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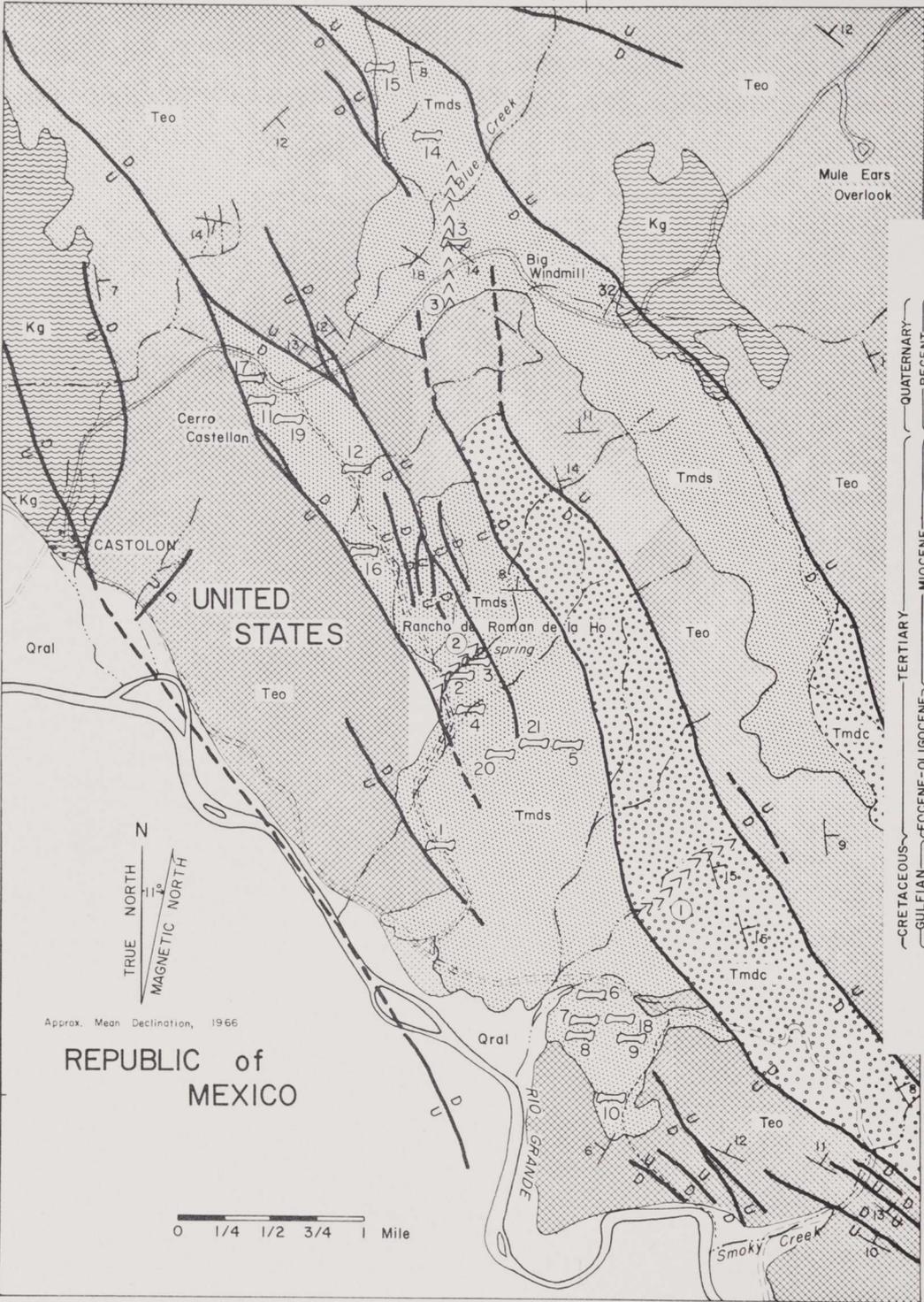
FURTHER STUDY OF CASTOLON
LOCAL FAUNA (EARLY MIOCENE)
BIG BEND NATIONAL PARK, TEXAS

By Margaret S. Stevens

December, 1977

Texas Memorial Museum/2400 Trinity/Austin, Texas 78705
W. W. Newcomb, Director

103° 28'



EXPLANATION

QUATERNARY - RECENT

Qral
Alluvium
Recent alluvium in stream channels

UNCONFORMITY

MIOCENE - DELAHO FORMATION

Tmdc
Tmdc, Smoky Creek Member, sandstone, conglomerate; Tmds, lower member, siltstone, sandstone, conglomerate

UNCONFORMITY

CRETACEOUS - GULFIAN - EOCENE-OLIGOCENE

Teo
Chisos, South Rim Formations, tuffs, flows, sediments

UNCONFORMITY

CRETACEOUS - GULFIAN

Kg
Aguja and Javelina Formations, sandstone and clay

5
Fossil locality

②
Measured section

Approx. Mean Declination, 1966

REPUBLIC of MEXICO

0 1/4 1/2 3/4 1 Mile



29° 05'

ARIKAREAN

Frontispiece.—Generalized geologic map of the Castolon area showing major faults and outcrop pattern of the Delaho Formation and adjacent rocks, Big Bend National Park, Texas (revised from Stevens et al., 1969). Fossil localities are numbered 1 through 21. Texas Memorial Museum locality numbers, the informal field names of each locality, and corresponding map numbers are:

- 40620, East side of Castolon Peak, 11.
- 40635, Rancho de Roman de la Ho, No. 2; type locality of the Delaho Fm., 2.
- 40686, Unnamed, 16.
- 40693, Unnamed, "Big Hill," 7.
- 40694, Rhino number two locality, 5
- 40715, "Millepede Draw," locality, 4.
- 40723, Lunch locality, 12.
- 40724, "Candelilla Draw" locality, 15.
- 40725, "Big Banks" locality, 14.
- 40726, Rhino number one locality, 3.
- 40736, Bench mark locality, 13.
- 40823, Northeast side of Castolon Peak, 17.
- 40849, *Priscocamelus* locality, "Big Hill," 9.
- 40871, Just over divide from Lance's locality, 8.
- 40879, Small dog locality, "Big Hill," 10.
- 40918, Rancho de Roman de la Ho, locality 1, 1.
- 40923, Lance's locality, "Big Hill," 6.
- 41460, "Hanging valley" locality, "Big Hill," 18.
- 41461, Southeast side of Castolon Peak, 19.
- 41462, New locality, or Sally's oreodont locality, 20.
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FURTHER STUDY OF THE CASTOLON LOCAL FAUNA
(ARIKAREEAN: EARLY MIOCENE)
BIG BEND NATIONAL PARK, TEXAS

By Margaret Skeels Stevens¹

ABSTRACT

The Castolon local fauna has been restudied in the light of newly discovered specimens from the Delaho Formation. These help to affix a more precise, later Arikareean age for the assemblage. Six new taxa, including new species of *Heloderma*, *?Brachyerix*, *Gregorymys*, *?Michenia*, and a new genus of sciurid and floridatragulid, are described. The oreodont *?Phenaco-coelus leptoscelos* (Stevens) is shown to be the remote ancestor of Barstovian and Clarendonian *Ustatochoerus*.

INTRODUCTION

Continued prospecting for fossil vertebrates in the lower part of the Delaho Formation since 1968 has resulted in recovery of specimens and taxa not reported by M. Stevens (*in* Stevens et al., 1969). All specimens reported here, except those from the Zoyatal local fauna from Aguascalientes, Mexico, come from the lower, unnamed, member of the Delaho Formation, exposed for several miles to the east and southeast of Castolon, Big Bend National Park. A reference map showing the aerial extent of the formation and its fossil localities is presented as the frontispiece. More detailed locality information is on file at the Texas Memorial Museum's Vertebrate Paleontology Laboratory at Balcones Research Center, Austin, Texas.

All specimen numbers not preceded by institutional acronyms in this report are in the Texas Memorial Museum collections. These are composite numbers in which the first part (five digits) is the locality number. The second part, which follows the locality number, is the specimen number. Hence, in what follows, locality numbers are included as part of the specimen number and are not repeated (except for holotype specimens) in the tabulations of each taxon described.

The Delaho Formation (Stevens, J. B., *in* Stevens et al., 1969) was deposited as bolson fill alluvium on an irregular surface produced by Arikareean basin and range faulting. When demonstrable, the base of the formation rests on Bee Mount Basalt (?Chadronian) of the Chisos Formation, and on Wasp Spring Flow Breccia or Burro Mesa Riebeckite Rhyolite (?Orellan-Whitneyan) of the South Rim Formation. Later Tertiary faulting has involved the Delaho Formation and preserves it as narrow grabens (frontis-

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piece) in the vicinity of Castolon, southward to and presumably into, Mexico. A thin basal conglomerate or conglomeratic volcarenite usually occurs, made up dominantly of the lithology of the basement rock. The lower member of the Delaho Formation becomes finer-grained and more silty higher in the sections. The highest part of the lower member is a medium fine unfossiliferous silt stone.

The upper, Smoky Creek member is predominantly a coarse conglomerate which represents depositional rejuvenation in the filling of the bolson, grading into finer, unfossiliferous deposits upward.

When their stratigraphic positions can be determined, the localities in the lower member usually occur in, or slightly above, the basal conglomeratic volcarenite, or in the immediate overlying silts. The localities are, however, often at different topographic positions because of faulting. Most specimens have come from locality 40635 (locality 2; see frontispiece) the type locality of the Delaho Formation.

All measurements in the tables are in millimeters, and were obtained by dial calipers. Illustrations were prepared by the author.

ABBREVIATIONS

AMNH	American Museum of Natural History, New York.
CM	Carnegie Museum of Natural History, Pittsburgh.
LACM (CIT)	Los Angeles County Museum, Los Angeles.
FMNH	Field Museum of Natural History, Chicago.
UCMP	University of California Museum of Paleontology, Berkeley.
N	Number of observations.
OR	Observed range.
\bar{X}	Arithmetic mean.
\bar{X}^{**}	Arithmetic mean with its standard error.
s	Standard deviation.
CV	Coefficient of variation.
a	Measurement is approximate.

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THE CASTOLON LOCAL FAUNA
Revised Faunal List

Class Reptilia

Order Chelonia

?*Geochelone* sp.

Order Squamata

**Heloderma texana* Stevens, sp. nov.

**Ctenosaura* or *Sauromalus* sp.

Class Mammalia

Order Marsupialia

*?*Peratherium* sp.

Order Insectivora

*?*Brachyerix hibbardi* Stevens, sp. nov.

Order Lagomorpha

Archaeolagus buangulus Dawson

Archaeolagus, cf. *A. acaricolus* Dawson

Order Rodentia

**Similisciurus maxwelli* Stevens, gen. et sp., nov.

**Gregorymys riograndensis* Stevens, sp. nov.

Heteromyidae, gen. et sp. indet.

Order Carnivora

?*Paroligobunis* sp.

*?*Nothocyon*, cf. *N. annectens* Peterson

Canidae, gen. et sp. indet.

Order Perissodactyla

Moschoedestes delahoensis Stevens

Order Artiodactyla

**Merychys*, cf. *M. calaminthus* Jahns

*?*Phenacocoelus leptoscelos* (Stevens)

**Priscocamelus wilsoni* Stevens

*?*Michenia australis* Stevens, sp. nov.

Stenomylus sp.

**Aguascalientia* sp.

Delahomeryx browni Stevens

**Nanotragulus ordinatus* (Matthew)

*Taxa marked with an asterisk are discussed in this paper.

SYSTEMATIC PALEONTOLOGY

Class Reptilia

Order Squamata

Suborder Lacertilia

Superfamily Varanoidea

Family Helodermatidae Gray

Heloderma Weigmann

*Heloderma texana*¹ sp. nov.

(Fig. 1, A-J; Table 1)

Holotype.—40635-123, an almost complete skull.

Referred specimens.—40635-119, cranial roofing bones; -137, frontal; -140, edentulous maxilla; -138, partial axis vertebra; and -158, nine articulated dorsal vertebrae.

Type locality.—Locality 40635 (Frontispiece)

Diagnosis.—*Heloderma texana* differs from *H. matthewi* of the middle Oligocene by its larger and more tuberculated osteoderms, osteoderms that are separated from each other by grooves, and by fewer maxillary teeth. *Heloderma texana* is distinguished from the living *H. suspectum* and *H. horridum* by its much smaller size, and by its more pustulate osteoderms.

Description.—The holotype consists of an almost complete and little distorted skull (Fig. 1, A-B, and G). The skull of *Heloderma texana* is low in profile, broad in the region of the orbits, and flattened. The pre- and post-frontals which form the dorsal margin of the orbit, are appressed in 40635-119, but are separated slightly by part of the frontal on the orbital rim of the holotype. Although Gilmore (1928) states that the family Helodermatidae is characterized by lizards that have the frontal excluded from the orbital margin, Bogert and Martin del Campo (1956) found this feature variable among samples of living *Heloderma suspectum* and *H. horridum*. The skull of *H. texana* has no supratemporal arch, but the postorbital bar is well developed. The ventral-lateral processes (subolfactory laminae) of the frontals are united by suture ventral to the olfactory bulbs, in typical helodermatid fashion (Fig. 1, C).

The parietals comprise a single shield without a pineal foramen. The parietal plate is relatively broad and similar in proportions to parietals of living species. The parietal of species of *Heloderma* from the Miocene or younger, is not as elongated as in *Eurheloderma* (Hoffstetter, 1957, p. 781; Fig. 5) from the late Eocene or early Oligocene of Europe.

¹*texana*, for the state of Texas.

The palate of *Heloderma texana* is characteristically helodermatid; its dental margin is bluntly rounded anteriorly, and it is approximately twice as wide as the snout is deep (Fig. 1, A, G). The vomers, palatines and pterygoids are elongated and are separated medially by a large palatal fenestra. The maxilla is excluded from the margin of the infraorbital vacuity. Although the palate of *Eurheloderma* is incompletely known, both its maxilla and pterygoid are similar to *Heloderma*. The basioccipital is slightly convex outward in *H. texana*, whereas in Recent *Heloderma* it is concave. It thus appears more varanid than in the living species.

Teeth of the holotype of *Heloderma texana* lack their apices and what remains of them is eroded. There appear to have been six widely spaced, pleurodont teeth which decrease in size posteriorly, with dilated, grooved bases attached to the maxilla. There also were very small, rudimentary teeth on the pterygoids as well, but only their attachments are preserved.

The maxillary teeth of 40635-123 are broken so that their pulp cavities can be seen. The cavities are oval with the long axis transverse to the length of the tooth row (Fig. 1, E), and appear to open toward the labial margins of the teeth. Recent *Heloderma* teeth were sectioned to provide a basis of comparison with those in the fossil. The pulp cavities of teeth of living *Heloderma* are transversely elongated as in the fossil. Perhaps the most notable feature of *Heloderma* is the development of the venom groove. This groove is formed by a fold of enamel along the anteroexternal margin of the upper teeth (Fig. 1, E, F). The fold of enamel produces the oval pulp cavity in Recent *Heloderma* teeth, and it is therefore reasonable to assume that oval pulp cavities in the fossil indicate that its teeth had venom grooves. Faint grooves can be made out on some of the teeth of *Heloderma texana*.

The skull of *Heloderma texana* is covered by osteoderms of varying size and roughness, depending on their position. The larger osteoderms are usually hexagonal and arranged serially, whereas those of smaller size are variable in shape and position. The larger osteoderms are not so flattened as those in the living species, but are more pustulate. The pustulate osteoderms are also more tuberculated, and the tubercles are separated from each other by deeper pits, than in living species. The larger osteoderms also tend to be less firmly attached to the underlying skull bones than the smaller osteoderms.

Several vertebrae have been referred to *Heloderma texana* on the basis of size and helodermatid morphology. An axis consists only of its centrum, 40635-138, but a series of dorsal vertebrae (-158) consists of complete vertebrae (Fig. 1, H-J). These vertebrae are wider than long, have low neural arches, relatively small neural canals, centra that are concave laterally and constricted slightly behind the condyle, and broad zygapophyses. They resemble but are much smaller than the vertebra figured and described by Estes (1963, Fig. 2) from the Thomas Farm local fauna. Although Estes noted that this vertebra is *Heloderma*-like, he referred it to the family Anguillidae.

Although it is difficult to determine the ontogenetic age of fossil lizards,

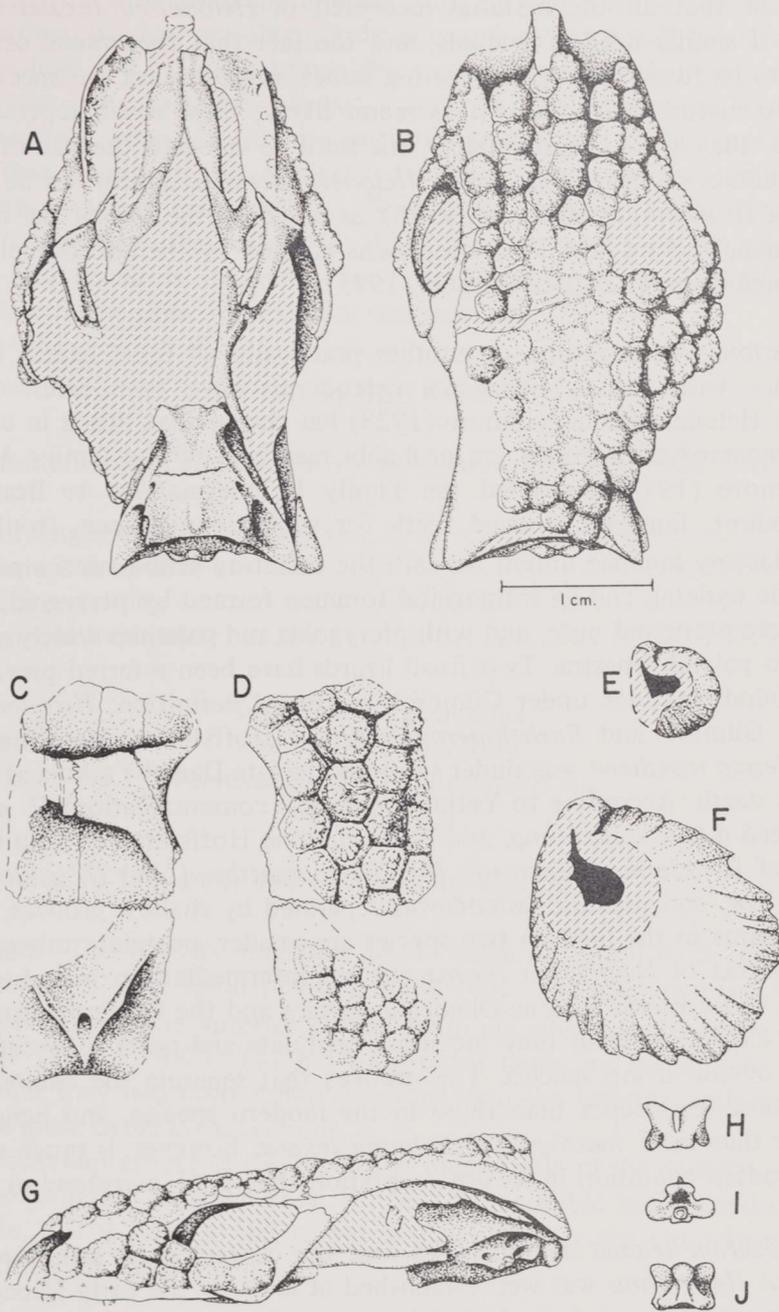


Fig. 1.—*Heloderma texana*, sp. nov. (A, B) ventral and dorsal view of skull, holotype, 40536-123; (C) ventral view of cranial roofing bones showing union of subolfactory laminae, 40635-119; (D) dorsal view of same specimen; (E) cross section of tooth of holotype; (F), cross section of comparable tooth in a Recent specimen of *Heloderma horridum*; (G) lateral view of skull, holotype; (H), (I), and (J), dorsal, anterior, and ventral views of vertebra, 40635-158. All X 2.

the fact that all the material recovered of *Heloderma texana* represent parts of similar-sized individuals, and the fact that the cranial osteoderms tend to be fused to their supporting bones, suggests that the specimens belong to mature individuals. If as seems likely, these fossils represent adult lizards, they were approximately one-third to one-half the size of average-sized adults of living *Heloderma*. *Heloderma texana* appears to be near the size of *H. matthewi* (Gilmore, 1928), as based on the size of the holotypic specimen, and on additional specimens studied by the late Daniel Yatkola (personal communication, October, 1975).

Discussion.—At one time or another practically all fossil lizards in North America with rugose, hexagonal osteoderms have been referred to the family Helodermatidae. Gilmore (1928) has shown that this is in error, and that most of these forms are probably members of the family Anguillidae.

Gilmore (1928) restricted the family Helodermatidae to lizards with pleurodont, fang-like grooved teeth for venom conveyance, frontals with subolfactory laminae united beneath the olfactory bulbs, no temporal arch, a single parietal, and an infraorbital foramen formed by pterygoid, palatine and ecto-pterygoid only, and with pterygoids and palatines widely separated by the palatal fenestra. Two fossil lizards have been referred previously to the Helodermatidae under Gilmore's restricted definition: *Heloderma matthewi* Gilmore and *Eurheloderma gallicum* Hoffstetter. New material of *Heloderma matthewi* was under study by the late Daniel Yatkola at the time of his death. According to Yatkola (personal communication) *H. matthewi* is indeed a true *Heloderma*, and *Eurheloderma* Hoffstetter is a junior synonym of *Heloderma* Weigmann. *Heloderma matthewi* and *H. gallicum* have large, low, and granular osteoderms separated by shallow grooves, whereas osteoderms in the modern two species are smaller, pustulate tubercles. The osteoderms of *Heloderma texana* are not intermediate in morphology between those of the Eocene-Oligocene species and the modern forms as one might expect; instead, they are more pustulate and more tuberculate than those of the living species. The grooves that separate the osteoderms of *H. texana* are deeper than those in the modern species, and hence much deeper than in *H. matthewi*. *Heloderma texana*, however, is much nearer to the modern condition in its ornamentation than is *H. matthewi* or *H. gallicum*.

Heloderma texana demonstrates that the characteristic structure of the skull of *Heloderma* was well established at least by the early Miocene, and that its structure, as is typical of lower vertebrates in general, has changed very little during the later Tertiary and Quaternary. *Heloderma* was much more widespread in North America during the middle Tertiary than it is at present, as indicated by occurrences in Colorado, Nebraska, Texas, and possibly in Florida. Clearly, Recent species of *Heloderma* exist as relic populations, extending from Arizona to the southern part of the west coast of Mexico (Bogert and Martin del Campo, 1956). The present-day distribution

of *Heloderma* results from preferential adaptation to, and systematic withdrawal within, tropical or subtropical xeric environments as these developed in the middle and later Tertiary. The occurrence of *Heloderma* in west Texas in the later Arikareean is but a stage in this withdrawal. The west Texas species is probably directly ancestral to, or very closely related to, species that were directly ancestral to the modern species, with little modification except size increase. According to Bogert and Martin del Campo the relative size of individuals of a given species or subspecies of modern *Heloderma* is dependent on the coincidence of maximum precipitation with the time of maximum temperature.

TABLE 1

Measurements of *Heloderma texana* sp. nov., holotype, 40635-123

Maximum length of skull as preserved	36.7
Maximum width of skull at orbits	20.5
Width between orbits	11.4
Maximum width of palate	12.5

Superfamily Iguanoidea
 Family Iguanidae Gray
Ctenosaurus sp. or *Sauromalus* sp.
 (Fig. 2, A-C)

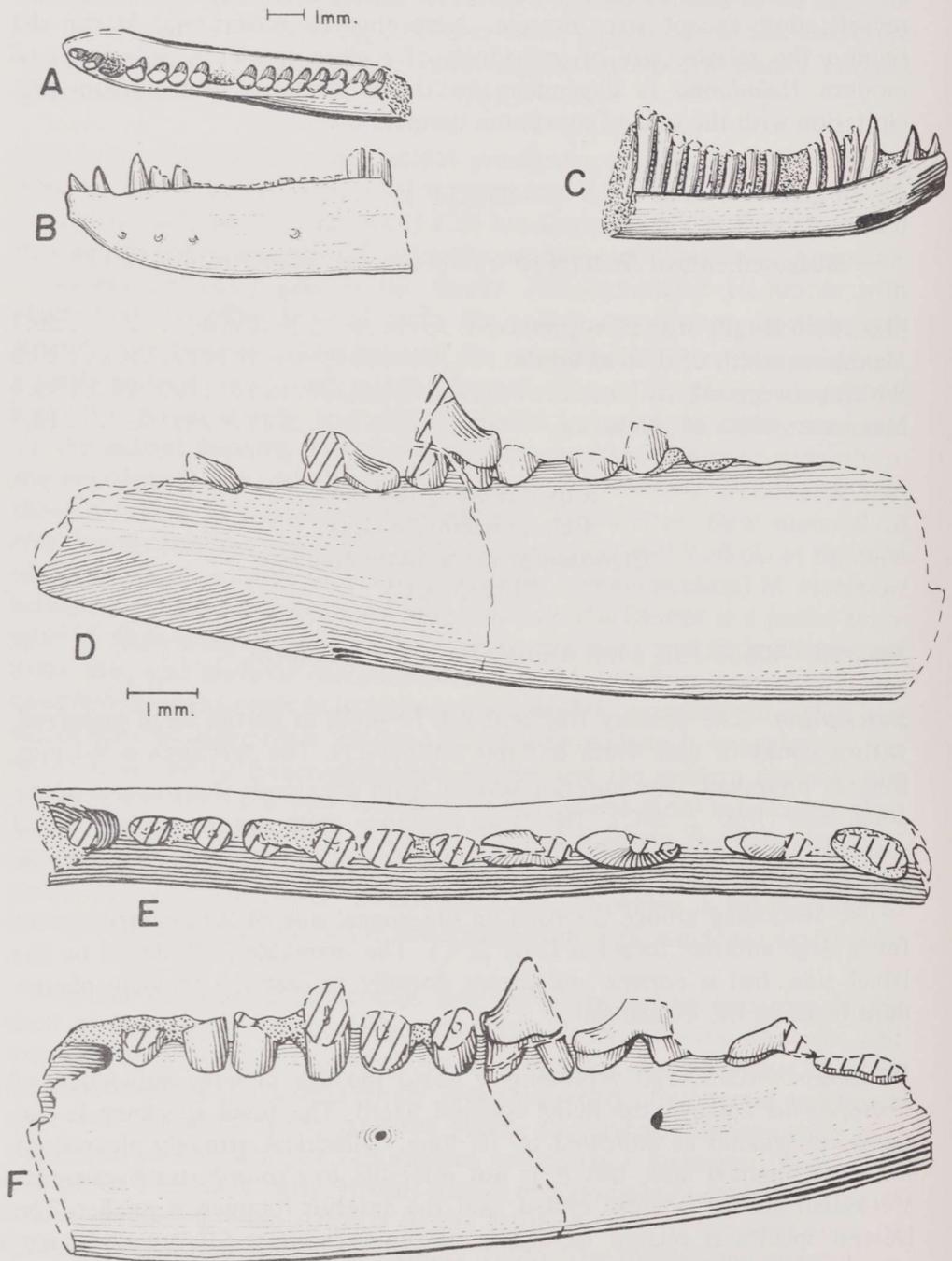
Material.—40635-155, a left dentary fragment with teeth.

Description.—The dentary fragment has 14 teeth or partial teeth preserved, with a count of nine teeth per five millimeters. The specimen is 9.4 mm. long as preserved. The anterior several teeth are simple sharp cones of unequal size (Fig. 2, A-C). The more posterior teeth are incomplete, but I suspect that they had more complex apices than the anterior teeth, because they have more ovoid cross sections.

The Meckelian groove is closed on the lingual side of the dentary, except for a large anterior foramen (Fig. 2, C). The mandible is flattened on the labial side, but is convex and curves dorsally to seat the strongly pleurodont teeth on the lingual side.

Discussion.—40635-155 represents a lizard the size of large individuals of *Crotophytus collaris*, the living collared lizard. The fossil specimen is certainly an iguanid as indicated by its long, cylindrical, strongly pleurodont teeth of unequal size, but it is not referable to *Crotophytus* because its Meckelian groove is more closed, and the anterior foramen is smaller. The Delaho species is related to lizards of the *Ctenosaura-Sauromalus* group,

probably closer to *Ctenosaura*. These are generalized, ground-dwelling, herbivero-omniverous, tropical and subtropical, subhumid or xeric iguanids of Mexico and the American far Southwest. *Ctenosaura*, *Sauromalus*, and *Heloderma* are sympatric today in certain parts of their ranges.



Class Mammalia
Order Marsupialia
Family Didelphidae Gray
Peratherium Aymard
? *Peratherium* sp.
(Fig. 2, D-F; Table 2)

Material.—40635-5, partial right mandibular ramus with an incomplete dentition.

Description.—Teeth of 40635-5 are poorly preserved and the identification of some is uncertain. The most anterior tooth preserved consists of the broken root of a canine, as determined by its large size and its oblique axis relative to the other teeth (Fig. 2, E). The canine is followed by P₁-P₃. The incomplete P₁ is a small, low tooth, with a smoothly sloping heel. Only the apex and part of the enamel on the anterior of P₂ is missing. It is a very narrow tooth with a rather low, medially ridged heel. A short diastema separates P₁ from P₂. The crown of P₃ is narrow, elongated, and rather high, with a higher heel than P₂. There are no cingula on any of these premolars.

The posterior root of each premolar is larger than the anterior root, whereas the roots of teeth that are molars are of equal size, as they are in Recent *Marmosa*, the mouse opossum. The roots belonging to the tooth posterior to P₃ are equal in size and more similar to those of the next posterior tooth, than they are to P₃. For this reason the tooth posterior to P₃ is believed to be M₁ and not P₄. If the teeth of 40635-5 are interpreted correctly, the mandible must belong to a didelphid similar to *Marmosa*, and not to an insectivore.

The mandibular ramus is slender, narrow, and evenly curved ventrally. Its symphysis is smooth and elongated, and ends under P₂, as in *Marmosa*. Two widely spaced mental foramina are present on the external side of the mandible. Although Tate (1933, p. 43) notes that position of the mental foramina is variable in *Marmosa*, their relative positions in the Delaho specimen are similar to those in living *M. mexicana* and *M. canescens* of Mexico, with the anterior foramen under the anterior root of P₂, and the posterior one under the posterior root of M₁.

Discussion.—Specimen 40635-5 is believed to be a marsupial allied to *Marmosa*. Although Tate (1933) says that no fossil *Marmosa* is known outside of its present range, and none has been reported older than late Pliocene, it is generally held that the long-ranging genus *Peratherium* is ancestral to it (Stock and Furlong, 1922, p. 317; McGrew, 1937, p. 451).

Fig. 2.—*Ctenosaura* or *Sauromalus* sp., 40635-155; (A) dorsal view, (B) labial view, and (C) lingual view of mandible fragment; X 4. ?*Peratherium* sp., 40635-5; (D) lingual view, (E) occlusal view, and (F), labial view of mandible; X 8.

Several species of Oligocene and early Miocene *Peratherium* have been described, but the incompleteness of the Castolon specimen hinders comparison to them. *Peratherium fugax* (Cope) is based on a palate with teeth, AMNH 5254, from the middle Oligocene. A referred specimen of this species, AMNH 5251, is more complete and consists of a well preserved mandible with most of its teeth, in addition to a palate. The spacing of the teeth, their size, and the diastema between P₁ and P₂ of 40635-5 is similar to that of the referred specimen of *P. fugax*. The morphology of the mandibles and absence of cingula on the premolars is similar in the Oligocene and Miocene forms.

The holotype of *Peratherium merriami* Stock and Furlong (1922, p. 311), from the early Arikareean part of the John Day Formation, consists of an incomplete skull associated with an incomplete mandible, UCMP 24240. The ramus, preserved posterior to P₂, is relatively larger than the Castolon specimen, its P₂ has a less flattened heel (see Stock and Furlong, 1922, Fig. 5), and its premolars are relatively narrower. The morphology of P₃ is otherwise similar, and the mental foramina have similar relative positions in both specimens.

Peratherium youngi McGrew (1937), from the late Arikareean Harrison Formation, is based on an isolated M³. Therefore no direct comparison between it and the Castolon mandible is possible. The holotype of *P. youngi*, FMNH P-25757, indicates an animal the size of *P. fugax*, for which associated upper and lower teeth are known. The Castolon species may turn out to be referable to *P. youngi* if and when adequate comparative material becomes available.

While *Peratherium* is widespread in the North American Tertiary, present-day *Marmosa* is restricted to Central and South America where tropical humid to subhumid climates are found. Certain species of *Ctenosaura*, *Heloderma*, and *Marmosa* are sympatric over some of their ranges in Mexico today.

TABLE 2

Measurements of ?*Peratherium* sp. 40635-5

Anterior margin of canine to posterior margin of M ₃	11.6
Anterior margin of P ₁ to posterior margin of P ₃	4.7
Alveolar diameter of M ₁ -M ₃	5.2
Maximum depth of jaw as preserved	3.1

Order Insectivora
Superfamily Erinaceoidea
Family Erinaceidae Fischer Von Waldheim
Subfamily Brachyericinae Butler
*?Brachyerix hibbardi*¹ sp. nov.
(Fig. 3, A-H; Fig. 4, A-C; Table 3)

Holotype.—40635-149, associated maxilla fragment with P³-M¹, cranium, and left mandible with incisor, P⁴-M³.

Type locality.—Locality 40635 (Frontispiece).

Diagnosis.—Differs from *Brachyerix macrotis* Matthew by slightly smaller size, wider P³, relatively less anteroposteriorly expanded P⁴ with the protocone longer than the hypocone, less anteroposteriorly attenuated M₂, and a rudimentary M₃.

Description.—The P³ is a relatively large tooth; three rooted and slightly narrower than long. The protocone is well developed, contrary to the condition found in *Brachyerix macrotis*, where it has been reduced to a mere cingulum. The paracone is the tallest cusp, and is connected to the metastyle by a crest. The parastyle is reduced, and is not connected to the paracone by a crest.

The P⁴ is a much larger tooth than P³, and is slightly narrower than it is long. Its paracone is almost as high as P⁴ is long, thus the cone is relatively more prominent than the paracone in *Brachyerix macrotis*. The paracone on the P⁴ of the type connects directly with the metastylar region by a crest. The metastyle is a low, not very prominent cuspule. The parastyle is a small, isolated cuspule developed on the faint anterior cingulum. The parastyle, although faint, is more prominent than in *Brachyerix macrotis*, and the apex of the paracone is situated more posteriorly. This is associated directly with the lesser anteroposterior attenuation of P⁴ of *?B. hibbardi* relative to the condition in *B. macrotis*.

The protocone of P⁴ of *?Brachyerix hibbardi* is slightly higher than the hypocone, unlike that in *B. macrotis*. The protocone is also the broader of the two cusps. Although the protocone and hypocone are distinct cusps, they are joined at depth (Fig. 3, B-C). Matthew (*in* Matthew and Mook, 1933, p. 3) notes that the genotypic specimen of *Brachyerix* lacks a hypocone, but it is apparent from his figure (mis-labeled *Brachyerix "montanus"*) that he probably confused the enlarged hypocone for the protocone, and regarded the true protocone as a style. Rich and Rich (1971, p. 26) have

¹*hibbardi*, specific name in memory of the late Professor Claude W. Hibbard, who did so much to increase our knowledge of fossil micro-mammals.

shown that the P⁴ of *Brachyerix*, when unworn, has a reduced protocone and an enlarged hypocone. Because the hypocone is less expanded in ?*B. hibbardi* than in *Brachyerix*, the posterolingual part of the P⁴ is less expanded. The broad P³, the relatively short but broad P⁴, and the prominence of the protocone of P⁴ in ?*B. hibbardi*, are similar to conditions in *Parveriscus montanus* Koerner (1940).

The M¹ is almost square, but is slightly wider than long, and is slightly longer than P⁴. The paracone is the third tallest cusp of the crown, not the tallest, as in *Brachyerix macrotis*. The paracone is slightly shorter than the metacone, and considerably shorter than the protocone, which is the tallest cusp (Fig. 3, B-C). The height of the paracone is approximately half the length of the tooth, as in *B. macrotis* and *Parveriscus montanus*. The paracone is anterolabial to the metacone, as it is in the other two species. The metacone is connected to the metastyle by a crest, which projects posterolabially as a metastylar spur; thus, the M¹ is more anteroposteriorly elongated labially than lingually. The shape of M¹ is more similar to that of *Parveriscus* than that in *Brachyerix*.

The protocone of M¹ is slightly anterior to the paracone, but its base does not expand anteromedially to the extent in *Brachyerix macrotis*. The relative anteromedial expansion of the protocone area of M¹ of ?*B. hibbardi* is more like the condition in *Parveriscus*. The anteromedial margin of M¹ of *B. macrotis* is closely adjacent to the posteromedial margin of P⁴, whereas in ?*B. hibbardi* these teeth are separated broadly (Fig. 3, B).

The hypocone is the lowest and smallest cusp on M¹ of ?*Brachyerix hibbardi*, as it is in the other two species. Because the protocone is not expanded anteromedially, the distances between the protocone and paracone, and between the hypocone and metacone are equal, and resemble the condition in *Parveriscus montanus* (Rich and Rasmussen, 1973, p. 25). The distance between the protocone and paracone is greater than between the hypocone and metacone in *Brachyerix*. No trace of the metaconule is apparent, but the slight posteromedial attenuation of the protocone wear-selene may indicate a raised area that might represent the metaconule. The protocone and hypocone are separated lingually, by a broad valley. A short lingual cingulum is present at the mouth of this valley. Slightly developed anterior and posterior cingula are present on M¹, and the prominent labial cingulum blends with the broad metastylar shelf. Anterior, posterior, lingual, and labial cingula are present on M¹ of *Parveriscus* and *Brachyerix*. Although M² is not preserved on 40635-149, a small, subtriangular M² is inferred to have been present (Fig. 3, E) to accommodate the talonid of M₂ and the M₃ (Fig. 3, D).

The lower jaw associated directly with the maxilla is almost complete, except for loss of bone in the posterior region, and loss of the tip of I₁ (Fig. 3, H). The lower incisor, believed to be I₁ (sensu McKenna and Holton, 1967, p. 2, and not I₂ of Butler, 1948), is a greatly enlarged, procumbent, rodent-like tooth. It is compressed laterally to form an ellipse in cross-

section, as in *Parveriscus* and *Brachyerix*. It is more compressed than I₁ of *Exallerix* McKenna and Holton (1967) from Mongolia. X-rays reveal that the incisor ends posteriorly beneath the posterior part of P₄. I₁ ends beneath the anterior root of P₄ in *Parveriscus*.

There are two large, matrix-filled alveoli anterior to P₄ in 40635-149 (Fig. 3, G), and what appears to be a third alveolus between these and I₁. I believe that this small alveolus represents a very small, shallow-rooted I₂ that is situated directly behind I₁, as in *Exallerix* and *Parveriscus*.

Because of phylogenetic loss of one or more of the premolars in members of the Erinaceidae, there is often confusion in identifying remaining teeth. The two large alveoli directly ahead of P₄ in 40635-149 either belong to two single-rooted teeth or to one double-rooted tooth. Because of the shapes of the alveoli, it is unlikely that they belong to a single tooth. The anterior of the two large alveoli is the larger, and its axis is oblique to the toothrow (Fig. 3, G). If this alveolus is for a single-rooted canine, then 40635-149 is similar to *Parveriscus* and *Exallerix* in that a P₂ separates the canine from P₄. I disagree with Rich and Rich (1971, Fig. 1) in their interpretation that the two large alveoli anterior to P₄ in *Brachyerix* belong to I₂ and a canine, because the small alveolus immediately anterior to the large alveoli in 40635-149 and just posterior to the incisor, is probably that for I₂. I suggest that their I₂ is the true canine, and that their canine is the P₂. If this is correct, then I₂, instead of P₂, has been lost phylogenetically in *Brachyerix*.

The second of the large alveoli that lies immediately ahead of P₄ in 40635-149, probably belongs to a single-rooted P₂ (see Butler, 1948, p. 463, for the reasons for calling this tooth P₂ and not P₃). As with *Parveriscus* and other Erinaceinae where P₂ is known to be present, the lower dental formula is I₁₋₂, C, P₂, P₄, and M₁₋₃ (Rich and Rasmussen, 1973). The dental formula for the mandible of *?Brachyerix hibbardi* is I₁₋₂ (reduced), C, P₂, P₄, and M₁₋₃ (reduced), and that for *Brachyerix* is I₁, C, P₂, P₄, and M₁₋₂.

The P₄ of *?Brachyerix hibbardi* is relatively large, with the protoconid the highest cusp of the tooth. It is as high as the tooth is long, which is similar to the proportions of P₄ in *Parveriscus*. The protoconid is much higher than the paraconid of P₄ in *Brachyerix*. The paraconid of P₄ in 40635-149 is located anterolingual to the protoconid, and it is a relatively larger cusp than its homologue in *Brachyerix*. It is separated from the protoconid by a notch as in *Parveriscus* and other Erinaceinae, as opposed to the condition in the typical Brachyericinae where the paraconid is reduced.

Although the metaconid of P₄ in 40635-149 is not well developed, there is a marked swelling on the tooth in the position of the metaconid. A similar swelling occurs on P₄ of *Parveriscus* of the Erinaceinae, and in *Brachyerix* of the Brachyericinae. P₄ is broadest across the short talonid. Two cuspules are located on the posterior edge of the talonid, one at its posterolabial side, and the other at its posterolingual side.

Unlike M₁ of *Parveriscus*, this tooth in *?Brachyerix hibbardi* is as elon-

gated as M₁ of *Brachyerix*. The prevallid shear of the trigonid of M₁ (the shear provided by the protoconid-paraconid crest) is almost as attenuated as it is in *Brachyerix*, one of the most advanced genera of hedgehogs in this feature. The anteroposterior diameter of the trigonid of M₁ of 40635-149 is approximately three-fifths the total anteroposterior length of the tooth, whereas in advanced *Brachyerix* the trigonid is two-thirds the length of M₁. The length of the trigonid in *Parveriscus* is about one-half the length of the tooth. Although the talonid is slightly broader than the trigonid of the Delaho species, as in *Brachyerix*, the width of the M₁ as a whole is relatively greater than it is in *Brachyerix*. Thus while the prevallid shear alignment is advanced in the direction of *Brachyerix*, the tooth is less specialized because it is broader.

The talonid of M₁ of ?*Brachyerix hibbardi* has two cusps. The ovoid entoconid is by far the tallest of the talonid cusps. It is almost as tall as the paraconid. The well-developed entocristid extends from the entoconid to the base of the metaconid, and prevents the talonid basin from opening lingually as it does in *Brachyerix*. The talonid basin of ?*Brachyerix hibbardi* opens posteriorly as it does in *Parveriscus*. The crescentic hypoconid is located posterolabially to the protoconid. A labial cingulum extends from the paraconid to the hypoconid, where it joins a posterior cingulum. Similar cingula occur in *Parveriscus* and *Brachyerix*.

As in *Brachyerix*, M₂ of ?*B. hibbardi* is two-thirds the length of M₁, but is relatively wider. The width of the trigonid is greater than its length, instead of being approximately equal as in *Brachyerix*. The trigonid of the Delaho hedgehog is longer anteroposteriorly than in *Parveriscus*, but the relative widths of the teeth are about the same. The attenuation of the trigonid of ?*B. hibbardi* is nearly the same as in *B. macrotis*.

The most notable feature of the mandible of ?*Brachyerix hibbardi* is the presence of a very small peg-like M₃ (Fig. 3, F-H). Its apex is presumed to be the protometaconid. A low and very small cusplule is present anterior to the protometaconid which may represent the paraconid. A talonid is not developed, but a slight labial cingulum extends around the tooth. The M₃ of *Parveriscus*, although reduced, has a better differentiated trigonid (Rich and Rasmussen, 1973, p. 40). Third molars are not present in *Brachyerix*.

The mandible of ?*Brachyerix hibbardi* is short and rather deep below the dental series. The ascending ramus is situated well behind the molar series, and rises steeply. The ascending ramus is bordered anteriorly by a prominent lateral flange, and the masseteric fossa is deep. The mandibular foramen is located beneath the middle part of P₄, as in *Parveriscus*, whereas in *Brachyerix* it is situated beneath the anterior root of M₁. The unfused symphyseal surface extends anterior from beneath P₄ in ?*B. hibbardi*, whereas in *Brachyerix* it terminates beneath M₁ (Rich and Rich, 1971). The symphysis in *Parveriscus* terminates between the canine and P₂ (Rich and Rasmussen, 1973).

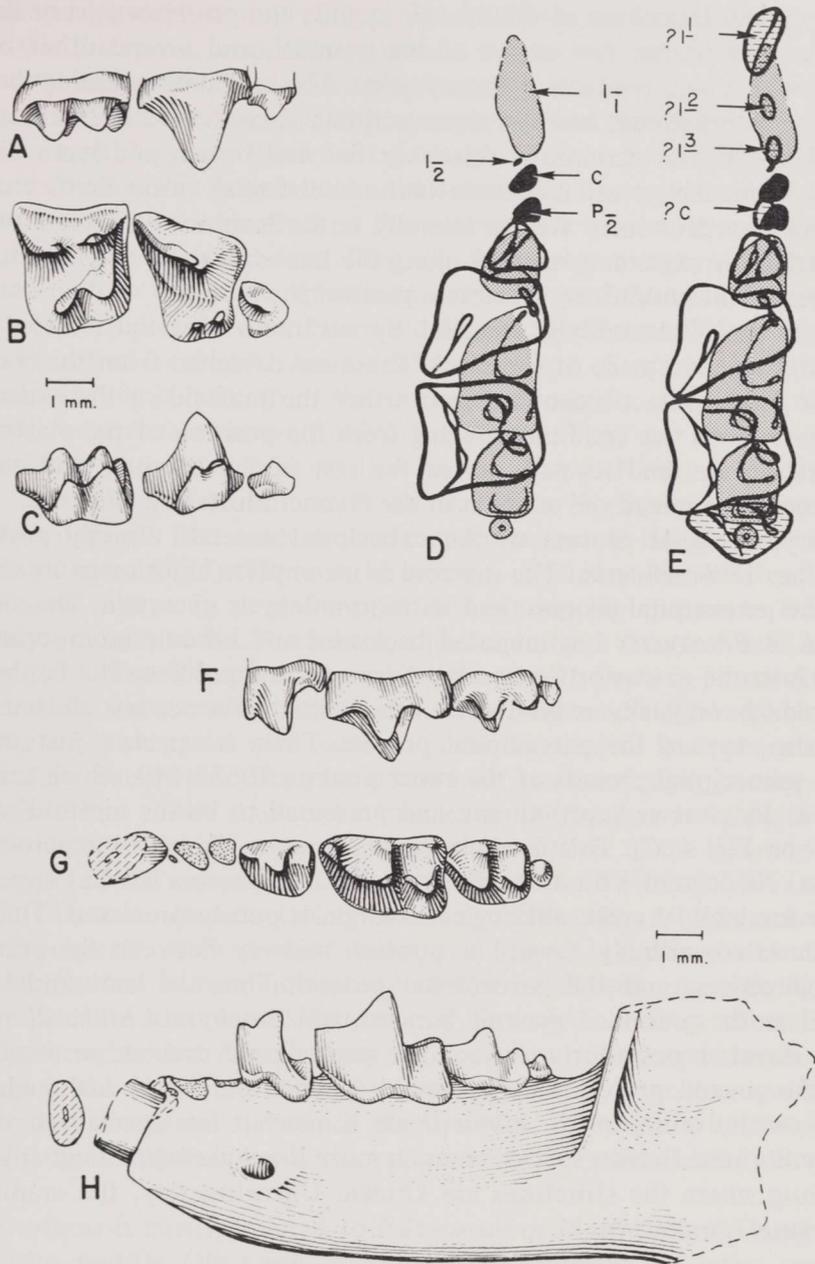


Fig. 3.—*Brachyerix hibbardi*, holotype, 40635-149: (A), (B), and (C) show labial, occlusal, and lingual views of P^3-M^1 ; (D) superposition of superior (heavy black lines) and inferior (stippled) dentition to show occlusion and position of unoccupied alveoli; (E) reconstruction of upper and lower dentition; (F), (G), lingual and occlusal views of lower teeth; (H) labial view of mandible with incisor and P_4-M_3 . All X 6.

The cranial fragments of 40635-149 include the posterior part of the cranium in two pieces, two pieces of the petrosal, and several other bits of bone that have no contacts with any other. The cranium, including the parietals, the interparietal, and the supraoccipital, is contained in one fragment (Fig. 4, A-C). The cranium is relatively flat and broad, and has a distinct sagittal crest. This crest merges into the lambdoidal crests that extend as thin and very prominent flanges laterally on both sides of the cranium. The interparietal is expanded laterally along the lambdoidal crest. There appears to be very faint sculpturing on certain parts of the parietal.

A left occipital condyle attached by suture to a partial mastoid bone makes up another piece of the skull. These are detached from the cranium, and no good contact exists between either the mastoid or the exoccipital and the rest of the cranium. Judging from the position of the mastoid-exoccipital suture, and its path across the rest of the cranium, the mastoid and exoccipital joined the cranium in the manner illustrated (Fig. 4).

The paroccipital process of the exoccipital extends directly posteriad, as it does in *Brachyerix*. The mastoid is incomplete anterior to its contact with the paroccipital process, and its morphology is uncertain. The mastoid process in *Brachyerix* has migrated backward and become incorporated directly into the posteriorly attenuated paroccipital process. The lambdoidal crest, which originally extended to the mastoid process, has shifted backward also, toward the paroccipital process. There is a process just anterior to the paroccipital process of the exoccipital on 40635-149, which is rounded ventrally, not very prominent, and presumed to be the mastoid process (arrow on Fig. 4, C). This is a very small structure close to the paroccipital process. Associated with this presumed mastoid process is what appears to be the lambdoidal crest, although its margin is poorly preserved. This crest extends lateroventrally toward a position midway between the presumed mastoid process and the paroccipital process. Thus the lambdoidal crest, as well as the presumed mastoid process, of *?Brachyerix hibbardi* appears to be directed posteriorly toward the paroccipital process, in association with the general posterior migration of the mastoid bone. Although these processes and crests in *?B. hibbardi* are somewhat less specialized than in *Brachyerix*, the Delaho species is much more *Brachyerix*-like than any other hedgehog where the structures are known. Unfortunately, the cranium of *Parveriscus* is unknown.

Discussion.—*?Brachyerix hibbardi* helps to clarify the mode, time, and place of origin of the subfamily Brachyericinae. Butler (1948, p. 488) included within the Brachyericinae the North American genus *Brachyerix* Matthew, and the Barstovian and Clarendonian genus *Metachinus* Matthew, because members of both are brachycephalic, have short faces, and have lost their third molar. Butler (1948) was uncertain about the affinities of North American (and Asian) *Parveriscus*, but thought that it was related either to *Brachyerix-Metachinus* of the Brachyericinae, or to *Amphichinus* or *Dimylechinus* of the Erinaceinae.

McKenna and Holton (1967, p. 2) expanded the Brachyericinae to include the European genus *Dimylechinus* Hurzeler (1944, p. 460), a hedgehog with many *Brachyerix*-like modifications, and their new genus *Exallerix*, also a form with *Brachyerix*-like features, from Mongolia.

The morphology of ?*Brachyerix hibbardi*, intermediate between *Parveriscus* and *Brachyerix*, suggests that the subfamily Brachyericinae evolved in North America from generalized *Parveriscus* that came in from Asia sometime during the late Oligocene. Rich and Rasmussen (1973, p. 44) have noted that middle Oligocene specimens described as *Palaeorinaceus minimus* Bohlin (1942, p. 23) from Taben-Buluk, western Kansu, China, and specimens identified as *Amphechinus (Palaeorinaceus) cf. minimus* (Bohlin) by Sulimski (1970, p. 64), from Nareen Bulak, Mongolia, are similar to specimens of *Parveriscus montanus* of North America. They are, however, slightly smaller than the oldest and smallest of the known North American specimens. Specimens identified as *P. montanus* in North America have been found in deposits that range in age from Arikareean to late Barstovian (Rich and Rasmussen, 1973). There is, however, a considerable amount of size increase and change in dental proportions among the specimens from successively younger rocks. *Parveriscus*, thus, came from Asia to North America during the latest Oligocene (or earliest Miocene?). Once in North America, the generally conservative main line of *Parveriscus* remained morphologically stereotyped, except for size increase, until the time of its apparent extinction in the Barstovian. The genus, however, produced a progressive lineage by at least the earlier Arikareean that leads to ?*Brachyerix hibbardi* of the later Arikareean, which in turn, produced *Brachyerix* of the Hemingfordian.

In spite of its antiquity, *Exallerix* McKenna and Holton (1967) of the middle Oligocene Hsanda Gol Formation of Mongolia, is a larger hedgehog than *Brachyerix*, with a much more specialized M₁. *Dimylechinus* of the late Aquitanian is morphologically similar to *Brachyerix*, although it is more specialized in some features and less specialized in others. Butler (1948) thought that *Dimylechinus* evolved from Oligocene *Amphechinus*. McKenna and Holton (1967) also thought that it came from within the Subfamily Erinaceinae to which *Amphechinus* belongs, but these authors thought that *Dimylechinus* itself was a member of the Subfamily Brachyericinae.

Parveriscus is closely related to *Palaeoscaptor* Matthew and Granger, also from the middle Oligocene Hsanda Gol Formation, and the two share similar proportions. *Palaeoscaptor* is probably best classified as a small and primitive member of the Subfamily Erinaceinae. *Parveriscus* appears to be transitional between the subfamilies Erinaceinae and Brachyericinae, but is probably best included within the Erinaceinae.

To include *Exallerix* and *Dimylechinus* in the Subfamily Brachyericinae makes the subfamily polyphyletic. The Brachyericinae appear to have evolved in North America no earlier than middle or later Arikareean. The highly specialized *Exallerix* of Mongolia is middle Oligocene in age. *Dimy-*

lechinus is a contemporary of *Brachyerix*, but the geographic distribution of this small hedgehog, confined to Europe, suggests that it has had a separate origin. It is possible that, like the Brachyericinae, the ultimate origin of *Dimylechinus* lies within *Palaeoscaptor-Parveriscus* of Asia. The *Brachyerix*-like modifications of *Dimylechinus* (and *Exallerix*) probably result from convergent specializations of their common *Palaeoscaptor-Parveriscus* Asian ancestors that migrated to different places at different times. Although the Brachyericinae had its origins within the Erinaceinae, a clear distinction between the two is not apparent until the late Arikareean. The Brachyericinae should be restricted to the North American genera *Brachyerix* and *Metachinus*.

TABLE 3

Measurements¹ of ?*Brachyerix hibbardi* sp. nov., holotype, 40635-149

<i>Upper teeth</i>	<i>Anteroposterior diameter</i>	<i>Transverse diameter</i>
P3-M1.....	4.65
P3.....	1.35	1.10
P4.....	2.48	2.32
M1.....	2.55	2.87
<i>Lower dentition and mandible</i>		
I ₁	1.45	0.98
I ₁ -M ₃ (posterior edge of incisor alveolus to posterior edge of M ₃).....		9.05
I ₁ -P ₄ (posterior edge of I ₁ to posterior edge of P ₄).....		3.83
M ₁ -M ₃ (lingual side).....	5.26
M ₁ -M ₂ (lingual side).....	4.62
P ₄	1.73	1.34
M ₁ (lingual).....	2.80
M ₁ (trigonid).....	1.75	1.65
M ₁ (talonid).....	1.80
M ₂ (lingual).....	2.05
M ₂ (trigonid).....	1.20	1.40
M ₂ (talonid).....	1.24
M ₃	0.66 (lingual)	0.60

¹Measurements taken as in Rich and Rasmussen (1973, fig. 1), when comparable, otherwise taken as indicated above.

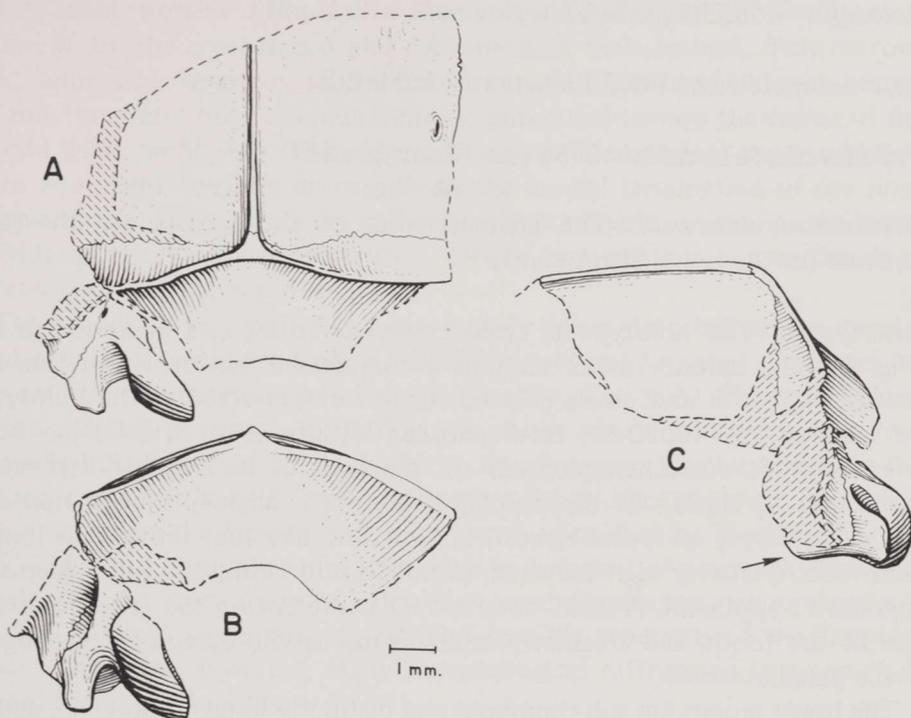


Fig. 4.—*Brachyerix hibbardi*, holotype, 40635-149, views of cranium; (A) dorsal, (B) posterior, and (C) lateral. Arrow points to the presumed mastoid process. All X 6.

Order Rodentia
 Family Sciuridae Gray
 Subfamily Sciurinae Baird
Similisciurus gen. nov.

Type species.—*Similisciurus maxwelli* sp. nov.

Diagnosis.—Differs from *Protosciurus* Black by its higher crowned, robust cheek teeth that have deep and constricted talonid basins, narrow hypoflexids, and remnants of ?hylophids.

Included species.—Type only.

*Similisciurus maxwelli*¹ sp. nov.
 (Fig. 5, A–G; Table 4)

¹*Similis*, like, and *sciurus*, a squirrel; *maxwelli*, for Dr. Ross A. Maxwell, who was the first superintendent of, and who did extensive geologic work in, Big Bend National Park.

Holotype.—40635-90, a left jaw fragment with M₁-M₃.

Referred specimen.—40620-39, an isolated left P₄.

Type locality.—Locality 40635 (see Frontispiece).

Similisciurus maxwelli.—The characteristics of the species are the same as those for the genus *Similisciurus*.

Description.—The holotype is broken anterior to P₄ and posterior to M₃ (Fig. 5). The anterior break sections a compressed incisor. Enamel on the incisor is smooth and cream-colored. P₄ is not preserved in the holotype. An isolated P₄, 40620-39, from another locality (Fig. 5, E-G) has been referred to *Similisciurus maxwelli* on the basis of its size and distinctive similarities to M₁-M₃ of the holotype. The P₄ is slightly smaller than M₁ of the holotype, in typical sciurid fashion, and like that tooth, it is longer than wide, relatively high crowned, although well worn, and has a deep and appressed hypoflexid. A small anteroconid is present on the anterior cingulum of the tooth, and a rather prominent mesostylid occurs posterolingual to the parametaconid.

The lower molars are sub-rhomboid and distinctly longer than wide, which is not characteristic of most of the Scuridae. The apices of the trigonid cusps of M₁-M₂ are rather close together, which produces a small trigonid crown, whereas these cusps on M₃ are more separated (Fig. 5, C). The anterolophid on M₁-M₂ is prominent and connected only to the paraconid. A large anteroconid (see Fig. 5, A for cusp nomenclature) is situated on the anterolophid and it is separated from the base of the parametaconid by a deep groove. Thus, the anterolophid is not confluent with the apex of the parametaconid. The anterolophid of M₃ communicates more directly with the parametaconid, but it is still separated from it by a notch.

The trigonid of M₁-M₂ tends to unite through a prominent metalophid (metalophid II). This lophid is a mutual development from the parametaconid and protoconid, and the two parts are separated from each other by a deep notch, which opens the trigonid basin posteriorly.

Hypoflexids of M₁-M₃ are notable for their depth and narrowness; thus, the ectolophid is little developed. The ectolophid is connected by a ridge to the protoconid on M₁-M₃, but it is connected to the hypoconid only on M₁. On M₂-M₃ the lophid terminates posteriorly at the base of the hypoconid, which is a large and distinct cusp on all molars. The hypoconid is especially large on M₃, where it is directed toward the talonid basin and incorporated into the "swollen" posterolophid. A mesoconid is developed slightly on M₂, but on M₃ the mesoconid is a relatively large cuspule. Entoconids are large and distinct cusps on the first two molars, but these are not separated from the posterolophid by clefts. The entoconid of M₃ is incorporated into the posterolophid. Very slight mesostylids occur on M₁ and M₂.

The most notable features of the lower cheek teeth of *Similisciurus maxwelli* are the great height and robustness of their crowns, their narrowness, appressed trigonids, and their deep and "pinched" talonid basins. A faint transverse ridge extends from the entoconid toward the center of the talonid basin on M₁-M₂. This ridge is best developed on M₁, and in addition there is a slight swelling or cuspule at the medial termination of the ridge on this tooth. These ridges are in the same topographic position as the hypolophids in the Prosciurinae (Wilson, 1949), but whether or not these are homologous structures is not known.

The mandible of *Similisciurus maxwelli* is rather deep below the alveolar border, and its masseteric fossa is deeply concave and bounded above and below by very prominent ridges that jut laterally (Fig. 5, A). The morphology of the masseteric fossa and its ridges is unlike anything seen in other true squirrels but it is remarkably similar to the corresponding structures in the genotype of *Cedramus*, *C. wardi* Wilson, of the middle Oligocene. *Cedramus* is a member of the Prosciurinae as presently classified by Black (1963, pp. 115, 230), and a member of a group that is thought to have no phylogenetic relationship to true squirrels. Like *Cedramus*, *Similisciurus* has entoconids that are distinct cusps (Fig. 5, B), and possible remnants of the ?hypolophids. There are, however, many morphological differences between their trigonids and ectolophids.

The deep branches of the masseter muscle of *Similisciurus maxwelli* end below and between M₁ and M₂, and the slip for the superficial branch extends slightly anterior to end below the hypoconid of M₁. The location of the masseter muscle in *S. maxwelli* is much more posterior and thus more primitive in position than in true squirrels with the exception of *ProtoSciurus* Black of the Oligocene and early Miocene.

Discussion.—Although *Similisciurus maxwelli* has some obviously primitive features, such as its longer than wide M₁ and M₂, its remnants of ?hypolophids, and its posteriorly positioned masseteric muscle, it is specialized in other ways. It is thought to represent a true squirrel of the Family Sciuridae, but one that is difficult to place within traditional sciurid classifications. Five genera of squirrels occur in the Arikareean of North America. These are *Protosciurus* Black, *Miosciurus* Black, *Tamias* Illiger, *Protospermophilus* Gazin, and *Miospermophilus* Black. All represent animals with widely separated cusps on their lower molars, shallow and broadly open talonid basins, and broad hypoflexids. All but *Protosciurus* have transverse, wider than long first and second molars, and masseteric fossae that end more anteriorly on the mandible. *Similisciurus* has no close similarity to any of the above genera with the possible exception of *Protosciurus*.

The oldest known true sciurid referable to *Protosciurus* is *P. mengi* Black, of the Orellan. *Similisciurus maxwelli* shows more general dental similarity to *P. mengi* than it does to the more contemporary *Protosciurus* of the Arikareean (*P. condoni*, *P. tecuyensis* (Bryant), and *P. rachelae* Black),

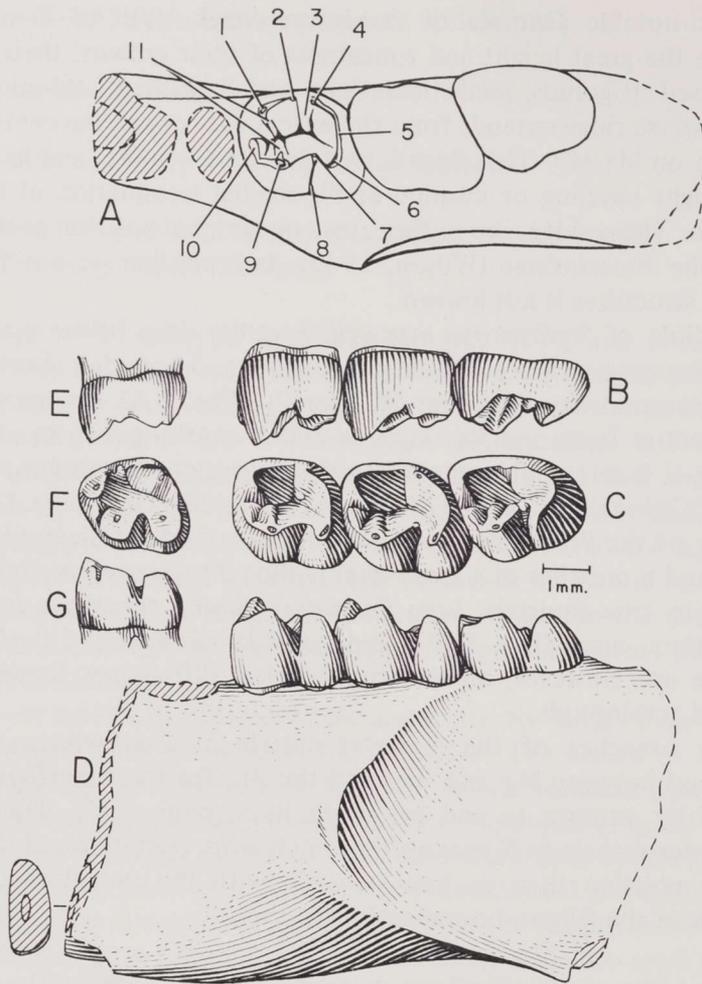


Fig. 5.—*Similisciurus maxwelli* gen. et sp., nov. holotype 40635-90: (A) dorsal view of holotype to show configuration of masseteric fossa and dental terminology; (1) parametaconid; (2) mesostylid; (3) ?hypolophid; (4) entoconid; (5) posterolophid; (6) hypoconid; (7) mesoconid; (8) hypoflexid; (9) protoconid; (10) anteroconid on anterolophid; and (11) metalophid. (B), (C), lingual and occlusal views of M_1 - M_3 of holotype; (D) labial view of mandible; (E), (F), (G), lingual, occlusal, and labial views of P_4 , 40620-39. All X 6.

which appear to be evolving toward typical tree squirrels. The similarities between *P. mengi* and *Similisciurus* include the position and development of homologous cusps, similar longer-than-wide first and second molars, and similar position of the masseter muscle on the mandible. These are features thought to be primitive for true squirrels. *Similisciurus* differs notably from *P. mengi* in its higher crowned, more massive teeth, its deeper and much

more appressed hypoflexids, in the development of the ridges that border the masseteric fossa, and in its larger size. The morphology of the masseteric fossa and its ridges is remarkably similar to the corresponding structures in the genotype of *Cedromus*, *C. wardi* Wilson, of the Orellan. *Cedromus* is a member of the Prosciurinae as classified by Black (1963, 115, 230), a group that Black thinks has no phylogenetic relationship to true squirrels.

Similisciurus maxwelli appears to be a primitive but very specialized true squirrel, possibly descended from *Protosciurus mengi* of the Oligocene. The high, massive teeth, with their crests, associated with great masseteric strength, suggest that *S. maxwelli* may have been a ground-dwelling, seed-crushing or grazing squirrel that was "experimenting" with occupancy of the same niche that was filled later in the Tertiary and Quaternary by the radiation of *Citellus* and *Cynomys*. Because it is more specialized in many features than *Citellus*, *Similisciurus maxwelli* cannot be ancestral to *Citellus* or to any other squirrel known to me.

TABLE 4

Measurements of *Similisciurus maxwelli* gen. et sp. nov., holotype, 40635-90 and 40620-39

	<i>Anteroposterior diameter</i>	<i>Transverse diameter</i>
Incisor	2.14	1.00
P4	2.25	2.06
M ₁	2.75	2.47
M ₂	2.88	2.68
M ₃	2.92	2.42
M ₁ -M ₃ , max. diam.....	7.75	
Depth of jaw below M ₁	6.37	

Family Geomyidae Gill
 Subfamily Entoptychyinae Miller and Gidley
Gregorymys Wood
*Gregorymys riograndensis*¹ sp. nov.
 (Figs. 6, A-B; 7, A-G; 8, A-G; Table 5)

Gregorymys sp., M. Stevens, in Stevens et al., 1969, p. 16.

Holotype.—40635-89, anterior part of skull with associated lower jaws.

Referred specimens.—40635-151, partial palate with P⁴-M³ and associated mandibles with P⁴-M₃; -107, nearly complete skull with unworn P⁴, M¹-M₃;

¹*riograndensis*, from the area of west Texas near the Rio Grande.

-116, anterior part of skull with P⁴; -150, rostrum of skull with incisors and P⁴; -118, palate with P⁴-M³; -38, jaw with P⁴-M₂; -39, jaw with P⁴-M₃; -95, jaw with P⁴-M₂; -91, jaw fragment with M₂-M₃; -135, jaw fragment with P⁴-M₁; -141, jaw with an unworn P⁴, and M₁-M₃; -181, -142, jaws with P⁴-M₃; -145, jaw with P⁴-M₂; -146, jaw with P⁴-M₂; -147, jaw with P⁴-M₃; -114, coprolite with crushed edentulous skull and some postcranial elements; and -105, coprolite with both edentulous mandibles and some postcranial material, and isolated fragments of limb bones.

Type locality.—Locality 40635 (see Frontispiece).

Diagnosis.—Differs from *Gregorymys douglassi* by slightly smaller size, lack of well defined upper incisor sulcus, and skull with a lower rostral vault.

Description.—Although it lacks the cranium, and the dentition is well worn, 40635-89 (Fig. 6; Fig. 8, C, F) is chosen as the holotype because it is the best specimen thus far recovered that has lower jaws associated with a skull. The most complete skull, 40635-107 (Fig. 7, A-C), belongs to a sub-adult individual where P⁴ is not fully erupted. Knowledge of the morphology of *Gregorymys riograndensis* is derived from interpretation of many topotypic specimens.

The skull is notable for its small size relative to other *Gregorymys*, for its short and low rostrum, and for its globular cranium which lacks interorbital crests even in old individuals. The rostrum is flattened dorsally, and is only moderately broad in the region of the rather narrow incisors. The rostrum of *G. riograndensis* does not jut upward and forward to the extent that it does in fossorial geomyoids.

The narrow upper incisors have orange-pigmented enamel. The sulcus, so characteristic of typical *Gregorymys*, is absent on the incisors of 40635-80 and -150, and it is only vaguely suggested on -107 and -116. The anterior face of the upper incisor is rounded as in *G. douglassi* Wood; not flattened as in advanced species of the genus.

The occlusal patterns of *Gregorymys* cheek teeth changes greatly as wear advances, as in other geomyoids. These changes are documented well for *G. riograndensis* because its many topotypic specimens represent individuals at various wear stages. P⁴ has three closely appressed cusps on the proto-loph, and the central cusp (protocone) is the largest (Fig. 8, A). A three-cusped proto-loph also occurs in other *Gregorymys*, as it does in *Entoptychus* (Rensberger, 1971, p. 113), but it is single-cusped in the earlier *Tenudomys* Rensberger (1973) and *Sanctimus* Macdonald (1970).

The metaloph of P⁴ of *Gregorymys riograndensis* has four cuspules of differing sizes. The metaloph is strongly arcuate, and its cuspules are obliterated soon after the tooth begins to wear. P⁴ is much larger than the molars, in typical *Gregorymys* fashion.

The lophs of the upper molars appear to have had three cuspsules each, when unworn, but no specimen has been recovered that has an unworn M¹ or M². P⁴-M³ are deeply sulcate labially; thus, the initial union of the protoloph with the metaloph begins lingually with wear, and the intervening sulcus retreats labially as wear continues (Fig. 8, A-C). This sulcus is basined medially; thus, at certain wear stages an isolated enamel lake or basin is formed on the crowns of the teeth. Such basins remain for a short time and then are removed by wear. Isolated enamel lakes are characteristic of *Gregorymys* at certain wear stages, and also of *Entoptychus* where, because of greater hypsodonty, they remain for a much longer period of time.

The roots of the upper and lower teeth of *Gregorymys riograndensis* have been exposed by preparation in the manner utilized by Rensberger (1971) to show their morphology. The roots of the upper molars are not thoroughly coalesced in the holotype (Fig. 8, C), or on 40635-118 and -151, but on -107 (Fig. 8, A) only M³ has divergent roots, hence this feature is variable among the Delaho population. The enamel margin of the upper cheek teeth of *G. riograndensis* is generally even around the base of the crowns, as in *Gregorymys*, primitive species of *Entoptychus*, and as in *Tenudomy*, *Pleurolicus*, *Schizodontomys*, and *Sanctimus*.

Morphology of the lower dentition of *Gregorymys riograndensis* has been discussed previously on the basis of two aged individuals (M. Stevens in Stevens et al., 1969), but with the acquisition of more material, the following additions are noted here. Five unworn or little worn P₄s of *G. riograndensis* show that a multicuspidate anterior cingulum, well separated from the protolophid by a sulcus, is present consistently (Fig. 8, D). The anterior cingulum bears three to four cuspsules, which vary in size. A shallow sulcus separates the most anterior of the cuspsules from the labial sets of two or three, and this sulcus persists for a short time after the cuspsules are worn away. A multicuspsate anterior cingulum is characteristic of *Gregorymys* and *Entoptychus*, but is absent in *Tenudomys*, *Pleurolicus*, *Schizodontomys*, and *Sanctimus*. The protolophid of P₄ has three to four cuspsules, and the metalophid has three. The protolophid and metalophid of the molars appear to have had three cusps each, when unworn, and an anterior cingulum on the anterolabial side of the protolophid. The anterior and posterior roots of P₄ are divergent. Enamel of P₄ extends down onto the forward face of the anterior root and down along the posterior face of the posterior root, similar to conditions in other *Gregorymys*. The enamel of M₁-M₃ extends down the posterior margin of the tooth toward the root only, hence in lingual view, the enamel margin is inclined (see Fig. 8, D-G). This feature, also characteristic of *Gregorymys*, is modified still more in advanced *Entoptychus*, but is absent in *Tenudomys*, *Pleurolicus*, *Schizodontomys*, and *Sanctimus*. Because *Entoptychus* carries this trend still farther in hypsodont teeth, the enamel becomes interrupted with wear, and the anterior parts of the molars lack enamel in occlusal view. Enamel interruption occurs at an ever-increasingly younger ontogenetic age in the progressively more advanced species of *Entoptychus*.

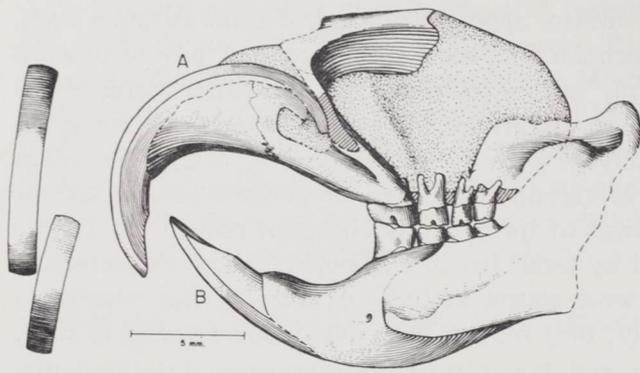


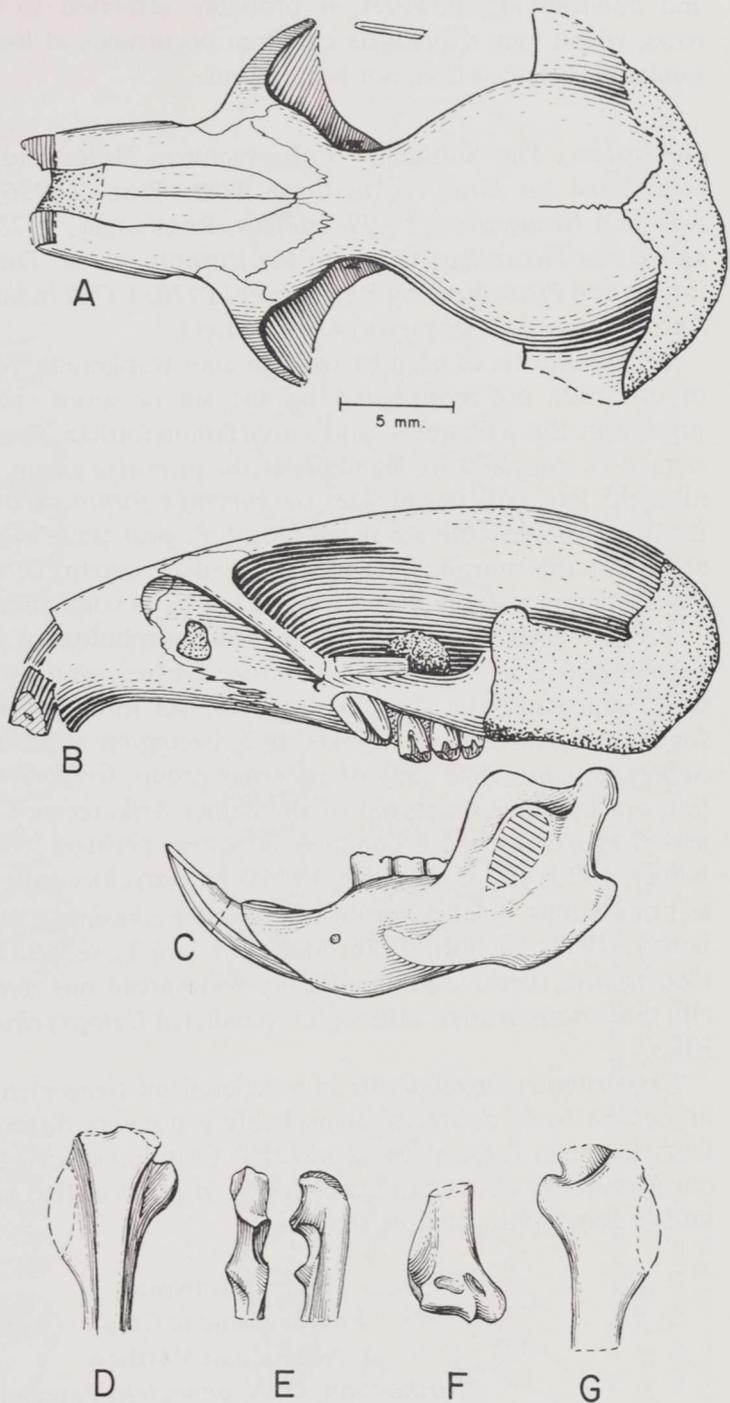
Fig. 6.—*Gregorymys riograndensis* sp. nov. (A), (B), lateral view of skull and associated mandible, and anterior view of upper and lower incisor, holotype, 40635-89. X 3.

Enamel interruption on M₁-M₃ has not been reported for *Gregorymys*. Two specimens, 40635-90, and -181, have enamel interrupted on M₁, or on M₁ and M₂ (Fig. 8, G). Similar interruptions would undoubtedly have occurred in other individuals of the Castolon geomyoid if death had not stopped dental attrition. Because of enamel inclination on the lower molars of other species of *Gregorymys*, enamel interruption undoubtedly would occur in these other species as well. Enamel inclination certainly is a function of greater hypsodonty of *Gregorymys-Entoptychus* relative to the other large geomyoids listed above.

The two individuals of *Gregorymys riograndensis* thus far recovered that have upper and lower teeth associated, 40635-89 and -151, show that while the enamel margins of the lower molars are inclined, the enamel around the base of the upper molars is generally parallel with the crowns. It is difficult to determine qualitatively the relative hypsodonty between the various species of *Gregorymys* because of lack of suitable preparation, and lack of information on dental wear changes among topotypic samples. A possible function of hypsodonty is indicated by sequence in the time of union of the protoloph(id)s and metaloph(id)s, time of formation of the isolated enamel lakes as a wave posteriorly, and the time of interruption of enamel. By the time the enamel becomes interrupted in M₁ and M₂ of *G. riograndensis*, the isolated enamel lakes have disappeared. In species of *Entoptychus* more advanced than *E. basilis* the enamel is interrupted by the time the lakes form (Rensberger, 1971, p. 128). Based on utilizing these criteria, *G. riograndensis* is slightly less hypsodont than *G. curtus* and *G. riggsi*, and much less hypsodont than *G. formosus*. No lower dentitions of *G. douglassi* are known to me, but judging from the upper teeth, *G. riograndensis* is perhaps slightly lower crowned.

The skull of *Gregorymys riograndensis* and the postcranial material that has been referred confidently to this species compare best with the living non-fossorial Heteromyidae. This indicates that *G. riograndensis* was not fossorial. The skull and postcranial elements are remarkably generalized, and suggest that the species foraged on the ground. Like all living geomyids

Fig. 7.—*Gregorymys riograndensis* sp. nov.
 (A) dorsal view of skull, 40635-107, as modified slightly by -116; (B) lateral view of skull, -107, but modified slightly by -116 in nasal region;
 (C) lateral view of mandible, -151;
 (D), (G), anterior and posterior views of partial femur, -163; (E) anterior and lateral views of partial ulna, -164; (F) anterior view of partial humerus, -165. All X 3.



and heteromyids, however, it probably retreated to self-constructed burrows, which may explain its common occurrence at locality 2, although articulated skeletons have not been found.

Discussion.—The Subfamily Entoptychinae Miller and Gidley (1918) was established for *Entoptychus* Cope. When Wood (1936) described *Gregorymys* and *Grangerimus* (= *Pleurolicus*, Rensberger, 1973), he referred these, as well as *Pleurolicus* Cope, to the Entoptychinae. The revisions of *Entoptychus* and *Pleurolicus* by Rensberger (1970, 1973) indicate to him that only *Entoptychus* and *Gregorymys* belong here.

Gregorymys is in need of revision and stratigraphic re-study. Three grades of evolution are represented by the six or seven species of *Gregorymys* present in the Arikareean and early Hemingfordian. *Gregorymys riograndensis* and *G. douglassi* are members of the primitive group, and both species are of early late Arikareean age. *Gregorymys formosus* of the early Hemingfordian illustrates the advanced morphological grade of *Gregorymys*. Whether or not the morphologically intermediate group, *G. curtus* and *G. riggsi*, are stratigraphically intermediate has yet to be confirmed.

Because *Gregorymys* seems an ideal morphological ancestor it has long been regarded as “ancestral” to *Entoptychus*, even though the two genera were approximately contemporaneous. As more information is obtained for later Arikareean geomyoids, it is becoming apparent that the ancestry of *Entoptychus*, like that of its sister group, *Gregorymys*, must be sought in a brachyodont geomyoid of the earlier Arikareean. Clearly, *Entoptychus* and *Gregorymys* had a common ancestry, perhaps from *Sanctimus* (Rensberger, 1973, 1973a; Nichols, 1976). *Entoptychus* arose and evolved rapidly as populations isolated within intermontane basins of the Northwest (Rensberger, 1971; Nichols, 1976; McKenna and Love, 1972). Its sibling group, *Gregorymys*, became geographically widespread but remained morphologically more conservative, although it paralleled *Entoptychus* in some characteristics.

Gregorymys riograndensis is a generalized *Gregorymys*, whose affinities lie nearest to *G. douglassi*. It probably is not very different morphologically from the stem form of the genus. The Castolon species does much to clarify our knowledge about primitive *Gregorymys*, as well as greatly extending the known geographic range of the genus.

Order Carnivora
Family Canidae Gray
cf. *Nothocyon* Matthew
? *Nothocyon*, cf. *N. annectens* Peterson
(Fig. 9; Table 6)

Nothocyon (Galecynus) annectens Peterson, 1907, p. 53.

? *Nothocyon*, cf. *N. lemur* (Cope), M. Stevens, in Stevens et al., 1969, p. 21.

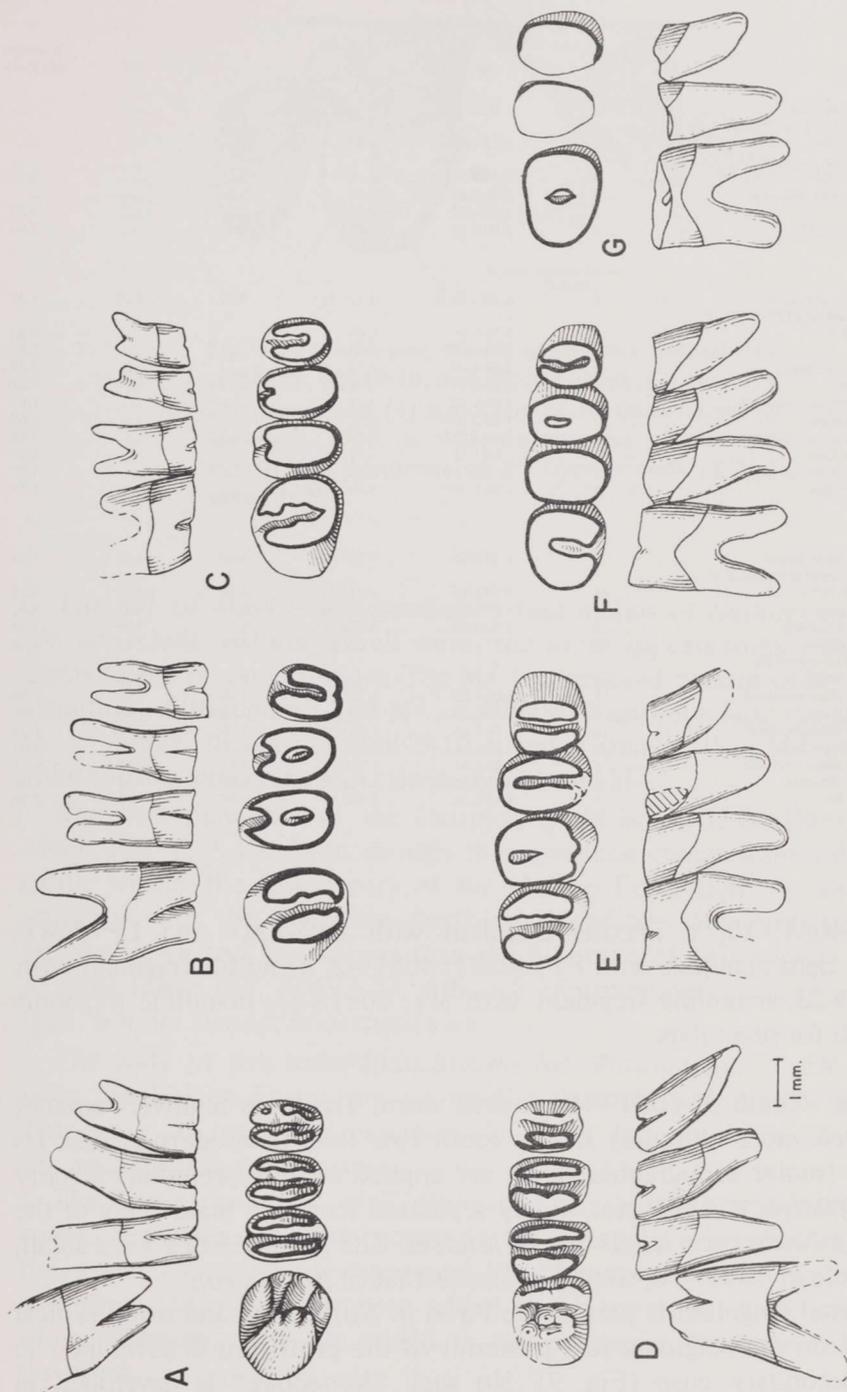


Fig. 8.—Changes in the occlusal pattern produced by wear on dentitions of *Gregorymys riograndensis*. (A) labial and occlusal views of P4-M₃, 40635-107; (B) same views of -118; (C) -89, holotype; (D) occlusal and lingual views of P4-M₃, 40635-141; (E) same views of -142; (F) -89, holotype; (G) -146, which has an interrupted enamel pattern on M₁ and M₂, typical of *Ertopychus*. All X 6.

TABLE 5

Measurements of topotypic sample of *Gregorymys riograndensis* sp. nov.

Skull	N	OR	\bar{X}^{**}	s	CV	Holotype 40635-89
Skull length; max observable	1	30.0
Length of rostrum; post. edge of incisor to anterior edge of P ⁴	2	9.12-10.17	9.65
Depth of skull; alveolar margin of P ⁴ to top of skull at orbits	3	8.36-9.30	8.76	8.63
Breadth of rostrum, max. trans. diam.	2	6.64-6.69	6.67
Interorbital diam.	2	4.50-4.70	4.60	4.50
Breadth of palate across P ⁴ s	3	5.00-6.53	5.83	5.95
<i>Upper teeth</i>						
Transverse diam. of upper incisor	5	1.32-1.54	1.42±.12	0.09	6.34	1.36
Length of anterior enamel of P ⁴ (EAP/, of Rensberger (1971:159))	4	0.75-1.05	0.90	0.80
P ⁴ -M ³ ; max. diam.	3	5.65-6.80	6.33	5.65
M ¹ -M ³ ; max. diam. (occlusal)	4	3.34-4.10	3.74	3.34
P ⁴ ; max. trans. diam.	5	2.00-2.30	2.15±.19	0.15	6.99	2.00
M ¹ ; anteroposterior diam. (occlusal)	4	1.02-1.42	1.26	1.02
M ¹ ; max. transverse diam.	4	1.86-2.20	2.02	2.00
M ² ; anteroposterior diam. (occlusal)	4	1.06-1.19	1.14	1.15
M ² ; max. transverse diam.	4	1.69-1.75	1.72	1.75
M ³ ; anteroposterior diam. (occlusal)	4	0.92-1.20	1.06	1.07
M ³ ; max. transverse diam.	4	1.40-1.50	1.46	1.45
<i>Lower teeth</i>						
Transverse diam. of lower incisor	8	1.23-1.43	1.32±.05	0.06	4.55	1.23
Length of anterior enamel of P ⁴ (EA/P of Rensberger (1971:159))	11	0.83-1.50	1.09±.13	0.20	18.53	1.20
P ⁴ -M ³ ; max. diam.	5	5.74-6.64	6.12±.48	0.39	6.33	6.02
M ¹ -M ³ ; max. diam. (occlusal)	5	3.60-4.00	3.77±.21	0.17	4.49	3.64
P ⁴ ; max. transverse diam.	10	1.52-1.93	1.77±.09	0.12	7.03	1.62
Height of paraconid of unworn P ⁴ ; apex to enamel margin	1	2.10
M ¹ ; anteroposterior diam. (occlusal)	11	1.06-1.38	1.25±.07	0.10	7.90	1.06
M ¹ ; max. transverse diam.	11	1.73-2.20	1.99±.10	0.15	7.49	1.96
M ² ; anteroposterior diam. (occlusal)	10	1.10-1.40	1.26±.06	0.08	6.17	1.25
M ² ; maximum transverse diam.	10	1.70-2.08	1.92±.09	0.12	6.40	1.90
M ³ ; anteroposterior diam. (occlusal)	6	0.98-1.44	1.21±.16	0.15	12.48	1.25
M ³ ; max. transverse diameter	6	1.45-1.70	1.53±.09	0.09	5.88	1.45
Depth of jaw below P ⁴	9	4.45-6.26	5.16±.45	0.59	11.38	5.10

Material.—40849-10, a maxilla fragment with RP³-RM² and LP⁴-LM¹; 40635-66, right mandible with P₃ and M₁; 40879-2, mandible fragment with M₁; 40693-23, mandible fragment with M₁; 40918-35, mandible fragment with alveoli for premolars.

Description.—Teeth of 40849-10 are well worn. The P⁴ is relatively smaller and oriented more obliquely in the tooth row than in modern canids. Its protocone (molar topographic terms are applied to this premolar) is only moderately large, and it is not widely separated from the main body of the tooth, as in *Nothocyon lemur* and *N. latidens*. The parastyle of P⁴ is a small, worn cuspule in 40849-10, similar in size to that of *Nothocyon*.

An internal cingulum is present on P₄ as in *Nothocyon* and other typical canids, but on the cingulum just posterior to the protocone is developed an elongate secondary cusp (Fig. 9). No such "hypocone" is developed in *Nothocyon lemur*, *N. latidens*, *N. geismarianus*, or any other species of typical *Nothocyon* known to me. This "hypocone," however, is similar, although slightly less developed, than the "hypocone" on P⁴ of the holotype, CM 1602, of ?*N. annectens*.

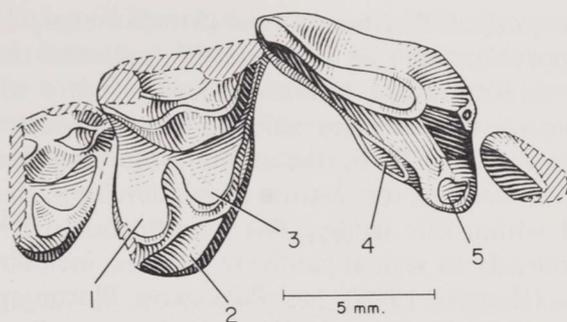


Fig. 9.—*?Nothocyon*, cf. *?N. annectens*; occlusal view of P³.M², 40849-10. X 4. (1) hypocone; (2) pericone; (3) protocone; (4) hypocone of P⁴ (tetartocone of Matthew, 1929, p. 471; deuterocone of some authors); (5) protocone of P⁴ (deuterocone of Matthew, 1929).

The M¹ of 40849-10 is similar to first molars of *Nothocyon lemur* and *?N. annectens*. Although well worn, the tooth appears to have had the usual cusps found in canid molars. The M² is a reduced version of M¹ in size and structure. Although P⁴ and M¹ of 40849-10 are very near the same size as in *N. lemur*, the M² of 40849-10 is much smaller than M² of *N. lemur*. *?Nothocyon annectens* has a similarly reduced M².

The best mandible of the Castolon canid is 40635-66 (Stevens et al., 1969, Fig. 7, A-C). Even though this specimen comes from a different locality within the lower part of the Delaho Formation, its teeth occlude properly with the maxillary dentition. Mandibles 40635-66 and 40879-2 are shallower and less robust than the holotype of *?Nothocyon annectens*. A third lower jaw, 40693-23, although approximately as deep as the holotype, is more slender in occlusal view.

The suite of five individuals known for *?Nothocyon*, cf. *?N. annectens* from the Delaho Formation are smaller than the holotype of this species. The range of individual variation, however, has not been established for *?N. annectens* in its type area.

The lower carnassial of *?Nothocyon*, cf. *?N. annectens* lacks accessory cusps. A similar condition occurs in the holotype, which shows that while the upper carnassial has developed the "hypocone" as an accessory cusp, additional cusps have not been added to the lower. In some canid lineages, when accessory cusps are added to one carnassial, they are also added to the other.

Discussion.—The first small carnivore remains found in the Delaho Formation were lower jaw fragments with teeth. These specimens are similar to a number of small canid species of the early Miocene, and they were identified

initially as *Nothocyon*, cf. *N. lemur* (Cope) (Stevens et al., 1969). Recovery of part of the upper dentition, in particular P⁴, indicates that the species is not comparable to *Nothocyon lemur*, because it has a more specialized P⁴. There has been a tendency for paleontologists to identify small fossil arctoids that have modified P⁴ by the addition of a hypocone, as members of the Procyonidae, because this feature is well developed in modern species currently placed within this family. The modification of P⁴, however, has occurred independently in several carnivore families, including the Canidae. Canid examples (Hough, 1948) are *Phlaocyon* Wortman and Matthew (1899); Peterson, 1924; McGrew, 1941) and *Aletocyon* Romer and Sutton (1927).

Peterson (1907), when he described the small dog from the Harrison Formation of Nebraska, included it within *Nothocyon* but he inserted as a subgenus Owen's (1847) generic name "Galecynus," which Cope (1881) had brought to North America and used extensively in later publications as a substitute name for the John Day species that he, Cope, had described originally as "*Canis*" *geismarianus*, "*C.*" *lemur*, and "*C.*" *latidens*. Whether Peterson simply wanted to carry on in print "*Galecynus*," or whether he intended it to amend the concept of *Nothocyon*, in view of his species' unusual P⁴, is unknown.

The canid from the lower part of the Delaho Formation is a small variant of *?Nothocyon annectens*. *?Nothocyon*, cf. *?N. annectens* from the Delaho Formation is slightly smaller and less robust than *?N. annectens* in most parameters, and its "hypocone" on P⁴ is slightly less well developed. The Delaho form appears to be a slightly less specialized (slightly earlier?) version of *?N. annectens* of the late Arikareean. The most likely ancestor for the Delaho species is *Nothocyon lemur* of the earlier Arikareean.

The similarity in morphology and increase in size is in accord with the known stratigraphic occurrence of *?Nothocyon*, cf. *?N. annectens* from the Delaho Formation, *?N. annectens* from the late Arikareean Harrison Formation, *Phlaocyon leucosteus* Matthew (1899) (Wortman and Matthew, 1899) from the early Hemingfordian, and *P. marslandensis* McGrew (1941) from the middle Hemingfordian. This similarity suggests that these species are drawn from stages in a single phyletic lineage. Within this series, P⁴ has a poorly developed parastyle, but the tooth becomes progressively more molarized as the hypocone enlarges. Also, with time, the P⁴ increases in size, the protocone achieves a more lingual position, the angle between the posterolingual margin of P⁴ and the anterior edge of M¹ decreases, and M¹ becomes progressively more quadrate. The lower sectorial, M₁, however, retains its normal canid trigonid and talonid. It is thus apparent that although the phlaocyonid lineage suggested above has its roots within *Nothocyon* of the early Arikareean, its early members are distinguishable by the later Arikareean.

I do not think that it is advisable, however, to identify the Castolon species, nor the Nebraska species, as members of *Phlaocyon*, as this would

corrupt the meaning of that distinctive genus. Clearly these animals represent transitional forms between *Nothocyon* of the earlier Arikareean and *Phlaocyon* of the early Hemingfordian, but because they are morphologically closer to *Nothocyon*, I have identified them as *?Nothocyon* in an attempt to indicate that they are atypical members of this group.

TABLE 6

Measurements of *?Nothocyon*, cf. *?N. annectens*

	40849-10
Anteroposterior diam. of P ⁴ (base of parastyle to posterior edge of metacone)	7.8
Transverse diam. of P ⁴ (normal to above measure)	4.9
Anteroposterior diam. of M ¹ (external margin)	5.6
Transverse diam. of M ¹ (normal to above measure)	7.5
Anteroposterior diam. of M ² (external margin)	3.0
Transverse diam. of M ² (normal to above measure)	4.9
Anteroposterior diam., P ³ -M ²	17.8 ^a
Anteroposterior diam., P ⁴ -M ²	14.9
	40635-66
Anteroposterior diam., P ₃	4.5
Transverse diam., P ₃	2.1
Anteroposterior diam., M ₁	8.2 ^a
Transverse diam., M ₁	3.6

Order Artiodactyla
 Family Merycoidodontidae Hay
 Subfamily Merychyinae Simpson
Merychys Leidy
Merychys, cf. *M. calaminthus* Jahns
 (Fig. 10, A-C; Table 7)

Merychys calaminthus Jahns, 1940, p. 187.

Merychys sp., M. Stevens, in Stevens et al., 1969, p. 29.

Material.—41464-1, palate with most of the cheek teeth associated with a partial mandible with P₄-M₃.

Description.—Specimen 41464-1 consists of a skewed palate with some of

its adjacent parts. The canine is relatively small, in typical *Merychus* fashion. The premolars are molarized and set obliquely in the tooth row (Fig. 10, B). Their orientation accounts for the short P¹-P⁴ diameter (Fig. 10, C). The individual premolars are no smaller than in *Merychus calaminthus*. When viewed labially, P¹-P³ are inclined backward as in *Merychus*. The structure of the canine, premolars, and molars of 41464-1 is typical of *Merychus*.

Teeth of 41464-1 are only moderately hypsodont. The Delaho *Merychus*, as indicated by its small size and little hypsodonty, belongs to one of the geologically older species of the genus (Fig. 10, C). There is a steady trend for size increase, relative decrease of width of the molars, decrease in relative premolar to molar diameters, and increased hypsodonty in successive species of *Merychus*, from the later Arikareean to the middle Hemingfordian. After this time the teeth of *Merychus* become stereotyped.

The associated mandible of 41464-1 and its dentition resemble closely specimens 40823-1 and 40694-1 reported on earlier (Stevens et al., 1969, p. 29).

Discussion.—*Merychus*, cf. *M. calaminthus* was identified originally as *Merychus* sp., because the first specimens obtained from the Delaho Formation consisted of partial mandibles with worn dentitions. It was noted that these jaws resemble *M. crabilli* Schultz and Falkenbach (1947) of the late Arikareean, *M. calaminthus* Jahns (1940) and small individuals of the more advanced and later species, *M. minimus* Peterson (1907). The adult dentition of 41464-1, which contains a little worn M³ (M₃ is damaged slightly), indicates that the Delaho species is not comparable to *M. minimus* (*M. minimus* sample based on means, Fig. 10, C-d, because its dentition is lower crowned.

Jahns (1940) selected several oreodont specimens recovered from the Tick Canyon Formation of Los Angeles County, California, as cotypes of *Merychus calaminthus*. Some of the cotypes consist of immature individuals, but his first mentioned specimen, LACM (CIT) 1383, is a palate with a nearly perfect adult dentition which serves as a lectotype of the species. Schultz and Falkenbach (1947, p. 189) described a second species as *M. crabilli*, based on a large sample of fine skulls and jaws of comparable geologic age and morphologically similar to, *M. calaminthus*. The specific separation of these two species was based on the fact that the type localities are widely separated, and on the fact that Schultz and Falkenbach (1947, p. 190) interpreted the California material as incomplete and immature.

Merychus "crabilli" is so similar to *M. calaminthus* in structure (Fig. 10, C-b, and 10, C-c), that it probably represents a northern High Plains population of that species (Stevens, in Woodburne et al., 1974, p. 19). *Merychus calaminthus* has been reported also from the Orocopia Mountain area of Riverside County, California (Woodburne and Whistler, 1973, p. 908), as well as from the lower part of the Hector Formation of San Bernardino County, California (Stevens, in Woodburne et al., 1974, p. 18).

The specimen that Schultz and Falkenbach (1968) reported as *Merychys* "crabilli ziaensis" from New Mexico probably is an old individual of *M. calaminthus*. It is thus apparent that *M. calaminthus* was widespread during the later Arikareean, and that populations extended from southern California eastward through New Mexico at least to west Texas, then northward to the northern High Plains.

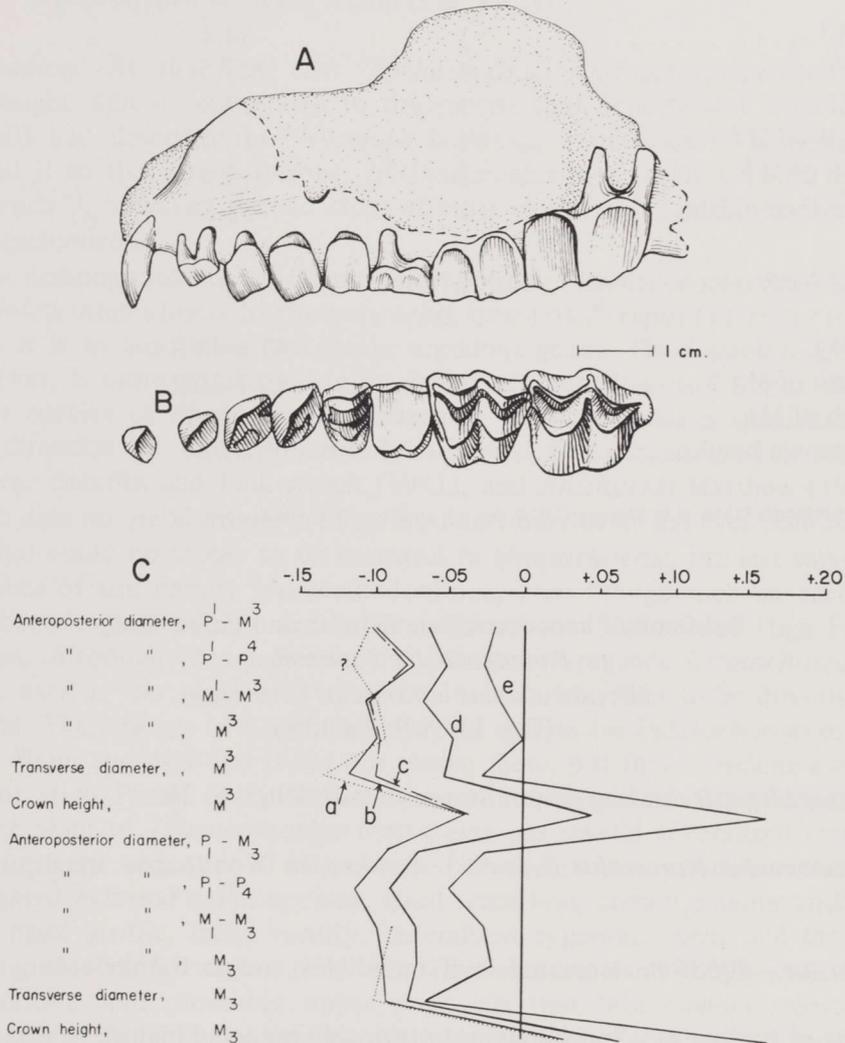


Fig. 10.—*Merychys*, cf. *M. calaminthus*, 41464-1. (A) lateral view of palate; (B) occlusal view of canine to M³. X 1. (C) ratio diagram, constructed in the manner devised by Simpson (1941), comparing 41464-1 (a) with other species of *Merychys*; (b) *M. "crabilli"* from the late Arikareean (based on means); (c) *M. calaminthus* from the late Arikareean, LACM (CIT) 1383, cotype; (d) *M. minimus* from the early Hemingfordian (based on means); (e) *M. elegans*, type species from the middle Hemingfordian (based on means). The standard species (vertical line) is *Paramerychys harrisonensis* (based on means).

TABLE 7

Measurements¹ of *Merychys*, cf. *M. calaminthus*
from the Delaho Formation

Upper teeth	N	OR	\bar{X}
P1-M ³	1	64.4
P1-P ⁴	1	?27.5
M1-M ³	1	37.8
Length of M ³	1	16.9
Width of M ³	1	12.0
M ³ , crown height	1	12.5 ^a
<i>Lower teeth</i>			
M ₁ -M ₃	3	41.6-43.8	42.9
Length of M ₃	3	19.7-20.2	20.0
Width of M ₃	3	9.1-9.6	9.3
M ₃ , crown height	1	12.7 ^a

¹Measurements taken as in Stevens (1970, fig. 3), and fig. 10, C, this paper.

Subfamily Phenacocoelinae Schultz and Falkenbach

Phenacocoelus Peterson

?*Phenacocoelus leptoscelos* (Stevens)

(Fig. 11, A-B; Table 8)

Hypslops leptoscelos Stevens, in Stevens et al., 1969, p. 26.

Phenacocoelus leptoscelos (Stevens), Stevens, in Woodburne et al., 1974, p. 10.

Holotype.—40635-8, associated skull, mandibles, and partial skeleton.

Referred specimens.—Specimens not previously reported include 40635-130, a slightly skewed skull with its dentition; 41461-1, a partial fractured skull and associated jaws; 40715-6, a crushed skull with a good dentition; 40620-37, a well-preserved mandible with teeth; and 41462-7, both mandibles of a sub-adult individual with teeth; and many other maxilla and mandibular fragments with teeth, as well as postcranial material.

Description.—The teeth of ?*Phenacocoelus leptoscelos* will not be discussed here as they have already been described in detail (Stevens, in Stevens et al.,

1969). Additional cranial material, however, adds to our knowledge of the skull morphology of this oreodont.

The skull of *?Phenacocoelus leptoscelos* is of medium size, has a well inflated and dorsally arched cranium, a concave nasal profile, an elongated external narial opening, a relatively shortened nasal bone, a moderately deep pre-orbital fossa with a vacuity, inflated but semi-depressed auditory bullae, and a sub-fanshaped occipital region (Fig. 11, A).

Discussion.—At the time that *?Phenacocoelus leptoscelos* was described, I thought that it was related to the species that Schultz and Falkenbach (1950) had described as "*Hypsiops luskensis*," and because of this I referred it to the genus *Hyslops*. *?Phenacocoelus leptoscelos* (as well as "*H. luskensis*"), however, has no close affinity to the type species of *Hyslops*, *H. brachymelis*.

As demonstrated by its cranial morphology, *?Phenacocoelus leptoscelos* is related more closely to *Phenacocoelus*, based on *P. typus* Peterson (1907), than it is to any other Arikareean oreodont genus. The Castolon species, however, is more specialized in its dental structure than is *P. typus* or any other species of *Phenacocoelus*. Dentally, *?P. leptoscelos* is specialized in the direction of *Ustatochoerus* Schultz and Falkenbach (1941), *Mediochoerus* Schultz and Falkenbach (1941), and *Brachycrus* Matthew (1901).

To date no oreodont older than very latest Barstovian has ever been reported that could be shown to be ancestral to *Ustatochoerus*, the last surviving member of the Family Merycoidodontidae, even though such an ancestor has been eagerly sought among Hemingfordian or Arikareean High Plains faunas. Although *Mediochoerus* and *Brachycrus* precede *Ustatochoerus* in time, each is too specialized along its characteristic lines to be directly ancestral. The absence of a suitable ancestral species for *Ustatochoerus* on the High Plains suggests that it did not evolve there, but that it became a member of High Plains Clarendonian faunas by immigration from elsewhere.

The skull of *?Phenacocoelus leptoscelos* has several generalized features that are very suggestive of *Ustatochoerus*. These features include its relatively elongated external narial opening, nasal retraction, arched cranium and concave nasal profile, facial vacuity, generalized zygomatic arch, and the sub-fanshaped occipital region (Fig. 11). Furthermore, the strongly molarized, hypsodont, and rhomboid upper premolars that bear cingula, constitute the same type of dental specializations one would expect to find in an ancestor of *Ustatochoerus* (Fig. 11, B-a, -b, -c).

The ratio diagram (Fig. 11, B) demonstrates that there is a regular trend, from the ustatochoerid *?Phenacocoelus leptoscelos* to *Ustatochoerus*, toward size increase, in the attenuation of the third molars associated with a decrease in relative width, an increase in hypsodonty, and in the increased relative width of the skull, a decrease in the relative length of the nasal bones, and an increase in the relative length of the external narial opening. Other morphological modifications include the broadening of the occipital

fan, and the flattening of the auditory bullae.

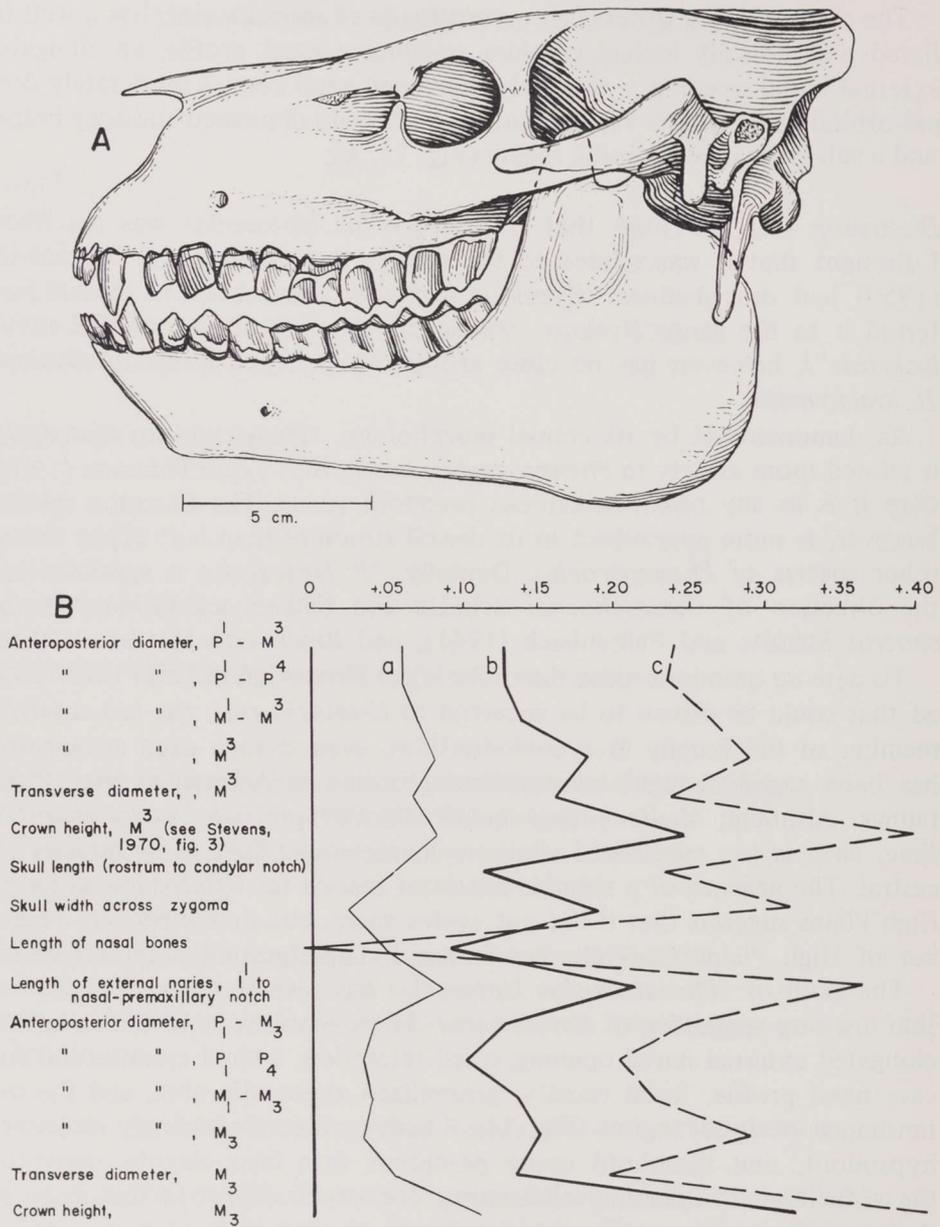


Fig. 11.—*Phenacocoelus leptoscelos* (Stevens). (A) skull based on holotype, 40635-8, but drawn to compensate for slight distortion; 40635-6, -26, and -130 were used as controls and to provide missing parts. X ½. (B) ratio diagram comparing ?*Phenacocoelus leptoscelos* (a), (based on means), with *Ustatochoerus*; (b) *U. medius* from the earliest Clarendonian, the oldest reported *Ustatochoerus* (based on means); (c) *U. major*, an advanced species from the middle Clarendonian (based on means). All measurements taken as in Table 8.

No other oreodont so far reported conforms so closely in morphology and proportions to the type of oreodont one would expect for an ancestor of *Ustatochoerus*, as does *?Phenacocoelus leptoscelos* of the later Arikarean of west Texas. Because of this resemblance, the Castolon species is interpreted to be a transitional form between *Phenacocoelus* and *Ustatochoerus*. A similar, but slightly larger oreodont, *Phenacocoelus*, cf. *P. leptoscelos*, has been reported from the early Hemingfordian Logan Mine local fauna of southern California by Stevens (*in Woodburne et al.*, 1974). This indicates that the early evolution of ustatochoerids was in the Southwest and adjacent Mexico.

TABLE 8

Measurements¹ of the total sample of *?Phenacocoelus leptoscelos* Stevens

Skull	N	OR	\bar{X}	s	CV	Holotype
Skull length, I ¹ to notch in condyles	2	178.2-192.5	185.4
Skull width, max. across zygoma	3	96.0-121.4	105.5	99.0
Depth of malar	7	15.1-19.4	16.9±1.61	1.74	10.38	17.9
Nasal length, max.	5	60.8-77.4	66.0±8.12	6.54	9.91	65.0
Length of external narial opening, alveolus of I ¹ to naso-premaxillary notch.	3	44.9-50.4	47.8
Postorbital constriction.	3	38.7-44.5	41.4	38.7
<i>Upper teeth</i>						
P1-M ³	6	86.7-104.2	92.8±6.78	6.46	7.00	91.3
P1-P4.	6	38.0-45.7	40.5±2.85	2.71	6.70	40.1
M ¹ -M ³	9	51.2-63.7	55.4±2.87	3.74	6.75	54.7
Length of M ³	12	23.0-30.7	25.0±1.46	2.30	9.21	23.3
Width of M ³	12	18.0-21.0	19.3±0.60	0.94	4.84	18.1
Height of M ³	6	15.7-17.4	16.3±0.68	0.65	3.98	15.9
<i>Lower teeth</i>						
P1-M ₃	8	87.9-109.1	95.9±5.44	6.51	6.78	98.2
P1-P4.	9	36.6-45.0	39.7±1.90	2.47	6.22	41.6
M ₁ -M ₃	10	52.0-63.7	57.3±2.50	3.49	6.10	57.9
Length of M ₃	11	23.8-29.5	26.7±1.29	1.92	7.20	27.3
Width of M ₃	12	11.2-14.1	13.2±0.53	0.87	6.35	12.7
Height of M ₃	5	12.9-18.3	16.3±2.61	2.10	12.94	17.7

¹Measurements of teeth taken as in Stevens (1970, fig. 3), and as in fig. 11, B, except as indicated, this paper.

Family Camelidae Gray
Subfamily Aepycamelinae Webb
Priscocamelus Stevens
Priscocamelus wilsoni Stevens
(Figs. 12-14, Table 9)

Priscocamelus wilsoni Stevens, in Stevens et al., 1969, p. 30.

Referred specimens.—Specimens collected after the original description of this species include 40918-47, a skull and jaw associated with a partial skeleton; 40879-8, associated, articulated front and hind limbs; and 41460-1, an almost complete palate with incisors to third molars.

Description.—The skull and jaw of *Priscocamelus wilsoni* is similar to that of *Oxydactylus campestris* Cook, except that it is approximately 20% smaller, and has a relatively shorter and steeper rostrum. Its dentition is unreduced. No I¹ has been recovered, but an alveolus for an obviously large I¹ is preserved in 40918-47. The second incisor is also large and has a broadened crown. This tooth is undamaged in 41460-1. The third incisor is larger than I², and is caniniform. A very short diastema separates I³ from I². The upper canine differs in size in the two specimens, but in both it is caniniform and slightly smaller than I³. A short diastema separates the canine from I³.

The first premolar is a small, double-rooted tooth of variable size in the three specimens that have it preserved. A very short diastema separates P¹ from the canine (Table 9). Behind P¹ is another short diastema, about the length of P². The C-P¹, and the P¹-P² diastemas of *Priscocamelus wilsoni* are shorter than those of any other oxydactyline camel (Fig. 14, D). The second and third premolars are trenchant, relatively long and narrow, and have more or less uninterrupted internal cingula. The brachydont upper molars of *P. wilsoni* are slightly longer anteroposteriorly than they are wide, and have very prominent styles and ribs.

The skull of *Priscocamelus wilsoni* has a very narrow, but short rostrum (Fig. 12, A, D). The margin of the external nares (Fig. 12, A) is much steeper than in *Oxydactylus campestris*. The nasal profile is practically straight, but the cranium, although incompletely preserved, is slightly arched. A shallow facial fossa occurs on the side of the face anterior to the orbit. This depression is similar to that found in *O. campestris*. The palate is invaded as far anteriorly as the middle of M² by a strongly V-shaped internal narial opening. Although the auditory bullae are poorly preserved, they are relatively large.

The lower cheek teeth of *Priscocamelus wilsoni* have been described elsewhere (M. Stevens, in Stevens et al., 1969), but the following observations about the anterior teeth and the mandible will be made here. The lower incisors are large and procumbent, especially I₃ (Fig. 12, B). The canine is

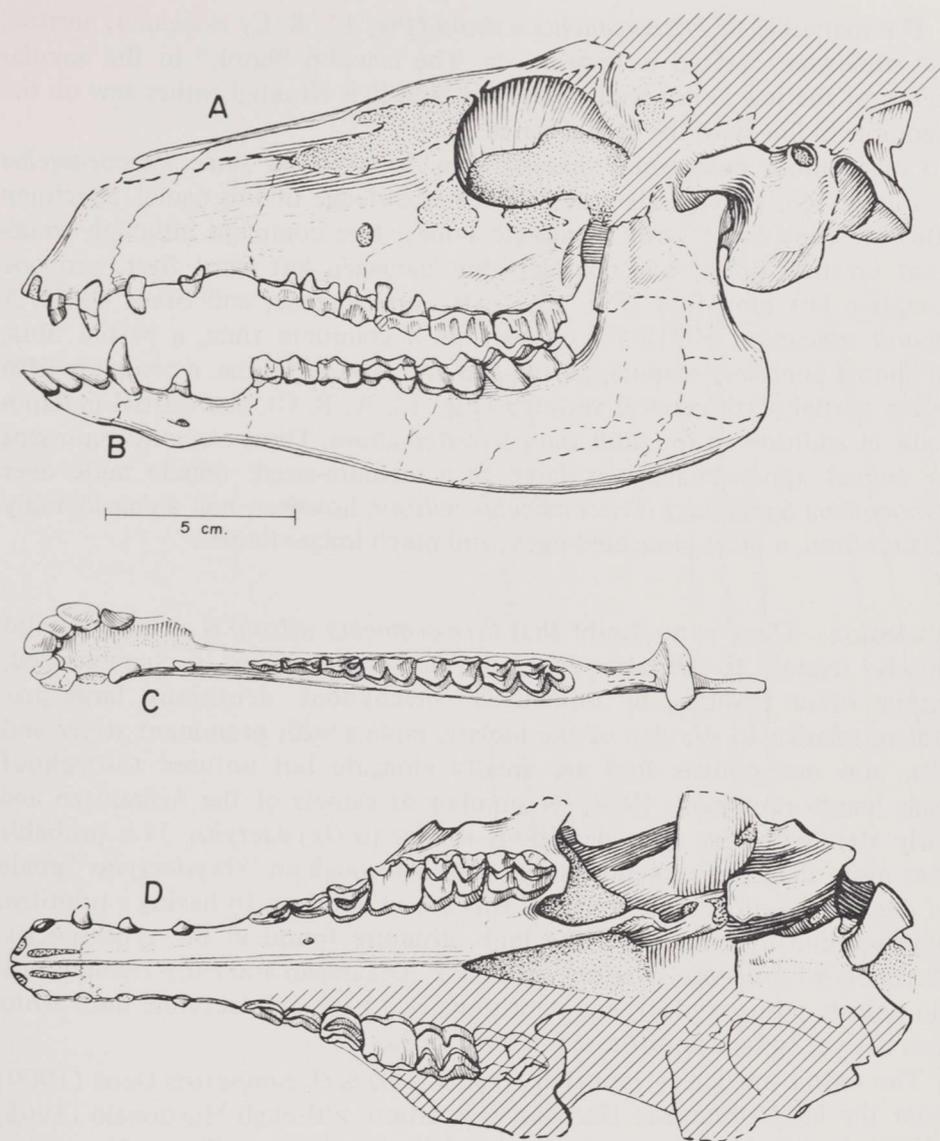


Fig. 12.—*Priscocamelus wilsoni*, 40918-47. (A) lateral view of skull; (B) lateral view of associated mandible; (C) occlusal view of mandible; (D) ventral view of skull (right side restored to eliminate crushing). All X ½.

directly posterior to I₃ with no diastema, and these vary in size although they are always large and caniniform. The C-P₁ diastema is variable in length, but it is not known to exceed the anteroposterior alveolar diameter of P₁. The first premolar is small and double-rooted. The P₁-P₂ diastema is the most variable diastema in *Priscocamelus wilsoni*. The diastemas in both jaws are the shortest known for an oxydactyline camel, and are reminiscent of the condition in Oligocene *Poebrotherium* (Fig. 14, D-a, b).

The mandible of *Priscocamelus wilsoni* (Fig. 12, B, C) is slender, narrow, and somewhat cervoid in appearance. The camelid "hook" in the angular region of the jaw is not well developed, and it is situated rather low on the mandible in line with the dental series.

Considerable postcranial material has been found since *Priscocamelus* was described, which adds much to our knowledge of this camel. Specimen 40879-8 consists of both inornate bones, two complete although somewhat crushed tibiae, one complete but damaged left front foot, and one complete left hind foot (Fig. 13, A, B), one scapula, and other bones. A second specimen, 40918-47, consists of a complete tibia, a partial tibia, an almost complete scapula, partial axis and atlas vertebrae, a complete fifth and a partial sixth cervical vertebra (Fig. 14, A, B, C), and partial metapodials, in addition to the skull and jaw noted above. These elements represent an animal approximately as large as a medium-sized, female mule deer (*Odocoileus hemionus*). *Priscocamelus wilsoni*, however, had a considerably smaller head, a more elongated neck, and much longer limbs.

Discussion.—There is no doubt that *Priscocamelus wilsoni* is an aepycamelid closely related to *Oxydactylus* Peterson. *Oxydactylus* is characterized, among other features, by unreduced, brachydont dentitions, large premolars relative to the size of the molars, molars with prominent styles and ribs, and metapodials that are greatly elongate but unfused throughout their length (Peterson, 1904). A number of camels of the Arikareean and early Hemingfordian have dentitions similar to *Oxydactylus*. It is probable that more than one camelid lineage passed through an "*Oxydactylus*" grade of dental evolution. *Priscocamelus wilsoni*, in addition to having a primitive oxydactyline dentition, has the limb structure found in the type species, *Oxydactylus longipes*. Whether other late Arikareean and early Hemingfordian camels with oxydactyline dentitions also have oxydactyline limb structure has yet to be demonstrated in most cases.

The oldest previously reported *Oxydactylus* is *O. campestris* Cook (1909) from the late Arikareean Harrison Formation, although Macdonald (1963, 1970) identified specimens from the earliest Arikareean Sharps Formation as *Oxydactylus* cf. *wyomingensis*. *Oxydactylus wyomingensis* (Loomis) is based on a very immature individual that probably came from the Harrison Formation in southeastern Wyoming. The type specimen of *O. wyomingensis* is advanced as demonstrated by its very elongate cervical vertebrae, which are longer than those of *Priscocamelus*, the length of its limbs, which, in spite of the individual's youth, are longer than those in *Priscocamelus*, and by the attenuation of its first and second molars. One would not expect to find these characteristics in a camel of earliest Arikareean age. "*Oxydactylus wyomingensis*" is probably a juvenile of *O. campestris*.

Priscocamelus wilsoni is related closely to *Oxydactylus campestris* but is smaller and more generalized in its rostral morphology. I originally thought

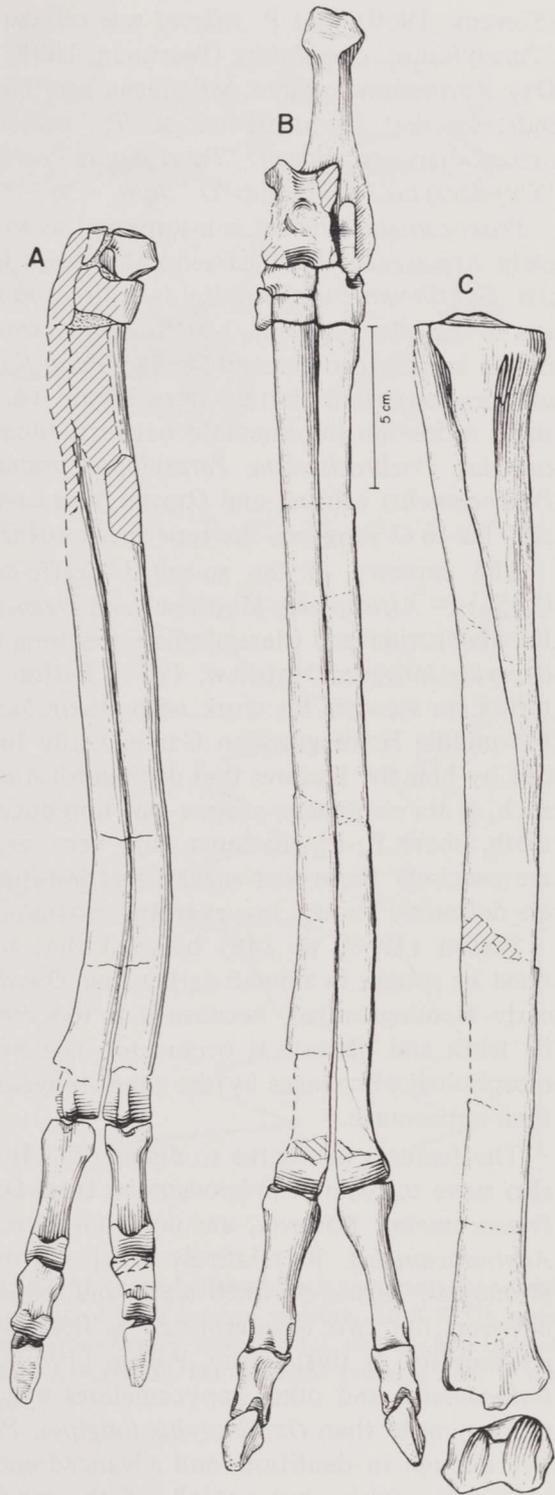


Fig. 13.—*Priscocamelus wilsoni*. (A) posterior view of left carpus-metacarpus and associated phalanges, 40879-8; (B) anterior view of left tarsus-metatarsus and its associated phalanges, 40879-8; (C) anterior and distal views of right tibia, 40918-47. All X ½.

(Stevens, 1969) that *P. wilsoni* was related closely to the *Oxydactylus*-like "*Paratylopus*" *cameloides* (Wortman, 1898) from the upper part of the John Day Formation, of late Arikareean age, but the new material of *P. wilsoni* indicates that the dentition of "*P.*" *cameloides* is more advanced but its metapodials are shorter. "*Paratylopus*" *cameloides* appears to be related to "*Oxydactylus*" *exilis* and "*O.*" *lulli*.

Priscocamelus wilsoni is interpreted as an intermediate taxon between the early Arikareean *Gentilicamelus sternbergi* (Cope) and *Oxydactylus campestris*. *Gentilicamelus sternbergi* is a direct descendant of *Paratylopus primaevus* of the late Oligocene, which, in turn, can be derived from *Poebrotherium* of the late Chadronian and Orellan. *Paratylopus primaevus* and *Gentilicamelus sternbergi* were omitted from Figure 14, D for the sake of simplicity, but their ratios are intermediate between those of *Poebrotherium* and *Priscocamelus*. *Poebrotherium*, *Paratylopus primaevus*, *Gentilicamelus sternbergi*, *Priscocamelus wilsoni*, and *Oxydactylus campestris* form a lineage that probably led to *O. longipes*, the type species of *Oxydactylus* (Fig. 14, D).

The ancestry of the so-called giraffe-camels, *Aepycamelus* Macdonald (1956) (= *Alticamelus* Matthew) and *Hesperocamelus* Macdonald (1949), of the Barstovian and Clarendonian, has long been thought to lie within *Oxydactylus longipes* (Matthew, 1901). Patton (1969) questioned this interpretation, in view of his work with *Australocamelus orarius*, a camelid from the middle Hemingfordian Garvin Gully local fauna of Texas. As pointed out by him the features that distinguish *Australocamelus* from *Oxydactylus*, such as its extremely narrow but unreduced premolars, very narrow cheek teeth, short P₁-P₂ diastema, and very slender, almost cervoid, mandible are precisely those that suggest relationship to the giraffe-camels. No limbs are definitely known, however, for *Australocamelus*.

Patton (1969, p. 148) believed that the ancestry of *Australocamelus* must be sought in animals earlier than *Oxydactylus longipes*, a species of the early Hemingfordian, because it is too conservative in the proportions of its teeth and because it occurs too late in time to accomplish the needed morphological changes by the time *Aepycamelus* and *Hesperocamelus* make their appearance.

The features that serve to distinguish *Australocamelus* from *Oxydactylus* also serve to separate *Priscocamelus* from *Oxydactylus*. *Australocamelus* and *Priscocamelus*, however, are not congeneric, because of the greater size of *Australocamelus*, its relatively much narrower and more anteroposteriorly attenuated, higher crowned teeth, and reduced styles and ribs. The similarity between the two is interpreted as the result of their ancestor-descendant relationship. If this is true, Patton (1969) is correct in his view that *Australocamelus* and other aepycamelines had their origin in an oxydactyline more remote than *Oxydactylus longipes*. *Priscocamelus wilsoni* is conservative enough in dentition, and advanced enough in foot structure, to be ancestral to certain, but not all, of the species currently placed within *Oxydactylus*. It is also a suitable ancestor for the later giraffe-like camels.

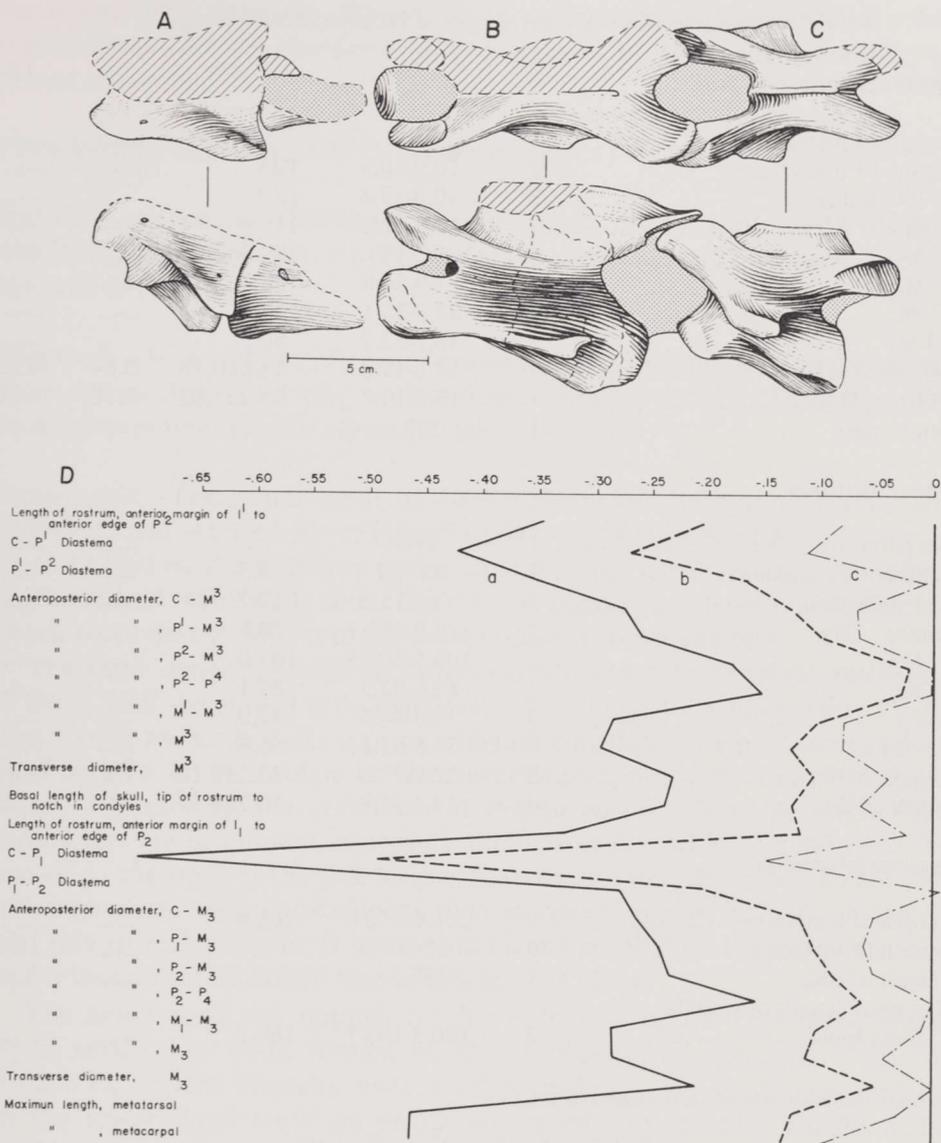


Fig. 14.—*Priscocamelus wilsoni*, 40918-47. (A) partial atlas and axis vertebrae; (B) partial presumed fifth cervical vertebra; (C) presumed sixth cervical vertebra. All X ½. (D) ratio diagram comparing *P. wilsoni* (b) with *Poebrotherium labiatum* (a), and the holotype of *Oxydactylus campestris* (c), of the late Arikareean. The standard (vertical line) is the type species of *Oxydactylus*, *O. longipes*.

TABLE 9

Measurements¹ of total sample of *Priscocamelus wilsoni*

<i>Upper dentition and skull</i>	N	OR	X**	s	CV
Length of rostrum	1	60.0
Canine-P ¹ diastema	2	10.2-10.5	10.4
P ¹ -P ² diastema	3	10.8-13.5	12.1
Canine - M ³	2	116.8-116.9	116.9
P ¹ -M ³	2	101.2-103.3	102.3
P ² -M ³	2	83.9-84.0	84.0
P ² -P ⁴	3	33.3-35.1	34.4
M ¹ -M ³	4	48.2-52.7	50.5
Length of M ³	7	17.2-19.8	18.6±0.78	0.84	4.52
Width of M ³	7	13.5-16.7	15.2±1.03	1.10	7.24
Skull length	1	228.6
<i>Lower dentition</i>					
Length of rostrum	1	54.5
Canine - P ₁ diastema	3	2.6-7.1	4.5
P ₁ -P ₂ diastema	3	7.4-15.2	10.7
Canine - M ₃	2	118.9-122.1	120.5
P ₁ -M ₃	2	106.5-107.5	107.0
P ₂ -M ₃	2	85.8-92.3	89.1
P ₂ -P ₄	3	29.6-34.6	32.0
M ₁ -M ₃	4	51.5-61.8	56.8
Length of M ₃	8	22.0-25.6	23.5±1.14	1.37	5.83
Width of M ₃	14	9.1-11.9	10.3±0.54	0.92	8.93
<i>Postcranial material</i>					
Length of metatarsus	2	262.0-270.0	266.0
Length of metacarpus	1	254.0
Length of tibia	1	332.5
Maximum length of scapula, along spine	2	180.5-198.*	189.2

¹Measurements taken as in fig. 14, D, except as noted.

Subfamily Camelinae Gray
 Tribe Protolabidini Zittel
Michenia Frick and Taylor
 ?*Michenia australis*¹ sp. nov.
 (Fig. 15, A-D; Table 10)

Camelidae, gen. et sp. indet., Stevens, in Stevens et al., 1969, p. 37.

Miotylopus gibbi (Loomis), McKenna and Love, 1972, p. 25-26.¹*australis*, southern, in reference to the southern distribution relative to other protolabines.

Holotype.—40871-1, a left mandible with P₂-M₃, a partial left M¹, the distal end of a humerus, the proximal end and other fragments of a left metacarpus with its unciform, and fragments of the right mandible, all of one individual.

Type locality.—Locality 40871 (see Frontispiece).

Referred specimens.—40693-24, upper cheek tooth series with P³-M³; 40620-20, mandible with P₃-M₃; 41460-3, partial mandible with P₂, broken M₁, and M₂-M₃.

Diagnosis.—Differs from *Michenia agatensis* by its smaller size, more prominent molar styles and ribs, and unfused metacarpal; from *Miotylopus* by its more prominent molar styles and ribs.

Description.—The upper teeth of 40693-24 are of appropriate size for the holotypic and referred lower jaws. The M¹, originally called M³ in Stevens et al. (1969) of the holotype is the same size and has the same morphology as the M¹ of 40693-24; thus, there is no reason to believe that the upper cheek teeth do not belong to the same species as the mandibles.

The third upper premolar of *?Michenia australis* is broad transversely, and it has a well developed although interrupted lingual cingulum (Fig. 15, A). The fourth premolar lacks a posterolingual cingulum. The protocones (damaged on M¹) of the molars are narrower anteroposteriorly than the hypocones, contrary to the condition in *Priscocamelus*. Molar parastyles and mesostyles are prominent, especially the mesostyles, which extend from the crown to the base of the enamel. Vertical ribs are well developed on M¹-M³, although these are less prominent than in *Priscocamelus*. The rib on the labial side of the paracone is more prominent than that on the metacone. The upper molars are described best as brachy-mesodont.

The lower teeth are notable for the reduction of the premolars, where P₂ is small. The basin formed by the entoconid and entostylid crests of P₃ and P₄, opens lingually instead of posteriorly, and the lingual margins of the lower cheek teeth are practically smooth, except that a slight metastylid is developed on the molars in a few individuals. A similar condition is found in *Michenia agatensis*, where the molar stylids are much reduced in contrast to the well developed molar styles in associated upper teeth (Frick and Taylor, 1971, p. 15).

The metapodials of *?Michenia australis* are known only from a few fragments of the left metacarpus, 40871-1. Only the proximal end of this metacarpus is preserved (Fig. 15, C), but it serves to demonstrate that the metapodial is unfused throughout its length. The fragments associated with this specimen indicate that the metapodial is delicate and slender.

Discussion.—*Miotylopus* Schlaikjer (1935), as characterized by its type

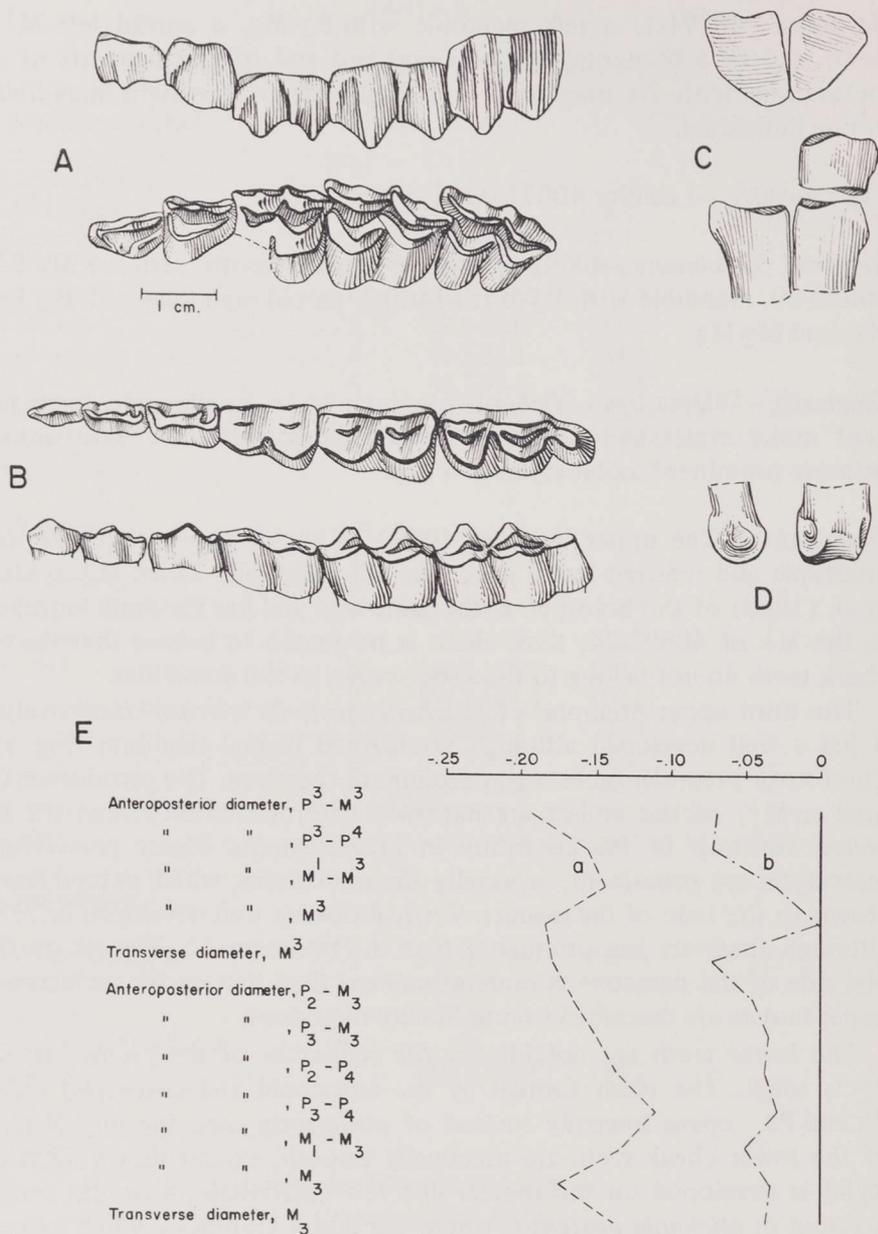


Fig. 15.—?*Michenia australis* sp. nov. (A) labial and occlusal view of upper cheek teeth, 40693-24; (B) occlusal and labial views of lower cheek teeth, holotype, 40891-1 (M₁ and M₂ partially restored from 40620-20); (C) anterior view of the proximal articular surface of left metacarpus, holotype, and anterior view of proximal end of left metacarpus with its unciform, holotype; (D) lateral and anterior view of presumed first phalange, holotype. All X 1. (E) ratio diagram comparing ?*Michenia australis* (a) with *M. agatensis* (b), from the early Hemingfordian (measurements from Frick and Taylor, 1971). The standard is *Oxydactylus longipes*.

species, *M. bathygnathus*, includes small Arikareean camelids that have reduced or absent molar style(ids) and ribs. The teeth of specimens 40871-1, 40620-20, and 41460-3, do not differ substantially from lower teeth of *Miotylopus gibbi* (Loomis), which prompted McKenna and Love (1972) to identify these specimens as this species. It is now known that this Delaho camelid cannot be referred to *M. gibbi* on the basis of the morphology of the upper teeth, because those of *Miotylopus* lack almost completely styles and ribs, and the Delaho form has these well developed. That lower teeth without stylids can belong to the same species as upper teeth which have well developed styles is demonstrated by the upper and lower teeth of the holotypic specimen of *?Michenia australis*. A similar condition is found in *M. agatensis*.

It is thus apparent that there are in the middle and later Arikareean two small camelid taxa that cannot be differentiated on lower teeth alone. Specimen 40871-1 is chosen as the holotype of the Delaho species, because it is the only specimen that has upper and lower teeth and at least part of a metapodial associated.

I believe this Delaho camelid is a small and primitive protolabine, possibly related to *Michenia* Frick and Taylor (1971). *Michenia* is based on *M. agatensis*, from the "Upper Harrison beds" of Peterson (1907), early Hemingfordian, Sioux County, Nebraska. This species also has been reported from the early Hemingfordian Logan Mine local fauna, Hector Formation, of southern California (Taylor, in Woodburne et al., 1974). *?Michenia australis* differs from *M. agatensis* only in smaller size, slightly more prominent molar styles and ribs, and unfused metacarpus.

Frick and Taylor (1971) envisioned *Dyseotylopus migrans* Stock (1935) from the upper part of the Sespe Formation as a possible ancestor for *Michenia agatensis*. Further study of the type of *Dyseotylopus migrans* by Taylor indicates to him that it has no affinity to *Michenia* (Taylor, personal communication, November, 1976).

?Michenia australis is a much better ancestor for *Michenia agatensis* than any other reported camelid. Whether or not such an ancestor-descendant relationship existed depends on knowledge of when metapodial fusion occurred and how consistent it was within populations of early protolabines. The ancestry of *?M. australis* of the later Arikareean in turn, may lie within "*Paratylopus*" *matthewi* (Lull) of the late Whitneyan, as this species appears to initiate a camelid lineage which decreases the size of the premolars, and reduces molar styles and ribs. "*Paratylopus*" *matthewi* differs from *?M. australis* only in its relatively wider and more brachydont molars.

A lower jaw fragment not referable to any described Arikareean genus was recovered from the lower part of the Delaho Formation. This jaw fragment represents an animal closely related to the artiodactyl from the Zoyatal local fauna of Mexico, that Dalquest and Mooser (1974) described as "*Miotylopus*" *wilsoni*. Because this species is not a miotylopine but a primitive floridatragulid, I have designated "*M.*" *wilsoni* the type species of a new genus.

TABLE 10

Measurements ¹ of total sample of *Michenia australis* sp. nov.

<i>Upper teeth</i>	N	OR	X	Holotype
P3-M ³	1	62.8
P3-P4	1	20.2
M1-M ³	1	45.4
Length of M ³	1	16.4
Width of M ³	1	13.6
<i>Lower teeth</i>				
P2-M ₃	1	78.7	
P3-M ₃	2	69.7-70.0	69.9	
P2-P4	1	27.4	27.4
P3-P4	2	20.0-20.5	20.3	20.0
M1-M ₃	2	44.0-50.3	47.2	44.0
Length of M ₃	3	17.7-20.9	20.3	20.3
Width of M ₃	2	9.4-9.7	9.6	9.4

¹Measurements taken as in fig. 15, E.

Subfamily Floridatragulinae Maglio
*Aguascalientia*¹ gen. nov.

Aguascalientia.—The characteristics of the genus are those of its type species, *A. wilsoni* (Dalquest and Mooser), a floridatragulid that differs from *Floridatragulus* White in its slightly shorter mandibular diastemas, the lack of a diastema between P₂ and P₃, and smaller size.

Aguascalientia wilsoni (Dalquest and Mooser)
(Fig. 16, A-E; Table 11)

Myotylopus wilsoni Dalquest and Mooser, 1974, p. 6.

Holotype.—41536-26 (see footnote 2), both mandibles with teeth, from the Zoyatal local faunule.

¹*Aguascalientia*, derived from the city of Aguascalientes, Mexico, the locality of its type species.
²Specimens of the Zoyatal local faunule were originally catalogued as part of the fossil collection of Midwestern University, MU, Wichita Falls, Texas; now curated in the Texas Memorial Museum collections.

Referred specimens.—41536-41, partial lower jaw with RP₂-RM₁; -30, isolated RM₂; -19, isolated LM₃; and a tentatively referred left tarsus, specimen -16.

Type locality.—Locality 41536. Miocene deposits in a quarry in the city of Aguascalientes, Mexico.

Description.—Dalquest and Mooser (1974) compared this camelid in detail only to *Miotylopus* and *Poebrotherium*, presumably because these are camels of suitably small size, although these authors note that the Mexican form differs substantially from these by its “very short premolars.” Dalquest and Mooser (1974) also referred several deciduous upper teeth to “*Miotylopus wilsoni*.” Restudy of these upper teeth indicates that they belong to an animal much too large to be “*M.*” *wilsoni*, because they are larger than deciduous upper teeth of *Priscocamelus*, a much larger camel. A search through the Aguascalientes collection failed to turn up any upper teeth that could be referred to *Aguascalientia*.

The holotype of *Aguascalientia wilsoni* has a large caniniform true canine. That this tooth is the canine and not a caniniform P₁ (characteristic of protoceratids) is demonstrated by the fact that a very small, single-rooted P₁ is present in the left mandible, 13 mm. behind the true canine, and the broken root of the RP₁ is preserved in its alveolus in the other jaw. Dalquest and Mooser (1974) state that no P₁ or its alveolus is present in the holotype.

A diastema approximating the length of M₁ extends from the canine to P₁ of *Aguascalientia wilsoni*. The corresponding distance in *Floridatragulus barbouri* equals the combined length of P₃-M₁. A second diastema from P₁-P₂ approximates the length of M₁-M₂; in *Floridatragulus* this distance equals the length of M₂-M₃. Nevertheless, the diastemas in *Aguascalientia* are exceptionally long relative to the size of the mandible and indicate that the animal had a very elongated rostrum.

The P₂ of *Aguascalientia wilsoni*, 41536-26 and -14, is slightly shorter anteroposteriorly than P₃, whereas in *Floridatragulus* it is equal to or slightly longer than P₃, and it has a very prominent parastyloid. The P₃ is similar to P₂ but larger and more bulbous, and its prominent parastyloid is inflected medially (Fig. 16, A, E). Contrary to the condition in typical camelids, P₄ of *A. wilsoni* is shorter anteroposteriorly than P₃, and bulbous.

The lower molars of *Aguascalientia wilsoni* are brachydont, and their anterior and posterior fossettes are not deep. Like the premolars, the molars are bulbous, and are oromerycid-like. The molars have a distinct metaconid that is well separated from the rest of the tooth, thus the metaconid crest remains separated from the other crests until the tooth is well worn. Intercolumnar tubercles are well developed on M₁ and M₂, and a tubercle is represented faintly on M₃.

The hypoconulid of M₃ of *Aguascalientia* is divided by two ridges. The major ridge is a continuation posteriorly of the hypoconid. The second

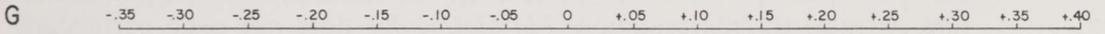
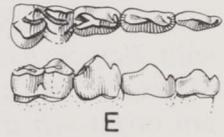
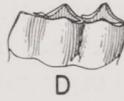
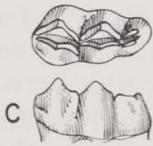
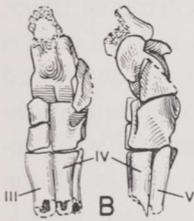
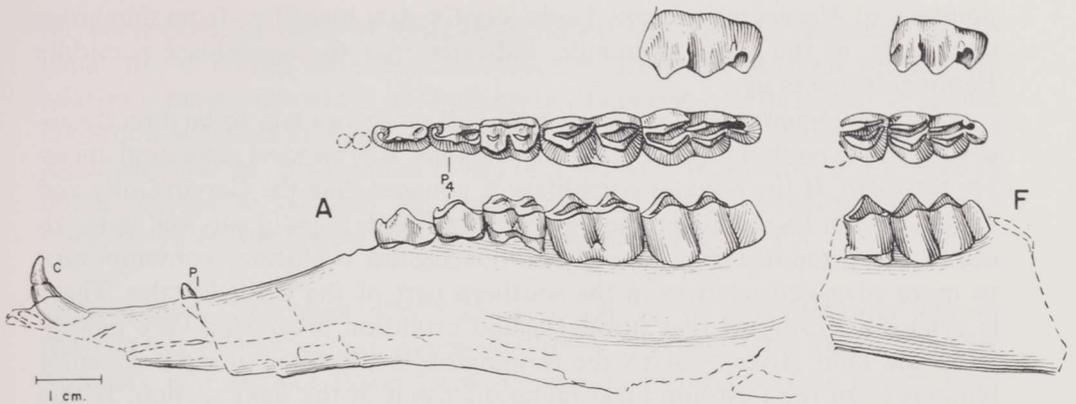
ridge, located lower down on the tooth, arises as a continuation of the entoconid, and it supports a distinct cuspule, like the cuspule found in the holotype of *Floridatragulus nanus* (Patton, 1969). The hypoconulid of a second individual of *A. wilsoni* (41536-19) has the second ridge more prominently developed and it contributes to the grinding surface of this little-worn tooth (Fig. 16, C). The hypoconulid morphology of *Aguascalientia* is similar to that of *Floridatragulus*, but it is also like the condition in synthetoceratines.

An incomplete tarsus has been referred tentatively to *Aguascalientia*, on the basis of its small size, and the fact that it is the tarsus of an artiodactyl, and cannot belong to an oreodont. The specimen, 41536-16, consists of the astragalus, partial calcaneum, cuboid, navicular, entocuneiform, and the proximal ends of the metatarsals III, IV, and V. The tarsus is tylopod in morphology, with metatarsals III and IV strongly developed. The most notable feature of this tarsus is that it retains a fairly large metatarsal V (Fig. 16, B); a lateral digit that is lost early in true camels, but which is present in oromerycids as well as in protoceratids. This tarsus indicates further that *Aguascalientia* is not related closely to true camels.

Discussion.—The species described by Dalquest and Mooser (1974) as “*Miotylopus*” *wilsoni*, cannot be referred to *Miotylopus* Schlaikjer on the basis of its greatly attenuated rostrum, its bulbous and foreshortened premolars, which leave P₄ the shortest of the series. Moreover, its bulbous molars have shallow fossettes with traces of intercolumnar tubercles. At first glance, the Mexican camelid appears protoceratid, but it differs from these in a number of details, including its caniniform and not incisiform true canine. *Aguascalientia* shows more similarity to *Floridatragulus* than to anything else yet described (Fig. 16, G-a).

Aguascalientia wilsoni is less specialized than *Floridatragulus*. To date, *Floridatragulus* has been reported from the middle Hemingfordian Thomas Farm local fauna, and from the succession of Hemingfordian to Barstovian faunas from the Texas Coastal Plain, reported by Patton (1969). Dalquest and Mooser (1974) suggested a Barstovian age for the Zoyatal local faunule based on interpretation of several taxa, most of which are known from very fragmentary material where size was the only criterion. In my opinion, the

Fig. 16.—*Aguascalientia wilsoni* (Dalquest and Mooser) gen. nov., from the Zoyatal local fauna, Aguascalientes, Mexico. (A) labial view of mandible, 41536-26, holotype, with canine, P₁, and P₃-M₃ (P₃ reversed); (B) anterior and inner view of left tarsus to show metatarsal V; (C) lingual and occlusal views of M₃, 41536-19; (D) labial view of same specimen; (E) labial and occlusal views of P₂-M₁, 41536-14; (F) *Aguascalientia* sp. 40693-25, from the lower part of the Delaho Formation. All X 1. (G) ratio diagram to compare various features of *Aguascalientia wilsoni* (a) with the holotype of *Floridatragulus barbouri* (b) from the lower part of the Thomas Farm quarry; the holotype of *F. dolichanthereus* (c) from the upper part of the Thomas Farm quarry; and 40693-25, (d) identified as *Aguascalientia* sp. The standard is *Oxydactylus longipes*.



Anteroposterior diameter, C - M₃
 " " , P₁ - M₃
 " " , P₂ - M₃
 " " , P₃ - M₃

Diastema, C - P₁
 " , P₁ - P₂

Diameter between P₁ and P₃

Anteroposterior diameter, P₃ - P₄

" " , P₂

Transverse " , P₂

Anteroposterior " , P₃

Transverse " , P₃

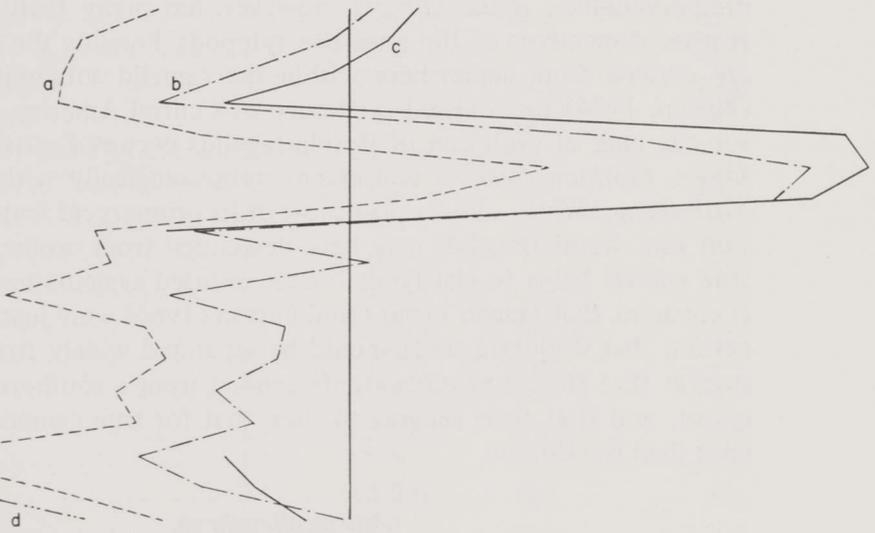
Anteroposterior " , P₄

Transverse " , P₄

Anteroposterior " , M₁ - M₃

" " , M₃

Transverse " , M₃



presence of *Merychys elegans* Leidy, confidently identified from numerous dentitions, in the Zoyatal faunule, indicates that the assemblage is middle Hemingfordian in age.

Although *Aguascalientia wilsoni* may still occur too late to be directly ancestral to the earliest species of *Floridatragulus*, it is an ideal structural ancestor for them. If the Zoyatal assemblage is younger than the Garvin Gully and Thomas Farm local faunas, then a primitive floridatragulid survived in Mexico, in the presumed area of early floridatragulid evolution, contemporary to more advanced relatives in the southern part of the United States. There is evidence to suggest that floridatragulid evolution progressed very rapidly from the later Arikareean to the Hemingfordian, in view of *Aguascalientia* remains from the Castolon local fauna discussed in the next section. If this is true, *A. wilsoni*, which is Hemingfordian in age, may be enough earlier than *Floridatragulus nanus* and *F. barbouri* to be directly ancestral to them. The problem lies in the fact that in Mexico, *Aguascalientia wilsoni* occurs with *Merychys elegans*, on which this age is based, whereas in the United States, *Floridatragulus* does not occur with *Merychys*. The apparent southern origin and distribution of primitive floridatragulids associated with apparent rapid evolution of the group explains their rarity in faunas of the United States.

The ancestors of *Floridatragulus* White have never been found. The peculiar morphology which combines advanced and primitive tylopod characters confuses its interpretation. *Floridatragulus* does not seem particularly oromerycid-like. *Aguascalientia*, however, has many features that are suggestive of members of the primitive tylopods. Possibly the Floridatragulinae are derived from somewhere within the camelid subfamily Oromerycinae (Wilson, 1974) that existed in Mexico or Central America, and for this reason the bulk of evolution of floridatragulids occurred outside of the United States. *Floridatragulus* is convergent morphologically with the true camel, *Nothokemas* White, and has lost most of its oromerycid features. The realization that floridatragulids may have descended from oromerycids instead of true camels helps to clarify the once confused systematics of the group. It is apparent that Maglio (1966) and Patton (1966) were justified in their suggestion that floridatragulids should be separated widely from true camels. I suggest that floridatragulids are descended from a southern oromerycid ancestor, and that their separation, like that for true camels, came about no later than the Eocene.

Aguascalientia sp.

(Fig. 16, F, G-d; Table 12)

Material.—40693-25, a left mandible fragment with partial M₂ and a complete M₃.

Description.—Specimen 40693-25 is approximately 15 percent smaller than

the corresponding parts of *Aguascalientia wilsoni*. The M₂, although incomplete, has a partial intercolumnar tubercle. Both the M₂ and the M₃ are relatively broad; the width of M₃ is greater than one-half its length. A similar condition is found in *Aguascalientia* and *Floridatragulus*. Because the M₃ of *Aguascalientia* sp. is so similar to M₃ in *A. wilsoni*, it will not be discussed in detail, except to say that the second crest of the hypoconulid is located lower down on the lingual side than in *A. wilsoni* (Fig. 16, F).

Discussion.—Specimen 40693-25 is so similar to *Aguascalientia wilsoni* that its placement within *Aguascalientia* is justified. The Delaho species probably is a distinct taxon from *A. wilsoni*, if for no other reason than its smaller size, but a formal description is deferred because of lack of knowledge about the anterior part of the mandible and the premolars.

TABLE 11

Measurements¹ of total sample of *Aguascalientia wilsoni*

Lower teeth	N	OR	\bar{X}	Holotype
Canine -M ₃	1	113.5	113.5
P ₁ -M ₃	1	93.7	93.7
P ₂ -M ₃	1	65.3	65.3
P ₃ -M ₃	1	58.3	58.3
Canine -P ₁ diastema	1	13.0	13.0
P ₁ -P ₂ diastema	1	24.2	24.2
Diam. between P ₁ and P ₃	1	31.2	31.2
P ₃ -P ₄	1	16.5	16.5
Length of P ₁	1	3.1	3.1
Length of P ₂	1	6.5
Width of P ₂	1	2.7
Length of P ₃	2	7.9-8.6	8.3	7.9
Width of P ₃	2	3.3-3.9	3.6	3.3
Length of P ₄	2	7.7-8.1	7.9	7.7
Width of P ₄	2	4.5-5.0	4.8	4.5
M ₁ -M ₃	1	32.6	32.6
Length of M ₁	2	9.6-9.6	9.6	9.6
Width of M ₁	1	7.2	7.2
Length of M ₂	2	13.2-13.4	13.3	13.2
Width of M ₂	2	8.1-8.9	8.5	8.9
Length of M ₃	2	17.9-18.1	18.0	18.1
Width of M ₃	2	9.1-9.5	9.3	9.1

¹Measurements taken as in fig. 16, G.

Aguascalientia sp. is the oldest floridatragulid yet reported. If identified correctly it demonstrates that the Floridatragulinae evolved rapidly from a very small, oromerycid-like ancestor in the later Arikareean, to large and specialized animals by the middle Hemingfordian.

TABLE 12

Measurements¹ of *Aguascalientia* sp., 40693-25

Length of M ₃	15.3
Width of M ₃	8.1

¹Measurements taken as in fig. 16, G.

Family Hypertragulidae Cope
Nanotragulus Lull
Nanotragulus ordinatus (Matthew)
 (Fig. 17, A-H; Table 13)

Hypertragulus ordinatus Matthew, 1907.

Nanotragulus ordinatus (Matthew), Matthew, 1926.

Nanotragulus, cf. *N. matthewi*, Stevens, in Stevens et al., 1969.

Material.—Specimens collected after 1969 include 40635-148, mandible with P₂-M₃; -86, mandible with P₃-M₃; -96, mandible with roots for P₂ and part of the rostrum, and M₁-M₂; -126, maxilla fragment with M²-M³; -187 and -188, rostra with P₁-P₂ diastema; and many other specimens.

Description.—Recovery of adult specimens of the Castolon *Nanotragulus* with more or less complete dentitions allows a firmer identification of the species than before. The description of this material will be limited to the premolars because the molars have been discussed fully elsewhere (Stevens, in Stevens et al., 1969).

Two rostra have been recovered, one of which contains a partial, caniniform P₁. Behind P₁ extends a diastema, approximating the length of M₃. The P₂ is somewhat caniniform, high above its alveolar border, and slightly recurved (Fig. 17, D). Specimens 40635-148 and -86, and the alveoli for -187 show that P₂ is set close to P₃ (Fig. 17, B, D, and F), as in species of *Nanotragulus* later than early middle Arikareean. Earlier species have a diastema between P₂ and P₃. The P₃ is lower than P₂, has a greater anteroposterior diameter, and a better developed posteromedial basin and crest. The P₃ of 40635-148 and -86 lack the external cingulum reported for the unerupted P₃ of 40918-18 (Stevens et al., 1969, Fig. 13), thus the cingulum must be variable. The P₄ is narrow and elongate, and its paraconid is directed sharp-

ly anteromedial. The metaconid is a very prominent and distinct cusp which communicates posteriorly with the entoconid via a prominent ridge. Unworn molars, especially M₃, are very high crowned (Fig. 17, B').

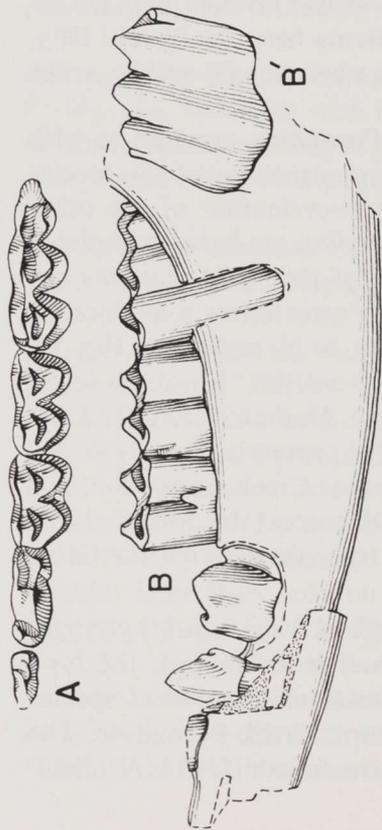
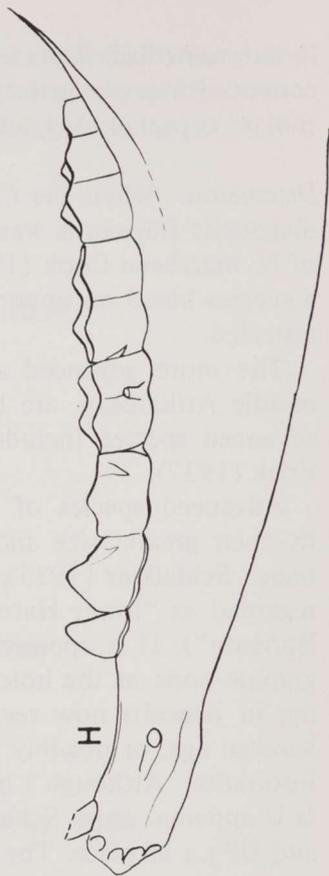
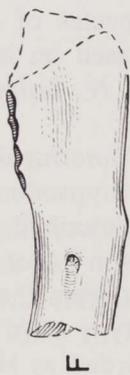
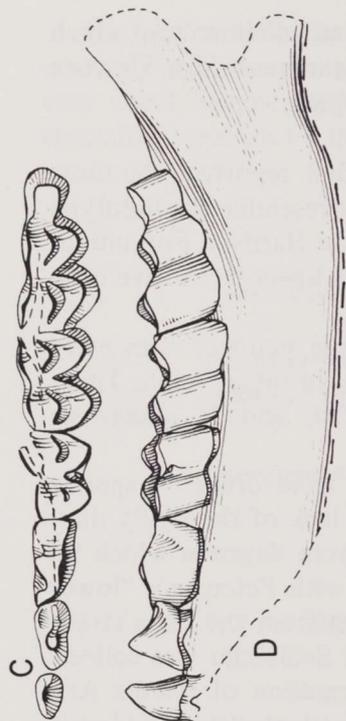
Discussion.—When the Castolon *Nanotragulus* was first reported, the most diagnostic fragments were upper teeth. These closely resemble the holotype of *N. matthewi* Cook (1934) from the late Arikareean Harrison Formation, a species based on upper teeth and one for which no lower teeth have been reported.

The more advanced species of *Nanotragulus*, those younger than early middle Arikareean, are based on isolated mandibles, or upper teeth. These advanced species include *N. ordinatus*, *N. matthewi*, and *N. albanensis* Frick (1937).

Advanced species of *Nanotragulus* are separated from primitive species by their greater size and hypsodonty, and by their lack of the P₂-P₃ diastema. Schlaikjer (1935) described *N. intermedius* from deposits which he regarded as "lower Harrison" (not to be confused with Peterson's "lower Harrison"). It is apparent from the fauna that comes from the same stratigraphic zone as the holotype of *N. intermedius* that Schlaikjer was collecting in deposits now regarded as Monroe Creek Formation of middle Arikareean age, or possibly from the upper part of the early Arikareean Gering Formation. Although I have not seen the type specimen of *N. intermedius*, it is apparent from Schlaikjer's illustrations that it is a juvenile with DP₃₋₄, and DP₃₋₄ in place. The holotype lacks the diastema between P₂ and DP₃, but it cannot be said that it would lack a diastema between P₂ and P₃, when these teeth fully erupted.

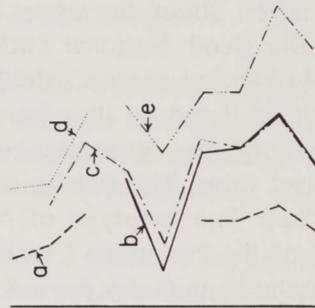
The material now available from the Delaho Formation provides us with information about the upper as well as the lower dentition of the species from Big Bend National Park. This encourages re-evaluation of the other later Arikareean species, which, except *N. intermedius*, are based on isolated dentitions. Based on its relatively large size, lack of the P₂-P₃ diastema and hypsodonty, the *Nanotragulus* from the Delaho Formation is a moderately advanced form. The Delaho species compares best to *N. orginatus* (Fig. 17, G-b, G-c). The holotype of *N. ordinatus* came from the "Lower Rosebud beds" of the Porcupine Creek area, South Dakota. Mathew's (1907) "Lower Rosebud" includes deposits which are regarded currently as early Arikareean Sharps Formation, middle Arikareean Monroe Creek Formation, and some deposits that are either Monroe Creek or Harrison (Macdonald, 1963, 1970). Macdonald (1963) reports *N. ordinatus* from the latter rocks (Monroe Creek or Harrison).

Figure 17, G, is a ratio diagram of several species of *Nanotragulus* younger than early Arikareean. The standard (vertical line) is *N. loomisi*, the type species, from the upper part of the Sharps Formation. The second species to the right (G-a) is *N. lulli* Frick, from the Monroe Creek Formation. The third (G-b) is the holotype of *N. ordinatus*, and the fourth (G-e) is *N. alban-*



1 cm.

0 +.05 +.10 +.15 +.20 +.25



G

Anteroposterior diameter, $M_1 - M_3$	
" " M_3	
Transverse diameter (max.), M_3	
Anteroposterior diameter, $P_2 - M_3$	
" " $P_2 - P_4$	
" " $P_3 - M_3$	
" " $M_1 - M_3$	
" " M_3	
Transverse diameter (max.), M_3	

TABLE 13

Measurements¹ of total sample of *Nanotragulus ordinatus*
from the Castolon local fauna

<i>Upper teeth</i>	N	OR	X**	s	CV
Length of M ³	3	8.4-8.7	8.5
Width of M ³	1	6.7
<i>Lower teeth</i>					
P ₂ -M ₃	1	36.0
P ₃ -M ₃	2	33.0-34.7	33.9
P ₂ -P ₄	1	11.5
M ₁ -M ₃	5	22.3-24.6	23.7±1.25	0.91	3.85
Length of M ₃	8	9.5-11.2	10.2±0.50	0.58	5.69
Width of M ₃	7	4.0-4.7	4.3±0.22	0.24	5.62
Crown height of M ₃ from apex of entoconid to base of enamel	1	10.3

¹Measurements taken as in fig. 17, G, except as noted.

ensis, presumably the youngest, late Arikareean, species of this series. The four species are probably in their correct stratigraphic order from left to right. Associated with their steady increase in general size (and greater hypsodonty, not shown because the holotypes have worn M₃s), is the tendency to eliminate the P₂-P₃ diastema, and to elongate M₃ anteroposteriorly.

The species of *Nanotragulus* from the Delaho Formation is morphologically indistinguishable from the holotype of *N. ordinatus*. Although no lower teeth have been reported for *N. matthewi* (Fig. 17, G-d), from the late Arikareean Harrison Formation, its upper teeth are slightly larger than upper teeth of the Castolon species, whose lower teeth are comparable to *N. ordinatus* in size. It is apparent that *N. matthewi* is related closely to *N. ordinatus*. *Nanotragulus matthewi* may be based on a large individual of *N. ordi-*

Fig. 17.—*Nanotragulus ordinatus* from the lower part of the Delaho Formation. (A) occlusal view of P₃-M₃, 40635-86; (B) lateral view of mandible of same specimen; (B) lingual view of M₃, same specimen; (C) occlusal view of P₂-M₃, 40635-148; (D) lateral view of same specimen. All X 2. (E) ratio diagram comparing Delaho sample of *Nanotragulus* (c) with other species; (a) *N. lulli* from the middle Arikareean, holotype; (b) *N. ordinatus* from the later Arikareean, holotype; (d) *N. matthewi* from the late Arikareean, holotype; (e) *N. albanensis* from the latest Arikareean, holotype. The standard is *N. loomisi*, the type species of the genus, from the early Arikareean.

natus, or it may have been drawn from a slightly later *Nanotragulus* population than that which yielded the holotype of *N. ordinatus*. The affinities of *N. matthewi* might be further clarified if we had upper teeth for *N. albanensis*. The type of this species presumably came from the upper part of the Harrison Formation (Lower Harrison of Frick, 1937). The lower teeth of *N. albanensis* are much larger than those of *N. ordinatus* (Fig. 17, G-e). Because the nanotragulid from the Delaho Formation is more similar to *N. ordinatus* it is transferred from *Nanotragulus*, cf. *N. matthewi*, to *N. ordinatus*.

AGE AND INTERPRETATION

There is no doubt that the Castolon local fauna is Arikareean, early Miocene, in age. Its members show more affinity with taxa of the later, rather than of the earlier half of this provincial age. An age of late middle Arikareean was suggested originally for the assemblage (Stevens, in Stevens et al., 1969). Further study of the fauna indicates that it is early late Arikareean in age.

Two taxa from the Castolon local fauna, *Archaeolagus*, cf. *A. acaricolus* (Dawson, in Stevens et al., 1969) and *Merychys*, cf. *M. calaminthus* are very similar to these species in the Tick Canyon Formation of southern California, regarded as late Arikareean. *Nanotragulus ordinatus* in its type area came from deposits of the middle or late Arikareean, but this species is slightly older than *N. albanensis* from the late Arikareean Harrison Formation, as based on morphology.

Several taxa in the Castolon local fauna, which belong to animal groups that usually have a wide geographic distribution and for this reason ought to be reliable age indicators, are more generalized morphologically than their relatives from the late Arikareean. These include *?Nothocyon*, cf. *?N. annectens*, *Priscocamelus wilsoni*, *Stenomylus*, and *Gregorymys riograndensis*.

A third group of taxa lacking comparable species from the late Arikareean but having relatives in the early Hemingfordian are considerably more primitive than those species. They include *?Brachyerix hibbardi* and *?Michenia australis*.

A fourth group from the Delaho Formation includes species that are members of lineages that originated and experienced their early evolution in areas outside of the classic Arikareean and Hemingfordian faunal regions, and are of little value for correlation. Nevertheless, they are of great phylogenetic interest. These include *?Phenacocoelus leptoscelos* and *Aguascalientia* sp., possibly *?Brachyerix hibbardi*, *Similisciurus maxwelli*, and the rhino *Moschoedestes* Stevens.

The final category of species from the Castolon local fauna belong to taxa of uncertain affinities, for example *Similisciurus* and *Moschoedestes*. *Moschoedestes*, a hypsodont, short-jawed rhinoceros, may be the remote ancestor for *Teleoceras* Hatcher, a hypsodont, short-jawed rhino of the late Mio-

cene and early Pliocene. *Moschoedestes* occurs with *?Phenacocoelus leptocelos*, the Arikareean ancestor for *Ustatochoerus*. *Ustatochoerus* on the northern High Plains occurs with *Teleoceras*, which suggests that some of the later Tertiary faunas of the High Plains are the result of faunal shift from the south to north. Another taxon of uncertain affinity from the Delaho Formation is *Delahomeryx* Stevens, a possible cervid. The incompleteness of the specimens of *?Peroligobunis* sp., *?Peratherium* sp., and the heteromyid inhibits evaluation of these forms.

The Castolon local fauna is the largest later Arikareean assemblage known within an area affected by the evolving Madro-Tertiary Geoflora (Axelrod, 1967). This flora set the stage in the early Miocene for certain vertebrates to undergo modifications that allowed them to invade successfully increasingly more xeric environment as it expanded and intensified during the North American Tertiary. Because the site of origin of aridity was in the Southwest and Mexico during the early Miocene, the ancestors for many late Tertiary High Plains mammals are found among early Miocene faunas of west Texas and California. None of the 22 species that comprise the Castolon local fauna indicates mesic environmental conditions, with the possible exception of *Aguscalientia*, a rare floridatragulid, perhaps with a preference for mesic, forest conditions.

Hundreds of individual bones and teeth have been found in the lower part of the Delaho Formation, but none of these remains are equid. I hold the same opinion that I held in 1969, that horses of the later Arikareean were not yet adapted well enough to xeric conditions to invade the area inhabited by the Castolon local fauna.

The Castolon local fauna shows relationships to other faunas of the Southwest, for example the Black Butte and Logan Mine local faunas (Woodburne et al., 1974), faunas where not a single horse bone has been reported. Although no flora is associated with the Castolon local fauna, the fossil vertebrates suggest that it was a subtropical acacia savanna, not unlike certain parts of Mexico today. As more information is obtained for the Castolon assemblage, it is becoming increasingly clear that the reptiles and *?Peratherium* sp. have affinity to their counterparts in the modern fauna of Mexico, where *Heloderma*, *Ctenosaura* (or *Sauromalus*), and *Marmosa* are sympatric in certain parts of their range.

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