Chapter 14

New Evidence of Miocene Protoceratidae Including a New Species from Chiapas, Mexico

S. DAVID WEBB,[1] BRIAN LEE BEATTY,[2] AND GEORGE POINAR, JR.[3]

ABSTRACT

We describe *Paratoceras tedfordi*, a new species of Protoceratidae from early Miocene amber-bearing sands near Simojovel, Chiapas, southern Mexico. The holotypic cranium weakly expresses maxillary plates, supraorbital rugosities, and a median occipital projection as in the type of *Paratoceras wardi*, and is interpreted as a female. Its short facial region, elongate premolars, and brachydont molars place it among the Protoceratinae, not Synthetoceratinae. We also describe new cranial and the first postcranial material of *Prosynthetoceras texanus* from Alum Bluff and Thomas Farm sites in Florida. Incorporating data from these new specimens, we consider highlights of protoceratid adaptive morphology including their elaborate male ossicones, tapirlike proboscis, brachydont to mesodont dentition, and limb features and proportions. We suggest that progressive protoceratids may be seen as ecological analogues of the Bushbuck of South Africa, a forest-adapted browser. Each of the three groups of horned Protoceratidae speciated allopatrically along latitudinal lines, with the northern branch becoming extinct earlier than its southern sister. Their greater proclivity toward survival in tropical latitudes explains the importance of Protoceratidae in the Gulf Coastal Plain during the Miocene, and evident higher abundance of *Paratoceras* in Central America.

INTRODUCTION

Protoceratidae comprise the rarest family of large mammals in the Neogene of North America. They range from the Uintan through the Hemphillian Land Mammal "Ages" of North America. Protoceratids become increasingly rare, if one can judge from the record, through the course of the Miocene. Because of their apparent rarity, the evolution and paleobiology of Protoceratidae have been shrouded in considerable darkness. In this paper, we describe a new species from southern Mexico (UCMP holotype: University of California Museum of Paleontology) as well as additional material from Florida (UF specimens: Florida Museum of Natural History).

We are very pleased to dedicate this work to Dr. Richard H. Tedford, and to name in his honor the newly described species. Dick has generously shared his encyclopedic knowledge of mammalian paleontology and stratigraphy with one of us for more than 40 years, and he has substantially contributed to the education of two subsequent generations of colleagues and students. We especially honor his profound contributions to the principles and practices of land-mammal biostratigraphy and systematics in North America, Asia, and Australia.

PREVIOUS STUDIES

The first of these remarkable animals to be described was *Protoceras celer*, named by Marsh (1891) from the late Oligocene of the White River Badlands. As the name implies, Marsh was intrigued by the structure of the horns or ossicones, which he compared most

[1] Distinguished Research Curator and Professor of Zoology and Geology, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611.
[2] Doctoral Candidate, Museum of Natural History, University of Kansas, Lawrence, KS 66045–2454.
[3] Professor, Department of Entomology, Oregon State University, Corvallis, OR 97331.

closely with those of a giraffe. Hereafter we refer to the protoceratid cranial armaments as ossicones, for, as explained below, they were surely not horn covered. Schlosser (1902) affirmed Marsh's view that *Protoceras* was a possible giraffid. The next two genera assigned to the Protoceratidae were the Miocene taxa *Syndyoceras cooki* Barbour (1905) and *Synthetoceras tricornatus* Stirton (1932). Each of these first three genera was represented by a solitary male individual, and was diagnosed primarily by its ossicones. Curiously, these first three genera appeared in ascending chronological order, underlining the impression that Protoceratidae had a simple linear (anagenetic) phylogeny.

The first hint that Protoceratidae had a more complex history came when Cook (1934) described *Pseudoprotoceras*, a presumed side branch that arose earlier than *Protoceras*. Frick (1937) added more Neogene forms, including the genus *Paratoceras*, the subgenus *Prosynthetoceras*, and several new species. Frick's monograph placed the five genera and one subgenus in three subfamilies, but provided virtually no discussion of their phylogenetic relationships. Simpson (1945: 266) found that Protoceratidae seemed "to represent very nearly a unit phylum." The last two generic additions to the Neogene Protoceratidae were *Lambdoceras* Stirton (1967) and *Kyptoceras* Webb (1981). The entire family, including five genera of basal protoceratids not considered here, was recently reviewed and placed in a modern cladistic framework by Prothero (1998).

Fossil evidence of this family is so rare that new material can substantially alter and improve our understanding of the group. Following the description of the new material noted above, we also consider some aspects of protoceratid paleobiology and biogeography.

SYSTEMATIC PALEONTOLOGY
ORDER ARTIODACTYLA OWEN, 1848
SUBORDER TYLOPODA ILLIGER, 1811
FAMILY PROTOCERATIDAE MARSH, 1891
SUBFAMILY PROTOCERATINAE MARSH, 1891
Genus *Paratoceras* Frick, 1937
***Paratoceras tedfordi*, sp. nov.**
Figures 14.1, 14.2, and 14.3; table 14.1

ETYMOLOGY: Named in honor of Dr. Richard H. Tedford.

HOLOTYPE: UCMP V99089/173300, mature female skull with left and right P3–M3 and alveoli of P2; missing rostrum anterior to diastema between P2 and presumed P1; also missing zygomatic arches. No other protoceratid material is associated with the holotype.

TYPE LOCALITY: The type cranium was collected in April, 1996, from the Simojovel area in the state of Chiapas, Mexico, from the amber-bearing beds of the Balumtum Sandstone of early Miocene age.

AGE: The amber-bearing conglomerates from this part of Chiapas are generally considered early Miocene, ranging in age between 22 and 26 Ma (Poinar, 1992).

DIAGNOSIS: Cranium short with centrally placed orbits, lacking elongate facial region found in Synthetoceratinae. Female skull with thickened posterior maxillary plates, supraorbital rugosities, and elaborate, posteriorly expanding median occipital projection similar to male *Paratoceras wardi*. No thickening or rugosity in region of parietal ossicones as seen in *Protoceras celer*. Cranium smaller, but palatal width broader, than in *P. wardi*. Molars brachydont and wider than long, as in other Protoceratinae but not Synthetoceratinae. Molars slightly larger than, but with similar morphology to those of *P. wardi*. Lingual cinguli on P3, P4, and M1–3 weaker than in *P. wardi*; interrupted by lingual cusps except on P4. P2 and P3 about 20% longer than in *P. wardi* and much longer relatively than in Synthetoceratinae.

DESCRIPTION OF CRANIUM: Although this cranium experienced considerable breakage on many of its elevated surfaces, as if tumbled in gravel, it was so densely mineralized that most of the skull and the dentition remain well preserved under a matrix of tightly cemented conglomerate. The overall length of the intact part of the cranium, along the vertex to the broken tip of the right maxillary, is 180 mm. The estimated true length is about 215 mm, assuming that the missing part of the rostrum had proportions similar to those of *Paratoceras wardi* (Patton and Taylor, 1973). If correct, this cranium was only about 8% shorter than in the type specimen of *P. wardi*. The large orbits occupy the central region of the skull, resembling in this regard other primitive selenodont artio-
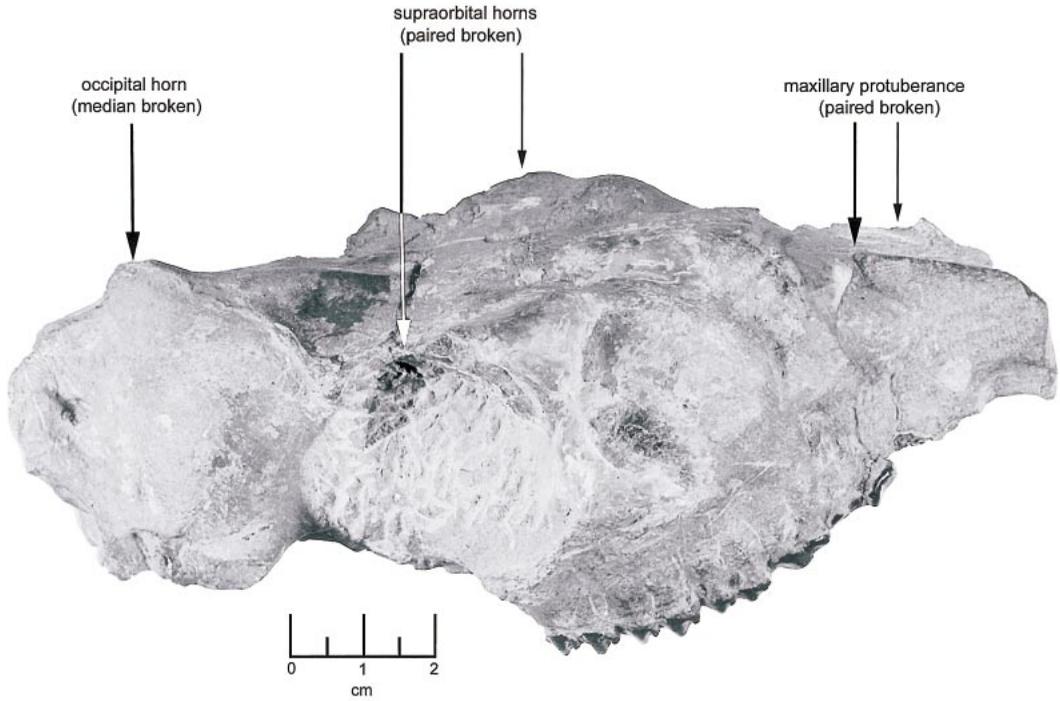
Fig. 14.1.   Oblique dorsolateral view of right side of holotype cranium of *Paratoceras tedfordi*, UCMP V99089/173300.
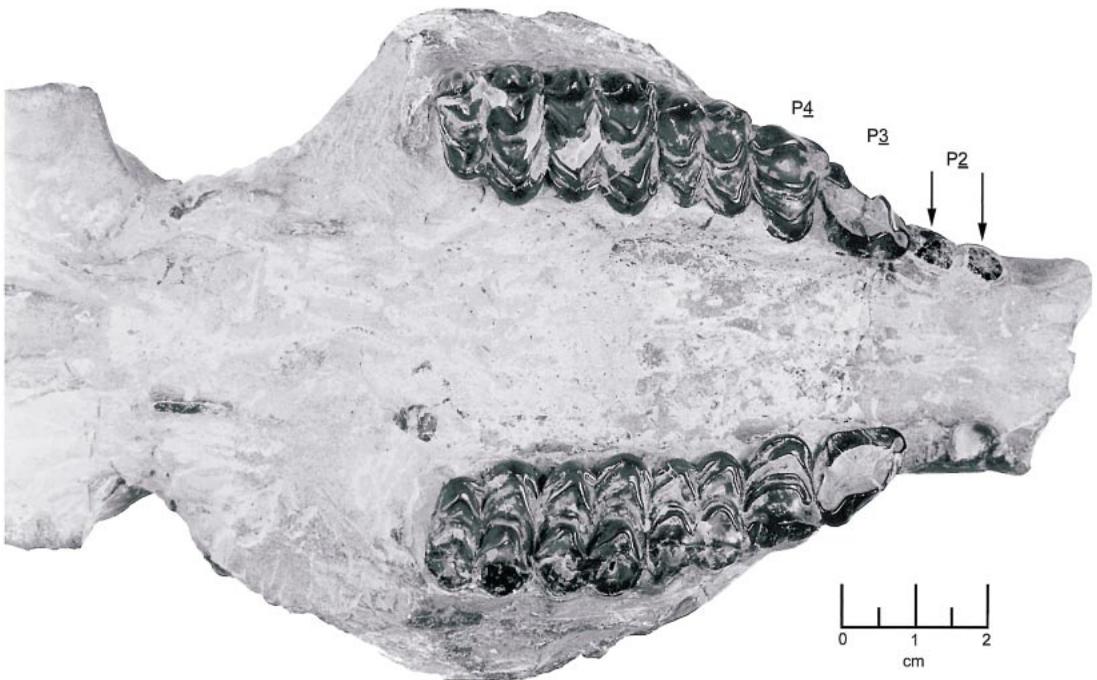

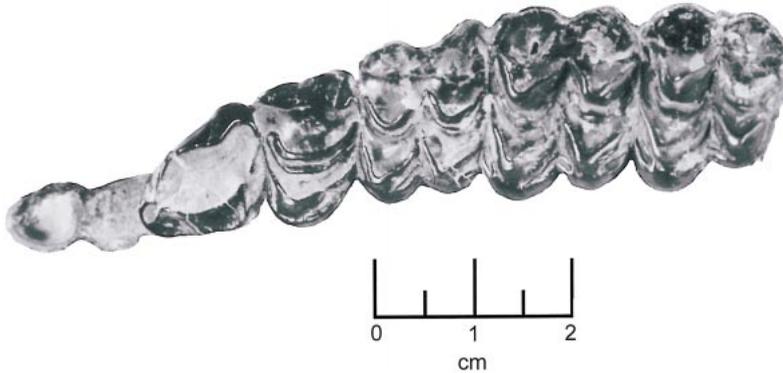Fig. 14.2.   Palatal view of holotype cranium of *Paratoceras tedfordi*.

Fig. 14.3. Occlusal view of left upper cheek teeth, P2 (alveoli) to M3 of holotype cranium of *Paratoceras tedfordi*.

dactyls including *P. wardi*. The oblique distance from the left postorbital bar to the nuchal eminence is 62.5 mm, which is considerably shorter than in *P. wardi* and more nearly in agreement with that dimension in *Protoceras celer* (Patton and Taylor, 1973). In the Chiapas skull the maximum cranial width across the supraorbital processes is 77.3 mm, but this is an underestimate due to minor breakage. The diameter across the masseteric crests, also slightly underestimated due to minor bone loss, is 88.3 mm. These dimensions indicate that the cranium of *Paratoceras tedfordi* is about 15% narrower than in *P. wardi* and probably also shorter.

Even though this cranium represents a female and is incomplete, it provides clear evidence of the peculiar ossicones characteristic of Protoceratidae. In particular it reveals rugosities in the maxillary, supraorbital, and occipital regions in exact agreement with ossicone positions in the rare genus *Paratoceras*. The right maxillary ascends about 35 mm

TABLE 14.1
**Measurements (mm) of Left Upper Dentition of
*Paratoceras tedfordi***

Length P2–M3	80.7
Length M1–M3	39.9
P3 length × width	16.6 × 9.9
P4 length × width	11.5 × 14.0
M1 length × width	12.4 × 13.9
M2 length × width	14.0 × 16.6
M3 length × width	14.5 × 17.0

above the P2 alveoli and there thickens dorsally. Although the exact dimensions of this maxillary rugosity are uncertain due to minor breakage, it attains a maximum thickness of 5.2 mm at its posterodorsal edge. The left side is also dorsally thickened, but is less fully preserved. Clearly these dorsally thickened maxillary bones represent the female expression of a rostral ossicone.

The second ossicone-like feature consists of greatly thickened supraorbital processes. The process on the right side is nearly 7 mm thick transversely at the point where it is broken.

An occipital ossicone is also expressed to some extent. The sagittal crest arises sharply from the convergence of the parietal crests on the midline about 30 mm posterior to a line between the postorbital bars. At this point the sagittal crest rises dorsally more than 10 mm and thickens posteriorly. The density and considerable thickness (about 10 mm) of the bone forming the posterior part of the sagittal crest indicate that it projected farther upward and thickened toward the nuchal eminence. These features indicate that the occipital region of this female skull weakly emulated the diagnostic occipital feature of the male cranium of *Paratoceras wardi*, which Patton and Taylor (1973: 369) characterized as a "bizarre occipital structure . . . that arises from the thickened and expanded dorsal border of the occipital bone and the dorsoposterior portion of the parietal bone." In this regard, the skull from Chiapas resembles that of *P. wardi* and differs from

known crania of Synthetoceratinae. There is no temporal crest dividing the posterolateral region of the cranium. This lays to rest the question, raised by Patton and Taylor (1973), of whether the temporal crest was lost only in males due to crowding by their bizarre ossicones.

Anterior to the P2 alveolus on the right side of the cranium is a circular fossa for *M. buccinator*; it is about 4 mm deep and 10 mm in diameter, a little smaller than that in *P. wardi*. The infraorbital foramen opens 12 mm above the posterior end of P3. The robust crest for *M. masseter* runs horizontally about 20 mm above the cheek teeth as in the type skull of *P. wardi*. Dorsal to the masseteric crest is a very large lacrimal fossa, about 35 mm long and 30 mm dorsoventrally, in which originated a large *M. levator nasolabialis*. The cranium lacks the peculiar bony excrescences and pittings so markedly developed on the facial and dorsal parts of the male *Paratoceras wardi* skull, perhaps indicating that those features are peculiar to adult males. The nasals are short, and each is retracted to a point about 3 mm posterior to the anterior end of the large lacrimal fossa. The intact length of the maxillary bones is greater than 45 mm long, but they are truncated anteriorly by breakage. The fractured upper edges of the maxillaries are separated by a long, parallel-sided gap 19 mm wide.

The ventral surface of this cranium provides few details other than overall dimensions and the well-preserved upper dentition. The palatal width between the third molars is 30.5 mm, which is nearly twice as wide as the corresponding dimension recorded (surely an error) for the type cranium of *P. wardi*. The following three lengths were measured as maximum distances from the anterior border of the foramen magnum: to posterior of M3 = 76.3 mm; to anterior of M1 = 122.6 mm; to anterior of P2 = 150.0 mm. These basal skull measurements bear a close resemblance to the same data for *P. wardi* (Patton and Taylor, 1973).

DESCRIPTION OF DENTITION: The molars are brachydont, wider than long and closely resemble those of *P. wardi*. Lingual cinguli are present on all five cheek teeth, but are not as strongly developed as in *P. wardi* and are interrupted by the lingual cusps on P3 and on M1–3.

Measurements (mm) of the left upper dentition (P2–M3) are indicated in table 14.1. The molar dimensions of *P. tedfordi* fall very close to those of *P. wardi*, and as in that species are wider than long. On the other hand, the premolar dimensions in *P. tedfordi* are about 20% greater in length than in *P. wardi* and nearly as much greater in width. P3 is tricuspate with a distinct parastyle and metastyle. P2, represented only by alveoli, is nearly as long.

DISCUSSION: The skull described here is the only protoceratid cranium known from south of Texas. The positions of the weakly expressed cranial ossicones identify it as the first known female skull of the rare genus *Paratoceras*. The hints of ossicones include thickening on the posterodorsal edges of the maxillary bones, paired rugosities in the supraorbital region, and a posteriorly expanding, median occipital projection. There is no evidence of a parietal ossicone, or equivalent thickened surface, as might be expected in a female skull of *Protoceras*. In female *Synthetoceras* a minor tuberosity develops at the posterolateral tip of the frontal, as seen in UF 16154 (Patton and Taylor, 1971), but the placement of this feature is quite different from that in the female skull of *Paratoceras*. Other diagnostic protoceratine features observed in this cranium are its brachycephalic proportions and its centrally placed orbits.

The upper dentition of the Chiapas skull is also readily recognized as protoceratine by its brachydont crowns, molars that are wider than long, and anterior premolars that are quite elongate. Detailed differences from the genotypic species, *Paratoceras wardi*, warrant recognizing *P. tedfordi* as a new species. Despite the fact that the skull is somewhat smaller than that of *P. wardi* in most dimensions, it has a broader palate and larger cheek teeth. The P2 and P3 are 20% longer than in *P. wardi*, these longer proportions indicating a more plesiomorphic stage than in that species. The age of *Paratoceras tedfordi* makes it the oldest known species of the genus, filling the space occupied by a question mark in the stratigraphic diagram presented by Patton and Taylor (1973).

SUBFAMILY SYNTHETOCERATINAE FRICK, 1937

Genus *Prosynthetoceras* Frick, 1937

Prosynthetoceras texanus Hay, 1924

See Patton and Taylor (1973) for synonymies.

Alum Bluff and Thomas Farm have yielded new material of *Prosynthetoceras texanus*, including the first postcranial evidence of this species in Florida. We treat the material from each area separately.

ALUM BLUFF

The sites at Alum Bluff in Leon County are known primarily for their paleobotanical samples of Barstovian age (Graham, 1964). A moderate number of vertebrate fossils also have been recovered from this same section in the Choctawhatchie Formation, a sandy facies below the Alum Bluff Formation proper, which is presumed to be of Middle Barstovian age (Puri and Vernon, 1964). Most of the vertebrate fauna consists of marine species, but included are a half dozen terrestrial vertebrate specimens, three of which represent *P. texanus*. The relative abundance of *P. texanus* among the land vertebrates from Alum Bluff is remarkably high.

UF200394: Partial left dentary with p4 to m2. The wear on the teeth indicates this individual was fully adult.

UF200395: Right dentary with p4 to m3, and alveoli for p3 and p2, as well as a complete diastema and edentulous symphysis. The teeth are not heavily worn compared to UF200394, indicating a different individual. The well preserved symphysis is noticeably spatulate. It measures 23.5 mm in length and 16.0 mm in width. Its maximum depth is 11.2 mm and the suture is dorsoventrally much thicker than in the Thomas Farm specimens.

UF124077: Fragment of rostral ossicone. This portion of the ossicone extends dorsally from just above the point where the maxillae have fused to just below where they bifurcate. This is indicated by its cross section and the direction of the grooves, particularly on its posterior side, which just begin to diverge laterally at the dorsal end of the specimen. The cross section changes from narrow anteriorly and wide posteriorly at the base to

wider (laterally) and shorter (anteroposteriorly).

DISCUSSION: In addition to these protoceratid fossils, the section at Alum Bluff produces a substantial leaf flora. The most abundant plant is *Sabalites*, a fan palm. A major component of the flora resembles the "hammock" plant association of present-day Florida, including *Ficus*, *Diospyros*, *Cinnamomum*, *Rhamnus*, and *Ulmus*. On the other hand, as reviewed by Graham (1964), an additional 42% of the species are now exotic to Florida, and indicate a strong tropical influence no longer present. Although this flora is not directly associated with the protoceratid specimens, it is reasonable to assume that they were associated in life with much the same vegetation.

THOMAS FARM

Thomas Farm is located 8 miles north of Bell in Gilchrist County, Florida. It has been extensively excavated and its fauna well studied since the late 1930s. Extensive work by field parties from the University of Florida added substantial new material during the past two decades. These efforts began in support of Ann Pratt's dissertation and also involved the Florida Paleontological Society, Inc. Most recently these activities have continued under the Pony Express program at the Florida Museum of Natural History, with yearly digs involving 40+ individuals. Florida records of *Prosynthetoceras* previously consisted only of four partial palates and dentaries, in Harvard's Museum of Comparative Zoology (Patton and Taylor, 1971).

UPPER MOLARS: UF185147, left M1; V5680–5, left M2; V5680–3, right M3; V7188, left M3. These upper molars are distinguishable from those of other selendont artiodactyls by their prominent, shelflike anterior cinguli, the strong styles between the protocone and metaconule, and their fused lingual roots. This last character was recently recognized by L. Barry Albright.

LOWER MOLARS: UF19894, right m3; UF203101, left m3. Lower molars of this species are more difficult to distinguish from those of other selenodont artiodactyls, except the m3. The m3 has a distinct hypoconulid with two well-formed rings of enamel em-

bracing a ring of dentine. This "double enamel loop" occurs in all Synthetocerinae and possibly in all of the Protoceratidae (Patton and Taylor, 1971).

UF176620: Right dentary with p3–m2 and partial m3. This dentary lacks a symphysis and is broken in mid-diastema, but shows p2 alveoli. The cheek teeth are only lightly worn, and the m3 appears recently erupted, indicating that this individual was relatively young.

UF176151: Right dentary with partial symphysis. The symphysis is broken and edentulous, not permitting accurate measurement of its width. Its length is 27.1 mm and its depth attains a maximum of 9.0 mm. This specimen has a relatively complete ascending ramus and angular region, revealing the masseter muscle attachment area. One peculiar developmental anomaly of this specimen is that p4 is rotated 180°, so that its proper labial side faces lingually. The tooth is fully rooted in this incorrect position.

UF203102: Right dentary with edentulous symphysis, p4–m3, plus alveoli of p2 and p3. The symphysis presents a deep suture and broadly spatulate form. Its measurements are length 31.1 mm, width 14.7 mm, and maximum depth 8.3 mm.

OSSICONES: Ossicones, horns, and antlers are considered diagnostic features of many ruminant groups and that also certainly applies to the Protoceratidae. In *P. texanus* the ossicone surfaces are excavated by numerous deep, wide grooves, presumed to have contained blood vessels. This indicates that the ossicones were not covered by a keratin sheath but by skin as in the Giraffidae. In *P. texanus* the frontal ossicone extends from the dorsal side of the orbit, curving medially and posteriorly at an ~60° angle from the orbit, then recurving anteriorly in the last ~5–6 cm. The ends of these ossicones are blunt and more robust at the ends, as in most giraffids.

UF44860: By comparison with complete skulls, particularly AMNH 53493, this specimen was identified as a distal end of a left frontal horn.

UF165026: This fragment of a rostral ossicone consists of the bridge of the ossicone as it surrounds the nasal passage, the smooth fusion of the two maxillae and a length of
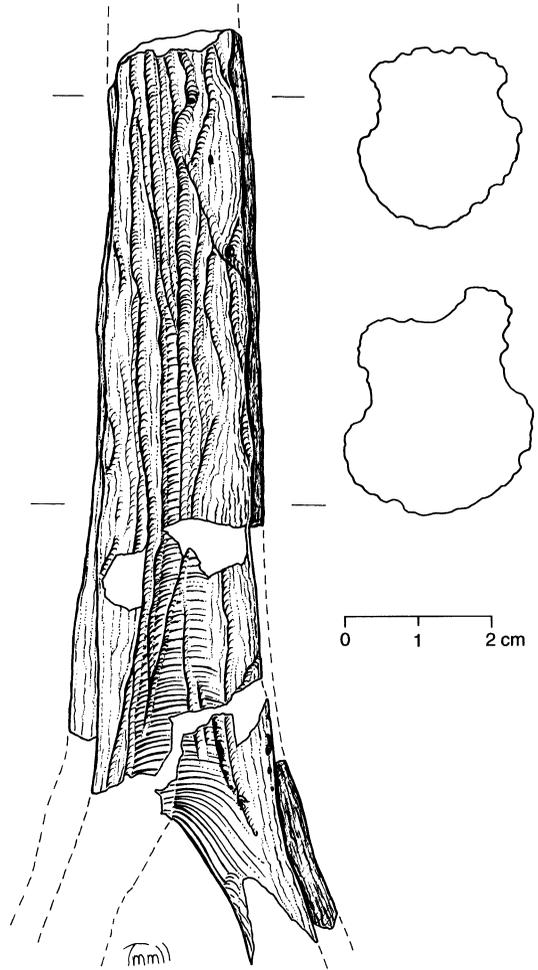

Fig. 14.4. Rostral horn of *Prosynthetoceras texanus*, UF 165026, from Thomas Farm.

ossicone that narrows transversely as it extends dorsally. It is not preserved to the point where the maxillae bifurcated dorsally. The cross section changes as one progresses dorsally from an equant, round anterior edge with a rectangular posterior edge to an increasingly flat (anteroposterior) cross section that is more convex on the anterior side and more concave on the posterior side. A strong set of lateral grooves separate the more rounded anterior side from the more rectangular posterior side (fig. 14.4).

POSTCRANIAL ELEMENTS: Although *Prosynthetoceras texanus* has been known for over 30 years, none of its postcranial skeleton has been described. In their monograph, Patton

and Taylor (1971) described the postcranial skeleton of *P. francisi* based on F:AM 32058. Here we describe the postcranial material of *P. texanus* from Thomas Farm. We identified elements of *P. texanus* by comparing them with other artiodactyls and with associated skeletal material of *P. texanus* and *P. francisi* at the AMNH.

Metacarpal III: Right UF182342 and UF188837, left UF185148. The metacarpals are shorter in length and narrower in cross section, especially in width, than the metatarsals. The proximal surface has a reniform facet on the dorsal edge that is slightly concave. The magnum facet is slightly convex. The adjacent space on the plantar process variably presents another facet, present in UF182342, but absent in the other two specimens. The dorsal edge of the proximal end is rounded as though for ligamentary attachment. The lateral side, which articulates with metacarpal IV, has two facets. The one nearer the dorsal edge is convex and downturned so as to support the metacarpal IV proximal surface, which in articulation rests ~3 mm distal to the proximal surface of the metacarpal IV. The second, more ventrally placed facet, is disc-shaped and also downturned, originating on the plantar process and articulating with the upturned sister facet on metacarpal IV. In *P. texanus* from Florida, the medial aspect of the proximal end has a groove for the metacarpal II. The groove extends only one-fifth of the way distally along the medial side of the shaft. This groove is much shorter than its homologue in *P. francisi*, where the groove for metacarpal II extends fully half the length of metacarpal III (Patton and Taylor, 1971). Also in *P. texanus*, a facet on the dorsal side of the groove faces ventrally to hold the metacarpal II in place.

At the distal end of metacarpal III, a strong carina emerges equally from either side of the fetlock joint, unlike those of the metatarsals described below. The carina sharply ends halfway around the distal articulation, such that the proximal phalangeal range of rotation extends from 175° dorsal to the surface of the metacarpal to a maximally flexed palmar position of −100° (fig. 14.5). We return to this feature under the discussion of morphological adaptations.
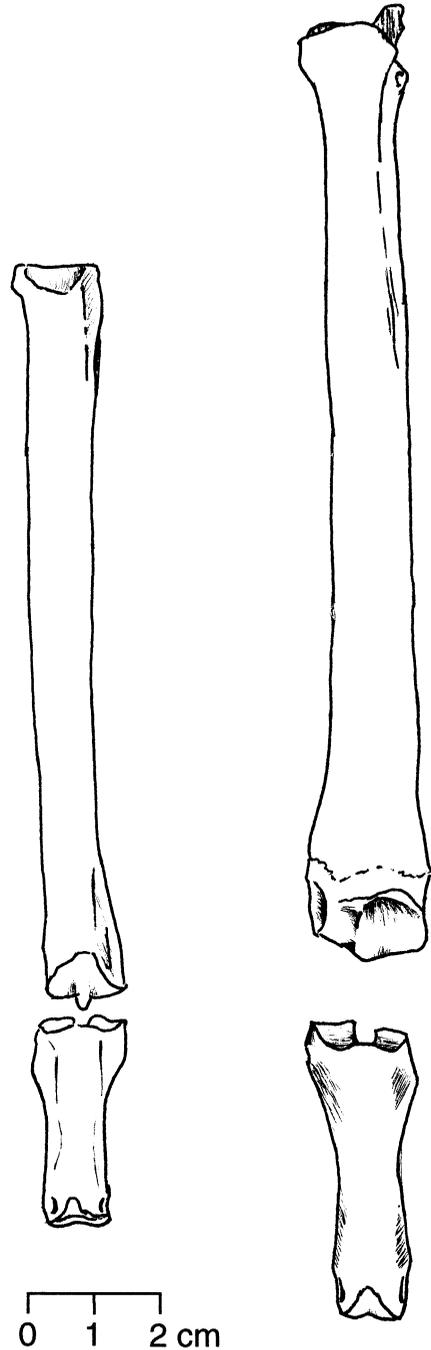
Metacarpal IV: Right UF187956; left

Fig. 14.5. Front foot (left): Metacarpal III, UF 188837 and proximal phalanx, UF 1387. Hind foot (right): Metatarsal III, UF 157888, and proximal phalanx, UF 203341 of *Prosynthetoceras texanus* from Thomas Farm Locality.

UF1278, UF 17607, UF199239. As for the third metacarpal, the proximal surface is characterized by an unciform facet that is slightly concave and triangular. An upturned facet on the medial side meets the downturned facet on the metacarpal III. A disc-shaped facet on the plantar process is upturned to articulate with the downturned sister on the metacarpal III. On the lateral edge there is a slight channel for articulation with metacarpal V; it extends only about one-quarter of the length of metacarpal IV. The smooth surface on the proximodorsal edge noted in the metacarpal III is not present in the metacarpal IV. The distal end is effectively the same as that of metacarpal III.

Proximal Phalanx (anterior): UF163081, UF164336, UF1413, UF1387, UF185143, UF-180981, UF185155, UF161172, UF186451, UF199687, UF185142, UF180628, UF-203479, UF10339, UF192627, V-10353. The differences that make it possible to distinguish between the anterior and posterior proximal phalanges are discussed below under the posterior proximal phalanges.

Patella: Right V-10657. The patella of *P. texanus* has an apex extending 0.7 cm above the proximal edge of the articular surface. That surface is convex along its lateral side; it becomes concave where it reaches around the medial condyle of the distal femur.

Navicular: UF163234, UF180161, UF-194110. As in all known protoceratids, the navicular and cuboid are separate. The medial surface of the navicular articulates with the cuboid by four facets, one in each corner. The facet for the medial condyle of the astragalus has a lip of articular surface that also articulates with the lateral condyle of the astragalus. The tuberosity of the navicular has an articular facet for the medial side of the cuboid; it lies posterodistally and is L-shaped, with the distal portion of the convex facet folded under to face more distally. The anteroproximal facet for the cuboid is not oval as in *P. francisi*, but rather tear-drop-shaped, with the point extending to the tip of the anterior spur. The posteroproximal facet is just like that in *P. francisi*, rectangular and slightly concave near the center. From this same medial view, the astragalar facet of the navicular projects proximally to form a posteroproximal tuberosity. The distal surface of the navicular has a large, slightly concave articular surface that extends from its anterior border to a bit more than halfway to the posterior edge.

Cuboid: V-6494, V-10182, V-10183, V-10184, V-10185, UF 173912, UF 185012. The cuboid of *P. texanus* differs in several ways from the cuboid of *P. francisi* (Patton and Taylor, 1971). The facet for the lateral condyle of the astragalus is lessened, with separate surfaces on the proximal and anterior sides. The calcaneal facet is similar to that in *P. francisi*, except that between the most proximal edge for the calcaneal facet and the anterior-facing posterior portion of the facet for the lateral condyle of the astragalus there is a valley. This valley extends distally to a small notch near the center of the lateral side of the anteromesial surface. Distally, a facet for the metatarsal IV is convex anteriorly and concave posteriorly. Another facet faces medially to articulate with the plantar process of metatarsal IV. Adjacent to this facet the groove for *M. peroneus longus* is much deeper and more notchlike than in *P. francisi*. Another patent difference from *P. francisi* is the plantar process, which extends much farther distally in *P. texanus*. Also the facet for the lateral condyle of the astragalus, especially the posteroproximal tuberosity for the lateral condyle of the astragalus, is more expansive in *P. texanus* than in *P. francisi*.

Ectomesocuneiform: UF165384, UF-171716, UF183804, UF183798, UF184507–184510, UF185597, UF187805, UF188035, UF189879, UF197378–197379, UF199469. In the Synthetoceratinae the ectocuneiform and mesocuneiform are fused into one bone, the ectomesocuneiform. The proximal surface is slightly convex with a slight lip on the anterior side. The distal surface is slightly more convex with a lip near the anteromedial side. The distal end has no articulation on the posterolateral fourth of the surface, though it has a slight tuberosity extending posterolaterally toward the plantar process of the cuboid.

Metatarsal III: UF188036 left, UF18436 right. The metatarsals in Protoceratidae do not fuse to form a cannon bone such as in modern Cervidae, and this allows one to observe a definitive character of Protoceratidae, an articular facet between metatarsal III and

IV. In metatarsal III the facet is in the form of a socket with an articular facet situated anteriorly; it meets the convex reniform facet on metatarsal IV. This character is particularly good for distinguishing metatarsals of protoceratids from those of camelids that have unfused metapodials, several of which coexist with *P. texanus* at Thomas Farm. In addition, because the intermetatarsal facet lies close to the durable proximal surface (within 1.5 cm in all specimens observed), this character is more likely to survive depositional processes. Another articulation on the lateral surface of the plantar process is a reniform facet that articulates with the plantar process of the metatarsal IV. The proximal surface has a facet that meets the ectomesocuneiform; it is C-shaped and convex on the medial side but progresses to being concave on the lateral edge. The plantar process also presents a facet for the navicular that is concave and curved medially.

Metatarsal IV: Right UF159888, UF-170930, UF173913, UF174981, UF180236; left V-10465, UF1517–1518. Metatarsal IV in this species is longer than metatarsal III. Its medial side is marked by a reniform facet projecting outward and dorsally toward the sister facet on the metatarsal III, and also by an oval-shaped facet on the plantar process to articulate with the metatarsal III. The lateral side of the plantar process has a facet facing 60° above the horizontal plane of the proximal surface to articulate with the plantar process of the cuboid. At a distance of ~6 mm, another cuboid facet on the dorsal edge is concave on the medial side and forms a lip posteriorly, facing at 40° to the plane of the proximal surface. The distal end of metatarsal IV is characterized by a carina that protrudes only halfway along the distal surface, extending posteriorly but not anteriorly. The articular surface on the medial side of the carina shows less relief from the carina than the lateral side. The carina itself forms a right angle with the plane of the proximal edge.

Proximal Phalanx (posterior): UF188422, V-10346, V-10347, V-10344, UF173904, UF303341, UF201656, UF201769, UF-171845, UF156232. The Synthetoceratinae differ from later Cenozoic Camelidae in having digits that are less flexible and more fully unguligrade. In the forefoot, the proximal surface of each proximal phalanx has a carinal groove that extends halfway up the articular surface. Distinguishing proximal phalanges of the forefoot from those of the hind foot is possible not only because the hind toes are longer and larger, but also because the proximal ends of the posterior proximal phalanges have more prominent lateral articular surfaces. This coincides with the differing relief of the two sides of the distal metatarsal on either side of the carina, described above. In the metacarpals, the two sides of the distal articular surfaces are equally recessed from the carina, and therefore the proximal phalanges are also more even. This results in greater flexibility in the front digits.

The distal ends of protoceratid proximal phalanges are also quite diagnostic. The distal clefts are just barely visible, and only on the ventral side, with a nearly flat surface at the distal end. The distal ends of proximal phalanges also differ between hind and forefeet. In the forefoot, the distal end of a proximal phalanx has its articular surface as wide as the shaft of the phalanx. In the hind foot, however, the proximal phalanx has a distal articulation that is only 70% as wide as the shaft.

Ungual Phalanx: UF188723. The distal phalanx of *Prosynthetoceras texanus* makes an angle of approximately 60° between its lateral edge and the proximal articular face, whereas its medial edge forms a right angle. The distal surface is planar with two nutrient canals along the lateral edge. The lateral edge also produces one main foramen toward the lower proximal edge of the hoof. The ungual phalanx forms a steep angled hoof, with a 45° angle from the plane of the ground to the dorsal surface. The coffin joint articular surface has a smooth shallow ridge at an angle of 65° to the horizontal.

DISCUSSION: The new material from Thomas Farm and Alum Bluff provides an opportunity for detailed comparisons between the Florida and Texas samples of *P. texanus*. Patton and Taylor (1971) compared measurements of the lower m3 to distinguish various species of *Prosynthetoceras* and *Synthetoceras*. Similar comparisons with the new Florida material cited above indicate that the Thomas Farm specimens correspond to the larger end of the Burkeville sample of *P. texanus*. The

single m3 from Alum Bluff also conforms to the larger range of the Burkeville *P. texanus*. Patton and Taylor (1971) suggested that the greater length of m3 in the Burkeville sample of *P. texanus*, as compared with that from Garvin Gully, indicated that it was a more progressive temporal subspecies. We suggest similarly that these new samples from Florida indicate that they belong to the younger stage of *P. texanus* evolution and add support to that distinction. Such close continuity in meristic data between Florida and Texas samples suggests that, at least during this part of the Hemingfordian, the synthetoceratines formed one continuous gene pool around the Gulf of Mexico. These data also tend to support Patton and Taylor's (1971: 168) suggestion that the Gulf Coastal Plain samples of *Prosynthetoceras* formed ''a virtually unbroken sequence leading to *Synthetoceras*.''

ADAPTIVE MORPHOLOGY

The name Protoceratidae is entirely appropriate, in the sense that among artiodactyls they are the ''first horns.'' They stem from the late Eocene (mainly Uintan) radiation of North American selenodont artiodactyls. This same radiation produced the Camelidae, the probable sister group of Protoceratidae (Webb and Taylor, 1980). The second great radiation of selenodont artiodactyls was late Oligocene in age and centered in Eurasia. There the true ruminants burst forth with true horns (Bovidae), deciduous antlers (Cervidae), and ossicones (Giraffidae), all convergent with, and quite separate from, the Protoceratidae. Their precocious attainment of ossicones and their sparse fossil record combine to heighten the curiosity of paleontologists about the evolutionary history and paleobiological modalities of the family Protoceratidae. Here we consider some highlights of their adaptive morphology.

OSSICONES: Perhaps the most familiar feature of Protoceratidae is their tendency to develop numerous paired outgrowths of bone from the dorsal cranial surface. Even in one of the earliest taxa, *Leptotragulus*, in which no ossicones occur, Norris (2000) recognized several cranial features suggestive of head-butting adaptations. He proposed that the broad, flattened frontal plane and the broad

occipital condyles with ventral stops indicated ''agonistic intraspecific behavior such as head-butting'' even among the earliest Protoceratidae (Norris, 2000: 341).

Within the Protoceratinae and Synthetoceratinae these behavioral proclivities may have been further developed, fostering the full development of diverse paired ossicones. *Paratoceras* species have three pairs, including maxillary, frontal, and occipital. In the maxillary and the occipital ossicones, two bases join to form a common midsagittal stalk. As shown above in *Paratoceras tedfordi*, the presumed female crania develop ossicones in the same positions as in male crania but they are expressed to a lesser degree. Similar sexual dimorphism appears in ossicones of subfamily Synthetoceratinae (Patton and Taylor, 1971). In the latter, the occipital ossicones have been lost, whereas the dorsal elaborations of the paired maxillaries are greatly extended. Both sets of ossicones have complex systems of deep grooves running along their length, suggesting similarity to the skin-covered ossicones of Giraffidae (fig. 14.4). This is clear evidence against the presence of true horns with their thick keratinous sheaths, and that is why we refer to the cranial armaments of Protoceratidae as ossicones.

The multiple ossicones of progressive Protoceratidae evidently were used both for display and for combat by prime age males (Webb, 1981). Thus the Protoceratidae seem to fall within the classical explanation of similar armaments in ruminants: They were promoted by sexual selection to help large successful males monopolize females. Among living ruminants, substantial sexual dimorphism featuring enlarged horns is particularly characteristic of moderately large, woodland ruminants. Strong dimorphism is less common at both ends of the habitat spectrum: on the one hand, in small, solitary, forest-dwelling species such as duikers, and on the other hand, in large, herding species of open-country habitats, where females tend to have enlarged horns as in Cape Buffalo (Jarman, 2000). Thus the strongly dimorphic and increasingly elaborate sets of horns in Miocene Protoceratidae signal a long history of sexual selection. It is also compatible with

their probable preference for woodland habitats.

PROBOSCIS: The nasal bones of *Protoceras*, *Paratoceras*, and the Synthetoceratinae are strongly retracted, typically as far back as the first molars. Such retracted nasals, along with a greatly enlarged pocket for the origin of a powerful set of *M. nasolabialis* muscles, ''indicate the presence of a large proboscidiform muzzle,'' according to Patton and Taylor (1973: 378). Janis (1982) and Prothero (1998) likewise considered the protoceratid feeding system to be adapted for mooselike browsing of semiaquatic vegetation. We affirm the morphological observations, but wish to suggest, as an equally appropriate model, the tapirs, which use their large muscular muzzles like a short trunk, taking in leaves and fruits from a wide array of tropical vascular plants (Eisenberg and Redford, 1999). We see no compelling reason to tie this morphology to semiaquatic feeding.

DENTITION: The cheek teeth of Protoceratidae are selenodont, as in several other artiodactyl families that appear in the middle and late Eocene. Selenodonty is an important specialization of the cheek teeth in which the cusps and cuspids become crescentic, providing an integrated set of shearing blades well adapted for chopping vegetation. Associated with selenodonty in living artiodactyls (namely Camelidae and the several families of living Ruminantia) is rumination, an elaborate set of digestive processes carried out in a multichambered stomach, by which symbiotic bacteria convert the otherwise undigestable structural sugars of plants, notably cellulose, into glucose. The cladistic relationships of artiodactyls allow us to attribute some form of rumination to any selenodont artiodactyls that fall within the Neoselenodontia as defined by Webb and Taylor (1980). There is thus a phylogenetic argument for attributing to the Protoceratidae a ruminating digestive system, perhaps similar to that of living Camelidae.

The upper molars of most Protoceratidae are characterized by strong lingual cinguli, a lingual style between the protocone and metaconule, and brachydont crowns with thick crenulated enamel. The lower molars are similar with strong interlobular stylids in most species. These are all hallmarks of soft-browsing ruminants, broadly comparable to the features of most Cervidae. There is a clear tendency in later Synthetoceratinae to substantially increase cheek tooth crown heights and to concomitantly reduce cinguli and interlobular styles in upper teeth and stylids in lowers. A progression of nearly unworn, third lower molar crown heights in selected Miocene Synthetoceratinae (fig. 14.6) illustrates *Prosynthetoceras texanus* from the late Hemingfordian Thomas Farm Site with a height of about 25 mm, *Synthetoceras tricornatus* from the early Hemphillian McGehee Farm Site with a height of about 35 mm, and *Kyptoceras amatorum* from the late Hemphillian of the Upper Bone Valley Fauna (50 mm). The fact that crown height increased greatly in Synthetoceratini and even more dramatically in Kyptoceratini implies some secular selection for coarser feeding capacity. While they probably persisted as tropical browsers, they may have been driven to cope with more marginal forage during increasing dry seasons.

Bob Feranec (University of Florida, personal commun.) determined the oxygen and carbon isotopes of an upper molar of *Kyptoceras amatorum*, UF 24008, from the Upper Bone Valley Formation. The δ^{18}O‰ value was 0.352; and the δ^{13}C‰ value was -11.94 obtained from the carbonate portion of the tooth enamel. These data are consistent with deep forest browsing.

We call attention to a diagnostic feature of all protoceratid upper molars: The anterolingual and posterolingual roots of each molar are fused to form an irregular anteroposterior dike. A typical example is an upper molar of *Prosynthetoceras texanus* (fig. 14.7). This character, here termed lingual radicozygy, was pointed out by Dr. L. Barry Albright. Initially we supposed that this feature was shared uniquely with ruminants and thus would add weight to the phylogenetic hypothesis that Protoceratidae are the sister group of Ruminantia. Further investigation, however, suggests that this is a primitive feature within the broad context of selenodont artiodactyls. Lingual radicozygy occurs in upper molars of virtually all early ruminants, including Moschidae such as *Machaeromeryx*. It also occurs in *Merycoidodon*, as well as in other oreodonts. It occurs in *Protylopus*,
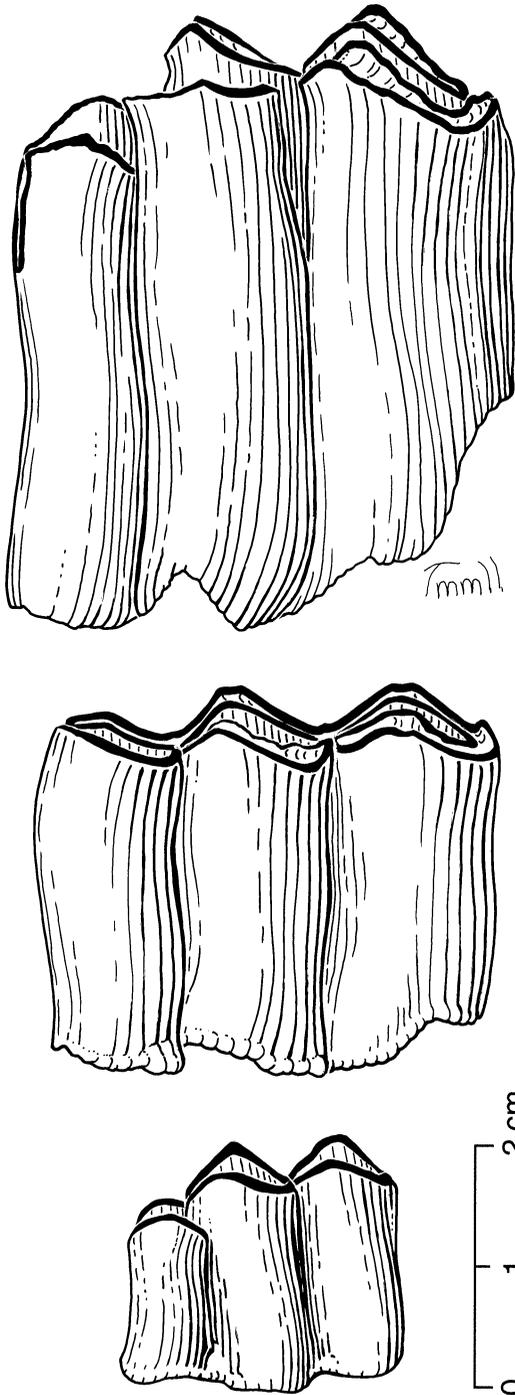
Fig. 14.6. Lateral views of little-worn right m3s of successively younger Mio-Pliocene protoceratids. Bottom: *Prosynthetoceras texanus*, UF 36455; middle: *Synthetoceras tricornatus*, UF 16157; top: *Kyptoceras amatorum*, UF 19894.
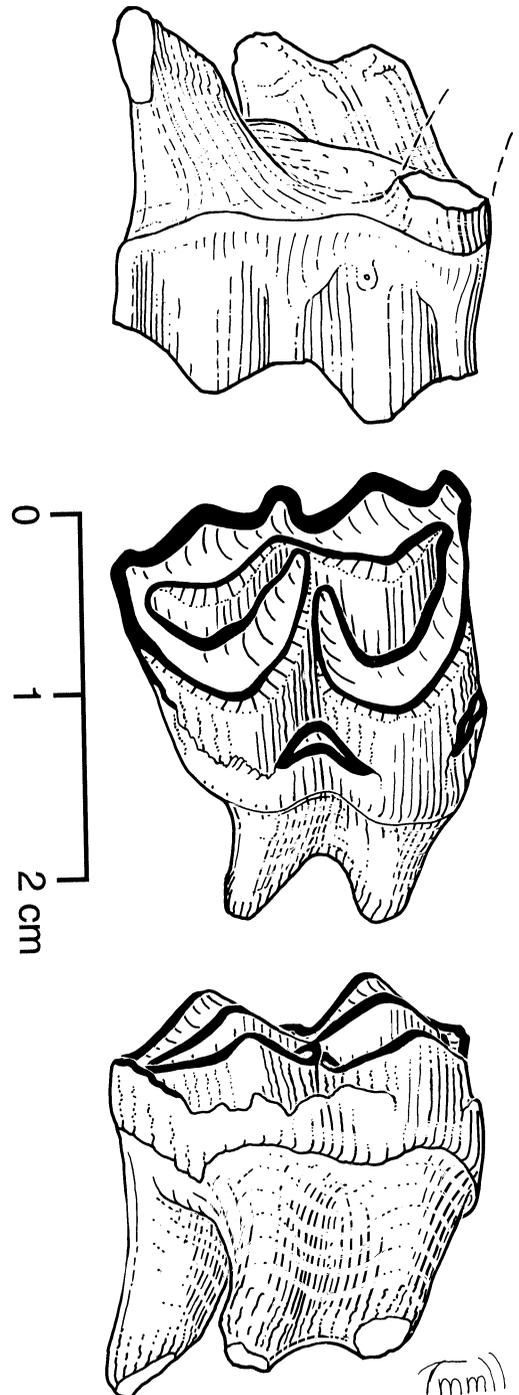
Fig. 14.7. Lateral, occlusal, and lingual views of right M3 of *Prosynthetoceras texanus*, V 5680–3, Thomas Farm locality, showing lingual radicozygy.

but is evidently lost in most other Camelidae. Incidentally, this provides a handy means of separating upper molars of *Floridatragulus*, a primitive camelid, from those of *Prosynthetoceras texanus*, with which it co-occurs. The origin and exact distribution of lingual radicozygy among diverse Eocene families warrants further study. It may have developed in early selenodonts as a mechanism to resist the strong lateral sweep of the battery of crescentic lower cheek teeth as they engaged during a transverse chewing stroke.

The mandible of Synthetoceratinae is notable for its long, unfused spatulate symphysis. We investigated the biological significance of an elongate spatulate symphysis in ruminants by observing its distribution among modern ruminant specimens in the AMNH and FLMNH Mammalogy collections. Our preliminary work showed diverse browsing and even several grazing species with long diastemata in the lower jaw and comparably spatulate symphyses. Similarly, Eisenmann (1998) found no simple functional explanations for the varied shapes of symphyses among diverse perisssodactyls.

LOCOMOTOR SYSTEM: The conservative nature of protoceratid limbs has long been recognized. With four functional digits on each foot and unfused central metapodials, protoceratid feet seem to play about the same conservative role among neoselenodonts as tapirid feet do among perissodactyls. Such pedal morphology was familiar in the Eocene but seems rather outmoded in a horned neoselenodont of the Mio-Pliocene.

Scott and Janis (1987: 6–7) state that protoceratids "resemble cervoid ruminants in general body proportions. . . ." The limb proportions of *Prosynthetoceras francisi* are known from two or more individuals from the Wright Farm, Garvin Gully Fauna of Texas, catalogued as F:AM 32058 and described by Patton and Taylor (1971). Table 14.2 gives the dimensions and ratios of the major limb elements.

Three features of these limb proportions are notable. First, the radius and tibia are the longest elements in the forelimb and hind limb respectively. Second, the metapodials are unusually short, making up just under one-quarter of the limb length. Third, the hind limb is about 20% longer than the fore-

TABLE 14.2
Limb Proportions (mm) in
***Prosynthetoceras francisi* (F:AM 32058)**

	Length	Percent
Fore limb		
Total length	462	100
Humerus	165	36
Radius	185	40
Metacarpal III	112	24
Hind limb		
Total length	555	100
Femur	192	34
Tibia	237	43
Metatarsal III	126	23

limb, based on the functional lengths of the three main limb bones in each. The proximal phalanges of the main digits add still further to this distinction, for in *Prosynthetoceras francisi*, the posterior proximal phalanges average 43.2 mm in length in comparison with 35.0 mm for the anterior proximal phalanges (Patton and Taylor, 1971).

Certainly the relative brevity of the distal elements indicates an animal that is not adapted for cursorial locomotion. Scott (1985) presented a thorough analysis of the adaptive significance of limb proportions in a broad array of living Bovidae. Assuming that similar adaptive regimes selected limb proportions in quasiruminants of the North American Tertiary, we can place the Synthetoceratinae in this scheme. The results clearly distinguish Synthetoceratines from swamp-adapted bovids such as the lechwes or the sitatunga (Scott, 1985). The most closely comparable limb proportions in bovids occur in the "Forest-cryptic" category. There, among a diversity of small forms, the duikers have similarly short distal elements. Even more closely comparable, based on Scott's data, are the larger forest-dwelling bovids, the bongo and especially the bushbuck, *Tragelaphus scriptus*. *Prosynthetoceras francisi* shares with the bushbuck the distinction of having the radius and tibia as the longest elements yet associated with short metapodials. Although body proportions suggest the bushbuck as the appropriate bovid analogue for *Synthetoceras*, its near relative the sitatunga, *Tragelaphus spekei*, inhabits papyrus

swamps. Thus the shift from bushland to swamp environments or the reverse may not be a large one. A key feature in postcranial osteology that can further test this distinction appears in the distal phalanges.

In *Prosynthetoceras texanus* and *P. francisi*, the distal ends of the proximal phalanges of both fore- and hind limbs have characteristic raised dorsal ridges. These indicate a limited range of flexibility, and an unguligrade posture. The articulation of this pastern joint in protoceratids closely resembles that in primitive camelids prior to the evolution of the padded, digitigrade arrangement of modern camelids (Webb, 1972). The distal ends of the ungual phalanges are narrow and sharply pointed. This is the very opposite of what we might expect if Synthetoceratinae were specially adapted to aquatic or swampy environments. The clear presence of such an adaptation in the sitatunga, and its absence in its congener, the bushbuck, strengthens the hypothesis that the absence of such swamp-adapted ungual phalanges is meaningful in *Prosynthetoceras francisi* and *P. texanus*.

Several peculiar features in the hind limb of Synthetoceratinae indicate unusually rigid limb architecture. The patella is unique among neoselenodonts in its horizontal extension around the medial condyle of the femur. This feature evidently restricted rotation of the tibia around the long axis of the hind limb. Also the posteromedial side of the calcaneum presents a greatly enlarged sustentacular facet, as noted previously by Stirton (1967). This facet facilitates a powerful extension of the hind foot. Another possible action would be, when the hind feet are planted, to raise the body vertically over the hind limbs. Between the sturdy proximal ends of the third and fourth metatarsals is a pair of reniform facets that hold them in place. This feature appears to be unique to protoceratids. It presumably helped lock the unfused major metatarsals together when they bore extra weight or torsion.

Evidently these adaptations in the patella, the calcaneum, and the metatarsals all worked toward making the hind limb stronger and more rigid. We speculate that they may have enhanced the ability of synthetoceratines to rear up on their hind legs, as high browsers. The extra length of the hind limb elements, exceeding those of the forelimb by about 20% (table 14.2), is consistent with this hypothesis.

The longer and stronger hind limbs of Protoceratidae may also be an adaptation for hind limb leaping. A gait emphasizing an extended suspension serves well in dense or broken woodland. Again the bushbuck may be an appropriate analogy, as it uses a bounding gait to manuever through woodland (Scott, 1985). The hind limb bounding hypothesis does not exclude the rearing hypothesis, and so we attribute both adaptations to Protoceratidae.

BIOGEOGRAPHIC PATTERNS

The horned members of the Protoceratidae consist of seven genera. *Protoceras* from the Late Oligocene and Early Miocene is the oldest and best known. These seven genera may be grouped as follows:

1. *Protoceras* and *Paratoceras*, not a recognized tribe, but, with addition of the probably hornless genus *Pseudoprotoceras*, forming the informal subfamily "Protoceratinae" (Prothero, 1998). In addition, the subfamily Synthetoceratinae includes two formally recognized tribes.
2. *Syndyoceras* and *Kyptoceras* form the tribe Kyptoceratini.
3. *Lambdoceras*, *Prosynthetoceras*, and *Synthetoceras* comprise the tribe Synthetoceratini (Webb, 1981; Prothero, 1998).

When the known distribution of each genus is mapped (figs. 14.8–14.11), the data suggest a recurring pattern of allopatric speciation on a latitudinal basis. Each suprageneric group has one taxon from the High Plains and another taxon from the Gulf Coastal Plain. In each instance, the southern taxon persists, whereas the northern taxon becomes extinct at a relatively early time. Thus, *Paratoceras* is the southern branch of the "Protoceratinae," and *Kyptoceras* is the southern branch of the Kyptoceratini (figs. 14.8, 14.9).

Within the tribe Synthetoceratini, the known pattern is a degree more complex, but nonetheless similar. *Prosynthetoceras* occurs earliest in the Arikareean Toledo Bend Local Fauna of east Texas (Albright, 1998). Meanwhile *Lambdoceras* appears with two north-
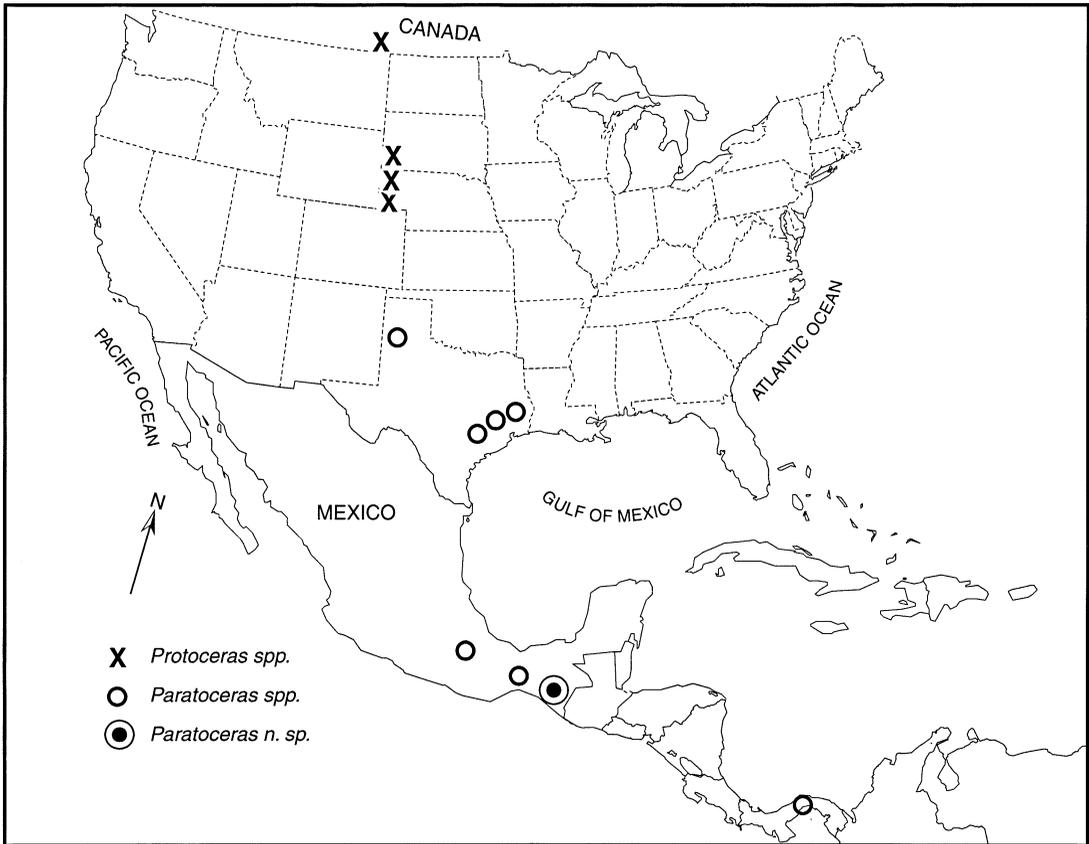
Fig. 14.8. Geographic distribution of Protoceratinae.

ern species and one southern species, *L. trinitiensis*. The latter persists in the Gulf Coastal Plain one mammal age after its northern sister taxa have disappeared (figs. 14.9, 14.10). The recurrent evolutionary pattern in the three clades of horned protoceratids begins with allopatric speciation along latitudinal lines, and is followed by early extinction of the northern branch, or more positively, with persistance of the southern branch.

The well-described records of middle and late Miocene protoceratids are mainly from the Gulf Coastal Plain of Texas and Florida (Patton and Taylor, 1971, 1973). Central American occurrences of Miocene Protoceratidae are less well known. When one makes allowances for the relatively impoverished nature of the overall record, however, the recurrence of Protoceratidae in Mexico and Panama becomes quite notable. They have been recorded at the following three middle

Miocene localities: Suchilquitongo in Oaxaca Valley (Ferrusquia-Villafranca, 1990), at El Gramal near the Isthmus of Tehuantepec (Wilson, 1967), and at Gaillard Cut in the Panama Canal Zone (Whitmore and Stewart, 1965). Indeed, in these limited samples from Central America, Protoceratidae are about as common as Equidae. Ferrusquia-Villafranca (1990) has indicated that, based on dental and mandibular evidence, these protoceratid records are mostly referable to *Paratoceras*. The new record of *Paratoceras tedfordi* from southern Mexico further emphasizes this biogeographic pattern. Jimenez-Hidalgo and Ferrusquia-Villafranca (2000) suggest that a rostrum with most of its cheek teeth from Suchilquitongo represents an unnamed new kyptoceratine. Thus, during the Miocene at least three clades of Protoceratidae speciated latitudinally and then retreated southward in
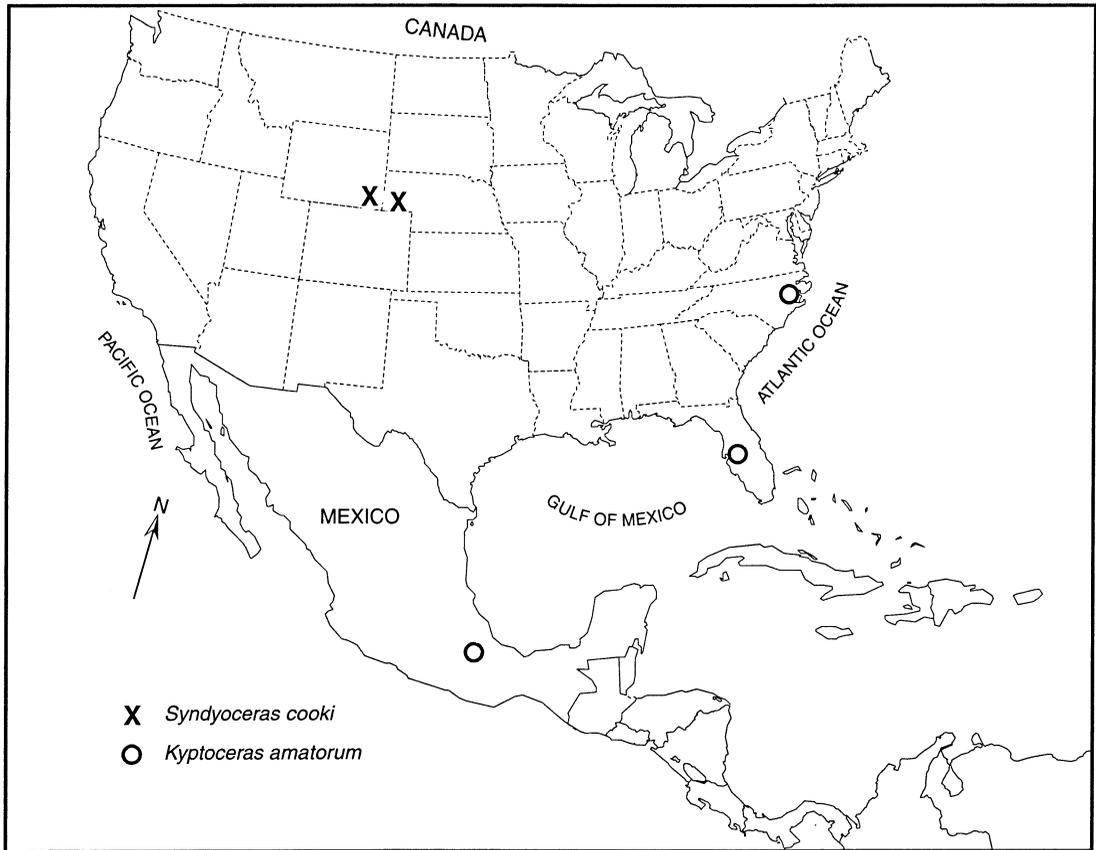
Fig. 14.9.   Geographic distribution of Kyptoceratini.

apparent association with humid subtropical habitats.

CONCLUSIONS

The new species *Paratoceras tedfordi* is represented by the first female skull of that genus. It comes from the amber-bearing beds near Simojovel, in the state of Chiapas, southern Mexico, and represents the oldest Miocene record of this rare genus.

New records of *Prosynthetoceras texanus* from Florida add to our knowledge of the osteology, especially the postcranial skeleton, of that species. The presence of this species at Alum Bluff associates it with the Alum Bluff Flora, reinforcing the probability that this species browsed on a rich subtropical flora.

The horned Protoceratidae, beginning with *Protoceras*, were noted for their precocious development of several paired ossicones, including the rostral (maxillary) horns that arched over the retreating nasal bones and met in the midline. The strongly dimorphic horns of Neogene protoceratids indicate persistent sexual selection for male competition by display and/or combat. Among modern ruminants, such medium-sized, highly dimorphic forms tend to inhabit woodland settings.

The retracted nasal bones and enlarged fossae for *M. nasolabialis* indicate that protoceratids had a short proboscis about like that of the Asiatic Tapir. This can be interpreted as a browsing adaptation, not necessarily as a device for aquatic feeding.

Synthetoceratine limb proportions indicate an analogy with the bushbuck, *Tragelaphus scriptus*, a medium sized bovid that bounds through woodland habitats. We find no post-
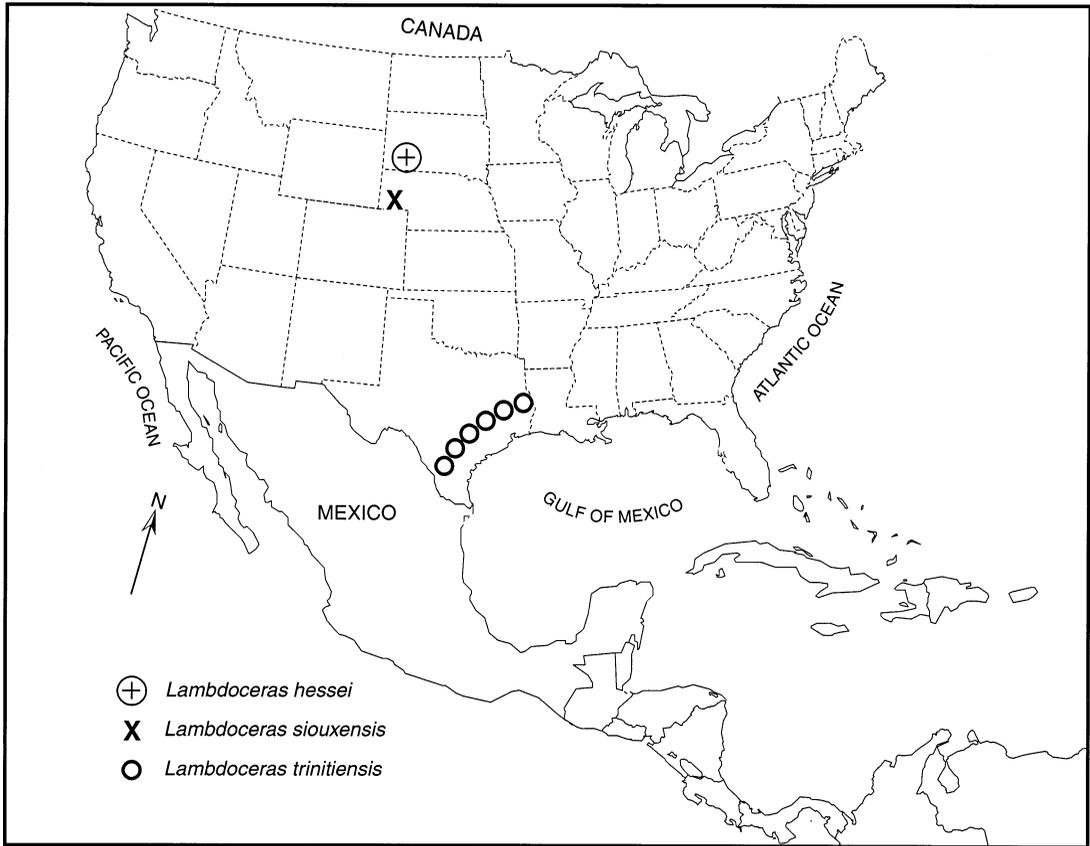
Fig. 14.10. Geographic distribution of *Lambdoceras* species.

cranial features that support the idea of a mooselike aquatic adaptation and some, such as the sharply pointed ungual phalanges, that tend to contradict it. This does not eliminate the possibility that some synthetoceratines may have frequented swamps and other aquatic settings. The relatively long and powerfully articulated hind limbs of synthetoceratines suggest two hypotheses: that they habitually reared up on their hind limbs to reach high browse, and that they characteristically used the hind limbs for a leaping style of locomotion in closed or broken woodlands.

The seven named genera of horned Protoceratidae fall into three clades: the Subfamily Protoceratinae with *Protoceras* and *Paratoceras*, and the Subfamily Synthetoceratinae with its two tribes, Kyptoceratini, including *Syndyoceras* and *Kyptoceras*, and Synthetoceratini, including *Lambdoceras*, *Prosynthetoceras* and *Synthetoceras*. Each of these clades had a northern branch and a southern branch, of which the latter endured much longer than the former. During the Miocene, while Synthetoceratinae became increasingly rare in the High Plains, the genera *Paratoceras* and *Kyptoceras* persisted in Central America. The fact that Protoceratidae were progressively restricted to lower latitudes during the Miocene and Pliocene further indicates their primary role as browsers in lush subtropical forests.
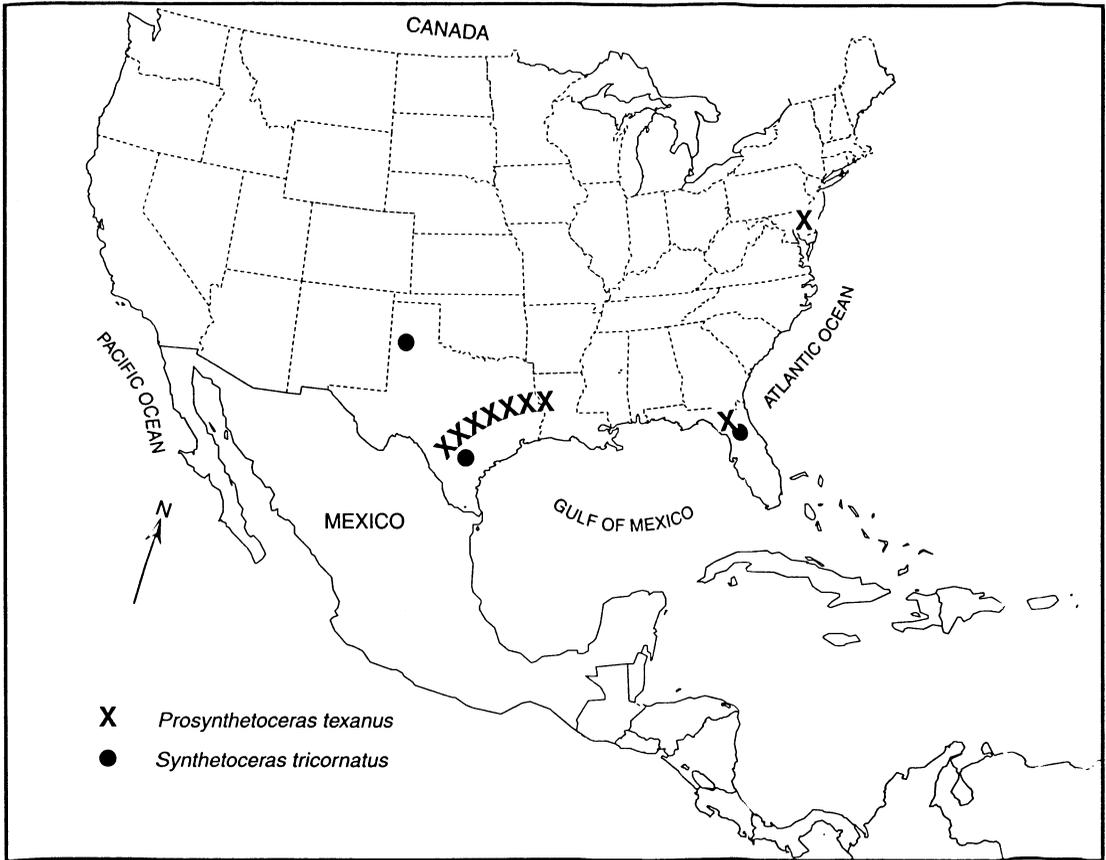
ACKNOWLEDGMENTS

Fig. 14.11.   Geographic distribution of Synthetoceratinae.

MacPhee, Clare Flemming, and John Alexander of the American Museum of Natural History, as well as to Dr. Robert Purdy of the Smithsonian Institution for assisting us with their respective collections. We thank Dave Bohaska at the Smithsonian Institution for calling our attention to the record of *Prosynthetoceras texanus* in the Calvert Formation. We are grateful to Bob Feranek and Bruce MacFadden for carbon isotope analysis of a *Kyptoceras amatorum* molar. Susan Trammell and Dale Johnson skillfully prepared the illustrations for this paper. We are indebted to the collector in Chiapas who found the holotype skull of *Paratoceras tedfordi*, and to the Mexican authorities who gave us permission to deposit it in the UCMP collections. This is contribution number 524 in Paleobiology from the Florida Museum of Natural History.

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