INTRODUCTION

Perissodactyla and proboscideans are grouped together in this chapter, following the grouping by Prothero, Manning, and Fischer (1988) of the "higher ungulates" or "par ungulates" at the level of the Perissodactyla and above. Perissodactyla and proboscideans are the two orders of higher ungulates with representative terrestrial members in the Tertiary of North America. The relationship of these orders to other higher ungulates, including the debate of the relationship of hyracoids to the perissodactyls, is discussed in the chapter on archean ungulates and ungulalete mammals (this volume, Chapter 15).

Present-day perissodactyls and proboscideans are all of large size (greater than 200 kg) to very large body size (greater than 1,000 kg), and all are folivorous herbivores with a hindgut system of cellulose fermentation. In both respects this contrasts with the artiodactyls, which represent the other extensive present-day ungulate radiation. Many artiodactyls (e.g., most suids) are omnivorous rather than folivorous, and folivorous artiodactyls have a primarily foregut system of fermentation (although they may also retain some hindgut fermentation, which is the pleisiomorphic condition for mammals).

Artiodactyls also include smaller forms (such as the Asian mouse deer, Trogontherium, with a body mass of as little as 2 kg), but their main diversity is in the 100-300 kg range. Only hippos, giraffes, and bison may exceed 1,000 kg in body mass today. Nor was there a much greater diversity of equiden-herbivores in artiodactyl history, although distinct forms of similar mass to large bison include late Cenozoic North American camelids and Old World sivatherine giraffids. In contrast, perissodactyls and proboscideans include the largest hoofed mammals ever known, with Oligocene indricotheres rhinocerotids, and Pleistocene mammoths attaining body masses of up to 20 t (Fotiolus and Kappelman, 1993).

The difference in the siting of the fermentation chambers foregut versus hindgut, has often been used to explain the relative evolutionary success (at least as perceived from the Recent) of artiodactyls versus other ungulates (Janis, 1978), but the true picture may not

16 kg simple (see summary chapter on Artiodactyla, this volume, Chapter 22, for discussion and review).

Perissodactyla and proboscideans also differ from artiodactyls in their specialization for locomotion. Proboscideans are graviportal, and living cetaceans (seals and whales) are mediportal at smaller sizes and graviportal at larger sizes. Equids are the only living curio-

sial perissodactyls, although some early Tertiary cetaceans (e.g., hyracoids and certain hipparions) were also moderately curiosial. In contrast, curiosial adaptations of the postcranial skeleton may be the primitive mode for artiodactyls (Rose, 1985). Only hippos could be described as graviportal among both living and fossil forms.

Present-day representatives of these groups consist only of the family Elephantiidae in the order Proboscidea and the families Equidae, Tapiridae, and Rhinocerotidae in the order Perissodactyla. Of these, only hippos have a recent representation in North America, although all living perissodactyl families were known during the Tertiary, as were nonelephantid proboscideans (with elephantids present in the Pleistocene). Today, dwarf hippos, reintroduced from Europe in the sixteenth century, thrive well enough in the North American west to be considered pests (Berger, 1986). Ex-

tinct perissodactyls found in North America in the Tertiary include bronchotheres, chalicotheres, and a variety of "hipparions" (including iseniotheres and various ceratotheres; see Colbert and Schoch, this volume, Chapter 39).

The Tertiary history of perissodactyls and proboscideans parallels that of the artiodactyls (see Chapter 22, this volume): a few North American endemics with their unique radiation, other North American appearances of taxa with a primarily Old World distribution, and the radiation of a number of unique Old World forms (especially during the early Tertiary).

Equids may well be of Old World origin because European equids predate the earliest known North American ones (see Hooker, 1994). Nevertheless, equids were a primarily North American radiation and did not comprise a significant component of the post-Benzie Old World faunas until the emigration of hippoanthine horses in the late Miocene (see MacFadden, 1992, for summary and
review). Bronzotheres also had their greatest diversification in North America. Unlike equids, they may have originated in this continent in the early Eocene, with later (middle Eocene) dispersal to Eurasia (see Mader, this volume, Chapter 36; Prothero and Schoch, 1989).

Tapirs apparently had their first appearance in North America (Prospirus and an undescribed tapiroid in the late Eocene) and, subsequent to the Oligocene occurrence of the European Protospirus, represent an exclusively North American radiation until the late Miocene (Schoch, 1989). Other moropomorphs, such as Incotolophidae and basal ceratomorphs (Semilaevis and Denticamotherium), appear to be uniquely North American (Schoch, 1989). In contrast, the majority of North American moropomorphs, such as chalicotheres and rhinocerosids, are of Eurasian origin with multiple immigrations into North America (Prothero and Schoch, 1989).

Finally, there was a diversification of Eurasian equids (equis and palaecothis), equid-related pachynotolophids, and basal ceratomorph lineages (e.g., leptohippids, deerocretids, and rodopogids) that were entirely of early Tertiary Old World occurrence (see Hooker, 1989, 1994; Schoch, 1989; Prothero and Schoch, 1989). They are not considered further in this chapter.

**SYSTEMATICS**

We consider only the interrelationships within the order Perissodactyla here. Figure 35.1 summarizes our current hypothesis of the interrelationships of perissodactyls. Relationships within the Ungulata as a whole are discussed in the chapter on archaic ungulates and ungulatulike mammals (this volume, Chapter 15), and relationships within the order Proboscidea are discussed in Lambert and Shoshani (this volume, Chapter 43). Relationships within the Equidae and the Hippomorpha are also ignored because equids are the only North American taxa in these groupings (see Hooker, 1989, 1994 for a review; also note brief discussion in Medwedev, this volume, Chapter 37).

This chapter focuses on the interrelationships among the major groups of perissodactyls: brontotheres, chalicotheres, equids, and ceratomorphs (rhinos and tapirs). The interrelationships and affinities of the various North American moropomorph taxa are extensively discussed in Colbert and Schoch (this volume, Chapter 39) and are not considered further here. A review of the history of ideas of perissodactyl interrelationships was presented by Schoch (1989a), and this section is largely a summary of that review.

The present-day concept of the Perissodactyla as comprising ungulates with a mesaxonic foot posture has its origin in Blainville (1815). Owen (1848) named the association of horses, tapirs, and rhinos the Perissodactyla, although taxa that hyracoids and various extinct other ungulates were originally included as perissodactyla. Previous to this, the living perissodactyls had been grouped with various other mammalian orders: Most commonly, tapirs and rhinos were grouped with other large-bodied, short-legged ungulates as "pachyderms"; horses were accorded their own stamnos, probably because of their economic and social importance (see references in Schoch, 1989a).
Wood (1934) was the modern originator of the notion of a division of living peristomial acanthocephalans into the suborders Hipposomophora (equids) and Echinorhynchus (horses and tapirs) (see also Wood, 1937). In this scheme, also followed by Simpson (1945), brotherhoods and chilicothorins were classified with equids in the Hipposomophora. Beristain (1945) maintained that brotherhoods and chilicothorins were sister taxa among the Hipposomophora. In contrast, Scott (1941) perceived a fundamental difference between clawed and hoofed peristomialacanthocephalans, creating the suborders Ancylopoda (chilicothorins) and Cheloniida (ceratomorphous and the remaining hipposomorphs).

Radinsky (1964) modified Scott's (1941) scheme to raise Hipposomophora and Ceratomorpho to equal subordinal rank with Anzylopoda. However, Schoch (1989) noted that Radinsky's perceived distinction of chilicothorins was based on his assignment of the genus Palaeomorpha to the Chilicothorinidae, an assignment that has since been questioned (see also discussion in Colbert and Schoch, this volume, Chapter 39).

In the early 1980s, both Schoch (1983, 1984, 1985) and Hooper (1984) independently came to the conclusion that chilicothorins shared derived characters with certain ceratomorphs. Schoch (1985) erected the suborder Meroponophora (including Anzylopoda and Ceratomorpho as infrataxons), leaving brotherhoods and equids as superfamilies within the suborder Hipposomophora. Hooker (1984) presented a rather more complex scheme, in which chilicothorins...
were recognized as the sister taxa to the lophiodontid "tapiroida" and bromotheres were considered as the sister taxa to all other perissodactyls.

Figure 35.1 is derived largely from Prothero and Schoch (1989) and presents an amalgam of the ideas of Schoch (1985, 1989a) and Hooper (1984, 1989). Prothero and Schoch (1989) consider hyracoids to be the sister taxa to other perissodactyls, dividing the Perissodactyla into the suborders Hyracoida and Mesaxonia. Within the Mesaxonia (equal to the Perissodactyla of common usage), Thalassotheromorpha (bromotheres), Hipparionomorpha (equoids and pachycephaloids), and Mioepomorpha (chalicotherioids, "tapiroids," and ceratomorphs) are granted equal status as infrorders. Within the Mioepomorpha, the parvorders Ancylopodida (choeriochoerids and lophiodontids) and Ceratomorpha (rhinochoeroids, Ursidae, Megatheriidae, and several Asian lineages) are recognized as sister taxa. Basal perissodactyl taxa include the North American family Ictidotheriidae and the Eurasian genus Kalakolosia (placed as more derived than the "tachychoeroids; not included in Figure 35.1.

Perhaps if hyracoids are excluded from the Perissodactyla (as suggested by, e.g., Novacek, Wyss, and McKenna, 1988; Shoshani, 1993), these infraordinal ranks would be raised from infraorder to suborder, and from parvorder to infrorders, respectively.
**EVCN**

Perissodactyla first appear in North America at the start of the Eocene, although they may be known from slightly earlier sediments in Europe (Hooker, 1994). The earliest Wastachian contains the equid *Hyracotherium* and the insectivore *Cardiolephas*. These taxa were joined in the later Wastachian by the equid *Xeniohippus*, the insectivorous *Homogalas*, and basal ornithomorphs such as *Hesperotherium* and *Hyracotherium*. In the latest Wastachian *Xeniohippus* was replaced by *Ochridhippus*, and there was the appearance of two new taxa: the bronchotherian *Estuoneutes* and the indeterminate perissodactyl *Lambdotherium* (these taxa were confined to the late Wastachian or nearly so) (see Figures 35.2, 35.4).

A more distinct faunal shift occurred at the start of the middle Eocene (Bridgerian), with the appearance of the larger, more derived bronchotherian *Palaenotherium*, the replacement of more primitive insectivores by *Insectolephas*, and the appearance of the first, true tapiroid *Melanites* (see Figure 35.4). *Hesperotherium* was rare in the early Bridgerian and did not survive this stage. By the late...
Bridgerian, bronchothere diversity increased, including the appearance of the first horned bronchothere Telmatherium. Basal triconodonts such as Hysipops and Selaeocodon were replaced by taxa such as Drammatherium and Dikilophodon, and the first amynodont rhynchocentrid was apparent (see Figures 35.3, 35.4).

The Urian marked the zenith of perissodactyly diversity in the family level, "Eomerychus" chalicotheres, the more derived tapiroid Colodon, and the first true tapiroid appeared in the early Uintian; bronchothere diversity increased to include larger, more specialized horned forms. By the late Uintian almost all bronchotheres were large, horned forms, and rhynchocentrid chirotheres made their first appearance (see Figures 35.3, 35.4). Ironically, during this

episode of perissodactyly diversification, the abundance of equids was low. Although represented by two genera in the early Uintian, and by Eophippus alone in the late Uintian (see Figure 35.2), the absolute numbers of fossil equids known from this time interval are very sparse, in contrast to the great abundance of individuals belonging to species of Hysipops in the early Eocene (see discussion in MacPadden, 1990; Janis, 1993).

There is little in the way of biogeographic variation during this earlier part of the Eocene, although perissodactyly in general appear to be sparsely represented in the California coast and northern Great Plains faunas. Note that rhynchodonts and tapiroids are found in California in the late middle Eocene; equids are absent.
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**Figure 35.3. (Cont.)**

**WHITE RIVER CHRONOFAUNA**

For the other groups discussed in this volume, a distinctive change is apparent at the start of the Chadronian (late Eocene), heralding the appearance of the "White River chronofauna" (see discussions in Chapters 4 and 22, this volume, relating to Tertiary North American chronofaunas). In contrast, a more distinctive change in perissodactyl diversity is seen earlier, in the late middle Eocene (Duchesnean), with a great reduction in generic diversity. By this time, "omnivorous" chalicotheres and hesperotheres were extinct, and bovids entered to the single genus *Duchesnianus* (unique to this time interval) (see Figure 35.4). The only remaining basal ceratomorph taxa was *Theratherium*, first appearing in the Duchesnean, although xenodontid and hymenodont rhinocerots maintained their late Uintan diversity. Distinctive additions include definitively rhinocerid genera (*Penetrigonias* and *Teleoceras*), and the "rebound" of the equids with the appearance of the *hypothetical* *Hoplohippus* (known only from the Duchesnean) and the archihippine *Mesolippus* (see Figures 35.5, 35.3).

Further, although less dramatic, change is apparent at the start of the Chadronian. Brontotheres reappear with the appearance of the extremely large, specialized eutrochotheres *Brenosoa,*
Table and diagram showing the biogeographic ranges of various groups of mammals, with notes on the Late Oligocene and Miocene epochs.
The earliest Archoohippus marked the last appearance of the hyracodontid Hynodon and the therocephalid Subhynodon, and the first definitive appearances of the equid Kalobaehippus and the tapirid Miospina. By the late early Eocene the first true chalicotheriid, Moropus, immigrated from Eurasia (see Figures 35.2, 35.3, 35.4). There is little in the way of biogeographical diversity in this Eocene/Oligocene time period, except for the relict survival of the tapirid Protospinus, and possibly also of the tapirloid Coelod, in the John Day faunas of the Pacific Northwest, after their extinction by the end of the Whitonian in the central Great Plains (see Figure 35.4). Rhinocerotids are virtually the only perissodactyls to be found in the California coast islands.

**RUNNINGWATER CHRONOFAUNA**

The early Miocene heralded the appearance of the "Runningwater chronofauna." The major change in perissodactyl diversity at this time was in the equids, with the appearance and radiation at this time of more derived anichterines such as Archaeohippus,
Dermatopseus, and Panorhippus. The large, specialized archifemurine Hypohippus first appeared in the early Hemingfordian. Mecopsippus was now extinct, although Mecopsippus survived as a rare faunal element through the early Hemingfordian. The earliest equine euques seems to be present at the start of the Miocene, although the genus Mecopsippus is not definitively known until the early Hemingfordian (see Figure 35.2).

Rhinoceroid diversity increased with the appearance of Mecopsippus in the early late Arikareean, although the similarly paired-horned Diceratherium continued to survive until the late Hemingfordian, and possibly into the early Barstovian. More rhinoeroid immigrants appeared in the early Hemingfordian, including the ceratotherines Floridaceros and Aphelops and the teloceratine Brachypohippus (see Figure 35.3). Chalicotheres were relatively abundant in this time period, with the appearance of Tylocephaloceras in the early Hemingfordian. Tapirs were the only surviving tapirids, with little change in their diversity over their Oligocene condition (see Figure 35.4).

In contrast to the patterns observed in other large mammals, where the Gulf Coast faunas were rather distinctive, there appears to be little biogeographical differentiation during this time period among perissodactyls. Note, however, that Aphelops is known only
from this region, and that *Protopinus* is known from here but is absent in the central Great Plains; *Mionipinus* shows the opposite pattern.

**CLARENDONIAN CHRONOFAUNA**

The late Hemingfordian (early late Miocene) represents the start of the Clarendonian chronofauna. Although proboscideans are generally thought to be absent from North America until the middle Miocene (e.g., Tedford et al., 1987), note the isolated occurrence of two specimens of the mammalid *Zygodentodon* in the late Hemingfordian (from the Massacre Lake Local Fauna in Nevada: locality NVB17) and the Deep River Local Fauna in Montana (locality NP42D). However, as also noted by Tedford et al. (1987), proboscideans are apparently absent from most areas until the late Barstovian. Even the well-sampled central Great Plains yields only one dubious proboscidean. *Gomphotherioid* proboscideans first appeared in the early Barstovian, with a diversification in the late Barstovian, including the appearance of the shovel-nosed *Serboodon* in the late Barstovian/early Clarendonian (see Figure 35.5).

Among the perissodactyls, the invasion of the Clarendonian chronofauna appears to be marked by new appearances, rather than by extinctions of earlier taxa (in contrast to other groups of large mammals). Equine *Aephipus* showed a diversity of species of *Merychippus,* representing both equines and hipparionine lineages of this paraphyletic genus. The hipparionine *Hipparion* and the equines *Prothomus* and *Calippus* appeared early in this time interval. Archontitheres remained modestly diverse, although more primitive archontitheres such as *Miohippus* were now extinct. In the early late Barstovian there was the appearance of a greater diversity of more derived equids: the hipparionine *Cornemhiphipus,* *Neohippus,* and *Parahippus,* and the equine *Plaihippus* (see Figure 35.2).

Rhinocerotid diversity was now almost entirely comprised of *rheutherines and teloceratines,* although *Diceratherium* survived into at least the late Hemingfordian. The short-legged, probably semiaquatic, grazing teloceratine *Telescerus* first appeared in the late Hemingfordian. *Dwarf rhinocerots* were common in the middle Miocene, with the appearance of the aceratherine *Pachyrhizus* in the early Barstovian and *Telescerus masdulimum* in the early late Barstovian (see Figure 35.3). Caihlotheres and tapirs continued to appear as rare elements of the fauna during the middle Miocene, with the appearance of the extant tapir *Tapirus* in the late late Barstovian (see Figure 35.4).

Perissodactyl diversity patterns showed a shift in the Clarendonian (early late Miocene), paralleling a similar shift in artiodactyl diversity (see Chapter 22, this volume), with a decline in the numbers of browsing taxa and an increase in the numbers of grazers, probably representing a reduction of woodland habitat.

Archontitheres persisted until the end of the Clarendonian, but were now represented only by the large, highly specialized genus *Hypohippus* and *Megahippus* (see also Janis, Gordon, and Illius, 1994), in contrast, the diversity of equine genera increased.

The early Clarendonian was the zenith of equine generic diversity, with seven sympatric taxa (all of which could be found in central Great Plains faunas). The derived equine *Dinoshippus,* sister taxon to the extant *Equus,* first appears in the early Clarendonian (see Figure 35.2).

Proboscideans remained moderately diverse among the proboscideans, with the appearance of the immigrant shovel-nosed *gomphotherine Plaihippus.* *Zygodentodon* was replaced by the larger, more specialized mammalid *Ammomys* (see Figure 35.3). Rhinocerotid generic diversity was little changed over their middle Miocene condition. Only one possible record of a chalicotherid is known from the Clarendonian, but tapirs persisted as occasional faunal elements.

There are few patterns of biogeographic variation in the Clarendonian chronofauna. The apparent continued survival of chalicotheres into the central Great Plains region alone is probably a sampling artifact. Dwarf rhinocerotids appear to be confined to southern and western regions in the Clarendonian. The Gulf Coast faunas do not appear to have acted as a refuge for the browsing archontitherine equids. Although sampling was poor during the late late Barstovian, *Megahippus* (Clarendonian) in the northern Great Plains and Pacific Northwest, perissodactyls (especially rhinocerots) were rather conspicuously underrepresented from these regions during this time period. Mammalid proboscideans appear to have been confined to the Gulf Coast and the Pacific Northwest during the Clarendonian.

**MIO-PLOCENE CHRONOFAUNA**

By the start of the Hemphillian, specialized browsing perissodactyls, such as archontitherine equids and chalicotheres, had become extinct. In contrast, the browsing rhinocerotid *Aepiplopus* survived, possibly indicative of a different habitat for this animal than for the other browsers (perhaps resembling the present-day savanna-swelling browsing rhinoceros, *Diceros bicornis*). Dwarf species of rhinocerots were now extinct. *Aepiplopus* and *Telescerus* survived into the earliest Pliocene, and there is a single record of a possible *Telescrus* from the early Blancan (see Figure 35.3). Apparently beasting all evolutionary odd, the extant tapir *Tapirus* (also a browser) continued the Pliocene, although it is only known from occasional specimens.

Grazing equids continued at moderate diversity through the late Miocene, although all species assigned to the genus *Merychippus* were now extinct. The monodactyl equine *Aepiplopus* appeared in the late early Hemphillian. Equid diversity showed a steady decline through the Mio-Pliocene chronofauna, however: *Prothomus* and *Hipparion* were extinct by the late Hemphillian, and the Gulf Coast faunas appeared to act as a refuge, especially during the early Pliocene, for genera such as *Cornemhiphipus,* *Neohippus,* *Calippus,* and *Parahippus.* The cause for this drop in diversity seems related to a major global change related to increased aridity and seasonality and the spread of lower productivity prairie grasslands (Curling, Wang, and Quade, 1993; MacFadden and Curling, 1994). The extant *Equus* first appeared in the Blancan and was virtually the only surviving genus by the end of the Pliocene (see Figure 35.2).

Proboscideans were diverse in the late Miocene, with the appearance of the shovel-nosed *Amebelodon* in the early early Hemphillian
and of other shovel-tusked taxa such as Zorynobolithos and Gnumaha-belodon, which may also have survived during the Hemphillian. However, shovel-tusked forms did not survive into the Pliocene. The gom- phothere Gomphotherium may have survived into the Pliocene only in the Gulf Coast faunas. The "New World" form Rhyncotherium may have been present as early as the earliest Hemphillian, joined by Stegosamotherium in the late Hemphillian. These New World forms, joined by Cuvierianus in the Blancan, formed the majority of Pliocene proboscidean diversity, although the mammutid Mammut was also present during the Pliocene (see Figure 35.5).

With the exception of the taxa mentioned here that survived only in Gulf Coast faunas into the Pliocene (various equid taxa and possibly Gomphotherium), there were few patterns of biogeographical variation. Rhipheoeradicae were known from latest Miocene Pacific Northwest faunas (perhaps their earlier apparent absence merely represents a sampling artifact). Despite the diver- sity of equids elsewhere on the continent, Pliohippus was almost the only equid known from the latest Miocene Pacific Northwest. In contrast, Dinohippus was almost the sole equid in northern Great Plains faunas. This apparent difference could well represent anoma- lous data because species of Dinohippus and Pliohippus are fre- quently mistaken for each other, and both genera are in exten- sive need of revision (see comments in MacPadden, this volume, Chapter 37).
SUMMARY

Perissodactyls were diverse in Eocene faunas, with a zenith of diversity at the family level in the Uinta. This late middle Eocene perissodactyl diversity comprised brontotheres, "omopodid" chalicotheres, and a diversity of tapirs and ceratotheres. Perissodactyls diversified, equal diversity was low at this time. A later Eocene reduction in perissodactyl diversity occurred slightly earlier (Duchesnean) in the fauna shifts seen in other large herbivores (early Chadronian). Extinctions at this time included chalicotheres and nontapirs "tapir-like" A "White River" (late Eocene-Oligocene) perissodactyl clade was comprised primarily of archontotheres, equids, and rhinoceros rhino- ceros. Brontotheres were prominent in large-scaled forms in the Chadronian, but did not survive to the Eocene. Amynodontids and baryconodont rhinocerotids were also absent diverse in the late Eocene and did not survive the Oligocene. A running-wild chaetothera, commencing in the early Eocene, was marked by the radiation of more large and specialized archontotheres, newly immigrant chalicotheroid chalicotheres, and a diversity of immigrant rhinocerotids. Change at the start of the Clarendonian fauna, in the late Heningfordian (late Eocene), contrasts with changes in faunal diversity seen in other large mammals at this time in that there were few genetic extinctions. However, this time was marked by the appearance of numerous new taxa, primarily representing the endemic diversification of equine equids and the immigration of the mammalian proboscideans. Proboscideans were not generally common in North America until the later middle Miocene, with gomphotherids appearing for the first time in the early Barstovian. Both large specialized archontotheres (including the probable grazing hippo mimic Teleoceras) and daintier rhinos were common in the middle Miocene, and a diversity of both browsing and grazing equids were apparent. By the Clarendonian (early late Miocene), although generic diversity of the grazing equine group was at its zenith, diversity was greatly reduced in the browsing archontotheres. Both archontotheres equids and chali- cotheres (also browsers) were extant by the end of the Clarendo- nian, but some browsers, such as the rhino Aepyceras and the tape tepitivas, survived. In the Miocene Pleistocene flora of equids and large rhinocerotids consisted during the late Miocene, but had declined by the Pliocene. The last North American rhinocerotid was known from the early Blancan, and by the late Blancan the extinct Equus was virtually the only surviving equid. The hoist Miocene saw a flour- ishing of shovel-headed proboscideans, but both these and regular gomphotherids were replaced by "New World form" gomphotheres in the Pliocene. The mammalian MMU survived from the late Miocene through the Pliocene. Tertiary perissodactyls and proboscideans do not exhibit profound patterns of biogeographical diversity, although perissodactyls appear to have been generally sparse in their distribution in the Northwest and along the California coast. The Gulf Coast fauna was not particularly distinctive in their perissodactyl and proboscidean components, except for the role that the Florida fauna appear to have played as a refuge for the earlier diversity of equine equids in the Pliocene and latest Miocene.

REFERENCES


