EVOLUTION OF TERTIARY MAMMALS OF NORTH AMERICA

VOLUME 1:
TERRESTRIAL CARNIVORES, UNGULATES, AND UNGULATELIKE MAMMALS

EDITED BY CHRISTINE M. JANIS,
KATHLEEN M. SCOTT, AND LOUIS L. JACOBS

29 Protoceratidae

DONALD R. PROTHERO

INTRODUCTION

The Protoceratidae were a middle Eocene to early Pliocene group of tylopods closely related to camels. They originated in North America in the early Uintan, during the great middle Eocene radiation of North American artiodactyls, and became extinct in the very latest Hemphillian. Thirteen valid genera are recognized, but typically only two or three genera were present at any given time. The Protoceratidae were a relatively long-ranging, but rare group throughout their history in most parts of North America.

Protoceratids began as small, primitive, hornless selenodont artiodactyls that are difficult to distinguish from contemporary Uintan oromerycids, oreodonts, and ruminants. Indeed, the oldest protoceratids were not removed from the leptomerycids and placed in the Protoceratidae until J. A. Wilson did so in 1974. Late Oligocene *Protoceras* sported enlarged canines and horns or hornlike protuberances on the maxilla, orbit, and parietals of male individuals. Later protoceratids all had some combination of horns, including the bizarre forked occipital "propeller" of *Paratoceras* and the rostral "slingshots" and orbital horns of the synthetoceratines (Figure 29.1). From the Whitneyan (mid-Oligocene) onward, protoceratids were very like some deer or antelopes in their skeletons and their range of body sizes (from 20–350 kg, according to Janis, 1982). However, they had unfused metapodials and relatively short legs compared to more gracile cursorial artiodactyls. According to Janis (1982), most Miocene protoceratids were mooselike folivorous browsers restricted to the more subtropical Gulf Coastal Plain. The only Miocene High Plains protoceratid, *Lambdoceras*, was a more deerlike tree browser. Protoceratids disappeared from North America in the latest Hemphillian, along with many other characteristically North American groups. These included dromomerycids, mylagaulid and eomyid rodents, most horses, rhinos, and antilocaprids, and many others; altogether, sixty-two genera became extinct (Webb, 1984). This extinction apparently corresponds to the cooling and loss of subtropical wooded habitat triggered by the Messinian crisis in worldwide climate.

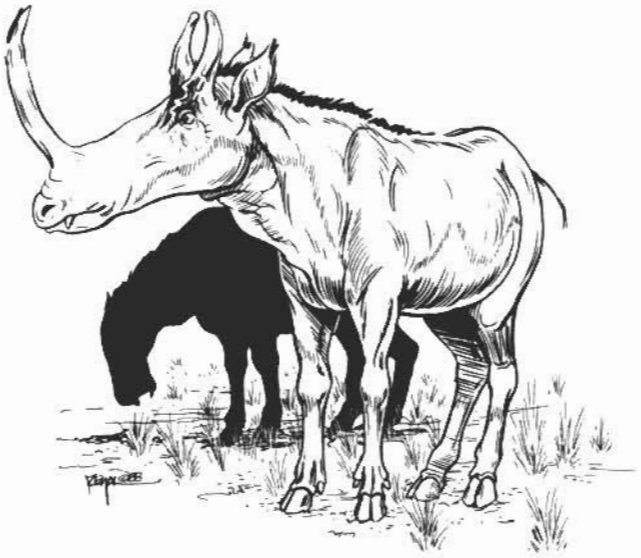


Figure 29.1. Restoration of *Synthetoceras*, by Brian Regal.

DEFINING FEATURES OF THE FAMILY PROTOCERATIDAE

CRANIAL

Although the horns and other cranial protuberances characterize the more advanced members of the family, they do not occur in the most primitive members. Aside from the horns, there are relatively few other features that are typical of protoceratids, and many of these are primitive. In the skull, there is a small facial vacuity, and the orbit is completely closed. The nasals are greatly retracted between the slender maxillae (to the level of P3 in *Heteromeryx*, and to the first molar in *Protoceras* and higher taxa). The upper incisors are lost in the more derived taxa. The diastema between the incisors and the second premolar becomes increasingly large, and the canine and first

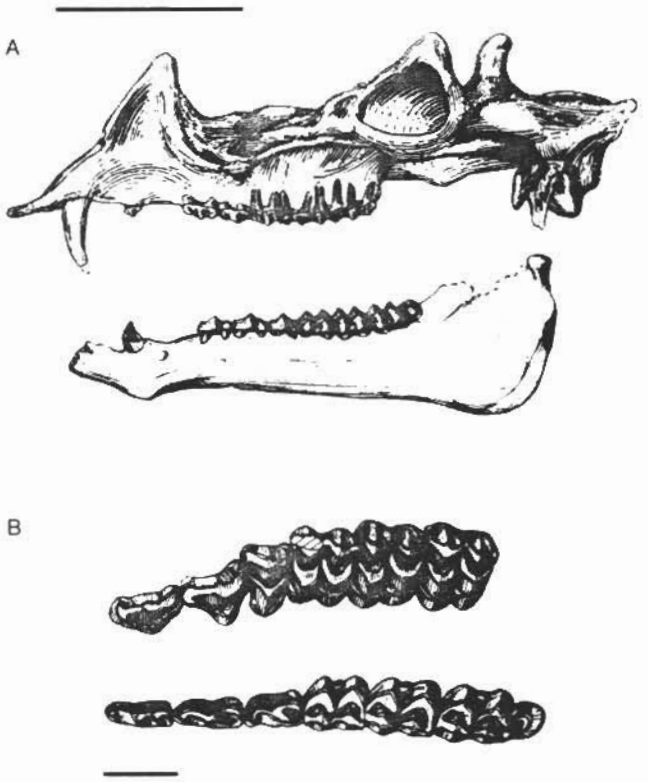


Figure 29.2. Skull and dentition of *Protoceras celer* from the Whitneyan of South Dakota. A. Left lateral view of male skull and jaws (scale bar = 5 cm). B. Crown views of upper and lower dentition (scale bar = 1 cm). (Modified from Patton and Taylor, 1973.)

premolar barely fill this gap; they are often reduced or lost. The jaw flexes downward at the symphysis. Although the jaw has the typical tylopod articular condyle, the coronoid process is shorter than in just about any other ungulate, and the angular process is rounded without the dorsal "hook" found in most tylopods. Like camels, protoceratids have distinctive winglike basioccipital processes just anterior to the occipital condyles that partially cover the hypoglossal foramina.

DENTAL

Most of the derived features that define the Protoceratidae are found in the dentition (Figure 29.2). These include an enlarged upper canine in males and caniniform P1/p1 isolated by diastemata. The primitively bunoselenodont upper molars are laterally wide and anteroposteriorly short. The paracone and metacone slope strongly lingually, with prominent parastyles and mesostyles and very strong lingual cingulum. In the lower molars, the anterior crest of the hypoconid and the posterior crest of the protoconid are directed lingually. Protoceratids are among the few Eocene artiodactyls with simple, completely selenodont teeth with no bifurcations of the lophs.

POSTCRANIAL

In the postcranial skeleton, protoceratid and camel vertebrae share a canal that passes through the neural arch rather than the transverse processes of the anterior cervical vertebrae. Through the history of the group, the limbs attain more cursorial proportions, but never to the degree seen in camels or pecoran ruminants. Originally, the radius and ulna were unfused, but they were completely fused in some synthetoceratines. The lateral metacarpals become somewhat reduced, but protoceratids always retain a fully four-toed manus. The astragalus develops a distinct distal keel, and the proximal side of the sustentacular facet is concave, a feature unique to the group. The cuboid and navicular remain separate, but the ecto- and mesocuneiforms are fused, as in other tylopods. The lateral metatarsals are more reduced than the lateral metacarpals, but vestiges are still evident. The metapodials never fuse into a cannon bone in this group. The keel at the distal end of the metatarsals is confined to the plantar surface and never extends anteriorly onto the volar surface, as in cursorial pecorans.

SYSTEMATICS

SUPRAFAMILY

The debate over the affinities of protoceratids has been one of the longest and most confused in the mammalian literature (see review in Patton and Taylor, 1973, pp. 401–2). *Protoceras* was the first member of the family to be described (Marsh, 1891), and Marsh suggested it might be related to giraffes. Osborn and Wortman (1892), Scott (1895, 1899), Wortman (1898), Matthew (1905), Colbert (1941), Stirton (1944), Simpson (1945), and most authors in the first half of this century tended to place protoceratids with ruminants, particularly hypertragulids, or within the Pecora. Loomis (1925, 1928) placed *Protoceras* with the camels, and Scott (1940) and Stirton (1967) began a modern revival of the idea that protoceratids were tylopods. Patton and Taylor (1971, 1973), in their extensive monographic review of the post-Eocene members of the family, further supported this idea. They did not include the Eocene members of the group within the family because Gazin (1955) had placed *Leptotragulus*, *Leptoreodon*, *Poabromylus*, and *Heteromeryx* within the Leptomerycidae, even though he considered them ancestral to protoceratids (Gazin, 1955, p. 14). Ironically, "leptotragulines" had long ago been considered tylopods by Wortman (1898), Matthew (1905), and Scott (1899). Wilson (1974), Golz (1976), and Black (1978) formalized the inclusion of the "leptotragulines" within the protoceratids, resulting in our modern conception of the group. Webb and Taylor (1980) produced some of the strongest evidence for the tylopod affinities of protoceratids.

INFRAFAMILY

Three subfamilial and two tribal names proposed for members of the Protoceratidae are still in use. The Synthetoceratinae was proposed by Frick (1937) for the taxa above node 9 in Figure 29.3, and their monophyly has never been in doubt. Webb (1981) divided this group into the tribes Kyptoceratini (node 10) and Synthetoceratini (node 11), and both of these clades are monophyletic. Patton and Taylor (1973) used the old name "Protoceratinae" as a taxonomic

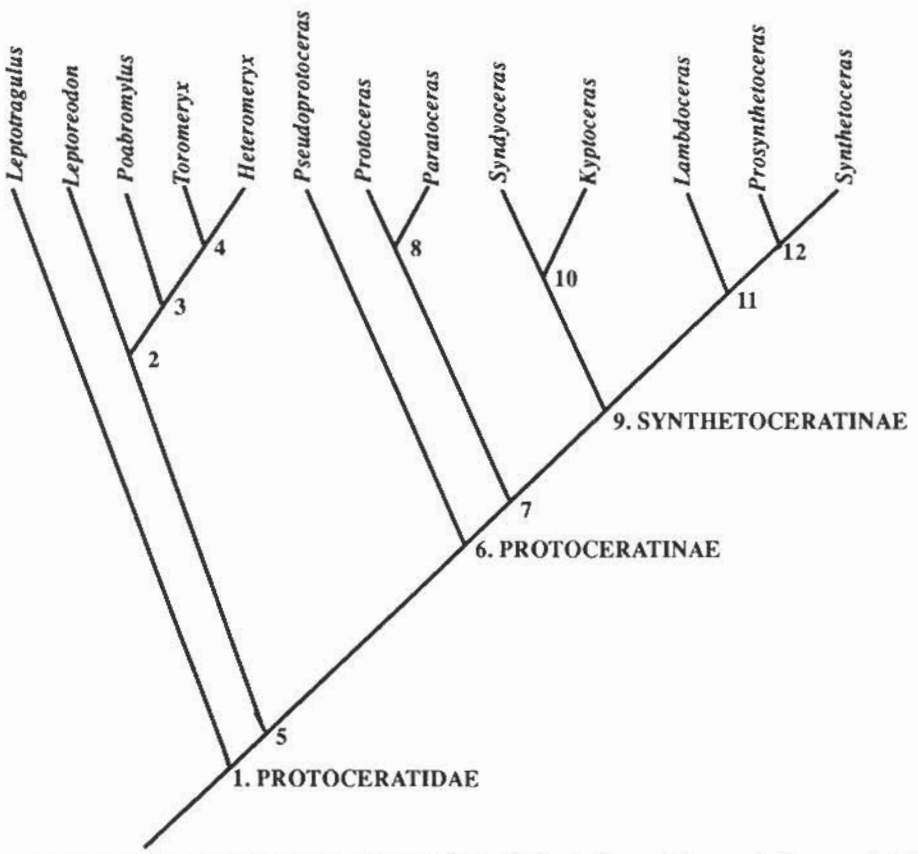


Figure 29.3. Interrelationships of the Protoceratidae. Characters at the nodes are as follows: (1) PROTOCERATIDAE: strong upper molar lingual cingula; short coronoid process on mandible; proximal side of sustentacular facet of astragalus concave. (2) p4 talonid closed posteriorly. (3) Anteriorly projecting p4 metaconid. (4) Weak columns in lingual valley of lower molars. (5) Brachydont teeth with thick enamel. (6) PROTOCERATINAE (emended): nasals retracted to level of molars. (7) Maxillary and orbital horns in males. (8) Maxillary horn a triangular laterally compressed flange. (9) SYNTHETOCERATINAE: Y-shaped rostral horn formed by fused maxillary flanges in males; longer muzzle and nasal bones; long orbital horns in males; small frontal protuberance including lacrimal bone in males; reduced premolars, and more hypsodont molars. (10) KYPTOCERATINI: rostral horn fused only at base, with no stalk; horns circular in cross section; orbital horns upright or anteriorly directed. (11) SYNTHETOCERATINI: rostral horn shaft fully developed by fusion of maxillaries; longer diastemata and reduced anterior premolars. (12) Rostral horn with longer shaft, more anteriorly directed; frontal horns sweep outward and backward; median pillar at base of crown between protoconid and hypoconid on m1–2.

wastebasket for the Oligocene taxa and *Paratoceras* (essentially the nonsynthetoceratine protoceratids, as defined by Patton and Taylor). If this group includes *Heteromeryx* and *Pseudoprotoceras*, it does not appear to be monophyletic. If the Protoceratinae is restricted to *Protoceras* and *Paratoceras*, then it is a valid taxon at node 8. Alternatively, the Protoceratinae could include the Synthetoceratinae and *Paratoceras* plus *Protoceras* at some rank between family and subfamily (node 7).

The "Leptotragulinae" (Zittel, 1893) has been widely used as a wastebasket name for the Eocene taxa, which have long been placed in the Leptomerycidae. There is clearly a monophyletic clade for most of these taxa at node 3, but unfortunately it does not include the genus *Leptotragulus*. If the hypothesis in Figure 29.3 is supported, then another name must be sought for this clade.

INCLUDED GENERA IN THE FAMILY PROTOCERATIDAE

The locality numbers listed for each genus refer to the list of unified localities in Appendix I. The acronyms for museum collections are listed in Appendix III.

The locality numbers may be listed in a couple of alternative ways. 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 PROTOCERATIDS

***Leptotragulus* Scott and Osborn, 1887**

Type species: Leptotragulus proavus Scott and Osborn, 1887.

Type specimen: PU 11501.

Characteristics: *Leptotragulus* and *Leptoreodon* are small, primitive protoceratids that differ only in features of the lower premolars. In *Leptotragulus*, the p4 metaconid is much weaker, and the anterior crest is more sharply flexed, with a strong parastylid. The same is true to a lesser degree in p3. The molars are very similar, and in most features, both of these genera are very similar to many other Uintan selenodont artiodactyls.

Average length of m2: 6.5–6.8 mm.

Included species: *L. proavus* (known from localities CP6A, CP6B); *L. medius* (localities CP6A, CP6B, CP29C, ?CP29D, [NP25A], [NP25B]); *L. clarki* (localities CP6A, CP6B, CP39IIB); "*L.*" *profectus* (probably referable to a

different genus, such as *Trigenicus* Douglass, 1903, according to Storer, pers. comm.) (localities SB44B, CP39B, CP83C, CP98C, NP10B, NP24C, NP24D, NP24E, NP27C).

Leptotragulus sp. is also known from localities NP9A, NP13, CC7, NP22, CP82.

***Leptoreodon* Wortman, 1898 (synonyms: *Camelomeryx*, *Merycodesmus*)**

Type species: *Leptoreodon marshi* Wortman, 1898.

Type specimen: AMNH 2064.

Characteristics: The differences between *Leptoreodon* and *Leptotragulus* were discussed earlier. *Leptoreodon* has a large, bulbous metaconid and a broadly flexed anterior crest on p4. The talonid basin on p4 also tends to be closed posteriorly. Both of these features indicate that *Leptoreodon* is a more derived protoceratid than *Leptotragulus*, and place it with higher protoceratids to the exclusion of *Leptotragulus*. The genera *Camelomeryx* and *Merycodesmus* (Scott, 1898) were synonymized with *Leptoreodon* by Gazin (1955).

Average length of m2: 6.6–9.5 mm.

Included species: *L. marshi* (known from localities CC4, CC5, SB43A, SB44A, CP6A, NP8); *L. major* (localities CC4, [CC5], SB43A, SB43B); *L. pusillus* (localities CC7C, [CC8], CC9B, [CC9C], SB42B, SB43A, SB43B); *L. edwardsi* (localities CC9A, SB43B); *L. stocki* (localities CC9A, CC9AA, CC9B, CC9BB); *L. leptolophus* (localities CC7C, [CC9A], SB42B, SB44A).

Leptoreodon sp. is also known from localities CC7B, CC9A, CC9B, CP6B, CP29C, NP9B, (NP22).

***Poabromylus* Peterson, 1931**

Type species: *Poabromylus kayi* Peterson, 1931.

Type specimen: CMNH 11753.

Characteristics: *Poabromylus* is very similar to *Pseudoprotoceras* in some features, leading Wilson (1974) to synonymize the two. Emry and Storer (1981) pointed out some important differences that distinguish the two genera. *Poabromylus* is more primitive than *Pseudoprotoceras* in having more slender cheek teeth, with p4 nearly as broad as m1 and weaker lingual stylids on the lower molars. The upper molar cingula are much more reduced than they are in *Leptoreodon*.

Average length of m2: 8.1–11.5 mm.

Included species: *P. kayi* (known from localities CP7C, CP42A, CP83A); *P. robustus* (locality NB2); *P. minor* (localities SB25B, SB44B, CP42A, CP83C); *P. golzi* (localities CP29D, [NP25A]).

Poabromylus sp. is also known from locality CP29C.

***Toromeryx* Wilson, 1974**

Type species: *Toromeryx marginensis* Wilson, 1974.

Type specimen: TMM 31281-7.

Characteristics: *Toromeryx* is larger than other Uintan protoceratids and has very prominent labial cingula. In general, the teeth are low and bulbous, with thick enamel. The ento- and metaconids are bunodont, but the proto- and hypoconids are selenodont. There are prominent recurved lingual stylids forming closed pockets, and the metaconid ridge is present on p4.

Average length of m2: 9.0 mm.

Included species: *T. marginensis* only (known from localities SB42B, SB44A).

***Heteromeryx* Matthew, 1905**

Type species: *Heteromeryx dispar* Matthew, 1905.

Type specimen: AMNH 12326.

Characteristics: Most primitive protoceratids are known only from teeth, jaws, and partial skulls, but *Heteromeryx* is known from a fairly complete skull with associated limbs (described by Matthew, 1905, and Scott, 1940). There are no horns or protuberances, but the narial notch is retracted to the level of P3, leaving long, delicate nasal bones. The upper canine is enlarged, and there are large diastemata anterior and posterior to the reduced P1. *Heteromeryx* is much larger than earlier Eocene protoceratids and differs from its contemporary *Pseudoprotoceras* in having larger, more complex P2–3, a strong protocone on P2, and less recessed nasals. It is considerably smaller than *Protoceras* or *Paratoceras* and also hornless (unless the type skull was from a female individual).

Average length of m2: 10.5 mm.

Included species: *H. dispar* only (known from localities SB44A, SB44B, CP83A, CP98A, CP98C).

"PROTOCERATINAE"

***Pseudoprotoceras* Cook, 1934**

Type species: *Pseudoprotoceras longinaris* Cook, 1934.

Type specimen: AMNH 81000.

Characteristics: Originally, *Pseudoprotoceras* was known only from a badly crushed partial skull from *Chadronia* Pocket, Dawes County, Nebraska. Wilson (1974) synonymized it with *Poabromylus*, but in a complete review of the genus, Emry and Storer (1981) revived the name and showed its distinctiveness (discussed earlier). They also referred two other species to this genus. *Pseudoprotoceras* has no horns or protuberances on the skull, although the only known skulls may be from female individuals. The nasals are retracted to the level of the first molar, and the upper canine is greatly enlarged. The cheek teeth are more hypsodont than in contemporary genera, without the thick enamel of *Heteromeryx*. The upper and lower molars are relatively large and broad compared to the premolars. The P2 lacks a protocone. The upper molars have no labial cingulum, but have a lingual column attached to the metaconule. The P4 has a strong metaconid directly anterolingually, and the lower molars have weak lingual stylids but no labial cingulids.

Average length of m2: 11.2–14.7 mm.

Included species: *P. longinaris* (known from localities CP39C, CP39F, CP42A, CP98A, CP98B, CP98C); *P. semicinctus* (locality NP10B); *P. taylori* (locality CP39F).

Pseudoprotoceras sp. is also known from locality NP9A.

***Protoceras* Marsh, 1891**

Type species: *Protoceras celer* Marsh, 1891.

Type specimen: YPM 11078.

Characteristics: Males of *Protoceras* can be recognized by their combination of triangular bony protuberances rising dorsally from the maxillary and supraorbital ridge and knoblike protuberances on the parietals (see Figure 29.2). *Protoceras* has a relatively posteriorly placed orbit in a skull with strong sagittal and parietal crests. The muzzle is very long, with greatly retracted nasals, and with P1 midway between the canine and P2. There are three lower incisors and an incisiform lower canine, with p1 nearly caniniform. The molars are elongate and slender and relatively low crowned. The robust ulna is fused with the radius only at the distal end. Most of these features easily distinguish both males and females of *Protoceras* from *Paratoceras*, and from *Pseudoprotoceras* and *Heteromeryx*.

Average length of m2: 11.0–14.2 mm.

Included species: *P. celer* (known from locality CP84B); *P. skinneri* (localities CP84C, CP85C, CP101); *P. neatodelpha* (locality CP103).

Protoceras sp. is also known from locality NP10CC.

Comments: *Protoceras* was the first genus of the family to be recognized, although the type specimen was from a female individual, so it did not have the horns of a male. This led to considerable taxonomic confusion and oversplitting, reviewed by Patton and Taylor (1973), who recognized only one genus and species from the Whitneyan.

***Paratoceras* Frick, 1937**

Type species: *Paratoceras macadamsi* Frick, 1937.

Type specimen: F:AM 32457.

Characteristics: *Paratoceras* has many unique features, but the most bizarre is the forked occipital horn in the male that resembles the propeller on a beanie. It also has small triangular maxillary protuberances and posteriorly recurved supraorbital horns. The orbit is shifted far forward, but the sagittal crest is weaker than in *Protoceras*. There are no parietal protuberances, and the parietal crests are weak. The muzzle is short with the P1 near the upper canine, and a longer P1–2 diastema. Only three lower incisiform teeth are present, so either i3 or the lower canine is lost. The molars are less elongate and more robust than in other protoceratids and are also higher crowned. The ulna is gracile, and fused most of its length to the radius.

Average length of m2: 11.5–18.2 mm.

Included species: *P. macadamsi* (known from locality SP2A); *P. wardi* (locality GC4E).

Paratoceras sp. is also known from locality CA7.

SYNTHETOCERATINAE

KYPTOCERATINI

***Syndyoceras* Barbour, 1905**

Type species: *Syndyoceras cooki* Barbour, 1905.

Type specimen: UNSM 1153.

Characteristics: *Syndyoceras* is most easily recognized by its rostral horn, which is formed by a symphysis of the maxillaries. Unlike the rostral horn of the Synthetoceratini, it does not fuse to form a long stem or trunk, but branches immediately above the base. There are long frontal horns that extend over the orbit and the curve dorsomedially but do not sweep backward as in the Synthetoceratini. The dentition is relatively low crowned, and the premolars are relatively large compared to other synthetoceratines. The limbs are relatively robust, and there is little reduction of the lateral metacarpals.

Average length of m2: 17.5–18.0 mm.

Included species: *S. cooki* only (known from localities CP52, CP103, CP104B).

***Kyptoceras* Webb, 1981**

Type species: *Kyptoceras amatorum* Webb, 1981.

Type specimen: UF 25711.

Characteristics: *Kyptoceras*, the last of the protoceratids from the latest Hemphillian, is actually closely related to Hemingfordian *Syndyoceras* and not to the Synthetoceratini of the later Miocene. This is shown by the rostral horn that diverges immediately above the base without a trunk, tall upright frontal horns, and the subcircular rather than laterally flattened cross section of the horns. *Kyptoceras* differs from all other protoceratids in that both the orbital and rostral horns tilt forward and the cheek teeth are extremely hypsodont. In addition, there is no exposure of the narial passage dorsally behind the rostral horn, as in all other protoceratids.

Length of m2: unknown. Length of M2: 28.6 mm.

Included species: *K. amatorum* only (known from locality GC13B, and possibly locality GC28 [could be *Synthetoceras*]).

SYNTHETOCERATINI

***Lambdoceras* Stirton, 1967**

Type species: *Lambdoceras hessei* Stirton, 1967.

Type specimen: UCMP 32372.

Characteristics: Like all other Synthetoceratini, *Lambdoceras* has a rostral horn formed by fusion of the maxillaries into a distinct shaft. Compared to others within the group, the shaft is relatively long and the fork is shorter. The frontal horns extend more directly out over the orbit, and the basal part is less triangular in cross section than in *Prosynthetoceras*. The lower premolars are relatively heavier, posteriorly wider and more wedge shaped than in *Prosynthetoceras*. The molars are primitively lower crowned, and the

lateral metatarsals are not as reduced as they are in *Prosynthetoceras*.

Average length of m2: 19.5–35.0 mm.

Included species: *L. hessei* (known from localities CP108B, CP88); *L. siouxensis* (localities CP110, CP111); *L. trinitiensis* (locality GC4E).

Lambdoceras sp. is also questionably known from locality CP114B.

Comments: *Lambdoceras* was the only synthetoceratine to persist in the High Plains after the Hemingfordian.

Patton and Taylor (1971) placed *Lambdoceras* as a subgenus of *Prosynthetoceras*, but their Figure 37 clearly shows that this makes *Prosynthetoceras* a horizontal wastebasket genus for all Barstovian and Clarendonian Synthetoceratini. For this reason, subsequent authors (e.g., Webb, 1981) have treated *Lambdoceras* as a valid genus, rather than as a subgenus of *Prosynthetoceras*.

***Prosynthetoceras* Frick, 1937**

Type species: *Prosynthetoceras francisi* Frick, 1937.

Type specimen: TAMU unnumbered.

Characteristics: *Prosynthetoceras* has a longer and more anteriorly directed shaft on the rostral horn than in more primitive synthetoceratines. The frontal horns arise posterior to the orbit and sweep outward and backward, with the basal part of the horn triangular in cross section. The lower premolars are laterally compressed compared to *Lambdoceras*. In the lower molars, the stylids are reduced, and there is a small median pillar at the base of the crown between the protoconid and hypoconid on m1–m2. The lateral metatarsals are completely reduced to proximal splints.

Average length of m2: 16.1–23.8 mm.

Included species: *P. francisi* (known from locality GC4E); *P. texanus* (= *P. rileyi*, *P. australis*) (localities GC2, GC3A, GC3B, GC4A, GC4D, GC5, GC8D, GC9A, GC9B, NC1A).

Prosynthetoceras sp. is also known from locality WM13.

Comments: Patton and Taylor (1971) considered *Lambdoceras* to be a subgenus of this genus and assigned most of the former members of the genus to *Prosynthetoceras* (*Prosynthetoceras*). For reasons given earlier, *Lambdoceras* is removed from subgeneric status, obviating the need for subgenera in *Prosynthetoceras*.

***Synthetoceras* Stirton, 1932**

Type species: *Synthetoceras tricornatus* Stirton, 1932.

Type specimen: UCMP 31520.

Characteristics: *Synthetoceras* has the longest and most anteriorly inclined rostral horn of any protoceratid. The frontal horns are like those of *Prosynthetoceras*, except that they are conspicuously knobbed. The p1–p4 diastema is extremely long, with p1–p2 lost. The p3 and p4 are proportionally smaller relative to the molars and have a high median protoconid. The molars are larger and higher crowned than those of *Prosynthetoceras*. The lateral metapodials are even further reduced than they are in *Prosynthetoceras*.

Average length of m2: 23.0–31.5 mm.

Included species: *S. tricornatus* only (known from localities GC6A, GC6B, GC11B, GC27, SP2A).

INDETERMINATE PROTOCERATIDS

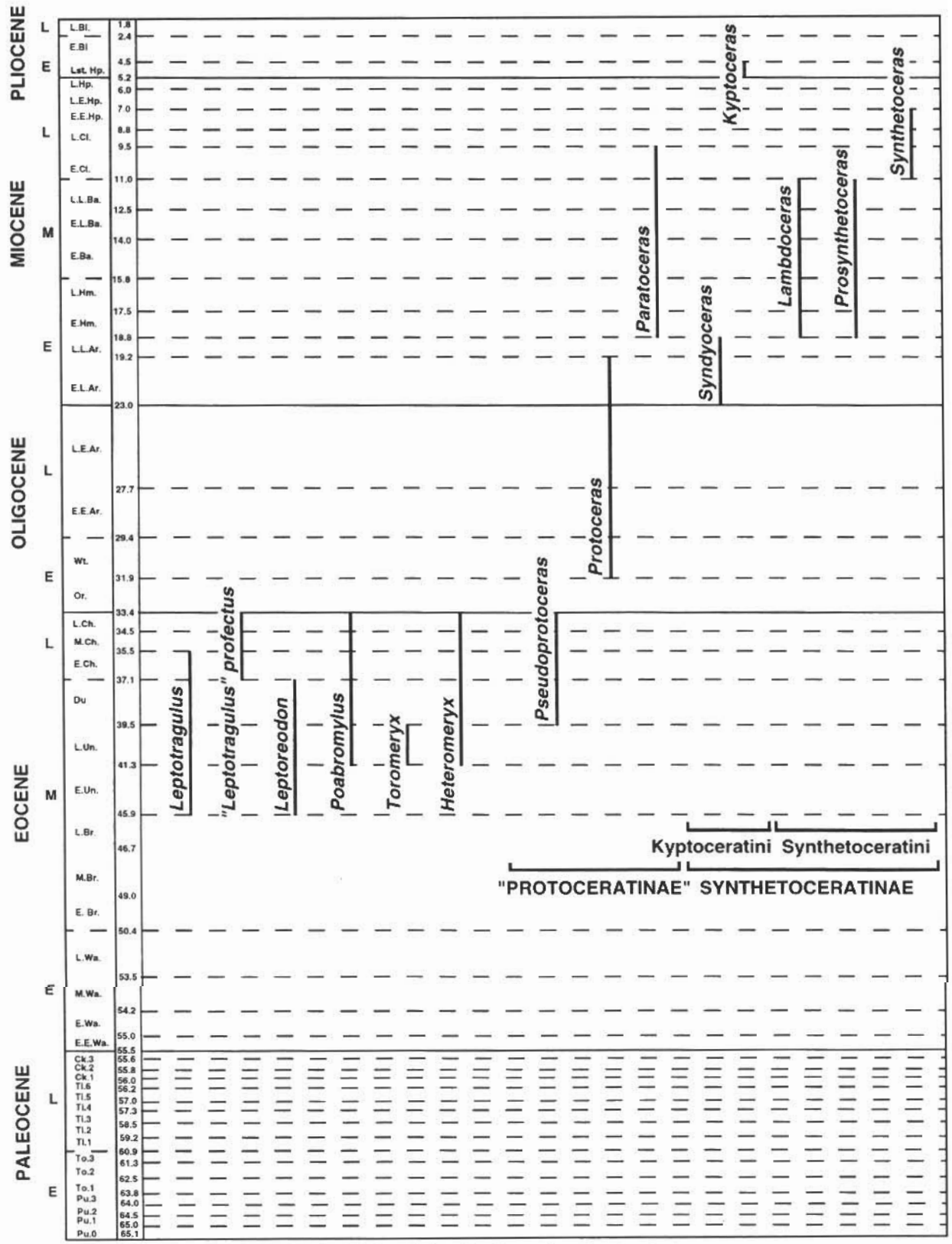
Fragmentary remains ascribed to protoceratids also have been reported from localities CA2, GC7, GC9C, CP114D, NP10C.

BIOLOGY AND EVOLUTIONARY PATTERNS

Protoceratids appeared in the Uintan (middle Eocene) as small, hornless forms that were very similar to a number of contemporary selenodont artiodactyls, such as the protoreodonts, agriochoeres, oromerycids, and hypertragulids. Although their skeletal anatomy is poorly known, presumably they were browsing herbivores that lived in the forested environments of the Uintan. When the climate changed in the late Eocene to a drier mix of forest and grassland (Berggren and Prothero, 1992; Prothero, 1994), protoceratids responded by becoming somewhat more hypsodont. They also began to show evidence of nasal retraction, implying that they must have had some sort of prehensile lip for browsing.

More importantly, they became restricted in distribution in the late Eocene (see Figure 22.5, 29.4). They are among the more common taxa in Uintan deposits of California, Utah, Saskatchewan, and Texas, and *Poabromylus* is one of the few taxa found in most Duchesnean localities. But *Pseudoprotoceras* and *Heteromeryx* are known from only a few specimens in a few Chadronian localities, and there are still no known Orellan protoceratids. During the later Oligocene, *Protoceras* actually occurs in the late Whitneyan "*Protoceras* channels" in only two places in the Big Badlands (Patton and Taylor, 1973, p. 355). The so-called "*Protoceras* channels" of Sheep Mountain Table and many other places in the Big Badlands yield no *Protoceras*, and there are none known from any other late Whitneyan channel deposit outside South Dakota. Arikareean protoceratids are similarly scarce, despite the great abundance of Arikareean deposits. By the Hemingfordian (late early Miocene), only *Lambdoceras* persisted in the High Plains; all other Miocene protoceratids are known from the subtropical coastal plains of Texas, Alabama, Florida, New Jersey, and Panama. Clearly, from the Oligocene onward, protoceratids were either very scarce and/or occupied habitats that have not been extensively sampled in the fossil record (outside the Gulf Coastal plain).

Some clues as to their habitat are given by their anatomy. According to Janis (1982, p. 286), they had purely folivorous molar wear and a broad, mooselike snout (suggested by their retracted nasals), which led Janis to propose that they fed on semiaquatic vegetation with little cellulose. Their relatively short limbs, with a persistently four-toed manus and unfused metapodials, suggest they were not open plains runners, but adapted for more brushy terrain. Only *Lambdoceras* persisted in the High Plains, and it had a narrower snout, suggesting a tree-browsing habitat (Janis, 1982).



Bl.=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 29.4. Temporal ranges of protoceratid genera.

Because horns were highly sexually dimorphic, there was probably extensive sexual selection for them, as is well documented in living horned ruminants. Apparently, their horns served the functions of both visual display and intraspecific combat (Webb, 1981). The horns of *Protoceras* are suited only for lateral display, but those of the Synthetoceratini are arranged for frontal display. Ruminants show a similar progression from lateral to frontal display. Most camelids and ruminants use a mixed strategy of biting, butting, poking, and neck wrestling in intraspecific combat between males, and the horns of protoceratids seem well designed for these purposes. Webb (1981, p. 364) has described how the horns of *Kyptoceras* were well suited for display and neck wrestling and pushing because their angle of attack would easily force males in combat to interlock without seriously gouging or killing their opponent. This kind of behavior is well documented in modern ruminants.

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