28. ORIGIN AND EVOLUTION OF THE PERISSODACTYLA: SUMMARY AND SYNTHESIS

DONALD R. PROTHERO and ROBERT M. SCHOCH

The Perissodactyla appear to have originated in Asia and/or Africa during the late Paleocene, where they diverged from their close relatives, the tethytheres (proboscideans, sirenians, desmostylians) and arsinoitheres. Contrary to many accounts, they are not as closely related to phenacodontids as they are to tethytheres, and perissodactyls did not come from Central America. Many unique synapomorphies strongly suggest that hyraxes (long considered "subungulates" related to elephants) are in fact perissodactyls. Since the Order Perissodactyla included the hyrax when it was created by Owen in 1848, we return the hyraxes to the Perissodactyla. The hyraxes were apparently the first group to split from the rest, and became isolated in Africa (along with tethytheres and arsinoitheres). There they underwent an endemic radiation, converging in some ways with bovids, pigs, tapirs, and chalicotheres; eventually they spread to Eurasia.

The non-hyracoid perissodactyls (Mesaxonia of Marsh, 1884) split into three major infraorders. The first group, the Titanotheriomorpha, was dominant in both Asia and North America during most of the later Eocene, migrating back and forth over the Bering Strait before finally becoming extinct during the Oligocene. The other two infraorders were widespread over Holarctica in the early Eocene, where they began to diverge into Hippomorpha (pachynolophids, equids, and palaeotheres) and Moropomorpha (isectolophids, lophiodonts plus chalicotheres, tapiroids *sensu lato*, and rhinocerotoids).

The hippomorph radiation began in the latest Paleocene and earliest Eocene with the "wastebasket" taxon *Hyracotherium*, which includes the most primitive pachynolophids, equids, and palaeotheres. If Hooker (this volume, Chapter 6) is correct, then the type species

of *Hyracotherium*, *H. leporinum*, is most closely related to palaeotheres, and the most primitive equids must be referred to another genus (possibly *Protorohippus*). After the early Eocene, equids became endemic to North America (with several back-migrations to Eurasia), while pachynolophids and palaeotheres became endemics which dominated Europe in the later Eocene. Both European groups were decimated during the early Oligocene ("la Grande Coupure") and disappeared by the mid-Oligocene.

The moropomorph radiation began with *Homogalax* and a number of "tapiroid" forms which were widespread over Holarctica in the early Eocene. By the mid-Eocene, they had diverged into a number of groups dominant in Asia and North America (isectolophids, ancylopods, lophialetids and other tapiroids *sensu lato*, and rhinocerotoids). Most of these groups reached their maximum diversity in the later Eocene of Asia, and then were decimated in the Oligocene. Chalicotheres, on the other hand, diversified in the Miocene of Eurasia, where they became large clawed herbivores adapted for pulling down branches on trees. Lophiodonts were closely related to chalicotheres, and were important tapir-like animals in Europe before their late Eocene extinction.

In the later Eocene of Asia and North America, rhinocerotoids diversified into amynodonts (some of which were large, aquatic forms with a proboscis), hyracodonts (long-legged forms which reached gigantic size in Asia), and rhinocerotids (true rhinoceroses). Amynodonts and hyracodonts were both severely affected by the late Eocene extinctions event, and were almost completely gone by the Oligocene. Rhinocerotids, on the other hand, began to dominate and radiate in the latest Eocene, filling the niches previously occupied by titanotheres and amynodonts in North America, and by

palaeotheres, tapiroids, and lophiodonts in Eurasia.

In the Miocene, equids and rhinocerotids were very diverse, and among the dominant large herbivores in Holarctica. Both were severely affected by the Messinian event at the end of the Miocene. During the Pleistocene, tapirs and equids crossed to South America via Panama. After the Pleistocene extinctions, only relicts of hyraxes in Africa, equids in Africa and Eurasia, rhinocerotids in Africa and southeast Asia, and tapirs in South America and southeast Asia were left from previously worldwide distributions of all of these groups. The wild populations of all of these groups (especially tapirs and rhinos) are now facing extinction from human population pressure and poaching.

Introduction

The Perissodactyl Workshop at the Fourth International Theriological Congress in 1985, and this resulting volume, brought together much new information about the Perissodactyla. Some of it radically changes the prevailing orthodoxies about the group which are still appearing in popular articles and books (e.g., Monroe, 1985; Savage and Long, 1986), textbooks (e.g., Carroll, 1988) and review articles (e.g., MacFadden, 1988). Many of these ideas have radical implications for mammalogy (e.g., the relationships of hyraxes, and our new perissodactyl classification) and evolutionary biology (e.g., revised ideas about horse evolution). In this chapter, we review the contributions to this volume, and place them in the larger context of much recent research about ungulate evolution. We have also compiled generic range charts of all the valid perissodactyl genera (Fig. 28.1), which necessitate a discussion of the diversification, biogeography and evolutionary patterns in the Perissodactyla through the entire Cenozoic. We hope this will help bring the next generation of textbooks and review articles up to date.

As this book went to press, new argon-argon dates from some of the classic North American terrestrial vertebrate-bearing sequences indicate that our later Eocene and Oligocene correlations will have to be

radically revised. These dates place the Duchesnean/Chadronian boundary around 36-37 Ma, the Chadronian/Orellan boundary around 33 Ma, the Orellan/Whitneyan boundary around 31.8 Ma, and the Whitneyan/Arikareean boundary around 29 Ma. At the same time, revised magnetostratigraphic correlations are in agreement with the increasing number of analyses that place the Eocene/Oligocene boundary at about 34 Ma. Although the revision of the timescale is not yet complete, it appears from these correlations that the Bridgerian, Uintan, and Duchesnean are middle Eocene, the Chadronian (classically considered early Oligocene) is actually late Eocene, and the Orellan, Whitneyan, and early Arikareean are early Oligocene. The Terminal Eocene Event is actually the Chadronian/Orellan extinction, although most authors (e.g., Prothero, 1985) have labeled this the "mid-Oligocene event." Similarly, the Duchesnean/Chadronian faunal turnover is actually the middle/late Eocene (Bartonian/Priabonian) event.

These radical changes in the timescale came too late to incorporate into most of the book. Except for this chapter and Chapter 10, it was impossible to rewrite the other chapters to reflect these new dates. Thus, for example, Mader (this volume, Chapter 25) refers to North American Oligocene brontotheres throughout his chapter, although it appears now that the extinction of brontotheres in North America occurred at the end of the Eocene. The range charts in this chapter (Fig. 28.1) were also finished long ago, and could not be completely redrawn at such a late stage in preparation of this book. Therefore, the reader is cautioned to read the terms "Eocene" and "Oligocene" in this book with the above revisions in mind, and substitute "late Eocene" whenever the author uses "early Oligocene" to mean Chadronian.

Origin of the Perissodactyla

Prior to this volume, the prevailing orthodoxy (e.g., Radinsky, 1966a; Sloan, 1970, 1987; Van Valen, 1978; Gingerich, 1976)

50	45	40	35	30	25	20	15	10	5	NALMA
Was	Brid	Uintan	Duch	Chad	Or	Wh	Arikareean	Hemng	Barstov.	Clar	Hemp	Blanc	NALMA
Cuis	Lut	Bartonian	Headon		Suev		Arvern	Agen	Orlean	Astarac	Vall	Turo	Rus	Vil	EURASIA
EOCENE				OLIGOCENE			MIOCENE				PLIO	PLE	EPOCHS

EQUOIDEA

"Hipparion"
Epuus
— AFRICA

Hyracotherium
Leptolophus
Lophiotherium
Anchitherium
Hipparion
Cymbalophus
Palaeotherium
Equus
Propalaeotherium
Pliolophus
Plagiolophus
"Hipparion"
Pachynolophus
Anchilophus
— EUROPE

Hipparion
Anchitherium
Gobihippus
Cormohipparion
Equus
Propalaeotherium
Sivalhippus
— ASIA

?Protorohippus
Nannippus
Orohippus
Protohippus
Mesohippus
Epihippus
Miohippus
"Merychippus"
Haplohippus
Hipparion
Parahippus
Onohippidium
Pseudhipparion
Anchitherium
Neohipparion
Archaeohippus
Hypohippus
Equus
Cormohipparion
Hypohippus
Megahippus
Calippus
Pliohippus
Dinohippus
Astrohippus
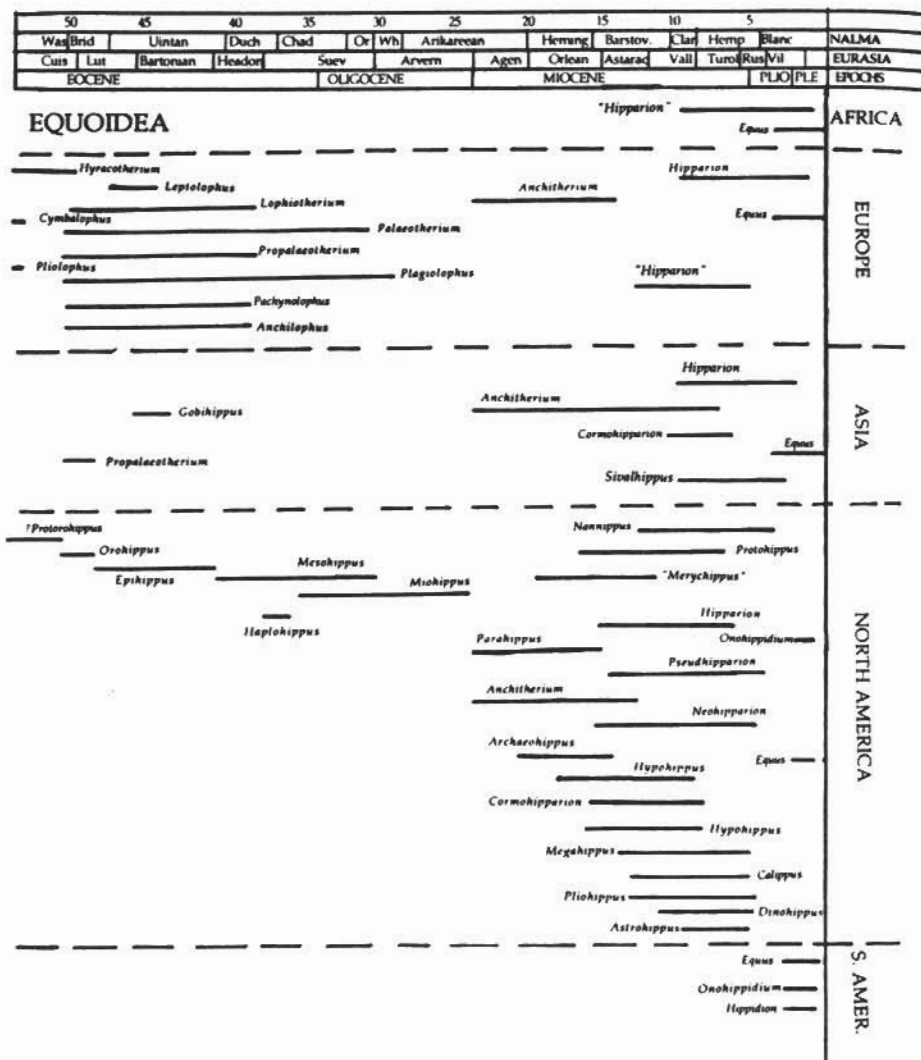— NORTH AMERICA

Equus
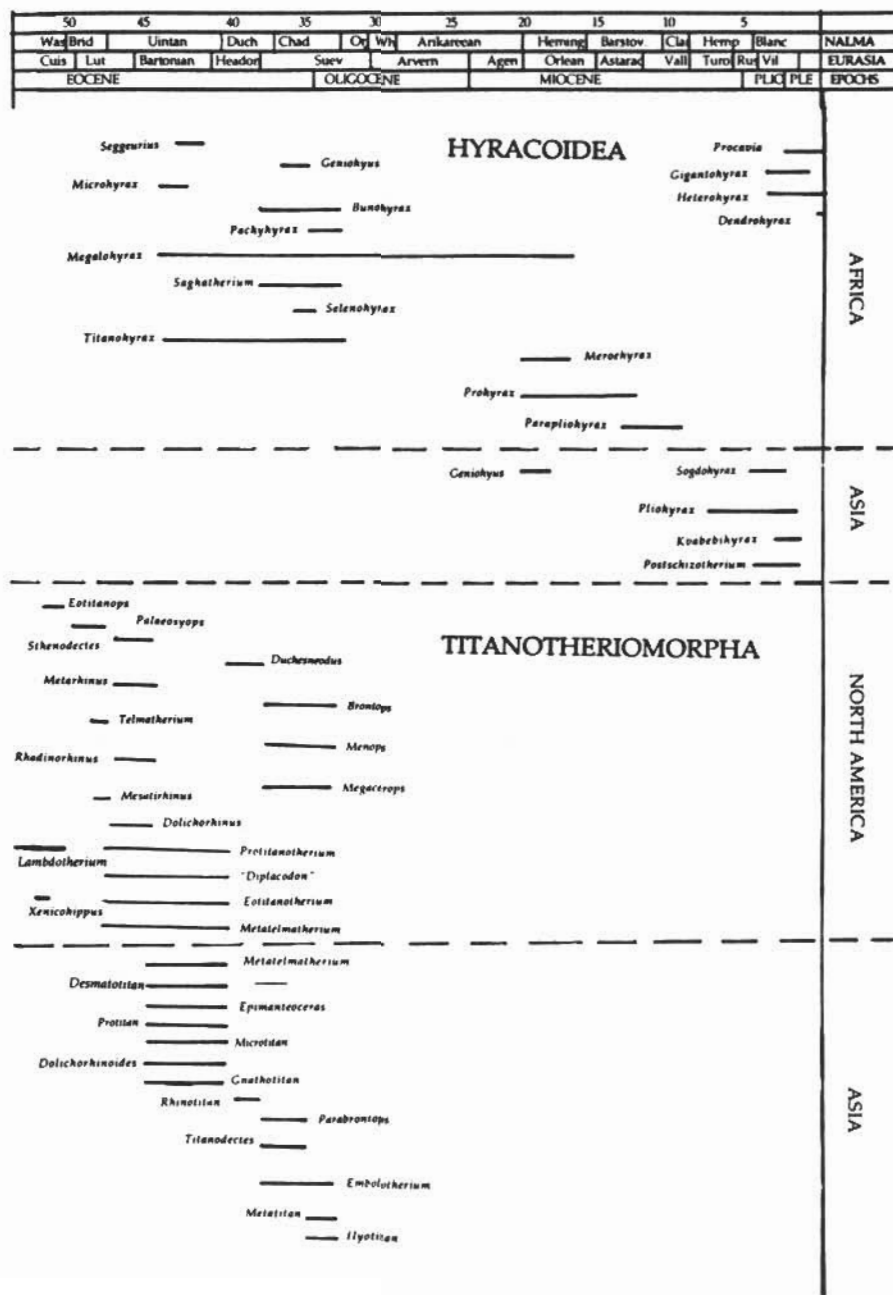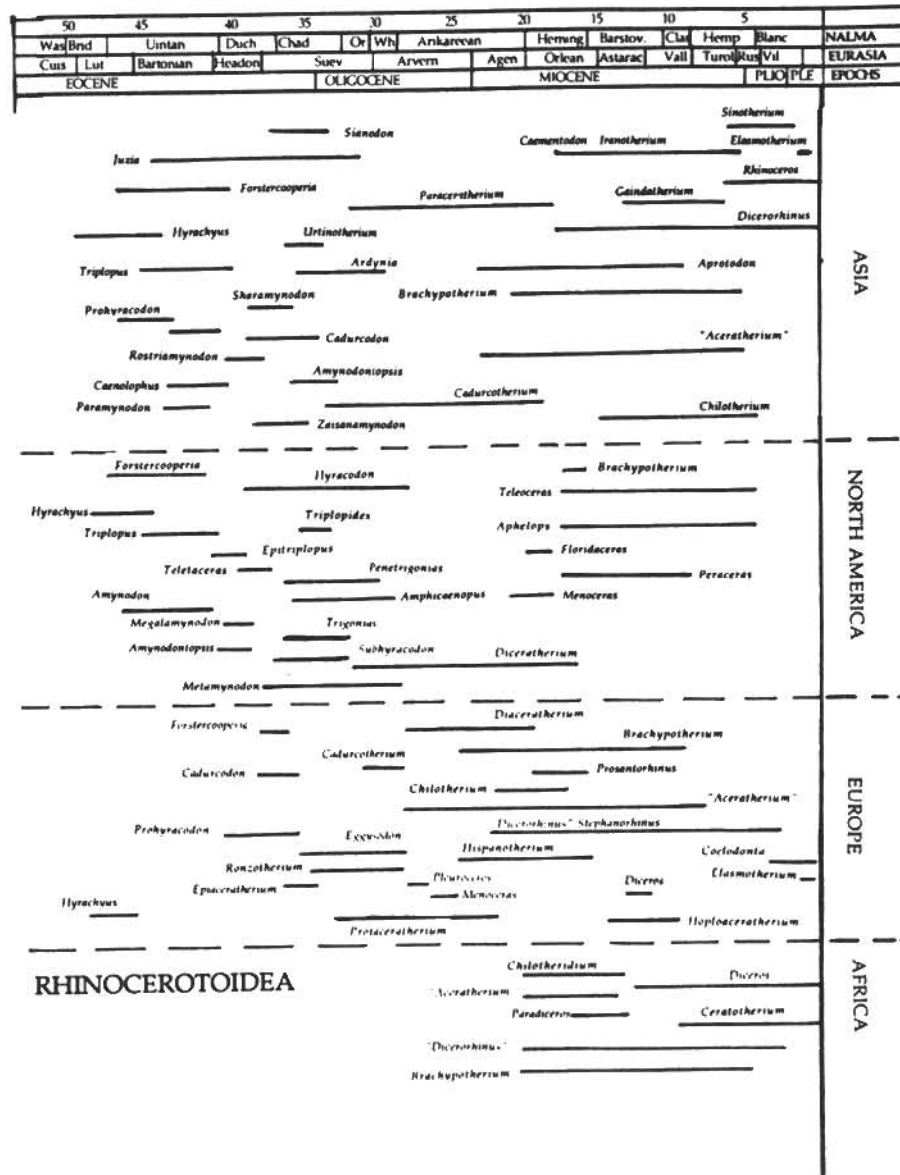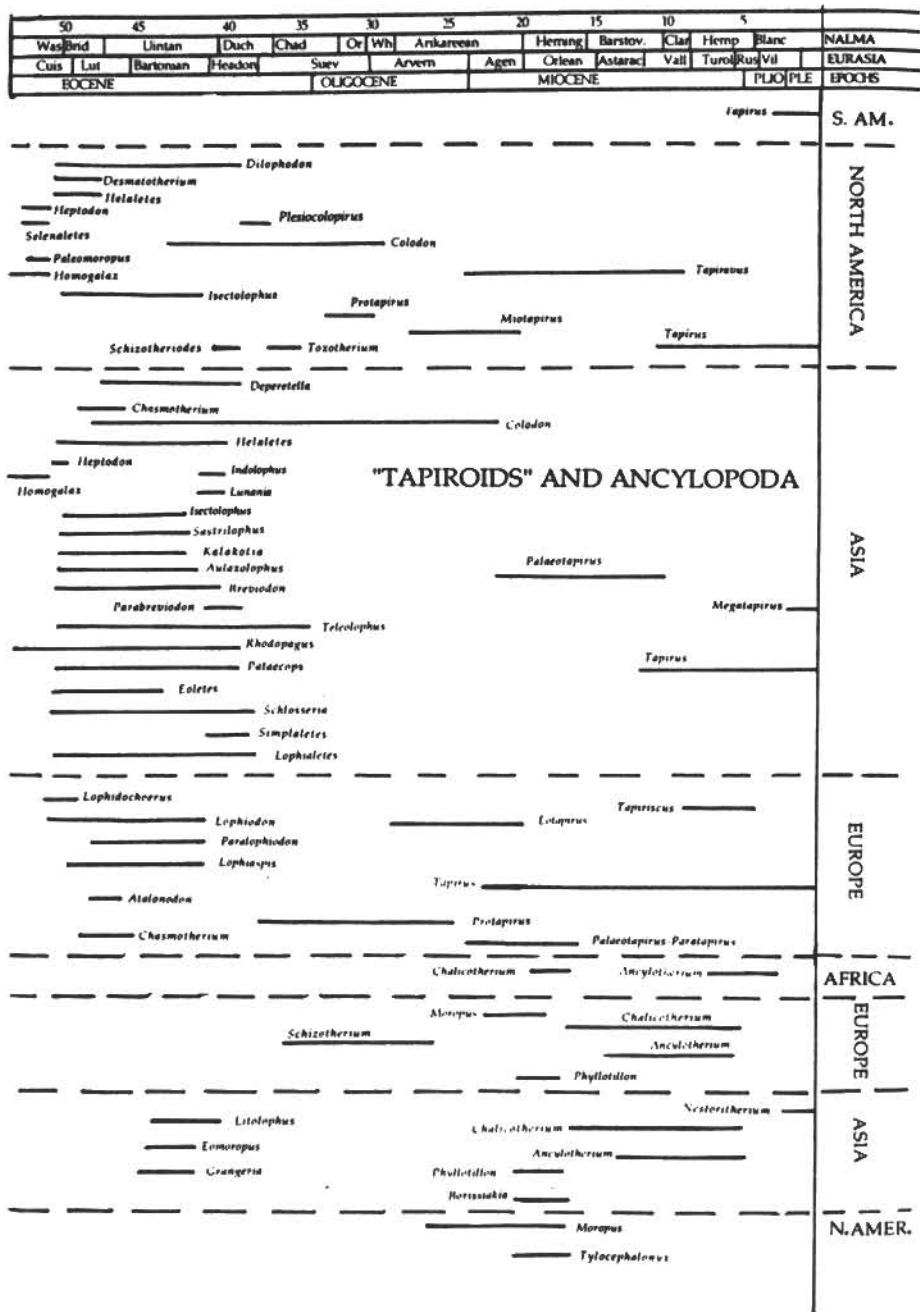Onohippidium
Hippidion
— S. AMER.

Fig. 28.1. Temporal ranges of valid perissodactyl genera discussed in this volume. Note that neither the timescale nor the ranges have been adjusted for the recent recalibration of the North American later Eocene-Oligocene (see p. 505). Timescale abbreviations: NALMA= North American land mammal "ages," as follows: Wasatchian, Bridgerian, Uintan, Duchesnean, Chadronian, Orellan, Whitneyan, Arikareean, Hemingfordian, Barstovian, Clarendonian, Hemphillian, Blancan. Eurasian chronology abbreviations for the following: Cuisian, Lutetian, Bartonian, Headonian, Suevian, Arvernian, Agenian, Orleanian, Astaracian, Vallesian, Turolian, Ruscinian, Villafranchian.

50	45	40	35	30	25	20	15	10	5	NALMA
Was	Brid	Uintan	Duch	Chad	Or	Wh	Arikareean	Hemng	Barstov.	Clar	Hemp	Blanc	NALMA
Cuis	Lut	Bartonian	Headon		Suev		Arvern	Agen	Orlean	Astarac	Vall	Turo	Rus	Vil	EURASIA
EOCENE				OLIGOCENE			MIOCENE				PLIO	PLE	EPOCHS

HYRACOIDEA

Seggeurius
Geniohyus
Procavia
Microhyrax
Gigantohyrax
Bunohyrax
Heterohyrax
Pachyhyrax
Dendrohyrax
Megalohyrax
Saghatherium
Selenohyrax
Titanohyrax
— AFRICA

Merohyrax
Prohyrax
Parapliohyrax
Geniohyus
Sogdohyrax
Pliohyrax
Kvabebihyrax
Postschizotherium
— ASIA

TITANOTHERIOMORPHA

Eotitanops
Palaeosyops
Sthenodectes
Duchesneodus
Metarhinus
Brontops
Telmatherium
Menops
Rhadinorhinus
Megacerops
Mesatirhinus
Dolichorhinus
Protitanotherium
Lambdotherium
"Diplacodon"
Eotitanotherium
Xenicohippus
Metatelmatherium
— NORTH AMERICA

Metatelmatherium
Desmatotitan
Epimanteoceras
Protitan
Microtitan
Dolichorhinoides
Gnathotitan
Rhinotitan
Parabrontops
Titanodectes
Embolotherium
Metatitan
Ilyotitan
— ASIA

50	45	40	35	30	25	20	15	10	5	
Was|Brid	Uintan	Duch	Chad	Or|Wh	Ankareean	Hemng	Barstov.	Cla|Hemp	Blanc	NALMA
Cuis|Lut	Bartonian	Headon	Suev	Arvern	Agen	Orlean	Astarac	Vall|Turol	Rus|Vil	EURASIA
EOCENE		OLIGOCENE			MIOCENE				PLIO|PLE	EPOCHS

S. AM.

Tapirus

NORTH AMERICA

Dilophodon
Desmatotherium
Helaletes
Heptodon
Plesiocolopirus
Selenaletes
Colodon
Palaeomoropus
Homogalax
Tapiravus
Isectolophus
Protapirus
Miotapirus
Schizotheriodes — Toxotherium
Tapirus

ASIA

Deperetella
Chasmotherium
Colodon
Helaletes
Heptodon
Indolophus
Homogalax
Lunania
Isectolophus
Sastrilophus
Kalakotia
Aulaxolophus
Breviodon
Palaeotapirus
Parabreviodon
Teleolophus
Rhodopagus
Tapirus
Pataecops
Eoletes
Megatapirus
Schlosseria
Simplaletes
Lophialetes

"TAPIROIDS" AND ANCYLOPODA

EUROPE

Lophidochoerus
Lophiodon
Tapiriscus
Lotapirus
Paralophiodon
Lophiaspis
Tapirus
Atalonodon
Protapirus
Chasmotherium
Palaeotapirus-Paratapirus

AFRICA

Chalicotherium — Ancylotherium

EUROPE

Moropus — Chalicotherium
Schizotherium — Anculotherium
Phyllotilon
Nestoritherium

ASIA

Litolophus
Chalicotherium
Eomoropus
Anculotherium
Grangeria
Phyllotilon
Borissiakia

N. AMER.

Moropus
Tylocephalonyx

50	45	40	35	30	25	20	15	10	5	
Was|Brid	Uintan	Duch	Chad	Or|Wh	Ankareean	Hemng	Barstov.	Cla|Hemp	Blanc	NALMA
Cuis|Lut	Bartonian	Headon	Suev	Arvern	Agen	Orlean	Astarac	Vall|Turol	Rus|Vil	EURASIA
EOCENE		OLIGOCENE			MIOCENE				PLIO|PLE	EPOCHS

ASIA

Sianodon
Juxia
Caementodon   Iranotherium   Elasmotherium
Forstercooperia
Rhinoceros
Paraceratherium   Gaindatherium
Hyrachyus   Urtinotherium
Dicerorhinus
Triplopus   Ardynia   Aprotodon
Prohyracodon   Sharamynodon   Brachypotherium
Cadurcodon   "Aceratherium"
Rostriamynodon
Caenolophus   Amynodontopsis
Paramynodon   Cadurcotherium   Chilotherium
Zaisanamynodon

NORTH AMERICA

Forstercooperia   Hyracodon   Brachypotherium
Hyrachyus   Triplopides   Teleoceras
Triplopus   Aphelops
Epitriplopus   Floridaceras
Teletaceras   Penetrigonias
Amynodon   Amphicaenopus   Menoceras   Peraceras
Megalamynodon   Trigonias
Amynodontopsis   Subhyracodon   Diceratherium
Metamynodon

EUROPE

Forstercooperia   Diaceratherium
Cadurcotherium   Brachypotherium
Cadurcodon   Prosantorhinus
Chilotherium
Prohyracodon   "Aceratherium"
Eggysodon   "Dicerorhinus" Stephanorhinus
Hispanotherium   Coelodonta
Ronzotherium   Diceros   Elasmotherium
Pleuroceros   Menoceras
Epiaceratherium
Hyrachyus   Hoploaceratherium
Protaceratherium

RHINOCEROTOIDEA

AFRICA

Chilotheridium   Diceros
"Aceratherium"
Paradiceros   Ceratotherium
"Dicerorhinus"
Brachypotherium

derived the Perissodactyla from the phenacodontids. Some went so far as to derive *Hyracotherium* from a known species (e.g., Sloan, 1987, implicated *Desmatoclaenus mearae*). Sloan (1970) and Gingerich (1976, pp. 86-88) speculated on paleoclimatological grounds that perissodactyls came from unknown phenacodontids living in the late Paleocene of Central America. Many of these "derivationist" scenarios were based on comparison of shared primitive characters predicated by the search for ancestral forms. They also tended to look only at dental evidence, and to neglect the possibility of migration from other regions. This practice has been likened by McKenna *et al.* (1977) to "connect-the-dots" art, and in the case of the perissodactyls, it led to erroneous conclusions.

Two important contributions have led to new conclusions concerning the origin of the perissodactyls. The first is the description of *Radinskya* (McKenna *et al.*, this volume, Chapter 3). Although McKenna *et al.* ultimately assigned it to the phenacolophid arsinoitheres, they pointed out that *Radinskya* shares some derived similarities with the perissodactyls. There is also a strong resemblance to the most primitive tethythere, the Chinese Paleocene form *Minchenella*, which was also once considered a phenacolophid (Domning *et al.*, 1986). The Chinese Paleocene fauna strongly suggests that arsinoitheres, tethytheres, and perissodactyls are very closely related.

This strikingly confirms the second line of evidence derived from cladistic analysis of the ungulates (McKenna and Manning, 1977; Prothero *et al.*, 1988). Prothero *et al.* (1988) considered all ungulate taxa, looking only at derived characters, and especially at the non-dental characters neglected in the phylogenies of Sloan (1970, 1987) and Van Valen (1978). They concluded that perissodactyls, arsinoitheres, and tethytheres were much more closely related to each other than they were to phenacodonts. A number of shared derived characters

support this contention (Prothero *et al.*, 1988, Table 8.1). Prothero *et al.* (1988) placed tethytheres and perissodactyls as closest sister-taxa, with arsinoitheres as the next outgroup. The evidence of *Radinskya* may place arsinoitheres nearer to perissodactyls.

This conclusion has been tested by recent detailed work on the petrosals of arsinoitheres. According to N. Court (pers. commun.), *Arsinoitherium* shares the most derived similarities in its petrosal with elephants, and does not resemble other tethytheres, hyracoids, or mesaxonians as closely. If this work is substantiated, then arsinoitheres might become another group of tethytheres. In addition, Court's work clearly shows that perissodactyls (including hyraxes), arsinoitheres, and tethytheres are a monophyletic group.

Putting this all together, it is clear that a group consisting of tethytheres, arsinoitheres, and perissodactyls (including hyraxes) was diversifying in the late Paleocene of eastern Asia. Prothero *et al.* (1988) labeled this group of higher ungulates the "Pantomesaxonia" of Franz (1924), following M. Fischer (1986). Unfortunately, we have since learned that Franz's usage of Pantomesaxonia included a heterogeneous, paraphyletic assemblage of non-artiodactyl ungulates, and so it does not seem appropriate to resurrect it as a name for the higher ungulates (node 47 in Fig. 8.1, Prothero *et al.*, 1988). Thus, we create the Grandorder Altungulata (new taxon) to include the higher ungulates: tethytheres, arsinoitheres, hyraxes, and mesaxonians (this volume, Chapter 29).

Since tethytheres, arsinoitheres, and hyracoids (the latter representing the perissodactyls) became African endemics in the Eocene and Oligocene, it seems likely that Africa may enter into this as well. Africa was separated from Eurasia by a narrow Tethyan seaway during the Paleocene (Savage and Russell, 1983). The fossil evidence from the Paleocene and Eocene of Africa is very poor, and presently does little to test this hypothesis. A small late

Paleocene fauna from Morocco (Cappetta *et al.*, 1978) contains no ungulates. The next-youngest assemblages are middle Eocene and already contain hyracoids, sirenians, and *Moeritherium* (Sudre, 1979; Savage, 1969).

At the present, two hypotheses seem plausible. One postulates that the Altungulata diverged in the late Paleocene of Asia (possibly closer to Tethys, but including China), and that their three earliest offshoots (tethytheres, arsinoitheres, hyracoids) crossed the Tethys and became isolated in Africa during the Eocene. However, it is not unreasonable to suggest that there may have been more connection between Africa and Eurasia across the Tethys than previously supposed. The Paleocene fauna reported by Cappetta *et al.* (1978) is not particularly endemic, but has similarities to the Chinese Paleocene (Sloan, 1987). In this case, there may have been common faunal elements on both sides of the Tethys during the Paleocene, and the tethytheres, arsinoitheres, and hyracoids became endemic to Africa in the Eocene when Tethys became a more difficult barrier to cross.

All of this does not deny the fact that phenacodonts have many derived similarities with perissodactyls and other altungulates. Some of these characters were discussed by Prothero *et al.* (1988). However, the evidence clearly shows that the phenacodont-altungulate split predates the diversification of altungulates in the late Paleocene. This is not surprising, since phenacodonts were found all over Holarctica by the early Paleocene, and were a very diverse group throughout that epoch. It is clear, however, that no known phenacodont was "ancestral" to the Perissodactyla or any other altungulate group, contrary to Sloan (1987), Van Valen (1978), and Radinsky (1969).

Hyracoids as Perissodactyla

Another striking new development has been the renewed evidence for the perissodactyl affinities of hyracoids. As reviewed by M. Fischer (this volume, Chapter 4), the idea

goes back a long way, and Owen included the hyrax when he coined the term "Perissodactyla" in 1848. For various reasons, the idea was less popular in this century, and most authors treated hyracoids as a separate order with no known affinities, or suggested that they might be related to elephants and other "subungulates." As more studies have been done on mammalian phylogeny in the last ten years, however, the case for hyrax affinities has undergone much more scrutiny. Some authors (e.g., Novacek, 1982, 1986; Novacek and Wyss, 1986; McKenna, 1987; Novacek *et al.*, 1988) have found morphological data, and others have found molecular data (discussed by M. Fischer, this volume, Chapter 4), which suggest that hyraxes are "paenungulates" related to elephants. Others, however, have suggested that hyracoids belong with other perissodactyls (McKenna, 1975b; McKenna and Manning, 1977; M. Fischer, 1986; this volume, Chapter 4; Prothero *et al.*, 1988). Although there are some morphological characters that seem to support tethythere-hyracoid affinities (Novacek, 1982, 1986; Novacek and Wyss, 1986; Novacek *et al.*, 1988), M. Fischer (1986; this volume, Chapter 4) argues that many of them are invalid or of doubtful taxonomic importance.

Similarly, the molecular evidence is not particularly strong, since it is based on very few amino acid substitutions and only sampled for a few proteins (Prothero *et al.*, 1988). The molecular data matrices of Wyss *et al.* (1987) reveal just how weak this molecular evidence is. Only one shared derived amino acid substitution in the α-lens crystalline, one substitution in α-hemoglobin, and possibly two in β-hemoglobin could be used to support hyrax-proboscidean affinities in the most parsimonious arrangements of the data. There are no data yet for hyracoids or proboscideans in several other key proteins: pancreatic ribonucleases, cytochrome c, fibrinopeptides A and B. There are no hyrax data for myoglobin. Thus, the molecular evidence

has a long way to go before it provides a strong case for hyrax-proboscidean affinities.

By contrast, M. Fischer has detailed an impressive array of striking and unique shared derived characters that occur only in hyracoids and mesaxonians. The most bizarre of these is the inflated Eustachian sac, a feature with uncertain functional significance and therefore little reason to suspect as a parallelism. M. Fischer showed that the detailed morphology of the hooves, the shoulder musculature, the appendages to the iris in the eye, and the retention of the tuber maxillaris after tooth eruption are among the many unique synapomorphies found only in hyraxes and mesaxonians. In addition, there are many skeletal features that can also be seen in the fossils, such as the strong dental similarities, and the feet with reduced first and fifth metapodials and enlarged third metapodials. Many features of the basicranium and cranial circulation (Cifelli, 1982; Wible, 1986, 1987), including the extrabullar internal carotid artery, the loss of the promontory and stapedial sulci, and the large, bridged tympanohyal, support hyracoid-mesaxonian affinities.

Novacek et al. (1988) found that some of M. Fischer's characters (such as the reduced acromion) do not occur in Hyracotherium (but this does not establish that they are absent from other primitive mesaxonians as well). In the latest incarnation of their "paenungulate" hypothesis, Novacek et al. (1988) support the monophyly of hyraxes and tethytheres with five characters (Novacek et al., 1988, Table 3.1). Most of these characters are open to question, however. For example, as M. Fischer (this volume, Chapter 4) points out, amastoidy also occurs in pangolins, whales, and dermopterans, and in some suids and rhinoceroses. Novacek et al. (1988) stand by their use of the serial carpus character, questioning M. Fischer's contention that it developed secondarily in hyraxes due to rotatory midcarpal joint. Even if M. Fischer's interpretation is wrong,

however, the serial carpus is still not a very strong character. As Gregory (1910, p. 452) pointed out, it also occurs in some rodents and insectivores, Hyaenodon, and some phenacodonts and meniscotheres. Indeed, within a genus, it is not even consistent. Radinsky (1966a) pointed out that Phenacodus primaevus has a serial carpus, but that of P. copei is alternating. And the zonary placentation character, as M. Fischer points out (this volume, Chapter 4), also occurs in aardvarks and carnivores.

This leaves only the posterior extension of the jugal, and the bifurcate M. styloglossus, as characters supporting hyrax-tethythere affinities. By contrast, most of the characters supporting hyrax-mesaxonian monophyly discussed previously (especially the Eustachian sac, iris appendages, detailed hoof morphology, and extrabullar internal carotid artery) are not only unique among the Eutheria, but truly bizarre and hard to imagine evolving in parallel.

Certainly, the next important step in testing this hypothesis is to find whether the hyracoid-mesaxonian features are found in their extinct sister-taxa. At the present, however, we feel that there is a sufficiently strong case for hyracoid-mesaxonian affinities to include the hyraxes in the perissodactyls. Consequently, we gave hyraxes full coverage in this volume, and placed hyraxes in the formal classification as a suborder of the Perissodactyla (Prothero and Schoch, this volume, Chapter 29). After all, hyraxes were in Owen's (1848) original definition of the Perissodactyla.

Some zoologists may object to the demotion of the long-established Order Hyracoidea and the confusion generated by redefining the Perissodactyla. However, this is one place where we feel a phylogenetic classification will do much more good than retaining the separate orders, with the implication that nothing is known of their relationships. With the new definition of the Perissodactyla, it becomes necessary to use a different term for

the non-hyracoid perissodactyls, and Marsh's (1884) long-established term Mesaxonia becomes available. Simpson (1945, p. 136) used this term as a monotypic superorder synonymous with Perissodactyla. However, it is certainly appropriate to use Mesaxonia in the sense Marsh (1884) intended: for horses, rhinos, tapirs, and their extinct relatives, but not hyraxes.
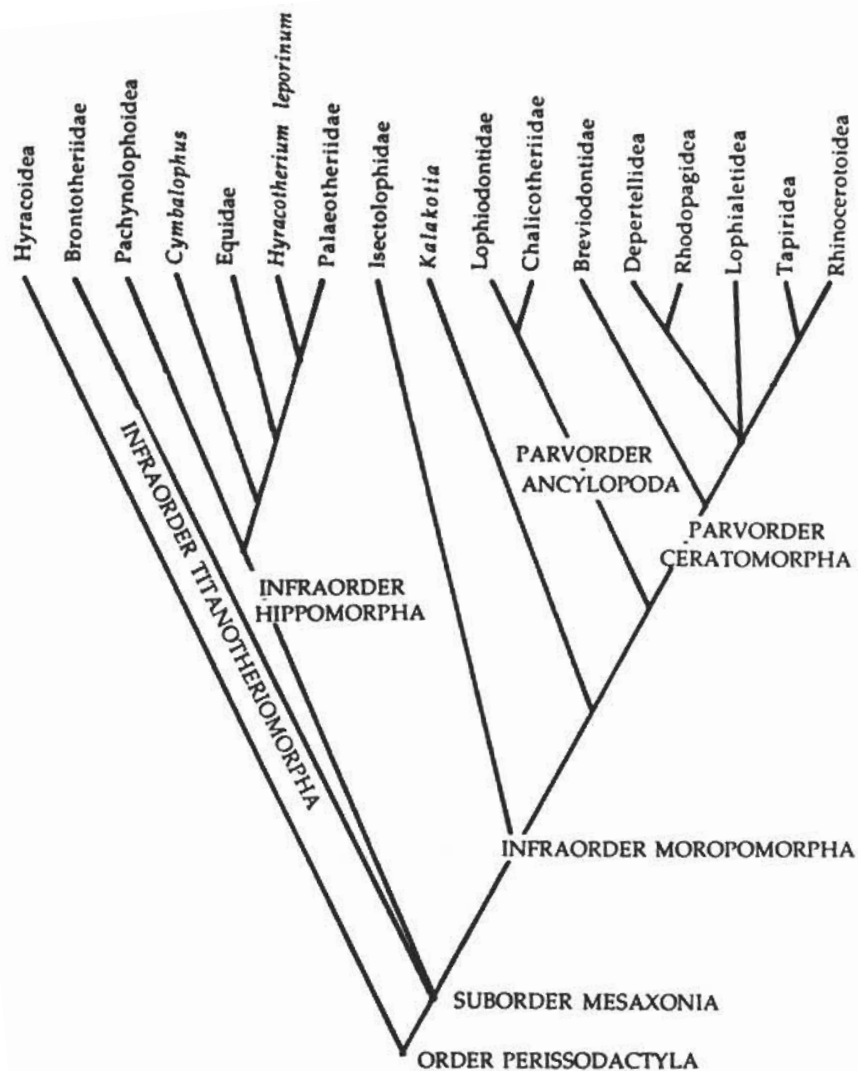
Hyraxes have a long and successful history that is only now beginning to be appreciated (Meyer, 1978; Rasmussen, this volume, Chapter 5). Most of their evolution took place in isolation in Africa, where they had no competition from other groups of ungulates. Consequently, they developed the ecological equivalents of pigs, bovids, anthracotheres, chalicotheres, tapirs, and some equids. They also ranged in body size from the housecat-sized Microhyrax to the rhino-sized Titanohyrax. This size range is already present in the earliest known hyraxes from the middle Eocene of Algeria. They reached the known peak of their success in the Oligocene of Africa, with as many as eight genera in the Fayum deposits of Egypt. In the early Miocene, artiodactyls and mesaxonians invaded from Eurasia and many hyraxes went extinct. By the late Miocene and Pliocene, a second radiation of large, hypsodont hyraxes spread widely over Eurasia, where they competed with chalicotheres and horses. Some developed eyes and nares on the top of the skull, possibly for an aquatic habitat, or enlarged tusk-like incisors. These hyraxes lasted until the Pleistocene in China, after which the group survived only in Africa. The Quaternary African forms include the huge Gigantohyrax, but the three living genera are all much smaller in body size. Even so, they are specialized in their ecological habits, even though they may be sympatric on the same rock outcropping or kopje. Procavia and Heterohyrax live mainly in areas of rocky scrub, whereas Dendrohyrax is arboreal. Because they live in rocky areas, they are not so severely threatened by human populations that have driven most other wild perissodactyls

to the brink of extinction.

Infraordinal relationships within the Mesaxonia

Schoch (this volume, Chapter 2) reviewed some of the early ideas about the relationships of the families of the Mesaxonia. The two most widely accepted subdivisions, Hippomorpha and Ceratomorpha of Wood (1937), have undergone many changes in meaning and acceptance. The Hippomorpha, originally consisting of horses, palaeotheres, titanotheres, and chalicotheres, has been discredited since there are no shared derived characters to support the monophyly of this grouping. The Ceratomorpha (tapiroids and rhinocerotoids), on the other hand, has been increasingly supported by shared derived characters as a good monophyletic group.

The most thorough and exhaustive effort to analyze all the shared derived characters of both the dentition and the rest of the skeleton in all the major infraordinal groups within the Mesaxonia is presented by Hooker (this volume, Chapter 6). He found three major divisions of the Mesaxonia: hippomorphs (horses, palaeotheres, and pachynolophids), "tapiromorphs" (= moropomorphs: isectolophids, chalicotheres, lophiodonts, and ceratomorphs), and titanotheres. Two rather weak characters appeared to unite the titanotheres and equoids, but Hooker chose not to use them, nor to create a group for titanotheres plus equoids. Thus, all three groups are here treated as infraorders in an unresolved trichotomy within the Suborder Mesaxonia. The Ceratomorpha are clearly supported as a monophyletic group in Hooker's analysis, but are a sister-group to the ancylopods (chalicotheres plus lophiodonts) within a larger group, the Moropomorpha (= Tapiromorpha sensu Hooker, this volume, Chapter 6). The Hippomorpha cannot be used in the old sense to include chalicotheres and titanotheres, but Hooker revised its contents to include pachynolophids, palaeotheres, and equids. In general, we find his

Hyracoidea
Brontotheriidae
Pachynolophoidea
Cymbalophus
Equidae
Hyracotherium leporinum
Palaeotheriidae
Isectolophidae
Kalakotia
Lophiodontidae
Chalicotheriidae
Breviodontidae
Depertellidea
Rhodopagidea
Lophialetidea
Tapiridea
Rhinocerotoidea

INFRAORDER TITANOTHERIOMORPHA

INFRAORDER HIPPOMORPHA

PARVORDER ANCYLOPODA

PARVORDER CERATOMORPHA

INFRAORDER MOROPOMORPHA

SUBORDER MESAXONIA

ORDER PERISSODACTYLA

28.2. Phylogenetic relationships of the major groups of perissodactyls. For discussion character states at the nodes, see text and also Hooker (this volume, Chapter 6).

conclusions well supported and convincing, and so have adopted his scheme in our classification. Our primary reservation is that there are a number of unique postcranial characters (cited by Borissiak, 1945, 1946) that seem to unite chalicotheres and titanotheres. The most striking of these is the fusion of the centrale to the scaphoid in the carpus. This character would have to be a parallelism in Hooker's scheme.

Infraorder Hippomorpha

The first infraorder covered in this book includes the diverse and successful equids, plus their sister taxa, the pachynolophids and palaeotheres. According to Hooker, they are united by the presence of a P^3 paraconule and by the proximity of the optic foramen to the posteroventral orbital foramina (MacFadden, 1976, Fig. 6). The pachynolophids (including "*Hyracotherium*" sp. from Rians, France) split off first, leaving the main group of hippomorphs, the Equoidea (i.e., equids and palaeotheriids; Hooker, this volume, Fig. 6.5; see also Fig. 29.2). The Equoidea (except for *Cymbalophus*) are united by several synapomorphies: a notched preparaconule crista and preparacrista junction on the upper molars and notched protocristid on the lower molars; and foramen ovale and medial lacerate foramen separated by a narrow bony bridge (MacFadden, 1976, Fig. 5). All equoids (including *Cymbalophus*) have broad, less tapered P_3 trigonids. The foramen ovale bridge is not known in *Cymbalophus*, so this character might apply to the entire Equoidea.

One of the striking results of Hooker's analysis is that the primitive hippomorph *Hyracotherium* (as presently constituted) appears to be a wastebasket taxon for all primitive pachynolophids, equids, and palaeotheres. The last revision of this genus (Kitts, 1956) did not consider the stratigraphic separation of the samples and is now thought to have lumped too many species together (Gingerich, 1980; Hooker, 1980). Hooker concludes that some species should be placed in the Pachynolophidae ("*Hyracotherium*" sp. from Rians), some as sister-taxon to the Palaeotheriidae (*Hyracotherium leporinum*, the type species), and some as independent genera ("*H.*" *cuniculum*, now *Cymbalophus*; "*H.*" *tapirinum*, which could be resurrected as *Systemodon* Cope, 1881; "*H.*" *vulpiceps*, which could be resurrected as *Pliolophus* Owen, 1858). Franzen (this volume, Chapter 7), on the other hand, views the character polarities differently. As a consequence, he restricts the content of the Palaeotheriidae considerably, and places pachynolophids, *Propalaeotherium*, and *Lophiotherium* in the equids.

It is unclear what generic name should be applied to the most primitive equids, such as "*Hyracotherium*" *vasacciense* and synonymous North American species. According to Bakker, Cooke, and Schain (unpublished manuscript, accepted but never resubmitted to this volume), the type species of *Eohippus*, *E. validus*, is related to chalicotheres, and is not a horse. Cope (1872a) originally named the common North American horse *Lophiotherium vasacciense*, but that genus refers to a European palaeothere. This animal was subsequently referred to the primate genus *Notharctus* (Cope, 1872b), and then to *Orotherium*, a Bridgerian genus that may be a synonym of *Orohippus* (Cope, 1873). The next available generic name that was applied to a Wasatchian equid is *Protorohippus* Wortman (1896), based on *Hyracotherium venticolum* Cope, 1881, from the Lost Cabin Member of the Wind River Formation (late Wasatchian). To our knowledge, this may be the first valid generic name for early Eocene equids from North America. Since the differences between these species are very slight and they share much symplesiomorphic similarity, we would not be surprised if there is resistance to breaking up the *Hyracotherium* wastebasket along cladistic lines. If the dental distinctions made by Hooker (this volume, Chapter 6) are valid, however, then we must conclude that *Hyracotherium* is more closely related to the palaeotheres,

and that the North American forms must be placed in a different genus. We leave it to the next reviser of Eocene horses to decide whether the first true horse should be called *Hyracotherium, Systemodon, Orotherium, Protorohippus*, or some other genus.

Once the hippomorphs began to radiate, they were widespread all over Holarctica in the early Eocene. *"Hyracotherium"* is among the commonest taxa in early Eocene deposits of North America and Europe. *"Hyracotherium" gabuniai* Dashzeveg, 1979 (regarded by Hooker, 1984, as a ceratomorph) and *Propachynolophus* are reported from the early Eocene of Mongolia and China. The entire early Eocene fauna was very cosmopolitan because of several Holarctic dispersal routes along Beringia, the Greenland-Barents Shelf, and via the Wyville Thompson Ridge through Greenland, Iceland, the Faeroes, and Scotland (McKenna, 1975a; 1983a, b). By the middle Eocene, however, there was increasing endemism. Europe began to be isolated, and its perissodactyl fauna came to be dominated by pachyno-lophids and palaeotheres (along with lophiodonts). These were the only significant perissodactyls in Europe until the Grande Coupure in the Oligocene brought in rhinos and other ungulate competitors. The later Eocene of Europe was the heyday for the non-equid hippomorphs, as described by Franzen (this volume, Chapter 7). Palaeotheres got to be quite large, and some *Palaeotherium* were very similar in size and morphology to the modern tapir, complete with retracted nasals (indicating a short proboscis) and selenolophodont molars. Specimens of *Propalaeotherium* from Messel, Germany, preserve soft anatomy and stomach contents indicating that palaeotheres browsed on leaves and fruits (Sturm, 1978). Although the lophiodonts were extinct by the middle Eocene, and pachynolophids and palaeotheres were severely decimated by the Eocene/Oligocene event, some taxa (*Palaeotherium, Pseudopalaeotherium, Plagiolo-*

phus) managed to persist into the early Oligocene. By the mid-Oligocene, however, all the non-equid hippomorphs were extinct.

Horse evolution

While Europe was the domain of endemic palaeotheres, pachynolophids, and lophiodonts during the middle and late Eocene, horses were found in the rest of Holarctica. Dashzeveg (1979) reported a horse he called *Gobihippus menneri* from the late Eocene of Mongolia, and Zdansky (1930) reported *Propalaeotherium sinense* from the middle Eocene of China. Most of the perissodactyls in the middle and late Eocene of Asia were not equoids, however, but tapiroids, amynodonts, hyracodonts, and chalicotheres. In North America, horses formed a fairly continuous lineage from *"Hyracotherium"* (= ?*Protorohippus*) to *Orohippus* (and the doubtfully distinct *Haplohippus*) to *Epihippus* in the middle and late Eocene. By the Oligocene, however, horses became much more diverse. Contrary to the popular myth of a single lineage of horses passing gradually through *Mesohippus* and *Miohippus*, Prothero and Shubin (this volume, Chapter 10) found that both of these horses were highly speciose, with many sympatric species spanning millions of years. Nor do the two genera intergrade. *Miohippus* is a distinctly larger horse with numerous distinguishing characters, and overlaps *Mesohippus* in temporal range by almost five million years.

By the late Oligocene, *Miohippus* split into two well-established groups, the persistently primitive, browsing anchitheriine horses, and the higher-crowned, more cursorial equines. There has been little recent work on the anchitheriines, yet they were a very successful group. They persisted in small numbers in North America, often living sympatrically with many species of equines. Since they were browsing horses, they subdivided the environment with the more grazing equines. Anchitheriines got to be quite large. One

species of *Hypohippus* was as big as a modern horse, and almost twice the size of its Miocene contemporaries. Contrary to popular notions that anchitheriines were slowly evolving, MacFadden (1986) has shown that the groups increased the occlusal surface area of their teeth, and corresponding body size, quite rapidly. Anchitheriines were also very successful at spreading around Holarctica. *Anchitherium* was the first post-Eocene horse to leave North America, occurring widely in the early Miocene of Europe and Asia. *Hypohippus* also traveled across the Bering Land Bridge to China, where it gave rise to the closely related *Sinohippus*. The small horse *Archaeohippus*, long thought to be an anchitheriine, is now considered to be an equine (Evander, this volume, Chapter 8; Hulbert, this volume, Chapter 11).

The beginning of the equine lineage through *Kalobatippus, Parahippus*, and *"Merychippus,"* is becoming better known (Evander, this volume, Chapter 8). One of the biggest problems is another taxonomic wastebasket, the mid-Miocene horse *"Merychippus."* According to Evander (1986), the type species of the genus, *M. insignis*, is based on two deciduous premolars and only a few specimens can be referred to this species with any confidence. Most of the Barstovian horses referred to this genus may have different generic allocations. This is even more critical when some species of *"Merychippus"* are sister taxa to various hipparionines, and others to some equinines (Hulbert, this volume, Fig. 11.1). According to Hulbert, for example, *"Merychippus" carrizoensis* and *"M." stylodontus* are sister-taxa of, and could be referred to, *Pliohippus, "M." coloradense* to *Pseudhipparion* or *Neohipparion*, and *"M." goorisi* to *Cormohipparion* or *Nannippus*.

Whatever nomenclature is finally adopted for these horses, it is clear that there was an enormous radiation of horses by the mid-Miocene. MacFadden (1985, 1986, 1988) reviewed much of the recent literature on evolutionary trends in Miocene horses, so there is no need to do so again

here. The biggest single area of controversy is over the systematics of hipparionine horses, which were extremely diverse and migrated repeatedly to the Old World during the Miocene (Woodburne, this volume, Chapter 12; Alberdi, this volume, Chapter 13). The primary argument concerns the use of morphological characters in hipparionine systematics. Prior to the work of Skinner, MacFadden, Woodburne, and Bernor, hipparionine systematics emphasized dental characters. Since there is a tremendous amount of parallelism in dental characters, and there was much oversplitting based on trivial differences in teeth, hipparionine systematics were a mess. The work of the scientists named above (summarized by Woodburne, this volume, Chapter 12) has used additional characters, particularly the facial fossa, as evidence of hipparionine relationships.

The controversy is far from settled. Many European workers are skeptical of the facial fossa as a character (discussed by Alberdi, this volume, Chapter 13), although many (but not all) North American workers use it. MacFadden (1980, 1984) demonstrated that the facial fossa was consistent within several quarry samples of horses (for example, *Hipparion tehonense* from Frick MacAdams Quarry, Clarendonian of Texas, or *Cormohipparion occidentale* from Hans Johnson Quarry, Clarendonian of Nebraska). Nevertheless, the controversy continues (e.g., Forstén, 1982, and reply by MacFadden and Skinner, 1982; Eisenmann *et al.*, 1987, and reply by MacFadden, 1987). MacFadden (this volume, Chapter 9) discusses the issue of character variability, and shows that equids (fossil and living) are no more variable than any other group of mammals. Thus, he supports his argument that the facial fossa is not overly variable within a single population. In our opinion, any analysis that is based on more characters should be preferred to those based on a single suite of characters, unless those additional characters can clearly be shown to be due to individual variation within populations.

Regardless of the taxonomy one adopts for hipparionines, it has become clear that there were several migrations of hipparionine horses to the Old World (Woodburne, this volume, Chapter 12). According to Woodburne, there were at least two different migration events. The first took place about 12 Ma (= million years ago) with the appearance of *Hippotherium primigenium* in the Vallesian of western Europe (derived from *Cormohipparion* in North America). It was followed by the migration of *Hipparion sensu stricto* (derived from North American *Hipparion sensu stricto*) about 9.5 Ma. This clearly demolishes the old notion that a single migration of hipparions from North America marked the beginning of the Vallesian (once thought to be the Mio-Pliocene boundary, but now considered late middle Miocene) all over the Old World (Berggren and Van Couvering, 1978). Surprisingly, references to the "*Hipparion* datum" are still widely found in the literature.

Horse diversity reached an all-time peak worldwide in the late Miocene (Clarendonian-Vallesian). By the beginning of the Pliocene, all of the anchitheriines, most of the hipparionines (except for *Calippus* in North America and several Old World hipparions), and many of the archaic equinines in North America (*Protohippus, Calippus, Astrohippus*, and *Pliohippus*) were extinct. The main lineage of Pliocene to Recent horse evolution took place in the Tribe Equini (the equinines), beginning with *Dinohippus*. One group, the hippidions (*Onohippidium* and *Hippidion*), had a highly retracted narial incision, and presumably some sort of snout. They evolved in South America after the late Pliocene reconnection of the Panamanian land bridge.

Another late Pliocene immigrant to South America was the living genus *Equus*, which spread widely all over the world after its origin in North America in the early Pliocene. *Equus* also spread to the Old World around 2.6 Ma (Lindsay *et al.*, 1980), whereupon it became common in al-

most all faunas. It entered Africa in the late Pliocene, where the zebras became diversified (Churcher and Richardson, 1978). *Equus* also spread widely over Asia in the Pleistocene. Because *Equus* is very abundantly represented all over the world in the Pleistocene, it has been subject to the same confusion in taxonomy as the hipparionines. This is due to oversplitting of taxa based on inadequate samples, usually isolated teeth. The conundrum of *Equus* systematics has not yet been completely resolved, but Winans (this volume, Chapter 14) attempts to resolve some of the problems of North American *Equus* by using multivariate morphometrics. Of the 59 named species, she reduces the complexity to just five distinct subgeneric groups, even fewer than recognized by Kurtén and Anderson (1980).

In terms of numbers of individuals, number of species, or ability to spread geographically, *Equus* is undoubtedly the most successful perissodactyl that ever lived. Ironically, it became extinct in its homeland, North America, during the megafaunal extinctions at the beginning of the Holocene. It also became extinct in South America, and greatly reduced in Eurasia. But as domesticated descendants of the Asian *E. przewalskii*, it has been reintroduced to these areas, as well as to places like Australia that have never had perissodactyls. Thanks to domestication, *Equus* is the only living perissodactyl that has increased in numbers and range, rather than having been diminished by the growth of human populations.

Infraorder Moropomorpha

The next great infraorder of mesaxonians is the Moropomorpha. This group includes not only the Ceratomorpha (tapiroids and rhinocerotoids), but also the ancylopods (chalicotheres and lophiodonts), as recognized by Hooker (1984; this volume, Chapter 6). Hooker defines the Moropomorpha (= Tapiromorpha *sensu* Hooker) by the loss of the lower molar lingual postcristid branch, and the development of the lower

molar hypolophid and upper molar metaloph. Both of these characters represent a precocious development of metaloph-hypolophid bilophodonty, a feature that is characteristic of nearly all moropomorphs.

Moropomorph systematics has long been in a very confused state, because of the tremendous amount of shared primitive similarity of most forms (as reviewed by Schoch, this volume, Chapters 2, 15). Much of this was cleared up by the monographs of Radinsky (1963, 1965), but his work still included some paraphyletic groups. In particular, the Family Helaletidae was long used as a wastebasket family to include all the non-isectolophid, non-tapirid "tapiroids." As is apparent from the phylogenies of Hooker (this volume, Chapter 6) and Schoch (this volume, Chapter 15), the various "tapiroids" are not a monophyletic group. Isectolophids are the most primitive sister-taxon of all other moropomorphs, but most of the "tapiroids" (*Breviodon*, deperetellids, rhodopagids, lophialetids *sensu stricto*, *Heptodon*) and Tapiroidea *sensu stricto* are united with the rhinocerotoids as the Ceratomorpha.

The Moropomorpha began with the early Eocene form *Homogalax*, which was very abundant in North American faunas, and also found in Asia (Chow and Li, 1965). By the late early Eocene, moropomorphs had begun to diversify into a variety of taxa, including the North American "tapiroids" *Heptodon, Helalates, Selenaletes, Plesiocolopirus, Desmatotherium, Dilophodon*, and *Isectolophus*, the ancylopod *Paleomoropus*, and the rhinocerotoid *Hyrachyus*. In the middle Eocene of Europe, there was a similar fauna which included the ancylopods *Lophiodon, Paralophiodon*, and *Lophiaspis*, the rhinocerotoids *Hyrachyus* and *Chasmotherium*, but no "tapiroids." Asian Middle Eocene faunas, on the other hand, contained few lophiodonts or equoids, but a great abundance of "tapiroids" (*Colodon, Helaletes, Deperetella, Teleolophus, Rhodopagus, Pataecops, Eoletes, Lophialetes, Schlosseria, Breviodon*), chalicotheres (*Grangeria*), and a

diversity of rhinocerotoids, including *Hyrachyus*, amynodonts (*Lushiamynodon, Caenolophus*) and hyracodonts (*Triplopus, Urtinotherium, Forstercooperia*). The Moropomorpha reached their maximum diversity in the later Eocene, especially in Asia and North America. By the early Oligocene, their diversity had declined greatly. Of the "tapiroids," only *Colodon* and *Protapirus* survived in North America, and *Colodon* and *Teleolophus* in Asia.

Each of these groups of moropomorphs developed different specializations. Many of the "tapiroid" families developed more and more strongly bilophodont molars, presumably for browsing. The true tapiroids, in addition, began to develop a deeply incised narial notch, presumably for support of a prehensile lip or proboscis. This tendency was carried to an extreme in the Family Tapiridae, which retract the nasals nearly to the top of the head, and greatly reduce the nasal bones. Tapirs changed very little after the Oligocene, remaining at a low diversity throughout the Tertiary of North America, Europe, and Asia. In the late Pliocene, they migrated across the Panamanian Isthmus along with many other North American forms, and became established in South America. They even reached the size of a rhino with the giant form *Megatapirus* from the Pleistocene of China. In the late Pleistocene, tapirs went extinct over most of their range except for one species in southeast Asia (the Malayan tapir, *Tapirus indicus*) and three species in South America. All four species are greatly endangered, primarily due to the destruction of their tropical rain forest habitat.

The Ancylopoda

Even more surprising is the conclusion that chalicotheres and lophiodonts were also primitive moropomorphs, unrelated to the palaeotheres or other equoids. Hooker (this volume, Chapter 6) modified Cope's (1889) taxon Ancylopoda for this group (originally constructed for the chalicotheres alone). According to Hooker, the

Ancylopoda is united by the shared possession of labially expanded M^3 parastyles, distal recurving of the upper molar protocone and hypocone, and lower molar protoconid and hypoconid. They also share many derived characters in the feet, first noticed by Osborn (1913).

The chalicotheres and lophiodonts typically occupied "no man's land" in perissodactyl classification. As reviewed by Schoch (this volume, Chapter 2), they were often allied with the hippomorphs (e.g., Simpson, 1945), with the titanotheres (e.g., Borissiak, 1945, 1946), or placed in their own suborder with no implication of relationships (e.g., Radinsky, 1964). Our classification (this volume, Chapter 29) reflects Hooker's conclusion that they are the sister-taxon of the Ceratomorpha, which includes most of the "tapiroids" (except isectolophids, *Kalakotia*, and *Aulaxolophus*) and rhinocerotoids. This is supported by derived characters, such as the distolingual position of the upper premolar metacone relative to the paracone, and the slight convergence of the upper molar metacone and hypocone, causing labial bending of the pre- and postmetacristae.

The close affinity of the chalicotheres and lophiodonts might also explain why there have been so many controversial forms that have been switched from one group to another. For example, *Paleomoropus* and *Lophiaspis* were assigned to the chalicotheres by Radinsky (1964), but were placed in the lophiodonts by K.-H. Fischer (1964, 1977). Similarly, *Toxotherium* and *Schizotheriodes* were placed in the tapiroids (Radinsky, 1964; Schiebout, 1977), amynodonts (Emry, 1979), or hyracodonts (Wilson and Schiebout, 1984), but Prothero *et al.* (1986) gave evidence to suggest that they, too, were lophiodonts. For the present, we place *Paleomoropus*, *Lophiaspis*, *Toxotherium*, and *Schizotheriodes* with the lophiodonts (Schoch, this volume, Chapter 15).

Even though they were more closely related to chalicotheres, lophiodonts converged on tapirids in many features. They reached their acme during the middle Eocene in Europe, where they were endemic forms, along with palaeotheres and pachynolophids. Some species of *Lophiodon* were rhino-sized, with huge bilophodont teeth and a tapir-like proboscis. Lophiodonts were reviewed by K.-H. Fischer (1964, 1977), although there has been little recent work on the group. Unlike the palaeotheres, pachynolophids, and "tapiroids," lophiodonts were extinct by the late Eocene, when the climate had begun to change worldwide.

Chalicotheres, on the other hand, had a unique ecological niche. They developed hook-like claws and long forelimbs, presumably for pulling down branches and browsing (Coombs, 1982, 1983). *Chalicotherium* itself had proportions much like a gorilla, and knuckle-walked with its claws held inward, like a ground sloth (Zapfe, 1979; see Fig. 24.2). Their first *bona fide* representatives are the "Eomoropidae," a paraphyletic group (discussed by Lucas and Schoch, this volume, Chapter 23) which is found in the late Eocene of both China and western North America. In the Oligocene, only *Schizotherium* is known, and it is restricted to Eurasia. Chalicotheres diversified and spread out in the early Miocene (Coombs, 1982; this volume, Chapter 24). They were a predominantly Eurasian group, although they were never particularly common, probably because they lived in a restricted forest habitat. Two subfamilies are recognized: the Schizotheriinae and the Chalicotheriinae. The Schizotheriinae had more hypsodont, elongated molars, and a special claw-retraction mechanism, but were not as gorilla-like in body proportions as the Chalicotheriinae. The chalico-theriine genus *Chalicotherium* spread to Africa in the early Miocene, and *Nestoritherium* was the last surviving member of the family, persisting until the Pleistocene in China. The schizotheriines spread to North America in the early Miocene (Hemingfordian), where well-known forms such as *Moropus* and the bizarre dome-skulled *Tylocephalonyx* oc-

curred (Coombs, 1978, 1979). By the Pliocene, schizotheriines were extinct in both North America and Eurasia, but *Ancylotherium* persisted in the Plio-Pleistocene of Africa. Our early hominid ancestors must have known the last of the chalicotheres in both Africa and China, but sadly, chalicotheres did not survive to join the horses, hyraxes, rhinos, and tapirs as members of the living fauna.

The Rhinocerotoidea

The largest and most ecologically diverse group of perissodactyls is the Rhinocerotoidea. Rhinocerotoids occupied an enormous range of ecological niches, from gigantic tree-top browsers (the indricotheres) to small, dog-sized running forms (the hyracodontines), to hippo-like river-dwelling grazers (some amynodonts, aceratherines, and teleoceratines), to forms with tapir-like proboscises (cadurcodontines). Although we associate rhinos with horns, most fossil rhinos were hornless. Indeed, the first horned rhinos had paired horns near the tip of their nasals, a feature that evolved twice independently. Surprisingly, there has been little detailed work on fossil rhinoceroses in over fifty years. Recently, however, there has been renewed interest in the group. Most of the recent research is reviewed by Prothero, Manning, and Hanson (1986) and Prothero, Guérin, and Manning (this volume, Chapter 16), so it is unnecessary to go over the details here.

The most primitive rhinocerotoid was *Hyrachyus*, which was widespread over Eurasia and North America in the middle Eocene. Although Radinsky (1966b, 1967, 1969) placed this taxon in the Tapiroidea based on shared primitive characters (see Hopson, this volume, Chapter 1), most authors have since placed it in the Rhinocerotoidea (Prothero *et al.*, this volume, Chapter 16). By the late middle Eocene, the three major families of rhinocerotoids had begun to diversify in North America and Asia. However, Europe was apparently cut off from Asia by the Turgai Straits in the late Eocene, allowing an endemic fauna of palaeotheres, lophiodonts, and pachynolophids (discussed earlier) to evolve. When immigrant rhinos and other ungulates entered Europe in the early Oligocene, these endemic perissodactyls went into decline.

The first family of rhinocerotoids was the Amynodontidae, reviewed by Wall (this volume, Chapter 17). Amynodonts were particularly common in late Eocene faunas of Asia, and slightly less common in North America. Beginning with primitive, long-faced forms like *Rostriamynodon* (Wall and Manning, 1986), they diverged into two subfamilies: the tapir-like cadurcodontines, which had a well-developed proboscis, and the more hippo-like, aquatic metamynodontines. Both subfamilies were reduced in diversity by the early Oligocene. In North America, only the hippo-like form *Metamynodon* survived to the mid-Oligocene, when it went extinct. In Asia, however, amynodonts persisted until the middle Miocene of Pakistan, where *Cadurcotherium* was the last survivor of this once diverse group.

The Family Hyracodontidae had a similar history of diversification and geographic dispersal. All hyracodontids, regardless of size, can be recognized by their long, slender metapodials. Beginning in the late Eocene with *Triplopus*, they were common in the middle and late Eocene of both Asia and North America. Three subfamilies are recognized. The hyracodontines were all small, cursorial forms, known primarily from North America. By the Oligocene, only *Hyracodon* was common in North America. It persisted until the end of the Whitneyan, the last of its group to go extinct. After the Grande Coupure, hyracodonts also migrated into Europe, where the small, tusked allaceropines were found (Heissig, this volume, Chapter 18).

The most spectacular hyracodonts were the indricotheres, which reached gigantic sizes. They are reviewed by Lucas and Sobus (this volume, Chapter 19). Heissig (this volume, Chapter 21) argued that the

indricotheres are rhinocerotids, because one specimen of *Forstercooperia* has a primitive tetradactyl manus, rather than the derived tridactyl condition. However, the hyracodontid affinities of indricotheres are clearly supported by their metapodial elongation, which persists even in gigantic forms that by all rights should have become graviportal. In addition, the enlarged incisors of indricotheres do not resemble the chisel-tusk incisor combination seen in rhinocerotids. Beginning with the small form, *Forstercooperia*, from the late Eocene of both Asia and North America (Lucas *et al.*, 1981), indricotheres became the largest land mammals to have ever lived, and were restricted to the Oligocene of Asia. The largest of them all was *Paraceratherium* (= *Baluchitherium*, *Indricotherium*, according to Lucas and Sobus, this volume, Chapter 19), which reached 18 feet (6 meters) at the shoulder, and could browse on the tops of trees. By the Miocene, indricotheres had vanished from Asia, the last of their family.

The most successful rhinocerotoids, however, were the true rhinoceroses (Family Rhinocerotidae), which include all five living species. According to Radinsky (1966b), the family is restricted to those forms with a chisel-like I^1 and a tusk-like I_2. The oldest known member of the family is *Telataceras* from the middle Eocene (Duchesnean) of Oregon, described by Hanson (this volume, Chapter 20). Hanson also refers specimens from the middle Eocene of California and Asia to this genus. By the early Oligocene, rhinocerotids had spread over Holarctica and begun to diversify, replacing groups that had been dominant in the middle Eocene, such as amynodonts, hyracodonts, palaeotheres, lophiodonts, and pachynolophids. As discussed by Heissig (this volume, Chapter 21), they included a variety of forms in Europe, such as *Ronzotherium* and *Epiaceratherium*. In North America, there were several genera, but the most successful was the *Subhyracodon-Diceratherium* lineage, which persisted for almost 20

million years.

In the late Oligocene of Europe, a number of distinct subfamilies and tribes of rhinocerotids began to diverge. There were the prehensile-lipped aceratheriines, the hippo-like teleoceratines, the paired-horned menoceratines, and the primitive members of the dicerorhinine lineage, which includes the living Sumatran rhino. In the early Miocene (Hemingfordian-Orleanian), several of these groups migrated to Asia and North America. Teleoceratines, aceratheriines, and dicerorhinines all became established in Asia in the early Miocene, where they were common elements of the fauna. North America first saw migration of the menoceratines from Europe in the latest Arikareean, followed by immigration of the aceratheriines and teleoceratines in the late Hemingfordian. The browsing aceratheriines *Aphelops* and *Peraceras*, and the grazing teleoceratine *Teleoceras* became important elements of nearly every North American Miocene fauna. Africa acquired teleoceratines, aceratheriines, and dicerorhinines in the mid-Miocene, and the endemic dicerotines (including the living African black and white rhinos) developed on that continent.

At the end of the Miocene, rhinos, like horses and many other land mammal groups, suffered greatly from the Messinian crisis and the terminal Miocene extinctions. With the exception of one Blancan rhino specimen from Beck Ranch in Texas, all of the aceratheriines and nearly all of the teleoceratines went extinct, thus wiping out the rhino fauna of North America. In Eurasia, only the rhinocerotines and dicerorhinines survived. In Africa, only the dicerotines and the last of the teleoceratines persisted until the Pliocene. The gap left by this extinction event was filled by a renewed radiation of Plio-Pleistocene rhinos, mostly from the dicerorhinines. These were widespread across Eurasia, culminating in the woolly rhinoceros, *Coelodonta*. Also characteristic of the Asian Pleistocene were the elephantine elasmotheres, which had a huge, single horn on their forehead.

They originated in China, but were restricted to Siberia and the Volga Basin and Poland in the Pleistocene. By the terminal Pleistocene extinction, most of these Eurasian rhinos became extinct.

Today, only relicts of this originally worldwide distribution of rhinos survive. Southeast Asia has two rhinocerotinines, the Indian rhino (*Rhinoceros unicornis*) and the Javan rhino (*R. sondaicus*). The last member of the long-lived dicerorhinine lineage survives in the Sumatran rhino, *Dicerorhinus sumatrensis*. In Africa, two dicerotines remain: the white rhino, *Ceratotherium simum*, and the black rhino, *Diceros bicornis*. All five of these species are being hunted to extinction by poachers, since their horns are extremely valuable (Penny, 1988). Ironically, although rhinos have long been the most diverse group of perissodactyls, they are now so threatened by humans that they may not outlast the less diverse horses, hyraxes, or tapirs.

Infraorder Titanotheriomorpha
The third and final major infraordinal group of mesaxonians includes the brontotheres (= titanotheres) and their primitive sister-taxon, *Lambdotherium*. Hooker (this volume, Chapter 6) created a new suborder, Titanotheriomorpha, for this group, although we have lowered it to infraordinal rank to coordinate it with the rest of the classification (Prothero and Schoch, this volume, Chapter 29). Hooker defines this group on the basis of the following shared derived characters: an overhanging occiput, the loss of the P^4 metaconule, the convergence of the upper molar paracone-protocone and metacone-hypocone, the flexion of the centrocrista, a centrocristal mesostyle, the notching of the preparaconule crista-paracrista and lower protocristid, and the lingual migration of the upper metaconule and the lower preultimate molar hypoconulid.

The affinities of titanotheres have long been controversial, although typically they were clustered with the equoids in the Hippomorpha, or with the chalicotheres

(see Schoch, this volume, Chapter 2). As discussed above, Hooker found two rather weak derived characters that appeared to support a relationship between titanotheres and hippomorphs (loss of I_3 distal cusp, upper molar cingular metastyle), but chose not to use this evidence to unite these two groups. Thus, we follow Hooker in classifying mesaxonians in an unresolved trichotomy of three infraorders: Hippomorpha, Moropomorpha, and Titanotheriomorpha (Fig. 28.2).

Of all the perissodactyl groups neglected over the last few decades, titanotheres have been the least studied. Although a few isolated papers have been published, there had been no significant reviews of the group since Osborn's 1929 monograph. Perhaps because this work was so intimidating in its size and the magnitude of its errors, and probably also because titanotheres are big and difficult to work with, it took sixty years before another scientist would critically evaluate Osborn's monograph *in toto*. Fortunately, we are able to include a revision of North American brontotheres by Mader (this volume, Chapter 25), the first and only significant review of the entire group since 1929.

Titanotheres apparently began with *Lambdotherium*, a fairly common taxon in the late early Eocene (late Wasatchian) of North America. There is some question as to whether *Lambdotherium* is really a titanothere. In an unpublished study, Wallace (1980) argued that *Lambdotherium* was really a palaeothere, but Hooker (this volume, Chapter 6) and Schoch and Lucas (1985) suggested that it had derived characters of the brontotheres. Whatever its affinities, Mader (this volume, Chapter 25) has shown that the rest of the Brontotheriidae, beginning with *Eotitanops* and *Palaeosyops*, are a good monophyletic group. *Eotitanops* is also found in the late Wasatchian, and *Palaeosyops* replaces it in the early middle Eocene (Bridgerian). Brontotheres then undergo a big radiation, diverging into several genera and spreading back and forth between North America and

Eurasia. By the late middle Eocene, they had become the largest land mammals in Eurasia and North America, sharing that niche with the uintatheres and amynodonts.

Osborn (1929) greatly oversplit the group, creating dozens of invalid species and genera, and dubious subfamilies he called "phyla." Mader (this volume, Chapter 25) reduces that mess to only seventeen valid North American genera, most from the Uintan (late middle Eocene). Lucas and Schoch (this volume, Chapter 27) show that a single quarry sample of *Duchesneodus* provides a good index of intrapopulation variability, which will be essential in future systematic studies of titanotheres. Unfortunately, there has been no similar revision of the Asian titanotheres, which were greatly oversplit by Granger and Gregory (1943) and by recent Chinese workers. We have not attempted to synonymize these invalid Asian genera in the classification adopted in this volume (Chapter 29), but the diversity of the group must surely be exaggerated. Whatever taxonomy is adopted, however, titanothere diversity was considerably reduced by the late Eocene (Chadronian). At that point, titanotheres reached their maximum size, and most had well-developed, paired blunt horns on their noses. Much work remains to be done on Chadronian titanotheres, since the best collections are still in their field wrappings in the Frick Collection of the American Museum of Natural History (New York). In Asia, the bizarre embolotheres, with their single blunt horn, were the culmination of the group in the ?Oligocene. A specimen of *Brachydiastematherium* is known from the Oligocene of Romania, but generally titanotheres are not found in European Eocene or Oligocene faunas (Lucas and Schoch, this volume, Chapter 26).

At the peak of their size and horn development, titanotheres became extinct. Earlier workers attributed their extinction to factors such as "racial senescence," but recent work has shown that the extinction of titanotheres coincides with the extinc-

tion of a number of archaic forms at the end of the Eocene (labeled the "mid-Oligocene event" by Prothero, 1985). Titanotheres were among the many victims of the terminal Eocene climatic event that resulted in global cooling and glaciation, lowered sea level, and resulting changes in vegetation (reviewed by Prothero, 1985). Once they became extinct, titanotheres were never truly replaced in North America. Oligocene and Miocene rhinos never reached their size. In Asia titanotheres competed with, and were succeeded by, the giant indricotheres, although both groups were extinct by the Miocene.

Acknowledgments

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