

35 Perissodactyla and Proboscidea

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INTRODUCTION

Perissodactyls and proboscideans are grouped together in this chapter, following the grouping by Prothero, Manning, and Fischer (1988) of the "higher ungulates" or "paenungulates" at the level of the Perissodactyla and above. Perissodactyls 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 archaic ungulates and ungulatelike mammals (this volume, Chapter 15).

Present-day perissodactyls and proboscideans are all of large (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 plesiomorphic condition for mammals).

Artiodactyls also include smaller forms (such as the Asian mouse deer, *Tragulid*, with a body mass of as little as 2 kg), but their main diversity is in the 10–300 kg range. Only hippos, giraffes, and bison may exceed 1,000 kg in body mass today. Nor was there a much greater diversity of megaherbivores in artiodactyl history, although extinct forms of similar mass to large bison include late Cenozoic North American camelids and Old World sivattherine giraffids. In contrast, perissodactyls and proboscideans include the largest land mammals ever known, with Oligocene indricothere rhinocerotoids and Pleistocene mammoths attaining body masses of up to 20 tons (Fortelius and Kappelman, 1993).

The difference in the siting of the fermentation chamber, 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, 1976), but the true picture may not

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

Perissodactyls and proboscideans also differ from artiodactyls in their specializations for locomotion. Proboscideans are graviportal, and living ceratomorphs (tapirs and rhinos) are mediportal at smaller sizes and graviportal at larger sizes. Equids are the only living cursorial perissodactyls, although some early Tertiary ceratomorphs (e.g., hyracodonts and certain tapiroids) were also moderately cursorial. In contrast, cursorial 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 Elephantidae in the order Proboscidea and the families Equidae, Tapiridae, and Rhinocerotidae in the order Perissodactyla. Of these, only tapirs 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, feral equids, reintroduced from Europe in the sixteenth century, thrive well-enough in the North American west to be considered pests (Berger, 1986). Extinct perissodactyls found in North America in the Tertiary include brontotheres, chalicotheres, and a variety of "tapiroids" (including isectolophids and various ceratomorphs; 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 own 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 equoids 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-Eocene Old World faunas until the emigration of hipparionine horses in the late Miocene (see MacFadden, 1992, for summary and

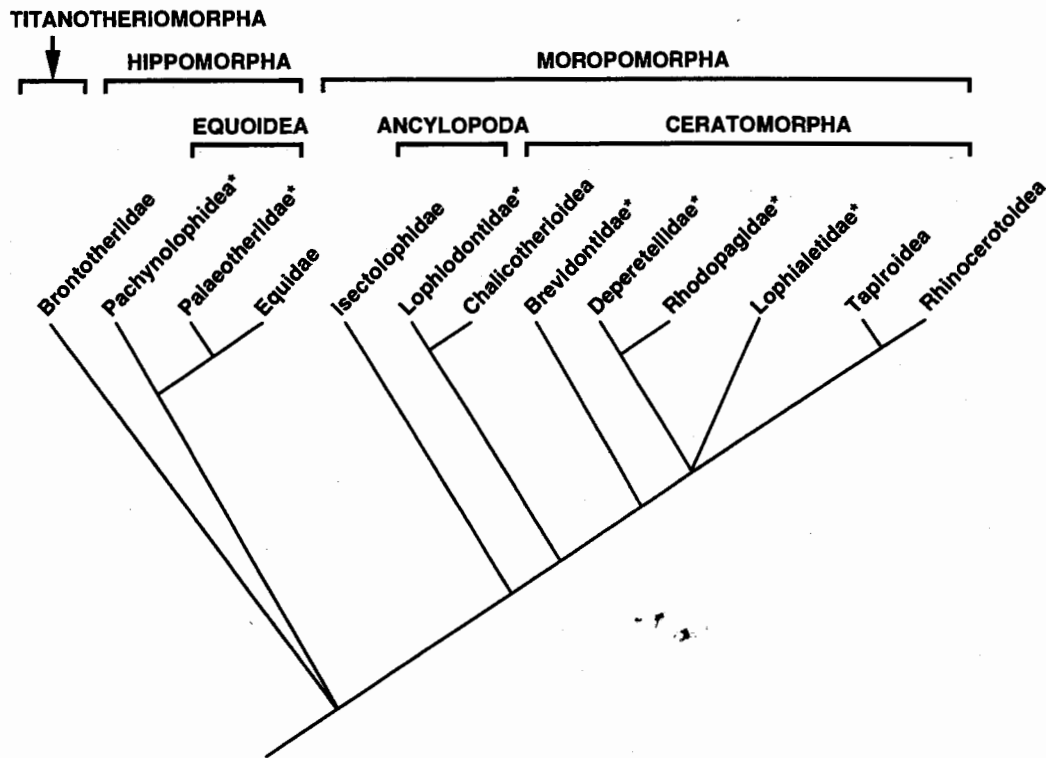


Figure 35.1. Interrelationships among perissodactyls. * indicates taxon not found in North America (but note that *Paleomoropus* has been considered to be a lophodontid [Schoch, 1989b] and that some of the earliest Eocene species of "*Hyacotherium*" may actually be palaeotheres [Hooker, 1994]).

review). Brontotheres 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).

Tapirids apparently had their first appearance in North America (*Protapirus* and an undescribed tapiroid in the late Eocene) and, subsequent to the Oligocene occurrence of the European *Protapirus*, represent an exclusively North American radiation until the late Miocene (Schoch, 1989b). Other moropomorphs, such as issectolophids, and basal ceratomorphs *Selenaletes* and *Desmatotherium*, appear to be uniquely North American (Schoch, 1989b). In contrast, the majority of North American moropomorphs, such as chalicotherioids and rhinocerotoids, are of Eurasian origin with multiple immigrations into North America (Prothero and Schoch, 1989).

Finally, there was a diversity of Eurasian equoids (equids and palaeotheres), equoid-related pachynolophids, and basal ceratomorph lineages (e.g., lophialetids, deperetellids, and rhodopagids) that were entirely of early Tertiary Old World occurrence (see Hooker, 1989, 1994; Schoch, 1989b; 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 ungulatelike mammals (this volume, Chapter 15), and relationships within the order Proboscidea are discussed in Lambert and Shoshani (this volume, Chapter 43). Relationships within the Equoidea and the Hippomorpha are also ignored because equids are the only North American taxon in these groupings (see Hooker, 1989, 1994 for a review; also note brief discussion in MacFadden, 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 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 (1816). Owen (1848) named the association of horses, tapirs, and rhinos the Perissodactyla, although note that hyracoids and various extinct other ungulates were originally included as perissodactyls. 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 status, probably because of their economic and social importance (see references in Schoch, 1989a).

MA	Land Mammal Age	Biogeographic Region										
		Central America (CA)	Gulf Coast (GC)	CA Central & Coast (CC)	Northern Great Basin (NB)	Southern Great Basin (SB)	Southern Great Plains (SP)	Central Great Plains (CP)	Northern Great Plains (NP)	Pacific Northwest (PN)	N. E. Coast (NC)	
1.8	Late Blancan	Na	Co, Na, Eq	Eq	Eq	Na, Eq	Na, Eq	Na, Eq			Eq	
2.4	Early Blancan	Eq		Eq	Eq, Hd, Di	Na, Ne, Di, Eq	Na, Eq	Na, Eq			Eq	
4.5	Late Hemphillian		Co, Na, Ne, Ps, As, Ca, Di			Na, Ne, As, Di	Na, Ne, As, Di	Na, Ne, Ps, Di				
5.2	Late Hemphillian			Na, Ne, As, Di, Pl	Di, Pl	Na, Ne, As, Di, Or	Co, Na, Ne, As, Di, Pl	Na, Ne, As, Di	Na, Ne, Di	Na, Ne, Pl		
6.0	Early Hemphillian		Co, Hp, Na, Ne, Ps, Ca, Di, Pr	Na, Ne, Di, Pl	Ne, As, Pl	Ne, As, Di	Co, Hp, Ne, As, Ca, Hd, Pl	Co, Hp, Na, Ne, As, Ca, Di, Pl, Pr		Ne, Pl		
7.0	Early Hemphillian	Co, Ca	Na, Ne, Ps, Ca, Pr	?Di or Pl	Co, Hp, Di	E?	?Co, Hp, Ne, Ca, Pl	Co, Hp, Na, Ne, Ca, Di, Pl	Na, Di	Pl		
8.8	Late Clarendonian	?Co	Co, Hp, Na, Ne, Ps, Ca, Pr	Mg, Co, Hp, Ne, Pl	Hh, Co, Hp, Ne, ?Pr, Pl	Ne or Co, Di, or Pl	Co, Hp, Ne, Ps, Ca, Pl	Hh, Co, Hp, Mx, Na, Ne, Ps, Ca, Pl, Pr		E?		
9.5	Early Clarendonian		Hh, Co, Hp, Ne, Ps, Ca, Di, Pl, Pr	Mg, Co, Hp, Pl	Hh, Mg, Co, Hp, Ne, ?Di, Pl	Hh, Mg, Co, Mh, Ne, ?Ps, Di, Pl	Hh, Co, Na, Ne, Ps, Ca, Di, Pl, Pr	Hh, Mg, Co, Hp, Mh, Na, Ne, Ps, Ca, Di, Pl, Pr	Hp, Mx	E?		
11.0	Late Barstovian		Hh, Mg, Co, Hp, Mh, Mp, Na, Ps, Ca, Pl, Pr	Hp, Mg	Mg, Co, Mg, Pl	Hh, Mh, Pl, Pr	Ar, Hh, Ka, Mg, ?Pa, Co, ?Hp, Mh, Ne, Ps, Ca, Pl, Pr	Hp, Mx	?Mp, Mx	Co, Mx		
12.5	Late Barstovian		?Co, Mp, Mh, Ca, Pr	Ar, Ka, Mh, Mg	Hh, Ka, Mg, Mg, Pl	Hh, Mg, Co, Mh, Ne, ?Di, Pl, Pr	Mh, Ps, Pl	Ar, Hh, Mg, Hp, Mh, Mg, Pl	De, Hh, Mh	Ar, ?Mx		
14.0	Early Barstovian	Mx	De, Hh, Ka, Hp, Mh, Mp, Ca, Pr	Ar, De, Hh, Ka, Mh, Mg	Ar, De, Hh, Pa, Mh, ?Mp, Mg, Pr	Hh, Ka, Mg, Mh, ?Mg	Ar, De, Hh, Ka, Pa, Mg, Mh, Ca, Mg	Ar, De, Hh, Hp, Mh, Mg, Pl	Ar, De, ?Hh, Pa, Mp, Mh	Ar, De, Mp, Mh		
15.8	Late Hemphordian		Ar, Ka, Mp	Ar, Hh, Pa, Mh, Mg	Ka, Pa, Mh, Mg	Ar, Mh, Pr	Ar, De, Hh, Ka, Pa, Mp, Mh	De, Hh, Pa, Mh, Mg				
17.5												

Figure 35.2. Biogeographic ranges of equids. A "box" (for a particular time period in a particular biogeographic region) with a cross through it means no fossil localities are known for that time period from that area; a single dashed line through the box means only scant fossil information is available (usually only a single, small, locality). Key: "Hyracotheriinae" are in italics: *Ep* = *Epihippus*, *Ha* = *Haplohippus*, *Hy* = *Hyracotherium*, *Or* = *Orohippus*, *Xe* = *Xenicohippus*. "Anchitheriinae" are in boldface: *Ar* = *Archaeohippus*, *De* = *Desmatippus*, *Hh* = *Hypohippus*, *Ka* = *Kalobatippus*, *Me* = *Mesohippus*, *Mg* = *Megahippus*, *Mi* = *Miohippus*, *Pa* = *Parahippus*. Equinae are in roman type. *Merychippus*: *Mh* = hipparionine *Merychippus* species, *Mp* = primitive *Merychippus* species (sensu stricto), *Mq* = equinine *Merychippus* species. Hipparionini are in plain roman type: *Co* = *Cormohipparion*, *Hp* = *Hipparion*, *Na* = *Nannippus*, *Ne* = *Neohipparion*, *Ps* = *Pseudhipparion*. Equini are in roman type underlined: *As* = *Astrohippus*, *Ca* = *Calippus*, *Di* = *Dinohippus*, *Eq* = *Equus*, *Hd* = *Hippidion*, *On* = *Onohippidium*, *Pl* = *Pliohippus*, *Pr* = *Protophippus*. E? = equid indet.

Wood (1934) was the modern originator of the notion of a division of living perissodactyls into the suborders Hippomorpha (equids) and Ceratomorpha (rhinos and tapirs) (see also Wood, 1937). In this scheme, also followed by Simpson (1945), brontotheres and chalicotheres were classified with equoids in the Hippomorpha. Borissiak (1945) maintained that brontotheres and chalicotheres were sister taxa among the hippomorphs. In contrast, Scott (1941) perceived a fundamental difference between clawed and hooved perissodactyls, creating the suborders Ancylopoda (chalicotheres) and Chelopoda (ceratomorphs and the remaining hippomorphs).

Radinsky (1964) modified Scott's (1941) scheme to raise Hippomorpha and Ceratomorpha to equal subordinal rank with Ancy-

lopoda. However, Schoch (1989a) notes that Radinsky's perceived distinctness of chalicotheres was based in part on his assignment of the genus *Paleomoropus* to the Chalicotherioidea, 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 Hooker (1984) independently came to the conclusion that chalicotheres shared derived characters with certain ceratomorphs. Schoch (1985) erected the suborder Moropomorpha (including Ancylopoda and Ceratomorpha as infraorders), leaving brontotheres and equoids as superfamilies within the suborder Hippomorpha. Hooker (1984) presented a rather more complex scheme, in which chalicotheres

MA	Land Mammal Age	Central America (CA)	Gulf Coast (GC)	CA Central & Coast (CC)	Northern Great Basin (NB)	Southern Great Basin (SB)	Southern Great Plains (SP)	Central Great Plains (CP)	Northern Great Plains (NP)	Pacific Northwest (PN)	N. E. Coast (NC)
MIOCENE	17.5	Early Hemingfordian Ar, / Ka	Ar, De, Hh, Ka, Pa, Mp			De, ?Mx		Ar, De, Hh, Ka, Pa, Mx	Ar, / Pa	Ar, Ka, Mi, Pa, Mx	Ar, Ka, Pa
	18.8	L. Late Arikarean	Ar, De, ?Pa	?Ar, Pa, ?Mx		Ar, Pa		De, Ka, Pa			
	19.2	E. Late Arikarean	?Pa	Ka				Ar, Ka, Mi, Pa	E? /	Ka, Mi	
OLIGOCENE	23.0	L. Early Arikarean						Mi	Mi	Ka, Me, Mi	
	27.7	E. Early Arikarean	Me	Mi				Ka, Mi, Me	?Me, Mi		
	29.4	Whitneyan						Mi	Me, Mi	Me, Mi	
	31.9	Orellan						Me, Mi	Me		
	33.4	Late Chadronian						Me, Mi	Me, ?Mi		
	34.5	Middle Chadronian						Me	Me		
EOCENE	35.5	Early Chadronian				Me		Me	Me, Mi		
	37.1	Duchesnean			Me	Ha, Me		Ep	Me	Ep, / Ha	
	39.5	Late Uintan				Ep		Ep	Ep		
	41.3										

Figure 35.2. (Cont.)

were recognized as the sister taxon to the lophiodontid "tapiroids" and brontotheres were considered as the sister taxon 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 Hooker (1984, 1989). Prothero and Schoch (1989) consider hyracoids to be the sister taxon to other perissodactyls, dividing the Perissodactyla into the suborders Hyracoidea and Mesaxonia. Within the Mesaxonia (equal to the Perissodactyla of common usage), Titanotheriomorpha (brontotheres), Hippomorpha (equoids and pachynolophoids), and Moropomorpha (chalicotherioids,

"tapiroids," and ceratomorphs) are granted equal status as infraorders. Within the Moropomorpha, the parvorders Ancylopoda (chalicotherioids and lophiodontids) and Ceratomorpha (rhinocerotoids, tapiroids, *Heptodon*, and several Asian lineages) are recognized as sister taxa. Basal moropomorph taxa include the North American family Isectolophidae and the Eurasian genus *Kalakotia* (placed as more derived than the isectolophids; 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 infraorder, respectively.

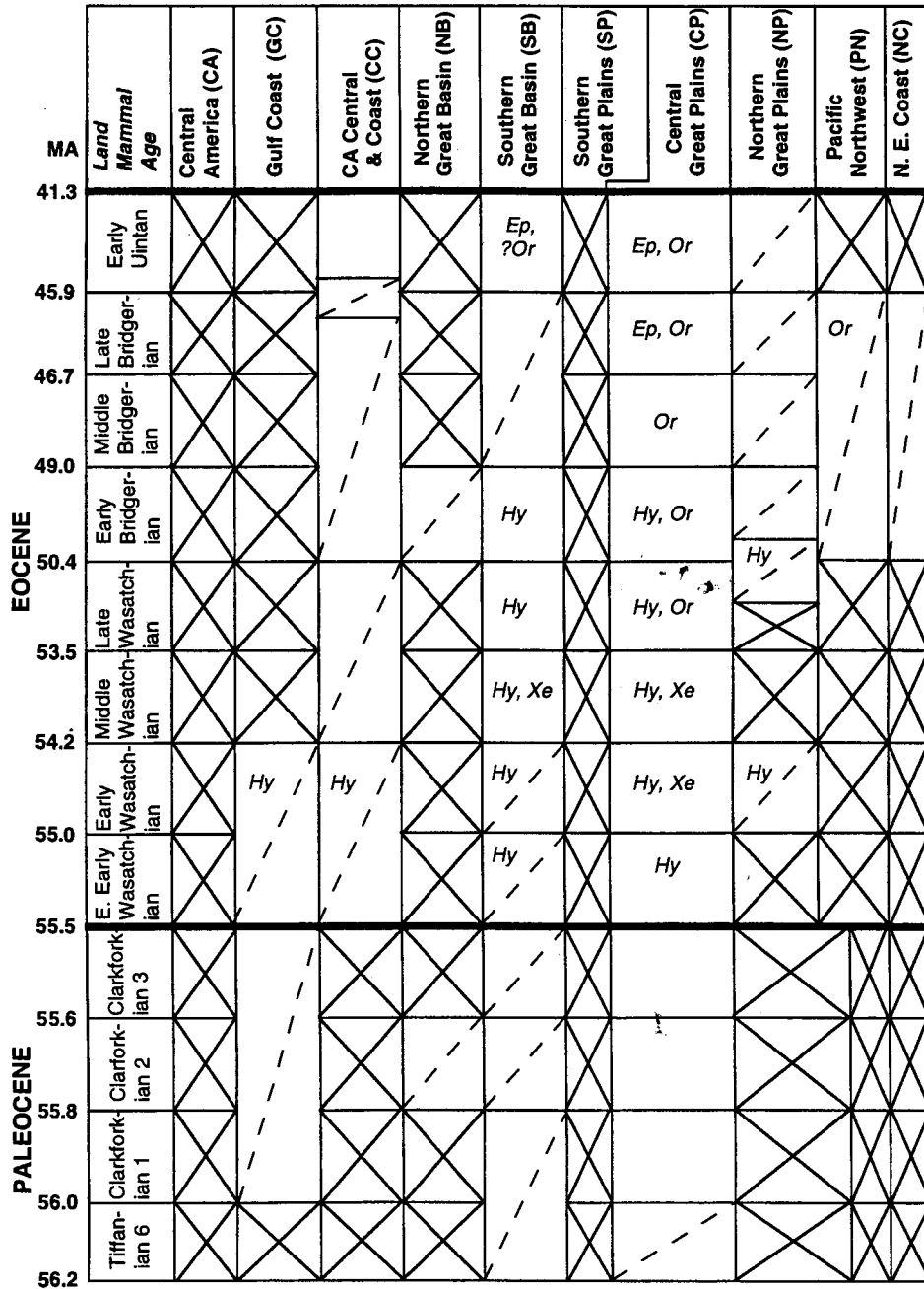


Figure 35.2. (Cont.)

EVOLUTIONARY AND BIOGEOGRAPHICAL PATTERNS

EOCENE

Perissodactyls 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 Wasatchian contains the equid *Hyracotherium* and the isctolophid *Cardiolophus*: These taxa were joined in the later Wasatchian by the equid *Xenicohippus*, the isctolophid *Homogalax*, and basal ceratomorphs such as *Hep-*

todon and *Hyrachyus*. In the latest Wasatchian *Xenicohippus* replaced by *Orohippus*, and there was the appearance of two new taxa: the brontothere *Eotitanops* and the indeterminate perissodactyl *Lambdaotherium* (these taxa were confined to the late Wasatchian 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 large derived brontothere *Palaeosyops*, the replacement of more primitive isctolophids by *Isectolophus*, and the appearance of true tapiroid *Heleletes* (see Figure 35.4). *Hyracotherium* disappeared in the early Bridgerian and did not survive this stage. By

MA	Land Mammal Age	Central America (CA)	Gulf Coast (GC)	CA Central & Coast (CC)	Northern Great Basin (NB)	Southern Great Basin (SB)	Southern Great Plains (SP)	Central Great Plains (CP)	Northern Great Plains (NP)	Pacific Northwest (PN)	N. E. Coast (NC)
1.8	Late Blancan										
2.4	Early Blancan					?Te					
4.5	Latest Hemphillian		Ap, Te			?Ap, Te		Ap, Te			
5.2	Late Hemphillian			Te	Te	?Ap, Te	Ap, Te	Ap, Te		Te	
6.0	L. Early Hemphillian		Ap, Te	Te	Ap, Te	Ap, Te	Ap, Te	Ap, Te		?Ap, Te	
7.0	E. Early Hemphillian	Te	Ap, Te		?Ap		Ap, Te	Ap, Te	Te	Te	
8.8	Late Clarendonian	?Te	Ap, Te	?Ap, Te	Ap, ?Pe, Te	R?	Pe, Te	Ap, Te			
9.5	Early Clarendonian		Ap, ?Te		Ap, ?Pe, Te	Ap, Pe, Te	Ap, Te	Ap, Pe, Te			
11.0	L. Late Barstovian		Ap, Pe, Te				Ap, Pe, Te	?Ap		Ap	
12.5	E. Late Barstovian		Ap, Pe, Te	?Ap	Pe	Ap, Pe	?Ap, Te	Pe, Te	Pe, Te	Ap, Pe, Te	Ap
14.0	Early Barstovian		Ap, Pe, Te	R?	Ap, Pe	Ap, Pe, Te	Ap, Pe, Te	Ap, Te	Ap, Te	Di, Te	
15.8	Late Hemphordian		Ap		Ap, ?Di	Ap, Pe		An, Ap, Br, Pe	Di		
17.5											

Figure 35.3. Biogeographic ranges of rhinocerotoids. A "box" (for a particular time period in a particular biogeographic region) with a cross through it means no fossil localities are known for that time period from that area; a single dashed line through the box means only scant fossil information is available (usually only a single, small, locality). Key: A mynodontidae are in boldface: **Ay** = *Amyrnodon*, **At** = *Amyrnodontopsis*, **Mt** = *Metamyron*, **Mg** = *Megalomyron*, "**Pr**" = "*Proceratops*." Hyracodontidae are in italics: *Ep* = *Epiplolophus*, *Fo* = *Forstercooperia*, *Hy* = *Hyracodon*, *Td* = *Triplopus*, *Tr* = *Triplopus*, *H?* = hyracodontid indet. Rhinocerotidae are in roman type: *Am* = *Amphicaenopus*, *An* = new aceratherine genus, *Ap* = *Aphelops*, *Br* = *Brachypotherium*, *Di* = *Diceratherium*, *Fl* = *Floridaceras*, *Me* = *Menoceras*, *Pe* = *Peraceras*, *Pt* = *Penetrigonas*, *Sh* = *Subhyracodon*, *Te* = *Teleoceras*, *Tg* = *Trigonas*, *Tt* = *Teletoceras*. *R?* = rhinocerotid indet.

gerian, brontothere diversity increased, including the appearance of the first horned brontotheriine *Telmatherium*. Basal ratomorphs such as *Heptodon* and *Selenaletes* were replaced by taxa such as *Desmatotherium* and *Dilophodon*, and the first amyronont rhinocerotoid was apparent (see Figures 35.3, 35.4).

The Uintan marked the zenith of perissodactyl diversity at the family level. "Eomorpid" chalicotheres, the more derived tapiroid *Blododon*, and the first true tapiroid appeared in the early Uintan; brontothere diversity increased to include larger, more specialized horned forms. By the late Uintan almost all brontotheres were large, horned forms, and hyracodontid rhinocerotoids made their first appearance (see Figures 35.3, 35.4). Ironically, during this

episode of perissodactyl diversification, the abundance of equids was low. Although represented by two genera in the early Uintan, and by *Epihippus* alone in the late Uintan (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 *Hyracotherium* in the early Eocene (see discussion in MacFadden, 1992; Janis, 1993).

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

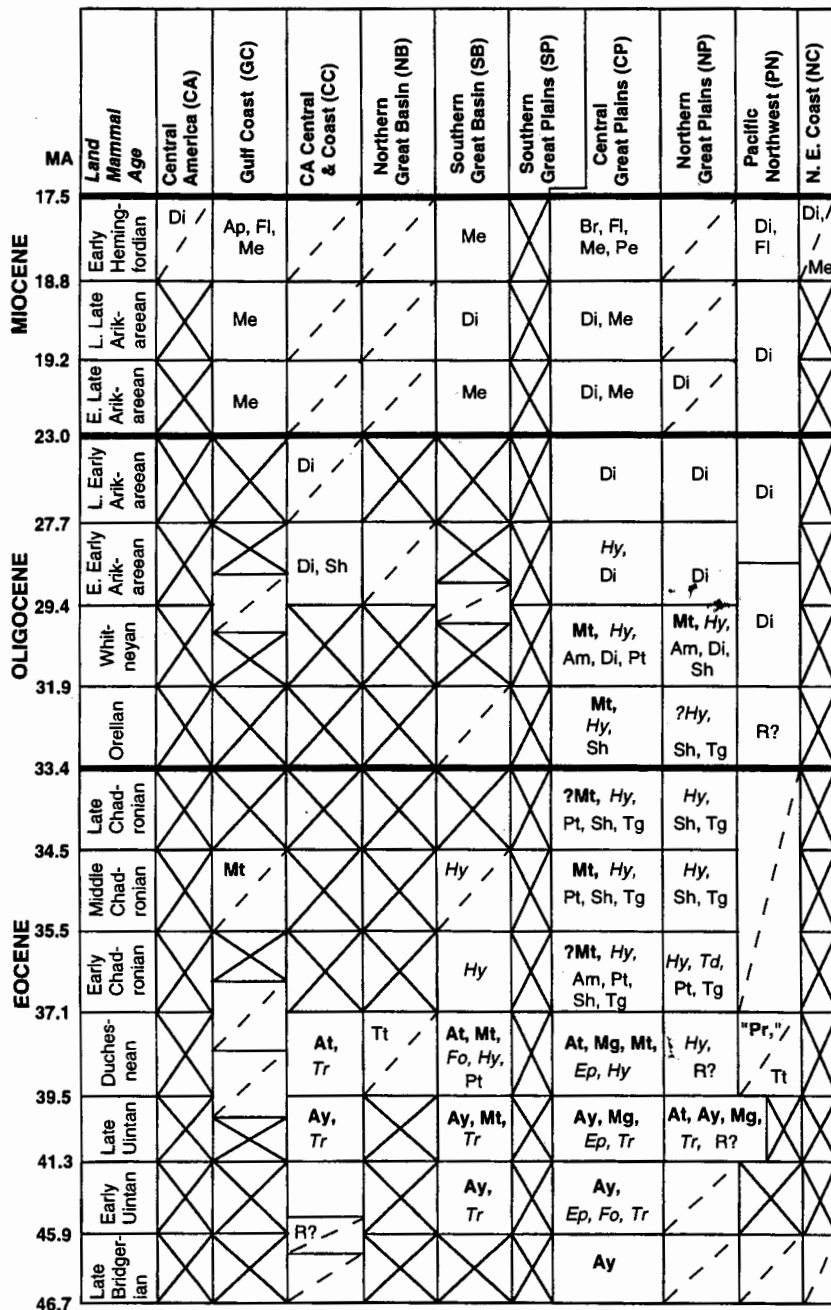


Figure 35.3. (Cont.)

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 summary 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, "eomorpid" chalicotheres and isctolophids were extinct, and brontotheres were reduced to the single genus *Duchesneodus*

(unique to this time interval) (see Figure 35.4). The only remaining basal ceratomorph taxon was *Toxotherium*, first appearing in the Duchesnean, although amynodontid and hyracodontid rhinocerotoids maintained their late Uintan diversity. Distinctive additions include definitive rhinocerotid genera (*Penetrigonas* and *Teletaceras*), and the "rebound" of the equids with the appearance of the hyracotheriine *Haplohippus* (known only from the Duchesnean) and the anchitheriine *Mesohippus* (see Figures 35.2, 35.3).

Further, although less dramatic, change is apparent at the start of the Chadronian. Brontotheres rediversified with the appearance of the extremely large, specialized eubrontotheres *Brontops*,

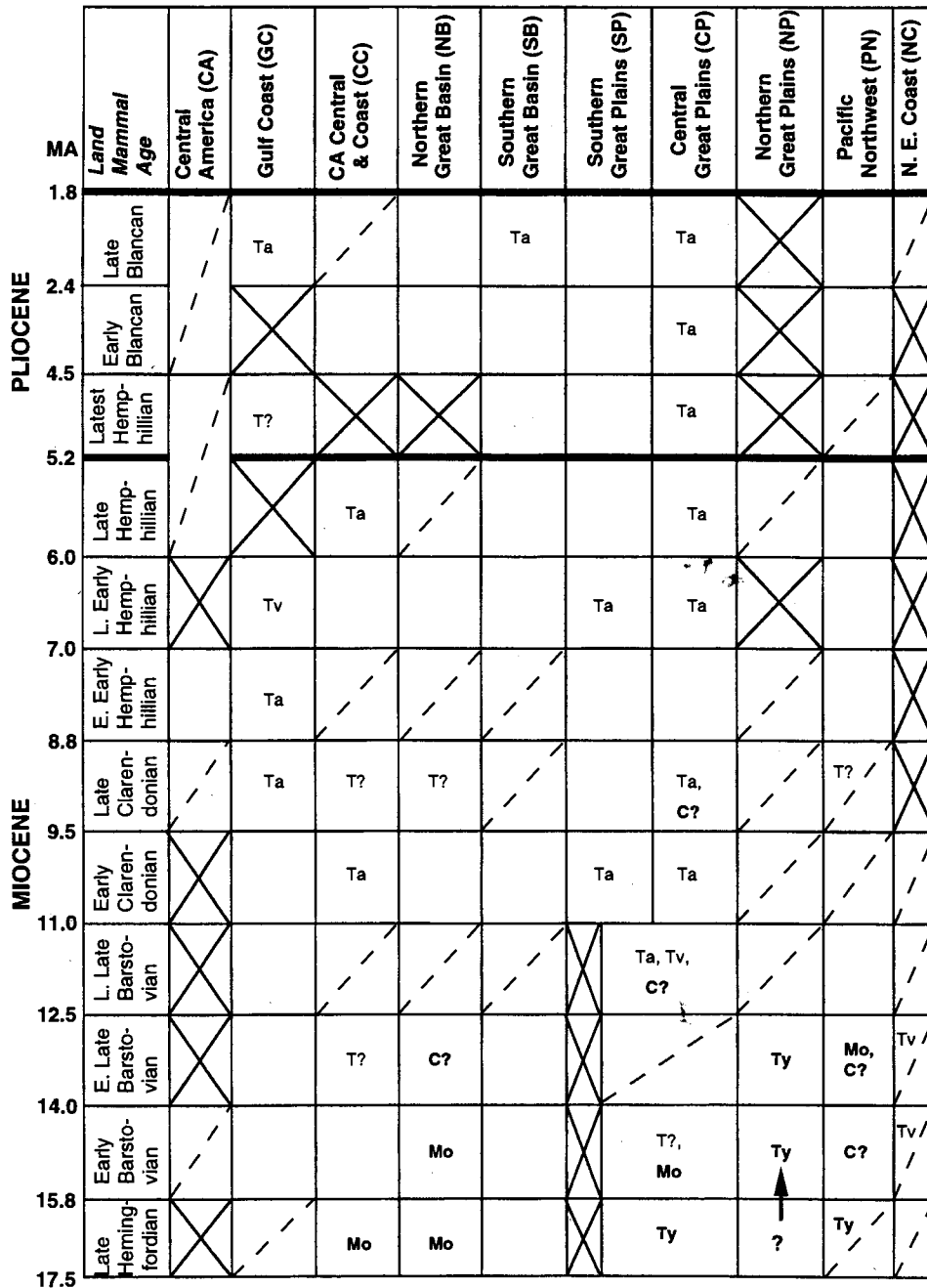


Figure 35.4. Biogeographic ranges of tapiroids, chalicotherioids, brontotheriids, and other perissodactyls. A "box" (for a particular time period in a particular biogeographic region) with a cross through it means no fossil localities are known for that time period from that area; a single dashed line through the box means only scant fossil information is available (usually only a single, small, locality). Key: "Tapiroids" are in roman type. Isectolophidae are in *italics* underlined: Ca = *Cardiolophus*, Ho = *Homogalax*, Is = *Isectolophus*. Basal ceratomorphs (and others) are in regular italics: *De* = *Desmatotherium*, *Di* = *Dilophodon*, *Fo* = *Fouchia*, *Hp* = *Heptodon*, *Hy* = *Hyrachyus*, *Pm* = *Paleomoropus*, *Se* = *Selenaletes*, *Sz* = *Schizotheriodes*, *Tx* = *Toxotherium*. Tapiroidea are in roman type underlined: Co = *Colodon*, He = *Helaletes*, Ht = *Heteraletes*. Tapiridae are in regular roman type: *Mi* = *Miotapirus*, *Ta* = *Tapirus*, *Tn* = new tapiroid genus, *Tv* = *Tapiravus*. T? = tapiroid indet. Chalicotherioids are in plain boldface: **Ep** = *Eomoropus*, **Gr** = *Grangeria*, **Mo** = *Moropus*, **Ty** = *Tylocephalonyx*. C? = chalicotheriid indet. Brontotheriidae are in boldface italics; horned taxa (Brontotheriinae) are underlined: **Br** = *Brontops*, **Dp** = "*Diplacodon*" *progressum*, **Du** = *Duchesneodus*, **Dx** = primitive diplacodont (sensu lato, genus undetermined), **Eo** = *Eotitanops*, **Et** = *Eotitanotherium*, **Eu** = eubronthere (genus undetermined), **Me** = *Mesatirhinus*, **Mg** = *Megacerops*, **Mn** = *Menops*, **Mr** = *Metarhinus* (= *Rhadinorhinus*), **Mt** = *Metatelmatherium*, **No** = *Notiotitanops*, **Pa** = *Palaeosyops*, **Pr** = *Protitanotherium*, **Pp** = *Protitanops*, **Sp** = *Sphenocoelus* (= *Dolicorhinus*), **St** = *Sthenodectes*, **Te** = *Telmatherium*. Perissodactyla incertae sedis are in boldface italics double underlined: **La** = *Lambdaotherium*.

Megacerops, and *Menops*. *Colodon* was the only surviving tapiroid. True tapiroids appear to be absent during the Duchesnean, but this may represent a sampling artifact because the tapiroid *Protapirus* is known from the late Uintan and Duchesnean, and tapiroids reemerged in the Oligocene (see Figure 35.4). Anchitheriines were now the only surviving equids, with the additional appearance of *Miohippus* in the early Chadronian (see Figure 35.2). Among the rhinocerotoids, amynodonts and hyracodonts were represented only by a single genus, *Metamynodon* and *Hyracodon*, respectively, but diversity increased among the rhinocerotoids, with the Chadronian appearance

of more derived genera such as *Trigonias*, *Amphicaenopus*, and the diceratheriine *Subhyracodon* (see Figure 35.3).

The transition from Eocene to Oligocene was marked by the extinction of the brontotheres and the appearance of the tapiroid *Protapirus*, but otherwise perissodactyl diversity was little affected. Some faunal changeover was apparent during the later Oligocene. The last definitive appearance of the tapiroid *Colodon*, the amynodontid *Metamynodon*, and the rhinocerotid *Penetrigonia* and *Amphicaenopus* was in the Whitneyan, and the rhinocerotid *Diceratherium* made its first appearance (see Figures 35.3, 35.4).

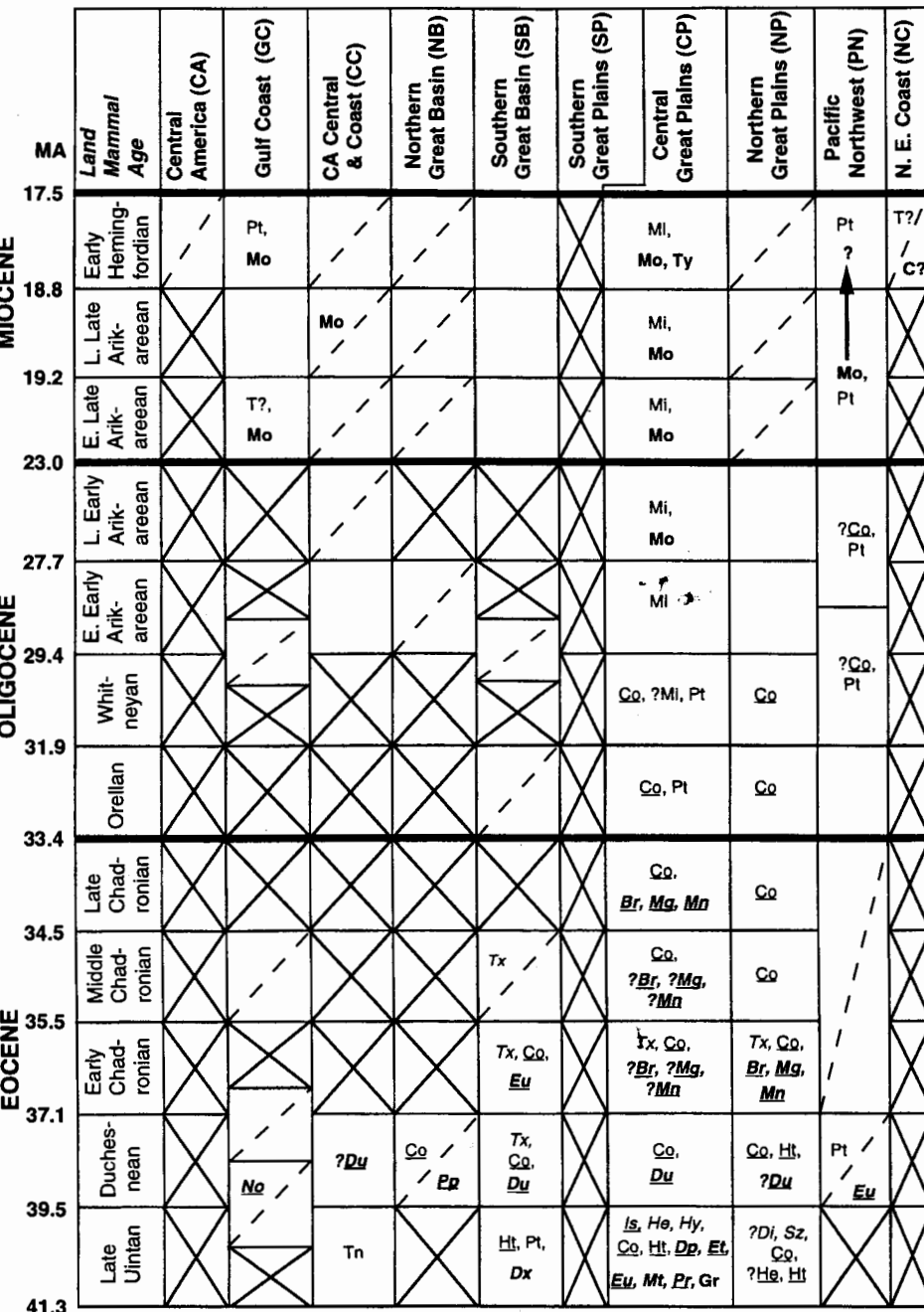


Figure 35.4. (Cont.)

The earliest Arikarean marked the last appearance of the hyracodontid *Hyracodon*, and the rhinocerotid *Subhyracodon*, and the first definitive appearances of the equid *Kalobatippus* and the tapirid *Miotapirus*. By the late early Arikarean 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 *Protapirus*, and possibly also of the tapiroid *Colodon*, in the John Day faunas of the Pacific Northwest, after their extinc-

tion by the end of the Whitneyan in the central Great Plains (see Figure 35.4). Rhinocerotids are virtually the only perissodactyls to be found in the California coast faunas.

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 anchitheriines such as *Archaeohippus*,

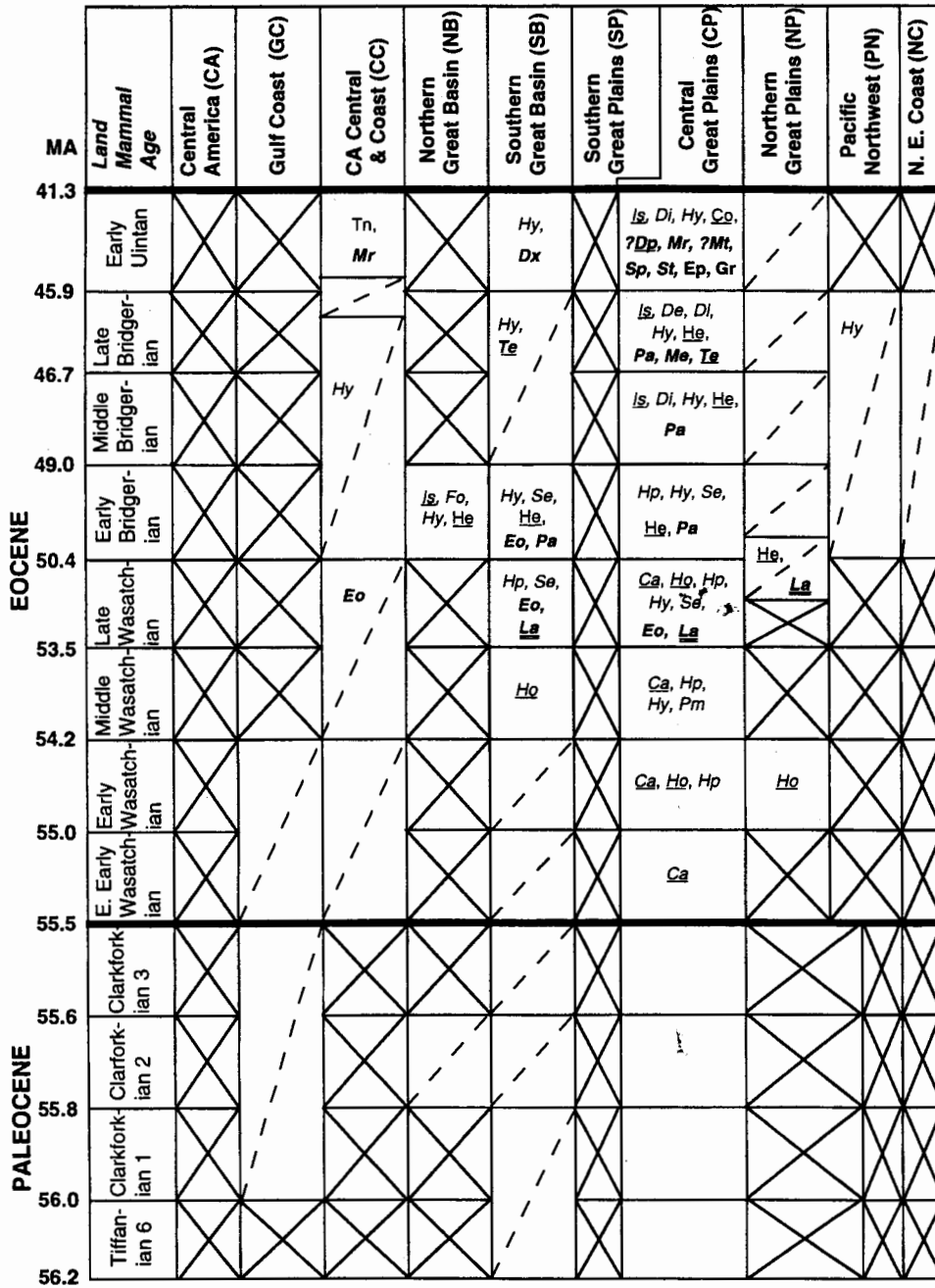


Figure 35.4. (Cont.)

Desmatippus, and *Parahippus*. The large, specialized anchitheriine *Hypohippus* first appeared in the early Hemingfordian. *Mesohippus* was now extinct, although *Miohippus* survived as a rare faunal element through the early Hemingfordian. The earliest equine equids may be present at the start of the Miocene, although the genus *Merychippus* is not definitively known until the early Hemingfordian (see Figure 35.2).

Rhinocerotid diversity increased with the appearance of *Meno-ceras* 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 rhinocerotid

immigrants appeared in the early Hemingfordian, including the aceratheriines *Floridaceras* and *Aphelops* and the teleoceratine *Brachypotherium* (see Figure 35.3). Chalicotheres were relatively abundant in this time period, with the appearance of *Tylocephalonyx* in the early Hemingfordian. Tapirids were the only surviving tapiroids, 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 *Protapirus* is known from here but is absent in the central Great Plains; *Miotapirus* 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 mammutid *Zygodolophodon* in the late Hemingfordian (from the Massacre Lake Local Fauna in Nevada [locality NB17] and the Deep River Local Fauna in Montana [locality NP34D]). 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. Gomphotheriid proboscideans first appeared in the early Barstovian, with a diversification in the late Barstovian, including the appearance of the shovel-tusker *Serbelodon* in the late Barstovian/early Clarendonian (see Figure 35.5).

Among the perissodactyls, the inception 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 equids showed a diversity of species of "*Merychippus*," representing both equinine and hipparionine lineages of this paraphyletic genus. The hipparionine *Hipparion* and the equinines *Protohippus* and *Calippus* appeared early in this time interval. Anchitheriines remained moderately diverse, although more primitive anchitheriines such as *Miohippus* were now extinct. In the early late Barstovian there was the appearance of a greater diversity of more derived equids: the hipparionines *Cormohipparion*, *Neohipparion*, and *Pseudhipparion*, and the equinine *Pliohippus* (see Figure 35.2).

Rhinocerotid diversity was now almost entirely comprised of aceratheriines and teleoceratines, although *Diceratherium* survived into at least the late Hemingfordian. The short-legged, probably semiaquatic, grazing teleoceratine *Teleoceras* first appeared in the late Hemingfordian. Dwarf rhinocerotids were common in the middle Miocene, with the appearance of the aceratheriine *Peraceras hessei* in the early Barstovian and *Teleoceras meridianum* in the early late Barstovian (see Figure 35.3). Chalicotheres and tapirids continued to appear as rare elements of the fauna during the middle Miocene, with the appearance of the extant genus *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.

Anchitheriine equids persisted until the end of the Clarendonian, but were now represented only by the very large, highly specialized, genera *Hypohippus* and *Megahippus* (see also Janis, Gordon, and Illius, 1994). In contrast, the diversity of equine equids increased. The early Clarendonian was the zenith of equine generic diversity, with ten sympatric taxa (all of which could be found in central

Great Plains faunas). The derived equinine *Dinohippus*, sister taxon to the extant *Equus*, first appears in the early Clarendonian (see Figure 35.2).

Gomphotheres remained moderately diverse among the proboscideans, with the appearance of the immigrant shovel-tusked gomphotherid *Platybelodon*. *Zygodolophodon* was replaced by the larger, more specialized mammutid *Mammuth* (see Figure 35.5). 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 anchitheriine equids. Although sampling was poor during the late late Barstovian and Clarendonian in the northern Great Plains and Pacific Northwest, perissodactyls (especially rhinocerotids) were rather conspicuously underrepresented from these regions during this time period. Mammutid proboscideans appear to have been confined to the Gulf Coast and the Pacific Northwest during the Clarendonian.

MIO-PLIOCENE CHRONOFAUNA

By the start of the Hemphillian, specialized browsing perissodactyls, such as anchitheriine equids and chalicotheres, had become extinct. In contrast, the browsing rhinocerotid *Aphelops* survived, possibly indicative of a different habitat for this animal than for the other browsers (perhaps resembling the present-day savanna-dwelling browsing rhinoceros, *Diceros bicornis*). Dwarf species of rhinocerotids were now extinct. *Aphelops* and *Teleoceras* survived into the earliest Pliocene, and there is a single record of a possible *Teleoceras* from the early Blancan (see Figure 35.3). Apparently beating all evolutionary odds, the extant tapirid *Tapirus* (also a browser) continued through 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 equinine *Astrohippus* appeared in the late early Hemphillian. Equid diversity showed a steady decline through the Mio-Pliocene chronofauna, however: *Protohippus* and *Hipparion* were extinct by the late Hemphillian, and the Gulf Coast faunas appeared to act as a refuge, especially during the Pliocene, for genera such as *Cormohipparion*, *Neohipparion*, *Calippus*, and *Pseudhipparion*. 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 (Cerling, Wang, and Quade, 1993; MacFadden and Cerling, 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-tusker *Amebelodon* in the early early Hemphillian

MA	Land Mammal Age	Central America (CA)	Gulf Coast (GC)	CA Central & Coast (CC)	Northern Great Basin (NB)	Southern Great Basin (SB)	Southern Great Plains (SP)	Central Great Plains (CP)	Northern Great Plains (NP)	Pacific Northwest (PN)	N. E. Coast (NC)
1.8	Late Blancan		Ma, Cu, Go, Mt	Rh	St	Ma, Cu, Rh, St	Rh, St	Ma, Rh, St		Ma, St	
2.4	Early Blancan			St	Ma	Cu, Rh, St	M?, St	Ma, Rh, St		Ma	
4.5	Latest Hemphillian		Ma, Rh, Go			Rh, St	Rh	G?			
5.2	Late Hemphillian			Ma, Rh, Go	Ma, ?Rh	Ma, Rh, St	Ma, Ak, Rh	Ma, Ak, ?Gn, Go		M?, G?	
6.0	L. Early Hemphillian		Ak, Am, To	Ma, Go	Ma	Ma, Go	Am	Am, To, ?Rh, Go		M?	
7.0	E. Early Hemphillian	Rh	Am, Go		Se		Am, ?Rh, Go	Am, Go	Am	Ma, Am	
8.8	Late Clarendonian	Go	Go	Go	Se, Go			Pl, Se, Go		Ma, G?	
9.5	Early Clarendonian		Ma, Gn, Go, Me	Go	Se, Go	Go	Go, Te	Eu, Go, Te			
11.0	L. Late Barstovian		M?, Go	Go	Se	G?		Zy, Eu, Go, Me			
12.5	E. Late Barstovian		P?		Zy, Go	Go, Me		Zy, Go	Zy, Go	M?, G?	Goy
14.0	Early Barstovian	Go	P?		Zy			P?		Go	
15.8	Late Hemphordian				Zy				Zy		
17.5											

Figure 35.5. Biogeographic ranges of proboscideans. A "box" (for a particular time period in a particular biogeographic region) with a cross through it means no fossil localities are known for that time period from that area; a single dashed line through the box means only scant fossil information is available (usually only a single, small, locality). Key: Mammutiidae are in boldface: Ma = *Mammut*, Zy = *Zygodolophon*. M? = mammutid indet. Gomphotheriidae are in roman type face: Ak = *Amebelodon* (*Konobelodon*), Am = *Amebelodon*, Pl = *Platybelodon*, Se = *Serbelodon*, To = *Torynobelodon*. "New World forms" are in italic: Cu = *Cuvieronius*, Rh = *Rhynchotherium*, St = *Stegomastodon*. Other gomphotheres are in regular roman type: Eu = *Eubelodon*, Gn = *Gnathabelodon*, Go = *Gomphotherium*, Me = *Megabelodon*. G? = gomphotheriid indet. Other elephantoids are in boldface italics: Mt = *Mammuthus*, Te = *Tetralophodon*. P? = proboscidean indet.

and of other shovel-tusked taxa such as *Torynobelodon* and *Gnathabelodon*, which may also have survived during the Hemphillian. However, shovel-tuskers did not survive into the Pliocene. The gomphotheres *Gomphotherium* may have survived into the Pliocene only in the Gulf Coast faunas. The "New World" form *Rhynchotherium* may have been present as early as the earliest Hemphillian, joined by *Stegomastodon* in the late Hemphillian. These New World forms, joined by *Cuvieronius* 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. Rhinocerotids were now known from latest Miocene Pacific Northwest faunas (perhaps their earlier apparent absence merely represents a sampling artifact). Despite the diversity 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 nomenclature bias because species of *Dinohippus* and *Pliohippus* are frequently mistaken for each other, and both genera are in extensive need of revision (see comments in MacFadden, this volume, Chapter 37).

SUMMARY

Perissodactyls were diverse in Eocene faunas, with a zenith of diversity at the family level in the Uintan. This late middle Eocene perissodactyl diversity comprised brontotheres, "eomorpid" chalicotheres, and a diversity of tapiroids and ceratomorphs: Perhaps paradoxically, equid diversity was low at this time.

A later Eocene reduction in perissodactyl diversity occurred slightly earlier (Duchesnean) to the fauna shifts seen in other large mammal groups (early Chadronian). Extinctions at this time included chalicotheres and nontapirid "tapiroids." A "White River" late Eocene–Oligocene perissodactyl chronofauna was comprised primarily of anchitheriine equids, tapirids, and rhinocerotine rhinocerotoids. Brontotheres were prominent as large specialized forms in the Chadronian, but did not survive the Eocene. A mynodontine and hyracodontine rhinocerotoids were also most diverse in the late Eocene and did not survive the Oligocene.

A Runningwater chronofauna, commencing in the early Miocene, was marked by the radiation of more larger and specialized anchitheriine equids, newly immigrant chalicotheriid chalicotheres, and diversity of immigrant rhinocerotids. Change at the start of the Clarendonian fauna, in the late Hemingfordian (late early Miocene), contrasts with changes in faunal diversity seen in other large mammals at this time in that there were few generic 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 mammutid proboscideans.

Proboscideans were not generally common in North America until the later middle Miocene, with gomphotheriids appearing for the first time in the early Barstovian. Both large specialized rhinocerotids (including the probable grazing hippo mimic *Teleoceras*) and dwarf rhinos were common in the middle Miocene, and a diversity of both browsing and grazing equids was apparent. By the Clarendonian (early late Miocene), although generic diversity of the grazing equine equids was at its zenith, diversity was greatly reduced in the browsing anchitheriines. Both anchitheriine equids and chalicotheres (also browsers) were extinct by the end of the Clarendonian, but some browsers, such as the rhino *Aphelops* and the extant tapir *Tapirus*, survived.

In the Mio-Pliocene chronofauna a diversity of equids and large rhinocerotoids continued during the late Miocene, but had declined by the Pliocene. The last North American rhinocerotoid was known from the early Blancan, and by the late Blancan the extant *Equus* was virtually the only surviving equid. The latest Miocene saw a flourishing of shovel-tusked proboscideans, but both these and regular gomphotheres were replaced by "New World form" gomphotheres in the Pliocene. The mammutid *Mammut* 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 faunas were not particularly distinctive in their perissodactyl and proboscidean components, except for the role that the Florida faunas appear to have played as a refuge for the earlier diversity of equine equids in the Pliocene and latest Miocene.

REFERENCES

- Berger, J. (1986). *Wild Horses of the Great Basin*. Chicago: University of Chicago Press.
- Blainville, de, H. M. D. (1816). Prodrôme d'une nouvelle distribution systématique du règne animal. *Bulletin des Sciences, Société Philomathique de Paris, Série 3*, 3, 105–124.
- Borissiak, A. (1945). The chalicotheres as a biological type. *American Journal of Science*, 243, 667–9.
- Cerling, T. E., Wang, Y., & Quade, J. (1993). Global ecological change in the late Miocene: expansion of C4 ecosystems. *Nature*, 361, 344–5.
- Fortelius, M., & Kappelman, J. (1993). The largest land mammal ever imagined. *Zoological Journal of the Linnean Society*, 107, 85–101.
- Hooker, J. J. (1984). A primitive ceratomorph (Perissodactyla, Mammalia) from the early Tertiary of Europe. *Zoological Journal of the Linnean Society*, 82, 229–44.
- (1989). Character polarities in early perissodactyls and their significance for *Hyracotherium* and infraordinal relationships. In *The Evolution of Perissodactyls*, eds. D. R. Prothero & R. M. Schoch, pp. 79–101. Oxford: Clarendon.
- (1994). The beginning of the equoid radiation. *Zoological Journal of the Linnean Society*, 112, 29–63.
- Janis, C. M. (1976). The evolutionary strategy of the Equidae, and the origins of rumen and cecal digestion. *Evolution*, 30, 757–74.
- (1993). Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics*, 24, 467–500.
- Janis, C. M., Gordon, I., & Illius, A. (1994). Modelling equid/ruminant competition in the fossil record. *Historical Biology*, 8, 15–29.
- MacFadden, B. J. (1992). *Fossil Horses: Systematics, Paleobiology, and Evolution of the Family Equidae*. Cambridge: Cambridge University Press.
- MacFadden, B. J., & Cerling, T. E. (1994). Fossil horses, carbon isotopes, and global change. *Trends in Ecology and Evolution*, 9, 481–5.
- Novacek, M. J., Wyss, A. R., & McKenna, M. C. (1988). The major groups of eutherian mammals. In *The Phylogeny and Classification of the Tetrapods, Vol. II: Mammals*, ed. M. J. Benton, pp. 31–71. Systematics Association Special Volume no. 35B. Oxford: Clarendon.
- Owen, R. (1848). Description of teeth and portions of jaws of two extinct Anthracotherioid quadrupeds (*Hyopotamys vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London*, 4, 103–41.
- Prothero, D. R., Manning, E. M., & Fischer, M. (1988). The phylogeny of the ungulates. In *The Phylogeny and Classification of the Tetrapods, Vol. II: Mammals*, ed. M. J. Benton, pp. 201–34. Systematics Association Special Volume no. 35B. Oxford: Clarendon.
- Prothero, D. R., & Schoch, R. M. (1989). Origin and evolution of the Perissodactyla: summary and synthesis. In *The Evolution of Perissodactyls*, eds. D. R. Prothero & R. M. Schoch, pp. 504–29. Oxford: Clarendon.
- Radinsky, L. B. (1964). *Paleomoropus*, a new early Eocene chalicothere (Mammalia, Perissodactyla), and a revision of Eocene chalicotheres. *American Museum Novitates*, 2179, 1–28.
- Rose, K. D. (1985). Comparative osteology of North American dichobunid artiodactyls. *Journal of Paleontology*, 59, 1206–26.
- Schoch, R. M. (1983). Relationships of the earliest Perissodactyls. *Geological Society of America, Abstracts with Programs*, 15, 144.
- (1984). Introduction. In *Vertebrate Paleontology*, ed. R. M. Schoch, pp. 1–16. New York: Van Nostrand Reinhold.
- (1985). *Concepts of the relationships and classification of major perissodactyl groups: notes for a workshop on fossil perissodactyls held at Fourth International Theriological Congress, Edmonton, Canada, August 1985*. Privately printed and distributed.

- (1989a). A brief historical review of perissodactyl classification. In *The Evolution of Perissodactyls*, eds. D. R. Prothero & R. M. Schoch, pp. 13–23. Oxford: Clarendon.
- (1989b). A review of the tapiroids. In *The Evolution of Perissodactyls*, eds. D. R. Prothero & R. M. Schoch, pp. 298–320. Oxford: Clarendon.
- Cott, W. B. (1941). Perissodactyla. The mammalian fauna of the White River Oligocene. *Transactions of the American Philosophical Society*, 28, 747–980.
- Shoshani, J. (1993). Hyracoidea-Tethytheria affinity based on myological data. In *Mammal Phylogeny: Placentals*, eds. F. S. Szalay, M. J. Novacek, & M. C. McKenna, pp. 235–56. New York: Springer-Verlag.
- Simpson, G. G. (1945). The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85, 1–350.
- Tedford, R. H., Skinner, M. F., Fields, R. W., Rensberger, J. M., Whistler, D. P., Galusha, T., Taylor, B. E., Macdonald, B. E., & Webb, S. D. (1987). Faunal succession and biochronology of the Arikareean through Hemphillian interval (late Oligocene through earliest Pliocene epochs) in North America. In *Cenozoic Mammals of North America*, ed. M. O. Woodburne, pp. 153–210. Berkeley: University of California Press.
- Wood, H. E., II (1934). Revision of the Hyrachyidae. *Bulletin of the American Museum of Natural History*, 67, 181–295.
- (1937). Perissodactyl suborders. *Journal of Mammalogy*, 18, 106.