

THE PROTOCERATINAE
(MAMMALIA, TYLOPODA,
PROTOCERATIDAE) AND THE
SYSTEMATICS OF THE
PROTOCERATIDAE

THOMAS HUDSON PATTON AND BERYL E. TAYLOR

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ABSTRACT

THE SYSTEMATICS of the subfamily Protoceratinae are revised and its evolution, phylogeny, and zoogeography outlined. The stratigraphic range of the subfamily extends from the Chadronian (early Oligocene) to the Clarendonian (middle Pliocene); geographically, the subfamily ranges from the northern Great Plains (South Dakota, Nebraska, Wyoming) southward to Texas and into Panama. The Protoceratinae now include four genera: *Hetero-*

meryx, *Pseudoprotoceras*, *Protoceras*, and *Paratoceras*. *Calops* Marsh is here synonymized with *Protoceras*; specific synonymies within each genus are also treated. Two new species of *Protoceras* are recognized: *P. skinneri* from South Dakota and Nebraska and *P. neatodelpha* from Wyoming. New skull and horn material allows an expanded description and diagnosis of *Paratoceras*, and a new species, *P. wardi*, from the Barstovian of the Texas Gulf Coastal Plain is erected.

INTRODUCTION

FEW OF THE MANY ARTIODACTYL groups represented in the North American Tertiary have so consistently defied taxonomic placement and so generally frustrated attempts to interpret their peculiar anatomy, as the Protoceratidae. From their appearance in the early Chadronian (early Oligocene) to their apparent extinction in the late Hemphillian (late Pliocene), the protoceratids display a variety of horns that in form and position are unequaled among any of their contemporaries. Although all the later protoceratids developed large and sweeping supra-orbital horns, the group is particularly distinguished by its strange maxillary armament. The arched bony plates on the upper surface of the maxillaries, which unite in some species to form a common trunked rostral horn, are unique features of the Protoceratidae. Although no other North American artiodactyl has such armament, the Uintatheriidae of the Dinocerata evolved maxillary horns roughly similar to those of the protoceratids.

Frick (1937) provided the first real review of the Protoceratidae. Under his single division, the Protoceratini, he included three subfamilies: the Protoceratinae, the Syndyceratinae, and the Synthetoceratinae. As revised by Frick, the Protoceratinae was composed of Marsh's genera *Protoceras* and *Calops*, the genus *Pseudoprotoceras* Cook, and a new genus, *Paratoceras* Frick. In this classification, Frick reduced *Calops* to a subgenus of *Protoceras*. Frick's Syndyceratinae was a monotypic subfamily, containing only the genus *Syndyceras* Barbour. The Synthetoceratinae was composed of the genus *Synthetoceras* Stirton and a new subgenus,

Prosynthetoceras Frick. Finally, a new genus, *Lambdoceras*, was erected by Stirton (1967, posthumously).

The more advanced protoceratids, represented by the Syndyceratinae and Synthetoceratinae, were combined into a single subfamily, the Synthetoceratinae (Patton and Taylor, 1971). As defined by us, the Synthetoceratinae includes the following genera: *Syndyceras* Barbour, *Prosynthetoceras* Frick, and *Synthetoceras* Stirton. We reduced Stirton's genus *Lambdoceras* to the rank of subgenus within *Prosynthetoceras*.

In the present paper, we have revised the remaining nominate subfamily, the Protoceratinae, to include the following genera: *Heteromeryx* Matthew, *Pseudoprotoceras* Cook, *Protoceras* Marsh, and *Paratoceras* Frick. We have also attempted to review the evolutionary history of the entire family and to present additional evidence to justify Scott's (1940) and Stirton's (1967) assignment of the family Protoceratidae to the suborder Tylopoda.

ACKNOWLEDGMENTS

Recognition is due the late Childs Frick for his perseverance in directing the field parties in their search for the rare protoceratids described in this report and for his revision of the Protoceratidae in 1937.

Deep appreciation is extended to Dr. Bobb Schaeffer, Drs. Malcolm C. McKenna, Richard H. Tedford, Messrs. Morris F. Skinner and Ted Galusha for critically reading the manuscript and giving helpful suggestions. It is a pleasure to acknowledge the benefits gained from the

many discussions with these gentlemen on the stratigraphy and correlation of the sedimentary rocks of the Great Plains and the Gulf Coastal Plain.

We are indebted to Dr. Frank C. Whitmore, Jr., United States Geological Survey, for permission to examine undescribed material from the Panama Canal Zone and to Dr. Elwyn L. Simons, Peabody Museum, Yale University, for the loan of specimens.

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ABBREVIATIONS

The following abbreviations are used to denote an institutional collection:

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History
F:AM, Frick American Mammals, Department of Vertebrate Paleontology, the American Museum of Natural History
HC, Harold Cook Collection (now incorporated with the American Museum of Natural History Collection)
PU, Princeton University
SDSM, South Dakota School of Mines
YPM, Peabody Museum, Yale University

MEASUREMENTS AND STATISTICS

N, sample size
OR, observed range
 \bar{X} , mean
S, standard deviation
V, coefficient of variation

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE OF THE PROTOCERATINAE

AS IS TRUE OF ALL the Synthetoceratinae, the members of the subfamily Protoceratinae are entirely North American.¹ Unlike the subfamily Synthetoceratinae, whose stratigraphic and geographic record is regular and relatively unbroken, the distribution of the genera comprising the Protoceratinae is marked by both stratigraphic and geographic discontinuities. The members are irregularly clustered in the Oligocene² and Miocene of Nebraska, Wyoming, and South Dakota, in the Miocene of coastal Texas and Panama, and in the Pliocene of the Texas Panhandle. No protoceratids have been found east of Texas. Although this distribution is doubtless influenced by the vagaries of geologic sampling, available evidence indicates that the Protoceratinae were less widely and less uniformly dispersed than their relatives, the Synthetoceratinae.

The Protoceratinae range from the Chadronian of the Great Plains, through the Hemingfordian of Panama and the early Barstovian of the Texas Coastal Plain, to the middle Clarendonian of the Texas Panhandle. Because of occasional confusion or uncertainty regarding particular fossil localities and their age designations, we have discussed each of the localities in the text that follows.

CHADRONIAN

Nebraska: The oldest record of the Protoceratinae is that of *Pseudoprotoceras longinarius* Cook, 1934. Cook (1934, p. 151) stated only that it came from the "Lower Chadron (Lower Oligocene) beds about 9 miles north of Crawford, Nebraska, in the same horizon and locality as the type of *Hypertragulus chadronensis*. . . ." He subsequently wrote that *H. chadronensis* came from the lower part of the Chadron Formation "only a few feet above the contact with the marine Pierre shales." The exposures from which the type was collected were later called the "Chadronia Pocket" and are well down in the

local section of the Chadron Formation but not at its base. Wood (1969, p. 17) concluded from his study of the rodents that the age of the "Chadronia Pocket" is "somewhat later than the Horsetail Creek [Colorado] and considerably later than the Pipestone Springs beds [Montana]." Clark, Beerbower, and Kietzke (1967, p. 57) correlated the Pipestone Springs fauna with the upper member (Peanut Peak) of the Chadron Formation of South Dakota.

Wyoming: Previously restricted to Nebraska, *Pseudoprotoceras* is now known from the Bates Hole region of central Wyoming as well. The specimens from this locality are being studied by Robert Emry of the National Museum of Natural History, Smithsonian Institution, who reports (personal commun.) that in the Flagstaff Rim section of the Bates Hole area of Wyoming, *Pseudoprotoceras* occurs stratigraphically near the middle of the section in beds that are about temporally equivalent to the Pipestone Springs, Montana (Main Pocket). Emry believes that these deposits are late Chadronian and probably almost equivalent to those of the Nebraska type locality of *Pseudoprotoceras longinarius*.

South Dakota: The genus *Heteromeryx dispar* Matthew, 1905, is the oldest protoceratine recorded from South Dakota. Matthew (1905, p. 23) generally cited the stratigraphic level as "the Titanotherium beds of the White River formation in South Dakota." A term first used by Leidy (1853), the *Titanotherium* bed (singular in Leidy's usage; later pluralized by Hatcher, 1893) corresponds to the entire Chadron Formation (see Harksen and Macdonald, 1969, p. 2). Under his specific characterization of *Heteromeryx*, however, Matthew (1905, p. 24) stated that the type came from "the Middle Titanotherium Beds on Indian Creek, Cheyenne River, S. Dakota." According to Clark, Beerbower, and Kietzke's (1967) correlation, the Middle *Titanotherium* beds are the equivalent of his Crazy Johnson Member of the Chadron Formation.

ORELLAN

No protoceratid remains have been recorded from deposits of this age.

¹We are using the term in the broadest sense to include Central America as far south as Panama.

²J. A. Wilson (personal commun.) reports a *Pseudoprotoceras*-like animal from the Oligocene of West Texas.

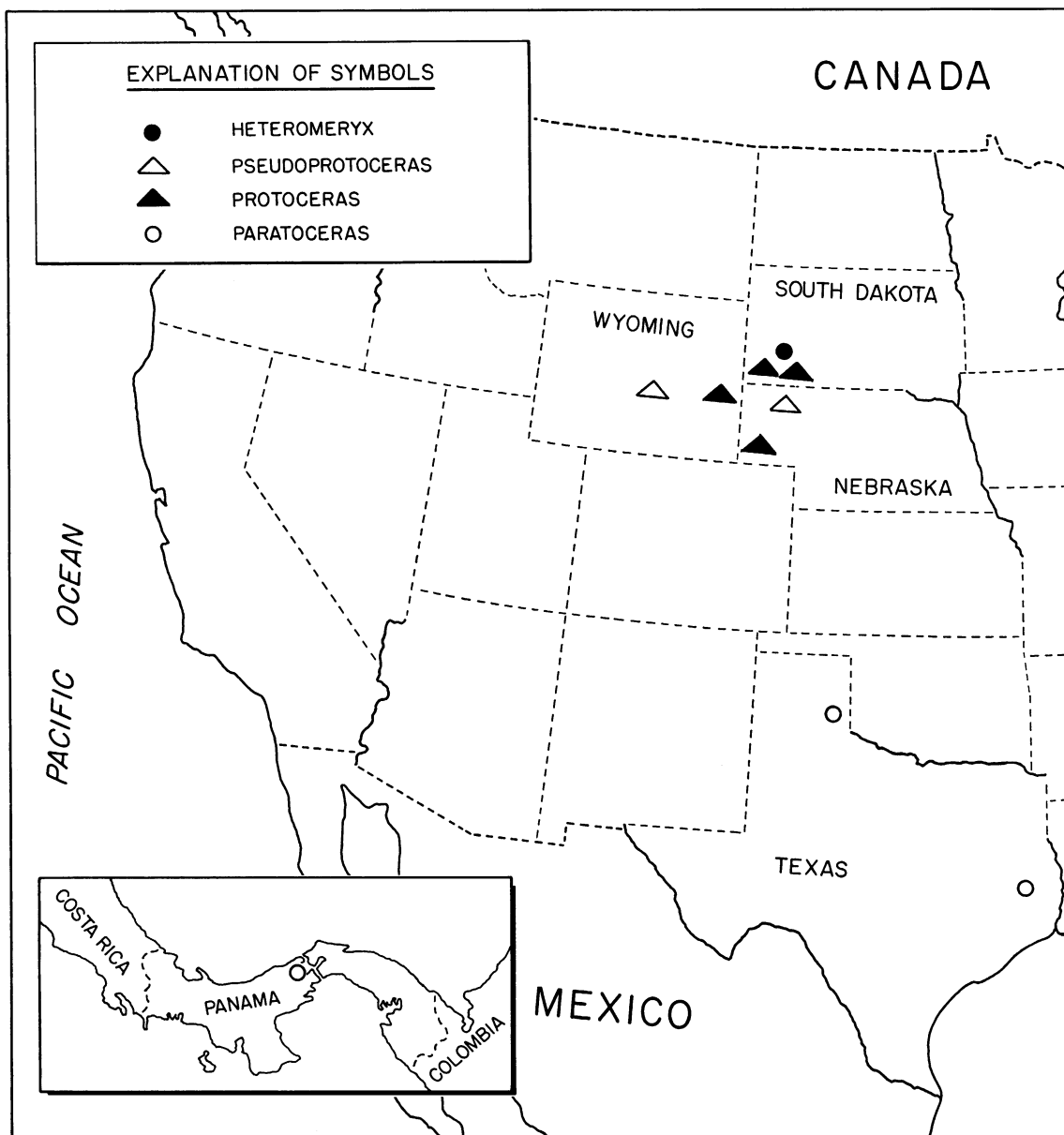


FIG. 1. Known geographic distribution of the Protoceratinae.

WHITNEYAN

South Dakota: The type genus, *Protoceras*, was originally described by Marsh (1891, p. 82) from "the upper part of the Oreadon beds of the Miocene" of South Dakota. This zone has since come to be known variously as "the Protoceras Bed" (Wortman, 1893, p. 96), "Protoceras sandstones" (Matthew, 1901, p. 370), and "Protoceras Channels" of various authors.

These beds are a part of the upper portion of Bump's (1956) Poleslide Member of the Brule Formation. The protoceratid taxa described by Marsh (1891, 1894a, 1897), including *Protoceras celer*, *P. nasutus*, *P. comptus*, *Calops cristatus*, and *C. consors*, were recovered from this same zone.

Protoceras channels occur in a number of areas in the Badlands of South Dakota, but the area on the northeast side of Cuny Table has yielded

the major part of the published specimens. Morris F. Skinner (personal commun.) reports that other channels on the south side of Sheep Mountain have been diligently searched by the Frick Laboratory field parties but have not yielded any *Protoceras*. A partial cranium of *Protoceras* was collected, however, from a channel deposit capping a butte in Jackson County, about 1 mile west of Cedar Pass. At this point, the channel was incised into the upper part of the Poleslide Member. The Rockyford Ash is not preserved above this particular outcrop but the study of nearby outcrops suggests that this channel deposit is situated stratigraphically below the Rockyford Ash.

ARIKAREEAN

South Dakota: In the past *Protoceras* was not known to occur outside the restricted locale and zone described above. Additional material collected in Fall River County by Skinner extends the distribution of this genus to beds that are equivalent to the upper part of the Sharps Formation. Skinner reports (personal commun.) that the Sharps Formation is temporally equivalent (in part) to the Gering Formation of Nebraska.

Nebraska: *Protoceras* is now recorded for the first time in the Miocene of western Nebraska. A specimen was collected in the Horse Creek area of Banner County, from deposits considered by Schultz and Falkenbach (1954, pp. 199–201)

to be temporally equivalent to the Gering Formation (early Arikareean). The early Miocene *Protoceras* specimens from Nebraska and South Dakota form the basis for description of a new species, *P. skinneri*.

Wyoming: In addition to the Nebraska occurrence, *Protoceras* is also recorded in an early Miocene deposit in eastern Wyoming. A partial skull (female), the type of a new species, *P. neatodelpha*, was taken from late Arikareean deposits that are temporally equivalent to the Harrison Formation (Frick and Taylor, 1968, p. 21) of Niobrara County.

HEMINGFORDIAN

Panama: Protoceratid material reported by Whitmore and Stewart (1965), from the Cucaracha Formation of the Panama Canal Zone, has been identified by us as belonging to *Paratoceras*. This record marks the first appearance of that genus in the protoceratine lineage. Whitmore and Stewart (1965, p. 182) assigned the Cucaracha Formation to the early middle Miocene (early Hemingfordian) on the basis of the land mammal assemblage recovered from the formation itself. They concluded: "Assignment of an age for the Cucaracha fauna must depend upon those members that resemble the geologically youngest forms found in dated sequences elsewhere. The Cucaracha oreodonts fall in this category, and are thus the basis on

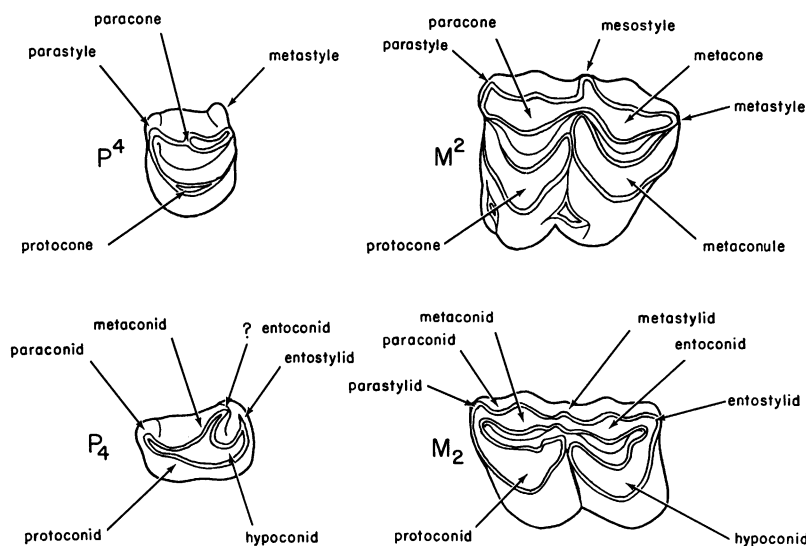


FIG. 2. Cusp terminology used herein follows that used for the synthetoceratine teeth (after Patton and Taylor, 1971, fig. 4).

which we regard the Cucaracha Formation as early Middle Miocene. This fauna was peripheral to the North American mammal fauna; therefore migration must have been to, rather than from, the Cucaracha area. Accordingly, any animals of pre-Middle-Miocene aspect in the Cucaracha fauna are regarded as relicts."

The general similarity of the Cucaracha *Paratoceras* with that from the early Barstovian of Texas supports Whitmore and Stewart's conclusion.

BARSTOVIAN

Texas: The genus *Paratoceras* is best represented by material recovered from early Barstovian deposits in the Texas Gulf Coastal Plain. This material, representing a new species, *P. wardi*, allows for the first time a description of the skull, horns, and upper dentition of this previously little known genus. The specimens were collected from the Trinity River Pit 1 in San Jacinto County, whose deposits have

yielded a fossil vertebrate assemblage distinct from the well-known Texas vertebrate biostratigraphic units that bracket them in time. Although incompletely studied, this local fauna occupies a position intermediate between the established Burkeville and Cold Spring faunas. On the basis of a study of fossil artiodactyls from this sequence, Patton (1969) concluded that the Burkeville and Cold Spring faunas were of medial Hemingfordian and medial Barstovian age, respectively. The Trinity River assemblage correlates most closely with the early Barstovian Lower Snake Creek fauna of Nebraska.

CLARENDONIAN

Texas: The type locality for *Paratoceras* is the Frick Laboratory Locality 17, Quarry 1, 10 miles north of Clarendon in Donley County, Texas. These deposits belong to the typical Clarendon sequence and are considered by most workers to be of early or middle Clarendonian age.

SYSTEMATICS

ORDER ARTIODACTYLA OWEN, 1848

SUBORDER TYLOPODA ILLIGER, 1811

FAMILY PROTOCERATIDAE MARSH, 1891

SUBFAMILY PROTOCERATINAE MARSH, 1891

INCLUDED GENERA: *Protoceras* Marsh, 1891; *Heteromeryx* Matthew, 1905; *Pseudoprotoceras* Cook, 1934; and *Paratoceras* Frick, 1937.

DISTRIBUTION: From Chadronian to Clarendonian of Panama, United States, and possibly Canada.¹

REVISED DIAGNOSIS: The Protoceratinae differ from the Synthetoceratinae, the other subfamily of the Protoceratidae, as follows: shorter proportioned skull with less elongate muzzle; shorter nasals; failure of the maxillary processes to unite to form a single shafted rostral horn; proportionally smaller frontal horns; stronger and more anteriorly extended masseteric crest in males; presence of cranial armament in males in the form of parietal hornlike protuberances in *Protoceras* and in an occipital horn in *Paratoceras*; P¹ present; relatively larger and more elongate P²⁻⁴₂₋₄ not showing the reduction in size or number characteristic of the Synthetoceratinae; lower-crowned molars with stronger lingual cingula above and more prominent intercolumnar pillars between the protoconid and hypoconid below.

GENUS *HETEROMERYX* MATTHEW, 1905

Heteromeryx MATTHEW, 1905, p. 23.

TYPE SPECIES: *Heteromeryx dispar* Matthew, 1905.

INCLUDED SPECIES: Type species only.

TYPE: AMNH 12326, crushed partial skull with P¹–M³ and parts of fore and hind limbs. Matthew (1905, p. 24) recorded the type from "the Middle Titanotherium Beds on Indian Creek, Cheyenne River, S. Dakota."

DISTRIBUTION: Chadronian of South Dakota.

¹A protoceratid may be represented by the type of *Leptomeryx semicinctus* Cope, 1889, from the *Titanotherium* Beds, Swift Current Creek, Saskatchewan, Canada. The writers have not seen the type but Matthew (1902, p. 214) observed, "This is clearly not *Leptomeryx*, and is distinct from any described White River genus (except possibly *Calops*, with which I am unable to compare it . . .)."

REVISED DIAGNOSIS: *Heteromeryx* differs from *Pseudoprotoceras* in having a larger, more complex P² and P³, a strong protocone on P², and less recessed nasals. The genus is distinguished from *Protoceras* and *Paratoceras* by its smaller size, longer nasals, and lack of hornlike protuberances.

DISCUSSION: The gender of the *Heteromeryx* is unknown, but even if it proves to be a female and hornless, it nonetheless differs from *Protoceras* in having weaker parietal crests. In contrast, the parietal crests on the female *Protoceras* skull are especially strong at the point where the hornlike protuberances arise in males. The muzzle of *Heteromeryx* is shorter than in *Protoceras*, with the position of P¹ about midway between the C/ and P², and less anteriorly situated than in *Paratoceras*. P² and P³ are larger than in *Protoceras* and both have a strong protocone; P² protocone is larger than that of both *Protoceras* and *Paratoceras*. Although the molars of the type of *Heteromeryx* are worn, they are very brachydont and apparently lower crowned than those of *Protoceras*. The ulna is strong and fused along its entire length with the radius in *Heteromeryx*, in contrast to a partially fused ulnoradius in *Protoceras* and a proportionally lighter ulna in *Paratoceras*.

The only other named species of *Heteromeryx* is *H. transversus* from the Cypress Hills Formation of Saskatchewan, Canada. First described as *Hypertragulus transversus* by Cope in 1889, the species was founded on the basis of two worn upper molars; it was not until 1891, however, that Cope figured (pl. 14, figs. 4–4a) one of the molars. According to Cope's original description, the *transversus* molars were almost twice the length (anteroposterior length 12 mm.; transverse diameter 15 mm.) of those of *H. calcaratus* Cope, then the only other known species of *Hypertragulus*. Cope described the type specimens as having among other general features, a small anterior cingular cusp, faint cingula on the anterior and posterior sides of the crescents but which do not extend around to their internal sides, and a lack of any buccal cingulum. In his revision of the Hypertragulidae, Matthew (1902, p. 316) questionably listed "*Hypertragulus transversus* Cope, stating, "It is not at all probable that this species is *Hypertragulus* or related

thereto." Apparently the only other treatment of this species was by Russell (1934, p. 66) who transferred it to *Heteromeryx*, remarking only that "the types of this species are hardly distinguishable from the M¹ and M² of *Heteromeryx dispar* Matthew. The Cypress Hills teeth are somewhat wider and more compressed anteroposteriorly."

Our comparisons indicate that the measurements of *H. transversus* molars (12 mm. by 15 mm.) are not significantly different from those of *H. dispar* (10.5 mm. by 14.5 mm.); however, morphologically the two forms are dissimilar. According to Cope's figure of the *H. transversus* molars, those of *H. dispar* show a stronger parastyle and metastyle. Moreover, Cope (1889, p. 155) stated, "Slight cingula on the anterior and posterior sides of the internal lobes which do not pass round their internal sides." This feature contrasts strongly with the molars of *H. dispar* which have a strong cingulum passing around the lingual side of the protocone and metaconule. In sum, it is clear that the minimal number and worn state of the *transversus* specimens precludes confident identification with any species; furthermore, it is evident that placement with any of the known species of *Hypertragulus* or *Heteromeryx* would at this time be highly conjectural. Therefore, it is our contention that *Heteromeryx* (= *Hypertragulus*) *transversus* be considered a *species inquirenda* (Stoll, et al., 1961) until such time more reliable specimens are available for study.

GENUS PSEUDOPROTCERAS COOK, 1934

Pseudoprotoceras Cook, 1934, p. 149.

TYPE SPECIES: *Pseudoprotoceras longinaris* Cook, 1934.

INCLUDED SPECIES: Type species only.

TYPE: AMNH 81000 (=HC 507), crushed anterior half of skull with C/ alveolus and P¹ (br.)-M³, astragalus, and navicular. Cook (1934, p. 151) reported the type from "Lower Chadron (Lower Oligocene) beds about 9 miles north of Crawford, Nebraska." The type is recorded in the American Museum catalogue from the "Chadronia Pocket, badland area, approximately 7.8 miles north of Crawford, Dawes County, Nebraska." Wood (1969, p. 2) stated, "The exposures at the 'Chadronia Pocket' are from a section a few feet thick, well down in the local section of the Chadron." As to the age of the deposits, Wood (p.17) concluded, "The

rodents of the *Chadronia* Pocket suggest a very short time interval before middle Oligocene. It seems quite possible that the Nebraskan Chadron, then, is somewhat later than the Horsetail Creek and considerably later than the Pipestone Springs beds." Clark, Beerbower, and Kietzke (1967, p. 57) correlated the Pipestone Springs fauna with that of the upper member (Peanut Peak) of the Chadron Formation of South Dakota.

DISTRIBUTION: Chadronian of Nebraska and Wyoming.

REVISED DIAGNOSIS: *Pseudoprotoceras* differs from *Heteromeryx* in having a smaller, less complex P² and P³ with P² lacking the protocone, and more retracted nasals.

Pseudoprotoceras is smaller than *Protoceras* and *Paratoceras* and differs from both in having no maxillary or frontal protuberances, although the large size of the C/ alveolus indicates that the type specimen is a male. P² in *Pseudoprotoceras* is simple and slenderer than in *Protoceras* and *Paratoceras*.

GENUS PROTCERAS MARSH, 1891

Protoceras MARSH, 1891, p. 81.

Calops MARSH, 1894a, p. 94.

Protoceras (*Calops*): FRICK, 1937, pp. 610, 613.

Calops: SCOTT, 1940, pp. 564-566.

Protoceras (including *Calops*): SIMPSON, 1945, p. 151.

TYPE SPECIES: *Protoceras celer* Marsh, 1891.

INCLUDED SPECIES: *Protoceras celer*, type species, *Protoceras skinneri*, new species, and *Protoceras neatodelpha*, new species.

DISTRIBUTION: Late Whitneyan of South Dakota, early Arikarean of South Dakota and Nebraska, and late Arikarean of Wyoming.

REVISED DIAGNOSIS: *Protoceras* differs from *Paratoceras* in having more posteriorly placed orbits; longer facial region; relatively shorter and less expanded cranium; relatively larger and more anteriorly situated maxillary protuberances; shorter more posteriorly placed triangular-shaped supraorbital protuberances; two hornlike parietal protuberances; no occipital horn; a stronger sagittal crest; three lower incisors and an incisiform canine, whereas *Paratoceras* is believed to have lost one of these four incisiform teeth; a longer muzzle with P¹ about midway between C/ and P²; a more elongate and slenderer P²⁻³ with stronger lingual cingulum on P²⁻³ and stronger protocone on P³; lower-crowned molars; a broader masseteric

fossa on the mandibular ramus; a proportionally heavier ulna that is fused only with the distal end of the radius; a relatively larger scaphoid facet on the radius, and a transversely narrower but anteroposteriorly longer lunar facet; a relatively larger fibular groove on the distal end of the tibia; a proportionally wider sustentacular facet on both the astragalus and the calcaneum; a heavier and more posteriorly projecting sustentacular process on the calcaneum; and a larger facet on the navicular for the entocuneiform.

Protoceras differs from *Heteromeryx* in having a larger, more elongate skull; an especially longer facial region; a more posteriorly placed orbit; a longer muzzle; maxillary, frontal, and parietal horns; proportionally smaller and less robust P²⁻³ with a weaker protocone on P³; brachydont molars, possibly slightly taller crowned than in *Heteromeryx*; and a partially fused radius and ulna.

Protoceras is larger than *Pseudoprotoceras* and differs in having a longer facial region; maxillary and supraorbital protuberances in the male; and a longer muzzle with P¹ about midway between C/ and P².

DISCUSSION: Until the description of *Protoceras* by O. C. Marsh in 1891, no horned artiodactyl had ever been known to occur in the White River Group of North America. First discovered by J. B. Hatcher from the "Miocene" (=Oligocene) of South Dakota, this new and strange creature was to usher in a long history of speculation about its unusual cranial morphology and its obscure ancestry. Of course, the most striking feature of *Protoceras* is the unique occurrence and arrangement of the paired hornlike protuberances of the males. The largest and most truly hornlike protuberances are those on the parietals just behind the orbits. In conformation and placement these horns are similar to those of giraffes. Another smaller pair occur as roughly triangular supraorbital "wings" which extend over the posterolateral border of the orbits. The most unusual of these protuberances, however, are the arched maxillary plates that rise above the open narial passage. These remarkable structures, duplicated only in *Paratoceras*, later gave rise to the even more spectacular single-trunked maxillary horn of the Synthetoceratinae.

Because of the exhaustive morphological descriptions previously given *Protoceras* by

Marsh (1891), Osborn and Wortman (1892), and Scott (1895, 1940), we include only the briefest description in the present report. Instead, we have limited systematic treatment of *Protoceras* to the discussion of generic and specific synonymy and the concomitant revised taxonomic diagnoses.

In 1894 Marsh (1894a, p. 94) in describing a new genus, *Calops*, gave only the following description: "In its general form and in most of its characters, this skull agrees so closely with the type of *Protoceras* as to suggest at once some affinity between the two. The dentition . . . is essentially the same. The high maxillary plates joining the sharp, pointed nasals; the deep lacrimal fossa; and the posterior orbit strongly closed behind, all suggest an ally of *Protoceras*, but the parietal ridges are here elevated into distinct crests, and are without horns." In a later paper, Marsh (1894b, p. 273) made some additional observations on the brain, dentition, and lower jaws of *Calops*, but made no effort to distinguish the features from those of *Protoceras*. In his final treatment of the protoceratids, Scott (1940, pp. 565-566) attempted to differentiate the hornless skull of *Calops* from that of female *Protoceras*: "[1] In the type-specimen of *P. celer* Marsh, the two parietal crests support a pair of very small, conical horn-like protuberances and this is the only skull of the kind that has yet been found, though many unquestionably female skulls are in the various collections. Presumably, the presence of these 'horns' was due to individual variation, though it may have been a specific distinction. In the two known skulls and *Calops* there is no trace of such prominencies. (2) In *Calops* the cranium is much more elevated, making the upper profile of the skull rise steeply from the nasals back to the vertex, from which point it declines very slightly to the summit of the inion. In consequence, the basi-cranial axis, with the occipital condyles, is much higher above the level of the teeth. Most skulls of *Protoceras* have suffered more or less deformation from down-crushing, which exaggerates this difference between the two genera. (3) In *Calops* the supraorbital foramina are minute, or absent, and the frontals are not grooved, whereas, in *Protoceras*, these foramina are conspicuous and deep vascular grooves lead forward from them. (4) The angle of mandible is more convex in *Calops* and extends somewhat farther behind the plane of the condyle. (5) The

individuals of *Calops* are decidedly smaller than any known species of *Protoceras*."

In contrast to the opinions of Scott and others, we contend that the genus *Calops* represents merely the female aspect of the earlier described *Protoceras* and that those characters used to differentiate the two taxa are actually manifestations of genetic continuity, i.e. sexual dimorphism, rather than genetic distinctions; (1) Scott's first point that, "though many unquestionably female skulls are in the various collections" the presence of the parietal horns is possibly "due to individual variation" is very odd in view of the fact that only two pages later (*op. cit.*, p. 567) he accepts Osborn and Wortman's (1892) demonstration of sexual dimorphism in the horns of the *Protoceras* skull. We contend, therefore, that the lack of parietal horns would be expected if the skulls assigned to *Calops* were considered to be those of females. (2) Scott himself provides part of the argument against his second point when he mentions the exaggerated differences in the level of the basi-cranial axis between the two genera brought about by deformation due to crushing. In uncrushed skulls of *Protoceras* (F:AM 40878, male; AMNH 1229, female) no such differences in profile are apparent. (3) The differences in development of vascular grooves leading from the supraorbital foramina are more apparent than real, as comparisons between crushed and uncrushed skulls reveal. (4) The presumed differences in the angle of the mandible between the two genera, even as Scott described them, are so slight as to be taxonomically meaningless. Moreover, they do not prevail in the additional complete specimen (F:AM 53521) found since Scott's statement. (5) Additional female *Protoceras* specimens (F:AM 40870; AMNH 1229) show that if all the skulls assigned to the female *Protoceras* and those assigned to *Calops* were grouped together, no significant difference in size (or morphology) would be detectable among them. The difference in size between "*Calops*" and *Protoceras* that Scott attributes to taxonomic divergence, we believe more properly reflects sexual dimorphism.

As recognized in the present report, *Protoceras* includes only three species: the type species, *P. celer*, a new species, *P. skinneri*, from the early Arikareean of South Dakota and Nebraska, and *P. neatodelpha*, new species, from the late Arikareean of Wyoming. We have placed the

genus *Calops* in synonymy with *Protoceras*; the long-standing species *C. cristatus*, *C. consors*, *P. nasutus*, and *P. comptus* we have put in specific synonymy with *P. celer*. Justification for this arrangement is included under the discussion of *P. celer*.

Protoceras celer Marsh, 1891

Figure 3; tables 1, 2

Protoceras celer MARSH, 1891, p. 81.

Protoceras comptus MARSH, 1894a, p. 93.

Calops cristatus MARSH, 1894a, p. 94.

Protoceras nasutus MARSH, 1897, p. 168.

Calops consors MARSH, 1897, p. 175.

TYPE: YPM 11078, partial female skull, with premaxilla missing and P²-M³(br.). The type was collected by J. B. Hatcher in 1894 from the *Protoceras* Beds, White River, South Dakota.

DISTRIBUTION: Late Whitneyan of South Dakota.

SELECTED REFERRED MATERIAL¹: *Protoceras* channels, Poleslide Member of the Brule Formation, head of Big Corral Draw, northeast of Indian Stronghold on the northeast side of Cuny Table, formerly Washington County, combined (1943) with Shannon County, South Dakota: YPM 11896, female skull, type of *Protoceras comptus*; YPM 11886, female skull, type of *Calops cristatus*; YPM 10161, fragment of left side of skull with maxillary protuberance, type of *Protoceras nasutus*; YPM 11885, female skull, type of *Calops consors*; YPM 10168, male skull; PU 10655, female skull and jaw; SDSM 2814, male skull; AMNH 1222, female skull and jaws; AMNH 584, female immature partial skull; AMNH 640, male posterior part of skull; AMNH 641, female partial skull; AMNH 643, male skull (figured by Osborn and Wortman, 1892, figs. 1, 2, 4; Scott, 1895, pl. 20); AMNH 645, female skull; AMNH 1220, female skull, jaws, and humeri; AMNH 1223, male skull; AMNH 1224, female skull; AMNH 1227, skull fragments and skeletal elements; AMNH 1228, male skull; AMNH 1229, female skull; AMNH 1230, male skull; AMNH 1232, female skull; AMNH 1236, female skull and skeleton; F:AM 53521, male skull, jaws, and articulated

¹In the case of specimens from other institutions, precise field data are lacking. It can only be assumed (see p. 354) that these specimens came from the above locality where the F:AM specimens were collected because this is the primary set of outcrops worked by the early collectors (M. F. Skinner, personal commun.).

skeleton; F:AM 53522, male partial skull; F:AM 53523, male skull; F:AM 53524, male partial skull; F:AM 53525, male partial skull; F:AM 53526, female partial skull, jaws, and partial skeleton; F:AM 53527, female partial skull and jaws; F:AM 53530, female posterior part of skull; F:AM 53531, male posterior part of skull; F:AM 53532, male partial cranium; F:AM 53533, male partial cranium; F:AM 53535, anterior part of skull; F:AM 53528, immature partial skull; F:AM 53529, immature partial skull; F:AM 53555–53557, three maxillae; F:AM 53536–53538, three mandibles; F:AM 53539–53549, 11 right mandibular rami; F:AM 53550–53552, three left mandibular rami; F:AM 53554, left ramus; F:AM 53558–53563, six immature rami; F:AM 53564–53565, two immature partial maxillae.

Protoceras channel, Poleslide Member of the Brule Formation, 1 mile west of Cedar Pass, Jackson County, South Dakota: F:AM 53566, partial cranium with broken parietal horns.

REVISED DIAGNOSIS: *Protoceras celer* averages about 20 percent smaller than *P. neatodelpha* and about 10 percent smaller than *P. skinneri*; P^2 differs from that of *P. skinneri* and *P. neatodelpha* in having a strong lingual cingulum and protocone, and from *P. neatodelpha* in having larger premolars relative to the size of the molars; P^3 metastyle smaller than that of *P. skinneri*; molars shorter crowned than in *P. neatodelpha*; mandible differs from that of *P. skinneri* in having a shorter P_1 – P_2 diastema and a shallower horizontal ramus below the molars.

DISCUSSION: Curiously, all the described species of the genera *Protoceras* and *Calops* were those erected originally by Marsh more than 75 years ago. This unusual circumstance probably reflects not only the relatively poor preservation of these taxa but also the remarkable morphological uniformity among the specimens variously assigned to them.

Marsh (1891, p. 82) initially described *Protoceras* from a single relatively well-preserved skull "from the upper part of the Oreodon beds of the Miocene" of South Dakota. The next year, Osborn and Wortman (1892) expanded the description of *Protoceras*, redefined the genus and family, and recognized the presence of sexual dimorphism in the characters of the *Protoceras* skull. Additional specimens available to them demonstrated that Marsh's type specimen was actually that of a female and, further,

allowed them to characterize the male *Protoceras* skull. In addition to the parietal protuberances originally described by Marsh on the female skull, the male skull described by Osborn and Wortman was shown to possess a second pair on the frontals and a third pair arising from the maxillaries. The male skull also differed from that of the female in having longer, more pronounced canine tusks. In 1894 Marsh described a new *Protoceras* species, *P. comptus*, from the same horizon in which *P. celer* was recovered. The skull, apparently that of a young female, was considered to differ from the type in its more elongate proportions and in the fact that the maxillary plates were not elevated and the posterior nares extended forward to between the first true molars. In the same paper, he described a new genus and species of protoceratid, *Calops cristatus*, also from the same horizon. Marsh (1894a, p. 94) believed the distinguishing feature of the new genus to be the parietal ridges which "are elevated into distinct crests, and are without horns." In a still later article, Marsh (1897) erected two new protoceratid species, *Protoceras nasutus* and *Calops consors*, again from the same horizon as *P. celer*. Marsh (p. 168) distinguished *P. nasutus* from the type species solely on the basis of the difference in cross sectional shape of the maxillary protuberances. He separated *Calops consors* from *C. cristatus* by emphasizing the more anterior placement of the orbit in the former species. By 1897 Marsh had described all the species of *Protoceras* (and *Calops*). He speculated little on the relationships of his two genera, either between each other or with other artiodactyl taxa. Through Osborn and Wortman's (1892) efforts, he was aware of the sexual dimorphism in the skull of *Protoceras* and he further (1897, p. 176) recognized the female gender of *Calops*: "The remains of *Calops* now known all appear to have pertained to females, and this naturally suggests the question—what the male skull was like, and especially whether it was provided with horns. The probabilities at present are in favor of the latter view, but it must be left to future discoveries to settle that point." Apparently Marsh never seriously considered the possibility that *Calops* could in reality be a female *Protoceras*; or that one of his *Protoceras* species (namely, *P. comptus*) might be a female counterpart to known *Protoceras* males. In the present report we attempt to demonstrate the likeliness of that possibility.

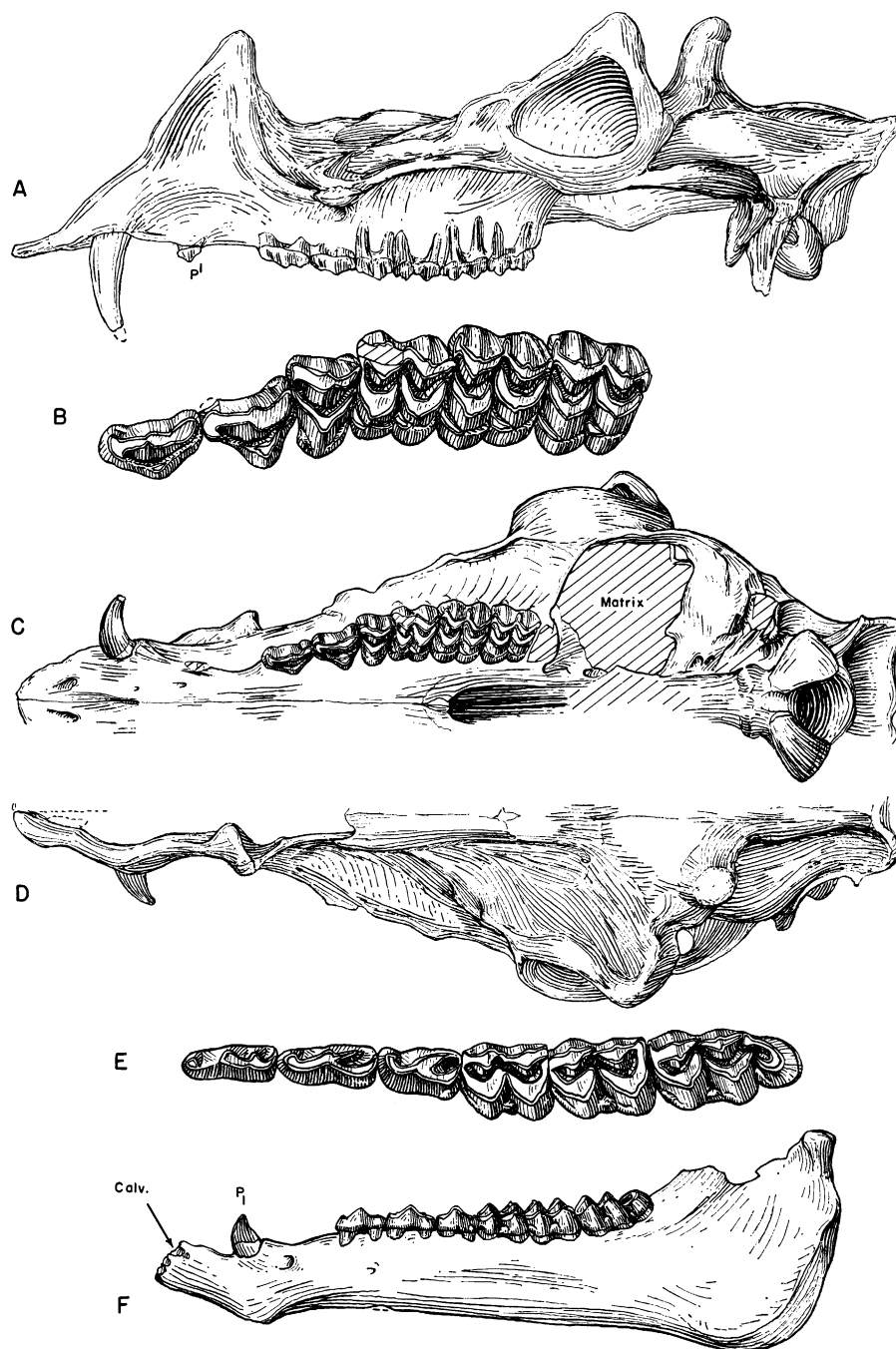


FIG. 3. *Protoceras celer*, referred, F: AM 53521, from basal *Protoceras* channel, northeast of Indian Stronghold, Shannon County, South Dakota. A. Lateral view. $\times \frac{1}{2}$. B. Occlusal view. $\times 1$. C. Palatal view. $\times \frac{1}{2}$. D. Dorsal view. $\times \frac{1}{2}$. E. Occlusal view. $\times 1$. F. Lateral view. $\times \frac{1}{2}$.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE UPPER DENTITION OF *Protoceras celer* FROM THE POESLIDE MEMBER OF THE BRULE FORMATION, SOUTH DAKOTA

	N	OR	\bar{X}	S	V
C					
Length	7	3.0- 9.5	6.79	3.041	44.82
Width	6	2.6- 5.3	3.88	1.061	27.32
P ¹					
Length	8	5.1- 7.6	5.96	0.933	15.62
Width	6	2.4- 2.8	2.57	0.137	5.32
P ²					
Length	11	11.0-13.8	12.84	0.919	7.16
Width	10	5.1- 7.5	6.18	0.850	13.75
P ³					
Length	16	11.1-14.4	12.86	0.883	6.87
Width	15	7.5-10.5	8.71	1.047	12.01
P ⁴					
Length	17	8.5-11.0	9.75	0.650	6.67
Width	15	10.0-12.8	11.69	0.770	6.59
M ¹					
Length	17	11.0-14.5	12.64	0.859	6.80
Width	16	12.0-15.3	13.93	0.827	5.93
M ²					
Length	17	11.8-15.4	13.82	0.960	6.95
Width	16	13.8-17.0	15.88	0.844	5.31
M ³					
Length	11	12.6-15.5	13.73	0.642	4.67
Width	16	13.3-17.5	15.99	1.014	6.35
P ² -P ⁴	11	31.0-36.0	34.18	1.647	4.82
M ¹ -M ³	17	35.0-42.7	38.74	2.368	6.11
P ² -M ³	11	67.5-74.5	71.41	2.700	3.78

We have provided above our reasoning for synonymizing *Calops* with *Protoceras*. At the specific level, then, we are left with five species: *P. celer*, *P. comptus*, *P. nasutus*, *P. cristatus*, and *P. consors*. Of these five species, the types of three (*P. comptus*, *P. cristatus*, and *P. consors*) are female skulls.

Calops (= *Protoceras*) *cristatus* was distinguished from *P. celer* exclusively on its lacking parietal horns as merely a dimorphic trait; the type is otherwise inseparable from the female *P. celer*. *Calops consors* was considered distinct from *C. cristatus* on the basis of the orbit being more anterior in the former, a taxonomically unimportant feature reflecting the youth of the type specimen, in which no anterior movement of the cheek dentition has yet taken place. The remaining type of *P. comptus*, a female skull, is inseparable from other *Protoceras* females; the

lack of elevated maxillary plates is typical of that gender; the other presumed distinguishing characters are demonstrably either a result of postmortem distortion or so slight as to be diagnostically meaningless. Thus, all the female *Protoceras* and *Calops* specimens and the taxa derived therefrom are inseparable from those assigned to *P. celer* and are, we believe, most properly synonymized with that species.

Other than *P. celer*, the only other *Protoceras* species based on a male skull is *P. nasutus*. Marsh's (1897, p. 168) complete original description of *P. nasutus* briefly stated that, "In a new species, *Protoceras nasutus*, the summits of the maxillary horn-cores are oval in section, as shown in cut 5." Marsh regarded this feature to be specifically distinct from the more triangular summits of the *P. celer* plates. Our examination of both types and additional specimens collected subsequently revealed no consistent distinctness in this character. At the summit of the maxillary plates of these specimens, all the cross

TABLE 2

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE LOWER DENTITION OF *Protoceras celer* FROM THE POESLIDE MEMBER OF THE BRULE FORMATION, SOUTH DAKOTA

	N	OR	\bar{X}	S	V
P ₁					
Length	7	3.9- 7.2	4.99	1.102	22.11
Width	4	2.3- 2.6	2.43	0.150	6.19
P ₂					
Length	8	9.5-14.5	12.24	1.417	11.58
Width	6	3.6- 4.3	3.90	0.245	6.28
P ₃					
Length	11	11.6-15.3	13.32	0.939	7.05
Width	9	4.0- 6.5	4.93	0.778	15.79
P ₄					
Length	14	10.0-13.3	11.69	0.819	7.01
Width	12	6.0- 7.1	6.60	0.354	5.37
M ₁					
Length	16	11.0-14.0	12.36	0.667	5.40
Width	14	8.9-11.5	9.71	0.640	6.58
M ₂					
Length	16	11.0-14.2	13.32	0.941	7.06
Width	14	9.6-12.0	10.62	0.665	6.26
M ₃					
Length	15	16.0-20.3	18.94	1.140	6.02
Width	12	9.9-11.1	10.48	0.391	3.73
P ₂ -P ₄	8	31.0-43.0	37.61	3.365	8.95
M ₁ -M ₃	14	38.5-48.4	47.48	11.865	24.99
P ₂ -M ₃	7	70.0-83.5	81.07	4.903	6.05

sections are oval, whereas a couple of centimeters below this, all become triangular. The little morphological variation observed in this character can doubtless be attributed to individual variation. An interesting feature long associated with *P. nasutus* but not mentioned by Marsh is the presumed sutural contact between the bases of the two maxillary plates. The first description of this widely accepted character apparently appeared in Scott's monograph on the fauna of the White River Oligocene (1940, p. 577). Despite Scott's remarks, the type specimen of *P. nasutus* (YPM 10161) possesses no such contact nor is there any evidence of the former presence of one. The inner margins of the maxillary plates do extend partly over the nasal canal and in crushed specimens probably do become closely appressed, but in the actual type and in other specimens (F:AM 40878 and 53521) morphologically almost inseparable from the type, no sutural union of the two plates is indicated. Although we agree with Scott (*op. cit.*) that such a union provided the basis for the evolution of the rostral horn in the subfamily Synthetoceratinae (Patton and Taylor, 1971, p. 211), we cannot find any evidence that the transition occurred among any of the known *Protoceras* species. Thus, we have synonymized *P. nasutus* with *P. celer*, the latter now being the sole valid species recognized in the Poleslide Member of the Brule Formation (Whitneyan) of South Dakota.

***Protoceras skinneri*, new species**

Figure 4; table 3

TYPE: F:AM 40247, crushed and incomplete left side of a female skull from P² to broken condyles with P²-M¹ and detached left M³; associated detached teeth including right P⁴, broken M¹ and M², M³ and left P², P⁴, M¹ broken, M², M³ broken, and fragments. The type was collected by Morris F. Skinner and Robert J. Emry from the Harris Ranch, just west of the Pine Ridge Reservation, southeast corner of Fall River County, South Dakota. It occurred 4 feet above a blue ash in a channel that cuts into the Brule Formation and is probably temporally equivalent to the upper part of the Sharps Formation or some part of the Gering Formation.

ETYMOLOGY: Named in honor of our esteemed colleague Morris F. Skinner.

DISTRIBUTION: Deposits equivalent in age to the upper part of the Sharps Formation or some part of the Gering Formation (early Arikareean) in Fall River County, South Dakota and Banner County, Nebraska.

REFERRED MATERIAL: F:AM 40248, right mandible with I₁-C alveoli, P₁-M₃ (P₂ alveolus and P₃ broken) and proximal half of humerus collected by C. H. Falkenbach who said (personal commun.) that it was obtained from 10 feet below the white layer, Horse Creek area, Banner County, Nebraska. Deposits in the Horse Creek area, where F:AM 40248 was collected, were considered to be temporally equivalent to the Gering Formation by Schultz and Falkenbach (1954, pp. 199-201).

DIAGNOSIS: Twenty percent larger than largest female of *P. celer*; P² differs from that of *P. celer* in lacking a strong lingual cingulum and protocone, and from *P. neatodelpha* in being larger relative to size of molars; P³ has a more pronounced and recurved metastyle than that of *P. celer* and *P. neatodelpha*; molars shorter crowned than those of *P. neatodelpha*.

DESCRIPTION

SKULL: Because the type specimen is that of a female, the cranial armament of this species is unknown. Preservation of the upper border of the orbit, however, serves to illustrate the smooth even border of this structure that is typical of female *Protoceras*. Because of the crushed condition of the type, it is difficult to reconstruct the partial skull, but it is evident that the orbit as figured (fig. 4) is situated both higher and more posteriorly relative to the molars than it was in life. The specimen also reveals the presence of a well-developed but unhorned parietal crest leading from the posterior border of the orbit to the prominent sagittal crest. The skull and dentition of *P. skinneri* are approximately 20 percent larger than that of the largest female specimen of *P. celer*.

Posteriorly, a conspicuous complex fossa is rimmed by a thickened lambdoidal crest. A temporal crest arises from the posterolateral edge of the lambdoidal crest and extends onto the long and produced paroccipital process. The two above-mentioned crests enclose the condyloid fossa, a very prominent feature common to all protoceratids. Situated between the paroccipital process and the postglenoid process is the small platelike auditory bulla. As in all

protoceratids, the dorsoposterior border of the external auditory meatus is walled by the squamosal. The zygomatic process of the squamosal supports a wide and gently curved glenoid fossa, the posterior edge of which is rimmed by a large and expanded postglenoid process. The ventral border of the jugal is expanded and sculptured for attachment of a large masseter muscle. Although the maxillary is badly crushed, it indicates the presence of the more lightly constructed masseteric ridge common to female protoceratids. The infraorbital foramen occurs above the level of the anterior edge of P⁴.

UPPER DENTITION: The incisive and caniniform dentition is lacking in the type of *P. skinneri*, but is presumed to be essentially like that of *P. celer*. P² is only partially erupted and is obscured posteriorly by a broken supernumerary premolar or an unshed dP², an anomalous retention (judged by wear on the molars) for an otherwise fully adult individual. P² of *P. skinneri* is similar to that of *P. celer* in having minor

cusps on either side of the parastyle, but differs from the latter in lacking a strong lingual cingulum and protocone. Although the lingual cingulum and protocone are variably developed in *P. celer*, they are generally larger than those of *P. skinneri*. As in all Protoceratinae, P² and P³ are elongate and possess a high paracone; also, P³ is wider than P² owing to the usual development of a protoconal cusp on the lingual cingulum. In *P. celer* this cusp is strongly developed; it is more weakly expressed in *P. skinneri*. P³ of *P. skinneri* also contrasts with that of *P. celer* in having a more pronounced and re-curved metastyle. Only in one *P. celer* female (YPM 11885) does P³ metastyle approach that of *P. skinneri*. In *Syndyoceras cooki*, P³ is more anteroposteriorly reduced and lacks a strong metastyle; in *Paratoceras wardi* there is similar foreshortening and an even smaller metastyle. P⁴ of *P. skinneri* closely resembles that of *P. celer* in morphology, differing only in its larger size relative to the molars. Very little difference is noted between the molars of *P. skinneri* and those of *P. celer*, except in the lesser development of lingual ingula of the latter species.

MANDIBLE: In general proportions the mandible of *P. skinneri* agrees closely with that of *P. celer*. In addition to its larger size, however, the *P. skinneri* mandible differs from that of *P. celer* in having a relatively longer P₁-P₂ diastema and a deeper horizontal ramus below the molars. Both species have a vertically slender diastema and a conspicuous symphyseal hook below P₁.

LOWER DENTITION: Unfortunately, much of the anterior dentition is missing in the sole *P. skinneri* mandibular ramus available. The incisive dentition is represented by four alveoli, indicating the presence of I₁₋₃ and an incisiform canine. A short (1 cm.) diastema separates /C alveolus from P₁. P₁ is caniniform and functional, exhibiting an abraded surface anteriorly; it is separated by a rather long, sharp diastema from P₂. The alveolus for P₂ indicates an elongate premolar and P₃ is a two-rooted elongate tooth similar to that of *P. celer*. P₄, in contrast, is more reduced and foreshortened than that of *P. celer*, resembling to some extent the proportions of P₄ in *Paratoceras* and the synthetoceratines. However, unlike *Paratoceras*, the *P. skinneri* P₄ has a more lingually flexed paraconid.

The molars of *P. skinneri* are badly worn, but except for their larger size, generally resemble those of *P. celer*. As in *P. celer*, accessory tubercles

TABLE 3

MEASUREMENTS (IN MILLIMETERS) OF THE UPPER AND LOWER TEETH OF *Protoceras skinneri*, NEW SPECIES, AND *Protoceras neatodelpha*, NEW SPECIES

	F:AM 40247 ^a			F:AM 40248			F:AM 40881 ^b	
	L	W		L	W		L	W
P ²	13.8	× 6.5	—	—	—	—	11.5	× 4.7
P ³	13.5	× 9.1	—	—	—	—	12.6	× (6.5) ^c
P ⁴	10.5	× 12.8	—	—	—	—	9.0	× 11.4
M ¹	13.5	× 14.5	—	—	—	—	14.0	× 15.5
M ²	(15.5+) ×	16.7	—	—	—	—	16.2	× 16.8
M ³	—	—	—	—	—	—	15.0	× 16.5
P ² -P ⁴	39.5	× —	—	—	—	—	34.6	× —
M ¹ -M ³	(44.0)	× —	—	—	—	—	42.9	× —
P ₁	—	—	6.2	× —	—	—	—	—
P ₂	—	—	—	—	—	—	—	—
P ₃	13.4	× 5.1	—	—	—	—	—	—
P ₄	12.5	× 7.0	(12.5)	× 7.0	—	—	—	—
M ₁	—	—	(12.0+)	× —	—	—	—	—
M ₂	(14.0)	× —	(14.5+)	× —	—	—	—	—
M ₃	21.0	× 11.0	20.5	× —	—	—	—	—
M ₁ -M ₃	(48.0)	× —	46.5	× —	—	—	—	—
P ₂ -M ₃	—	—	(84.0)	× —	—	—	—	—

^aType of *Protoceras skinneri*, new species.

^bType of *Protoceras neatodelpha*, new species, from Wyoming.

^cMeasurements enclosed in parentheses are approximate.

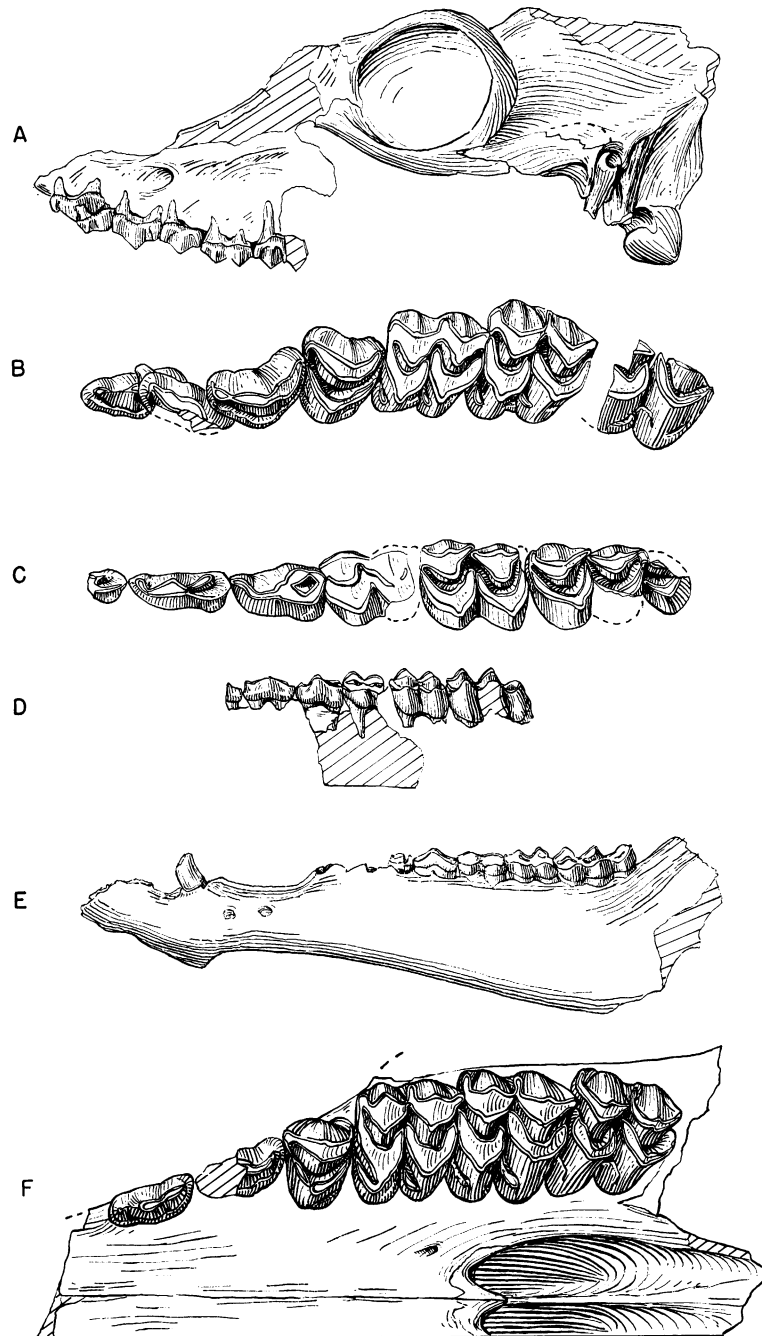


FIG. 4. *Protoceras skinneri*, new species, and *Protoceras neatodelpha*, new species. A-E, *Protoceras skinneri*. A-D. Type, F:AM 40247, crushed partial skull and associated detached teeth. A. Lateral view. $\times \frac{1}{2}$. B. P²-M³, occlusal view. $\times 1$. C. Broken P²-M³, occlusal view. $\times 1$. D. Lateral view. $\times \frac{1}{2}$. E. Right ramus with P₁-M₃ (P₂ alv.), F:AM 40248, lateral view, reversed. $\times \frac{1}{2}$. F. *Protoceras neatodelpha*, type, F:AM 40881, partial skull with P²-M³, occlusal view. $\times \frac{1}{2}$.

appear between the protoconid and hypoconid crescents in each molar.

***Protoceras neatodelpha*, new species**

Figure 4; table 3

TYPE: F:AM 40881, partial skull with P²–M³ from deposits equivalent in age to the Harrison Formation, north of Keeline, Niobrara County, Wyoming.

HYPODIGN: Type specimen only.

ETYMOLOGY: From the Greek *neatos* (youngest) and *adelphē* (sister).

DISTRIBUTION: Late Arikareean deposits, temporally equivalent to the Harrison Formation, Niobrara County, Wyoming.

DIAGNOSIS: Premolars, especially P², smaller relative to the size of the molars than in *P. celer* and *P. skinneri*; P³ with less pronounced metastyle; molars taller crowned than in *P. celer* and *P. skinneri*, with lingual cingulum failing to continue around the protocone and metaconule.

DESCRIPTION

SKULL: The partially preserved type specimen (F:AM 40881) is sufficiently intact to indicate a hornless female *Protoceras*. The parietal crest is weakly developed near the orbit, but becomes more pronounced near its juncture with the sagittal crest. A masseteric ridge is visible above the premolars, and anteromesial to the ridge a relatively large preorbital fossa is indicated. Unfortunately, no other feature is preserved adequately enough to warrant description.

UPPER DENTITION: Although none of the anterior upper dentition of *P. neatodelpha* is preserved, it is assumed to be like that of other *Protoceras* species. The entire cheek dentition, P²–M³, however, is available for description. The most noteworthy aspect of the premolars of *P. neatodelpha* is their reduction relative to the size of the molars. Whereas the molars are roughly the size of the large *P. skinneri*, the premolars are no larger than those of *P. celer*; in fact P² and P³ of some specimens of *P. celer* are larger than those of *P. neatodelpha*. P² of *P. neatodelpha* is especially small and has retained only a weak lingual cingulum, in contrast to the more strongly developed cingula of *P. celer* and *P. skinneri*. No trace of a protoconal cusp, like that present in *P. celer*, is visible on *P. neatodelpha*. P³ is only partially preserved in *P. neatodelpha*, but

apparently is not so transversely wide as that of *P. celer* or *P. skinneri*; it also lacks the pronounced metastyle common to those species. Although proportionally smaller, P⁴ is morphologically similar to that of *P. celer* and *P. skinneri*.

The upper molars of *P. neatodelpha* are typically protoceratid in the development of strong styles and accessory cusps. They differ from *P. celer* and *P. skinneri*, however, in being taller crowned and in having differently expressed lingual accessory cusps. In *P. celer* these cusps join around the entire protocone and metacone crescents; in *P. skinneri* they are present on both the anterior and posterior walls of the protocone and metacone; in *P. neatodelpha* they are apparently restricted to the anterior walls of those cusps.

GENUS *PARATOCERAS* FRICK, 1937

Paratoceras Frick, 1937, p. 608.

TYPE SPECIES: *Paratoceras macadamsi* Frick, 1937.

INCLUDED SPECIES: Type species, *Paratoceras wardi*, new species, and an undescribed species from Panama noted on page 368.

KNOWN DISTRIBUTION: Hemingfordian of Panama, early Barstovian of the Texas Coastal Plain and the Clarendonian of the Texas Panhandle.

DIAGNOSIS: Differs from other genera of the subfamily in having smaller, more posteriorly situated pointed maxillary protuberances in the male, with the rims of the maxillary plates thicker than in *Protoceras*; longer and gently recurved supraorbital horns, widely flared at the base and tapering to a bulbous tip in the male, roughly similar to those of the Synthetoceratinae; no parietal protuberances; a transversely forked occipital horn in the male; extremely weak parietal ridges and a faint sagittal crest; a probable loss of one lateral incisiform tooth (?I₃ or /C); a more forwardly placed P¹ with the diastemata shorter between C and P¹ and longer between P¹ and P² than in *Protoceras*; a more robust P²⁻³ with P³ lacking a prominent protocone; a posteriorly wider and more wedge-shaped P₄, similar in shape to that of the synthetoceratines; taller-crowned molars; and a less broadly expanded masseteric region of the mandibular ramus.

Limbs of *Paratoceras* differ from those of *Protoceras* in having a proportionally more slender ulna that is fused for most of its length

with the radius; relatively smaller scaphoid facet on the radius and a transversely wider but anteroposteriorly shorter lunar facet; relatively smaller fibular groove on the distal end of the tibia; relatively narrower sustentacular facet on both the astragalus and the calcaneum; weaker and less posteriorly projecting calcaneal sustentacular process and a smaller navicular facet for the entocuneiform. The smaller facet for the entocuneiform would seemingly indicate that this tarsal may be more reduced in *Paratoceras*, which in turn, suggests that metatarsal II, articulating with the entocuneiform, may also be more reduced than in *Protoceras*. Reduction of the vestigial digits in the pes of *Paratoceras* is further indicated by a shallower depression on the proximal part of metatarsals III and IV for digits II and V.

DISCUSSION: The genus *Paratoceras* was erected by Frick (1937, p. 608) on the basis of a mandibular ramus recovered from the MacAdams Ranch Quarry near Clarendon, Donley County, Texas. The type specimen (F:AM 32457) is a partial right ramus containing P_2 – M_3 but missing both the ascending ramus and the symphyseal region anterior to P_2 .

Frick's (1937, p. 608) entire description consisted of the following: "The genus is based on a mandibular ramus which evidently belonged to a somewhat smaller form, and one with a quite different dentition, from *Synthetoceras*. The closeness of the p_2 to the posterior border of the symphysis, the extreme compression of the premolars, the anteroposterior elongation of p_3 relative to p_4 and the low molar crowns at once recall the White River genus *Protoceras*. The p_2 – m_3 distance actually but slightly exceeds that of a large individual of the latter." Elsewhere, Frick (p. 596) made the following comparison: "It is of smaller size . . . and differs markedly from *Synthetoceras* in the large and non-reduced premolars and low-crowned molars, in these characters more resembling *Protoceras* of the White River."

Fortunately, the distinctly large lower premolars of *Paratoceras* have proved sufficiently diagnostic to allow easy separation of this genus from other protoceratids, at least when dealing with lower jaws. Nothing else was known of the genus, and it was presumed that its other characters resembled those of its contemporary and almost contemporary relatives, *Synthetoceras* and *Prosynthetoceras*. Since Frick's description,

however, excellent well-preserved material belonging to *Paratoceras* was recovered by N. Z. Ward of the former Frick Laboratory of the American Museum of Natural History from the Trinity River Quarry in San Jacinto County, Texas. These specimens include a remarkable skull, preserved almost completely intact, demonstrating a peculiarity of cranial armament for *Paratoceras* equally as bizarre as that of the synthetoceratines.

This and other new specimens allow us to present a description and revised diagnosis of the genus *Paratoceras* and a discussion of its relationship with other members of the Protoceratinae.

The genus presently contains two species, the type species, *P. macadamsi*, from the Clarendon beds of the Texas Panhandle (Clarendonian) and *P. wardi*, new species, from the late Miocene (Barstovian) of the Texas Coastal Plain. A third and apparently specifically distinct form from the middle Miocene Cucaracha Formation of the Panama Canal Zone will be described by Frank Whitmore (United States Geological Survey) in a forthcoming publication.

***Paratoceras wardi*, new species**

Figures 5–12 (14 in part); tables 4–6

TYPE: F:AM 40249, an almost complete skull with left orbital horn, occipital horn and C(alv.)– M^3 . The type is from Trinity River Pit 1, 7 miles northeast of Cold Spring (latitude $30^{\circ}40'15''N$, longitude $95^{\circ}03'10''W$), San Jacinto County, Texas. The quarry is situated on the south bank of the Trinity River, about 1000 feet downstream from the mouth of Prayer Creek, directly below a high point or bluff known locally as Pine Island Hill. Trinity River Pit 1 is in the upper part of the Fleming Formation and lithologically 225 to 300 feet below the lithic zone from which the published Cold Spring Fauna of Wilson (1956) was derived, according to the unpublished stratigraphic data of M. F. Skinner on file in the American Museum of Natural History; see discussion on page 356.

ETYMOLOGY: Named in honor of N. Z. Ward, who collected the type and most of the referred material.

DISTRIBUTION: From the upper part of the Fleming Formation (early Barstovian) in San Jacinto and Walker counties, Texas.

REFERRED MATERIAL: Trinity River Pit 1, upper part of the Fleming Formation, San Jacinto County, Texas: F:AM 40250, left maxilla with P^2 alveolus- M^3 ; F:AM 40251, right partial maxilla with P^4 - M^3 ; F:AM 40252, left immature maxilla with C- P^1 erupting and dP^2 - M^3 (broken germ); F:AM 40253, left partial maxilla with P^3 - M^1 ; F:AM 40254, left detached M^3 germ; F:AM 40255, right detached M^3 ; F:AM 40256, left mandible with P_1 (root)- M_3 ; F:AM 40749, left mandible with P_1 alveolus- M_3 (P_2 - P_3 alveoli); F:AM 40750, right mandible with P_1 - M_3 ; F:AM 40751, right partial mandible with P_1 root and P_2 broken- M_3 ; F:AM 40752-40755, four partial mandibles with P_4 - M_3 ; F:AM 40756, right partial mandible with M_1 - M_3 ; F:AM 40757, right partial mandible with dP_4 broken- M_3 (P_4 germ); F:AM 40758, left mandibular fragment with M_2 ; F:AM 40759, right immature partial mandible with P_1 erupting and dP_2 - dP_4 ; F:AM 40760, right mandibular fragment with M_2 - M_3 ; F:AM 40762-40763, two humeri; F:AM 40764-40765, two partial humeri; F:AM 40766, ulna and radius; F:AM 40767, radius and incomplete ulna; F:AM 40768, partial ulna and radius; F:AM 40769, incomplete metacarpal III; F:AM 40856, associated right partial femur and left tibia; F:AM 40857-40861, five partial femora; F:AM 40862-40864, three partial tibiae; F:AM 40865-40866, two left astragali; F:AM 40867-40868, two left calcanea; F:AM 40869-40870, two right calcanea; F:AM 40871, right navicular; F:AM 40872-40873, two left metatarsals III; F:AM 40874, right metatarsal III; F:AM 40875, right metatarsal IV; F:AM 40876, left partial metatarsal IV; F:AM 40877, proximal phalanx.

From exposures on the road near Gospel Hill, 4 miles south of Riverside, Walker County, Texas: F:AM 40761, right partial mandible with M_1 - M_3 .

DIAGNOSIS: Differs from *P. macadamsi* in having dentition about 25 percent smaller; shorter-crowned dentition; a longer muzzle, especially longer P^1 - P^2 diastema; a stronger lingual cingulum on P^2 ; a shallower horizontal ramus; and a posteriorly narrower and less wedge-shaped P_4 .

DESCRIPTION

HORNS: As is true of all protoceratids, the skull of *Paratoceras* is characterized primarily by

its peculiar cranial armament. In addition to the standard supraorbital horns and a pair of *Protoceras*-like maxillary protuberances, *Paratoceras* possesses a truly remarkable forked horn jutting upward from the occiput. Again, as is true of the whole family, the cranial horn development apparently is restricted to males. Whereas no female skull actually is known of *Paratoceras*, this assumed sexual dimorphism is amply demonstrated by other genera in the family.

The bizarre occipital structure mentioned above arises from the thickened and expanded dorsal border of the occipital bone and the dorsoposterior portion of the parietal bone. Just above its short base the horn forks transversely into two laterally compressed tines, giving the horn the appearance of a slingshot. The anterior edge of each tine is almost straight, whereas the dorsal and posterior edges are more gently curved. Midway along the anterior edge is a rather prominent and roughened linear tuberosity, the function of which is presently uncertain, but which closely resembles a muscle attachment; it probably served for distal attachment of the temporalis muscle, a unique configuration if interpreted accurately. The ventral (lateral) surface of each tine is concave, forming a shallow sulcus that also resembles a surface for muscle attachment; this feature also apparently is associated with the temporalis. The sulcate portion of the ventral surface tapers proximally into a deepened pit at the posterior base of the horn. This pit is separated by a wall of thickened bone from the posterior rim of the large fossa for attachment of the main part of the temporalis muscle, which in *Paratoceras* extends upward onto the base of the horn. As mentioned, other attachments, probably ligamentous, appear on the tines of the horn. Although part of the bone in this region is broken away, a wide but shallow groove apparently leads from the aforementioned pit down the posterolateral surface of the lambdoidal crest into the condyloid fossa.

Foramina for nerve and blood supply to the horn and its covering occur in two main pairs. Anteriorly, two foramina are situated at the base of the fork on either side of the sagittal plane. The posterior pair occur at the base of the inner, or dorsal, surface of the forks. The entire surface of the occipital horn is covered with tiny pits, similar to those on the palate (fig. 5). These tiny

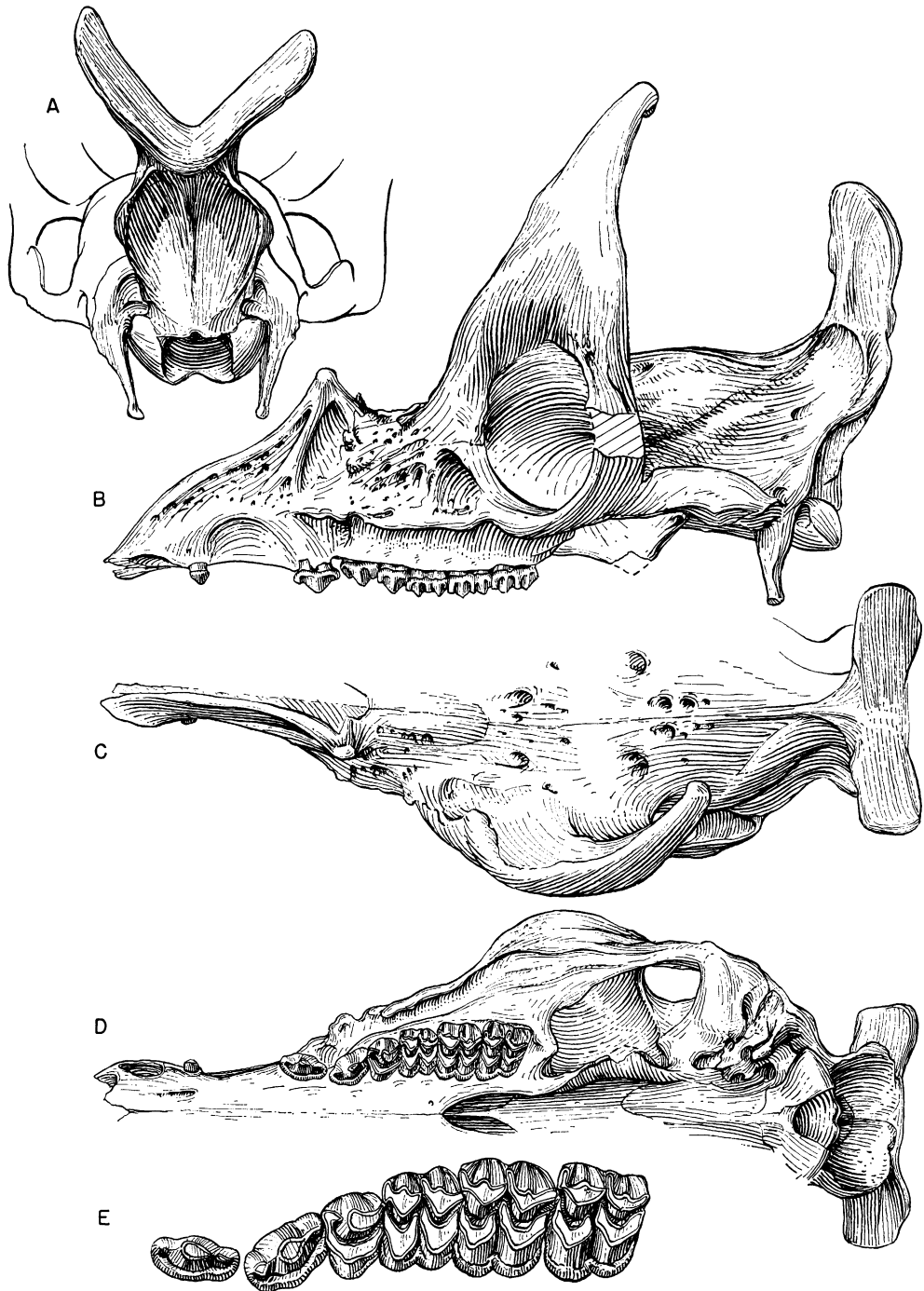


FIG. 5. *Paratoceras wardi*, new species, type, F:AM 40249, from Trinity River Pit 1, San Jacinto County, Texas. A. Posterior view of skull. $\times \frac{1}{2}$. B. Lateral view. $\times \frac{1}{2}$. C. Dorsal view. $\times \frac{1}{2}$. D. Palatal view. $\times \frac{1}{2}$. E. P²-M³, occlusal view. $\times 1$. (See figs. 6-8).

foramina apparently are associated with attachment of the skin covering, much like those occurring on giraffid horns.

The supraorbital horns of *Paratoceras* are roughly similar to those of the Synthetoceratinae (Patton and Taylor, 1971). They are gently recurved, rather widely flared and triangular in cross section at the base, and taper toward a slightly bulbous tip. Also as in the synthetoceratines, the horn surface is longitudinally grooved and sculptured, reflecting for the most part the course of blood vessels beneath the skin covering. The *Paratoceras* supraorbital horn differs from that of the synthetoceratines in that it is relatively shorter, more tapered, and possesses a strongly rugose anterior edge. A sharp medial ridge, which acts as a strengthening strut, divides the dorsal surface into two broad sulci. The geometry and sculpturing of the sulci, in addition to the shape of the anterior rugosity, strongly suggest muscle attachments; we presently believe, however, this possible function to be unlikely. The distal part of the supraorbital horn is much narrower, becoming oval in cross section toward the end. A small recurved knob caps the tip, much as in the synthetoceratines.

The lateral surface of the supraorbital horn is relatively smooth; the longitudinal vascular grooving is very similar to that in the synthetoceratines. Some of these grooves lead into (or from) several nutrient foramina opening on the lateral surface. The only deep sculpturing on the surface of the horn is encountered on the supraorbital process of the frontal bone, which serves as the posterior buttress for the horn. Function of this sculpturing is not yet understood.

The maxillary "horns" or protuberances of *Paratoceras* are remarkably similar but arise more posteriorly than their homologues in *Protoceras*. Retention of this persistent structure is all the more paradoxical in view of the extreme and striking evolutionary changes occurring in the rest of the skull. As in *Protoceras*, the maxillary horns are formed by the arching of the dorsal border of the maxillary bones into two anteroposteriorly flattened plates with a slight lateral flare. In *Paratoceras* the rims of the plates are thickened to a much greater extent than those in *Protoceras*; they are also more pointed at their apexes. Unlike *Protoceras*, the maxillary plates in *Paratoceras wardi* are strengthened by a prominent buttress of thickened bone running

from the base of the maxillary plates to its apex. The flat parts of the maxillary plates between the thickened rims are quite thin with their lateral surface roughened and pocked. In the only maxillary specimen known of the type species, *P. macadamsi*, the buttressing of the maxillary plate is not developed; surface irregularity of the plate is present, but is not so pronounced as in *P. wardi*. There are no foramina in the maxillary plates of the type skull of *P. wardi*; they are, however, present in a maxilla (F:AM 53519) of *P. macadamsi* (p. 393).

SKULL¹: The shape and proportions of the skull of *Paratoceras* are similar to those of other protoceratids, despite the great differences in cranial armament. As in *Prosynthetoceras*, the frontal region is broad and low with a distinctly attenuated face and muzzle. Just anterior to the orbits, the skull tapers rapidly toward the muzzle; it becomes narrowest at the diastema, then flares toward the canines. As in the Synthetoceratinae, the facial (frontal) region of *Paratoceras* is unelevated; in fact, it appears to be depressed slightly below the facio-cranial axis, but some of this may be attributable to post-mortem distortion. Unlike the synthetoceratines, the *Paratoceras* skull is characterized by more forwardly placed orbits and a longer, more expanded cranium. In the synthetoceratines the orbits are situated completely behind the molars, but in *Paratoceras* the anterior rim of the orbit reaches a point above the posterior edge of M². The braincase is larger relative to overall skull size than in any other protoceratid; it is also unique among the protoceratids in the near absence of a sagittal crest. Only at the anterior base of the occipital horn is there a slight development of such a crest. *Paratoceras* also lacks a temporal crest, a structure which is highly developed in the synthetoceratines. Absence of these two cranial crests in *Paratoceras* is very unusual in view of their prominence in other protoceratid genera. Apparently much of their function as muscle attachments has been assumed by the occipital horn (see above). There is, however, a large, flared lambdoidal crest extending ventrally from the posterolateral base of the occipital horn into the condyloid fossa. Behind this crest, the supraoccipital region is scooped into a broad complex fossa similar to,

¹For the purpose of description, the Protoceratinae skulls and jaws will be oriented so that the long axis of the head is in a horizontal position.



FIG. 6. *Paratoceras uardi*, new species, type, F:AM 40249. Lateral view. $\times \frac{3}{4}$. (See figs. 5, 7, and 8.)

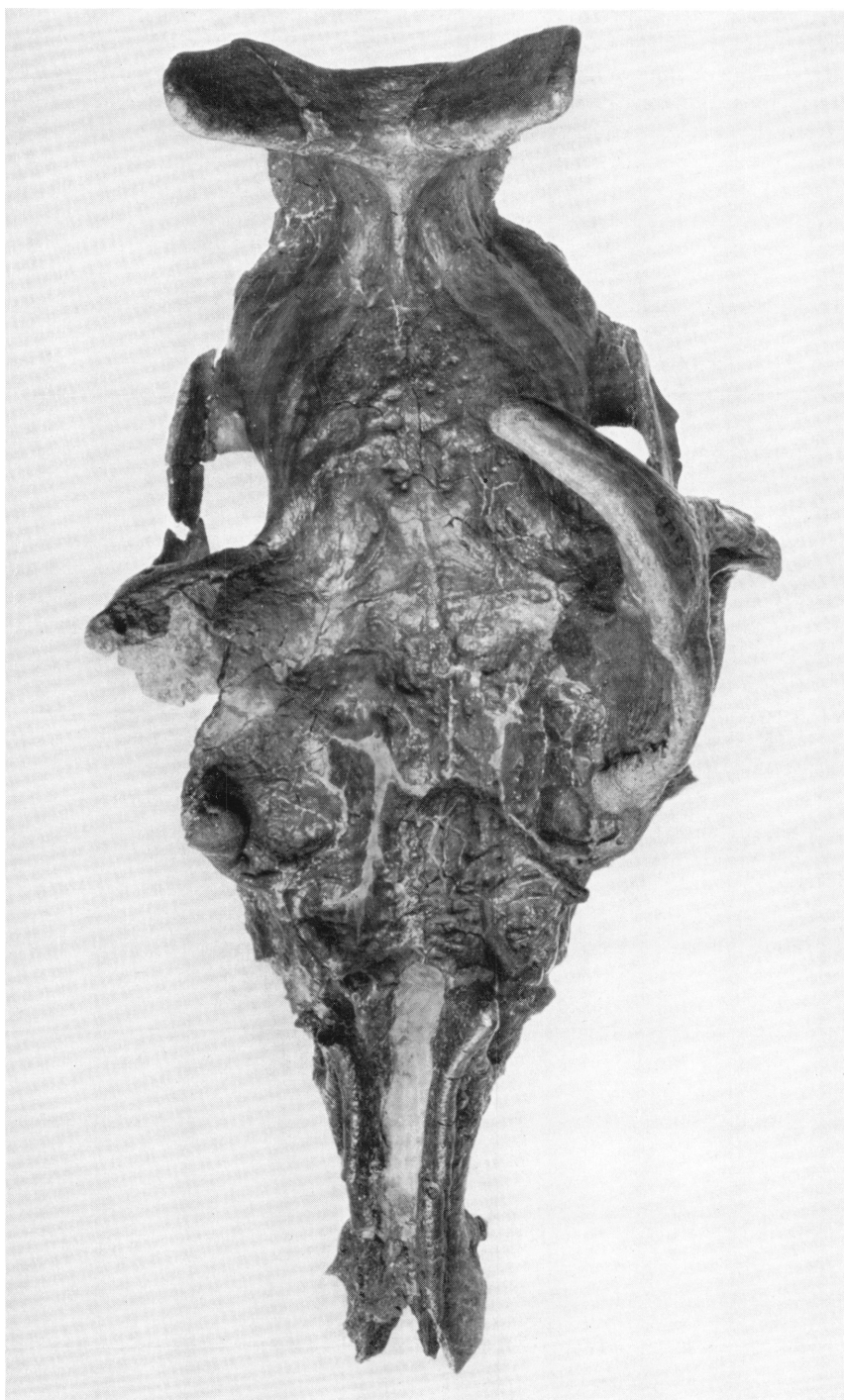


FIG. 7. *Paratoceras wardi*, new species, type, F:AM 40249. Dorsal view. $\times \frac{3}{4}$. (See figs. 5, 6, and 8.)

but not so deep as, that found in the synthetoceratines. The breadth and depth of this structure apparently is directly related to the number and size of horns the neck muscles must support. The upper portion of the fossa is divided by a sharp vertical ridge; the lateral border of the fossa is the lambdoidal crest, which disappears toward the foramen magnum. In contrast to the concave complexus fossa, the surface just above the foramen magnum becomes slightly convex. The foramen magnum itself is of almost rectangular shape; its dorsal border, as in *Protoceras*, is marked by a prominent median notch, the sides of which are thickened into small processes. The intercondyloid incisure is broad and rounded. Like other protoceratids, the occipital condyles are large, project posteriorly, and are inflected slightly mesially. Large occipital condyles are widely separated and placed well under the overhanging supraoccipital. The articular surface of the condyles extends anteriorly onto the basioccipital, as in *Protoceras* and the cervids. Also as in *Protoceras*, the dorsolateral border of the condyles is strongly notched, and just anterior to each notch occurs the large condyloid foramen.

The basioccipital of *Paratoceras* resembles that of *Protoceras* in its shape, in its large size, and in the presence of a shallow groove along its ventral, or basilar, surface. This groove, leading from the intercondyloid incisure, is not always present in *Protoceras* but is sometimes replaced by a faint keel (Scott, 1940, p. 370). The exoccipitals are low, laterally flared, and enclose a deep fossa on each side. Posteriorly the surface of the exoccipital is forward of, and separated from, the external occipital protuberance by the posterolateral edge of the lambdoidal crest. This concave surface, the condyloid fossa, is bordered anterolaterally by the temporal crest and the paroccipital process. Ventrally, the condyloid fossa is marked by a shallow sulcus occurring just above the condyle and extending to the dorsomesial edge of the paroccipital process. This sulcus is probably associated with the attachment for either the lateral atlanto-occipital ligament or the rectus capitus dorsalis muscle. Dorsally the condyloid fossa is perforated by a rather large opening for the condyloid canal. Long, slender, and laterally compressed paroccipital processes are similar to those of *Protoceras*. They do not, however, possess the lateral flare characteristic of the Syntheto-

ceratinae. The lateral edge of the paroccipital process continues into the temporal crest, which joins the lambdoidal crest at the ventrolateral base of the supraoccipital horn. At its root, just behind the auditory meatus, the paroccipital process is roughened for attachment of the digastric and/or sternomastoid muscles. The supraoccipital is high and narrow and thickens at its upper extremity to form the base of the supraoccipital horn. In *Protoceras* the supraoccipital is thickened dorsally and is filled with diploe. A cross section of the *Paratoceras* supraoccipital horn reveals the same diploetic structure.

The braincase of *Paratoceras* is large and bulbous and is roofed almost entirely by the parietals. In several ways the *Paratoceras* braincase differs markedly from that of *Protoceras*. Except for a faint ridge at the base of the supraoccipital horn it lacks a sagittal crest. Further, no trace of a parietal crest or parietal protuberances marks the cranium as in *Protoceras*. The most prominent feature of the parietals is the smooth bands of bone leading from each temporal fossa and converging onto the supraoccipital horn, marking the placement of the large temporalis muscle. As indicated by the distribution of the smooth bone, the posterior part of the muscle extended well up onto the supraoccipital. In fact, ligamentous attachments, apparently for the temporalis, seem to occur on the anterior edges of each tine of the supraoccipital horn, a strange and unusual occurrence indeed if this interpretation is correct. Posterolaterally, the parietals are marked by a large foramen, from which a wide but shallow channel emerges and leads toward the supraoccipital horn. Dorsally, the parietals are unaffected by the temporalis muscle group. Near the midline of the cranium, at the suture with the frontal bones, the parietals are perforated by several pits, the largest of which appears to pierce the skullcap. Just anterior to these, two similarly large perforations occur on the frontals on either side of the midline. These, like other such puzzling skull markings, are not understood by us.

Contact of the parietal with the squamosal is obscured in the type but appears to have been low on the cranium. The contact apparently occurs just above the large, vertically slender foramen (supraglenoid) that stands on the root of the zygomatic process of the squamosal.



FIG. 8. *Paratoceras wardi*, new species, type, F:AM 40249. Ventral view. $\times \frac{3}{4}$. (See figs. 5-7.)

Delineation of the contacts between the parietals, alisphenoids, and orbitosphenoids is mostly obscured by postdepositional fractures in the skull, preventing a reliable comparative description of these elements. The pterygoid (hamular) processes are thin, rather widely flaring, and considerably smaller and less attenuated than those of modern Pecora and Camelidae. Pronounced pterygoid tubercles mark the extreme anterolateral edges of the cranium. As Stirton (1932, p. 148) noted in *Synthetoceras*, these attachments for the pterygoid muscle are apparently more massive than in other artiodactyls. Just inside this structure is the large foramen orbito-rotundum. Above this foramen occur the foramen lacerum anterius and the optic foramen.

The glenoid fossa is wide, slightly convex, and practically unbounded by the kind of rimming flanges in modern deer and camels that apparently allow great freedom of movement for mandibular articulation. At the posteromesial border of the glenoid or mandibular fossa, a

small rim is developed, which in part, protects the postglenoid foramen. Mesially, the rim thickens to a small tuberosity, the postglenoid or retroglenoid process, which serves for attachment of the capsular ligament of the temporomandibular joint and which also prevents posterior dislocation of the mandible.

Between the glenoid cavity and the paroccipital process is a small uninflated, platelike auditory bulla; it is extremely well preserved in the type, and the ventral surface is highly sculptured with various grooves, pits, and flanges. Of these features, the two most prominent flanges occur on the anterolateral border just behind the glenoid fossa and on the posterior border behind the postglenoid foramen.

The most anterior part of the bulla, the styli-form process, which in other artiodactyls with small or medium-sized bullae is generally a slim projection (Whitmore, 1953, p. 133), is a wider and irregularly shaped structure in *Paratoceras*. As in the living cervids, bovids, and some oreodonts, the styli-form process of *Paratoceras*

TABLE 4

SKULL MEASUREMENTS (IN MILLIMETERS) OF *Paratoceras wardi*, NEW SPECIES, AND *Protoceras celer* MARSH (THE MEASUREMENTS ARE ORTHOGONAL PROJECTIONS)

	F:AM 42049 ^a	AMNH 643 ^b	F:AM 53521
Median length			
Foramen magnum to premaxilla border (basilar)	(209) ^c	201.0	203.0
Occipital crest to anterior border of premaxilla (vertex)	(245)	231.0	234.0
Postorbital to anterior premaxilla border (facial)	(153)	162.0	(166)
Postorbital to occipital crest (cranial)	97.5	71.3	(69)
Occipital crest to tip of nasals	(155)	130.6	143.0
Nasofrontal suture to tip of nasals	(35)	28.6	29.0
Anterior border, foramen magnum to posterior of M ³	75.0	(66)	(68)
Anterior border, foramen magnum to anterior border of posterior nares	99.0	85.0	89.0
Anterior border, foramen magnum to anterior of M ¹	114.5	101.0	105.0
Anterior border, foramen magnum to anterior of P ²	149.0	131.5	138.0
Anterior border, foramen magnum to anterior of C	188.0	180.0	182.0
Width			
C to C (width of muzzle)	31.0	(36)	33.0
Postorbital width, widest point of supraorbital process	115.0	102.0	(98)
Cranium, maximum width	60.8	(54.5)	57.0
Height			
Maxillary protuberance, height above alveolar border of maxilla	54.0	64.0	57.0
Frontal horn, height above the superior border of orbit	70.0	12.0	11.5
Parietal horn, height above parietal ridge	—	22.5	19.5
Occipital horn, height above the occipital crest	43.0	—	—

^aType (F:AM 42049) of *Paratoceras wardi*, new species.

^bAMNH 643 and F:AM 53521 *Protoceras celer* Marsh, referred.

^cMeasurements in parentheses are approximate.

forms a portion of the wall of the ostium tympanicum tubae. Again as in living Artiodactyla, the styliform probably also served for attachment of the levator veli muscle (Whitmore, 1953, p. 133). The mesial border of the styliform process is incised by a smooth, round notch, which may have served for reception of the eustachian tube. Also in this region are the foramina for the external and internal carotid vessels. The auditory bulla of *Paratoceras*, as in all protoceratids, fits relatively loosely between the squamosal, basioccipital, and the paroccipital process and forms the ventral wall, or floor, of the external auditory meatus. No attempt has been made to section the auditory bulla, but it is presumably hollow, as in *Protoceras*.

The squamosal of *Paratoceras* plays a smaller role in the formation of the cranial wall than in other Artiodactyla. Its suture with the parietal is not discernible but apparently lies just above the root of the zygomatic process. The part of the zygomatic process of the squamosal leading to the glenoid fossa is wide, thick, and horizontally flattened; from the lateral edge of that fossa to the junction of the postorbital process of the frontal, the zygoma is relatively thin and vertically placed. The external surface of the zygomatic process of the squamosal is pitted and sculptured, indicating strong attachment for the deep masseter muscle. Below the orbit, the jugal is very widely expanded; its ventral surface is longitudinally grooved, whereas its anterolateral surface is pitted and roughened into a crest which extends into the facial, or masseteric, crest. Both of these features again indicate the presence of a strongly developed masseter muscle. As in *Protoceras* and the synthetoceratines, the orbit, which is completely encircled in bone, is rimmed posteriorly more by the postorbital process of the frontal than by the jugal. This contrasts sharply with other Artiodactyla, in which the postorbital process usually reaches only halfway down the posterior wall of the orbit. The roof of the orbit is formed by the supraorbital horn. Anterior articulation of the jugal is obscured by the roughening of the bone forming the anterior rim of the orbit. The anterolateral wall of the orbit is pierced ventrally by the maxillary, sphenopalatine, and posterior palatine foramina. Immediately above these foramina is a large deep fossa, apparently for reception of the lacrimal sac. The opening for the lacrimal canal is situated near the orbital

rim dorsolateral to the fossa for the lacrimal sac. The facial part of the lacrimal bone is almost entirely occupied by a deep, broad depression for reception of the external lacrimal gland. Apparently the lacrimal does not contact the nasal in *Paratoceras*, nor is it separated from that bone by any kind of vacuity, as is common in modern deer and antelope.

The frontals of *Paratoceras*, which are large, broad, and oddly sculptured, give rise to and support the recurved frontal, or supraorbital, horns. As in the synthetoceratines, the medial facial part of the frontals is depressed below the level of the cranium and the nasals. This condition also is prevalent to a lesser degree in some camelids. Anteromesial to the anterior rim of each frontal horn is a large deep pit, or fossa, approximately 1 cm. in diameter. The function of this fossa is uncertain, but it probably contained some kind of facial gland, as is common among ruminant artiodactyls. No internal drainage is visible; position of this fossa, however, on the face just above the lacrimal fossa suggests the possibility of some association of function between the two glands. This fossa is apparently absent in most *Protoceras* skulls, but a hint of its presence over the orbit is seen in the only well-preserved skull of *Calops* (= *Protoceras*; YPM 11885). From the two large, symmetrically placed pits straddling the midline just anterior to the frontoparietal suture to the frontomaxillary and frontonasal sutures, most of the frontal bone of the *Paratoceras* skull is covered with a wide variety of shapes and sizes of pits, grooves, holes, and other irregularities. Some of this unique sculpturing is symmetrical across the sagittal plane, but some occurs randomly. Furthermore, it occurs not only on the frontals but on the nasals and maxillaries as well. The only other mammal known to us possessing similar bone sculpturing is the South American paca (*Cuniculus paca*), in which the zygoma and part of the facial and cranial regions are similarly affected. The most strongly sculptured part of the frontals is the narrow area just posterior to the nasals. This region is slightly depressed and forms a structural extension of the nasal area onto the frontal bones. Some of the smaller pits are randomly distributed and oriented, but the deeper ones in this area open anteriorly. This last feature may offer some clue as to their possible functional significance. Contact between the frontals and nasals is made

along a slightly posteriorly indented suture at a level roughly coincident with that of the anterior edge of the orbital horn.

The nasals of *Paratoceras*, like those of all protoceratids, are extremely retracted. Less than 2.5 cm. in length, they extend forward only to the posterior base of the maxillary plates. The nasomaxillary suture is not discernible, and because the area of contact is only partly obscured by breakage, we believe that this suture may have been partially fused. Breakage and offset of bone along what must have been this contact indicate the size and shape of the nasals, but does not necessarily indicate an unfused contact. Instead, it seems that it remained a zone of relative weakness. Sculpturing is present on the surface of the nasals but is less conspicuous than on other facial bones. The extremely retracted nasals of *Paratoceras*, shorter than in any other protoceratid genus except *Protoceras*, indicate the presence of a large proboscisiform muzzle. Other morphological clues relating to the development of a proboscis are discussed below.

More than in any other feature, *Paratoceras* resembles *Protoceras* in the development of bony plates on the dorsal borders of the maxillaries. These strange protuberances form a flared arch of bone on either side of the open nasal passage and are separated at their base over the nasal canal. The dorsal borders of the plates (described earlier) are rimmed by thickened bone. As is true of most of the cranial bones, these rims are diploetic internally. Each plate also is buttressed by a column of thickened bone running from the anterolateral base of the plate to its apex; the apex is also thickened for strength. Except for the arched plates, the most striking feature of the maxillaries of *Paratoceras* is the exceedingly strong development of the masseteric ridge. Although present in all protoceratids, especially *Protoceras*, no other selenodont artiodactyl possesses such a marked facial crest. In *Paratoceras*, the ridge extends forward from the zygomatic arch to a point above the anterior edge of P³. The ridge is greatly thickened, and its outer edge curls sharply to form a half-tunnel, indicating a strong attachment for a powerful masseter muscle. Unlike *Protoceras*, no horizontal inflection of the face above the ridge is present. In contrast to the rest of the maxillary, the bone below the ridge, i.e. that part forming the masseter attachment surface, is smooth. The

infraorbital foramen is situated near the anterior end of the masseteric ridge at a point above the anterior end of P³. From its opening, the dorsal nasal branch of the intraorbital artery ascends anterodorsally to furnish blood to the enlarged muzzle, including what must have been a strong levator nasolabialis muscle; the lateral nasal branch leads anteriorly to supply the upper lip. The posterolateral surface of the maxillary is also marked by several large venous channels; the largest, the dorsal nasal, descends from the posterior branch of that vein, and just before it drops over the lip of the masseteric ridge, receives the angularis oculi. The latter appears to be formed by branches leading from both above and below the supraorbital horn. These veins and others, including the lateral nasal, infraorbital, and dorsal labial, join together to form the facial vein, which leads posteriorly in a large groove protected by the overhanging curl of the masseteric ridge. Above the shelf of the diastema of P¹-P², the maxilla is constricted to form a semicircular fossa. Limits of this fossa are determined by the course of the alveolus for the large, recurved canine. Dorsal to the canine root, the anterodorsal border of the maxillary descends gently in a broad curve from the maxillary plate. The round, thickened border of the maxillary is relatively smooth except for the presence of numerous small pits. Below the rim, the plate is sculptured by an irregular lattice of bony braces and struts, presumably adding strength to this otherwise delicate structure.

Flat palatine processes of the maxillaries support virtually the entire bony palate. The pre-maxillae are missing and probably broken at the maxillary suture. The palatines constitute only a very thin rim of the choanal border, and no posterior nasal spine is present. The posterolateral border of the bony palate forms a distinct notch, the choanal, or posterior narial notch, which follows the palatomaxillary suture and is situated between the palatine bone and the pterygoid process. This notch is more anteriorly placed in *Paratoceras*, reaching the level of the anterior edge of M², than in the camelids and cervids. The thin vomer is visible in the choanal notch, and in its lack of vertical depth it resembles more that of the camelids than of the Pecora. If correctly identified, the anterior palatine foramen does not occur at the palatomaxillary suture as it does in the ruminants, but is situated just posterior to P¹. A deep palatine

groove leads forward from the palatine foramen. The entire palatal surface is marked by the kind of small pits that occur so ubiquitously on the skull of *Paratoceras*.

UPPER DENTITION: C, P¹⁻⁴, M¹⁻³. Characters of the upper dentition of *Paratoceras wardi*, and in part for the whole genus, are based on three specimens: a complete upper dentition, except for canines, preserved in the type skull (F:AM 40249); a partial right maxilla with P⁴-M³ (F:AM 40251); and a partial left maxilla with P³-M¹ (F:AM 40253).

Only the canine alveolus is preserved in the available specimens of *P. wardi*; the shape and extent of the alveolus reveals the presence of a long, recurved canine with a root socket extending as far back as P². The canine tusk in the maxillary specimen of *P. macadamsi* (F:AM 53519) shows that the *Paratoceras* canine is typically protoceratid in having a trihedral shape and a sharp, pointed tip. The sharp leading edge of the canine is broken anterolaterally; the postero-internal surface shows wear, indicating abrasion with the anterior edge of the caniniform first lower premolar.

As in *Protoceras*, but unlike the synthetoceratines, *Paratoceras* possesses P¹. Small, laterally compressed, and consisting simply of a paracone, it is implanted by two parallel roots. Two diastemata of equal length separate P¹ from C/ and P² in *Protoceras*. P¹ in *Paratoceras* is much closer to C/, forming a long diastema between P¹ and P². Although much slimmer than P² of the synthetoceratines, the *Paratoceras* P² is generally more robust than that of *Protoceras*. Small anterior and posterior cusps are present on either side of the paracone and are joined lingually by a strong basal cingulum running the length of the crown. A very slight development of cingula is observed at the buccal base of the terminal cusps. No protocone is present like that seen on the lingual base of P² in some *Protoceras* specimens. Except for its greater transverse thickness, P³ in *Paratoceras* is very similar to P². The submolariform P⁴ consists of an external crest and an internal crescent. Although not so prominent as in the synthetoceratines, both parastyle and metastyle are present; each is separated buccally by a small valley, forming a broad rib on the paracone. A thick cingulum occurs on the posterolingual base of the protocone; a much smaller one appears on the anterior base of this cusp.

The upper molars of *Paratoceras* are typically protoceratid in their extreme brachydonty and retention of strong accessory cusps. In crown height, they are only slightly more advanced than those of *Protoceras*; certainly they exhibit no tendency toward the taller crowns acquired by their contemporary relatives, the synthetoceratines. The external crests are marked by a strong parastyle and mesostyle, and a more weakly expressed metastyle. A strong median rib is present on both paracone and metacone. Lingually, the base of the internal crescents of M² and M³ is rimmed by a heavy cingulum extending around the entire lingual half of the tooth. On M¹, this accessory structure is limited to a median pillar between the protocone and metaconule crescents and a thin cingulum on the base of the anterior and posterior walls of the tooth. In the strong development of accessory cusps on the upper molars, *Paratoceras* is more primitive than the synthetoceratines and even exceeds some specimens of *Protoceras* in this respect. All three molars are broader than they are long, and all are tapered from the base of the crown to the occlusal surface.

MANDIBLE: The mandible of *Paratoceras* is intermediate in general shape between that of the more primitive *Protoceras* and the graceful, more advanced one of the synthetoceratines. The horizontal ramus is long, slender, and delicate, reflecting the long premolar-molar series and their brachydont condition. The lingual surface is slightly concave below the level of the tooth roots. Anteriorly, the premolar series are separated from the caniniform P₁ by a thin, relatively short diastema, whose sharp superior border drops below the level of the main alveolar border. A very short diastema separates P₁ and the incisiform series. In their shortness, the diastemata of *Paratoceras* resemble those of *Protoceras* and *Syndyoceras* more than they do the extremely long diastemata of *Synthetoceras* and advanced species of *Prosynthetoceras*. Despite some crushing of this region in all the *Paratoceras* specimens, the incisive alveolar border widens and becomes mildly spatulate. The mandibular symphysis of *Paratoceras* appears never to have fused. As in the synthetoceratines, the symphyseal articular surface is heavily pocked by the interconnecting facets and projections for loose articulation of the two rami. The hooklike posterior border of the symphysis projects below the mesial contour of the mandible at the level

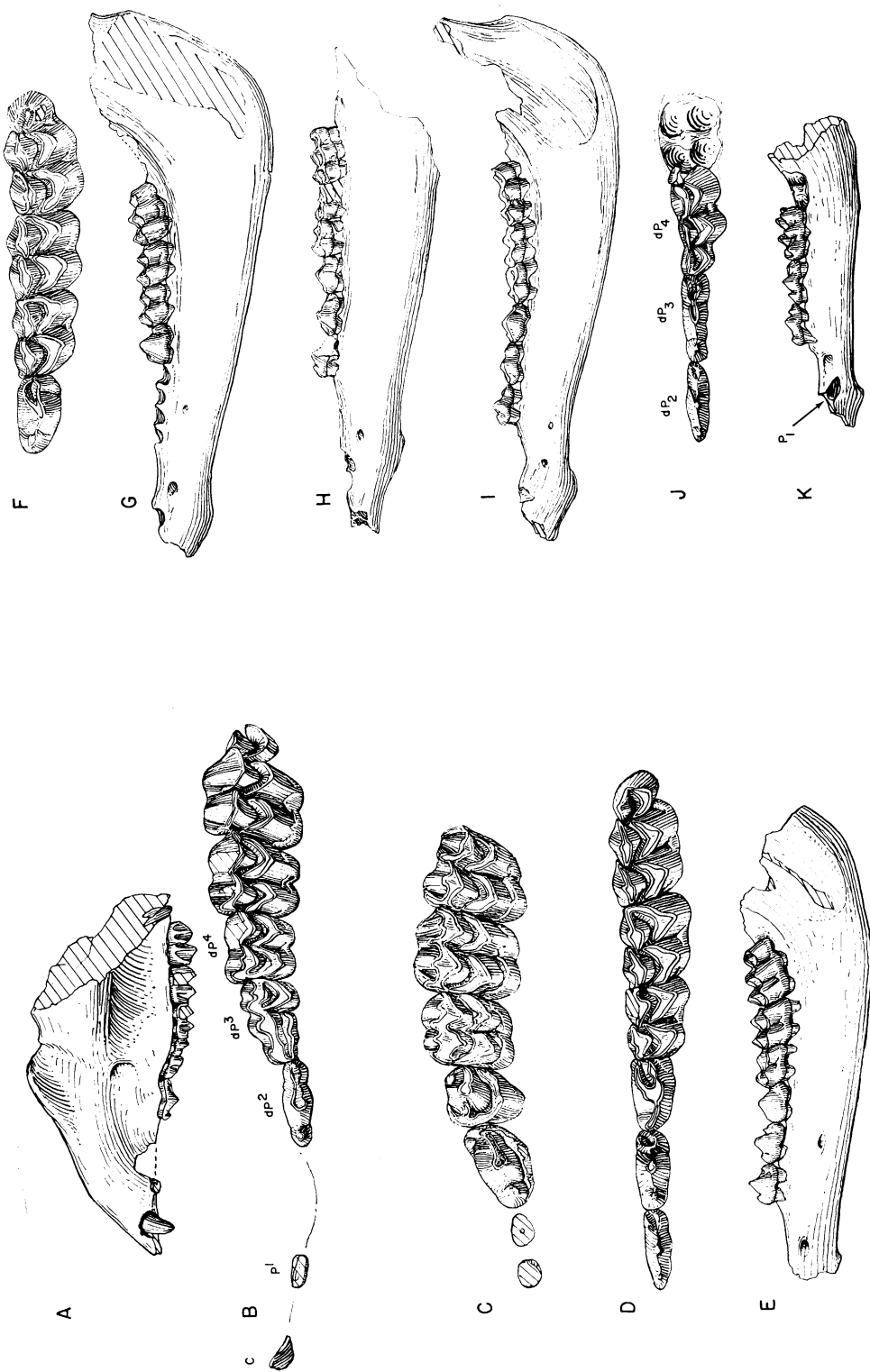


FIG. 9. *Paratoceras wardi*, new species, referred, from Trinity River Pit 1, San Jacinto County, Texas. A-B. Left immature maxilla with C-P₁ erupting and dP₂-M₃ broken germ, F:AM 40252. A. Lateral view. $\times \frac{1}{2}$. B. Occlusal view. $\times \frac{1}{2}$. C. P₂ alveolus-M₃, F:AM 40250, occlusal view. $\times 1$. D-E. Left partial ramus, F:AM 40256. D. P₂-M₃, occlusal view. $\times \frac{1}{2}$. E. Lateral view. $\times \frac{1}{2}$. F-G. Left partial ramus, F:AM 40749. F. P₄-M₃, occlusal view. $\times 1$. G. Lateral view. $\times \frac{1}{2}$. H. F:AM 40751, lateral view, reversed. $\times \frac{1}{2}$. I. F:AM 40750, lateral view, reversed. $\times \frac{1}{2}$. J-K. Right immature ramus with P₁ germ and dP₂-dP₄, F:AM 40759. J. DP₂-dP₄, occlusal view, reversed. $\times 1$. K. Lateral view. $\times \frac{1}{2}$.

of the forward edge of the large anterior mental foramen. This large process probably served for insertion of the genio-hyoideus muscle. Posterior mental foramina may or may not be present.

Although it lacks the broadly expanded masseteric region characteristic of *Protoceras*, the ascending ramus of *Paratoceras* does not possess the strangely canted and attenuated ascending ramus of the synthetoceratines. The fossa for insertion of the masseter is large, but shallow, and demarcated posteriorly and vertically by a conspicuous rim. In every available specimen the coronoid process is broken; however, because of the low position of the glenoid cavity and basicranium, it may be presumed to have been short, as it is in the other protoceratid genera. The angle is only slightly developed and is placed high on the ascending ramus near the condyle. The articular surface of the condyle is limited almost entirely to the dorsal and posterior portions of that structure, once again reflecting the low placement of the glenoid cavity and basicranium.

LOWER DENTITION: I_2 , C, P_{1-4} , M_{1-3} . In the mandibular specimens referred to *P. wardi*, none has the complete incisive alveolar part preserved, precluding determination of the precise incisor count. The complete dentition posterior to this, however, is present or indicated, and consists of the incisiform canine, four premolars, and three molars. In only two specimens, F:AM 40751 and F:AM 40749, are the incisive alveoli indicated, and in each of these the maximum incisor count is apparently three, suggesting that either the lateral incisor (I_3) or the incisiform canine has been lost in *Paratoceras*.¹ If indeed, one of the incisors is lost, it is a unique trait for a protoceratid genus, for all the other genera retain a full incisiform series. In any event, the remaining incisors must have been very small and delicate, as indicated by the relatively minute size of the incisive alveoli. This feature is anticipated in *Protoceras*, as described by Osborn and Wortman (1892, p. 359): "The inferior incisors present delicate spatulate crowns; the median incisors are slightly larger than the lateral incisor, which is very delicate. The canine has precisely the same delicate structure as the lateral incisor." The caniniform P_1 of *Paratoceras* is generally smaller than

that of *Protoceras* and the synthetoceratines. In only one specimen (F:AM 40749) does the alveolus for P_1 indicate a tooth comparable in size to that of *Protoceras*. Scott (1940, p. 568) noted the effects of sexual dimorphism on this tooth in *Protoceras*, pointing out that in "the female P_1 resembles the corresponding tooth in the upper jaw, but is rather smaller and is implanted by a single root. In the male P_1 is large and caniniform and abraded the posterior face of the upper canine." All the specimens with P_1 alveolus preserved in the Trinity River sample indicate the presence of a definite, but small, caniniform tooth except for the above ramus (F:AM 40749). Judging from wear facets on the upper canine, P_1 of *Paratoceras* also occluded with the posterior face of the canine.

It is the characters of the lower premolars that particularly distinguish the mandibular dentition of *Paratoceras* from that of other protoceratid genera, and it was upon these characters that Frick (1937, p. 608) originally erected the genus. The lower premolars are long and compressed for a Miocene protoceratid, but nonetheless, they are strong, robust teeth. All are two rooted. Although they are considerably more elongate than the reduced premolars of *Syndyoceras*, *Prosynthetoceras*, and *Synthetoceras*, *Paratoceras* premolars are shorter and thicker than those of *Protoceras*. Only in the foreshortening of P_4 does *Paratoceras* resemble its protoceratid relatives. The thin elongate P_2 is almost equal in length to P_3 . The bladelike anterior cusp (paraconid) is separated by a distinct notch from the high, pointed protoconid. In *Protoceras*, *Syndyoceras*, and *Prosynthetoceras* the paraconid forms an anterolingual flexid; in *Paratoceras*, this cusp is oriented directly forward. It is lost completely in *Synthetoceras*. The posterior end of the tooth is characterized by separated hypoconid and entoconid crests, forming a posteriorly breached fossettoid. P_3 differs from P_2 in its larger size, relatively greater posterior width, and in the entoconid forming a distinct cusp rather than a crest. It also lacks an anterior flexid. P_4 is slightly wedge-shaped and resembles that of the synthetoceratines in its foreshortening, its thickness, and in the presence of anterolingual flexid; this flexid, however, is not strongly developed as that of *Protoceras*. The entoconid and hypoconid form two parallel posteriorly directed crests that extend more than halfway up the side of the

¹No specimens of *P. macadamsi* preserve the incisive dentition; the incisive dentition of *P. wardi* is therefore extended provisionally to characterize that of *P. macadamsi*.

protoconid. In *Protoceras* and the synthetoceratines, these crests curve lingually, with the hypoconid crest forming a posterior entostylid.

In contrast to the synthetoceratines, *Paratoceras* retains brachydonty of the lower molars. The hypoconid and protoconid crescents are symmetrical and directed slightly forward. Stylids are reduced in comparison with those on the upper molars; a small, low parastylid and a very inconspicuous entostylid are present. The metaconid crest overlaps that of the entoconid to form a limited metastyle. As in all protoceratids, median pillars are developed on the *Paratoceras* lower molars between the protoconid and hypoconid crescents; they are not nearly so strongly expressed, however, as those in the synthetoceratines and also differ from the latter in retaining accessory pillars on M_3 . In addition to the dromomerycids, only *Paratoceras* and *Floridatragulus* among the large North American Miocene artiodactyls possess the accessory pillars on M_3 .

As in *Protoceras*, small anterior cingula appear on the base of the protoconid crescents of the lower molars; these are also absent in the synthetoceratines. A significant character of the lower molars is the presence of a double enamel loop on the hypoconulid of M_3 , which with wear encloses a fossettid. This feature, described by Patton (1969, p. 168) and emphasized by Patton and Taylor (1971, p. 146) is "characteristic of the ruminants, is not present in the camelids (except in the problematical *Floridatragulus*), but occurs in all protoceratids. In this regard M_3 of *Prosynthetoceras* resembles that of the genus *Floridatragulus*, which is often found in association, but is distinguishable from it on the basis of the strong anterior cingulum, the accessory pillar between the protoconid and hypoconid, and the lower crown height of the latter. Another contemporary genus, *Nothokemas*, possesses an M_3 which converges on the above-mentioned condition of *Prosynthetoceras* and *Floridatragulus*, in that it approaches the formation of a double enamel loop on the hypoconulid. In *Nothokemas*, however, this is accomplished by the posterior extension of the entoconid."

LIMBS: Definitely associated limbs¹ and dentition of *Paratoceras* are yet to be found. We are referring to *Paratoceras wardi* limbs that have the general protoceratid characters and are com-

¹For the purpose of description and comparison, all limbs are described from a vertical (standing) position.

TABLE 5

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE UPPER DENTITION OF *Paratoceras wardi*, NEW SPECIES, FROM THE UPPER PART OF THE FLEMING FORMATION, SAN JACINTO COUNTY, TEXAS

	N	OR	\bar{X}	S	V
P^3					
Length	3	11.7–13.0	12.53	0.723	5.77
Width	3	7.2–8.6	7.93	0.702	8.85
P^4					
Length	4	9.1–9.5	9.35	0.191	2.05
Width	4	11.8–12.6	12.20	0.365	2.99
M^1					
Length	5	11.1–12.5	11.82	0.507	4.29
Width	5	13.0–14.0	13.52	0.356	2.64
M^2					
Length	4	12.2–13.3	12.73	0.457	3.59
Width	4	15.2–16.0	15.50	0.356	2.30
M^3					
Length	3	12.5–12.8	12.60	0.173	1.37
Width	3	15.2–16.6	15.87	0.702	4.43
M^1-M^3	3	35.0–36.5	35.77	0.751	2.10

paring them with *Protoceras celer*. Distinguishing characters that immediately place the limbs in the Protoceratidae are: (1) exceptionally strong ulna not fully co-ossified with the radius, (2) unfused metacarpals III and IV; unfused metatarsals III and IV with articular facets for rudimentary metatarsals II and V, (3) failure of the carina on the metacarpal to extend to the anterior surface of the facet, (4) strong distal keel on the astragalus, and (5) separate cuboid and navicular. The above characters are unlike those of the cervids for which these limbs might be mistaken but like those of all members of the Protoceratidae. Judging by the length of the unassociated limbs referred to *P. wardi*, the front limb is proportionally short compared with the rear limb. Osborn and Wortman (1892, p. 359) noted a similar disparity in length between the front and rear limbs of *Protoceras*. In general, the limbs allocated to *Paratoceras* show a striking similarity to those of the earlier occurring *Protoceras*.

FRONT LIMBS: Three humeri and one partial humerus (F:AM 40762–40765), ranging in length from 127.5 mm. to 131 mm., are referred to *P. wardi*. The length of the humeri is within the range of *Protoceras celer*. Humeri of two partial skeletons of the latter measure 122 mm. (F:AM 53521) and 137 mm. (F:AM 53527). The head of the humerus of *Paratoceras* is strongly convex

TABLE 6

MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF THE LOWER DENTITION OF *Paratoceras wardi*, NEW SPECIES, FROM THE UPPER PART OF THE FLEMING FORMATION, SAN JACINTO COUNTY, TEXAS

	N	OR	\bar{X}	S	V
P ₂					
Length	2	12.1–12.2	12.15	0.071	0.58
Width	2	4.3– —	4.30	0.000	0.00
P ₃					
Length	3	12.2–12.7	12.50	0.265	2.12
Width	3	5.0– 5.2	5.07	0.115	2.28
P ₄					
Length	8	11.0–12.0	11.50	0.334	2.90
Width	8	6.0– 7.0	6.74	0.346	5.14
M ₁					
Length	11	10.7–11.8	11.11	0.295	2.65
Width	11	8.2–10.0	9.40	0.603	6.42
M ₂					
Length	12	11.5–12.5	12.11	0.281	2.32
Width	10	8.5–11.9	10.58	0.864	8.16
M ₃					
Length	12	16.2–18.0	17.02	0.648	3.81
Width	12	9.5–11.5	10.76	0.528	4.91
P ₂ –P ₄	3	35.3–36.0	35.60	0.361	1.01
M ₁ –M ₃	11	38.0–41.0	39.55	1.040	2.63
P ₂ –M ₃	3	73.8–76.8	75.53	1.504	1.99

anteroposteriorly and projects posteriorly well beyond the plane of the shaft. All three humeri have the greater and lesser tuberosities broken near the base, but the remnants indicate that their position corresponds to those of *P. celer*, with the same faint, narrow bicipital groove separating the tuberosities. A weak deltoid ridge (fig. 10), slightly stronger than in *P. celer*, rises just beneath the head of the humerus and extends anterodistally but disappears before the middle of the shaft. Although the deltoid ridge is weak, it tends to be stronger than in *P. celer*. The shaft is short and heavy as in *P. celer*, with the proximal one-third laterally compressed; near the middle, the shaft is more cylindrical with the distal part widening just above the trochlea. An extremely weak lateral condyloid crest is similar to that of *P. celer*. The trochlea closely resembles that of *P. celer* with the width ranging from 27.5 mm. (F:AM 49763) to 30.3 mm. (F:AM 40764). The trochlea is slightly oblique to the upright shaft with the proximal border of the smaller lateral condyle descending slightly below the level of the larger medial condyle. A deep groove similar to that of

P. celer separates the lateral and mesial condyles of the trochlea. A prominent ridge runs straight back to the posterior border of the trochlea (as in all protoceratids) and marks the lateral condyle of the trochlea. In the cervids, this condylar ridge is directed more laterally and terminates at the anterolateral border of the trochlea. Lateral and mesial epicondyles are weak as in *P. celer*, but the coronoid fossa tends to be shallower than in the latter. In *Paratoceras wardi*, the olecranon fossa is deep but unperforated.

Two ulnae-radii are referred to *P. wardi*. Compared with *Protoceras celer*, the length of the radii of *P. wardi* (130 and 131.5 mm.; F:AM 40767 and F:AM 40766) is shorter, and the ulna is proportionally lighter relative to the radius. Not only is the ulna of *P. wardi* (fig. 10) comparatively lighter throughout its entire length than that of *P. celer*, but the distal articular surface for the cuneiform is also proportionally smaller compared with that for the lunar. The ulna and radius are co-ossified for most of their length; their separation near the proximal end is equivalent to about 20 percent of the total length of the radius. In contrast, the ulna and radius of *P. celer* are separate for most of their length and co-ossified only near the distal end. The proportionally lighter ulna, which is almost entirely fused with the radius, and a smaller articular surface for the cuneiform in *Paratoceras wardi*, indicate that more weight was borne by the radius, and the front foot was, therefore, less widely spread laterally than in *P. celer*.

In *P. wardi*, the olecranon process (fig. 10E) is relatively longer and projects more posteriorly than in *P. celer*. The greater sigmoid cavity is an undivided articular surface that tends to be smaller and less semicircular than in *P. celer*. The proximal end of the radius is divided into three articular surfaces. Although the proximal end is expanded transversely, similar to that of *P. celer*, the proximolateral facet projects less laterally. Transverse diameter of the proximolateral facet of the radius, which articulates with the lateral condyle of the humerus, is proportionally less than that of *P. celer*. However, the articular surface for the mesial condyle of the humerus is similar to that of *P. celer*. The shaft of the radius in *P. wardi* is almost uniform in size throughout its length and proportionally more robust compared with the ulna of *Protoceras*

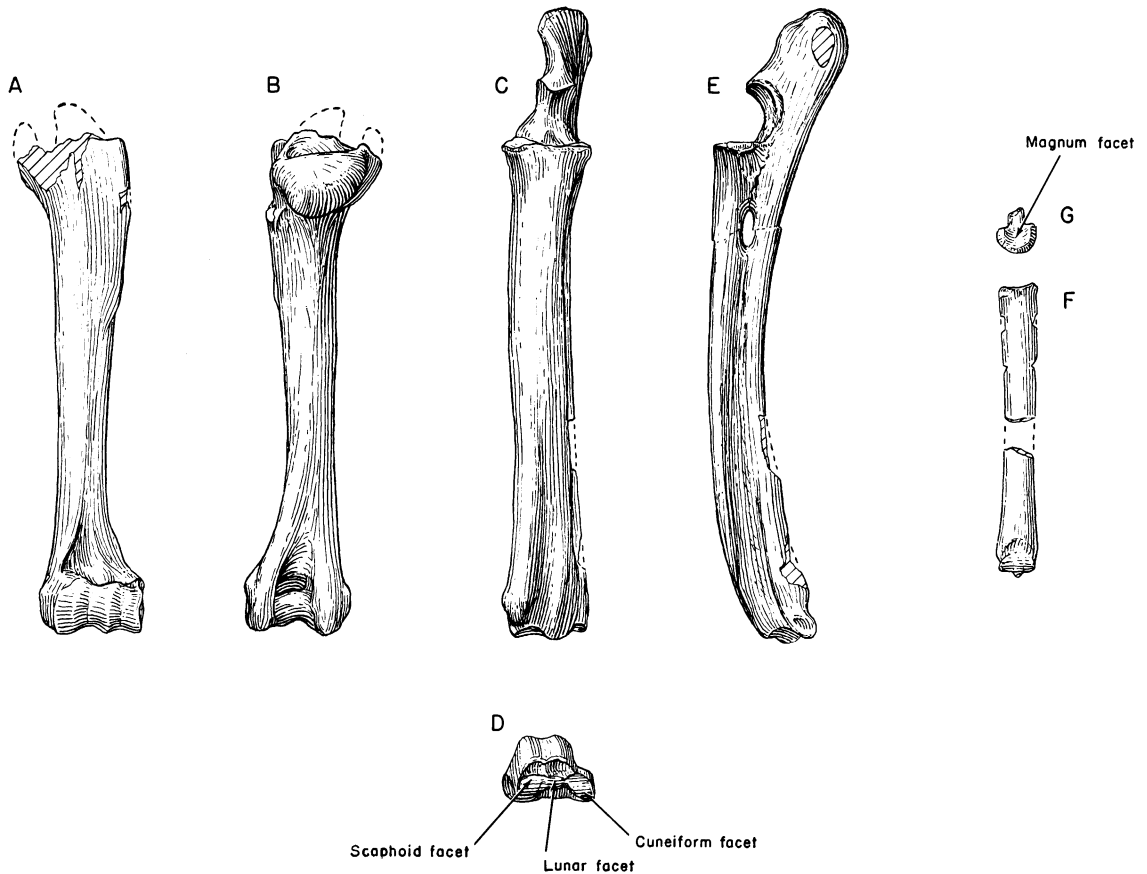


FIG. 10. *Paratoceras wardi*, new species, from Trinity River Pit 1, San Jacinto County, Texas. A-B. Right humerus, F:AM 40763. A. Anterior view, reversed. B. Posterior view, reversed. C-E. Left ulnoradius, F:AM 40766. C. Anterior view. D. Distal view. E. Lateral view. F-G. Right incomplete metacarpal III, F:AM 40769. F. Anterior view, reversed. G. Proximal view, reversed. All $\times \frac{1}{2}$.

celer. The shaft is strongly curved anteriorly displaying a marked bicipital rugosity. A low ridge on either side of the anterior distal end of the radius encloses a slightly rugose concave attachment for the extensor tendons. Distally, the radius consists of two articular facets for the scaphoid and the lunar. In *P. wardi*, the scaphoid facet resembles that of *P. celer* but is proportionally smaller. The lunar facet, however, is relatively larger; it is transversely wider but anteroposteriorly narrower than in *P. celer*; it is also more centrally situated with a slightly more concave articular surface. Although the boundary of the facet for the scaphoid and the lunar is clearly outlined, no distinct ridge separates the two articular surfaces, as is sometimes found in

P. celer. The facet for the cuneiform is confined to the ulna as in *Protoceras*.

The metacarpus of *Paratoceras wardi* is represented only by an incomplete third metacarpal (F:AM 40769), but presumably contains four digits, as in *Protoceras celer*. This third metacarpal (fig. 10) consists of associated proximal and distal parts that are believed to be of one individual. The proximal articular surface of metacarpal III is but little expanded, as in *P. celer*, with the anteroposterior length (11.8 mm.) slightly exceeding the transverse diameter (10.5 mm.). In fact, the magnum from a partial skeleton (AMNH 1227) of *P. celer* articulates almost perfectly with the third metacarpal referred here to *P. wardi*. On the proximal

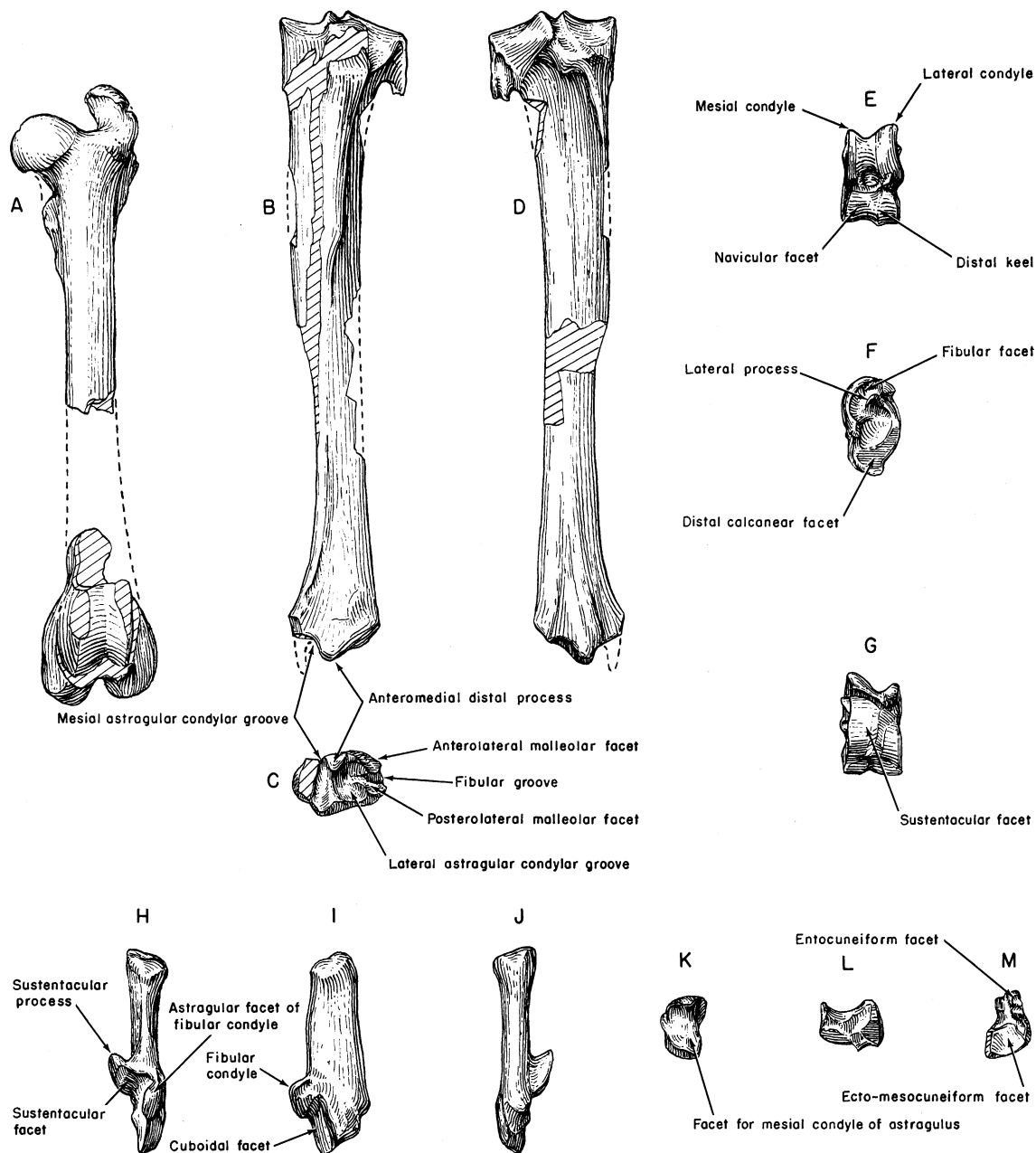


FIG. 11. *Paratoceras wardi*, new species, from Trinity River Pit 1, San Jacinto County, Texas. A-D. Left associated incomplete femur and tibia, F:AM 40856. A. Anterior view. B. Anterior view. C. Distal view. D. Posterior view. E-G. Left astragalus, F:AM 40865. E. Anterior view. F. Lateral view. G. Posterior view. H-J. Left calcaneum, F:AM 40867. H. Anterior view. I. Lateral view. J. Posterior view. K-M. Right navicular, F:AM 40871. K. Proximal view, reversed. L. Lateral view, reversed. M. Distal view, reversed. All $\times \frac{1}{2}$.

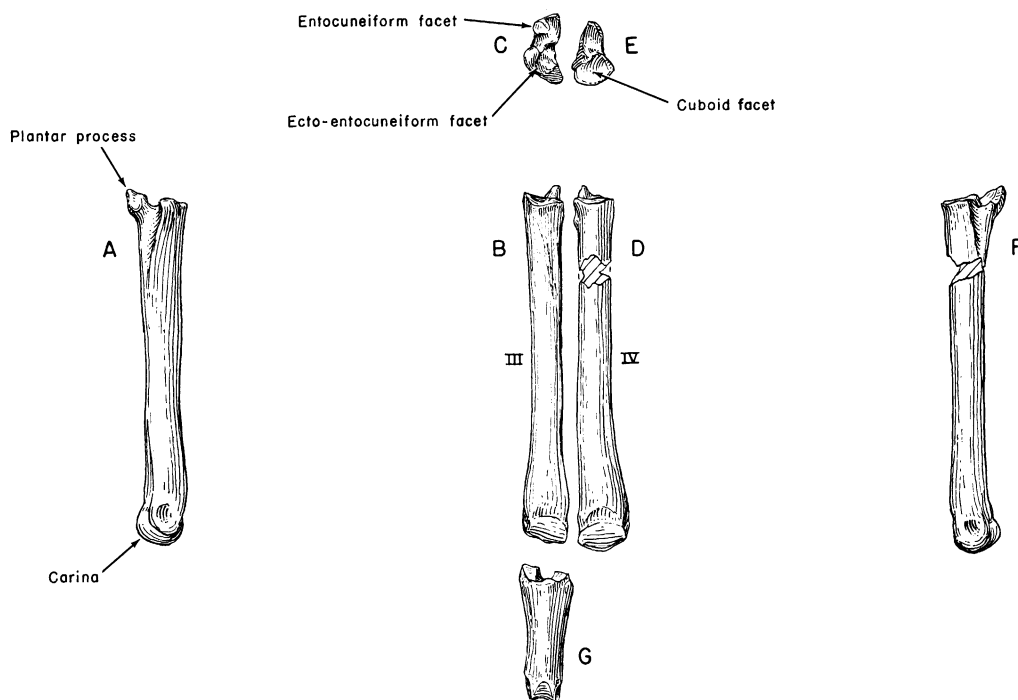


FIG. 12. *Paratoceras wardi*, new species, from Trinity River Pit 1, San Jacinto County, Texas. A–C. Left metatarsal III, F:AM 40872. A. Mesial view. B. Anterior view. C. Proximal view. D–F. Right metatarsal IV, F:AM 40875. D. Anterior view, reversed. E. Proximal view, reversed. F. Lateral view, reversed. G. Proximal phalanx of metatarsal III or IV, F:AM 40877, anterior view. All $\times \frac{1}{2}$.

surface, the magnum facet is concave with the mesial and lateral borders slightly elevated to about the same level. The posterior half of the facet for the magnum narrows abruptly with the transverse diameter equal to about half of the diameter at the widest point. On the proximo-lateral side of metacarpal III are two facets for metacarpal IV and another small anterolateral facet for articulation with the unciform. The anterolateral facet is small and undercut to overlap and articulate with the proximal mesial facet of metacarpal IV; the posterior facet is cylindrical—even smaller than the anterior facet. On the mesial side of metacarpal III is a well-defined depression for metacarpal II that gradually disappears on the proximal half of the shaft as in *P. celer*. The third metacarpal is so similar to that of *Protoceras* that we are compelled to conclude that *Paratoceras* also probably had a well-developed metacarpal II, with the length approaching that of metacarpal III. On the mesial side, the facet for the articulation of metacarpal II is so badly eroded that compari-

son with *Protoceras* is not possible. A prominent carina on the distal trochlea is mostly confined to the posterior and distal surfaces, but unlike *Protoceras*, a trace of the carina can also be detected on the anterodistal surface.

REAR LIMBS: Six partial femora including one (F:AM 40856, fig. 11A) associated with a tibia are referred to *Paratoceras wardi*. Proximal and distal ends of the femur are remarkably like those of *Protoceras celer*. Enough of the femur is preserved to show that it was probably short and stocky as in *P. celer*. On an extremely short neck is a well rounded head marked by an oval depression for the ligamentum teres. The greater trochanter is large and massive (antero-posterior diameter 19 mm., F:AM 40857) and rises above the level of the head. Although the bridge between the head and the greater trochanter is short, it tends to be longer than in *P. celer*. A large, deep digital fossa extends laterally to undercut the strong intertrochanteric ridge connecting the greater and lesser trochanters. On the lower border of the digital

fossa is a large posteriorly projecting lesser trochanter. The trochlear groove for the patella is broad and rather shallow with the mesial crest projecting more anteriorly and much broader than the lateral crest. In *P. wardi*, the condyles of the trochlea are narrow and project less posteriorly behind the plane of the shaft than in *P. celer*. The lateral condyle is almost vertical, but the mesial condyle is more oblique relative to the shaft. Above the lateral condyle is a shallow rugose digital extensor fossa.

One tibia (F:AM 40856, fig. 11) associated with a partial femur, and three partial tibiae are referable to *Paratoceras wardi*. The tibia is remarkably similar to *Protoceras celer*, but averages smaller; the length from the proximo-mesial condyle to the anteromedial distal process is 183 mm. The proximal surface of the tibia resembles *P. celer* with the femoral facets rather narrow. The mesial condyle is smaller and deeply concave; the lateral condyle is antero-posteriorly longer with the posterolateral border projecting more posteriorly for attachment with the fibula than in *P. celer*. From the size of the proximal part of the fibula that is co-ossified with the tibia, we surmise that the fibula possibly could have extended for most of the length of the tibia or for its full length, as seen occasionally in *P. celer* (F:AM 53521). Although somewhat crushed, it is evident that the anterior crest of the tibia is less produced anteriorly than in *P. celer*. Allowing for the crushing, we see that the shaft curves slightly anteriorly and laterally as in *P. celer*. The distal end of the tibia conforms closely to *P. celer*, except for the more reduced fibular groove, which is so shallow that it is a mere rugose depression. The small distal fibular depression indicates that the distal part of the fibula of *P. wardi* was more reduced than in *P. celer*, but the proximal end of the fibula, as stated above, appears to be proportionally as strong as in *P. celer*. A distinct distal facet for the malleolar bone is present on each side of the fibular depression. These facets indicate that the malleolar is not fused with the tibia, and judging by the space for the malleolar, it is unreduced, approximating in size that of *P. celer*. The distal end of the tibia is expanded transversely with the mesial condylar facet for the astragalus narrower than the lateral facet. A prominent ridge, continuous with a strong anteromedial distal process, separates the two facets. Deep anteroposterior condylar facets for the astragalus

along with the interlocking connection with the astragalus and calcaneum would permit little, if any, lateral motion and restrict movement to a fore-aft direction. The mesial malleolus is broken near the base, but its size and position appear similar to that of *P. celer*. A prominent groove for the tendon flexor digitalis longus fades out on the posteromesial surface of the shaft about 35 mm. above the distal end. The anterodistal surface of the shaft for the tendon of tibialis anticus is concave.

Two astragali, each measuring 29 mm. along the lateral side, are referred to *Paratoceras wardi*. Compared with *Protoceras celer*, the astragalus averages smaller, and the sustentacular facet is proportionally narrower. The lateral condyle (fig. 11E) of the proximal trochlea, which articulates with the tibia, is higher and wider than the mesial condyle. The difference in height of the condyles is similar to that in *P. celer*, but the groove separating the condyles tends narrower and deeper. In *P. wardi* the posterior extremity or tuberosity of the mesial condyle is narrower than that of *P. celer*, in which this tuberosity is distally directed and more transversely expanded. This transverse shelflike expansion of the posterior tuberosity of the mesial condyle in *P. celer* would permit more rotational movement between the tibia and astragalus. On the distal trochlea of the astragalus of *P. wardi*, the facet for the cuboid is relatively narrow and only about one-third the width of the navicular facet. The distal trochlea of *P. wardi* is mesially deflected with a strong distal keel on the lateral side as in *P. celer*. Both the deflection and the strong distal keel are characteristic of all protoceratids. A weak transverse process occurs on the anterodistal end of the mesial condyle. This process is weaker in *P. wardi* than in *P. celer* and absent in the synthetoceratines. Anteriorly, the interarticular fossa is narrow and deep. Laterally, the distal calcaneal facet is short but extends more posteriorly than in *P. celer*. The sustentacular facet is long and narrow with a relatively smaller articular surface for the calcaneum than in *P. celer*. It is marked by a prominent vertical groove that is slightly past center toward the mesial side. Parallel to the groove is a noticeably strong ridge that marks the mesial extent of the facet.

Four calcanea, with the total length ranging from 56.5 mm. (F:AM 40868) to 59.2 mm. (F:AM 40869), are referred to *Paratoceras wardi*.

Although the calcaneum (fig. 11) of *P. wardi* is similar to that of *Protoceras celer*, the sustentacular facet is transversely narrower with a lighter, less posteriorly projecting sustentacular process. Also, the calcaneal fibular condyle is anteroposteriorly shorter, transversely narrower, and more elevated than in *P. celer*. No malleolar of *P. wardi* is known, but the small, elevated fibular condyle of the calcaneum indicates that the fibular facet is relatively smaller and deeper than in *P. celer*. The tuber calcis has low lateral and mesial tuberosities and a smooth almost flat anterior tuberosity. Posteriorly, the lateral and mesial tuberosities are separated by the vertical plantar sulcus, which quickly fades out on the shaft, as in *P. celer*. In comparison, the calcaneal shaft of *P. wardi* is more laterally compressed and less robust, with the anterior border much narrower. The transverse dimension of the sustentacular facet of the four referred calcanea ranges between 9 and 9.5 mm. and is relatively narrower than in *P. celer*. The sustentacular facet is almost semicircular, anteroposteriorly concave, and slightly convex transversely with the mesial border lower. Projecting posteriorly is an equally strong but less massive sustentacular process. The astragalar-capitulum facet is almost flat, narrowed medially, and widened distally, where a sharp ridge separates it from the cuboid facet. As in *P. celer*, the cuboid facet is narrow, anteroposteriorly elongate, and slightly concave. The distal half of the cuboid facet is almost flat transversely with the proximal half sloping mesially.

Only one navicular (F:AM 40871, fig. 11) is referred to *Paratoceras wardi*. As in all protoceratids, the navicular and cuboid are separate. The proximal facet of the navicular is semicircular in outline and anteroposteriorly concave for the mesial trochlea of the astragalus. A low ridge near the lateral border of the facet articulates with the prominent groove on the distal trochlea of the astragalus. Anteriorly, the navicular is transversely narrow but gradually widens toward the midpoint; it is vertically deep (8.5 mm.) and anteromesially marked by a horizontal groove. In mesial view, the posterior border of the astragalar facet projects sharply upward with the distal mesial surface marked by a sharp V-shaped distal spur that indicates the point of contact between the ecto-mesocuneiform and the entocuneiform. The posterior

surface of the navicular is irregular and narrowed distally toward a short plantar (posterior) spur that is less prominent than in *P. celer*. On the lateral side of the navicular of *P. wardi* are three facets for the cuboid. The anteroproximal and anterodistal facets are relatively small, flat, anteroposteriorly elongate surfaces. By far the largest is the posterior facet for the cuboid, which extends almost the entire vertical length of the posterior border of the navicular. The posterior facet is a narrow flat surface with the anteroposterior length of the distal half gradually increasing. A wide interosseous fossa separates the anterior and posterior facets and continues onto the distal surface of the navicular. The distal surface of the navicular of *P. wardi* appears to have three separate facets similar to that of the synthetoceratines. The anterior facet is large, somewhat rounded, having a slightly convex surface with the transverse diameter relatively greater than in *P. celer*. Posteriorly, the facet is marked by a low ridge that interrupts the articular surface suggesting a separate facet. Posterior to this ridge, a narrow articular surface continues onto the distal spur which indicates the point of contact between the ecto-mesocuneiform and the entocuneiform. Despite this low ridge, it is most likely one articular surface for the combined ecto-mesocuneiform as in *Protoceras* and the synthetoceratines. At this point, a sharp V-shaped distal spur separates the ecto-mesocuneiform and entocuneiform facets. The posterior navicular facet for the entocuneiform is anteroposteriorly elongate and transversely narrow. The entocuneiform facet in *P. wardi* is smaller with the posterior border projecting less distally than that of *P. celer*. A smaller facet for the entocuneiform suggests that this tarsal may be more reduced than in *P. celer*, and this in turn, suggests that the metatarsal II, which articulates with the entocuneiform, may also be more reduced. In fact, this is supported by the smaller depression on the referred metatarsal III (F:AM 40874) for the vestigial lateral metatarsal II.

The metatarsus of *P. wardi* is represented by metatarsals III and IV, which are not fused as in *P. celer*. Both metatarsal III and IV (fig. 12) are marked by a depression on the proximal end, indicating that vestigial metatarsals II and V were present but reduced, as are the proximal splints of *P. celer*. In *P. wardi*, however, the depression on the functional metatarsals for

vestigial digits II and V is relatively smaller than in *Protoceras celer*.

Three third metatarsals, ranging in length from 91 mm. (F:AM 40872) to 95 mm. (F:AM 40874), are referred to *Paratoceras wardi*. Width of the proximal end of metatarsal III is 10.8 mm. (F:AM 40872, fig. 12A-C), and the proximal facet for the ecto-mesocuneiform is anteroposteriorly concave with slightly elevated lateral and mesial borders. The plantar process is elevated above the level of the ecto-mesocuneiform facet and bears a vertically elongate, slightly concave facet for the entocuneiform. The entocuneiform facet slopes mesially at an approximate 45 degree angle to the long axis of the metatarsal and is relatively smaller than that of *P. celer*. Mesially, metatarsal III has a deep proximal depression for a vestigial metatarsal II. On the anteroproximal border of the depression is a small concave facet for metatarsal II. Near the proximal end is a deep, slightly rugose depression that diminishes distally and fades out on the shaft about 13 mm. below the proximal facet (F:AM 40874). In *P. wardi* the depression on metatarsal III is relatively smaller and less distally extended than in *P. celer*. On the proximolateral surface of metatarsal III are two facets for metatarsal IV. The small concave anterior facet is situated on the anterior border of the depression about 5 mm. below the proximal end. The second facet for metatarsal IV is a vertically elongate lateral facet on the plantar process. Laterally, the shaft of metatarsal III is flattened to allow close approximation of the two central metatarsals, a condition similar to that of *P. celer*, as noted by Scott (1940, p. 353). The transverse diameter near the middle of the shaft (F:AM 40874) is only 8.5 mm., but increases toward the distal end where it measures 12.3 mm. at the point of contact with the distal facet. In *P. wardi*, a strong carina on the posterior surface of metatarsal III passes across the distal surface, disappearing on the anterodistal surface of the trochlea, as in *P. celer*. The carina on the metatarsals is stronger and extends more anteriorly onto the trochlea than on the metacarpals.

One right metatarsal IV (F:AM 40875, fig. 12D-F) measuring 92.5 mm. from the cuboid facet to the distal carina and a left proximal half of metatarsal IV are referred to *P. wardi*. This fourth metatarsal articulates almost perfectly with right metatarsal III (F:AM 40874)

mentioned above. Because the metatarsal IV is the shorter in this instance, it probably represents a smaller individual, if the length of metatarsal IV slightly exceeds that of metatarsal III, as it does in *P. celer*. Metatarsal IV of *P. wardi* differs primarily from *P. celer* in having a relatively smaller articular surface on the plantar process for the cuboid and a proportionally smaller proximolateral depression for the vestigial metatarsal V.

Width of the proximal end of metatarsal IV is 10.2 mm., slightly less than metatarsal III (F:AM 40874). The proximal facet for the cuboid is anteroposteriorly concave with the lateral border higher than the mesial. A prominent plantar process rises above the anterior cuboid facet. On the lateral surface of the plantar process is a vertically oblique, elongate, narrow facet for the distally projecting plantar spur of the cuboid. The proximolateral surface of metatarsal IV is marked by a shallow depression for a vestigial metatarsal V; on its anteroproximal border this depression has a small facet for the vestigial digit. The depression for metatarsal V is smaller than the corresponding depression on metatarsal III for metatarsal II. A similar difference in size of the depressions on metatarsals III and IV of *Protoceras celer* was noted by Scott (1940, p. 353). On the anteromesial surface of metatarsal IV, about 2.5 mm. below the cuboid facet, is a small mesially projecting facet that articulates with a small concave facet on metatarsal III. A second, small, vertically elongate facet for metatarsal III is situated on the posterior part of the plantar process. Mesial and posterior surfaces of the shaft are flattened; the distal trochlea has a strong carina that corresponds closely to the previously described metatarsal III.

One proximal phalanx (F:AM 40877, fig. 12G) of digit III or IV of the pes is referred to *Paratoceras wardi*. Total length of the proximal phalanx is 34 mm.; the length of the proximal phalanx of the pes is presumably greater than that of the manus, as in *Protoceras celer*. The proximal facet (width, 11.5 mm.) articulates closely with a left metatarsal III, F:AM 40872 (distal trochlear articular width, 12 mm.). The proximal facet of the first phalanx is higher on the lateral side and deeply grooved anteroposteriorly for a prominent carina. Although the carinal groove is posteriorly deep, it fades out

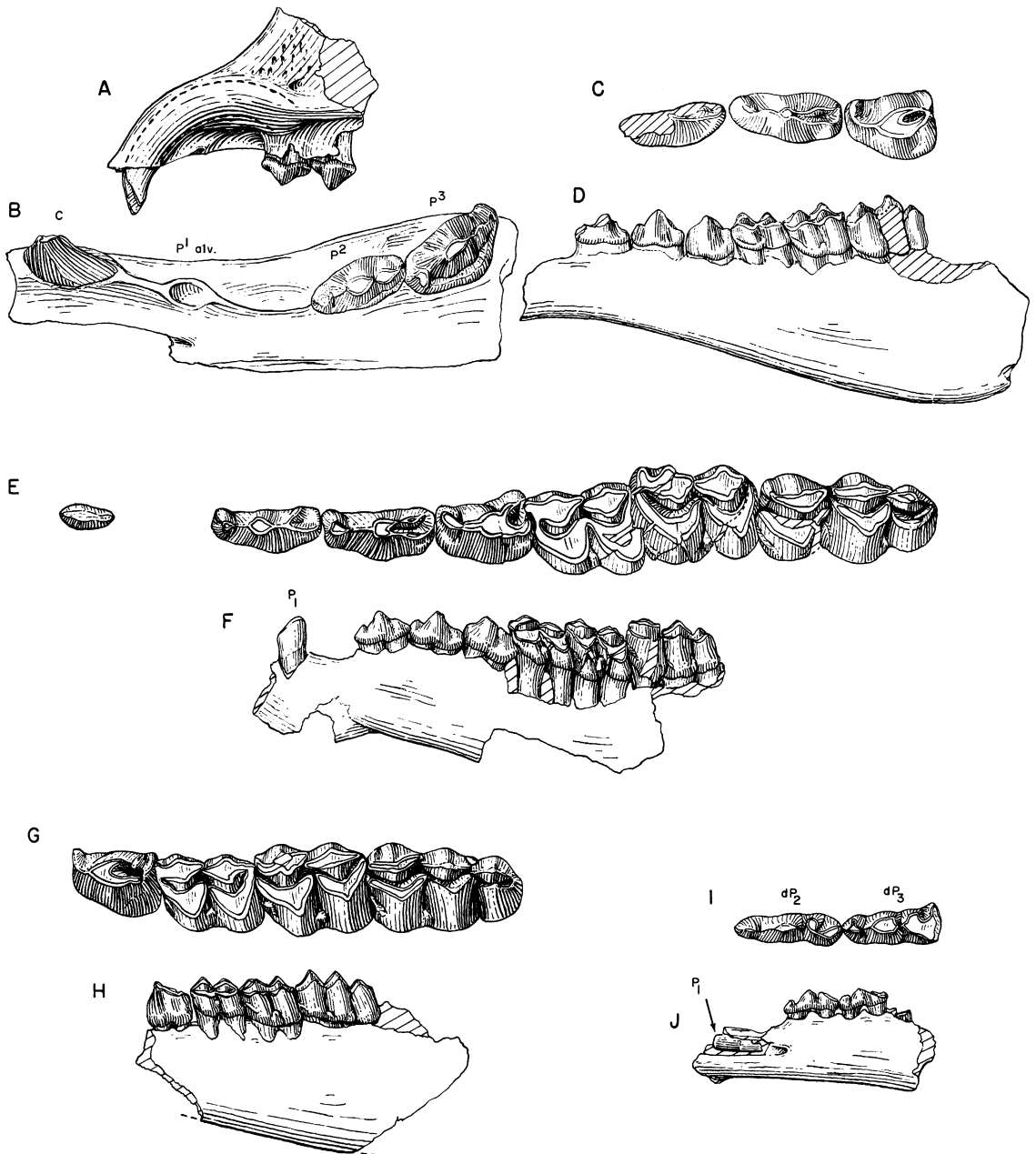


FIG. 13. *Paratoceras macadamsi* from Donley County, Texas. A-B. Right partial maxilla with C and P¹ alveolus-P³, F:AM 53519. A. Lateral view, reversed. $\times \frac{1}{2}$. B. Occlusal view, reversed. $\times 1$. C-D. Type, right ramus with P₂-M₃, F:AM 32457. C. P₂-P₄, occlusal view, reversed. $\times \frac{1}{2}$. D. Lateral view, reversed. $\times \frac{1}{2}$. (Both views of F:AM 32457 after Frick, 1937, fig. 65, in part.) E-F. Left ramus with P₁-M₃, F:AM 53516. E. Occlusal view. $\times 1$. F. Lateral view. $\times \frac{1}{2}$. G-H. Left partial ramus with P₄-M₃, F:AM 33409. G. Occlusal view. $\times 1$. H. Lateral view. $\times \frac{1}{2}$. I-J. Right immature partial ramus with P₁ and dP₂-dP₃, F:AM 53520. I. DP₂-dP₃, occlusal view, reversed. $\times 1$. J. Lateral view, reversed. $\times \frac{1}{2}$.

near the middle of the proximal facet, corresponding to the termination of the carina on the anterior surface of the distal trochlea of the metatarsus. The distal trochlea of the proximal phalanx is narrow (8.9 mm.) with a prominent anteroposterior median groove. Articular surface of the distal trochlea of the proximal phalanx is restricted anteriorly but extends proximally high on the posterior surface, a characteristic of all the protoceratids.

DISCUSSION: *P. wardi* occurs only in the incompletely described Trinity River local fauna (not yet formally established) of the Texas Coastal Plain (Patton and Taylor, 1971, p. 127). This local fauna lies stratigraphically between the previously established Burkeville and Cold Spring faunas (*sensu* Wilson, 1956; Patton, 1969) and is regarded by us as being of early Barstovian age. The relationship of *P. wardi* to the undescribed species from the Hemingfordian of Panama (Whitmore, personal commun.) is presently unknown. The later occurrence of *P. wardi*, however, allows possible derivation from the Central American form. It is, of course, possible, and even likely, that the species represented by the Panamanian specimens was more widely distributed than its fossil record indicates. Thus, it may have been present, but, because of ecologic bias or some other factor limiting preservation, is unrecorded in earlier Coastal Plains deposits. Certainly either it or its antecedent species had to "pass through" Texas and northern Central America to reach Panama. Just when and how long this dispersal took place is presently unknown except to say that it was at least no later than an early Hemingfordian event.

Perhaps the greatest value in the discovery of *Paratoceras wardi* lies in the fact that it reveals for the first time generic characters of the skeleton other than those of the lower jaw. Previously diagnosed only on the basis of its large, unreduced premolars and low-crowned molars, *Paratoceras* is now seen to represent a greater morphologic departure from other protoceratid genera. This is especially visible in the configuration of the skull and cranial armament. Even among a group of animals renowned for its bizarre horn development, *Paratoceras* attracts special attention. All protoceratid genera possess horns or hornlike protuberances on the maxillaries and supraorbital borders, but only *Paratoceras* developed a forked horn on the occiput. In

only one other artiodactyl group, the Cranio-ceratinae, is there a parallel evolution of an occipital horn. In North America all members of the Cranio-ceratinae have a single-shafted occipital horn, but in Europe a palaeomerycid, *Triceromeryx pachecoi* (de Villalta Comella, Crusafont Pairó, and Lavocat, 1946), from Spain has a bifurcated occipital horn. The palaeomerycid horn is robust and long shafted, whereas in *Paratoceras* the occipital is extremely short shafted with relatively longer and more compressed forks. It is curious that forking was so persistent (and unique) a theme in the evolution of protoceratid horns; perhaps it is as genetically fixed as branching is among the antlers of the cervids. Another remarkable feature of the occipital horn is its participation in the origin of the mandibular musculature (see evolution and phylogony). This qualifies as an extraordinary secondary adaptation in the evolution of horns; superposed on an already unusual structure, it is all the more noteworthy.

Aside from its morphological and functional significance, the genus *Paratoceras* (as revealed by *P. wardi*) is also important in that it represents a heretofore incompletely recognized distinct phylogenetic lineage among the Protoceratidae. Previously the genus was known to depart from *Protoceras* only in dental differences, the other above-mentioned distinctions disclose an evolutionary offshoot of considerable extent and duration. Now, instead of being known by just a few mandibular specimens from the Texas Panhandle, we recognize the genus in collections from the Texas Coastal Plain and as far south as Panama.

Paratoceras macadamsi Frick, 1937

Figures 13, 14A-C; table 7

Paratoceras macadamsi FRICK, 1937, p. 609, fig. 65.

TYPE: F:AM 32457, right partial mandible with P₂-M₃ (broken) from Location 17, Quarry 1,¹ 10 miles north of Clarendon on the east side of Carrol Creek in the NW $\frac{1}{4}$, NE $\frac{1}{4}$, sect. 7, Blk. C-3, G.C. and Santa Fe Railway Survey, Donley County, Texas.

DISTRIBUTION: Clarendonian of the Texas Panhandle.

¹Location 17, Quarry 1 is synonymous with Mac-Adams Quarry, and Location 17, Quarry 2 and Canyon, Texas Museum's Grant Quarry are a continuation of the same channel deposit.



FIG. 14. A–C. *Paratoceras macadamsi* Frick. A. Right maxilla, F:AM 53519. (See fig. 13A and B.) B. Left partial ramus, F:AM 53518, reversed. C. Type, right ramus, F:AM 32457 (see fig. 13C, D). D. *Paratoceras wardi*, new species. Right ramus, F:AM 40750. (See fig. 9I.) All lateral views. $\times 1$.

REFERRED MATERIAL: From the type locality; F:AM 53519, right partial maxilla with C and P¹(alveolus)-P³; F:AM 53516, left mandible with P₁-M₃; F:AM 33409, left partial mandible with P₄-M₃; F:AM 53515, right partial mandible with P₁(broken)-M₁; F:AM 53518, left partial mandible with P₁-P₄; F:AM 53517, left mandibular fragment with P₁; F:AM 53520, right immature partial mandible with P₁ germ and dP₂-dP₃.

DIAGNOSIS: Differs from *P. wardi* in having approximately 25 percent larger dentition; taller-crowned molars; a shorter muzzle, especially shorter P¹-P² diastema; weaker and less complete lingual cingulum on P²; a deeper horizontal ramus; and a posteriorly thicker and more wedge-shaped P₄.

DESCRIPTION: Although the type mandibular specimen described by Frick in 1937 has been the sole basis for recognition of this species (and up until now, the genus), subsequently collected material from the type locality allows us to enlarge the original description.

MAXILLA: The only known specimen of the skull of *P. macadamsi* consists of the right maxilla containing C and P¹ (alveolus)-P³ (F:AM 53519, fig. 13A-B). In virtually every respect it compares closely in morphology to *P. wardi*. The upper border of the maxilla is expanded dorsally into a thin, arched plate of bone that was obviously unconnected to its opposite counterpart. The dorsal rim has a rounded, free border that is slightly thicker than the rest of the plate. The labial surface of the maxillary plate is rough and pitted, but this preserved part lacks the elaborate sculpturing and bracing typical of *P. wardi*. A prominent foramen penetrates the labial surface of the plate, probably conducting the facial branches of the intraorbital vessels. Another, larger, foramen occurs ventrally on the lingual face of the plate.

As in *P. wardi* and in *Protoceras celer* most of the anterolabial part of the maxilla serves as a sheath to contain the enlarged canine and canine root. The root extends posteriorly in a wide arc to abut on the roots of P²; the bony sheath for this root forms a prominent bulge along the labial surface of the maxilla. The bulge continues posteriorly into the strongly developed masseteric ridge. Below the bulge at the level of the posterior diastema the maxilla is strongly pinched lingually. Two subequal maxillary

diastemata are formed by an isolated P¹ separating C from P². In ventral view, the labial border of the maxilla flares outwardly from P² to the canine, so that the canine is more laterally placed than the cheek dentition.

The palatine process of the maxilla is only partially preserved. It is apparently narrowest just anterior to P², and, as is true of *Protoceras*, it is very flat transversely and anteroposteriorly. The palatine process meets the vertical plate of the maxilla at a very sharp angle. Scott (1940, p. 575), describing the same bone in *Protoceras*, gave the following interpretation: "The faintly marked rugose ridges which indicate the limits of the soft palate in front of the premolars, are in many existing ruminants placed quite close to the median line, so that part of the ventral surface of the maxillary was not covered by the soft tissue. In *Protoceras*, on the other hand, these ridges run along the angle formed by the meeting of the horizontal and vertical surfaces of the bones, which thus do not curve into each other as gently as in the modern forms mentioned."

TABLE 7
MEASUREMENTS (IN MILLIMETERS) AND STATISTICS OF
THE LOWER DENTITION OF *Paratoceras macadamsi*,
DONLEY COUNTY, TEXAS

	N	OR	\bar{X}	S	V
P ₁					
Length	2	7.7- 7.8	7.75	0.071	0.91
Width	2	3.5- —	3.50	0.000	0.00
P ₂					
Length	4	15.0- 16.0	15.38	0.435	2.83
Width	4	5.6- 6.0	5.83	0.171	2.93
P ₃					
Length	3	15.6- 16.7	16.03	0.586	3.65
Width	3	6.9- 7.3	7.07	0.208	2.95
P ₄					
Length	4	13.0- 14.4	13.65	0.597	4.38
Width	3	9.1- 9.9	9.43	0.416	4.41
M ₁					
Length	4	14.4- 15.5	14.73	0.519	3.52
Width	4	11.2- 12.5	11.78	0.675	5.73
M ₂					
Length	3	16.5- 18.2	17.23	0.874	5.07
Width	3	12.8- 13.2	13.03	0.208	1.60
M ₃					
Length	3	22.0- 25.0	23.10	1.652	7.15
Width	3	12.5- 13.7	13.27	0.666	5.02
P ₂ -P ₄	2	45.0- 46.4	45.70	0.990	2.17
M ₁ -M ₃	3	52.8- 58.0	55.17	2.631	4.77
P ₂ -M ₃	2	99.5-104.5	102.00	3.536	3.47

Scott (*op. cit.*) also remarked on the unusual position of the posterior palatine foramina which in *Protoceras* "are placed just internal to P¹ and from them deeply marked vascular grooves run forward to the incisive foramina. These, perhaps, represent the foramina which in *Merycoidodon* and *Bothriodon* occur opposite P³."

This unusual position for the posterior palatine foramen obtains also in *P. macadamsi*, except that in the one maxillary specimen available, another much smaller foramen occurs just posterior to it and is connected to the larger one by a shallow vascular groove. No posterior foramen is observed in *P. wardi*.

UPPER DENTITION: The partial right maxilla described above contains the canine and P¹ (alveolus)-P³.

The canine of *Paratoceras* is known only from the *P. macadamsi* maxilla, that tooth being indicated only by large alveolus in *P. wardi*. Like that of *Protoceras*, the *Paratoceras* canine is trihedral in cross section. This shape is also roughly similar to that in the oreodonts, but the protoceratine canine is longer, more compressed, and slenderer than in the oreodonts. Also as in *Protoceras* and the oreodonts, the *Paratoceras* canine is worn on the posterior face of the tooth, indicating that the first lower premolar had become the caniniform tooth in the lower series. Like *Protoceras* and unlike the oreodonts, the *Paratoceras* canine is strongly flared laterally, no doubt forming part of the male threat and display complex, along with the cranial horns. The

upper premolars of *P. macadamsi* differ little in proportions from those of *P. wardi*, the chief distinction lying in the greater absolute size of the former. P² lacks the complete lingual cingulum present in *P. wardi*. No discernible differences in P³ exist between the two species.

MANDIBLE: The poorly preserved mandibular specimens of *P. macadamsi* reveal only the greater depth of the mandible of this species compared to that of *P. wardi*.

LOWER DENTITION: I₂, C₂, P₁₋₄, M₁₋₃. The most notable feature of the lower dentition of *P. macadamsi* is its increase in crown height over that of *P. wardi*. This probably also accounts for the relative increase in the depth of the mandible. As in *P. wardi*, the anterior crest (paraconid) of P₂ and P₃ is separated by a distinct notch from the high, pointed protoconid. In *P. macadamsi* a strong anterolingual flexid is present on P₃ (F:AM 53516). Also as in *P. wardi*, and in contrast to *Protoceras celer* and the synthetoceratines, the posterior crests (hypoconid and entoconid) are parallel and oriented anteroposteriorly, displaying no lingual curve. Buccally, the posterior base of P₄ in *P. macadamsi* develops a stronger cingulum than that of *P. wardi*. The primary differences between the premolars of the two species is in the greater crown height and posterior thickness of P₃ and P₄.

The lower molars of *P. macadamsi* differ from those of *P. wardi* only in the greater crown height and occasional absence of an internal pillar on M₃ of the former.

EVOLUTION AND PHYLOGENY

THE PHYLOGENETIC HISTORY of the Protoceratinae spans a segment of geologic time ranging from Chadronian (early Oligocene) to late Clarendonian (early Pliocene). In contrast, the history of the Synthetoceratinae is recorded only from the late Arikarean (early Miocene) to early Hemphillian (medial Pliocene). The phylogeny of the Synthetoceratinae involves only a single linear succession with comparatively minor geographic differentiation, whereas that of the Protoceratinae contains the primitive *Pseudoprotoceras*, an adequate prototype for all later protoceratid evolution, and, in addition, two well-differentiated lineages, *Protoceras* and *Paratoceras*.

The earlier genera, *Pseudoprotoceras* and *Heteromeryx*, adequately fulfill the morphologic and chronologic requirements necessary for all later radiation: they possess the most primitive features and occur in the oldest rocks. Both genera possess simple, relatively slender and elongate skulls. Both are also hornless and lack facial and cranial crests, but possess retracted nasal bones and slightly arched maxillary borders. It is especially the last characters that distinguish them as protoceratids and anticipate the principal characteristics of the family. However, *Pseudoprotoceras* rather than *Heteromeryx* is placed in the direct ancestral position for later protoceratid evolution, primarily because of its simpler dentition, more retracted nasals, and longer arched muzzle. Additionally, *Heteromeryx* possesses a strongly fused ulnoradius, a more advanced feature than the partially fused ulnoradius of later occurring genera. This character removes *Heteromeryx* from a directly ancestral position. Unfortunately, we have no record of the limbs of *Pseudoprotoceras*.

The origin of the type genus *Protoceras* is obscure, for no transitional forms are known between it and its probable ancestor *Pseudoprotoceras*. It is apparent, however, that the transition took place sometime between Chadronian and late Whitneyan. It is also apparent that an important evolutionary development during this period involved the acquisition of horns or hornlike structures on different parts of the skull. We have previously discussed various aspects of *Protoceras* evolution (Patton and Taylor, 1971, p. 209), some of which bear repeat-

ing here. All *Protoceras* males possess the unique bony protuberances that characterize the skull of that genus and all later protoceratids. Although subject to some variation, the bony processes of *Protoceras* males fall into two primary groups: rostral and cranial. The cranial protuberances rise from the temporal crests of the parietals and from the supraorbital borders of the frontals. The rostrals rise from the dorsal borders of the maxillaries. A third and smaller set of protuberances occurs on the male skull of *P. celer* at the anterolateral borders of the frontals near the suture with the nasals and lacrimals. These are faintly indicated in the female and do not persist in the later protoceratines or synthetoceratines. Unfortunately, only *P. celer* of the three presently recognized *Protoceras* species, is represented by male skulls. All that we know of horn evolution within the genus, therefore, is restricted to evidence supplied by that species. The horn evolution of the other protoceratine, *Paratoceras*, was distinct from that of *Protoceras*, involving emphasis on different structures. Thus, unlike the Synthetoceratinae in which horn evolution follows a single progression of morphological steps, that of the Protoceratinae is composed of two divergent types, each of which must have evolved separately from some simple-horned unknown common ancestor that followed *Pseudoprotoceras*.

The protoceratine horns (indeed, those of the entire family) are simple structures growing directly from the dermal bones. Although similar in appearance to giraffid horns, they apparently did not develop from the "ossicones" characteristic of that family. Like the giraffes, however, and probably like the titanotheres and dinoceratids, they may have been covered with tough skin. Available evidence precludes the presence of any kind of sheath, deciduous or permanent.¹ The size, shape, placement, and sexually dimorphic expression of these structures indicate that they served as part of threat display and as fighting organs involving social ranking of males. According to Geist's (1966) classification, they correspond to Stage I in the evolution of horn types, i.e., they are simple and

¹ The functional morphology of protoceratid horns will be covered in more detail in another paper.

TABLE 8

SUMMARY OF DIAGNOSTIC CHARACTERS OF THE PROTOGERATINAE

	<i>Heteromeryx</i>	<i>Pseudoprotoceras</i>	<i>Protoceras</i>	<i>Paratoceras</i>
Skull proportions	Short with less posteriorly placed orbits, shorter facial region than in <i>Protoceras</i>	Facial region less elongate than in <i>Protoceras</i>	Posteriorly placed orbits, elongate facial region, extremely short cranium	More forwardly placed orbits, less elongate facial region and longer more expanded cranium than in <i>Protoceras</i>
Maxillary protuberances	None	None	Relatively large bony plates of varying form	Smaller, more pointed, and more posteriorly situated
Supraorbital protuberances	None	None. Elongate rugose convex area above, slightly anterior of orbit	Short triangular-shaped projections arising on dorso-posterior rim of orbit	Longer, almost erect but gently recurved, tapering horns with bulbous tips arising from superior rim of orbit
Parietal protuberances	None	?	Two almost erect hornlike protuberances arising just posterior to orbit from strong parietal crests in male	Parietal protuberances absent; parietal crests weak in male
Occipital horn	?	?	None	Almost erect transversely forked occipital horn arising from occiput of male skull
Sagittal crest	Moderate	?	Strong	Extremely weak
Lower incisor teeth	?	?	Three incisors and an incisor form canine	? Broken alveoli indicating only three incisor teeth present with either I ₃ or C believed lost
Muzzle	Moderately long, approximating that of <i>Pseudoprotoceras</i> with P ¹ about midway between C and P ²	Moderately long with P ¹ slightly closer to C than P ²	Long with P ¹ about midway between C and P ²	Shorter with P ¹ nearer C, and longer diastema between P ¹ and P ²
p ₂ -p ₃	Proportionally larger and more robust than in <i>Pseudoprotoceras</i> and <i>Protoceras</i> ; strong protocone on P ² and P ³	Similar to <i>Protoceras</i> but smaller	Elongate with lingual cingulum; P ³ strong protocone	Less elongate, more robust; P ³ without protocone
P ₂ -P ₃ Molars	? Very brachydont, with worn molars of the type appearing lower crowned than in <i>Protoceras</i>	? As in <i>Protoceras</i> but smaller	Elongate and slender Low crowned	Less elongate and more robust Taller crowned
Mandibular ramus	?	?	Broadly expanded masseteric region	Less expanded
Ulna	Well-developed ulna fused with radius along its entire length	?	Strong ulna with only distal end fused with radius	Lighter ulna fused most of its length with radius

small and are probably employed by swinging the head up and sideways, dealing the opponent a blow on the side. In contrast to the more posteriorly placed horns, the anterior arched protuberances on the maxillaries probably served, not as offensive bruising organs, but rather as protection for the proboscideiform muzzle. The morphological steps between *Pseudoprotoceras* and *Protoceras* probably also reflect a change to a social structure involving small, relatively independent groups approaching the gregariousness of small herds. This conclusion is supported by (1) the evolution of horns, which is normally a concomitant to hierarchical confrontation between males of herding ungulates, and (2) the numerical abundance of fossil specimens in such deposits as the *Protoceras* channels of the Poleslide Member of the Brule Formation. Although *Protoceras* specimens are rare in an absolute sense, they are found in abundance in the *Protoceras* channels. This may reflect either strong habitat preference or ecological conditions.

Irrespective of the horns, the skull of *Protoceras* departs from those of other Oligocene artiodactyls in ways that Scott (1895, p. 309) regarded as being "modernized": (1) the cranium is shortened and rounded; (2) the orbit is shifted backward to lie completely behind the line of the molar teeth; (3) the facial region is elongated, due not only to the shifting of the orbit, but also to the lengthening of the muzzle; and (4) greater flexure of the basifacial-basiscranial axis. Although these characters largely persist in later forms, they are outweighed by the shift toward evolution of male cranial and rostral armament, especially among the synthetoceratines. Among the females, the skull of *P. celer* differs little from those of *P. skinneri* and *P. neatodelpha*. Those general skull characters described above by Scott are apparently not sexually dimorphically expressed but apply equally well to females. Unlike that of the horned males, the evolution of the female *Protoceras* skull involved little change from the Whitneyan to the Arikareean.

The dentition of *Protoceras* has been described in general terms by Patton and Taylor (1971, p. 209): "Except for the lack of upper incisors, *Protoceras* possesses a full dentition. In the upper jaw there are no traces of alveoli in the premaxillaries. The canine of the male is a large curved tusk, comparable in development to that of *Hydropotes*, *Moschus*, and *Tragulus*. The premolars are unreduced and the molars are quite

brachydont, robust, and complicated by accessory styles and tubercles. The lower jaw of *Protoceras* is relatively deep and robust, possesses a normal rounded and expanded angle and has a relatively short diastema. The lower dentition consists of three incisors, an incisiform canine, a caniniform P_1 , P_2 - P_4 , and M_1 - M_3 . As is true of upper dentition, the molars are unreduced and primitively constructed, with both accessory stylids and tubercles."

Evolutionary changes in the dentition of *Protoceras* species were relatively minor. A progressive reduction of the lingual cingulum and the protocone of P^2 and P^3 occurred from *P. celer* through *P. neatodelpha*, but other than a general increase in crown height few consistent trends are observed in this sequence. We have also previously summarized the evolutionary stage of *Protoceras* limbs (Patton and Taylor, 1971, p. 209). Unfortunately, no limb bones of the later-occurring species of *Protoceras* are presently known, precluding the determination of evolutionary trends in these structures. Because of this lack of adequate preserved material, especially limbs and male skulls, we are unable to determine the nature and extent of dispersal and evolution of *Protoceras* species after *P. celer*. Certainly the discovery of any kind of *Protoceras* later than Whitneyan was unexpected. Its unsuspected but now undoubted occurrence as late as the late Arikareean, coupled with its scanty preservation and biased sampling, tantalizes rather than informs. The conservatism of the female skulls of *P. skinneri* and *P. neatodelpha* provides no real clue as to what, if any, changes occurred on the skull of corresponding males. For the present we can say only, that the genus was more widespread, geographically and chronologically, than previously thought, and that during the time represented by its fossil record it accumulated cranial morphological differences sufficiently distinctive to warrant recognition of three successional species, *P. celer*, *P. skinneri*, and *P. neatodelpha*. Without any real evidence to the contrary, we assume these forms to represent "chronospecies," i.e., they are related by direct genetic descent rather than representing two distinct lineages branching from *P. celer*. This opinion is based on their close geographic proximity, morphological similarity, and their separation in successive biostratigraphic units.

Unquestionably the greatest gap in our knowledge of protoceratine evolution lies in the

origin of the genus *Paratoceras*. Morphologically, it combines the skull features of both the protoceratines and synthetoceratines. The nasals are retracted and the maxillaries are arched into bony protuberances similar to those of *Protoceras*; over the orbits, however, are widely flared and recurved horns characteristic of the Synthetoceratinae. In other features, especially the development of a unique occipital horn, the genus departs from both groups to a degree that almost warrants separate subfamilial status. The above-mentioned similarities to *Protoceras*, however, compel us to conclude that its phylogenetic affinities are closer to the Protoceratinae and are best expressed by inclusion in that group.

The earliest record of *Paratoceras* is in the medial Hemingfordian of Panama. We can state only that the Panamanian population, as yet unstudied, is specifically different from the present recognized species, *P. wardi* and *P. macadamsi*. Its geographic and chronologic distribution, however, suggests a close phyletic relationship with *P. wardi* from the Barstovian of the Texas Coastal Plain. The latter species, described in the present report, reveals for the first time the distinctive cranial morphology of the genus. It has already been noted that the *Paratoceras* muzzle is characterized by highly retracted nasal bones and dorsally arched maxillaries that form two separate bony protuberances similar to those of *Protoceras*. Unlike *Protoceras*, however, the parietal protuberances are lacking; and instead of short frontal protuberances, *Paratoceras* has large, flared, and recurved horns extending out over each orbit. Although similar to the frontal or supraorbital horns of the synthetoceratines, the *Paratoceras* frontal horn is distinct and peculiar to the genus. Longitudinal vascular grooving on these horns indicate that they, like all other protoceratid horns, were covered with thick skin.

The strongly forked occipital horn of *Paratoceras* is fascinating not only for its unique structure and position, but also because it participates in the origin of the temporal musculature, again an unduplicated evolutionary phenomenon, so far as we are aware. Another puzzling and unique feature of the *Paratoceras* skull is the intensive sculpturing of the upper face, including the maxillaries, nasals, anterior portion of the frontals and parietals. We have arrived at no truly satisfactory explanation for the functional adaptation of this feature and can only presume

that it was involved in the origins of ligaments for muscles of the proboscidiiform muzzle. The evolution of the occipital horn is also difficult to interpret, primarily because of its small size and unusual placement. Such a horn would seem to have little value as an intimidatory device, but then it is difficult to assess its visual impact in social herds where juvenile-adult and male-female encounters demand immediate and definite recognition. The supraorbital horns alone could provide this sign unless the presence of other similarly horned species required even further distinctness. Another possible, if extraordinary, explanation for the evolution of this horn lies in its relationship to the temporal musculature. As described before, the anterior edge of each tine is marked by a prominent and roughened tuberosity that closely resembles a muscle attachment. Further, the ventral (lateral) surface of each tine is concave, forming a shallow sulcus that also resembles a surface for muscle attachment. Several other features outlined earlier also support this observation. It is interesting, therefore, to speculate on the adaptive relationship between the horn and the temporalis muscles. Did it serve to provide greater surface area for the origin of the temporalis muscles, much as the sagittal crest serves in many other mammals? Was the horn already evolved before the temporal musculature "took advantage" of this additional surface area for attachment? Or did the two evolve in some coadaptive fashion, each giving impetus to the other? Most, if not all, of these questions could be answered if we had a female skull of *Paratoceras*. If, however, the relationship between the horn and the temporal muscles is critical, then we would expect it to obtain in females as well as males. If the horn is a sexually dimorphic trait in *Paratoceras*, then we must assume the horn-temporal-muscle relationship to be adventitious, a circumstance as odd as the horn itself.

Acquisition of skull and horn features as distinctive as those of *Paratoceras* indicates that the genus branched off from *Protoceras* or some pre-*Protoceras* form at a very early stage. It is doubtful that *Paratoceras* evolved from any known *Protoceras* species; it is more likely that its divergence from the lineage that eventually led to *Protoceras* took place at least during the early Whitneyan, or perhaps as early as the late Orellan. From that point on the evolution of its cranial armament must have departed rapidly

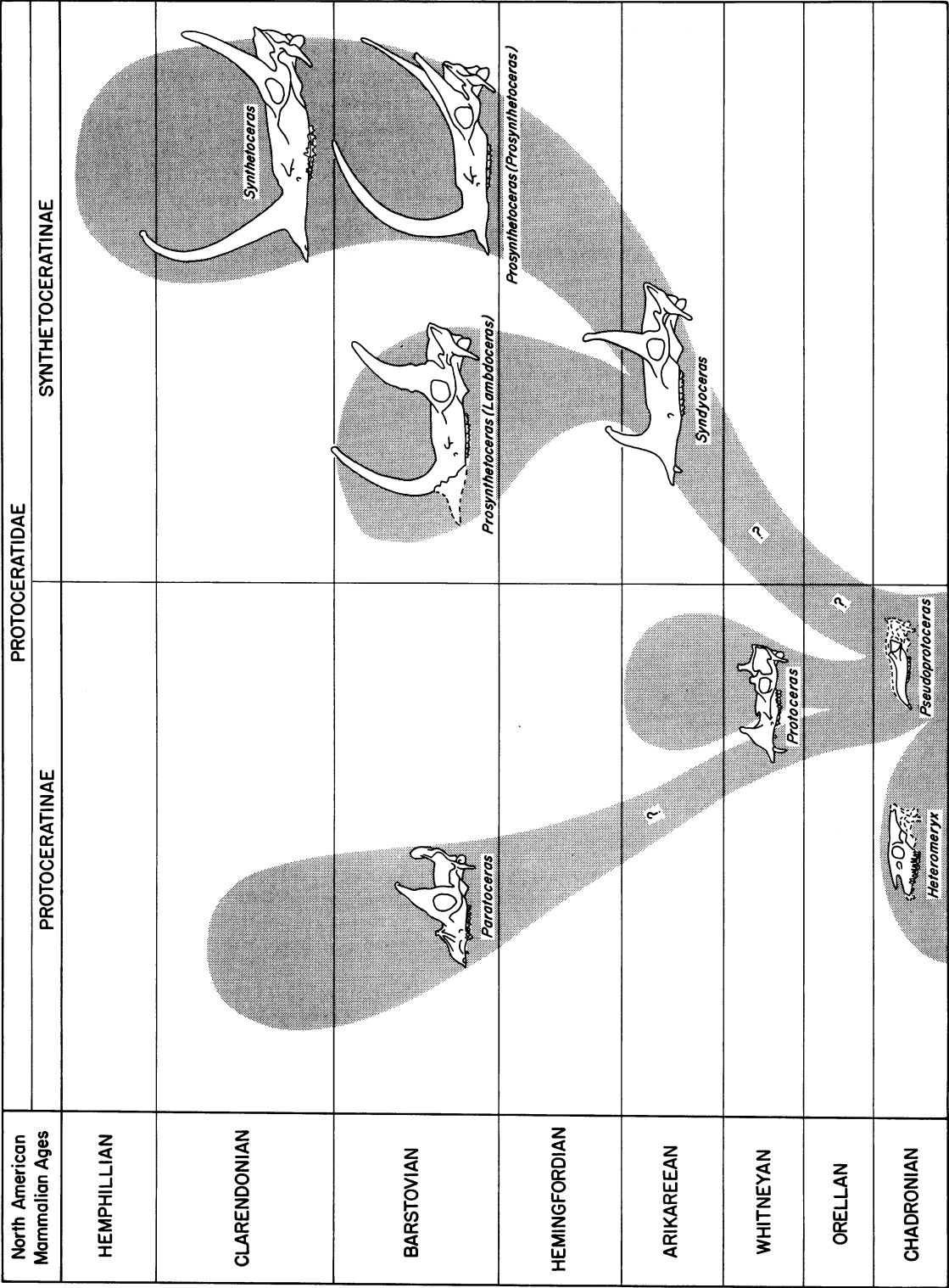


Fig. 15. Suggested phylogeny of the Protoceratidae.

from that of *Protoceras*, although the muzzle shows a roughly parallel progression. Because we have no record of *Paratoceras* in the Great Plains, and because the genus appears only in Texas and Central America, we assume that it dispersed southward soon after its divergence from the *Protoceras* lineage. Alternatively, we must also consider the possibility of an early *Protoceras* population in southern latitudes that gave rise to *Paratoceras*, but having no fossil record. Yet another, but presently unverifiable, possibility is that the *Pseudoprotoceras*-like form reported by Wilson (personal commun.) from the Oligocene of west Texas was the ancestor of *Paratoceras*. In any event, it is clear that much, if not all, *Paratoceras* evolution occurred south of the Great Plains, a circumstance shared in large part by the subfamily Synthetoceratinae. The spotty distribution pattern of *Paratoceras* is, like most fossil records, probably more artificial than real. Although the geographic and chronologic distribution of the genus extends from the Hemingfordian of Panama (undescribed species, p. 368) through the Barstovian of the Texas Coastal Plain (*P. wardi*) to the Clarendonian of the Texas Panhandle (*P. macadamsi*), a more continuous distribution through time and space among the once-living populations is likely. Lamentably, that segment of the Texas stratigraphic section most critical to our understanding the origin and center of dispersal of *Paratoceras* is either uninformative or missing entirely. The early Oligocene-early Miocene sequence in west Texas has produced only the aforementioned *Pseudoprotoceras*-like form, while that time span is very poorly represented or absent in the otherwise abundantly fossiliferous Texas Coastal Plain. Just how widespread, however, and what evolutionary changes took place between the three species is presently indeterminable, primarily because of the inadequacies of geologic sampling. We only recognize specific differences accumulated during the time represented by their fossil record; how this temporal and geographic isolation affected the evolutionarily critical and taxonomically important skull and horn features, is unknown.

The most puzzling aspect of *Paratoceras* distribution is its restricted occurrence in the relatively extensive and well-known biostratigraphic units of the Texas Coastal Plain. *Paratoceras* appears only in the incompletely described Trinity River local fauna, an assemblage that lies stratigraphically between the Burkeville and

Cold Spring faunas (Patton and Taylor, 1971, pp. 127, 207). This genus, like *Prosynthetoceras* (*Lambdoceras*), is not recorded in any of the other well-sampled units that comprise the Coastal Plain succession; other protoceratids, however, are abundantly preserved in the bracketing deposits (Patton and Taylor, 1971).¹ What events led up to and succeeded this apparently anomalous configuration are entirely conjectural. The biotic assemblages represented by the Garvin Gully, Burkeville, Cold Spring, and Lapara Creek faunas are for the most part sequential and patterned (Patton, 1969). In contrast the Trinity River local fauna contains elements that are not only new to the region but are also unique in the succession. These forms appear so suddenly and are so short-lived that they suggest either (1) a rapid southward dispersal of northern Great Plains forms [e.g. *P. (Lambdoceras)* and *Paratoceras*], owing to a relatively abrupt opening of an ecologically suitable route; these transients were unable to displace the established forms, such as *Prosynthetoceras*, and were eventually extirpated, or (2) the Gulf Coastal Plain biostratigraphic succession is so ecologically biased as to give us only a constricted view of what was going on over most of the region at any one time. To address the second interpretation first, we would suggest that the general geographic uniformity of fossil occurrence that led Wilson (1956) to set up the sequence of units in the first place argues against localized ecological bias in fossil sampling. This is not to say that an ecotone consistently unsampled because of a regionally peculiar configuration cannot occasionally be recorded; in fact, this would create the very kind of anomalous occurrence we are faced with here. On the other hand, largely random sampling hypothesized under (2) would give us none of the interpretive and predictive capacity we use in the Gulf Coast sequence. The first interpretation appears to be more consistent with all that we know of this region; but it is not totally satisfactory, because of the apparently excessive rapidity of the events that may have occurred. It is also, unfortunately, the most difficult to document. A stratigraphic succession in the Texas Panhandle comparable with that of the Coastal Plain would go a long way toward solving this problem.

¹Still other undescribed forms occur in the Trinity River local fauna that are absent from other Coastal Plain deposits.

SYSTEMATIC RELATIONSHIPS OF THE PROTOCERATIDAE

HISTORICAL REVIEW

SINCE MARSH'S FIRST DESCRIPTION (1891) of the genus *Protoceras* confusion has surrounded the systematic affinities of the family Protoceratidae. Few mammalian phyla have so consistently defied systematic placement as this strange group. Prophetically, Marsh's (1891, pp. 81–82) initial remarks included only the briefest appraisal: "This animal was apparently a true ruminant . . . the animal represented by this skull is very distinct from any hitherto described . . . The characters now known suggest affinities with the giraffes, but indicate a distinct family, which may be called the Protoceratidae."

The following year, Osborn and Wortman (1892, p. 369) in a more extensive treatment of the family, compared the Protoceratidae with the Tragulina and the Pecora and reservedly concluded that: "there are no marked affinities in the direction of any of these families. In the possession of bony protuberances on the parietals which are probably processes of this bone and not developed separately as in the Giraffe, in the general architecture of the skull, together with so many primitive characteristics of the feet, this genus apparently occupies a distinct position and cannot be consistently referred to either the Tragulina or the Pecora as at present constituted and defined. The possession of multiple horns suggests the possible relationship of the family to the Sivatheriidae, but the likeness does not extend to other features of the skull.

"That it represents a distinct family there can be little doubt. Of its successors, we know nothing whatever, and our ignorance is equally great in the matter of its ancestry."

In 1895 Scott presented an even more exhaustive analysis of protoceratid relationships, comparing the group primarily with the same Pecora and Tragulina. He concluded (pp. 358–365) that the skull of *Protoceras* exhibits a remarkable assemblage of characters, some more primitive than the tragulines, some extremely modernized and advanced like those among the higher Pecora, and some peculiar to itself. Although consideration of the skull features alone might indicate referral of the protoceratids to the Pecora, Scott believed that the configuration of primitive and advanced characters argue against

such a move. On the same grounds, Scott (1895, p. 360) also rejected the possibility of the genus being a transitional form; in such a form he believed we should find "an association of features like those of *Tragulus* and *Gelocus*, on the one hand, and of the lower Pecora, such as *Moschus*, on the other." Scott contended that *Protoceras* could have only a remote connection with the Pecora and, as a consequence, any suggested relationship with members of that group are illusory. He believed that its position as a connecting link between the tragulines and the deer is precluded, moreover, by having more primitive feet than the former and a more advanced skull than the latter.

Scott (*op. cit.*, pp. 364–365) then compared *Protoceras* with *Leptomeryx*, *Hypertragulus*, and *Hypisodus* and inferred a natural relationship among these genera. He considered these to comprise a family of White River selenodonts, "each of whose genera has become more or less specialized in a way peculiar to itself, and with a tendency to simulate the Pecora in some respect or other, yet always retaining a number of primitive features."

Scott believed that *Protoceras* represents a divergent offshoot of the same stock which, while retaining in most respects the foot-structure belonging to the common ancestor of all these genera, has, at the same time, paralleled the higher Pecora in many features of the skull.

In a more confident interpretation of *Protoceras* affinities, and following up on his earlier conclusions, Scott (1899, pp. 19, 21) presented the following important remarks: "Professor Marsh ('91, p. 82) has proposed the formation of a separate family for the reception of this extraordinary genus, but this seems hardly necessary, for in essentials *Protoceras* does not differ more from *Leptomeryx* or *Hypertragulus* than they do from each other, despite its bizarre appearance. . . . Aside from the extraordinary peculiarities of the skull, especially in the male sex, *Protoceras* displays an unmistakable likeness to *Leptomeryx* and *Hypertragulus*, a likeness which is apparent in the vertebral column, the limb-bones, the feet, and the dentition. Combined with these are certain resemblances to *Peobrotherium*, fewer and less striking ones to the oreodonts, and a number

to the Pecora. It should be remembered, however, that the pecoran characteristics, which are almost exclusively confined to the skull, are such as are found only in the *higher* Pecora, the Cavicornia, and do not occur in the deer. It may seem quite absurd to regard *Protoceras* as an aberrant member of the Tylopoda, but, as will be shown in the sequel, it is highly probable that such is the correct view of its relationships. I am glad to find myself in agreement with Dr. Wortman on this point, for in the paper already cited he speaks of the early cameloids, *Protoceras* and *Leptomeryx* ('98, p. 102).'' In the same paper, Scott placed *Protoceras* alongside *Leptomeryx*, *Hypertragulus*, *Hypisodus*, *Leptoreodon*, *Camelomeryx*, and *Oromeryx* in the family Leptomerycidae, which he included in the Tylopoda. In itself an interesting departure from the then-prevailing classification, Scott (*op. cit.*, p. xi) took an even more radical step by declaring that, "with the possible exception of the oreodonts and agriochoerids, all of the strictly indigenous North American selenodonts are derivatives of the tylopodan stem." We shall return to this point later in the discussion.

In 1905 Matthew referred *Protoceras* and his new genus, *Heteromeryx*, to the Hypertragulidae, a family which was roughly synonymous with Scott's Leptomerycidae. Unable to accept Scott's (1899) tylopodan persuasion, Matthew (1905, p. 25) regarded the group "as an entirely independent offshoot of the primitive ruminant stock, without especially near relations to any other group. . . ." He considered the distinguishing characteristics of the family to be the combination of a functionally tetradactyl manus with a didactyl pes.

The description of the genus *Syndyoceras* in 1905 shed little light on the problem; in fact, Barbour (1905, p. 798) was led to say only that, "*Syndyoceras* seems to be remotely related on the one hand to *Protoceras* of the Oligocene, and on the other hand to modern antelope." With the exception of Loomis's (1925, 1928) brief referral of *Protoceras* to the camels, it was not until 1932, when Stirton described the genus *Synthetoceras*, that the problem of protoceratid ancestry and relationships was resurrected. The well-preserved *Synthetoceras* from Clarendon, Texas, provided a new dimension to protoceratid phylogeny, but provided little information on the family's ancestry; in fact, Stirton (1932, p. 154) concluded his study by remarking only on the un-

certain relationship between the Protoceratidae and the Hypertragulidae, finally leaving the question open to future discoveries.

The most extensive systematic review of the Protoceratidae was included in Childs Frick's treatment of North American horned ruminants; however, while Frick did much to expose previously undescribed material, he completely avoided any reference to familial relationships. In contrast, Colbert (1941) speculated on the relationships of artiodactyl families, including the Protoceratidae, but made no specific comparisons with that family. His only comment was that the protoceratids were derived from the Hypertragulidae. However, his more general argument has considerable bearing on our discussion.

Probably the most important treatment of protoceratid systematics was that of Scott (1940), whose views on artiodactyl phylogeny were the product of study over a protracted period (see Scott, 1895, 1899). Unquestionably Scott's most important contribution was his contention that the Protoceratidae, as well as the hypertragulids and oreodonts, are not ruminants, as has been the usual claim, but are more properly placed in the Tylopoda. Because of their relevance to our own conclusions, Scott's opinions are integrated into the more comprehensive discussion which follows.

Stirton (1944) suggested that the suborder Pecora be subdivided into three superfamilies, Traguloidea, Cervoidea, and Bovoidea. Under this arrangement, the Protoceratidae were included in the Traguloidea along with the Amphimerycidae, Hypertragulidae, Tragulidae, and Gelocidae.

Finally, the discovery and description by Stirton (1967) of a new genus of protoceratid, *Lambdoceras* (reduced to subgeneric status by Patton and Taylor, 1971), again stimulated speculation on the origin and affinities of the family, completely reordering Stirton's previous ideas. In this paper Stirton, without acknowledging Scott's (1940) prior classification, also claimed tylopodan heritage for the Protoceratidae. Like those of Scott, his views are more fully outlined in the subsequent discussion.

GENERIC COMPARISONS

It is obvious that systematic placement of the Protoceratidae has been highly problematical. However, notwithstanding the peculiarities

attaching to the family in its own right, it is equally obvious that much of the difficulty arises from the complexities of artiodactyl systematics in general. Without attempting to arrive at any sweeping rearrangement of the Artiodactyla in the present report, we nonetheless must re-examine the basis for classification of several important groups. Because *Protoceras* and its early relatives, *Pseudoprotoceras* and *Heteromeryx*, have been compared to, and allied with, such a disparate array of taxa, a re-examination of its relationships to the genera with which they are most frequently compared is now warranted.

With the exception of Osborn and Wortman's (1892), Loomis's (1928), Scott's (1940), and Stirton's (1967) classification of the Protoceratidae with the Tylopoda, most authors have placed the family in the Ruminantia, variously within the Tragulina and Pecora. Therefore, so that the position of the protoceratids may be more fully understood, a comparison is made with members of both the Tragulina and Pecora. In evaluating those protoceratid characters that appear to be most diagnostic with respect to other groups, we find that those of the limbs are especially useful, primarily because of their relative evolutionary conservatism when compared with features of the skull and dentition. Genera used in this comparison include *Archaeomeryx*, *Leptomeryx*, *Tragulus*, *Hypertragulus*, and *Leptotragulus*. Conclusions drawn from these comparisons follow immediately after this discussion.

Archaeomeryx: Matthew and Granger (1925) described and referred *Archaeomeryx* to the Hypertragulidae. After a thorough osteological study of the genus, Colbert (1941, p. 9) concurred that Matthew and Granger were fully justified in this family assignment. Unlike all other members of the Hypertragulidae, *Archaeomeryx* possessed functional upper incisors. In *Hypertragulus*, vestigial upper incisors are indicated by minute alveoli, but *Protoceras* has no trace of these teeth. The upper canine is of medium size in both *Archaeomeryx* and *Hypertragulus*, whereas *Protoceras* has a large upper canine that is "tusk-like" in the male. Colbert observed that seemingly the first upper premolar had been lost in *Archaeomeryx*, and in this respect the loss of P¹ was a less primitive condition than in *Hypertragulus* or *Protoceras*. The premolars in *Archaeomeryx* are similar to those of *Hypertragulus* except for the larger internal cusp (protocone) on P³

which recalls a condition seen in *Leptotragulus* and *Leptomeryx*. The upper molars are quadricuspid, low crowned, and lack the protoconule present in *Amphimeryx*. Compared with those of *Hypertragulus*, the upper molars of *Archaeomeryx* are lower crowned, the parastyle is equally developed, but the mesostyle which is lacking in *Hypertragulus*, is prominent and the metastyle is less strongly developed on M³. The lower incisors and incisiform canine of *Archaeomeryx* are without diastemata, whereas P¹ is caniniform and isolated by diastemata, as in *Hypertragulus* and *Protoceras*. The lower premolars (two through four) are basically like those of *Hypertragulus* but are in an uninterrupted series and less trenchant. P⁴ metaconid of *Archaeomeryx* is stronger than that of either *Hypertragulus* or *Protoceras*. The lower molars are quadricuspid and brachyodont, lower crowned than in *Hypertragulus*, and, despite the difference in size, appear proportionally similar in crown height to *Protoceras*.

The limbs of *Archaeomeryx* strongly resemble those of *Hypertragulus*. The radius and the relatively heavy ulna are separate. Lack of co-ossification of the radius and ulna indicates a more primitive stage of development than either *Hypertragulus* or *Protoceras*. In the latter, the distal end of the radius and ulna are co-ossified, but in *Hypertragulus* the radius and ulna are completely fused. Unfortunately, the carpals are missing in the manus of *Archaeomeryx*, but four unfused digits are present. Because of crushing, it is not clear whether metacarpal I was ever present, but Colbert concluded that the pollex was probably suppressed. If this is the case, *Archaeomeryx* would be more advanced, in this respect, than *Hypertragulus*, which retains the pollex. In *Archaeomeryx* metacarpals II and V are relatively heavier than in *Hypertragulus* and proportionally similar to those of *Protoceras*. Colbert (1941, p. 8) observed that the fibular facets on the tibia showed probable unconnected proximal and distal vestiges of the fibula. In contrast, *Hypertragulus* has both ends of the fibula co-ossified with the tibia, and *Protoceras* has the proximal end of the fibula co-ossified with the tibia, although the distal malleolar bone is separate. As in *Hypertragulus*, the astragalus in *Archaeomeryx* lacks the distal keel and the upper and lower ginglymi are parallel. On the other hand, the astragalus in *Protoceras* has a distal keel and the condyles of the distal trochlea are not parallel but instead are slightly deflected.

A completely fused cuboid and navicular in *Archaeomeryx* is typical of all members of the Hypertragulidae but unlike the protoceratids and camelids, in which these tarsals are separate. The ectocuneiform in *Archaeomeryx* is separate, apparently including the combined ecto-mesocuneiform as in *Hypertragulus* and *Protoceras*. A well-developed entocuneiform is present in *Archaeomeryx* and indicated in *Hypertragulus*; a relatively large entocuneiform is present and separate from the ecto-mesocuneiform in *Protoceras*. The pes in *Archaeomeryx* has four separate digits. Metatarsals II and V are slender lateral splints that extend almost the full length of metatarsals III and IV and are proportionally similar to those of *Hypertragulus*. Strangely, the development of the lateral metatarsals in *Archaeomeryx* and *Hypertragulus* is less advanced than in the otherwise primitive foot of *Protoceras*, in which these lateral metatarsals are reduced to proximal splints.

As observed by Matthew and Granger (1925) and Colbert (1941) the characters of *Archaeomeryx* are very close to *Hypertragulus* with the exception that *Archaeomeryx* is more primitive than *Hypertragulus* in possessing functional upper incisors and lower-crowned molars. Colbert pointed out that *Archaeomeryx* is more advanced than *Hypertragulus* in the closure of the orbit and the apparent loss of P¹. Examining the limb characters and foot structure, we again see a close resemblance to *Hypertragulus*. But certain characters in *Archaeomeryx*, such as the completely separate ulna, proportionally stronger metacarpals II and V, and indication of unfused proximal and distal vestiges of the fibula as shown by the articular facets on the tibia, are all more primitive characters than those found in *Hypertragulus*. Colbert (1941, p. 7) concluded that the pollex was probably suppressed in *Archaeomeryx*, in which case it would be more advanced than *Hypertragulus*, which retains five metacarpals. Skeletal features of *Archaeomeryx* that show a more primitive condition than *Protoceras* are: (1) the completely free ulna, (2) apparently unco-ossified proximal end of fibula and tibia, and (3) the almost full-length lateral metatarsals II and V in contrast to proximal splints of *Protoceras*. However, the cuboid and navicular are fused in *Archaeomeryx*, a condition that would seemingly preclude any ancestral relationship with the later occurring protoceratids, in which these tarsals remain separate.

Leptomeryx: In many ways *Leptomeryx* from the Chadron and Brule formations is more advanced than either of its contemporaries, *Pseudoprotoceras* and *Protoceras*. In *Leptomeryx* the dentition is more cervid-like and the foot structure more specialized than any other ruminant in North America. Although most authors have placed *Leptomeryx* with the Hypertragulidae, Matthew (1908, p. 552) considered *Leptomeryx* a primitive genus of pecoran stock related to the Cervidae. He reasoned that because of the cervid-like dentition and specialized foot structure, *Leptomeryx* was the only early North American form that could have been ancestral to the Cervidae.

Except for the vestigial upper incisors and the lower first premolar, the dentition of *Leptomeryx* is basically pecoran. In contrast, the dentition of *Protoceras* has more in common with that of *Hypertragulus*. In *Leptomeryx* the upper incisors are vestigial, but in *Protoceras* these teeth are missing altogether. Both *Protoceras* and *Leptomeryx* have lower incisors, but in the latter I₁ is larger relative to the other incisors and is more procumbent than that of *Protoceras*. The lower canine is incisiform in both *Leptomeryx* and *Protoceras*; however, the upper canine is strongly caniniform and large in the male *Protoceras* but vestigial in *Leptomeryx*. Furthermore, *Protoceras* and *Hypertragulus* have a strong caniniform P₁ and a strong P¹; P₁ in *Leptomeryx* is weak and less caniniform, and P¹ is lost. Absence of P¹ and a weaker, less caniniform P₁ sets *Leptomeryx* apart from *Protoceras* and *Hypertragulus*, suggesting a more pecoran relationship. The molars in *Protoceras*, on the other hand, are transversely broad and extremely brachyodont—basically similar to the smaller molars of *Leptomeryx*. The upper molars of *Protoceras* have a prominent parastyle, mesostyle, and strong median vertical ribs similar to *Leptomeryx*.

In comparing the limbs of *Leptomeryx* with *Protoceras*, the feet of *Leptomeryx* are strongly pecoran and for the most part, more specialized than those of *Protoceras*. However, this is not true with regard to the ulna of *Leptomeryx*, which is well developed but completely free from the radius, unlike *Protoceras*, in which the distal end of the ulna is co-ossified with the radius. Despite the otherwise specialized foot structure in *Leptomeryx*, the unattached ulna indicates a more primitive stage of development. In *Leptomeryx* the manus is highly specialized and has fewer carpals than those in *Protoceras*. As noted

by Osborn and Wortman (1892, p. 268), the magnum and trapezoid are coalesced in *Leptomeryx* and there is no evidence that the trapezium was present. A more primitive condition is seen in *Protoceras* in which the magnum, trapezoid, and trapezium are all separate. Furthermore, the position of the carpals in *Leptomeryx* differs from that of *Protoceras* in the lateral shifting of the lunar to rest exclusively on the unciform, contacting the magnum only laterally. In *Protoceras* the lunar rests almost equally on the magnum and unciform. *Leptomeryx* and *Protoceras* have four unfused metacarpals, but *Leptomeryx* metacarpals II and V are proportionally more slender than those of *Protoceras*. The fibula in *Leptomeryx* is closely comparable, in degree of reduction, with that of *Protoceras*. In both taxa, a rudiment of the proximal end of the fibula generally is attached to the tibia; most of the shaft is suppressed and the distal malleolar is present although not co-ossified with the tibia. Curiously, the pes in *Leptomeryx* is much more specialized than the manus. In *Leptomeryx*, the astragalus lacks the distal keel and the upper and lower ginglymi are parallel; the astragalus in *Protoceras* has a strong distal keel, and the condyles of the distal trochlea are slightly deflected. The presence of a fused cuboid and navicular in *Leptomeryx* is in distinct contrast to the more primitive condition of a separate cuboid and navicular found in all the protoceratids. *Leptomeryx* and *Protoceras* have the ectocuneiform and mesocuneiform fused, but the entocuneiform is separate and proportionally larger in *Protoceras* than *Leptomeryx*. Fusion of both the cuboid and navicular and the ectocuneiform and mesocuneiform in *Leptomeryx* indicates that the tarsals are more pecoran in character than those of *Protoceras*. The pes in *Leptomeryx* is immediately distinguishable from the Tertiary genera under discussion by the fusion of the third and fourth metatarsals to form a cannon-bone. Metatarsals II and V are represented by proximal splints. A more primitive condition of the pes is seen in *Protoceras*. Here metatarsals III and IV are separate and proximal splints II and V are less reduced than in *Leptomeryx*.

Hence, certain characters such as the fused trapezoid and magnum, the apparent loss of the trapezium in the manus, the fused cuboid and navicular, and the reduced entocuneiform in the pes, all indicate that the feet of *Leptomeryx* are

much more specialized than those of *Protoceras*. Further, a more advanced stage of development is also seen in the medapodials. In *Leptomeryx*, metacarpals II and V are proportionally more slender than those of *Protoceras* and unlike the latter, metatarsals III and IV are fused to form a cannon-bone.

Hypertragulus: Although *Protoceras* shares many similarities with *Hypertragulus*, some characters indicate fundamental differences between *Protoceras* and its Oligocene contemporary. In both *Hypertragulus* and *Protoceras*, the lower incisors are present. In *Protoceras*, however, the upper incisors are missing, whereas in *Hypertragulus* they may or may not be present. Both taxa have similar specialization of the canines and P₁; in males the upper canines are large and functional but the lower canine is incisiform, and the first lower premolar is caniniform. The premolars in *Hypertragulus* are extremely specialized for an Oligocene artiodactyl, reduced in size, trenchant, with P₂ isolated by diastemata. In contrast, *Protoceras* has extremely large, less sharp premolars and no diastema between P₂ and P₃. The molars in *Protoceras* are relatively lower crowned than in *Hypertragulus*. In *Protoceras*, the parastyle and metastyle are weak, and the mesostyle is strong, in contrast to *Hypertragulus*, in which the parastyle and metastyle are extremely strong, but the mesostyle is absent. Skulls of *Protoceras* and *Hypertragulus* exhibit fundamental differences, moreover, that places in question the relationship of these two genera not only with each other, but even as descendants of a common Eocene ancestor. In addition to the numerous paired bony protuberances on the male skull, *Protoceras* differs from *Hypertragulus* in the strongly closed, and more posteriorly situated orbits, proportionally longer frontals, shorter parietal area, and uninflated bullae.

Numerous significant differences exist in comparing the limbs and foot structure of *Protoceras* and *Hypertragulus*. In *Protoceras*, the manus is quadridactyl and metacarpals II and V are functional and proportionally stronger than in *Hypertragulus*. The ulna is heavy and only the distal end is co-ossified with the radius in *Protoceras*, whereas in *Hypertragulus* the ulna is relatively lighter and fully co-ossified with the radius. In *Protoceras*, the proximal end of the fibula is co-ossified with the tibia, the fibula shaft is extremely reduced or incomplete, and the distal malleolar bone is not co-ossified with

the tibia as in *Hypertragulus*. Furthermore, the distal condyles of the astragalus in *Protoceras* are slightly deflected mesially and have a prominent distal keel, whereas in *Hypertragulus* the upper and lower ginglymi are parallel, and the distal keel is lacking. The cuboid and navicular are fused in *Hypertragulus*, as in all pecorans, but are separate in *Protoceras*. Strangely, the pes in *Protoceras* is far too specialized in comparison to the manus with its four functional digits. In *Protoceras*, metatarsals II and V are reduced to proximal splints in contrast to *Hypertragulus* which retains almost full length slender metatarsals II and V.

Certain characters of *Hypertragulus*, such as retention of metacarpal I and the almost full length metatarsals II and V, indicate a more primitive stage of development than *Protoceras*. On the other hand, *Protoceras* appears less advanced than *Hypertragulus* in that the ulna and radius are only partially co-ossified, metacarpals II and V are proportionally stronger, and the cuboid and navicular are separate.

Tragulus: For an evaluation of primitive or advanced characters, it is helpful to compare recent *Tragulus* with *Hypertragulus*. Both *Hypertragulus* and *Tragulus* have hornless skulls of similar size. In a comparison of these genera with *Archaeomeryx*, Colbert (1941, p. 4) pointed out that size itself is an important character and the limited size increase between the Oligocene *Hypertragulus* and the recent *Tragulus* is less than in most mammals during this period of time, and is indicative of the slight amount of structural evolution that has taken place within this group. The upper incisors in *Tragulus* are missing and the upper canine is large and "tusk-like," whereas in *Hypertragulus* the upper incisors are vestigial and the canine is proportionally smaller. Unlike *Hypertragulus*, the first upper premolar is missing in *Tragulus*, but upper premolars two through four are basically similar to those of *Hypertragulus*. The molars in *Tragulus* are brachydont but slightly taller crowned than in *Hypertragulus*. The upper molars in *Tragulus* differ from *Hypertragulus* in a weaker parastyle, strong mesostyle (absent in the latter), and a weak metastyle on M³; an exceptionally strong metastyle is characteristic of M³ of *Hypertragulus*.

In *Tragulus*, the lower molars have a stronger entostyloid than in *Hypertragulus*. The lower canine is incisiform in both genera. In *Tragulus*, P₁ is missing. P₂-P₄ are situated in a closed series

and P₂ is not isolated by diastemata as in *Hypertragulus*. Furthermore, the premolars in *Tragulus* are more complex and less trenchant than in *Hypertragulus*.

Limbs of recent *Tragulus* show a surprising number of primitive features. In *Tragulus* the humerus is very similar in size and form to that of *Hypertragulus*, but the ulna, which is proportionally similar in size to the radius, is not so fully co-ossified with the radius. Although both the proximal and distal ends of the ulna are fused with the radius in *Tragulus*, a distinct outline separates each bone. This partial co-ossification of the ulna and radius obviously shows a more primitive stage of development than the fully fused radius and ulna in *Hypertragulus*. *Tragulus* has less separate carpals than *Hypertragulus*. In *Tragulus* the trapezoid is not separate and the trapezium is not present. In *Hypertragulus* the trapezoid, magnum, and trapezium are all separate, and unlike *Tragulus* metacarpals III and IV are not fused to form a cannon-bone. The pollex, which is present in *Hypertragulus*, is absent in *Tragulus*. As in *Hypertragulus*, the manus lacks the artiodactyl symmetry; metacarpal III is longer than metacarpal IV but metacarpals II and V are approximately paired.

The femur is short and relatively heavy as in *Hypertragulus*; the neck is short, the great trochanter rises slightly above the ball of the femur, and the second trochanter is extremely prominent, projecting strongly backward and slightly inward. The trochlea for the patella is long and narrow with the mesial and lateral crests of almost equal length and more symmetrical than in *Hypertragulus*, which has a relatively longer mesial crest. In both genera the tibia is slightly longer than the femur, and the proximal and distal vestiges of the fibula are co-ossified with the tibia. In marked contrast to *Hypertragulus*, the pes in *Tragulus* is distinguished by fused metatarsals III and IV and extremely delicate nonfunctional lateral digits II and V. Despite the presence of vestigial lateral digits II and V, the fusion of metatarsals III and IV is more advanced than *Hypertragulus*. Flexibility of the pes in recent *Tragulus* is more limited than in *Hypertragulus* because the cuboid, navicular, and ecto-mesocuneiform are all co-ossified; only the entocuneiform is separate. In *Hypertragulus* the cuboid and navicular are fused but separate from the fused ecto-mesocuneiform.

Looking at the skeleton of *Tragulus*, we are immediately impressed by certain features that recall the ancient hypertragulids. In general, the size and stature resemble *Hypertragulus*; the rear limb is especially long relative to the front limb. However, a more primitive stage of development is indicated by the partial co-ossification of the ulna and radius. The most strikingly primitive feature of *Tragulus* is the presence of lateral digits in both manus and pes. Although lateral digits II and V are delicate and not functional, it is unexpected to find these present in a recent member of the Tragulidae. On the whole, the skeletal features of *Tragulus* are advanced. The upper incisors and both upper and lower first premolars are missing. Metacarpals III and IV are fused as are the trapezoid and magnum; the trapezium is absent. In the pes of *Tragulus*, the metatarsals III and IV are fused and the hallux, which is present in *Hypertragulus*, is missing. Furthermore, the cuboid, navicular, and ecto-mesocuneiform are all fused in *Tragulus*.

Leptotragulus: Gazin (1955, p. 14) found that the dentition of *Leptotragulus* completely meets all the structural requirements necessary to qualify as the ancestor of the Protoceratidae. Stirton (1967, p. 25) concurred that the base heritage of the Protoceratidae "is very close to, or in common with, that of the Camelidae, in or near the genus *Leptotragulus*." We compared *Protoceras* and *Leptotragulus* dentitions, and found that weak upper and lower incisors are present in *Leptotragulus*, but that upper incisors are missing in *Protoceras*. In *Leptotragulus* the canines resemble those of *Protoceras*. The upper canine is relatively large and caniniform, similar to the tusklike canine of the male *Protoceras*, and the lower canine is incisiform as in the latter. P_1^1 in *Leptotragulus* are isolated by diastemata, as in *Protoceras*; P_1^1 is compressed, trenchant, and more caniniform than in *Protoceras*, but P_1^1 is caniniform as in the latter. P_{2-4}^2 are sharp and basically similar to those of *Protoceras*. The diagnostically important P_4 is of especial interest because it is very similar to that of *Protoceras*. It has a well-developed paraconid, a high, pointed protoconid, and a lingual crest running posteriorly from the peak of the protoconid to enclose a narrow posterior valley. A weak metaconid may occur near the midpoint of the lingual crest. The molars of *Leptotragulus* are even more similar to *Protoceras* than are the premolars. In

Leptotragulus the molars are extremely brachydont, anteroposteriorly narrow, and transversely wide. The paracone and metacone slope strongly inward, the parastyle and mesostyle are prominent, and the lingual cingulum is exceptionally strong.

The limbs of *Leptotragulus* are similar to the protoceratids and have more in common with the Tylopoda than the Ruminantia. In *Leptotragulus* the ulna is strong and completely free from the radius, whereas in *Protoceras* the distal end of the radius and ulna are co-ossified. The basic characters of the pes in *Leptotragulus* strongly resemble those of *Protoceras*. Fragmentary associated evidence shows that the astragalus has a distal keel, as in the protoceratids, but unlike the hypertragulids. Also, unlike the hypertragulids, the cuboid and navicular in *Leptotragulus* are separate as they are in both protoceratids and camelids. Furthermore, the ecto- and mesocuneiforms appear to be indistinguishably coalesced, also as in the protoceratids and camelids. Behind the ecto-mesocuneiform and adjacent to the posterior part of the cuboid is space for a large entocuneiform as in *Protoceras*. In *Leptotragulus*, metatarsals III and IV are unfused, as in *Protoceras*, and the sulci on the proximal ends of both III and IV indicate that metatarsals II and V were present but reduced to proximal splints similar to those of *Protoceras*. Also as in the latter, the keel on the distal ends of the metatarsals is confined to the plantar surface.

In sum, the mildly trenchant premolar and brachydont molars in *Leptotragulus* strongly resemble those of the protoceratids. The upper molars are anteroposteriorly short and transversely wide and proportionally similar to those of *Protoceras*. They further resemble *Protoceras* by having a prominent parastyle and mesostyle and a strong lingual cingulum. The limbs of *Leptotragulus* have even more in common with the protoceratids than the dentition. The pes is basically the same as in the protoceratids. The tarsals of *Leptotragulus* and *Protoceras* have a distal keel on the astragalus, a separate cuboid and navicular and a large entocuneiform. Metatarsals III and IV are unfused in *Leptotragulus* and metatarsals II and V are believed to be reduced to proximal splints similar to those of *Protoceras*. Hence, the characters of both the dentition and the limbs of late Eocene *Leptotragulus* foreshadow those of the Oligocene protoceratids.

CONCLUSIONS

A synthesis of the above comparisons leads us to several conclusions regarding protoceratid affinities. Numerous differences noted between the Protoceratidae and members of the Pecora make the likelihood of any relationship with that group remote. The protoceratids differ from those groups included in the Pecora as follows: (1) presence of P^1 , at least in earlier genera, and caniniform P_1 , except in *Synthetoceras*, that occludes behind upper canine, (2) talonid basin opening posteriorly or posterolingually in P_3 and P_4 , (3) separate magnum and trapezoid, (4) separate trapezium, (5) strong lateral metacarpals II and IV, (6) unfused metacarpals and metatarsals III and IV, (7) failure of the carina on the metacarpal to extend to the anterior surface of the facet, (8) lack of the short transverse process at the anterodistal end of the mesial condyle of the astragalus, (9) strong distal keel on the astragalus, and (10) separate cuboid and navicular.

The other ruminant group to which the protoceratids are most often referred is the Tragulina (excluding the problematical Hypertragulidae, see Historical Review). The Protoceratidae differ from the Tragulina in the following fundamental characters: (1) retention of P^1 , (2) a caniniform P_1 , (3) separate trapezoid, (4) separate trapezium (no trapezium in tragulids), (5) unfused metacarpals and metatarsals, (6) strong distal keel on astragalus, (7) axes of upper and lower ginglymi of astragalus not parallel, and (8) separate cuboid and navicular.

It is clear, then, that in many fundamental and diagnostically consistent characters, especially those of the limbs, the Protoceratidae differ significantly from those groups commonly and historically included in the Pecora and Tragulina.¹ Moreover, it is equally clear that most of those characters that separate the protoceratids from the Pecora and Tragulina serve also to ally them firmly with the Tylopoda (*sensu* Simpson,

1945). Those characters common to both protoceratids and camelids include: (1) separate navicular and cuboid, (2) separate magnum and trapezoid, (3) unfused metacarpals III and IV, as in *Poebrotherium* and some later camelids, e.g., *Miolabis*, (4) termination of the carina on the metacarpals before it reaches the anterior surface of the facet, (5) a shallow carinal groove on the proximal end of the first phalanx of the manus ending before the middle of the facet, (6) articular surfaces on the distal end of the metacarpal are nearly parallel on either side of the carina, (7) shallow pastern facet with a weak middle ridge on the second phalanx of the manus, (8) strong distal keel on the astragalus, (9) united ecto-mesocuneiform, (10) separate and well-developed entocuneiform, and (11) unfused metatarsals III and IV, as in *Poebrotherium*, *Oxydactylus*, and *Miolabis*.

Thus, we conclude that the above combination of tooth and limb characters strongly recommends placement of the Protoceratidae in the Tylopoda. Although previously suggested by Scott (1899, 1940) and Stirton (1967), we believe that we have assembled enough evidence, especially that based on the heretofore relatively poorly studied limbs, to substantiate this claim.

In searching for the origins of the protoceratids, we agree with Gazin (1955, p. 14) that the Uintan genus *Leptotragulus* is the likely ancestor. Gazin reasoned that the dentition of *Leptotragulus*, especially in the structure of the premolars, met all the essential requirements. Stirton (1967, p. 25) suggested that the base heritage of the Protoceratidae lay in or near the genus *Leptotragulus*, and he placed the family in the suborder Tylopoda. In classifying the Protoceratidae with the Tylopoda, Stirton put great emphasis on the separation of the navicular and cuboid, which are united in the earliest known ruminants. Our own more extensive study of the limb structure of *Leptotragulus* and *Protoceras* shows more clearly that the characters of *Leptotragulus* strongly foreshadow those of *Protoceras* and even show fundamental similarity to those of the much later *Synthetoceras*. In the late Eocene, the ulna of *Leptotragulus* is strong and completely free from the radius. The ulna of *Protoceras* is also strong but the distal end is co-ossified with the radius. Surprisingly, a similarly primitive condition is found in the ulna and radius of the Pliocene *Synthetoceras*, in which the ulna is conspicuously strong and never fully

¹In recent classifications, Simpson (1945) ranked the Tylopoda as a separate suborder; within the suborder Ruminantia, he included two infraorders, Tragulina (including the Protoceratidae) and Pecora. Romer (1966), on the other hand, listed the Tylopoda (including the Protoceratidae) and Pecora as the infraorders of the same suborder Ruminantia. He subdivided the Pecora into three superfamilies: Traguloidea, Cervoidea, and Bovoidae.

co-ossified with the radius, an unfused condition that is unlike both camelids and cervids. Basically, the pes of *Leptotragulus* is similar to that of *Protoceras*, and even *Synthetoceras*. Comparing the tarsals of *Leptotragulus*, *Protoceras*, and *Synthetoceras*, we find that they all have a distal keel on the astragalus and lack parallel upper and lower ginglymi. Furthermore, they all have a separate navicular, solidly fused ecto-mesocuneiform, and space for a large and separate entocuneiform. Metatarsals III and IV are unfused in *Leptotragulus*, and laterals II and V are reduced to proximal splints, as in *Protoceras* and *Synthetoceras*. Except for the lack of a co-ossified ulna and radius, the limbs are characteristically camelid and unlike the ruminants. The limbs, and especially the foot structure of the most advanced member of the Protoceratidae, are primitive. After observing the small degree of structural change in the limbs between the Oligocene protoceratids and the Pliocene synthetoceratines, it is evident that the characters of protoceratid limbs preserve the ancestral condition to a greater and more reliable degree than the dentition. Therefore, we agree with Gazin (1955) that the dentition of the late Eocene *Leptotragulus* has all the basic requirements to be ancestral to the protoceratids, but we are more impressed by the fact that the limbs of *Leptotragulus* have even more in common with the protoceratids.

The placement of the Protoceratidae in the Tylopoda naturally raises the question of what actually constitutes the suborder Tylopoda. Osborn (1910), Matthew (1929), Colbert (1941), and Simpson (1945) agreed in restricting the Tylopoda to contain only the xiphodonts and true camels, a view that is most generally held

today. Others, notably Scott (1940) and Stirton (1967) expanded the Tylopoda to include various other ruminant groups. Scott (1940) held the extreme view in this regard in considering all North American selenodonts to be tylopods. In recent years, only Romer (1966) approached this widely expanded definition of the Tylopoda, but presented very little evidence for his arrangement. Our ideas tend to parallel roughly those of Scott and Stirton, that is, we concur that the Camelidae, Oromerycidae, Leptotragulinae, and of course, the Protoceratidae, belong within the Tylopoda. Our opinion is founded primarily on the similarity of limb structure shared by these groups. The Hypertragulidae, to which the protoceratids have often been compared, are particularly difficult to assign and undoubtedly require a much more thorough study before confident placement can be made. At present, it is unclear to us whether the group, which is entirely North American, belongs with the Old World tragulines, which probably include only the Amphimerycidae, Gelocidae, and Tragulidae, or the Pecora, which should include the Palaeomerycidae, Giraffidae, Antilocapridae, Cervidae, and Bovidae. The further question of whether such groups as the cainotheres, anoplotheres, xiphodonts, agriocheres, and oreodonts are in reality true tylopods is a fascinating one but is obviously beyond the scope of this paper. Emerging clearly from this discussion are the complexities of artiodactyl systematics; add to this the vagaries and inconsistencies of the geologic record and the problem becomes even further convoluted. It is obvious that final disposition of the various fossil ruminant groups is not yet settled.

CLASSIFICATION OF THE FAMILY PROTOCERATIDAE

ORDER ARTIODACTYLA OWEN, 1848

SUBORDER TYLOPODA ILLIGER, 1811

Family Protoceratidae Marsh, 1891

Subfamily Protoceratinae Marsh, 1891 (=Protoceratidae Marsh, 1891; Protoceratinae Zittel, 1893).

Heteromeryx Matthew, 1905. Early Oligocene.

Heteromeryx dispar Matthew, 1905. Chadronian (early Oligocene), South Dakota.

Pseudoprotoceras Cook, 1934. Early Oligocene.

Pseudoprotoceras longinaris Cook, 1934. Chadronian (early Oligocene), Nebraska.

Protoceras Marsh, 1891 (Including *Calops* Marsh, 1894). Late Oligocene.

Protoceras celer Marsh, 1891 (including *Protoceras comptus* Marsh, 1894; *Calops cristatus* Marsh, 1894; *Protoceras nasutus* Marsh, 1897; *Calops consors* Marsh, 1897). Whitneyan (late Oligocene), South Dakota.

Protoceras skinneri, new species. Early Arikareean (early Miocene), South Dakota and Nebraska.

Protoceras neatodelpha, new species. Late Arikareean (early Miocene), Wyoming.

Paratoceras Frick, 1937. Medial Miocene–early Pliocene.

Paratoceras, undescribed species. Hemingfordian (medial Miocene), Panama (Frank C. Whitmore, personal commun.).

Paratoceras wardi, new species. Early Barstovian (late Miocene), Texas.

Paratoceras macadamsi Frick, 1937. Clarendonian (early Pliocene), Texas.

Subfamily Synthetoceratinae Frick, 1937

Syndyoceras Barbour, 1905. Early Miocene.

Syndyoceras cooki Barbour, 1905. Late Arikareean and early Hemingfordian (early to medial Miocene), Nebraska and Wyoming.

Prosynthetoceras Frick, 1937. Medial to late Miocene.

Prosynthetoceras (*Prosynthetoceras*) Frick, 1937. Medial Hemingfordian to medial Barstovian (medial to late Miocene), Texas and Florida.

P. (Prosynthetoceras) texanus (Hay, 1924) (including *Dromomeryx texanus* Hay, 1924; *Dromomeryx angustidens* Hay, 1924; *Merycodus grandis* Hay, 1924; *Protolabis francisi* Hay, 1924; cf. *Miolabis* sp. indet.: Simpson, 1932; ?*Cranioceras texanus*: Frick, 1937; ?*Synthetoceras rileyi* Frick, 1937; *Blastomeryx texanus*: Wood and Wood, 1937; *Syndyoceras australis* White, 1941; ?*Syndyoceras texanus*: Hesse, 1942; *Nothokemas grandis* White, 1947; *Synthetoceras (Prosynthetoceras) douglasi* White, 1947; cf. *Miolabis tenuis*: Ray, 1957; *Synthetoceras (Prosynthetoceras) rileyi australis*: Maglio, 1966; *Prosynthetoceras texanus*: Patton, 1967). Medial Hemingfordian (medial Miocene), Texas and Florida.

P. (Prosynthetoceras) francisi Frick, 1937. Barstovian (late Miocene), Texas.

P. (Lambdoceras) Stirton, 1967. Medial to late Miocene.

P. (Lambdoceras) hessei Stirton, 1967. Hemingfordian (medial Miocene), South Dakota.

P. (Lambdoceras) trinitensis Patton and Taylor, 1971. Barstovian (late Miocene), Texas.

P. (Lambdoceras) siouxensis Frick, 1937. Barstovian (late Miocene), Nebraska.

Synthetoceras Stirton, 1932. Early to late Pliocene.

Synthetoceras tricornatus Stirton, 1932. Clarendonian (early Pliocene), Texas; Hemphillian (late Pliocene), Florida and Alabama.

SUMMARY

CHADRONIAN TAXA of the Protoceratinae fulfill the morphologic and temporal requirements for the radiation of all members of the Protoceratidae. Earliest occurring protoceratids are distinguished by the arched bony plates on the upper surface of the maxillaries that develop into hornlike protuberances in later species of the Protoceratinae and unite to form a rostral horn in the Synthetoceratinae.

Remains of the North American subfamily Protoceratinae are known from deposits of Chadronian to Clarendonian age. The geographic range of the subfamily extends from the northern Great Plains (South Dakota, Nebraska, and Wyoming) southward to Texas and the Panama Canal Zone.

Taxonomic changes within the Protoceratinae proposed here include (1) the removal of *Hypotragulus transversus* Cope from the genus, *Heteromeryx*, (2) the placement of *Calops* Marsh in synonymy with *Protoceras*, (3) the synonymy of *Protoceras comptus* Marsh, *Calops cristatus* Marsh, *Protoceras nasutus* Marsh, and *Calops consors* Marsh with *Protoceras celer*, all from the same stratigraphic unit.

The Protoceratinae now includes four genera. *Heteromeryx* Matthew and *Pseudoprotoceras* Cook are monotypic and known only from the Chad-

ronian (early Oligocene). *Protoceras* Marsh previously restricted to the Whitneyan (late Oligocene) of South Dakota is here recorded from the early Miocene. We describe two new Arikareean species, *Protoceras skinneri* from South Dakota and Nebraska, and *Protoceras neatodelpha* from Wyoming.

Paratoceras was originally described by Frick (1937) from a jaw collected in Clarendonian sediments in the panhandle of Texas. A new species, *Paratoceras wardi*, is described from the early Barstovian deposits of the Gulf Coastal Plain of Texas. The geographic and temporal range of *Paratoceras* is extended to include an undescribed species from Hemingfordian deposits of the Panama Canal Zone (Whitmore, personal commun.). A lower jaw, all that was known of *Paratoceras*, is here supplemented by the description of the skull and limbs of *P. wardi*.

The systematic position of the Protoceratidae is discussed and possible protoceratid relationships to the Tragulina and Pecora are considered. Additional evidence supports Scott's (1940) and Stirton's (1967) assignment of the family Protoceratidae to the suborder Tylopoda, and probable derivation in or near the Uintan tylopod *Leptotragulus*.

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