EVOLUTION OF TERTIARY MAMMALS OF NORTH AMERICA

VOLUME 1:
TERRESTRIAL CARNIVORES, UNGULATES, AND UNGULATELIKE MAMMALS

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INTRODUCTION

The Rhinocerotidae was one of the most successful groups of mammals in North America. After the extinction of stegomastoids in the late Eocene, rhinos were the largest land mammals on the continent until the appearance of mastodonts 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 Paraceratherium), proboscidean-sized browsers (most of the acriatheres), four independent examples of dwarfing (Pemphoner suillus, Teleoceras meridians, and new undescribed species of Teleoceras and Diceratherium), pig-sized herding rhinos (Menoceras arkaeaeus; see Figure 42.3) 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, Triceroceras, has been erected by Haisin (1989) to refer to the most primitive North American rhinocerotids from the Clarion Formation of Oregon. By the latest Eocene (Columbiaan) and early Oligocene, there were several rhino genera represented in the High Plains: Trigonias, Parapterium, Subhyraco, and Amphicynodon. In the Whitmanian and Arkamean (later Oligocene through earliest Miocene), however, rhino diversity was reduced to three genera, Diceratherium, which persisted from 31-37 Ma, the longest unopposed reign of any rhino. In the latest Arkamean, the pig-sized rhino Menoceras arkaeaeus (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 fauna were in great flux, and there was considerable change in the rhinos as well. Diceratherium and Menoceras became extinct as invading acriatheres (Floridanus, Paracer, Antelope, and a new undescribed genus) and teleoceratines (Brachypotherium) established themselves. From the late Hemingfordian until the late Hemphillian (latest Miocene), the rhino fauna were "true elements of the "Cenomanian or "Cretaceous" fauna of the... (Truitt, 1970; Webb, 1984; Tedford et al., 1987). There was a single genus of browsing acriatheres, typically Antelope, and grazing hippolike teleoceratines (typically Teleoceras) in nearly every North American locality of Barstovian, Cenomanian, 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 eomylid rodents, most horses, and antilopids, totaling 62 genera (Webb, 1984). One isolated tooth scrap from the Blancan of Texas is known (Madden and Dalquest, 1995), 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 extant 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 regions on the skull surface, it is clear that horns were present in only a few groups. Paired nasal flanges occur in Deinotherium, and small paired horns (independently derived) in Mammuthus. Teleoceratines have a small terminal nasal horn, and male Paraceratherium simum has the only aecraterine 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-maxillary nasal contact is lost. The nasals are long and slender, and in the aecraterines, the nasal 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 mandible condyle is broad, flat, the surface, and horizontal.

DENTAL

As reviewed by Prothero, Manning, and Hanson (1986), the Rhinocerotidae are defined by the presence of a chisel-shaped 11 occluding with a tuskslike 2. On M3, the mescone is extremely reduced or absent, and the posterior cingulum is absent. 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 n-shaped pattern formed by the junction of the premolars, metaconids, and euctyleph. In very derived forms, these teeth can become very hypsodont and develop various internal ridges (cretes, anterocretes, and cristae) to increase surface area (see Prothero, Manning, and Hanson, 1986, Figure 6). Prenive rhino premaxillars were not fully mobilized, so there may be fewer connecting the protocone and hypocone. In the past, the subtle differences in premaxillars were used to separate the two genera (e.g., Wood 1937). Quarry samples show that most of this premaxillary variation is normal intraspecific variability, and thus the species listed here reflect considerable lumping. Lower teeth, on the other hand, have the stereotyped L-shaped premaxillary and metaconid, which changes only in the bone marrow oviduct.

POSTCRANIAL

When prospecting in almost any Olignyce or Misocene locality, rhino postcraniatal bones are easily recognized by their size and robustness compared to any other mammal of the time (except titanothere and matriodons, which were even larger). Only Mammuthus and the dwarf species became more gracile, but even their bones cannot be mistaken for any other mammal. In particular, the rhino has a fused intervertebral sacral and a deep hip notch in the anteromedial margin of the transverse process. There are also deep dorsal and ventral notches on the anterior articulation of the atlas. The neural process of the proximomolar tuberosity of the hamates is very long and posteroomedially inclined. The limbs in teleocrater are very robust and proximodistally shortened; this is espeically true of the manus and pes. Most rhinocerotids had tridactyl feet, but the most primitive ones, like Triceratops, still retain a functional fifth metacarpal. These have three rear in a few individuals of the aecraterines Aepyceras, Paraceratherium, and Floridaceras, possibly as an atavism (Prothero, Manning, and Hanson, 1986, p. 359). Teleoceratines also have a posterior articulation of the scapulohumeral and lunar.

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

Figure 42.2. Ontogeny of the Ovuliferous Rhinoceratinae, Lagodamalis ovuliferous. A: Skull (after Osborn, 1930) (scale bar = 50 cm); B: Skull (after Scott, 1931) (scale bar = 1 m).
SYSTEMATICS

SUPRAFAMILY

The Hyracodontidae are the closest sister taxon to the Rhinocerosidae. The two groups are united by the following derived features: reduced parassyles; 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 naso-tal notch and loss of I1. Presumably, these rhinos had a periscopial lip or snout for browsing. The tribe Teleocentridae are highly derived and easily recognized by their short, stout, proximodorsally compressed limbs and feet, broad brachycephalic skulls with flaring lambdoid crests, and nasal bones with a U-shaped crest section supporting a small terminal tower. They also have an elongate calcaneal tuber and a posterior articulation of the scapulohumeral ligament.

In the past, there was a polyphyletic subfamily "Casuromorphia" for all the primitive taxa; it has no legitimacy (even the name Cyno- pus is invalid). Until recently, Diceratherium and Monoceras were placed together in a subfamily Diceratheriidae for the paraphyletic group.

Figure 42.3. Interrelationships of the North American Rhinocerotidae. Characters at the nodes are as follows: (1) RHINOCEROTIDAE: I1 reduced shaped; I2 toothless; very reduced M3 metacone; M1–2 cristate lost; premaxillary–nasal contact lost; reduced posterior cingulum on M3; shorter posterior ectoloph on M1–2. (2) M1–3 paraconule folds more open; antroconules enlarged; M3 metacone lost; I3, lower canine lost in adults; metacone ridges on molars; loss paracone and metacone cingula separate and reduced on premolars; greater hypsodonty; postcarnassial process on ramus: broad ascending ramus on dentary, with uniaxial posterior border; long, posteroventrally curved process on anterior tuberculum of humpy. (3) Broad paraangular crest, laterally flared lateral buccal crests; concave dorsal skull profile; long nasals. (4) Extended rec- croris; anteroventrally inflected basi- ceratid; long, flattened postorbital process. (5) Threed upper and lower incisors, upper canine lost; metacone ridges of P2–4 lost; P2 reduced; mandible continous; midventral flange on ramus. (6) Shallower anterior notch on atlas. (7) Upper premolars fully bilophodont; overall size increase. (9) ACRERATIDAE: I1 cristate; I2 reduced; large distal posteros of M1; fifth metaconule enlarged. 10. Premaxillary–nasal lost; I3 lost; nasal incision over anterior P4. 11. (11) Dental skull profile flattened. (12) TELECERATIDAE: TELEOLATIRIDAE; mesoplates shortened; carpal and tarsal compresed dorsoventrally; strong antroconules; broad cristae on metaconules; lamina edge of nasals downturned and thinned, resulting in U-shaped crest section; calcaneal tuber elongate; brachycephalic skull; nasal incision returned to level of anterior P3; P3 lost in some Teleoceras.
rhinos (Petersen, 1920). Tanner (1969) showed that the two genera were very distinct, and Prothero, Manning, and Hat-son (1986) and Prothero and Manning (1987) have shown that they are only distantly related. A large suite of derived characters (Figure 42.3, note 7) unites Menoceras with higher rhinos, and the paired horn condition is a parallelism. The Dioceratheriinae includes only Diocerasorthium sense stricto and Subhynoconas, and Menoceras is grouped with European Pleurocoerus in the subfamily Menocerinae (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 questionable from that locality, thus implying some doubt that the taxon is actually present at that locality, either in the genus or the species level.

BASAL RHINOCEROTIDS

Telesercus Hamson, 1899

Type species: Telesercus radinikyi Hamson, 1899.

Type specimen: UCMP 129000.

Characteristics: Small rhinoceros with 11/2 elioal tusk combination, but these are not as enlarged as they become in large rhinoceroses. Telesercus has an unreduced anterior dental series, sharp creases between molar pararadontes, more lingually inflected molar metastem axes, and low connexion of lower molar metapodia to protolophids. There is a marked posterior diastema and a single-rooted P1.

Average length of m2: 20.5–24.8 mm.

Included species: T. radinikyi (known from locality PN78B), T. mortizali (locality NLBY).

Penetrigonus Tanner and Martin, 1976 (synonymy: Caenopus in part; Subhynoconas, in part)

Type species: Penetrigonus budlami Tanner and Martin, 1976.

Type specimen: USNM 62049.

Characteristics: Penetrigonus is readily distinguished from Telesercus not only by its larger size, but also by a whole suite of more advanced rhinoceros characters (Figure 42.3, note 2), including a completely developed rhinoceros [twc] complex, the absence of an M3 metacoon, the loss of 13 and the lower canine, and the characteristic features of the mandible and hornum.

Average length of m2: 25.0–27.4 mm.

Included species: P. budlami (known from localities SB44B), CP9C, CP9G, CP9MC, CP7A2A, CP8CA, CP9BA; P. agnus (locality NP1B); P. daktorens (localities CP9C, CP9ED, CP86B).

Comments: Small Oligocene rhinoceroids that are slightly larger than Telesercus but smaller than any species of Subhynoconas or Trigonias have been incorrectly referred to a number of genera. The first valid name to be proposed for this group was Penetrigonus, although the original diagnosis was based on invalid differences in upper premolar crenata. Ignoring the premolars, these are distinct features in the size and the reduction of the phallicula that unite this genus.

In their concept of Penetrigenus, Prothero, Manning, and Hanson (1986) included not only the type, but also specimens from the Vedder Formation (locality CP82A) and Staffsgaff Rim, LGree Creek (localities CP93C, CP93G), and Beaver Divide area of Wyoming (locality CP7501C), the Pondera Local Fauna of Texas (locality SB44B), and specimens referred to Subhynoconas agnus by Russell (1982). "Caenopus" daktorens probably also belongs in this genus.

Trigonias Lucas, 1900

Type species: Trigonias sobrensis Lucas, 1900.

Type specimen: USNM 3924.

Characteristics: The medium-larger Chladonia rhino, Trigonias, is known from a number of complete skeletons. It retains all the anterior teeth except for I1 and the lower canine. The skull profile is distinctively concave and saddle shaped, with large sagittal crest and broad lambdoid crests. It is one of the few Dioceratheriinae rhinos that retain a functional fifth metacarpal.

Average length of m2: 37.0–50.0 mm.

Included species: T. sobrensis (known from localities CP66B, CP83A, CP83B, CP9BA, NP10B, NP22C, CP24A, NP10B); T. woffi (localities CP82A, CP9BA).

Trigonias sp. is also known from localities NB24C, NB27D, CP3901F, CP90B, NP124C, NP27D.

Comments: Trigonias was once generally overlooked by Gregory and Cook (1924) because of slight premolar variations within a single population, but this view is evidence is now grounds for regarding most premolar differences as unipopulational. Besides the type species, only the much larger T. woffi is valid.

Amphicerasous Wood, 1927

Type species: Amphicerasous platyccephalus (Osborn and Woodward, 1894).

Type specimen: AMNH 542.

Characteristics: Amphicerasous is a precociously large rhinoceros from the Chladonias and Whitiways of the South Dakota Big Badlands and from Stark County, North
Dakota. It has a very broad, doliochoeophoral shell with flaring lamellate exists. The adults are relatively short, with no lateral arches, and the posterior dorsal part of the premedian isolate is reduced, allowing the individuals to contact the nasal inclusions. The lower jaw has a strongly procumbent i2 tooth and is nearly cylindrical in cross-section. The first two upper premolars are very primitive, but i2 is nearly completely incisoriform.
Average length of n2: 46.0–50.0 mm
Included species: A. playfordi (known from localities CP93A, CP94B, NP51A)

Comments: It is peculiar that this rhino is known from the Chadronian and Whitby, but not from the Lowermost Orellan. Because it was probably a large, amphibious form, found in river channel sandstones, perhaps it was driven from its home in the Orellan by the amphibious amphiodont rhinocerous Megameryxodon.

DICERAHERINAE
Subhynodon Brandt, 1878 (synonym: Cenoceras, in part)
Type species: Subhynodon occidentalis (Leidy, 1850).
Type specimen: USNM 114.

Characteristics: Subhynodon is easily distinguished from other Chadronian and Orellan rhinos by its larger size (except for Amphiceras, which is much larger). It is also distinguished from more primitive rhinos by the loss of i3 and the upper canine, and a modified P5 (Figure 42.3, node 5). It has a markedly condyloid tooth, broad, flat surfaced, and slightly horizontal. The posterior end of the process faces anteriorly. The four teeth are completely tridactyl.
Average length of n2: 290–350 mm
Subhynodon sp. is also known from localities CC12, NP24C, NP24D, NP25B.

Comments: Subhynodon is the commonest largest Chadronian and Orellan rhinoceros, but it is a taxon that has been greatly misunderstood. Over a century, the invalid name "Cenoceras" (Cope, 1860) has been attached to this rhino, and it still appears in recent works (e.g., Russell, 1962). Wilson and Schoch (1984) have shown that the nomenclature of Subhynodon, and many of its synonyms (provoc), is preparation.

Like Trigonias and Hyrpania, Subhynodon was oversplit into several invalid species and genera based on slight variations of muscularization of the upper premolars. The large Orellan quarry sample from the Harvard Poyall River, Gosher Co., Wyoming (locality CP92C), clearly shows that most of the "species" based on premolar variability are in 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 (synonym: Subhynodon, in part)
Type species: Diceratherium armatus Marsh, 1875.
Type specimen: YPM 10003.

Characteristics: Typical Diceratherium armatum is a large rhino with paired "massae" on the tips of the nasals on males. This was previously considered to be the nasal bone of the much smaller rhino, Megameryx, but most Megameryx 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 n2: 31.0–47.0 mm
Included species: D. armatum (as D. mastodon) known from localities CC31, CP93, CP95, CP95A, CP96, CP96A, NP56B, PN9C, PN6D, "D. tridactylum" (as Subhynodon tridactylum) (localities CP42D, CP98B, CP98C, CP98E, CP98K, NP51A), D. annectens (localities CC98, CP98, CP99, CP95A, CP95B, CP95C, CP95D), D. steinhoffi (localities CP95, CP99, CP95D), D. mastodon (localities CC13, CP95, CP95A, CP95B, NP9D, NP9E), D. armatum, D. armatum (locality CP104A, CP104B, NP10D, NP19B), D. sp. (locality CP101).

Diceratherium sp. is also known from localities "CA1, CA7, NB1D, SB2, SB4, CP96B, NP13B", "NP3D", "NP4E", "NP5G".

Comments: Diceratherium gives rise to Diceratherium in the Whitby (13 Ma) and this genus then persists into the Hemingfordian and possibly the early Tunbridgeian (about 17 Ma), a record too generic to be of use. As with Subhynodon, the taxonomy of Diceratherium has long been easily misunderstood.

Nevertheless, identification is usually unambiguous because it was the practicality the only rhino present through the Whitby and most of the Arkhangelsk. This low in generic diversity was compensated for by several parallel species that persisted unchanged (through most of the Arkhangelsk: D. armatum, the large type species, and D. steinhoffi, a smaller species. There is also a few dwarf species (Prothero, in preparation) from the earliest Arkhangelsk (formerly considered the Granger Formation at Roundhouse Rock, Nebraska, but now correlated with the "brown siltstone" member of the Briare Formation, according to Snehart et al., 1985) and a late Arkhangelsk to early Hemingfordian species, D. mastodon. In this study, the Whitby species "Subhynodon tridactylum is also referred to Diceratherium because some maxilla clearly show the beginnings of the nasal ridge forms.

Rhinocerotidae
MENOCERATINAE

Mencerus (Troll, 1921) (synonymy: Dicercerithorium, in part: Mesochoristes)

Type species: Mencerus anikarensis (Barbour, 1906).
Type specimen: UNSM 6208.

Characteristics: Mencerus was long confused with Dicercerithorium because both have paired horns at the tips of their nasals (Peter, 1920). As already discussed, the horns are not homologous in detail, and apparently they were independently derived. Mencerus shows many other characters (Figure 42.3, node 7) that clearly show it is a much more derived rhino than Dicercerithorium since rhino.
Indeed, in female skulls without the paired horns, Mencerus was often mistaken for more derived rhinos.
Average length of m2: 31.0-46.0 mm.

Comments: Pig-sized Mencerus anikarensis (usually mislabeled "Dicercerithorium anikarensis") immigrated to North America in the late Anikare era and is by far the commonest mammal in the famous Agate Bone bed. It evolved to smaller species. This barbouri, in the early Heming- fordian, which has been badly oversplit (M. "fullbuckii", M. "warslandensis", and the Croatan rhino, "Mesochoristes"), None of these synonomies 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, Mencerus disappeared as the wave of immi- grate aceratherines and teloceratinae apparently drove it out in the mid-Hemingfordian.

ACERATHERINAE

Floridacer in Wood, 1964

Type specimen: MCZ 149.

Characteristics: Floridacerus is the first aceratherine whose functional fifth maxillary was noted (Wood 1964). Its aceratherine affinities are somewhat equivocal. The only available material is badly crushed, so the degree of nasal retraction is difficult to determine. Unlike any other aceratherine, if had an upper 11, as indicated by a diastasis face on the lower tank.
Average length of m2: 47.2 mm.
Included species: F. whiti (only known from localities GC3, GC10D, CP106, PN9).

Comments: Floridacerus is an unusually large Hemingfordian rhino, known primarily from the Thomas Farm Local Fauna in Florida (locally GC8). 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, Aplocheles and Proceratoceras.

New genus (Prothero, in preparation)

Characteristics: Galusha (1977) briefly described a speci- men: (FAM 9554) from the early late Hemingfordian Box Butte Formation, Box Butte Co., Nebraska (locality CP107). It differs from all other aceratherines in its much smaller, extreme nasal retraction (to the level of anterior M), a feature paralleled only in the latest, most derived Aplo- cheles, and its uniquely that 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's unknown. Average length of m2: 41.0 mm.

Aplocheles, Cape, 1874

Type species: Aplocheles megadusos (Cope, 1873).
Type specimen: AMNH 8290.

Characteristics: Aplocheles has the derived features of a dor- sally arched nasal frontal profile and an unusually long di- asterism between the lower tank and the first lower premaxilla. Like almost all aceratherines, it lacks a chisel-shaped 1.
Average length of m2: 41.0-43.0 mm.

Aplocheles sp. is also known from localities GC5D, (GC5F), (GC5A), GC9B, GC10C, GC11B, GC12C, GC12E, NB20, NB21, NR20A, NR20B, NR25B, SB34A, SB35, CP127, (NP1), NP42, NP38B, NP38H, NP13).

Comments: Aplocheles 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. megadusos, persists with little change from the late Hemingfordian to the late Cimarronian. In the Hemphillian, the genus gets noticeably larger, with more hypodont teeth and more extreme nasal retraction. Aplocheles, a browser, is typically found with the grazing Telocerinus in most North American Miocene localities, although it is smaller numbers. It reached its acme in the latest Hemphillion, when it occurred in great numbers in the Panhandle of Texas (Coffee Ranch, locally SP13, and comparable localities) and Kansas (Eton Quarry) (locality CP123D). Telocerinus, by contrast, was rare at this time.
Rhinocerotidae

Ponorcaea Cope, 1880 (synonyms: Diceratherium, in part),
Apheles, in part; Telocerus, in part)

Type species: Peroceras supercilium Cope, 1880.
Type specimen: AMNH 8380.

Characteristics: Peroceras is characterized by a brachycephalic skull with a preorbital lambdoid crest and occipital, shortened nasals, flat dorsal skull profile, an upturned syn- physis in females, a short lower diastema, and lingual cin- gula on the lower cheek teeth. Average length of m2: 31.0-60.0 mm.


Peroceras sp. is also known from localities SB34A, PGOA.

Comments: Peroceras has long been one of the most mis- understood rhinos of North America. The type species is the most robust, derived species of the genus, and the primitive members have been incorrectly referred to Apheles, Acraceras, and Diceratherium. Prothero and Manning (1987) cleared up some of the confusion, and further discussion will be presented by Prothero (in prepara- tion).

Three species are currently recognized. The primitive, medium-sized species, P. pseudofuscus (= "Diceratherium jamaicensis," "Apheles monotonus"), overtops in size and morphology with A. mcaleadas. Most specimens of the primate Hemphillianian and Barstovian P. peroceras are hard to distinguish from A. mcaleadas from the same deposits. There is a dwarf species, P. teucer, from the Texas Gulf Coastal Plain (Prothero and Sereno, 1980; Prothero and Manning, 1987), and the large type species, P. supercil- ium (= P. "teucer"; P. "teucer"), which paralleled the teloceratine in many features. During the Barstovian and early Clarendonian, P. supercilium is most common in northern localities, such as South Dakota, northern Ne- braska, and Montana and is not found in southern localities except in New Mexico and California. If it competed with Telocerus for the same large-bodied aquatic grazier niche, then it was less successful because it was much more rare than Telocerus and died out in the Clarendonian.

TELOCERATINAE: TELEOCERATINI

Brachyoterium Röger, 1904

Type species: Brachyoterium brachysurus (Lartet, 1837).

Type specimen: Unavailable.

Characteristics: Brachyoterium differs from Telocerus in having a slender post tympanic process with a ventral edge that is level with the postorbital process. There are strong lingual cingula on the upper premolars, and M2 is approx- imately equal to length of M3. The distal limb elements, especially the second metapodial, are longer and less re- bus than is typical of Telocerus. In all other features, it shows the typical teloceratine anatomy of a robust, short- limbed skeleton and a brachyphyll tooth with relatively hypsodont teeth and flaring lambdoid crest. Average length of m2: 44.0-54.0 mm.

Included North American species: B. americanum (known from localities CP17, CP107, CP108A, CP120B).

Comments: Yaskula and Tanner (1979) assigned late Hem- phillianian teloceratines from the Martin Canyon Local Fauna of northeast Colorado (locality CP17) to Brachy- ototrium americanum (gender corrected). It is unquestion- able, the most primitive teloceratine from North America, although whether it is truly Brachyoterium is still debatable. For the present, all of the late Hemphill- ian teloceratine material is referred to Brachyoterium americanum; truly Barstovian material is referred to Tele- ceras medicorhini.

Telocerus Hatcher, 1894

Type species: Telocerus major Hatcher, 1894.

Type specimen: PU 10645.

Characteristics: Telocerus is easily recognized by its char- acteristically robust and proximodistally shortened limbs and feet, and by its brachycephalic skull with broad flaring lambdoid crest and brachygnathic arches. The nasal bones are U-shaped in cross section, and typically there is a small horn rugosity at the tip of the nasals. The upper 11 is still present, unlike the condition in the a- ceratherines. The cheek teeth are usually very hypsodont, with the molars greatly enlarged at the expense of the pre- molars. The p2 is lost in most species of Telocerus. The nasal incisor is retracted to the level of interior P1, much shallower than in derived aiceratherines. In addition to the robustness of the limbs, Telocerus has an elongate canals te tube and an articulation between the scapulod and humerus. Average length of m2: 50.0-63.0 mm.

Included species: T. major (known from localities GC1B, SB252, SP2A, CP90A, CP114D, CP114A, CP114B, CP114D, NP41B, NP7); T. mediterraneus (localities GC1F, GC1E, GC1D, GC1C, GC1B, GC1A, GC1), T. forsteri (localities [C19], NB27A, NB31B, NP45, SB31B, [SP1B], [SP4C], SP3A, CP116B, CP116C, CP116D, CP116E, CP123C, CP127, [PN12]); T. telocerus (localities GC11A, GC11B).

T. hitchi (is T. "teucer") (localities GC13B, GC13C, GC13D, GC14, NC31, BB3D, SB3C, SB5A, SB5B, CP116D, CP114E); T. n. sp. A: (localities [SB32B, SB32F, SB32D]; T. n. sp. B: [SP7D, SB16, CP123C]).

Telocerus sp. is also known from localities (CA3), CA4,
elge seem 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 C7, GC3, GC5, GC19L, GC22C, SB47, SB48, SB52, CS54B, CS54A, CS168, NP9A, NP10BB, NP22, NP95A, NP25B, NP25C, NP68B, NP13, NP16.

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 Monoceros was much smaller than contemporary extant and extinct species. Eocene and Oligocene rhinocerotids have relatively low-crowned teeth and efficient cutting incus chisel-like comb structures for browsing, and most of them are found in river channel sandstones. Clark, Boochower, and Katzke (1967) found that Sabrhyacodon was more abundant in the near-stream facies of the Big Rodlands than in the swampy plain; it was absent from the open plain. Xyrapax and Amphibolophodon are known exclusively from river channel deposits. As the tiannathères, antyodontids, and other large-bodied browsers disappeared during the late Eocene and the Oligocene, only the rhinocerotids persisted in the browsing, near-stream niches (Figure 35.3). By the Oligocene, the conditions were drier, and overall mammalian diversity was in an all-time low (Prothero, 1985; Stucky, 1990). During most of this time, Diacronothium was the only large-bodied mammal in North America, apparently hiding in what remained of the riparian woodlands. Judging from the large numbers of these rhinos in quarters such as the Big Well, Kokernot Co., Wyoming (locality 5CP25), they may have formed herds. Diacronothium was the first North American rhino to show significant sexual dimorphism in horns or task development, so it probably had a more complicated social structure than its more solitary predecessors.

The large Antarctotherian (Upper Harrison Formation, Agate Springs, Quarry, locality CP10A4), the first of the early Miocene immigration events, brought the tiny European Monoceros on the scene. Judging from its great abundance in these quarters, it probably lived in large herds, with subequal numbers of males and females. By contrast, the true Diceratherium was very rare and apparently looking ground to the invader. It is unknown from the rest of the Hesperitherium (late early Miocene), although it may occur in the late Hesperitherium in Railroad Canyon, Idaho (locality NP19B). Monoceros, in turn, tried to compete with a mid-Hesperitherium wave of immigrant archontitheres and teleoceratines and was gone before the late Hesperitherium. By the late Hesperitherium, the archontitheres Apheropus and Paraceratherium and the teleoceratine Brachytherium had established the dominant rhino lineages for the rest of the Miocene.

From the late Hesperitherium to the late Miocene (latest Miocone), North American rhinos show the browser-grazer pair combinations that are typical of savannah everywhere, including the modern East African savanna. The browser typically feeds on...
Figure 42A. Temporal ranges of North American rhinoceroid genera.
medium- and high-level leaves and tender shoots uses a pre- bensile lip and prehensile for the purpose. Aceraceritina, particularly Aepholhos and pumilus Pursh, performed this role in the North American Miocene savannas. These rhinos have a greatly enlarged nasal cavity for anchoring muscles of a prehensile lip and have replaced their upper incisors with a nipping pad, as modern rhinos and rinoceronts have. The modern browsing black rhino is rather solitary with a wide home range, and with few exceptions, most Aepholhos are found in small numbers in any given quarry. Wright (pers. comm.) has found that Aepholhos has relatively low infant mortality at the Lave site in Florida (GC1A), which is comparable to the population structure of the brown Dicerorhinus. 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 herder like hippos. Wright (pers. comm.) found that the Lone Bone Hill Teleocerus 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 Poi- son Ivy Quarry locality CP116A rhinos even contain grass seeds (Voorhies and Tornam benz, 1979). Although modern white rhinos are not as aquatic as Teleocerus or hippos, they are efficient grazers that live in small herds. The brower-grazer pair combination was very successful, for similar pairs were found in most Miocene sav- annas in Eurasia and Africa, usually involving a browsing Acraceritina or Dicerorhinus and a grazing Rhyacodaws or Chlorotherium. When the savannas disappeared from North America in the early Pliocene, w'c did the rhinos. Today the brower-grazer pairs are found only in the East African savanna, one of the few remaining species. 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 Pliocene units of South Dakota, Nebraska, Kansas, Oklahoma, and Texas than they are in the intermontane localities in Califor- nia, Oregon, and Nevada (see Figure 35.3). There are many Miocene localities from the intermontane region, with a great abund- ance of camels, horses, and mammoths, but rhinos are extremely rare, because this cannot be due to sampling, it is apparent that rhino preferred the open savanna of the Plains to the more wooded habitats of the intermontane states. There are few Miocene local- ities east of the Mississippi, but Florida produces rhinos in great numbers. Besides this overall trend, certain species clearly had biogeo- graphic preferences. The dwarf species of Perusorcas and Teleocerus were found mainly in the Texas Gulf Coastal Plain, which had a pe- culiar endemic fauna that lived in the swampy, wooded backsw amendment (Prothero and Sorensen, 1980). These dwarfs were analo- gous to the dwarfs that occurs when savanna mammoths adapt to the warmer biotopes and resources of the forest, as happens with pygmy hippos, forest stumps, and Cape buffalo, and many small island dwarfs, Perusorcas superfleecius, in contrast, is found almost exclusively in more northerly Barstovian and Clarendonin local- ities, especially in Montana, South Dakota, and Nebraska; it was absent from Florida or Texas. Florida had endemism in much of its fauna, and Teleocerus pertenuis was also a Florida endemism. The Rio Grande rift was remarkably rich in Perusorcas (all three species) and had its own endemic, prehistoric species of Teleocerus (Teleocerus "it. sp. No. 1"). 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 Aepholhos magnolus and few Frequently Teleocerus or Perusorcas. Further details of this biogeographic picture are pre- sented elsewhere.

REFERENCES