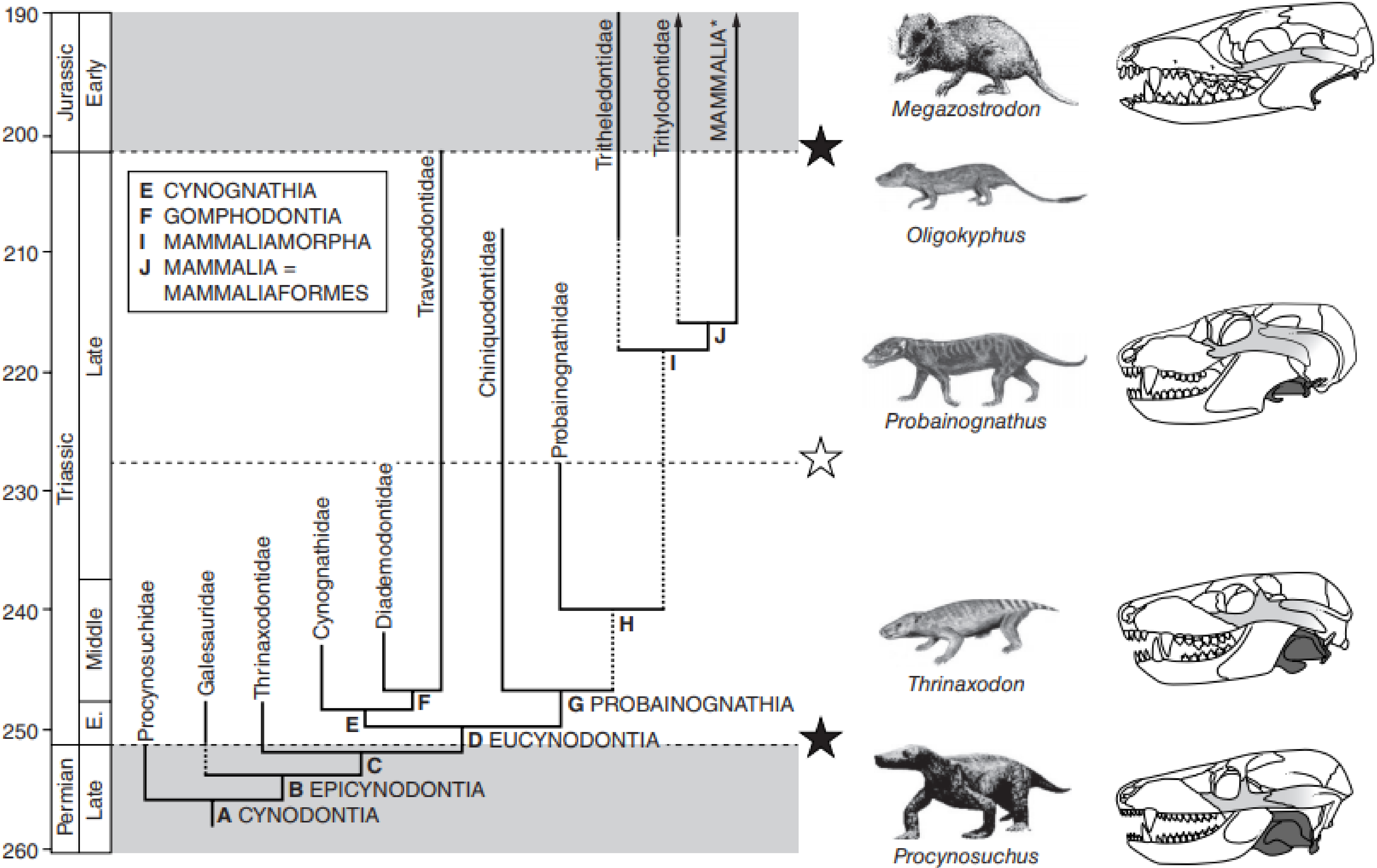
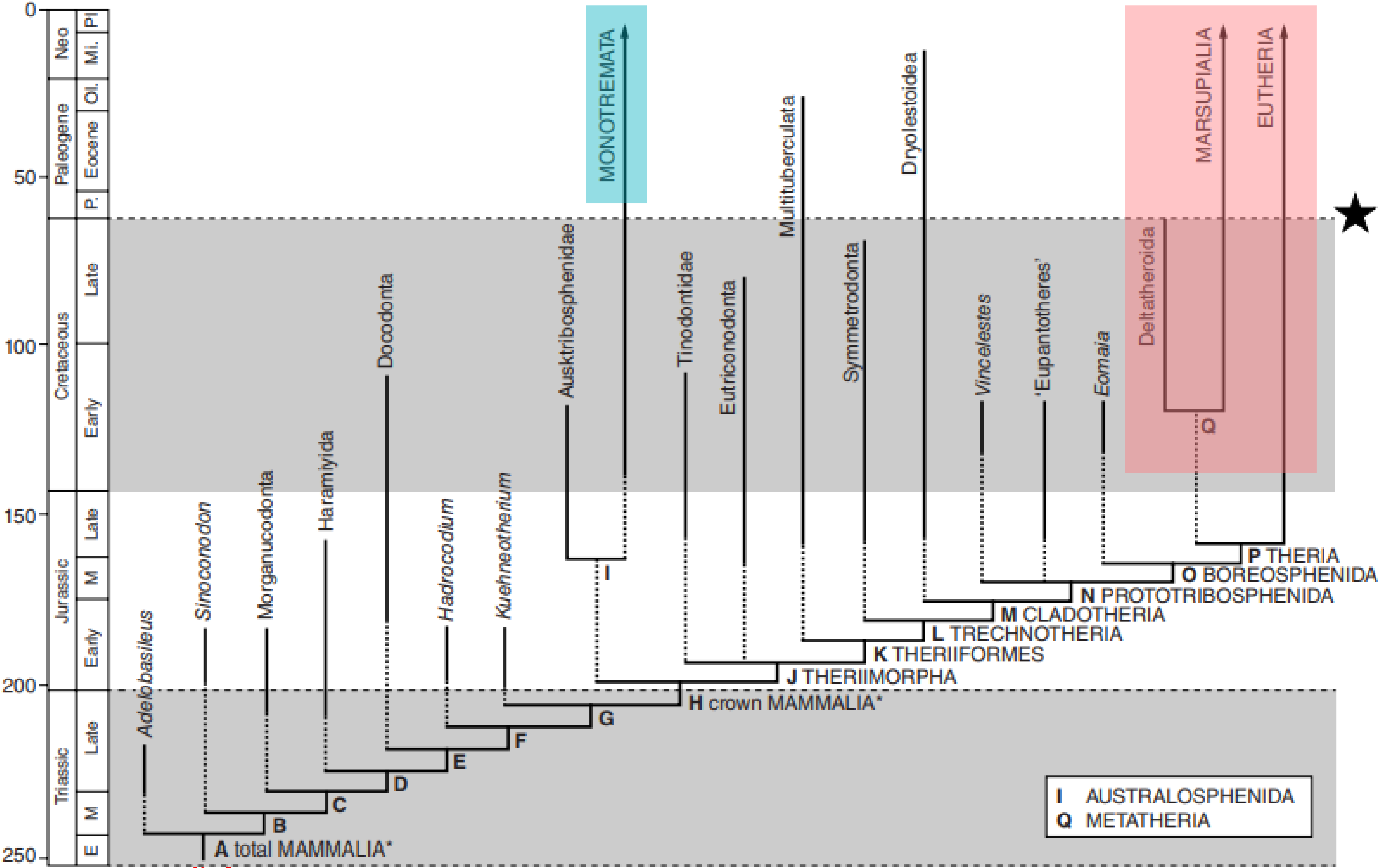
Mamaliaformes

Mamaliaformes (Rowe 1988): The most inclusive clade containing *Mus musculus* but not *Tritylodon longaevus* or *Pachygenelus monus.*

Mammalia (Linneaeus 1758): The least inclusive clade containing *Ornithorhynchus anatinus* and *Mus musculus*.


190
200
210
220
230
240
250
260
Jurassic
Early
Triassic
Late
Middle
E.
Permian
Late
E CYNOGNATHIA
F GOMPHODONTIA
I MAMMALIAMORPHA
J MAMMALIA = MAMMALIAFORMES
Procynosuchidae
Galesauridae
Thrinaxodontidae
Cynognathidae
Diademodontidae
Traversodontidae
Chiniquodontidae
Probainognathidae
Tritheledontidae
Tritylodontidae
MAMMALIA*
A CYNODONTIA
B EPICYNODONTIA
C
D EUCYNODONTIA
E
F
G PROBAINOGNATHIA
H
I
J
Megazostrodon
Oligokyphus
Probainognathus
Thrinaxodon
Procynosuchus

Synapomorphies are from Botha *et al*. (2007) for basal taxa, and Hopson and Kitching (2001), Abdala (2007), and Liu and Olsen (2010) for the remainder (convergences marked*): **A CYNODONTIA**, contact between nasal and lacrimal, frontal excluded from the orbital margin, double occipital condyle, angle of dentary at same level or posterior to postorbital bar, reflected lamina of angular a smooth plate with slight depressions, notch at base of coronoid process; **B EPICYNODONTIA**, facial process of septomaxilla short, interpterygoid opening absent, zygomatic arch moderately deep dorsoventrally, lateral crest of dentary incipient, masseteric fossa in dentary extends to the angle; **C**, foramen incisivum present, maxilla covers vomer in palatal view, bony palate complete, foramen on external surface of lower jaw between dentary and angular absent, reflected lamina of the angular hook-like; **D EUCYNODONTIA**, lateral crest of dentary well developed, dentary–surangular dorsal contact closer to cranio-mandibular joint, surangular–squamosal articulation with mandible reduced, upper postcanine series extends below orbit; **E CYNOGNATHIA**, carotid artery foramen in basisphenoid absent, canine serrations, lateral crest of dentary well developed, zygomatic arch very deep, infraorbital process is descendant process of jugal, posterior extension of squamosal dorsal to squamosal sulcus well developed; **F GOMPHODONTIA**, inferior margin of jugal in the zygomatic arch is well developed and high, upper tooth series extends below orbit*, postcanine occlusion by tooth-to-tooth contact because of widened postcanines, upper postcanine teeth widened*, transverse crest in upper postcanines with two cusps; **G PROBAINOGNATHIA**, bony palate extends to posterior margin of tooth row or behind, ectopterygoid absent, upper tooth series extends below orbit*; **H**, incipient maxillary platform lateral to dentition in posterior portion of the teeth row, upper postcanine teeth widened*, posterior postcanine teeth lack a strongly curved main cusp; **I MAMMALIAMORPHA**, prefrontal absent, postorbital bar absent, paroccipital process differentiated into anterior and posterior processes, mediolateral thickening of anterior margin of coronoid process, mandibular symphysis unfused, zygomatic arch slender, upper postcanine teeth have buccal cingulum; **J MAMMALIA**, fusion of prootic and opisthotic at an early ontogenetic stage, lateral flange vascular canal present venous drainage exiting from the back of the cavum epiptericum, completely divided postcanine roots. Source: Cynodont restorations adapted from various sources. Skulls drafted by S. Mitchell in Ruta *et al*. (2013). Abbreviations: E, Early. Dashed lines and star symbols indicate extinction events.



Mamaliaformes

Cladogram showing the postulated relationships of the major groups of mammals, and of the Mesozoic groups in particular, based on the work of Luo *et al*. (2002, 2011), Zhou *et al*. (2013), and O'Leary *et al*. (2013). Synapomorphies: **A MAMMALIA**, well-developed jaw articulation between squamosal and dentary, double-rooted cheek teeth, medial wall of orbit enclosed by orbitosphenoid and ascending process of palatine, expansion of brain vault in parietal region, squamosal large, tabular bone absent, occipital condyles large and separated by a notch or groove, trigeminal nerve exits all in anterior lamina of petrosal and well behind alisphenoid, alisphenoid makes broad contact with frontal; **B**, petrosal promontorium; **C**, cheek teeth divided into premolars and molars, precise cusp-to-cusp occlusion developed through wear, mandibular symphysis reduced, diphyodont dentition (juvenile and adult only); **D**, groove for replacement dental lamina absent, five or fewer upper postcanine teeth, petrosal lateral flange and crista parotica connected, occiuput sloping anterodorsally, procoracoid foramen absent, extratarsal spur present, hair preserved; **E**, jugular fossa absent, paroccipital process extending ventral to cochlear housing; **F**, overhanging medial ridge above postdentary trough absent; **G**, no unambiguous synapomorphies; **H crown MAMMALIA**, presence of occlusal surfaces that match precisely between upper and lower molars upon eruption, distinctive masseteric fossa with well – defined ventral margin, cochlear canal elongate, ossified pila antotica separating cavum epiptericum from braincase is absent (except multituberculates), astragalus and calcaneus in partial superposition (except *Ornithorhynchus* and *Jeholodens*), greatly enlarged gyrencephalic cerebral hemispheres; **I AUSTRALOSPHENIDA**, tribosphenic molars with continuous and shelf-like mesial cingulid that extends to the lingual side of the molar rather than cingulid cusps, ultimate lower premolar with fully developed trigonid, transversely wide talonid, talonid placed posterior to the trigonid; **J**, **THERIIMORPHA**, postdendary trough absent, separate scars for surangular/prearticular absent, Meckelian sulcus vestigial or absent, pterygoid fossa on dentary present, medial pterygoid shelf present; **K THERIIFORMES**, acromion process of scapula strongly downturned, proximal head of humerus is spherical and inturned, proximal head of femur ball-like, inturned and set off on a constricted neck, calcaneal tuber is longer than wide; **L TRECHNOTHERIA**, hypertrophied postvallum/ prevallid shearing mechanism, squamosal with postglenoid depression, petrosal, post-tympanic recess present, caudal tympanic process present, atlas rib absent in adults, moderate torsion (30°–15°) of humerus, pelvic acetabulum with complete rim (without cotyloid notch, greater trochanter directed dorsally; **M CLADOTHERIA**, angular process of dentary well-developed and posteriorly positioned, paraconid shorter than metaconid, talonid has at least one cusp, interclavicle absent; **N PROTOTRIBOSPHENIDA**, broad contact between alisphenoid and frontal, cochlea is elongated and coiled up to 360°; **O BOREOSPHENIDA**, absence of postdentary trough and scars for the postdentary bones (except coronoid) in the dentary, tribosphenic molars, talonid placed posterior to the trigonid on lower molars, distinctive cingulid cuspule; **Q THERIA**, tribosphenic molar, anterior lamina of prootic is absent, acetabulum bears an inverted U-shaped articular region for the femoral head, astragalus with distinctive neck, calcaneum with enlarged sustentacular process; **R METATHERIA**, three premolars, postnatal tooth replacement limited to third premolar. angular process that is equal to half but less than the length of the dentary ramus. Abbreviations: E, Early; Mi, Miocene; Mid, Middle; Neo, Neogene; Ol, Oligocene; P, Paleocene; Pl, Pliocene/Pleistocene. Dashed lines and star symbols indicate extinction events.

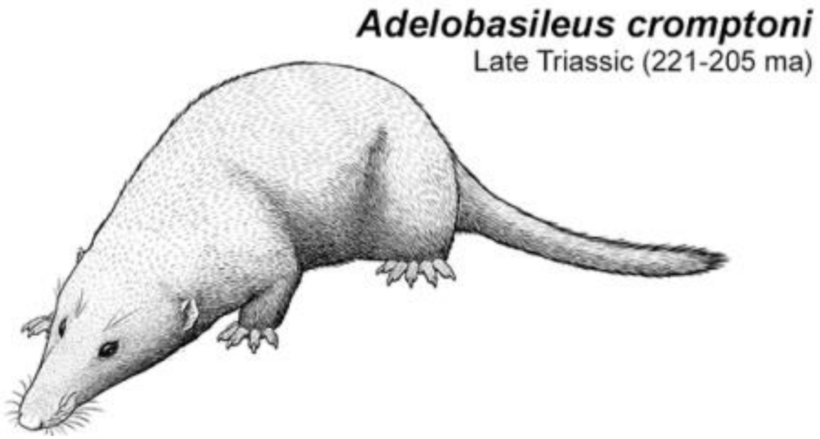
BOX 10.3 RELATIONSHIPS OF THE MESOZOIC MAMMALS

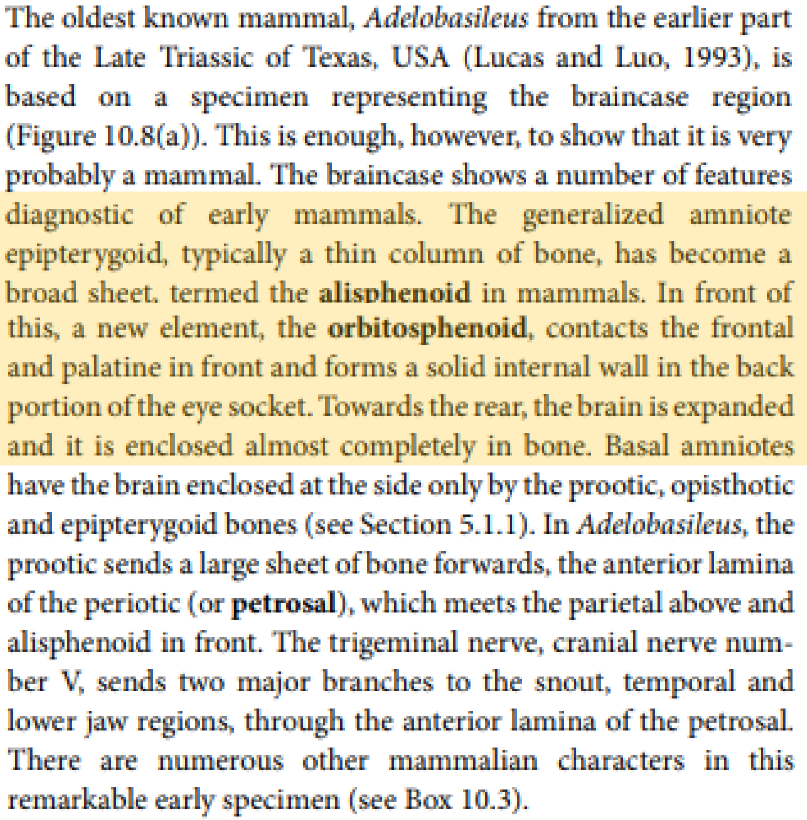
A traditional view of mammalian evolution was that the group was diphyletic, that is, it had two ancestral lines, one leading to the 'therians' and the other to the 'prototherians'. The 'therians', those forms with a triangular array of cusps on the molars, included *Kuehneotherium*, the symmetrodonts, marsupials and placentals. The 'prototherians' had the molar cusps aligned and included the morganucodontans, docodontans, triconodontans, multituberculates and monotremes.

The first cladistic analyses (Kemp, 1983; Rowe, 1988) disproved this view, showing that 'prototherians' are not a clade, and suggesting that monotremes are more closely related to marsupials and placentals than *Morganucodon*. The linear alignments of tooth cusps in *Morganucodon*, multituberculates, docodontans and triconodontans are plesiomorphic characters that do not indicate close relationships to monotremes.

All cladistic analyses agree that the three living mammal groups are arranged as (Monotremata (Marsupialia + Placentalia)), with the Marsupialia plus Placentalia forming the clade Theria. A key question has been the relationships of various extinct clades, notably the Multituberculata. Kemp (1983) found multituberculates, and most Mesozoic taxa, as outgroups to the clade of modern mammals, whereas others (Luo *et al*., 2002, 2011; Zhou *et al*., 2013) find a broad separation between Monotremata and its closest outgroups (Australosphenida) and Theria and its closest outgroups (Boreosphenida). Averianov *et al*. (2013) find an alternative arrangement of taxa within Trechnotheria, with a clade comprising Symmetrodonta and Meridiolestida as sister to Cladotheria, and *Vincelestes* classed as a dryolestid.

Adelobasileus




The oldest known mammal, *Adelobasileus* from the earlier part of the Late Triassic of Texas, USA (Lucas and Luo, 1993), is based on a specimen representing the braincase region (Figure 10.8(a)). This is enough, however, to show that it is very probably a mammal. The braincase shows a number of features diagnostic of early mammals. The generalized amniote epipterygoid, typically a thin column of bone, has become a broad sheet, termed the **alisphenoid** in mammals. In front of this, a new element, the **orbitosphenoid**, contacts the frontal and palatine in front and forms a solid internal wall in the back portion of the eye socket. Towards the rear, the brain is expanded and it is enclosed almost completely in bone. Basal amniotes have the brain enclosed at the side only by the prootic, opisthotic and epipterygoid bones (see Section 5.1.1). In *Adelobasileus*, the prootic sends a large sheet of bone forwards, the anterior lamina of the periotic (or **petrosal**), which meets the parietal above and alisphenoid in front. The trigeminal nerve, cranial nerve number V, sends two major branches to the snout, temporal and lower jaw regions, through the anterior lamina of the petrosal. There are numerous other mammalian characters in this remarkable early specimen (see Box 10.3).

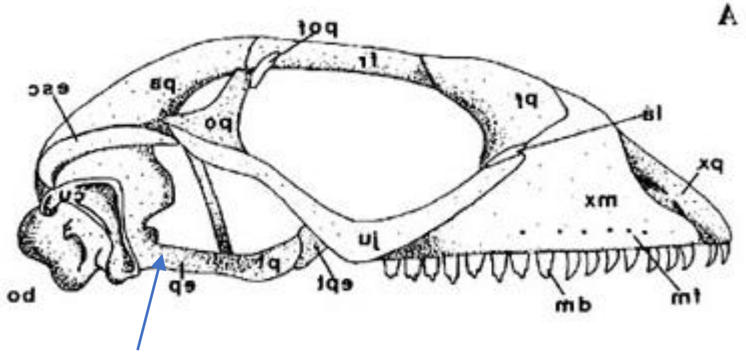
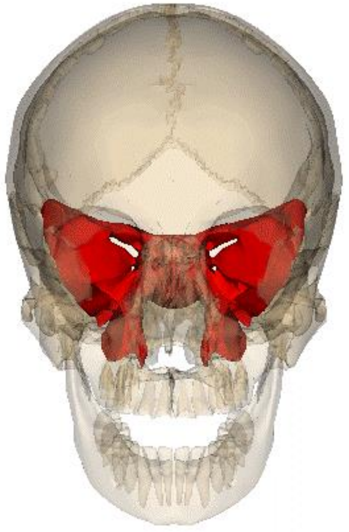
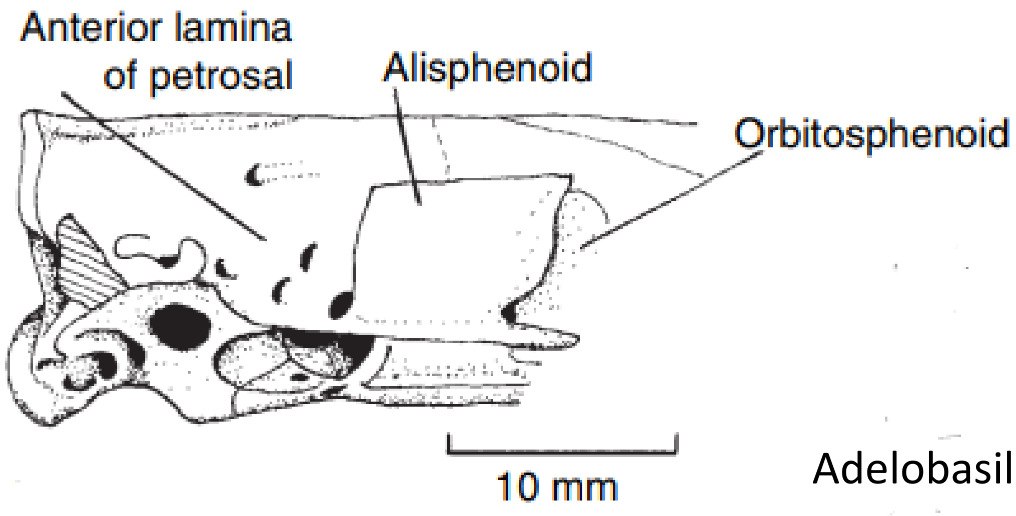


FIGURA 1: Vista lateral del cráneo de A: Microlophus atacamensis MZUC 25108. B: Microlophus quadrivittatus MZUC 25116. Abreviaturas utilizadas: (bo) basioccipital, (cu) cuadrado, (dm) dientes maxilares, (ept) ectopterigoides, (ep) epipterigoides, (esc) escamoso, (fm) forámenes maxilares, (fr) frontal, (ju) yugal, (la) lacrimal, (mx) maxilar, (pa) parietal, (pof) postfrontal, (po) postorbital, (pf) prefrontal, (px) premaxilar, (pt) pterigoides. LR:



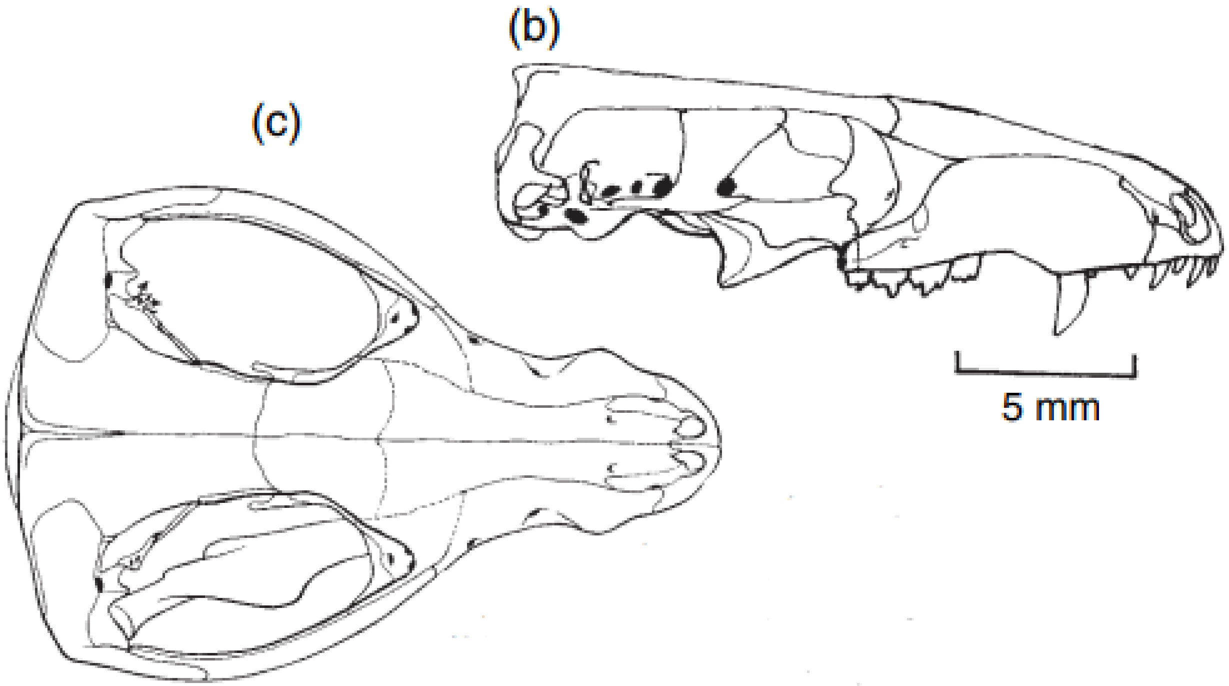


Adelobasileus

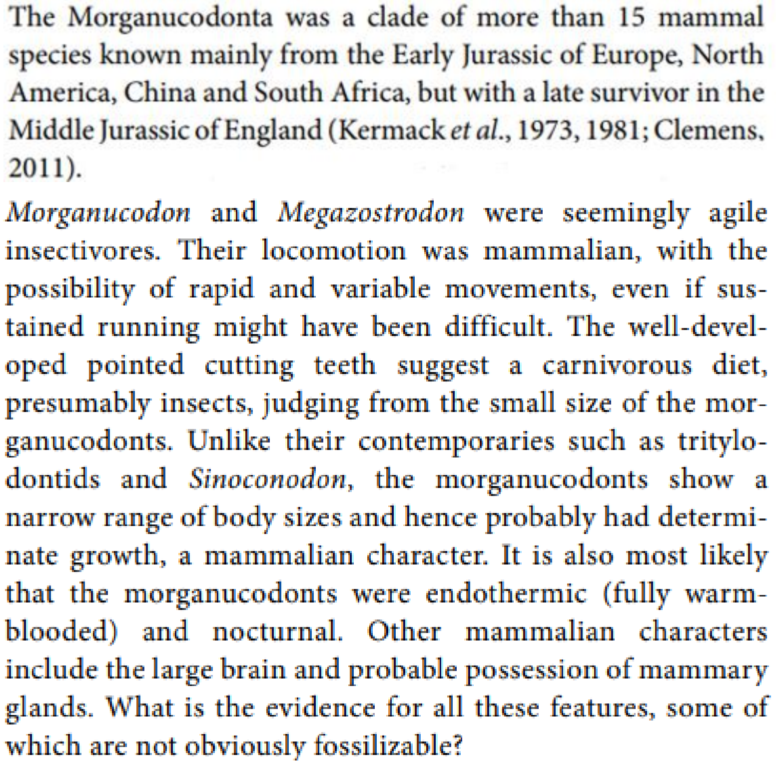
Sinoconodon

Sinoconodon rigneyi
Early Jurassic (196-189 ma)

Sinoconodon from the Early Jurassic of China (Figure 10.8(b,c)) also appears to occupy a basal position in mammalian phylogeny (Crompton and Luo, 1993; Zhou *et al.*, 2013). It shows all the braincase features (Figure 10.8(b)) seen in *Adelobasileus*, and the rest of the skull shows a fully developed jaw joint between the dentary and squamosal and a fully developed petrosal promontorium for the inner ear cochlea. These are the classic mammalian characters. The back part of the skull is expanded (Figure 10.8(c)) and the orbit and lower temporal fossa are a single opening, bounded by a slender zygomatic arch. The cheek teeth, however, did not occlude precisely. Some posterior cheek teeth appear to have been replaced in the adult, accompanied by sustained, slow growth of the skull late in the individual's life. These are plesiomorphic features of the indeterminate growth of cynodonts.



Morganucodonta

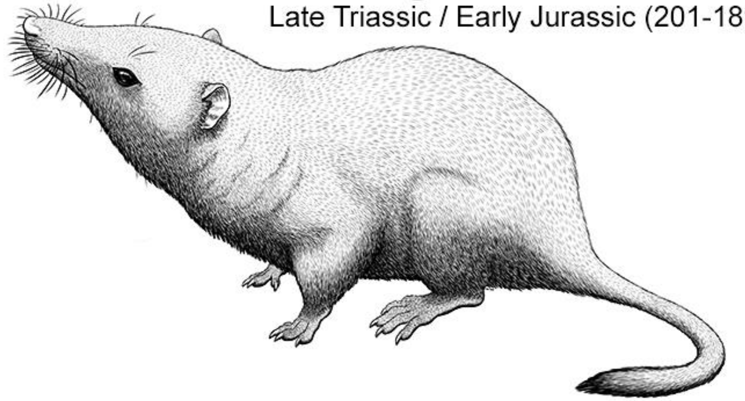


The Morganucodonta was a clade of more than 15 mammal species known mainly from the Early Jurassic of Europe, North America, China and South Africa, but with a late survivor in the Middle Jurassic of England (Kermack *et al.*, 1973, 1981; Clemens, 2011).

Morganucodon and *Megazostrodon* were seemingly agile insectivores. Their locomotion was mammalian, with the possibility of rapid and variable movements, even if sustained running might have been difficult. The well-developed pointed cutting teeth suggest a carnivorous diet, presumably insects, judging from the small size of the morganucodonts. Unlike their contemporaries such as tritylodontids and *Sinoconodon*, the morganucodonts show a narrow range of body sizes and hence probably had determinate growth, a mammalian character. It is also most likely that the morganucodonts were endothermic (fully warm-blooded) and nocturnal. Other mammalian characters include the large brain and probable possession of mammary glands. What is the evidence for all these features, some of which are not obviously fossilizable?

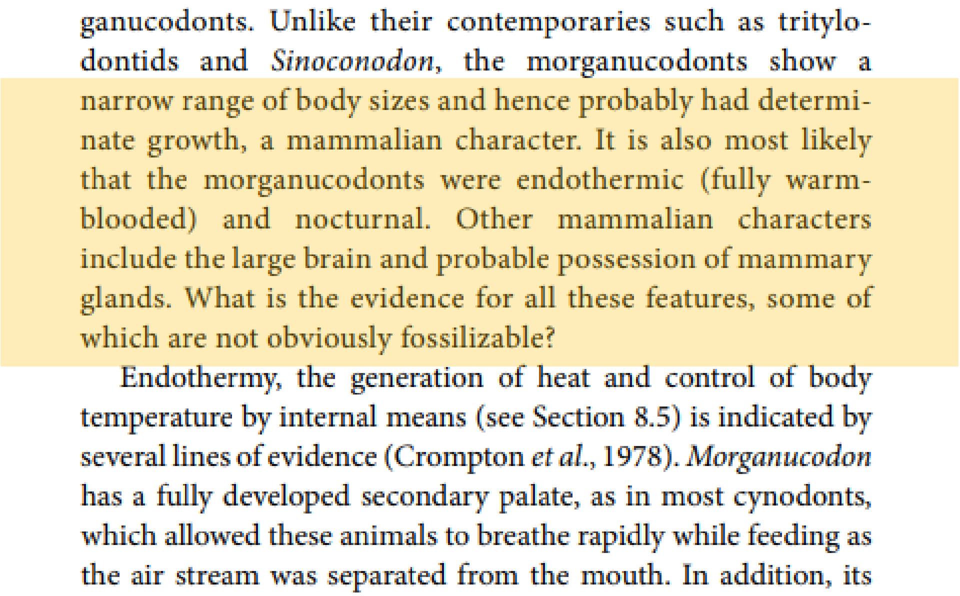
Se pueden inferir características que no son tan obvias mirando los fósiles

- Carnívoros, probablemente insectívoros.
- Crecimiento determinado
- Endotérmicos
- Nocturnos
- Probablemente con glándulas mamarias

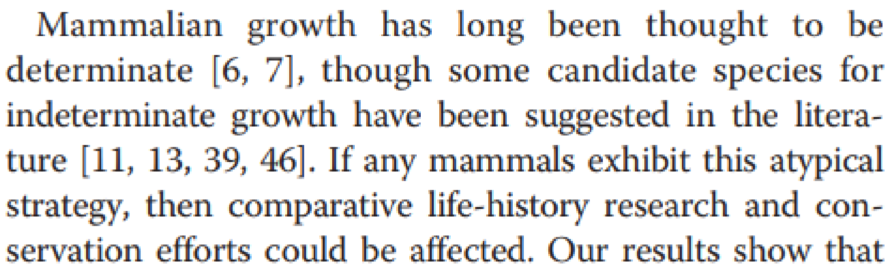


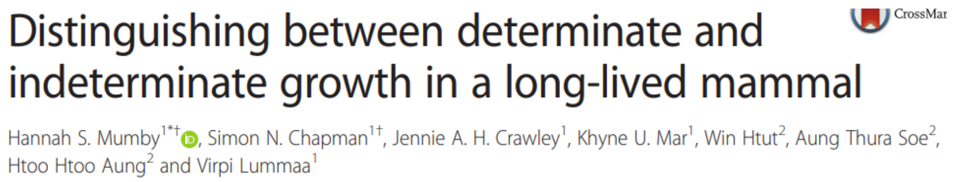
Megazostrodon rudnerae
Late Triassic / Early Jurassic (201-189 ma)

Crecimiento determinado


ganucodonts. Unlike their contemporaries such as tritylodontids and *Sinoconodon*, the morganucodonts show a narrow range of body sizes and hence probably had determinate growth, a mammalian character. It is also most likely that the morganucodonts were endothermic (fully warm-blooded) and nocturnal. Other mammalian characters include the large brain and probable possession of mammary glands. What is the evidence for all these features, some of which are not obviously fossilizable?

Endothermy, the generation of heat and control of body temperature by internal means (see Section 8.5) is indicated by several lines of evidence (Crompton *et al*., 1978). *Morganucodon* has a fully developed secondary palate, as in most cynodonts, which allowed these animals to breathe rapidly while feeding as the air stream was separated from the mouth. In addition, its


Mammalian growth has long been thought to be determinate [6, 7], though some candidate species for indeterminate growth have been suggested in the literature [11, 13, 39, 46]. If any mammals exhibit this atypical strategy, then comparative life-history research and conservation efforts could be affected. Our results show that


Distinguishing between determinate and indeterminate growth in a long-lived mammal

Hannah S. Mumby[1*†], Simon N. Chapman[1†], Jennie A. H. Crawley[1], Khyne U. Mar[1], Win Htut[2], Aung Thura Soe[2], Htoo Htoo Aung[2] and Virpi Lummaa[1]

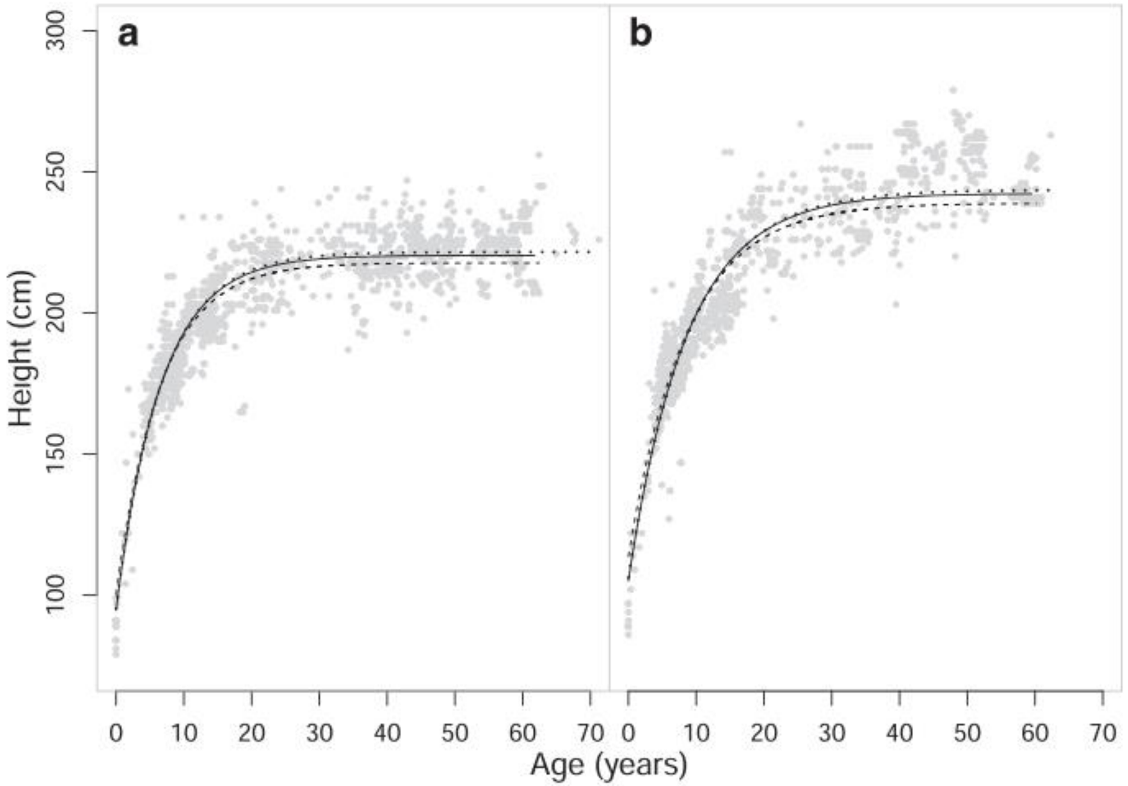


Fig. 1 Height growth curves of **a**) females and **b**) males. Solid curves are derived from average measurements of captive-born elephants (*n* = 170 and 159); dotted curves are derived from average measurements of all elephants, of both wild- and captive-birth origin (*n* = 240 and 189); Dashed curves are derived from all captive-born elephants, including historic height data, and take ID into account (*n* = 22 and 26). Points are from all the elephants of that sex

Endotermia

nate growth, a mammalian character. It is also most likely that the morganucodonts were endothermic (fully warm-blooded) and nocturnal. Other mammalian characters include the large brain and probable possession of mammary glands. What is the evidence for all these features, some of which are not obviously fossilizable?

Endothermy, the generation of heat and control of body temperature by internal means (see Section 8.5) is indicated by several lines of evidence (Crompton *et al.*, 1978). *Morganucodon* has a fully developed secondary palate, as in most cynodonts, which allowed these animals to breathe rapidly while feeding as the air stream was separated from the mouth. In addition, its bone histology shows fibro-lamellar bone formed early in its life, so indicating a high metabolic rate and high growth rate (Chinsamy and Hurum, 2006).

METABOLIC RATE

The body proportions, size, and dentition of early mammals resemble those of modern insectivores, which suggests a broadly similar way of life and physiology. Their general similarity with primitive modern mammals suggests a comparable metabolic rate and body temperature. Crompton, Taylor, and Jagger (1978) argued that the body temperature of early mammals may have been lower than even the most primitive of living mammals, the monotremes, which have a temperature of only 30 to 32°C. Nevertheless, if they were endotherms and maintained a relatively constant body temperature, they would have had a fairly high metabolic rate simply because of their small size.

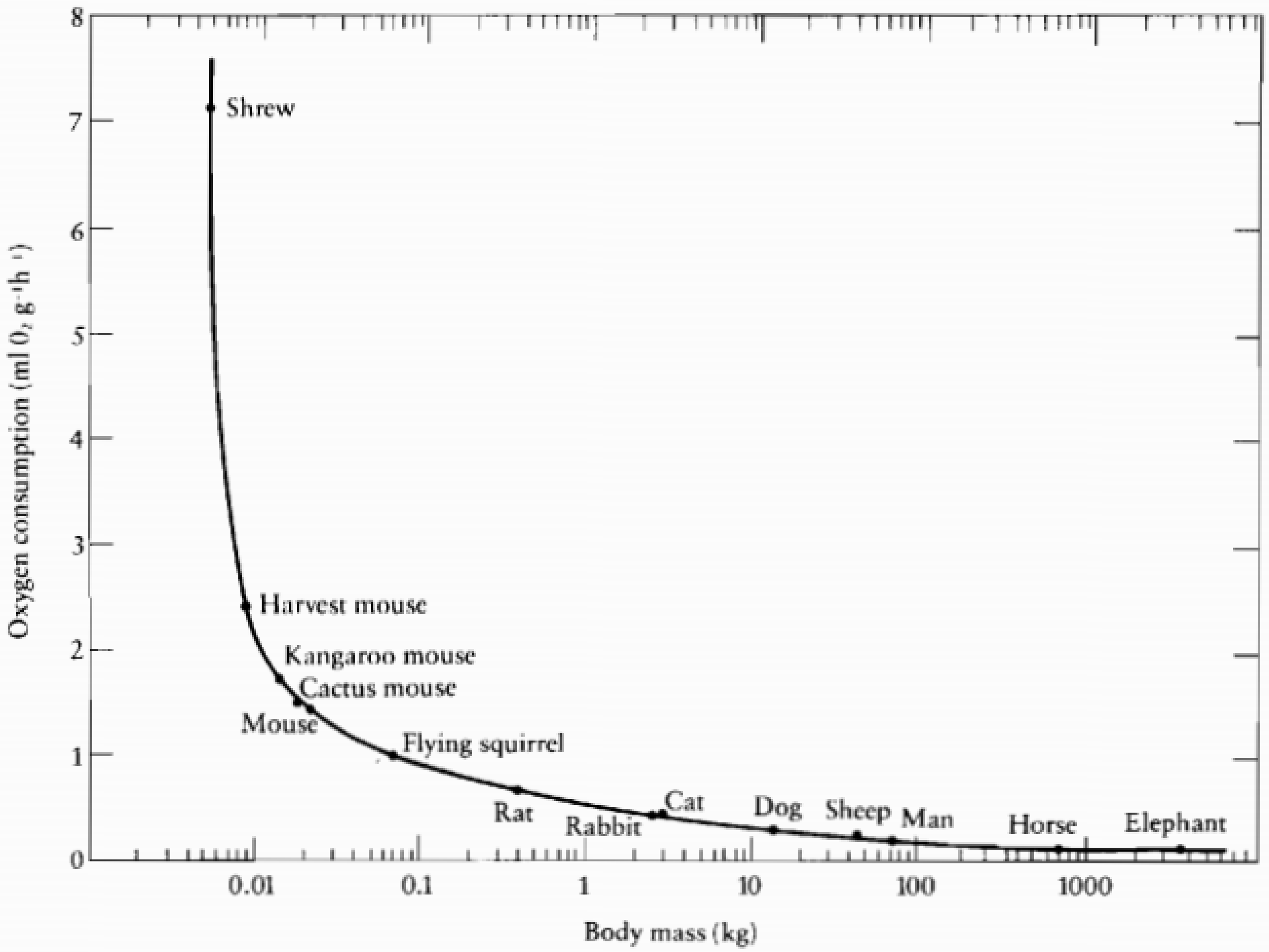
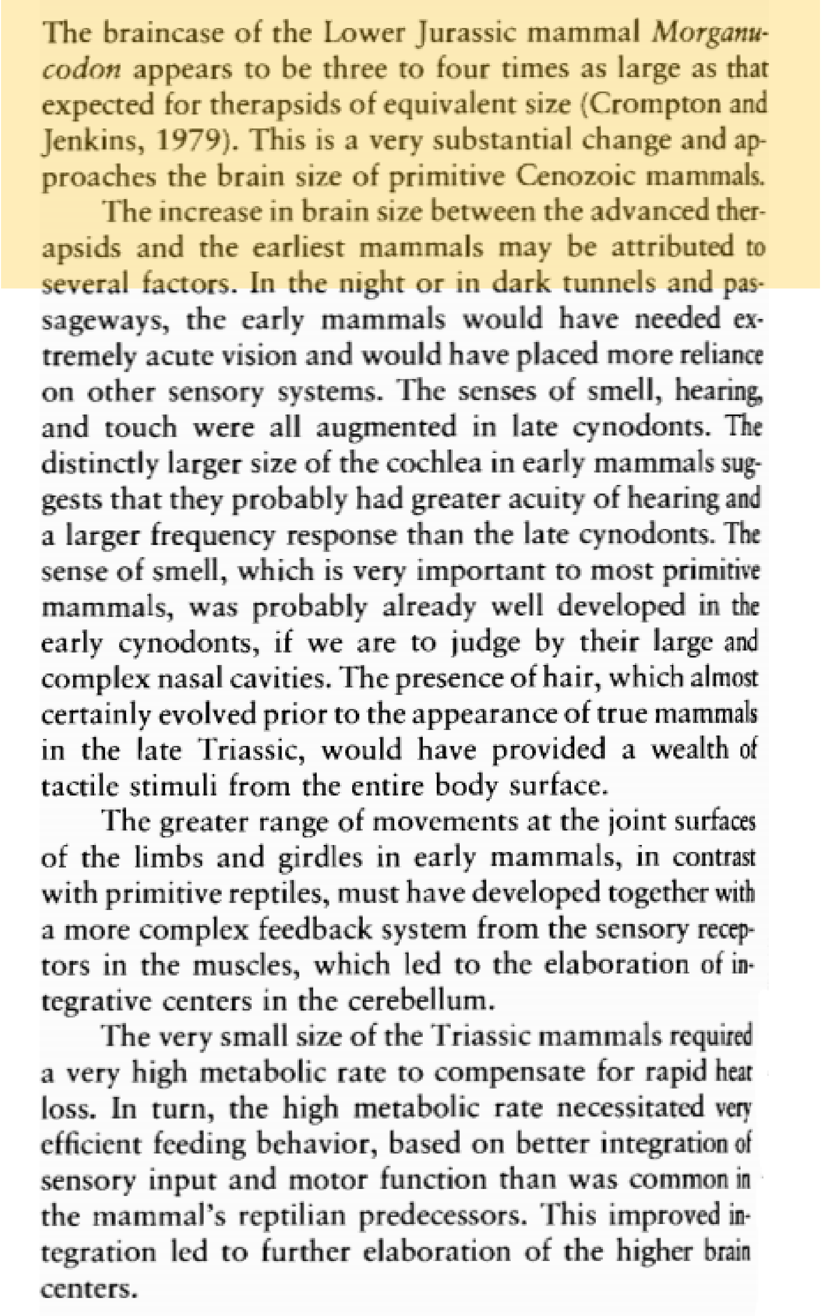


Figure 18-9. OBSERVED RATES OF OXYGEN CONSUMPTION OF VARIOUS MAMMALS. The oxygen consumption per unit body mass increases rapidly with decreasing body size. Note that the abscissa is logarithmic while the ordinate has an arithmetic scale. *From Schmidt-Nielsen, 1975.*

Nocturnos



The braincase of the Lower Jurassic mammal *Morganucodon* appears to be three to four times as large as that expected for therapsids of equivalent size (Crompton and Jenkins, 1979). This is a very substantial change and approaches the brain size of primitive Cenozoic mammals.

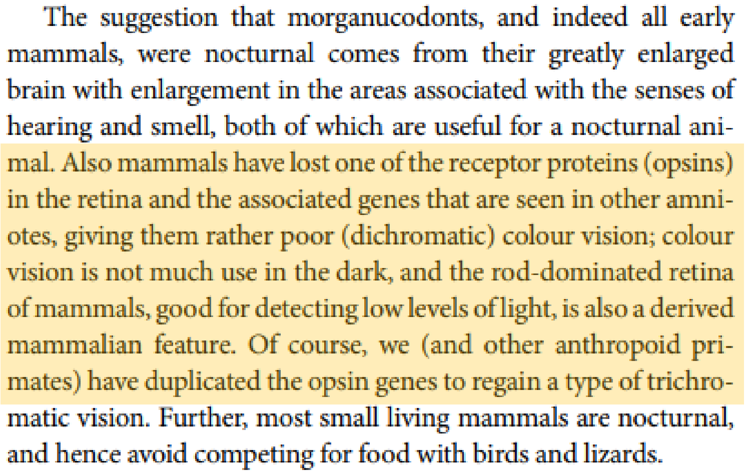
The increase in brain size between the advanced therapsids and the earliest mammals may be attributed to several factors. In the night or in dark tunnels and passageways, the early mammals would have needed extremely acute vision and would have placed more reliance on other sensory systems. The senses of smell, hearing, and touch were all augmented in late cynodonts. The distinctly larger size of the cochlea in early mammals suggests that they probably had greater acuity of hearing and a larger frequency response than the late cynodonts. The sense of smell, which is very important to most primitive mammals, was probably already well developed in the early cynodonts, if we are to judge by their large and complex nasal cavities. The presence of hair, which almost certainly evolved prior to the appearance of true mammals in the late Triassic, would have provided a wealth of tactile stimuli from the entire body surface.

The greater range of movements at the joint surfaces of the limbs and girdles in early mammals, in contrast with primitive reptiles, must have developed together with a more complex feedback system from the sensory receptors in the muscles, which led to the elaboration of integrative centers in the cerebellum.

The very small size of the Triassic mammals required a very high metabolic rate to compensate for rapid heat loss. In turn, the high metabolic rate necessitated very efficient feeding behavior, based on better integration of sensory input and motor function than was common in the mammal's reptilian predecessors. This improved integration led to further elaboration of the higher brain centers.

El neurocráneo era mucho más grande (3-4 veces) que el esperado para un terápsido de tamaño corporal similar.

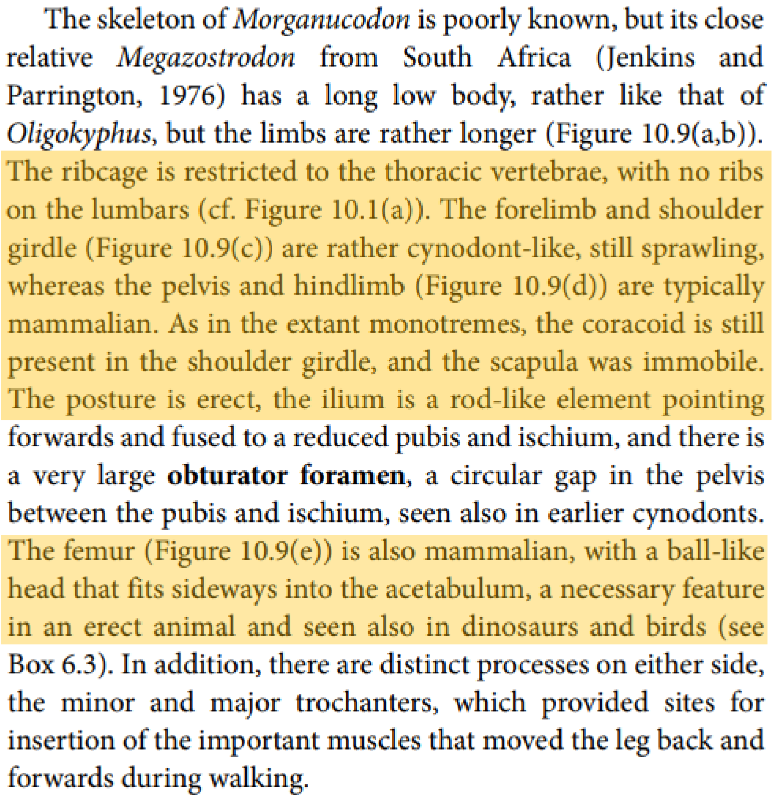
Cerebro más grande asociado a especializaciones de sentidos diferentes a la vista, útiles para la noche: audición, olfato, tacto.



The suggestion that morganucodonts, and indeed all early mammals, were nocturnal comes from their greatly enlarged brain with enlargement in the areas associated with the senses of hearing and smell, both of which are useful for a nocturnal animal. Also mammals have lost one of the receptor proteins (opsins) in the retina and the associated genes that are seen in other amniotes, giving them rather poor (dichromatic) colour vision; colour vision is not much use in the dark, and the rod-dominated retina of mammals, good for detecting low levels of light, is also a derived mammalian feature. Of course, we (and other anthropoid primates) have duplicated the opsin genes to regain a type of trichromatic vision. Further, most small living mammals are nocturnal, and hence avoid competing for food with birds and lizards.

Los mamíferos son dicrómatas, perdieron una de las opsinas.
La visión en colores no es muy útil en la noche.
La retina es mucho más rica en bastones

Morganucodonta



The skeleton of *Morganucodon* is poorly known, but its close relative *Megazostrodon* from South Africa (Jenkins and Parrington, 1976) has a long low body, rather like that of *Oligokyphus*, but the limbs are rather longer (Figure 10.9(a,b)). The ribcage is restricted to the thoracic vertebrae, with no ribs on the lumbars (cf. Figure 10.1(a)). The forelimb and shoulder girdle (Figure 10.9(c)) are rather cynodont-like, still sprawling, whereas the pelvis and hindlimb (Figure 10.9(d)) are typically mammalian. As in the extant monotremes, the coracoid is still present in the shoulder girdle, and the scapula was immobile. The posture is erect, the ilium is a rod-like element pointing forwards and fused to a reduced pubis and ischium, and there is a very large **obturator foramen**, a circular gap in the pelvis between the pubis and ischium, seen also in earlier cynodonts. The femur (Figure 10.9(e)) is also mammalian, with a ball-like head that fits sideways into the acetabulum, a necessary feature in an erect animal and seen also in dinosaurs and birds (see Box 6.3). In addition, there are distinct processes on either side, the minor and major trochanters, which provided sites for insertion of the important muscles that moved the leg back and forwards during walking.

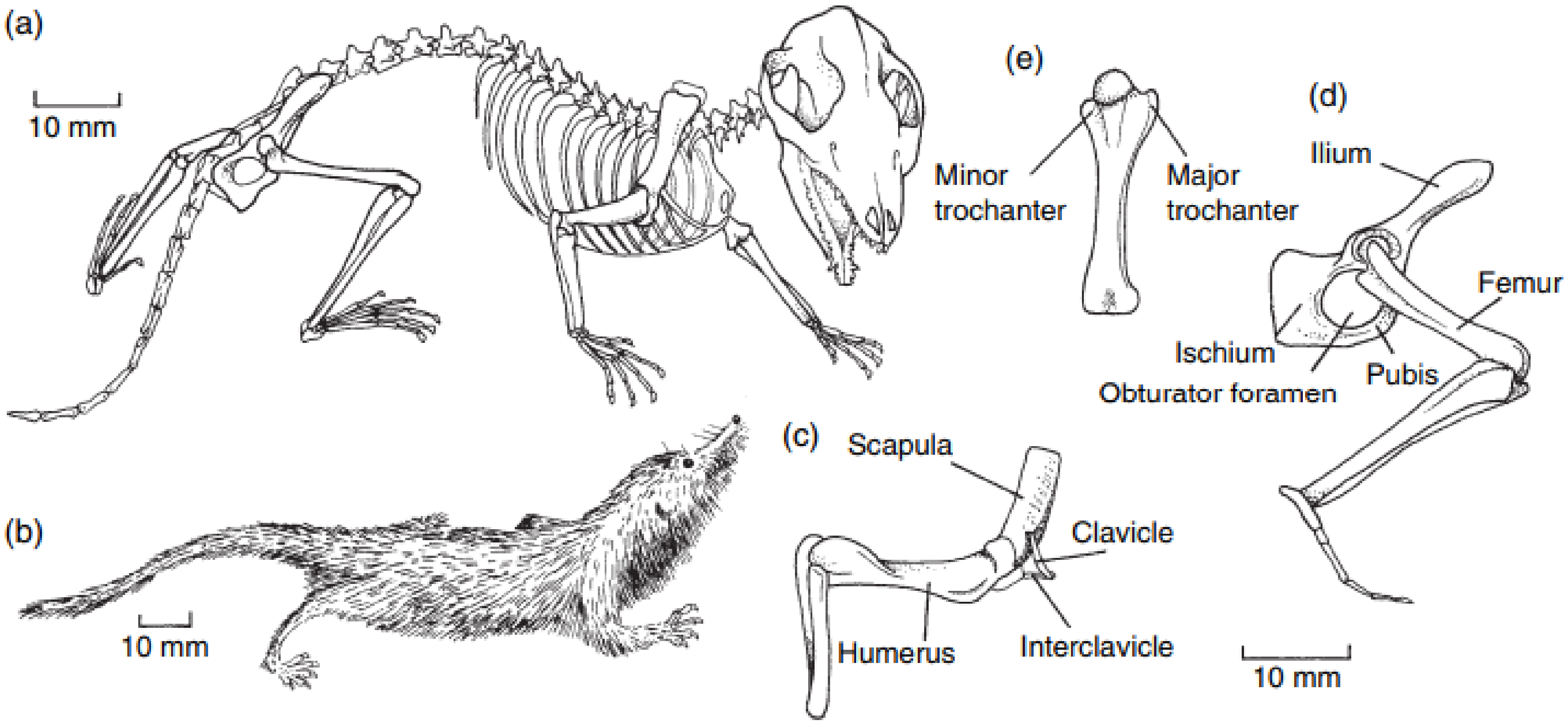
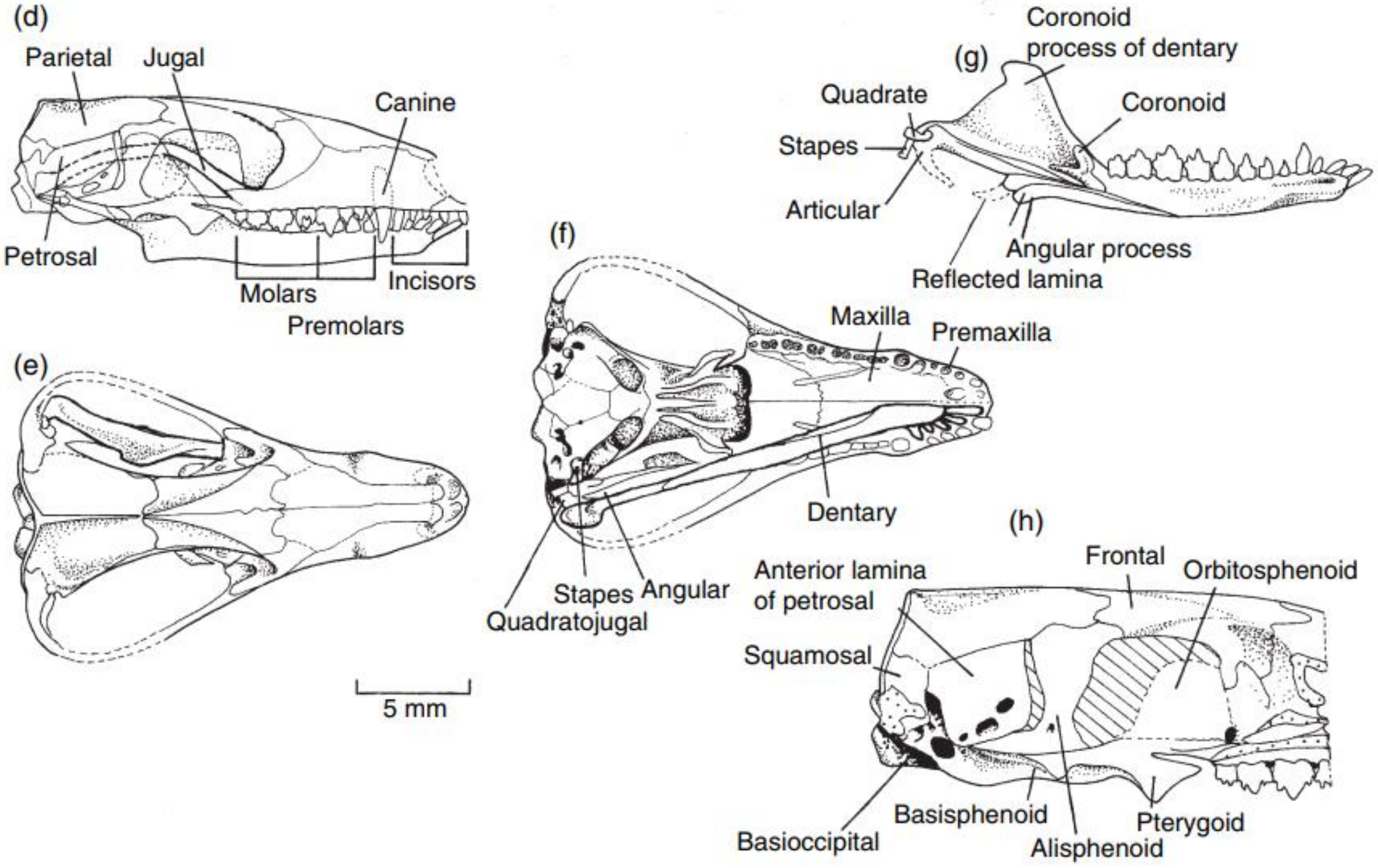
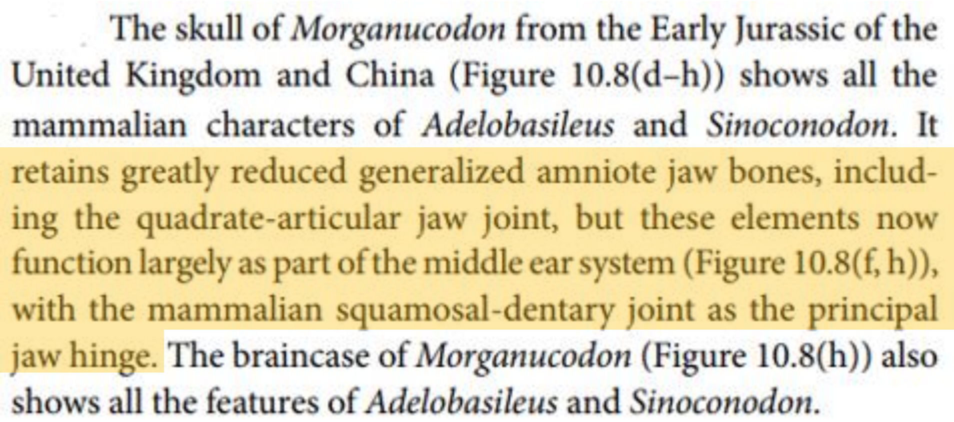


Figure 10.9 The skeleton of morganucodonts: (a) skeleton of *Megazostrodon*; (b) body restoration; (c) forelimb and pectoral girdle; (d) hindlimb and pelvic girdle of *Morganucodon*; (e) femur. Source: Adapted from Jenkins and Parrington (1976).

→ Costillas restringidas a las vértebras torácicas
→ Miembros delanteros despatarrados, traseros erguidos.
→ Cintura pectoral con coracoides

Morganucodonta





The skull of *Morganucodon* from the Early Jurassic of the United Kingdom and China (Figure 10.8(d–h)) shows all the mammalian characters of *Adelobasileus* and *Sinoconodon*. It retains greatly reduced generalized amniote jaw bones, including the quadrate-articular jaw joint, but these elements now function largely as part of the middle ear system (Figure 10.8(f, h)), with the mammalian squamosal-dentary joint as the principal jaw hinge. The braincase of *Morganucodon* (Figure 10.8(h)) also shows all the features of *Adelobasileus* and *Sinoconodon*.

BOX 10.2 JAW JOINT TO MIDDLE EAR

One of the most spectacular evolutionary transitions is the modification of the ‘reptilian’ jaw joint of basal cynodonts into two of the three ear ossicles of mammals (Allin, 1975; Kemp, 2005; Takechi and Kuratani, 2010; Luo, 2011). The jaw joint in *Thrinaxodon* (illustration I(a,c)) is between the quadrate in the upper jaw and articular in the lower jaw, as in the generalized gnathostome condition, but the quadrate is much reduced. The surangular, just behind the coronoid process of the dentary, comes very close to the squamosal, and the stapes touches the quadrate, as in gnathostomes more widely.

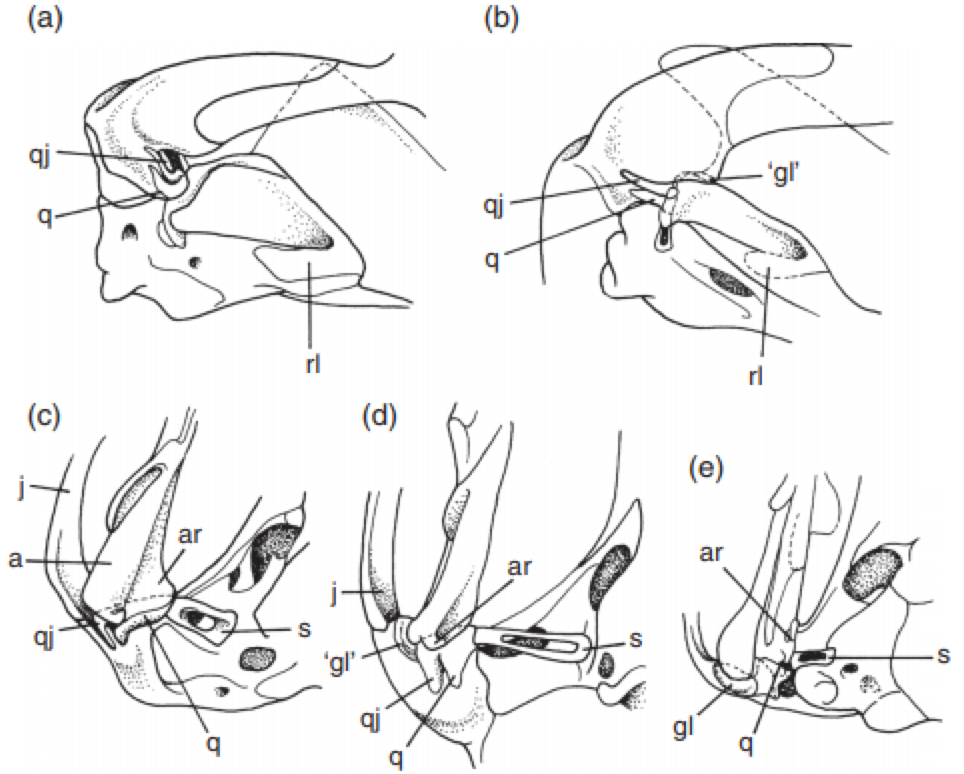
A few subtle changes in *Probainognathus* (illustration I(d)) mark the beginnings of the switch. The surangular now meets the squamosal in a special hollowed facet, the glenoid, which allowed rocking movements. The articular forms part of a narrow rod (including the reduced angular, prearticular and surangular), which is loosely held in a groove on the inside of the dentary. By this stage the ‘reptilian’ jaw joint, and a new joint, are both present, very close together, and apparently functioning in tandem.

The next stage is seen in the mammal *Morganucodon* (illustration I(b,e)), in which the dentary contacts the squamosal. The surangular loses contact with the squamosal and is replaced by a distinctive enlarged process of the dentary, the condylar process, that fits into the glenoid on the squamosal.

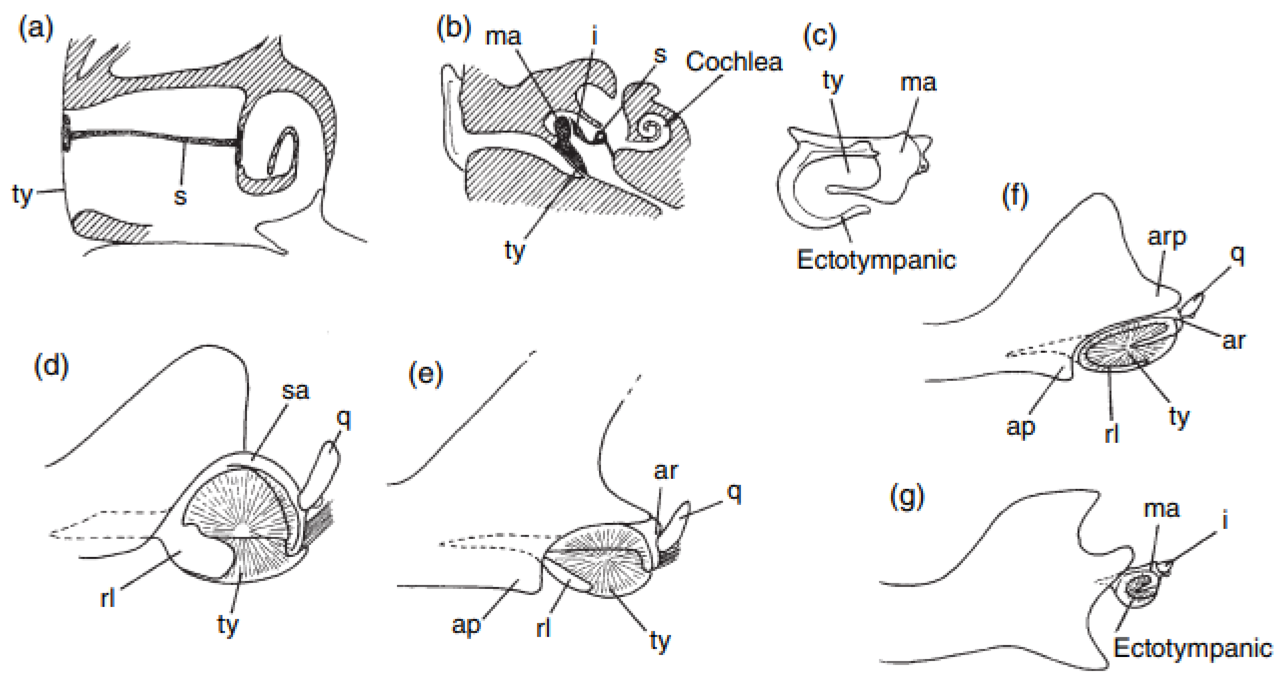
In typical reptiles and birds, the eardrum, or tympanum, is a circular sheet of skin held taut in the curve behind the quadrate. Sound is transmitted to the inner ear within the braincase in the form of vibrations across the middle ear space by the stapes, a rod of bone extending from the tympanum to the inner ear (illustration II(a)). In modern mammals, sound is transmitted via a set of three tiny bones within the middle ear, the **auditory ossicles**: the **malleus**, **incus** and **stapes**, or hammer, anvil and stirrup (illustration II(b)). The tympanum is held taut by the curved **ectotympanic,** which sits just behind the squamosal–dentary jaw joint (illustration II(c)). The mammalian stapes is the same as the generalized amniote stapes, the malleus is the articular and prearticular, the incus the quadrate and the ectotympanic the angular. The generalized amniote jaw joint is present within our middle ear, and the close association explains why we can still hear our jaw movements when we chew.

The evolution of the cynodont and mammalian jaw joint and middle ear was reconstructed as a four-stage process by Allin (1975). He assumed that the angular, articular and quadrate bones were already involved in sound conduction in therapsids (illustration II(d,e)). He restored a large tympanic membrane beneath the dentary, held taut by the reflected lamina of the angular below and the surangular above. Vibrations of the tympanum passed through the articular and quadrate to the stapes. In other words, the lower jaw was a key part of the hearing equipment of early cynodonts. The tympanum became smaller and was pushed behind the new squamosal–dentary jaw joint in early mammals (illustration II(f,g)). At the same time, the articular–quadrate crank became reduced and separated from the rest of the skull and lower jaw, and moved fully into a separate auditory passage.

These transformations had been predicted from early embryological studies, and the development of modern mammals shows four processes that contribute to the separation of the middle ear from the jaw (Takechi and Kuratani, 2010; Luo, 2011). First, the developmental precursors of the three ear ossicles are displaced medially from the lower jaw. Second, the developing middle ear is displaced behind the dentary-squamosal joint. Third, the middle ear shows negative allometry with respect to the mandible (the middle ear elements are relatively large in early embryos, but the mandible grows faster in later stages). Fourth, Meckel's cartilage is reabsorbed to permit the middle ear to be disconnected from the mandible. Meckel's cartilage, originating from the first branchial arch, serves as scaffolding for the development of mandibular and middle ear elements. Normal development of Meckel's cartilage includes its eventual reabsorption, and the production of the ear bones, and these stages in development are controlled by a complex series of signals from many structural and some homeobox genes (Takechi and Kuratani, 2010; Luo, 2011) that direct development first according to the generalized vertebrate model, and then impose modifications to bring about separation of primary mandible and middle ear.



(I) Evolution of the mammalian jaw joint: (a,b) posterolateral and (c–e) ventral views of the posterior right-hand corner of the skull and lower jaw of (a,c) the early cynodont *Thrinaxodon*, (d) the later cynodont *Probainognathus* and (b,e) the early mammal *Morganucodon*, showing the move of the quadrate and articular towards the middle ear region. Abbreviations: a, angular; ar, articular; gl, glenoid; j, jugal; q, quadrate; qj, quadratojugal; rl, reflected lamina; s, stapes; sa, surangular. Source: Adapted from Crompton and Hylander (1986).



(II) Structure of the ear, in vertical section, in (a) a typical reptile and (b) a mammal; (c) the ear ossicles of a modern mammal in lateral view; (d–g) Allin's (1975) theory for the origin of the mammalian jaw joint and middle ear system; lateral views of the posterior portion of the lower jaw of (d) an early cynodont; (e) an advanced cynodont; (f) an early mammal; and (g) a modern therian mammal. Abbreviations as in illustration (I); and: ap, angular process; arp, articular process; i, incus; ma, malleus; s, stapes; ty, tympanum. Source: (a–c) Adapted from various sources. (d–g) Adapted from Allin (1975).

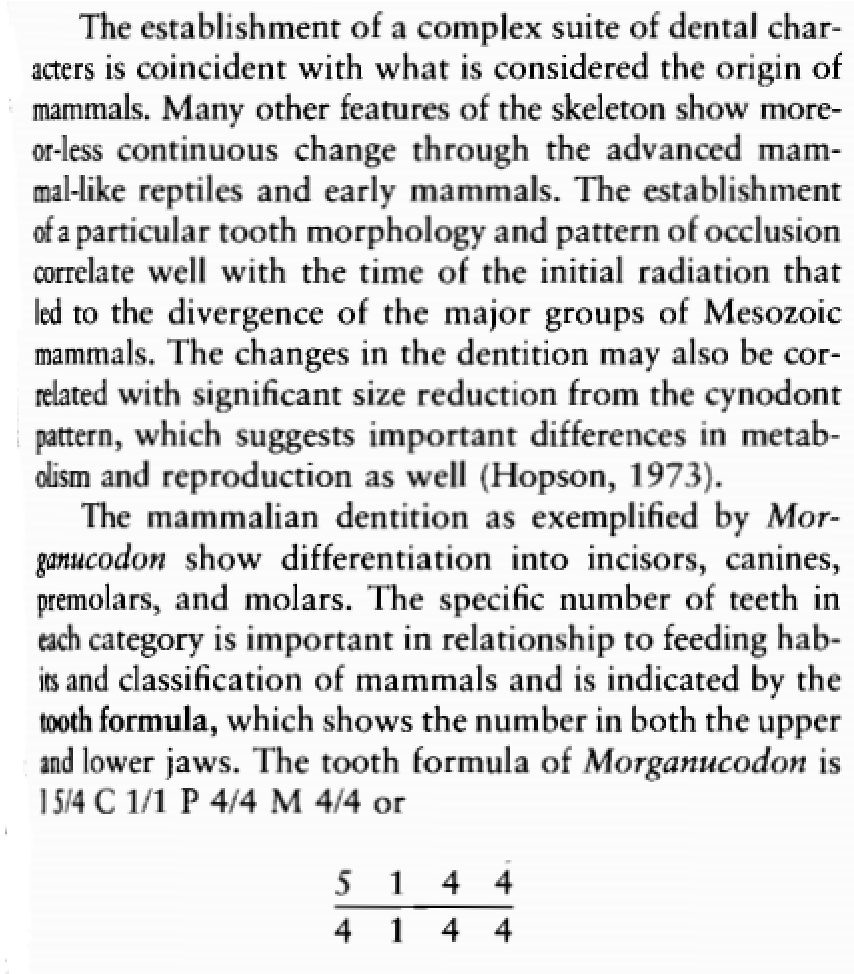
¿Cuál es cuál?

Malleus Martillo	Incus Yunque	Stapes Estribo
Articular + prearticular	Cuadrado	

Tímpano soportado por el ectotimpánico (= angular)

Tímpano soportado por el cuadrado

Dentición

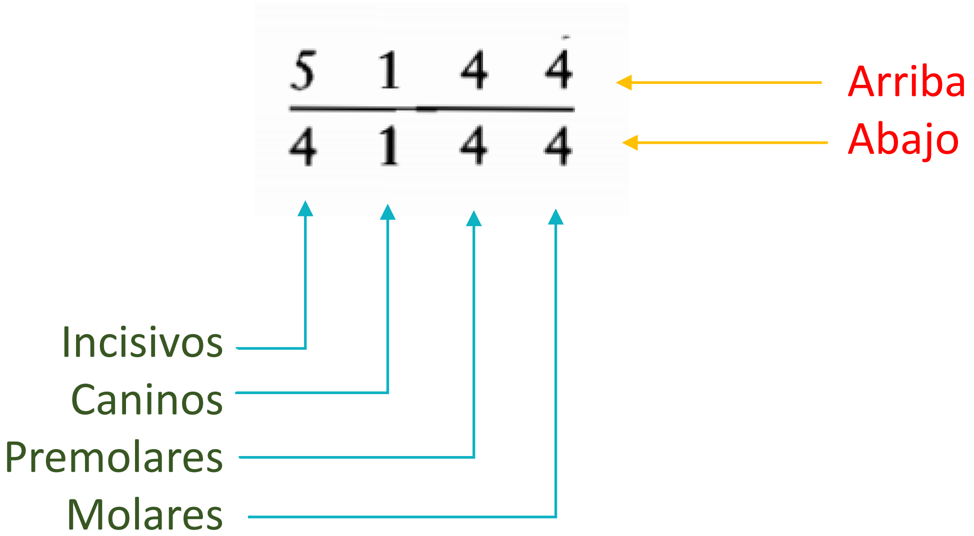


The establishment of a complex suite of dental characters is coincident with what is considered the origin of mammals. Many other features of the skeleton show more-or-less continuous change through the advanced mammal-like reptiles and early mammals. The establishment of a particular tooth morphology and pattern of occlusion correlate well with the time of the initial radiation that led to the divergence of the major groups of Mesozoic mammals. The changes in the dentition may also be correlated with significant size reduction from the cynodont pattern, which suggests important differences in metabolism and reproduction as well (Hopson, 1973).

The mammalian dentition as exemplified by *Morganucodon* show differentiation into incisors, canines, premolars, and molars. The specific number of teeth in each category is important in relationship to feeding habits and classification of mammals and is indicated by the **tooth formula,** which shows the number in both the upper and lower jaws. The tooth formula of *Morganucodon* is I 5/4 C 1/1 P 4/4 M 4/4 or

$$\frac{5\quad 1\quad 4\quad 4}{4\quad 1\quad 4\quad 4}$$

- → Se establece una morfología dental particular
- → Patrón de oclusión



$$\frac{5\quad 1\quad 4\quad 4}{4\quad 1\quad 4\quad 4}$$

Arriba
Abajo

Incisivos
Caninos
Premolares
Molares

Dentición

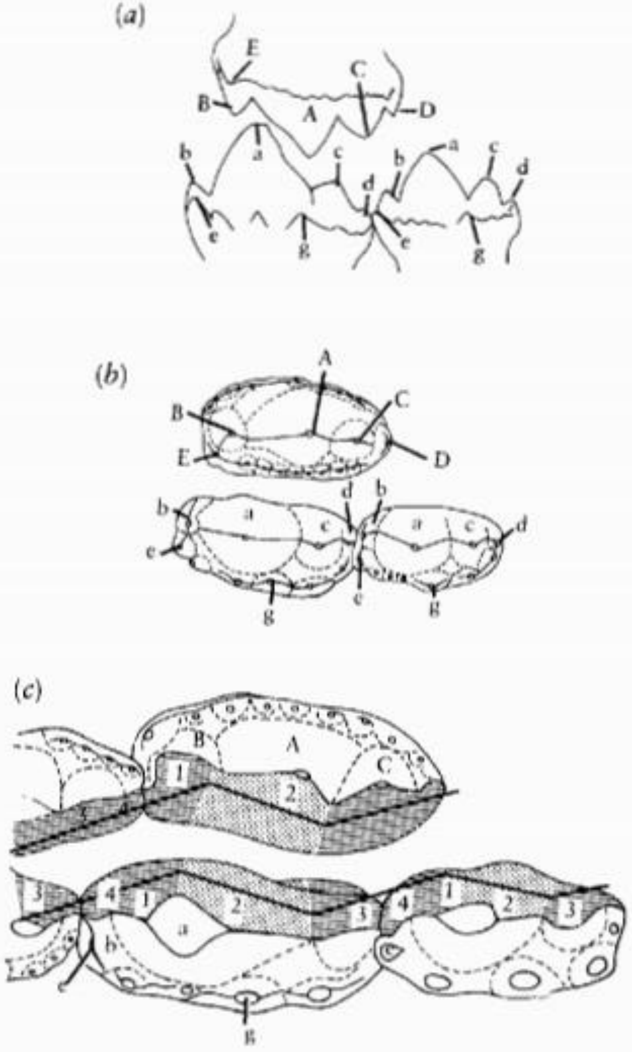
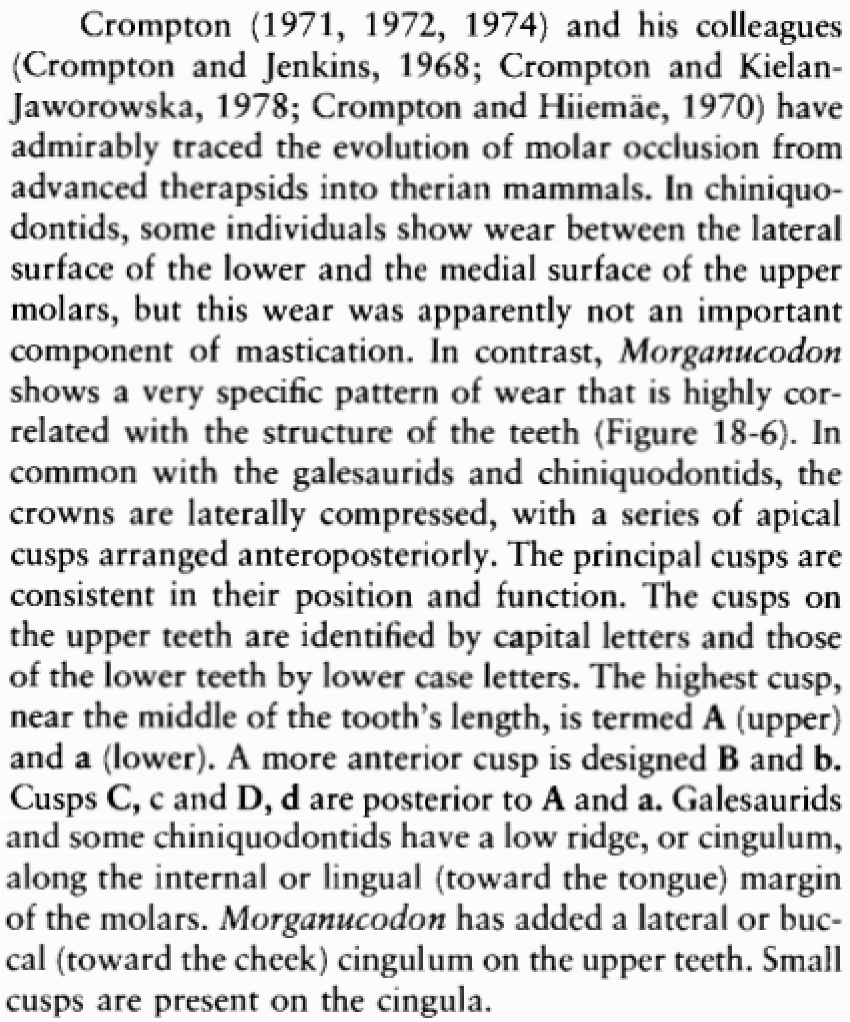
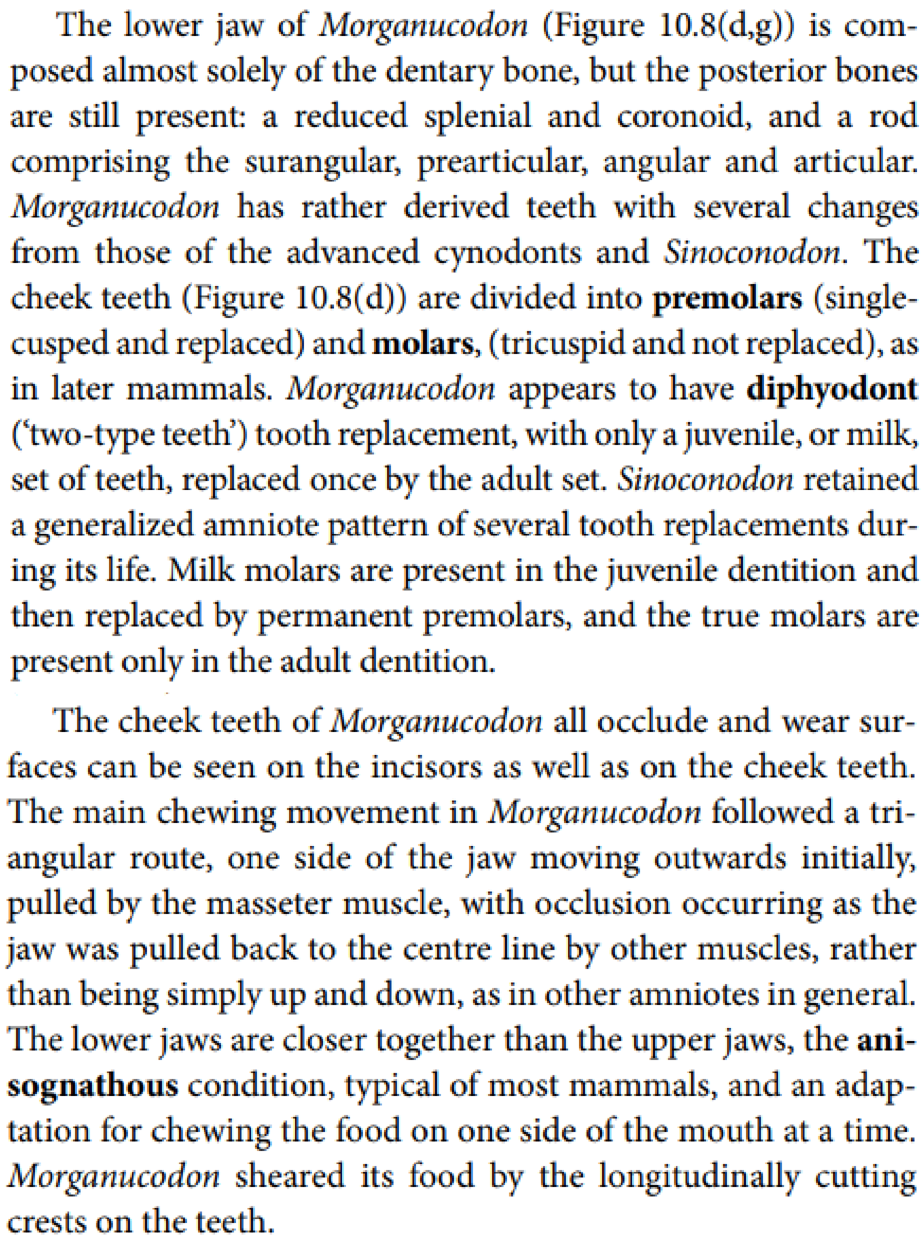


Figure 18-6. (*a* and *b*) Upper and lower molar teeth of *Morganucodon* in internal and occlusal views. (*c*) Occlusal views of two upper and three lower molars. The wear facets form two sides of "wide-angled" reversed triangles. The orientation of these wear facets is illustrated by the thick black lines. *From Crompton and Jenkins, 1968.* Anterior to left.



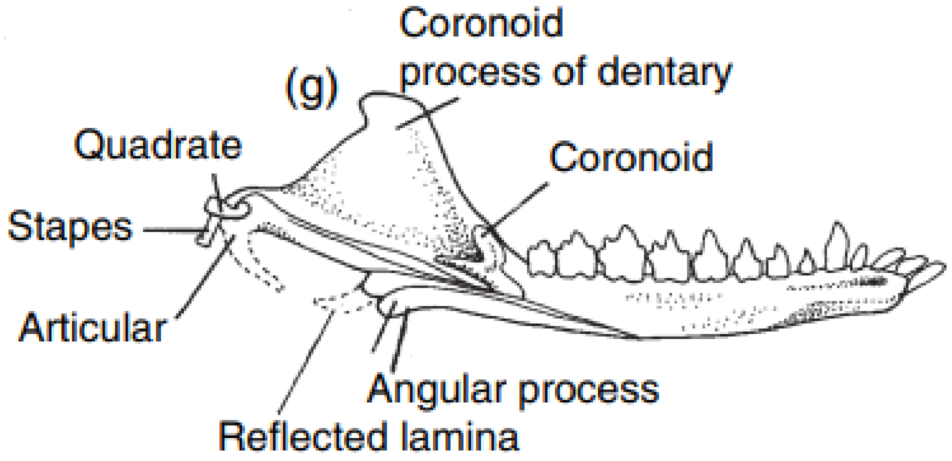
Crompton (1971, 1972, 1974) and his colleagues (Crompton and Jenkins, 1968; Crompton and Kielan-Jaworowska, 1978; Crompton and Hiiemäe, 1970) have admirably traced the evolution of molar occlusion from advanced therapsids into therian mammals. In chiniquodontids, some individuals show wear between the lateral surface of the lower and the medial surface of the upper molars, but this wear was apparently not an important component of mastication. In contrast, *Morganucodon* shows a very specific pattern of wear that is highly correlated with the structure of the teeth (Figure 18-6). In common with the galesaurids and chiniquodontids, the crowns are laterally compressed, with a series of apical cusps arranged anteroposteriorly. The principal cusps are consistent in their position and function. The cusps on the upper teeth are identified by capital letters and those of the lower teeth by lower case letters. The highest cusp, near the middle of the tooth's length, is termed **A** (upper) and **a** (lower). A more anterior cusp is designed **B** and **b.** Cusps **C,** c and **D, d** are posterior to **A** and **a.** Galesaurids and some chiniquodontids have a low ridge, or cingulum, along the internal or lingual (toward the tongue) margin of the molars. *Morganucodon* has added a lateral or buccal (toward the cheek) cingulum on the upper teeth. Small cusps are present on the cingula.

Morganucodonta



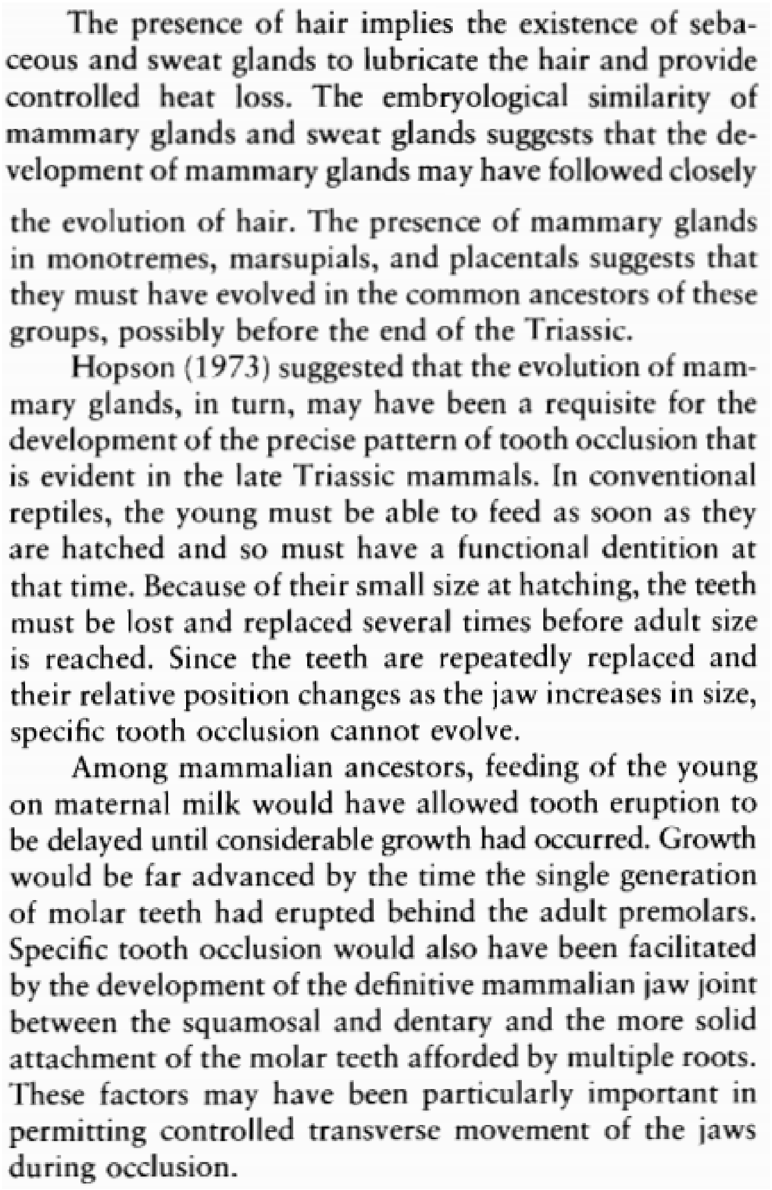
The lower jaw of *Morganucodon* (Figure 10.8(d,g)) is composed almost solely of the dentary bone, but the posterior bones are still present: a reduced splenial and coronoid, and a rod comprising the surangular, prearticular, angular and articular. *Morganucodon* has rather derived teeth with several changes from those of the advanced cynodonts and *Sinoconodon*. The cheek teeth (Figure 10.8(d)) are divided into **premolars** (single-cusped and replaced) and **molars**, (tricuspid and not replaced), as in later mammals. *Morganucodon* appears to have **diphyodont** ('two-type teeth') tooth replacement, with only a juvenile, or milk, set of teeth, replaced once by the adult set. *Sinoconodon* retained a generalized amniote pattern of several tooth replacements during its life. Milk molars are present in the juvenile dentition and then replaced by permanent premolars, and the true molars are present only in the adult dentition.

The cheek teeth of *Morganucodon* all occlude and wear surfaces can be seen on the incisors as well as on the cheek teeth. The main chewing movement in *Morganucodon* followed a triangular route, one side of the jaw moving outwards initially, pulled by the masseter muscle, with occlusion occurring as the jaw was pulled back to the centre line by other muscles, rather than being simply up and down, as in other amniotes in general. The lower jaws are closer together than the upper jaws, the **anisognathous** condition, typical of most mammals, and an adaptation for chewing the food on one side of the mouth at a time. *Morganucodon* sheared its food by the longitudinally cutting crests on the teeth.



Difiodoncia: dientes de leche que luego se cambian por dientes adultos.

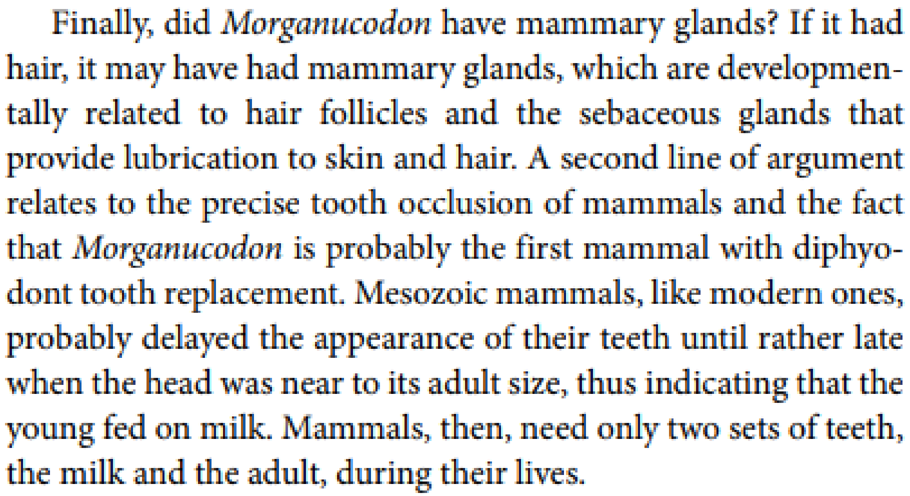
Glándulas mamarias



The presence of hair implies the existence of sebaceous and sweat glands to lubricate the hair and provide controlled heat loss. The embryological similarity of mammary glands and sweat glands suggests that the development of mammary glands may have followed closely the evolution of hair. The presence of mammary glands in monotremes, marsupials, and placentals suggests that they must have evolved in the common ancestors of these groups, possibly before the end of the Triassic.

Hopson (1973) suggested that the evolution of mammary glands, in turn, may have been a requisite for the development of the precise pattern of tooth occlusion that is evident in the late Triassic mammals. In conventional reptiles, the young must be able to feed as soon as they are hatched and so must have a functional dentition at that time. Because of their small size at hatching, the teeth must be lost and replaced several times before adult size is reached. Since the teeth are repeatedly replaced and their relative position changes as the jaw increases in size, specific tooth occlusion cannot evolve.

Among mammalian ancestors, feeding of the young on maternal milk would have allowed tooth eruption to be delayed until considerable growth had occurred. Growth would be far advanced by the time the single generation of molar teeth had erupted behind the adult premolars. Specific tooth occlusion would also have been facilitated by the development of the definitive mammalian jaw joint between the squamosal and dentary and the more solid attachment of the molar teeth afforded by multiple roots. These factors may have been particularly important in permitting controlled transverse movement of the jaws during occlusion.



Finally, did *Morganucodon* have mammary glands? If it had hair, it may have had mammary glands, which are developmentally related to hair follicles and the sebaceous glands that provide lubrication to skin and hair. A second line of argument relates to the precise tooth occlusion of mammals and the fact that *Morganucodon* is probably the first mammal with diphyodont tooth replacement. Mesozoic mammals, like modern ones, probably delayed the appearance of their teeth until rather late when the head was near to its adult size, thus indicating that the young fed on milk. Mammals, then, need only two sets of teeth, the milk and the adult, during their lives.

- Oclusión precisa de dientes.
- Difiodoncia.

Los mamíferos mesozoicos probablemente pueden haber retrasado la salida de dientes hasta bastante tarde, cuando la cabeza estaba más cercana al tamaño adulto → las crías deben haberse alimentado de leche

Haramiyida

One group of early mammals has become remarkably well known thanks to new finds from China. For a long time, the clade Haramiyida was known only from isolated teeth and jaws from the Late Triassic and Jurassic of Europe, Africa, and Greenland. Then, a series of complete skeletons of haramiyids were reported from the Middle and Late Jurassic of China. Two come from the Tiaojishan Formation (latest Middle Jurassic) of northern China, *Megaconus* (Zhou *et al.*, 2013) and *Arboroharimaya* (Zheng *et al.*, 2013). *Megaconus* was about 27 cm long (Figure 10.10(a,b)), and *Arboroharimaya* perhaps 35 cm long. The first was interpreted as a ground-dweller, the second as a tree-climber because of its grasping feet and hands. Both show evidence that haramiyids were the first herbivorous mammals, having longitudinal cusp rows on the upper molars that occlude alternately with those of the lower molars (Figure 10.10(c-e)). These authors differ in their views on haramyid relationships, Zhou *et al.* (2013) positioning them outside crown Mammalia (see Box 10.3), whereas Zheng *et al.* (2013) argued that the broad grinding molars indicate relationships with multituberculates, and so a position within crown Mammalia.

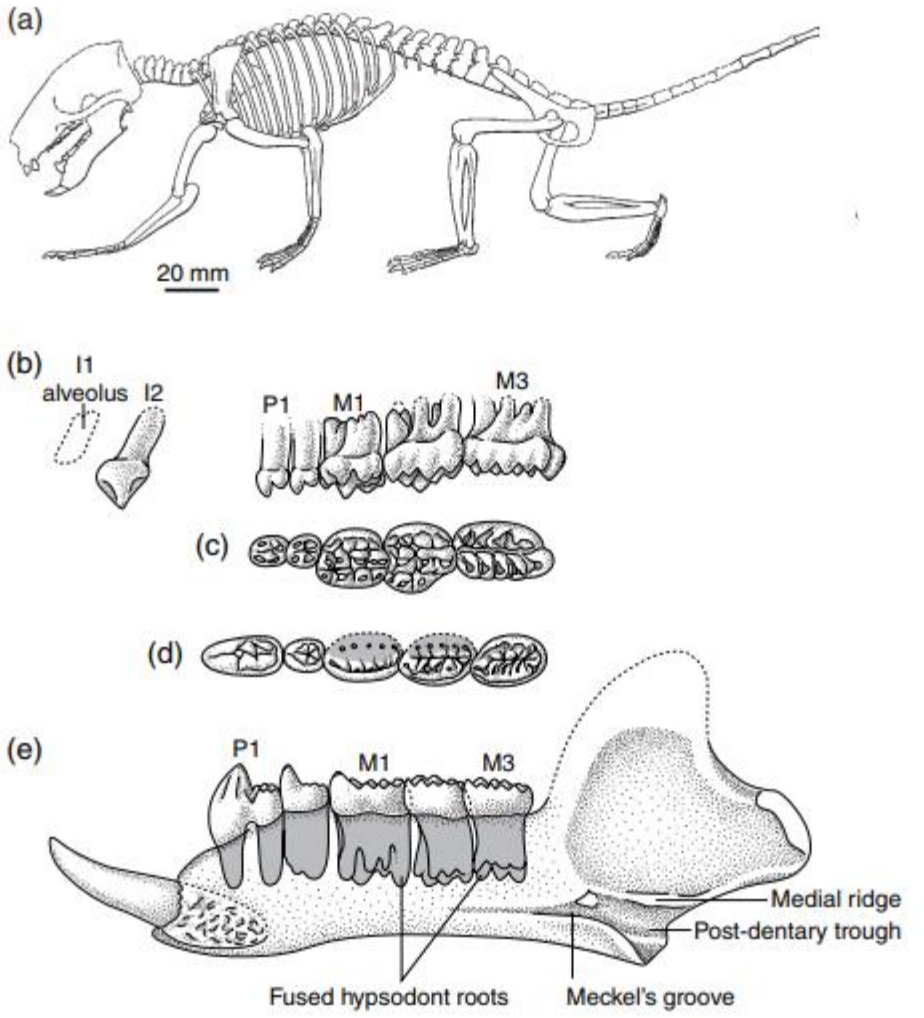


Figure 10.10 Jurassic basal mammals: (a–e) the haramiyid *Megaconus*, (a) reconstruction of skeleton, (b) lingual (medial) view of the upper dentition, (c) occlusal view of the upper cheek teeth, (d) occlusal view of the lower cheek teeth, (e) and the whole mandible in lingual (medial) view;

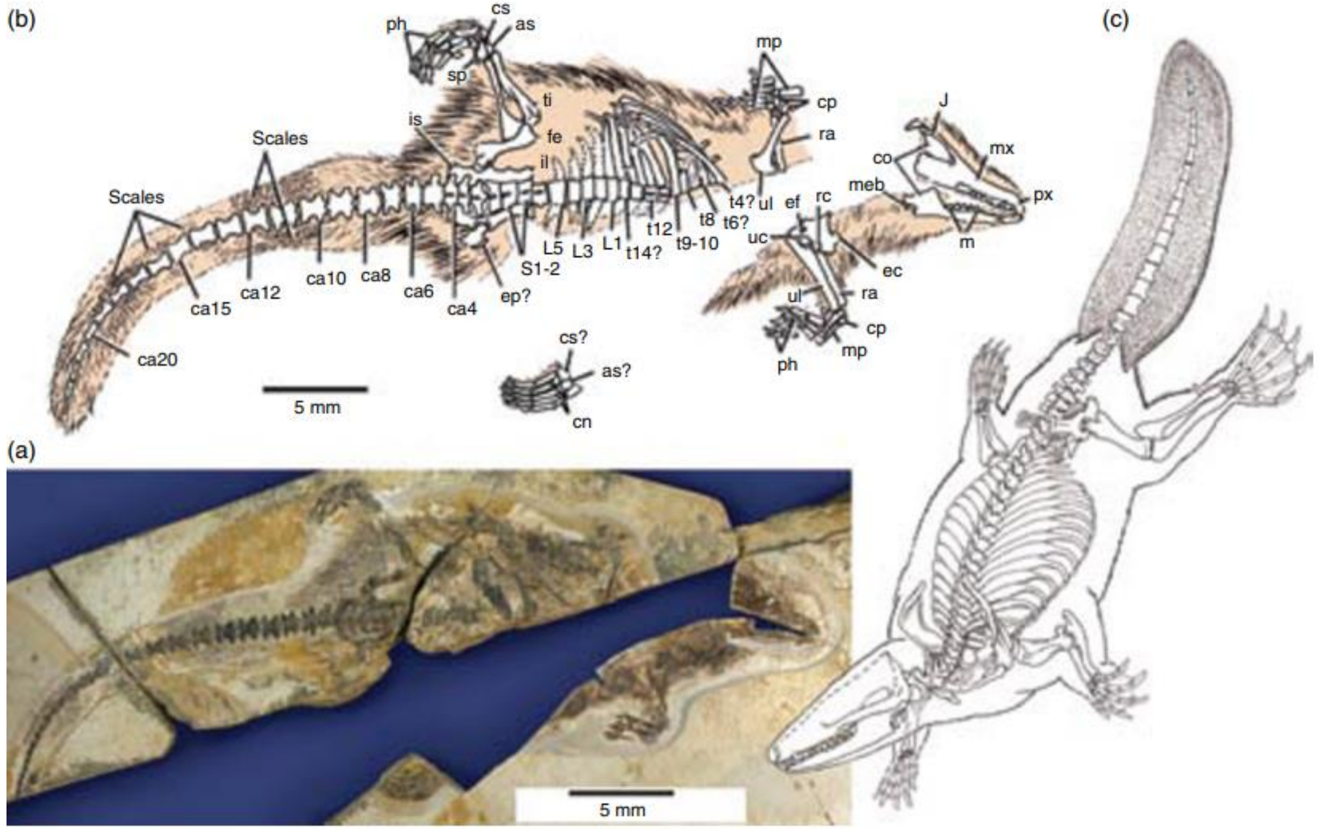
Docodonta

The docodontans, about 12 species from the Middle and Late Jurassic of Europe, Asia and North America were known originally from isolated jaw bones (Figure 10.11(c)). These showed how the teeth converged on a functionally tribosphenic-like structure (Luo and Martin, 2007). Recent finds include more complete specimens from Portugal and China. The Portuguese Late Jurassic *Haldanodon* was a tiny, perhaps 10-cm-long, ground dweller that shows adaptations for digging, including stout and short limb bones and humeri with greatly expanded distal joints and strong deltopectoral crests (Martin, 2005). The braincase is more derived than that of morganucodonts in having an elongate and curved cochlear canal, no anterior paroccipital process, and constriction of the squamosal (Ruf *et al.*, 2013). *Castorocauda* from the Middle Jurassic of China (Ji *et al.*, 2006) was a remarkable docodontan, the first mammal to show substantial adaptations for swimming (see Box 10.4).

There are always remarkable new fossils from China, and the Jurassic mammals from that country have revolutionized our understanding of Mesozoic mammal evolution (see Section 10.3.1, Box 10.3). The docodontan *Castorocauda* was no different (Ji *et al.*, 2006). The remarkable fossil (see Illustration a, b) shows a 43-cm long somewhat beaver-like animal, with adaptations for swimming (and burrowing) and with a poison spur on its ankle.

The fossil comes from the Middle Jurassic Jiulongshan Formation, and was associated with pterosaurs, a theropod dinosaur, lissamphibians, and insects. It preserves nearly all of the skull and skeleton. The first two molars are narrower than in other docodontans, and have recurved cusps in line, interpreted as a plesiomorphic feature retained in *Castorocauda* to help it grasp fish and other aquatic prey. The body was covered with fur, and the tail outline is broad, and covered with interspersed guard hairs and scales, as in a modern beaver. The limbs are short and powerful, with adaptations for swimming and digging. *Castorocauda* may have been 50 cm long and weighed 500 g, similar in size and shape to a modern otter, and perhaps showing similar adaptations to swimming and hunting in fresh waters.

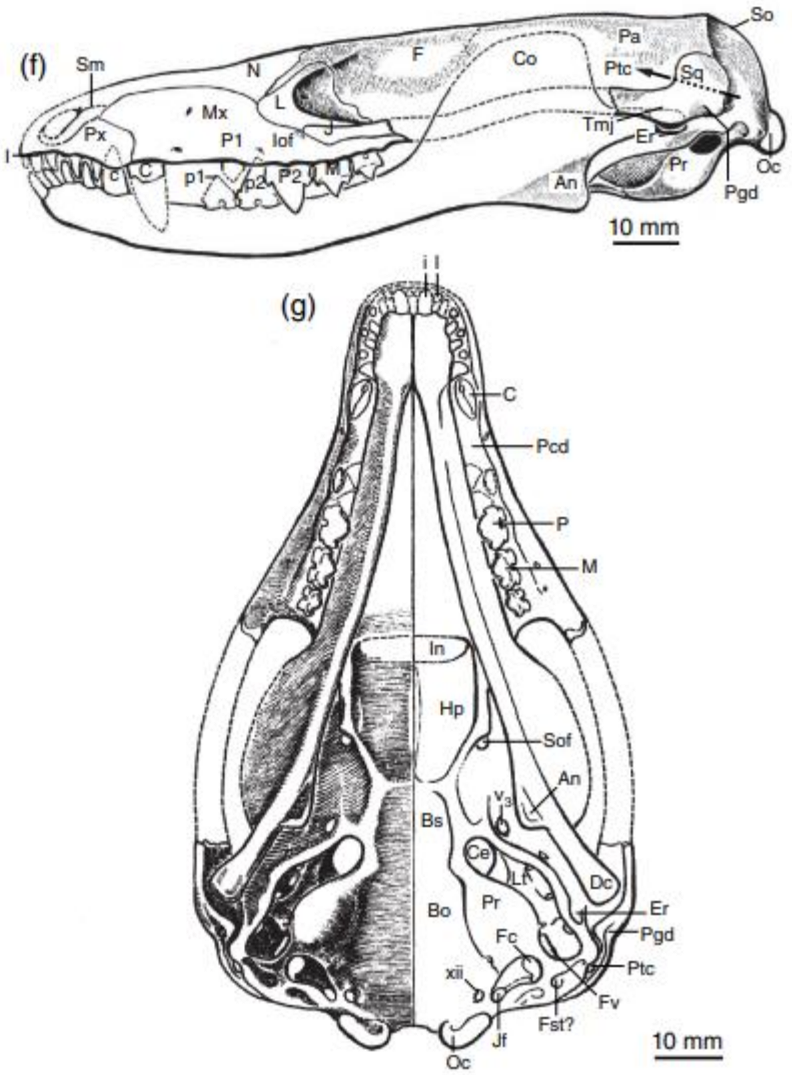
Castorocauda had a poison spur on its ankle, a feature also seen in the haramiyid *Megaconus* (Zhou *et al.*, 2013), in multituberculates, and in many other Mesozoic mammals (Hurum *et al.*, 2006). This interpretation is based on the structure of the astragalus, which carries a bony base and a keratin spur. Perhaps such a feature was plesiomoerphic for mammals. The modern platypus (see Section 10.3.2) has such a spur, which develops initially in both males and females, but is retained only in the adult male, and delivers poison. This is perhaps an offensive weapon in male–male fights, as well as being used in defence.



The first swimming mammal *Castorocauda*, showing the original specimen (a), an outline drawing of this specimen showing skeleton and surrounding hair (b), and a reconstruction as a swimmer and burrower (c). Abbreviations: as, astragalus; ca, caudal vertebrae; cn, ento-, meso-, and ecto-cuneiforms; co, coronoid process of dentary; cp, carpals; cs, calcaneus; ec, ectepicondyle and supinator shelf (humerus); ef, entepicondyle foramen; ep?, probable epipubis; is, ischium; J, jugal; L1-6, lumbar ribs 1 to 6; m, molars; meb, manubrium of malleus; mp, metacarpals; mx, maxilla; px, premaxilla; ra, radius; rc, radial condyle; S1-2, sacrals 1 and 2; sp, extratarsal ("poisonous") spur; t4-t14 (preserved ribs through thoracic 17); uc, ulnar condyle; ul, ulna. See Colour plate 10.2. Source: Ji *et al.* (2006). Reproduced with permission from the American Association for the Advancement of Science.

Hadrocodium

Hadrocodium from the Early Jurassic of China (Luo *et al*., 2001) appears to fall phylogenetically between Docodonta and crown Mammalia (see Box 10.3). This tiny mammal, known only from its tiny skull (Figure 10.10(f,g)) was probably little more than 32 mm long and weighed perhaps 2 g. Its importance rests in its relatively large brain, and in its derived ear structure in which the postdentary trough has entirely disappeared and the middle ear ossicles are entirely separated from the lower jaw for the first time. Note that this separation between jaw and ossicles seems to have happened independently several times in early mammals, and certainly between monotremes ands therians.



(f,g) skull of *Hadrocodium* in lateral (f) and ventral (g) views. Source: Luo *et al*. (2001). Reproduced with permission from the American Association for the Advancement of Science.

Kuehneotherium

Kuehneotherium from the Early Jurassic of South Wales (Kermack *et al*., 1968) has been difficult to interpret because its remains consist of isolated teeth and jaw fragments. The genus has gained some notoriety, however, because the three principal cusps of its teeth are arranged in a very shallow triangle and this was once said to be a forerunner of the tribosphenic molar, important in later mammalian evolution (see Section 10.3.2). The upper and lower molar teeth (Figure 10.11(a,b)) have a main central pointed cusp and smaller accessory cusps placed low on the shoulders of the main cusp.

A small group of Jurassic and Cretaceous mammals, Tinodontidae, formerly classed as symmetrodontans, appear to follow next phylogenetically (see Box 10.3). *Tinodon* shares some superficial similarities in its teeth with *Kuehneotherium*.

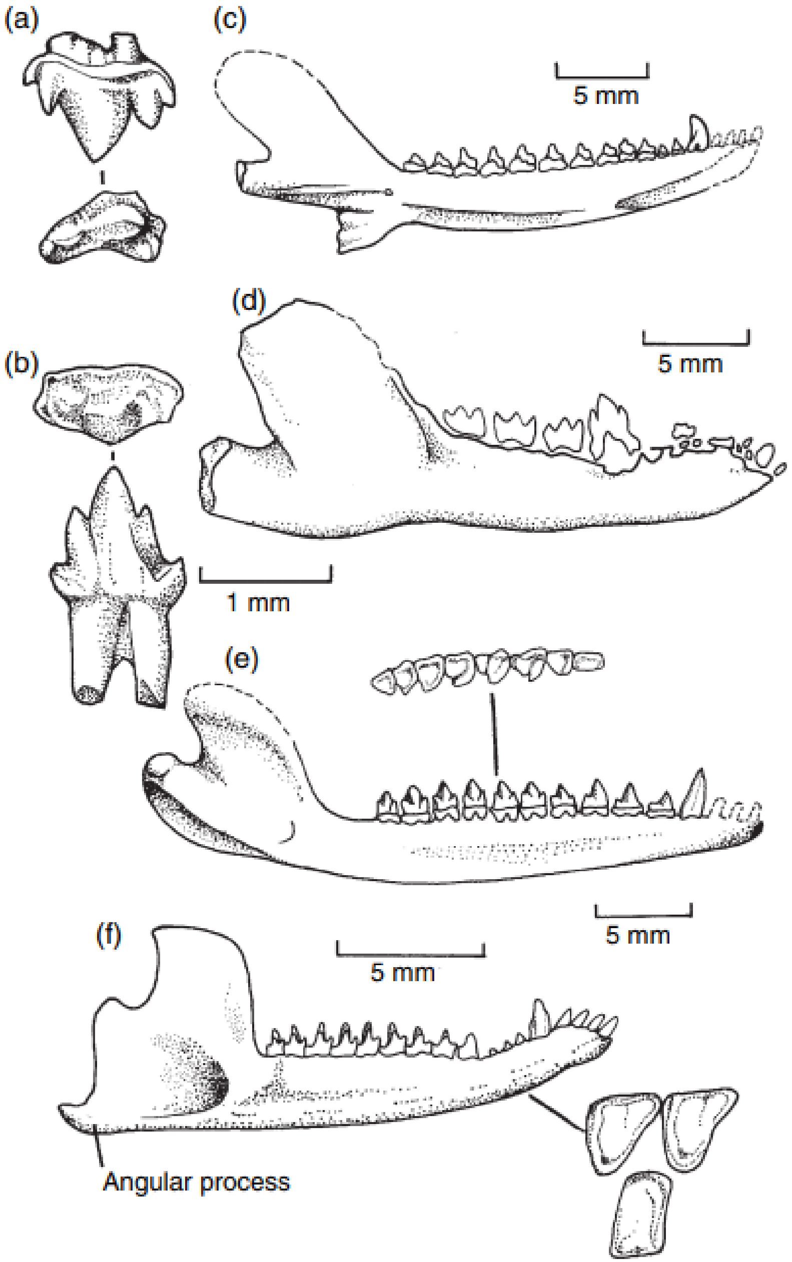
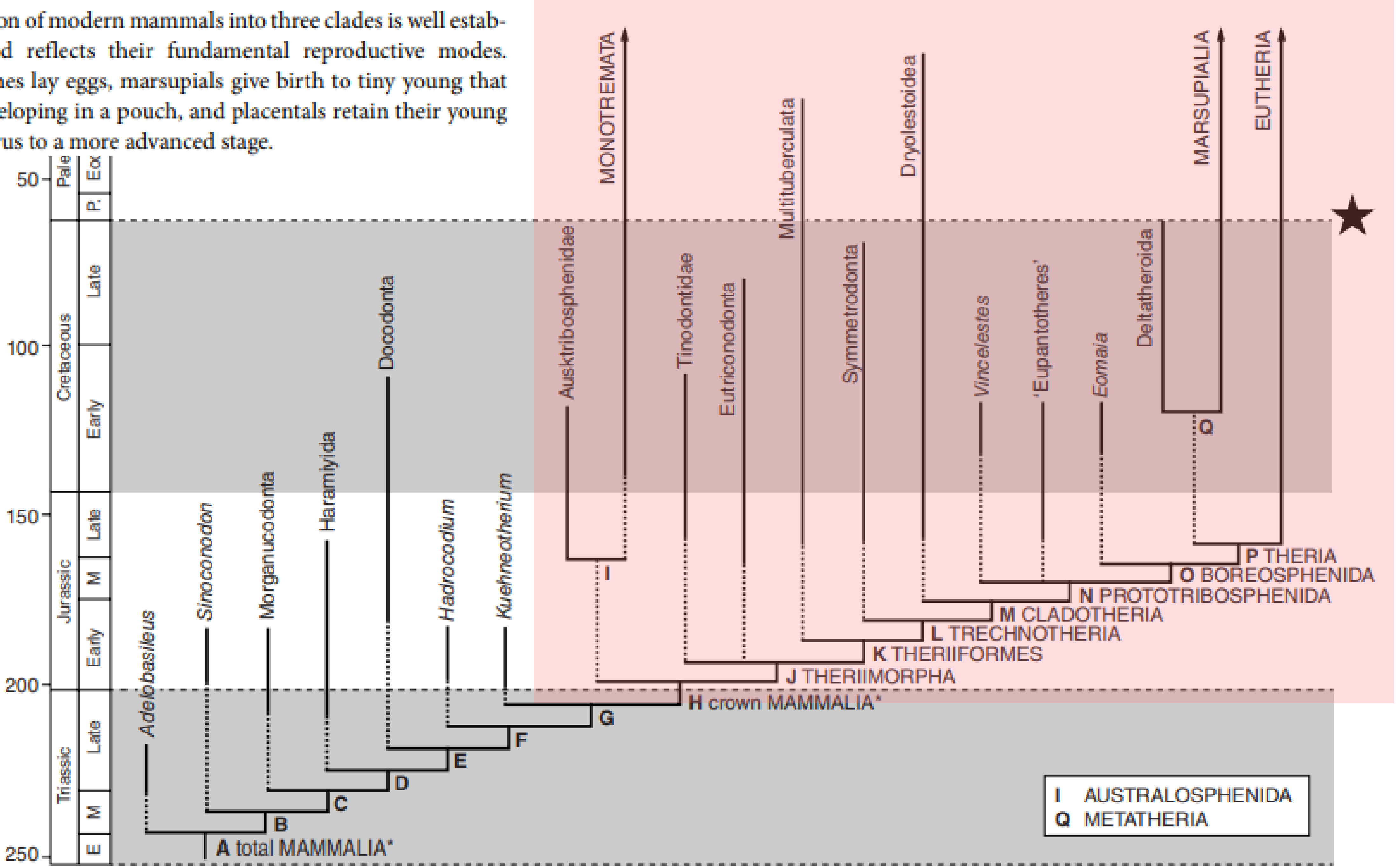


Figure 10.11 Mesozoic mammals: (a) upper molar of *Kuehneotherium* in medial and occlusal views; (b) lower molar of *Kuehneotherium* in medial and occlusal views; (c) lower jaw of the docodontan *Docodon*, in medial view; (d) lower jaw of the triconodontan *Triconodon* in lateral view; (e) lower jaw of the symmetrodont *Spalacotherium* in lateral view and occlusal view of the molars; (f) lower jaw of the dryolestid *Crusafontia* in medial view and occlusal view of two upper and one lower cheek tooth. Source: (a,b) Adapted from Kermack *et al.* (1968). (c) Adapted from Woodward (1898). (d) Adapted from Flower and Lydekker (1891). (e) Adapted from Cassiliano and Clemens (1979). (f) Adapted from Krebs (1994).

The division of modern mammals into three clades is well established, and reflects their fundamental reproductive modes. Monotremes lay eggs, marsupials give birth to tiny young that finish developing in a pouch, and placentals retain their young in the uterus to a more advanced stage.



Tribosphenic molar

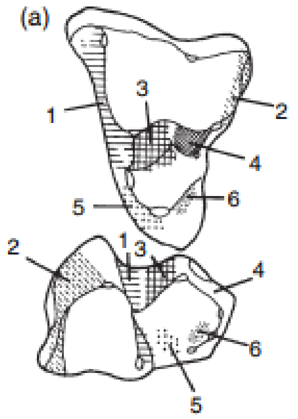
A key evolutionary acquisition of mammals was the tribosphenic molar (Figure 10.13), in which a newly evolved cusp of the upper molar, the **protocone** macerates food in a facing basin of the lower molar, the **talonid**. The name tribosphenic (literally, 'rubbing-wedge') refers to the derived mortar-and-pestle type of occlusal action of these teeth. The occlusal surface is a triangle of three cusps with the point facing outwards in a lower molar, followed by the talonid basin in which the inward-facing point of the triangle of an upper molar, the protocone, occludes.

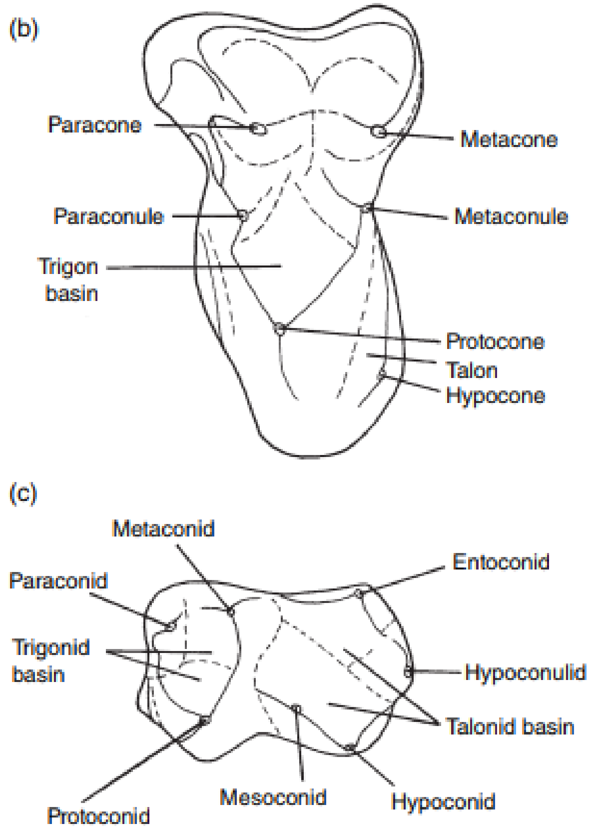
The evolution of the tribosphenic molar has been much discussed. Therians (marsupials and placentals) share the tribosphenic molar (Box 10.3), and at one time the modern monotremes were treated as quite distinct, perhaps with a separate origin deep in the Triassic, because they show a more linear arrangement of cusps in adult molars. Palaeontologists tried to divide the teeth of the various Mesozoic forms (see Section 10.3.1) into linear and tribosphenic patterns.

Then, a number of Cretaceous teeth from Australia, assigned to Ausktribosphenidae (see Section 10.3.3), appeared to show a kind of tribosphenic pattern and were placed variously on the line to Monotremata or to Theria. The resolution (Luo *et al.*, 2002, 2003; Davis, 2011) appears to be that crown-group mammals divide into two clades that diverged in the Jurassic, the Australosphenida based in the southern hemisphere, and the Boreosphenida based in the northern hemisphere. Each clade evolved a kind of tribosphenic tooth, but these tooth types differ in details, and the basal members of each clade had more simple teeth.

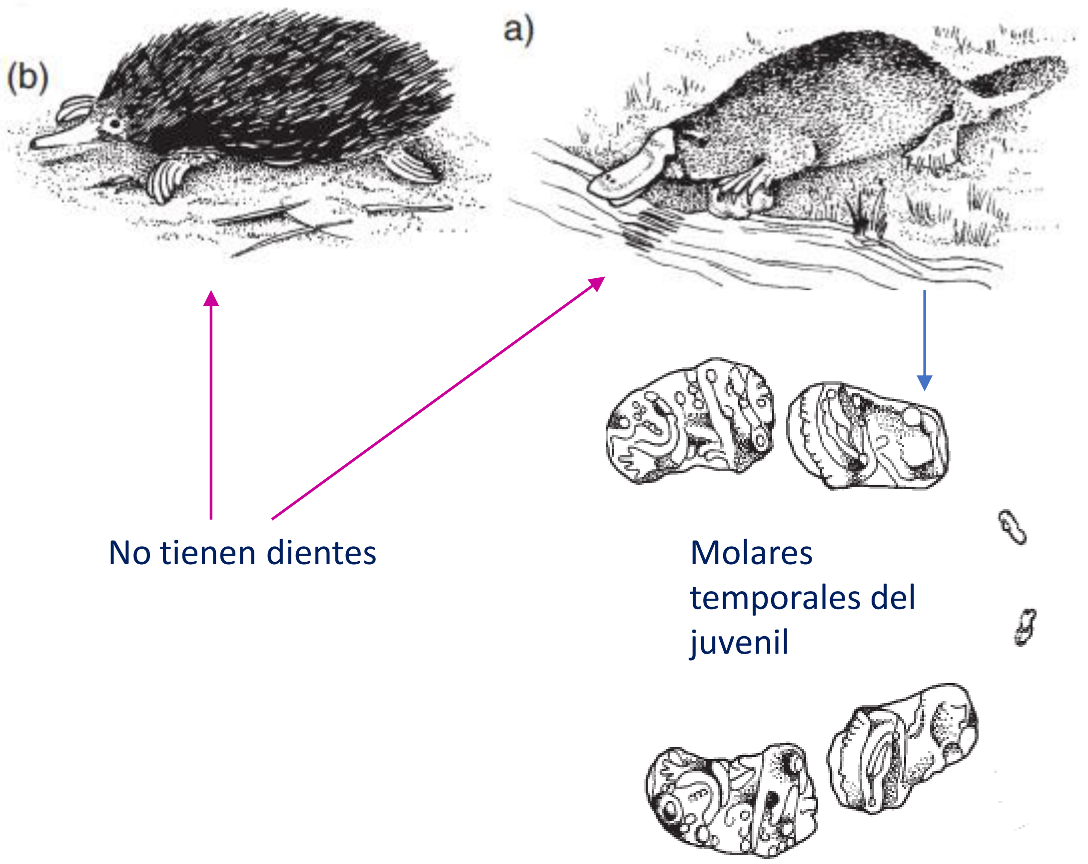
Figure 10.13 The tribosphenic molar: (a) the tribosphenic Cenozoic placental mammal *Didelphodus*, showing the postulated sequence of assembly of shearing surfaces on both upper (top) and lower (bottom) molars; (b,c) nomenclature of the main cusps, ridges and basins, of the Late Cretaceous placental mammal *Gypsonictops* (b) upper and (c) lower molars. Source: Adapted from Bown and Krause (1979).

The tribosphenic molar (Figure 10.13(a)) has six shearing surfaces. The nomenclature of the cusps, ridges and facets of typical mammalian molar teeth such as these is complex (Figure 10.13(b,c)). The main terms to note are for the triangles of three cusps: the **paracone** (anterolateral), **metacone** (posterolateral) and **protocone** (medial) in the uppers, and the **paraconid** (anterointernal), **metaconid** (posterointernal) and **protoconid** (external) in the trigonids of the lowers. The talonid, occupying the posterior half of lower molars, is bounded by the **entoconid** (medial), **hypoconid** (lateral) and the **hypoconulid** (posterior).



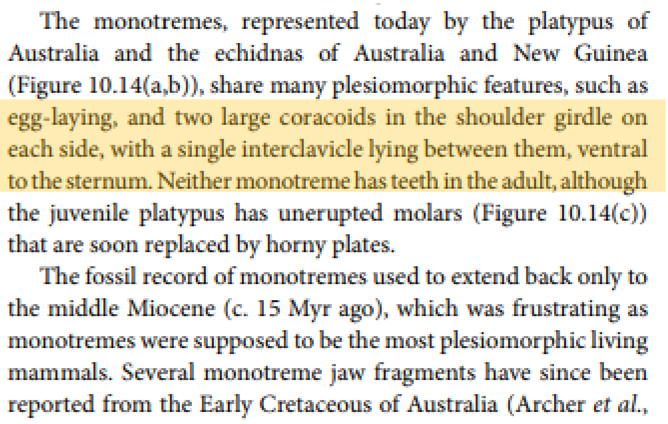


Australosphenida → Ausktribosphenidae + Monotremas

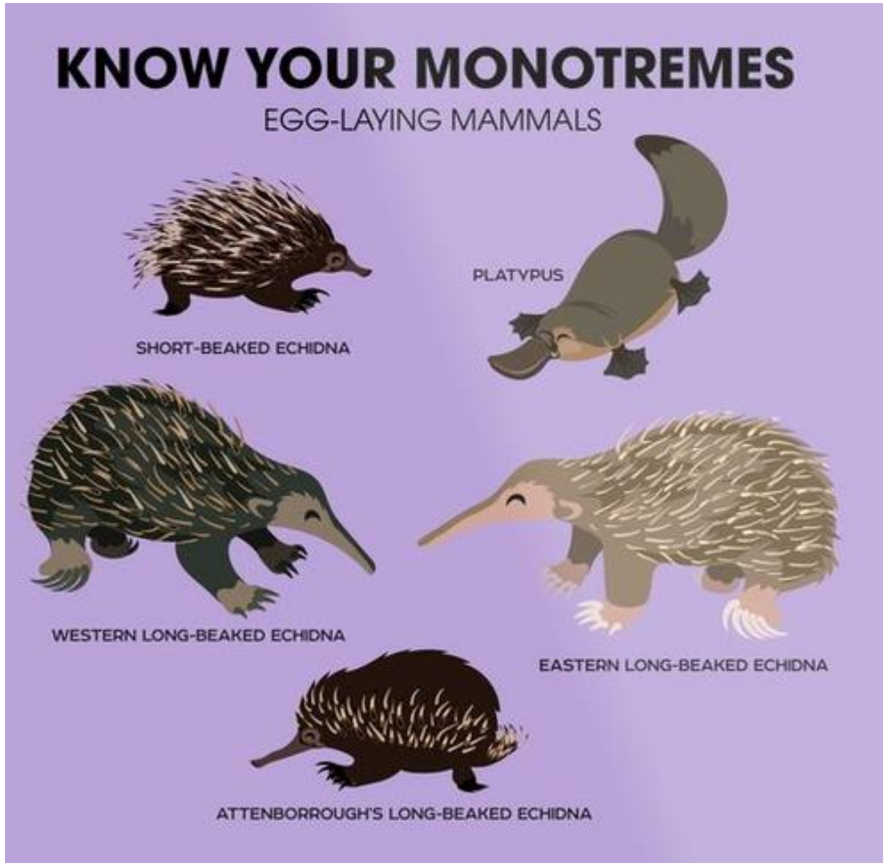


No tienen dientes

Molares temporales del juvenil


The monotremes, represented today by the platypus of Australia and the echidnas of Australia and New Guinea (Figure 10.14(a,b)), share many plesiomorphic features, such as egg-laying, and two large coracoids in the shoulder girdle on each side, with a single interclavicle lying between them, ventral to the sternum. Neither monotreme has teeth in the adult, although the juvenile platypus has unerupted molars (Figure 10.14(c)) that are soon replaced by horny plates.

The fossil record of monotremes used to extend back only to the middle Miocene (c. 15 Myr ago), which was frustrating as monotremes were supposed to be the most plesiomorphic living mammals. Several monotreme jaw fragments have since been reported from the Early Cretaceous of Australia (Archer *et al.*,



Australosphenida → Ausktribosphenidae + Monotremas

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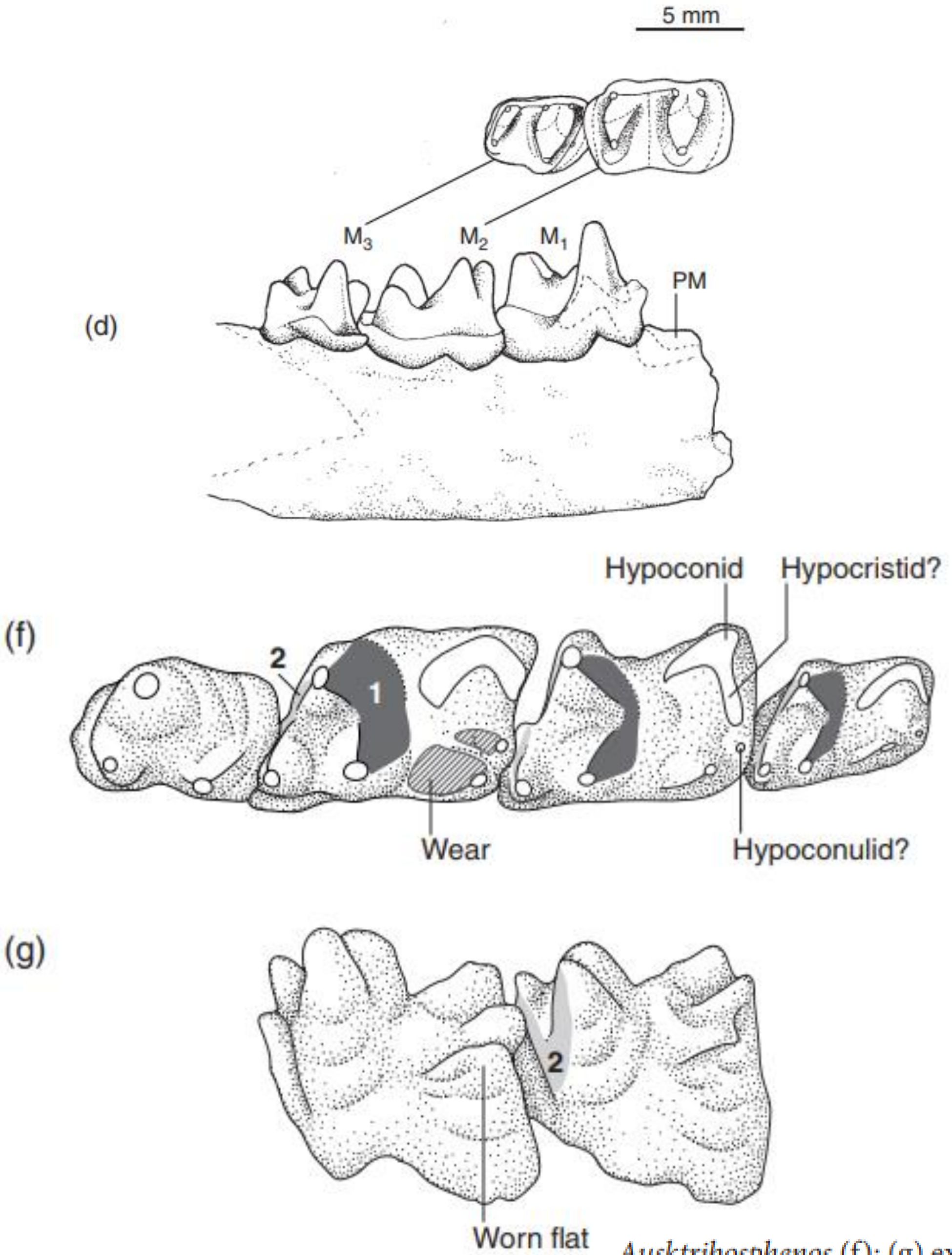
Platypus teeth have also been found in the Palaeocene of Argentina. This suggests a Gondwanan origin for the group and fits with a suggestion that monotremes arose in Australia, and that some of them migrated across Antarctica to South America, where they existed perhaps for only a short time.

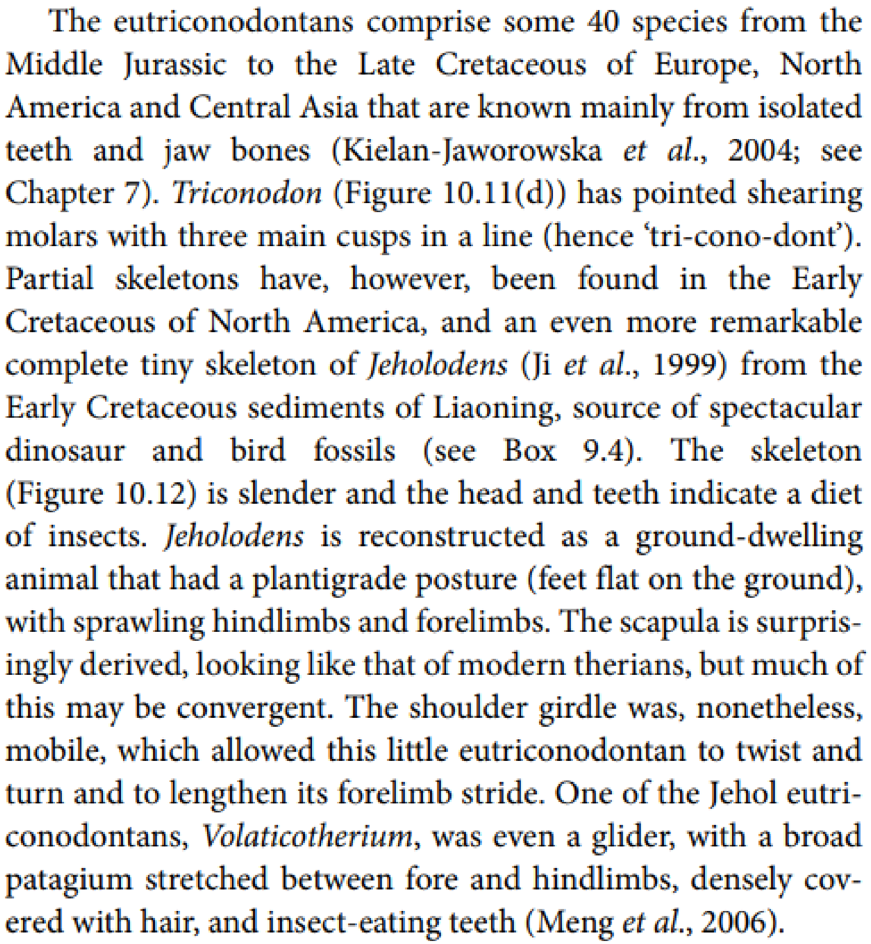
The origin of monotremes has long been debated. The discovery of teeth and jaw fragments in the Middle Jurassic of Madagascar (*Ambondro*) and South America (*Asfaltomylos*), and the Early Cretaceous of Australia (*Ausktribosphenos*, *Bishops*), have clarified the situation. These teeth, many of which are superficially tribosphenic (see Section 10.3.2), are assigned to Ausktribosphenidae, and they and Monotremata to Australosphenida (Luo *et al.*, 2002, 2003; Davis, 2011). These show molar occlusal surfaces whose facets are limited to a shearing function and do not appear to be present within the talonid basin (Figure 10.14(e–h)), as in the true tribosphenic tooth of Boreosphenida.



(d) jaw fragment of *Steropodon*,

Ausktribosphenos (f); (g) external view of upper molars 1–2 of *Ausktribosphenos*;

Eutriconodonta



The eutriconodontans comprise some 40 species from the Middle Jurassic to the Late Cretaceous of Europe, North America and Central Asia that are known mainly from isolated teeth and jaw bones (Kielan-Jaworowska *et al.*, 2004; see Chapter 7). *Triconodon* (Figure 10.11(d)) has pointed shearing molars with three main cusps in a line (hence 'tri-cono-dont'). Partial skeletons have, however, been found in the Early Cretaceous of North America, and an even more remarkable complete tiny skeleton of *Jeholodens* (Ji *et al.*, 1999) from the Early Cretaceous sediments of Liaoning, source of spectacular dinosaur and bird fossils (see Box 9.4). The skeleton (Figure 10.12) is slender and the head and teeth indicate a diet of insects. *Jeholodens* is reconstructed as a ground-dwelling animal that had a plantigrade posture (feet flat on the ground), with sprawling hindlimbs and forelimbs. The scapula is surprisingly derived, looking like that of modern therians, but much of this may be convergent. The shoulder girdle was, nonetheless, mobile, which allowed this little eutriconodontan to twist and turn and to lengthen its forelimb stride. One of the Jehol eutriconodontans, *Volaticotherium*, was even a glider, with a broad patagium stretched between fore and hindlimbs, densely covered with hair, and insect-eating teeth (Meng *et al.*, 2006).

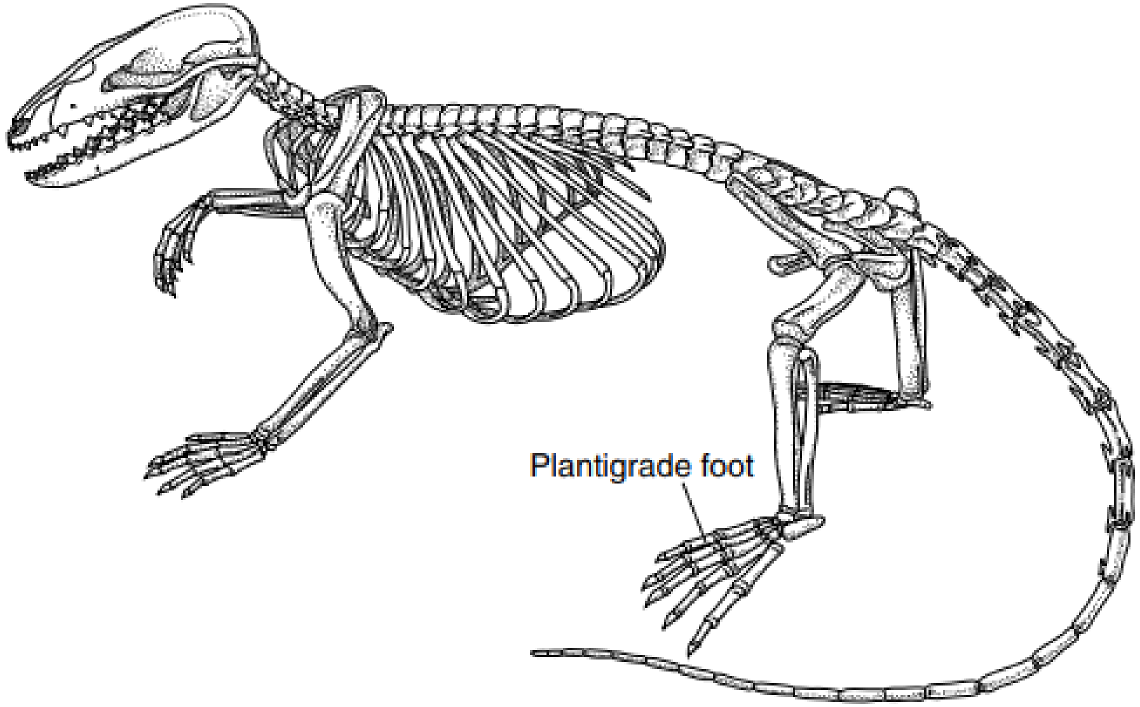
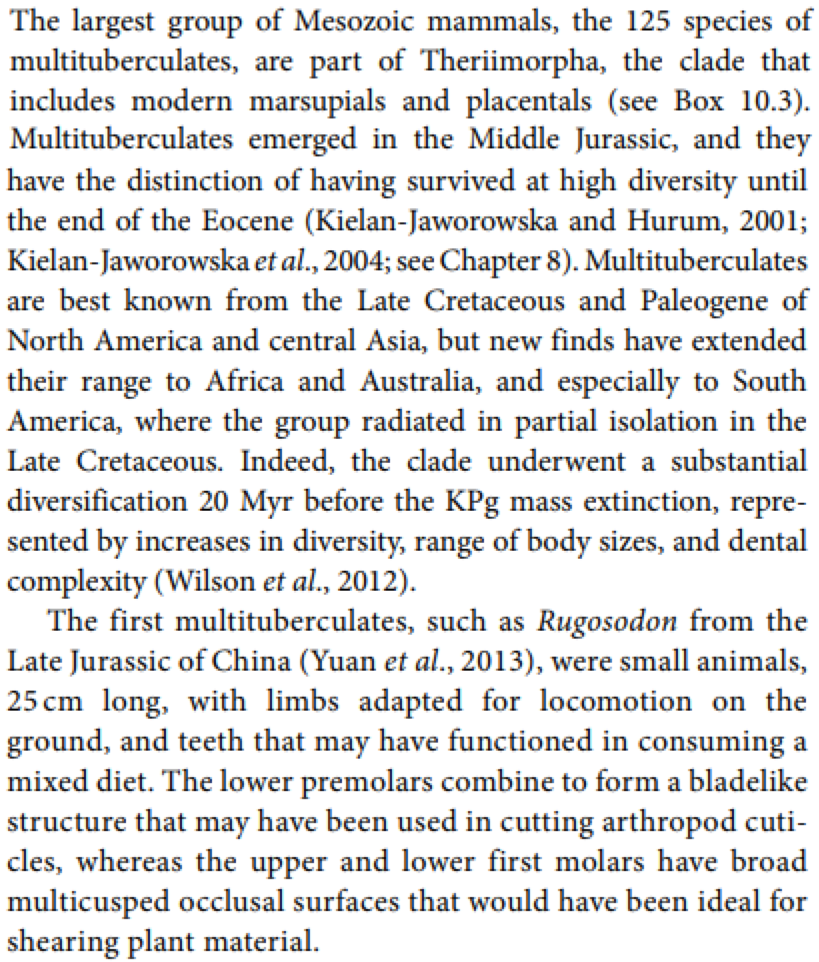


Figure 10.12 Skeleton of the triconodontan *Jeholodens* in left lateral view, restored from a nearly complete specimen from the Early Cretaceous of China. Source: L. Zhe-xi, Field Museum of Natural History, Chicago, IL, USA. Reproduced with permission.

Multituberculados



The largest group of Mesozoic mammals, the 125 species of multituberculates, are part of Theriimorpha, the clade that includes modern marsupials and placentals (see Box 10.3). Multituberculates emerged in the Middle Jurassic, and they have the distinction of having survived at high diversity until the end of the Eocene (Kielan-Jaworowska and Hurum, 2001; Kielan-Jaworowska *et al.*, 2004; see Chapter 8). Multituberculates are best known from the Late Cretaceous and Paleogene of North America and central Asia, but new finds have extended their range to Africa and Australia, and especially to South America, where the group radiated in partial isolation in the Late Cretaceous. Indeed, the clade underwent a substantial diversification 20 Myr before the KPg mass extinction, represented by increases in diversity, range of body sizes, and dental complexity (Wilson *et al.*, 2012).

The first multituberculates, such as *Rugosodon* from the Late Jurassic of China (Yuan *et al.*, 2013), were small animals, 25 cm long, with limbs adapted for locomotion on the ground, and teeth that may have functioned in consuming a mixed diet. The lower premolars combine to form a bladelike structure that may have been used in cutting arthropod cuticles, whereas the upper and lower first molars have broad multicusped occlusal surfaces that would have been ideal for shearing plant material.

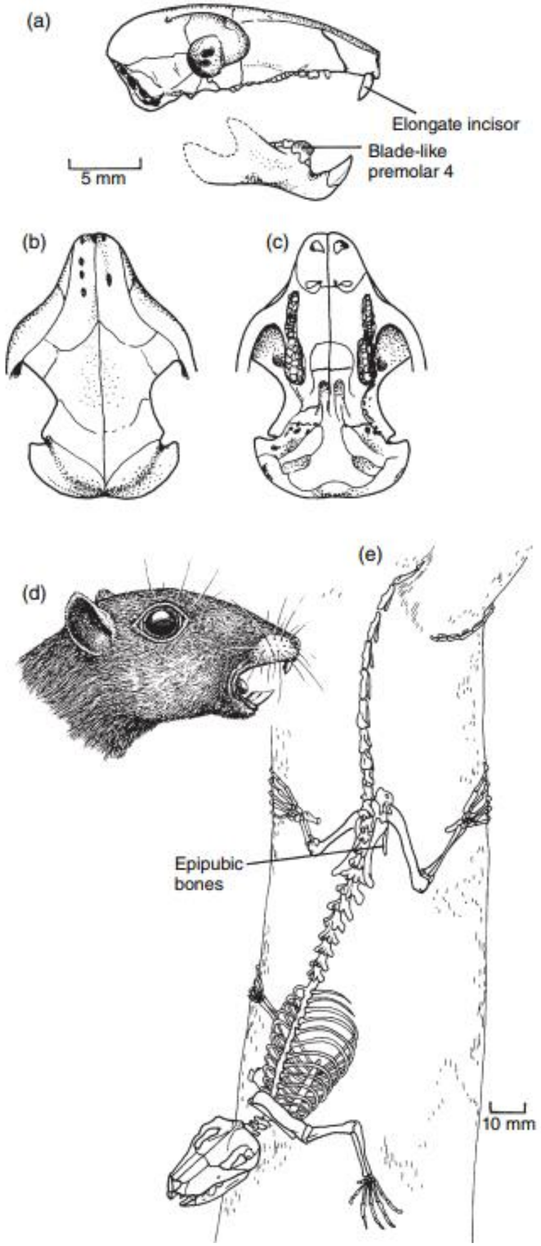
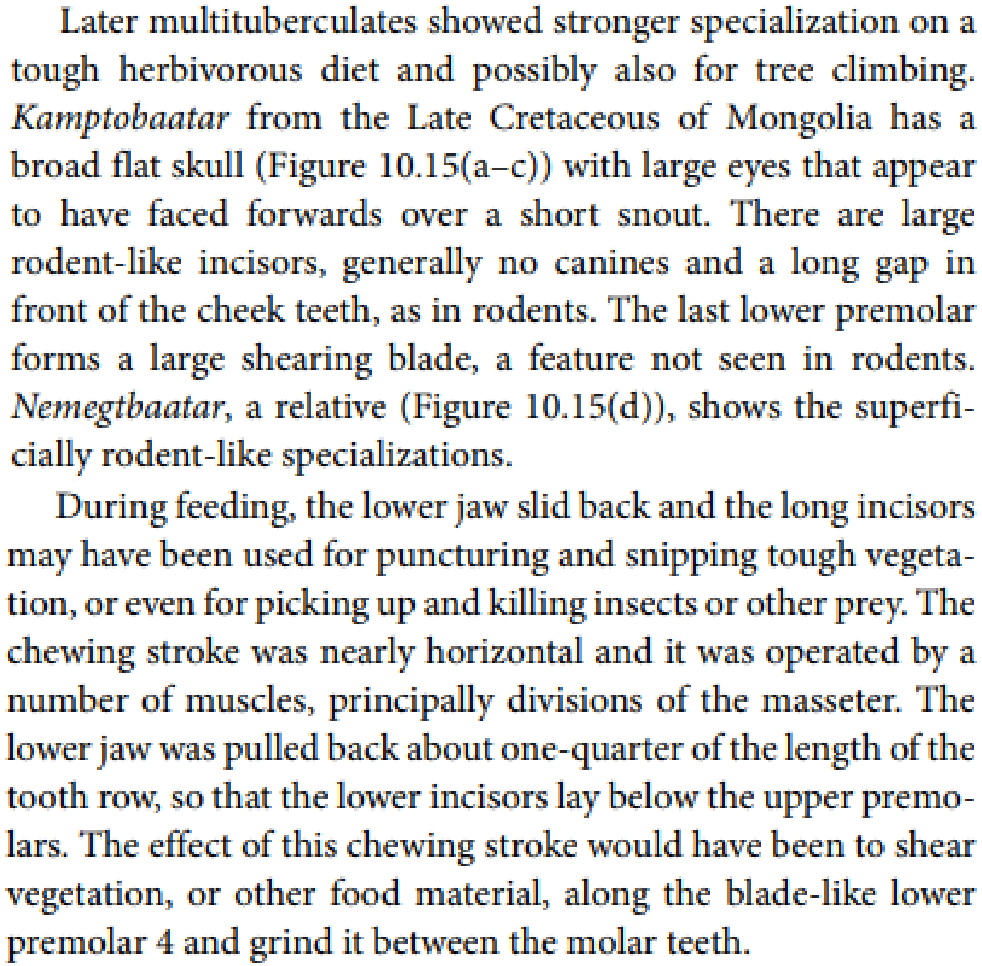


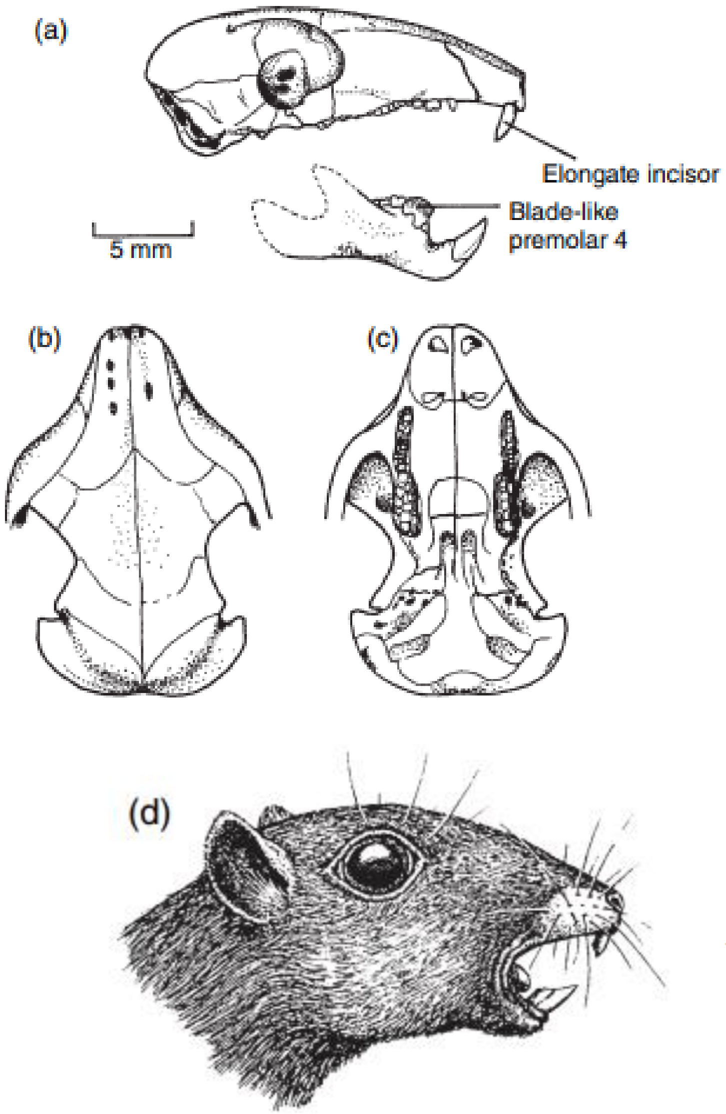
Figure 10.15 The multituberculates: (a–c) skull of *Kamptobaatar* in lateral, dorsal and ventral views; (d) restored head of *Nemegtbaatar*; (e) reconstructed skeleton of *Ptilodus* descending a tree trunk. Source: (a–c) Adapted from Kielan-Jaworowska (1971). (d) Z. Kielan-Jaworowska, formerly, Institute of Paleobiology, Warsaw, Poland. Reproduced with permission. (e) Adapted from Krause and Jenkins (1983).

Multituberculados



Later multituberculates showed stronger specialization on a tough herbivorous diet and possibly also for tree climbing. *Kamptobaatar* from the Late Cretaceous of Mongolia has a broad flat skull (Figure 10.15(a–c)) with large eyes that appear to have faced forwards over a short snout. There are large rodent-like incisors, generally no canines and a long gap in front of the cheek teeth, as in rodents. The last lower premolar forms a large shearing blade, a feature not seen in rodents. *Nemegtbaatar*, a relative (Figure 10.15(d)), shows the superficially rodent-like specializations.

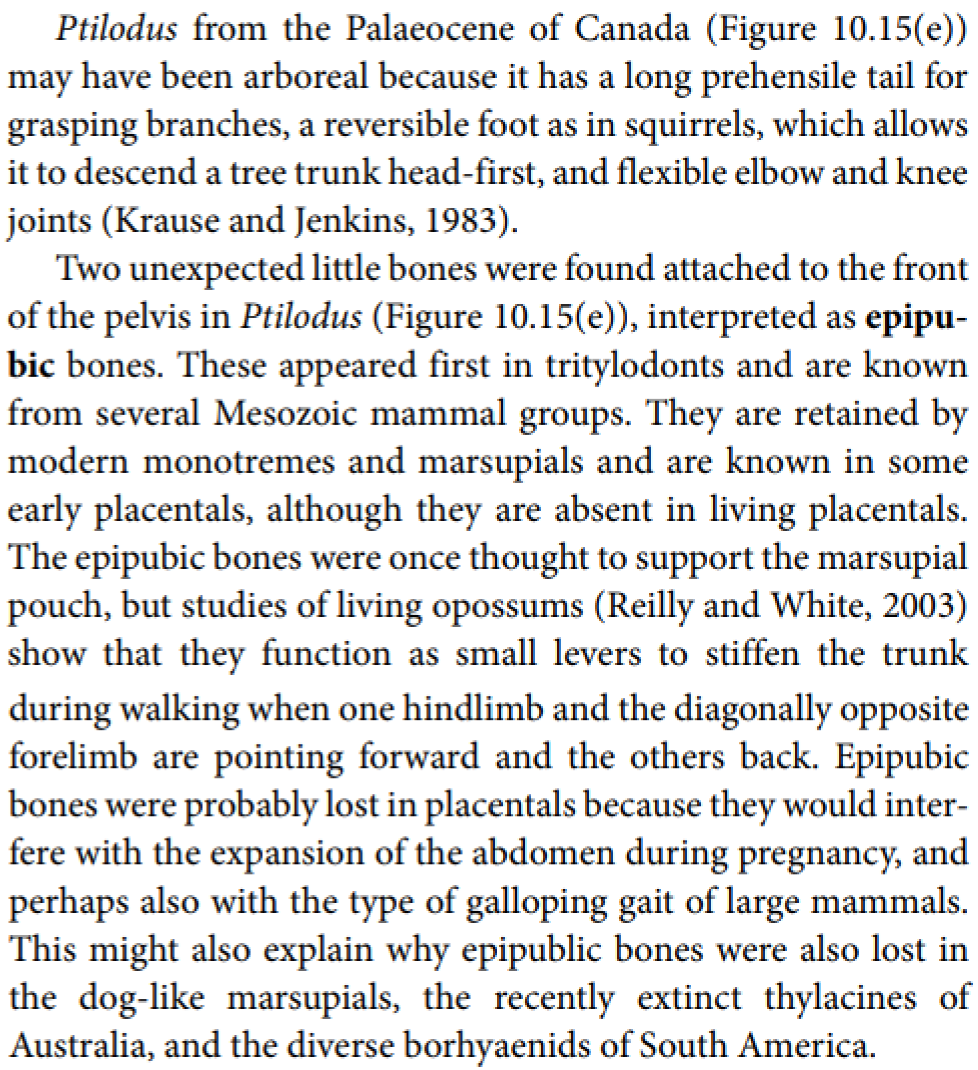
During feeding, the lower jaw slid back and the long incisors may have been used for puncturing and snipping tough vegetation, or even for picking up and killing insects or other prey. The chewing stroke was nearly horizontal and it was operated by a number of muscles, principally divisions of the masseter. The lower jaw was pulled back about one-quarter of the length of the tooth row, so that the lower incisors lay below the upper premolars. The effect of this chewing stroke would have been to shear vegetation, or other food material, along the blade-like lower premolar 4 and grind it between the molar teeth.



Kamptobaatar

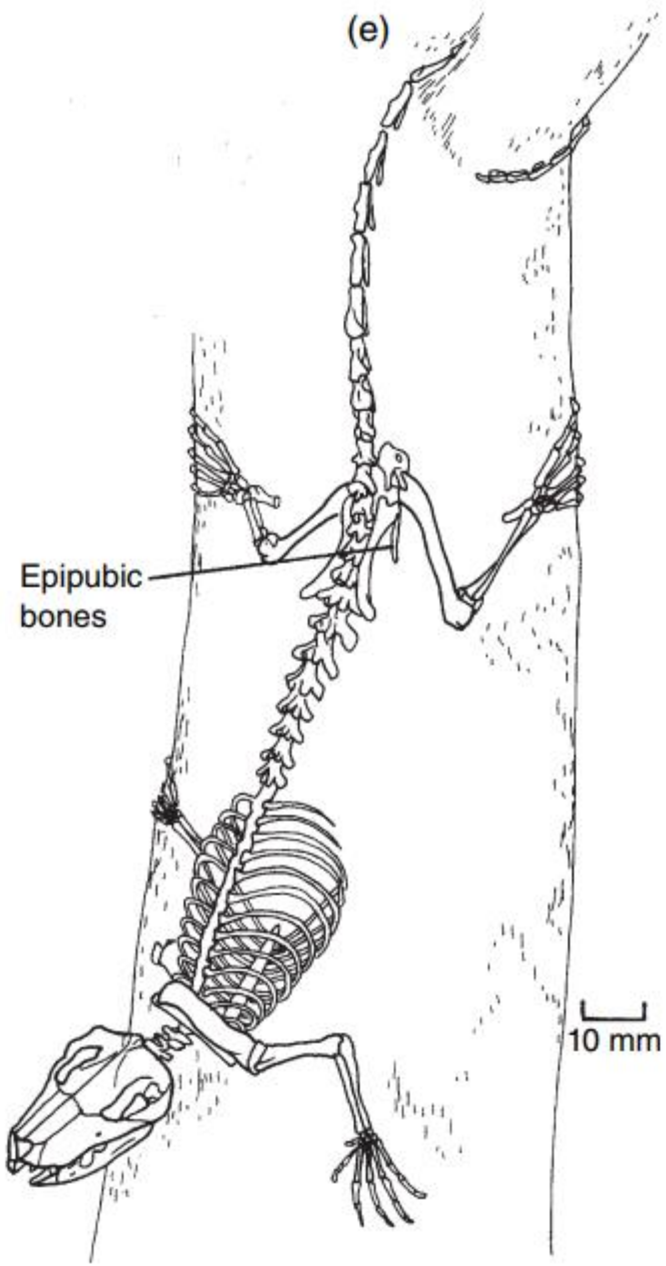
Nemegtbaatar;

Multituberculados

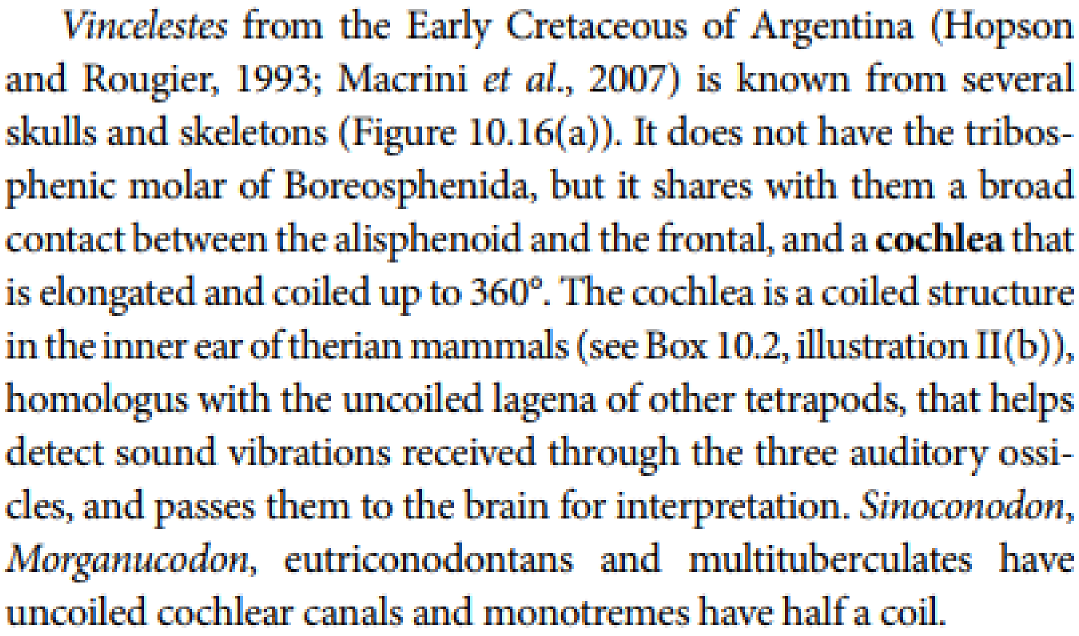


Ptilodus from the Palaeocene of Canada (Figure 10.15(e)) may have been arboreal because it has a long prehensile tail for grasping branches, a reversible foot as in squirrels, which allows it to descend a tree trunk head-first, and flexible elbow and knee joints (Krause and Jenkins, 1983).

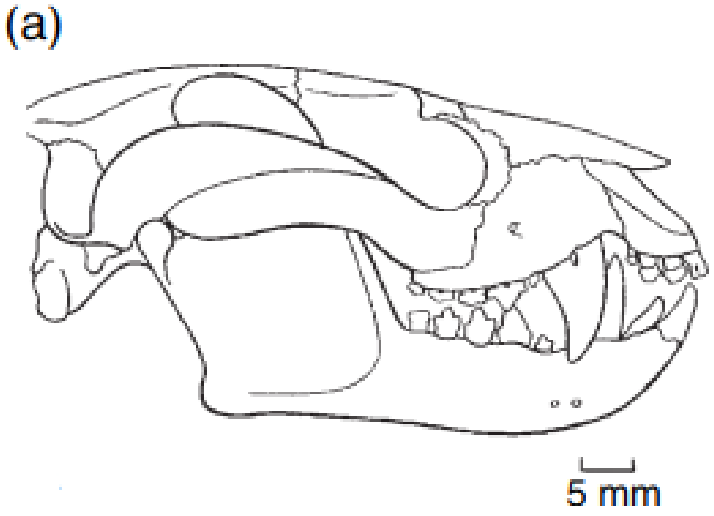
Two unexpected little bones were found attached to the front of the pelvis in *Ptilodus* (Figure 10.15(e)), interpreted as **epipubic** bones. These appeared first in tritylodonts and are known from several Mesozoic mammal groups. They are retained by modern monotremes and marsupials and are known in some early placentals, although they are absent in living placentals. The epipubic bones were once thought to support the marsupial pouch, but studies of living opossums (Reilly and White, 2003) show that they function as small levers to stiffen the trunk during walking when one hindlimb and the diagonally opposite forelimb are pointing forward and the others back. Epipubic bones were probably lost in placentals because they would interfere with the expansion of the abdomen during pregnancy, and perhaps also with the type of galloping gait of large mammals. This might also explain why epipublic bones were also lost in the dog-like marsupials, the recently extinct thylacines of Australia, and the diverse borhyaenids of South America.



Vincelestes

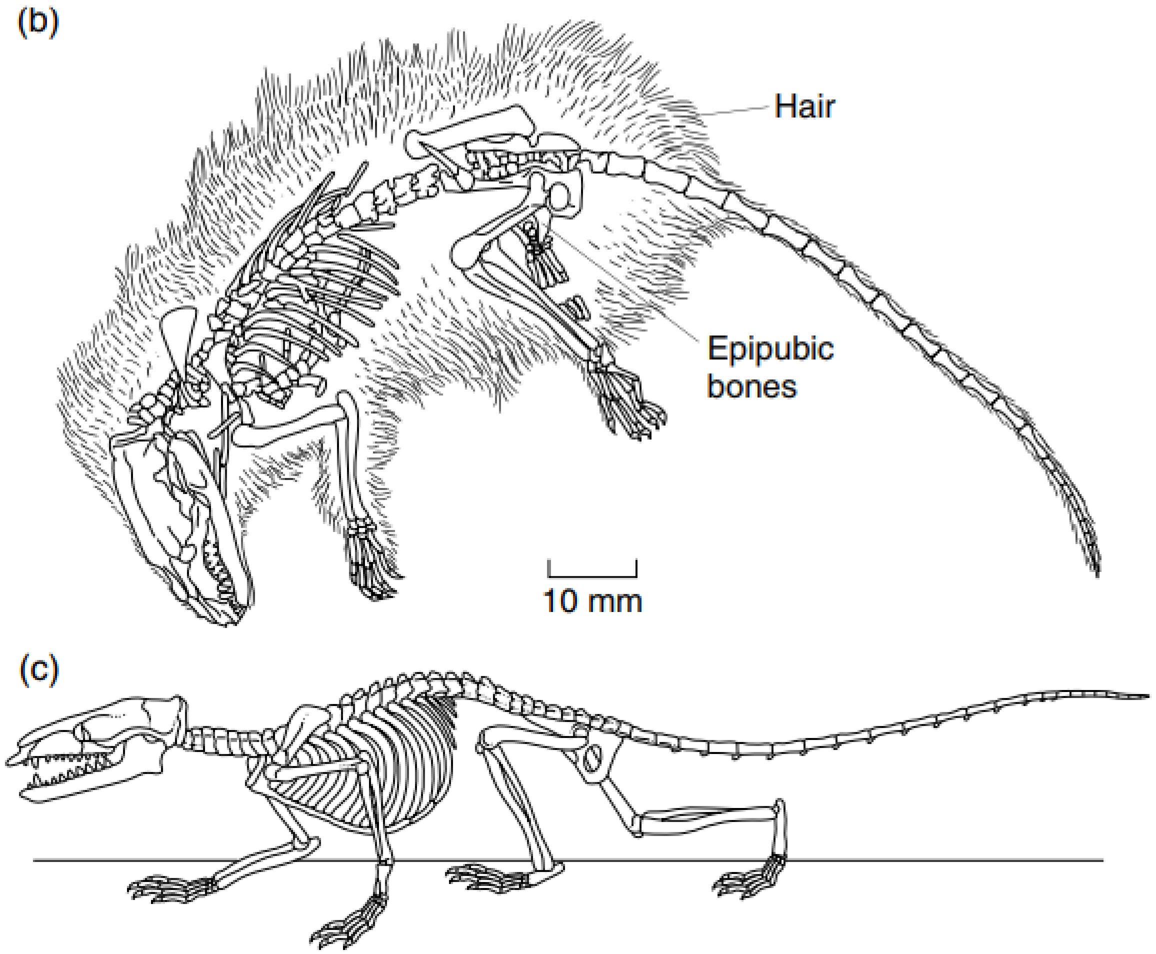


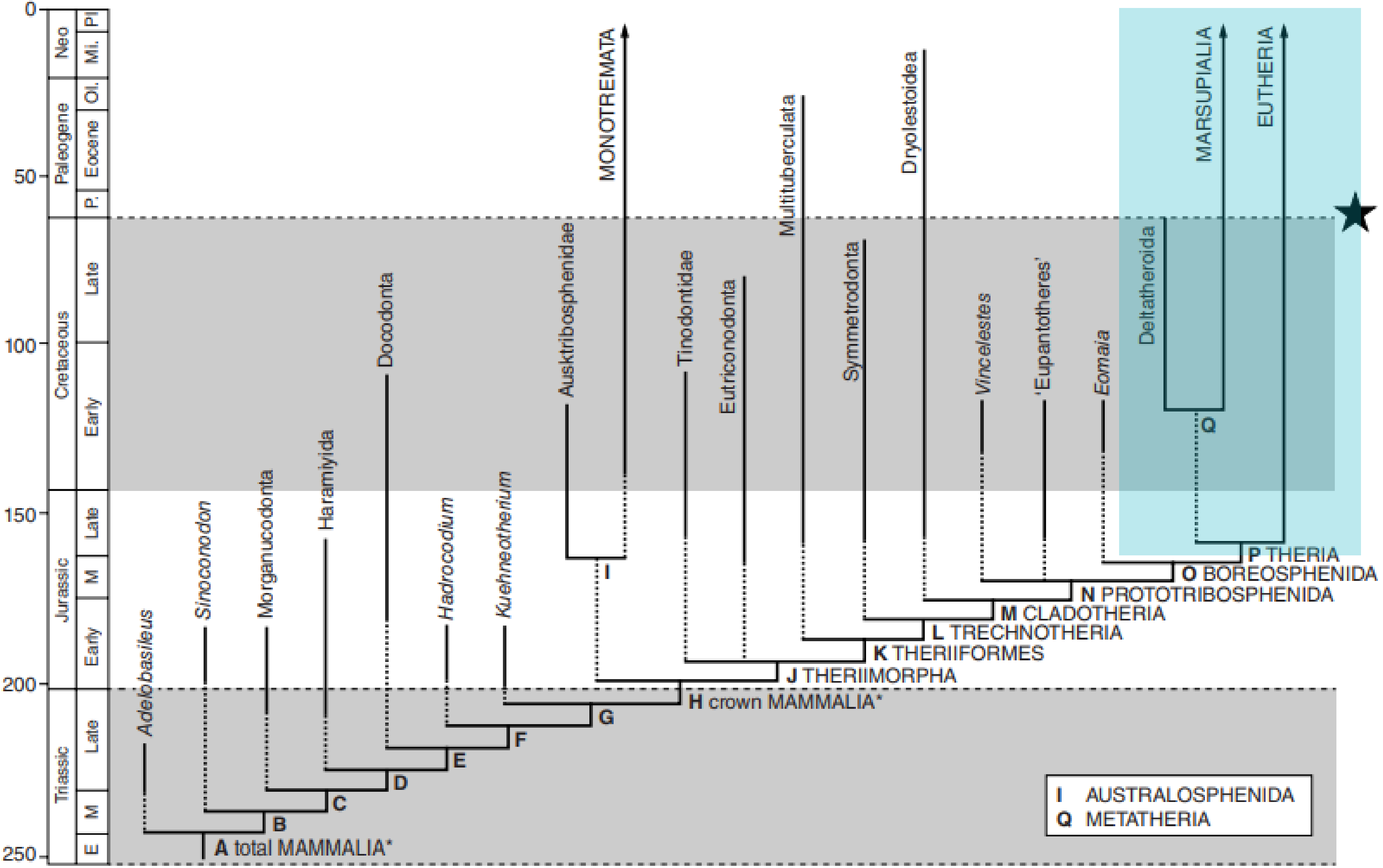
Vincelestes from the Early Cretaceous of Argentina (Hopson and Rougier, 1993; Macrini *et al*., 2007) is known from several skulls and skeletons (Figure 10.16(a)). It does not have the tribosphenic molar of Boreosphenida, but it shares with them a broad contact between the alisphenoid and the frontal, and a **cochlea** that is elongated and coiled up to 360°. The cochlea is a coiled structure in the inner ear of therian mammals (see Box 10.2, illustration II(b)), homologus with the uncoiled lagena of other tetrapods, that helps detect sound vibrations received through the three auditory ossicles, and passes them to the brain for interpretation. *Sinoconodon*, *Morganucodon*, eutriconodontans and multituberculates have uncoiled cochlear canals and monotremes have half a coil.



Eomaia

The major clade Boreosphenida, members of which have tribosphenic molar teeth (see Section 10.3.2), emerged by the Middle Jurassic, as indicated by the oldest eutherian *Juramaia* (see Section 10.3.7). The most complete basal boreosphenidan is *Eomaia* ('dawn mother') from the Early Cretaceous Yixian Formation of China. When it was first reported (Ji *et al.*, 2002), *Eomaia* was interpreted as a placental mammal, a remarkable find that extended the range of placentals by some 40 Myr. However, new phylogenetic analyses (e.g. Luo *et al.*, 2003) place it as a member of Boreosphenida, and sister to Theria (see Box 10.3). *Eomaia* is a shrew-sized animal, some 16 cm long that weighed perhaps 20 g. The exceptionally well-preserved fossil (Figure 10.16(b,c)) shows that *Eomaia* had hair, which is not a surprise. It also retains the epipubic bones that are typical of modern monotremes and marsupials, but are lost in modern placentals (see Section 10.3.4). *Eomaia* was an agile little animal and it might have been a climber – its finger and toe bones are long and the claws are strongly curved and laterally compressed, features that help in grasping twigs.

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Sinoconodon
Morganucodonta
Haramiyida
Docodonta
Hadrocodium
Kuehneotherium
Ausktribosphenidae
MONOTREMATA
Tinodontidae
Eutriconodonta
Multituberculata
Symmetrodonta
Dryolestoidea
Vincelestes
'Eupantotheres'
Eomaia
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L TRECHNOTHERIA
M CLADOTHERIA
N PROTOTRIBOSPHENIDA
O BOREOSPHENIDA
P THERIA
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