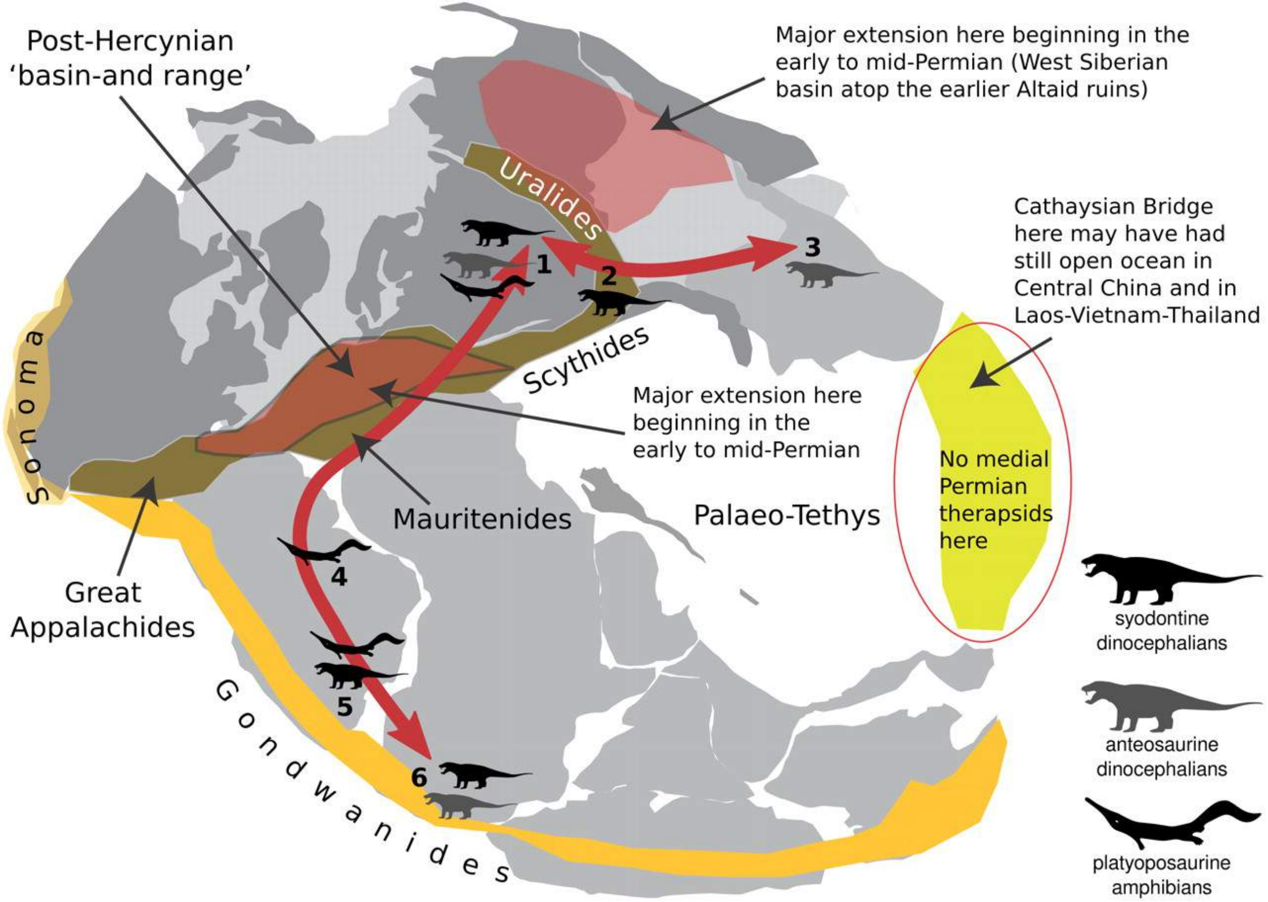


Figure 1 Diagrammatic representation of the cladistic terminology used in this paper. Synapsida (S) includes all fossil and Recent taxa that are more closely related to living mammals (M) than they are to living reptiles (R). Major synapsid subclades include Therapsida (T) and Cynodontia (C), both of which include mammals as their extant representatives. Synapsids that are not therapsids (i.e., nontherapsid synapsids) are a paraphyletic group traditionally termed “pelycosaurs” (P). Because fossil synapsids show a blend of mammalian and reptilian characteristics, the latter actually being retentions of the primitive amniote condition, the term “mammal-like reptile” was often employed. In phylogenetic phraseology, the term mammal-like reptiles corresponds to nonmammalian synapsids. Features diagnosing the clades Synapsida, Therapsida, and Cynodontia are discussed in the text.


Texas Permian red beds
EARLY PERMIAN - 270 MA
Karoo basin

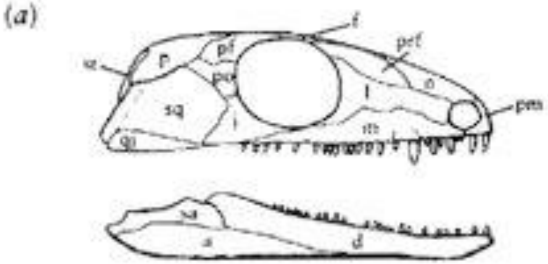


Reconstruction of Pangaea showing anteosaurid dinocephalians and platyoposaurid temnospondyles during the Middle Permian. Probable dispersal routes are indicated by red arrows. 1, Russian Platform; 2, southern fore-Urals, Kazakhstan; 3, Ordos Basin, China; 4, Parnaíba Basin, Brazil; 5, Paraná Basin, Brazil; 6, Karoo Basin, South Africa. The map is considerably modified from ref. 48 after new geological data

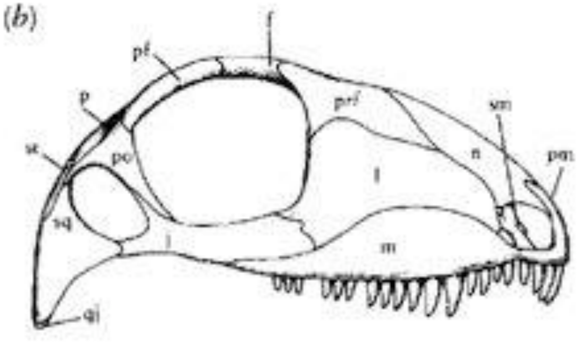
- Caninos acentuados
- Dientes grandes
- Alargamiento procesos tranversos: Mayor musculatura axial. Menos ondulación lateral?
- Tres osificaciones de escapula-coracoides, hasta estadios tardíos

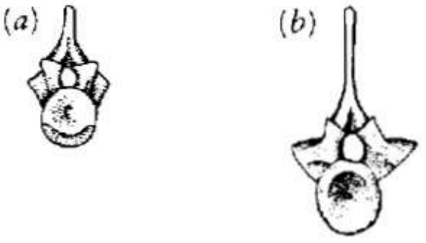
mammals, the elaboration of axial musculature above and below the transverse processes helps limit lateral undulation of the trunk and support the vertebral column as an arch above the girdles. Lateral undulation of the column remained an important attribute of locomotion in most synapsids, but the elongation of the transverse processes may indicate more active support of the column on the girdles than was the case in other early amniotes. The

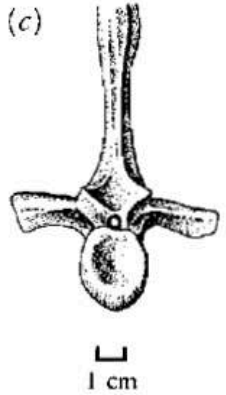
(*a*)

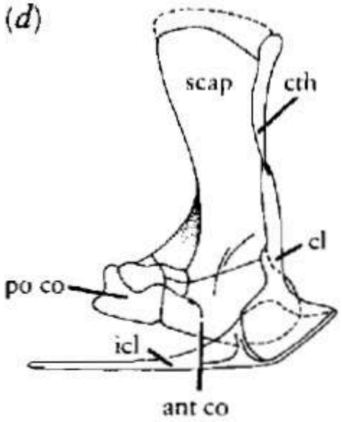


(*b*)





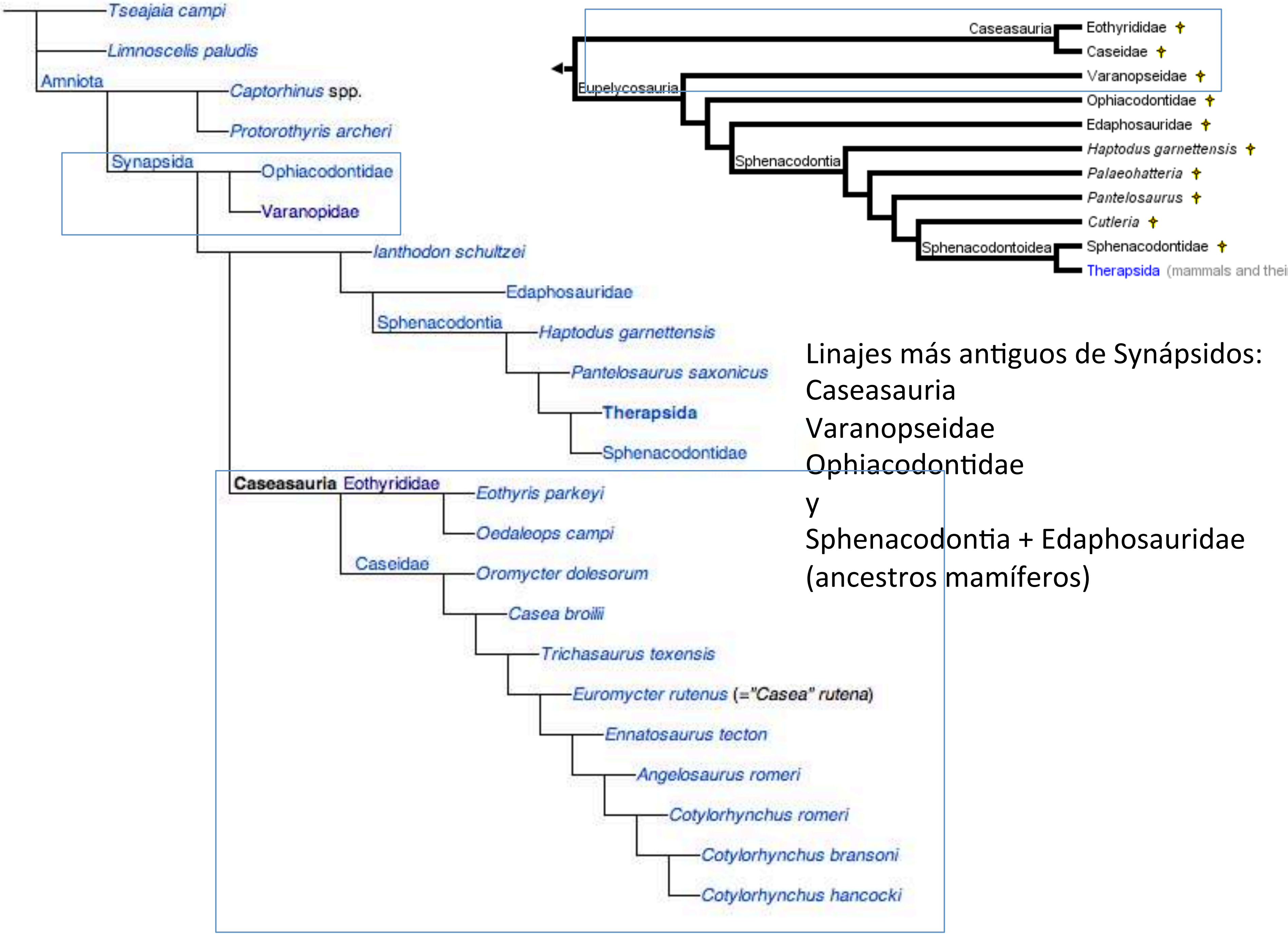




In pelycosaurs, we can identify three centers of ossification in the scapulocoracoid: an anterior and a posterior coracoid as well as the scapula (Figure 17-4*d*). In adult protorothyrids, the scapulocoracoid is ossified without a trace of subdivision, but there are three distinct elements in young individuals of several Pennsylvanian genera. Coossification appears to be progressively delayed in pelycosaurs so that sutures are evident between the elements in more mature specimens.

Primitive pelycosaurs have two pairs of sacral ribs, and the blade of the ilium is narrow and directed posteriorly. Several advanced pelycosaur groups have one or two additional pairs of sacral ribs and a broad iliac blade to support their greater body size.

The configuration of the articulating surfaces of the girdles and limbs of all pelycosaurs indicate a sprawling posture like that of the most primitive tetrapods, which were discussed in Chapter 9.



Linajes más antiguos de Synápsidos:
Caseasauria
Varanopseidae
Ophiacodontidae
y
Sphenacodontia + Edaphosauridae
(ancestros mamíferos)

Uno de los linajes más antiguos de pelicosaurios son los Caseasauria, de cabeza corta y ancha. Se dividen en los carnívoros Eothyridae y los herbívoros Caseidae. Los Eothyridae sólo se conocen por los cráneos de *Eothyris* y *Oedalops*. Se hace evidente un rasgo ancestral de los synápsidos, la diferenciación de caninos de gran tamaño.

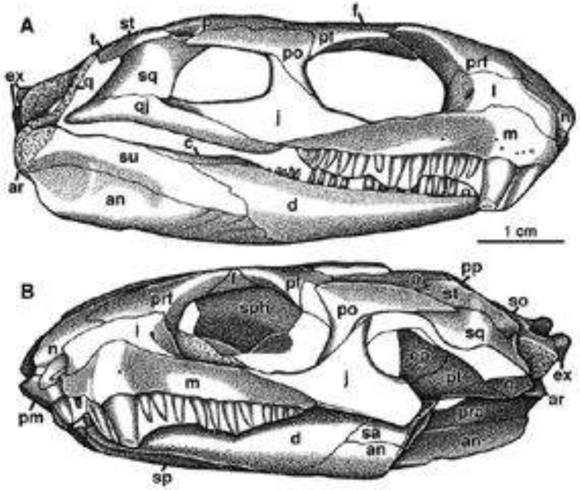


FIGURE 2. Specimen drawings of *Eothyris parkeyi* Romer, MCZ 1161 in (**A**) right lateral, and (**B**) left lateral views, respectively. For anatomical abbreviations see Figure 1.

Caseasauria: Maxila por borde ventral del ojo

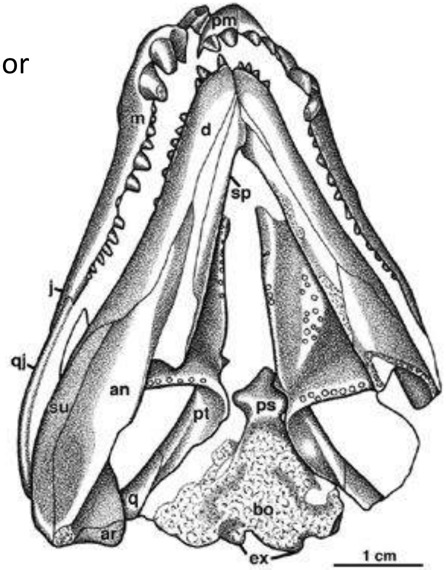


FIGURE 3. Specimen drawing of *Eothyris parkeyi* Romer, MCZ 1161 in palatal view. For anatomical abbreviations see Figure 1.

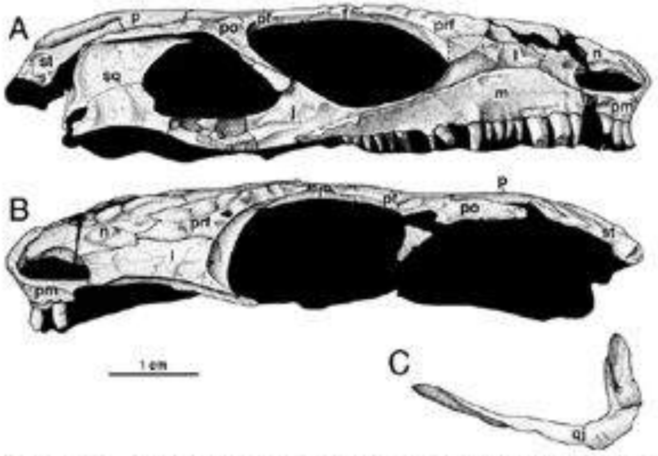


FIGURE 6. Specimen drawings of *Oedaleops campi* Langston, UCMP 35758, in (**A**) right lateral, and (**B**) left lateral views, respectively. **C**, the quadratojugal bone, which was attached to the ventral side of the skull. For anatomical abbreviations see Figure 1.

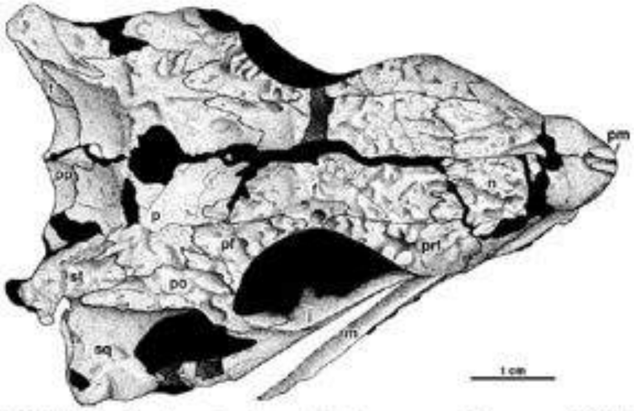
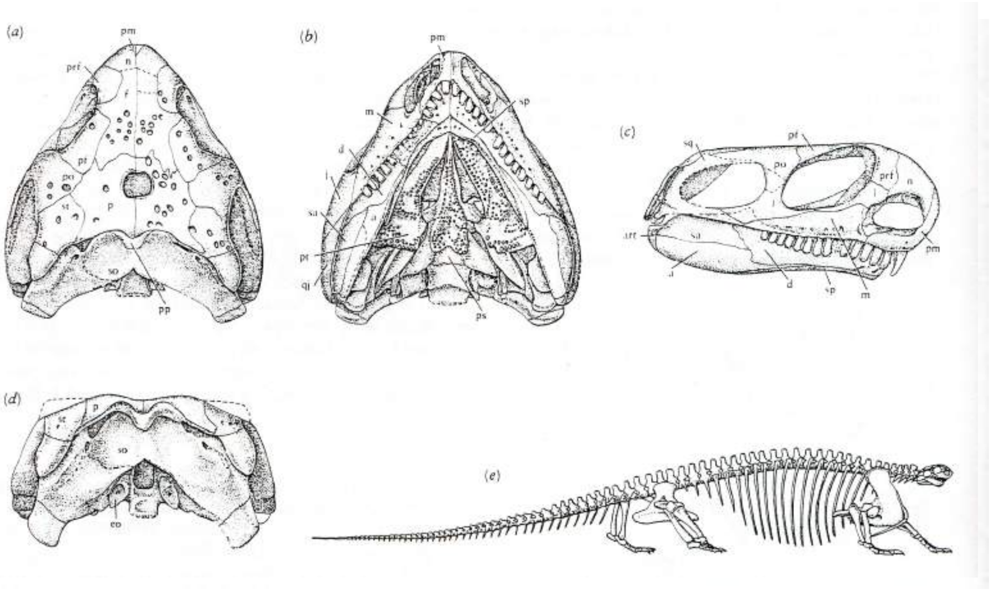
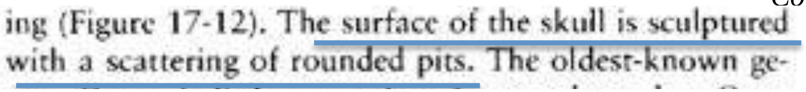


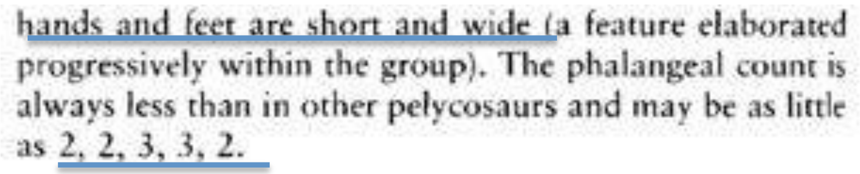
FIGURE 7. Specimen drawing of *Oedaleops campi* Langston, UCMP 35758, in dorsal view. For anatomical abbreviations see Figure 1.

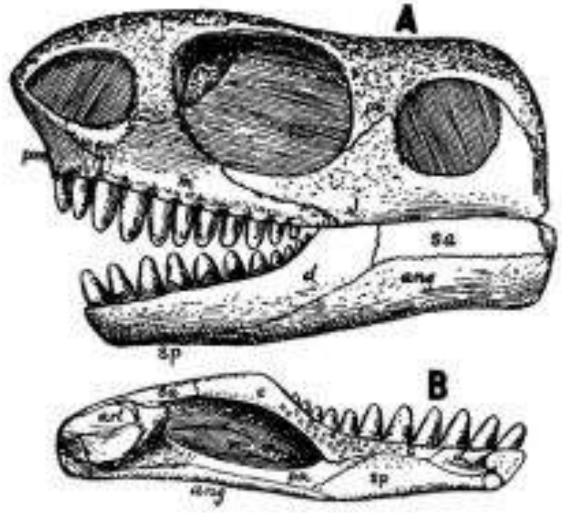
Caseidae



Cotylorhynchus


ing (Figure 17-12). The surface of the skull is sculptured with a scattering of rounded pits. The oldest-known ge-

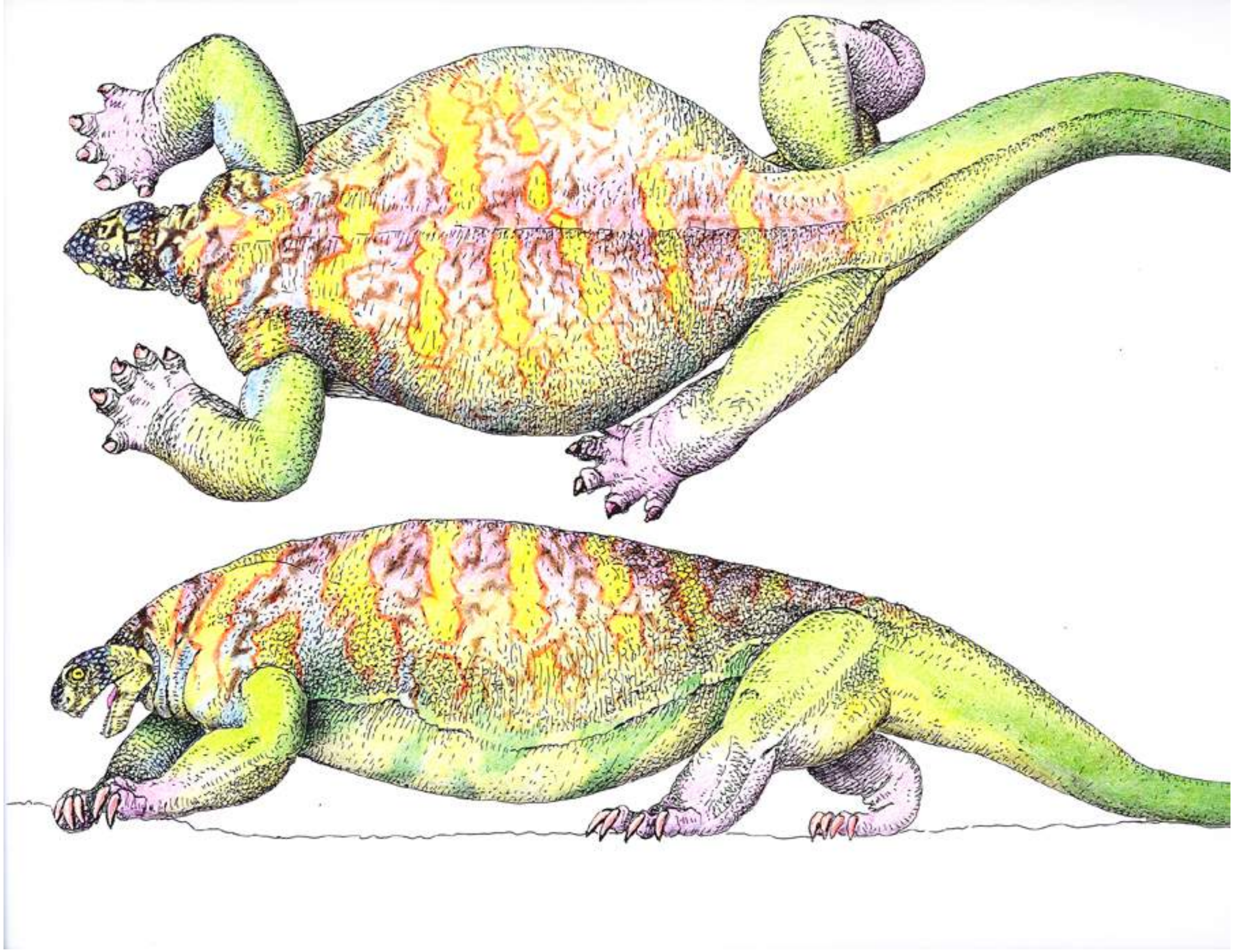

hands and feet are short and wide (a feature elaborated progressively within the group). The phalangeal count is always less than in other pelycosaurs and may be as little as 2, 2, 3, 3, 2.



Casea

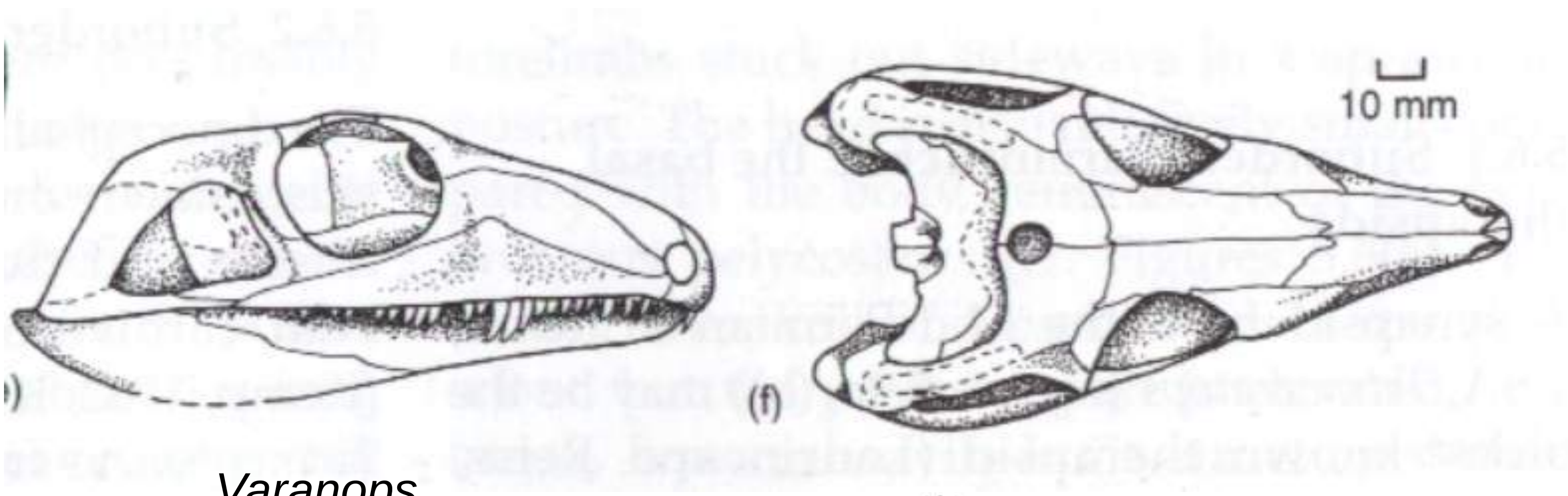
Los Caseidae se caracterizan por sus **diminutas cabezas** y **anchos cuerpos** asociados al tracto digestivo de un herbívoro. **Extensión anterior del cráneo más allá de los dientes. Pérdida de los caninos.**

Hay placa de dientes sobre el paladar pero ausentes en las mandíbulas

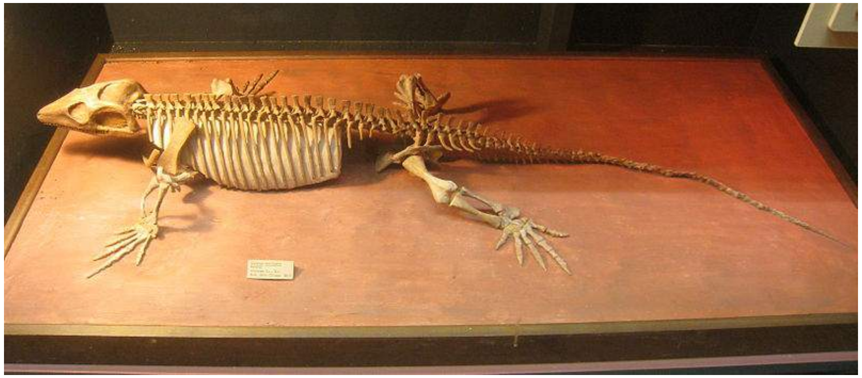


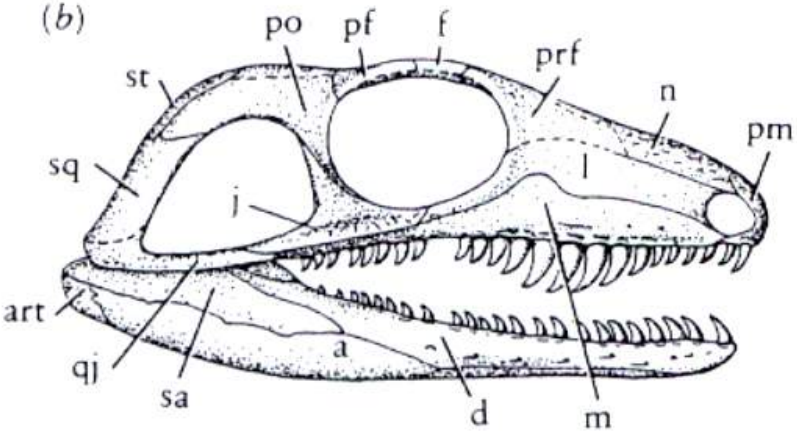
Caseidae;
Cotylorhynchus

Otros de los linajes más antiguos de pelicosaurios son los Ophiacodontidae y los Varanopidae. Los Varanopidae presentan cráneo más alargado, esqueleto más ligero y extremidades más largas y ágiles. Es otro caso de convergencia hacia el nicho de las lagartijas actuales**. La dentición se extiende más hacia posterior, hasta debajo de la fenestra temporal.**



Varanops





Aerosaurus

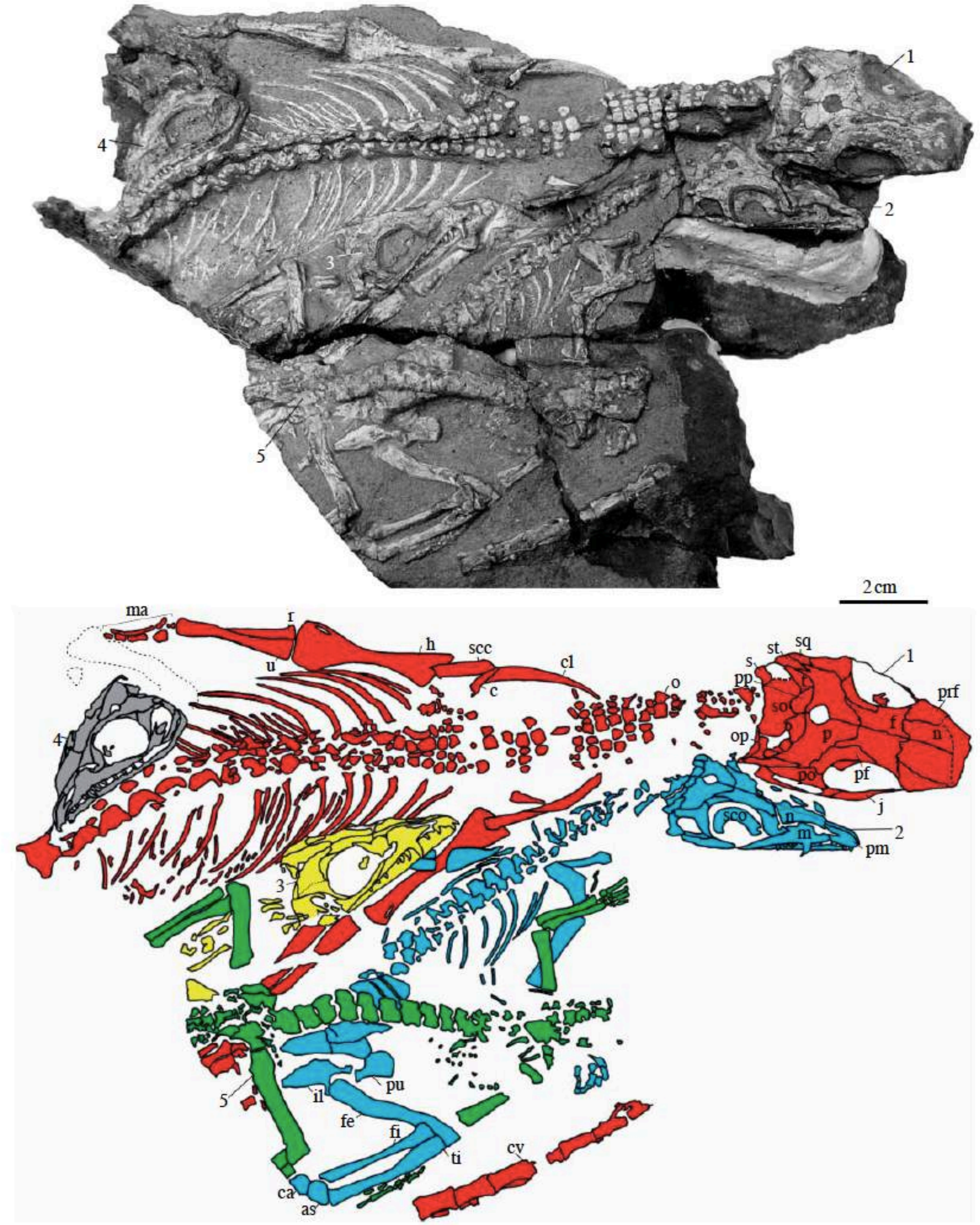


Figure 1. The varanopid specimen SAM-PK-K8305. Numerals indicate individuals: leader lines point to the skulls of individuals 1–4, whereas that for individual 5 points to its hip region because the anterior half of its skeleton, including the skull, is missing. as, astragulus; c, cleithrum; ca, calcaneum; cl, clavicle; cv, caudal vertebra; f, frontal; fe, femur; fi, fibula; h, humerus; il, ilium; j, jugal; m, maxilla; ma, manus; n, nasal; o, osteoderm; op, opisthotic; p, parietal; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; pu, pubis; r, radius; s, stapes; scc, scapulocoracoid; sco, scleral ossicles; so, supraoccipital; sq, squamosal; st, supratemporal; ti, tibia; u, ulna.

Familia de Varanopidos

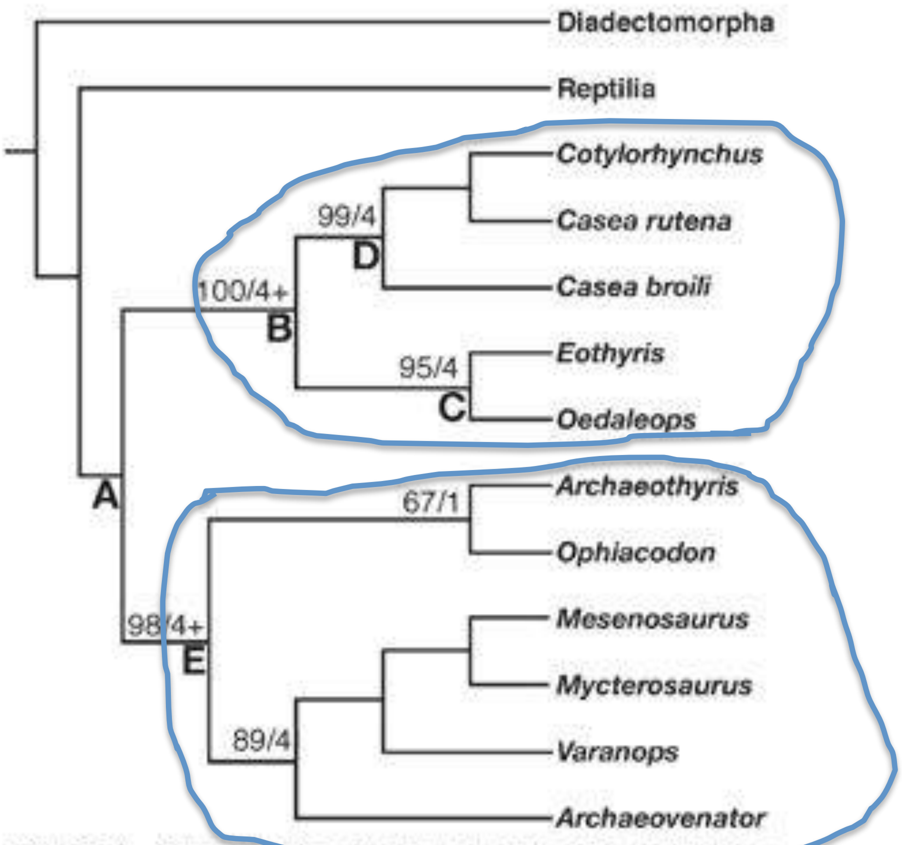


FIGURE 9. Synapsid phylogeny. The monophyly of the Eothyrididae was tested by submitting a data matrix of 13 taxa and 69 morphological characters (Appendix 1) to a phylogenetic analysis using parsimony (PAUP*, Version 4.0b10). The morphological characters were polarized in 13 taxa according to the outgroup criterion. Reptilia and Diadectomorpha have been chosen as outgroups. All characters have the same weight, and all multistate characters were unordered. Tree length 140 steps, CI 0.701, HI 0.3429, RI 0.8093, RC 0.5723. The numbers at selected nodes indicate bootstrap values and decay indices, respectively. Major Nodes: A, Synapsida; B, Caseasauria; C, Eothyrididae; D, Caseidae; E, Eupelycosauria.

Hay una divergencia temprana de dos principales linajes de synápsidos:

Los Caseasauria

Los **Eupelycosauria**

Los Ophiacodontidae son los primeros Macrodepredadores:

- mayor tamaño corporal
- mayor tamaño del cráneo
- caninos acentuados
- dientes grandes
- región postorbital mas corta y alta: mordida más grande y rápida (pero menos fuerte)
  Hocico largo, angosto: “meatcleaving face”

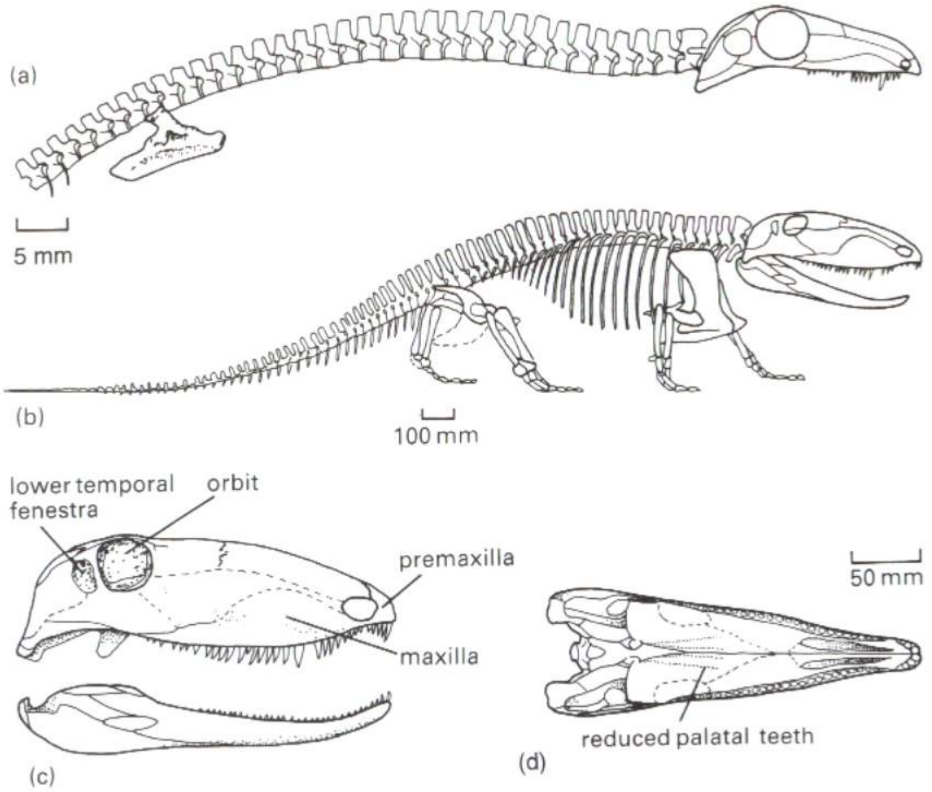
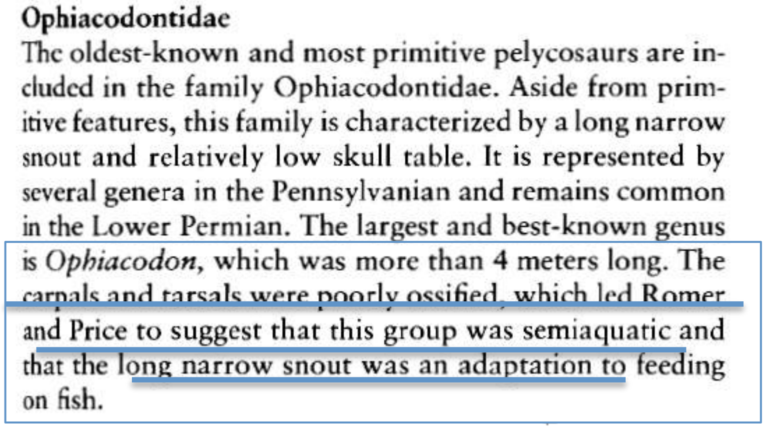


Fig. 5.5 The ophiacodonts (a) *Archaeothyris* and (b–d) *Ophiacodon*: (a) partial skull and skeleton in lateral view; (b) skeleton; (c, d) skull in lateral and ventral views. (Modified from Romer and Price, 1940 and Reisz, 1986.)

Los Ophiacodontidae incluye los representantes más antiguos conocidos de los Synapsida, el género *Archaeothyris* del carbonífero tardío.
Se ha hipotetizado una dieta de peces y tetrapodos en vez de insectos.



Ophiacodontidae

The oldest-known and most primitive pelycosaurs are included in the family Ophiacodontidae. Aside from primitive features, this family is characterized by a long narrow snout and relatively low skull table. It is represented by several genera in the Pennsylvanian and remains common in the Lower Permian. The largest and best-known genus is *Ophiacodon*, which was more than 4 meters long. The carpals and tarsals were poorly ossified, which led Romer and Price to suggest that this group was semiaquatic and that the long narrow snout was an adaptation to feeding on fish.

Acuáticos?

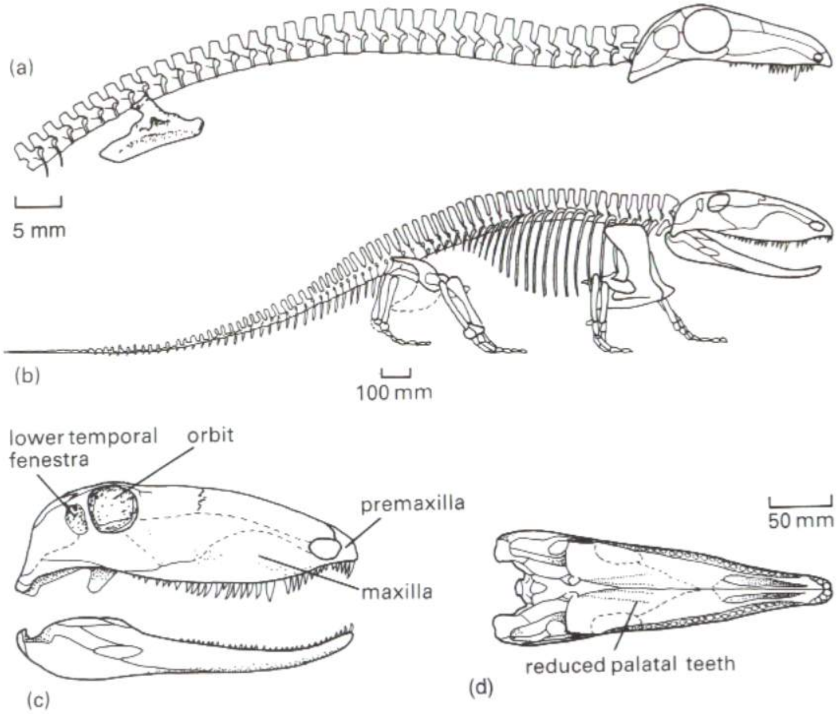
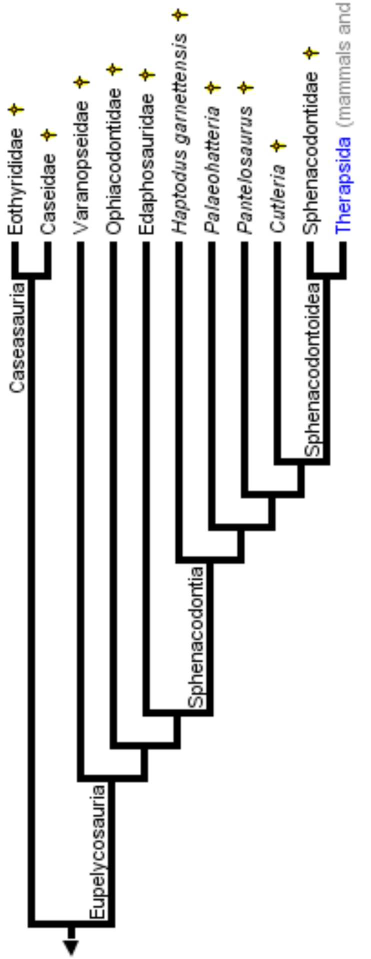
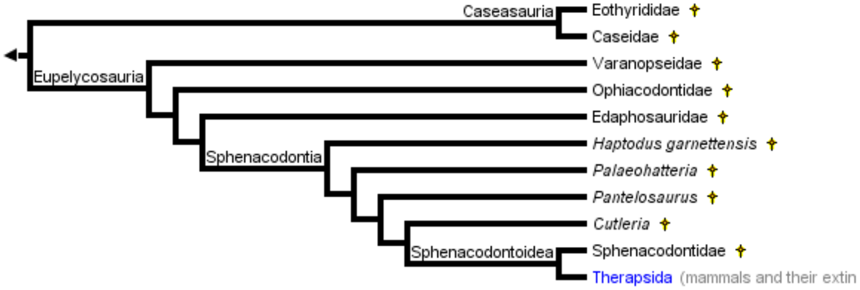


Fig. 5.5 The ophiacodonts (a) *Archaeothyris* and (b–d) *Ophiacodon*: (a) partial skull and skeleton in lateral view; (b) skeleton; (c, d) skull in lateral and ventral views. (Modified from Romer and Price, 1940 and Reisz, 1986.)

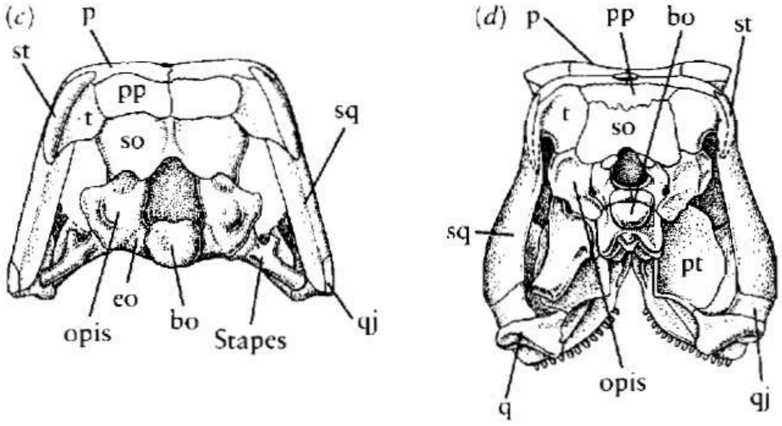




Hay menor integración de huesos en la región occipital en Eupelycosaurios tempranos.

Los demás pelycosaurios (edaphosauria + sphenacodontia) integran los huesos en una estructura de placa que incopora al supraoccipital, procesos paraoccipitales anchos, y los huesos dérmicos del borde del cráneo.

Hyomandilbular es grande en todos.



Paleothyris *Ophiacodon*

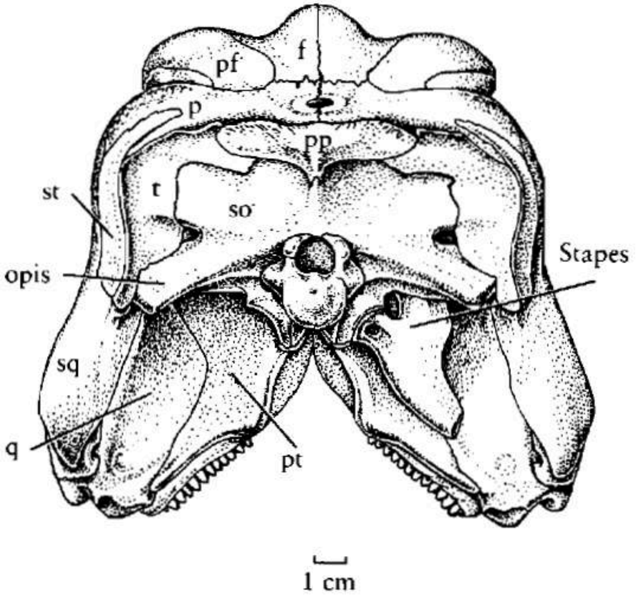


Figure 17-3. OCCIPUT OF THE LOWER PERMIAN PELYCOSAUR *DIMETRODON*. This genus shows the platelike nature of the supraoccipital, which is fused to the opisthotic and suturally attached to the tabular. The stapes is a massive element. Abbreviations as in Figure 8-3. *From Romer and Price, 1940.*

Edaphosauridae

Edaphosauridae. Herbívoros de cráneo corto y pequeño, pero con dentición muy diferente a Caseidae: Placas de dientes en las mandíbulas, abundante dentición palatal.

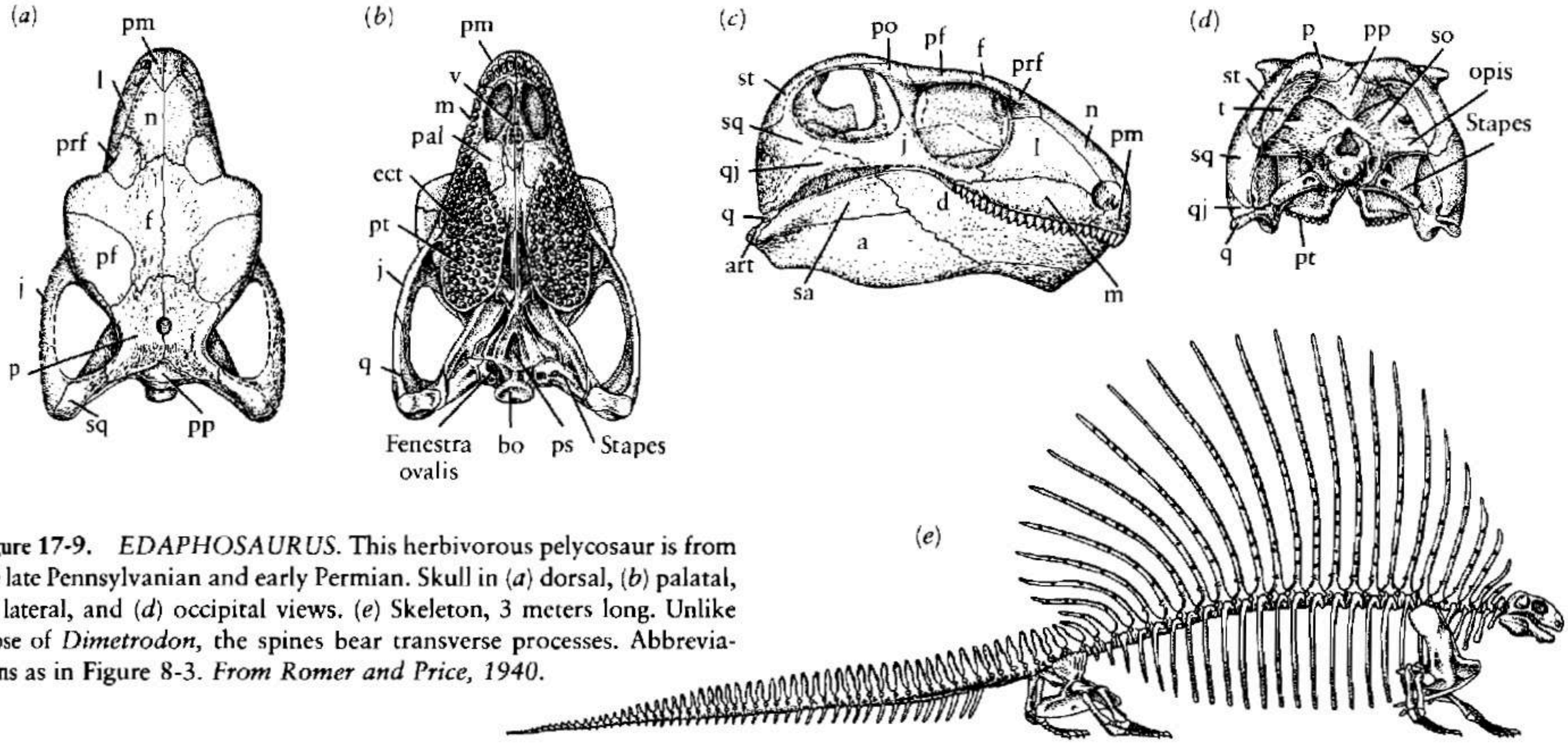
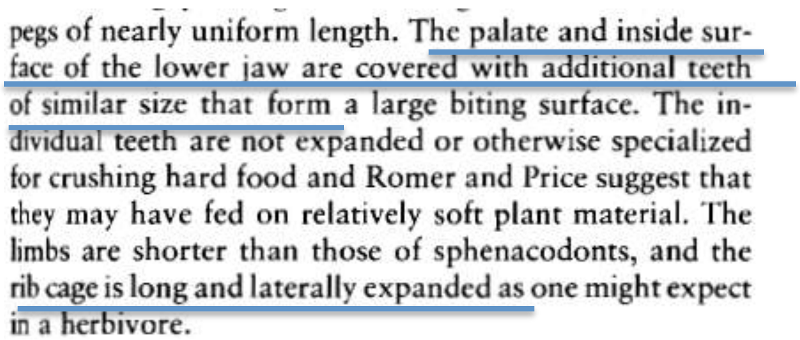


Figure 17-9. *EDAPHOSAURUS*. This herbivorous pelycosaur is from the late Pennsylvanian and early Permian. Skull in (*a*) dorsal, (*b*) palatal, (*c*) lateral, and (*d*) occipital views. (*e*) Skeleton, 3 meters long. Unlike those of *Dimetrodon*, the spines bear transverse processes. Abbreviations as in Figure 8-3. *From Romer and Price, 1940.*



pegs of nearly uniform length. The palate and inside surface of the lower jaw are covered with additional teeth of similar size that form a large biting surface. The individual teeth are not expanded or otherwise specialized for crushing hard food and Romer and Price suggest that they may have fed on relatively soft plant material. The limbs are shorter than those of sphenacodonts, and the rib cage is long and laterally expanded as one might expect in a herbivore.

Los Edaphosauridae presentan el desarrollo de una vela probablemente involucrada en termorregulación. **Cada espina neural posee además proyecciones “ornamentales” hacia los lados.** Los Edaphosauridae son predominantemente herbívoros, con dientes romos, mandíbulas profundas en las que la articulación de la mandíbula se encuentra por debajo de la línea de los dientes. *Ianthosaurus* es un Edaphosaridae basal del carbonífero que presenta una vela con proyecciones, **pero retiene la dentición carnívora ancestral.**

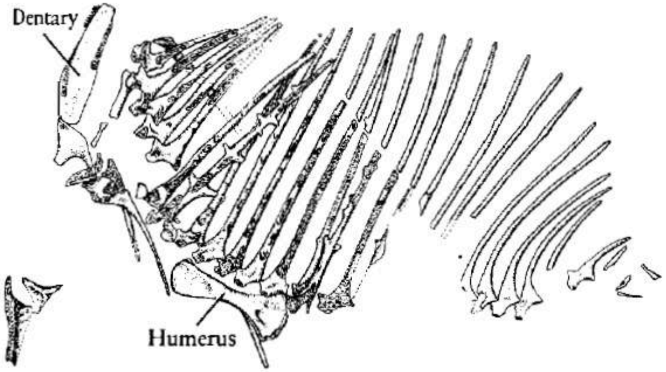


Figure 17-10. INCOMPLETE SKELETON OF *IANTHOSAURUS*, × ⅓. This primitive edaphosaur is from the Upper Pennsylvanian. The dentition resembles that of early carnivorous pelycosaurs. *From Reisz and Berman, 1986.*

SPHENACODONTIA

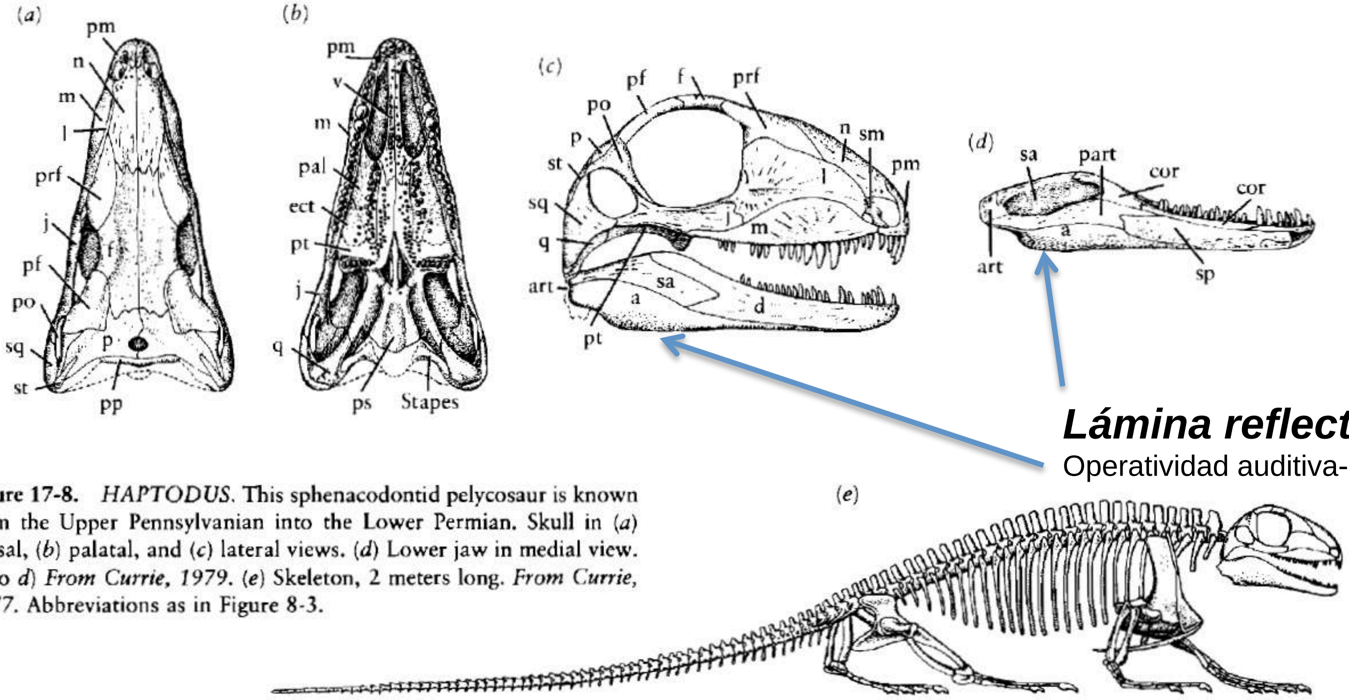
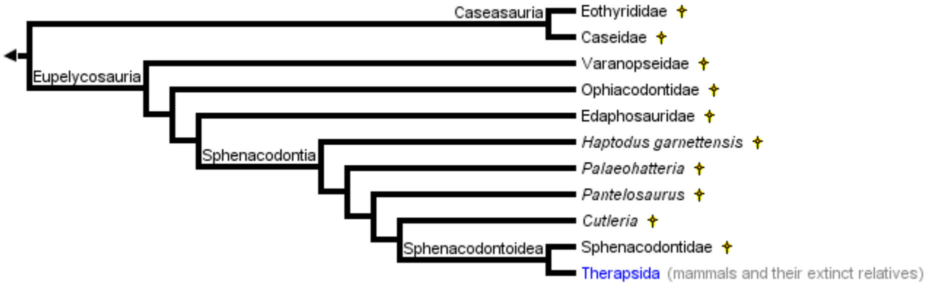


Figure 17-8. *HAPTODUS*. This sphenacodontid pelycosaur is known from the Upper Pennsylvanian into the Lower Permian. Skull in (*a*) dorsal, (*b*) palatal, and (*c*) lateral views. (*d*) Lower jaw in medial view. (*a* to *d*) *From Currie, 1979*. (*e*) Skeleton, 2 meters long. *From Currie, 1977*. Abbreviations as in Figure 8-3.

Lámina reflectada del angular

Operatividad auditiva-mecanoreceptora



Sphenacodontidae

Phylogenetically, the most important of the pelycosaur families are the sphenacodonts. They appear in the middle or late Pennsylvanian and are the dominant terrestrial carnivores in the Lower Permian. At some stage in their history they gave rise to the therapsids. The best-known sphenacodonts are the Lower Permian genera *Dimetrodon* (Figure 17-5) and *Sphenacodon*, which exceed 3 meters in length. The skull is typically much deeper than in the ophiacodonts and the canine teeth are greatly enlarged. To support the dentition, the maxilla extends far up on the snout and separates the lacrimal bone from the margin of the external nares.

The jaw articulation is well below the level of the tooth row in sphenacodonts, the articular is greatly enlarged, and the articulating surface extends far down on the medial face of the lower jaw. A feature that is unique to sphenacodonts is the presence of a reflected lamina of the angular (Figure 17-6), which can be associated with the development of the middle ear in later synapsids and mammals.

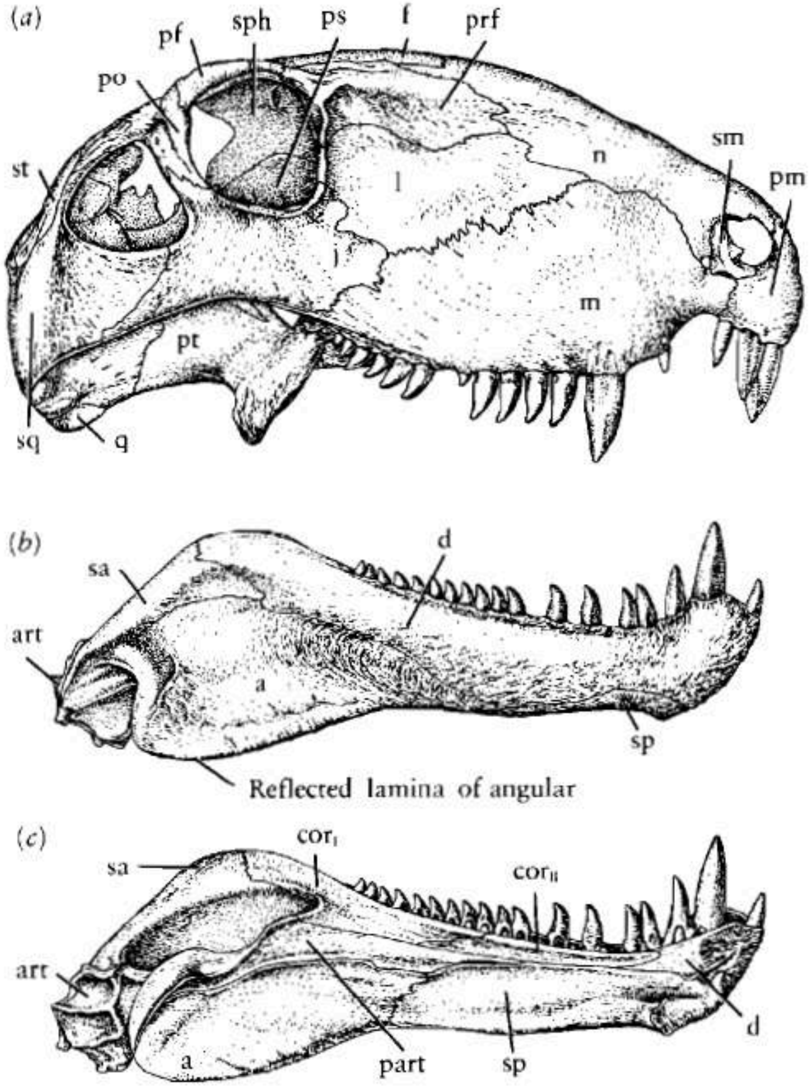
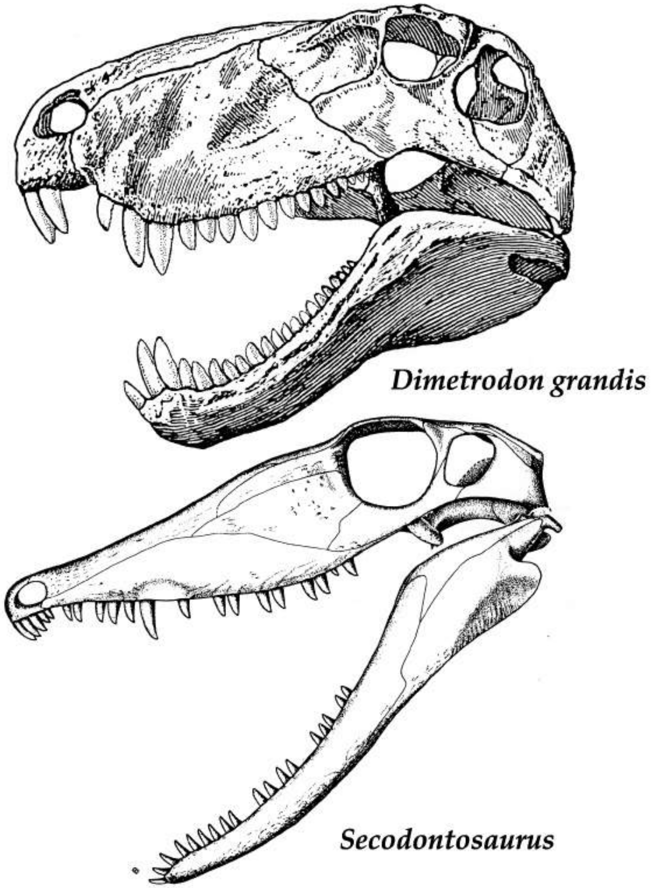
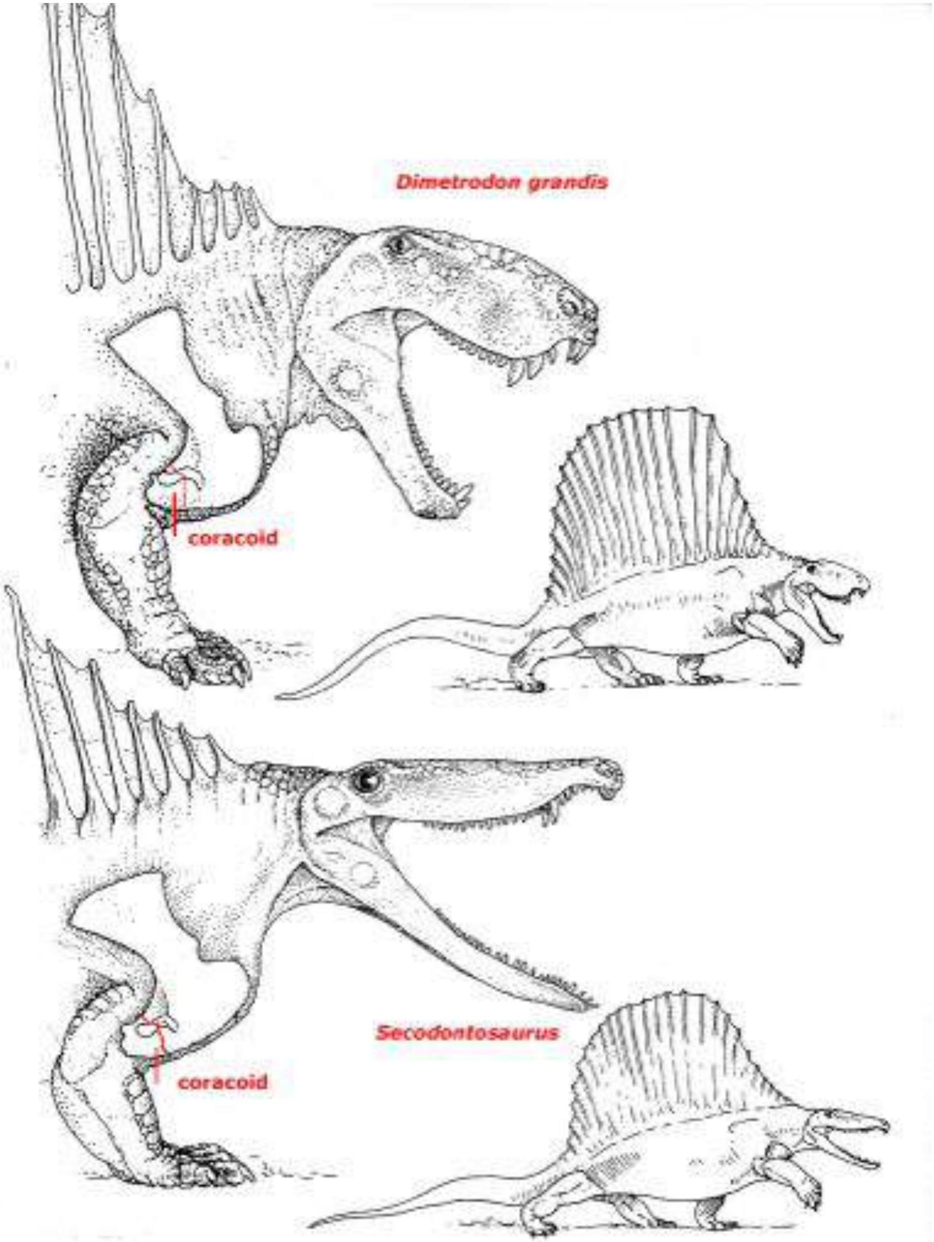
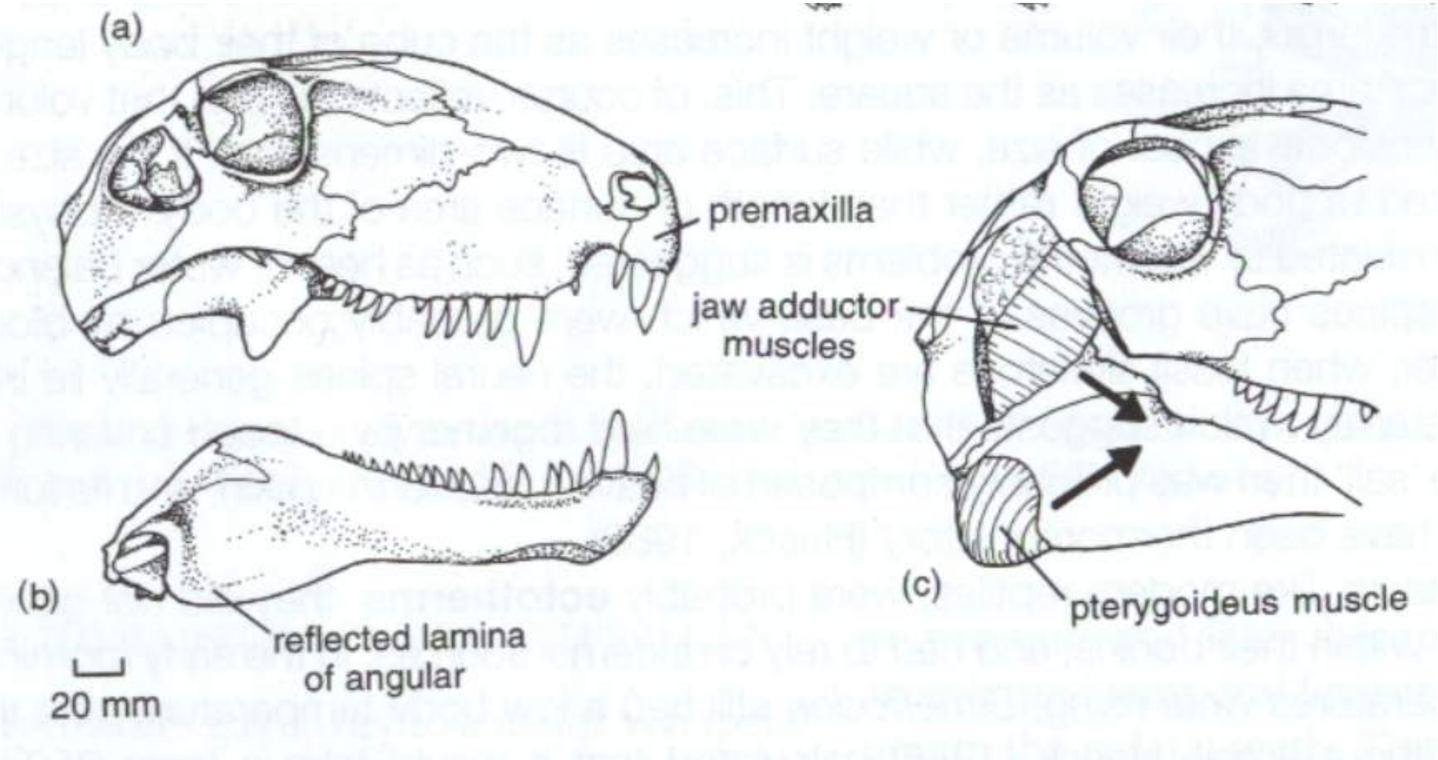


Figure 17-6. (*a*) Skull of *Dimetrodon*, in lateral view. (*b*) Lateral and (*c*) medial views of the lower jaw, ×¼. Abbreviations as in Figure 8-3. *From Romer and Price, 1940.*


Dimetrodon grandis
Secodontosaurus


Dimetrodon grandis
coracoid
Secodontosaurus
coracoid

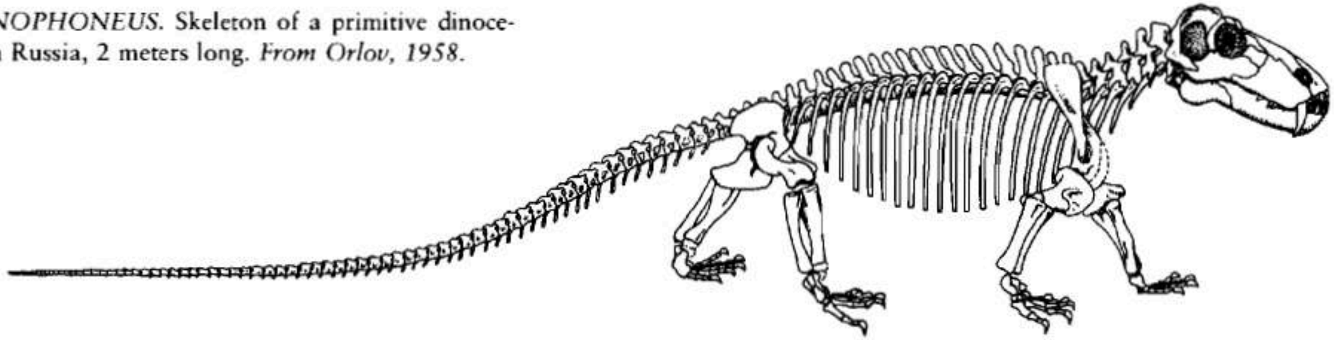
Los Sphenacodontidae *p*resentan un sitio de inserción externo del músculo pterygoideo, tal que este gira desde el interior y abre la mandíbula.



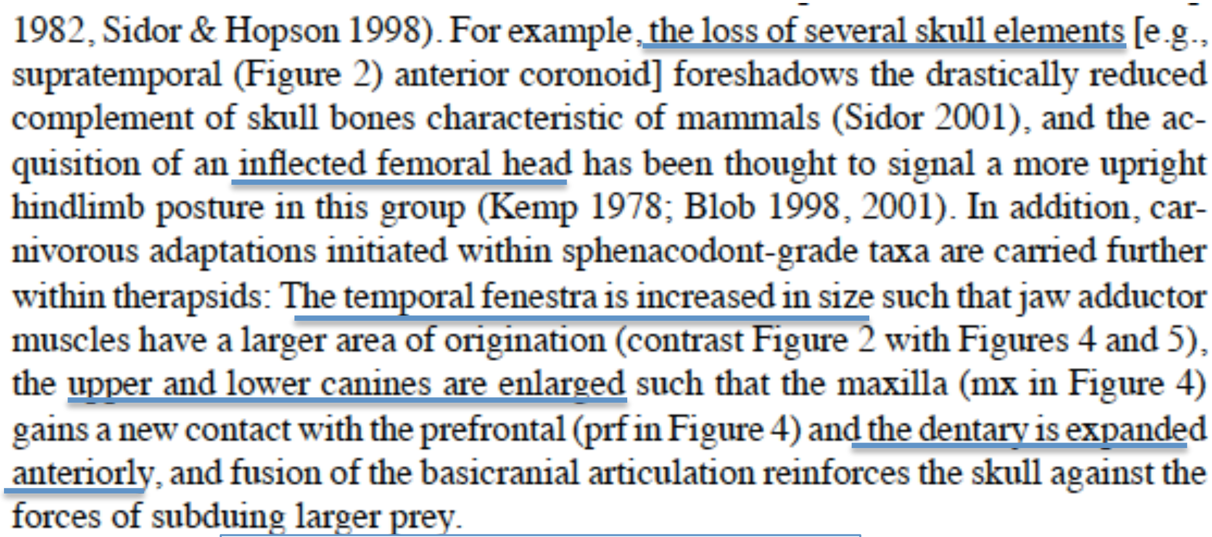
Therapsida

Characters: Large head with relatively rigid skull; $ long dorsal process of premaxilla [B&S, H&P] [RS01]; $ septomaxilla with posterodorsal facial process separating nasal & maxilla [B&S, H&P, ***contra LR96]; $ maxilla enlarged, separating nasal & lacrimal [B&S, H&P]; $ maxilla contacts prefrontal (except Tetraceratops) [LR96] [RS01]; $ enlarged temporal fenestra [B&S, H&B] [RS01]; $ upper margin of fenestra forms concave, ventrolaterally facing surface (for origin of jaw adductors?) [LR96]; $ pineal foramen raised on prominent boss [B&S, H&P] [RS01]; $ supratemporal absent [B&S, H&P] [RS01]; $ squamosal with groove on posterior [B&S, H&P]; $ quadrate reduced [LR96]; $ braincase firmly sutured to back of dermal skull roof [LR96]; dentary anteriorly expanded [RS01]; anterior coronoid absent [RS01]; $ posterior coronoid ventrally shifted & fails to form dorsal margin of jaw in medial view [RS01]; $ reflected lamina of angular bone notched dorsally [B&S, H&P] [RS01]; $ reflected lamina with pattern of ridges on lateral surface; $ vomer expanded transversely between choanae [B&S, H&P]; vomer with concave ventral surface; at least partial secondary palate; $ posteromedian flange of pterygoid present behind the interpterygoid vacuity [LR96]; $ pterygoid short & palatines meet at midline (except Tetraceratops) [LR96]; $ interpterygoid vacuity shortened [B&S, H&P, LR96]; basicranial articulation fused [RS01]; $ parasphenoid ventral plate ridged & lacks central groove (except Tetraceratops) [LR96]; $ precanine teeth absent; $ premaxillary teeth of equal size (except Tetraceratops) [LR96]; enlarged canine dentition [RS01]; $ upper canine length increased [B&S] $ no more than twelve upper postcanine teeth [LR96]; $ teeth absent from ectopterygoid [LR96]; $ palatal teeth restricted to raised denticle fields (except Tetraceratops) [LR96]; heavy body; $ intercentra absent from trunk [RS01]; more than 3 sacral vertebrae; tail reduced; limb girdles reduced and more mobile; limbs more slender, but fairly short; limbs held more vertically; $ scapular blade slender [RS01]; $ pectoral glenoid deepened & rounded [RS01]; $ humeral head rounded, not screw-shaped [RS01]; expanded iliac blade; $ acetabulum deepened & rounded [RS01]; $ inturned head of femur [RS01]; general reduction of ventral components (e.g. clavicle -- indicative of more upright posture); inflected femoral head [RS01]; development of greater trochanter on femur (with iliac blade, indicates gluteal hindlimb musculature); phalanges shorter (used as lever, rather than holdfast); possibly had hair; increased metabolic rate probable; found in terrestrial habitats with nearly world-wide distribution.***

Figure 17-17. *TITANOPHONEUS.* Skeleton of a primitive dinocephalian therapsid from Russia, 2 meters long. *From Orlov, 1958.*



Therapsida:



1982, Sidor & Hopson 1998). For example, the loss of several skull elements [e.g., supratemporal (Figure 2) anterior coronoid] foreshadows the drastically reduced complement of skull bones characteristic of mammals (Sidor 2001), and the acquisition of an inflected femoral head has been thought to signal a more upright hindlimb posture in this group (Kemp 1978; Blob 1998, 2001). In addition, carnivorous adaptations initiated within sphenacodont-grade taxa are carried further within therapsids: The temporal fenestra is increased in size such that jaw adductor muscles have a larger area of origination (contrast Figure 2 with Figures 4 and 5), the upper and lower canines are enlarged such that the maxilla (mx in Figure 4) gains a new contact with the prefrontal (prf in Figure 4) and the dentary is expanded anteriorly, and fusion of the basicranial articulation reinforces the skull against the forces of subduing larger prey.

septomaxilla with posterodorsal facial process separating nasal & maxilla

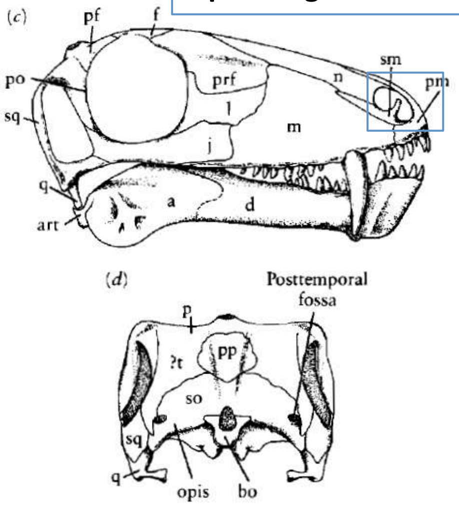
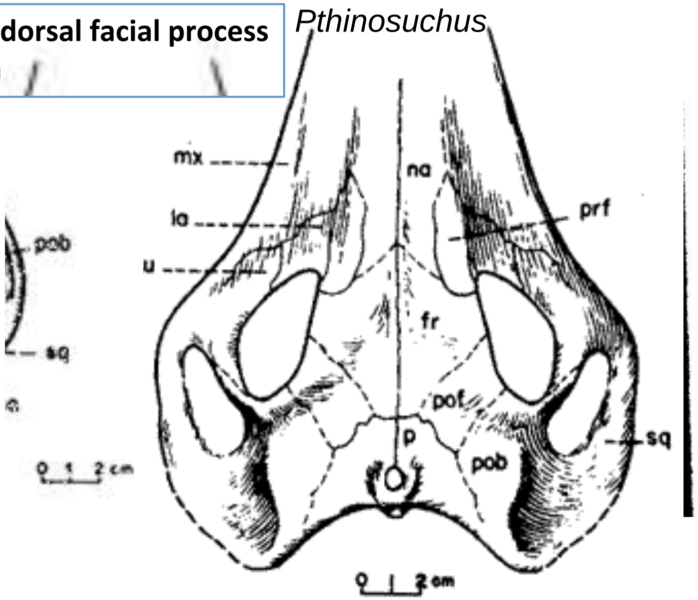
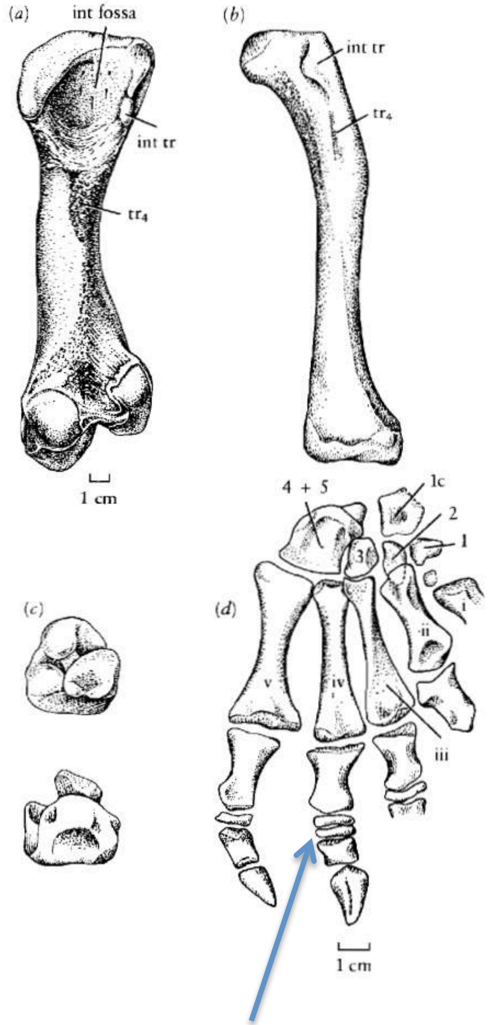


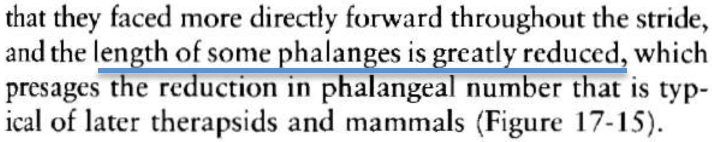
Figure 17-13. SKULL OF THE PRIMITIVE THERAPSID *BIARMOSUCHUS*. (*a*) Dorsal, (*b*) palatal, (*c*) lateral, and (*d*) occipital views, × ⅓. Abbreviations as in Figure 8-3. *From Sigogneau and Chudinov, 1972.*

Pthinosuchus

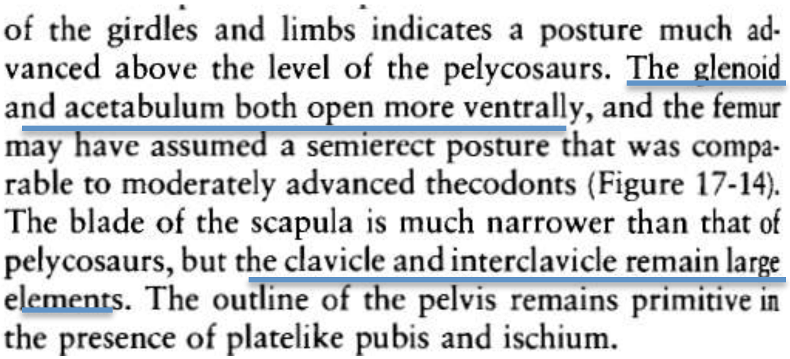


Pineal foramen raised on a boss or “chimney”





that they faced more directly forward throughout the stride, and the length of some phalanges is greatly reduced, which presages the reduction in phalangeal number that is typical of later therapsids and mammals (Figure 17-15).



of the girdles and limbs indicates a posture much advanced above the level of the pelycosaurs. The glenoid and acetabulum both open more ventrally, and the femur may have assumed a semierect posture that was comparable to moderately advanced thecodonts (Figure 17-14). The blade of the scapula is much narrower than that of pelycosaurs, but the clavicle and interclavicle remain large elements. The outline of the pelvis remains primitive in the presence of platelike pubis and ischium.

Narrowing of scapular blade
Loss of intercentra

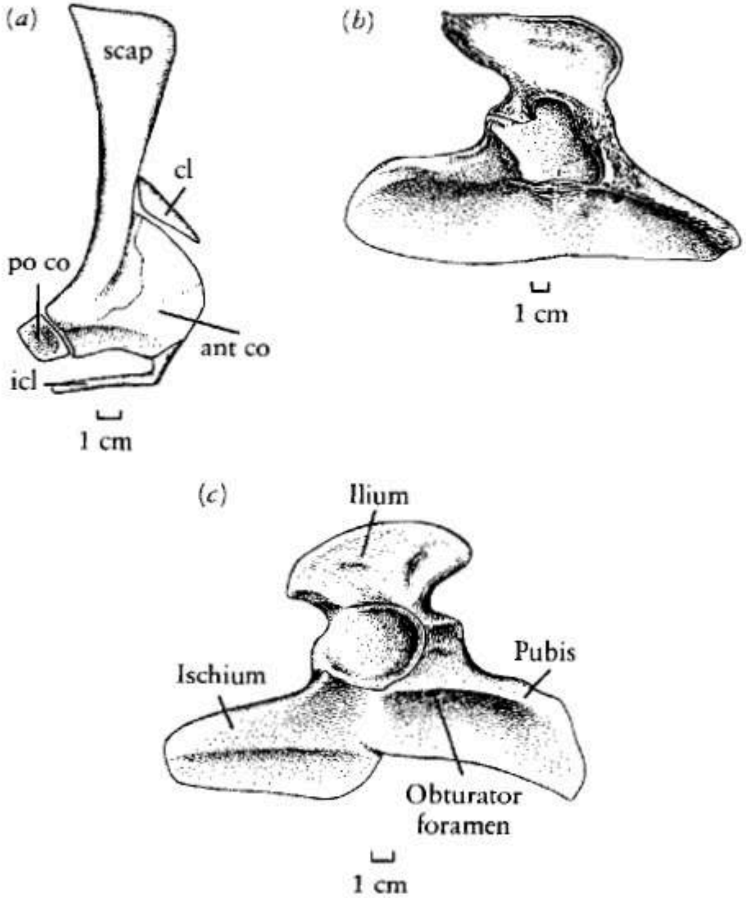


Figure 17-14. GIRDLES OF PELYCOSAURS AND THERAPSIDS. (*a*) Shoulder girdle of the therapsid *Biarmosuchus*. Abbreviations as in Figure 17-4. *From Sigogneau and Chudinov, 1972.* (*b*) Pelvis of the pelycosaur *Dimetrodon*. *From Romer and Price, 1940.* (*c*) Pelvis of the therapsid *Biarmosuchus*. *From Sigogneau and Chudinov, 1972.*

Tetraceratops: Cercano a Therapsida?

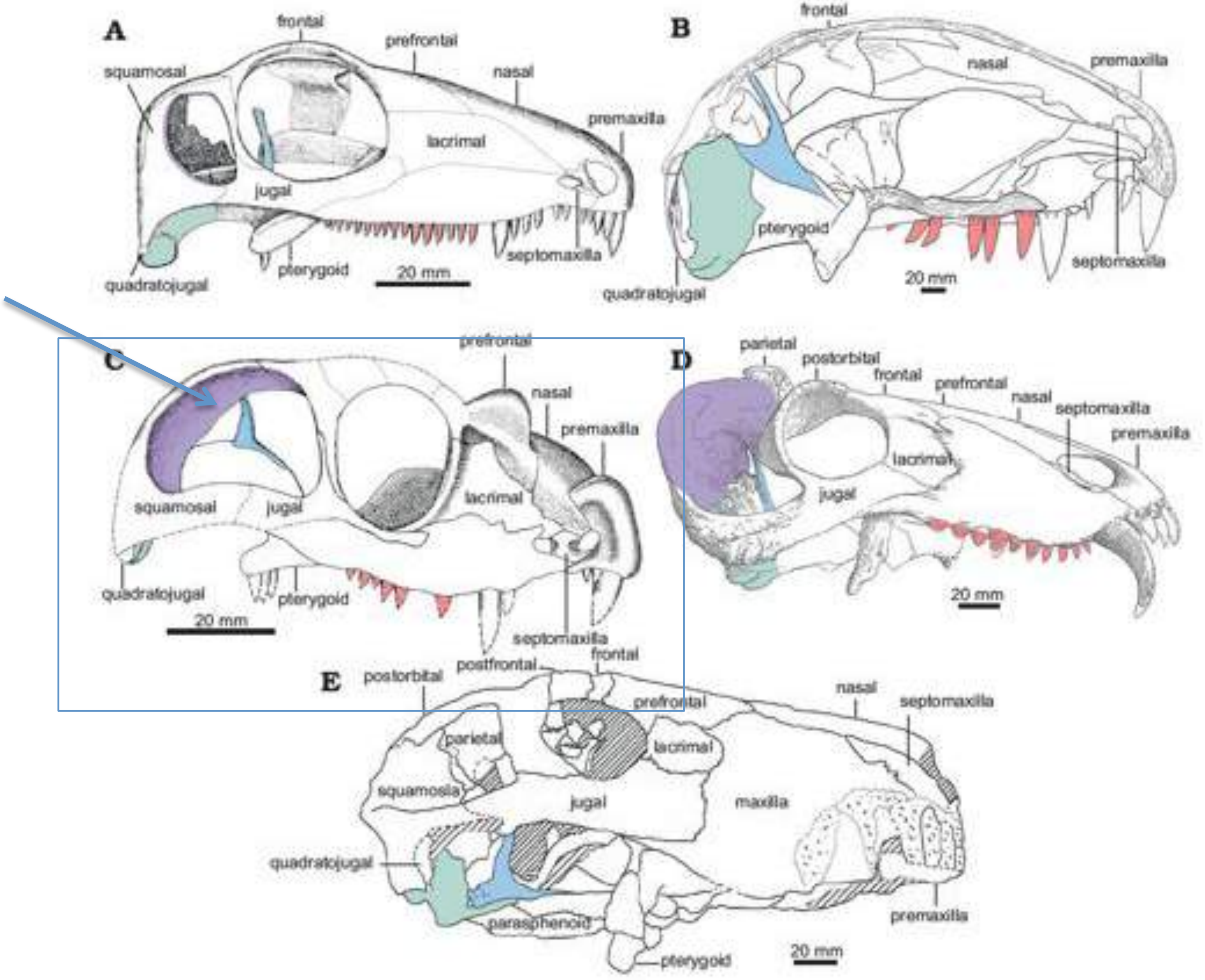


Fig. 4. Reconstructions (A–D) or specimen drawings (E) in lateral view of synapsid skulls. A. *Haptodus garnettensis* Currie, 1977 (modified from Laurin 1993). B. *Dimetrodon limbatus* Cope, 1877, sagittal section (modified from Romer and Price 1940). C. *Tetraceratops insignis* Matthew, 1908 (modified from Laurin and Reisz 1996). D. *Syodon efremovi* Orlov, 1940 (modified from Orlov 1958). E. *Lycaenops angusticeps* (Broom, 1913) UCMP 42701 (modified from Laurin 1998). The quadrate is colored in green, epipterygoid in blue, upper postcanines in orange, and upper margin of the temporal fenestra in purple.

known in any other therapsid. However, the presence of a greatly elongated dorsal process of the premaxilla, septomaxilla with a long facial process, maxilla which is increased in height so as to contact the prefrontal, and ventral surface of

clade, suggests that the initial evolutionary radiation of therapsids occurred in Laurasia.

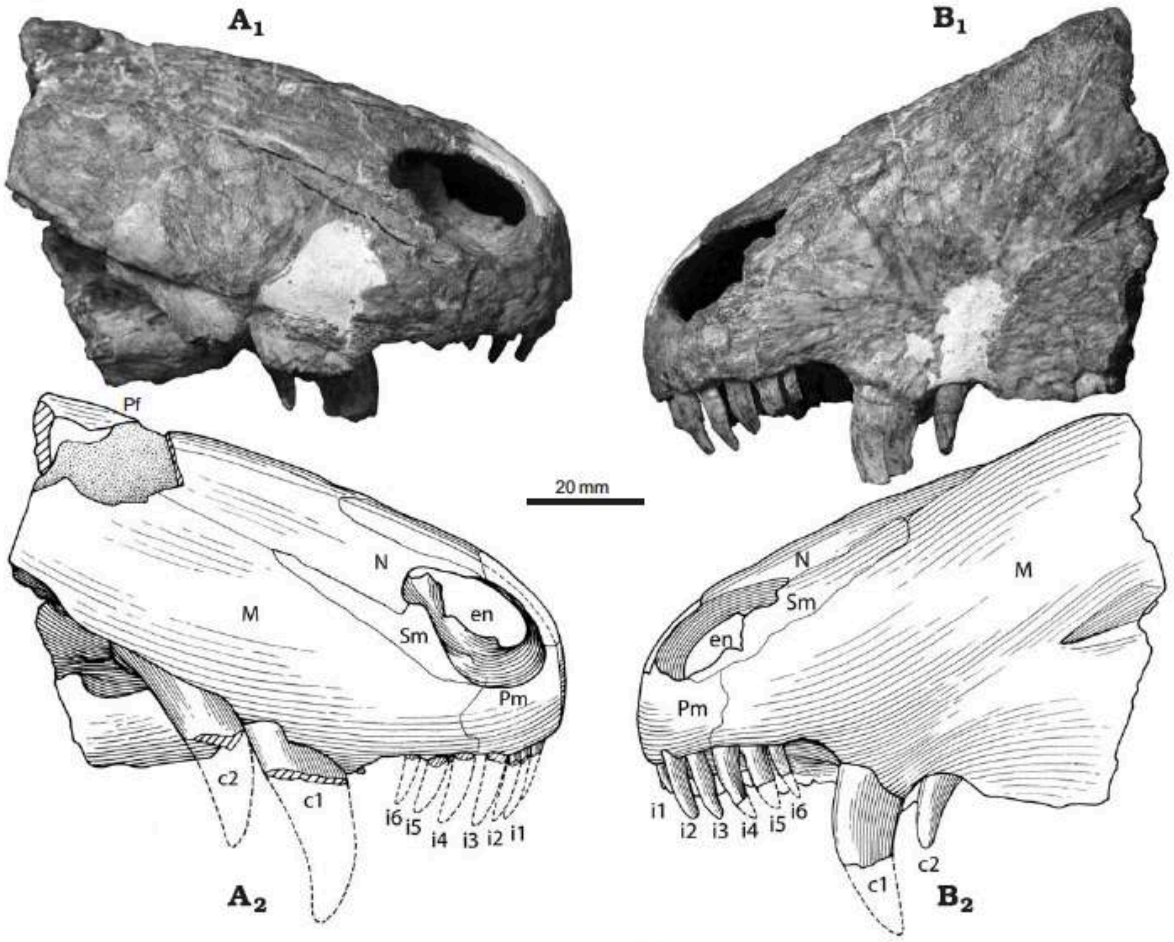
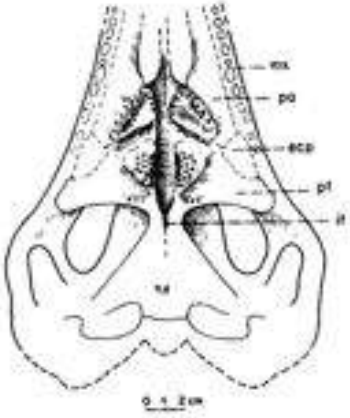
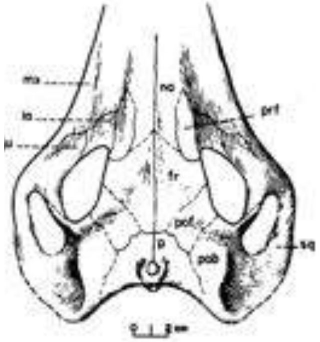


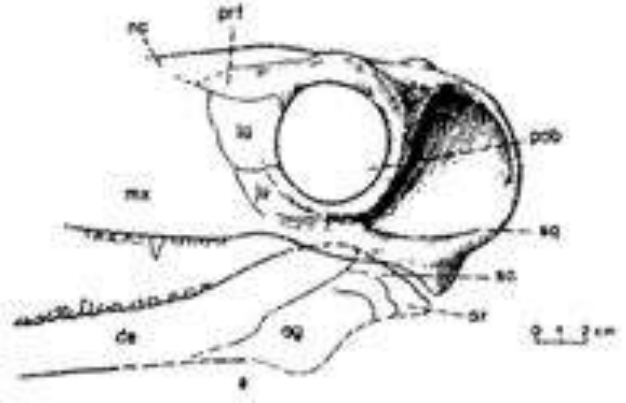
Fig. 2. Partial skull of the basal therapsid *Raranimus dashankouensis* gen. et sp. nov., IVPP V15424 (holotype) from Middle Permian Xidagou Formation, Dashankou, Xumen, Gansu, China in right lateral (**A**) and left lateral (**B**) views.. Photographs (A_1, B_1) and explanatory drawings (A_2, B_2). Abbreviations: c1–2, canine 1–2; ch, choana; en, external naris; i1–6, incisor 1–6; M, maxilla; N, nasal; p1–3, postcanine 1–3; Pf, prefrontal; Pl, palatine; Pm, premaxilla; Pt, pterygoid; rc, replacement canine; ri, replacement incisor; Sm, septomaxilla; sp, small precanine maxillary tooth; V, vomer.





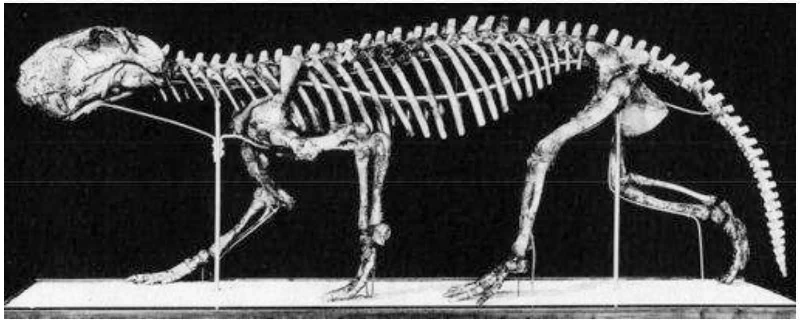
Phthinosuchus

(pero es pobremente conocido y no muy referido en la literatura moderna)

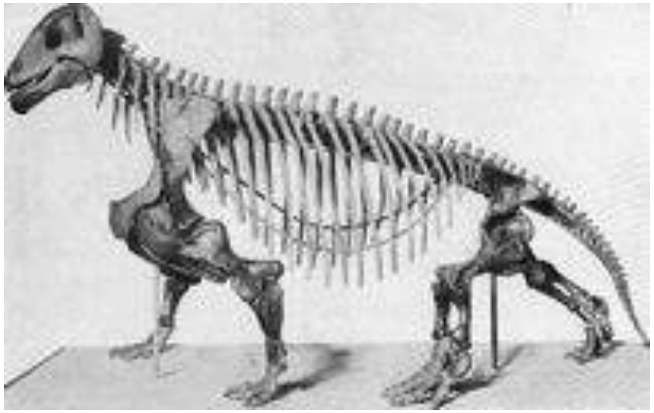


Existen 4 linajes principales de Terápsidos

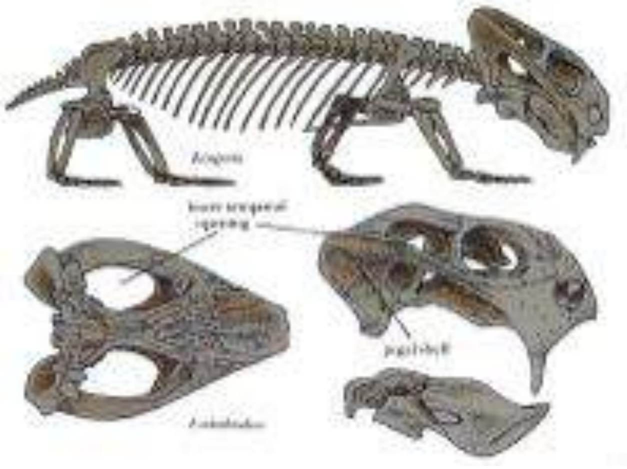
Biarmosuchia (Eotitanosuchia)



Theriodonta



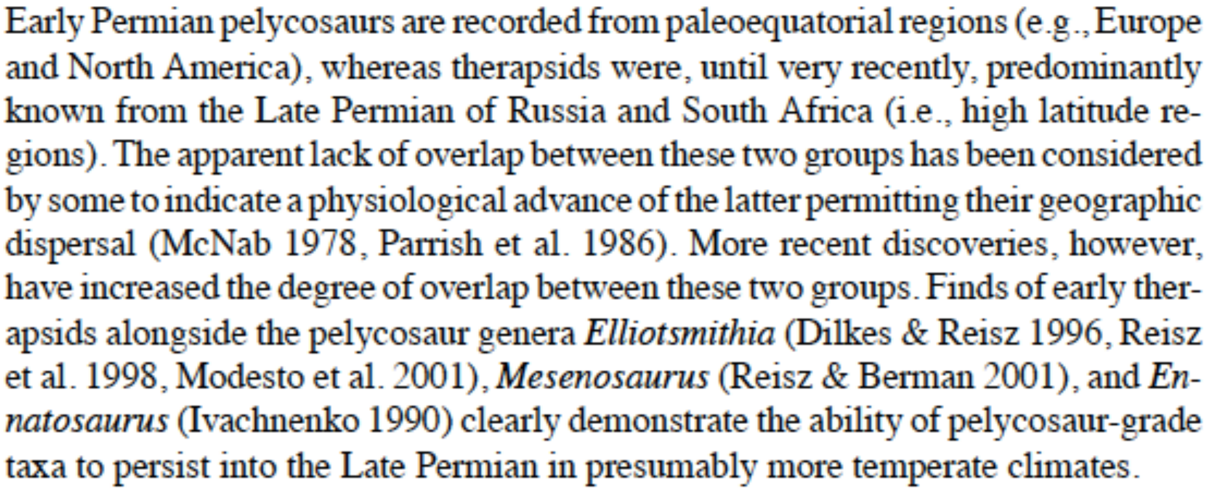
Dinocephalia



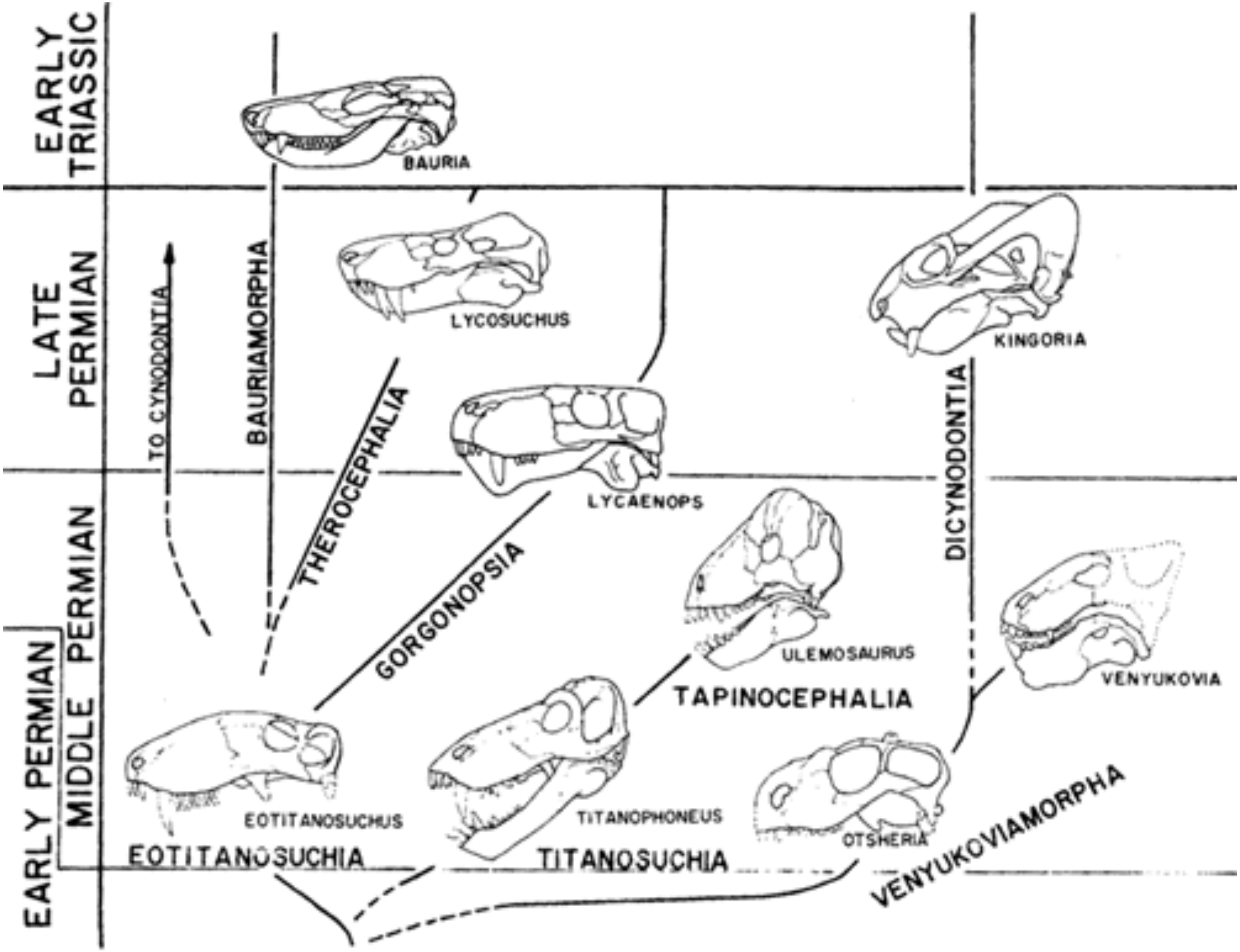
Anomodontia

Los Biarmosuchia son probablemente grupo hermano de Theriodontia. Se debate si Anomodontia es grupo hermano de Theriodonta+Biarmosuchia, o grupo hermano de Dinocephalia.

Segregación geográfica de Pelycosaurios y Terápsidos?



Early Permian pelycosaurs are recorded from paleoequatorial regions (e.g., Europe and North America), whereas therapsids were, until very recently, predominantly known from the Late Permian of Russia and South Africa (i.e., high latitude regions). The apparent lack of overlap between these two groups has been considered by some to indicate a physiological advance of the latter permitting their geographic dispersal (McNab 1978, Parrish et al. 1986). More recent discoveries, however, have increased the degree of overlap between these two groups. Finds of early therapsids alongside the pelycosaur genera *Elliotsmithia* (Dilkes & Reisz 1996, Reisz et al. 1998, Modesto et al. 2001), *Mesenosaurus* (Reisz & Berman 2001), and *Ennatosaurus* (Ivachnenko 1990) clearly demonstrate the ability of pelycosaur-grade taxa to persist into the Late Permian in presumably more temperate climates.



Phylogeny of noncynodont therapsids with skulls of representative forms.

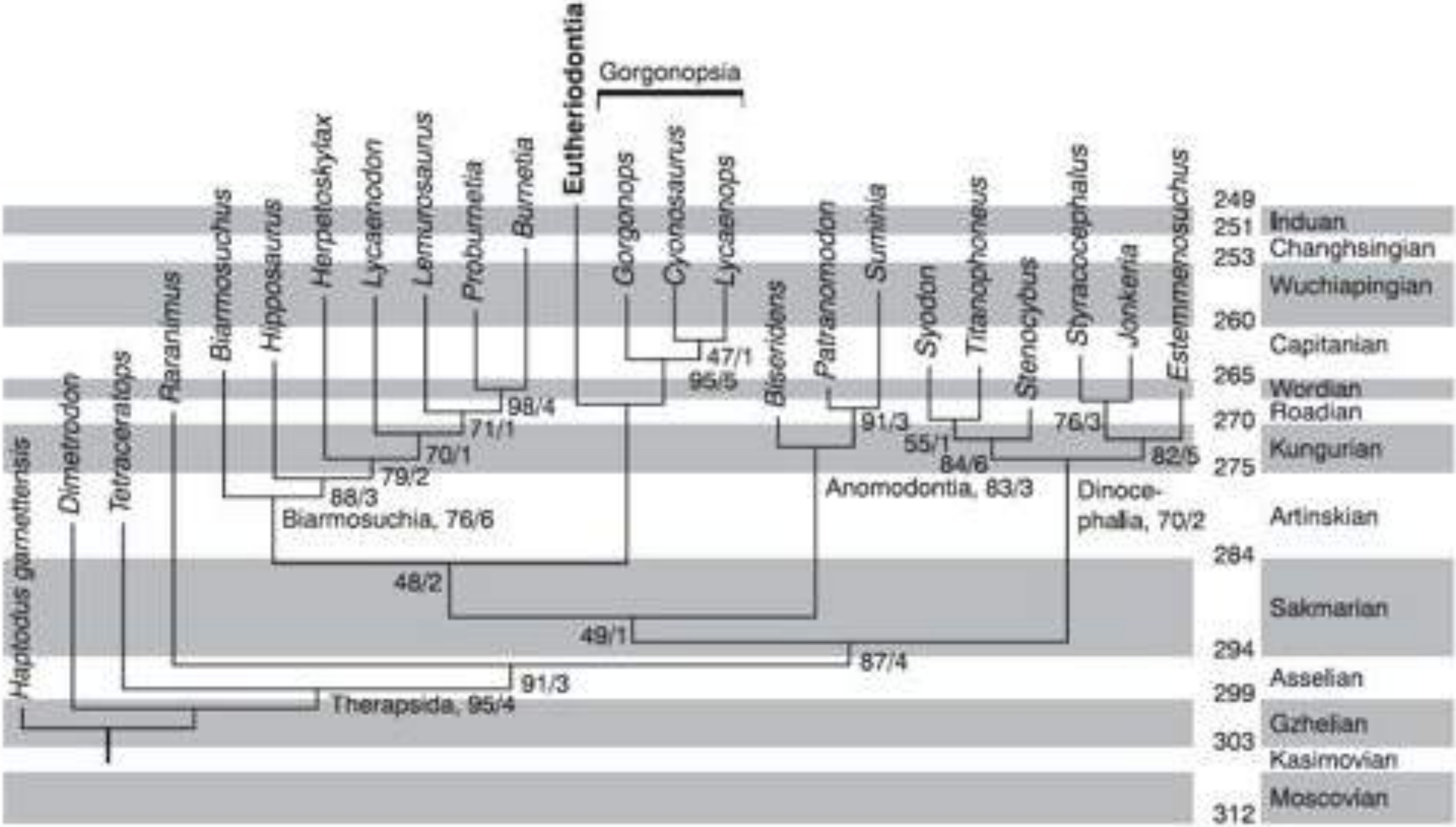
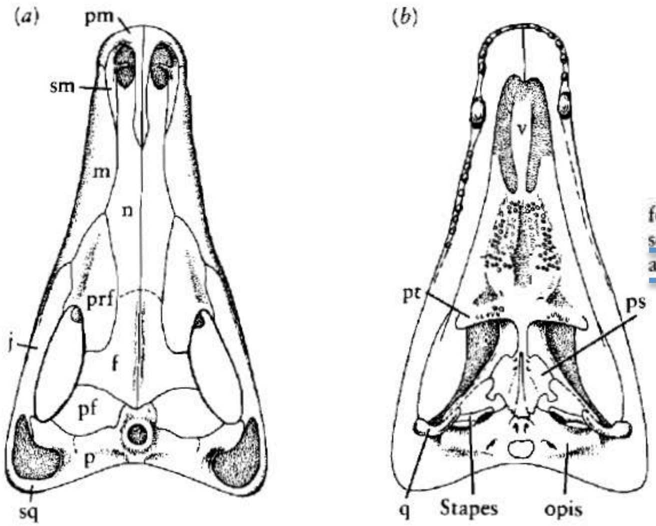
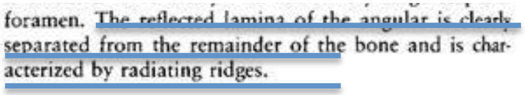


Fig. 5. Time-calibrated tree displaying the relationship between *Haptodus*, *Dimetrodon*, *Tetraceratops*, and 20 other therapsids. The putative position of Eutheriododontia (a taxon that includes Therocephalia and Cynodontia, the latter including Mammalia) was added after the analysis, in the position suggested (for Cynodontia) by Liu et al. (2009). The bootstrap and Bremer support values are also included. The branch lengths are approximate but reflect geological time.

Biarmosuchia (previamente Eotitanosuchia, Pthinosuchia)




foramen. The reflected lamina of the angular is clearly separated from the remainder of the bone and is characterized by radiating ridges.

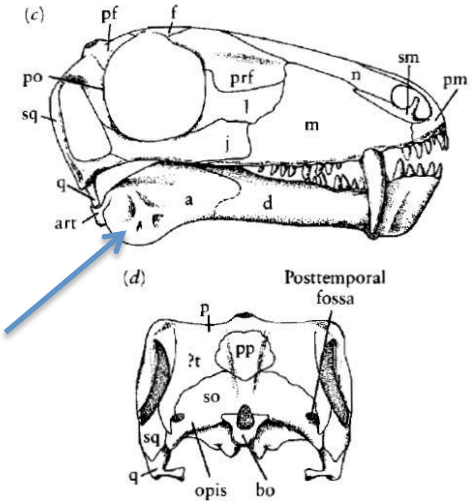
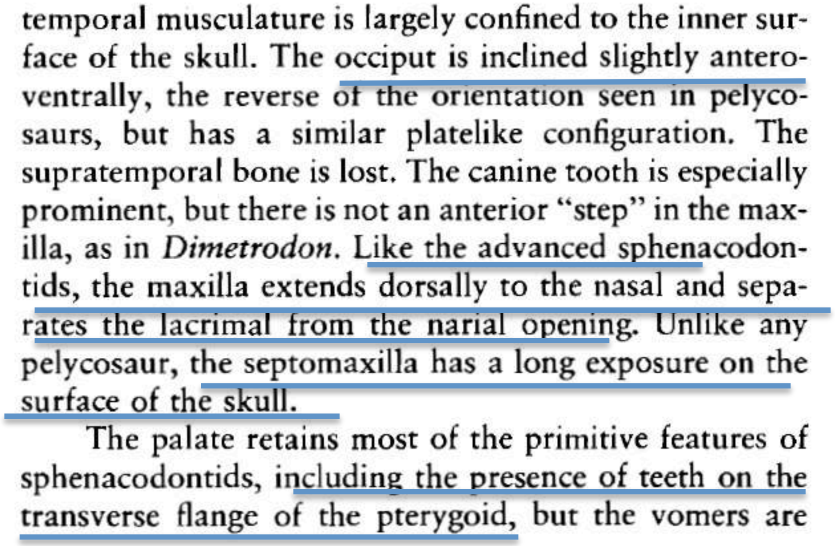
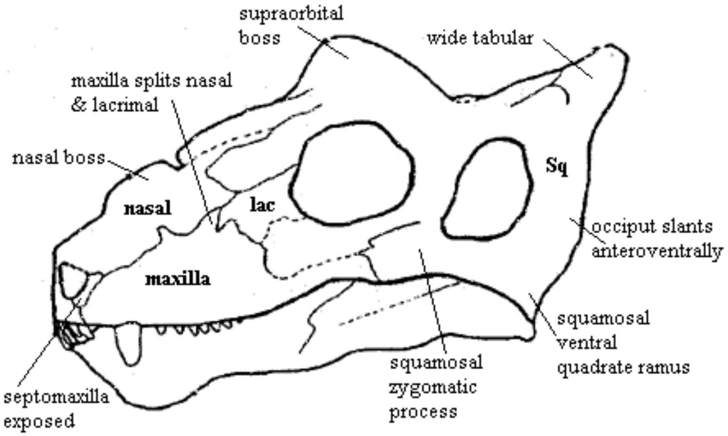


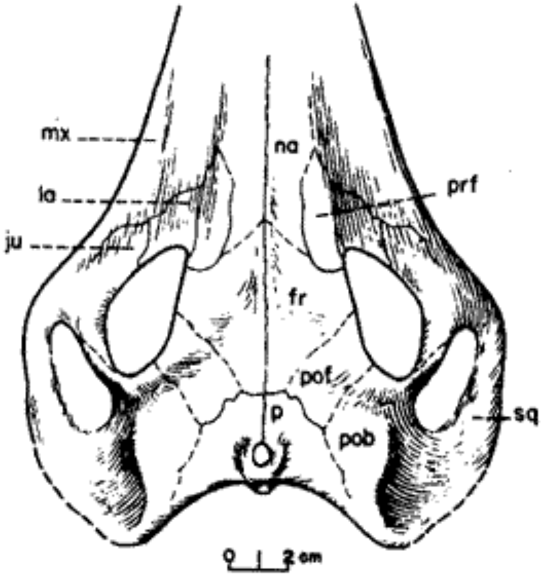
Figure 17-13. SKULL OF THE PRIMITIVE THERAPSID *BIARMOSUCHUS*. (*a*) Dorsal, (*b*) palatal, (*c*) lateral, and (*d*) occipital views, × ⅓. Abbreviations as in Figure 8-3. *From Sigogneau and Chudinov, 1972.*

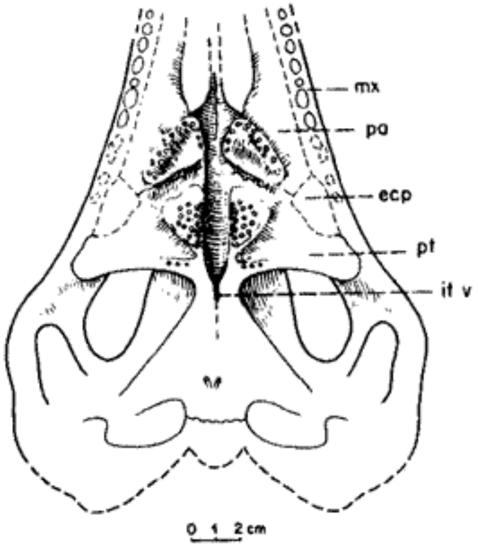

temporal musculature is largely confined to the inner surface of the skull. The occiput is inclined slightly anteroventrally, the reverse of the orientation seen in pelycosaurs, but has a similar platelike configuration. The supratemporal bone is lost. The canine tooth is especially prominent, but there is not an anterior "step" in the maxilla, as in *Dimetrodon*. Like the advanced sphenacodontids, the maxilla extends dorsally to the nasal and separates the lacrimal from the narial opening. Unlike any pelycosaur, the septomaxilla has a long exposure on the surface of the skull.

The palate retains most of the primitive features of sphenacodontids, including the presence of teeth on the transverse flange of the pterygoid, but the vomers are

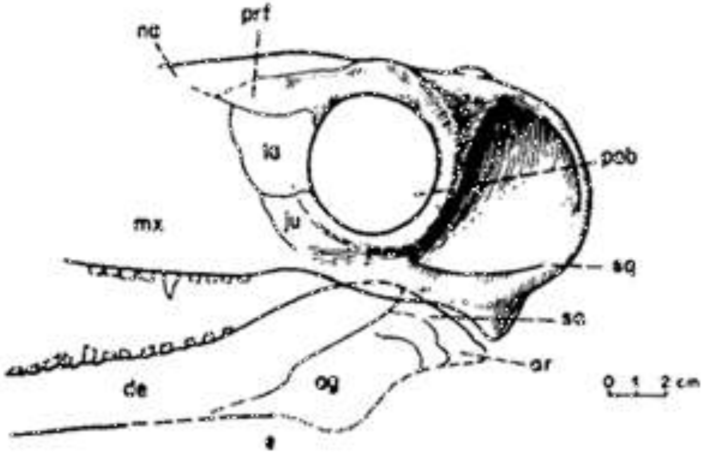


Proburnetia skull in anterolateral view. From Barghusen & Sidor (2001).

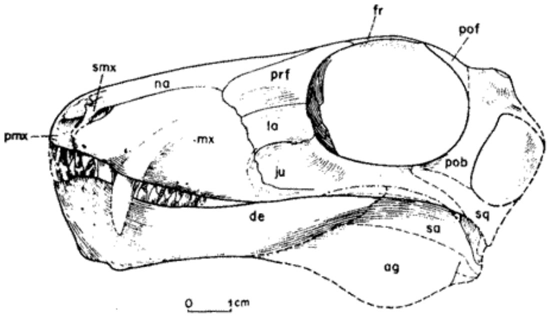




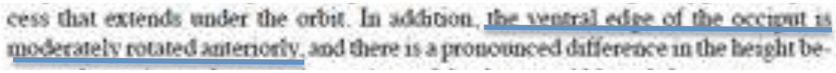
Pthinosuchus



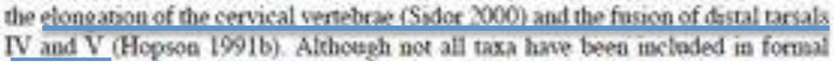
Biarmosuchia: “Ictidorhinidae”



Ictidorhinus

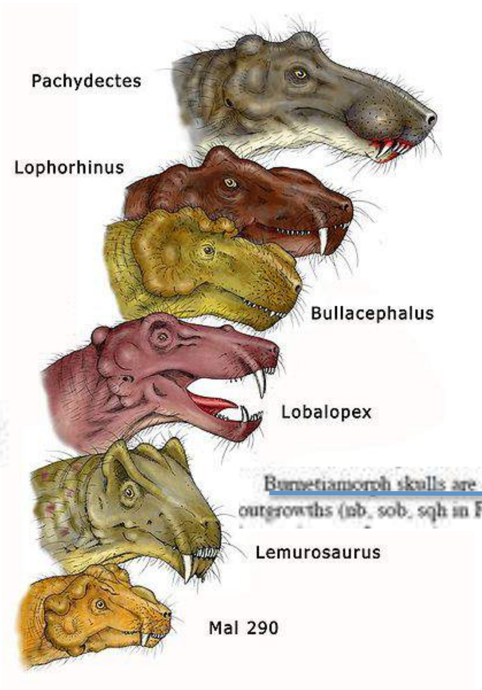


cess that extends under the orbit. In addition, the ventral edge of the occiput is moderately rotated anteriorly, and there is a pronounced difference in the height be-



the elongation of the cervical vertebrae (Sidor 2000) and the fusion of distal tarsals IV and V (Hopson 1991b). Although not all taxa have been included in formal

Biarmosuchia: Burnetiamorpha



Burnetiamorph skulls are adorned with numerous protuberances and horn-like outgrowths (nb, sob, sqh in Figure 4). For much of this group's history, however,

Burnetia

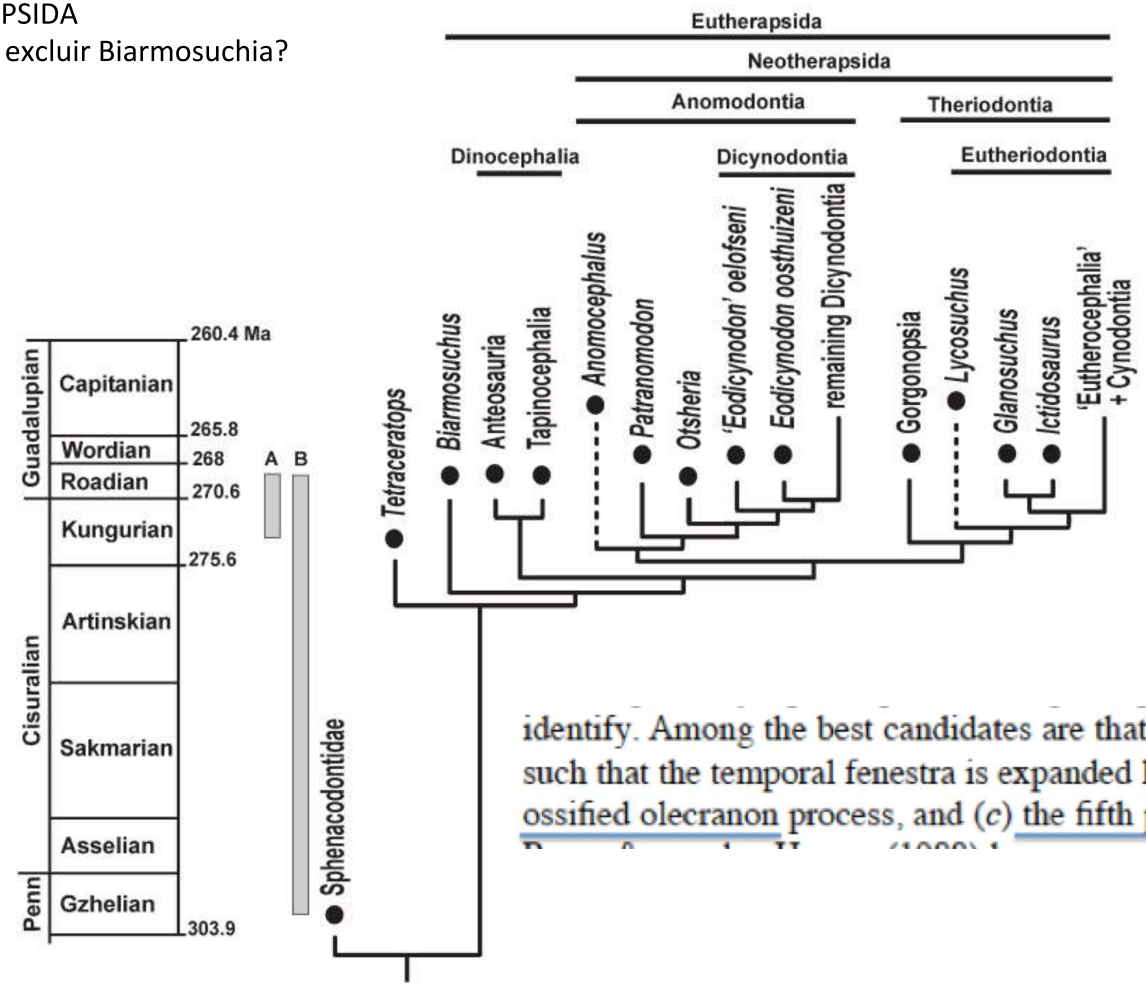
Biarmosuchia: Eotitanosuchia

They seem to be more advanced than the Biarmosuchia in that the temporal opening behind the eye socket, although small, is still somewhat larger than the biarmosuchians, being expanded in the upper rear (posterodorsal) margin, allowing the area of attachment of the adductor (jaw closing) muscles to be visible from the dorsal (top) view looking down. The eotitanosuchian bite was stronger and more efficient than the biarmosuchian bite.

Eotitanosuchus

EUTHERAPSIDA

Se puede excluir Biarmosuchia?



identify. Among the best candidates are that (*a*) the zygomatic arches are bowed such that the temporal fenestra is expanded laterally, (*b*) the ulna lacks a distinct, ossified olecranon process, and (*c*) the fifth pedal digit has only three phalanges.

TEXT-FIG. 4. Cladogram showing therapsid relationships and earliest records of the groups (filled circles). These records correspond to the therapsids recovered from the *Eodicynodon* AZ, South Africa; the Mezen and Ocher assemblages, Russia; and the Xidagou fauna, China. Dashed lines in the branches of *Lycosuchus* and *Anomocephalus* indicate that the taxa are not recorded in the Wordian, but their basal placement in the phylogeny of Eutheriodontia and Anomodontia, respectively, suggests that they should be present at that age. *Biarmosuchus* is the oldest (and the only Wordian) representative of the Biarmosuchia. Phylogenetic relationships of the taxa follow Rubidge and Sidor (2001) except for Anomodontia, which follows Modesto and Rubidge (2000) and Modesto *et al.* (2003), and the paraphyly of 'Therocephalia', which follows Abdala (2007). Grey bars indicate temporal gap without record of therapsids including (A) and excluding (B) *Tetraceratops* as a basal therapsid (see text). Time scale from Gradstein and Ogg (2004).

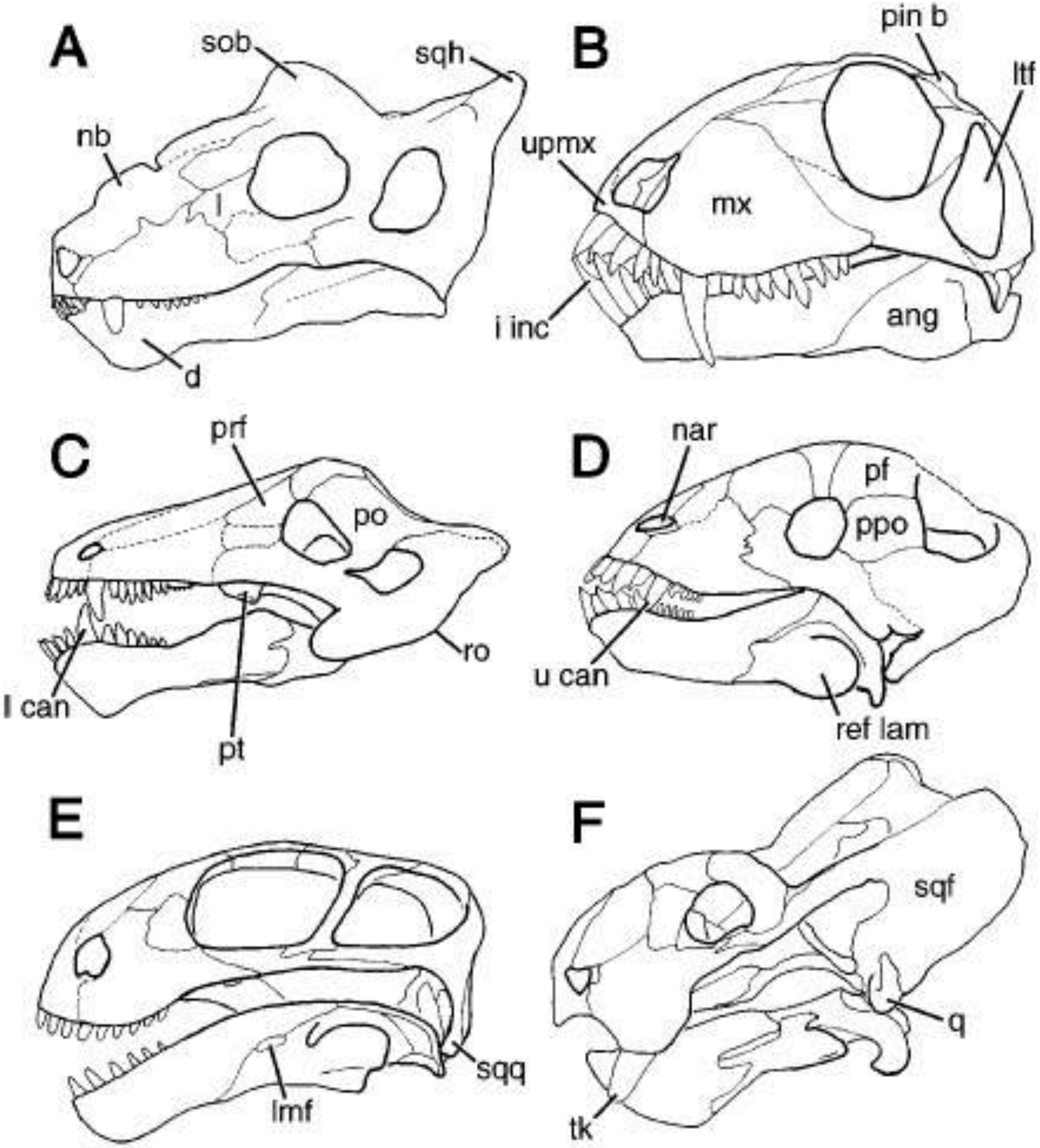


Figure 4 Skulls of selected nontheriodont therapsids in lateral view (not to scale). (*A*) the burnetiamorph biarmosuchian *Proburnetia*; (*B*) the anteosaurid dinocephalian *Stenocybus*; (*C*) the tapinocephalian dinocephalian *Styracocephalus*; (*D*) the basal tapinocephalid dinocephalian *Tapinocaninus*; (*E*) the basal anomodont *Patranomodon*; (*F*) the advanced dicynodont *Kannemeyeria*. Anatomical abbreviations: ang, angular; d, dentary; i inc, intermeshing incisors; l, lacrimal; l can, lower canine; lmf, lateral mandibular fenestra; ltf, lateral temporal fenestra; mx, maxilla; nar, external naris; nb, nasal boss; pf, postfrontal; pin b, pineal boss; po, postorbital; ppo, pachyostosed postorbital bar; pt, transverse flange of the pterygoid bone; ref lam, reflected lamina of the angular; ro, anteriorly rotated occiput; sob, supraorbital boss; sqf, squamoal fossa for jaw adductor musculature; sqh, squamosal horn; sqq, quadrate process of squamosal; tk, tusk-like upper canine; u can, upper canine; upmx, upturned premaxilla. Reconstructions modified from the following original sources: (*B*) Cheng & Li (1997); (*C*) Rubidge & van den Heever (1997); (*D*) Rubidge (1991); (*E*) Hopson (1994); (*F*) Renaut; 2000.

DINOCEPHALIA

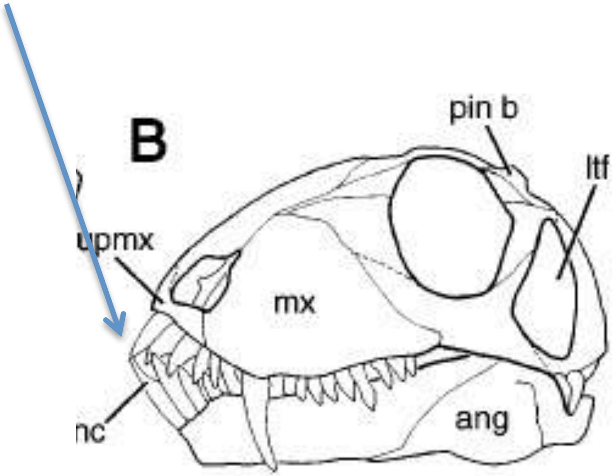
Dinocephalians

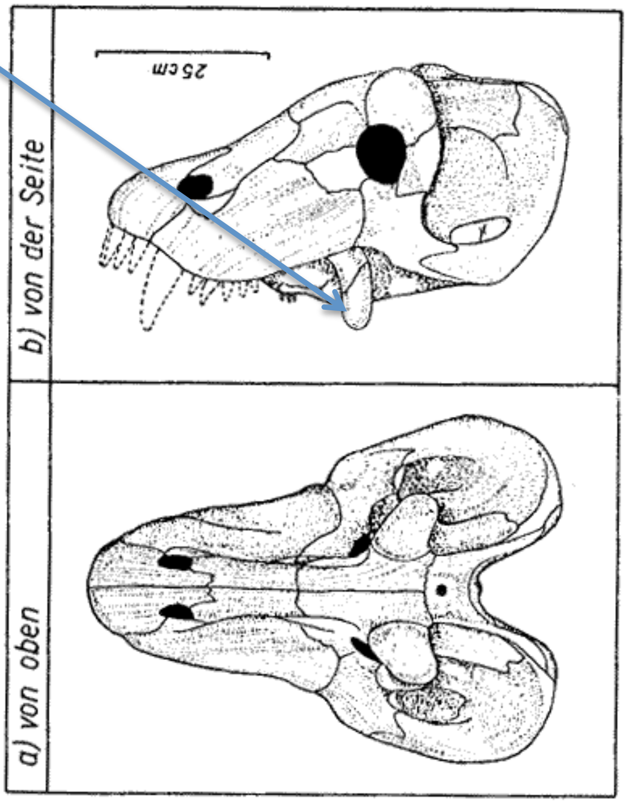
The dinocephalians were contemporary with the primitive carnivorous biarmosuchids and include some of the earliest herbivorous therapsids. They are confined to the Upper Permian but are known in southern Africa as well as Russia. They left no descendants.

Famosos por formas derivadas con paquiostosis craneal

a preorbitally positioned transverse flange of the pterygoid (pt in Figure 4), the lack of ridges and fossae on the lateral surface of the reflected lamina (ref lam

intermeshing upper and lower incisors





Anteosauridae: *Anteosaurus*

Tapinocephalidae: *Ulemosaurus*

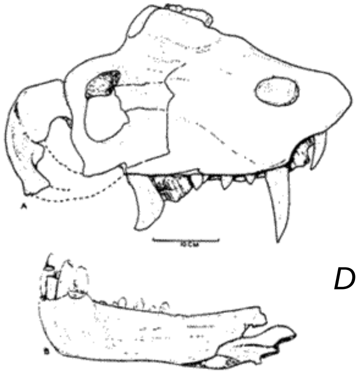
Dos grupos dinocéfalos:

ANTEOSAURIA (parafilético?)

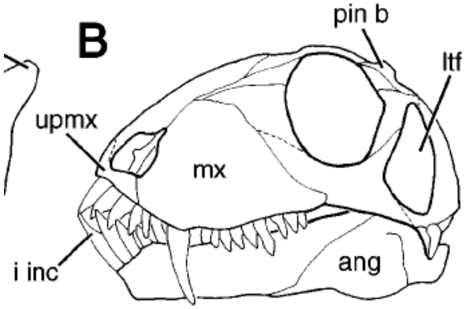
TAPINOCEPHALIA (herbívoros)

Algunos anteosauria derivados tienen **paquiostosis craneal**, todos los Tapinocephalia tienen

Anteosauria

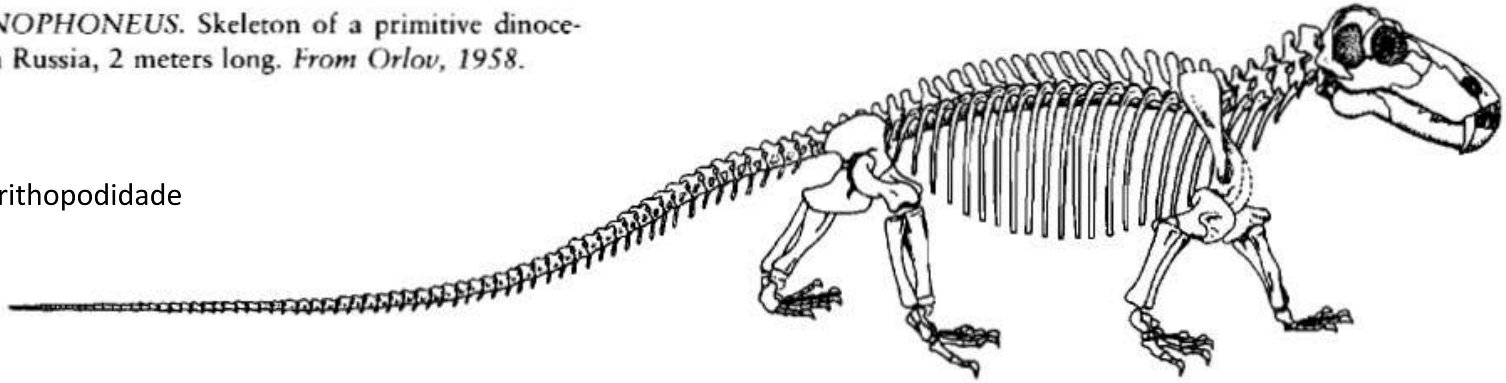


Doliosaurus



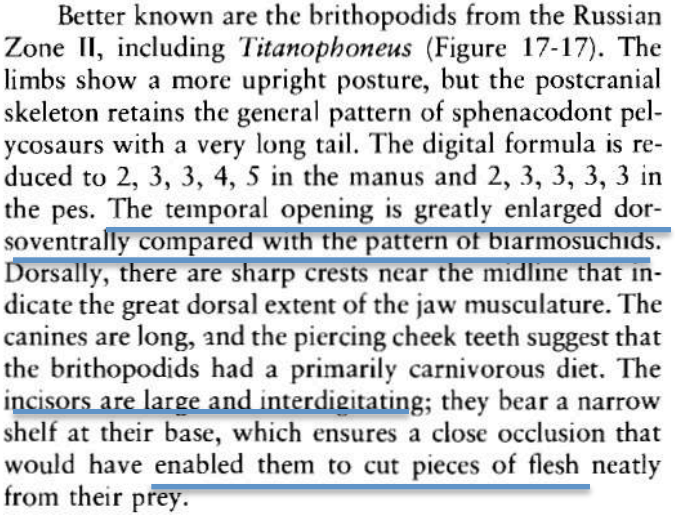
Stenocybus

Figure 17-17. *TITANOPHONEUS*. Skeleton of a primitive dinocephalian therapsid from Russia, 2 meters long. *From Orlov, 1958*.

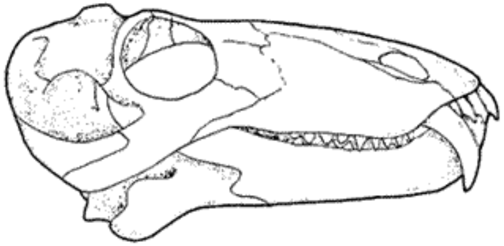


Brithopodidade

Dinotitan

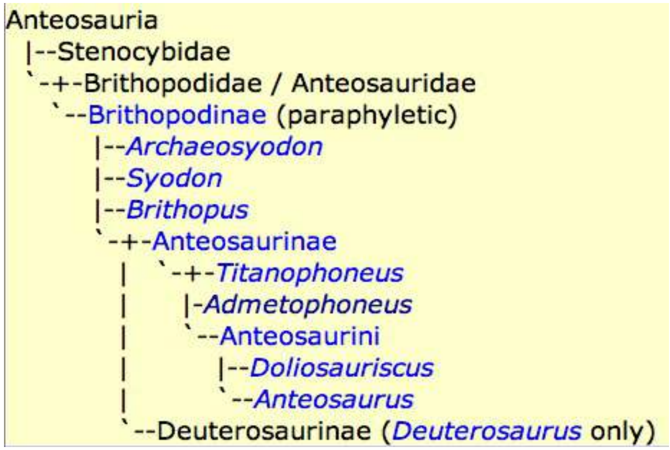


Better known are the brithopodids from the Russian Zone II, including *Titanophoneus* (Figure 17-17). The limbs show a more upright posture, but the postcranial skeleton retains the general pattern of sphenacodont pelycosaurs with a very long tail. The digital formula is reduced to 2, 3, 3, 4, 5 in the manus and 2, 3, 3, 3, 3 in the pes. The temporal opening is greatly enlarged dorsoventrally compared with the pattern of biarmosuchids. Dorsally, there are sharp crests near the midline that indicate the great dorsal extent of the jaw musculature. The canines are long, and the piercing cheek teeth suggest that the brithopodids had a primarily carnivorous diet. The incisors are large and interdigitating; they bear a narrow shelf at their base, which ensures a close occlusion that would have enabled them to cut pieces of flesh neatly from their prey.

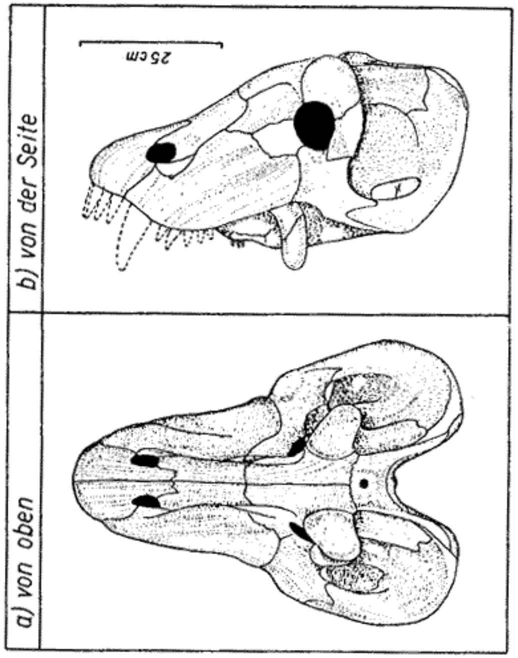


Syodon

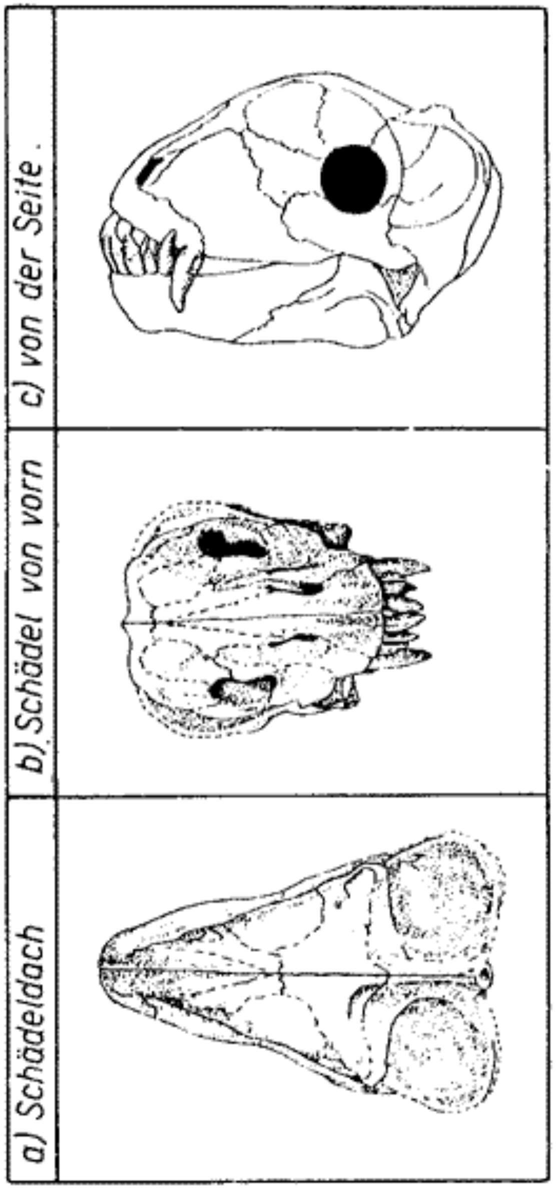
Anteosaurios derivados, de cabeza gruesa



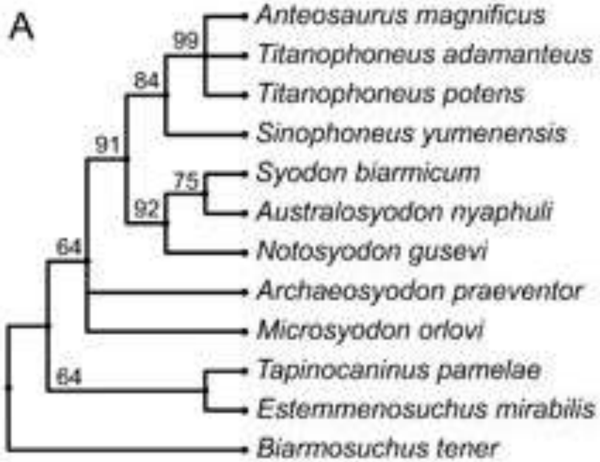
```
Anteosauria
  |--Stenocybidae
  `-+-Brithopodidae / Anteosauridae
    `--Brithopodinae (paraphyletic)
       |--Archaeosyodon
       |--Syodon
       |--Brithopus
       `-+-Anteosaurinae
         |   `-+-Titanophoneus
         |     |-Admetophoneus
         |     `--Anteosaurini
         |        |--Doliosauriscus
         |        `--Anteosaurus
         `--Deuterosaurinae (Deuterosaurus only)
```



Anteosaurus



Deuterosaurus



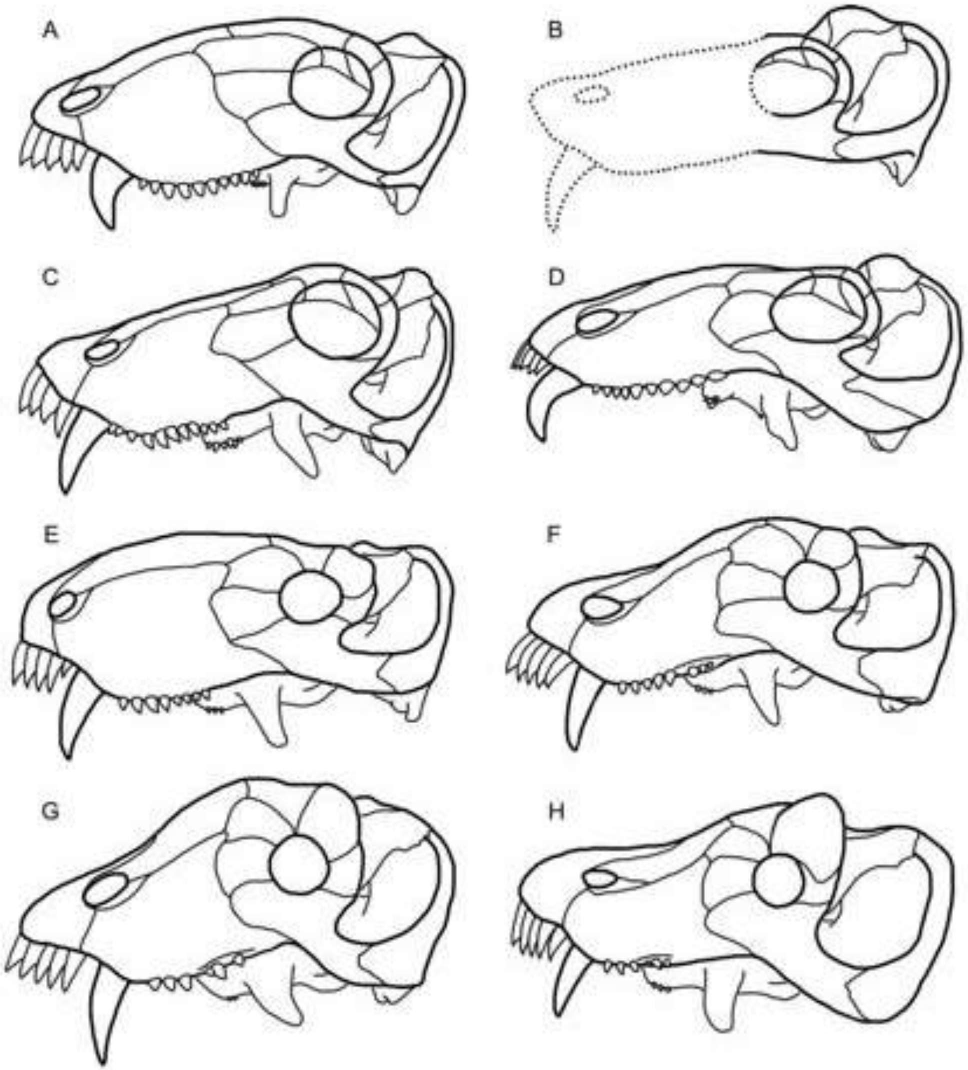
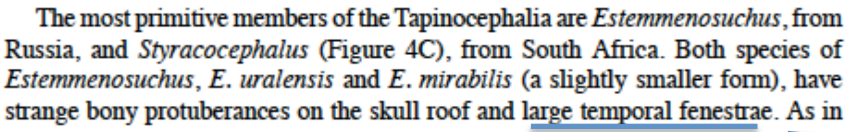


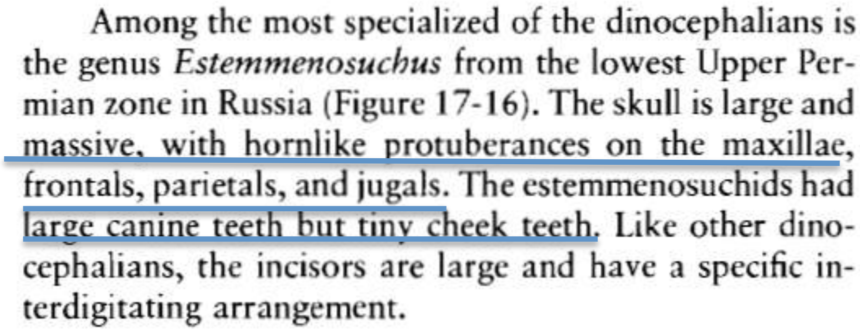
Figure 30. The skulls of all valid anteosaurid species (excluding *Microsyodon orlovi*) reconstructed in left lateral view. **A,** *Archaeosyodon praeventor*; **B,** *Notosyodon gusevi*; **C,** *Australosyodon nyaphuli*; **D,** *Syodon biarmicum*; **E,** *Sinophoneus yumenensis*; **F,** *Titanophoneus potens*; **G,** *Titanophoneus adamanteus*; **H,** *Anteosaurus magnificus*.

basales

Estemmenosuchidae



The most primitive members of the Tapinocephalia are *Estemmenosuchus*, from Russia, and *Styracocephalus* (Figure 4C), from South Africa. Both species of *Estemmenosuchus*, *E. uralensis* and *E. mirabilis* (a slightly smaller form), have strange bony protuberances on the skull roof and large temporal fenestrae. As in



Among the most specialized of the dinocephalians is the genus *Estemmenosuchus* from the lowest Upper Permian zone in Russia (Figure 17-16). The skull is large and massive, with hornlike protuberances on the maxillae, frontals, parietals, and jugals. The estemmenosuchids had large canine teeth but tiny cheek teeth. Like other dinocephalians, the incisors are large and have a specific interdigitating arrangement.

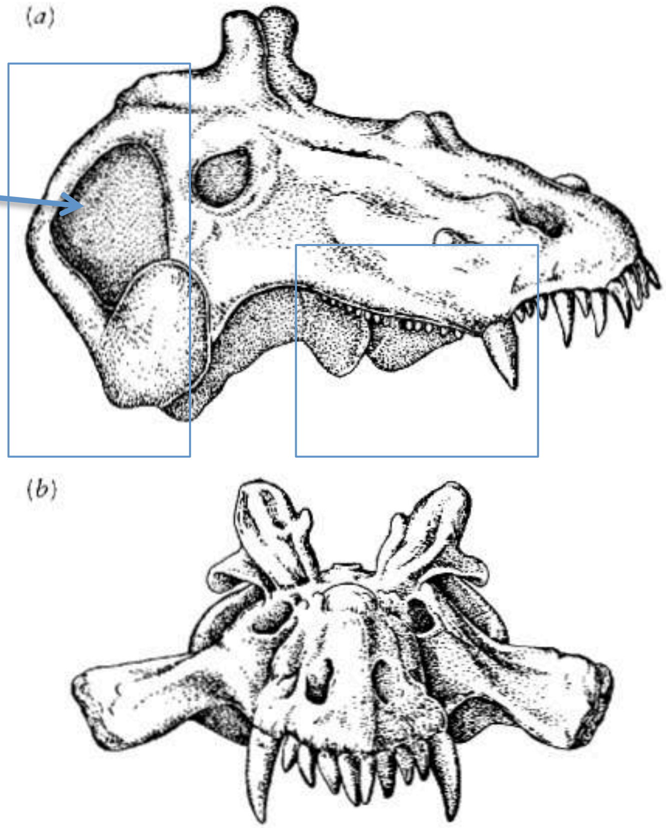
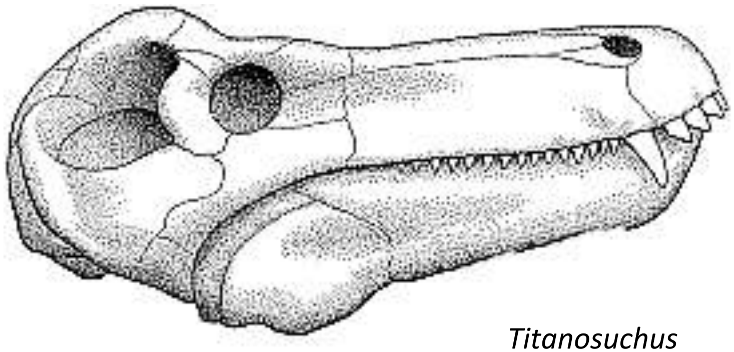
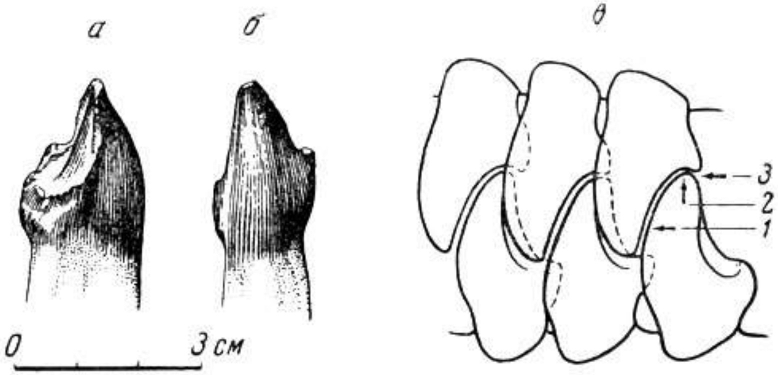


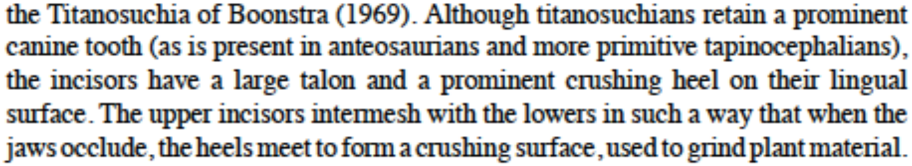
Figure 17-16. THE SKULL OF *ESTEMMENOSUCHUS*. (*a*) Lateral and (*b*) anterior views. It is one of the oldest-known therapsids, coming from the lowermost Upper Permian of Russia. The small size of the cheek teeth suggests that it was a herbivore. Its specific affinities are unknown. *From Chudinov, 1965. By permission of the University of Chicago Press.* Skull 80 cm long.

Titanosuchia + Tapinocephalidae



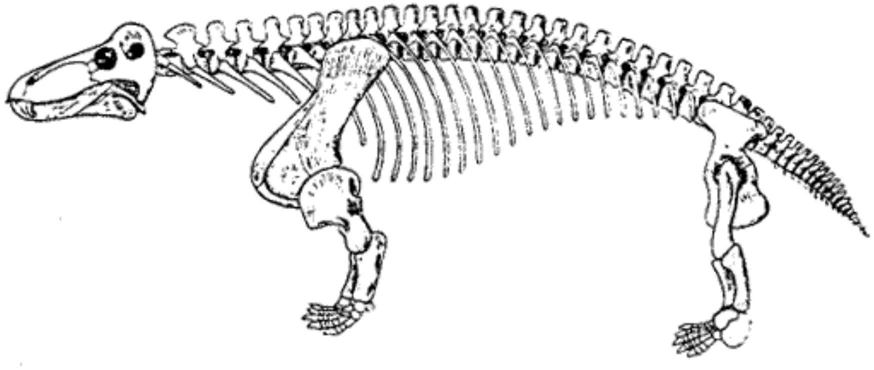
Titanosuchus





the Titanosuchia of Boonstra (1969). Although titanosuchians retain a prominent canine tooth (as is present in anteosaurians and more primitive tapinocephalians), the incisors have a large talon and a prominent crushing heel on their lingual surface. The upper incisors intermesh with the lowers in such a way that when the jaws occlude, the heels meet to form a crushing surface, used to grind plant material.

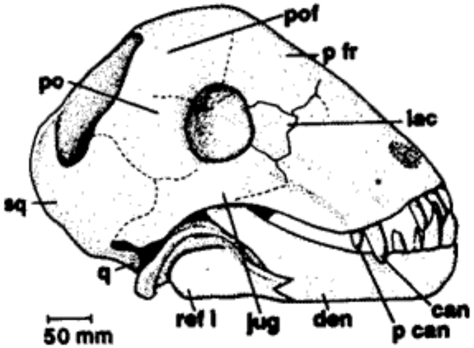
"Talones" trituradores en incisivos de especialización herbívora



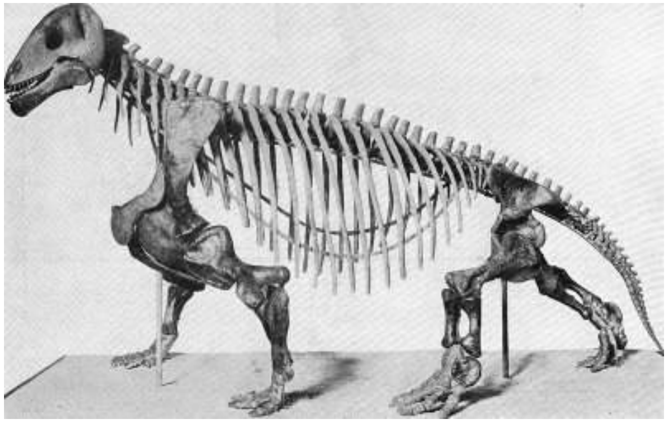
Jonkeria: Pérdida total de dentición

Tapinocephalidae

Ulemosaurus



Tapinocaninus: Tapinocephalidae basal, aún presenta caninos



Moschops

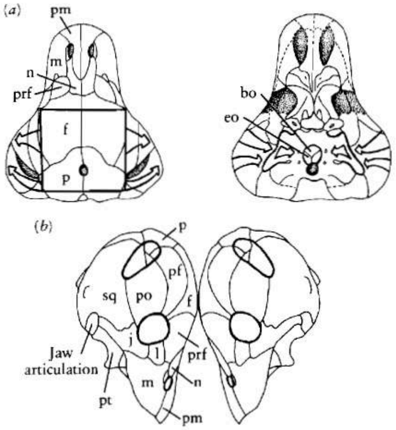
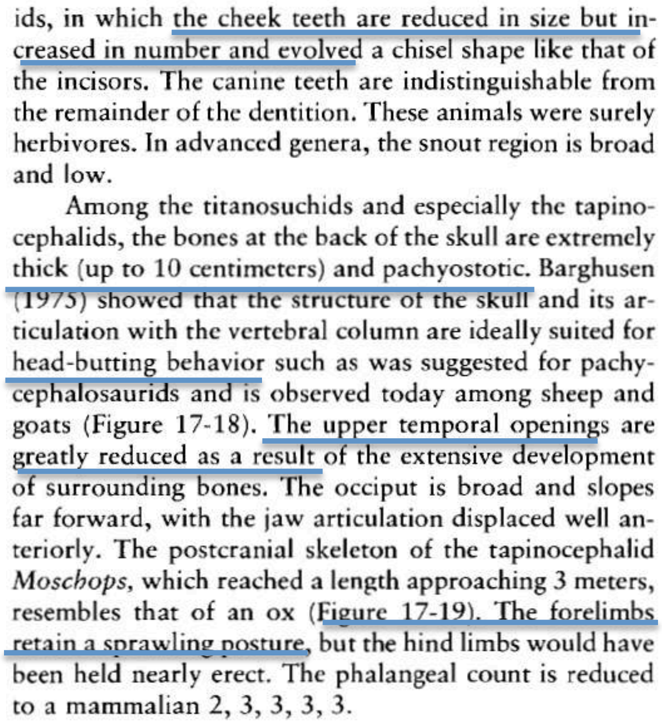


Figure 17-18. (*a*) Skull of the dinocephalian *Moschops* showing areas of dorsal thickening and distribution of forces produced when head butting. (*b*) Orientation of skulls at time of contact. Abbreviations as in Figure 8-3. *From Barghusen, 1975.*



ids, in which the cheek teeth are reduced in size but increased in number and evolved a chisel shape like that of the incisors. The canine teeth are indistinguishable from the remainder of the dentition. These animals were surely herbivores. In advanced genera, the snout region is broad and low.

Among the titanosuchids and especially the tapinocephalids, the bones at the back of the skull are extremely thick (up to 10 centimeters) and pachyostotic. Barghusen (1975) showed that the structure of the skull and its articulation with the vertebral column are ideally suited for head-butting behavior such as was suggested for pachycephalosaurids and is observed today among sheep and goats (Figure 17-18). The upper temporal openings are greatly reduced as a result of the extensive development of surrounding bones. The occiput is broad and slopes far forward, with the jaw articulation displaced well anteriorly. The postcranial skeleton of the tapinocephalid *Moschops*, which reached a length approaching 3 meters, resembles that of an ox (Figure 17-19). The forelimbs retain a sprawling posture, but the hind limbs would have been held nearly erect. The phalangeal count is reduced to a mammalian 2, 3, 3, 3, 3.

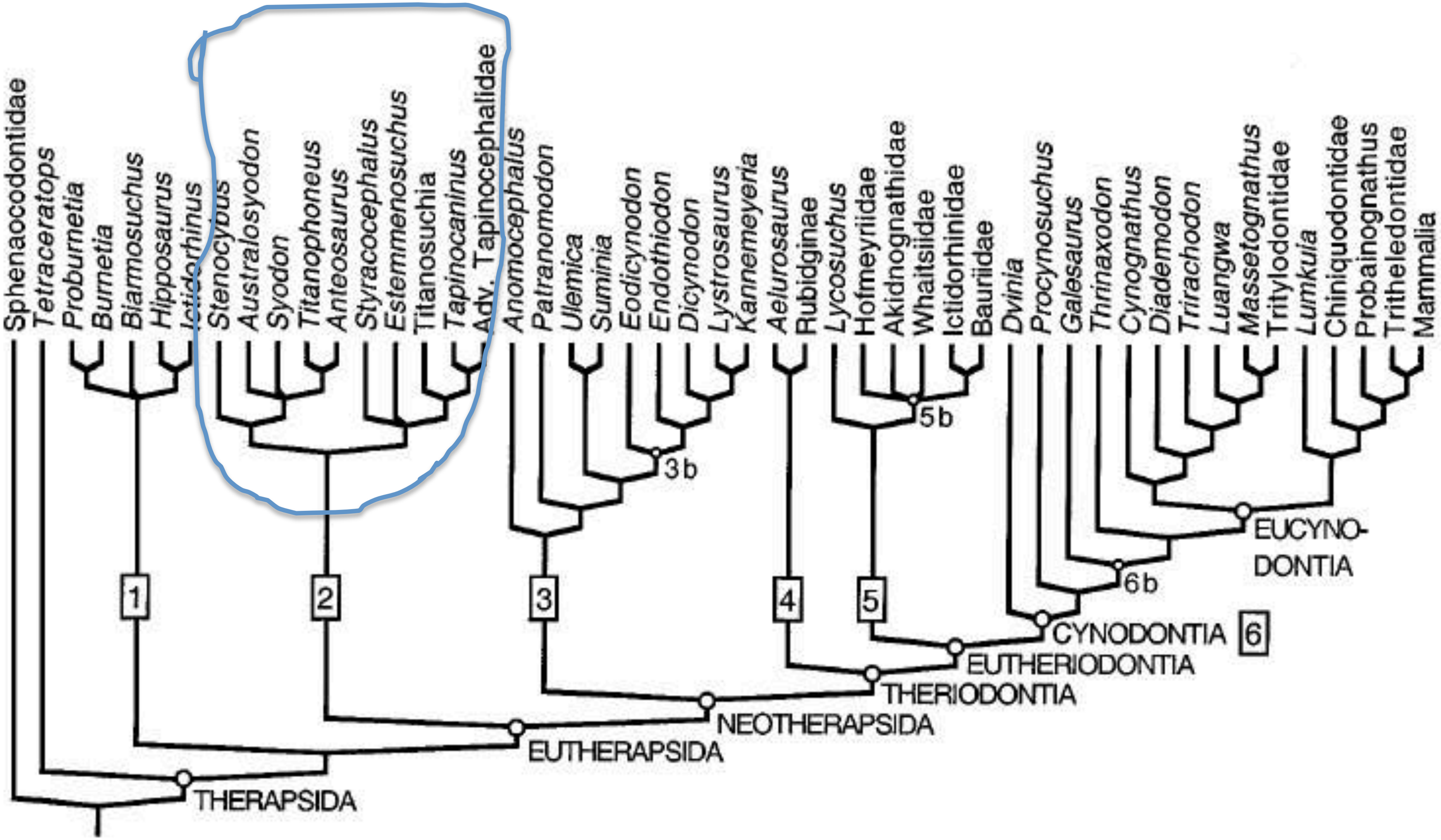


Figure 3 Cladogram of the therapsid groups considered in the text. 1, Biarmosuchia; 2, Dinocephalia; 3, Anomodontia; 3b, Dicynodontia; 4, Gorgonopsia; 5, Therocephalia; 5b, Eutherocephalia; 6, Cynodontia; 6b, Epicynodontia. This cladogram is by no means exhaustive. For example, only the most derived pelycosaur family is shown here (e.g., Sphenacodontidae). Relationships depicted here are based on those proposed by Hopson (1991, 1994), Rubidge & van den Heever (1997), Sidor & Hopson (1998), Modesto et al. (1999) and B. S. Rubidge & C. A. Sidor (unpublished data). See text for further details.

Neotherapsida?: Anomodontia + Theriodontia

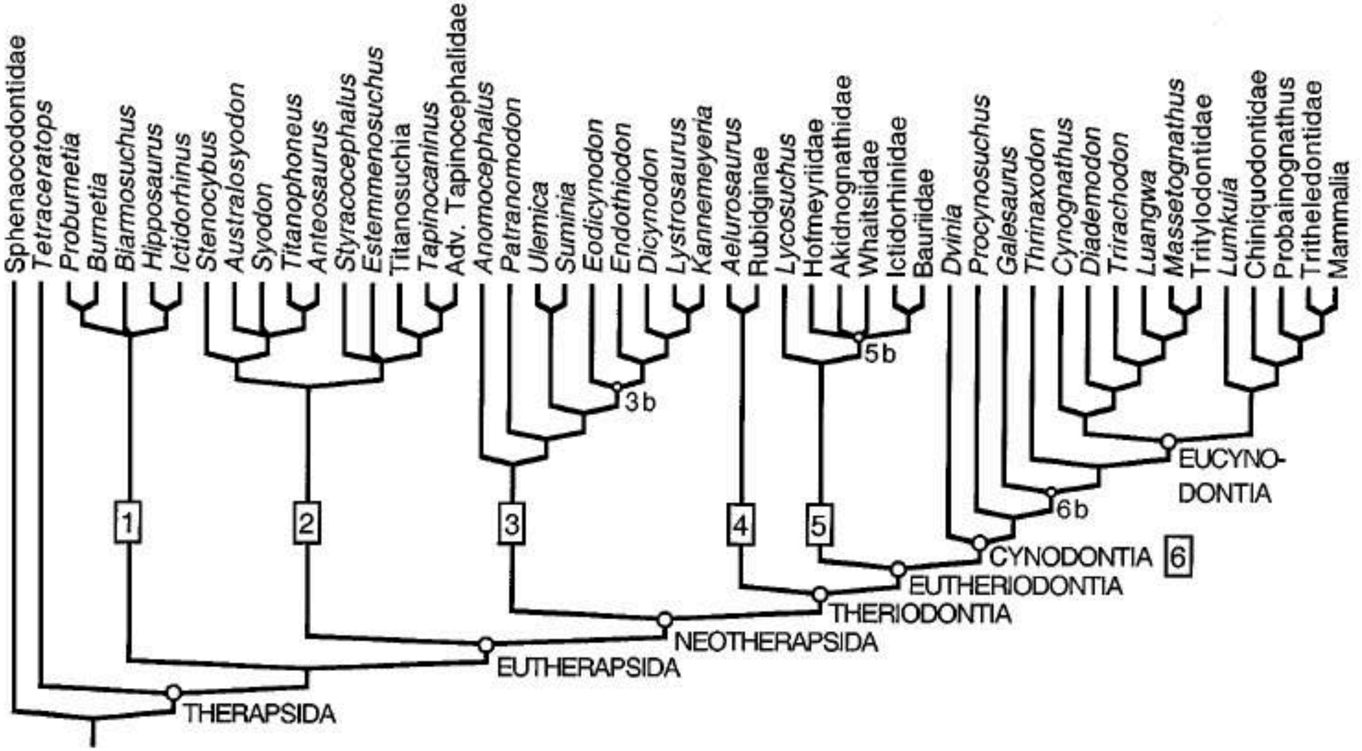


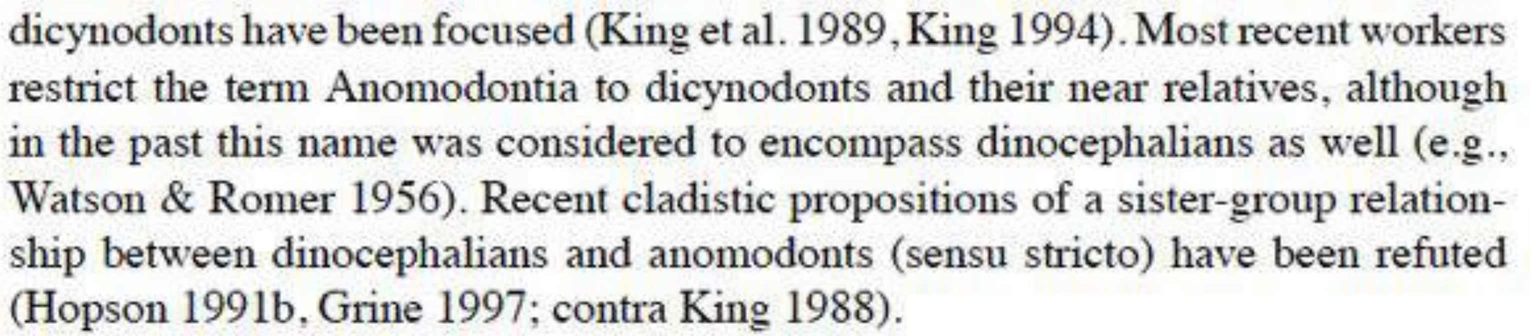
Figure 3 Cladogram of the therapsid groups considered in the text. 1, Biarmosuchia; 2, Dinocephalia; 3, Anomodontia; 3b, Dicynodontia; 4, Gorgonopsia; 5, Therocephalia; 5b, Eutherocephalia; 6, Cynodontia; 6b, Epicynodontia. This cladogram is by no means exhaustive. For example, only the most derived pelycosaur family is shown here (e.g., Sphenacodontidae). Relationships depicted here are based on those proposed by Hopson (1991, 1994), Rubidge & van den Heever (1997), Sidor & Hopson (1998), Modesto et al. (1999) and B. S. Rubidge & C. A. Sidor (unpublished data). See text for further details.

ANOMODONTIA **Herbívoros de hocico corto.** Dorsally elevated zygomatic arch and septomaxilla lacking elongated posterodorsal process between nasal and maxilla. **Los Dicynodontia son sus representantes más abundantes, con dientes reducidos o ausentes, excepto los caninos**

Dicynodontia:

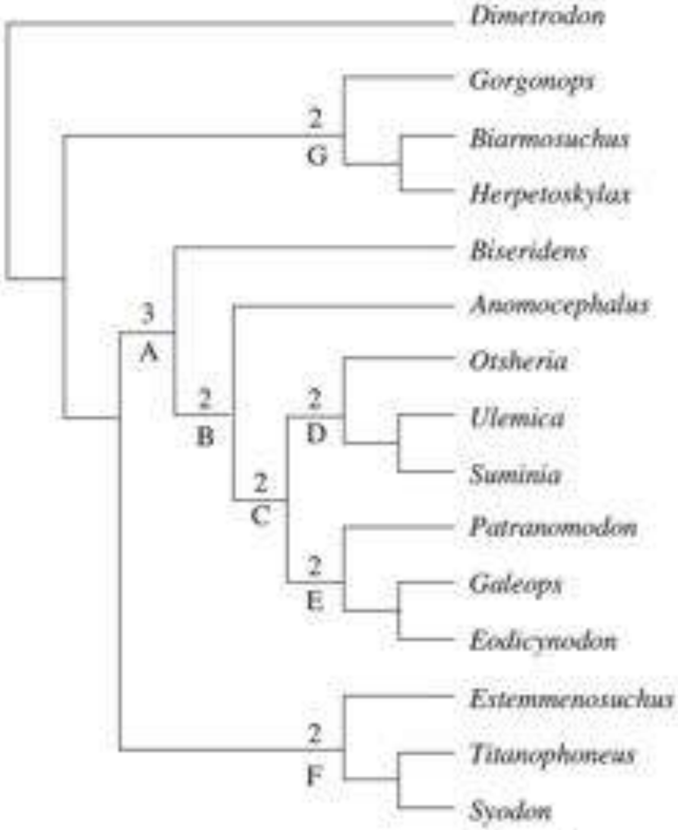
Lystrosaurus

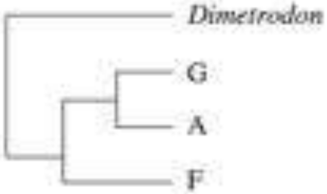
Tiarajudens



dicynodonts have been focused (King et al. 1989, King 1994). Most recent workers restrict the term Anomodontia to dicynodonts and their near relatives, although in the past this name was considered to encompass dinocephalians as well (e.g., Watson & Romer 1956). Recent cladistic propositions of a sister-group relationship between dinocephalians and anomodonts (sensu stricto) have been refuted (Hopson 1991b, Grine 1997; contra King 1988).

Biseridens: anomodonto más basal





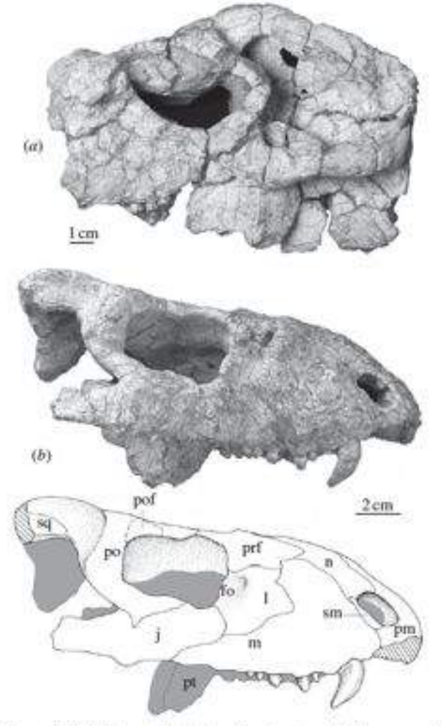
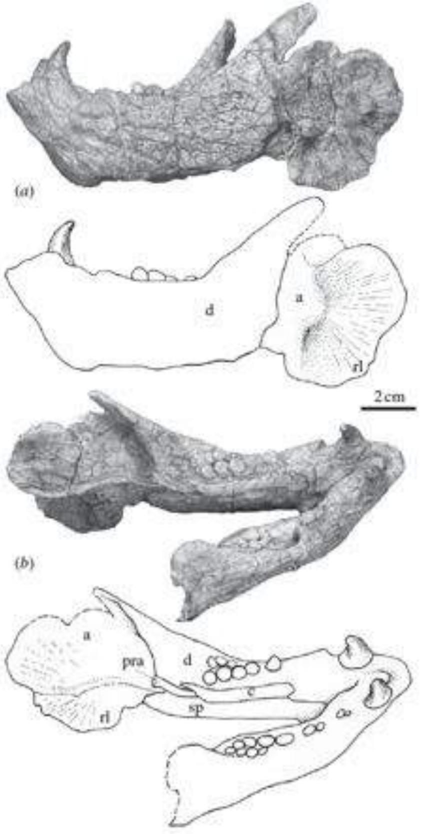


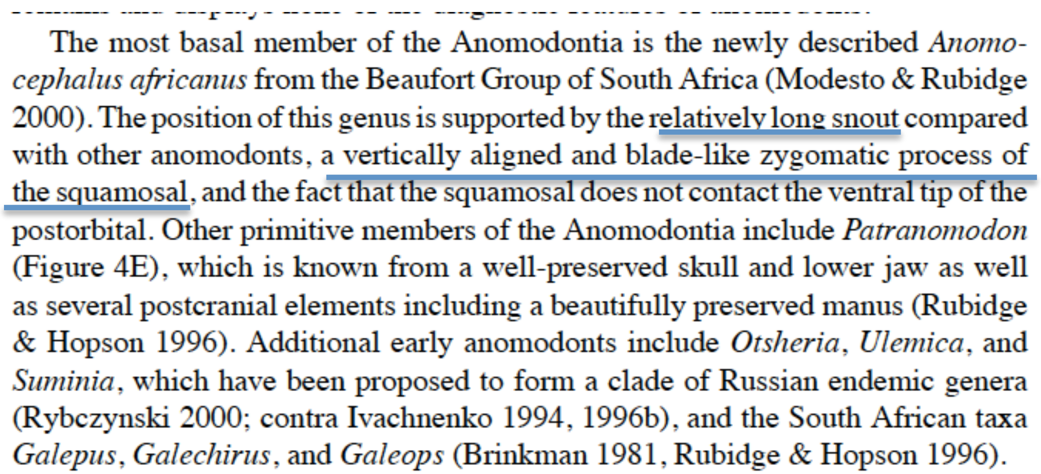
Figure 3. *Biseridens qilianicus* in lateral view. (*a*) Photograph of the holotype IGCAGS V 632 and (*b*) photograph and interpretative drawing of IVPP V 16013. Abbreviations as in figure 1.



El árbol inferior es igualmente parsimonioso: Dinocefalia+Anomodontia, a exclusión de Theriodontia

The following synapomorphies distinguish ***Biseriden***s as an anomodont and not an eotitanosuchian as previously described: **short snout; dorsally elevated zygomatic arch and septomaxilla lacking elongated posterodorsal process between nasal and maxilla**. The presence of a differentiated tooth row; denticles on vomer, palatine and pterygoid; contact between tabular and opisthotic; lateral process of transverse flange of pterygoid free of posterior ramus **and absence of mandibular foramen** exclude it from other anomodonts.

Anomodontos basales



The most basal member of the Anomodontia is the newly described *Anomocephalus africanus* from the Beaufort Group of South Africa (Modesto & Rubidge 2000). The position of this genus is supported by the relatively long snout compared with other anomodonts, a vertically aligned and blade-like zygomatic process of the squamosal, and the fact that the squamosal does not contact the ventral tip of the postorbital. Other primitive members of the Anomodontia include *Patranomodon* (Figure 4E), which is known from a well-preserved skull and lower jaw as well as several postcranial elements including a beautifully preserved manus (Rubidge & Hopson 1996). Additional early anomodonts include *Otsheria*, *Ulemica*, and *Suminia*, which have been proposed to form a clade of Russian endemic genera (Rybczynski 2000; contra Ivachnenko 1994, 1996b), and the South African taxa *Galepus*, *Galechirus*, and *Galeops* (Brinkman 1981, Rubidge & Hopson 1996).

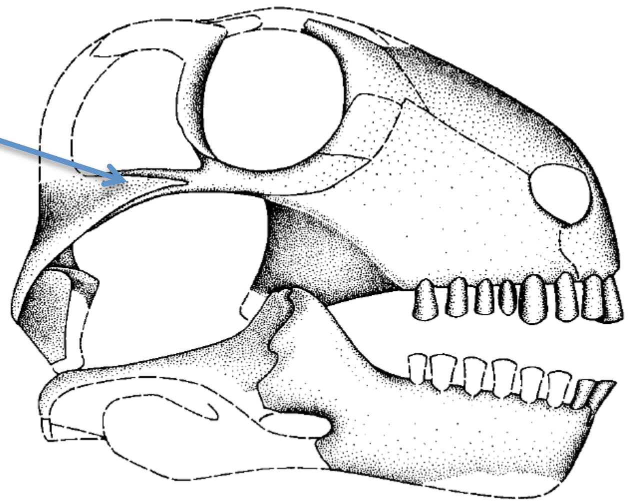
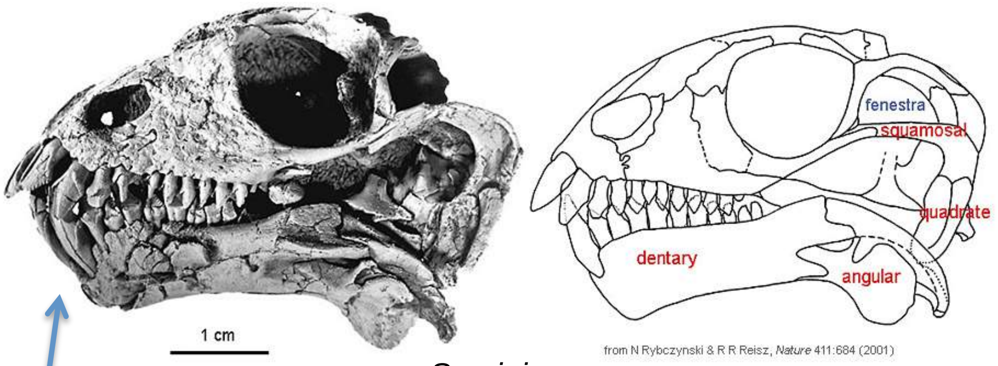


Figure 2. *Anomocephalus africanus* gen. et sp. nov. Reconstruction of the skull in right lateral view, two-fifths natural size. The outline of the quadrate flange of the pterygoid, known only from small, widely separated fragments, is omitted for clarity.

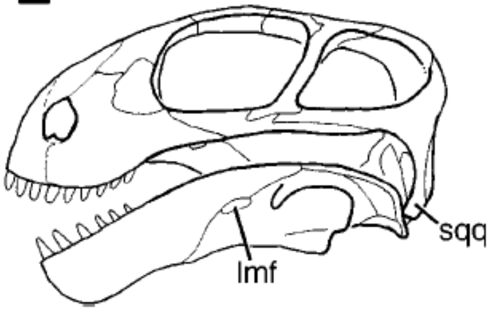


from N Rybczynski & R R Reisz, *Nature* 411:684 (2001)

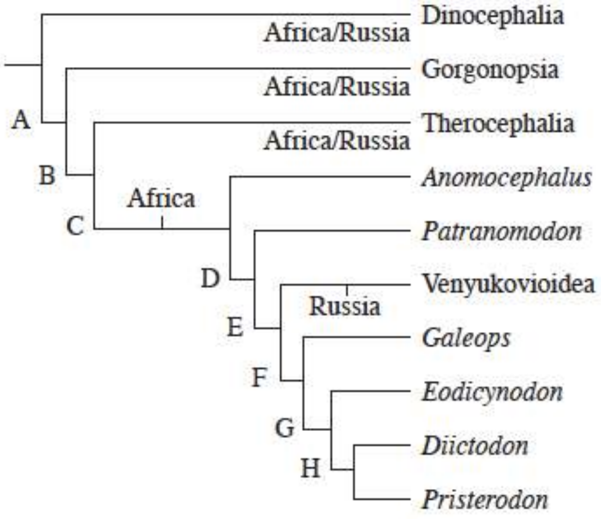
Suminia

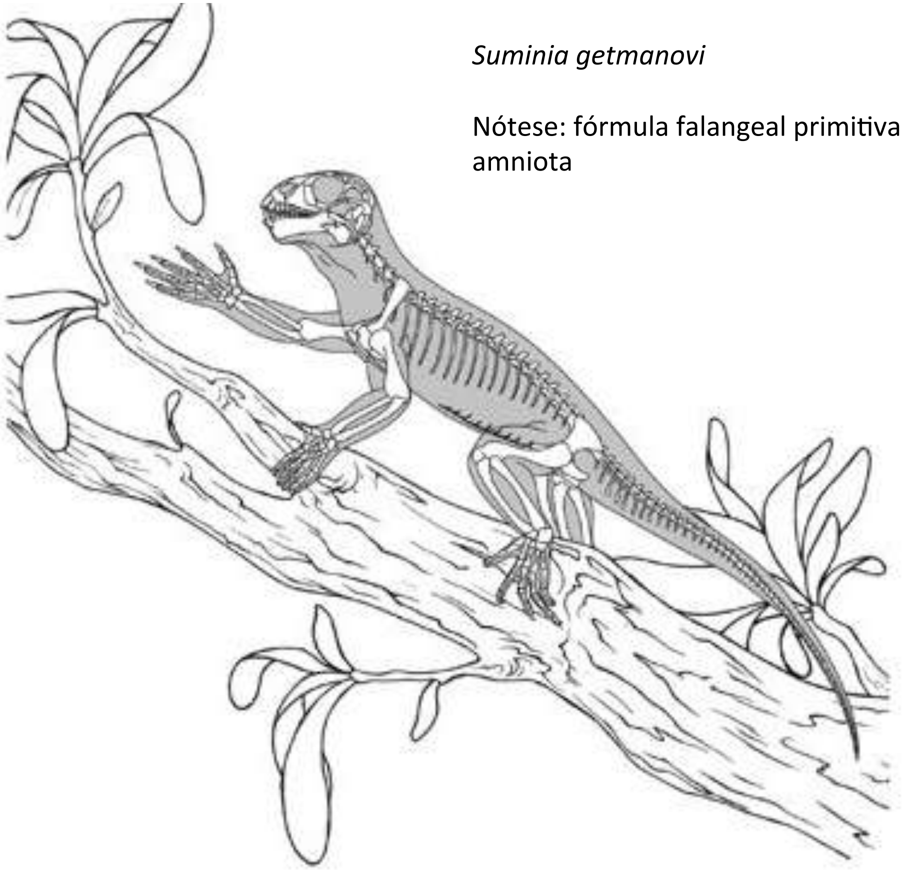
Incisivos interdigitantes!

E



Patronomodon





Suminia getmanovi

Nótese: fórmula falangeal primitiva para amniota

VENJUKOVIAMORPHA

ADVANCED HERBIVOROUS THERAPSIDS: THE ANOMODONTS

Venjukoviamorphs

The dinocephalians did not survive the end of the Permian. Most herbivorous therapsids belong to a distinct assemblage, the Anomodontia. The earliest members of this group are known in the early Russian beds and are represented by the genus *Otsheria* in Zone I and *Venjukovia* in Zone II (Figure 17-20). The skulls of these genera are small and short, superficially resembling the herbivorous pelycosaurs. The zygomatic arch is located high on the cheek and exposes the adductor musculature widely between the cheek and the lower jaw. The temporal openings have expanded posteriorly beyond the level of the occipital condyle, but they do not extend as far dorsally as those of early dinocephalians. The canine teeth are reduced and the cheek teeth are short and blunt.

The premaxillae form a broad shelf of bone anterior to the internal nares. The palate is primitive in retaining a movable basicranial articulation and a distinct transverse flange of the pterygoid, but it has lost the denticles that occupied the margin of the flange in the more primitive therapsids.

Like the latter anomodonts, the coronoid bone is lost from the lower jaw and a large mandibular foramen is evident. The dentary bones in *Venjukovia* are fused at the symphysis.

As herbivorous forms, it was long thought that the venjukoviamorphs might form a link between the primitive dinocephalians and later anomodonts. Barghusen (1976) pointed out that *Venjukovia* is more primitive than the earliest known dinocephalians in not having the adductor musculature expanded over the dorsal skull table behind the orbits. In contrast, *Venjukovia* initiated the spread of a lateral sheet of the adductor mandibulae externus, which originates on the lateral surface of the squamosal and inserts on the lateral surface of the lower jaw. Many of the specializations for a herbivorous diet are clearly different in these two groups and evolved separately. There is no evidence to ally the anomodonts with any other particular group of primitive therapsids.

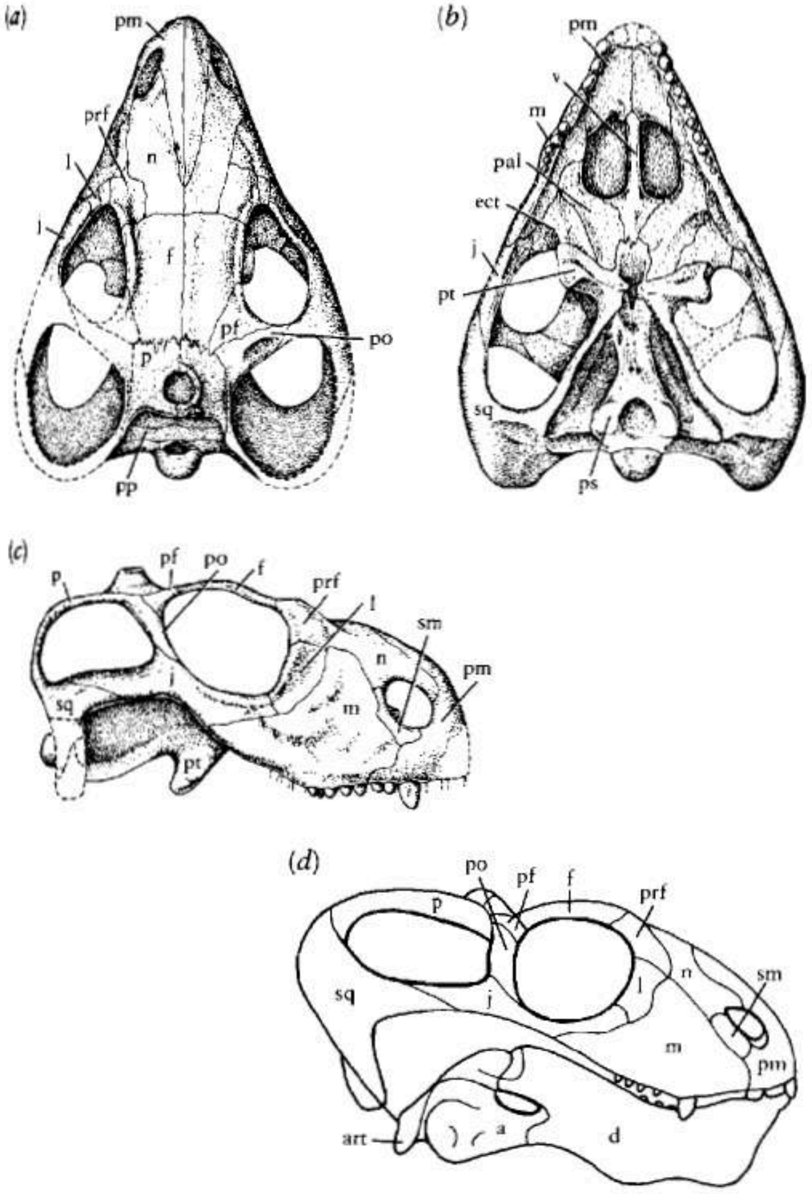


Figure 17-20. SKULLS OF PRIMITIVE UPPER PERMIAN ANOMODONTS. *Otsheria* in (*a*) dorsal, (*b*) palatal, and (*c*) lateral views, × ½. *From Chudinov, 1960.* (*d*) *Venjukovia* in lateral view, × ½. *From Barghusen, 1976.* Abbreviations as in Figure 8-3.

DROMASAURIA

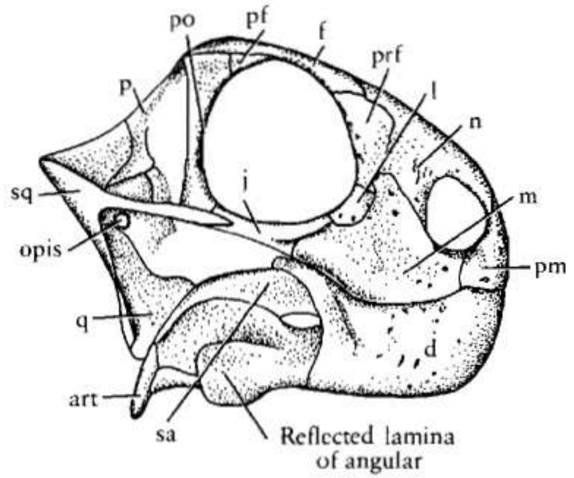


Figure 17-21. SKULL OF THE DROMASAUR *GALEOPS*. This small, agile herbivore is related to the dicynodonts. Natural size. Abbreviations as in Figure 8-3. *From Brinkman, 1981.*

ure 17-21) appears superficially like that of the venjukoviamorphs, with a high and narrow zygomatic arch, narrow postorbital bar, and narrow squamosal. It is relatively short and there is a partial secondary palate that is formed by the premaxillae. Canine teeth are not prominent and premaxillary teeth are progressively lost within the group. In contrast with venjukoviamorphs and dicynodonts, the postorbital does not extend back to the squamosal. The adductor musculature expands out of the temporal opening dorsally, and the lateral surface of the lower jaw is grooved to suggest an area for insertion of a superficial layer of the external adductor.

The limbs are long and slender, in contrast with the dicynodonts, and dromasaurs lack the key changes in the jaw apparatus that characterize that group.

Basal anomodonts have traditionally been placed in either Dromasauria or Venyukovioidea (Watson & Romer 1956). The former group was comprised of the southern African taxa *Galechirus*, *Galepus* and *Galeops*, whereas the latter consisted of the Eastern European taxa *Otsheria* and *Venyukovia* (the latter nomen is commonly misspelt '*Venjukovia*': Ivakhnenko 1994, 1996). Both groups were regarded as monophyletic (Brinkman

However, the analysis of *Patranomodon*, from the base of the Beaufort Group and then the most basal anomodont known, led Rubidge & Hopson (1990) to conclude that both Dromasauria and Venyukovioidea were paraphyletic. A corollary of their evaluation of basal anomodont

Dicynodonts

The most numerous, diverse, and long-lived anomodonts were the dicynodonts, which appeared at the very base of the Upper Permian sequence in southern Africa, became worldwide in distribution in the Lower Triassic, and continued to the end of the Triassic. They were by far the most abundant of terrestrial vertebrates in the late Permian and early Triassic but lost ground by the mid-Triassic, perhaps in competition with rhynchosaurs and herbivorous cynodonts.

large genera, the rear limbs were held erect, but the fore limbs were sharply bent at the elbow. In all members, the phalangeal count was reduced to 2, 3, 3, 3, 3. The postcranial skeleton varied in relationship to body weight and to different ways of life that ranged from semiaquatic to subterranean, but the skull shows a remarkable consistency in its proportions that is related to a unique specialization of the feeding apparatus.

premaxilla and anterior portion of the dentary are edentulous in *Eodicynodon*. Both of these areas are pock-marked with numerous foramina that suggest the presence of a horny covering in life. Adding to their unusual appearance, the dicynodont dentition consists of paired, tusk-like upper caniniforms (tk in Figure 4) and a vestigal complement of small postcanine teeth. These features, in addition to their characteristic sliding jaw joint, have been traditionally regarded as underlying the success of dicynodonts (Crompton & Hotton 1967, Barghusen 1976, King 1994).

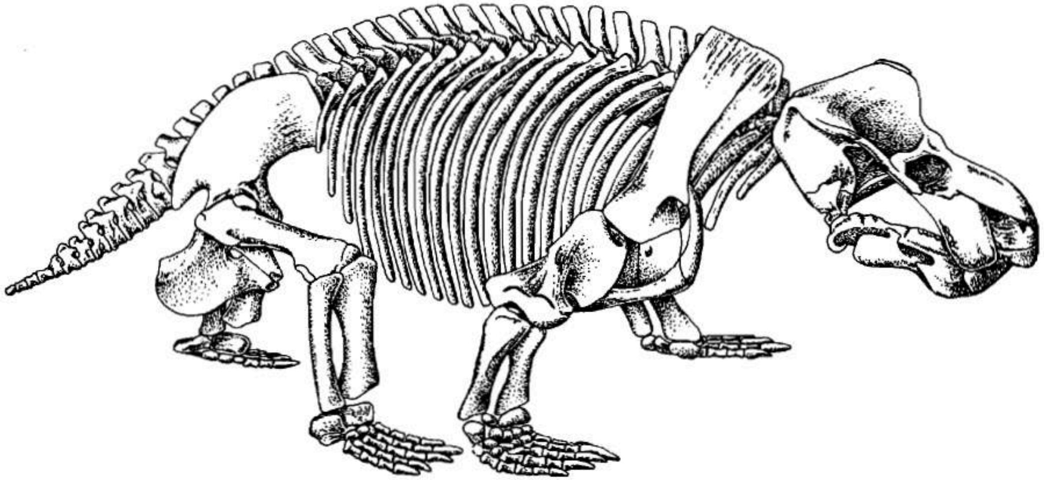


Figure 17-25. SKELETON OF THE LARGE DICYNODONT *KANNEMEYERIA*. From the Lower Triassic of southern Africa, approximately 3 meters long. *From Pearson, 1924. By permission of the Zoological Society of London.*

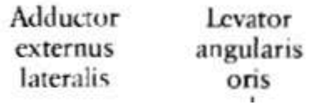
rial, but the specific diet must have been different in genera such as *Lystrosaurus*, which is thought to have been semiaquatic, huge terrestrial animals such as *Kannemeyeria* from the Lower Triassic (Figure 17-25) and *Placerias* from the Upper Triassic, which have the body proportions of large grazing or browsing mammals, and small forms with wedged-shaped skulls such as *Cistecephalus* and *Kawingasaurus*, in which the limbs and girdles suggest a burrowing habitus (Cox, 1972, Cluver, 1978).

ARTICULACIÓN DESLIZANTE DE LA MANDÍBULA

The configuration of the jaw articulation differs significantly from that of venjukoviamorphs. The articulating surface of the articular is approximately twice as long as that of the quadrate. The surface of both bones is convex in lateral view but grooved longitudinally, which indicates that the articulating surface of the lower jaw was translated across that of the quadrate, in contrast with the simple hinge joint of most tetrapods.

The shape of the jaws and temporal region shows that the major muscles that opened and closed the mouth were oriented nearly horizontally, which suggests that anterior and posterior movements of the jaw were of great importance (Figure 17-23).

Within the anomodonts, a major new muscle mass has evolved. Already in the venjukoviamorphs, the adductor mandibulae externus was widely exposed laterally. Barghusen (1976) identified a depression on the lateral surface of the lower jaw into which inserted a superficial portion of this muscle. The origin may have been in the process of shifting from the medial surface of the back of



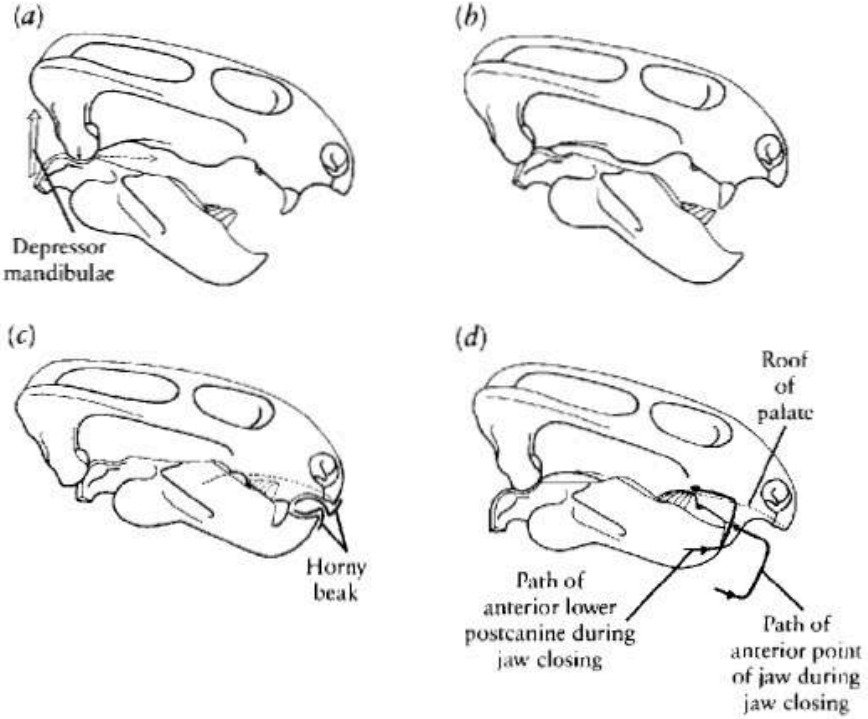
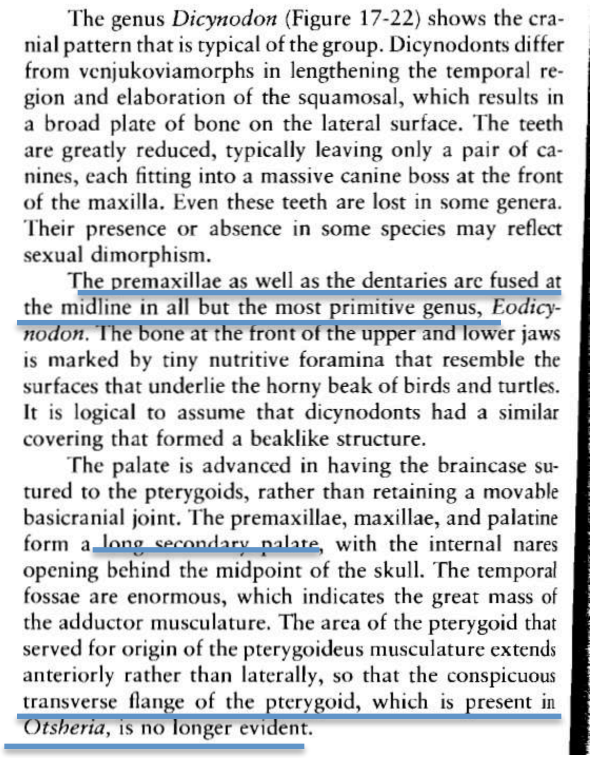


Figure 17-24. LATERAL VIEW OF THE SKULL IN THE PRIMITIVE DICYNODONT *EMYDOPS*. Stages in the masticatory cycle are illustrated. (*a*) Depression and beginning of protraction. Dashed arrow indicates direction of jaw movement. (*b*) Full protraction and beginning of elevation. (*c*) Beak bite and beginning of retraction. (*d*) Complete retraction. *From Crompton and Hotton, 1967.*



The genus *Dicynodon* (Figure 17-22) shows the cranial pattern that is typical of the group. Dicynodonts differ from venjukoviamorphs in lengthening the temporal region and elaboration of the squamosal, which results in a broad plate of bone on the lateral surface. The teeth are greatly reduced, typically leaving only a pair of canines, each fitting into a massive canine boss at the front of the maxilla. Even these teeth are lost in some genera. Their presence or absence in some species may reflect sexual dimorphism.

The premaxillae as well as the dentaries are fused at the midline in all but the most primitive genus, *Eodicynodon*. The bone at the front of the upper and lower jaws is marked by tiny nutritive foramina that resemble the surfaces that underlie the horny beak of birds and turtles. It is logical to assume that dicynodonts had a similar covering that formed a beaklike structure.

The palate is advanced in having the braincase sutured to the pterygoids, rather than retaining a movable basicranial joint. The premaxillae, maxillae, and palatine form a long secondary palate, with the internal nares opening behind the midpoint of the skull. The temporal fossae are enormous, which indicates the great mass of the adductor musculature. The area of the pterygoid that served for origin of the pterygoideus musculature extends anteriorly rather than laterally, so that the conspicuous transverse flange of the pterygoid, which is present in *Otsheria*, is no longer evident.

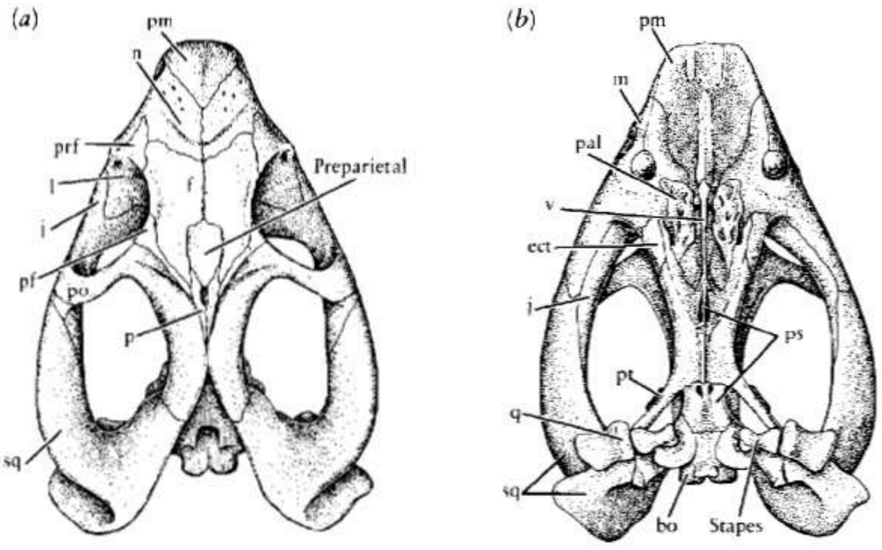
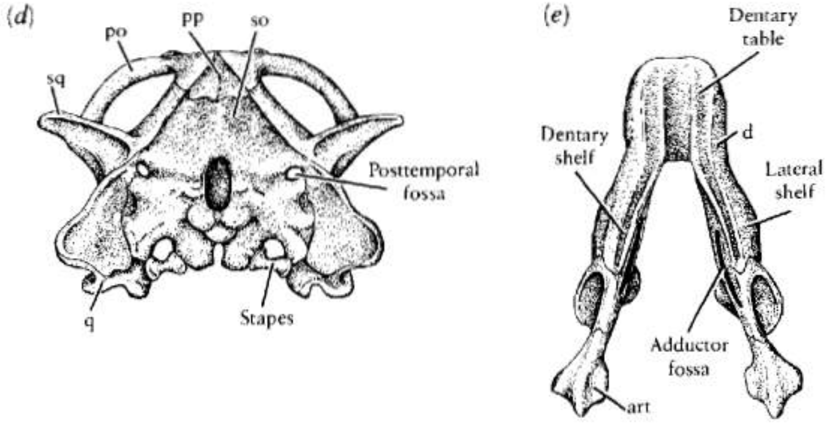
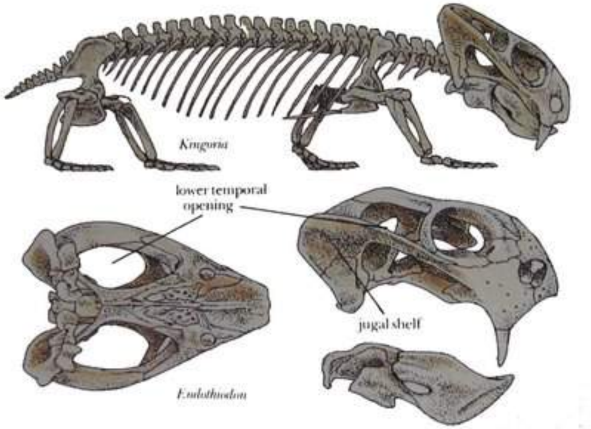


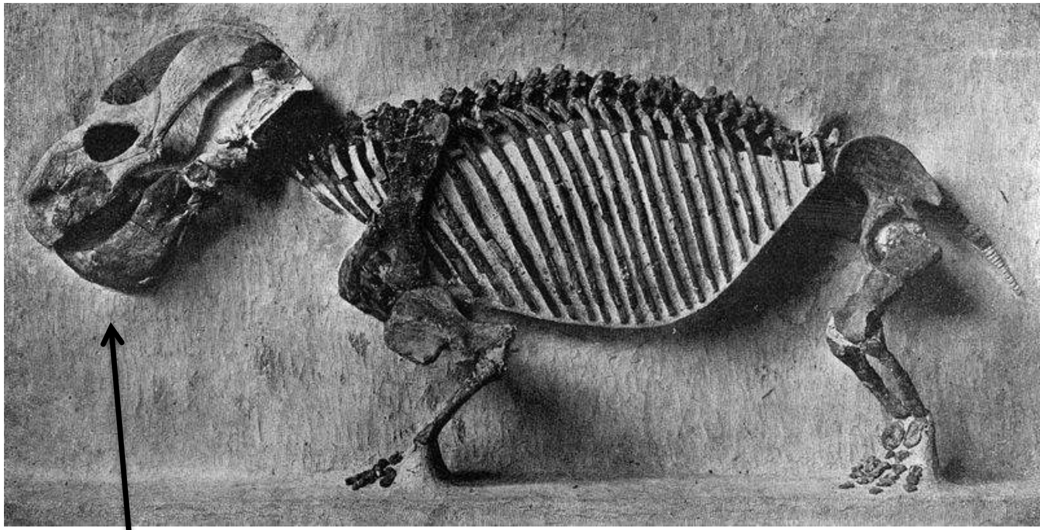
Figure 17-22. SKULL AND LOWER JAWS OF THE ADVANCED ANOMODONT *DICYNODON*. Skull in (*a*) dorsal, (*b*) palatal, (*c*) lateral, and (*d*) occipital views, $\times\frac{3}{8}$. (*e*) Lower jaw in dorsal view, $\times\frac{1}{2}$. Abbreviations as in Figure 8-3. *From Cluver and Hotton, 1981.*



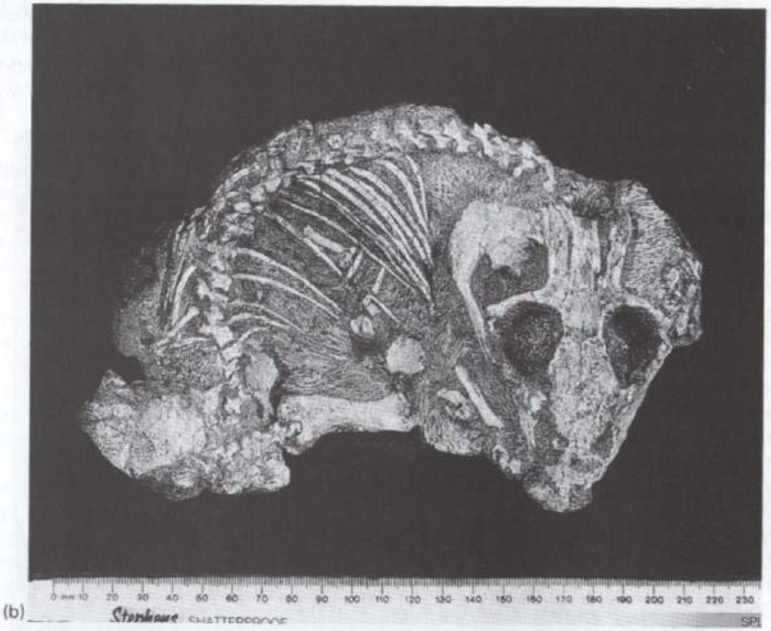
Placerias

edges. Advanced dicynodonts loose the cheek teeth entirely and shearing is limited to the more anterior region, which is increased in surface area. Neither grinding nor chewing occurred in this group; the food was comminuted entirely by shearing.





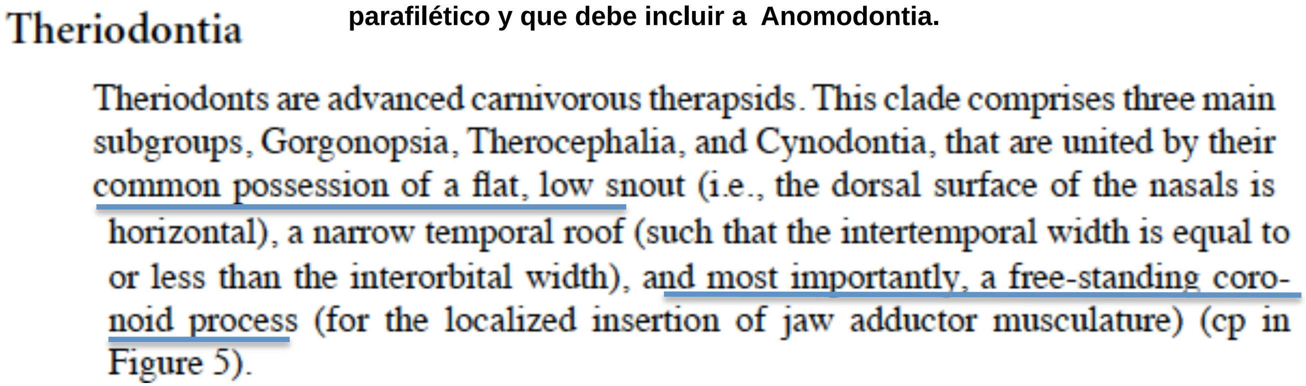
Formas derivadas **sin colmillos**



Dicynodont burrows from the Late Permian, Karoo basin, South Africa: (a) part of a corkscrew-shaped living burrow (matchbox is 50mm long); (b) skeleton of a curled-up Oudenodon, *overwhelmed by a flash-flood (skeleton is 200mm long). (Courtesy of Roger Smith.)*

THERIODONTA

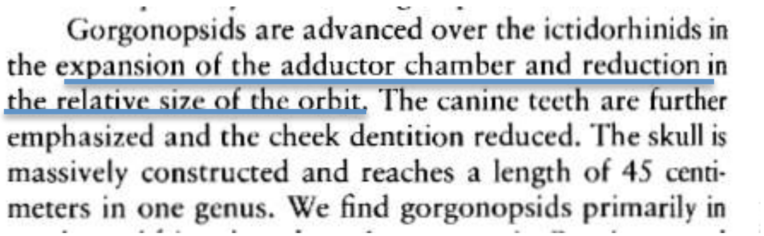
La monofilia del grupo esta discutida, algunos creen que es parafilético y que debe incluir a Anomodontia.



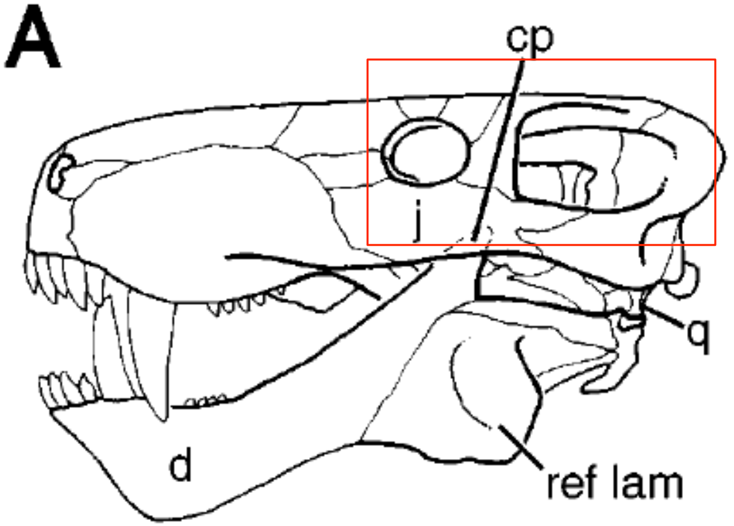
Theriodontia

Theriodonts are advanced carnivorous therapsids. This clade comprises three main subgroups, Gorgonopsia, Therocephalia, and Cynodontia, that are united by their common possession of a flat, low snout (i.e., the dorsal surface of the nasals is horizontal), a narrow temporal roof (such that the intertemporal width is equal to or less than the interorbital width), and most importantly, a free-standing coronoid process (for the localized insertion of jaw adductor musculature) (cp in Figure 5).

GORGONOPSIA:
THERIODONTOS BASALES



Gorgonopsids are advanced over the ictidorhinids in the expansion of the adductor chamber and reduction in the relative size of the orbit. The canine teeth are further emphasized and the cheek dentition reduced. The skull is massively constructed and reaches a length of 45 centimeters in one genus. We find gorgonopsids primarily in



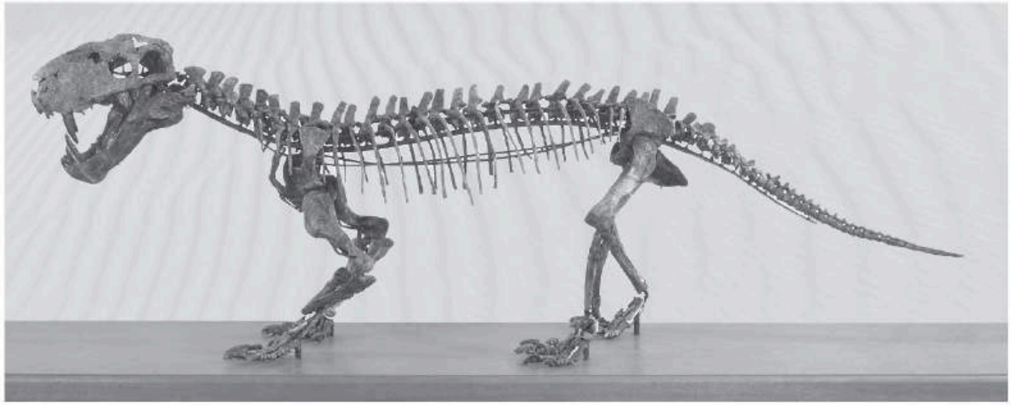


Fig. 1. The type skeleton of "*Aelurognathus*" *parringtoni* (von Huene, 1950), GPIT RE/7133, as mounted at the Palaeontological Museum of Tübingen University. – Total length is about 170 cm.

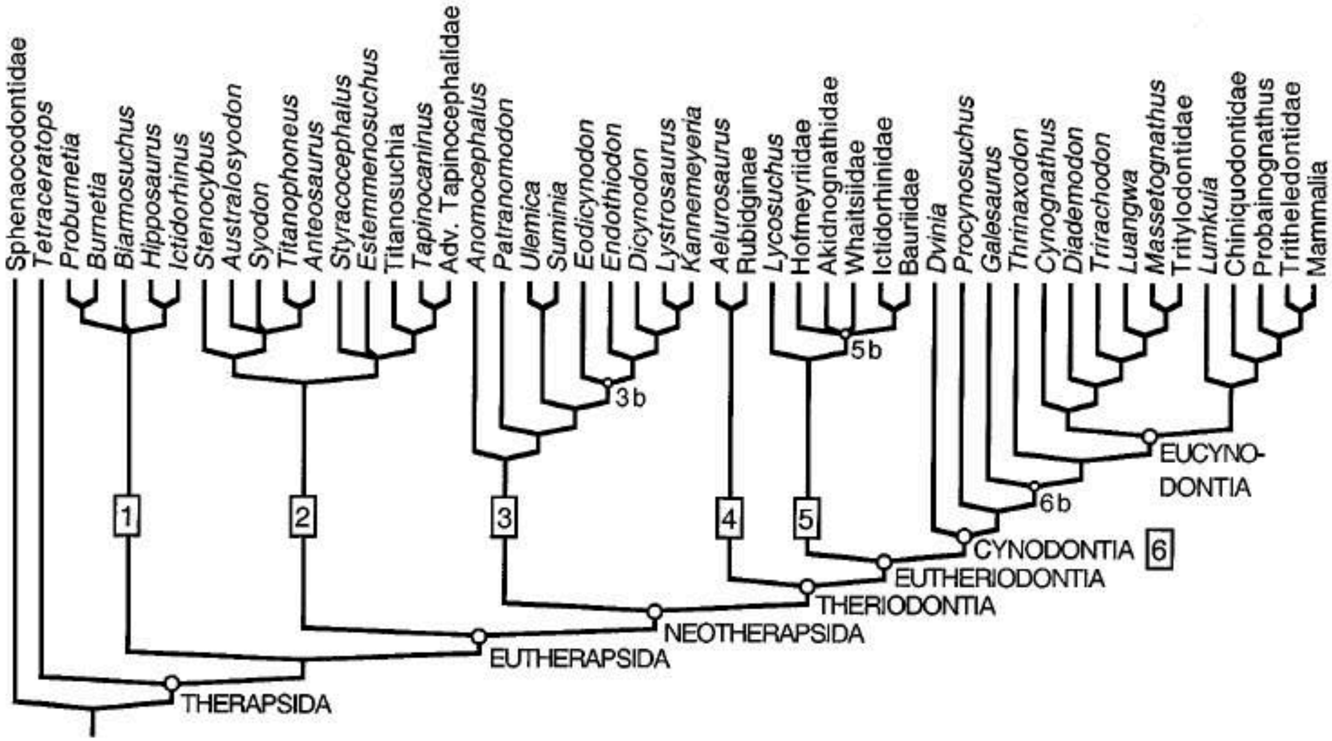
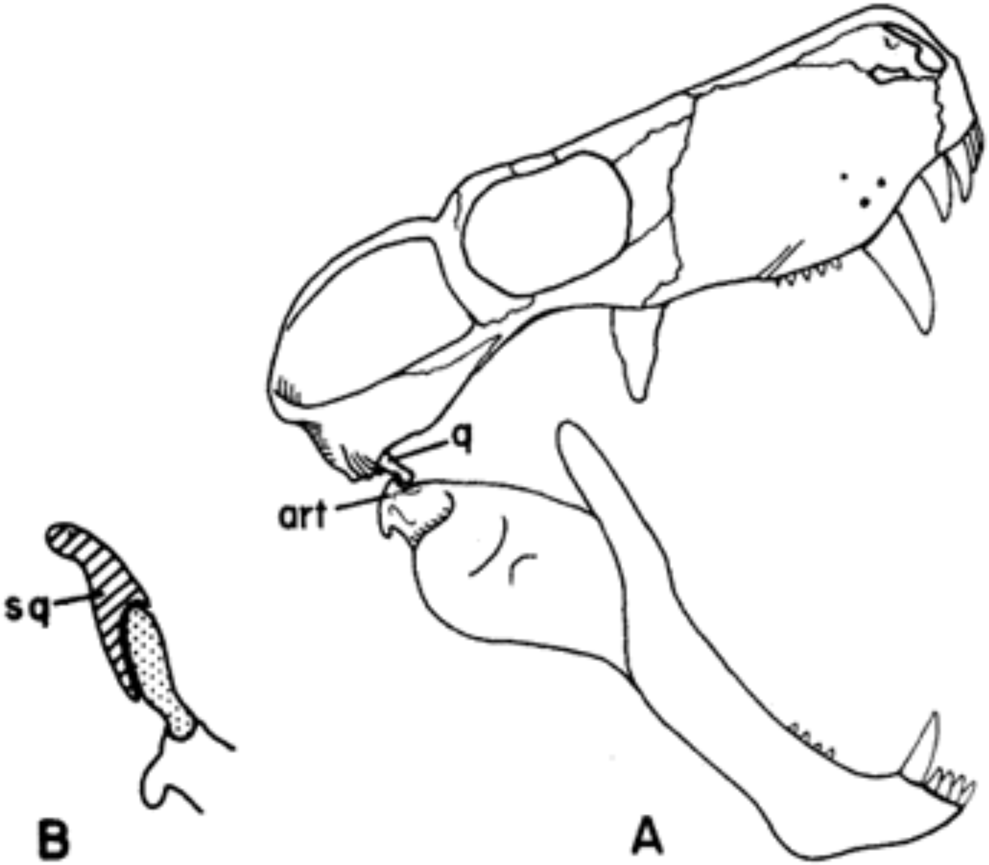


Figure 3 Cladogram of the therapsid groups considered in the text. 1, Biarmosuchia; 2, Dinocephalia; 3, Anomodontia; 3b, Dicynodontia; 4, Gorgonopsia; 5, Therocephalia; 5b, Eutherocephalia; 6, Cynodontia; 6b, Epicynodontia. This cladogram is by no means exhaustive. For example, only the most derived pelycosaur family is shown here (e.g., Sphenacodontidae). Relationships depicted here are based on those proposed by Hopson (1991, 1994), Rubidge & van den Heever (1997), Sidor & Hopson (1998), Modesto et al. (1999) and B. S. Rubidge & C. A. Sidor (unpublished data). See text for further details.

process. The lower jaw of gorgonopsians is also highly diagnostic; the reflected lamina of the angular (ref lam in Figure 5) has an attached dorsal margin and bears a unique system of lateral ridges including a near-vertical, anterior ridge in front of a deep, pocket-like depression.



features are clear: (*a*) Gorgonopsians possessed a quadrate (q in Figure 5) that was only loosely attached to the skull (i.e., they lacked a sutural connection between the quadrate and squamosal), and (*b*) when the jaw was fully opened, the shape

Gorgonopsia: “Dientes de sable”,
Con amplio rango de motilidad para abrir la mandíbula. Cola reducida en comparación a dinocéfalos carnívoros, extremidades más esbeltas

Tartarian saber-toothed protomammals of the Late Permian. These five-hundred-pound gorgonopsians had warm-blooded evolutionary style.

of the bone. Allin suggested that all the postdentary elements vibrated as a unit. The movement of the articular would be translated to the quadrate, which was only loosely attached to the squamosal. The loose attachment of the quadrate is only explicable in relationship to its mobility in consort with the bones in the lower jaw. In turn, the quadrate would have activated the stapes, which is still a large element but is lightened by the presence of a very large opening for the stapedial artery.

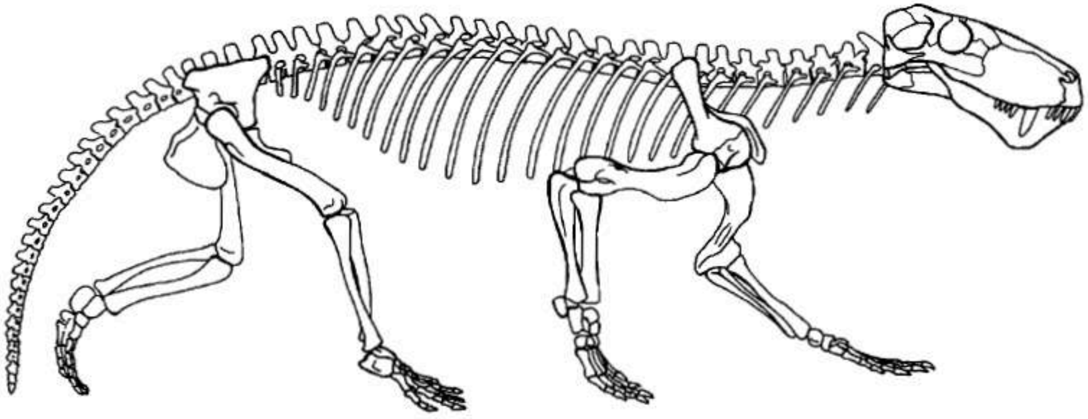
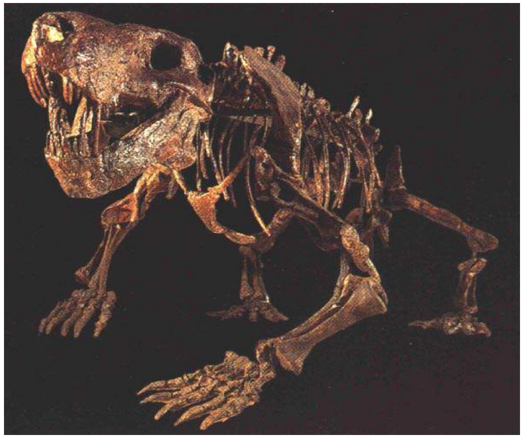
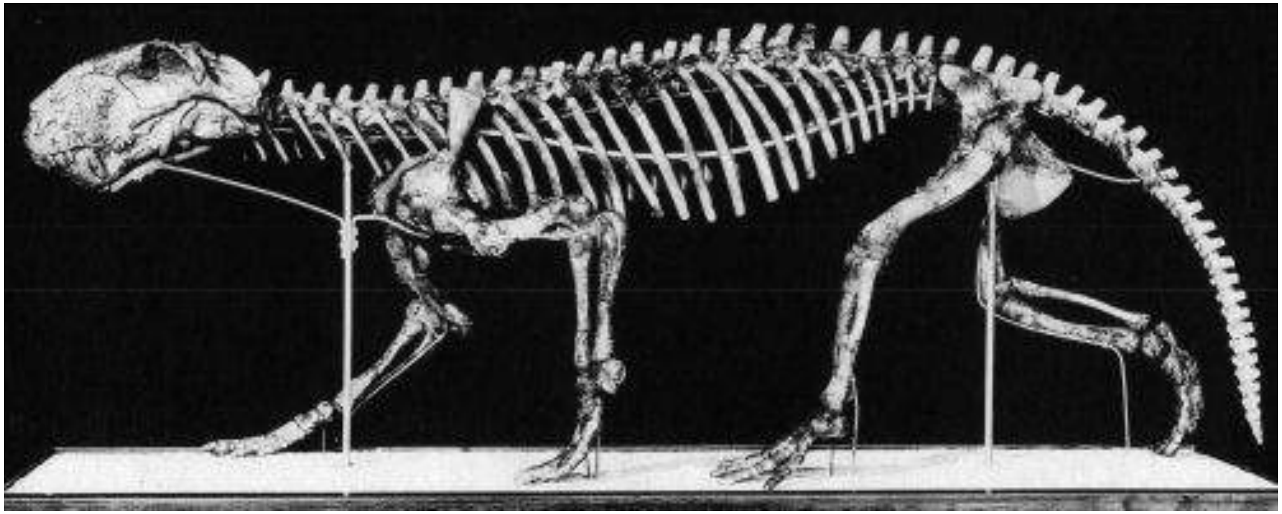
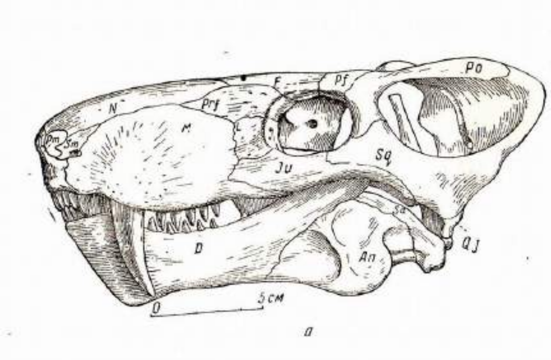


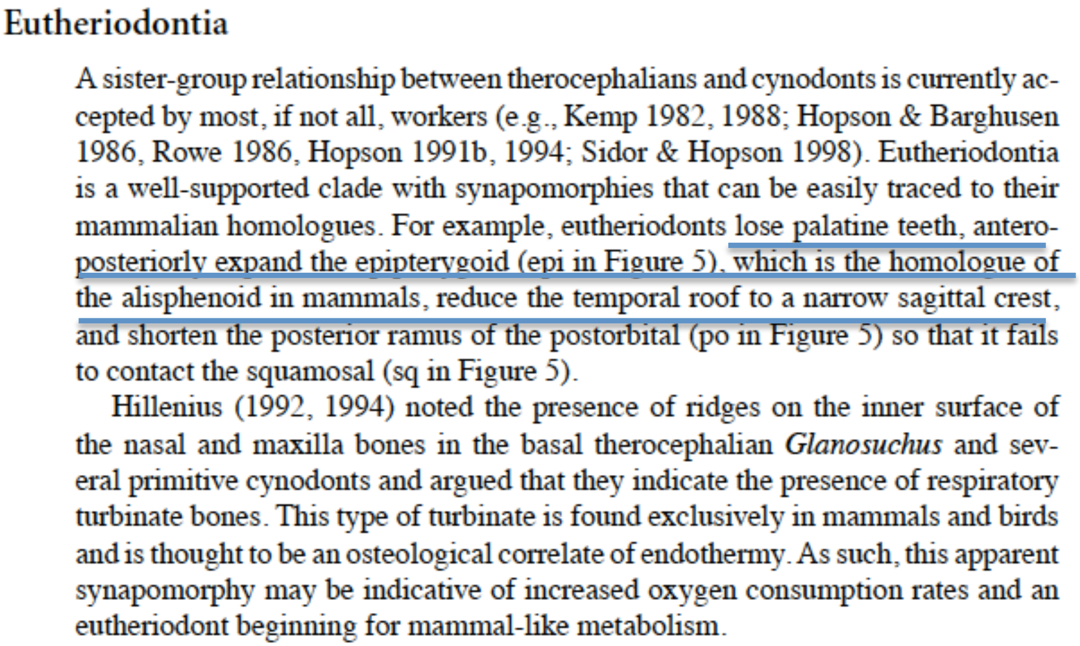
Figure 17-27. SKELETON OF THE GORGONOPSID *LYCAENOPS*, ORIGINAL 1 METER LONG. *From Colbert, 1948.*







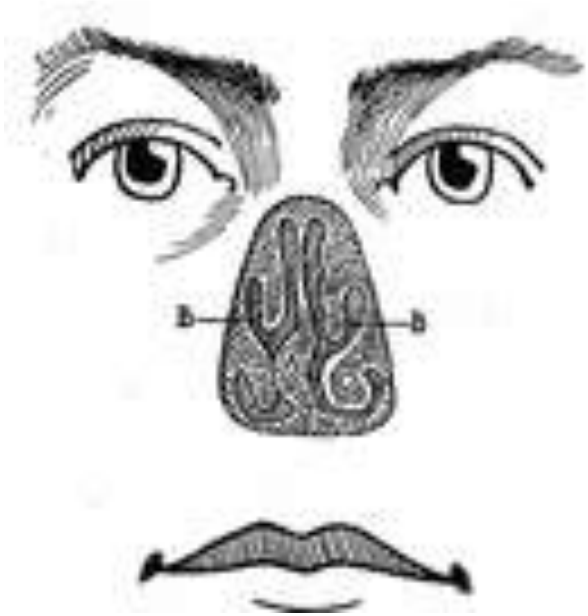
Inostrancevia



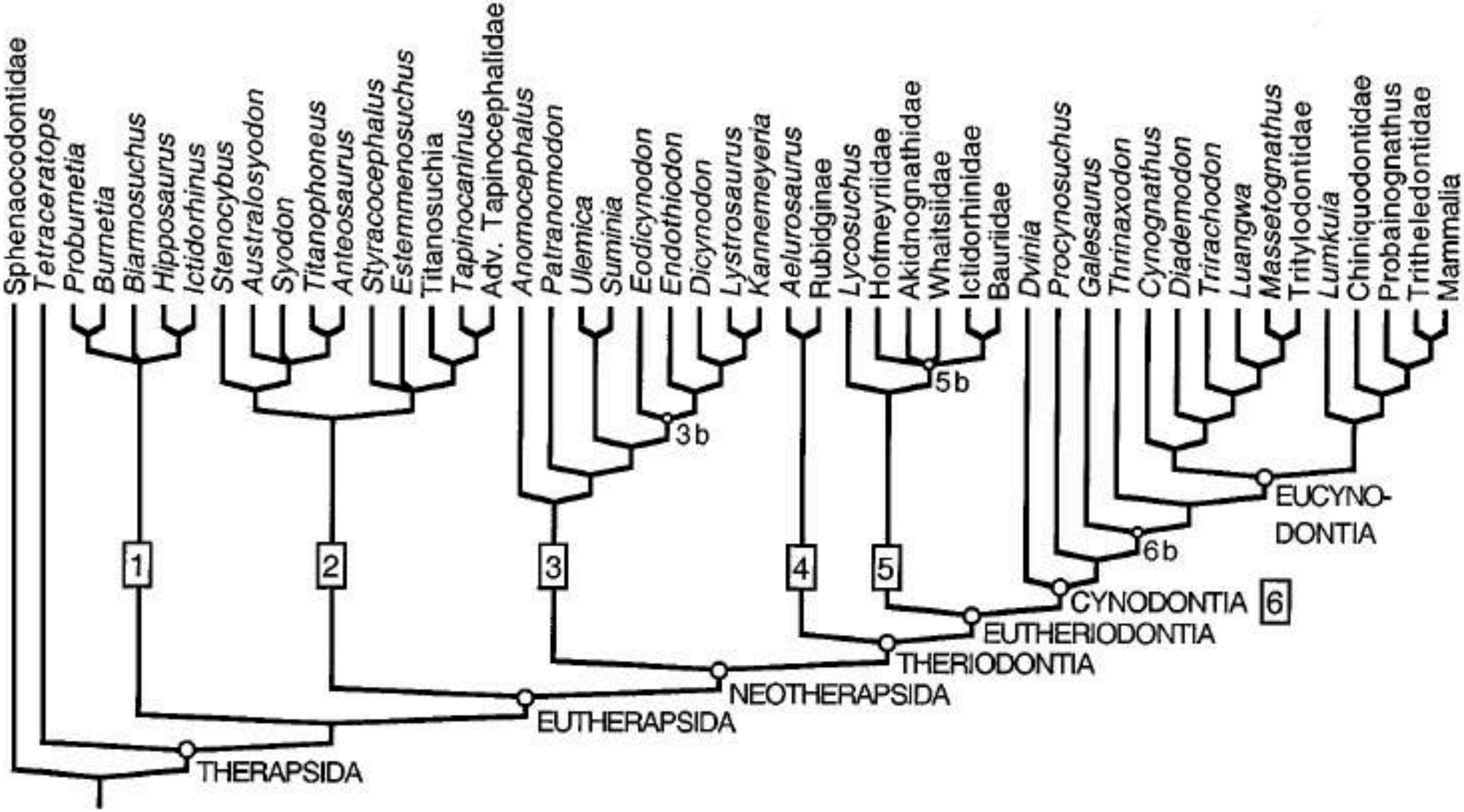
Eutheriodontia

A sister-group relationship between therocephalians and cynodonts is currently accepted by most, if not all, workers (e.g., Kemp 1982, 1988; Hopson & Barghusen 1986, Rowe 1986, Hopson 1991b, 1994; Sidor & Hopson 1998). Eutheriodontia is a well-supported clade with synapomorphies that can be easily traced to their mammalian homologues. For example, eutheriodonts lose palatine teeth, anteroposteriorly expand the epipterygoid (epi in Figure 5), which is the homologue of the alisphenoid in mammals, reduce the temporal roof to a narrow sagittal crest, and shorten the posterior ramus of the postorbital (po in Figure 5) so that it fails to contact the squamosal (sq in Figure 5).

Hillenius (1992, 1994) noted the presence of ridges on the inner surface of the nasal and maxilla bones in the basal therocephalian *Glanosuchus* and several primitive cynodonts and argued that they indicate the presence of respiratory turbinate bones. This type of turbinate is found exclusively in mammals and birds and is thought to be an osteological correlate of endothermy. As such, this apparent synapomorphy may be indicative of increased oxygen consumption rates and an eutheriodont beginning for mammal-like metabolism.



Eutheriodonte derivado,
mostrando turbinales



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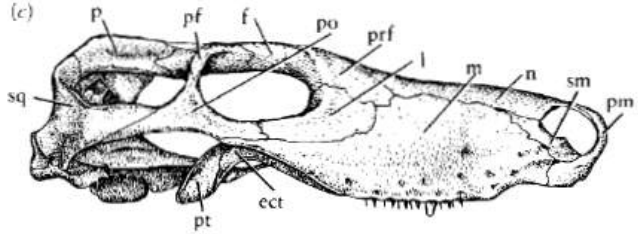
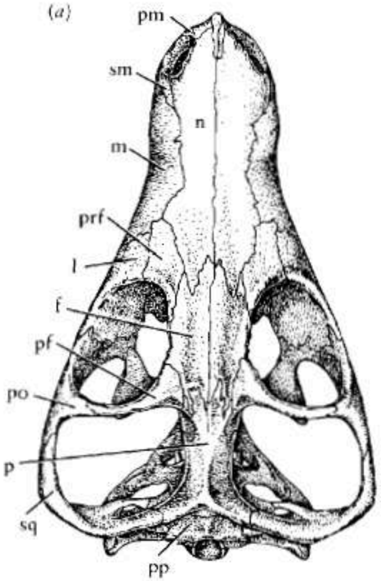
Therocephalia (monofilético)





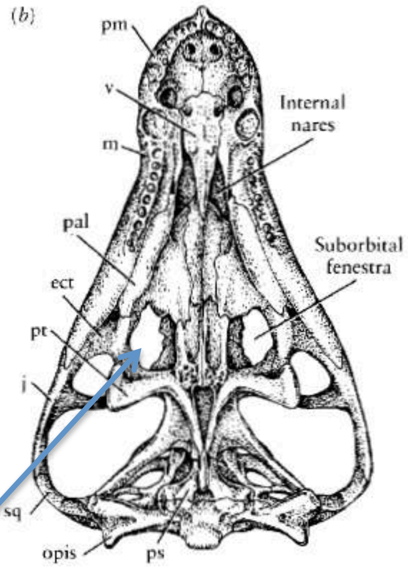


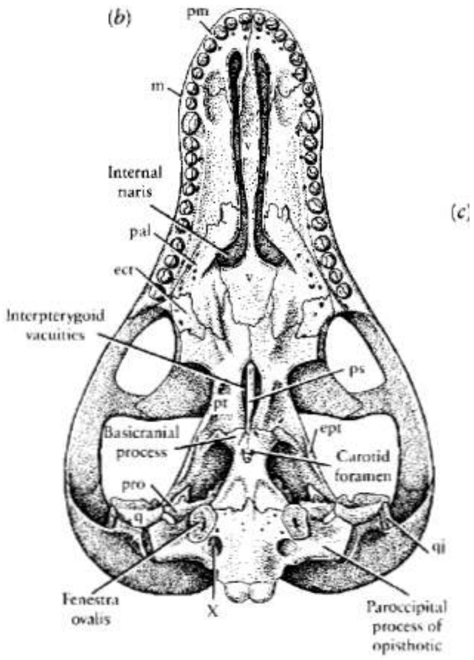
Figure 17-28. SKULL OF THE LOWER TRIASSIC THEROCEPHALIAN *REGISAURUS*. (*a*) Dorsal, (*b*) palatal, and (*c*) lateral views, × ⅔. Abbreviations as in Figure 8-3. *From Mendrez, 1972.*

By their first appearance in the fossil record, early taxa such as *Lycosuchus* and *Scylacosaurus* share several synapomorphies with all other therocephalians that indicate the monophyly of this group. Most notably, bilateral fenestrae (termed suborbital vacuities) are developed in the palate between the pterygoid, ectopterygoid, and palatine bones. In addition, the stapes is rod-like, lacking a stapedial foramen. Postcranially, the ilium of all therocephalians possesses a distinct, finger-like process that emanates from the bone's anterior margin.

Two much more advanced groups of carnivorous therapsids, the therocephalians and cynodonts, appear in the Upper Permian of Russia and southern Africa. We have not established the specific origin and interrelationships of these groups. They may have evolved separately from primitive carnivorous therapsids.

The therocephalians were much more diverse than the gorgonopsians, including small, possibly insectivorous forms (the scaloposaurids) (Figure 17-28), large carnivores (the pristerognathids), and the herbivorous bauriids. They range from the base of the Upper Permian sequence to the end of the Lower Triassic and are known in China, Antarctica, Russia, and southern and eastern Africa. Mendrez (1972, 1974, 1975, 1979) published detailed descriptions of several genera.

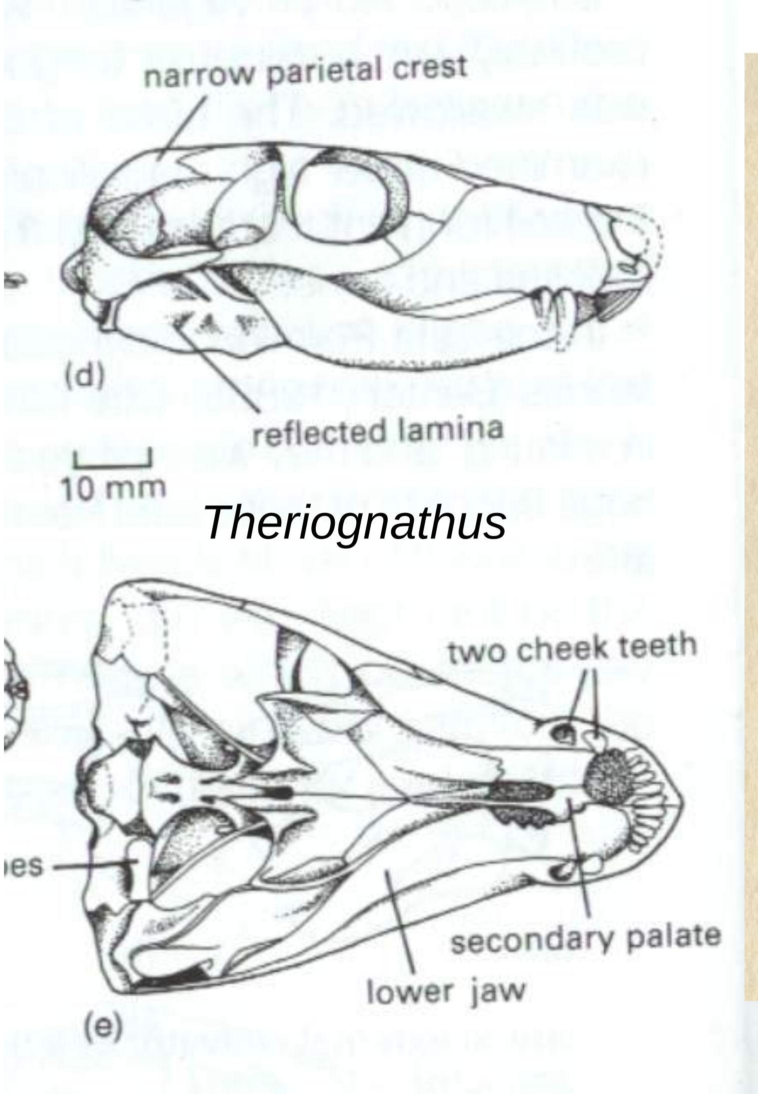
In contrast with the gorgonopsians, the jaw musculature in early therocephalians expanded dorsally over the braincase, leaving only a narrow sagittal crest between the adductor chambers. Both therocephalians and cynodonts developed a secondary palate, but this structure evolved in different ways in the two groups. In primitive therocephalians (Figure 17-28*b*), the vomer participates along with the premaxillae and maxillae, but the palatine remains dorsal in position. In primitive cynodonts (see Figure 17-30*b*), the vomer remains dorsal to the secondary palate, which incorporates the palatine in its posterior border. In both groups, the epipterygoid is expanded as a plate of bone lateral to the braincase.



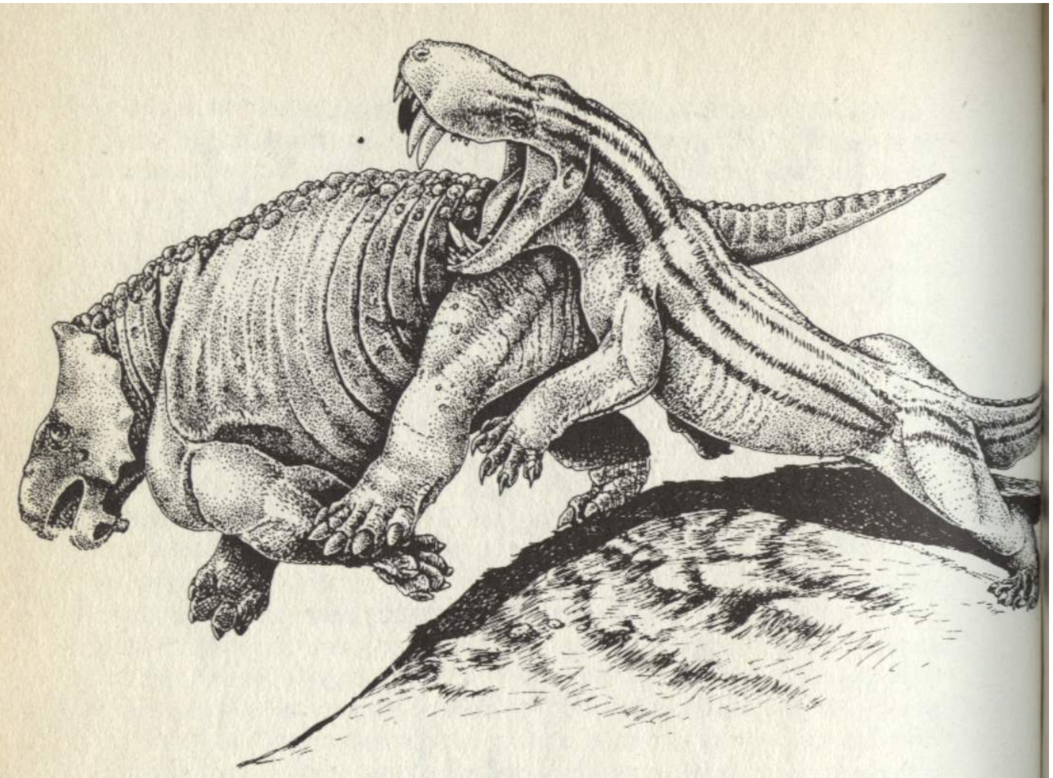
Cynodontia: *Procynosuchus*

Therocephalia

Lámina del angular más cercana al extremo posterior de la mandíbula.
Presencia de un paladar secundario **compuesto del vómer y maxilares**

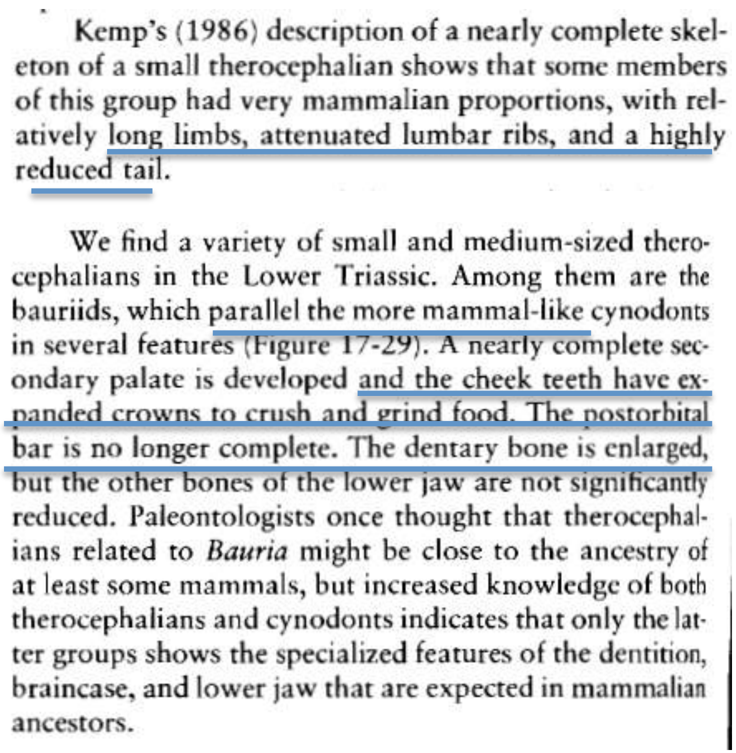


Theriognathus



A Kazanian scene: *Trochosaurus*, a protomammal, attacks an herbivorous pareiasaur.

TEROCÉPHALOS DERIVADOS: Paralelismos con mamíferos



Kemp's (1986) description of a nearly complete skeleton of a small therocephalian shows that some members of this group had very mammalian proportions, with relatively long limbs, attenuated lumbar ribs, and a highly reduced tail.

We find a variety of small and medium-sized therocephalians in the Lower Triassic. Among them are the bauriids, which parallel the more mammal-like cynodonts in several features (Figure 17-29). A nearly complete secondary palate is developed and the cheek teeth have expanded crowns to crush and grind food. The postorbital bar is no longer complete. The dentary bone is enlarged, but the other bones of the lower jaw are not significantly reduced. Paleontologists once thought that therocephalians related to *Bauria* might be close to the ancestry of at least some mammals, but increased knowledge of both therocephalians and cynodonts indicates that only the latter groups shows the specialized features of the dentition, braincase, and lower jaw that are expected in mammalian ancestors.

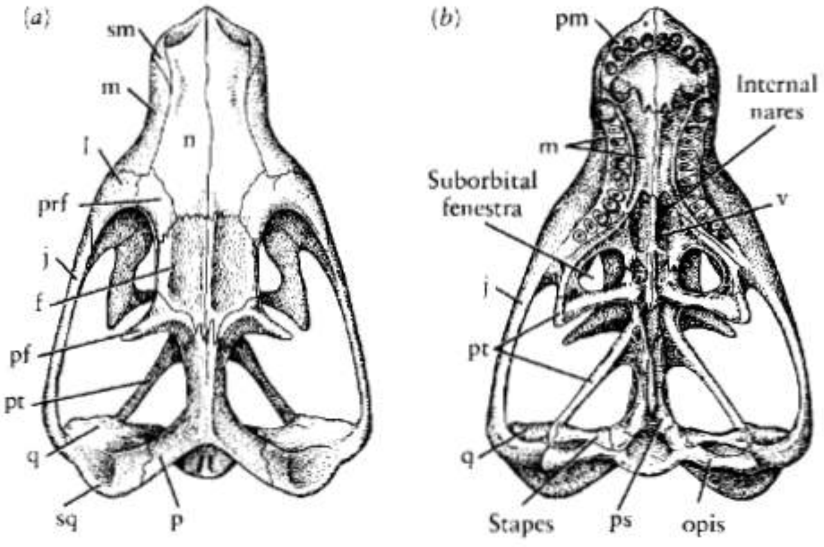
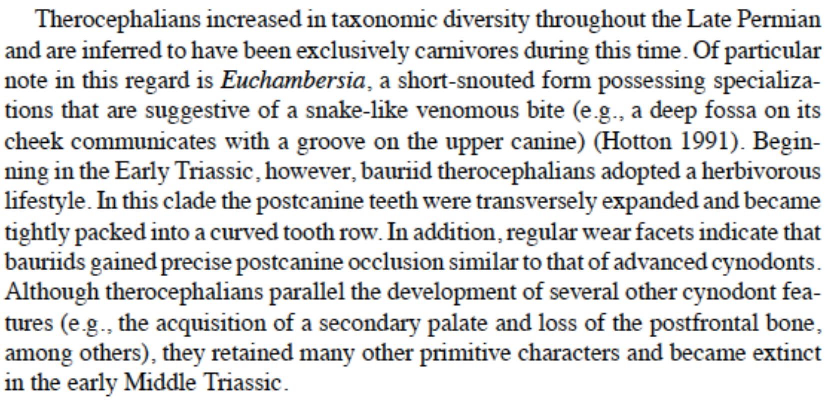
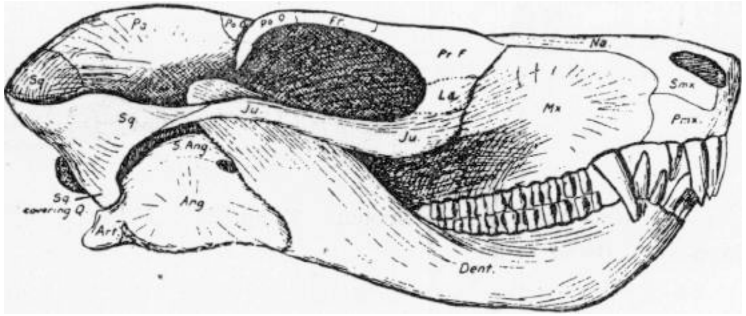


Figure 17-29. SKULL OF THE HERBIVOROUS THEROCEPHALIAN *BAURIA*. (*a*) Dorsal and (*b*) palatal views, × ½. Abbreviations as in Figure 8-3. *Drawn on the basis of sketches of Mendrez-Carroll.*



Therocephalians increased in taxonomic diversity throughout the Late Permian and are inferred to have been exclusively carnivores during this time. Of particular note in this regard is *Euchambersia*, a short-snouted form possessing specializations that are suggestive of a snake-like venomous bite (e.g., a deep fossa on its cheek communicates with a groove on the upper canine) (Hotton 1991). Beginning in the Early Triassic, however, bauriid therocephalians adopted a herbivorous lifestyle. In this clade the postcanine teeth were transversely expanded and became tightly packed into a curved tooth row. In addition, regular wear facets indicate that bauriids gained precise postcanine occlusion similar to that of advanced cynodonts. Although therocephalians parallel the development of several other cynodont features (e.g., the acquisition of a secondary palate and loss of the postfrontal bone, among others), they retained many other primitive characters and became extinct in the early Middle Triassic.



Cynodontia

Paladar formado por maxilar y palatino
Dentarios más de 90% de la mandíbula

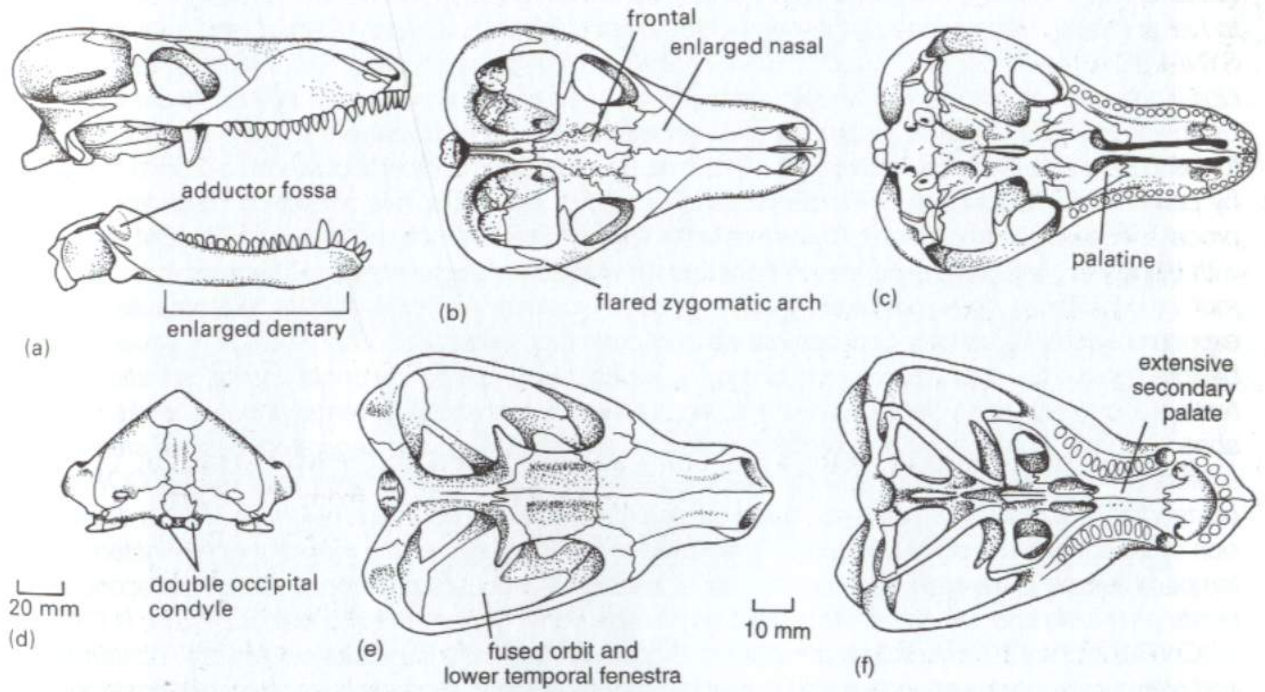


Fig. 5.13 The early cynodont *Procynosuchus*, skull in (a) lateral, (b) dorsal, (c) ventral, and (d) occipital views; (e, f) the herbivorous therocephalian *Bauria*, skull in dorsal and ventral views. [Figures (a–d) after Kemp, 1979; (e, f) modified from Carroll, 1987.]

have lost the sutural connection between the dentary and the other jaw bones, which appear to be able to move independently to at least a limited degree. The progressive reduction in size and loose attachment of the postdentary bones has long been an enigmatic aspect of the evolution of mammals. The most plausible explanation is that elaborated by Allin (1975) in relationship to the origin of the mammalian middle ear.

División de adductor en masetero y temporalis!

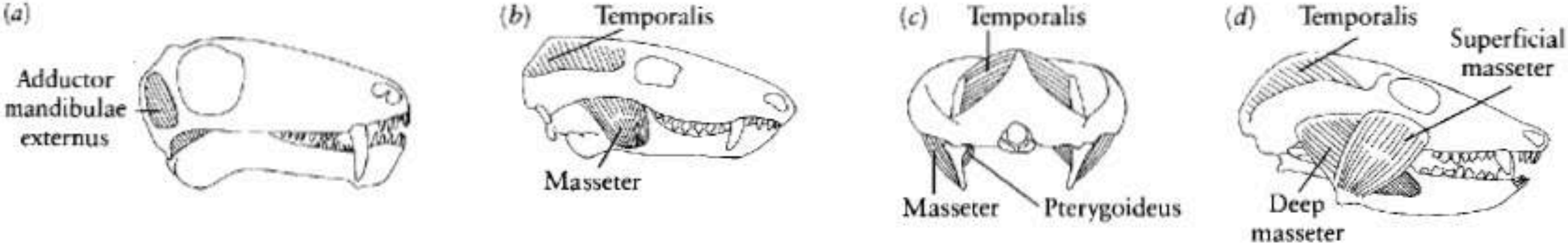
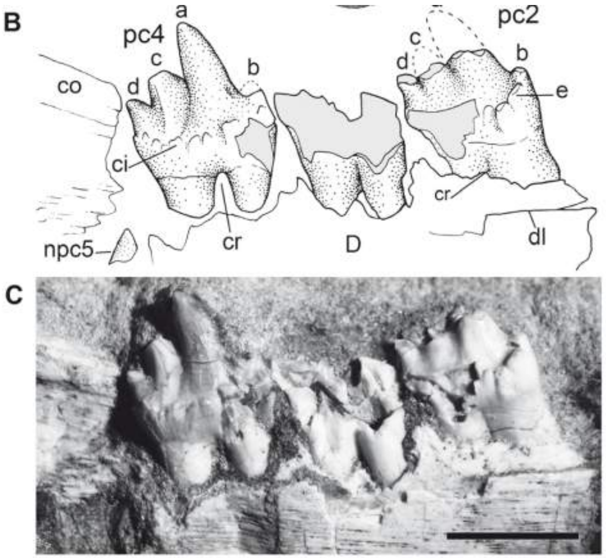
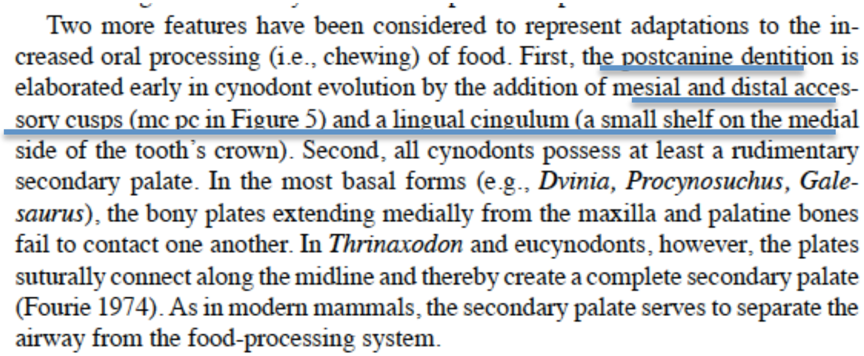


Figure 17-31. EVOLUTION OF THE MAMMALIAN JAW-CLOSING MUSCULATURE. Of the three major elements of the adductor musculature in primitive tetrapods described in Chapter 9, the adductor mandibulae internus and the adductor mandibulae posterior are both very much reduced in the ancestry of mammals. The major muscles that originate from the adductor chamber in mammals are all derived from the adductor mandibulae externus. In primitive therapsids, as illustrated by *Biarmosuchus*, (*a*), the externus, as in primitive amniotes, consists of a single functional unit that is entirely contained within the adductor chamber and inserts on the dorsal and medial surface of the back of the lower jaw. In primitive cynodonts such as *Thrinaxodon*, (*b*), the zygomatic arches are bowed laterally and the superficial portion of the externus inserts on the lateral surface of the lower jaw. Its origin has shifted to the inside surface of the zygomatic arch. With the separation of the adductor mandibulae into two functional units, the medial portion, which originates on the skull roof and the lateral surface of the braincase, is now termed the temporalis. The lateral portion is designated the masseter. In posterior view, (*c*), we see that the force of the masseter acts to pull the lower jaw laterally as well as dorsally, thus balancing the medially directed force produced by the temporalis. (*d*) In more advanced cynodonts such as *Probainognathus*, the masseter has split into two units. The fibers of the deep masseter, like the single element in *Thrinaxodon*, are oriented nearly parallel with those of the temporalis. The fibers of the newly elaborated superficial masseter are oriented obliquely anteriorly.

Mesial
(anterior)




Two more features have been considered to represent adaptations to the increased oral processing (i.e., chewing) of food. First, the postcanine dentition is elaborated early in cynodont evolution by the addition of mesial and distal accessory cusps (mc pc in Figure 5) and a lingual cingulum (a small shelf on the medial side of the tooth's crown). Second, all cynodonts possess at least a rudimentary secondary palate. In the most basal forms (e.g., *Dvinia, Procynosuchus, Galesaurus*), the bony plates extending medially from the maxilla and palatine bones fail to contact one another. In *Thrinaxodon* and eucynodonts, however, the plates suturally connect along the midline and thereby create a complete secondary palate (Fourie 1974). As in modern mammals, the secondary palate serves to separate the airway from the food-processing system.

CYNODONTES BASALES:

Procynosuchidae

The Upper Permian procynosuchid cynodonts show marked advances in the development of a secondary palate, complex cheek teeth, and changes in the jaw and temporal region that indicate the initial steps in reorganizing the jaw musculature toward a mammalian pattern. The secondary palate in *Procynosuchus* (Figure 17-30*b*) is formed by ventral and medial extensions of the premaxilla, maxilla, and palatine. They do not meet at the midline and do not continue to the back of the tooth row. However, a fleshy secondary palate probably completed the separation of the air passage from the mouth.

The cheek teeth are multicuspate and superficially resemble the molars of late Triassic mammals. The crowns of the teeth are elongate, with a series of linearly arranged cusps. The upper and lower teeth do not occlude with one another and are continuously replaced, as in most reptiles.

The temporal opening is enormous, which indicates the presence of very large muscles to close the jaws. In contrast with other groups of therapsids, the lower temporal bar, or zygomatic arch, extends laterally beyond the level of the dentary. This extension allows the insertion of jaw muscles on the lateral surface of the dentary. This also occurred in dicynodonts, but as a result of raising the zygomatic arch above the level of the tooth row rather than by its lateral extension. The dentary of cynodonts has a high coronoid process that is recessed laterally for muscle insertion. In mammals, the muscle that occupies this position is termed the deep masseter and the recess for its insertion is termed the masseteric fossa.

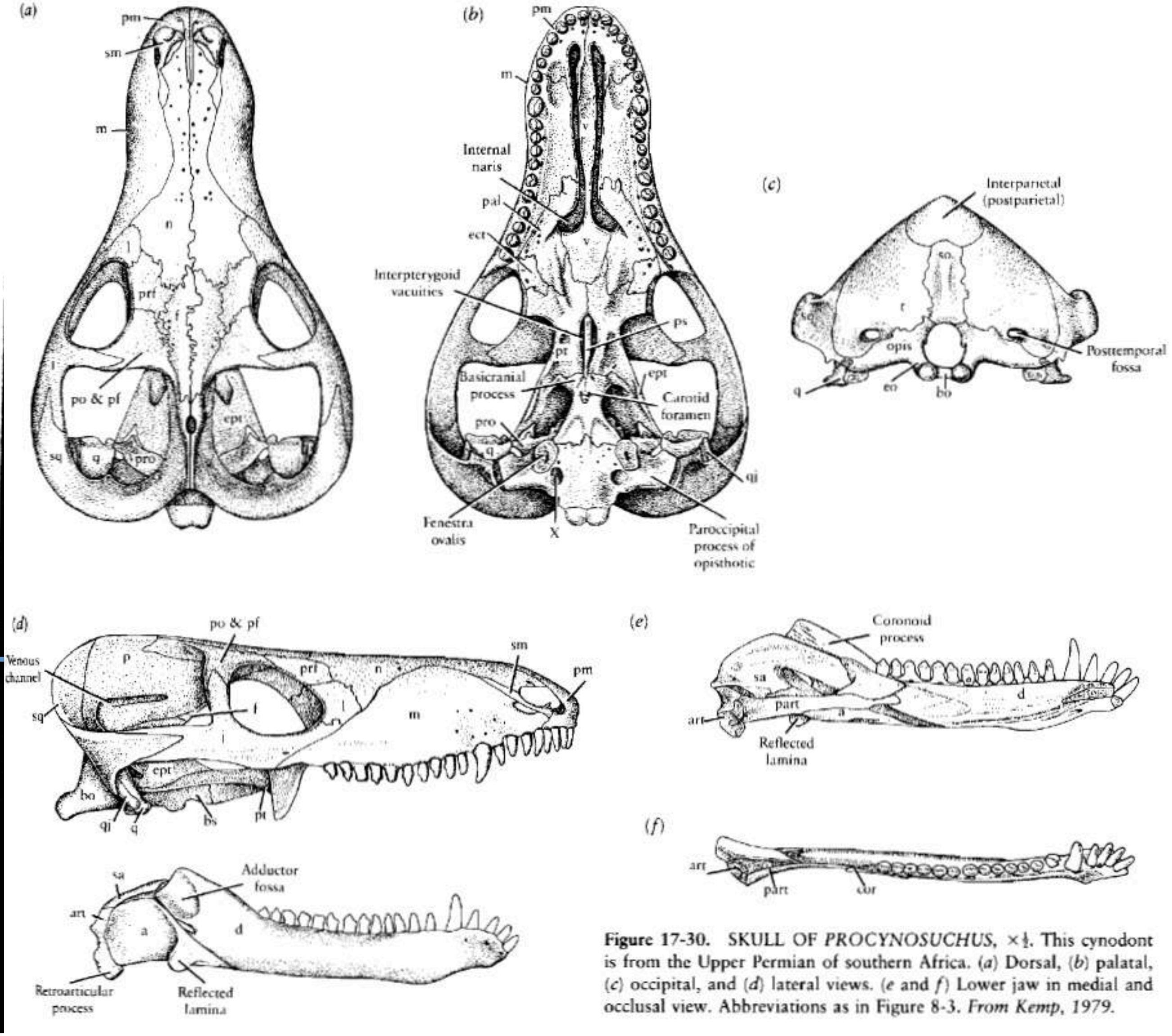


Figure 17-30. SKULL OF *PROCYNOSUCHUS*, ×½. This cynodont is from the Upper Permian of southern Africa. (*a*) Dorsal, (*b*) palatal, (*c*) occipital, and (*d*) lateral views. (*e* and *f*) Lower jaw in medial and occlusal view. Abbreviations as in Figure 8-3. *From Kemp, 1979.*

Several other cynodont apomorphies can be interpreted as consequences of a more refined set of jaw-closing muscles. The parietal bone extends ventrally to more extensively contribute to the sidewall of the braincase, and the epipterygoid is expanded to alisphenoid-like proportions and makes a new contact with the frontal (f in Figure 5). In addition, the origination site of the *m. temporalis* on the parietal crest is elongated anteriorly so as to incorporate the pineal foramen.

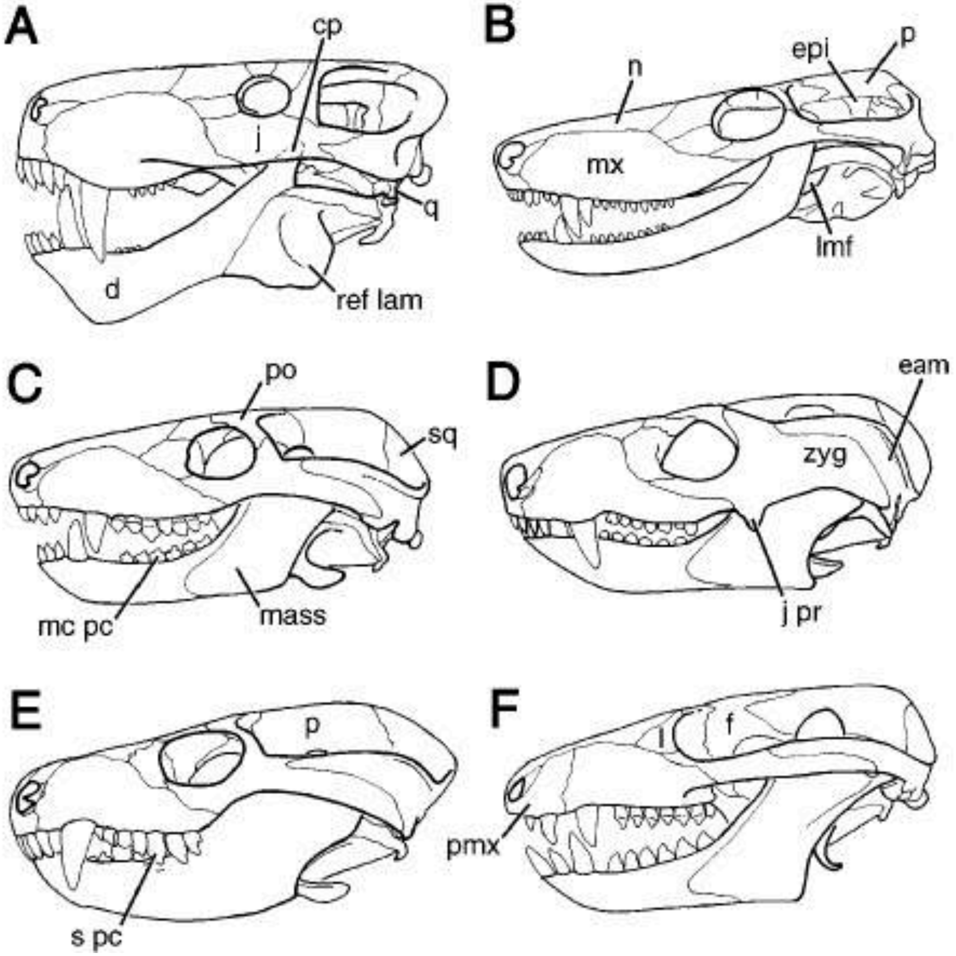


Figure 5 Skulls of selected theriodonts in lateral view (not to scale). (*A*) the gorgonopsian *Leontocephalus*; (*B*) the eutherocephalian *Ictidosuchoides*; (*C*) the basal cynodont *Thrinaxodon*; (*D*) the basal cynognathian *Trirachodon*; (*E*) the basal probainognathian *Lumkuia*; (*F*) the tritheledontid *Pachygenelus*. Anatomical abbreviations: cp, coronoid process of the dentary; d, dentary; eam, fossa on the squamosal termed the external auditory meatus; epi, epipterygoid; f, frontal; j, jugal; j pr, jugal suborbital process; l, lacrimal; lmf, lateral mandibular fenestra; mass, masseteric fossa; mc pc, multicusped postcanine teeth; mx, maxilla; n, nasal; p, parietal; pmx, premaxilla; po, postorbital; q, quadrate; ref lam, reflected lamina of the angular; s pc, sectorial postcanine teeth; sq, squamosal; zyg, zygomatic arch (composed of the jugal and squamosal bones). Reconstructions modified from the following original sources: (*A*) Sidor & Hopson (1998); (*B*) (*C*) (*D*) (*F*) Hopson (1994); (*E*) Hopson & Kitching (2001).

this group (Crompton & Parker 1978). In cynodonts more derived than *Dvinia* and *Procynosuchus* (Epicynodontia sensu Hopson & Kitching 2001) (clade 6b in Figure 3), the masseteric fossa is enlarged such that it approaches the ventral margin of the mandible (mass in Figure 5).

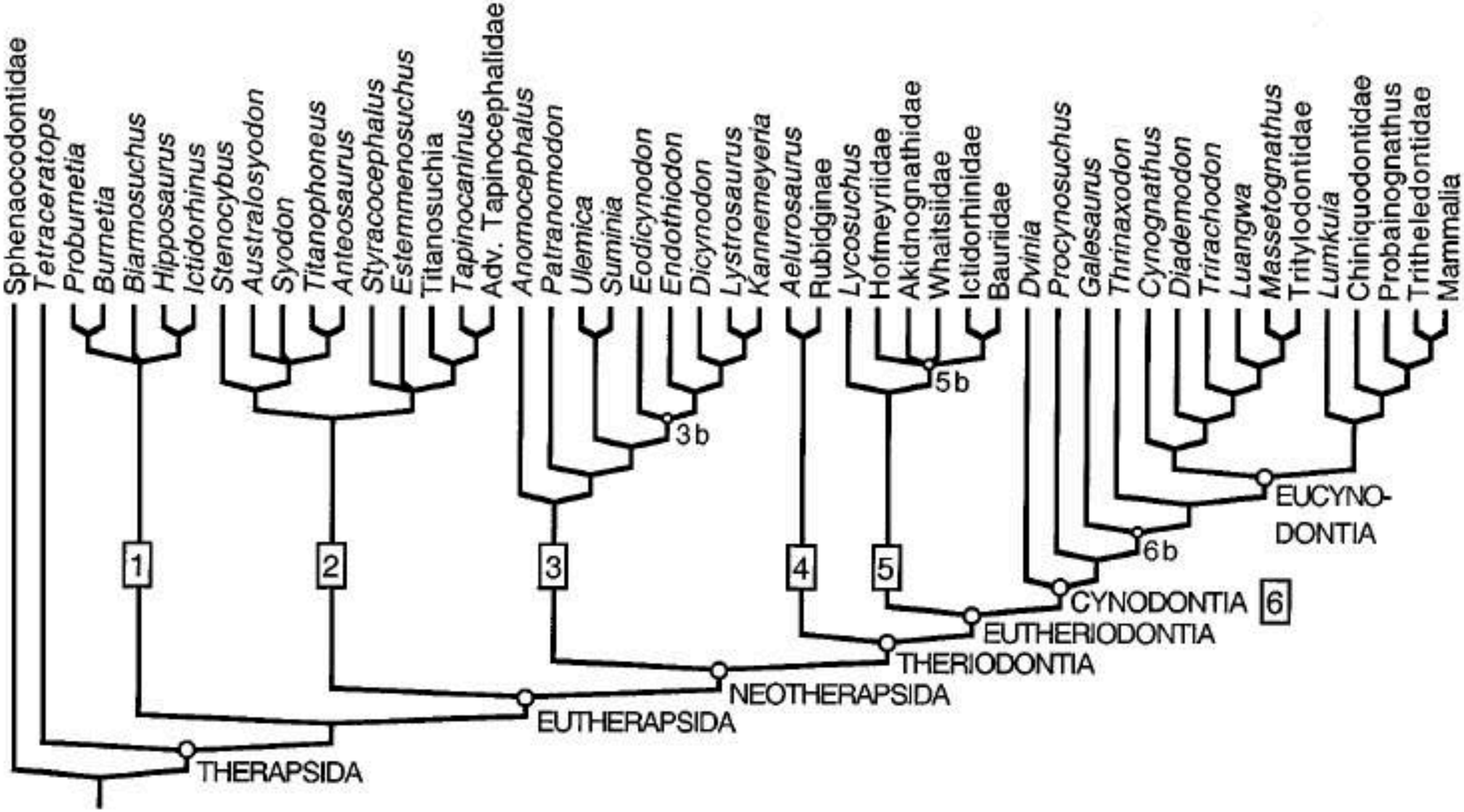


Figure 3 Cladogram of the therapsid groups considered in the text. 1, Biarmosuchia; 2, Dinocephalia; 3, Anomodontia; 3b, Dicynodontia; 4, Gorgonopsia; 5, Therocephalia; 5b, Eutherocephalia; 6, Cynodontia; 6b, Epicynodontia. This cladogram is by no means exhaustive. For example, only the most derived pelycosaur family is shown here (e.g., Sphenacodontidae). Relationships depicted here are based on those proposed by Hopson (1991, 1994), Rubidge & van den Heever (1997), Sidor & Hopson (1998), Modesto et al. (1999) and B. S. Rubidge & C. A. Sidor (unpublished data). See text for further details.

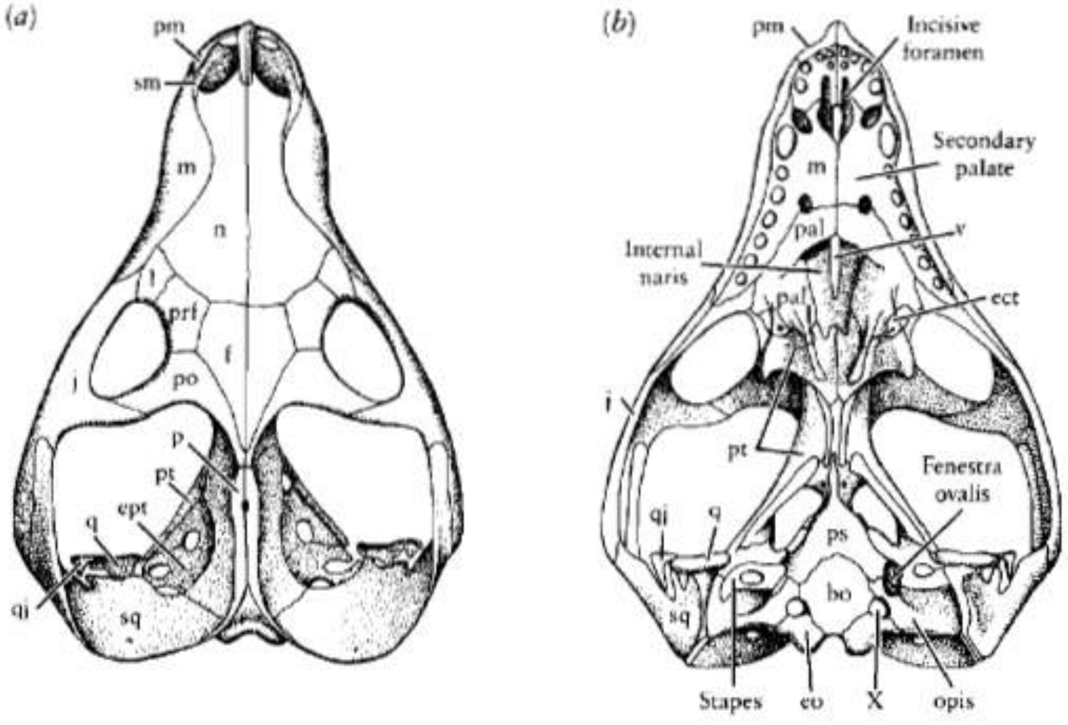
THRINAXODON ("galesauridae")

Thrinaxodon was a lightly built, active carnivore, approximately 50 centimeters in length. The trunk is long, with 27 presacral vertebrae, and the limbs are relatively short. The shortness of the limbs is accentuated by the plantigrade posture of the feet. The general appearance brings to mind the proportions of a mustelid carnivore.

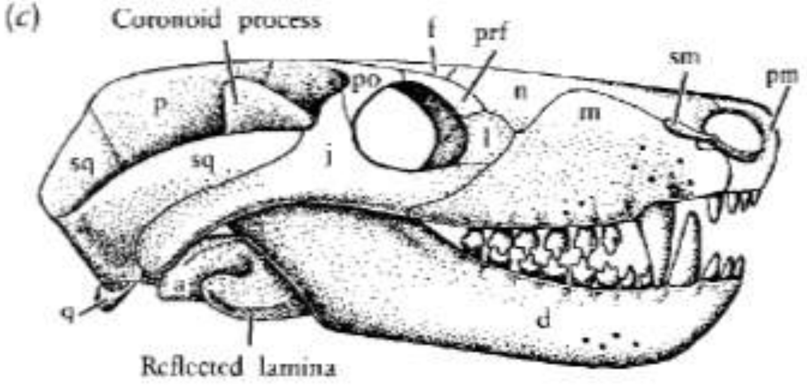
The skull is about 10 centimeters long, and the adductor chamber occupies nearly half of its length (Figure 17-32). The two sides are separated by a very narrow braincase that forms a sharp sagittal crest that still retains a pineal opening. The squamosal expands broadly around the back of the adductor chamber and forms the lateral surface of the occiput. As in *Procynosuchus*, a single area of ossification occupies the position of the postorbital and postfrontal of more primitive therapsids. This bone meets the prefrontal above the orbit.

Thrinaxodon is advanced over the procynosuchids in the formation of a solid secondary palate, with sutural attachment of the maxillae and palatines at the midline beneath the nasal passage. The pterygoids meet at the midline and close the interpterygoid vacuity in adults. The dentition has a nearly mammalian appearance. There are four upper and three lower incisors, a number that is retained in most more advanced cynodonts. Canine teeth are present in both upper and lower jaws, although they are not as large as those of more primitive theriodonts. There are seven to nine cheek teeth. The crowns are laterally compressed and marked by a series of linearly arranged cusps. However, in contrast with mammals, the teeth are still replaced regularly and do not show a specific pattern of occlusion.

The lower jaw is dominated by the dentary, with a coronoid process that extends dorsally above the zygomatic arch. The masseteric fossa reaches to its base. The postdentary bones are not greatly reduced but, like those of *Procynosuchus*, lose sutural contact with the dentary and can move separately. The reflected lamina of the angular is still a large structure that extends laterally from the remaining bone surface. As in primitive reptiles, the articular forms the entire surface for articulation with the skull. The quadrate and closely linked quadratojugal are greatly reduced and fit loosely into adjacent sockets at the base of the squamosal.



"Galesaurid"



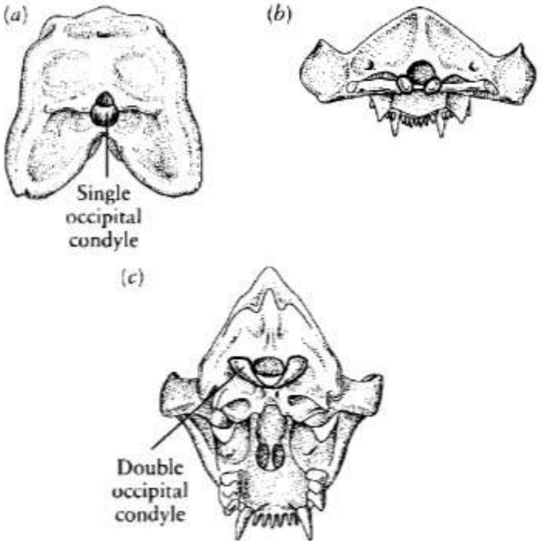


Figure 17-33. The articulation between the skull and the cervical vertebrae changes significantly between pelycosaurs and mammals. (*a*) In primitive pelycosaurs, the occipital condyle is a single hemispherical structure located directly below the foramen magnum. (*b*) Within the therapsids, the condyle splits to form a paired structure. (*c*) The area of articulation moves dorsally in mammals, so that the hinge line passes midway in the height of the foramen magnum to minimize tension on the nerve cord when the skull is flexed dorsally or ventrally. Pairing of the occipital condyle precludes lateral flexion and rotation at this point. *Redrawn from Jenkins, 1971.*

The Origin of the Mammalian Atlas-Axis Complex

Among therapsids, there is a marked change in the nature of the mobility of the head on the trunk. The pattern in primitive amniotes (see Chapter 10) is retained with little modification throughout the pelycosaurs and into the primitive therapsids (Figure 17-33 and 17-34). The occipital condyle is a roughly hemispherical structure that is situated beneath the foramen magnum. The atlas arches and intercentrum form an incomplete ring that fits about it like the socket of a ball-and-socket joint. The mobility of this joint was limited by the proatlas, whose paired elements formed a link between articulating surfaces on the exoccipitals and the paired atlas arches. This linkage restricted both rotation and dorsoventral flexion between the skull and the trunk.

Among primitive therapsids, mobility is achieved by a limited amount of rotation and flexion at each point of articulation between the skull and the anterior elements of the cervical series. In mammals, the two movements are concentrated between different elements of the atlas-axis complex. Dorsoventral flexion in an arc as great as 90 degrees occurs primarily between the occipital condyle and the atlas. This mobility is achieved among the cynodonts and early mammals by division of the originally single occipital condyle into two articulating surfaces that shift progressively from a position beneath the foramen magnum to positions on either side of this opening. In primitive amniotes, flexion at this joint would cause a considerable stretching at the top of the spinal cord and compression at its base. As the condyles moved dorsally to reach the midpoint of the height of the foramen magnum, these forces on the spinal cord were minimized. The paired nature of the condylar surface effectively precludes rotation and lateral bending at this joint. In *Thrinaxodon*, the condyle is clearly paired, but the proatlas is retained. The articulating surfaces are still in a relatively ventral position throughout the cynodonts.

The restriction of rotation between the head and the atlas is compensated for by specialization of the atlas-axis articulation. In primitive therapsids, rotation between these elements is limited by the well-developed zygapophyseal joints between the atlas and axis arches. The zygapophyses are reduced in early cynodonts. In addition, the centrum

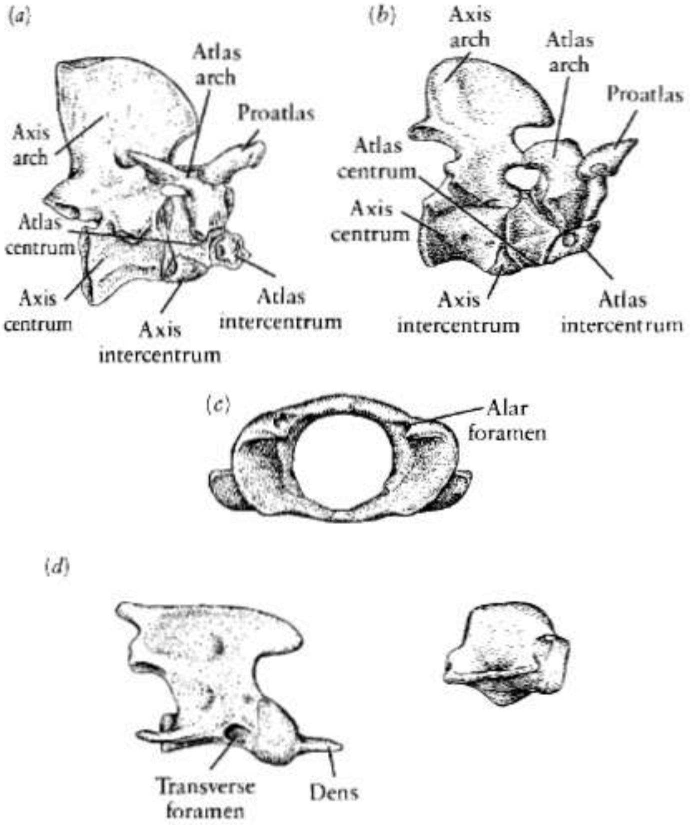
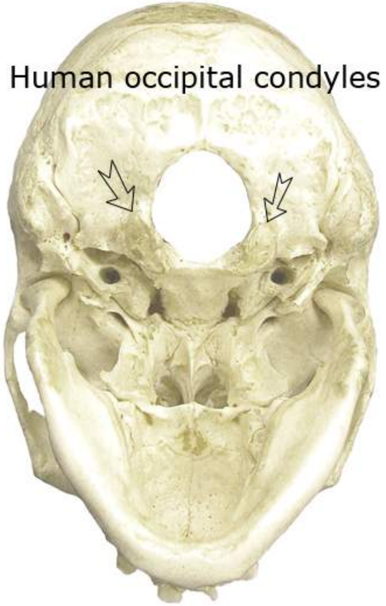
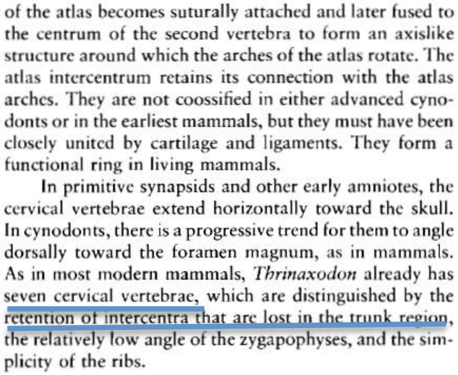


Figure 17-34. CHANGES IN THE ATLAS-AXIS COMPLEX BETWEEN PELYCOSAURS AND MAMMALS. (*a*) The pelycosaur *Ophiacodon*. Limited flexion and rotation are possible at a series of joints between the occipital condyle and the cervical vertebrae. The link between the proatlas and the occiput limits dorsoventral flexion and rotation between the skull and the atlas. The atlas arch restricts rotation between the atlas and the axis. *From Romer and Price, 1940.* (*b*) The cynodont *Thrinaxodon*. The zygapophyseal articulation between the atlas and axis is simplified to allow rotation between these elements. The pleurocentra of the atlas and axis are closely integrated to form an axis around which the atlas arch and intercentrum can rotate. *Modified from Jenkins, 1970.* (*c* and *d*) Modern mammals. (*c*) Anterior view of atlas of a cat. (*d*) Lateral view of atlas-axis complex separated to show articulating surfaces. The atlas arch and intercentrum have fused to form a ring-shaped structure. The anterior surface restricted movement by the skull to flexure in the vertical plane. Rotation and lateral flexure occur between the atlas and the axis.

Condilo occipital doble, 7 cervicales

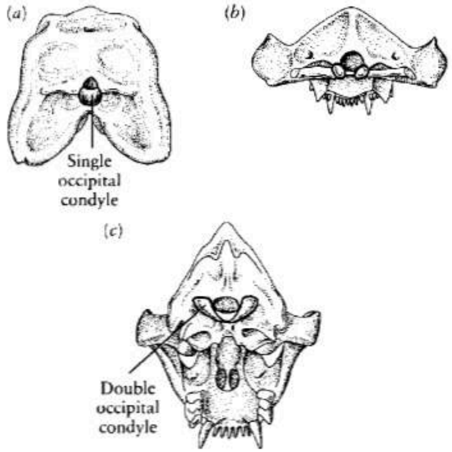


Cynodonte derivado (human!)



of the atlas becomes suturally attached and later fused to the centrum of the second vertebra to form an axislike structure around which the arches of the atlas rotate. The atlas intercentrum retains its connection with the atlas arches. They are not coossified in either advanced cynodonts or in the earliest mammals, but they must have been closely united by cartilage and ligaments. They form a functional ring in living mammals.

In primitive synapsids and other early amniotes, the cervical vertebrae extend horizontally toward the skull. In cynodonts, there is a progressive trend for them to angle dorsally toward the foramen magnum, as in mammals. As in most modern mammals, *Thrinaxodon* already has seven cervical vertebrae, which are distinguished by the retention of intercentra that are lost in the trunk region, the relatively low angle of the zygapophyses, and the simplicity of the ribs.



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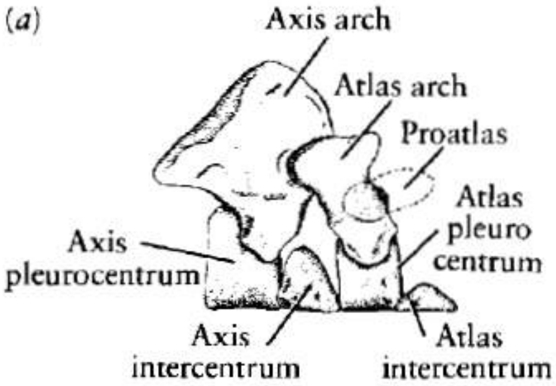
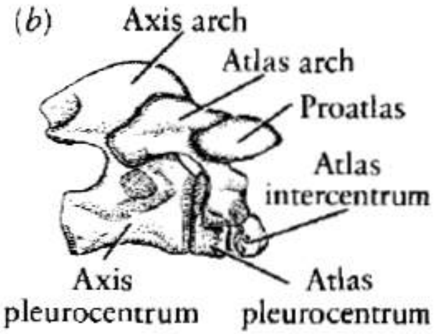
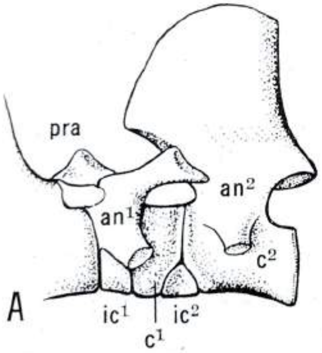
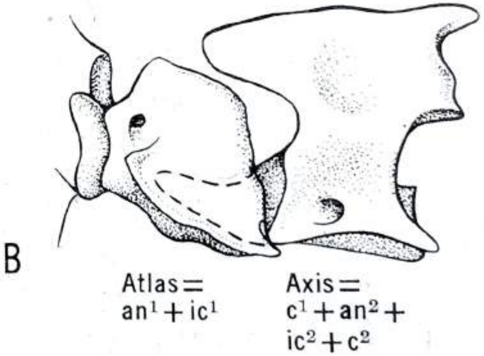


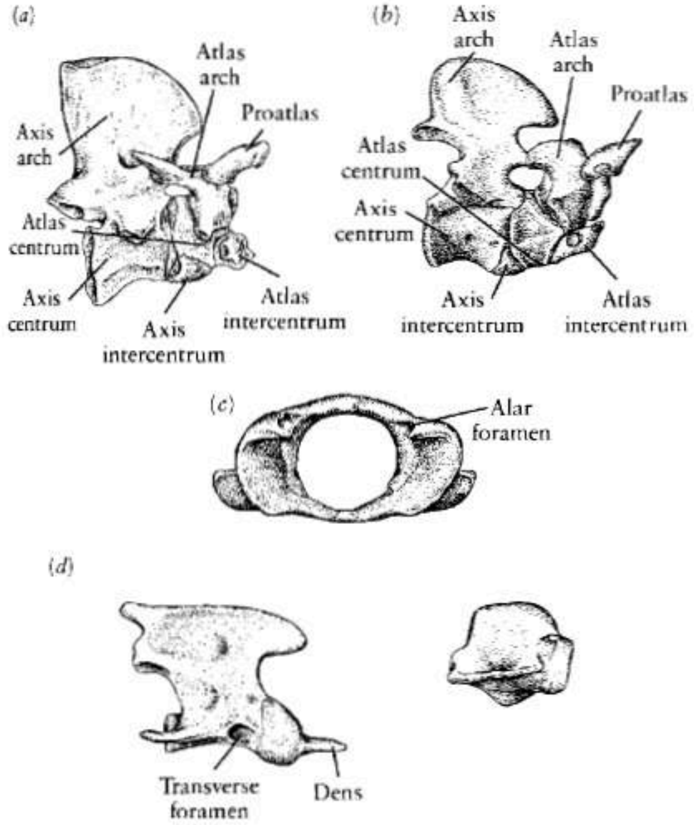
Reptiliomorpha



Protorothyridae







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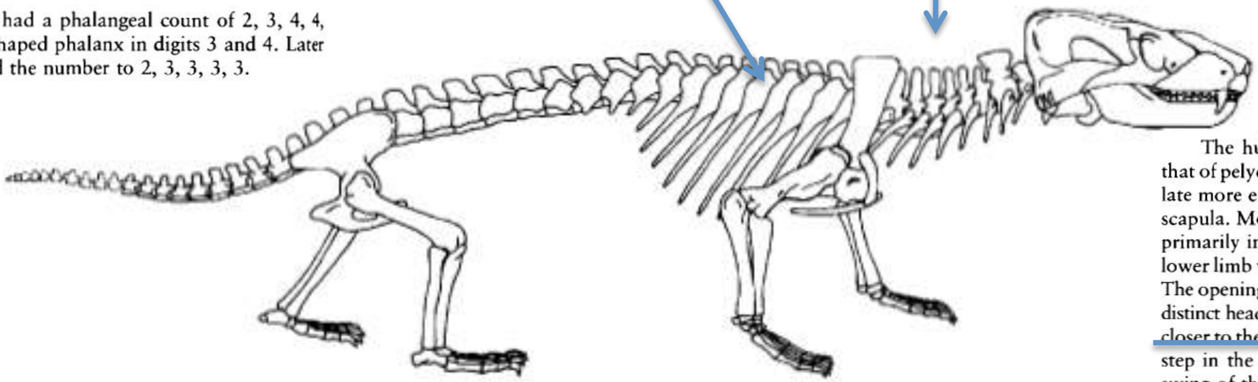
17-35). The ribs in the lumbar region consist of only the costal plate, without any shaft. The costal plates are logically associated with establishing greater rigidity of the column so that the trunk region could be held persistently off the ground. Their presence also suggests a reduction in the degree of lateral undulation of the column (Kemp, 1982). The costal plates are progressively reduced in several lineages of more advanced cynodonts, which may be attributed to a progressive elaboration of the epaxial musculature to support the trunk, without the need to rely on the expanded ribs. It may be recalled that the earliest terrestrial vertebrates, the ichthyostegids, had extremely broad ribs to support the trunk, but they were reduced in subsequent amphibian lineages.

Región lumbar diferenciada

facultative and even habitual bipedality. In contrast, the tail was progressively shortened in cynodonts. The elaboration of costal plates and more effective trunk musculature may have enabled the cynodonts to shorten the tail early in their evolution, but this shortening precluded the development of bipedality at the therapsid level. Some late therapsids did redevelop a long tail, but it was a slender appendage like that of modern rodents, without the heavy musculature of their reptilian ancestors.

In primitive amniotes, the broad ventral blade of the clavicle and the robust T-shaped interclavicle served to resist the strong medially directed force that resulted from the laterally oriented limbs. These dermal elements remain large throughout the cynodonts and into primitive mammals, which indicates that the forelimbs continued to exert a substantial medial force as a result of their sprawling posture. In the living monotremes, these bones have retained an essentially cynodont pattern.

Thrinaxodon had a phalangeal count of 2, 3, 4, 4, 3, with one disk-shaped phalanx in digits 3 and 4. Later cynodonts reduced the number to 2, 3, 3, 3, 3.



Costal plate: proximal rib expansion

7 cerv!!!

The humerus remains a heavy, complex bone, like that of pelycosaurs. The head is deflected dorsally to translate more effectively the force of the limbs to the vertical scapula. Movement of the humerus would have still been primarily in the horizontal plane and the function of the lower limb would have been similar to that in pelycosaurs. The opening of the glenoid and the development of a more distinct head would have allowed the humerus to be moved closer to the body when it was retracted, a necessary initial step in the development of the mammalian fore-and-aft swing of the limb.

Figure 17-35. SKELETON OF THE LOWER TRIASSIC CYNODONT *THRINAXODON*, ½ METER LONG. Greatly widened ribs probably served to support the trunk and to limit lateral undulation. *From Jenkins, 1984.*

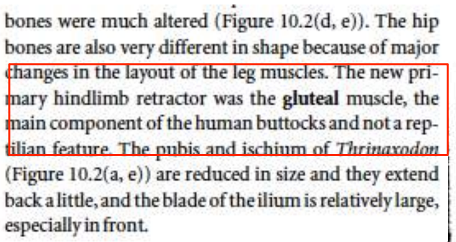
Galesaurid

Archosaurs retain the long tail that is characteristic of primitive amniotes. As the limbs achieved a more habitually upright posture among advanced thecodonts, the maintenance of an arched trunk was achieved by the counterbalancing of the long heavy tail. The weight of the tail also enabled some thecodonts and dinosaurs to achieve

of the femur. In cynodonts, the pubis and ischium were reduced rather than elaborated, but the iliac blade was expanded, especially in an anterior direction, to increase the area of origin for both protractors and retractors that have a much different mechanical arrangement than those of dinosaurs.

The changes in cynodonts were already well underway at the base of the Triassic, at which time the early archosaur *Chasmatosaurus* retained a pelvis that was similar to that of the most primitive diapsids.

Thrinaxodon



bones were much altered (Figure 10.2(d, e)). The hip bones are also very different in shape because of major changes in the layout of the leg muscles. The new primary hindlimb retractor was the **gluteal** muscle, the main component of the human buttocks and not a reptilian feature. The pubis and ischium of *Thrinaxodon* (Figure 10.2(a, e)) are reduced in size and they extend back a little, and the blade of the ilium is relatively large, especially in front.

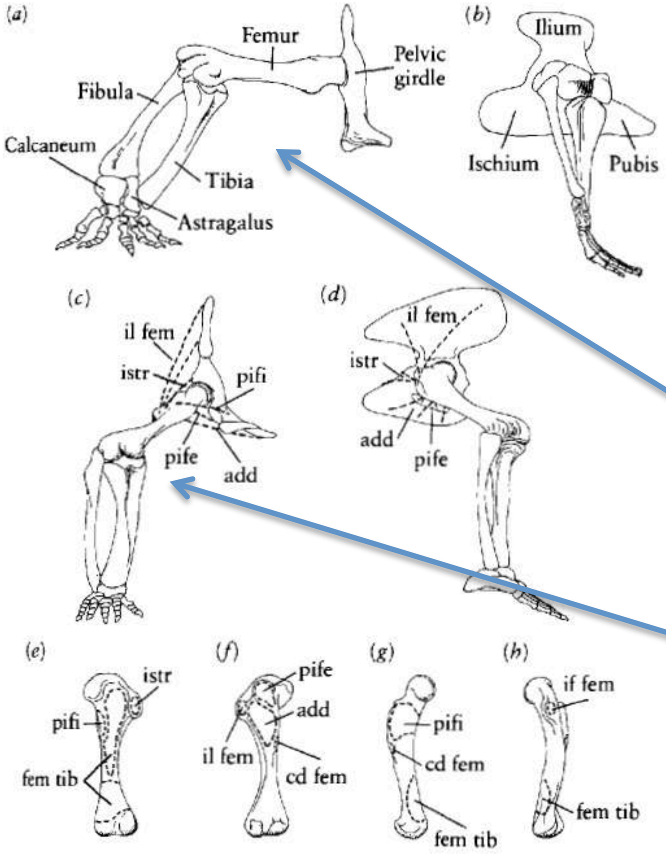
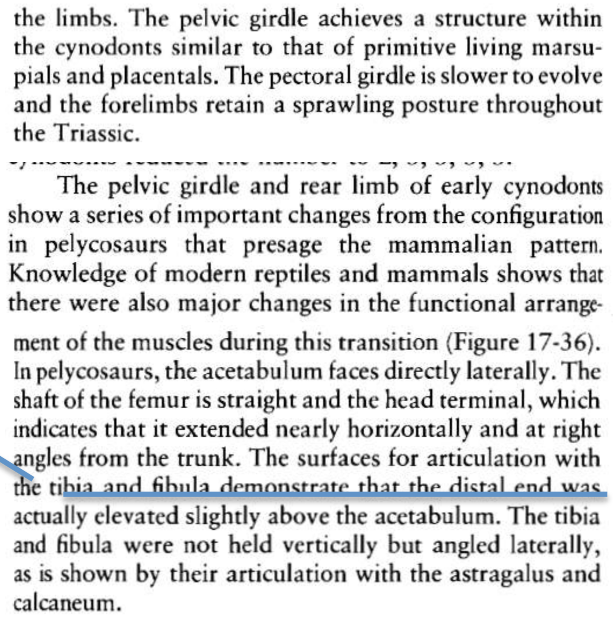
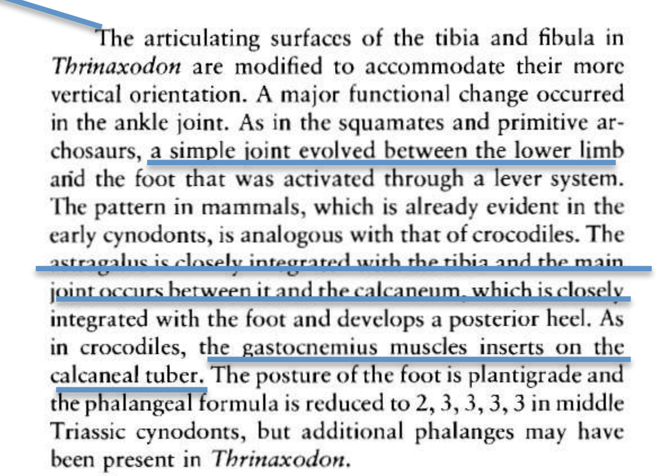


Figure 17-36. THE PELVIC GIRDLE AND REAR LIMB. Changes in their structure and function between pelycosaurs and cynodonts. (*a*) Anterior and (*b*) lateral views of the pelvis and rear limb of the pelycosaur *Dimetrodon*. (*c*) Anterior and (*d*) lateral views of the pelvis and rear limb of the cynodont *Thrinaxodon*. (*e*) Dorsal, (*g*) ventral, (*g*) anterior, and (*h*) posterior views of the femur of *Thrinaxodon* showing the position of muscle attachments. The orientation of the major muscles changes to facilitate more effective fore-and-aft movement of the limb, which is drawn closer to the body. The posture of the foot also changes in this transition from digitigrade to plantigrade. In *Thrinaxodon*, the calcaneum serves as a lever to ventroflex the foot. Abbreviations as follows: add, adductor musculature; cd fem, caudofemoralis; fem tib, femorotibialis; il fem, iliofemoralis; istr, ischiotrocantericus; pife, puboischiofemoralis externus; pifi, puboischiofemoralis internus. *From Jenkins, 1971.*



the limbs. The pelvic girdle achieves a structure within the cynodonts similar to that of primitive living marsupials and placentals. The pectoral girdle is slower to evolve and the forelimbs retain a sprawling posture throughout the Triassic.

The pelvic girdle and rear limb of early cynodonts show a series of important changes from the configuration in pelycosaurs that presage the mammalian pattern. Knowledge of modern reptiles and mammals shows that there were also major changes in the functional arrangement of the muscles during this transition (Figure 17-36). In pelycosaurs, the acetabulum faces directly laterally. The shaft of the femur is straight and the head terminal, which indicates that it extended nearly horizontally and at right angles from the trunk. The surfaces for articulation with the tibia and fibula demonstrate that the distal end was actually elevated slightly above the acetabulum. The tibia and fibula were not held vertically but angled laterally, as is shown by their articulation with the astragalus and calcaneum.



The articulating surfaces of the tibia and fibula in *Thrinaxodon* are modified to accommodate their more vertical orientation. A major functional change occurred in the ankle joint. As in the squamates and primitive archosaurs, a simple joint evolved between the lower limb and the foot that was activated through a lever system. The pattern in mammals, which is already evident in the early cynodonts, is analogous with that of crocodiles. The astragalus is closely integrated with the tibia and the main joint occurs between it and the calcaneum, which is closely integrated with the foot and develops a posterior heel. As in crocodiles, the gastocnemius muscles inserts on the calcaneal tuber. The posture of the foot is plantigrade and the phalangeal formula is reduced to 2, 3, 3, 3, 3 in middle Triassic cynodonts, but additional phalanges may have been present in *Thrinaxodon*.

Origen del tubérculo calcáneo!

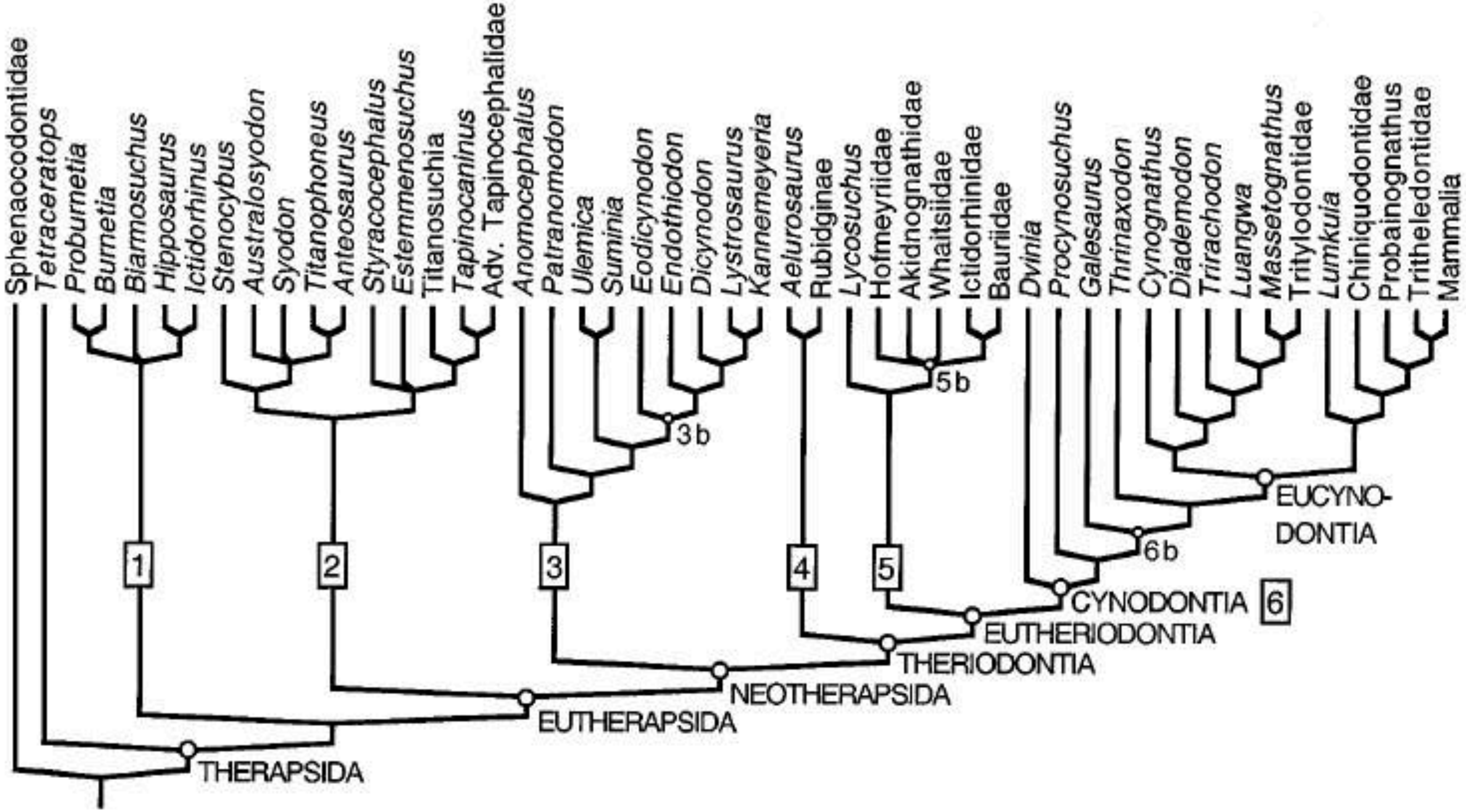
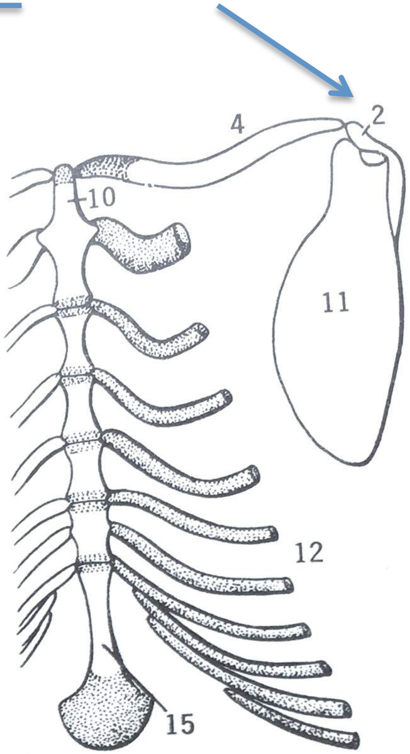


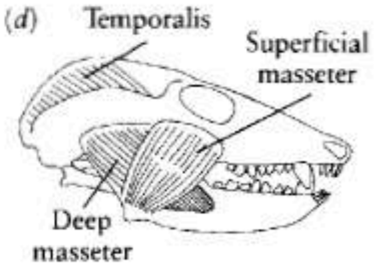
Figure 3 Cladogram of the therapsid groups considered in the text. 1, Biarmosuchia; 2, Dinocephalia; 3, Anomodontia; 3b, Dicynodontia; 4, Gorgonopsia; 5, Therocephalia; 5b, Eutherocephalia; 6, Cynodontia; 6b, Epicynodontia. This cladogram is by no means exhaustive. For example, only the most derived pelycosaur family is shown here (e.g., Sphenacodontidae). Relationships depicted here are based on those proposed by Hopson (1991, 1994), Rubidge & van den Heever (1997), Sidor & Hopson (1998), Modesto et al. (1999) and B. S. Rubidge & C. A. Sidor (unpublished data). See text for further details.

EUCYNODONTIA

Cynodonts more derived than *Thrinaxodon* (Figure 5C) have been termed the Eucynodontia (Kemp 1982, 1988) and are characterized by a number of features that produce an increasingly mammal-like skull and postcranial skeleton. Important modifications include: (*a*) an enlarged dentary and reduced, more rod-like, postdentary bones, (*b*) the fusion of the dentaries at the mandibular symphysis, (*c*) a supplementary contact between the surangular and squamosal lateral to the quadrate-articular jaw joint, (*d*) the formation of an acromion process on the leading edge of the scapula, and (*e*) the acquisition of the mammalian phalangeal formula.



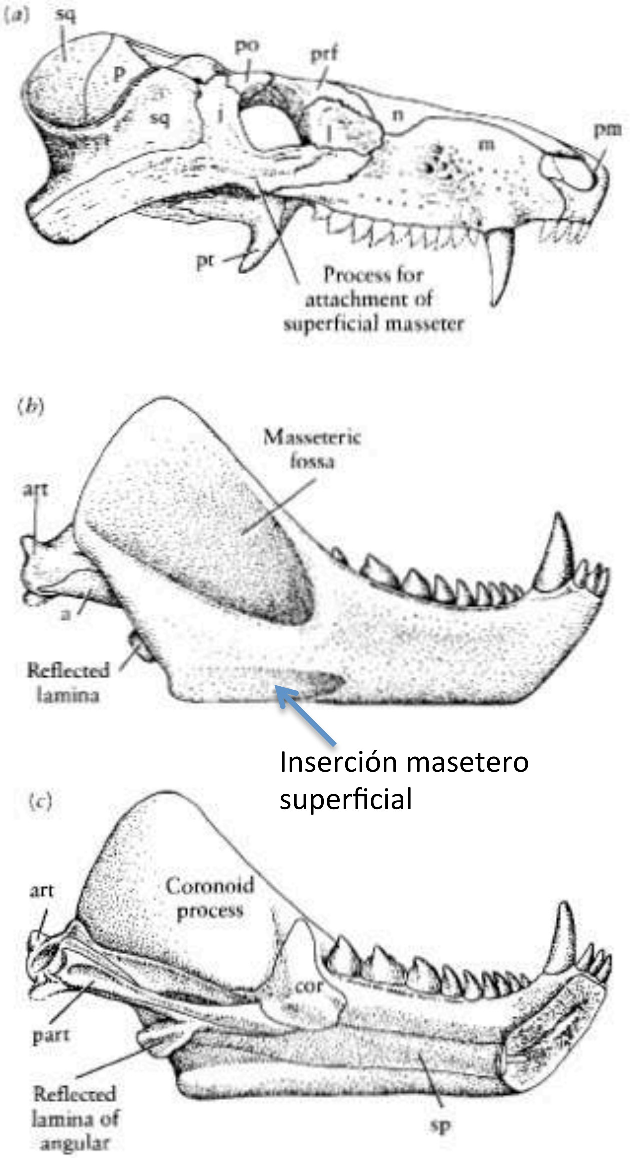
D, Didelphys



Masetero superficial

Although the lower jaw has a superficially mammalian appearance, closer examination shows that the dentary is accompanied by a number of smaller bones that are united in a narrow bar, which fit into a groove on its medial surface. This bar is made up of the articular, prearticular, angular, and surangular. The coronoid remains a flat plate of bone that overlaps the anterior end of the rod. The jaw articulation is formed in primitive reptilian fashion by the articular and quadrate.

The postcranial skeleton was very similar to that of *Thrinaxodon*, except for proportional differences that were associated with the greater weight of the body.



Inserción masetero superficial

Figure 17-37. (*a*) Skull and (*b* and *c*) lower jaw of the large cynodont *Cynognathus*, maximum length 40 centimeters. Abbreviations as in Figure 8-3. (*a*) *From Broili and Schröder, 1934.* (*b* and *c*) *From Kermack, Mussett, and Rigney, 1973.*

Cynodontes

“Gomphodontos”

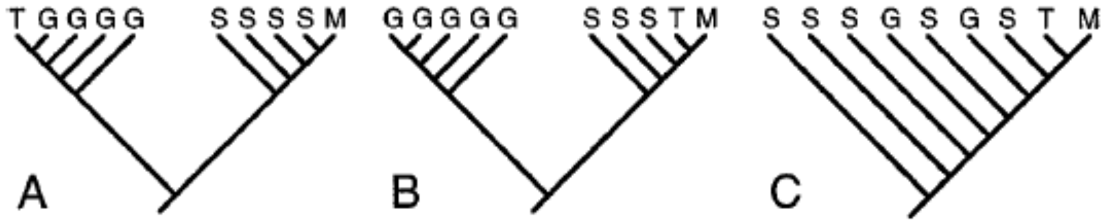
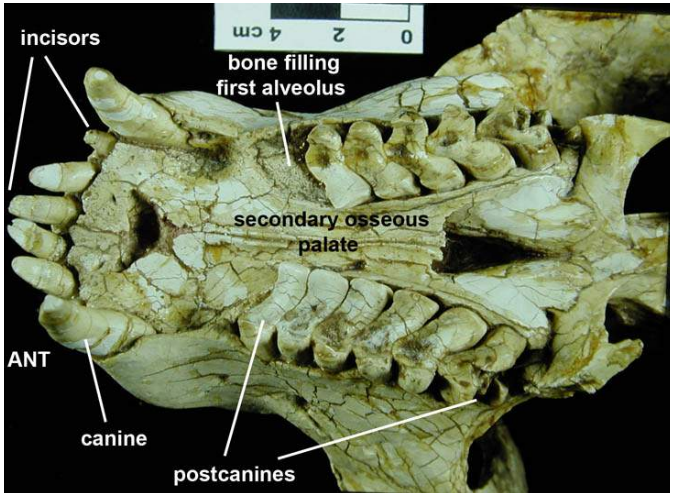
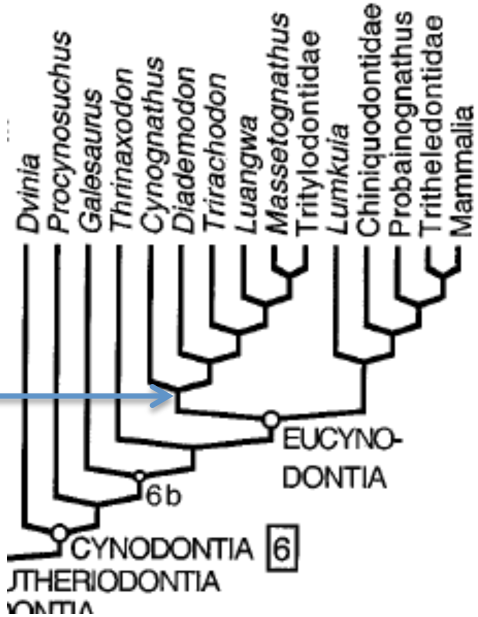


Figure 6 Diagrammatic representation of three hypotheses of advanced cynodont phylogeny. (*A*) The traditional hypothesis (cf. Crompton & Ellenberger 1957, Hopson & Kitching 1972, Hopson 1991); (*B*) that of Kemp (1982, 1983); (*C*) that of Rowe (1988, 1993; see also Gauthier et al. 1988). G, herbivorous, gomphodont cynodonts; T, tritylodontids (the teeth of which are morphologically gomphodont); S, cynodonts with sectorial postcanine teeth; M, early mammals (which have sectorial teeth). The following taxa are characterized by transversely-expanded (gomphodont) postcanine teeth in Figure 3: *Diademodon*, *Trirachodon*, *Luangwa*, *Massetognathus*, and *Tritylodontidae*; all other cynodonts have sectorial (slicing) postcanine teeth. Although we favor the hypothesis depicted in (*A*), advanced cynodont systematics lacks consensus, and further work is required.

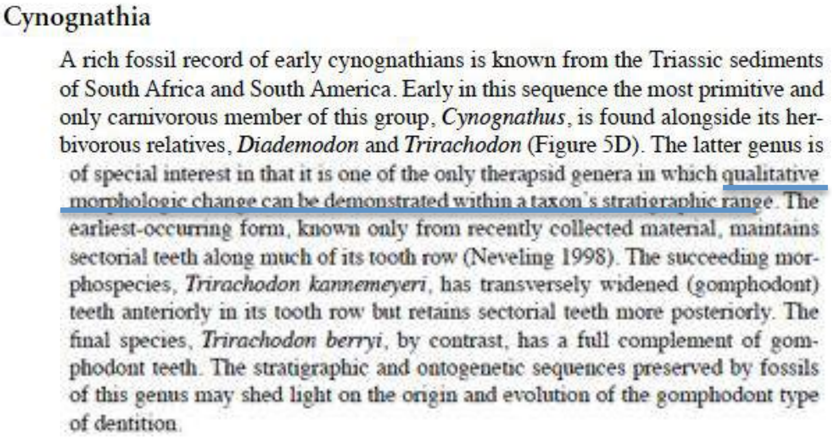


Cynognathia



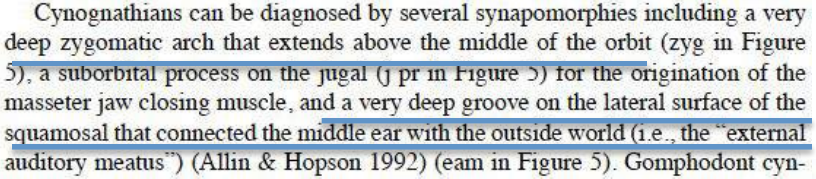
Dentición Gomphodonta: dientes lateralmente expandidos, más anchos que largos (como en Bauria)

“Sectorial”: Cortante



Cynognathia

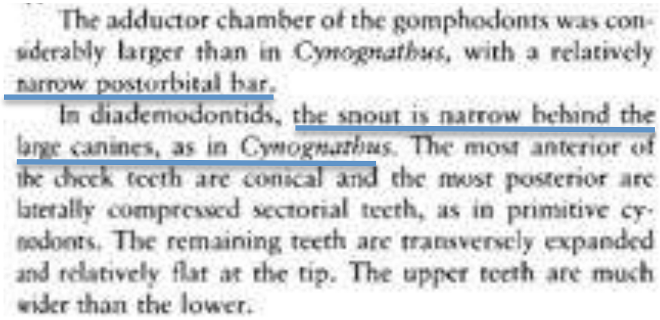
A rich fossil record of early cynognathians is known from the Triassic sediments of South Africa and South America. Early in this sequence the most primitive and only carnivorous member of this group, *Cynognathus*, is found alongside its herbivorous relatives, *Diademodon* and *Trirachodon* (Figure 5D). The latter genus is of special interest in that it is one of the only therapsid genera in which qualitative morphologic change can be demonstrated within a taxon's stratigraphic range. The earliest-occurring form, known only from recently collected material, maintains sectorial teeth along much of its tooth row (Neveling 1998). The succeeding morphospecies, *Trirachodon kannemeyeri*, has transversely widened (gomphodont) teeth anteriorly in its tooth row but retains sectorial teeth more posteriorly. The final species, *Trirachodon berryi*, by contrast, has a full complement of gomphodont teeth. The stratigraphic and ontogenetic sequences preserved by fossils of this genus may shed light on the origin and evolution of the gomphodont type of dentition.



Cynognathians can be diagnosed by several synapomorphies including a very deep zygomatic arch that extends above the middle of the orbit (zyg in Figure 5), a suborbital process on the jugal (j pr in Figure 5) for the origination of the masseter jaw closing muscle, and a very deep groove on the lateral surface of the squamosal that connected the middle ear with the outside world (i.e., the "external auditory meatus") (Allin & Hopson 1992) (eam in Figure 5). Gomphodont cyn-

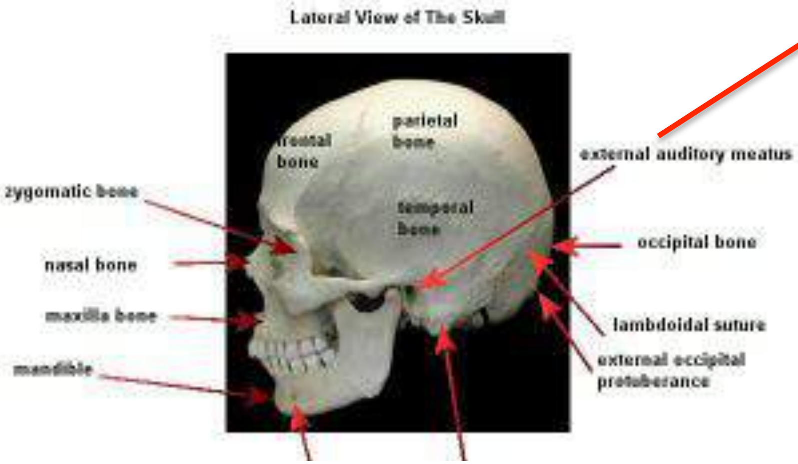
Formas de Cynognathia basales herbívoras: presentan al menos algunos dientes lateralmente expandidos (condición de "Gomphodontos")

Trirachodon: Cambio a la dentición gomphodonta en la variación intra-genérica, en perfecta secuencia estratigráfica. Primero todos sectoriales, luego dientes anteriores gomfodontos, después todos gomfodontos



The adductor chamber of the gomphodonts was considerably larger than in *Cynognathus*, with a relatively narrow postorbital bar.

In diademodontids, the snout is narrow behind the large canines, as in *Cynognathus*. The most anterior of the cheek teeth are conical and the most posterior are laterally compressed sectorial teeth, as in primitive cynodonts. The remaining teeth are transversely expanded and relatively flat at the tip. The upper teeth are much wider than the lower.



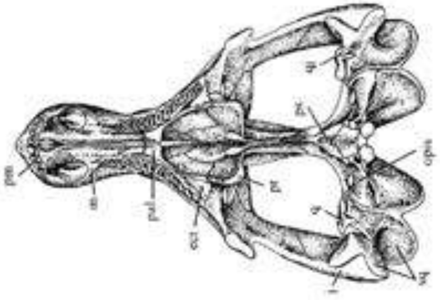
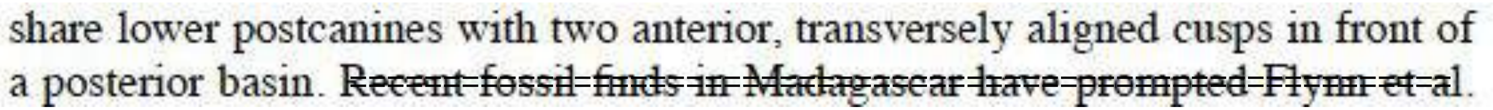
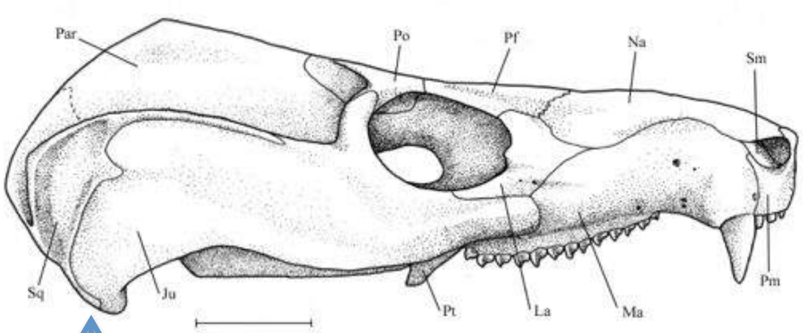


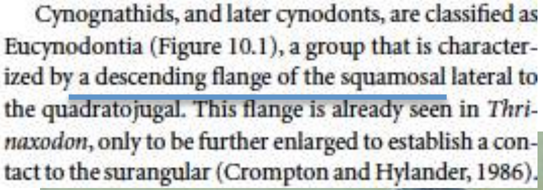
Figure 17-38. PALATE OF THE LOWER TRIASSIC GOMPHODONT *DIADEMODON*, ×1. Abbreviations as in Figure 8-3. From Brink, 1963.

Traversodontidae: Cynognathia derivados con dentición gomphodonta.

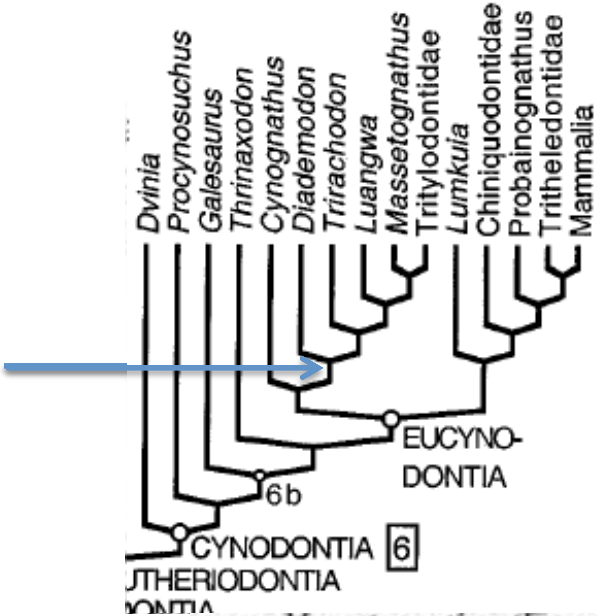

share lower postcanines with two anterior, transversely aligned cusps in front of a posterior basin. ~~Recent fossil finds in Madagascar have prompted Flynn et al~~.

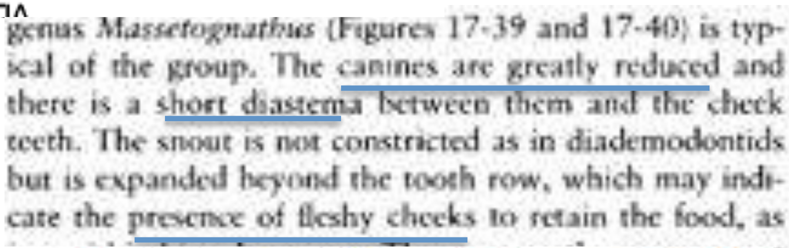


Massetognathus


Cynognathids, and later cynodonts, are classified as Eucynodontia (Figure 10.1), a group that is characterized by a descending flange of the squamosal lateral to the quadratojugal. This flange is already seen in *Thrinaxodon*, only to be further enlarged to establish a contact to the surangular (Crompton and Hylander, 1986).

Exaeretodon




genus *Massetognathus* (Figures 17-39 and 17-40) is typical of the group. The canines are greatly reduced and there is a short diastema between them and the cheek teeth. The snout is not constricted as in diademodontids but is expanded beyond the tooth row, which may indicate the presence of fleshy cheeks to retain the food, as

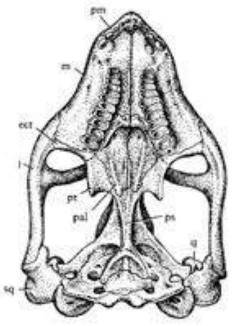
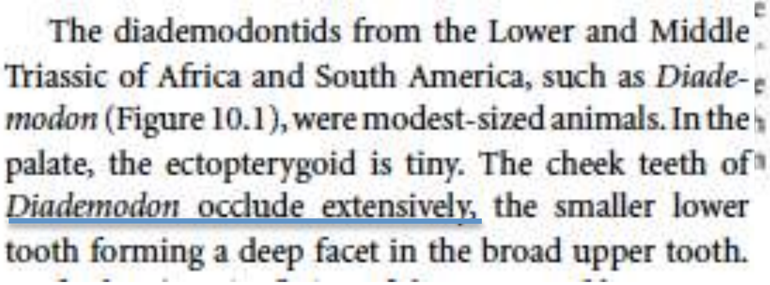


Figure 17-40. PALATE OF THE HERBIVOROUS CYNODONT *MASSETOGNATHUS*. Abbreviations as in Figure 8-3. From Romer, 1967.


The diademodontids from the Lower and Middle Triassic of Africa and South America, such as *Diademodon* (Figure 10.1), were modest-sized animals. In the palate, the ectopterygoid is tiny. The cheek teeth of *Diademodon* occlude extensively, the smaller lower tooth forming a deep facet in the broad upper tooth.

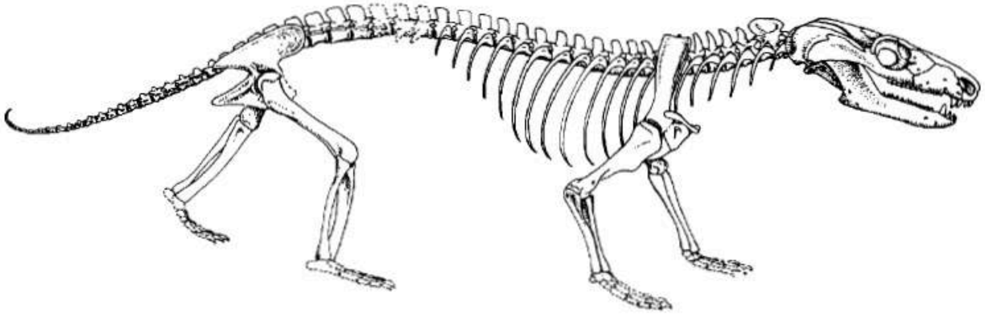
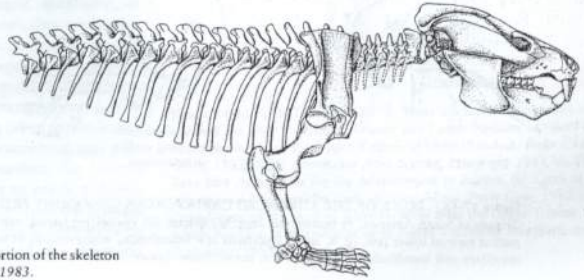


Figure 17-39. SKELETON OF THE SOUTH AMERICAN GOMPHODONT CYNODONT *MASSETOGNATHUS*, ×¼. *From Jenkins, 1970.*



ure 17-42. *KAYENTATHERIUM.* Anterior portion of the skeleton
the Lower Jurassic tritylodont, ×¼. *From Sues, 1983.*

Primitive diademodontids retain broad costal plates in the lumbar region like those of the galesaurids, but the plates are absent from the cervical and anterior thoracic ribs. In contrast, advanced traversodontids have reevolved the slim ribs of typical reptiles. The vertebral column is specialized in the presence of accessory articulating surfaces that may have helped to support the trunk. The epaxial musculature, situated between the neural spines and the transverse processes, has probably become further elaborated. The ilium is elongated anteriorly and supported by up to four sacral ribs.

Traversodontids survive nearly to the end of the Triassic (Hopson, 1984). We know them from the Lower to the Upper Triassic in South America, the Middle Triassic of East Africa, and the Upper Triassic of North America, India (Chatterjee, 1983), and southern Africa.

10.2(g)), *Massetognathus* has an erect mammalian hindlimb and sprawling reptilian forelimb, as in *Probelesodon* (Figure 10.2(f)), and the lumbar ribs are reduced (such ribs are absent in mammals). The reduction and loss of lumbar ribs probably indicate the evolution of a **diaphragm** in these forms. In modern

PROBAINOGNATHIA (incluye mamíferos)

Most of the major features of the mammalian skull evolved among the carnivorous cynodonts. The chiniquodontids still retain the postorbital and prefrontal bones, but they are lost in both trithelodonts and tritylodonts. With the loss of the postorbital bar, the temporal opening becomes confluent with the orbit in these groups, as in the early mammals.

Among the chiniquodontids, the secondary palate extended posteriorly to essentially the same extent as in primitive mammals. Important changes in the dentition between cynodonts and mammals will be discussed in the following chapter.

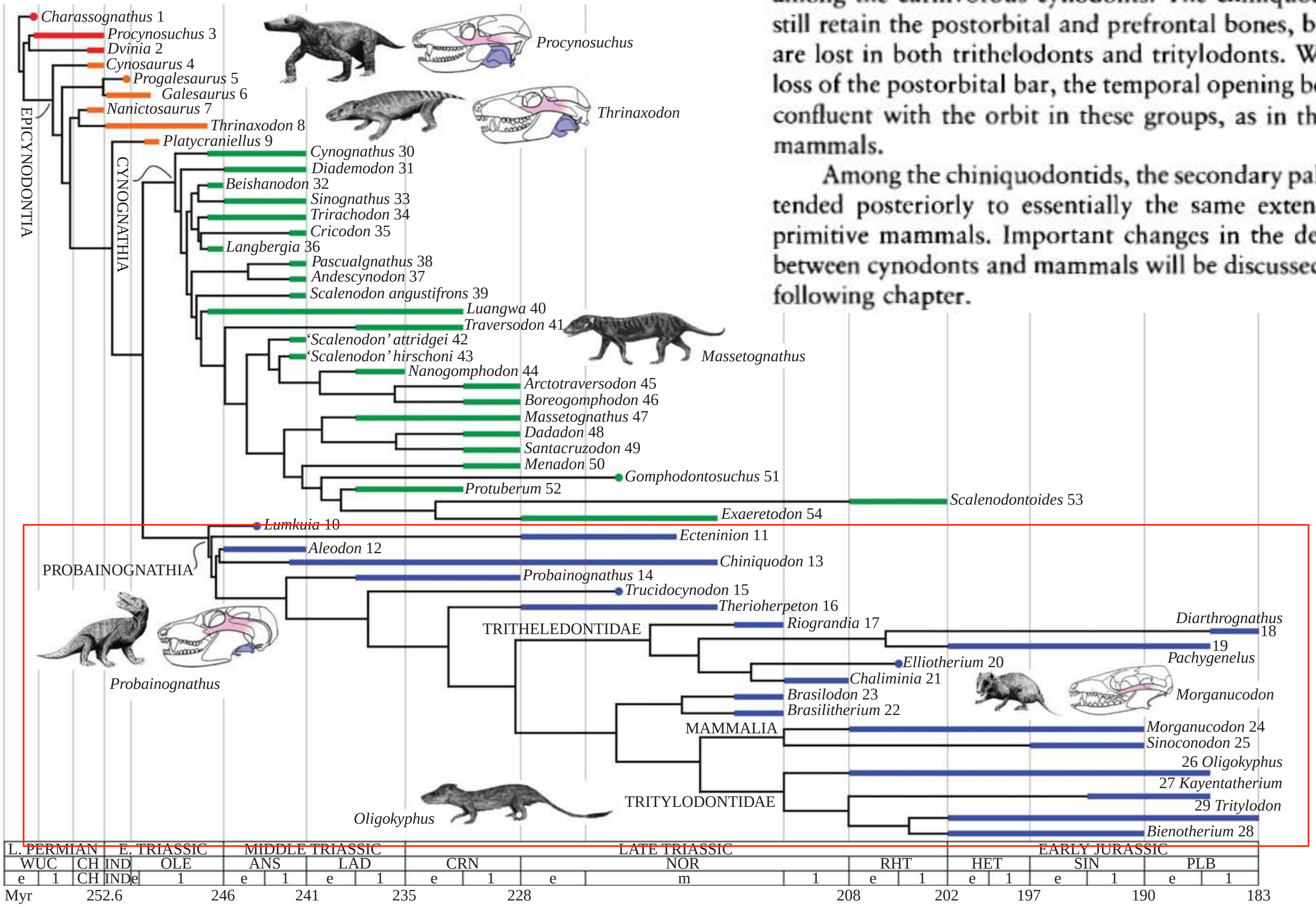


Figure 1. Cynodont tree plotted onto a stratigraphic scale; rectangular bars or dots show the known observed ranges of taxa; e, early; m, middle; l, late; each taxon is identified by a number, for ease of comparisons with the plots in figure 2*a*–*c*. For stage abbreviations, see §2d.

Si el fulcrum de la oclusión está por detras del PLMA, el efecto es positivo (aplica fuerza sobre la articulación mandibular)
Si queda delante, el efecto es –

El masetero superficial tiene una acción contraria al temporalis

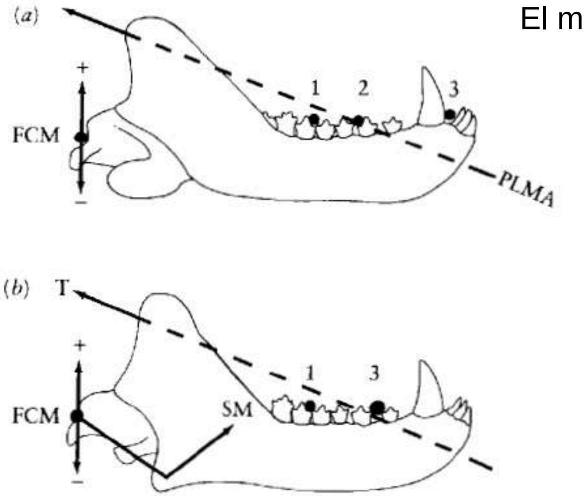
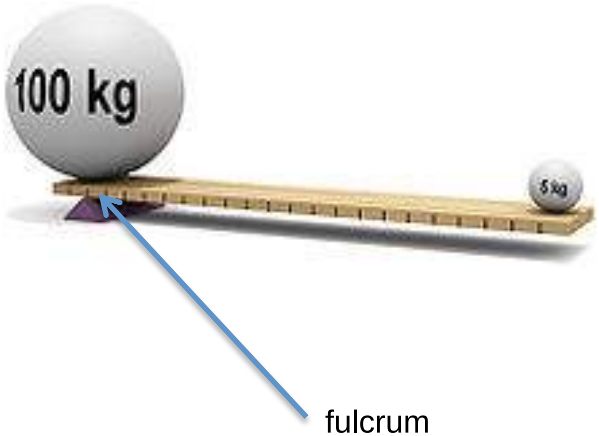


Figure 17-49. RESOLUTION OF FORCES ON THE JAW JOINT OF A MAMMAL-LIKE REPTILE. *Based on the bi-fulcral model of Bramble, 1978.* Abbreviations as follows: PLMA, projected line of muscle action, extended anteriorly from the temporalis; FCM, fulcrum of craniomandibular joint; T, temporalis; SM, superficial masseter; 1, 2, 3, occlusal fulcra. (*a*) When the occlusal fulcrum is at 3, near the front of the mouth, contraction of the temporalis places a positive force on the jaw articulation. When the occlusal fulcrum is at 1, near the back of the jaw, the force on the jaw articulation is negative. When the occlusal fulcrum is directly in line with the projected line of muscle action, the force on the jaw articulation is neutral. (*b*) Representation of the counterbalancing of forces produced by the temporalis and the superficial masseter. The superficial masseter, whose force is represented by the arrow SM, acts at nearly right angles to the temporalis, T. When the occlusal fulcrum is near the front of the jaw, 3, the force on the jaw joint is negative, and when it is at 1, the force is positive. There will be a position near the middle of the jaw where the forces of the temporalis and superficial masseter neutralize one another.



fulcrum

El aumento progresivo del proceso coronoide permitio eliminar la presion positiva al morder con los dientes anteriores, y luego en todos los dientes

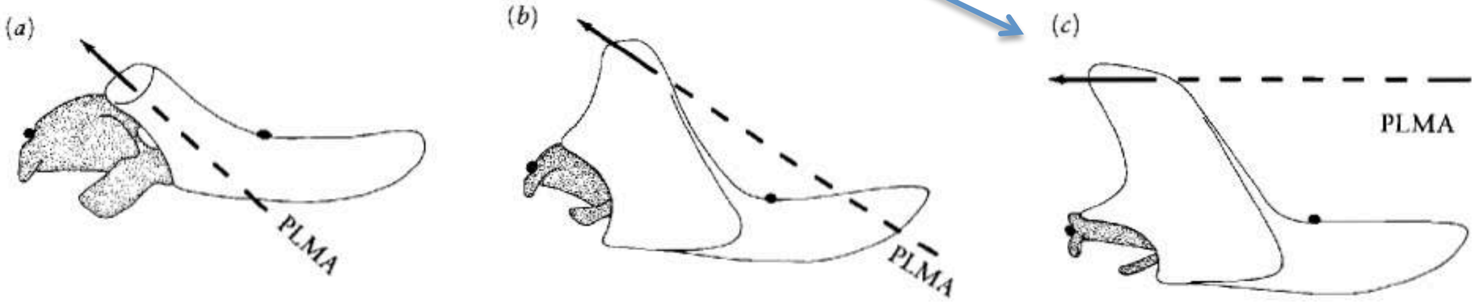


Figure 17-50. JAWS OF THREE CYNODONTS. The way in which the progressive heightening of the coronoid process changes the forces acting on the jaw joint is shown. Only the temporalis is considered. (*a*) In *Procynosuchus*, the projected line of muscle action crosses the lower jaw behind the teeth row, and the force on the jaw joint is positive no matter where the food is bitten. (*b*) In *Trirachodon*, the projected line of muscle action intersects the middle of the tooth row, so that a more anterior bite will produce a positive force but a more posterior bite will produce a negative force. (*c*) In *Probainognathus*, the projected line of muscle action passes over the end of the jaw, and the force on the jaw joint will be negative no matter where the food is bitten. With the evolution of the superficial masseter, cynodonts were able to exert a progressively stronger bite on the food while the jaw articulation was stressed to a smaller extent. This process explains how the extradentary elements could have been reduced in late therapsids in relationship to the evolution of the mammalian middle ear. Abbreviation as in Figure 17-49. *From Bramble, 1978.*

Evolución previa de huesos art. mandibulares

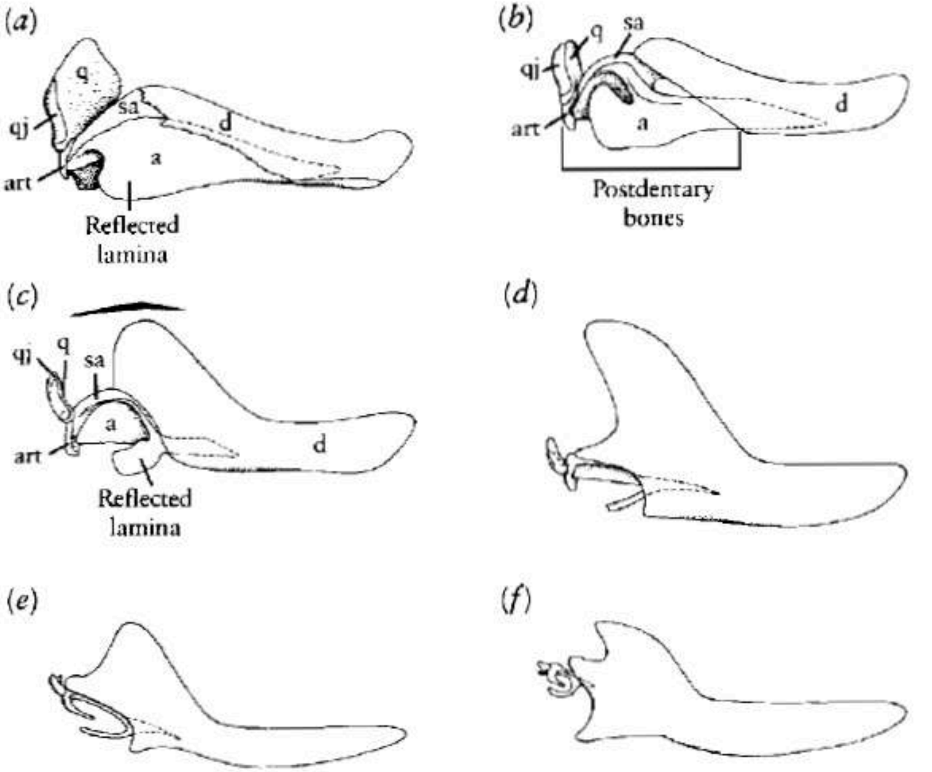


Figure 17-47. PROGRESSIVE CHANGES IN THE STRUCTURE OF THE JAW AND ELEMENTS OF THE MIDDLE EAR FROM PELYCOSAURS TO MAMMALS. All in lateral view. (*a*) The sphenacodont pelycosaur *Dimetrodon*. All the elements of the lower jaw are suturally attached. The angular bears a reflected lamina. (*b*) Condition of an advanced therocephalian. Postdentary bones are no longer suturally attached to the dentary, but they remain very large. (*c*) *Thrinaxodon*, a primitive cynodont. (*d*) The advanced cynodont *Probainognathus*. (*e*) An early Jurassic mammal, *Morganucodon*. (*f*) Hypothetical reconstruction of a Jurassic panthothere. The ear ossicles are not known in the immediate ancestors of placentals and marsupials, but they would have been about this size. Abbreviations as in Figure 8-3. *From Allin, 1975.*

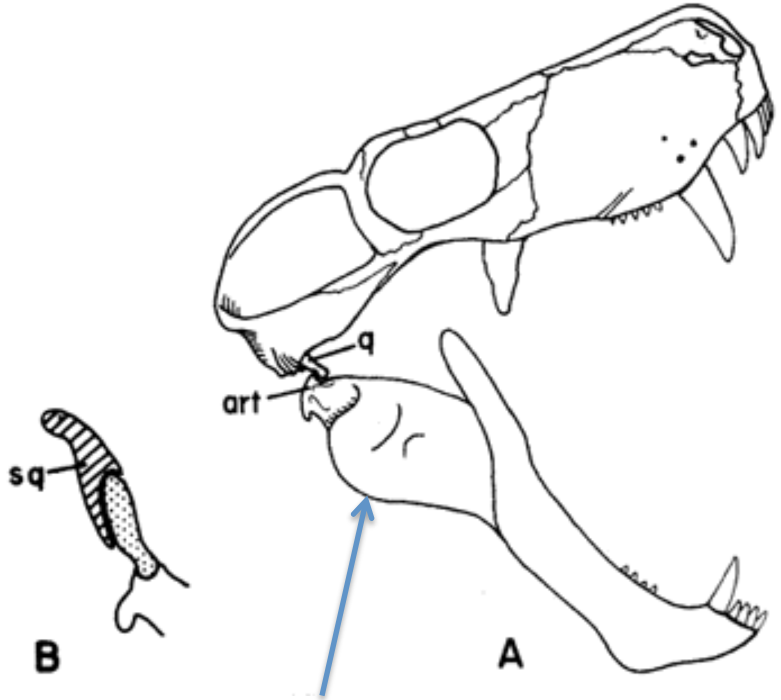


Lámina del angular

Cuadrado suelto

In later cynodonts—both the herbivorous gomphodonts and tritylodonts and the carnivorous chiniquodontids—the postdentary bones are further reduced. The angular is reduced to a narrow rod that lies parallel with the prearticular and surangular. The reflected lamina consists of a narrow process that extends posteroventrally toward the retroarticular process of the articular. Together, these processes form an incomplete ring. According to Allin, the large bony surface of the reflected lamina in early cynodonts was replaced by a membrane (the tympanum) that stretched to the articular. These elements form a structure that is comparable, except for its larger size, with the tympanic ring and malleus in modern mar-

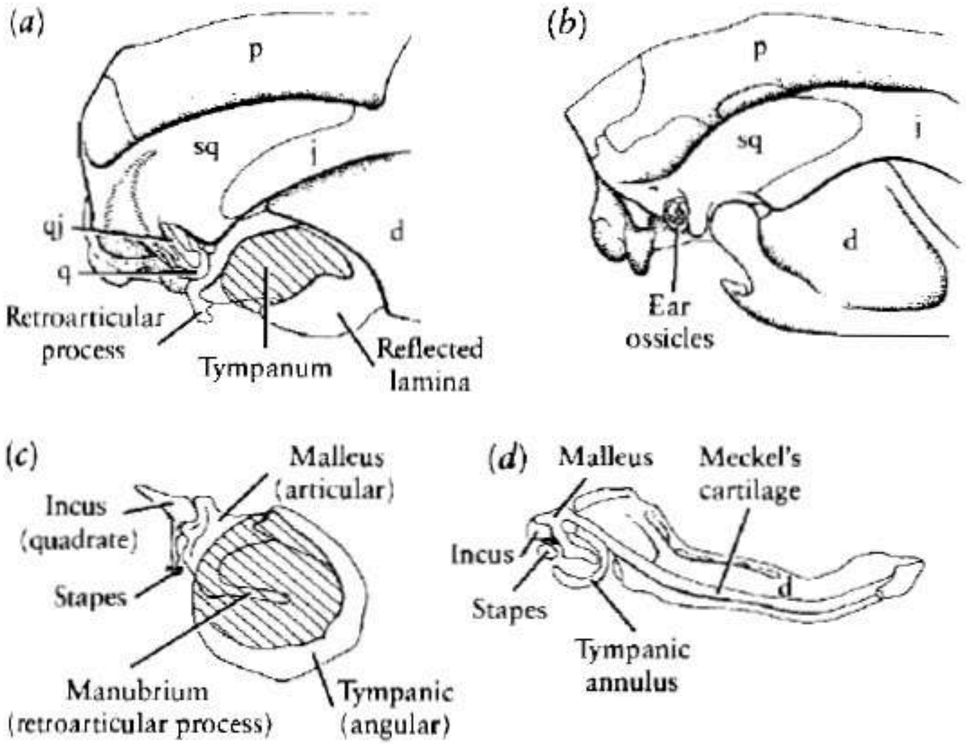


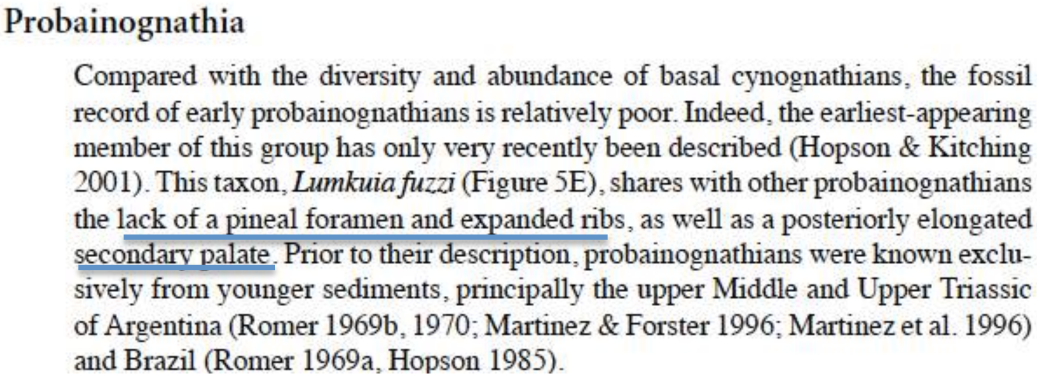
Figure 17-48. (*a*) Jaw and ear region in a mammal-like reptile, *Thrinaxodon*, and (*b*) a living opossum. (*c*) Enlarged view of ear ossicles in the opossum. (*d*) Medial view of the jaw in a fetal mammal to show the parallel between the ontogenetic development of the middle ear and jaw joint complex with the phylogenetic origin of this structure. Abbreviations as in Figure 8-3. *From Crompton and Jenkins, 1979. By permission of the University of California Press.*

The ear ossicles in adult mammals are functionally very distinct, since they do not serve a role as elements in the jaw articulation, as was the case in all therapsids. Indicative of this evolutionary transformation, the function of these bones changes in every generation of marsupials. During their development in the pouch, the malleus and incus retain the reptilian role of the articular and quadrate. Only when the young leave the pouch do these bones separate from the lower jaw and enter the middle ear.

In *Probainognathus,* the surangular and dentary extend back to the squamosal to form a second jaw articulation. As the dentary is further elaborated, we can recognize two functional jaw joints, a medial reptilian joint, which consists of the articular and quadrate, and a lateral mammalian joint, which is formed by the dentary and squamosal. Both are retained in early mammals (see Chapter 18). It is not yet certain when the malleus and incus became incorporated into the middle ear, but the grooves on the medial surface of the dentary that indicate their position of attachment in early Jurassic mammals are missing in Upper Jurassic genera.

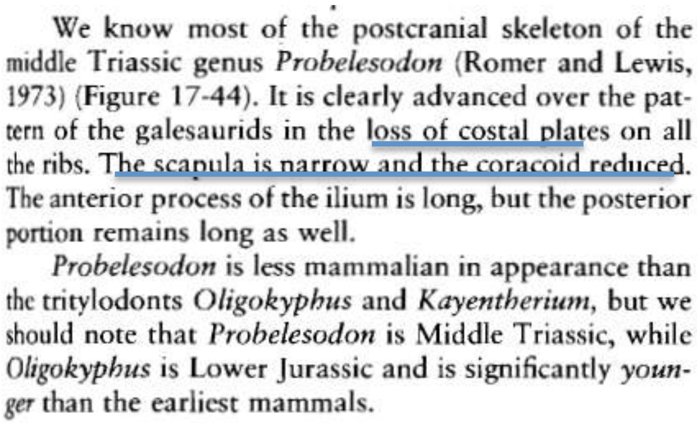
PROBAINOGNATHIA BASALES

Probainognathidae, Chiniquodontidae



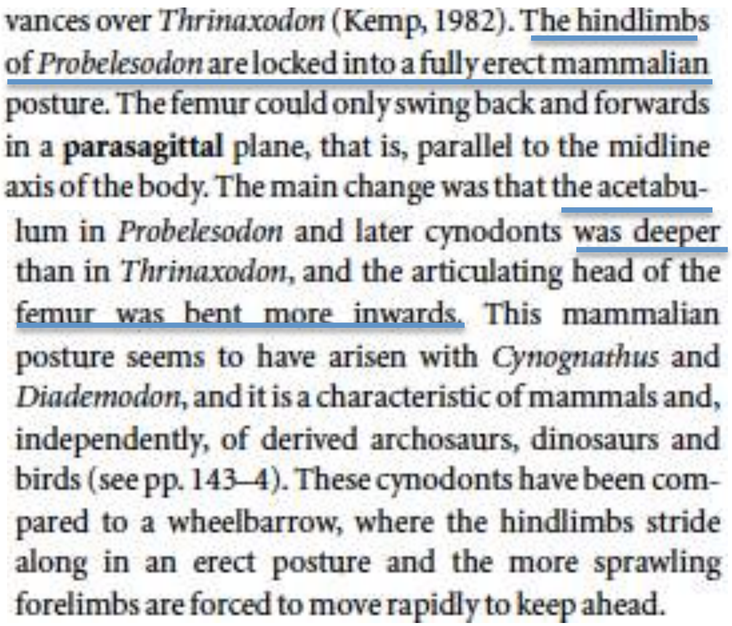
Probainognathia

Compared with the diversity and abundance of basal cynognathians, the fossil record of early probainognathians is relatively poor. Indeed, the earliest-appearing member of this group has only very recently been described (Hopson & Kitching 2001). This taxon, *Lumkuia fuzzi* (Figure 5E), shares with other probainognathians the lack of a pineal foramen and expanded ribs, as well as a posteriorly elongated secondary palate. Prior to their description, probainognathians were known exclusively from younger sediments, principally the upper Middle and Upper Triassic of Argentina (Romer 1969b, 1970; Martinez & Forster 1996; Martinez et al. 1996) and Brazil (Romer 1969a, Hopson 1985).



We know most of the postcranial skeleton of the middle Triassic genus *Probelesodon* (Romer and Lewis, 1973) (Figure 17-44). It is clearly advanced over the pattern of the galesaurids in the loss of costal plates on all the ribs. The scapula is narrow and the coracoid reduced. The anterior process of the ilium is long, but the posterior portion remains long as well.

Probelesodon is less mammalian in appearance than the tritylodonts *Oligokyphus* and *Kayentherium*, but we should note that *Probelesodon* is Middle Triassic, while *Oligokyphus* is Lower Jurassic and is significantly *younger* than the earliest mammals.



vances over *Thrinaxodon* (Kemp, 1982). The hindlimbs of *Probelesodon* are locked into a fully erect mammalian posture. The femur could only swing back and forwards in a **parasagittal** plane, that is, parallel to the midline axis of the body. The main change was that the acetabulum in *Probelesodon* and later cynodonts was deeper than in *Thrinaxodon*, and the articulating head of the femur was bent more inwards. This mammalian posture seems to have arisen with *Cynognathus* and *Diademodon*, and it is a characteristic of mammals and, independently, of derived archosaurs, dinosaurs and birds (see pp. 143–4). These cynodonts have been compared to a wheelbarrow, where the hindlimbs stride along in an erect posture and the more sprawling forelimbs are forced to move rapidly to keep ahead.

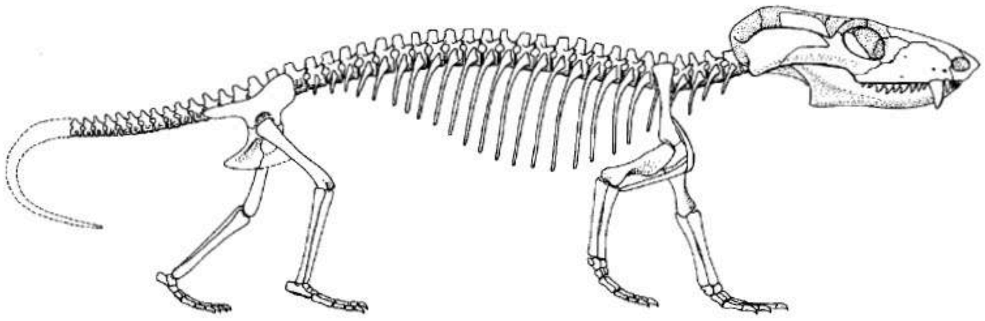
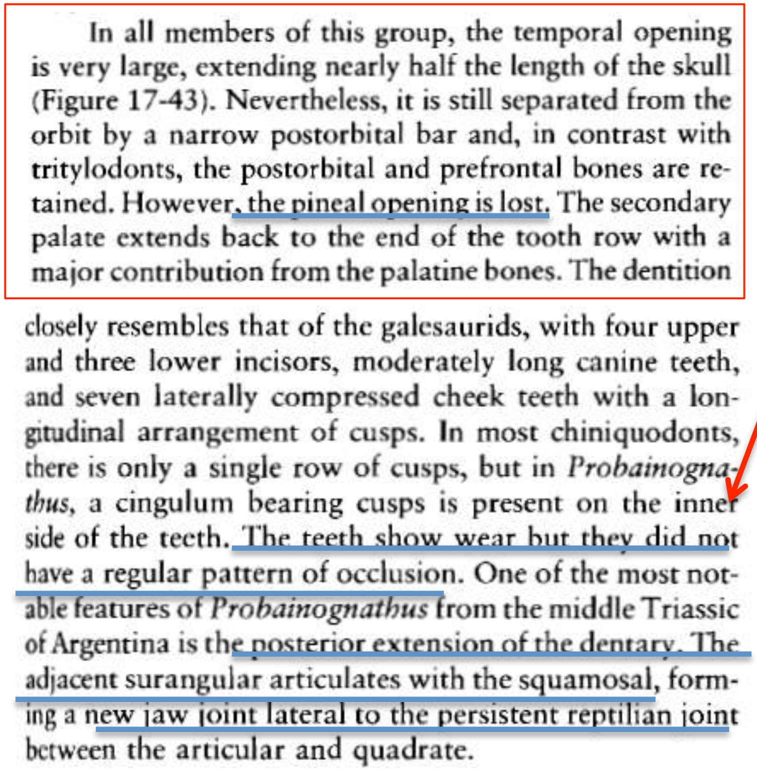
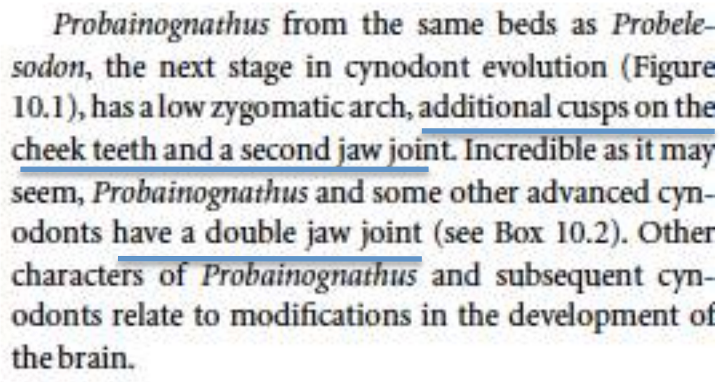


Figure 17-44. *PROBELESODON*. Skeleton of the advanced carnivorous cynodant from the Middle Triassic of South America, 65 centimeters long. *From Romer and Lewis, 1973.*



In all members of this group, the temporal opening is very large, extending nearly half the length of the skull (Figure 17-43). Nevertheless, it is still separated from the orbit by a narrow postorbital bar and, in contrast with tritylodonts, the postorbital and prefrontal bones are retained. However, the pineal opening is lost. The secondary palate extends back to the end of the tooth row with a major contribution from the palatine bones. The dentition closely resembles that of the galesaurids, with four upper and three lower incisors, moderately long canine teeth, and seven laterally compressed cheek teeth with a longitudinal arrangement of cusps. In most chiniquodonts, there is only a single row of cusps, but in *Probainognathus*, a cingulum bearing cusps is present on the inner side of the teeth. The teeth show wear but they did not have a regular pattern of occlusion. One of the most notable features of *Probainognathus* from the middle Triassic of Argentina is the posterior extension of the dentary. The adjacent surangular articulates with the squamosal, forming a new jaw joint lateral to the persistent reptilian joint between the articular and quadrate.

Polifiodoncia



Probainognathus from the same beds as *Probelesodon*, the next stage in cynodont evolution (Figure 10.1), has a low zygomatic arch, additional cusps on the cheek teeth and a second jaw joint. Incredible as it may seem, *Probainognathus* and some other advanced cynodonts have a double jaw joint (see Box 10.2). Other characters of *Probainognathus* and subsequent cynodonts relate to modifications in the development of the brain.

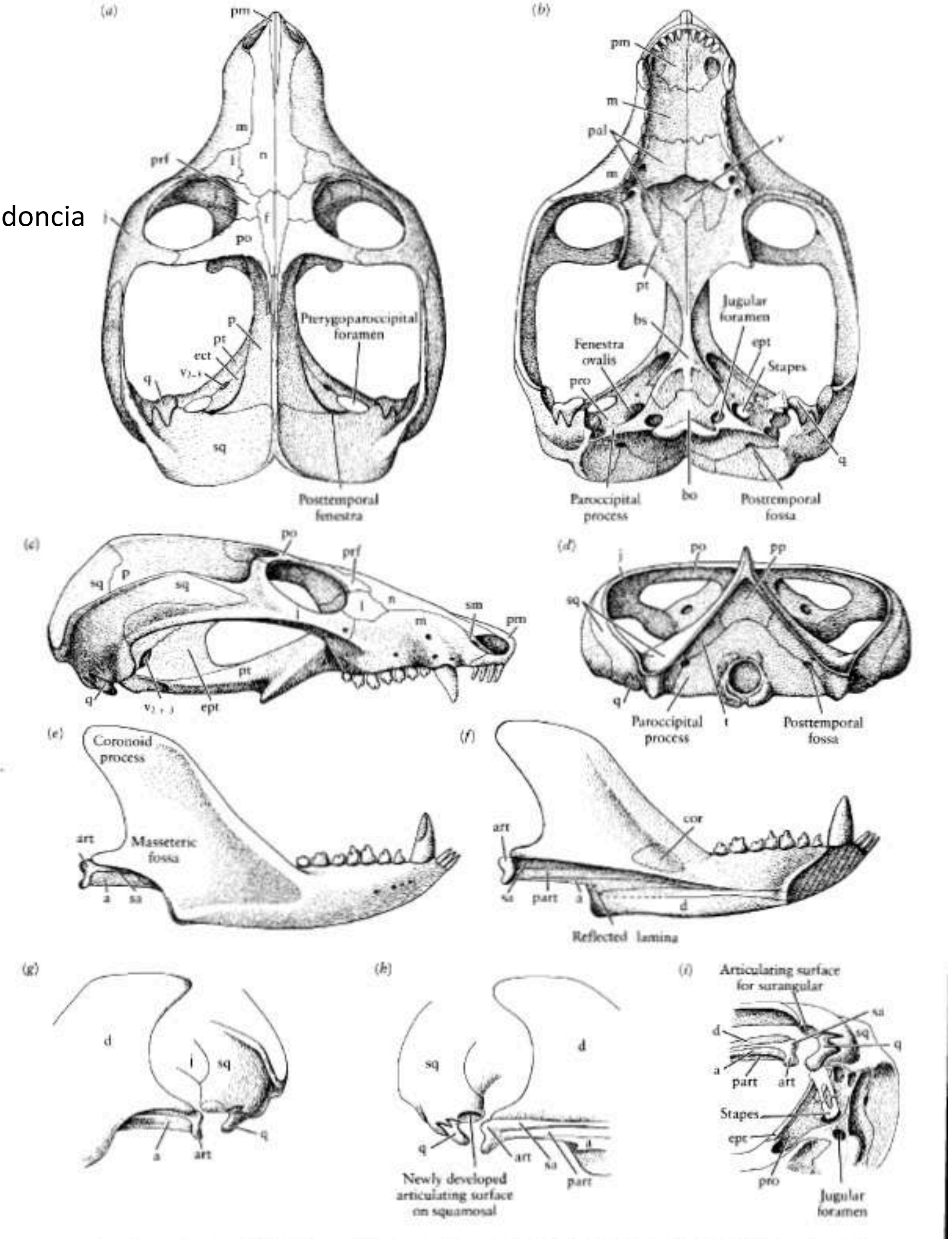


Figure 17-43. SKULL OF THE ADVANCED CARNIVOROUS CYNODONT *PROBAINOGNATHUS*. From the Middle Triassic of South America, 9½ centimeters long. (*a*) Dorsal, (*b*) ventral, (*c*) lateral, and (*d*) occipital views. (*e*) Lateral and (*f*) medial view of lower jaw. (*g*, *h*, and *i*) Details of jaw articulation. Abbreviations as in Figure 8-3, plus: V_{2+3}, openings for maxillary and mandibular branches of Vth nerve. *From Romer, 1970.*

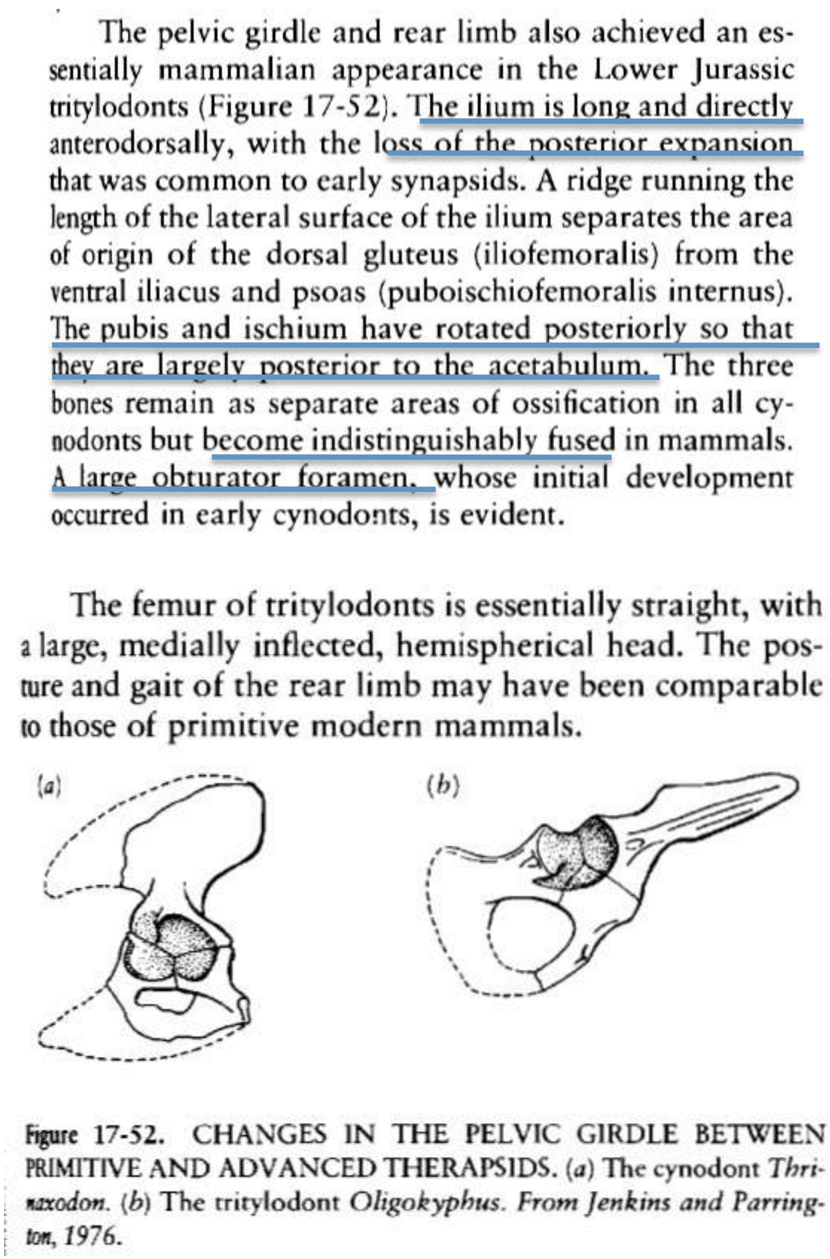
Mammaliomorpha: Más cercanos
a mamíferos que a diademodontoides (cynognathidae) , chiniquodontidos y probainognathidos.

Comparten un ileon anteriormente proyectado y rotación posterior del pubis por debajo del acetábulo

Comunicación de la órbita con la apertura temporal

Mammaliomorpha basales:

Tritylodontes, Trithelodontes, Brasilodontidos y Dromatheriidos



The pelvic girdle and rear limb also achieved an essentially mammalian appearance in the Lower Jurassic tritylodonts (Figure 17-52). The ilium is long and directly anterodorsally, with the loss of the posterior expansion that was common to early synapsids. A ridge running the length of the lateral surface of the ilium separates the area of origin of the dorsal gluteus (iliofemoralis) from the ventral iliacus and psoas (puboischiofemoralis internus). The pubis and ischium have rotated posteriorly so that they are largely posterior to the acetabulum. The three bones remain as separate areas of ossification in all cynodonts but become indistinguishably fused in mammals. A large obturator foramen, whose initial development occurred in early cynodonts, is evident.

The femur of tritylodonts is essentially straight, with a large, medially inflected, hemispherical head. The posture and gait of the rear limb may have been comparable to those of primitive modern mammals.

Figure 17-52. CHANGES IN THE PELVIC GIRDLE BETWEEN PRIMITIVE AND ADVANCED THERAPSIDS. (a) The cynodont *Thrinaxodon*. (b) The tritylodont *Oligokyphus*. *From Jenkins and Parrington, 1976.*

TRITHELODONTIDAE

been adequately described. The skull ranges from 3 to 6 centimeters long, the temporal opening (as in tritylodonts) is confluent with the orbit, and the postorbital and prefrontal bones are lost. In *Diarthrognathus*, the frontal extends ventrally anterior to the orbit to reach a dorsal process of the palatine that extends up from the palatal surface. The dentary appears to have made contact with the squamosal. As Gow (1980) described, the dentition is unlike that of chiniquidontids and mammals in the relatively great width of the cheek teeth (Figure 17-45). In *Pachygenelus* there are only two pairs of upper and lower incisors, although *Chaliminia* has three uppers, behind which is a diastema. *Theioherpeton* from South America appears to be the most mammalian of them all with a small, low skull that has very narrow zygomatic arches and narrow, crowned cheek teeth with partially divided roots. *Diarthrognathus* and *Chaliminia* appear to have retained an interpterygoid vacuity, a feature that was present only in very primitive cynodonts, but its expression in the trithelodonts may be a result of their very small size, which may favor the retention of juvenile characters.

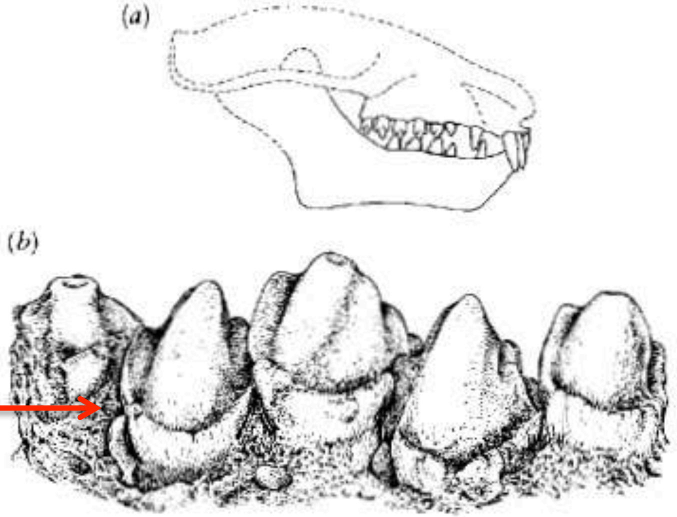
Because of the incomplete nature of most genera in this group, we are not certain that they are closely related. Nevertheless, they appear to show the closest approach to a mammalian morphology among small carnivorous cynodonts, which are otherwise the most appropriate ancestors of mammals.

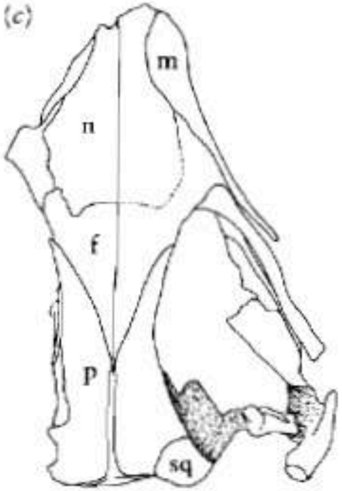
Articulación es casi completamente Dentario-Escamosa

No hay barra postorbital

No hay sínfisis entre los dentarios

Cingulum externo en los dientes





slender zygomatic arch, enlargement of the nasal cavity, the formation of a bony wall between the eyeballs and

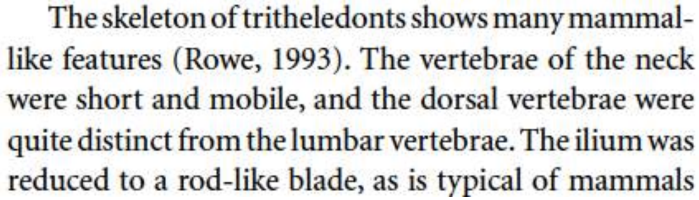
Tritheledontids (Figure 5F) are poorly understood as a group, although they have played an important role in understanding the origin of mammals (Crompton 1963, Luo 1994). Although its homology with that of mammals remains controversial, the dentary of the derived tritheledontid, *Pachygenelus*, appears to have made a contact with the squamosal, although an articular fossa is not present (Hopson 1994). This contact foreshadows the condition in early mammals such as *Morganucodon* and *Sinoconodon*, in which a well-developed dentary-squamosal jaw joint functions beside the primitive quadrate-articular jaw joint (Crompton & Luo 1993).

Figure 17-45. TRITHELODONTS. These advanced carnivorous cynodonts are from the Upper Triassic and Lower Jurassic. (*a*) Skull of *Pachygenelus* from the Upper Triassic of North America. *From Chatterjee, 1983. With permission from* Science. *Copyright 1983 by The American Association for the Advancement of Science.* (*b*) Teeth of a specimen of *Pachygenelus* from southern Africa. *From Gow, 1980.* (*c*) Dorsal view of the skull of *Theioherpeton* from the Upper Triassic of South America. Abbreviations as in Figure 8-3. *From Bonaparte and Barberena, 1975.*

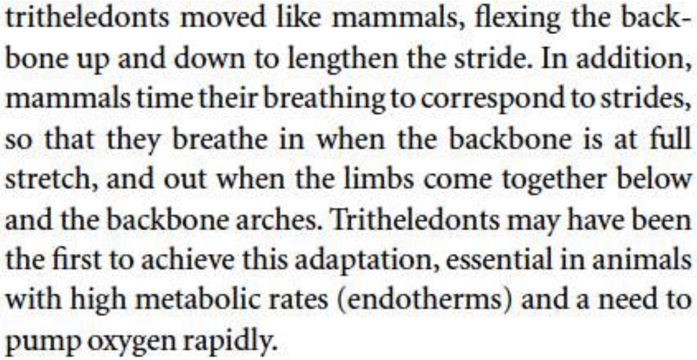
Trithelodontidae (Ictidosauria)

Locomoción a “saltitos” respiratorios
Ileon alargado

Chaliminia

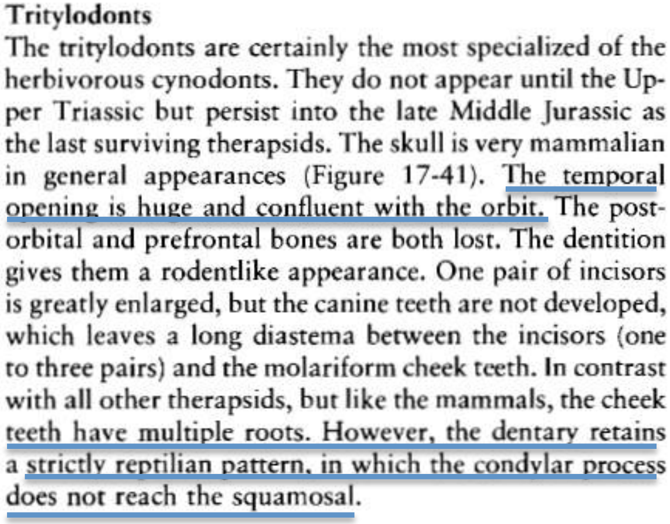


The skeleton of tritheledonts shows many mammal-like features (Rowe, 1993). The vertebrae of the neck were short and mobile, and the dorsal vertebrae were quite distinct from the lumbar vertebrae. The ilium was reduced to a rod-like blade, as is typical of mammals



tritheledonts moved like mammals, flexing the backbone up and down to lengthen the stride. In addition, mammals time their breathing to correspond to strides, so that they breathe in when the backbone is at full stretch, and out when the limbs come together below and the backbone arches. Tritheledonts may have been the first to achieve this adaptation, essential in animals with high metabolic rates (endotherms) and a need to pump oxygen rapidly.

TRITYLODONTIDAE



Tritylodonts

The tritylodonts are certainly the most specialized of the herbivorous cynodonts. They do not appear until the Upper Triassic but persist into the late Middle Jurassic as the last surviving therapsids. The skull is very mammalian in general appearances (Figure 17-41). The temporal opening is huge and confluent with the orbit. The postorbital and prefrontal bones are both lost. The dentition gives them a rodentlike appearance. One pair of incisors is greatly enlarged, but the canine teeth are not developed, which leaves a long diastema between the incisors (one to three pairs) and the molariform cheek teeth. In contrast with all other therapsids, but like the mammals, the cheek teeth have multiple roots. However, the dentary retains a strictly reptilian pattern, in which the condylar process does not reach the squamosal.

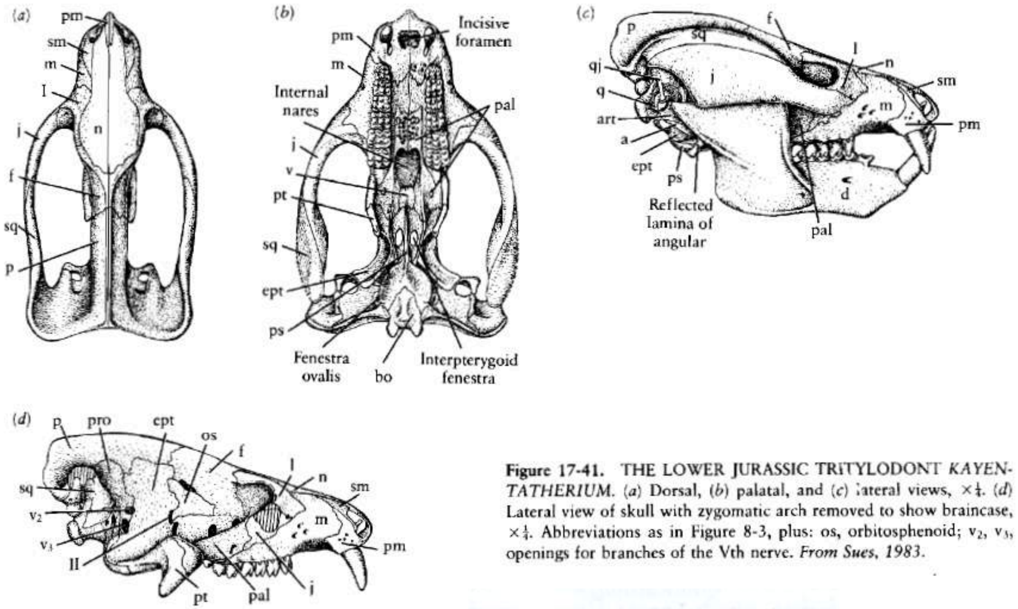
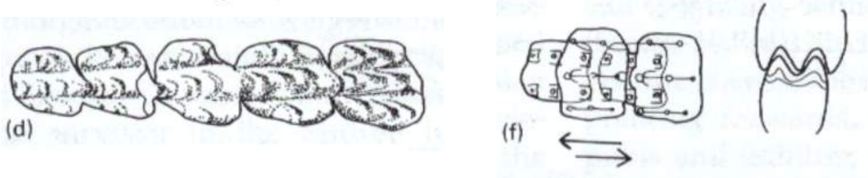


Figure 17-41. THE LOWER JURASSIC TRITYLODONT *KAYENTATHERIUM*. (*a*) Dorsal, (*b*) palatal, and (*c*) lateral views, ×¼. (*d*) Lateral view of skull with zygomatic arch removed to show braincase, ×¼. Abbreviations as in Figure 8-3, plus: os, orbitosphenoid; v_2, v_3, openings for branches of the Vth nerve. *From Sues, 1983.*



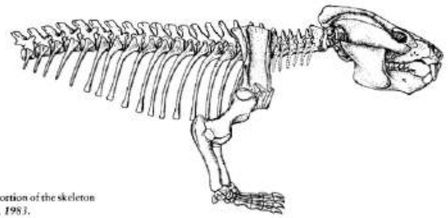
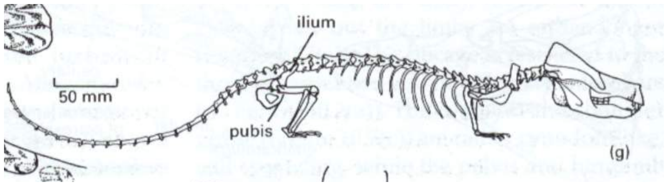
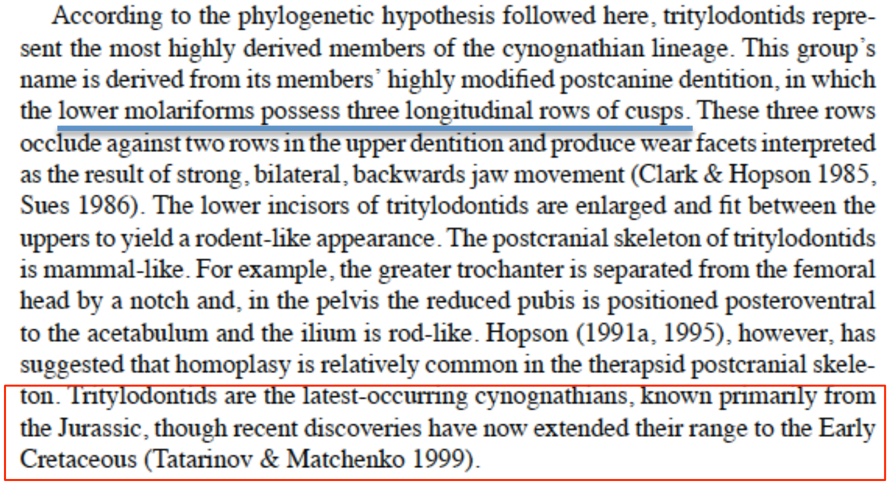
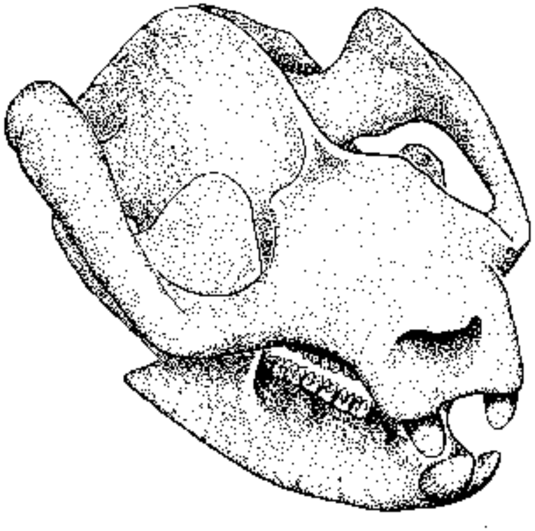


Figure 17-42. *KAYENTATHERIUM*. Anterior portion of the skeleton of the Lower Jurassic tritylodont, ×⅙. *From Sues, 1983.*

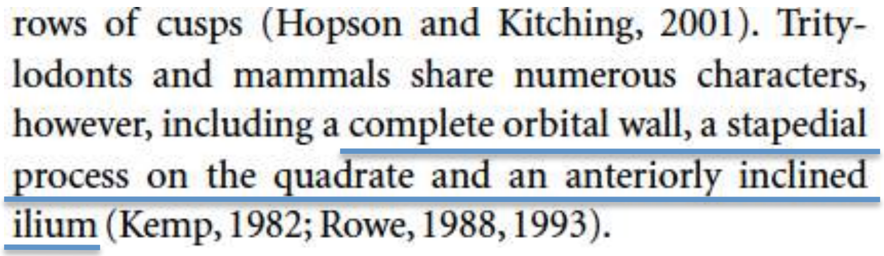




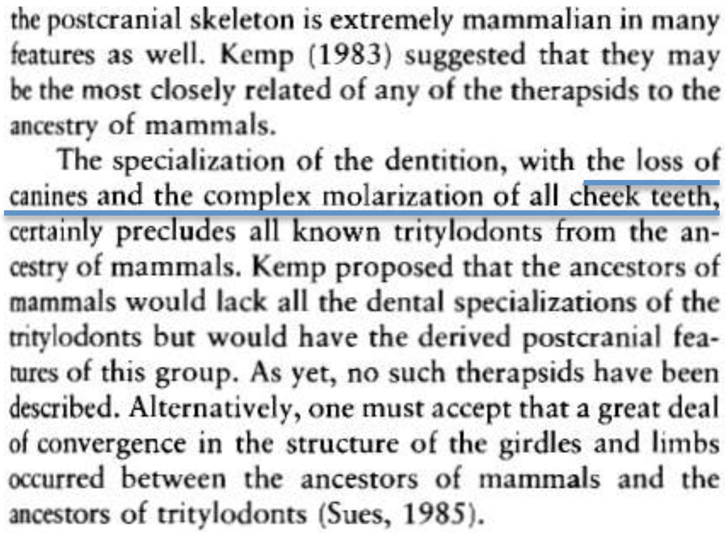
According to the phylogenetic hypothesis followed here, tritylodontids represent the most highly derived members of the cynognathian lineage. This group's name is derived from its members' highly modified postcanine dentition, in which the lower molariforms possess three longitudinal rows of cusps. These three rows occlude against two rows in the upper dentition and produce wear facets interpreted as the result of strong, bilateral, backwards jaw movement (Clark & Hopson 1985, Sues 1986). The lower incisors of tritylodontids are enlarged and fit between the uppers to yield a rodent-like appearance. The postcranial skeleton of tritylodontids is mammal-like. For example, the greater trochanter is separated from the femoral head by a notch and, in the pelvis the reduced pubis is positioned posteroventral to the acetabulum and the ilium is rod-like. Hopson (1991a, 1995), however, has suggested that homoplasy is relatively common in the therapsid postcranial skeleton. Tritylodontids are the latest-occurring cynognathians, known primarily from the Jurassic, though recent discoveries have now extended their range to the Early Cretaceous (Tatarinov & Matchenko 1999).



Tritylodon



rows of cusps (Hopson and Kitching, 2001). Tritylodonts and mammals share numerous characters, however, including a complete orbital wall, a stapedial process on the quadrate and an anteriorly inclined ilium (Kemp, 1982; Rowe, 1988, 1993).



the postcranial skeleton is extremely mammalian in many features as well. Kemp (1983) suggested that they may be the most closely related of any of the therapsids to the ancestry of mammals.

The specialization of the dentition, with the loss of canines and the complex molarization of all cheek teeth, certainly precludes all known tritylodonts from the ancestry of mammals. Kemp proposed that the ancestors of mammals would lack all the dental specializations of the tritylodonts but would have the derived postcranial features of this group. As yet, no such therapsids have been described. Alternatively, one must accept that a great deal of convergence in the structure of the girdles and limbs occurred between the ancestors of mammals and the ancestors of tritylodonts (Sues, 1985).