THE CRANIUM OF *LEPTOTRAGULUS,* A HORNLESS PROTOCERATID (ARTIODACTYLA: PROTOCERATIDAE) FROM THE MIDDLE EOCENE OF NORTH AMERICA

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ABSTRACT—*Leptotragulus,* from the upper middle Eocene of North America, is the most plesiomorphic member of the Protoceratidae, an enigmatic group of selenodont artiodactyls. Until now *Leptotragulus* was known primarily from teeth, limb bones and a few skull fragments. A previously undescribed series of crania shows that *Leptotragulus* exhibits the typical protoceratid skull morphology, with a broad, flattened forehead, pronounced lambdoid crests enclosing a deep complexus fossa, and broad occipital condyles with a pronounced anteroventral margin. It is suggested that these features, which are suited to forms of agonistic, intraspecific behaviour such as head-butting, may indicate that the evolution of such behaviour occurred comparatively early in the history of the protoceratids. Study of the anatomy of the otic region in *Leptotragulus* suggests that there are a number of similarities in periotic morphology between leptotragulines and plesiomorphic ruminants such as hypertragulids and leptomerycids, which may indicate a sister group relationship between the Protoceratidae and the Ruminantia.

INTRODUCTION

The long-running debate over the affinities of protoceratids, an endemic clade of artiodactyls from the middle Eocene to early Pliocene of North and Central America, is one of the longest and most confused disputes in the history of mammalian systematic biology (Prothero, 1998). The group can be viewed as the first attempt by artiodactyls at a pecoran ruminant-like cranial Bauplan (Janis, 1990). Indeed, for much of the first part of this century, protoceratids were classed as ruminants. The first member of the group to be described, *Protoceras* (Marsh, 1891) was originally thought to be related to giraffes. Later authors, including Osborn and Wortman (1892), Scott (1895, 1899), Wortman (1898), Matthew (1905), Colbert (1941), Stirton (1944), and Simpson (1945), tended to place the Protoceratidae with the ruminants, particularly the hypertragulids or leptomerycids. In later years, however, the idea that protoceratids were members of the Tylopoda has prevailed (Scott, 1940; Stirton, 1967; Patton and Taylor, 1971, 1973; Webb and Taylor, 1980), and remains the consensus view today (Janis et al., 1998; Prothero, 1998). This is largely based on the presence of one character, penetration of the neural arch pedicles of cervical vertebrae 2–6 by the vertebral artery, which is also seen in camelids, and by the absence of a second character, fusion of the cuboid and navicular, which is a synapomorphy of ruminants (Webb and Taylor, 1980). Despite this, the systematic placement of the Protoceratidae remains unstable (Fig. 1). A large-scale cladistic study of the Artiodactyla by Gentry and Hooker (1988) produced ambiguous results for protoceratids, grouping them with either ruminants or camelids according to the methodology employed. A recent study of the basicranium of the early Miocene synthetoceratine protoceratid *Syndyoceras cooki* (Joeckel and Stavas, 1996), while not providing conclusive proof of the ruminant affinities of the Protoceratidae, emphasized the considerable differences in cranial anatomy between camelids and protoceratids.
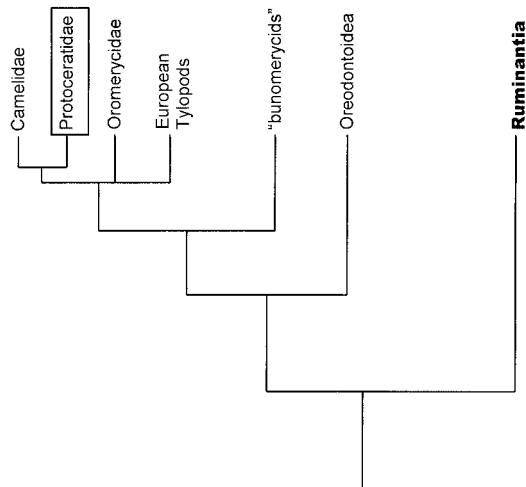
The first members of the Protoceratidae appear in the middle Eocene (Prothero, 1998). Of these, the most plesiomorphic taxon is *Leptotragulus.* Leptotragulines were originally grouped with the camelids (Wortman, 1898; Scott, 1899; Matthew, 1905). Gazin (1955) included *Leptotragulus,* together with the other leptotraguline genera, *Leptoreodon, Poabromylus* and *Heteromeryx,* in the Leptomerycidae, even though he considered them ancestral to protoceratids. Wilson (1974), Golz (1976), and Black (1978) placed these taxa within the Protoceratidae, which is the generally accepted position today (Prothero, 1998). Characters uniting the Protoceratidae are: possession of strong lingual cingula on the upper molars; a short coronoid process on the mandible; and a concavity of the proximal side of the sustentacular facet of the astragalus (Prothero, 1998). The early forms lack the cranial ''appendages'' seen in the more derived protoceratine and synthetoceratine protoceratids. As Prothero (1998) suggests, the ''Leptotragulinae'' are almost certainly a paraphyletic group, with *Leptoreodon, Poabromylus,* and *Heteromeryx,* forming a monophyletic group that excludes *Leptotragulus. Leptotragulus* itself may well be the sister group of all protoceratids (Prothero, 1998). However, rather than erecting new names to cover these taxa, this paper will continue to use ''leptotraguline'' as convenient shorthand for the non-protoceratine protoceratids.

As the most plesiomorphic members of the Protoceratidae, leptotragulines have the potential to provide important information on character polarities within the protoceratids and to cast light on the question of the tylopod versus ruminant affinities of the group. Unfortunately, leptotraguline basicrania are extremely rare in museum collections (Joeckel and Stavas, 1996). Recently, however, the author had the opportunity to work on collections of material from Leota Quarry, a middle Eocene site 1.6 km (1 mile) North of New Leota Post Office, in Uinta County Utah, which were made by R.V. Witter during the 1940s. Leota Quarry is part of the lithostratigraphically defined Uinta 'C' zone, termed by Osborn (1929) the ''*Diplacodon-Protitanotherium* zone.'' The material, which is housed in the vertebrate paleontology collections of the Museum of Comparative Zoology, Harvard University, and the Princeton Museum (now at the Peabody Museum, Yale), includes a number of complete and partial crania of *Leptotragulus,* which are described below.

Institutional Abbreviations—**ACM**, Pratt Museum, Amherst College; **MCZ**, Harvard University Museum of Comparative Zoology vertebrate paleontology collections, **MCZ M**, mammal collections; **OUM**, Oxford University Museum of

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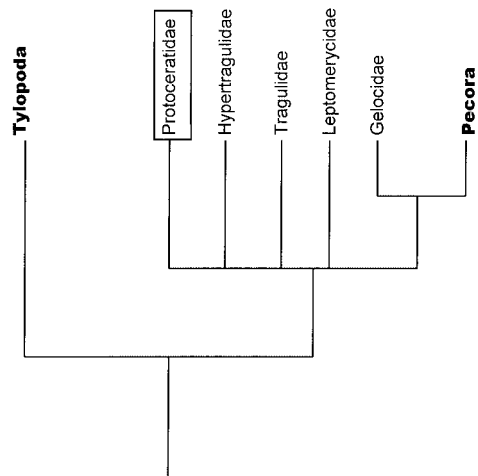
FIGURE 1. Alternative schemes for the placement of the Protoceratidae within the Artiodactyla. **A**, Protoceratids as members of the tylopod radiation and sister group of the Camelidae, as favored by Webb and Taylor (1980). **B**, protoceratids as members of the ruminant radiation (inferred from Scott, 1940, by Joeckel and Stavas, 1996). Membership of Tylopoda follows Norris (1999).

Natural History zoological collections; **YPM-PU**, Princeton Collections, Department of Vertebrate Paleontology, Peabody Museum, Yale University.

MATERIALS

Descriptions were made of the following specimens of *Leptotragulus*:

1. *Leptotragulus* sp., MCZ 5303, a largely complete skull, associated with a fragmentary pelvic girdle, from Leota Quarry, R.V. Witter and party, 1940. The specimen is recorded as being from strata "45' below *Diplacodon* SS." The skull is in generally good condition, but shows some signs of lateral compression, together with right-to-left shear.

2. *Leptotragulus* sp., MCZ 5304, consisting of a complete skull, a substantial fragment of the left mandible, and seven smaller fragments of mandibular bone, from Harn Quarry, 1

mile North of New Leota, R.V. Witter and party, 14 August, 1940. The skull is in almost perfect condition, with negligible crushing. The auditory bullae were absent on both the left and right hand sides. Mechanical preparation was carried out on the otic region of the right hand side.

3. *Leptotragulus ?clarki,* MCZ 5364, an almost complete skull from Leota, 1940. The skull is lacking cheek teeth and zygomatic arch on the right hand side, and there has been some damage to the dorsal surfaces of the rostrum and braincase. There has been some lateral compression and right-to-left hand shear. Mechanical preparation was carried out on the otic region of the left-hand side.

4. *Leptotragulus* sp., MCZ 21428, a fragmentary skull from Leota Quarry (Section 13, T7S, R20E), R.V. Witter and party, 1940. The specimen consists of a large part of the right braincase wall (including periotic, parietal and part of the squamosal), a fragment of premaxilla and maxilla bearing the right C1 and P1–3, a fragment of maxilla bearing M1–3, a mandibular fragment bearing P2–3 and various bone fragments. The canine was relatively small and M3 only partially erupted, suggesting that this animal was a juvenile female. The inner surface of the braincase wall was mechanically prepared to reveal the endocranial surface of the periotic.

5. *Leptotragulus medius,* YPM-PU 16391, a complete skull from Leota Ranch, T7N, R20E, 11.2 km (7 miles) N.E. of Ouray, Uinta County, Utah, R.V. Witter and party, 1946. The skull is crushed dorso-ventrally, with some damage to the dentition. The endocranial cast was exposed by Leonard Radinsky in 1974.

6. *Leptotragulus medius,* YPM-PU 16392, a complete skull with associated mandible from Leota Ranch, R.V. Witter and party, 1946. Skull and lower jaw are crushed laterally. Presence of Dp4 plus an unerupted m3 in the mandible suggests that this specimen was a juvenile. The cranial roof and occipital region are absent.

7. *Leptotragulus medius,* YPM-PU 16397, a complete skull with associated mandible and atlas from Leota Ranch, R.V. Witter and party, 1946. Skull and lower jaw are crushed laterally. Atlas is still attached to the rear of the skull. Some deciduous teeth are present, so the specimen is a juvenile.

Specimens of *Leptotragulus* were compared with a variety of living and extinct artiodactyls, including: *Agriochoerus antiquus* (YPM-PU 11429), *Agriochoerus matthewi* (YPM-PU 14251), *Alces alces* (MCZ M 1707), *Antilocapra americana* (MCZ M 14352, 39440), *Bunomeryx elegans* (MCZ 5306, 5311, 5313), *Cainotherium commune* (MCZ 5161, YPM-PU 11579, 11679, 12266), *Camelus dromedarius* (MCZ M 57837), *Capra nubiana* (MCZ M 11478), *Dama dama* (MCZ 59126), *Giraffa camelopardis* (OUM 21475), *Hippopotamus amphibius* (MCZ M 5020, 10017), *Homacodon vagans* (YPM-PU 13129), *Hypsiops breviceps* (ACM 7101), *Leptoreodon gracilis* (YPM-PU 11225), *Leptoreodon marshi* (YPM-PU 11226), *Lama glama* (MCZ M1746, 1881, 29878, OUM 2959), *Prodesmatochoerus periculorum* (MCZ 17398, ACM 9254), *Prolibytherium magnieri* (NHM M21901), *Protoceras celer* (YPM-PU 10168, 11078), *Protoreodon annectens* (MCZ 3342), and *Tragulus javanicus* (OUM 5673).

THE CRANIUM OF *LEPTOTRAGULUS*

The cranium of MCZ 5304 shows little or no distortion compared with the other specimens examined, and forms the basis of the description. Characters are augmented and confirmed by reference to the other specimens. *Leptotragulus* is a small artiodactyl, with a mean condylobasal length of 88.6 mm (n = 3). Overall, the skull is elongate, flattened in profile, and comparatively broad in the postglenoid and jugal regions (Fig. 2). The rostrum tapers gradually anteriorly, with a marked constric-
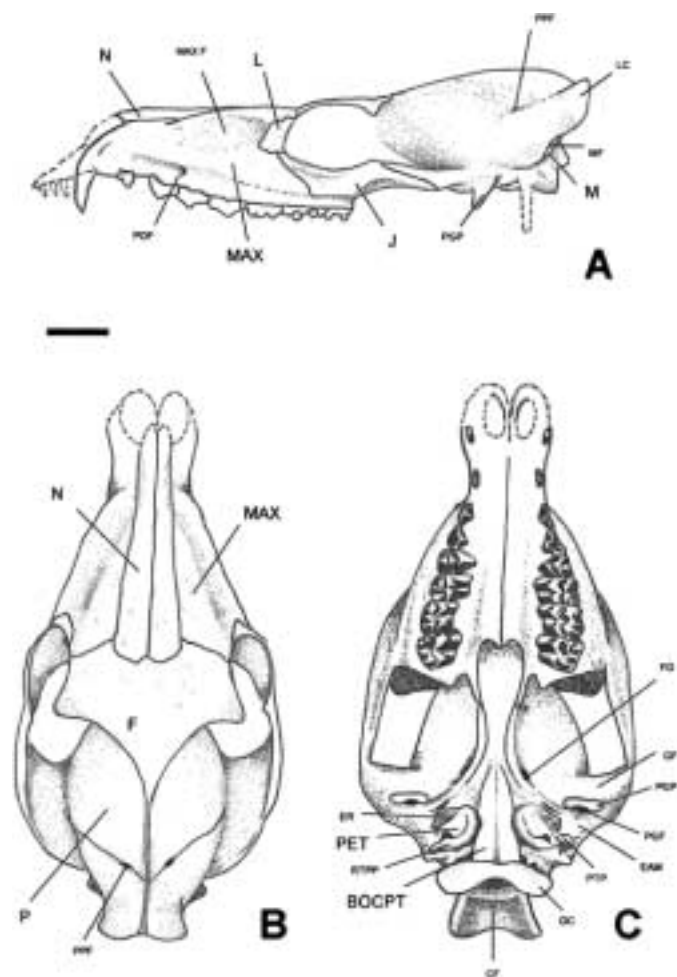
FIGURE 2. Reconstruction of the cranium of *Leptotragulus,* based primarily on MCZ 5304, with additions from other specimens. Dotted lines indicate areas not preserved in the specimen. Auditory bullae were absent in all specimens studied. **A**, lateral view, **B**, dorsal view, **C**, ventral view. **Abbreviations: CF**, complexus fossa; **EAM**, external auditory meatus; **ER**, epitympanic recess; **FO**, foramen ovale; **GF**, glenoid fossa; **J**, jugal; **L**, lacrimal; **LC**, lambdoid crest; **M**, mastoid wing of periotic; **MAX**, maxilla; **MAX F**, maxillary fossa; **MF**, mastoid foramen; **N**, nasal; **OC**, occipital condyle; **P**, parietal; **PET**, petrosal wing of periotic; **PGF**, post-glenoid foramen; **PGP**, post-glenoid process; **POF**, pre-orbital foramen; **PPF**, post-parietal foramen; **PTP**, post-tympanic process of squamosal; **RTPP**, rostral tympanic process of periotic. Scale bar equals 10 mm.

tion anterior to P2. Using the method described by Webb (1965), the cheek teeth: rostrum: basicranium ratio for *Leptotragulus* is 1:0.6:1.15, indicating that the skull has a comparatively short rostrum and shows little or no compression of the postglenoid region. Flexion of the basifacial axis downward from the basicranial axis is approximately 15°, comparable to those of the oromerycid *Montanatylopus* (Joeckel and Stavas, 1996) and the Uintan homacodont *Bunomeryx* (Norris, 1999), but considerably less than that of more derived protoceratids (Joeckel and Stavas, 1996). Unlike the majority of protoceratid genera, *Leptotragulus* had no cranial appendages.

The dentition of *Leptotragulus* is described in detail by a number of authors, notably Scott and Osborn (1887), Scott (1899), Gazin (1955), and Black (1978), and will not be considered in detail here. There are, however, a number of points that are worthy of note. There are pronounced diastemata be-

tween C1 and P1, and between P1 and P2. The upper molars are laterally wide and anteroposteriorly short and exhibit a higher degree of selenodonty than is seen in contemporaneous homacodonts, such as *Bunomeryx* (Wortman, 1898; Stucky, 1998). They have strong lingual cingula. The canine was large in all specimens examined, with the exception of MCZ 21428. It is possible that this individual was a female, as sexual dimorphism in the canine teeth is a feature of protoceratids (Prothero, 1998). However, the fact that M3 was only partially erupted in this specimen suggests that it was also a juvenile. In the absence of data on the growth and development of the skull in protoceratids, it is possible that the small size of the canine was due to immaturity.

The nasal bones are narrow and more-or-less consistent in width along the length of the rostrum (Fig. 2B). There is no evidence of the nasal retraction seen in more derived protoceratids (Scott, 1940). The premaxillae are badly damaged in MCZ 5304, but reference to the other specimens suggest that they are narrowed dorsally, with the ascending ramus of the premaxilla being greatly reduced. The suture between the premaxilla and the maxilla follows the curving anterior margin of the canine. The most unusual feature of the rostrum of *Leptotragulus* is the great expansion of the maxilla dorsally and caudally, where it forms much of the dorsal surface of the snout. It is this expansion that gives the skull its flattened profile, and also exaggerates the constriction of the rostrum anterior to P2. The maxilla has an extensive suture with the frontal, blocking contact between the lacrimal and nasal bones. There is an extensive, shallow maxillary fossa anterior to the lacrimal, and a single pre-orbital foramen, which lies just dorsal to the anterior root of P3. The anteriorly directed sulcus that leads from this foramen is bordered dorsally by a very pronounced ridge, which runs from just caudal to the pre-orbital foramen to a point just dorsal of P1.

The zygomatic arches are broad and transversely flattened. Despite the flexion in the basicranial-basifacial axis of the skull, there is very little curvature in the arch. About half the arch is formed from the jugal, with the suture with the squamosal lying just caudal to the postorbital bar. The bar is incomplete, with a moderately well-developed frontal process, but only very limited development of a jugal process. A pronounced masseteric crest runs from the jugal onto the surface of the maxilla. Unlike the situation described by Webb (1965) in camelids, the origin of the masseter is neither vertical nor horizontal, but somewhere between these two extremes. This reflects the extent to which the ventral margin of the orbit is bowed outwards in *Leptotragulus.*

The frontals are flattened dorsally. There is no noticeable flaring over the orbits and supra-orbital sulci appear to be poorly-developed or absent. The cranium is ovate and dorso-ventrally flattened. Two moderately well developed parietal crests arise from the postero-dorsal margins of the orbits, fusing at the apex of the cranium to form a high-arching sagittal crest. In contrast to the smooth curve of the sagittal crest, the profile of the cranium dips sharply, before rising to the high occiput. A foramen lies in the furrow formed by this dip, interpreted as the post-parietal foramen (Whitmore, 1953). The occiput overhangs the rear face of the cranium by a considerable distance. The lambdoid crests are very pronounced and are bowed outwards, enclosing a deep complexus fossa. This gives the supra-occipital region a semi-circular, arched appearance that is characteristic of protoceratids (Patton and Taylor, 1971, 1973).

The glenoid fossa is broad, with a gently convex articular surface. It is bordered posteriorly by a long, low postglenoid process, and mesially by a low, anteromedially directed ridge, which is a continuation of the pterygoid flange. The small, ovate foramen ovale lies close to the lateral edge of this ridge. A breakage of the glenoid region in two of the specimens ex-

amined (MCZ 5364, YPM-PU 16391) revealed a deep sinus, lying dorsal to the glenoid fossa, between the periotic and the squamosal; it is also visible, in transverse section, in the fragment of braincase wall in MCZ 21428. This space is identified as the sinus venosus temporalis, a structure that has also been reported from the Arikareean synthetoceratine protoceratid *Syndyoceras cooki* (Joeckel and Stavas, 1996), as well as the oreodont *Prodesmatochoerus periculorum* (Whitmore, 1953), the early camelid *Poebrotherium wilsoni* (Whitmore, 1953), as well as the modern *Llama* (Joeckel and Stavas, 1996). The sinus in *Leptotragulus* is, however, much larger than any in the foregoing taxa. An elongate gap in the basicranium, lying just medial to the postglenoid process in MCZ 5304, is interpreted as the foramen jugulare spurium, one of two openings into the sinus venosus temporalis (Whitmore, 1953).

The postglenoid process is not as robust a structure as in, for example, the Uintan homacodont tylopod *Bunomeryx* (Norris, 1999). Posteriorly, it is penetrated by a small, vertically-directed postglenoid foramen. The external auditory meatus is roofed by the squamosal. Unlike the condition seen in many plesiomorphic artiodactyls (Coombs and Coombs, 1982; Norris, 1999) there is no lateral flare of the meatus. It is delineated posteriorly by a robust post-tympanic process of the squamosal.

The auditory bulla was absent in all the specimens seen, suggesting that, like the bulla of more derived protoceratids, the ectotympanic was a comparatively small structure (Joeckel and Stavas, 1996; Patton and Taylor, 1971, 1973), which was only loosely attached to the basicranium. According to Scott (1898), the bullae of ''*Parameryx*'' (=*Leptotragulus*) are hollow and smaller than those of early camelids. Unfortunately, as he later discovered (Scott, 1899), the specimen that he studied was a cranium of the oromerycid *Protylopus*. Thus the leptotraguline bulla remains undescribed.

Because of the absence of bullae, the tympanic face of the periotic was completely exposed on the ventral surface of the basicranium (Fig. 3A). The cochlear body is a broad, ventrally-flattened structure. Medially, it is demarcated by a very substantial rostral tympanic process, which encloses the fenestra cochleae posteromedially. This process arises anteriorly from the raised, triangular promontorium. The fenestra cochleae is subtriangular in shape, with the ventral rim being greatly thickened and anteriorly withdrawn. This has the effect of making the fenestra ventrally directed. The paths of the two branches of the entocarotid artery can be discerned as shallow depressions on the surface of the promontorium. The stapedial artery sulcus is moderately well defined; the sulcus of the promotorial artery, which appears to follow the lateral margin of the rostral tympanic process, is less clear. The tegmen tympani is broadly exposed lateral to the cochlear body. A slit-like opening, which lies anterolateral to the large, ovate epitympanic recess (Fig. 3A), and is separated from the recess by a narrow septum, is interpreted as the foramen jugulare spurium (see above). The fossa of the stapedial muscle is narrow. The fenestra vestibuli is small and partially hidden by the lateral wall of the cochlear body. The fossa muscularis tensor tympani is mostly pocketed in the lateral wall of the tegmen tympani, as described by Webb and Taylor (1980) in a number of groups of hornless ruminants. In MCZ 5364 the ventral margin of this pocketed area is ridged, suggesting the presence of two elements: a dorsal, petrosal component (the tensor tympani) overlying a ventral, squamosal component, termed the ''facies epitympanica'' by Whitmore (1953). A smaller, laterally-directed cavity, lying just caudal to the external auditory meatus, is identified as the incisura tympanica, a structure that Whitmore (1953:133) reported to be present in pecorans, but absent in camelids and tragulids.

Like other protoceratids (Joeckel and Stavas, 1996), the canalicular portion of the periotic of *Leptotragulus* is massive and bony. The endocranial surface of the periotic has an enormously
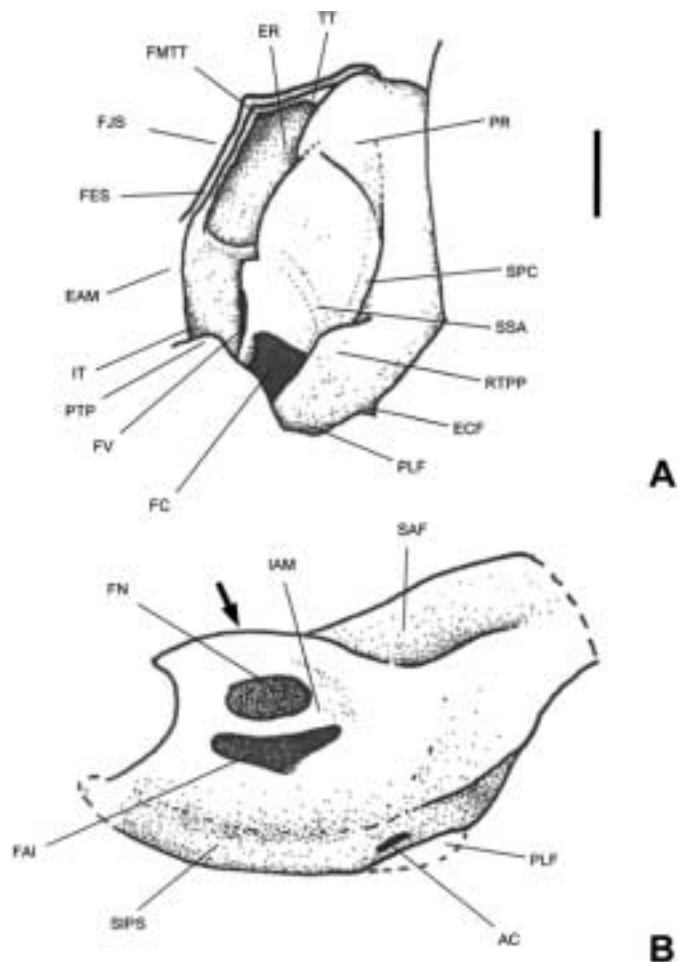

FIGURE 3.   Periotic of *Leptotragulus*. **A**, tympanic face, from MCZ 5304. **B**, endocranial surface, from MCZ 21428. Black arrow in **B** marks the position of the crest separating the cerebral and cerebellar faces. **Abbreviations:** as for Figure 1, together with: **AC**, acqueductus cochleae; **ECF**, entocarotid foramen; **FAI**, foramen acousticus inferius; **FC**, fenestra cochleae; **FES**, facies epitympanica of squamosal; **FJS**, position of foramen jugulare spurium; **FMTT**, fossa muscularis tegmen tympani; **FN**, opening of facial nerve canal; **FV**, fenestra vestibuli; **IAM**, internal auditory meatus; **IT**, incisura tympanica; **PLF**, posterior lacerate foramen; **PR**, promontorium; **SAF**, subarcuate fossa; **SIPS**, sulcus of the inferior petrosal sinus; **SPC**, sulcus of the promontorial canal; **SSA**, sulcus of the stapedial artery; **TT**, tegmen tympani. Scale bar equals 2 mm.

thickened ventro-mesial margin, which is grooved for the passage of the inferior petrosal sinus. Unlike the condition seen in tylopods (Joeckel and Stavas, 1996; Norris, 1999), there is no sign of a ventrally directed flange roofing the petrobasilar canal; the transition from the ventral to mesial faces of the periotic is smoothly rounded. Posteriorly, a shallow sulcus notching the ventral surface marks the position of the posterior lacerate foramen; the sulcus is pierced by a single foramen, identified as the opening of the aqueductus cochleae. The internal auditory meatus is very large. The rounded facial canal lies almost directly dorsal to the foramen acousticus inferius, the two openings being enclosed within an extensive, shallow meatal depression. The cerebellar and cerebral faces of the periotic are separated by a marked crest. The subarcuate fossa, which lies on the cerebral face, is shallow and lacks a mastoid fossa; it is bounded medially by the low swelling of the ampulla of the anterior semicircular canal. The mastoid portion of the periotic
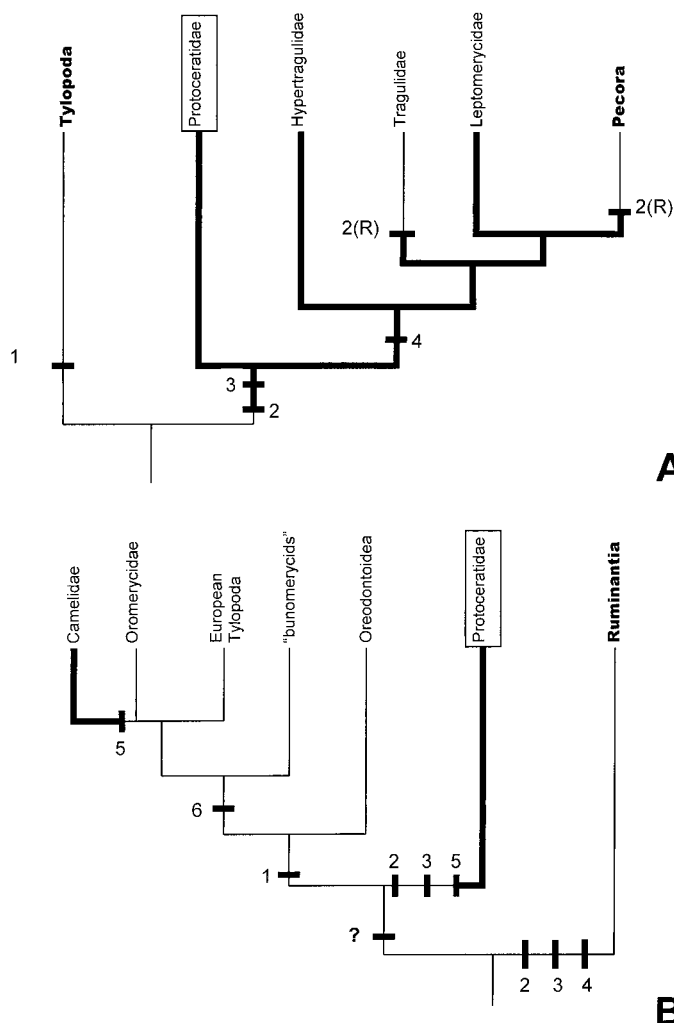
FIGURE 4. Character distributions within two alternative schemes for artiodactyl systematics. **A**, protoceratids as the sister group of ruminants; **B**, protoceratids as the sister group of tylopods. **Character States:** 1, petrosal flange roofs petrobasilar canal; 2, massive expansion of rostral tympanic process of periotic; 2(R), reversion to ancestral state from character 2; 3, crest separates cerebellar and cerebral faces of periotic; 4, fusion of cuboid and navicular; 5, vertebrarterial canal passes through neural arch pedicels of cervical vertebrae; 6, presence of a deep mastoid fossa on the endocranial surface of the periotic. Dark lines in **A** indicate the distribution of character 2 within a ruminant + protoceratid clade, requiring a single origination and two independent losses of character 2. Dark lines in **B** show the distribution of character 5 within a ruminant + tylopod clade, requiring two independent originations of character 5. In addition, two independent originations of characters 2 and 3 are required to support the scheme shown in 4B. Note that there is no character defining the protoceratid + tylopod clade.

is exposed laterally as a thin, horizontally aligned strip, lying between the squamosal and the supraoccipital (Fig. 2A). The elongate mastoid foramen lies on the dorsal margin of this exposure.

The palatal bones terminate posteriorly at a point level with the anterior root of M3 (Fig. 2C). The basisphenoid is gently convex along the midline anteriorly, and is depressed laterally by the shallow sulci of the eustachian tubes. The basioccipital of *Leptotragulus* is robust. The ventral surface has a median groove which continues onto the posterior portion of the basisphenoid, a feature seen in other protoceratids (Scott, 1940; Joeckel and Stavas, 1996) but which is generally absent in ca-

melids and ruminants (where the ventral surface carries a subdued, mid-line keel). Swelling of the basioccipital lateral to these grooves may indicate the presence of paired sinuses, as seen in CT scans of *Syndyoceras* (Joeckel and Stavas, 1996). The entocarotid foramen is visible as a small notch in the lateral surface of the basioccipital. It is separate from the larger posterior lacerate foramen (Fig. 2C).

The paroccipital process of the exoccipital was missing in all the specimens examined. The occipital condyles are broad and flattened, with a pronounced anteroventral lip.

DISCUSSION

One of the most striking aspects of the cranium of *Leptotragulus* is the extent to which it resembles the crania of more derived protoceratids. Despite the antiquity of this genus, it already possesses a suite of distinctive characters. These include the flattened profile of the skull; expansion of the maxilla postero-dorsally; very pronounced, convex supraoccipital crests; and broad occipital condyles with a well developed anteroventral lip. In other respects, however, *Leptotragulus* exhibits distinctly plesiomorphic traits: there is little or no retraction of the nasals; the rostrum is comparatively short; the postorbital bar is incomplete; and there is little or no compression of the postglenoid portion of the skull. Moreover, the moderate level of basicranial-basifacial flexion (15°) is comparable with other Uintan artiodactyls, such as *Bunomeryx* (16°: Norris, 1999), rather than the higher levels of flexion seen in more derived protoceratids (21°–25°: Joeckel and Stavas, 1996).

One intriguing possibility is that the derived features shown by *Leptotragulus* reflect the evolution of agonistic, intraspecific behaviour of the type implied by the elaborate cranial appendages of the later protoceratids. The broad occipital condyles, for example, are remarkably similar to those of camelids. Webb (1965) has hypothesized that this feature is associated with head-butting behaviour and the subsequent need for strengthening of the occipital-atlanteal joint. Patton and Taylor (1971: 142) suggested that the characteristically deep complexus fossa of protoceratids, which is further emphasized by the outwardly flaring lambdoid crests, was a indictor of strong dorsal neck muscles, needed to lift the heavy, horned heads of advanced protoceratids. In the case of *Leptotragulus,* which has a small, hornless skull, it is more likely that strengthening of the neck muscles was another feature associated with the evolution of head-butting. Finally, there is the expansion of the postero-dorsal portion of the maxilla, leading to the formation of a characteristically broad, but flattened forehead. In horned protoceratids, this forehead area forms part of the broad base of the frontal horns. In the absence of horns, however, it is possible that the flattened area was the point of contact during fighting.

The presence of a pronounced bony ridge on the maxilla of *Leptotragulus,* lying anterior and dorsal to the pre-orbital foramen, is a more problematic feature. In synthetoceratine protoceratids, there is often a pronounced bony tubercle in this position. Stirton (1932) believed that this structure served as the origin of the levator nasolabialis muscle. In contrast, Patton and Taylor (1971) suggested that its main purpose was to provide protection for the infraorbital branch of the maxillary artery, which is greatly enlarged to provide a blood supply to the rostral horn. Neither of these explanations fits the situation in *Leptotragulus.* The lack of nasal retraction suggests that *Leptotragulus* did not possess the sort of enlarged, mobile upper lip that would require an extensive levator nasolabialis muscle, while the absence of a rostral horn would seem to negate the requirement for a complex maxillary arterial system. It may be that all protoceratids have a tendency to develop bony ridges on the rostrum, which is elaborated in the more derived forms to produce the various horns and other cranial appendages typ-

ical of the group. It is worth noting, however, that a similar ridge was present in the two specimens of *Leptoreodon* (a hornless protoceratid which is contemporaneous with *Leptotragulus*) that were studied by the author (YPM-PU 11225, 1126), which terminated in a bony tubercle. The anterior margin of this tubercle is grooved by a dorsally directed sulcus, presumably the path of the pre-orbital branch of the maxillary artery. This raises the possibility that soft-tissue protuberances were present on the snouts of the ''hornless'' early protoceratids, and that the various sulci and tubercles seen in both *Leptotragulus* and *Leptoreodon* are a reflection of the blood supply required by such structures.

From the outset, one of the most important aspects of this study of *Leptotragulus* was the extent to which this early protoceratid could cast light on the disputed question of the higher-level affinities of the Protoceratidae. In essence, there are two conflicting hypotheses. The first, as espoused by Patton and Taylor (1973) and Webb and Taylor (1980), is that protoceratids are members of the Tylopoda, and are closely related to camelids (Fig. 1A). This view is widely accepted today (Janis et al., 1998; Prothero, 1998), but is supported by comparatively few synapomorphic characters. The majority of the similarities cited by Patton and Taylor (1973), such as the possession of an unfused cuboid and navicular by both camelids and protoceratids, are symplesiomorphic. Webb and Taylor (1980) provided only two synapomorphic characters for the Tylopoda, of which one, the presence of a three-chambered stomach lacking a reticulum, cannot be assessed in fossil taxa and may also be symplesiomorphic. The remaining character is the pattern of arterial passage through cervical vertebrae 2–6, with the vertebral artery passing through the neural arch pedicles rather than the transverse processes of the vertebrae.

The second hypothesis, most recently proposed by Joeckel and Stavas (1996) is, in effect, a reversion to the earliest ideas about protoceratid affinities, namely that their affinities lie with the Ruminantia (Fig. 1B; Osborn and Wortman, 1892; Scott, 1895, 1899; Wortman, 1898; Matthew, 1905; Colbert, 1941; Stirton, 1944; Simpson, 1945). Joeckel and Stavas (1996) provided a set of characters drawn from the cranium of *Syndyoceras* which served to emphasize the differences between protoceratids and camelids, together with two possible synapomorphies linking protoceratids and ruminants, namely the presence of a strong dorsal crest separating the cerebral and cerebellar faces of the petrosal, and the reduction of the subarcuate fossa. A study of the Uintan tylopod *Bunomeryx* by the author (Norris, 1999) suggests that reduction of the subarcuate fossa might be symplesiomorphic within artiodactyls: however, other characters of *Bunomeryx* provided evidence for the existence of a tylopod clade uniting oreodonts, bunomerycids, camelids, oromerycids, and a number of European forms, but excluding protoceratids.

In summary, therefore, both hypotheses are supported by a single skeletal synapomorphy, and a much larger set of characters that serve to emphasize the distance between protoceratids and both ruminants and tylopods. Furthermore, protoceratids lack the distinctive synapomorphies that unite tylopods (petrosal flange roofs petrobasilar canal—Joeckel and Stavas, 1996: Norris, 1999) or ruminants (fused cuboid and navicular—Webb and Taylor, 1980). Protoceratids are, however, members of the monophyletic Neoselenodontia (Webb and Taylor, 1980), which also contains the ruminants and tylopods. There are three possible phylogenetic scenarios: (1) protoceratids are the sister group of the Ruminantia; (2) protoceratids are the sister group of the Tylopoda; or (3) protoceratids are the sister group of Ruminantia and Tylopoda. However, there are no known characters supporting the third hypothesis.

The hope expressed by at least one previous study (Joeckel and Stavas, 1996) was that the study of leptotraguline basicran-ia might provide characters that would unambiguously link protoceratids either to ruminants or camelids. As has been discussed above, the principal impression gained from the study of the cranium of *Leptotragulus* is the remarkable extent to which this middle Eocene form possesses the distinctive cranial characters of later protoceratids. However, there are some areas that provide wider phylogenetic insights. The structure of the periotic, for example, is very reminiscent of that of early ruminants. Points of similarity include the presence of a marked ridge between the cerebellar and cerebral faces (also noted in *Syndyoceras* by Joeckel and Stavas, 1996), which is seen in the majority of ruminants (but which is also present in the European tylopods *Anoplotherium* and *Diplobune*; Dechaseaux, 1969:fig. 3); and a large rostral tympanic process and ventrally-orientated fenestra cochleae, both of which have been described by Webb and Taylor (1980) from the periotics of the hornless ruminants *Hypertragulus, Archaeomeryx,* and *Leptomeryx.*

The most striking resemblance between the *Leptotragulus* and the hypertragulids and leptomerycids is the very great size of the rostral tympanic process, which is large enough to form part of the medial wall of the hypotympanic sinus. The presence of the rostral tympanic process itself is likely to be a widely-distributed character within the Artiodactyla. Coombs and Coombs (1982), for example, reported the presence of ''a strong ventral ridge'' running along the medial edge of the promontorium in *Gobiohyus,* and similar, albeit weaker structures in *Diacodexis* and *Homacodon,* and noted that a similarly positioned ridge in modern artiodactyls marks the contact of the bulla with the promontorium. The distinctive feature in the case of *Leptotragulus,* however, is not the presence of the process per se, but its massive development, and it is this feature that links it with both *Hypertragulus* and the leptomerycids. The presence of the ventrally-directed fenestra rotunda may also be associated with the massive thickening of the bone in this area and the retraction of the ventral margin of the fenestra, a feature noted by Webb and Taylor (1980) in *Hypertragulus, Archaeomeryx* and (to a lesser extent) *Leptomeryx,* but which is absent in the four early/middle Eocene taxa studied by Coombs and Coombs (1982).

Regarding the possible tylopod affinities of the protoceratids, the only remains of *Leptotragulus* described to date are the cranium (in this paper), the dentition (Scott and Osborn, 1887; Gazin, 1955; Wilson, 1974; Golz, 1976; Black, 1978), and the limbs (Scott and Osborn, 1887). Without information on the axial skeleton, it is impossible to provide any new information on the all-important question of the pattern of vertebrarterial circulation, identified by Webb and Taylor (1980) as a tylopod synapomorphy. Certainly, in those protoceratid taxa for which cervical vertebrae are available, the vertebral artery passes through the neural arch pedicle and runs for almost half the length of the vertebra inside the neural canal. This condition is also seen in camelids and xiphodonts (Gentry and Hooker, 1988) but not, crucially, in any of the other taxa with tylopod affinities for which cervical vertebrae have been described (cainotheres, anoplotheres, dacrytheres, oromerycids, and oreodonts). This is an important point, because it means that the pattern of vertebrarterial circulation cannot be used as a synapomorphy to unite the protoceratids with a wider tylopod clade; it is only a potential synapomorphy of a camelid + xiphodont + protoceratid clade within the Tylopoda. As discussed above, other features of the protoceratid cranium, particularly in the ear region, serve only to emphasize the distance between protoceratids and the tylopods, which raises the possibility that the structure of the cervical vertebrae may have evolved independently in camelids and protoceratids. There are other features of the cervical vertebrae, such as development of a spout-like odontoid process and fusion of the atlanteal articular surfaces,

which are seen in the axis of both camelids and advanced ruminants and are almost certainly convergent.

If protoceratids prove to be the sister group of ruminants, then there are some interesting implications for artiodactyl biogeography. The earliest known ruminants date from the late Uintan, 41.3 Ma (Webb, 1998). The sudden appearance of ruminants in the fossil record of North America, combined with the absence of any obvious candidate for a sister group in the middle Eocene faunas of the continent, has led some authors to suggest that ruminants originated in Eurasia. To date, however, although both hypertragulids and leptomerycids have been found in late Eocene deposits in central and southern Asia (Savage and Russell, 1983) none have been found which pre-date the Uintan forms from North America (Webb and Taylor, 1980; Webb, 1998). The 'homacodontine' artiodactyl *Mesomeryx,* which Stucky (1998) identifies as having ruminant affinities, first appears in the early Uintan, 44.1 Ma (Prothero, 1996). In contrast, the oldest known fossils of *Leptotragulus* are found some 45.9 Ma, which would push the latest date for a common ancestor of the ruminant + protoceratid clade back into the Bridgerian. It also raises the possibility that tylopods + ruminants are, in fact, a North American group, an idea which was prevalent in the early and middle years of this century (e.g., Scott, 1940) but which is now dismissed as "chauvinism" (Webb, 1998:467).

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