

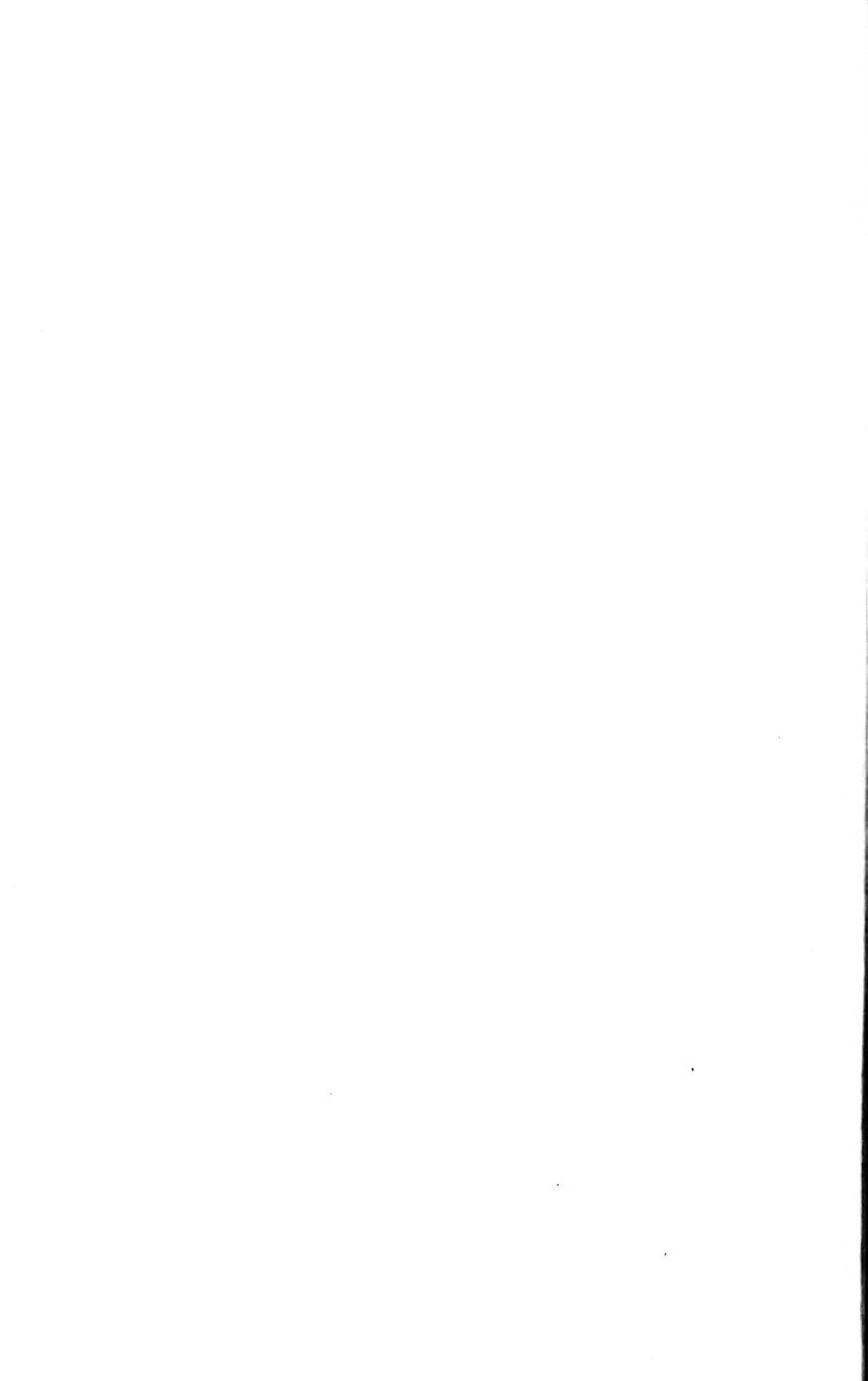
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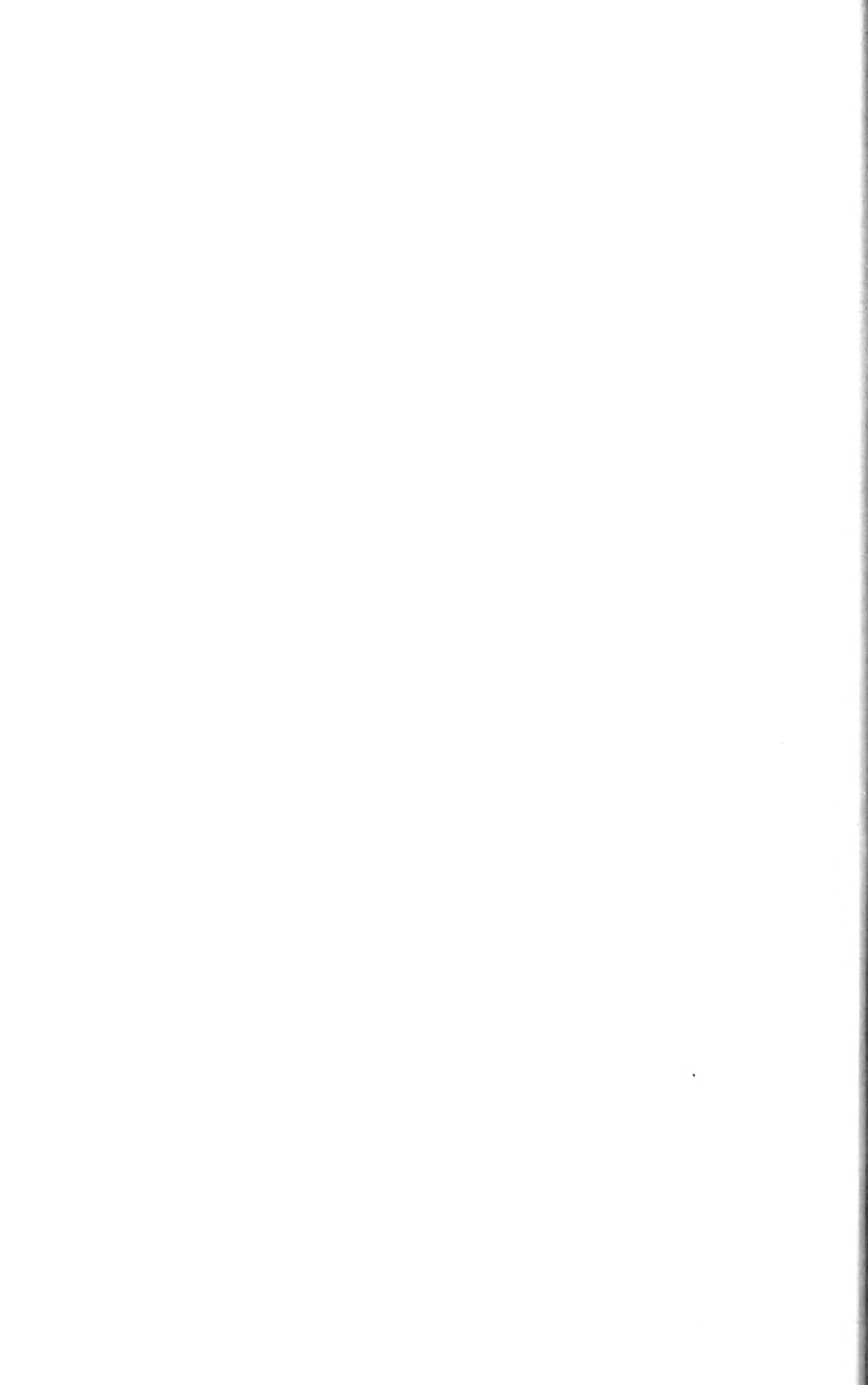
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ERRATA: *Annals of Carnegie Museum*, Vol. 45.

Page 43 - Title of paper: for Mississippian read Mississippian.

Page 258 - *Atopomys salvelinus* [as new species name] should be in bold-face type, i.e., **Atopomys salvelinus**.

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CARNEGIE MUSEUM OF NATURAL HISTORY

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VOLUME 45

DECEMBER 16, 1974 COMP. ZOOLOGICAL LIBRARY ARTICLE 1

JAN 13 1975

VARIATION OF THE SHAPES OF BIRDS' EGGS WITHIN THE CLUTCH: CORRECTION OF AN ERROR

F. W. PRESTON¹

In 1972 T. H. Manning of Merrickville, Ontario, called my attention to an error in a paper I wrote with Eric J. Preston (Preston, F. W., and E. J. Preston, 1953. Variation of the shapes of birds' eggs within the clutch. *Ann. Carnegie Mus.*, 33(5): 129-139). The denominators, m and n, of the first two equations of page 137 had been interchanged. This slip had escaped the authors and referees in 1953, and so far as I know had escaped any readers for twenty years until Mr. Manning noticed it. My former associates, John M. McCormick and Theodore C. Baker, now both of Toledo, agreed with Mr. Manning, and new calculations were made. W. J. Winans, using the University of Pittsburgh high-speed computer, and E. Harvey Barnett, using the Corning Glass Works computer at Corning, each recomputed Table II of the 1953 paper, using the data of Table I. (The original work was done on a desk calculator.) The two new sets of calculations agree, and show that the original qualitative conclusions as to what is significant and what is not were sound. This is fortunate rather than creditable. A substantial fraction of the numerical values were, of course, in error. A revised table is presented here (Table 1). I have no reason to think that in another twenty years further errors will be discovered.

¹Box 49, Meridian Station, Butler, Pennsylvania 16001.

Submitted for publication January 28, 1974.

In the third equation of page 135, delete the large ("curly") brackets. They, too, are an error, but they are so obviously out of place that it is unlikely they would mislead anyone.

My confession of error does not commit Eric J. Preston, who has not been consulted. If he had been, he would no doubt have agreed.

The accidental interchange of the denominators was carried over into another paper (Gemperle, M. H., and F. W. Preston. 1955. Variation of shape in the eggs of the Common Tern in the clutch-sequence. *Auk*, 72: 184-197). A new table has been computed for these data also, and a correction has been published in that journal (Preston, F. W. 1974. Ancient error in a 1955 *Auk* paper. *Auk*, 91: 417-418).

Back issues of many *Annals of Carnegie Museum* articles are available, and a few early complete volumes and parts are listed at half price. Orders and inquiries should be addressed to: Publications Secretary, Carnegie Museum, 4400 Forbes Avenue, Pittsburgh, Pa. 15213.

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CAMPYLOGNATHOIDES LIASICUS (QUENSTEDT), AN UPPER LIASSIC PTEROSAUR FROM HOLZMADEN— THE PITTSBURGH SPECIMEN

JAN 6 13 1975

PETER WELLNHOFER¹

HARVARD
UNIVERSITY

INTRODUCTION

In 1903, Carnegie Museum obtained an excellently preserved pterosaur, which was included in the collection purchased from the Belgian Baron de Bayet. In 1897, the skeleton without the skull and a part of the cervical vertebral column had been found in the Upper Liassic "Posidonienschiefer" near Holzmaden (Württemberg, Germany). Bernard Hauff (1921: plate legend 19) reported that one year later the isolated skull with some cervical vertebrae was discovered in exactly the same horizon and only a few meters away from the skeleton. When he prepared the specimen, Hauff put the skull into the skeleton slab as it is shown today. Hauff also (1921: Pl. 19) published the only existing photograph of this specimen. Although it has been mentioned by numerous authors as the "Pittsburgh specimen of *Campylognathus*" there has been no thorough investigation of it. Plieninger (1907: 222) published only some details about the sternum and the gastralia, and von Huene (1914: 60), who studied the specimen personally, figured and described only the skull. Finally Colbert (1969: 20) dealt with the measurements of certain skeletal elements in comparison with his rhamphorhynchid pterosaur from Cuba.

Among the five known specimens of the genus *Campylognathoides* the Pittsburgh specimen is the most complete. It provides new information about the skull and the pelvis, on the basis of which some previous opinions can now be corrected.

¹Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich.

Submitted for publication November 14, 1972.

The investigation of this specimen became possible when Carnegie Museum of Natural History invited me to be a Visiting Museum Specialist, from May to November, 1972. For this opportunity I express my thanks and appreciation to the Director of the Museum, Dr. M. Graham Netting; to the Associate Director, Dr. James L. Swauger; and especially to the Curator of Vertebrate Fossils, Dr. Mary R. Dawson, who was very helpful in examining the English text. My thanks are also extended to Prof. Dr. R. Hoffstetter, who kindly sent me some photographs of the *Campylognathoides* specimen of the Muséum National d'Histoire Naturelle in Paris.

Class Reptilia
Order Pterosauria
Suborder Rhamphorhynchoidea
Family Rhamphorhynchidae

Campylognathoides Strand 1928¹

Type: *Campylognathus zitteli* Plieninger, 1895

At the present time there are five known specimens of the genus. The first one was described by Quenstedt (1858: 299) under the name *Pterodactylus liasicus*. It consists only of isolated bones of a forelimb from the Upper Liassic of Wittberg near Metzingen (Württemberg). Today it is preserved in the Museum für Geologie und Paläontologie of the University of Tübingen. In 1893 the second specimen was found near Holzmaden and described by Plieninger (1895) as *Campylognathus zitteli*. It is a nearly complete skeleton, kept in the Staatliches Museum für Naturkunde in Stuttgart. In his monograph on the "Pterosaurier der Juraformation Schwabens," Plieninger (1907: 222) also assigned the third specimen, the one in Pittsburgh, to this species. The fourth *Campylognathoides* from Holzmaden, now an Uppsala University specimen, consisting of a mandible, a scapulocoracoid, a wing-arm, tibia and fibula, and two feet, was assigned by Wiman (1923: 45) to *Campylognathus liasicus*. The fifth specimen is a well-preserved, nearly complete skeleton, also from Holzmaden, and today in the Muséum National d'Histoire Naturelle in Paris. It is not yet described, but Hauff (1953) and Augusta & Burian (1961) published a photograph of it.

DESCRIPTION AND DISCUSSION, PITTSBURGH SPECIMEN

Campylognathoides liasicus (Quenstedt)

SYNONYMY

1858 *Pterodactylus liasicus*.—Quenstedt: 299.

1907 *Campylognathus liasicus*. (Quenstedt).—Plieninger: 218, Pl. 14.

¹*Campylognathus* Plieninger, 1895, is preoccupied.

- 1907 *Campylognathus zitteli* F. Plien.—Plieninger: 222, Fig. 1 (non *C. zitteli* Plieninger 1895).
1921 *Campylognathus zitteli* F. Plien.—Hauff: 38, Pl. 19.)
1923 *Campylognathus liasicus*.—Wiman: 45, Pl. 2.
1971 *Campylognathoides liasicus* (Quenstedt).—Wild: 187, Table 3.

MATERIAL

A nearly complete skeleton. Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania, USA. CM 11424 (Fig. 13).

HORIZON AND LOCALITY

Lower Toarcian, "Lias Epsilon," "Posidonienschiefer." According to Hauff (1921: 38) the skeleton was found in his quarry VII near Holzmaden, Württemberg. It came from the so-called Fleins (II 3), which is part of the middle section of the "Lias Epsilon." This "Fleins" consists of a bituminous limestone layer 18 cm thick (Hauff, 1921: 6). It is the same layer in which the type specimen of *Campylognathoides zitteli* was discovered.

PRESERVATION

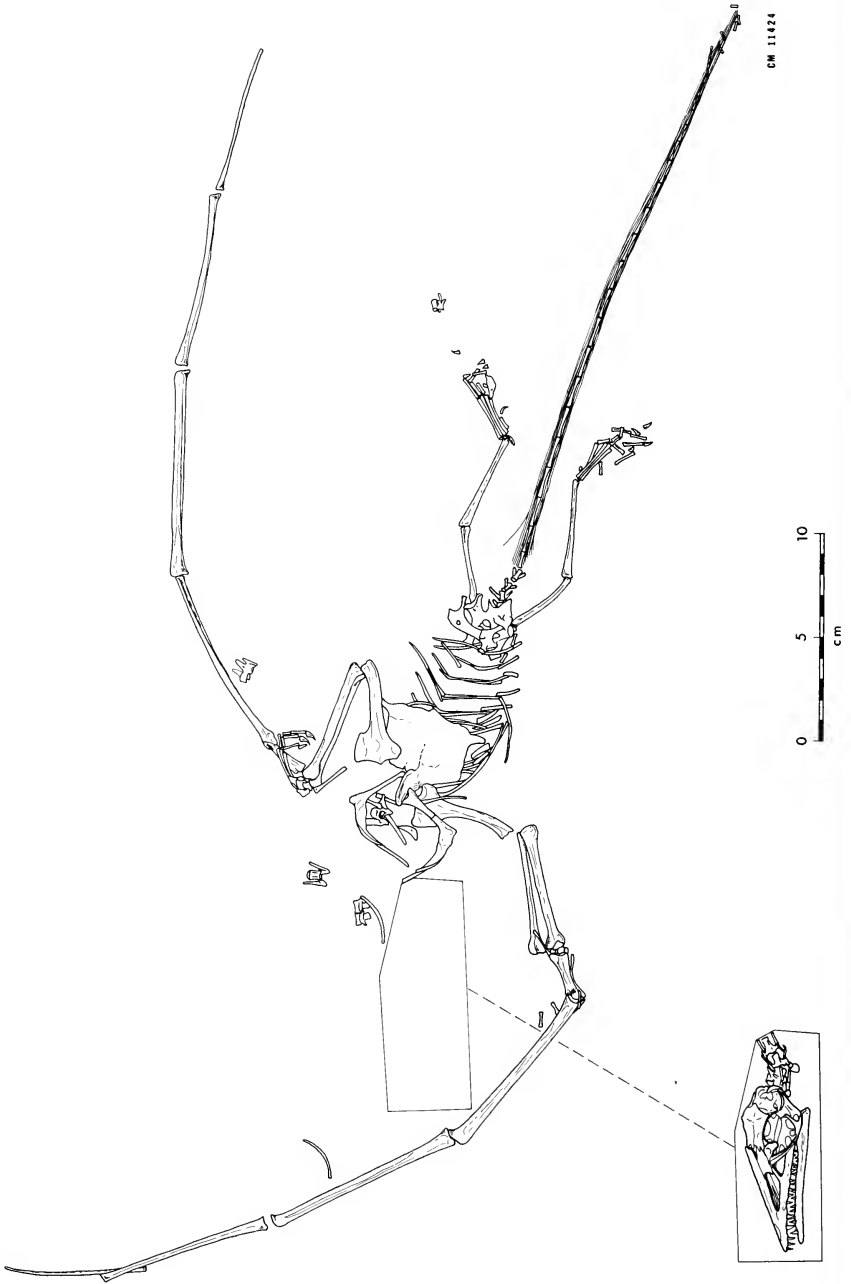
The skeleton lies on a dark slab 17¼ inches by 29¼ inches in size. Its ventral side is exposed. The elements of the appendicular skeleton—the sternum, the pelvis, and the tail—are still in almost original position. It is noteworthy that the presacral vertebral column is lacking, a condition that Hauff (1921: 38) also found in most of the other pterosaurs from Holzmaden. Nonetheless, the pelvis, hind limbs, and tail are in a fairly natural position relative to the wing arms and the sternum, as if the vertebrae were present. Only the gastralia span the space between the sternum and the pelvis. Both scapulocoracoids are still united with the sternum and lie nearly symmetrically, but they are dislocated to the front of the sternum. Three cervical and three dorsal vertebrae are isolated at different parts of the skeleton.

The original position of the skeleton was as shown in Figure 1. The skull, connected with the first five cervical vertebrae, was situated a few meters away and was put into the slab later, as mentioned above. Because of the possibility that the skull and the postcranial skeleton came from different individuals, it is necessary to prove that it was correct to unite both in one specimen. There are two facts, especially, that justify Hauff's procedure. First, finds of pterosaurs in Holzmaden are extremely rare. Second, the skull was connected with cervical vertebrae I to V, and the following vertebrae VI to VIII were found together with the skeleton. Thus there should be no doubt about the unity of the skull and the postcranial skeleton.

No imprints of any soft parts or of the wing membranes are recognizable.

THE SKULL (FIGS. 2 & 3)

The skull and the mandible are exposed on their left sides. Because of compression, parts of the skull roof are also visible. Some of the palatal elements could be prepared through the skull openings. The skull roof is broken between the premaxilla and the frontal. In relation to the



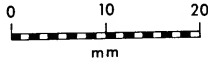
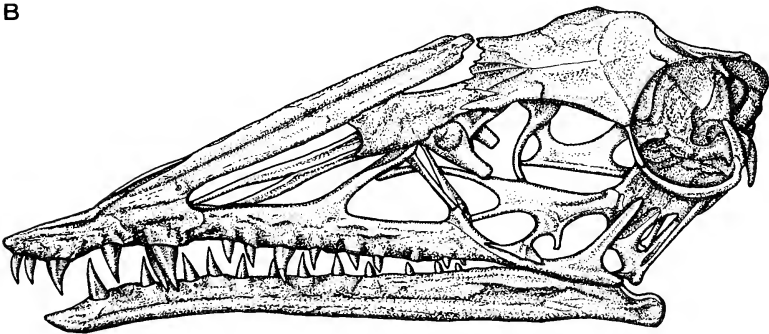
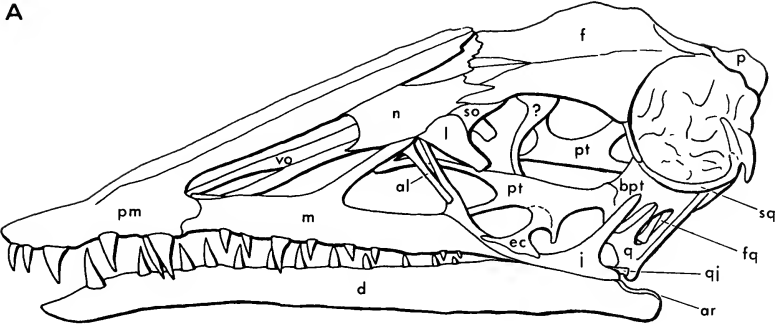


Fig. 2. A, B. *Campylognathoides liasicus*. CM 11424. Skull. A. Interpretation of skull structures. B. Specimen as preserved. Abbreviations: *al*, adlacrimal; *ar*, articular; *bpt*, basiptyergoid; *d*, dentary; *ec*, ectopterygoid; *f*, frontal; *fq*, foramen quadrati; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *p*, parietal; *pm*, premaxilla; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *so*, supraorbital; *sq*, squamosal; *vo*, vomer.

←
Fig. 1. *Campylognathoides liasicus*. CM 11424. Original position of skeleton, ventral view, showing area in which the dislocated skull was placed.

front of the skull, the braincase is turned downward, compressing the orbit dorso-ventrally. The premaxillae form the tip of the snout and extend backward between the frontals to above the middle of the orbit. The premaxillae also dorsally surround the fairly large external nares, as well as forming their front margins. Posterior to the fourth tooth, the premaxillo-maxillar suture is visible. The ventral margins of both the external naris and the antorbital fenestra are formed by the maxilla. Its ascending process separates these two openings. The external naris is clearly larger than the antorbital fenestra. The jugal is distinctly bounded by the maxilla, and forms the lower margin of the orbit. It sends a short process posteriorly toward the quadrate, where a small part of the quadratojugal is also preserved. The lower temporal fenestra was probably surrounded by the jugal, the quadrate, the squamosal, and the postorbital. The postorbital is not preserved. The squamosal extends anteriorly as a curved process, forming the postorbitosquamosal bar and separating the lower and the upper temporal fenestrae. In reference to other rhamphorhynchids in my reconstruction (Fig. 3), I made the squamosal partly cover the postorbital. Apparently the upper temporal fenestra was very large. It is bounded by the frontal, the postorbital, the squamosal, and the parietal. Its upper margin with the parietal cannot be recognized, but probably there was a smooth transition. The frontal also forms the upper margin of the orbit, meeting anteriorly the premaxilla, the nasal, and the supraorbital. The anterior margin of the orbit is formed by the lacrimal and a presumed adlacrimal, both of which cover the ascending process of the jugal.

Concerning the position and interpretation of certain skull elements there are some differences from von Huene's opinions (1914: 60). They involve the outlines and positions of the nasal, the lacrimal, the supraorbital and the quadratojugal. The adlacrimal, which could indeed be taken to be a prefrontal, has no posterior process as shown in von Huene's Figure 3 (p. 60). The suture that he assumed separated the nasal and his lacrimal is not a real suture. I recognize it only as a fracture in the nasal. Therefore the nasal extends posterior to the frontal. The bones projecting into the orbit are two easily distinguishable structures. In my interpretation, agreeing with Plieninger (1907: 223), they are the supraorbital and the lacrimal. Von Huene saw only the supraorbital, although in different shape, but did not consider the ventral process of the lacrimal. Another question concerns the original position of these two elements. Plieninger (1907: 223) let them project into the orbit, which is indeed the position found in the fossil skull. Von Huene (1914: 60) also believed that the supraorbital projects freely into the orbit in analogy to *Dimorphodon*, *Crocodylus* and the ratites. In my opinion, the present position of the lacrimal and the supraorbital are caused by post-mortem compression of the skull; that is, the supra-

orbital is pushed below the frontal, also turning the lacrimal backward. In the reconstruction these two elements are shown as I know them in *Dorygnathus* and the Upper Jurassic rhamphorhynchids. This same position of the lacrimal and the supraorbital occurs even in *Pterodactylus* (Wellnhofer, 1970: 17). Finally, it is not the quadratojugal at the point marked by von Huene, but rather the quadrate turned dorsoventrally. The quadrate is expanded medially and perforated by a large oval foramen. The real quadratojugal had to be very small, forming a ventral connection between the jugal and the quadrate.

Twelve teeth are preserved in the upper jaw. The first visible tooth is the first premaxillary tooth of the right side. Next to the fourth tooth appears the corresponding one of the opposite side. There are four teeth in the premaxilla, of which the fourth tooth is the strongest of the entire dentition. The first three teeth are placed more or less upright in the jaw; the fourth is tilted slightly backward. All the teeth are rather curved and have posteriorly turning, pointed tips. At the base their cross section is slightly oval, lacking sharp edges. Their surface is smooth. There is a gap behind the fourth tooth opposite two teeth in the lower jaw. An alveolus is not recognizable, probably having been closed by compression. Behind two smaller teeth follows the largest one

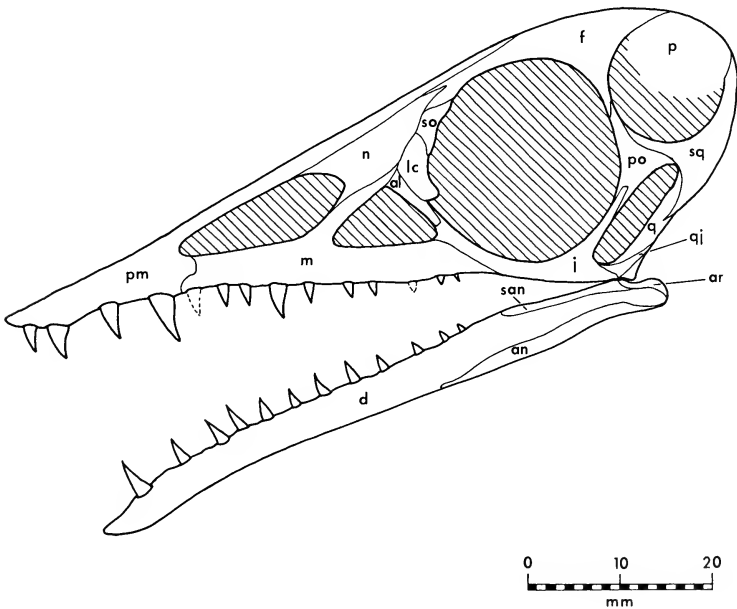


Fig. 3. *Campylognathoides liasicus*. CM 11424. Reconstruction of skull. Abbreviations as in Fig. 2 and: *an*, angular; *po*, postorbital; *san*, surangular.

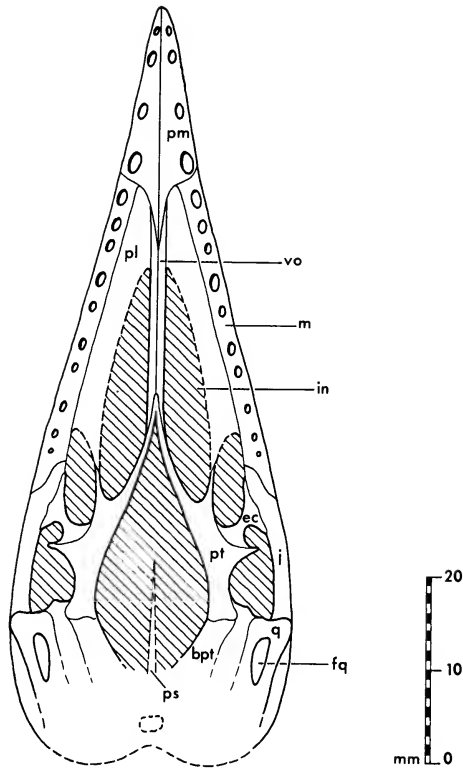


Fig. 4. *Campylognathoides liasicus*. CM 11424. Reconstruction of palate. Abbreviations as in Fig. 2 and: *in*, internal naris; *pl*, palatine; *ps*, parasphenoid.

of the maxilla, then three small teeth, again a gap, then two very small teeth. Probably there were 14 teeth in the upper jaw—4 in the premaxilla and 10 in the maxilla.

THE PALATE (FIG. 4)

Certain structures of the palate are visible through the openings of the orbit, the antorbital fenestra, and the naris. The pterygoids, the ectopterygoids, and the vomers are especially distinguishable. In the reconstruction of the palate, the positions of the mandibular articulation, the vomers, and the pterygoids are definite. Uncertain in position and shape are the palatines and the occipital and sphenoidal regions. Based on the existing elements, however, it is possible to obtain a fairly positive reconstruction of the palate.

The largest elements are the pterygoids, which extend medially and anteriorly between the vomers, and form a common tip. The interpterygoid vacuity might have been smaller or larger than reconstructed, depending on the breadth of the skull. Laterally the pterygoid extends a process anteriorly to the palatine. The postpalatine vacuity is closed posteriorly by the ectopterygoid, which widens at its end. Posteriorly there is another lateral pterygoid process that does not meet the jugal. The stalk-like base of the pterygoids is supported posteriorly by the basipterygoid. The outline of the basipterygoid cannot be recognized posteriorly. Medially the quadrate broadens winglike, adjoining the pterygoid and the basipterygoid. The vomers are very long and narrow. Between the vomers the premaxillae extend anteriorly and the pterygoids posteriorly as pointed tips. The palatine projects only with a small rim at the front margin of the external naris and is almost covered by the maxilla. Therefore, the palatine cannot be much broader than the maxilla is high, and must be fairly narrow and long, resulting in large internal nares that correspond in size to the external ones.

THE MANDIBLE

The lower jaw has 12 teeth on each side. The tip of the mandible (5 mm) is toothless. The first tooth is the largest one. It is upright in the jaw, as are all the lower teeth, and has a posteriorly directed tip. The following seven teeth are fairly equal in spacing and size. The lower tooth row bites inside the upper one. The last four teeth are comparatively small. Laterally there are depressions between the teeth in which the teeth of the upper jaw fit, allowing the beak to close a little more than it does in the present position. The retroarticular process is robust. Apparently the articular was small, but the sutures between the articular, the angular, and the surangular are hardly distinguishable. The rami of the mandible narrow anteriorly and are slightly curved ventrally toward the tip of the symphysis.

THE VERTEBRAL COLUMN

All the vertebrae are procoelous. The first five cervical vertebrae are still united with the skull as preserved. The occiput, especially the squamosal part, covers the atlas. There is a trough-shaped bone, 2.5 mm in diameter, squeezed between the quadrate and the squamosal. It could be interpreted as an intercentrum between the atlas and the axis. Because the anterior cervical vertebrae are turned laterally, the short neural spine of the axis can be observed. The third vertebra shows a much larger spine, directed backward. The axis bears ribs, as do the following cervical vertebrae. The ribs articulate with the strong anteriorly situated transverse processes of the vertebrae. The cervical ribs extend farther posteriorly than the corresponding vertebral centra. The

cervical vertebrae measured across the transverse processes, are slightly narrower than they are long. The posterior cervical vertebrae, associated with the skeleton, are situated beside the left carpus, between the scapulocoracoids, and close to the first phalanx of the left wing finger.

All parts that are preserved of the dorsal vertebral column are two articulated vertebrae from the lumbar region and the last lumbar vertebra, still connected with the sacrum. Their neural spines are broadened on top, and rise vertically. The sacrum apparently consists of four vertebrae compactly connected with the ilia. As preserved, most of the sacrum is covered by the prepubes and the right ischiopubis.

The first caudal vertebra and one of its transverse processes can be observed beneath the right ischiopubis. Three vertebrae are a little removed from their natural articulation. Exposed ventrally, they extend as long oblique transverse processes posteriorly. The fairly straight remaining caudal vertebral column (Fig. 14E) is enclosed in a shaft of numerous "ossified tendons." These are elongated rodlike, ossified (or possibly calcified) processes of both the prezygapophyses and the post-zygapophyses and of the chevrons. All processes bifurcate—as demonstrated by Ostrom (1969)—which must have given some kind of elastic stability. Mobility of the tail was made possible only by the anterior four caudal vertebrae, which lack long processes and are not enveloped by the rodlike extensions of the following vertebrae. Posteriorly, the length of the vertebral centra increases markedly. The maximum length of 15 mm is reached by the ninth vertebra and continues to the fourteenth one. Then the length of the centrum decreases gradually to 4.5 mm in the thirty-third vertebra. The tip of the tail, probably consisting of five more vertebrae, is missing. The last seven caudal vertebrae present are dislocated. The entire length of the tail was approximately 32.5 cm.

THE RIBS

There are cervical ribs from the axis back. They are relatively strong and have anterior processes covered laterally by the preceding ribs. The ribs of the fifth cervical vertebra are 8 mm in length. They are not separated from the vertebrae, even in the isolated ones, showing that the cervical ribs were fairly closely connected to the vertebrae.

Most of the dorsal ribs have been lost along with the dorsal vertebral column. Two ribs are dislocated, lying beside the second phalanx of the wing finger and beside the two isolated dorsal vertebrae. Their proximal articulation is not preserved. Remains of dorsal ribs are also recognizable between the scapulocoracoids and beside the sternum. The anterior ones were apparently dichoccephalous and strong, the posterior ones fairly thin and without discernible articulations.

Next to the sternum several short, broad sternal rib segments are also preserved, some of them still in connection with the sternal plate. Plieninger (1907: 222), who figured and described this part of the skeleton, supposed that the gastralria were also connected with the sternum by such segments, since they are located beside some of the gastralria. In any case, it is extraordinary that these mostly cartilaginous rib segments are ossified at all. The conclusion is that this individual was an adult.

THE STERNUM (FIGS. 5, 14A)

The sternal plate, exposed ventrally, is almost rectangular and has two short processes on the posterior lateral edges. The anterior margins merge into the sternal keel. Its front end is obtuse and rounded. Posteriorly the upper rim changes to a flat medial keel that disappears in the middle of the sternal plate. The surface of the originally slightly arched sternal plate is grained. The curved posterior margin projects in the middle as a tip. The ventral space between the sternum and the pelvis is occupied by the gastral skeleton. It consists of six arches, each composed of one curved middle element and two rodlike lateral elements, all ending in points and partly overlapping each other. Structures similar in shape and position have been found in *Rhamphorhynchus* and the pterodactyls.

THE PECTORAL GIRDLE (FIG. 6)

The scapula and coracoid are firmly fused as a strong hooked element. Both scapulocoracoids lie more or less symmetrically in front of the sternum, showing their medial surfaces. The free articular ends of the coracoids are expanded to 7.5 mm, forming an articular surface with the sternum. Judging from their present position, the articular surfaces with the sternum were located dorsally at the base of the sternal keel, possibly one behind the other. This would be the same position described by Wiman (1923: 47) in a Holzmaden *Dorygnathus* now in Uppsala. The glenoid cavity for the humerus seems to be formed by the scapular part. The articular surface of the cavity is located mainly on the lateral side, which is not visible. The scapular blade narrows to a flattened, laterally broadened bone bearing a more curved, sharp edge, which runs medially and disappears 12 mm from the free end of the ventral margin.

THE FORELIMBS (FIGS. 7, 8, 14C)

HUMERUS: Both humeri lie nearly symmetrically beside the sternum, showing their median sides. Proximally, the right humerus is covered by the coracoid and a rib, but it shows very well the saddle-shaped articular head. The proximal margin shows a middle projection from

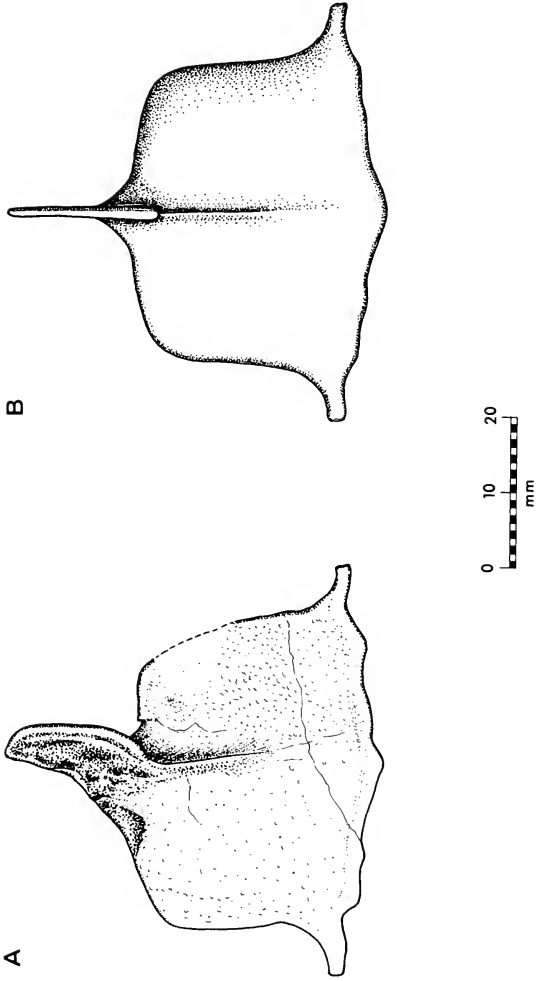


Fig. 5. A, B. *Campylognathoides litasicus*. CM 11424. Sternum. A. As preserved, showing lateral side of the sternal keel. B. Reconstruction of sternum, ventral view.

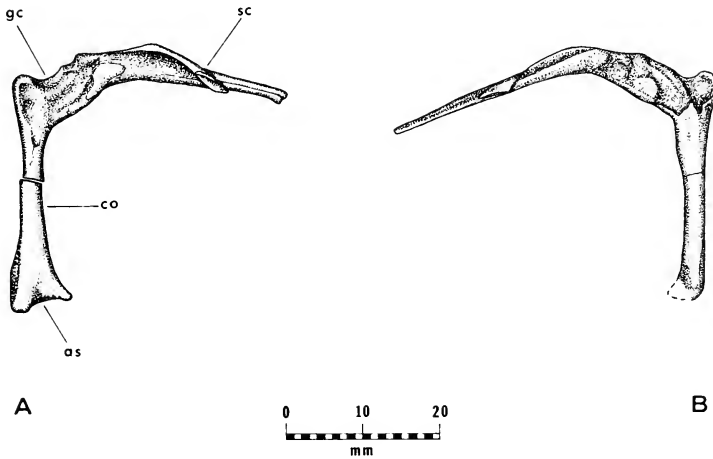


Fig. 6. A, B. *Campylognathoides liasicus*. CM 11424. Scapulocoracoids. A. Right scapulocoracoid, medial view. Articular end of coracoid is twisted, showing the articular surface in posterior view. B. Left scapulocoracoid, medial view. Abbreviations: *as*, articular surface of the coracoid against the sternum; *co*, coracoid; *gc*, glenoid cavity; *sc*, scapula.

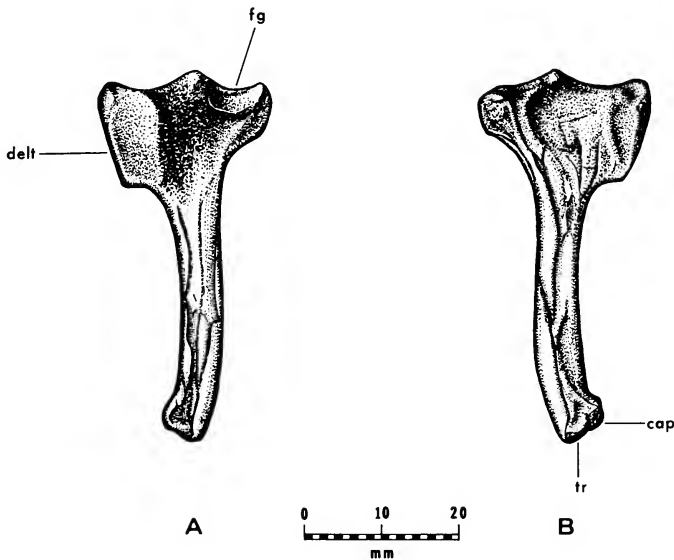


Fig. 7. A, B. *Campylognathoides liasicus*. CM 11424. Humeri. A. Right humerus, medial view. B. Left humerus, medial view. Abbreviations: *cap*, capitellum; *delt*, deltopectoral crest; *fg*, fossa glenoidalis; *tr*, trochlea.

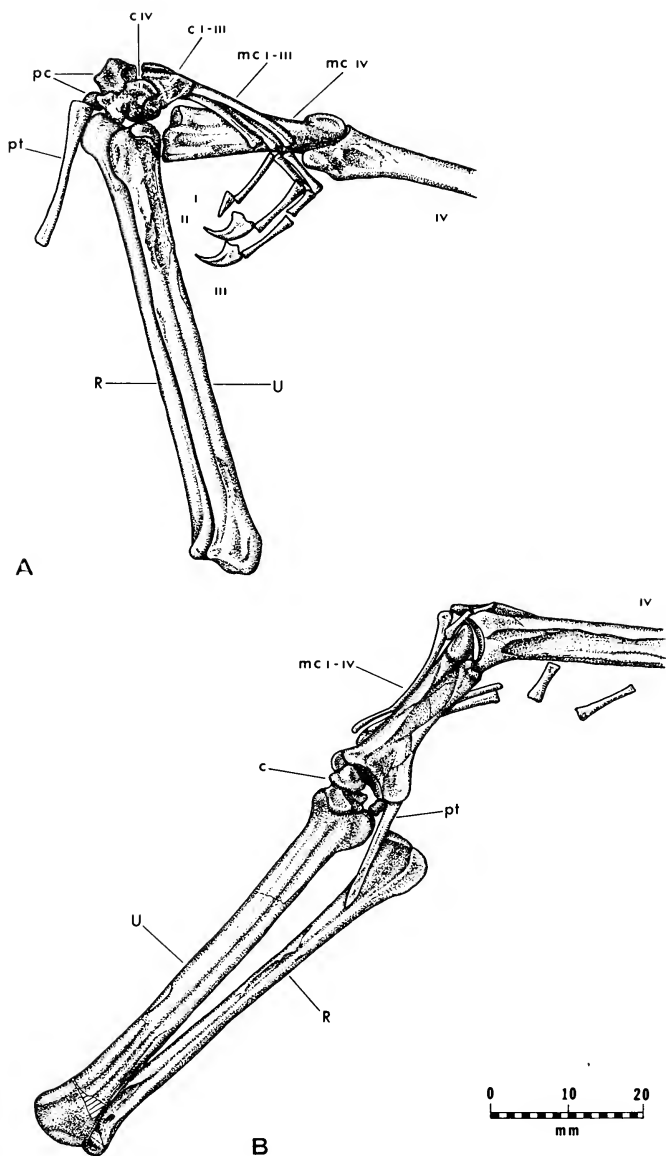


Fig. 8. A, B. *Campylognathoides liasicus*. CM 11424. Radius, ulna, carpus, metacarpus, and digits. A. Left limb. B. Right limb. Abbreviations: c, carpals; mc, metacarpals; pc, proximal carpals; pt, pteroid; R, radius; U, ulna; I, II, III, IV, digits I-IV.

which the deltopectoral crest extends 13 mm and the internal process 10 mm. The deltopectoral crest is a powerful expansion, 14 mm long measured parallel to the shaft. In its distal section the shaft is slightly curved. The position of the trochlea and the capitellum is oblique to the shaft, forming an angle of about 55° .

FOREARM: In the left forearm the radius and ulna are close together. In the right one both are distally separated. The two elements have very broad articulations. The proximal ulnar articulation surpasses that of the radius. When in contact with the oblique articular surface of the humerus, the maximum possible extension between humerus and forearm was at an angle of about 105° . Proximally, the left ulna shows a tendency to an olecranon-like process.

CARPUS: Although pushed out of their natural position, the carpals are easily distinguished, especially the structures of the left carpus. Both proximal and distal rows consist of two carpals. The smallest proximal carpal is a globular element nearly 2 mm in diameter. The larger one, probably originally situated more at the ulnar side, is more cubical and bears several concave articular facets. It is about 3.5 mm in diameter. The two proximal carpals form a complex, 12 mm broad and about 6 mm high. Although not fused, they seem to be very closely connected. The element interpreted as carpal IV is 7 mm wide and distally bears two articular facets facing the metacarpal of the wingfinger. The carpal supporting metacarpals I to III is also 7 mm wide and laterally spans carpal IV. On the radial side of the proximal row of the carpus a pteroid bone articulates, 20 mm in length and slightly curved.

METACARPUS: As usual, the major structure in the metacarpus is the metacarpal of the wingfinger. In the right limb it is exposed from its posterior side, in the left limb from its lateral side. On the base there is a thickening, especially dorsoventrally. In the right arm the articular connection to the first phalanx of the wingfinger is twisted out of its natural position at an angle of about 90° . Thus the distal pulley-like articular surface is partly exposed, but the posterior process of the proximal articulation of the phalanx still meets the pulley. Dorsally the pulley is oval in outline, expanding posteriorly. Ventrally it is covered by the process of the first wing phalanx. The metacarpals of the three small fingers are only slender splints, averaging 1.2 mm in diameter.

PHALANGES: The phalangeal formula of the manus is 2-3-4-4, as is usual in pterosaurs. The first three small digits are still articulated only in the left manus, but are turned over posteriorly. They support relatively strong claws with a broad base that is convex in the middle. The concave margin of the claw is strengthened by a swelling; the tips are sharp and pointed.

The phalanges of the wingfingers are in natural articulation, except for the fourth phalanx of the right wingfinger, which is lying proximally beneath the preceding phalanx. Because of the strong post-mortem compression, the profile of the phalanges is not well preserved, but the anterior edge, visible in the left basal phalanx, seems to be relatively sharp. Posteriorly there was a groove, dorsally and ventrally limited by sharp edges, on the attachment for the wing membrane. The cross section seems thus to be similar to that in *Nesodactylus* from the Upper Jurassic of Cuba (Colbert, 1969: 16, Fig. 10A). Proximally the first phalanx of the wingfinger has a strong anterior process that prevents the wingfinger from over-extending to the front. The bipartite articular socket is bounded posteriorly by a short process, which fit inside a superficial groove just beneath the pulley-like articulation of metacarpal IV when the wing was folded back.

The articulations between the wing phalanges are obtuse and thickened only posteriorly. In life there was not much mobility between them. The first and second wing phalanges are straight, the third is curved slightly anteriorly, and the fourth one slightly posteriorly. The largest phalanx is the second, as in all other specimens of *Campylognathoides* and also of *Dorygnathus*. When the wingarm was folded, the points of bending were between the humerus and forearm and between the fourth metacarpal and first phalanx of the wingfinger.

THE PELVIC GIRDLE (FIGS. 9, 14B)

The highly compressed pelvis is exposed ventrally, but all elements can be identified. Therefore, a rather positive reconstruction of the pelvis is possible. The ilia extend anteriorly as slender pointed blades. The postacetabular processes of the ilia extend posteriorly in short, pointed extremities. The sacral vertebrae are fused with the ilia by robust sacral ribs, leaving foramina between them. Though mostly covered, the length of the pelvis compared to the length of the last dorsal vertebrae suggests that there must have been four sacrals as in *Campylognathoides zitteli* (Plieninger, 1895: 214). The ischiopubes are fused with the ilia without any visible sutures, as plates arched posteriorly and medially. They approached ventrally but did not connect. The element interpreted by Plieninger (1895: 214; 1907: 223) as the ischium is the ischiopubis. Because of this interpretation Plieninger developed an incorrect reconstruction of the pelvis of *Campylognathoides*, assuming a deep sinus separating his supposed ischium and pubis. Based on Plieninger's interpretation, Kuhn (1967: 28) tentatively erected a new subfamily for *Campylognathoides*. But the Pittsburgh specimen shows very clearly that there is a fused ischiopubis plate, so the pelvis of *Campylognathoides* had basically the same construction as that of the Upper Jurassic *Rhamphorhynchus*.

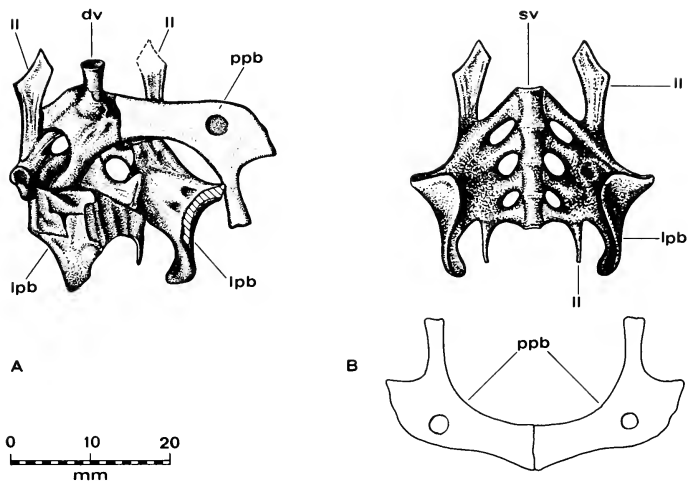


Fig. 9. A, B. *Campylognathoides liasicus*. CM 11424. Pelvis. A. Specimen as preserved. B. Reconstruction, ventral view. Abbreviations: *dv*, dorsal vertebra; *il*, ilium; *ipb*, ischiopubis; *ppb*, prepubis; *sv*, sacral vertebrae.

The prepubes crossing the sacrum and the left ilium are very broad and heavy. The prepubis expands fanlike laterally and especially medially to a thin bony plate rising from a stick-like base. There is a circular fenestra, 2.5 mm in diameter, in the prolongation of the shaft. Medially the prepubis is obtuse where it originally met the opposite element.

THE HIND LIMBS (FIGS. 10, 14D)

The hind legs are still in their natural position. The femora articulate in the pelvis, but the phalanges of the pes are dislocated.

FEMUR: The ilia partly cover the proximal articulations of the femora. Distal to the head there is a slight constriction followed by a trochanteric thickening, the trochanter externus. The shaft is slightly curved and distally thickened to the condyles. Anteriorly the distal condyles are separated by a deep intercondylar fossa for attachment of the tendon quadriceps femoris.

TIBIA AND FIBULA: The tibiae are slender and not curved. The fibulae are covered by the tibiae except at the distal end of the right tibia, where the fibula projects laterally. Thus, the fibula is as long as the tibia and forms its own distal condyle.

TARSUS: The tarsus is not completely preserved. In the right pes there are only two small distal tarsals, and in the left pes three globular distal ones. It is not possible to determine whether the flat ossicle, 5 mm long and situated proximal to the fifth toe, is metatarsal V or an ele-

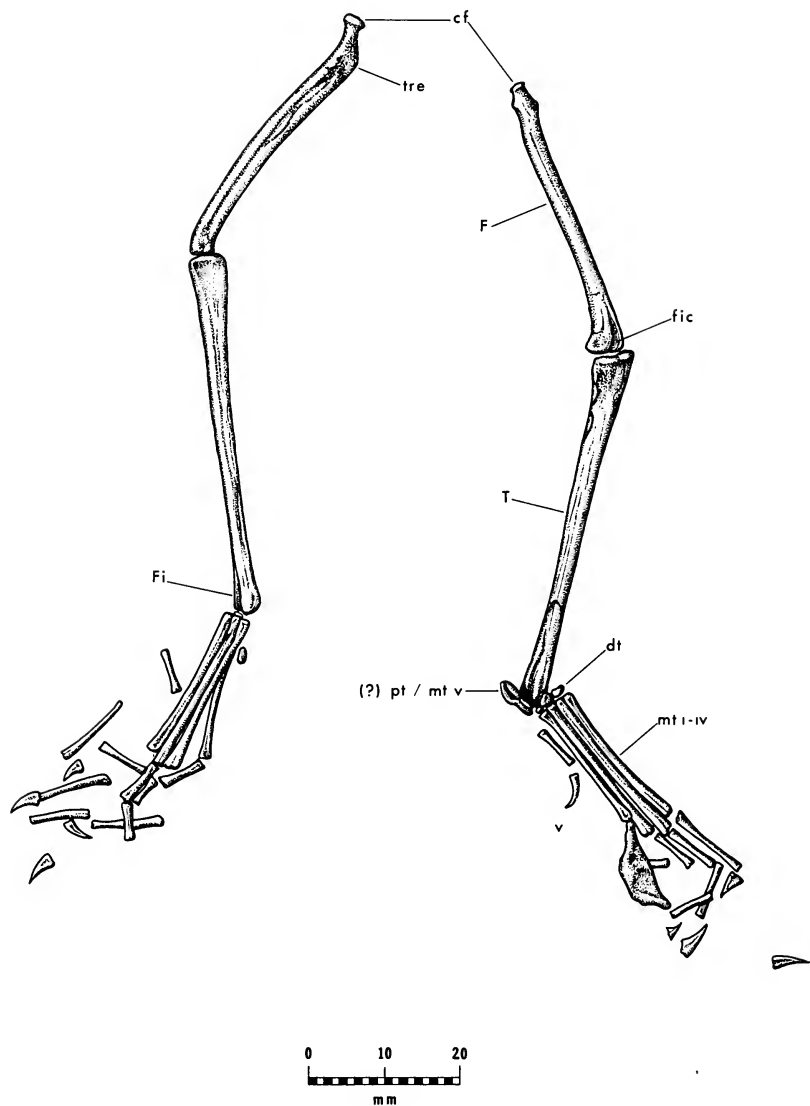


Fig. 10. *Campylognathoides liasicus*. CM 11424. Hind legs as preserved, ventral view. Abbreviations: *cf*, caput femoris; *dt*, distal tarsals; *F*, femur; *Fi*, fibula; *fic*, fossa intercondylaris; *mt*, metatarsals; *pt*, proximal tarsals; *tre*, trochanter externus; *V*, fifth toe.

ment of the proximal row of the tarsus. The corresponding elements in the opposite foot are lacking. Possibly the proximal row of the tarsus is fused with the tibia as it is in *Campylognathoides zitteli* (Plieninger, 1895: 216).

METATARSUS: Metatarsals I to IV are long, slender splints with well-developed distal articulations. Lying close together, they have flattened contact facets against the adjacent metatarsals, so they were possibly very close in position.

PHALANGES: The phalanges of the feet are dislocated but almost all present. The phalangeal formula must have been 2-3-4-5-2, which is the usual one in all rhamphorhynchoids. The distal phalanges of toes I to IV are small, slightly curved claws. The fifth toe consists of a long proximal phalanx and a distal phalanx that is bent medially and pointed like a claw.

The fourth toe of the left foot is peculiar. Instead of phalanges, a bony plate articulates with the fourth metatarsal, 13 mm in length and broadened medially to 4 mm. Since four claws are preserved, this bone must also have supported a claw. This is apparently a deformity of the fourth toe in which the four phalanges have grown together, forming a single broad bone.

TABLE I
MEASUREMENTS (IN MM) OF *Campylognathoides liasicus*, CM 11424

Skull		
Length	83	
Height across the postorbitals	29	(restored)
External naris, length	19	
External naris, height	6	
Preorbital fenestra, length	10.5	
Preorbital fenestra, height	6.0	
Orbit, length	20	
Orbit, height	21.5	(restored)
Number of upper teeth (4 pm, 10 m)	14	(restored)
Mandible		
Length	66.3	
Height in the middle of the ramus	4.2	
Retroarticular process, length	5	
Toothless tip, length	5	
Number of lower teeth	12	
Vertebral column		
Cervical vertebra II, length of centrum	4	
Cervical vertebra III, length of centrum	5.5	
Cervical vertebra IV, length of centrum	8.0	
Cervical vertebra V, length of centrum	8.4	
Cervical vertebra VI, length of centrum	8.5	
Cervical vertebral column, length	53	(restored)
Dorsal vertebra, length of centrum	5.2	
Dorsal vertebra, height of neural spine	5.7	

TABLE 1, *cont'd.*

Sacrum, length	18	(restored)
Caudal vertebra 1, length of centrum	—	
Caudal vertebra 2, length of centrum	3.7	
Caudal vertebra 3, length of centrum	5.0	
Caudal vertebra 4, length of centrum	5.8	
Caudal vertebra 5, length of centrum	8.3	
Caudal vertebra 6, length of centrum	12.3	
Caudal vertebra 7, length of centrum	14.2	
Caudal vertebra 8, length of centrum	14.7	
Caudal vertebra 9, length of centrum	15.0	
Caudal vertebra 10, length of centrum	15.0	
Caudal vertebra 11, length of centrum	15.0	
Caudal vertebra 12, length of centrum	15.0	
Caudal vertebra 13, length of centrum	15.0	
Caudal vertebra 14, length of centrum	15.0	
Caudal vertebra 15, length of centrum	14.6	
Caudal vertebra 16, length of centrum	14.3	
Caudal vertebra 17, length of centrum	14.0	
Caudal vertebra 18, length of centrum	13.1	
Caudal vertebra 19, length of centrum	11.7	
Caudal vertebra 20, length of centrum	10.1	
Caudal vertebra 21, length of centrum	9.2	
Caudal vertebra 22, length of centrum	8.0	
Caudal vertebra 23, length of centrum	7.5	
Caudal vertebra 24, length of centrum	7.2	
Caudal vertebra 25, length of centrum	6.9	
Caudal vertebra 26, length of centrum	6.2	
Caudal vertebra 27, length of centrum	6.0	
Caudal vertebra 28, length of centrum	5.8	
Caudal vertebra 29, length of centrum	5.6	
Caudal vertebra 30, length of centrum	5.4	
Caudal vertebra 31, length of centrum	5.2	
Caudal vertebra 32, length of centrum	5.0	
Caudal vertebra 33, length of centrum	4.5	
Total length of tail	325	(restored)
Sternum, length	49.7	
Sternal plate		
Breadth, anteriorly	38	
Breadth, posteriorly	55	
Sternal keel, height	9	
Breadth	1.5	
Length	18.5	
Scapula, length (approx.)	37	
Coracoid, length (approx.)	30	
Medial breadth	3.0	
Distal breadth	7.5	
Humerus		
Length	50.3	
Breadth across deltopectoral	22.8	
Medial breadth of the shaft	5.9	
Radius, length	59.5	
Medial breadth of the shaft	3.2	

TABLE I, *cont'd.*

Ulna, length	60.3			
Medial breadth of the shaft	5.2			
Carpus, length (approx.)	7			
Pteroid, length	20			
Metacarpal I, length	19.5			
Metacarpal II, length	21			
Metacarpal III, length	22			
Metacarpal IV, length	23			
Proximal breadth	10.0			
Medial breadth	5.0			
Distal breadth	5.6			
Digit I, phalanges 1 - 2	8.5	5		
Digit II, phalanges 1-3	5.0	8.2	5.0	
Digit III, phalanges 1-4	6.5	4.5	8.1	5.0
Digit IV, phalanges 1-4 (wingfinger)	93.3	96.0	84.5	69.6*
Wingfinger, total length	343.4			
Pelvis				
Ilium, length	27			
Preacetabular process, length	15			
Postacetabular process, length	8			
Prepubis, height	15.5			
Breadth	20			
Femur				
Length	37.6			
Breadth, distally	4.8			
Diameter of head (approx.)	2			
Medial breadth of the shaft	2.6			
Tibia				
Length	47.4			
Breadth, proximal	5			
medial	2.7			
distal	4			
Metatarsal I, length	20.5			
Metatarsal II, length	22.0			
Metatarsal III, length	21.6			
Metatarsal IV, length	17.8			
Digit I, phalanges 1-2	11.0	4.0		
Digit II, phalanges 1-3	7.7	7.6	4.5	
Digit III, phalanges 1-4	7.6	—	—	—
Digit IV, phalanges 1-5	6.5	4.5	5.5	—
Digit V, phalanges 1-2	6.0	4.5		
Pes, total length (approx.)	45			
Wingspan (restored)	920			
Total length (restored)	535			

*By mistake Colbert (1969: 21) gave the measurement of the fourth wingphalanx as 96.6 mm.

SYSTEMATIC POSITION

In his description of *Campylognathoides zitteli* Plieninger (1895: 218; and 1907: 234) pointed out the differences between *Campylognathoides* and *Dorygnathus*. The differences separating these two genera appear especially in the morphology of the skull, dentition, mandible, sternum, shoulder girdle, and pelvis. With regard to these differences, the Pittsburgh specimen is a typical *Campylognathoides*. Both genera are also distinct in the proportions of certain skeletal segments. The first wing phalanx of *Campylognathoides* is much longer than its forearm, in contrast to *Dorygnathus* in which the forearm is always longer than the first wing phalanx.

For determination of species we must first examine the type specimen of *Campylognathoides zitteli*. In it we can recognize a much larger external naris relative to the preorbital fenestra. Furthermore, there are four premaxillary teeth and probably ten maxillary teeth, as in the Pittsburgh specimen. It is remarkable that in both specimens the fourth upper tooth is the strongest one. Also the lower jaw has the same toothless tip and is slightly curved ventrally. However, there are differences in the number of lower teeth, *C. zitteli* having 19 and the Pittsburgh specimen only 12 teeth in the mandible. Besides, the largest lower tooth in *C. zitteli* is the first one, not the second one as in the Pittsburgh specimen and the Paris specimen. Based on Plieninger's observations (1895: 204) and my own study of the Pittsburgh specimen, it is not possible that the quadratojugal of *Campylognathoides* was as expanded as shown in Arthaber's (1921) restoration. There, the quadratojugal forms the entire anterior margin of the infratemporal fenestra. Actually, it could have been only a small element connecting the jugal and the quadrate ventrally. Also, the prefrontal as figured by Arthaber is not visible. In this place, between the frontal and external naris, there is only one bony structure, the nasal. Von Huene (1914: 60) did not distinguish a prefrontal.

The shape of the scapula as described by Plieninger in *C. zitteli*, bearing a sharp dorsally turned edge medially, is close to the Pittsburgh *Campylognathoides*, as is the distal broadening of the coracoid articulation and, so far as I can see, the shape of the sternal keel. The pelvis of *C. zitteli*, exposed from its dorsal side, shows shorter and broader ilia. It is uncertain how much the ischiopubial plates agree, because of different preservation. The prepubes, important for comparison, are entirely lacking in *C. zitteli*.

The type specimen of *C. zitteli* is much larger than the Pittsburgh *Campylognathoides* and the other three specimens of the genus. Comparative measurements of all five specimens are given in Table 2.

The precaudal dorsal vertebral column is not preserved in any of the five specimens, and so we have no reference length for allometric in-

TABLE 2
Comparative measurements (in mm) of the specimens of *Campylognathoides*

	<i>C. liasicus</i> , Type, Quenstedt 1858 Tübingen	<i>C. liasicus</i> , Plieninger 1907 Pittsburgh	<i>C. liasicus</i> , Wiman 1923, Uppsala	<i>C. liasicus</i> , Hauff 1953 Paris*	<i>C. zitteli</i> , Type, Plieninger 1895, Stuttgart
Skull	—	83	—	90	130
Mandible	—	66.3	66	72	115
Humerus	42	50.3	55	53	70 (restored)
Ulna	52	60.3	65	64	82
Metacarpal IV	19	23	23	24	30
Digit IV	—	—	—	—	—
Phalanx 1	82.5	93.3	95	97	185
Phalanx 2	—	96.0	102	102	209
Phalanx 3	—	84.5	—	87	165
Phalanx 4	55	69.6	—	69	121.5
Femur	—	37.6	40	38	65
Tibia	—	47.4	53	47	88

*Measurements taken from photographs.

TABLE 3
Comparative skeleton proportions in the specimens of *Campylognathoides*

	<i>C. liasicus</i> Tübingen	<i>C. liasicus</i> Pittsburgh	<i>C. liasicus</i> Uppsala	<i>C. liasicus</i> Paris	<i>C. zitteli</i> Stuttgart
Ulna/Humerus	1.24	1.20	1.18	1.20	1.17 (restored)
Ulna/Metacarpal IV	2.74	2.63	2.83	2.66	2.73
Ulna/Tibia	—	1.27	1.23	1.36	0.93
Tibia/Femur	—	1.26	1.33	1.24	1.35
Ulna/Phalanx I of Digit IV	0.63	0.65	0.68	0.66	0.44
Femur/Ulna	—	0.62	0.62	0.59	0.79

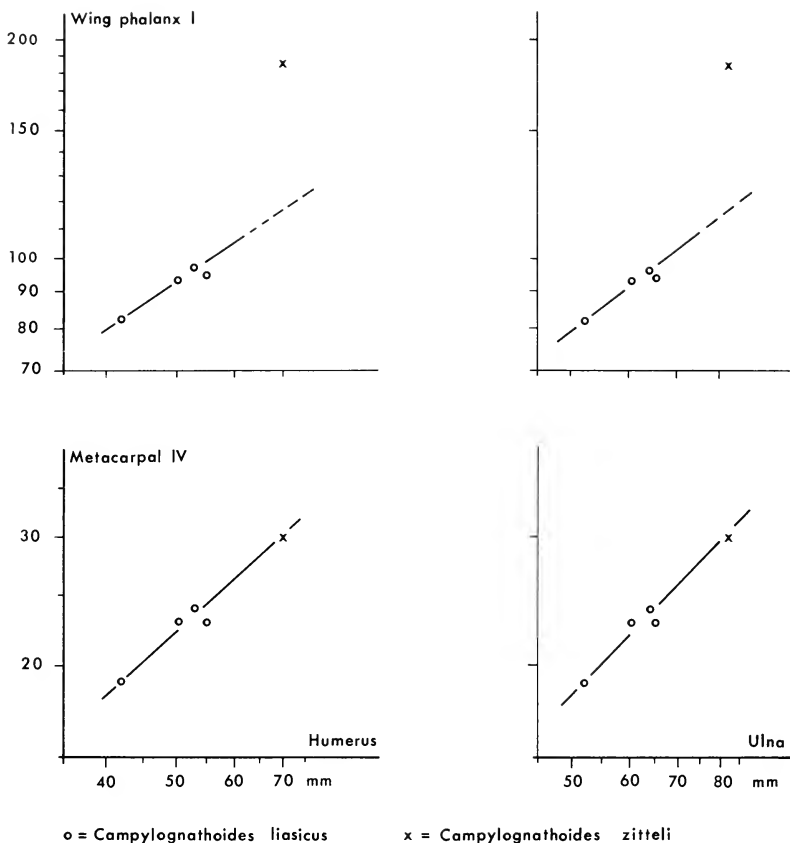


Fig. 11. Diagrams showing allometric growth of metacarpal IV and wing phalanx I relative to growth of humerus, left row, and ulna, right row. Based on all five specimens of the genus *Campylognathoides*. The length of the humerus of *C. zitteli* is restored.

vestigations. The length of the humerus, usually growing isometrically with the dorsal vertebral column (Wellnhofer, 1968: 119), could also be used, but unfortunately the humerus of *C. zitteli* is not completely preserved. Assuming that the ratio between the length of the humerus and the length of the ulna is the same, as it is fairly constant in the other four specimens, the length of the humerus of *C. zitteli* can be calculated as 70 mm.

The diagrams shown in Figures 11 and 12 reflect the allometric growth of metacarpal IV, the first wing phalanx, the femur, and the tibia compared to the length of the humerus or the length of the ulna. The growth of the metacarpal shows no specific difference in any of the

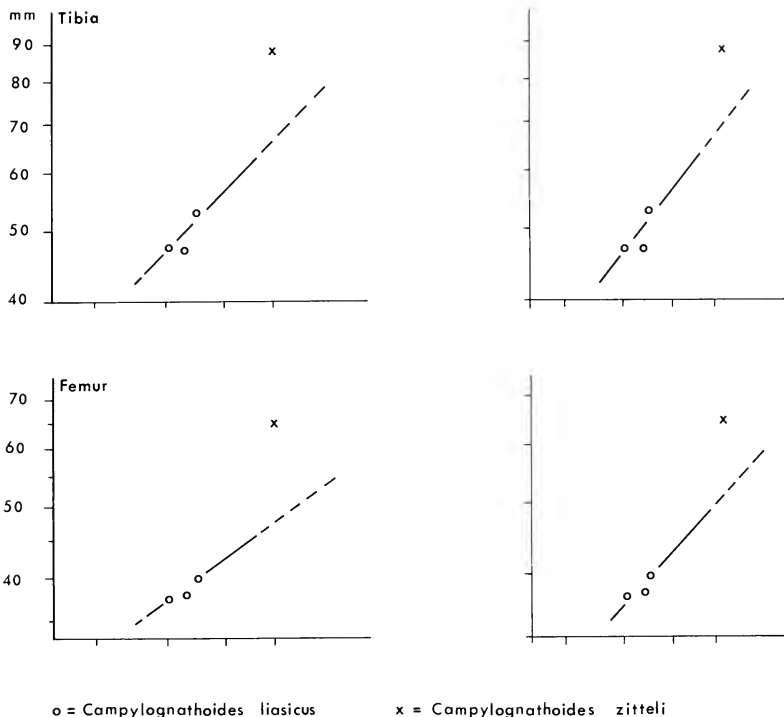


Fig. 12. Diagrams showing allometric growth of femur and tibia relative to growth of humerus, left row, and ulna, right row. Based on all five specimens of the genus *Campylognathoides*. The length of the humerus of *C. zitteli* is restored.

five specimens. However, with regard to the first wing phalanx and the femur it is apparent that these bones become much bigger in *C. zitteli* than in the other four specimens. The fact that they cannot be juvenile forms of *C. zitteli* can be proved by the Pittsburgh specimen. Also, the tibia is relatively longer in *C. zitteli* than in the comparable specimens from Pittsburgh, Uppsala, and Paris. Comparative proportions of some skeletal elements are given in Table 3.

The four smaller specimens are relatively close in their numerical values and are clearly distinct from *C. zitteli*. Exceptions are the ratio between the femur and the tibia and between the metacarpal and the ulna, which are more or less constant in all specimens. But in *C. zitteli* the tibia is larger than the ulna and in the other specimens it is smaller. Though generally longer than the ulna, the first wing phalanx reaches more than twice the length of the ulna in *C. zitteli*. Thus *C. zitteli* is not only absolutely larger but also has relatively longer hindlegs and longer wingfingers than the four remaining specimens. The specimens from

Tübingen, Uppsala, Paris, and Pittsburgh are not specifically distinct from one another. They are separable from *C. zitteli* as *Campylognathoides liasicus* (Quenstedt) (Wiman, 1923: 45; Wild, 1971: 187).

SYSTEMATIC POSITION OF *Campylognathoides*

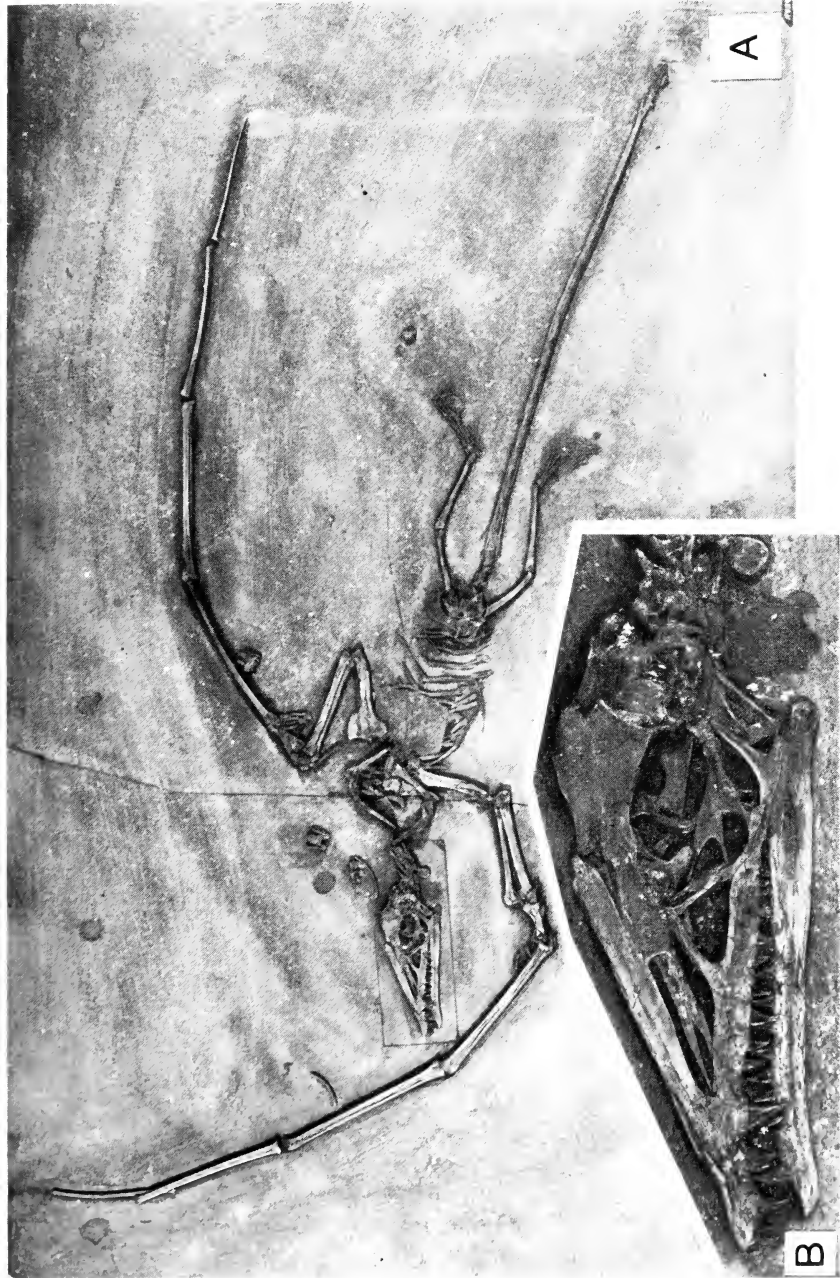
Based on the Pittsburgh specimen, it is possible to get a clear idea about the structure of the *Campylognathoides* pelvis for the first time. There is no fundamental difference between it and the pelvis of *Dorygnathus* and *Rhamphorhynchus*. Although the form of the prepubes is somewhat different, all three genera have an undivided ischiopubial plate. The opinion, valid until now, that the ischium and the pubis of *Campylognathoides* were separate, has to be corrected. Therefore, *Campylognathoides* should not be placed in its own subfamily (Kuhn, 1967: 28). In general the question is whether or not this characteristic is significant systematically at all, since, for example, the ischium and pubis are fused to an ischiopubis in the Upper Jurassic species *Rhamphorhynchus muensteri* (Goldfuss) but not in *R. longicaudus* (Muenster), which shows a deep sinus separating both elements.

With regard to its present phylogenetic position, *Campylognathoides* seems to be fairly isolated. No direct connection is possible either to the earlier genera, e. g., the Lower Jurassic *Dimorphodon*, or to the later Upper Jurassic rhamphorhynchids. *Campylognathoides* is also clearly distinct from contemporary forms, as has been already demonstrated for *Dorygnathus*. In *Parapsicephalus* from the Upper Liassic of Whitby (England) the preorbital fenestra is the largest skull opening, in contrast to *Campylognathoides*. Although the postcranial skeleton is not known, there are relatively close similarities in the palate as it is figured by von Huene (1914: 59). *Campylognathoides* and *Parapsicephalus* are similar in the form of the slender vomers, the long internal nares bounded laterally by the palatines, and the long medial pointed tips of the pterygoids, although *Parapsicephalus* is not known well enough to deduct a closer relationship.

The ancestors of *Campylognathoides* are not known. *Dimorphodon* from the Lower Liassic of Lyme Regis (England) is out of the question. Its skull is larger, the snout higher, the external nares larger than the orbits, the quadrate is a more vertical position, and the dentition, especially that of the mandible, is completely different from *Campylognathoides*.



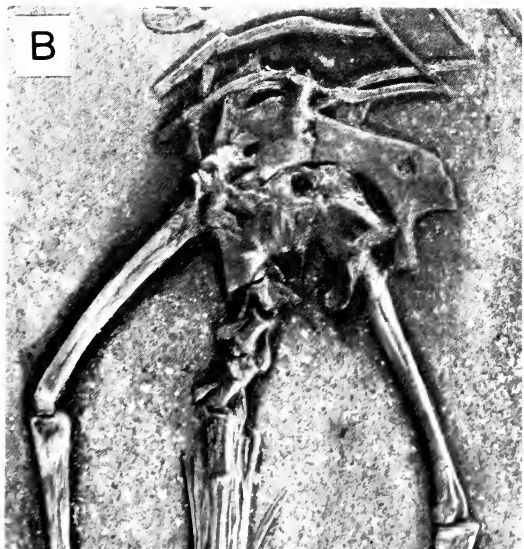
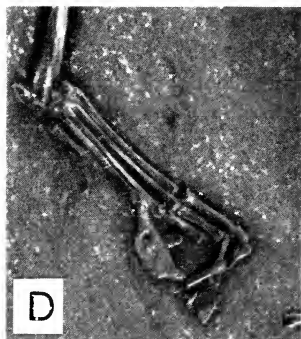
Fig. 13. *Campylognathoides liasicus* (Quenstedt), Upper Liassic, Holzmaden, CM 11424. A. Skeleton, approximately X 1/3. B. Skull, actual size.



We may ask whether *Campylognathoides* itself could be taken as an ancestor of the Upper Jurassic rhamphorhynchoids, especially since the genus *Rhamphorhynchus* from the Solnhofen lithographic limestone is very well known and represented by numerous specimens. There are common characteristics in the pelvis (not in *R. longicaudus*), except the prepubes, which are much more slender in *Rhamphorhynchus*, and in the shoulder girdle. The limb bones are at any rate morphologically very similar in all rhamphorhynchoids. The skull of *Rhamphorhynchus* is lower, more elongated, with toothless pointed tips, and forwardly directed, long teeth. The external naris is relatively small, as is the preorbital fenestra. The quadrate is more horizontal. Although all these differences could be interpreted as a result of evolutionary change during the uppermost Liassic, the entire Middle Jurassic, and most of the Upper Jurassic, restrictively *Dorygnathus* seems to be a more probable ancestor of *Rhamphorhynchus*, since it also has long, forwardly directed teeth and long toothless tips of the jaws.

Scaphognathus, also from the Upper Jurassic Solnhofen limestone, has a high skull, a more vertical quadrate, and large preorbital fenestrae like *Campylognathoides*. Also, the teeth are more or less upright in the jaws. The palate, especially, with its long, slender vomers and the medial tips of the pterygoids extending between them, is remarkably similar to that in *Campylognathoides*, although there are some differences. The external nares of *Scaphognathus* are smaller than the orbits, the teeth are slender and long, and reduced to eight in the upper jaw and to five in the mandible. Furthermore, the ischium and the pubis were not fused, as shown by a specimen kept in the "Museum am Solenhofer Aktienverein" in Solnhofen (Maxberg). Thus, *Campylognathoides* must be eliminated as a possible ancestor of *Scaphognathus*. We must wait for more discoveries, especially from the Middle Jurassic, to elucidate satisfactorily the phylogenetic relationships between the different genera of the Rhamphorhynchoidea.

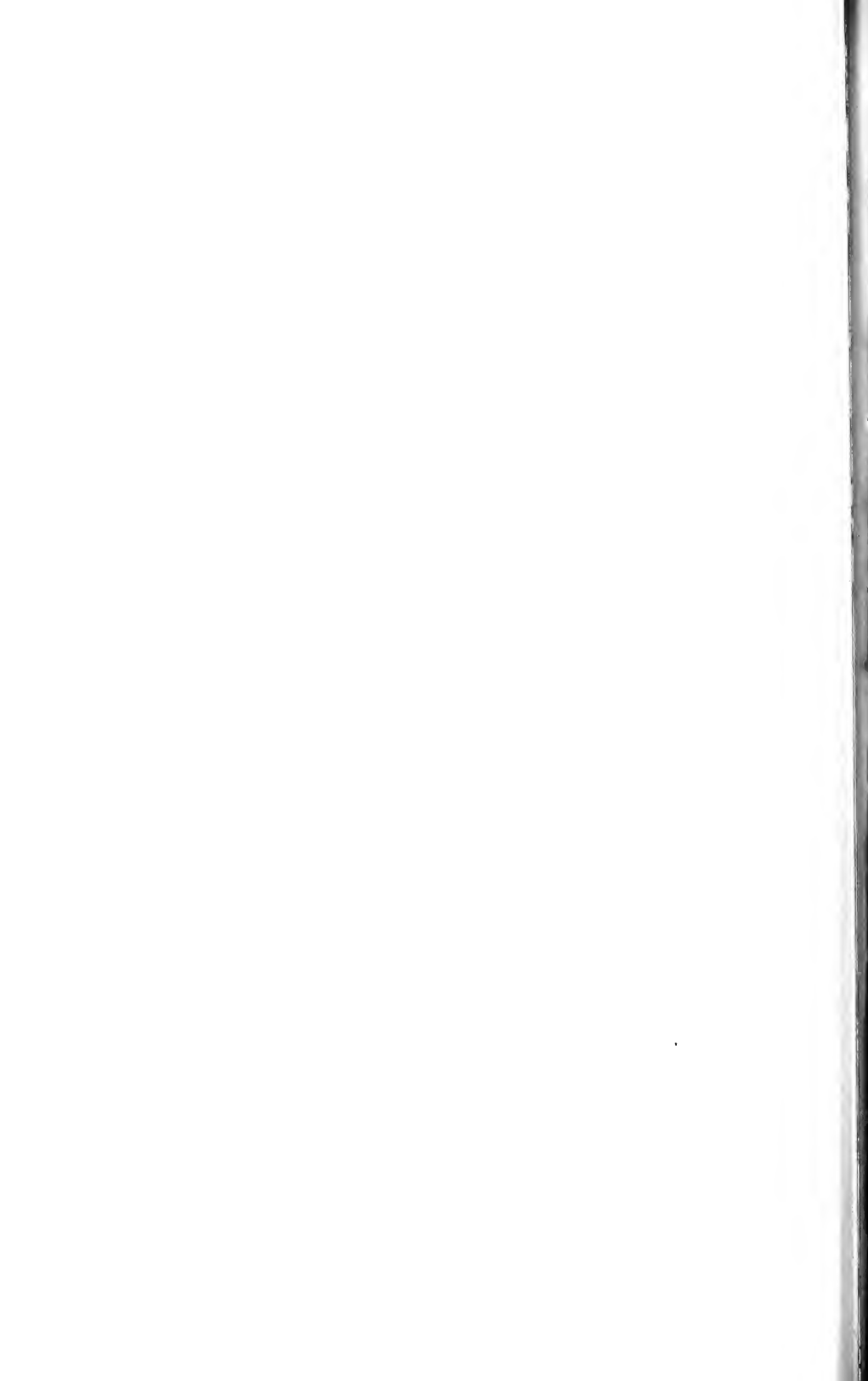
Fig. 14. *Campylognathoides liasicus* (Quenstedt), Upper Liassic, Holzmaden, CM 11424. A. Sternum showing the articulation of both coracoids on the dorsal side of the sternal keel. B. Pelvis region, ventral view. C. Left carpus, metacarpus, digiti and pteroid. D. Left foot, showing the abnormal shape of the fourth toe. E. Proximal section of the caudal vertebral column, showing the rodlike extensions of the zygapophyses and chevrons. All figures natural size.



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GEOGRAPHIC VARIATION IN THE FLAME MINIVET (*PERICROCOTUS FLAMMEUS*) ON THE ISLAND OF MINDANAO, PHILIPPINES (AVES: CAMPEPHAGIDAE)

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Curator of Birds

The Flame Minivet (*Pericrocotus flammeus*) ranges from the Indian subcontinent across the mainland of southern Asia to Indonesia and the Philippines. It is highly polytypic: 17 races were admitted by Deignan (1960). The most recent work on Philippine birds (duPont, 1971: 243-244) lists five subspecies (one described after Deignan's list appeared) from that archipelago, of which two are attributed to the large island of Mindanao: *P. f. johnstoniae* Ogilvie-Grant, 1905, and *P. f. gonzalesi* Ripley and Rabor, 1961. They are said to be endemic to Mount Apo and Mount Katanglad respectively, and no other Mindanao localities are mentioned for this species. This restriction was obviously an oversight, as duPont himself has reported the species from two localities in northern Misamis Oriental Province and from Lake Lanao, Lanao Province (Meyer de Schauensee and duPont, 1962: 161). In point of fact, *Pericrocotus flammeus* is widely distributed on the island of Mindanao, having been collected at localities from Mount Mayo, Davao Province, at the southeastern corner of the island, to at least as far west as Mount Sugarloaf in the east-central part of the Zamboanga Peninsula (see Fig. 1). Altitudes shown on labels I have examined range from less than 1000 feet at Lanuza, Surigao del Sur Province, to 7000 feet on Mount Apo.

The chief geographically variable character in this species on Mindanao is the color of males. All have the head, foreback, much of the

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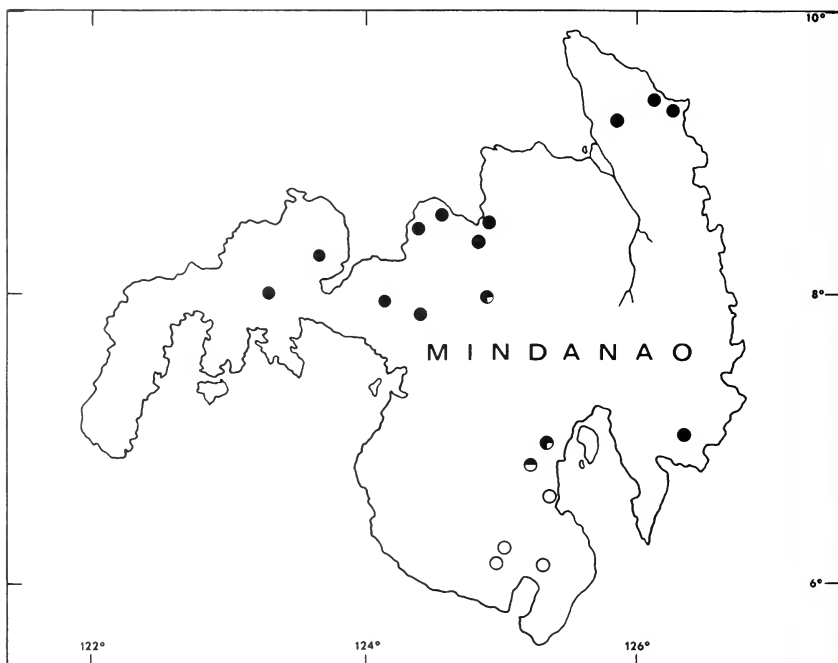


Fig. 1. Distribution of Mindanao specimens of *Pericrocotus flammeus* examined. Open circles = *P. f. neglectus*. Spot $\frac{1}{2}$ black = Mount Apo = *P. f. johnstoniae*. Spots $\frac{1}{4}$ black = (south) Mount McKinley; (north) Mount Katanglad, type locality of *P. f. gonzalesi* (see text). Black spots = *P. f. gonzalesi*.

wing, and the basal and central part of the tail glossy black. The mid-back to upper tail coverts, underparts beyond the throat, wing speculum, and distal portions of the rectrices vary from lemon yellow to rich orange, although no Mindanao population is as deeply orange or red-orange as are the more northern Philippine races *P. f. leytensis* Steere and *P. f. novus* McGregor.

Males from most of Mindanao have the variable areas mentioned above orange in color, with the underparts always somewhat paler than the back, wings, and tail. In southern Mindanao the orange color of males is replaced by lemon yellow, slightly washed with orange on the rump only. This yellow population has been completely overlooked in the literature, although specimens have been collected by several expeditions, at least as far back as the Hachisuka expedition of 1930. Deignan (1946:514-515) strongly (and, as we now know, erroneously) emphasized *marchesae* of the Sulu Archipelago as "the one race with a pure yellow male."

In females of all Mindanao populations, the black heads and backs of males are replaced by gray, the brightly colored areas are invariably yellow, the yellow of the underparts extends anteriorly to include the throat, and there is a yellow band across the forehead at the base of the bill. Within Mindanao, geographic variation in females is expressed chiefly in bill size.

As indicated above, two names are in current use for Flame Minivets of Mindanao. Their type localities could hardly be more unfortunate from the nomenclatorial viewpoint. Specimens from Mount Apo (= *johnstoniae*) are almost perfect intermediates between the orange and yellow populations, and are somewhat variable as would be expected of such intermediates. The cotypes in the British Museum (Natural History), which I have examined, are well illustrated in the plate accompanying the paper by Ogilvie-Grant (1906: pl. XIX, facing p. 480). Two other males from Mount Apo now before me are rather more yellowish beneath than the male cotype. The wing and tail markings of Mount Apo birds are pale orange, the rump somewhat deeper, and the underparts rich yellow, variably washed with orange. Ripley and Rabor (1961: 8) described their new *gonzalesi* as differing from *johnstoniae* of Mount Apo "in the male by being more richly orange-yellow on undersurface, wing edgings, and tail . . . *gonzalesi* is a very well-marked intermediate . . . representing a discontinuous cline in a stage from the lemon-yellow or egg-yellow populations, *johnstoniae* and *marchesae* of Sulu, and the rich vermilion orange of *novus* and *leytensis*." The authors gave the range of *gonzalesi* only as "Mount Katanglad, central Mindanao from 4,000 to 5,000 feet." The Mount Katanglad population does, indeed, represent a stage along a cline, but actually part of the cline exists *within* Mindanao. The type specimen of *gonzalesi* and another adult male from Mount Katanglad are absolutely indistinguishable from a male from Mount McKinley, Davao Province, a peak at the northern edge of the complex of peaks that also includes Mount Apo to the south (Hoogstraal, 1951). They are distinctly paler and less deeply orange than males from anywhere within a great arc extending from Mount Mayo, southeastern Davao Province, north through Surigao, west through Misamis Oriental and Lanao Provinces, to the Zamboanga Peninsula. Although males from within this arc vary somewhat, they are relatively consistent and are uniformly brighter than the Mount McKinley and Mount Katanglad specimens. Ideally we should be able to use only two names for Flame Minivets of Mindanao: one for the orange birds found throughout most of the island in the west, north, and east; and one for the lemon-yellow birds of the south, simply describing the area of intergradation between these two in central Mindanao. Unfortunately, both of the presently available names are based on populations from within this area of intergradation. Mount Apo

birds are so precisely intermediate in color that the name *johnstoniae* cannot possibly be applied to either the orange or yellow populations. It seems best to restrict the name to the birds of Mount Apo itself. Although the name *gonzalesi* is also based on a population along the cline of intergradation, the birds of Mount Kantanglad are clearly closer to the orange populations than to the yellow. Rather than restrict the name *gonzalesi* to one portion of the orange-yellow cline and thus be forced to use four names for Mindanao subspecies, I prefer to broaden the concept of Ripley and Rabor and call all the Mindanao populations with orange males *gonzalesi*.

The yellow population of southern Mindanao remains to be discussed. As stated above, it has not been mentioned in the literature. Specimens in the Hachisuka collection were identified as "*johnstoniae*," while those in subsequent collections have been labelled "*marchesae*." The latter is a yellow but quite distinct subspecies confined to the island of Jolo in the Sulu Archipelago. The yellow Mindanao birds may appropriately be called:

***Pericrocotus flammeus neglectus*, new subspecies**

HOLOTYPE: AMNH 783646, collected at Sitio Balisong, Barrio Kablon, Tupi, Cotabato Province, Mindanao, 23 February 1962, by members of the Philippine National Museum - American Museum of Natural History expedition (field no. 179).

CHARACTERS: Males differ from all other Philippine races of the species except *marchesae* of Jolo in having the underparts, lower back, and markings of wings and tail yellow rather than some shade of orange; at most, the central part of the rump is slightly washed with yellow-orange. Males differ from *marchesae* in having all yellows distinctly less rich — lemon yellow rather than egg yellow. Both sexes differ from *gonzalesi* (in the expanded sense used here) in having somewhat shorter bills (see list of measurements below). Females of *neglectus* are close to those of *gonzalesi* in color, but have the yellow of the underparts, on the average, less intense and somewhat greener in hue. The females of both these races are very different from those of *marchesae*. In the latter, the upperparts, instead of being bluish gray with no gloss, are blue-black as in males. This is true only of definitively plumaged female *marchesae*. First-year females are dark, dull gray above, somewhat browner (less blue) than females of *neglectus* and *gonzalesi*; as in other Campephagidae, this age class is recognizable by its more pointed rectrices and light tips to the tertials. Deignan (1946:515, 521-522) erroneously described a gray-backed first-year female *marchesae* as a variant adult. Females of both age classes of *marchesae* are richer yellow below than those of the Mindanao races.

MEASUREMENTS: Wings were measured flat, and bills from the forehead, both to the nearest 0.5 mm. In males, only adults were measured. In females, no significant difference was found between first-year and older birds in wing and bill measurements, so age classes were combined. Ranges and means (in parentheses) are given.

P. f. neglectus: 11 males wing 78.5 - 83.5 (80.6); 10 males bill 15.5 - 17.5 (16.75); 7 females wing 75 - 82 (78.2); 7 females bill 15 - 17.5 (16.4).

P. f. johnstoniae: 2 males wing 79.5, 80.5; 2 males bill 17, 17.5; 2 females wing 77.5, 79; 2 females bill 17, 18.5.

P. f. gonzalesi: 27 males wing 79 - 84 (81.0); 26 males bill 16.5 - 18.5 (17.7); 17 females wing 76 - 82 (79.5); 16 females bill 17.5 - 19 (17.9).

P. f. marchesae: 4 males wing 78.5 - 79.5 (79.0); 3 males bill 16 - 17 (16.7); 3 females wing 79 - 80.5 (79.8); 3 females bill 15.5 - 16.5 (16.0).

Although the sample of *johnstoniae* is small, it can be seen that this form is intermediate between *neglectus* and *gonzalesi* in bill size as well as in color.

RANGE of *neglectus*: Southeastern Cotabato and southwestern Davao Provinces, Mindanao Island, Philippines. Much of southern Mindanao is unknown ornithologically, and the range of this race is undoubtedly more extensive than suggested by the list of localities from which it is presently known.

REMARKS: The syntypes (or cotypes) of *Pericrocotus johnstoniae* Ogilvie-Grant are a pair, male and female, in the British Museum (Natural History) collection at Tring. In accordance with the practice of this museum, only one of the syntypes has been segregated and placed with the type collection. As indicated by Warren and Harrison (1971: 265), it is the female syntype of *johnstoniae* that has been so segregated, while the male remains in the main collection. This was an unfortunate choice, as the females of this group of minivets, as shown above, are not entirely separable by color, and, although *neglectus* and *gonzalesi* females are generally separable on bill size and often by color, *johnstoniae* is intermediate between these two forms. The male of *johnstoniae*, on the other hand, is easily recognizable by its nearly exact intermediacy in color between the strikingly different *neglectus* and *gonzalesi*. I therefore take this opportunity to designate formally as lectotype the male syntype of *Pericrocotus johnstoniae* Ogilvie-Grant, BM(NH) 1905-11-26-83.

It should be noted that the color plate accompanying the original description of *Pericrocotus marchesae* (Guillemard, 1885: pl. XVIII, facing p. 247) is much too orange. This plate was reproduced in Hachisuka (1935: pl. 50, facing p. 362) with little if any improvement.

In the original description of *gonzalesi*, Ripley and Rabor (1961: 8) stated that "two females appear to bear this difference out [more richly orange-yellow on the undersurface, wing edgings, and tail than *johnstoniae*], although in one specimen the difference is only readily ob-

servable in the color of the tail." Although sexed as female on the label, YPM 62374, which is more richly colored than females of *johnstoniae*, is in fact an immature male. The *only* female in the type series of *gonzalesi* does not differ in tail color, to my eye, from other Mindanao females of this species.

Finally, the catalogue number of the holotype of *gonzalesi* was given in the original description (Ripley and Rabor, *loc. cit.*) as YPM no. 58896. This number does not now appear on the label of the holotype, which is numbered YPM 61785. I am informed by my colleague, Dr. Mary Heimerdinger Clench, who was at Yale at the time, that the type specimens in the collection from which *gonzalesi* came were renumbered after the description of *gonzalesi* was published, and the later (higher) catalogue number is to be considered correct.

SPECIMENS EXAMINED (all localities mentioned except for those of *marchesae* are on the island of Mindanao, and are arranged from west to east by province): *neglectus*: Cotabato: Sitio Balisong, Barrio Kablon, Tupi [vicinity of Mount Matutum], 13; Tucay E-el, Mount Matutum, 2; "Salangani" [= apparently near Gogong; collected 22 January 1930; see itinerary of collector in Hachisuka, 1931: 91], 2. Davao: Padada, 1.

johnstoniae: Davao: Mount Apo, various localities [including types], 8.

gonzalesi: Zamboanga del Sur: Mount Sugarloaf, 8. Misamis Occidental: Catagan [foothills of Mount Malindang], 3. Lanao del Sur: Lumba-Bayabao, Piapayungan Mountains, 9; Lake Lanao, 1. Misamis Oriental: Camp Dunque, Tuod, Manticao, 6; Malibato, Opol, 2; Barrio Civilog, 3; Anakan, 2. Bukidnon: Mount Katanglad, Malaybalay [including type], 4. Agusan: Mount Hilong-hilong, 5. Surigao del Sur: Sibahay, Lanuza, 1; "Car-Can-Mad-Lan area" [= Carrascal, Cantilan, Madrid, Lanuza], 7. Davao: Mount McKinley, 2; Mount Mayo, 2.

marchesae: Sulu Archipelago: Jolo [including type], 9.

Also series of *novus* and *leytensis* in AMNH and DMNH.

ACKNOWLEDGEMENTS: My discovery of the distinctiveness of *neglectus* occurred while I was studying a collection of Mindanao birds at the American Museum of Natural History (AMNH) through the courtesy of Dean Amadon and Charles O'Brien. The type of *johnstoniae* and other specimens were examined at Tring through the courtesy of Ian Galbraith of the British Museum (Natural History) (BMNH). Specimens were examined at and borrowed from the Delaware Museum of Natural History (DMNH) through the courtesy of John E. duPont, and he and D. S. Rabor (temporarily at DMNH) helped me identify Mindanao collecting localities. Additional specimens were borrowed through the kind cooperation of the following colleagues: Emmet R. Blake (Field Museum of Natural History), Frank B. Gill (Academy of Natural Sciences of Philadelphia), S. Dillon Ripley (Ripley collection, including former Hachisuka collection), Eleanor H. Stickney (Peabody Museum of Natural History, Yale University [YPM]), and Richard L. Zusi (U. S. National Museum of Natural History).

SUMMARY

Most of the Philippine Island of Mindanao is occupied by a race of *Pericrocotus flammeus* in which adult males are black and orange. The name *P. f. gonzalesi*, although based on a somewhat intermediate population, is advocated for this race. Southern Mindanao is inhabited by a black and yellow race, here described and named *P. f. neglectus*, which is somewhat similar to *P. f. marchesae* of the island of Jolo. The oldest name for any Mindanao population of this species, *johnstoniae*, is here restricted to the population of Mount Apo, which is precisely intermediate in color between *gonzalesi* and *neglectus*. The male syntype of *johnstoniae* is designated as lectotype, on the grounds that females are insufficiently distinctive.

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JAN 13 1975

SQUATINACTIS CAUDISPINATUS, A NEW ELASMOBRANCH FROM THE UPPER MISSISSIPPIAN OF MONTANA

RICHARD LUND¹

Research Associate, Section of Vertebrate Fossils

RAINER ZANGERL²

INTRODUCTION

Among the elasmobranchs so far discovered in the lagoonal Bear Gulch limestones of central Montana (Melton, 1971) there is a small shark of unmistakably batoid habitus with very much enlarged pectoral fins and an apparent tail spine something like that in modern sting-rays. The skeleton is preserved on two slabs (and partial counterplates, Fig. 1) of impure limestone, lithologically reminiscent of the "Faule" layers (see, for example, Walther 1904) of the Jurassic lithographic limestone sequences at Solnhofen, Bavaria. Unfortunately, the two slabs do not make contact with each other, so that we do not know how much of the skeleton is missing in the interval. Although there are Paleozoic sharks that lacked pelvic fins (for example *Agassizodus*, unpublished information) we suspect that this region of the skeleton was present, but lost in the process of collecting this individual. Much of the counterplate was also lost and with it most of the front end of the skull.

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As in Solnhofen occurrences, the skeleton is a reddish-brown color contrasting with the beige background of the limestone. Both calcified cartilage prisms and denticles are somewhat translucent and extremely brittle. Although the vertebral column is present, the individual elements composing it are preserved so indistinctly that it is impossible to give an adequate description.

SYSTEMATICS

Class Chondrichthyes

Subclass Elasmobranchii

Family *Squatinactidae*, new family

Squatinactis, new genus

DIAGNOSIS: Sharks of batoid habitus with very much enlarged pectoral fins and basipterygial cartilages arched around the gill openings somewhat as in *Squatina*. Anterior radials of the pectoral fins fused, forming a flat cartilage plate. Skull probably flattened dorso-ventrally; snout blunt. Teeth of cladodont design, very thin base and with high but variable number of cusps; mouth cavity armored with mucous membrane denticles of irregular crown relief and a tendency to form aggregates involving two or more denticles; posterior region of roof of mouth armored with a triangular plate consisting of basally fused mucous membrane denticles. Tail region of the vertebral column bearing a stout spine. Skin incompletely covered with dermal denticles of simple structure and regionally differing size; aggregates involving several denticles occur.

Squatinactis caudispinatus, new species

DIAGNOSIS: As for genus.

TYPE: Univ. Montana, Vertebrate No. 3333, an articulated skeleton divided on plate and incomplete counterplate. Pelvic region probably not calcified.

HORIZON AND LOCALITY: Bear Gulch Limestone, Lower Pennsylvanian; south of Becket, Fergus County, central Montana (Melton, 1971).

DESCRIPTION

SKULL AND VISCERAL SKELETON

The preserved parts of the skull and visceral skeleton show that the entire complex was articulated at the time of burial. Precise identification of what is presently visible and in what view, however, is more difficult. On the right side of the skull in Fig. 1, one can vaguely discern the outline of an orbit, and medially adjacent to it two cartilage pieces that represent beyond doubt a palatoquadrate and Meckel's cartilage, and adjacent thereto, the dorso-ventrally collapsed palatoquadrate. The central area of the skull consists of a pavement of structures of varying shapes and sizes, including an approximately triangular plate (Fig. 3a). The surface of this pavement is fairly flat and covered, here



Fig. 1. *Squatinactis caudispinatus*, Univ. of Montana (UM) 3333, dorsal view.





and there, with calcified cartilage prisms that appear to have once formed a layer over it. Removal of one of the pavement structures revealed its opposite side, which displays an irregular relief (Fig. 3b). The substance of these elements is clearly different in appearance from the calcified cartilage prisms. It is dense and nearly translucent, and each element contains one or more canals that open to the (presently visible) flat sides of the structures.¹ The location of these pavement elements and the nature of their substance strongly suggest that they are dentine denticles presently seen in basal view. If this is correct, they would have to be the mucous membrane denticles of the roof of the mouth cavity with the remnants of the braincase still adhering to them in a number of places. This would mean that most of the braincase was lost with the counterplate and that we are observing the dorsal side of the armor of the roof of the mouth, the armor consisting of aggregates of mucous membrane denticles including a solid triangular plate. The occurrence of aggregates of mucous membrane denticles and the formation of relatively large plates is known in iniopterygian holocephalians (Zangerl and Case, in press), but to our knowledge has never been observed in an elasmobranch before (Nelson, 1970).

Very few dentition teeth are visible. Two of them are located near the tip of the snout, which is almost completely missing (Fig. 4a), and one about midlength of the jaws on the right side of the skull (Fig. 4b). Surprisingly, these teeth are cladodont to diademodont in structure. One of the anterior teeth is elaborately provided with nine sharp cusps, a large middle cusp, followed in size by the outermost cusps. Between these, on either side, there is a group of three cusplets, the middle one being the largest (Fig. 4a). Next to this tooth there is a fragment of a smaller one with one large cusp and two broken smaller ones. The tooth found at midlength of the jaw has broken cusps, but there is no question as to its structure. It is asymmetrical and consists of a large cusp, flanked on one side by two smaller cusplets and on the other by a single smaller cusp (Fig. 4b). *Squatina* thus displays the rather curious combination of sharp, delicate-looking cladodont teeth on the jaws with a pavement of rough-crowned, variously fused mucous membrane denticles on the palate.

Behind the area of the dental pavement there are a number of narrow cartilage rods (about seven on the right side, four or five on the left) that are more or less antero-posteriorly oriented (Fig. 2). Several of

¹The pavement element that had been removed for inspection of the opposite side was later cleared in toluene and mounted on a slide with damar. Although this treatment rendered the substance nearly transparent, the internal canal system is not visible.



Fig. 2. *Squatina caudispinatus*, UM 3333, dorsal view. Scale equals 20 mm.

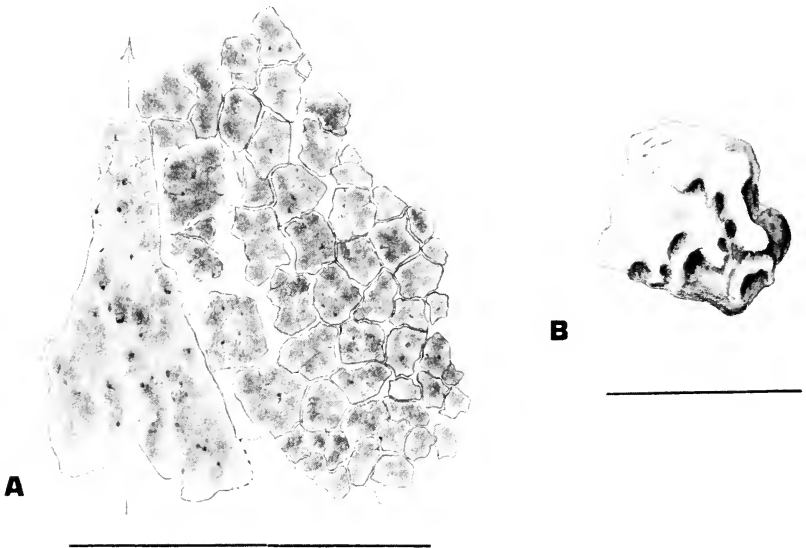


Fig. 3. a. *Squatinactis caudispinatus*, pavement of mucous membrane dental aggregates from roof of mouth cavity, dorsal (aboral) view. Arrow indicates anterior. Scale equals 5 mm. b. single denticular aggregate, oral view. Scale equals $\frac{1}{2}$ mm.

these are accompanied by dental aggregates. We interpret these elements as branchial arch pieces, and their arrangement suggests that the gill openings faced ventrally and laterally as in the modern *Squatina*.

SHOULDER GIRDLE, AND PECTORAL FINS

Both scapulocoracoids are present but their dorsal ends are concealed among flattened branchial elements. The scapular portion of each is moderately broad where exposed. The coracoid portion tapers rapidly to a point and stands at a right angle to the scapular portion. A "heel" projects postero-laterally from this boot-shaped shoulder girdle for articulation with the basiptyerygium of the pectoral fin. There is no junction between coracoids, and no evident cartilaginous connection between scapular cartilages and vertebral column, as in the rays (Goodrich, 1958). The first few vertebral neuropophyses are enlarged, perhaps to support ligamentous connections with the scapular processes.

The basiptyerygium of the pectoral fin consists of four elements arranged in an antero-posterior series. The first is sub-triangular and bears a distal component, morphologically a radial. The second and third basiptyerygial cartilages are much elongated and distally pointed, and serve, functionally, both as basiptyerygial elements and as radials

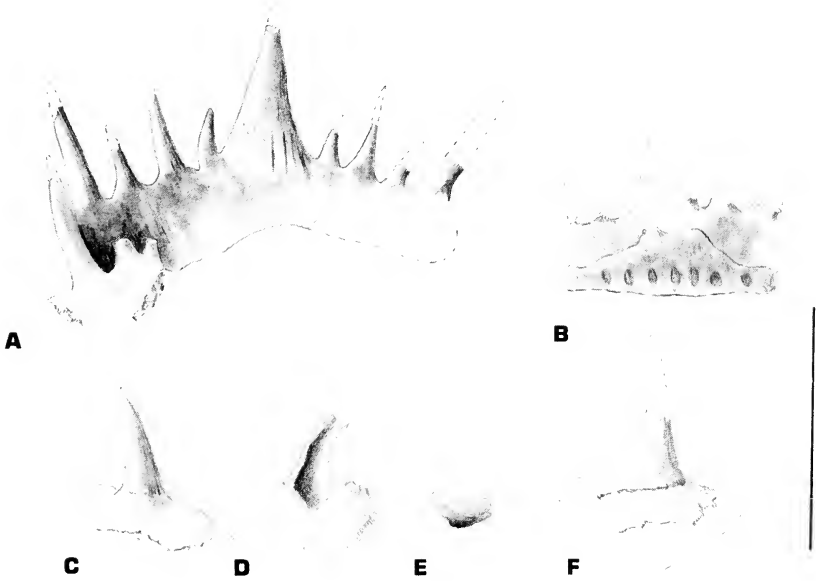


Fig. 4. *Squatinactis caudispinatus*, teeth and head denticles. a. Tooth from front end of skull. b. Tooth from mid-length of jaws. c - f. Denticles from posterior surface of head. Scale equals 1 mm.

(Fig. 5). The posterior basiptyerygial cartilage plate is squarish in outline and bears well developed joint facets proximally and distally. The distal facet forms a joint with a flat cartilage plate that represents the proximally fused radials 2 to 13 (Fig. 5). Radials 14 to 20 seem to lack an articular connection on the basiptyerygium.

The long axis of the *Squatinactis* pectoral fin forms a right angle with the longitudinal axis of the animal. It appears to have been very flexible, judging from the slenderness of the radials and their wide spacing. The anterior half of the fin skeleton, behind the head region, is peculiarly specialized. The basiptyerygial cartilages are curved around the posterior margin of the gill region, a condition reminiscent of the gill openings and pectoral fin relationship in *Squatina* (Fig. 6).

In *Squatina* the antero-medial edge of the pectoral fin is thick, and when applied against the gill region (for example, in a preserved specimen) effectively seals the gill openings laterally, while permitting the ventral ends of the gill slits to remain open. In terms of separating afferent from efferent respiratory water this anatomical construction is of considerable significance to a bottom dweller, at rest, whose gill openings are on the side of the body, next to the spiracle, rather than on the ventral side as in the batoids.

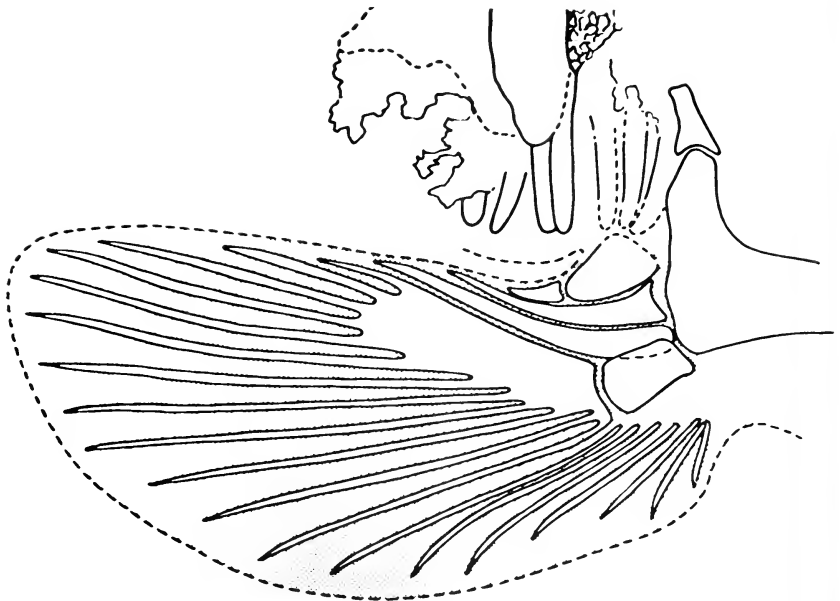


Fig. 5. *Squatinactis caudispinatus*, pectoral fin.

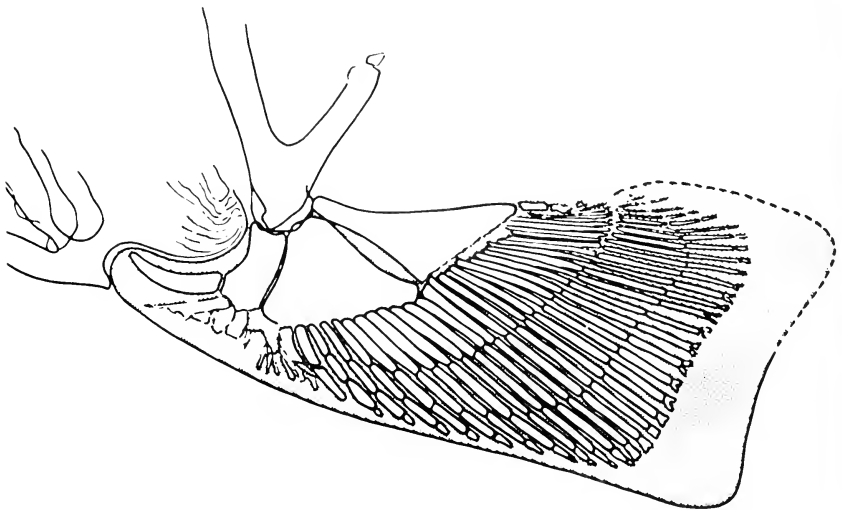


Fig. 6. *Squatina japonica*, FMNH 59306, tracing from radiograph.

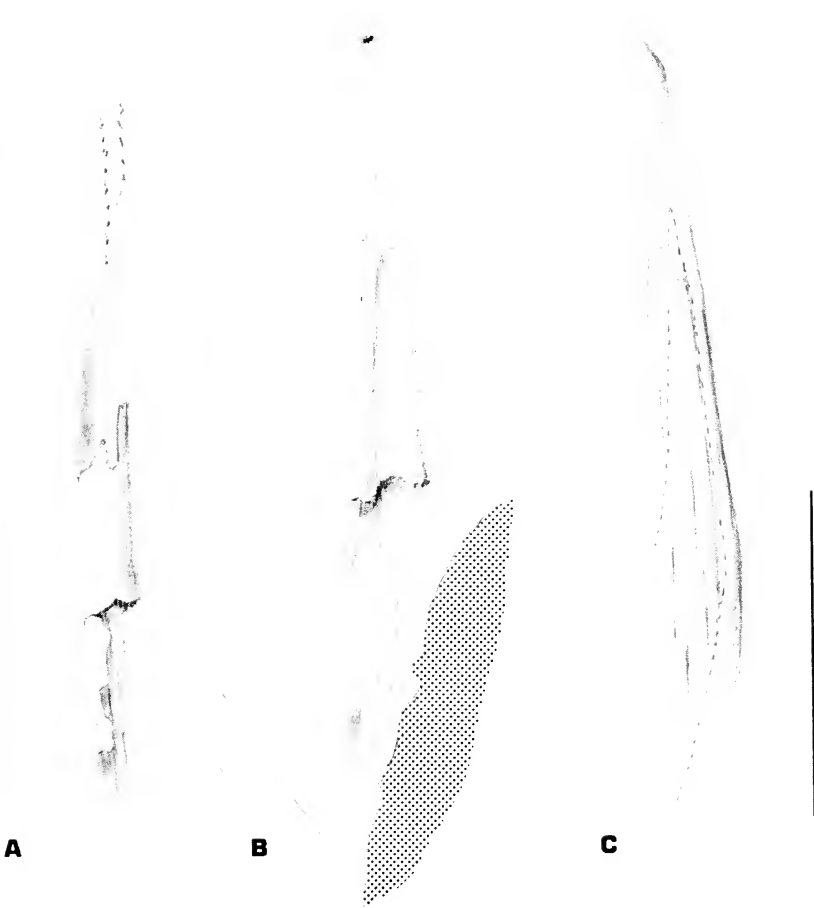


Fig. 7. *Squatinactis caudispinatus*, spine. a, b. Views from plate and counterplate. c. Reconstruction. Scale equals 10 mm.

In *Squatinactis*, the long jaws and anterior inclination of the ventral portions of the branchial arches combine to give the appearance of a branchial apparatus very similar to and convergent upon that of *Squatina*.

AXIAL SKELETON

The vertebral column anteriorly appears to consist of antero-posteriorly expanded neural arch pieces and possibly some calcifications in the ventral sheath of the notochord. All this, however, is so indistinct

that no adequate description is possible. About 30 vertebrae can be counted on the slab that contains the skull, and probably there were more than 30, in that portion, plus those in the tail.

The tail section bears an interesting spine supported upon a long, low basal plate of calcified cartilage (Figs. 1, 2, and 7). The spine lies at an angle of about 25° to the base of the plate. The spine is presently divided on plate and counterplate. It is long and slender, tapering to a sharp point which is bent slightly backwards. The posterior face of the spine back of its point is provided with two parallel rows of serrations flanking a longitudinal groove. The mid-section of the spine (on the plate) is broken longitudinally, showing the relatively smooth-walled internal cavity, which does not seem to extend to the apex of the spine. The surface of the spine was ornamented with both pronounced and delicate longitudinal ridges of different extent (Fig. 7). No proximal posterior furrow can be found on the spine corresponding to the basal cartilage.

DERMAL DENTICLES

Dermal denticles are located on the head (Fig. 8), dorsal, and ventral surfaces of the pectoral fins, and along the body of *Squatina*. The location of denticles on the body cannot be established with certainty. Poor preservation of the vertebrae and sharp changes in direction of the vertebral column make use of the dorsal spine unreliable for orientation anteriorly. There are, however, two series of denticles along the vertebral column, and a patch of rectangular denticular aggregates behind the pectoral fins, similar to those that form the pavement in the mouth (Fig. 3). There is a line of a few large denticles separate from, but parallel to the vertebrae, at one side (Fig. 1). This line of denticles is associated with the patch of aggregates and a few calcified cartilage rods on an isolated patch of counterplate matrix, and is also interspersed with very small denticles anteriorly. There is reason to believe that denticles and plates of this size may have lain along the back of the animal (Bendix-Almgreen, 1971). Closely associated with the vertebral column, but generally on the opposite side, is a tight group of intermediate sized denticles. Comparison with several recent skates reveals that denticles are common dorsally, but ventrally may be confined to the pectoral and pelvic fins. It is probable that this is the condition in *Squatina* as well.

The shape of the dermal denticles is striking. They are hollow cones with sharp, slender crowns and widely-flaring bases (Fig. 7). On the pectoral fins, where denticles are distributed most densely along the anterior margins, the largest are near the antero-distal margins, smaller ones in the central parts of the fins. The largest denticles have the same structure as the smaller ones.

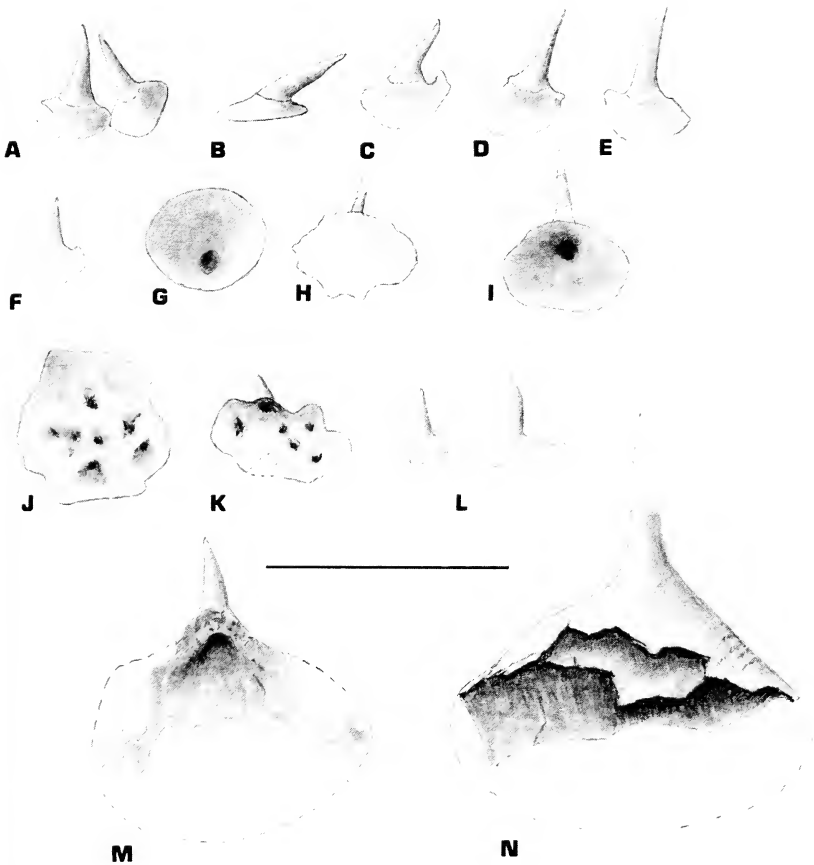


Fig. 8. *Squatinactis caudispinatus*, UM 3333, dermal denticles. a - f. From proximal part of pectoral fin. g, h, i. From distal part of pectoral fin. j, k. Denticular aggregates from presumed dorsal surface. l, m, n. Presumed dorsal denticles.

CONCLUSIONS

FEEDING:

The teeth along the jaws of *Squatinactis* are delicate, piercing structures, of the sort useful for injuring a soft bodied or chitin-covered invertebrate or a small fish, while the pavement aggregates form a weak buccal mill. The delicacy of the dentition precludes a durophagous diet, indicating that *Squatinactis* probably fed on small annelids, crustaceans, and occasional small fish, all of which are common in the Bear Gulch fauna.

LOCOMOTION

The flattened head, broad pectoral fins, and whiplike tail, and extremely posteriorly placed fin spine, are features that indicate a batoid habitus. It is striking, however, that the pectoral fin radials are slender, widely spaced, and unjointed, while the pectoral girdle shows no signs of bracing by fusion in the midline. The mode of propulsion of *Squatina* would seem to be analogous to that of the modern Squatinidae, Pristidae, Rhinobatidae and Torpedinidae, where lateral undulation of trunk and tail would provide a significant proportion of power, while pectoral fin motion would supplement the power and provide horizontal stability in planing (Bigelow and Schroeder, 1953).

RELATIONSHIPS

Squatina represents an adaptive type different from all others so far recognized in the Paleozoic, and it is thus difficult to assess its phyletic relations within this group. The most interesting features are clearly associated with a partial gill-closing mechanism, described above, that has since been independently evolved again in the Mesozoic-to-Recent angel sharks (*Squatina*). The similarity between these anatomical constructions permits by analogy the conclusion that *Squatina*, like *Squatina*, had a dorso-ventrally flattened body, and was a benthic shark.

A recent review of structural designs among Paleozoic elasmobranchs as exemplified by the morphology of their pectoral fins clearly showed that *Squatina* does not fit into any of a number of basic fin designs, although the phalacanthous pattern comes the closest (Zangerl, in press). Much as in *Squatina*, the dentition teeth are small and very delicate, cladodont to diademodont in structure. The conical, dermal denticles with widely flaring, hollow bases are of lepidormorial simplicity in their structure and are similar to the denticles of many modern sharks. The caudal spine is notably peculiar in that it does not have a posterior, proximal furrow (behind the pulp cavity) for the reception of the basal cartilage, as is typical of the fin spines of phalacanthous as well as modern sharks. Since the structure here described as a cartilage base is rather badly preserved, our interpretation as such may, of course, be wrong.

In summary, although *Squatina* has all the attributes of a Paleozoic shark, the most that can be said about its phylogenetic ties is that it represents a batoid specialization at the cladodont level of elasmobranch organization and that it probably evolved from sharks of phalacanthous design.

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ARTICLE 5

HISPANIOLAN BOAS OF THE GENUS *EPICRATES* (SERPENTES, BOIDAE) AND THEIR ANTILLEAN RELATIONSHIPS

BRUCE R. SHEPLAN¹ AND ALBERT SCHWARTZ²

The boid snakes of the genus *Epicrates* Wagler, 1830, occur in the neotropics from Costa Rica to Argentina and in the West Indies. Only one species, *E. cenchria* Linnaeus, with nine subspecies, occurs in Central and South America, including the islands of Trinidad, Tobago, and Margarita (Peters and Orejas-Miranda, 1970:107). The West Indian forms include the following currently accepted named populations (in order of date of description):

- angulifer* Cocteau and Bibron, 1840
- inornatus* Reinhardt, 1843
- striatus* Fischer, 1856
- fordii* Günther, 1861
- strigilatus* Cope, 1862
- chrysogaster* Cope, 1871
- gracilis* Fischer, 1888
- monensis* Zenneck, 1898
- subflavus* Stejneger, 1901
- granti* Stull, 1933
- relicquus* Barbour and Shreve, 1935
- fosteri* Barbour, 1941
- exsul* Netting and Goin, 1944

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The interrelationships and variation of the Antillean taxa have never been carefully defined, and there are various interpretations of the relationships of these taxa to each other. Stull (1935) recognized five species: *angulifer*, *gracilis* (including *monensis*), *inornatus* (including *fordii* and *granti*), *striatus* (including *chrysogaster* and *strigilatus*), and *subflavus*. Mertens (1939:74) suggested another arrangement: *angulifer* (including *striatus*, *chrysogaster*, *relicquus*, and *strigilatus*), *inornatus* (including *subflavus*, *fordii*, *monensis*, and *granti*), and *gracilis*. Cochran (1941:313 *et seq.*) used the combinations *E. s. striatus*, *E. inornatus fordii*, and *E. g. gracilis* for the three Hispaniolan forms. Schwartz (1968a) regarded the Bahamian taxa *exsul* and *chrysogaster* as distinct species. Most important was his allocation of *chrysogaster* to specific rank, instead of treating it as a subspecies of either *angulifer* or *striatus*. Stimson (1969) followed Stull's arrangement, with the addition of subsequently named forms.

The systematics of Antillean *Epicrates* are still in a chaotic state. No author has ever compared specimens of all Antillean taxa, and existing diagnoses of Antillean forms (with the exception of *exsul*) are at best casual.

It is truly remarkable that modern diagnoses of these snakes do not exist. Although conceptual "diagnoses" are prevalent among those concerned with these boids, detailed formal descriptions and scale counts of the various taxa are not available. This is especially true of the Bahamian forms currently associated with *angulifer* (*strigilatus*, *fosteri*, *relicquus*, and *chrysogaster*). Even *striatus* and nominate *angulifer* are poorly known and inadequately diagnosed by modern standards. Stull (1935) and Stimson (1969), in their un-annotated checklists of the Boidae, reallocated names without giving rationales for their actions.

We present here modern definitions and descriptions of the recognizable taxa. We have examined living specimens of all Antillean taxa with the exceptions of *chrysogaster* and *monensis*. Since Hispaniola contains the maximum number (three) of sympatric species, and since we have made extensive collections on that island and on Cuba and the Isla de Pinos, these islands are logical points of departure for the study of West Indian *Epicrates*. We have ample material from these islands, as well as from throughout the Bahamas, so it seems appropriate to review *Epicrates* as it occurs in these three major centers of differentiation, with limited comments on peripheral taxa.

METHODOLOGY

In contrast to the better-known colubrid snakes, boids lack relatively constant scutellar characteristics. Such counts as supra- and infra-labial scales, dorsal scale rows behind the head, at midbody and an-

terior to the vent are all extremely variable in *Epicrates*, and it is difficult to define taxa by these characters. Accordingly, we have emphasized *modal* (rather than *absolute*) differences in scale characters. In many instances, these characteristics are strongly, in others less strongly, modal. By giving frequencies of each category (see Tables 1-8) we show how strong the modes are in our samples. Obviously, the smaller the samples, the less reliable are the modes.

In the tables, all counts do not necessarily reflect the total variation in any particular series, since, for instance, snakes with incomplete tails are commonplace, and the data for this count (and its associated ventrals + subcaudals) may involve far fewer specimens than shown in N.

We have employed the following measurements and scale counts:

1. Snout-vent length, in millimeters. In each case we cite the largest male and female measured, but larger snakes probably exist or existed in nature (or in collections, see discussion of *E. angulifer*). Therefore, our maximum-size records should be treated with caution. There are, however, obvious trends in size between Antillean species, with two major groups involved — one of small-to-moderate-sized species, and a second of large-to-very-large species.

2. Sex was determined by dissection or by the presence of extruded hemipenes. The hemipenis is described for each species from extruded or partially extruded organs. In several taxa we have seen no males with extruded hemipenes, or the organs are incompletely extruded.

3. Ventral scales were counted in the manner proposed by Dowling (1950).

4. Unpaired subcaudals were counted on complete tails. From some areas, boas with complete tails are rare in collections, and data on this character are incomplete.

5. Ventrals + subcaudals has been used as an index figure, since in many instances it serves to intensify subtle differences.

6. Intersupraocular scales are the scales that lie between the supraoculars, and fill the space occupied by the frontal in most snakes.

7. Pre-intersupraocular scales are the prefrontals of orthodox colubrid usage. The scales bordering the intersupraocular(s) are multiple, and in many instances not conspicuously enlarged.

8. Post-intersupraocular scales are those that border the intersupraocular(s) posteriorly, in the space filled by the parietal in most other snakes. Using three counts in an anterior to posterior sequence (pre-intersupraoculars/intersupraoculars/post-intersupraoculars) we construct formulae (i.e., 3-1-5) that characterize populations.

*9. Supralabial and infralabial scales. Both these counts show broad variation, but usually with strong modal frequencies. (In this count and others marked with an asterisk, we counted each side of the head as a

separate unit, and we refer to these individual counts as "series." Thus, a single snake contributes two series of supralabials, infralabials, loreals, etc.)

*10. Number of supralabials entering the eye. In all taxa except *angulifer*, which usually has the supralabials separated from the eye by a row of lorilabials, one to three supralabials enter the eye. There are strongly modal classes, both of total number of supralabials entering (i.e., two or three scales), and of which scales are involved (i.e., supralabials 6-7 or 7-9). We also noted which supralabial is most often associated with eye penetrance.

*11. Loreal scales. These are most often 1 or 2, occasionally 3. In all cases, loreal number is strongly modal.

*12. Scales in the circumorbital series. We counted all scales (including supraoculars and supralabials) in contact with the eye. This count is strongly modal.

13. Dorsal scale rows, counted behind the head, at midbody, and anterior to the vent. Of all counts in *Epicrates*, these show the least reliability since the amount of variation in any population (or indeed on any snake) is great. Accordingly we have not stressed differences in dorsal scale counts except where they are virtually dichotomous.

14. Number of blotches on the body (between occiput and vent), and on the tail. Pattern plays an important part in the differentiation of species and subspecies of *Epicrates*, but there are pitfalls that make blotch counts unreliable. In Bahamian populations body blotches are extensively fused, and they can be discerned only by counting the remnant pale interspaces. In western Cuban populations the pattern is so faded and pale that accurate counts cannot be made, even though a pattern is present. We characterize body blotches as "subcircular," "ovate," or "angulate," depending upon our impression of the blotch shape. The ventrad extent of blotches has been recorded as whether they reach the dorsal-ventral junction. The presence or absence of secondary lateral series of smaller blotches has also been noted, and whether these blotches are fused (usually posteriorly) with the primary dorsal blotches. In many populations variation in dorsal pattern seems infinite, and we have, after describing the basic pattern, supplied descriptions of some common modifications.

In addition, we have included available data on coloration in life, ecology, distribution (both geographic and altitudinal), reproduction, position of the umbilicus in neonates, and food habits in nature (determined from stomach contents).

SYSTEMATIC REVIEW

Epicrates angulifer Cocteau and Bibron
Epicrates angulifer Cocteau and Bibron, 1840, 8: pl. 25.

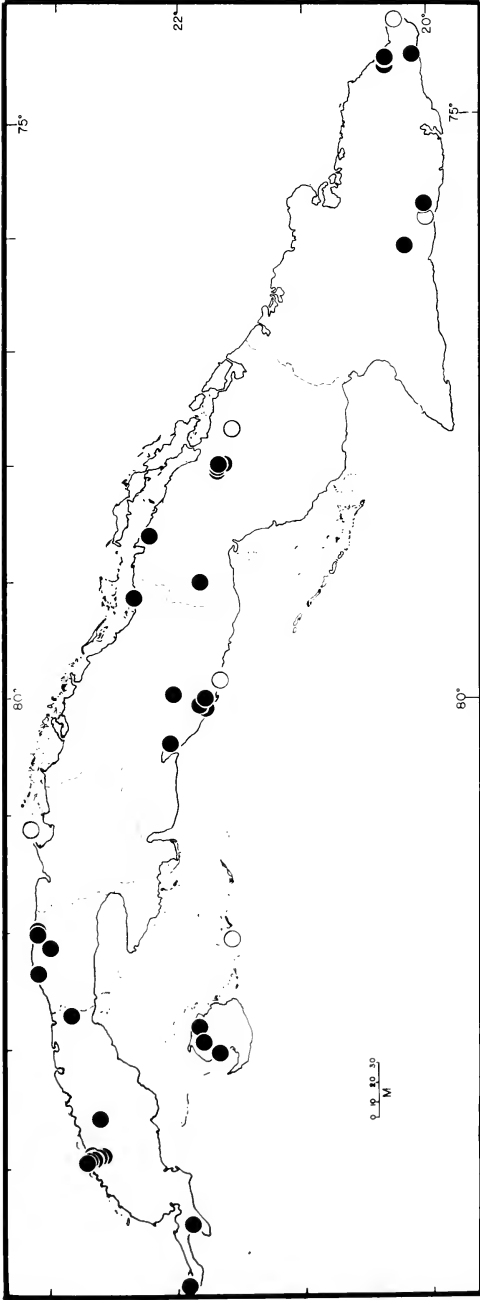


Fig. 1. Map of Cuba, showing localities for *Epicrates anguifer*. Solid symbols represent specimens examined. Hollow symbols represent literature records.

TYPE LOCALITY: Cuba; holotype - Muséum National d'Histoire Naturelle 3292.

DEFINITION: A large species of *Epicrates* (males to 1743 mm, females to 2250 mm, snout-vent length), with 272 - 292 ventral scales in males, 268 - 290 in females; 45 - 55 subcaudal scales in males, 46 - 54 in females; ventrals + subcaudals 321 - 347 in males, 316 - 339 in females; intersupraocular scales modally 3, pre-intersupraocular scales modally 3, post-intersupraocular scales modally 4; dorsal-scale row on neck 44 - 54, 53 - 69 at midbody, 28 - 38 anterior to vent, the lowermost scale row not alternating a large and a small scale for each ventral scute; supralabials modally 14 with none entering the eye in most instances, the supralabials and eye separated by a complete row of lorilabials; infralabials modally 17; loreal modally 1; circumorbital series modally composed of 8 scales; dorsal pattern consisting of from 42 to about 65 appressed angulate dark-brown to black markings on a yellowish to yellowish-tan ground, but often (western Cuba) without any dark colors in the dorsal pattern, the pattern composed of an indeterminate number of medium-brown to pale-tan, much-fused markings; tail patternless above, or with up to 12 dorsal darker markings.

DISTRIBUTION: Cuba (widespread geographically and altitudinally) and the Isla de Pinos (Fig. 1); probably occurring on many offshore islands and cays, but reported only from Cayo Cantiles in the Archipiélago de los Canarreos (Garrido and Schwartz, 1969).

VARIATION: The series of 55 *E. angulifer* has been divided into five geographic lots for comparison: Isla de Pinos; and Pinar del Río, Habana-Matanzas, Las Villas-Camagüey, and Oriente provinces (See Table 1).

Snout-vent length of the largest male (AMNH 82913) is 1743 mm; of the largest female (AMNH 82909), 2250 mm. Both are from Pinar del Río Province. We examined other "huge" specimens (for example, USNM 12538) that are so badly coiled that accurate measurements were impossible, so it is likely that our maximum measurements may be superseded. Barbour and Ramsden (1919:187) cited records from the Ciénaga de Zapata of 6400 mm, and another of 4570 mm that Gundlach possessed. They also reported 2740 mm specimens taken in 1913 and 1915. Although these measurements are presumably of total, rather than snout-vent lengths, we have not examined specimens of comparable size, although we have little doubt that such specimens may exist.

Data on scutellar variation in the five geographic lots of *E. angulifer* are presented in Tables 1 and 3-8. There is a slight west-east cline in number of ventrals in both sexes, with low counts in the west and high counts in the east, but the Oriente region is represented by a single female, and we cannot be certain that the trend seen in the five Oriente males is equally demonstrable in females. The low-count male is from Pinar del Río, the high-count male from Oriente. The low-count female is from Pinar del Río, the high-count female from Las Villas-Camagüey. Male extremes in subcaudals also are from Pinar del Río and Oriente, whereas both extremes in female subcaudals are from the Pinar del Río series. The single Oriente female also has 54 subcaudals. In ventral + subcaudal counts the male extremes are from Pinar del Río and Oriente, and the female extremes are from Pinar del Río (low) and Las Villas-Camagüey and Oriente (high).

Intersupraocular scales are modally 3 (26 snakes), but specimens from the Isla de Pinos and Habana have bimodes (2 and 3 scales). Pre-intersupraoculars are modally 3 (24 snakes), except in the sample from Habana where the local mode is 4. Post-intersupraoculars are modally 4 (27 snakes), but local samples have modes of 3 (Isla de Pinos, Habana). Dorsal-scale-row counts are relatively uniform, except that Isla de Pinos snakes generally have slightly lower midbody counts (53-63, elsewhere 56-69). Of the entire series, only two snakes (from the Isla de Pinos) have less than 30 dorsal scales anterior to the vent.

Supralabials are modally 14 (56 series) in all samples except that from Oriente, where there is a bimode (13 and 14). No supralabials regularly enter the eye (93 series), since these scales are usually separated from the eye by a complete row of lorilabials. Fifteen series, however, have one supralabial entering the eye. In most cases (13) this is supralabial 7, whereas in two cases supralabial 8 is involved. The highest incidence of this character is in the Oriente series, where half the series has eye-supralabial contact (5 of 10 series). Three of six Oriente individuals have bilateral contact between the supralabials and the eye. The other instances of this contact include 4 of 16 series from the Isla de Pinos specimens and 6 of 42 series in Pinar del Río specimens. Between Habana and Camagüey none of 40 series shows supralabial penetration into the eye. Possibly this aberrant (for *angulifer*) condition is limited to the Isla de Pinos and eastern and western Cuba. Infra-labials are modally 17 (35 series), but the Isla de Pinos and Oriente samples show modalities of 16. Note that 16 supralabials occur with almost the same frequency as do 17 supralabials.

The circumorbital series is modally composed of 8 scales, but the Isla de Pinos and Habana samples have 8 and 9 as a bimode. The loreal scales show a strong mode of 1 (103 series), with rare variants of 2 loreals (six series) and 3 loreals (one series).

It is in dorsal coloration that *E. angulifer* shows the most striking variation. There are two distinctive dorsal patterns, and to a large extent they are geographically correlated. In Pinar del Río Province, *E. angulifer* shows a dorsal pattern consisting of a very faded series of dorsal angulate markings, appressed, with a ventrolateral row of irregularly shaped secondary blotches. Snakes from this general region lack dark-brown-to-black pigments in the dorsal pattern, so that pattern details are very difficult to distinguish, and counts of dorsal blotches are impossible. Occasional snakes (AMNH 76555) from this area are somewhat darker, but the pattern is still obliterated because of the absence of dark blotch boundaries. This pale pattern begins to be replaced in Habana Province and is further and more completely replaced in Las Villas and Camagüey by snakes with well-developed dorsal angulate markings and secondary side blotches. In our Habana series, two

snakes are pale and two are dark; in our Las Villas-Camagüey sample, one is pale and 12 are dark. All the Oriente snakes are dark-patterned. Thus there seems to be a west-east cline, with pale snakes commonest in the west and dark snakes in the east. We would have little hesitancy in naming the eastern population of darkly-patterned snakes except that (1) we are unable to correlate these pigmental traits with any differences, even mean ones, in scutellation; and (2) the Isla de Pinos snakes apparently show both patterns, with dark dorsa predominant. One Isla de Pinos snake (CM 282) is pale, whereas all others are dark; it is possible that this very old specimen is truly faded from its time in preservative. Nonetheless, we are reluctant to name a new subspecies of this widely-ranging snake until more material is available. It is of interest that the plate in the original description shows a pale and faded snake, so there is little question that the nominate form, should a new subspecies be named, will be the western pale population.

In those snakes whose dorsal pattern allows dorsal blotch counts, the variation is between 42 and about 65 on the body, and between 5 and about 12 on the upper surface of the tail. The angulate markings in *E. angulifer* are so arranged that any count is very difficult and this, coupled with the faded appearance of western snakes, renders this count of even less importance than in other *Epicrates*.

The pattern is variable dorsally, from indiscriminately patterned and faded individuals to snakes whose dorsal angulate markings are black and very prominent against a tan-to-brown or yellowish-tan ground. The blotches begin on the neck and continue to the tip of the tail, the more distal caudal blotches forming complete rings near the tail tip. A lateral series of irregularly shaped angulate blotches reaches the dorsal-ventral junction but does not extend onto the venter. All blotches may be hollowed centrally, or they may be solidly dark. The head is usually tan or yellowish tan and unmarked, but in extreme individuals dark brown or black suffusions, or irregular and indiscriminate markings may be present. The chin, throat, and anterior ventrals are yellowish to cream, but more posteriorly the ventrals become heavily suffused with gray to produce tan-to-brown scales with pale clear edges. In the faded snakes, the foregoing pattern details are all much obscured.

The hemipenis of *E. angulifer* (based upon AMNH 82915: = 589 in the collection of Herndon G. Dowling) is long and stout, and has a series of seven or eight heavy and serrate-edged flounces on the non-sulcate surface. Proximal to these is a weak flounce that subtends a stout basal papilla about opposite to the sulcus spermaticus. The organ is strongly bifurcate distally for about one-third its length, and the sulcus divides basal to the bifurcation of the organ. The margins of the

sulcus, both before and after its division, are stout, and the sulcus is deeply entrenched. The bifurcate portion of the hemipenis is covered by a series of about seven weakly defined rows of coarse papillae. An incompletely extruded hemipenis (AMNH 77769) resembles the above description closely. This general description of hemipenial structure and pattern applies, with slight modification, to all other Antillean *Epicrates*.

REMARKS: Stull (1935:396) considered *E. angulifer* a distinct species, and no one has seriously questioned this assignment with the exception of Mertens (1939:74) who combined *angulifer* with *striatus*, *chrysogaster*, *relicquus*, and *strigilatus*. Stimson (1969:11) disregarded Mertens's allocation and followed Stull. We see no reason to combine *E. angulifer* with *E. striatus* or any other Antillean taxon, since it is eminently distinct from all other species in having, among other features, the eye usually completely separated from the supralabials by a row of lorilabials and few subcaudals.

There is some question about the author and original citation of *E. angulifer*. Stull (ibid.) cited the name as proposed by Bibron (Cocteau and Bibron, 1840:215, pl. 25). Stimson (op. cit.) gave Bibron as the author, and the original description as on page 215 in de la Sagra, with no mention of the plate. Smith and Grant (1958) laboriously considered all alternatives for both authorships and dates of the reptile names in the de la Sagra work, and we follow their rationale in dating the name from 1840, attributing it to Cocteau and Bibron, and citing the plate as the original indication. If the Spanish (rather than French) edition is used as the prior source of these Cuban names by Cocteau or Bibron or both (and Smith and Grant consider that the Spanish edition antedated the French edition), then the formal verbal description begins on page 129 rather than 215.

Epicrates angulifer is widespread in Cuba and its satellite islands, occurring also on the Isla de Pinos and probably on both the northern and southern *cayerías*, although it has been reported only from Cayo Cantiles in the Archipiélago de los Canarreos. The species occurs from sea level to elevations of about 305 meters in the Sierra de los Organos, and probably at higher elevations in the Sierra de Purial and associated ranges between Sabanilla and Baracoa in Oriente Province, between Sevilla and La Gran Piedra in the Sierra de la Gran Piedra in southern Oriente, near Topes de Collantes in Las Villas Province in the Sierra de Trinidad, and at somewhat lower elevations in the Sierra de Cubitas in northern Camagüey Province.

Like most other Antillean *Epicrates*, *angulifer* is typically a snake of wooded situations, like *monte* (broad-leaf forest), at both high and low elevations. Specimens are regularly seen on roads at night and rarely

are encountered abroad during the day. One snake (AMNH 96042) was secured from a tree branch, 9.2 meters above the ground, where it was coiled and resting during the day in *monte*. Individuals are often associated with caves, rocky cliffs, and their talus. In such situations, *E. angulifer* finds not only shelter but food, since bats form a portion, possibly a major portion in the case of some cavernicolous individuals, of the boa's diet. A specimen from Finca Morales (AMNH 77773), taken near the entrance of a cave at night, contained two *Mormoops blainvillei*, two *Phyllonycteris poeyi*, one *Brachyphylla nana*, and one small unidentifiable bat. The state of digestion indicated that at least the five identifiable bats had been very recently taken by the snake. Hardy (1957) noted that *E. angulifer* feeds on *Phyllonycteris*, and observed the boas constricting or swallowing their prey. The gastrointestinal tracts of other *E. angulifer* examined contain *Rattus* or domestic chickens, both pullets and half-grown adults.

Hardy (1957) also commented on the large number (41) of *E. angulifer* secured at Cueva de las Majáes near Trinidad. These snakes, collected in eight visits there, were active and more easily secured in the evening or at night. In particularly favorable situations, *E. angulifer* appears to be common.

No young snakes are in the series examined by us, so there are no data on the umbilical position in this species. A gravid female from San Vicente was taken to the laboratory in September 1959 and gave birth to four young (one dead at parturition) on November 4. By the following day, these small snakes were capable of aggressive striking behavior. On November 17, the three snakes had total lengths between 600 and 610 mm and were able to exude a very mild musk. One young individual shed for the first time on December 11.

Epicrates striatus Fischer

Homalochilus striatus Fischer, 1856, Abh. Nat. Ver. Hamburg, 3:102.

TYPE LOCALITY: Originally Santo Domingo and St. Thomas, here restricted to the vicinity of Santo Domingo, Distrito Nacional, Dominican Republic. Syntypes formerly in HZM, now lost (*in litt.*, W. Lädiges, May 24, 1971).

DEFINITION: A large species of *Epicrates* (males to 2330 mm, females to 2055 mm, snout-vent length), with 270 - 299 ventral scales in males, 266 - 298 in females; 76 - 102 subcaudals in males, 76 - 94 in females; ventrals + subcaudals 353 - 390 in males, 343 - 387 in females; intersupraocular scales 1 or 2, pre-intersupraocular scales modally 3 or 5, post-intersupraocular scales modally 5; dorsal scale rows on neck 34 - 49, 35 - 65 at midbody, 22 - 31 anterior to vent, the lowermost scale row not alternating a large and a small scale for each ventral scute; supralabials modally 14 or 15, with usually two (modally 7 - 8 or 8 - 9) or three (7 - 9) supralabials entering eye; infralabials modally 18 or 19; loreals modally 1 or 2; body blotches 60 to about 122, but dorsum often virtually patternless or with blotches so fused as to be uncountable and revealed only by remnants of pale interspaces; tail blotches absent to 28.

DISTRIBUTION: Hispaniola, including Ile de la Gonâve, Ile-à-Vache, and Ile de la Tortue (Fig. 2); the Bahama Islands (Bimini Islands, Andros, Berry Islands, New Providence including Rose Island, Eleuthera, Long, Cat, Exuma Cays, Ragged Islands; Fig. 3).

REMARKS: Stull (1935:397-398) combined *E. striatus* and *E. strigilatus* Cope from the Bahama Islands. Mertens (1939:74) further combined these two taxa with *E. angulifer* Cocteau and Bibron. We do not concur in this latter action, since the Cuban *angulifer* is a distinctive snake (see discussion above), but we follow Stull in her arrangement of *striatus* and *strigilatus*.

As with *Anolis distichus* Cope, which also occurs both in Hispaniola and the Bahama Islands (Schwartz, 1968a:261-263), there are not only differences between *E. striatus* from these two major segments of its range, but also several well-defined subspecies in each major area. Definition of the species *E. striatus* is difficult because the two geographical segments have different modalities in several characters.

Our analysis suggests that *E. striatus* is a north island (*sensu* Williams, 1961) snake, which has invaded the Haitian Tiburon Peninsula on one hand and the Bahama Islands on the other. In addition, the species occurs on the Hispaniolan satellites of Gonâve, Vache, and Tortue, and in the latter case has differentiated sufficiently to be considered nameworthy. We recognize three subspecies of *E. striatus* on or associated with Hispaniola, and five subspecies in the Bahama Islands.

There are two junior synonyms of *E. striatus*: *multisectus* Cope, 1862, from unknown locality, and *versicolor* Steindachner, 1863, from "Colombia." The holotype of *multisectus* has been examined for us by Edmond V. Malnate. Its scale counts, general habitus, and pattern confirm *multisectus* as a strict synonym of *E. striatus* (see discussion under *E. s. striatus*). *Epicrates versicolor*, although considered by Cochran (1941:314) a synonym of *E. striatus striatus*, apparently does not apply to that form. Examination of the detailed scutellar descriptions and figures, as well as the description of the pattern of *versicolor*, leaves little doubt that this name is a synonym of *strigilatus* and that the holotype was brought to Europe from some Bahamian island, rather than from Colombia or Hispaniola. If at some future time the Bahamian snakes presently regarded as *E. striatus strigilatus* are subdivided, then *versicolor* will require further consideration.

We have examined 126 specimens of *E. striatus* from Hispaniola (including the satellite islands) and 74 specimens from the Bahama Islands. Since we consider *E. striatus* on the "north island" of Hispaniola (*sensu* Williams, 1961; derived from the separation of Hispaniola into two islands in past geologic time) to be the basic stock for the balance of the subspecies, we discuss that taxon first.

Epicrates striatus striatus Fischer

Homalochilus multisectus Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, 14:70. Type locality unknown, here restricted to the vicinity of the city of Santo Domingo, Distrito Nacional, Dominican Republic; holotype Academy of Natural Sciences of Philadelphia 10315.

DISTRIBUTION: Hispaniola (including Ile de la Gonâve), except the western end of the Tiburon Peninsula in Haiti, Ile-à-Vache, and Ile de la Tortue.

DEFINITION: A subspecies of *E. striatus* characterized by the combination of large size (males to 1865 mm, females to 1737 mm), moderate number of ventrals in both sexes (272 - 293 in males, 273 - 298 in females), modally 2 intersupraocular scales, modally bordered anteriorly by 5 scales, posteriorly by 5 scales, modally 15 supralabials with two supralabials (8 - 9) entering the eye, modally 11 scales in the circumorbital series, and modally 2 loreals; pattern usually a series of 60 to 97 bold and contrasting dark rectangles on a tan-to-yellowish-tan ground, and usually without pale dorsal median spots or dots on the neck, or prominent lateral longitudinal stripes on the anterior portion of the body.

VARIATION: Our series of 96 *E. s. striatus*, including specimens from Hispaniola north of the Cul de Sac-Valle de Neiba plain, the Península de Barahona, the region around Pétienville, and Ile de la Gonâve (six specimens), shows the following. The largest male has a snout-vent length of 1865 mm (ASFS X2512), and the largest female, 1737 mm (ASFS V23989). Mertens (1939:74) reported a female with a snout-vent length of 1860 mm. Among our specimens are several that are very large, possibly even larger than the two extremes noted above, but these are either poorly preserved snakes or skins without measurements in life. Although longer snakes than those cited as maxima doubtless exist, our general impression is that *E. s. striatus* does not reach so large a size as some of the other subspecies (See tables for variation in scutellation).

The dorsal pattern of *E. s. striatus* is extremely variable, but the variations seem uncorrelated with geography or ontogeny. Basically, the dorsal pattern consists of 60 to 97, more or less subcircular, ovate to angulate brown blotches or spots outlined by dark brown to black, forming an essentially complete series of dorsal saddles. The blotches are often modified, by alternation, into a chain-like pattern. Below this major series of dorsal blotches there is usually a secondary series of smaller angulate blotches on the lower sides, lying at the apices of the primary dorsal blotches. The upper side of the tail is blotched, with as many as 28 blotches. The colors and pattern configuration are the same as on the body, except that no lateral row of secondary blotches occurs. The venter is gray to brown, with scattered to regular dark-brown to dark-gray markings that form longitudinal short lines or line segments. The entire ventral pattern is extremely variable. Although the neck lacks the lateral stripe typical of the Bahamian populations, a stripe is indicated in some specimens by elongate members of the secondary

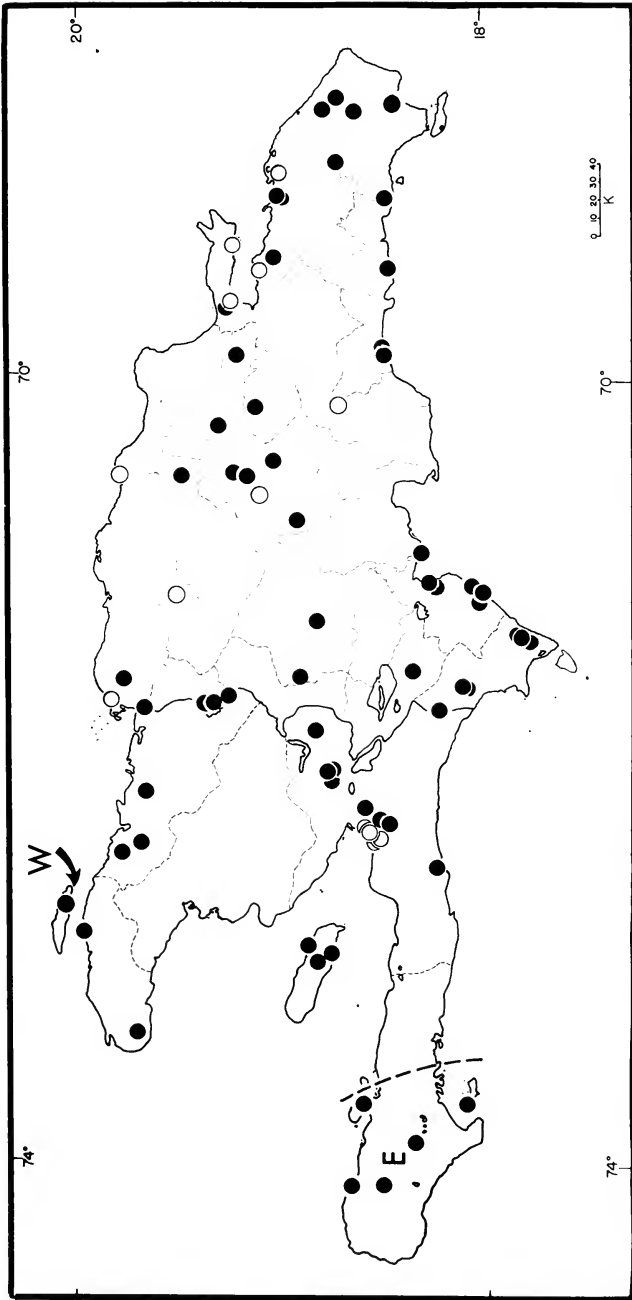


Fig. 2. Map of Hispaniola, showing localities for *Epicrates striatus*. Solid symbols represent specimens examined. Hollow symbols represent literature records. All symbols represent *E. s. striatus* except: W = *E. s. warreni*; E = *E. s. exagistius*.

blotch series arranged in a roughly linear fashion. In some young specimens (ASFS V1352) there is a bold lateral stripe on the anterior eighth of the body. Cochran (1941:317) commented upon this stripe in young *E. striatus* from Haiti. Even much larger snakes may have prominent lateral lines, so this condition is not restricted to juveniles.

The dorsal pattern is extremely variable, and the above description hardly does justice to the many variants in the long series at hand. The blotches are regularly dark and boldly contrasting with the paler ground color, and in some specimens (ASFS V2033) so fused that they can be discerned only by the pale interspace remnants. In this individual also, the neck has a dorsal median series of pale interspace blotches. A larger snake (ASFS V814) also has this pale neck-blotch condition, a pattern typical of most Bahamian populations. Although in general Bahamian populations of *E. striatus* are distinguished by the lateral anterior body stripe and the dorsal pale neck blotches, both these chromatic conditions occur in some specimens from Hispaniola.

The upper side of the head is virtually patternless, but it may be more or less marbled with dark and light brown. A postocular dark line or stripe is moderately prominent in some individuals, and there may be an additional short dark line on the upper temporal region. Those snakes that do not have fused dorsal blotches on the neck may have a pale sharp transverse bar delimiting the first dorsal neck blotch from the darker head coloration. In some especially dark snakes, the tail is solidly black or very dark brown above, without evidence of pattern except for a few scattered pale tan scales.

In a series of six males and seven females, all litter mates (ASFS V30273-84) except one female (MCZ 43817), the umbilicus lies on ventrals 185 - 200 in the males and between ventrals 184 and 196 in the females. The twelve litter mates, removed from a gravid female, have snout-vent lengths of 370 - 382 mm in six males and 299 - 379 mm in six females.

The hemipenis of *E. s. striatus* (based on ASFS V814) is short and stout, extending for about the length of eight subcaudal scales, and is deeply bifurcate; there are about six flounces on the basal undivided portion of the hemipenis, the more distal flounces decorated with marginal serrations; the bifurcations are closely set with low rounded papillae that are less prominent near the sulcus; the sulcus is divided at the base of the bifurcation and ends blindly near the apex of each fork. The absence of a basal spine or enlarged papilla on the side of the hemipenis opposite the sulcus is noteworthy, although there is a single low rounded papilla in this position.

The holotype of *Homalochilus multisectus* Cope is a young male with a snout-vent length of 492 mm and a tail length of 105 mm. There are 294 ventrals and 87 subcaudals (ventrals + subcaudals, 381).

Supralabials are 15/17, infralabials 21/19. The circumorbital series contain 10 and 11 scales, and supralabials 8 - 9 enter the orbit on both sides. Loreals are bilaterally 2. Intersupraoculars are 5, bordered anteriorly by 7 scales and posteriorly by 7 scales. Dorsal scale rows are 42 - 58 - 27. There are about 83 body blotches and about 23 tail blotches. We have no doubt that *multisectus* is a synonym of *striatus*, although the ventral count is one scale greater than that for our series of 44 male *E. s. striatus*. The presence of 2 loreal scales and entrance into the eye of supralabials 8 - 9 bilaterally suggest strongly that *multisectus* is identical with *E. s. striatus*. Cope (1862:71) did not compare *H. multisectus* with *E. striatus*, nor despite the abundance of scutellar details that he gave for the type specimen, is there any indication of which counts or facts Cope regarded as diagnostic.

Epicrates s. striatus is widely distributed on Hispaniola north of the Cul de Sac-Valle de Neiba plain (Fig. 2). The subspecies also occurs in the Sierra de Baoruco and its associated more mesic southern foothills, and near Oviedo, but there are no records from the very arid lowlands of the Península de Barahona. There is only one record from the xeric Cul de Sac-Valle de Neiba plain. *E. s. striatus* occurs in the mesic oases within the plain. There are two specimens from near Pétienville in southeastern Haiti that we associate with *E. s. striatus*. These snakes are from the northern ranges of the Massif de la Selle. A single specimen from near Jacmel on the southern coast of the base of the Tiburon Peninsula we also consider *E. s. striatus*, although in depth of dorsal pigmentation it seems to approach the western Tiburon subspecies. This subspecies of mesic forested situations, which is elsewhere restricted to the "north island," has likely reached the Península de Barahona by crossing the eastern end of the Valle de Neiba, possibly along the Río Yaque del Sur. This eastern portion of the Valle de Neiba is more mesic and better wooded than elsewhere, and such conditions have probably allowed penetration of the nominate subspecies onto the "south island" in this region. Similar situations occur in *Ameiva taeniura* (Schwartz, 1967) and *Uromacer catesbyi* (Schwartz, 1970a). The occurrence of *E. s. striatus* near Pétienville and Jacmel likewise is probably correlated with more mesic conditions in the extreme western Cul de Sac.

Specimens from Ile de la Gonâve do not differ in coloration, pattern, or scutellation from mainland snakes, although all the high counts for dorsal scale rows are from the short Gonâve series. Considering the wide distribution of *E. s. striatus*, the subspecies appears to be relatively constant in characteristics and shows little obvious variation correlated with geography. Perhaps the Gonâve population has recently arrived on that island, and there has not been sufficient time for differentiation.

E. s. striatus is an inhabitant of mesic and usually forested situations, although the forests need not be dense or high. Fairly dry forests, like those in the vicinity of Pepillo Salcedo, Oviedo, Boca Chica, and Boca de Yuma support populations of *E. s. striatus*, although we have the impression that the snake is more common in mesic areas. *E. s. striatus* occurs from sea level at many localities to elevations of about 1220 meters near Constanza in the Cordillera Central and in the Sierra Martín García. Snakes are most commonly encountered foraging at night. Active snakes have been taken in a banana grove, in tangled vines 2.1 to 2.7 meters above the ground, crawling in trees 1.5 meters to 6.1 meters above the ground, in a small roadside shrub, and in comparatively low-to-moderate heights in shrubs, trees, and bushes. One snake was found dead on a road in xeric scrub near Elías Piña, so that, in the upland Valle de San Juan, such arid habitats are not ignored. During the day, *E. s. striatus* has been taken in a rotten palm log adjacent to a mesic cacao grove, in a dry log overlooking the Río Yaque del Norte, in a large hollow log adjacent to a cornfield surrounded by mesic high-canopied *cafetal*, in the straw roofing of a fallen shack, and in a rotten tree stump.

Three specimens of *E. s. striatus* have been recorded as erythristic. Two of these (ASFS X8110, ASFS X9276) are from southwest of Miches, El Seibo Province, Dominican Republic. The third individual (ASFS V18525) is from near La Mata, Sánchez Ramírez Province. One of the Miches snakes was recorded in life as dull orange-ventrally, with the dorsum darker orange with grayish orange blotches. In 1971, Fowler and Schwartz saw a freshly-killed erythristic *E. s. striatus* east of Sabana de la Mar in this same region, and Fowler and Sheplan attempted to secure native help at Las Cañitas in collecting "*culebras coloradas*" (= "red snakes,") a name that was readily understood by local inhabitants. Apparently, there are demes of *E. s. striatus* that have this peculiar coloration. The Sabana de la Mar-La Mata localities are some 90 kilometers apart. All erythristic snakes are from the eastern end of the island.

Females taken between June 13 and August 27 were gravid. These gravid females varied in snout-vent length from 1313 mm to 1672 mm, and the number of embryos or fetuses varied between 8 very small young in the smallest female (1313 mm) to 31 embryos in the largest (1672 mm). Between these extremes, the number of embryos include 5, 9, 12 (two females), 14, 17, 18, and 19.

***Epicrates striatus exagistus*, new subspecies**

HOLOTYPE: MCZ 125603, an adult female from Camp Perrin, Département du Sud, Haiti, one of a series collected July 24-26, 1962, by native collectors. Original number ASFS X3780.

PARATYPES: Dépt. du Sud, Haiti: ASFS X3779, ASFS X3781-88, same data as holotype; ASFS V9678, Jérémie, March 18, 1966, native collector; USNM 60603, Moline, January 28, 1918, W. L. Abbott; USNM 60604, Les Basses, January 9, 1918, W. L. Abbott. Ile-à-Vache (western end), Haiti: ASFS X3789-91, August 6, 1962, native collectors.

DISTRIBUTION: Western end of the Tiburon Peninsula and Ile-à-Vache, Haiti.

DEFINITION: A subspecies of *E. striatus* characterized by the combination of moderate size (males to 1711 mm, females to 1635 mm snout-vent length), moderate number of ventrals in both sexes (271 - 285 in males, 273 - 286 in females), modally 2 intersupraocular scales, modally bordered anteriorly by 6 scales, posteriorly by 5 scales, modally 15 supralabials with one or two supralabials (8 or 7 - 8) entering the eye, modally 10 or 11 scales in the circumorbital series, and modally 1 loreal: pattern extremely faded with dorsal and tail blotches very obscure, usually faint and not outlined with dark brown or black and uncountable except in young snakes and exceptional adults; body blotches 74 - 86; dorsum tan and virtually unpatterned, without pale dorsal median spots or dots on the neck, or prominent lateral longitudinal stripes on the anterior portion of the body.

DESCRIPTION OF HOLOTYPE: An adult female with a snout-vent length of 1520 mm and a tail length (incomplete) of 63 mm; ventral scales 273, tail incomplete, anal scale entire; supralabials 14/15, infralabials 19/19; loreals 1/1; supralabials 7 - 8 entering the eye on the left side, 8 - 9 on the right side; 2 intersupraocular scales, bordered anteriorly by 6 scales, posteriorly by 5 scales; circumorbital series with 10 scales on the right side and 11 on the left; dorsal-scale-row formula 36 - 41 - 26; dorsum unpatterned tan with only the most vague indications of dorsal blotches as dim, slightly darker tan, irregular markings; venter gray, darker posteriorly and with scattered dark-gray subcircular to square spots; top of head concolor with dorsum; chin and throat immaculate cream, the gular scales gray-centered.

VARIATION: The series of paratypes plus the holotype consists of four males and 12 females; of these, three males are from Ile-à-Vache. The largest male (ASFS X3781) has a snout-vent length of 1711 mm, and the largest female (ASFS X3783) a snout-vent length of 1635 mm; both are topotypes. Data on variation in scale counts are given in Tables 1, and 3-8.

The dorsum is virtually unicolor in most specimens. Juveniles are pallid, but more distinctly marked dorsally than adults. At most in adults, there may be a vague or faint indication of the dorsal body blotches in the form of irregular darker-tan-to-brownish angulate lines across the back. Some adults (USNM 60603) are more darkly patterned.

COMPARISONS: Aside from its faded pattern and apparently smaller size, *E. s. exagistus* differs from *E. s. striatus* in several ways. The modal head scale formula of 6-2-5 in *exagistus* differs from the 5-2-5 formula in *striatus*. The modal conditions of 8 or 7 - 8 (rather than 8 - 9) supralabials entering the eye and the very high modality of a single loreal are both distinctive features of the Tiburon snakes. Although *striatus* has lower extremes of subcaudals in both sexes, it also has higher extremes in subcaudals in both sexes. Considering the small number of *exagistus* examined, we have de-emphasized presumed differences in ventral and subcaudal counts. Such differences will have

to be supported by additional material. However, the pale coloration, faded pattern, and loreal, supralabial, and head scale differences serve well to distinguish *exagistus* from *striatus*.

REMARKS: *E. s. exagistus* is known only from the western end of the Haitian Tiburon Peninsula, and on Ile-à-Vache (Fig. 2). The localities where the nominate subspecies and *exagistus* most closely approach each other are Jacmel on the southern coast near the base of the Tiburon Peninsula and either Les Basses or Ile-à-Vache near the tip of the peninsula — distances of approximately 130 kilometers. Like *E. s. striatus*, *exagistus* is primarily a snake of mesic wooded situations; one specimen was secured by Richard Thomas in woods at night as it crossed a paved road.

Seven females from Camp Perrin, collected July 24 - 26, were gravid, with from 7 to 18 fetuses. The females ranged in snout-vent length from 1420 mm to 1635 mm. There is no correlation between snout-vent length and litter size, since both of the small females (1420 mm) had the upper extreme in number of embryos, whereas one of the largest females (1520 mm) had only seven embryos.

E. s. exagistus occurs from sea level (Ile-à-Vache; Jérémie) to about 305 meters at the type locality. Moline lies in the northern foothills of the Massif de la Hotte, possibly at an elevation higher than that of the type locality.

The name *exagistus* is derived from the Greek for "mystical," in reference to the fact that in *vodoun* (voodoo), snakes are associated with the loa Damballa (Leyburn, 1966:148); *Epicrates striatus* is the largest and most conspicuous serpent in Haiti.

Epicrates striatus warreni, new subspecies

HOLOTYPE: MCZ 125604, an adult female from vicinity of Palmiste, Ile de la Tortue, Haiti, taken August 15 - 27, 1970, by native collector for C. R. Warren. Original number ASFS V20364.

PARATYPES: ASFS V20367-78, young removed from MCZ 125604; USNM 59437, Ile de la Tortue, February 1, 1917, W. L. Abbott.

DISTRIBUTION: Ile de la Tortue, Haiti.

DEFINITION: A subspecies of *E. striatus* characterized by a combination of (presumably) moderate size (no adult males known, females to 1411 mm snout-vent length), high number of ventrals in both sexes (284 - 299 in males, 287 - 298 in females), modally 2 intersupraoculars, modally bordered anteriorly by 5 scales, posteriorly by 4 scales, modally 15 supralabials with two supralabials (8 - 9) entering the eye, modally 11 scales in the circumorbital series, and modally 2 loreals; pattern faded and pale and dorsal blotches extremely confluent, when countable between 67 and 81 on the body; lateral neck stripe weakly developed or absent in both adults and juveniles, and a row of pale median dorsal neck blotches present.

DESCRIPTION OF HOLOTYPE: An adult female with a snout-vent length of 1411 mm and tail length (complete) of 264 mm; ventral scales 291, subcaudal scales 89, ventrals + subcaudals 380; anal scale entire; supralabials 14/15, infralabials 18/18; loreals 2/2; supralabials 7 - 8 entering eye on left side, 8 - 9 on right side; 2 intersupraocular scales, bordered anteriorly by 5 scales and posteriorly by 5 scales; circumorbital series with 11

scales on both sides; dorsal scale rows 45 - 55 - 29; dorsal pattern composed of faded brown rhombs, not outlined with black to dark brown, and greatly fused on the neck and approximately anterior quarter of body, leaving a series of pale middorsal spots of ground color to mark the edges of the darker markings; posteriorly, dorsal blotches more apparent and separated by tan dorsal ground color but still not individually apparent due to extensive fusions; tail solid dark-brown-to-black above and without obvious pattern; venter gray, becoming darker gray posteriorly and with scattered dark-gray rectangular blotches, each restricted to a ventral scute and often aligned to give the impression of short dark dashes; lateral neck stripe restricted to region immediately behind head; no clear series of secondary lateral blotches that apparently are fused with the complex darker dorsal pattern.

VARIATION: The series of *E. s. warreni*, including the holotype, consists of seven juvenile males and two adult and four juvenile females. Eleven juveniles were removed from the holotype at the time of preservation and were then quite well developed and active despite the presence of large amounts of yolk. One juvenile (ASFS V20378) is deformed and cannot be sexed. Mr. Warren had several other adult *Epicrates* from Tortue, which the junior author casually examined in life. These snakes were equally pale, and we have no doubt that the Tortue population of *E. striatus* is characteristically pale dorsally (For variation in scutellological characters see tables 1 and 3-8).

The juvenile male paratypes vary in snout-vent length between 310 mm and 385 mm, and the umbilici lie on ventrals 189 to 197. The female juveniles vary in snout-vent length between 360 mm and 370 mm, and the umbilici lie on ventrals 188 to 195.

The only other adult *E. s. warreni* is a female, USNM 59437, a skin without measurements. This snake resembles the holotype closely, except that it is even paler, perhaps due to the length of time since preservation. Like the holotype, it lacks a neck stripe and secondary lateral blotches, and has a series of pale median dorsal nuchal spots or markings due to extensive fusion of the pattern anteriorly. The juveniles are all extremely pale, but with the pattern elements well shown. The dorsal blotches are more apparent than in adults, but the lack of a neck stripe and the anterior blotch fusions are conspicuous.

COMPARISONS: The three Hispaniolan subspecies - *striatus*, *exagistus*, *warreni* - show a graded series in dorsal pattern intensity, with *striatus* at the dark and contrasting extreme and *exagistus* at the very pallid and faded extreme. *E. s. warreni* stands between these two subspecies in pattern intensity, but not geographically. Whereas *striatus* is a well and prominently marked snake, and *exagistus* is a very pale and faded snake, *warreni* shows the pattern but in a faded and much fused (especially anteriorly) form. Only *warreni* regularly has median neck sports or dots. In *striatus* (although this condition occurs as a variant) the angulate dorsal blotches continue to the head in most specimens.

The head scale formulae of the three taxa differ: *striatus* has a head scale formula of 5-2-5, *exagistus* 6-2-5, and *warreni* 5-2-4. Since *war-*

reni is surely a direct derivative of geographically adjacent *striatus*, the similarities between the head-scale formulae of these two subspecies are to be expected. In *striatus* there are 4 pre-intersupraoculars in 27 series versus 51 with 5 scales in this position, whereas in *warreni* there are 10 snakes with 5 pre-intersupraoculars, no snakes with 4, and only one snake with 3.

All Hispaniolan subspecies of *E. striatus* have a mode (or bimode) of two supralabials entering the eye. In *exagistus* the usual supralabials involved in eye penetration are 7 - 8, whereas in *warreni* and *striatus*, they are 8 - 9. Both *warreni* and *striatus* have 2 loreals, in contrast to 1 loreal in *exagistus*.

E. s. warreni is completely separable from *E. s. exagistus* on the basis of ventrals + subcaudals (see Table 1).

REMARKS: Our knowledge of the herpetofauna of Ile de la Tortue has been due principally to the efforts of C. Rhea Warren, who has made extensive collections there in the vicinity of the settlement of Palmiste. There are now 25 species of amphibians and reptiles known from Tortue, but the amount of subspecific endemism is relatively slight (Schwartz, 1970b). There are local subspecies of *Leiocephalus schreibersi* Gravenhorst, *Diploglossus costatus* Cope, *Ameiva chryso-laema* Cope, *Uromacer catesbyi* Schlegel, and *Dromicus parvifrons* Cope. Although Mr. Warren's Tortue collections have not been intensively studied, there are several other species that apparently have diverged at a subspecific level on Ile de la Tortue.

We have no personal knowledge of the habitat of *E. s. warreni*, but we presume that, like its relatives on Hispaniola, it too is an inhabitant of mesic forested situations. Schwartz (1970c:785), quoting Warren's comments, noted that Palmiste is in a mesic region.

Epicrates striatus in the Bahama Islands

We have combined the snakes presently assigned to the taxa *fosteri* and *strigilatus* in the Bahama Islands with *E. striatus* from Hispaniola, since there is a general community of scutellar and pattern details that occurs in all. On the other hand, the Bahamian group differs from the Hispaniolan group in several respects: the intersupraocular scale is modally 1 (rather than 2); the pre-intersupraoculars are modally 3 (rather than 5 or 6); both supra- and infralabials are modally less (14 and 18) in the Bahamas than they are in Hispaniola (15 and 19); supralabials 7-8 are most often involved in eye penetration in the Bahamas, whereas 8-9 are so involved in Hispaniola (except for *E. s. exagistus* which has 7-8); Bahamian circumorbitals are modally 10, but these scales are modally 11 in Hispaniola; and finally, Bahamian snakes modally have 1 loreal (like *exagistus*, but unlike *striatus* or *warreni* with 2). In ventral, subcaudal, and ventrals + subcaudals counts, the

Bahamian snakes overlap Hispaniolan snakes greatly (Table 1).

The presence of a well-expressed lateral line on the neck or anterior portion of the body is a constant Bahamian pattern feature. In some populations this stripe forms a conspicuous element of the dorsal pattern, extending far posteriorly on the body. Secondly, almost all Bahamian populations (one exception) have the anterior blotches fused into a series of pale median dorsal neck dots or spots. It should be noted that the latter pattern feature occurs in *warreni* and in some specimens of *striatus*. The lateral neck stripe also occurs variably in *E. s. striatus*, so that neither pattern feature is exclusively Bahamian.

The number of subspecies to be recognized in the Bahama Islands is problematical. Only two names (*strigilatus*, based on New Providence material; *fosteri*, based on Bimini Islands material) are presently in use, and there is no problem in differentiating these taxa on the basis of coloration. *Epicrates striatus strigilatus* is brown-to-gray, and *fosteri* is very-dark-gray-to-black. One other population (Ragged Islands) is named below. But there are specimens of *E. striatus* from other islands: we have examined specimens from the Berry Islands, Andros, Eleuthera, the Exuma Cays, and Long and Cat islands. Although populations of *E. striatus* on some of these islands are readily assigned to already-named taxa, it is obvious that on others there has been sufficient divergence to consider the populations distinct subspecies. This is the typical picture of intra-Bahamian variation in reptiles. We are handicapped in that few specimens are available, an exception being the Bimini Islands. Finally, variation throughout much of the Bahamas appears to be in pattern, color, and intensity of both these features, rather than in scutellation. We stress these points to emphasize that our interpretation of *E. striatus* in the Bahama Islands is conservative, and might well be different if we had more material from several islands.

Epicrates striatus strigilatus Cope

Homalochilus strigilatus Cope, 1862, 14:71.

Epicrates versicolor Steindachner, 1863, 22(2):89. Type locality "Columbia;" holotype, Naturhistorisches Museum Wien 18930.

TYPE LOCALITY: New Providence Island, Bahama Islands; syntypes, Academy of Natural Sciences of Philadelphia 10237 and 10239.

DISTRIBUTION: The Bahama Islands: New Providence, Rose Island, Eleuthera, Long Island, and the Exuma Cays.

DEFINITION: A subspecies of *E. striatus* characterized by the combination of moderate size (males to 1445 mm, females to 1780 mm snout-vent length), moderate number of ventrals in both sexes (274 - 295 in males, 274 - 288 in females), modally 1 intersupraocular scale (but modally 2 intersupraocular scales on New Providence), modally bordered anteriorly by 3 scales, posteriorly by 5 scales (although 6 is the mode on Long Island), modally 14 supralabials with two or three scales (7 - 8 or 7 - 9) entering the eye, modally 10 scales in the circumorbital series, and modally 1 loreal; pattern consisting of about 68 to 122 much-fused medium-brown to dark-gray dorsal blotches, usually count-

able only by the pale interblotch spaces that are reduced to a series of middorsal pale spots or blotches or angulate markings, most prominent on the neck but extending far posteriorly in some specimens; a prominent dark-brown-to-dark-gray or almost black lateral stripe on the neck, extending for about the anterior quarter to third of the body in some specimens.

VARIATION: Our series of *E. s. strigilatus* consists of 12 specimens from New Providence including Rose Island, 12 from Eleuthera, 5 from Long, and 3 from Great Exuma and Compass Cay in the Exuma Cays (Fig. 3). The largest male (MCZ 96793) is from Eleuthera, and has a snout-vent length of 1445 mm; the largest female (LDO 8-6804) is from Great Exuma and has a snout-vent length of 1780 mm. As in other populations of large boas, these extremes may well be below maximum size. In four juvenile females from New Providence, the umbilici lie on

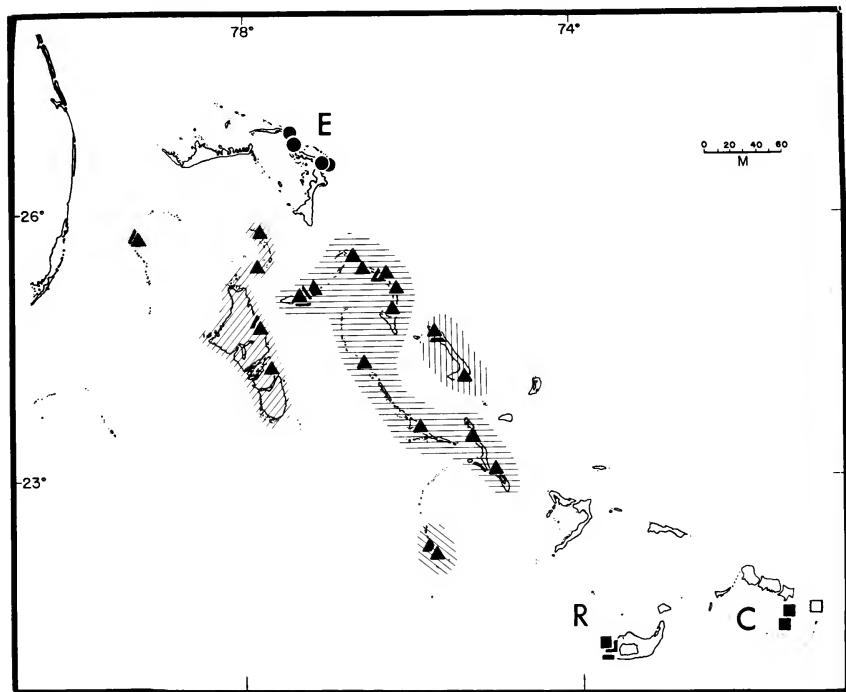


Fig. 3. Map of the Bahama Islands, showing distributions of three species and subspecies of *Epicrates*, as follows: *E. striatus* (triangles); *E. s. fosteri* - stippling (upper left); *E. s. fowleri* - diagonal lines from upper right to lower left; *E. s. strigilatus* - horizontal lines; *E. s. ailurus* - vertical lines; *E. s. mcraniei* - diagonal lines from upper left to lower right. E = *E. exsul* (solid circles). C = *E. c. chrysogaster* (solid squares represent specimens examined, hollow square represents literature record); R = *E. c. relicquus* (solid squares).

ventrals 187 to 194; no male juvenile *strigilatus* are available (See tables 1 and 3-8 for data on scutellar variation in the four geographic samples of *E. s. strigilatus*).

Body blotches are very often uncountable, or can be reckoned only from the pale interspace remnants. Blotches vary from about 68 on New Providence to about 122 on Eleuthera, with Long Island snakes having intermediate counts between 78 and 102. Tail blotches are absent in some specimens and maximally are 22; both extremes occur in New Providence. Blotch counts are the weakest of characteristics on which to subdivide Bahamian *E. striatus*, since significant counts cannot be taken on most specimens.

The dorsal pattern of *E. s. strigilatus* is difficult to describe, since it is highly modified from the basic *E. striatus* pattern. Basically, the pattern consists of a large number of angulate dark markings, brown to dark gray in color, on a paler (tan to gray) ground. These angulate markings are outlined in dark brown to dark gray, from about midbody posteriorly. Anteriorly, the angulate markings are always extensively fused, so that on the neck and anterior quarter to third of the body the markings are no longer discernible. Their positions are indicated only by small pale oval or angulate interblotch areas that are the color of the ground on the remainder of the body. This results in the neck and anterior portion of the body having a median series of pale spots, dots, small angulate areas, or other such indicators of the interblotch regions, whereas the blotches are no longer determinable. There is a secondary ventro-lateral series of dark-brown-to-dark gray angulate blotches, but these are irregular, usually fused with the dorsal darker pattern, and not clearly defined. A regular pattern feature is the presence of a dark lateral neck stripe, involving 2 or 3 dorsal scale rows, which extends from just behind the head at the level of the mouth posteriorly for about the anterior quarter or third of the body. This dark stripe is bordered above by a pale (tan-to-gray) concomitant stripe that makes the dark stripe appear even more prominent. Posteriorly, the stripe breaks up into a series of irregular dark markings that become the secondary ventrolateral series of blotches. The venter is pale and usually immaculate, although it may be much suffused with gray, especially posteriorly. The upper surface of the head is unmarked, although there usually are some paler suffusions on a darker ground, but these do not form a definite pattern.

This description of the basic *strigilatus* pattern is general, and most snakes show some variation in this pattern. Some individuals (MCZ 42268) have the dorsal pattern composed of scales of three colors: pale, medium brown, and black. The result is a very complex dorsal pattern that defies description. In many other snakes, especially topotypes, the dorsal pattern seems much less contrasting, and the dorsal scales are

generally divisible only into pale and medium-dark scales. Even here, however, the pale interblotch remnants are often bordered by scales that are darker than any others on the dorsum. Anteriorly, the lowermost four dorsal scale rows below the neck stripe are usually immaculate, but in some snakes (MCZ 42268) there are small irregular dark blotches in this area. In others, the pale stripe above the dark neck stripe is sharply bordered above by a dark longitudinal stripe, which gives the neck a quadrilineate appearance (UMMZ 117026). These accessory dark neck stripes are absent in other individuals, and in extreme cases (ASFS V23469) the lower dark neck stripes are very short and become fragmented to form a series of dark secondary angulate blotches on the lower sides. The variants seem endless, and there appears to be no correlation with geography.

REMARKS: We have collected very few *E. s. strigilatus* ourselves and our knowledge of the habitats occupied by this most widespread of the Bahamian subspecies is meagre. Two snakes from New Providence were secured at night, one crawling in a bush in scrub and the other in a tree in coppice. (In Bahamian terminology, "scrub" refers to a treeless or virtually treeless vegetation type; "coppice" refers to stands of tropical hardwood trees.) Since the Bahamas are in general far more xeric than optimum habitats occupied by *E. striatus* on Hispaniola, all the Bahamian subspecies must be more tolerant of arid conditions than the Hispaniolan subspecies. Still, at least one of our New Providence snakes was taken in a wooded situation, which suggests that *E. s. strigilatus* may frequent woods throughout its Bahamian range. The large number of specimens from Hatchet Bay, Eleuthera, is probably due at least in part to the extensive poultry-raising industry at that locality. Natives there told the junior author that *Epicrates* was locally abundant, the snakes being attracted to the area by the multitude of chickens. In fact, *Epicrates striatus* is known as "fowl snake" throughout the Bahamas, doubtless because of its predilection for this kind of food.

The range we attribute to *E. s. strigilatus* (Fig. 3) includes most of the islands on the east side of the Great Bahama Bank, east of the Tongue of the Ocean, with the exception of Cat Island and the Ragged Islands, both of which are inhabited by other distinctive subspecies. Like many Bahamian reptiles and amphibians, *E. striatus* does not cross the Crooked Island Passage. The genus reappears in the southeastern Bahamas on Great Inagua and the Turks and Caicos groups. *E. striatus* is absent from Rum Cay and San Salvador, both of which stand on isolated banks. It does not occur on the Little Bahama Bank, part of which is occupied by *E. exsul*. The species may occur on Green Cay on the eastern edge of the Tongue of the Ocean. That isolated islet has a poorly known but remarkably diverse herpetofauna.

Epicrates striatus ailurus, new subspecies

HOLOTYPE: AMNH 77015, an adult female, from Alligator Cay, Bennett's Harbour, Cat Island, Bahama Islands, taken March 24, 1953 by George B. Rabb (original number VV-AMNH 3809).

PARATYPES: Cat Island, Bahama Islands: MCZ 39481-82, Arthur's Town, July-August, 1935, W. J. Clench; MCZ 39483, Bennett's Harbour, July-August, 1935, W. J. Clench; ASFS V11146, Port Howe, November 4, 1966, native collector; ASFS V11163, 0.8 km. N Port Howe, November 3, 1966, R. Thomas.

DISTRIBUTION: Cat Island, Bahama Islands.

DEFINITION: A subspecies of *E. striatus* characterized by the combination of moderate size (males to 1560mm, females to 1640 mm snout-vent length), moderate number of ventrals in both sexes (283 - 293 in males, 280 - 285 in females), modally 1 intersupraocular scale, modally bordered anteriorly by 3 or 4 scales, posteriorly by 3 to 7 scales (no mode), modally 14 supralabials with two scales (7 - 8) entering the eye, modally 10 scales in the circumorbital series, and modally 1 loreal; pattern consisting of a long, prominent lateral neck stripe, extending over one third the length of the body, dorsal blotches completely fused and indeterminate except by their pale remnant interspaces, which occur on the neck as a series of dark-bordered oval or circular median dorsal markings, and posteriorly as a median longitudinal dorsal stripe extending far onto the tail.

DESCRIPTION OF HOLOTYPE: An adult female with a snout-vent length of 1640 mm and tail (incomplete) of 290 mm; ventral scales 280, tail (incomplete) with 84 subcaudal scales, anal scale entire; supralabials 14/14, infralabials 18/18; loreals 1/- (one side damaged); supralabials 7 - 8 entering the eye bilaterally; 1 intersupraocular scale, bordered anteriorly by 3 scales, posteriorly by 3 scales; circumorbital series with 10 scales on the left side, 11 on the right; dorsal-scale-row formula 40 - 47 - 25; dorsum (as preserved) very dark gray with a broad middorsal band, darker gray (almost black centrally) with a series of about 97 pale oval, circular, or more or less angulate pale median spots or blotches from the occiput as far as the posterior third of the body, beyond which these spots are fused into a solid pale middorsal stripe that extends to about the tip of the tail; the dark middorsal band bordered ventrally by a solid black stripe anteriorly, that posteriorly becomes increasingly irregular and fragmented and finally extends ventrolaterally to combine with the remnants of the lateral neck stripe, resulting in the middorsal dark band having grossly serrate edges that extend ventrally to within two or three dorsal scales of the ventrals; lateral neck stripe dark and prominent, joined on the temporal region by a dark vertical band to the anterior continuation of the dark dorsal band margin, extending about two-thirds of the length of the body, becoming broader and slightly fragmented, the posterior third to quarter extremely fragmented and combined with the dark edge of the dorsal band; scattered dark scales, small or large blotches along the length of the body among the pale scales below the lateral dark stripe and adjacent to the ventrals; venter pale anteriorly, suffused with gray posteriorly, and with dark gray scattered quadrate or subrectangular markings restricted to individual ventrals, becoming more intense posteriorly and forming, on the underside of the tail, a median dark line which near the tip forms the black underside of the tail; head grayish, with a pair of pale lateral areas and pale lores, a dark preorbital V, and a dark line from the temples to the supraorbital scale on each side.

VARIATION: The series of *E. s. ailurus* consists of three males and three females. Variation in scutellar characteristics is given in Tables 1 and 3-8.

In dorsal pattern the series is like the type in most details. Typical is the dark middorsal band with median pale spots or blotches, either

continuing through the entire length of the body, or more often fused to form a pale middorsal stripe that extends onto the tail. Also typical is a very dark (black) neck stripe that extends far back onto the body and even beyond, is easily discernible as a prominent series of black blotches. No snake shows any indication of angulate dorsal blotches; blotch positions can be ascertained only by the pale median dorsal markings. Even this method fails because of fusion of these pale interspaces posteriorly. The head markings described for the holotype are constant, with basically a postorbital and a post-supraocular dark stripe present. The major variant in pattern in the paratypic series is the absence of a very dark border to the middorsal dark band.

COMPARISONS: The differences between *ailurus* and *strigilatus* (also *striatus*, *exagistus* and *warreni*) are primarily in pattern. No other subspecies has complete obliteration of the dorsal angulate blotches resulting in either a middorsal series of pale spots or blotches or the fusion of these interspace remnants posteriorly into a middorsal stripe. The neck stripe is far more bold and extends farther posteriorly in *ailurus* than it does in *strigilatus*. In general, *ailurus* is a boldly and contrastingly patterned snake in comparison with the less contrastingly angulate-blotched *strigilatus*. When the scale counts of *ailurus* are compared with those of all populations of *strigilatus* there appear to be no differences, although the counts of ventrals in *ailurus* fall toward the upper extreme of these counts in *strigilatus*. Differences between *ailurus* and the Hispaniolan subspecies basically are ones of pigmentation and pattern. In fact, *ailurus* and *exagistus* are extremely different in these features. It is unnecessary to compare *ailurus* and the Hispaniolan subspecies of *E. striatus* in detail, since *ailurus* is distinctly a member of the Bahamian complex of the species.

REMARKS: We have named *E. s. ailurus* because it is consistently different from all other Bahamian populations. Although some of its features occur in diluted form in some *E. s. strigilatus*, on the whole the two taxa are very different.

Cat Island, although surely originally a portion of the Great Bahama Bank, now is separated from it (Fig. 3). The fauna of Cat suggests that it has been fairly well isolated from the balance of the Great Bank islands. In some cases (*Ameiva auberi*, McCoy, 1970) Cat has very distinctive subspecies of otherwise widely-ranging Bahamian species; in others (*Sphaerodactylus decoratus*, Thomas, 1968; *Anolis distichus*, Schwartz, 1968b), the Cat Island populations show peculiar mélanges of characteristics of populations of adjacent islands and defy any orthodox nomenclatural treatment. Schwartz (1968a) has suggested that Cat Island has had a history somewhat different from that of the balance of the islands that are more or less associated with it on the Great Bank.

Since we have not collected *E. s. ailurus* ourselves, we have no first-hand knowledge of its coloration in life. The two specimens secured by Thomas lack field or habitat data. The holotype, however, was taken from a crevice in a large limestone block adjacent to a sandy beach (Rabb and Hayden, 1957:39). Presumably, like other members of the species, *ailurus* inhabits wooded situations or coppice.

The name *ailurus* is Greek for "cat," in allusion to the island upon which this subspecies occurs.

***Epicrates striatus mcraniei*, new subspecies**

HOLOTYPE: UMMZ 118033, a subadult male, from Margaret Cay, Ragged Islands, Bahama Islands, taken September 7, 1957 by Robert Hanlon.

PARATYPES: Little Ragged Island, Ragged Islands, Bahama Islands: ASFS V22851, November 16, 1970, J. R. McCranie; ASFS V23468, November 17, 1970, J. R. McCranie.

DISTRIBUTION: Little Ragged Island and Margaret Cay, Bahama Islands.

DEFINITION: A subspecies of *E. striatus* characterized by the combination of small size (single male specimen with snout-vent length of 1330 mm, largest female 1540 mm), low number of ventrals in both sexes (270 in male, 266 - 271 in females), modally 2 intersupraocular scales, modally bordered anteriorly by 3 scales, posteriorly by 4 to 6 scales (no mode), modally 14 supralabials with two scales (7 - 8) entering the eye, 10 or 11 scales (no mode) in circumorbital series, and modally 1 loreal; dorsal pattern consisting of about 80 to 92 well defined and unfused dark-brown to very dark gray angulate blotches, clearly separated by pale-gray to grayish-tan interspaces, and without a median series of dorsal dots or spots on the neck or anterior portion of the body; lateral neck stripe absent or at best represented by a very short black line followed along the body by a series of irregularly shaped and placed black secondary blotches on a very pale gray ground.

DESCRIPTION OF HOLOTYPE: A subadult male with a snout-vent length of 1330 mm and tail length (complete) of 220 mm; ventral scales 270, subcaudal scales 83, ventrals + subcaudals 353, anal scale entire; supralabials 14 on the left side, uncountable on the right, infralabials 19 on the left side, uncountable on the right; loreals 1/1; supralabials 8 - 9 entering the eye on the left side, 7 - 8 on the right side; 2 intersupraocular scales, bordered anteriorly by 3 scales, posteriorly by 6 scales; circumorbital series with 10 scales on the right side, 11 scales on the left side; dorsal scale row formula 41 - 50 - 26; dorsum (as preserved but probably little changed from the living condition as observed in the paratypes) a combination of black angular markings and gray-to-whitish gray interspaces, about 80 angulate markings on the body and about 18 on the upper surface of the tail; no central fusion of the black blotches (although lateral margins may touch or fuse slightly) so there is clear differentiation between the black blotches and the pale-gray interspaces and no indication of a median series of pale middorsal dots or spots; upper surface of head marbled with very dark gray and paler gray, but without definite pattern; dark neck stripe restricted to about 15 dorsal scales, followed by a series of irregularly spaced and sized black secondary blotches which continue on the sides of the tail but are much paler posteriorly; a series of much paler and smaller gray ventrolateral blotches on the lower sides; venter pale creamy, but much suffused with gray and without quadrate or rectangular spots or blotches.

VARIATION: Variation in scutellation is shown in Tables 1 and 3-8. The two paratypes were seen in life by the junior author. One (ASFS V22851) was recorded as being very dark gray and pale grayish tan dorsally, with the labials pale yellow and the venter creamy with dark-

gray marbling and stippling. The throat was immaculate pale cream. The other (ASFS V23468) had dark brown blotches on a grayish-tan ground. The blotches were almost black peripherally. The venter was cream, stippled and clouded with gray. The head was brown above, marbled with white and cream. The pattern details of these two paratypes agree closely with the holotype. The dorsal pattern is very dark on a pale ground, there is no median fusion of dark blotches, and thus there are no middorsal pale spots or blotches. The dark dorsal blotches are distinct and well separated by pale ground color. The lateral neck line is short, even shorter than in the holotype, and in a very short distance degenerates into a longitudinal series of lateral blotches or blotch fragments.

COMPARISONS: *E. s. mccraniei* is distinguished from all other Bahamian subspecies of *E. striatus* by having 2 intersupraocular scales, very dark coloration, no dorsal blotch fusion (and thus without median neck markings), and extreme reduction of the lateral neck stripe. The subspecies also stands at the lower extreme in ventral counts and in ventrals + subcaudals in both sexes. In having an angulate dorsal pattern and 2 intersupraoculars, *mccraniei* most closely resembles *E. s. striatus*, but it differs from that subspecies in having 1 rather than 2 loreals, 14 rather than 15 supralabials, supralabials 7 - 8 rather than 8 - 9 entering the eye, and much different color: dark browns, blacks, and grays rather than browns and tans. Both sexes of *mccraniei* have fewer ventrals than do both sexes of *striatus*, although additional specimens of the Bahamian subspecies will doubtless show some overlap in this character (Table 1). Ventrals + subcaudals in *mccraniei* are distinctly lower than similar counts in *striatus*. *E. s. mccraniei* differs greatly from *exagistus*, in pattern and color, and is very different in color from *warreni*.

REMARKS: One of our major reasons for combining the Bahamian subspecies with Hispaniolan *E. striatus* is the discovery of *E. s. mccraniei*. This subspecies combines both Bahamian and Hispaniolan characteristics, and occupies the Bahamian islands (the Ragged Islands) that are closest to Hispaniola (although they are much closer to Cuba than to Hispaniola; other islands in the Bahamian Archipelago are closer to the Hispaniolan coast but are not occupied by *E. striatus*). It is remarkable that such a distinctive subspecies occurs on a string of cays that at one time were undoubtedly connected to Long Island (Fig. 3), one of the land masses now occupied by *E. s. strigilatus*. Long Island *strigilatus* show no approach to *mccraniei* even though they differ in some respects (such as having 6 post-intersupraoculars) from topotypical *strigilatus*.

The herpetofauna of the Ragged Islands is just becoming fairly well known. The Ragged Islands support a typical Great Bahama Bank fau-

na, but there are several species that have differentiated there (*Ameiva auberi*, McCoy, 1970; *Sphaerodactylus decoratus*, Schwartz, 1972). Doubtless, as the McCranie-Porras material is further studied, it will be shown that other widespread Bahamian species have differentiated subspecifically on this long chain of islands and islets.

One of the paratypes was secured by McCranie at dusk as it extended its head from a cranny in a rock wall adjacent to a well. The other paratype was secured the following day in the same rock wall, as it too put out its head. The rock wall surrounds a buttonwood (*Conocarpus*) swamp.

Epicrates striatus fosteri Barbour

Epicrates striatus fosteri Barbour, 1941, 18: 64.

TYPE LOCALITY: North Bimini, Bahama Islands; holotype, MCZ 46054.

DISTRIBUTION: North Bimini, South Bimini, East Bimini, and Easter Cay, Bahama Islands.

DEFINITION: A subspecies of *E. striatus* characterized by the combination of large size (males to 2330 mm, females to 1895 mm snout-vent length), moderate number of ventrals in both sexes (272 - 286 in males, 269 - 282 in females), modally 1 intersupraocular scale, modally 14 supralabials with 3 scales (7 - 9) entering the eye, modally 10 scales in the circumorbital series, and modally 1 loreal; dorsal pattern consisting of a dark-brown-to-black band resulting from the almost complete fusion of the dorsal angulate markings, the positions of these markings shown only by dorsal median pale-brown-to-grayish-tan oval to angulate interspaces, the more posterior ones more angulate and the more anterior ones more oval; lateral neck stripe prominent, extending for about the anterior third of the body and concolor with the dorsal dark color but set off from that dorsal color by a longitudinal stripe of pale ground color.

VARIATION: No other Bahamian *Epicrates* has been so poorly diagnosed as *fosteri*. Barbour (1941:64) noted only that it has "the ground color black—black as a raven's wing—with a pearly iridescence of extraordinary beauty." *Epicrates s. fosteri* is a very distinctive snake and is well represented in collections since it is common on all four islands where it occurs. (Fig. 3). We have examined more *fosteri* (a total of 25 including the holotype) than any other subspecies of *E. striatus* from the Bahamas. *Epicrates s. fosteri*, as Barbour pointed out, is a dark snake, in contrast to the generally brown-to-gray snakes from most other Bahamian islands (exceptions being Andros, the Berry Islands, and the Ragged Islands). There is no question of the distinctness of *fosteri* from *strigilatus*, *ailurus*, and *mccraniei*, and it forms one member of a pair of subspecies that occupies islands west of the Tongue of the Ocean.

Our series consists of 20 males and five females. There are two juveniles, female litter mates, with snout-vent lengths of 230 mm and 330 mm. The smaller is deformed, and the umbilicus on the larger lies on ventral 192. Details of scutellation are shown in Tables 1 and 3-8.

Body and tail blotches cannot be counted because of the extensive

fusions between them; but pale interspace counts vary between about 66 to 108 on the body, and tail blotch counts range from 4 to 16, the variation due to the degree of fusion of the dorsal caudal markings.

Barbour's comments on the color of *E. s. fosteri* require emendation. Rarely is a black *fosteri* encountered. The dorsum is most often very dark brown to very dark gray, with the light interspaces grayish tan to paler gray. Nevertheless, the dark dorsal color of *fosteri* is indeed distinctive. The complete fusions of the basic angulate dorsal markings is likewise distinctive. In addition, the lower sides have strongly angulate dark-brown-to-dark-gray blotches, which form a secondary series, resulting at least in part from disintegration of the dark lateral neck stripe posteriorly. These secondary blotches are most often fused posteriorly with the dark dorsal pattern to give a jagged and grossly serrate pattern which extends to the dorsal-ventral junction. The lateral neck stripe is as dark as the dorsum, and separated on the neck and anterior portion of the body by a more dorsal pale stripe, with the result that the neck stripe is especially prominent and boldly delineated. In most specimens, the neck stripe disappears at about the anterior third of the body and disintegrates into a series of irregularly sized and spaced angulate markings. Posteriorly, these fuse with the dorsal color as noted above. Below this secondary series of markings there may be another longitudinal series of smaller and usually slightly paler blotches, which also may fuse posteriorly with the entire dorsal pattern. The median dorsal pale interspaces tend to be subcircular or oval dots or spots on the neck, but become increasingly angulate posteriorly. These interspaces on the tail may be demonstrated by only a few scattered pale scales on an otherwise very dark ground. The upper surface of the head is concolor with the dorsum, but the temples are usually very pale, and the median dorsal series of pale dots extends to the occiput or slightly beyond. The chin and throat are immaculate cream to very pale gray, and this color continues onto the anteriormost ventrals. Posteriorly, the venter is heavily suffused with dark gray, and may be vaguely to strongly marked with darker-gray-to-dark-brown quadrate or subrectangular spots. These spots are limited to individual ventrals, and are often aligned to give a vaguely lineate appearance to the venter. In addition, some snakes (ASFS V21986) have pale quadrate areas on the ventrals, so that there may be three colors - pale cream, gray, dark gray - forming a checkered appearance.

This description is only general, since there are many modifications in the series before us. For example, the neck stripe may be restricted anteriorly (ASFS V7121) and may almost immediately break down into the series of secondary lateral blotches. The dorsal color is variable, but in almost all snakes tends to very dark brown to almost black. None of our material, either preserved or alive, is solid black as Barbour's

diagnosis implies. The juvenile coloration does not differ strikingly from that of adults, except that the colors are somewhat paler, although never so pale as they are in juvenile *strigilatus*.

COMPARISONS: *Epicrates s. fosteri* differs from all subspecies thus far discussed (except *mccraniei*) in its very dark dorsal coloration. No other population of *E. striatus* from Hispaniola or east of the Tongue of the Ocean approaches *fosteri* in this character. From *mccraniei*, which is also dark, *fosteri* may be easily distinguished by (1) complete fusion of dorsal blotches rather than complete separation as in *mccraniei*, (2) 1 rather than 2 intersupraoculars, and (3) higher ventrals and ventrals + subcaudals counts (see data in Table 1). *Epicrates s. fosteri* differs also from all other Bahamian and Hispaniolan populations in having three supralabials (7 - 9) entering the eye; all other subspecies modally have two supralabials (7 - 8, 8 - 9) entering the eye, although it should be recalled that topotypical *strigilatus* modally have three supralabials (7 - 9) entering the eye, and that this condition occurs as a bimode in Long Island *strigilatus*.

REMARKS: A series taken by Richard Thomas and Dennis R. Paulson (ASFS X4805-X4810) was secured in coppice on South Bimini, with the exception of one snake that was taken crossing a road at night in mangroves. Like its relatives elsewhere, *fosteri* is basically a snake of forested situations, although it may be encountered some distance from optimal habitat. A small individual (ASFS V7121, 860 mm snout-vent length) contained a catbird (*Dumetella*) in its stomach. Two litter mates (ASFS V8074-V8075) were born to a female in captivity on September 4. The female was about 2.0 meters long, and the total litter consisted of 17 snakes.

***Epicrates striatus fowleri*, new subspecies**

HOLOTYPE: MCZ 125605, an adult male, from Fresh Creek, Andros Island, Bahama Islands, taken September 7, 1970, by Danny C. Fowler. Original number ASFS V20366.

PARATYPES: Andros Island, Bahama Islands: ASFS V20365, 0.8 km S Fresh Creek, September 5, 1970, D. C. Fowler; ASFS V15175, Mangrove Cay, east shore, 3.2 km S airstrip, April 25, 1968, P. M. Baker; ASFS V20461, 3.7 km S Stanniard Creek, May 16, 1971, A. Schwartz; AMNH 2923-24, 1908, Drs. Dahlgren and Meuller; MCZ 5819, no collector or date. Berry Islands, Bahama Islands: ASFS V22303, Chub Cay, spring 1970, gift of D. W. Thornton; ASFS V22304, Great Harbour Cay, May 5, 1970, native collector.

DISTRIBUTION: Andros Island and the Berry Islands, Bahama Islands.

DEFINITION: A subspecies of *E. striatus* characterized by the combination of large size (males to 1260 mm, females to 2055 mm snout-vent length), moderate number of ventrals in both sexes (273 - 282 in males, 271 - 276 in females), modally 1 intersupraocular scale, modally 15 supralabials with 2 scales (7 - 8) entering the eye, modally 10 scales in the circumorbital series, and always 1 loreal; dorsal pattern consisting of a very dark-brown-to-dark-gray or almost black middorsal band representing the fused angulate blotches, leaving ovate to angulate paler (gray to tan) interspaces, lateral neck stripe prominent and dark but short and disintegrating into a series of lateral dark secondary blotches before the anterior third of the body.

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 1260 mm and tail length of 240 mm; ventral scales 282, subcaudal scales 85, ventrals + subcaudals 367, anal scale entire; supralabials 15/15, infralabials 18 on the left side, 19 on the right, loreals 1/1; supralabials 7 - 8 entering the eye bilaterally; 1 intersupraocular scale, bordered anteriorly by 4 scales, posteriorly by 5 scales; circumorbital series with 11 scales on the right side, 13 scales on the left; dorsal scale row formula 40 - 51 - 27. Dorsum very dark brown (almost black) with no indication of angulate dark blotches that are fused to each other, leaving about 96 paler (brown) ovate to angulate interspaces in a middorsal series from occiput to vent, and 17 pale interspaces on the tail; head unicolor with dorsum and with a few median pale brown occipital spots and a black neck stripe that begins at the angle of the jaws and, after being almost immediately broken, continues for about 3 centimeters on the neck, then is fragmented into a secondary series of irregularly spaced and sized blotches that continue for a short distance then fuse with the darker edges of the dorsal pattern to give a serrate effect on the posterior half of the body; tail very dark brown above, the pale interspace markings restricted to small areas of about four or fewer scales; chin, throat, and anterior ventrals cream, becoming suffused posteriorly with dark gray, so that they are irregularly mottled with gray and marked by some darker gray margins at the dorsal-ventral junction; underside of tail with a dark-gray median stripe composed of a lineate series of dark-gray quadrate blotches on the subcaudals.

VARIATION: The series of *E. s. fowleri* consists of four males and three females from Andros and one male and one female from the Berry Islands. Scutellogical details are in tables 1 and 3-8.

With one exception (ASFS V15175, see below), all paratypes agree closely with the holotype in pattern and color. *Epicrates s. fowleri* is a very dark snake, much like *fosteri*, with the dorsal blotches much fused and determinable only by their remnant pale interspaces. These number about 78 to about 112 on the body and from about 9 to 17 on the tail. The neck stripe is regularly short, and promptly fragments into a series of secondary lateral blotches. Of the two Berry Island snakes, one (ASFS V22304) lacks any clear indication of the neck stripe, the pattern being fragmented at its very inception. The other (ASFS V22303) has a more extensive neck stripe which, however, quickly disintegrates into a series of elongate stripe-like pieces, which in turn dissolve into the customary series of secondary blotches and more posteriorly fuse with the dorsal pattern. Colors involved in all but the exceptional specimen noted above are dark browns and blacks. ASFS V20461 was described in life as dorsally dark-brown-to-black with the interspaces and lower sides brown, with white scales intermixed. The chin and throat were immaculate yellow and the venter much suffused with darker gray posteriorly.

Only one *Epicrates* (ASFS V15175) is known certainly to have come from Mangrove Cay, that portion of Andros Island that lies between Middle Bight and South Bight, and is thus completely isolated from other *fowleri* localities. Although there are no precise locality data on the MCZ and AMNH *fowleri*, they conform to our diagnosis of the

subspecies. The Mangrove Cay specimen, a female with a snout-vent length of 980 mm, was in life dorsally patternless medium brown with a bluish-gray lateral stripe from just posterior to the jaw articulation to halfway along the body. There are some small darker brown blotches below the lateral stripe and a few widely scattered black scales dorsally, but otherwise the snake is patternless. One of the old specimens (MCZ 2923) exhibits a similar appearance, but this may be due to fading after a long time in preservative.

Central Andros (Mangrove Cay) and South Andros (south of South Bight) are both extensive land masses, cut off completely by the east-west bight system on Andros. It is possible that snakes on these islands have diverged from their relatives on North Andros, whence all recently taken and well-documented Andros snakes have come. Only additional southern material can confirm this postulate. On the other hand, the Mangrove Cay snake may only be aberrant in color and pattern.

COMPARISONS: *E. s. fowleri* differs from all other Bahamian and Hispaniolan subspecies (except *fosteri* and *mccraniei*) in its dark dorsal coloration and fused dorsal blotches. In *mccraniei*, the dorsal angulate blotches are distinct, and there are 2 intersupraoculars and modally 14 supralabials. These two subspecies are very different in pattern and not easily confused. In addition, the ventrals + subcaudals counts in *mccraniei* lie below the lower extreme of these counts in *fowleri* (*mccraniei* male 353, *fowleri* males 358 - 367; *mccraniei* female 343, *fowleri* females 352 - 359). Additional *mccraniei* will probably show some overlap with *fowleri* in these counts.

The more pertinent comparisons of *fowleri* are with adjacent *fosteri*. These two subspecies are very similar in dorsal color and pattern, although *fosteri* has longer lateral neck stripes than does *fowleri*. Two scutellar differences of importance are the presence of 14 supralabials of which 7 - 9 enter the eye in *fosteri*, in contrast to 15 supralabials of which 7 - 8 enter the eye in *fowleri*. The mode of three supralabials entering the eye is very strong (34 of 52 series) in *fosteri*, whereas only one of 18 series has three supralabials entering the eye in *fowleri*.

REMARKS: Two specimens from the Berry Islands do not differ appreciably in scale counts or color and pattern from Andros *fowleri*. In both cases only two (rather than three) supralabials enter the eye, and the neck stripe, as noted above, is very short and quickly fragmented. We see no reason to consider the Berry Islands snakes as *fosteri*, and here consider them *fowleri*. Interestingly, one other reptilian species (*Anolis distichus*) has a subspecies common to Andros and the Berry Islands but a different subspecies on the Biminis (Schwartz, 1968b). Although the Berry Islands and Andros are both close to New Providence, they lie on the west side of the Tongue of the Ocean, whereas New Providence lies on the east side of this deep break in the Great

Bahama Bank (Fig. 3). The similarities of the subspecies west of the Tongue (*fosteri*, *fowleri*) stand in strong contrast to those on the east side of the Tongue (*strigilatus*, *ailurus*). *Epicrates s. mccraniei* differs from both these groups, although it lies on the east side of the Tongue.

One paratype (ASFS V20365) was taken under a large boat hatch lying on sand and leaves, about 5 meters from the shore in a *Coccoloba-Casuarina* stand. The holotype was secured after a heavy nocturnal deluge as it crawled in an ornamental oleander tree about 2.5 meters above the ground. The Stanniard Creek snake (a female) was taken May 16, 1971, at night, on an unpaved road in pinewoods after an all-day rain. It was very inactive. Upon preservation, 35 slightly embryonated eggs were taken from the snake. The Great Harbour Cay snake was crawling on the road during the late morning. Apparently, *E. s. fowleri* tolerates a wide variety of habitats.

South Andros is quite different ecologically from North Andros. The former area is vegetationally dense coppice, and the latter is primarily pinelands on a limestone substrate. There are as yet no specimens of *Epicrates* from South Andros, although the natives there assured the junior author that "fowl snakes" do indeed occur in that region.

Epicrates chrysogaster Cope

Homalochilus chrysogaster Cope, 1871, 11:557.

TYPE LOCALITY: "Turk's Island" (perhaps meaning Grand Turk Island, Turks Islands, although the species has not been reported or collected there subsequently); holotype, Academy of Natural Sciences of Philadelphia 10322.

DEFINITION: A large species of *Epicrates* (males to 810 mm, females to 1310 mm snout-vent length), with 245 - 275 ventral scales in males, 249 - 270 ventral scales in females, 79 - 88 subcaudals in males, 74 - 83 subcaudals in females; ventrals + subcaudals 320 - 363 in males, 327 - 339 in females; intersupraocular scales modally 2, pre-intersupraocular scales modally 3, post-intersupraocular scales modally 3; dorsal scale rows 33 - 37 on neck, 39 - 47 at midbody, 19 - 27 anterior to vent, the lowermost scale row not alternating a large and a small scale for each ventral scute; supralabials modally 14 with either two scales (7 - 8) or three scales (6 - 8) entering the eye; infralabials modally 16; loreals modally 2; circumorbital series modally composed of 11 scales; dorsal pattern extremely variable, from a series of 38 to 77 angulate dorsal blotches (often very reduced) to four longitudinal gray stripes; tail blotches, when present, from about 6 to 20.

DISTRIBUTION: The Turks and Caicos Islands, and Great Inagua Island (including Sheep Cay) in the extreme southeastern Bahama Islands (Fig. 3). In the Turks Islands, known only from the indefinite type locality, and in the Caicos Islands only from "Ambergris Cay" and Long Cay off South Caicos, but presumably widespread throughout these two island groups.

REMARKS: The most distinctively patterned of the Antillean *Epicrates* is *E. chrysogaster*. Some specimens are longitudinally striped, but this is not a constant pattern feature. Some individuals are more orthodoxly patterned with a series of dorsal angulate blotches, but these may be small and restricted, so that the snakes appear virtually patternless.

Although *relicquus* Barbour and Shreve has been considered (1) a distinct species, (2) a subspecies of *E. striatus* (Barbour, 1937), or (3) a subspecies of *E. angulifer* (Mertens, 1939), we have no doubt that this Great Inagua taxon is most closely related to *E. chrysogaster* and should be considered conspecific with it. Schwartz (1968a) considered *E. chrysogaster* distinct from related Antillean boas (*angulifer*, *striatus*) and raised it to specific rank. We here consider that *chrysogaster* and *relicquus* comprise one species, which is endemic to the extreme south-eastern Bahamas and the Turks and Caicos islands. Most remarkably, Barbour and Shreve (1935) did not compare *relicquus* with adjacent *chrysogaster*, but rather with *E. striatus*, a species from which *relicquus* is easily distinguished and eminently distinct. Although it seems likely that *E. chrysogaster* is a derivative of *E. striatus* (see discussion below), we feel strongly that the differences between *striatus* and *chrysogaster* are specific rather than subspecific.

Epicrates chrysogaster chrysogaster Cope

DISTRIBUTION: Caicos Islands (and possibly Turks Islands).

DEFINITION: A subspecies of *E. chrysogaster* characterized by the combination of low number of ventral scales (245 in one male, 249 - 259 in five females), low number of ventrals + subcaudals (320 in one male, 327 - 339 in four females), low number of dorsal scale rows at midbody (39 - 43), modally 14 supralabials with usually three supralabials (modally 6 - 8) entering the eye, modally 15 infralabials, and a pattern consisting of either a series of angulate to ovate dorsal blotches without a secondary lateral row, or a series of four longitudinal dark-gray stripes, the two dorsal stripes at about the level of the central portions of the position of the blotch series and the lateral pair of stripes on the lower sides, in about the position of a secondary series of lateral blotches.

VARIATION: The series consists of one male and five females. The male (MCZ 42408) has a snout-vent length of 590 mm, and the largest female (MCZ 11989) has a snout-vent length of 1220 mm. One other (presumed) female is represented only by its anterior half, so that body counts are not available for this individual. Scutellogical variation is shown in Tables 2 - 8.

Five of the series of *E. c. chrysogaster* have a blotched pattern.

(1) MCZ 11990 has the most elaborate pattern, consisting of a series of more or less ovate-to-slightly-angulate blotches that are usually arranged in a series of saddles or partial saddles (i.e., without complete alternation). The blotches are brown with slightly darker edges. These dorsal blotches involve about the 15 middorsal scale rows, and fall far short of the dorsal-ventral junction. The lower sides are almost immaculate tan, with occasional widely scattered small brown spots. The head is clear tan above, with a pair of small brownish occipital spots. The venter is immaculate cream.

(2) UMMZ 117027 is much like the above snake except that the dorsal blotches are much more restricted laterally, and there is a

strong tendency toward fusion and alternation of blotches. The lower sides are immaculate, and there is a narrow but clear postocular dark-brown stripe across the temporal region.

(3) MCZ 11992 is a large adult, and it too has restricted dorsal blotches, but the blotches are more angulate and much more difficult to delimit since they are much invaded by tan ground color.

(4) MCZ 41049 is a young snake that is almost patternless, the dorsal pattern limited to a series of widely scattered medium-brown spots on a tan ground. The lower sides are patternless and the head has a dark postorbital stripe. Blotch counts in this series of 4 snakes vary between 38 and 77 on the body, and about 6 to 17 on the tail.

(5) MCZ 11991 is the half-specimen noted above. It shows an almost complete loss of dorsal pattern, the blotch sites indicated by small isolated patches of dark scales.

Two snakes are longitudinally striped. The smaller of these (MCZ 42048) has prominent broad paramedian gray stripes, three scales wide, from the occiput to near the tip of the tail. On the distal portion of the tail the two stripes fuse so that the tail becomes totally dark dorsally. The lateral stripes are much finer, involving only one scale row, and are separated from the dorsal stripes by about 4 scale rows. These lateral stripes begin on the neck and extend to above the vent. The head is patternless except for a postocular dark line, and the venter is immaculate. A larger striped snake (MCZ 11989) is similar, except that the stripes are less apparent.

The two *E. c. chrysogaster* patterns seem not to be correlated with geography, since both lined and blotched snakes occur on "Ambergris Cay." Admittedly, the latter is actually two separate cays, and the precise source of the specimens is unknown. Certainly the two patterns are not ontogenetic, since the two striped snakes include an adult and a juvenile. The appearance of blotch fusion on the Long Cay snake suggests that the longitudinal lines might have resulted from fusion of blotches and suppression of other portions of the pattern. Cope's (1871:558) description of the holotype shows that it too is a blotched snake. The range of variation in the snakes with blotched patterns is likewise suggestive of high variability in dorsal pattern within the subspecies. So little material of *chrysogaster* is available from these islands that further speculation is futile.

COMPARISONS: *E. c. chrysogaster* differs from its immediate neighbor *E. striatus* in having fewer ventral scales (245 in one male *chrysogaster*, 270 - 299 in male *striatus*; 249 - 259 in female *chrysogaster*, 266 - 298 in female *striatus*). The two species also differ in head-scale formulae (3-2-3 in *E. c. chrysogaster*, 5-2-5 and 3-1-5 in the Hispaniolan and Bahamian segments of *E. striatus*), modally fewer infralabials (16 in *E. c. chrysogaster*, 18 and 19 in the two segments of *E. striatus*).

Supralabial 7 usually is involved with eye penetrance in *E. c. chrysogaster*, whereas supralabial 8 has this distinction in *E. striatus*. In addition, the pattern in *E. c. chrysogaster* is quite different from that of both segments of *E. striatus*: the southeastern species differs from Bahamian *E. striatus* in lacking a neck stripe, extensive fusion of dorsal body blotches, and prominent secondary blotches, whereas it differs from Hispaniolan *E. striatus* in lacking both prominent secondary blotches and large and conspicuous angulate dorsal blotches.

REMARKS: We have not collected or seen live specimens of *E. c. chrysogaster*. Cope (1871:558) noted that the holotype was light fawn above, golden yellow below, and the blotches deep brown, with darker edges. The junior author has visited both of the Ambergris Cays and Long Cay. Western Little Ambergris is flat and grassy, whereas eastern Big Ambergris is more rugged and overgrown with shrubs, grasses, and cacti, on a limestone base. Long Cay is higher and more rugged than either of the Ambergris Cays. Apparently *E. c. chrysogaster* is a snake of barren and xeric situations in comparison to habitats occupied by most other Antillean *Epicrates*.

Epicrates chrysogaster relicquus Barbour and Shreve

Epicrates relicquus Barbour and Shreve, 1935, 40(5):362.

TYPE LOCALITY: Sheep Cay off the northwest coast of Great Inagua, Bahama Islands; holotype, MCZ 37891.

DISTRIBUTION: Great Inagua Island (including Sheep Cay), Bahama Islands.

DEFINITION: A subspecies of *E. chrysogaster* characterized by the combination of high number of ventral scales (269 - 275 in two males, 270 in one female), high number of ventrals + subcaudals (363 in one female), high number of dorsal scale rows at mid-body (46 - 47), modally 14 supralabials with modally two sublabials (modally 7 - 8) entering the eye, modally 17 infralabials; pattern consisting of a series of angulate dorsal blotches which may be fused to each other or to the prominent ventrolateral series of secondary blotches that extend almost to the dorsal-ventral junction.

VARIATION: The series of *E. c. relicquus* is composed of two males and one female. The larger male (ASFS V20458) has a snout-vent length of 810 mm, and the female (ASFS X4815) a snout-vent length of 1310 mm. Variation in scale counts is shown in Tables 2-5, 7, 8.

Dorsally, *E. c. relicquus* is apparently not so variable as the nominate subspecies. The dorsum in ASFS V20458 was recorded as tan above, with the blotches darker brown. The venter was cream, suffused with gray, especially laterally. The dorsal pattern consists of a series of 65 to 67 dorsal angulate markings, which when best expressed are dark-edged and pale centrally. These blotches are much fused and alternated middorsally to give a chain-like effect. There is a secondary lateral series of angulate blotches, smaller than the dorsal blotches and almost reaching the dorsal-ventral junction. These secondary blotches may be partially fused (especially posteriorly) with the primary dorsal blotches,

so that the dorsal pattern reaches almost to the ventral scutes. The head is unpatterned except for a pair of paramedian occipital dark spots and a vague postorbital dark line. In the large adult (ASFS X4815), the entire dorsal pattern is very faint and almost obliterated by invasion of dorsal tan ground color. This snake very much resembles faintly blotched specimens of *E. c. chrysogaster*. The dorsal blotches may continue onto the tail, where one specimen has 20 caudal blotches and the others have the tail so irregularly blotched that significant counts cannot be taken.

COMPARISONS: *E. c. relicquus* is distinguished from *E. c. chrysogaster* in several ways: the former has a more complete dorsal pattern, since it has a series of lateral secondary blotches (absent in the nominate subspecies) and the dorsal blotches are more extensive and more angulate (rather than ovate). One extreme in the dorsal pattern of *relicquus* resembles the similar extreme in *chrysogaster*. Midbody scale rows in *relicquus* are more numerous (46 - 47) than in *chrysogaster* (39 - 43), and *relicquus* modally has more (17) infralabials than does *chrysogaster* (15). Finally, the two subspecies differ in that *relicquus* modally has two supralabials (7 - 8) entering the eye, whereas *chrysogaster* modally has three supralabials (6 - 8) entering the eye. No *relicquus* has the typical *chrysogaster* 6 - 8 combination (in fact, only two series in *relicquus* show involvement of three supralabials), and only four (of 14) series of supralabials in *chrysogaster* have the typical 7 - 8 supralabial mode of *relicquus*. Supralabial 7 modally enters the eye in *chrysogaster*, whereas supralabial 8 modally has this position in *relicquus*.

REMARKS: No specimen of *E. chrysogaster* has the hemipenis completely extruded, but ASFS V20458 has the organ partially extruded. There are three flounces on the exposed and undivided non-sulcate portion of the organ, and proximal to the first flounce is a prominent basal papilla. The sulcus spermaticus is deeply entrenched. Doubtless the organ is bifurcate as in other Antillean *Epicrates*.

The junior author has visited Great Inagua and Sheep Cay. The former is a relatively mesic and well-wooded island, where *Epicrates* appears to be unaccountably rare, since the habitat seems excellent for the species. Sheep Cay, on the other hand, is a low and swampy islet, hardly separated from Great Inagua itself, with some restricted low coppice and mangroves. The greater portion of Sheep Cay is covered with low, dense grass. The male *E. c. relicquus* was secured (by a native for Donald W. Buden) from inside a log near a *Cocos* grove.

Epicrates inornatus Reinhardt

Boa inornata Reinhardt, 1843, 10:253.

Piesigaster boettgeri Seoane, 1881, 12:218. Type locality, "Mindanao, Philippine Islands"; type specimen unknown.

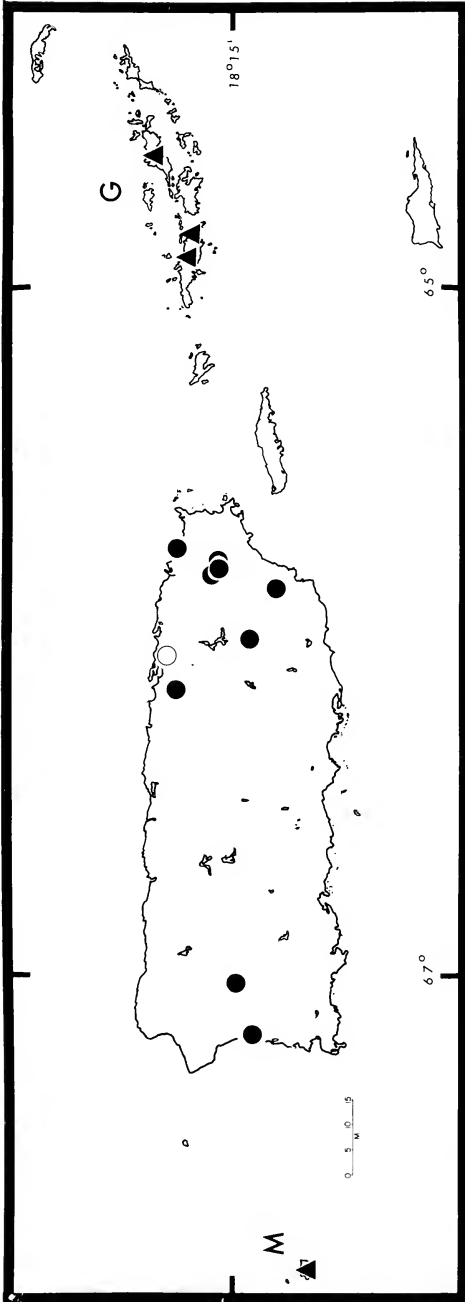


Fig. 4. Map of Greater Puerto Rico, including Isla Mona and the Virgin Islands. *Epicrates inornatus* - circles (solid circles represent specimens examined. Hollow circle represents literature record). *Epicrates monensis* - triangles; M = *E. m. monensis*; G = *E. m. granti*.

TYPE LOCALITY: Puerto Rico; syntypes, Universitetets Zool. Mus. København R.5597-5598, R.55101.

DISTRIBUTION: Puerto Rico (Fig. 4).

DEFINITION: A very large species of *Epicrates* (males to 1860 mm, females to 1750 mm snout-vent length), with 263 - 273 ventral scales in males, 258 - 267 in females, 66 - 74 subcaudal scales in males, 68 - 75 in females; ventrals + subcaudals 329 - 338 in males, 326 - 339 in females; intersupraocular scale always 1, pre-intersupraocular scales modally 2, post-intersupraocular scales modally 2; dorsal scale rows 31 - 34 on the neck, 38 - 42 at midbody, 21 - 25 anterior to vent, the lowermost scale row not alternating a large and a small scale; supralabials modally 11 with usually one supralabial (modally 6) entering the eye; infralabials modally 12; circumorbital series modally 8; loreals almost always 1; body blotches 66 - 73; tail blotches 12 - 26; many large adults virtually patternless.

VARIATION: Although *E. inornatus* is peripheral to our area of primary interest, we have included it because it has been previously associated nomenclatorially with *E. monensis* and *E. granti*. We have examined nine males and four females but no juveniles, and we are unaware of any young *E. inornatus* in American collections. The largest male has a snout-vent length of 1860 mm (MCZ 4645) and the largest female a snout-vent length of 1750 mm (MCZ 4646). Variation in scale counts is shown in tables 2 - 8.

Color and pattern are especially variable. Stejneger (1904:690-691) recorded the color of an adult male (USNM 27734) as "Nearly uniform 'bistre' with ventrals and subcaudals darker, narrowly pale-edged behind; above numerous indistinct cross bars (70-80 from neck to vent) of dusky color with one or two scales nearly black, thus emphasizing the spots, of which all the component rows (dorsal, dorsolateral, lateral and ventrolateral) are recognizable; the crossbars increase in width posteriorly; a blackish postocular band indistinctly connected with medio-lateral faint longitudinal line on the neck; supralabials fading into pale brownish gray at the commissure; slight traces of rufous on rostral and other shields of face; iris silvery gray clouded with dusky." Another male snake (USNM 27456) Stejneger reported as showing hardly "any traces of bars or spots; general color above, chestnut, darkest on the median region and tail, gradually becoming lighter toward the ventrals; the latter brownish-slate color with pale edges; throat and chin mottled dull rufous and brownish slate; scattered obscure dusky spots on flanks." Schmidt (1928:pl.4) has an excellent photograph of an adult that appears to be very dark and completely patternless.

Grant (1932) reported on several specimens. Two from the Río Mameyes were marked with dorsal spots, "decidedly and clearly outlined with very dark brown, the center light walnut color but darker than the brown body color." Another specimen from Río Piedras was a "light tan color" and its "dorsal spots are lighter instead of darker than the body color, with a suggestion of a darker border." Of a young snake,

Grant remarked that it was "impossible to count accurately the dark spots on the specimen because they were so broken up."

In our series of 14 *E. inornatus* (one an unsexed tanned skin) this variation is amply confirmed. Six specimens are patterned, much as described by Stejneger and Grant. There is a series of narrow angulate dorsal blotches that do not reach the dorsal-ventral junction and are greatly hollowed centrally, with prominent black-to-very-dark-brown edges. This series is, in addition, bordered ventrolaterally by another series of smaller blotches that may be fused into a ventrolateral dark line, especially on the neck. The head is virtually patternless dark, stippled brown or gray, except that an occipital bar may be faintly indicated, and it may pass posteroventrally to join with a small ventrolateral secondary blotch or the ventrolateral neck line. The venter in these snakes is very dark brown to gray, heavily stippled or overlaid with dark brown. Although these subadult and adult snakes are rather boldly patterned, the pattern shows a degree of dissolution that does not occur elsewhere in the Antillean members of the genus. Grant's comments upon one juvenile examined by him and its photograph (Grant, 1932:pl. 38), suggest that a series of confused dorsal blotches is also the basic juvenile pattern.

The balance of our series consists of patternless or virtually patternless snakes. Some (ASFS X4516) show vague remnants of the dorsal pattern, but others, like MCZ 4848, have no dorsal pattern whatsoever. The latter is not an exceptionally large snake (snout-vent length 1360 mm). Although most of the largest *E. inornatus* are patternless, this is not the sole condition in very large specimens. These changes are ontogenetic, but the unicolor condition is reached at various stages in individual lives, rather than at a constant snout-vent length. The largest *E. inornatus* (MCZ 4645 - snout-vent length 1860 mm) is a patterned male, but patterned snakes are about evenly divided between males and females of various sizes. The largest female (MCZ 4646) is unpatterned. We assume that patterned versus unpatterned condition is not correlated with sex, but rather with increasing size. There is no evidence that it is geographical, since both types occur in the same general area. Among a series of five snakes from Bayamón, one is patterned and four are unpatterned.

COMPARISONS: For comparison between *E. inornatus* and *E. mohnensis*, see the discussion of the latter species.

In many ways, *E. inornatus* resembles Jamaican *E. subflavus*. The two species were long confused until Stejneger (1901) differentiated *subflavus* from *inornatus*. We have examined only three female *E. subflavus* (ASFS V11164-65, ASFS V19601), since we consider this taxon peripheral to our problem. Thus our comments are based upon limited material. *E. subflavus* and *E. inornatus* differ in that *subflavus* has a

higher ventral count (279 - 280 versus 258 - 267 in *inornatus*) and a greater number of subcaudals (74 - 83 versus 68 - 75). These differences are intensified in ventral + subcaudal counts (female *subflavus* 354 - 363, female *inornatus* 326 - 339). Both species have the same pre-intersupraocular/intersupraocular/post-intersupraocular formula: 2-1-2. All dorsal scale row counts are comparable (31-33, 39-44, and 20-23 in *subflavus*; 31-34, 38-42, and 21-25 in *inornatus*). Supralabials are modally 11 in *inornatus*, 12 in *subflavus*; infralabials are modally 12 in *inornatus*, 12 and 14 in *subflavus*. Both species have supralabial 6 usually entering the eye, although the number of supralabials entering the eye in *inornatus* is usually 1, whereas in *subflavus* it is usually 2 or 3 (either supralabials 5 - 6 or 6 - 8). The circumorbital series in *inornatus* is composed of 8 scales, whereas in *subflavus* there are modally 9 scales in this position.

E. subflavus also differs from *E. inornatus* in pattern. Stejneger (1901:469) noted that the color of *subflavus* is "pale yellowish, with numerous blackish dorsal and lateral cross bars in zigzag, anteriorly quite broken and obscure, posteriorly strongly marked and extended so as to make the ground color appear blackish." Basically, *E. subflavus* is a pale yellow snake with weakly demonstrated dorsal angulate markings anteriorly, and more or less solid black posteriorly. This coloration and pattern bear little resemblance to those of *E. inornatus*. Yet the two snakes seem very similar in habitus. We are not suggesting that they be regarded as subspecies, but rather that *E. subflavus* is more closely related to *E. inornatus* than to any other Antillean taxon.

REMARKS: The hemipenis of *E. inornatus* (based upon ASFS X4516) is short, extending about the length of five subcaudals, and bifurcate, with four frounces basally, and with a stout basal papilla or lobe on the non-sulcate surface proximal to the first frounce. As far as can be determined, the bifurcate sections of the organ are studded with rather elongate papillae which seem widely spaced compared to those of other smaller Antillean *Epicrates*. The sulcus spermaticus divides at the bifurcation of the organ. The hemipenis is not fully extruded, so that apical details are unknown.

E. inornatus is widely distributed geographically. The species occurs from sea level to elevations of about 1050 meters (El Yunque). The only specimen collected by the junior author was from dense tropical deciduous forest, but considering the localities, it is doubtful whether the species is restricted to such densely wooded situations.

Epicrates monensis Zenneck

Epicrates monensis Zenneck, 1898, 64:64.

TYPE LOCALITY: Isla Mona; syntypes, 5 specimens formerly in the HZM, now destroyed (*in litt.*, W. Lädiges, February 18, 1971).

DEFINITION: A moderate-sized species of *Epicrates* (males to 770 mm, females to 570 mm snout-vent length, but Meerwarth (1901) reported that one of the syntypes had a snout-vent length of 1010 mm), with 261 - 269 ventral scales in males, 261 - 266 in females, 80 and 81 subcaudal scales in males, 82 - 84 in females; ventrals + subcaudals 345 - 347 in males, 345 - 348 in females; intersupraocular scale modally 1, pre-intersupraocular scales modally 3, post-intersupraocular scales modally 5; dorsal scale rows 34 - 39 on neck, 39 - 47 at midbody, 23 - 31 anterior to vent, the lowermost scale row not alternating a large and a small scale; supralabials modally 13 with usually two supralabials (modally 6 - 7) entering eye; infralabials modally 15; circumorbital series modally 11; loreals modally 1; body blotches 47 - 73, tail blotches about 10 to 22.

DISTRIBUTION: Isla Mona and the Virgin Islands (Fig. 4); in the latter chain known from St. Thomas and Tortola, but presumed to occur elsewhere in the archipelago.

COMPARISONS: *Epicrates monensis* and *Epicrates inornatus* differ as follows: *E. inornatus* has a much shorter tail with fewer subcaudals (males 66 - 74, females 68 - 75) than *E. monensis* (males 80 - 81, females 82 - 84). This difference is reflected in the ventrals + subcaudals counts in the two species (*E. monensis* males 342, females 345 - 348; *E. inornatus* males 329 - 338, females 326 - 338). Pre-intersupraoculars in *E. inornatus* are modally 2, whereas this count occurs rarely in *E. monensis*; the same is true of post-intersupraoculars which are almost always 2 in *E. inornatus*, a count that does not occur in *E. monensis*. In *E. inornatus*, supralabials are modally 11, in contrast to 13 in *E. monensis*, and infralabials are modally 12 in *E. inornatus*, modally 15 in *E. monensis*. The circumorbital series in *E. inornatus* is modally 8 scales, but modally 11 scales in *E. monensis*. *E. inornatus* and *E. m. monensis* resemble each other in that most often only one supralabial (modally 6, but also 5 or 7) enters the eye (18 of 26 series), although two supralabials (5 - 6, 6 - 7) enter the eye in 8 of 26 series. Supralabial 6 is most intimately associated with eye entrance in *E. inornatus*, where it makes the contact in 24 of 26 series. In *E. monensis*, supralabial 7 enters the eye in 11 of 16 series. *Epicrates inornatus* is much larger than *E. monensis*. Large subadult *inornatus* resemble *monensis* since the dorsal pattern is composed of a series of angulate dorsal blotches. These blotches, however, do not reach the dorsal-ventral junction as they do in *E. monensis*. In addition, there is a strong tendency in *E. inornatus* to have a secondary row of small blotches on the lower sides, a condition not observed in *E. monensis*. Head patterns in the two species are difficult to compare, since in all our *E. inornatus*, the head pattern is obscure. Remnants of an occipital U are discernible in *E. inornatus* subadults, but in all our specimens the head pattern is so overlaid with darker pigment that other details cannot be determined.

Association of *E. monensis* with *E. gracilis* is untenable in view of the strong lateral body compression and alternating large-and-small scales in the first dorsal scale row in *E. gracilis*. The two species also differ strikingly in pattern, which in *E. gracilis* is much less extensive.

The tail in *gracilis* is much longer with consequently many more subcaudal scales (90 - 111 in *E. gracilis*, 80 - 84 in *E. monensis*), and there are many fewer ventrals + subcaudals in *E. monensis* (342 - 348) than in *E. gracilis* (364 - 415). The pre-intersupraocular/intersupraocular/post-intersupraocular formula is modally 4 - 1 - 2 in *E. gracilis* and 3 - 1 - 5 in *E. monensis*. Infralabials are modally 13 in *E. gracilis*, 15 in *E. monensis*. Supralabial 6 is most intimately associated with the eye in *E. gracilis*, whereas supralabial 7 has this position in *E. monensis*.

Although *E. monensis* grossly resembles *E. fordii*, in that both are prominently blotched snakes, they differ in many details. The blotches are angulate in *E. monensis* and ovate or subcircular in *E. fordii*. Generally, *E. fordii* has more body (58 - 92) and tail blotches (13 - 27) than *E. monensis* (47 - 73 and about 10 - 22). *E. fordii* has fewer ventrals than *E. monensis* (*E. fordii* males 231 - 261, females 236 - 259; *E. monensis* males 261 - 269, females 261 - 266). Neck and midbody dorsal scale rows are fewer in *E. fordii* (28 - 35, 31 - 39) than in *E. monensis* (34 - 39, 39 - 47). The supralabial and infralabial modes are both 14 in *E. fordii*, but are 13 and 15 respectively in *E. monensis*. *E. fordii* has 10 scales in the circumorbital series and 2 loreals. *E. monensis* has 11 circumorbital scales and 1 loreal.

These comparisons of *E. monensis* with *E. inornatus*, *E. gracilis*, and *E. fordii*, all suggest strongly that *E. monensis* forms a distinctive unit within Antillean *Epicrates*. Despite its disjunct distribution, we feel that *E. monensis* (including *granti*) merits specific status.

REMARKS: No other complex within Antillean *Epicrates* is more puzzling than those taxa associated with Greater Puerto Rico — *inornatus* Reinhardt, *monensis* Zenneck, and *granti* Stull. Part of the problem is that there are very few specimens of the latter two taxa. Destruction of the five syntypes of *monensis* during World War II reduced by more than half the number of specimens available. A second factor is the huge size of all *inornatus* we have studied, in comparison with the much smaller *monensis* and *granti*. None of our *monensis*, for example, approaches the size of 1010 mm mentioned by Meerwarth for one of the syntypes (sex not mentioned). Even this large *monensis* does not approach the much greater size of *inornatus*, although our *inornatus* sample is biased in favor of large snakes. Another factor is that the pattern in *inornatus* becomes increasingly obscure with advanced age and larger size, and there are no small specimens of *inornatus* known to us. Grant (1932:pl. 38) showed a photograph of a *monensis* and an *inornatus* of comparably small sizes, but the markings on the young *inornatus* are very poorly depicted. Thus we have no concept of the juvenile and subadult pattern of *inornatus*. All these factors might have influenced our decisions regarding the relationships of these three popula-

tions. On the other hand, there are scutellar differences and similarities between *monensis*, *inornatus*, and *granti* that yield a logical arrangement of this complex of forms.

Stejneger (1904:688-694) considered *inornatus* and *monensis* as distinct species. He did not follow the arrangement of Meerwarth (1901), who considered *monensis* a "variety" of *E. fordii*. Stejneger also pointed out that *monensis* and *chrysogaster* might be closely related, but he rejected Zenneck's (1898) contention that *monensis* and *chrysogaster* might be only different *Zeichnungsformen*. Schmidt (1926: 158-159) reported on the sixth specimen of *monensis* and suggested that *monensis* might be allied to *fordii* from Hispaniola. (Later, Schmidt (1928:130-133) maintained *monensis* and *inornatus* as distinct species and commented that on Isla Mona, *E. monensis* "with *Cyclura* . . . is a conspicuous link with the Hispaniolan fauna.") His reference is doubtless due to Zenneck's comparison of *monensis* with *fordii*, with which Schmidt felt *monensis* might be allied.

Grant (1932) also kept *monensis* and *inornatus* as distinct species. He collected three specimens of *monensis*, the seventh, eighth, and ninth to reach collections. Grant presented pigmental, pattern, and scutellar details on both *inornatus* and *monensis*. Stull (1933) named *E. inornatus granti* on the basis of one badly damaged specimen from Tortola in the Virgin Islands. Her comparisons were with *E. inornatus*, from which species *granti* differs abundantly, but she made no comparisons with *E. monensis*, which might have been more pertinent. Later, Stull (1935), in her checklist of boids, considered *granti* and *inornatus* as subspecies, along with *fordii*. She also regarded *monensis* as a subspecies of *gracilis*, a most peculiar course. Finally, Mertens (1939:74), without presenting detailed evidence, considered *fordii*, *granti*, *monensis*, and *subflavus* as subspecies of *inornatus*. He thus acknowledged that there were resemblances between all three boas of the Greater Puerto Rico area.

Our examination of 3 *monensis*, 6 *granti*, and 13 *inornatus* suggests that *monensis* and *granti* have a community of characteristics that differentiate them from *inornatus*. Accordingly, we separate this complex into two species: *E. monensis* (including *granti*) and *E. inornatus*. This arrangement poses one major problem: the range of *E. inornatus* divides that of *E. monensis* into two sections - Isla Mona on one hand and the Virgin Islands on the other. This situation is puzzling, but it may be explained by postulating that Puerto Rico was at one time inhabited by two species of *Epicrates*, a very large one, and a smaller one that has disappeared. Hispaniola today has two small species and one large species. We reject association of *monensis* (or *granti* or *inornatus*) with any of the Hispaniolan species, most especially *E. gracilis* or *E. fordii*.

Epicrates monensis monensis Zenneck

DISTRIBUTION: Isla Mona.

DEFINITION: A subspecies of *E. monensis* characterized by the combination, usually, of 3 post-intersupraocular scales, low number of dorsal scale rows (39 - 42) at midbody, 1 - 0 supralabials enter the eye, and low number of body (47 - 56) and tail (about 10 - 14) blotches.

VARIATION: The three specimens of *E. m. monensis* include one male and two females. We have been unable to locate the third Grant specimen, which presumably is in some American collection. The male has a snout-vent length of 720 mm, the ventrals number 264, and the tail is incomplete. The larger female is damaged so that an accurate count cannot be taken, but it has about 261 ventral scales. The undamaged female has 266 ventrals and 82 subcaudals, and a ventral + subcaudal count of 348. Ventrals in the syntypic series (no sexes given) were 259 - 266, according to Meerwarth (Stejneger, 1904:693), and the subcaudals in two specimens were 79 and 82. Other scutellar variation is shown in Tables 2 - 8.

The dorsal pattern of *E. m. monensis* consists of a series of blotches that are angulate rather than ovate or subcircular, extending from the dorsal midline to the junction of the dorsal and ventral scales. In all specimens some blotches are divided longitudinally to produce a scattered series of isolated dark ventrolateral blotches. The blotches may be saddle-like, and thus bridge the middorsal line, or they may be staggered to give a chain-like effect. Both conditions occur at various regions on the same snake. The blotches are outlined in dark, and are pale centrally. The smallest snake (UMMZ 74414) shows the central paling least, and we assume that, as in *E. fordii*, there is increased paling with increasing size. The head pattern is obsolescent, and at best there is a very weakly delineated loreo-postocular line. One constant feature, however, is the presence of a pair of dark transverse bars at the level of the occiput. In some instances, these bars may join with the small ventral portion of the first body blotch to give an inverted U-shaped head-and-neck figure that is broken at the dorsal midline. This characteristic marking is well shown by Stejneger (1904:figs. 153 and 157, and less diagrammatically in Fig. 154). The venter is almost immaculate, with a few scattered dark flecks or short longitudinal lines. Some of the dorsal blotches extend for a very short distance onto the lateral margins of the ventrals. The chin and throat are patternless. The tail continues the dorsal body blotching, some of the posteriormost caudal blotches forming complete or almost complete rings around the tail.

Epicrates monensis granti Stull, new combination

Epicrates inornatus granti Stull, 1933, (267): 1.

TYPE LOCALITY: Tortola Island, British Virgin Islands; holotype, MCZ 33847.

DISTRIBUTION: The Virgin Islands (known from St. Thomas and Tortola).

DEFINITION: A subspecies of *E. monensis* characterized by the combination of 5 post-intersupraocular scales, high number of dorsal scale rows (41 - 47) at midbody, usually two supralabials entering the eye, and high number of body (61 - 73) and tail (20 - 22) blotches.

VARIATION: Our series of *E. m. granti* includes four males and two females, all from St. Thomas in the American Virgin Islands with the exception of the holotype. The largest male (ASFS V8070) has a snout-vent length of 770 mm; the largest female (VINP 1484) has a snout-vent length of 470 mm. Scutellar variation is shown in tables 2 through 8.

The Tortola holotype, a male, shows some variation from the St. Thomas series in several scale counts. This snake sets the upper limit of ventrals in males, has the highest counts of neck, midbody, and posterior dorsal scale rows, and is the only snake with 3 scales bordering the intersupraocular posteriorly. This snake also is the only specimen which has one supralabial (7) entering the eye unilaterally. It is not unlikely that specimens from elsewhere in the Virgin Islands will ultimately be shown to be recognizably different from topotypic *E. m. granti*.

In most pattern details, *E. m. granti* closely resembles the nominate subspecies. The dorsal pattern consists of a series of angulate dorsal blotches that reach from the dorsal midline to the junction of the dorsal scales with the ventral scales. These blotches may be saddles or may alternate, giving a chain-like effect, and the more ventral portions of some of them may be cut off to give a short series of randomly located ventrolateral blotches. The head is patternless dorsally, but young snakes (ASFS V3640) show the same dark U-shaped occipital bar as in *monensis*. The loreo-postocular stripe is at best very faint in juveniles, and completely absent in larger individuals. The venter is variably patterned. It may be immaculate or heavily stippled with dark brown. The underside of the tail may have almost complete rings, especially distally, resulting from the ventral continuation of the dorsal caudal blotches.

COMPARISONS: *Epicrates m. monensis* and *E. m. granti* resemble each other so closely in dorsal pattern that it is difficult to separate them. The much-reduced head pattern and more often complete occipital U in *granti* appear to be the only major pattern features that differentiate the two subspecies. In scutellation and blotch counts, the taxa are easily distinguishable. *Epicrates m. granti* has a higher number of dorsal scale rows at midbody (41 - 47; 39 - 42 in *monensis*), and higher body-blotch counts (61 - 73) than in *monensis* (47 - 56). Tail blotches are more numerous in *granti* (20 - 22) than in *monensis* (about 10 - 14). Ventrals and subcaudals are comparable in the two forms. *E. m. granti* usually has 5 post-intersupraocular scales (versus modally 3 in *monen-*

sis). Perhaps the major structural difference between the two subspecies is the entrance into the eye of but one or no scale in *monensis*, in contrast to the modal entrance of two scales into the eye in *granti*.

REMARKS: One *E. m. granti*, secured by Richard Thomas on St. Thomas, was noted in life to have the dorsum dark brown, with the blotches darker brown, somewhat paler centrally. The venter was cream-colored, but much stippled with brown. This snake was secured at night as it climbed in a viny tangle about 2.4 meters above the ground in moderately mesic woodlands.

No male *E. monensis* has the hemipenis completely everted. ASFS V8070, however, has a partially everted hemipenis, flounced proximally, with a stout basal lobe on the non-sulcate surface.

Epicrates fordii Günther¹

Pelophilus fordii Günther, 1861, :142.

Chilabothrus maculatus Fischer, 1888, 5: 33.

Type locality, "Cap-Haïtien and Gonaïves, Haiti", syntypes lost except for HZM 52.

TYPE LOCALITY: "Western Africa," here restricted to the vicinity of Port-au-Prince, Dépt. de l'Ouest, Haiti; holotype, BMNH 1946.1.1.55.

DEFINITION: A moderate-sized species of *Epicrates* (males to 860 mm, females to 730 mm snout-vent length), with 231 - 261 ventral scales in males, 236 - 259 in females, 69 - 85 subcaudals in males, 70 - 89 in females; ventrals + subcaudals 308 - 343 in males, 312 - 341 in females; intersupraocular scales almost always 1, pre-intersupraocular scales modally 3, post-intersupraocular scales modally 3; dorsal scale rows 28 - 35 on neck, 31 - 39 at midbody, 18 - 23 anterior to vent, the lowermost scale row not composed of alternating large and small scales; supralabials modally 13 with usually two supralabials (modally 6 - 7) entering eye; infralabials modally 14; circumorbital scales modally 10; loreals almost always 2; body blotches 58 - 92, tail blotches 13 - 27.

DISTRIBUTION: Hispaniola, where known from four general regions: the Cul de Sac-Valle de Neiba plain and the associated eastern Llanos de Azua and as far northwestward in Haiti as Gonaïves; the Valle de Cibao in northwestern Dominican Republic; Cap-Haïtien in north-central Haiti; Môle St. Nicholas on the Presqu'île du Nord-Ouest in extreme northwestern Haiti. Also known from Ile de la Gonâve and Ile à Cabrit (Fig. 5). Unknown from the "south island," except along the northern slopes of the Morne l'Hôpital in Haiti and the Sierra de Baoruco in the Dominican Republic.

REMARKS: Cochran (1941:320-21) examined very few *Epicrates fordii* since there were only six specimens in American collections. She also included data on seven other specimens, the holotype and two additional specimens in the British Museum (Natural History), and the four syntypic specimens of *Chilabothrus maculatus* Fischer, three of which are from Cap-Haïtien and Gonaïves in Haiti. We have examined 65 specimens of *E. fordii*, but this is only a fraction of the living individ-

¹Editorial policy of the *Annals* requires adherence to the International Rules of Zoological Nomenclature, hence the original spelling of *fordii* is retained here contrary to the author's preference for *fordi*.

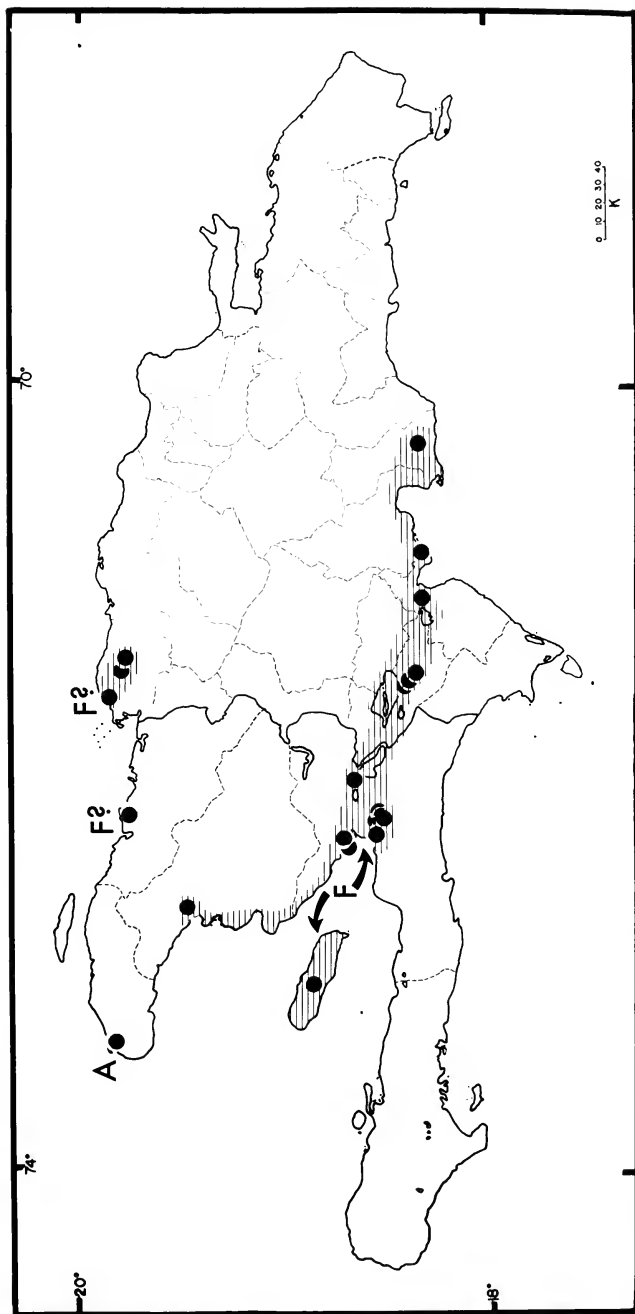


Fig. 5. Map of Hispaniola, showing (solid circles) localities of specimens of *Epicrates fordii* (F). Range of *E. f. fordii* is shown by horizontal lines; localities whence *E. fordii* is known but where the status of the populations is unsure are questioned. A = *E. f. agametus*.

uals of this snake that have reached the United States in the past seven years, since *E. fordii* has been commonly collected in Haiti in the vicinity of Port-au-Prince. Under suitable ecological situations (primarily xeric), *E. fordii* is an abundant snake.

It is unfortunate that, aside from a long series from the Cul de Sac Plain in Haiti, we have relatively small lots of snakes from elsewhere. This makes it difficult to assess geographic variation within the species. To make matters worse, three of the syntypes of *C. maculatus* have been destroyed. The exception is one male (HZM 52) that we have examined. This snake is labeled as having come from "North America" and is presumably the *vierte kleines Stück* noted by Fischer (1888:33) without precise locality data. Finally, additional Cap-Haïtien and Gonaïves specimens are limited to three (MCZ 37601 and ZMB 28576 - two snakes), so that the status of the name *maculatus* remains in doubt. We have resolved this situation to our satisfaction, basing our conclusions solely on the extant syntype (HZM 52), despite the inconclusiveness of its locality data.

When sufficient material has accumulated from throughout the range of *E. fordii*, the species will undoubtedly be shown to have diverged into at least three nameworthy populations: one in the Cul de Sac-Valle de Neiba, a second in the Valle de Cibao, and a third on Presqu'île du Nord-Ouest. We can assess at this time only the variation in the Cul de Sac-Valle de Neiba sample. This population we regard as *E. f. fordii*, along with the single Gonâve snake, the snake from Ile à Cabrit, and the two snakes from Gonaïves. We have also compared the five Valle de Cibao specimens with the Cul de Sac-Valle de Neiba snakes, and because of its distinctive characters, have named the Môle St. Nicholas specimen (see below) as a new subspecies.

Epicrates fordii fordii Günther

DISTRIBUTION: Hispaniola, including the Cul de Sac-Valle de Neiba plain, Llanos de Azua, Gonaïves, Ile de la Gonâve, and Ile à Cabrit in Haiti and the Dominican Republic.

DEFINITION: A subspecies of *E. fordii* characterized by the combination of low number of ventral scales in both sexes (231 - 255 in males, 236 - 259 in females), low number of ventrals + subcaudals (310 - 339 in males, 312 - 341 in females), and low number of body blotches (58 - 88).

VARIATION: The series of 61 *E. f. fordii* includes 48 snakes from the Cul de Sac Plain, nine snakes from the Valle de Neiba-Llanos de Azua, one snake from Gonaïves, one snake from Ile à Cabrit, and one snake from Ile de la Gonâve. The largest male has a snout-vent length of 785 mm (ASFS V13726) and the largest female has a snout-vent length of 730 mm (ASFS V13715). Both are from north of Pétionville, Haiti. The Cul de Sac series also includes two litters, one of seven, and the other of six snakes. In the first series the snout-vent lengths vary between 165 and 195 mm, and in the second litter between 194 and 204

mm. The umbilici of these 13 snakes plus four additional small snakes from Haiti vary in position in eight males between ventrals 167 and 180, and in nine females between ventrals 175 and 183.

Throughout the Cul de Sac-Valle de Neiba plain and the Llanos de Azua, there is an east-west cline in number of ventral scales, with Dominican snakes (Valle de Neiba + Llanos de Azua) having slightly higher numbers of ventrals than in Haitian (Cul de Sac) snakes. This trend is even more pronounced in number of subcaudal scales, thus ventrals + subcaudals counts intensify the differences between the two samples. For example, Haitian males (including the Gonâve specimen) have 231 - 255 ventrals, 69 - 81 subcaudals, and 310 - 334 ventrals + subcaudals. Dominican males have 238 - 254 ventrals, 73 - 85 subcaudals, and 311 - 339 ventrals + subcaudals. Haitian females (including the Cabrit specimen) have 236 - 257 ventrals, 70 - 81 subcaudals, and 312 - 334 ventrals + subcaudals, whereas Dominican females have 247 - 259 ventrals, 76 - 89 subcaudals, and 325 - 341 ventrals + subcaudals. The trends toward higher scale numbers in Dominican snakes are apparent. Further scutellar details are given in tables 2 - 8.

Body blotches vary between 58 and 88 in the Haitian snakes and between 63 and 74 in the Dominican snakes. Tail blotches in the Haitian snakes range from 13 to 27, and in Dominican snakes from 16 to 27. Blotch counts are inconsistent. Although these blotches are usually discrete, in many individuals they are variously combined to give a chain-like effect, which makes blotch counting difficult. The counts were taken paramedially, in an effort to avoid the pitfalls of the chain-effect patterns.

The Gonâve male in all counts falls within parameters set by mainland specimens. On the other hand, the Cabrit female sets the high count for ventrals in female *E. f. fordii* (257). The highest number of ventrals in mainland female *E. f. fordii* is 255.

Color notes from living snakes from Manneville (ASFS V8201) and Ile à Cabrit (ASFS V10312) show the variation in coloration in *E. f. fordii*. The Manneville snake was noted by Richard Thomas as light gray dorsally, with dorsal blotches and saddles milk-chocolate brown (slightly paler than Pl. 15 A 12, Maerz and Paul, 1950), outlined in black and limned with paler gray. The lower sides were paler gray, and the venter dark gray, with both sides and venter having brown spots, flecks, and streaks. The Cabrit snake was noted by the junior author as pale brown dorsally, varying to pale tan on the sides. The blotches were brown with darker brown edges. The venter was dirty white, the central portion of each ventral suffused with gray. The iris was grayish with some brownish flecks.

The major pattern variation is in the intensity of the dorsal blotches. In young snakes the blotches are solid and somewhat reddish-brown

in color, but with increasing size they become more "hollowed" (= paler) centrally with dark borders, and in turn may be set off around their periphery by an area paler than the dorsal ground color. The lower sides have a series of irregular blotches or markings of the same color as the dorsal blotches, followed ventrally by a series of much smaller dark-brown markings. The latter are more or less apparent on the ventral scales, depending upon intensity of the ventral coloration. The head pattern (best seen in juveniles) consists of a loreo-postocular stripe that ends abruptly on the temporal region, and a complex scroll-like or lyre-shaped figure on the top of the head. This figure is basically dark brown, variously invaded and eroded by vermiculate pale lines or line-fragments. In adults only the loreo-postocular line remains distinct. The dark dorsal head pattern ends abruptly posteriorly and appears to be the first of the series of dorsal blotches. All cephalic pale markings are absent or very obscure in adults, although the dark head area may retain peripheral evidence of encroachment of pale pigment in its irregular edges.

Although the dorsal blotches are ovate or subcircular and usually discrete over much of the body, in most snakes there is some local fusion of blotches with a resulting alternating chain-like effect. In other individuals, some of the dorsal blotches are inverted Y's, the arms extending ventrally and the stem dorsally. There may be discrete alternating smaller blotches (portions of the primary dorsal series) isolated from their "parent" blotches. None of these variants is sufficiently constant to delimit any population, and a series of sibling neonates (ASFS V11355-V11362) shows all kinds and degrees of fusions and modifications of the dorsal blotch system. Regardless of these modifications, the impression of *E. f. fordii* is of a dorsally blotched snake, the blotches brown, outlined in black or darker brown, on a gray-to-tan or pale-brown ground.

REMARKS: The hemipenis (based on ASFS V20606) is short, extending the length of about seven or eight subcaudal scales, and is deeply bifurcate. The basal undivided portion has five conspicuous flounces and a very prominent basal lobe, which is sharply pointed, on the non-sulcate surface. The bifurcate section of the hemipenis is closely studded with many low, rounded, blunt papillae that extend to the sulcus spermaticus. The sulcus is bifurcate at the bifurcation of the hemipenis, the two branches of the sulcus extending to, and ending blindly near the apices of the bifurcations.

We have secured very few *E. f. fordii* ourselves, and most specimens handled by us or by others in our field parties have been secured by natives. Thus, detailed habitat data are few. The specimens we took were the Ile à Cabrit snake obtained by Richard Thomas in the base of a grass tussock in *Acacia*-cactus scrub during the day, and the speci-

men from Duvergé secured by Thomas beneath the thin outer layer of a fire-scarred cabbage palm about 1.5 meters above the ground. The Palo Alto snake was found dead on a road in a mesic *Musa* grove, but this is an exceptional occurrence in a very mesic artificial situation in an otherwise xeric region. The snake from Limonal was taken by a native from under a rock on a grassy hillside. Our impression is that *E. f. fordii* is a snake of xeric situations, and the abundance of specimens from the Cul de Sac and associated lower northern foothills of the Morne l'Hôpital confirms this contention. Specimens from Duvergé and Manneville are from below sea level in the Cul de Sac-Valle de Neiba plain, but the species is not restricted to such low elevations. Occurrence at Puerto Escondido and Limonal shows that *E. f. fordii* occurs to elevations of about 305 meters in less harsh and slightly more mesic habitats.

The snake from Manneville contained a young rat (*Rattus*) in its stomach. A female from Frères (ASFS V11354) gave birth to seven young (ASFS V11356-62) in captivity on June 25, and a female from near Pétionville (ASFS V24338) was gravid on June 16.

Two nomenclatorial problems remain. The holotype of *E. fordii* was reported to have 253 ventrals and 70 subcaudals (ventrals + subcaudals 323) by Günther (1861:142). We have not examined the holotype, but Boulenger (1893:98) considered it a female, and in addition to Günther's counts, gave 33 scale rows at midbody. The subcaudal and ventrals + subcaudals counts suggest that the specimen originated within the Haitian range of *E. fordii*, rather than in the Dominican section. We have no hesitancy in restricting the type locality to the Port-au-Prince area since the holotype agrees with snakes from this general area.

The situation with the name *maculatus* Fischer is more complex. This name was based upon specimens from Cap-Haïtien and Gonaïves, but the only extant syntype (HZM 52) is without precise locality data. This syntype is a male with 249 ventrals and 78 subcaudals (ventral + subcaudals 327). Both these counts fall within the parameters for the syntypic series given by Cochran (1941:321). It seems likely that the extant syntype came from the Cul de Sac area in Haiti.

The two Gonaïves specimens (ZMB 28576) are a male with 253 ventrals, 75 subcaudals, and 328 ventrals + subcaudals, and a juvenile female with 249 ventrals, 77 subcaudals, and 326 ventrals + subcaudals. Both these snakes, which may be interpreted as topotypes of *maculatus*, fall within the parameters of Haitian *E. fordii*. Certainly there is no doubt that the *maculatus* syntype and the Gonaïves topotypes are closest in all counts to the Cul de Sac-Valle de Neiba material. Accordingly, we *pro tem* consider *maculatus* Fischer a strict synonym of *fordii* Günther, with the proviso that additional material from north-central

Haiti (Cap-Haitien) might well change this assignment (see further discussion under "Remarks" in next section).

***Epicrates fordii agametus*, new subspecies**

HOLOTYPE: MCZ 62656, an adult male, from Môle St. Nicholas, Département du Nord-Ouest, Haiti, taken July 26, 1960, by A. Stanley Rand and James D. Lazell.

DISTRIBUTION: Known only from the type locality, but probably occurs throughout the Presqu'île du Nord-Ouest, Haiti.

DEFINITION: A subspecies of *E. fordii* characterized by the combination of high number of ventral scales (261 in only specimen known), high number of ventrals + subcaudals (343), and high number of body blotches (92).

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 860 mm and tail 170 mm; ventral scales 261, 82 unpaired subcaudal scales, anal scale entire; supralabials 13/14, infralabials 16/15; loreals 2/2, preoculars 2/2, postoculars 6/7; circum-orbital scales 10/13; 1 intersupraocular scale, bordered anteriorly by 3 scales and posteriorly by 5 scales; supralabials 6 - 7 and 7 - 8 entering the eye; dorsal-scale-row formula 33 - 38 - 22; 92 dark dorsal body blotches and 17 dark dorsal tail blotches; ventrals + subcaudals 343.

Dorsum (as preserved) dull grayish tan, the dorsal dark blotches medium brown, outlined with black, the blotches occasionally fused across the back to form saddles, or in some areas with alternate fusions giving a chain-like effect; lower sides with a longitudinal series of irregular dark markings, with a third longitudinal series, much less clearly defined, at about the junction of the dorsal and ventral scales; venter dull gray with some diffuse and irregularly placed darker spots posteriorly; dorsal and ventral surfaces of tail continuing the same patterns and colors as the body; a dark brown loreo-postocular stripe; upper surface of head darker gray, with some vague pale-gray vermiculations entering the dorsal head coloring posteriorly; chin and throat almost patternless except for dark-gray smudging on the mental and infralabial scales.

COMPARISONS: The single *E. f. agametus* lies above all other specimens of *E. fordii* in number of ventral scales (261 versus a high count of 255 in CM 38849 from "Etang Manneville") and in ventrals + subcaudals (343 versus a high count of 339 in ASFS V14940 from Limonal). The body blotches likewise are greater in number (92) than in any other *E. fordii*, where the high body blotch count is 88 in a male (CM 38838) from "Etang Manneville." Despite the relatively small difference in number of body blotches between *agametus* and *fordii*, we feel strongly that this is a valid difference between these two taxa, since only 18 of 61 *E. f. fordii* have body blotch counts above 70 (mean = 68.3). The holotype of *E. f. agametus* is the largest specimen of either sex of *E. fordii* known. It is possible that, considering the long series of the nominate subspecies available, *E. f. agametus* reaches a larger size than *E. f. fordii*.

There appear to be no differences in color or pattern between *fordii* and *agametus*, but such comparisons are tenuous when based on only one individual which was not seen by us in life. The name *agametus* is derived from the Greek for "bachelor" in reference to the unique male holotype.

REMARKS: Since neither of us has visited the Presqu'île du Nord-Ouest, we are unfamiliar with the habitat where the holotype of *E. f. agametus* was taken. However, Lazell (1961) noted that the Môle St. Nicholas area is "arid," and he implied that *Acacia* is common there. This is the sort of ecological situation where *E. fordii* occurs most abundantly elsewhere.

The Presqu'île du Nord-Ouest is a secondary center of endemism in Hispaniola. Among endemic reptiles are *Sphaerodactylus shrevei* Lazell (1961), a peculiar gecko whose closest relative is *S. rhabdotus* Schwartz (1970d) from the Valle de Neiba. Endemic subspecies include *Ameiva lineolata perplicata* Schwartz, *A. chrysolaeama defensor* Schwartz and Klinikowski, and *Diploglossus curtissi diastatus* Schwartz. *Epicrates fordii agametus* is the fifth species that shows differentiation in this remote and isolated area.

Epicrates fordii appears to have a disjunct distribution in northern and western Haiti, although we admit that this may be more apparent than real. The closest records of *E. fordii* to Môle St. Nicholas are Gonaïves, Dépt. de l'Artibonite, and Cap-Haïtien, Dépt. du Nord - respectively distances of 67 and 130 kilometers airline. Both these localities were represented in the type-series of *Chilabothrus maculatus* (= *E. f. fordii*). We have examined one specimen (MCZ 37601, female) from Cap Haïtien, which may be considered topotypic *maculatus*. This snake has 254 ventrals and an incomplete tail. Its ventral count lies within the known range for *E. f. fordii*. The number of body blotches (76) is no higher than occasionally encountered in *E. f. fordii*, and there is no reason to interpret the Cap-Haïtien specimen as intermediate between *fordii* and *agametus*.

There remains for discussion the short series from the Valle de Cibao in the northwestern Dominican Republic. This suite consists of the following snakes from Monte Cristi Province: AMNH 40114-16, Monte Cristi; MCZ 43680, 24 km E Monte Cristi; and ASFS V1268, eastern edge, Villa Vásquez. The series is composed of one female (MCZ 43680) and four males.

The largest male (AMNH V40115) has a snout-vent length of 600 mm, and the female a snout-vent length of 460 mm. The ventral counts of the four males (233 - 241) fall in the lower half of the range of ventral counts (231 - 255) in male *E. f. fordii* (and far below that of the holotype of *agametus*). The single Cibao female with 246 ventrals is also at about the midpoint of the range of this count in female *E. f. fordii* (236 - 259). In ventrals + subcaudals, the Cibao males (308 - 316) are at and below the lower extreme of this count in *E. f. fordii* (310 - 339), and the female (319) lies near the lower extreme in female *E. f. fordii* (312 - 341). In no other counts or pattern details do these snakes differ from *E. f. fordii*, and they lie at the opposite extreme of variation

from *agametus* in the species. We have little doubt that more material from the Valle de Cibao will reveal that this arid valley is inhabited by a subspecies of *E. fordii* which characteristically has ventral counts lower than those of *E. f. fordii* and *E. f. agametus*. We refrain from naming this population since the amount of overlap in counts between Cibao specimens and *E. f. fordii* is great.

The specimen from Villa Vásquez was recorded in life as grayish tan dorsally, with brown blotches outlined in black. The venter was dark brown, a color that we have not recorded in *E. f. fordii*, which regularly has a gray venter. Thus, the Cibao population may possess a different ventral coloration than other *E. fordii*. The Villa Vásquez snake was found dead on a road in a transitional area between the naturally xeric Valle de Cibao and the artificially more mesic (because of irrigation for rice culture) region east of Villa Vásquez.

Epicrates gracilis Fischer

Chilabothrus gracilis Fischer, 1888, 5:35.

TYPE LOCALITY: Cap-Haïtien, Département du Nord, Haiti; syntypes - formerly in HZM; now destroyed (*vide* W. Lädiges, *in litt.*, February 18, 1971).

DEFINITION: A moderate-sized species of *Epicrates* (males to 870 mm, females to 905 mm snout-vent length), with 271 - 304 ventral scales in males, 271 - 296 in females, 91 - 111 subcaudals in males, 90 - 102 in females; ventrals + subcaudals 368 - 415 in males, 364 - 396 in females; intersupraocular scale always 1, pre-intersupraocular scales modally 4, post-intersupraocular scales modally 2; dorsal scale rows 27 - 42 on neck, 33 - 47 at midbody, 21 - 29 anterior to vent, the lowermost scale row alternating a large and a small scale for each ventral scute; supralabials modally 13 with usually two supralabials (modally 6 - 7) entering eye; infralabials modally 13; circumorbital scales modally 11; loreals modally 1; body blotches 62 - 100, tail blotches 21 - 35.

DISTRIBUTION: Hispaniola, where known from scattered localities on the Tiburon Peninsula in Haiti, the north Haitian coast at the type locality, and the northern, eastern, and extreme southwestern Dominican Republic (Fig. 6); unreported from any Hispaniolan satellite island.

REMARKS: Cochran (1941:323) regarded *E. gracilis* as an "exceedingly rare snake." She examined only five specimens from American collections and included data on the two syntypes in the Hamburg Zoologisches Museum. Mertens (1939:75) examined one additional specimen (from Santiago, Dominican Republic), and another specimen without definite locality in the HZM. No other records of the species have appeared in the literature.

Recent collecting by us and companions has resulted in the assembling of specimens of *E. gracilis* from nine localities in the Dominican Republic and two localities in Haiti. The Museum of Comparative Zoology has newly acquired specimens from three Haitian localities on the Tiburon Peninsula, and the United States National Museum has material from two new Haitian localities. We have borrowed all specimens with locality data (with the exception of MCZ 43655 from Sosúa,

which is no longer available) and have assembled 51 *E. gracilis*. Although this material encompasses 19 localities, they are peculiarly localized: one suite of specimens is from the Tiburon Peninsula in Haiti and the Península de Barahona in the Dominican Republic, and thus from the Hispaniolan "south island" (*sensu* Williams, 1961), and the remainder is from the northern to eastern Dominican Republic, from Monte Cristi and Dajabón provinces in the west to La Altagracia Province in the east. There are no published records or specimens of *E. gracilis* from Haiti north of the Cul de Sac Plain, with the exception of the now-lost syntypes from Cap Haïtien on the northern Haitian littoral, nor are there specimens or records from the Dominican Republic south of the Cordillera Central, with the exception of the Península de Barahona. Our sample, then, can be divided into "north and south island" material, although in neither case do we have specimens from throughout one of the paleoislands.

E. gracilis is locally abundant. The longest series is that secured by D. C. Leber and natives at Camp Perrin in Haiti, where 12 snakes were collected. The second longest series is from near Palo Verde in extreme northwestern Dominican Republic, whence we have 7 specimens taken by Richard Thomas in two nights' collecting. Because of its arboreality and brown cryptic coloration *E. gracilis* may be difficult to detect, even where it is quite common. We have secured only one specimen active by day. All but three others were taken at night. The distinctly laterally compressed body of *E. gracilis* strongly indicates that it is a climber, and its nocturnal activities suggest that it rarely comes to the ground and remains in above-ground situations during the day. Of three *E. gracilis* taken while resting during the day, one was in a pile of rocks, another in a solution hole in a limestone rock, and the third in a knot-hole in a fence post adjacent to a wooded ravine.

Stull (1935:397) suggested that *E. gracilis* and *E. monensis* were conspecific, but Mertens (1939:74) felt that they were not. Certainly *gracilis* and *monensis* differ in body shape (*monensis* is not laterally compressed) and in dorsal pattern (*monensis* has a pattern of staggered, nearly rectangular blotches, whereas *gracilis* has a pattern of more or less circular blotches). Even more important, as both Mertens (1939:75) and Cochran (1941:323 and Fig. 93) pointed out, *E. gracilis* has a series of alternating large and small scales in the first scale row. This is not the case in *monensis* or in any other Antillean *Epicrates*. As a result of this condition, *gracilis* has smaller dorsal scales than most other *Epicrates*. We feel that the alternating large-and-small first row of dorsal scales in *gracilis* is sufficiently distinct structurally to separate *E. gracilis* as a species from all others. In pattern, however, *E. gracilis* is remarkably like *E. exsul*. Schwartz (1968a:260) suggested that the latter might "represent a long-separated Hispaniolan element

on the Little Bahama Bank." *Epicrates exsul*, despite its chromatic and pattern similarities to *E. gracilis*, lacks the alternating large-and-small row of first dorsal scales, and differs from *gracilis* in other scutellar details. Nevertheless, *E. gracilis* and *E. exsul* resemble each other much more closely than either does any other *Epicrates*.

Our material shows that on Hispaniola there are two distinctive subspecies of *E. gracilis*. One is restricted to the historical "south island" (Tiburón Peninsula and Península de Barahona), and the other to Haiti and the Dominican Republic north of the Cul de Sac-Valle de Neiba plain. Although the syntypes of *E. gracilis* are no longer extant, the counts given for these specimens by Boulenger (1893:98) and Cochran (1941:324), as well as their locality, suggest that the nominate subspecies occurs on the Hispaniolan "north island" (see comments below).

Epicrates gracilis gracilis Fischer

DISTRIBUTION: Hispaniola, north of the Cul de Sac-Valle de Neiba plain.

DEFINITION: A subspecies of *E. gracilis* characterized by the combination of small size (males to 700 mm, females to 718 mm snout-vent length), low number of ventrals in both sexes (271 - 286 in both males and females), low number of subcaudals in both sexes (91 - 97 in males, 92 - 102 in females), and ventrals + subcaudals low (368 - 377 in males, 364 - 384 in females).

VARIATION: The series of *E. g. gracilis* consists of 7 males and 18 females, of which 5 males and 15 females have complete tails. The largest male (AMNH 42997) has a snout-vent length of 700 mm, the largest female (USNM 66713) a snout-vent length of 718 mm. Scutellar variation is shown in tables 2 through 8.

The body is laterally compressed and distinctly deeper than broad. The head is small and is set off from the body by the slender neck. The ground color is tan, with the 62 to 100 dorsal blotches and 21 to 35 tail blotches dark brown. The body blotches are ovate to subcircular and may form complete narrow dorsal saddles, paramedian dorsal pairs, or staggered dorsal pairs - all conditions occurring on the same snake (e.g., ASFS V1370). There is a second more lateral row of dark markings that are extremely variable in expression. These markings may be blotch-like, dots, spots, or even diagonal and irregular dashes. All occur on the same snake. In some snakes they are barely discernible. The venter is yellow-tan to brownish, and it is almost patternless except for some scattered brownish suffusions which are regularly present. The head pattern is best seen in juveniles (ASFS V1371, ASFS V1410, AMNH 44743). In simplest form this pattern consists of a median dark-brown stripe beginning between the eyes and extending posteriorly onto the occiput, a dark transverse line before the eyes across the base of the snout, a pair of dark lines behind the eye, the more dorsal extending onto the temples, the more ventral forming a diagonal line to

the angle of the jaws, all followed by an inverted U-shaped dark figure on the occiput. One of the juveniles (ASFS V1410) has all the cephalic elements present but also shows much additional dark cephalic patterning between the basic figures, so that the head is complexly marked with dark brown dots, lines, and figures. All the basic pattern elements of the head persist into most large adults, although they become more obscure with increased size. The clarity of the cephalic pattern in adults is negatively correlated with the depth of the brown dorsal pigmentation. Snakes with dark ground colors show the head pattern less distinctly. The iris is pale buff. Two juveniles from Palo Verde were recorded in life as having the venter orange and the dorsal orange-tan and tannish orange. Young *E. g. gracilis* are more brightly colored than adults.

In three juveniles, the position of the umbilicus is extremely variable. All specimens are females, and the umbilicus involves ventrals 177 and 178 in one snake, 201 to 203 in another, and 211 to 213 in the third. The two snakes that set the umbilical parameters are from the same locality.

REMARKS: Our field notes on *E. g. gracilis* reveal the habits and habitat of the snake. All but one were secured at night. The exceptional individual was secured southeast of Sosúa in the early afternoon as it crawled on a barbed-wire fence adjacent to an orange grove. The long series from near Palo Verde was collected at night in riparian forest adjacent to the Río Yaque del Norte. The snakes were secured in trees on branches and in vine tangles from 0.6 to 2.4 meters above the ground. The specimen from Higüey was taken as it crawled between two shrubs 1.2 meters above the ground on a cutbank adjacent to a pasture. The snake from Santiago de la Cruz was found at a height of 3.7 meters in a tree along the edge of a stream. The specimen from Pepillo Salcedo was found in a small tree near the Laguna de Salodillo. Finally, another snake from Sosúa was taken from the trunk of a large *Ficus* adjacent to the road in a grassy pasture with a few scattered bushes. The apparent association of *E. g. gracilis* with woods adjacent to bodies of water suggests that the snake is mesophilic, and that its habitat is basically lowland deciduous woods. Fortunately, this sort of wooded situation persists today primarily along stream and lake margins. The highest elevation from which we have specimens of *E. g. gracilis* is 122 meters, east of Santiago de la Cruz. Most records are from coastal or near-coastal localities, the major exception being Merten's record from Santiago, which is in the interior Valle de Cibao at an elevation of about 175 meters.

Cochran (1941:324) gave ventral and subcaudal counts for the two HZM syntypes of *E. gracilis*. The two specimens had 282 and 289 ventrals, and 100 and 103 subcaudals, respectively. There is little doubt

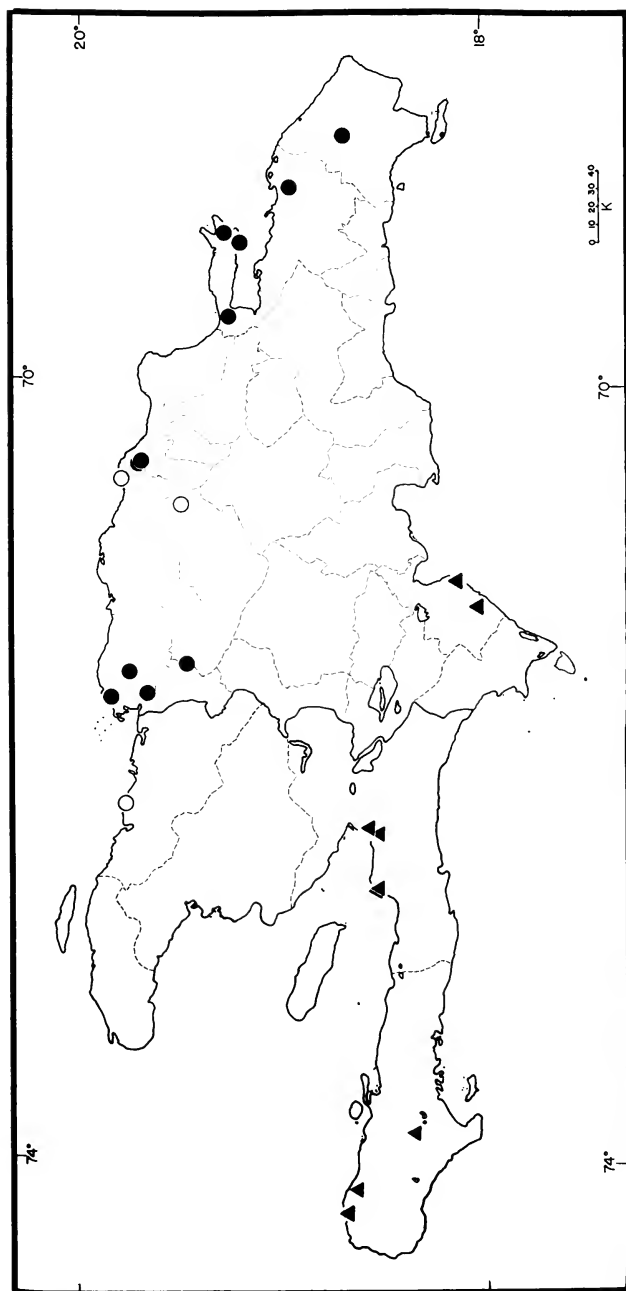


Fig. 6. Map of Hispaniola, showing ranges of *Epicrates gracilis gracilis* (circles) and *E. g. hapalus* (triangles). Solid symbols represent specimens examined. Hollow symbols represent literature records.

that these two snakes were females since both counts (especially the subcaudals) in both snakes fall close to the parameters set by Dominican *E. gracilis*. However, ventrals + subcaudals in these two snakes (382, 392) are near or above the upper extreme (384) of female *E. g. gracilis*.

***Epicrates gracilis hapalus*, new subspecies**

HOLOTYPE: MCZ 125602, an adult male, from Camp Perrin, Département du Sud, Haiti, one of a series collected July 28, 1962, by native collectors. Original number ASFS X3250.

PARATYPES: Haiti: ASFS X3243-49, X3251, same data as holotype; ASFS X2805-06, same locality as holotype, July 24, 1962, D. C. Leber, native collectors; MCZ 64781, Mayette, near Jérémie, Dépt. du Sud, December 12, 1960, L. Whiteman; ASFS V25005, 11.2 km W Jérémie, Dépt. du Sud, June 19, 1971, R. Thomas; MCZ 65095-97, Ça Ira, Dépt. de l'Ouest, March 15, 1961, L. Whiteman; MCZ 116757-59, Léogâne, Dépt. de l'Ouest, spring, 1969, collector unknown; USNM 117277, Diquini, Dépt. de l'Ouest, March 17, 1943, A. Curtiss; USNM 123987, Diquini, Dépt. de l'Ouest, November 23, 1946, A. Curtiss; USNM 118035, near Port-au-Prince, Dépt. de l'Ouest, August 1943, A. Curtiss.

ASSOCIATED SPECIMENS: Dominican Republic, Barahona Province: 5.3 km NE La Ciénaga (ASFS V30814); 7.7 km W Paraíso, 153 meters (ASFS V30952-53, ASFS V31029).

DISTRIBUTION: Hispaniola; known from the Tiburon Peninsula in Haiti, and the Península de Barahona in the Dominican Republic.

DEFINITION: A subspecies of *E. gracilis* characterized by the combination of large size (males to 870 mm, females to 905 mm snout-vent length), high number of ventrals in both sexes (278 - 304 in males, 279 - 296 in females), high number of subcaudals in both sexes (96 - 111 in males, 90 - 100 in females), and ventrals + subcaudals high (376 - 415 in males, 373 - 396 in females).

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 705 mm and tail 356 mm; ventral scales 293, 100 unpaired subcaudal scales, anal scale entire; supralabials 13/13, infralabials 13/13; loreals 1/1, preoculars 1/3, postoculars 6/6; circum-orbital scales 11/12; 1 intersupraocular scale, bordered anteriorly by 3 scales and posteriorly by 2 scales; supralabials 6 - 7 and 6 - 8 entering eye; dorsal-scale-row formula 35 - 44 - 26; 86/82 dark-brown body blotches and 24 dark dorsal tail blotches; ventrals + subcaudals 393.

Dorsum brown with darker brown subcircular to ovate blotches, in places forming continuous dumbbell-shaped dorsal saddles, paired and occasionally staggered; lateral surfaces with small and diffuse widely scattered dark markings, without definite shape or distribution; top of head with a dark median spot anterior to eyes, an irregular pair of fine lines from posterior to the eyes to the occiput, and a broad dark line on each side from the posterior margin of the eye to the upper temporal region; venter brown, heavily clouded with dark gray except on about first 10 ventrals, which are clear tan to brownish; left hemipenis partially extruded.

VARIATION: Including the holotype, there are 10 male and 16 female *E. g. hapalus*. The largest male (ASFS X3246) has a snout-vent length of 870 mm, the largest female (ASFS X3243) 905 mm. Scutellar variation is shown in tables 2 through 8.

COMPARISONS: Size and scutellation differentiate *hapalus* from the nominate subspecies. *E. g. hapalus* is a much larger snake in both sexes.

es: male *gracilis* reach a maximum snout-vent length of 700 mm, whereas male *hapalus* reach 870 mm. Of the 10 male *hapalus*, four are larger than the largest of the seven male *gracilis*. Differences in snout-vent length are even more pronounced in females. The largest female *gracilis* has a snout-vent length of 718 mm and the largest female *hapalus* measures 905 mm. Seven of the 16 female *hapalus* have a snout-vent length in excess of that of the largest of the 18 female *gracilis*. These data strongly suggest that differences in size are not sample artifacts, but reflect real differences in body size between the two populations.

Males of the two subspecies are readily differentiated on the basis of number of ventral scales: 271 - 286 in male *gracilis*, 278 - 304 in male *hapalus*. The samples are small, but the means (278.6 in *gracilis*, 290.6 in *hapalus*) are quite different, despite the degree of overlap of the extremes. In females, the ventrals in *gracilis* are 271 - 286 and 279 - 296 in *hapalus*. Although there again is an overlap in female ventrals, the higher counts and means (278.7 in female *gracilis*, 286.8 in female *hapalus*) are apparent. Ventrals + subcaudals intensify the differences in total underbody scale counts between the two subspecies. In males, this count is 368 - 377 (mean 362.6) in *gracilis* and 376 - 415 (mean 395.6) in *hapalus*, almost complete separation. In females, ventrals + subcaudals are 364 - 383 (mean 375.3) in *gracilis* and 373 - 396 (mean 383.3) in *hapalus*.

E. g. hapalus also has more dorsal scale rows at the neck and midbody than does *E. g. gracilis*. In *hapalus*, the neck counts are 31 - 42 and the midbody counts are 34 - 47, whereas these counts are 27 - 38 and 33 - 42 in *gracilis*. The extreme variation in number of dorsal scale rows in boids renders these differences of less value than in colubrids, for example, but the larger number of dorsal rows in *hapalus* seems likely correlated with the generally larger size and greater bulk of that subspecies. In *gracilis*, the modal number of supralabials is 12 (21 series), whereas only nine series of *hapalus* have supralabial counts of 12. The supralabial mode in *hapalus* is 13 (23 series), whereas 13 supralabials occur in 18 series in *gracilis*. All other counts are comparable in the two subspecies.

There is no striking difference in color or pattern between *gracilis* and *hapalus*. The latter is generally a brown snake with darker brown blotches, but some specimens (e.g., ASFS X3251) are paler (tan). The head pattern of the single male juvenile (USNM 118035, whose umbilicus lies on ventrals 217 - 219) is like that described for *E. g. gracilis* juveniles except that it is much more diffuse and less well defined. Our impression is that the head pattern in *hapalus* is much less clear in adults than it is in adult *gracilis*, but the general features are comparable.

REMARKS: We can say very little concerning the habits of *E. g. hapalus*. Most ASFS specimens were collected by natives, but David C. Leber secured one individual at Camp Perrin during the day in a rock-pile 6.1 meters from a native house in a cultivated area. This is the only instance we know of a specimen of *E. gracilis* being taken on the ground. Richard Thomas secured a female near Jérémie in a solution hole in a limestone rock, where the snake was wedged in a tight ball-like coil. Of the four Dominican specimens, one was secured by the senior author during the day from a knot-hole in a fence post adjacent to a wooded ravine. The three snakes from Paraíso were collected at night in rich mesic streamside forest: the junior author took one on a sapling limb 2.1 meters above the ground, D. C. Fowler took another in a vine tangle 1.5 meters above the ground, and Fowler secured the third in a large roadside vine tangle 4.6 meters above the ground. All were active.

The hemipenis of *E. gracilis* (based upon ASFS X3246, a paratype of *E. g. hapalus*) is short, extending the length of about eight or nine subcaudal scales, and is deeply bifurcate. The basal undivided portion has five conspicuous flounces and a very prominent basal lobe, which is sharply pointed, on the non-sulcate surface. The bifurcate section of the hemipenis is closely studded with many low, rounded, blunt papillae which extend to the sulcus spermaticus. The sulcus divides at the bifurcation of the hemipenis, the two branches of the sulcus extending to, and ending blindly near, the apices of the hemipenis.

The lack of specimens of *E. gracilis* from the area between Port-au-Prince and Santiago de la Cruz in the Dominican Republic (Fig. 6) might suggest that, in this intervening area, intermediates between *gracilis* and *hapalus* occur, and that the southern population, here regarded as nomenclatorially recognizable, might merely be the extreme southern portion of a northeast-southwest cline, of which the central portion is unrepresented by specimens. Such may well be the case, but in our defense we point out that the sexual extremes of *hapalus*, with the highest number of ventrals and ventrals + subcaudals, are a male (USNM 118035) from Port-au-Prince and a female (USNM 123987) from Diquini. Both these localities are at the base of the Tiburon Peninsula, geographically in a region where one might expect (were *gracilis* and *hapalus* clinal) dilution of the high *hapalus* counts. We have little doubt that *hapalus* and *gracilis* are two distinct populations that differ from each other in scutellation, but not in color and pattern. Of the pair, *E. g. gracilis* is the "north island" cognate of *E. g. hapalus*.

The four snakes from the Península de Barahona are included with *E. g. hapalus* since in size they best agree with that taxon. However, the lower limits of ventral counts in both male and female *hapalus* are set by snakes from this short series (male, ASFS V30953, 278 ventrals; fe-

male, ASFS V30952, 279 ventrals) and the same is true of ventrals + subcaudals. It is possible that these Barahona snakes represent extreme intergrades between *hapalus* and *gracilis*. There are no specimens of *E. gracilis* closer than 150 kilometers to the west (Port-au-Prince, Diquini, Ça Ira) in Haiti, although apparently suitable habitat occurs abundantly between the eastern coast of the Peninsula de Barahona and the base of the Tiburon Peninsula. Only additional material from this intervening area will confirm our suppositions regarding the eastern Barahona *E. gracilis*.

Most localities for *E. g. hapalus* are coastal or nearly so. The type locality, however, lies at about 305 meters on the southern slopes of the Massif de la Hotte. The Tiburon Peninsula is generally mesic, particularly at its western end. The snakes from Paraíso and La Ciénaga were all taken in mesic situations. In general we assume that the habitats occupied by *E. g. hapalus* do not differ strikingly from those noted for the nominate subspecies.

The name *hapalus* is from the Greek for "gentle, delicate," in reference to the nature of these snakes.

Epicrates exsul Netting and Goin

Epicrates exsul Netting and Goin, 1944, 30(6): 71.

TYPE LOCALITY: Near Blackrock (approximately 26° 49' N lat. and 77° 25' 30" W long.) on the east coast of Great Abaco Island, Bahama Islands; holotype - CM 21408.

DEFINITION: A moderate-sized species of *Epicrates* (males to 566 mm, females to 810 mm snout-vent length), with 243 - 251 ventral scales in males, 236 - 246 in females, 72 - 75 subcaudals in males, 69 - 72 in females; ventrals + subcaudals 316 - 326 in males, 305 - 317 in females; intersupraocular scales modally 2, pre-intersupraocular scales modally 5, post-intersupraocular scales modally 4; dorsal scale rows 28 - 33 on neck, 35 - 40 at midbody, 19 - 22 anterior to vent, the lowermost row not alternating a large and a small scale; supralabials modally 13, with usually three supralabials (modally 6 - 8) entering eye; infralabials modally 14 or 15; circumorbital scales modally 10; loreals modally 1; body blotches 41 - 57, tail blotches 13 - 16.

DISTRIBUTION: Great Abaco Island (including Elbow Cay) and Little Abaco Island, on the Little Bahama Bank, Bahama Islands (Fig. 3). Unknown from Grand Bahama Island but expected there, as well as on other islands and islets on the Little Bahama Bank.

VARIATION: The series of *E. exsul* consists of seven specimens, of which three are males and four are females. The largest male (CM 45450) has a snout-vent length of 566 mm, the largest female (AMNH 73005) 810 mm. In general body configuration, the species is laterally compressed, and in life is some shade of brown to tan with from 41 to 57 subcircular-to-ovate middorsal blotches on the body and 13 to 16 irregularly shaped blotches on the tail. In some specimens (ASFS V8961), the dorsal blotches are much reduced, incomplete, and widely separated, whereas in others (AMNH 72982), the blotches are transversely elongate ovals, well delineated, and evenly spaced. Most speci-

mens have, in addition to the dorsal blotches, a very irregular series of small dark-brown ventrolateral spots. Portions of this series, even at best expression, are absent from long sections of the pattern, so that continuity of the series is often haphazard. The head is unpatterned dorsally. The throat and venter are paler (pinkish tan in ASFS V8961) than the dorsum, and always immaculate. There may be a few scattered dark-brown scales in the lowermost row of dorsals. Scutellar variation is shown in tables 2 through 8.

Since there is only one specimen available from Little Abaco, it is impossible to compare the populations of *E. exsul* on Little and Great Abaco. However, the following data are of interest. The Little Abaco specimen (CM 45450) is the largest male *exsul* (the larger of the two Great Abaco males has a 525 mm snout-vent length), it has the only pre-intersupraocular scale count of 3 (all other snakes have 5 scales in this position), and has the only post-intersupraocular count of 3 (4 or 5 on Great Abaco). The Little Abaco male also sets the low parameters of anterior and posterior dorsal scale rows (28 on neck, 19 before vent). The scale differences between this snake and those from Great Abaco suggest that some differentiation has taken place.

REMARKS: No male has the hemipenes completely extruded. However, CM 45450 has the left hemipenis partially everted. As exposed, the structure is small and there are five flounces on the non-sulcate surface, of which the basal flounce has a conspicuous projecting triangular lobe almost precisely opposite the sulcus. The sulcus is simple and undivided as far as can be seen and is deeply entrenched.

Epicrates exsul appears to be distinctly uncommon on Great Abaco. The junior author with Donald W. Buden spent the period of April 10 - 14, 1965, collecting on that island. Although they traveled by automobile extensively along the length of Abaco and collected at various promising localities, they secured but one snake, dead on a road near Treasure Cay. The habitat at the site was burnt-over pinewoods on one side of the road and cut-over pine with a scrubby understory on the other. Most of northern and central Abaco is pinewoods on a sandy to limestone base. Netting and Goin (1944:73) noted that the holotype was secured along the margin of a clearing in pinewoods and that two other individuals were seen but escaped "into crevices in the knife-edged, eroded rocks." With increasing interest in the herpetofauna of the Bahama Islands, it is remarkable that apparently only six more snakes have been secured since the holotype was taken.

The herpetofauna of the Little Bahama Bank was discussed by Schwartz (1968a). There are six reptiles known from this bank: one *Sphaerodactylus*, one *Anolis*, one *Leiocephalus*, and three snakes (*Typhlops*, *Epicrates*, *Alsophis*), an altogether depauperate fraction of the typical Great Bahama Bank herpetofauna. Two facts are possibly sig-

nificant. First, *E. exsul* is regarded as a portion of the old "Great Bank" fauna (Schwartz, 1968a:264), which has persisted on the Little Bank as a refugium. Second, *E. exsul* is apparently absent from Grand Bahama Island. All other Little Bank species of amphibians and reptiles occur on the two major Little Bank islands (Grand Bahama, Great Abaco) except *E. exsul*. Considering the short distance (about 16 kilometers) between Little Abaco and Grand Bahama, and that even this distance is studded with a series of minor cays, islands, and islets; that there is a floral and physiographic identity between these two islands; and that within the past decade Grand Bahama has been under development, especially at its western end, by various American and Bahamian interests, it seems especially peculiar that *E. exsul* remains unknown there. It is possible that the species is truly absent from Grand Bahama or that it is somehow peculiarly limited in distribution, perhaps to the less well-known eastern end. Along these lines, it is suggestive (as Schwartz, 1968a:266 pointed out) that Great Abaco represents the northernmost portion of the Bahamian seaward volcanic arc. Perhaps *E. exsul* persisted on Great (and Little?) Abaco during periods when Grand Bahama and other Little Bank islands were submerged, and the snake has not reached Grand Bahama.

DISCUSSION

The nine species of Antillean *Epicrates* that we recognize may be conveniently divided into two groups: (1) a group of large and robust snakes (*angulifer*, *striatus*, *chrysogaster*, *subflavus*, *inornatus*), and (2) a group of small to medium-sized, more slender snakes (*monensis*, *fordi*, *gracilis*, *exsul*). Maximally sized adults of the former group reach snout-vent lengths of 2330 mm in males and 2250 mm in females. Among the four smaller species, maximally sized males reach a snout-vent length of 870 mm and females a length of 905 mm (see comment on *E. m. monensis*).

It is likely that Antillean *Epicrates* have been derived from continental *E. cenchria*. Such a pattern of origin for most (but not all) Antillean reptiles and amphibians (i.e., from the continent to the islands) is almost a certainty, considering the geological history of the major continental land masses in contrast to that of the West Indies. Although we have no doubt that this pattern is repeated in *Epicrates*, there is little to ally any Antillean species with *E. cenchria*. In pattern, *cenchrria* has a series of circular or subcircular dorsal blotches and one or two secondary lateral series of smaller blotches, a trilineate head pattern, and a different basic dorsal color (reddish brown) in comparison to the generally more drab and sombre tones of Antillean species. In scutellation *E. cenchria* has a low number of both subcaudal and ventral scales.

The eye is in contact with the supralabials. In size, *E. cenchria* resembles the group of large Antillean *Epicrates*.

We postulate that the two size groups are in fact divergent lineages of Antillean *Epicrates*, although in neither case is the total sequence within the lineage clear. Also, we are presented with the problem of *E. angulifer* which, in its usually complete row of lorilabials, differs markedly from mainland *E. cenchria*, although it is fairly certain that *angulifer* is the basic stock for West Indian *Epicrates*. It is difficult to relate the pattern, coloration, and scutellation of *angulifer* to that of *cenchria*, although both have a short tail and relatively low number of subcaudals. This is slim evidence indeed on which to suggest a relationship. We can only assume that ancestral *Epicrates* possessed a complete lorilabial row that has been retained only in *angulifer*, and lost in *cenchria* and other Antillean species. It is of course possible that *angulifer* is ancestral to all other large *Epicrates*, including *cenchria*, but this supposes Antillean origin of the genus, with subsequent invasion of and differentiation upon the continental land mass. This is not impossible, but the idea is not especially appealing historically.

Assuming that *E. angulifer* is the primitive Antillean member of the genus, we derive two series of large species from it: *inornatus-subflavus* and *sriatus-chrysogaster*. Of these two species pairs, we consider the former more closely related to each other. *Epicrates inornatus* and *E. subflavus* stand out among large Antillean *Epicrates* in that both have head-scale formulae of 2-1-2. Both are large snakes (in excess of 1800 mm snout-vent length), both have a moderate number of dorsal-scale rows at midbody (38 - 42 in *inornatus*, 39 - 44 in *subflavus*), and one loreal. Of the two species, *subflavus* has a greater number of both ventrals and subcaudals, more supralabials (11 versus 12), 9 rather than 8 scales in the circumorbital series, and two or three (rather than one) supralabials entering the eye. Both species most often have supralabial 6 involved with eye entrance, a condition that occurs in no other large Antillean species (but does occur in the small *E. gracilis*). The coloration and style of body pattern are quite different in these two species, and they have both obviously been long-separated from each other and from *E. angulifer*. However, the very fact that they were so long confused, until Stejneger's (1901) description of *subflavus*, is evidence of their close similarity. We interpret *E. subflavus* and *E. inornatus* as more closely related to each other than to any other Antillean *Epicrates*, and as an early independent line of West Indian boid evolution derived from *E. angulifer* or proto-*angulifer* stock.

The geographical separation of *subflavus* (Jamaica) and *inornatus* (Puerto Rico) is puzzling. This widely disjunct distribution suggests that they were indeed an early derivative or arrival, which has persist-

ed on widely-separated islands. However, as Darlington (1957:514) pointed out concerning the Greater Antillean mammal fauna, there is a possibility that Jamaica has served as Antillean port-of-entry for some mainland species, with subsequent migration therefrom. We interpret *subflavus* as an early insular invader from the mainland, which later dispersed to Puerto Rico (with differentiation there) but did not reach Hispaniola. The alternative explanation, that *subflavus* and *inornatus* are independent derivatives of *angulifer*, seems less reasonable.

The case for a sequence of *angulifer-striatus-chrysogaster* is much more convincing. In this instance, we must consider *E. striatus* in terms of its Hispaniolan and Bahamian populations, although we are convinced that these two segments are properly arranged as groups of subspecies, rather than as distinct species. Of the members of the large species-group of Antillean *Epicrates*, only *striatus* has occasional specimens with a complete lorilabial row, a feature that occurs very regularly (but not constantly) in *angulifer*. Among the Hispaniolan subspecies of *E. striatus* a complete lorilabial row occurs most commonly in (western) Tiburon *exagistus*, whereas in *angulifer* eye-supralabial contact occurs most frequently in Oriente Province in extreme eastern Cuba. Elsewhere in Hispaniola, complete lorilabial series occur only in nominate *striatus* as a rare variant. The head-scale formula of *angulifer* is 3-3-4, whereas Hispaniolan *striatus* has a formula of 5-2-5 and Bahamian *striatus* has 3-1-5. More detailed analysis of this variation in *E. striatus* shows that *E. s. striatus*, which we consider the basic Hispaniolan-Bahamian stock, has a head-scale formula of 5-2-5, whereas *exagistus* has 6-2-5 and *warreni* 5-2-4. Within the Bahamian populations, head-scale formulae are 3-1-5 (*strigilatus*, *fosteri*, and *fowleri*), and, most important, 3-2-? in *mccraniei*. Of the Bahamian populations only *mccraniei* retains the two intersupraoculars typical of ancestral *striatus*. Considering all the satellite subspecies of *E. striatus*, there has been primarily a reduction from two to one intersupraocular in the Bahamas (except for *mccraniei*). All populations derived from *E. s. striatus* show reduction in head scales, with the exception of *exagistus*, which has increased pre-intersupraoculars to 6.

Of the Hispaniolan subspecies of *E. striatus*, the nominate subspecies has the highest upper extreme of midbody dorsal-scale counts (65), whereas all other subspecies (*warreni*- 61, *exagistus*- 57) have lower upper extremes. *Epicrates angulifer* has the highest number of midbody scales (53 - 69) of all the large Antillean *Epicrates*. In number of loreals, basal *E. s. striatus* has 2, and this condition occurs also in *warreni*, but *exagistus* and all Bahamian subspecies have 1 loreal. Supralabials are 15 in *E. s. striatus*, and in derived *exagistus* and *warreni* as well. However, this number is reduced to 14 in all Bahamian taxa except *fowleri*. Basal *E. s. striatus* has 19 infralabials, and this condi-

tion persists in *warreni* and *exagistus*. The number is reduced to 18 in *strigilatus* and *ailurus*, but 19 persists in *fosteri* and *fowleri*. Supralabials 8 and 9 enter the eye in nominate *striatus* and in *warreni*, but *exagistus* has supralabials 7-8 in this position, and the Bahamian subspecies have either 7-8 (*ailurus*, *mccraniei*, *fowleri*) or 7-9 (*strigilatus*, *fosteri*). Regardless of the number of supralabials entering the eye, supralabial 8 is most intimately associated with eye entrance in all populations of *E. striatus*. Circumorbital scales are 11 in all Hispaniolan *E. striatus*, and 10 in all Bahamian subspecies (with the exception of a mode of 11 in Eleutheran *strigilatus*). In number of ventrals, we find the same general pattern. *Epicrates s. striatus* has a moderate number of ventral scales, whereas *exagistus* has a lower number and *warreni* a higher number of ventrals. The Bahamian populations likewise have generally moderate numbers of ventrals, with the lowest counts in southern *mccraniei* and the highest counts in northeastern *strigilatus* and *ailuris*.

In summary, we suggest that *E. striatus* is a derivative of *E. angulifer*, which has differentiated on the subspecific level in three directions: Tiburon Peninsula (=“south island”) *exagistus*, Tortue *warreni*, and basic (=“north island”) *striatus*. In addition, there has been invasion of the Great Bahama Bank, resulting in three basic “styles” of boas: (1) west of the Tongue of the Ocean, very dark boas with the typical Bahamian *striatus* fused dorsal pattern (*fosteri* and *fowleri*); (2) east of the Tongue of the Ocean, tan-to-pale-gray boas with typical Bahamian *striatus* fused dorsal pattern (*strigilatus* and *ailurus*); and (3) *mccraniei*, which lies more or less east of the Tongue of the Ocean but is dark in dorsal color and lacks the typical Bahamian *striatus* fused dorsal pattern and retains the distinctly angulate blotches and unfused dorsal pattern of Hispaniolan basal *E. s. striatus*. Concomitant with these color and pattern differences have gone changes (generally reductions) of number of scales in most populations derived from *E. s. striatus*.

We interpret *E. chrysogaster* as another population derived from *E. striatus*, on Great Inagua and the Turks and Caicos Islands. Schwartz (1968a) considered *chrysogaster* a member of the “primal southeastern fauna” in the Bahamian Archipelago. The 19 species included in this fauna, which occurs on islands south of the Crooked Island Passage, were regarded as an old southeastern Bahamian fauna whose relationships were not clearly shown (=not subspecifically related) to presumably ancestral species on the Greater Antilles. *Epicrates chrysogaster* differs from ancestral *E. striatus* in many ways, both in scutellation and in pigmentation. Most striking in *chrysogaster* are the quadrilineate individuals. Even in blotched individuals, the blotches are widely separated and reduced, and the secondary row of lateral blotches is absent in one subspecies (*chrysogaster*). The head scale formula is

3-2-3, in contrast to 5-2-5 in Hispaniolan *E. striatus* and 3-1-5 in Bahamian *E. striatus*. In *E. chrysogaster*, as in Bahamian *E. striatus*, there has been reduction of both pre- and post-intersupraoculars, although Bahamian *E. striatus* has retained the ancestral number of 5 post-intersupraoculars. Ventral scales in *E. chrysogaster* are fewer than in most populations of *E. striatus*. In circumorbital series and number of loreals *E. chrysogaster* resembles Hispaniolan *E. striatus* (11 circumorbitals, 2 loreals), but both supra- and infralabials are fewer than in Hispaniolan *E. striatus* (14 and 16, versus 15 and 19). *Epicrates chrysogaster* has the same number of supralabials (14) as Bahamian *E. striatus*, but has fewer infralabials (16 versus 18). Supralabials entering the eye are two in *E. striatus*; the scale most intimately associated with eye entrance is supralabial 8. In *E. chrysogaster*, either two or three supralabials enter the eye (depending upon the subspecies); supralabials 7 and 8 are the scales most intimately associated with eye entrance. Although *E. chrysogaster* resembles both the Hispaniolan and Bahamian segments of *E. striatus* in some ways, we feel that it merits specific rank. We find no reason to alter Schwartz's previous hypothesis that *E. chrysogaster* is a distinctive member of the old southeastern Bahamian fauna, but we add that probably *E. chrysogaster* was derived from Hispaniolan *E. striatus*.

The four smaller-sized species (*exsul*, *gracilis*, *fordii*, and *monensis*) are widely scattered geographically. *Epicrates exsul* occurs only on the Little Bahama Bank, far removed from any other known population of small *Epicrates*, and *monensis* has a split distribution on Isla Mona and the Virgin Islands. The origin of this group of snakes remains even more of a puzzle than that of the large *Epicrates*. We suggest that together they represent an old sidebranch of *Epicrates*, specializing in small size and arboreality (*gracilis*). In general, this group has fewer ventrals than do species of the large group. A major exception is that *gracilis* has a very high number of ventrals (perhaps an adaptation to arboreality), whereas *chrysogaster* has a very low number of ventrals among larger species. Certainly, the most distinctive of the smaller *Epicrates* is *gracilis*. Not only does it have a high number of ventrals, but in addition is very long-tailed, with consequent high number of subcaudals. It alone has the first dorsal scale row alternating a large and a small scale for each ventral. These characteristics set *E. gracilis* apart from other members of the complex, and indeed from all other *Epicrates*. Although we might assume that *E. gracilis* is the primitive member of this complex, it seems more likely that its differences from *exsul*, *fordii*, and *monensis* are adaptations to arboreality. Head-scale formulae for the four smaller boids are: *exsul* 5-2-4, *gracilis* 4-1-2, *fordii* 3-1-3, and *monensis* 3-1-3 or 3-1-5. Only *exsul* retains the two intersupraocul-

lars that we consider primitive in the *angulifer-striatus-chrysogaster* complex. Considering the remote area inhabited by *exsul*, we assume that it is a long-isolated remnant population that has persisted *in situ* (Schwartz, 1968a). Although the closest relationships of *exsul* are with *gracilis*, we do not suggest that one of these snakes is a derivative of the other, but rather that both are derived from some proto-*exsul* stock. One line of this stock persists as *exsul* on the Little Bahama Bank, and the other (*gracilis*) persists on Hispaniola and has become highly adapted for arboreality. The similarities between these two species in coloration and pattern we regard as due to close relationship, rather than to convergence.

If *exsul* and *gracilis* represent one line of smaller boa radiation, then *monensis* and *fordii* represent another. Of this pair, we consider *monensis* the more primitive, since it has a more complete and "typical" Antillean *Epicrates* pattern of angulate dorsal markings and has more ventral scales than does *fordii*. *Epicrates fordii* has a modified dorsal pattern composed of ovate or subcircular paired blotches, and fewer ventral scales. The head-scale formulae of the two species are similar. The post-intersupraoculars in *monensis* number either 3 or 5, whereas these scales number 3 in *fordii*. Of the two species, *monensis* reaches a larger size than does *fordii*. *Epicrates fordii* has 2 loreals and 10 circumorbitals, in contrast to 1 loreal and 11 circumorbitals in *monensis*.

Within the group of smaller *Epicrates*, the number of supralabials is low (13 or 14) and the number of infralabials is also low (13, 14, or 15). Among the large boas, only *inornatus-subflavus* have lower counts (supralabials 11 and 12, infralabials 12 or 14). Among the smaller *Epicrates* the range of number of supralabials entering the eye varies between 1 (*monensis*) and 3 (*exsul*), although the most common condition in the group is 2. Supralabial 7 is the scale that is most intimately associated with eye entrance in all species except *gracilis*, which has supralabial 6 in this position. It is supralabial 6 that enters the eye in *inornatus-subflavus*, whereas in the other large *Epicrates* supralabial 8 has this distinction.

In summary, we postulate the following history of Antillean *Epicrates*: (1) invasion (from Central America) of a primitive proto-*angulifer* stock with a short tail and complete lorilabial row; (2) very early division of this stock into (A) a group of boas that lost the lorilabial row (*inornatus*, *subflavus*) and was broadly distributed in Jamaica and Puerto Rico and perhaps elsewhere where it no longer persists, (B) a second group that retained the lorilabial row (*angulifer*), and (C) a third group of smaller boas; (3) derivation of *striatus* on the Hispaniolan "north island" from *angulifer* and subsequent invasion of the Hispaniolan "south island" (*exagistus*) and Ile de la Tortue (*warreni*); (4)

invasion of the islands of the southeastern Bahamian Archipelago by the *striatus* group and differentiation into *chrysogaster* (including *relicquus*); (5) a later invasion of the Great Bahama Bank by Hispaniolan "north island" *striatus*, giving rise to three "types" of subspecies (*fosteri-fowleri*, *strigilatus-ailurus*, *mccraniei*); (6) early division of the smaller boas (C) into two lines (*exsul-gracilis*, *monensis-fordii*). One line penetrated the Bahamas, persists on the northern Little Bahama Bank (*exsul*), also remained on Hispaniola, and specialized for arboreality (*gracilis*). The second line consists of a primitive pair of boas, of which one (*monensis*) has a split distribution on Isla Mona and the Virgin Islands (to the west and east of Puerto Rico, a distribution resulting from the presumed extinction of a proto-*monensis* stock on Puerto Rico and the other (*fordii*) derived from this proto-*monensis* stock on Hispaniola.

Hispaniola seems to have been ideally located geographically and ideally diverse ecologically to harbour three sympatric species. One of these (*striatus*) has been derived from more western *angulifer*, another (*fordii*) from more eastern *monensis*, and the third (*gracilis*) represents a highly divergent arboreal derivative of a proto-*exsul* stock that evolved locally on Hispaniola. Among these three species, *E. striatus* is a large snake, widespread geographically and primarily an inhabitant of mesic forested situations. *Epicrates fordii*, in contrast, is a denizen of more arid and open areas and is not associated with forested situations. Finally, *E. gracilis* is a small and distinctly arboreal snake, which is (even more than *E. striatus*) distinctly associated with mesic wooded habitats. Although both *E. striatus* and *E. gracilis* occur sympatrically and syntopically, direct competition between them is minimized by the much larger size and consequently much larger prey items which *E. striatus* ingests. Such a dichotomy in prey size may be even more striking, since evidence suggests that *E. striatus* eats (at least as adults) primarily homoiotherms, whereas *E. gracilis* ingests poikilotherms (lizards, frogs).

The remote geographic isolation of *E. exsul* and the absence of other small *Epicrates* in the Bahamas is of interest. The history of the islands has been such that the Great and Little Bahama Banks have been exposed for only a relatively short time, and presumably this accounts for the absence of any other small *Epicrates* on the Great and Little Bahama banks. Apparently the Abacos were a refugium for very few reptiles, far less than the islands south of the Crooked Island Passage, and *E. exsul* is one of that meagre number (Schwartz, 1968a:264-265). With re-emergence of these banks, the Great Bank was invaded by *E. striatus* from Hispaniola, but differentiation seems to have been lesser than in the *striatus-chrysogaster* radiation in the southeastern part of the ar-

chipelago. Why *E. gracilis* and *E. fordii* have not invaded the Bahamas is not clear. These islands are not especially suited to the mesic forest situation that harbors *E. gracilis* in Hispaniola today, but the Great Bank islands surely seem suitable for *E. fordii*. This species may have been a relatively recent arrival in Hispaniola and simply has not had time or opportunity to reach the Bahamas.

The scattered distribution of small boas in the West Indies bespeaks an old occupancy with extinction on various intermediate islands. Outstanding is the absence of small *Epicrates* in Puerto Rico where, considering the distribution of *E. monensis*, one is to be expected. If the herpetofauna of the southeastern Bahamas and the Turks and Caicos islands is indeed old, it is remarkable that these islands do not harbor a small boa of this complex. The Turks and Caicos islands are so poorly known herpetologically, however, that the absence of a small *Epicrates* there is hardly confirmed.

Certainly of the two groups of Antillean *Epicrates*, the group of large snakes is the most successful in terms of area occupied and degree of differentiation. The persistence of an old stock (*inornatus-subflavus*) on two islands and the sequential series of *angulifer-striatus-chryso-gaster* accounts for most of the land mass of the Greater Antillean (including the Bahamas) region. These large snakes are absent only from some of the southeastern Bahamas (Rum Cay, San Salvador, Plana Cays, Atwoods Cay, Mayaguana); the Little Bahama Bank; Cay Sal Bank; the Cayman Islands; Navassa Island between Hispaniola and Jamaica; apparently from the Hispaniolan satellites of Isla Beata, Isla Catalina, and the Cayemites; and apparently from the Virgin Islands and the Puerto Rican satellites. Many details — especially in the cases of the Puerto Rican and Hispaniolan satellites — remain to be verified, since it is likely that large *Epicrates* occur at least on the Hispaniolan satellites and possibly also on some of the more mesic Puerto Rican satellites.

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SPECIMENS EXAMINED

Epicrates angulifer

CUBA, Pinar del Río Province, Ensenada de Cajón (AMNH 82913); 18 km W Cayuco (AMNH 82908); Viñales (AMNH 77766); San Vicente (AMNH 76555, AMNH 77770-71, AMNH 82903-07, AMNH 82911, AMNH 96039, + one snake in the collection of Dennis R. Paulson); 4 km N San Vicente (AMNH 77767); 3 km N San Vicente (AMNH 77768, AMNH 82909); Valle de Ancón (AMNH 82910); San Diego de los Baños (USNM 27498); Guanajay (USNM 27434); HABANA PROVINCE, La Habana (USNM 12538); Boca de Jaruco (AMNH 83373); 3.2 km E Boca de Jaruco (AMNH 82899); 10.9 km W Jaruco (AMNH 82900-01); LAS VILLAS PROVINCE, no further locality (USNM 55875); Soledad (AMNH 77772, AMNH 82902); 4 km W, 8 km N Trinidad (AMNH 77774-75); Finca Morales, 12.8 km NW Trinidad (AMNH 77773); 4.0 km S Topes de Collantes (AMNH 96040); 9.6 km S Manicaragua (AS 444); Cueva de Caguanges, Punta Caguanes (AMNH 82912); CAMAGÜEY PROVINCE, 1.0 km W Majagua, Río Majagua (AMNH 77777); 13.4 km E Morón (AMNH 82902); 8.8 NE Banao (AMNH 77778); Los Paredones (AMNH 83366); Paso de la Trinchera (AMNH 96041); Paso de Lesca (AMNH 96042); ORIENTE PROVINCE, 3.0 km SE, thence 11.2 km NE Sevilla (AMNH 83367); 35.8 km W Santiago de Cuba (AMNH 82261); 24 km S Sabanilla (AMNH 83369); 4.5 km W Baracoa (AMNH 83370-71); Baracoa (USNM 51425); ISLA DE PINOS, no further locality (CM 282, CM 1545, CM 1702, CM 41533); just W Nueva Gerona, east base, Sierra de las Casas (AMNH 82914-15); 14.1 km SSW Nueva Gerona (AMNH 82916); Los Indios (MCZ 11738).

Epicrates striatus striatus

HAITI, DEPT. DU NORD-OUEST, Bombardopolis, 305 meters (USNM 59436); Port-de-Paix (USNM 59437); *Dépt. du Nord*, 1.6 km SSW Limbé (ASFS V10016); Port Margot (ASFS V10308, ASFS V10315-18); ca 5 km SW Limonade (ASFS V10054-59); DEPT. DE L'OUEST, 14.9 km SE Mirebalais (ASFS V23987-88); 10.2 km SE Mirebalais (ASFS V23989); 8.0 - 11.2 km S. Mirebalais (ASFS V23990-92); 12.8 km E Lascahobas (ASFS V26602); 1.1 km E Croix des Bouquets (ASFS V8146); 3.2 km N Pétienville (ASFS V9679); Morne Calvaire, 1.6 km SW Pétienville, (702 meters) (ASFS X2062); near Jacmel (MCZ 8613); ILE DE LA GONÂVE, Etroits (ASFS X2512); Ti Palmiste, 6 km from (= north) Pointe à Raquettes (MCZ 80832); Degoute (MCZ 96179-81); vicinity of Picmi (ASFS V26800); DOMINICAN REPUBLIC, *Monte Cristi Prov.*, 1 km S Palo Verde (ASFS V1352, ASFS V1402-05); 5 km SE Pepillo Salcedo (ASFS V17710); DAJABÓN PROV., Restauración (ASFS V18005, ASFS V18362); Colonia Agrícola Mariano Cestero, 7 km N Restauración (ASFS V18003-04); Villa Anacaona (ASFS V18360-61); ESPAILLAT PROV., 2 km N Puesto Grande (ASFS V18064); SAMANÁ PROV., 8.0 km NW Sánchez (ASFS V34269, ASFS V36144); DUARTE PROV., 5.6 km SW San Francisco de Macorís (ASFS V4427); 3 km W Azucey (ASFS V16085); SÁNCHEZ RAMÍREZ PROV., 1 km SE La Mata (ASFS V18525); EL SEIBO PROV., 5.6 km S Sabana de la Mar (ASFS X8111); 2.1 km SW Miches (ASFS X9276); 5.3 km SW Miches (137 meters) (ASFS X8110); LA ALTAGRACIA PROV., 4.7 km NW La Enea (ASFS V1121); 1.6 km NE Higüey (ASFS V814); 13.0 km NNE Higüey (ASFS V813); 18 km N Higüey (ASFS V13813); 1.6 km NW Boca de Yuma (ASFS V29060); SAN PEDRO DE MACORÍS PROV., 24.8 km E San Pedro de Macorís, Río Cumayasa (ASFS V28924); DISTRITO NACIONAL, Santo Domingo (ASFS V13906); 5.1 km E Santo Domingo, from Río Ozama (ASFS V2458); 11 km E Boca Chica (ASFS V28581); LA VEGA PROV., ca. 8.0 km W Constanza (ASFS X8915); 12 km NE Jarabacoa (610 meters) (ASFS V4315); 4.8 km S La Vega, Guaiguí, (92 meters) (ASFS V33697); AZUA PROV., Barreras (ASFS V21269-70, ASFS V21415); Sierra Martín García, 1220 meters above Barreras (ASFS V21222); SAN JUAN PROV., 17 km E Eliás Piña (ASFS V14585); Barranca (ASFS V21623); INDEPENDENCIA PROV., Puerto Escondido (ASFS V20931); BARAHONA PROV., Barahona (ASFS V30660); 6.6 km SW Barahona (ASFS V30244); La Ciénaga (ASFS V2); Hermann's finca, Paraíso (MCZ 43817); 7.7 km W Paraíso (ASFS V31318); PEDERNALES PROV., 19.2 km SW Enriquillo (ASFS X9784, ASFS X9998-X10000); 21.0 km SW Enriquillo (ASFS V4426); Oviedo (viejo) (ASFS V30272-84); 24 km NE Cabo Rojo, (610 meters) (ASFS V16762); 23.5 km N Cabo Rojo, (580 meters) (ASFS V30090); 19 km N Pedernales, (305 meters) (ASFS V2696).

Epicrates striatus strigilatus

BAHAMA ISLANDS, NEW PROVIDENCE, no further locality (MCZ 6242, MCZ 7091, MCZ 126770-71, USNM 36596, USNM 31982); Nassau (MCZ 26788, USNM 27457, AMNH 2691); Yamacraw Beach (ASFS V10382); 0.5 km E Nassau East (ASFS V10748); ROSE ISLAND (UMMZ 117026); ELEUTHERA, Harbour Island airstrip, north end of island (ASFS 17404); 8.0 km SE James Cistern (ASFS 17468, ASFS 17483); James Cistern (ASFS 17544); Hatchet Bay Plantation (ASFS 17469, ASFS 17504-06); Hatchet Bay (UMMZ 99223 - 2 specimens); 0.8 km N Rock Sound (ASFS V7101); main road between Savannah Sound and Palmetto Point (MCZ 96793); LONG ISLAND, Simms (MCZ 42265); Clarence Town (MCZ 42266-69); EXUMA CAYS, Compass Cay (ASFS V23469); GREAT EXUMA, Bahama Sound, south of The Forest (ASFS V7102); 0.8 km SW junction with Queen's Highway on northern portion of Moss Town Road (LDO 8-6804).

Epicrates striatus fosteri

BAHAMA ISLANDS, NORTH BIMINI, near Alicetown (CM 21962, MCZ 46054-58, MCZ 46178. MCZ 46054 is holotype); Easter Cay (CM 34177); EAST BIMINI, near East Well

(CM 37593); southern tip (cm 34198); SOUTH BIMINI, no other locality (ASFS V7121, ASFS X4805-10); western end (ASFS V8074-75, ASFS V21986); East End (CM 34158-59); Black Lands (CM 32532, CM 32574); water tower (CM 34125).

Epicrates chrysogaster chrysogaster

CAICOS ISLANDS, Ambergris Cay (MCZ 11989-92, MCZ 42048-49); Long Cay, off South Caicos (UMMZ 117027).

Epicrates chrysogaster relicquus

BAHAMA ISLANDS *Great Inagua*, Mathew Town (ASFS X4815); ca. 16 km N Mathew Town (ASFS V20458); SHEEP CAY (MCZ 37891 - holotype).

Epicrates inornatus

PUERTO RICO, Mayagüez (USNM 72749); Las Marías (USNM 29583); Bayamón (MCZ 4645-48 - five specimens); Caguas (USNM 27734); Humacao (USNM 27769); El Yunque (AMNH 63631); headwaters, Río Mameyes (MCZ 37298-99); 3.5 km SW Sabana, (305 meters) (ASFS X4516); near Luquillo (USNM 27456).

Epicrates monensis monensis

ISLA MONA (FMNH 267, UMMZ 74413-14).

Epicrates monensis granti

AMERICAN VIRGIN ISLANDS, *St. Thomas*, Pelican Beach Point (ASFS V3640); 1.9 km SE Hoffman (ASFS V8070); Vessup Bay Estate Development (VINP 1483-84); nr. Red Hook (WPM 1569); BRITISH VIRGIN ISLANDS, *Tortola*, (MCZ 33947 - holotype of *granti*).

Epicrates fordii fordii

HAITI, DÉPT. DE L'ARTIBONITE, Gonaïves (ZMB 28576 - 2 specimens); DÉPT. DE L'OUEST, Port-au-Prince (USNM 84291); 3.2 km N Pétienville (ASFS V13715-16, ASFS V13726-28); 1.6 km NW Pétienville (ASFS V24337-44); ca. 1.6 km NE Pétienville (ASFS V26789, ASFS V26793); Pétienville (ASFS V25006); Frères (ASFS V11354-62); Ste. Philomène (USNM 117278); Hatte Lathan (USNM 123994-95); Manneville (ASFS V8201); "Étang Manneville" (CM 33837-41, CM 38843-53); Ile à Cabrit (ASFS V10312); ILE DE LA GONÂVE (USNM 75924); DOMINICAN REPUBLIC, INDEPENDENCIA PROV., 6 km W Duvergé (ASFS V20493); Puerto Escondido (ASFS V20606, ASFS V20872, ASFS V20936); 10 km NW Puerto Escondido (ASFS V20801); AZUA PROV., Barreras (ASFS V21450, ASFS V31272); PERAVIA PROV., Limonal (ASFS V14940); BARAHONA PROV., 3.0 km N Palo Alto (ASFS V30573); "North America" (HZM 52 - syntype of *Chilabothrus maculatus*).

Epicrates gracilis gracilis

DOMINICAN REPUBLIC, MONTE CRISTI PROVINCE, 1 km S Palo Verde (ASFS V1370-71, ASFS V1406-10); 5 km SE Pepillo Salcedo (ASFS V1627); DAJABÓN PROVINCE, 8 km E Santiago de la Cruz, (122 meters) (ASFS V1302); PUERTO PLATA PROVINCE, 10 km SE Sosúa (ASFS V1720); 11 km SE Sosúa (ASFS V1725); SAMANÁ PROVINCE, 8.0 km NW Sánchez (ASFS V36137); Samaná (MCZ 43687); Rojo Cabo (USNM 55025); no further locality (AMNH 43006, AMNH 44743, AMNH 44834); EL SEIBO PROVINCE, Jovero (USNM 66713); LA ALTAGRACIA PROVINCE, 1.6 km NW Higüey (ASFS V812); "Santo Domingo" (HZM 6022); "Samaná or Monte Cristi" (AMNH 42996-43000).

Epicrates exsul

BAHAMA ISLANDS, GREAT ABACO ISLAND, near Blackrock (CM 21408 - holotype); 14.4 km NW Treasure Cay (ASFS V8961); Marsh Harbour (AMNH 79014); Hopetown (AMNH 72981-82; AMNH 73005); LITTLE ABACO ISLAND, Black Point (CM 45450).

TABLE I
 • MEASUREMENTS AND SCALE COUNTS OF ANTILLEAN *Epicrates*

	N	MAX S-V L (MM)	No. VENTRALS	No. SUBCAUDALS	No. VENTRALS + SUBCAUDALS
<i>angulifer</i>					
Isla de Pinos (4 m, 3 f., 1 unsexed)	8	m. - 1555 f. - 1480	278-285 271-283	46 47	329 318
Pinar del Río (7 m, 14 f.)	21	m. - 1743 f. - 2250	272-284 268-284	45-52 46-54	321-333 316-334
Habana-Matanzas (2 m, 3 f.)	5	m. - 1415 f. - 1987	278 281-287	47-49 46-52	325-327 328-339
Las Villas- Camagüey (4 m, 11 f.)	15	m. - 1663 f. - 1882	274-283 276-290	47-51 49-53	323-333 327-339
Oriente (5 m, 1 f.)	6	m. - 1631 f. - 1445	279-292 279	48-55 54	331-347 333
<i>striatus</i>					
<i>striatus</i> (44 m, 52 f.)	96	m. - 1865 f. - 1737	272-293 273-298	76-96 76-94	358-382 358-384
<i>exagistus</i> (4 m, 10 f.)	14	m. - 1711 f. - 1635	271-285 273-286	80-85 86-88	355-370 362-363
<i>warreni</i> (7 m, 6 f.)	13	m. - - f. - 1411	284-299 287-298	88-102 89-94	375-390 377-387
<i>strigilatus</i>					
New Providence + Rose I. (4 m, 7 f.)	11	m. - 1260 f. - 1350	274-295 274-288	83-91 80-87	367-386 357-373
Eleuthera (7 m, 5 f.)	12	m. - 1445 f. - 1140	279-285 276-287	82-86 80-87	362-369 356-373
Exuma Cays (3 f.)	3	f. - 1780	275-278	82-83	358-361
Long (3 m, 2 f.)	5	m. - - f. - -	277-280 277-280	79-83 81	356-360 358
<i>ailurus</i> (3 m, 3 f.)	6	m. - 1560 f. - 1640	283-293 280-285	80-85 81	368-373 366
<i>mccraniei</i> (1 m, 2 f.)	3	m. - 1330 f. - 1540	270 266-271	83 77	353 343
<i>fosteri</i> (20 m, 5 f.)	25	m. - 2330 f. - 1895	272-286 269-282	84-91 87-93	362-373 362-372
<i>fowleri</i> (5m, 4 f.)	9	m. - 1260 f. - 2055	273-282 271-276	82-86 76-88	358-367 352-359

N = No. of individuals

Max S-V L = Maximum snout-vent length

m. = male; f. = female.

TABLE 2
MEASUREMENTS AND SCALE COUNTS OF ANTILLEAN *Epicrates* (cont'd.)

	N	MAX S-V L (MM)	No.		
			VENTRALS	SUBCAUDALS	VENTRALS + SUBCAUDALS
<i>chrysogaster</i>					
<i>chrysogaster</i> (1 m, 5 f., 1 unsexed)	6	m. - 590 f. - 1220	245 249-259	79 74-83	320 327-339
<i>relicquus</i> (2 m, 1 f.)	3	m. - 810 f. - 1310	269-275 270	88 -	363 -
<i>inornatus</i> (9 m, 4 f.)	13	m. - 1860 f. - 1750	263-273 258-267	66-74 68-75	329-338 326-339
<i>monensis</i>					
<i>monensis</i> (1 m, 2 f.)	3	m. - 720 f. - 570	264 266	- 82	- 348
<i>granti</i> (3 m, 2 f.)	5	m. - 770 f. - 470	261-269 261-265	80-81 82-84	342 345-347
<i>fordii</i>					
<i>fordii</i> <i>Cul de Sac,</i> <i>Cabrit,</i> <i>Gonave</i> (20 m, 28 f.)	48	m. - 785 f. - 730	231-255 236-257	69-81 70-81	310-334 312-334
<i>fordii</i> <i>Valle de</i> <i>Neiba +</i> <i>Llanos de</i> <i>Azua</i> (3 m, 6 f.)	9	m. - 775 f. - 630	238-254 247-259	73-85 76-89	311-339 325-341
<i>agametus</i> (1 m.)	1	m. - 860	261	82	343
<i>gracilis</i>					
<i>gracilis</i> (7 m, 18 f.)	25	m. - 700 f. - 718	271-286 271-286	91-97 92-102	368-377 364-384
<i>hapalus</i> (10 m, 15 f.)	25	m. - 870 f. - 905	278-304 279-296	96-111 90-100	376-415 373-396
<i>exsul</i> (3 m, 4 f.)	7	m. - 566 f. - 810	243-251 236-246	72-75 69-72	316-326 305-317

N = No. of individuals

Max S-V L = Maximum snout-vent length

m. = male; f. = female.

TABLE 3

	SCALE COUNTS, ANTILLEAN <i>Epicrates</i>														
	NO. PRE-INTERSPRAOCLAR			NO. INTERSPRAOCLAR			NO. POST-INTERSPRAOCLAR			NO. DORSAL SCALE ROWS					
	2	3	4	1	2	3	4	5	6	7	8	9	NECK	MIDBODY	POSTERIOR
<i>angulifer</i>															
Isla de Pinos	3	5		4	4		5	3					46-52	53-63	28-36
Pinar del Rio	4	6	4	3	5	9	4	10	4	1			44-53	57-69	30-38
Habana-Matanzas	1	3		2	2	2		2	1				45-50	61-69	31-38
L.V.-Camaguey	3	8	2	1	5	8	1	9	5				47-54	56-68	32-38
Oriente	4			1	1	3		4	1				47-51	62-67	32-37
<i>striatus</i>															
<i>striatus</i>	8	27	51	9	1	3	78	9	7	1	1	8	31	35	17
<i>exagistius</i>															
<i>warreni</i>	1		10	2	1	12	3	13	3	2	4	9	2	34-43	39-57
<i>strigilatus</i>															
(New Prov., Rose)	6	1	5	4	6	1	1	1	6	2	2	1	36-43	49-54	24-27
(Eleuthera)	2	7	2	1	7	5			3	6	3		36-43	47-56	25-27
(Exumas)	1	1	1	1	11	1			11	1			42-43	49-54	27
(Long)	3	1	1	4	4				1	1	2		39-45	49-53	27-28
<i>ailurus</i>	1	2	2	1	5	1	1	1	1	1	1	1	37-41	47-51	24-26
<i>micraniei</i>	2	2	1	3	3				1	1	1	1	39-41	43-50	26-27
<i>fosteri</i>	16	6	3	13	9	3	1	4	3	9	7	1	36-41	42-54	25-28
<i>fowleri</i>	1	4	3	1	7	2			2	2	3	2	38-42	45-53	25-27
<i>chrysogaster</i>															
<i>chrysogaster</i>	2	3	1	1	3	4			5	1	2	1	33-37	39-43	23-25
<i>relucqius</i>	1	1	1	1	1	2			1	1	1		36-37	46-47	19-27
<i>inornatus</i>	10	3		13			13		12	1			31-34	38-42	21-25
<i>monensis</i>															
<i>monensis</i>	1	1	1	2	1				2	1			36-39	39-42	24-26
<i>granii</i>	4	1		4	1	4	1	1	2	2			34-38	41-47	23-31
<i>fordii</i>															
<i>fordii</i>	2	45	3	49	1			8	25	10	6	1	28-34	32-38	18-23
(Haiti)	9			9					8	1			29-35	31-39	19-23
(Dom. Rep.)	1			1							1		33	38	22
<i>agametius</i>															
<i>gracilis</i>															
<i>gracilis</i>	12	12	1	25	8	1	1	15	8	1	1	1	27-38	33-43	21-28
<i>haplatus</i>	9	12	5	26	13	9	3	13	9	3	1	1	31-42	34-47	22-29
<i>exsul</i>	1	6			3	2	1	1	5	1			28-33	35-40	19-22

Modes or bimodes in bold face.

TABLE 4
SCALE COUNTS, ANTILLEAN *Epicrates*

	NO. SUPRALABIALS						
	11	12	13	14	15	16	17
<i>angulifer</i>							
Isla de Pinos			5	9	1	1	
Pinar del Río		1	15	17	7		
Habana-Matanzas			4	6			
Las Villas-Camagüey		1	6	18	5		
Oriente			4	4	2		
<i>striatus</i>							
<i>striatus</i>			12	37	66	48	16
<i>exagistus</i>			1	6	19	5	1
<i>warreni</i>				2	12	11	3
<i>strigilatus</i>							
(N. Prov. + Rose I.)			2	10	7	5	
(Eleuthera)	1	3	6	11	3		
(Exumas)			3	3			
(Long)				5	2	1	
<i>ailurus</i>			1	8	3		
<i>mccraniei</i>		1		3	1		
<i>fosteri</i>		1	9	20	17	3	
<i>fowleri</i>			1	7	9	1	
<i>chrysogaster</i>							
<i>chrysogaster</i>			3	9	1	1	
<i>relicquus</i>			1	3	2		
<i>inornatus</i>	14	7					
<i>monensis</i>							
<i>monensis</i>			4	2			
<i>granti</i>		1	3	4			
<i>fordii</i>							
<i>fordii</i>							
(Haiti)	1	19	58	19	3		
(Dom. Rep.)		2	9	5			
<i>agametus</i>			1	1			
<i>gracilis</i>							
<i>gracilis</i>	4	21	18	4			
<i>hapalus</i>	4	10	23	14	1		
<i>exsul</i>		1	8	1			

Modes in boldface.

TABLE 5
SCALE COUNTS, ANTILLEAN *Epicrates*

	NO. INFRALABIALS											
	11	12	13	14	15	16	17	18	19	20	21	22
<i>angulifer</i>												
Isla de Pinos			1	1	3	6	3	2				
Pinar del Río				2	8	11	17	3	1			
Habana-Matanzas					2	3	4					
Las Villas-												
Camagüey				1	7	6	11	18	1			
Oriente					2	4	3	1				
<i>striatus</i>												
<i>striatus</i>					1	3	15	41	59	42	20	4
<i>exagistus</i>							2	6	15	6	3	
<i>warreni</i>						1	3	10	10	4		
<i>strigilatus</i>												
(N. Prov. +												
Rose I.)							2	14	8			
(Eleuthera)						2	9	9	4			
(EXumas)						3	1	2				
(Long)						2	2	4	1	2		
<i>ailurus</i>						2	2	4	2	2		
<i>mccraniei</i>								2	2	1		
<i>fosteri</i>						5	9	14	19	3		
<i>fowleri</i>							3	7	8			
<i>chrysogaster</i>												
<i>chrysogaster</i>				3	5	4	3					
<i>relicquus</i>						2	3	2				
<i>inornatus</i>	3	12	9	3								
<i>monensis</i>												
<i>monensis</i>				1	4	1						
<i>granti</i>			1	2	5	1						
<i>fordii</i>												
<i>fordii</i>												
(Haiti)			3	13	44	18	8					
(Dom. Rep.)				3	9	3	1					
<i>agametus</i>					1	1						
<i>gracilis</i>												
<i>gracilis</i>	7	13	21	4								
<i>hpalus</i>	3	8	23	12	5	1						
<i>exsul</i>			1	5	5	2						

Modes or bimodes in boldface.

TABLE 6
SCALE COUNTS, ANTILLEAN *Epicrates*

	NO. SUPRALABIALS ENTERING EYE										MODAL NO. SCALES	NO. OF SUPRALABIAL					
	0	5	6	7	8	9	5-6	6-7	7-8	8-9			9-10	4-6	5-7	6-8	7-9
<i>angulifer</i>																	none
Isla de Pinos	12		4														none
Pinar del Rio	36		6														none
Hab.-Matanzas	10																none
L.V.-Camaguey	30																none
Oriente	5		3	2													none
<i>striatus</i>																	
<i>striatus</i>	3		3	27	8												two
<i>exagistus</i>	3		2	9	1												two
<i>warreni</i>																	two
<i>strigilatus</i>																	two
(New Prov. + Rose I.)																	
(Eleuthera)																	two
(Exumas)			2														three
(Long)																	two or three
<i>ailurus</i>																	two
<i>mccraniei</i>																	two
<i>josteri</i>																	three
<i>fowleri</i>																	two
<i>chrysogaster</i>																	
<i>chrysogaster</i>																	three
<i>granti</i>																	two
<i>inornatus</i>	1	16	1														one
<i>monensis</i>																	
<i>monensis</i>	2	2	2														one
<i>granti</i>			1														two
<i>jordii</i>																	
<i>jordii</i>																	
(Haiti)																	
(Dom. Rep.)																	
<i>agamerus</i>																	
<i>gracilis</i>																	
<i>gracilis</i>																	two
<i>hapalus</i>																	two
<i>exsul</i>																	two
<i>gracilis</i>																	three
<i>gracilis</i>																	two
<i>hapalus</i>																	two
<i>exsul</i>																	three

Modes in boldface.

TABLE 7
SCALE COUNTS, ANTILLEAN *Epicrates*

	CIRCUMORBITAL SCALES							
	7	8	9	10	11	12	13	14
<i>angulifer</i>								
Isla de Pinos		8	8					
Pinar del Río		31	9	2				
Habana-Matanzas		5	5					
Las Villas Camagüey		25	4	1				
Oriente		10		1				
<i>striatus</i>								
<i>striatus</i>			4	19	92	58	13	1
<i>exagistus</i>			1	11	11	6	1	
<i>warreni</i>				4	23	1		
<i>strigilatus</i>								
(New Prov. + Rose I.)				11	10	3		
(Eleuthera)		1	2	14	7			
(Exumas)				1	4	1		
(Long)				5	3	1		
<i>ailurus</i>			1	7	3			
<i>mccraniei</i>				3	3			
<i>fosteri</i>			4	22	19	3	2	
<i>fowleri</i>				9	4	3	1	
<i>chrysogaster</i>								
<i>chrysogaster</i>			4	5	4	1		
<i>relicquus</i>					2	2	2	
<i>inornatus</i>	2	12	5	3				
<i>monensis</i>								
<i>monensis</i>				1	4	1		
<i>granti</i>				2	7			
<i>fordii</i>								
<i>fordii</i>								
(Haiti)		1	10	47	30	12		
(Dom. Rep.)			2	5	7	1	1	
<i>agametus</i>				1				
<i>gracilis</i>								
<i>gracilis</i>			1	18	20	5	2	1
<i>hapalus</i>			3	12	24	7	3	1
<i>exsul</i>				11	1			

Modes or bimodes in boldface.

TABLE 8
SCALE COUNTS, ANTILLEAN *Epicrates*

	LOREALS			
	1	2	3	4
<i>angulifer</i>				
Isla de Pinos	15	1		
Pinar del Río	40	2		
Habana-Matanzas	10			
Las Villas-Camagüey	28	1	1	
Oriente	10	2		
<i>striatus</i>				
<i>striatus</i>	67	112	10	
<i>exagistus</i>	25	5		
<i>warreni</i>	3	25		
<i>strigilatus</i>				
(New Prov. + Rose I.)	23	1		
(Eleuthera)	23	1		
(Exumas)	6			
(Long)	9			
<i>ailurus</i>	8	2		
<i>mccraniei</i>	6			
<i>fosteri</i>	47	3		
<i>fowleri</i>	14			
<i>chrysogaster</i>				
<i>chrysogaster</i>	4	10		
<i>relicquus</i>		6		
<i>inornatus</i>	25	1		
<i>monensis</i>				
<i>monensis</i>	6			
<i>granti</i>	8	1		
<i>fordii</i>				
<i>fordii</i>				
(Haiti)	8	84	8	
(Dom. Rep.)	1	14	1	2
<i>agametus</i>		2		
<i>gracilis</i>				
<i>gracilis</i>	39	8		
<i>hpalus</i>	51	1		
<i>exsul</i>	12	2		

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ARTICLE 6

PALEONTOLOGY AND GEOLOGY OF THE BADWATER CREEK AREA, CENTRAL WYOMING

Part 8. The rodent *Microparamys* (Mammalia)

MARY R. DAWSON

Curator, Section of Vertebrate Fossils

INTRODUCTION

The family Ischyromyidae is represented in the Badwater Creek Upper Eocene not only by the large ischyromyids described by Black (1971), but also by the small *Microparamys dubius*. This species, originally described (Wood, 1949:558) from Wood locality (see Black and Dawson, 1966, for location of this and other localities mentioned here), is now known in the Badwater localities from additional isolated teeth, only three from the type locality, but more adequate samples from localities 5, 5A, and 6. The species occurs also in Upper Eocene deposits in the Uinta Basin (Dawson, 1966:99-102).

The specimens described here are in the vertebrate paleontological collections of Carnegie Museum of Natural History (CM) and Amherst College (ACM). Illustrations are by Linda Trueb. This study and associated field work were supported by grants GB-1266, GB-4089, GB-7801, and GB-30840X from the National Science Foundation, and by grants from the Childs Frick Corporation and the Gulf Oil Corporation.

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Family Ischyromyidae
Microparamys Wood, 1959

Three middle and late Eocene species of *Microparamys*, *M. minutus*, *M. dubius*, and *M. tricus*, form a relatively conservative, morphologically similar assemblage of probably closely related forms. Their differences, so far as known, are mainly in size and in development of crests, which tend to be more pronounced in the late Eocene species.

Microparamys dubius (Wood, 1949)

Sciuravus dubius Wood, 1949:558.

Microparamys dubius (Wood, 1949), Dawson, 1966:99.

TYPE: ACM 10020, right M_1 .

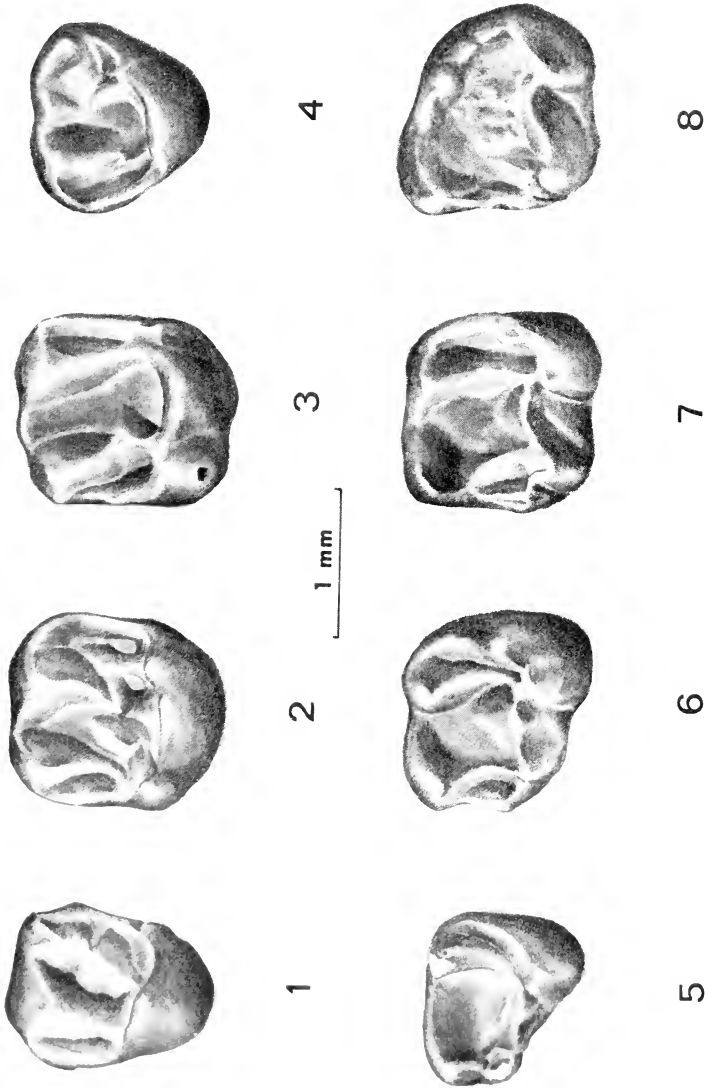
REFERRED SPECIMENS: ACM 10021, M_2 ; CM 14571-73, 14630, 14788-96, 137 isolated upper and lower teeth.

LOCALITIES: Wood (type) locality (5 teeth); 5(42 teeth); 5A(57 teeth); 6(35 teeth); Badwater Creek area, Natrona County, Wyoming. (Also known from White River Pocket, Utah.)

AGE: Late Eocene.

DESCRIPTION AND COMPARISONS OF NEW MATERIAL: Previous descriptions of *M. dubius* (Wood, 1949; Dawson, 1966) were based on lower teeth and a lower jaw. The new Badwater specimens add information on upper teeth and a greater understanding of morphological variation within the species. All specimens of *M. dubius* from the Badwater localities are isolated teeth. In size range (Table 1) *M. dubius* is very near the sample of *M. minutus* from the middle Eocene Powder Wash locality (Dawson, 1968:335-341).

P^3 is not known. P^4 (Fig. 1) is compact anteroposteriorly, with paracone and metacone close together and no mesostyle between them. The hypocone is indicated only by a slight swelling on the posterior cingulum. There is a prominent metaconule. The first two molars are generally quadrate in outline, but the hypocone is distinctly less well developed than the protocone. As in other species of *Microparamys* the anterior and posterior cingula are well developed. A loph extends buccally from protocone to just anterior to the paracone (Fig. 2, probably M^1) or to the paracone (Fig. 3, probably M^2). The mesostyle is small or absent, depending at least in part on stage of wear. The metaloph, which has one or sometimes two well developed metaconules, is usually directed to the protocone, but in some specimens is directed toward the hypocone. As in *M. minutus* and *M. tricus*, the lophs appear to wear away rapidly. As in *M. minutus*, M^3 (Fig. 4) has a well developed anterior cingulum and prominent paracone-protoloph. There is usually a swelling indicating some development of a hypocone on the posterior cingulum, and a variable ridge usually extends into the talon basin from just anterior to the hypocone swelling. The talon tends to be slightly elongated but never so elongated as in some specimens of *M. minutus*.



Figs. 1-8. *Microparamys dubius*, occlusal views of teeth.
 Fig. 1: CM 14571, left P₁. Fig. 2: CM 14572, right M¹ or M². Fig. 3: CM 14573, right M¹ or M². Fig. 4: CM 14630, left M³. Fig. 5: CM 14788, left P₁. Fig. 6: CM 14789, left M₁ or M₂. Fig. 7: CM 14790, left M₁ or M₂. Fig. 8: CM 14791, left M₁. Line equals 1 mm.

In total, the upper cheek teeth share many features with those of *M. tricrus* and *M. minutus*. The hypocone and metaloph may be slightly more prominent, and M^3 is less elongated than in *M. minutus*. *Microparamys tricrus* is larger than *M. dubius* but seems similar in upper tooth morphology. However, since *M. tricrus* is known from a specimen with well-worn teeth, detailed comparisons with it are not possible. *Microparamys perfossus* from the Early Oligocene (Wood, 1974:13-17) is larger than *M. dubius* and differs also in having U-shaped protocone and hypocone. It seems closer to the incompletely known *Microparamys* sp. D (Wood, 1962: 165-166) than to *M. minutus*, *M. tricrus*, and *M. dubius*.

Like the upper cheek teeth, the lower teeth share a number of characters with those teeth of *M. minutus* and *M. tricrus*. On the trigonid of P_4 (Fig. 5) the metaconid is more prominent than the protoconid. The mesoconid is only a small swelling on the ectolophid. In most specimens there is a distinct lophid from entoconid toward hypoconid, but in some the lophid extends back to the posterior cingulum. M_1 and M_2 are similar, but a narrower trigonid on M_1 (Fig. 6, probably M_1) may differentiate it from M_2 (Fig. 7, probably M_2). The well-developed anterior cingulum has a buccal swelling. There is no metastylid. The hypolophid, extending to or toward the hypoconid, is well developed and separate from the posterior cingulum. The mesoconid is small, but distinct on the ectolophid. The posterior protoconid arm is variable in development, usually but not always closing the trigonid basin posteriorly. M_3 (Fig. 8) has a posteriorly expanded talonid that shows a distinct entoconid and frequently some development of a lophid from entoconid into the basin. The ectolophid is usually distinct, but the mesoconid is usually small.

The greatest difference between *M. dubius* and *M. minutus* in the lower cheek teeth is in the distinct hypolophid between entoconid and hypoconid in *M. dubius*. In this feature *M. dubius* is closer to *M. tricrus*. The Early Oligocene species *Microparamys perfossus* also seems to have a more prominent hypolophid than in *M. minutus* and has some development of a mesolophid, absent in *M. dubius*.

DISCUSSION: The record of *Microparamys* from Upper Eocene deposits along Badwater Creek is now relatively good, but unfortunately the type locality of *M. dubius*, Wood locality, has yielded only three teeth in addition to the two originally described from there. This topotype sample is inadequate to provide a good estimate of morphological variation from that locality, but on the basis of the known material, the samples from localities 5, 5A, and 6 merit no separation at the specific level.

Microparamys is a long ranging genus in North America. Its oldest known representative is the incompletely known *Microparamys* sp. A from the earliest Eocene (Graybullian) of Wyoming (Wood, 1962:160-161), and its youngest is *M. perfossus* from the Early Oligocene of Texas (Wood, 1974:12-17). The Middle Eocene *M. minutus* and the Late Eocene

M. dubius and *M. tricus* seem to be closely related, relatively conservative species, and even the Early Oligocene *M. perfossus*, though distinctive especially in morphology of the upper molars, is not far from this group.

Microparamys, which may have had an ancestry near that of sciuravids, was the main ischyromyid in North America to enter the small rodent niche in the Middle and Late Eocene, when it seems to have competed successfully with the small sciuravids and cylindrodontids. Although it persisted into the Early Oligocene in the more southern part of its range, its distribution and extinction may have been related to development of the eomyids, which have a North American history showing appearance in the Late Eocene and a strong radiation in the Early Oligocene.

The history of *Microparamys* in Europe is quite different, although there too the genus first appeared in the Early Eocene. By the middle Eocene *Microparamys* had given rise to and been replaced by the Gliridae (Hartenberger, 1971). The final disappearance in the Late Oligocene of the primitive glirid *Gliravus* has been related to a Late Oligocene radiation of eomyids in Europe (Hartenberger, 1971:133), as an interesting parallel to the possible effect of an earlier eomyid radiation on *Microparamys* in North America. Of course the more modernized glirids persisted through the Late Oligocene to the Recent in Europe.

TABLE I.
MEASUREMENTS OF *Microparamys dubius*, IN MM.

	Anteroposterior	Width ¹
CM 14571, P ³	1.15	1.49
CM 14572, M ¹ or 2	1.42	1.59
CM 14573, M ¹ or 2	1.42	1.57
CM 14630, M ³	1.36	1.29
CM 14788, P ₄	1.19	0.75-1.12
ACM 10021, M ₂	1.46	1.32-1.42
CM 14789, M ₁ or 2	1.36	1.19-1.42
CM 14790, M ₁ or 2	1.39	1.39-1.42
ACM 10020, M ₁	1.53	1.36-1.15
CM 14791, M ₁	1.49	1.36-1.25

¹For lower teeth, width of trigonid precedes width of talonid.

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VOLUME 45

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ARTICLE 7

PALEONTOLOGY AND GEOLOGY OF THE BADWATER CREEK AREA, CENTRAL WYOMING

Pt. 9. Additions to the cylindrodont rodents from the late Eocene

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Research Associate, Section of Vertebrate Fossils

In an earlier description of the late Eocene cylindrodonts present in the Badwater faunas, two specimens from locality 6 were referred to *Pareumys* sp. (Black, 1970a:209). At the time, no upper cheek teeth that might belong to that species were recognized. Later, while studying the ischyromyids in the Badwater faunas (Black, 1971), one maxillary fragment with M¹-M³ and three isolated upper molars were encountered, all from locality 6, which appear to pertain to *Pareumys*. This additional material establishes the presence of a new species of *Pareumys* at Badwater somewhat similar to *Pareumys milleri* known from the Myton Member of the Uinta Formation in northeastern Utah.

Since 1969 much additional work has been done at Badwater, particularly at locality 20 (Black, 1969) where a K/Ar date of 41.2 ± 1.4 m. y. has been obtained on a tuff immediately below the fossil-bearing silts. Included in the assemblage from locality 20 are at least two and possibly three species of cylindrodonts. Two species are represented by excellent jaws, and this material is described here.

The cylindrodonts from locality 20 are all somewhat more advanced than those from the other Badwater late Eocene localities, and this is

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seen in other taxa as well. This suggests that the fauna from locality 20 is somewhat younger than that from localities 5, 6, 7, Wood and Rodent. The date of 41.2 ± 1.4 m. y. is close to that suggested for the Uintan-Duchesnean boundary, 40 million years (McKenna, Russell, West, Black, Turnbull, Dawson, and Lillegraven, 1973). If this is indeed the case, the classic Uinta B and C faunas would be older, with Uinta B possibly at 45-46 m. y. and Uinta C at 43-44 m. y.

Specimens are in the Carnegie Museum of Natural History (CM) and Texas Tech University Museum (TTU-P) collections. This research was supported by National Science Foundation grants GB-7801 and GB-30840X and by the Institute of Museum Research, Texas Tech University. All measurements are in millimeters. When two transverse measurements are given, the first is the width across the protoloph or metalophid, the second is the width across the metaloph or hypolophid.

Family *Cylindrodontidae*
Genus *Pareumys* Peterson
Pareumys cf. *P. guensburgi*
Figures 1-4

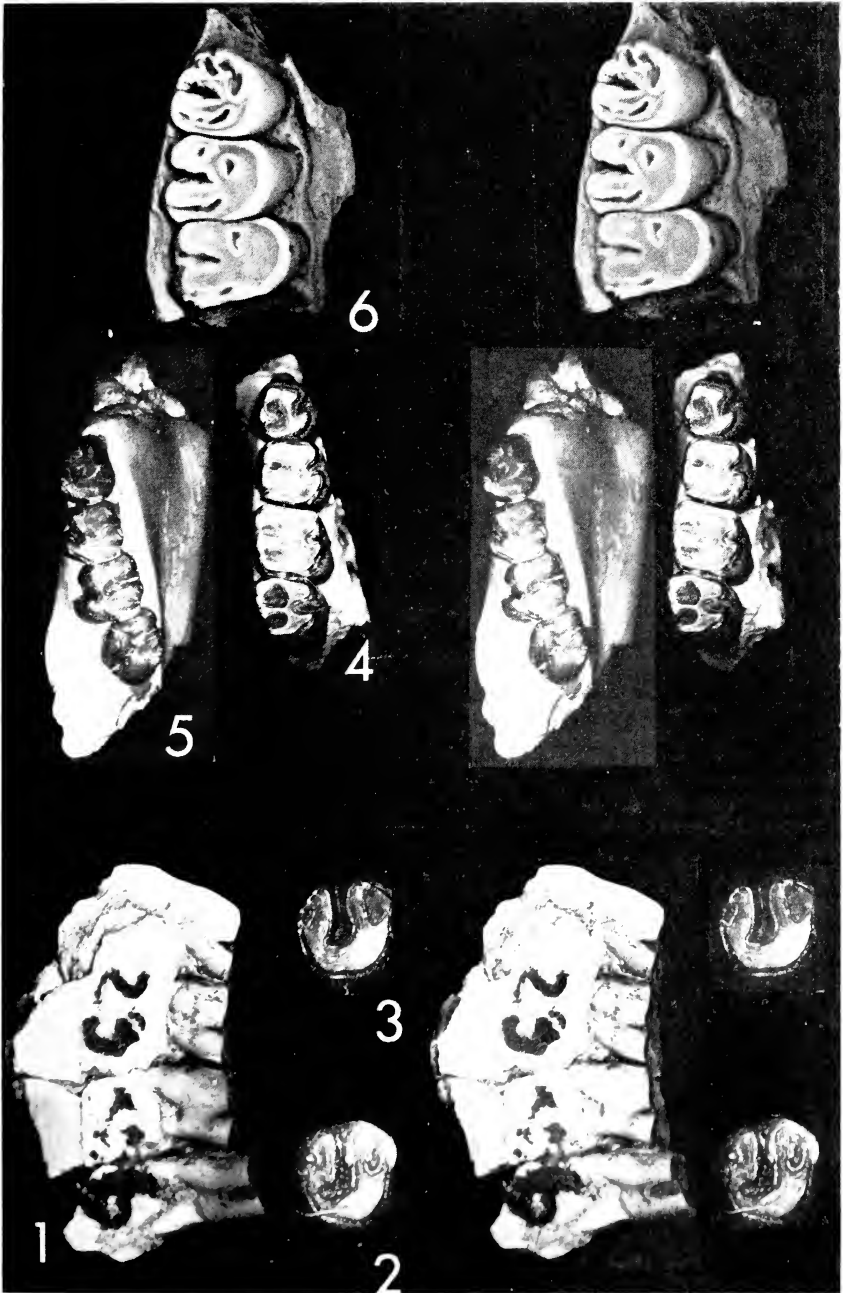
REFERRED SPECIMENS: CM 23806, RP₁-M₁; ; TTU-P 6118, RM¹⁻²; 6119, RM¹⁻²; 6120, LM₂.
HORIZON AND LOCALITY: Late Eocene, ?Duchesnean, all from locality 20, Hendry Ranch Member, Tepee Trail Formation.

DESCRIPTION: The lower cheek teeth here referred to *Pareumys guensburgi* (Black, 1970b) are so similar in size and morphology to the La Point type specimen as to be almost identical. The slight differences in measurements are easily attributable to differences in measuring technique. CM 23806 has both M¹ and M² extremely worn, even more so than in the type of *P. guensburgi*. On P₁ of the Badwater specimen the hypolophid is not complete as it is in the type specimen. In other features the lower cheek teeth agree completely.

The two upper molars are unilaterally hypsodont with a broad straight internal border that has no trace of separation of the protocone and hypocone down the lingual face of the teeth, quite in contrast to the condition in *Jaywilsonomys* (Ferrusquia-Villafranca and Wood, 1969). Both teeth are moderately worn, however, and there could have been a slight separation when unworn. On both upper molars the metalophid is incomplete with a valley between the metaconule and the internal face of the protocone-hypocone. The metaconule connects posteriorly to the posterior cingulum. A small pit is isolated at the posterobuccal corner of the teeth between the posterior cingulum and metacone. At the stage of wear rep-

→

Figs. 1-4. *Pareumys* cf. *P. guensburgi*. 1. Lateral view, CM 23806, x5. 2. TTU-P 6118, RM¹⁻², x5. 3. TTU-P 6119, RM¹⁻², x5. 4. CM 23806, RP₁-M₃, x5. Fig. 5, *Pseudocylindrodon* near *P. tobeyi*, CM 23805, LP₁-M₃, x5. Fig. 6, *Pareumys lewisi*, Type, CM 14407, LM¹-M₃, x5.



resented, the metaconule is rather indistinct within the metalophid but was certainly never as large as in *Jaywilsonomys*. There is no mesostyle on either tooth.

DISCUSSION: At the time Ferrusquia-Villafranca and Wood (1969) published their paper on *Jaywilsonomys* from the early Oligocene of Chihuahua, Mexico, the description of *Pareumys guensburgi* (Black, 1970b) was in press. There are a number of similarities between *P. guensburgi* and the smaller of the two species of *Jaywilsonomys*, *J. pintoensis*. Both species have cheek teeth that are higher crowned than those of other species of *Pareumys* and with hypoconids displaying a definite anterior torsion. However, the species are distinct in that there is no lingually displaced and separate hypocone on the molars of *P. cf. P. guensburgi*. Although the lower molars of all known specimens of *Pareumys guensburgi* are well worn, there does not appear to have been any metalophid (metalophid 11 of Wood) across the rear of the trigonid basin except in FMNH (Field Museum of Natural History) PM 14978 where there is a short protoconid spur on M_2 . In *Jaywilsonomys* the metalophid is interrupted, but distinct metaconid and protoconid spurs remain. These are evidently essentially absent in *P. guensburgi*.

Because of the absence of a distinct, lingually displaced hypocone on the upper molars, I prefer to retain the Utah and Badwater specimens in the genus *Pareumys*. They do, however, appear to be close to the possible ancestry of *Jaywilsonomys*, although too advanced in metalophid reduction to be in the main line of descent.

MEASUREMENTS IN MM. OF *Pareumys* CF. *P. guensburgi*

	TTU-P 6118	TTU-P 6119
RM ^{1 or 2}		
a-p	2.50	2.50
tr	3.05	3.20
	CM 23806	
P ₁ a-p	2.00	
tr	1.60	
tr	2.15	
M ₁ a-p	2.25	
tr	2.15	
tr	2.55	
M ₂ a-p	2.45	
tr	2.45	
tr	2.60	
M ₃ a-p	2.35	
tr	2.50	
tr	2.40	

***Pareumys lewisi*² new species**

Figure 6

TYPE: CM 14407, left maxillary fragment with M¹-M³.

HYPODIGM: Type and CM 16881, 16883, 19745, all upper molars; CM 15989 and 15990, lower molars.

HORIZON AND LOCALITY: Late Eocene, Uintan, all from locality 6, Hendry Ranch Member, Tepee Trail Formation.

DIAGNOSIS: Larger than *Pareumys milleri*; not as hypsodont as *P. guensburgi*; lophids of lower molars low; no distinct hypocone on M¹-M³; metaloph with connection to posterior cingulum and protocone.

DESCRIPTION: The upper molars are unilaterally hypsodont with the lingual crown height being about twice that of the buccal height. Unworn teeth showing little interdental wear are almost square in occlusal outline. The type, CM 14407, is of an old individual and shows considerable interdental wear. This combination of interdental wear with occlusal wear changes the occlusal outline from square to transversely elongate. There is no distinct hypocone, but the internal border is straight and swollen along its entire length. The anterior cingulum is raised into a rather high, heavy crest, and immediately behind it is a deep, very narrow valley between the anterior cingulum and protoloph. The protoloph passes straight across the crown of the tooth from the paracone to the protocone, and except for CM 19745 there is no evidence of a protoconule within this loph. The metaloph is short and joins the inner slope of the protocone through a very thin ridge about half way down the inner face of that cusp. The metaconule is large and is joined not only to the internal face of the protocone but also posteriorly to the posterior cingulum. With advanced wear two small lakes are formed. One lies between the metaconule, posterior cingulum and protocone. The central valley between the metaloph and protoloph is narrow but deep and opens onto the external face of the teeth. The mesostyle is variously developed. In one specimen it is quite small and fused into the posterior face of the paracone (CM 16883), whereas in the type and also in CM 19745 the mesostyle is separate from both the paracone and the metacone, and partially dams the central valley.

The third upper molar is the smallest of the upper molars, with a reduced metacone and posterior cingulum area. As on M¹ and M², the metaconule is quite large and joined to both the protocone and the posterior cingulum. The central valley between the protoloph and metaloph on M³ is completely closed buccally.

The lower molars have been described (Black, 1970a:209-211) and this description is repeated here:

"Both molars are low crowned and have low lophids, much lower than those of *Pseudocylindrodon tobeyi*. The hypolophids are somewhat lower than those of *Pareumys milleri* or *P. grangeri*. The two Badwater teeth are appreciably longer than wide, another *Pareu-*

²Named for Arnie Lewis, who found the type specimen.

mys character in contrast to *Pseudocylindrodont*. The hypoconids of *Pareumys* sp. are not swollen nor do they show any anterior torsion as they do in the higher-crowned cylindrodonts. The posterolophids are low and the hypoconulids indistinct. The central and posterior valleys are broad and shallow. There is no metastylid. On CM 15990 the posterior protoconid arm passes into the metaconid slope isolating the trigonid basin from the talonid. These two teeth are slightly larger than either the first or second molars of *Pareumys milleri* or *P. grangeri* and the cusps and crests of the Badwater specimens are somewhat lower than in the Uinta species. In all other respects, however, they are quite close to CM 2938, the type of *P. milleri*."

AFFINITIES: The relationships of the upper teeth here assigned to *Pareumys lewisi* were not recognized at the time the manuscript on the Badwater cylindrodont rodents was completed. In that paper (Black, 1970a) I assigned the two lower molars from locality 6 to *Pareumys* sp., but the upper molars were then thought to pertain to a new species of *Plesispermophilus* (Black and Dawson, 1966; Dawson, 1968:367). Therefore this material was not critically examined at the time of preparation of the manuscript on cylindrodonts. It is now obvious that these specimens do pertain to a cylindrodont rodent and the material is sufficient to warrant description of a new species of *Pareumys*.

Pareumys lewisi is a large species of the genus. Although not as large as *P. guensburgi* of the late Duchesnean (Black, 1970b), it is larger than *P. milleri*, *P. grangeri*, and *P. troxelli* (Burke, 1935) of the Uintan. Its cheek teeth are lower crowned than those of *P. guensburgi* and they display complete metalophids on the lower molars with no anterior twisting of the hypoconids. The upper molars are similar to those referred to *Pareumys* near *grangeri* by Wilson (1940, Plate 1, Figs. 4 and 5) but they are considerably larger. The lower molars are not as hypsodont as are those of *P. guensburgi*. In most respects *P. lewisi* appears to be closer to *P. milleri* than to *P. guensburgi*.

MEASUREMENTS IN MILLIMETERS

Pareumys lewisi

	CM 14407		CM 19745	CM 16883	CM 16881
M ¹ a-p	2.25	M ¹ or 2			
tr	3.25	a-p	2.20	2.30	2.35
		tr	3.00	3.10	3.00
M ² a-p	2.20				
tr	3.25				
M ³ a-p	2.25				
tr	2.90				
	CM 15989	CM 15990			
M ₁ or 2					
a-p	2.55	2.55			
tr	2.35	2.30			
tr	2.40	2.30			

Pareumys sp.

MATERIAL: CM 25405, RM₁-M₂; TTU-P 4885, RM₃ from locality 20.

DISCUSSION: The RM₁-M₂ is very badly worn. As far as can be discerned these two specimens are morphologically similar to the specimens referred to *P. guensburgi*. However, they are significantly larger than known material of that species. They may either represent a third species of *Pareumys* or merely an extremely large individual of *P. guensburgi*.

MEASUREMENTS IN MM.

	CM 25405	TTU-P 4885
M ₁ a-p	2.45	
tr	—	
tr	—	
M ₂ a-p	3.00	
tr	2.80	
tr	2.85	
M ₃ a-p		3.00
tr		2.70
tr		2.50

Genus *Pseudocylindrodon* Burke
Pseudocylindrodon near *P. tobeyi*

Figure 5

REFERRED SPECIMENS: CM 23805, LP₁-M₃; TTU-P 4882, RM¹⁻²; 6122, LM¹⁻²; 6121, RM¹⁻²; 4884, RdP₁; 4883, RM₁₋₂.

HORIZON AND LOCALITY: Late Eocene, late Uintan, all from locality 20, Hendry Ranch Member Tepee Trail Formation.

DESCRIPTION: The specimens from locality 20 are all slightly smaller than those previously described for *Pseudocylindrodon tobeyi* from the Wood and Rodent localities, closely approaching in size specimens of *P. medius* and *P. neglectus* (Black, 1965:12-13). In most characters of the occlusal surface these teeth show only the most minor changes from the conditions in *P. tobeyi*. The cheek teeth appear to be more hypsodont with the lingual valleys more nearly closed and the hypocone somewhat more swollen than in *P. tobeyi*. There is a strong hypolophid on P₄, as in *P. medius*, and as seen in one specimen of *P. tobeyi*. Metastylids are absent on the lower molars as in *P. tobeyi* and *P. medius*.

The portion of the mandible preserved in CM 23805 is quite similar to that of *P. medius*, although it is somewhat larger. The mandible is rather short and stout with only a weakly defined masseteric fossa, which terminates below the anterior end of M₂. The mental foramen is single, as in *P. medius*, rather than double, as in *P. neglectus*.

DISCUSSION: This sample is extremely close in morphology to the teeth of *P. tobeyi*, but the population represented appears to be some-



Fig. 7. *Pseudocylindrodon medius*, x10. CM 10954, LP₁-M₃.

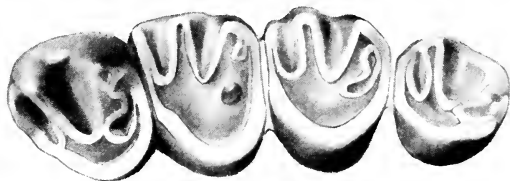


Fig. 8. *Pseudocylindrodon medius*, x10. CM 10000, LP⁴-M³.

what advanced over that known from the Wood and Rodent localities. There is every indication that this represents evolution in place over what is probably no more than a 1 to 2-million-year period.

In such characters as a decrease in size, increase in hypsodonty and greater closure of the lingual valley of the molars, this lineage is moving towards the condition seen in *P. medius* from McCarty's Mountain, Montana. *P. tobeyi* and *P. near P. tobeyi* also resemble *P. medius*, and differ from *P. neglectus* in the presence of a hypolophid on P₄, in the absence of metastylids on the lower molars, and in having a single mental foramen.

The sequence *Pseudocylindrodon tobeyi* to *P. near P. tobeyi* to *P. medius* appears to be an excellent example of phyletic speciation within a limited geographic area of northwestern Wyoming and southwestern Montana. The measurements given of *P. medius* are taken from an unpublished manuscript on the McCarty's Mountain rodents, and illustrations of *P. medius* (Figs. 7-8) are included for comparative purposes. It

would appear that most of the evolutionary history of *Pseudocylindrodon* has been restricted to the intermontane Rocky Mountain region covering a period of probably no more than 6-7 million years from approximately 43 or 44 million years to 36 or 37 million years ago.

MEASUREMENTS IN MM. OF *Pseudocylindrodon*

	<i>P. tobeyi</i> (Means)	<i>P. nr. P. tobeyi</i>	<i>P. medius</i> (Means)
M ¹ or ² a-p	1.92	1.71 (TTU-P 4882)	1.75
tr	2.11	2.28	2.20
dP ₄ a-p		1.90 (TTU-P 4884)	
tr		1.15	
tr		1.50	
P ₁ a-p	1.94	1.86 (CM 23805)	1.86
tr	1.23	1.33	1.21
tr	1.85	1.83	1.75
M ₁ a-p		1.75	1.71
tr	M ₁ or ₂	1.44	1.63
tr	a-p 1.96	2.03	1.79
	tr 1.69		1.90
M ₂ a-p		1.79	1.70
tr	tr 1.95		
tr		1.68	1.69
tr		2.00	1.99
M ₃ a-p	2.06	1.75	1.71
tr	1.81	1.69	1.58
tr	1.74	1.60	1.49

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VOLUME 45

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ARTICLE 8

STETHACANTHUS ALTONENSIS (ELASMOBRANCHII) FROM THE BEAR GULCH LIMESTONE OF MONTANA

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INTRODUCTION

Among the fossil fish remains described from the Mississippian of Illinois around a century ago were a series of compressed triangular spines that were assigned to the genera *Physonemus* and *Oracanthus*. The spines were thin-walled, concave anteriorly, and variably ornamented. Subsequent discoveries from the Mississippian of Ohio included a large series of unornamented spines pertaining to *Physonemus altonensis*, for which Newberry (1889) erected the genus *Stethacanthus*. The spines, which were crushed into various asymmetrical shapes, included two with portions of fins attached, which were thought to represent the pectoral fin spines of an unknown shark. While additional spines assignable to *Stethacanthus* were named by Hussakoff (1913) from the Mississippian of Kentucky, no additional information on the identity of *Physonemus* or *Stethacanthus* has emerged since then.

A field party from the University of Montana, working in the Middle Carboniferous, uncovered a male and a female *Stethacanthus altonensis* in the Bear Gulch Limestone, Tyler formation, Big Snowy Group, of Fergus County, Montana (Melton, 1971). The almost flawless male, MV 2830, consists of neural and visceral cranium, axial, and appendicular skeletons back to the level of the pelvic fin and of the middle of the second dorsal fin. The female, CM 23654, a & b, while more poorly preserved, lacks only the first dorsal fin and the tip of the tail. A Field

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Museum of Natural History party, working in Westphalian rocks of Indiana, obtained a female *Stethacanthus* seen on X-rays through shale, also lacking the tail. The Montana specimens form the basis of this report.

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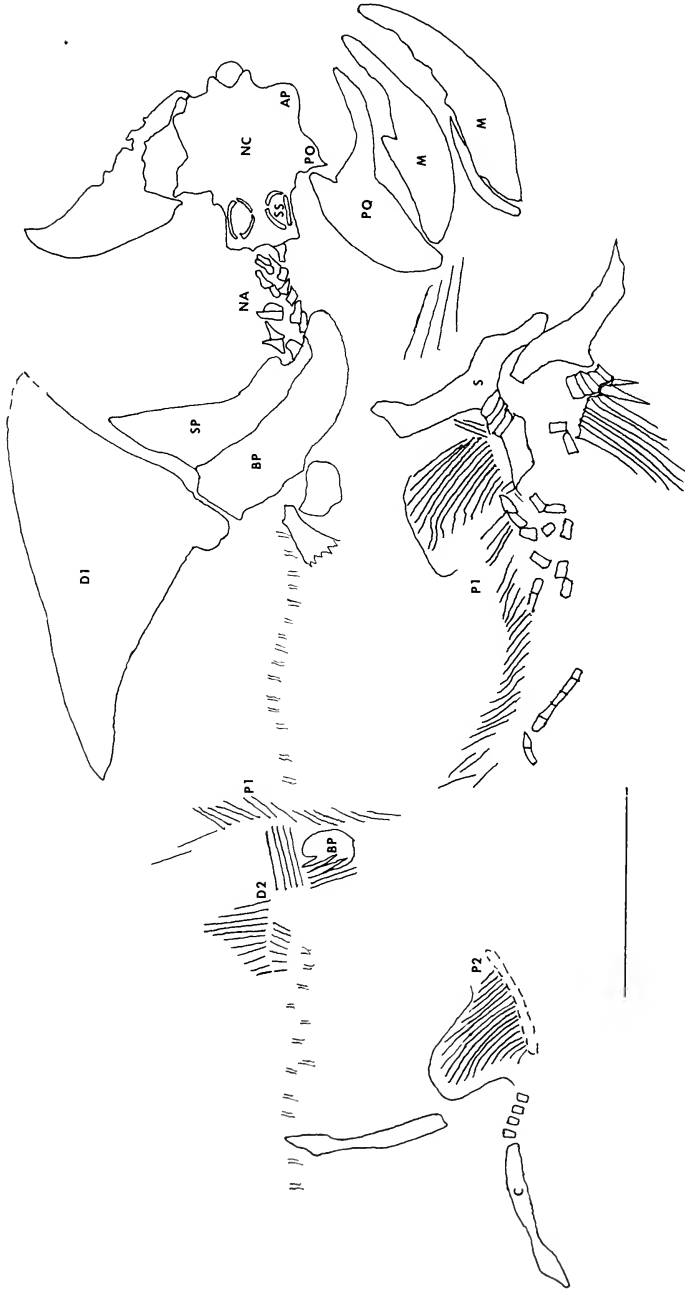
ABBREVIATIONS: AMNH, American Museum of Natural History, New York. CM, Carnegie Museum of Natural History, Pittsburgh. FMNH, Field Museum of Natural History, Chicago. MV, University of Montana Vertebrate collection.

SYSTEMATICS

There are almost as many classifications of Paleozoic chondrichthyan fish as there are taxa in this group represented by adequate specimens (Romer, 1966; Glikman, 1967; Patterson, 1965; Moy-Thomas, 1939; Moy-Thomas & Miles, 1971; Zangerl, in press). New taxonomic schemes have tended to be simply rearrangements based upon the same materials, the fossil record of the class consisting largely of isolated spines and teeth. The recently collected Bear Gulch limestones contain a chondrichthyan fauna of unprecedented diversity, superbly preserved, with at least ten taxa represented by whole individuals. *Stethacanthus* is the only Bear Gulch material that resembles a true selachian. Until study of the remaining forms is complete and published, a few remarks are necessary to justify the classification used below.

The term Elasmobranchiomorpha (Miles, 1971) signifies a relationship between Arthrodira and Chondrichthyes. The Bear Gulch fauna shows that there is no basis in fact for such classification, as the arthrodirids are now understood. There is a clear justification for retaining a subclass Elasmobranchii to separate elasmobranchiate and operculate chondrichthyans. Ordinal assignments within the Paleozoic Elasmobranchii, like the Cladodontida (Glikman, 1967), based solely upon the form of the pectoral fin, prove to be meaningless when other character complexes are known, e.g., the nature of the dorsal fins, caudal fins, and even the jaws. Zangerl's suggestion of an anacanthous division (see

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 Fig. 1 *Stethacanthus altonensis*, M.V. 2830. Abbreviations: AP, antorbital process; BP, basal plate; C, clasper; D1, first dorsal fin; D2, second dorsal fin; M, Meckel's cartilage; NA, neural arches of first vertebrae; NC, neurocranium; P1, pectoral fin; P2, pelvic fin; PO, postorbital process; PQ, palatoquadrate; S, scapulocoracoid; SP, first dorsal-fin spine; SS, semicircular canals. Scale is 5 inches. Other pelvic fin omitted for clarity.



discussion below), is basically a slight rearrangement of Glikman's (1967) orders Cladoselachida and Cladodontida, and is adopted here informally and provisionally. *Stethacanthus* represents an experiment in elasmobranch evolution that is significantly divergent enough to warrant family-level separation.

Class Chondrichthyes
Subclass Elasmobranchii
Division Anacanthida Zangerl, in press
Family **Stethacanthidae**, new family

DIAGNOSIS: Elasmobranchii with first dorsal spine followed by radiating radial supported fin, second dorsal fin with spine vestigial or absent, radials along the axis of the pectoral fin, jaw suspension amphistylic.

TYPE GENUS: *Stethacanthus*, Newberry, 1889, only genus.

Family Stethacanthidae
Genus *Stethacanthus* Newberry, 1889

TYPE SPECIES: *Physonemus altonensis* St. John and Worthen, 1875.

DIAGNOSIS: A cladodontoid shark with a short rostrum, broad supraorbital region, and short otic region. Palatoquadrate cartilage with a high otic ramus articulating with the postorbital process; hyomandibular narrow. Teeth on the jaws cusped, of cladodont type, cusps fluted with the central cusp longest, the lateral cusps of moderate length and the intermediate cusps very small. Scapulocoracoid of normal selachian type, pectoral fin composed of 5 (10?) narrow anterior basals, a broad basal plate and a long segmented metapterygial axis; radials unjointed, long and gently tapering outward in the basal portion, uniformly short and blunt along the lateral edge of the metapterygium, and very thin along the mesial edge of the metapterygium. First dorsal fin with a large, thin-walled compressed spine, unornamented and concave anteriorly, fitted over a long basal plate and articulating at its base with the apex of a high triangular fin. Second dorsal fin with a very small, anterior basal plate apparently lacking a spine, followed by a series of basidorsals, each of which supports one radial. Caudal fin with strong hypochordal lobe, epichordal lobe with rhombic neural arches and thin neural spines, vertebral column well sheathed in calcification back to the level of the first dorsal spine and with short neural arches, very poorly calcified posteriorly. Entire dorsum of head and dorsal edge of first dorsal fin covered with enlarged single cusped denticles, the bases of which are fitted mosaically; no shagreen elsewhere in skin. Secondary sexual differentiation present, the first dorsal fin and spine of the male twice the size of that of the female, and the denticle belt on the dorsal fin of the male bearing a median row of elongate denticles.

INCLUDED SPECIES: *S. altonensis*; *S. exilis* Hussakoff, 1913; *S. humilis* Hussakoff, 1913.

GEOLOGIC RANGE: Lower Mississippian through Middle Pennsylvanian, of Ohio, Kentucky, Illinois, Indiana, Iowa, Oklahoma, and Montana.

Stethacanthus altonensis (St. John & Worthen) 1875.

Physonemus altonensis St. John & Worthen, 1875.

Stethacanthus altonensis Newberry, 1889.

Stethacanthus tumidus Newberry, 1889.

Stethacanthus productus Newberry, 1897.

Stethacanthus compressus Newberry, 1897.

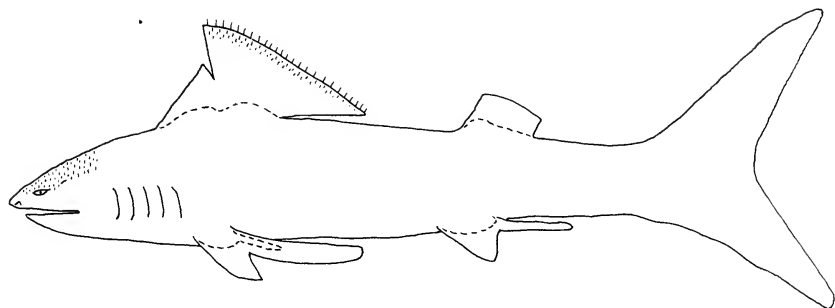


Fig. 2 *Stethacanthus altonensis*, composite restoration. Approx. 1/11 natural size.

TYPE SPECIMEN: FMNH UC 27404, St. John and Worthen (1875), Pl. 19, Fig. 1, the first of two illustrated syntypes, is hereby designated the lectotype of *S. altonensis*.

REFERRED SPECIMENS: MV 2830, male; CM 23654, female; FMNH PF 2207, female.

DIAGNOSIS: Largest species of genus.

DISCUSSION: The genus *Stethacanthus* was established for a series of large thin-walled, cartilage-cored spines from the Mississippian of the mid-continental United States. Distortion of the spines resulting from decomposition of the cartilage and subsequent compression during burial was evidently common, and generally produced a distinct pseudoasymmetry. This asymmetry led Newberry (1889) to believe that the spines were from pectoral and pelvic fins, a belief that is dispelled by the intact specimens (Fig. 1).

Differences in the size and shape of the spines were the basis for specific differentiation in the absence of external ornamentation. Most differences in shape between specimens representing different "species" is attributable to postmortem distortion. Differences in size may be attributable to age or sexual dimorphism. Newberry (1889) established the genus *Stethacanthus*, designating *Physonemus altonensis* St. John and Worthen (1875) as the type species. Newberry (1889) also established the species *S. tumidus*, based upon a series of spines from the Ohio Mississippian. The spine of MV 2830, the male, is almost identical to the type specimen of *S. altonensis* FMNH UC 27404, as well as to the cotype of *S. tumidus* Newberry, AMNH 212. The spine of FMNH PF 2207, a female very slightly larger in head length than MV 2830, is half the size of the latter although not differentiable on the basis of shape.

The whole specimens, therefore, fit the first illustrated and named specimen of *Stethacanthus altonensis* (St. John and Worthen). *S. tumidus* Newberry cannot be distinguished from *S. altonensis*, and further, the present lack of a valid morphological basis for distinguishing one species of *Stethacanthus* from another suggests that most named species of *Stethacanthus* should be considered synonyms of *S. altonensis*. *S.*

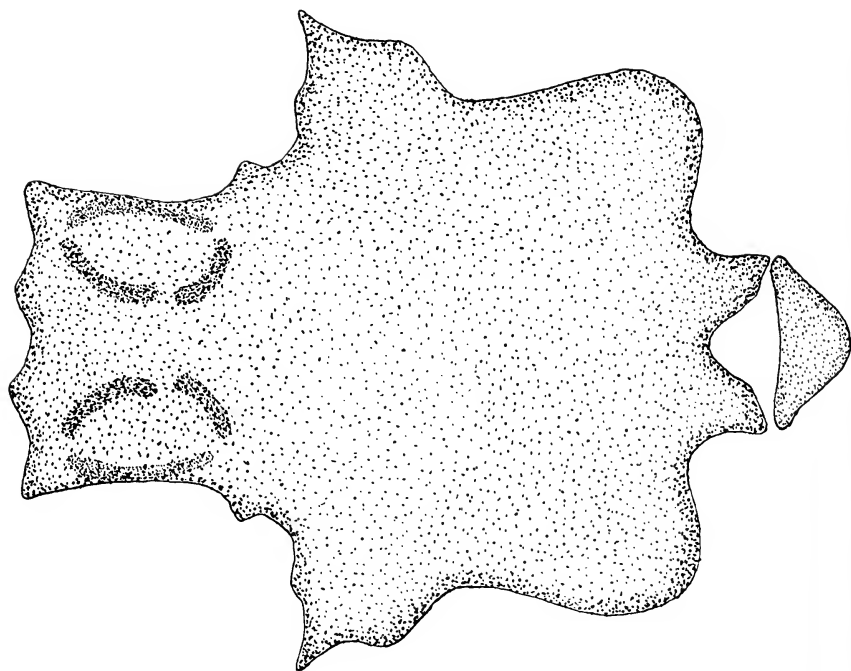


Fig. 3 *Stethacanthus altonensis*, M.V. 2830, chondrocranium, dorsal view.

humilis and *S. exilis* (Hussakoff, 1913) are too small to be safely placed into synonymy, however, and are provisionally retained.

DESCRIPTION

HEAD: The chondrocranium (Fig. 3), as revealed from the dorsal aspect, is distinctively different from those of contemporaneous elasmobranchs. The preotic portion of the braincase is twice the length of the otic region. There is a short, rounded, and distinct rostrum, behind which the antorbital process is sharply pointed distally, and extends almost as far from the midline as does the postorbital process. The interorbital wall forms a deep concavity that is almost completely roofed by supra-orbital cartilage. The postorbital process is prominent and bears a well-developed articular fossa for the otic ramus of the palatoquadrate distally along its posterior margin. The process is notched at the base, possibly for the passage of the spiracular canal. The skulls of the Montana specimens are dorsoventrally flattened and do not show any indications of nerve foramina. All six semicircular canals are present in the male, as are the vestibules and the endolymphatic fossa. There are no appreciable differences in proportions between the otic region of *S. altonensis* and the modern *Squalus acanthias*.

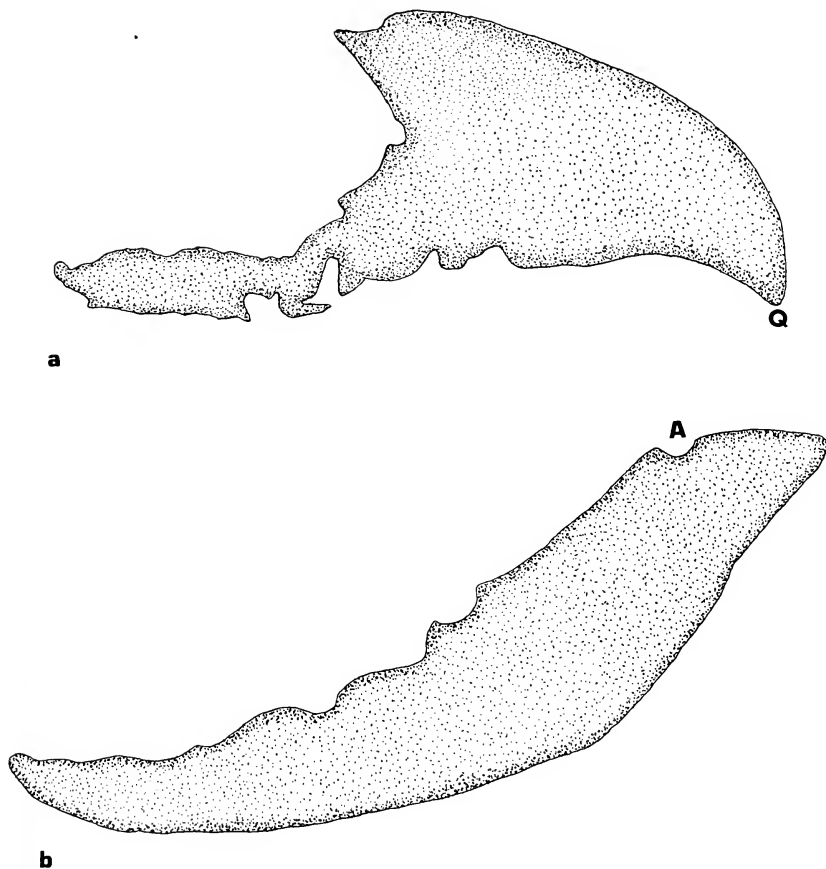


Fig. 4 *Stethacanthus altonensis*, M.V. 2830, a. palatoquadrate, left. Q-quadrate process; b. Meckel's cartilage, left. A-articular fossa.

The palatoquadrate (Fig. 1, 4a) is $2\frac{1}{2}$ times as long as its maximum height at the otic ramus. The palatine ramus represents slightly less than half the length of the element, and is quite low, while the posteroventral corner of the orbital margin bears an elevated, slightly anterodorsally concave facet or basal process. There are prominent grooves along the anterior two-thirds of the ventral margin of the palatoquadrate, for the reception of at least seven tooth families. No teeth are found in place, however. The quadrate process forms a boss on the posteroventral corner. Meckel's cartilage (Fig. 4b) is low in profile, articulates with the palatoquadrate cartilage at its posterodorsal corner, and bears teeth and grooves for tooth families for at least two-thirds of its length.

While there is a distinct branchial region visible in each specimen,

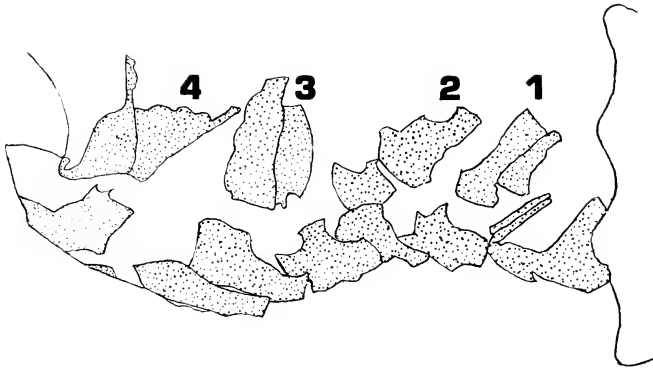


Fig. 5 *Stethacanthus altonensis*, M.V. 2830. First vertebrae, with neurocranium to the right.

few details can be made out except for denticles and a substantial ceratohyal. The hyomandibular is narrow proximally and narrower distally. The hyomandibular probably fitted into a groove on the posterodorsal edge of the mesial surface of the palatoquadrate, as in *Acanthodes* (Miles, 1968).

AXIAL SKELETON: The vertebral column is strongly sheathed in calcifications from the occiput to a point under the origin of the first dorsal-fin spine, and weakly calcified with very fine rhombs from there back to the beginning of the tail. The first five vertebrae have moderately high neural arches topped by short neural spines at the rear of each arch. Intercalary cartilages, if present, were not calcified. The centra themselves have a thin film of calcification, indicating some constriction of the notochord, but the details are not clear. Low basapophyses are sturdily calcified and extend the length of the centra. Posterior to the dorsal spine, the form of the vertebrae is not preserved, but the neural spines seem to maintain a uniform height at least back to the second dorsal fin.

DORSAL FIN: The first dorsal fin (Fig. 6) constitutes one of the strangest features of this remarkable fish. The spine, as illustrated by Newberry (1889, pls. 24, 25) and St. John and Worthen (1875, Pl. 19) is roughly a broad right triangle with the hypotenuse concave anterodorsally, the base lying over a cartilaginous plate for its entire length, and a vertically oriented articulation for the fin along the height of the triangle. The outer surface of the spine is unornamented, and a prominent horizontal shoulder marks the insertion of middorsal musculature upon the front of the spine. Articulation of the spine with the fin is accomplished in two ways. At the rear of the basal plate is a very strongly calcified process that receives a convex condyle from the fin,

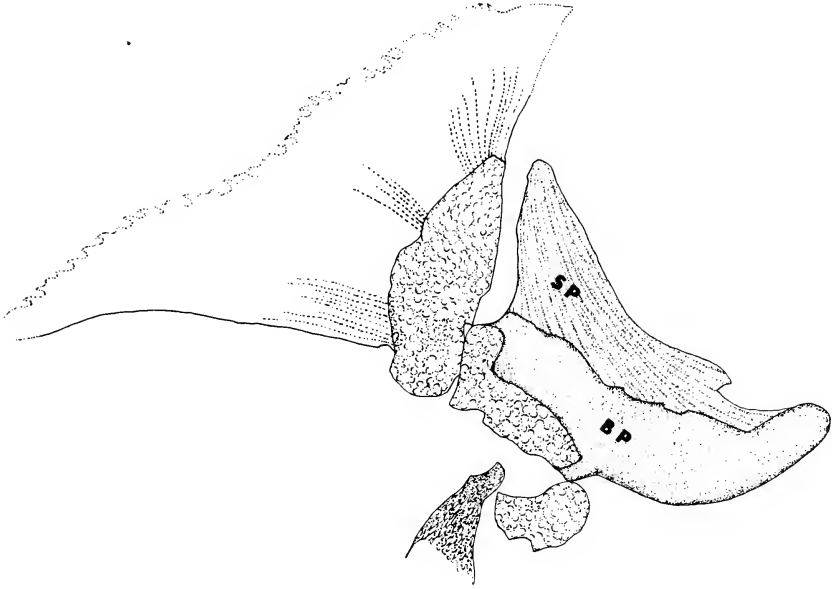


Fig. 6 *Stethacanthus altonensis*, M.V. 2830, first dorsal fin and spine. Abbreviations are as in Fig. 1.

apparently allowing a degree of anteroposterior rotation of the body of the fin in the midsagittal plane. Above the basal plate the dorsal half of the posterior margin of the spine is tongued to fit a presumed groove along the anterior edge of the fin, allowing lateral deflection of the fin. The fin itself is also triangular, with the apex directed anteroventrally and produced into a convex articular condyle. The fin is composed of long, thin, calcified tubes radiating from the apex, sheathing a calcified cartilage core along the anterior edge of the fin. The posterodorsal margin bears a belt of up to nine rows of enlarged dermal denticles, the bases of which are arranged mosaically (see below).

The second dorsal fin is disturbed and incomplete, and differs strikingly from the first. A small calcified plate lies at the anterior end of the fin. Posteriorly the distal radials increase gradually in thickness and height. The radials are each supported by a basidorsal, of which there are at least 24 in the Montana female. There is no evidence of a discrete spine.

PECTORAL GIRDLE AND FIN: The scapulocoracoid cartilage is typically selachian, short and broad dorsal to the narrow articular process, with a ventral ramus narrowing between the articular process and the midline.

The basal elements of the fin (Figs. 7, 8) consist of 5 (10?) narrow

basals increasing in length posteriorly, followed by a large pentagonal basal plate. The basal plate is followed by an axis of 16 elements of approximately equal lengths but decreasing in width to thin rods at the posterior end. The first 10 radials of the body of the fin are supported by the anterior basals, the remaining 6 are supported upon processes arising from the basal plate, and all taper gradually toward their tips. Each axial element supports two blunt radials laterally, and an undetermined number of very fine radials mesially.

The pectoral fin is similar to that of *Cladodus nielsoni* (Schaeffer, 1967) in general form. It differs in most details, as in the distribution of



Fig. 7 *Stethacanthus altonensis*, M.V. 2830, pectoral fins and girdles, as preserved. A-articulation.

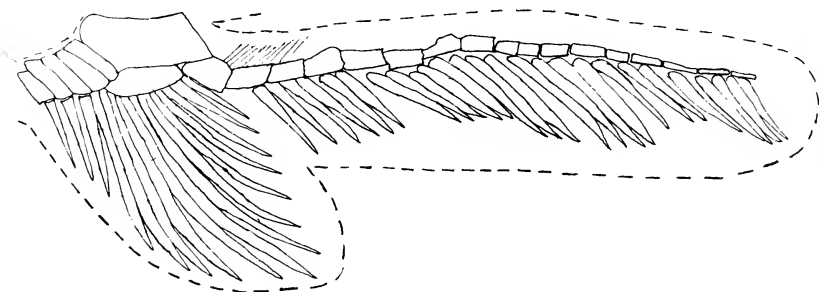


Fig. 8 *Stethacanthus altonensis*, M.V. 2830, right pectoral fin, restored.

radials relative to supports in the body of the fin, the presence of 7 more axial elements, and in the presence of radials along both the lateral and mesial edges of the axis of the fin.

The presence of a complete complement of axial radials clearly indicates that in this expression of the cladodont type of fin the axis was completely free from the body wall.

PELVIC FIN: One pelvic fin and two claspers of the male are well preserved, the girdle and other pelvic fin having been folded and crushed. The pelvic fin (Fig. 1) is somewhat smaller than the basal lobe of the pectoral fin, and consists of 18 unjointed, tapering radials. The clasper (Fig. 9) is separated from the body of the fin by about four blocks of calcified cartilage. While the clasper is evidently a compound structure, the precise morphology of its parts is obscured because of crushing.

CAUDAL FIN: The endoskeleton of the caudal fin (Fig. 10) is of heterocercal design and separated into discrete epichordal and hypochordal lobes. The hypochordal lobe consists of about 15 apparently unjointed, broad radials supported upon thick haemal spines. There is a slight central region of 10 thin haemal elements, the first four of which support short, thin radials. The notochordal axis is capped by more than 20 short, thick, rhombic neural arches, to the edge of the slab, each of which was overlain by a long, stout, neural spine laid back at a steep angle.

The tail is similar to that of *Cladoselache* in the presence of rhombic neural arches overlain by spines, although the *Cladoselache* condition is far more specialized. In form and general outline, the tail of *Stethacanthus* resembles that of *Ctenacanthus costellatus* (Glikman, 1967), which also shows completely separate epichordal and hypochordal lobes, indicating a deeply forked and almost symmetrical outline. The tail of *Stethacanthus* shows more structural unity of the epichordal lobe than that of *Ctenacanthus*, and approaches a functionally homocercal condition (Lund, 1967).

TEETH AND DENTICLES: The teeth of *Stethacanthus altonensis* (Fig. 11a) are typically cladodont in form, 5-cusped, the central cusp largest, the two extreme lateral cusps smaller, and the intermediate cusps very small. The cusps are strongly striated vertically, with the striations running from the base to the crown of each cusp, and finer on the labial sides of the cusps than on the lingual sides. The cusps are rounded in cross section, and curve inward slightly. They most closely resemble those of *Cladodus turritus* Newberry and Worthen, 1866.

Branchial denticles (Fig. 11b) are compressed, strongly striated vertically, posteriorly curved, and a very small, thin, flat base. Successive cusps are added posterior to the older cusps and may overlap the older cusps at the base.

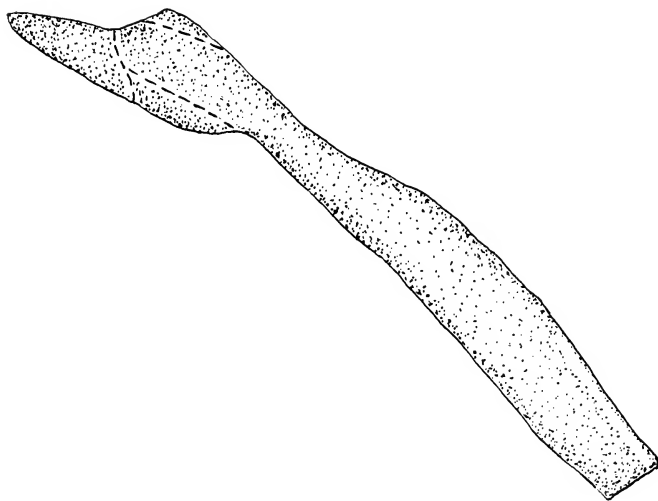


Fig. 9 *Stethacanthus altonensis*, M.V. 2830, clasper.



Fig. 10 *Stethacanthus altonensis*, C.M. 23654, Caudal fin, restored.

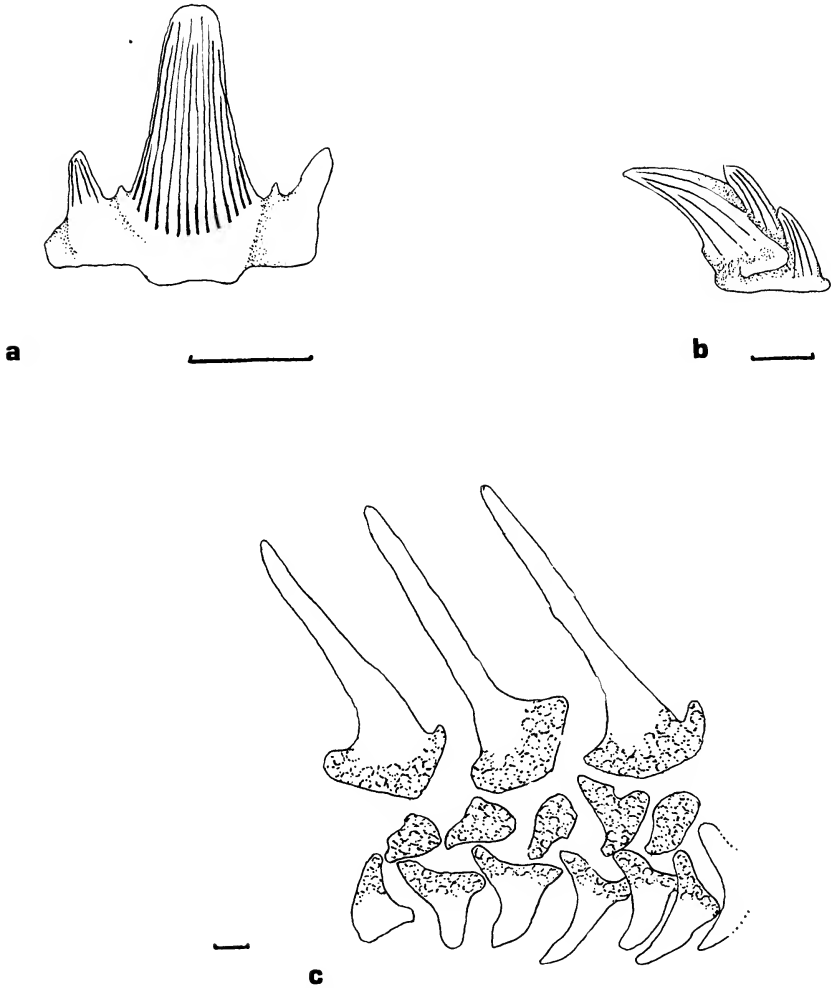


Fig. 11 *Stethacanthus altonensis*, M.V. 2830; a., tooth; b, branchial denticle; c, portion of denticle belt from middle of first dorsal fin. Scale is 2 mm.

There is no trace of normal shagreen denticles like those found in the skin of some sharks. *Stethacanthus* is peculiar among known sharks, however, in having modified denticles covering the dorsal surface of the head and the upper edge of the first dorsal fin. The denticles on the head are relatively uniform in size, about as high as the central cusps on the teeth, rounded in cross section, somewhat curved posteriorly, and are smooth and monocuspid. The cusps are higher than the width of their

bases. The denticles on the edge of the dorsal fin are also smooth and monocuspid, and have polygonal bases fitted together in a mosaic pattern (Fig. 11c). The belt of denticles is between seven and nine denticles wide at the anterior end of the fin, tapering to four or five denticles wide at the posterior end. In the male, the lateral denticles are each shorter than the width of their base and are strongly curved posteriorly. The denticles increase in height and decrease in curvature toward the midline of the fin, so that the denticles of the midline row achieve a height of approximately 2 cm. These denticles are straight and bluntly pointed. The remarkable differentiation of the median row of denticles is not present in the female, which reinforces the presumed secondary sexual nature of the size difference in the first dorsal fins and spines. The precise function of the denticles on the top of the head and the edge of the fin is not known.

FORM AND FUNCTION OF *Stethacanthus*

Stethacanthus represents a significantly different design from previously known Paleozoic sharks in the form of pectoral and first dorsal fins. The presence of radials along the axis of the pectoral fin contrasts strongly with the condition in the ctenacanth sharks and previously reported cladodont sharks (Schaeffer, 1967), and is not similar to the archipterygial fin of xenacanth. Unlike the latter type of fin, a new functional unit has been added posterior to the unaltered lifting plane (Gray, 1968). The plane pectoral fin chiefly controls vertical pitch, more specifically acting to lift the anterior part of the body to compensate for lift posterior to the center of gravity generated by a heterocercal tail (Gray, 1968, p. 69).

The motion of the axial portion of the fin would be limited by the fin web chiefly to a vertical plane, producing either elevation or depression of the fin axis relative to the fish. Segmental axial musculature located on the dorsal and ventral surfaces of the axis would be axial elevators and depressors. It would be reasonable to assume that radial musculature in the form of extensors and flexors would be present superficially on dorsal and ventral surfaces. The action of the radial musculature would serve to widen or narrow the surface area of the fin presented to the water.

Depression of the axial lobes of both pectoral fins would cause the fish to pitch downward in forward travel, all other control surfaces being neutral. Elevation of both axial lobes would produce an elevation of the head, while unilateral action of one fin could produce a banked turn. It is improbable that the axial lobes functioned independently of the remaining control surfaces of the body, but they are seen as analogous in action to the ailerons of an airplane.

The *Stethacanthus* type of pectoral fin represents a morphological intermediate between the plane pectoral fin of *Cladosepache*, for example, and the functionally quite different archipterygium of the pleuracanth. The pleuracanth pectoral fin, articulated by a proximal joint and lacking a plane portion, seems to have been modified for sculling in concert with a diphycercal tail and elongate dorsal fin, as a supplement to anguilliform swimming. The association between a reduction of heterocercality of the caudal fin and freeing of the pectoral fins from their function of compensation in pitch has recurred in the crossopterygians, lepidosirenid lungfish, and among the actinopterygians, as well as among the elasmobranchs. There is no indication that such a functional transition has occurred or is incipient in *Stethacanthus*, however.

The pectoral fin of *Stethacanthus* is most similar to that of *Cladodus nielsoni* (Schaeffer, 1967), differing from it chiefly in the possession of a radial-supported fin along the axis. It is clear that the axis of the *Stethacanthus* pectoral fin was free from the body wall, and it is tempting to suggest a similar condition for the pectoral fin of *Cladodus*. No information exists to support this idea, and there seems little functional benefit in the possession of a whiplike axis, but it is highly improbable that the axis of a pectoral fin would be anchored in the body wall, where it would serve no function at all.

A fixed first dorsal fin provides neutral stability, allowing changes of direction through small angles without compensation (Gray, 1968). *Stethacanthus* differs in one important regard from the elasmobranch model in that the fin was vertically hinged upon the spine and motion was limited to horizontal rotation about the anteroventral apex. Musculature probably originated upon the base of the spine and inserted radially upon the fin, to adduct and abduct the fin. The anterior end of the first dorsal spine lay approximately above the sixth vertebra, quite close to the skull. The center of gravity of the fish must have been located posterior to the joint between the spine and the fin. It is clear that the first dorsal fin of *Stethacanthus* must have played an active part in turns, in contrast with the fixed fin of other sharks.

The mechanics of turning involved the power provided by body and tail motion, and control surfaces anterior to the center of gravity, in the form of pectoral and first dorsal fins. These features all indicate an adaptive experiment towards high maneuverability in a fusiform fish, an unusual combination. Stability in tight turns would seem to be a real difficulty under this particular design. It does not seem to help the stability problem significantly that the caudal fin approaches homocercality somewhat with the strengthening of the ventral lobe. In the absence of rigorous hydrodynamic tests, one can only speculate upon the complexity of this design in comparison with the elegant, if somewhat less maneuverable, design of modern sharks.

RELATIONSHIPS

Knowledge of whole-body morphology of Paleozoic elasmobranchs is so limited that little taxonomic meaning can be gleaned from any single form. Zangerl (in press) grouped them into organizational complexes, a useful first step in understanding their early radiation. *Stethacanthus* is placed in the anacanthous division, and five other groups are delimited to include roughly all major aspects of the known radiation. Of the six divisions, the phalacanthous, xenacanthous, and edestid seem to be natural assemblages of closely related taxa; the bradyodonts are chiefly unknown; a *Squatina*-like form (Lund and Zangerl, 1974) is not clearly related to any other group; and the anacanthous group contains a diverse assemblage of individualistic genera.

The phalacanthous forms fit Schaeffer's (1967) morphocline leading to the modern sharks. They have two narrow, fixed, dorsal-fin spines followed by large basal plates, a relatively narrow based pectoral fin trending toward the tribasal type, a complete squamation of mosaically arranged placoid denticles, and a simple heterocercal caudal fin. Secondary sexual differentiation is unknown. *Ctenacanthus* and *Tristychius* are typical phalacanthus.

The anacanthous group, as typified by "*Cladodus*," *Cladoselache*, *Stethacanthus*, "*Physonemus*" *falcatus*, and *Symmorium*, has a dorsal spine or spines lacking an orthodontine surface; may tend toward specializations of the first dorsal fin or spine, or both, with retention of a basidorsal-radial second dorsal-fin support system; toward a long, free axis of the pectoral fin; and reduction of the squamation to localized, specialized patches. Secondary sexual differentiation is present, at least in *Stethacanthus*.

The xenacanthids show specialization in the position of the first dorsal-fin spine, merger of probably primitively basidorsal-radial supported first and second dorsal fins, tends toward transformation of the free pectoral axis into an archipterygium, reduction or elimination of the squamation, a diphyrcercal tail, and no known secondary sexual differentiation.

The suspensorium of all three groups is amphistylic, and the feeding mechanism is essentially similar throughout. All possess teeth derivable from a coronodontid design, if this is primitive, and two possess cladodont teeth. While the braincases differ in proportion (Schaeffer, 1967; Romer, 1964), they are all "shark-like." *Bandringa rayi* (Zangerl, 1969), a long-snouted form and an undescribed Bear Gulch batoid-like form, both phalacanth derivatives, are extremes within this design. The three groups share this suite of characters in common, and share them with no other chondrichthyan group. This assemblage comprises the subclass Elasmobranchii.

Stethacanthus demonstrates derived states for most of the character complexes in the subclass that are not associated with the basic predacious feeding mechanism. Ancestral squamation was undoubtedly complete, and probably without significant sexual differentiation. Development of the free pectoral axis into a separate functional unit complete with rays is advanced only slightly over the condition in *Cladodus nielseni* (Glikman, 1967). The rather unusual dorsal-fin spine could be derived from something like that of *Cladoselache*. The presence of radials in the first dorsal fin, and basidorsals and radials in the second dorsal fin compares with the xenacanth condition, and is also found in *Chondrenchelys* (Moy-Thomas, 1939) and possibly in chimaeroids (Glikman, 1967). There seems to be no reason to believe that the phalacanth condition is primitive for either the Chondrichthyes or for the Elasmobranchii.

SUMMARY

Stethacanthus altonensis (St. John and Worthen), first described as a spine genus from the Carboniferous of the United States, is an anacanthous shark of specialized design. The originally described spine is the first dorsal fin spine, which is followed by a mobile, triangular fin of radiating elements. The second dorsal fin lacks a distinct spine, and is of basidorsal-radial construction. The chondrocranium is proportioned as in the modern *Squalus*, the suspensorium is amphistylic and the teeth are cladodont. The pectoral fin is cladodont in design, but the axis has two radials for each segment laterally and a large number of fine radials mesially. The axis is a functionally separate part of the fin. Claspers are present in the male. The caudal fin has a strong ventral lobe of thick, hypochordal radials, while the dorsal lobe is supported by short, well-calcified neural spines. The dorsal surface of the head and the posterodorsal edge of the first dorsal fin are covered by monocuspid denticles, which are lengthened along the midline of the fin in the male. The first dorsal fin and spine are considerably larger in the male than in the female.

Adaptations in pectoral and first dorsal-fin structure are believed to center around increased maneuverability. Comparisons with other chondrichthyans leads to the conclusion that a basidorsal-radial dorsal fin structure may be primitive for the Chondrichthyes.

The unusual adaptations of *Stethacanthus* are a strong indication of a more varied adaptive radiation among Paleozoic sharks than has heretofore been suspected.

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ARTICLE 9

PALEONTOLOGY AND GEOLOGY OF THE
BADWATER CREEK AREA, CENTRAL WYOMING

Part 10. A late Paleocene mammal fauna
from the Shotgun Member of the
Fort Union Formation

LEONARD KRISHTALKA¹, CRAIG C. BLACK², AND D. W. RIEDEL³

A small outcrop of the Fort Union Formation along Badwater Creek at the western end of Cedar Ridge, T. 39N., R. 89W., was first noted by Tourtelot in 1953. This occurrence of Fort Union sediments was mentioned by Keefer (1961:1315; 1965a: A29) and was described as being some 1600 feet thick with the base of the section terminated by faulting and the top truncated by sediments of early Eocene age. In 1961 Keefer noted a fossil plant locality in this section, but no vertebrates were known to occur in the Shotgun Member as exposed at this locality. Gard (unpublished thesis completed in 1969), mapped the Shotgun outcrops, which extend northwest along the Cedar Ridge Fault into the SW-1/4, Sec. 9, T. 39N., R. 89W.

In 1963 fossil vertebrates of Paleocene age were first discovered along Badwater Creek just east of the Natrona-Fremont County line in the Shotgun Member (erroneously called the Shotgun Butte Member by Black and Dawson, 1966: 301, 302) of the Fort Union Formation. Using washing techniques (Black and Dawson, 1966) two to three tons of matrix from this locality have now been washed, and some four hun-

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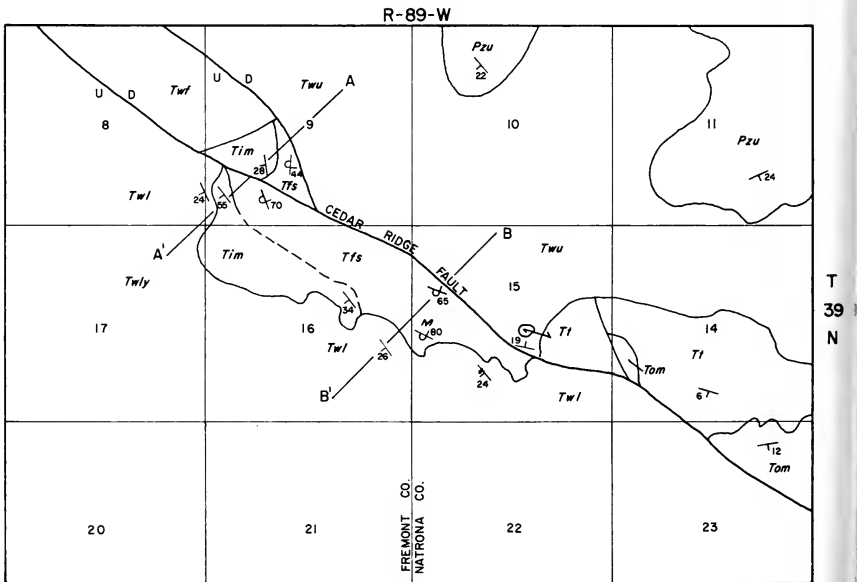
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dred mammalian specimens have been recovered, together with shark teeth, osteichthyan vertebrae, crocodylian fragments, various gastropods, and pelecypods and reworked ammonite fragments.

GEOLOGY OF THE FORT UNION FORMATION

In the vicinity of the vertebrate fossil locality (SW 1/4, Sec. 15, T. 39N., R. 89W.) the overturned beds of the Shotgun Member crop out (Text-fig. 1) as a narrow band of deeply dissected siltstones, claystones, and sandstones. In the lowest 250 feet of outcrop, yellowish-gray sandstones and silty sandstones form several sharp low ridges. Other lenticular sandstones are widely scattered in the upper exposures. The siltstones and claystones are predominantly light gray to olive gray but some beds are dark reddish-brown. Weathering gives the outcrop a general grayish-orange aspect. Some of the siltstones contain limonite-filled worm burrows. Carbonized leaf fragments are common in others. These outcrops are overlain by coarse boulder conglomerates in the Lysite Member of the Wind River Formation, with about 90 degrees of angular unconformity and over 120 feet of erosional relief, but farther to the northwest the same sequence of Shotgun strata is overlain



Text-fig. 1. Sketch map showing relationships of the Shotgun Members of the Fort Union Formation (TFs) to the Indian Meadows (Tim), Tepee Trail (Tt), and Wind River (Twl, Twly and Twu) formations. Tertiary "Oligo-Miocene" and Palaeozoic undifferentiated are also indicated. The vertebrate faunal locality is indicated (M) in Section 15, T39N., R. 89W. The geology has been compiled by D. W. Riedel.

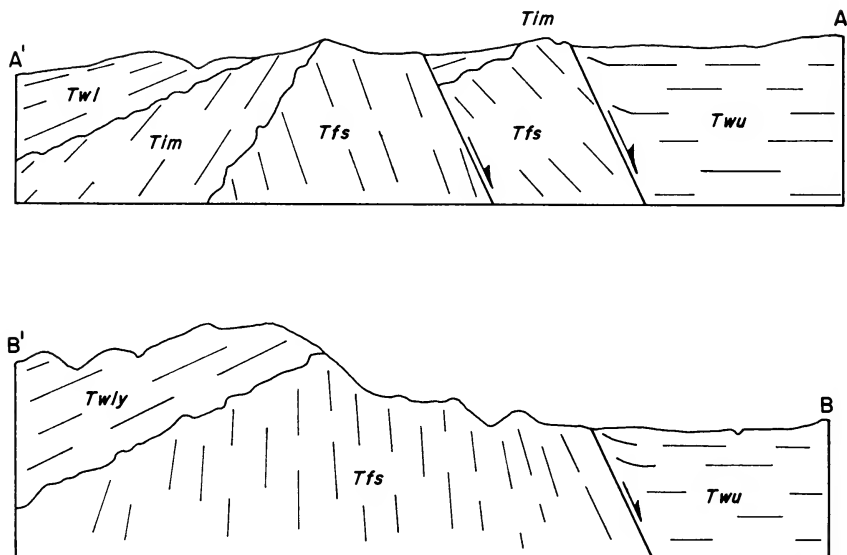
by conglomerates and mudstones of the Indian Meadows Formation with no more than 55 degrees of angular unconformity.

Across Badwater Creek, in the SW 1/4, Sec. 9, T. 39N., R. 89W., a very similar sequence of siltstones, claystones, and interbedded sandstone grades upward into a zone of thin conglomerates containing cobbles of siliceous shale and oil-stained sandstone. These beds are overlain by conglomerates and algal ball limestones of the Indian Meadows Formation with angular unconformity ranging from 55 degrees at the western edge to more than 100 degrees at the eastern edge. No fossils have yet been found in these rocks, but their lithology, overturned attitude, and relations to the overlying Indian Meadows Formation show that they are part of the Shotgun Member.

The greatest thickness of unfaulted Shotgun outcrop is in the vicinity of the vertebrate locality, where Keefer (1965a) measured 1600 feet of strata. Nearly 2300 feet of similar rocks were penetrated in the Pure Oil Co. Badwater 2-A well located about 2½ miles down dip (Keefer, 1965a, pl. 3). As much as 2000 feet of Shotgun strata may be present in the SW 1/4, Sec. 9, T. 39N., R. 89W., but the lower part of the section is cut by a fork of the Cedar Ridge Fault so that no accurate measured section can be obtained.

The complex relationships (Text-fig. 2) of the Shotgun Member to other strata in the Badwater area are largely the result of subsidence of the Wind River Basin throughout early and middle Tertiary time, and the uplift and overthrusting of the Bighorn Mountains that accompanied and followed it. The geologic history of the area has been discussed by Keefer (1965a, 1965b, and 1966), Paape (1961) and Tourtelot (1957).

During Fort Union time subsidence caused the Wind River Basin to become landlocked, or nearly so, and a large lake formed in the northeastern part. Siltstones, claystones, and sandstones of the Shotgun Member accumulated along the lake margin, interfingering with and prograding over the offshore deposits of the Waltman Shale Member. Uplift of the Bighorn Mountains may have begun in latest Paleocene or earliest Eocene time, causing erosion of Mesozoic rocks and deposition of the conglomerates in the uppermost part of the Shotgun Member. By earliest Eocene time the uplift had created localized thrust faults that upturned and overturned the beds of the Shotgun Member toward the west and southwest in the Badwater area. Rapid erosion of the Bighorn front during early Eocene time truncated the Shotgun strata and formed coarse alluvial fans of the Indian Meadows Formation. This deposition was interrupted by a great episode of thrust faulting that affected the basin margin from the Owl Creek Mountains to the Casper Arch, and further tilted the rocks in the Badwater area so that boulder conglomerates of the Lysite Member of the Wind River



Text-fig. 2. Cross-sections A-A' and B-B' shown in Text-fig. 1, illustrating the relationships of the Tertiary rock units. Abbreviations as in Text-fig. 1.

Formation overlies the Indian Meadows beds with up to 26 degrees of angular unconformity. Further erosion during Wind River time breached the Precambrian core of the Bighorn Range, changing the lithic composition of the sediments in the Wind River Formation from limestones and sandstones in the Lysite Member to sandstones and conglomerates of granite, gneiss, and schist in the Lost Cabin Member. Both subsidence and uplift had nearly ended by late Wind River time, and the uppermost clastic sediments of the Lost Cabin Member were masked and buried by fine-grained volcanic debris transported from the Absaroka region. All the younger tuffaceous strata of the late Eocene Tepee Trail, Oligocene White River, and Miocene Split Rock Formations are fine-grained and relatively thin, and are separated from Lost Cabin strata and from each other by only modest angular and erosional unconformities. The structural evolution of the Badwater area was completed in post-Miocene time by normal faulting that lowered the Bighorn Mountains and the Tertiary sediments north of the Cedar Ridge Fault relative to the Wind River Basin, placing the Split Rock Formation in contact with Lysite beds and the uppermost Wind River strata against those of the Shotgun Member.

ACKNOWLEDGEMENTS

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MAMMALIAN FAUNAL LIST

Multituberculata

Ptilodus sp.

Ectypodus sp. nr. *E. tardus*

Mesodma sp.

Cf. *Mesodma*

Microcosmodon conus

Marsupialia

Peradectes protinnominatus

Insectivora

Leptictid sp.

Palaeoryctid sp.

Aphronorus fraudator

Apatemys kayi

Cf. *Talpavus*

Cf. *Scenopagus*

Primates

Plesiadapis farisi

Phenacolemur frugivorus

Carpolestes sp.

Condylarthra

Chriacus pelvidens

Mimotricentes sp.

Cf. *Litomylus*

Phenacodaptes sabulosus

Ectocion osbornianum

Phenacodus cf. *primaevus*

Phenacodus sp.

Class Mammalia

Order Multituberculata

Suborder Ptilodontoidea

Family Ptilodontidae

Ptilodus Cope, 1881a

Ptilodus sp.

Figures 1-5

REFERRED SPECIMENS: P¹, 12491, 16128, 16138, 16144; P², 12455, 12453, 12488, 16130, 16129, 16132, 16136, 16179, 16146, 16145, 16143, 16140, 16137, 16134, 16185, 16141, 16147, 12487, 12489, 23693; P³, 16135; P⁴, 16133, 16124, 16125, 16121, 16187, 16126; M¹, 16182, 16165, 16163, 23686, 23692; M², 12454; P₄, 12490, 12449, 12450, 12452, 12451, 16120, 23685; M₁, 16150, 16180, 16152, 16148, 16156, 16191, 23684, 23687-23691; M₂, 16186, 16162, 16161, 16159.

DESCRIPTION: P¹ in occlusal view resembles an isosceles triangle with the apex directed anteriorly. Three cusps occur on the crown, one

anteriorly and a transverse pair posteriorly. The crown of CM 16138 is wider and less nearly triangular than the other referred P¹'s, and has a slight anteroexternal bulge.

The crown of P² has a gently sloping posterior shelf, is subquadrate in occlusal outline, and bears four cusps, one pair occurring anteriorly, and one pair posteriorly. The cusps are either pyramidal, conical, or crest-like. Variation also occurs in their size and distance from one another.

P³ (CM 16135, AP 3.5, TR 2.1) is elongate and slightly hourglass-shaped in occlusal outline. The crown bears nine cusps in two longitudinal rows. One row consists of five cusps, and the other of four. The internal cusps are laterally compressed and joined together almost to their apices. The cusps of the external row are pyramidal and more nearly separate.

None of the five referred P⁴'s is complete. Four are anterior fragments, and one (CM 16121) is a posterior fragment. A composite P⁴ (of CM 16121 and CM 16125) has an approximate cusp formula of 0:6:9. The anterior fragments have a small anteroexternal bulge, but do not bear any external cusps. The medial cusps, of which the second is largest and opposite the second internal cusp, are conical and separate from one another at their bases. The medial cusps are lower than the internal cusps. The anterointernal cusps are laterally compressed, become progressively higher posteriorly, and are joined to one another almost to their apices. On the posterior fragment, five internal and three medial cusps are preserved. The last medial cusp is opposite the groove between the penultimate and antepenultimate internal cusps.

The most nearly complete of the referred M¹'s is CM 16165 (TR 2.1), a posterior fragment with three external, five medial, and five internal cusps. The external and medial cusps are pyramidal, with the medial cusps wider and slightly more massive than the external ones. The internal cusps are smaller and more nearly conical than those in the other rows, and progressively decrease in size posteriorly. On CM 16163, a worn anterior fragment of M¹, only the external and internal rows are preserved, each with four cusps. An approximate cusp formula of a composite M¹ (CM 16165 and CM 16163) is 10:11:8.

The cusp formula on M² is 1:3:4 (CM 12454; AP 3.0, TR 2.8). The crown is triangular in occlusal outline and slightly concave anteriorly. The medial cusps are large, subcrescentic, and well separated from one another. The internal cusps are small, and conical to pyramidal. The first three are close together, but well separated from the fourth.

Only one specimen of P₄ is complete (CM 12449; AP 6.4). The blade bears 12 serrations, although one or two additional ones may have been obliterated by wear. In lateral view, the crest profile is long, very low, and not symmetrical. The anterior slope is longer and more gently in-

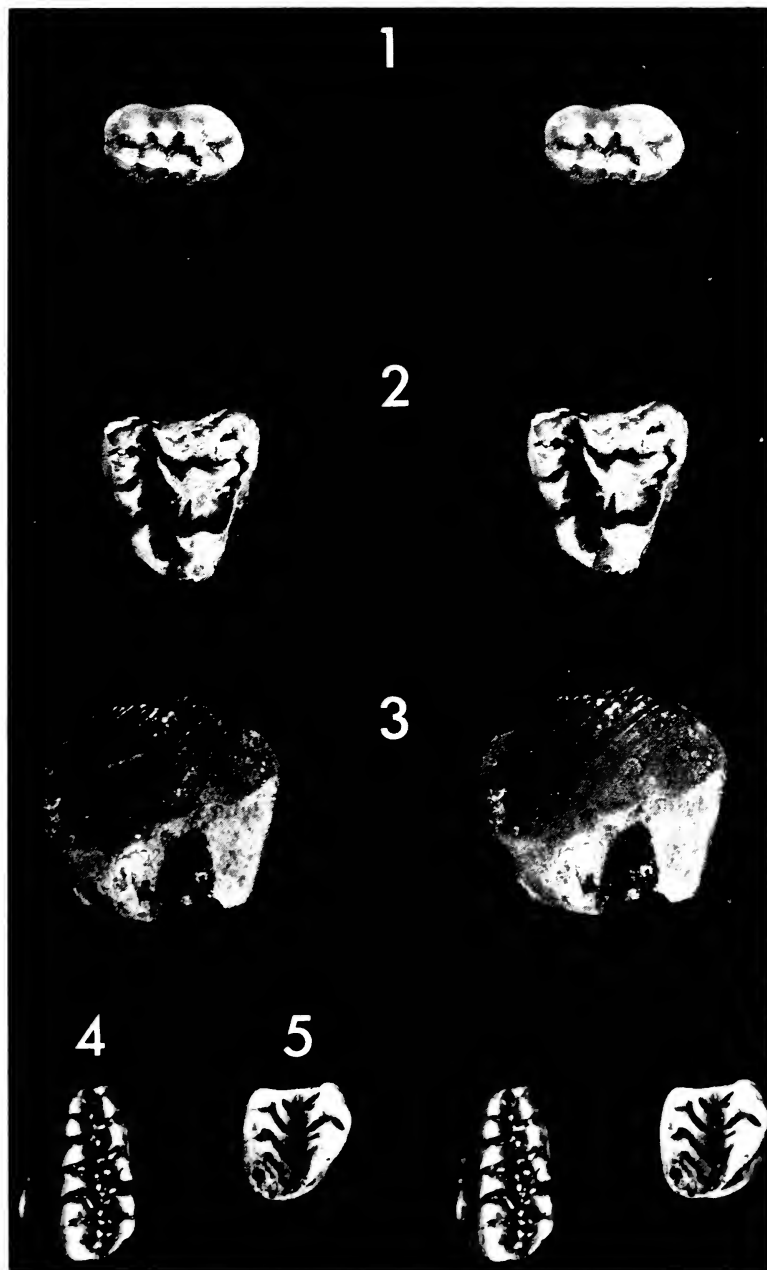


Plate 1. Figs. 1-5. *Ptilodus* sp. 1. P¹, CM 16135, occlusal view, approx. X 5. 2. M², CM 12454, occlusal view, approx. X 7. 3. P⁴, CM 12449, external view, approx. X 5. 4. M₁, CM 16191, occlusal view, approx. X 7. 5. M₂, CM 16162, occlusal view, approx. X 7.

clined than the posterior slope. The sixth serration is highest on the blade. The distance from the top of the anterobasal concavity to the first serration is more than one-third of the length of the crown. The first ridge originates from the base of the first serration, and posteroventrally directed ridges are absent.

The cusp formula of M_1 is 6:5 (CM 16191; AP 3.3, TR 1.6). Anteriorly the crown narrows only slightly, so that the lateral borders of the crown are essentially parallel. The cusps of the external row progressively increase in size posteriorly. The first four are pyramidal, the fifth is sub-crescentic, and the sixth, which appears to be formed by the union of two cusps, is the longest cusp on the crown. The cusps of the internal row are higher and more laterally compressed than the external cusps. The first four internal cusps are well separated from one another, whereas the fourth and fifth are united along most of their height. Two accessory cuspules occur on M_1 , one anterior to the first external cusp, and a larger one anterior to the first internal cusp.

The cusp formula of M_2 is 4:2 (range, AP 2.0-2.2; TR 1.9-2.0). The external cusps are joined and subequal in size, but are demarcated medially by three deep grooves. The internal cusps, of which the first is largest and tallest on the crown, are more nearly separate. A single groove occurs on the medial face of the first internal cusp, and two are present on that of the second.

COMMENTS: Except for P^3 (CM 16135), all teeth described here are like *Ptilodus* in size and crown morphology. P^3 , with 9 cusps arranged in two longitudinal rows, more nearly resembles that of *Prochetodon cavus*. The maximum number of cusps known for P^3 of *Ptilodus* is 7, which occurs on only one specimen of *P. montanus* (Simpson, 1937). In addition, P^3 of *Ptilodus* is invariably narrower than P^2 . CM 16135 is much wider than the isolated P^2 's described here. The remaining teeth resemble *Ptilodus* and differ from *Prochetodon* as follows: four cusps on P^2 instead of three; slightly wider P^4 , which is straight in lateral aspect instead of concave; and absence of a deep groove on the anterior slope of P^4 . Molars of *Prochetodon* have never been described. However, apart from M_1 , the molars referred here do not differ significantly from those of *Ptilodus wyomingensis* in size, cusp formula, and crown morphology. The 6:5 cusp formula for M_1 is slightly higher than the 6:4 formula recorded for *P. wyomingensis*. P^4 , in lacking a third row of cusps and a pronounced anteroexternal bulge, closely resembles that of *P. wyomingensis*, but is slightly narrower than the latter. The narrowness of P^4 , the relatively higher cusp formula of M_1 , and the curious *Prochetodon*-like structure of P^3 suggest that the species of *Ptilodus* represented by these isolated teeth is more advanced than *P. wyomingensis* and perhaps was derived from the latter.

Family Ectypodontidae

Ectypodus Matthew and Granger, 1921*Ectypodus* sp. near *E. tardus* (Jepsen, 1930b)

Figures 6-10

REFERRED SPECIMENS: P⁴, 16175; M¹, 23694; M², 16167, 16177, 16181, 23695, P₄, 16119, 16176, 23696-23699; M₁, 16178.

DESCRIPTION: The cusp formula of P⁴ is 2:6 (CM 16175, AP 2.5). The internal crest is moderately high in lateral profile, with straight anterior and posterior slopes. The last cusp is highest on the blade, and a tiny posterobasal cuspule is present. The first external cusp is small and occurs opposite the first internal cusp. The second external cusp, conical and larger than the first, is situated opposite the second internal cusp.

The M¹ cusp formula is 9:11:8 (CM 23694, AP 3.9, TR 1.8). In lateral aspect the crown is slightly concave. The internal row begins anteriorly at the level of the fourth medial cusp and is approximately two-thirds of the length of the tooth. The cusps in all three rows are pyramidal, but those of the medial row are broader at the base.

M² is triangular in occlusal outline and has a cusp formula of 1:3:3 (range, AP 2.0, TR 2.1). In both the medial and internal rows the first two cusps are appressed, and the third nearly separate. The medial and internal cusps are subcrescentic, with the former relatively larger and extremely broad at the base. The second medial cusp is highest on the crown. On CM 16181 the first internal cusp bears a small bump on its anterior face.

Both the complete referred P₄'s have 11 serrations (CM 16119, AP 3.0; CM 16176, AP 2.9). In lateral aspect, the anterior profile of the blade is short, high, and sharply convex. The posterior slope is relatively longer, much lower, and nearly straight. The fourth serration is highest on the crown. Although the posterolabial surface of the blade is quite worn on both specimens, a single posteroventrally directed groove can be discerned originating from between the ultimate and penultimate serrations.

The cusp formula of M₁ is 7:5 (CM 16178, AP 2.8, TR 1.3). In occlusal view, the two rows of cusps diverge posteriorly. The external cusps, worn well below the height of the internal cusps, become progressively longer anteriorly from the sixth cusp. In the internal row the cusps are pyramidal, the first and second cusps, as well as the fourth and fifth, are appressed, and the third cusp is the largest on the crown. The largest intercusp valley occurs between the third and fourth internal cusps.

COMMENTS: The high anterior and low posterior profile of P₄ is characteristic of *Ectypodus* and *Mimetodon*. P₄ of *Mimetodon* bears three posteroventrally directed grooves on the posterolabial part of the blade.

P_4 referred here bears only one. In its lateral profile, number of serrations, and size, P_4 closely agrees with that of *Ectypodus tardus*, known from the Eocene of Colorado (McKenna, 1960) and Wyoming (Jepsen, 1930b), and with *E. powelli*, known from a number of Tiffanian localities in Montana and Wyoming.

P^4 , with a cusp formula of 2:6, a moderately high blade, and ultimate internal cusp highest, agrees only with that of *Ectypodus*, among known Tertiary ectypodontids, and especially with *E. tardus*. P^4 of *E. powelli* has not been described. M^1 and M_1 referred here are significantly larger than those of *E. tardus* and *E. powelli*, but are closer in cusp formula (M^1 , 9:11:8; M_1 , 7:5) to the former (M^1 , 8:9:6; M_1 , 7-8:4). Whereas the larger size and cusp formulae of the molars imply morphologic distinction from *E. tardus*, affinity to this species is inferred from the extreme similarity of P^4 and P_4 to those of *E. tardus*. The Badwater Paleocene species of *Ectypodus* is clearly closely related to *E. tardus*, and may have been near, or part of, its ancestral lineage.

Mesodma Jepsen, 1940

Mesodma sp.

Figures 11-14

REFERRED SPECIMENS: P^4 , 23702, 16122, 16183; M^1 , 16164; M^2 , 16160; 16189, 23700; M_1 , 23701, 16154, 16155, 16157, 16188.

DESCRIPTION: The cusp formula of P^4 is 3:6 (CM 16122, AP 1.9). In occlusal aspect, the crown is essentially rectangular, has a narrow anteroexternal bulge and is slightly constricted medially. The internal crest is straight and runs posteroexternally from the anterointernal corner of the crown. In lateral view, the blade profile is extremely low. The anterior and posterior slopes are straight, the latter very short. The ultimate internal cusp, when unworn, is the highest point of the blade. Posterobasal cuspules are not present. The three external cusps are conical, become progressively larger posteriorly, and occur opposite the first three internal cusps, respectively.

The cusp formula of the only referred M^1 of *Mesodma* sp. is 8:10:6 (CM 16164, AP 2.4, TR 1.2). In the external row, the anterior cusps are subconical and the posterior ones pyramidal. The penultimate cusp is largest. Similarly, anterior medial cusps are small, low and sub-crescentic, whereas posteriorly the cusps are larger, taller, and fully crescentic. The ultimate medial cusp is the highest on the crown. The internal row provides approximately two-thirds of the internal border of the crown and originates anteriorly at the level of the fourth medial cusp. The first two and last internal cusps are small and conical; the third, fourth, and fifth cusps are much larger and pyramidal.

The cusp formula of M^2 is 1:3:3 (range AP 1.1-1.2, TR 1.1-1.2). In

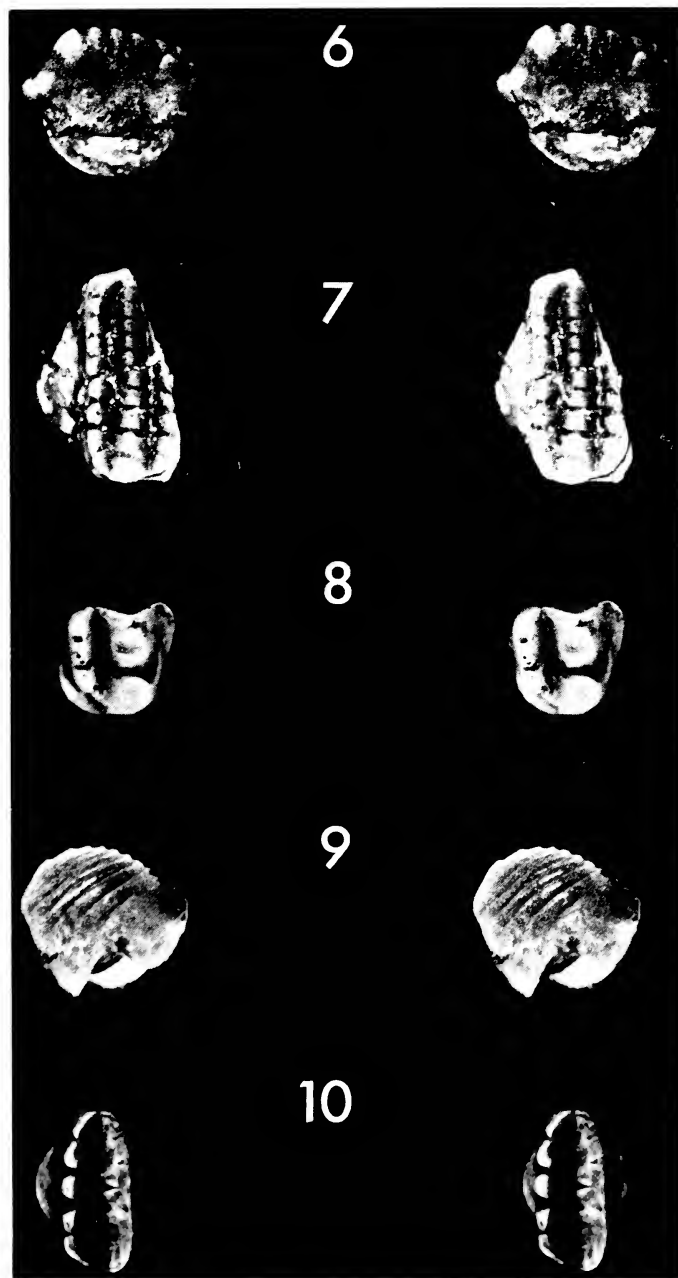


Plate 2. Figs. 6-10. *Ectypodus* sp. nr. *E. tardus*. 6. P⁴, CM 16165, external view, approx. X 10. 7. M¹, CM 23694, occlusal view, approx. X 7. 8. M², CM 16177, occlusal view, approx. X 7. 9. P⁴, CM 16176, external view, approx. X 7. 10. M¹, CM 16178, occlusal view, approx. X 7.

occlusal aspect the crown is wider than long and concave anteriorly. A relatively wide cingulum connects the single small external cusp to the last medial cusp. The medial cusps, of which the first two are appressed, are subcrescentic, and progressively increase in height posteriorly. The internal cusps, slightly lower than the medial ones, are pyramidal and gradually become smaller posteriorly.

The cusp formula on M_1 is 7:4-5 (range AP 2.1-2.3, TR 0.9). Anteriorly, in occlusal view, the crown narrows only slightly, and the two rows of cusps are essentially parallel. Posteriorly, the last internal cusp occurs opposite the penultimate external cusp so that the cingulum joining the last cusp of each row is oriented extremely obliquely. In the external row the first cusp is smallest and conical, the second to fourth are subcrescentic, the fifth and sixth cusps are crescentic, and the last cusp is short and crest-like. The internal cusps are larger and taller than the medial ones, and pyramidal in shape.

COMMENTS: The *Mesodma*-like features of P^4 described here are: cusp formula, 3:6; internal blade of extremely low profile, with straight short posterior slope, and ultimate cusp highest. The molars are referred to *Mesodma* sp. on the basis of size association with P^4 , and their similarity in cusp formulae and crown morphology to *Mesodma* sp. F, known from the Cypress Hills Tiffanian of Alberta (Krishtalka, 1973); Gidley Quarry, Montana; and Shotgun Local fauna, Wyoming (R. E. Sloan, personal communication).

Cf. *Mesodma*
Figure 15

REFERRED SPECIMEN: P^4 , 16118.

DESCRIPTION: CM 16118 (AP 3.5, approx.), a left P^4 , is intermediate in size between P^4 of *Ptilodus* sp., and *Ectypodus* sp., near *E. tardus*. The cusp formula is 1:7. The posterior part of the base of the tooth below the last internal cusp is broken away, but the posterior slope appears to have been straight and short. The anterior slope of the blade is straight and very low in lateral profile, with the ultimate cusp highest on the blade. The internal cusps are large, well-defined, and increase in size posteriorly. The external cusp, large and pyramidal, occurs opposite the second and third internal cusps. A tiny bump is situated anterior to the external cusp, but is not large enough to be included in the cusp formula.

COMMENTS: Features of this large, isolated P^4 that imply affinity with *Mesodma* include the very low profile of the internal crest, the straight anterior and posterior slopes, a relatively low cusp formula, and the relative height of the last internal cusp (highest on the blade). The last two features are also characteristic of P^4 of *Ectypodus*, although the lateral profile of the internal crest on P^4 of *Ectypodus* is considerably

higher than that of *Mesodma* and CM 16118. Only two Paleocene species of *Mesodma* are known: *M. ambigua*, from the Mantua Lentil, Polecat Bench Formation, Wyoming, and *Mesodma* sp. P (including *Mesodma* sp. described in this paper) from Tiffanian localities in Alberta, Montana, and Wyoming. CM 16118 is much larger than P⁴ of *Mesodma* sp. P. P⁴ is unknown in *M. ambigua*. If CM 16118 indeed represents a large species of *Mesodma*, it is the first such record for the Late Paleocene.

Suborder Taeniolabidoidea

Family Eucosmodontidae

Microcosmodon Jepsen, 1930a

Microcosmodon conus Jepsen, 1930a

Figures 16-20

REFERRED SPECIMENS: M¹, 16149, 23703; M², 16168; P₄, 16123; M₁, 16151, 16153, 16158, 16166; M₂, 16171.

DESCRIPTION: The cusp formula on M¹ is 7:8:8 (CM 16149; AP 2.2, TR 1.2). The internal row is a high narrow cingulum, with the individual cusps developed as crenulations along its apex. This internal ridge is one-half the length of the tooth and originates anteriorly at the level of the fifth medial cusp. The medial and external cusps are well worn but appear to have been more robust than those on M¹ of *Mesodma* sp.

The cusp formula on M² (CM 16168; AP 1.3, TR 1.1) is 1:3:4, and differs perhaps significantly from that of *Mesodma* sp., which is 1:3:3. In occlusal aspect, the crown is longer and less transverse than M² of *Mesodma* sp., and the cingulum joining the external cusp to the last medial cusp is much narrower. The medial cusp are subcrescentic, and the internal cusps form a continuous crest.

CM 16123 (AP 1.8), the only P₄ referred to *Microcosmodon conus*, is heavily worn, but 5 large, cusp-like serrations can be discerned. Characteristically, there are no ridges on the external or internal faces of the blade. In lateral outline, the blade is arcuate and appears to have been almost symmetrically so when unworn. Anteriorly, the blade only slightly overhangs the root, and a basal concavity is absent. A postero-basal crescent, convex ventrally, occurs on the labial surface of the blade. The crown does not overhang the posterior root.

The cusp formula of M₁ is 7:4 on three specimens (range AP 1.9-2.0, TR 0.9) and 6:4 on CM 16166 (AP 1.8, TR 0.9). In occlusal view, the posterior border of the crown is only moderately oblique and is much wider than the anterior edge. The two rows of cusps converge anteriorly. This condition differs from M₁ of *Mesodma* sp., on which the two rows of cusps are more nearly parallel and the posterior edge of the crown is very oblique. The external cusps are subcrescentic and the first is the smallest on the crown. The internal cusps are pyramidal and much higher than the external ones. The last internal cusp is massive

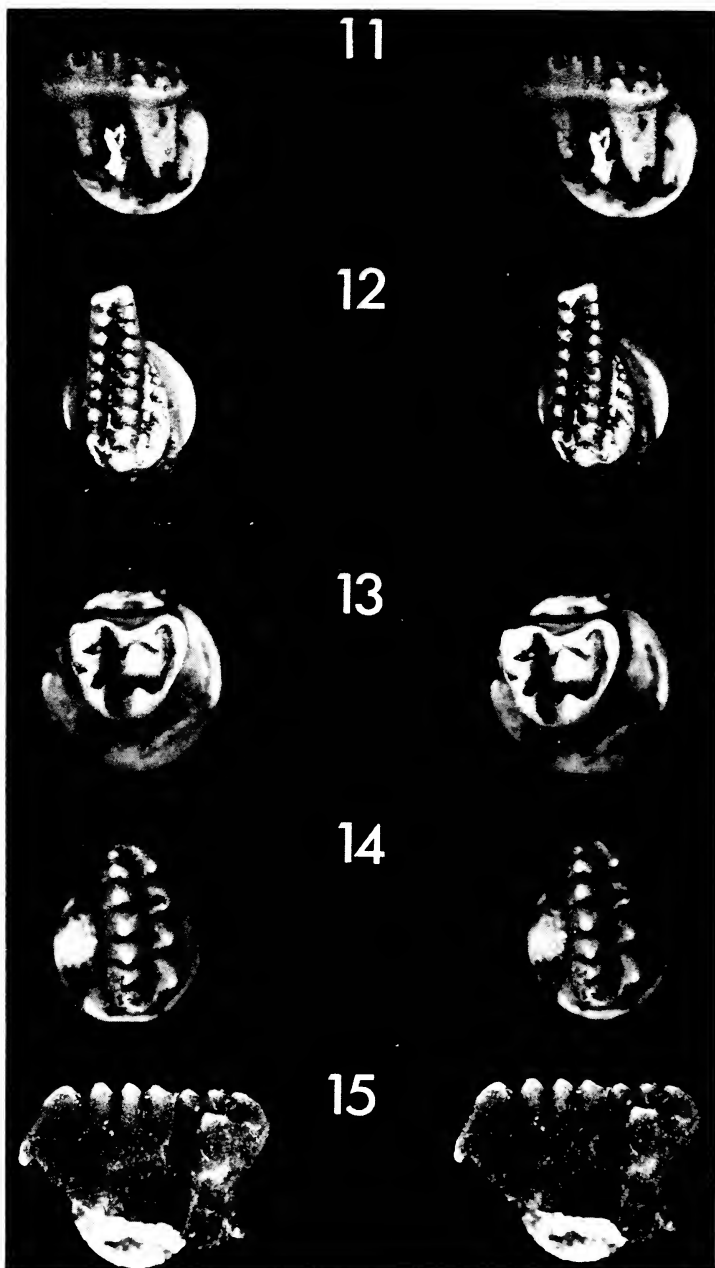


Plate 3. Figs. 11-14. *Mesodma* sp. 11. P⁴, CM 16122, external view, approx. X 10. 12. M¹, CM 16164, occlusal view, approx. X 10. 13. M², CM 16189, occlusal view, approx. X 10. 14. M₁, CM 16155, occlusal view, approx. X 10. Fig. 15. Cf. *Mesodma*. P₄, CM 16118, external view, approx. X 10.

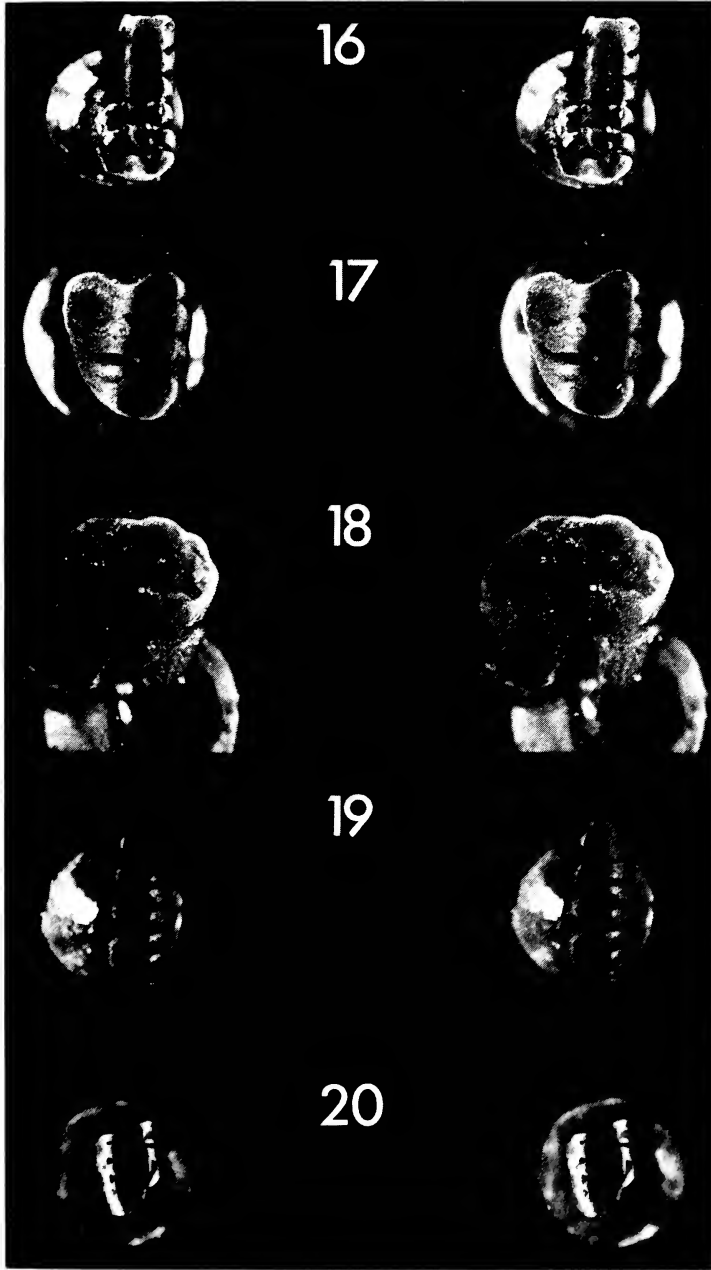


Plate 4. Figs. 16-20. *Microcosmodon conus*. 16. M^1 , CM 16149, occlusal view, approx. X 10. 17. M^2 , CM 16168, occlusal view, approx. X 15. 18. P_1 , CM 16123, external view, approx. X 15. 19. M_1 , CM 16149, occlusal view, approx. X 10. 20. M_2 , CM 16171, occlusal view, approx. X 10.

and appears to be the union of two cusps.

The cusp formula on CM 16171 (AP 1.2, TR 0.9), a heavily worn M_2 , is 4:2. The crown is rather elongate in occlusal outline.

COMMENTS: Among Tertiary multituberculates known to us, only *Microcosmodon* possesses a P_4 with 5 cusp-like serrations, no anterobasal concavity, and no external and internal ridges. Although similar in outline and serration count, P_4 of *Pentacosmodon* is much larger and bears well developed labial and lingual ridges. The lower molars are referred to *M. conus* on the basis of size association with P_4 and similarity of cusp formula and crown shape to described M_1 and M_2 of *M. conus* (Jepsen, 1940). M^1 , with a short internal crenulated crest and robust medial and external cusps, differs significantly from M^1 of *Mesodma* sp., and appears eucosmodontine in character. M^2 is narrower, more elongate, and has a higher cusp formula than that of *Mesodma* sp. Future recovery of associated upper and lower dentitions of *M. conus* may, however, prove the tentative referral of these isolated upper molars to *M. conus* to be incorrect.

Infraclass Metatheria
Order Marsupicarnivora
Family Didelphidae

Peradectes Matthew and Granger, 1921
Peradectes protinnominatus McKenna, 1960

Figure 21

REFERRED SPECIMENS: M^3 , 23705; molar trigonids, 23706-23709.

DESCRIPTION: CM 23705, a labial fragment of M^3 (AP 1.6) bears a well-developed metacone, a paracone, and four styler cusps. The paracone is worn well below the height of the metacone, but the size of its base implies that the metacone and paracone were subequal in height. Styler cusp C is very weak and is the smallest of the styler cusps. Cusp D is well developed and is slightly larger than cusp B. Cusp A is intermediate in size between cusps B and C.

On the referred trigonid fragments, the protoconid is the tallest cusp, with the metaconid higher than the paraconid.

COMMENTS: M^3 resembles *Peradectes*, and differs from *Peratherium* in possessing subequal paracone and metacone. The tiny styler cusp C on M^3 implies affinity to the Wasatchian *Peradectes protinnominatus* rather than the Tiffanian *P. elegans*, in which cusp C is well developed. The teeth described here are larger than those of *P. pauli* (Gazin, 1956a), which is known only from the lower dentition.

Three didelphid molars from the Tiffanian of Alberta, Canada, were described by Krishtalka (1973) as *Peradectes* cf. *elegans*. However, University of Alberta No. 5760, an M^1 , bears a tiny styler cusp C and,

along with the two lower molars, should be referred to *P. protinnominatus*.

Infraclass Eutheria
Order Insectivora
Family Leptictidae
Leptictid sp.
Figure 22

REFERRED SPECIMENS: M¹ or M², 16230, 23704.

COMMENTS: The two referred specimens are lingual fragments of upper molars that bear an anteroposteriorly compressed protoconid, a small hypocone on a wide hypoconal shelf, long protocristae, and an extremely weak anterior cingulum. Compared to known Tiffanian leptictids, the molar fragments are larger than *Diacodon pearcei* (Gazin, 1956a) and *Palaeictops septentrionalis* (Russell, L. S., 1929). As in *Palaeictops*, the protocone is high and anteroposteriorly compressed. However, these specimens cannot be assigned to *Palaeictops* with any degree of certainty until more complete material is recovered.

Family Pentacodontidae
Aphronorus Simpson, 1935
Aphronorus fraudator Simpson, 1935

REFERRED SPECIMENS: M², 16219, 16235; M₂, 23715 (AP 2.4; TR 1.8).

COMMENTS: The three molars referred to *Aphronorus* are much smaller than those of *A. orieli* (Gazin, 1969) but closely agree in size and morphology with M² and M₂ of *A. fraudator*, described by Simpson (1935, 1937) from the Torrejonian of Montana. The first occurrence of *Aphronorus* in Tiffanian deposits was reported from the Shotgun Local Fauna, Wyoming, by D. E. Russell (1967). Examination of Shotgun material and personal communication with Craig Wood, Harvard University, indicate the occurrence of both *A. fraudator* and *A. orieli* in the Shotgun fauna.

Family Palaeoryctidae
Palaeoryctid sp.
Figure 23

REFERRED SPECIMENS: M₁ or M₂, 16221, 23710-23714 (range, AP 2.3-2.7, TR 2.0).

DESCRIPTION: All but one (CM 16221) of the referred specimens are extremely worn lower molars. Discernible palaeoryctid characters are the very high trigonid, the relatively narrower and shorter talonid, and the simple, arc-shaped posteristid. On CM 16221 the paraconid is highly compressed anteroposteriorly and occurs considerably internal relative to the metaconid. The protoconid and metaconid are well devel-

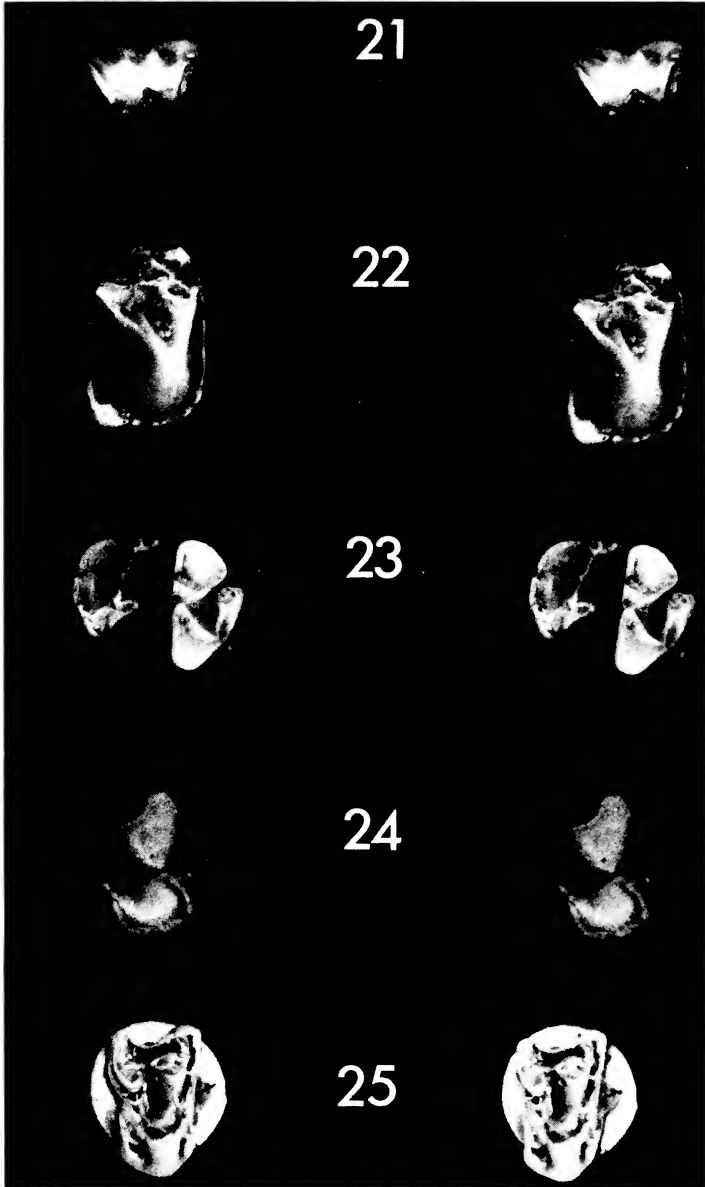


Plate 5. Fig. 21. *Peradectes protinnominatus*. External $\frac{1}{2}$ of M^3 , CM 23705, occlusal view, approx. X 10. Fig. 22. *Leptictid* sp. Internal $\frac{1}{2}$ of M^1 or M^2 , CM 23704, occlusal view, approx. X 10. Fig. 23. *Palaeoryctid* sp. M_1 or M_2 , CM 23713, occlusal view, approx. X 10. Figs. 24-25. *Apatemys kayi*. 24. M_1 or M_2 , CM 16218, occlusal view, approx. X 10. 25. M^2 , CM 16231, occlusal view, approx. X 10.

oped, with the metaconid relatively lower, less robust, and more posterior in position. The hypoconid forms the highest point on the talonid, and the cristid obliqua is median on the posterior wall of the trigonid.

COMMENTS: These lower molars fall within the range in size of *Avunculus* Van Valen, 1966, and *Gelastops* Simpson, 1935, but cannot be assigned to either genus until more complete material is recovered. The authors follow MacIntyre (1966), Szalay (1968), and McKenna (1969) in classifying palaeoryctids as Insectivora rather than Delta-theridia (Van Valen, 1965, 1966).

Family Adapisoricidae

Talpavus Marsh, 1872

Cf. *Talpavus*

Figures 26-28

REFERRED SPECIMENS: M¹ or M², 16226, 16227, 23719; P₄, 23718; M₁, 12495, 23717; M₂, 23716; M₃, 16210.

DESCRIPTION: The referred upper molars are small, lingual fragments that bear a well developed protocone, a small hypocone, and distinct conules. The protocone leans anteriorly and is not anteroposteriorly compressed. The hypocone, which is on the posterior cingulum, is separate from and posterolingual to the protocone. The protocristae and conulecristae are sharp and distinct. The precingulum is narrow and terminates lingually in a tiny cuspule.

P₄ (CM 23718; AP 1.7, TR 1.1) is submolariform, with a tricuspid trigonid and a relatively wide but unbasined talonid. The three trigonid cusps are extremely worn but appear to have been well developed when complete. The talonid is shorter than and approximately three-fourths as wide as the trigonid. The hypoconid is worn flat, the hypoconulid is small and medial, and the entoconid is well developed and is the highest of the three talonid cusps. The postcristid is slightly arcuate.

The trigonid on M₁ (CM 12495; AP 1.8, TR 1.2) is narrower than the talonid. The paraconid is moderately developed and is compressed anteroposteriorly. As on P₄, the entoconid is much higher than the worn hypoconid and the hypoconulid is small and central on the postcristid.

M₃ (CM 16210; AP 1.8, TR 1.2) is extremely worn, so that the diagnostic features of the paraconid cannot be discerned. However, as on P₄ and M₁, the hypoconid is worn flat, below the height of the entoconid.

COMMENTS: The authors follow Robinson's (1968a, 1968b) classification of adapisoricid and nyctitheriid insectivores. The teeth closely resemble *Talpavus* in that the talonid on P₄ is large and unbasined, the paraconid is anteroposteriorly compressed on M₁, and the entoconid is much higher than the hypoconid on P₄, M₁, and M₃. This condition differs from that of *Leptacodon* and other nyctitheriids in which the talonid on P₄ is relatively narrow, the hypoconid on M₁₋₃ is higher than the

entoconid, and the hypoconulid occurs slightly lingual to the midline. Relative to *Talpavus* and the present sample, the talonid on P_4 of *Entomolestes* (Adapisoricidae) is narrower, and the paraconid on the lower molars is not as compressed anteroposteriorly.

The upper molars from Badwater are approximately one-half as large as those of *T. sullivanii* (Guthrie, 1971), and are tentatively referred to cf. *Talpavus* on the basis of size association with the lower molars and their adapisoricid-like characters: the anterior leaning protocone, a distinct posterolingual hypocone, and sharply defined conules and cristae.

In comparable parts of the dentition, cf. *Talpavus* is slightly larger than the Bridger *Talpavus nitidus*, much smaller than *T. sullivanii*, but close in size to *T. (Leipsanolestes) seigfriedti* (Simpson, 1928) from the Bear Creek Tiffanian of Montana. According to Simpson (1928), the paraconid on P_4 of *T. seigfriedti* is rudimentary, the talonid is narrow and simple, and the hypoconulid on $M_{1,2}$ is not definite. This condition differs from, and seems more primitive than, that described above for cf. *Talpavus*.

Scenopagus McKenna and Simpson, 1959

Cf. *Scenopagus*

Figure 29

REFERRED SPECIMEN: M^1 , 16222 (AP 1.9; TR 2.6).

DESCRIPTION: The crown of CM 16222 is constricted anteroposteriorly across the conules and is considerably longer labially than lingually. The labial and lingual borders of the crown are nearly parallel and oriented obliquely posterobuccally. The anterior and posterior margins of the crown are respectively convex and concave in parallel fashion along the lingual two-thirds of the tooth. The three major cusps are well developed: the paracone is tall, conical, and nearly vertical in stature; the metacone is somewhat lower, compressed labiolingually, and leans posteriorly; the protocone is large, leans anterolabially, and possesses a long lingual slope. The hypocone, quite small and conical, forms the lingual end of the narrow postcingulum. The conules are pyramidal in structure and well developed, each with distinct pre- and postconule-cristae. The parastyle is a low, somewhat enlarged shelf and forms the anteriormost extension of the crown. There is no metastyle and the ectoflexus is extremely shallow. The short precingulum does not extend to the lingual margin of the crown. Both the pre- and postcingula narrow labially and terminate at the level of the conules. The paracingulum and metacingulum are broad, but do not, respectively, extend completely around the base of the paracone and metacone. The postmetacrista is straight in occlusal view, and runs directly posterolabially, with no flexure. There is no preparacrista.

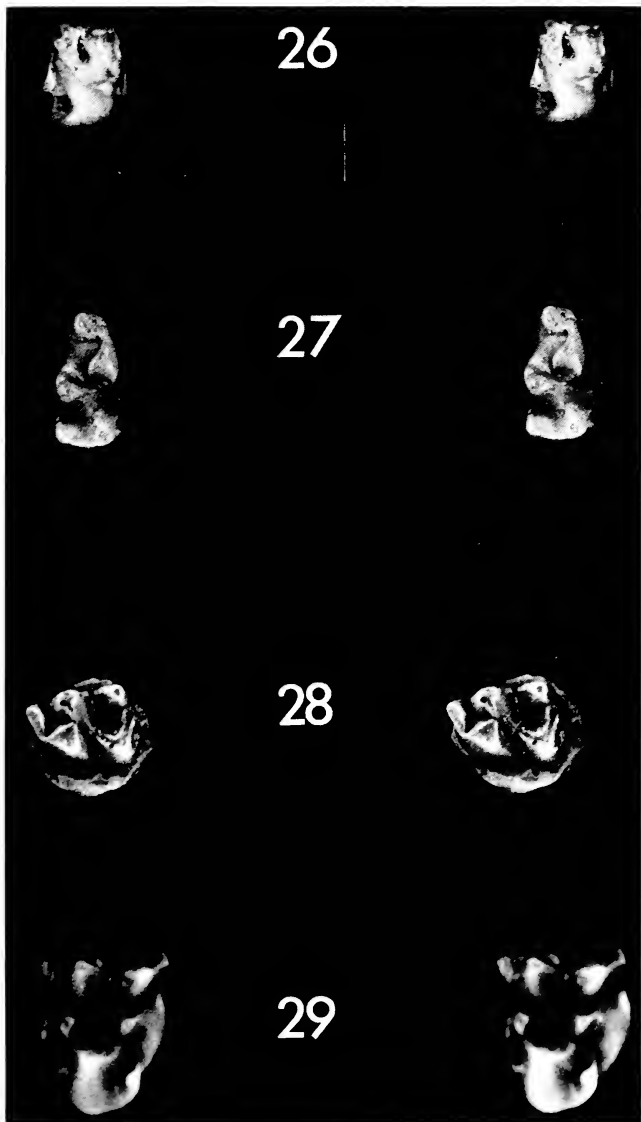


Plate 6. Figs. 26-28. Cf. *Talpavus*. 26. M^1 or M^2 , CM 16226, occlusal view, approx. X 10. 27. P_4 , CM 23718, occlusal view, approx. X 10. 28. M_1 , CM 12495, occlusal view, approx. X 10. Fig. 29. Cf. *Scenopagus*. M^1 , CM 16222, occlusal view, approx. X 10.

COMMENTS: This upper first molar is of the adapisoricid-nyctitheriid-type in crown shape and cusp morphology. Among early Tertiary adapisoricids and nyctitheriids (including *Leptacodon*) known to us, CM 16222 most closely resembles M¹ of *Scenopagus* (McKenna and Simpson, 1959), previously known only from Eocene horizons. The absence of a distinct metastyle, and the small hypocone and postcingulum on CM 16222 obviates referral of this molar to a known species of *Scenopagus*, all of which possess a large metastyle, and a large hypocone at the lingual end of a broad postcingulum. In all other characters, CM 16222 and M¹ of *Scenopagus* are very similar: significantly, a shallow ectoflexus, a flaring parastylar salient, absence of a preparacrista, hypocone separate from the protocone, and a labiolingually compressed metacone that is drawn posterolabially into a high postmetacrista. These shared characters suggest that this latest Paleocene species of cf. *Scenopagus*, represented by CM 16222, may have been temporally and morphologically close to the ancestry of the earliest known Eocene species of *Scenopagus* (from the Lost Cabin), with enlargement on the upper molars of the hypocone, metastyle, and postcingulum developing in these lineages by Eocene time.

Among other known adapisoricids and nyctitheriids, CM 16222 only superficially resembles M¹ of *Leptacodon tener* and *Talpavus*. Comparison of CM 16222 with McKenna's (1963) reconstruction of the type of *L. tener* revealed the following differences: a greater degree of crown constriction across the conules on CM 16222, a much shallower ectoflexus, a posterolabial (in contrast to a posterolingual) orientation of the lingual margin of the crown, a straight (rather than flexed) postmetacrista, a slightly more conical metacone, and narrower, shorter anterior and posterior cingula. Upper molars of Eocene *Talpavus* (Guthrie, 1971; and CM 12397, partial left maxilla with M¹⁻³, Willwood Fm., Big Horn Basin, Wyo.) and *Entomolestes* (Guthrie, 1971) differ from CM 16222 (and upper molars of *Scenopagus*) in possessing a weaker, lower postmetacrista, a distinct preparacrista, and a conical, uncompressed metacone. Finally, CM 16222 is distinct from the fragmentary upper molars assigned in this paper to cf. *Talpavus* in its larger size, smaller hypocone, and in the posterolabial, instead of posterolingual, orientation of the lingual margin of the crown.

Family Apatemyidae
Apatemys Marsh, 1872
Apatemys kayi (Simpson, 1929)
Figures 24-25

REFERRED SPECIMENS: M², 16231; M₁ or M₂, 16218.

DESCRIPTION: The M² (CM 16231, AP 1.3; TR 2.0) is quadrate in

occlusal outline, quite transverse, and slightly constricted antero-posteriorly at the level of the conules. The ectoflexus is deep and symmetrically concave, producing distinct metastylar and parastylar saillents. The protocone occurs anterior to the midline, and its base forms the lingual extent of the crown. The lingual border of the tooth, from the base of the protocone to that of the hypocone, is oriented obliquely posterobuccally. The hypocone is large and conical, and is situated directly posterior to the protocone. A moderately broad stylar shelf occurs between the labial edge of the crown and the well-developed, conical paracone and metacone. The paracone is taller than the metacone, broader at the base, and slightly more labial in position. Although they are badly worn, the conules appear to have been subequal in size, with the paraconule situated more lingual than the metaconule. Both the paracingulum and metacingulum are broad. The paracingulum extends to the parastyle, whereas the metacingulum terminates lingual to the metastyle. A high and broad postmetacrista runs from the posterior side of the metacone to the metastyle. The anterior and posterior cingula are narrow and do not extend labially beyond the level of the conules.

The referred lower molar (AP 1.9, TR 1.2) possesses the characteristic lingual apatemyid curve, and a squared trigonid with an anterolabial cusp. The trigonid is low, and narrower than the talonid. The protoconid and metaconid are subequal with the metaconid more posterior. The paracristid extends directly anteriorly from the protoconid to a tiny, ridge-like anterolabial cusp, which in turn is joined to the anterolingual paraconid by a lateral cristid. The paraconid occurs substantially medial relative to the metaconid. The hypoconid is small and the entoconid and hypoconulid are broken away. The cristid obliqua is medial on the posterior wall of the trigonid, and the talonid basin is not symmetrical, but slopes to its deepest point at the posterolingual part of the base of the metaconid.

COMMENTS: Among known Paleocene and Eocene apatemyids, the molars described here closely resemble *Apatemys* in the corresponding parts of the dentition. In contrast to *Labidolemur* (Matthew and Granger, 1921) and *Jepsenella* (Simpson, 1940), M^2 (CM 16231) possesses a hypocone, well developed conules, a larger metastyle, and a more quadrate occlusal outline, and CM 16218 (M_1 or M_2) has a much lower trigonid (McKenna, 1963; West, 1972). Both molars agree in size with *A. kayi*, known from the Tiffanian Bear Creek fauna, Montana.

Except for the Late Eocene *A. uintensis*, West (1973) recently synonymized all of the other known species of *Apatemys* as *A. bellus*, and considered the high coefficients of variation for the resultant sample of *A. bellus* as a corollary of the great temporal and geographic range of

the species. We believe that these high C.V. values (generally between 10-20) warrant continued separation of the species of *Apatemys* until more evidence for their synonymy is found.

Order Primates
Suborder Plesiadapoidea
Family Plesiadapidae
Plesiadapis Gervais, 1877
Plesiadapis farisi Dorr, 1952

REFERRED SPECIMENS: I, 16273, 16286; P³, 16243, 16245, 16268, 16277, 16272, 23720; P⁴, 12472, 16251, 16242, 16204, 16246, 23721; M¹⁻², 16194; M¹, 12484-12486, 12480, 16193, 16197, 16207, 16253, 16283, 16266, 23722, 23723; M², 23724, 16203, 16255, 16198, 16199; M³, 16275, 12479, 23725-23732; P₃, 16284; P₄, 16249, 16248, 23733, 23734; M₁₋₂, 12471; M₁, 23735, 12481-12483, 16285, 16267, 16265, 16247; M₂, 12459, 16256, 16270, 12469, 12470, 16254, 16206; M₃, 16250, 16281, 16252, 16282, 12477, 12478, 23736, 23740; fragments of molars and premolars, 23741.

MEASUREMENTS: P³, AP 2.2-2.7, TR 2.8-3.3; P⁴, AP 2.4-3.0, TR 3.9-4.1; M¹, AP 3.2-3.5, TR 4.3-4.7; M², AP 3.5-3.8, TR 5.2-5.8; M³, AP 3.2-3.7, TR 4.5-5.4; P₃, AP 2.4, TR 2.2; P₄, AP 2.5-2.8, TR 2.4; M₁, AP 3.0-3.6, TR 2.7-3.1; M₂, AP 3.3-3.8, TR 3.0-3.5; M₃, AP 5.0-5.3, TR 2.9-3.5.

COMMENTS: A detailed treatment of the isolated teeth of *P. farisi* from Badwater is unnecessary, as this species has been adequately described by Dorr (1952, 1958). The diagnostic features of the isolated teeth are as follows: P³⁻⁴ are transverse, bear a distinct and elongate paraconule, and confluent paracone and smaller metacone. On M¹⁻³ the hypocone is not a distinct cusp, and the mesostyle is a weak ridge. P₄ is simple, with no metaconid or paraconid. The trigonid is slightly narrower than the talonid on M₁₋₂, and the labial walls of the protoconid do not exhibit the exaggerated slope characteristic of *P. jepseni* and *P. anceps* (Gazin, 1956a; 1956b). On M₃ the posterior lobe of the talonid is nearly as broad as the anterior lobe.

In contrast to *P. farisi* and the teeth described here, P₄ in *P. dubius* and *P. rubeyi* bears an incipient metaconid, P⁴ in *P. cookei* and P³ in *P. anceps* and *P. fodinatus* lack a paraconule, and P³⁻⁴ in *P. gidleyi* are less transverse, with the paraconule slightly weaker and less distinct.

Family Paromomyidae
Phenacolemur Matthew, 1915
Phenacolemur frugivorus (Matthew and Granger, 1921)

REFERRED SPECIMENS: P⁴, 16288; M¹, 16259, 23742-23744; M¹ or M², 16293-16295, 16287; M², 16260, 12499, 12497; M³, 16274, 16278, 16261; P₄, 16289; M₁, 12498, 16264, 16296, 16292, 16290, 23745, 23746; M₂, 16262, 16291, 16269, 16257, 16258, 16271, 23747; M₃, 16263, 16297, 23748, 23750.

MEASUREMENTS: P⁴, AP 1.9, TR 2.3; M¹, AP 1.9-2.0, TR 2.8-2.9; M², AP 1.7-1.9, TR 2.6-3.0; M³, AP 1.7-2.3, TR, 1.9-2.3; P₄, AP 1.6, TR 1.0; M₁, AP 1.8-2.1, TR 1.4-2.0; M₂, AP 1.8-2.1, TR 1.5-1.8; M₃, AP 2.6-2.7, TR 1.4-1.7.

COMMENTS: The isolated teeth closely agree in size and morphology with *P. frugivorus*, well known from Tiffanian localities in Wyoming, Colorado, Montana, and Alberta (Simpson, 1955; Krishtalka, 1973). *P. frugivorus*, including these specimens from Badwater, is smaller than other Tiffanian and Wasatchian species of *Phenacolemur*, and possesses simpler, less robust fourth premolars and a smaller hypoconal shelf on M^{1-2} . Although the molars of *P. frugivorus* and *P. mcgrewi* (Robinson, 1968c) from the Late Eocene of Badwater, are very close morphologically, the difference in size between M^1 and M^2 of *P. frugivorus* is not as great as in *P. mcgrewi*. The ratio of average length of $M^1:M^2$ and $M_1:M_2$ for *P. mcgrewi* is 1.66 and 1.50, respectively. That for *P. frugivorus* from Badwater is 1.1 and 1.0, respectively.

Family Carpolestidae
Carpolestes Simpson, 1928
Carpolestes sp.

REFERRED SPECIMEN: P⁴, 16170.

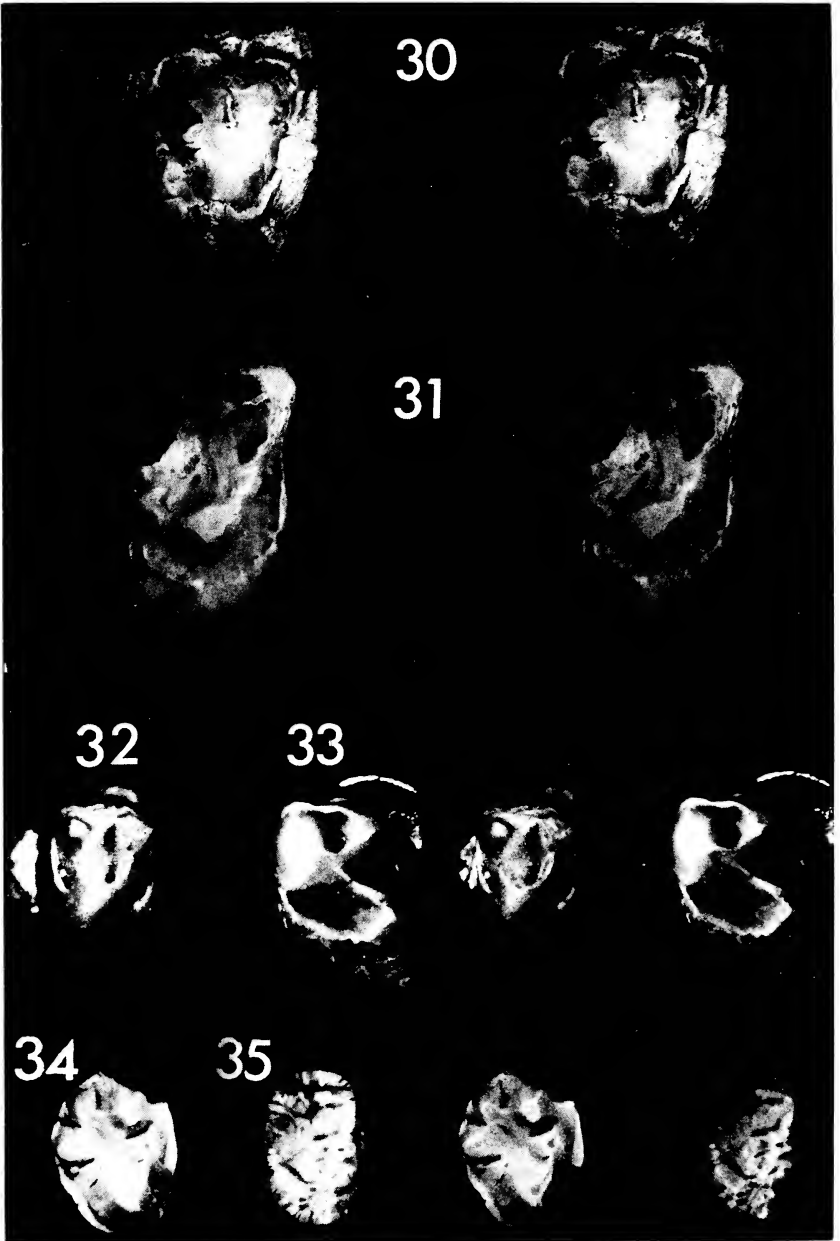
DESCRIPTION: CM 16170 is a labial fragment of a carpolestid P⁴ (AP 1.6). Six small cusps, subequal in height, are joined along the labial edge of the crown. The largest intercusp valley occurs between the second and third anterior cusps. The median ridge is preserved on CM 16170 but is well worn. It extends across the length of the crown internal to the labial cusps, and terminates anteriorly in a small cuspule. A round wear facet, which occurs anteriorly near the broken lingual margin of the crown, corresponds to the cuspule on the anterior cingulum of known carpolestid P⁴'s.

COMMENT: CM 16170 closely resembles P⁴ of both *Carpodaptus* and *Carpolestes*. However, it agrees with *Carpolestes* and differs from *Carpodaptus* in that the labial row of cusps is not arcuate in lateral view, and is nearly straight rather than lingually convex in occlusal aspect.

Among described species of *Carpolestes*, P⁴ is known only in *C. dubius* (Jepsen, 1930a) where it is much longer than CM 16170. The fragment may represent P⁴ of *C. nigridens* (Simpson, 1928) or *C. aquilae* (Simpson, 1929), the known dentitions of which are smaller than in *C. dubius*.

Order Condylarthra
 Family Arctocyoniidae
Chriacus Cope, 1883
Chriacus pelvidens (Cope, 1881b)
 Figures 30-31

REFERRED SPECIMENS: M¹, 16240; M², 23751.



DESCRIPTION: In occlusal view, CM 16240, an M¹ (AP 7.7, TR 8.5) is nearly quadrate, with a slightly concave posterior margin and a shallow ectoflexus. The cingulum is continuous around the edge of the crown and bears a large hypocone posterior to the protocone, a small parastyle and a comparatively weaker metastyle. The protocone is large, broad at the base, and occurs anterolingually. The metacone and paracone are subequal, conical, and bunodont, and the conules are well developed.

On M², CM 23751 (AP approximately 7.0, TR 8.3), the metacone and the posterolabial corner of the crown are broken away. Relative to M¹, M² is slightly shorter, the anterior margin of the crown is gently concave, the cingulum is not continuous lingual to the protocone, and hypocone is more lingual in position.

COMMENTS: These teeth are larger than those of *C. truncatus*, but agree closely in size and crown morphology with *C. pelvidens*, known from both Torrejonian and Tiffanian horizons.

Mimotricentes Simpson, 1937

Mimotricentes sp.

Figures 36-40

REFERRED SPECIMENS: M¹, 12492, 16239; M² 12457, 12456, 23752, 23753; M³, 16205; M₁, 12458, 23754; M₂, 23755-23757.

DESCRIPTION: M¹ is quadrate in occlusal view. The protocone is large and crescentic, the paracone and metacone are subequal and conical, and the hypocone is large and bunodont and does not extend lingually beyond the protocone. The metaconule is much larger than the paraconule and lacks a premetaconulecrista. Both paraconulecristae are absent. The parastyle is stronger than the metastyle and juts anteriorly beyond the margin of the precingulum. The cingulum is continuous around the protocone on CM 16239 (AP 6.3, TR 6.5), but is discontinuous on CM 12492 (AP 6.3, TR 6.7). The ectocingulum is incomplete at the ectoflexus in both specimens. Accessory cuspsules occur on the postcingulum at the labial and lingual margins of the base of the hypocone.

On M² (CM 12457; AP 6.9, TR 8.1) the crown is more transverse than on M¹, the hypocone and conules are weaker, the parastyle is stronger, the ectoflexus is shallower, and the ectocingulum is continuous labially.

←

Plate 7. Figs. 30-31. *Chriacus pelvidens*. 30. M¹, CM 16240, occlusal view, approx. X 3. 31. M², CM 23751, occlusal view, approx. X3. Figs. 32-33. Cf. *Litomylus*. 32. M¹ or M², CM 16224, occlusal view, approx. X 10. 33. M₁ or M₂, CM 23763, occlusal view, approx. X 10. Figs. 34-35. *Phenocodus* sp. 34. M³, CM 23783, occlusal view, approx. X 3. 35. M₃, CM 16200, occlusal view, approx. X 2.

The parastylar area is broken away on CM 16205, the single referred M^3 . Relative to M^1 and M^2 , the paracone is larger and higher than the metacone on M^3 , the paraconule is much stronger than the metaconule, and the hypocone is absent.

The specimens referred to M_1 and M_2 are isolated trigonid fragments. The trigonid cusps are large, conical, and bunodont, with subequal protoconid and metaconid and smaller paraconid. On M_1 the paraconid is somewhat anteroposteriorly compressed and joined to the protoconid by a strong paracristid. On M_2 the paraconid is more nearly conical and more posteromedial in position. The paracristid is weaker on M_2 than on M_1 and the metaconid is less posterior relative to the protoconid. The enamel on all the referred molars is rugose.

COMMENTS: Van Valen and Sloan (1965) referred all species of *Tricentes* (except the type species, *T. crassicolidens*) to *Mimotricentes*. The specimens described here are larger in comparable parts of the dentition than *M. fremontensis* and *M. subtrigonus*, but are close in size to *M. latidens* and *M. angustidens*, of which only the lower dentitions have been adequately described and figured (Simpson, 1937). The characters that distinguish these two species (relative widths of talonid and trigonid on M_1 and M_2) are not discernible on these fragmentary lower molars.

Family Hyposodontidae
Cf. *Litomylus* Simpson, 1935
Figures 32-33

REFERRED SPECIMENS: M^1 or M^2 , 16224, 16228, 23758-23761; M_1 or M_2 , 23762, 23763.

DESCRIPTION: All the referred upper molars are lingual fragments. The protocone is crescentic, sharp, and anterolingual in position. The conules, preserved on CM 16224, are well defined, with sharp pre- and postconulecristae. The precingulum is very short, and ends lingually just buccal to the base of the protocone. The postcingulum is well developed and ridge-like, and curls anterolingually toward the base of the protocone. The hypocone is tiny, and is formed by the expansion of the lingual end of the postcingulum. A weak groove occurs between the hypocone and protocone on the posterolingual face of the latter. In occlusal view the crown of the upper molar fragments is essentially rectangular, with a straight lingual margin, and anterior and posterior borders that converge labially.

The two lower molars thought to pertain here are also fragmentary, with the trigonid and part of the talonid preserved on CM 23763. The protoconid and metaconid are conical, but the metaconid is taller and broader at the base. Significantly, the paraconid is extremely reduced and merely forms the lingual end of a small, ridge-like paracristid,

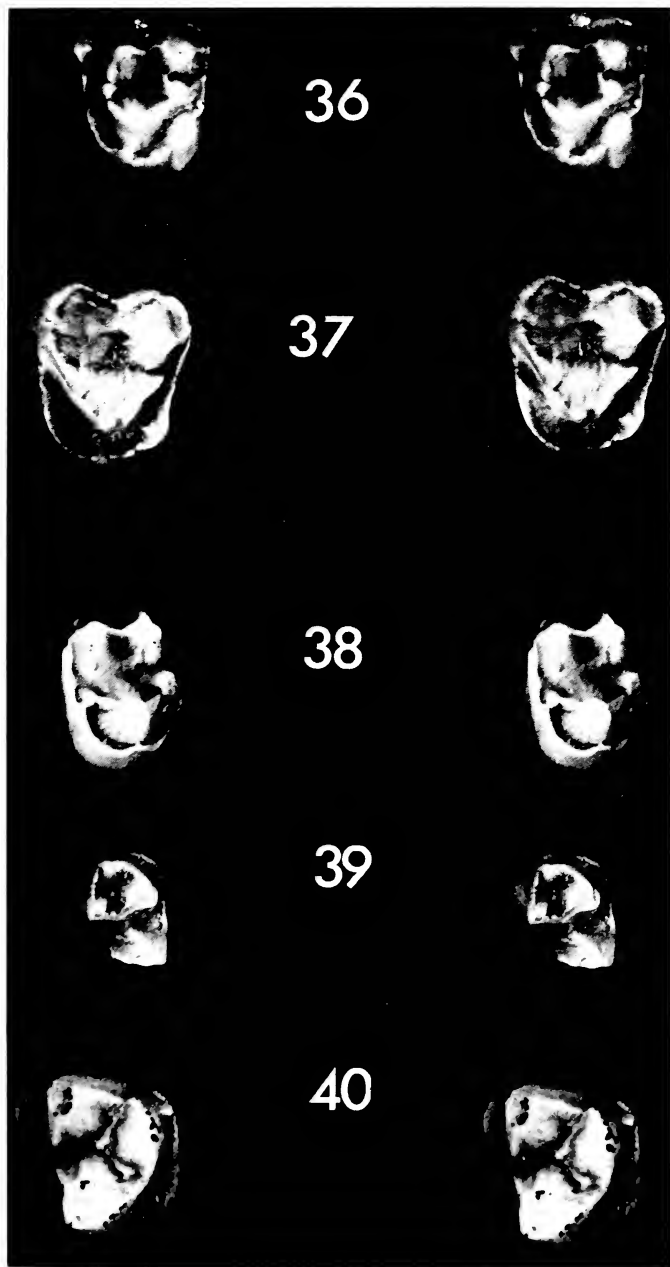


Plate 8. Figs. 36-40. *Mimotricones* sp. 36. M¹, CM 12492, occlusal view, approx. X 3. 37. M², CM 12457, occlusal view, approx. X 3. 38. M³, CM 16205, occlusal view, approx. X 3. 39. M¹, CM 12458, occlusal view, approx. X 3. 40. M₅, CM 23755, occlusal view, approx. X 5.

which extends between the anterior part of the base of the protoconid and metaconid.

COMMENTS: The fragments of the upper molars are *Litomylus*-like in the slight medial constriction of the crown, the sharp crescentic structure of the protocone and conules, and the occurrence of a tiny hypocone on a narrow postcingulum. The partial lower molars resemble *Litomylus* in the extreme reduction of the paraconid and the straight, short ridge-like nature of the paracristid. However, the referred material is considerably smaller in comparable parts of the dentition than known species of *Litomylus* and is too fragmentary to be definitely assigned to that genus.

Phenacodaptes Jepsen, 1930a

Phenacodaptes sabulosus Jepsen, 1930a

REFERRED SPECIMENS: M², 16201, 23764-23766; M₂, 16276; M₃, 23767.

COMMENTS: The referred upper and lower molars closely resemble those of *P. sabulosus*, described by Jepsen (1930a) and Gazin (1959). Comparison of the Badwater material with casts of Princeton University Nos. 17591 and 14398 (partial upper and lower dentitions, respectively, of *P. sabulosus* from Silver Coulee) revealed no significant differences in size or crown morphology.

Family Phenacodontidae

Ectocion Cope, 1882

Ectocion osbornianum Cope, 1882

REFERRED SPECIMENS: M¹ or M², 23778, 23779, 23780; M³, 16209; M₁, 23781.

DESCRIPTION: On the referred upper first or second molars, all of which are lingual fragments, the crown narrows internally and has a long lingual slope. The protocone and hypocone are large and bunodont and occur at the anterolingual and posterolingual corns of the rectangular crown. The conules are well developed, with the metaconule slightly anterior relative to the hypocone. On M³ the hypocone is absent, the paracone is about twice as large as the metacone, the conules are strong, and a well developed mesostyle is present.

CM 23781, an M₁ trigonid, bears subequal and bunodont protoconid and metaconid. Although the paraconid is not a definite cusp, the paracristid is strong, and characteristically slopes ventrolingually towards (while being separate from) the anterior part of the base of the metaconid. A distinct metastylid occurs on the posterolingual slope of the metaconid.

COMMENTS: West (1971) considered *Gidleyina* to be congeneric with *Ectocion*. The rectangular occlusal outline of the partial upper molars differs from the subquadrate condition of M¹ and M² of *Phenacodus* and species previously referred to *Gidleyina*, but resembles *Ectocion*

sensu stricto in this respect. The molars from Badwater are larger than molars of *E. parvus*, but they do not differ significantly from *E. osbornianum*, which is known from Late Tiffanian and Wasatchian deposits of Wyoming and Colorado, and from the Late Tiffanian of Alberta.

Phenacodus Cope, 1873

Phenacodus cf. *primaevus*

REFERRED SPECIMENS: M², 12475; M³, 23782; molar fragments, 23768-23777.

COMMENTS: Two species of *Phenacodus* are represented in the collection. Although the material is fragmentary, the molars show a distinct size bimodality. The larger fragments are closest in size to *P. primaevus*, which is known from Tiffanian and Wasatchian horizons. A well developed mesostyle occurs on CM 12475, a partial M², and the metaconule is large and only slightly internal relative to the metacone. On CM 23782, a fragment of M³, the metaconule occurs significantly more posterior relative to the metacone, than on M².

Phenacodus sp.

Figures 34-35

REFERRED SPECIMENS: M³, 23783; M₃, 16200.

COMMENTS: The smaller species of *Phenacodus* is represented by a complete lower and partial upper third molar. M₃ (CM 16200; AP 10.3, TR 7.3) and M³ are within the size range of *P. almiensis* (Gazin, 1942) and *P. ?bisonensis* (Gazin, 1956a) but cannot be assigned to either species until more complete material is recovered.

AGE OF THE FAUNA

Of the 22 species in the Badwater fauna, two (*Peradectes protinnominatus* and cf. *Scenopagus*) were previously known only from the Eocene, two (*Ectocion osbornianum* and *Phenacodus primaevus*) occur in late Paleocene and early Eocene rocks, and three (*Ptilodus* sp., *Ectypodus* sp. nr. *E. tardus*, and cf. *Talpavus*) possess dental features that seem to imply a late Paleocene or early Eocene stage of development. The remaining 15 species are either known only from late Paleocene deposits, or are undoubtedly of late Paleocene aspect in tooth morphology. The presence of many Paleocene, together with a number of Eocene, forms in the Badwater fauna suggests that the Badwater locality represents a previously unsampled latest Tiffanian facies. The assemblage compares most closely, although only in part, with the late Tiffanian faunas from Silver Coulee, Dell Creek, and Clark Fork, and provides the earliest known record of *Peradectes protinnominatus* and possibly *Scenopagus*. *Ectypodus* sp. nr. *E. tardus*, cf. *Talpavus* and cf. *Scenopagus* appear to be intermediate between late Paleocene and early Eocene members of those lineages. *Ptilodus* sp. is more advanced

than *P. montanus* and *P. wyomingensis* and seems to parallel the late Tiffanian *Prochetodon* in the development of P³. *Microcosmodon conus* and *Mesodma* sp., as well as the primates *Plesiadapis farisi*, *Phenacolemur frugivorus*, and *Carpolestes* sp. are reliable indicators of a late Paleocene age. Apart from *Ectocion osbornianum* and *Phenacodus* cf. *P. primaevus*, which occur in both late Tiffanian and Wasatchian deposits, the Badwater condylarths correspond to those recovered from other latest Paleocene localities.

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ARTICLE 10

TAXONOMY AND GEOGRAPHIC DISTRIBUTION OF *PEROMYSCUS MANICULATUS NUBITERRAE* RHOADS (MAMMALIA: RODENTIA)

GORDON L. KIRKLAND, JR.¹

INTRODUCTION

The deer mouse, *Peromyscus maniculatus*, is one of the most common and widely distributed small mammals in North America. Over its range, which extends from southern Mexico to the Arctic and from coast to coast, the deer mouse exhibits considerable morphological and ecological variation, with 28 continental and 38 insular subspecies recognized (Hall and Kelson, 1959). Some of these geographic races, quite distinct and associated with recognizable barriers, probably represent incipient or proto-incipient species. Other less distinct forms warrant serious re-evaluation so that a clearer picture of the systematics and taxonomy of the deer mouse may be obtained in the future. This paper presents the results of an examination of the taxonomic status and distribution of the cloudland deer mouse, *Peromyscus maniculatus nubiterrae*, a little-studied form that inhabits the higher elevations of the Appalachian Mountains from New York to Georgia. Major emphasis is placed on the relationships between the cloudland deer mouse and the morphologically and ecologically similar woodland deer mouse, *Peromyscus maniculatus gracilis* (LeConte).

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LITERATURE

P. m. nubiterrae has been infrequently studied or used as a laboratory animal. Most work published on this form has concerned new localities and status reports in state mammal surveys, along with references to habitat selection (Bailey, 1946; Barbour, 1941; Cady, 1941; Coleman, 1948; Gifford and Whitebread, 1951; Golley, 1962, 1966; Grimm and Roberts, 1950; Handley and Patton, 1947; Kellogg, 1939; Komarek and Komarek, 1938; Odum, 1949; Paradiso, 1969; Richmond and Roslund, 1949; Roslund, 1951; Wilson, 1945; Wilson and Friedel, 1942). Notable exceptions are the coverage of this subspecies by Osgood (1909), plus Linzey's (1970) examination of early growth and development, Kirkland and Linzey's (1973) notes on reproductive success, and Bradshaw and George's (1969) description of the karyotype.

By comparison, *P. m. gracilis* is a well-known and much-studied form. King (1969) provides an overview of the abundant and varied research conducted on this subspecies.

METHODS AND MATERIALS

Data for this study were obtained from *Peromyscus maniculatus* specimens housed in Carnegie Museum of Natural History (CM), the National Museum of Natural History (USNM), the Museum at Michigan State University (MSU), and the Shippensburg State College Vertebrate Museum (SSC). External measurements (given in mm) for total length, tail length, body length (total length minus tail length), hind foot length, ear length, and weight (given in gm) were obtained from tags accompanying specimens. Because ear length and weight frequently were not recorded, these characters are represented in the statistics by smaller sample sizes than are other external characters. Only specimens judged to be adults, i.e., having a total length of at least 160 mm, as suggested by Linzey's (1970) data, were used in the study. A total of 806 specimens was examined: 595 *P. m. nubiterrae*

TABLE 1
COMPOSITION BY SEX AND PLACE OF ORIGIN OF SPECIMENS EXAMINED

Subspecies	No. skulls		No. skins		State	Museum
	M ¹	F ²	M	F		
<i>P. m. nubiterrae</i>			7	7	Georgia	USNM
			24	15	Maryland	USNM
	4	6	14	13	Kentucky	USNM
	27	23	183	144	Pennsylvania	CM
	9	1	30	33	N. Carolina	USNM
	2	8	11	10	N. Carolina	CM
	6	4	16	22	Tennessee	USNM
			11	6	Virginia	USNM
	6	4	28	21	W. Virginia	USNM
			54	46	324	271
<i>P. m. gracilis</i>	15	5	6	4	Michigan	MSU
			10	8	Michigan	USNM
	6	4	14	14	N. Hampshire	USNM
	2	1	10	9	New York	USNM
	7	6	11	19	New York	SSC
	1	3	17	11	Ontario	CM
	19	31	28	50	Pennsylvania	CM
			50	50	96	115

¹M = Males.

²F = Females.

and 211 *P. m. gracilis* (Table 1).

I examined 100 skulls of each subspecies (Table 1). Ten measurements were taken on each skull, using Helios dial micrometers (1/20 mm calibration). The skull measurements included:

1. Greatest length: from the anterior tip of the nasals to the posterior-most portion of the braincase.
2. Condylbasal length: from the anterior base of the incisors to the posterior point of the occipital condyle.
3. Interorbital breadth: the shortest distance between the orbits.
4. Cranial breadth: the width of the braincase at its widest point.
5. Maxillary tooth row: length of the cheek tooth row from the anterior base of M¹ to the posterior base of M³.
6. Nasal: the greatest anterior-posterior length of the nasal bones.
7. Shelf of bony palate: length of the palate from the posterior edge of the incisive foramen to the posterior edge of the palate.
8. Diastema: length of the space between the anterior base of M¹ and the posterior-lateral base of the incisor.
9. Palatine slits: the greatest length of the incisive foramen.
10. Postpalatal length: distance from the posterior medial edge of the palate to the anterior edge of the foramen magnum.

EXTERNAL AND SKULL MORPHOLOGY

P. m. nubiterrae and *P. m. gracilis* are exceedingly similar in morphology and ecology. Hamilton (1943) describes *P. m. nubiterrae* as "not well characterized, but being a peripheral form, has slight differences which set it off from *gracilis* to the north." Osgood (1909) describes *P. m. nubiterrae* as being similar to *P. m. gracilis* but slightly smaller and with a broader, better-defined middorsal dusky area. Osgood also notes that the skull of *P. m. nubiterrae* is similar to that of *P. m. gracilis* but decidedly smaller. The data obtained in this study confirm these previous observations. *P. m. nubiterrae* is, indeed, very similar to *P. m. gracilis* and possibly is better defined geographically than morphologically or ecologically.

Tables 2 and 3 contain the means, standard errors, standard deviations, coefficients of variation and ranges for six specimen tag measurements of 595 *P. m. nubiterrae* (324 males; 271 females) and 211 *P. m. gracilis* (96 males; 115 females). Comparisons of sexes within subspecies reveal that females tend to be larger than males. In both subspecies the hind foot measurement for males was greater than that for females, but the difference was not significant (Student's t-test; Tables 2 and 3). Because of the significant sex differences in both species for total length, body length, weight, and tail length in *P. m. gracilis*, all comparisons between subspecies were made between samples of the same sex.

Statistical comparisons of the two subspecies using Student's t-test reveal that female *P. m. gracilis* are significantly larger than female *P. m. nubiterrae* in all six measurements (Table 4). In males, *P. m. gracilis* averaged larger than *P. m. nubiterrae* in all measurements but weight. The differences were significant for total length, hind foot length, and body length. The overlap of the range of measurements for each character is large, ranging from 63% for the hind foot of females to 90% for the body length of males. In general, males of each subspecies seem to be somewhat less differentiated than the females. In males the overlap for the six characters averages 83.5%, while in females it averages 70.6%. The coefficients of difference for external measurements range from .12 to .32 (Table 4). This is far below the level of 1.28 suggested by Mayr (1969) for distinguishing subspecies. Thus, data from the external measurements confirm that on the average, *P. m. nubiterrae* is slightly smaller than *P. m. gracilis*.

The same size relationship between *P. m. nubiterrae* and *P. m. gracilis* is evident in the data from the 10 skull characters examined. Tables 5 and 6 contain, respectively, statistics for the skull measurements of *P. m. nubiterrae* and *P. m. gracilis*. The differences in skull measurements are not as pronounced as in the skin measurements. *P. m. nubiterrae* females average larger than males in nine of ten characters,

TABLE 2
UNIVARIATE STATISTICAL COMPARISON OF EXTERNAL MEASUREMENTS OF ADULT *P. m. nubiterrae*

Measurement	N	Mean	S.E.	S.D.	C.V.	Range	t-ratio
Males:							
Total length	324	174.88	.46	8.37	4.79	160-202	4.45***
Tail length	324	89.34	.36	6.49	7.27	70-111	1.95
Hind foot	324	20.69	.05	.81	3.94	19-25	1.83
Ear length	199	18.75	.09	1.25	6.65	15-22	1.46
Body length	324	85.50	.27	4.94	5.78	74-102	5.27***
Weight	189	17.79	.08	1.07	6.03	13-24	2.18*
Females:							
Total length	271	178.15	.58	9.58	5.38	160-205	
Tail length	271	90.38	.39	6.47	7.15	70-109	
Hind foot	270	20.57	.05	.77	3.74	18-23	
Ear length	171	18.57	.09	1.11	6.00	15-22	
Body length	271	87.79	.34	5.64	6.43	74-101	
Weight	150	18.37	.28	3.44	18.72	12-29	

*Significant at .05 level.

***Significant at .001 level.

TABLE 3
UNIVARIATE STATISTICAL COMPARISON OF EXTERNAL MEASUREMENTS OF ADULT *P. m. gracilis*.

Measurement	N	Mean	S.E.	S.D.	C.V.	Range	t-ratio
Males:							
Total length	96	176.79	.80	7.87	4.45	161-196	5.06***
Tail length	96	88.19	.57	5.56	6.30	74-105	4.32***
Hind foot	96	21.29	.12	1.16	5.45	18-25	1.17
Ear length	67	19.04	.13	1.08	5.70	14-21	1.43
Body length	96	88.59	.56	5.49	6.20	72-103	3.68***
Weight	37	17.37	.37	2.24	12.89	14-23.5	4.37***
Females:							
Total length	115	183.53	1.02	10.89	5.90	160-221	
Tail length	115	91.96	.64	6.89	7.50	74-117	
Hind foot	115	20.99	.21	10.82	2.27	17-25	
Ear length	96	19.36	.16	1.60	8.25	14-24	
Body length	115	91.60	.58	6.25	6.82	78-110	
Weight	63	20.42	.50	3.88	19.02	12-33.5	

***Significant at the .001 level.

TABLE 4
COMPARISON¹ OF MEANS OF SIX EXTERNAL MEASUREMENTS OF *P. m. gracilis* AND
P. m. nubiterrae (g.—n.).

Variable	N	g.—n.	t-ratio	% Overlap	C.D.
Males:					
Total length	420	1.91	1.99*	83	.12
Tail length	420	1.51	1.57	76	.13
Hind foot	420	.60	5.70***	86	.30
Ear length	266	.29	1.70	75	.12
Body length	420	3.09	5.25***	90	.30
Weight	226	-.42	1.76	86	.13
Females:					
Total length	386	5.38	4.84***	74	.26
Tail length	386	1.58	2.15*	74	.12
Hind foot	385	.42	2.70**	63	.14
Ear length	267	.79	4.75***	70	.29
Body length	386	3.81	5.87***	64	.32
Weight	213	2.05	3.81***	79	.28

*Significant at .05 level.

**Significant at .01 level.

***Significant at .001 level.

¹Student's t-test with percent overlap of range, and coefficient of differentiation after Mayr, 1969.

while *P. m. gracilis* females average larger than males in seven of ten characters. The only significant difference is in the cranial breadth of *P. m. gracilis*, in which males exceed females. The reason for this difference is not evident.

Comparison of the subspecies reveals that *P. m. gracilis* is significantly larger than *P. m. nubiterrae* in seven of ten characters in each sex (Table 7). The width of the interorbital constriction is the only character in which the mean for both sexes is greater in *P. m. nubiterrae*, but this greater difference is significant only in males. The overlap in measurements for the ten characters averages 61% in males and 70.3% for females. In this statistic, the females of the two subspecies appear to be about as equally differentiated as in skin measurements. However, the overlap range for skull-characters in males is much less than for skin measurements. This suggests that males may be more differentiated in skull morphology than in external anatomy. The coefficients of difference range from .05 for the cranial breadth in females to .62 (Table 7). The coefficients of difference average .40 in males and .31 in females. Once again these levels are below those normally accepted for subspecies differentiation (Mayr, 1969).

The analysis of skin and skull measurements verifies the observations of earlier workers. *P. m. nubiterrae* is slightly smaller than *P. m. gracilis*. Although populations of the two subspecies may be distin-

TABLE 5
STUDENT'S T-TEST OF CRANIAL MEASUREMENTS OF *P. m. nubiterrae* BY SEX

Measurement	N	Mean	S.E.	S.D.	C.V.	Range	t-ratio
Males:							
Condylobasal length	54	21.88	.10	.75	3.42	20.05-23.65	1.35
Greatest length	54	24.46	.09	.64	2.63	23.1-25.9	.58
Cranial breadth	54	11.33	.05	.38	3.32	10.2-12.15	.00
Interorbital breadth	54	3.90	.02	.13	3.42	3.65-4.3	.00
Maxillary tooth row	54	3.42	.02	.13	3.91	3.1-3.65	1.81
Nasal	54	9.71	.05	.37	3.83	8.85-10.5	.33
Shelf of bony palate	54	4.02	.04	.26	6.55	3.55-4.85	1.73
Palatine slits	54	4.58	.04	.27	5.80	3.85-5.25	1.77
Diastema	54	6.49	.04	.29	4.52	5.85-7.1	.48
Postpalatal length	54	8.56	.05	.34	4.02	7.7-9.6	1.80
Females:							
Condylobasal length	46	22.10	.13	.88	3.98	20.3-23.55	
Greatest length	46	24.55	.13	.90	3.65	22.55-26.5	
Cranial breadth	46	11.33	.04	.29	2.60	10.8-11.9	
Interorbital breadth	46	3.90	.02	.14	3.63	3.55-4.2	
Maxillary tooth row	46	3.48	.03	.19	5.53	3.2-4.45	
Nasal	46	9.74	.08	.53	5.46	8.55-10.8	
Shelf of bony palate	46	3.93	.04	.26	6.53	3.35-4.5	
Palatine slits	46	4.73	.04	.30	6.33	4.1-5.85	
Diastema	46	6.54	.05	.33	5.10	5.8-7.4	
Postpalatal length	46	8.69	.06	.38	4.33	8.05-9.6	

TABLE 6
STUDENT'S T-TEST OF CRANIAL MEASUREMENTS OF *P. m. gracilis* BY SEX

Measurement	N	Mean	S.E.	S.D.	C.V.	Range	t-ratio
Males:							
Condylobasal length	50	22.71	.08	.59	2.60	21.4-23.9	.77
Greatest length	50	25.19	.19	.64	2.52	23.8-26.25	.00
Cranial breadth	50	11.53	.05	.32	2.78	10.95-12.4	3.28**
Interorbital breadth	50	3.80	.03	.18	4.69	3.5-4.3	1.81
Maxillary tooth row	50	3.47	.02	.14	3.98	3.1-3.8	1.33
Nasal	50	10.02	.06	.42	4.27	9.05-11.2	.22
Shelf of bony palate	50	4.10	.03	.21	5.17	3.6-4.5	.49
Palatine slits	50	4.88	.04	.29	5.93	4.3-5.6	1.12
Diastema	50	6.85	.04	.29	4.23	6.3-7.4	1.46
Postpalatal length	50	8.92	.04	.31	3.52	8.2-9.45	.82
Females:							
Condylobasal length	50	22.81	.10	.70	3.08	21.6-24.45	
Greatest length	50	25.19	.10	.71	2.82	23.7-26.65	
Cranial breadth	50	11.36	.05	.32	2.85	10.65-11.95	
Interorbital breadth	50	3.86	.02	.15	3.84	3.55-4.15	
Maxillary tooth row	50	3.43	.02	.16	4.56	3.1-3.85	
Nasal	50	10.04	.07	.49	4.87	8.95-11.4	
Shelf of bony palate	50	4.08	.03	.20	4.86	3.65-4.45	
Palatine slits	50	4.95	.05	.33	6.71	3.65-5.7	
Diastema	50	6.94	.05	.33	4.69	6.1-7.6	
Postpalatal length	50	8.98	.06	.41	4.59	8.0-9.95	

**Significant at .01 level.

TABLE 7
COMPARISON¹ OF MEANS OF TEN CRANIAL MEASUREMENTS OF *P. m. gracilis* AND
P. m. nubiterrae (g.—n.).

Variable	N	g.—n.	t-ratio	% Overlap	C.D.
Males:					
Condylobasal length	104	.88	6.24***	58	.62
Greatest length	104	.73	5.83***	67	.57
Cranial breadth	104	.24	3.50***	55	.34
Interorbital breadth	104	-.10	3.33***	81	.32
Maxillary tooth row	104	.05	1.89	39	.19
Nasal	104	.31	4.01***	62	.10
Shelf of bony palate	104	.08	1.71	69	.17
Palatine slits	104	.30	5.48***	52	.54
Diastema	104	.36	6.27***	52	.62
Postpalatal length	104	.36	5.56***	66	.55
Females:					
Condylobasal length	96	.71	4.39***	47	.41
Greatest length	96	.64	3.90***	70	.40
Cranial breadth	96	.07	.48	85	.05
Interorbital breadth	96	-.04	1.33	92	.17
Maxillary tooth row	96	-.05	1.39	49	.14
Nasal	96	.30	2.89**	65	.29
Shelf of bony palate	96	.15	3.20**	71	.33
Palatine slits	96	.22	3.40***	73	.35
Diastema	96	.41	6.12***	72	.62
Postpalatal length	96	.29	3.60***	79	.37

**Significant at .01 level.

***Significant at .001 level.

¹Student's t-test with percent overlap of range, and coefficient of differentiation after Mayr, 1969.

guished statistically on the basis of most skull and skin measurements, it is difficult to assign individual specimens to either subspecies on the basis of these characters because of the extensive overlap between them. In identifying single individuals, characteristics other than skin and skull measurements should be used.

COLOR COMPARISONS

Some authors have used dorsal coloration as a key character in distinguishing between *P. m. nubiterrae* and *P. m. gracilis* (Osgood, 1909; Hamilton, 1943). *P. m. nubiterrae* is described as having a darker, broader middorsal stripe; however, both subspecies exhibit considerable variation in color intensity and width of the middorsal stripe.

The stripe in *P. m. nubiterrae* often exceeds one-half the width of the back, while in *P. m. gracilis* it is often less than one half. In addition, the contrast between the sides and the back stripe is often lacking in *P. m. gracilis*, so that no back stripe is evident.

Specimens of the two races from Pennsylvania are darker and more frequently have a noticeable middorsal stripe than do *P. m. gracilis* from New York and New Hampshire. In *P. m. nubiterrae*, the middorsal stripe becomes more distinct in populations south of Pennsylvania. This suggests a north-south gradient for dorsal coloration, with intermediate populations in Pennsylvania being the most similar.

On the basis of specimens at the National Museum of Natural History, it is possible to differentiate non-Pennsylvania specimens with regularity on the basis of dorsal coloration. *P. m. gracilis* from New Hampshire are consistently lighter than *P. m. nubiterrae* from Georgia, North Carolina, Tennessee, Kentucky, Virginia, Maryland, and West Virginia. Compared to a series of 28 from New Hampshire, only 10 of 326 specimens from Georgia to Maryland were lighter than the darkest specimen from New Hampshire.

Thus, with the exception of specimens from Pennsylvania, dorsal coloration and the appearance of the middorsal stripe are the best characters by which specimens of the two subspecies may be distinguished without long series. Over most of its range, *P. m. nubiterrae* has a conspicuously darker dorsum with a more distinct middorsal stripe.

BREEDING CHARACTERISTICS

Although there is no evidence that *P. m. nubiterrae* and *P. m. gracilis* differ in reproductive characteristics in the wild, they do exhibit marked differences in reproductive success in the laboratory. *P. m. nubiterrae* is an excellent breeder, while *P. m. gracilis* is fair to poor (Kirkland and Linzey, 1973). This differential breeding success under laboratory conditions is exhibited by Pennsylvania and non-Pennsylvania individuals of the two subspecies. The results of recent cross matings between males of one subspecies and females of the other suggest that the lack of breeding success in *P. m. gracilis* may be due to female inhibition. Male *P. m. gracilis* will successfully mate with female *P. m. nubiterrae*, but previously reproductively successful *P. m. nubiterrae* males do not mate successfully with female *P. m. gracilis*. This differential breeding success in the laboratory is one of the most important and consistent distinctions between *P. m. nubiterrae* and *P. m. gracilis*. It indicates that these two subspecies represent differentiated gene pools, in spite of obvious morphological similarities.

KARYOTYPES

Differences in karyotypes between *P. m. gracilis* and *P. m. nubiterrae* have been reported by Bradshaw and Hsu (1972). *P. m. nubiterrae* has either 34 or 36 banded autosomes, while *P. m. gracilis* has either

36 or 38. According to Bradshaw and Hsu, there appears to be a north-south cline for autosome number in these two subspecies. In *P. m. nubiterrae* from North Carolina, the autosome number is typically 34 to 36. In Pennsylvania 36 autosomes are present, and the number increases to 36 to 38 for *P. m. gracilis* specimens from Vermont and New Hampshire. In *P. m. nubiterrae*, specimens with 34 biallelic autosomes occur more frequently than do specimens with 36. These data provide further evidence of differentiated gene pools and of clinal gradients in *P. maniculatus* along the Appalachian Mountains.

DISTRIBUTION

P. m. nubiterrae is restricted to the mountains of the Appalachian chain, and occurs in ten states: Georgia, South Carolina, North Carolina, Tennessee, Kentucky, Virginia, West Virginia, Maryland, Pennsylvania, and New York. A disjunct population of *P. m. nubiterrae* may exist adjacent to Pymatuning Swamp in Crawford County, Pennsylvania. Thirteen specimens (CM) collected in March and April, 1932, from 2 miles S.W. of Linesville and the south edge of Pymatuning Swamp are typical of *P. m. nubiterrae*. Although *P. m. nubiterrae*'s north-south range extends nearly 650 miles, its east-west distribution is probably less than 175 miles at its widest point. An examination of capture localities from the literature and museum specimens (see Specimen Localities and Literature Records below) reveals that the cloud-land deer mouse is somewhat more restricted in its distribution than Hall and Kelson (1959) suggest (Figure 1). This is particularly true for its absence from the Tennessee Valley, although *P. m. nubiterrae* occurs in a small section of mountains in the eastern portion of Tennessee. *P. m. nubiterrae* tends to live at higher elevations, but the data of Wilson (1945) suggest that it may occur as low as a 900 foot elevation in Virginia. Most workers conclude that it is most abundant above the 2500-3500-foot level in the forests of the Canadian Zone. Its occurrence at lower elevations is limited to cool shaded valleys.

P. m. gracilis has a more northern distribution, which extends from northeastern Pennsylvania through New York and much of northern New England. It also extends westward through southern Canada to Michigan, Wisconsin, and Minnesota (Hall and Kelson, 1959). Within this range, *P. m. gracilis* inhabits cool, deciduous, boreal forests (Klein, 1960).

The interface between the ranges of *P. m. nubiterrae* and *P. m. gracilis* is located in north-central Pennsylvania. In this region there is undoubtedly some intergradation between the two subspecies (Grimm & Whitebread, 1952; Benton & Altman, 1964). The current boundary between the two subspecies, as drawn by Hall and Kelson (1959), is based on Roslund's (1951) designation of 23 deer mice from Bradford

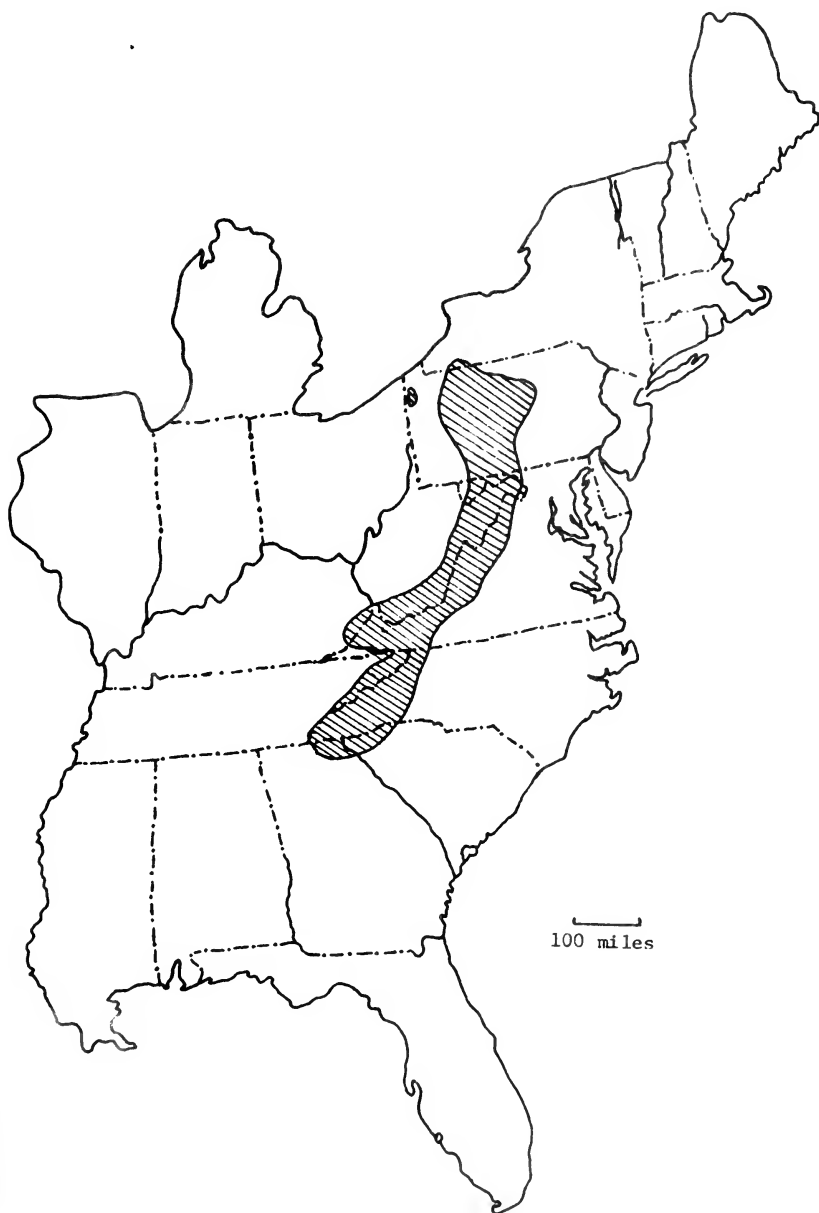


Fig. 1. Range of *Peromyscus maniculatus nubiterrae*.

and Sullivan counties as *P. m. nubiterrae*. I believe that these specimens (CM 32281; 32300-03; 32519-21; 32523-24; 32526-27; 32529-30; 32532; 32534; 32535; 32539; 32541-44; 32553) should be redesignated as *P. m. gracilis*. There are no obvious color differences between the 23 specimens in question and specimens of either subspecies from Pennsylvania. However, the means of the skin measurements are more similar to those of the 78 *P. m. gracilis* from northern Pennsylvania than to the 307 *P. m. nubiterrae* from western Pennsylvania (Table 8). None of the differences are significant. The redesignation of these specimens results in a constriction of the northern and eastern borders of *P. m. nubiterrae* until the range corresponds more or less with the unglaciated portions of central Pennsylvania. Thus in Pennsylvania *P. m. gracilis* is restricted to the glaciated portions of the northeastern part of the state.

TABLE 8
COMPARISON OF *P. maniculatus* FROM BRADFORD AND SULLIVAN COUNTIES TO
P. m. gracilis AND *P. m. nubiterrae* FROM ELSEWHERE IN PENNSYLVANIA.¹

n=	<i>P. maniculatus</i> Bradford & Sullivan co.'s 23	<i>P. m. gracilis</i> Northeastern Pennsylvania 78	<i>P. m. nubiterrae</i> Central and western Pennsylvania 307
	Mean	Mean (diff.)	Mean (diff.)
Total length	179.96	182.27 (+2.31)	176.88 (-3.08)
Tail length	92.61	93.01 (+.50)	90.83 (-1.78)
Body length	87.35	89.26 (+1.91)	86.04 (-1.31)
Hind-foot length	21.04	21.28 (+.24)	20.74 (-.30)
Ear length	19.61	19.07 (+.54)	18.73 (-.88)
		Σdiff 5.50 mm	Σdiff 7.35 mm

¹Sexes combined.

SUBSPECIES FORMATION

Using normal taxonomic criteria, it is difficult to justify the recognition of two extremely similar subspecies whose current range interface (Hall and Kelson, 1959) does not correspond with a major physiographic or biological barrier. An appropriate solution under these circumstances might be to designate *P. m. nubiterrae* and *P. m. gracilis* as a single subspecies, *P. m. gracilis*, which exhibits typical north-south character gradients. However, if the 23 previously mentioned Bradford and Sullivan counties, Pennsylvania, specimens (CM) are actually *P. m. gracilis* and not *P. m. nubiterrae*, then the subspecies boundary corresponds with the farthest advance of the Wisconsin Ice Front. The existence of the two forms as separate gene pools then may be justified on historical grounds.

The area now occupied by *P. m. nubiterrae* was not glaciated. However, *P. m. nubiterrae* was probably shifted southward along the Appalachians during the late Pleistocene. Guilday (1971) has documented the southward displacement of an arctic-subarctic mammal fauna into the central Appalachians. Any southward displacement of *P. m. nubiterrae* may have been tempered by altitudinal shifts into lowland areas.

The region now occupied by *P. m. gracilis* was totally covered by ice during the Pleistocene. During the Wisconsin glaciation, the stock from which the current *P. m. gracilis* is derived must have resided in the range of one or more of the other current subspecies of *P. maniculatus* (or their parental stocks), or in an area in the East or Midwest that was then ecologically suitable. In the East, *P. m. gracilis* may have resided in Pleistocene refugia in New Jersey. Braun (1947, 1964) has documented boreal forest elements in New Jersey during the Pleistocene. Wetzel (1955) has concluded that the presence of *Synaptomys cooperi* on the Delmarva Peninsula and southward on the Virginia-North Carolina coast provides evidence of an Atlantic Coast refugium for boreal species during the Pleistocene.

I propose that these subspecies were formed during the late Pleistocene when *P. m. gracilis* was pushed south and east into a coastal refugium, while *P. m. nubiterrae* continued to reside in the unglaciated part of the Appalachian Mountains. This period of separation during the Wisconsin permitted the development of the behavioral differences reflected in the independent breeding responses under laboratory conditions. The extremely similar morphology of the two forms has resulted from living under similar environmental conditions over a long period of time. The higher elevations in the southern Appalachians are and have been similar in vegetation and climate to the northern areas currently inhabited by *P. m. gracilis*.

OTHER SUBSPECIES

In addition to its geographical proximity and close relationship to *P. m. gracilis*, *P. m. nubiterrae* is partially sympatric with the Prairie Deer Mouse, *Peromyscus maniculatus bairdii* (Hoy and Kennicott). The latter race has extended its range eastward, apparently in response to extensive clearing of forests (Paradiso, 1969). *P. m. bairdii* exhibits strong preferences for open grassland habitats and seldom ventures into forest areas (Harris, 1952; Wecker, 1963). Thus, although geographically sympatric, the two races are ecologically separated (Hall and Kelson, 1959; Paradiso, 1969).

P. m. nubiterrae and *P. m. bairdii* are also morphologically distinct. *P. m. bairdii* is one of the short-tailed grassland races of deer mice, and its external measurements markedly distinguish it from the longer-tailed, larger-bodied *P. m. nubiterrae*. In Pennsylvania the ranges of

the standard skin measurements for *P. m. bairdii* are: total length, 121-160 mm; tail length, 50-70 mm.; hind-foot length, 16-19 mm.; ear length, 12-14 mm. (Doutt, et al., 1973). There is thus no overlap with measurements of *P. m. nubiterrae*.

SUMMARY

Peromyscus maniculatus nubiterrae occupies a range along the higher elevations of the Appalachian Mountains from New York to Georgia, predominantly in areas that were not glaciated. It is poorly differentiated from *P. m. gracilis*, which occupies a range to the north and east of *P. m. nubiterrae* that was once glaciated. On the basis of skull and external morphology, it is difficult to justify the retention of *P. m. nubiterrae* as a separate subspecies. Dorsal coloration is the best character by which to distinguish between these two forms. *P. m. nubiterrae* tends to have a darker and more distinct middorsal stripe.

An additional criterion for retaining *P. m. nubiterrae* as a subspecies separate from *P. m. gracilis* is the success attained in its differential breeding in the laboratory. This distinction suggests genetic differences between *P. m. nubiterrae* and *P. m. gracilis* that are not observed in external and skull morphology. Karyotypic differences have also been observed between the two subspecies. These differences were probably acquired during the late Pleistocene when, it is hypothesized, *P. m. gracilis* occupied a refugium in New Jersey, while *P. m. nubiterrae* occupied an Appalachian range.

SPECIMEN LOCALITIES AND LITERATURE RECORDS

The localities of the 595 skins and 100 skulls of *P. m. nubiterrae* examined in this study are listed below. Museums housing each group of specimens examined are listed at the end of these sections. County records from a search of the literature are also given.

GEORGIA. Specimens examined: Rabun County, Rabun Bald. Towns County, Brass-town Bald (USNM). Literature records: Lumpkin; Rabun; Towns; Union; White counties (Golley, 1962).

KENTUCKY. Specimens examined: Harlan County, Black Mountain (USNM).

MARYLAND. Specimens examined: Garrett County, Grantsville; 6 mi. N Frostburg (USNM). Literature records: Allegany; Garrett counties (Paradiso, 1969).

NORTH CAROLINA. Specimens examined: Clay County, 12½ mi. E Hayesville (USNM). Haywood County, 7½ mi. S Waynesville (CM). Macon County, Highlands; 10 mi. W Franklin - Wayah Bald (USNM). Mitchell County, near summit Roan Mt. (CM); 7½ mi. SW town of Roan Mountain, Carter Co., Tennessee; and Glen Ayre, Roan Mt. (USNM). Rutherford County, Cove Creek. Transylvania County, Pisgah Forest - Bent Creek Experimental Station. Watauga County, Grandfather Mt.; 7½ mi. N Elk Knob. Yancey County, Mt. Mitchell; 3½ mi. S Mt. Mitchell summit (USNM). Literature records: Jackson; Macon counties (Odum, 1949). Buncombe; Henderson; Macon; Mitchell; Swain; Transylvania counties (Brimley, C.S., 1944-46).

PENNSYLVANIA. Specimens examined: Bedford County, 6 mi. NW Immler; 7 mi. NW Immler; 2 mi. E Osterburg. Cambria County, 5 mi. N Ebensburg; 5 mi. NNE Ebensburg;

5½ mi. NE Ebensburg; 5 mi. NE Ebensburg; 1¼ mi. SW Patton. Cameron County, 8 mi. NNW Emporium - Three Mile Run. Centre County, 2.3 mi. SE Woodward - Cherry Run. Clearfield County, McGees Mills; 4 mi. NW Cessna Run; 0.7 mi. SE McGees Mills. Crawford County, S edge Pymatuning Swamp; 2 mi. SW Linesville. Fayette County, ¼ mi. S Ohiopyle; 4 mi. SE Ohiopyle; 2½ mi. NW Markleysburg; 2 mi. E Markleysburg; 2 mi. NW Markleysburg. Forest County, Brookston. Huntingdon County, 5 mi. NE McAlveys Fort; 5½ mi. NE McAlveys Fort. Indiana County, 8½ mi. SE Indiana; Cessna Run - 4 mi. NW Glen Campbell; Glen Campbell. Jefferson County, 5½ mi. NE Sigel; 8 mi. NE Sigel - Heath Station. Lycoming County, 6½ mi. S Nisbet. McKean County, 10 mi. SW Bradford - Sugar Run; Sugar Run; 3 mi. N Clermont - Red Mill Run; 4 mi. E Clermont. Mifflin County, 5 mi. W Milroy. Potter County, 4 mi. SW Ulysses - Gold; 8 mi. NE Coudersport; 4 mi. NW Costello; Costello; 6½ mi. S Ulysses - Buckseller Run; 5½ mi. SW Ulysses - Cobb Hill; 5½ mi. SW Ulysses - Rapple Hollow; 7½ mi. SW Ulysses - Woodcock Run. Somerset County, 2 mi. SSE Somerset; ½ mi. W Bakersville; 8 mi. NW Somerset; 10 mi. NW Somerset; 5½ mi. WSW Jennerstown; 5 mi. WSW Jennerstown; 4½ mi. NW Salisbury; 5 mi. NW Salisbury. Warren County, 5 mi. E Columbus - Benson Swamp; 5 mi. N Kinzua; 2½ mi. N Kinzua. Westmoreland County, 6 mi. SSE Laughlinton; Laughlinton; ½ mi. SSE Rector - Lynn Run; 3 mi. SSE Rector; 2 mi. SSE Rector; 7¾ mi. S Laughlinton - Bald Knob Tower; 1½ mi. SSE Rector - Lynn Run; 5 mi. SE Rector; 6 mi. S Laughlinton; 4½ mi. SSE Rector; ½ mi. ESE Laughlinton (CM).

TENNESSEE. Specimens examined: Carter County. Cocke County, Snake Den Mt.; 4½ mi. SE Cosby - Low Gap; Old Black Mt.; Inadu Knob; Mt. Guyot. Johnson County, Holston Mts.; 3½ mi. NE Shady Valley - Holston Mt. (USNM). Literature records: Blount; Carter; Cocke; Johnson; Sevier; Sullivan counties (Kellogg, 1939).

VIRGINIA. Specimens examined: Bedford County, Peak of Otter. Giles County, Mountain Lake. Grayson County, Mt. Rogers - Troutdale. Page County, Skyland. Rappahannock County, Devil's Stairs - Washington (USNM). Literature records: Dickenson; Giles; Grayson; Highland; Page; Rappahannock; Smyth; Tazewell; Wise counties (Bailey, 1946). Augusta; Bedford; Giles; Grayson; Highland; Page; Rappahannock; Shenandoah; Smyth; Tazewell; Washington; Wise counties (Handley and Patton, 1947).

WEST VIRGINIA. Specimens examined: Greenbrier County, White Sulphur Springs. Mercer County, Flat Top. Pocahontas County, Cranberry Glades; Dubbin - Middle Mt. Raleigh County, SW of Pemberton - Windy Gulf; Flat Top Mt. Randolph County, Cheat Bridge. Pendleton County, Spruce Knob (USNM). Tucker County, 2 mi. S Parsons (SSC). Literature records: Monongalia County (Wilson, 1945).

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ARTICLE 11

EOCENE FOSSIL MAMMALIA FROM THE SAND WASH BASIN, NORTHWESTERN MOFFAT COUNTY, COLORADO

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INTRODUCTION

A small, biostratigraphically significant assemblage of fossil vertebrates has been accumulated over the past 50 years from the Sand Wash Basin of northwestern Moffat County, Colorado. The Sand Wash deposits that yielded these fossils appear to be an outlier of the much better known Washakie Formation of the Washakie Basin to the north, and there are numerous faunal similarities as well. The mammals provide evidence suggesting that faunas representing both Bridgerian and Uintan land-mammal ages may be recognized in the Sand Wash beds.

The previously published record of Sand Wash Eocene vertebrates is incomplete. This paper documents the entire mammalian fauna known to us, updates and consolidates taxa that have been previously published, and examines the biostratigraphic position of the Sand Wash fauna.

HISTORY OF STUDY

Fossil vertebrates from the Sand Wash Basin were first collected by Carnegie Museum of Natural History parties directed by Earl Douglass and including J. Leroy Kay in 1922, 1923, and 1924. These collec-

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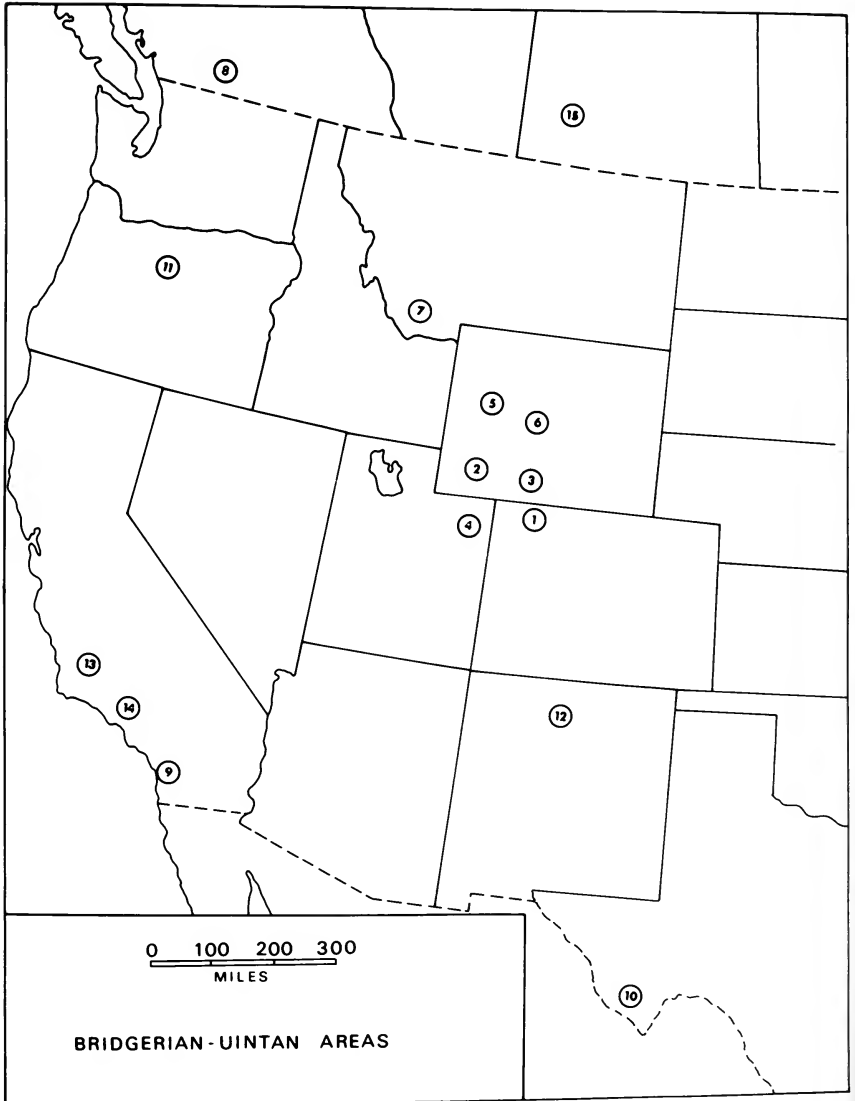


Fig. 1 Distribution of Bridgerian and Uintan mammalian fossil-producing areas in western North America. Areas indicated as follows: 1. Sand Wash Basin; 2. Green River Basin; 3. Washakie Basin; 4. Uinta Basin; 5. Togwotee Pass; 6. Wind River Basin; 7. Southwestern Montana; 8. Princeton; 9. San Diego; 10. Big Bend; 11. Clarno; 12. Galisteo; 13. Sespe; 14. Poway; 15. Swift Current Creek.

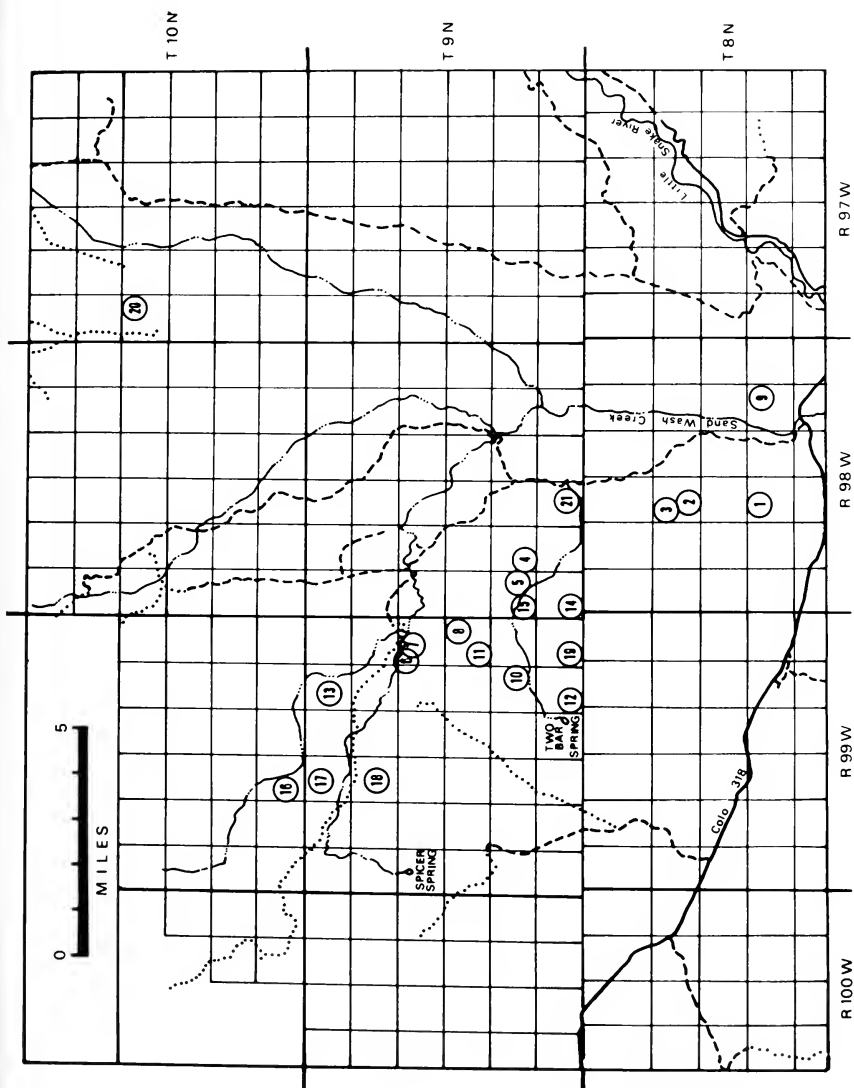


Fig. 2. Outline map of part of the Sand Wash Basin, western Moffat County, Colorado. Heavy solid lines=paved highways; heavy dashed lines=graded roads; heavy dotted lines=trails; light solid lines=flowing streams; light interrupted lines=intermittent streams; numbers=fossil vertebrate localities.

tions were incidental to studies of the nearby later Tertiary Brown's Park Formation. For the most part, locality data are inadequate for precise relocation of the sites visited by the Douglass parties. This early collection was not mentioned in any previous publication.

In 1924 and 1925 Denver Museum of Natural History parties, under the supervision of Harvey Markman, made a substantial collection, mostly of large mammals from several localities in the northwestern part of the Sand Wash Basin. Three papers resulted: Abel and Cook (1925) and Cook (1926a,b). These described one condylarth, one uintathere, and several titanotheres, almost all of which were considered to be new genera or species. Since then, *Hyopsodus* (Gazin, 1968) and the uintatheres (Wheeler, 1961) have been reviewed and the Sand Wash specimens placed in previously recognized taxa.

More recently, taxonomically more diversified collections have been made for the University of Colorado Museum and Carnegie Museum of Natural History. One of us (Dawson) spent several weeks in the area in 1961, opening localities 1, 2, and 3 (see Fig. 2 for locations), and revisiting the Spicer's Spring area worked by Markman. P. O. McGrew found a small vertebrate locality (loc. 20) in 1962, and turned the specimens over to Carnegie Museum. Localities 1 and 3 were revisited briefly by a party from Carnegie Museum and the American Museum of Natural History in 1963, and locality 3 again by Carnegie Museum in 1964. In 1972, both authors and M. C. McKenna revisited localities 1, 2, and 3, and discovered two others, localities 4 and 5. West again worked in Sand Wash Basin in 1973, revisiting most of the Markman localities (10-19). He also found four additional sites (6-9), one of which, locality 9, is readily collectible by screen-washing. Early in the spring of 1973, a specimen referred below to *Parahyus* sp. was given to the Denver Museum by a Moffat County resident. Its locality is designated loc. 21.

The specimens collected by Dawson in 1961 are in the University of Colorado Museum; those collected by all parties since 1961 are in Carnegie Museum of Natural History, as are the Douglass and Kay collections. The Markman collection, plus the recently collected specimen of *Parahyus*, remains in the Denver Museum of Natural History.

ACKNOWLEDGEMENTS

We thank the staff of the Department of Geology of the Denver Museum of Natural History (Messrs. Jack Murphy and K. Don Lindsey) and the University of Colorado Museum (Drs. Peter Robinson and Judith Van Couvering) for access to specimens in their respective charges. Drs. Edward J. McKay and Richard Mauger contributed unpublished data on the geology of the Sand Wash Basin. John Sutton and Helen McGinnis prepared the photographs. This research was supported by NSF grant GB20263A1 to West, and NSF grant G14254 to Dawson.

The following museum abbreviations are used below:

DMNH - Denver Museum of Natural History

UCM - University of Colorado Museum, Boulder

CM - Carnegie Museum of Natural History, Pittsburgh

GEOLOGICAL SETTING

The Sand Wash Basin is an isolated area of about 600 square miles of middle-to-late Eocene lacustrine and fluvial rocks in northwestern Moffat County, Colorado (Fig. 1). The most recent mapping, by Edward J. McKay of the U. S. Geological Survey, shows well the southern fault contact with middle Tertiary rocks (Brown's Park Fm.) and the eastern onlap onto the earlier Eocene Green River and Wasatch Formations. McKay's maps do not extend to the northern and western sides of the Sand Wash Basin. For these areas reference must be made to Sears and Bradley (1924) and Sears (1924). Maps of Sears and Bradley show conformability of the later beds over the Green River formation in those directions as well. The nearest presumably correlative rocks are in the Washakie Basin, north of the Wyoming line, about 15 miles north of the north end of the Sand Wash Basin (Roehler, 1973).

McKay (letter to West, October 30, 1972) follows earlier work and uses the term Bridger Formation for the Sand Wash post-Green River Formation rocks. However, he agrees with Roehler that, "the 'Bridger' of the Sand Wash and Washakie Basins are lithologically and faunally alike, and key beds can be traced from one basin to the other; and although faunas are alike in the Green River and Washakie Basins, the lithologies differ. For this reason, Roehler suggests the name Washakie for rocks of Bridger age in the Washakie Basin. If the Survey adopts Roehler's new name, I'll use it in the Sand Wash Basin."

All the fossil mammal localities are in rocks mapped by McKay as "upper Bridger." This designation is, however, of local importance only, and should not be construed to be necessarily equivalent to the Green River Basin Twin Buttes Member of the Bridger Formation. We have noted some lithologic variations across the basin within the "upper Bridger." To the northwest there is much more channelling, producing striking green sandstone deposits, with prominent overbank deposits adjacent to them. These are rich in bone, and appear to be the lithologies exploited by the Markman parties whose localities all were in that part of the exposure area (Fig. 2). To the southeast the sediment seems considerably finer, shows relatively less channelling, and floodplain and lacustrine environments are predominant.

Markman (in Cook, 1926b:12) believed that all his specimens were recovered from no more than 200 feet of vertical section. He did not, however, report any materials from the southern and eastern part of the basin, where additional localities were found more recently. These are

up to a few hundred feet lower, topographically, than some of the Markman localities, and are down strike from them. Unfortunately, ground cover and faulting make positive correlations across the basin difficult. It may be that the southeastern localities are significantly lower in the section than the northwestern ones.

OCCURRENCE OF FOSSILS

Fossil bone is not abundant in the Sand Wash Basin, but is present in most places. Turtles are the most frequently encountered vertebrates, and several kinds, both terrestrial and aquatic, are present. In the northwestern part of the basin only a few scraps of smaller mammals have been encountered, while larger perissodactyls and uinatheres predominate. Farther southeast, large mammals continue to be a significant part of the assemblage, but remains of small organisms, fish, amphibians and reptiles, as well as mammals, occur more frequently. Fossil wood is common throughout Sand Wash Basin.

The 21 vertebrate fossil localities in the Sand Wash Basin are indicated approximately in Fig. 2. The precise locality data are on file in the Department of Geology, Milwaukee Public Museum, and the Section of Vertebrate Fossils, Carnegie Museum of Natural History.

FAUNAL LIST

- Marsupicarnivora
 - Didelphidae
 - Peratherium marsupium*
- Insectivora
 - Pantolestidae
 - Pantolestes natans*
- Carnivora
 - Miacidae
 - Viverravus minutus*
 - Viverravus* sp.
 - Uintacyon vorax*
- Primates
 - Adapidae
 - Notharctus robustior*
 - Omomyidae
 - Washakius* sp.
- Rodentia
 - Ischyromyidae
 - Leptomys bridgerensis*
 - Ischyromyid sp.
 - Sciuravidae
 - Tillomys* sp. cf. *T. senex*
- Condylarthra
 - Hyopsodontidae
 - Hyopsodus despiciens*

- Perissodactyla
 Equidae
Orohippus sylvaticus
 Heleletidae
Hyrachyus modestus
Hyrachyus small species
Isectolophus sp. cf. *I. latidens*
 Brontotheriidae¹
Tanyorhinus blairi
Tanyorhinus bridgeri
Tanyorhinus harundivorax
Tanyorhinus sp.
Telmatherium accola
Telmatherium advocata
Manteoceras foris
Manteoceras pratensis
Metarhinus sp.
 Dinocerata
 Uintatheriidae
Eobasileus cornutus
 Artiodactyla
 Dichobunidae
Homacodon sp. cf. *H. vagans*
Parahyus sp.

¹See following discussion of these particular assignments.

SYSTEMATIC PALEONTOLOGY

Class Mammalia

Subclass Metatheria

Order Marsupicarnivora

Family Didelphidae

Peratherium marsupium (Troxell, 1923)

Two molar teeth (CM 23193, locality 1, and CM 23194, locality 9) are assigned to this species. CM 23193, M², has a well developed stylar cusp C, but is so worn that the degree of development of the other stylar cusps cannot readily be seen. The presence of cusp C prevents assignment to *Peratherium knighti* (McGrew, 1959:147-148). In its size (length 2.3 mm, width 2.3 mm) as well as the size of the lower molar, CM 23194 (length 2.0 mm, anterior width 0.7 mm, posterior width 0.6 mm), there is a good fit with *Peratherium marsupium* from the Green River Basin (West, 1973:80).

Peratherium marsupium occurs through Bridgerian time. The phylogenies of Eocene didelphids are so poorly understood that this species is of little biostratigraphic significance.

Subclass Eutheria

Order Insectivora

Family Pantolestidae

Pantolestes natans Matthew, 1909

This is the single representative of Insectivora in the Sand Wash collection. The size of both UCM 21475 (locality 2) and CM 23189 (locality 1) places this form among the middle-to-large *Pantolestes* of Matthew (1909). Comparison with a suite of *Pantolestes* molars from the Green River Basin shows that the Sand Wash specimens are larger than the average from the Bridger Formation. The most reasonable assignment for these specimens is in *P. natans*, a late Bridgerian species. The genus is also known from post-Bridgerian rock in Uintan deposits of the Uinta Basin.

Order Carnivora

Family Miacidae

Viverravus minutus Wortman, 1901

An isolated highly sectorial P_4 (CM 14915, locality 3) is referred here. It is a slender tooth (6.4 mm long, 3.0 mm wide) with a pronounced posterior hypoconid. The genus is known definitely only from the Bridgerian, and this species is reported from throughout the Bridgerian.

Viverravus sp.

An isolated M^2 (CM 23199, locality 2) is tentatively placed in this genus. It is a simple tooth with no hypocone and only the paraconule visible. It is most similar morphologically to *V. minutus*, the tiniest of the later Bridgerian miacids, but this single tooth does not permit secure species identification.

Uintacyon vorax Leidy, 1872

Fig. 3

This species is represented by a dentary fragment (CM 23191, locality 4) with P_4 - M_1 and roots of all post-canine teeth. There is a short diastema between C and P_1 and between P_1 and P_2 . P_2 and P_3 are sub-equal in size and double-rooted. P_4 is sectorial, with a well developed hypoconid. M_1 has a high paraconid and a well developed enclosed talonid basin. M_2 is double-rooted, while the much smaller M_3 has only a single root. There are two mental foramina, one beneath the anterior root of P_2 and the other beneath the anterior root of P_3 . The symphysis is long and stout. *Uintacyon vorax* is a Bridgerian species, but the genus is also known from Uintan rocks at Myton Pocket, Uinta Basin, Utah.

Order Primates

Family Adapidae

Notharctus robustior (Leidy, 1872)

One specimen (UCM 33360) with M^1 and M^2 is definitely *N. robustior*, and a second (UCM 33394), a lower molar trigonid, is tentatively

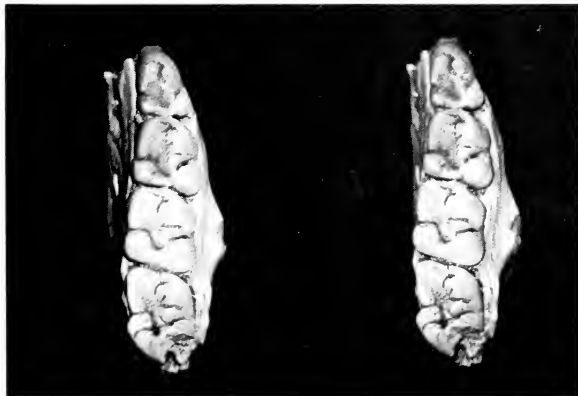
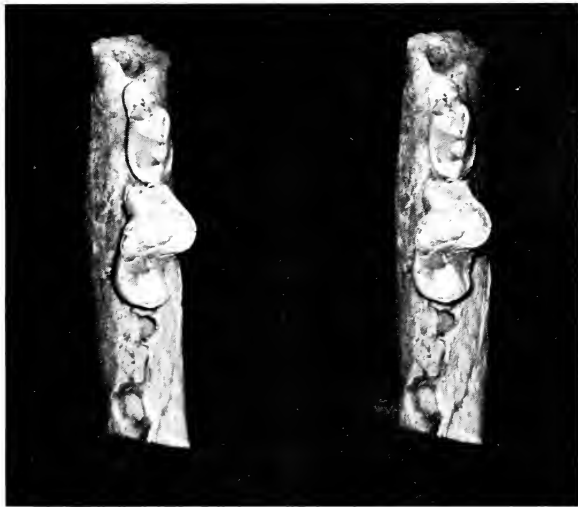


Fig. 3. (top) *Uintacyon vorax*, part of CM 23191, right jaw with P_4 - M_1 (stereophotographs).
Fig. 4. (bottom) *Leptotomus bridgerensis*, CM 14907, right jaw with dP_4 , $M_{1,3}$ (stereophotographs). Line equals 1 cm.

placed here. Both were found at locality 3. Both the size and topography of these teeth conform to those of *N. robustior* (Robinson, 1957). *Notharctus* is well known from the late Wasatchian through Bridgerian, and has recently been reported in an early Uintan fauna in the Washakie Basin (Turnbull, 1972).

Family Omoyidae

Washakius sp.

A single lower first molar (CM 23200, locality 20) is assigned to *Washakius*. It is similar in size to Bridgerian *W. insignis*, but enough of the enamel is spalled off to render insecure a precise species identification. *Washakius* is a common Bridgerian genus, and has also been reported from a Uintan locality (Poway) in southern California.

Order Rodentia

Most of the rodent specimens from these Sand Wash localities and all that are relatively completely represented by upper and lower jaws with teeth are referable to *Leptotomus bridgerensis*. A few other fragmentary remains may represent two other ischyromyid taxa, and one tooth represents the Sciuravidae. The lack of diversity of the rodent fauna from the Sand Wash Basin is striking in contrast to the situation in the Green River Basin, from which more varied ischyromyids and sciuravids as well as cylindrodontids are known. Whether this difference reflects more complete collecting in the Green River Basin or has some paleoecologic basis is uncertain at present.

Family Ischyromyidae

Leptotomus bridgerensis Wood, 1962

Fig. 4

SPECIMENS: CM Nos. 14905-14907, 16098; UCM Nos. 33351-33353, 33361, 33380, 33386, 33390, 33917. All locality 3.

One of the most characteristic features of *Leptotomus*, the shape of the lower incisor [convex and narrow anteriorly, widest about two thirds of the distance from the anterior face (Wood, 1962:64)] typifies the lower jaws referred here. Upper and lower cheek teeth, though not greatly different from those of *Paramys*, are morphologically similar to previously known specimens of *Leptotomus bridgerensis*. In size this sample overlaps Wood's sample (1962:90-91) in about half of their measurements but ranges larger in the remainder. In spite of this difference, the overlap and morphological resemblance support reference to *Leptotomus bridgerensis*, already known from the Green River and Washakie Basins.

One lower jaw, CM 14907, has dP_4 , previously unknown in this species. It is a slender tooth, relatively elongate in the trigonid, and has an

anterior cingulum curving anteriorly and linguad from the protoconid. This specimen also exhibits the wrinkled enamel characteristic of early stages of wear.

The lower jaws referred here are variable in development of the maseteric fossa, which is distinct in all specimens but more heavily ridged in jaws of the older individuals.

It is interesting to note that *Leptotomus bridgerensis*, the species most adequately represented in the Sand Wash fauna, is the only ischyromyid reported (Wood, 1962) from Bridgerian deposits in the Washakie Basin, suggesting that environments sampled in these two basins may be similar.

Ischyromyid spp.

Two specimens, an isolated incisor (UCM 33369, locality 3) and a jaw fragment with incisor (UCM 33918, locality 3), represent two additional rodent taxa, probably ischyromyid. One has a relatively wide incisor and the other, a larger form, has an incisor that is widest posteriorly. The specimens, which are not referable to *Leptotomus*, are not adequate for positive generic identification.

Family Sciuravidae

Tillomys sp. cf. *T. senex* Marsh, 1872

One lower molar tooth, probably M_2 (CM 23197, locality 20), is close in size and morphology to the Bridgerian species *Tillomys senex*. It is to be hoped that additional small mammalian remains might be recovered from this locality, which was found and collected by P. O. McGrew.

Order Condylarthra

Family Hyopsodontidae

Hyopsodus despiciens Matthew, 1909

Hyopsodus markmani Abel and Cook, 1925:34

Hyopsodus despiciens Gazin, 1968:15

SPECIMENS: UCM Nos. 33307-33349, 33354, 33356, 33357-33359, 33372, 33378; CM Nos. 14887-14903, 14908, 16097, 16100-16101, 23190, locality 3; CM Nos. 23185-23186, locality 2.

Abel and Cook (1925) described a new species, *H. markmani*, from the Sand Wash Basin, DMNH 486 as the holotype. However, Gazin (1968:28-29) pointed out that DMNH 486, instead of being $M^1 - M^2$, as described originally, is actually $dP^4 - M^1$, and that it represents the already known late Bridgerian species *H. despiciens*, as do the other eight specimens collected by Markman. We concur with the synonymy. *Hyopsodus despiciens* is by far the most common species in the collections from the southern and eastern Sand Wash localities.

TABLE 1.
DISTRIBUTION OF SAND WASH FAUNA BY LOCALITY¹

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
<i>Peratherium marsupium</i>	1	2																				
<i>Pantolestes natans</i>	1 ²																					
<i>Viverravus minutus</i>	1	1							1													
<i>Viverravus</i> sp.																						1
<i>Uintacyon vorax</i>				1																		
<i>Notharctus robustior</i>		2																				1
<i>Washakius</i> sp.																						1
<i>Leptotomus bridgerensis</i>		12																				
<i>Ischyromyid</i> sp.		2																				1
<i>Tillomys</i> sp. cf. <i>T. senex</i>		2	72									X ³										1
<i>Hyopsodus despiciens</i>			6	1																		1
<i>Orohippus sylvaticus</i>			2																			
<i>Hyrachyus modestus</i>																						
<i>Hyrachyus</i> small sp.																						
<i>Isectolophus</i> sp. cf. <i>I. latidens</i>	1																					
<i>Tanyorhinus blairi</i>																						?
<i>Tanyorhinus bridgeri</i>																						X
<i>Tanyorhinus harundinivorax</i>										X												X
<i>Tanyorhinus</i> sp.																						X

¹Localities numbered as in Fig. 2.

²Number of determined specimens from each locality in CM and UCM 1961 and post-1961 collections.

³Presence at a locality in older collections.

TABLE 2.
TEMPORAL DISTRIBUTION OF SAND WASH EOCENE MAMMALIAN GENERA

	Bridger A-B	Bridger C-D	Washakie A (lower)	Washakie B (upper)	Wagonhound	Myton
<i>Peratherium</i>	X	X		X		
<i>Pantolestes</i>	X	X			X	X
<i>Viverravus</i>	X	X				
<i>Uintacyon</i>		X				X
<i>Notharctus</i>	X	X	X	X		
<i>Washakius</i>	X	X				
<i>Leptotomus</i>		X	X	X	X	X
<i>Tillomys</i>		X				
<i>Hyopsodus</i>	X	X	X	X	X	
<i>Orohippus</i>	X	X	X			
<i>Hyrachyus</i>	X	X	X	X	X	
<i>Isectolophus</i>		X			X	X
<i>Tanyorhinus</i>				X	X	
<i>Telmatherium</i>			X		X	
<i>Manteoceras</i>			X	X	X	
<i>Metarhinus</i>			X	X	X	
<i>Eobasileus</i>			X	X	X	
<i>Homacodon</i>		X	X			
<i>Parahyus</i> ¹						

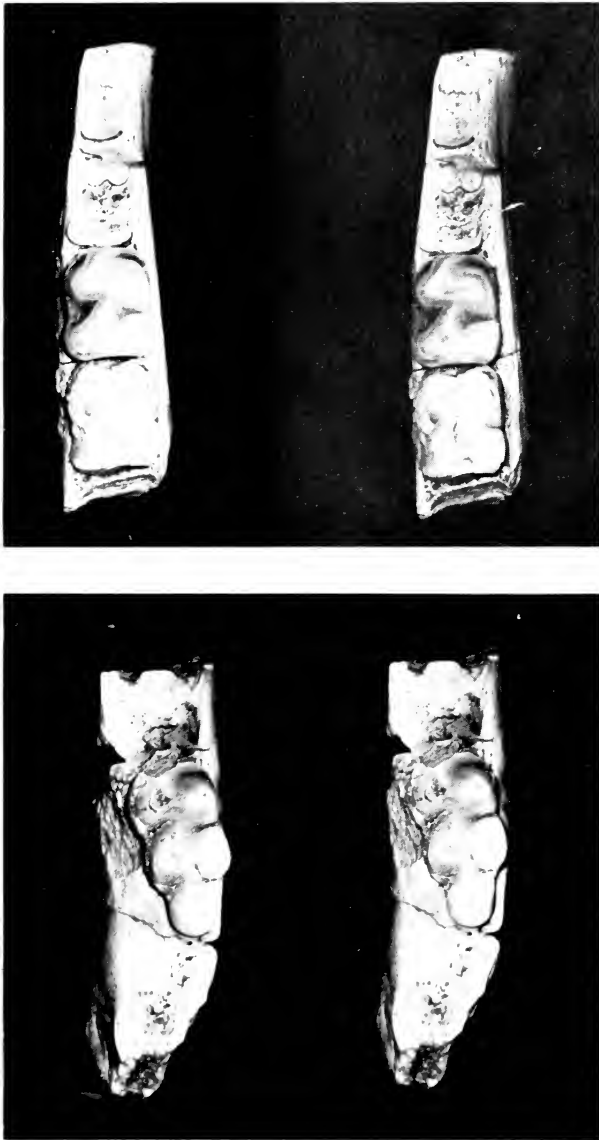
¹Locality of type of *P. vagus* uncertain, possibly Uintan of Washakie Basin (McKenna, 1972:93); referred specimen from Bridgerian-Uintan Tepee Trail Formation (Lewis, 1973; McKenna, 1972).

Order Perissodactyla
Suborder Equoidea
Family Equidae
Orohippus sylvaticus Leidy, 1870
Figs. 5, 6, 7

SPECIMENS: UCM 24303, 33363, 33366, 33381, 33386, 33389, locality 3; CM 23188, locality 4; CM 23198, locality 20.

These specimens are placed in *O. sylvaticus* rather than *O. agilis*, which is approximately the same size, because of the broad heel on M_3 and the subequal anterior and posterior widths of P_4 on which the anterior end is markedly narrower in *O. agilis* (Kitts, 1957). *O. sylvaticus* is later Bridgerian in age, and *Orohippus* is succeeded in the Uintan by the more advanced *Epihippus*, characterized by greater molarization of the premolars.

Suborder Tapiroidea
Family Heleletidae
Subfamily Hyrachyinae
Hyrachyus modestus Leidy, 1870



Figs. 5, 6. *Orohippus sylvaticus*, UCM 24301, left jaw with P₄-M₁, M₃ (stereophotographs).
 Fig. 5, P₄-M₁. Fig. 6, M₃. Line equals 1 cm.

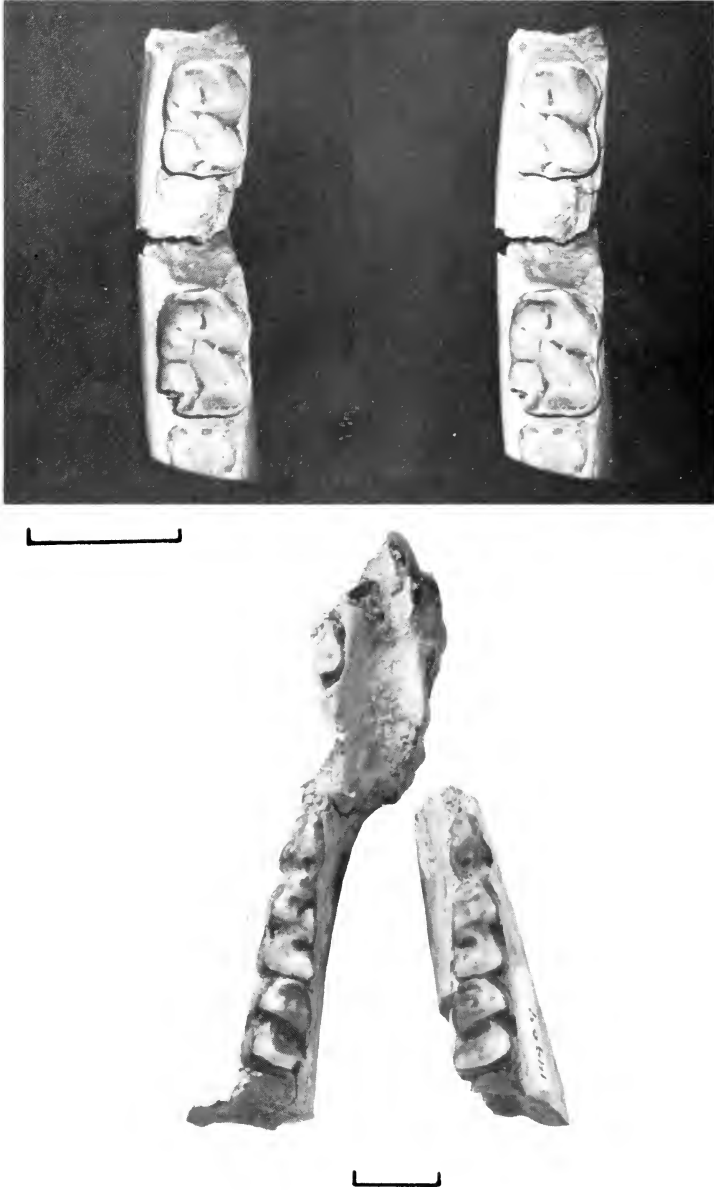


Fig. 7. (top) *Orohippus sylvaticus*, UCM 24302, right jaw with P₄, M₂ (stereophotographs). Line equals 1 cm.
 Fig. 8. (bottom) *Hyrachyus*, small sp., CM 14904, jaws with right and left dP₃₋₄, M₁. Line equals 1 cm.

One badly broken dentary fragment, UCM 33382 (locality 3), appears to represent this species. Its size is appropriate (Radinsky, 1967) but it is too fragmentary for further comments. UCM 33388 (locality 3), a broken upper molar, probably also may be assigned to *H. modestus*.

Hyrachyus small species

Fig. 8

Two well-preserved dentaries (UCM 33355, locality 1, and CM 14904, locality 3) may document a new species of *Hyrachyus*. CM 14904 has dP_3 , dP_4 , and M_1 in both rami. The permanent incisors and canine are in early stages of eruption, and thus do not provide reliable measurements.

These materials represent an animal too small to be placed realistically in either recognized species of *Hyrachyus* (Radinsky, 1967), and do not belong to any other known helaetid (*Isectolophus*, *Dilophodon*, for example). A new species of *Hyrachyus* may be represented, but definite determination should await more complete, mature specimens.

Isectolophus cf. *I. latidens* Osborn, Scott, and Speir, 1878

CM 11381 is a nearly complete skull of a very young tapiroid, having dP^{2-4} and unworn M^1 preserved. It is currently under study by W. D. Turnbull. Although precise locality information is lacking for the specimen, greenish sandstone matrix adhering to the skull suggests that it came from the northwestern group of localities near Spicer Spring. Immaturity make identification of the skull difficult, but in size of M^1 (length, 11.5 mm; width, 12.2 mm) the specimen is closer to the range of the Bridgerian species *I. latidens* than to that of the Uintan *I. annectens* (Radinsky, 1963:22-25).

Subclass Brontotherioidea

Family Brontotheriidae

Cook (1962b) recognized considerable diversity among the Sand Wash titanotheres. Unfortunately his paper was published while Osborn's 1929 monograph on the titanotheres was in press, so the Sand Wash taxa were not worked into Osborn's grand synthesis. Cook did not make adequate comparative studies of the Sand Wash specimens, so many of his species characterizations are inadequate. A thorough revision of titanotheres is greatly needed, with attention to individual and sexual variation of these animals. It would be premature and would only add to nomenclatorial confusion to do more in this study than suggest possible synonymies.

Tanyorhinus blairi Cook, 1926

Tanyorhinus bridgeri Cook, 1926

Tanyorhinus harundivorax Cook, 1926

Tanyorhinus sp.

The genus *Tanyorhinus* and these three species were described as new by Cook. His generic comparison was with *Dolichorhinus*, the well-known early Uintan narrow-skulled genus. Our review of Cook's material and comparison of it with specimens of *Dolichorhinus* in the Carnegie Museum collections suggest that Cook's generic characteristics may be attributed to individual variation, sexual dimorphism, wear stages of the teeth, and post-mortem crushing. Therefore, we believe that *Tanyorhinus* may realistically be included within *Dolichorhinus*.

The three species of *Tanyorhinus* proposed by Cook seem to be biologically unnecessary. *T. blairi* and *T. bridgeri* appear to be sexual dimorphs, with *T. blairi* probably the male. The holotype of *T. blairi* differs from that of *T. bridgeri* in being a bit larger and more robust. *T. harundivorax* is represented by a single dentary fragment, less worn than specimens of Cook's other two species. It is difficult to maintain this as specifically separate. It appears to us to be simply a younger individual of the species represented by the much more complete material of *T. blairi* and *T. bridgeri*.

Telmatherium accola Cook, 1926

Telmatherium advocata Cook, 1926

Telmatherium is a well-established genus from the Wagonhound. We concur with Cook's generic assignment, even though he himself was not positive of it (1926b:16). We question the biological necessity for two species, again for the reason of sexual dimorphism. The holotype of *T. advocata* seems more robust than the holotype of *T. accola*. Our preference is to recognize a single Sand Wash species of *Telmatherium*.

Manteoceras foris Cook, 1926

Manteoceras pratensis Cook, 1926

Manteoceras sp.

Fig. 9

This genus is known from both Bridgerian and early Uintan times, as it is frequently found in the Green River, Washakie, and Uinta Basins. Several specimens in the Carnegie Museum collection are more complete than those available to Cook, and permit more careful study. CM 11380 and CM 11382 share attributes of both Bridgerian *M. manteoceras* and Uintan *M. uintensis*.

The holotype (DMNH 487) of *M. foris* is a dentary with deciduous teeth. Cook differentiated it from *M. pratensis* by the shape and simplicity of the premolars, which apparently were not recognized as deciduous. It is now preferable to regard the Sand Wash specimens of *Manteoceras* as individuals of a single species. Until a larger sample is available, it is not possible to determine whether *M. manteoceras* or *M. uintensis* is the more appropriate species designation for this material.

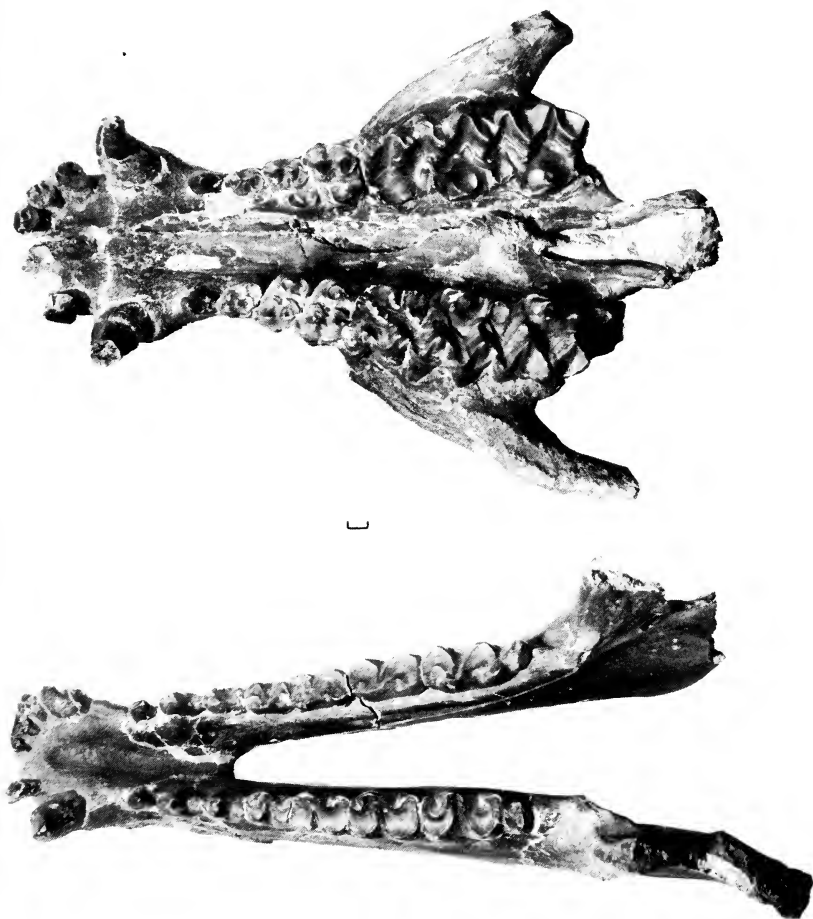


Fig. 9. *Manteoceras pratensis*, CM 11382, partial skull and lower jaw. Line equals 1 cm.

Metarhinus sp.

Fig. 10

A single maxillary fragment with P¹ to M¹ (CM 26287, locality 9) belongs to *Metarhinus*, a titanotherine genus not in Cook's collection. The specific assignment remains uncertain for lack of complete molar teeth. This genus, like other titanotheres discussed above, appears in both Bridgerian and early Uintan faunas, and is further evidence for the critical biostratigraphic position of the Sand Wash fauna.



Fig. 10. *Metarhinus* sp., CM 26287, right maxilla with P¹-M¹. Line equals 1 cm.

Order Dinocerata
Family Uintatheriidae
Eobasileus cornutus Cope, 1872

Uintacolotherium blayneyi Cook, 1926a:7
Eobasileus cornutus Wheeler, 1961:53

Cook (1926a) described a presumed new uintathere, *Uintacolothe-rium blayneyi*, based on DMNH 495 and other specimens. Wheeler (1961:52-55, 61) reviewed the uintatheres and synonymized Cook's material with *Eobasileus cornutus*. This suggests an early Uintan age for at least some Sand Wash mammals. *Eobasileus* is readily differentiated from *Uintatherium* by its size and the relative development of the horns.

Order Artiodactyla

Family Dichobunidae

Homacodon sp. cf. *H. vagans* Marsh, 1872

A right dentary fragment (UCM 33392) with M_2 and an isolated lower molar (CM 14963), both from locality 3, may be compared to *Homacodon vagans*. Size and morphology are readily comparable to the materials of this species described by Sinclair (1914:286). The prominent separation of the hypoconulid from the main part of the talonid and the fusion of the paraconid and metaconid that characterize *H. vagans* are readily seen in these specimens. The species is late Bridgerian.

Parahyus sp.

One specimen, consisting of a well-preserved dentary and fragments of the skull, is tentatively referred to *Parahyus*, the enigmatic bunodont artiodactyl recently discussed by Lewis (1973) and McKenna (1972). Thus far, Sand Wash locality 21 has produced only this specimen, which was collected by a Moffat County resident and given to the Denver Museum of Natural History.

The Sand Wash *Parahyus* is smaller than *P. vagus* as described by both Sinclair (1914) and Lewis (1973). Of those artiodactyls of more certain geographic and geologic provenance, the specimen most closely resembles Bridgerian *Helohyus* from the Green River Basin, although it clearly is not referable to any known species of that genus. As it is at present under study by K. Don Lindsey of the Denver Museum of Natural History, we simply indicate its occurrence in the Sand Wash assemblage as *Parahyus* sp.

DISCUSSION

Of primary interest is the age of the faunal assemblage outlined above. As indicated by Table 2, the elements of the Sand Wash fauna occur in both Bridgerian and Uintan rocks. The large mammals, especially the perissodactyls and uintatheres, suggest a Uintan Age, while the smaller mammals are far more suggestive of late Bridgerian time. As mentioned earlier, most of the large mammals were collected in the northwestern part of the basin (*Hyopsodus* is the only small mammal from that region), while the smaller mammals were collected farther south and east.

Several explanations for this distribution may be suggested. First, inadequacy of collecting may explain the absence of small mammals accompanying the titanotheres and uintatheres in the northwestern part of the basin. This is unlikely, as a number of competent field paleontologists have carefully examined the Markman localities near Two Bar and Spicer's Springs with identical lack of success in recovering small vertebrates. The nature of the sample does then seem to reflect adequately the preserved fauna.

Second, there may be a significant stratigraphic distance between the large mammal ("Uintan") localities and the small mammal ("Bridgerian") localities. This would then suggest two discrete time-stratigraphic units in the Sand Wash Basin Eocene, something that is difficult to demonstrate geologically. If the northwestern part of the basin is indeed substantially younger than the southern part, the range of *Hyopsodus despiciens* must then be extended into the later Eocene.

Third, perhaps the most realistic interpretation of Sand Wash mammals involves the readily observable facies differences across the basin, and the association of the mammals with different paleoenvironments. The particular situations of the fossil assemblages suggest that the "Uintan" and "Bridgerian" assemblages represent two rather different ecosystems that were in existence at approximately the same time. What geologic evidence there is more strongly supports this position than that of a large stratigraphic differential across the basin.

If this alternative is valid, the particular biostratigraphic position of the Sand Wash mammals brings into question the adequacy of the conventional terms "Bridgerian" and "Uintan" as descriptive devices. This fauna would fall on the Bridgerian-Uintan boundary as traditionally understood, and thus is adequately defined by neither term.

Finally, the last two suggestions can be considered simultaneously. Perhaps there is a time difference accompanied by ecologic variation. This would readily accommodate the distributional discrepancies.

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THE LATE PLEISTOCENE ARVICOLINE RODENT *ATOPOMYS*

RICHARD J. ZAKRZEWSKI¹

INTRODUCTION

The arvicoline genus *Atopomys* was described and named by Patton (1965) on the basis of two M_1 's from a small fissure in Texas, now referred to as Fyllan Cave. The genus is characterized, in part, by small size, confluency of the first and second alternating triangles on the lower molars, and well-developed dentine tracts. It has been suggested that *Atopomys* was derived from the arvicoline *Nebraskomys*, which it resembles primarily in the occlusal pattern (Hibbard, 1970).

Remains of both of these genera are rare in the fossil record. *Nebraskomys* is known from the Rexroad local fauna (late Pliocene of Kansas) and the Sand Draw local fauna (early Pleistocene of Nebraska). *Atopomys* is known from Fyllan Cave (Kansan), the lower levels of Trout Cave in West Virginia, and Cumberland Cave in Maryland (both questionably Illinoian). Additional material has been obtained from Fyllan Cave by Ernest L. Lundelius, Jr., University of Texas at Austin; and from Cumberland Cave as a result of the continuing excavations under the direction of John E. Guilday, Carnegie Museum of Natural History. The Cumberland Cave find became the impetus for this study.

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All additional materials are isolated teeth, but they refine the diagnostic characters and degree of variation expected for the genus. Differences between the Texas and eastern forms prompt the naming of a new species for the latter.

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I am especially indebted to John E. Guilday of Carnegie Museum of Natural History (CM) for suggesting this study and for the loan of specimens in his care. Ernest L. Lundelius, Jr., of the University of Texas at Austin (UTBEG), and the late Claude W. Hibbard of the University of Michigan (UMMP) kindly lent specimens in their care. Jerry R. Choate and Michael E. Nelson reviewed the manuscript.

SYSTEMATIC PALEONTOLOGY

Order Rodentia Bowdich, 1821

Family Arvicolidae Gray, 1821

Genus *Atopomys* Patton, 1965

TYPE SPECIES: *Atopomys texensis*.

HORIZON AND TYPE LOCALITY: The holotype, an isolated RM_1 (UTBEG 40682-1), was excavated from a fissure fill in the Edwards formation (Cretaceous) exposed in the Texas Crushed Stone Company quarry on Balcones Trail in Austin, Travis County, Texas. The fissure deposit is composed largely of brown-to-red silty clay of Pleistocene (Kansan) age. The material from the site is referred to as the Fyllan Cave local fauna.

SUPPORTIVE MATERIAL: Specimens consist of isolated molars found in Fyllan Cave, Trout Cave (3½ miles southwest of Franklin, Pendleton County, West Virginia), and Cumberland Cave (½ mile south of Corriganville, Allegany County, Maryland). Catalog numbers of the holotype, paratypes, and referred material are listed below.

EMENDED GENERIC DIAGNOSIS: A small vole with rooted teeth, cementless re-entrant angles, and well developed dentine tracts (Fig. 1, g, h). The enamel along the occlusal surface is variable in thickness both on and among specimens (Fig. 1).

The M_1 (Fig. 1, a, g, h) consists of a posterior loop, three alternating triangles, and an anterior loop. The posterior loop is generally closed off from the alternating triangles. The first alternating triangle opens broadly into the second, and in some instances the triangles are almost confluent (directly opposite each other rather than alternating). The relationship between the second and third triangle varies, but generally the third is isolated from the first two, and opens broadly into the anterior loop. The anterior loop is relatively simple, and sometimes slightly crenulated. Occasionally, a nubbin of a fourth triangle is present. Pits and prism folds are absent.

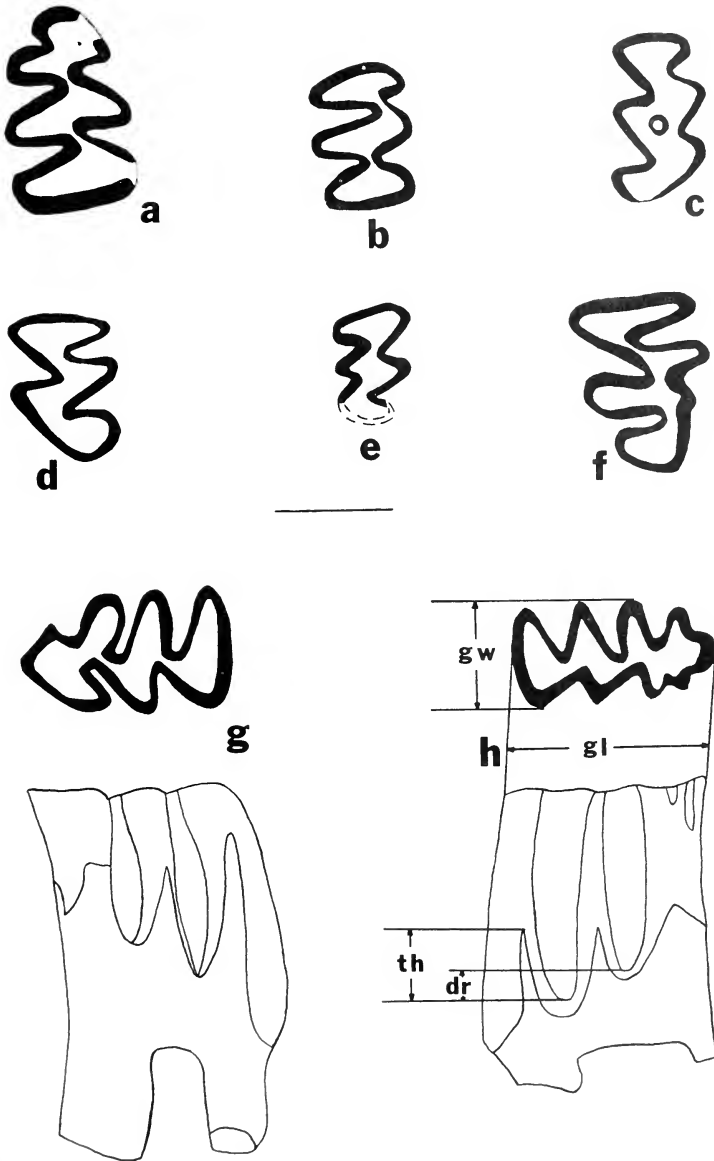


Figure 1. *Atopomys* and *Nebraskomys* isolated molars: a-e, g; *A. salvelinus*; a, M_1 , CM24226; b, M_2 , CM24544; c, M^1 , CM12540; d, M^2 , CM24229; e, M^3 , CM24231; g, M_1 , holotype, CM20040. h, *A. texensis*, M_1 holotype, UTBEG 40682-1. f, *N. mcgrewi*, M^3 , UMMP V57227. gl=greatest length; gw=greatest width; th=dentine tract height; dr=depth of second lingual re-entrant angle. Horizontal line=1 mm.

The M_2 (Fig. 1b) consists of a posterior loop and four alternating triangles. The first is confluent with the second, and the third is confluent with the fourth. These sets are separate from each other, imparting a trilophate appearance to the tooth. The tooth is strongly curved labially from its midline toward the roots, which suggests that the lower incisor passes from the lingual to labial side near the M_2 . The M_3 is unknown.

The M^1 consists of an anterior loop and four broadly open alternating triangles (Fig. 1c). The enamel along the occlusal surface is variable, ranging inconsistently from thick to thin. A pit is present on one specimen (Fig. 1c). The M^1 generally has two roots, but there is evidence of fusion of the anterior root with a median one, and in one instance three roots are present.

The M^2 consists of an anterior loop and three alternating triangles (Fig. 1d). It has two roots.

The M^3 consists of an anterior loop, two alternating triangles, and a reduced posterior loop (Fig. 1e). The first triangle opens broadly into the second with some suggestion of confluency. The tooth has two roots.

Atopomys is distinguished from *Nebraskomys*, the only North American genus it closely resembles, by the occlusal shape of the M^3 . In the M^3 of *Nebraskomys* (Fig. 1f) the alternating triangles are not as confluent, nor is the posterior loop as reduced, as in *Atopomys* (Fig. 1e). In *Atopomys* all the teeth are more hypsodont relative to the length of the tooth and the dentine tracts are better developed on the sides of the teeth than they are in *Nebraskomys*.

Atopomys texensis Patton, 1965

Atopomys texensis Patton, 1965:466-468.

Microtine indet. Patton, 1965:468-469.

HOLOTYPE: RM_1 , UTBEG 40682-1

PARATYPE: RM_1 , UTBEG 40682-2

HORIZON AND TYPE LOCALITY: Same as for genus.

ADDITIONAL MATERIAL: UTBEG 40682-6, 9, 19, 20, 22, M_1 s; UTBEG 40682-4, 21, M_2 s; UTBEG 40682-3, 5, 14, M^1 s.

EMENDED DIAGNOSIS: *Atopomys texensis* is distinguished from the other species in the genus by its less-developed dentine tracts, slightly more complex anterior loop, and the fact that the second internal reentrant consistently is not as deep on the M_1 (Fig. 1h).

Atopomys salvelinus, new species

HOLOTYPE: CM20040, LM_1 . Fig. 1g.

HORIZON AND TYPE LOCALITY: Nine to 10 feet below the surface from fill in Trout Cave.

PARATYPES: All paratypes are isolated teeth. Trout Cave: 8-9 feet below surface, CM20039 (M_1) and CM24544 (M_2); 9-10 feet below surface, CM24545 and 24546 (M_1 s); 10-11 feet below surface, CM20041 and 24547 (M_1 s), CM24548 (M^1). Cumberland Cave: CM24226 (M_1), CM12539, 12542, 12544, and 24230 (M_2 s), CM12538, 12540, 12541, 12543, 24227 and 24228 (M^1 s), CM24229 (M^2), CM24231 (M^3).

DIAGNOSIS: *Atopomys salvelinus* is distinguished from *A. texensis* by its better developed dentine tracts, simpler anterior loop, and deeper second internal re-entrant on the M_1 (Fig. 1g).

DESCRIPTION OF HOLOTYPE: The holotype consists of a posterior loop, three alternating triangles, and a simple anterior loop. The posterior loop is closed off from the alternating triangles. The first alternating triangle opens broadly into the second, and the two triangles are almost confluent. The third triangle is closed off from the first two alternating triangles and opens broadly into the anterior loop. The anterior loop is simpler and more oval than in the type series of *Atopomys texensis*. The enamel is thick and consistent around the occlusal surface. The length is 1.69 mm, width 1.05 mm, height of crown 1.68 mm, and the height of the dentine tract on the posterior loop 1.24 mm. The last measurement is almost twice that of the type of *A. texensis*, which measures 0.66 mm.

ETYMOLOGY: *Salvelinus* is the generic name for the brook trout (Pisces) and is used here in a geographic sense to refer to Trout Cave.

INTER- AND INTRA-SPECIFIC VARIATION: The general occlusal pattern of the teeth was described in the generic diagnosis. One of the major differences between the two species is that the M_1 s of *Atopomys texensis* have an anterior loop that is slightly more complex. Four of the five undamaged M_1 s of *A. texensis* exhibit crenulations or additional small re-entrants. In the holotype (Fig. 1h) and paratype a rectangular-shaped nubbin that could be interpreted as a fourth triangle is present. This nubbin is separated from the anterior loop by a shallow re-entrant. Patton (1965) incorrectly considered this re-entrant to represent a prism fold. A true prism fold, if present, would be found on the rectangular nubbin. Although these crenulations are lost relatively rapidly in the ontogeny of *A. texensis*, they do not represent ontogenetic differences between it and *A. salvelinus*, because specimens of similar ontogenetic age in the latter taxon lack any crenulations on the anterior loop. In fact, in *A. salvelinus* there appears to be a reduction of the anterior loop in the sense that the third triangle becomes incorporated into the loop in some instances. This feature can best be seen in CM24226, the M_1 from Cumberland Cave (Fig. 1a). Differences in mensural data for M_1 (Fig. 1h) are shown in Table 1.

The M^1 that Patton (1965) described as "Microtine indet.," because its enamel is differentiated into thin and thick tracts and because its dentine tracts are high, is considered to pertain to the genus *Atopomys*. Examination of additional M^1 s revealed that the enamel is dif-

ferentiated on these teeth, as in Patton's original specimen, and that the differentiation is not consistent as to location of thickness.

Another interesting character found on one of the M^1 's (CM12540) of *A. salvelinus* from the Cumberland Cave is the presence of a shallow enamel pit between the first and second alternating triangles (Fig. 1c). This is the first arvicoline tooth, other than an M^1 or M^3 , that I have seen with an enamel pit on the occlusal surface.

RELATIONSHIPS: Although *Atopomys salvelinus* is more advanced than *A. texensis* with regard to development of dentine tracts, the relatively simple nature of the anterior loop in the former suggests that *A. texensis* is not directly ancestral to *A. salvelinus*. While it is not impossible for a simpler pattern to be derived from a relatively more complex one, this would be the first evidence of such a trend in the evolution of the arvicolines. A similar argument could be used in considering the ancestral relationship of *Nebraskomys* to *Atopomys*. Reduction in the length of the M^1 and in loop development on the M^3 must have occurred if the former gave rise to the latter. Again, while this would not be impossible, it would be unprecedented in arvicoline phylogeny. Therefore, it seems probable the resemblance in the occlusal pattern between *Nebraskomys* and *Atopomys* is the result of parallelism.

HABITAT AND CORRELATION

Because *Atopomys* is rare and the local faunas in which it is found are not well understood, the habitat preferences of the genus cannot be established with any certainty at this time.

Guilday (personal communication) reports that the Trout Cave material was discovered between the 8- and 10-foot levels of a 12-foot-deep stratified sequence. A poorly-defined flowstone at the 5-foot level separates the 12-foot sequence into two lithic units. Many of the taxa found below the flowstone are equivalent to those found in the Cumberland Cave local fauna.

The Cumberland Cave local fauna is definitely pre-Wisconsin in age and thought to be Illinoian (Guilday, 1971). Guilday (personal communication) reports that a date of 250,000 B.P. has been obtained for the Cumberland Cave local fauna based on the racemization of amino acids in a horse phalanx. But, because this process is temperature-dependent, the date should be considered as a minimum one. White (1970) suggests a middle Illinoian age or older for those faunas, e.g., the Cumberland Cave, that contain the erethizonid genus *Coendu*.

Patton (1965) tentatively considered the Fyllan Cave local fauna to be Kansan in age. Hibbard had suggested this age to him as a maximum, a conclusion based on the stage of evolution of the rabbits in the Fyllan Cave local fauna, and supported by the presence of *Pedomys llanensis* in that fauna. *P. llanensis* is known from the Cudahy local fauna (Kansan) of Kansas and its equivalents in the Great Plains.

If the Cumberland Cave local fauna had been located on the Great Plains, the association of *Ondatra annectens*, *Neofiber*, and *Atopomys*, and the lack of *Microtus pennsylvanicus*, would suggest a pre-Illinoian age. Because of the geographic position of Cumberland Cave and the lack of other pre-Wisconsin faunas in the area with which it can be compared, the determination of the exact age is moot.

TABLE 1. MEASUREMENTS (in mm) of M_1 in *Atopomys* and *Nebraskomys*

	Taxon	N	O. R.	X	S_x	S. D.
Greatest length	<i>A. salvelinus</i>	7	1.45-1.72	1.64	0.04	0.10
	<i>A. texensis</i>	4	1.63-1.91	1.76	0.06	0.12
	<i>N. mcgrewi</i>	4	2.07-2.28	2.15	0.04	0.09
	<i>N. rexroadi</i>	1		2.16		
Greatest width	<i>A. salvelinus</i>	5	0.77-1.12	0.99	0.06	0.14
	<i>A. texensis</i>	6	0.85-1.08	0.92	0.04	0.09
	<i>N. mcgrewi</i>	4	1.13-1.29	1.19	0.04	0.08
	<i>N. rexroadi</i>	1		1.17		
Dentine tract height (see fig. 1h)	<i>A. salvelinus</i>	4	1.24-1.42	1.34	0.05	0.09
	<i>A. texensis</i>	4	0.60-0.74	0.68	0.03	0.06
	<i>N. mcgrewi</i>	3	0.48-0.49	0.49	0.00	0.01
	<i>N. rexroadi</i>	1		0.16		
Depth of second lingual re-entrant angle (see fig. 1h)	<i>A. salvelinus</i>	7	0.00-0.19	0.14	0.03	0.07
	<i>A. texensis</i>	5	0.24-0.32	0.28	0.02	0.04
	<i>N. mcgrewi</i>	4	0.22-0.27	0.24	0.01	0.02
	<i>N. rexroadi</i>	1		0.26		

N=sample size; O.R.=observed range; X=mean; S_x =standard error of mean; S.D.=standard deviation.

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ARTICLE 13

PALEONTOLOGY AND GEOLOGY OF THE BADWATER CREEK AREA, CENTRAL WYOMING

Part 11. Late Eocene Marsupials

TAKESHI SETOGUCHI¹

INTRODUCTION

In this, the eleventh in a series of papers dealing with vertebrates from Badwater Creek, Wyoming, three species of didelphid marsupials are described. All specimens are from the Hendry Ranch member of the Tepee Trail Formation (Tourtelot, 1957) and are of late Eocene or Uintan age. Specimens of these didelphids have been found at all localities of this level and include both isolated teeth and partial jaws. There are approximately 150 didelphid teeth and jaws in the Badwater collections at Carnegie Museum of Natural History, at the University of Colorado Museum, and at the Museum of Texas Tech University.

The purpose of the present paper is twofold: First to describe the didelphids from the late Eocene of North America that have not been previously described, and second, to present criteria, other than size, that can be used for the separation of species known only from the lower dentition. The upper dentition of *Peratherium* shows a typical dilambdodont tooth pattern. That of *Nanodelphys* shows less dilambdodonty. In animals with dilambdodont upper teeth, the lower molars have a hypoconid with a very sharp buccal angle that occludes with the ectoloph of the upper teeth. These teeth either lack a hypoconulid or have this cusp displaced (Robinson, 1968). The lower molars of *Peratherium* show this pattern. In relation to the less well-developed dilambdodonty

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of the upper molars of *Nanodelphys*, displacement of the hypoconulid is less emphasized in the lower dentition of *Nanodelphys*. These characteristic differences in lower dentition reflect the degree of the development of dilambdodonty of the upper dentition among didelphid marsupials.

I follow van Valen (1966, Fig. 1) for the terminology of molars.

The following abbreviations have been used: CM, Carnegie Museum of Natural History; TTU-P, Vertebrate Paleontology collection of Texas Tech University Museum.

ACKNOWLEDGEMENTS

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SYSTEMATIC ACCOUNT

Class Mammalia

Superorder Marsupialia

Order Marsupialia

Family Didelphidae Gray, 1821

Genus *Peratherium* Aymard, 1850

Peratherium cf. *P. marsupium* (Troxell, 1923)

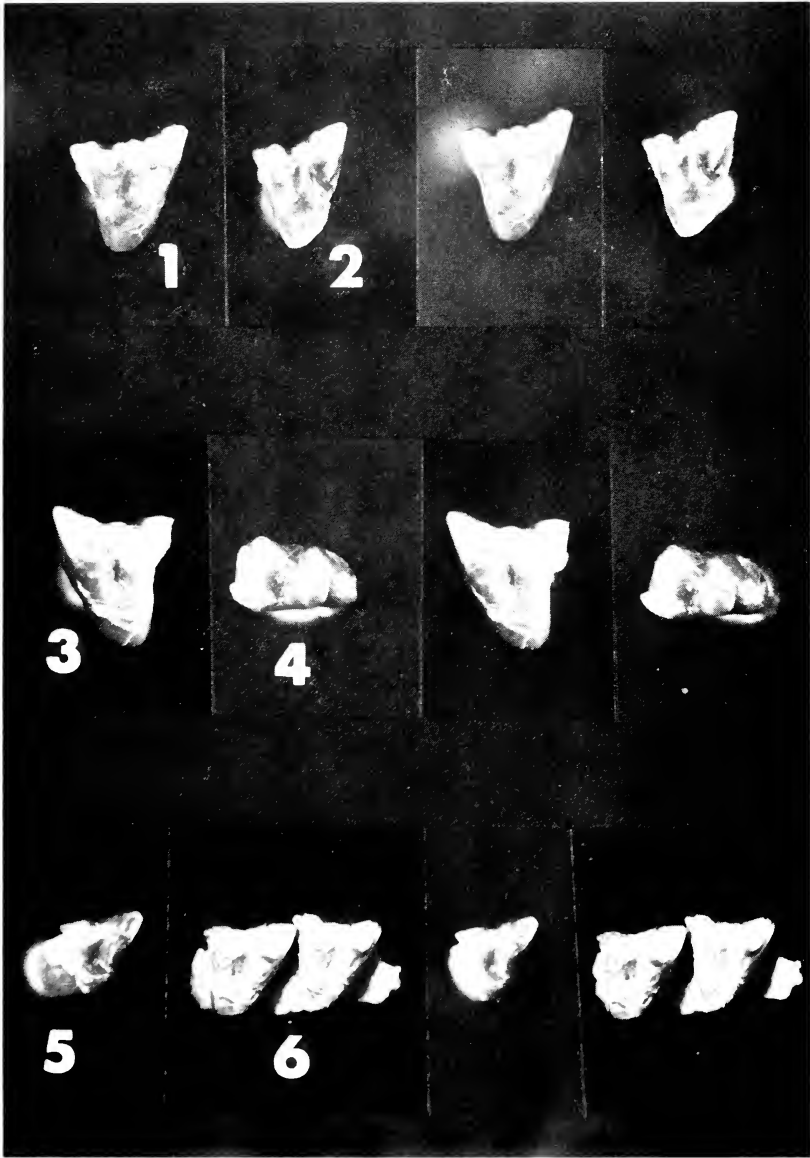
(Figs. 1, 2, 3 & 4, Table 1)

MATERIALS: M¹ — CM 23786; M² — TTU-P 1238, CM 15709, CM 23803; M³ — CM 23785, TTU-P 1375; M₁ — CM 23790, CM 23791, CM 23792; M₄ — CM 23793.

LOCALITIES: Loc. 6, 20, & Rodent, Badwater Creek, Wyoming.

AGE: Late Eocene.

DESCRIPTION: Molars are larger than those of *Peratherium knighti*. The general morphology of upper molars agrees with the corresponding molars of *P. knighti*. The morphology of the protocone, the paracone, and the metacone is very similar to that in *P. knighti*. However, the morphology of the styler shelf is different from that of *P. knighti*. On M¹, styler cusp A is a small ridge that runs anteroposteriorly and is situated just anterior to styler cusp B. Styler cusp B is situated just buccal to the anterior crest of the paracone. Posterior to styler cusp B and buccal to the apex of the paracone, the buccal ridge of the styler shelf is widely grooved. This groove runs downwards on the concave buccal surface of the styler shelf. Posterior to the groove, and, buccal and slightly anterior to the notch formed by the paracone and the metacone, a small cusp is present on the buccal edge of the styler shelf.



Figs. 1-4. *Peratherium* cf. *P. marsupium*: Fig. 1, CM 23786, left M^1 ; Fig. 2, TTU-P 1238, left M^2 ; Fig. 3, CM 23785, right M^3 ; Fig. 4, CM 23790, left M^1 (all about 5x).

Figs. 5-6. *Peratherium* cf. *P. knighti*: Fig. 5, CM 23787, left M^1 ; Fig. 6, TTU-P 1237, left maxillary fragment with M^{2-3} (all about 5x).

This cusp is lower than both styler cusps B and C. Just posterior to this cusp, styler cusp C is present. This small cusp and styler cusp C share the common base. Styler cusp C is conspicuous and situated just buccal to the notch formed by the paracone and the metacone. Styler cusp D is situated posterior to styler cusp C and lower than styler cusp C. Styler cusp E is present posterobuccal to styler cusp D and near the apex of the metastyle. Styler cusp E is smaller than styler cusp D and separated from styler cusp D by a wide and shallow groove. Styler cusps B, C, and D lie in an almost straight anteroposterior line.

M² is somewhat compressed anteroposteriorly. Styler cusp B is stout. Posterior to styler cusp B, the styler shelf is grooved buccally. This groove runs downwards on the concave buccal surface of the styler shelf. Styler cusp C is situated buccal to the notch between the paracone and the metacone. Styler cusp C is compressed buccolingually and connects to styler cusp D posterobuccal to it. Styler cusp D is as large as styler cusp C. No styler cusp E is seen. Styler cusps C and D occur on the extreme buccal border of the crown.

All M³s at hand are well worn. Apparently styler cusps B and C are stout. Between these styler cusps a wide groove is present. Undulation on the buccal surface of the styler shelf posterior to styler cusp C indicates the presence of styler cusp D. No indication of styler cusp E is present. Styler cusps occur on the buccal border of the styler shelf so that the styler shelf is rather wide.

The morphology and the size of the lower teeth is identical to those of the middle Eocene *Peratherium marsupium*. The hypoconid is crescentic. The crista obliqua runs anterolingually from the apex of the hypoconid and connects to the protolophid just posterior to the apex of the protoconid. The postcrisid runs lingually and continues to form the hypoconulid. The hypoconulid forms a horizontal, posteriorly directed ledge. It is situated posterior to the entoconid and slightly buccal to it. The hypoconulid lies far below the entoconid at almost the same level as the talonid basin. The crista obliqua and the postcrisid do not form acute narrow ridges. Thus the talonid basin is shallow and opens posteriorly across the flattened hypoconulid.

DISCUSSION: The upper molars of early Tertiary didelphids usually show significant morphological differences between species while the structure of the lower molars remains relatively constant. Size is about the only criterion that can be used for the separation of species known only from lower dentitions. The size of the present Badwater specimens is very close to that of *Peratherium marsupium* of the middle Eocene (Troxell, 1923; Simpson, 1928). Only the lower dentition of *P. marsupium* has been adequately figured. Although there is a considerable time span between the middle and late Eocene, the Badwater specimens are thought to be conspecific with *P. marsupium*.

Peratherium cf. *P. knighti* McGrew, 1959
(Figs. 3, 4, 5 & 6, Table 1)

MATERIALS: right maxillary fragment with M^{2-3} — CM 23788; left maxillary fragment with M^{2-3} — TTU-P 1237; M^1 — CM 15995, CM 23787, TTU-P 1244, TTU-P 1353, TTU-P 1355, TTU-P 1357; M^2 — CM 16006, CM 16895, CM 23804, CM 23784, TTU-P 1352, TTU-P 1358, TTU-P 5966; M^3 — CM 23831, TTU-P 1346, TTU-P 1349, TTU-P 1351; M^4 — CM 23832, CM 23833, TTU-P 1348, TTU-P 1350, TTU-P 1365, TTU-P 1366; left mandibular fragment with $M_{2,4}$ — CM 23794; right mandibular fragment with M_2 — CM 15711; DP_3 — CM 23935, CM 23936, CM 23937; M_1 — CM 16889, CM 18225, CM 23789, CM 23834, CM 23835, CM 23837, TTU-P 2426, TTU-P 2428, TTU-P 2432, TTU-P 2450, TTU-P 2445, TTU-P 5967; M_2 — CM 16888, CM 16891, CM 21633, CM 21634, CM 23795, CM 23836, TTU-P 2425, TTU-P 2426, TTU-P 2427, TTU-P 2429, TTU-P 2434, TTU-P 5965; M_3 — CM 23794, TTU-P 2424, TTU-P 2429, TTU-P 5968.

LOCALITIES: Loc. 5, 5A, 5 # front, 5 # back, 6, 20, & Wood, Badwater Creek, Wyoming.

AGE: Late Eocene.

DESCRIPTION: M^1 is elongated anteroposteriorly. The protocone is crescentic and forms a right angle at the anterolingual corner of the crown. The anterior crest extends linguobuccally along the anterior surface of the paracone, forming the anterior cingulum. There is no trace of a protoconule. The anterior cingulum, near the anterolingual face of the paracone, is very narrow, but the portion buccal to this becomes slightly wider and rises to the anterobuccal corner of the crown. Just lingual to the anterobuccal corner of the tooth, a shallow socket is opened anteriorly, which accepts the posterior corner of the antecedent premolar. Styler cusps are arranged along the extreme buccal border of the tooth. Styler cusp A is a small, anteroposteriorly elongated ridge, situated just buccal to the anterior cingulum. Styler cusp B is low and robust, and is situated posterior to styler cusp A. From the anterolingual corner of styler cusp B, a crest runs lingually to connect with the anterior crest of the paracone. Posterior to styler cusp B and anterior to the notch between the paracone and the metacone, a small and widely opened groove separates styler cusp B from the other posteriorly situated cusps. Styler cusp C is situated just buccal to the notch formed by the paracone and the metacone. Styler cusp C is connected to styler cusp D with a low ridge between them. Styler cusp D is linguobuccally compressed and situated buccal to the anterior crest of the metacone. Styler cusp D runs posterobuccally, making the styler shelf broad posteriorly. No styler cusp E is seen. The buccal face of the styler shelf is almost smooth. Buccal to the groove between styler cusps B and D the styler shelf is concave. The paracone is considerably smaller and lower than the metacone, and both are crescentic. From the apex of the paracone a crest runs buccally toward styler cusp B. The protocone, the paracone, and styler cusp B lie in an almost straight transverse line. Another crest runs posterobuccally from the apex of the paracone and joins anterolingually to the crest from the metacone

at a nearly right angle, forming a V-shaped notch. The posterolingual face of the metacone forms the buccal half of the posterior surface of the tooth. No posterior cingulum is present. A ridge runs from the apex of the protocone to the metaconule, which is crescentic and rounded. The area surrounded by proto-, para-, and metacone is basined. Between the metacone and the metaconule a narrow, shallow groove runs anteroposteriorly.

The M^2 agrees almost exactly with M^1 in general morphology. The protocone is more compressed anteroposteriorly than in M^1 . The groove posterior to stylar cusp B is deeper, and this makes stylar cusp B stouter than in M^1 . Stylar cusp C is much more elongated anteroposteriorly and small stylar cusp D is situated more posteriorly. The metacone is taller and more sharply crescentic than in M^1 . The latter feature makes the stylar shelf shorter posteriorly. Thus, M^2 is more compressed anteroposteriorly than in M^1 . The metaconule is more conspicuous and the groove between it and the metacone is wider.

The M^3 is much more compressed anteroposteriorly than in M^1 and M^2 . Stylar cusps C and D are conspicuous and share the common base. The buccal side of the tooth is broadly concave. The metacone approaches the paracone in size, but the former is taller. The buccal surface of the stylar shelf is smooth, not crenulated as it is in *Peratherium marsupium*. The protocone is somewhat more compressed anteroposteriorly than on M^2 , and the metaconule is much more conspicuous.

The M^4 is very narrow anteroposteriorly. The protocone and the paracone are well developed, but the metacone is greatly reduced. The stylar shelf is depressed, and a conical stylar cusp C is situated midway along the posterobuccal border of the shelf. The posterior stylar cusps are lost.

The morphology of the lower teeth is almost identical to that of *Peratherium marsupium*, but the size is significantly smaller.

Three teeth (CM 23935, 23936, and 23937) are identified as DP_3 s on the basis of their small size and basic similarity to permanent lower molars of *Peratherium*. The paraconid is a well defined cusp, situated at the anterior corner of the tooth. It is elongated transversely. One crest descends linguoposteriorly and another crest descends buccoposteriorly from the apex of the paraconid. The paraconid is clearly separated by a groove from the anterior ridge of the protoconid. No anterior cingulum is present. The protoconid is stout and higher than the paraconid. The protoconid is a triangular cusp. A crest runs from the apex of the protoconid anteriorly towards the posterobuccal base of the paraconid. A short crest runs linguoposteriorly from the apex of the protoconid to the apex of the rudimentary metaconid. The metaconid is not completely separated and shares a common base with the

protoconid. This crest continues to run posteriorly from the metaconid, and forms an acute ridge connecting with the entoconid. The entoconid is well below the metaconid, but almost as high as the paraconid. The hypoconulid is posterobuccal to the entoconid and forms a horizontal, posteriorly directed ledge. It lies far below the entoconid at almost the same level as the talonid basin. The hypoconulid is separated from the entoconid by a shallow groove that runs posterolingually from the talonid basin. The hypoconid is crescentic and situated just buccal to the entoconid. Anterior to the midline between the hypoconid and the entoconid is the protoconid. The crista obliqua is not well defined but it is clearly connected to the posterobuccal base of the protoconid. The posterior cingulum runs from the hypoconulid basobuccally to the buccal base of the hypoconid. No buccal cingulum is seen. The roots of the specimens are broken.

DISCUSSION: The Badwater specimens show considerable variation in molar size. Among them, CM 23784 (right M²) is very close in size to the corresponding molar of the type specimen of the Bridgerian *Peratherium knighti*. The Badwater specimens also show a wide variation in morphology. In some, the metaconule is well defined, and in others there is almost no trace of the metaconule. In some specimens, styler cusp C is united to styler cusp D as a mere ridge anterior to it. In others it is small but well defined. These differences in morphology, however, probably are no more than individual variation, and do not imply specific differences. In all specimens the styler cusps are low and are situated on the extreme buccal borders on the molars. These specimens are almost identical to the Bridgerian *Peratherium knighti*.

TOOTH CHARACTERISTICS OF *Peratherium*: The upper dentition of *Peratherium* shows a typical dilambdodont tooth pattern with the paracone and the metacone joined in a "W" shaped ectoloph. In animals with dilambdodont upper teeth, the lower molars have a hypoconid with a very sharp buccal angle that occludes in the "W" of the upper teeth, and either lack a hypoconulid or have this cusp displaced (Robinson, 1968:130). The lower molars of *Peratherium* show this pattern. The hypoconulid is displaced lingually and situated posterior to the entoconid. This characteristic feature of the hypoconulid reflects the high degree of the development of dilambdodonty of the upper dentition.

Genus *Nanodelphys* McGrew, 1937

Nanodelphys cf. *N. minutus* McGrew, 1937

(Figs. 9, 10, 11, 12 & 13, Table I)

MATERIALS: DP³ — CM 25037, CM 26467, CM 23850, CM 23851, CM 23852, TTU-P 1360, TTU-P 1362, TTU-P 1364; left maxillary fragment with M²⁻³ — CM 19748, CM 23794; M¹ — TTU-P 1250, TTU-P 1367; M² — CM 15671; M³ — CM 16007; M₁ — CM 18216, TTU-P 2416, TTU-P 2420; M₂ — CM 23844, TTU-P 2413; M₃ — CM 23843, CM 23845, TTU-P 2415, TTU-P 2418; M₄ — CM 23846, CM 23847, TTU-P 2414, TTU-P 2417.

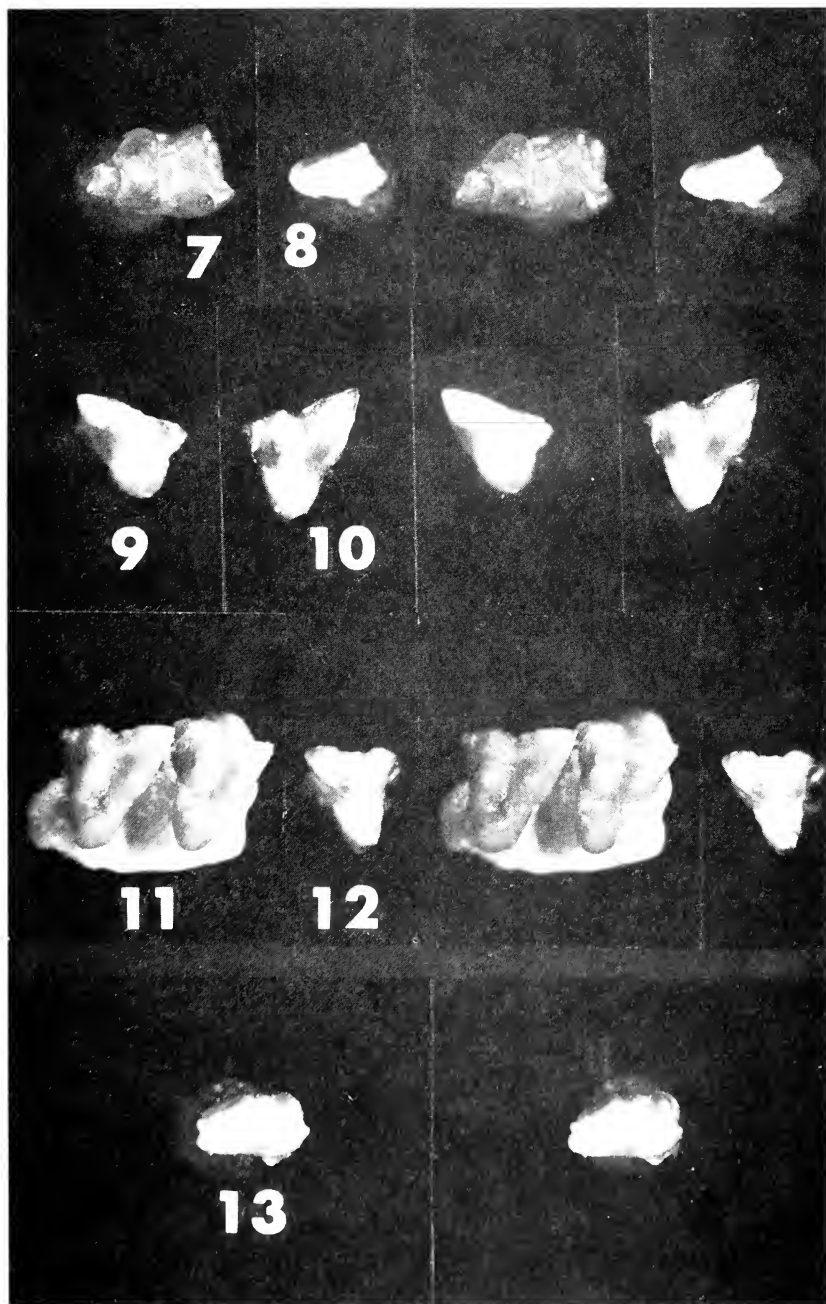
LOCALITIES: Loc. 5A, 5 # front, 5 # back, 6, 20, & Wood, Badwater Creek, Wyoming.
AGE: Late Eocene.

DESCRIPTION: DP³ is elongated anteroposteriorly. The protocone is stout, high, crescentic, and somewhat compressed linguobuccally, forming an obtuse angle at the lingual corner of the tooth. A crest runs from the apex of the protocone to a very small protoconule situated lingual to the lingual face of the paracone. A rather broad anterior cingulum is situated anterior to the paracone and forms the anterobuccal corner of the tooth. The cingulum lies lower than the stylar shelf and does not connect with it. Buccal to the paracone no stylar shelf is seen. The paracone is slightly smaller and lower than the metacone. Both are conical cusps. A crest runs posterobuccally from the paraconal apex. This crest forms the anterobuccal border of the stylar shelf. Stylar cusp C is not present. Buccal to the metacone, stout and obliquely elongated stylar cusp D extends posterobuccally. Anterior to stylar cusp D, a shallow groove separates stylar cusp D from the buccal surface of the paracone. There are no cusps posterior to stylar cusp D. The stylar shelf extends only posteriorly to the metacone. The paracone and the metacone are widely separated from each other, with a broad U-shaped notch between them. These crests run anteroposteriorly between the apexes of the paracone and the metacone and form the metaconal apex to the posterobuccal corner of the tooth. The latter crest, stylar cusp D, and the crest posterior to stylar cusp D form the border of the posterior half of the stylar shelf. A posterior ridge from the apex of the protocone runs to a small metaconule situated lingual to the metacone. Between the metacone and metaconule there is a broad and very shallow groove. The area surrounded by the protocone, protoconule, paracone, metacone, and metaconule is deeply basined.

The M¹ is elongated anteroposteriorly. The protocone is stout, high, and crescentic, and forms a nearly right angle at the lingual corner of the tooth. A crest runs almost basobuccally from the apex of the protocone and forms the anterior cingulum along the anterior base of the paracone. The crest becomes narrower just anterior to the apex of the paracone. Buccal to this, the crest becomes broader and extends to reach the anterobuccal corner of the tooth. The buccal half of the cingulum is excavated anteriorly, making a shallow notch to accept the posterobuccal corner of the antecedent premolar. On the anterobuccal corner, no stylar cusp is seen. Stylar cusp B is large and anteroposteriorly elongated, lying buccal to the paracone. Posterior to stylar

Figs. 7-8. *Peratherium* cf. *P. knighti*: Fig. 7, CM 23936, right DP₁; Fig. 8, TTU-P 2426, right M₁ (all about 10x).

Figs. 9-13. *Nanodelphys* cf. *N. minutus*: Fig. 9, TTU-P 2426, right DP₃; Fig. 10, TTU-P 1250, left M₁; Fig. 11, CM 19748, left maxillary fragment with M²⁻³; Fig. 12, CM 16007, right M₃; Fig. 13, CM 23845, right M₁ (all about 10x).



cuspid B there is a deep and wide excavation. Styler cuspid C is not present. Buccal to the metacone is a tiny, linguobuccally compressed styler cuspid that lies at the extreme buccal edge of the tooth. This makes the styler shelf broad posteriorly. No styler cuspid posterior to styler cuspid D is seen. The paracone and the metacone are of equal size, conical, and tall. A crest runs buccally from the apex of the paracone and forms the anterior border of the styler shelf. No metaconule or posterior cingulum is seen.

The M² has almost the same feature as M¹, although the former is much more compressed anteroposteriorly. The protocone forms an acute angle at the lingual corner of the tooth. Styler cuspid B is the largest. It is conical and situated slightly lingually, not on the extreme buccal border of the shelf. Posterior to the styler cuspid B there is a deep, wide excavation. On some specimens a rudimentary, anteroposteriorly elongated styler cuspid C is present on the posterior face of the excavation and just anterior to styler cuspid D. On others, styler cuspid C is completely missing. The styler shelf protrudes buccally and widens posteriorly. A rather prominent metaconule is present. Between the metaconule and the lingual base of the metacone, a wide, shallow groove runs anteroposteriorly. The area surrounded by the proto-, para-, and metacone and the metaconule is deeply basined. No posterior cingulum is present.

On M³ styler cuspid B is reduced to an anteroposterior elongated ridge buccal to the paracone. This makes the styler shelf broad anteriorly. Posteriorly to styler cuspid B there is a deep, wide excavation as on M¹ and M², but the excavation is notched buccally. Styler cuspid C is completely lost and only a small trace of styler cuspid D is seen on the extreme buccal border of the tooth. Thus, the styler shelf is broader on M³ than on M¹ and M². The portion lingual to the base of the metacone is broken. The area surrounded by the proto-, para-, and metacone is also deeply basined, as on M².

No M⁴s are recognized in this sample.

The size of lower molars is significantly smaller than that of lower molars of *Peratherium knighti*. The paraconid is situated more anteriorly than in *Peratherium*, so that the trigonid is wider anteroposteriorly in *Nanodelphys* than in *Peratherium*. The hypoconid forms an acute angle with the entoconid and the crista obliqua is concave buccally. In relation to this, the hypoflexid is wide anteroposteriorly and excavates the talonid basin buccally. The posteristid runs from the hypoconid posterolingually and connects with the hypoconulid. The hypoconulid is situated posterobuccal to the entoconid. The hypoconulid is a little lower than the hypoconid and is as high as the entoconid. A ridge runs between the hypoconulid and entoconid. The talonid is rather deeply basined. It is completely blocked posteriorly by the posteristid and the hypoconulid.

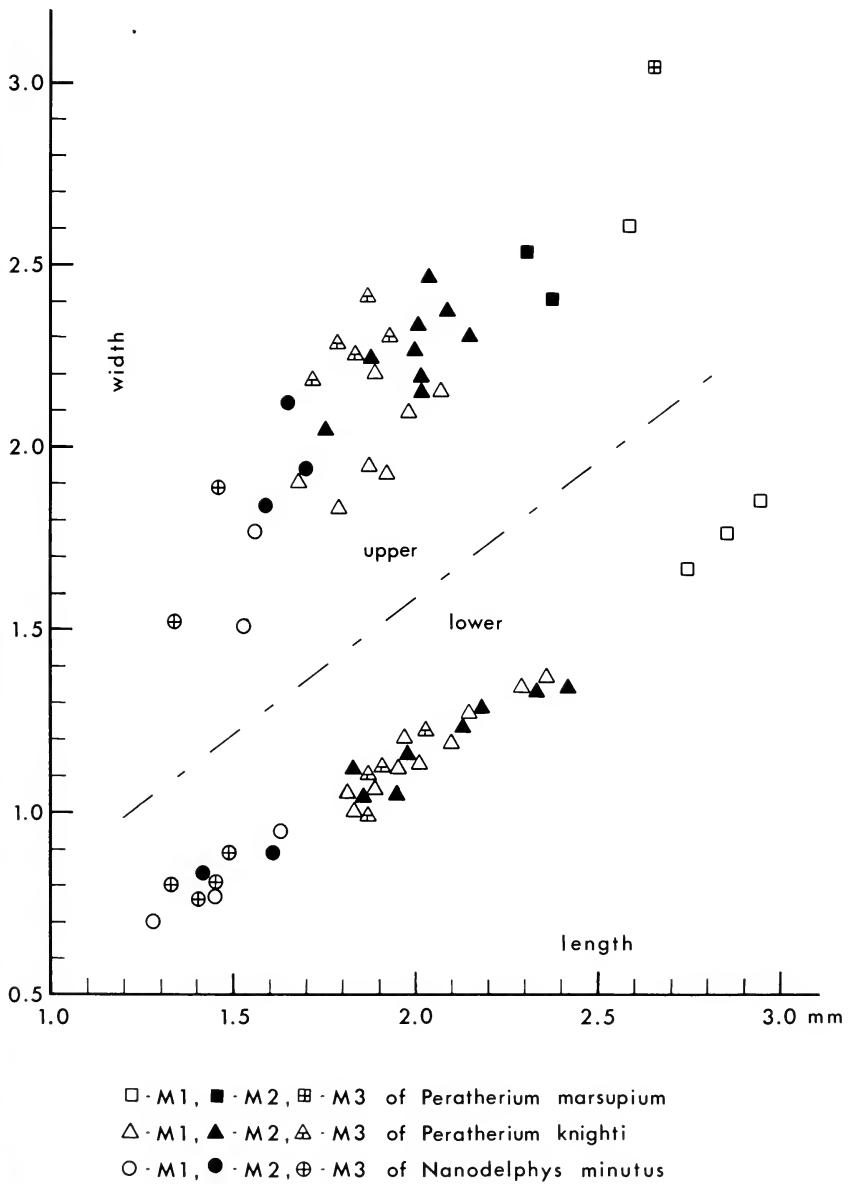


Fig. 14. Size-frequency graph of molars.

TOOTH CHARACTERISTICS: The upper dentition of *Nanodelphys* shows less dilambdodonty. The paracone and the metacone are more conical than in *Peratherium*. In relation to the less well-developed dilambdodonty of the upper molars of *Nanodelphys*, it seems that displacement of the hypoconulid is less emphasized in the lower dentition of this genus.

TABLE I. TOOTH DIMENSIONS (MEASUREMENTS IN MM)

	Number of Specimens	Observed Range of Length	Mean Length	Observed Range of Width	Mean Width
<i>Peratherium</i> cf. <i>P. marsupium</i>					
Upper Molars					
M ¹	1	2.59	—	2.60	—
M ²	1	2.38	—	2.40	—
M ³	1	2.66	—	3.04	—
Lower Molars					
M ₁	3	2.75-2.95	2.853	1.66-1.85	1.756
<i>Peratherium</i> cf. <i>P. knighti</i>					
Upper Molars					
M ¹	6	1.68-2.07	1.885	1.83-2.15	1.971
M ²	9	1.75-2.15	1.996	2.04-2.46	2.253
M ³	6	1.72-1.93	1.842	2.18-2.41	2.273
Lower Molars					
DP ₃	3	1.38-1.70	1.493	0.81-0.95	0.870
M ₁	10	1.83-2.36	2.040	1.03-1.37	1.178
M ₂	8	1.83-2.42	2.084	1.03-1.34	1.194
M ₃	4	1.87-2.03	1.928	0.99-1.22	1.108
<i>Nanodelphys</i> cf. <i>N. minutus</i>					
Upper Molars					
DP ³	5	1.33-1.50	1.428	1.35-1.47	1.418
M ¹	2	1.53-1.56	1.545	1.51-1.77	1.640
M ²	3	1.59-1.70	1.647	1.84-2.12	1.967
M ³	2	1.34-1.46	1.400	1.52-1.89	1.705
Lower Molars					
M ₁	3	1.28-1.63	1.453	0.70-0.95	0.807
M ₂	2	1.43-1.61	1.520	0.83-0.89	0.860
M ₃	4	1.33-1.49	1.420	0.76-0.89	0.815

CONCLUSIONS

No lower dentition of *Nanodelphys* has been described. The upper molars of early Tertiary didelphids usually show significant morphological differences between species. On the basis of morphological differences of upper molars, three species of didelphid marsupials from the late Eocene of Badwater, Wyoming, are recognized. Upper molars of these three species can be grouped into three size categories (Fig. 14). The largest group is *Peratherium marsupium*, the second largest *P. knighti*, and the smallest *Nanodelphys minutus*. Lower molars from Badwater can also be grouped into three size categories, correlative with the size groups of upper molars. It is thus safe to conclude that the smallest group of lower molars belongs to *Nanodelphys minutus*.

The lower molars of *Nanodelphys* can be distinguished from those of *Peratherium* on morphological grounds other than that of size. In *Peratherium*, the hypoconulid forms a horizontal, posteriorly directed ledge directly posterior to the entoconid, and the talonid basin opens posteriorly across the flattened hypoconulid. In *Nanodelphys*, however, the hypoconulid is raised posterobuccally to the entoconid and blocks the talonid basin posteriorly. The characteristic differences of the lower dentition reflect the degree of the development of dilambdodonty of the upper dentition among didelphids. And, in turn, these characteristic differences between these two major types reflect generic differences between *Peratherium* and *Nanodelphys*.

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ARTICLE 14

SOLVED AND UNSOLVED PROBLEMS IN THE *SPOROPHILA LINEOLA/BOUVRONIDES* COMPLEX (AVES: EMBERIZIDAE)

PAUL SCHWARTZ¹

The relationships and taxonomic treatment of the white-cheeked, black-and-white seedeaters, *Sporophila lineola* and *S. bouvronides*, have never been satisfactorily resolved. Within the complex, which is distributed through most of South America, the two characters most obviously subject to variation—the extent (or absence) of white on the crown, and the amount (or absence) of dark mottling or barring on the white underparts—appear to vary in a continuous sequence from one extreme to the other, with no correlation either with one another or with any clear-cut geographic pattern. Birds more or less “typical” of *lineola* and *bouvronides* are illustrated in Haverschmidt (1968:414-415). Many birds of the *bouvronides* kind are mottled on the chest rather than only on the sides as shown in the figure on page 415.

Meyer de Schauensee (1952:175-181) reviewed the problem and proposed treating the forms as one species, with nominate *lineola* (broadly white-crowned, usually with unmottled underparts) occupying Brazil south of the Amazon and east of the Tapajoz, eastern Bolivia, Paraguay, and northern Argentina; roughly the southeastern half of the complex's total range. He limited *bouvronides* (essentially black-crowned; more or less mottled underparts) to the islands of Trinidad

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and Tobago. At the same time he revived *restricta* (essentially black-crowned; unmottled underparts), a form from northeastern Colombia that Hellmayr (1938:212) had synonymized with *bouvronides*. The highly variable population (as seen in museum collections) of northern and western Amazonia, Venezuela, and the Guianas he treated as hybrid between *restricta* and *lineola*.

Subsequent to Meyer de Schauensee's 1952 revision, Phelps and Phelps (1963:405) treated *lineola* and *bouvronides* as separate species, as they had in the earlier edition of their Venezuelan list; Meyer de Schauensee (1966:507-508) gave a simplified version of his former proposal, considering continental *bouvronides*-like birds as individual variants of nominate *lineola*; Haverschmidt (1968:414-415) believed two species were involved; and Paynter (1970:139-140), referring to "this vexing species," followed essentially the later treatment of Meyer de Schauensee.

I have worked with this complex in Venezuela since 1957, chiefly since 1972. I believe I can now with some confidence suggest the basic solution to the problem. My investigations, however, have disclosed some previously unsuspected sub-problems, and until they are resolved, some pieces of the puzzle will remain missing. By presenting this preliminary report I hope to stimulate interest leading to a more rapid total solution.

THE BASIC SOLUTION

Field work and programmed collecting have established that in north-central Venezuela from, roughly, June/July to November/December there are present two distinct, coexisting populations of this complex, one of them breeding (B) and the other non-breeding (X). Both populations are migratory and from January to May neither is present except as represented by marginal vagrants. Both show characteristics of long-distance migrants, not just off-season wanderers like the other common *Sporophilae* that breed throughout this region. X, however, may possibly do some wandering after arrival in the region. Both populations arrive and depart at about the same time, although B arrives somewhat earlier and departs somewhat later than X.

In other parts of northern Venezuela the periods of presence and absence may vary slightly from the regime indicated, and the arrivals and departures of the breeding and non-breeding populations may be less coincidental, but their relative status remains the same.

Through studies of wild and captive birds I have been able to define reasonably well the characters of these populations. Work in progress should permit delineating them completely, but for purposes of the present paper I indicate that B is essentially black-crowned, while X is invariably white-crowned. These letters are used for the Venezuelan

populations under discussion, and are not to be construed as necessarily applying to other black- and white-crowned populations. Fuller characterizations and more detailed analyses of plumage variations will appear in a future publication, in which I will also present data substantiating the basic solution to this problem, proposed preliminarily in the present paper.

The situation of a heterogeneous community structure deriving from the coincidental presence in the same region of two or more distinct migratory populations apparently applies to most of Amazonia and northern South America. Recognizing this dissolves much of the former confusion and should open the way to more effective future investigation.

UNSOLVED PARTS OF THE PROBLEM

As a breeding bird, B extends across northern Venezuela (and probably all northern South America), south to at least 7° N lat, but perhaps not much farther south than that. Where it spends the non-breeding season is not yet known. A brief preliminary review of some museum collections suggests this may be in Amazonia.

The total extent of the "wintering" range of the X population is undetermined. Its breeding range is unknown, or at best, uncertain. There is a hint from preliminary information that this could be in northeastern Amazonia, i.e., Cayenne and contiguous regions, but in any case logic suggests it is somewhere in Amazonia, *sensu lato*, or south of there.

The birds' vocalizations have proved useful up to now and will be an important tool for future work. These sounds will be discussed later in greater detail, but it is necessary to consider briefly here the primary song in order to demonstrate the nature of some still-remaining pieces of this puzzle.

In the B population the primary song consists of short, intermediate, and long phrases, any one individual employing all at one time or another. The short phrase, while showing some individual and geographic variation, is basically consistent in pattern throughout the B population. It is the phrase most frequently used, when one considers an individual's total singing time, and may be the principal species-specific element of primary song. It is a rather simple "vocal rattle": a slower or faster "dididididee" or "krrrrrrre," sometimes with no terminal "chirp," sometimes with more than one. This is the song usually described in the literature. Longer phrases usually begin with the short phrase motif, then continue with variations, the longest being fairly complex. A recording of one common dialect of the B song-pattern group is presented in Schwartz ([1964]).

The birds of Trinidad have this same song pattern (from the literature and a recording by David Snow). Other than this, the only extra-Venezuelan song I have heard is that presented by Frisch ([1962]), who

informs me that it was recorded in central São Paulo state, Brazil, well within the range of birds now thought of as nominate *lineola* and thus presumably of a white-crowned bird (black-crowned birds are unknown from this region of Brazil, or from anywhere south of Amazonia). This song is very similar to that of Venezuelan B, clearly a part of that song-pattern group. In playback experiments Venezuelan B generally reacts to this Brazilian song with the same intensity as to its own. [Author's note: After this paper was originally submitted for publication I received most opportunely from J.C.R. Magalhães a fine recording of a "Bigodinho," made 16 February 1975 at his farm, Fazenda Barreiro Rico, in central São Paulo state. He indicated it was of "an extremely territorial adult male with a white crown." This bird's song is virtually identical to that given by breeding, black-crowned birds in Venezuela.]

From the time I first became interested in this problem I looked closely at all the singing white-cheeked seedeaters I encountered (in Venezuela) without ever seeing any with more than a trace of white in the crown. Not until early July, 1966, in northern Bolívar state, did I finally encounter broadly white-crowned birds. These were in foraging flocks, which is typical of seedeaters outside the breeding season. All "adult" males in these flocks were white-crowned. Birds of both sexes were collected. All had small gonads in non-breeding condition. During the same period, in the same region, I also found singing, territorial birds, all of which were black-crowned. One that was collected had large testes in breeding condition. These circumstances, coupled with the similarity of song already evident from Frisch's Brazil record, suggested a solution to the confusion about the complex: both forms belonged to a single species, but white-crowned birds in northern South America were off-season migrants from south of the Amazon.

However, when several trappers and fanciers of local birds subsequently told me that "white crowns" sing in Venezuela, hence (according to their interpretation) must also nest, further investigation of the problem was indicated. Although this has shown the solution to be less simplistic than it had earlier seemed, I am now fully convinced that X (previously identified in this paper as a population of birds with white crowns that "winters" in northcentral Venezuela) does not nest in northern Venezuela. But it does sing. It is interesting that its song pattern is distinctly different and, although generally related, seems not to belong to the B song-pattern group. Its short phrase consists of several spaced, short whistles followed by a rattle that is somewhat different from the rattle of B, sounding more like "dit dit dit drdrdrdr."

This same X song pattern has been heard and recorded from a number of individuals at two separate "wintering" sites in Venezuela (central Carabobo and, 200 km to the south, southwestern Guárico), and throughout the year from captive birds. No other song type has been heard from

X birds. Captive B birds sing the B song pattern throughout the year, indicating that the different X song is not explainable as an off-season variation that continues in captivity.

Because of their "inverted" life cycles it is difficult to assess the relationship of B and X. The inference from song playback experiments and observations of wild and captive birds is that they behave as distinct species. The different song-pattern of X may have evolved through character displacement to provide an isolating mechanism between B and X. Considering the temporal and geographical disparity between the normal breeding periods of these migratory populations this last suggestion may seem unlikely. We do not, however, know their past history, nor do we yet know their complete present story. In the course of other work I found that a female *Sporophila minuta* hatched in October (banded as a nestling), bred successfully the following June (age eight months). Thus precocious X females hatched in January or February on the normal X nesting grounds might be attracted to breed with B males in September or October if the songs of B and X were the same, or vice versa if B and X similarly occur together at the opposite end of their migration routes. Chances of the circumstances permitting such interbreeding would probably normally be minimal. They would increase, however, should the breeding region of X lie in northern Amazonia and meet or closely approach the southern limit of the breeding range of some black-crowned populations. In such a region the two forms would probably more nearly approach synchrony of breeding periods, under similar climatic (hence availability of food) influence. This would provide an opportunity for the development of character displacement, with the reinforcement of reproductive isolation between the two populations through the evolution of divergent primary song.

However much B and X may appear to be separate species, we do not know how they behave toward other populations. Based on the similarity of vocal characters and song response in Venezuela, I am obliged to think that B could be conspecific with the São Paulo population, hence possibly (but not necessarily) with the whole array of breeding populations in eastern Brazil. The question then arises: what is the status of X as a breeding bird with respect to the São Paulo population, which is generally similar in appearance but has a B-type song? The distinct song of X may be only a well differentiated dialect that intergrades through connecting populations with that of central São Paulo. If so, we may have a "ring species," and B and X would have to be considered conspecific even though their direct interactions may be as distinct species. I believe no "ring species" has yet been convincingly demonstrated in the western hemisphere. Thus there is a particular interest in determining the status and place of X within the complex, as well as whether there are populations nesting across Amazonia in such a

way as to establish a link between the breeding populations of northern South America and those south of Amazonia.

To judge from comments by Haverschmidt (1968) and Young (1929:243), a situation at least somewhat similar to that described above for Venezuela appears to apply also to Surinam and Guyana. From field work in the border region I have little doubt that the breeding population of Guyana corresponds to the same B population of Venezuela, and would guess that Surinam breeding birds do too. However, we do not know whether the "wintering" white-crowned birds of Surinam, Guyana, or even extreme eastern Venezuela come from the same vocal-pattern population as do the central Venezuelan X birds.

The situation in Cayenne requires investigation. Black-crowned birds have not yet been reported from there and Kenneth Parkes informs me that in Carnegie Museum of Natural History there are Cayenne specimens of white-crowned birds from the period January-May. The breeding condition of those birds is not indicated on the labels or in the field notes of the collector, S.M. Klages, but the temporal coincidence, when considered in the context of other partial and preliminary information, suggests that Cayenne may lie within the breeding region for the Venezuelan X, the Guyana and Surinam white-crowned birds, or both. If so, it points to northeastern Amazonia, perhaps northern Amazonia generally, as this breeding region.

Any or all populations south of Amazonia may have bearing on the essential problem. For example, I have been informed by J.D. Frisch, J.C.R. Magalhães, and H. Sick that the breeding populations of southeastern Brazil are migratory. Although not surely known, it is believed that they migrate northward to Amazonia. They could thus contribute to the heterogeneous appearance of collections from that region. In any case, these populations should be studied before our understanding of the *S. lineola* complex can be considered thorough.

The movements of the birds nesting in the extreme southern and southwestern part of the complex's range are also poorly known (*vide* F. Contino, C.C. Olrog, *in litt.*). Our ignorance about the entire complex is almost complete.

NEED FOR COOPERATION

I may find partial answers to some of the remaining problems, or may make reasonable deductions, leading thereto, once I have completed detailed examination of existing collections. Many specimens, however, are inadequately labeled as to exact locality, date, or breeding condition of the bird when collected. Furthermore, museum collections give no clue as to voice.

There is need for adequate material from as many localities as possible throughout South America and from throughout the year. Gathering

such vast material within a reasonable time is probably beyond the means of any one person. Therefore I present the problem in its present state with the hope that others resident in or traveling to regions of possible interest (especially Amazonia, *sensu lato*, entire eastern Brazil, and the Guianas), may be able to obtain some of the needed information and thus contribute toward the total solution. It would appear that the matter has interest beyond that of alpha taxonomy. Among other things, should future investigation establish that the migratory B and X populations occur together in the breeding range of X, as they do in the breeding range of B (i.e., that each "winters" in the breeding range of the other), it would disclose a most unusual condition. A possibly similar case seems to be suggested by Olrog (1965:271,272).

Optimally, specimens should be of males in "adult" plumage (pied plumage also acceptable), with accurate information about locality, date, condition of testes (measurements), and fat deposition, and be linked to recordings of the bird's song before it was collected, or even to written transcriptions of song-pattern. Specimens without recordings or song descriptions (but otherwise fully labeled as indicated) are still very useful. So too are carefully identified and labeled recordings without specimens. These could serve to point out possible breeding localities of birds with the X song-pattern and in general to map song patterns. In the case of recordings made where specimens may not be collected, an effort should be made to observe not only the plumage pattern of the singing bird, but also its behavior; to determine, through territorial interaction—natural or in reaction to recorded song playback—or other evidence, whether it may be a breeding bird. Non-breeding seedeaters may sing on the "wintering" grounds, but this appears to be social singing and the birds do not display breeding season territoriality. Note, too, that some actually breeding birds may react indifferently or not at all to song playback, depending upon the phase of the breeding cycle in which they are found.

Banding may provide important information and should be done in spite of the low probability of returns. Vast, largely unoccupied regions are involved, although the custom of trapping these birds for cage purposes may increase the probability of band recoveries. In this regard I have banded about 100 birds, most of them in "female" plumage, with U.S. Fish & Wildlife or colored bands, and hope to be able to increase such efforts in 1975. Field observers should be on the alert for banded birds in any plumage.

Additionally, an effort should be made to learn what grass seeds are used for food and whether there is a predominant kind among them. These birds are not ground foragers, but glean seeds directly from the spikes, so it is not difficult to determine, with care, from which plants they feed. The observer's emphasis should be on native grasses, for the

birds may readily utilize some widely spread introduced species such as *Panicum maximum*.

I am indebted to Otto Huber for reading critically a draft of this paper, and to Mary H. Clench and Kenneth C. Parkes for their careful and pertinent editing of the final version. Marilyn Niedermeier kindly typed the last draft. To avoid lengthy repetition, other acknowledgments will appear in the detailed publication that will follow completion of current studies. Opportunely received contributions of information, sent to me or published independently, will also be incorporated in that paper.

SUMMARY

The systematics of the *Sporophila lineola/bouvronides* complex has never been satisfactorily resolved. Investigations of wild and captive birds in Venezuela disclose that the heterogeneous appearance of series presently in museum collections is an artifact, the result of the coincidental presence in the same region of biologically discrete, migratory populations which, when properly separated, are clearly definable. The investigations have also discovered some previously unsuspected sub-problems within the complex.

The detailed results of these studies, which are still in progress, will be presented in a future paper, the purpose of the present publication being to indicate the basic solution to this long-standing problem, and to point out some fundamentally important unsolved aspects, with the hope that others resident in or traveling to regions of possible interest may be able to gather data toward the total solution.

RESUMEN

La sistemática del complejo *Sporophila lineola/bouvronides* nunca ha quedado resuelta satisfactoriamente. Las investigaciones de campo y con aves en cautiverio, efectuadas en Venezuela, revelan que la apariencia heterogénea de las series existentes en colecciones de museos es una condición artificial que ha resultado por la presencia coincidente en la misma región de distintas poblaciones migratorias, las cuales son claramente definibles. Estos estudios, además, han descubierto varios sub-problemas no sospechados dentro del complejo.

Los resultados detallados de estas investigaciones, aún en curso, serán presentados en un trabajo futuro, siendo el motivo de la presente publicación indicar la solución básica de este antiguo problema; además de señalar algunos aspectos, aún no resueltos, de importancia fundamental para la aclaración definitiva, con la esperanza de que otros investigadores que residan o viajen a regiones de interés puedan obtener datos conducentes a una solución final.

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ARTICLE 15

PALEONTOLOGY AND GEOLOGY OF THE BADWATER CREEK AREA, CENTRAL WYOMING

Part 12. Description and Review of Late Eocene
Multituberculata from Wyoming and Montana

LEONARD KRISHTALKA AND CRAIG C. BLACK

Section of Vertebrate Fossils

INTRODUCTION

Remains of a late Eocene multituberculate were first discovered (Robinson, et. al., 1964) at two Badwater localities, 5 and 5A, in the Hendry Ranch Member of the Tepee Trail Formation (as used by Tourtelot, 1957). There is now almost overwhelming evidence that these sediments do not represent eastern equivalents of the Tepee Trail Formation. Rather, these volcanic rich silts and clays were probably deposited at the same time as, or somewhat later than, the volcanic conglomerates of the Wiggins Formation, which overlies the Tepee Trail Formation in its type area (Love, 1939). But until a thorough geologic review of the area can be completed, we shall continue to follow Tourtelot's usage. The multituberculate remains were described by Sloan (1966) as *Parectypodus lovei*. *P. lovei* has also been reported (Black, 1967) from the late Eocene Shoddy Springs local fauna, Climbing Arrow Formation, Montana, but this material has not been described or discussed in systematic detail. A larger sample of multituberculate teeth has since been recovered from three different Badwater localities, 6, 20, and Wood. Our re-examination of the late Eocene multituberculate remains from Wyoming and Montana indicates the occurrence of a greater diversity of

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taxa than hitherto reported, and provides evidence for referral of *Parectypodus lovei* to *Ectypodus*.

All measurements are given in millimeters. Abbreviations are as follows: CM, Carnegie Museum of Natural History; UCM, University of Colorado Museum; UCMP, University of California Museum of Paleontology; KU, University of Kansas Museum of Natural History.

SYSTEMATIC DESCRIPTION

Family Neoplagiulacidae Ameghino, 1890

Ectypodus Matthew and Granger, 1921

The genus *Parectypodus* was named by Jepsen (1930), but he later (1940) synonymized it with *Ectypodus*. McKenna (1960) reviewed the species of *Ectypodus* in some detail and concurred with Jepsen's conclusions. But Sloan (1966) claimed that the genoholotype of *Parectypodus*, *P. simpsoni*, was distinct from other species of *Ectypodus*, and revived the genus to include *P. simpsoni*, *P. laytoni*, and the late Eocene *P. lovei*. Additional species may be referred to *Parectypodus* in Sloan's unpublished manuscript concerning Puercan multituberculates (Sloan, 1966).

The extensive definition of *Parectypodus* presented by Sloan (1966) utilizes only characters of the fourth premolars. Only five posterior fragments of P₄ comprise the fourth premolar sample in the original collection of multituberculate remains from Badwater, and these do not lend themselves to the criteria of Sloan's diagnosis. Two partial fragments of P⁴ and a nearly complete P₄, subsequently recovered from Badwater and the Shoddy Springs locality, do not agree with the description of these teeth given for *Parectypodus*. Rather, as described below, they closely resemble *Ectypodus* in comparable parts of the dentition (McKenna, 1960; Krishtalka, 1973). All material described by Sloan (1966) from Badwater localities 5 and 5A as *P. lovei*, as well as additional material from locality 6 and Wood are here referred to *Ectypodus lovei*. Material recovered from the Climbing Arrow Formation, Montana, and Badwater locality 20 seems distinct from *E. lovei*, and is here assigned to *Ectypodus* sp. Available material does not warrant description of a new species.

Ectypodus lovei (Sloan, 1966)

Figures 1-8, Table 1

Parectypodus lovei Sloan, 1966

TYPE: CM 15126, right M₁.

REFERRED SPECIMENS: P₄, UCM 28358, CM 15053, 15629, 16980, 16984, 27626; M₁, UCM 27096, 28359, CM 15129, 16982, 16983, 17513, 18256, 21336; M₂, CM 21335; P₃, CM 21641, 27628; M¹, UCM 25681, 27076, 28360, CM 15084, 15085, 15133, 16981, 21334, 21640; M², UCM 25255, 27094, CM 15054, 15086, 21642.

HORIZON AND LOCALITY: Late Eocene, Badwater localities 5, 5A, 6, Wood, Hendry Ranch Member, Tepee Trail Formation, Natrona County, Wyoming.

DESCRIPTION AND DISCUSSION: The five posterior fragments of P_4 from localities 5 and 5A described by Sloan (1966) are of little diagnostic value. Neither the standard length, nor the height of the first serration above the anterior enamel base can be measured, nor can the number of serrations be counted or reliably estimated. The orientation of the ridges at the posterolabial corner of P_4 is similar in most ectypodontids except for *Mimetodon*. However, the angle formed at the posterodorsal corner of P_4 , between the slope and the vertical posterior border of the blade, may be indicative of the generic affinities of P_4 among certain ectypodontids (Krishtalka, 1973, from Sloan, pers. comm.). The slope is quite steep in *Parectypodus* (approximately 140 degrees), but less so in *Ectypodus* and *Mesodma* (approximately 110-125 degrees). The five posterior fragments of P_4 referred here to *E. lovei* have a posterior angle of approximately 120 degrees. These fragments are also included in *E. lovei* through parsimony, by tentative association with the remaining isolated teeth from localities 5 and 5A, all of which seem attributable to one species.

In terms of numbers of complete isolated teeth, the record of lower first molars from Badwater is best. All but one have a cusp formula of 6:4, with labial and lingual margins that converge anteriorly and are more nearly straight than convex. The cusps on M_1 are crescentic, and the length-to-width ratio ranges from 1.66 to 1.75. M_1 's of *E. lovei* are smaller than are those referred below to *Ectypodus* sp. They also possess a lower cusp formula, a more nearly straight external border, and more nearly parallel labial and lingual margins in occlusal view. Sloan (1966) correctly noted that M_1 of *E. lovei* closely resembles UCMP 44009, M_1 of *E. tardus* from the early Eocene Four Mile fauna (McKenna, 1960). This, and the diagnostic structure of P^4 described below, imply that the multituberculate remains from Badwater localities 5, 5A, 6 and Wood are more closely allied to *Ectypodus* than to *Parectypodus*.

Only CM 21336, RM_1 from locality 6, with a cusp formula of 7:4, more nearly resembles M_1 of *Ectypodus* sp. CM 21336, however, is tentatively referred to *E. lovei*, since the remaining sample of isolated teeth from locality 6 resembles the comparable teeth of *E. lovei* from localities 5 and 5A. A second M_1 from locality 6, CM 18256, is extremely worn, but in size and cusp formula (6:4) is typical of *E. lovei*. If CM 21336 is properly an M_1 of *E. lovei*, the range of variation in M_1 of that species is large, and its structure may imply the ancestry of the younger *Ectypodus* sp. from *E. lovei*. On the other hand, a larger sample from locality 6 may imply the presence of both species of *Ectypodus* at one horizon.

M_2 of *E. lovei* was not known at the time of Sloan's (1966) original description. Three specimens of M_2 have since been recovered, one of

E. lovei from locality 6, and two of *Ectypodus* sp. from the Climbing Arrow Formation. CM 21335, RM₂ from locality 6, is much shorter than M₂ from Montana, and possesses a lower cusp formula (3:2 as opposed to 4:2). The anterior end of CM 21335 is of suitable width and shape to abut against the posterior end of M₁ of *E. lovei*.

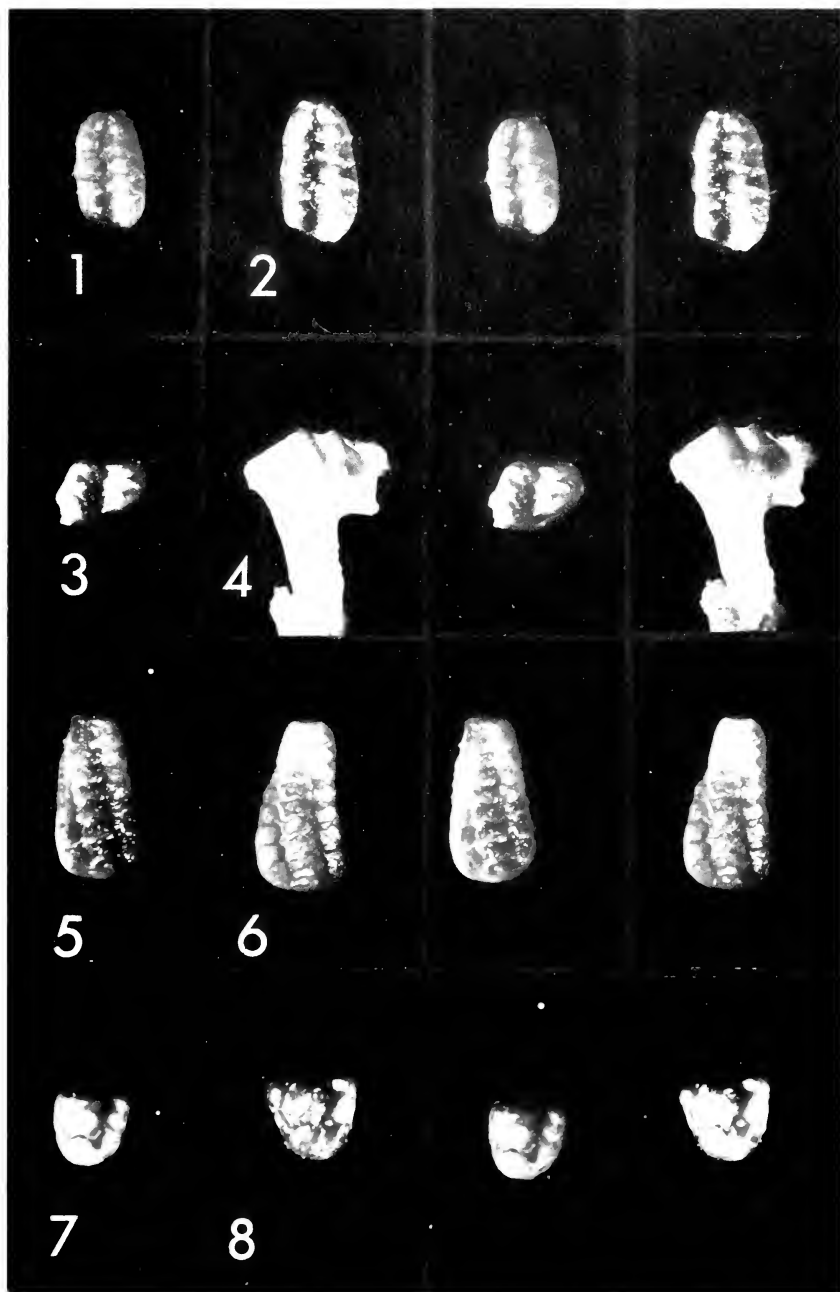
Upper fourth premolars of *E. lovei* did not occur in the original sample from Badwater. One specimen, CM 21641 from locality 5A, comprises approximately the posterior three-quarters of P⁴, which is highly diagnostic in ectypodontids (Krishtalka, 1973). The preserved anterior profile of CM 21641 is straight and bears four cusps, of which the last is highest on the crown. The posterior slope is straight and short, and a posterobasal cuspule appears to have been present in the unworn condition. Among ectypodontids known to us, these features are diagnostic of P⁴ of *Ectypodus*. In contrast, on P⁴ of *Parectypodus* and *Neoplagiulax*, the anterior slope is convex in labial view, the antepenultimate or penultimate cusp is highest in the internal row, and the posterior slope is concave. On P⁴ of *Mesodma*, as in *Ectypodus*, the anterior profile is straight and the ultimate internal cusp is highest on the crown. The posterior slope, however, is usually convex in *Mesodma*, and the anterior profile is lower than in *Ectypodus*.

A second specimen, CM 27628 from locality 6, comprises approximately the anterior one-quarter of P⁴ and preserves the first three cusps of the internal row and two external cusps. The latter are situated opposite the second and third internal cusps, respectively. CM 27628 is of a size and structure consistent with that of CM 21641, the posterior fragment of P₄ from locality 5A.

M¹ of *E. lovei* is known from 10 specimens, only two of which are complete. The cusp formula is 7:9-10:5-6, which is very similar to that of *E. tardus* from Four Mile (McKenna, 1960). The cusps are crescentic and progressively decrease in size anteriorly in each row. The most variable character on M¹ is the length of the internal row and its point of origin anteriorly from the medial row. The internal row originates at the level of the fourth and fifth medial cusps on UCM 25681 (cusp formula 7:10:5), the third medial cusp on CM 21334 (cusp formula 7:9:6) and CM 21640 (an anterior fragment), and the second medial cusp on CM 15133 (an anterior fragment). M¹ of *E. lovei* is shorter than M¹ of *Ectypodus* sp. described below, and possesses fewer cusps in the external row (7:9-10:5-6 as opposed to 9:9:6).



Figs. 1-8. Stereophotographs of teeth of *Ectypodus lovei*, all approx. x 10. Fig. 1. CM 15126, RM₁, occlusal view. Fig. 2. CM 21336, RM₁, occlusal view. Fig. 3. CM 21335, LM₂, occlusal view. Fig. 4. CM 21641, LP⁴, labial view. Fig. 5. CM 21334, LM¹, occlusal view. Fig. 6. UCM 25681, LM¹, occlusal view. Fig. 7. CM 15086, RM₂, occlusal view. Fig. 8. CM 21642, RM₂, occlusal view.



The four specimens of M^2 from Badwater localities 5 and 5A that were described by Sloan (1966) are here assigned to *E. lovei*. The cusp formula is 1:3:3, but the external cusp is extremely weak, low and flattened; and, as Sloan points out, it is merely part of the crest that forms the anteroexternal corner of the crown. In occlusal view, the crown is very nearly triangular except for the posterior margin, which is not angular but conspicuously rounded. The reverse is true of M^2 , referred below to *Ectypodus* sp., on which the external cusp is more distinct and the posterior margin of the crown not rounded, but angular.

Ectypodus sp.

Figures 9-14, Table 2

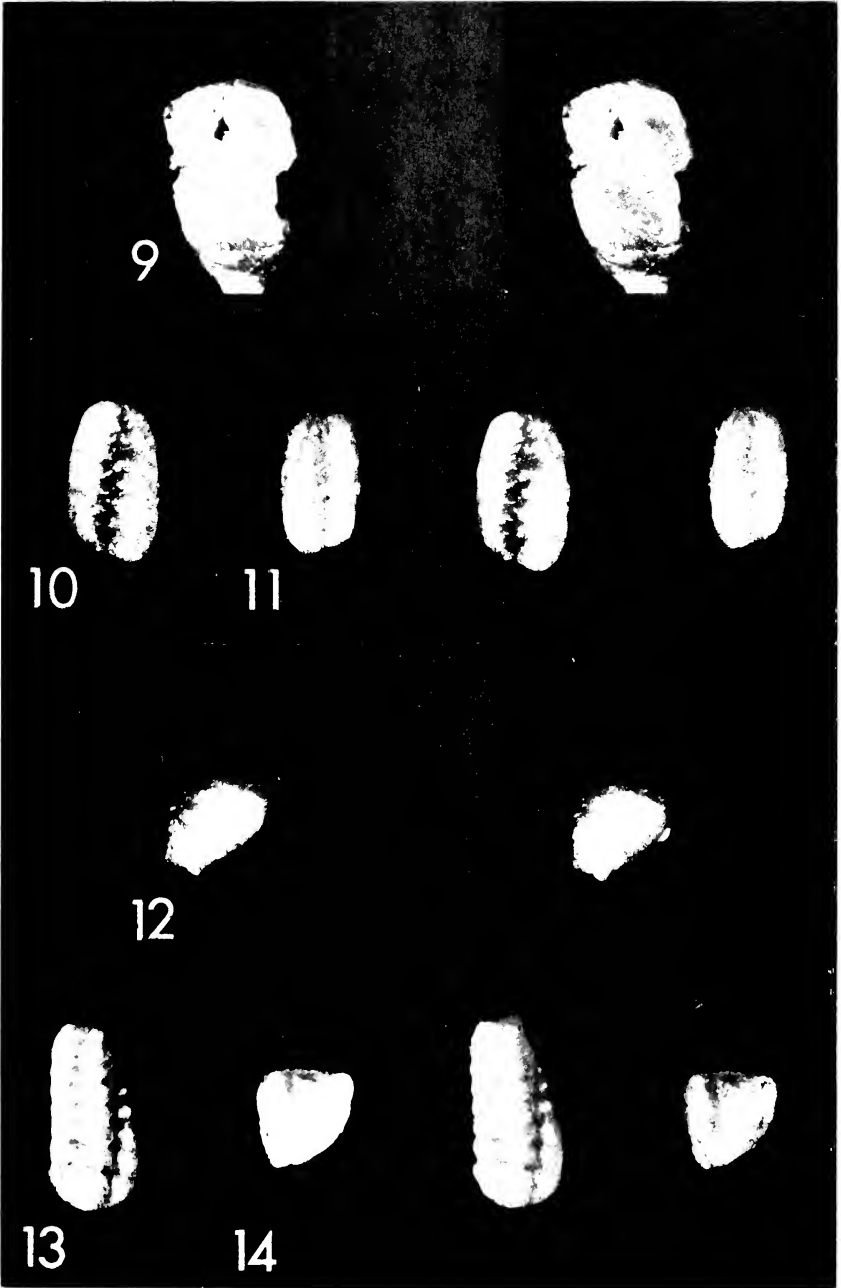
REFERRED SPECIMENS: P_4 , CM 18842, 18843, 21270, 21271, 27627, KU 17128; M_1 , CM 18841, 18844, 18845, 18847, 21273, 21275, 26266, KU 17131; M_2 , CM 21272, 21274; M^1 , CM 18846, 27629, KU 17130, 17132, 17179; M^2 , CM 26265.

HORIZON AND LOCALITIES: Late Eocene, Badwater locality 20, Hendry Ranch Member, Tepee Trail Formation, Natrona County, Wyoming; Climbing Arrow Formation, Shoddy Springs, Jefferson County, Montana.

DESCRIPTION AND DISCUSSION: Four fragments of P_4 have been recovered from Shoddy Springs, and two from locality 20. Two of the former (CM 18843, CM 21271) appear to be fragments of the same blade. The fracture pattern as well as the ridges on both the labial and lingual face of each fragment match extremely well when the two are united along the line of breakage. The anterior profile of this P_4 , although somewhat altered by wear, is lower than that of *Parectypodus*, higher than that of *Mesodma*, but consistent with that of *Ectypodus*, e.g., P_4 of *E. tardus* from Four Mile (McKenna, 1960), or *E. powelli* (Jepsen, 1940). The ratio of the height of the first serration above the anterior enamel base (1.0 mm) to the standard length (3.2 mm) is 0.32, which is very close to that for known species of *Ectypodus* (0.33) and much lower than the 0.50+ value for *Parectypodus* (Sloan, 1966). Similarly, as in *Ectypodus*, the labial height of enamel at the anterior root (2.3 mm) is characteristically less than the standard length of P_4 , whereas in *Parectypodus* it is greater (Sloan, 1966). The characters of P_4 of *Ectypodus* are from R. E. Sloan, completed manuscript on Puercan multituberculates from the San Juan Basin, which is referred to by Sloan, 1966). P_4 of *Ectypodus* sp. bears 10 serrations, as in *E. tardus* and *E. powelli*. P_4 of known species of *Parectypodus* have 12-14 serrations. The remaining fragments of P_4 from Climbing Arrow and locality 20 closely resemble the nearly complete P_4 of *Ectypodus* sp.

→

Figs. 9-14. Stereophotographs of teeth of *Ectypodus* sp. Fig. 9. CM 18843 and 21271, RP_1 , approx. x 5, labial view. Fig. 10. CM 26266, RM_1 , approx. x 10, occlusal view. Fig. 11. CM 18847, LM_1 , approx. x 10, occlusal view. Fig. 12. CM 21274, LM_2 , approx. x 10, occlusal view. Fig. 13. CM 18846, RM^1 , approx. x 10, occlusal view. Fig. 14. CM 26265, LM^2 , approx. x 10, occlusal view.



Of the eight specimens of M_1 referred to *Ectypodus* sp., seven are complete. Six were recovered from Climbing Arrow and two from locality 20. All the isolated teeth have a cusp formula of 7:4 except for CM 26266, the only complete M_1 from locality 20, which has 8 cusps in the external row. Characteristically, the external margin of the crown is convex, with a distinct bulge occurring at the level of the fifth and sixth external cusps. This condition differs from the more nearly straight labial margin of the crown on M_1 of *E. lovei*. M_1 of *Ectypodus* sp. is also longer and wider than that of *E. lovei*, and has one or two more cusps in the external row. The length-to-width ratio of M_1 of *Ectypodus* sp. ranges from 1.6-1.8 and, as such, overlaps that of *E. lovei* (1.66-1.75).

The two M_2 's referred here to *Ectypodus* sp. are from Climbing Arrow. They are longer and have a higher cusp formula (4:2) than M_2 of *E. lovei* (3:2).

Of the five specimens of M^1 , only one, CM 18846, from Climbing Arrow, is complete. The remaining four teeth are posterior fragments from locality 20 that yield little taxonomic information. CM 18846 is longer and has a higher cusp formula (9:9:6) than that of *E. lovei* (7:9-10:5-6). This is consistent with the larger size and higher cusp formula of M_1 and M_2 of *Ectypodus* sp. compared with that of *E. lovei*. As in *E. lovei*, the cusps on CM 18846 and the fragmentary teeth from locality 20 are crescentic, but they are also slightly broader at the base, especially in the medial row. The internal row on CM 18846 originates at the level of the second medial cusp.

The single M^2 of *Ectypodus* sp., from locality 20, shares the same structure and cusp formula (1:3:3) with M^2 of *E. lovei*, but is appreciably longer and wider.

REMARKS AND CONCLUSIONS

The diagnostic criteria of Tertiary ectypodontid taxa given in the literature are almost exclusively concerned with the morphology of the fourth premolars (Sloan, 1966). This is of little value when considering a sample of mostly isolated molars and a few fragments of P4. As such, identification of the late Eocene multituberculates from Wyoming and Montana with any degree of confidence is problematical. The entire sample is very small, and is composed of only isolated teeth, most of which are fragmentary. Remains of each tooth type have not been recovered from each locality. Except for a single M_1 from locality 6, however, the isolated teeth comprising upper and lower $M1$ and $M2$ seem, in each case, to represent two morphological groups. These groups segregate into two sets of localities. All multituberculate teeth from Badwater localities 5, 5A, 6, and Wood seem referable to one species, *Ectypodus lovei*. Those from locality 20 and Shoddy Springs appear to represent a descendent species of *Ectypodus*, with molars of relatively larger size and

higher cusp formula. This is consonant with the growing evidence (Black, 1974) that the mammalian fauna from locality 20 is younger and more advanced than the fauna from localities 5, 5A, 6 and Wood. Larger samples of multituberculate remains from these localities would enhance the record of the range of variation of late Eocene species of *Ectypodus*. The present evidence does not deny the possibility of both species of *Ectypodus* occurring at locality 6, or the presence of a third species of *Ectypodus* at Shoddy Springs.

Before the discovery of their remains in late Eocene deposits, multituberculates were thought to have become extinct in the early Eocene (Jepsen, 1930, 1949). It would be premature and perhaps naive to view this as merely a temporal range extension of the Altheria, and thus to discount the possibility of the existence of a diversity of ectypodontids in western North America during the middle and late Eocene, perhaps surviving into the Oligocene, in ecological situations that have not been extensively sampled in the past (Black, 1967).

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The authors would like to express their gratitude to Dr. R. E. Sloan, Department of Geology, University of Minnesota, for kindly allowing the use of information from a completed manuscript, some of which, by similar permission, has already appeared in print (Krishtalka, 1973). We would also like to thank the following for access to and loan of material in their care: Dr. Mary Dawson, Carnegie Museum of Natural History; Dr. Peter Robinson, University of Colorado Museum; and Dr. Larry Martin, The University of Kansas. Field parties from these three institutions as well as from Texas Tech University were responsible for collecting the material used in this study. This work was supported by the National Science Foundation, Grants GB-7801 and GB-30840X, and by the Graduate School of Texas Tech University.

TABLE 1.
MEASUREMENTS AND CUSP FORMULAE OF UPPER AND LOWER MOLARS OF *Ectypodus lovei*

		Locality	Length	Width	Cusp formula
M ₁	UCM 28359	5A	1.5	0.9	6:4
	CM 16983	5	1.55	0.9	6:4
	CM 16982	5A	—	0.8	—
	CM 15129	5A	1.5	0.9	6:4
	CM 15126	5A	1.5	0.9	6:4
	CM 17513	Wood	1.4	0.8	6:4
	CM 18256	6	1.6	1.0	6:4
	CM 21336	6	1.75	1.0	7:4
M ₂	CM 21335	6	0.8	1.0	3:2
M ¹	UCM 25681	5A	2.2	1.1	7:10:5
	UCM 28360	5A	—	1.2	—
	CM 15085	5A	—	1.0	—
	CM 15084	5	—	1.2	—
	CM 16981	5	—	1.0	—
	CM 21334	6	2.1	1.1	7:9:6
M ²	UCM 25255	5A	0.9	0.9	1:3:3
	UCM 27094	5A	1.0	1.0	1:3:3
	CM 15086	5A	0.9	0.9	1:3:3
	CM 15054	5	0.9	1.0	1:3:3
	CM 21642	6	1.0	1.1	1:3:3

TABLE 2.
MEASUREMENTS AND CUSP FORMULAE OF UPPER AND LOWER MOLARS OF *Ectypodus* sp.

		Locality	Length	Width	Cusp formula
M ₁	CM 21275	Climbing Arrow	—	0.9	—
	CM 18847	Climbing Arrow	1.7	1.0	7:4
	CM 18844	Climbing Arrow	1.85	1.1	7:4
	CM 18841	Climbing Arrow	1.6	1.0	7:4
	CM 18845	Climbing Arrow	1.6	1.0	7:4
	CM 21273	Climbing Arrow	1.7	1.0	7:4
	CM 26266	20	1.95	1.2	8:4
	KU 17131	20	1.8	1.0	7:4
	M ₂	CM 21272	Climbing Arrow	—	1.0
CM 21274		Climbing Arrow	1.1	1.1	4:2
M ¹	KU 17179	20	—	1.1	—
	KU 17132	20	—	1.1	—
	CM 27629	20	—	1.25	—
	CM 18846	Climbing Arrow	2.4	1.1	9:9:6
M ²	CM 26265	20	1.2	1.2	1:3:3

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ARTICLE 16

PALEONTOLOGY OF THE EARLIEST OLIGOCENE DEPOSITS IN JACKSON HOLE, WYOMING

Part 1. Rodents exclusive of the Family Eomyidae

JOHN F. SUTTON AND CRAIG C. BLACK

Section of Vertebrate Fossils

INTRODUCTION

During the summer of 1971, Sutton began field work in Jackson Hole in connection with continuing broad research on faunas of intermontane, potentially high altitude, aspect (Robinson et al., 1968). Attempts were being made to look at all the accessible outcrops of the Miocene Colter Formation. Near the end of the summer, a small outcrop of Oligocene deposits was discovered along Pilgrim Creek in the Teton National Forest, Jackson Co., Wyoming. This outcrop lies between the lower part of the Colter Formation and another outcrop. The latter was thought to be a Miocene intrusive, although recently there have been doubts about its intrusive nature (J. D. Love, personal communication). Pilgrim Creek has cut down through the Miocene contact on the south bank and mudslides have covered the remaining contacts.

The outcrop appears to be composed, at least partially, of landslide deposits, as there are unbedded coarse pebbles, clays, and large quartz grains throughout half of the deposit. The remainder of the outcrop, which is much finer grained, seems to be less disturbed, but no bedding or structure can be seen. Both areas of the outcrop yield the same vertebrate fossils, most of which appear to be Chadronian in age. The assemblage, however, is perhaps slightly different from other Chadronian faunas, like those from Pipestone Springs and McCarty's Mountain in Montana. Some of the species appear to be transitional between late Eocene and early Oligocene forms.

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Very few jaws have been recovered from these deposits. Most of the specimens are isolated teeth. The bone scrap is usually broken into extremely small pieces and is generally angular rather than rounded. Indications are that the bone was broken after deposition.

The locality was revisited briefly during the summers of 1972, 1973, and 1974. In 1971, approximately 200 pounds of matrix were washed and a few teeth recovered from the concentrate. Additional samples were washed in successive visits, so that perhaps 14,000 pounds of matrix have been washed from the site to date. Not all the concentrate from the 1974 season has been processed.

Washing has produced a varied micromammalian assemblage represented almost entirely by isolated teeth. Considering the limited amount of outcrop and its coarse nature, it is extremely doubtful that future work will provide substantially more complete material for any of the species present. During the spring high-water stages of 1974, some 50% of the productive portions of the outcrop was eroded and lost down Pilgrim Creek.

While the small-mammal fauna is rather diverse, this paper deals with rodents exclusive of the family Eomyidae. Other groups will be dealt with in later contributions.

This work was supported by grants GB-7801 and GB-30840X from the National Science Foundation to Black, and in 1973, by a grant to Sutton from the Graduate School of Texas Tech University. All specimens are in the collections of Carnegie Museum of Natural History. The following abbreviations are used throughout: KU, The University of Kansas; CM, Carnegie Museum of Natural History; UCMP, University of California, Berkeley, Museum of Paleontology; USNM, United States National Museum of Natural History; a-p, anteroposterior; tr, transverse. Where two transverse measurements are given, the first is the anterior loph (id) and the second is the posterior loph (id). All measurements are in millimeters, and were taken with a filar micrometer.

Following are the rodents from the Pilgrim Creek fauna discussed in this paper:

Ischyromyidae

Ischyromys cf. *I. veterior*

Cylindrodontidae

Pseudocylindrodon nr. *P. medius*

Cylindrodon cf. *C. fontis*

?Sciuridae

Sciurid indet.

Aplodontidae

Spurimus sp.

Prosciurus vetustus

Prosciurus cf. *P. relictus*

Prosciurus sp.

Heteromyidae

Heliscomys cf. *H. vetus*

?Castoridae

Pipestoneomys cf. *P. bisulcatus*

Family indet.

Griphomys sp.

SYSTEMATIC REVIEW

Family Ischyromyidae Alston, 1876

Genus *Ischyromys* Leidy

Ischyromys cf. *I. veterior*

Figures 1-7, Table 1

MATERIAL: CM 27564, LP₄; 27565, RP₄; 27558, LM^{1 or 2}; 27563, LM^{1 or 2}; 27566, RM^{1 or 2}; 27572, LM^{1 or 2}; 27560, RM₃; 27561, RP₄; 27562, LP₃; 27571, LP₄; 27573, LM_{1 or 2}; 27557, RM_{1 or 2}; 27567, LM_{1 or 2}; 27568, LM_{1 or 2}; 27569, LM_{1 or 2}; 27570, RM_{1 or 2}; 27555, LM₃.

DESCRIPTION: The upper premolars are typical of *I. veterior* in that they have the extended anterior cingulum and distinct lingual notch with subequal protocone and hypocone. The metaloph is flexed anteriorly before it joins the hypocone, as Wood (1937) points out. In contrast to Wood's description, however, there is no excavation or concavity of the paracone on the premolars or any of the molars. The protoconule is distinguishable on the upper teeth, but is less well developed on CM 27564, 27566, and 27572. CM 27566 also has a distinct mesostyle on the buccal margin of the tooth. The M³ is similar to the other molars, but is slightly narrower across the metaloph.

The lower premolars are elongate and narrow anteriorly with a posteriorly closed trigonid. The trigonid is open anteriorly. The remainder of the tooth is well developed, with a strong hypolophid and posterior cingulum that meets the entoconid. The buccal groove is deep and posteriorly directed. The molars are not elongate and are typical of *Ischyromys* as adequately described by Wood (1937) and Howe (1966). There are indications of a spur running from the posterior face of the protoconid into the anterior basin on CM 27567 and CM 27557. This structure is only slightly developed and is difficult to see. On CM 27573, however, the spur is well developed and extends far into the basin where it is met by another very short spur arising on the anterior side of the hypolophid. The M₃ is similar in construction to the anterior molars except for the posterior narrowing of the tooth.

DISCUSSION: The teeth fall within the range for *I. veterior* (Black, 1968) in most cases and appear to be generally a good representation of

that species. Some of the teeth, however, exhibit tendencies that are reminiscent of *I. douglassi* (Black, 1968) from McCarty's Mountain, Montana. Several of the lower molars have the spur on the back of the protoconid, and several have a well developed hypoconulid, characters found in *I. douglassi*. It is possible that we are dealing with a population of *I. veterior*-like rodents that gave rise at a later date to the distinct species *I. veterior* and *I. douglassi*. The Pilgrim Creek *Ischyromys* thus seems to be older than either the Pipestone Springs or McCarty's Mountain, Montana, forms.

TABLE 1. MEASUREMENTS OF *Ischyromys* CF. *I. veterior*

		N	X	O.R.
P ⁴	a-p	2	3.23	3.00-3.47
	tr	2	3.09	2.90-3.28
	tr	2	2.73	2.57-2.90
M ^{1 or 2}	tr	4	3.33	3.08-3.65
	tr	3	2.65	2.55-2.70
	tr	3	2.54	2.30-2.74
M ³	a-p	1	3.20	—
	tr	1	2.71	—
	tr	1	2.10	—
P ₄	a-p	3	3.54	3.33-3.66
	tr	3	2.26	2.11-2.45
	tr	3	2.60	2.47-2.63
M _{1 or 2}	a-p	7	3.15	2.80-3.50
	tr	7	2.62	2.25-2.95
	tr	6	2.81	2.37-3.00
M ₃	a-p	1	2.90	—
	tr	1	2.78	—
	tr	1	2.39	—

Family Cylindrodontidae Miller and Gidley, 1918

Genus *Pseudocylindrodon* Burke*Pseudocylindrodon* nr. *P. medius*

Figures 13-17, Table 2

MATERIAL: CM 27531, LP⁴; 27532, LM^{1 or 2}; 27534, LP₁; 27535, LM_{1 or 2}; 27536, LM_{1 or 2}; 27537, RM_{1 or 2}; 27538, RM_{1 or 2}; 27539, LM₃; 27540, RM₃.

DESCRIPTION: The cheek teeth are in general quite similar to those of *Pseudocylindrodon medius* (Burke, 1938; Black, 1974) although they do exhibit some minor differences.



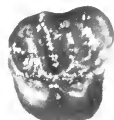
Figs. 1-7. *Ischyromys* cf. *I. veterior*. All x 4. 1. CM 27564, LP⁴. 2. CM 27566, RM^{1 or 2}. 3. CM 27560, RM³. 4. CM 27567, LM_{1 or 2}. 5. CM 27573, LM_{1 or 2}. 6. CM 27568, LM_{1 or 2}. 7. CM 27555, LM₃. Figs. 8-10. *Spirimus* sp. All x 7. 8. CM 27552, RdP⁴. 9. CM 27551, LP⁴. 10. CM 27548, LP₄.



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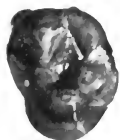
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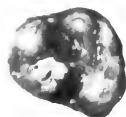
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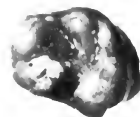
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In the upper fourth premolar there is no indication of a posteriorly divided metaloph spur or much sign of a distinct metaconule. The metaloph is, however, complete. In the one upper molar the mesostyle is large, the metaloph complete, and the metaconule indistinct. There is no posterior spur from the metaloph.

The lower fourth premolar is very close to that of *P. tobeysi* (Black, 1970, fig. 13), but is somewhat larger. The lower first and second molars are closer in size to those of *P. tobeysi* than to those of *P. medius*. Morphologically, the lower molars appear to be closer to those of *P. medius* in the degree of central and posterior valley closure and in the size and direction of the hypoconid, although one tooth, CM 27538, resembles an M_1 of *P. tobeysi* more than it does those of *P. medius*. The sample also appears to be slightly higher crowned than are the molars of *P. tobeysi*. M_3 is also quite similar to M_3 of *P. medius*.

DISCUSSION: Specimens of *Pseudocylindrodon* from Pilgrim Creek are intermediate in size and morphology between specimens referred to *P. near P. tobeysi* (Black, 1974) from Badwater locality 20 dated at 41.2 ± 1.4 m.y. and the sample of *P. medius* from McCarty's Mountain considered to be of earliest Oligocene age. They are more primitive than any of the material referred to *Pseudocylindrodon* from the Vieja Group, Texas (Wood, 1974).

Genus *Cylindrodon* Douglass

Cylindrodon cf. *C. fontis*

Figures 18-20, Table 2

MATERIAL: CM 27545, RP₄; 27541, 27542, 27543, RM^{1 or 2}; 27533, RP₄; 27544, 27546, LM_{1 or 2}.

DESCRIPTION AND DISCUSSION: These teeth are all very similar to those of *Cylindrodon fontis* from McCarty's Mountain, Montana. They may be slightly smaller and lower crowned, but the sample size is much too small to be certain of this.

Family ?Sciuridae Gray, 1821

Sciuridae gen. et sp. indet.

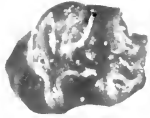
Figure 21

MATERIAL: CM 27584, LP₁. (a-p 1.62, tr 1.39, tr 1.39).

DESCRIPTION: In this lower premolar, the metaconid dominates the trigonid, being about twice the size of the protoconid. The trigonid is



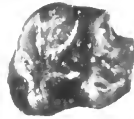
Figs. 11-12. *Spurimus* sp. All x 7. 11. CM 27549, RM_{1 or 2}. 12. CM 27526. LM₃. Figs. 13-17. *Pseudocylindrodon* nr. *P. medius*. All x 7. 13. CM 27531, LP₄. 14. CM 27534, LP₄. 15. CM 27538, RM_{1 or 2}. 16. CM 27539, LM₃. 17. CM 27535, LM_{1 or 2}. Figs. 18-20. *Cylindrodon* cf. *C. fontis*. All x 7. 18. CM 27544, LM_{1 or 2}. 19. CM 27543, RM^{1 or 2}. 20. CM 27533, RP₄.



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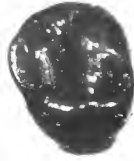
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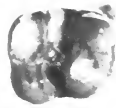
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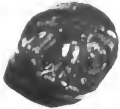
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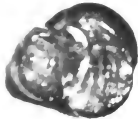
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open both anteriorly and posteriorly, with a low anterolophid extending forward. There is a small mesostylid, and the entoconid, although incorporated into the posteroloph, is still distinguishable. The mesoconid is strong and is located in the middle of the lingually displaced ectolophid. The talonid basin is smooth and deepest lingual to the hypoconid. There is no hypolophid developed, only a slight swelling at the base of the entoconid.

DISCUSSION: The only other Chadronian form to be referred (questionably) to the Sciuridae is *Protosciurus jeffersoni* from Pipestone Springs, Montana (Black, 1965). CM 27584 has no hypolophid, and is 30% smaller than *P. jeffersoni*. The absence of the hypolophid effectively removes CM 27584 from the Prosciurinae, since it is a feature found in virtually all members of the subfamily. In addition, the shape and configuration of the tooth more clearly resembles sciurids than prosciurines.

TABLE 2. MEASUREMENTS OF *Pseudocylindrodon* NR. *P. medius*

CM material	a-p	tr	tr
27531 LP ⁴	2.00	2.00	1.77
27532 LM ¹ or 2	1.73	1.45	1.62
27534 LP ₂	2.38	1.43	1.96
27535 LM ₁ or 2	1.89	1.49	1.90
27536 LM ₁ or 2	1.69	1.48	1.70
27537 RM ₁ or 2	1.68	1.42	1.64
27538 RM ₁ or 2	2.10	1.35	1.60
27539 LM ₃	1.80	1.40	1.63
27540 RM ₃	1.63	1.53	1.28
<i>Cylindrodon</i> cf. <i>C. fontis</i>			
27545 RP ⁴	1.93	1.76	1.43
27541 RM ¹ or 2	1.76	1.77	1.77
27542 RM ¹ or 2	1.68	1.62	1.83
27543 RM ¹ or 2	2.00	1.83	1.62
27533 RP ₂	1.79	1.13	1.92
27544 LM ₁ or 2	1.89	1.70	1.71
27546 LM ₁ or 2	2.32	—	—

Family Aplodontidae Trouessart, 1897
Subfamily Prosciurinae (Wilson, 1949)

We here follow Rensberger (1975:11) in considering the Prosciurinae to be a subfamily of the Aplodontidae rather than a distinct family (Wahlert, 1974) or a subfamily of the Ischyromyidae (Black, 1968).

Genus *Spurimus* Black*Spurimus* sp.

Figures 8-12, Table 3

MATERIAL: CM 27552, RdP⁴; 27551, LP⁴; 27548, LP₃; 27549, RM_{1 or 2}; 27550, LM_{1 or 2}; 27526, LM₃.

DESCRIPTION: The upper dentition is represented by a deciduous fourth premolar and a permanent premolar. The deciduous tooth is broadly triangular with a wide anterior cingulum. The protoloph is complete and the metaloph is incomplete with a distinct metaconule. A small mesostyle is present. There is no hypocone, but rather a wide sweeping posteroloph ending at the posterolingual base of the metacone. There are no other deciduous premolars known for *Spurimus*.

The permanent P⁴ is molariform, but has no hypocone. The protoloph and metaloph are complete. The protoconule, however, is not discernible, and the metaconule is joined to the protocone and metacone by thin crests, as in *S. scottii* (Black, 1974). The anterior cingulum is smaller than in either of the described species of *Spurimus*.

P₄ is elongate and narrow anteriorly, with the protoconid and metaconid distinct and separated by a notch, as in *S. selbyi*. The hypolophid is strong, and there is a swelling in the posterolophid that represents the hypoconulid. The lower molars are similar to the premolar except that they are slightly larger and the trigonid basin is closed anteriorly and posteriorly, forming a pit between the protoconid and metaconid, which are more widely separated than in the premolar. M₃ narrows posteriorly and there is no evidence of a hypoconulid.

DISCUSSION: Many of the characters agree with *Spurimus scottii*, such as the structure of the metaloph, nature of the trigonid, and the large, shallow, buccal groove on the lower molar. The structure of the P₃ trigonid, however, is more representative of *S. selbyi* (Black, 1971). With the small sample recovered here it is best that no specific assignment of these specimens be made. A larger sample would reflect the variability present in the population and allow for better comparison with known material from the Badwater, Wyoming, localities.

TABLE 3. MEASUREMENTS OF *Spurimus*

CM material	a-p	tr	tr
27552 RdP ⁴	2.00	1.68	1.54
27551 LP ⁴	1.97	2.30	2.23
27548 LP ₃	2.22	1.34	1.85
27549 RM _{1 or 2}	2.35	1.95	2.20
27550 LM _{1 or 2}	2.30	1.64	1.97
27526 LM ₃	2.20	1.72	1.60

Genus *Prosciurus* Matthew*Prosciurus vetustus*

Figures 22-23, Table 4

MATERIAL: CM 27579, RM^{1 or 2}; 27577, RM³; 27578, LM³; 27583, LM³.

DESCRIPTION AND DISCUSSION: The upper molar teeth have high, relatively free protocones, and hypocones are very small. Mesostyles are present and well developed on all the teeth. The characteristic double metaconules are also present on these teeth. The lower molar is broken, but compares favorably with Black's (1965) description in that it is wide anteriorly, has a well-developed hypolophid and a small mesostylid, and the metaconid is continuous anteriorly with the anterior cingulum.

These four teeth agree with Black's (1965) and Wood's (1937) description of *P. vetustus*. The presence of the double metaconules and the appropriate size leave little doubt that this assignment is correct.

Prosciurus cf. *P. relictus*

Figure 24

MATERIAL: CM 27576, RM^{1 or 2} (a-p 1.92, tr 1.31, tr 1.31).

DESCRIPTION: This single specimen differs, by the presence of a lingual cingulum and the absence of a mesostyle, from other prosciurines recovered. Wood (1937) discusses a similar form from Pass Creek, Montana, of about the same size, that has a lingual cingulum, but also a small mesostyle. The absence of the mesostyle is a character found in *P. saskatchewaensis* (Wood, 1937). *P. saskatchewaensis*, however, is somewhat larger and does not possess the lingual cingulum.

DISCUSSION: The presence of this form in these earliest Oligocene sediments further complicates the prosciurine picture. It is the right size and has the same lingual cingulum as *P. cf. P. relictus* (Wood, 1937), but it lacks the mesostyle. Presence or absence of a mesostyle is known to be a variable character in some groups of rodents and we have therefore assigned this tooth to Wood's *P. cf. P. relictus*, based on the development of the lingual cingulum and the size.

Prosciurus sp.

Figures 25-27, Table 3

MATERIAL: CM 27580, LM^{1 or 2}; 27585, RM^{1 or 2}; 27581, LP₄.

DESCRIPTION: The upper molars are slightly anteroposteriorly compressed, with well developed protocones, protoconules, and single metaconules. Comparisons with *P. relictus* (KU 545, P⁴ - M¹ from the Brulé of Nebraska) indicate that CM 27580 is more transverse, and that the lingual margin of the anterior cingulum is not as well developed.

CM 27585 is slightly larger than *P. relictus* and has a better development of the hypocone and a more prominent mesostyle.

The lower premolar is quite distinctive, with a high open trigonid, exceptionally well-developed metastylid and metaconid, short slit-like talonid, and a short hypolophid appressed to the posterolophid. The protoconid and metaconid are well developed and set much more widely than in *P. relictus*, resulting in a nearly square occlusal outline of the tooth.

DISCUSSION: These teeth, while probably not representing the same species, show peculiarities that do not allow their ascription to any form thus far reported: (1) The upper molars, while agreeing most closely with *P. relictus*, are more transverse, and differ in construction of the anterior cingulum; (2) the metastylid, trigonid, and talonid basin of the lower premolar are distinctly different from those in any described form.

TABLE 4. MEASUREMENTS OF *Prosciurus*
Prosciurus vetustus

CM material	a-p	tr	tr
27579 M ¹ or 2	2.0*	2.32*	2.32
27577 RM ³	1.80	2.10	1.80
27578 LM ³	2.05	2.15	2.15
27583 LM ₃	2.00	1.62*	—
<i>Prosciurus</i> sp.			
27580 LM ¹ or 2	1.37*	—	1.90
27585 RM ¹ or 2	1.78*	2.50	2.33
27581 LP ₄	1.95	1.47	1.71*

*Specimens damaged.

Family Heteromyidae Allen and Chapman, 1893

Genus *Heliscomys* Cope

Heliscomys cf. *H. vetus*

Figure 28, Table 5

MATERIAL: CM 27547, LP⁴ - M¹.

DESCRIPTION: This single maxillary fragment was the only *Heliscomys* material recovered from the Pilgrim Creek deposits. The upper premolar is typical of *Heliscomys*, being triangular in occlusal outline. There is a short posterior cingulum connecting the base of the hypocone and metacone, and there is a small accessory cuspule developed anteroexternal to the protocone. The cuspule is similar to that described by Wood (1935) for *H. gregoryi*.

The molar is wider than long, with a well-developed anterior cingulum passing lingually, ending in a weakly defined protostyle. A short posterior cingulum is also present. The transverse valley is deeper than the antero-posterior valleys, and is not blocked lingually. The paracone and metacone are set anteriorly respective to their lateral counterparts. All the cusps are distinct and free for most of their height.

DISCUSSION: CM 27547 is a good match for the specimens described by Black (1965) from Pipestone Springs, Montana, but is more transverse. USNM 181413, not seen by Black, is similar to other Pipestone specimens, but the central valley is blocked lingually. The presence of the accessory cuspule and the blocking of the central valley are characters that occur randomly in populations of *Heliscomys*. Galbreath (1953) indicated that his sample of *H. vetus* from NE Colorado contained specimens with these characteristics. After looking at a large sample of *Heliscomys* collected by Galbreath since 1953 we find that these characters do occur in various states of development throughout the population. With this in mind it may be worthwhile to re-examine other species of *Heliscomys*, such as *H. gregoryi*, where these characters are considered to be diagnostic.

TABLE 5. MEASUREMENTS OF *Heliscomys* cf. *H. vetus*

	CM 27547	M ¹
	P ⁴	
a-p	0.85	p.88
tr	0.60	1.07
tr	1.07	1.07

Family indet.

Genus *Griphomys* Wilson, 1940

Griphomys sp.

Figure 29

MATERIAL: CM 27527, RM₃ (a-p 1.27, tr 1.15, tr 1.05).

DESCRIPTION: The lower molar is rectangular with a metalophid and hypolophid formed by anteroposterior compression of the primary cusps. The anterior cingulum is complete, there is no metaconid, and the ectolophid is incomplete. The tooth is essentially bilophate in structure.

DISCUSSION: *Griphomys* has been reported in the literature only from the Sespe Formation in California (Wilson, 1940; Lindsay, 1968). Wilson had no third molars in his sample, but Lindsay's specimen (UCMP 79479) shows a better development of the anterior cingulum than our CM 27527. UCMP 79479 also has a short lophid running anteriorly from the midline of the metalophid. CM 27527 has a lophid extending from the hypoconid into the central basin. The Pilgrim Creek

specimen is slightly larger (0.10 mm) in all dimensions than the California material. This occurrence provides little to help explain the problematical nature of *Griphomys* but does indicate that it was more widespread than originally thought. It has also been tentatively noted to occur in the late Eocene Badwater faunas (M.R. Dawson, personal communication). If this record proves to be *Griphomys*, its history becomes more complicated, existing in the late Eocene of California and Wyoming and surviving into the early Oligocene, at least in Wyoming.

Wood (1974:79-90) has suggested that *Griphomys* and *Meliakrouniomys* are related, and that both are members of the family Eomyidae. Emry (1972) placed *Meliakrouniomys* in the Heteromyidae. One new tooth of *Griphomys* from Pilgrim Creek, Wyoming, has no bearing on the familial position of the genus. We have therefore left *Griphomys* without familial assignment.

Family ?Castoridae Gray, 1821
Genus *Pipestoneomys* Donohoe
Pipestoneomys cf. *bisulcatus*
Figure 30

MATERIAL: CM 27575, RM² (a-p 1.70, tr 1.23, tr 0.88).

DESCRIPTION: The paracone is the highest of the primary cusps, and the metacone is smaller and more lingually displaced. Both the protocone and hypocone are low and lophlike and are continuous with the anteroloph and posteroloph, respectively. A deep lingual groove is continuous, with an anterior lake system that opens labially between the paracone and anteroloph. There are two lakes in this system, one labial and one lingual, forming an hourglass shape between the paracone and protocone. The mesoloph extends from the anterior arm of the hypocone to the posterior margin of the paracone. The metaloph is complete and extends from the hypocone to the base of the metacone and the posteroloph, isolating two posterior lakes.

DISCUSSION: *Pipestoneomys* is known from two other localities in North America: Pipestone Springs, Montana (Donohoe, 1956; Black, 1965), and Crawford, Nebraska (Alf, 1962). This single occurrence of *Pipestoneomys* adds little to the understanding of the genus, but does compare favorably with Donohoe's (1956) description of *P. bisulcatus* except for crown proportions. CM 27575 is much less transverse, especially across the metaloph, where it tapers to meet what must be a small M³.

AGE OF THE PILGRIM CREEK FAUNA

The faunal evidence seems to indicate that the Pilgrim Creek locality is of earliest Oligocene age. The majority of forms discussed here agree reasonably well with those found in either the Pipestone Springs local



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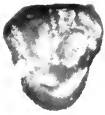
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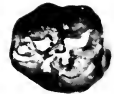
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fauna or the McCarty's Mountain fauna, both of Chadronian age in Montana. None of the Kishenehn, La Point, or Cypress Hills faunas have comparable rodent assemblages, so comparisons are difficult. Once the Bates Hole rodents are described, more accurate age assignments for other early Oligocene assemblages will be possible, as the Bates Hole sequence provides a number of K-Ar dates through the White River Formation (Emry, 1973). The ischyromyid material would indicate an age slightly older than either of these localities since there seems to be a "mix" of characters of *I. douglassi* and *I. veterior* in the same population, allowing for speculation concerning the ancestral nature of the Pilgrim Creek specimens. The prosciurines do not present a clear picture of the age of this fauna, since there are representatives that compare closely to the Orellan *P. relictus*.

Griphomys, while represented by only one tooth, is known only from the Eocene of California and tentatively from Locality 20 at Badwater, Wyoming (41.2 m.y.). The cylindrodonts, especially *Pseudocylindrodont*, are intermediate in size and morphology between those from Badwater, *P.* near *P. tobeysi*, and *P. medius* of McCarty's Mountain. They are more primitive than the *Pseudocylindrodont* material from the Vieja Group (Wood, 1974, 33-46). They suggest an age slightly older than McCarty's Mountain for this fauna. Therefore, it seems probable that this fauna is older than McCarty's Mountain, considered to be of earliest Oligocene age, yet younger than the Badwater Locality 20 fauna of latest Eocene age. The faunal elements not discussed in this contribution, as well as those covered here seem to indicate a very early Oligocene age for this fauna, perhaps earlier than for any fauna yet reported for the Oligocene.

ACKNOWLEDGEMENTS

The authors thank the Jackson Hole Biological Research Station (University of Wyoming and New York Zoological Society), under the direction of Dr. L. Floyd Clarke (1971-72) and Dr. Oscar Paris (1973-74), for providing research space and living accommodations during the course of this study. We also wish to thank Jere Sutton and Kris Krisktalka for invaluable field service in collecting and transporting the

←
 Fig. 21. ?Sciuridae, CM 27584, LP₁, x 7. Figs. 22-23. *Prosciurus vetustus*. All x 7. 22. CM 27579, RM^{1 or 2}. 23. CM 27578, LM³. Fig. 24. *Prosciurus* cf. *P. relictus*, CM 27576, RM^{1 or 2}, x 7. Figs. 25-27. *Prosciurus* sp. All x 7. 25. CM 27585, RM^{1 or 2}. 26. CM 27581, LP₁. 27. CM 27580, LM^{1 or 2}. Fig. 28. *Heliscomys* cf. *H. vetus*, CM 27547, LP⁴ - M¹, x 10. Fig. 29. *Griphomys* sp. CM 27527, RM₃, x 15. Fig. 30. *Pipestoneomys* cf. *P. bisulcatus*, CM 27575, RM², x 7.

matrix. In addition, we express our appreciation to the National Forest Service for permission to carry out this work in the Teton Wilderness Area. The authors have both benefitted greatly from discussions and field excursions with Dr. J. D. Love of the U. S. Geological Survey. Specimens were loaned by Dr. Larry D. Martin, University of Kansas; Dr. Robert Emry, National Museum of Natural History; and Dr. E. C. Galbreath, Southern Illinois University.

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