


Laurasiatheria

Por Luis Vega Jorquera
Magíster en Ciencias Biológicas


Pholidota

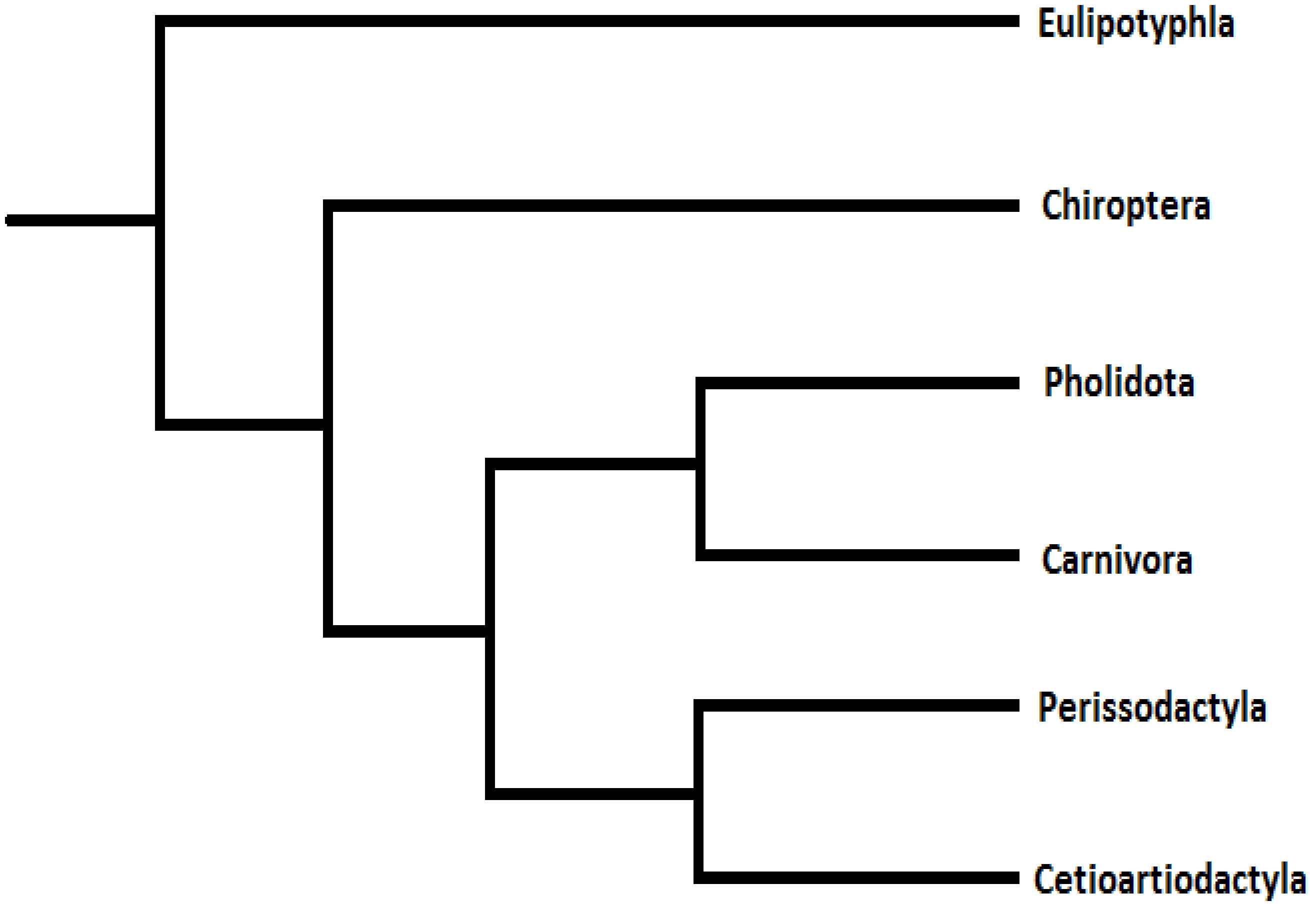
Chiroptera

Cetioartiodactyla

Carnivora

Eulipotyphla

Perissodactyla


Eulipotyphla
Chiroptera
Pholidota
Carnivora
Perissodactyla
Cetioartiodactyla

Eulipothyphla

Soricidae

Solenodontidae

Talpidae

Erinaceidae

Nesophontidae †

(a)

(b)

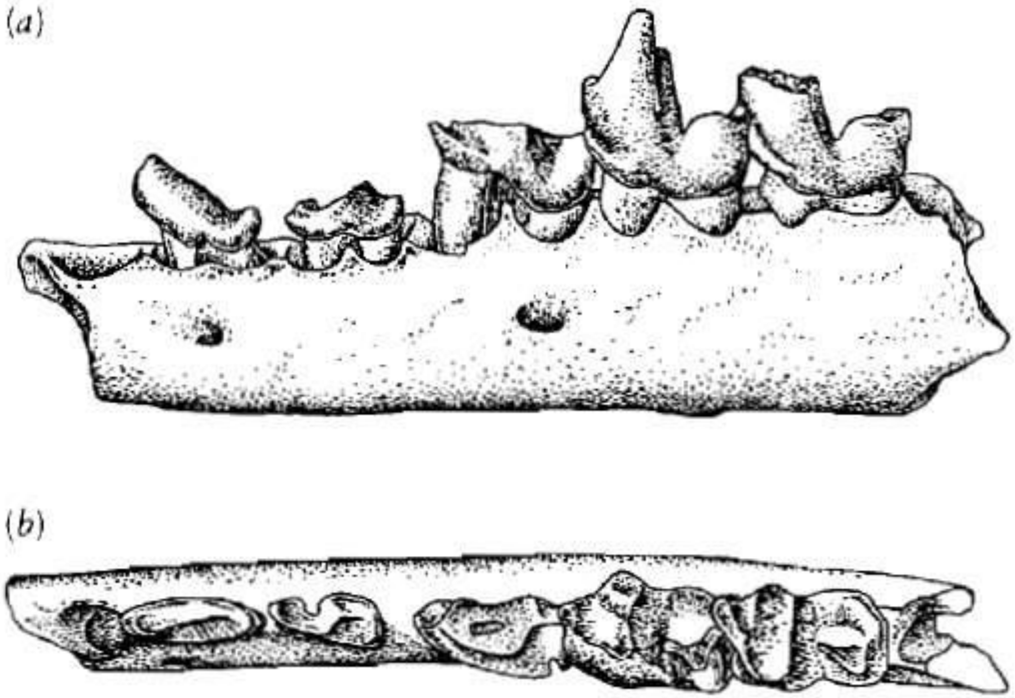
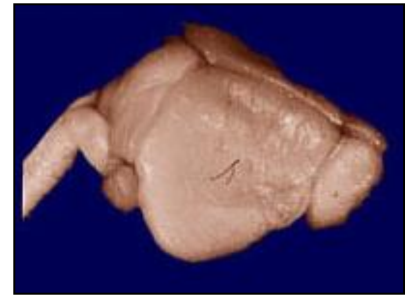


Figure 20-22. *BATODON*. Lower jaw of the possible soricomorph insectivore from the Upper Cretaceous. (*a*) Lateral and (*b*) occlusal views, ×3. *From Clemens, 1973.*

These authors recognize *Batodon* (Figure 20-22) from the Upper Cretaceous of North America as the earliest-known soricomorph on the basis of its dentition. Three

Plesiomorfías:

Biologists have long recognized that shrews, moles, hedgehogs, and their less-well-known relatives—the tenrecs and African golden mole—are among the most primitive living placentals. The brain is small, and the cerebral hemispheres are smooth and do not expand over the cerebellum. The testes are abdominal, inguinal, or in a sac in front of the penis. Some genera retain a cloaca. The skull is primitive in the absence of a postorbital bar and the auditory bulla is rarely ossified. The number and configuration of the teeth in primitive genera resemble the pattern in the early "Proteutheria." The feet are usually plantigrade and pentadactyl, with the pollex and hallux not opposable.



Sinapomorfías:

The following are shared derived characters of the Insectivora as so restricted. The pattern of the skull wall medial to the orbit is modified in association with the small size of the eye and the relatively large nasal capsule. The maxilla is widely expanded, but the palatine is much reduced. The lacrimal has no facial wing. The orbitosphenoid is anterior to the braincase. The jugal is absent or markedly reduced. In several groups, the zygomatic arch is lost or incomplete. A postglenoid foramen is usually present for passage of the external jugular vein. There is a large pyriform fenestra between the otic capsule and the basisphenoid and the bony dorsum sellae is absent. The pubic symphysis is reduced.

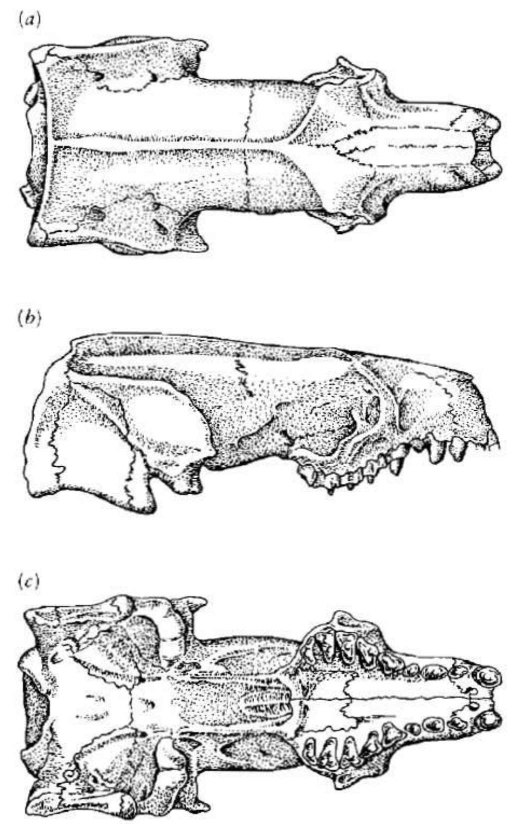
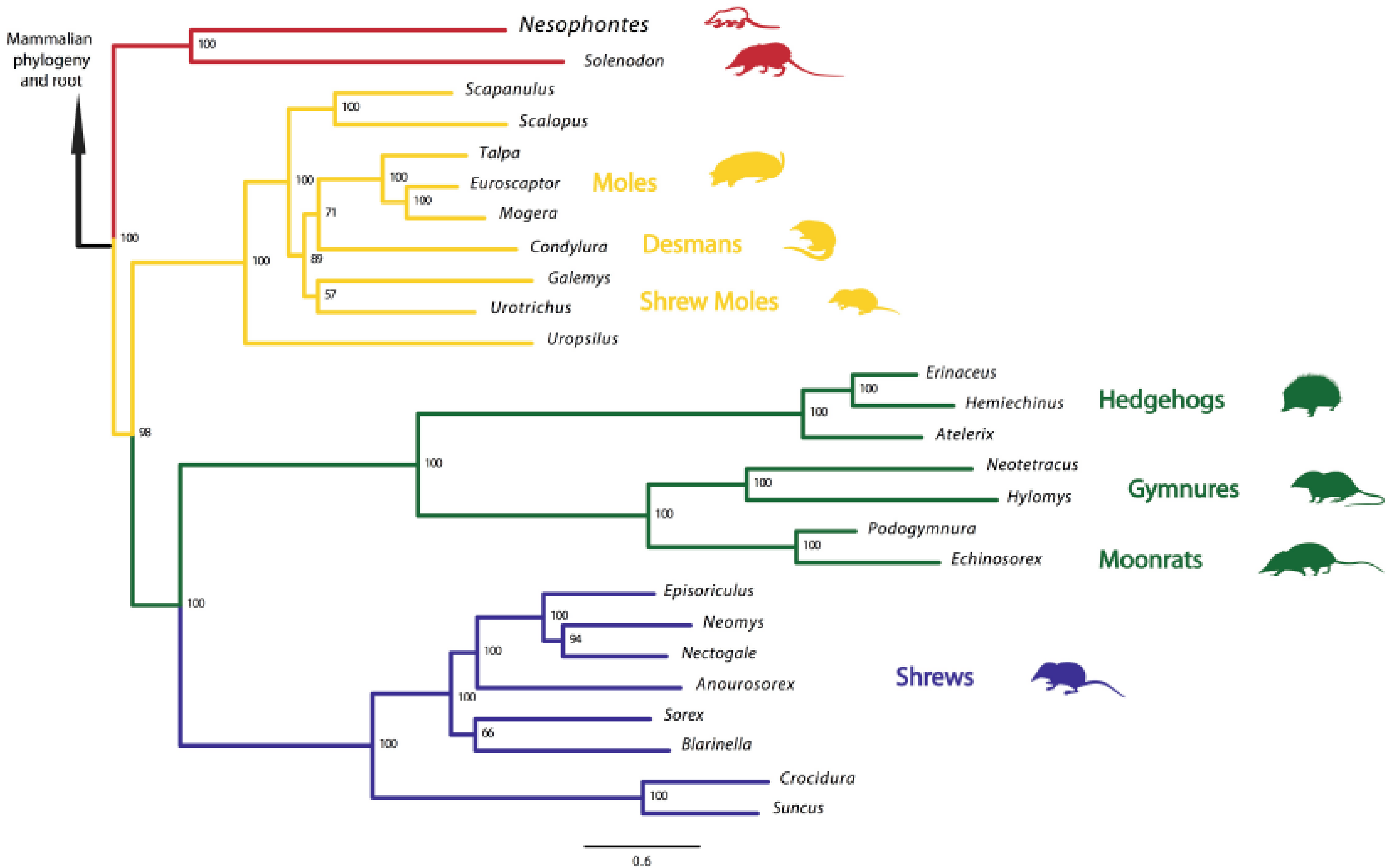


Figure 20-23. SKULL OF *APTERNODUS*, A PRIMITIVE INSECTIVORE. (*a*) Dorsal, (*b*) lateral, and (*c*) palatal views. *From McDowell, 1958.*



Mammalian phylogeny and root
Nesophontes
Solenodon
Scapanulus
Scalopus
Talpa
Euroscaptor
Mogera
Moles
Condylura
Desmans
Galemys
Urotrichus
Shrew Moles
Uropsilus
Erinaceus
Hemiechinus
Hedgehogs
Atelerix
Neotetracus
Gymnures
Hylomys
Podogymnura
Echinosorex
Moonrats
Episoriculus
Neomys
Nectogale
Anourosorex
Shrews
Sorex
Blarinella
Crocidura
Suncus
0.6

Solenodon

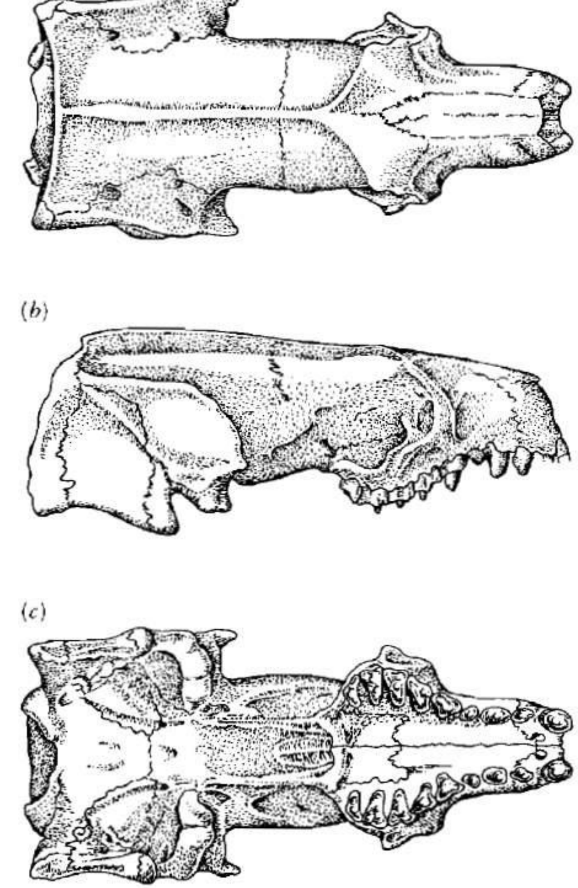


Figure 20-23. SKULL OF *APTERNODUS*, A PRIMITIVE INSECTIVORE. (*a*) Dorsal, (*b*) lateral, and (*c*) palatal views. *From McDowell, 1958.*

Diente dilambdóntido: Cúspides en forma de W

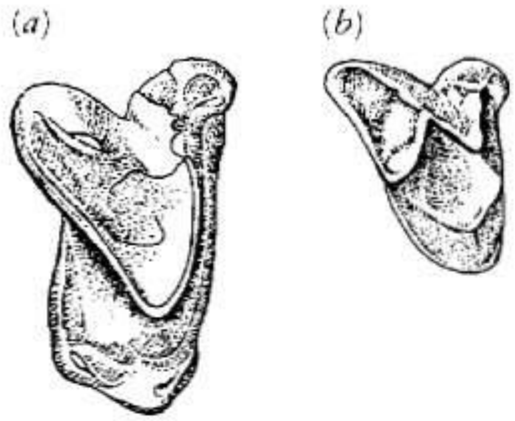
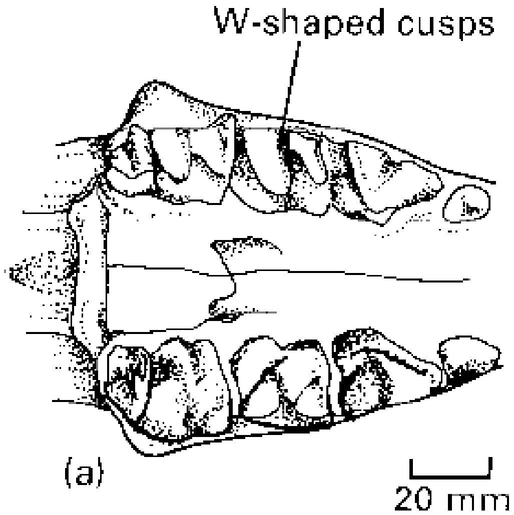


Figure 20-24. ZALAMBDONTY AND DILAMBDONTY AS ILLUSTRATED BY THE UPPER MOLARS OF INSECTIVORES. (*a*) The zalambdont molar of *Solenodon* and (*b*) the dilambdont molar of *Nesophontes*. From McDowell, 1958.

Diente dilambdóntido convergente con stem placentarios (*Zalambdalestes* , *Palaeoryctes*) y marsupiales (*Necrolectes, Notoryctes*)

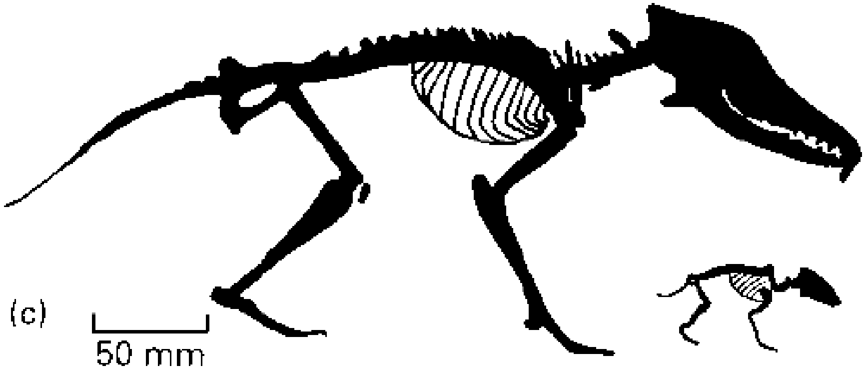
Talpidae

The shrews (soricomorphs) arose in the Mid-Palaeocene. Late Cretaceous records of insectivores are debated (Archibald, 2003). The palate of the Oligocene shrew *Domnina* (Figure 10.30(a)) shows the W-shaped pattern of ridges on the upper molar teeth that is typical of the group. The moles, closely related to the shrews, arose in the Eocene. The forelimbs, which are used in burrowing, are broad and paddle-like, and the mole humerus (Figure 10.30(b)) is a very characteristic broad bone with large processes for the attachment of powerful muscles.

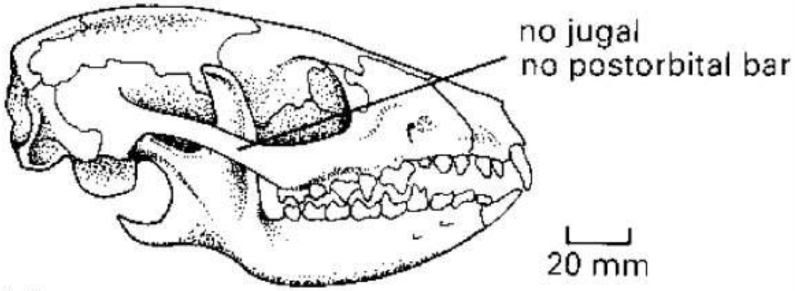


Erinaceidae

The hedgehogs (erinaceomorphs) arose in the Eocene. The most spectacular hedgehog was *Deinogalerix*, a long-limbed dog-sized animal (Figure 10.30(c)) from the late Miocene, which was probably covered with stiff hair rather than spines (modified hairs). *Deinogalerix* was five times as long as the European hedgehog *Erinaceus* and it must have been a dramatic sight as it charged about the hot grasslands of southern Italy. The skull of *Erinaceus* (Figure 10.30(d)) shows some derived characters of the Insectivora (Butler, 1988), such as the loss of the jugal and the absence of a postorbital process (present in most placentals).



(c)

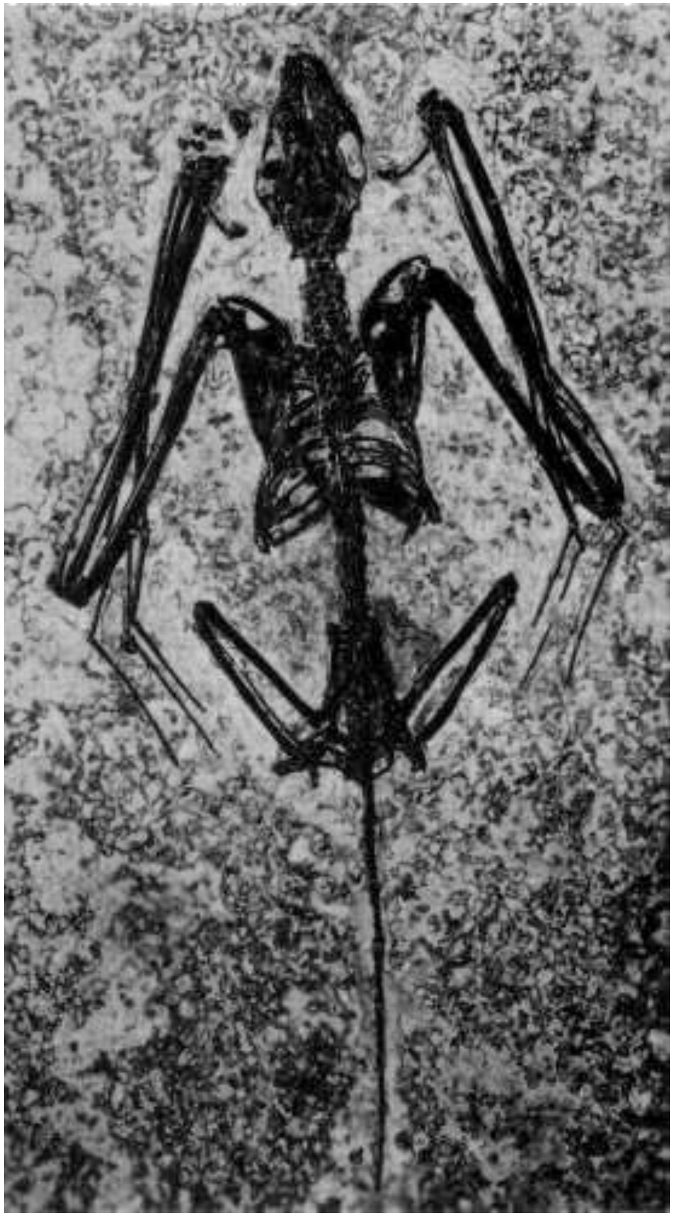


(d)

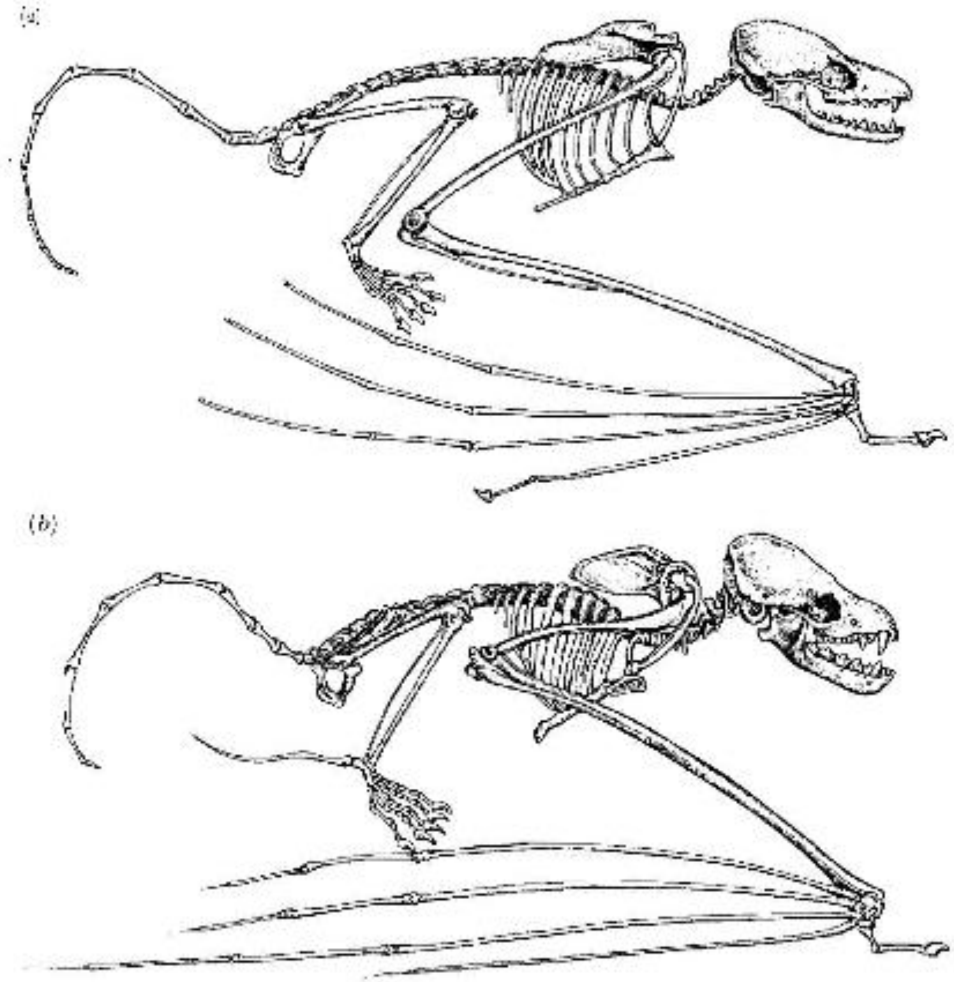
Chiroptera

Bat remains have been found in the latest Palaeocene, but the oldest well-known form is the early Eocene *Icaronycteris* (Figure 10.30(e)). Already all the key microchiropteran features are there: the humerus, radius (and fused ulna) and digits are all elongated, and the flight membrane is supported by the spread fingers 2–5 (digit 1, the thumb, is much shorter). The shoulder girdle is modified to take the large flight muscles on the expanded scapula on the back and the broad ribs and sternum on the front. The hindlimbs are strong, and the feet are turned backwards so that *Icaronycteris* could hang upside down as modern bats do. The eyes are large and the ear region shows specializations for echolocation. The modern bat groups arose mainly in the late Eocene and Oligocene, but remains are often scrappy.

The teeth of earlier bats, from the Paleocene of France, which Russell, Louis, and Savage (1973) described, show a pattern that could be readily derived from that of Upper Cretaceous eutherians such as *Cimolestes*, with transversely expanded upper molars and the talonid well lower than the trigonid. The presence of a W-shaped ectoloph corresponds closely to the pattern of mid-Paleocene to late Eocene nyctitheriid soricomorphs (Figure 20-28). This finding provides the strongest evidence for specific insectivore-bat affinities and is not contradicted by other skeletal features.



Icaronycteris



great elongation of digits 2 through 5. The scapula has assumed a dorsal position. As in modern bats, most of the cranial sutures are obliterated. A relatively small number of features are less well developed than in modern bats. The dental formula of

$$\frac{2\quad 1\quad 3\quad 3}{3\quad 1\quad 3\quad 3}$$

includes one or more teeth that are lost in all modern bats. The ribs have not coalesced and the elements of the sternum are neither fused nor keeled. A primitive phalangeal count of 2, 3, 3, 3, 3 is retained in both the forelimbs and rear limbs. The terminal phalanges of digits 2 through 5 of the manus are very short and blunt, whereas they are more slender in modern bats.

Figure 20-27. BATS. (*a*) The early Eocene bat *Icaronycteris*. (*b*) The modern bat *Myotis*. Both × 1. *From Jepsen, 1970.*

- Presenta alas adaptadas para el vuelo, pero la morfología del oído sugiere ausencia de ecolocación.
- Principios de quilla en el manubrium
- Garras en todos los dedos

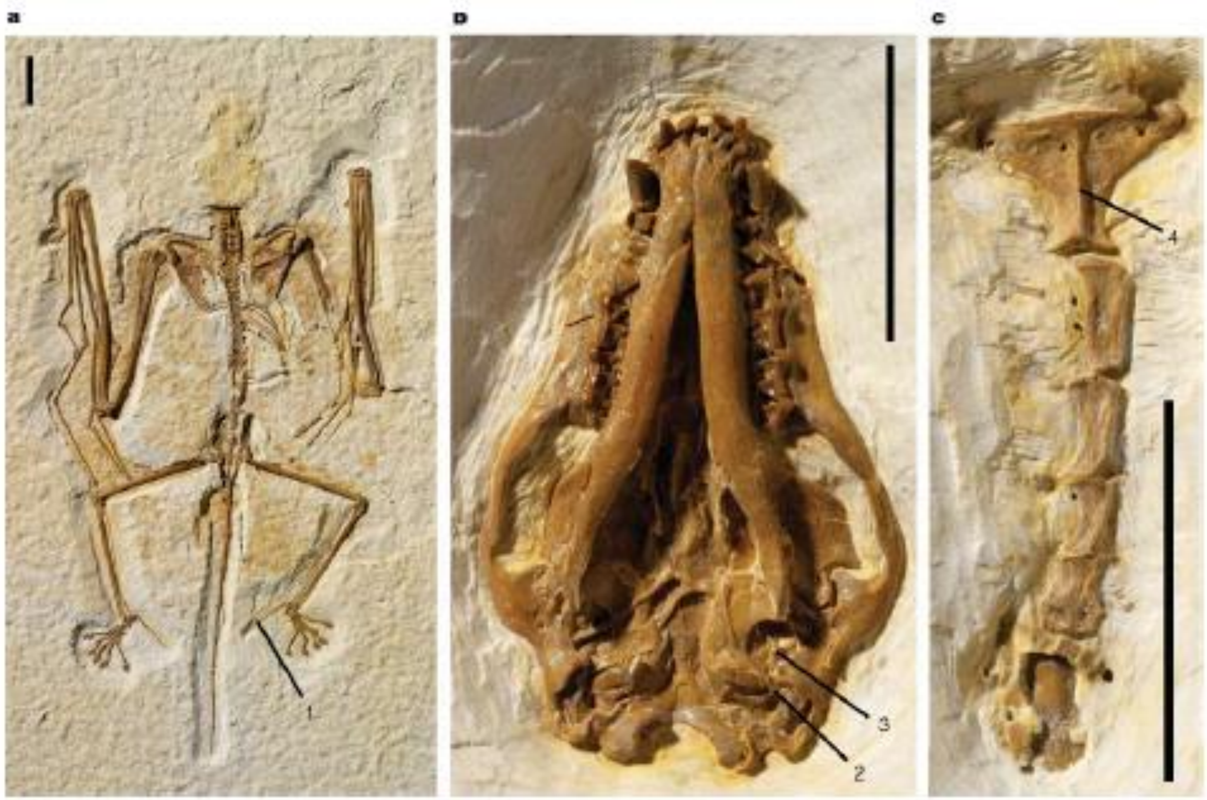


Figure 1 | Holotype of *Onychonycteris finneyi* (ROM 55351A). **a**, Skeleton in dorsal view. **b**, Skull in ventral view. **c**, Sternum in ventral view. Scale bars, 1 cm. All elements are preserved on a single slab with the skeleton exposed on one side, and the skull and sternum on the reverse. The counter-part slab (ROM 55351B, not shown) preserves impressions of parts of the dorsal aspect of the skeleton. Features labelled: 1, calcar; 2, cranial tip of stylohyal; 3, orbicular apophysis of malleus; 4, keel on manubrium of sternum.

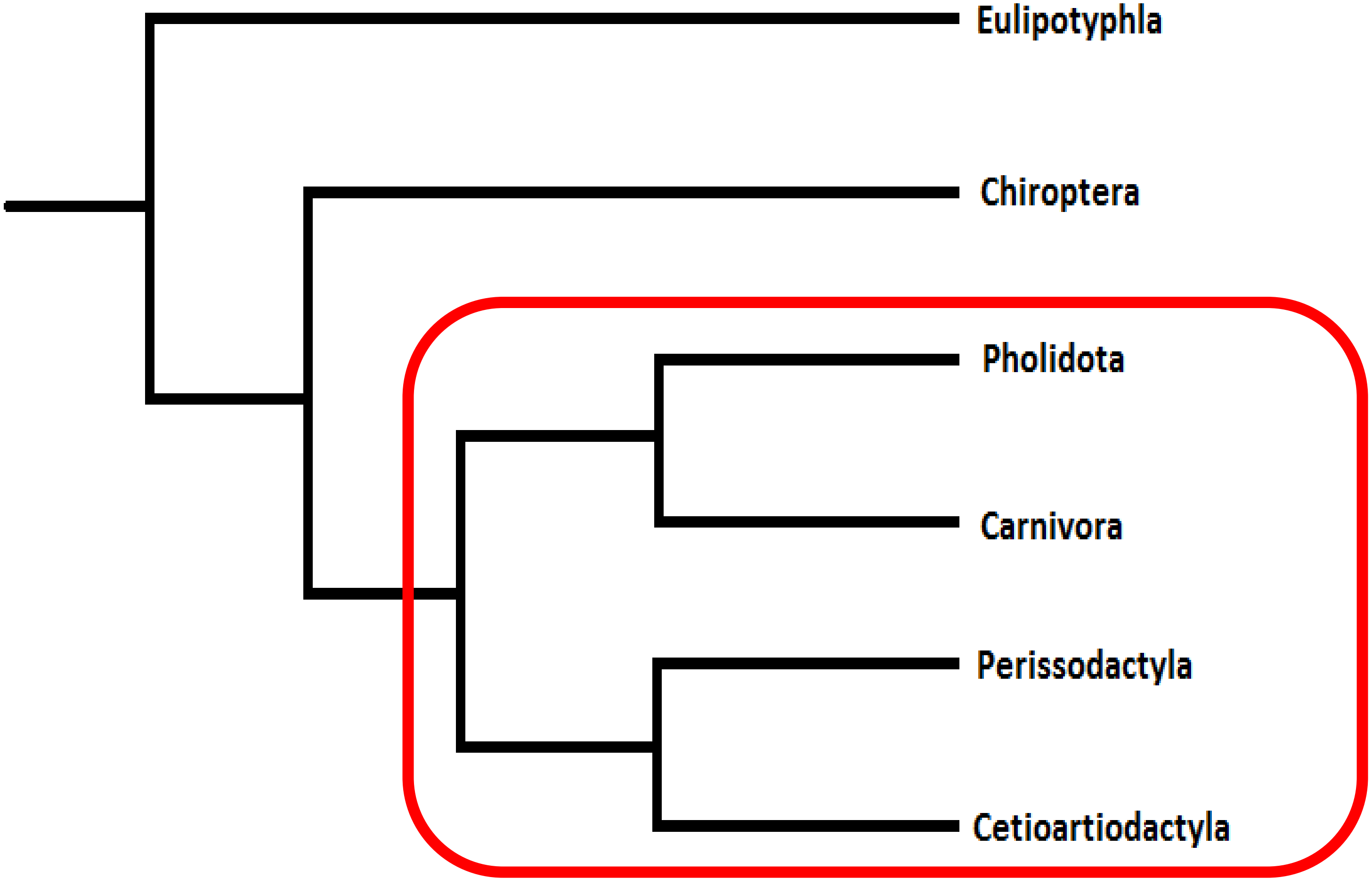
En un momento se sugirió que podrían ser 2 grupos separados, que inventaron el vuelo independientemente.

Evidencia molecular sugiere que Microchiroptera es parafilético, y que Megachiroptera estaría anidado dentro del grupo de todos los demás murciélagos.

Microchiroptera

Megachiroptera

Feruungulata:



“Condylarthros”: Grupo parafilético, incluye taxa basales de feruungulata que no pertenecen otros grupos más específicos.

Presentan características tanto de herbívoros como carnívoros.

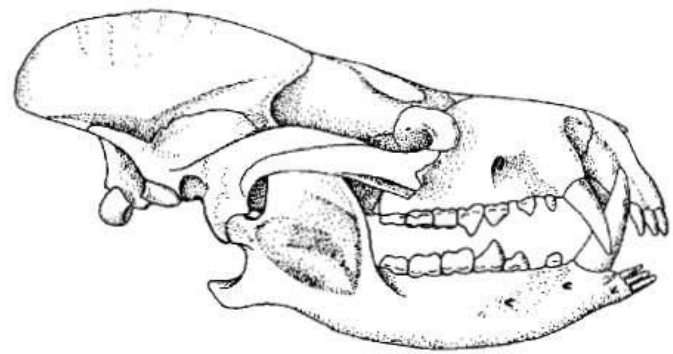
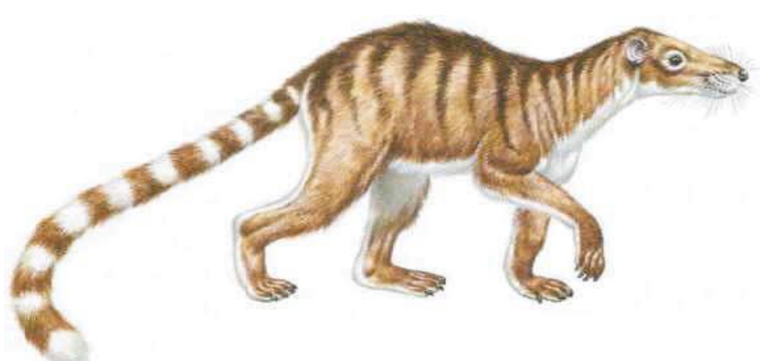
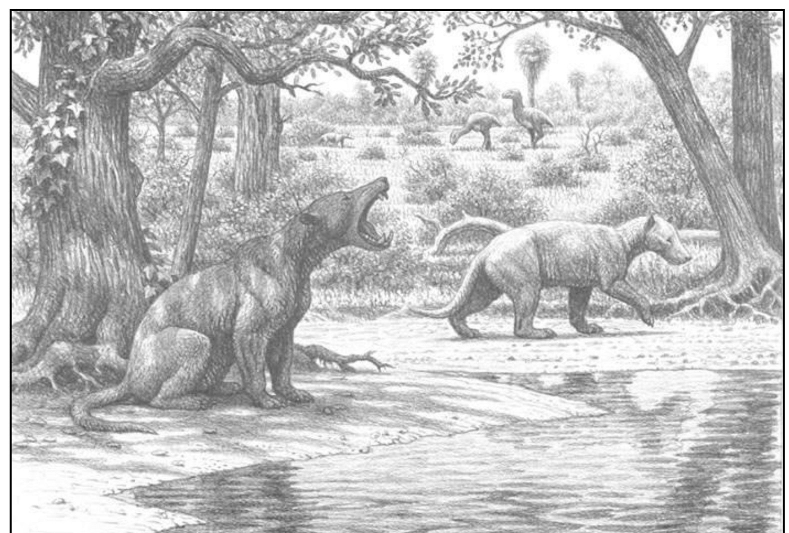


Figure 21-2. SKULL OF *ARCTOCYON*, A PRIMITIVE CONDYLARTH, ×¼. *From Russell, 1964.*



Chriacus



Arctocyon

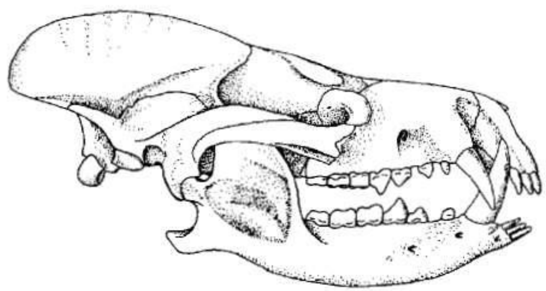


Figure 21-2. SKULL OF *ARCTOCYON*, A PRIMITIVE CONDYLARTH, ×⅓. *From Russell, 1964.*

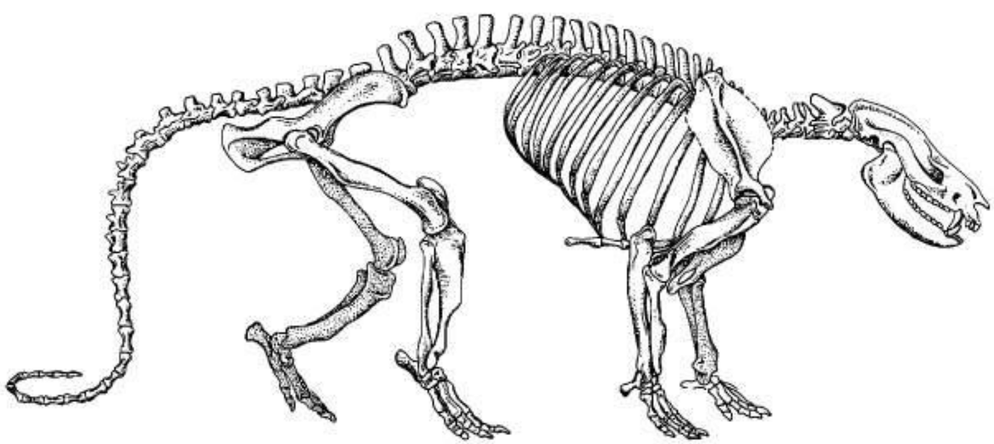
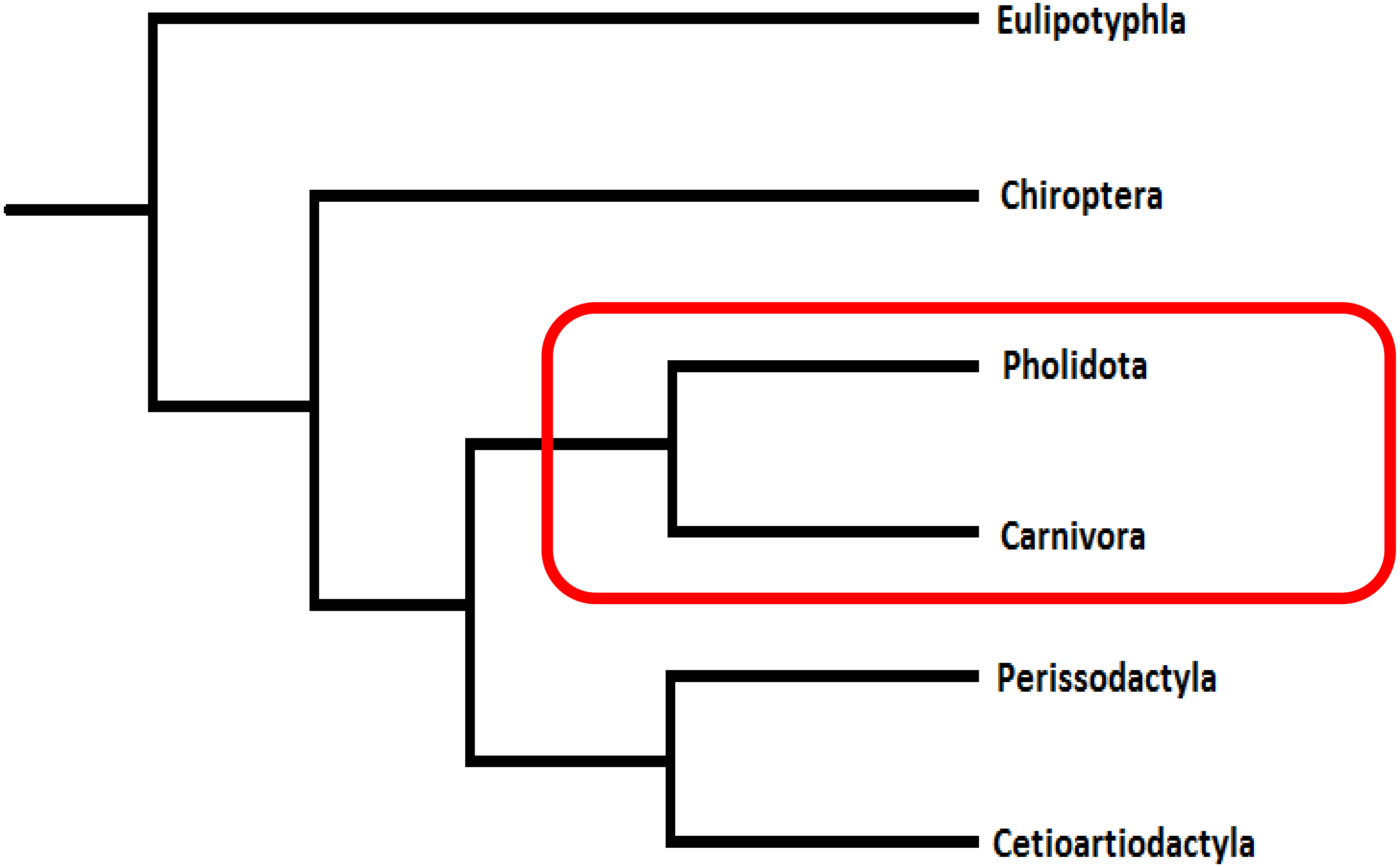
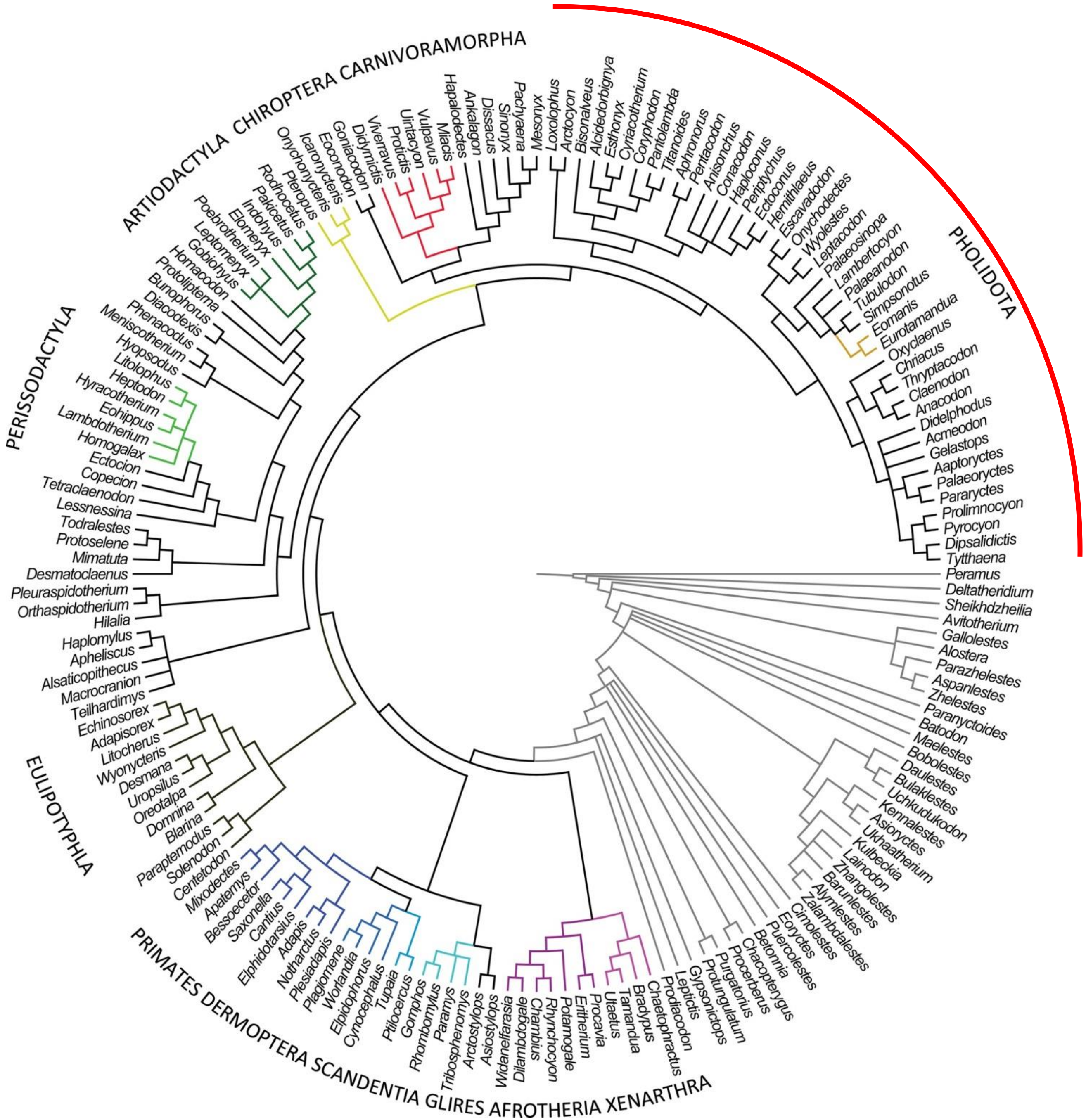


Figure 21-4. SKELETON OF THE PALEOCENE CONDYLARTH *ECTOCONUS*. This genus exemplifies the primitive pattern for ungulates. Length about 2 meters. *From Gregory, 1951 and 1957.*

Condylarths represent a grade of ungulate evolution that is more advanced than Zhelestidae but less so than extant ungulate groups. They seem to have few, if any, derived characteristics that are not also found in one or more of the more advanced ungulate taxa. Most condylarths have rather generalized skulls with moderately long snouts and prominent sagittal and occipital crests. The dental formula is usually unreduced from the primitive condition (3.1.4.3/3.1.4.3), and the canines are generally prominent. The molars of most condylarths are broad, low-crowned, and bunodont, with narrow stylar shelves, low mesiodistally compressed trigonids, and rather broad talonid basins. The conules tend to be prominent, and a hypocone is variably developed. The incisors and premolars are usually simple, although the last premolar is often molarized. These dental features suggest an omnivorous diet that included an increasing proportion of vegetable matter. The skeleton is also generalized, with moderately robust limbs that are usually neither elongate nor much shortened, and pentadactyl feet, which bore hoofs in some forms but claws in others. Most were terrestrial, with some, such as phenacodontids, showing incipient cursorial features; others (many arctocyonids) were adapted for scansorial or arboreal lifestyles.

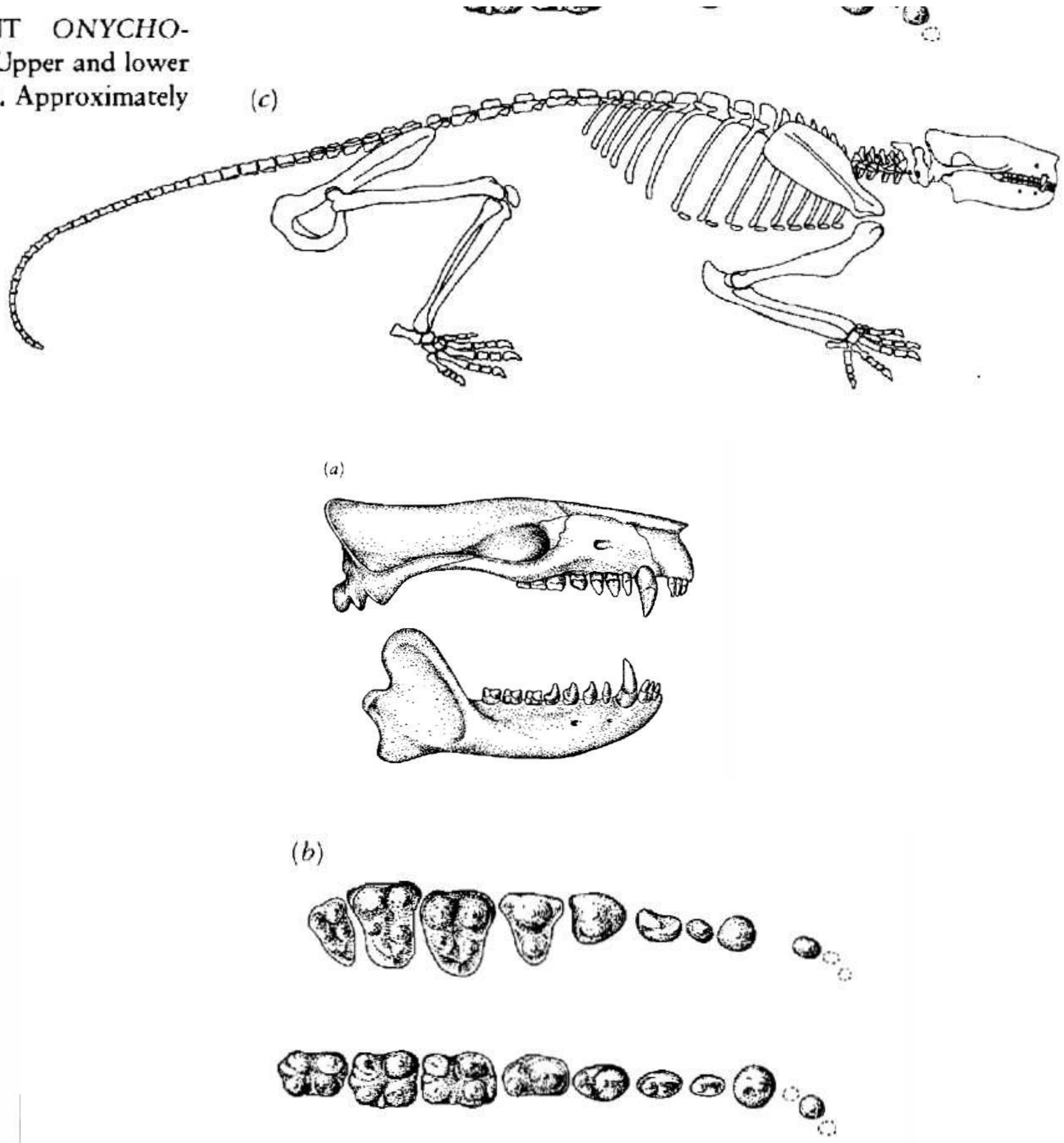
Ferae:


Eulipotyphla
Chiroptera
Pholidota
Carnivora
Perissodactyla
Cetioartiodactyla


ARTIODACTYLA CHIROPTERA CARNIVORAMORPHA
PHOLIDOTA
PERISSODACTYLA
EULIPOTYPHLA
PRIMATES DERMOPTERA SCANDENTIA GLIRES AFROTHERIA XENARTHRA
Onychonycteris
Icaronycteris
Eoconodon
Goniacodon
Didymictis
Viverravus
Protictis
Uintacyon
Vulpavus
Miacis
Hapalodectes
Ankalagon
Dissacus
Sinonyx
Pachyaena
Mesonyx
Loxolophus
Arctocyon
Bisonalveus
Alcidedorbignya
Esthonyx
Cyriacotherium
Coryphodon
Pantolambda
Titanoides
Aphronorus
Pentacodon
Anisonchus
Conacodon
Haploconus
Periptychus
Ectoconus
Hemithlaeus
Escavadodon
Onychodectes
Wyolestes
Leptacodon
Palaeosinopa
Lambertocyon
Palaeanodon
Tubulodon
Simpsonotus
Eomanis
Eurotamandua
Oxyclaenus
Chriacus
Thryptacodon
Claenodon
Anacodon
Didelphodus
Acmeodon
Gelastops
Aaptoryctes
Palaeoryctes
Pararyctes
Prolimnocyon
Pyrocyon
Dipsalidictis
Tytthaena
Peramus
Deltatheridium
Sheikhdzheilia
Avitotherium
Gallolestes
Alostera
Parazhelestes
Aspanlestes
Zhelestes
Paranyctoides
Batodon
Maelestes
Bobolestes
Daulestes
Bulaklestes
Uchkudukodon
Kennalestes
Asioryctes
Ukhaatherium
Kulbeckia
Lainodon
Zhangolestes
Barunlestes
Alymlestes
Zalambdalestes
Cimolestes
Eoryctes
Puercolestes
Betonnia
Chacopterygus
Procerberus
Purgatorius
Protungulatum
Gypsonictops
Leptictis
Prodiacodon
Chaetophractus
Bradypus
Tamandua
Ulaetus
Procavia
Eritherium
Potamogale
Rhynchocyon
Chambius
Dilambdogale
Widanelfarasia
Asiostylops
Arctostylops
Tribosphenomys
Paramys
Rhombomylus
Gomphos
Ptilocercus
Tupaia
Cynocephalus
Elpidophorus
Worlandia
Plagiomene
Plesiadapis
Notharctus
Adapis
Elphidotarsius
Cantius
Saxonella
Bessoecetor
Apatemys
Mixodectes
Centetodon
Solenodon
Parapternodus
Blarina
Domnina
Oreotalpa
Uropsilus
Desmana
Wyonycteris
Litocherus
Adapisorex
Echinosorex
Teilhardimys
Macrocranion
Alsaticopithecus
Apheliscus
Haplomylus
Hilalia
Orthaspidotherium
Pleuraspidotherium
Desmatoclaenus
Mimatuta
Protoselene
Todralestes
Lessnessina
Tetraclaenodon
Copecion
Ectocion
Homogalax
Lambdotherium
Eohippus
Hyracotherium
Heptodon
Litolophus
Hyopsodus
Meniscotherium
Phenacodus
Diacodexis
Burophorus
Protolipterna
Homacodon
Gobiohyus
Leptomeryx
Poebrotherium
Elomeryx
Indohyus
Pakicetus
Rodhocetus
Pteropus

Taeniodonta:

Figure 20-13. THE PRIMITIVE TAENIODONT *ONYCHODECTES*. (*a*) Skull and lower jaw in lateral view. (*b*) Upper and lower dentition in occlusal view. (*c*) Skeleton in lateral view. Approximately the size of an opossum. *From Schoch, 1982.*



eton. The limbs are moderately long but without evidence of cursorial adaptations. They may have been adept at climbing and had some capacity for digging. The ulna and radius are unreduced and unfused. The carpals are unreduced, unfused, and alternating. One specialization is the elaboration of the astragalocalcaneal complex for extreme plantar flexion, a character shared with the leptictids, *Cimolestes* and *Procerberus*. The feet are plantigrade, with five digits each bearing unfissured claws. The tail is long and heavy.

The skull is primitive in the absence of a postorbital bar. The dentition is complete, without trace of a diastema, and the canine is only moderately enlarged. The cheek teeth are primitive in their basically tritubercular configuration. The premolars are sectorial, but the molar cusps are reduced, as would be appropriate in an animal that grinds its food. More importantly, the cheek teeth are higher crowned than in primitive eutherians, with the enamel extending lingually on the upper molars and labially on the lowers to provide the greater wearing surfaces necessary for an omnivorous to herbivorous diet. The upper molars are transversely narrow, with the protocones, protoconules, and metaconules small and lingually placed; the stylar shelves are reduced. In contrast with most other herbivorous groups, neither the upper nor the lower teeth have cingula primitively, and the hypocone is absent.

Taeniodonta:

By the early Eocene, genera such as *Stylinodon* (Figure 20-14) had become highly specialized in their dentition and postcranial skeleton and reached the size of a bear. Patterson (1949) suggested that the rate of evolution of the dentition, illustrated through a series of progressive stages, may have been among the most rapid in any mammalian group. In *Stylinodon*, all the teeth are rootless and ever growing. One upper and one lower incisor have been lost. The canine is by far the largest tooth. Like the incisors, it bears enamel only on the anterior surface, which forms a sharp, chisel-like blade. The canine is greatly expanded posteriorly in a manner that is unique among mammals to provide a large crushing surface. The premolars are molariform and all the cheek teeth rapidly lose their crowns through wear, so they appear as cylinders of dentine with only a thin surrounding edge of enamel.

The diet of taeniodonts was tough and highly abrasive. The well-developed claws, especially on the forelimbs, and the elaboration of large areas for muscle attachment suggest that they were used for digging food from the ground. Schoch suggested that the advanced taeniodonts may have resembled the aardvark in digging abilities.

The fossil record of taeniodonts is entirely limited to western North America. Previous reports from other areas are based on misidentified specimens. They are not known after the middle Eocene. Schoch and Lucas (1981) suggest that their rarity in most localities may be due to their living in a poorly sampled environment, such as the uplands, away from the typical areas of deposition.

Lillegraven (1969) and McKenna (1973) suggest that taeniodonts may be the sister group of *Cimolestes*.

(c)

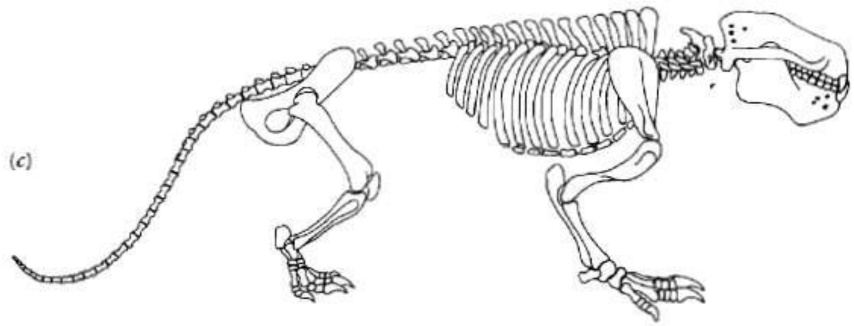
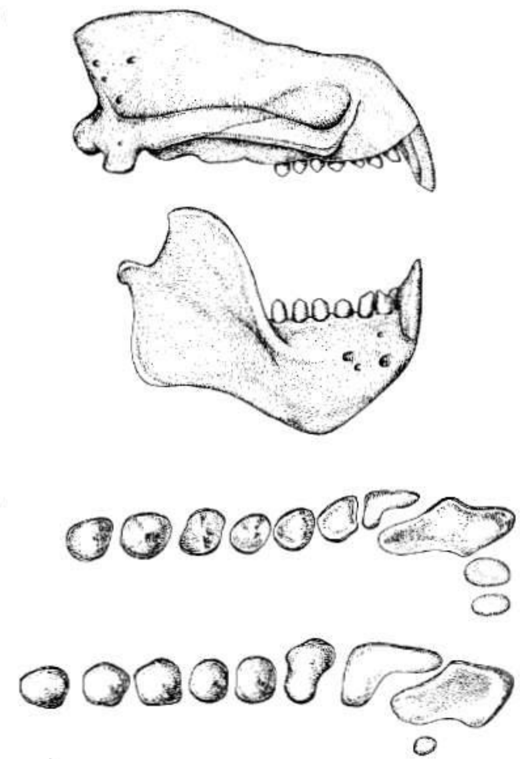
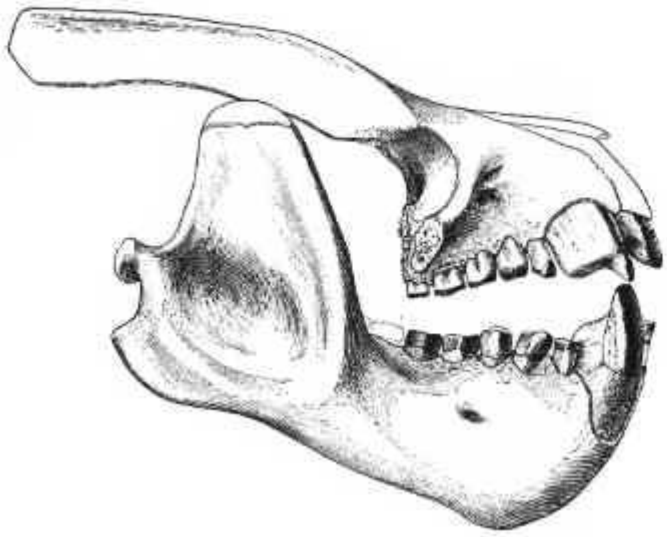


Figure 20-14. THE ADVANCED TAENIODONT *STYLINODON*. (*a*) Skull in lateral view. (*b*) Upper and lower dentition in occlusal view. (*c*) Skeleton the size of a bear. *From Schoch, 1982.*

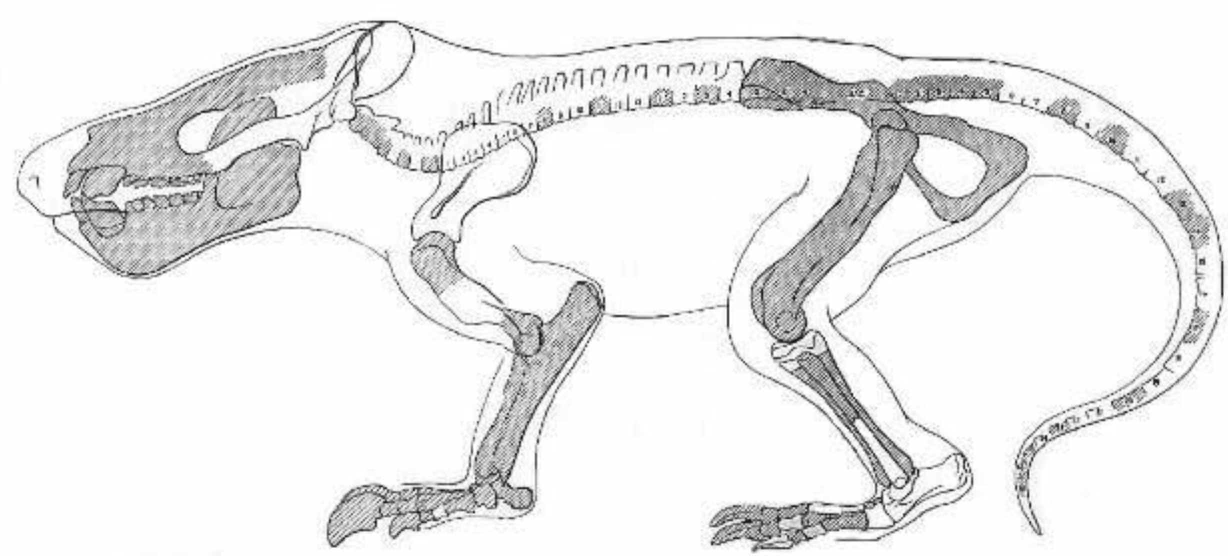
(a)

(b)





Psittacotherium



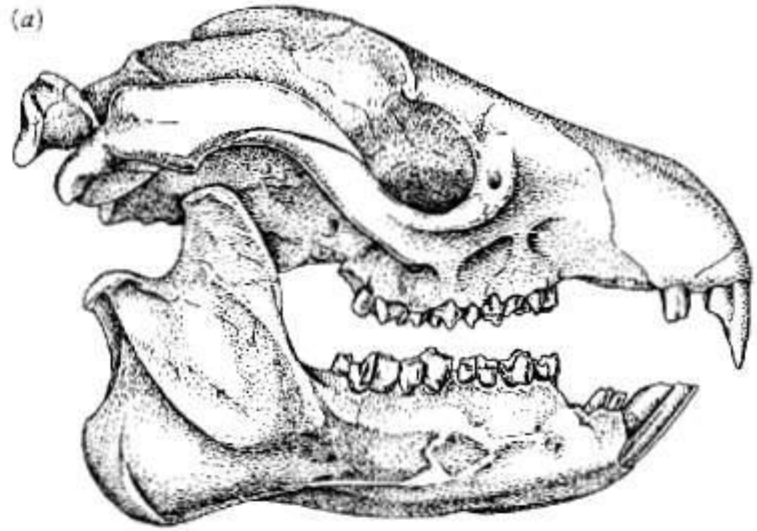
Tillodontia:

The tillodonts constitute a second group of rare herbivores that were once thought to be closely related to the taeniodonts. They too have chisel-shaped anterior teeth, but the most highly specialized teeth are the second incisors, not the canines. It is clear that herbivorous adaptations occurred separately in these two groups and not from a similarly specialized common ancestor.

meters long. The second incisors are greatly enlarged, rootless, and ever growing. Like the incisors of taeniodonts, the enamel is limited to the anterior surface. The other anterior teeth are reduced or lost, leaving a wide diastema anterior to the cheek teeth. The buccal side of the lower cheek teeth and the lingual side of the uppers are arcuately columnar, while the opposite side bears low cusps. They are rapidly worn away, which suggests a highly abrasive diet. Gazin (1953) hypothesized a rodentlike anterior-posterior excursion of the mandible.

The skull is primitive in the small size of the braincase and absence of a postorbital bar, but the basicranium is shorter than in primitive eutherians.

(a)



(b)

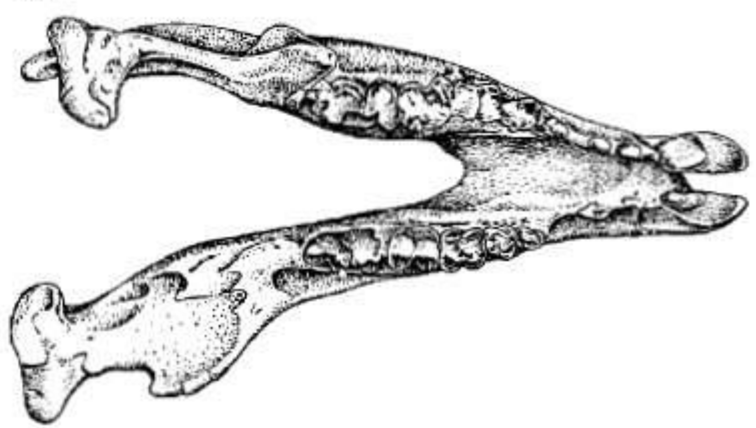
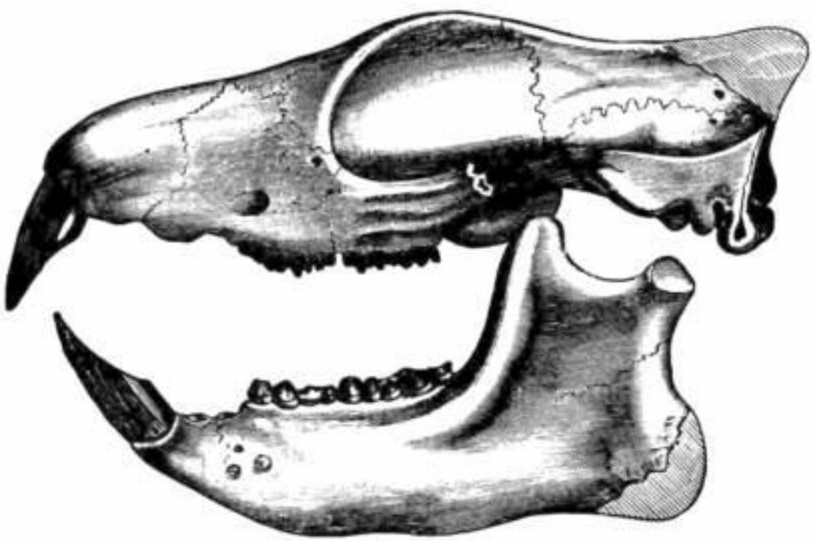


Figure 20-15. (a) Skull of the Eocene tillodont *Trogosus*, 30 centimeters long. (b) Lower jaw of *Tillodon* in occlusal view. *From Gazin, 1953. By permission of Smithsonian Institution Press, Smithsonian Institution, Washington, D.C.*



Tillodon

Trogosus

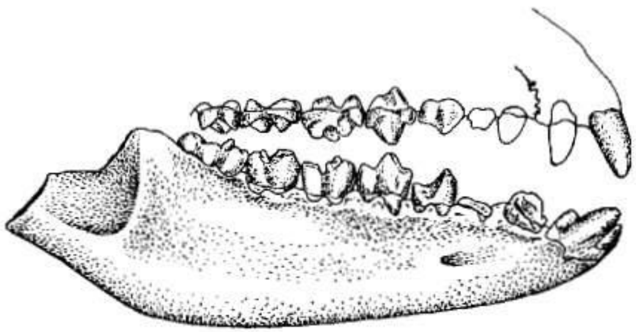


Figure 20-16. The dentition of the Lower Eocene tillodont, *Esthonyx* × ⅔. *From Gazin, 1953. By permission of Smithsonian Institution Press, Smithsonian Institution, Washington, D.C.*

Gunnell, 1979; Stucky and Krishtalka, 1983) shows the initial elaboration of the second incisors, but a diastema has not yet developed. When unworn, the cheek teeth show a primitive pattern that is not far removed from Upper Cretaceous eutherians, except for greatly expanded hypoconal and periconal shelves.

talonid. Derived features shared by tillodonts and *Deltatherium* include reduction of the entoconid and upper molar conules and hypertrophy of the upper molar parastylar and metastylar shear surfaces.

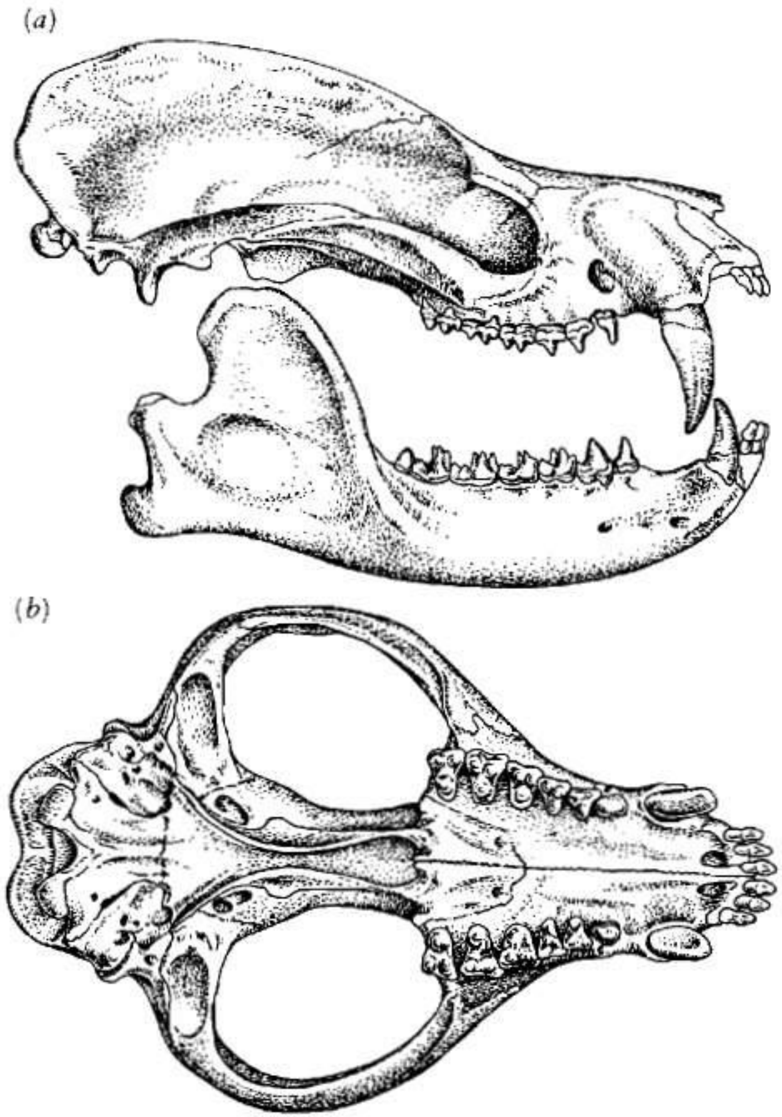


Figure 20-17. SKULL OF THE PRIMITIVE EUTHERIAN *DELTATHERIUM*. (*a*) Lateral and (*b*) palatal views. This genus has long been classified among the ungulates, but the dentition retains the features of "proteutherians." *From Matthew, 1937.*

Pantodontidae:

The pantodonts were a much more diverse and well-known assemblage. Eleven families are recognized from the Paleocene and they extend into the Lower Oligocene in Asia. Early knowledge was based primarily on large forms from North America, including the sheep-sized *Pantolambda* (Figure 20-18) and the rhinoceros-sized *Titanoides* (Figure 20-19) and *Coryphodon*. The limbs are short and stout. The feet are generally primitive, with five spreading digits. *Titanoides* bears claws, but other genera have small hoofs.

Our knowledge of pantodonts has recently been greatly expanded by the discovery in Asia of a number of smaller forms, some as little as a rat (Chow, Chang, Wang, and Ting, 1977). *Bemalambda* is one of the best-known members of the order. Another genus may have had a tapirlike proboscis (Ting, Schiebout, and Chow, 1982).

The dentition is primitively complete without a diastema. All genera can be recognized by the V-shaped lophs on upper premolars 3 and 4, and the W-shaped pattern of the molar lophs. The teeth show relatively little wear, which suggests a nonabrasive diet (Coombs, 1983).

Cifelli suggested that the pantodonts and tillodonts evolved separately from forms like *Deltatherium*. Zhou and Wang (1979) suggested a common ancestry in the Upper Cretaceous. McKenna (1975) traced pantodonts directly to *Cimolestes*, in common with taeniodonts, but associates tillodonts with primitive ungulates.

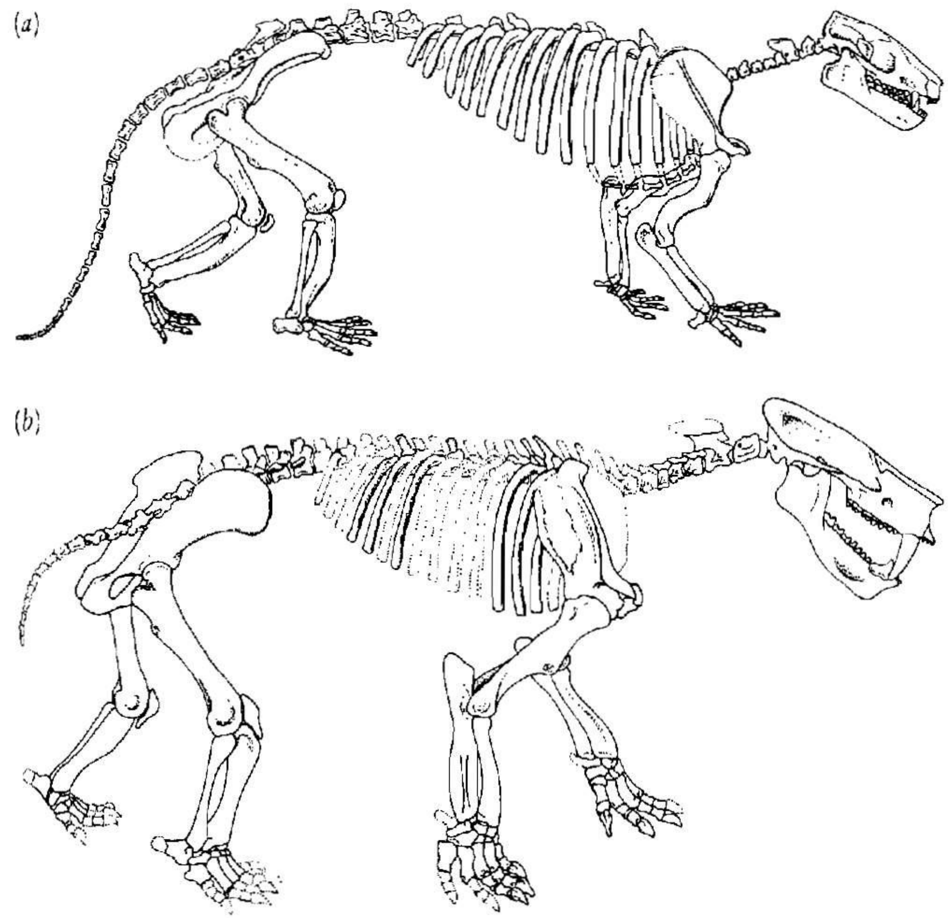
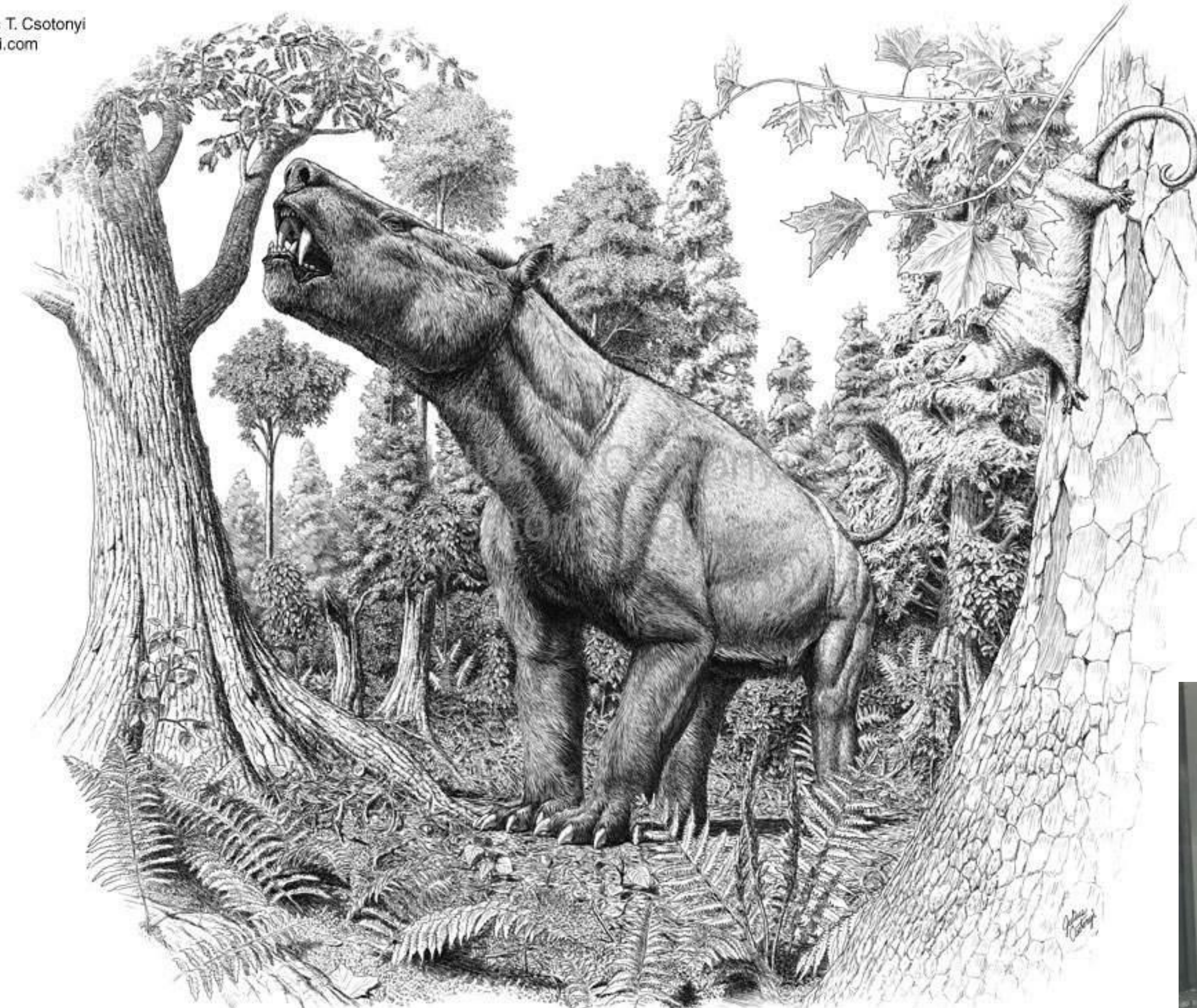


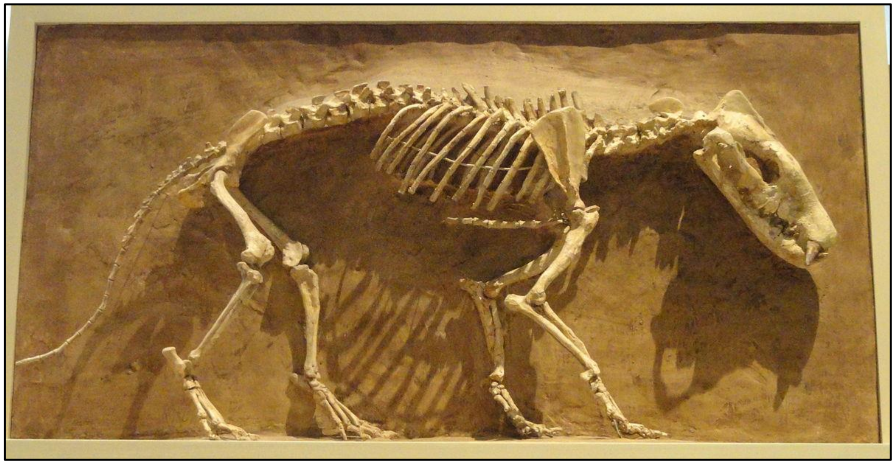
Figure 20-19. PANTODONTS. (*a*) Skeleton of *Pantolambda*, $\times \frac{1}{12}$. (*b*) Skeleton of the clawed pantodont *Titanoides*, $\times \frac{1}{16}$. *From Simons, 1960.*

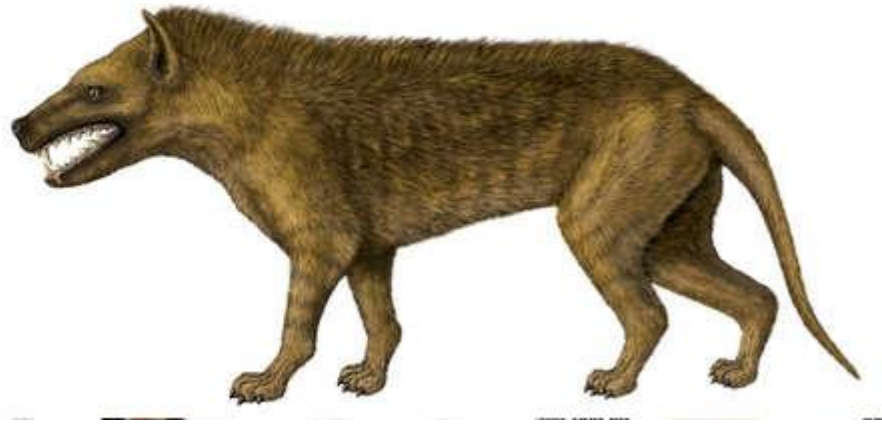



gettyimages

Creodonta:

Grupo carnívoro, con dientes carnasiales similares a los desarrollados en Carnivora, pero en una posición diferente (molar superior 1y 2, molar inferior 2 y3).





Hyaenodon

Creodonta:

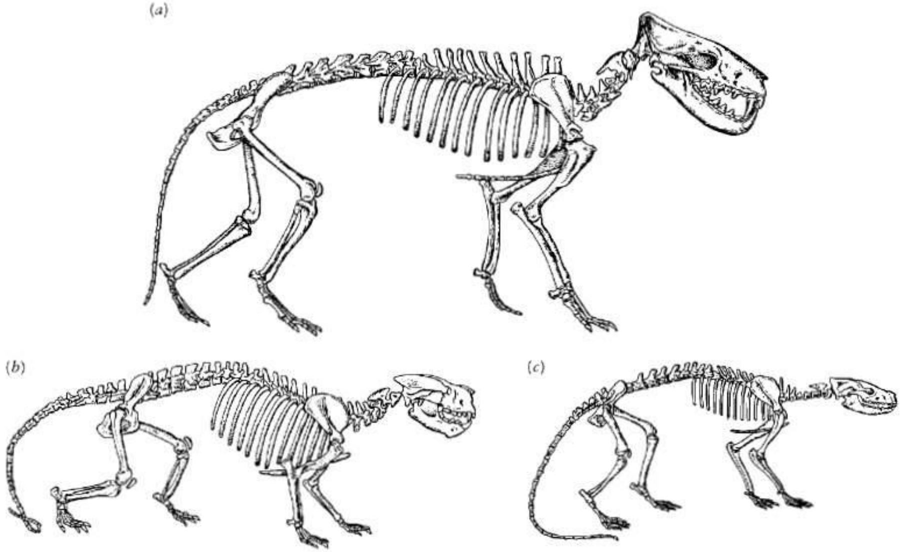


Figure 20-55. SKELETAL RESTORATION OF OXYAENIDS AND HYAENODONTS. (*a*) *Hyaenodon.* (*b*) *Patriofelis.* (*c*) *Sinopa. From Gregory, 1957.*

The two families of creodonts, the Oxyaenidae and Hyaenodontidae, appear in the late Paleocene and are common throughout the Eocene. Oxyaenids, which may have originated in North America, were generally small, with long bodies and short limbs. In contrast with the hyaenodontids, they have lost the third molar. The posture of the feet was plantigrade with spreading toes. Hyaenodontids, which were more common in the Old World, include genera in which the body proportions were comparable with those of felids, canids, and hyaenids (Figure 20-55). Some reached the size of large bears. Like other primitive eutherians, the creodonts lacked an auditory bulla and five digits were retained on both the forelimbs and hind limbs (Figure 20-56).

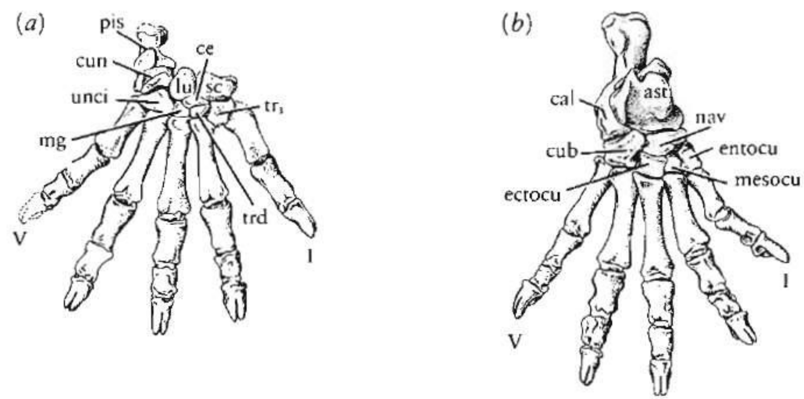


Figure 20-56. FEET OF THE CREODONT *PATRIOFELIS.* (*a*) Front. (*b*) Rear. Abbreviations as follows: ast, astragalus; cal, calcaneum; ce, centrale; cub, cuboid; cun, cuneiform; ectocu, ectocuneiform; entocu, entocuneiform; lu, lunar; mesocu, mesocuneiform; mg, magnum; nav, navicular; pis, pisiform; sc, scaphoid; trd, trapezoid; trz, trapezium; unci, unciform; I, V, metacarpals and metatarsals. *From Gregory, 1957.*

Creodonta: Oxaenydae

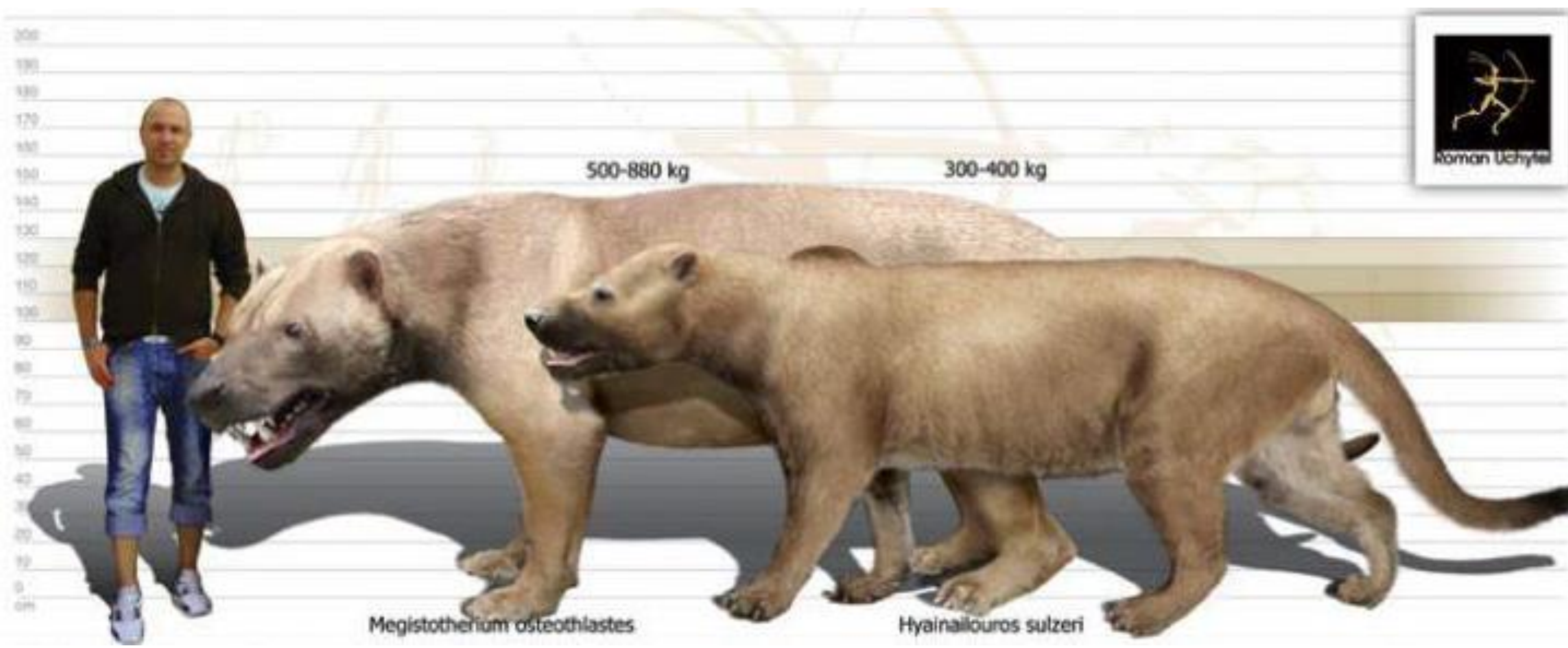
Patriofelis

Machaeroides, **Machairodinae**

Creodonta: Hyaenodontidae

Más diversos que Oxaenydae. Más de 50 géneros en 4 familias: Proviverridae, Limnocyonidae, Hyaenodontidae y Hyainailouridae.

Extremidades más gráciles, en ocaciones digitígrados.



Pholidotamorpha: Paleonodonta

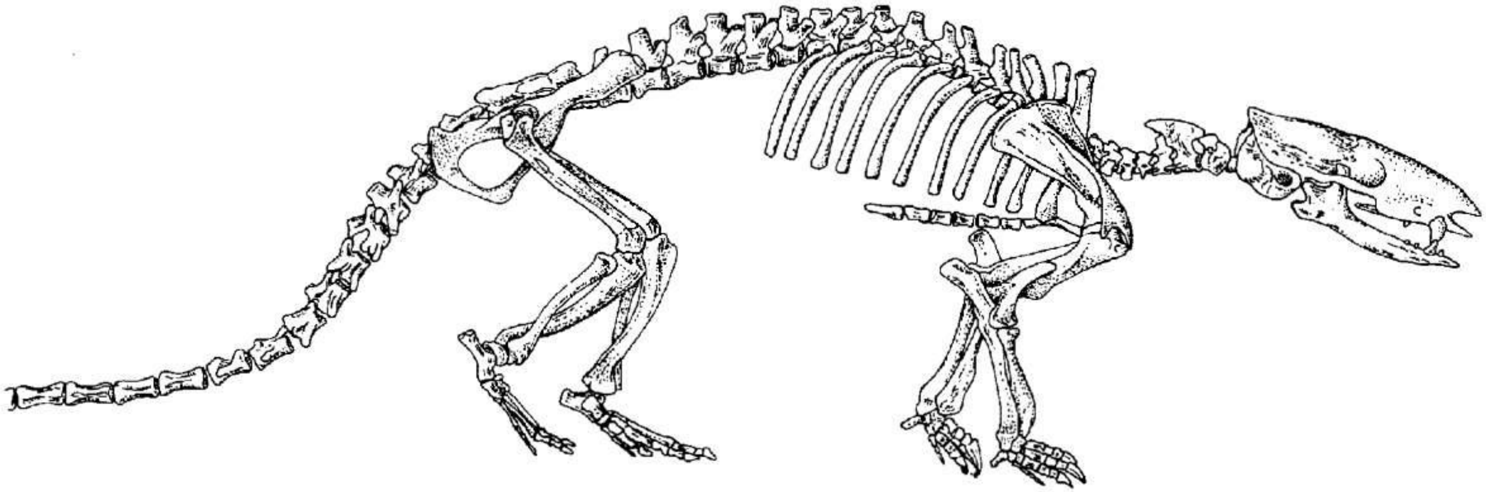


Figure 21-92. SKELETON OF THE EOCENE PALAEANODONT *METACHEIROMYS*. The original was 2 meters long. *From Simpson, 1931.*

early Tertiary North American Palaeanodonta. The best-known member of this group is the Eocene genus *Metacheiromys* (Figure 21-92). It resembles the xenarthrans in the loss of enamel and the reduction of the number of cheek teeth. The limbs are primitive but characterized by tuberosities which suggests that they were used in digging. Simpson pointed out a number of features that he believed showed incipient development toward the xenarthrous condition, including extra areas of vertebral articulation, a thickening of the posterior margin of the scapular spine, and the structure of the pelvis. None of these reach the stage of development of the earliest-known South American xenarthran, and Emry (1970) contended that they do not indicate close relationships.

In any case, *Metacheiromys* is too late and too specialized in the loss of all but two of the cheek teeth to be considered directly ancestral. The most primitive member of the Metacheiromyidae is *Propalaeanodon* from the Upper Paleocene (Rose, 1979) (Figure 21-93*a*). It consists of a lower jaw with seven teeth and a possibly associated humerus that suggests a digging habit. The enamel is already all but lost and the crowns of the teeth have no cusps, in common with the early South American armadillos. The ramus of the jaw is also relatively slender.

Pholidotamorpha: Paleonodonta

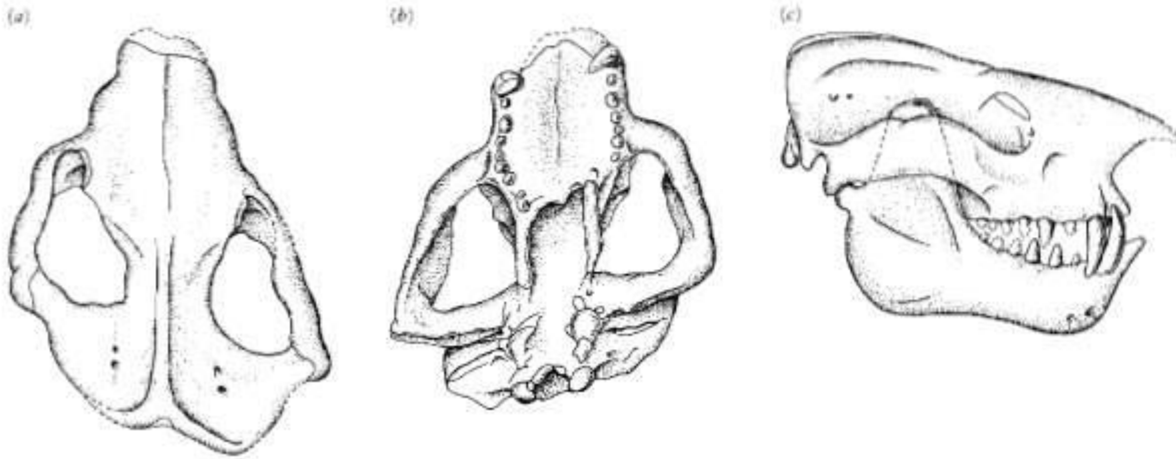


Figure 21-95. SKULL OF *ERNANODON* FROM THE LATE PALEOCENE OF CHINA. (*a*) Dorsal, (*b*) palatal, and (*c*) lateral views, × ⅘. *From Radinsky and Ting, 1984.*

The Epoicotheriidae is a second family of palaeanodonts that also appears in the Upper Paleocene. The Eocene and Oligocene members are highly specialized as subterranean burrowers, showing a degree of specialization of the skull, vertebrae, and limbs that is comparable to that of the African golden mole and some burrowing rodents (Figure 21-94) (Rose and Emry, 1983). The den-

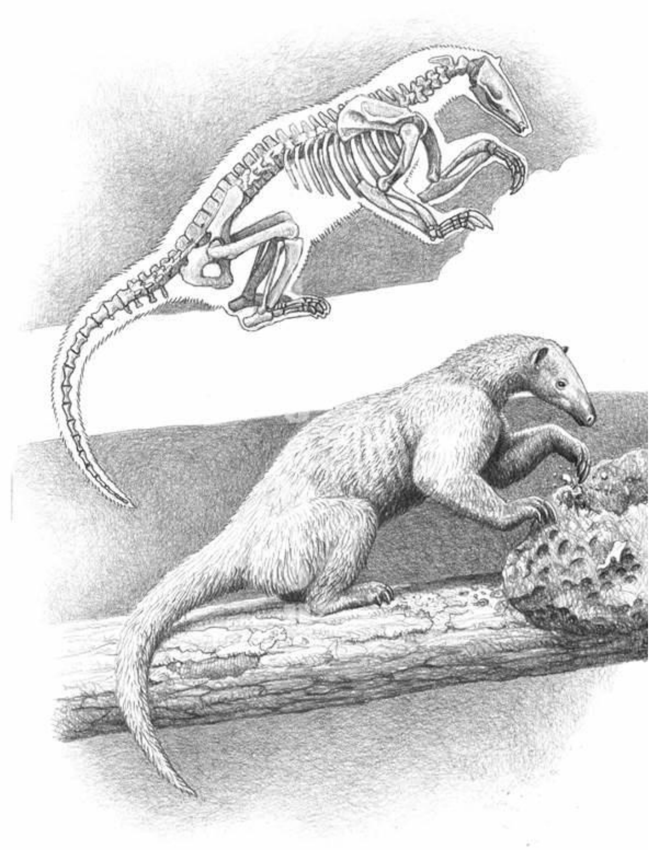
large canine. It seems possible that the otherwise isolated Upper Paleocene genus from China *Ernanodon* (Radinsky and Ting, 1984) may be related to the epoicotheres (Figure 21-95). The skull superficially resembles that of some sloths in the presence of both upper and lower caniniform teeth, but the lower tooth bites in front of the canine in both *Ernanodon* and the epoicothere, as in most mammals, whereas it bites behind the upper tooth in the sloth.

Pholidota:

Cráneo de forma tubular, mandíbula angosta y sin dientes.

Presentan placas de queratina sobre todo el cuerpo a modo de armadura.

Pholidota



Eurotamandua

Pholidota

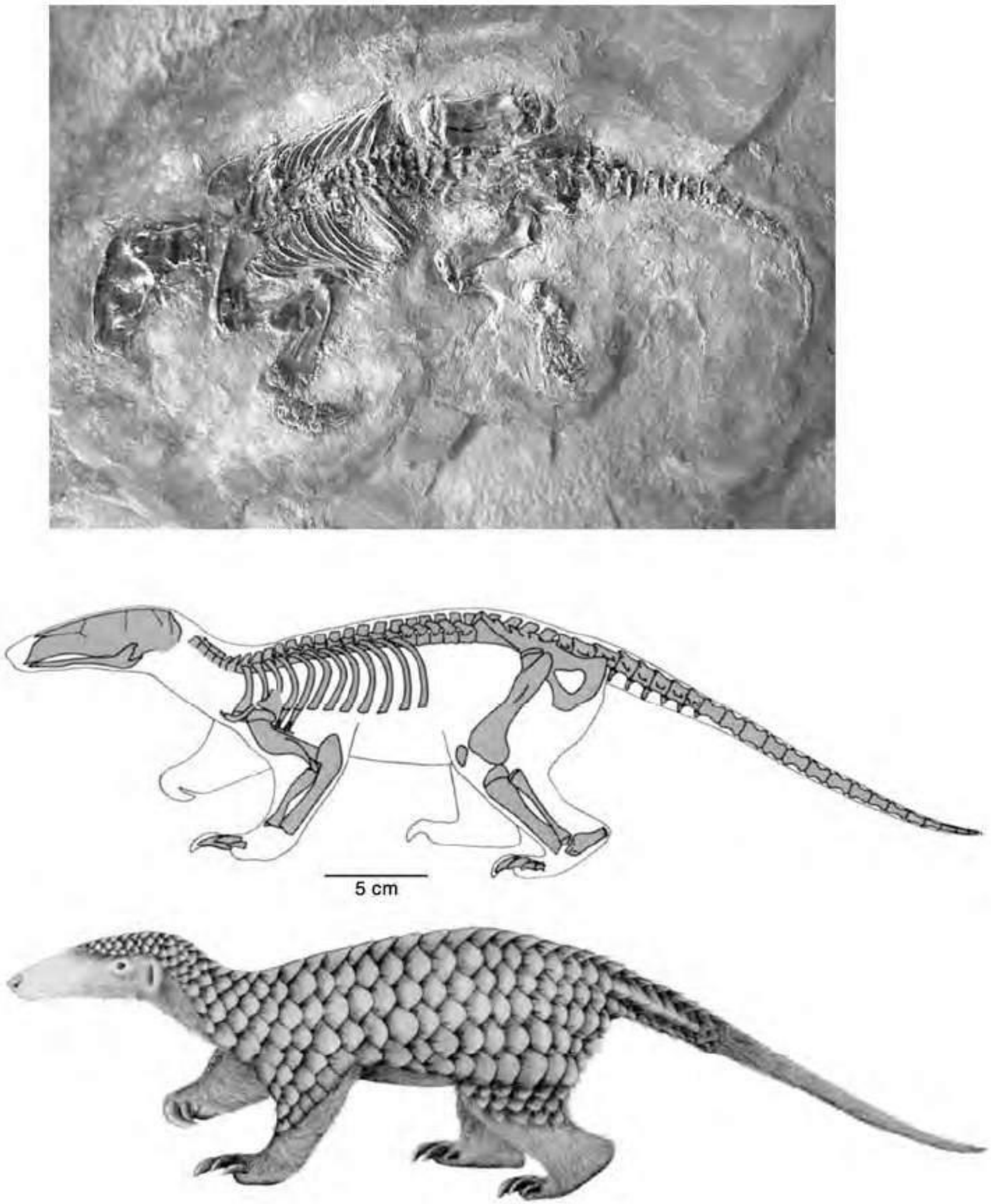


Fig. 11.5. Primitive pholidotan *Eomanis* from the middle Eocene of Messel, Germany. (Photograph courtesy of G. Storch; restorations from Storch, 1978.)

Eomanis

Mesonychia

Carnívoros con similitudes dentales a los ancestros de los cetáceos.

Mesonychia

There were no large mammalian carnivores in the early Paleocene. Oxyaenids and hyaenodontids appeared only in the late Paleocene, and members of the Carnivora were still relatively small until the Oligocene. In the absence of other large carnivores in the early Cenozoic, this role was taken by a family within the ungulate assemblage, the Mesonychidae.

life. The limbs were specialized for cursorial locomotion (Figure 21-28). The metapodials were closely integrated and the posture of the foot was digitigrade. However, all mesonychids are thought to have retained hoofs rather than claws, and the terminal digits, like those of condylarths, are deeply fissured.

The middle Paleocene genus *Dissacus,* which is known from Europe, Asia, and North America, was more primitive, retaining a plantigrade posture and five digits in the manus. Even this genus was fairly large, with the skull

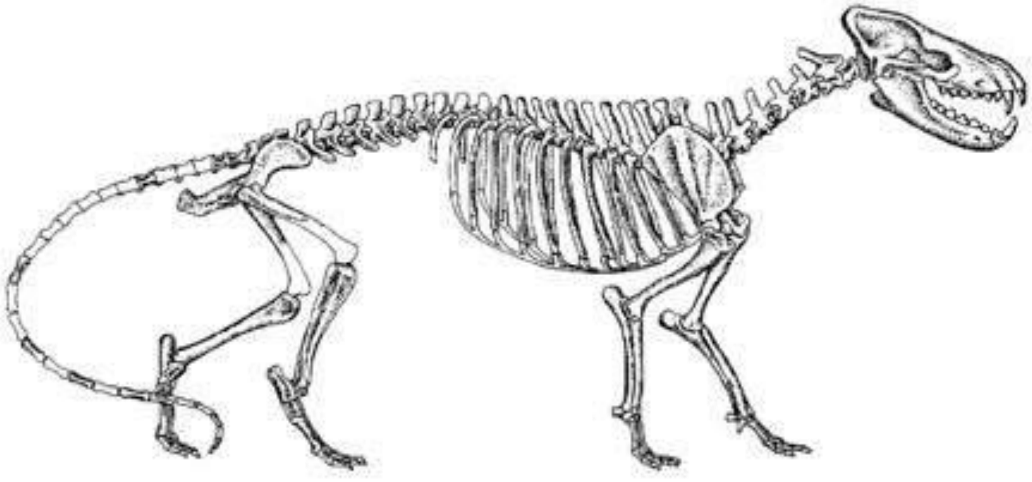


Figure 21-28. *MESONYX.* Skeleton of a carnivorous mesonychid from the Eocene of North America. *From Scott, 1888.*

Mesonychia

nearly 20 centimeters long. The large temporal fossa and high sagittal crest in *Harpagolestes* and *Mesonyx* and the low position of the mandibular condyle and its hingelike action are typical of carnivores and suggest a very strong bite (Figure 21-29). The dentition has some specialized features in common with members of the Carnivora as well. The lower molars are laterally compressed blades and both the upper and lower teeth have carnassial notches that in modern carnivores serve to hold the flesh as it is torn from the bone. However, in occlusal view, one can see that the upper molars retain a basically triangular pattern, with no development of carnassials.

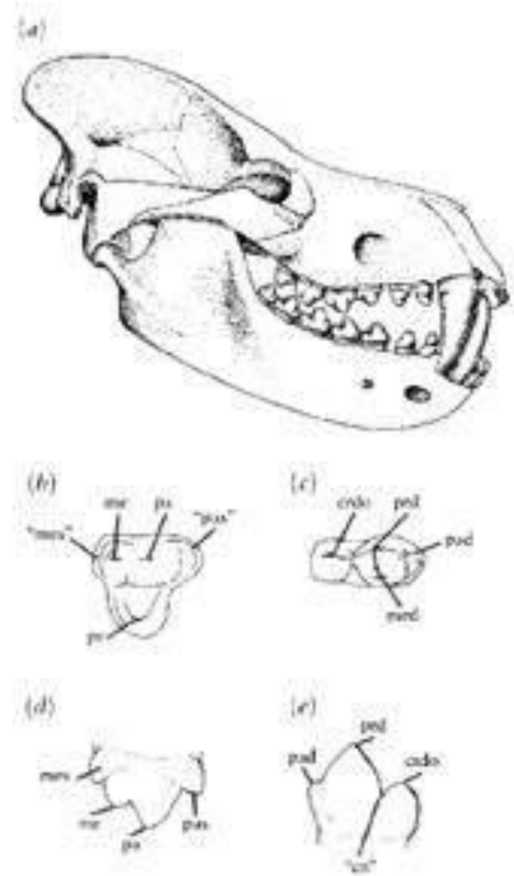


Figure 21-29. (*a*) Skull of the mesonychid *Harpagolestes*. (*b* to *e*) Molar teeth of the middle Paleocene mesonychid *Dissacus*. (*b*) and (*d*) are occlusal and buccal views of right upper molar. (*c*) and (*e*) are occlusal and buccal views of left lower molar. Abbreviations as follows: "cn," analogous feature to the carnassial notches of the carnivoran and hyaenodontan trigonids; crdo, cristid obliqua, the crest formed by the buccal wall of the talonid; me, metacone; med, metaconid; "mes," mestastyle; pa, paracone; pad, paraconid; "pas," parastyle; pr, protocone; prd, protoconid. *From Szalay, 1969b.*

Only a relatively few, small mesonychids had sharp cusps. In most genera, the teeth are massive and the cusps blunt, which gives the general appearance of the teeth in hyaenids and suggests that they were bone-crushing scavengers. Others may have been bearlike omnivores. *An-*

Carnivoramorpha

The living meat-eaters, cats, dogs, hyaenas, weasels and seals are members of the Order Carnivora. These animals are characterized by the possession of a pair of **carnassial** teeth on each side of the jaws: the upper premolar 4 and the lower molar 1 are enlarged as longitudinal blades that shear across each other like a powerful pair of scissor blades (Figure 10.38(a,b)). Certain forms that crush bones, such as the hyaenas, have broad premolars with thick enamel and powerful jaw adductors. Bone-crushing dogs have broad molars. The canine teeth are generally long and used in puncturing the skin of prey animals, whereas carnivores use their incisors for grasping and tearing flesh, as well as for grooming.

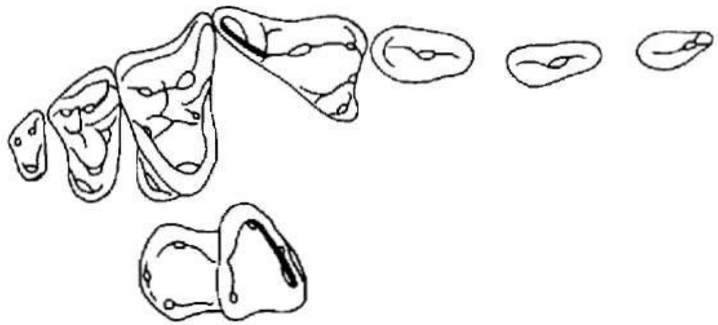
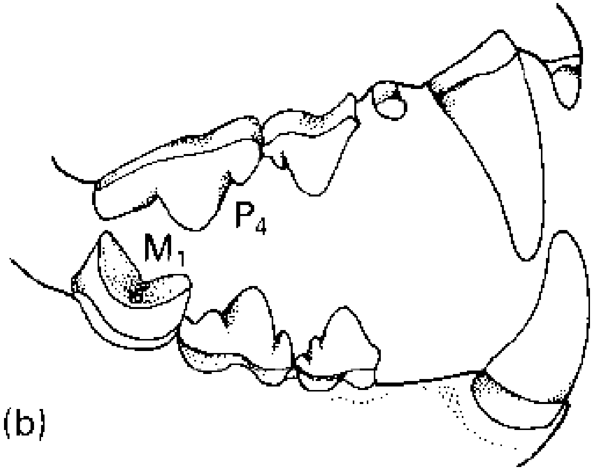


Figure 20-53. CARNASSIAL TEETH IN THE ORDER CARNIVORA. Heavy line indicates position of carnassial blades on last upper premolar and first lower molar of the primitive carnivore *Miacis*. *From Savage, 1977.*



Carnivoramorpha

We first recognize members of the order Carnivora in the early and middle Paleocene. They are characterized by the specialization of the last upper premolar and first lower molar for shearing. This specialization is first shown by the presence of a well-developed metastyle blade at the posterior angle of the premolar, which sheared against the anterior surface of the trigonid of the first lower molar. The protocone of P^4 is located far forward of the paracone. The posterior molars are reduced. All of the early carnivores were small—comparable in size to a weasel or small cat. They are primitive in lacking ossification of the auditory bulla; the scaphoid, lunar, and centrale of the carpus remain separate, in contrast with their fusion in more advanced carnivores.

Among the primitive Carnivora, two families are recognized, the Viverravidae from the Lower Paleocene into the Oligocene and the Miacidae, which appears first in the earliest Eocene. Both are Holarctic in distribution.

Although appearing earlier in time, the Viverravidae are more specialized in the loss of the third molar in both upper and lower jaws. The viverravid *Protictis* (Figure 20-57) has a small skull and extremely high, sharp cusps, which suggest an insectivorous diet.

Miacids are clearly distinct when they first appear in the Lower Eocene of Europe and North America. Gingerich (1980b) suggests that they may have immigrated from Asia where they are also known in the early Eocene. The miacids are generally more similar to the derived carnivore families and assumed dominance over the Viverravidae by the end of the Eocene. Most are poorly known, but a complete articulated skeleton was described from the middle Eocene of Germany (Springhorn, 1980) (Figure 20-58). The limbs are relatively short, the trunk is elongate, and the feet are plantigrade.

Figure 20-58. *PAROODECTES.* Skeleton of the miacid carnivore from the Middle Eocene of Germany, ×⅛. *From Springhorn, 1980.*

All the advanced families are distinguished from the miacids and viverravids by ossification of the auditory bulla, but this structure shows different patterns of evolution in each family. According to Hunt (1974), all living carnivores have at least three elements of the bulla: the dermal ectotympanic and both a rostral and caudal entotympanic. The ossification of the bulla was probably associated with an increase in hearing ability. The greater acuity of other mammals with large bullae has been established physiologically (Lay, 1972).

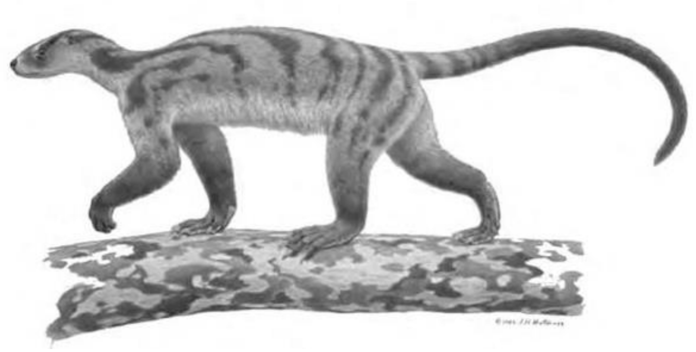
Carnivoramorpha

Viverravidae:

Pérdida del molar 3

Presenta la articulación fíbula-calcaneo

Bulla no osificada



Mustelodon, **Viverravidae**

Miacidae:

Retención del molar 3

Pérdida de la articulación fíbula-calcaneo

Bulla no osificada

Vulpavus, **Miacidae**

Carnivora:

the modern carnivore families are advanced in the development of an ossified auditory bulla and at least some increase in relative brainsize (Radinsky, 1973, 1975, 1977). All the modern families have fused the scaphoid and lunar bones in the carpus, which suggests more effective running and support of their generally larger body size, although

Two major groups of advanced carnivores are recognized on the basis of differences in the nature of the bulla together with changes in the carotid circulation that can be observed in the bones of the basicranial region. In the Aeluroidea (or Feloidea), including viverrids, felids, and hyaenids, the main branch of the internal carotid is reduced or lost, with the arterial circulation to the brain coming primarily from the external carotid in conjunction with the evolution of a countercurrent exchanger in the vicinity of the orbit, which apparently cools the blood entering the brain.

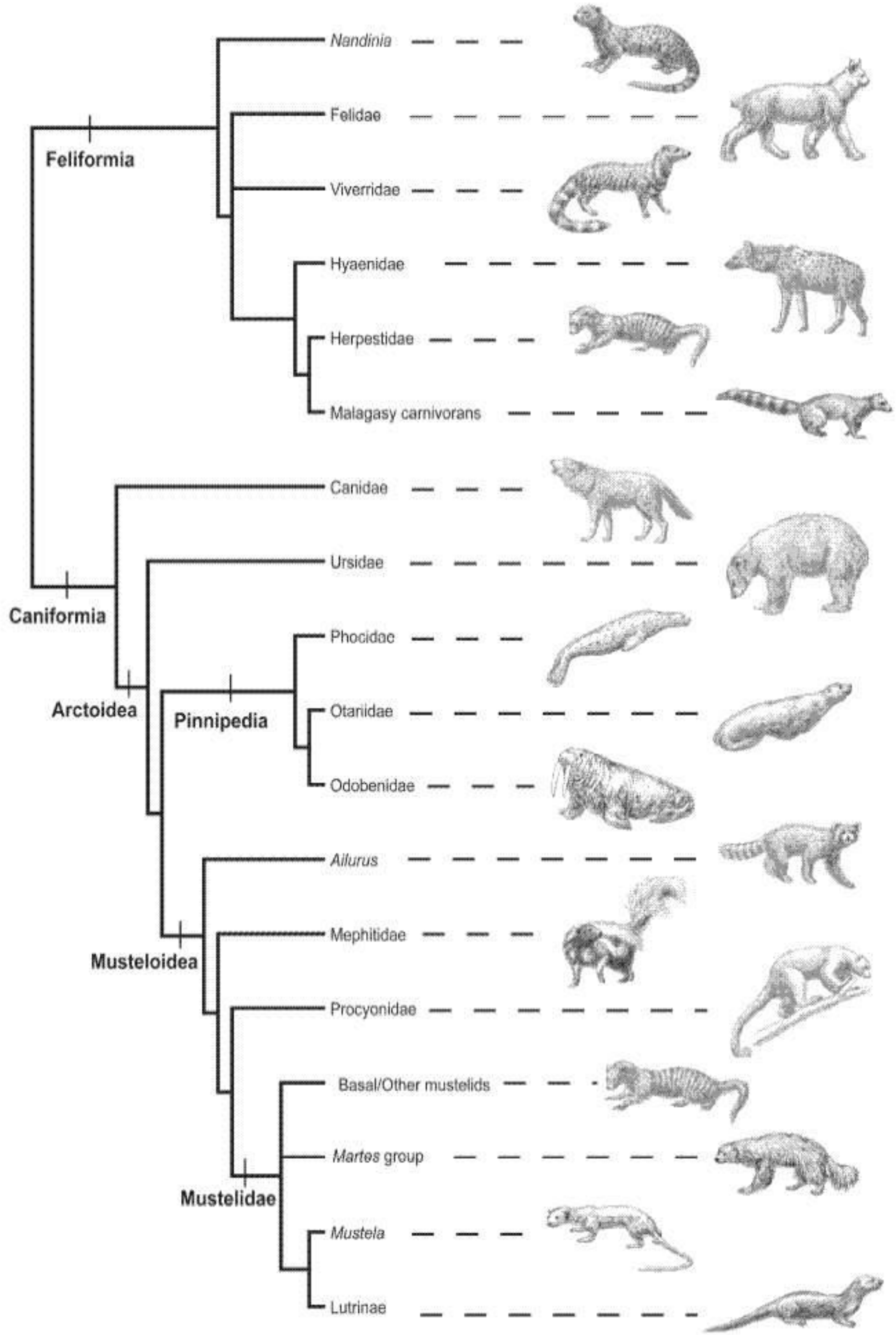
In felids and viverrids, both the ectotympanic and the caudal entotympanic contribute to the formation of a septum that divides the bulla into anterior and posterior chambers. In hyaenids, the septum is formed primarily by the ectotympanic, and the chamber of the middle ear is increased by expansion into the mastoid.

In the arctoids (also termed canoids), which include the Canidae, Procyonidae, Ursidae, and Mustelidae, as well as the marine carnivores, the internal carotid remains an important artery and the auditory bulla is not clearly divided into two chambers. Canids have an incomplete division of the bulla, and there is no septum in procyonids and mustelids.

Feliformia*:* Viverridae

Caniformia*:* Procyonidae

Carnivora:



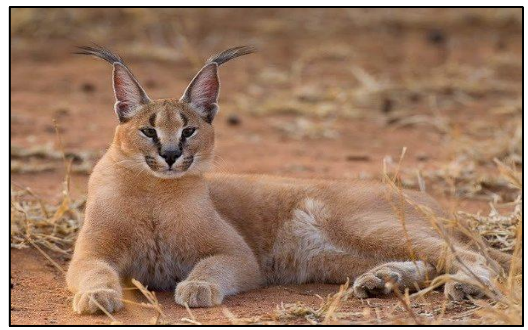
Nandinia
Felidae
Viverridae
Hyaenidae
Herpestidae
Malagasy carnivorans
Feliformia
Canidae
Ursidae
Phocidae
Otariidae
Odobenidae
Caniformia
Arctoidea
Pinnipedia
Ailurus
Mephitidae
Procyonidae
Basal/Other mustelids
Martes group
Mustela
Lutrinae
Musteloidea
Mustelidae

Carnivora: Feliformia

Hyenidae

Herpestidae

Nandiniidae



Felidae

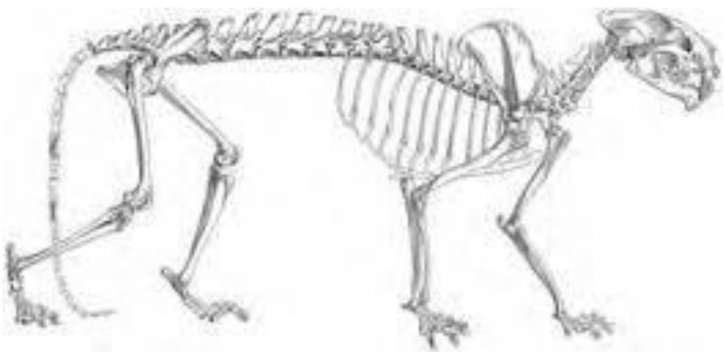
Eupleridae

Viverridae

Feliformia: Nimravidae

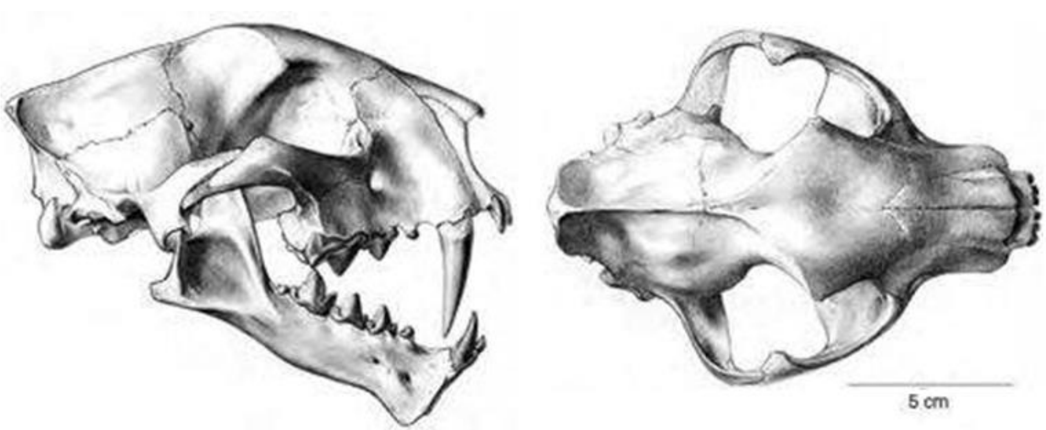
‘Falsos Gatos’. Feliformes basales.

Bula auditiva pobremente o no osificada.

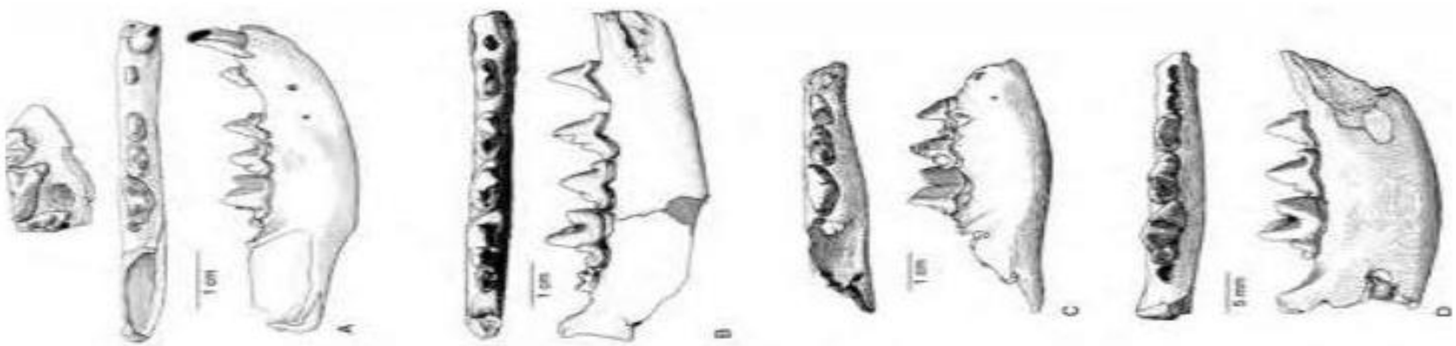


Dinictis

Hoplophoneus



Feliformia:



(A) *Stenoplesictis,* right upper and lower teeth **Stem Viverridae-Stem Feliformia**
(B) *Asiavorator,* left P2–M2 **Viverridae**
(C) Proailurus, right P3–M1 **Felidae-Viverridae**
(D) Stenogale, left P3–M1 **Felidae**

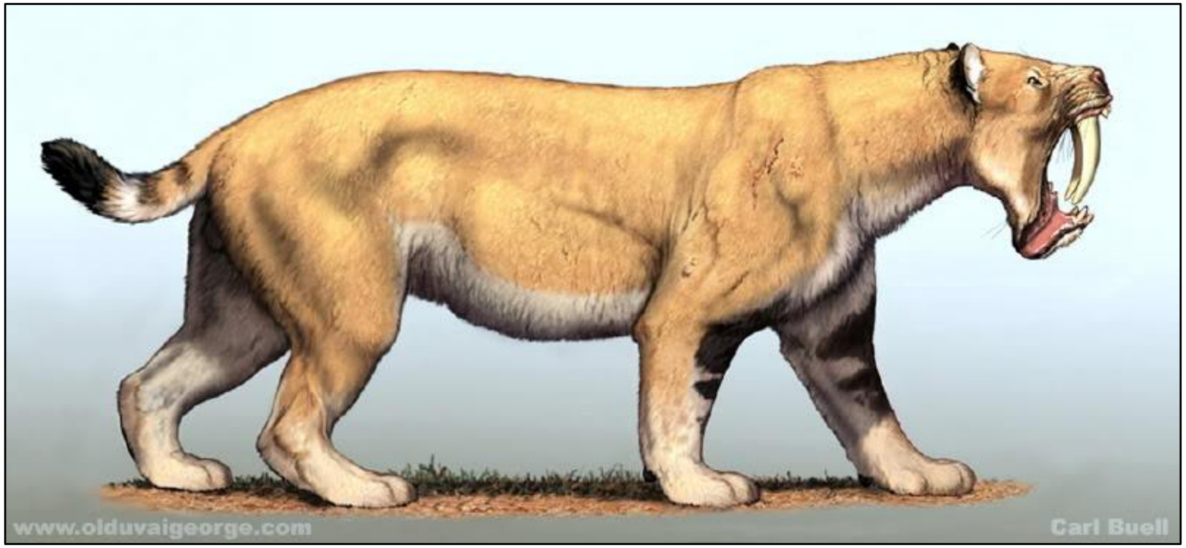
Stenoplesictis

Proailurus

Feliformia: Felidae

Barbourofelidae: Stem Felidae

Barbourofelis



Feliformia: Felidae

Pantherinae

Felinae

Machairodontinae

Feliformia: Machairodontinae

Smilodon

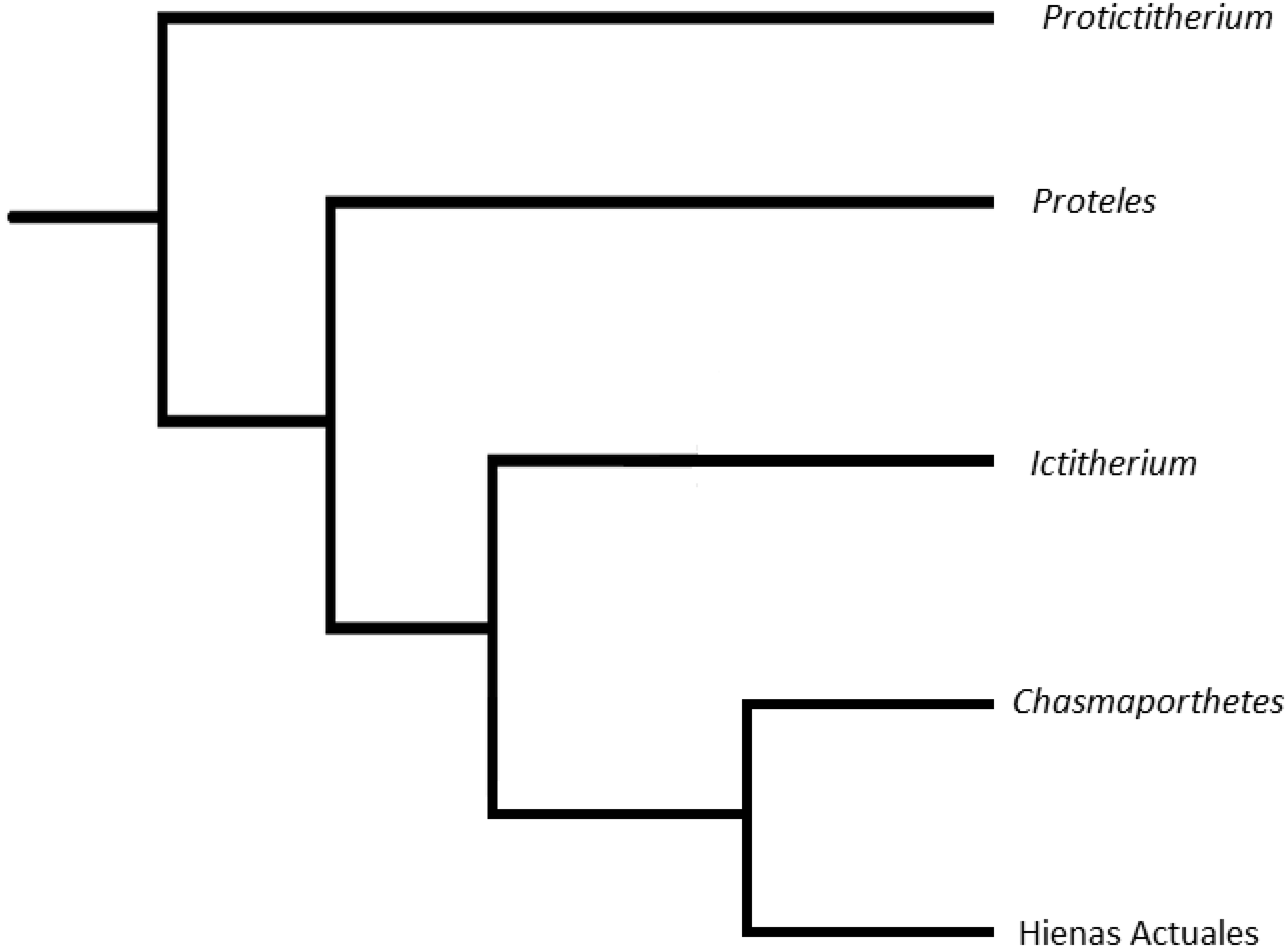
Feliformia: Percrocutidae

Grupo relacionado a Hyenidae.

Conocidos principalmente por mándíbulas y dientes.

Dinocruta

Feliformia: Hyenidae

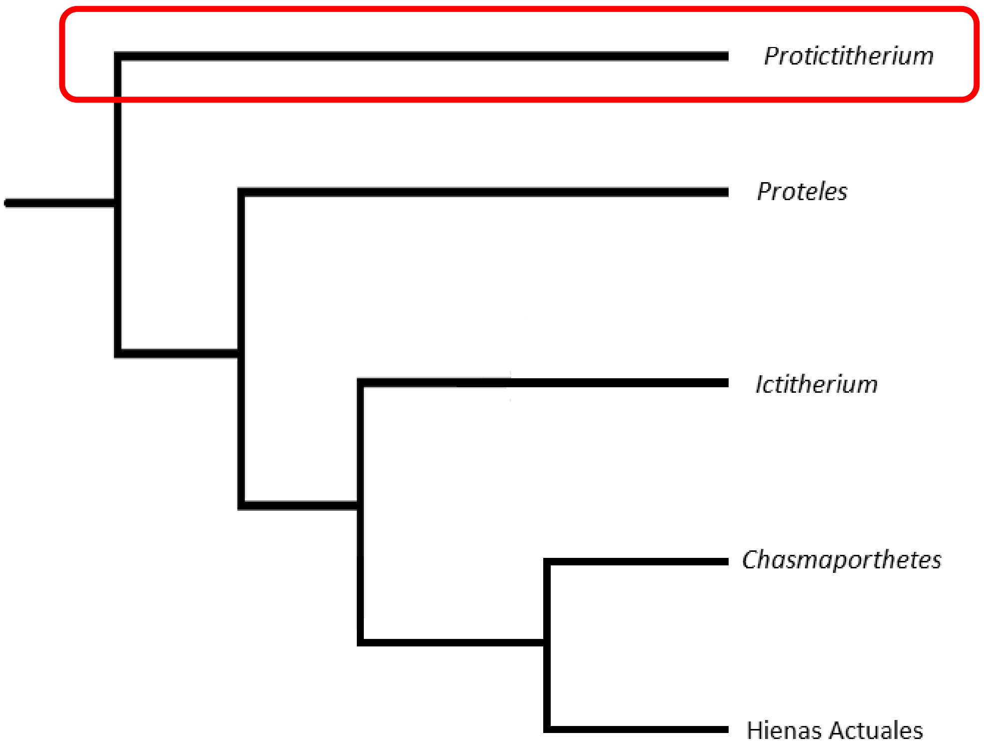


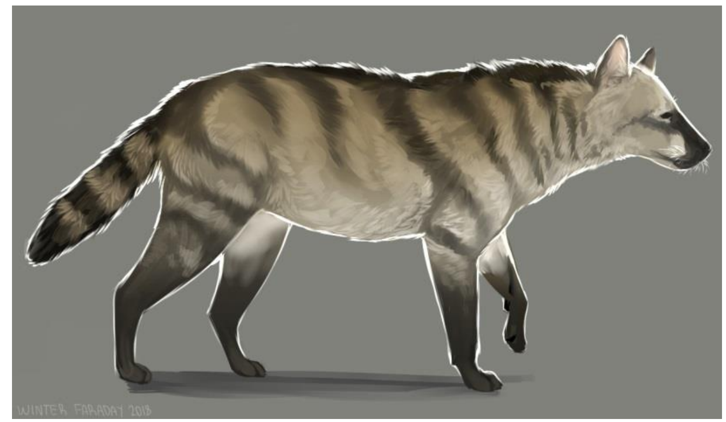
Feliformia: Hyenidae

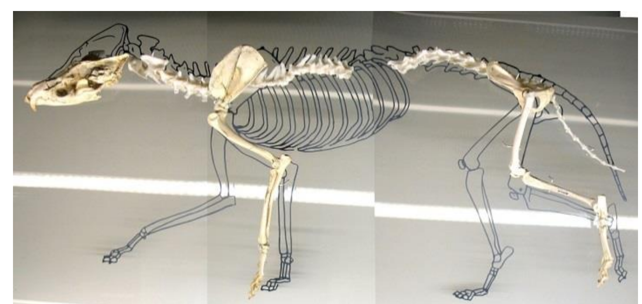
Formas basales con forma de civeta.

Arborícolas. Insectivoras.

Garras retractables.







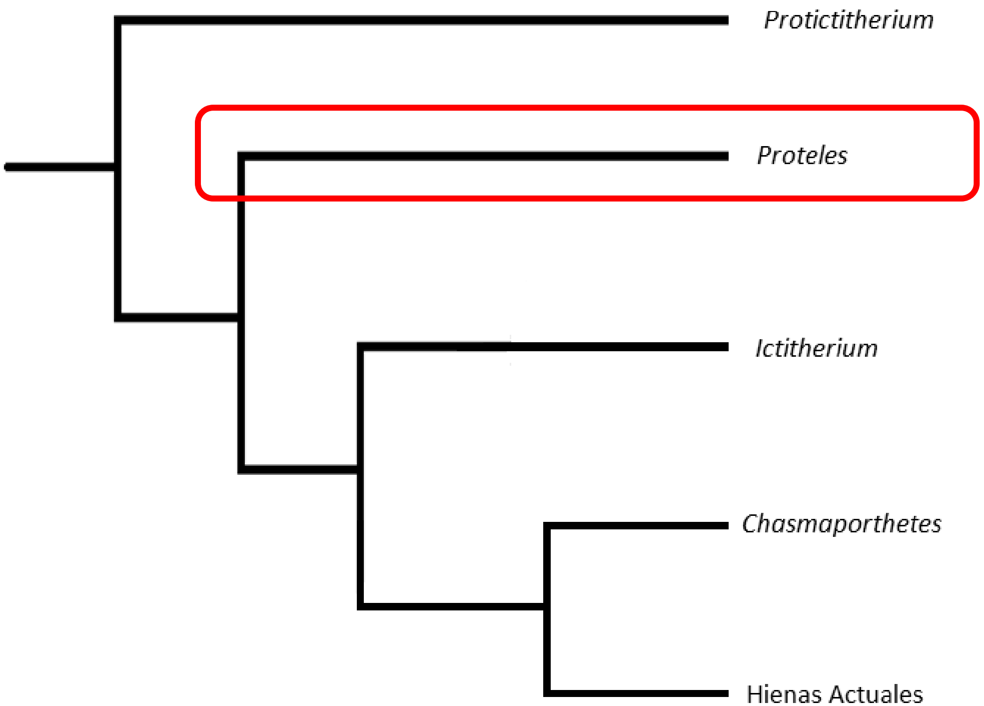
Protictitherium

Feliformia: Hyenidae

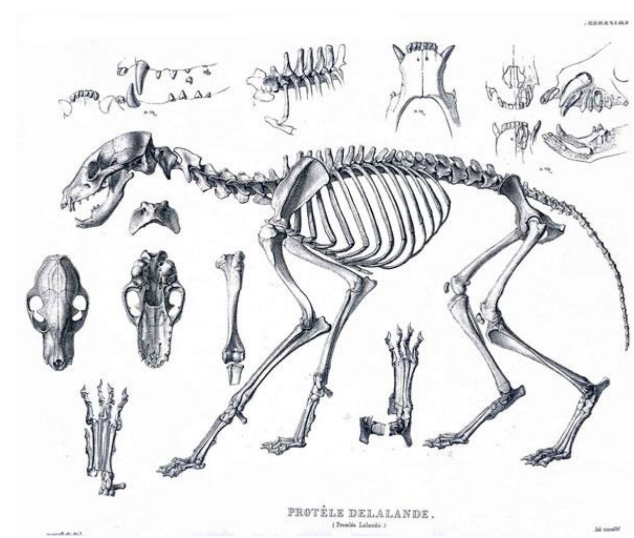
Formas pequeñas, con patas delanteras más largas que las traseras.

Insectivoro. Terrestre.

Vivo en la actualidad.

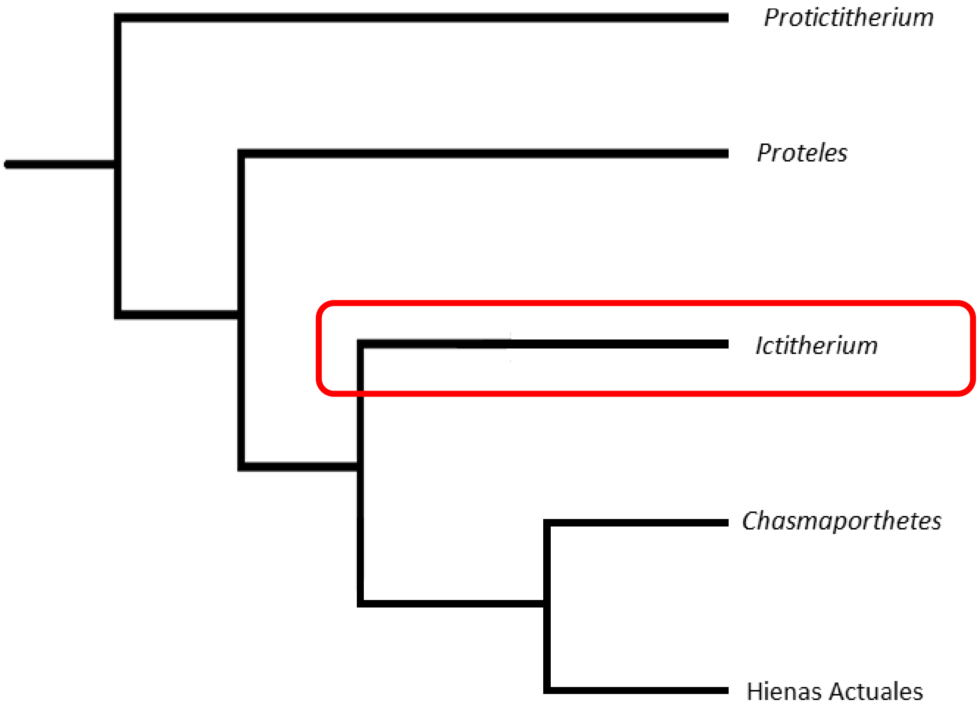


Proteles



Feliformia: Hyenidae

Hyenas gráciles, con forma similar
a la de un perro.



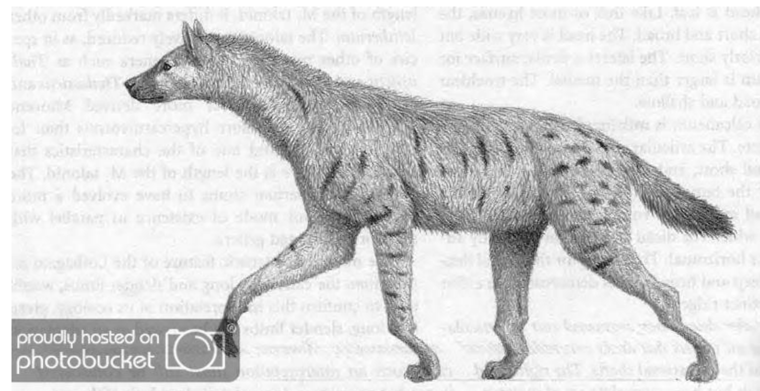


Figure 7.20 Restoration of *Ictitherium ebu* sp. nov. by Mauricio Antón. Shoulder height = 60 cm.

Ictitherium

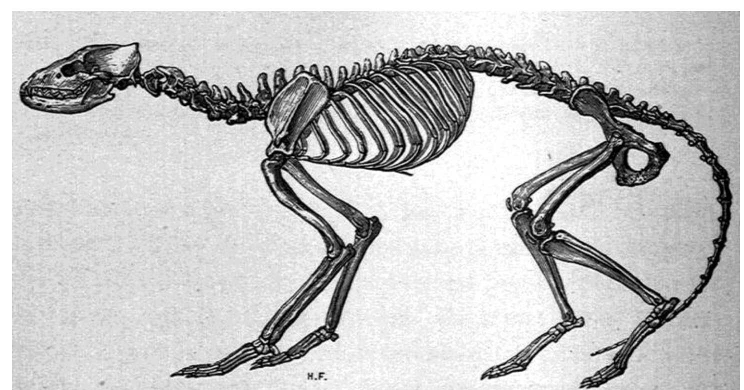
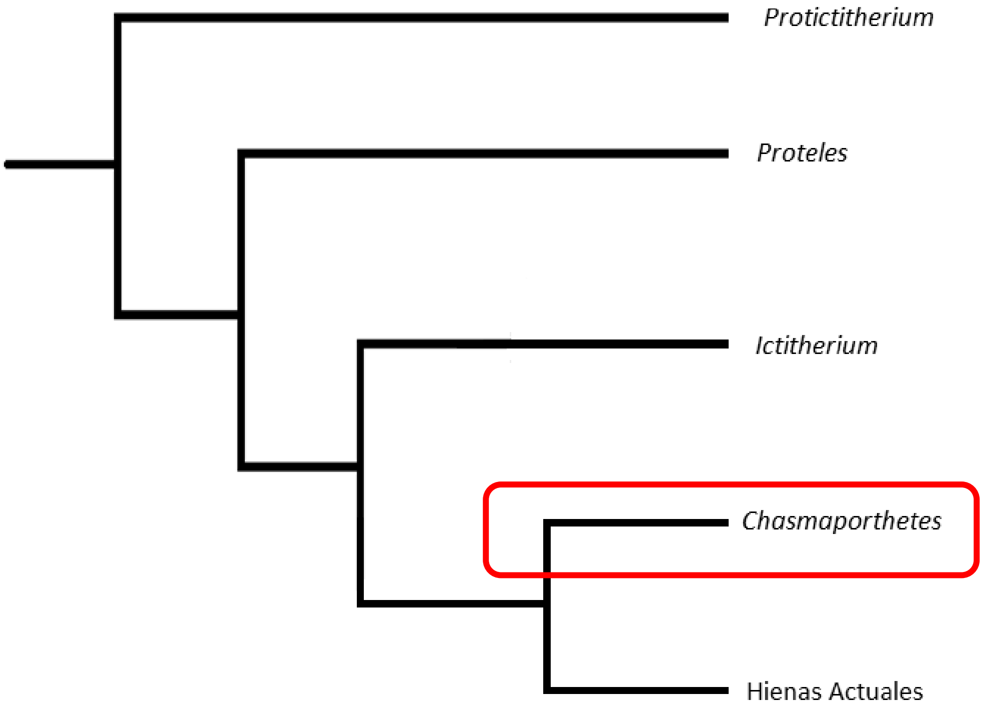
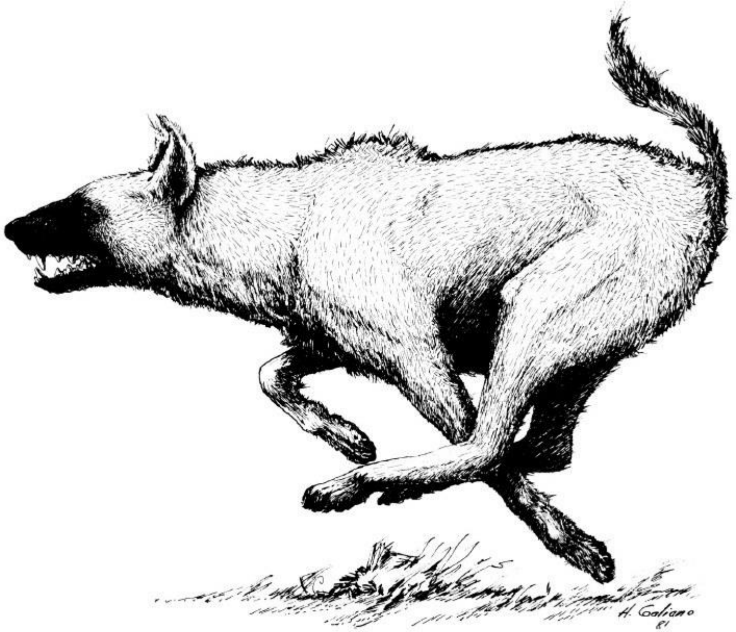


Fig. 274. — Restauration du squelette de l'*Ictitherium robustum*, à 1/9 de grandeur. — Miocène supérieur de Pikermi.

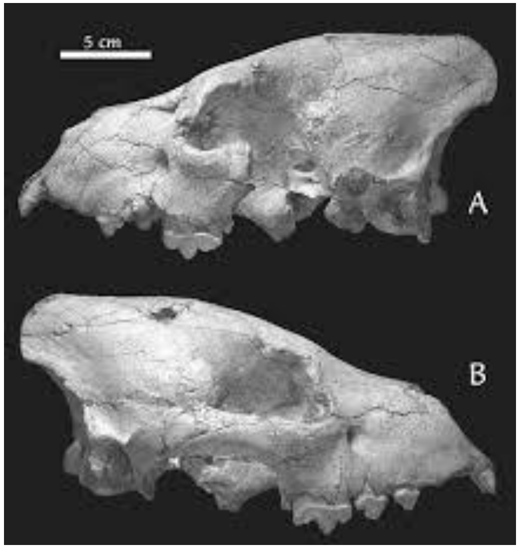
Feliformia: Hyenidae

Hyenas corredoras, tipo guepardo.



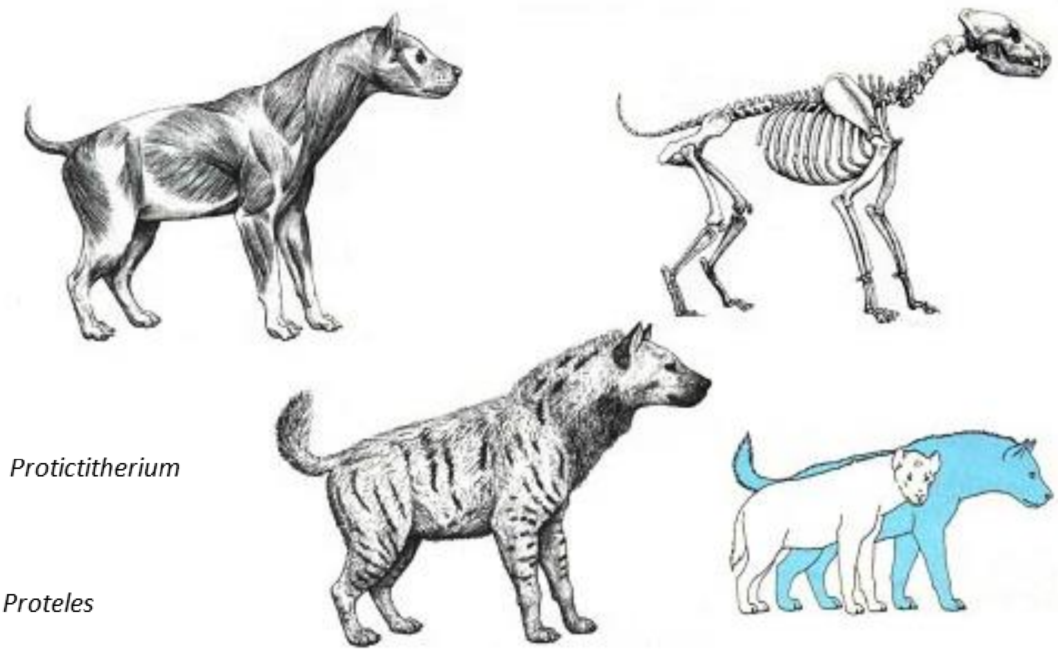


Chasmapothetes

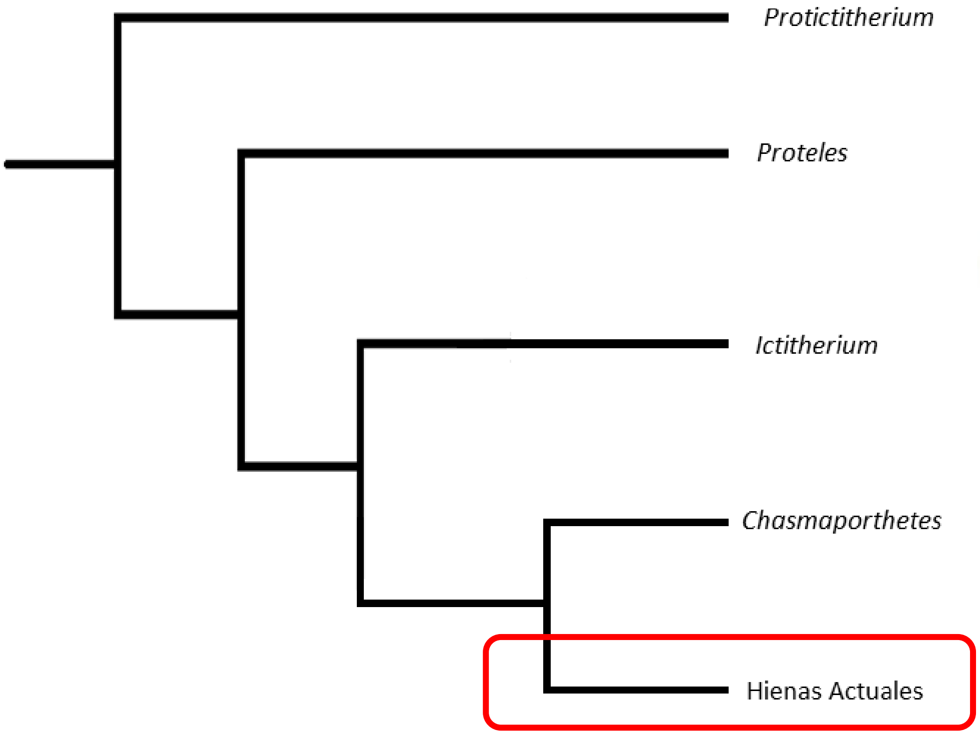


Feliformia: Hyenidae

Hienas carroñeras, rompe huesos.



Pachycrocuta brevirostris



Caniformia

Chrysocyon brachyurus, **Canidae**

Ailuropoda melanoleuca, **Ursidae**

Hydrurga leptonyx, **Pinnipeda**

Ailurus fulgens, **Ailuridae**

Mephitis mephitis, **Mephitidae**

Nasua nasua, **Procyonidae**

Taxidea taxus **Taxinae, Mustelidae**

Gulo gulo, **Martinae, Mustelidae**

Lutra lutra, **Lutrinae, Mustelidae**

Caniformia: Amphycyonidae

The amphicyonids are an assemblage of medium-to-very-large-sized genera that are known from the early Oligocene to the early Pliocene. They are common in North America and also known in Africa and Eurasia. The bulla shows a primitive arctoid pattern and they were previously placed in the Canidae.

Hunt (1977) and Ginsburg (1977) suggested that amphicyonids are closely related to the ursids, because both of these groups are specialized in having an enlarged inferior petrosal sinus with an excavation in the basioccipital. In bears, this opening houses a loop of the internal carotid that forms a countercurrent exchanger with an adjacent vein to cool the blood going into the brain. The structure of the opening in amphicyonids suggests a comparable function.

Radinsky (1980) described the endocasts of 10 amphicyonid genera that showed a progressive expansion and increased infolding of the neocortex and an increase in relative braincase from an EQ of 0.6 to 0.7 in the Oligocene to 1.19 to 1.4 in the late Miocene, as well as other features that show strong parallels with changes observed in the canids.

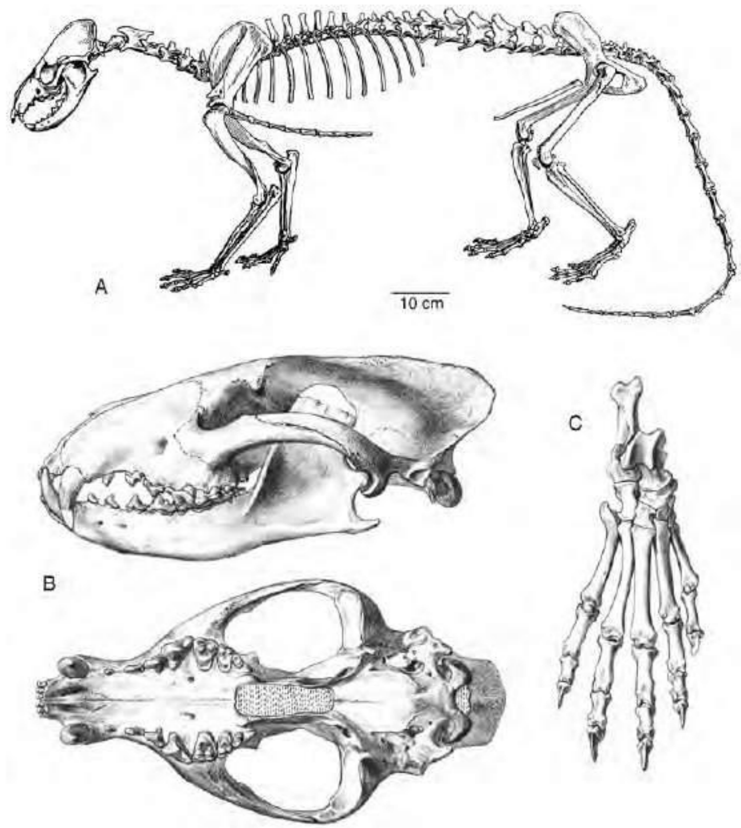
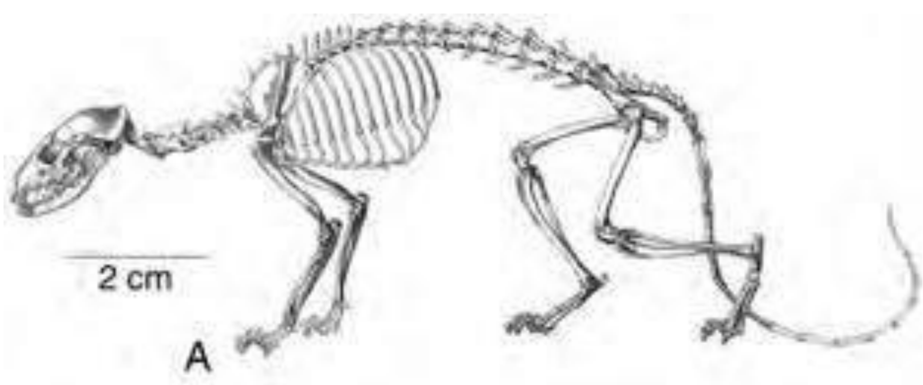


Fig. 8.18. Amphicyonid *Daphoenus*: (A) skeleton; (B) skull; (C) right foot. Scale applies to A. (From Scott and Jepsen, 1936.)

Caniformia: Canidae

Bula auditiva totalmente osificada, formada por el entotimpánico caudal, con contribuciones de otros huesos. El entotimpánico caudal forma un séptum parcial.

Formas modernas pierden las clavículas.



Hesperocyon, **Hesperocyonines**

Caniformia: Canidae

Bula auditiva totalmente osificada, formada por el entotimpánico caudal, con contribuciones de otros huesos. El entotimpánico caudal forma un séptum parcial.

Formas modernas pierden las clavículas.

Aelurodon, **Borophaginae**

Epicyion, **Borophaginae**

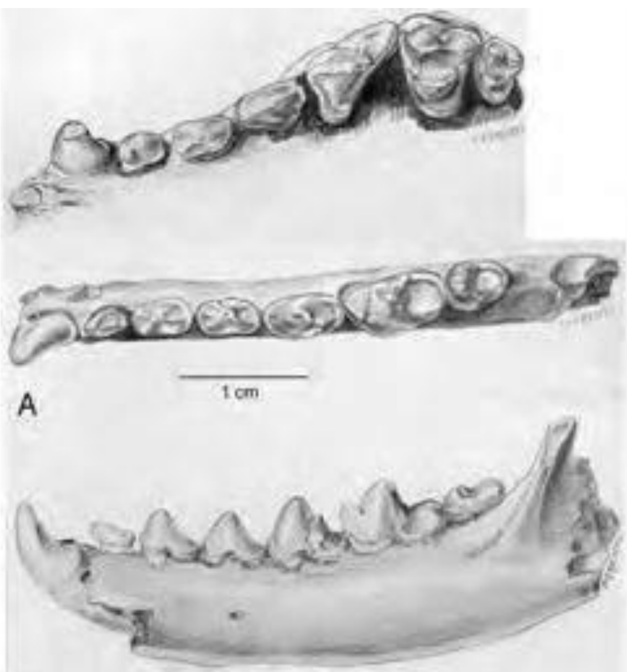
Borophaginae aún conservan el 5° dedo del pie.

Caniformia: Arctoidea

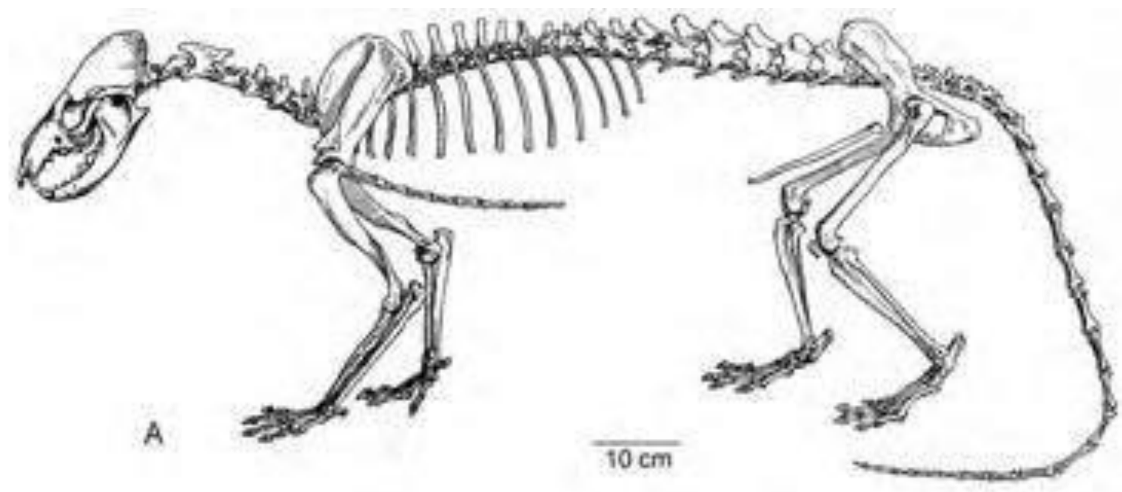
Poseen una fossa suprameatal (un agugero en la pared dorsolateral de la cavidad del oído medio)

Pierden el molar 3.

La mayoría tiene una buya auditiva de una única cámara formada por el ectotímpánico.



Parictis, **Amphicynodontinae**



Daphoneus, **Amphycyonidae**

Ursidae

Bears appear in the middle Oligocene in Europe. *Ursavus* from the middle Miocene appears close to the ancestry of modern bears. The giant Panda *Ailuropoda* is probably an early offshoot of the Ursidae and is first known in the late Miocene of Europe (Thenius, 1979).

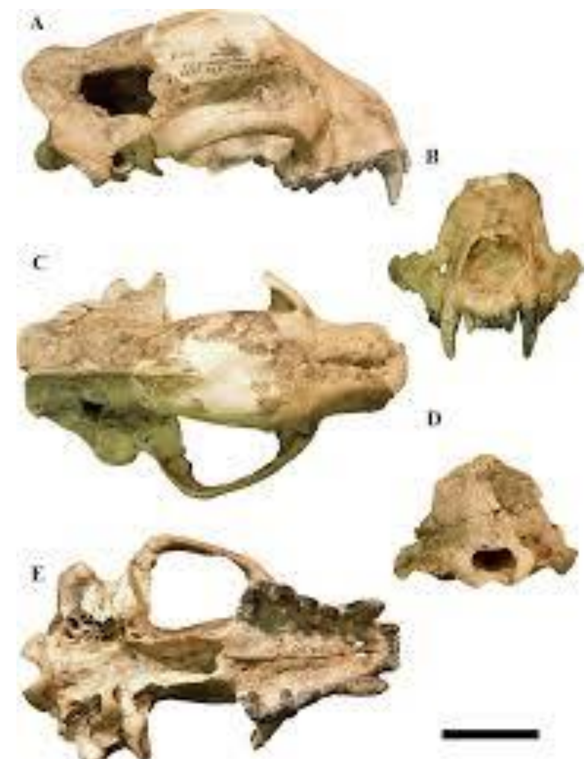
Hemicyon, **Hemicyontidae (stem Ursidae)**

Procyonidae, Mephitidae, Ailuridae

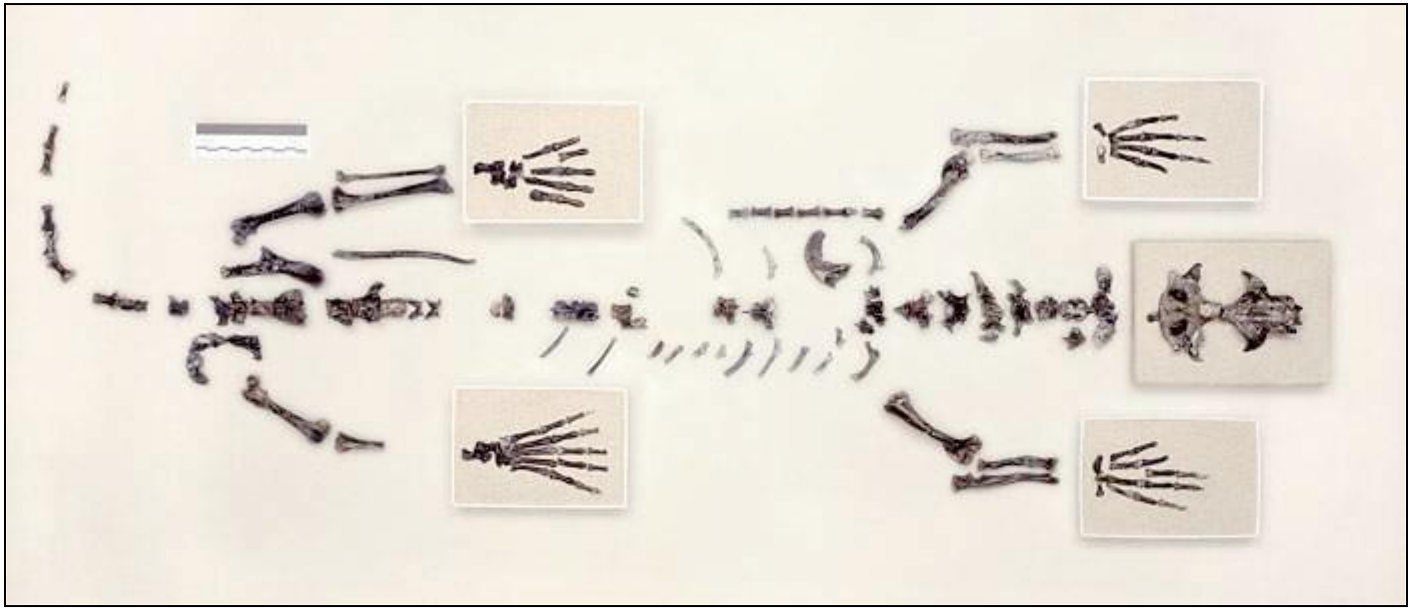
Procyonids (raccoons and their allies) are questionably identified from the early Oligocene, although their remains are easily confused with those of mustelids. The skull proportions of this group vary greatly, but they can be recognized by the blunting of the cusps and the squaring of the molars, which are associated with an omnivorous diet. The lesser panda *Ailurus* (which is sometimes placed in a separate family) apparently arose from the early procyonids and appears in the middle and late Miocene of Asia and Europe.

Mustelidae

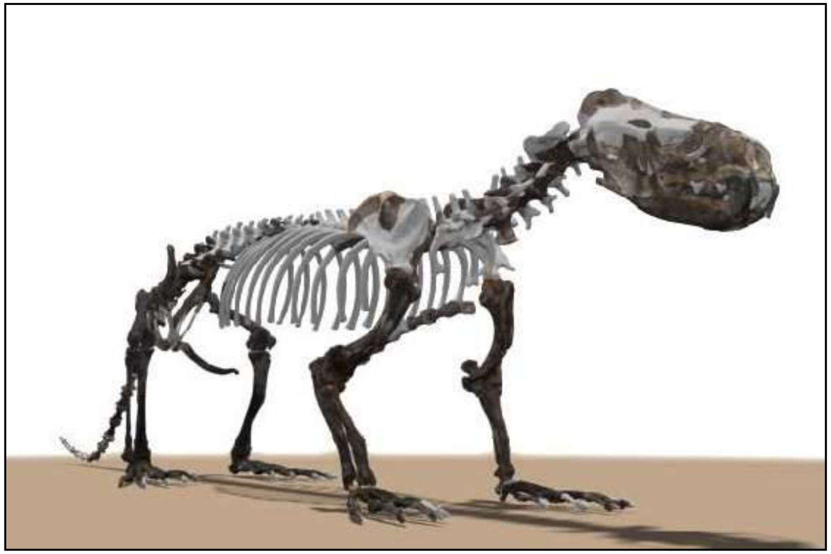
Megalictis



Pinnipedia: Semantoridae



Puijila



Pinnipedia: Semantoridae

Posee caracteres específicos de pinnipedos, como presentar solo 4 pares de incisivos, y tener el último molar reducido y ubicado hacia la línea media.

Pinnipedia: Enialarctidae, Desmatophocidae

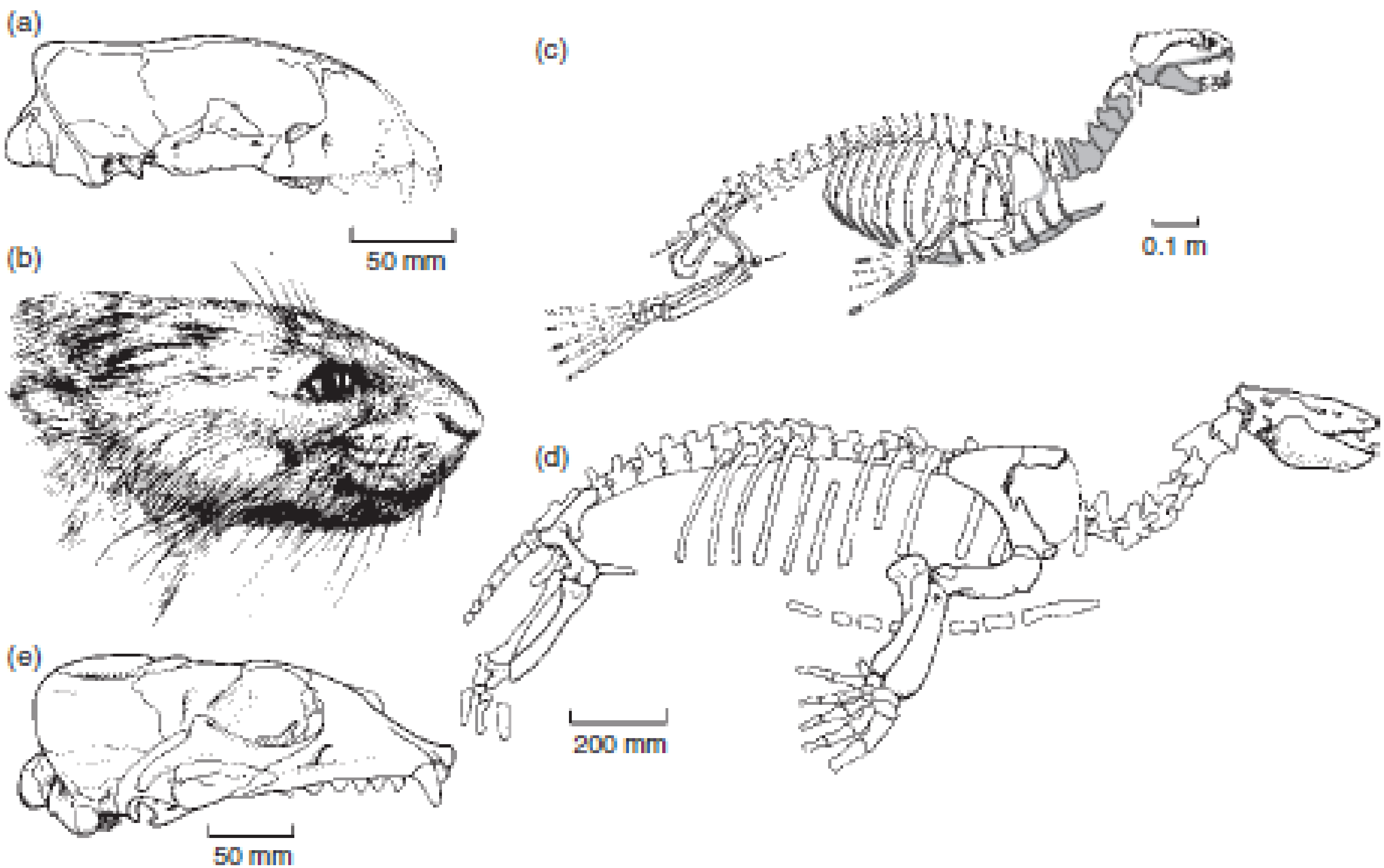
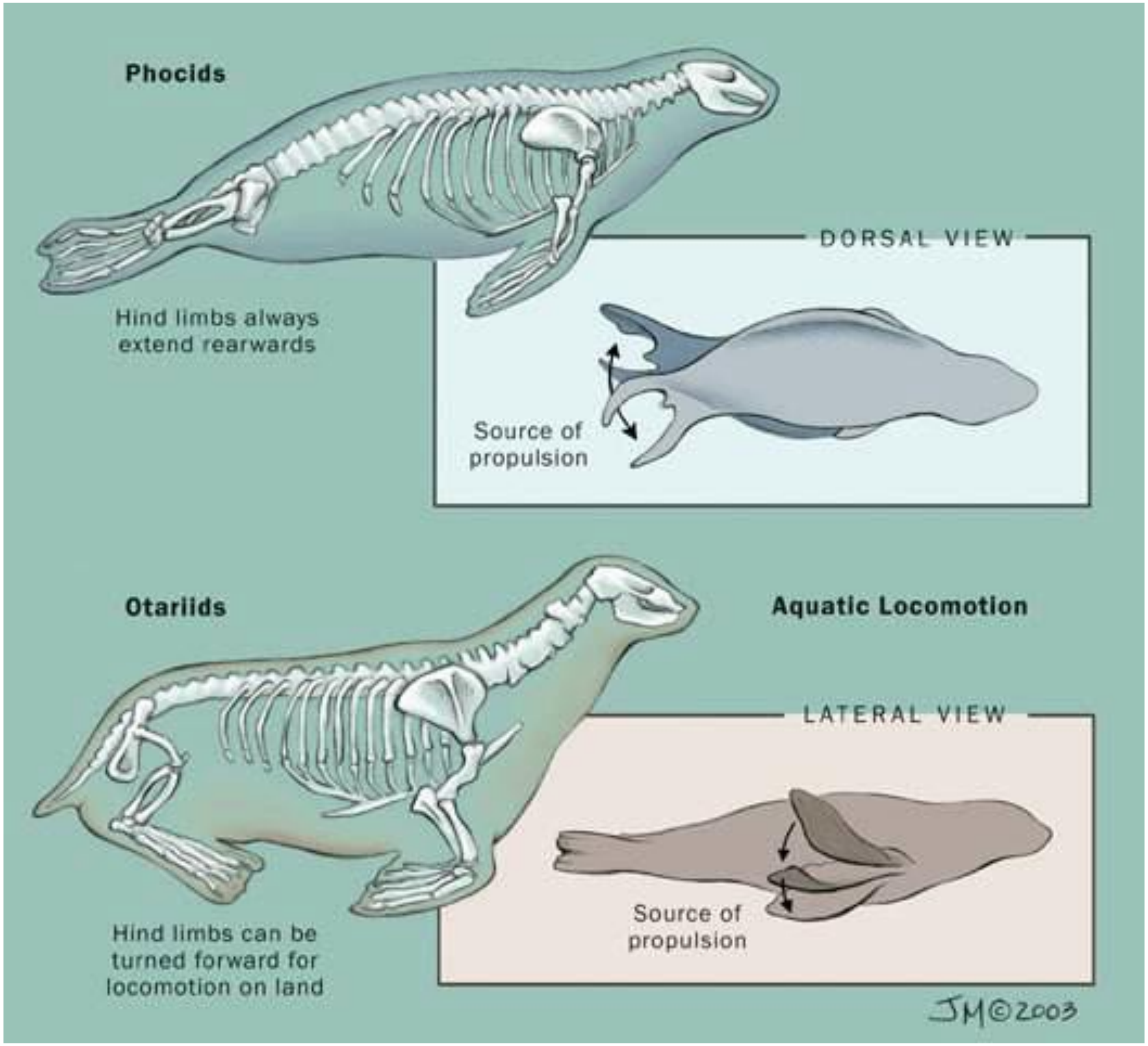


Figure 10.44 Fossil pinnipeds: (a–c) skull, restored head and skeleton of the late Oligocene and early Miocene enaliarctid *Enaliarctos*; (d) skeleton of the early Miocene desmatophocid *Allodesmus*; (e) skull of the late Miocene sealion *Thalassoleon*. Source: (a,b) Adapted from Mitchell and Tedford (1973). (c) A. Berta, San Diego State University, San Diego, CA, USA. Reproduced with permission. (d) Adapted from Mitchell (1975). (e) Adapted from Repenning and Tedford (1977).

Pinnipedia

Pinnipedia


Phocids
Hind limbs always extend rearwards
DORSAL VIEW
Source of propulsion
Otariids
Aquatic Locomotion
LATERAL VIEW
Source of propulsion
Hind limbs can be turned forward for locomotion on land
JM©2003

Pinnipedia: Phocidae

No poseen oído externo.

Aletas sirven poco para andar en tierra.

Phoca

Piscophoca

Mirounga

Pinnipedia: Otarioidea

The walruses (Odobenidae) succeeded the desmatophocids. They are first known approximately 14 million years ago, represented by the genus *Neotherium*. *Imagotaria*, which lived adjacent to the west coast of North America from 9 to 12 million years ago, probably includes the ancestors of the living species (Figure 20-63). In these forms, the simplified cheek teeth have only a single root. Most of the history of the Odobenidae is recorded around the Pacific Basin. The walruses established themselves in the North Atlantic between 8 and 5 million years ago and then reentered the North Pacific about 1 million years ago.

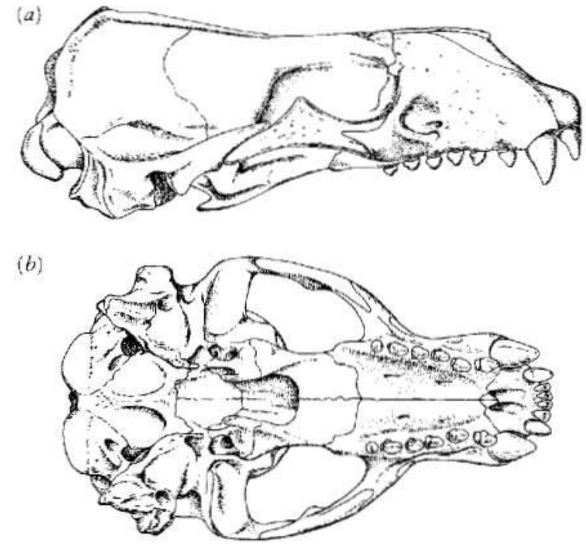
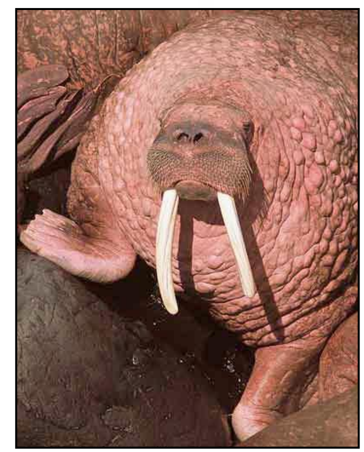


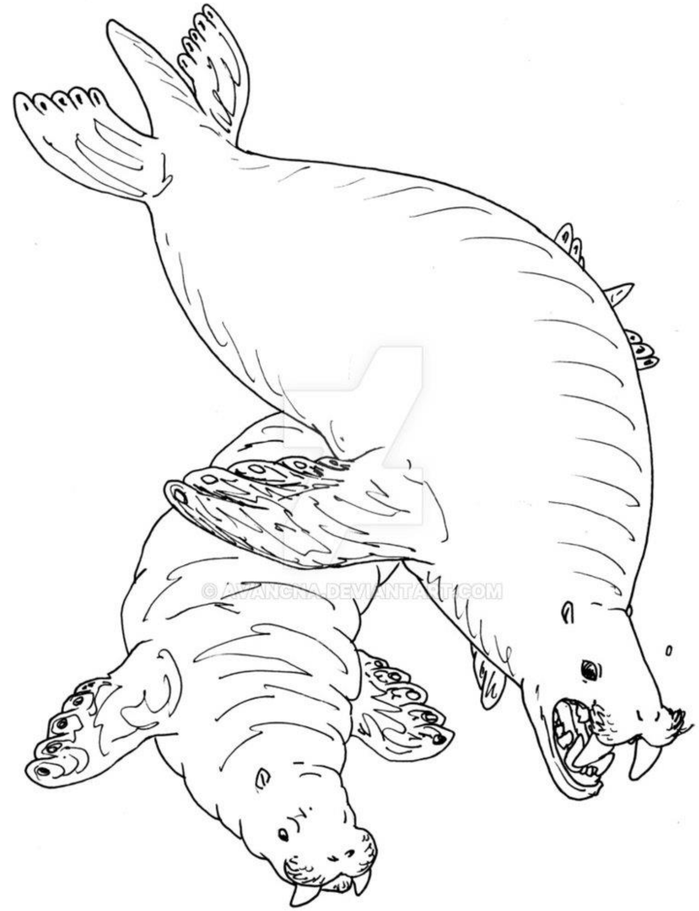
Figure 20-63. SKULL OF *IMAGOTARIA*. This genus is an ancestor of the modern walrus from the Miocene of western North America. (*a*) Lateral and (*b*) palatal views. Original 30 centimeters long. *From Repenning and Tedford, 1977.*

The Otariidae (fur seals and sea lions) are first represented by *Pithanotaria* from beds that are 11 million years old. Members of this genus are small and primitive in some respects, but they are already unmistakable otariids in the form of the postcranial skeleton. *Thalassoleon* is a well-known genus from the late Miocene (Figure 20-64). The modern genus *Eumetopias* is known from Japan at least 2 million years ago.



Pinnipedia: Otarioidea

Neotherium



Pithanotaria