

# EVOLUTION OF TERTIARY MAMMALS OF NORTH AMERICA

VOLUME 1:  
TERRESTRIAL CARNIVORES, UNGULATES,  
AND UNGULATELIKE MAMMALS

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## 42 Rhinocerotidae

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### INTRODUCTION

The Rhinocerotidae was one of the most successful groups of mammals in North America. After the extinction of titanotheres in the late Eocene, rhinos were the largest land mammals on the continent until the appearance of mastodons in the mid-Miocene. They occurred in enormous herds, especially in the High Plains Miocene, and some quarries yield thousands of their bones. Rhinocerotids were very diverse ecologically. There were large hippolike grazers (*Teleoceras*, *Brachypotherium*, and *Peraceras superciliosum*); prehensile-lipped browsers (most of the aceratherines); four independent examples of dwarfing (*Peraceras hessei*, *Teleoceras meridianum*, and new undescribed species of *Teleoceras* and *Diceratherium*); pig-sized herding rhinos (*Menoceras arikareense*; see Figure 42.1); and many other less specialized kinds. Rhinocerotids occupied the large-bodied herbivorous niches in North America from the early Oligocene to the end of the Miocene, and many other niches besides.

The family Rhinocerotidae first appears in North America, probably as immigrants from Asia, in the Duchesnean (late middle Eocene) of Oregon, California, and Texas. A new genus, *Teletaceras*, has been erected by Hanson (1989) to refer to the most primitive North American rhinocerotids from the Clarno Formation of Oregon. By the latest Eocene (Chadronian) and early Oligocene, there were several rhino genera represented in the High Plains: *Trigonias*, *Penetrigonias*, *Subhyracodon*, and *Amphicaenopus*. In the Whitneyan and Arikareean (later Oligocene through earliest Miocene), however, rhino diversity was reduced to one genus, *Diceratherium*, which persisted from 31–17 Ma, the longest unopposed reign of any rhino. In the latest Arikareean, the pig-sized rhino *Menoceras arikareense* (misidentified as *Diceratherium cooki* in most books and museum labels) immigrated from Europe. It occurs in large numbers at the famous Agate Springs Quarries in Nebraska.

During the Hemingfordian (late early Miocene), North American mammal faunas were in great flux, and there was considerable

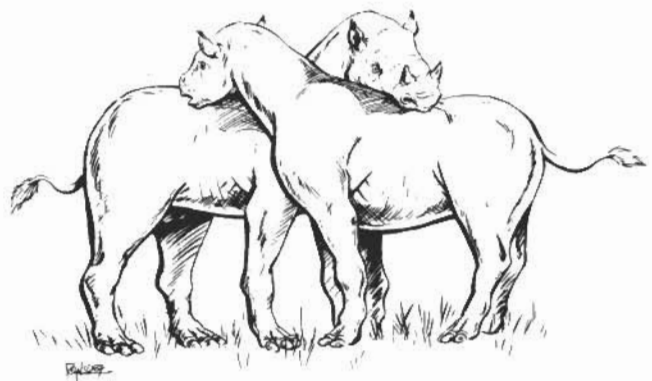


Figure 42.1. Restoration of *Menoceras*, by Brian Regal.

change in the rhinos as well. *Diceratherium* and *Menoceras* became extinct as invading aceratherines (*Floridaceras*, *Peraceras*, *Aphelops*, and a new undescribed genus) and teleoceratines (*Brachypotherium*) established themselves. From the late Hemingfordian until the late Hemphillian (latest Miocene), the rhino faunas were stable elements of the “Clarendonian chronofauna” (Tedford, 1970; Webb, 1984; Tedford et al., 1987). There was a single genus of browsing aceratherine (typically *Aphelops*) and grazing hippolike teleoceratine (typically *Teleoceras*) in nearly every North American locality of Barstovian, Clarendonian, or Hemphillian age.

At the end of the Hemphillian, rhinoceroses were nearly extinct in this continent, along with the extinction of protoceratids, dromomerycids, mylagaulid and eomyid rodents, most horses, and antilocaprids, totaling 62 genera (Webb, 1984). One isolated tooth scrap from the Blancan of Texas is known (Madden and Dalquest, 1990), but no other rhinos are known after the Hemphillian. This extinction was probably related to the loss of subtropical wooded habitat during the cooling and drying associated with the Messinian worldwide climatic event.

## DEFINING FEATURES OF THE FAMILY RHINOCEROTIDAE

### CRANIAL

Despite the popular association of rhinos with horns, most extinct rhinos were hornless. Rhino horns are made of agglutinated hair loosely attached to a rugose area on the skull, so they are rarely preserved. Nevertheless, from the rugosities on the skull surface, it is clear that horns were present in only a few groups. Paired nasal flanges occur in *Diceratherium*, and small paired horns (independently derived) in *Menoceras*. Teleoceratines have a small terminal nasal horn, and male *Peraceras superciliosum* is the only aceratherine to bear a horn. Instead, rhinocerotids must be defined on a large suite of cranial, dental, and postcranial characters.

The skull is low and saddle shaped, with broad parasagittal crests and laterally flared lambdoid crests (Fig. 42.2). The premaxillary-nasal contact is lost. The nasals are long and slender, and in the aceratherines, the narial notch is deeply retracted. The dentary has a broad ascending ramus with a straight posterior border and a distinct postcondylar process, a unique rhinocerotid synapomorphy. The mandibular condyle is broad, flat surfaced, and horizontal.

### DENTAL

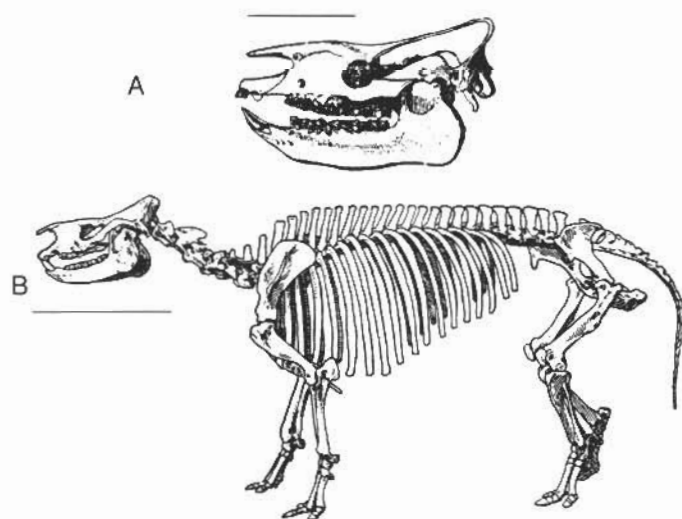
As reviewed by Prothero, Manning, and Hanson (1986), the Rhinocerotidae are defined by the presence of a chisel-shaped I1 occluding with a tusklike i2. On M3, the metacone is extremely reduced or absent, and the posterior cingulum is short. In most rhinocerotids except the most primitive ones, the other incisors and canines are lost. The upper cheek teeth are the most characteristic part of the anatomy. The molars typically have the diagnostic  $\pi$ -shaped pattern formed by the junction of the protoloph, metaloph, and ectoloph. In very derived forms, these teeth can become very hypsodont and develop various internal ridges (crochets, antecrochets, and cristae) to increase surface area (see Prothero, Manning, and

Hanson, 1986, Figure 6). Primitive rhino premolars were not fully molarized, so there may be crests connecting the protocone and hypocone. In the past, the subtle differences in premolars were used to oversplit the group (e.g., Wood, 1927). Quarry samples show that most of this premolar variation is normal intrapopulation variability, and thus the species lists here reflect considerable lumping. Lower teeth, on the other hand, have the stereotyped L-shaped protolophid and metalophid, which changes only in becoming more hypsodont.

### POSTCRANIAL

When prospecting in almost any Oligocene or Miocene locality, rhino postcranial bones are easily recognized by their size and robustness compared to any other mammal of the time (except titanotheres and mastodonts, which were even larger). Only *Menoceras* and the dwarf species became more gracile, but even their bones cannot be mistaken for any other mammal. In particular, the rhino axis has a fused intervertebral canal and a deep alar notch in the anteromedial margin of the transverse process. There are also deep dorsal and ventral notches on the anterior articulations of the atlas. The medial process of the proximolateral tuberosity of the humerus is very long and posteromedially inflected. The limbs in teleoceratines are very robust and proximodistally shortened; this is especially true of the manus and pes. Most rhinocerotids had tridactyl feet, but the most primitive ones, like *Trigonias*, still retain a functional fifth metacarpal. This bone also reappears in a few individuals of the aceratherines *Aphelops*, *Peraceras*, and *Floridaceras*, possibly as an atavism (Prothero, Manning, and Hanson, 1986, p. 359). Teleoceratines also have a posterior articulation of the scaphoid and lunar.

Most of the systematics in this chapter is based on Prothero, Manning, and Hanson (1986), Prothero and Manning (1987), Prothero, Guérin, and Manning (1989), and Prothero (in a complete monograph on the North American Rhinocerotidae, which is currently in preparation).



**Figure 42.2.** Osteology of the Orellan rhinocerotid *Subhyracodon occidentalis*. A Skull (after Osborn, 1898) (scale bar = 50 cm). B. Skeleton (after Scott, 1941) (scale bar = 1 m).

## SYSTEMATICS

## SUPRAFAMILY

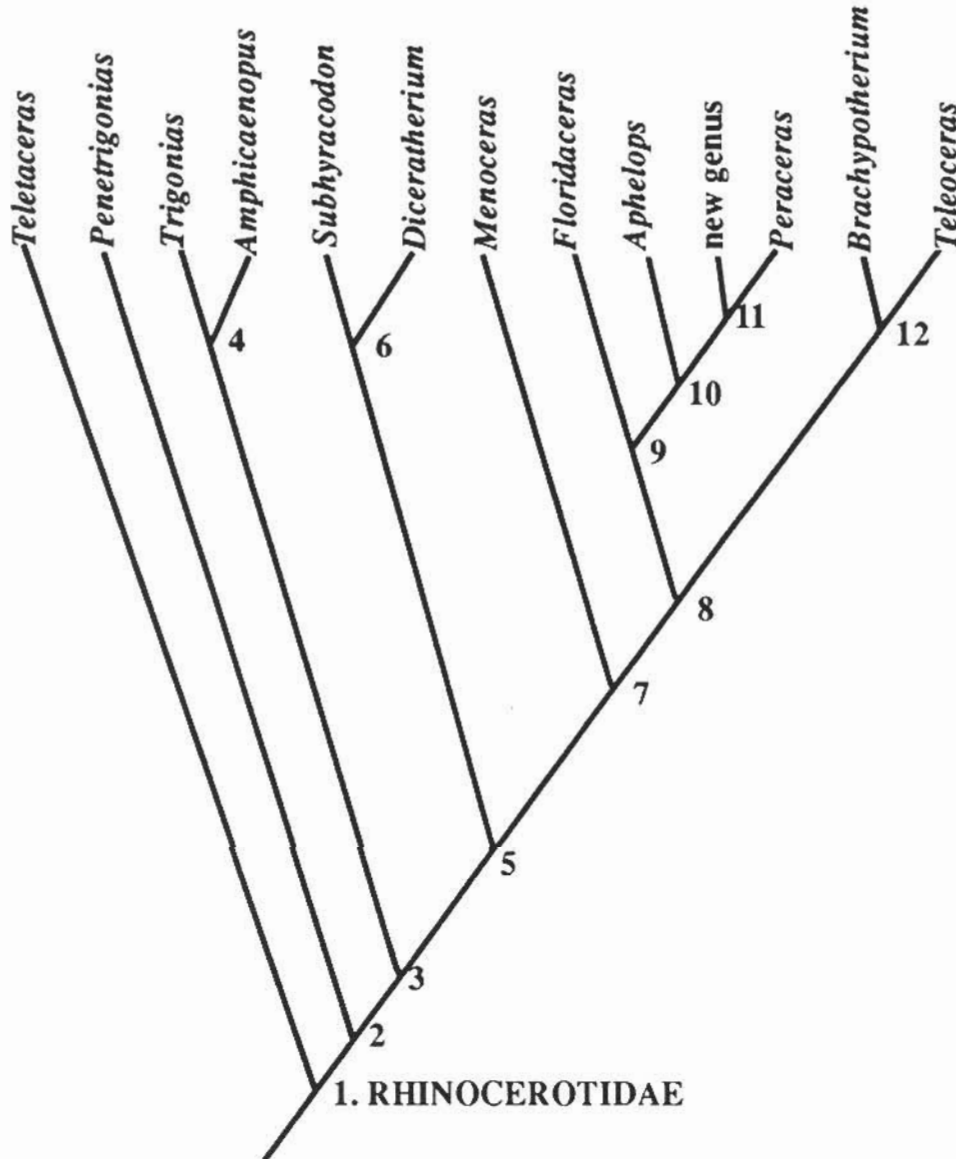
The Hyracodontidae are the closest sister taxon to the Rhinocerotidae. The two groups are united by the following derived features: reduced parastyles; longer cheek tooth series relative to skull length; M1–M2 metacone flange lengthened; M3 metacone reduced and lingually deflected.

## INFRAFAMILY

A number of subfamilies and tribes have been proposed within the

Rhinocerotidae, but only a few are monophyletic (Figure 42.3). The subfamily Aceratheriinae is easily recognized by their retracted narial notch and loss of I1. Presumably, these rhinos had a prehensile lip or snout for browsing. The tribe Teleoceratini are highly derived and easily recognized by their short, stout, proximodistally compressed limbs and feet, broad brachycephalic skulls with flaring lambdoid crests, and nasal bones with a U-shaped cross section supporting a small terminal horn. They also have an elongate calcaneal tuber and a posterior articulation of the scaphoid and lunar.

In the past, there was a paraphyletic subfamily “Caenopinae” for all the primitive taxa; it has no legitimacy (even the name *Caenopus* is invalid). Until recently, *Diceratherium* and *Menoceras* were placed together in a subfamily Diceratheriinae for the paired-horned



**Figure 42.3.** Interrelationships of the North American Rhinocerotidae. Characters at the nodes are as follows: (1) RHINOCEROTIDAE: I1 chisel shaped; i2 tusklike; very reduced M3 metacone; M1–2 cristae lost; premaxillary-nasal contact lost; reduced posterior cingulum on M3; shorter posterior ectoloph on M1–2. (2) M1–3 parastyle folds more open; anterochets enlarged; M3 metacones lost; i3, lower canine lost in adults; metacone ribs on molars lost; paracone and metacone ribs separate and reduced on premolars; greater hypsodonty; postcondyloid process on ramus; broad ascending ramus on dentary, with straight posterior border; long, posteromedially curved process on anterolateral tuberosity of humerus. (3) Broad parasagittal crests; laterally flared lambdoid crests; concave dorsal skull profile; long nasals. (4) Extended occiput; anterodorsally inflected basicranium; long, flattened postglenoid process. (5) Third upper and lower incisors, upper canine lost; metacone ribs of P2–4 lost; P2 molarized; mandibular condyle broader, flat surfaced and nearly horizontal; distal condyle of humerus more asymmetrical; dorsoventrally compressed posterior articular surface on atlas; postglenoid process faces anteriorly; fifth metacarpal reduced to vestige. (6) DICERATHERIINAE: long, broad supraorbital ridges; paired nasal ridges in males. (7) Strong crochet present; I2 lost; reduced sagittal crest; premaxillary further reduced; nasal incision over posterior P2; basicranium shortened relative to palate; upper molar lingual cingula weak or absent;

shallow anteroventral notch on atlas. (8) Upper premolars fully bilophodont; overall size increase. (9) ACERATHERIINAE: medial flange of i2 reduced; long diastema posterior to i2; fifth metacarpal enlarged. (10) Premaxillary reduced; I1 lost; nasal incision over anterior P4. (11) Dorsal skull profile flattened. (12) TELEOCERATINAE: TELEOCERATINI: metapodials shortened; carpals and tarsals compressed dorsoventrally; strong anterochets; broad zygomatic arches; lateral edge of nasals downturned and thinned, resulting in U-shaped cross section; calcaneal tuber elongate; brachycephalic skull; nasal incision retracted to level of anterior P3; p2 lost in some *Teleoceras*.

rhinos (Peterson, 1920). Tanner (1969) showed that the two genera were very distinct, and Prothero, Manning, and Hanson (1986) and Prothero and Manning (1987) have shown that they are only distantly related. A large suite of derived characters (Figure 42.3, node 7) unites *Menoceras* with higher rhinos, and the paired-horn condition is a parallelism. The Diceratheriinae includes only *Diceratherium* sensu stricto and *Subhyracodon*, and *Menoceras* is grouped with European *Pleuroceros* in the subfamily Menoceratinae (Prothero, Manning, and Hanson, 1986; Prothero, Guérin, and Manning, 1989).

#### INCLUDED NORTH AMERICAN GENERA IN THE FAMILY RHINOCEROTIDAE

The locality numbers listed for each genus refer to the list of unified localities in Appendix I. The locality numbers may be listed in a couple of alternative ways. The acronyms for museum collections are listed in Appendix III.

Parentheses around the locality (e.g., [CP101]) mean the taxon in question at that locality is cited as an "aff." or "cf." the taxon in question. Parentheses are usually used for individual species, thus implying the genus is firmly known from the locality, but the actual species identification may be questionable. Question marks in front of the locality (e.g., ?CP101) mean the taxon is questionably known from that locality, thus implying some doubt that the taxon is actually present at that locality, either at the genus or the species level.

#### BASAL RHINOCEROTIDS

##### *Teletaceras* Hanson, 1989

Type species: *Teletaceras radinskyi* Hanson, 1989.

Type specimen: UCMP 129000.

Characteristics: Small rhinocerotid with I1/i2 chisel-tusk combination, but these are not as enlarged as they become in later rhinocerotids. *Teletaceras* has an unreduced anterior dental series, sharp creases between molar parastyles and paracones, more lingually inflected molar metacone axes, and low connection of lower molar metalophids to protolophids. There is a marked postcanine diastema and a single-rooted p1.

Average length of m2: 20.5–24.8 mm.

Included species: *T. radinskyi* (known from locality PN5B); *T. mortivallis* (locality NB2).

##### *Penetrigonia* Tanner and Martin, 1976 (synonyms: *Caenopus* in part; *Subhyracodon*, in part)

Type species: *Penetrigonia hudsoni* Tanner and Martin, 1976.

Type specimen: UNSM 62049.

Characteristics: *Penetrigonia* is readily distinguished from *Teletaceras* not only by its larger size, but also by a whole suite of more advanced rhinocerotid characters (Figure 42.3, node 2), including a completely developed rhinocerotid incisor complex, the absence of an M3 metacone, the loss of i3 and the lower canine, and the characteristic features of the mandible and humerus.

Average length of m2: 25.0–27.4 mm.

Included species: *P. hudsoni* (known from localities [SB44B], CP39C, CP39G, CP39IIC, CP42A, CP83A, CP98A); *P. sagittatus* (locality NP10B); *P. dakotensis* (localities CP39C, CP68D, CP84B).

Comments: Small Oligocene rhinocerotids that are slightly larger than *Teletaceras* but smaller than any species of *Subhyracodon* or *Trigonia* have been incorrectly referred to a number of genera. The first valid name to be proposed for this group was *Penetrigonia*, although the original diagnosis was based on invalid differences in upper premolar crests. Ignoring the premolars, there are distinct features in the size and the reduction of the premaxilla that unite this genus.

In their concept of *Penetrigonia*, Prothero, Manning, and Hanson (1986) included not only the type, but also specimens from the Yoder Formation (locality CP42A) and Flagstaff Rim, Ledge Creek (localities CP39C, CP39G), and Beaver Divide areas of Wyoming (locality CP39IIC), the Porvenir Local Fauna of Texas (locality SB44B), and specimens referred to "*Subhyracodon*" *sagittatus* by Russell (1982). "*Caenopus*" *dakotensis* probably also belongs in this genus.

##### *Trigonia* Lucas, 1900

Type species: *Trigonia osborni* Lucas, 1900.

Type specimen: USNM 3924.

Characteristics: The medium- large-sized Chadronian rhino, *Trigonia*, is known from a number of complete skeletons. It retains all the anterior teeth except for i3 and the lower canine. The skull profile is distinctively concave and saddle shaped, with low sagittal crests and broad lambdaoid crests. It is one of the few nonaceratherine rhinos that retain a functional fifth metacarpal.

Average length of m2: 37.0–50.0 mm.

Included species: *T. osborni* (known from localities CP68B, CP83A, CP83B, CP98A, NP10B, NP27C, CP42A, NP10B); *T. wellsii* (localities CP83A, CP98A).

*Trigonia* sp. is also known from localities NB24C, NB27D, (CP39F), CP98B, NP24C, NP27D.

Comments: *Trigonia* was once grossly oversplit by Gregory and Cook (1928) based on slight premolar variations within a single population, but this same evidence is now grounds for regarding most premolar differences as intrapopulational. Besides the type species, only the much larger *T. wellsii* is valid.

##### *Amphicaenopus* Wood, 1927

Type species: *Amphicaenopus platycephalus* (Osborn and Wortman, 1894).

Type specimen: AMNH 542.

Characteristics: *Amphicaenopus* is a precociously large rhinocerotid from the Chadronian and Whitneyan of the South Dakota Big Badlands and from Stark County, North

Dakota. It has a very broad, dolichocephalic skull with flaring lambdoid crests. The nasals are relatively short, with no lateral notches, and the posterodorsal part of the premaxillary is reduced, allowing the maxilla to contact the nasal incision. The lower jaw has a strongly procumbent i2 tusk and is nearly cylindrical in cross section. The first two upper premolars are very primitive, but P4 is nearly completely molarized.

Average length of m2: 46.0–50.0 mm.

Included species: *A. platycephalus* only (known from localities CP83A, CP84B, NP51A).

Comments: It is peculiar that this rhino is known from the Chadronian and Whitneyan, but not from the intervening Orellan. Because it was probably a large, amphibious form, found in river channel sandstones, perhaps it was driven from its habitat in the Orellan by the amphibious amynodontid rhinocerotoid *Metamynodon*.

## DICERATHERIINAE

### *Subhyracodon* Brandt, 1878 (synonyms: *Caenopus*, in part)

Type species: *Subhyracodon occidentalis* (Leidy, 1850).

Type specimen: USNM 114.

Characteristics: *Subhyracodon* is easily distinguished from other Chadronian and Orellan rhinos by its larger size (except for *Amphicaenopus*, which is much larger). It is also distinguished from more primitive rhinos by the loss of I3 and the upper canine, and a molarized P2 (Figure 42.3, node 5). It has a mandibular condyle that is broader, flat surfaced, and nearly horizontal. The postglenoid process faces anteriorly. The feet are completely tridactyl.

Average length of m2: 29.0–39.0 mm.

Included species: *S. occidentalis* (known from localities CP40B, CP41A, CP41B, CP68C, CP84A, CP99A, NP50C); *S. mitis* (localities CP39C, CP39G, CP39IIC, CP40A, CP41A, CP42A, CP68B, CP83A, CP83B, CP83C, CP98, NP29C); *S. kewi* (locality CC9C).

*Subhyracodon* sp. is also known from localities CC12, NP24C, NP24D, NP32B.

Comments: *Subhyracodon* is the commonest larger Chadronian and Orellan rhinocerotid, but is a taxon that has been greatly misunderstood. For over a century, the invalid name "*Caenopus*" (Cope, 1880) has been attached to this rhino, and it still appears in recent works (e.g., Russell, 1982; Wilson and Schiebout, 1984) because there has been no comprehensive systematic work on Oligocene rhinos since Scott (1941). Lucas, Schoch, and Manning (1981, p. 835) formally placed "*Caenopus*" in synonymy with *Subhyracodon*, and my work substantiates this (Prothero, in preparation).

Like *Trigonias* and *Hyracodon*, *Subhyracodon* was oversplit into several invalid species and genera based on slight variations of molarization of the upper premolars. The large Orellan quarry sample from the Harvard Fossil Re-

serve, Goshen Co., Wyoming (locality CP42C), clearly shows that most of the "species" based on premolar variants belong to the same population. The species list here reflects a more modern concept of taxonomy and will be formally substantiated elsewhere (Prothero, in preparation).

### *Diceratherium* Marsh, 1875 (synonyms: *Subhyracodon*, in part)

Type species: *Diceratherium armatum* Marsh, 1875.

Type specimen: YPM 10003.

Characteristics: Typical *Diceratherium armatum* is a large rhino with paired flanges on the tips of the nasals on males. This was previously confused with the rounded nasal bosses of the much smaller rhino, *Menoceras*, so most *Menoceras* was incorrectly labeled *Diceratherium* (as discussed earlier). Besides the nasal ridges and the completely molarized upper premolars, few derived characters distinguish *Diceratherium*.

Average length of m2: 31.0–47.0 mm.

Included species: *D. armatum* (= *D. matutinum*) (known from localities CC9D, CC13, CP48, CP50, CP51A, CP52, CP84C, CP85C, CP101, NP10C, NP34C, NP36A, NP36B, PN6C, PN6D, PN6E); *D. tridactylum* (= *Subhyracodon tridactylum*) (localities CP42D, CP84B, CP99B, CP99C, NP51A); *D. annectens* (localities CC9D, CP48, CP50, ?CP51A, CP52, CP84C, CP101, NP34C, PN6C, ?PN6D, ?PN6E, NC1A); *D. niobrarense* (localities CC13, CP103, CP104A, CP104B, NP10D, PN19B); *D. n. sp.* (locality CP101).

*Diceratherium* sp. is also known from localities ?CA1, CA7, NB3D, SB2, SB4, CP86B, (NP33B), (NP34D), (PN6F), PN6G.

Comments: *Subhyracodon* gives rise to *Diceratherium* in the Whitneyan (31 Ma) and this genus then persists into the Hemingfordian and possibly the early Barstovian (about 17 Ma), a record for generic longevity among rhinos. As with *Subhyracodon*, the taxonomy of *Diceratherium* has long been badly misunderstood.

Nevertheless, identification is usually unambiguous because it was the practically the only rhino present through the Whitneyan and most of the Arikarean. This low in generic diversity was compensated for by several parallel species lineages that persisted unchanged through most of the Arikarean: *D. armatum*, the large type species, and *D. annectens*, a smaller species. There is also a new dwarf species (Prothero, in preparation) from the earliest Arikarean (formerly considered the Gering Formation at Roundhouse Rock, Nebraska, but now correlated with the "brown siltstone" member of the Brule Formation, according to Swinehart et al., 1985) and a late Arikarean to early Hemingfordian species, *D. niobrarense*. In this study, the Whitneyan species "*Subhyracodon*" *tridactylum* is also referred to *Diceratherium* because some male skulls clearly show the beginnings of the paired nasal ridges.

## MENOCERATINAE

### *Menoceras* (Troxell, 1921) (synonyms: *Diceratherium*, in part; *Moschoedestes*)

Type species: *Menoceras arikareense* (Barbour, 1906).

Type specimen: UNSM 62008.

Characteristics: *Menoceras* was long confused with *Diceratherium* because both have paired horns at the tips of their nasals (Peterson, 1920). As already discussed, the horns are not homologous in detail, and apparently they were independently derived. *Menoceras* shows many other characters (Figure 42.3, node 7) that clearly show it is a much more derived rhino than *Diceratherium* sensu stricto. Indeed, in female skulls without the paired horns, *Menoceras* was often mistaken for more derived rhinos.

Average length of m2: 31.0–46.0 mm.

Included species: *M. arikareense* (known from localities GC3A, GC3B, GC8B, ?GC8C, CP51A, CP84C, CP103, CP104A, CP104B); *M. barbouri* (= *M. "cooki," M. "marslandensis,"* and "*Moschoedestes delahoensis*") (localities GC5, GC8D, SB29B, SB46, CP71, CP88, CP105, CP106, NC1A, NC2).

Comments: Pig-sized *Menoceras arikareense* (usually mislabeled "*Diceratherium cooki*") immigrated to North America in the late Arikarean and is by far the commonest mammal in the famous Agate bone bed. It evolved to a slightly larger species, *M. barbouri*, in the early Hemingfordian, which has been badly oversplit (*M. "falkenbachi," M. "marslandensis,"* and the Castolon rhino, "*Moschoedestes*"). Some of these synonymies were demonstrated by Prothero and Manning (1987), and others are forthcoming (Prothero, in preparation). After spreading over much of the continent from New Mexico to Florida in the early Hemingfordian, *Menoceras* disappeared as the wave of immigrant aceratherines and teleoceratines apparently drove it out in the mid-Hemingfordian.

## ACERATHERIINAE

### *Floridaceras* Wood, 1964

Type species: *Floridaceras whitei* Wood, 1964.

Type specimen: MCZ 4046.

Characteristics: *Floridaceras* is the first aceratherine whose functional fifth metacarpal was noted (Wood, 1964). Its aceratherine affinities are somewhat equivocal. The only skull material is badly crushed, so the degree of nasal retraction is difficult to determine. Unlike any other aceratherine, it had an upper I1, as indicated by a thegosis facet on the lower tusk.

Average length of m2: 47.2 mm.

Included species: *F. whitei* only (known from localities GC5, GC8D, CP106, PN6H).

Comments: *Floridaceras* is an unusually large Hemingfordian rhino known primarily from the Thomas Farm Local Fauna in Florida (locality GC5). Most of its anatomy sug-

gests that it was one of several immigrant aceratherines in the early Hemingfordian which eventually lost out to the dominant genera, *Aphelops* and *Peraceras*.

### New genus (Prothero, in preparation)

Characteristics: Galusha (1975) briefly described a specimen (F:AM 95544) from the early late Hemingfordian Box Butte Formation, Box Butte Co., Nebraska (locality CP107). It differs from all other aceratherines in its smaller size, extreme nasal retraction (to the level of anterior M1, a feature paralleled only in the latest, most derived *Aphelops*), and its uniquely flat dorsal skull profile. It cannot be referred to any existing genus, so Prothero (in preparation) will erect a new genus to contain this material. Although it is one of the earliest aceratherines known, it is also one of the most derived.

The m2 is unknown. Average length of m2: 41.0 mm.

### *Aphelops* Cope, 1874

Type species: *Aphelops megalodus* (Cope, 1873).

Type specimen: AMNH 8292.

Characteristics: *Aphelops* has the derived features of a dorsally arched nasal-frontal profile and an unusually long distastema between the lower tusk and the first lower premolar. Like almost all aceratherines, it lacks a chisel-shaped I1.

Average length of m2: 41.0–63.0 mm.

Included species: *A. megalodus* (known from localities GC3B, GC4B, GC4C, GC4D, GC4E, NB6B, [NB20A], NB25B, NB29, SB32A, SB32B, SB32D, SB32F, CP75B, [CP75C], CP76, CP78, CP90A, CP108B, CP110, CP114A, CP114B, CP114C, CP114D, CP116A, CP116B, ?NC3B); *A. malacorchinus* (localities GC11A, GC11B, SB32G, SP1B, SP1C, SP3A, CP76, CP78, CP116A, CP116B, CP116C, CP123C); *A. mutilus* (localities GC11C, GC12II, GC13A, SB34C, SB58A, SB58B, SP1D, SP3B, SP4A, CP115C, CP116D, CP116F, CP123D).

*Aphelops* sp. is also known from localities GC6D, (GC8F), (GC9A), GC9B, GC9C, GC10B, GC12I, ?CC23, NB7D, (NB9), (NB11), NB17, NB19C, NB23C, NB27B, (SB43A), SB55, CP127, (NP11), NP42, PN8B, (PN9B), PN13.

Comments: *Aphelops* is the most common and best known aceratherine in North America. Three successive species are recognized here, each becoming progressively larger from the late Hemingfordian to the late Hemphillian. The primitive species, *A. megalodus*, persists with little change from the late Hemingfordian to the late Clarendonian. In the Hemphillian, the genus gets noticeably larger, with more hypsodont teeth and more extreme nasal retraction. *Aphelops*, a browser, is typically found with the grazing *Teleoceras* in most North American Miocene localities, although in smaller numbers. It reached its acme in the latest Hemphillian, when it occurred in great numbers in the Panhandle of Texas (Coffee Ranch, locality SP3B, and comparable localities) and Kansas (Edson Quarry) (locality CP123D). *Teleoceras*, by contrast, was rare at this time.

**Peraceras Cope, 1880 (synonyms: *Diceratherium*, in part);  
*Aphelops*, in part; *Teleoceras*, in part)**

Type species: *Peraceras superciliosum* Cope, 1880.

Type specimen: AMNH 8380.

Characteristics: *Peraceras* is characterized by a brachycephalic skull with a procumbent lambdoid crest and occiput, shortened nasals, flat dorsal skull profile, an upturned symphysis in females, a short lower diastema, and lingual cingula on the lower cheek teeth.

Average length of m2: 31.0–61.0 mm.

Included species: *P. superciliosum* (= *P. "crassus," P. "troxelli"*) (known from localities NB23B, SB32D, SB32F, SB34A, [SP1A], CP71, CP73C, CP76, CP89, CP90A, CP114A, CP114B, CP114C, CP114D, ?CP116, NP41B); *P. profectum* (= "*Diceratherium jamberi," "Aphelops montanus"*) (localities ?NB7C, NB18, SB32A, SB32B, SB32D, SB32F, CP71, CP108B, CP110, CP114B, NP42); *P. hessei* (localities GC4B, GC4C, GC4D, GC4E, GC10A, SB32D).

*Peraceras* sp. is also known from localities SB34A, PN9A.

Comments: *Peraceras* has long been one of the most misunderstood rhinos of North America. The type species is the most robust, derived species of the genus, and the primitive members have been erroneously referred to *Aphelops*, *Aceratherium*, and *Diceratherium*. Prothero and Manning (1987) cleared up some of the confusion, and further discussion will be presented by Prothero (in preparation).

Three species are currently recognized. The primitive, medium-sized species, *P. profectum* (= "*Diceratherium jamberi," "Aphelops montanus"*), overlaps in size and morphology with *A. megalodus*. Most specimens of the primitive Hemingfordian and Barstovian *P. profectum* are hard to distinguish from *A. megalodus* from the same deposits. There is a dwarf species, *P. hessei*, from the Texas Gulf Coastal Plain (Prothero and Sereno, 1980; Prothero and Manning, 1987), and the large type species, *P. superciliosum* (= *P. "crassus," P. "troxelli"*), which paralleled the teleoceratines in many features. During the Barstovian and early Clarendonian, *P. superciliosum* is most common in northern localities, such as South Dakota, northern Nebraska, and Montana and is not found in southern localities except in New Mexico and California. If it competed with *Teleoceras* for the same large-bodied aquatic grazer niche, then it was less successful because it was much more rare than *Teleoceras* and died out in the Clarendonian.

## TELEOCERATINAE: TELEOCERATINI

### ***Brachypotherium* Roger, 1904**

Type species: *Brachypotherium brachypus* (Lartet, 1837).

Type specimen: Unavailable.

Characteristics: *Brachypotherium* differs from *Teleoceras* in having a slender post-tympanic process with a ventral edge

that is level with the postglenoid process. There are strong lingual cingula on the upper premolars, and M2 is approximately equal in length to M3. The distal limb elements, especially the second metapodials, are longer and less robust than is typical of *Teleoceras*. In all other features, it shows the typical teleoceratine anatomy of a robust, short-limbed skeleton and a brachycephalic skull with relatively hypsodont teeth and flaring lambdoid crests.

Average length of m2: 44.0–54.0 mm.

Included North American species: *B. americanum* (known from localities CP71, CP107, CP108A, CP108B).

Comments: Yatkola and Tanner (1979) assigned late Hemingfordian teleoceratines from the Martin Canyon Local Fauna of northeast Colorado (locality CP71) to *Brachypotherium americanum* (gender corrected). It is unquestionably the most primitive teleoceratine from North America, although whether it is truly *Brachypotherium* is still debatable. For the present, all of the late Hemingfordian teleoceratine material is referred to *Brachypotherium americanum*; early Barstovian material is referred to *Teleoceras medicornutum*.

### ***Teleoceras* Hatcher, 1894**

Type species: *Teleoceras major* Hatcher, 1894.

Type specimen: PU 10645.

Characteristics: *Teleoceras* is easily recognized by its characteristically robust and proximodistally shortened limbs and feet, and by its brachycephalic skull with broad flaring lambdoid crests and broad zygomatic arches. The nasal bones are U-shaped in cross section, and typically there is a small horn rugosity at the very tip of the nasals. The upper I1 is still present, unlike the condition in the aceratherines. The cheek teeth are usually very hypsodont, with the molars greatly enlarged at the expense of the premolars. The p2 is lost in most species of *Teleoceras*. The nasal incision is retracted to the level of anterior P3, much shallower than in derived aceratherines. In addition to the robustness of the limbs, *Teleoceras* has an elongate calcaneal tuber and an articulation between the scaphoid and lunar.

Average length of m2: 50.0–63.0 mm.

Included species: *T. major* (known from localities GC6B, SB32G, SP2A, CP90A, CP114D, CP116A, CP116B); *T. medicornutum* (localities GC4C, GC4D, GC4E, NB7C, [CP75C], [CP76], CP87B, CP110, CP114A, CP114D, NP41B, PN7); *T. meridianum* (localities GC4B, GC4C, GC4D, GC4E, NB7C, CP114A); *T. fossiger* (localities [CA9], NB27A, NB31, NP45, SB31B, [SP1B], [SP1C], SP3A, CP116B, CP116C, CP116D, CP116E, CP123C, CP127, [PN12]); *T. proterum* (localities GC11A, GC11B); *T. hicksi* (= *T. "ocotensis"*) (localities GC13B, GC13C, CC37, CC40, CC41, NB33, SB11, SB34C, SB58A, SB62, SP1D, CP78, CP116D, CP116E); *T. n. sp. A.* (localities SB32B, SB32D, SB32F); *T. n. sp. B.* (SP1D, SP3B, CP123D).

*Teleoceras* sp. is also known from localities (CA3), CA4,



(GC10B), (GC12II), GC13A, GC27, CC25B, CC26B, CC36, CC37, CC38, NB19C, NB23C, NB27C, SB32G, SB34A, SB60, SP1A, (SP1F), (CP56), CP76, CP87B, CP114C, CP115D, CP116F, NP38E, PN9A, PN11, PN13, PN14, PN15.

Comments: *Teleoceras* is by far the most abundant and best known Miocene rhinoceros from North America. It is known from enormous quarry samples all over the continent, including complete articulated individuals in death poses killed during an ash fall, from Ashfall Fossil Bed, Antelope Co., Nebraska (locality CP116A; Voorhies and Thomasson, 1979; Voorhies, 1981).

The taxonomy of *Teleoceras* was in great confusion, but Prothero (in preparation) has simplified this considerably. By my count, there are eight valid species in North America, including two that are new. Overall, the *Brachypotherium-Teleoceras* lineage shows a general size increase from *Brachypotherium americanum* in the late Hemingfordian to *T. medicornutum* of the Barstovian, *T. major* of the Clarendonian, and *T. fossiger* of the early Hemphillian. After reaching maximum size in the early Hemphillian, the remaining species are smaller: *T. proterum*, the Florida endemic, and *T. hicksi*, the late Hemphillian species. Two dwarf species of *Teleoceras* are known: *T. meridianum* of the Texas Gulf Coastal Plain Barstovian, and *Teleoceras* n. sp. B from the latest Hemphillian of Guymon, Oklahoma. There is a new endemic species of *Teleoceras* from the Barstovian and Clarendonian of the Santa Fe Group of New Mexico, which differs from contemporary *T. medicornutum* in having unusually short nasals and robust premaxillae, apparently for some sort of prehensile lip, as is seen in aceratherines.

*Teleoceras* was unquestionably a successful analogue of the hippopotamus, which lives in large herds in the riverbed during the day and comes out at night to graze along the riverbanks. This is suggested not only by their occurrence in river channels and their hippolike build, but also by their population structure (D. Wright, pers. comm.). *Teleoceras* occurs in large numbers in just about every Miocene locality in the High Plains after the Hemingfordian, usually accompanied by the browser *Aphelops*. Contrary to popular belief, *Teleoceras* did not disappear before *Aphelops* in the latest Hemphillian. It just happens to be scarce in the richest late Hemphillian quarries, such as Coffee Ranch and Edson. Actually, *Teleoceras* reached its maximum geographic extent in the latest Hemphillian, even if it is scarce. It occurs in the Mt. Eden Local Fauna in southern California, Panaca Local Fauna in Nevada, Keams Canyon and Jeddito Local Fauna in Arizona, the Chamita Formation in New Mexico, the Wray localities in Colorado, the Snake Creek Formation in Nebraska, the Sawrock Local Fauna in Kansas, Coffee Ranch Local Fauna and the Guymon area in the Texas-Oklahoma Panhandle, the Upper Bone Valley Formation in Florida, and in Yepomera and Ocote in Mexico. As discussed earlier, the extinction of *Teleoceras* and *Aph-*

*elops* seems to be related to the climatic and floral changes triggered by the Messinian worldwide climatic event.

## INDETERMINATE RHINOCEROTIDS

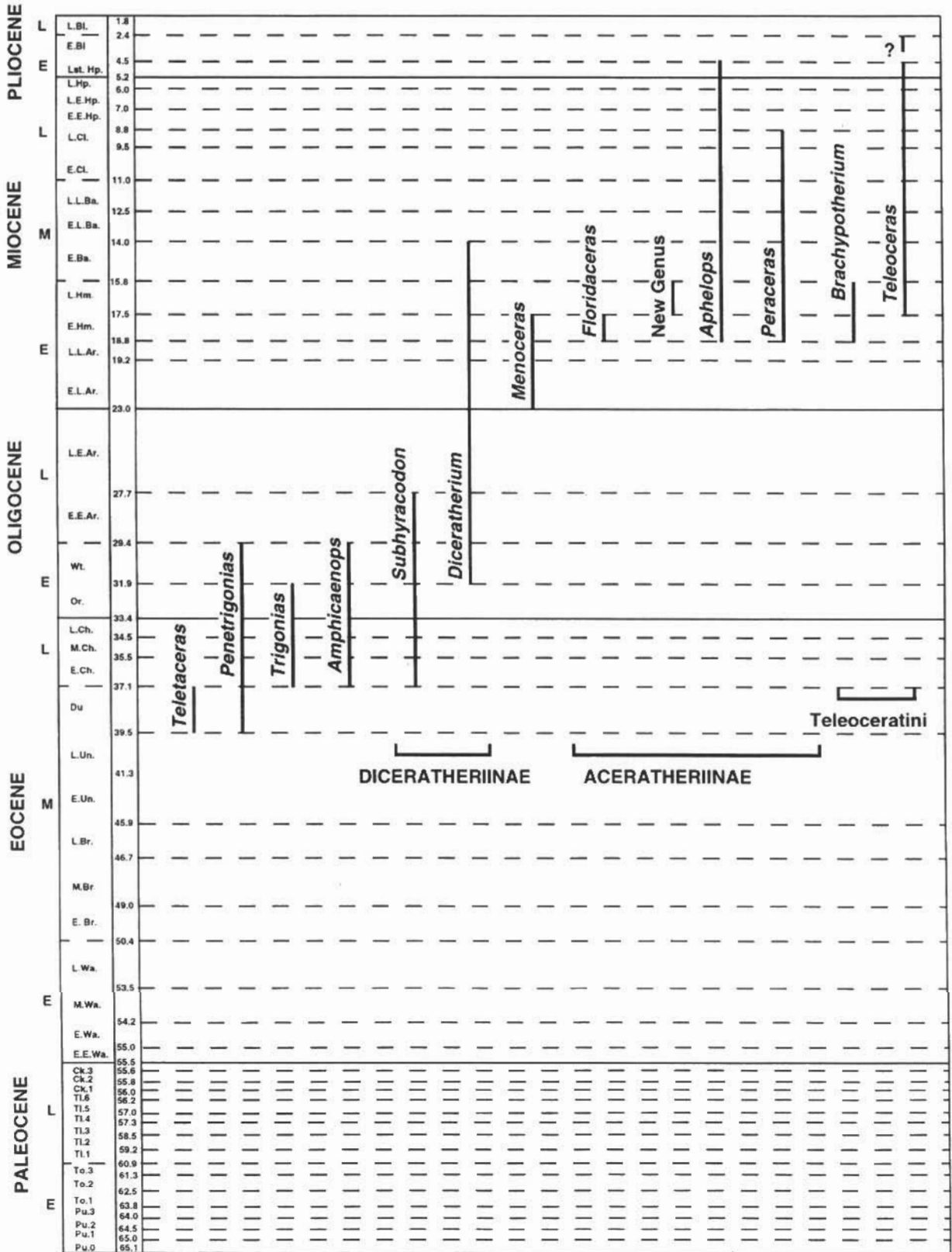
Fragmentary remains ascribed to rhinocerotids have been reported from localities CA7, GC8E, CC3, CC19II, CC21C, SB47, SB48, SB52, CP54B, CP87A, CP116E, NP9A, NP10BB, NP22, NP25A, NP25B, NP25C, PN6B, PN13, PN16.

## BIOLOGY AND EVOLUTIONARY PATTERNS

North American rhinoceroses showed a considerable variety of ecological adaptations. Most were relatively large-bodied herbivores and among the largest animals of their ecosystem, but the pig-sized *Menoceras* was much smaller than contemporary entelodonts and chalicotheres. Eocene and Oligocene rhinocerotids have relatively low-crowned teeth and efficient cutting incisor chisel-tusk combinations for browsing, and most of them are found in river channel sandstones. Clark, Beerbower, and Kietzke (1967) found that *Subhyracodon* was more abundant in the near-stream facies of the Big Badlands than in the swampy plain; it was absent from the open plain. *Trigonias* and *Amphicaenopus* are known exclusively from river channel deposits. As the titanotheres, amynodonts, and other large-bodied browsers disappeared during the late Eocene and the Oligocene, only the rhinocerotids persisted in the browsing, near-stream niche (Figure 35.3). By the Arikarean, the conditions were drier, and overall mammalian diversity was at an all-time low (Prothero, 1985; Stucky, 1990). During most of this time, *Diceratherium* was the only large-bodied mammal in North America, apparently hiding in what remained of the riparian woodland. Judging from the large numbers of these rhinos in quarries such as 77 Hill, Niobrara Co., Wyoming (locality CP52), they may have formed herds. *Diceratherium* was the first North American rhino to show significant sexual dimorphism in horns or tusk development, so it probably had a more complicated social structure than its more solitary predecessors.

In the late Arikarean (Upper Harrison Formation, Agate Springs Quarry, locality CP104A), the first of the early Miocene immigration events brought the tiny European *Menoceras* on the scene. Judging from its great abundance in these quarries, it probably lived in large herds, with subequal numbers of males and females. By contrast, true *Diceratherium* was very rare and apparently losing ground to the invader. It is unknown from the rest of the Hemingfordian (late early Miocene), although it may occur as late as the Barstovian in Railroad Canyon, Idaho (locality PN19B). *Menoceras*, in turn, had to compete with a mid-Hemingfordian wave of immigrant aceratherines and teleoceratines and was gone before the late Hemingfordian. By the late Hemingfordian, the aceratherines *Aphelops* and *Peraceras* and the teleoceratine *Brachypotherium* had established the dominant rhino lineages for the rest of the Miocene.

From the late Hemingfordian to the late Hemphillian (latest Miocene), North American rhinos show the browser-grazer pair combinations that are typical of savannas everywhere, including the modern East African savanna. The browser typically feeds on



Bi.=Blancan, Hp. = Hemphillian, Cl.= Clarendonian, Ba.= Barstovian, Hm.= Hemingfordian, Ar. = Arikareean, Wt. =Whitneyan, Or.= Orellan, Ch. = Chadronian, Du.= Duchesnean, Un. = Uintan, Br. = Bridgerian, Wa. = Wasatchian, Ck. = Clarkforkian, Ti. = Tiffanian, To. = Torrejonian, Pu. = Puercan.

Figure 42.4. Temporal ranges of North American rhinocerotid genera.

medium- and high-level leaves and tender shoots and uses a prehensile lip and/or trunk for the purpose. Aceratherines, particularly *Aphelops* and primitive *Peraceras*, performed this role in the North American Miocene savanna. These rhinos have a greatly retracted nasal incision for anchoring muscles of a prehensile lip and have replaced their upper incisors with a nipping pad, as modern rhinos and ruminants have. The modern browsing black rhino is rather solitary with a wide home range, and with few exceptions, most *Aphelops* are found in small numbers in any given quarry. Wright (pers. comm.) has found that *Aphelops* has relatively low infant mortality at the Love site in Florida (locality GC11A), which is comparable to the population structure of the browser *Diceros*.

By contrast, there is little doubt that teleoceratines were good analogues of the modern hippo. Not only was their body very hippo-like, but they are found in great numbers in river channel deposits, indicating that they were gregarious herders like hippos. Wright (pers. comm.) found that the Love Bone Bed *Teleoceras* had a very high infant mortality, like that of hippos. Their teeth are very high crowned and suitable for grazing, and the throat cavities of the Poison Ivy Quarry (locality CP116A) rhinos even contain grass seeds (Voorhies and Thomasson, 1979). Although modern white rhinos are not as aquatic as *Teleoceras* or hippos, they are efficient grazers that live in small herds. The browser-grazer pair combination was very successful, for similar pairs were found in most Miocene savanna localities in Eurasia and Africa, usually involving a browsing *Aceratherium* or *Dicerorhinus* and a grazing *Brachypotherium* or *Chilotherium*. When the savannas disappeared from North America in the early Pliocene, so did the rhinos. Today the browser-grazer pairs are found only in the East African savanna, one of the few remaining on earth.

Because of the wide geographic spread of North American Miocene localities, it is possible to examine rhino biogeography as well. The most striking fact is that rhinos are far more abundant in the Plains states of South Dakota, Nebraska, Kansas, Oklahoma, and Texas than they are in the intermontane localities in California, Oregon, and Nevada (see Figure 35.3). There are many good Miocene localities from the intermontane region, with a great abundance of camels, horses, and mastodonts, but rhinos are extremely rare. Because this cannot be due to sampling, it is apparent that rhinos preferred the open savanna of the Plains to the more wooded habitats of the intermontane states. There are few Miocene localities east of the Mississippi, but Florida produces rhinos in great numbers.

Besides this overall trend, certain species clearly had biogeographic preferences. The dwarf species of *Peraceras* and *Teleoceras* were found mainly in the Texas Gulf Coastal Plain, which had a peculiar endemic fauna that lived in the swampy, wooded habitat near the coast (Prothero and Sereno, 1980). These dwarfs were analogous to the dwarfing that occurs when savanna mammals adjust to the more limited spaces and resources of the forest, as happens with pygmy hippos, forest elephants and Cape buffalo, and many island dwarfs. *Peraceras superciliosum*, in contrast, is found almost exclusively in more northerly Barstovian and Clarendonian localities, especially in Montana, South Dakota, and Nebraska; it was absent from Florida or Texas. Florida had endemism in much of its

fauna, and *Teleoceras proterum* was also a Florida endemic. The Rio Grande rift was remarkably rich in *Peraceras* (all three species) and had its own endemic, prehensile-lipped species of *Teleoceras* (*Teleoceras* "n. sp. A" earlier). The details of the faunas from the Miocene of California, Oregon, Nevada, and Arizona have not been fully worked out yet, but if the fauna has any rhinos at all, typically they include *Aphelops megalodus* and less frequently *Teleoceras* or *Peraceras*. Further details of this biogeographic picture are presented elsewhere.

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