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**REVISION OF THE EXTINCT PSEUDOCERATINAE
(ARTIODACTYLA: RUMINANTIA: GELOCIDAE)**

S. David Webb

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REVISION OF THE EXTINCT PSEUDOCERATINAE (ARTIODACTYLA: RUMINANTIA: GELOCIDAE)

S. David Webb

ABSTRACT

The Pseudoceratinae is a North American clade of small, hornless ruminant artiodactyls known from the late middle Miocene to the earliest Pliocene. Two genera and three species are recognized: *Pseudoceras skinneri* Frick 1937 (including *P. potteri* Frick 1937 and *P. wilsoni* Frick 1937 as junior synonyms); *Floridameryx floridanus* new genus and species; and *Floridameryx klausii* (Frick 1937), new combination. Originally regarded as small, aberrant members of the Camelidae, cranial (especially basicranial), dental, and postcranial characters clearly place the Pseudoceratinae instead within the artiodactyl suborder Ruminantia, and more precisely within the extinct family Gelocidae. Among the derived ruminant (pecoran) character states exhibited by the pseudoceratines, the following are most notable: broad postglenoid process; fully developed odontoid process of axis; lack of upper incisors; forelimb length nearly equal to that of hindlimb; third and fourth metacarpals and metatarsals fully fused into cannon bones with well developed distal keels; metatarsal with deep, distally bridged anterior groove; fused cuboid and navicular; and parallel-sided astragalus. *Floridameryx* differs from *Pseudoceras* by having a wider skull with weaker parietal and sagittal crests, reduced premolars, higher crowned molars, and shorter metatarsals.

The Withlacoochee River 4A locality in north-central Florida produces the largest population sample of pseudoceratines, with a minimum of 26 individuals represented, and is the only known site to have a pseudoceratine as the most common ungulate. About half of the mandibles bear small, procumbent, incisiform canines, as is typical in advanced ruminants, while the other half have large, upright canines which occluded with the upper canines. This is interpreted as sexual dimorphism, with the former morphology presumably representing females and the latter males. The abundance of pseudoceratines in the Withlacoochee 4A fauna, seen in its paleoecological context, is attributed to a preference for very mesic, densely forested environments.

Key Words: *Pseudoceras*, Ruminantia, Gelocidae, osteology, Miocene, Florida, Hemphillian

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INTRODUCTION

In May 1967, scuba-diving paleontologists from the Florida Museum of Natural History discovered a rich concentration of bones representing a new genus and species of the extinct subfamily Pseudoceratinae in sediments beneath the Withlacoochee River in central Florida. This new pseudoceratine was the most common species at the site, known as Withlacoochee River 4A (at ca. 28° 59' N; 82° 21' W). Seven seasons of underwater collecting produced about 700 specimens representing at least 26 individuals of the new taxon and nearly all of its skeleton, including many elements previously unknown in any pseudoceratine.

In the original description, Frick (1937) assigned the Pseudoceratinae to the Camelidae. Simpson (1945) followed this assignment, but with a query. The new Florida sample shows clearly that the Pseudoceratinae belong with the hornless Ruminantia rather than with the Camelidae. An intriguing irony accompanies Frick's original assignment. Although he relegated Pseudoceratinae to an appendix under the rubric of Camelidae (Frick 1937:648-652), the volume in which they were presented was his great tome "Horned Ruminants of North America". Perhaps Frick and his assistants knew subconsciously that they were dealing with ruminants after all, albeit ones without horns.

The primary basis for Frick's assignment of Pseudoceratinae to Camelidae was the upright lower canine tooth, evident in the holotype mandible of *Pseudoceras skinneri*. In the Withlacoochee River 4A sample, however, this feature occurs in 12 of the 22 complete mature rami; in the other 10 rami the lower canine tooth is smaller and incisiform as in typical Ruminantia (In many of these mandibles the actual canine is absent, but its size and orientation can be inferred from the alveolus). The new sample demonstrates that the nature of the lower canine cannot be used absolutely as a criterion distinguishing Camelidae from Ruminantia. In this instance it would lead to the absurdity of dividing an otherwise unified population into Camelidae and Ruminantia. The differences in lower canine morphology are instead interpreted to be sexual dimorphism.

It was evident to the author as early as 1970 that the Withlacoochee River 4A sample of Pseudoceratinae had important implications for the phylogeny of hornless ruminants. It took another decade and two trips to Europe to pursue those implications. Taylor and Webb (1976) and Webb and Taylor (1980) were both attempts to penetrate some of the mysteries of lower ruminant phylogeny.

Based on their findings Webb and Taylor (1980:154) asserted that *Pseudoceras* was a North American gelocid. Tedford et al. (1987:189; 2004:216-217) likewise recognized *Pseudoceras* as an immigrant gelocid, and McKenna and Bell (1997) classified it within the Gelocidae. A gelocid origin for *Pseudoceras* was also noted by Webb (1998) in a review article on the fossil hornless ruminants of North America. The morphologic evidence for this relationship is formally presented here for the first time.

The following review of the Pseudoceratinae consists of three parts. First is a systematic revision of the extinct subfamily, taking into account undescribed fossil collections from Florida and elsewhere in North America. The second section provides an osteological description of the subfamily based primarily on the rich sample from Withlacoochee River 4A. And the third part features relationships, tracing the evolution of Pseudoceratinae back to their probable origins among lower Pecora in the Oligocene and Miocene of Eurasia.

ABBREVIATIONS AND DEFINITIONS

This paper is based primarily on fossils catalogued in the vertebrate paleontology collection of the Florida Museum of Natural History, University of Florida, Gainesville (abbreviated as **UF**). Other relevant paleontological collections and their abbreviations are: **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; **F:AM**, Frick Collection, American Museum of Natural History, New York; **TMM**, Texas Memorial Museum, University of Texas, Austin; and **UNSM**, Nebraska State Museum, University of Nebraska, Lincoln.

All measurements are given in millimeters (mm). Standard abbreviations of **I** for incisor, **C** for canine, **P** for premolar, and **M** for molar are used; a preceding **D** indicates a deciduous tooth; and the following numeral the relative tooth position (M2 = upper second molar). Upper case letters denote upper teeth; whereas lower case letters refer to mandibular teeth. **n** denotes sample size; **s**, sample standard deviation; and **x**, sample mean.

Definitions and boundaries of North American Land Mammal Ages and biochronology of North American fossil localities follow Tedford et al. (2004), with the exception of McGehee Farm, which is regarded as earliest Hemphillian (Hh1) as in Tedford et al. (1987) for the reasons outlined by Hulbert and Whitmore (2006). Following Tedford et al. (2004), **CI** denotes the Clarendonian Land Mammal Age and **Hh** the Hemphillian; numbers following these abbreviations signify a subage, e.g., **CI3** equates to the late Clarendonian.

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen 1848

Suborder RUMINANTIA Scopoli 1777

Family GELOCIDAE Schlosser 1886

Subfamily PSEUDOCERATINAE Frick 1937

Included Genera.—*Pseudoceras* Frick 1937 and *Floridameryx*, new genus.

Diagnosis.—Diminutive hornless ruminants. Skulls of traguloid proportions, sharing many gelocid features. Dental formula I 0/3, C 1/1, P 3/3, M 3/3. Lower incisors procumbent and spatulate; lower canines upright and occluding with upper canines in presumed males, procumbent and incisiform in presumed females; short diastemata; p1 absent; p2-p4 with weakly developed lingual cuspids as in Gelocidae, tending to posterolingually oriented metaconid and transverse compression as in *Bachitherium*; length of premolar series relatively shorter than in most Gelocidae, ranging from 55 to 70 percent of molar series; molars with gelocid pattern, crenulated enamel, numerous cingula and stylids, mesodont to incipiently hypsodont, and transversely compressed. Cementum often present in contrast with *Gelocus*. Postcranial skeleton broadly comparable to that of *Moschus*, with forelimbs nearly equal in length to hindlimbs. Astragalus parallel-sided and cubic in proportions. Metapodials fused into cannon bones with complete distal keels. Metatarsus with distally enclosed anterior gutter, unlike *Moschus*.

Distribution.—Late middle Miocene to early Pliocene of North and Central America (Clarendonian and Hemphillian Land Mammal Ages).

Genus *Pseudoceras* Frick 1937Type Species.—*Pseudoceras skinneri* Frick 1937.

Distribution.—Late middle Miocene to late Miocene of High Plains, Gulf Coastal Plain, and Central America (C11 to Hh2).

Generic Diagnosis.—Skull narrower than in *Floridameryx*, with stronger parietal and sagittal crests, longer occipital overhang, and bulla broadly appressed against basioccipital. Length of premolar series about 65 to 70 percent of molar series. Molars mesodont and not markedly compressed. Metatarsus about ten percent longer than that of *Floridameryx floridanus*.

Etymology.—*Pseudo*, Gr., false; *ceras* (or *keras*), Gr., horn (neuter); in reference to the false resemblance to horned ruminants or to Protoceratidae.

Included Species.—The type species only (see below).

Pseudoceras skinneri Frick 1937*Pseudoceras wilsoni* Frick 1937:651.*Pseudoceras potteri* Frick 1937:652.*Blastomeryx elegans* Matthew and Cook 1909, Patton (1969), in part, Texas specimens only.

Holotype.—F:AM 33723, left mandibular ramus with i3, c, p2-m3.

Type Locality.—East Kat Quarry, Cherry County, Nebraska.

Discussion.—The holotypes and referred specimens of *Pseudoceras wilsoni* and *Pseudoceras potteri* came from the same stratigraphic unit (Merritt Dam Member of Ash Hollow Formation) and the same region of Nebraska as the holotype of *Pseudoceras skinneri* and are here regarded as synonyms of *P. skinneri*. Supposed differences among the three noted by Frick (1937), such as postcanine diastema length, represent ordinary variation within the same species, as demonstrated in the larger pseudoceratine sample from Withlacoochee River 4A. An important specimen, only briefly mentioned by Frick (1937:243, 651), is F:AM 33720, a nearly complete skull from Hans Johnson Quarry, there tentatively referred to *Pseudoceras*.

Another series of specimens from the Merritt Dam Member in northern Nebraska are present in the University of Nebraska Collection and were briefly mentioned by Frick (1937:649). The best example is UNSM 26606, a left mandible collected by F. Walker Johnson from the *Platybelodon barnumbrowni* locality on the east side of Snake River.

An additional pair of mandibles (evidently of one individual) from Cherry County are F:AM 53365 and 53368. These come from Clayton Quarry (Burge level), and thus document the earliest records of *Pseudoceras skinneri* in the C11 (Tedford et al. 2004).

The youngest records (Hh2) of *P. skinneri* come from FT-40 and FT-49, the *Amebelodon fricki* sites in northern Nebraska where a series of dentaries, UNSM 46059-46063, compare closely with the C13 samples. In four mature lower dentitions premolar length averages 20.5 mm and molar lengths average 29 mm, giving a ratio of about 0.68. Leite (1990) recorded another specimen of similar faunal age from the Lemoyne local fauna in Keith County, Nebraska.

Evidently the earliest accession of a diagnostic specimen of *Pseudoceras skinneri* was made by Alexander Agassiz in October 1882. Agassiz had received a shipment of specimens from Charles H. Sternberg including the right mandible of a small ruminant from Prairie Dog Creek near Logan, Phillips County, Kansas. Agassiz catalogued it as MCZ 3313 and

identified it (in ink) as *Blastomeryx scotti*. The six cheek teeth clearly represent *P. skinneri*, with the premolar series measuring 20.4 and the molars 31.7 in length.

In the southern Great Plains the best sample of *Pseudoceras skinneri* comes from the C13 Higgins Locality in Lipscomb County, Panhandle of Texas. This population appears to have significantly larger body size than the northern plains samples of similar age. The clearest evidence comes from three adult metatarsals, F:AM 95232, 95234 and 95237, that average 128 mm in length, about eight percent larger than the northern Nebraska metatarsals. Conceivably this sample deserves recognition as a larger species; on the other hand, it seems preferable to regard the size difference as clinal variation within the same species, a pattern documented in other Clarendonian ungulates (Webb 1969a).

On the Gulf Coastal Plain of Texas, the C12 Lapara Creek Fauna includes at least one clear record of *Pseudoceras skinneri*. A right mandible, TMM 30896-496 from Buckner Ranch in Bee County, was referred by Patton (1969) to *Blastomeryx elegans* but the premolars are diagnostic of *Pseudoceras*. If one includes the alveoli for p2, the length of the little-worn premolar series measures 22 mm, and that of the molar series is 31 mm, thus falling within the range of the northern Nebraska series of *P. skinneri*. The two other small ruminant specimens cited by Patton (1969) probably also represent Pseudoceratinae.

Hulbert and Whitmore (2006) recorded *Pseudoceras* sp., based on an astragalus, at the Hh2 Mauvilla local fauna in Alabama. However, with the proposed recognition of two genera of pseudoceratines in this work, the very limited Mauvilla sample is now only diagnostic to the subfamily level.

Pseudoceras skinneri also occurs in the Love Bone Bed, Alachua County, Florida, another C13 record (Webb et al. 1981). A diagnostic example is a complete metatarsal, UF 25007, with a length of 119.5, which compares very closely with specimens from Nebraska. Additional specimens include UF 24990, m1; UF 24999, three isolated molars; UF 25000, two fused thoracic vertebrae; UF 25001, a scapula; UF 25002, two humeri; UF 25003, two radii; UF 25004, a complete metacarpus; UF 25005, six metacarpal fragments; UF 25006, a distal end of a tibia; UF 25008, four astragali; and UF 25009, three phalanges.

The range of *Pseudoceras skinneri* extends south into Honduras where it occurs in the Hh2 fauna from the Gracias Formation. There Webb and Perrigo (1984) reported ten specimens, and illustrated UF 18041, a right

mandibular ramus with m2-m3. These teeth measure slightly larger than the equivalent teeth in the type specimen from Nebraska.

Floridameryx n. gen.

Type Species.—*Floridameryx floridanus*, new species.

Included Species.—*Floridameryx klausii* (Frick 1937), new combination.

Distribution.—Late Miocene of New Mexico (C12) and late Miocene to earliest Pliocene of Florida (Hh1-Hh4).

Generic Diagnosis.—Skull wider than in *Pseudoceras*, with weaker parietal and sagittal crests, no occipital overhang, and bulla separated by a gap from basioccipital. Length of premolar series about 55 percent of molar series. Molars incipiently hypsodont, with modest cementum, and tending to transverse compression. Metatarsals about ten percent shorter than in *Pseudoceras*.

Etymology.—Florida, honoring the state; *meryx* (or *meryco*), Gr., masculine sheep, or, more generally, ruminant.

Floridameryx floridanus n. sp.

Pseudoceras sp., Webb (1998), in part; Tedford et al. (2004:207); Webb et al. (2008).

Pseudoceras n. sp., Hulbert and Webb (2001:269-270; fig. 13.39).

Holotype.—UF 13832, male left ramus with c1, p2-p4, m1-m3 in little-worn condition, from Withlacoochee River 4A, Marion-Citrus county line, Florida, collected by UF field parties led by N. Tessman in 1968.

Allotype.—UF 19395, female left ramus with i1, p2-4, m1-m3 in little-worn condition, from Withlacoochee River 4A, collected by S. D. Webb and H. Converse in 1970. The use of an allotype instead of a paratype in this case emphasizes the systematic importance of sexual dimorphism in this species.

Known Distribution.—Late Miocene to earliest Pliocene of Florida (Hh1-Hh4).

Referred specimens.—The extensive sample of material from the type locality is listed in the Appendix. Several other sites in Florida also produce material referable to this species. Haile 6A: UF 2181, m1; and UF 25436, a medial phalanx. McGehee Farm Site: UF 11002, a metacarpus; and UF 25437, an astragalus. Both of these sites are in western Alachua County and are early Hemphillian (Hh1) in age, thus slightly older than

the Hh2 type locality (Hulbert 2005; Hulbert & Whitmore 2006).

The Hh4 Palmetto Fauna, previously recognized as the classic “Bone Valley Fauna” of Polk County, also includes *Floridameryx floridanus* (Webb et al. 2008: therein listed as “*Pseudoceras* sp.”), the youngest definitive records of the subfamily. Perhaps the most diagnostic specimen is a complete metatarsus, UF 133997, from the Whidden Creek local fauna. Measuring 105.5 mm in length, it falls neatly within the size range of the Withlacoochee River 4A sample, and is about ten percent shorter than metatarsi of *Pseudoceras skinneri*. Other Palmetto Fauna specimens are listed in Webb et al. (2008).

Diagnosis.—Smaller than *Pseudoceras skinneri*. Differs from *Floridameryx klausi* by having incipiently hypsodont molars and lower molars with flattened lingual walls strongly compressed in transverse dimensions. Short premolars, metaconid long with flat lingual wall. Lower premolar series averages 15 mm long; lower molar series about 28 mm long. Mean unworn metaconid height of m3 8.8 mm; mean length, 13.0 mm; mean width, 4.5 mm.

Etymology.—“Floridian”. This species name honors the special kind of paleontological wealth that Florida often provides. The richest sample of pseudoceratines by far comes from the Withlacoochee River 4A site which also gives a special insight into the paleoecology of this species.

Discussion.—The large sample of *Floridameryx floridanus* from Withlacoochee River 4A forms the principal basis for the osteology (below). The Withlacoochee River 4A local fauna is late early Hemphillian (Hh2) in age (Becker 1985; Tedford et al. 1987, 2004). The minimum number of individuals, based on the proximal end of left metatarsals, is 26, but surely many more contributed to the large sample.

The setting in which *Floridameryx floridanus* occurs so abundantly consists of a freshwater pond or oxbow lake cut deeply into the surrounding Eocene limestone, now exposed in the bottom of the Withlacoochee River. The vertebrate remains were scattered through massive green clays and occasionally concentrated in thin beds of silt. The composition of this local fauna suggests an unusual paleontological community. Many common species at Withlacoochee 4A are exceedingly rare or unknown elsewhere, and conversely, species that are abundant in most Hemphillian faunas are rare or absent. When present, pseudoceratines are typically a very rare component of North American ungulate faunas, but *F. floridanus* is

by far the most common species found at Withlacoochee River 4A. As is typical of early Hemphillian faunas in Florida, equids are very diverse (8 species), but Withlacoochee River 4A is the only site where *Hipparion* cf. *tehonense* and the diminutive *Nannippus morgani* are common (28% and 9% of identifiable teeth, respectively) (Hulbert 1988, 1993). The most common carnivore is the diminutive borophagine canid, *Borophagus orc* (Webb 1969b), an appropriate-sized predator to have hunted *F. floridanus* and *N. morgani*. Larger mammals at this site include *Thinobadistes*, *Pliometanastes*, *Enhydritherium*, *Indarctos*, *Machairodus*, *Cormohipparion*, *Protohippus*, *Amebelodon*, *Aphelops*, *Teleoceras*, *Tapirus*, and *Aepycamelus* (Webb 1969; Wolff 1977; Becker 1985; Hulbert 1988, 1993, 2005). The vertebrate fauna also includes several perciform fishes, numerous amphibians, various freshwater turtles and snakes, *Alligator*, several sizes of tortoises, and an extinct egret, *Egretta subfluvia* (Becker 1985). The probable habitat adjacent to the freshwater pond where material accumulated was subtropical deciduous forest (a Florida “hammock”). Evidently this was the preferred habitat of *Floridameryx floridanus*.

Floridameryx klausi (Frick 1937), new combination
Pseudoceras klausi Frick 1937:652; Galusha and Blick (1971:109).

Pseudoceras sp., Tedford et al. (2004:200).

Holotype.—F:AM 31997, right ramus with p2 roots, and p3-m3 in medium wear, from Round Mountain Quarry, Chamita Formation, Santa Fe County, New Mexico.

Known Distribution.—Late Miocene (Cl2) of New Mexico.

Referred Specimens.—Two figured mandibles and thirteen other rami and partial rami as cited in Frick (1937:652). The two upper dentitions, there questionably referred, also represent *Floridameryx klausi*.

Diagnosis.—Differs from *Floridameryx floridanus* by having mesodont molars; lower molars with partly flattened lingual walls and less compressed in transverse dimensions. Short premolars, metaconid not as long or as flattened as in *Floridameryx floridanus*. Lower premolar series about 16 mm long; lower molar series about 28 mm long. Unworn m3 metaconid height about 7.5 mm; mean length, 12.6 mm; mean width, 5.2 mm.

Discussion.—*Floridameryx klausi* closely resembles *Floridameryx floridanus* in size and premolar reduction but is less progressive in a number

of dental features. The crown height of m3 in the slightly worn type mandible is 7.4 mm; and that tooth in even earlier wear in F:AM 33782 measures 7.5 mm high. Comparable measurements in eight specimens of *F. floridanus* ranged from 8.4 to 9.5 with a mean of 8.8. Thus, *F. klausii* had not attained the degree of hypsodonty that occurs in *F. floridanus*.

A related distinction is the degree to which the lower molars are transversely compressed. At the widest point, the mean width of m3s of *Floridameryx klausii* measures 5.2 mm. Although the m3s of *F. floridanus* are slightly longer than those of *F. klausii*, their mean width is 4.5 mm, nearly four standard deviations (0.21) less than in *F. klausii*. Similar comparisons between maximum widths of the second lower molars yield 5.1 in *F. klausii* and 4.6 in *F. floridanus*, a difference of nearly three standard deviations. Thus, in transverse compression as in hypsodonty, *F. klausii* molars are less progressive than those of *F. floridanus*.

The entire known sample of *Floridameryx klausii* was collected by Frick Laboratory parties from the Round Mountain Quarry near San Ildefonso, New Mexico. That quarry produces excellent samples of a limited variety of taxa. Although the quarry is isolated from the continuous stratigraphic sections studied by Galusha and Blick (1971), the fauna is regarded as middle Clarendonian (Cl2) in age on biochronologic grounds (Tedford et al. 2004).

If *Floridameryx klausii* is indeed middle Clarendonian in age, it lived about four million years earlier than *Floridameryx floridanus*. The differences between these two species consist of relatively minor differences that would be expected as progressions in a single evolving lineage. On the other hand, those changes took place at a sufficiently rapid rate, and the gap in the known record is sufficiently large, to permit a reliable specific distinction.

During their brief span the Pseudoceratinae diversified modestly. The earliest records from the early Clarendonian in northern Nebraska (Burge Fauna) are slightly smaller and more brachyodont than typical *Pseudoceras skinneri* from the late Clarendonian, thus representing a plausible ancestral condition for all subsequent North American pseudoceratines. This species survived with few changes, other than a modest increase in hypsodonty, through the late early Hemphillian.

Floridameryx diverged from *Pseudoceras* as its cranial proportions broadened and its premolar series (and face) were abbreviated. During its recorded history *Floridameryx* increased in hypsodonty at about the same rate as *Pseudoceras*. Its size increased only

moderately so that it remained smaller than *Pseudoceras skinneri*. *Floridameryx* first appears in the middle Clarendonian as *F. klausii* from Round Mountain quarry in New Mexico. Its subsequent records (as presently known) are confined to Florida. By late early Hemphillian time, when the large sample of *Floridameryx floridanus* was preserved at Withlacoochee River 4A, this genus showed further increases in the degree of hypsodonty and in the transverse compression of its molars, but had made no fundamental new departures. The latest Hemphillian samples from the Palmetto Fauna reveal no significant changes from the much better late early Hemphillian samples.

Confinement of *Floridameryx* to one site in New Mexico and a few sites in Florida suggests a very limited (largely peripheral) geographic range. By contrast *Pseudoceras* occurs widely through the midcontinent and southward (through unknown ranges) to Honduras. Neither genus seems to have ranged into or west of the Rocky Mountain Province.

OSTEOLOGY OF THE PSEUDOCERATINAE

The following descriptive osteology is based primarily on the rich sample of *Floridameryx floridanus* from the Withlacoochee River 4A site in Florida (see Appendix). The major exceptions are cranial features taken from the previously undescribed skull of *Pseudoceras skinneri*, F:AM 33720 from Hans Johnson Quarry in northern Nebraska. Unless otherwise stated, all comments refer to the UF sample of *F. floridanus*.

As the subsequent section on Relationships will suggest, the Pseudoceratinae represent a branch of the extinct family Gelocidae. Nonetheless, in many parts of the following description comparisons are made with more distantly related ruminant taxa, especially *Moschus* and *Tragulid*, for the simple reason that these living genera are better known and more widely available as standards of comparison. I have added some descriptive details regarding *Gelocus* to supplement that available in the literature and to facilitate comparison with the Pseudoceratinae. The phylogenetic significance of many osteological features will be interpreted in the section on Relationships.

GENERAL FEATURES OF THE SKULL

The skulls of Pseudoceratinae generally resemble those of other hornless ruminants. Among living forms, the relevant comparisons are with Tragulidae and Moschidae. The small size, absence of frontal

appendages, large orbits near the mid-length of the skull, short rostrum, and enlarged upper canines all suggest at once that the heritage of Pseudoceratinae lies among the primitive ruminants.

The size range of pseudoceratine crania falls between *Hyemoschus* and *Moschus*. No pseudoceratine is as small as the various species of *Tragulus* nor small members of the extinct Hypertragulidae such as *Hypisodus*. On the other hand, no known Pseudoceratinae attain the size of the large extinct tragulids *Dorccatherium* and *Dorcabune*. Thus, the size range of the Pseudoceratinae lies near the mode for primitive ruminants.

The absence of horns or antlers in Pseudoceratinae is confirmed in five crania, one of *Pseudoceras skinneri* and four of *Floridameryx floridanus* (Fig. 1). Large upper canines occur consistently, as in other hornless ruminants, including Tragulidae, Hypertragulidae, Gelocidae, and Moschidae. Presumably sabre-like upper canines served as weapons of defense in all of these groups that lack horns, antlers or other frontal appendages.

Pseudoceratinae have the primitive ruminant proportions with a short face on a relatively longer braincase. More than a century ago Kowalevsky (1876) and Rutimeyer (1883) observed that the braincase (including orbits) is longer than the facial portion of the skull in Tragulidae, Gelocidae, and other primitive ruminants. The orbits are relatively large, while the zygomatic processes of the jugal, squamosal, and frontal bones are very slender. The anterior root of the zygomatic arch is set low, just above the molar roots, and the masseteric crest is weak. A lacrimal vacuity separates the maxillary from the frontal bone and also the lacrimal from the nasal bone, in the same relationship that is found in Hypertragulidae, Gelocidae, and Moschidae, but not in any of the Tragulidae.

The cranial vault is only moderately inflated, about as in living Tragulidae. The parietal, sagittal, and mastoid crests are even stronger than in living members of that family and much stronger than in higher ruminants. In general, the crests resemble those in Hypertragulidae. The parietal crests form a triangular posterior skull table with postorbital apices, emphasized by strong postorbital constrictions. The basicranium is much wider than in Tragulidae. The bullae are somewhat more inflated than in Moschidae, about as in most Hypertragulidae; they do not approach the degree of inflation found in Tragulidae. The bullae are hollow, not cancellous as in Camelidae. The glenoid fossa is broad with a broad postglenoid process and crest, closely resembling the

condition in Gelocidae, Moschidae and higher ruminants. The facial portion of the skull is flexed downward on the braincase, more than in Tragulidae, about as in Moschidae, but not to the extent seen in most horned ruminants.

RESTORATION OF THE WITHLACOOCHEE *FLORIDAMERYX* CRANIUM

Before proceeding to a detailed description of the cranium, it is necessary to comment on the restoration of the specimen shown in Figure 1. Despite the excellent sample of *Floridameryx floridanus* from Withlacoochee River 4A, some cranial features remain in doubt. The “hinge region” between the braincase and the facial region was restored almost in its entirety; and the pterygoids, lacrimals, and nasals are virtually unknown. While most features of the braincase and orbitotemporal region are well represented in UF 13834, it is an adolescent specimen, in which cranial flexion may be exaggerated, and some dimensions are smaller than in fully adult specimens. The dimensions, as restored, were derived from two less complete but mature specimens, namely UF 19257, an excellent braincase lacking the orbital and sphenoid regions, and UF 19258, an interorbital-frontal portion of a cranium.

The upper jaws and palate of the Withlacoochee skull (Fig. 1) were restored using UF 13836 and 13833, right and left premaxillary-maxillary series, respectively. Slight differences in wear indicate that these represent different individuals. The width of the palate across the molars was determined partly from UF 19265, a maxillary with well-worn teeth, in which the distance from the midline to the labial wall of M3 was just over 18 mm. Further concordant estimates were derived from the occlusal relationships between the upper and lower canines and from the contact between the incisive processes in UF 13836 and 13833.

The restoration of the nasal and lacrimal bones is largely hypothetical (Fig. 1D-E). The posterior overlapping suture of the nasals on the frontals is clearly demonstrated in two crania, UF 13834 and 19258. The position of the posterolateral corner of the lacrimal is presumably marked by the supraorbital notch as in most other selenodont artiodactyls. The width of the nasals anteriorly is constrained by the preserved dorsal portions of the premaxillary and maxillary in UF 13836 and 13833.

The most uncertain aspect of this cranial restoration was the relationship between the facial portion of the skull and the braincase. A solution was provided by the relationship between the glenoid fossa and the cheek tooth row, which was determined from the large sample

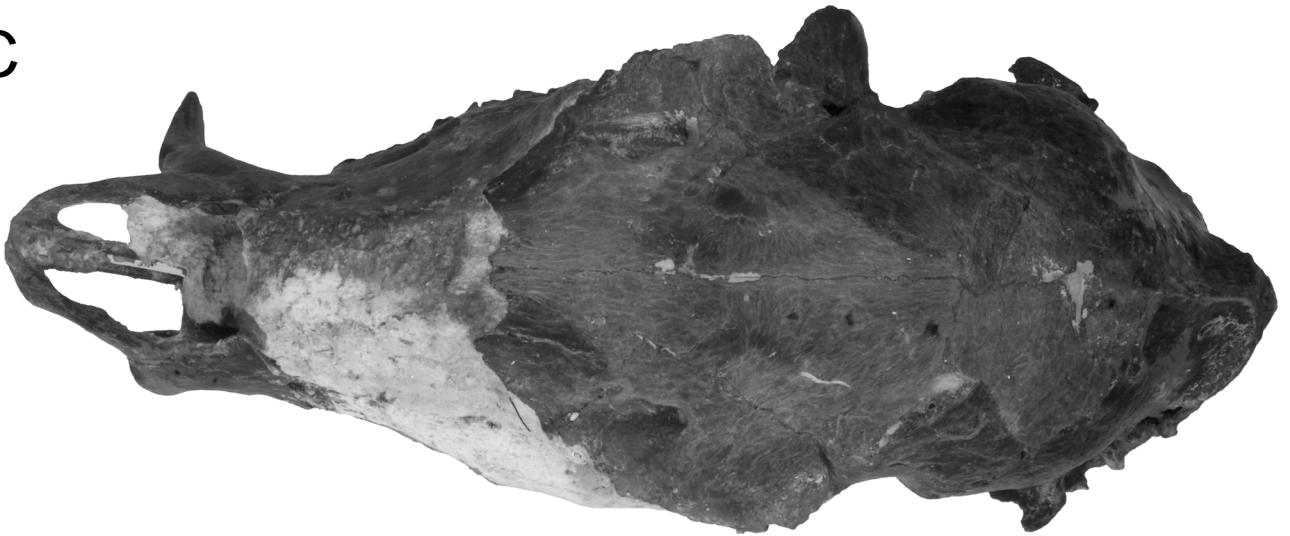
A



B



C



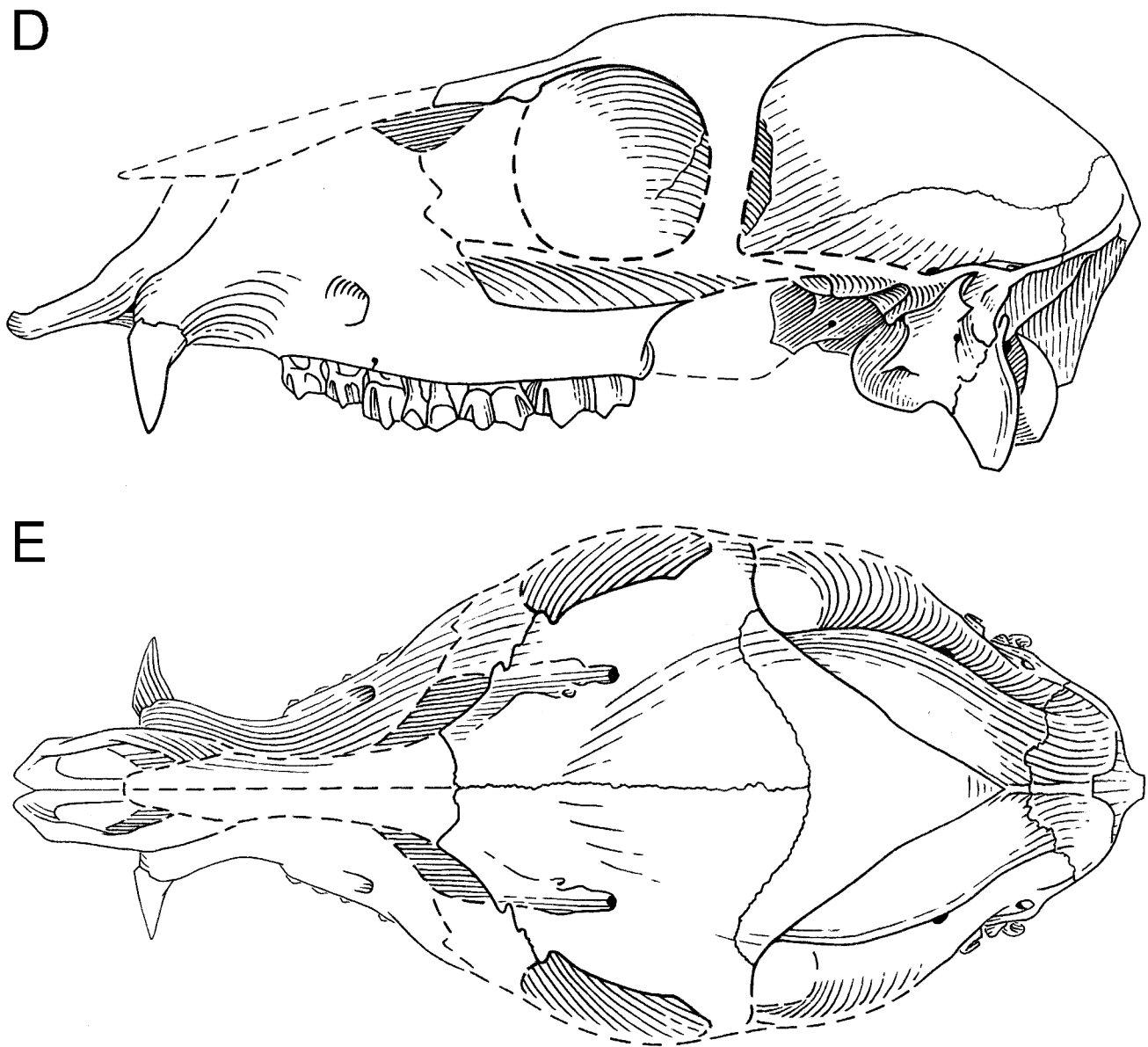


Figure 1. Composite cranium of *Floridameryx floridanus* new genus and species, from the Withlacoochee River 4A Site, Florida. It is made up of UF 13834 (braincase, frontals, and orbits), 13833 (left premaxilla and maxilla), and 13838 (right premaxilla and maxilla); other regions reconstructed. The three specimens are most likely from three different individuals. A, right lateral (reversed), B, ventral, and C, dorsal views of the cranium. D, lateral, and E, dorsal views of an idealized reconstruction of the skull, showing sutures between major skull elements.

of undistorted mature mandibles. When this relationship was satisfied, several other relationships across the “hinge region” were concordant. These included the outline of the orbit which is nearly circular, the zygomatic arch as a nearly horizontal surface, the projection of the palate across the pterygoid region to the base of the alisphenoid, and the congruence of the frontal profile with the nasal projection along the upper edge of the maxillary. Because these relationships were satisfied

in well-preserved specimens, restored features such as cranial flexion and cranial length must be constrained within the normal range of mature specimens of *Floridameryx floridanus*.

PREMAXILLA

In the Pseudoceratinae, each premaxilla consists of an obliquely ascending facial portion and a horizontal palatal portion (Fig. 1). The long, narrow facial portion

curves upward around the narial opening. The aperture thus formed is somewhat taller than wide, about as in *Moschus* and not so deep as in higher ruminants. Although the upper edge in available specimens is broken, the premaxilla evidently contacted the nasal bone broadly, unlike *Hyemoschus* where the maxillary bone intervenes, or *Cephalophus* where it only touches the nasal. In lateral view, the posterior margin along the maxillary follows a gentle sigmoid curve, convex dorsally and concave ventrally near the canine. The suture consists of a thin lamella of the premaxilla clasped between inner and outer layers of the maxilla. This tongue-in-groove structure, characteristic of all ruminants, evidently enables the premaxillary-maxillary junction to withstand considerable stress on the incisive region. The premaxilla has no direct contact with the canine alveolus as it often does in *Moschus*.

The palatal portion of the premaxilla is well-preserved and shows clearly that no upper incisors were present (Fig. 1B). It is somewhat longer than in Tragulidae and is not so strongly downturned. On the other hand, the incisive region is much shorter than in *Moschus*, or especially than in any higher ruminant. The vertical height of the premaxilla diminishes in the incisive region, but it does not become flattened and broadened as in *Moschus* and especially in higher ruminants. On the contrary, the bone anterolateral to the incisive foramen is deeper than it is wide. Presumably the horny cropping pad had not developed to such an important degree as in more advanced ruminants, especially in grazers. The palatal exposure of the premaxilla is unusually limited. The palatine processes, which join together in the midline, are frail and short. Likewise the incisive foramina, most of which they enclose, are only about 10 mm long. With respect to these short, narrow premaxillae, the Pseudoceratinae more nearly resemble the Tragulidae and *Cephalophus* than even such primitive ruminants as *Moschus* and *Dremotherium*.

MAXILLA

The maxilla covers much of the facial region and most of the palate and supports the entire upper dentition. The anterior tip of the palatal portion forms the posterolateral margin of the incisive foramen in the usual manner. The large upper canine is completely and firmly surrounded by the maxillary bone (Fig. 1). The anterior border of the facial portion, which is sutured to the premaxilla, ascends obliquely to meet the nasal bone. The root of the canine curves posterodorsally just within the upper margin of the maxilla. The anterior end of the infraorbital canal opens 6 mm above the P3. It

occupies the same position in the skull of *Pseudoceras skinneri* as in one juvenile and seven adult specimens of *Floridameryx floridanus*. This contrasts with the usual position of the infraorbital foramen above and often anterior to the P2 in most other ruminants, including Moschidae and Tragulidae. The rest of the facial portion of the maxillary is plain, marked only by a gentle horizontal convexity above the molars, and a weak facial crest extending forward from the jugal bone onto the posterior edge of the maxilla. This posterior facial portion of the maxilla is surprisingly shallow in view of the considerable hypsodonty of the molars. The depth from the jugal suture to the alveolar border of the M3 ranges from 5.5 to 6.5 mm in mature specimens of *F. floridanus*.

The alveolar border of the maxilla follows a gently convex course curving ventrally and labially. The weakly developed maxillary tuberosity projects posteromedially behind the molars. The palatine suture crosses the midline opposite M1 and turns posteriad adjacent to the posterior molars. The anterior palatine foramen emerges at the maxillo-palatine suture rather than within the palatine as it does in Tragulidae. In *Moschus* and the Cervidae, the position of this foramen is even farther anterior, lying entirely within the maxilla, as noted by Rutimeyer (1883). The forward passage of the palatine nerves and arteries are marked by short but deep grooves on the palatal surface of the maxillary bone. The palatine portion of the maxilla is noticeably arched dorsally and widens posteriorly adjacent to the palatine. A prominent diastematal crest curves lingually between the canine and the premolars. This crest is stronger than in Tragulidae and more closely approaches the midline, thus resembling Moschidae and higher ruminants.

NASAL

The nasals are inadequately preserved in pseudoceratine crania; only their posterior contact with the frontals need be described. Each nasal forms a V-shaped dentate suture with the frontal, the posteriormost point lying lateral to the midline. The lateral edge of each nasal lies about 2 mm medial to the course of the supraorbital canal. The nasal is separated from the lacrimal by the frontal bone and by a lacrimal vacuity.

LACRIMAL

The lacrimal bone is fully preserved only in the skull of *Pseudoceras skinneri*, F:AM 33720. It forms a broad plate on the side of the face immediately anterior to the orbit, and it occupies an almost equal area inside the orbit. The facial portion of the lacrimal is large and flat as in Moschidae and Tragulidae. In many

artiodactyls and in most higher ruminants, by contrast, this area is deeply depressed for a facial gland. A large lacrimal vacuity is present, whereas in Tragulidae it is absent. The vacuity is preserved only in *Pseudoceras skinneri*. In *Floridameryx floridanus* the vacuity is clearly indicated by the smoothly finished anterolateral margins of the frontals. The vacuity, underlain by the ethmoturbinal bones, has about the same width as the facial exposure of the lacrimal bone. Its long dimension extends anteroventrally as in most ruminants. In the skull of *P. skinneri* the upper margin of the lacrimal bone, along the frontal suture, measures 9 mm, while the ventral margin, along the maxilla and jugal, is about 13 mm long. A lacrimal fossa for the lacrimal duct lies just inside the orbit and leads into a single anteriorly directed foramen, as in *Moschus*.

FRONTAL

The frontal contributes more to the skull roof than any other bone (Fig. 1). It does not reach posteriorly to the orbit as in most horned ruminants, thus resembling *Moschus* and Tragulidae. Presumably the posterior extension of the frontal in higher ruminants is correlated with the development of antlers and horns from that bone.

The anterior, W-shaped contact with the nasals lies well in front of the orbit. In *Pseudoceras skinneri*, F:AM 33720, the frontals reach even farther forward than the lacrimal, about 20 mm ahead of the orbit. In *Floridameryx floridanus* crania they extend only about 15 mm anterior to the orbit. In three specimens the midline penetration of the nasals between the frontals is only about 3 or 4 mm, whereas in *Moschus* the depth is about 10 mm in most specimens. The lateral margin of the frontal extends posterolaterally forming the upper wall of the lacrimal vacuity; there it turns posteriorly along the dentate suture with the lacrimal bone and enters the anterodorsal corner of the orbit.

The frontal does not extend onto the side of the face below the upper rim of the orbit as it does in most higher ruminants. In this respect, the Pseudoceratinae resemble *Moschus*. The frontal contributes a major part of the inner wall of the orbit. The orbital walls are not in such close contact as in Tragulidae or in *Cephalophus*. Rather they are well separated in *Pseudoceras skinneri*, closely resembling *Moschus* in this respect; the walls are even more widely separated in *Floridameryx* crania.

Inside the orbit the frontal slopes steeply in a medioventral direction. It narrows toward its ventral edge and forms a U-shaped contact with the pterygoid

and alisphenoid. The ethmoidal foramen lies anterior to its normal position in higher ruminants, almost touching the lacrimal.

The dorsal exposure of the frontals is dominated by a strong dome-like convexity much like that in *Moschus*. Each supraorbital foramen is large, often complexly subdivided, and leads forward into a deep longitudinal groove. A small median foramen occurs near the anterior end of the frontals in some specimens. The postorbital process of each frontal is at least 7 mm thick near its dorsal origin and descends nearly 15 mm to its suture with the jugal.

JUGAL

This fragile bone is completely preserved only in the skull of *Pseudoceras skinneri*, F:AM 33720. The largest portion of the jugal contributes to the floor of the orbit. Posteriorly it bifurcates in the usual manner to produce an ascending postorbital process and a horizontal zygomatic process.

The large suborbital portion of the jugal forms a nearly horizontal plate about 12 mm wide that rises gently toward the lacrimal bone in front of the orbit. From its ventral surface this plate gives origin to the masseter muscle, a strong masseteric crest marking the lateral edge. The masseteric plate is only about 2 mm thick. The anteriormost part of the jugal extends 5.8 mm in front of the orbit along a nearly horizontal contact with the lacrimal bone. In lateral view this antorbital portion of the jugal remains rather shallow, not exceeding 8 mm in depth.

Within the orbit, the jugal contact lies only about 1 mm below the lacrimal foramen. The anterolateral contact with the maxillary is by a dentate suture, but medially, against the alveolar region of the maxillary, the contact follows a linear course. The maxillary extends a long splint-like process posteriorly along the ventro-medial edge of the jugal to a point posterior to the postorbital bar.

The postorbital process of the jugal rises dorsally and slightly anteriorly, whereas in most ruminants and tragulids the postorbital bar slopes posteriorly. The contact between the frontal and jugal lies in the lower third of the orbital opening as in Moschidae and Cervidae generally, not in the upper third as in Tragulidae. The zygomatic process of the jugal underlies the squamosal and tapers to a point opposite the anterior edge of the glenoid fossa. The masseteric crest follows this process and continues as a strong crest onto the glenoid portion of the squamosal as in *Moschus* and most ruminants.

PALATINE

The palatal exposure of the palatine extends from the M2 to a point about 15 mm behind the M3. The apex of the internal nares lies opposite the posterior edge of the M3 as in *Moschus* and higher ruminants generally. In Tragulidae, by contrast, the palatines meet at the midline for nearly their full length and, as noted by Rutimeyer (1881), the nares open behind the orbits. The anterior palatine foramen borders the anterior margin of the palatine, whereas in Tragulidae this foramen opens wholly within the palatine.

The orbital exposure of the palatine rises to nearly the middle of the orbit. It contacts the alveolar portion of the maxilla laterally and makes an extensive intraorbital contact with the frontal. The posterior opening of the large infraorbital canal lies low on the medial side of the alveolar region between the maxillary and palatine bones as in *Moschus* and higher ruminants, whereas in Tragulidae it lies directly above the alveolar region, dorsolateral to its position in other ruminants. In Tragulidae, the palatine bone extends laterally above the maxillary to the infraorbital canal, whereas in Pseudoceratinae, *Moschus*, and higher ruminants the lacrimal bone occupies that position. The sphenopalatine foramen is relatively small and low, as in higher ruminants, and in strong contrast to the situation in Tragulidae. The posterior palatine foramen opens in the normal position below the sphenopalatine foramen.

PTERYGOID

This bone is preserved only as a minute piece in the skull of *Pseudoceras skinneri*. Nonetheless traces of its attachments to the medial wall of the alisphenoid, and to the palatine, presphenoid, and basisphenoid, may be recognized. It evidently occupied a trapezoidal area on the medial wall of the pterygoid region, reinforcing the alisphenoid-palatine connection. The pterygoid thus resembles that of *Moschus*; it is not so reduced as in *Hyemoschus* nor so strongly reflected as in *Tragulus*.

VOMER

The vomer is represented only by traces of its contact with the presphenoid. Evidently the posterior portion is weak and does not extend far posteriorly.

PRESPHENOID

At its posterior end the presphenoid is subcircular in cross-section. In the middle portion, where it is covered by the vomer, it becomes transversely

compressed; and at the anterior end it broadens again to buttress the ethmoid region.

ORBITOSPHEOID

The ventral and anteroventral portions of this bone are fused tightly onto the sides of the presphenoid. The orbitosphenoid occupies the posteroventral part of the orbital inner wall, posterior to the palatine. The contact between the orbitosphenoid and frontal bones follows a sigmoid course, rising from the midorbital region toward the postorbital bar. The orbitosphenoid broadly contacts the parietal in the posterior part of the orbital wall, much as in *Moschus*, and not as in Tragulidae where the alisphenoid intervenes. The posteroventral wall of the orbitosphenoid borders the alisphenoid. The left and right orbitosphenoids are widely separated across the midline except at their bases. This contrasts with the Tragulidae in which these bones are fused at the midline. The optic foramen pierces the ventral wall of each orbitosphenoid midway between the anterior and posterior margins. The optic foramen also partly excavates the posterodorsal surface of the presphenoid just anterior to the optic chiasma.

ALISPHEOID

The alisphenoid borders the anterolateral edge of the basisphenoid and extends wings or processes in three different directions. One wing extends posteriorly under the bulla; one ascends into the orbitotemporal region; and the third passes anteroventrally as the pterygoid process. The pterygoid process of the alisphenoid joins the palatine to form the posterolateral edge of the hard palate. In UF 19257 and 13834, suture scars indicate the position of the small pterygoid bones on the medial wall of the alisphenoids.

From the pterygoid portion of the alisphenoid an unusually strong crest extends posteriorly along the edge of the basisphenoid to connect with the anteromedial wall of the auditory bulla. This crest forms the medial wall of a channel for the eustachian tube and the tensor tympani muscle. A much shorter and lower longitudinal ridge on the alisphenoid forms the lateral wall of the eustachian canal. The large foramen ovale lies dorsolateral to the eustachian canal and occupies much of the width of the posterior wing of the alisphenoid. The foramen ovale faces ventrolaterally and slightly anteriorly. Anterior to this foramen and at the base of the pterygoid process are one or two moderate-sized foramina for the subsphenoidal veins. Similar foramina are common but variable in *Moschus* and Cervidae. A narrow bridge of the alisphenoid (only about 3 mm wide),

separates the pterygoid wing of the alisphenoid from the ascending wing. It faces anteroventrally and is taller than wide (about 6 mm x 4 mm). The anterodorsal wall of the foramen is formed by the orbitosphenoid bone.

The ascending portion of the alisphenoid contacts the orbitosphenoid in the posteroventral corner of the orbital chamber, but only for a short distance (about 9 mm). As in *Moschus* and higher ruminants, the alisphenoid gives way dorsally to the parietal which occupies the upper postorbital region. A strong prominence for the lateral pterygoid muscle occupies the area lateral to the sphenoidal fissure and a crest passes posteriorly from it onto the squamosal as in most ruminants. From the tip of this crest, the alisphenoid-squamosal suture passes posteromedioventrally into the tympanic region. The ascending wing of the alisphenoid (covering the lateral wall of the braincase) is smaller than its posterior wing (covering the ventral wall of the braincase).

PARIETAL

The parietal occupies a greater portion of the braincase than in higher ruminants, in which the frontal is more expanded. In this respect Pseudoceratinae resemble other hornless ruminants including the Gelocidae, Moschidae, Hypertragulidae, and Tragulidae. Likewise, along its contact with the frontal the parietal is concave anteriorly, whereas in higher ruminants it is usually convex. The dorsal aspect of the parietal is divided quite distinctly into a flat anterior and a crested posterior part. The anterior part is continuous with the frontal and forms the posterior triangular portion of the skull table. In the posterior part, the parietal crests connect the postorbital bars to the sagittal crest. The sagittal crest and the adjacent parts of the parietals slope downward toward the nuchal eminence. The parietals meet the supraoccipital bones 8 to 10 mm short of the nuchal eminence.

The parietals form much of the lateral wall of the braincase (Fig. 1D-E). They include both the narrowest part, across the postorbital constriction, and the widest part, above the glenoid fossa. The difference in width between these two parts is, as in *Moschus*, far more dramatic than in higher ruminants. The anterior edge of each parietal follows a vertical suture from the postorbital bar ventrally behind the orbit meeting the frontal for about 5 mm. It extensively contacts the orbitosphenoid. The anteroventral corner of the parietal meets the alisphenoid along a sinuous suture less than 5 mm long, just above the level of the zygomatic arch. The long ventral margin of the parietal rises gently as it passes

posteriorly toward the nuchal eminence. Finally, the parietal meets the supraoccipital along a vertical contact about 12 mm long.

SQUAMOSAL

The upper edge of the squamosal overlaps the parietal and supraoccipital along the side of the braincase. The suture passes anterodorsally from the middle of the mastoid crest (about 13 mm below the nuchal eminence in UF 19257, about 14 mm in F:AM 33720) and follows the edge of the supraoccipital for 7 or 8 mm. There it meets the parietal forming a long descending contact below the widest part of the cerebral expansion. A narrow tongue of the squamosal turns ventromedially to enter the posteroventral corner of the orbit where it is tightly fused with the alisphenoid. At this point the squamosal is very thick and assists the alisphenoid in supporting a strong tubercle for the lateral pterygoid muscle. The tubercle is strong as in *Moschus* but does not reach the extremely well-developed condition seen in Tragulidae and Protoceratidae (Patton & Taylor 1973:376). The squamosal suture then turns posteriorly along the lateral edge of the alisphenoid, nearly touching the foramen ovale, and passes to the bulla and mastoid region.

The zygomatic-glenoid portion of the squamosal extends laterally 8 to 10 mm beyond the widest part of the braincase. It is supported by anterior and posterior crests. The posterior zygomatic crest is an anterior continuation of the mastoid crest as it turns anteriorly and widens above the ear region. It becomes still wider and thicker above the glenoid fossa. The splint-like zygomatic process of the squamosal overlaps that of the jugal. The zygomatic process thus spans a 12 mm gap between the glenoid fossa and the postorbital bar, where the squamosal terminates.

The glenoid fossa is nearly rectangular in outline (Fig. 1B), being about 15 mm wide and 6 mm long. In this respect the Pseudoceratinae differ from most other ruminants. The longitudinal channel for the capsular ligament on the medial side of the glenoid fossa is present, as in virtually all ruminants, but it is not as strongly developed as in *Moschus*. The glenoid fossa is bounded posteriorly by a very broad, very strong postglenoid process. It is about 10 mm wide and nearly 5 mm deep in both *Pseudoceras* and *Floridameryx*. The relative size of the process is greater than in any other ruminants, although it most closely resembles that in *Mazama* and other Cervidae. The postglenoid foramen is small, relatively smaller even than in Tragulidae, and in striking contrast to the large foramina in *Moschus* and higher

ruminants. The lateral side of the postglenoid process turns anteriorly and joins a strong zygomatic crest, thus enclosing the lateral side of the glenoid fossa. This lateral glenoid crest is only weakly developed in *Moschus* and some higher ruminants. This strong lateral crest, the broad and deep postglenoid process, and the concave glenoid surface evidently provided the Pseudoceratinae with an extraordinarily secure jaw articulation, presumably a feature related to powerful occlusion of the enlarged canines in presumed males.

A supraglenoid foramen opens above the zygomatic crest posterior to the glenoid region. In the skull of *Pseudoceras skinneri* it is over 3 mm in diameter and in *Floridameryx floridanus* it is only slightly less. This foramen is minute or absent in Tragulidae and in most higher ruminants, but a moderate-sized supraglenoid foramen occurs as a variable feature in *Moschus* and *Cephalophus*. This foramen evidently provides an alternative to the postglenoid foramen as a route for venous drainage from the lateral cerebral region. In *Moschus* and higher ruminants, a large excavation above the external auditory meatus, the suprameatal fissure, provides still another alternative route, but this excavation is not developed in Pseudoceratinae nor in Tragulidae.

Above the external auditory meatus and behind the zygomatic arch is the post-tympanic neck of the squamosal. In most primitive artiodactyls this region is prominent, whereas in most ruminants it is weakly developed in comparison with the mastoid process immediately posterior to it. It is likewise very weak in Pseudoceratinae. Instead, a long tubular meatus dominates this area.

AUDITORY BULLA

The bulla has a spheroidal outline in Pseudoceratinae. It lacks the anteromedial-posterolateral elongation observed in *Moschus* and most higher ruminants. It is hollow and moderately inflated; the degree of inflation lies between the extremely swollen condition in *Cephalophus* or the Tragulidae and the flattened condition of *Moschus* and most Cervidae. In size and degree of inflation it resembles the bulla of *Hydropotes*, although it is constructed quite differently. The medial wall of the bulla touches the basioccipital broadly in *Pseudoceras*, whereas in *Floridameryx* a small fissure bounds the bulla medially. The long tubular meatus rises posterodorsolaterally so that its lip touches the posterior edge of the zygomatic crest. It is longer and more nearly vertical than in *Moschus* or any higher ruminants, and it is unique in attaining the level of the

zygomatic crest. Its aperture faces dorsally and posteriorly rather than laterally and posteriorly as in most ruminants. The tympanohyal process lodges at the base of the tubular meatus where it fuses with the lateral wall of the bulla. In most other ruminants the tympanohyal process lies farther posteriad, close to or in contact with the paroccipital process. In *Moschus*, *Hydropotes*, and *Cephalophus*, however, the tympanohyal is set anterolaterally near the base of the meatus, as in Pseudoceratinae. The styliiform process is weakly developed and blunt, in contrast with that of *Moschus* and most Cervidae.

PERIOTIC

The following description is based on a petrosal removed from UF 19257 (Fig. 2). After study and illustration (Fig. 2), it was reattached to the skull. This dense disc-shaped bone is covered ventrally and laterally by the bulla and is inseparably fused with the mastoid along its lateral margin. Its medial margin lies just dorsal and lateral to the basioccipital. The medial margin does not contact the basioccipital and lacks the strong process and notch which in *Tragulus* contact the basioccipital and form part of the median lacerate foramen. Posteromedially, behind the posterior lacerate foramen, the periotic is braced against the basioccipital, about as in *Moschus*. The periotic is somewhat longer than wide, its long axis diverging posterolaterally from the long axis of the skull at an angle of about 45 degrees. The ventral surface of the periotic faces anteroventrolaterally in the usual manner.

The structural details of the periotic are complex partly because of the intricate structures of the middle and inner ear, and partly because of the diverse cranial nerves and vessels that commute through this part of the braincase. The ventral face of the periotic lies in a plane essentially parallel to that of the endocranial face and is separated from it by a thickness of about 4 mm. The ventral (basicranial) aspect will be described first (Fig. 2A).

The globose promontorium dominates the ventral aspect of the periotic. The contours of its surface closely follow the first two cochlear whorls, the posterior being the larger. A third complete whorl is present anteriorly, but is too small to be reflected by the promontorial contours. The gentle swale between the first two cochlear whorls reveals no trace of any vessels or nerves in any of the specimens at hand. As in ruminants generally, no branch of the internal carotid artery crossed the promontorium.

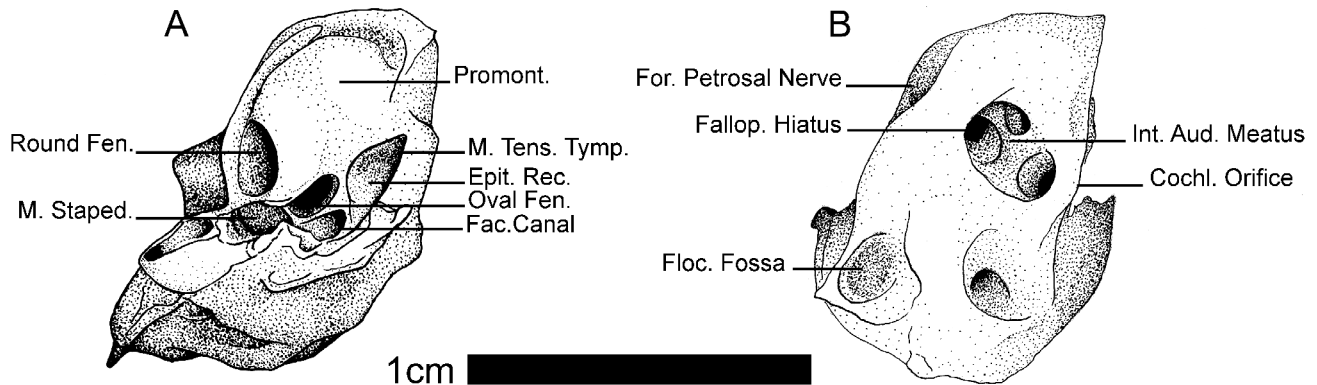


Figure 2. Left Periotic of *Floridameryx floridanus*, UF 19257, from the Withlacoochee River 4A Site in A, basicranial, and B, endocranial, views. Promont.(Promontorium), Round Fen.(Round Fenestra), M.Staped. (Stapedial Muscle Fossa), M.Tens. Tymp. (chamber for Tensor Tympani Muscle), Epid. Rec. (Epitympanic Recess), Oval Fen. (Oval Fenestra), Fac. Canal (Facial Canal Opening), For. Petrosal Nerve (Foramen Petrosal Nerve), Fallop. Hiatus (Fallopian Hiatus), Floc. Fossa (Flocular Fossa), Int. Aud. Meatus (Internal Auditory Meatus), Cochl. Orifice (Cochlear Orifice).

The rounded medial edge of the periotic is thin and forms a relatively narrow band beside the promontorium. In *Moschus*, by contrast, the band is much wider and thicker. The closest comparison in this feature is with Tragulidae where, although not smoothly rounded, the medial edge of the periotic is narrow and thin. Presumably, this feature is related to the development of a substantially inflated bulla, which protects the medial edge of the periotic by covering it ventrally.

The round fenestra (*fenestra cochleae*) faces directly posteriad as in *Moschus* and Cervidae. In Tragulidae, on the other hand, it faces posterolaterally. The ventral lip of the fenestra nearly conceals the aperture in Pseudoceratinae, whereas in most ruminants it is well exposed. Facing the fenestra posteriorly is a high bony wall, formed from the mastoid, resembling that in most higher ruminants, but missing in Tragulidae. Likewise, a bony curtain separates the entrance to the round fenestra laterally from the fossa for the stapedial muscle. In this feature, also, the Pseudoceratinae resemble most higher ruminants and differ from Tragulidae.

The deep fossa for the stapedial muscle lies posterolateral to the round fenestra. It is not as elongate transversely as in *Moschus* and the Cervidae but is more deeply pocketed. In particular, the lateral edge of the stapedial fossa is marked by a steep wall well above the level of the facial canal, a feature not observed in Cervidae or *Moschus*, but more nearly approached in other Gelocidae and in Tragulidae.

The oval fenestra (*fenestra vestibulae*) lies anterolateral to the round fenestra. A distinct bony crest extends along the edge of the promontorium from the

round to the oval fenestra, evidently serving as an attachment for part of the stapedial muscle. I have not observed such a strong crest in other ruminants, although a weakly developed crest commonly occurs in *Moschus*.

The long axis of the fenestra ovale parallels the cochlear axis. In Pseudoceratinae, as in Tragulidae, the aperture is nearly circular, in contrast with *Moschus* and the Cervidae in which the length is fully twice the width. The fenestra ovale is pressed closely against the wall of the promontorium. The bevelled edge for the stapes footplate thins considerably along the medial side as in Tragulidae, whereas in *Moschus* and Cervidae the bevelled edge is continuously broad. Corresponding features of the stapes itself are described below.

The facial canal emerges through the ventral surface of the periotic immediately posterolateral to the fenestra ovale. In Tragulidae the facial canal emerges farther forward, anterolateral to the fenestra ovale, but in this feature the Pseudoceratinae resemble higher ruminants. In *Floridameryx*, the opening of the facial canal lies well below the level of the oval fenestra and is separated from it by a crest. The difference in elevation is much less in Tragulidae, Cervidae, and *Moschus*, and in them no crest sets off the facial canal. The facial canal may be followed anterodorsally as it passes above the lateral side of the fossa for the tensor tympani muscle. In the Pseudoceratinae, the small epitympanic recess lies well forward of the facial canal opening. It lies lateral to the tensor tympani fossa and is essentially continuous with it. This same arrangement is found in other Gelocidae, in *Moschus*, and in higher ruminants. In the Tragulidae, on the other hand, the epitympanic recess lies lateral or posterolateral to the

facial canal, entirely separated from the tensor tympanic fossa. In Pseudoceratinae and other Gelocidae, an unusually prominent crest separates the opening of the facial canal from the tensor tympani fossa. In Tragulidae, by contrast, the facial canal emerges within the fossa, and no line of demarcation can be detected. In *Moschus* and higher ruminants the condition is intermediate, in that the canal opens posterior to the edge of the fossa but the boundary is marked only by a subtle decrease of slope or at most a faint crest.

In Pseudoceratinae, the tensor tympani muscle is housed in a large spheroidal chamber anterior to the fenestra ovale and the ventral opening of the facial canal. The medial side of the chamber is represented by the flattened bone surface covering the distal cochlear whorls. The anteroposterior length of the chamber is no greater than its transverse width, as in other Gelocidae, but in marked contrast with *Moschus* and most Cervidae in which the chamber is longer than wide and extends as far anteriorly as the terminal cochlear whorl. This hemispherical tensor tympani chamber is relatively and absolutely much larger and more deeply pocketed into the roof of the middle ear in Pseudoceratinae and other Gelocidae than in Tragulidae; resembling in that regard *Moschus* and most higher ruminants.

A general explanation of several special features of the gelocid periotic is lateral compression of the middle ear by the mastoid wall. This forces the epitympanic recess anterior to the facial canal and makes it join the muscular fossa. The facial foramen is shifted posteromedially so that it opens immediately below the fenestra ovale. It also causes the facial canal to curve around toward the round fenestra. And finally, the muscular chamber is tucked more deeply under the anterolateral wall of the periotic.

The endocranial side of the periotic (Fig. 2B) consists of a thinner ventromedial portion including the internal auditory meatus, and a thicker dorsolateral portion housing the semicircular canals. The internal auditory meatus is in fact a common orifice for several canals passing from the brain through the periotic. It is divided by a low bony ridge into a smaller lateral fossa and a larger medial fossa. This dividing ridge is low as in *Gelocus*, *Moschus*, and most Cervidae, not prominent as in Tragulidae. The lateral fossa within the internal auditory meatus contains two openings. A small posterior opening enters the vestibular canal, through which the superior ramus of the vestibular nerve reaches the outer ampulla of the utriculus. The large anterior opening provides passage for the facial nerve via the Fallopian

Hiatus as it passes ventrally along the lateral side of the cochlea and then turns posteriad into the tympanic cavity as described above.

The medial fossa within the internal auditory meatus contains one large and two small openings. The large opening, the internal acoustic pore, conducts the acoustic nerve anteroventrally to the organ of Corti within the cochlea. The two smaller openings pass laterally through the wall of the periotic into the middle region of the cochlea. These features in Pseudoceratinae closely resemble those in most ruminants.

A rather large cochlear orifice opens into the medial edge of the periotic about 2.5 mm medial to the internal auditory meatus. It opens ventrally inside the cochlea near the round fenestra as in other ruminants. In the specimen of *Floridameryx*, these two orifices are about half a millimeter apart. On the lateral edge of the periotic, a slit-like opening passes posteriorly into the periotic bone. This Fallopian hiatus represents the entry of the superficial petrous nerve into the Fallopian aqueduct about midway between its endocranial and tympanic openings. It closely resembles the hiatus in other Gelocidae, *Moschus*, and most higher ruminants, but differs from the Fallopian hiatus in Tragulidae, for in that family the hiatus lies more nearly on the tympanic face than on the edge of the endocranial face, and it has a more anterior position than in Gelocidae or higher ruminants.

The dorsolateral portion of the periotic has an irregular surface reflecting the adjacent surface of the cerebellum and, laterally inside the periotic, the semicircular canals. Raised ridges forming a Y-pattern represent the superior semicircular canal passing dorsolaterally, the posterior semicircular canal fading away posteriorly, and the common root of these two canals. Of three lateral cerebellar lobes represented by fossae, only the floccular fossa is very distinct. It lies largely within the arc of (and ventral to) the superior semicircular canal. It is almost hemispherical with a diameter of about 3.5 mm and a depth of about 2.5 mm. The resemblance of this floccular fossa to that of *Moschus* is very close. As Sigogneau (1968) has observed, a deep floccular fossa is found in *Moschus* and *Hydropotes*, but not in other modern Cervidae. An even deeper floccular fossa occurs in other Gelocidae. Since a very deep floccular (or subarcuate) fossa also occurs in Hypertragulidae and Camelidae, as well as Cainotheriidae and Xiphodontidae, it is evidently a primitive feature shared by many early selenodont artiodactyls.

In Tragulidae, however, the morphology on the endocranial side of the semicircular canal is markedly different. The only deep fossa that might be homologous to the floccular fossa lies posterodorsal (not ventral) to the superior semicircular canal. Other features in this region also differ radically in Tragulidae, as compared with Gelocidae and Moschidae. For example, a large canal, presumably for the superior petrosal vein, passes through the upper portion of the periotic lateral to the semicircular canals; in Pseudoceratinae, as in most ruminants, no such canal exists.

MASTOID

The mastoid is difficult to describe, partly because it is largely overlapped by the squamosal anteriorly and dorsally and by the occipital posteriorly and ventrally, and partly because the suture lines bounding it fuse early and often become obscure. Fortunately, however, one specimen of *Floridameryx*, UF 13834, is a juvenile with parts of the squamosal missing, so that both mastoids are well delineated. The lateral face of the mastoid is broadly expanded (over 9 mm wide) under the cover of the squamosal and rises to nearly the same height along the mastoid crest of the squamosal. Only the thickened posterior edge of this face (about 2 mm wide) is exposed posterior to the squamosal, and anterior to the exoccipital. This posterior exposure most closely resembles that in *Moschus* and most higher ruminants; it is much narrower and strongly crested compared with the mastoid in Tragulidae.

This narrow exposure makes up the ventral half of the mastoid crest of the squamosal. From the junction of the squamosal and supraoccipital it extends anteroventrally to the bifurcation of the mastoid and zygomatic crests, just behind the external auditory meatus. There it gives off a smaller crest that proceeds ventrally down to the tip of the small mastoid process. At this point the mastoid exposure is extremely narrow, being sandwiched between the post-tympanic neck of the squamosal and the base of the paroccipital process. The emergence of the stylomastoid canal marks the squamosal-mastoid junction about 6 mm below the external auditory meatus and nearly the same distance anterior to the tip of the mastoid process. The narrow posterior edge of the mastoid is overlapped by the exoccipital to which it is fused. The mastoid foramen may open at the upper end of the mastoid-paroccipital suture, but in Pseudoceratinae it is minute or absent. The lower edge of the lateral wall of the mastoid is solidly fused with the periotic bone even in young specimens.

OCCIPITAL

The dorsal portion of the occipital is notable for its prominent external occipital protuberance. The protuberance is heavy and diamond-shaped, most closely resembling that in *Tragulid* and smaller than that in *Moschus*. The anterior point connects with the sagittal crest of which the occipital part is between 9 and 10 mm long. The dorsal surface of each occipital forms a trapezoidal surface. The anterior side descends nearly vertical for about 12 mm bordering the parietal. At the squamosal the occipital border turns posteroventrally to the mastoid bone and forms the high mastoid crest along a straight suture of nearly 7 mm length. In the development of the occipital protuberance and sagittal and mastoid crests, the Pseudoceratinae resemble *Gelocus* and *Moschus*, whereas in higher ruminants these features are largely subdued.

The posterior aspect of the occipital forms an almost perfect equilateral triangle. It has a more pointed apex than in *Moschus*; and the region is much wider than tall and the upper apex is very broadly rounded, as in higher ruminants.

A strong median occipital crest extends ventrally from the posterior point of the diamond-shaped external occipital protuberance about as in *Moschus*. At the lower end on either side of the midline a tubercle for the atlanto-occipital muscle is weakly defined. The major nuchal muscle attachment areas occupy most of the posterior aspect of the cranium. The upper pair are for the nuchal ligament and complexus muscles. The lateral third of the occipital region is set off by a vertical crest for the splenius and obliquus muscles.

EXOCCIPITAL

The condyle and the paroccipital process are the principal features of the exoccipital. The condyles agree in their disposition and shape with those of most ruminants. The ventral condylar surface terminates anteriorly in a transverse ridge as in horned ruminants. It is somewhat stronger in *Floridameryx* than in *Pseudoceras*. Such a ventral condylar ridge does not occur in Tragulidae but is found in *Moschus* and *Dremotherium*. Meade (1906) interpreted these as stop mechanisms for horned ruminants, but their occurrence in Merycoidodontidae, Moschidae, Camelidae, and Protoceratidae suggests that they originated earlier in artiodactyls with enlarged canine teeth (Webb 1965).

The paroccipital process in both *Pseudoceras* and *Floridameryx* is unusually large and posteriorly reflected. It slopes so strongly posteroventrally that the tip lies almost directly lateral to the point of the occipital

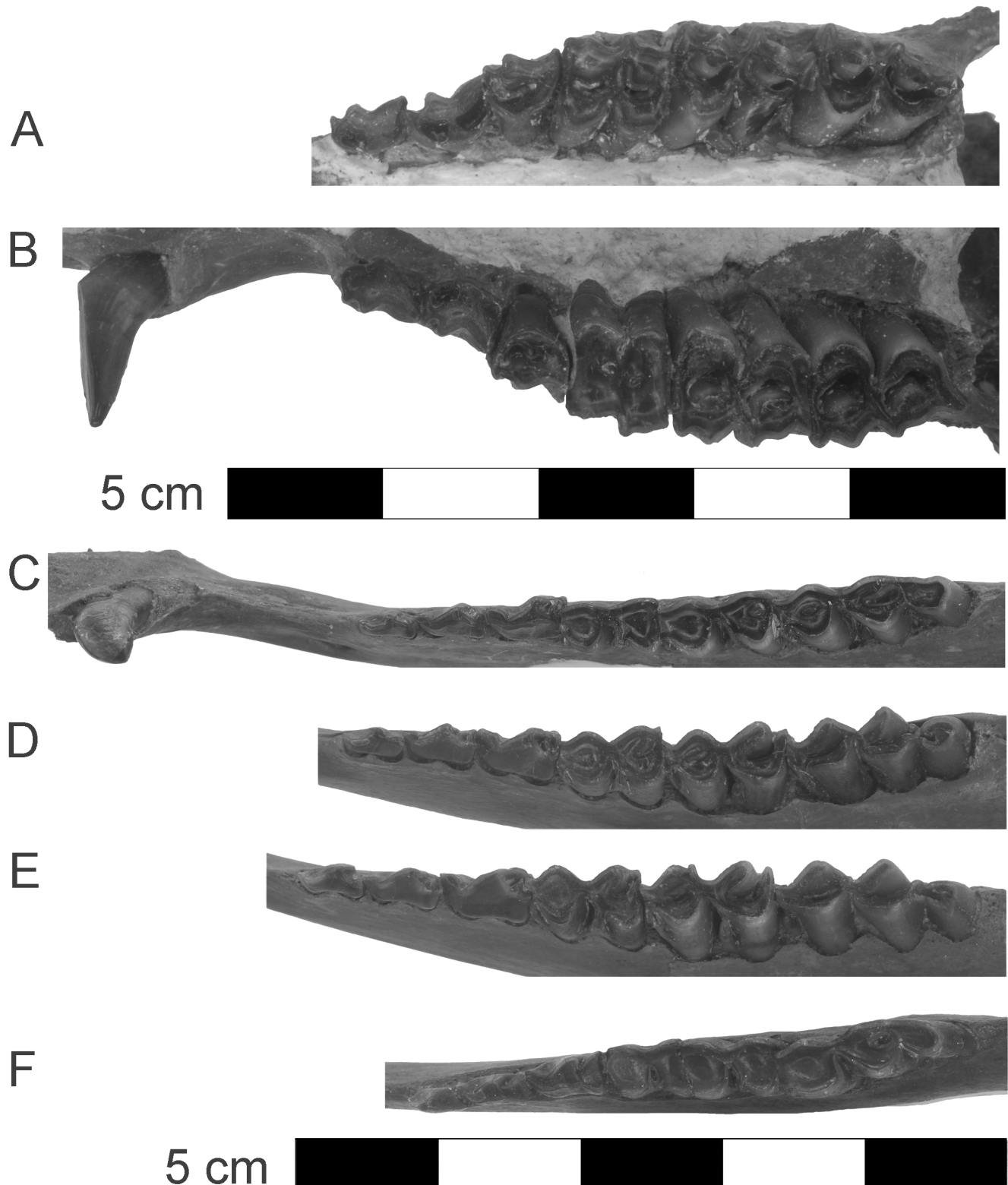


Figure 3. Occlusal views of upper and lower teeth of *Floridameryx floridanus* from the Withlacoochee River 4A Site, Florida. A. UF 13833, left maxilla with P2-M3. B. UF 13836, right maxilla with C1, P2-M3. C. UF 13832 (holotype), left c1, p2-m3. D. UF 19395 (allotype), left p2-m3. E. UF 225879, left p2-m3. F. UF 225882, right (reversed) p2-m3. Lateral views of mandibles shown in Figure 4. Upper scale bar is for the maxillae, lower scale bar is for the mandibles.

condyles. The blade-like process is expanded anteroposteriorly. It tapers from a maximum width of over 9 mm to a blunt tip. Its length, from its base near the mastoid process to its tip is about 14 mm. It curves slightly medially near the tip. Because of its strongly posterior orientation, the tip of the paroccipital process does not extend below the level of the basioccipital, as in *Moschus* and most other ruminants.

The condyloid fossa is narrow and deeply pocketed between these structures. It contains two relatively large foramina, the condyloid foramen and the hypoglossal foramen. The former is smaller and provides the ventral exit of the occipital canal from the braincase. The latter is larger, lies farther anteroventral, and transmits the hypoglossal nerve and the posterior meningeal branch of the occipital artery.

BASIOCCIPITAL

A pair of shallow concavities, each with a broad trapezoidal outline, marks the basioccipital region. They provide the origin for the various cervical flexor muscles which are considerably enlarged. Their arrangement in broad concavities closely resembles the condition in *Moschus*, and differs considerably from that in Tragulidae with their narrow basicranii. In the skull of *Pseudoceras skinneri* the bulla is broadly appressed against the lateral edge of the basioccipital, while in specimens of *Floridameryx floridanus* it is continuously separated by a gap of no less than a millimeter, about as in *Moschus*. The anterolateral edge of the basioccipital is emarginate, forming the medial wall of the jugular canal and immediately anterior to it the median lacerate foramen for the carotid artery and nerve.

BASISPHEOID

The anterior edge of the basioccipital is solidly fused with the basisphenoid in the three available specimens. The line of fusion is marked by a pair of basilar tubercles, moderately developed about as in *Moschus* and *Dremotherium*. As Sigogneau (1968) has observed, these tubercles are absent in higher ruminants, but are well developed in Tragulidae. They are separated by a groove that passes along the midline. The ventral surface of the basisphenoid is convex, and it narrows as it passes anteriorly between the pterygoid processes.

UPPER DENTITION

The dental formula is I0, C1, P2-P4, M1-M3 (Figs. 1B, 3A-B). The complete absence of upper incisors is

confirmed in *Floridameryx* by premaxillae that lack alveoli, including UF 13833 and 13836.

The upper canines appear to be of two sizes, dimorphism that is more fully documented in the lower dentition. Only the larger, presumably male, upper canines are adequately represented. The anteroposterior diameter of the root just above the crown ranges from 5.1 to 5.5 mm in four specimens of *Floridameryx floridanus*. The transverse diameter ranges from 3.2 to 3.7 mm in the same sample. The upper canine alveolus in UF 19270, however, is only 2.7 mm in anteroposterior diameter by 2.4 mm in transverse diameter. Presumably this specimen represents a female.

A remarkable feature of the male upper canine is heavy occlusal wear on the anterior face, as in Tayassuidae. The wear plane is nearly vertical and transverse, but with slight lingual and ventral beveling (Fig. 3B). One nearly unworn upper canine (UF 19272) exhibits a strong anterior crest with a small wear facet beginning near the tip. Others have nearly half the crown worn away from tip to base.

The root of a mature upper canine (UF 19271) is completely closed and had ceased to grow. The root is 16.2 mm long, while the heavily worn crown is 5.7 mm long. The canine makes a gentle spiral along its length. The root arcs forward and downward, assuming an essentially vertical position where the crown emerges from the maxillary. The tip of the canine is twisted outward around its own axis, so that the tip lies about 6 mm lateral to the root and to the cheek teeth. Evidently when the canine first erupts the tip receives the initial wear, but as it continues to emerge the tip twists downward and posterolabially so that the wear facet gradually shifts dorsolingually onto the anterior crown face.

P2 and P3 are long, bladelike teeth with a high secant labial wall (Fig. 3A-B). The parastyle is small but distinct and produces a persistent labial rib. The high principal cusp is the paracone. On the labial wall it forms a very prominent rib, set off by deep grooves before and behind. The paracone is broadly connected to an oblique bladelike metacone, which accounts for more than half of the tooth length. The paracone-metacone blade greatly resembles that of a carnivore carnassial, and it surely had a shearing function. The deep postparaconal groove functioned in much the same manner as the carnassial groove, that is to facilitate clearing the "blade." The long labial shearing facet slopes about 60 degrees above the horizontal in newly

erupted teeth, but declines to less than 30 degrees in well-worn teeth.

The lingual structures of P2 and P3 are relatively weak. They consist of a minute midlingual protocone supported by a small lingual root. The entire lingual margin is reinforced by a continuous cingulum which is especially strong at the anterolingual and posterolingual ends. As the premolars wear down, the protocone soon disappears as a distinct cusp, and forms a cross link between the labial blade and the lingual cingulum (Fig. 3A). At the same time anterolingual and posterolingual fossettes appear. In advanced wear, the posterolingual fossette is completely destroyed.

P4 consists of two crescentic cusps forming, in effect, a half molar, as in most artiodactyls (Fig. 3A-B). This tooth is three-rooted, as are P2 and P3, but here the protoconal root is very well developed. The posterolabial root is the weakest. The labial wall has a strong parastyle, an even stronger paracone, and, separated by a considerable gap, an elongate metacone. These labial structures partly resemble their counterparts in P2 and P3, but the carnassial function is much weaker. The fossette is large and persistent, but unlike higher ruminants, it occupies an anterior rather than a central position. One or a few minute ephemeral posterior fossettes sometimes are present in early wear stages. P4 has a higher crown than the preceding premolars.

The upper molars closely resemble one another and may be described together. Each successive molar, however, increases in height and length over the preceding (Fig. 3A-B). In *Floridameryx floridanus* the crown height of a slightly worn M1 (UF 19263) measured along the mesostyle, is about 4.3, while M2 measures 6.8, and a faintly worn M3 reaches a height of 8.1. An unworn M3 (UF 19262) measures 8.5 mm high. The upper molars are transversely compressed, a feature that is more obvious in the longer proportioned posterior molars.

The paracone and metacone are narrow subcircular cusps, as is clearly indicated by their pinched appearance within the fossettes. Nonetheless they produce a high bicrescentic ectoloph. Labially these cusps produce a prominent parastyle, paraconal rib, and mesostyle, only a weak metaconal rib, and a moderate metastyle. The M3 metastyle is stronger and grooved posterolabially. The paraconal rib is not reflected forward, nor does it join the parastyle as in Tragulidae.

The lingual cusps are crescentic or somewhat angular, with their vertices directed anterolingually. The adjacent midlingual limbs do not join each other directly and firmly, as one might expect in such hypsodont taxa.

Instead, the posterior limb of the protocone and the anterior limb of the metaconule often proceed separately toward the mesostyle, thinning as they do so. The midlingual valley, therefore, tends to be quite deep, often extending labially to the center of the fossettes in early wear stages. The nature of this midlingual commissure is weak but extremely variable. For example, in each molar of UF 19264 the posterior limb of the protocone is short, posteriorly directed, and does not reach the metaconule until a very late wear stage. The molar protocones of this specimen thus resemble those in *Gelocus* and *Tragulus*. In UF 19265, while the adjacent limbs are about as poorly united, it is the anterior limb of the metaconule that is short, anteriorly directed, and fails to join the protocone until a very late wear stage. In either event, the midlingual commissure is weak and variable in Pseudoceratinae.

The fossettes are simple crescents with no folds or processes. They persist for most of the crown height, only disappearing during about the last 2 mm of wear. A short endostyle is usually present. It decreases in size from the M1 to the M3 and is often absent or obscure on M3. The endostyle arises at the anterolingual base of the metaconule and may or may not touch the base of the protocone. No cingulum is present on pseudoceratine upper molars. Thin cementum usually covers upper and lower cheek teeth; it is especially evident in the fossettes.

The deciduous upper premolars are preserved in two maxillaries, UF 19262 and 19264. The only evidence of DP2 unfortunately is the posterior alveolus which indicates that it was a narrow tooth. The anterior portion of DP3 is narrow, consisting only of two closely appressed labial cusps. They are not elongate nor well-separated as in tragulids. It is impossible to identify an anterolingual cingulum due to the advanced wear stage of this tooth; if it had such a cingulum it was weak. The posterior portion of DP3 is molariform with a weak but distinct protocone. This tooth is 6.2 long and 4.7 wide in both specimens. The broad molariform pattern of the posterior portion of DP3 closely resembles that in *Gelocus*, *Bachitherium* and *Prodremotherium* and foreshadows the more fully molariform condition of deciduous premolars in higher Pecora.

DP4 is fully molariform and about equals the first upper molar in length and width. It differs from true molars only in its much lower crown, thinner enamel and weaker mid-lingual cusp. In UF 19262 DP4 measures 6.2 long and 5.9 wide; in UF 19264 these dimensions are 6.3 by 6.0. DP4 in Pseudoceratinae presents essentially the same morphology as in

Bachitherium and *Prodremotherium* (Geraads et al. 1987).

LOWER DENTITION

The dental formula is i1-i3, c1, p2-p4, m1-m3. The first lower incisor has an expanded spatulate crown, with a horizontal wear surface 5 mm wide and 5 mm deep in UF 19395 (Fig. 4B). The lateral edge of the incisor flares widely, whereas the medial edge is nearly straight. This moderately worn incisor has an anterior face of thickened enamel about 8 mm long, inclined at an angle of about 30 degrees above the horizontal. The root is about 9 mm long and tapers rapidly to a diameter of about 2 mm.

The i2 and i3 are much smaller than the first. One well-preserved dentary, UF 225886, reveals a heavily worn i2 in the same horizontal plane as the i1. It is 2.7 mm wide, and the anterior enamel face is still 5.1 mm long. The root is only 1.7 mm wide and 2.5 mm in dorsoventral diameter. The i3 is not preserved in the *Floridameryx* sample, but the alveoli suggest that it is a smaller replica of the i2.

The permanent incisors of *Floridameryx floridanus* erupted quite late in life. The tip of an unerupted i2 lies deep in the crypt of UF 13832, in which the m3 had already fully erupted. The i1 is unerupted in two mandibles (UF 225895 and 225896) with m2 lightly worn. Evidently the i1 began to erupt at about the same time the m3, and the i2-i3 did not emerge until the m3 had become well worn.

The most remarkable dental feature of the Pseudoceratinae is the presence in males of a strong upright lower canine that occludes against the anterior face of the upper canine (Figs. 3C, 4B). In all other known pecorans, by contrast, the lower canine is incisiform. Although quite evident in the type of *Pseudoceras skinneri*, this upright lower canine does not occur in all pseudoceratines. For example, a right mandible of *Pseudoceras* (F:AM 53365) from Clayton Quarry in Nebraska has an incisiform canine. The allotype of *F. floridanus* also illustrates the presumed female morphotype (Fig. 4).

The nature of lower canine dimorphism is elucidated by the large sample of *Floridameryx floridanus* mandibles from Withlacoochee River 4A. As shown in Figure 5, about half of the mandibles support large upright lower canines with vertical wear facets on their posterior surfaces. Presumably these mandibles represent male individuals. Other mandibles have slender procumbent lower canines and presumably represent females. Both types are about equally

represented at all ages, using the wear stage of m1 as an indication of age. A subtle tendency for higher mortality in probable males than females may be noted in this figure. This pattern is familiar in ruminant species in which young males become social outcasts and thus experience heavier selection than young females who generally enjoy the security of the herd. The caniniform lower canine does not change ontogenetically but evidently is a sex-linked (male) character. The presumed female lower canines are incisiform as in other ruminants.

The male lower canine is recurved and attains a total length of over 15 mm. The crown is about 7 mm high in both *Pseudoceras* and *Floridameryx* and leans outward from the plane of the mandible at an angle of about 20 degrees. It bears a crest that passes from the tip down the anterior face and curves anteromedially near the base. The medial side is nearly flat, with two faint concavities running vertically. In old individuals heavy wear extends vertically from the tip down the posterior face of the canine. In very old specimens, such as UF 225886, the wear extends down onto the root and produces a notch more than 1 mm deep in the posterior profile of the canine. Wear striations extend obliquely from dorsolingual to ventrolabial across the posterior face of the canine. On the lingual side, nearly horizontal grooves cut into the enamel just above the presumed gum line. In old individuals, such as UF 225911, the groove cuts completely through the lingual enamel of the canine from the anterior face to the posterior wear face. Presumably these grooves resulted from abrasion by vegetation and adhering sediments as they were pulled into the mouth by the tongue. Scott (1940:381) noted similar abrasion in *Archaeotherium* canines and attributed them to pulling sand-laden roots.

The postcanine diastema, ranging from about 15 to 20 mm (Fig. 4; Table 1), is relatively short compared with the diastemata in *Moschus*, Cervidae, or other higher ruminants. It is about the same relative length as in the Tragulidae.

The lower premolar series is noticeably reduced in length relative to the molar series in Pseudoceratinae (Figs. 3-4; Table 1). This premolar abbreviation reaches its extreme in *Floridameryx floridanus*, but even in *Pseudoceras skinneri* the premolars are short as compared with those in other primitive ruminants. Loss of the p1 has contributed to this abbreviation. A dp1 does exist; in one juvenile dentary it appears as a small leaf-shaped tooth immediately anterior to a nearly identical dp2. Within the premolar series, size increases from anterior to posterior as in *Moschus* and higher

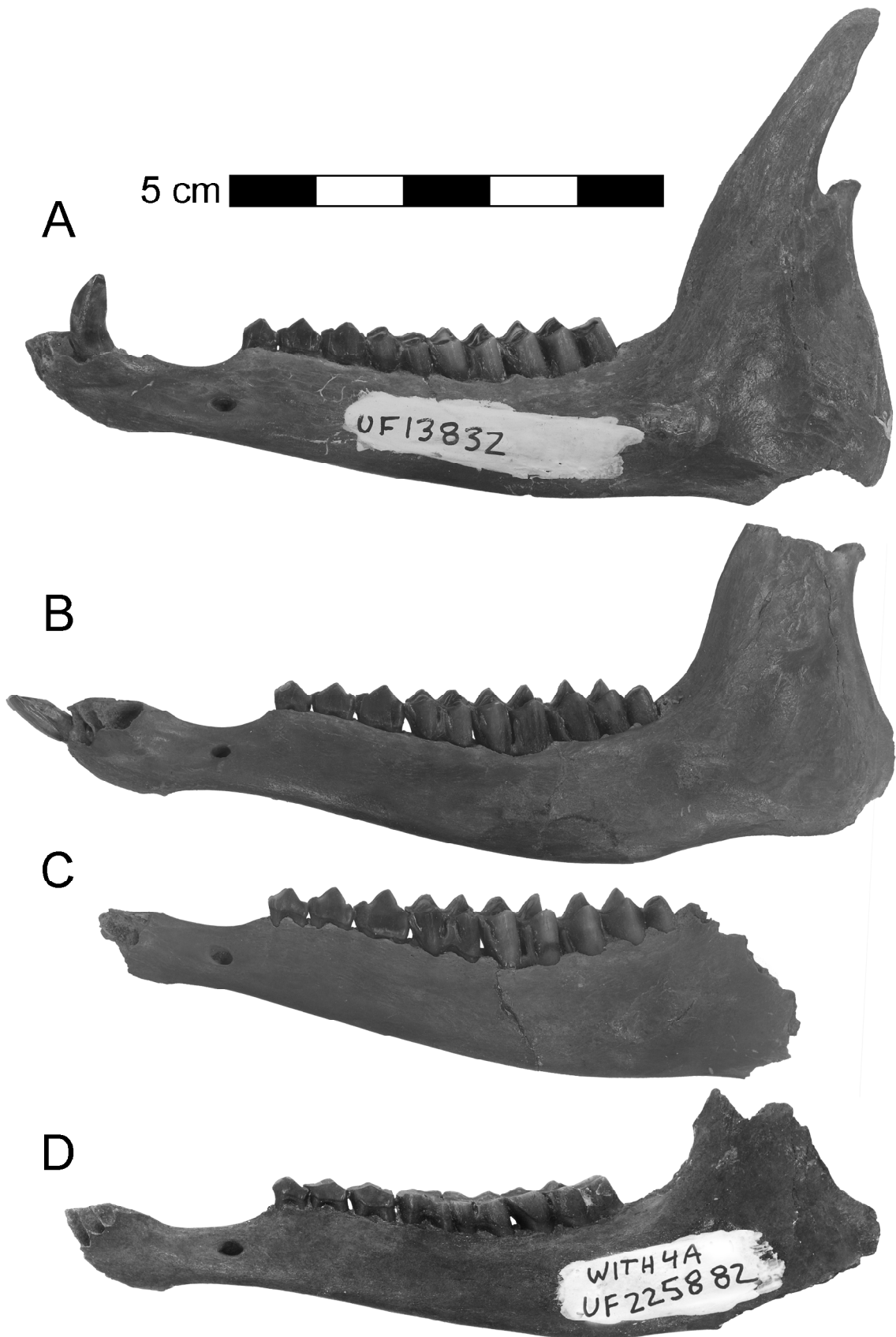


Figure 4. Mandibles of *Floridameryx floridanus* from the Withlacoochee River 4A Site, Florida in lateral view. Occlusal views of these specimens are Figure 3C-F. A. UF 13832 (holotype). B. UF 19395 (allotype). C. UF 225879. D. UF 225882 (reversed).

Table 1. Measurements of dentitions of *Floridameryx floridanus* from Withlacoochee River 4A, Florida. Abbreviations for measurements: DIA, length of postcanine diastema; LM, length of molar row; LP, length of premolar row. Detailed measurements of individual cheekteeth in *Pseudoceras* and *Floridameryx* are beyond the scope of this paper, but are available upon written request from the Department of Vertebrate Paleontology at the Florida Museum of Natural History.

Maxilla				Mandible			
Light wear				Light wear			
	LP	LM		LP	LM	DIA	
x	17	24	x	15	30	16	
n	4	5	n	7	6	6	
Medium Wear				Medium Wear			
	LP	LM		LP	LM	DIA	
x	17.5	26	x	15	27	15.5	
n	1	2	n	6	6	6	
Heavy Wear				Heavy Wear			
	LP	LM		LP	LM	DIA	
x	17	23	x	15	27	18	
n	3	3	n	3	4	1	

ruminants generally, but in marked contrast with conditions in Tragulidae and more primitive selenodonts.

The premolars are constructed on a tragulid- or camelid-like pattern, altogether different from that of *Moschus*, Cervidae, or other higher ruminants. Each premolar is narrow, wedge-shaped, lacks multiple lingual folds, and has a distinct peak in its profile (Fig. 4). The enamel on the premolars and molars is faintly crenulated.

The p2 is a narrow tooth with three relatively simple cuspids in an anteroposterior row. The paraconid is low and slightly inflected to the lingual side. The central cuspid (metaconid) is the tallest one. From its lingual wall projects a rib which is probably homologous with the posterolingual crest on more posterior premolars. The talonid is low and broad. On its lingual side, a minute entoconid and a posterior transverse crest enclose a minute fossettid.

The p3 is an enlarged and especially broadened version of p2 (Fig. 3C-E). The paraconid is extended anterolingually to form a paralophid crest. The metaconid rises centrally above the other cusps and extends from its posterior slopes a strong posterolabial and a weak lingual crest. The broad talonid is enclosed labially by the metaconid crest. A small entoconid occupies the center of the basin. A small talonid valley opens posterolingually between the entoconid and the posterior

transverse crest. After moderate wear stages, however, it becomes a posterolingual fossettid.

The p4 differs from p3 in its larger size and in some structural details (Fig. 3C-E). The paralophid is stronger and encloses a very small trigonid basin bounded lingually by a minute cingulum. The metaconid sends off a strong posterolingual crest which passes posteriad and with the entoconid forms a complete posterolingual wall. The talonid valley is enclosed in very early wear stages to form a long narrow fossettid which trends posterolingually.

The lower molars are moderately high-crowned and strongly compressed transversely. They are only a little higher-crowned than lower molars of some other progressive Gelocidae such as *Prodremotherium*. But the strong compression of pseudoceratine molars gives the impression of much greater height. Moreover, because hypsodonty is a ratio of crown height to occlusal area, the Pseudoceratinae are surely among the most hypsodont of hornless ruminants, rivaled only by the hypertragulid *Hypisodus*.

The molars increase in size and height from the m1 to m3 (Figs. 3-4). Nonetheless, they may be described together, as there are few other differences between them. The metaconid and entoconid are elongate and rather strongly flattened. They thus contrast strongly with the bulbous lingual cusps of

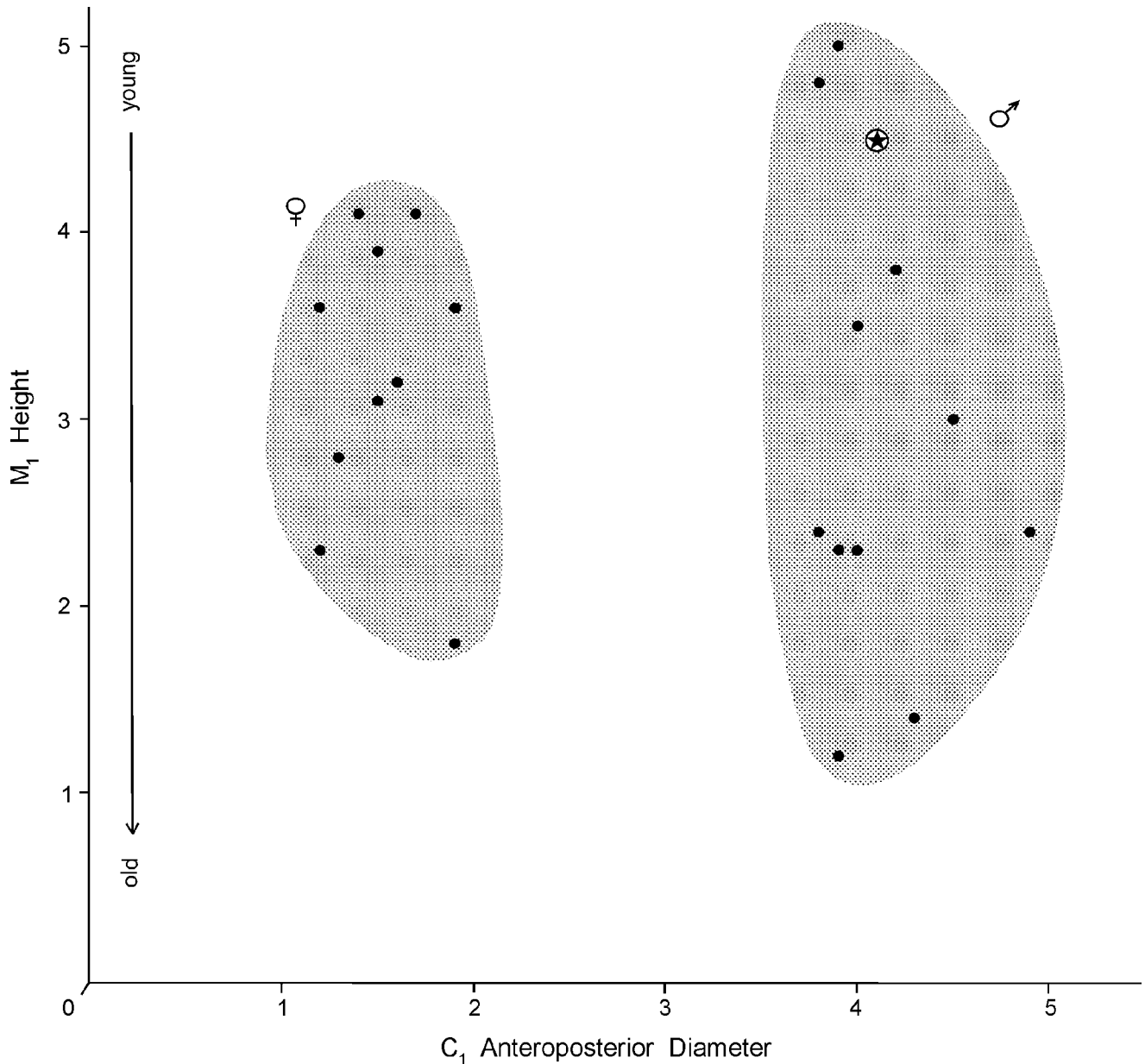


Figure 5. Variation by age and sex in the Withlacoochee River 4A sample of *Floridameryx floridanus*, based on 22 mature dentaries; sex determined by dimorphic canine size, age by wear heights of m1. The holotype specimen is indicated by the star.

Gelocus. The flatness of the wall is broken by two features: (1) a small but sharp parastylid that persists even into moderately advanced stages of wear; and (2) a persistent groove separates the metaconid from the entoconid. No metastylid is present. Neither the metaconid nor the entoconid shows any trace of the folding so characteristic of *Dorcatherium* or other Tragulidae.

Perhaps the most remarkable feature of pseudoceratine lower molars is the lingual opening of the posterior fossettid. This feature is commonly observed in the m2 and m3, but it also occurs frequently

in the m1 in early wear stages. This posterolingual opening is created by the failure of the posterior horn of the hypoconid to join the entoconid. This suggests that pseudoceratine lower molars developed their hypsodont condition prematurely, as it were, from primitive ruminant stock in which the hypoconid was still conical.

The protoconid and hypoconid each present more angular labial faces than in *Gelocus* or *Tragulus*. No accessory folds, such as found in Tragulidae (especially *Dorcatherium*) or Palaeomerycidae, occur in the Pseudoceratinae. A strong protostylid (anterolabial cingulum) rises steeply from the anterolabial surface of

the protoconid and persists into moderately advanced stages of wear. In Tragulidae, on the other hand, it is weak and ephemeral. The median ectostylid is tall and well developed on the first two molars but is weak or absent on the m3. The tip of the ectostylid has nearly the same height as the hypoconid; in later wear stages it may be incorporated with that cusp, thereby adding an anterolabial fold to its normal curve (see m1 in Fig. 3C). No hypostylid (posterolabial cingulum) occurs, in contrast with the condition often observed in Tragulidae.

The m3 differs from the m1-m2 mainly in the presence of a third lobe. In Pseudoceratinae, this lobe consists of a simple subcircular loop of enamel (the hypoconulid) attached to the posterior wall of the hypoconid labially and, at a much lower level, to the entoconid lingually. In early wear stages, this heel appears to be made of two weakly joined enamel segments, one lingual and one labial. Even in later wear stages a posterior sulcus may be seen, seemingly representing a line of fusion between these two portions. There are never two concentric enamel walls as in *Moschus*, Cervidae, and higher ruminants. In the simple structure of the third lobe of m3, the Pseudoceratinae resemble other Gelocidae, especially *Prodremotherium*.

The deciduous lower incisors and canines are not represented in any known pseudoceratines.

The third and fourth deciduous lower premolars are present in an unworn stage in UF 17416. A broken alveolus in this same jaw represents dp2 and suggests that its length is about 4. The dp3 measures 5.5 long and 1.9 wide. It is distinguished from p4 only by its lower crown and by its less complete metaconid blade. This tooth generally resembles that of other gelocids (Geraads et al. 1987) and differs markedly from the long three-cusped dp3 of tragulids.

The dp4 has the long three-lobed structure characteristic of all artiodactyls. It is 9.1 mm long and 3.1 wide. The two posterolingual cuspids form strong crescents but the anterolingual cuspid is weak posteriorly. Likewise the anterolabial cuspid is weaker than the two more posterior labial cuspids. The posterior edges of all three labial cuspids flare outward preventing complete connection with the opposing lingual crescents. In this respect dp4 resembles the peculiarly primitive structure of the permanent molars of pseudoceratines.

MANDIBLE

The horizontal ramus is long, about as shallow as in most cervoids, and bowed upward. Its depth decreases gradually from a maximum below the last molar to a minimum beneath the diastema (Fig. 4). The

masseteric fossa is shallow but nonetheless distinct. Its outline is subtriangular with the anteroventral apex below and just behind the end of the last molar. This apex is distinguished by a strong tuberosity for insertion of the principal tendon of the deep masseter muscle. Beneath the masseteric tuberosity the jaw becomes shallower, producing a ventral concavity as in most giraffoids and cervoids. Behind this, the masseteric insertion occupies a large semicircle; the jaw deepens and the ventral edge becomes correspondingly convex. On the ventral and posterior margins of the masseteric insertion area is a distinct peripheral muscle scar for the superficial masseter.

The mandibular condyle lies 10 to 15 mm above the cheek tooth row. Its neck turns mediad so that the condyle lies entirely medial to the plane of the rest of the ascending ramus, as in higher ruminants but in contrast to the Tragulidae.

The condyle is remarkably narrow with a transverse diameter of only 7.0 mm and anteroposterior diameter of 0.5 mm. The articular surface is nearly flat. In Tragulidae, by contrast, the condyle resembles a transversely oriented hemicylinder with a convex articular surface and a width fully twice the length. The coronoid process rises in a tall graceful curve posteriorly and slightly laterally to a point about 20 mm above the condyle. The process tapers somewhat toward its dorsal tip.

AXIAL SKELETON

The atlas (Fig. 6A) broadly resembles a small version of an atlas of a cervid such as *Odocoileus*. The most notable difference is the convex outline of the lateral wings, in contrast with the straight margins in the larger cervid specimens. The axis (Fig. 6B) falls within the same progressive morphological stage ascribed by Webb and Taylor (1980) to *Moschus* and the Cervidae. This includes full development of the odontoid process into a subcircular "spout", and dorsal expansion of the adjacent atlantal articulation almost equal to the top of the neural canal. In UF 13828 the hatchet-shaped dorsal crest is about 28.8 mm long and the articular length of the centrum is 38.5, making the axis the longest cervical vertebra. The intermediate cervicals are of moderate length, ranging in length from about 28 to 30 mm along their centra. The seventh cervical (Fig. 6C) is shorter (25.2 mm long) and more robust. It has a short, posteriorly directed neural spine.

Figures 6D and 6E illustrate representative anterior and posterior thoracic vertebrae, respectively. A relatively small (presumably young) thoracic from the

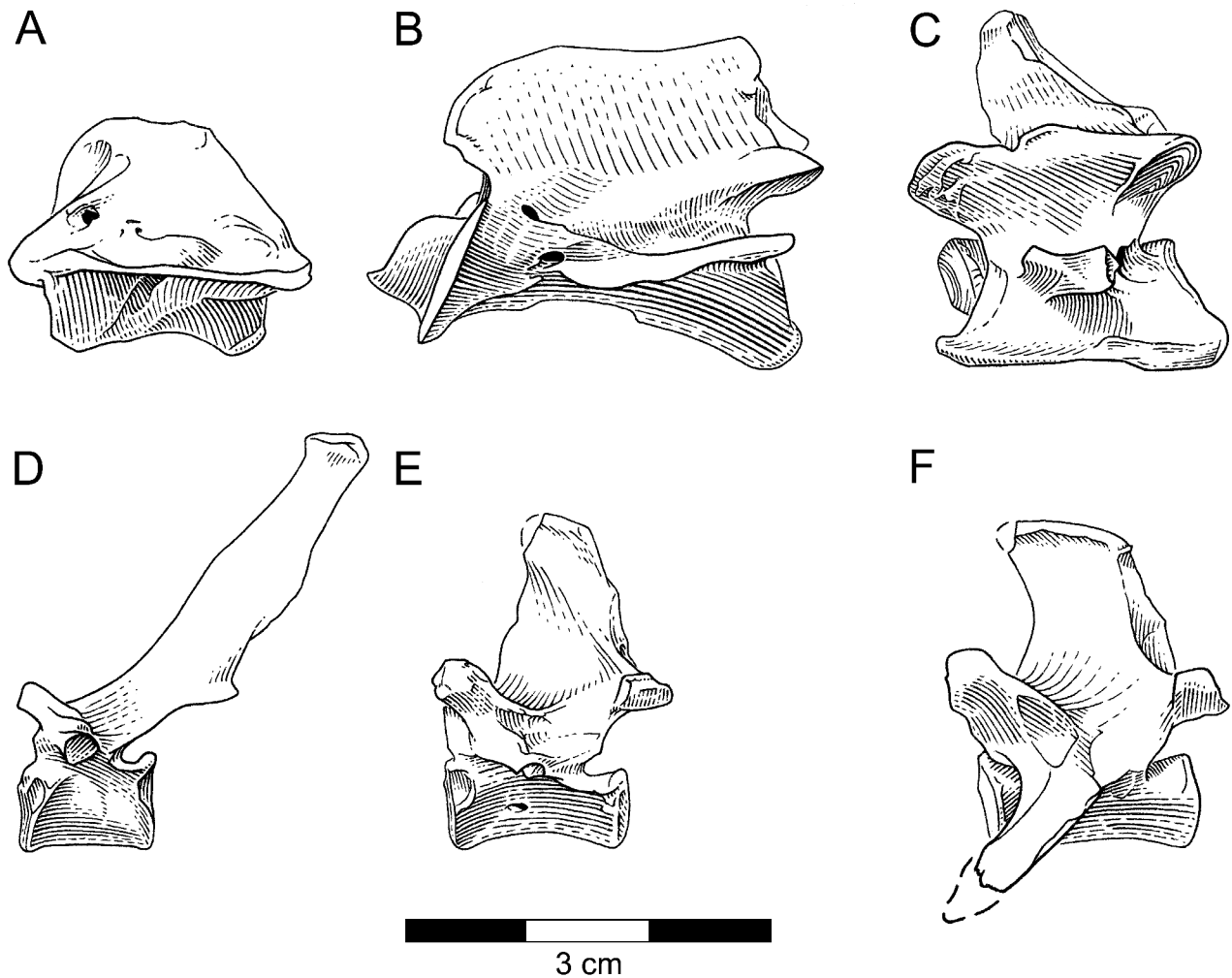


Figure 6. Left lateral views of A, UF 225937, atlas; B, UF 225938, axis; C, UF 225950, seventh cervical vertebra; D, UF 226233, anterior thoracic vertebra; E, UF 226234, posterior thoracic vertebra; and F, UF 226236, lumbar vertebra of *Floridameryx floridanus* from the Withlacoochee River 4A Site.

middle of the series, UF 225920, indicates that the neural spines were relatively tall in *Floridameryx*. Although its centrum is only 13.1 mm long, the spine reaches 41 mm above the top of the centrum. The spine slopes posterodorsally at an angle of about 25 degrees from the plane of the neural canal.

The lumbar vertebrae (Fig. 6F) show a remarkable range from narrow centra near the anterior end of the series to very broad specimens representing the posterior end of the series. For example the widths of some anterior lumbar centra measure about 12 mm, whereas in UF 226236 the width is 16.5 mm. The maximum widths of the free transverse processes range between 50 and 52 mm. The zygapophyses of the lumbar vertebrae are very tightly curled inward indicating strong defense against dislocation by hind limb thrusts during leaping or galloping.

The sacrum (Fig. 7) has even broader centra. For example, in UF 24173, the anterior width is 19 mm. In

that individual the sacrum is made up of four fused vertebral segments, but in others there are five. The sacrum narrows rapidly toward the tail, so that the posterior segment in UF 24173 is only 12 mm wide and 11 mm high. It arches downward and the neural canal becomes minute suggesting a fairly short tail. Various caudal elements are preserved, but there are not enough to give a sense of the overall proportions.

FORELIMB

Measurements of the major forelimb elements are provided in Table 2 and they are illustrated in Figure 8. The scapula is about 80 mm long, and the anteroposterior dimension of the glenoid cavity is 17 mm. The humerus is relatively stocky (Fig. 8B-C). The olecranon process of the ulna (Fig. 8D-E) adds another 16 mm to the functional length of the forelimb. In a sample of more than a dozen well-preserved radioulnae, only two, UF

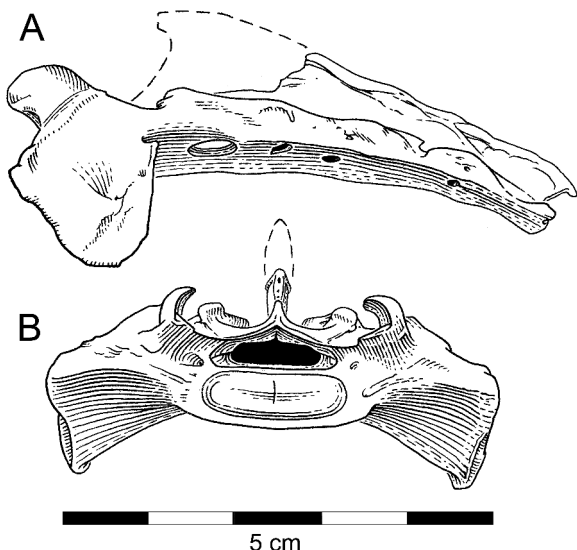


Figure 7. A, lateral and B, anterior views of UF 225981, sacrum of *Floridameryx floridanus* from the Withlacoochee River 4A Site.

18954 and 18955, had the ulna associated with the proximal end of the radius. The former of these had exostoses that artificially prevented separation. The shaft of the ulna was evidently very frail but extended the complete length of the radius, as indicated by

attachment scars along the posterolateral face of most radii, and its distal end did not fuse with the radius.

The third and fourth metacarpals are fully fused into a cannon bone (Fig. 8F-G) even in young individuals with unfused distal epiphyses. The distal keels extend fully (180 degrees) from the anterior to the posterior face of each metacarpal. An anterior groove is evident on all specimens, although it becomes very faint on the most mature individuals. About 7 mm from the distal midline, a small foramen enters a closed gully (Fig. 8F). At the proximomedial end of the metacarpus on the plantar surface a triangular facet about four mm on each side represents a vestigial second metacarpal.

The proximal surface of the third metacarpal gives credible evidence that the trapezoid and magnum are fused in *Floridameryx*. Careful examination of the medial side of that articulation on all available specimens shows no line of separation, encouraging the presumption that this fusion was present as in most ruminants. Direct evidence of the smaller carpal elements are missing in the Withlacoochee River sample, because the skeletal material is not articulated, and the smaller elements were seldom recovered in the underwater excavations.

The phalanges of Pseudoceratinae are those of an ordinary, small, cloven-hoofed ruminant. The few such elements available in this collection do not allow

Table 2. Comparative measurements of forelimb (in mm). DW, distal width; L, length; OL, olecranon length; PW, proximal width

	<i>Floridameryx floridanus</i> With. 4A				<i>Gelocus communis</i> *	<i>Bachitherium cf. insigne</i> *
					Ronzon	Cereste
Humerus	L	PW	DW		L	L
x	79.1	16.3	17.0		109	146
s	1.8	3.1	0.7		—	—
n	15	15	15		1	1
Radio-ulna	L	PW	DW	OL	L	L
x	98.2	15.8	15.3	16.1	87	141
s	4.1	0.6	0.8	1.3	—	—
n	13	18	15	13	1	1
Metacarpal	L	PW	DW		L	L
x	97.9	13.2	12.8		76	109
s	2.0	0.4	0.4		—	—
n	14	20	18		1	1

* after Geraads et al. (1987, p. 64)

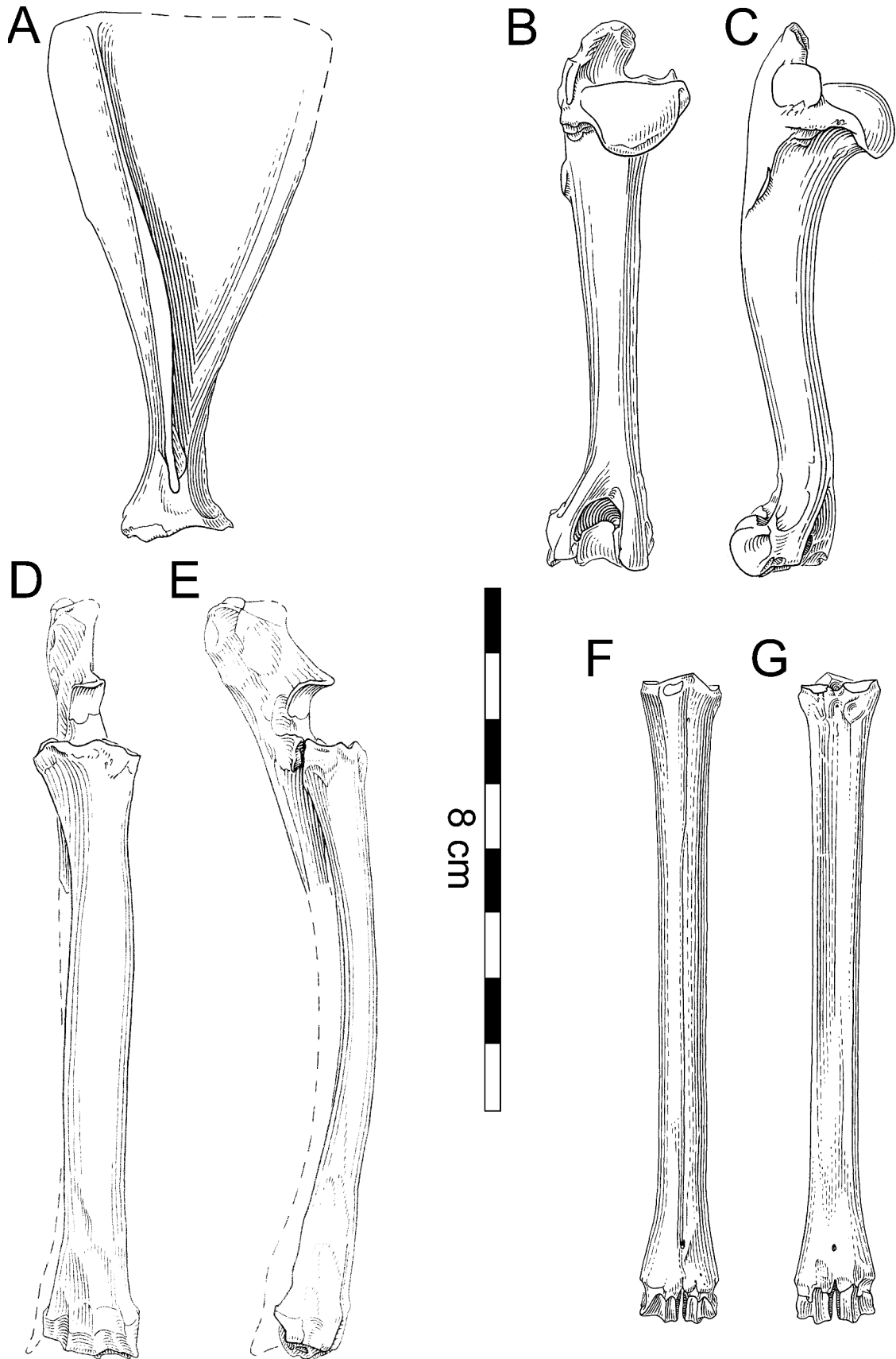


Figure 8. Forelimb elements of *Floridameryx floridanus* from the Withlacoochee River 4A Site. Lateral view of A, UF 17403, left scapula; B, anterior and C, lateral views of UF 13827, left humerus; D, anterior and E, lateral views of UF 18955, left radioulna; and F, anterior and G, posterior views of UF 226038, left metacarpus.

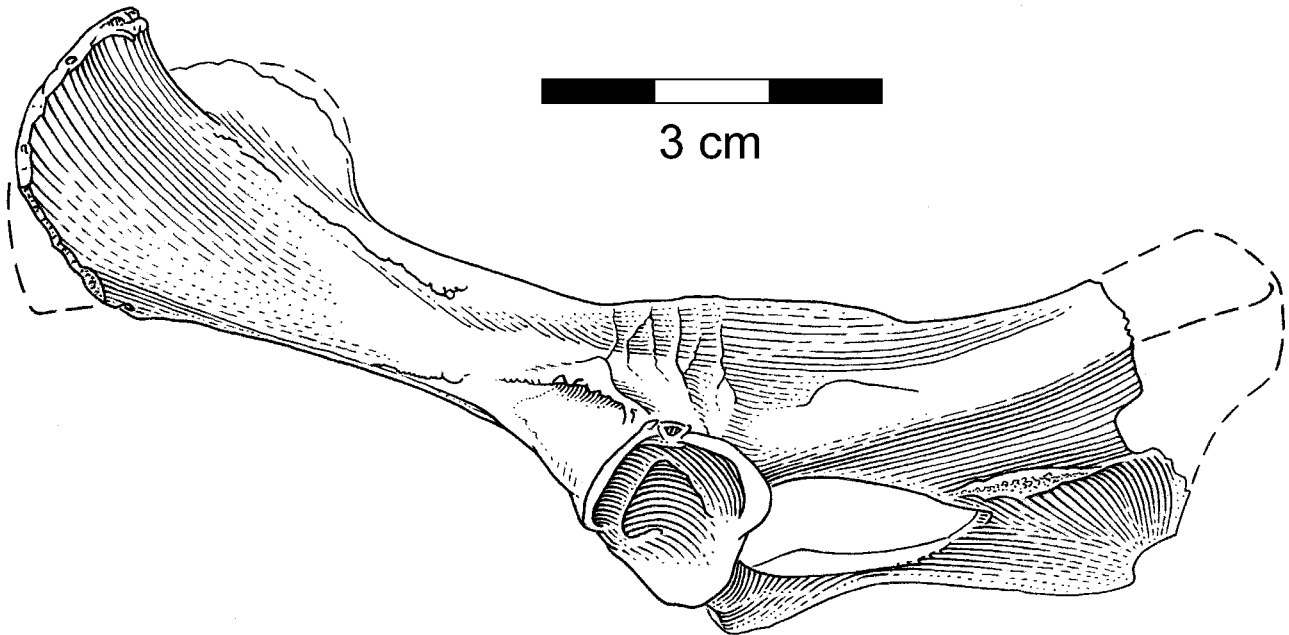


Figure 9. Lateral view of UF 201847, left pelvis of *Floridameryx floridanus* from the Withlacoochee River 4A Site.

Table 3. Comparative measurements of hind limb (in mm). DW, distal width; L, length; PW, proximal width.

	<i>Floridameryx floridanus</i> With. 4A			<i>Gelocus communis</i> * Ronzon	<i>Bachitherium</i> cf. <i>insigne</i> * Cereste
Femur	L	PW	DW	L	L
x	116.9	26.4	22.8	130	184
s	4.3	1.4	2.8	—	—
n	7	11	12	1	1
Tibia	L	PW	DW	L	L
x	134.2	25.5	17.0	135	216
s	3.8	2.7	0.6	—	—
n	15	23	24	1	1
Metatarsus	L	PW	DW	L	L
x	103.3	13.5	15.0	90	142
s	3.0	0.5	0.6	—	—
n	26	36	34	1	1

* after Geraads et al. (1987, p. 64)

us to distinguish between those of the fore- and hind feet.

HIND LIMB

Measurements of the major hind limb elements are provided in Table 3 and they are illustrated in Figures

9-12. The pelvis (Fig. 9) represents a relatively progressive stage of ruminant locomotor evolution. Its overall length can be estimated as greater than 100 mm, based on various well-preserved anterior and posterior portions. The iliac blade is well expanded in proportion to the blade connecting it to the acetabulum, the former

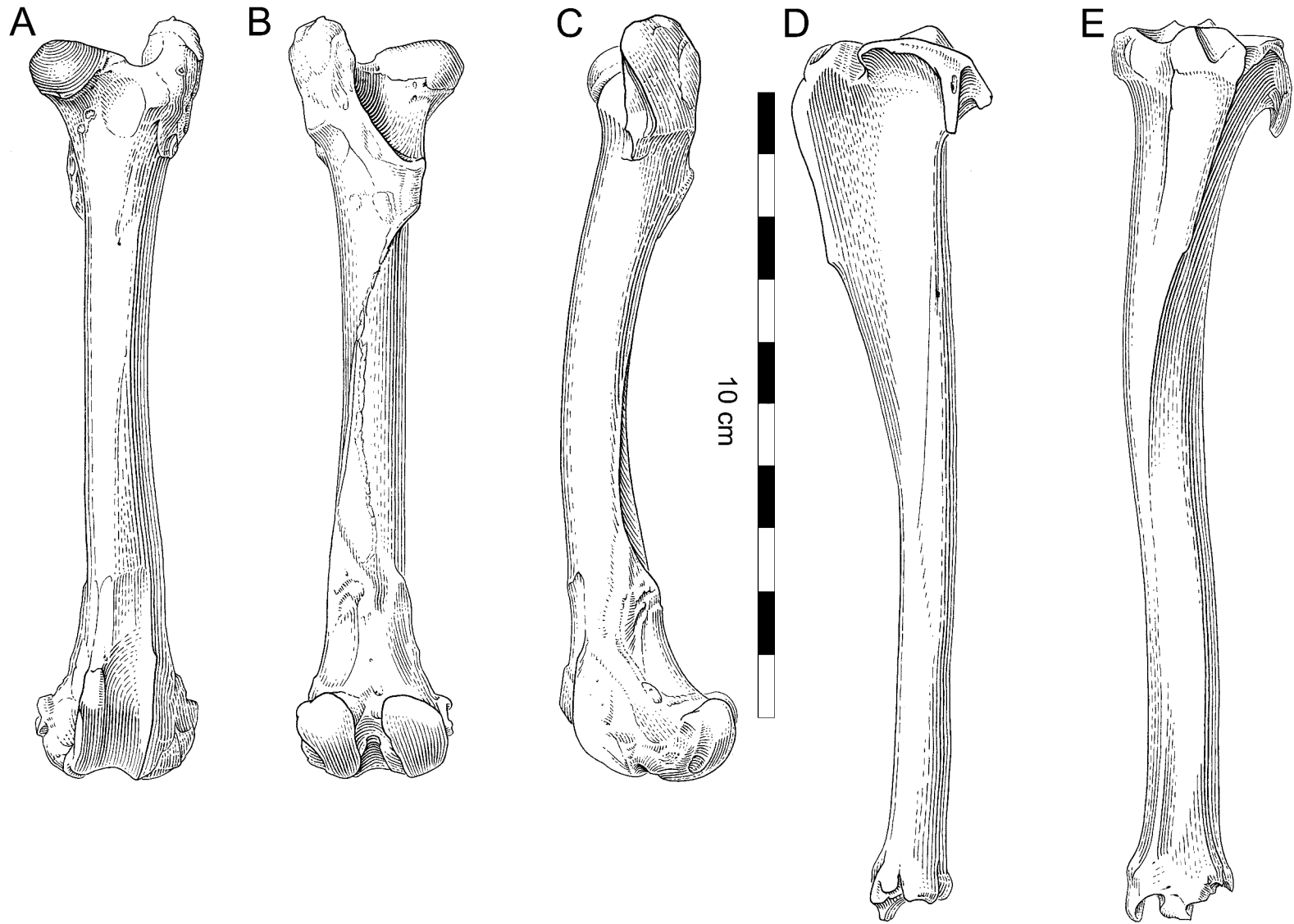


Figure 10. A, anterior, B, posterior, and C, lateral views of UF 226095, left femur; and D, lateral and E, anterior views of UF 18956, left tibia of *Floridameryx floridanus* from the Withlacoochee River 4A Site.

having a diagonal expanse of about 40 mm and the latter a minimum dorsoventral diameter of only about 12 mm in UF 13819, a mature left pelvis. Directly dorsal to the acetabulum and posterior to the greater sciatic notch is a widely convex region more than 15 mm deep, featuring strong tendinous scars for the ischial musculature, most importantly a powerful *M. iliopsoas*. Despite its small scale this region closely resembles the homologous area in *Odocoileus* and other progressive cervids. The functional significance of these features will be considered further below.

The femur (Fig. 10A-C) and tibia (Fig. 10D-E) are gracile, not unlike those of a miniature cervid. Five examples of the patella are known in *Floridameryx*. Each has a tear-drop shape and measures about 18 mm long, 13 mm wide and about 8 mm thick near the proximal end. Other than their shorter proportions the patellae broadly resemble those of *Moschus* and the Cervidae.

The fibula is represented at its proximal end by a vestige of bone extending distally from the posterolateral corner of the tibia (Fig. 10E). In several individuals it forks into two processes of which the more lateral attains a length of 7 to 9 mm. The distal end of the fibula, as in most other ruminants, forms a malleolar bone that forms a sliding articulation with the calcaneum, and lodges on its medial side in a notch on the distolateral corner of the tibia. The stages of its transformation within hornless ruminants were discussed by Webb and Taylor (1980). In *Floridameryx*, the distal fibula is only known by two examples, but its morphology and function are readily inferred from the corresponding surface of the calcaneum. That articulation consists of a relatively large proximal convexity and a very small distal surface that is nearly flat. The corresponding surface of the malleolar bone has not progressed to the fully concavo-convex pattern of cervids and other progressive ruminants. It more closely resembles the transitional arrangement in *Gelocus*.

The metatarsus (Fig. 11) is fully fused except in a few specimens that are presumably fetal. At the proximal end on the plantar face, a small rugosity on the lateral side and another more prominent one on the medial side probably represent the vestigial fifth and second metatarsals respectively. These proximal rudiments are smaller than those in *Leptomeryx* (Webb & Taylor 1980:144). The line of fusion between the third and four metatarsals leaves a deep groove on the anterior surface of the metatarsus which enters a closed gully 6 to 8 mm above the base of the distal epiphyses (Fig. 11A). At the point where the groove enters the “gully foramen” it is nearly 2 mm in diameter. In juvenile

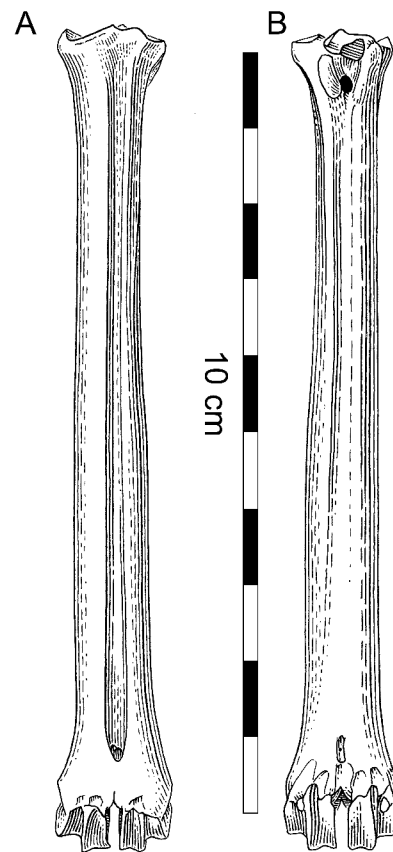


Figure 11. A, anterior and B, posterior views of UF 226164, left metatarsus of *Floridameryx floridanus* from the Withlacoochee River 4A Site.

specimens lacking distal epiphyses the gully has not been fully bridged. As in the metacarpus the distal articulations of the metatarsus in adult specimens are strongly keeled.

The cubonavicular bone (Fig. 12A-B) is fully fused and has the proportions typical of advanced ruminants. The astragalus (Fig. 12C-E) is parallel-sided and short-coupled (nearly cubic) as in progressive pecorans (Webb and Taylor 1980). The one probably primitive feature of the astragalus (and calcaneum) is the narrowness of the sustentacular surface. In contrast with *Moschus* and most Cervidae, this surface does not extend medially beyond the rest of the bone. Presumably the expanded sustentaculum in more advanced pecorans is an adaptation for greater support of the foot especially during leaping and galloping. The only non-pecoran feature of the calcaneum (Fig. 12F-H) concerns the articulation for the malleolar and has been discussed above.

LOCOMOTOR ADAPTATIONS

The limb proportions of *Floridameryx* can be seen in Tables 2-4. In 1972 my laboratory assistant, Chandra

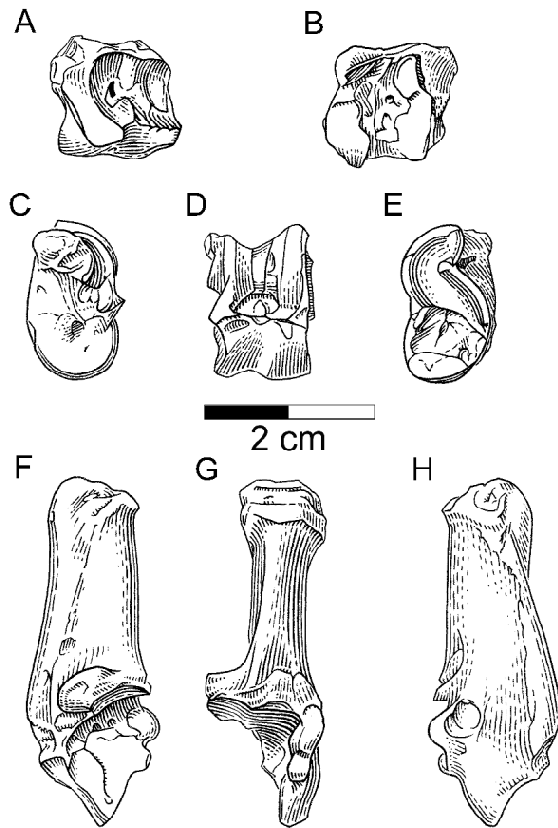


Figure 12. Tarsal elements of *Floridameryx floridanus* from the Withlacoochee River 4A Site. A, proximal and B, distal views of UF 226197, left cubonavicular; C, medial, D, anterior, and E, lateral views of UF 226185, left astragalus; and F, medial, G, anterior, and H, lateral views of UF 226176, left calcaneum.

Aulsbrook, and I assembled a composite skeleton (UF 201847) from the Withlacoochee River 4A collection. From that skeleton, now on exhibition in the Hall of

Florida Fossils at Powell Hall on the UF campus, one gets a much clearer general impression of the nature of this animal (Fig. 13). Striking features of this skeleton are the two nearly equal pairs of long, straight limbs and the long, straight back. It looks, in other words, much like a small deer, and much less like *Tragulus*, a mouse deer. The latter have short forelimbs, tucked-up hind limbs, and strongly flexed backs, producing a posture much like that of a rabbit. I return to a fuller discussion of this point in another section below.

RELATIONSHIPS

The Pseudoceratinae are a rare and relatively short-lived group of hornless ruminants. On the basis of present records, they are confined geographically to North and Central America. The subfamily exhibits a puzzling array of primitive and progressive characters. The upright lower canine in male mandibles suggested to Frick (1937) affiliation with Tylopoda rather with Ruminantia. On the other hand, many progressive features of the skeleton, such as keeled metapodials and front limb length nearly equal to hind, suggest comparison with horned or antlered ruminants. The balance of osteological evidence indicates something in between, namely that Pseudoceratinae fall within the hornless Pecora.

Now that the osteology of Pseudoceratinae has been described, its resemblance to Tylopoda may be recognized as retained primitive (plesiomorphic) characters. For example, an upright lower canine is common to most mammals. It is modified in special ways among various derived lineages, including most of the Ruminantia.

Pseudoceratinae share many derived characters (synapomorphies) with the Ruminantia. Prominent examples of ruminant synapomorphies are absence of upper

Table 4. Limb proportions in *Floridameryx floridanus*. Percentage is the mean length of each individual limb element divided by the sum of the means of the three elements for that limb in Tables 2 and 3.

Forelimb	Percent	N
Humerus	28.7	15
Radioulna	35.7	13
Metacarpus	35.6	14
Hind Limb	Percent	N
Femur	32.9	7
Tibia	37.9	15
Metatarsus	29.2	26
Fore/Hind Ratio	77	

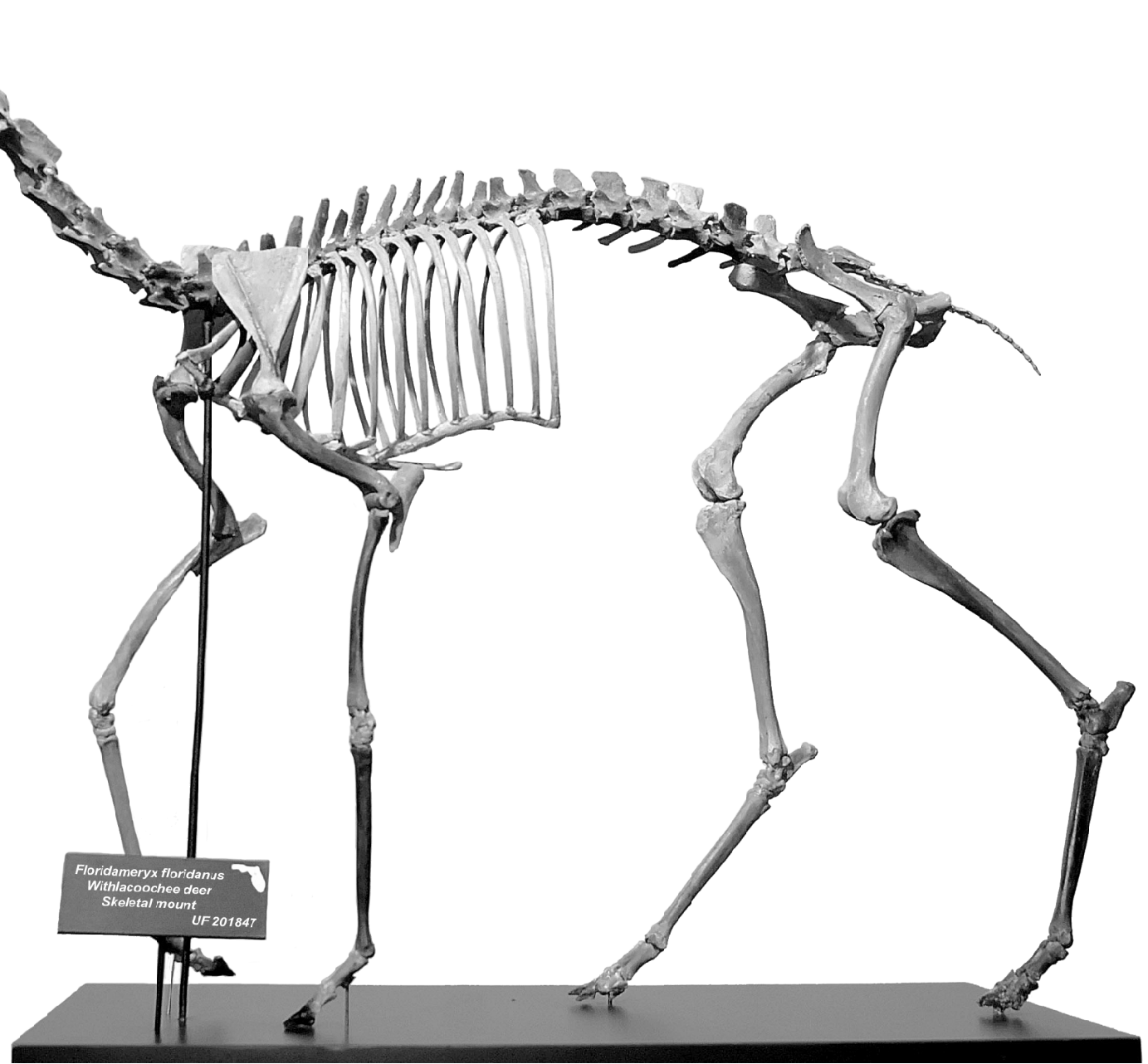


Figure 13. Composite mounted skeleton of *Floridameryx floridanus*, UF 201847, from Withlacoochee River 4A collection, on permanent public display at the Florida Museum of Natural History. Skull is a cast of the specimens in Figure 1; a few other elements are either casts or restored, but most of the postcranial skeleton is original fossil material.

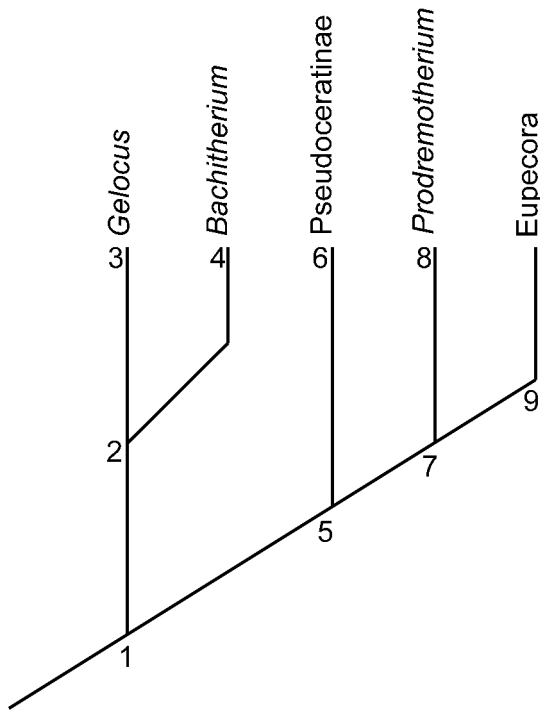


Figure 14. Cladogram of lower Pecora, modified from Geraads et al. (1987). Synapomorphies at numbered positions on the cladogram: 1) narrow posterolateral exposure of mastoid; DP3 with strong lingual cingulum; talonid of dp3 complex; strong metaconid on lower premolars; lateral metapodials incomplete or absent; astragalus parallel sided. 2) fibular facet of calcaneum convex. 3) simple p1. 4) caniniform p1; C1 with strong crest; proximal end of metatarsals nearly circular. 5) elongate odontoid process; crescentic protocone on upper premolars; p1 absent; increasing hypsodonty with cementum on cheek teeth; metacarpals fused; metapodial keels complete; astragalus cubic. 6) lower premolars with posteriorly directed metalophids. 7) supraglenoid foramen present; upper canine flattened and sigmoidal; limbs elongate with forelimb length nearly equal to hindlimb length. 8) metalophid on lower premolars; p4 with four strong lingual crests; lower molars with closed trigonids. 9) elongate facial region; lacrimal fossa for facial gland; upper canines reduced; *Palaeomeryx*-fold on lower molars.

incisors; fusion of trapezoid and magnum in the carpus; and fusion of cuboid and navicular in the tarsus. Also it is evident that Pseudoceratinae lack cranial appendages and thus lie basal to the higher Pecora, including the great diversity of horned, antlered, and ossiconed ruminants.

The first cladogram to present an hypothesis about interrelationships of lower ruminants was by Webb and

Taylor (1980). Above Tragulina, they placed Gelocidae and Moschidae as the basal families of Pecora. The second such cladogram was produced by Geraads et al. (1987:fig. 45). It added many significant comparisons among the Neoselenodontia. Its special feature was a detailed phylogenetic arrangement of the genera *Gelocus*, *Bachitherium* and *Prodremotherium*. The part of their cladogram representing the relationships among hornless Pecora is adopted here (Fig. 14). In this edition, however, Pseudoceratinae are inserted just above *Gelocus* and *Bachitherium*, and just below *Prodremotherium*. The branch points, presented in this figure caption, have been renumbered. Many of the morphological features (synapomorphies) assigned to the branch points are direct translations of the original evidence provided by Geraads et al. (1987). This provides a phylogenetic framework for Pseudoceratinae, and explains why it is appropriate to assign this subfamily to the family Gelocidae.

Inflation of the genus *Bachitherium* to its own family within Tragulina was proposed by Janis (1987) after Geraads et al. (1987) was in press. This awkward timing explains the inability of the latter paper to comment upon the former. In this cladogram (Fig. 14), the close affiliation of *Gelocus* and *Bachitherium* do not warrant a family distinction for the latter.

Gelocus communis from the early Oligocene at Ronzon, near Le Puy in southern France, provides a fundamental reference point in the evolution of hornless ruminants. In his classic work on *Gelocus*, Kowalevsky (1876) documented many key points that placed it near the ancestry of higher ruminants. *Gelocus* and several closely related genera range from the Lutetian through Aquitanian in Europe and also occur in Asia and Africa (Hamilton 1973; Vislobokova & Daxner-Höck 2002). In view of the considerable gap in space and time between early Oligocene *Gelocus* in Eurasia and late Miocene to early Pliocene Pseudoceratinae in North America, it is not surprising that many intervening steps remain obscure.

In interpolating the Pseudoceratinae into this phylogeny we begin with the basicranial region, then review some general aspects of the dentition, and finally look at key features of the postcranial skeleton. In the basicranium most features of the Pseudoceratinae broadly resemble those of *Gelocus* and are considerably advanced over those of the Tragulidae (Fig. 15). Most obvious are the greater width of the basioccipital and the breadth across the otic capsules. The square shape of the glenoid fossa with a prominent postglenoid process is another synapomorphy shared by *Gelocus*,

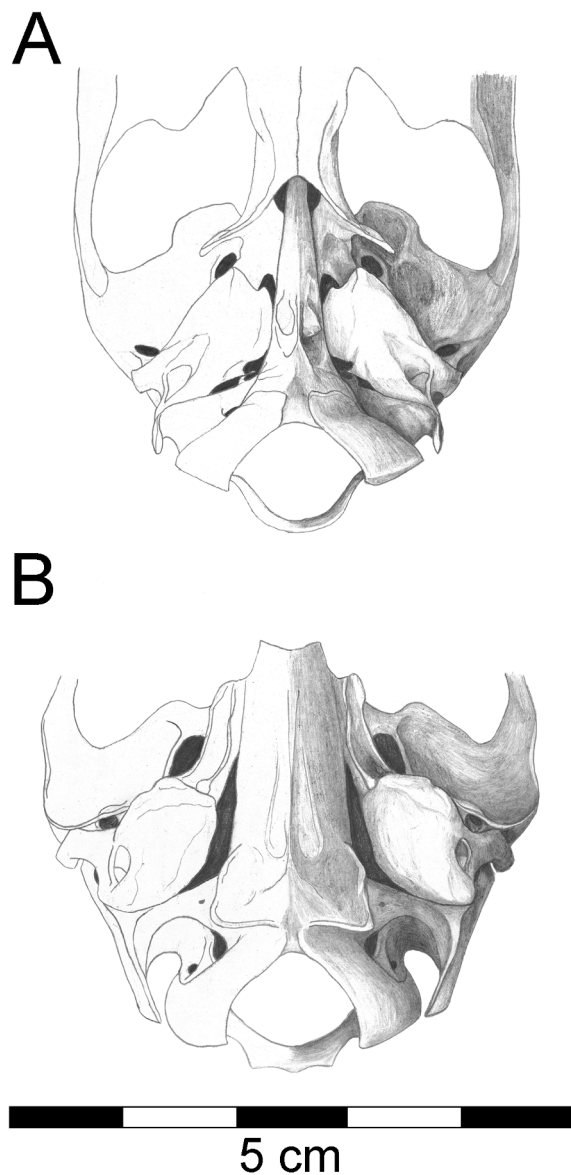


Figure 15. Basicranial sketches of A, *Tragulus javanicus* and B, *Floridameryx floridanus* (UF 19257).

Pseudoceratinae, Moschidae and Eupecora (higher ruminants).

Several synapomorphies shared by *Gelocus*, *Bachitherium*, Pseudoceratinae and *Prodremotherium* may be noted in the ear region. The anteromedial rim of the periotic is thickened and broadly fused with the squamosal. The internal carotid artery was wholly abandoned, whereas in Tragulidae a major branch of that artery ascends along the medial wall of the bulla. In Gelocidae, the tensor tympani fossa is continuous with the epitympanic recess and is separated by a crest from the more posteriorly placed opening of the facial canal. In Tragulidae, by contrast, the tensor tympani fossa is continuous with the facial canal opening (Webb & Tay-

lor 1980). The external auditory meatus is tubular and rises almost vertically to the level of the zygomatic arch in Gelocidae and most Pecora, whereas groups lower on the ruminant tree have the external auditory meatus lower and more posteriorly directed. The mastoid exposure lies along the lateral edge of the occipital in Gelocidae, including Pseudoceratinae, and most pecoran ruminants, whereas in *Lophiomeryx*, Hypertragulidae and Tragulidae it is larger and extends anteriorly along the lateral wall of the skull.

Viret (1961) emphasized the diagnostic value of the anterior cheek teeth in clarifying phylogenetic relationships among hornless ruminants. In *Gelocus*, p1 is a small premolariform tooth in continuity with the cheek tooth series. The dp1 in *Floridameryx* has the same relationship. The fact that p1 is subsequently lost in various ruminant families may diminish its significance, for it is probably a plesiomorphous feature among Gelocidae. It is noteworthy that even a few higher ruminants, for example the giraffoids *Propalaeoryx* and *Heterocemas* retain a simple p1 (Hamilton 1973), as in *Gelocus*. *Bachitherium* has autapomorphically enlarged the p1 so that it occludes against the posterior face of the upper canine. Geraads et al. (1987) correctly describe this as a caniniform first lower premolar. The loss of p1 is a feature shared by *Prodremotherium* and Pseudoceratinae.

In the almost bladelike lower premolars of *Gelocus* one can recognize the antecedents of lingual structures that become more important later. The paralophid, metalophid, and posterolophid, and also the faint hypolophid, are overshadowed by the high anteroposterior slopes of the protoconid. The lower premolars of Pseudoceratinae exhibit the same basic pattern as in *Gelocus* except that the degree of transverse compression is considerably exaggerated. The long metalophid and transverse compression of the lower premolars present striking resemblances between *Pseudoceras*, *Floridameryx* and *Bachitherium*. In *Prodremotherium*, the lower premolars are shorter, flatter crowned, and the lingual lophids longer than in *Gelocus*, indicating that it had progressed one step farther toward the lower premolar morphology of *Dremotherium* and other Eupecora.

The presence of upright lower canines in presumed male Pseudoceratinae provides an important clue to the phylogeny of lower ruminants. Presumably this character state is primitive, as it occurs throughout other groups of artiodactyls and in other orders of mammals. If an upright lower canine had been lost and only later reacquired in Pseudoceratinae, it is unlikely that it could

have regained its precise occlusion with the anterior face of the upper canine. It seems more likely that this is a retained primitive character. If so, it places definite constraints on the phylogenetic position of Pseudoceratinae within lower ruminant phylogeny.

The following sequence of adaptive changes in the arrangement of the lower canine in the history of lower Pecora may be inferred. An incisiform lower canine was acquired in females very early in ruminant history. This adaptation for improved food-gathering evidently coincided with reduction of the upper incisors and development of an upper cropping pad. Meanwhile, in males an enlarged upper canine had developed and was used both for defense of the herd and in intraspecific combat. In its primitive mode it occluded anteriorly with the lower canine and posteriorly with the p1. In the common ancestor of the Tragulidae and Hypertragulidae, however, the lower canine in males became incisiform as in females. Then, in Hypertragulidae, the p1 strengthened its occlusal relationship with the enlarging upper canine; whereas, in Tragulidae, an increasing diastema isolated the upper canine from the p1, which retained its primitive form. Meanwhile, the primitive dimorphic lower canine condition continued in the common ancestors of the Moschidae and the Pseudoceratinae. Probably as the canines took on a more important role in male behavior and breeding success, they were further enlarged and their self-sharpening mode of occlusion refined. On the other hand, within the evolution of the Moschidae the male upper canine became so greatly enlarged that its occlusion with the lower was difficult to maintain. At this point in the phylogeny, an upright lower canine became disadvantageous and selection for an incisiform (female-like) lower canine became intense. Also, at this point, the long upper canine became loose-socketed, a condition that is retained in tusked Cervidae (Janis & Scott 1987). Today an incisiform lower canine occurs in all living ruminants, both male and female.

This proposed sequence of events in the evolution of pecoran canines requires further evidence before it can be fully accepted. *Gelocus* itself could provide crucial evidence, but at present the exact nature of its canines is not well documented. Insofar as they are known, the lower canines appear to be incisiform, but since, to this author's knowledge, only two mandibles with alveoli are known, they may both represent females. Filhol (1877) attributed to *Gelocus communis* some upper canines each with a strong wear facet on its anterior face, and he figured one example. If this attribution is correct, it constitutes indirect evidence that

some (presumably male) *Gelocus* had caniniform lower canines. Several other genera from the Phosphorites of Quercy, including *Lophiomeryx*, *Bachitherium* and *Prodremotherium*, consistently have incisiform lower canine teeth. Likewise *Dremotherium* shares the incisiform condition of the lower canine with Eupecora. In summary, retention of an upright lower canine in male Pseudoceratinae must be an ancient feature, possibly shared with *Gelocus*, and one that is quite anachronistic by late Miocene time.

The lower molars of Pseudoceratinae are narrow ("transversely compressed") with strong metastylids as in *Prodremotherium*, as noted by Geraads et al. (1987). A *Palaeomeryx*-fold in lower molars is not usually present in Pseudoceratinae, but is shared by *Prodremotherium* and many higher pecorans (Geraads et al. 1987).

Finally we turn to the postcranial evidence of Pseudoceratine to shed light on its affinities. In many postcranial features Pseudoceratinae fall somewhere among the more progressive Gelocidae or even parallel with the Moschidae. For example, the metapodials of Pseudoceratinae are fully keeled and fused at an early stage of development, about as in *Dremotherium*. The second and fifth metatarsals are reduced to minute vestiges, thus advanced well beyond the condition described by Kowalevsky (1876) in *Gelocus communis*. The metapodials are also longer than in *Gelocus* (Tables 2-3).

The presence of a closed gully at the distal end of an anterior groove on the metatarsus has important phylogenetic significance as established by Leinders and Heintz (1980). It is evidently a synapomorphy of Cervidae, Dromomerycidae and Antilocaprinae. The absence of a metatarsal groove and gully in *Moschus* is also a derived condition, possibly representing a synapomorphy with Bovidae. Thus the presence of a deep metatarsal gully in adult Pseudoceratinae implies an affiliation with probable pre-cervoid stock within Gelocidae.

Kowalevsky (1876) properly emphasized the importance of locomotor adaptations to properly understanding the phylogeny of hornless ruminants. Tragulidae, with their short limbs and short distal limb proportions, progress by hare-like leaping. Some of the principal anatomical correlatives of this locomotor style include relatively short, broad forefeet, primarily for landing and turning rather than for leaping; high head carriage with strong cervical dorsiflexion; a flexible, arched lumbar region; an underslung pelvis; a deeply flexed, spring-like hindlimb; and relatively strong eversion of

the hind foot (Gambarian 1974; Hildebrand 1985). A traguloid mode of locomotion was evidently characteristic of most small artiodactyls in the early Cenozoic. For example, Hurzeler's (1937) description of Cainotheriidae emphasizes many features that are both leporid-like and tragulid-like.

Gelocidae span a considerable variety of transitional forms toward a longer-limbed, straight-backed pecoran stature. Their morphology and proportions indicate progressive adaptation for fast gaits with extended suspension, such as the rotary gallop of a deer. Such gaits in ungulates have been analyzed by Gambarian (1974) and Hildebrand (1985). The simplification of the joints in feet, especially in the forelimbs, are toward simple hinge-like mechanisms that are restricted to fore-and-aft motion. The fundamental reason, as noted by Hildebrand (1985:43), is that "The faster a quadruped moves, the smaller its base of support can be." The loss of side toes and reduction of the ulna and fibula are clearly aspects of this general trend. Coupled with the obvious trends in fore- and hind limbs, one also sees advances in the axial skeleton and especially the pelvis. The deep ischial region above the acetabulum and the greatly expanded ilia indicate powerful iliopsoas muscles for deer-like leaping. In such features, described above, Pseudoceratinae have progressed beyond *Gelocus* itself, and are comparable with the more progressive Gelocidae, or even the Moschidae.

Limb proportions in Pseudoceratinae also fall somewhere in the midst of the complex progression of Gelocidae and Moschidae. In its forelimb, the radius and metacarpus of *Floridameryx* each account for about 36 percent of the combined humerus+radius+metacarpus length (Table 4). Equivalent data for a single species of *Gelocus* are not yet adequately known. In *Floridameryx* the hind limb proportions, derived in similar fashion, are 38 percent for the tibia and 29 percent for the metatarsus. In *Gelocus communis* the hind limb proportions are 38 percent for the tibia and 26 percent for the metatarsus, thus retaining a bit more length in the proximal limb segment. In view of the vast gaps in time and space between *Gelocus communis* and *Floridameryx floridanus*, these are surprisingly similar proportions, suggesting a similar stage of skeletal evolution among these lower pecorans.

The previous descriptions and comparisons indicate that Pseudoceratinae share many special features with *Gelocus*. They also share some synapomorphies (or parallelisms) with Moschidae (and thereby often with various higher ruminants). It seems reasonable to view

the Pseudoceratinae as a North American clade that branched from earlier (Oligo-Miocene) Eurasian stock somewhere within the Gelocidae. An appropriate taxonomic solution, based on the known facts, is to place the Pseudoceratinae as a distinct subfamily within the Gelocidae.

Finally, we may ask whether there are any intermediate fossils more closely linking *Gelocus* from the Oligocene of Europe and the Pseudoceratinae from the late Miocene and Pliocene of North America. Two possible answers deserve brief consideration. One is the enigmatic genus *Bachitherium* known mainly from France. The other involves a pair of poorly known genera from Mongolia.

First, with regard to *Bachitherium*, it seems clear that Webb and Taylor (1980) were premature in their assignment of this genus to the Leptomerycidae, even if they were correct in wishing to remove it from the previous assignment to Hypertragulidae (Lavocat 1951; Viret 1961). Bouvrain and Geraads (1985) announced the discovery of a skeleton of *Bachitherium cf. insigne* from Cereste and Geraads et al. (1987) clarified its relationships to other Neoselenodontia. In the same year Ginsburg and Huguency (1987) assigned an important Stampian-aged sample of two species of *Bachitherium* to the Tragulidae with a query. Janis (1987:209) considered *Bachitherium*, in the progressive nature of the odontoid process of the axis and in most features of its postcranial skeleton, "to be at a leptomerycid/gelocid grade of evolution", and attempted to solve the manifold possible affinities of this genus by placing it in its own monotypic family, Bachitheriidae.

The lower premolars of *Bachitherium* are very distinctive. They have strongly inflected parastylids and long, posteriorly directed metaconids, the parallel metaconids and entoconids enclosing long, narrow valleys. The left mandibular ramus of *Bachitherium insigne* Filhol, figured and described by Ginsburg and Huguency (1987), closely resembles the mandibles with complete dentitions of *Pseudoceras skinneri*. Despite obvious differences in the anterior part of the lower dentition, with the lower caniniform tooth in *Bachitherium* being the lower premolar, but in presumed male Pseudoceratinae, the lower canine, the two groups appear closely related.

This cladistic analysis is far from complete, and much remains to be learned about the flowering of the Gelocidae. The family remains something of a "scrapbasket". Besides *Gelocus*, *Bachitherium*, *Pseudoceras*, *Floridameryx* and *Prodremotherium*, it includes at least a handful of other genera even after

removal of *Lophiomeryx* to its own family by Janis (1987). *Paragelocus*, *Pseudogelocus*, *Phanero-meryx*, *Gobiomeryx* and *Pseudomeryx*, for example, are poorly known osteologically. Nonetheless they hint at an important evolutionary ferment among lower Pecora in Eurasia during the Oligo-Miocene.

The genera *Pseudomeryx*, a possible gelocid, and *Palaeohypsodontus*, a possible bovid, both from the mid-Tertiary of Central Mongolia (Trofimov 1957, 1958; Vislobokova & Daxner-Höck 2002) might have some distant affiliation with Pseudoceratinae. In each Mongolian form, the lateral compression and precocious hypsodonty of their molars hint at a similar combination of primitive and progressive features as in North American Pseudoceratinae. After comparing these two genera with Tragulidae, Gelocidae, and Bovidae, Trofimov (1957:140) noted that “etaient capable de se nourrir d’herbes assez dures.” Subsequently, one such species of primitive little ruminants from the Asian steppe might have reached the central plains of North America in the middle Miocene, and there extended its tenuous existence. The extinction of these precocious pecorans took place first in Asia and later in North America, as the inevitable pressure of competition from more progressive horned ruminants bore down upon them.

CONCLUSIONS

The subfamily Pseudoceratinae appeared in North America at the beginning of the Clarendonian land mammal age. *Pseudoceras skinneri* spread widely throughout the High Plains, the Gulf Coast, and as far south as Honduras. *Floridameryx*, a smaller genus with shorter premolars relative to its molars, appeared first in the Round Mountain Quarry, middle Clarendonian of New Mexico, as *Floridameryx klausi*, and later as *Floridameryx floridanus* in early and late Hemphillian sites of Florida. Chronologically the Pseudoceratinae range from early Clarendonian through late Hemphillian, a span of about seven million years. They are almost certainly immigrants to North America, presumably reaching this continent about 12 million years ago when they appear abruptly in the record.

Both known genera of Pseudoceratinae appear to have become extinct by the end of Hemphillian. This coincides with a very large number of extinctions of browsing or mixed-feeding ungulate genera in the North American record (Tedford et al. 1987; Webb et al. 1995; Janis et al. 2000). These major extinctions at the end of the late early and latest Hemphillian represent a marked interval of desiccation at about the end of the Miocene. If pseudoceratine habitats are correctly interpreted as

stream-border forests, then such desiccation might be expected to have drastically reduced the living space and food resources available to them. Thus the seven million-year history of the Pseudoceratinae ended as abruptly as it began.

Despite the original assignment of the subfamily Pseudoceratinae to the family Camelidae, the relatively complete osteological sample of *Floridameryx floridanus* from Withlacoochee River 4A clearly demonstrates the affiliation of this subfamily with hornless ruminants including Gelocidae and Moschidae from Eurasia. A surprising arrangement of the lower canines in which males have upright, self-sharpening fangs, but females have procumbent incisiform teeth as in higher ruminants, suggests that such dimorphism may have been present in other taxa (possibly *Gelocus* and *Bachitherium*) during the Oligocene and early Miocene ascent to higher ruminants.

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APPENDIX I

The following are all of the major specimens of *Floridameryx floridanus* n. gen. and sp. from the Withlacoochee River 4A site, Marion-Citrus county line, Florida, in the UF collection.

Braincases: UF 13834, 19257.

Frontals, R & L: UF 19258.

Premaxilla: UF 19270.

Premaxillae & maxillae (associated): UF 13833, 13836.

Maxillae: UF 13831, 19261-19269.

Mandibles: UF 13832, 17414-17416, 19395, 225874-225908.

Upper canines: UF 19271-19273.

Lower canine: UF 225911.

Lower third molars: UF 225909-225910.

Atlas vertebrae: UF 225912-225914, 225930, 225936-225937.

Axis vertebrae: UF 225915-225916, 225931, 225938-225939.

Cervical vertebrae: UF 225917, 225932, 225940-225953.

Thoracic vertebrae: UF 225918-225921, 225933, 225954-225968, 226233-226234.

Lumbar vertebrae: UF 225922-225929, 225934, 225969-225980, 226235-226236.

Sacra: UF 17401, 24173, 225981-225983.

Ribs: UF 13816, 17402.

Scapulae: UF 13820, 17403, 226052-226064.

Humeri: UF 13827, 17406, 18953, 225984-225994.

Radioulnae: UF 18954-18955.

Radii: UF 13818, 225995-226018.

Proximal ulnae: UF 13817, 226019-226030.

Metacarpals: UF 13822, 17407, 18951, 226031-226051.

Pelves: UF 13819, 17412, 226065-226070.

Femora: UF 13821, 17411, 27382, 226071-226103.

Patellae: UF 13825, 226231-226232.

Tibiae: UF 13815, 17410, 18956, 226104-226130.

Astragali: UF 13824, 17408, 226185-226194.

Calcanea: UF 13826, 226172-226184.

Cubonaviculars: UF 226195-226197.

Metatarsals: UF 226131-226171.

Proximal phalanges: UF 13823, 226198-226229.

Distal phalanges: UF 17409, 226230.

Mounted composite skeleton: UF 201847 (includes numerous elements that are not catalogued individually and a cast of the composite skull made from UF 13834, 13833, and 13836).