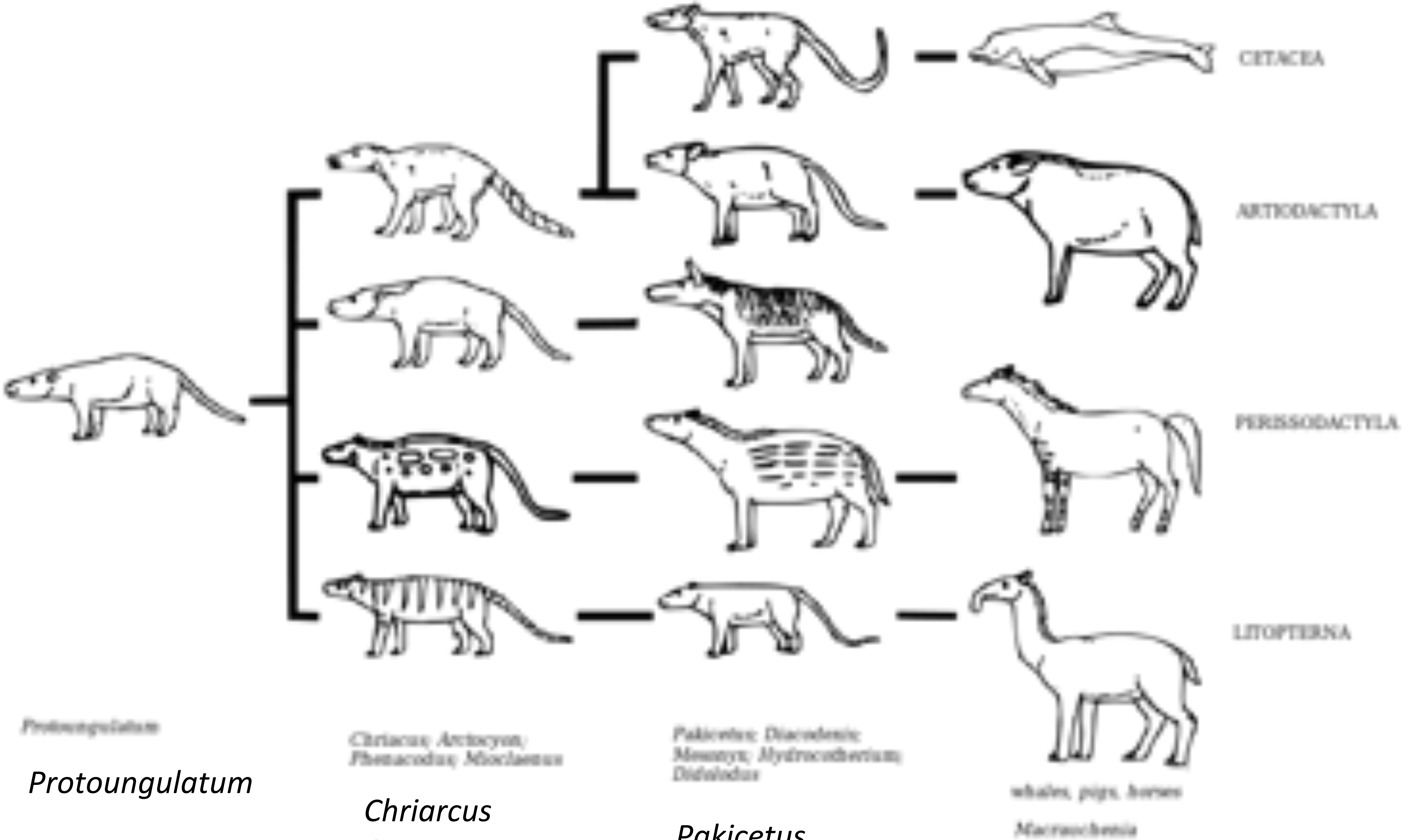


Protoungulatum

Chriarcus
Arctocyon
Phenacodus
Mioclaenus

Pakicetus
Diacodexis
Mesonyx
Hydrocotherium
Didolodus

Ballenas
Cerdos
Caballos
Macrauchenia

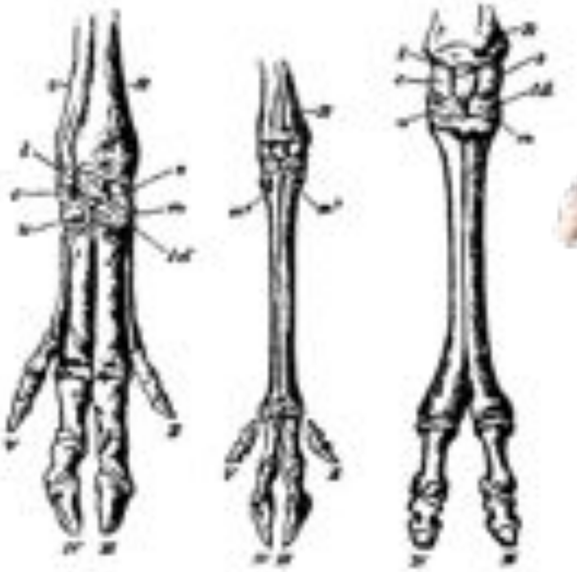
Perissodactyla:

Brontotheriidae

Megacerops (Brontotherium)

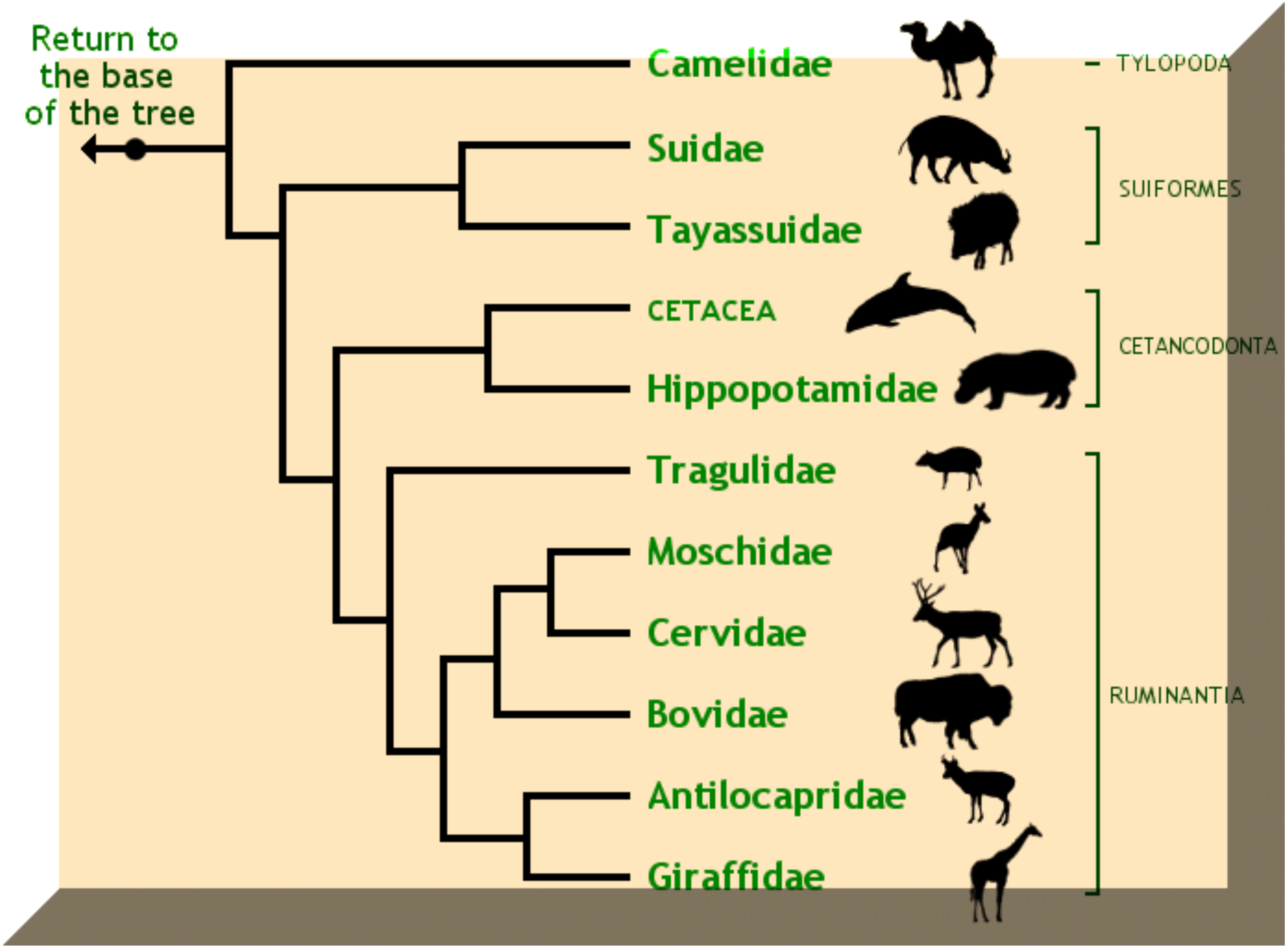
ARTIODACTYLA

Aprox 27 familias, 10 actuales. Desde el eoceno más temprano



Paraxónicos:
apoyados sobre
dedos 3 y 4 más
desarrollados

?



Filogenia molecular

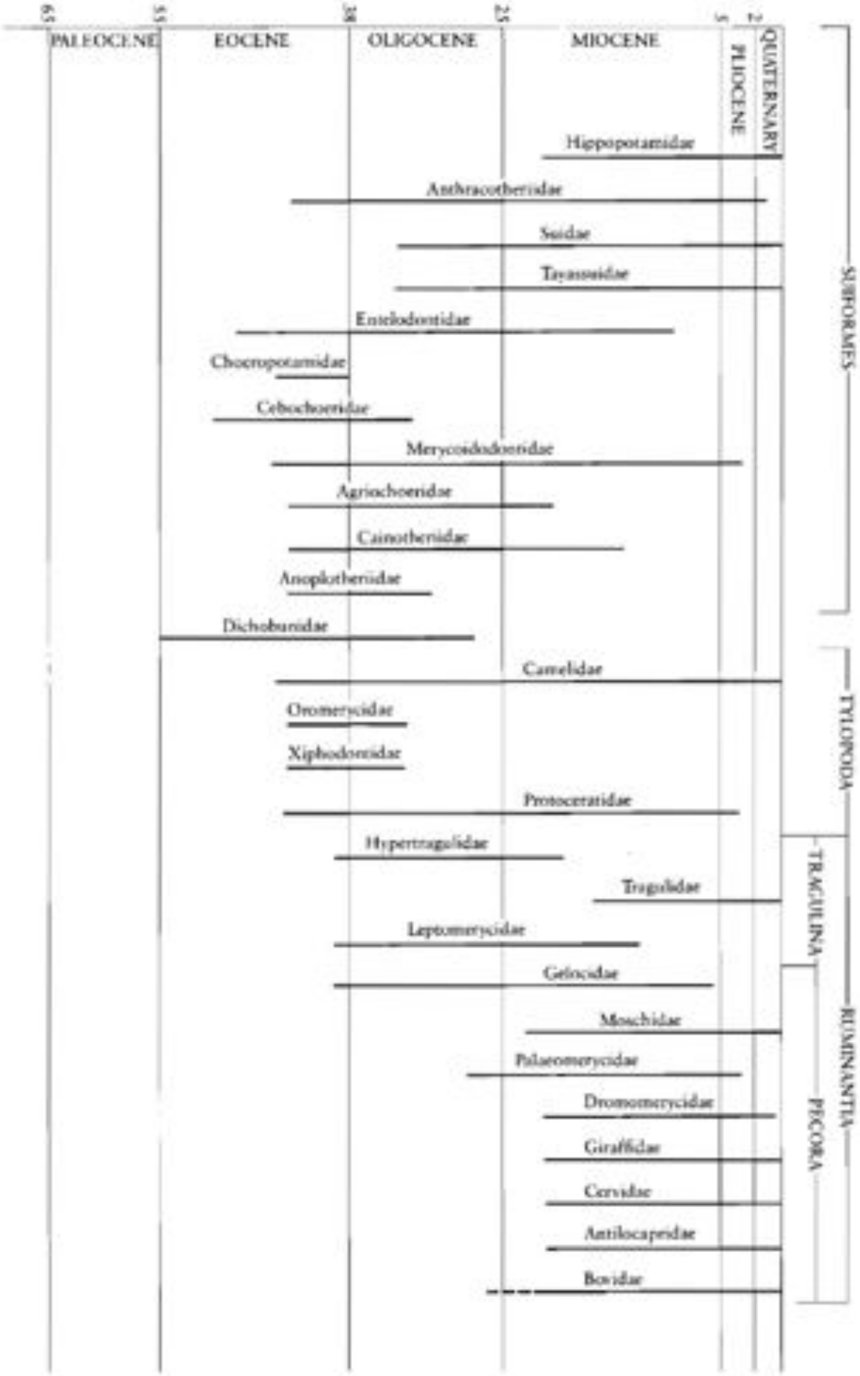
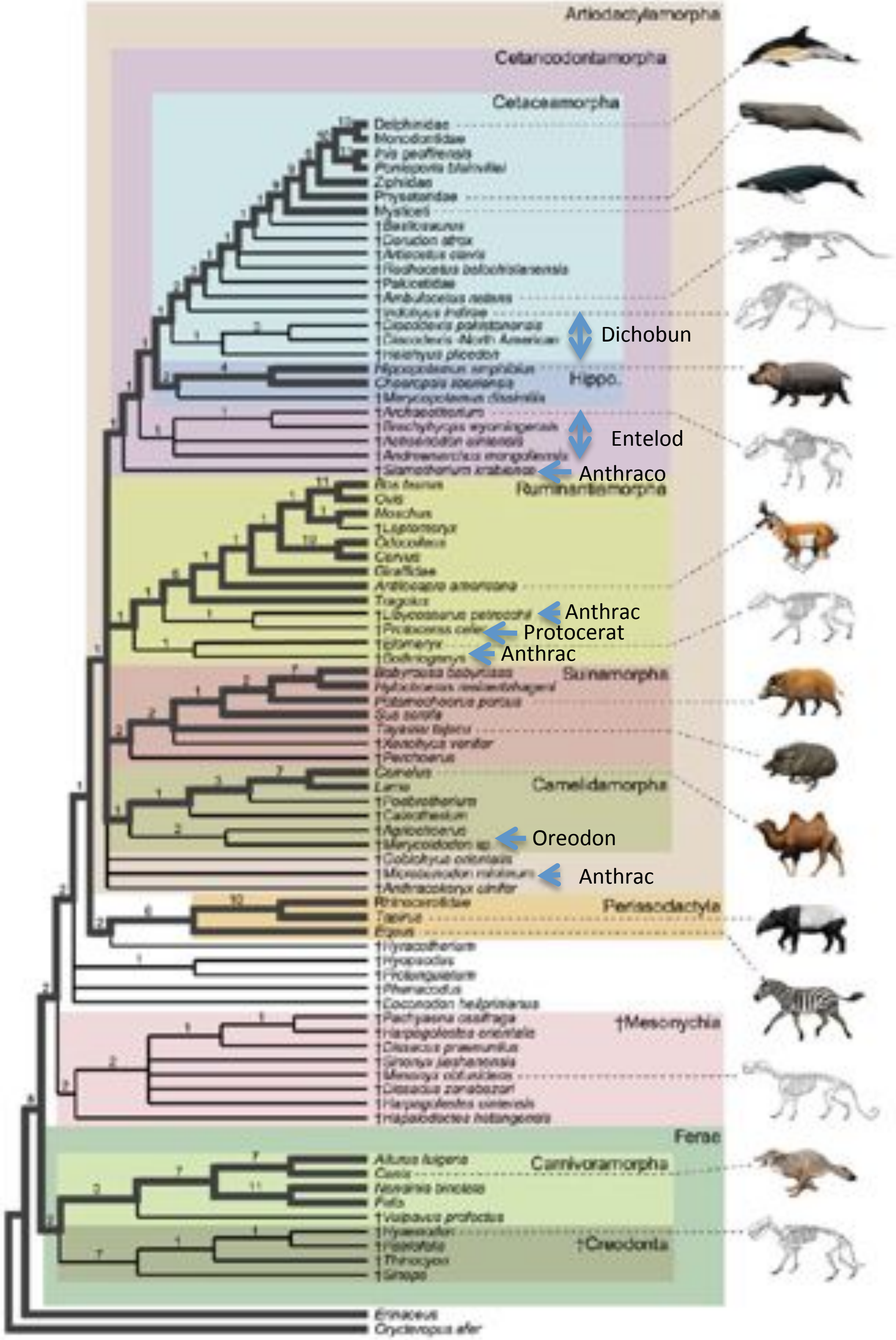


Figure 21-9. STRATIGRAPHIC RANGES OF ARTIODACTYL FAMILIES.

Artiodactyls radiated extensively in all the northern continents in the early and middle Eocene; approximately 20 families appeared by the late Eocene. By the end of the Eocene, all of the major groups of artiodactyls had emerged. Modern members of the order can be conveniently classified in three major groups: the suborder Suiformes, including the modern pigs, peccaries, and the hippopotamus; the Tylopoda (camels and llamas); and the Ruminantia, including tragulids, giraffes, deer, and the diverse assemblage of antelopes and cattle.

EVIDENCIA TOTAL



Es posible que los Cetáceos estén anidados dentro de Artiodactyla, sean su grupo hermano, o 2do outgroup. Hay acuerdo que los cetáceos son “ungulados” muy cercanos, pero mientras no se resuelvan los detalles no está claro cómo usar el nuevo término **Cetartiodactyla** (pese a que esté de moda reemplazar Artiodactyla por este término). Abajo, excelentes definiciones independientes de esta polémica.

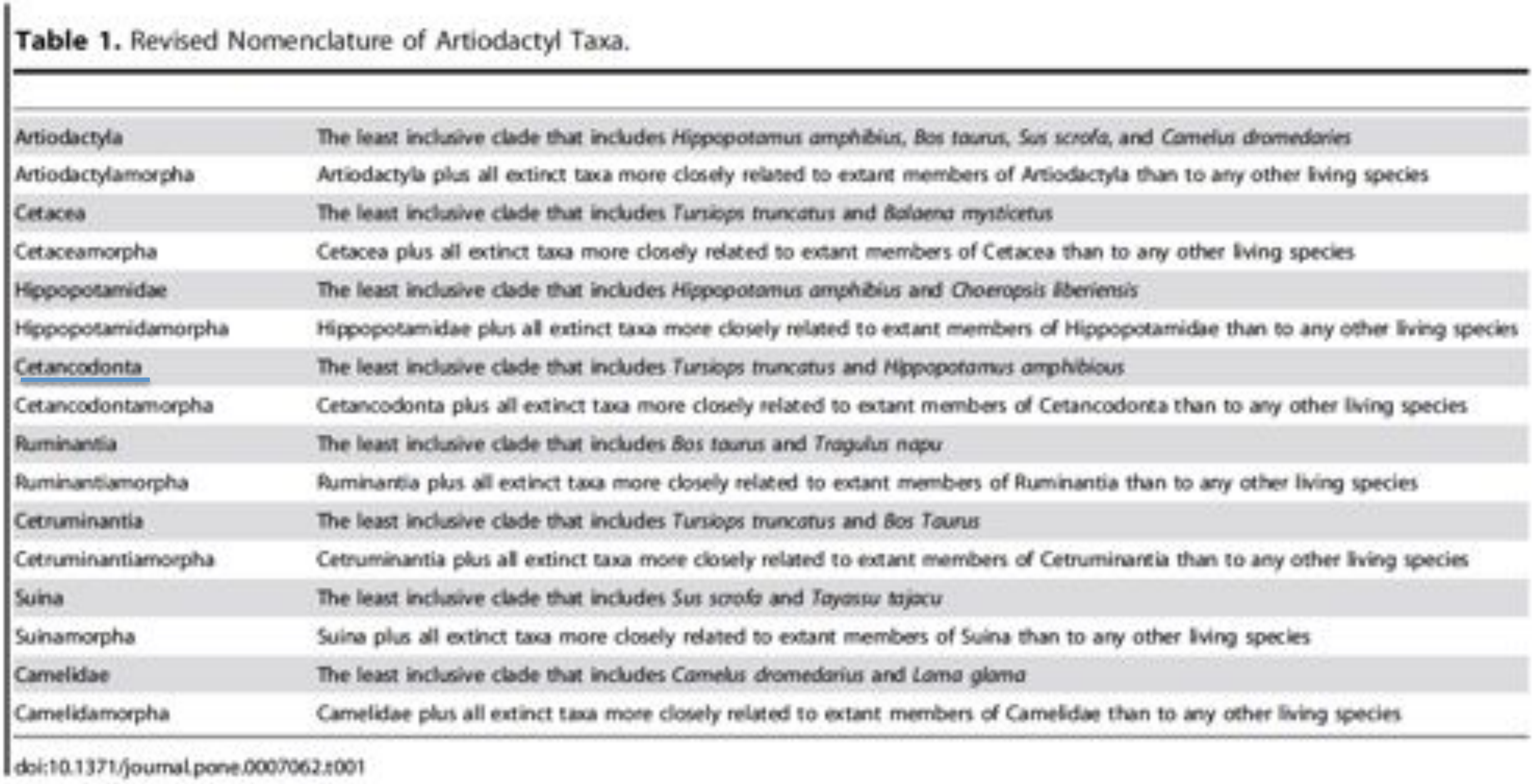


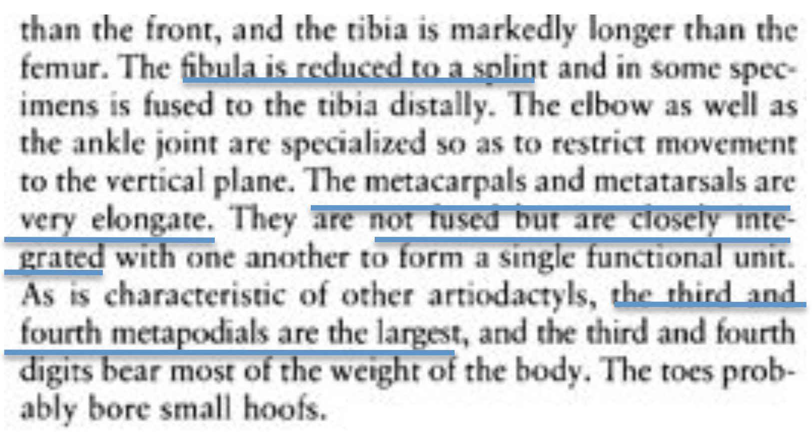
Table 1. Revised Nomenclature of Artiodactyl Taxa.

Artiodactyla	The least inclusive clade that includes *Hippopotamus amphibius, Bos taurus, Sus scrofa*, and *Camelus dromedaries*
Artiodactylamorpha	Artiodactyla plus all extinct taxa more closely related to extant members of Artiodactyla than to any other living species
Cetacea	The least inclusive clade that includes *Tursiops truncatus* and *Balaena mysticetus*
Cetaceamorpha	Cetacea plus all extinct taxa more closely related to extant members of Cetacea than to any other living species
Hippopotamidae	The least inclusive clade that includes *Hippopotamus amphibius* and *Choeropsis liberiensis*
Hippopotamidamorpha	Hippopotamidae plus all extinct taxa more closely related to extant members of Hippopotamidae than to any other living species
Cetancodonta	The least inclusive clade that includes *Tursiops truncatus* and *Hippopotamus amphibious*
Cetancodontamorpha	Cetancodonta plus all extinct taxa more closely related to extant members of Cetancodonta than to any other living species
Ruminantia	The least inclusive clade that includes *Bos taurus* and *Tragulus napu*
Ruminantiamorpha	Ruminantia plus all extinct taxa more closely related to extant members of Ruminantia than to any other living species
Cetruminantia	The least inclusive clade that includes *Tursiops truncatus* and *Bos Taurus*
Cetruminantiamorpha	Cetruminantia plus all extinct taxa more closely related to extant members of Cetruminantia than to any other living species
Suina	The least inclusive clade that includes *Sus scrofa* and *Tayassu tajacu*
Suinamorpha	Suina plus all extinct taxa more closely related to extant members of Suina than to any other living species
Camelidae	The least inclusive clade that includes *Camelus dromedarius* and *Lama glama*
Camelidamorpha	Camelidae plus all extinct taxa more closely related to extant members of Camelidae than to any other living species

doi:10.1371/journal.pone.0007062.t001

Cetancodonta: creado por evidencia molecular que indica que los cetáceos son afines a los hipopótamos

“Dichobunidae” (parafilético). 1eras formas muy pequeñas y ágiles, de extremidades alargadas



than the front, and the tibia is markedly longer than the femur. The fibula is reduced to a splint and in some specimens is fused to the tibia distally. The elbow as well as the ankle joint are specialized so as to restrict movement to the vertical plane. The metacarpals and metatarsals are very elongate. They are not fused but are closely integrated with one another to form a single functional unit. As is characteristic of other artiodactyls, the third and fourth metapodials are the largest, and the third and fourth digits bear most of the weight of the body. The toes probably bore small hoofs.

Diacodexis ya es paraxónico como todos los Artiodactylos modernos

Plesiomorfías: Clavícula presente, ulna completa no fusionada al radio, cuboide y navicular separados, mano y pie de 5 dedos, tercer trocanter, metapodiales no fusionados

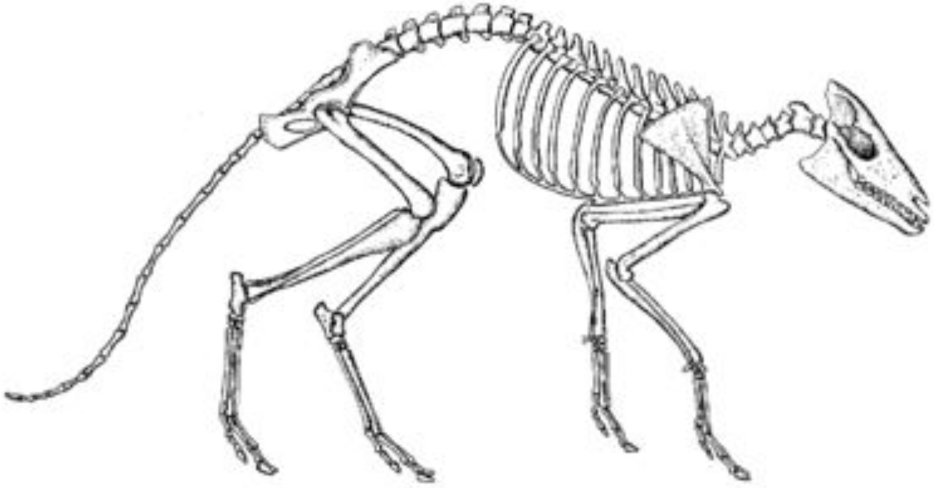


Figure 21-10. SKELETON OF THE LOWER EOCENE ARTIODACTYL *DIACODEXIS*, ABOUT THE SIZE OF A RABBIT. The limb structure is very specialized for cursorial locomotion. *From Rose, 1982. With permission from* Science. *Copyrigh 1982 by the American Association for the Advancement of Science.*

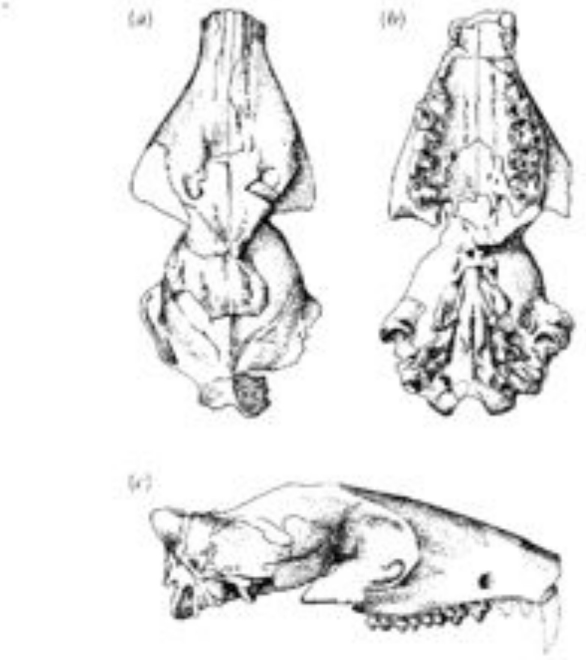
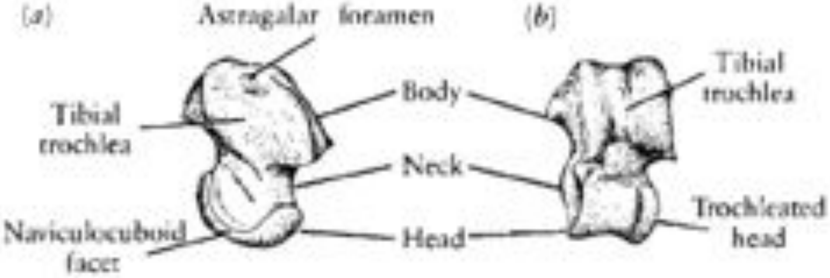


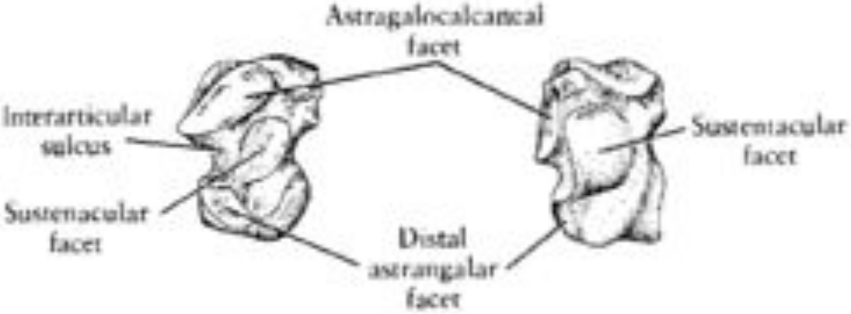
Figure 21-13. SKULL OF THE PRIMITIVE ARTIODACTYL *HOMACODON.* (*a*) Dorsal, (*b*) palatal, and (*c*) lateral views, × ½. This genus may be close to the ancestry of several advanced artiodactyl families. *From Sinclair, 1914.*

Diacodexis puede incluso ser Cetaceomorpha

Fusión y reducción de la Ulna en la evolución de perisodátilos



Vista anterior



Vista posterior (palmar)

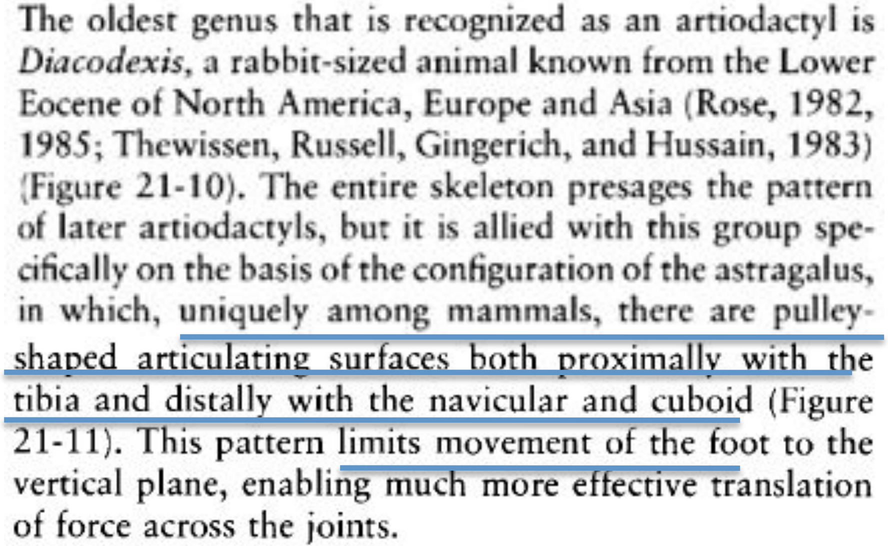
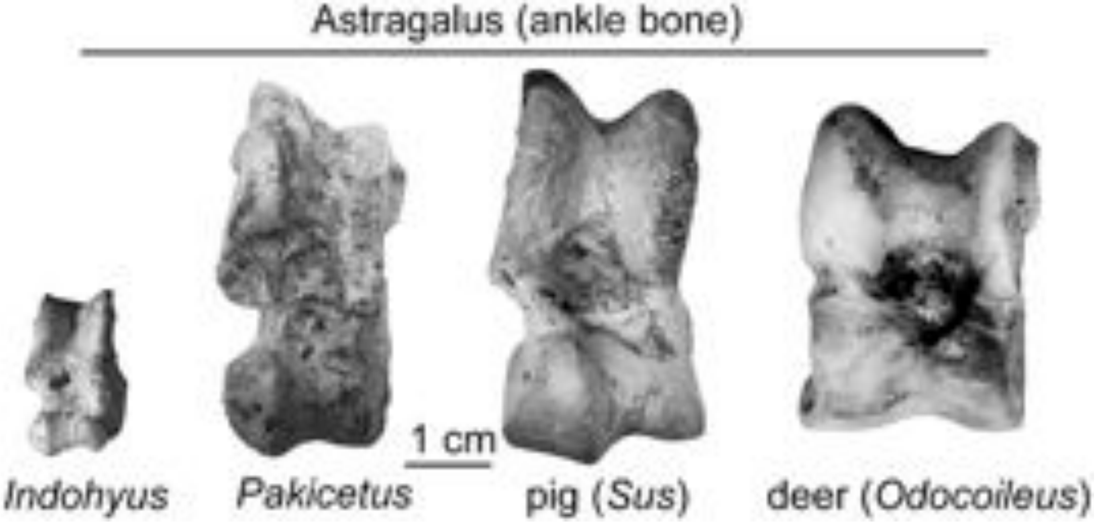
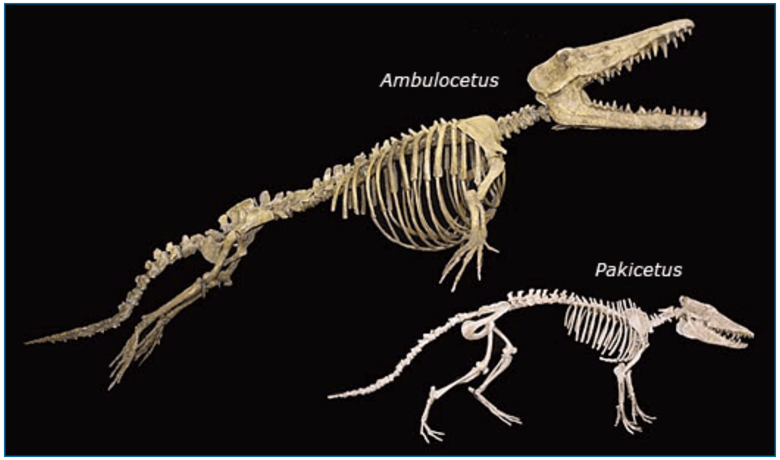

The oldest genus that is recognized as an artiodactyl is *Diacodexis*, a rabbit-sized animal known from the Lower Eocene of North America, Europe and Asia (Rose, 1982, 1985; Thewissen, Russell, Gingerich, and Hussain, 1983) (Figure 21-10). The entire skeleton presages the pattern of later artiodactyls, but it is allied with this group specifically on the basis of the configuration of the astragalus, in which, uniquely among mammals, there are pulley-shaped articulating surfaces both proximally with the tibia and distally with the navicular and cuboid (Figure 21-11). This pattern limits movement of the foot to the vertical plane, enabling much more effective translation of force across the joints.

Figure 21-11. Comparison of the astragalus of (*a*) the hyopsodont *Choeroclaenus* and (*b*) the primitive artiodactyl *Diacodexis*. The proximal and distal articulating surfaces of *Diacodexis* are in the shape of a pulley, which allows controlled flexion in the vertical plane between the lower leg and the foot. *From Schaeffer, 1947.* (*c*) Foot of a primitive artiodactyl, the oreodon *Agriochoerus*. *From Scott, 1940.*

El astrágalo de los artiodactylos es ***absolutamente distintivo.***

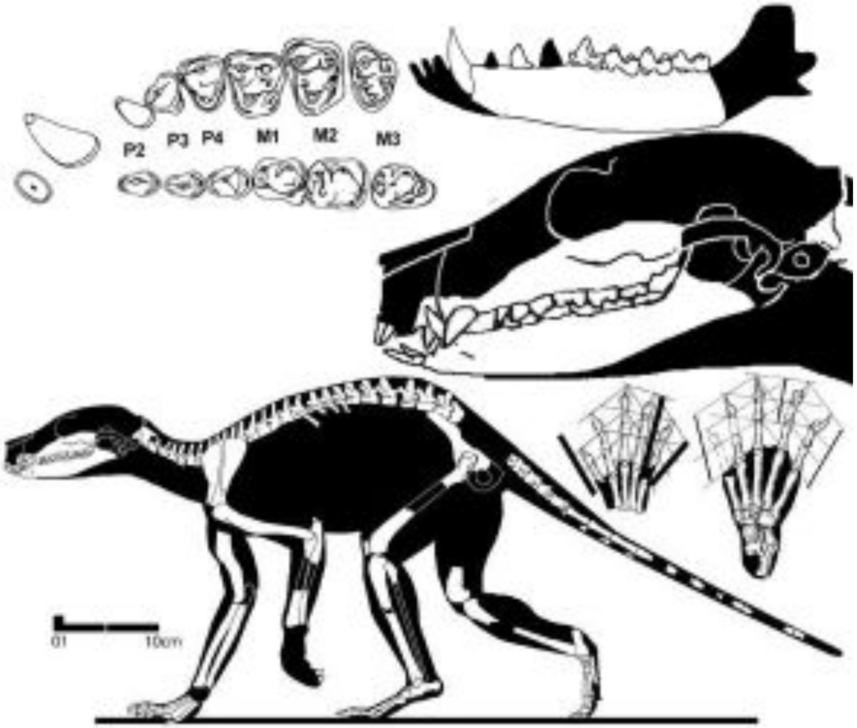
Su presencia en stem cetaceos como *Pakicetus y Rhodocetus* indica afinidades artiodáctilas de los Cetáceos (apoyada además por la evidencia molecular)





Pakicetus

Arctocyonidae: "Condilartros" carnívoros-omnívoros del Paleoceno-Eoceno, propuestos como ancestros de Artiodactyla (Serían Artiodactylomorpha).



Chriacus

Arctocyon

La dentición de los Dichobunidae sugiere afinidad con Arctocyonidae como *Chriacus*

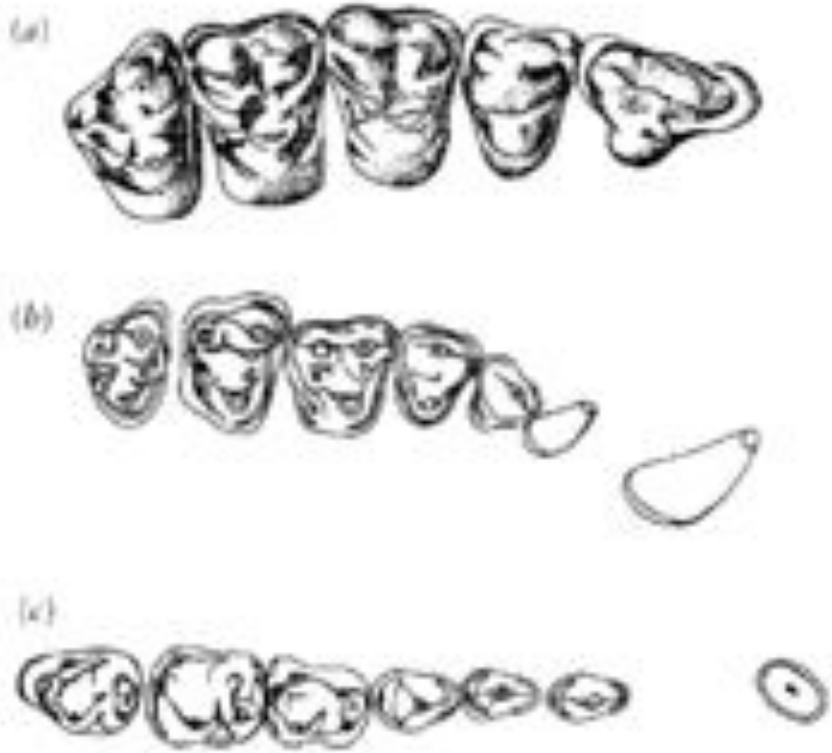
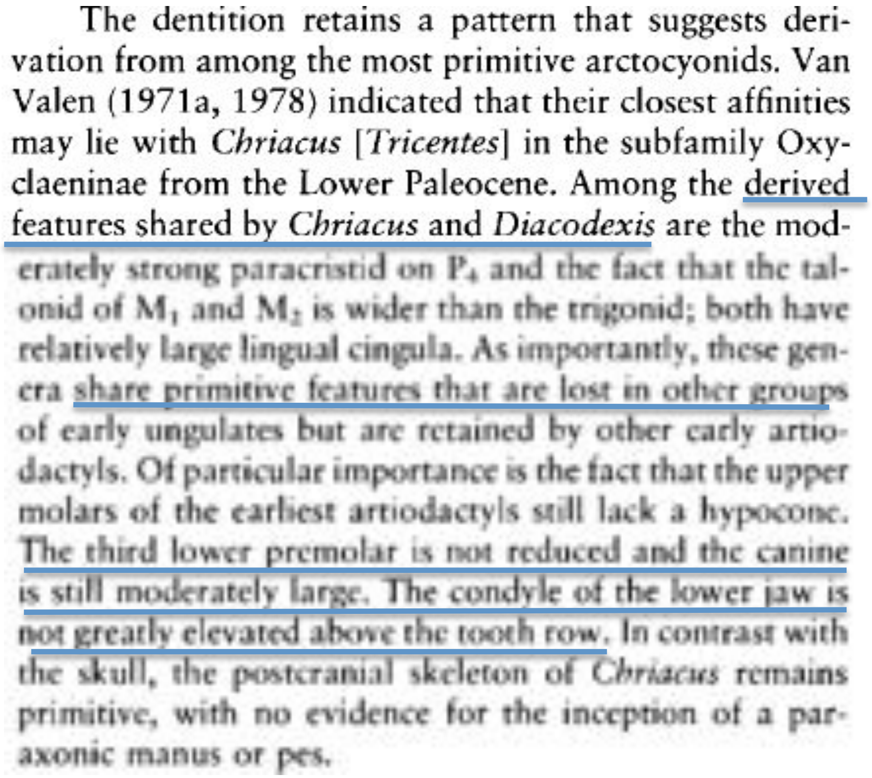
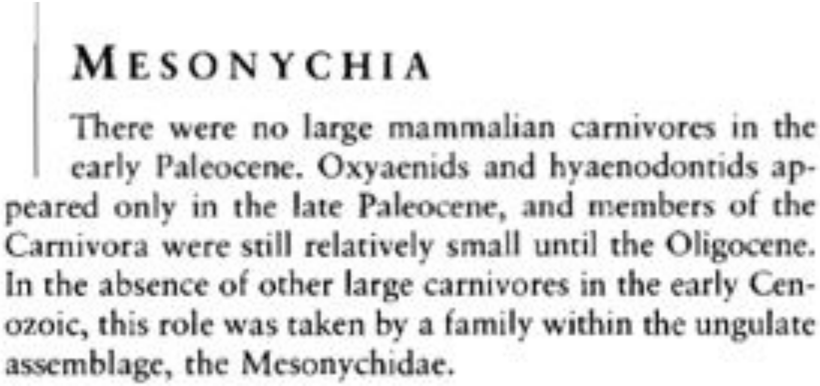


Figure 21-12. (*a*) Upper molars and posterior premolars of the earliest artiodactyl *Diacodexis*, ×3. *From Sinclair, 1914.* (*b*) Upper dentition of the oxyclaenine arctocyonid *Chriacus* [*Tricentes*], which is close to the pattern of primitive artiodactyls, ×1. *From Matthew, 1937.* (*c*) Lower dentition of *Chriacus*. *From Matthew, 1937.*



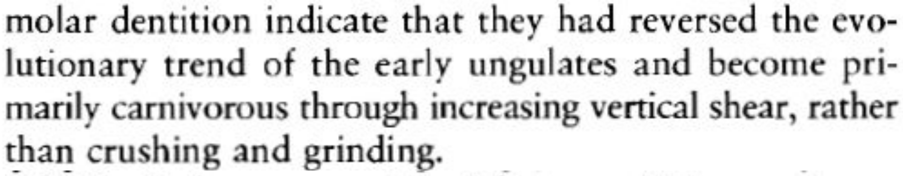
The dentition retains a pattern that suggests derivation from among the most primitive arctocyonids. Van Valen (1971a, 1978) indicated that their closest affinities may lie with *Chriacus* [*Tricentes*] in the subfamily Oxyclaeninae from the Lower Paleocene. Among the derived features shared by *Chriacus* and *Diacodexis* are the moderately strong paracristid on P_4 and the fact that the talonid of M_1 and M_2 is wider than the trigonid; both have relatively large lingual cingula. As importantly, these genera share primitive features that are lost in other groups of early ungulates but are retained by other early artiodactyls. Of particular importance is the fact that the upper molars of the earliest artiodactyls still lack a hypocone. The third lower premolar is not reduced and the canine is still moderately large. The condyle of the lower jaw is not greatly elevated above the tooth row. In contrast with the skull, the postcranial skeleton of *Chriacus* remains primitive, with no evidence for the inception of a paraxonic manus or pes.



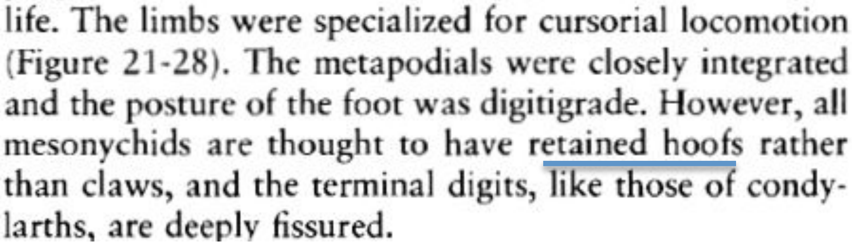
MESONYCHIA

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.

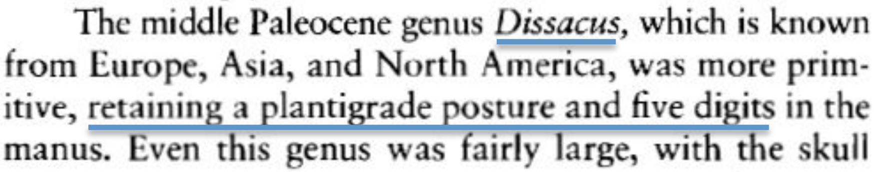
- Se consideran derivados de los condilartros arctocyonidos, triisodontinos.
- Semejanzas dentales con stem cetaceos



molar dentition indicate that they had reversed the evolutionary trend of the early ungulates and become primarily carnivorous through increasing vertical shear, rather than crushing and grinding.



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

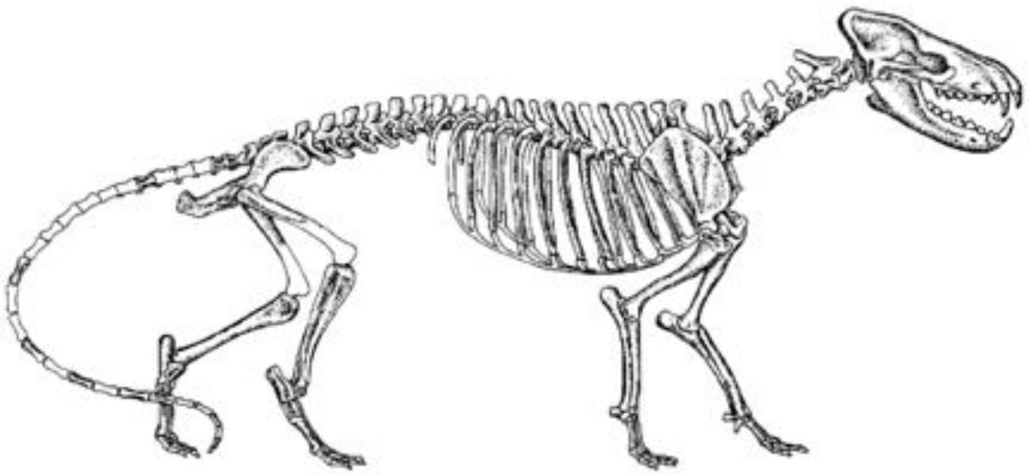
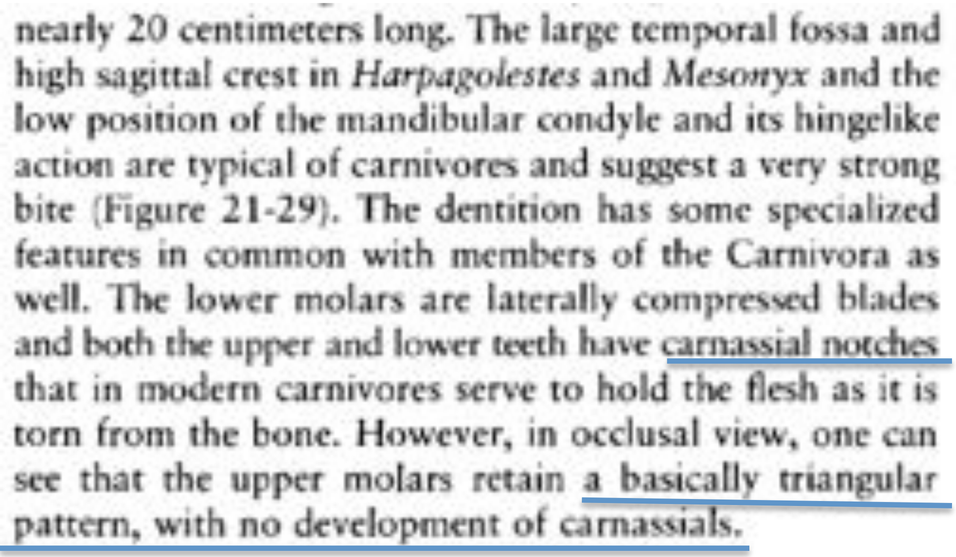
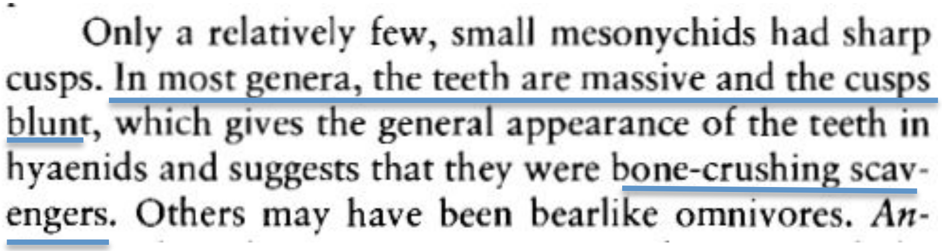


Figure 21-28. *MESONYX.* Skeleton of a carnivorous mesonychid from the Eocene of North America. *From Scott, 1888.*

Algunas convergencias con la dentición de Carnivora.



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.



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-*

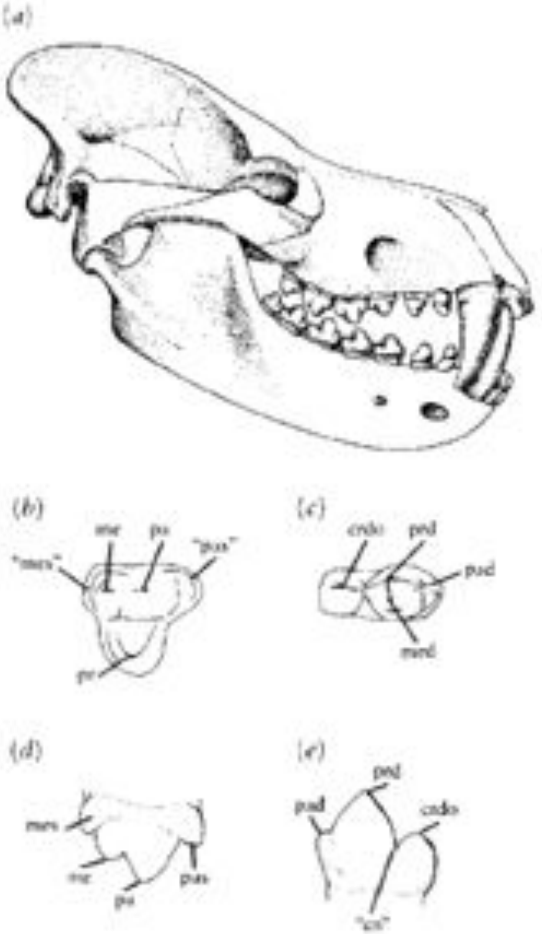
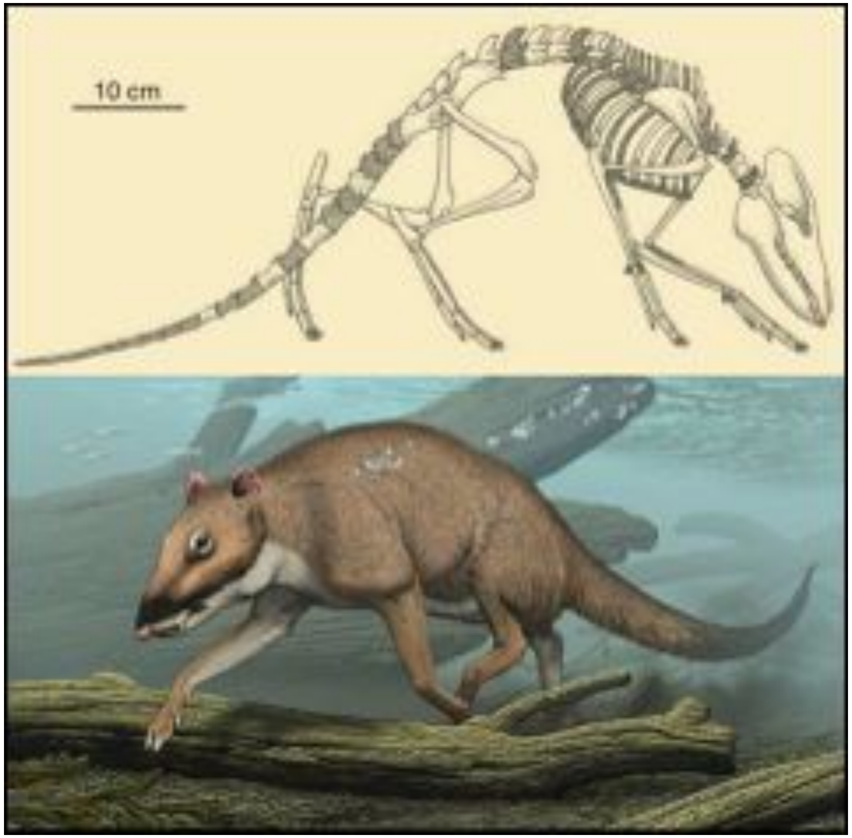


Figure 21-29. (*a*) Skull of the mesonychid *Harpagolestes*. (*b* to *e*) Molar teeth of the middle Paleocene mesonychid *Dissacus*. (*b*) and (*d*) are occlusal and buccal views of right upper molar. (*c*) and (*e*) are occlusal and buccal views of left lower molar. Abbreviations as follows: "cn," analogous 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.*

El astrágalo-calcáneo de mesoníquidos es primitivo, el de stem cetacea es tipicamente artiodáctylo

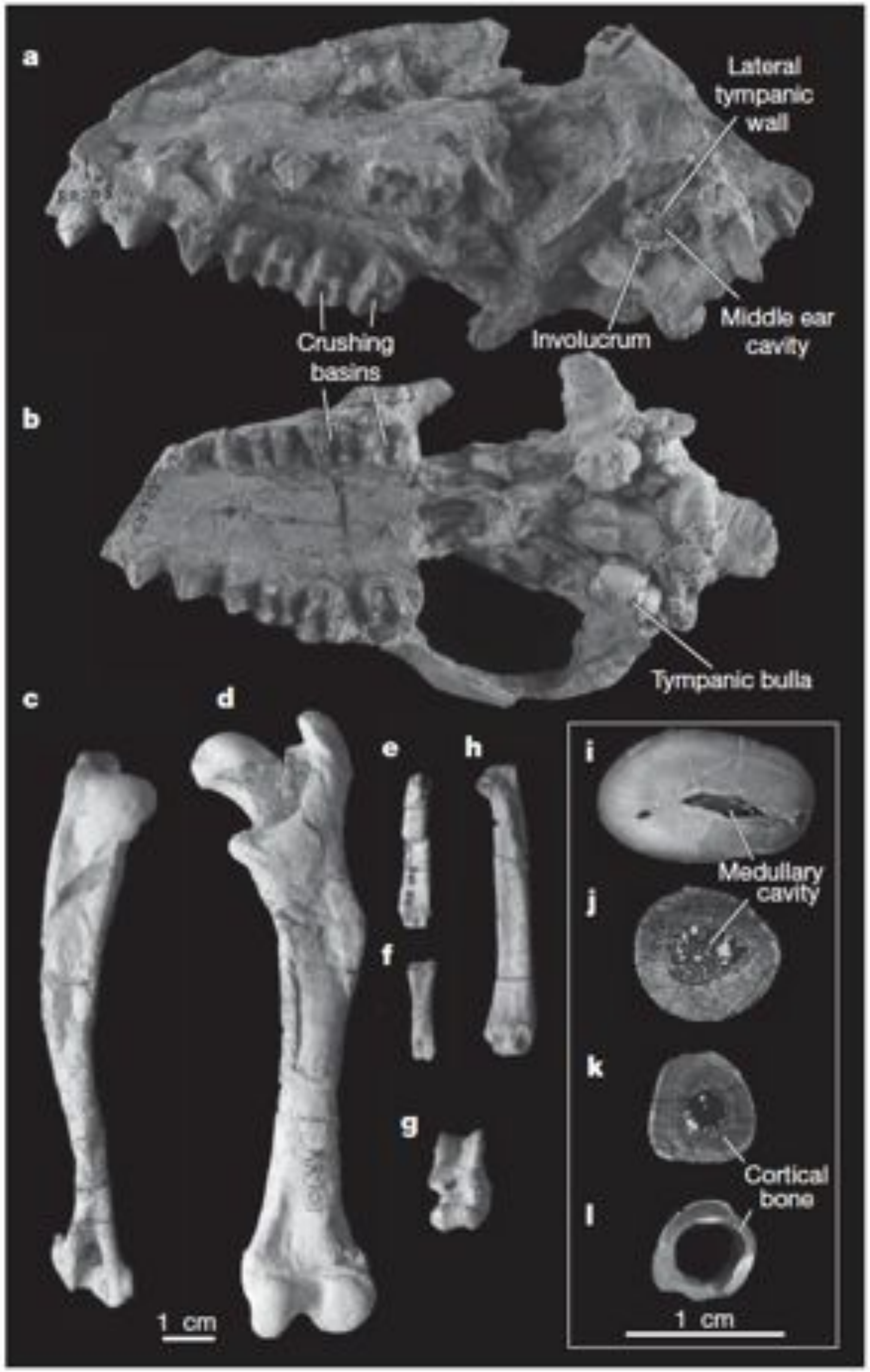
Raoellidae. Antiguamente considerados una forma de Dichobunidae. Actualmente se consideran Cetaceomorfos,

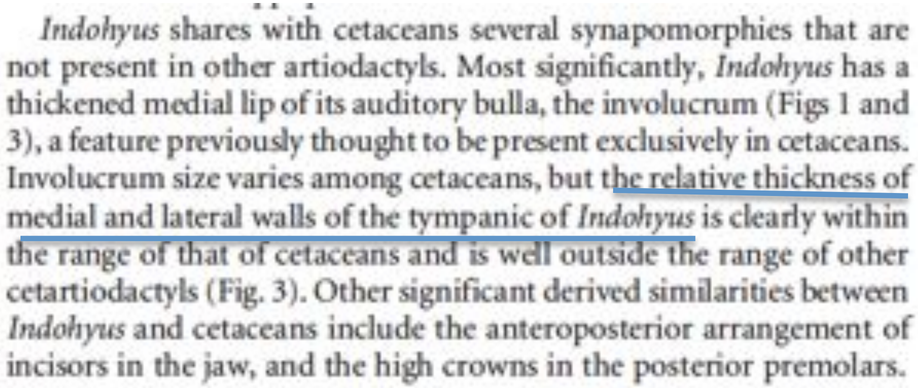


δO18 values and **osteosclerotic bones** indicate that the raccoon-like Indohyus was habitually aquatic, but δC13 values suggest that it rarely fed in the water.

Indohyus

Engrosamiento medial de la bulla: involucrum




Indohyus shares with cetaceans several synapomorphies that are not present in other artiodactyls. Most significantly, *Indohyus* has a thickened medial lip of its auditory bulla, the involucrum (Figs 1 and 3), a feature previously thought to be present exclusively in cetaceans. Involucrum size varies among cetaceans, but the relative thickness of medial and lateral walls of the tympanic of *Indohyus* is clearly within the range of that of cetaceans and is well outside the range of other cetartiodactyls (Fig. 3). Other significant derived similarities between *Indohyus* and cetaceans include the anteroposterior arrangement of incisors in the jaw, and the high crowns in the posterior premolars.

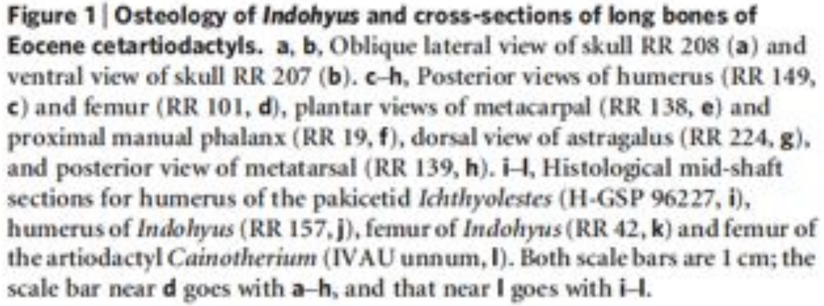
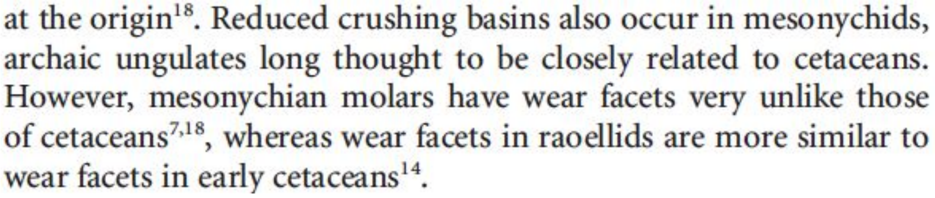
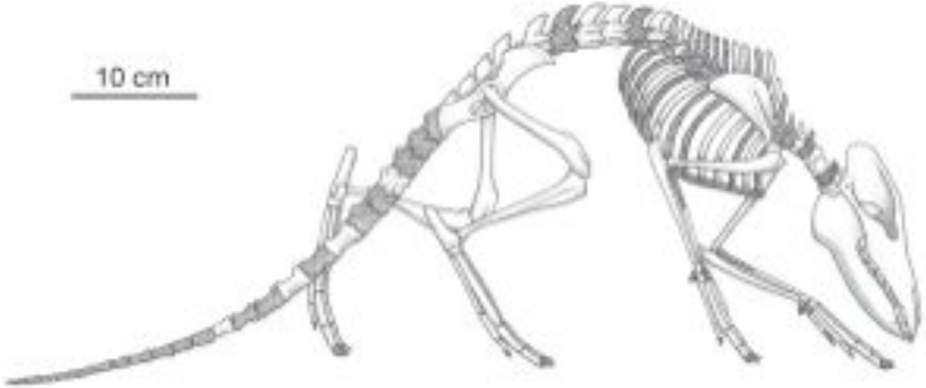
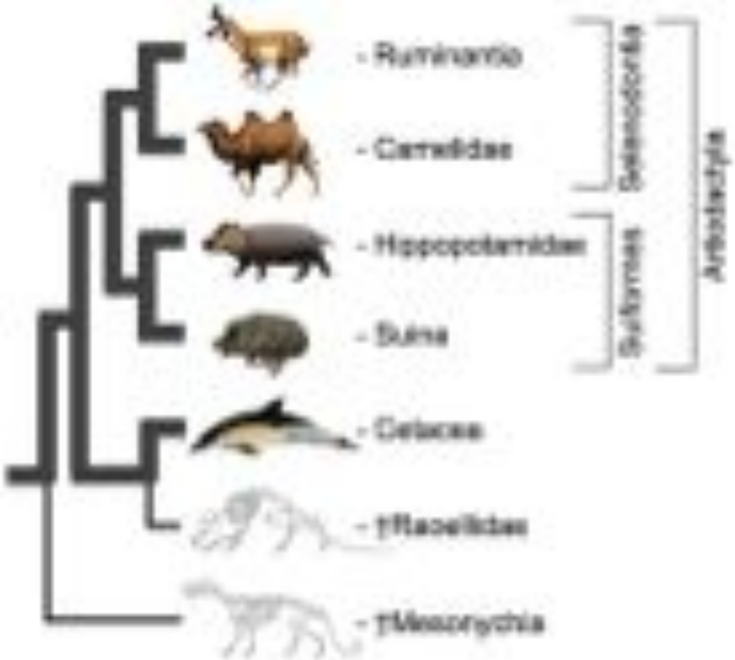


Figure 1 | Osteology of *Indohyus* and cross-sections of long bones of Eocene cetartiodactyls. **a**, **b**, Oblique lateral view of skull RR 208 (**a**) and ventral view of skull RR 207 (**b**). **c**–**h**, Posterior views of humerus (RR 149, **c**) and femur (RR 101, **d**), plantar views of metacarpal (RR 138, **e**) and proximal manual phalanx (RR 19, **f**), dorsal view of astragalus (RR 224, **g**), and posterior view of metatarsal (RR 139, **h**). **i**–**l**, Histological mid-shaft sections for humerus of the pakicetid *Ichthyolestes* (H-GSP 96227, **i**), humerus of *Indohyus* (RR 157, **j**), femur of *Indohyus* (RR 42, **k**) and femur of the artiodactyl *Cainotherium* (IVAU unnum, **l**). Both scale bars are 1 cm; the scale bar near **d** goes with **a**–**h**, and that near **l** goes with **i**–**l**.

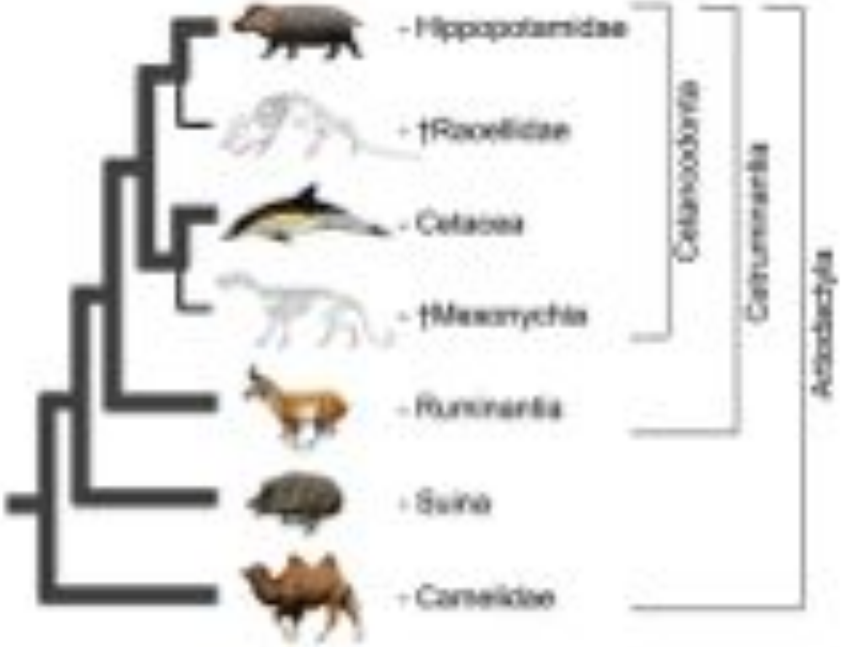

at the origin[18]. Reduced crushing basins also occur in mesonychids, archaic ungulates long thought to be closely related to cetaceans. However, mesonychian molars have wear facets very unlike those of cetaceans[7,18], whereas wear facets in raoellids are more similar to wear facets in early cetaceans[14].



Otros artiodáctilos semiacuáticos: Los Tragulidae (ruminantia basales) e Hipopótamos.

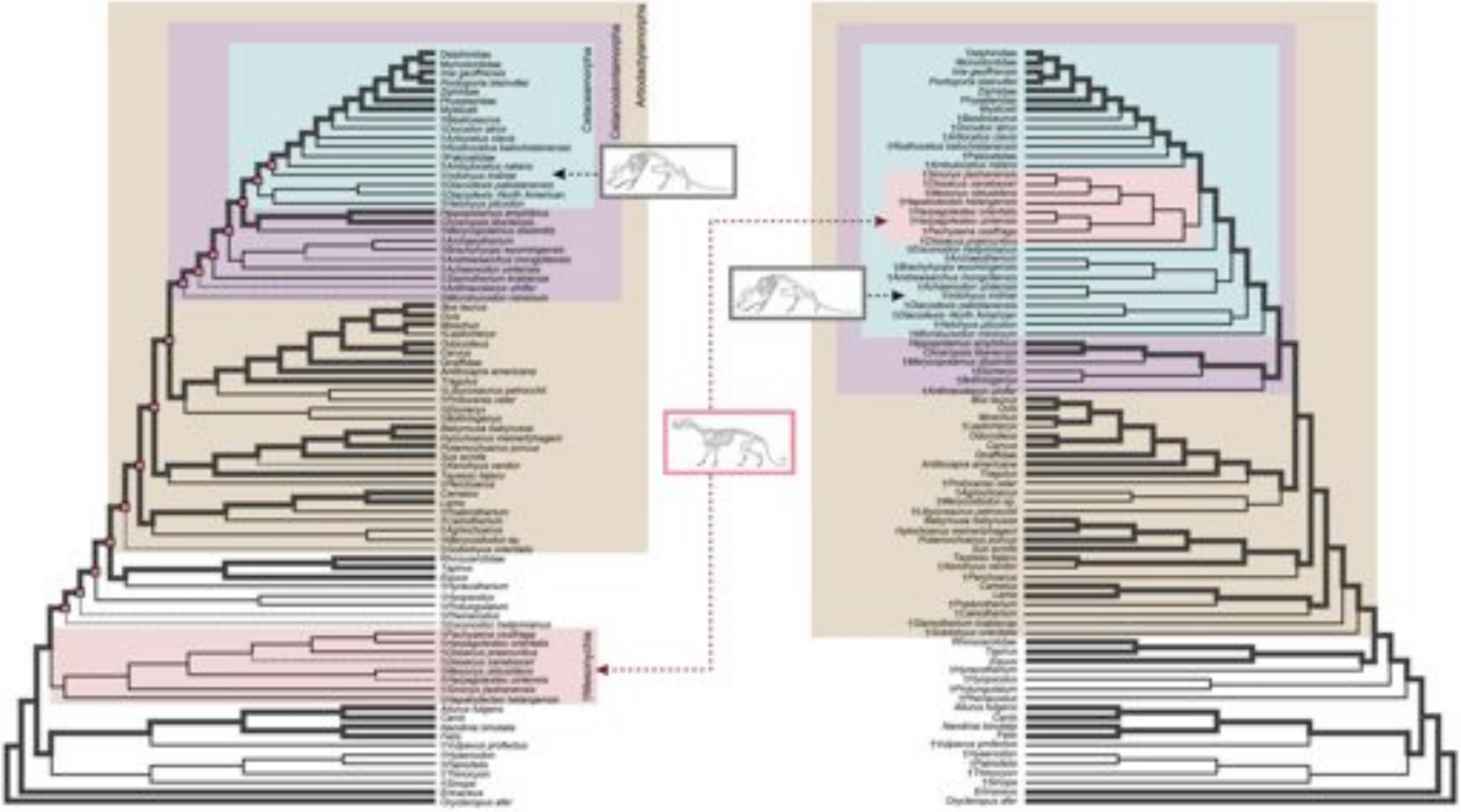


A) Thewissen et al., 2007



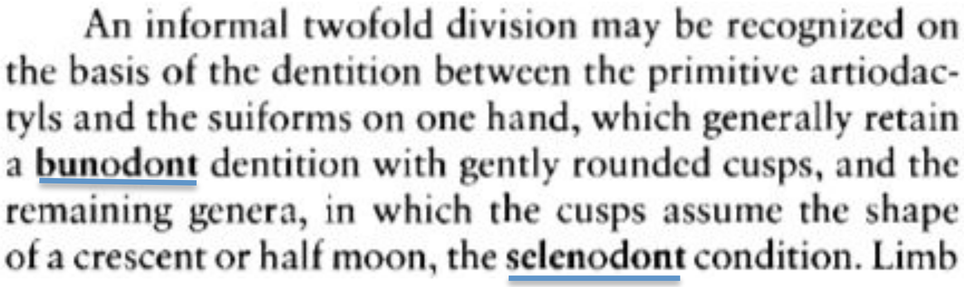
B) O'Leary and Gatesy, 2008

Posiciones inestables en el árbol mixto.



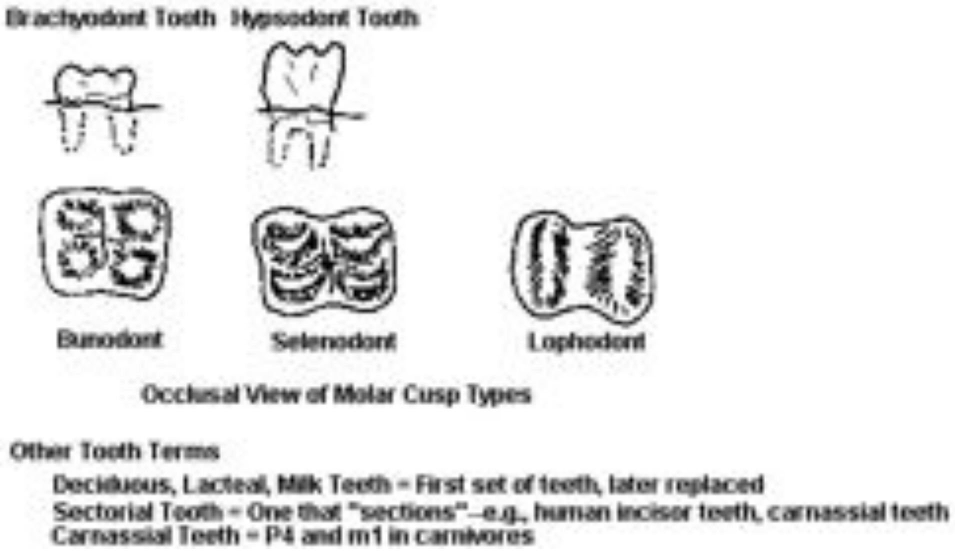
A) A most parsimonious tree; 57,269 steps

B) Two steps beyond minimum length; 57,271 steps



An informal twofold division may be recognized on the basis of the dentition between the primitive artiodactyls and the suiforms on one hand, which generally retain a **bunodont** dentition with gently rounded cusps, and the remaining genera, in which the cusps assume the shape of a crescent or half moon, the **selenodont** condition. Limb

Ciervo selenodonte
(Ruminantia)



Other Tooth Terms

Deciduous, Lacteal, Milk Teeth = First set of teeth, later replaced
Sectorial Tooth = One that "sections"–e.g., human incisor teeth, carnassial teeth
Carnassial Teeth = P4 and m1 in carnivores

Pecarí bunodonte
(Suiformes)

Existen muchísmas formas que han sido clasificadas como “Suiformes” por sus dientes pero bunodontes, pero es una plesiomorfía (condición primitiva, no sirve para agrupar)

La dentición Bunodonta es derivada respecto a la de Diacodexidae, teniendo cuspides más bulbosas de los molares, y un cíngulo más continuo. Además los artiodactylos "bunodontos" suelen tener mayor tamaño corporal. Existen muchas formas que han sido clasificadas como "Suiformes" por tener dentición Bunodonta pero esto es una plesiomorfía para artiodactylos corona. Por ej, actualment se considera que muchos "suiformes" son en realidad más cercanos a los cetáceos.

Los **"Anthracotheriidae"** son un grupo de artiodáctilos basales bunodontos de asia (eoceno), norteamérica (oligoceno-mioceno) y áfrica (oligoceno-plioceno), con 4 dedos en la pata trasera,, de patas cortas, no corredores, y tafonomía que sugiere vida anfibia. Aunque tradicionalmente considerados como Suiformes, los últimos análisis indican que en realidad son parafiléticos, conteniendo formas relacionadas a los hipopótamos (Cetacodontomorfa) sino además ruminantomorphos y artiodáctylos basales a todos los grupos.

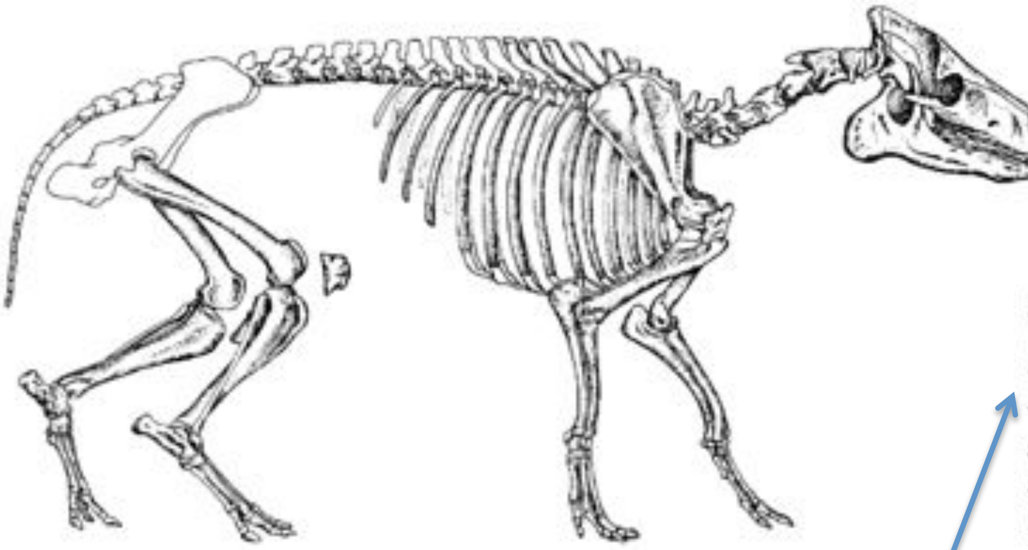
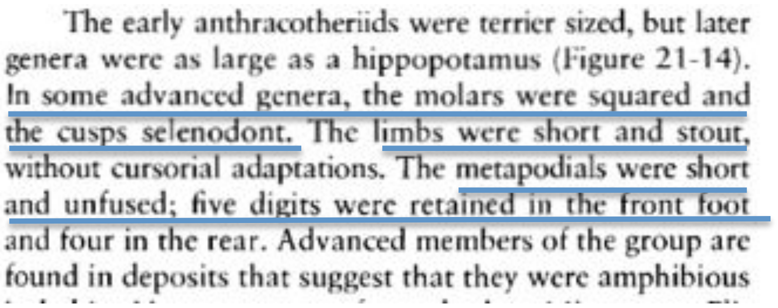


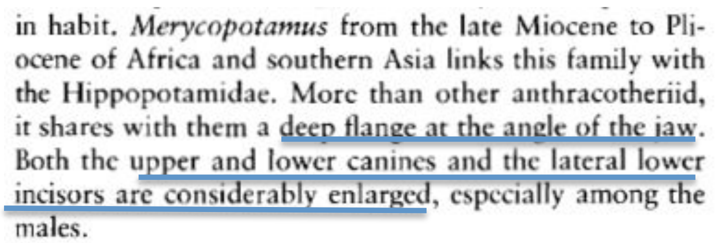
Figure 21-14. THE ANTHRACOTHERID *ANCODUS*. From the Oligocene of western North America, $\times\frac{1}{10}$. *From Scott, 1894.*



The early anthracotheriids were terrier sized, but later genera were as large as a hippopotamus (Figure 21-14). In some advanced genera, the molars were squared and the cusps selenodont. The limbs were short and stout, without cursorial adaptations. The metapodials were short and unfused; five digits were retained in the front foot and four in the rear. Advanced members of the group are found in deposits that suggest that they were amphibious

Ancestros de formas selenodontas?

Hippopotamidae



in habit. *Merycopotamus* from the late Miocene to Pliocene of Africa and southern Asia links this family with the Hippopotamidae. More than other anthracotheriid, it shares with them a deep flange at the angle of the jaw. Both the upper and lower canines and the lateral lower incisors are considerably enlarged, especially among the males.

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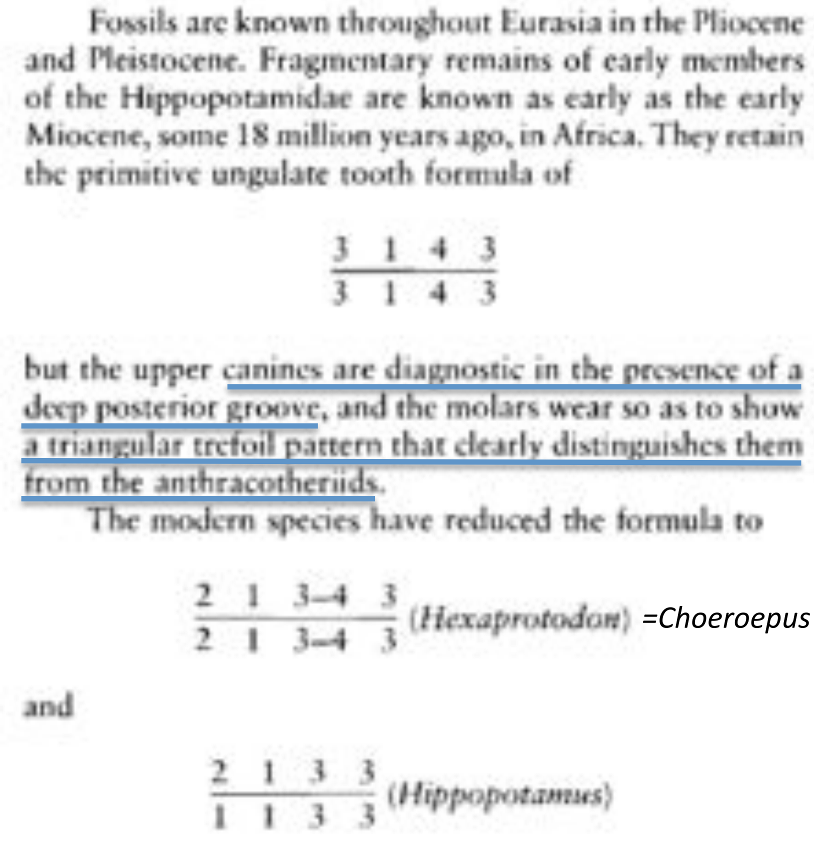

Fossils are known throughout Eurasia in the Pliocene and Pleistocene. Fragmentary remains of early members of the Hippopotamidae are known as early as the early Miocene, some 18 million years ago, in Africa. They retain the primitive ungulate tooth formula of

$$\frac{3\quad 1\quad 4\quad 3}{3\quad 1\quad 4\quad 3}$$

but the upper canines are diagnostic in the presence of a deep posterior groove, and the molars wear so as to show a triangular trefoil pattern that clearly distinguishes them from the anthracotheriids.

The modern species have reduced the formula to

$$\frac{2\quad 1\quad 3\text{–}4\quad 3}{2\quad 1\quad 3\text{–}4\quad 3}$$ (*Hexaprotodon*) *=Choeroepus*

and

$$\frac{2\quad 1\quad 3\quad 3}{1\quad 1\quad 3\quad 3}$$ (*Hippopotamus*)

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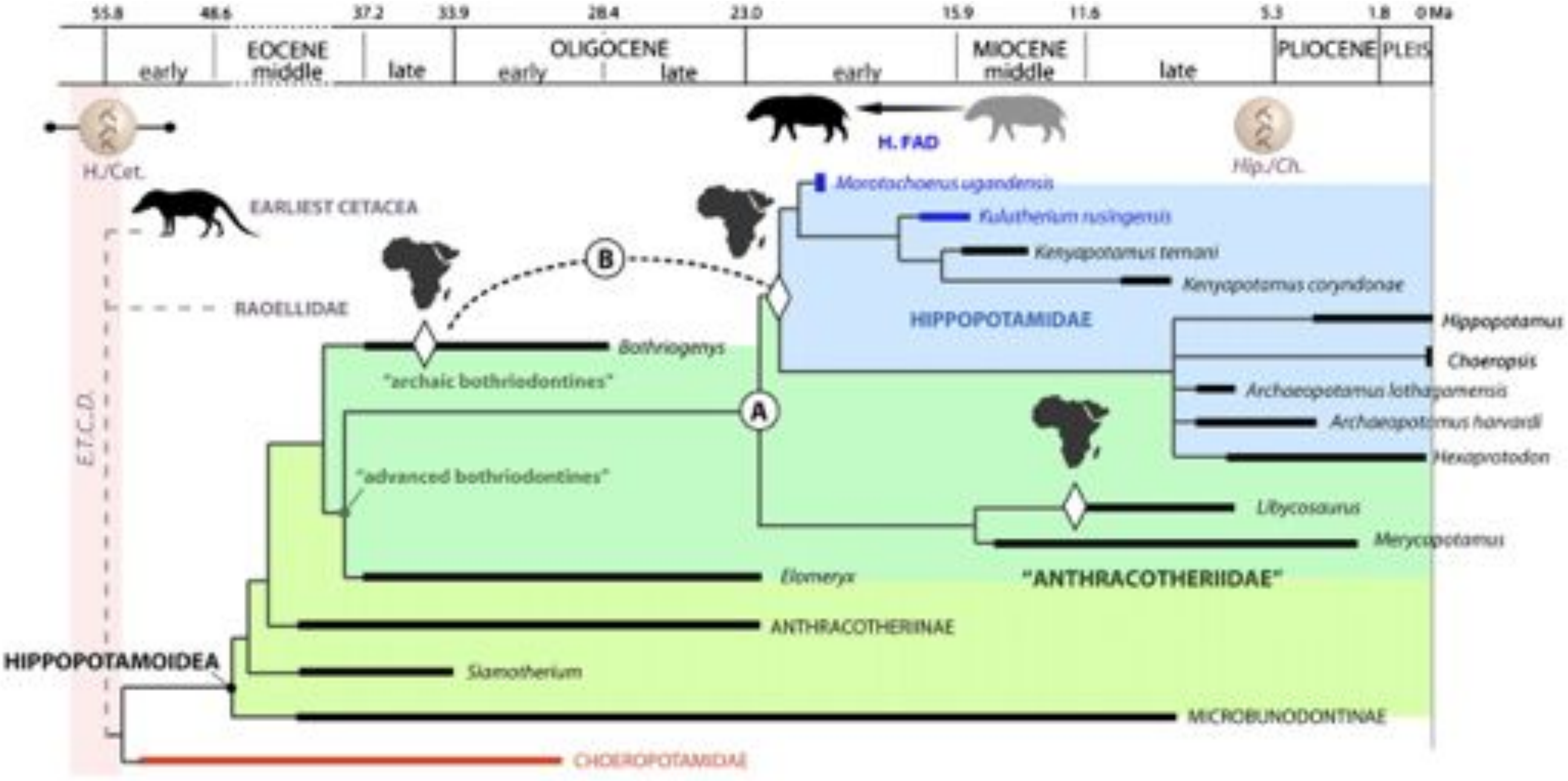
Dentición única: A peculiar cheek tooth pattern distinguishes the Hippopotamidae from all other extant and extinct ungulates and over the years it has been acknowledged through a diversity of terms (e.g., subbunodont, bunoselenodont, trefoliate, bunodont/bilophodont).

Al igual que a los anthracotheridos, a los Hipoppotamidae se les consideraba tradicionalmente como Suiformes. Sin embargo la evidencia molecular los coloca firmemente junto a los Cetáceos, definiendo el clado Cetancodonta que implicaba un “gap” en el registro fósil. Los últimos análisis morfológicos son más amigables, mostrando que ciertas formas del mioceno temprano consideradas como anthracotheridos y suiformes (Morotochoerus, Kulutherium) son Hippomorphos, cerrando parte del “gap”. El anthracotherido *Siamotherium* es un Cetancodontomorpho basal.



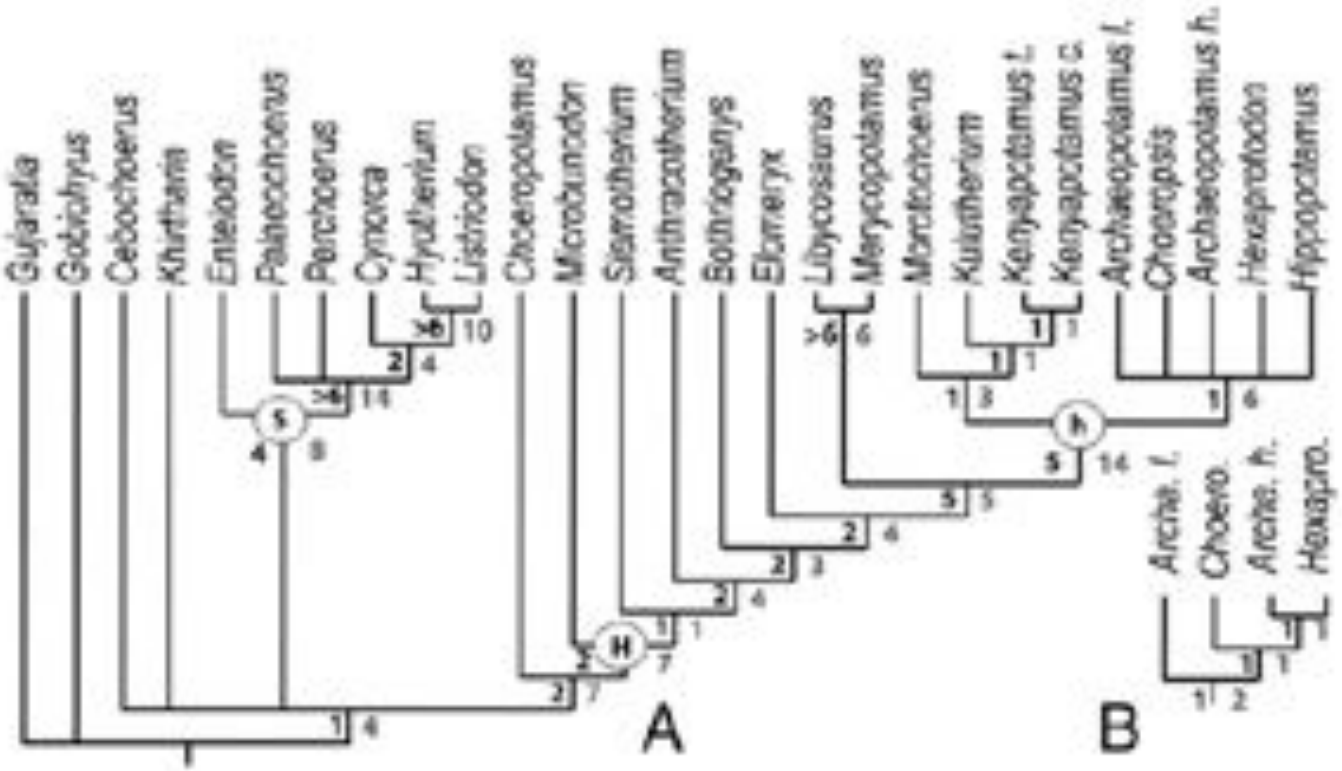


Fig. 2. Phylogeny of hippopotamoids based on the consensus of 78 parsimonious trees (consensus tree length = 234; CI = 0.39; RI = 0.75). (*A*) whole data matrix; (*B*) relationships within Hippopotaminae when excluding *Hippopotamus*. H, Hippopotamoidea; h, Hippopotamidae; S, Suina. Shaded numbers indicate nonambiguous synapomorphies, and solid numbers indicate Bremer support. Abbreviations: *Archaeopotamus h, A. harvardi*; *Archaeopotamus l., A. lothagamensis*; *Kenyapotamus c., K. coryndonae*; *Kenyapotamus t., K. ternani.*

Según trabajos recientes la dentición única de los Hipopótamos tiene una historia evolutiva compleja: Son derivados de "anthracotheridos" derivados con dentición selenodonta!

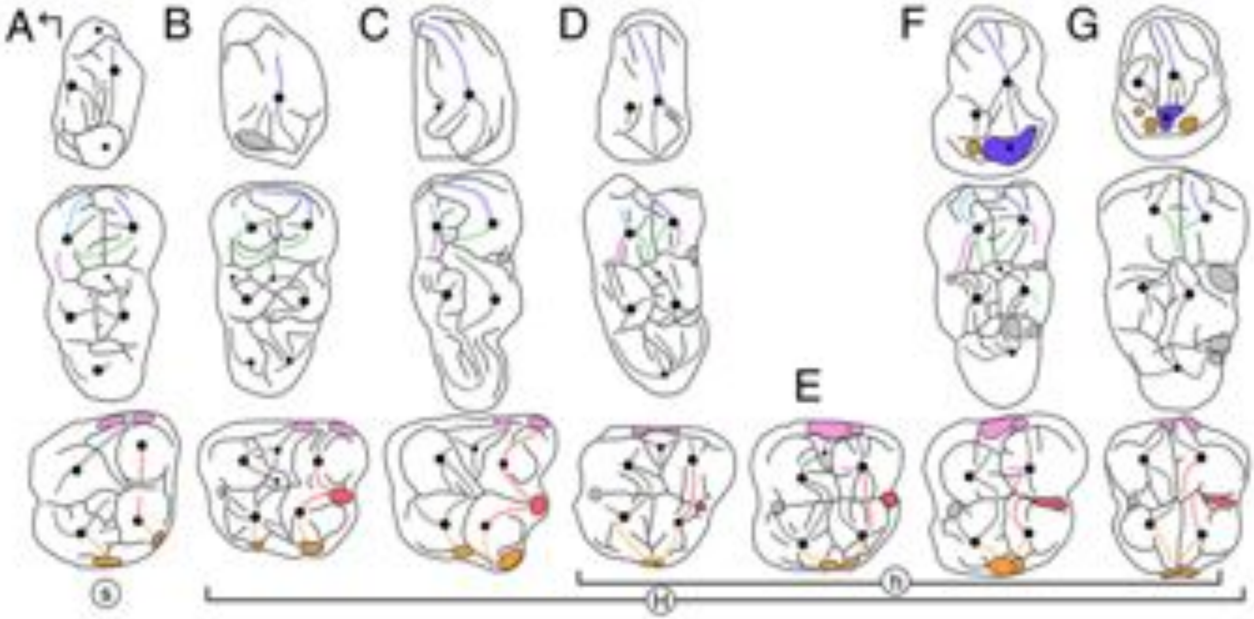


Fig. 3. Sketches of p4, lower and upper molars (from top to bottom) of (*A*) *Palaeochoerus*, (*B*) *Choeropotamus*, (*C*) *Bothriogenys*, (*D*) *Morotochoerus*, (*E*) *Kulutherium*, (*F*) *Kenyapotamus*, and (*G*) *Hexaprotodon*. H, Hippopotamoidea; h, Hippopotamidae; s, Suoidea. Color correspondence: upper molars, red, postparacrista and premetacrista; pink, parastyle and mesiostyle; and orange, metastyles and distostyles; lower cheek teeth, dark green, postmetacristid and postprotocristid; light green, postectohypocristids; light blue, premetacristid; blue, preprotocristid; purple, postectoprotocristid and postectometacristid; violet, hypoconid; and brown, accessory conulids. The arrow indicates mesial (to top) and lingual (to left) directions.

Bunodonty and selenodonty are classically viewed as primitive and derived tooth patterns, respectively. It is for this reason that a differentiation of the bunodont Hippopotamidae from the most selenodont subfamily of anthracotheriids, the Bothriodontinae (48, 49), has not been supported by many contributions (e.g., ref. 43). This hypothesis would indeed imply relatively complex changes in the cheek tooth pattern, as discussed by Boisserie and Lihoreau (44) and Boisserie et al. (22). The inclusion of Morotochoerus and Kulutherium within the Hippopotamidae is particularly important in this regard, because it allows for a description of the nature and timing of these changes from ~21 million years onward.

ENTELODONTA. “Killer pigs”. Típicamente considerados Suiformes, pero pueden ser Cetancodontomorpha

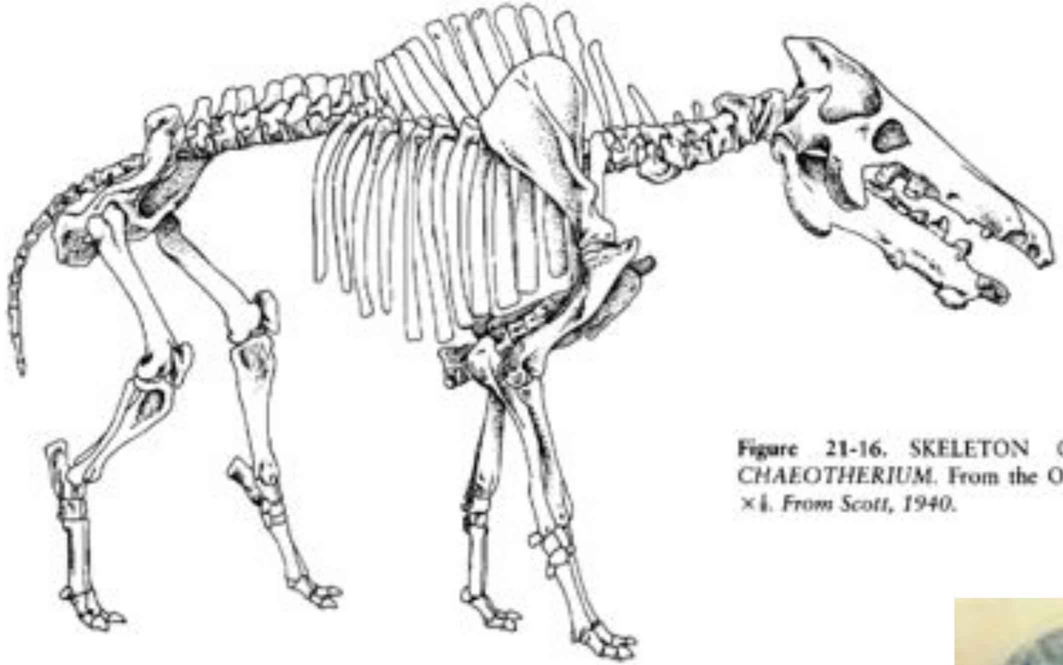


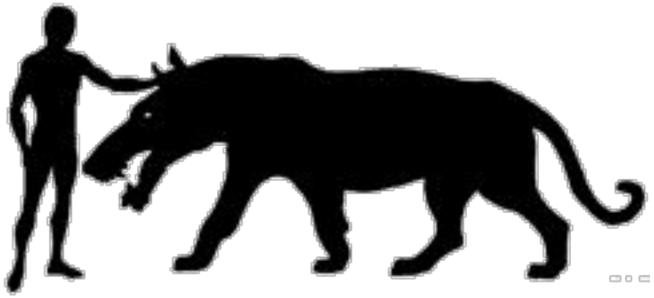
Figure 21-16. SKELETON OF THE ENTELODONT *ARCHAEOTHERIUM*. From the Oligocene of western North America, ×[illegible]. *From Scott, 1940.*

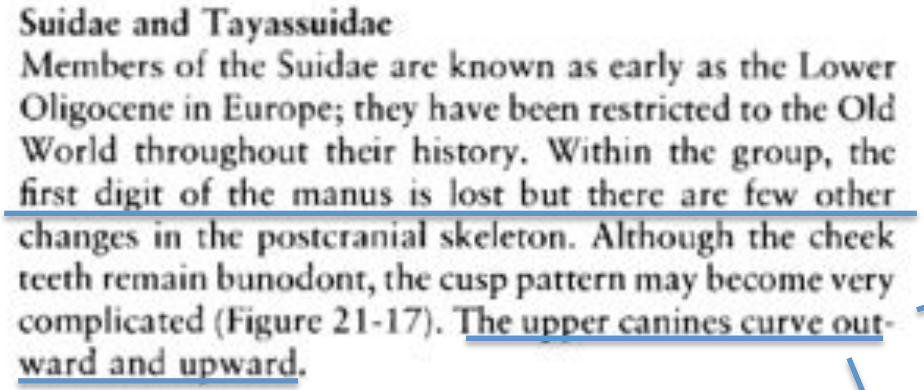
The entelodonts, which extended into the early Miocene, were common in North America and Europe. They were large animals, with the skull reaching nearly 1 meter long. They are characterized by the presence of bony processes from the lower jaw and zygomatic arch (Figure 21-16).

Se consideran omnívoros/depredadores

Archaeotherium

Andrewsarchus de mongolia, tradicionalmente considerado un mesoníquido, es ubicado como un entelodonto por los análisis más recientes





Suidae and Tayassuidae

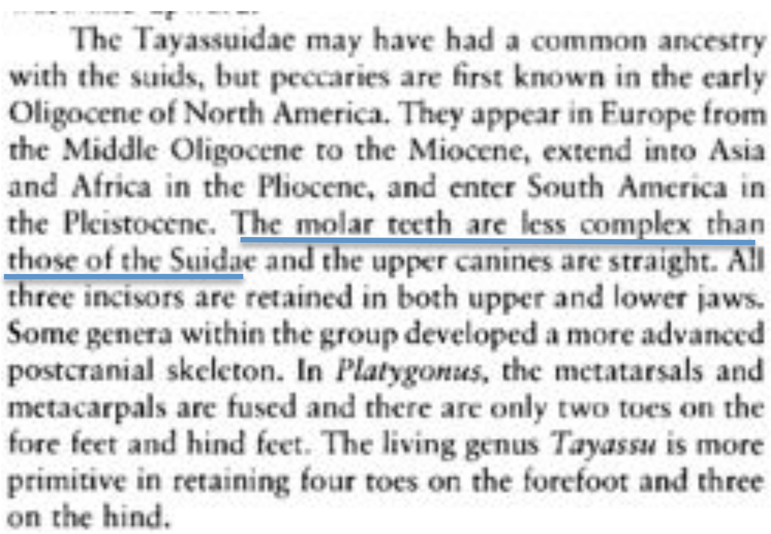
Members of the Suidae are known as early as the Lower Oligocene in Europe; they have been restricted to the Old World throughout their history. Within the group, the first digit of the manus is lost but there are few other changes in the postcranial skeleton. Although the cheek teeth remain bunodont, the cusp pattern may become very complicated (Figure 21-17). The upper canines curve outward and upward.

Figure 21-17. (*a*) Skull of the Oligocene peccary *Perchoerus* from western North America. *From Scott, 1940.* (*b* and *c*) Upper and lower dentition of *Perchoerus. From Scott, 1940.* (*d*) Complex cheek teeth of the suid *Nyanzachoerus. From Harris and White, 1979.*

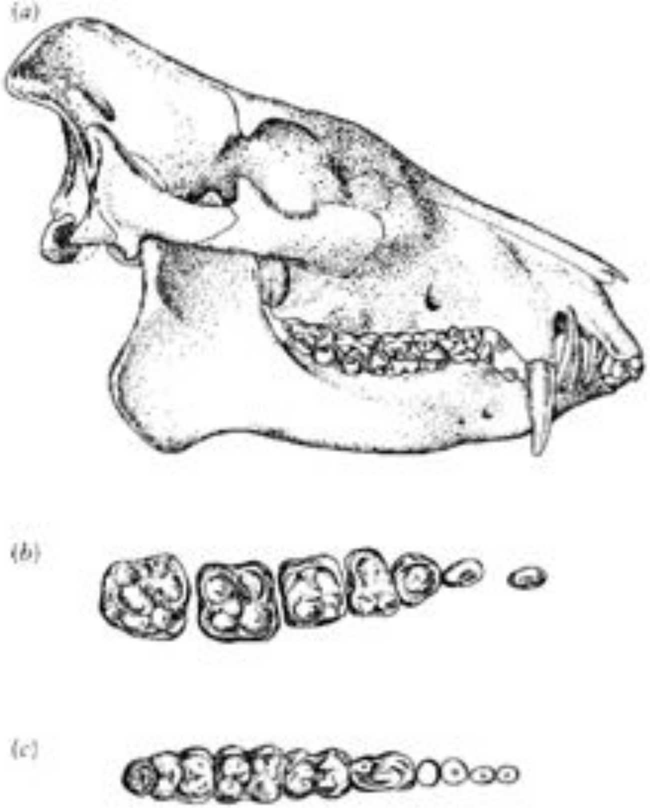
Domestic pig

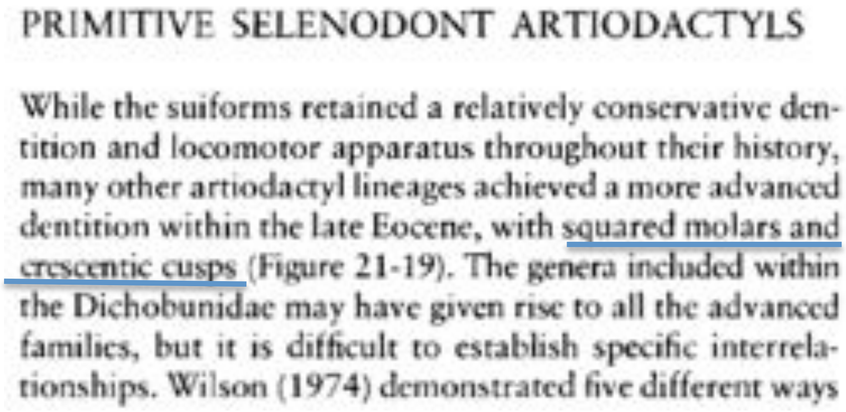
Babirusa

Warthog



The Tayassuidae may have had a common ancestry with the suids, but peccaries are first known in the early Oligocene of North America. They appear in Europe from the Middle Oligocene to the Miocene, extend into Asia and Africa in the Pliocene, and enter South America in the Pleistocene. The molar teeth are less complex than those of the Suidae and the upper canines are straight. All three incisors are retained in both upper and lower jaws. Some genera within the group developed a more advanced postcranial skeleton. In *Platygonus*, the metatarsals and metacarpals are fused and there are only two toes on the fore feet and hind feet. The living genus *Tayassu* is more primitive in retaining four toes on the forefoot and three on the hind.



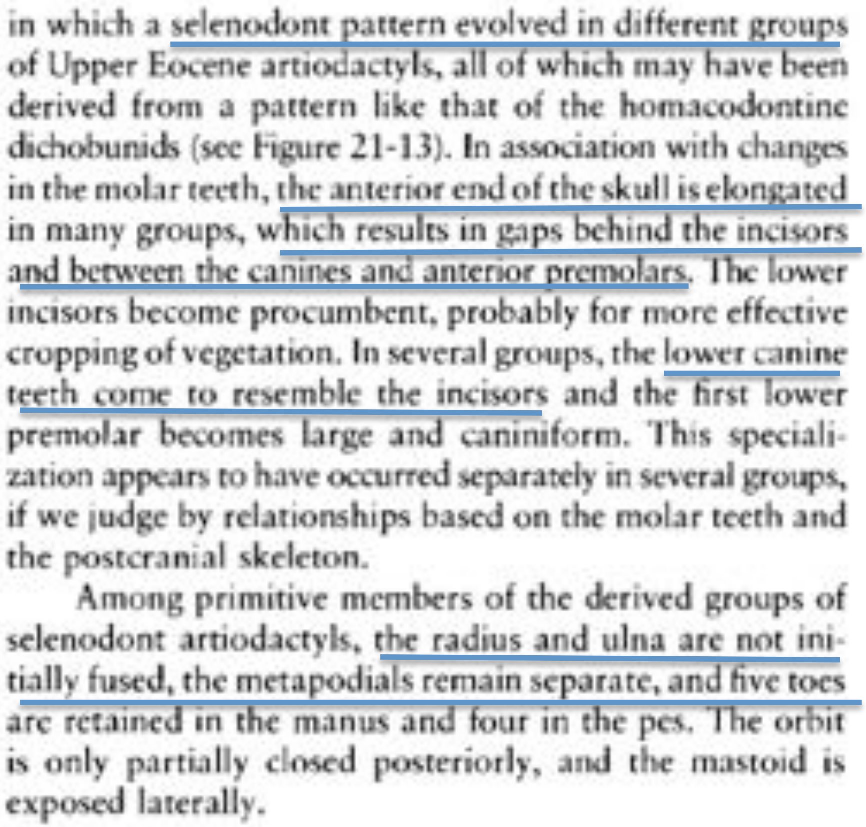


PRIMITIVE SELENODONT ARTIODACTYLS

While the suiforms retained a relatively conservative dentition and locomotor apparatus throughout their history, many other artiodactyl lineages achieved a more advanced dentition within the late Eocene, with squared molars and crescentic cusps (Figure 21-19). The genera included within the Dichobunidae may have given rise to all the advanced families, but it is difficult to establish specific interrelationships. Wilson (1974) demonstrated five different ways

Selenodoncia y especialización cursorial convergente

Grupos con distintas mezclas de rasgos primitivos y derivados, que indica paralelismo. Relaciones son inciertas

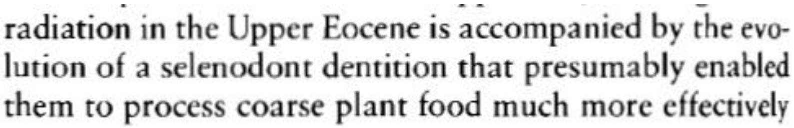


in which a selenodont pattern evolved in different groups of Upper Eocene artiodactyls, all of which may have been derived from a pattern like that of the homacodontine dichobunids (see Figure 21-13). In association with changes in the molar teeth, the anterior end of the skull is elongated in many groups, which results in gaps behind the incisors and between the canines and anterior premolars. The lower incisors become procumbent, probably for more effective cropping of vegetation. In several groups, the lower canine teeth come to resemble the incisors and the first lower premolar becomes large and caniniform. This specialization appears to have occurred separately in several groups, if we judge by relationships based on the molar teeth and the postcranial skeleton.

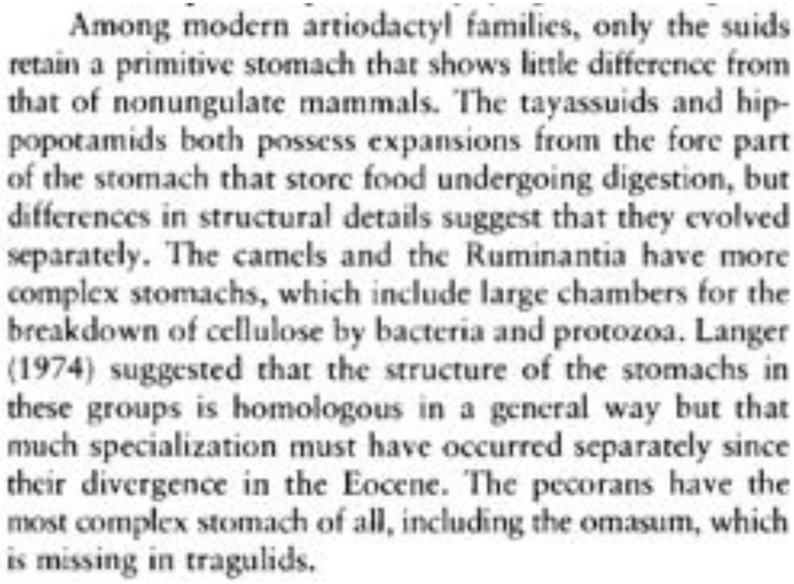
Among primitive members of the derived groups of selenodont artiodactyls, the radius and ulna are not initially fused, the metapodials remain separate, and five toes are retained in the manus and four in the pes. The orbit is only partially closed posteriorly, and the mastoid is exposed laterally.

Hemos visto bunodontes, ahora en adelante hablaremos de Artiodactylos de dentición **Selenodonta**

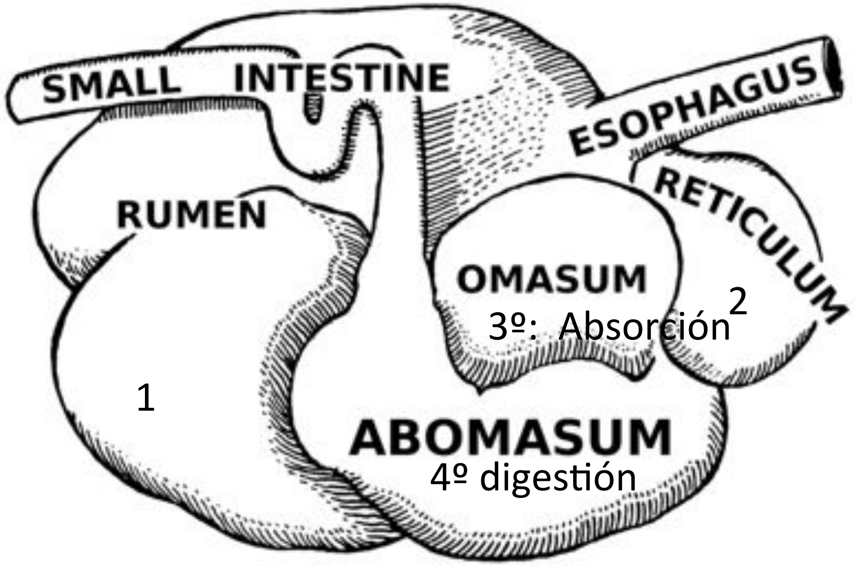
RUMINANTIA



radiation in the Upper Eocene is accompanied by the evolution of a selenodont dentition that presumably enabled them to process coarse plant food much more effectively



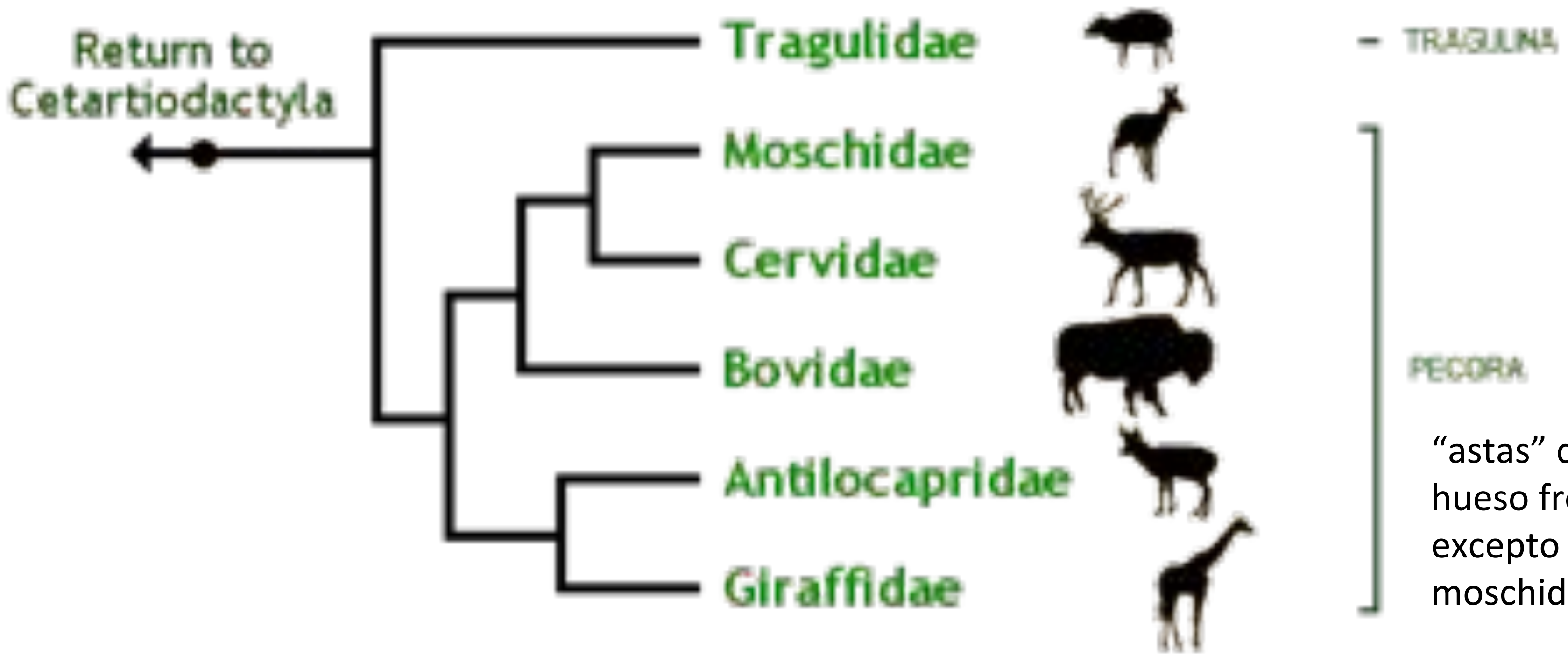
Among modern artiodactyl families, only the suids retain a primitive stomach that shows little difference from that of nonungulate mammals. The tayassuids and hippopotamids both possess expansions from the fore part of the stomach that store food undergoing digestion, but differences in structural details suggest that they evolved separately. The camels and the Ruminantia have more complex stomachs, which include large chambers for the breakdown of cellulose by bacteria and protozoa. Langer (1974) suggested that the structure of the stomachs in these groups is homologous in a general way but that much specialization must have occurred separately since their divergence in the Eocene. The pecorans have the most complex stomach of all, including the omasum, which is missing in tragulids.



1 y 2 : Fermentación

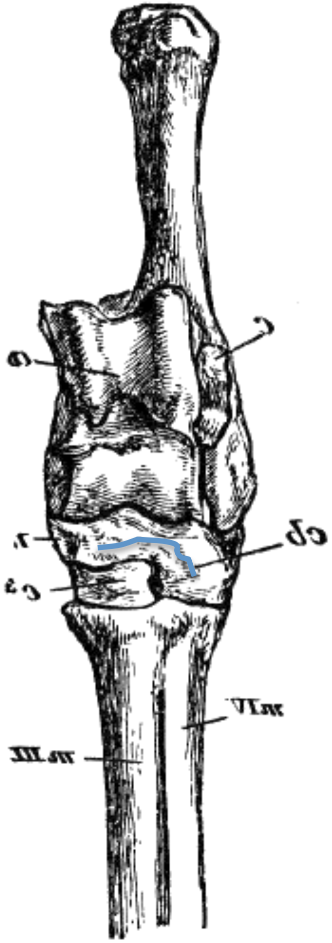
Los cetaceos también tiene un foregut, fermentador en mysticeti!!!

RUMINANTIA actuales: TRAGULIDAE (CHEVROTAINS) Y PECORA

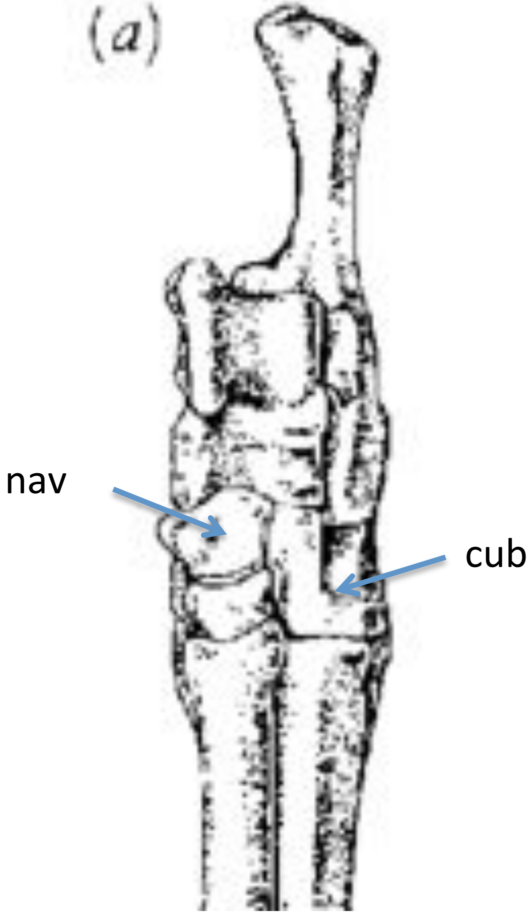


"astas" del
hueso frontal,
excepto
moschidae

Fusión del navicular y cuboide



Cervus (Ruminantia)



Proebrotherium (Camelidae)

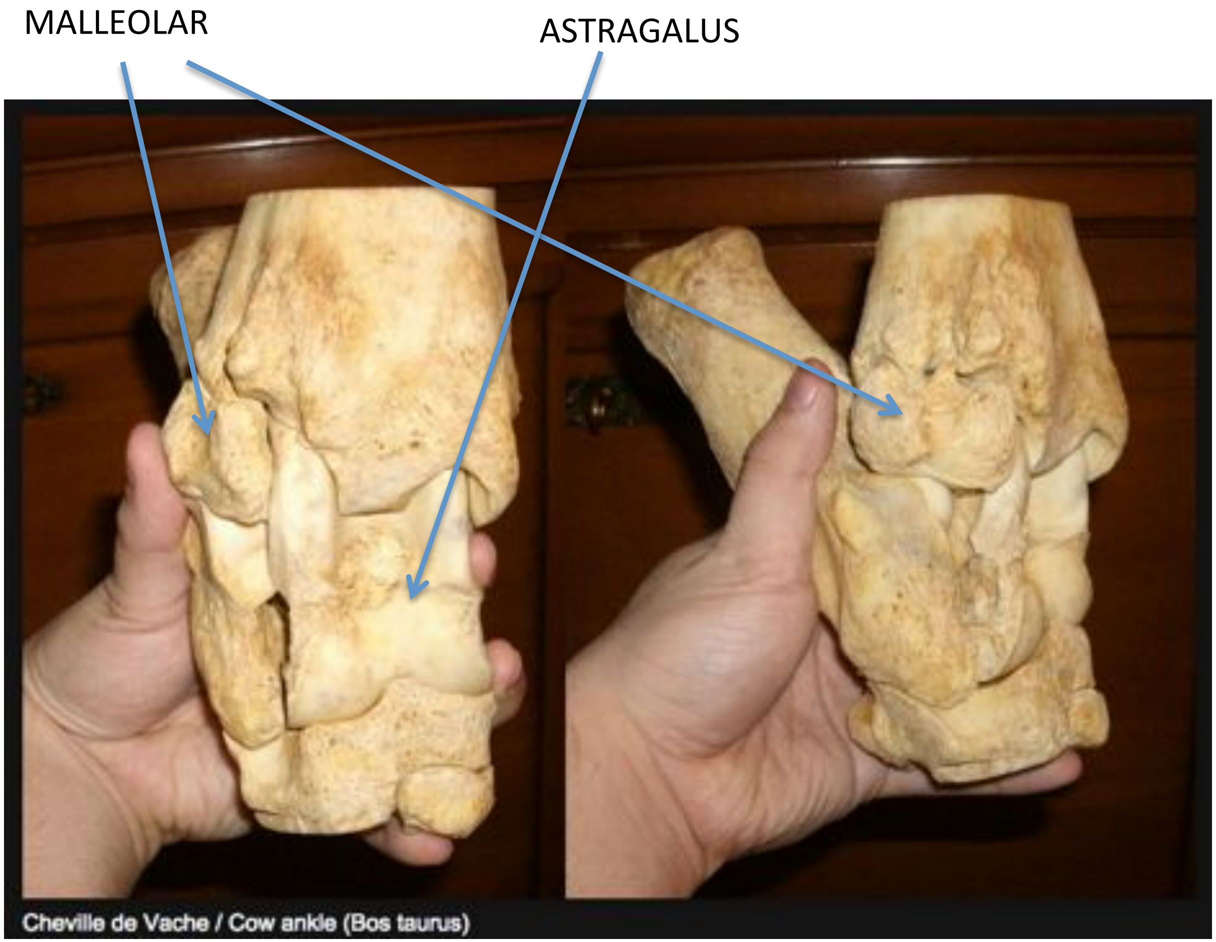
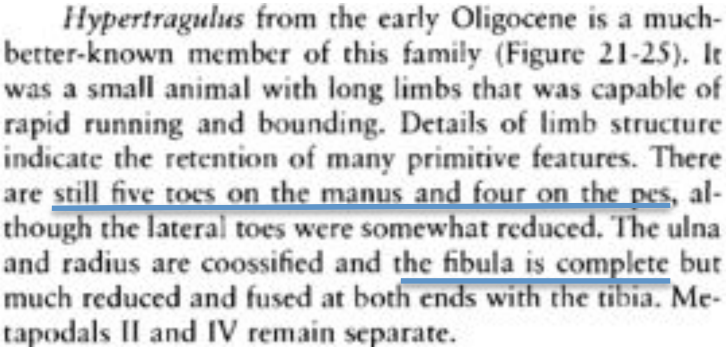
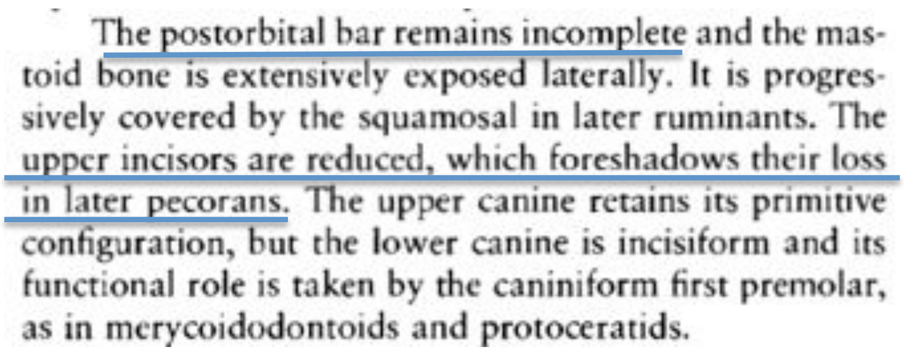


Fig.6.Maleollar bone in camel (A) and cow (B)

In Ruminantia the fibula is represented by: a proximal osseous nucleus that is attached to the lateral condyle of the tibia, a fibrous cord that represents the body and is destroyed by boiling, and an independent bone at distal extremity named malleolar bone (Fig.6).



Hypertragulus from the early Oligocene is a much-better-known member of this family (Figure 21-25). It was a small animal with long limbs that was capable of rapid running and bounding. Details of limb structure indicate the retention of many primitive features. There are still five toes on the manus and four on the pes, although the lateral toes were somewhat reduced. The ulna and radius are coossified and the fibula is complete but much reduced and fused at both ends with the tibia. Metapodals II and IV remain separate.



The postorbital bar remains incomplete and the mastoid bone is extensively exposed laterally. It is progressively covered by the squamosal in later ruminants. The upper incisors are reduced, which foreshadows their loss in later pecorans. The upper canine retains its primitive configuration, but the lower canine is incisiform and its functional role is taken by the caniniform first premolar, as in merycoidodontoids and protoceratids.

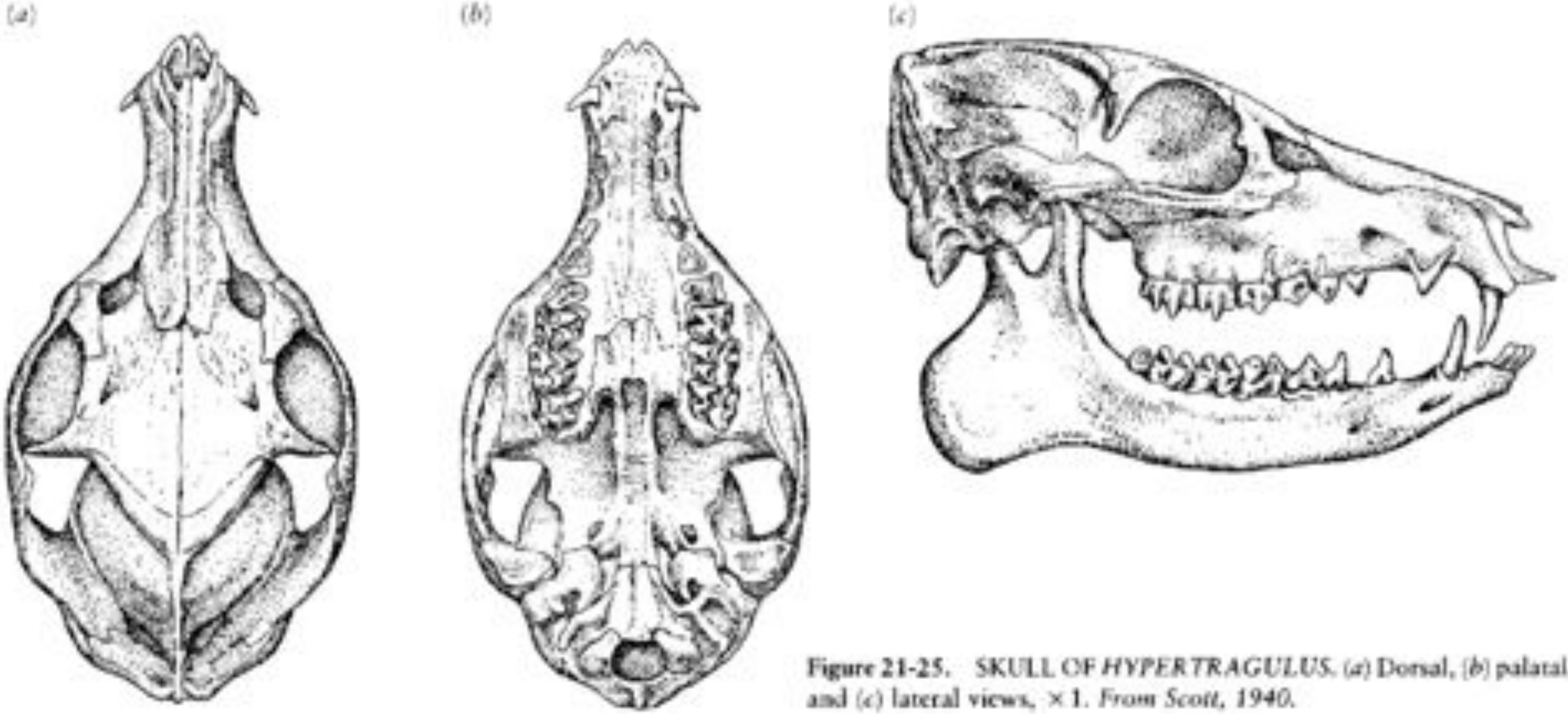


Figure 21-25. SKULL OF *HYPERTRAGULUS.* (*a*) Dorsal, (*b*) palatal, and (*c*) lateral views, × 1. *From Scott, 1940.*

Hypertragalus ya presenta la fusión cuboide-navicular

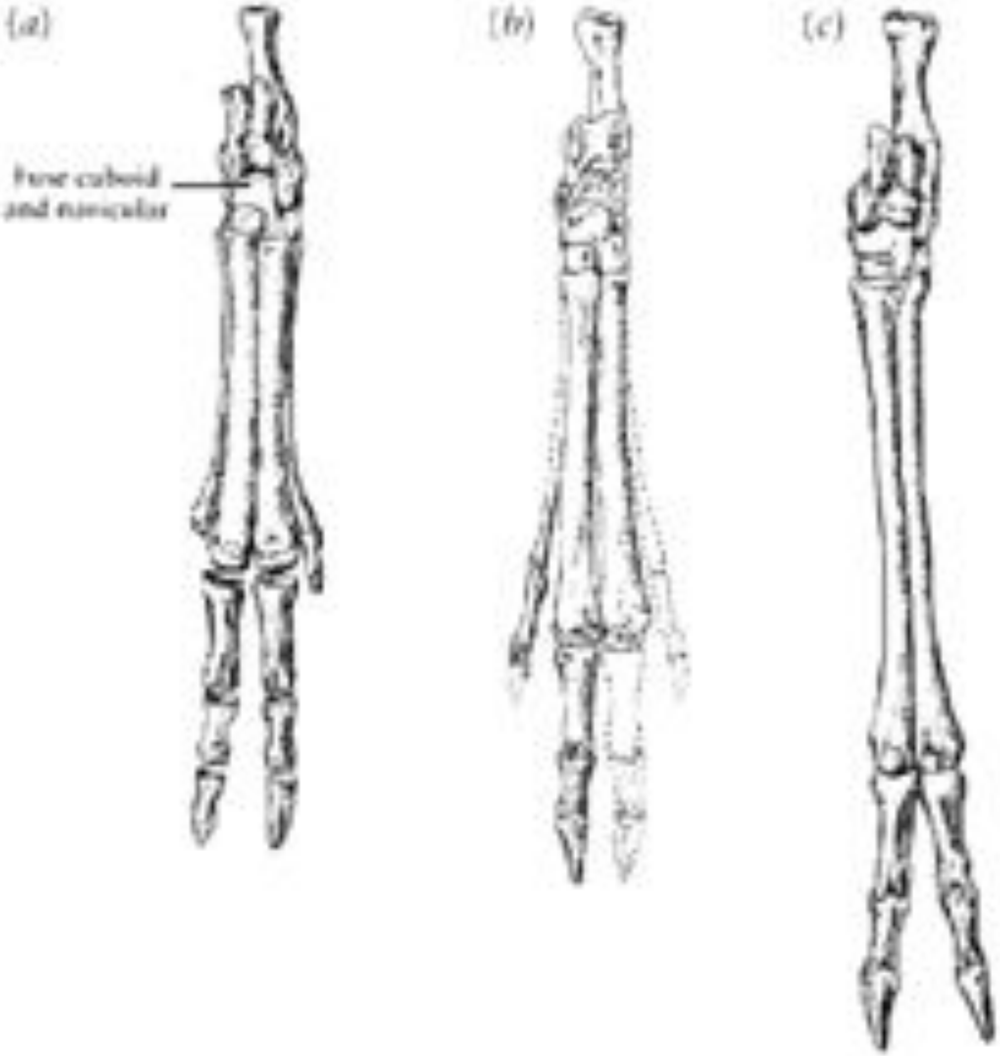
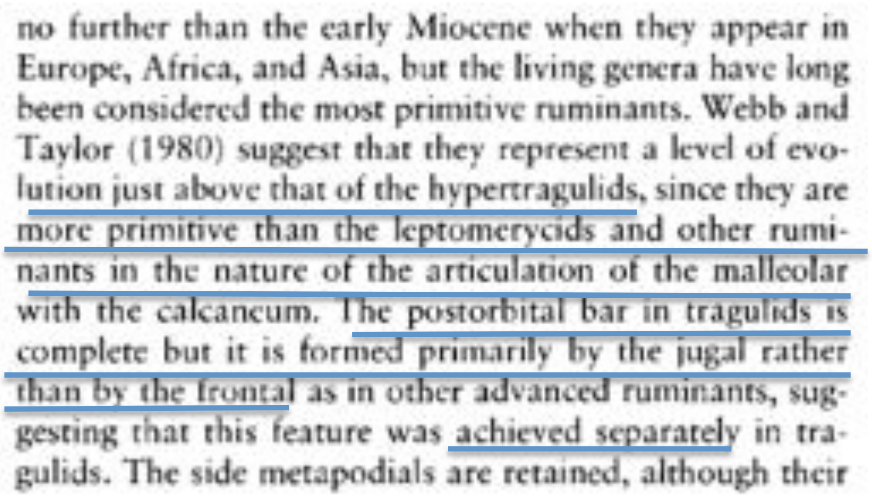


Figure 21-24. (*a*) Rear foot of the primitive ruminant *Hypertragulus* from the Oligocene of North America showing fusion of cuboid and navicular. *From Scott, 1940.* (*b*) Foot of *Archaeomeryx*. *From Colbert, 1941b.* (*c*) Foot of *Leptomeryx*. *From Scott, 1940.*

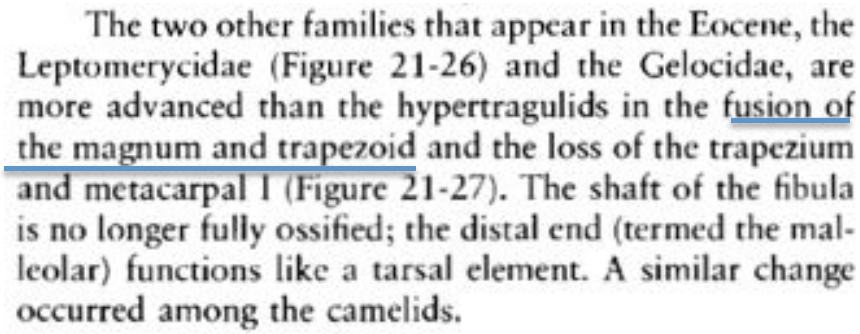
TRAGULIDAE



no further than the early Miocene when they appear in Europe, Africa, and Asia, but the living genera have long been considered the most primitive ruminants. Webb and Taylor (1980) suggest that they represent a level of evolution just above that of the hypertragulids, since they are more primitive than the leptomerycids and other ruminants in the nature of the articulation of the malleolar with the calcaneum. The postorbital bar in tragulids is complete but it is formed primarily by the jugal rather than by the frontal as in other advanced ruminants, suggesting that this feature was achieved separately in tragulids. The side metapodials are retained, although their

Pérdida de los incisivos superiores

Leptomerycidae y Gelocidae: Más cercanos a Pecora



The two other families that appear in the Eocene, the Leptomerycidae (Figure 21-26) and the Gelocidae, are more advanced than the hypertragulids in the fusion of the magnum and trapezoid and the loss of the trapezium and metacarpal I (Figure 21-27). The shaft of the fibula is no longer fully ossified; the distal end (termed the malleolar) functions like a tarsal element. A similar change occurred among the camelids.

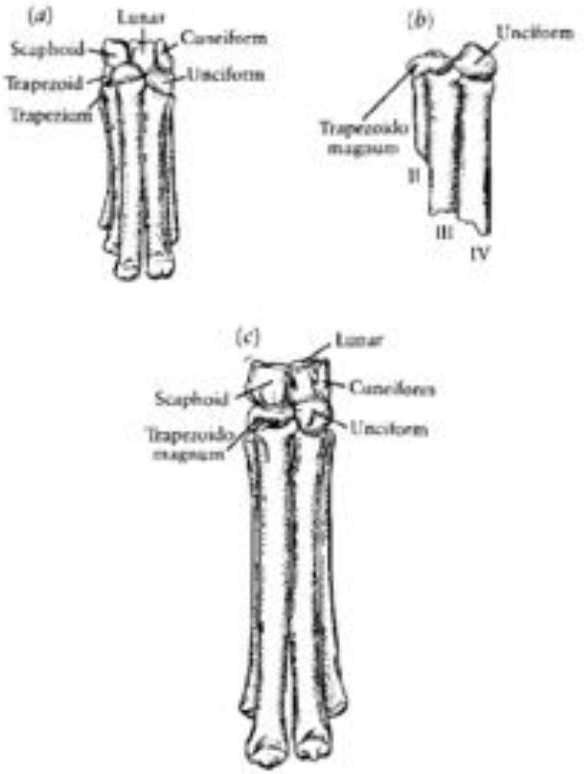


Figure 21-27. MORPHOLOGICAL CHANGES IN THE FRONT FEET OF HORNLESS RUMINANTS. (a) *Hypertragulus*. (b) *Archaeomeryx*. (c) *Leptomeryx*. *From Webb and Taylor, 1980.* I to V, metacarpals.

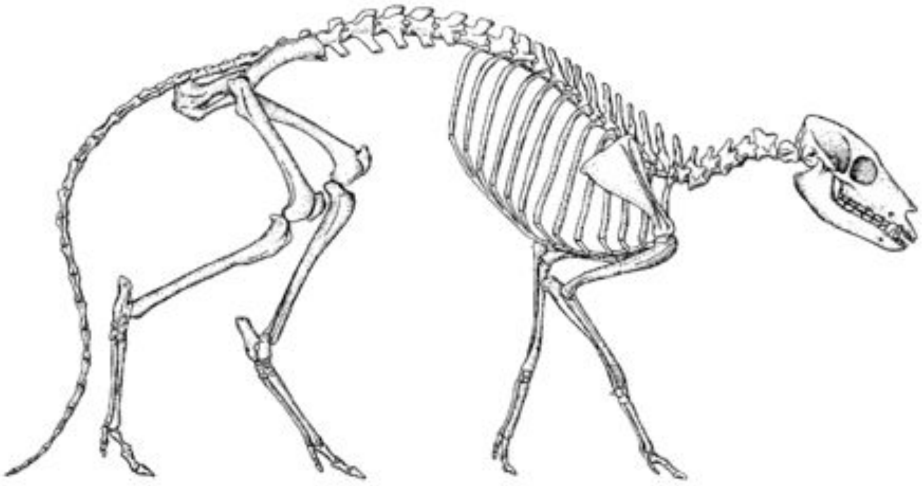
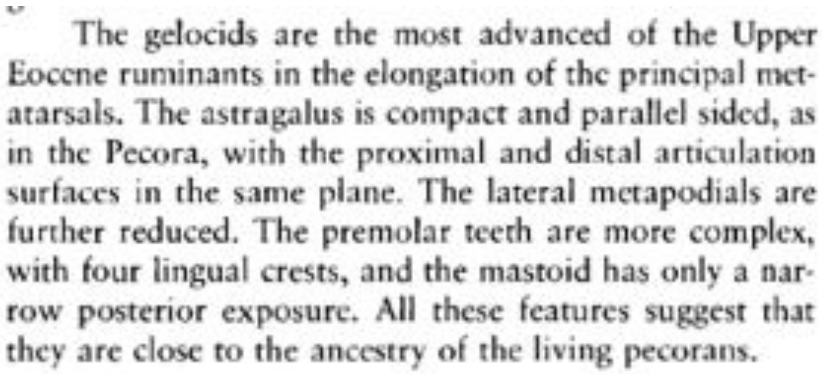


Figure 21-26. *ARCHAEOMERYX*. Skeleton of a member of the primitive ruminant family Leptomerycidae, ×⅓. *Colbert, 1941b.*



The gelocids are the most advanced of the Upper Eocene ruminants in the elongation of the principal metatarsals. The astragalus is compact and parallel sided, as in the Pecora, with the proximal and distal articulation surfaces in the same plane. The lateral metapodials are further reduced. The premolar teeth are more complex, with four lingual crests, and the mastoid has only a narrow posterior exposure. All these features suggest that they are close to the ancestry of the living pecorans.

Moschidae “Ciervos del agua”

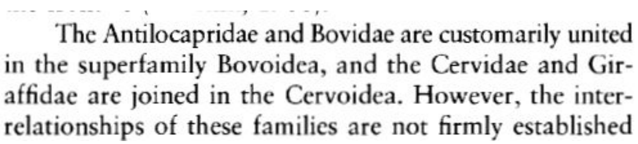
La posición filogenética permanece incierta, pero el análisis combinado más reciente los ubica como grupo hermano de los Pecora.

these canines are held loosely in their sockets, with their movement controlled by facial muscles. The buck can draw them backwards out of the way when eating. In aggressive encounters, he thrusts his canines out and draws in his lower lip to pull his teeth closer together. He then presents an impressive two-pronged weapon to rival males.

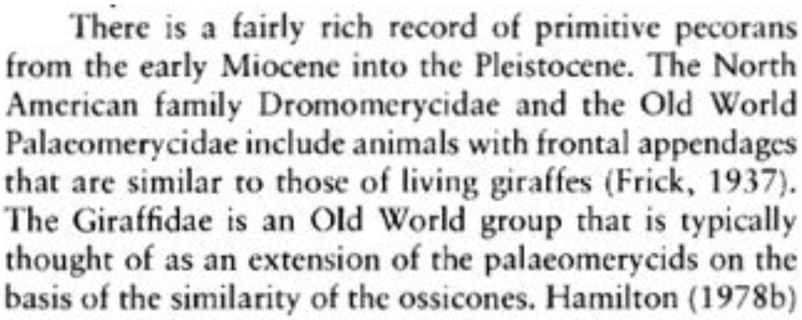
Pecora

Four families of pecorans are recognized in the modern fauna—the Cervidae, Giraffidae, Antilocapridae, and Bovidae—all of which can be distinguished by the nature of their frontal appendages. The Bovidae alone are said to have true **horns** consisting of a conical bony horn core surrounded by a keratin sheath; neither are shed. The Antilocapridae, the pronghorned "antelope" of North America, has the same elements but the sheath is shed annually and both core and sheath may be forked. Giraffes have a bony horn core but it is covered with skin rather than a keratin sheath. The term **ossicone** is applied to this structure. Ossicones may be in the shape of a simple spike, as in the living giraffe and okapi, or they may be forked or palmate as in diverse late Cenozoic genera of the Old World. Cervids characteristically have forked bony structures, termed **antlers** that are shed annually. They are attached to a pedicel extending from the skull that is comparable to the ossicone of giraffes. The horn cores of bovids and giraffids develop separately and later fuse to the skull. The antlers of cervids develop as outgrowths of the frontals (Bubenik, 1966).

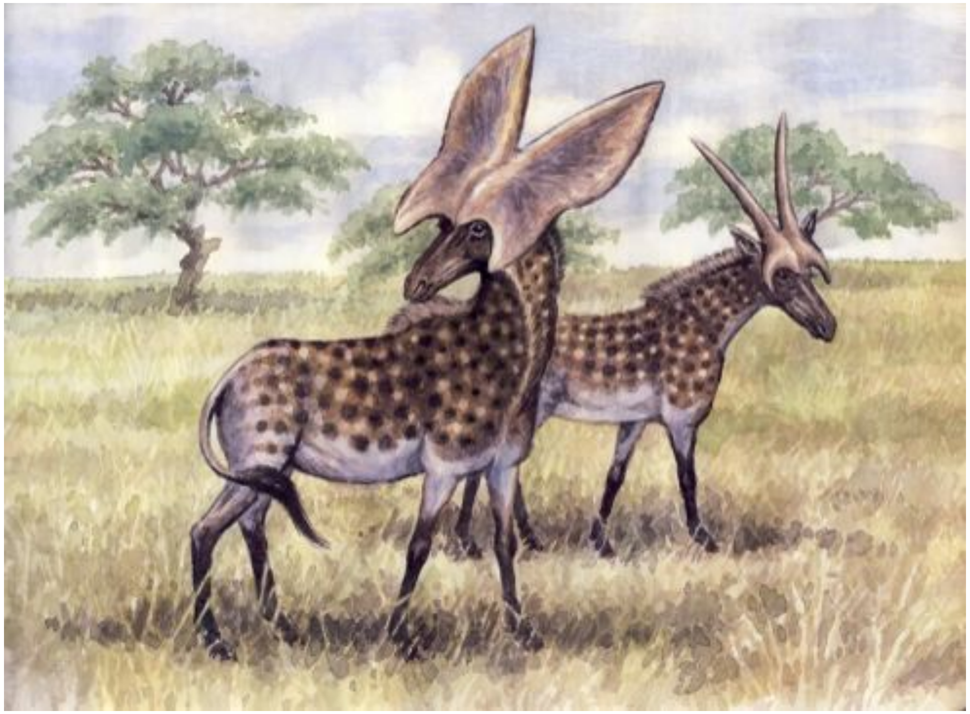
Palaeomerycidae: ancestros de las Giraffidae



The Antilocapridae and Bovidae are customarily united in the superfamily Bovoidea, and the Cervidae and Giraffidae are joined in the Cervoidea. However, the interrelationships of these families are not firmly established

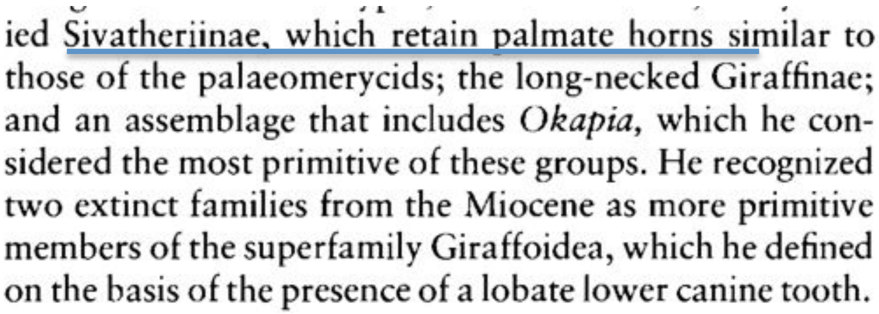


There is a fairly rich record of primitive pecorans from the early Miocene into the Pleistocene. The North American family Dromomerycidae and the Old World Palaeomerycidae include animals with frontal appendages that are similar to those of living giraffes (Frick, 1937). The Giraffidae is an Old World group that is typically thought of as an extension of the palaeomerycids on the basis of the similarity of the ossicones. Hamilton (1978b)

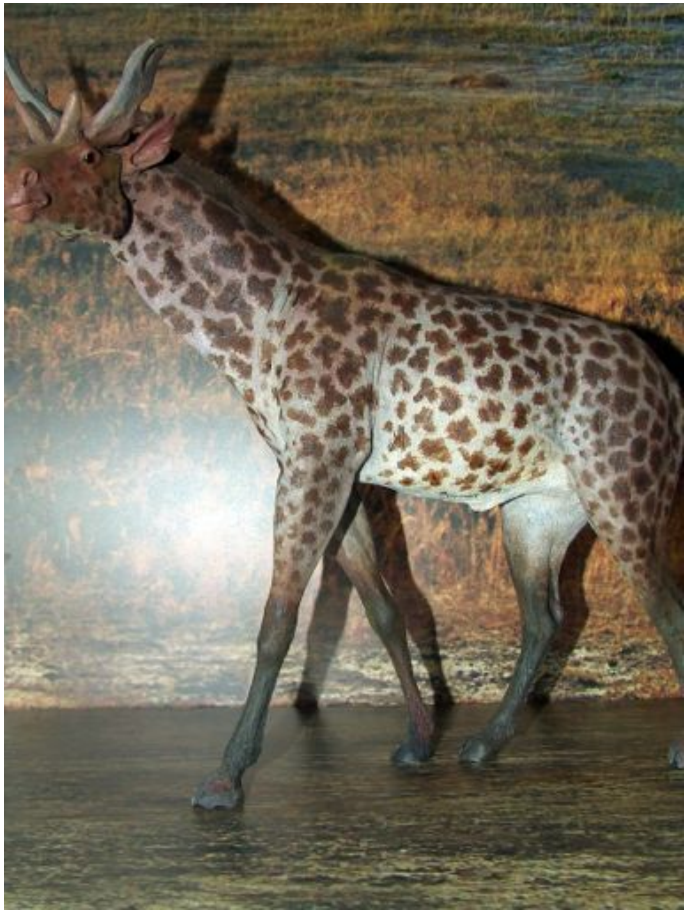


Prolybitherium, con ossiconos "palmados"

Giraffidae



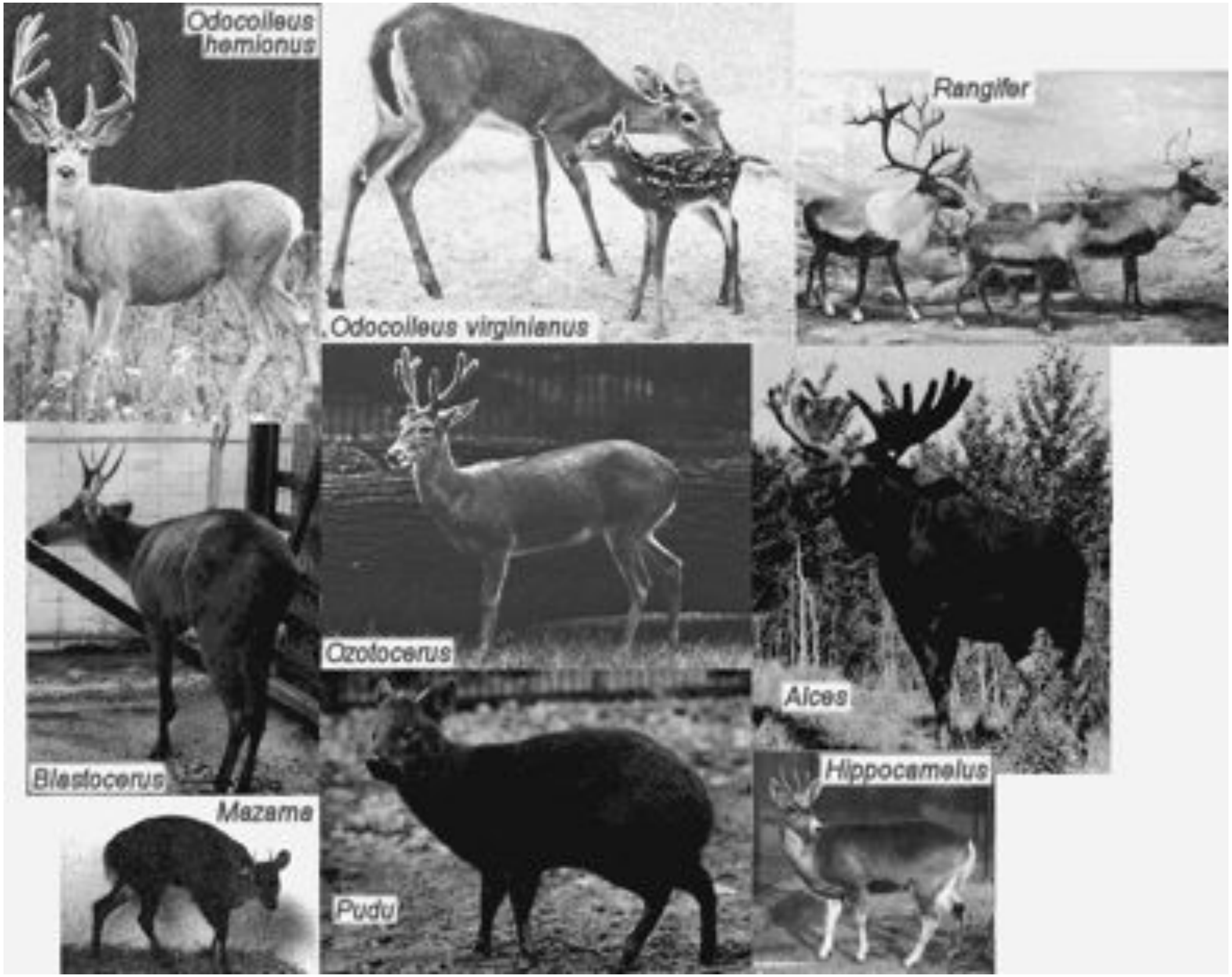
ied Sivatheriinae, which retain palmate horns similar to those of the palaeomerycids; the long-necked Giraffinae; and an assemblage that includes *Okapia*, which he considered the most primitive of these groups. He recognized two extinct families from the Miocene as more primitive members of the superfamily Giraffoidea, which he defined on the basis of the presence of a lobate lower canine tooth.



Sivaatherium

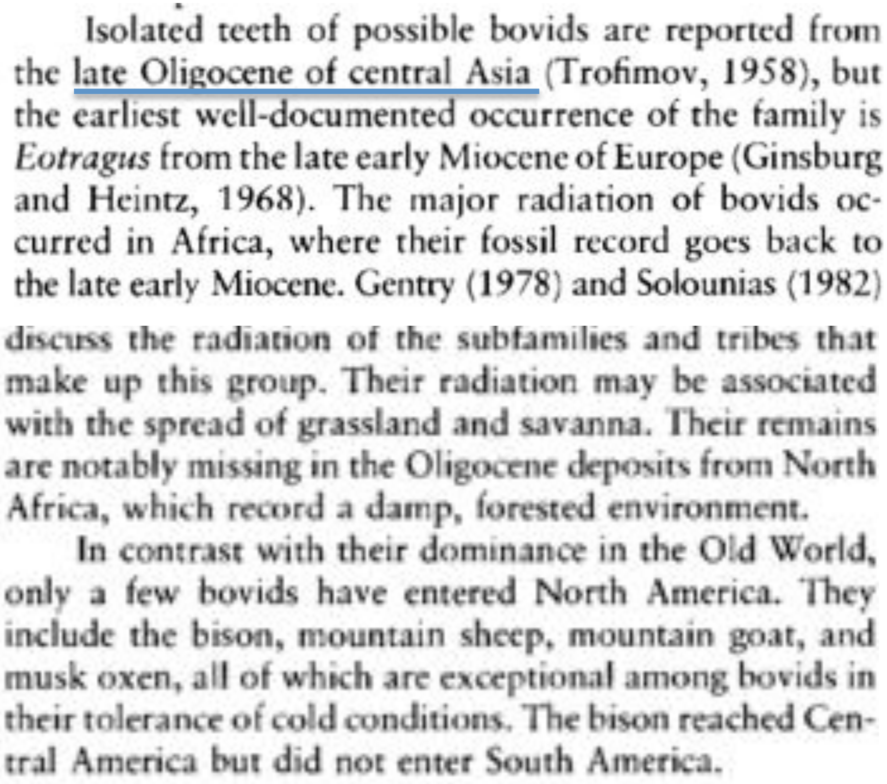
Okapia

Clearly identifiable deer appear in the Lower Miocene of Europe, Asia, and Africa. In contrast with giraffids and bovids, the cervids are limited primarily to the North Temperate region. They spread into North America at the close of the Cenozoic and extended into South America after the emergence of the Panama Land Bridge.



The North American antilocaprids also emerged in the early Miocene and were moderately diverse until the late Cenozoic when, perhaps as a result of competition from the immigrant bison, they were reduced to a single genus, *Antilocapra*. Leinders and Heintz (1980) cite shared derived characters of the lacrimal duct that suggest a close relationship to the cervids.

BOVIDAE



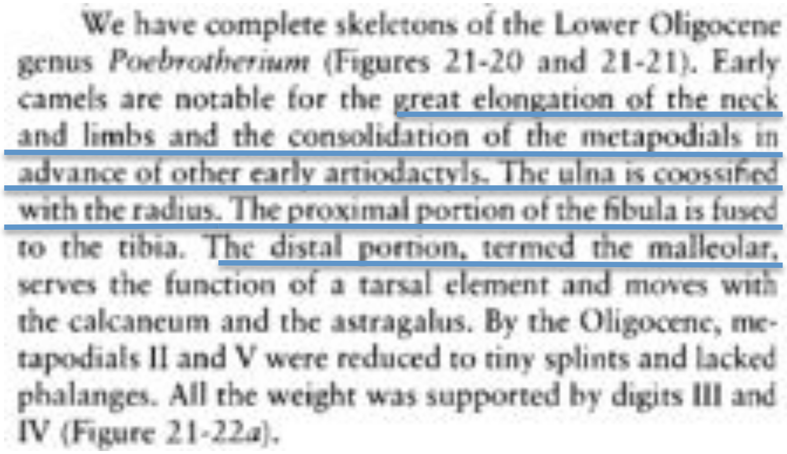
Isolated teeth of possible bovids are reported from the late Oligocene of central Asia (Trofimov, 1958), but the earliest well-documented occurrence of the family is *Eotragus* from the late early Miocene of Europe (Ginsburg and Heintz, 1968). The major radiation of bovids occurred in Africa, where their fossil record goes back to the late early Miocene. Gentry (1978) and Solounias (1982) discuss the radiation of the subfamilies and tribes that make up this group. Their radiation may be associated with the spread of grassland and savanna. Their remains are notably missing in the Oligocene deposits from North Africa, which record a damp, forested environment.

In contrast with their dominance in the Old World, only a few bovids have entered North America. They include the bison, mountain sheep, mountain goat, and musk oxen, all of which are exceptional among bovids in their tolerance of cold conditions. The bison reached Central America but did not enter South America.

TYLOPODA (camelidomorpha) Grupo amplio que incluye a **Camelidae** y quizás, familias fósiles posiblemente cercanas Oreodontoidea, Oromerycidae, Xiphodontidae y Protoceratidae

CAMELIDAE

an upper lip that is split in two with each part separately mobile



We have complete skeletons of the Lower Oligocene genus *Poebrotherium* (Figures 21-20 and 21-21). Early camels are notable for the great elongation of the neck and limbs and the consolidation of the metapodials in advance of other early artiodactyls. The ulna is coossified with the radius. The proximal portion of the fibula is fused to the tibia. The distal portion, termed the malleolar, serves the function of a tarsal element and moves with the calcaneum and the astragalus. By the Oligocene, metapodials II and V were reduced to tiny splints and lacked phalanges. All the weight was supported by digits III and IV (Figure 21-22*a*).

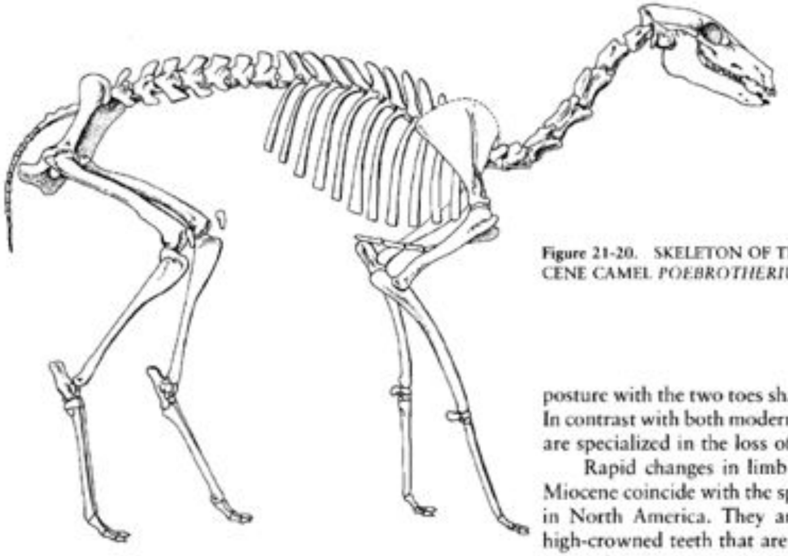


Figure 21-20. SKELETON OF THE NORTH AMERICAN OLIGOCENE CAMEL *POEBROTHERIUM*. *From Scott, 1940.*

posture with the two toes sharply bent and widely spread. In contrast with both modern suids and ruminants, camels are specialized in the loss of ligaments joining the toes.

Rapid changes in limb structure during the middle Miocene coincide with the spread of steppe and grassland in North America. They are correlated with a shift to high-crowned teeth that are capable of grinding abrasive vegetation.

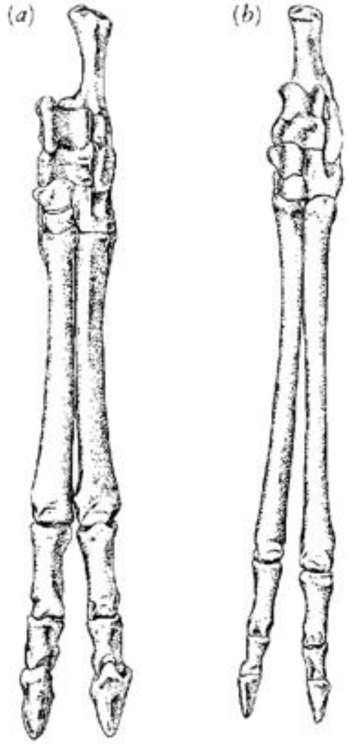
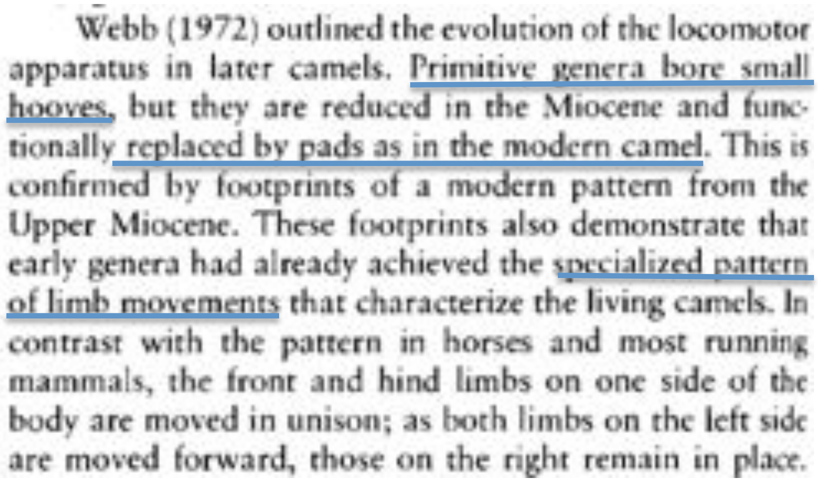
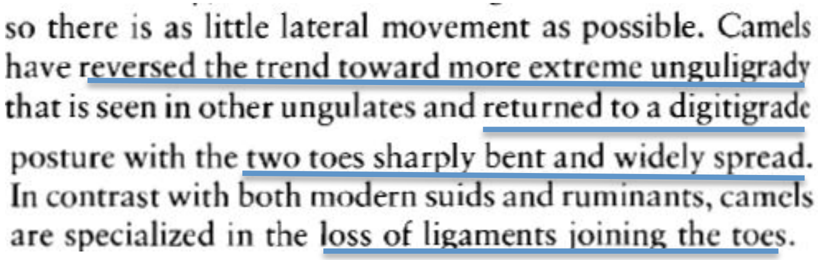


Figure 21-22. REAR FEET OF SELENODONT ARTIODACTYLS. (*a*) The Oligocene camelid *Poebrotherium*. (*b*) The protocerid *Protoceras*. *From Scott, 1940.*

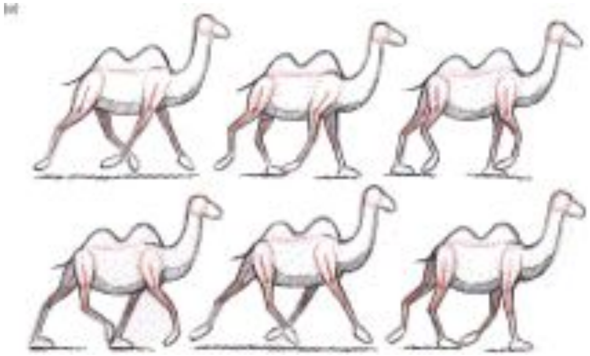
Their dentition shows traces of vesitigial central incisors in the upper jaw, and the third incisors are developed into canine-like tusks. Camelids also have true canine teeth and tusk-like premolars which are separated from the molars by a gap.



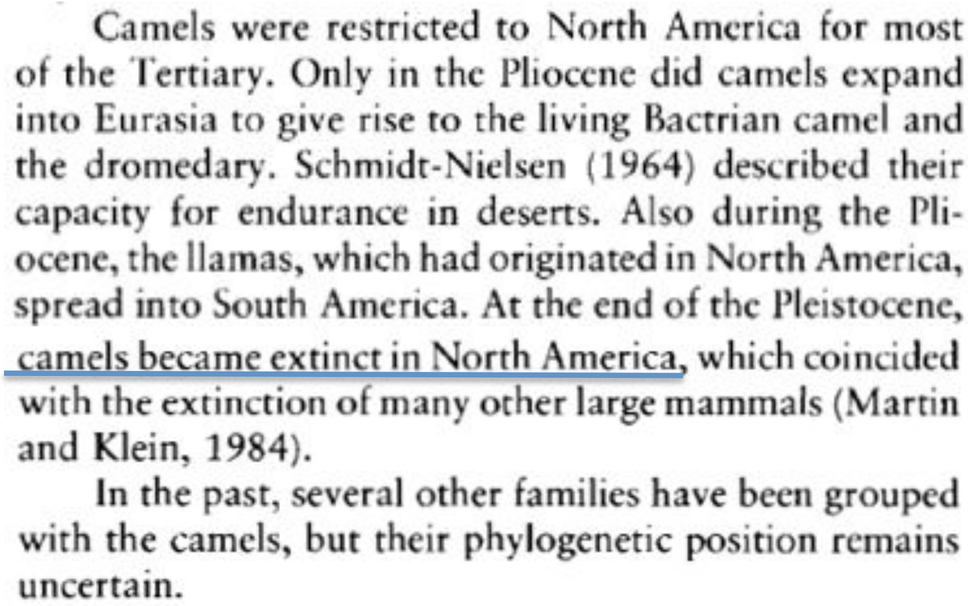
Webb (1972) outlined the evolution of the locomotor apparatus in later camels. Primitive genera bore small hooves, but they are reduced in the Miocene and functionally replaced by pads as in the modern camel. This is confirmed by footprints of a modern pattern from the Upper Miocene. These footprints also demonstrate that early genera had already achieved the specialized pattern of limb movements that characterize the living camels. In contrast with the pattern in horses and most running mammals, the front and hind limbs on one side of the body are moved in unison; as both limbs on the left side are moved forward, those on the right remain in place.



so there is as little lateral movement as possible. Camels have reversed the trend toward more extreme unguligrady that is seen in other ungulates and returned to a digitigrade posture with the two toes sharply bent and widely spread. In contrast with both modern suids and ruminants, camels are specialized in the loss of ligaments joining the toes.



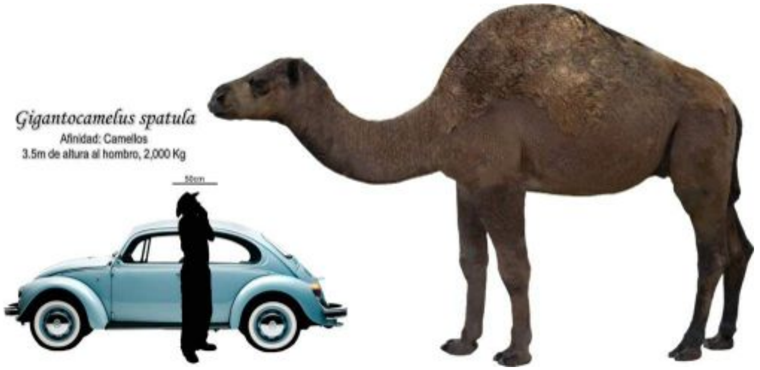
“Pacing”



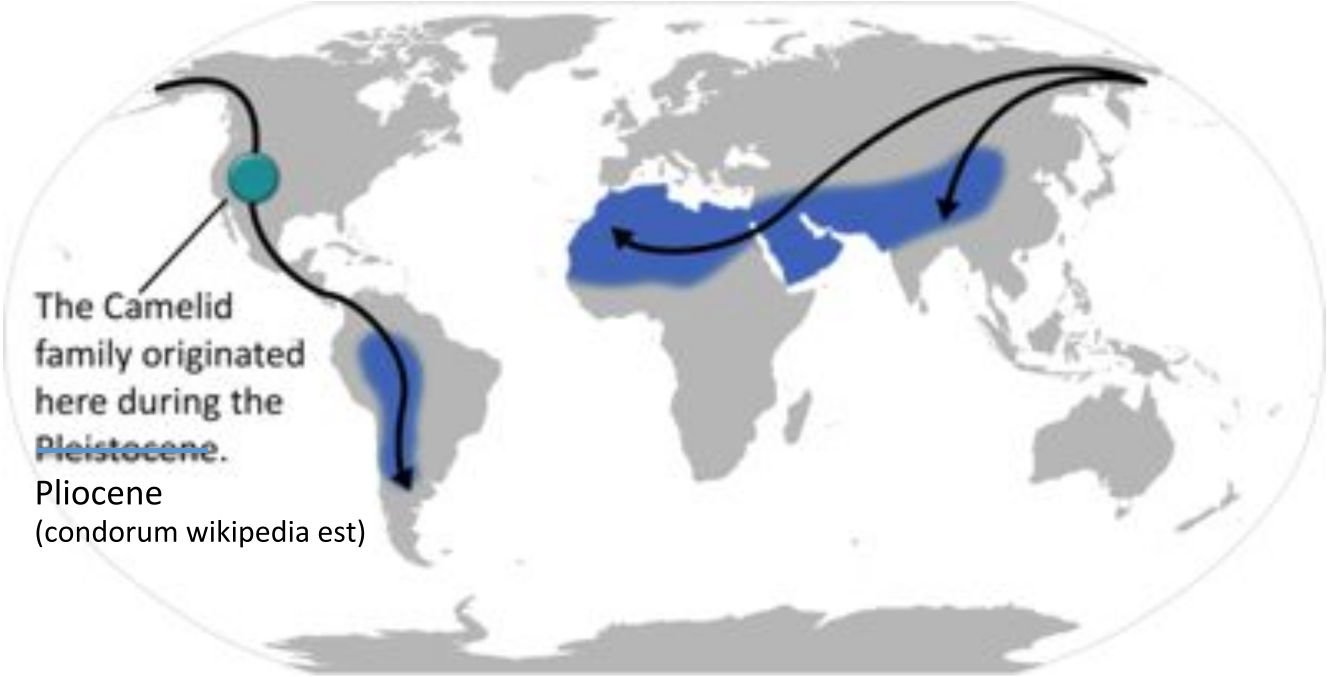
Camels were restricted to North America for most of the Tertiary. Only in the Pliocene did camels expand into Eurasia to give rise to the living Bactrian camel and the dromedary. Schmidt-Nielsen (1964) described their capacity for endurance in deserts. Also during the Pliocene, the llamas, which had originated in North America, spread into South America. At the end of the Pleistocene, camels became extinct in North America, which coincided with the extinction of many other large mammals (Martin and Klein, 1984).

In the past, several other families have been grouped with the camels, but their phylogenetic position remains uncertain.

Géneros sudamericanos:
Lama (Llama y Guanaco)
Vicugna (Vicuña y Alpaca)



Norteamérica:
Gigantocamelus
(Titanotylopus)



Pliocene
(condorum wikipedia est)

Oreodontoidea (Merycoidodontoidea)

CAMELIDAMORPHA?

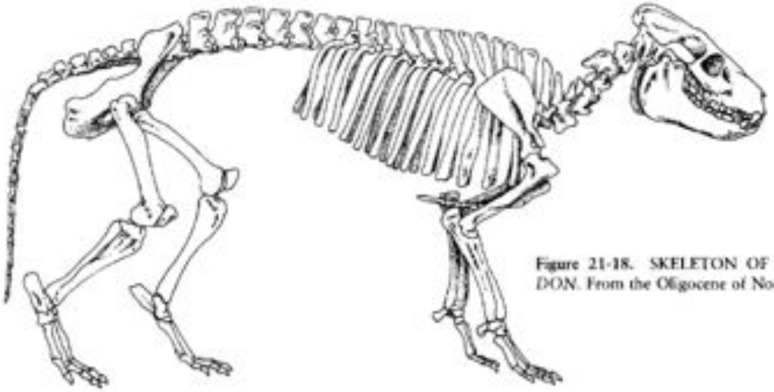


Figure 21-18. SKELETON OF THE OREODON *MERYCOIDODON*. From the Oligocene of North America, ×¼. *From Scott, 1940.*

Merycoidodontoidea

The Merycoidodontoidea were a common and diverse assemblage that we know from the late Middle Eocene into the Pliocene; they were entirely restricted to North America. Most were the size and proportions of pigs and sheep, with relatively short limbs and primitive feet (Figure 21-18).

Throughout the group, the face remained short and gaps did not develop between the anterior teeth (Figure 21-19). The labial crests of the upper molars were the first to become highly crescentic, but in most members of the group both the upper and lower molars bear four large crests. The upper incisors are reduced, the lower incisors and canines are procumbent, and the first lower premolar assumes the function of the canine.

oerids are differentiated by a progressive development of selenodonty, molarization of the premolars, and reduction of the hypocone. The ungual phalanges of *Diplobunops* and *Agriochoerus* are long and laterally compressed—more like claws than the hoof-bearing feet of other artiodactyls (see Figure 21-11). It has been suggested

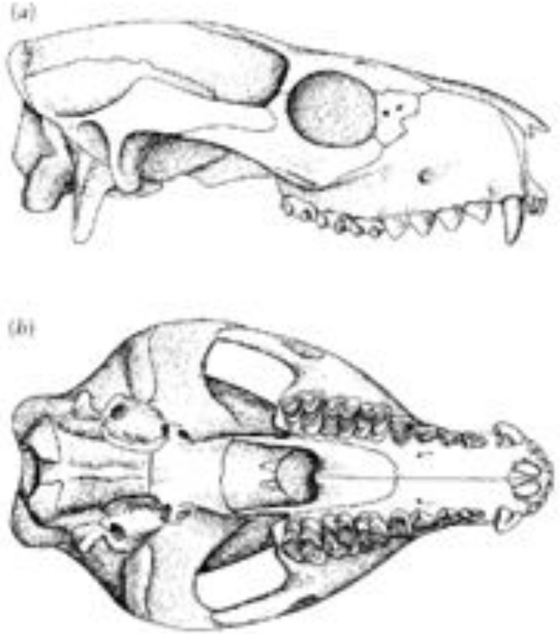


Figure 21-19. SKULL OF THE OREODON *BATHYGENYS*. (*a*) Lateral and (*b*) palatal view. *From Wilson, 1971.*

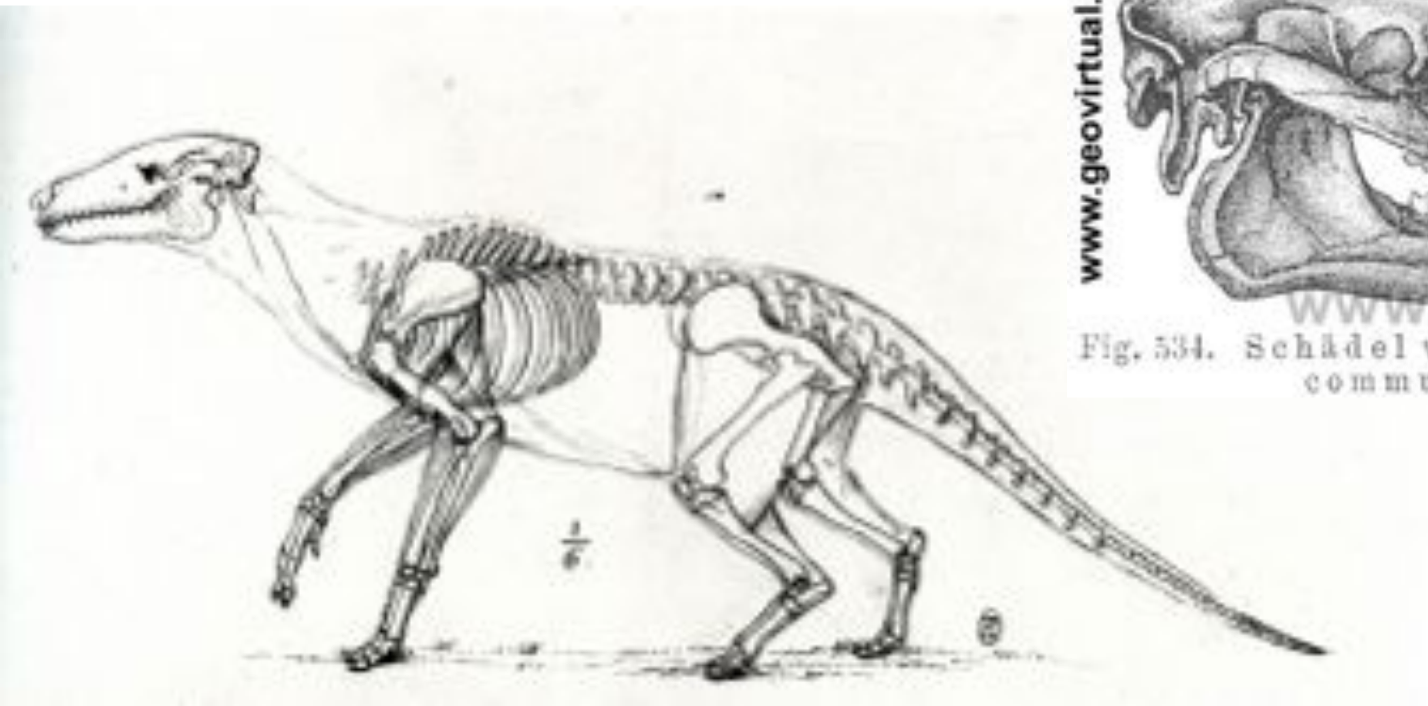


Fig. 534. Schädel von Anoplotherium commune Cuv.

Romer sugirió que el oreodonto *Anoplotherium* (de cara + larga) sería cercano a los Camelidae.

La combinación de evidencia (fósiles + molecular) favorecen esta interpretación, colocando a los oreodontos hacia la base de camelidomorpha, pero la evidencia fósil disponible por sí sola no la apoya

Camelidamorpha?

Oromerycidae

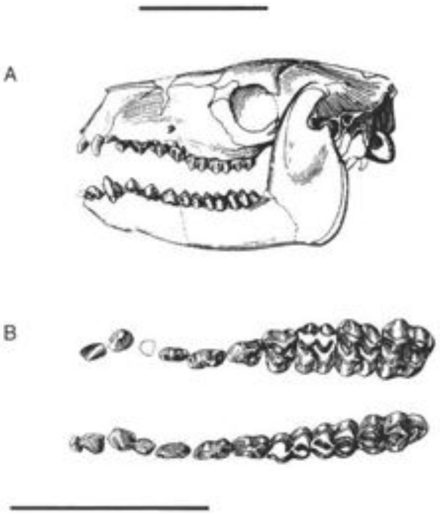


Figure 28.2. A. Skull and jaws of *Eotylopus reedi* (UW 216), a representative and relatively completely known oromerycid (scale bar = 5 cm). B. Crown view of dentition of *Eotylopus reedi* (scale bar = 5 cm). (Modified from Prothero, 1986.)

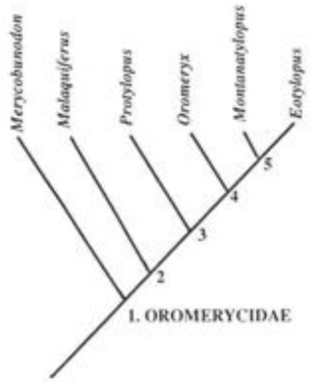


Figure 28.3. Interrelationships within the Oromerycidae. Characters at the nodes are as follows: (1) OROMERYCIDAE: Deep lingual cleft separating metaconid from entoconid on m3. (2) Lose hypocone; weak upper molar cingula; plicate enamel. (3) Stronger selenes; higher crowned, more rectangular upper molars. (4) Upper molars narrow posteriorly. (5) Much larger size; lose enamel plications.

p3, which does not place it with any group. The affinities of this taxon are indeterminate.

The oromerycids are distinguished from all other early North American selenodontids in having a bifurcate protocone; the entoconid is joined by a crest to the metaconid. Selenodonty is further elaborated within this group.

Figure 28.1. Restoration of *Protylopus*, by Brian Regal.

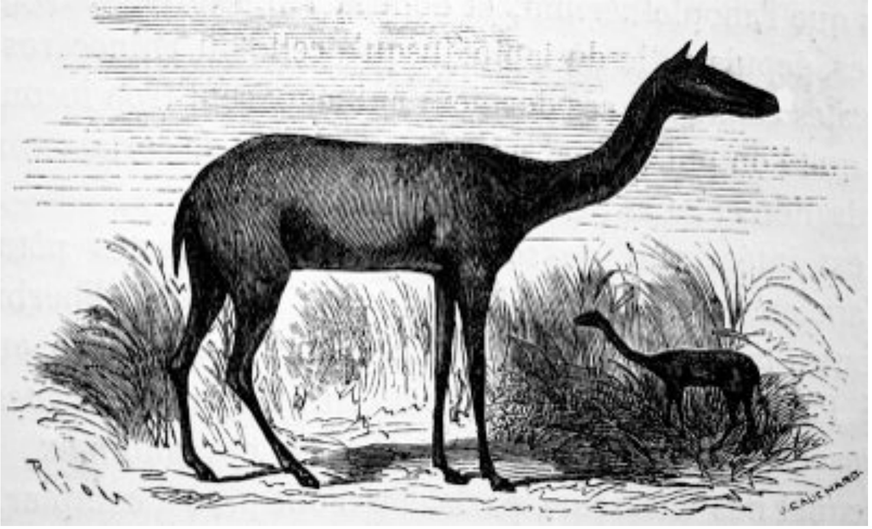
(Figure 28.1). They had no cranial appendages or locomotory specializations. Indeed, they are so primitive in skull, dentition, and skeleton that they have long been confused with primitive camels and protoceratids. Although *Oromeryx* was described by Marsh in

ceratids. The skull (Figure 28.2A) is like that of most primitive tylopods, with a short, broad rostrum, incomplete postorbital bar, and no facial or lacrimal vacuities. Like other tylopods, the bulla is inflated and filled with cancellous bone.

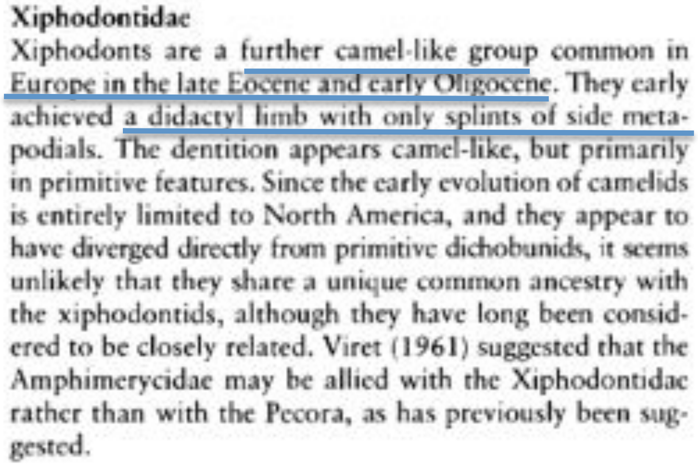
Eocene and early Oligocene of North America. The metapodials are not fused and the manus is still four toed, but the lateral toes of the pes are greatly reduced. Within

those of camels. The only noticeable specialization is the fusion of the radius and ulna, which happened independently in a number of advanced ungulates. The manus has four fully-developed metacarpals, although the central two are more robust. The fibula is reduced to a nodule. The lateral metatarsals have been so reduced that the foot is essentially didactyl.

Camelidamorpha?



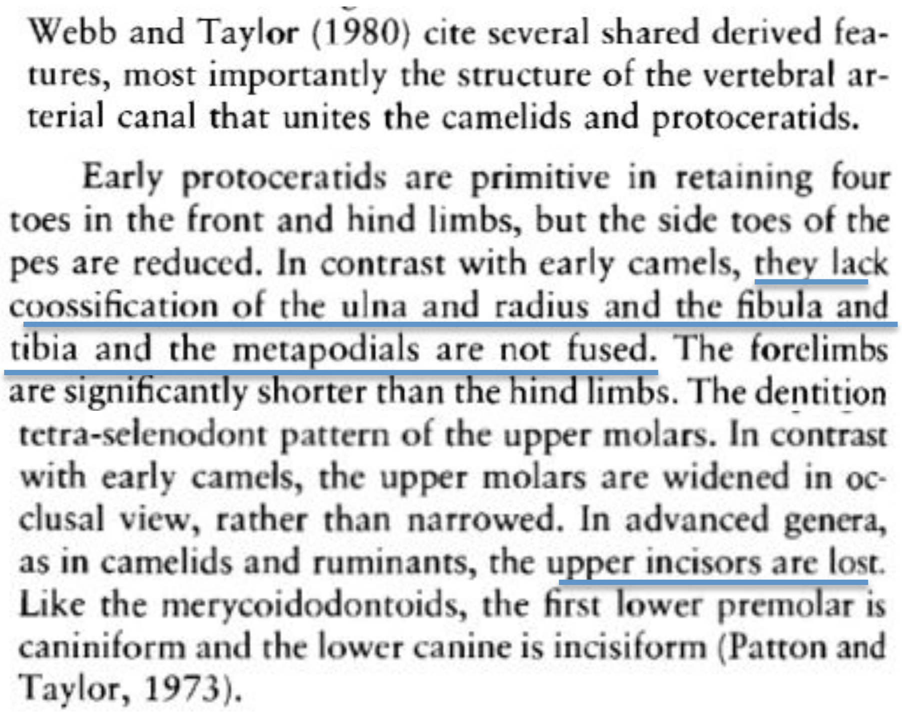
Xiphodon



Xiphodontidae

Xiphodonts are a further camel-like group common in Europe in the late Eocene and early Oligocene. They early achieved a didactyl limb with only splints of side metapodials. The dentition appears camel-like, but primarily in primitive features. Since the early evolution of camelids is entirely limited to North America, and they appear to have diverged directly from primitive dichobunids, it seems unlikely that they share a unique common ancestry with the xiphodontids, although they have long been considered to be closely related. Viret (1961) suggested that the Amphimerycidae may be allied with the Xiphodontidae rather than with the Pecora, as has previously been suggested.

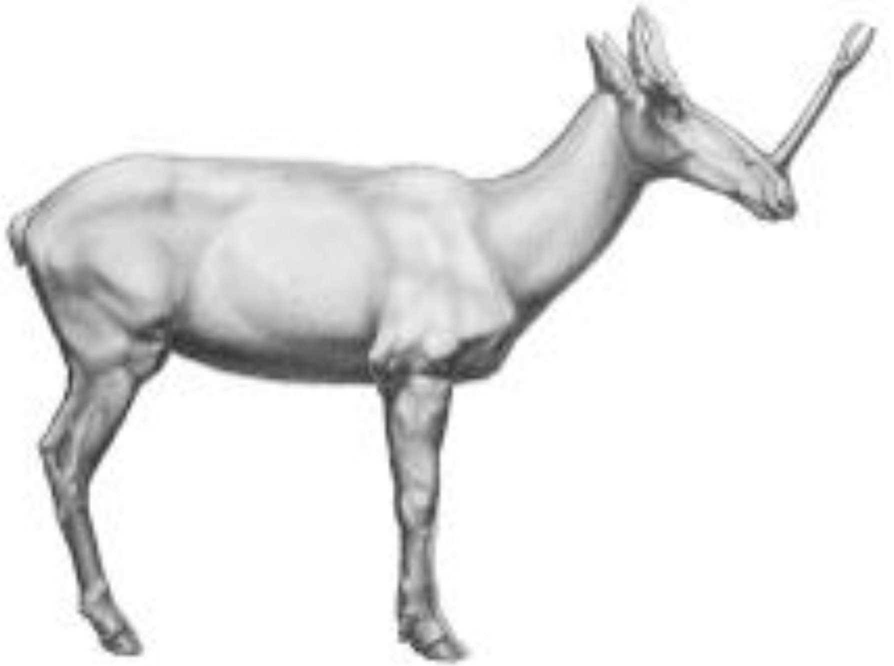
PROTOCERATIDAE



Webb and Taylor (1980) cite several shared derived features, most importantly the structure of the vertebral arterial canal that unites the camelids and protoceratids.

Early protoceratids are primitive in retaining four toes in the front and hind limbs, but the side toes of the pes are reduced. In contrast with early camels, they lack coossification of the ulna and radius and the fibula and tibia and the metapodials are not fused. The forelimbs are significantly shorter than the hind limbs. The dentition tetra-selenodont pattern of the upper molars. In contrast with early camels, the upper molars are widened in occlusal view, rather than narrowed. In advanced genera, as in camelids and ruminants, the upper incisors are lost. Like the merycoidodontoids, the first lower premolar is caniniform and the lower canine is incisiform (Patton and Taylor, 1973).

Ruminantiamorpha según análisis mixto.
Según fósiles, outgroup a Ruminantia + Camelidamorpha



Syndyoceras

Advanced protoceratids, such as *Paratoceras* (Figure 21-23) are characterized by the development of bony protuberances in a variety of bizarre patterns. They may extend from the temporal crests of the parietal, the supraorbital border of the frontal, and the dorsal border of the maxilla (Webb, 1981).

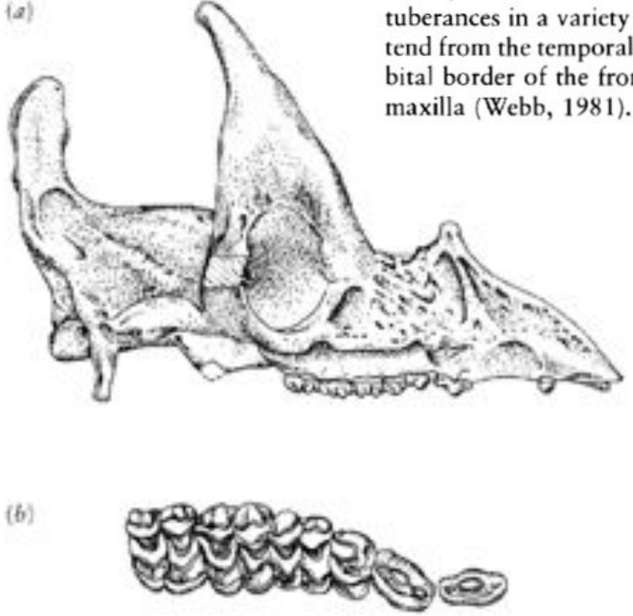
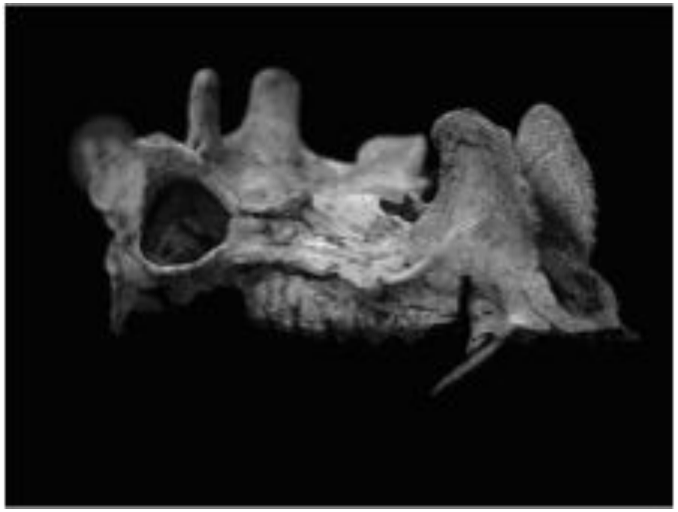


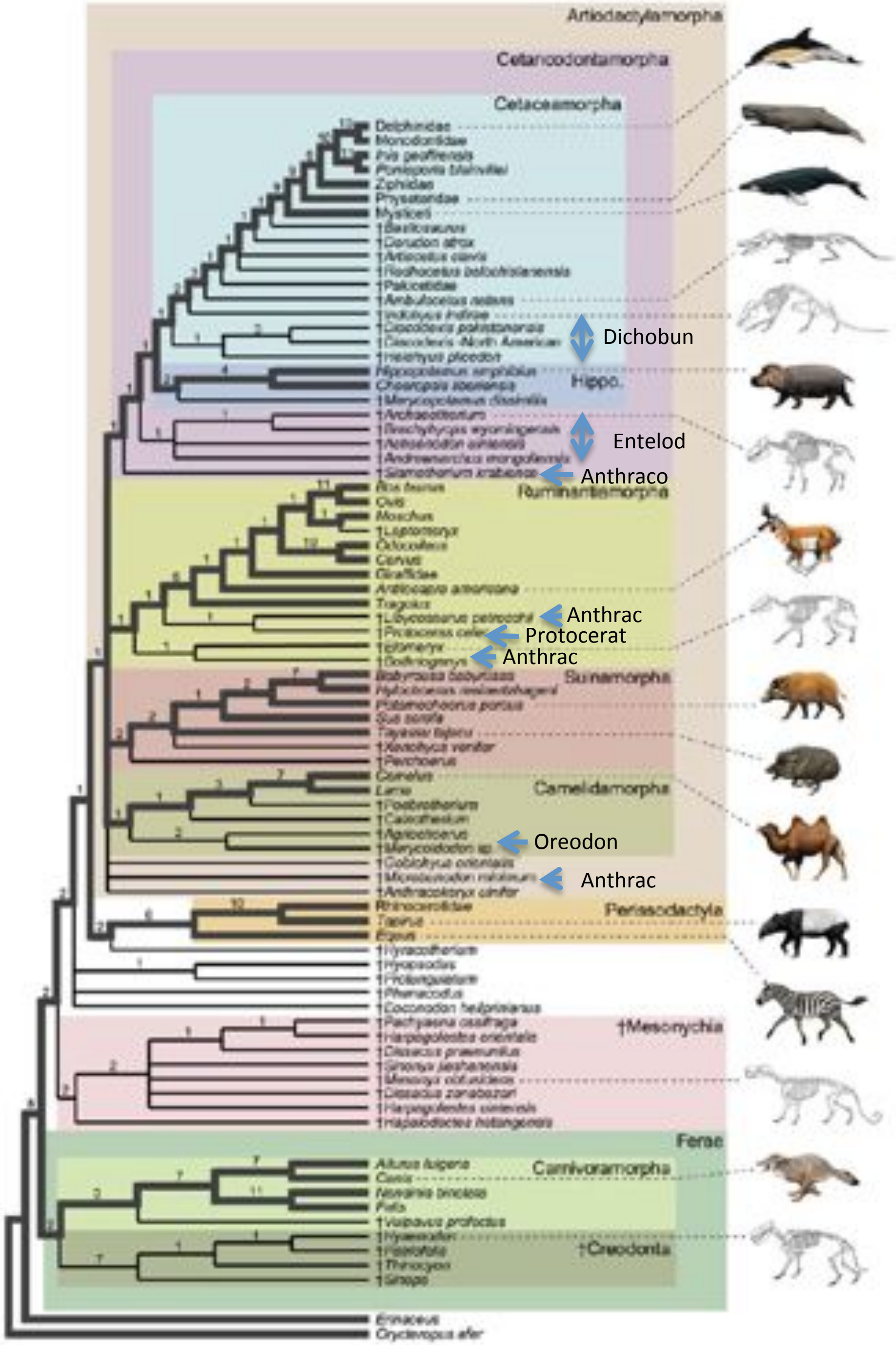
Figure 21-23. (*a*) Skull of the protocerid *Paratoceras* from the Miocene of North America. (*b*) Teeth of the same genus. *From Patton and Taylor, 1973.*

Synthetoceras



Protoceras

EVIDENCIA TOTAL



Dichobun

Entelod

Anthraco

Anthrac

Protocerat

Anthrac

Oreodon

Anthrac

DATA FOSILIZABLE

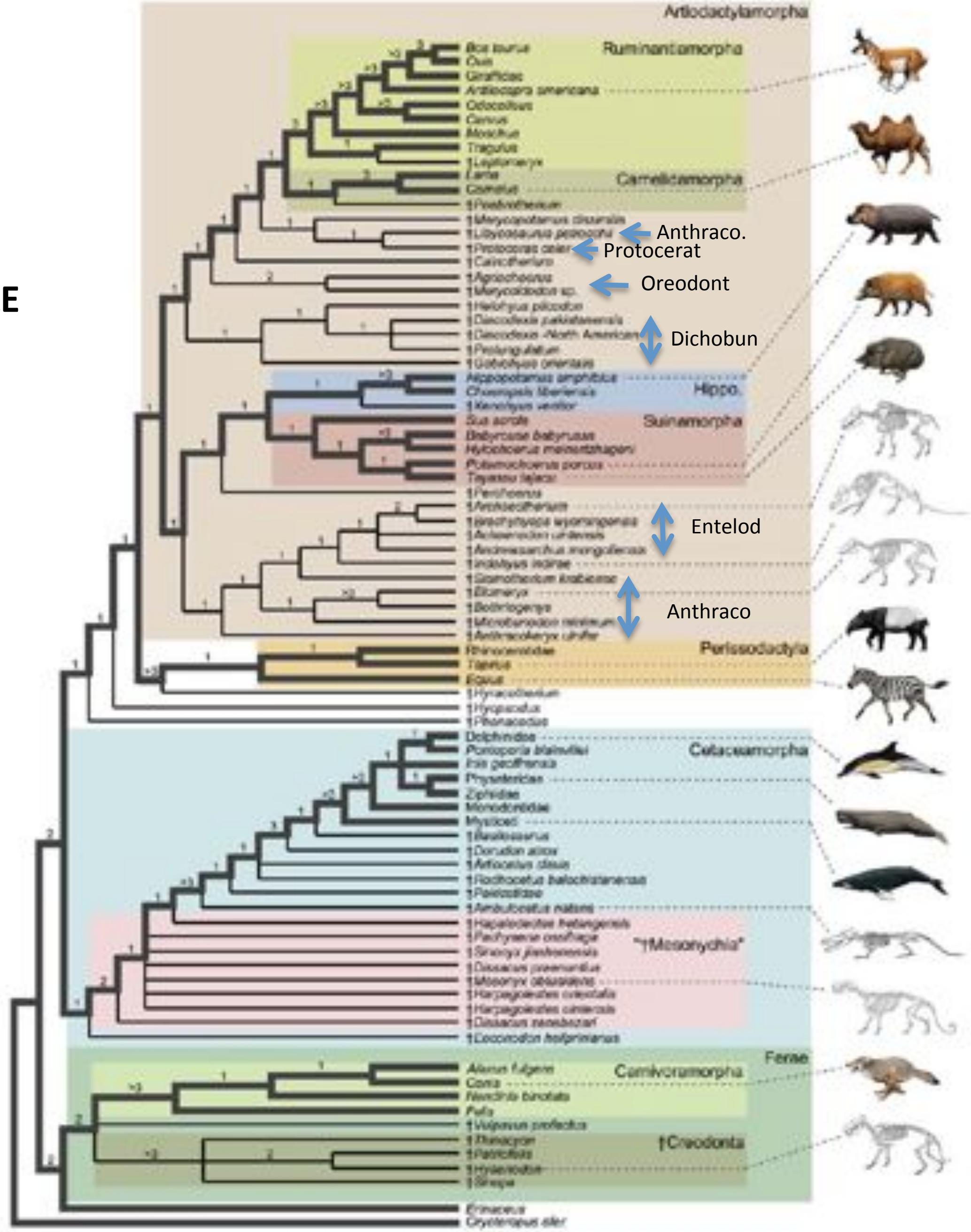


Figure 5. Strict consensus of the 48 minimum length trees for the equally-weighted parsimony analysis of 606 characters observable in fossils (3,722 steps). Note that both Selenodontia (Ruminantia + Camelidae) and Suiformes (Hippopotamidae + Suina) are supported, in contrast to the total evidence analysis (Figure 2). Colored boxes that delimit taxonomic groups are as in Figure 2 (Hippo. = Hippopotamidamorpha).
doi:10.1371/journal.pone.0007062.g005

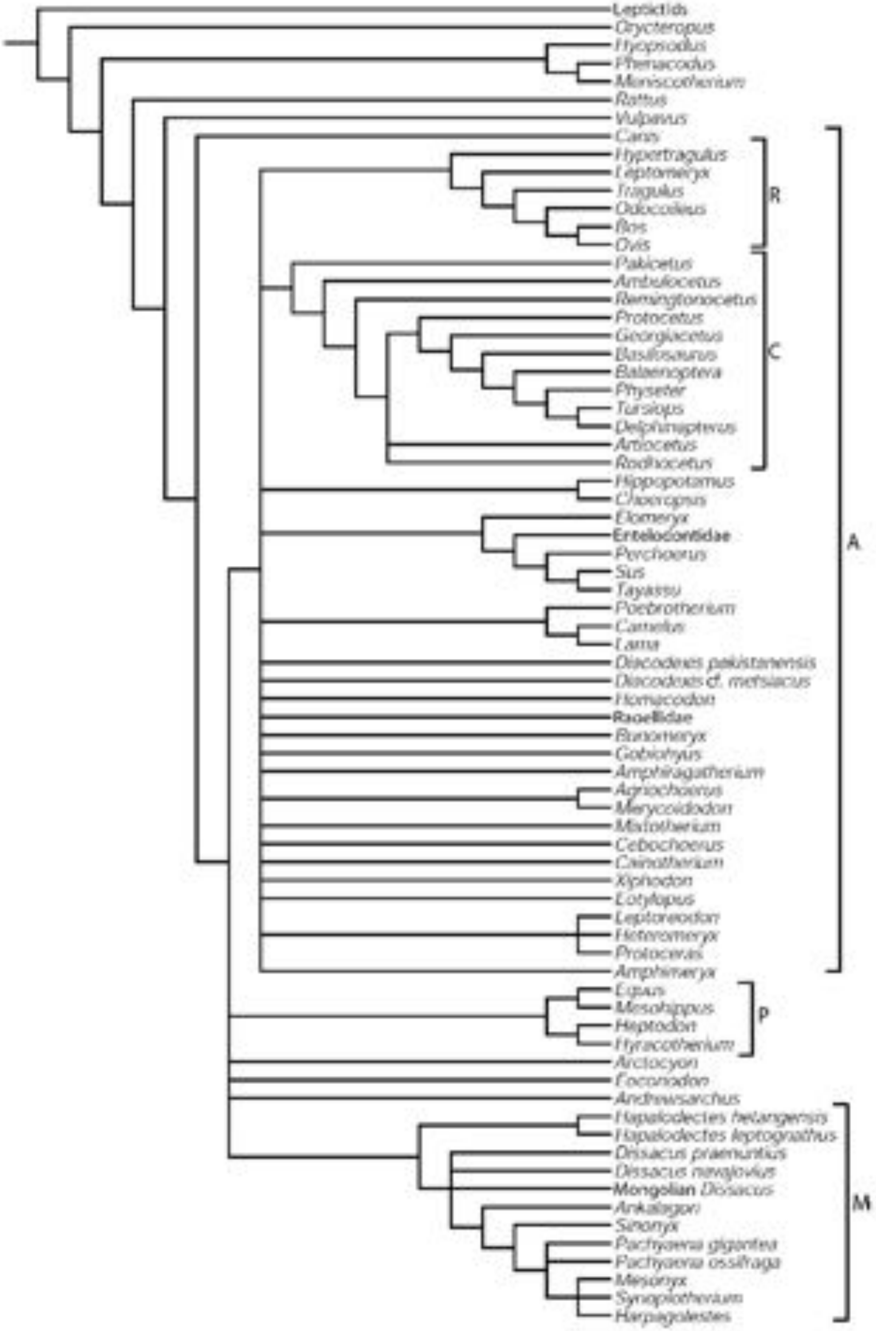


Fig. 2. Strict consensus of 8,910 most parsimonious trees for the intrinsic dataset. Each most parsimonious tree is 33,468 steps in length and supports the exclusion of Mesonychia from Cetartiodactyla. *Taxon abbreviations*: A, Cetartiodactyla; C, Cetacea; M, Mesonychia; P, Perissodactyla; R, Ruminantia.