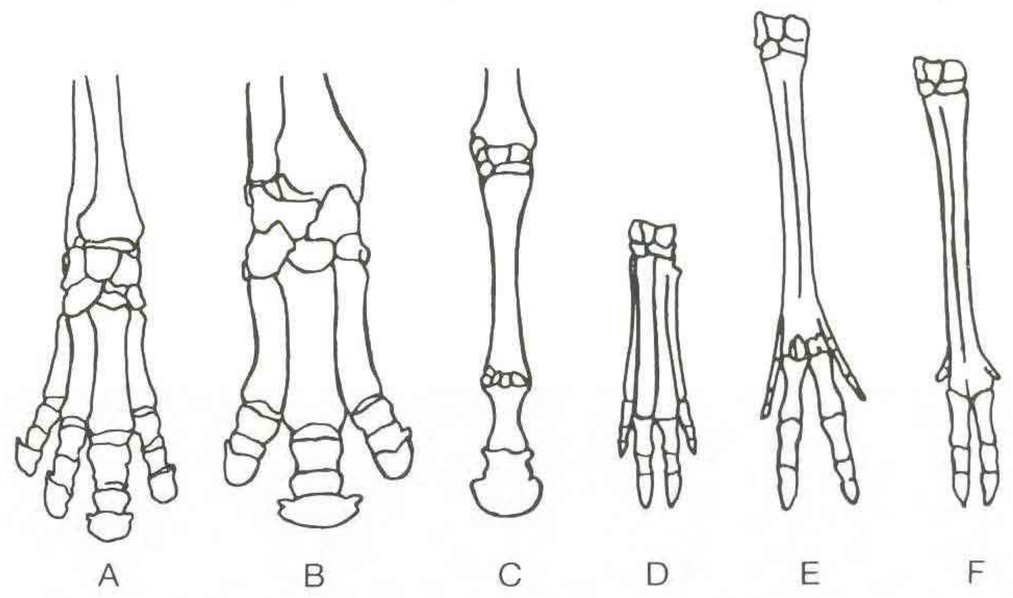
CHAPTER 12

Hoofed herbivores

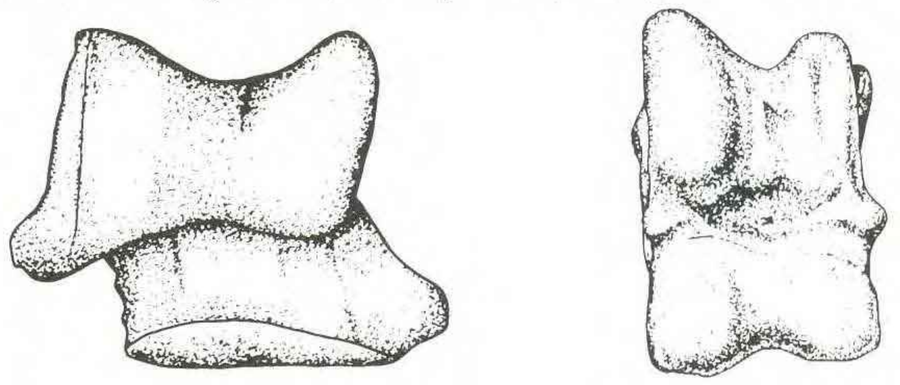
One third of all known mammalian genera are herbivores and more than half of these belong to two orders – the Perissodactyla and the Artiodactyla, meaning odd toed and even toed; one or three toes are usual in perissodactyls (tapirs, rhinos and horses) while two or four toes are usual in artiodactyls (pigs, camels, deer, giraffe, cattle, antelopes, goats and many others). This vast array of herbivores is formally classified into 12 families and there are double that number of extinct families. They range from rabbit-size to the bison, with many large extinct forms; one rhinoceros was the largest known land mammal. Their origins are probably in the Palaeocene and the fossil record for both orders is good. Perissodactyls are dominant in the early Tertiary, with the artiodactyls gradually taking over until today there are only six genera of perissodactyls but around 80 artiodactyl genera. The families appear mostly to have arisen on northern continents and later spread southward into Africa and South America; none ever reached Australia. Most early Tertiary stocks are rooters and browsers, many dying out to be replaced by colonizers of the savannahs and open grassland habitats of the later Tertiary. Diversification into a very wide range of habitats was achieved by major anatomical and physiological adaptations. Limbs tended to elongate, particularly the feet, many became digitigrade and even unguligrade; the number of hoofed toes was reduced to three, two or even one. These modifications, combined with alterations in the ankle joints and fusion of the paired limb bones, enabled the herbivores to exploit fully a vast range of terrains, move efficiently over long migrations and rapidly escape predators.

The dentitions of early genera were almost complete; in later stocks upper incisors are often lost, the lower incisors biting against a hard pad. There is also a tendency for the canines and anterior premolars to be reduced, leaving a diastema in front of the battery of grinding teeth, which become high crowned, develop complex cusp patterns and add cementum to the crown. The dental changes, which usually involve elongation of the face, reach their acme among the horses.

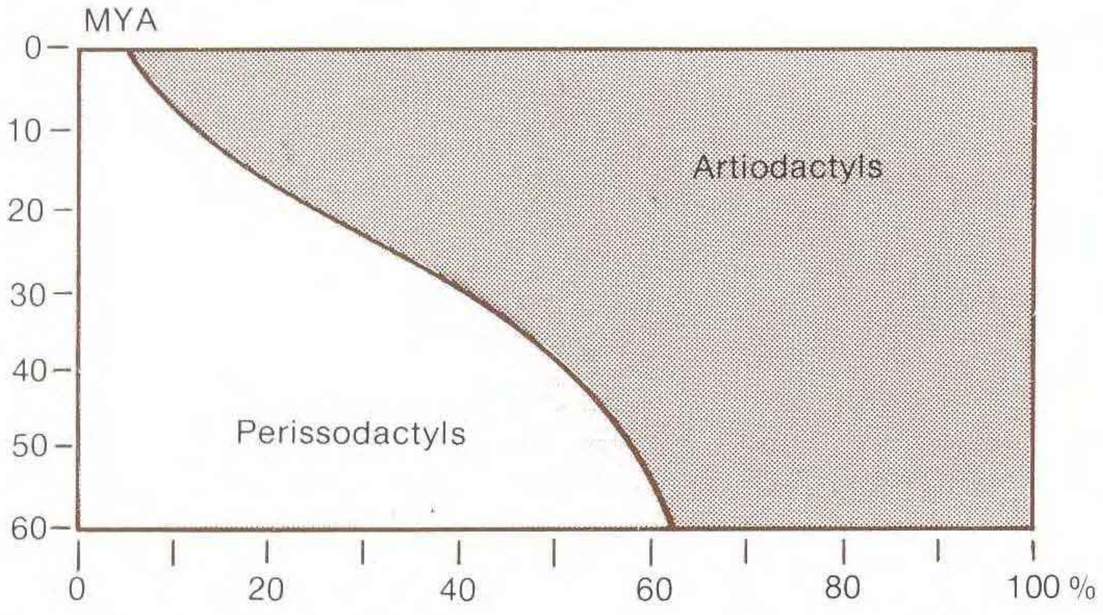
The alimentary canal or gut of herbivores is much more complex than that of insectivores or carnivores. Digestion of cellulose is made possible only by the presence of micro-organisms in the gut. The stomachs of many ruminant artiodactyls are subdivided into a series of chambers allowing specialized functions associated with ruminating or redigestion of food before it is passed



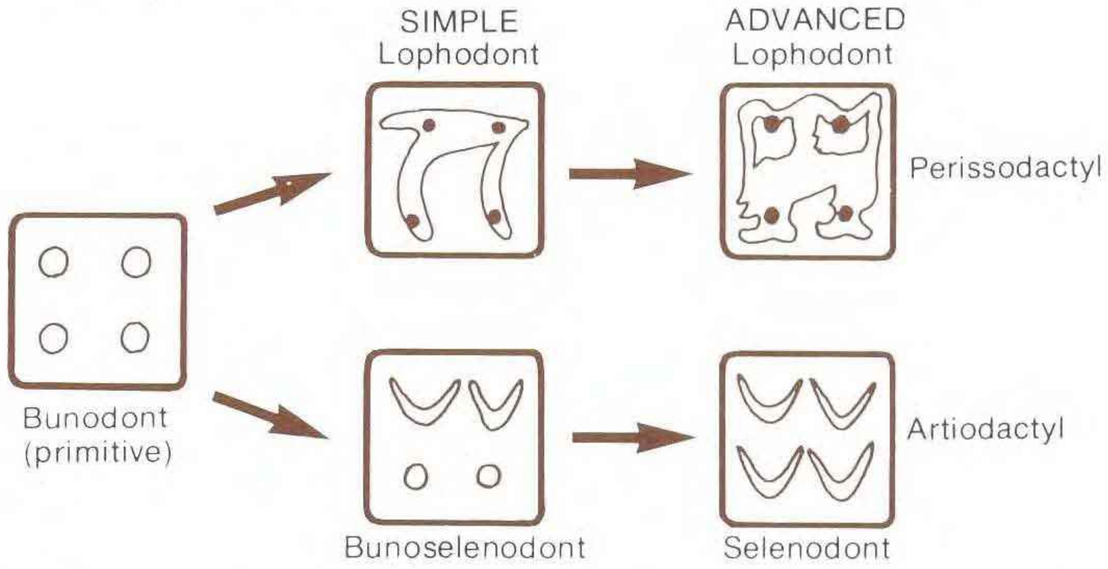
Forefoot of both odd (A–C) and even (D–F) toed ungulates to show the reduction of the digits in each. A Tapir (4 toes); B Rhinoceros (3 toes); C Horse (1 toe); D *Leptomeryx* (2 toes and 2 reduced toes); E *Blastomeryx* (2 toes and 2 vestigial toes); F *Merycodus* (2 toes).



The astragalus (ankle bone) of a perissodactyl (left) and an artiodactyl (right). The double pulley (top and bottom) is characteristic of the artiodactyl astragalus.



The relative abundance of odd (perissodactyl) and even (artiodactyl) toed ungulates through Caenozoic time: beginning 60 million years ago faunas were dominated by perissodactyls, but as time progressed these were gradually replaced by artiodactyls so that today they make up 90 per cent of ungulate faunas.



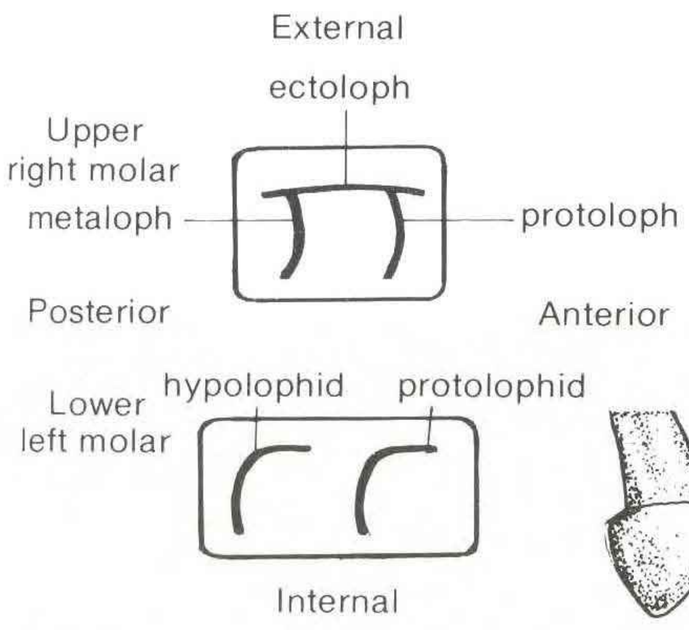
Diagrammatic sequence of evolutionary changes from a simple four cusped bunodont ancestral form of molar tooth into typical perissodactyl and artiodactyl patterns.

to the intestines. Thus ruminants make very efficient use of the vegetation they consume; almost nothing is wasted.

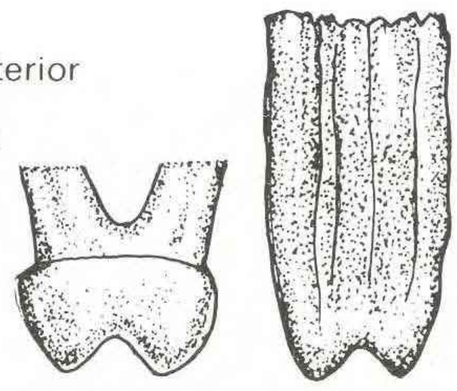
Several lineages independently develop skull outgrowths, primarily as defence mechanisms. Horns develop in both sexes in bovids (cattle and antelopes for example). A pair of conical bony outgrowths develops on the frontal skull bones; in life these are covered with a horny sheath. The horns may be straight, curved or spiral but never branch and are permanent, not shed annually. By contrast, antlers develop in cervids (deer), usually only in the male though they are present in both sexes of reindeer. They are paired, branching, bony outgrowths of the frontal skull bones, lacking a horny sheath; they grow and are shed annually. Ossicones in giraffes are bony outgrowths with a permanent covering of skin. In rhinoceroses the nasal 'horn' is composed of compact hair and so does not fossilize. Several extinct stocks (e.g. titanotheres, uintatheres and protoceratids) had bony skull outgrowths, usually referred to loosely as 'horns'; they were never shed, some were branched, their number and head site varied, they were usually larger in the male, but whether they were covered in skin or horn is unknown.

All early members of these two orders were small and hornless. When they reached a weight of about 20 kg, horns began to develop and sexual dimorphism appears. It is probable that early taxa were forest dwellers; as they moved out into woodlands, savannah and grasslands many became territorial and in consequence needed some defence for the herd.

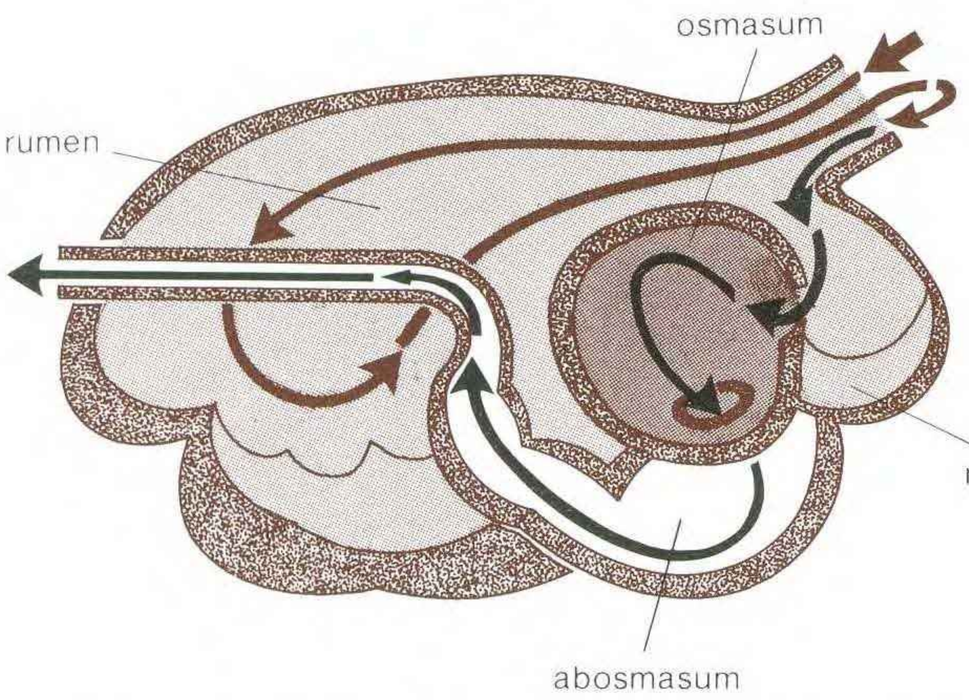
Domestication of wild animals is one of the greatest achievements of mankind. In western Asia by the seventh millenium BC (about 9000 years ago) goats and sheep were being domesticated, to be followed by cattle, pigs, horses and camels. Over the succeeding millenia man was to alter these herbivores by selective breeding for his own ends. Their importance in the economy of man is perhaps most clearly reflected in the dramatic rise in human populations from around 100 million people in the Neolithic (about 10 000 years ago) when domestication began, to a staggering 4500 million today. Domestication of livestock must rank with crop cultivation and medicine as one of the three major factors in this explosion.



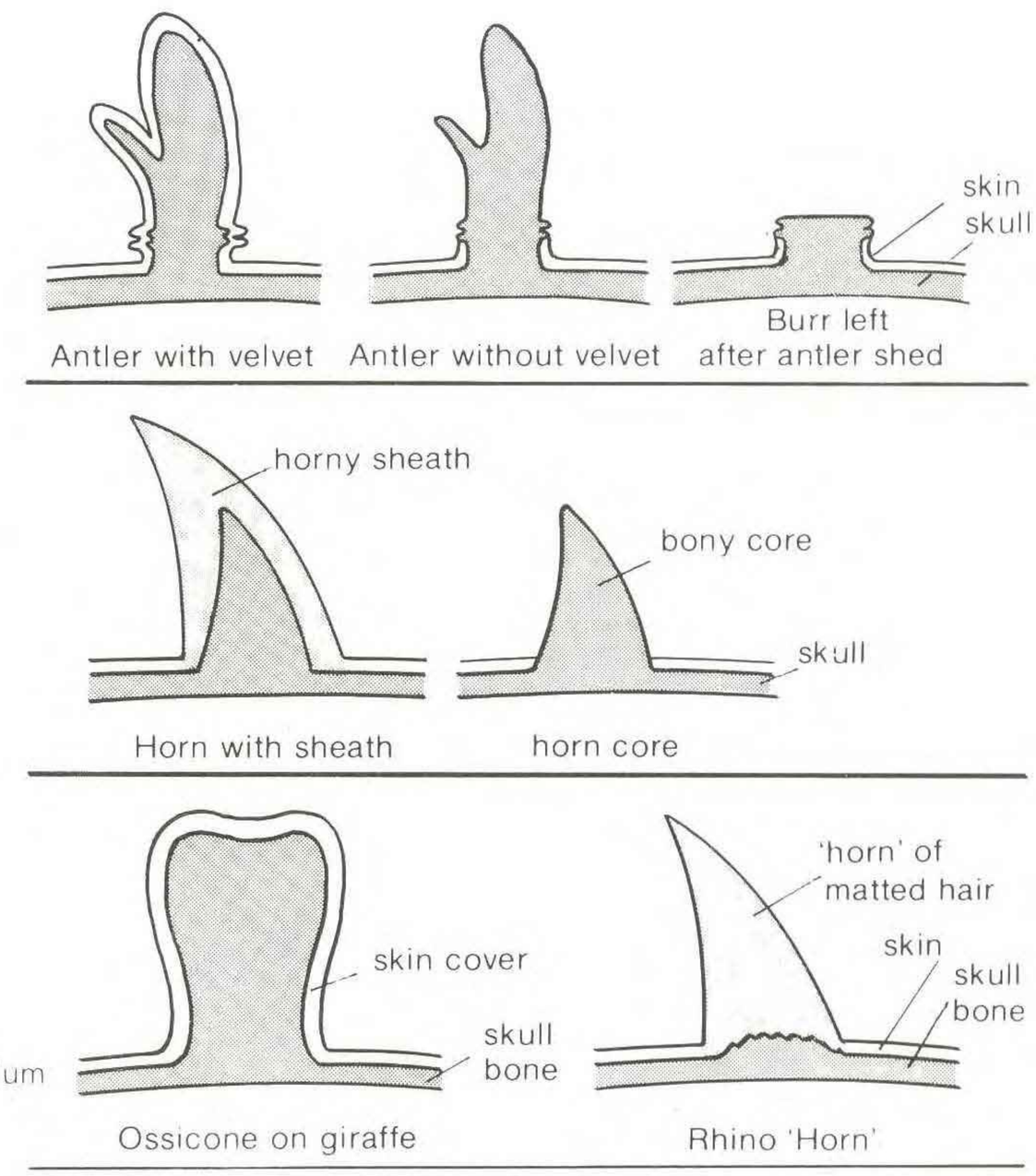
The basic pattern of the upper and lower molar teeth as seen in tapirs and rhinoceroses.



Early and primitive ungulate teeth are all brachydont (low crowned, left) and most advanced forms are hypsodont (high crowned).



Diagrammatic representation of a ruminant stomach. The black arrows follow the food from the mouth into the first two stomach chambers – the rumen and reticulum. The rumen is a fermenting vat where micro-organisms break down the cellulose plant material and produce amino acids and proteins. After regurgitation and chewing of the cud, the food follows the brown arrows to the third chamber – the osmasum – where excess water is removed, and then to the fourth chamber – the abosmasum – where conventional digestion proceeds before the residue passes into the intestine.



Ungulate skull outgrowths.
Top: antlers grow annually on male deer (rarely on female), and are shed each spring. They are branched bony structures with a skin covering during growth. When shed a burr is left on the head.
Middle: horns grow on male and female bovids (cattle, sheep, antelopes). They have a bony core and a horny sheath. They do not branch and are not shed.
Bottom, left: ossicones develop in giraffes; they may or may not branch, they have a skin covering during life and are not shed.
Bottom, right: rhinoceroses may have one or two 'horns'; these are composed of matted hair, are larger in males and continue to grow throughout life.

Odd toed ungulates

Also known as the Perissodactyla or Mesaxonia, in these animals the axis of weight bearing passes through the middle or third digit. Most members are three toed, but the later horses have eliminated the lateral digits to become one toed. There are five major stocks – tapirs, rhinoceroses, horses, and the extinct brontotheres and chalicotheres. Of the 14 families only three survive today (tapirs, rhinoceroses and horses). The order had its peak in the Eocene but by the end of Oligocene times ten of the 14 families were extinct. The perissodactyls dominated the medium- and large-sized herbivores of the early Tertiary. They have a good fossil record in North America and Eurasia, with later members penetrating southward to Africa and South America.

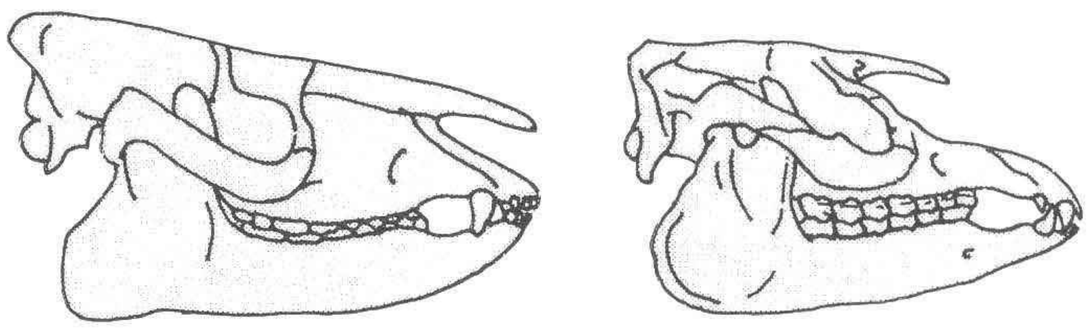
ODD TOED HERBIVORES

		Examples
Order PERISSODACTYLA		
Suborder CERATOMORPHA		
Superfamily Tapiroidea		
Family	† Helaletidae	† *Heptodon*
	Tapiridae	*Tapirus*
	† Hyrachyidae	† *Hyrachyus*
Superfamily Rhinocerotoidea		
Family	† Hyracodontidae	† *Hyracodon*
		† *Forstercooperia*
		† *Indricotherium*
	† Amynodontidae	† *Metamynodon*
		† *Cadurcodon*
	Rhinocerotidae	† *Caenopus*
		† *Teleoceras*
		† *Aceratherium*
		† *Coelodonta*
		† *Elasmotherium*
Suborder ANCYLOPODA		
Superfamily Chalicotheroidea		
Family	† Eomoropidae	† *Litolophus*
	† Chalicotheriidae	† *Moropus*
		† *Chalicotherium*
Suborder HIPPOMORPHA		
Superfamily Equoidea		
Family	† Palaeotheriidae	† *Palaeotherium*
	Equidae	† *Hyracotherium*
		† *Mesotherium*
		† *Miohippus*
		† *Anchitherium*
		† *Hypohippus*
		† *Parahippus*
		† *Merychippus*
		† *Hipparion*
		† *Pliohippus*
		† *Hippidion*
		Equus
Superfamily Brontotheroidea		
Family	† Brontotheriidae (Titanotheres)	† *Eotitanops*
		† *Palaeosyops*
		† *Brontotherium*

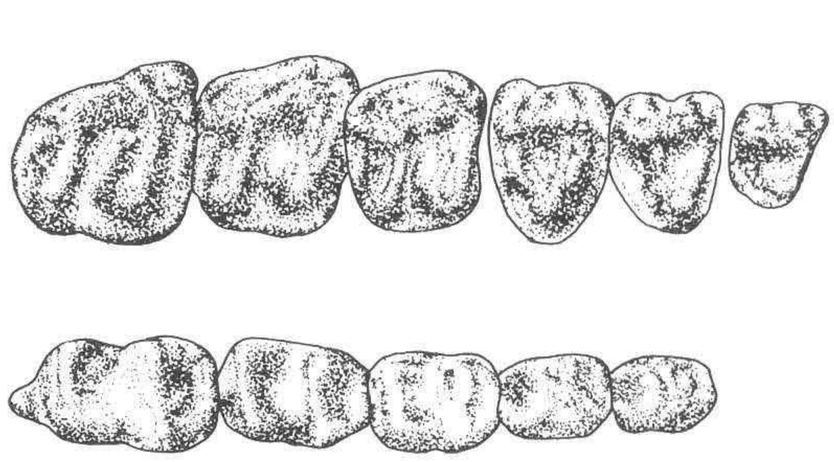
Tapirs

The first tapirs appear in the early Eocene at the same time as the first horses and chalicotheres, with brontotheres and rhinoceroses present before the end of the Eocene. This implies an origin and early differentiation of the order back in the Palaeocene. *Heptodon* is one of the earliest tapirs and from the early Eocene of Wyoming are known skulls and a partial skeleton. The living tapir, despite some 55 million years of 'evolution', still bears a remarkable similarity to its ancestor. *Tapirus* is about twice the size of *Heptodon*; it retains four toes on the fore foot and three on the hind foot; the toes are hoofed with a supporting pad. The ulna and fibula are complete and unfused. All these limb characters of the living tapir are seen in its Eocene ancestor *Heptodon*. The skulls are also similar in structure, except that there was no proboscis in *Heptodon*. The dentition of tapirs is complete though a small diastema exists; the upper canine is reduced and the lateral incisor has become caniniform. In *Tapirus* all but the first premolar have become molariform, but the molars in both *Heptodon* and *Tapirus* are closely similar. The basic tapiroid (and rhinocerotoid) pattern is a three loph upper molar, the lophs or ridges arranged as in the Greek letter pi π; the lower molars have two transverse lophids.

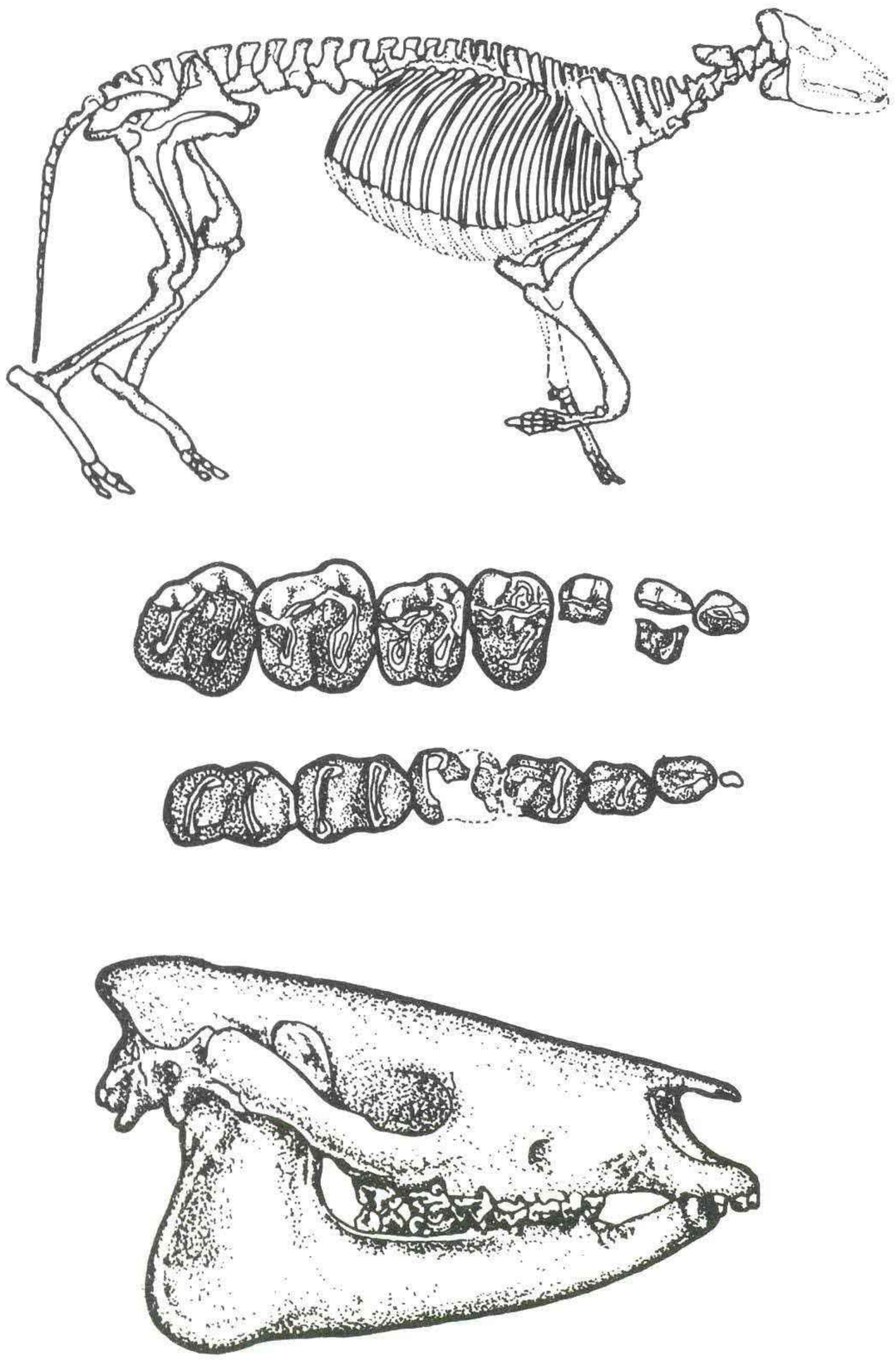
Tapirs are tropical browsing mammals, living in forests and woodlands near water; they survive today in Central and northern South America and in south-east Asia, remnants of a once widespread distribution. Tapirs persisted in the warmer parts of North America, Europe and Asia until late Pleistocene times.



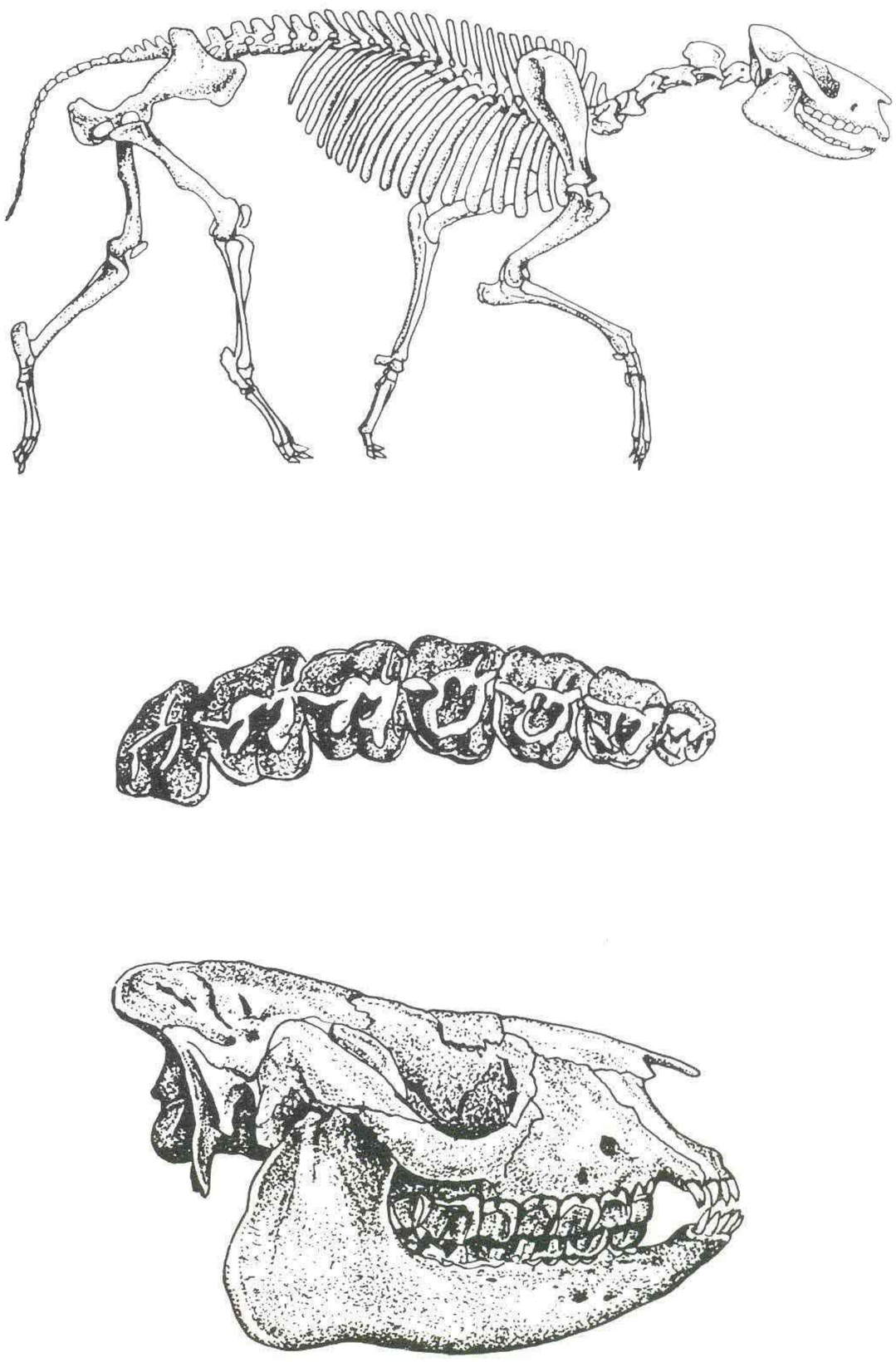
Left: skull of *Heptodon* (length 20 cm), a primitive tapir from the early Eocene, and right skull of *Tapirus* (length 36 cm), a living tapir. The nasal bones (above the eyes) on the living tapir are indicative of a well developed proboscis. (After Radinsky)



Top, the upper, and above, the lower cheek dentition of *Heptodon*; although the earliest known tapir, it shows characteristic tapir features; the upper molars have a π pattern and each of the lower molars has two transverse lophs. (After Radinsky).



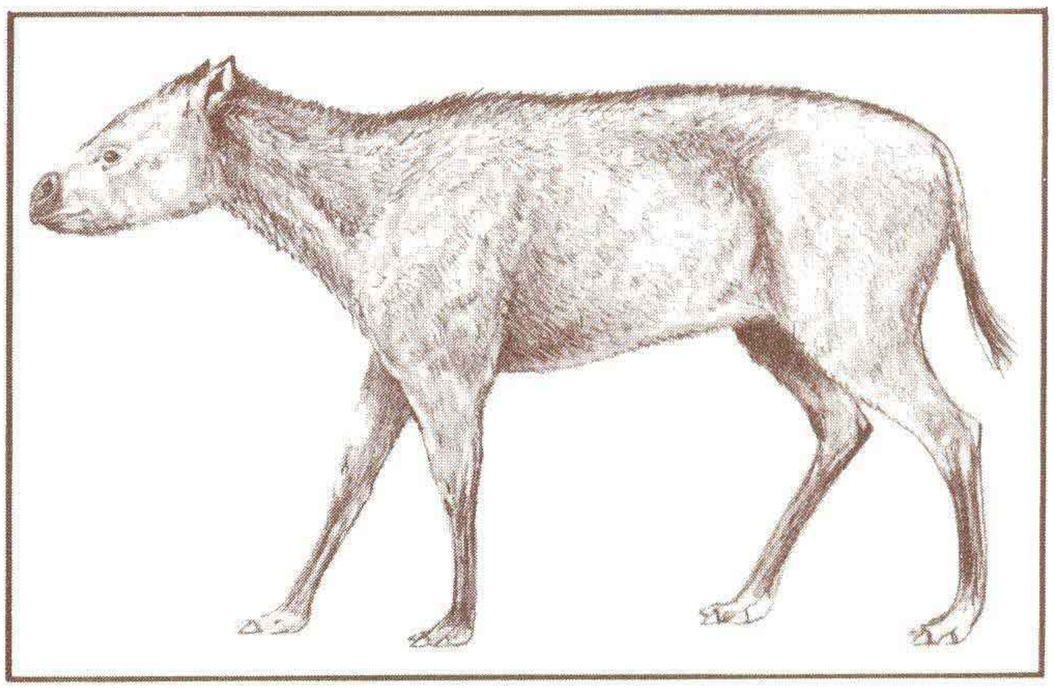
Skeleton (overall length 1.6 m), cheek dentition and skull (length 30 cm) of *Hyrachyus*. The nasal incision is larger than in *Heptodon* and the teeth show traces of rhinocerotoid characters. (After Wood).



Skeleton (length 1.5 m), dentition and skull (length 27 cm) of *Hyracodon*, a running rhinoceros from the Oligocene of North America. This animal was lightly built like a horse, had three toes on each foot and the posterior premolars are molarized. (After Scott).

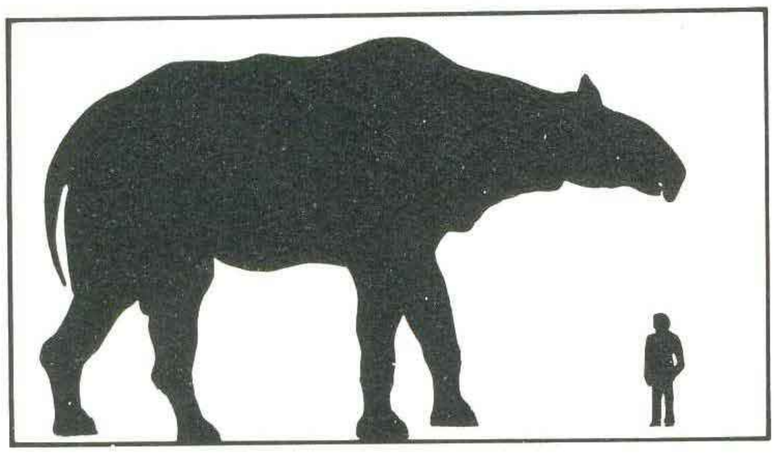
Rhinoceroses

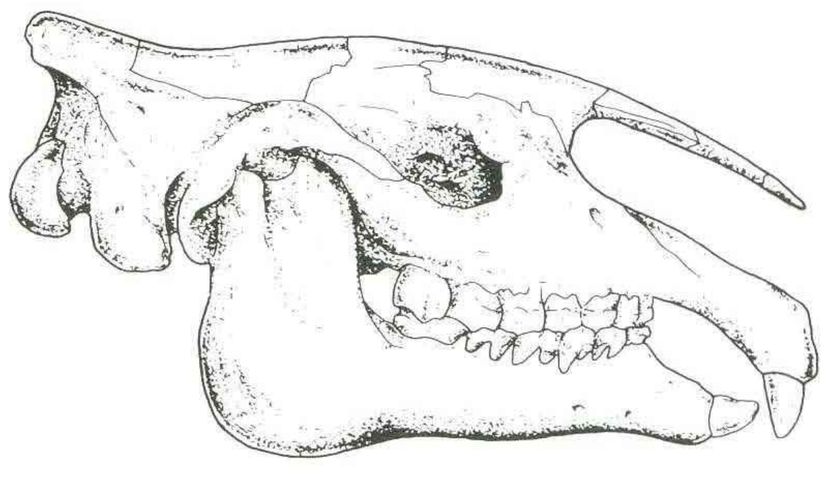
From a tapiroid close to *Hyrachyus* arose two lineages of rhinocerotoids – the hyracodontids and amynodontids – both stocks abundant in the Eocene and Oligocene of North America and Asia. The hyracodontids comprise about a dozen genera; most of these were medium-sized like *Hyracodon*. Their elongate almost slender limbs and light build parallels that of horses, and like them they were cursorial. Their posterior dentition with progressive molarization of the premolars and increase in crown height was little changed from that of tapirs, though there were many variations in the anterior teeth. The incisors were primitively spatulate and equal-sized and the canines of moderate size. However, in Oligocene times in Asia there arose from a hyracodont close to *Forstercooperia* a series of gigantic hornless rhinoceroses, which may be grouped in the subfamily Indricotherinae. They ranged from Caucasia, through



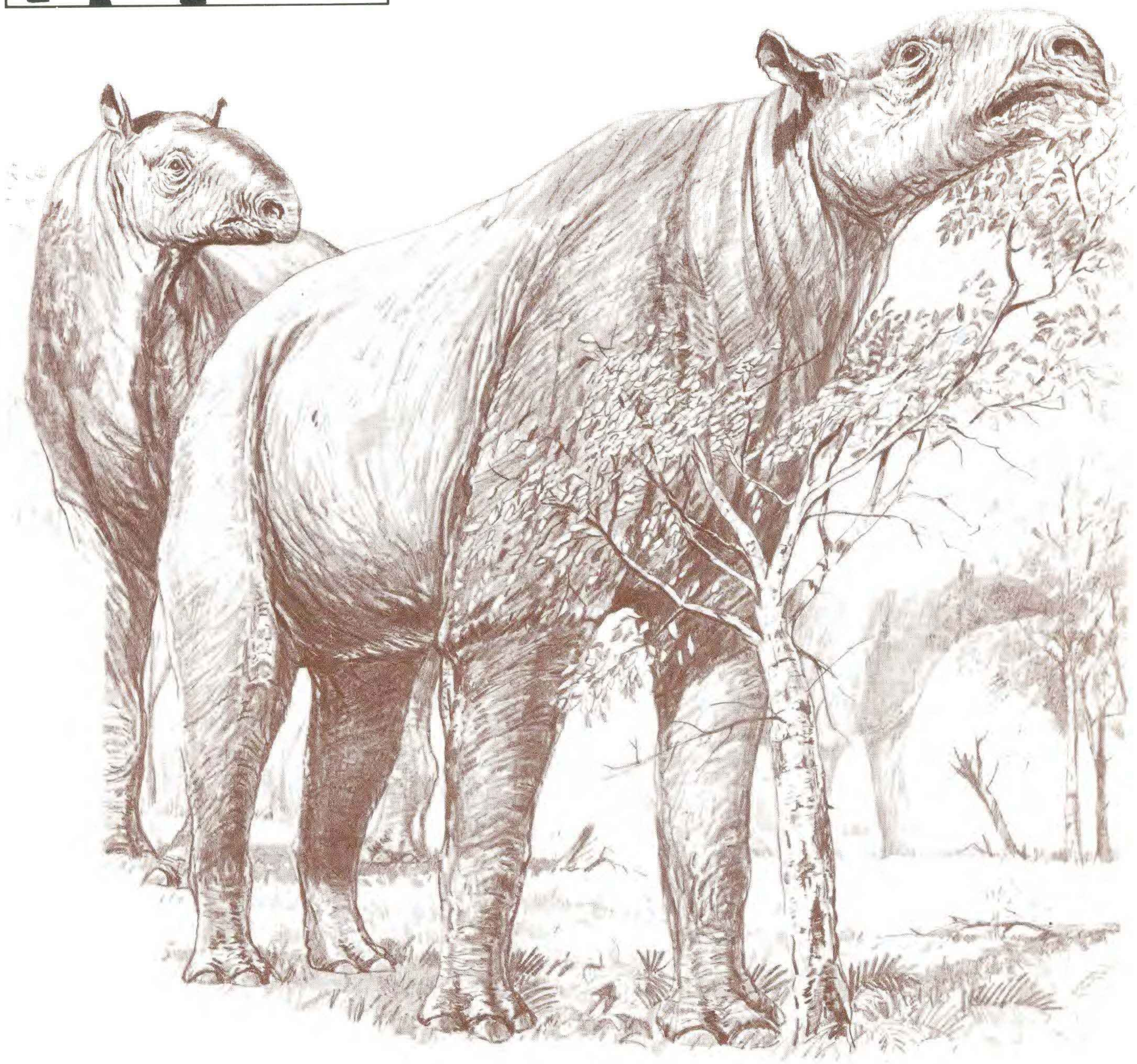
Restoration of *Hyracodon*, a hornless three toed running rhinoceros of the Oligocene period.

Central Asia and Baluchistan to China. *Indricotherium* (= *Baluchitherium*) is the largest land mammal that ever lived. This rhinoceros stood 5·4 m at the shoulder; with its long neck and 1·3 metre-long skull it could reach to browse on vegetation over eight metres above the ground. With a probable weight of around 30 tonnes it was four and a half times as heavy as the heaviest recorded elephant (6·6 tonnes) and nearly twice the estimated weight of the heaviest mammoth.





Skull (after Granger & Gregory), size comparison and restoration of the 35-million-year-old rhinoceros from Central Asia *Indricotherium* (= *Baluchitherium*), the largest land mammal that ever lived.



The second Palaeogene lineage of rhinoceroses comprised the amynodontids, a compact group of about ten genera with large heavy bodies, short stocky limbs and short faces with prominent canine tusks. Among their number was *Metamynodon* which had prehensile lips and *Cadurcodon* with a short tapir-like proboscis. This, combined with the very hippopotamus-like skeleton found among members of this family, strongly suggests a semi-aquatic habitat.

The great radiation of Palaeogene rhinoceroses was all but over by the close of the Oligocene, leaving only a few stragglers to see the earliest Miocene times in Asia. However, there arose from among the hyracodontids during the Oligocene a lineage with distinct specializations of the incisor teeth, namely the development of chisel-shaped I^1 and procumbent hypertrophied lanceolate or tusk-like I_2; these were to form the basis of a second great radiation of rhinoceroses in the Neogene – the Rhinocerotidae. They comprise about 50 genera, including four present-day survivors; they were abundant in North America, Eurasia and Africa during the Miocene and the Plio-Pleistocene, and adapted to a wide range of habitats, climates and diets. Many were browsers as were earlier rhinoceroses, but some became specialized grazers. Some had thick coats of long hair, many had 'horns' which were composed of matted hair and do not fossilize, but a bony protuberance on the skull is indicative.

Caenopus is representative of the early rhinocerotids in the early Oligocene of North America. It was very tapir-like with short stout limbs, four-toed front feet and three-toed hind feet; the last premolar was molarizing and the cheek teeth were low crowned. *Teleoceras* was a hippopotamus-like rhinoceros from the Miocene of North America. It had a bony rugosity on the nasal bone implying the presence of a horn; though *Teleoceras* was similar in size to living rhinoceroses, it had a brain that was twice as large. *Aceratherium* and its allies were medium-sized rhinoceroses abundant in the Miocene of Eurasia and Africa. They were hornless, had reduced incisor teeth and had subhypsodont molars suggesting a mixed diet of foliage and grasses.

Restoration of the Ice Age woolly rhinoceros, *Coelodonta antiquitatis*, a large furry rhino with two nasal horns that roamed the tundra of Palaearctica during the late Pleistocene.

Opposite: restoration of *Elasmotherium*, a very large rhinoceros from the mid Pleistocene of the steppes of southern Siberia; the single horn on the forehead could reach 2 metres in length.