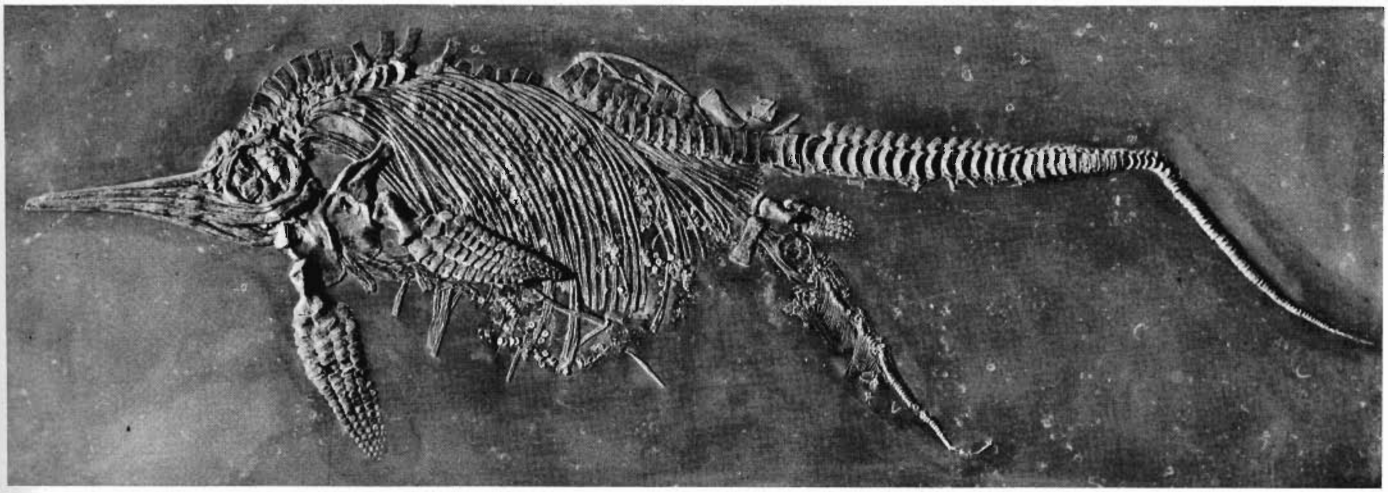
VERTEBRATE PALEONTOLOGY AND EVOLUTION



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W. H. FREEMAN AND COMPANY | NEW YORK

Library of Congress Cataloging-in-Publication Data

Carroll, Robert L.
Vertebrate paleontology and evolution.
Includes index.
1. Vertebrates, Fossil. 2. Vertebrates—Evolution. I. Title.
QE841.C254 1987 566 86-31808
ISBN 0-716-71822-7

Printed in the United States of America.
3 4 5 6 7 8 9 0 HL 6 5 4 3 2 1 0 8 9 8

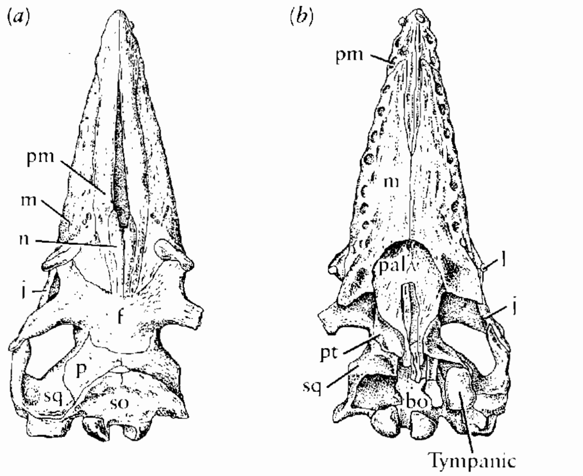


Figure 21-37. SKULL IN DORSAL AND PALATAL VIEWS OF THE PRIMITIVE OLIGOCENE WHALE *AETIOCETUS.* Although teeth are retained, the pattern of the skull is otherwise typical of primitive mysticete whales. Abbreviations as in Figure 8-3. *From Emlong, 1966.*

the most abundant living family and include the minke and giant blue. This group is known from the late Miocene. The Eschrichtiidae, which include the gray whale, has a fossil record going back to the late Miocene, but the small size of the skull is a primitive feature that may suggest an even earlier origin. The number of families gives an inflated impression of the diversity of modern mysticetes, for there are only 8 living genera with fewer than 15 species.

PERISSODACTYLA

THE ORIGIN OF PERISSODACTYLS

Only six genera of perissodactyls remain in the modern fauna. The living horses, tapirs, and rhinos represent but a small fraction of the numerous lineages that were common in the early Cenozoic (Figure 21-38).

Perissodactyls are known from the earliest Eocene and their ancestry can be traced with little question to the condylarth family Phenacodontidae. Van Valen (1978) suggested that phenacodontids may in turn be derived from the loxolophine arctocyonids at the base of the Paleocene. He distinguished early members of the Loxolophinae from other arctocyonid subfamilies by the possession of relatively low-crowned and transverse lower molars; the trigonid basins lack a central crest, and the M_1 paraconids do not project forward. *Loxolophus* (Figures 21-39 and 21-40) has a rather doglike skull, with large canines and a short diastema behind the first premolar.

Phenacodus from the late Paleocene and early Eocene has been considered a typical condylarth (Figures 21-41). The limbs are relatively long but unspecialized. Both manus and pes are pendactyl but digits I and V are reduced. The middle Paleocene genus *Tetraclaenodon* is less completely known but occupies a position closer to the ancestry of the perissodactyls. Although it is the most advanced phenacodont that is not too specialized to have given rise to perissodactyls, it is still significantly more primitive than the earliest members of that group.

Hyracotherium, which was common in the Lower Eocene, is the best-known primitive perissodactyl. Radinsky (1966) described a number of changes between *Tetraclaenodon* and *Hyracotherium.* The most important involve the dental and locomotor apparatus.

The molars of *Hyracotherium* have relatively higher and more acute cusps and ridges and the crests connecting the cusps are better developed (Figure 21-42). The protocone-metaconule connection has been lost, but a crest has developed that joins the hypocone and metaconule. These changes result in the elaboration of two oblique transverse crests, an anterior protoloph and posterior metaloph. In the lower teeth, the hypoconulid has been displaced posteriorly, leaving the posterior side of the hypoconulid and entoconid clear for shear against the anterior side of the metaloph.

The third upper molar is enlarged to the size of the second and has added a hypocone. The lower third molar becomes larger than the second. These changes would have resulted in an increase in the amount of shear and a decrease in crushing.

Elaboration of the angle of the jaw suggests increased importance of the masseter-pterygoid complex relative to the temporalis, as in most mammalian herbivores. This complex contributes to transverse movements of the jaws, in contrast to the vertical movement produced by the temporalis, which is emphasized in carnivores.

In *Tetraclaenodon* (Figure 21-43), the mobility of the forelimb is already restricted relative to that of more primitive mammals. The elements of the carpus alternate with one another, which adds strength to the carpus but reduces its mobility. The scaphoid rests partly on the magnum and the lunar partly on the unciform. In *Hyracotherium,* the length of the forearm relative to the humerus is increased and the carpals have more extensive areas of articulation. There is increased overlap between the cuneiform and the scaphoid and between the unciform and magnum. The first digit is lost and the fifth is reduced; the third digit has assumed the major role in support of the foot. The metacarpals are much longer than those of *Phenacodus.*

Similar changes in proportions can be seen in the rear limb. The tarsus is narrow and more compact. The astragalus, calcaneum, and navicular are radically modified to eliminate the possibility of lateral movement of the foot. The astragalo-navicular articulation is saddle shaped, which is a unique and diagnostic feature of the perissodactyls. The first and fifth toes are lost. In these features, early perissodactyls are advanced over the contemporary

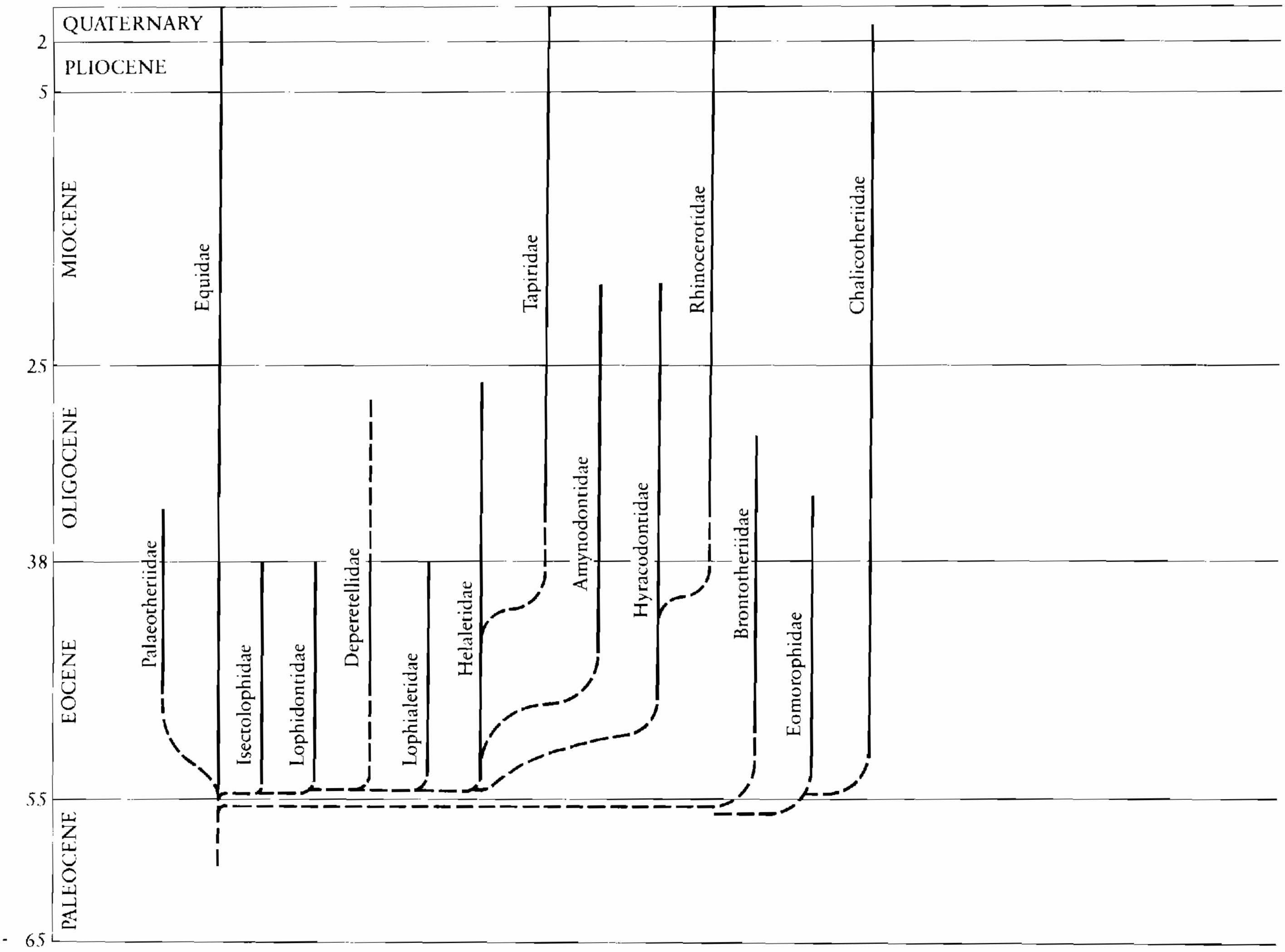


Figure 21-38. STRATIGRAPHIC RANGES OF PERISSODACTYL FAMILIES.

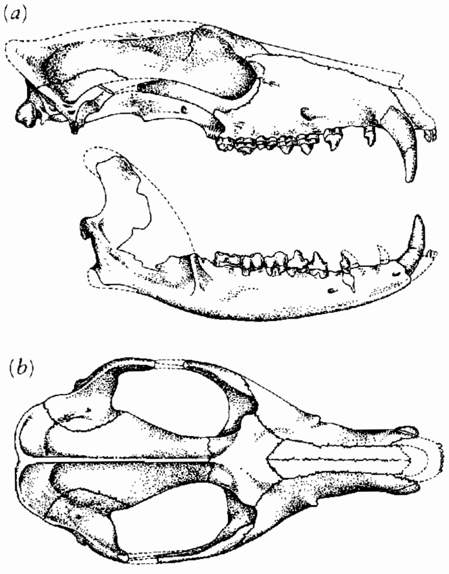


Figure 21-39. (*a*) Lateral and (*b*) dorsal views of the skull of the arctocyonid *Loxolophus*, which may be close to the ancestors of the phenacodonts and so to the perissodactyls. *From Matthew, 1937.*

artiodactyls and distinguished from them in the emphasis that is placed on the third digit, a pattern termed **mesaxonic.**

Radinsky estimated that the changes from *Tetraclaenodon* to *Hyracotherium* took place in less than 5 million years—considerably more rapidly than other changes within the order in the subsequent 55 million years. As in the case of the artiodactyls, Radinsky considers that the change in foot structure and other modifications for cursorial locomotion were more significant

Figure 21-40. (*a* and *b*) Upper and lower dentition of *Loxolophus*. *From Matthew, 1937.*

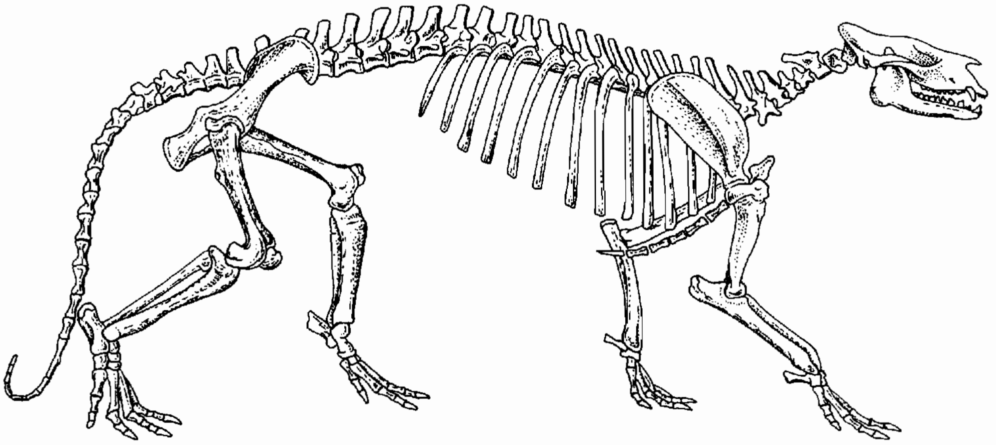


Figure 21-41. SKELETON OF THE CONDYLARTH *PHENACODUS. From Gregory, 1951 and 1957.*

than changes in the dentition in accounting for the great success of perissodactyls in the early Eocene.

The absence of intermediates between *Tetraclaenodon* and *Hyracotherium* in North America suggests that the actual transition may have taken place in some other part of the world. As in the case of the artiodactyls, one might debate whether it is more useful to consider that the origin of perissodactyls occurred when the definitive ankle morphology evolved or at the earlier time when the ancestral phenacondont lineage first diverged from the ancestors of other ungulate groups.

Hyracotherium varied from 25 to 50 centimeters in height at the shoulder. The orbit is midway in the length of the skull and lacks a postorbital bar. The teeth are low crowned (brachydont) and basically bunodont, despite the initial development of cross lophs. The premolars are not molariform. A short diastema is present but all the incisors are retained, as is the case in modern equids. Endocasts demonstrate that the brain is significantly advanced over that of condylarths in its relative size and expanded neocortex (Radinsky, 1976). Most skeletal features of *Hyracotherium* may be close to the ancestral pattern for all perissodactyls. MacFadden (1976) showed that the confluence of the foramen ovale and the middle lacerate foramen and the migration of the optic foramen close to, or confluent with, a group of posteroventral foramina are derived features that demonstrate that *Hy-*

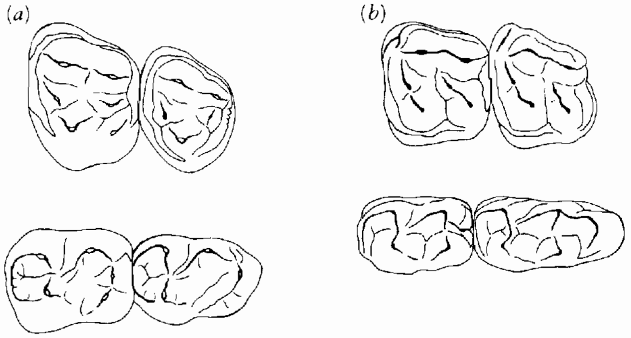


Figure 21-42. Upper and lower second and third molars of (*a*) *Tetraclaenodon* and (*b*) *Hyracotherium*. These teeth show the transition from the condylarth to the primitive perissodactyl pattern. *From Radinsky, 1966.*

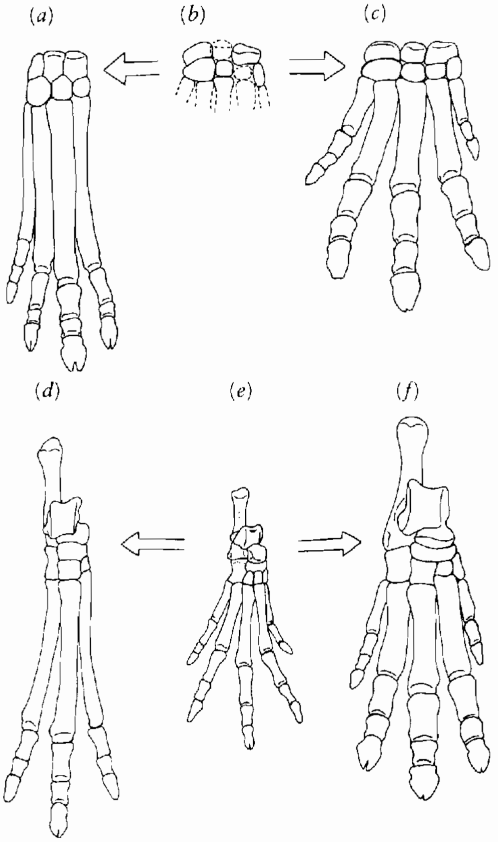


Figure 21-43. CHANGES IN THE LIMB STRUCTURE BETWEEN PHENACODONTS AND PRIMITIVE PERISSODACTYLS. (*a*) Front feet of *Hyracotherium*, (*b*) *Tetraclaenodon*, and (*c*) *Phenacodus*. (*d*) Hind feet of *Hyracotherium*, (*e*) *Tetraclaenodon*, and (*f*) *Phenacodus*. *From Radinsky, 1966.*

racotherium belongs to the same monophyletic group as other members of the family Equidae.

Representatives of three superfamilies of perissodactyls are known in the Lower Eocene. In addition to the equid *Hyracotherium,* we find the tapiroid *Homagalax* and the chalicotheroid *Paleomoropus* (a group whose later members are characterized by the elaboration of long claws) (Radinsky, 1969). The early brontotheroids (rhinolike forms with large bony protuberances on the skull) appeared in the later part of the early Eocene, and the Rhinocerotoidea is known from the beginning of the late Eocene. Fourteen perissodactyl families had differentiated by the end of the Eocene. In strong contrast with the Artiodactyla, the subsequent history of this group shows a progressive reduction in diversity.

Although later members of the perissodactyl superfamilies are very distinct from one another, the early Eocene forms are differentiated primarily by small differences in the pattern of molar cusps (Figure 21-44). Equids retain a distinct protoconule and metaconule. In the early tapiroids, these cusps join the protoloph and metaloph and the protolophid and hypolophid are elaborated in the lower molars. The chalicotheroids retain the protoconule and protocone as distinct cusps, but the metaconule merges with the hypocone to form a high, unbroken metaloph. Brontotheroids have a strong mesostyle and a w-shaped ectoloph; the metaconule is absent and the protoconule is reduced. The functional significance of these changes in cusp pattern is discussed by Butler (1952) in relationship to different patterns of mastication and particular types of food. The early perissodactyl genera were also differentiated to some degree by differences in size.

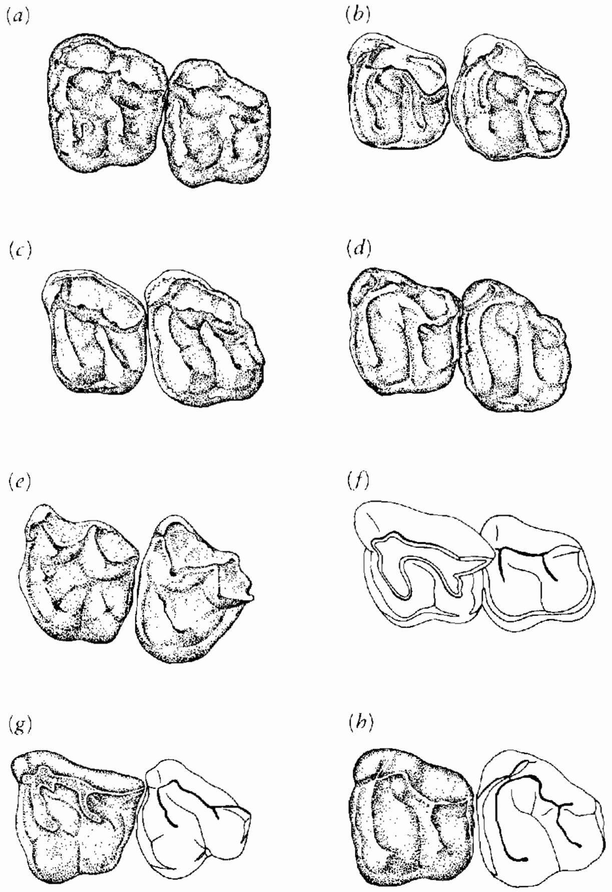


Figure 21-44. SECOND AND THIRD UPPER MOLARS OF EARLY PERISSODACTYLS. (*a*) *Hyracotherium.* (*b*) *Paleomoropus,* a chalicotherioid. (*c* and *d*) *Homogalax* and *Heptodon,* both tapiroids. (*e*) *Eotitanops,* a brototherioid. (*f, g,* and *h*) The rhinocerotoids *Amynodon, Hyracodon,* and *Hyrachyus. From Radinsky, 1969.*

The three initial groups underwent subsequent radiation within the Eocene.

TAPIROIDS

Although tapirs are the most conservative of living perissodactyls, they are but one surviving lineage of a diverse assemblage in the Eocene. The early tapiroids are distinguished from the equid *Hyracotherium* by elaboration of the cross lophs and some molarization of the premolars. They were common in all the northern continents in the early Eocene. Subsequently, separate families differentiated in North America, Europe, and Asia. Short-lived, little-differentiated groups include the Isectolophidae in North America, the Lophidontidae in Europe, and the Deperetellidae and Lophialetidae in Asia. In the Asian families, the manus became tridactyl and the metapodials were relatively long and slender.

Both isectolophids and a second family common in North America in the middle to late early Eocene, the Helaletidae, may be traced to *Homagalax.* The early helaletid genus *Heptodon* (Figure 21-44*d*) has a sharp-crested transverse protoloph and metaloph that meet the ectoloph, a pattern that is common to all later tapiroids. It is also advanced in the presence of a postcanine diastema. *Heptodon* appears to be at the base of a dichotomy leading in one direction to the Rhinocerotoidea and in another to the modern family Tapiridae. *Helaletes,* which is known from the middle Eocene of North America and the early late Eocene of Asia, is close to the origin of modern tapirs. As in *Tapirus,* this genus shows a deep nasal incision, which indicates development of a short proboscis. Other helaletids survived until near the end of the Oligocene. All other early tapiroid families became extinct at the end of the Eocene.

Radinsky (1965) detailed the changes in the skeleton between the Eocene tapiroid *Heptodon* and the Recent genus *Tapirus.* The main advances in the skull are associated with the elaboration of the proboscis and were essentially completed by the Oligocene (Figure 21-45). Postcranially, most changes can be attributed to the larger size of the modern genus, but we can see some cursorial adaptations, including the fusion of the radius and ulna and the loss of the acromium, which in noncursorial mammals supports the clavicle. As in all other tapiroids, the modern tapirs retain brachydont cheek teeth and a rela-

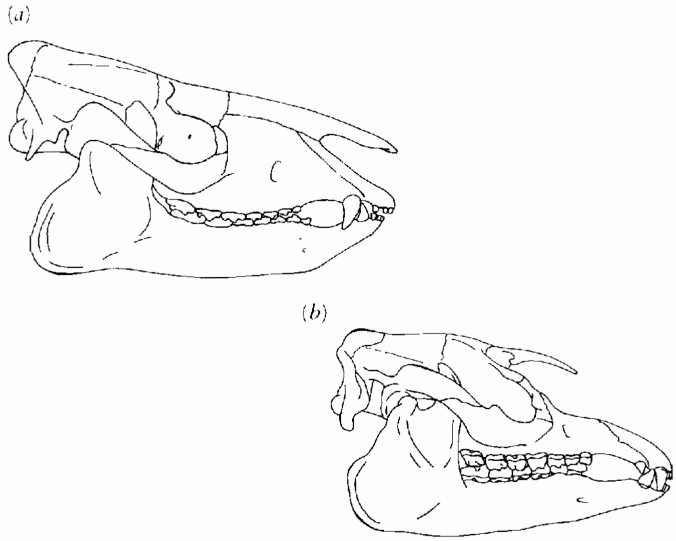


Figure 21-45. SKULLS OF TAPIROIDS. (*a*) *Heptodon*, from the Eocene and (*b*) the modern genus *Tapirus*. *From Radinsky, 1965.*

tively primitive pattern of the feet. The earliest tapirid, *Prototapir*, appears in the early Oligocene in Europe and the Middle Oligocene in North America. The modern genus *Tapirus* is known first in the late Miocene of China and is common in North and South America during the Pleistocene (Dawson and Krishtalka, 1984).

RHINOCEROTOIDEA

Ancestral rhinoceroses can be recognized from the beginning of the late Eocene in North America and Asia. Primitive genera were tapirlike in size and body form, but the teeth show an increase in shearing function that, as in the case of early selenodont artiodactyls, is associated in some groups with subsequent increase in size and greater cursorial adaptation. The teeth of the early rhinos are differentiated from those of the tapiroids in being higher crowned; the ectolophs of the first and second molars are long and flat and the paralophids and metalophids are high (Figure 21-44*f*, *g*, and *h*). Shearing along the ectoloph is enhanced and horizontal shearing becomes important. The morphology of the molar teeth among the Rhinocerotoidea is fairly conservative, but there is considerable variation of the pattern of the incisors and canines, which Radinsky (1969) used to characterize each of the families (Figure 21-46).

Advanced characters of the molars are initiated in some variants of a late middle Eocene species of the helaletid tapiroid *Hyrachyus*. They are elaborated in two late Eocene families, the Hyracodontidae and the Amynodontidae. Radinsky (1969) suggests that this pattern may have evolved separately from different lineages, which would make the Rhinocerotoidea, as it is generally understood, polyphyletic. One might solve this problem by referring the Amynodontidae to the Tapiroidea and restricting the Rhinocerotoidea to the Hyracodontidae and their descendant, the modern family Rhinocerotidae.

The structure and general habitus of the amynodontids are like those of other rhinoceroses and so will be considered in this section. This family is distinguished by increasing hypsodonty and further elaboration of ectoloph shear; the canines are usually large and erect and the incisors are small and pointed. The molars are transversely compressed. The skull is massive and the antorbital portion shortened. As in other rhinos, there is progressive size increase in most lineages, although some genera remain small. The limbs remain conservative, with the manus remaining tetradactyl; no cursorial adaptations are evident beyond those already present in tapirs. Amynodontids were common and diverse in the early Oligocene of North America and especially in Asia, but they did not survive to the end of that epoch.

The hyracodontids, which Radinsky (1967) reviewed, were small- to medium-sized forms that show some cursorial specializations. The pes is long and slender and the manus tridactyl. They are distinguished from the amynodonts dentally by the fact that the third upper molar is triangular in outline rather than squared, and the ectoloph is confluent with the metaloph. Within the family, most lineages show an increase in hypsodonty and the premolars become more molariform. The canines are smaller and the incisors are spatulate or pointed. A variety of lineages, some of which were highly cursorial, evolved during the late Eocene and early Oligocene. Two genera

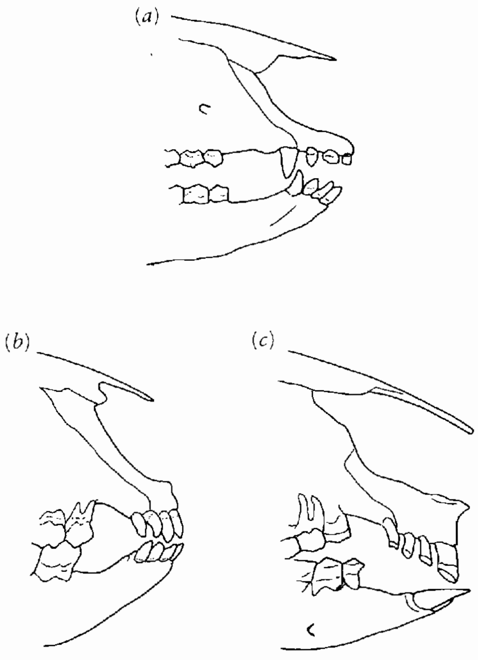


Figure 21-46. SPECIALIZATION OF THE ANTERIOR TEETH IN RHINOCEROTOIDS. (*a*) *Hyrachyus*, a tapiroid, showing a primitive perissodactyl condition. (*b*) *Hyracodon*, a hyracodontid rhinocerotoid. (*c*) *Trigonias*, a primitive rhinocerotid. *From Radinsky, 1969.*

were common in both North America and Asia in the late Eocene, but subsequent evolution proceeded separately in both areas. In the Oligocene, the Asian genus *Indricotherium* was gigantic. This family did not survive the Oligocene.

The ancestry of the modern family Rhinocerotidae is apparently to be found among primitive hyracodontids in which the manus retained four digits. Early members are recognized by the chisel-shaped upper incisor and the enlarged, procumbent second lower incisor. The other incisors and canines are reduced or lost. The Rhinocerotidae was common and diverse throughout the northern hemisphere in the Oligocene and Miocene. The central Asian genus *Indricotherium* from the late Oligocene and early Miocene was the largest known land mammal, standing 5 meters tall at the shoulder, with a skull that was 1.2 meters long. Like other primitive rhinos this genus lacked horns. *Teleoceras* was a common late Miocene and Pliocene form from North America that had the proportions of a hippopotamus. Rhinos became extinct in North America after the Pliocene but remained widespread and diverse in the Old World into the late Pleistocene.

The fossil record of rhinos since the Miocene is well documented in Africa (Hooijer, 1978). The black and white rhinos, *Diceros bicornis* and *Ceratotherium simum*, are among the most long-lived modern ungulate species. Their transition from more primitive African species occurred approximately 4 million years ago. The divergence between these rhinoceros genera occurred at least 12 million years ago.

Dicerorhinus, which is now restricted to southeast Asia and Indonesia, was present in Europe in the early Miocene and appeared in Africa more than 20 million years ago. The genus *Rhinoceros* is known from the late Pliocene. The now extinct woolly rhinoceros *Coelodonta*, which is illustrated in neolithic cave paintings in Europe, was widespread in Eurasia during the Pleistocene.

Throughout their history, rhinos have included both browsing and grazing forms that were capable of exploiting a fairly wide range of diets. The actions of humans, both in direct predation and by widespread destruction of habitats, have placed all five of the surviving rhino species in danger of extinction. A revised phylogeny of the Rhinocerotoidea is proposed by Prothero, Manning and Hanson (1986).

BRONTOTHERIOIDEA

During the early Cenozoic, the most spectacular perissodactyls in North America and Asia were the brontotheres or titanotheres (Figure 21-47). From dog-sized forms in the late early Eocene, they reached the size of a rhinoceros by the time of their extinction in the middle Oligocene. Accompanying the great increase in overall size was an inordinate increase in the size of bony projections from the front of the skull. Stanley (1974) described the evolution of these structures for intraspecific combat in relationship to progressive adjustment to the increase in total body size.

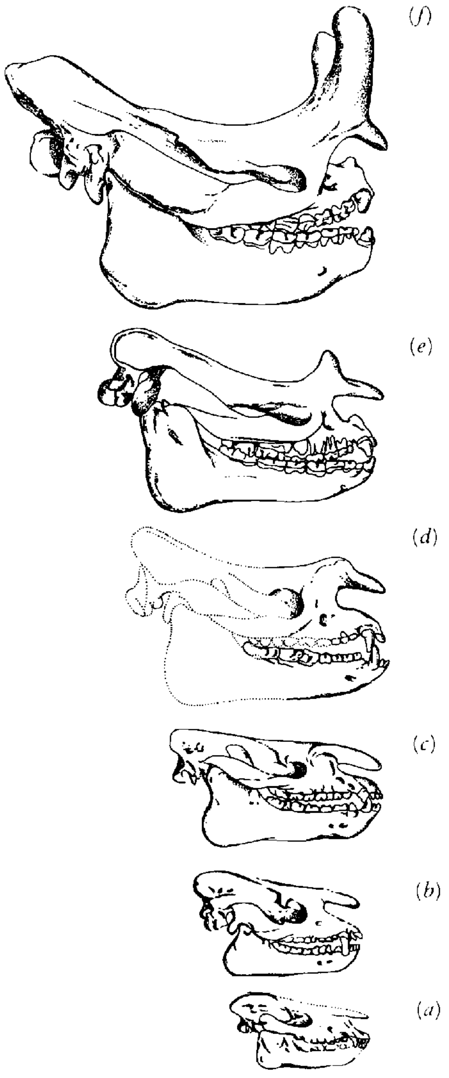


Figure 21-47. ELABORATION OF THE "HORNS" OF TITANOTHERES. (*a*) *Eotitanops*, Lower Eocene. (*b*) *Limnohyops*, Middle Eocene. (*c*) *Manteoceras*, Middle Eocene. (*d*) *Protitanotherium*, Upper Eocene. (*e*) *Brontotherium leidyi*, Lower Oligocene. (*f*) *Brontotherium gigas*, Lower Oligocene. *From Stanley, 1974.*

Eotitanops from the latter part of the early Eocene had already evolved the W-shaped ectoloph that was characteristic of this group throughout its history. The body size increased by 50 percent by the middle Eocene. As in the Rhinocerotoidea, brontotheres show a progressive shortening of the anterior portion of the skull. By the late middle Eocene, the bones were elaborated as hornlike structures. The phylogeny of titanotheres established by Osborn (1929) indicates that large size and elaboration of the "horns" occurred independently in three related subfamilies between the middle Eocene and the early Oligocene. In relationship to their large body size, the limbs remained little modified and four digits were retained in the manus.

CHALICOTHEROIDEA

Advanced chalicotheroids include some of the most bizarre ungulates. *Chalicotherium* from the Miocene of Europe had limb proportions and specializations of the pelvic girdle that would have enabled it to assume a semibipedal stance comparable to that of a gorilla (Figure 21-48). Zapfe (1979) and Coombs (1983) suggested that it may have been adapted to browsing on tall trees.

Moropus, in which the body proportions were more horselike, is characterized by the presence of large claws on both the forelimbs and hind limbs that were retractable like those of a cat (Figure 21-49). *Chalicotherium* also had claws on the rear limbs. It has been suggested that their claws were used to dig up tubers or roots, but the teeth do not show extensive wear as would be expected if they ate food from the ground. No other elements of the skeleton are specialized like those of known digging forms. The fusion of the ulna and radius precludes twisting of the lower arm. The forelimbs may have been used to bring vegetation to the mouth.

Tylocephalonyx from the Miocene of North America resembled *Moropus* in general proportions, but the skull was greatly thickened posteriorly like the dome of *Pachycephalosaurus* and may have been used in intraspecific head butting (Coombs, 1979).

Chalicotheres are represented in the early Eocene by members of the primitive family Eomoropidae, which are known from both North America and Asia (Radinsky, 1964). Their dentition resembles that of later chalicotheres in possessing a W-shaped ectoloph that enhances vertical shear. The lower molars have a double-V pattern of crests and surfaces for crushing against the protocone. Chalicotheroids remain conservative in not evolving molariform premolars. It is not known whether or not the eomoropids had yet developed claws.

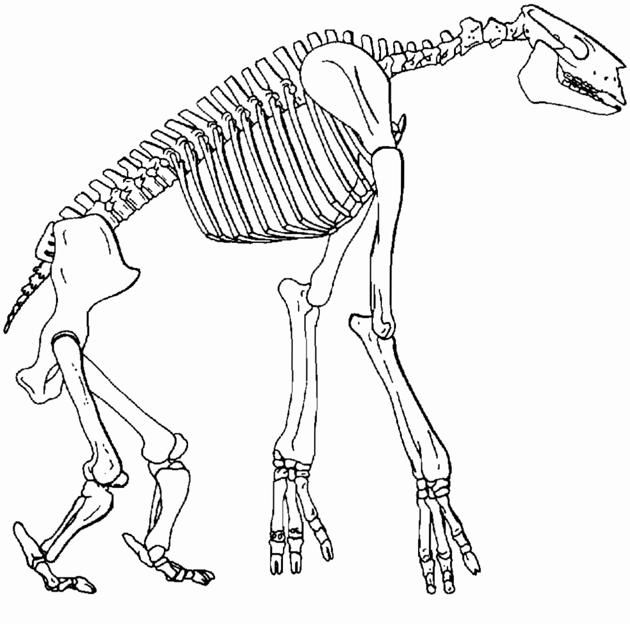


Figure 21-48. CHALICOTHERIUM FROM THE MIOCENE OF EUROPE. This genus is thought to have been capable of a partially bipedal posture and browsed from trees. *From Coombs, 1983.*

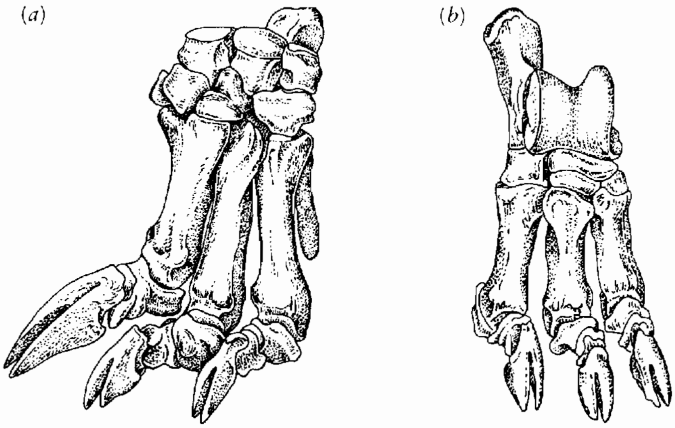


Figure 21-49. (*a*) Forefoot and (*b*) hind foot of the chalicothere *Moropus. From Gregory, 1951 and 1957.*

The family Chalicotheriidae is recognized from the latest Eocene and continued into the Pleistocene in Asia and Africa (Butler, 1978). After the Eocene, most of the history of this group was restricted to the Old World. Only a few genera close to *Moropus* were represented in North America during the Miocene (Coombs, 1978).

EQUOIDEA

The extensive fossil record of the family Equidae provides an excellent example of long-term, large-scale evolutionary change. Changes in body size, skull proportions, dentition, limb structure, and relative brain size have all been thoroughly documented (Simpson, 1961; Edinger, 1948; Radinsky, 1976, 1984).

Early work suggested that horses constituted a single assemblage that progressed relatively steadily from the small-sized *Hyracotherium* [*Eohippus*], with low-crowned teeth and four toes on the front feet and three on the rear, to the modern genus *Equus,* which has high-crowned teeth and whose manus and pes are reduced to a single toe. Subsequent research has demonstrated a much more complex radiation, with many divergent lineages of browsers and grazers overlapping one another in time (Figure 21-50).

Hyracotherium is known from the base of the Eocene in both North America and Europe. The equids were among the most abundant mammals during the early Eocene in North America, where the evolution of the horse is best documented. Several early genera were also common in Europe where a divergent family (or subfamily), the Palaeotheriidae, is recognized. *Palaeotherium* is distinguished by a W-shaped ectoloph and oblique, sharp-crested cross lophs. With wear, the molars functioned like

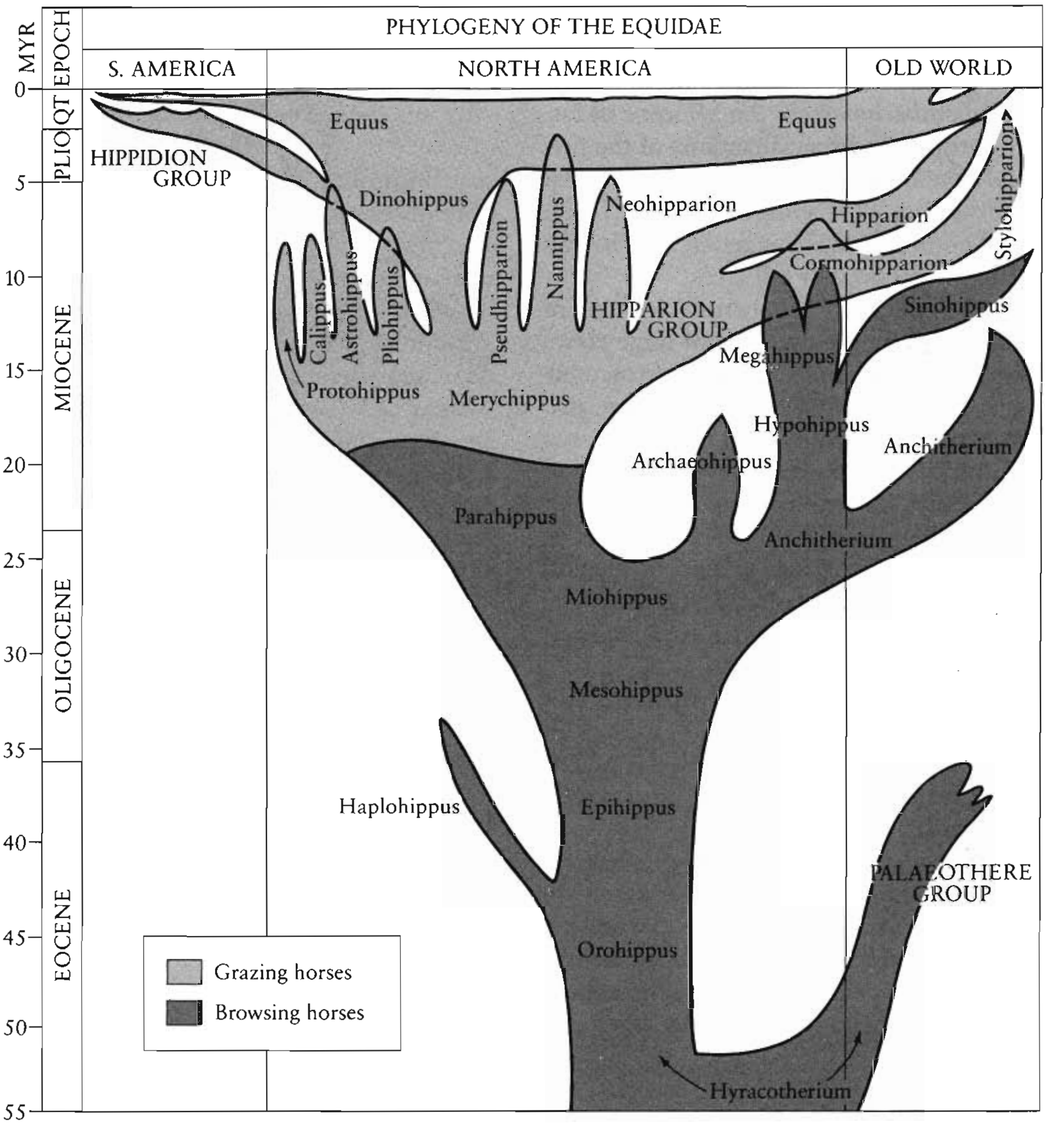


Figure 21-50. PHYLOGENY OF THE HORSE. *From MacFadden, 1985.*

those of solenodont artiodactyls. *Palaeotherium,* which was the largest equoid of the Eocene, also molarized its premolars. European equoids became extinct early in the Oligocene, leaving only the family Equidae to represent this group for the remainder of the Cenozoic.

Only a single lineage of equids is known in the Eocene of North America, represented by *Orohippus* and *Epihippus,* which are successors of *Hyracotherium* in the Middle and Upper Eocene. They show moderate size increase and progressive molarization of the premolars.

Mesohippus was the characteristic equid of the North American Oligocene. It was the size of a sheep and had lost the fourth toe of the manus. The teeth were now clearly lophodont. The ectoloph is prominent but does not have the W-shape of chalicotheres and brontotheres. All but the small first premolar had become molariform (Figure 21-51). However, the cheek teeth remained low crowned and so were better suited for browsing than grazing. From *Mesohippus,* one line, including the genus *Anchitherium,* migrated to Eurasia in the early Miocene and gave rise to species that are known in China as late as the Pliocene. All members of this lineage retained conservative features of the dentition and limbs.

A more progressive line led via *Parahippus* to the characteristic Miocene genus *Merychippus.* Within the 5 to 10 million years of the range of *Parahippus,* most of the major changes in cranial proportions leading to the modern horse were accomplished (Radinsky, 1984) (Figure 21-52). The teeth became high crowned to resist the greater wear of a diet of hard grasses. To accommodate the long roots of the cheek teeth (about 60 percent their length in modern horses), the jaws and face became deepened and the tooth row was displaced anteriorly relative to the orbit and the jaw articulation. The zygomatic arch was strengthened by the completion of the postorbital bar. The high-crowned teeth were supported by a newly elaborated tissue, **cement,** which is soft but tough and serves to support the hard but brittle columns of enamel. The pattern of the molar and premolar lophs approached those of the modern horse. The muzzle was elongated to

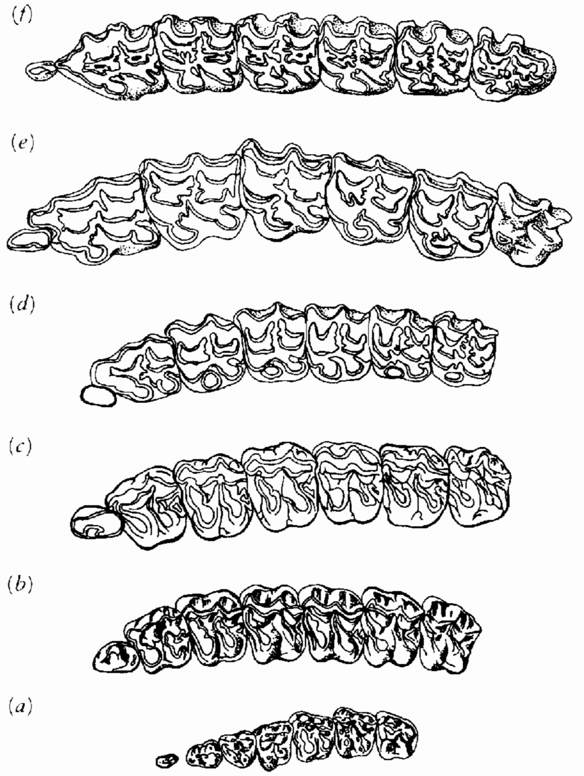


Figure 21-51. CHANGES IN THE DENTITION WITHIN THE EQUIDAE. (*a*) *Orohippus*, middle Eocene. (*b*) *Mesohippus*, Oligocene. (*c*) *Miohippus*, Miocene. (*d*) *Merychippus*, Miocene. (*e*) *Pliohippus*, Pliocene. (*f*) *Equus*, Pleistocene. *From Gregory, 1951 and 1957.*

extend the reach of the enlarged incisors. In contrast with the pecorans, the upper as well as lower incisors are retained in the most progressive perissodactyls.

Three toes are retained in *Merychippus*, but the larger central one evidently bore most of the weight (Thomason, 1986). The configuration of the manus and pes indicates that a strong elastic ligament, like that of modern horses, passed behind the central digit. The ligament stretched as the foot struck the ground, and its elastic energy assisted in ventroflexion of the foot to increase the force of the next stride (Camp and Smith, 1942). These specializations of the dentition and limbs point to *Merychippus* as a rapidly running, grazing animal of the newly expanded North American prairies. *Merychippus* was overshadowed in the late Miocene by a diversity of grazing genera that are divisible into the three-toed hipparions and the monodactyl equines. *Hipparion* is distinguished by the isolated protocone in its upper cheek teeth and by a deep depression or fossa in front of the orbit. *Hipparion* spread from North America into Eurasia and Africa. The appearance of *Hipparion* has been used as an indicator of the Miocene-Pliocene boundary in Europe and much of Asia, but this history is complicated by the probability that more than one lineage migrated to the Old World (MacFadden and Skinner, 1981; MacFadden, 1984a). Hipparions persisted in Africa into the Pleistocene.

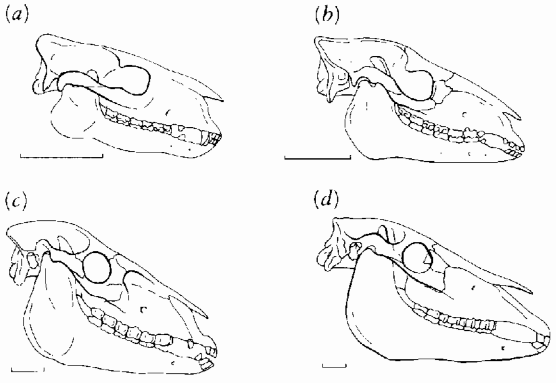


Figure 21-52. SKULLS OF REPRESENTATIVE EQUIDS THAT SPAN THE EVOLUTIONARY HISTORY OF THE FAMILY. (*a*) *Hyracotherium*. (*b*) *Mesohippus*. (*c*) *Merychippus*. (*d*) *Equus*. Note progressive changes in proportions. The greatest change occurs between *Mesohippus* and *Merychippus*. Scale bars equal 5 centimeters. *From Radinsky, 1984.*

A separate branch from *Merychippus* led to the late Miocene and Pliocene genus *Pliohippus*, in which the lateral toes became vestigial (Figure 21-53) and hypsodonty was further increased. One descendant lineage of *Pliohippus* with relatively short limbs, exemplified by *Hippidion*, diversified in South America in the late Pliocene. Another line gave rise to the dominant Pleistocene genus *Equus*, which appeared approximately 3.5 million years ago.

Equus quickly spread to Europe, Asia, Africa, and South America (Eisenmann, 1980). Surprisingly, this genus became extinct in the New World at the end of the Pleistocene, whereas nine species still live in the Old World including the wild Asian horse, four species of asses, and four zebras.

Among the perissodactyls, only the horses have been common and widespread in the late Cenozoic. Janis (1976) discussed the dietary limitations that might have been imposed on perissodactyls by the character of their digestive system. In contrast with most living artiodactyls, they do not ruminate and their efficiency in extracting nutrients from plant material is significantly lower. Perissodactyls all possess a fermentation chamber, the caecum, but it is posterior rather than anterior to the stomach, opening between the small intestine and the colon. In contrast with

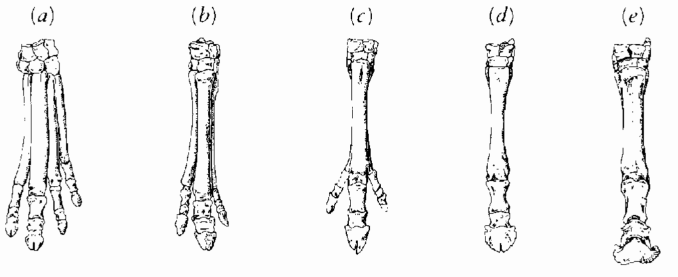


Figure 21-53. EVOLUTION OF THE FRONT FOOT IN THE EQUIDAE. (*a*) *Hyracotherium*. (*b*) *Miohippus*. (*c*) *Parahippus*. (*d*) *Pliohippus*. (*e*) *Equus*. *From Gregory, 1951 and 1957.*

artiodactyls, food passes relatively rapidly through the digestive tract. This enables them to eat very large amount of fibrous foods that are low in nutritive value, but they are relatively less efficient in handling foods of lower fiber content than are the artiodactyls. Bell (1969) described the ecological relationship in which horses feed on highly fibrous grasses and thereby make other food more accessible to artiodactyls. Janis argued that the greater efficiency of feeding on fibrous material by modern horses restricted the number of species that might have evolved to make use of this type of food. In contrast, artiodactyls are much more selective feeders, and so many species have been able to evolve and coexist in the same general area.

AFRICAN UNGULATES

Africa was never as completely isolated as Australia or South America, but in the early Tertiary there was certainly much more continuous movement of mammals between North America and Eurasia than between either of these continents and Africa (Maglio, 1978).

As yet, little is known of Paleocene mammals in Africa (Cappetta, Jaeger, Sabatier, Sigé, Sudre, and Vianey-Liaud, 1978). The late Eocene and Oligocene fauna shows a considerable diversity of forms, including some highly specialized groups that indicate a significant period of prior evolution.

A limited number of lineages appear to have entered Africa in the early Tertiary; these included prosimian primates, creodont carnivores, and possibly several lineages of early condylarths. Orders typical of the northern continents such as artiodactyls, perissodactyls, insectivores, and the Carnivora were almost certainly later immigrants that were highly differentiated before they entered Africa.

Other groups appear to have differentiated in Africa. The elephants and their close relatives within the order Proboscidea are the best known and are most specifically associated with Africa. The hyraxes or conies differentiated there, as did the short-lived, rhinoceroslike embrithopods. Although early fossils are not known, the aardvarks have been confined to Africa for most of their history. Fossils of early sirenians are common in northern Africa, which suggests that their origin may be associated with the margins of that continent.

Because of this geographical association, it has long been thought that many of these African groups shared a close ancestry. Simpson (1945) used the term Subungulate to unite proboscideans, hyraxes, embrithopods, and sirenians. When the desmostylians, a marine group from the Pacific Basin, were recognized as a distinct order, they too were included in this assemblage. McKenna (1975) grouped the Proboscidea, Sirenia, and Desmostylia in the Mirorder Tethytheria. This classification has been further substantiated by Novacek (1986) and Domning, Ray, and McKenna (1986). The history of mammals in Africa has been reviewed comprehensively by Maglio and Cooke (1978). Recent discoveries have extended the fossil record of some of these groups and demonstrated probable affinities with earlier Asian forms.

PROBOSCIDEA

The Proboscidea includes only two surviving species, the African elephant, *Loxodonta africana,* and the Asian elephant *Elephas maximus.* Proboscideans were an important and very widespread group for most of the Cenozoic, and until the end of the Pleistocene they were common in North and South America and throughout Eurasia, as well as Africa. Their early history—until the end of the early Miocene—was confined to Africa.

The oldest currently known proboscideans are from the early Eocene of southern Algeria (Mahboubi, Ameur, Crochet, and Jaeger, 1984). The skull of this (as yet unnamed) genus shows the high profile common to elephants. The nasal opening is posterior in position, indicating the initiation of a trunk, and the second upper incisors are enlarged (although not yet of elephantine proportions, (see Figure 21-54*a*)). The upper canines are re-

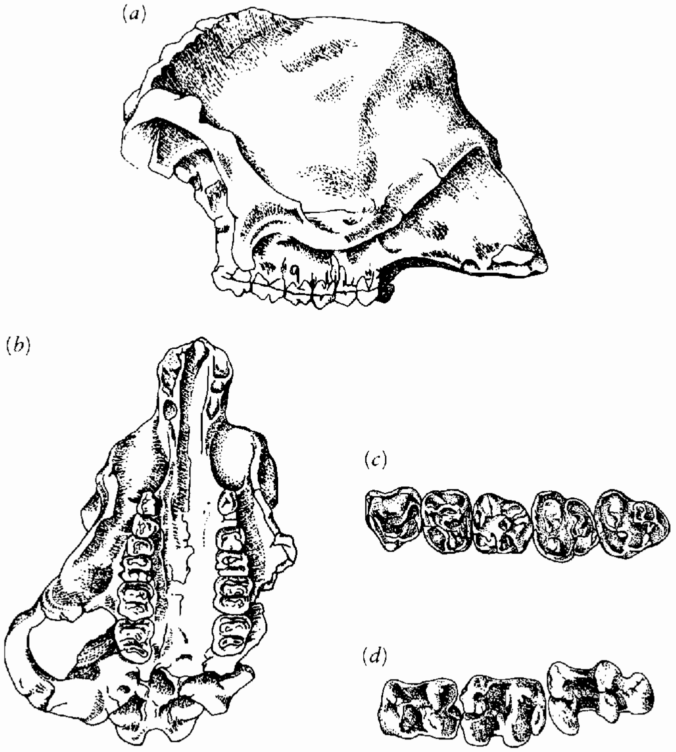


Figure 21-54. SKULL OF A NEWLY DISCOVERED PROBOSCIDEAN FROM THE EARLY EOCENE OF ALGERIA. (*a*) Lateral and (*b*) palatal views. The entire skeleton was less than 1 meter tall. *From Mahboubi, Ameur, Crochet, and Jaeger, 1984. Reprinted by permission from* Nature. *Copyright © 1984. Macmillan Journals Ltd.* (*c* and *d*) Teeth of members of the family Anthracobunidae, which may be related to the ancestry of elephants. (*c*) Posterior upper teeth of *Anthracobune. From West, 1983.* (*d*) Lower molars of *Jozaria,* $\times\frac{1}{2}$. *From Wells and Gingerich, 1983.*

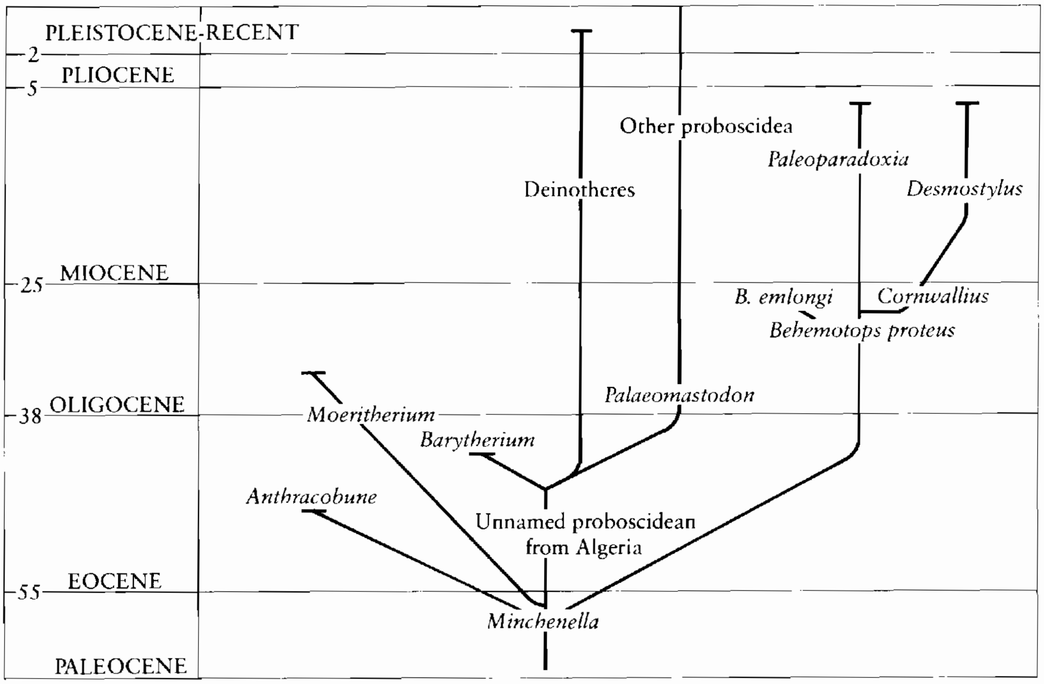


Figure 21-55. SIMPLIFIED PHYLOGRAM OF PROBOSCIDEA AND DESMOSTYLIA. *From Domning Ray and McKenna 1986. By permission of Smithsonian Institution Press, Smithsonian Institution, Washington, D.C., 1986.*

duced and separated from the premolars by a long diastema; the first premolar is lost. The molars are distinguished by two well-developed transverse lophs. As in other primitive proboscideans, the second lower incisors are also significantly enlarged, spatulate, and procumbent. The third lower incisor is reduced and the canine is lost.

The occiput is high, with a broad nuchal crest for muscles to support a heavy skull. The bones of the head are already pneumatized and as in later proboscideans, the auditory meatus is high.

Although it is only about 1 meter tall, the postcranial skeleton shows the graviportal adaptations common to later proboscideans. The forelimb is extremely robust and the radius is fixed in a pronating position. The femur is longer than the humerus and much longer than the tibia. The astragalus and calcaneum are closely similar to those of later Eocene and early Oligocene proboscideans.

The only feature that seems to remove this genus from direct ancestry to later proboscideans is the presence of a deep submaxillary fossa, which is not reported in other early members of the order.

These Lower Eocene fossils are definitely close to the ancestry of later proboscideans. Much less-well-known genera from the early to middle Eocene of the Indian subcontinents have molar teeth of a similar pattern, which West (1983) and Wells and Gingerich (1983) suggest may link them to more primitive ungulates from the Paleocene. Members of the family Anthracobunidae (Figure 21-54*c*) have molars that are dominated by four massive, blunt cusps arranged so as to form two transverse ridges. The addition of a small entoconid II presages the proboscidean condition. However, the anterior teeth give no clue of proboscidean affinities. The canines were large and the incisors unspecialized. The dental count is typical of primitive eutherians. Some genera may have been as large as a pig or tapir. The anthracobunids might be relicts of the ancestral stock that gave rise to the proboscideans, but they are clearly too late to be directly ancestral and do not show the initiation of any typically proboscidean characters. The ancestry of the anthracobunids may lie with genera such as *Minchenella* from the late Paleocene of China, which Zhang (1978, 1980) placed in the condylarth family Phenacolophidae. Although *Minchenella* is known only from lower jaws, Domning, Ray, and McKenna (1986) argue that the transversly broadened hypoconulid shelf of the lower third molar with a small entoconid II is a sufficiently significant derived feature to establish its affinities with both the Proboscidea and a second order of aquatic mammals, the Desmostylia (Figure 21-55).

Order Proboscidea
  Suborder Gomphotherioidea
    Family Gomphotheriidae: late Eocene to middle Pleistocene
    Family Elephantidae: late Miocene to Recent
  Suborder Mammutoidea
    Family Mammutidae: early Miocene to sub-Recent
    Family Stegodontidae: middle Miocene to late Pleistocene

There is a rich record of proboscideans from the Upper Eocene and Lower Oligocene of northern Africa. These are already large animals and have most of the postcranial specializations that are common to the modern species. The limbs are columnar, with the distal elements short. The bones lack medullary cavities, and the manus and pes are short and pentadactyl.

These early proboscideans have been classified in a single genus, *Palaeomastodon* within the Gomphotheriidae, although they show extensive variability and may include the ancestors of several subsequent lineages.

The Gomphotheriidae is considered a long-living ancestral stock that gave rise to a succession of other groups. Primitively, they have long spatulate incisors in the elongate lower jaws, as well as tusks in the upper jaws (Figure 21-56). The teeth are bunodont, with up to seven pairs of rounded cusps. In contrast with their early Eocene ancestors, they have lost all trace of canine teeth. The fossil record of proboscideans is poor for most of the Oligocene but rich in the Miocene, by which time all the major lineages had emerged. At the end of the early Miocene, Africa joined Asia and the proboscideans began their migrations to the ends of the earth (Figure 21-57). Descendants of early gomphotheriids reached all continents

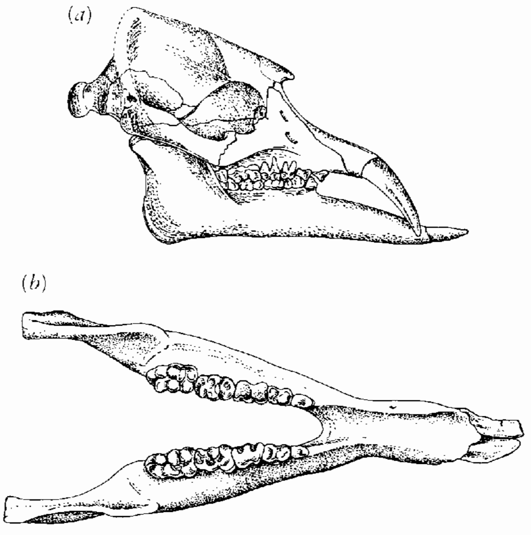


Figure 21-56. (*a*) Skull and (*b*) lower jaws of the gomphotheriid proboscidean *Palaeomastodon* from the Upper Eocene of North Africa. *From Andrews, 1906.*

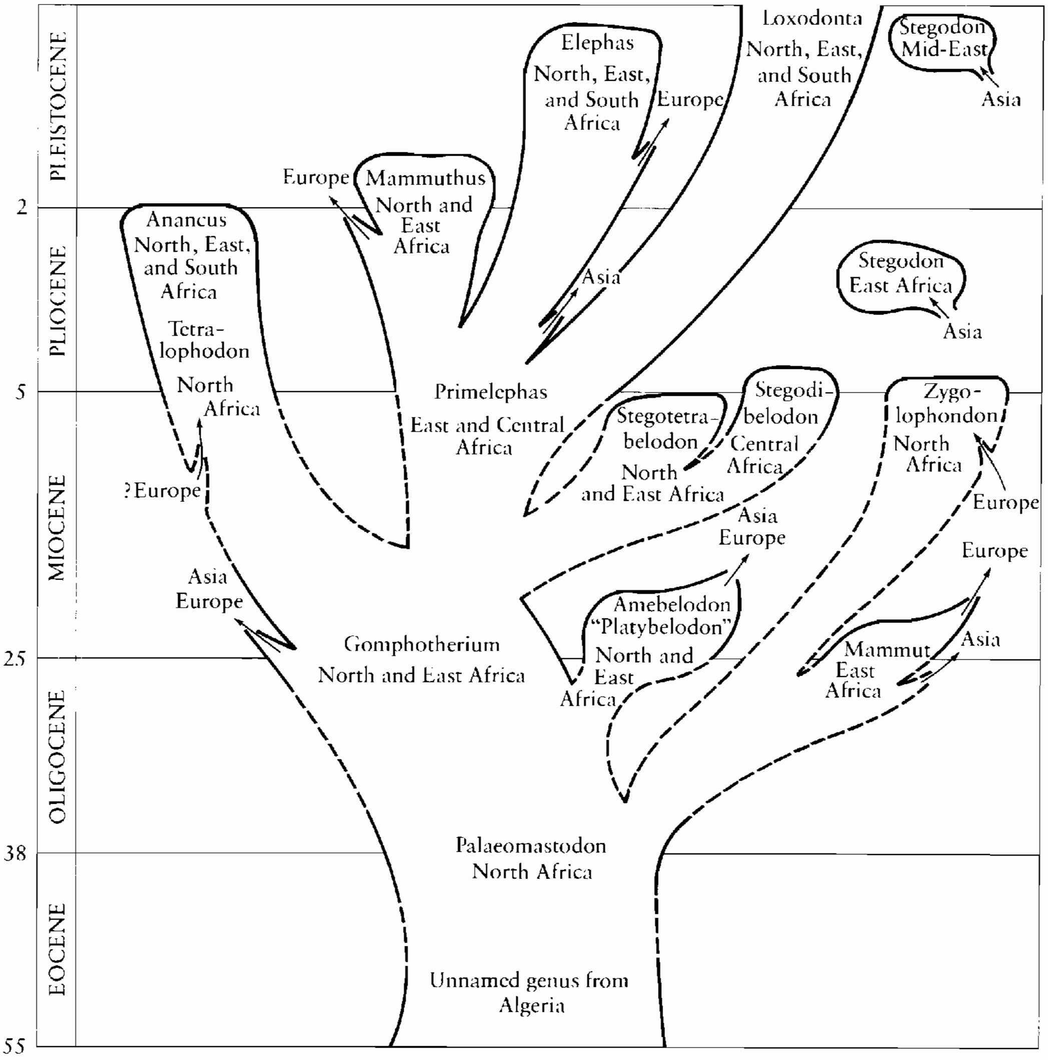


Figure 21-57. PHYLOGENY OF THE PROBOSCIDEA SHOWING THEIR GEOGRAPHICAL DISTRIBUTION. *From Coppens, Maglio, Madden, and Beden, 1978. Reprinted by permission of Harvard University Press.*

except Australia and Antarctica. The Gomphotheriinae extended into Asia, Europe, and North America; the Cuvierienoninae originated in North America and spread into South America; and the Anancinae rose in Africa and spread into Europe and parts of Asia. The latter two subfamilies approached the pattern of modern elephants in the loss of their lower tusks, elongation of their molars, and deepening of their skulls.

The surviving family Elephantidae is recognizable as early as the late Miocene. It is characterized by a unique pattern of tooth structure and succession that is not evident in other proboscideans. The molar teeth are so long that the anterior portion erupts and becomes functional while the posterior portion is still undergoing development. As the teeth form at the back of the jaw, they move forward and replace the earlier formed teeth that are lost at the front. In early genera, which are placed in the subfamily Stegotetrabelodontinae, the premolars are functional, as in other proboscideans, but in advanced elephants they are suppressed. Instead, the deciduous cheek teeth tend to become molariform and function as the molars develop. Only one and one-half pairs of teeth are functional at a time in their relatively short jaws.

The teeth of the primitive genus *Stegotetrabelodon* retain evidence of two two longitudinal rows of cusps that were common to primitive proboscideans (Figure 21-58). The cusps are anteroposteriorly compressed. With wear, the two halves become confluent, as in modern elephants. In the most derived elephant species, the wooly mammoth, there may be as many as 30 plates in the last molar. Each plate is composed of a compressed loop of enamel surrounding the dentine and separated by cementum. The hard enamel forms a series of shearing blades that, with wear, stand above the softer dentine and cementum.

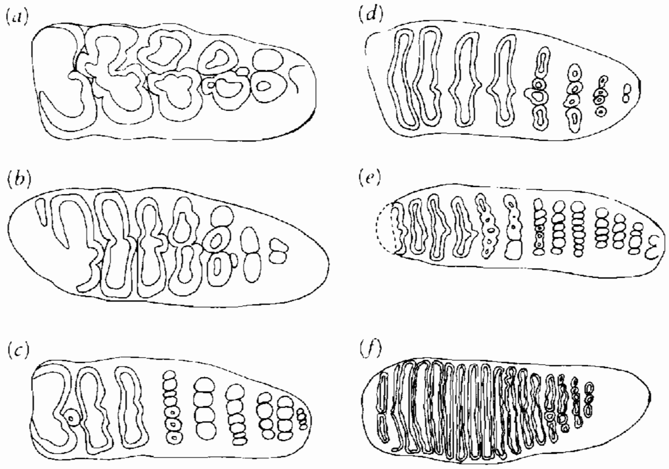


Figure 21-58. CHANGES IN THE MOLAR CUSPS OF PROBOSCIDEANS. These species show progressive consolidation of the gomphothere cone-pairs, loss of the median cleft, fusion of accessory columns, increase in plate number, and thinning of enamel. (*a*) *Gomphotherium.* (*b*) *Stegotetrabelodon.* (*c*) *Primelephas.* (*d*) *Mammuthus subplanifrons.* (*e*) *Mammuthus africanavus.* (*f*) *Mammuthus primigenius.* Similar changes occurred in the genus *Elephas. From Maglio, 1973.*

In early genera, each molariform tooth bears only as many plates as there were rows of cusps in advanced gomphotheres (five to seven in the last molar). They were also primitive in retaining very long tusks in the lower jaws. The subfamily Elephantinae appeared in the latest Miocene, represented by the genus *Primelephas* from east and central Africa, which is distinguished by the short symphysis of the lower jaw and reduction or loss of the premolars. This primitive lineage gave rise to three derived genera by the middle Pliocene, *Elephas, Loxodonta,* and *Mammuthus. Loxodonta* was highly advanced when it first appeared, but unlike other late Tertiary proboscideans, it showed little change within the genus and never left Africa. *Loxodonta africana* is now confined to the area south of the Sahara but lived in Egypt during predynastic times. *Elephas* spread out of Africa in the mid-Pliocene and is now restricted to southern Asia. Its African record is very complete during the Pliocene and Pleistocene and shows a sequence of rapidly evolving forms within a single lineage. *Mammuthus,* which is distinguished by spirally twisted tusks and a wrinkled or wavy pattern of the enamel, was common in North America and Eurasia, where it persisted into the late Pleistocene.

The suborder Mammutoidea paralleled the Elephantidae in many features of the dentition but did not evolve their specialized pattern of serial tooth replacement. Like the Elephantidae, they lost the lower tusks and shortened the jaw symphysis while elaborating molars that showed a platelike structure. However, the entire tooth is formed prior to eruption. They appear in Africa in the early Oligocene. The Mammutidae were common in North America and Eurasia as well as Africa and persisted into the sub-Recent. The Stegodontidae were a primarily Asian group that reentered Africa several times during their history. Their teeth remained low crowned, with thick enamel.

DEINOTHERIOIDEA AND MOERITHERIOIDEA

Two distinct groups, the Deinotherioidea and the Moeritherioidea, may have diverged before the Gomphotherioidea and Mammutoidea but may nevertheless be included within the Proboscidea (Figure 21-55).

The Deinotheriodea, which were present in the Old World from the early Miocene to the end of the Pleistocene, have long been considered a divergent suborder within the Proboscidea. They were specifically excluded by Maglio (1973) and by Coppens, Maglio, Madden, and Bedey, (1978), but Mahboubi, Ameur, Crochet, and Jaeger (1984) and Domning, Ray, and McKenna (1986) argued that they shared a close common ancestry.

The deinotherioids were elephantine in size and limb structure. They are clearly distinguished from other proboscideans by the absence of upper tusks and the presence of large, recurved tusks in the lower jaws (Figure 21-59).

The posterior position of the narial opening indicates the presence of a proboscis, but the shape of the skull is very distinct from that of typical elephants. The occiput is extended far ventrally to permit attachment of large muscles to ventroflex and rotate the skull. As in the gomphotheriids, the molar teeth are bilophodont. They remain low crowned throughout the history of the group. The teeth show considerable variability in both of the recognized genera but no progressive evolutionary change except for general increase in size. Harris (1976) showed that the anterior teeth were used for crushing and the posterior for shearing.

Typical members of this group are not known in Africa or elsewhere until the early Miocene and no possible ancestors are recognized in the Oligocene, although typical proboscideans are fairly well known during this time. Harris (1978) suggested that the Upper Eocene genus *Barytherium,* which is known from North Africa, is a plausible relative of this group on the basis of the similarity of the cheek teeth. This genus was assigned a more distant relationship by Mahboubi and his colleagues on the basis of the discovery of Lower Eocene proboscideans.

Deinotherioids extended into Europe and Asia in the late Miocene and Pliocene but were never as common or widespread as the elephants.

Moeritherium, which we know from the Upper Eocene and Oligocene of northern Africa (from Senegal to Egypt), has long been associated with the proboscideans, but it also shares some features with a later group of marine mammals, the Desmostylia.

Moeritherium was less than 1 meter tall with fairly lightly built limbs. Their structure and the discovery of many specimens in marine deltaic deposits suggests that *Moeritherium* was amphibious in habits. The dentition is similar to that of the earliest proboscideans in having both the upper and lower second incisors greatly enlarged and, like them, there are upper but no lower canines (Figure 21-60). The six pairs of cheek teeth are bilophodont.

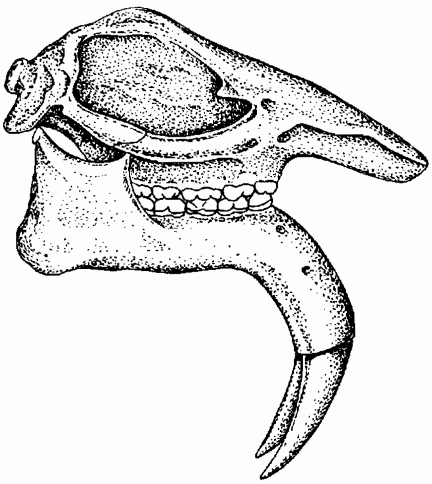


Figure 21-59. SKULL OF *DEINOTHERIUM. From Harris, 1978. Reprinted by permission of Harvard University Press.*

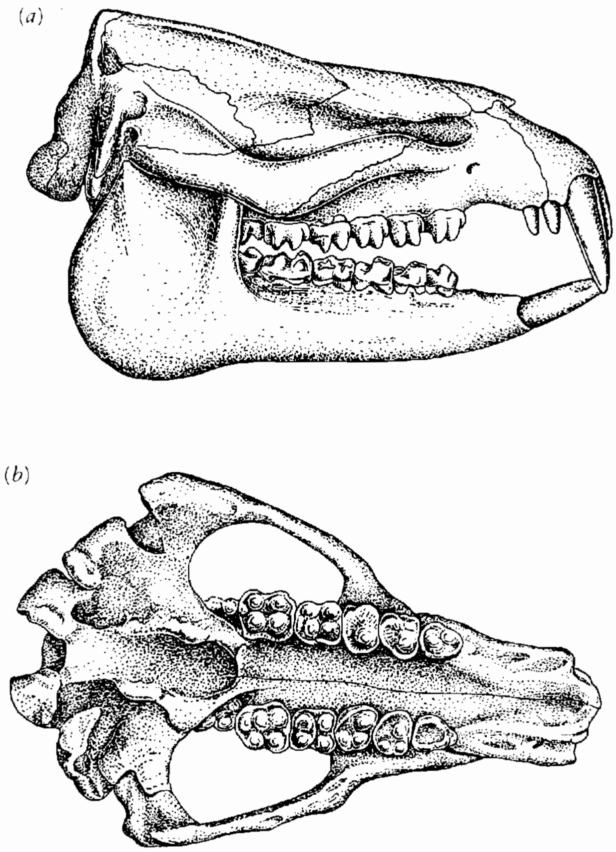


Figure 21-60. THE EARLY PROBOSCIDEAN *MOERITHERIUM.* (*a*) Restoration of skull in lateral view. (*b*) Palate. *From Andrews, 1906.*

In contrast with other early proboscideans, the skull is low and only weakly pneumatized but the external auditory meatus is high. There is no evidence of a trunk.

Moeritheres may be relicts of an early stage in the evolution of the proboscideans. Domning, Ray, and McKenna (1986) point out features in which they are divergent from later proboscideans, including loss of the third lower incisor, loss of the lacrimal bone, and the shortening of the anterior portion of the skull. They retain primitive characters that indicate that they diverged from early tethytheres close to the point of origin of the desmostylians.

DESMOSTYLIA

Desmostylians were long known only from isolated teeth consisting of a number of cusps that developed as closely placed enamel cylinders (Figure 21-61*c*). They were found in marine deposits and, as they somewhat resemble the teeth of some sirenians, it was assumed that they were closely related. The discovery of associated postcranial

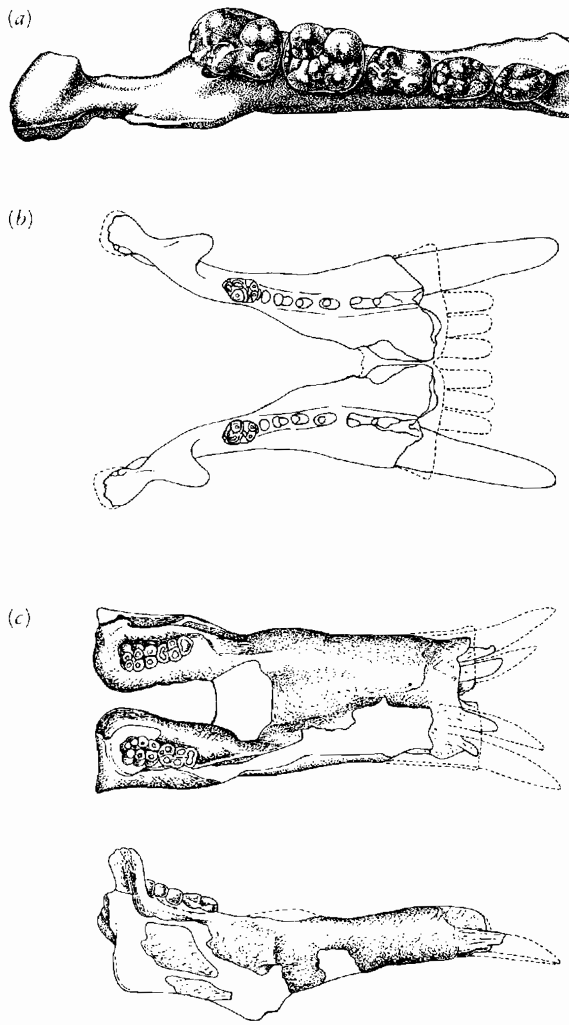


Figure 21-61. LOWER JAWS OF DESMOSTYLIANS. (*a*) Occlusal view of the lower jaw of the primitive Upper Oligocene desmostylian *Behemotops proteus.* Note similarity with the teeth of the primitive proboscidean *Moeritherium,* 25 centimeters long. *From Domning, Ray and McKenna, 1986.* (*b*) Occlusal view of the lower jaw of *Behemotops emlongi.* Anterior cheek teeth are represented by empty alveoli. The anterior dentition resembles that of *Desmostylus;* the relative length of the jaw is much shorter, but the symphyseal region broader. These proportions resemble the modern hippopotamus, 50 centimeters long. *From Domning, Ray and McKenna, (1986.)* (*a* and *b*) *By permission of Smithsonian Institution Press. Smithsonian Institution, Washington, D.C., 1986.* (*c*) Dorsal and lateral views of the lower jaws of *Desmostylus,* from the Middle Miocene. The cheek teeth are restricted to the back of the jaw, leaving a long diastema behind the tusklike canines. *From Reinhart, 1959.*

material demonstrated that they had a totally different body form, with both front and hind limbs that were well developed but with hands and feet that were somewhat specialized as paddles (Figure 21-62). These animals may have been amphibious or perhaps somewhat seal-like in habits. Elaboration of the incisors, elongation of both the upper and lower jaws, and the long diastema anterior to the cheek teeth give them the look of primitive elephants. However, the fact that the canine teeth are also elaborated as tusks rules out close relationship with typical proboscideans. Desmostylians are known only in the Upper Oligocene and Miocene and are restricted to the margins of the North Pacific ocean. *Palaeoparadoxia* and *Desmostylus* were common in the Miocene. The Upper Oligocene genus *Behemotops,* which was recently described by Domning, Ray, and McKenna (1986), appears close to the ancestry of later desmostylians and demonstrate close affinities with the base of the proboscidean assemblage. Domning, Ray, and McKenna suggest that desmostylians were amphibious herbivores that fed on marine algae and that the earlier genera depended to a large extent on plants exposed in the intertidal zone.

It is fairly easy to conceive of a common, Paleocene ancestor for typical proboscideans, moeritherioids, and desmostylians that was already distinct in the elaboration of the anterior dentition and the bilophodont arrangement of the molar cusps. It is more difficult to envisage that common ancestor also showing significant derived features in common with other African groups such as embrithopods, sirenians, and hyraxes.

EMBRITHOPODA

Embrithopods are known primarily from a single locality in the Oligocene of Egypt. *Arsinoitherium* is known from the entire skeleton (Figure 21-63). Although it is elephantine in its general form, the skull is entirely different. It is dominated by two gigantic bony processes that arise from the nasals and a much smaller pair that is medial to the orbits. The teeth form a nearly uniform series without tusks, conspicuous canines, or a significant diastema. They retain a full primitive dental formula of

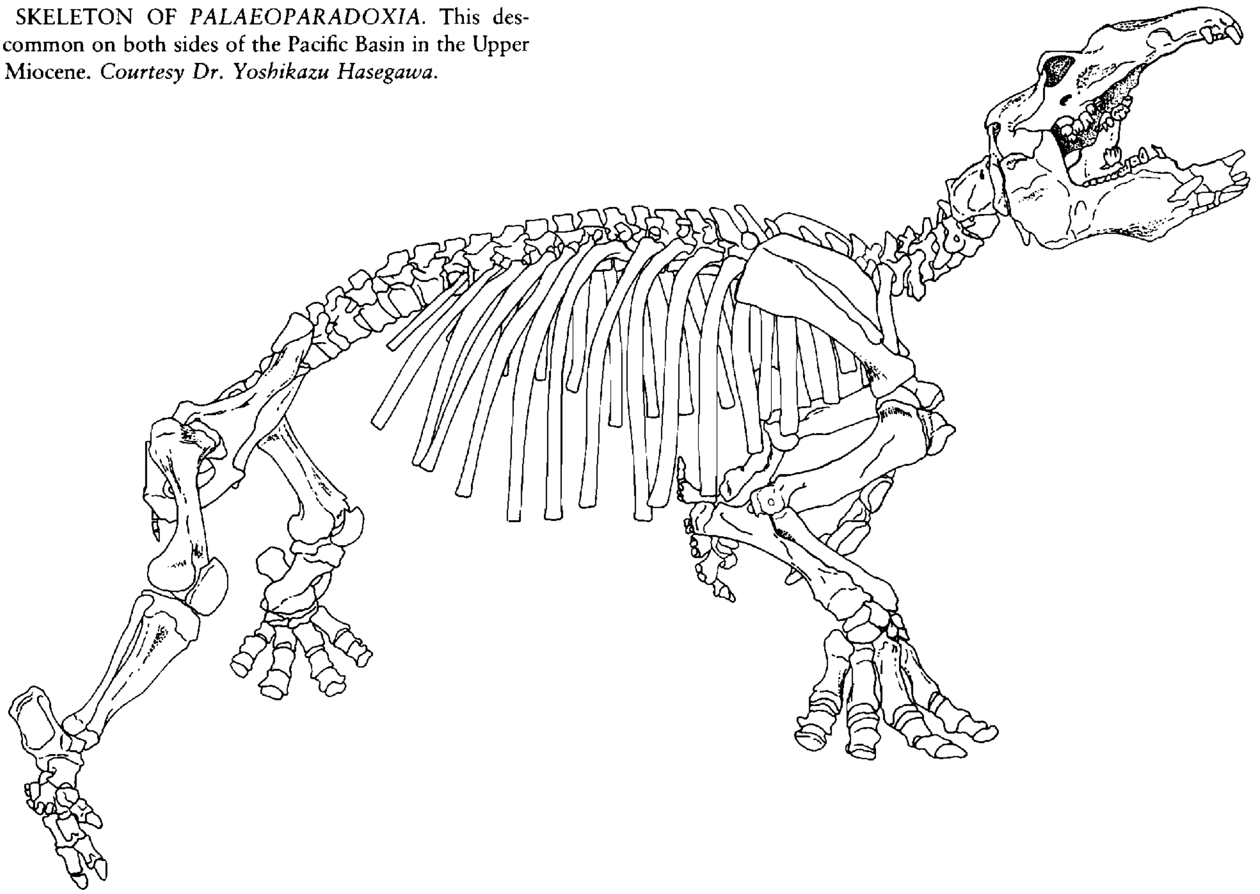
$$\frac{3\quad 1\quad 4\quad 3}{3\quad 1\quad 4\quad 3}$$

The molar teeth are conspicuously bilophodont and high crowned.

Until recently, no remains of embrithopods had been described outside Africa. In 1977, McKenna and Manning suggested that the Upper Paleocene or Lower Eocene Mongolian genus *Phenacolophus* might be related to the ancestry of *Arsinioitherium. Phenacolophus* is represented by remains of a skull that is approximately 15 centimeters long and some postcranial elements. Both the upper and lower teeth are bilophodont (Figure 21-64*a*). Unlike *Arsinioitherium,* the canines are enlarged. Limb elements are short, stocky, and primitive.

Sen and Heintz (1979) described material from several localities in north central Turkey and Romania that can be assigned to the Arsiniotheriidae with much greater assurance (Figure 21-64*d*). The specimens are smaller than the Egyptian genus and somewhat more primitive in details of the dental anatomy. The most significant difference is the absence of horns.

Figure 21-62. SKELETON OF *PALAEOPARADOXIA.* This desmostylian was common on both sides of the Pacific Basin in the Upper Oligocene and Miocene. *Courtesy Dr. Yoshikazu Hasegawa.*



On the basis of available evidence, one could argue that the Embrithopoda originated in Asia and migrated to Africa, or that the group originated in Africa and spread into Asia at an early stage in evolution, before the emergence of horned forms. Bearing in mind the rarity of fossils from the Paleocene in Africa, an Asian origin seems a simpler explanation. Both the Turkish and African forms come from deposits that suggest amphibious habits.

Both embrithopods and proboscideans are suggested as being derived from members of the condylarth family Phenacolophidae, which have large blunt molar cusps arranged so as to form transverse lophs.

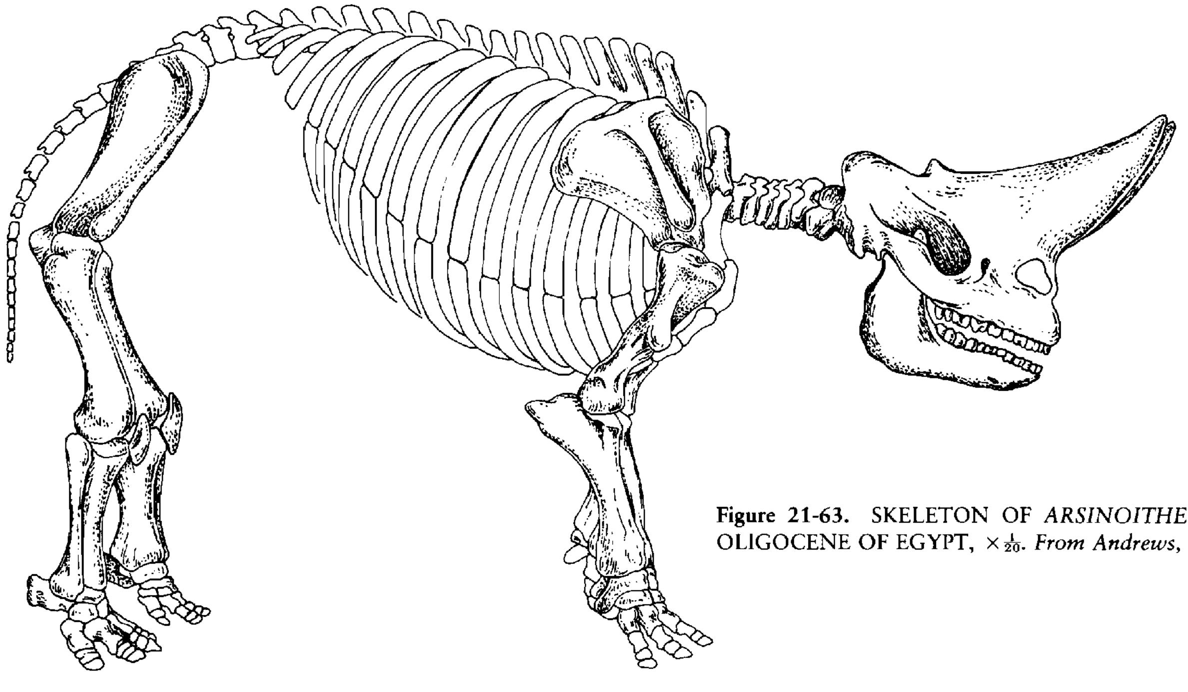


Figure 21-63. SKELETON OF *ARSINOITHERIUM* FROM THE OLIGOCENE OF EGYPT, ×$\frac{1}{20}$. *From Andrews, 1906.*

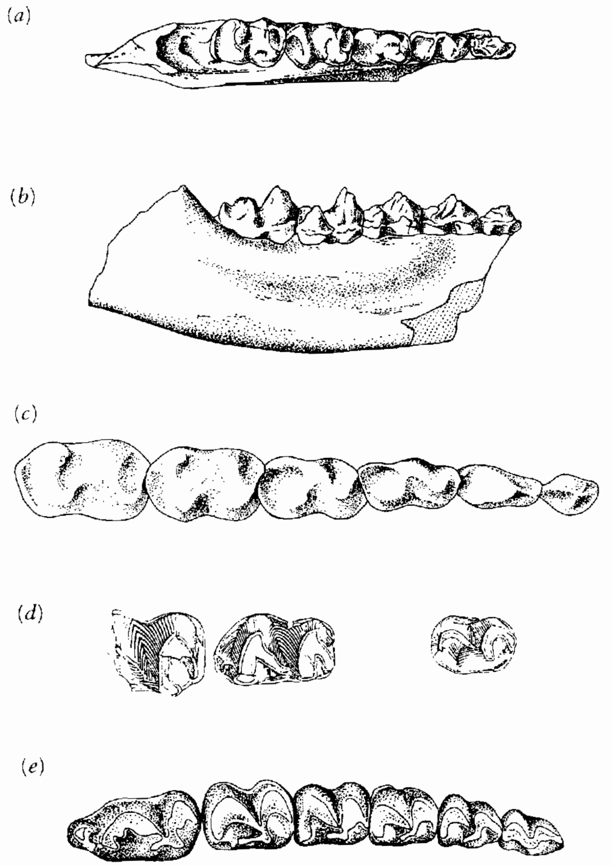


Figure 21-64. POSSIBLE RELATIVES OF *ARSINOITHERIUM.* (*a*) Occlusal and (*b*) lateral views of the lower jaw of *Phenacolophus,* a condylarth from the Upper Paleocene or Lower Eocene of Mongolia. *From Matthew and Granger, 1925.* (*c*) Composite reconstruction of lower cheek teeth of *Phenacolophus. From McKenna and Manning, 1977.* (*d*) Lower cheek teeth of the late Eocene of Oligocene Romanian arsinoithere *Crivadiatherium. From McKenna and Manning, 1977.* (*e*) Lower cheek teeth of *Arsinoitherium. From Andrews, 1906.*

SIRENIANS

Sirenians have long been thought to have some affinities with proboscideans and embrithopods, but the current evidence does not seem very convincing.

Sirenians superficially resemble whales in having a fusiform body, forelimbs that are specialized as paddles, and a horizontal tail fluke. They differ from all other specialized marine mammals in adhering to a strictly herbivorous diet. They are primarily coastal in distribution. Only four species survive today, *Dugong dugon* of the Indopacific basin, and three species of manatee: *Trichechus inunguis* in the Amazon basin, *T. manatus* in the Caribbean and along the northern coast of South America, and *T. senegaliensis* on the west coast of Africa. Stellar's sea cow, *Hydrodamalis,* was a dugong that lived along the northern margin of the Pacific ocean until its extinction in the eighteenth century.

Sirenians lack sonar, although the periotic, like that of whales, is not solidly fused to the skull and is dense and expanded. All sirenians going back to the Lower Eocene are characterized by massive, pachyostotic ribs that significantly increase the body weight. Horizontal stability is increased by elongation of the lungs and a horizontal diaphragm. Compression of the thoracic cavity permits sirenians to sink with a minimum of effort. Unlike whales, they are not active divers.

In all modern sirenians, the rostrum and the end of the lower jaw are deflected ventrally. This feature is most conspicuous in the dugong, which feeds on bottom-hugging sea grasses. Living dugongs have two or three pairs of cheek teeth that are open rooted but lack enamel. The manatee has up to eight teeth that are functional at a time in each jaw ramus. These teeth are steadily replaced by new teeth that erupt at the back of the jaw; as many as 20 cheek teeth may erupt in each jaw. In some genera, there are tusklike upper teeth that appear to be comparable to the first incisors in contrast to the tusks in elephants, which form from the second incisors.

Sirenians first appear in the fossil record in the Lower Eocene of Hungary (Kretzoi, 1953). Their remains are fragmentary but include the pachyostotic ribs that are a hallmark of the group.

The Middle Eocene *Prorastomus* from Jamaica, the only genus in the family Prorastomidae, shows the most primitive cranial pattern yet known. The lower jaw is straight, and there is only a slight deflection of the rostrum. The skull is pachyostotic. The dental count of

$$\frac{3\quad 1\quad 5\quad 3}{3\quad 1\quad 5\quad 3}$$

is striking in the retention of a fifth premolar, which is lost in all other post-Cretaceous groups of placentals. Aside from pachyostotic ribs and vertebrae, no definitely attributable postcranial remains are known to indicate the degree of aquatic adaptation attained at this stage of sirenian evolution.

Apart from the primitive nature of the skull, with its general similarities to condylarths, these early sirenids do not show any features that demonstrate specific relationships with other placental orders. The cheek teeth are bilophodont like those of early proboscideans and members of the Anthracobunidae, but this feature evolved separately in several other orders. The retention of five premolars in all Eocene species raises the possibility of derivation from a very primitive stock of late Cretaceous or early Tertiary eutherians, without close affinities with any other advanced mammalian orders. The early distribution of sirenians suggests an origin along the shores of the ancestral Tethys Sea rather than specifically from African progenitors.

Most Middle and Upper Eocene sirenians are placed in the genus *Protosiren,* which is reported from Java, India, Europe, and southeastern North America (Domning, Morgan, and Ray, 1982). They argue that the family Protosirenidae is ancestral to both living families. The postcranial skeleton is already essentially modern.

Dugongids are represented in the middle Eocene by *Eotheroides* from North Africa (Figure 21-65); like other Eocene genera, it still retains five premolars. It is placed in the subfamily Halitheriinae, which has a scattered record throughout the early Tertiary in Africa, Europe, and both the Atlantic and Pacific shores of the New World (Domning, 1978). The Dugonginae, which is represented today by a single species of the genus *Dugong* in the Indo-Pacific basin, has no fossil record.

Although most sirenians were tropical in distribution throughout their history, one lineage, the Hydrodamalinae, became adapted to life around the shores of the North Pacific in the late Cenozoic. The origin of this group lies with halitherine dugongids, which are known along the western shores of North America since the early Miocene (Domning, 1978). The earliest hydrodamalinae, *Dusisiren* (Figures 21-66 and 21-67) appeared about 19 million years ago. A series of species provide a nearly continuous morphological sequence leading to the modern genus *Hydrodamalis*, which appeared 7 million years ago. In this sequence, the size increases from 2 to 3 meters to over 9 meters (probably an accommodation to living in cold waters) and the cheek teeth are completely lost as are the phalanges of the front limb. Domning attributes the change in dentition to feeding on softer plants, including kelp and other brown-red algae, as was observed by early explorers in the Arctic. Heavy insulation with blubber made them so bouyant that they apparently did not dive at all.

In the late Pliocene, *Hydrodamalis* was known from the Japanese archipelago around the North Pacific to northern Mexico. The range of the group has apparently been progressively reduced over the last 20,000 years. The last animals were killed about 1768.

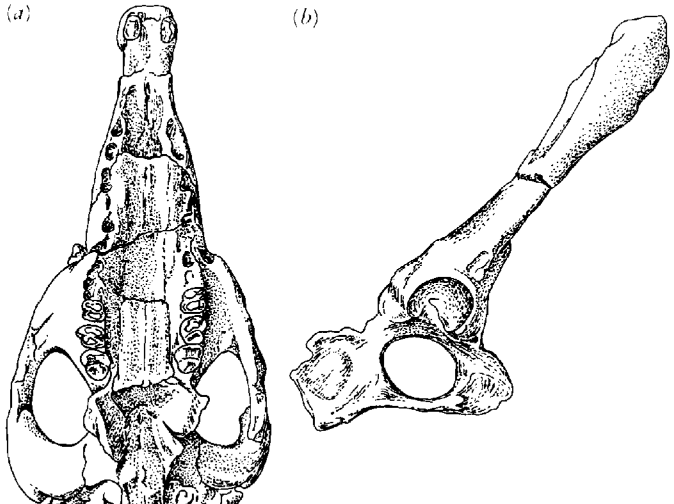


Figure 21-65. (*a*) Palate of the sirenid *Eotheroides* from the middle Eocene of North Africa. (*b*) Pelvic girdle of *Eotheroides*. *From Andrews, 1906.*

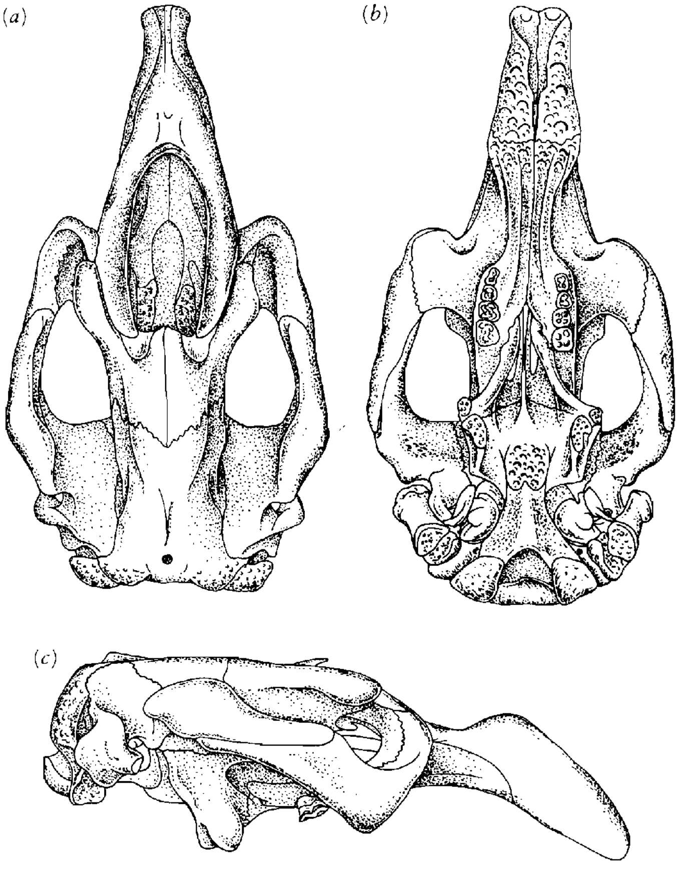


Figure 21-66. (*a*) Dorsal, (*b*) palatal, and (*c*) lateral views of the skull of *Dusisiren*, an early Miocene ancestor of Stellar's sea cow. *From Domning, 1978.*

Domning (1982) recently reviewed the evolution of the manatees (Trichechidae). Their ancestry probably lies in primitive dugongids or possibly protosirenids that were isolated in the South American area in the early Tertiary, at which time the Amazon Basin was open to both the Atlantic and Pacific Oceans. The first possible member of the modern family is *Potamosiren* from the Middle Miocene. This genus has reduced the cheek teeth to molars 1 to 3, as in most dugongids. The feature of continuous cheek tooth replacement, which is fed by indefinite toothgerm division, is established in *Ribodon* by the late Miocene. Domning attributed selection for the changing dental pattern to feeding on siliceous aquatic grasses in the Amazon Basin, in contrast with the less-abrasive sea grasses eaten by the dugongs.

Movement of the teeth from the back to the front of the jaw and the loss of permanent premolars are features in common with members of the Elephantidae, but they clearly evolved independently in the two groups, and the sirenians are distinct in the continuous replacement of the molars.

Dugongids preceded the manatees in the Caribbean, where they were present for most of the Tertiary. They became extinct in the Atlantic and Mediterranean at the end of the Cenozoic, possibly as a result of climatic de-

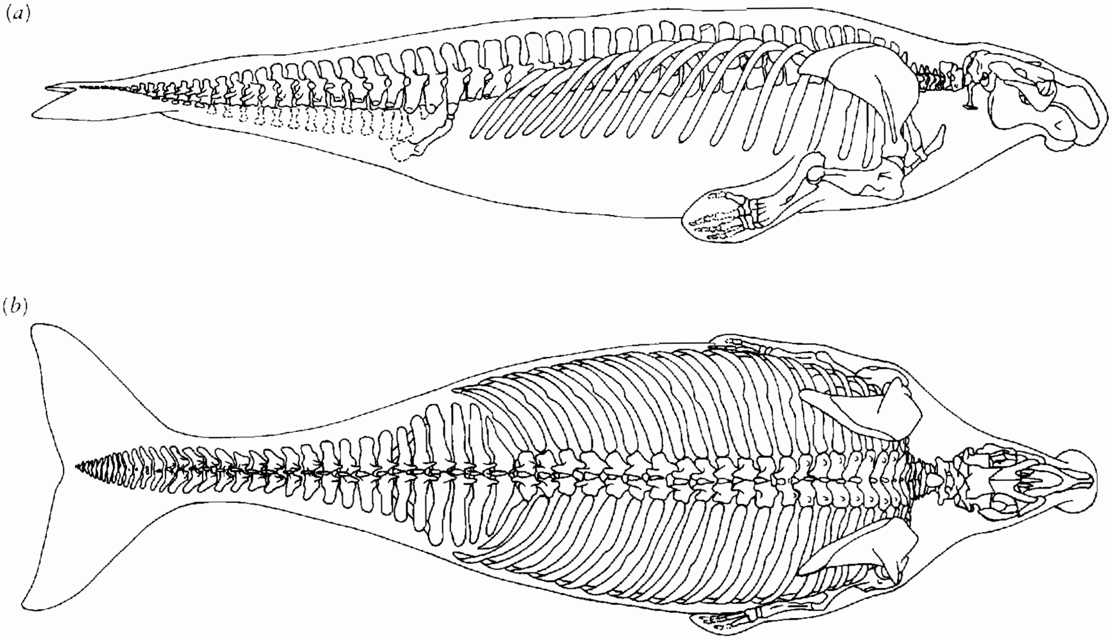


Figure 21-67. SKELETON OF *DUSISIREN.* (*a*) Lateral and (*b*) dorsal views. Original was 4 meters long. *From Domning, 1978.*

terioration leading to the Pleistocene glaciation. The last record of dugongids in the Atlantic Basin is in the late Miocene, whereas manatees evidently entered that ocean from South America in the Pliocene.

HYRACOIDEA

The hyracoids or conys are superficially rabbitlike forms whose history has been confined largely to Africa, although they are also known in limited areas of Europe and Asia.

They appear first in the Upper Eocene of North Africa (Sudre, 1979). In the early Oligocene, Lower Fossil Wood Zone of the Fayum, Egypt, they make up approximately half the fauna, but by the Upper Fossil Wood Zone, they account for only 16 percent of the specimens. Their importance continues to dwindle through the Cenozoic (Meyer, 1978). Today, there are three genera that are restricted to Africa and the near East.

The current fossil record provides little evidence of the specific origin of the group and little to confirm affinities with the other "African" orders.

The dentition of hyraxes for most of their history maintained nearly the primitive eutherian formula, with loss of only the lateral lower incisors. The most important specialization is that the central upper incisor is a triangular, recurved tusk that grows from a persistant pulp cavity. The enamel on the lingual side is present when the tooth first erupts but is rapidly worn down. As in rodents, this tusklike medial incisor is sharpened by contact with the lower incisor. The upper incisor is always larger in the male than in the female. There may be a short diastema behind the incisors but the rest of the dentititon is of uniform height. The cusps are bunodont to lophodont, with a distinctly perissodactyl appearance in some genera (Figure 21-68).

The modern genera are omnivorous. Some are arboreal and others live among the rocks. All climb well with the help of moist foot pads.

The postcranial skeleton is distinctive in the great length of the vertebral column, with 20 to 23 thoracic and 4 to 9 lumbar vertebrae. In contrast, the tail is exceedingly short. There are five toes on the manus and three on the pes. All bear flat nails except the inside digit of the pes, which has a claw. The posture is plantigrade, with the rear limbs kept in a crouch.

The abundant early Tertiary fossils are included in the extinct family Pliohyracidae. We first find the modern Procaviidae in the Miocene. The lateral incisors and canines are lost in the Pleistocene and Recent species. Sudre agrees with the frequently suggested idea that hyraxes originated from the Condylarthra but does not support affiliation with proboscideans and sirenians. Current work by Fischer (Prothero, Manning, and Fischer, 1986) supports close affinities between hyraxes and perissodactyls.

TUBULIDENTATA—THE AARDVARK

The aardvark, or earth pig, is known from a single modern species, *Orycteropus afer,* which is widespread in Africa south of the Sahara. It has a heavily built, generally archaic skeleton, with limbs that are specialized for digging. There are four toes on the manus, five on the pes, and

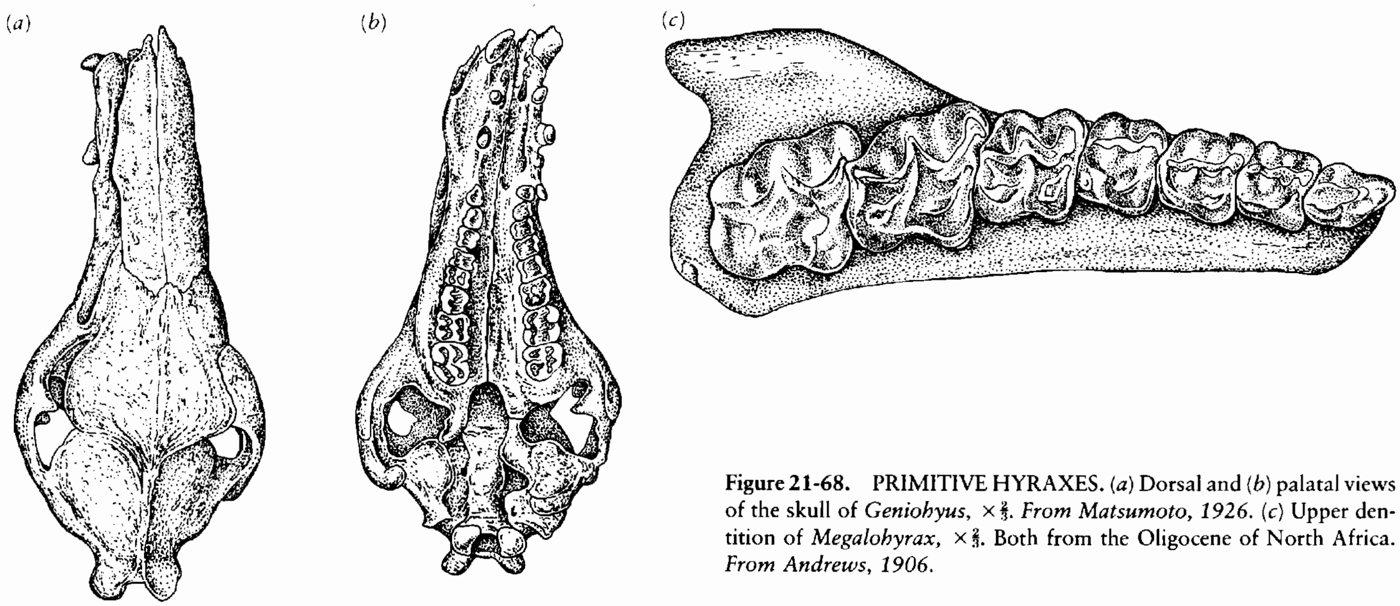


Figure 21-68. PRIMITIVE HYRAXES. (*a*) Dorsal and (*b*) palatal views of the skull of *Geniohyus*, $\times\frac{2}{3}$. *From Matsumoto, 1926.* (*c*) Upper dentition of *Megalohyrax*, $\times\frac{2}{3}$. Both from the Oligocene of North Africa. *From Andrews, 1906.*

the clavicle is retained. The limb bones show conspicuous tuberosities for muscle attachment.

The aardvark lives in burrows and feeds primarily on termites that it digs from the ground. Its sense of smell is extremely acute. The incisors and canines are lost, as is the enamel from all the teeth. The cheek teeth are large and unique among mammals in being composed of numerous hexagonal prisms of dentine that form around tubular pulp cavities. The absence of enamel is compensated for by continuous growth of the cheek teeth. The teeth and lower jaws are much better developed than in ant-eating specialists in other orders.

Aardvarks are of special phylogenetic interest in being almost certainly African in origin, but without special skeletal resemblance to the other groups whose origin or early evolution has been associated with Africa: sirenians, elephants, and hyraxes. They are also clearly distinct phylogenetically from the other groups that are highly committed to feeding on ants—the South American Myrmecophagidae and the pangolins.

Aardvarks nevertheless show a similar pattern of enamel loss to that of South American xenarthrans and the North American palaeanodonts (which will be discussed in a later section). Patterson (1975, 1978) discussed

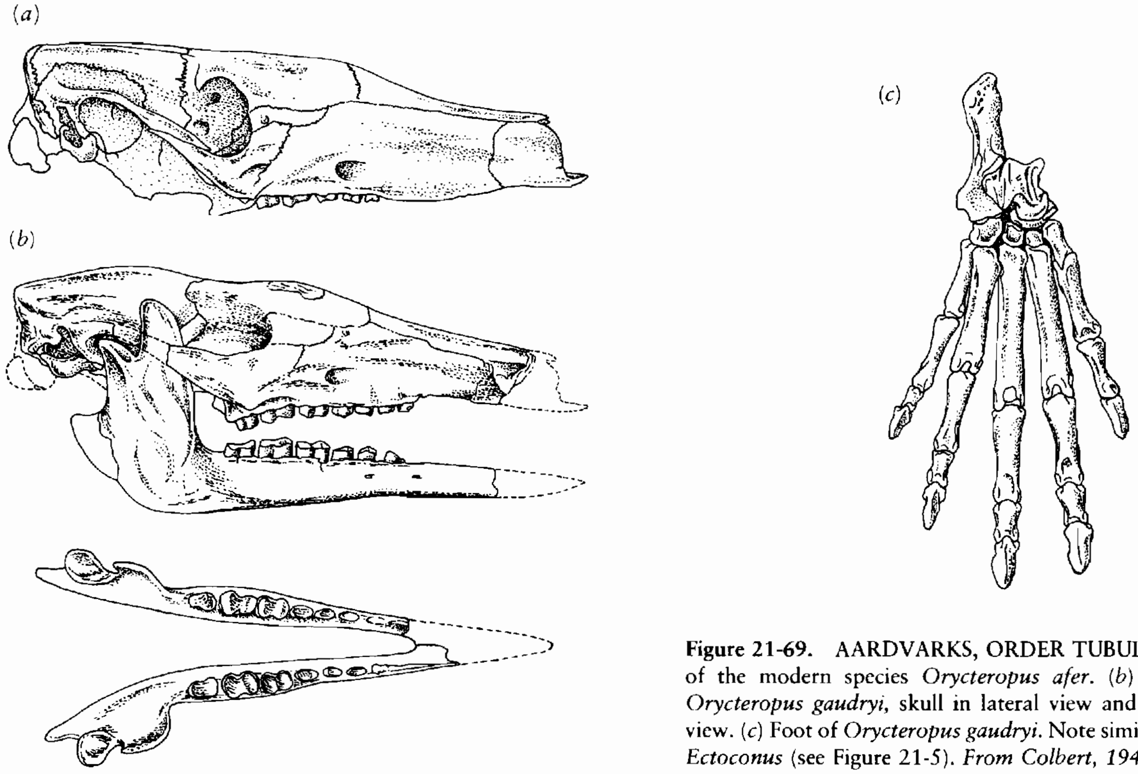


Figure 21-69. AARDVARKS, ORDER TUBULIDENTATA. (*a*) Skull of the modern species *Orycteropus afer*. (*b*) The Miocene species *Orycteropus gaudryi*, skull in lateral view and lower jaw in occlusal view. (*c*) Foot of *Orycteropus gaudryi*. Note similarity to the condylarth *Ectoconus* (see Figure 21-5). *From Colbert, 1941a.*