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CAPTORHINID REPTILES FROM THE EARLY PERMIAN OF NEW MEXICO, WITH DESCRIPTION OF A NEW GENUS AND SPECIES

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Abstract

A new genus and species of single-tooth-rowed captorhinid, *Rhiodenticulatus heatoni,* is based on two skulls and partial postcranial skeletons collected from the Lower Permian Cutler Formation near Arroyo de Agua, north-central New Mexico. A cladistic analysis of its relationships to other single-tooth-rowed captorhinids suggests that it is a primitive sister taxon to *Labidosaurus* and *Eocaptorhinus.* The dentition of *R. heatoni,* however, exhibits several unique derived features which are interpreted as representing an adaptation to a specialized diet.

Puercosaurus obtusidens Williston, 1916, the only previously described captorhinid from New Mexico, is declared a *nomen dubium* because the holotypic left dentary is indeterminate, and there is no basis for accepting that it and the two poorly preserved captorhinid skulls found at a different locality and referred to the species by Williston (1916) are conspecific. Additional captorhinid remains have been collected recently from the Lower Permian Cutler, Abo, and Sangre de Cristo formations at widely scattered localities in central and northern New Mexico. Though these specimens, as well as the skulls referred to "*Puercosaurus obtusidens,*" are too poorly preserved to be assigned to existing or new taxa, they do indicate that the Captorhinidae was diverse and widely distributed in the Lower Permian of New Mexico.

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INTRODUCTION

Published accounts of captorhinid reptiles from the late Paleozoic of New Mexico have been limited to two reports (Williston, 1916; Langston, 1953). Williston (1916) described a small captorhinid, *Puercosaurus obtusidens,* on the basis of three poorly preserved and incomplete specimens, a left dentary and two skulls, collected from the Cutler Formation in the Rio Puerco drainage in the north-central part of the state. Further discoveries of captorhinids were not made until 1934–1935, when collecting was resumed by field parties from the University of California, Berkeley. While conducting extensive field work in the Lower Permian Cutler Formation of the same area, three moderately well preserved specimens, including two skulls with jaws and articulated postcranial materials were found at the well known Camp quarry near the small village of Arroyo de Agua (see Langston, 1953, for histories and vertebrate assemblages of well known localities of the area). The only published report of these specimens was a brief reference to them by Langston (1953) in a discussion of the age of the late Paleozoic vertebrate-bearing strata of New Mexico. Here he notes (1953: 410) "a small romeriid cotylosaur possibly referable to *Puercosaurus obtusidens* is more primitive than *Romeria texana* of the middle Wichita (Putnam)" of the Lower Permian of Texas. Extensive collecting by the authors during the past several years in the Lower Permian deposits throughout New Mexico has resulted in the discovery of additional captorhinid remains from the Cutler, Abo, and Sangre de Cristo formations.

Taxonomic evaluation of the undescribed captorhinid materials of New Mexico has necessitated a reexamination of the type specimens of *Puercosaurus obtusidens* Williston (1916). The partial left dentary, designated by Williston as the holotype, is not only indeterminate, but also provides no basis for considering it conspecific with the two partial, crushed skulls referred by him to the species. Even though the two referred skulls are undoubtedly captorhinids, they are too poorly preserved to be assigned to an established or new taxon. Under these circumstances *P. obtusidens* is judged a *nomen dubium.* On the other hand, the specimens collected by the University of California, Berkeley, are sufficiently well preserved and unique to be referred to a new genus and species, *Rhiodenticulatus heatoni.* With the exception of the types of this species, all other Lower Permian captorhinid specimens from New Mexico are too incomplete to recommend assignment to existing or new taxa. Yet, they exhibit sufficient variation to indicate that the group was probably quite diverse and widely distributed in New Mexico during the Early Permian.

Throughout the text the abbreviations CM, FMNH, and UCMP are used to refer to collections of the Carnegie Museum of Natural History, Field Museum, Chicago, and the Museum of Paleontology, University of California, Berkeley, respectively.

SYSTEMATIC PALEONTOLOGY

Class Reptilia
Order Cotylosauria
Suborder Captorhinomorpha
Family Captorhinidae
Genus ***Puercosaurus*** Williston, 1916
Puercosaurus obtusidens Williston, 1916, *nomen dubium*

Puercosaurus obtusidens Williston, 1916:189–192, fig. 37A–D.

Remarks.—The original description of *Puercosaurus obtusidens* Williston (1916) was based on poorly preserved and incomplete specimens—an incomplete dentigerous left dentary, FMNH 743, designated as the holotype and two severely crushed skulls, FMNH 745, referred to the species (Fig. 6; only one of the skulls is figured). Williston (1916) illustrated the mandible and one of the two skulls, but a partial reconstruction of the skull was based on both skulls. Although the specimens were collected from the Lower Permian Cutler Formation near Arroyo de Agua in the Rio Puerco drainage area, north-central New Mexico, the holotypic dentary is from the well known Miller bonebed (see Langston, 1953, for description of locality), whereas the referred skulls were apparently found at least several kilometers away along the Rio Puerco (Williston, 1916). The holotypic dentary is too poorly preserved and incomplete to be reasonably certain that it belongs to that family. Further, the holotypic dentary and referred skulls do not exhibit any unique features in common which would demonstrate that they are conspecific. In view of these circumstances *P. obtusidens* is declared here a *nomen dubium.* Though the skulls FMNH 745 are sufficiently complete to recognize their captorhinid affinities, assignment to either a known or new species is not possible.

Genus ***Rhiodenticulatus,*** new genus

Type species.—*Rhiodenticulatus heatoni,* new species.

Etymology.—From the Greek *rhio,* nose, and *denticulatus,* with small teeth, referring to the relatively small teeth of the premaxilla.

Diagnosis.—Small captorhinid that differs from all other single-tooth-rowed captorhinids in the following features: 1) premaxillary dentition reduced to three teeth which are subequal in size and equal to or smaller than precanine maxillary teeth; 2) reduction of maxillary dentition to 11 teeth; 3) number of precanines reduced to two; 4) extremely large

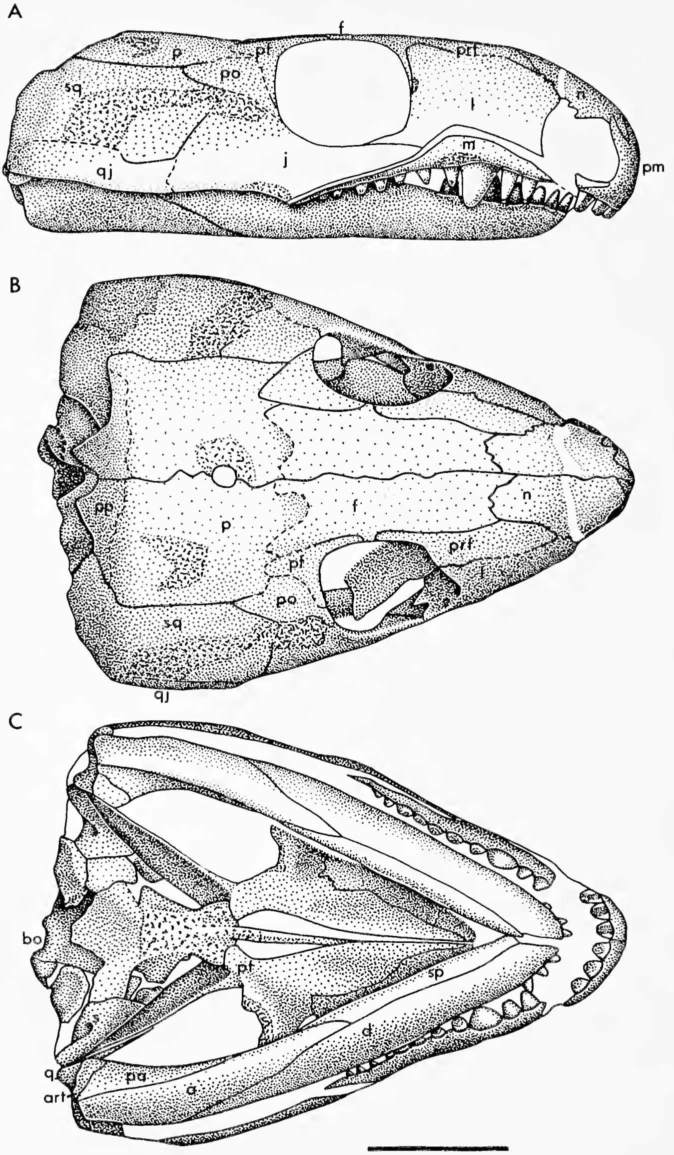


Fig. 1.—*Rhiodenticulatus heatoni,* holotype, UCMP 35757. Skull in A, lateral, B, dorsal, and C, ventral views. Abbreviations: a, angular; art, articular; bo, basioccipital; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pa, prearticular; pf, postfrontal; po, postorbital; pp, postparietal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; sp, splenial; sq, squamosal. Scale = 1 cm.

single canine with basal diameter as much as twice that of any postcanine; 5) very broad lacrimal with a height (measured at the highest level of the dorsal expansion of the maxilla) to length (shortest distance between orbit and naris) ratio of .65 to .73; and 6) prefrontal extends far anteriorly to a level about 84 to 90% of the distance from the orbit to the naris. Distinguished from *Labidosaurus* and *Eocaptorhinus* by its proportionately narrower skull postorbitally. Straight occipital margin of skull table separates it from *Romeria* which has a bilateral parietal embayment and from *Labidosaurus* and *Eocaptorhinus* which have a median embayment. Differs from *Romeria* and *Protocaptorhinus* in having a long, low rectangular quadratojugal with a longitudinal length that is approximately four times the height. Pointed postcanine teeth of *Rhiodenticulatus heatoni* are distinguishable from the blunt teeth of *Labidosaurus* and *Eocaptorhinus*.

Rhiodenticulatus heatoni, new species

Etymology.—Named in honor of the late Malcolm J. Heaton in recognition of his significant contributions to our understanding of the morphology and phylogenetics of the Captorhinidae.

Holotype.—UCMP 35757: partial, articulated skeleton that includes skull with closely joined lower jaw, vertebral series with ribs from the axis to the seventh caudal, pectoral and pelvic girdles, right humerus and proximal ends of ulna and radius, femora, left tibia, fibulae, and tarsi; skull not attached to postcranial skeleton.

Paratypes.—UCMP 40209: skull with closely joined lower jaw, missing left postorbital cheek region and posterior half of left mandible.

UCMP 40210: partial, articulated postcranial skeleton preserved in three small segments: 1) a series of seven postaxial cervical and dorsal vertebrae with ribs, essentially complete pectoral girdle, and proximal ends of humeri; 2) series of six vertebrae that includes the last two presacrals, two sacrals with ribs, and the first two caudals, and pelvis; and 3) portion of the left hindlimb, including proximal two thirds of femur and nearly complete tibia. It is quite likely that UCMP 40209 and UCMP 40210 belong to the same individual.

Horizon and locality.—All specimens are from the Cutler Formation exposures of the Rio Puerco drainage, Rio Arriba County, north-central New Mexico. An Early Permian Wolfcampian age is generally accepted for these exposures. Although the holotype and paratypes are listed as coming from UCMP Camp quarry locality V-2814, Langston (1952: 98) notes that they were probably not found in the main bone level of the quarry, but rather as float on the slope of Loma Salazar a few feet away and presumably at or just above the quarry bone level. The Camp quarry is located in SW1/4NE1/4NE1/4 sec. 8, T. 22 N., R. 3 E., about

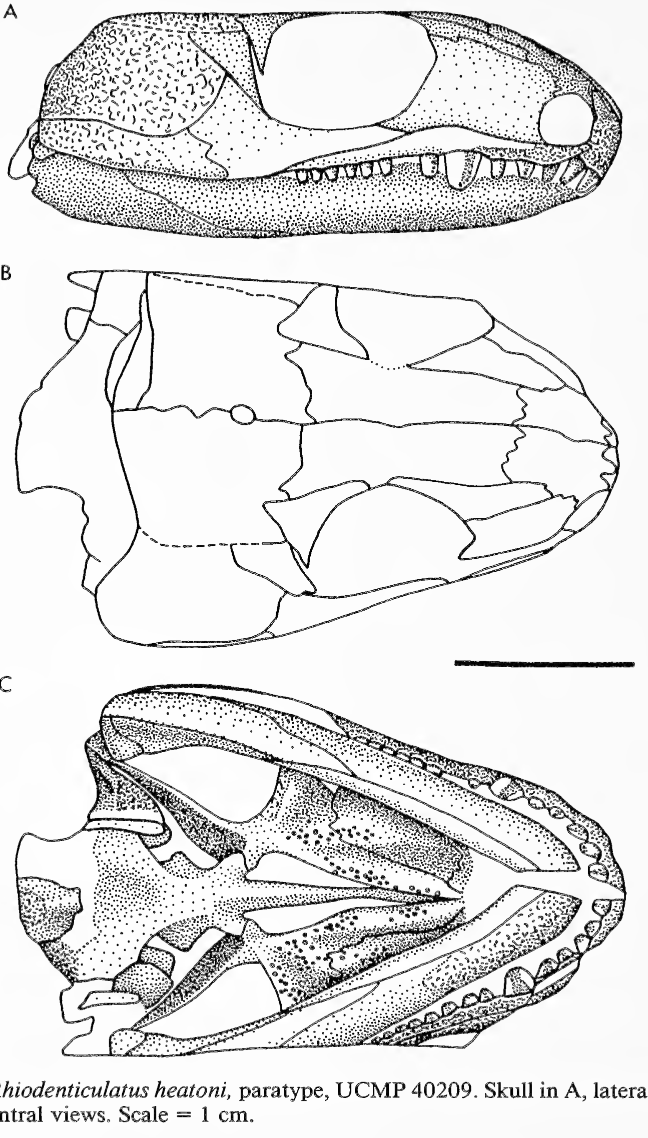


Fig. 2.—*Rhiodenticulatus heatoni,* paratype, UCMP 40209. Skull in A, lateral, B, dorsal, and C, ventral views. Scale = 1 cm.

1.1 km southeast of Arroyo de Agua. All three specimens are preserved in red, indurated concretionary nodules.

Description

Skull.—Specimens of *Rhiodenticulatus heatoni* exhibit the general structural pattern seen in all captorhinids and, therefore, aside from a few structures, Figs. 1, 2 eliminate the need for a detailed description of its anatomy. The skulls of the holotype UCMP 35757 and paratype UCMP 40209 have suffered little distortion, but most of the superficial features of the skulls, such as sculpturing, have been lost due to weathering and excessive preparation performed prior to this study. In UCMP 40209 the left postorbital region was removed in the late 1930s in an attempt to study the braincase in thin section. The extent of ossification of the appendicular and axial portions of the holotypic skeleton suggests that it is a mature individual. The skulls are triangular, with the postorbital width being only about 80 to 82% of the midline length. The occipital margin of the skull stable is straight.

The downturned premaxilla possesses three teeth. In the paratype UCMP 40209 (Fig. 2A) the anterior end of the right maxilla greatly overlaps the lateral surface of the maxillary process of the premaxilla, making it appear as though the third premaxillary tooth originates from the anterior end of the maxilla. Although imperfectly preserved, the premaxillary teeth obviously had the shape of sharply pointed pegs, were subequal in size, and were approximately the same size as, or even possibly slightly smaller than, the precanine maxillary teeth. Anteriorly the maxilla forms the ventral rim of the naris, gradually expands to a moderate midlength dorsal swelling, and then tapers to a posterior terminus at, or just short of, the level of the posterior margin of the orbit. The right and left maxillae of the holotype possess 10 and 11 teeth, respectively, whereas both maxillae of UCMP 40209 possess 11. In both skulls the third tooth forms an extremely large canine relative to any of the other marginal teeth, with a basal diameter equal to, or greater than, twice that of any of the postcanines. In the holotype the precanines are slightly larger than the largest postcanines. The postcanines exhibit a steady decrease in size posteriorly. As in the premaxilla, the maxillary teeth have the form of sharply pointed pegs. In neither skull is it possible to observe directly that only a single row of marginal maxillary teeth is present. Indirect evidence for a single row is present, however, in that the teeth form a straight row along the outermost margin of the jaw, the postcanines exhibit a steady decrease in size, and there does not appear to be sufficient space for an additional tooth row on the alveolar shelf of the maxilla.

The lacrimal is unusual in being very broad. The ratio of its height (measured at the level of the dorsalmost expansion of the maxilla) to length (measured as the shortest distance between the orbit and naris) is about .65 in the holotype and about .73 in UCMP 40209. There is a correspondingly narrower lateral exposure of the prefrontal as a result of the expanded height of the lacrimal. The prefrontal is also very long and extends anteriorly along the dorsal margin of the lacrimal to a level that is about 90 and 84% of the distance between the orbit and the naris in the holotype and UCMP 40209, respectively. A long ventral process of the prefrontal can be seen in the holotype extending along the medial margin of the lacrimal on the anterior orbital rim. The prefrontal and postfrontal are separated by only a small lateral process of the frontal on the dorsal rim of the orbit. The frontals have a long, narrow rectangular outline. Measured from the level of their orbital contribution, the length of the anterior portion of the frontal is almost one and one half times that of the posterior portion. The pineal opening in both skulls is large and positioned anterior of the midlength of the union of the parietals. The supratemporals are not preserved in either skull. The presence of the postparietal is indicated only in the holotype and then only as an impression of its ventral surface; its suture with the parietal is therefore uncertain. The anterior ends of the right jugals of both skulls appear to wedge between the lacrimal and maxilla, rather than forming the step-like sutural encroachment onto the lateral surface of the dorsal margin of the maxilla seen in other captorhinids (Heaton, 1979). This is undoubtedly due to imperfect preservation, however, inasmuch as the standard condition is present on the nonfigured left side of the holotypic skull. The quadratojugal has the outline of a long, low rectangle, with the length exceeding the height by about four times.

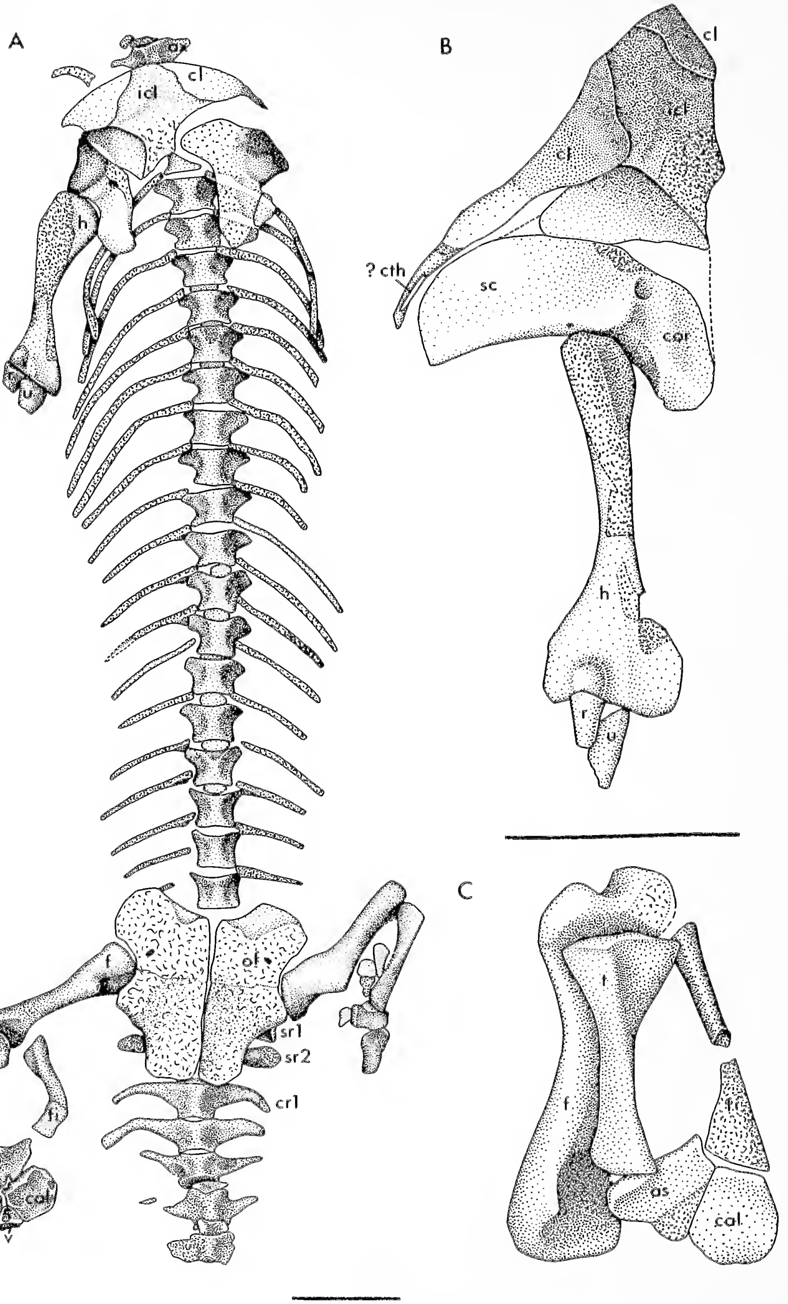
Description of the palate is limited by the attached jaws. As in all captorhinids there is no ectopterygoid, and the rectangular palatine probably extends posteriorly to the subtemporal fossa. The presence of a medial jugal process cannot be determined. The denticle fields of the palate are preserved only in the paratype UCMP 40209. There is a scattering of denticles along the posterior border of the transverse flange of the pterygoid. There are also two faint, denticle bearing ridges; one extends along the medial border of the palatal ramus of the pterygoid, and a second extends obliquely anterolaterally across the palatal ramus of the pterygoid and onto the palatine. The three columns of irregularly arranged denticles converge toward the basicranial articulation. Denticles also appear to be present on the parasphenoid.

The braincases of the holotype and UCMP 40209 are exposed in ventral and occipital views and, though poorly preserved for the most part, do not appear to exhibit any noteworthy differences from the standard captorhinid construction. Both stapes of the holotype and the right of UCMP 40209 are exposed in ventral view and are well enough preserved to deserve comment. Though the footplates are not fully exposed, they appear to conform closely to those of *Ecocaptorhinus* (Heaton, 1979) and *Captorhinus* (Fox and Bowman, 1966). It has the form of a broadly oval disk that thins toward its periphery. The disk is drawn out posterolaterally into a cone-like structure, with the apex being smoothly continuous with the columella. The cross-sectional shape of columella, which remains unchanged throughout its short length, is that of a mediolaterally flattened blade having a vertical height about three times its horizontal width. A large stapedial foramen pierces the proximal end of the columella at a slightly anteromedial angle from the vertical. Occipital view of the holotypic skull (not drawn) clearly reveals the dorsal process of the left stapes just distal to the stapedial foramen. It is very narrow, tapers to a point distally, and curves slightly medially.

The mandibles of both skulls are visible in partial lateral view and in ventral view; their sutural pattern and shape show no deviation from those of other captorhinids. The posterior ends of the mandibles are too damaged to determine whether or not a retroarticular process was present. Dentary teeth are visible only in the holotype, but unfortunately only the anterior half of the series is visible, and these are only partially exposed. The first three teeth exhibit a marked increase in size posteriorly, with the third tooth probably being the largest of the entire series. On the basis of basal diameter, the fourth and fifth teeth are slightly smaller than the third, whereas the sixth appears to be equal to the third in size. The seventh and eighth decrease further in size, as undoubtedly does the remaining unexposed portion of the series. It is estimated that the dentary of the holotype held 14 or 15 teeth.

Postcranial skeleton.—Whereas the skull of *Rhiodenticulatus heatoni* exhibits notable differences from those of other captorhinids, the opposite appears to be true of the postcranial skeleton; this is not unexpected inasmuch as this characterizes the history of captorhinids (Heaton and Reisz, 1980).

The holotype appears to possess a complete, articulated vertebral column from the axis to the sixth caudal vertebra (Fig. 3). Unfortunately, the column is exposed only in ventral view, and small segments of the series are hidden by the pectoral and pelvic girdles. Despite this, it can be safely estimated that the entire presacral column consisted of 25 vertebrae. The centra are slightly pinched laterally, and except for what is believed to be the axial centrum the ventral midlines are still broadly rounded in transverse section; the axial centrum has a distinct keel-like ventral midline. The wing-like transverse processes exhibit a gradual reduction in their lateral extent posteriorly in the column. The ventral surface of the processes slope anteroventrally, and the lateral width narrows as the processes extend to the anterior rim of the centrum. Both ends of the centra are slightly beveled to accommodate the intercentra, giving them a slightly keystone appearance in lateral view. The intercentra are variably displaced dorsally into the notochordal canals of the centra, where attempts to fully expose them would result in damage to the centra. As a result, many of the intercentra appear to be absent, whereas those that are partially exposed vary in size and have a lozenge-shaped outline. The first chevron occurs between caudals three and four.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The string of seven postaxial cervical and dorsal vertebrae of UCMP 40210 are exposed in dorsal view only (Fig. 4A) and undoubtedly include postaxial cervicals. Although poorly preserved, the neural arches exhibit the swollen appearance so typical of captorhinids. The neural spines are barely developed and appear as mere nubbins. The zygapophyses are widely spaced from the midline, giving the neural arches the typical lateral expansion of captorhinids. The transverse processes extend laterally beyond the zygapophyses. Only the badly weathered neural arches are exposed in the UCMP 40210 vertebral series which includes the second to last presacral to the second caudal (not figured), and they reveal no important differences from the far anterior presacral of the same specimen.

The ribs of the holotype and paratype UCMP 40210 are moderately well preserved, but the expansion of the heads is rarely visible, and the shafts frequently appear as narrow rods. The heads of the postaxial cervical ribs appear to be holocephalous and articulate in part with the intercentra. The rib shafts of the cervicals of UCMP 40210 are expanded into blade-like structures, whereas the more posterior rib shafts of the holotype are subcircular in cross-section. The ribs of the anterior half of the presacral column are more strongly curved posteroventrally than those of the posterior half. The sacral ribs are straight, thick, and greatly expanded distally. The anterior caudal ribs of the holotype are fused to the centra, curve strongly posteriorly, are thicker than the presacral ribs, and quickly decrease in length more posteriorly in the column.

The greater portions of the pectoral girdles are preserved in both the holotype and paratype UCMP 40210, and together they exhibit most of the important features of this structure (Figs. 3A, B, 4B). The head of the interclavicle is roughly diamond-shaped, and the long, thin stem is nearly complete in UCMP 40210, missing only a small part of the distal end. The ventral plates of the clavicles are not complete, but impressions on the interclavicles indicate that they were broad and met medially; there is also no indication of a prominent, thumb-like posterior process diverging from the main body of the ventral plate as has been described in *Labidosaurus* (Williston, 1917) and *Captorhinus* (Holmes, 1977). The narrow dorsal stem is directed abruptly dorsally

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Fig. 3.—*Rhiodenticulatus heatoni,* holotype, UCMP 35757. A, ventral view of postcranial skeleton, B, right lateral view of shoulder region, and C, lateral view of left hindlimb. Abbreviations: as, astragalus; ax, axis; cal, calcaneum; cl, clavicle; cor, coracoid; cr, caudal rib; cth, cleithrum; f, femur; fi, fibula; h, humerus; icl, interclavicle; lc, lateral centrale; of, obturator foramen; r, radius; sc, scapula; sr, sacral rib; t, tibia; u, ulna; 2, 4, 5, distal tarsals; iii, iv, v, metatarsals. Scales = 1 cm.

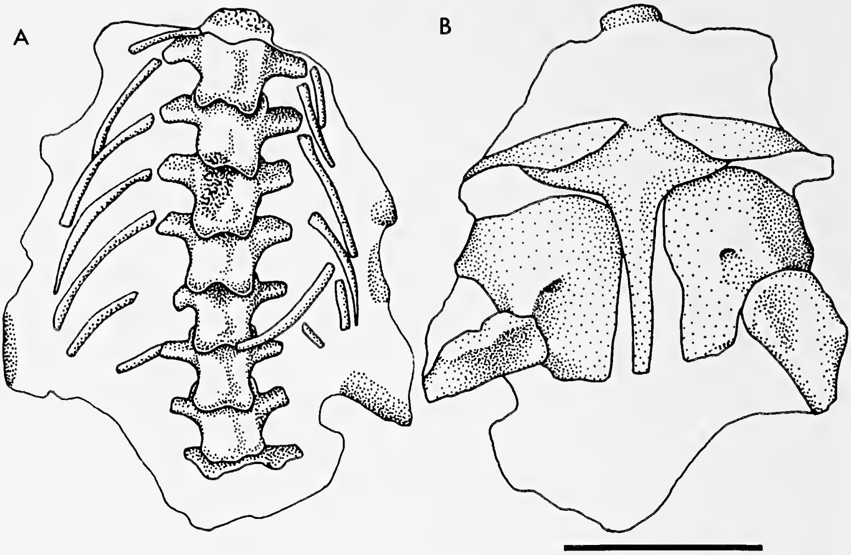

Fig. 4.—*Rhiodenticulatus heatoni,*paratype, UCMP 40210. A, dorsal view of series of seven far anterior presacral vertebrae with ribs, and B, ventral view of pectoral girdle with proximal ends of humeri preserved in a single nodule.

at nearly a right angle to the ventral plate. As in *Captorhinus* (Holmes, 1977), a distinct, posteriorly directed flange-like expansion of the ventral half of the dorsal stem for the clavicular deltoid muscle is clearly seen in the holotype. What may be a portion of the cleithrum is present on the distal end of the dorsal stem of the right clavicle of the holotype. There are no visible sutural divisions of the endochondral portion of the pectoral girdle. The scapular blade curves dorsally rather abruptly from the essentially horizontal coracoid plate. The anterior and posterior margins of the scapular blade are essentially straight and parallel to each other except for the anterodorsal corner being broadly curved. The anterior coracoid portion expands a short distance anteriorly beyond the scapular blade as a smoothly rounded plate. A coracoid foramen located ventromedially to the anterior buttress of the glenoid and a supraglenoid foramen on the posterior margin of the lateral surface of the scapular blade just above the supraglenoid buttress are clearly visible in the holotype and UCMP 40210.

Essentially all that is visible of the pelves of the holotype and UCMP 40210 is the worn ventral surface of the puboischiadic plate (Fig. 3A); the less complete pelvis of UCMP 40210 is not figured. In both specimens osssification along the puboischiadic suture appears to be complete in that there are no open spaces. The sutural division between the pubis and ischium is barely discernable in the holotype. The anterior border of the puboischiadic plate is moderately concave. The ischium is slightly longer and narrower than the pubis. A short distance from the ventral rim of the acetabulum the pubis is perforated by the obturator foramen.

The humerus is best represented in the holotype (Fig. 3A, B). It is poorly preserved, but exhibits the same general configuration as those of *Captorhinus* and *Eocaptorhinus* except that the shaft and distal head have a more slender appearance. Its length, about 1.8 cm, is approximately 90% of that of the femur. All other forelimb elements are either too incomplete to comment on or are absent. The hindlimb and pes are preserved only in the holotype (Fig. 3A, C). The preservation of the femora allows recognition of only some of the major features of this element. Except in being considerably more slender, particularly the shaft, the femur is very similar to that of *Captorhinus.* It is about 2.0 cm long, has a minimum shaft diameter of about 1.3 mm, and a maximum width of the distal head of 4.3 mm. The head appears rather massive, with a well developed intertrochanteric fossa. The popliteal area is a smooth, broadly concave depression. Though the internal trochanter is well developed, there appears to no distinct step or notch between it and the head. The tibiae and fibulae of the holotype are present, but only those of the left limb are well preserved. The tibia and fibula appear to be identical to those of *Captorhinus* except in being noticeably more slender. In typical primitive reptilian fashion the tibia is much shorter, 11.0 mm, than the femur, roughly 55% of its length. The mediolateral width of the massive proximal end is about 45% of the length, whereas anteroposterior width of the distal end is about 36% of the length; the narrowest mediolateral width of the shaft is about 0.8 mm. A deep groove divides the anterior face and articular surface of the expanded proximal end; the groove is bounded medially by a prominent cnemial crest. The lateral margin of the tibia is bowed slightly medially away from the fibula. The left fibula is about 12.3 mm long and the mediolaterally expanded proximal and distal ends are about 2.5 and 3.5 mm wide, respectively; the narrowest mediolateral width of the shaft is about 1.1 mm. The medial margin of the fibula is strongly concave and the lateral margin only very slightly convex, giving it the appearance of being bowed laterally away from the tibia.

The tarsi of the holotype are well ossified. The right, exposed in ventral view (Fig. 3A), is nearly complete, missing only the first distal tarsal, whereas the left is represented only by the dorsally exposed calcaneum and astragulus (Fig. 3C). The tarsal elements conform closely to the pattern seen in *Captorhinus* (Peabody, 1951) except for two apparent deviations; the fourth distal tarsal is relatively smaller and the fifth which is relatively larger than in *Captorhinus.* The typical pattern in primitive reptiles is for the fourth distal to be considerably larger than the other distal tarsals. In *Rhiodenticulatus,* however, the fourth distal is roughly equal in size to the fifth. The extreme proximal ends of the third, fourth, and fifth metatarsals are all that remains of the rest of the right pes.

DISCUSSION

Placement of *Rhiodenticulatus heatoni* within the Captorhinidae of the suborder Captorhinomorpha is unquestionable. It should be made clear, however, that we follow Heaton (1979), Gaffney and McKenna (1979), Reisz (1980), and Heaton and Reisz (in press) in the assignment of genera in the two recognized captorhinomorph families, the Early Pennsylvanian to Early Permian Protorothyrididae (=Romeriidae of many authors) and Early to Late Permian Captorhinidae. The captorhinids are differentiated from the protorothyridids by their low, wide, massive skull, hooked premaxillae, loss of tabulars and ectopterygoids, fully ossified paroccipital processes, stoutly built postcranial skeleton, 25 presacral vertebrae with swollen neural arches and low neural spines, absence of cleithra, thumb-like process on the ventral plate of clavicle, short stoutly built limbs, absence of a supinator process of humerus, and wide manus and pes. Presently, about 14 genera of captorhinids are recognized. Among these, however, only four genera, *Romeria, Protocaptorhinus, Eocaptorhinus,* and *Labidosaurus,* could conceivably be confused with *Rhiodenticulatus,* because they possess single-rowed, marginal dentitions.

Clark and Carroll (1973) and Heaton (1979) presented nearly identical phylogenies in which the series of successively later occurring, single-tooth-rowed captorhinids *Romeria, Protocaptorhinus,* and *Eocaptorhinus* forms a single, continuous, phylogenetic lineage depicting transitional morphological stages that links the protorothyridids with the later occurring, multiple-tooth-rowed *Captorhinus.* Among the captorhinids with multiple-rowed marginal dentitions, *Captorhinus* is the only genus known in great detail and is also generally accepted as the most primitive. *Labidosaurus,* the least understood of the single-tooth-rowed captorhinids, is not included in Heaton's (1979) phylogenetic scheme, but is depicted in Clark and Caroll's (1973) phylogenetic tree as the end member of an offshoot from *Protocaptorhinus.* Gaffney and McKenna (1979:7) criticized the systematic methodology used by Clark and Carroll, and Heaton as being "stratophenetic" (*sensu* Gingerich, 1976) in which "similar morphologies are arranged stratigraphically and connected using usually implicit rather than explicit criteria, to form what are interpreted as ancestor-descendant lineages."

Gaffney and McKenna, without altering the basic phylogenies of Clark and Carroll, and Heaton, reexpressed them in the form of a cladogram and, thus, as a testable hypothesis. Our only serious reservation of their cladogram of the Captorhinidae is the position of *Labidosaurus* as a member of the clade containing *Protocaptorhinus.* As brought out below, *Labidosaurus* shares with *Eocaptorhinus* and *Captorhinus* several derived features of the skull not seen in *Protocaptorhinus.* Further, restudy of *Labidosaurus* is greatly needed before its phylogenetic reltionships can be accurately evaluated. Despite this, the cladogram of Gaffney and McKenna presents a reasonable understanding of the evolutionary relationships of the captorhinids and, along with the detailed morphological studies of the known captorhinomorphs by Carroll and Baird (1972), Clark and Carroll (1973), Heaton (1979), and Olson (1984), provides a basis for assessing the polarity of several character states of *Rhiodenticulatus heatoni.*

The maxillary dentitions of the holotype and paratype UCMP 40209 of *Rhiodenticulatus* are unique among the single-tooth-rowed captorhinids in possessing: 1) a single, extremely large canine whose basal diameter is equal to, or greater than, twice that of any of the postcanines; 2) 11 teeth; and 3) two precanines. It can also be noted that among the protorothyridids only the Pennsylvanian *Cephalerpeton* exhibits a similar specialization toward a greatly reduced number (16) of maxillary teeth that includes a low number (four) of precanines (Reisz and Baird, 1983). Protorothyridids typically possess, as does *Romeria,* a pair of prominent, subequal canines, yet their basal diameters are far less than twice that of the largest postcanines. Although a single tooth may be designated as a canine in *Protocaptorhinus* and *Labidosaurus,* it is not as prominent as either of the paired canines of *Romeria. Eocaptorhinus* also exhibits a single, prominent canine, and although the first through third postcanines may be noticeably shorter, their basal diameters are only slightly smaller than that of the canine. In the holotypic skull of *Rhiodenticulatus,* having a midline length of about 38 mm, the basal diameter of the canine is about 2.2 mm. This is larger in both absolute and relative measurements than the canines of *Romeria* and *Protocaptorhinus,* in which the basal diameters range from roughly 1.2 to 1.7 mm for skulls 50 to 53 mm in midline length. On the other hand, though the maximum basal diameter of the canines in *Eocaptorhinus* and *Labidosaurus* may be as much as 2.6 and 3.0 mm, respectively, their midline skull lengths are as much as two and four times greater than that of *Rhiodenticulatus.*

Previous authors (Clark and Carroll, 1973; Heaton, 1979) have noted that there is a general reduction in the number of maxillary teeth in successively later occurring, single-tooth-rowed captorhinids. Approximate maxillary tooth counts for *Protorothyris, Romeria, Protocaptorhinus, Labidosaurus,* and *Eocaptorhinus* are 24–30, 22–23, 18–22, 14–18, and 17–22, respectively. The maximum of 11 maxillary teeth in *Rhiodenticulatus* can only be interpreted as a unique derived character. Probably related to this trend is the unique occurrence in *Rhiodenticulatus* of only two precanines. Protorothyridids typically possess five precanines, but as many as seven or eight have been described in *Paleothyris* (Carroll, 1969). A further slight reduction in the number of precanines occurs in the successively later occurring captorhinids; *Romeria prima* possesses six precanines, *R. texana, Protocaptorhinus,* and *Labidosaurus* four or five, *Eocaptorhinus* three or occasionally four, and *Captorhinus* three or rarely four.

The lacrimal of *Rhiodenticulatus* may be unique among all captorhinomorphs in having an unusually large height to length ratio. The height was measured at the level of the dorsalmost expansion of the maxilla, whereas the length was taken as the shortest distance between the orbit and naris. Despite the small errors expected in making these sorts of measurements, the height to length ratios of .65 and .73 for the holotype UCMP 35757 and paratype UCMP 40209, respectively, are considerably greater than those of other single-tooth-rowed captorhinids, which range from about .25 to .40. In the protorothyridids *Paleothyris* and *Protorothyris,* the lacrimals are very long and narrow, and have a height to length ratio of about .17. The fact that in *Rhiodenticulatus* the ratio is smaller for the larger holotype than for the paratype, suggests that the ratio decreases somewhat with growth or increase in size. This notion is reinforced in *Romeria texana,* where the ratios for an adult and juvenile described by Clark and Carroll (1973) are .27 and .40, respectively.

The extreme anterior extent of the prefrontal along the dorsal margin of the lacrimal in *Rhiodenticulatus* also sets it apart from all other captorhinids. In the holotype UCMP 35757 and paratype UCMP 40209 the prefrontal extends anteriorly to a level that is 90 and 84% of the distance from the orbit to the naris, respectively, whereas in other captorhinids and in *Protorothyris* this measurement ranges from approximately 43 to 58%. It might be suspected that the greater anterior extension of the prefrontal in *Rhiodenticulatus* is due to removal, either as a result of weathering or mechanical preparation, of that portion of the nasal overlying its anterior end. In *Eocaptorhinus,* for example, where additional exposure of the prefrontal could conceivably increase its preorbital length by as much as 28% (Heaton, 1979), the anterior extension of the prefrontal would increase from about 44 to 56% of the distance between the orbit and naris. As pointed out by Heaton (1979), in Clark and Carroll's (1973) illustration and reconstruction of the holotype of *Romeria texana* the prefrontals appear unusually long due to the exposure of that portion of their anterior ends normally overlapped by the nasals. For this reason we used Heaton's (1979) reconstruction of *Romeria texana* in calculating the relative anterior extension of the prefrontal. In the holotype and paratype UCMP 40209 of *Rhiodenticulatus* both pairs of prefrontals have identical lateral exposure configurations, strongly suggesting that they have not been significantly distorted in this way by weathering or excessive preparation.

Rhiodenticulatus exhibits several shared derived features with other advanced single-tooth-rowed captorhinids. Its possession of only three premaxillary teeth is considered advanced among the captorhinids in view of the general trend within the captorhinomorphs toward reduction in the number of premaxillary teeth. Protorothyridids typically have five or six premaxillary teeth, although *Protorothyris archeri* appears to have four and *Cephalerpeton* only three (Reisz and Baird, 1983). Premaxillary tooth counts for *Romeria prima, R. texana, Protocaptorhinus, Labidosaurus,* and *Eocaptorhinus* are 4, 5, 4 or 5, 3, and 4 or 5, respectively. The premaxilla of *Captorhinus* typically possesses four teeth and rarely three or five. *Rhiodenticulatus* is also similar to the more derived captorhinids *Labidosaurus, Eocaptorhinus,* and *Captorhinus* in having a long, narrow, rectangular quadratojugal in which the longitudinal length exceeds by almost four times the height, and the dorsal margin tends to be straight. As pointed out by Heaton (1979), in the more primitive *Romeria* and *Protocaptorhinus* the dorsal margin of the quadratojugal tends to be more convex. Heaton also noted that in the reconstruction of *Romeria prima* by Clark and Carroll (1973) this feature is erroneously exaggerated and is actually not significantly different from that of *R. texana* and *Protocaptorhinus.* More notable, however, is the shorter length of the quadratojugals of *Romeria* and *Protocaptorhinus,* so that the length exceeds the height by no more than two and one half times. The quadratojugals of the protorothyridids tend to be more like those of the more primitive captorhinids. The straight occipital margin of the skull table of *Rhiodenticulatus,* seen also in *Protocaptorhinus,* is a derived feature with respect to the bilateral parietal embayment of the occipital margin of *Romeria* and the protorothyridids. On the other hand, *Rhiodenticulatus* is viewed as primitive with respect to the median embayment of the occipital margins of *Labidosaurus, Eocaptorhinus,* and *Captorhinus.*

Rhiodenticulatus exhibits at least two characters that link it with the more primitive captorhinids *Romeria* and *Protocaptorhinus,* and exclude it from the more advanced *Labidosaurus, Eocaptorhinus,* and *Captorhinus.* It has been noted by several authors (Clark and Carroll, 1973; Heaton, 1979) that in the evolution of the captorhinids there is a marked trend toward relative widening of the postorbital region of the skull. In *Labidosaurus, Eocaptorhinus,* and *Captorhinus,* the postorbital lateral expansion of the skull becomes so pronounced that the lateral margin of the skull in dorsal view is noticeably concave, whereas in *Romeria, Protocaptorhinus,* and *Rhiodenticulatus* it is essentially straight. *Labidosaurus, Eocaptorhinus,* and *Captorhinus* are advanced over *Romeria, Protocaptorhinus,* and *Rhiodenticulatus* in exhibiting the shared derived feature of blunt (rather than sharply pointed) postcanine maxillary teeth (Olson, 1984).

Finally, there is one unique feature of *Rhiodenticulatus* with respect to all other single-tooth-rowed captorhinids which on first consideration seems unquestionably primitive, its possession of small premaxillary teeth of subequal size. In all captorhinids the premaxillary teeth exhibit a steady but dramatic increase in size anteriorly, with the anterior teeth reaching sizes equal to, or greater than, the maxillary canine. Though *Rhiodenticulatus* is like its protorothyridid predecessors in this character, implying a primitive state, the alternative interpretation that it represents an evolutionary reversal is argued below.

On the basis of the above character state analysis we conclude that the most plausible relationship of *Rhiodenticulatus heatoni* to other captorhinids is that depicted by the cladogram of Fig. 5 in which it is the primitive sister taxon to *Labidosaurus, Eocaptorhinus,* and *Captorhinus* (plus all other multiple-tooth-rowed forms). We recognize, however, that the cladogram possesses a few weaknesses. First, several of the nodes are defined by only a single character. Second, there are at least two notable contradictions between the cladogram and the character state analysis presented. Perhaps the most obvious is the possession by *Rhiodenticulatus* of small, subequal premaxillary teeth. The cladogram requires that this character be interpreted as the result of a secondary reduction in tooth size, or an evolutionary reversal, rather than more simply, as our character analysis implies, a primitive character. The likelihood that such an event occurred, however, seems very reasonable in light of the several derived modifications of the dentition of *Rhiodenticulatus* noted: 1) a single, extremely large canine, 2) reduction of the maxillary dentition to 11 teeth, 3) reduction in the number of precanines to two, and 4) reduction of the premaxillary dentition to three teeth. Of these, the first three are judged unique to *Rhiodenticulatus* among the single-tooth-rowed captorhinids, whereas the last also occurs in *Labidosaurus.* It should be noted here, however, that in our opinion it seems quite likely that the reduction in the number of premaxillary teeth to three in *Rhiodenticulatus* and *Labidosaurus* was achieved independently given the otherwise marked differences between their dentitions. A second possible inconsistency between the

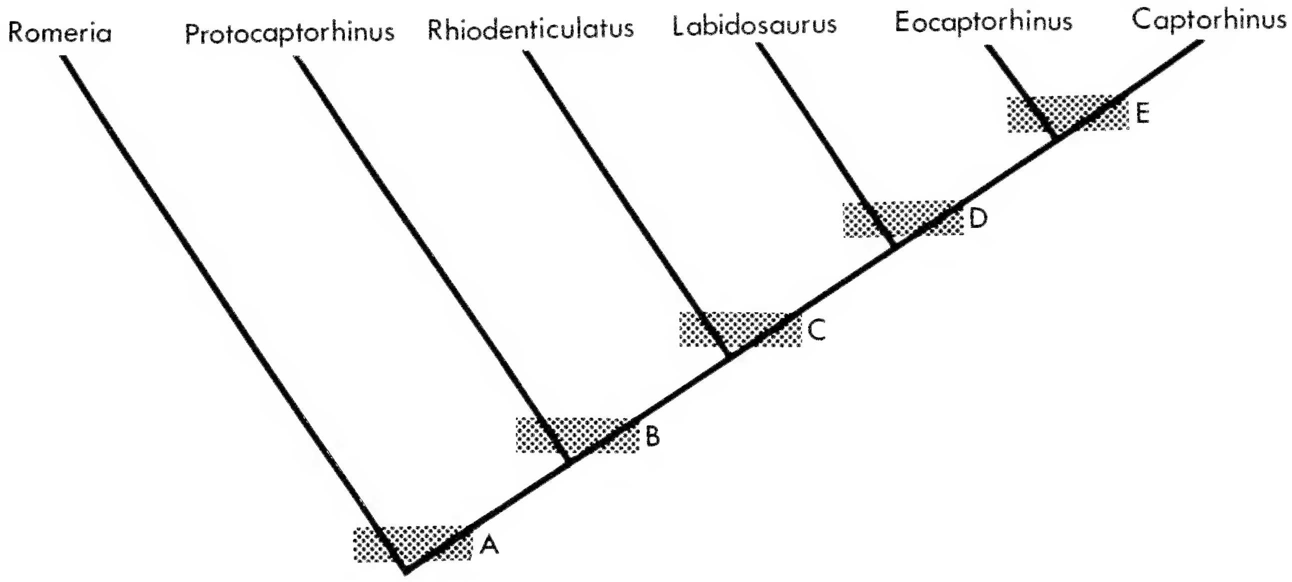

Fig. 5.—Cladogram illustrating possible relationships of *Rhiodenticulatus heatoni.* Shared derived characters: A, hooked premaxilla, loss of tabular, loss of ectopterygoid, supinator process of humerus absent, clavicle with thumb-like process, reduced dentition; B, straight occipital margin of skull table; C, elongate quadratojugal; D, retroarticular process present, median embayment of occipital margin of skull table, marked expansion of postorbital cheek region, blunt postcanines; E, anteroposteriorly elongate retroarticular process.

placement of *Rhiodenticulatus* in the cladogram and our character state analysis concerns the unique derived features of its dentition. If, as suggested above, the extremely large, single canine, 11 maxillary teeth, and two precanines of *Rhiodenticulatus* represent the most advanced stages of general trends within the single-tooth-rowed captorhinids, then it could be argued that these features indicate an advanced sister taxon relationship with *Labidosaurus* and *Eocaptorhinus* as well. This interpretation is rejected, however, in favor of the alternative argument that these unique features of the dentition of *Rhiodenticulatus,* as well as its relatively small, few premaxillary teeth, probably reflect an adaptation to a specialized diet not present in the other single-tooth-rowed captorhinids.

OTHER NEW MEXICO CAPTORHINIDS

In recent years the authors have collected additional captorhinid remains from the Lower Permian Cutler, Abo, and Sangre de Cristo formations at widely scattered localities in northern and central New Mexico. Although these specimens, as well as the two crushed and incomplete skulls referred to "*Puercosaurus obtusidens*" by Williston (1916), are too poorly preserved to be assigned safely to an existing taxon or made the basis of a new one, they permit the recognition of at least three possible morphotypes, one each from the Cutler, Abo, and Sangre de Cristo formations. These specmiens are, therefore, important as indicators of the diversity and spatial range of the captorhinids in the Lower Permian of New Mexico.

Indeterminate Cutler Captorhinid

All the indeterminate captorhinid specimens from Cutler Formation of the Rio Puerco drainage, Rio Arriba County, in the north-central part of the state are considered together as though pertaining to a single form distinct from *Rhiodenticulatus heatoni* of the same area. This is done despite the fact that the indeterminate specimens exhibit some differences from each other. It is realized that future discoveries may indicate that the differences between them may be due to either the presence of more than one undescribed species, or distinct growth stages of the same species, or both. If conspecificity is being masked by ontogenetic growth stages, then it is also conceivable that one or more of the indeterminate Cutler specimens may prove to be conspecific or congeneric with *R. heatoni.* This possibility is given some support by the presence in a few of the unassigned Cutler specimens of at least one feature considered derived in *R. heatoni,* the single, greatly enlarged canine. The unassigned Cutler specimens include:

FMNH 745, two crushed and very incomplete skulls referred to "*Puercosaurus obtusidens*" by Williston (1916), who illustrated only one, the same skull shown here in

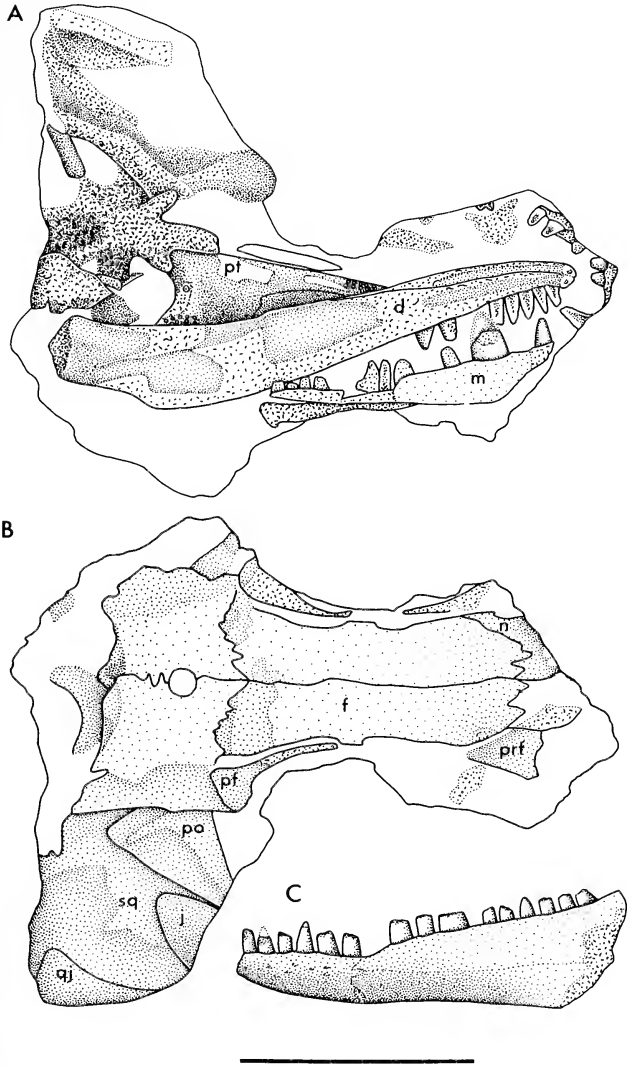

Fig. 6.—"*Puercosaurus obtusidens*" Williston (1916). A, dorsal, and B, ventral views of referred skull FMNH 745. C, lateral view of holotypic dentary FMNH 743. Abbreviations: d, dentary; f, frontal; j, jugal; m, maxilla; pf, postfrontal; po, postorbital; prf, prefrontal; pt, pterygoid; qj, quadratojugal; sq, squamosal. Scale = 1 cm.

Fig. 6A, B. Their exact locality is unknown, and according to Williston (1916) they were found by Mr. Miller in 1911 on the Rio Puerco a few miles below Arroyo de Agua. The holotypic left dentary of "*P. obtusidens*" (Fig. 6C) is too incomplete to assign to the Captorhinidae with reasonable certainty.

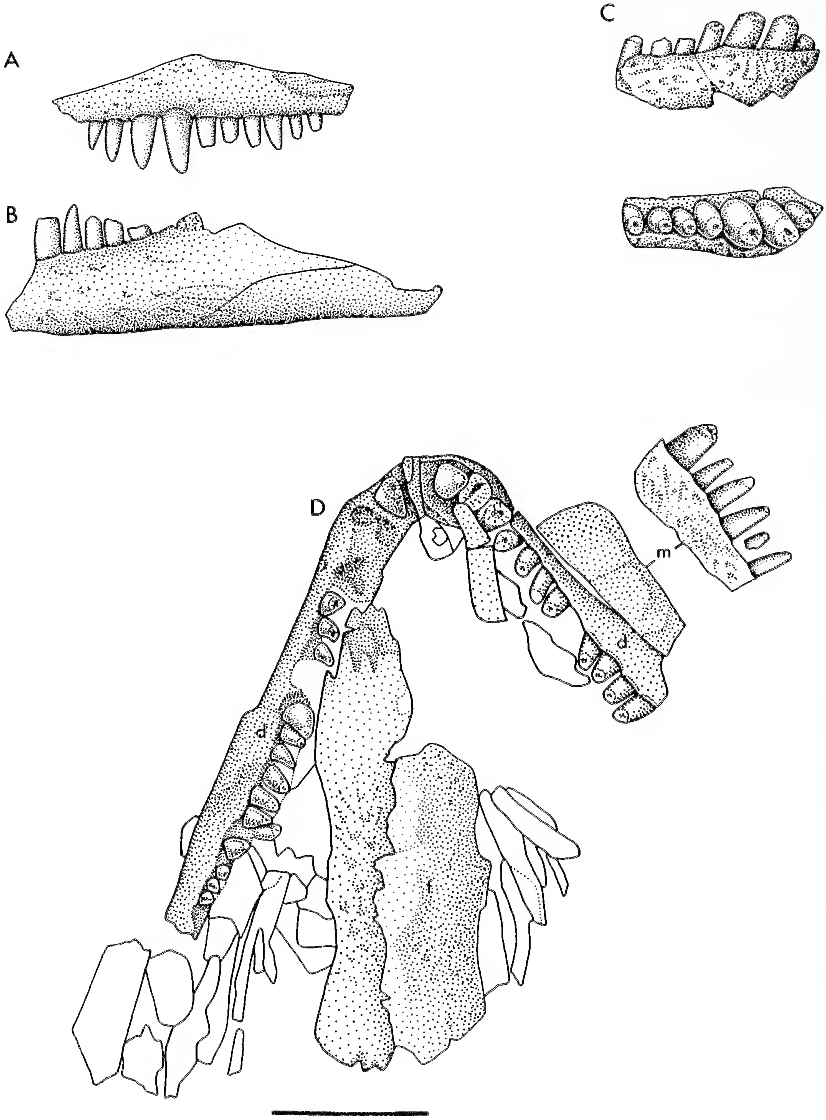

Fig. 7.—Indeterminate captorhinid from the Cutler Formation. A, lateral view of partial left maxilla, B, lateral view of posterior portion of left dentary, and C, lateral and dorsal views of anterior portion of right dentary of CM 28592. D, partial skull CM 28591 showing mainly paired frontals in dorsal view, dentaries in ventral view, and small portion of left maxilla in both medial and lateral views. Abbreviations: d, dentary; f, frontal; m, maxilla. Scale = 1 cm.

CM 28591, a partial skull (Fig. 7C, D); CM 28589, fourteen dorsal vertebrae, most of which are articulated in strings of two or three, and associated fragments of ribs and appendicular elements (Fig. 8A). These vertebrae are indistinguishable from those of *R. heatoni,* as are those of most captorhinids, but are included here because they were found in very close proximity to CM 28591 in NE¼SW¼NE¼ sec. 5, T. 22 N., R. 3 E. about 1.5 km northeast of Arroyo de Agua.

CM 28592, partial left maxilla (Fig. 7A), small portion of both dentaries (Fig. 7B), presacral vertebra, and left humerus (Fig. 8C). These elements undoubtedly belong to a single individual and were collected in N¼SW¼SE¼ sec. 8, T. 22 N., R. 3 E. about 1.6 km southeast of Arroyo de Agua.

The left premaxilla of the figured skull of FMNH 745 (Fig. 6) appears to have held four teeth as Williston (1916) described; this estimate takes into account an unoccupied space. The premaxillary teeth, as in *Rhiodenticulatus,* are very small relative to the pre- and postcanines of the maxilla. Accounting for spaces, the maxilla of FMNH 745 held approximately 13 to 15 teeth, including two or possibly three precanines, one extremely large canine, and 10 or 11 postcanines that decrease gradually in size posteriorly. As in *Rhiodenticulatus,* the basal diameter of the canine is about twice that of any of the postcanines. The dentition of the partial left maxilla of CM 28592 (Fig. 7A) is considerably different, however, in that the canine is relatively smaller when compared to the postcanines, and the third or posteriormost precanine is nearly as large as the canine, producing a double canine appearance. A segment of the right maxilla of CM 28591 (Fig. 7D) shows the canine as dominating the postcanines in size, though not as greatly as in *Rhiodenticulatus.* The maxillary dentitions of FMNH 745, CM 28591, and CM 28592 are single rowed, and the teeth appear as simple, sharply pointed pegs except for a slight, posterior curvature of the tips. The frontals of FMNH 745 and CM 28591 (Figs. 6B, 7D) are complete, and their very narrow contribution to the orbital rim is clearly discernable. As in *Rhiodenticulatus,* the portion of frontal anterior to its contribution to the orbital rim is considerably larger than that which is posterior. In FMNH 745 the pineal foramen appears to be more centrally positioned along the median parietal suture than in *Rhiodenticulatus.* The dentary dentition is well preserved in CM 28591 except for most of the teeth lacking their tips; the more complete right dentary is estimated to have held about 18 teeth. The first tooth is extremely small in typical captorhinid fashion, the second and third are subequal in size and much larger than the others of the series, and the following teeth do not exhibit an obvious size pattern except for the last three being greatly reduced. The anterior seven teeth preserved on the fragment of right dentary of CM 28592 (Fig. 7C) exhibit the same size relationships as in CM 28591. In contrast, the first five teeth of the left dentary of the FMNH 745 are of subequal, moderate size. The dentary teeth also have the form of simple, sharply pointed pegs.

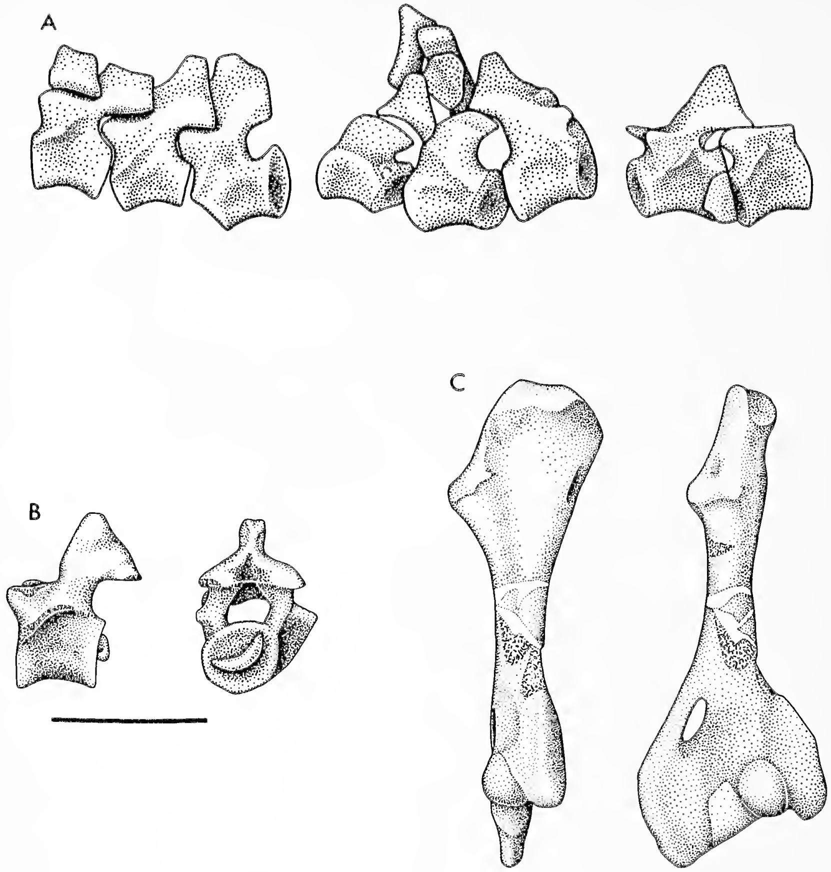

Fig. 8.—Indeterminate captorhinid from Cutler Formation. Presacral vertebrae of A, CM 28589, and B, CM 28592. C, dorsal proximal and distal ventral views of left humerus CM 28592. Scale = 1 cm.

The presacral vertebrae of CM 28589 and CM 28592 (Fig. 8A, B) are alike and as far as comparisons will allow like those of *Rhiodenticulatus*. The neural spine is small, triangular in lateral view, and distinctly set off from the neural arch, which has the expected swollen appearance. The zygapophyses extend slightly beyond the lateral margins of the centra, and their articular facets are essentially horizontal. There is no evidence of a suture between the neural arch and centrum. The transverse process is positioned on the anterodorsal quadrant of the lateral surface of the centrum. In lateral view the process is a thin, ridge-like structure whose base extends anteroventrally to the centrum

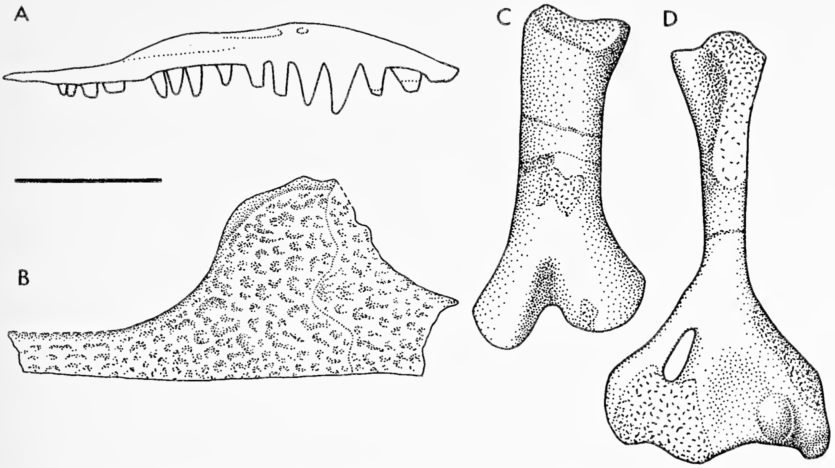

Fig. 9.—Indeterminate captorhinid CM 41707 from the Abo formation. A, medial view of left maxilla, B, lateral view of left jugal, C, dorsal view of distal half of right femur, and D, distal ventral view of left humerus. Scale = 1 cm.

rim. In anterior view its lateral projection diminishes as it extends to the centrum rim, giving it a wing-like appearance. The ends of the centra are beveled slightly so as to give them a slightly keystone appearance in lateral view. The lateral surfaces of the centra are moderately concave in horizontal section, producing a spool-shaped appearance. The only clearly visible intercentrum is seen in the vertebra of CM 28592 (Fig. 8B); it has a low, narrowly triangular outline in lateral view and a crescent-shaped outline in anterior view.

The only appendicular element of the indeterminate specimens from the Cutler Formation worthy of description is the well preserved left humerus of CM 28592 (Fig. 8C). It differs from those of *Eocaptorhinus* and *Captorhinus* (Holmes, 1977) mainly in having a more gracile form, but in this feature is also like that of *Rhiodenticulatus.* The proximal and distal ends are relatively narrower, and the entepicondyle extends far more distally beyond the radial condyle than in *Eocaptorhinus* or *Captorhinus.*

Indeterminate Abo Captorhinid

A second possible New Mexico captorhinid form for which there is insufficient morphological information to assign to either an existing or a new taxon is based on a single specimen, CM 41707, collected from the Abo Formation about 20 km northeast of Socorro in the central part of the state in SE¼NE¼W¼ of sec. 14, T. 2 S., R. 3 E. CM

41707 consists of disarticulated elements of the skull and postcranial skeleton of an individual that are randomly associated and densely concentrated in a small, strongly indurated, red concretion. Only those elements close to the outer surface of the concretion were prepared and include: a left maxilla, left jugal, anterior half of the right mandible, a presacral vertebra, ribs, greater part of the left humerus, distal half of right femur, and several unidentified fragments. Only a few of the above elements are figured here (Fig. 9). The left maxilla (Fig. 9A), although poorly preserved, retains an accurate outline of its dentition, which consists of 14 teeth and at least one unoccupied space; in this feature it is like the maxilla of the indeterminate Cutler specimen FMNH 745. As in *Rhiodenticulatus,* there are two moderate sized precanines. Although the third tooth is the largest of the series and should be considered a canine, the fourth tooth is nearly as large, giving CM 41707 a distinctly double canine appearance like that in the partial left maxilla of the indeterminate Cutler specimen CM 28592. The basal diameter of neither canine of CM 41707, however, exceeds that of the largest postcanine as greatly as does the single, enlarged canine of *Rhiodenticulatus.* The teeth gradually decrease in size from the first canine to the seventh tooth; this is followed first by four somewhat larger, subequal teeth and then by the last three and smallest teeth of the series. The jugal (Fig. 9B) is like that of other captorhinids. A smooth flange on the dorsal margin of the posterior plate clearly indicates the position of the overlaping postorbital, and the spike-like projection on the posterior margin marks the point of separation between the jugal-squamosal and jugal-quadratojugal contacts.

The anterior half of the right mandible (not figured) is exposed in lateral and dorsal view, and the first 16 teeth are present, though many are represented by only their bases. As in the captorhinids *Eocaptorhinus* and *Captorhinus,* the first tooth is extremely small, the second moderate sized, and the third is greatly enlarged and dominates the entire series, having a basal diameter of about 2 mm and a height of about 5 mm. The fourth tooth is the second largest of the series, with a basal diameter of about 1.5 mm and an estimated height of 2.5 mm, whereas the fifth is greatly reduced and about equal to the second in size. Teeth 6, 7, and 8 are of subequal, moderate size, the larger ninth tooth appears to have been about the size of the third tooth, and the remaining seven teeth steadily decrease in size posteriorly. All the dentary teeth appear to have the form of simple pointed pegs and are aligned in a single row. As in *Eocaptorhinus* and *Captorhinus,* the first three teeth lean obliquely forward and the fourth is nearly vertical. The one partial vertebra appears to be typical of captorhinids. The left humerus of CM 41707 (Fig. 9D) is nearly complete, missing only a

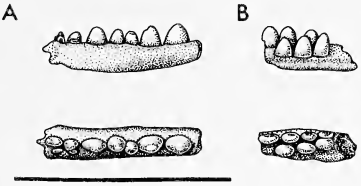

Fig. 10.—Indeterminate captorhinid from the Sangre de Cristo Formation. Lateral and ventral views of maxillary fragments A, CM 28594, and B, CM 28595. Scale = 1 cm.

portion of its proximal end. The shaft is more slender and the entepicondyle possibly less expanded than those of *Eocaptorhinus* or *Captorhinus.* The entepicondyle extends distally only slightly beyond the radial condyle. In contrast, the distal half of the right femur (Fig. 9C) is very stoutly constructed, especially in comparison with *Eocaptorhinus* and *Captorhinus.*

Indeterminate Sangre de Cristo Captorhinid

Numerous fragments of captorhind maxillae and dentaries have been collected from the Lower Permian Sangre de Cristo Formation approximately 50 km southeast of Santa Fe in the northeastern part of the state in NE¼ sec. 36, T. 14 N., R. 13 E. Two of the maxillary fragments are figured (Fig. 10), and they clearly indicate that the captorhinid from this locality had at least two rows of teeth. In one (CM 28594, Fig. 10A) the broken edges of a second row of teeth can be seen lateral to the posterior end of the main row. Medial wear facets of the teeth, which are more evident on the other fragment (CM 28595, Fig. 10B), give them the same blunt, peg-like outlines seen in *Eocaptorhinus* and multiple-tooth-rowed forms such as *Captorhinus.* These two features of the dentition indicate clearly that the Sangre de Cristo captorhinid remains are of a distinct and more advanced taxon than the other representatives of the family in New Mexico.

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DESCRIPTION OF THE LOWER JAW OF *STEGOSAURUS* (REPTILIA, ORNITHISCHIA)

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Abstract

Description of a well preserved lower jaw of *Stegosaurus* reveals previously unknown structural details. Although comparisons between the lower jaw of *Stegosaurus* and those of other stegosaurs are greatly limited, they strongly suggest a close comformity. The lower jaw of *Stegosaurus* exhibits the most primitive grade of organization among the ornithischians with one noticeable exception, the retention of an intercoronoid in ceratopsians.

Introduction

During the past several years there has been a renewed effort by the Carnegie Museum of Natural History to prepare the remaining dinosaur materials collected by that institution over 60 years ago (1909–1922) at what is now Dinosaur National Monument. During the routine preparation of one of the blocks, field no. 83, an almost complete, excellently preserved left mandible of *Stegosaurus* was unexpectedly discovered. Earl Douglass, who was in charge of the quarrying operations, had identified the contents of field no. 83 as "Dinosaur. vertebra, rib, etc.," and preparation of the block was, therefore, subsequently

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postponed because it was thought to contain little of importance. Although *Stegosaurus* is one of the most common of the Morrison dinosaurs, skull material is extremely rare. To date, only one complete skull and lower jaw have been found, that of the type specimen of *Stegosaurus stenops* (USNM 4934) from the Felch quarry (YPM quarry 1; see Ostrom and McIntosh, 1966) at the entrance of Garden Park, about 13 km north of Canyon City, Colorado. It was originally described briefly by Marsh (1887) and later in much greater detail by Gilmore (1914). Several braincases of *Stegosaurus* have been found, but the anterior half of a right dentary (USNM 4935) from the "stegosaur" quarry (YPM quarry 13; see Ostrom and McIntosh, 1966), about 6.5 km east of Como Bluff, Wyoming, is otherwise the only other mandible known. The mandible described herein lacks only the predentary and teeth, and is noteworthy in exhibiting structural details heretofore unknown in other specimens.

The following abbreviations are used to refer to repositories of specimens: CM, Carnegie Museum of Natural History; USNM, National Museum of Natural History; and YPM, Yale Peabody Museum.

SYSTEMATIC PALEONTOLOGY

Class Reptilia
Order Ornithischia Seeley, 1888
Suborder Stegosauria Marsh, 1877
Family Stegosauridae Marsh, 1880
Genus ***Stegosaurus*** Marsh, 1877
Stegosaurus sp.

Specimen.—CM 41681, left mandible lacking predentary and dentition.

Horizon.—Morrison Formation, Late Jurassic.

Locality.—Dinosaur National Monument (originally called the Carnegie quarry), about 10 km north of Jensen, Uintah County, Utah. CM 41681 was found under the fourteeth cervical vertebra of the type skeleton of *Apatosaurus louisae* Holland, CM 3018, at the co-ordinates F to G-54 on the quarry map published by Gilmore (1936).

Collector.—Earl Douglass and party, 1910.

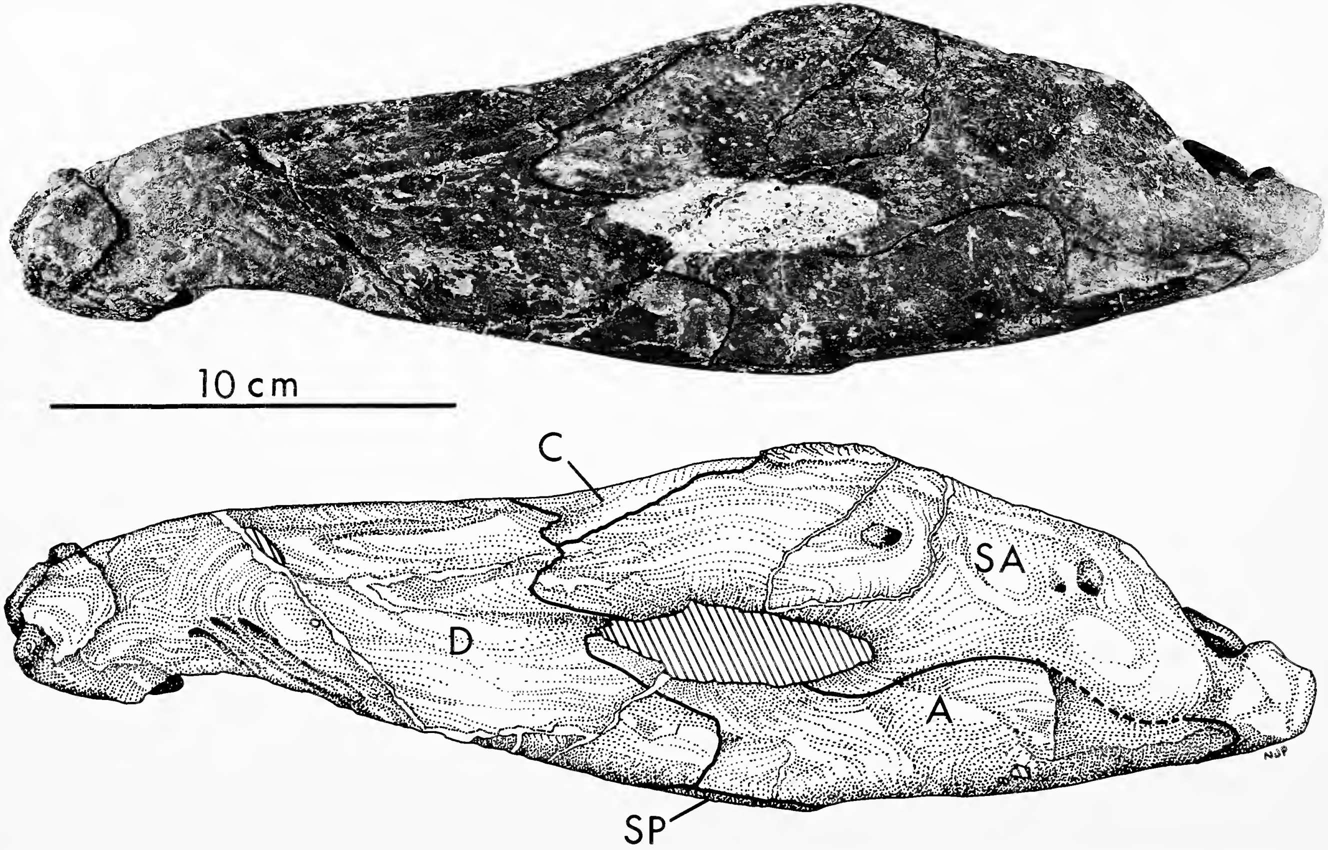
Assignment.—Descriptions and illustrations by Marsh (1887) and Gilmore (1914) of the holotypic lower jaw of *Stegosaurus stenops* USNM 4934, although containing several errors that will be brought out in the text below, and by Gilmore (1914) of the right dentary of *Stegosaurus* sp. USNM 4935 leave little or no doubt about the assignation of CM 41681 to this genus. It can also be noted that there exists no known dinosaur from the Late Jurassic whose lower jaw could be confused with that of *Stegosaurus*.

DESCRIPTION

As Figs. 1–3 indicate, the left mandible CM 41681 is complete except for the absence of the one unpaired element of the lower jaw, the median predentary, and the dentition. The mandible is well preserved and the sutures delineating the seven elements that comprise it, except those of the articular, are clearly discernable. The mandible is narrowly compressed in transverse section. In lateral or medial view the mandible is shallow, exhibiting a gradual dorsal and ventral expansion posteriorly from the symphysis to a maximum depth at about three-fifths its length, then gradually narrows at about the same rate posteriorly to the end of the retroarticular process. Whereas the expansion of the dorsal margin is somewhat angular in outline, that of the ventral margin is smoothly convex. There is no development of a distinct coronoid process, but rather there is a low coronoid eminence whose apex is formed by the surangular. The plate-like anterior end of the mandible turns abruptly medially and slightly ventrally, and with the symphysis inclined posteroventrally the joined mandibles would have a scoop-like appearance. It has not been possible to identify the small rectangular plate of bone adhering to the medial surface of the anterior end of the dentary; it might be part of the adjoining left dentary.

The sutures of the lateral surface of the mandible (Fig. 1) are, for the most part, clearly defined and need little comment. The articular-surangular suture is not evident, and a portion of the angular-surangular suture is restored on the basis of impression. The dentary, surangular, and angular border a very large, horizontally elongate, oval mandibular foramen. A very thin, short strip of the splenial is visible on the midventral margin of the mandible. Three shallow, parallel grooves occur shortly posterior of the point where the anterior end of the dentary curves medially. Each deepens slightly as it extends 1 to 2 cm anterodorsally from the inferior jaw margin and ends at a small foramen that pierces the dentary at a very low angle. Three relatively small foramina are located near the dorsal border of the surangular; two closely spaced smaller ones are located a considerable distance posterior to a larger one. They undoubtedly penetrate to the medial side of the surangular. Galton (1974) has described similar foramina in the ornithischian dinosaur *Hypsilophodon* and suggested that they may have transmitted cutaneous branches of the inferior alveolar nerve as in modern lizards (Oelrich, 1956).

In medial view (Fig. 2) all seven elements of the mandible are visible. The dentary is the largest of the jaw elements. Its upper half, above the Meckelian canal, is remarkably thick, having a triangular cross-sectional outline with the apex directed medially to form a dorsal, shelf-like surface (Fig. 3). Posteriorly much of the medial edge of the


10 cm
C
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D
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dorsal shelf is occupied by a series of 20 closely spaced alveoli. The remaining anterior portion of the medial edge of the shelf takes the form of a thin, knife-like ridge that continues to the symphysis. The slightly concave dorsal shelf of the dentary faces dorsomedially at its posterior end, but because of a gradual twisting as it is followed anteriorly, the shelf faces directly dorsally just beyond its midlength and then anteriorly at the symphysis. Along most of the length of the dorsal shelf, mainly at the level of the alveoli, is a series of about nine foramina of varied sizes, which might be interpreted as mental foramina. The posteriormost pair of foramina are located at the anterior end of a prominent, 3 cm long groove that deepens anteriorly. The orientation of the alveolar series suggests that the teeth were directed mainly medially and only slightly dorsally. Directly below the series of alveoli is a series of foramina; they are apparently arranged so that each foramen lies opposite an alveolus, but they do not occur the entire length of the alveolar series.

The Meckelian canal of the dentary is exposed medially as it emerges from beneath the anterior margin of the splenial, becoming progressively shallower as it extends nearly to the symphysis. The large, subrectangular, plate-like splenial has a sinuous, overlapping suture with the dentary anteriorly. There is a deep, narrow emargination of the anterior border of the splenial at the level of the Meckelian canal. The splenial-prearticular contact is also very sinuous; a moderate sized inframandibular foramen is located on this suture. The posterodorsal corner of the splenial appears to enter narrowly the rim of the adductor fossa. Its ventral margin contacts the dentary along the ventral edge of the mandible, whereas more posteriorly it wraps a short distance around the ventral edge to contact the angular on the lateral surface of the mandible. A large foramen of unknown function penetrates the splenial in a posterodorsal direction near its anteroventral border. What may be a large foramen is located near the middorsal margin of the splenial. A small portion of the angular wraps around the ventral edge of the mandible and is visible in medial view. Although a sutural contact between the prearticular and articular cannot be discerned, the prearticular undoubtedly formed the greater part of the ventromedial border and the articular the posterior border of the large, oval adductor fossa. The coronoid is roughly triangular in medial view, with its longer side forming a substantial portion of the dorsal margin of the mandible. It also contributes greatly to the anteromedial border of the adductor

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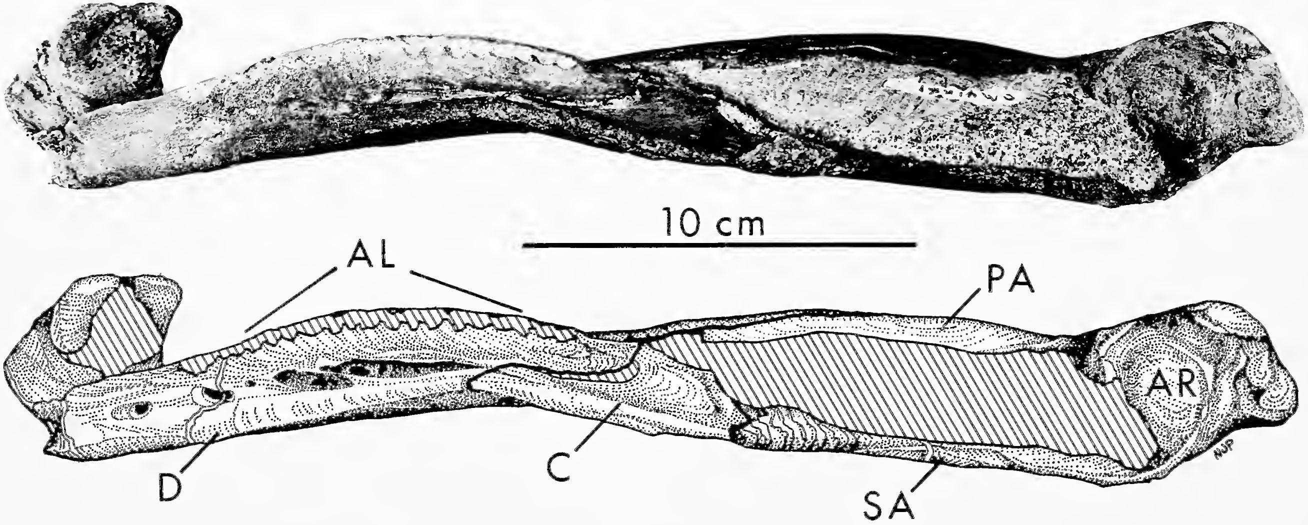
Fig. 1.—Photograph and illustration of left mandible of *Stegosaurus* CM 41681 in lateral view. Abbreviations: A, angular; C, coronoid; D, dentary; SA, surangular; SP, splenial.


10 cm
AL
PA
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D
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fossa. There is no indication that an intercoronoid was present. Just posterior to the coronoid there is a small, triangular, thickened area on the medial surface of the surangular apex of the coronoid eminence. This thickened area undoubtedly marks the site of concentrated attachment of jaw adductor musculature. The slightly concave articular surface of the articular is subcircular in outline. At its posteromedial border is a stout, dorsally directed triangular process. The retroarticular process is short and bluntly rounded.

COMPARISON AND DISCUSSION

The *Stegosaurus* mandible CM 41681 exhibits three features of particular interest that are not noted or shown in earlier descriptions or illustrations of the genus (Marsh, 1887; Gilmore, 1914): a large, external mandibular foramen; presence of a large coronoid bone; and a very weakly developed coronoid process with the apex formed by the surangular.

Several orders of reptiles have small fenestrae on the external surface of the mandible, but the presence of a large external mandibular foramen located at the intersection of the dentary, angular, and surangular, as in *Stegosaurus,* is rare. Such a foramen is found in crocodiles, prosauropods, theropods, and some thecodonts, but among ornithischians it has been reported only in the primitive ornithopod *Fabrosaurus* (Thulborn, 1970) and the stegosaur *Huayangosaurus* (Dong et al., 1982; Zhou, 1983). The external mandibular foramen of *Fabrosaurus* and CM 41681 are very similar except that in the former the dentary forms the anterior half or more of its margin. *Huayangosaurus,* from the Middle Jurassic of China, is the only stegosaur in which an external mandibular foramen has previously been described (Dong et al., 1982; Zhou, 1983). Although the formaen in *Huayangosaurus* is relatively smaller than that in CM 41681, it has the same general outline shape and precisely the same position and relationships to the surrounding dentary, surangular, and angular. Owen (1863) did not find evidence of the mandibular foramen in the primitive armored ornithischian *Scelidosaurus,* and recent preparation using modern chemical techniques has clearly indicated the absence of the foramen (Charig, 1979). *Scelidosaurus* has often been considered a stegosaur, but Charig (1979:126), who is currently restudying this animal, has remarked that

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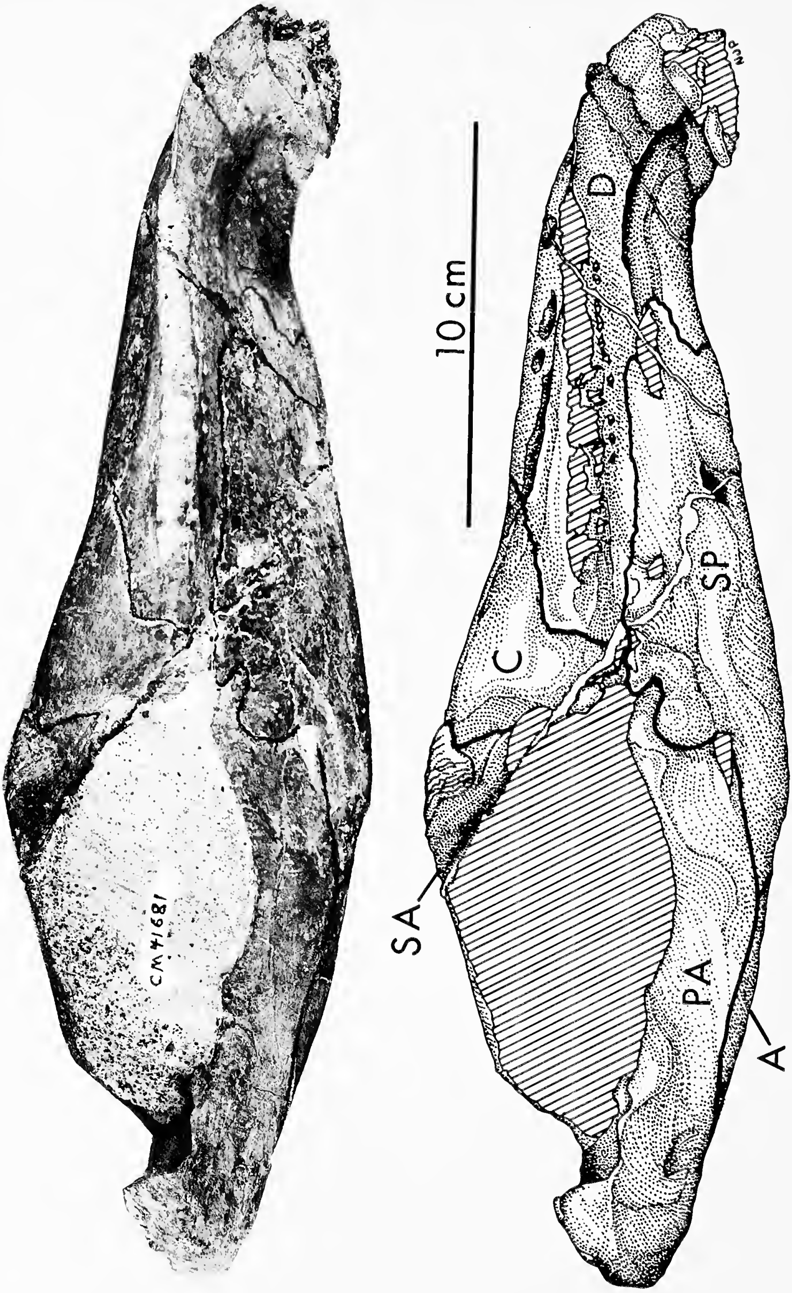
Fig. 2.—Photograph and illustration of left mandible of *Stegosaurus* CM 41681 in dorsal view. Abbreviations: AL, alveoli; AR, articular; C, coronoid; D, dentary; PA, prearticular; SA, surangular.


CM 41681
10 cm
NJP
D
SP
C
SA
PA
A

"It has often been regarded as an ancestral stegosaur; it might be an ancestral ankylosaur; it could be neither."

Gilmore (1914) presumed that a separate coronoid bone was present in *Stegosaurus,* but was unable to verify this on the basis of the then only known complete jaw of the genus, that of the holotype of *S. stenops* (USNM 4934). It is, therefore, gratifying that relatively large coronoid is clearly evident in CM 41681. Owen (1863) stated that the lower jaw of *Scelidosaurus* includes a coronoid, but did not describe it or indicate it in his figures (pls. 46, 47). Although the presence of a coronoid has not been demonstrated in other stegosaurs, there is no basis for suggesting its absence. On the contrary, there is increasing evidence that a coronoid element was present in all ornithischians except the hadrosaurs. It has been explicitly reported in the ornithopods *Hypsilophodon* (Galton, 1974), *Camptosaurus* (Gilmore, 1909), *Iguanodon* (Dollo, 1883), and *Ouranosaurus* (Taquet, 1976), in the ceratopsians *Protoceratops, Montanoceratops, Centrosaurus,* and *Triceratops* (Brown and Schlaikjer, 1940), in the ankylosaur *Edmontonia* (Gilmore, 1930; Russell, 1940) (=*Panoplosaurus* of Coombs, 1978), and in the pachycephalosaur *Stegoceras* (Gilmore, 1924). The presence of a second coronoid element, the intercoronoid, has also been found by Brown and Schlaikjer (1940) in the Protoceratopsidae and Ceratopsidae. The intercoronoid, which apparently occurs in all saurischians (for example, *Plateosaurus, Brachiosaurus, Camarasaurus, Allosaurus, Tyrannosaurus,* and others), has not been reported in any other ornithischian group, and we are unable to find any evidence for its presence in CM 41681.

Among the ornithischians the coronoid of the ankylosaur *Edmontonia* (Gilmore, 1930; Russell, 1940) resembles most closely that of *Stegosaurus* in shape, size, and position, but important differences are evident. The anterior extension of the coronoid in *Edmontonia* lies medial to the posterior end of the tooth row, whereas in *Stegosaurus* it lies lateral to the tooth row. In *Edmontonia,* as well as in other ankylosaurs, and the pachycephalosaur *Stegoceras* (Gilmore, 1924) the surangular is expanded dorsally into a broadly rounded but prominent coronoid process; only in *Edmontonia,* however, is the coronoid clearly shown to curve upward onto the leading edge of the process. In *Stegosaurus,* on the other hand, the dorsal margin of the mandible rises gradually and evenly to the apex of the very low coronoid eminence whose apex is formed by the surangular. With the exception of *Fabro-*

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Fig. 3.—Photograph and illustration of left mandible of *Stegosaurus* CM 41681 in medial view. Abbreviations: A, angular; C, coronoid; D, dentary; PA, prearticular; SA, surangular; SP, splenial.

saurus (Thulborn, 1970), ornithopods possess a large, shaft-like coronoid process formed mainly by the dentary, that extends dorsally from the main body of the bone; the summit of the process may even curve anteriorly. There is a suboval coronoid on the medial surface of the process except in hadrosaurs, which appear to lack this element (Lull and Wright, 1942; Ostrom, 1961). In *Fabrosaurus* the dentary forms the apex of a low coronoid eminence; there is no distinct coronoid process. Within the ornithopods there is an apparent trend toward reduction and loss of the coronoid. The coronoid is relatively large in the primitive *Fabrosaurus* and *Hypsilophodon,* but in advanced forms it is greatly reduced, as in *Ouranosaurus,* and apparently lost in hadrosaurs.

Only one difference between CM 41681 and previous descriptions of the lower jaw of *Stegosaurus* is possibly noteworthy. The *Stegosaurus* right dentary USNM 4935 possesses 23 alveoli (Gilmore, 1914), whereas that of CM 41681 has 20. Whether this should be regarded as an individual variation or as having taxonomic significance is not known. It can be noted, however, that the USNM 4935 right dentary is approximately 20% larger than that of CM 41681, and the difference in their tooth counts may be related to size. What little is known about the jaws of other stegosaurs suggests that they compare closely with that of *Stegosaurus.* Though the descriptions of the jaw of *Huayangosaurus* (Dong et al., 1982; Zhou, 1983) are very brief, the accompanying figures of its lateral surface suggest that it probably differs in only minor ways from that of *Stegosaurus*—it may have a slightly more prominent coronoid process, but with the apex still apparently formed by the surangular; the teeth appear to be vertically oriented; a lateral exposure of the coronoid is not indicated; and the anterior end of the mandible curves more strongly ventrally. The stegosaurs *Kentrurosaurus* (Hennig, 1936), *Tuojiangosaurus* (Dong et al., 1983), and *Chungkingosaurus* (Dong et al., 1983) are known only from incomplete dentaries. The dentary of the *Kentrurosaurus* resembles very closely that of *Stegosaurus* in the position, shape, and development of the Meckelian canal, but the slightly larger alveoli suggest that it may have held fewer teeth. All that can be said of the dentaries of the latter two genera is that they were long and low, as in *Stegosaurus.*

The possession of a large external mandibular fenestra, large coronoid, and very weakly developed coronoid process in which the apex is formed by the surangular can be justifiably interpreted as primitive ornithischian features, inasmuch as they occur in a wide range of thecodonts. The above comparisons, therefore, indicate that the lower jaw of *Stegosaurus,* as is probably true of other stegosaurs, exhibits the most primitive grade of organization among the ornithischians with one conspicuous exception, the retention of the intercoronoid in the ceratopsians.

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VOLUME 55 23 MAY 1986 ARTICLE 3

BIOCHEMICAL AND MORPHOLOGICAL DIFFERENTIATION IN SPANISH AND MOROCCAN POPULATIONS OF *DISCOGLOSSUS* AND THE DESCRIPTION OF A NEW SPECIES FROM SOUTHERN SPAIN (AMPHIBIA, ANURA, DISCOGLOSSIDAE)

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Abstract

Biochemical and morphological divergence among Moroccan and Iberian populations suggests that populations of *Discoglossus* inhabiting these regions are not conspecific. Northern Moroccan *Discoglossus* are assigned to *D. pictus*; *Discoglossus galganoi* Capula et al. 1985 inhabits the Iberian peninsula to the north of the Guadalquivir River basin, and the *Discoglossus* population residing to the south of the Guadalquivir River basin on Iberia is described as a new species. An evolutionary scenario for Iberian and Moroccan populations, consistent with the biochemical and morphological data, is inferred from the physiogeographic history of the region.

Introduction

Until recently only two species of *Discoglossus* were thought to inhabit Europe. Spanish, French, and Sicilian populations were called *D. pictus,* and populations inhabiting Corsica, Sardinia, Elba, and Monte Argentario, Italy, were called *D. sardus* (Knoepffler, 1961*a,* 1961*b,* 1962). Recent electrophoretic examinations of *Discoglossus* have, how-

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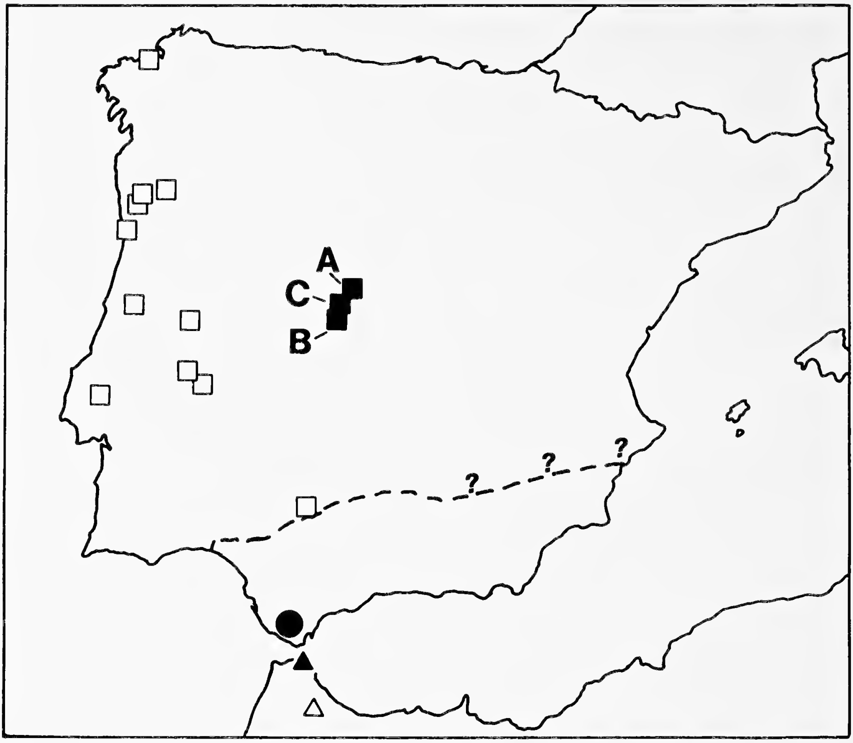

Fig. 1.—Localities of examined specimens of *Discoglossus galganoi* (squares), *D. pictus* (triangles), and *D. jeanneae* (circle). Dotted line traces the presumed northern limit of *D. jeanneae*; see Discussion for further explanation.

ever, revealed two additional species, *D. montalentii* from Corsica (Lanza et al., 1984) and *D. galganoi* from north of the Guadalquivir River basin in Spain and Portugal (Capula et al., 1985).

My interest in *Discoglossus* was initially focused on the amount of genetic differentiation that accumulated between European and African populations after the formation, 5–7 million years ago, of the Strait of Gibraltar (Busack, 1986). Because my electrophoretic study revealed substantial genetic differentiation between Spanish and Moroccan samples, the morphologies of these populations were also compared. Biochemical and morphological data indicate that Iberian populations to the north and to the south of the Guadalquivir River basin are not conspecific, and that neither is conspecific with populations inhabiting northern Morocco. The data supporting this conclusion are presented in the following pages, together with a description of a second species from Spain, and a hypothetical reconstruction of the evolutionary history of Iberian and Moroccan forms of *Discoglossus*.

Table 1.—*Protein systems examined by electrophoresis; enzymes are arranged by Enzyme Commission number.*

Protein (abbreviation)	Enzyme Commission number	Electro-phoretic conditions
Albumin (Ab)	—	B
(Oxidoreductases)		
Alcohol dehydrogenase (Adh)	1.1.1.1	A
Glycerol-3-phosphate dehydrogenase (Gpd)	1.1.1.8	D
L-Lactate dehydrogenase (Ldh)	1.1.1.27	F
Malate dehydrogenase (Mdh)	1.1.1.37	F
Malate dehydrogenase (Me)	1.1.1.40	F
Isocitrate dehydrogenase (Icd)	1.1.1.42	E
Phosphogluconate dehydrogenase (Pgd)	1.1.1.44	E
Glutamate dehydrogenase (Glud)	1.4.1.3	D
Superoxide dismutase (Sod)	1.15.1.1	D
(Transferases)		
Aspartate aminotransferase (Aat)	2.6.1.1	D
Hexokinase (Hk)	2.7.1.1	G
Creatine kinase (Ck)	2.7.3.2	G
(Hydrolases)		
Esterase (Est)	3.1.1.1	B
Esterase-D (Est-D)	3.1.1.1	B
Acid phosphatase (Acp)	3.1.3.2	G
Fructose-bisphosphatase (Hdp)	3.1.3.11	D
N-Acetyl-Beta-glucosaminidase (Hex)	3.2.1.30	G
Dipeptidase I, L-Leucyl-L-Alanine (La)	3.4.11	B
Dipeptidase III, L-Leucylglycyl-glycine (Lgg)	3.4.11	C
Dipeptidase IV, L-Phenylalanyl-L-Proline (Pap)	3.4.11	B
Adenosine deaminase (Ada)	3.5.4.4	A
(Lyases)		
Fructose-bisphosphate-aldolase (Ald)	4.1.2.13	H
Aconitate hydratase (Acon)	4.2.1.3	E
(Isomerases)		
Mannose-6-phosphate isomerase (Mpi)	5.3.1.8	E
Glucose-6-phosphate isomerase (Gpi)	5.3.1.9	F
Phosphoglucomutase (Pgm)	5.4.2.2	E

A = Histidine, pH 7.8 gel and electrode buffer (Harris and Hopkinson, 1976), 150v/3h.
B = LiOH A + B, pH 8.2 gel and LiOH A, pH 8.1 electrode buffer (Selander et al., 1971), 300v/3h.
C = Poulik, pH 8.7 gel and borate, pH 8.2 electrode buffer (Selander et al., 1971), 250v/3h.
D = Tris citrate II, pH 8.0 gel and electrode buffer (Selander et al., 1971), 130v/4h.
E = Tris citrate II, pH 8.0 + NADP gel and tris citrate II, pH 8.0 electrode buffer (Selander et al., 1971), 130v/4h.
F = Tris citrate III, pH 7.0 gel and electrode buffer (Ayala et al., 1972), 180v/3h.
G = Tris citrate III, pH 7.0 + 15% glycerine gel and tris citrate III, pH 7.0 electrode buffer (Ayala et al., 1972), 180v/3h.
H = Tris citrate III, pH 7.0 + NAD + 2-mercaptoethanol gel and tris citrate III, pH 7.0 electrode buffer (Ayala et al., 1972), 180v/3h.

MATERIALS AND METHODS

Electrophoresis.—One individual was collected from north of the Guadalquivir River basin in Ávila Province, Spain, at San Martín del Pimpollar (40°22′N, 5°03′W; Fig. 1, square C). Seven specimens were collected south of the Quadalquivir River basin in Cádiz Province, Spain (Fig. 1, circle), near the towns of Facinas (36°08′N, 5°42′W, 5 specimens) and Benalup de Sidonia (36°20′N, 5°49′W, 2 specimens). Specimens collected in Têtouan Prefecture at Chechaouene (35°10′N, 5°16′W; Fig. 1, open triangle; 5 specimens) and in the vicinity of Tleta Tarhremt (35°47′N, 5°28′W; Fig. 1, closed triangle; 5 specimens) represent northern Moroccan populations.

Specimens were sacrificed in the field and samples of heart and liver were removed, frozen, and stored in liquid nitrogen (−196°C). In the laboratory, tissues were transferred to a freezer (−76°C) until used in electrophoresis two to 12 months later. Tissue samples were pooled for each animal. Proteins were separated electrophoretically in horizontal starch gels (11.5% hydrolyzed starch, Sigma Chemical Co.) and localized by standard histochemical staining procedures (Ayala et al., 1972; Harris and Hopkinson, 1976; Selander et al., 1971; Table 1). Genetic interpretations of allozymic data were based on criteria developed by Selander et al. (1971). Multiple loci within a protein system were numbered with "1" designating the most anodally migrating set of allelic products. Alleles of a locus were lettered, with "a" representing the most anodally migrating product. Data resulting from the electrophoretic analysis are summarized in Table 2.

Two methods were used to analyze genetic relationships among populations of *Discoglossus.* The first distinguishes patterns of allele distribution among populations that occur as a result of chance association from those that occur too frequently to be chance phenomena. If all patterns of allele distribution are equally probable, the probability, P, that a particular pattern will occur is $1/S_n$ where S_n is the sum of the number of possible patterns of allele distribution. In the case of the three populations of *Discoglossus* being compared, $S_n = 7$ for three items combined three at a time, two at a time, and one at a time. The probability of observing a specific pattern of allele distribution, r, two or more times is given by summing the terms of the binomial expansion:

$$\mathrm{b}(r) = \binom{m}{r} P^r (1 - P)^{m-r},$$

where r is the number of replications seen for a given pattern of allele distribution, m is the total number of alleles in the data set, and $\binom{m}{r}$ is the number of possible combinations of m alleles taken r at a time (Straney, 1980; Patton and Smith, 1981).

The second method is the computation of estimates of, and standard errors for, the unbiased minimum genetic distance ($\hat{D}$; Nei, 1978, 1971, respectively) between *Discoglossus* populations. Allele frequency data (Table 2) were used directly for the computation of genetic distances and their standard errors.

Morphology.—Capula et al. (1985:tables 2, 4) published comprehensive tables of morphological measurements for *D. galganoi.* I have used the data in these tables to elucidate the morphological features of *D. galganoi* and to make direct assessments of morphological differentiation between *D. galganoi* and other taxa.

Spanish specimens I personally examined were representative of the same Cádiz Province populations as my electrophoretic samples, but collected earlier (between 1969 and 1972). Moroccan specimens included those used for electrophoresis as well as additional material from the same sites. Straight-line measurements of snout–urostyle (SUL), snout (anterior corner of the eye to the tip of the snout), head (posterior angle of the jaw to the tip of the snout), eye (horizontal diameter from posterior corner to anterior corner), tibia, femur, hand (proximal aspect of the central metacarpal tubercle to the tip of the third digit), and foot (proximal aspect of the metatarsal tubercle to the tip of the third digit) lengths were taken to 0.1 mm with dial calipers. Head width (angle of jaws), interorbital (between the anterior corner of the eyes), and internarial (center to center) distances were also recorded.

Frogs are sometimes sexually dimorphic in many characters and sexes were analyzed separately. The effect of having limited numbers of individuals of each size representing each sex of each population was minimized by converting each character measurement to natural logarithms; the variance of ln-transformed data estimates intrinsic variability and is unaffected by size (Lewontin, 1966; Moriarty, 1977). Transformed data representing each character were subjected to covariance analysis in which snout–urostyle length was selected as the independent variable. Although allometry is correctly assessed only from the study of growth of an individual, I used individuals of different sizes from a population to obtain estimates of allometric coefficients. Identification of dissimilarities in the allometric growth influence by using transformed data is acceptable for comparing populations (Thorpe, 1976).

Linear regression analysis, in which the measurement data were left untransformed, was then performed for variables demonstrating significant differences in allometric growth. For ease of presentation and interpretation, only the resulting slope and intercept values are reported in Table 4. Significance levels for all statistical tests were set (*a priori*) at 0.05 and probabilities are those for committing a Type I error in a two-tailed test.

RESULTS

Biochemical Comparisons

Aat1, Aat2, Acp2, Ada, Est-D, Hdp, Me, Pgm, and Sod were monomorphically expressed among all three populations I examined. Table 2 summarizes the distribution of allozymes at the 25 polymorphic loci I was able to score unambiguously.

Populations of *Discoglossus* residing to the north and to the south of the Guadalquivir River basin in Spain and those inhabiting northern Morocco are genetically well differentiated. Fifteen of 87 alleles identified among these *Discoglossus* samples are shared among all populations. Spanish *Discoglossus* residing north of the Quadalquivir River basin share 17 alleles with individuals from northern Morocco and 23 alleles with *Discoglossus* residing south of the Guadalquivir River basin in Spain. Populations inhabiting the area south of the Guadalquivir River basin share 29 alleles with *Discoglossus* inhabiting northern Morocco (Table 3).

Seventy alleles, however, differentiate between individuals of *Discoglossus* from north of the Guadalquivir River basin in Spain and those from northern Morocco, 64 alleles differentiate individuals from north of the Guadalquivir River basin and those from south of the Guadalquivir River basin in Spain, and 58 alleles differentiate individuals living to the south of the Guadalquivir River basin in Spain from those inhabiting northern Morocco (Tables 2 and 3). The distribution of these alleles contributes to a genetic distance ($\hat{D}$) of 0.74 ± 0.18 between the Spanish sample from north of the Guadalquivir River basin and the northern Moroccan samples, 0.39 ± 0.12 between Spanish samples residing to the north and to the south of the Guadalquivir

Table 2.—*Genic variation within and among samples of* Discoglossus.

		D. jeanneae	*D. galganoi*	*D. pictus*
Number of specimens		7	1	10
Mean heterozygosity per locus		0.16	0.03	0.16
Percentage of loci polymorphic		38.2	2.9	44.1
Locus and alleles				
Ab1	a	0.86	1.00	0.95
	b	0.14	0.00	0.00
	c	0.00	0.00	0.05
Ab2	a	1.00	1.00	0.00
	b	0.00	0.00	1.00
Acon	a	0.57	0.00	1.00
	b	0.29	0.00	0.00
	c	0.14	0.00	0.00
	d	0.00	1.00	0.00
Acp1	a	0.00	0.00	0.10
	b	1.00	1.00	0.90
Adh	a	1.00	1.00	0.80
	b	0.00	0.00	0.20
Ald	a	0.00	1.00	0.00
	b	0.86	0.00	1.00
	c	0.14	0.00	0.00
Ck	a	0.57	0.00	0.10
	b	0.00	0.00	0.10
	c	0.43	0.00	0.75
	d	0.00	0.00	0.05
	e	0.00	1.00	0.00
Est	a	0.00	0.00	0.20
	b	0.00	0.00	0.40
	c	0.29	0.00	0.40
	d	0.14	0.00	0.00
	e	0.57	1.00	0.00
Glud	a	0.00	1.00	0.20
	b	1.00	0.00	0.80
Gpd	a	0.00	1.00	0.00
	b	0.07	0.00	0.00
	c	0.93	0.00	0.50
	d	0.00	0.00	0.50
Gpi	a	1.00	1.00	0.90
	b	0.00	0.00	0.10
Hex	a	0.00	0.00	0.10
	b	1.00	1.00	0.00
	c	0.00	0.00	0.90
Hk1	a	1.00	1.00	0.00
	b	0.00	0.00	1.00
Hk2	a	0.00	1.00	0.00

Table 2.—*Continued.*

		D. jeanneae	*D. galganoi*	*D. pictus*
	b	1.00	0.00	0.00
	c	0.00	0.00	1.00
Icd1	a	0.00	0.00	0.10
	b	0.86	0.00	0.85
	c	0.14	0.00	0.05
	d	0.00	1.00	0.00
Icd2	a	0.00	0.00	1.00
	b	0.00	0.50	0.00
	c	1.00	0.50	0.00
La	a	0.00	0.00	0.10
	b	0.57	1.00	0.90
	c	0.43	0.00	0.00
Ldh1	a	1.00	1.00	0.00
	b	0.00	0.00	1.00
Ldh2	a	1.00	0.00	1.00
	b	0.00	1.00	0.00
Lgg	a	0.00	0.00	1.00
	b	1.00	1.00	0.00
Mdh1	a	0.14	0.00	0.00
	b	0.29	0.00	0.00
	c	0.43	0.00	0.00
	d	0.14	0.00	0.00
	e	0.00	1.00	0.60
	f	0.00	0.00	0.30
	g	0.00	0.00	0.10
Mdh2	a	0.71	0.00	0.90
	b	0.29	0.00	0.10
	c	0.00	1.00	0.00
Mpi	a	0.00	0.00	0.50
	b	0.71	1.00	0.50
	c	0.29	0.00	0.00
Pap	a	0.29	0.00	0.00
	b	0.71	1.00	0.00
	c	0.00	0.00	1.00
Pgd	a	0.86	0.00	0.50
	b	0.00	0.00	0.40
	c	0.14	0.00	0.10
	d	0.00	1.00	0.00

River basin, and 0.39 ± 0.12 between Spanish samples from south of the Guadalquivir River basin and those from northern Morocco.

Morphological Comparisons

Between sexes.—The 19 male and 8 female specimens in the sample of *D. galganoi* examined by Capula et al. (1985) do not demonstrate

Table 3.—*Number of replications of the seven possible patterns of allele distribution present among the three populations of* Discoglossus. *Patterns replicated eight times or more do not occur as a result of chance association (*$b \leq 0.05$*, see Materials and Methods) but only alleles shared between two or more populations are informative.*

D. galganoi	*D. jeanneae*	*D. pictus*	Number
X	X	X	15
	X		14
X			10
		X	24
X		X	2
X	X		8
	X	X	14

sexual dimorphism. There were no significant differences in allometry identified by the covariance analysis.

While no significant difference was found in the distribution of SUL between 14 male and 16 female *Discoglossus* from south of the Guadalquivir River basin in Spain, the allometric relationship between SUL and foot length is significantly different between the sexes of this population ($F = 6.61$, $P < 0.05$). The foot length of a female with an SUL of 45 mm (an intermediate size in the sample of adults of either sex) is approximately 95% the length of the foot of an equivalent-sized male.

Five male and six female *Discoglossus* from northern Morocco demonstrated sexual dimorphism in the allometric relationship between SUL and snout length. While no significant differences were identified between male and female SUL in these samples, the relationship between SUL and snout length is significantly different between sexes ($F = 16.39$, $P \ll 0.05$). At an SUL of 45 mm, the snout length of a female specimen is approximately 86% of the snout length of an equivalent-sized male.

Between populations.—Male specimens of *D. galganoi* differ from male *Discoglossus* from northern Morocco in the allometric growth relationship between SUL and snout ($F = 68.01$, $P \ll 0.05$), head ($F = 63.57$, $P \ll 0.05$), tibia ($F = 10.66$, $P < 0.05$), femur ($F = 16.90$, $P \ll 0.05$) and hand lengths ($F = 55.07$, $P \ll 0.05$) and in the growth relationships of SUL and head width ($F = 5.84$, $P < 0.05$) and SUL and internarial distance ($F = 8.05$, $P < 0.05$). Female specimens representing these populations differ in the allometric relationship between SUL and head ($F = 39.56$, $P \ll 0.05$) and eye ($F = 28.73$, $P \ll 0.05$) lengths.

Male specimens of *D. galganoi* differ from males from south of the Guadalquivir River basin in Spain in the allometric growth relationship

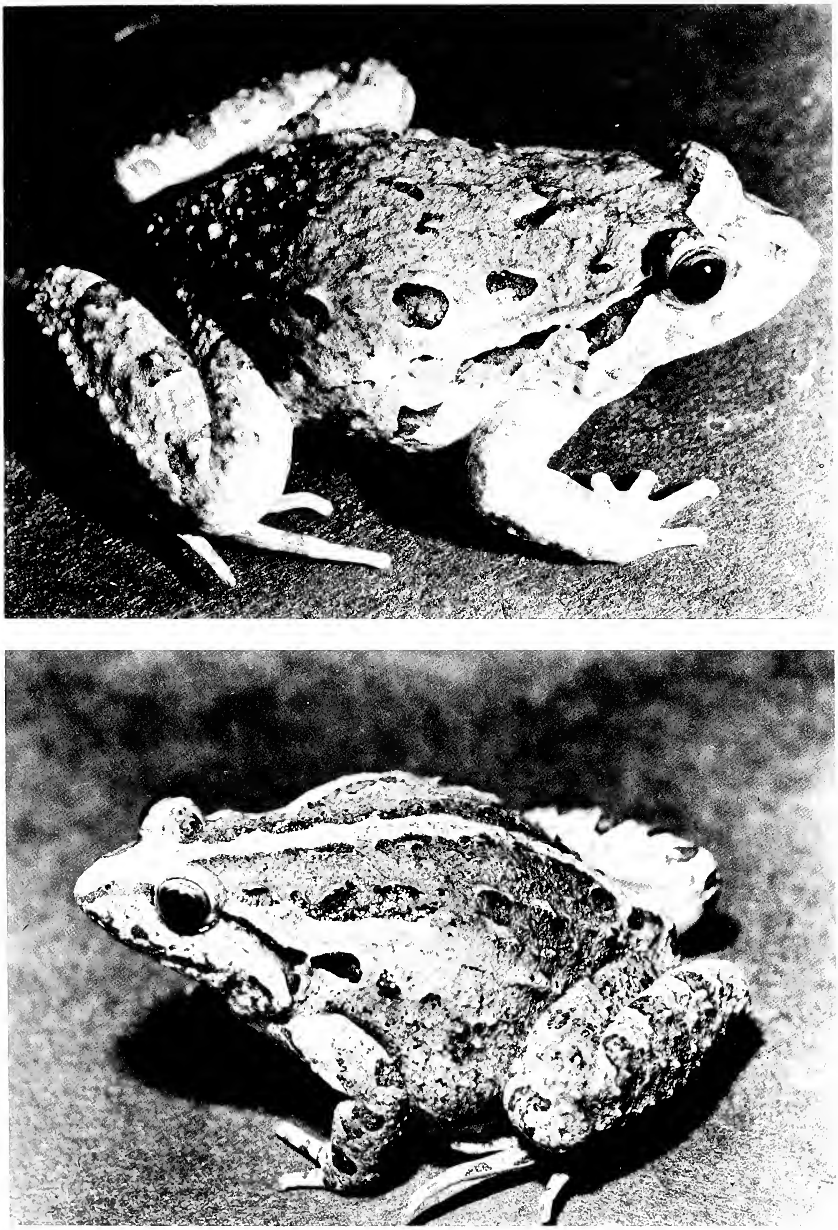

Fig. 2.—Spotted (upper) and striped (lower) color phases of *Discoglossus jeanneae.*

of SUL and snout (F = 224.33, $P \ll 0.05$), head (F = 54.76, $P \ll 0.05$), tibia (F = 11.29, $P \ll 0.05$), femur (F = 7.08, $P < 0.05$), and hand lengths (F = 45.82, $P \ll 0.05$), and in the allometric relationship between SUL and internarial distance (F = 5.63, $P < 0.05$). Female specimens representing these populations differ in the allometry between SUL and head length (F = 72.34, $P \ll 0.05$), SUL and hand length (F = 77.57, $P \ll 0.05$), and between SUL and internarial distance (F = 12.62, $P \ll 0.05$).

Male specimens from south of the Guadalquivir River basin in Spain and those from northern Morocco differ only in the allometric growth relationship between SUL and snout length (F = 16.47, $P \ll 0.05$). The allometric growth relationship between SUL and all examined morphological characters is not different in female specimens drawn from these populations.

SYSTEMATIC CONSIDERATIONS

Northern Moroccan populations.—Lanza et al. (1984) demonstrated that specimens of *Discoglossus* from near Barika, Algeria, are genetically very similar to those from Sicily, the type locality of *D. pictus* (Nei's average genetic identity = 0.93, Nei's $D = 0.07$). Although Capula et al. (1985:table 7) do not provide a table of allele frequencies with which I might directly compare results, they do list 12 loci that distinguished Algerian and Tunisian *D. pictus* from Iberian *D. galganoi.* Three of these 12 loci (Ada, Aat1, and Acp2) were found to be monomorphic among populations I compared, and seven were not considered in my study. Only two of these 12 loci (Icd2 and Ldh1) distinguished between Moroccan and Iberian populations in my study. While it is possible that not all Moroccan, Algerian, Tunisian, and Sicilian populations are conspecific, at this time it is zoogeographically and systematically conservative to consider populations of *Discoglossus* inhabiting North Africa and Sicily *D. pictus* Otth, 1837.

Iberian populations residing north of the Guadalquivir Basin.—The albumin immunological distance obtained when specimens from Villaviciosa and Arenas de San Pedro, Spain (Fig. 1A, B, respectively), were compared to those representing *D. pictus* from Tleta Tarhremt, Morocco (Fig. 1, closed triangle), was 17 units (Maxson and Szymura, 1984:249). The unbiased genetic distance (Nei's $\hat{D}$) between one individual I collected from San Martín del Pimpollar, Spain (Fig. 1C), and *D. pictus* from northern Morocco was 0.74 ± 0.18. Capula et al. (1985) reported a genetic distance (Nei's D) of 0.58 between their pooled samples representing Portugal and central Spain and those from Algeria and Tunisia.

It is apparent from genetic (Capula et al., 1985:table 9) and mor-

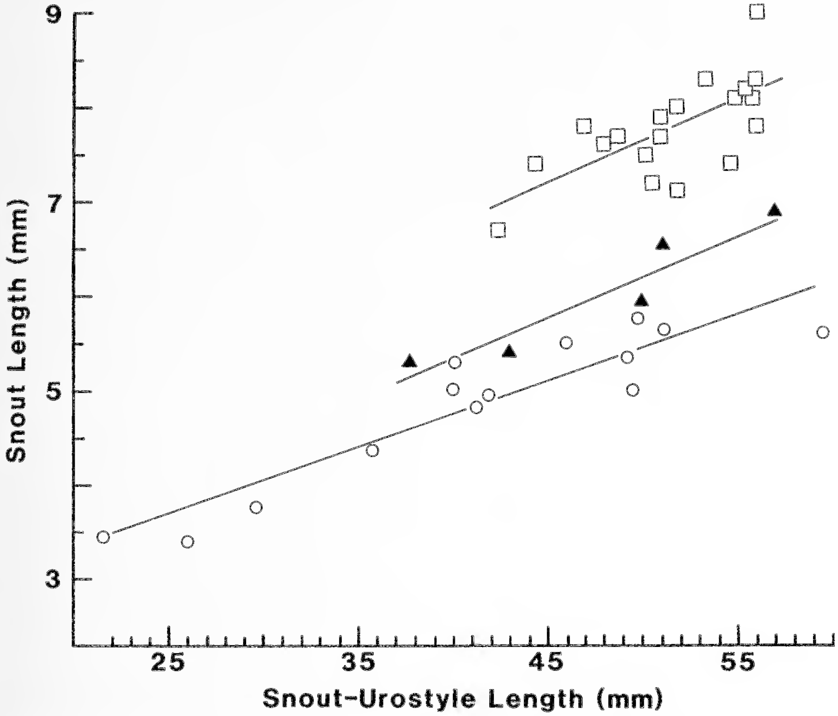

Fig. 3.—Snout length regressed on snout-urostyle length in male *Discoglossus galganoi* (squares), *D. pictus* (triangles), and *D. jeanneae* (circles). See Table 4 for regression coefficients.

phological comparisons (this study, Results) that Iberian populations of *Discoglossus* residing north of the Guadalquivir River basin are clearly differentiated from those inhabiting northern Morocco and are deserving of the species status recently ascribed to them by Capula et al. (1985). Whether or not, however, the specimens Maxson and Szymura (1984) and I examined biochemically (Fig. 1A–C) actually represent *D. galganoi* is unclear. Until data with which to further assess the taxonomic status of Iberian populations residing to the north of the Guadalquivir River basin become available, these populations are best referred to *D. galganoi* Capula et al., 1985.

Iberian populations residing south of the Guadalquivir Basin.—*Discoglossus* from south of the Guadalquivir River basin in Spain are morphologically and genetically different from both Moroccan *D. pictus* and *D. galganoi* (Tables 2, 3, and Results). I consider the extent of these differences to be representative of species level differentiation and designate the new species herewith.

Table 4.—*Estimates of slope (b) and intercept (a) obtained when measurements derived from various morphological features (y) were regressed againts snout–urostyle length (x) in* Discoglossus galganoi, D. jeanneae, *and* D. pictus. *Linear regression results are reported only for those allometric growth characteristics that differed significantly in an analysis of covariance; an analysis of variance technique (Sokal and Rohlf, 1981:471) was used to assess the hypothesis that each linear regression was significant (values of F_s and associated significance levels* [P] *for this statistical test are provided).*

	D. galganoi		*D. jeanneae*		*D. pictus*	
Statistics	Males	Females	Males	Females	Males	Females
			Head length			
b ± SE	0.24 ± 0.04	0.20 ± 0.04	0.20 ± 0.02	0.18 ± 0.03	0.16 ± 0.04	0.20 ± 0.06
a ± SE	2.40 ± 2.14	4.51 ± 1.61	2.60 ± 0.65	3.10 ± 1.26	3.77 ± 1.72	2.39 ± 2.34
F_s, P	34.97, $\ll 0.05$	31.36, $\ll 0.05$	168.67, $\ll 0.05$	45.29, $\ll 0.05$	20.86, < 0.05	12.25, $= 0.05$
			Head width			
b ± SE	0.33 ± 0.04	—	—	—	0.23 ± 0.03	—
a ± SE	0.15 ± 1.95	—	—	—	4.30 ± 1.54	—
F_s, P	74.52, $\ll 0.05$	—	—	—	49.79, < 0.05	—
			Snout length			
b ± SE	0.09 ± 0.02	—	0.07 ± 0.01	—	0.09 ± 0.02	—
a ± SE	3.14 ± 1.15	—	1.90 ± 0.35	—	1.86 ± 0.81	—
F_s, P	16.26, $\ll 0.05$	—	75.05, $\ll 0.05$	—	26.84, < 0.05	—
			Internarial distance			
b ± SE	0.05 ± 0.01	0.04 ± 0.01	$0.05 \pm 4.41 \times 10^{-3}$	0.06 ± 0.01	0.04 ± 0.01	—
a ± SE	0.55 ± 0.59	0.76 ± 0.43	0.36 ± 0.19	0.42 ± 0.44	0.97 ± 0.41	—
F_s, P	17.46, $\ll 0.05$	20.43, < 0.05	158.89, $\ll 0.05$	36.11, $\ll 0.05$	26.70, < 0.05	—

Table 4.—*Continued.*

Statistics	*D. galganoi*		*D. jeanneae*		*D. pictus*	
	Males	Females	Males	Females	Males	Females
			Eye length			
b ± SE	—	0.08 ± 0.01	—	—	—	0.07 ± 0.01
a ± SE	—	0.59 ± 0.69	—	—	—	0.15 ± 0.53
F_s, P	—	27.53, $\ll 0.05$	—	—	—	37.86, <0.05
			Tibia length			
b ± SE	0.34 ± 0.07	—	0.40 ± 0.04	—	0.29 ± 0.04	—
a ± SE	9.96 ± 3.58	—	4.88 ± 1.52	—	10.50 ± 1.76	—
F_s, P	24.26, $\ll 0.05$	—	126.55, $\ll 0.05$	—	63.62, <0.05	—
			Femur length			
b ± SE	0.29 ± 0.08	—	0.41 ± 0.02	—	0.18 ± 0.04	—
a ± SE	9.65 ± 4.39	—	2.39 ± 0.84	—	12.40 ± 2.00	—
F_s, P	11.72, $\ll 0.05$	—	428.16, $\ll 0.05$	—	18.46, <0.05	—
			Hand length			
b ± SE	0.10 ± 0.02	0.10 ± 0.02	0.13 ± 0.01	0.11 ± 0.02	0.10 ± 0.02	—
a ± SE	2.72 ± 1.15	2.72 ± 0.96	−0.09 ± 0.33	0.81 ± 0.71	1.25 ± 0.83	—
F_s, P	19.80, $\ll 0.05$	21.59, <0.05	299.02, $\ll 0.05$	51.28, $\ll 0.05$	36.64, <0.05	—

Discoglossus jeanneae, new species

(Fig. 2)

Holotype.—Carnegie Museum of Natural History (CM) 54657, an adult female, along highway C-440, 15 km ESE Alcalá de los Gazules, Cádiz Province, Spain, 6 April 1971, Stephen D. Busack.

Paratypes (21, all from Cádiz Province, Spain).—CM 52126, female, along highway C-440, 12.9 km ESE Alcalá de los Gazules, 18 October 1969; CM 52128–52129, two females, along highway C-440, 13.8 km WNW Los Barrios, 18 October 1969; CM 52475–52476, two males, along highway C-440, 6.6 km NW Algeciras, 10 January 1970; CM 53087, male, along highway C-440, between 7.6 and 7.7 km NW Los Barrios, 12 March 1970; CM 53119, male, along highway CA-221, 21.2 km ENE Facinas, 10 April 1970; CM 53324, male, along highway C-440, 9.01 km NW Los Barrios, 18 June 1970; CM 53884a–d, 4 females, along highway C-440, between 4.0 km WNW Casas del Castaño and 5.0 km WNW Los Barrios, 8 October 1970; CM 54244, female, along highway C-440, between 19 km ESE Alcalá de los Gazules and 1 km WNW Casas del Castaño, 18 November 1970; CM 54581, female, and CM 54582, male, along highway C-440, between 3.7 and 11.4 km WNW Los Barrios, 19 March 1971; CM 54608–54610, three females, along highway CA-P-2112, between 12.6 and 14.2 km NNE Benalup de Sidonia, 2 April 1971; CM 54704, male, along highway C-440, 0.3 km WNW Casas del Castaño, 16 May 1971; CM 55742–55743, two males, and CM 55744, female, along highway C-440, between 18.4 and 22.7 km WNW Los Barrios, 15 January 1972.

Diagnosis.—*Discoglossus jeanneae* is similar in coloration and pattern to *D. galganoi* and *D. pictus,* but is distinguished from them by biochemical and morphological characters. *Discoglossus jeanneae* and *D. pictus* share no alleles at six electrophoretic loci (Ab2, Hk1, Hk2, Icd2, Ldh1, and Lgg), *D. jeanneae* and *D. galganoi* share no alleles at three loci (Glud, Hk2, and Ldh2).

Male *D. jeanneae* have a shorter snout than males of either *D. pictus* or *D. galganoi* of similar SUL (Fig. 3, Table 4). Male *D. jeanneae* also have a greater head length, a shorter internarial distance, and shorter tibia, femur, and hand lengths than male *D. galganoi* of comparable SUL (Table 4). Female *D. jeanneae* have a shorter head and hand lengths, and shorter internarial distances, than *D. galganoi* of similar SUL (Table 4).

Description of holotype.—An adult female with the following measurements (mm): SUL 47.9, snout length 5.1, head length 10.8, head width 15.1, horizontal diameter of eye 4.1, interorbital distance 7.5, internarial distance 3.0, tibia length 23.4, femur length 21.7, hand length 5.9, foot length 15.1. Choanae oblong and relatively large; prevomerine dentigerous processes in two nearly straight series, each with 11 teeth, located just behind the choanae and separated by a distance less than half that of the diameter of a choana. Tongue roundish, thick, scarcely free behind. Nostrils dorsal, much closer to the tip of the snout than to the eye, horizontal diameter of the eye slightly greater than the distance from the naris to the eye. Tympanum indistinct. Fingers rel-

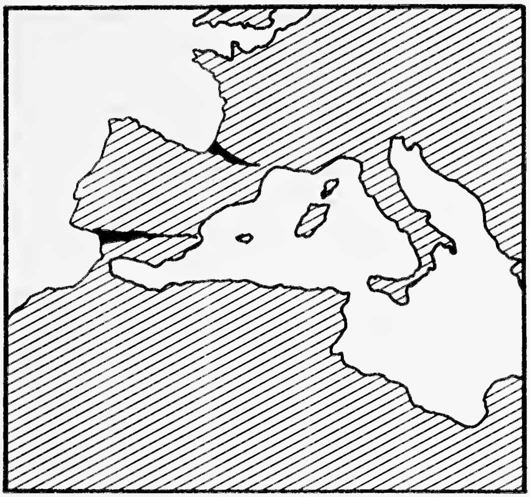

Fig. 4.—A Lower Miocene reconstruction of the Iberian peninsula and North Africa; heavily blackened areas indicate marine incursions (after Illies, 1975).

atively short, unwebbed; III, IV, II, I in order of decreasing length. Three prominent palmar tubercles, the largest at the base of finger IV, the next largest at the base of finger I, and the smallest in the center. Toes slender, very slightly webbed, IV, III, V, II, I in order of decreasing length. No subarticular tubercles, no tarsal fold; small ellipsoidal metatarsal tubercle. Heels overlap slightly when femora are held at right angles to the body axis. Skin of dorsum with several irregularly positioned diminutive, pustules, skin of venter smooth.

Coloration of holotype (*in alcohol*).—The ground color of the top of the head is citrine drab from mid-eye to snout. Beginning at mid-eye, and continuing to just below the area of front limb insertion, a dark olive patch reminiscent of a large italicized "X" appears on a ground color of a lighter shade of dark olive. A prominent (6.5 mm in length) and elongated teardrop-shaped patch of chaetura drab angles ventroposteriorly from the posterior corner of the eye. This patch, and the ground color of the "X," are edged in citrine drab. Small faint patches shaped as triangles oriented with the base down appear along the upper lip; a light stripe extends from the front corner of the eye through the nostril.

Colored as the "X," a lightly-horned, heart-shaped, shield extends over the central dorsum. The upper half of the shield is edged in citrine drab on a ground color of lighter dark olive; intense asymmetrical patches of dark olive line the lower "V" and the upper and outer curves of this shield. A broken dorsolateral line of citrine drab is present.

In lateral view, an ovoid dark olive blotch appears below the dorsolateral line and just above the area of insertion of the front limb. The interaxillary region is light deep olive blending into dark olive buff towards the venter; the dark olive buff blends into buffy brown in the region of the groin. The venter is deep olive buff and unpatterned.

The upper surfaces of the hind legs are clove brown with irregular transverse blotches of fuscous black; upper surfaces of the front legs are citrine drab with three deep olive transverse blotches.

Pattern polymorphism (*in alcohol*).—Spotted individuals are most common, striped specimens are less common (Fig. 2), and occasionally an unpatterned *D. jeanneae* is found. Unstriped individuals exhibit either a complete or broken anteriodorsal "X." All have a teardrop eye patch, triangular blotches on the upper labium, and, in varying degrees of distinction, a stripe extending from the front corner of the eye through the nostril. A broken dorsolateral line of citrine drab also appears, at times faint, at times pronounced, in all unstriped individuals.

Unstriped individuals have a ground color which varies from citrine drab to light dark olive to fuscous. Coloration on the posterior portion of the dorsum varies from a pattern in which prominent spots are connected to suggest a shield-like shape to a simple pattern of widely spaced and barely discernable spots. Ventral coloration is generally unpatterned deep olive buff; some specimens, however, demonstrate olive or clove brown pigmentation of varying intensity on the lower jaw and upper pectoral region.

In the striped paratype (CM 53119), the "X" and shield symmetry are broken by a medial stripe of citrine drab. The resultant halves of the "X" and shield merge on either side of the medial stripe to form two solid regions of dark olive, one on the right, one on the left, and each between the medial stripe and the dorsolateral region. The small ovoid blotch found below the dorsolateral ridge and above the area of limb insertion in spotted individuals is continuous with the teardrop eye patch and forms a single blotch in this specimen. The eye-nostril stripes and upper labial triangles are pronounced and, along the dorsolateral region, there is a prominent citrine drab stripe extending from the eye to the groin. The outer edge of this stripe exhibits the darker coloration reminiscent of the dark olive upper and outer curves of the heart-shaped shield described for the holotype.

Etymology.—Jeanne A. Visnaw accompanied me during four months of field work in Spain and Morocco during 1982; in spite of what she learned during her first trip abroad, Jeanne again accompanied me in 1983. While the husbands and wives of graduate students often contribute substantially to the success of their spouses, few routinely sacrifice as much or give as unselfishly as my wife has. I dedicate this new Spanish frog to her.

DISCUSSION

Physiogeographic changes have been extensive in this area of the western Mediterranean region in the last few million years. The Betic Cordillera (an alpine ridge located on the Spanish Meseta between Cádiz in the west and Alicante in the east) was subjected to folding and extensively restructured during Miocene-Pliocene. Lower Miocene Atlantic waters flowed to the Mediterranean through what is now the Guadalquivir River basin (Figs. 4–5; Berggren and Van Couvering, 1974; Illies, 1975; Le Pichon et al., 1972), Neogene sedimentation filled the younger, western portion (Córdoba-Sevilla) of the Guadalquivir Basin and the northern portion began to emerge from considerable depth at the end of the Miocene (Tjalsma, 1971:120–125), and Pliocene events allowed Atlantic waters to form the Strait of Gibraltar (Fernix et al., 1967; Hsü, 1983; and Mantura, 1977).

Geologic events such as these have a direct effect on sexually reproducing organisms. The rate at which genetic divergence accumulates between populations is believed to be a function of the time those populations have been separated (Zuckerkandl and Pauling, 1965). If this is true, the more genetically differentiated two populations of terrestrial anurans are, the longer they have been separated. Of the three patterns of allele distribution that are phylogenetically informative among these three populations of *Discoglossus, D. galganoi* and Moroccan *D. pictus* share only two, *D. galganoi* and *D. jeanneae* share 8, and *D. jeanneae* and Moroccan *D. pictus* share 14 (Table 3). If unbiased genetic distance units ($\hat{D}$) are considered, Moroccan *D. pictus* are separated from *D. galganoi* by 0.74 ± 0.18 units and *D. jeanneae* is separated from both *D. galganoi* and Moroccan *D. pictus* by 0.39 ± 0.12 units (Fig. 5). *Discoglossus galganoi* and Moroccan *D. pictus* are probably not sister species.

Males of *D. galganoi* are more morphologically differentiated from males of *D. jeanneae* and males of *D. pictus* than are female *D. galganoi* from female *D. jeanneae* or *D. pictus.* The allometric growth relationship between SUL and 10 morphological characters were compared among males and females of these three species and male *D. galganoi* differ from Moroccan *D. pictus* in seven such relationships, females differ in only one. Male *D. galganoi* differ from *D. jeanneae* in six allometric relationships, females differ in three. Male *D. jeanneae* appear to be little changed from Moroccan *D. pictus,* however, as only one allometric relationship is clearly different; female *D. jeanneae,* on the other hand, demonstrate no differences among any of the 10 allometric growth relationships when compared with female *D. pictus.*

The fossil record of *Discoglossus* is limited. Middle Miocene remains from Beni-Mellal, Morocco, referred to the genus *Discoglossus* by Vergnaud-Grazzini (1966), have been reassigned to the extinct discoglossid

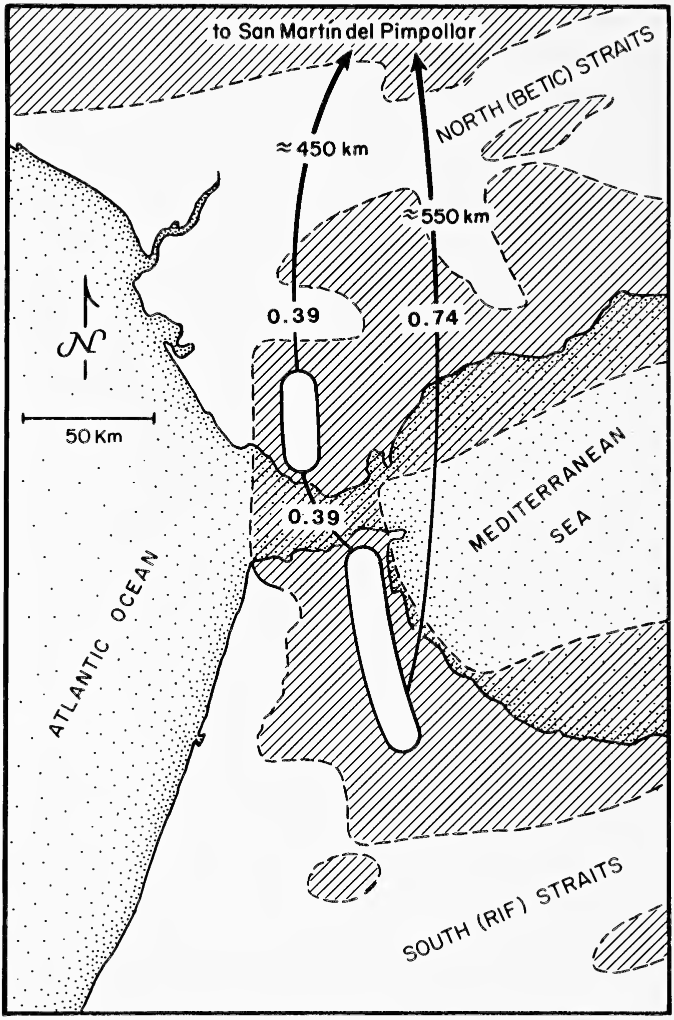

Fig. 5.—A mid-Miocene reconstruction of the Gibraltar area (after Fernix et al., 1967). Shaded areas represent emergent land; geographic and unbiased genetic distances between sampled populations of *Discoglossus* are indicated.

genus *Latonia* by Sanchiz and Alcover (*in litt.*); as a result, fossil representatives of *Discoglossus* are unknown in North Africa. The Lower Miocene *Discoglossus troschelii* from Rott, Germany, was considered conspecific with *D. pictus* (=? *galganoi*) from Spain (Boulenger, 1891). Neogene specimens from Escobosa de Calatañazor (Soria), Venta del Moro (Valencia), and Alcoy (Alicante), Pliocene samples from El Arquillo II (Teruel), and mid-Pleistocene specimens from Arganda (Madrid), attest to the age, persistence without morphological change, and widespread nature of *D. pictus* (=? *galganoi*) throughout prehistoric Iberia (Sanchiz, 1977*a*, 1977*b*).

The electrophoretic and morphological data coincide well with one evolutionary scenario that may be inferred from the geographic history of the region. The ancestral stock of *D. galganoi,* which once populated the Spanish Meseta, and that of *D. pictus-D. jeanneae,* which once populated an area now known as southern Spain and northern Morocco, suffered temporal and climatic separation dating from the Lower Miocene. The Pliocene formation of the Strait of Gibraltar then divided ancestral *D. pictus-D. jeanneae* populations into two populations which evolved to become *D. jeanneae* and *D. pictus.*

Additional research is clearly necessary before we can fully understand the evolutionary history, distributional limits, and taxonomy of Iberian and North African *Discoglossus.* Until additional data becomes available, however, conservative limits for the distribution of *D. jeanneae* may be drawn. These would include the northern edge of the Guadalquivir River basin (Fig. 1, dotted line), regions inundated during Miocene flooding that currently lay to the east of the headwaters of the Guadalquivir River (Fig. 1, dotted line with question marks), and the shores of the Atlantic Ocean and the Strait of Gibraltar.

ACKNOWLEDGMENTS

I wish to extend my gratitude to Benedetto Lanza, who provided me with a manuscript copy of the description of *D. galganoi,* and to D. B. Wake and M. M. Frelow of the Museum of Vertebrate Zoology, University of California, Berkeley, who provided facilities, financial support, and assistance during the electrophoretic analysis. L. R. Maxson graciously provided immunological data and a copy of her and Szymura's unpublished manuscript, C. J. McCoy and E. J. Censky generously provided sustenance and lodging during a visit to Pittsburgh, D. B. Wake, L. R. Maxson, and T. Uzzell reviewed and improved earlier versions of the manuscript, Lezlie Skeetz assisted in translating the patterns and colors of *D. jeanneae* into words, G. M. Christman prepared Figure 5, and Alfredo Salvador assisted with a portion of the field work in Spain. Travel funds were provided by a National Science Foundation dissertation improvement grant (DEB 81-20868) and a National Geographic Society research grant (2600-83). Specimens in Spain were collected under authority of permits 888 (1982) and 22061 (1983) issued by the Instituto Nacional para la Conservación de la Naturaleza, Madrid. Collecting in Morocco was authorized by letter from the Embassy of Morocco to the United States, Mohamed Benjelloun, economic counsellor.

SPECIMENS EXAMINED

D. jeanneae.—(Electrophoretic Analysis): SDB 1556, 1691, 1905, 1906, 1930, 1949, 1954, and 1989 at the Universidad de León, Spain. (Morphological Analysis): Carnegie Museum of Natural History (CM) 52125–52129, 52475–52477, 52537, 52626, 53087–53088, 53119–53120, 53324, 53884 (4 specimens), 54244, 54581–54582, 54608–54610, 54657, 54704, and 55742–55743.

D. galganoi.—(Electrophoretic Analysis): SDB 1691 at the Universidad de León.

D. pictus.—(Electrophoretic Analysis): SDB 1773 (2 specimens) and SDB 1774 (3 specimens) at the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); MVZ 186124–186125 and 186132–186134. (Morphological Analysis): MVZ 186124–186134.

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YANOMAMA MATERIAL CULTURE IN THE CARNEGIE MUSEUM OF NATURAL HISTORY. PART II. WEARING APPAREL AND FESTIVAL ARTIFACTS

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ABSTRACT

The Carnegie Museum of Natural History has one of the largest, most inclusive, and best documented collections of Yanomama material culture in the world. The collection, consisting of two accessions comprising 572 specimens, spans a 5 year period from 1979 to 1984. This corpus of material documents not only traditional Yanomama material culture, but also shows the changes it has undergone due to the introduction of Western goods and materials. Part I dealt with material culture categories related to Food Procurement and Household Articles (Couture-Brunette, 1985). Part II deals with Wearing Apparel and Festival Artifacts; and Part III will deal with Foreign Influence and Miscellaneous Constructions.

INTRODUCTION

The Yanomama Indians inhabit an area of approximately 30,000 (Smole, 1976:3) to 100,000 (Migliazza, 1972:20) square miles in northern Brazil and southern Venezuela. They are one of the largest Indian populations in the Amazonian rain forest. In spite of their large population, they have been able to remain isolated and unacculturated until the present due to their settlement locations off major waterways in the Guyana Shield area. There is no agreement on the total number of Yanomama. While Chagnon (1974:1) estimates a total population

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of 10,000, Saffirio (1985:36) feels that 16,400 in 320 villages is closer to the true number.

All Yanomama speak four mutually intelligible languages and several dialects. The group has been called by several names; terms such as "Waica," "Xiriana," "Shamatari," and "Yanoama," have all been used to designate this family of languages. "Yanomamo," "Yanam," "Sanuma," and "Yanomam" actually denote only one dialect or language within the larger group. Thus "Yanomama" is used to refer to the entire family of languages (Migliazza, 1972:33). The Catrimani River Yanomama of Brazil, from whom the Carnegie Museum of Natural History collections have come, belong to the linguistic group "Yanomam." They inhabit areas of the Federal Territory of Roraima and the State of Amazonas.

Since the construction in the mid 1970s of Brazilian Highway BR 210, the Perimetral Norte, deep into Yanomama territory in Brazil, acculturation has been proceeding at a rapid rate. The introduction of Western goods, beliefs, and diseases has brought about profound and permanent changes in the Yanomama lifestyle (Saffirio, 1980; Saffirio et al., 1983). Like many South American groups before them the Yanomama are substituting Western material culture in replacement of their traditional technology. This loss of native crafts is documented in the Carnegie Museum of Natural History collections.

Giovanni Saffirio, a member of the Consolata Society for Foreign Missions, arrived at a mission post on the Catrimani River in 1968. He was the collector of Yanomama material culture for Carnegie Museum of Natural History. He has recently been awarded his Ph.D. in the Department of Anthropology at the University of Pittsburgh, and has since returned to the Catrimani Mission.

Collection I, accession number 32703, was made during 1979–80, while collection II, accession number 32735, took place in 1984. Every effort was made to secure as complete a representation of Yanomama material culture as possible, with a wide range in variation among specimens. As a result, the Carnegie Museum of Natural History has one of the largest, best documented, and most inclusive collections in the world.

The Catrimani River Yanomama Indians of South America, and the Carnegie Museum of Natural History collections of Yanomama material culture, have been presented in more detail in the Part I article (Couture-Brunette, 1985). Part II covers the Wearing Apparel and Festival Artifacts segment of the collection.

The classification of an artifact as either an item of wearing apparel or a festival artifact is based on the function of the artifact, regardless of its method of construction. Some specimens which served the same

Fig. 1.—Women's aprons, an item of everyday apparel. Accession 32735.

purpose were constructed differently based on their use as an item of everyday wear or as a festival artifact. In these cases the entire group of specimens was placed in the category where it was most often used. In this manner, separation of like artifacts was avoided. Two examples, one from each of the Festival Artifacts and Wearing Apparel categories, will illustrate this placement. Women's aprons are worn every day, but certain aprons in the Carnegie Museum of Natural History collection are made specifically for festivals. All aprons were placed into the Wearing Apparel category in order to discuss the "apron" group as a whole. Highly decorated aprons which were intended for festival usage are separately indicated.

It proved impossible to explain fully all manufacturing terminology and methods of the many different materials (basketry, cordage, knots) used in construction of the specimens. Standard references were used–Emery (1980) when discussing the cordage, Adovasio (1977) for the basketry, and Shaw (1972) for knot descriptions.

Numbers for the types of cordage and letters for the knots are used throughout the analysis (Couture-Brunette, 1985:tables 1 and 2). All knots are illustrated (Couture-Brunette, 1985:fig. 4). "S" and "Z" twist in cordage is also illustrated (Couture-Brunette, 1985:fig. 5).

Some of the cordage consists of a number of spun and plied yarns which were combined by twisting. Rather than list these varying numbers of yarns as separate constructions, they were combined in one cordage type (see Couture-Brunette, 1985:table 1), with the number of plies referred to in parentheses after the cordage type number. For example, cordage type #12(4) consists of four pieces of 2 ply s spin Z twist yarns, all combined in an S twist. Similarly, cordage type #13(4) is composed of four pieces of 3 ply s spin Z twist yarns, combined in an S twist. Cordage types #5 and #6, as well as types #11 through #15, all consist of varying numbers of plies, and will be used with parenthetical numbers indicative of these.

All Yanomama words in the text are set in italics. Spelling follows Saffirio (1980, 1985). Due to the great number of Yanomama languages and dialects, these words are specific to the Catrimani River villages only.

WEARING APPAREL

Men and women do not wear an abundance of clothing. The only item which men wear every day is a string around the waist, to which they tie their penis foreskin. Occasionally men will also wear a "belt" of native cotton. Women wear cotton "aprons" which consist of a thick belt in the back with a short fringe in the front.

Both men and women pierce their ears. Women also pierce the center and corners of their lower lip, and the nasal septum. Everyday "jewelry" consists of straws worn in the lip holes, and straws or bunches of grass in the nose and ears. Feather earrings are worn by both men and women, usually during festivals.

Traditionally, necklaces are made from seeds, shells, feathers, and other animal parts strung on *yamaasik* fiber cordage or cotton string. Only men wear necklaces made from animal parts, although women utilize feathers and shells in earrings, necklaces, and aprons.

Many men and women have begun to wear Western shorts and T shirts since the arrival of Westerners on a frequent basis on Brazilian Highway BR 210. Young men no longer pierce their ears, and women near the highway do not pierce their lips or nose (Saffirio, 1980; Saffirio et al., 1983). Increasing numbers of necklaces and earrings are made from trade beads and scrap metal acquired from Westerners.

Women's Clothing

"Aprons" (Figs. 1–2), which are worn every day, are a sign of a woman's modesty. They are made by women from beginning to end; the cotton is spun and the cordage is plied and twisted by them. Women also wear armbands made from flowers, grasses, or cotton.

*Aprons (*pesimak*).*—For analytical purposes, the elements of the apron

Fig. 2.—Beaded woman's apron, CMNH number 32703-12. This would be worn during a festival.

were divided into three separate constructions—belt, fringe, and cord. The "belt" is the back portion of the apron. It is constructed in the same manner as the cotton hammock (Couture-Brunette 1985: figs. 28, 29). Stakes are placed in the ground the necessary distance apart, and one continuous strand of cotton yarn is wrapped back and forth. The ends are then tied with a cotton cord, and the stakes are removed. Belts contain approximately 150 warp strands. They average twice the length of the front portion of the apron: the "fringe." This is constructed by folding short pieces of cordage in half over a length of cotton cord. The pieces are then twined tightly with cotton or *yamaasik* string just below the cord. One end of the fringe cord is tied permanently to the belt. The term "cord" denotes both the cord over which the fringe is folded and twined, and the cord which ties the two ends of the belt together. In most cases these two pieces of cordage are not the same, differing usually in the number of plies contained within the twisted rope.

Decorative seeds, beads, shells, or feathers are occasionally tied to each end of the fringe. The entire apron is sometimes dyed with *nara* (a reddish dye) in shades of brown, yellow, red, or orange.

Table 1.—*Yanomama women's aprons in the collections of Carnegie Museum of Natural History.*

Accession number	Cordage			Knots	Twining		Length (cm)	
	Cord	Belt	Fringe		Belt	Fringe	Belt	Fringe
32703								
-12	#12 (5)	#9	#10	A(2), C, G, H	S slant	none	45.6	27.4
-13	#13 (3, 4)	#9	#13 (2)	A(2), C	none	Z slant	33.0	16.5
-14A	#13 (7)	#14 (4)	#11 (3)	J(4), A(2), C	S slant	S slant	40.2	17.7
-14B	#13 (7, 8)	#9	#13 (2)	A(8), C	none	S slant	41.9	18.7
-14C	#20; 13 (6)	#9	#13 (2)	A(8), C, H(5)	none	Z slant	50.3	20.6
-15A	#13 (7, 8)	#9	#13 (2)	A(8), F	none	S slant	44.4	25.4
-15B	#13 (7, 8)	#9	#13 (2)	A(8), F	S slant	S slant	48.5	22.4
-44A	#13 (4)	#9	#13 (2)	A(6), C	none	S slant	31.4	18.1
-44B	#13 (11)	#9	#13 (2)	A(7), C	none	S slant	47.2	26.4
-44C	#13 (10)	#9	#13 (2)	A(6), C	none	S slant	47.0	21.4
-44D	#15 (3)	#9	#13 (2)	A(7), C	none	Z slant	50.0	26.0
-44E	#13 (5, 6)	#9	#13 (2)	A(4), C	none	S slant	47.0	25.5
-44F	5 strand sennit; #13 (4)	#9	#13 (2)	A(4), J, C	none	Z slant	42.6	19.4
-44G	#13 (5, 6, 8, 10)	#9	#13 (2)	A(3), C	S slant	S slant	42.4	30.0
-44H	#13 (19, 21, 23)	#9	#13 (2)	A(6), E, C	S slant	S slant	51.0	26.5
-44I	#13 (2); 14 (2); 15	#9	#13 (2)	A(3), C, H(2)	none	S slant	39.4	10.7
-44J	#13 (4)	#9	#13 (2)	A(7), C	none	S slant	25.8	18.9
-44K	#13 (6, 7, 12)	#9	#13 (2)	A(7), C, H	none	S slant & plaiting	46.3	22.2
-44L	#13 (7); 11 (4)	#7	#13 (2)	A, C, G(2)	none	Z slant	28.4	19.4
-44M	#11 (6); 13 (3)	#9	#13 (2)	A(6), C	S slant	S slant	40.4	15.8
-44N*	#13 (2)	#11 (3)	#14 (2)		Z slant	S slant	35.5	16.5
-44O	#13 (11); 15 (7)	#7; 9; 10	#15 (2)	A, C, E	S slant	S slant	47.6	25.6
-44P	#13 (6)	#9	#13 (2)	A(7), C	Z slant	S slant	51.2	21.6

Table 1.—*Continued.*

Accession number	Cordage			Knots	Twining		Length (cm)	
	Cord	Belt	Fringe		Belt	Fringe	Belt	Fringe
-44Q	#13 (3, 7)	#9	#13 (2)	A(6), C	S slant	S slant	42.7	15.5
-44R	#13 (10)	#9	#13 (2)	A(6), C	S slant	S slant	41.2	25.5
-44S	#13 (5, 9)	#9	#13 (2)	A(3), E	Z slant	Z slant	44.0	16.9
-44T	#13 (4)	#9	#13 (2)	A(3), C, E	none	S slant	36.1	14.6
-44U	#13 (7)	#9	#13 (2)	A(6), C, J	S slant	S slant	40.5	19.2
32735								
-197	#13 (3, 5)	#9	#13 (2)	A(4), C	S slant	S slant	44.8	25.0
-236	#13 (5); 15 (2)	#9	#13 (2)	A(8), C, G	none	S slant	39.0	19.0
-237	#13 (11)	#9	#13 (2)	A(9), C	none	S slant	46.5	27.5
-288	#13 (4, 5)	#9	#13 (2)	A(8), F	none	S slant	50.4	19.9
-289	#13 (5)	#9	#13 (2)	A(5), C, G	none	S slant	47.5	22.7
-290	#13 (4, 5)	#9	#13 (2)	A(2), C	S slant	S slant	55.1	22.9
-291	#13 (3, 5)	#9	#13 (2)	A(7), C, E	S slant	Z slant	26.9	12.5
-292†	#13 (8, 13)	#9	#13 (2)	A(8), C, F, G	S slant	S slant	47.2	21.4
-293	#3; 13 (4)	#9	curassow feathers	A(3), E, J, G	S slant	stitching	32.5	18.0
-294	#13 (4)	#7; 9	#13 (2)	A(9), C	S slant	S slant	36.6	20.3
-295	#13 (9, 33)	#9	#13 (2)	A(3), C, J(4)	S slant	S slant	50.2	20.6
-296	#13 (10); 14 (4)	#9	#14 (2)	A(2), C, J(6)	none	S slant	47.2	20.4
-297	#13 (4, 6)	#9	#13 (2)	A, H(13), G	S slant	S slant	51.0	24.4
-298	#13 (5); 16	#7; 9	#13 (2)	A(4), C, J(3), G	Z slant	S slant	47.9	24.8
-299	#13 (8, 10)	#8	#13 (2)	A(4), C, E, J(2)	S slant	S slant	50.1	23.9
-300	#13 (6, 8)	#7	#13 (2)	A(4), E, J(2)	none	S slant	42.9	23.9

* Commercial 18 strand braided rope.

† Two halves of fringe made by two people (?); cordage and decoration are both different.

The aprons are fairly standardized in construction, although some cordage variation is apparent in Table 1. The belt cordage is the most consistent element in all aprons. Of the 27 specimens in collection 32703, 24 of them (89%) used cordage type #9 for the belt, either alone or in combination with another type. Cordage types #10, #11(3), and #14(4) were each used on one belt, and type #7 (in combination with type #9) was used on two. Fourteen of the 16 aprons from the 32735 collection (87.5%) used cordage type #9 on the belt. Two belts used a combination of cordage types #9 and #7, and one belt used type #8.

Twelve of the collection I belts have occasional rows of twining to hold the warp yarns together. Of these belts, 75% of the twining is S slant and 25% is Z slant (Couture-Brunette, 1985:fig. 15). Ten of the collection II belts have rows of twining, 90% S slant and 10% Z slant. This mixture of S and Z slant twining is interesting in view of the fact that 100% of the basketry twining is S slant. Stitch slant in twining is a recognizable attribute, which is standardized over a cultural area (Adovasio, 1977:30). It is unusual to find this variation in the aprons, which utilize twining only incidentally, and not in the twined basketry. There, the greater number of specimens and the greater amounts of twining would make some variation more understandable.

The cordage used on the fringe is generally the same cordage present on the belt, but is doubled back on itself and re-twisted. For example, 2 ply s spin Z twist cotton cordage (type #9), the most common belt cordage, is doubled and S twisted to produce the 2 ply s spin z plied S twisted cordage of type #13(2), the most common fringe cordage. This cordage is present on 24 of the 27 collection I aprons and 14 of the 16 collection II aprons.

The twining which secured the pieces of fringe to the cord is S slant on 78% of the 32703 aprons and Z slant on 22%. Of the 32735 fringes, 87.5% of the aprons have S slant twining, and one each are Z slant and stitched.

The most interesting fact about the twining on both belts and fringes is the fact that S slant twining on one is often paired with Z slant twining on the other. This can also be seen on Table 1, where eight of the 32703 aprons, representing 67% of the belts which have twining, pair S slant twining on the belt with S slant twining on the fringe. One apron exhibits Z slant twining on both belt and fringe, while two of the aprons, 17% of the belts which have twining, combine Z slant twining on the belt with S slant twining on the fringe. The same is true of the 32735 aprons; of the 10 belts with twining, 70% of them have S slant twining on both belt and fringe, 10% pair S slant on the belt with Z slant on the fringe, and 10% pair Z slant on the belt with S slant on the fringe. One of the aprons utilizes S slant twining on the belt and stitching on the fringe. These facts suggest that belts and fringes are made by different women, given the standardization of stitch slant in twining which was discussed earlier. This deduction was later confirmed by the collector (Saffirio, personal communication).

The cords, which tie the ends of the belt and serve as the "backbone" to the fringe, are different from one another on 16 of the collection I aprons (59%) and 13 of the collection II aprons (81%). These differences are generally exhibited in the number of plies contained in the cord; if this variance is regarded as a function of cord diameter they are as standardized as the other apron elements. Cordage type #13(variable number of plies) is used on 25 of the 27 collection I aprons in at least one of the two possible places (belt or fringe) and on all of the collection II aprons on either the belt or fringe. The number of s spin Z twist plies used in cordage type #13 was widely variable, with four to eight the most common amount. Of the 32703 aprons, cordage type #13 with six to eight plies was the most popular, whereas on the 32735 aprons four and five plies were more often used. One apron in the 32703 accession used a five strand sennit cord and another exhibited a commercially braided cord. One of the 32735 aprons used cord made from *yamaasik* fiber.

Knot type "A" was the most popular knot present on the aprons. Nearly all of the cords were finished off with this knot on each string end. Knot type "C," the second most popular knot, was used to attach the fringe to the belt on 23 of the 27 collection I aprons and 12 of the 16 collection II aprons. The other knots present on the aprons were generally used to attach decorative elements to the fringe. Occasionally the fringe had additional pieces of cordage attached to the main cord with knot type "H," the lark's head.

Taking all these facts into consideration, the "standard" apron consists of cordage type #9 on the belt, cordage type #13(2) on the fringe, and cordage type #13(variable number of plies) making up the cord. Twenty-two of the 27 aprons in collection I, 81%, are standard. The percentage was even higher for the 32735 aprons, where 14 of the 16 aprons, 87.5%, are standard.

The two accessions differ more in their mode of decoration than in their method of construction. These decorative differences between collections I and II are a reflection of collection bias; the earlier 32703 accession contains more aprons which were worn every day, while many festival aprons were collected for the later 32735 accession.

Only four specimens from collection I have decorative accessories added to the apron. Two aprons (32703-44E and -440) have shells strung on cotton or *yamaasik* string and tied to each fringe end, whereas one apron (-14C) has patches of curassow skin and feathers tied to each fringe end. The fourth apron, -12, is an entirely different construction (Fig. 2). The belt is standard cordage type #9 and the cord is type

Fig. 3.—Two traditional women's necklaces of *tirimoku* seeds, CMNH numbers 32703-7A and B (left). Right, two *aroariki,* men's necklaces worn for protection against evil spirits and spells, CMNH numbers 32703-8A and B.

#12(5). The fringe, however, consists of a 27.4 by 13.2 cm beaded rectangle in red, white, and light and dark blue. There are red (cordage type #10) and black (cordage type #9) tassels at each corner, and a small red fringe along the bottom of the apron (cordage type #10). The beaded design is a geometric motif with opposing triangles within bands of contrasting color. The beadwork on an apron such as this is very intricate and time consuming, and the apron was very expensive to purchase from the maker. It was brought from Themaim, a Maxikopiutheri woman from the Mucajai River, in December 1979.

Most of the collection II aprons are decorated with beads, *tirimoku* seeds, shells, and feathers tied to each fringe end. Feathers are the most popular decorative elements; specimens 32735-291, -296, and -300 use toucan, curassow, and lovely cotinga feathers to decorate each fringe end, and the fringe on apron -293 is constructed entirely from curassow feathers stitched to the cord. Aprons -297, -298, and -299 used curassow and toucan feathers in combination with beads, shells, and seeds. Apron -294 utilizes strings of beads and seeds at each fringe end, while -288 makes use of strings of seeds.

Fig. 4.—Three *kotho,* belts for boys and men. From top: 32703-16B, -16C, and -16A.

The fringe on apron -292 appears to have been made by different women. While the cordage, type #13(2), is the same throughout the fringe, the diameter of both the spun and plied yarns is quite different. Likewise, the decorations at each end of the fringe are different; one side has shells strung on cordage types #9 and #13(5), whereas the other side decoration is beads and seeds. This suggests that decorative elements on aprons may be specific to individual women, another deduction later confirmed by the collector (Saffirio, personal communication).

Armbands.—Most of the decorative arm ornaments worn by women are composed of highly perishable flowers or grasses; therefore, no specimens of these are present in the Carnegie Museum of Natural History collections. The only women's armbands in the collection are a pair of cotton armbands for a young girl. Although at first glance they appear to be loom woven cloth, the fabric structure is actually plain interlinking crossed right over left (Emery, 1980:61). This circular method of construction produces a seamless, stretch fabric.

32735-21 A&B, *wao kik,* owned by Yaikom. Pink cotton girl's armband, seamless, cordage type #9. D—10.1 cm.

Necklaces.—The Carnegie Museum of Natural History collection contains three traditional seed necklaces (Fig. 3). These are rarely made by women today because of the availability of trade beads.

32703-7A, bought from a Hewenahipiutheri woman, December 1979. *Tirimoku* seeds on cordage type #12(3) tied with three knot "A"s. L—40.6 cm.
32703-7B, same as 32703-7A except cordage type #3 tied in knots "A" and "G." L—55.9 cm.
32735-35, *yanuak,* woman's necklace. Fourteen loops of small, round black seeds strung on cordage type #3 tied in knot "F." Two knot "A"s one string end. L—43.8 cm.

Men's clothing

The penis string is the only item of clothing considered essential for everyday men's wear (Saffirio, personal communication). Occasionally men will also wear a "belt" of native cotton (Fig. 4). Initially this is made by women in the same fashion as the belt portion of the women's apron. But after the ends have been tied and the stakes removed, the entire length of the belt is very tightly wrapped with *yamaasik* or cotton string every 2 to 5 cm. The belt is often dyed red or brown with *nara.*

*Belts (*kotho*).*

32703-16A, man's belt. Cordage type #9 belt; cordage #13(5,6) cord. Loose warps, no wrapping. L—56.6 cm.
32703-16B, man's belt, from Mahuku of Hewenahipiutheri village, December 1979. Cordage type #7 belt with cordage type #9 tie every 2 cm. Cordage type #3 cord tied at each end with knots "E," "G," and "F." Yarns dyed red with *nara*; three purple serpentine lines painted down belt length. L—73.2 cm.
32703-16C, boy's belt. Cordage type #9 belt; cordage type #13(4) cord. Belt wrapped with green commercial string every 3 cm. Tied each end with knots "A," "F," and "H." L—38.6 cm.
32703-301, boy's belt. Cordage type #7 belt; cordage type #13(6) cord. Tightly wrapped with cordage type #1 every 2 cm; tied with knots "A"(4) and "E"(2). Dyed red with *nara.* L—36.2 cm.

Necklaces.—These necklaces (Fig. 5) are worn only by men, because they are made of animal parts from game the men have hunted and killed.

32703-9, *thihi nak,* jaguar tooth necklace from Paxeko, a 30 year old good hunter in Hewenahipiutheri village. Cordage type #3, knot "E"(?). L—36.9 cm.
32703-10, *opo nak,* from Iropitheri village November 1979. Armadillo teeth tied to cordage type #1 with knot "E." L—39.4 cm.
32735-43, *opo sina.* Cordage type #3 necklace, with pendant of two armadillo tails tied to untwisted *yamaasik* fiber with knots "A" and "E." L—37.9 cm.
32735-84, necklace of cordage type #3 with pendant of two cock of the rock bird upper beaks and crests stitched together with commercial pink thread. Tied together with knots "G" and "F." L—36.5 cm.

FESTIVAL ARTIFACTS

This category includes all items used at feasts and for ritual or spiritual purposes. Items of clothing (feather armbands, headbands, and

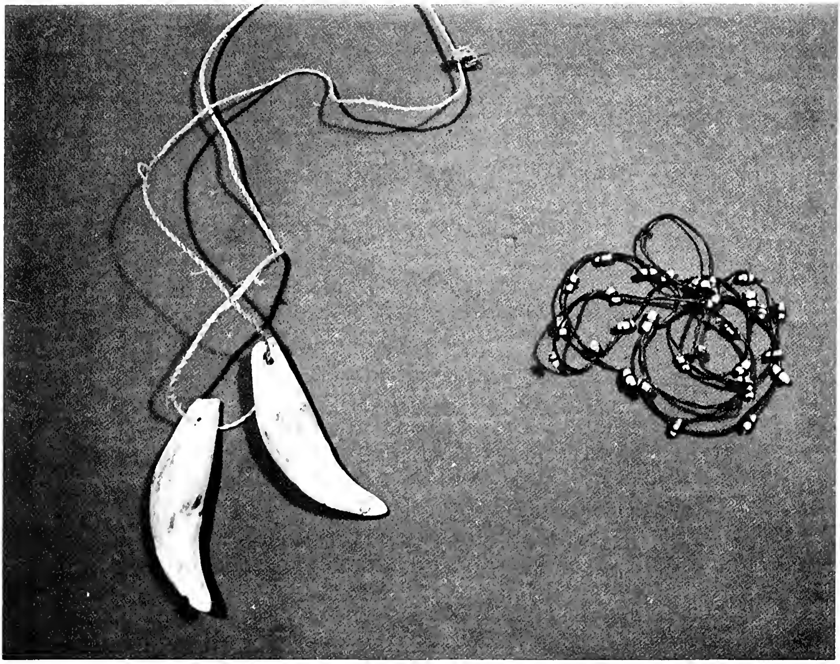

Fig. 5.—Two necklaces made from animal parts, and thus worn only by men. CMNH numbers 32703-9 (left) and 32703-10 (right).

earrings) worn only during festivals are included, although highly decorated women's aprons, usually worn during festivals, are grouped into the "Wearing Apparel" category with the rest of the aprons as discussed previously.

Feasts, which can last up to a week, are primarily political events among the Yanomama. Although each village is self-sufficient in terms of daily life and food procurement, alliances with other villages are promoted for marriage alliances and cooperative warfare. The Catrimani River Yanomama follow a prescriptive bilateral cross-cousin marriage rule and use an "Iroquois-Dravidian" kinship system (Chagnon, 1977:56; Saffirio, 1985:118). However, one village often does not provide enough cross-cousins to satisfy this rule. A man must frequently seek a wife outside of his own village as a result (Smole, 1976: 76, 94). When he finds an eligible female, he is obliged to reciprocate to her father or brothers with his own sister. Alliances between villages are strengthened by the double tie (Chagnon, 1977:55).

Warfare is another situation calling for village alliances. Several villages may band together to fight a common enemy, or one village may flee to an ally when warfare drives them out of their own territory.

They are occasionally forced to live in the allied village for a lengthy period of time—up to several years—until their new gardens begin to produce (Chagnon, 1977:97ff).

Both the Brazilian Indian Agency (FUNAI) and missionary groups have discouraged warfare among the Yanomama in recent years. As a result, ritual chest pounding duels during festivals are currently replacing fatal raiding parties (Saffirio, personal communication). The duels allow the Yanomama to settle grievances among themselves or with allied villages. These duels are usually performed during the festivals.

Body Decoration

Festival wear consists of feather or animal skin armbands and headbands for men and feather earrings for men and women. In addition, both sexes paint themselves elaborately and cover their hair with bird down.

Paint.—Yanomama men and women paint their bodies frequently during the dry season and almost daily during the rainy season with black (*nara uxirim*) and red (*nara wakirim*) paint. Body painting is especially colorful and elaborate during feasts, so the paints and storage equipment were placed into the Festival category.

Red body paint is made from seeds (*nara moko*) of the *Bixa orellana* tree. These have a greasy red outer covering, which is rubbed off and molded into a ball (Fig. 14) or made into a thick liquid to be stored in gourds.

32735-93, black paint gourd, owned by Carrera. End sealed with wax. String through hole below gourd neck: cordage type #3 tied in two knot "A"s. L—10.7 cm W–8.1 cm.

32735-342, black paint gourd? sealed with leaf plug. Neck wrapped with scotch tape, no string. L—11.2 cm W—7.7 cm.

32703-29, lump of red paint. L—5.9 cm.

32735-310, same as 32703-29. L—7.0 cm.

32735-311, same as 32703-29. L—7.8 cm.

32703-23, red paint gourd sealed with wax. Cordage type #3 through hole in gourd neck, knot "A" on visible end. L—18.8 cm W—11.6 cm.

Apparel.—Festival armbands for women are made of leaves and flowers; none of these are present in the Carnegie Museum of Natural History collection. Festival armbands for men are made from bird feathers and body parts.

White bird down feathers (*horomaep*) are also used by both Yanomama men and women. They coat the hair with resin, and then cover their heads with the white down. The down on women occupies only a fringe around the head, but men apply it to completely cover the hair. The down is stored in gourds (*horokoto*), and retrieved by poking a stick into the cut-off top.

Fig. 6.—Feather earrings (*kurakaas sina*) worn by men and women during festivals. All are accession 32735.

32703-20A, *horokoto* with *horomaep*, from Mahuku of Hewenahipiutheri village December 1979. Top cut off; hole for tie string through neck. L—15.4 cm.

32703-20B, same as 32703-20A. L—16.5 cm.

32703-20C, same as 32703-20A. L—19.3 cm.

32703-21C, corked with wad of leaves. Cordage type #11(3) tied through hole with knot "F"(?). L—12.4 cm.

32703-52A, collected 1979–80. Cordage type #3 tied in neck hole with knot "A." L—15.1 cm.

32703-52B, same as 32703-52A. L—15.4 cm.

32735-106, top cut off; no hole in neck for cordage. L—12.9 cm.

32735-107, corked with leaf wad; cordage type #4 tied through hole with knots "E" and "A." L—12.1 cm.

32735-108B, two holes drilled through neck; cordage type #3 threaded through both holes and tied inside gourd with unidentifiable knot. L—16.6 cm.

32735-108B, no stopper; cordage type #9(?) through hole. L—25.1 cm.

As has been discussed previously, men wear items made from animal body parts such as wings, skins, teeth, and tails. Women, however, are permitted to wear feather earrings. These earrings, also worn by men, consist primarily of single feathers inserted into pieces of straw (Fig. 6). Sometimes the feathered end of the straw is smeared with resin,

Table 2.—*Yanomama feather earrings in the collections of Carnegie Museum of Natural History.*

Type	Accession number	Feathers (number)	Cordage	Length (cm)
seisi sina	32735-46 A&B	lovely cotinga	#2	9.5
	-47 A&B	lovely cotinga	*yamaasik*	11.2
	-53 A&B	lovely cotinga	*yamaasik*	11.0
	-54 A&B	lovely cotinga	*yamaasik*	17.0
kurakaas sina	-55 A&B	parrot (single)	none	16.5
	-56 A&B	parrot (single)	none	17.0
	-57 A&B	parrot (single)	none	16.6
	-58 A&B	parrot (single)	resin	19.4
	-59 A&B	parrot (single)	resin	19.7
	-60 A&B	parrot (single)	*yamaasik*	22.5
	-61 A&B	parrot (single)	*yamaasik*	21.4
	-62 A&B	parrot, curassow	*yamaasik*	15.6
	-63 A&B	parrot, curassow	*yamaasik*	17.7
	-64 A&B	parrot, curassow	*yamaasik*	17.3
	-65 A&B	curassow (two)	none	13.4
	-66 A&B	curassow (two)	none	9.9
	-67	curassow (two)	none	12.8
	-68 A&B	curassow (two)	none	11.3
	-69 A&B	curassow (two)	none	11.3
	-70 A&B	curassow (two)	none	11.5
	-71 A&B	toucan, parrot, curassow	#2 (?)	18.7
	-72 A&B	parrot, toucan	none	14.3
	-73 A&B	parrot, curassow	#1	15.0
	-74 A&B	guan, curassow	#1	12.2
	-75 A&B	parrot (single)	none	11.9
	-76 A&B	parrot (single)	none	11.6
	-77 A&B	guan (single)	none	7.2
	-78 A&B	guan (single)	none	10.0
	-79 A&B	guan (single)	none	11.7
	-80 A&B	parrot (single)	none	11.3
	-81 A&B	guan (single)	none	11.6
	-82 A&B	curassow (two)	none	12.4
	-83 A&B	guan, curassow	*yamaasik*	13.0

either to protect underlying fiber wrapping or to hold the unwrapped feather in place.

Table 2 presents the data for the two types of feather earrings. The first, *seisi sina,* consists of lovely cotinga bird skin and feather patches wrapped to pieces of wood, which is used in place of straw because of the weight of the earring. One pair of earrings is wrapped with the rare Z twist *yamaasik* fiber cordage, whereas the others are secured with unplied *yamaasik.*

The second type of earring, *kurakaas sina,* utilizes a variety of feath-

Fig. 7.—*Ara sina,* man's festival armband made from bird feathers.

ers. Parrot and curassow are the most popular types, whereas toucan and guan are occasionally present. The commonest earring is the single or paired feather inserted into straw, seen in 21 of the 29 pairs. Eight pairs have a single earring in the center surrounded by a "bouquet" of curassow or toucan feathers.

Nine pairs use fiber wrapping to secure the feathers, and two pairs have resin coating the inserted end. The unplied *yamaasik* is again the most popular wrapping, but two pairs use S twist *yamaasik,* and one pair utilizes the rare Z twist *yamaasik* fiber.

Men's clothing.—Men wear both arm- and head-bands during festivals. These are made by the men from bird or other animal parts. There are two types of armbands. The first, *ara sina,* consists of one to four long red tail feathers from the macaw (*Ara macao*) tied to pieces of

Table 3.—*Yanomama* ara sina *armbands in the collections of Carnegie Museum of Natural History.*

Accession number	Macaw feathers	Bunched feathers	Cordage type	Length (cm)
32703-6A	four	parrot & macaw	#1	66.1
-6B	four	white-winged guan	#1	65.6
-6C	four	macaw, parrot, and white-winged guan	#1	64.2
-35A	three	parrot	#1	67.5
-35B	three	white-winged guan	#1	59.4
-35C	four	white-winged guan	#1	67.7
-35D	three	white-winged guan	#1	65.6
-35E	three	white-winged guan	#1	63.0
-35F	four	macaw, parrot and white-winged guan	#1	64.0
-35 G	three	macaw	#1	68.7
32735-121A	four	white-winged guan	#1	60.9
-121B	four	white-winged guan	#1	66.7
-122A	four	white-winged guan	#1	51.8
-122B	four	white-winged guan	#1	64.1
-123	one	white-winged guan	#1	60.4
-124	one	parrot & white-winged guan	#9	61.6
-125	three	white-winged guan	#1	69.5
-126	three	white-winged guan	#1	68.0
-127	four	white-winged guan	#1	52.1
-128A	three	white-winged guan	#1	62.9
-128B	three	white-winged guan	#1	66.4
-129A	three	white-winged guan	#1	68.4
-129B	three	white-winged guan	#1	66.1
-130A	four	white-winged guan	#1	66.2
-130B	four	white-winged guan	#1	62.0
-131A	three	white-winged guan	#1	64.7
-131B	three	white-winged guan	#1	64.6
-132A	four	macaw & parrot	#1	54.3
-132B	four	parrot	#1	68.6
-133A	four	macaw	#1	68.4
-133B	four	macaw	#1	69.6
-134A	four	parrot	#1	58.9
-134B	four	parrot	#1	72.2
-135A	four	parrot	#1	76.7
-135B	four	parrot	#1	60.0
-136A	four	macaw & parrot	#1	61.8
-136B	four	macaw & parrot	#1	59.0
-137A	four	parrot	#1	65.2
-137B	four	parrot	#1	53.9
-138	three	parrot	#1	69.7
-139	three	macaw	#1	62.0
-140	three	parrot	#2	63.5

Table 3.—*Continued.*

Accession number	Macaw feathers	Bunched feathers	Cordage type	Length (cm)
-141	three	parrot	#1	65.6
-142A	four	parrot	#1	63.1
-142B	three	parrot	#1	57.3
-143A	three	parrot	#1	65.9
-143B	three	parrot	#1	72.0
-144A	three	parrot	#1	67.4
-144B	three	parrot	#1	63.3
-145A	four	parrot	#1	65.5
-145B	four	parrot	#1	61.4
-146A	four	parrot	#1	57.9
-146B	four	parrot	#1	51.2
-147	two	parrot	#2	65.8
-148	four	parrot	#1	59.2
-149A	four	parrot	#1	59.2
-149B	four	parrot	#1	58.5
-150A	four	parrot	#1 and #2	51.4
-150B	four	parrot	#1	59.2
-151A	three	parrot	#1	61.9
-151B	three	parrot	#1	58.9
-152A	three	parrot	#1	71.1
-152B	three	parrot	#1	64.2
-153A	three	parrot	#1	69.9
-153B	three	parrot	#1	59.4
-154A	three	parrot	#1	66.5
-154B	three	parrot	#1	67.4
-155A	three	parrot	#1 and #2	70.8
-155B	three	parrot	#1	67.3

bamboo or palm wood (Fig. 7). Bunches of parrot (*Amazona* sp.), curassow (*Crax alector*), or white-winged or piping guan (*Aburria pipile*) feathers are tied in a "bouquet" at the base of the longer macaw feathers. The armband is then tied around the upper arm with the long red feathers pointing upwards. They are worn in pairs, with usually one on each arm.

Table 3 presents the data for the *ara sina* armbands. Length, corresponding to the height of the long red tail feathers when worn, is not a critical factor in matching pairs of armbands; six pairs differ in size between pieces by 10 cm or more. It is more important to match the feathers, both in number of long red macaw feathers and in color and species of the "bouquet" feathers. All but two sets of armbands matched both the number of long red macaw feathers and the "bouquet" feathers

Fig. 8.—*Yaro sina,* man's festival armband made from bird tails.

on both armbands. One pair, 32735-142A & B, matched four long red macaw feathers on one armband with three on the other. Only 32735-132A & B did not match the "bouquet" feathers on the two armbands.

An interesting application of these facts can be tested with accession 32703 armbands, which were not delivered in pairs. Utilizing the criteria discussed above for matching pairs, it can be suggested that pairs are composed of specimens -6B and -35C, and -6C and -35F. Both of these pairs then have matched macaw and "bouquet" feathers. Both the macaw and the "bouquet" feathers match on three specimens (-35B, -35D, and -35E); any two of these three could form a pair of armbands. The "bouquet" feathers of -6A and -35A or -35G are somewhat matched. Whatever the pairs of the last two groupings, it is clear that the armbands from accession 32703 are not completely paired; the final set of, for instance, -35E and -35G is composed of completely unmatched "bouquet" feathers.

Cordage type #1 is clearly the choice to wrap the feathers to the wood. Cordage type #2, the rare Z twist *yamaasik* fiber, is present on four armbands, and s spin Z twist cotton cordage, type #9, on one. Interestingly, pairs 32735-150A & B and -155A & B utilize both S

Table 4.—*Yanomama* yaro sina *armbands in the collections of Carnegie Museum of Natural History.*

Accession number	Wings	Tails	Other	Cordage	Knots
32703-54	macaw, toucan	toucan		#9, 11 (3), 14 (2)	A(3), J(2), C, H(3)
-55	toucan	toucan	macaw	#9, 11 (3), 13 (2)	A(5), E, K, C(3), ?
-56	macaw	toucan		#11 (3), 14 (2)	A(4), J(2), C, G, E
-60	guan, macaw	guan, toucan	toucan	#9, 12 (17)	A(2), F, J(2), E, C
-64	parrot, guan	toucan	toucan	#9, 11 (3)	A(2), C(2), J(2), E
-65	guan	toucan		#3, 9, 13 (2)	A, J(3), H(6)
-93	macaw, toucan, guan, parrot			#1, 9, 13 (2, 4)	A(2), J(2), G, E, C, K

Fig. 9.—*Yaro sina,* man's festival headband made from bird skins, wings, and tails.

and Z twist *yamaasik* fiber on one armband of the pair, whereas the other exhibits standard S twist *yamaasik* fiber. It is possible that these armbands which utilize mixed cordages were made by two individuals, one of whom wrapped the long red macaw feathers to the wood while the other attached the "bouquet" feathers. Accession 32703 armbands use S twist *yamaasik* fiber exclusively.

The second type of men's armband, the *yaro sina* (Fig. 8), is composed of bird wings, tails, and skin. Aracari (*Pteroglossus pluricinctus*), parrot, toucan (*Ramphastos rucanus*), and macaw wings, tails, and skins are tied together to lengths of string. These lengths are tied around the upper arm, leaving the wings dangling.

Men usually wear the *yaro sina* armbands as a pair, one on each arm. Thus the armbands discussed in Table 4 are actually pairs of

Table 5.—*Yanomama* yaro sina *headbands in the collections of Carnegie Museum of Natural History.*

Accession number	Wings and tails	Headpiece	Cordage	Knots	Length* (cm)
32703-57	parrot	curassow	#13 (3)	A(3), C, F	32.4
-58	parrot	curassow	#13 (3)	A(3), C, F, J	24.2
-59	none	curassow (2)	#12 (6)	F	34.8
-61	toucan	none	#10	H, K	
-62	none	curassow	#11 (3)		25.7
-63	none	curassow	#11 (3)	K	25.1
-66	parrot, curassow	curassow	#13 (3)	A(3), C, F	38.0
-67	toucan, guan	curassow	#13 (3)	A(2), C, J	23.5
-68	toucan, guan, macaw, parrot	curassow	#3, 5 (3)	E, F, H, C(2)	30.4

* "Length" refers to the length of the headpiece.

armbands, which have been tied together. Some effort was made to balance the armbands; a pair with a toucan tail on one armband will be partnered with a toucan tail on the other. Only the smaller guan or parrot wings are occasionally present on one member of the pair but not the other.

Table 4 indicates that toucan tails are the parts used most consistently by all who make the *yaro sina* armbands. Only one specimen uses another bird tail in addition to the toucan tails, and all armbands but 32703-93 have toucan tails on them. Macaw wings are the second most popular bird part, present on four of the seven armbands. When the other parts are considered, primarily skins with feathers from the breast or head, macaw parts are present on five of the seven armbands.

Cordage type #9, the 2 ply s spin Z twist cotton, is used on six of the seven armbands. Cordage type #11(3) is present on four specimens, and type #13(2) on three. Only two armbands exhibit *yamaasik* fiber cordage, and only in minor amounts.

An interesting fact about the *yaro sina* armbands stems from the variation possible in their mode of construction. There are many types of cordage to choose from, and even more knots which can be used. As with stitch slant in twining, discussed previously, knots tend to reflect individual choice. Taking these facts into consideration, armband pairs 32703-54 and -65 were probably made by the same man. Both armbands used knot "H" exclusively to the the string to the bird parts. None of the other specimens uses knot "H" in this fashion; in fact, none of the other specimens uses knot "H" in any fashion. A lark's head is not a "fixed" knot, but rather a suspended knot capable of movement along another piece of string. Although it can be rendered relatively immobile by the tightness of the tie, it is unusual to find it used as a method of permanent attachment. The specimens are not

Fig. 10.—Incomplete *yaro sina* headbands, consisting of just the curassow skin headband.

overly similar in any other attribute; they both make heavy use of toucan parts, as do many of the other *yaro sina* armbands; they both use cordage types #9 and #13(2), which are the first and third most popular cordages; and one uses *yamaasik* fiber cordage, found on one other specimen. Nevertheless, the attachment of the parts to the string is unusual enough to merit special attention, and use of the rare lark's head knot is a distinguishing characteristic which links these two pairs of armbands and separates them from the others.

The second item of men's festival apparel is the headband made of bird parts or monkey skin. While the monkey headbands are simply made of skinned monkey tails, the feather *yaro sina* headbands, like the *yaro sina* armbands, are complex constructions of bird wings and tails tied to cotton or fiber cordage (Fig. 9). The band which passes across the forehead is made of curassow skin and feathers. A string is tied at each end of the band to make the head size adjustable, and the bird wings and tails dangle at each temple.

The *yaro sina* headbands are not as balanced as the *yaro sina* armbands; little effort was made to place similar wings and tails at each temple. As can be seen on Table 5, many of the headbands (32703-

Fig. 11.—*Wisa sina,* man's festival headband made from a skinned black saki monkey tail. Accession 32735.

58, -59, -62, and -63) consist of just the curassow headband with no dangling parts (Fig. 10). Although bands are occasionally worn this way, it is usual to complete them with other bird parts at the temples. The reverse situation is found on 32703-61, which consists only of the earpieces to a headband; it has not yet been added to, or has been detached from, the curassow band.

Cordage type #13(3) is the most popular cordage used on the *yaro sina* headbands, present on four of the nine specimens. The rest of the cordage consists of two pieces of cordage type #11(3), and one each of types #12(6), #10, #3, and #5(3). In this respect the *yaro sina* headbands differ from the *yaro sina* armbands; cordage usage on the armbands was very consistent, with cordage type #9 present on six of the seven armbands, type #11(3) on four, and type #13(2) on three. *Yamaasik* fiber was used on one headband. Knot "A" was the most popular knot in total number of ties, whereas knots "C" and "F" were used on the greatest number of headbands.

A second type of headband, also utilizing feathers, is woven of *masik* vine. Curassow and toucan feathers are inserted into the weave in

Fig. 12.—*Horokoto* with *yakoana,* hallucinogenic drug storage gourd. CMNH number 32703-22B.

patches of red, yellow, and black. This headband is not adjustable to different sizes.

32735-20, *mayop ahuk,* owned by Tixo. Band is tied at four points with cordage types #1 and #3 in knots "F"(2) and "A." A 12 cm length in the back of the headband has no feathers. D—18.0 cm.

Other festival headbands consist of skinned monkey tails (Fig. 11). The fur piece is flattened, and an adjustable string is tied at each end.

32735-194, *wixa sina.* Black saki monkey skin tied with cordage type #3 in knot "H" at one end. L—(tail only) 42.7 cm.
32735-195, same as -194 but string tied with knot "E." L—41.2 cm.
32735-196, *wixa sina* tied with cordage type #19 in knot "C." L—36.9 cm.

Drug Containers

Most men use hallucinogenic drugs—*yakoana*—during festivals, although shamans make frequent use of them when performing shamanistic rituals. The drug (*Virola* sp.), also known as *ebene,* is made from inner tree bark (Chagnon et al., 1971:72–74). The latex from the tree is used as the poison on monkey arrows (Couture-Brunette, 1985: 501).

Fig. 13.—Chest pounding tools. From top: *paruk xayau,* CMNH number 32703-25A; *paruk xayau,* CMNH number 32703-25B; *suhumuk,* CMNH number 32703-25C.

The moist scrapings are mixed with ashes and kneaded into a ball, with saliva providing additional moisture if necessary. It is then placed over the fire on a container to dry (Chagnon, 1977:23). The residue is ground into a powder, and stored in gourd containers until needed (Fig. 12).

32703-22A, *horokoto* with *yakoana,* from Mahuku of Hewenahipiutheri village, December 1979. Corked with ball of wax; cordage type #9 through hole. Knot "A" inside gourd; two knot "A"s other end. L—14.2 cm.

32703-22B, same as 32703-22A but corked with roll of animal hide. Cordage type #3 through hole in neck; tied with knot "E." Outside of gourd covered with resin. L—15.9 cm.

32735-102, sealed with wax. Cordage type #3 through neck hole; two knot "A"s one end and three on the other. L—11.4 cm.

32735-103, brown wood cork. Hole drilled in neck; no string. L—15.1 cm.

32735-104, owned by Mahuku. Top sealed with wax, no hole or string. Split down side. L—12.4 cm.

32735-105, top sealed with wax. Cordage type #3, no visible knots. L—15.3 cm.

32735-341, sealed with wax. L—12.2 cm.

The drug is blown into the nostrils with a *mokamosi,* a hollow cane tube. One end of the tube is lined with wax while the other is unmodified. The tube is loaded with a dose of *yakoana,* and the receiver places

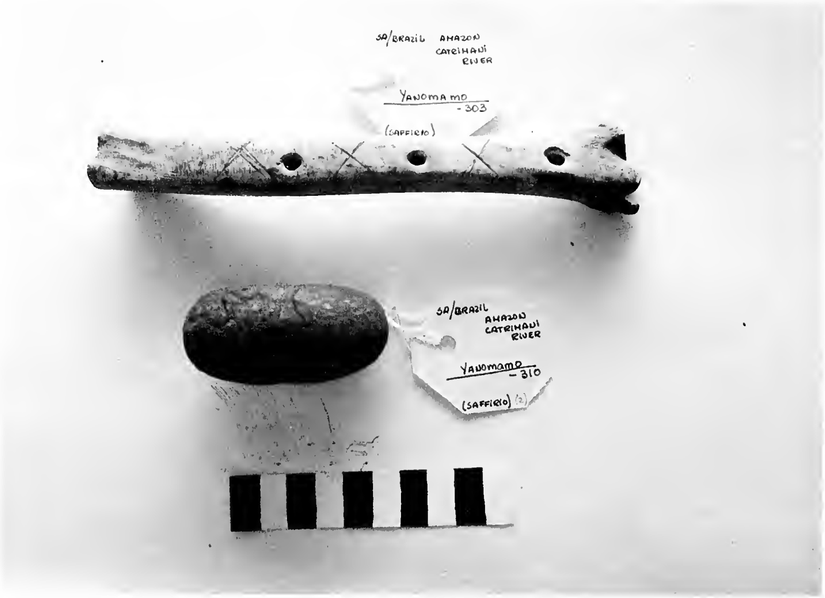

Fig. 14.—*Haya maro,* deer bone flute (top) and *nara wakirim,* lump of red body paint (bottom). Accession 32735.

the waxed end inside one nostril. Another man expels a powerful gust of air into the cane. A man will take a few doses of the drug at a time in each nostril.

32703-41, collected in 1979–80. Lengthwise cracks and splits along the sides of the tube. L—88.4 cm.
32735-89, four parrot feathers in the waxed end. L—69.8 cm.
32735-90, same as 32735-89. L—69.0 cm.

Chest Pounders

Ritual chest pounding duels during festivals have replaced much of the revenge warfare among the Catrimani Yanomama. Blows are delivered with the aid of chest pounders (*paruk xayau*), wood branches which are smoothed and polished (Fig. 13). No effort is made to trim off protruding stubs, and the ends may be pointed or flat.

32703-25A, from Akasi and Paruk of Uxiutheri village, November 1979. Ends unpointed. L—35.9 cm.
32703-25B, same as 32703-25A but both ends pointed. L—40.4 cm.
32735-109, owned by Carlos. Both ends pointed; approximately 5 cm from each end red and yellow toucan feathers are wrapped onto the pounder with cordage type #1. L—22.1 cm.

32735-263, one end pointed and other rounded. Cordage type #9 wrapped 10 times around one end. L—28.9 cm.
32735-264, ovoid, both ends pointed. Small hole partially drilled into one side. "ME" carved on other side. L—18.2 cm.
32735-265, forked. Two top ends pointed, other (bottom) end flat. L—20.2 cm.

A second type of ritual dueling tool, *suhumuk,* is used in a different fashion. This object, also made of wood, is blade shaped with pointed ends and serrated teeth in the center (Fig. 13). Both ends are grasped by one man, who then hugs his opponent and digs the teeth into his back while the opponent does the same.

32735-25C, from Akasi and Paruk of Uxiutheri village, November 1979. Four teeth; one end pointed, other flat. L—38.5 cm.
32735-191, four teeth; both ends pointed. L—77.6 cm.
32735-31, *maama suhumuk,* stone found by Honi on the path near the Arapari River (KM 135 of Highway BR 210). Honi said these were not longer used in dueling, but were made and used by ancestors. L—23.4 cm.

Miscellaneous Festival Accessories

The Yanomama use two kinds of musical instruments, both of them flutes. The first is a deer bone flute (Fig. 14). Its use is restricted to festivals, when it is played by the guests as they draw near the host village. The leg bone is hollowed and holes are drilled into one side. The joint forms a natural closure for one end, while the other end of the flute is open. The flute is usually reddened with *nara.* The second flute, which is a child's toy imitation of the ritual flute, will be discussed in Part III as a miscellaneous construction.

32703-49A, *haya maro,* collected 1979-80, 2 holes drilled in top. L—12.4 cm.
32703-49B, same as 32703-49A but three holes drilled in top. L—15.1 cm.
32703-49C, same as 32703-49B. L—14.6 cm.
32735-50, two drilled holes and one natural hole, faint traces of *nara.* L—18.2 cm.
32735-51, same as 32735-50. L—17.8 cm.
32735-52, three drilled holes, reddened with *nara.* L—18.9 cm.
32735-303, three drilled holes alternate with three "X"s scratched onto the surface. Reddened with *nara.* L—19.0 cm.
32735-304, same as 32735-303. L—19.4 cm.

Two necklaces, although occasionally worn outside of festivals, are intimately associated with the spirit world and were thus grouped in the Festival category with the drug equipment. The first, *aroariki* (Fig. 3), is worn for protection against evil spells and spirits. It is composed of cut pieces of tubers which have been dyed brown. The pieces are threaded on brown dyed string.

32703-8A, from Puuxim of Wakathautheri village. Cordage type #10, eight knot "A"s. L—35.4 cm.
32703-8B, same as 32703-8A. Cordage type #3, with knots "A"(5), "E"(2), and "J"(2). L—38.2 cm.

The other type of necklace, *marasik,* is worn by men. It acts as an aphrodisiac, attracting partners of the opposite sex. It consists of cut pieces of tubers, which are dyed red and tied to reddened cotton string.

32735-44A, cordage type #11(3) tied around center of each tuber in knots "E," "G," and "F." Ends tied together with two knot "A"s. L—70.0 cm.

32735-44B, same as 32735-44A but string tied around tubers with knot "E." Ends tied together with knot "E." L—69.1 cm.

ADDITIONAL COMMENTS

The two categories of Wearing Apparel and Festival Artifacts are intimately related, inasmuch as most festival artifacts are items to be worn. The division of specimens into selected categories was intended to reflect the function of the artifact. However, in two cases the construction of the specimen outweighed the functional aspects. Specifically, the women's aprons and the body paint groups were discussed together under one category, although in function each group should have been separated. In the case of the aprons, this combined discussion followed a constructional basis. Everyday and festival aprons are made the same way, and differ only in the added decorative elements. As this was the case, the "apron" group was combined into one discussion section under "Wearing Apparel" rather than presenting separate but identical constructional data in two categories. The "body paint" group was similarly combined for the same reasons.

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I wish to thank Dr. Giovanni Saffirio for his invaluable advice and explanations on particularly puzzling specimens. Drs. James B. Richardson and David R. Watters kindly read through initial drafts and provided helpful comments. Dr. Hugh H. Genoways and the staff of the Section of Mammals, Drs. Kenneth Parkes and D. Scott Woods of the Section of Birds, and Dr. Juan Parodiz and Ms. Jay Tripp of the Section of Malacology assisted in the identification of materials used in manufacture of many of the artifacts. Ms. Nancy Perkins of the Division of Exhibits drafted the knots as well as the cordage/basketry twist examples. Specimen photographs were taken by Ms. Barbara Gundy; all other photographs are used with the kind permission of Giovanni Saffirio.

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STANDARD KARYOLOGY OF NINE SPECIES OF VESPERTILIONID BATS (CHIROPTERA: VESPERTILIONIDAE) FROM THAILAND

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Abstract

Karyotypes of nine species of vespertilionid bats from Thailand are described. *Pipistrellus mimus* (2n = 34, FN = 46), *Tylonycteris robustula* (2n = 32, FN = 50), *Murina leucogaster* (2n = 44, FN = 50), and *Miniopterus schreibersi* (2n = 46, FN = 52) have karyotypes essentially identical to ones previously reported from other regions. *Pipistrellus pulveratus* (2n = 32, FN = 50) is reported for the first time and differs by six Robertsonian fission/fusion events from the primitive *Myotis*-like karyotype. Karyotypes

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for *Hesperoptenus tickelli* (2n = 32, FN = 50) and *H. blanfordi* (2n = 34, FN = 60) are reported for the first time and parallel the extreme morphological differences between the two species. *Harpiocephalus mordax* (2n = 40, FN = 62) is very distinct from other members of the subfamily Murininae but is apparently derived from a *Murina*-like ancestor. *Kerivoula papillosa* (2n = 38, FN = 52) though considered little differentiated from primitive vespertilionines has a relatively highly derived karyotype similar to *Vespertilio*.

INTRODUCTION

The family Vespertilionidae is distributed worldwide in temperate and tropical regions. It is the largest family in the order Chiroptera including approximately 33 genera and 313 Recent species (Koopman, 1984). Thirteen genera and 34 species are known to occur in Thailand (Lekagul and McNeely, 1977).

Previous karyotypic studies led Pathak and Sharma (1969) to suggest that the family has two very different patterns of chromosomal variability. Some genera such as *Myotis* exhibit remarkable homogeneity with all examined species having 2n = 44, FN = 50 or 52. Others such as *Pipistrellus* (2n = 26, 28, 30, 32, 34, 36, 38, 42, 44 and FN = 44, 46, 48, 50, 52) are much more heterogeneous. These studies, however, mostly have been restricted to New World (Baker and Patton, 1967; Bickham, 1979*a,* 1979*b*) and European (Bovey, 1949; Capanna and Civitelli, 1970; Fedyk and Fedyk, 1970; Zima, 1978) species. Karyotypic data for African, Australian, and Asian vespertilionids are sparse. For example, karyotypes have been reported for only one species of vespertilionids from Thailand (Harada et al., 1982*b*).

This study presents standard karyotypes of nine species in seven genera and four subfamilies from Thailand. Karyotypes of five of these species have been reported from other regions (Pathak and Sharma, 1969; Manna and Talukdar, 1965; Yong et al., 1971; Bickham and Hafner, 1978; Harada and Kobayashi, 1980; Harada, 1973; Ando et al., 1977). New data are presented for four species and one subfamily.

MATERIALS AND METHODS

All animals were collected in Thailand using mist nets. Upon capture, all animals were subcutaneously injected with a weak solution of baker's yeast, sugar, and water (Lee and Elder, 1980) to stimulate bone marrow mitosis. Twenty-four hours later, animals were sacrificed and humeri removed. Karyotypes were prepared in the field from bone marrow cells suspended in a hypotonic solution (0.075 M KCl) for approximately 25 min and then fixed in a 3:1 solution of methanol : glacial acetic acid (Baker et al., 1982). Three to four drops of the fixed cell suspension were dropped onto clean, dry microscope slides and ignited with a match. After the flaming suspension extinguished itself, any remaining liquid was carefully drained away and slides were stained in a 2% solution of Geimsa in 0.01 M phosphate buffer. Diploid (2n) and fundamental (FN) numbers were determined from counts of a minimum of 10 mitotic spreads. Description of chromosome morphology follows the nomenclature of Patton (1967). All specimens were prepared as museum skins and skulls or alcoholics and are housed in the Carnegie Museum of Natural History (CM), the Texas Cooperative Wildlife Collection, Texas A&M University (TCWC), or The Museum, Texas Tech University (TTU).

Specimens Examined

Pipistrellus mimus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, 15°29'N, 99°18'E (CM 88129 M, 88130 F); Huai Kha Khang Wildlife Sanctuary, 2.7 km S Khao Nang Rum Wildlife Research Station, 15°27'N, 99°18'E (CM 88132 M); Huai Kha Khang Wildlife Sanctuary, 1.5 km W Khao Nang Rum Wildlife Research Station, 15°29'N, 99°17'E (CM 88131 M).

Pipistrellus pulveratus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, 3.7 km S, 1 km E Khao Nang Rum Wildlife Research Station, 15°27'N, 99°18'E (CM 88134 F, CM 88136 F).

Tylonycteris robustula.—Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 88149 F, CM 88151 F, CM 88152 F, CM 88140 F, TTU 41257 F, TK 21416 F).

Hesperoptenus blanfordi.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, 15°19'N, 99°18'E (CM 88114 M, TTU 41255 F); Huai Kha Khang Wildlife Sanctuary, 1.5 km W Khao Nang Rum Wildlife Research Station (TK 21279 F).

Hesperoptenus tickelli.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, 3.7 km S, 1 km E Khao Nang Rum Wildlife Research Station, 15°27'N, 99°18'E (CM 88119 M, TK 21193 M); Huai Kha Khang Wildlife Sanctuary, 2.0 km S Khao Nang Rum Wildlife Research Station, 15°30'N, 99°16'E (CM 88117 M).

Kerivoula papillosa.—Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 90°58'E (CM 88164 F).

Miniopterus schreibersi haradai.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, 2.7 km S Khao Nang Rum Wildlife Research Station, 15°30'N, 99°16'E (CM 88156 M); Huai Kha Khang Wildlife Sanctuary, 3.7 km S, 1 km E Khao Nang Rum Wildlife Research Station, 15°27'N, 99°18'E (CM 88157 M).

Murina leucogaster.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88162 F, CM 88163 F).

Harpiocephalus mordax.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88159 F).

Results

Table 1 is a summary of the known standard karyotypic data for the family Vespertilionidae including those reported here. The standard karyotypes of eight species representing seven genera and four subfamilies are presented in Figs. 1–3. A brief description of these karyotypes follows.

Subfamily Vespertilioninae

Pipistrellus mimus (2n = 34, FN = 46; Fig. 1a).—Four animals examined have a karyotype that consists of six pairs of large metacentric to submetacentric chromosomes and one large subtelocentric pair. There are nine pairs of acrocentric chromosomes ranging in size from medium

Table 1.—*A summary of known standard karyotypic data for the family Vespertilionidae. SM—submetacentric, M—metacentric, ST—subtelocentric, and A—acrocentric.*

Taxon	2n	FN	X	Y	Authority
Subfamily Vespertilioninae					
Myotis auriculus	44	52	SM	A	Bickham, 1979*b*
Myotis austroriparius	44	50	SM	SM	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Myotis bechsteini	44	52	M	A	Zima, 1978
Myotis blythi	44	52	SM	A	Baker, 1970
	44	50	SM	A	Baker et al., 1974
Myotis brandti	44	50	SM	A	Zima, 1982
Myotis californicus	44	50	SM	SM	Baker and Patton, 1967
Myotis capaccinii	44	50	—	—	Manfreddi Romanini et al., 1975
Myotis dasycneme	44	52	M	A	Zima, 1978
Myotis daubentonii	44	50–52	SM	A	Bovey, 1949
	44	54	SM	—	Fedyk and Fedyk, 1970
	44	52	M	A	Zima, 1984
Myotis elegans	44	50	SM	SM	Baker and Patton, 1967
Myotis emarginatus	44	50	SM	A	Bovey, 1949
	44	56	M	A	Radjhabli et al., 1969, 1970
	44	52	M	A	Zima, 1978
Myotis evotis	44	50	SM	SM	Baker and Patton, 1967
	44	52	SM	A	Bickham, 1979*b*
Myotis fortidens	44	50	SM	A	Osborne, 1965
Myotis frater	44	50	SM	A	Harada and Yoshida, 1978
Myotis grisescens	44	50	SM	A	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Myotis horsfieldi	44	50	SM	A	Harada and Kobayashi, 1980
Myotis hosonoi	44	52	SM	A	Harada, 1973
	44	50	SM	A	Harada and Yoshida, 1978
Myotis keaysi	44	50	SM	A	Bickham, 1979*b*
	44	50	—	—	Baker and Bickham, 1980
Myotis keenii	44	50	SM	SM	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Myotis leibii	44	50	SM	SM	Baker and Patton, 1967
Myotis lucifugus	44	50	SM	SM	Baker and Patton, 1967
Myotis macrodactylus	44	52	SM	A	Harada, 1973
	44	52*	SM	A	Obara et al., 1976*a*
	44	50	SM	A	Harada and Yoshida, 1978

Table 1.—*Continued.*

Taxon	2N	FN	X	Y	Authority
Myotis milleri	44	52	SM	—	Reduker et al., 1983
Myotis myotis	44	50	M	A	Bovey, 1949
	44	50	SM	A	Bickham and Hafner, 1978
	44	50	SM	A	Iliopoulou-Georgudaki and Giagia, 1984
Myotis mystacinus	44	56	M	A	Radjhabli et al., 1969, 1970
Myotis nattereri	44	50	SM	—	Ando et al., 1977
	44	50	SM	—	Harada and Yoshida, 1978
	44	52	SM	A	Zima, 1978
Myotis nigricans	44	50	SM	SM	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
	44	50	SM	A	Baker and Bickham, 1980
Myotis oxygnathus	44	56	M	A	Radjhabli et al., 1969, 1970
	44	50	SM	A	Bickham and Hafner, 1978
Myotis pruinosus	44	52	SM	ST	Harada and Uchida, 1982
Myotis sodalis	44	50	SM	—	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Myotis thysanodes	44	50	SM	SM	Baker and Patton, 1967
	44	52	SM	A	Bickham, 1979*b*
Myotis velifer	44	50	SM	SM	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Myotis (*Pizonyx*) *vivesi*	44	50	SM	SM	Baker and Patton, 1967
Myotis volans	44	50	SM	SM	Baker and Patton, 1967
Myotis yumanensis	44	50	SM	—	Baker and Patton, 1967
	44	50	SM	A	Bickham, 1979*b*
Lasionycteris noctivagans	20	28	SM	A	Baker and Patton, 1967
	20	28	SM	A	Bickham, 1979*a*
Pipistrellus abramus	26	44	ST	A	Takayama, 1959
	26	44	A	A	Harada, 1973
	26	44	A	A	Obara et al., 1976*b*, 1976*c*
Pipistrellus affinus	36	50	SM	A	Pathak and Sharma, 1969
Pipistrellus babu	36	50	M	A	Dulic, 1981
Pipistrellus endoi	38	50	A	—	Ando et al., 1977
	38	50	A	—	Ando et al., 1980
Pipistrellus hesperus	28	46	SM	A	Baker and Patton, 1967
Pipistrellus kuhli	44	50	SM	A	Capanna, 1968
	44	50	SM	—	Baker et al., 1974
	44	50	SM	A	Zima, 1982
Pipistrellus mimus	34	—	—	—	Manna and Talukdar, 1965

Table 1.—*Continued.*

Taxon	2N	FN	X	Y	Authority
	38	48	M	A	Pathak and Sharma, 1969
	34	46	SM	A	This study
Pipistrellus mordax	34	46	M	A	Pathak and Sharma, 1969
Pipistrellus nanus	36	50	M	A	Peterson and Nagorsen, 1975
Pipistrellus nathusii	44	51	SM	A	Bovey, 1949
	42	50	M	—	Fedyk and Ruprecht, 1976
	42	50	M	A	Zima, 1978
Pipistrellus pipistrellus	42	51	M	A	Bovey, 1949
	44	50	M	—	Fedyk and Ruprecht, 1976
	44	50	M	A	Zima, 1978
	44	50	SM	A	Zima, 1982
	44	52	M	A	Zima, 1984
Pipistrellus savii	44	50	SM	A	Capanna, 1968
	44	50	—	—	Park and Won, 1978
	44	50	SM	A	Zima, 1982
Pipistrellus pulveratus	32	50	SM	—	This study
Pipistrellus subflavus	30	56	SM	A	Baker and Patton, 1967
	30	50	SM	—	Bickham, 1979*a*
Nyctalus furvus	44	50	SM	A	Ando et al., 1977
	44	50	SM	A	Harada et al., 1982*a*
Nyctalus lasiopterus	42	50	SM	A	Tsuchiya et al., 1972
	42	50	SM	A	Harada, 1973
	42	50	SM	A	Ando et al., 1977
	42	50	SM	A	Harada et al., 1982*a*
Nyctalus leisleri	46	54	SM	—	Fedyk and Fedyk, 1970
Nyctalus noctula	42	50	SM	A	Dulic et al., 1967
	42	50	SM	A	Vorontsov, 1969
	42	50	M	A	Zima, 1978
	42	50	M	M	Zima, 1984
Eptesicus andinus	50	48	SM	A	Baker and Patton, 1967
Eptesicus brasiliensis	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Baker et al., 1982
Eptesicus capensis	32	50	SM	A	Peterson and Nagorsen, 1975
Eptesicus circumdatus	50	48	SM	—	Heller and Volleth, 1984
Eptesicus diminutus	50	48	SM	A	Williams, 1978
Eptesicus furinalis	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Williams, 1978
Eptesicus fuscus	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Bickham, 1979*a*
Eptesicus guadeloupensis	50	48	SM	A	Genoways and Baker, 1975

Table 1.—*Continued.*

Taxon	2N	FN	X	Y	Authority
Eptesicus hottentotus	50	48	SM	—	Peterson and Nagorsen, 1975
Eptesicus japonensis	50	48	SM	SM	Ando et al., 1977
Eptesicus lynni	50	48	SM	A	Bickham, 1979*a*
Eptesicus nilssoni	50	48	—	—	Ando et al., 1977
	50	50	M	A	Zima, 1978
	50	48	M	—	Zima, 1982
Eptesicus serontinus	50	48	SM	A	Baker and Patton, 1967
	50	48	SM	A	Vorontsov, 1969
	50	52	SM	SM	Fedyk and Fedyk, 1970
	50	48	SM	—	Baker et al., 1974
	50	48	SM	A	Bickham, 1979*a*
	50	48	SM	—	Baker and Bickham, 1980
Vespertilio murinus	38	50	M	A	Vorontsov, 1969
	38	54	M	A	Zima, 1978
	38	50	—	—	Obara and Saitoh, 1977
Vespertilio orientalis	38	50	M	A	Ando et al., 1977
	38	50	SM	A	Obara and Saitoh, 1977
Vespertilio superans	38	50	M	A	Vorontsov, 1969
	38	50	M	A	Zima, 1978
Histiotus montanus	50	48	SM	A	Williams and Mares, 1978
Tylonycteris pachypus	46	52	A	M	Yong et al., 1971
Tylonycteris robustula	32	52	A	M	Yong et al., 1971
	32	52	A	M	This study
Hesperoptenus blanfordi	34	60	A	—	This study
Hesperoptenus tickelli	32	46	ST	M	This study
Nycticeius humeralis	46	48	SM	A	Baker and Patton, 1967
	46	48	SM	A	Bickham, 1979*a*
Scotoecus hindei	30	50	ST	SM	Nagorsen et al., 1976
Rhogeessa genowaysi	42	50	SM	SM	Baker, 1984
Rhogeessa parvula	44	50	SM	SM	Baker and Patton, 1967
	44	50	SM	—	Bickham and Baker, 1977
Rhogeessa tumida	42	50	SM	SM	Baker and Patton, 1967
	30	50	—	—	Baker, 1970
	42	50	SM	SM	Bickham and Baker, 1977
	34	50	SM	SM	Bickham and Baker, 1977
	32	50	SM	SM	Bickham and Baker, 1977
	30	50	SM	ST	Bickham and Baker, 1977
	34	50	—	—	Baker and Bickham, 1980
	30	50	—	—	Baker and Bickham, 1980
	52	52	—	—	Honeycutt et al., 1980
	34	50	SM	—	Baker et al., 1985
	32N	50	SM	—	Baker et al., 1985
	32B	50	SM	—	Baker et al., 1985
	30	50	SM	A	Baker et al., 1985

Table 1.—*Continued.*

Taxon	2N	FN	X	Y	Authority
Scotophilus dinganii	36	52	A	M	Schlitter et al., 1980
	36	62[1]	—	—	Peterson and Nagorsen, 1975
Scotophilus heathi	36	52	M	A	Sharma et al., 1974
Scotophilus kuhlii	36	52	M	A	Pathak and Sharma, 1969
	36	48	M	A	Harada et al., 1982*b*
Scotophilus temminckii	36	52	SM	A	Pathak and Sharma, 1969
	36	48	SM	A	Harada and Kobayashi, 1980
Scotophilus viridis	36	54	A	M	Schlitter et al., 1980
Lasiurus borealis	28	46	SM	A	Baker and Patton, 1967
	28	48	SM	A	Baker and Mascarello, 1969
	28	48	SM	A	Bickham, 1979*a*
Lasiurus cinereus	28	46	SM	A	Baker and Patton, 1967
	28	48	SM	A	Bickham, 1979*a*
Lasiurus ega	28	48	SM	A	Bickham, 1979*a*
Lasiurus ega panamensis	28	46	A	A	Baker and Patton, 1967
Lasiurus ega xanthinus	28	46	SM	A	Baker and Patton, 1967
Lasiurus intermedius	26	40	SM	A	Baker and Patton, 1967
	26	42	A	A	Baker, 1970
Lasiurus seminolus	28	48	SM	A	Baker and Mascarello, 1969
	28	48	SM	A	Bickham, 1979*a*
Barbastella barbastellus	32	52	—	—	Matthey and Bovey, 1948
	32	50	M	A	Bovey, 1949
	32	50	SM	A	Capanna et al., 1968
	32	52	SM	A	Zima, 1978
Barbastella leucomelas	32	50	SM	A	Ando et al., 1977
Plecotus auritus	32	52	—	—	Matthey and Bovey, 1948
	32	50	M	A	Bovey, 1949
	32	54	SM	A	Fedyk and Fedyk, 1970
Plecotus auritus auritus	32	54	M	A	Ando et al., 1977
	32	52	M	A	Zima, 1978
Plecotus auritus sacrimontis	32	50	M	A	Harada, 1973
Plecotus austriacus	32	50	SM	A	Baker, 1970
	32	54	SM	A	Fedyk and Fedyk, 1970
	32	50	SM	A	Baker et al., 1974
	32	52	M	A	Zima, 1978
Plecotus phyllotis	30	50	—	—	Baker and Patton, 1967
	30	50	SM	A	Baker and Mascarello, 1969
Idionycteris phyllotis	30	50	SM	—	Bickham, 1979*a*
	30	50	SM	—	Stock, 1983

Table 1.—*Continued.*

Taxon	2N	FN	X	Y	Authority
Plecotus rafinesquii	32	50	A	A	Baker and Mascarello, 1969
Plecotus townsendi	32	48	—	—	Baker and Patton, 1967
	32	50	A	A	Baker and Mascarello, 1969
	32	50	A	A	Bickham, 1979*a*
	32	50	A	A	Stock, 1983
Euderma maculatum	30	50	SM	A	Williams et al., 1970
	30	50	SM	—	Stock, 1983
Subfamily Miniopterinae					
Miniopterus australis	46	50	SM	A	Harada and Kobayashi, 1980
Miniopterus magnater	46	50	SM	A	Harada and Kobayashi, 1980
Miniopterus schreibersi	46	50	—	—	Matthey and Bovey, 1948
	46	50	SM	A	Baker et al., 1974
	46	50	SM	A	Bickham and Hafner, 1978
	46	50	SM	A	Bickham, 1979*a*
	46	50	SM	A	Harada and Kobayashi, 1980
Miniopterus schreibersi haradai	46	52	SM	A	This study
Miniopterus schreibersi fuliginosus	46	52	SM	A	Harada, 1973
Subfamily Murininae					
Murina aurata	44	60	SM	A	Ando et al., 1977
Murina leucogaster	44	50	—	—	Harada, 1973
	44	58	SM	A	Ando et al., 1977
	44	50	SM	A	This study
Harpiocephalus mordax	40	62*	—	—	This study
Subfamily Kerivoulinae					
Kerivoula papillosa	38	52**	—	—	This study
Subfamily Nyctophilinae					
Antrozous pallidus	56	50	SM	A	Bickham, 1979*a*
Bauerus dubiaquercus	44	52	SM	A	Engstrom and Wilson, 1981

* Obara et al., 1976*a,* report on inversion polymorphism in chromosome 5.

** Includes sex chromosomes in FN.

[1] Examination of the figure in Peterson and Nagorsen (1975) gives a FN = 52. This probably represents a typographical error.

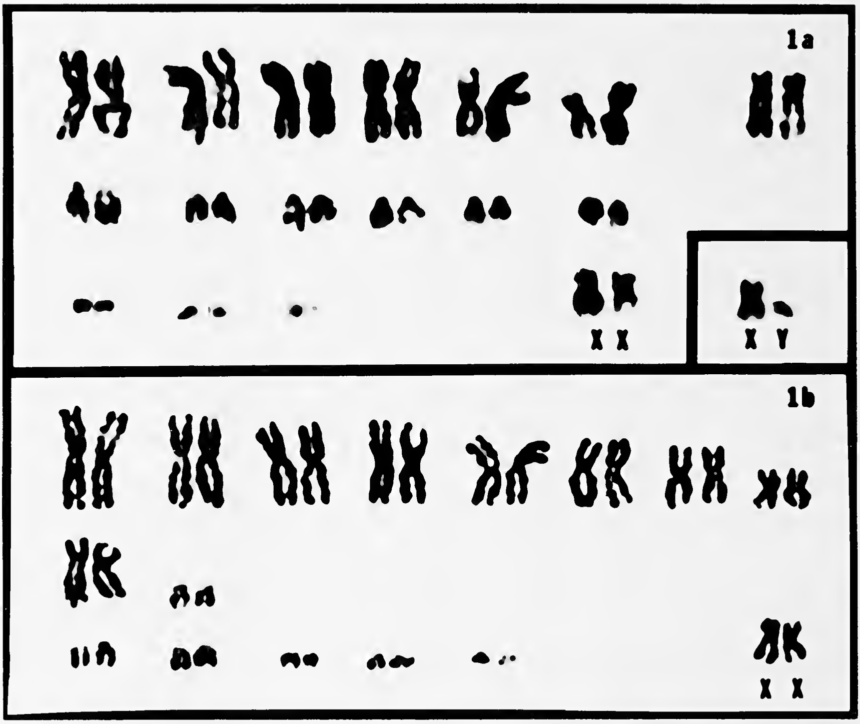

Fig. 1.—The standard karyotypes of: a) *Pipistrellus mimus* F (CM 88135), 2n = 34, FN = 46, inset *P. mimus* M (CM 88131); b) *Pipistrellus pulveratus* F (CM 88136), 2n = 32, FN = 50.

to minute. The X is medium-sized and submetacentric and the Y is small and acrocentric.

Pipistrellus pulveratus (2n = 32, FN = 50; Fig. 1b).—The autosomal complement includes eight pairs of metacentric or submetacentric chromosomes ranging in size from large to medium. There is one large pair and one small pair of subtelocentric chromosomes, and five pairs of acrocentric chromosomes ranging from medium-sized to small. The X is medium-sized and submetacentric.

Tylonycteris robustula (2n = 32, FN = 50; Fig. 2a).—The karyotype shown here is similar to that reported by Yong et al. (1971), but there are slight differences. Both studies report 2n = 32 with nine pairs of metacentric to submetacentric chromosomes. However, our specimens had one pair of medium-sized subtelocentric chromosomes and five pairs of acrocentric chromosomes ranging from medium-sized to minute, whereas Yong et al. (1971) reported two pairs of subacrocentric

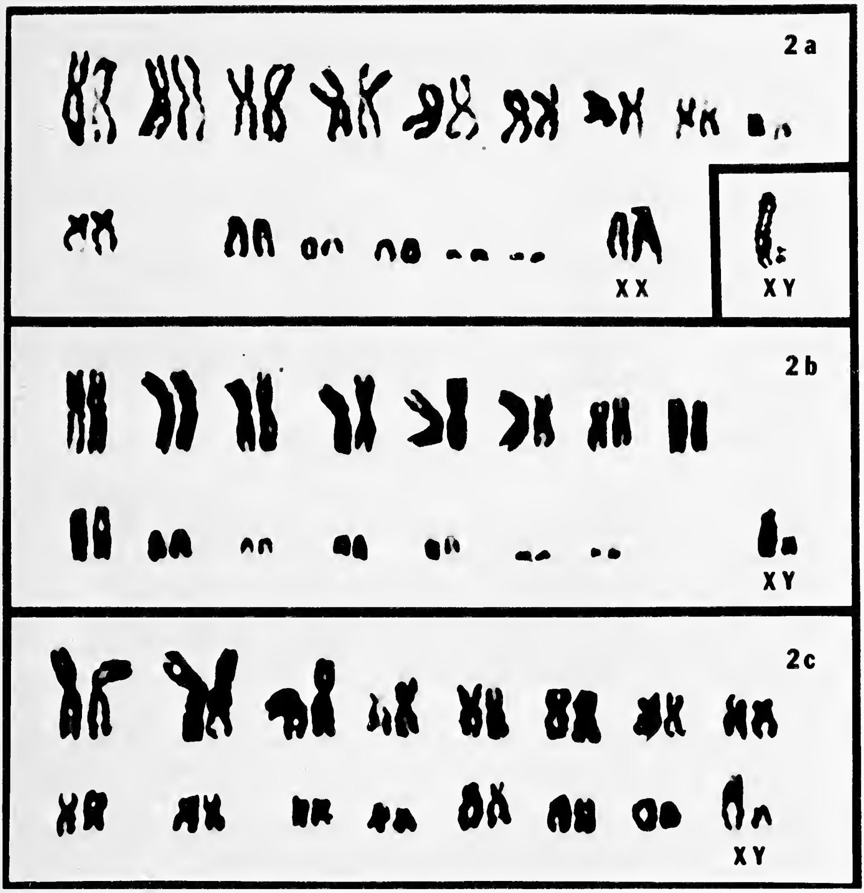

Fig. 2.—The standard karyotypes of: a) *Tylonycteris robustula* F (TK 21416), 2n = 32, FN = 50; inset *T. robustula* M. (CM 88152); b) *Hesperoptenus tickelli* M (TCWC 47481), 2n = 32, FN = 46; c) *Hesperoptenus blanfordi* F (CM 88114), 2n = 34, FN = 60.

and two pairs of acrocentric chromosomes. The X is large and acrocentric and the Y is a small metacentric chromosome.

Hesperoptenus tickelli (2n = 32, FN = 46; Fig. 2b).—The autosomal complement contains eight pairs of metacentric to submetacentric chromosomes ranging from large to medium-sized. There also are seven pairs of medium-sized to minute acrocentric chromosomes. The X is a large subtelocentric and the Y is a small metacentric chromosome.

Hesperoptenus blanfordi (2n = 34, FN = 60; Fig. 2c).—The autosomal complement includes 13 pairs of metacentric to submetacentric chromosomes gradually decreasing in size from large to small. There is one pair of medium-sized subtelocentric chromosomes and two pairs of medium-sized acrocentric chromosomes. The X is a medium-sized subtelocentric chromosome, and the Y is a small subtelocentric chromosome.

Subfamily Kerivoulinae

Kerivoula papillosa (2n = 38, FN = 52; Fig. 3a).—Metacentric to submetacentric chromosomes include three large pairs, one medium-sized pair and one small pair. There is one medium-sized pair and one large pair of subtelocentric chromosomes, and 12 pairs of acrocentric chromosomes grading from large to small. The sex chromosomes were not identified in this species, but are probably the medium-sized pair of submetacentric chromosomes. The fundamental number includes the presumed sex chromosomes.

Subfamily Miniopterinae

Miniopterus schreibersi haradai (2n = 46, FN = 52; Fig. 3b).—The autosomal complement includes two large and one medium-sized pairs of metacentric chromosomes, and one medium-sized pair of subtelocentric chromosomes. There are 18 acrocentric pairs ranging from large to small. One medium-sized acrocentric pair has a secondary constriction near the centromere. The X is a medium-sized submetacentric chromosome. Other reports of karyotypes from *Miniopterus schreibersi* (Harada, 1973; Ando et al., 1977; Bickham and Hafner, 1978) identified the smallest pair of chromosomes as biarmed. This was not apparent from our preparations; however, the medium-sized subtelocentric pair of chromosomes we observed is evidently unique to Thai *Miniopterus schreibersi* and is not seen in European (Bickham and Hafner, 1978) or Japanese (Harada, 1973) populations.

Subfamily Murininae

Murina leucogaster (2n = 44, FN = 50; Fig. 3c).—There are two pairs of large metacentric, and two pairs of medium-sized to small submetacentric autosomes. The autosomal complement is completed by 17 acrocentric pairs ranging from large to small. The X is medium-sized and submetacentric. This karyotype is similar to that of *Murina leucogaster* from Atesu, Japan (Harada, 1973), but the third largest

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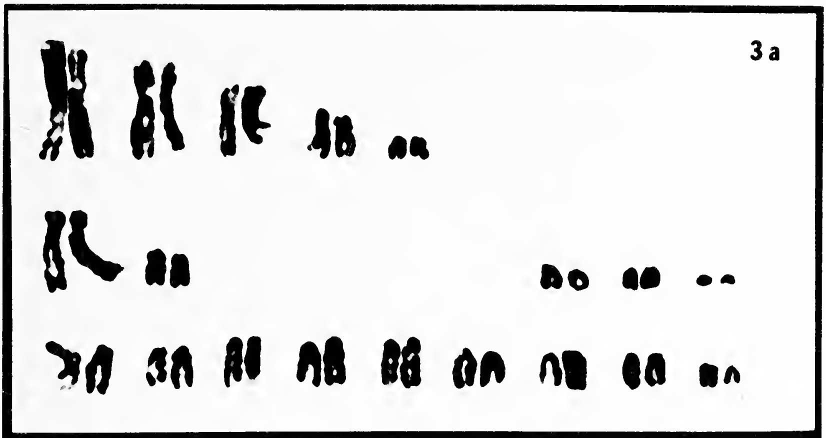
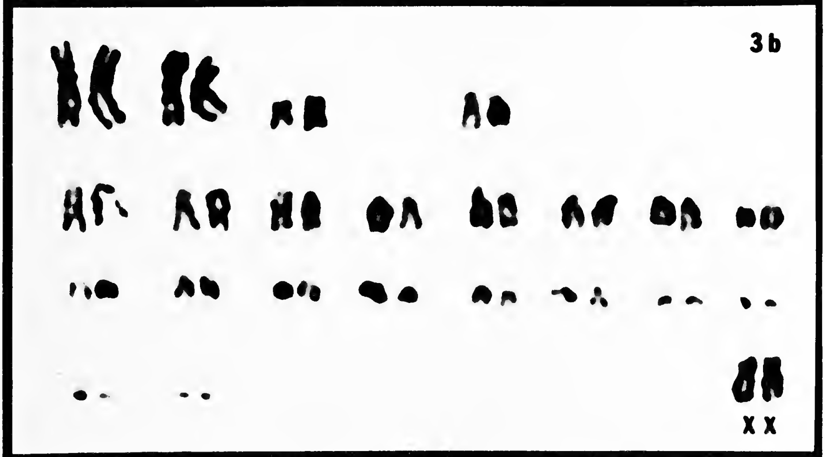
Fig. 3.—The standard karyotypes of: a) *Kerivoula papillosa* F (CM 88164), 2n = 38, FN = 52 (FN includes sex chromosomes); b) *Miniopterus schreibersi haradai* F (CM 88157), 2n = 46, FN = 52; c) *Murina leucogaster* F (CM 88163), 2n = 44, FN = 50.


3a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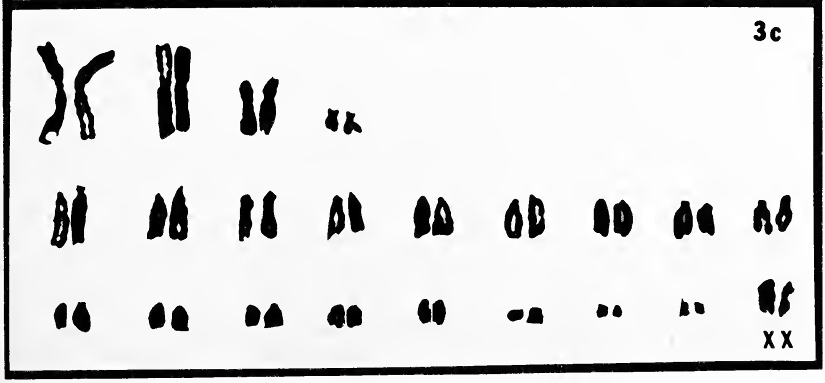
3c

chromosome is considerably smaller in our material than in the Japanese bats.

Harpiocephalus mordax (2n = 40, FN = 62).—Poor field preparation of *Harpiocephalus mordax* made chromosome analysis difficult, but counts of metaphase spreads consistently gave a diploid number of 40. The chromosomal complement includes three large pairs, one medium-sized pair and two small pairs of metacentric to submetacentric chromosomes and five pairs of subtelocentric chromosomes. There are nine pairs of acrocentric chromosomes gradually decreasing from large to small. The single individual examined was a female, so sex chromosomes could not be identified but are probably the medium-sized pair of submetacentric chromosomes. The fundamental number includes the presumed sex chromosomes.

DISCUSSION

This karyological study is consistent with earlier studies (Capanna and Civitelli, 1970; Baker and Patton, 1967; Pathak and Sharma, 1969; Bickham, 1979*b*), which have indicated extensive chromosomal variability between genera in vespertilionid bats. Within genera for which karyotypic data have been obtained on more than one species, three different patterns of chromosomal variability are apparent. Of the 15 genera (Table 1) for which more than one species have been karyotyped, 11, including members of three subfamilies, can be characterized as conservative genera. These are genera in which all species have the same or nearly the same standard karyotype. *Myotis* (2n = 44, FN = 50, 52) and *Eptesicus* (2n = 50, FN = 48, with the exception of *E. capensis*) are typical representatives of this pattern. *Scotophilus, Vespertilio, Barbestella, Lasiurus, Plecotus, Miniopterus,* and *Murina* also exhibit this pattern. Genera exhibiting the second pattern of variation are interspecifically variable. Five genera currently fill this group (Table 1). *Pipistrellus* has nine different diploid numbers among the 15 species that have been karyotyped. *Nyctalus,* with data from four species, shows three different karyotypes and *Tylonycteris* and *Hesperoptenus* each has two different karyotypes for two species. The third pattern is one of intraspecific variability and is best documented in the genus *Rhogeessa* (Table 1). Three species possess at least nine different karyotypes. *Rhogeessa parvula* has a 2n = 44, FN = 50 karyotype, and *R. genowaysi* has 2n = 42, FN = 50. *R. tumida,* however, has 2n = 30, 32a, 32b, 34, 42, 44, 52 and FN = 50, 52).

Pipistrellus exhibits such wide variability that even with karyotypes for approximately one third of the recognized species no real patterns of karyotypic relationships are evident within the genus. Several species share the *Myotis*-like 2n = 44, FN = 50 karyotype considered primitive for the family (Bickham, 1979*a*, 1979*b*; Baker and Patton, 1967). Many of the other karyotypes can be related to each other and to the primitive *Myotis*-like karyotype on the basis of Robertsonian fusions and fissions. *Pipistrellus pulveratus* has a karyotype of 2n = 32, FN = 50 in two individuals. The karyotypes appear to differ from the primitive *Myotis*-like karyotype by six Robertsonian fission-fusion events.

The karyotype of *P. mimus* cannot be so directly derived from the *Myotis*-like primitive. Manna and Talukdar (1965) reported a karyotype of 2n = 34 from southwestern India and Pathak and Sharma (1969) found 2n = 38, FN = 48 for the same species in northeastern India. We found 2n = 34, FN = 46 for four individuals from northwestern Thailand. This karyotype can be derived from the 2n = 38 karyotype through one centric fusion and the loss, possibly through tandem fusion, of one small pair of acrocentric chromosomes. The 2n = 38 karyotype has 6 pairs of large metacentric to submetacentric chromosomes and 12 pairs of acrocentric chromosomes. The Thai karyotypes have an additional biarmed chromosome that is subtelocentric and three fewer pairs of acrocentrics. Neither karyotype can be derived from the *Myotis*-like primitive karyotype without the loss or tandem fusion of at least one pair of acrocentric chromosomes. These data support the suggestion of Pathak and Sharma (1969) that translocations other than Robertsonian fusions may play an important role in chromosomal evolution in some groups of *Pipistrellus.* These authors also suggest that the two karyotypic forms of *P. mimus* may represent cryptic species. Cryptic species differentiated by karyotypes have been discovered for the family among the many karyotypic forms of *Rhogeessa* (Baker, 1984), so this explanation of karyotypic variation in *P. mimus* is not unreasonable. An alternative explanation of the chromosomal variability observed in *P. mimus* may involve intraspecific variability. This phenomenon is very rare among vespertilionids but is well documented within the genus *Rhogeessa.* In either case, *P. mimus* merits comprehensive cytogenetic study throughout its range in southern Asia.

Our karyotype of *Tylonycteris robustula* is slightly different from that reported by Yong et al. (1971). The extremely small chromosomes they consider biarmed are probably acrocentric. The *T. robustula* autosomal karyotype readily can be derived from the *Myotis*-like primitive condition by a series of six centric fusions. The X chromosome, however, has experienced a pericentric inversion to an acrocentric condition and the Y, either a pericentric inversion or the addition of a heterochromatic short arm making it biarmed. An acrocentric or subtelocentric X chromosome is rare among the Vespertilionidae occurring in only two species of *Pipistrellus,* two species of *Scotophilus, Scotoecus hindei,* two species of *Lasiurus,* two species of *Plecotus,* and two species of *Hesperoptenus* (Table 1). *Tylonycteris robustula* also has diploid and fundamental numbers in common with the two *Plecotus.* The karyotypes are at least superficially the same, except both *Plecotus* have acrocentric rather than biarmed Y chromosomes. Assumptions of homology on the basis of standard karyotypes must be made with caution, however (Bickham and Baker, 1977; Baker et al., 1985; Haiduk and Baker, 1982). The similarities between the plecotine genus, *Plecotus,* and the vespertilionine genus *Tylonycteris* are likely the result of convergence. Tate (1942) considered *Tylonycteris* and *Philetor* as derived from an ancestor similar to the *Pipistrellus joffrei* group. Neither *Philetor* nor any members of the *P. joffrei* group have been karyotyped for comparison, however.

The genus *Hesperoptenus* is poorly understood systematically. Four species are currently recognized, two of which are known from only a few specimens. The more common forms, *H. tickelli* and *H. blanfordi,* are very different from one another morphologically. Tate (1942) commented that if the genus was not polyphyletic it at least contained strongly differentiated species. *Hesperoptenus blanfordi* and *H. tickelli* also are karyologically distinct. Whereas the two species have similar diploid numbers, *H. blanfordi* has one of the highest FNs reported for the family, and *H. tickelli* has an FN of 52, among the most commonly found in the family. To derive one karyotype from the other would require one fission/fusion event and five pericentric inversions or heterochromatic additions. The *H. tickelli* karyotype can be derived from the *Myotis*-like primitive karyotype through four Robertsonian fusions and the loss or tandem fusion of two pairs of acrocentrics. There also has been a pericentric inversion changing the primitive biarmed X to a derived subtelocentric configuration. The Y is a derived small metacentric chromosome, either through pericentric inversion or heterochromatic addition. The *H. blanfordi* karyotype is more difficult to derive from the *Myotis*-like primitive requiring at least five Robertsonian fusions and five pericentric inversions in the autosomal complement. The X chromosome also is inverted to an acrocentric condition. The more parsimonious scenario might consist of *H. tickelli* diverging from the *Myotis*-like ancestor with *H. blanfordi* being a highly divergent offshoot of *H. tickelli.* Chromosomal data support the conclusion that *H. tickelli* and *H. blanfordi,* at best, are only distantly related. Ryan (1966) and Koopman (1971) thought *Hesperoptenus* was closely related to *Glauconycteris* and *Chalinolobus.* Hill (1976) considered dental differences between the three genera to be too great and considered *Hesperoptenus* more closely aligned with the genus *Scotophilus. Hesperoptenus tickelli* and some *Scotophilus* have FN and uniarmed X chromosomes in common. *H. tickelli* has one fewer pair of biarmed chromosomes and one fewer pair of acrocentric chromosomes than *Scotophilus,* however. No species of *Glauconycteris* or *Chalinolobus* have been karyotyped for comparison.

Our karyotype of *Miniopterus schreibersi haradai* agrees well with previous reports. Miniopterinae is considered the most derived subfamily of the Vespertilionidae, even being accorded familial status by some authors (Mein and Tupinier, 1977) yet the karyotype found throughout this subfamily differs from the primitive *Myotis*-like karyotype by a single Robertsonian fission and two pericentric inversions (Bickham and Hafner, 1978). Harada (1973) found in *M. s. fuliginosus,* and we found in *M. s. haradai,* a medium-sized subtelocentric chromosome apparently unique to Thai members of the species.

Members of the subfamily Murininae have been regarded as a specialized offshoot of an early *Myotis*-like ancestor (Miller, 1907). The subfamily contains two genera, *Murina* and *Harpiocephalus.* All members of *Murina* karotyped so far have had a standard karyotype essentially identical to the 2n = 44 *Myotis*-like primitive, agreeing with the early divergence of Murininae from the vespertilionine line. Tate (1941) considered the second genus, *Harpiocephalus,* as a very specialized offshoot of the line leading to *Murina,* and Miller (1907) termed *Harpiocephalus* as one of the most aberrant genera of the family. The *Harpiocephalus* karyotype is derived from the primitive *Myotis*-like karyotype and the *Murina* karyotype by two possible pericentric inversions indicating that *Harpiocephalus* probably evolved from a *Murina*-like ancestor rather than diverging earlier from the line leading to *Murina.*

The subfamily Kerivoulinae has been considered the least specialized of the vespertilionid subfamilies being closely related to the "least progressive" genera of the subfamily Vespertilioninae (Tate, 1941). The karyotype of *Kerivoula papillosa* can be derived from the primitive *Myotis*-like karyotype through two Robertsonian fusions and the loss or tandem fusion of one pair of acrocentric chromosomes.

Within the Vespertilionidae, *Kerivoula* shares a similar standard karyotype with the Japanese *Pipistrellus endoi* and members of the genus *Vespertilio.* In the past, the entire genus *Pipistrellus* has been considered a part of *Vespertilio,* but Zima (1978) considers the distinctive karyotype of *Vespertilio* as justification for separate generic status. Ando et al. (1980) suggest *P. endoi* may be a link between the genus *Vespertilio* and its *Pipistrellus*-like ancestor. The subfamily Kerivoulinae may have a similar link to its *Pipistrellus*-like ancestor here. There are no other data to link the three, however, and postulation of a common origin is only speculative.

Unquestionably, Robertsonian fusions and fissions have played a major role in chromosomal evolution of the family Vespertilionidae

(Bickham, 1979*a*). However, the standard karyotypes reported here indicate a greater importance for non-Robertsonian rearrangements such as inversions and translocations as evolutionary mechanisms than was previously thought (Bickham, 1979*a*; Bickham and Baker, 1977). Pericentric inversions, tandem fusions, or heterochromatic additions apparently have occurred in *Tylonycteris robustula, Miniopterus schreibersi haradai, Kerivoula papillosa,* and *Harpiocephalus mordax* in their evolution from the 2n = 44 ancestral karyotype. *Hesperoptenus tickelli* and *H. blanfordi* may show an especially high incidence of pericentric inversions, requiring up to five possible inversion events to be derived from the ancestral karyotype. Examination of these standard karyotypes emphasizes how poorly understood are vespertilionid karyological relationships. Speculations about relationships based on standard karyotypes can be misleading, however. G-band analysis has indicated that constant genera such as *Myotis* are indeed as constant as was assumed from standard karyotypes (Bickham, 1979*b*). It also has pointed out extreme chromosomal differences where standard karyotypes indicated homology (Baker et al., 1985). Chromosomal banding analysis should allow a more accurate assessment of the mechanisms of chromosomal evolution seen in the family Vespertilionidae. G-banding also will provide a means to test apparent homologies between groups such as *Kerivoula* and *Vespertilio.* The extensive variability between, and possibly within, species of *Pipistrellus* also will be much better characterized by G-banding. Comparison of conserved and derived chromosome sequences revealed by G-banding is imperative to an understanding of systematic relationships among the Vespertilionidae.

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RESULTS OF THE CARNEGIE MUSEUM OF NATURAL HISTORY EXPEDITIONS TO BELIZE. I. SYSTEMATIC STATUS AND GEOGRAPHIC DISTRIBUTION OF *SIBON NEILLI* (REPTILIA, SERPENTES)

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Abstract

The nominal species *Sibon neilli* Henderson, Hoevers and Wilson (type-locality, "vicinity of Belize City, Belize") is shown to be a southern subspecies of *Sibon sanniola* Cope (type-locality, "Chichen Itza, Yucatan, Mexico"), confirming the arrangement proposed by Kofron (1985). *Sibon sanniola neilli* differs from *Sibon s. sanniola* in having a banded, rather than spotted, color pattern, and higher ventral and subcaudal scale counts.

Introduction

Sibon neilli Henderson, Hoevers, and Wilson (1977) is an enigmatic member of the snake fauna of Caribbean Central America. The species was described from a unique type-specimen, collected in "the vicinity of Belize City, Belize District, Belize." Henderson et al. (1977) recognized that *Sibon neilli* is very similar to *S. sanniola,* a species endemic to the northern part of the Yucatan Peninsula, but diagnosed *S. neilli* on the basis of higher ventral and subcaudal scale counts, a different pattern of supralabial, postocular, and temporal scale contacts, and a banded color pattern. Kofron (1985), without examining addi-

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Table 1.—*Ventral and subcaudal scale counts in* Sibon sanniola *and* S. neilli.

Population	Ventrals		Subcaudals	
	♂♂	♀♀	♂♂	♀♀
*S. sanniola**	145–159 (Mean = 153.7 ± .64) N = 26	144–160 (Mean = 151.8 ± .79) N = 24	67–83 (Mean = 75.0 ± .61) N = 24	58–74 (Mean = 65.0 ± .82) N = 23
*S. neilli***	162		88	
*S. neilli****	153–162 (Mean = 159) N = 3	146, 157	83–89 (Mean = 86.7) N = 3	70, 81

* Yucatán and Quintana Roo, México.

** Holotype only.

*** All Belize and Guatemala specimens, except FMNH 4247.

tional specimens of *S. neilli* and without comment, considered *S. neilli* a subspecies of *Sibon sanniola.*

During field work in Belize in 1984 we collected a specimen of *Sibon* at Chaa Creek, Cayo District, that has the characteristic banded dorsal pattern of *S. neilli.* In addition, there is a specimen in Carnegie Museum of Natural History from El Petén, Guatemala, that also fits the description of *Sibon neilli.* I have compared these specimens with the holotype and previously only known specimen of *S. neilli,* with all other *Sibon* of this group available from Belize, and with an extensive series of *Sibon sanniola* from Yucatán and Quintana Roo, México (see Specimens Examined).

Results

Ventral and subcaudal scale counts.—Data summaries for ventral and subcaudal scale counts for *Sibon sanniola* and *Sibon neilli* are presented in Table 1. Both the ventral and subcaudal counts for the holotype of *Sibon neilli* exceed the known ranges for these counts in *S. sanniola,* as pointed out by Henderson et al. (1977). The range of ventral counts for males in the "southern" population overlaps the range for the "northern" population, as do the ranges of ventral counts for females in the two populations. Subcaudal counts in males barely overlap in the two populations, and overlap slightly in females. Although the sample size for the southern population is small, it appears that the differences in segmental counts are consistent. A specimen from "British Honduras" (FMNH 4247, male) has 153 ventrals and 67 caudals, both counts within the ranges for the northern population.

Supralabial-postocular-temporal contact.—The holotype of *Sibon neilli* has 9-9 supralabials, with the 4th, 5th, and 6th entering the orbit. The 7th supralabial is in contact with the lower postocular and the primary temporal. Henderson et al. (1977) regarded the 7th supralabial-postocular-temporal contact as a distinctive character of *S. neilli,* stating that it "occurs occasionally in *S. sanniola,* but in no other species of *Sibon.*" In reality, this is the contact pattern that is most common in *Sibon sanniola.* In a series of 51 *S. sanniola* from Yucatán and Quintana Roo the 7th supralabial contacts only the lower postocular and primary temporal 88% of the time (right and left sides of the head scored separately). In the remaining 12% the upper tip of the 7th supralabial, posterior angle of the lower postocular, and anterior tips of the primary and secondary temporals make a single point contact. In specimens with the more common pattern, the anterior tip of the primary temporal makes a broad contact with the postocular, preventing contact of the 7th supralabial with the secondary temporal.

Fig. 1.—*Sibon sanniola neilli* (CM 105981), Chaa Creek, Cayo Dist., Belize; from a Kodachrome photo of the living specimen by Paul S. Freed.

Color pattern.—The holotype of *Sibon neilli* has a series of 34 dark dorsal crossbands on a lighter ground color, faded almost to white in the specimen. The widest crossbands are 2½ scales long at the middorsal line, and taper to about 1½ scales at the lowermost dorsal scale rows. The edges of the bands are jagged, not straight. The bands extend ventrally only to the outer ends of the ventral scales. The center of the belly is marked with a series of roughly paired, longitudinal dark "dashes," each usually two ventral scales long. There are about 21 dark crossbands on the tail, which become increasingly crowded toward the tail tip. The dark nuchal band extends ventrally to the edges of the ventrals, and anteriorly as a middorsal dark bar that reaches the frontal scale. The holotype is much faded, resulting in enhanced contrast between the dorsal dark bands and the interspaces (Henderson et al., 1977:fig. 1).

The specimen from Chaa Creek, Belize (CM 105981), has 42 dorsal body bands that taper ventrally from 2½ to 1½ scales wide, and 22 bands on the tail. The nuchal band has a broad anterior extension that reaches the parietals, and the top of the head is lighter brown. The sides of the head are much lighter. The belly is lightly marked with indistinct brown smudges. The only significant difference between the pattern of this specimen and that of the holotype is the amount of contrast between the dorsal bands and the interspaces. In life, the dorsal bands of CM 105981 were medium brown, and the interspaces dark tan, providing minimal contrast (Fig. 1).

The specimen from Las Cañas, Guatemala (CM 58282), has 38 barely discernible dark bands on the body, and a banded tail. The bands are only slightly darker than the medium brown ground color. The head and nuchal pattern are typical, and the belly is moderately well-marked with longitudinal dashes.

The typical color pattern of *Sibon sanniola* is a series of dark, light-edged middorsal spots, frequently fused to form an irregular "zig-zag" line, on a light brown to ash gray background. The lateral and ventrolateral spot series may either persist, be reduced, or fade completely. The tail is spotted along the middorsal line. The belly typically is marked with pairs of dark longitudinal dashes. The nuchal band, with anterior extension onto the head, is as described for *Sibon neilli.*

A juvenile specimen from Xunantunich, Belize (MCZ 56994, 180 mm total length), has a pattern of about 47 middorsal spots (many fused), and two series of lateral dark spots on each side. A very similar pattern occurs in juvenile *S. sanniola* (CM 49739, 140 mm; CM 49754, 156 mm). This suggests that the banded adult pattern of *S. neilli* may result from ontogenetic fusion of the dorsal, lateral, and ventrolateral spot series, which remain discrete in *S. sanniola.*

CONCLUSIONS

In size, habitus, and most details of scutellation *Sibon neilli* and *Sibon sanniola* are identical. The supposedly diagnostic arrangement of supralabial, postocular, and temporal scales of *S. neilli* actually is consistent with the pattern usually found in *S. sanniola.* Only the color pattern and numbers of ventral and subcaudal scales are distinctive characters of the *S. neilli* population. Although Kofron (1983) shows the range of *S. sanniola* (including *S. neilli*) as being continuous from northern Yucatán and Quintana Roo southward into Belize and El Petén, no specimens are available from the critical areas where intergradation would be expected (Lee, 1980 and personal communication). The southernmost precise locality for *Sibon sanniola* is Felipe Carrillo Puerto, Quintana Roo (Peters, 1953), although FMNH 4247 from "British Honduras" has both scale counts and color pattern typical of *S. sanniola.* The range of *S. neilli* extends from coastal central Belize (Belize City), southwestward into El Petén, Guatemala. Despite the apparent hiatus, I assume that the range of the species is continuous, as there is no ecological discontinuity between southern Quintana Roo and central Belize, and I interpret the morphological differences between the southern and northern populations as clinal variation within a single species.

Clinal variation is common in colubrid snake species that have extensive latitudinal ranges on the Yucatan Peninsula. Such clinal variation typically involves either the color pattern or segmental counts, or both. Examples are *Conophis lineatus* (Wellman, 1963), *Leptodeira frenata* (Duellman, 1958), *Ninia sebae* (Schmidt and Rand, 1957), and *Leptophis mexicanus* (Oliver, 1948), to cite a few of many species that illustrate this variational pattern. I conclude that Kofron (1985) was correct in allocating the name *Sibon neilli* to the southern population of *Sibon sanniola* that is characterized by a banded color pattern and higher ventral and subcaudal scale counts.

SPECIMENS EXAMINED

Sibon sanniola neilli.—BELIZE: Belize Dist., vicinity of Belize City (MPM 8929, holotype). Cayo Dist., Chaa Creek, 5 mi. S San Ignacio (CM 105981); vicinity of Augustine (MPM 8208); Xunantunich (MCZ 56994). GUATEMALA: El Petén, Las Cañas (Municipality San Luis) (CM 58282). Total 5 specimens.

Sibon sanniola sanniola.—BELIZE: "British Honduras" (FMNH 4247). MÉXICO: Quintana Roo, Pueblo Nuevo X-Cán (CM 45778–45785, 46844–46845, 46881–46883, 49056, 49062, 49136, 49154, 49159, 49163). Yucatán, Chichén Itza (FMNH 20609, 20613, 26988, 36257–36258, 36268, 36272, 36276, 36285, 36287, 36289, 36296); Kantunil (FMNH 36264, 36286, 36288, 36270); Libre Unión (FMNH 36259, 36262, 36266, 36273, 36278, 36280–36283, 36290, 36294–36295); Pisté (CM 46955–46958, 47004, 47142–47148, 49734–49741, 49742–49748, 49749–49756); Progreso (FMNH 40734–40735); Yokdzonot (FMNH 36261, 36263, 36265, 36267, 36269, 36271, 36274–36275, 36277, 36279, 36284, 36290–36293, 36297). Total 101 specimens.

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KARYOTYPES OF ELEVEN SPECIES OF MOLOSSID BATS FROM AFRICA (MAMMALIA:CHIROPTERA)

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Abstract

Standard karyotypic data are reported for 11 species of molossid bats collected from Somalia and Cameroun, Africa. Chromosomal data are reported for the first time for *Chaerephon ansorgei, C. aloysiisabaudiae, Mops midas, M. spurrelli, M. thersites, M. brachypterus, M. petersoni, M. demonstrator,* and *M. nanulus* (all were formerly members of the genus *Tadarida*). Karyotypes for two of the species we examined have been reported previously. Although our data corroborate the karyotype of *C. pumila* described by Dulic and Mutere (1973), our karyotypic analysis of *M. condylurus* differs substantially from that presented by these authors. In addition to these data, we provide a summary of the available karyotypic data for molossid bats studied to date.

Introduction

The Molossidae is a group of insectivorous, swift-flying bats that live in tropical and temperate parts of the world. More than half of the 91 or so extant species have been regarded as members of the genus *Tadarida* (Corbet and Hill, 1980); the remaining species are spread among

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Table 1.—*Summary of karyotype morphology for 11 species of African molossid bats. Letter designations are: M—metacentric, SM—submetacentric, ST—subtelocentric, A—acrocentric.*

Species	Large M	Medium M	Medium ST	Small ST	Medium–small A	X	Y	FN
Chaerephon ansorgei	1	3	4	2	13	ST	A	66
Chaerephon aloysiisabaudiae	1	3	4	2	13	SM	A	66
Chaerephon pumila	1	2	3	0	17	SM	A	58
Mops midas	1	3	4	2	13	SM	A	66
Mops condylurus	1	3	4	2	13	SM	A	66
Mops spurrelli	1	3	4	1	14	SM	—	64
Mops thersites	1	3	3	1	15	SM	ST	62
Mops brachypterus	1	3	0	0	19	SM	—	54
Mops petersoni	1	3	0	0	19	SM	A	54
Mops demonstrator	1	2	1	0	19	SM	A	54
Mops nanulus	1	2	1	0	19	SM	A	54

11 other genera. Until recently, taxonomic assignments and systematic relationships among the family members had not been examined worldwide. Freeman (1981), based upon a phenetic study of morphological traits, provided the first major review of the family. She restricted the genus *Tadarida* to include only nine species and assigned the remainder to *Chaerephon, Mops, Mormopterus* and *Nyctinomops* (all former subgenera of *Tadarida*).

Karyotypic data for the Molossidae are available for 25 species, only six of which are inhabitants of the Old World. In this paper we analyze the karyotypes of 11 African molossid species belonging to the genera *Chaerephon* and *Mops,* and summarize the chromosomal data (Tables 1 and 2) now available for 35 species representing 10 of the 12 genera recognized by Freeman (1981).

METHODS AND MATERIALS

Standard karyotypes were obtained in the field from bone marrow preparations (Patton, 1967) of live caught animals. A minimum of five representative chromosome spreads were examined from each individual to determine diploid (2n) and fundamental numbers (FN). Photomicrographic enlargements of suitable spreads were used in the final analyses.

Chromosomes were divided into large and medium-sized metacentric, medium and small subtelocentric, and medium to small acrocentric morphological classes. Determination of centromere position was difficult because differential contraction of nearly acrocentric chromosomes caused variation in the number of countable arms. We follow Warner et al. (1974) in being conservative in the determination of biarmed versus acrocentric conditions and reiterate their warning that FN values are somewhat arbitrary and subjective.

Taxonomic designations follow Honacki et al., 1982 (see Freeman, 1981).

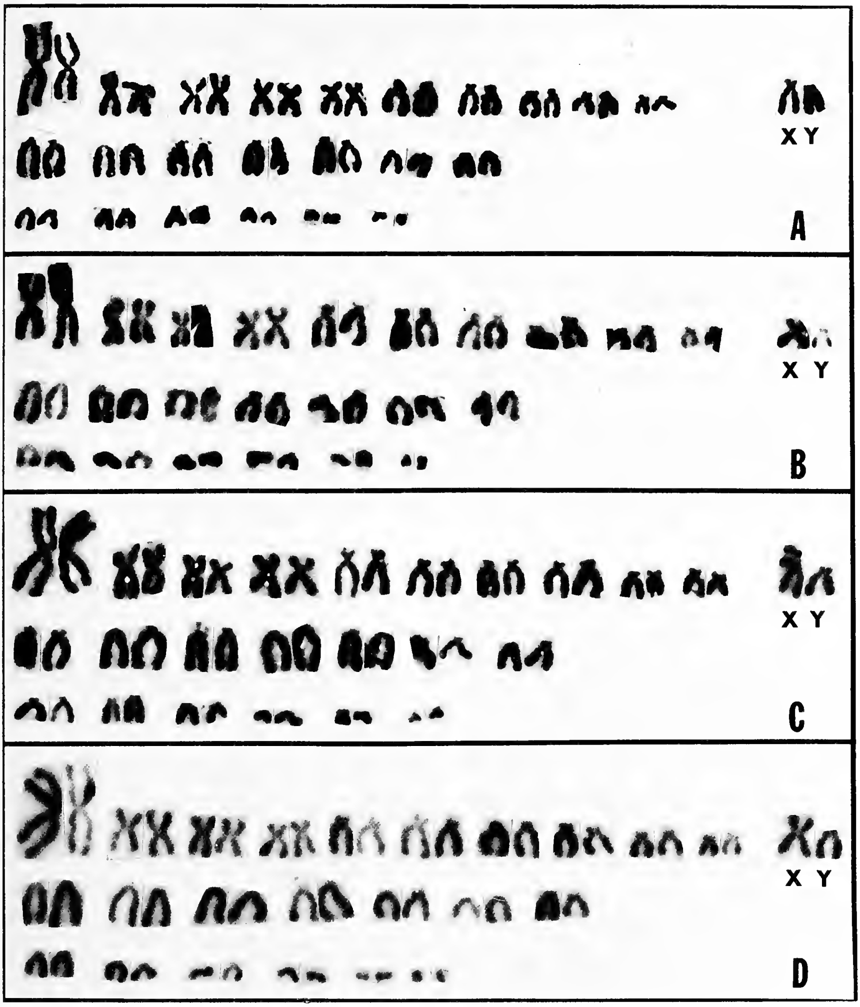

Fig. 1.—Representative karyotypes of A) *Chaerephon ansorgei* from Cameroun, B) *Chaerephon aloysiisabaudiae* from Cameroun, C) *Mops midas* from Somalia, and D) *Mops condylurus* from Somalia.

SPECIES ACCOUNTS

A summary of the chromosomal morphology for the species examined in this study is presented in Table 1. Representative karyotypes are presented in Figs. 1–3.

All species examined in this study were characterized by a diploid number of 48. Fundamental numbers ranged from 54 to 66. All of these species had, minimally, four biarmed autosomal elements including one large pair of metacentric and at least one medium-sized pair of metacentric chromosomes. In all cases the large metacentric pair was twice the size of the next largest chromosome pair. The X chromosomes were medium-sized and submetacentric or subtelocentric in all species; the Y chromosome was medium-sized and acrocentric in all but one species.

A brief description of the karyotypes for each species reported herein follows.

Chaerephon ansorgei (Thomas, 1913)

Fig. 1A, 2n = 48; FN = 66; 1♂

The autosomal complement includes one pair of large metacentric, three pairs of medium metacentric, four pairs of medium subtelocentric, and 13 medium to small acrocentric chromosomes. The X chromosome is medium-sized and subtelocentric, and the Y is medium-sized and acrocentric.

Chaerephon aloysiisabaudiae (Festa, 1907)

Fig. 1B, 2n = 48; FN = 66; 1♂

The karyotype of this species is identical to *C. ansorgei* except the X chromosome in *C. aloysiisabaudiae* appears submetacentric rather than subtelocentric.

Chaerephon pumila (Cretzschmar, 1826)

2n = 48; FN = 58; 8♂♂, 6♀♀

The karyotype of our specimens is identical to that reported for this species by Dulic and Mutere (1973).

Mops midas (Sundevall, 1843)

Fig. 1C, 2n = 48; FN = 66; 3♂♂, 3♀♀

This species is karyotypically identical to the above-mentioned *Chaerephon* species and shares the submetacentric condition of the X chromosome observed in *C. aloysiisabaudiae.*

Mops condylurus (A. Smith, 1833)

Fig. 1D, 2n = 48; FN = 66; 4♂♂, 5♀♀

The karyotype of *M. condylurus* is identical to both *M. midas* and *C. aloysiisabaudiae.*

Mops spurrelli (Dollman, 1911)

Fig. 2A, 2n = 48; FN = 64; 3♂♂

The chromosomal complement from female specimens of *M. spurrelli* differ from *M. condylurus* in the absence of one less small subtelocentric pair and the presence of an extra acrocentric pair. The X chromosome is submetacentric.

Mops thersites (Thomas, 1903)

Fig. 2B, 2n = 48; FN = 62; 3♂♂, 4♀♀

The autosomes are nearly identical to *M. spurrelli* but there is one less medium-sized subtelocentric and one additional acrocentric pair present. The X chromosome is submetacentric but the Y appears to be subtelocentric instead of the more commonly observed acrocentric condition.

Mops brachypterus (Peters, 1852)

Fig. 3A, 2n = 48; FN = 54; 1♀

The autosomes of the female specimen examined consist of one large pair of metacentric, three pairs of medium-sized metacentric and 19 medium to small acrocentric pairs. Although morphologically similar to *M. thersites,* it differs chromosomally by lacking subtelocentric pairs and having additional acrocentric pairs. The X chromosome presumably is submetacentric.

Mops petersoni (El Rayah, 1981)

Fig. 3B, 2n = 48; FN = 54; 1♂, 1♀

In addition to being morphologically similar, this species is karyotypically identical to *M. brachypterus.*

Mops nanulus J. A. Allen, 1917

Fig. 3C, 2n = 48; FN = 54; 2♂♂, 2♀♀

M. nanulus differs from *M. petersoni* and *M. brachypterus* by having one less medium-sized metacentric pair and the presence of a medium-sized subtelocentric pair. The sex pair is identical to *M. petersoni.*

Mops demonstrator (Thomas, 1903)

Fig. 3D, 2n = 48; FN = 54; 1♂

The karyotype of this species is identical to *M. nanulus.*

DISCUSSION

Until Freeman's (1981) recent revision of the Molossidae, phylogenetic relationships and taxonomic assignments within the family

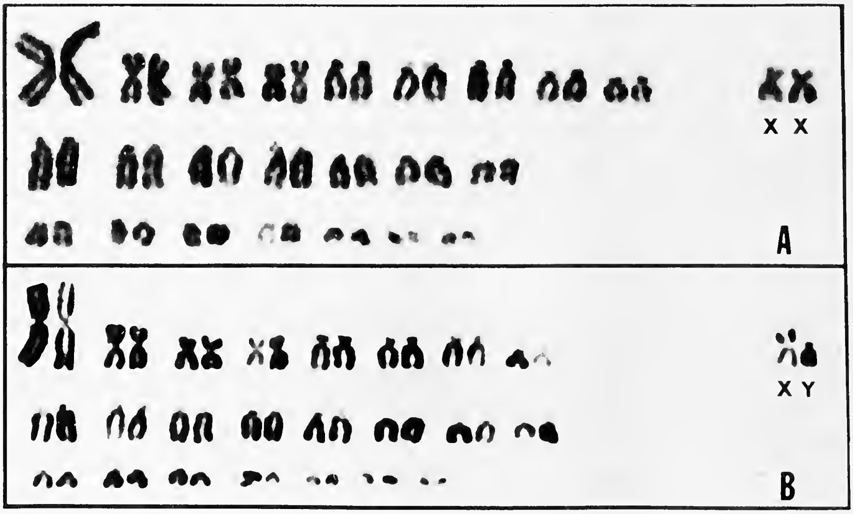

Fig. 2.—Representative karyotypes of A) *Mops spurrelli* from Cameroun, B) *Mops thersites* from Cameroun.

were largely unexplored. Warner et al. (1974) suggested that chromosomal studies might be beneficial in evaluating these relationships. Chromosomal data now available for 36 molossid species representing 10 of 12 genera recognized by Freeman (1981) are summarized in Table 2.

We detected no intraspecific chromosomal variation within any of the species examined in this study. This is noteworthy for two reasons. First, our karyotypes of *M. condylurus* (FN = 66) from Afgoi, Somalia, differ substantially from the karyotype of this species (FN = 56) reported from Kisubi, Uganda, by Dulic and Mutere (1973). These localities are several hundred kilometers apart and this suggests either that considerable geographic variation in the karyotype occurs within this species or there are two species currently recognized as *M. condylurus.* Secondly, our data support the specific distinctiveness of *M. spurrelli* and *M. nanulus.* Freeman (1981) recognized the morphological similarity between these two taxa and noted Koopman's (1975) suggestion that they might be conspecific. Our data indicate that *M. nanulus* (FN = 54) and *M. spurrelli* (FN = 66) differ by five pairs of biarmed chromosomes, and considering the scarcity of intraspecific karyotypic variation within this family, it would seem likely that the two taxa are specifically distinct.

Variation in FN for the species we examined ranged from 54 to 66 (Table 1). These karyotypes can be conveniently divided into three

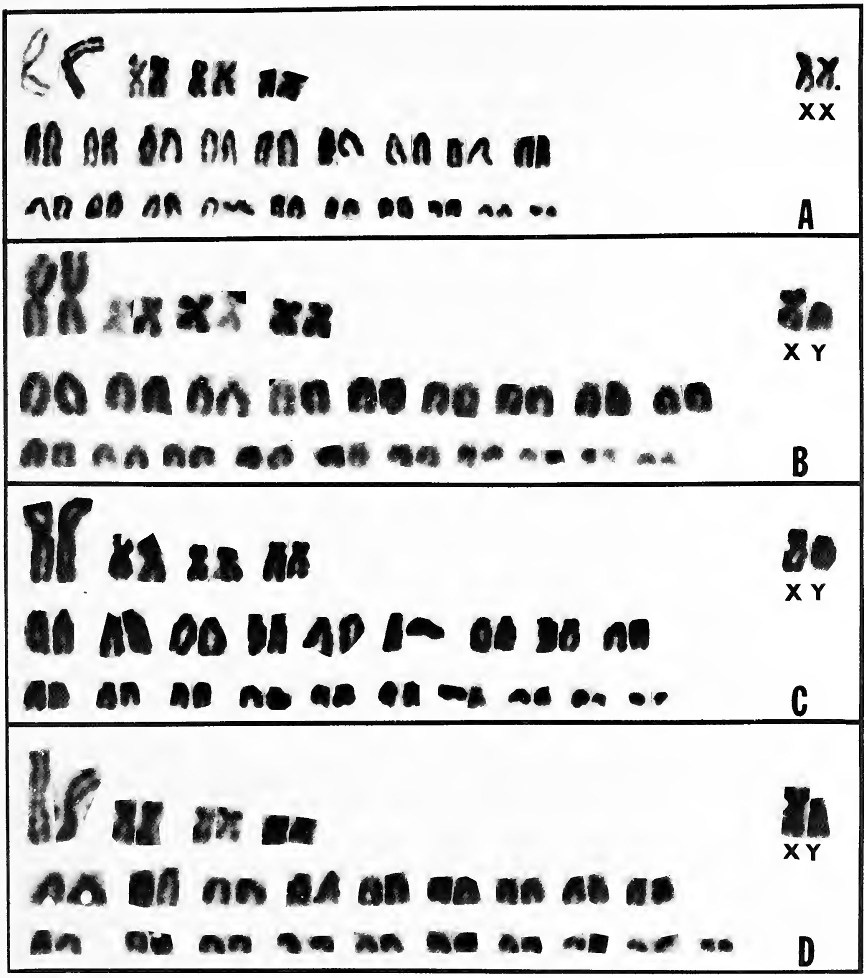

Fig. 3.—Representative karyotypes of A) *Mops brachypterus* from Cameroun, B) *Mops petersoni* from Cameroun, C) *Mops nanulus* from Cameroun, and D) *Mops demonstrator* from Cameroun.

groups. The high FN group (FN = 62–66) includes both species of *Chaerephon* and four of eight *Mops* species. Within this group, differences between the FN = 62–66 karyotypes apparently involve the absence of medium and small subtelocentric autosomes. Our examination of *Chaerephon pumila* (FN = 58) agrees with the karyotype of this species reported by Dulic and Mutere (1973), and forms an intermediate FN group. Again, differences between the intermediate and

Table 2.—*Summary of molossid karyotype data.*

Species	2n	FN	Reference
Chaerephon aloysiisabaudiae[1]	48	66	This study
Chaerephon ansorgei[1]	48	66	This study
Chaerephon bivittata[1]	48	54	Peterson and Nagorsen, 1975
Chaerephon plicata[1]	48	54	Harada and Kobayashi, 1980; Harada et al., 1982
Chaerephon pumila[1]	48	58	Dulic and Mutere, 1973; this study
Eumops auripendulus	42	62	Warner et al., 1974
Eumops glaucinus	38	64	Warner et al., 1974
	40	64	Warner et al., 1974
Eumops perotis	48	56	Baker, 1970; Warner et al., 1974
	48	58	Wainberg et al., 1974
Eumops underwoodi	48	56	Warner et al., 1974
Molossops abrasus	34	60	Warner et al., 1974; Gardner, 1977
Molossops greenhalli	34	—	Linares and Kiblisky, 1969
	34	60	Baker, 1970; Warner et al., 1974
Molossops temminckii	42	56	Gardner, 1977
Molossus ater	48	58	Warner et al., 1974
Molossus molossus	48	56	Baker and Lopez, 1970
	48	58	Warner et al., 1974
Molossus rufus	48	58	Wainberg et al., 1974
Molossus sinaloa	48	58	Warner et al., 1974
Mops brachypterus[1]	48	54	This study
Mops condylurus[1]	48	66	This study
	48	56	Dulic and Mutere, 1973
Mops demonstrator[1]	48	54	This study
Mops midas[1]	48	66	This study
Mops nanulus[1]	48	54	This study
Mops petersoni[1]	48	54	This study
Mops spurrelli[1]	48	64	This study
Mops thersites[1]	48	62	This study
Mormopterus kalinowskii[1]	48	56	Warner et al., 1974
Mormopterus setiger[1]	48	54	Warner et al., 1974
Nyctinomops aurispinosus[1]	48	58	Warner et al., 1974
Nyctinomops femorosacus[1]	48	58	Warner et al., 1974
Nyctinomops laticaudatus[1]	48	58	Warner et al., 1974
Nyctinomops macrotis[1]	48	58	Warner et al., 1974
	48	56	Baker, 1970
Otomops martiensseni	48	56	Dulic and Mutere, 1973
Promops centralis	48	58	Warner et al., 1974
Promops nasutus	40	54	Wainberg, 1966
Tadarida brasiliensis	48	—	Painter, 1925
	48	54	Kniazeff et al., 1967
	48	56	Warner et al., 1974; Baker et al., 1982
Tadarida fulminans	48	54	Peterson and Nagorsen, 1975

[1] Indicates species formerly recognized as *Tadarida,* see Freeman (1981).

high FN forms appear to be in the absence of small subtelocentric pairs plus the absence of one pair of medium-sized metacentrics. The low FN group (FN = 54) includes *M. brachypterus, M. petersoni, M. demonstrator,* and *M. nanulus.* Karyotypic morphologies of the latter two are identical and differ from the former pair in having one fewer medium-sized metacentric pair and an additional pair of medium-sized subtelocentric chromosomes.

Whether or not these karyotype associations reflect phylogenetic relationships within genera is difficult to assess from standard karyotypic data. Phylogenetic interpretations based on chromosomal data necessarily require identification of homologous pairs using differential staining techniques (see Haiduk et al., 1981). There is, however, little concordance between Freeman's (1981) phenetic classification and the patterns of karyotypic morphology for these species. Within *Chaerephon,* Freeman's (1981) analysis clusters *C. ansorgei* (FN = 66) with *C. bivittata* (FN = 54, Peterson and Nagorsen, 1975). *C. aloysiisabaudiae* (FN = 66) then joins the cluster followed by *C. pumila* (FN = 58, Dulic and Mutere, 1973; this study) several junctures later, and further still, by *C. plicata* (FN = 54, Harada and Kobayashi, 1980; Harada et al., 1982). Similarly, within the genus *Mops, M. demonstrator* (FN = 54) clusters phenetically with *M. condylurus* (FN = 66); *M. brachypterus* (FN = 54) and *M. thersites* (FN = 62) pair together. These disparities suggest the possibility that either morphological and chromosomal characters are evolving at different rates, or that the taxonomic relationships of these taxa need to be reexamined.

Karyotypic stability for bats, in general, has been recognized by several authors (Peterson and Nagorsen, 1975; Gardner, 1977; Baker, 1978; Baker et al., 1982; Baker and Bickham, 1980; Bickham, 1979*a,* 1979*b*; Bickham and Baker, 1979) and has been suggested for the Molossidae, specifically, by Warner et al. (1974) and Dulic and Mutere (1973). Of the 36 molossid species for which chromosomal data are available only seven species have diploid numbers other than 2n = 48 (Table 1). The modal occurrence of 2n = 48 chromosomes in both Old and New World genera plus the similarity between this number and the proposed primitive diploid number for the Vespertilionidae (Baker, 1970) led Warner et al. (1974) to propose 2n = 48 as primitive for the Molossidae. Our documentation of the 2n = 48 karyotype in 11 Old World molossid species further supports this diploid value as primitive for the family.

SPECIMENS EXAMINED

Chaerephon aloysiisabaudiae.—CAMEROUN: 16 km S, 2 km E Yaounde (3°43′N, 11°32′E), (1♂ CM 58678).

Chaerephon ansorgei.—CAMEROUN: 25 km S, 13 km E Garoua, (9°05'N, 13°30'E), (1♂ CM 58679).

Chaerephon pumila.—CAMEROUN: 24 km S, 13 km E Garoua (9°05'N, 13°30'E), (1♂ CM 58724); SOMALIA: Libsoma Farm 6 km S, 17 km W Afgoi (2°05'N, 44°58'E), (3♂♂ CM 85438, 85439–85440; 2♀♀ CM 85441–85442); SOMALIA: Bulo Burti (3°51'N, 45°34'E), (4♂♂ CM 85455–85456, CM 85459–85460; 4♀♀ CM 85457–85458, 85461–85462).

Mops brachypterus.—CAMEROUN: 25 km S, 3 km E Yaounde (3°38'N, 11°33'E), (1♀ CM 58687).

Mops condylurus.—SOMALIA: Libsoma Farm, 6 km S, 17 km W Afgoi (2°05'N, 44°58'E), (4♂♂ CM 85423, 85408–85409, 85424; 5♀♀ CM 85410–85411, 85412, 85425–85426).

Mops demonstrator.—CAMEROUN: 2 km W Ngaoundere (7°20'N, 13°34'E), (1♂ CM 58681).

Mops midas.—SOMALIA: Libsoma Farm, 6 km S, 17 km W Afgoi (2°05'N, 44°58'E), (3♂♂ CM 85429, 85436, 85428; 3♀♀ CM 85427, 85430).

Mops nanulus.—CAMEROUN: 25 km S, 13 km E Garoua (9°05'N, 13°30'E), (1♂ CM 58694); CAMEROUN: 24 km S, 13 km E Garoua (9°05'N, 13°30'E), (1♂ CM 58692; 2♀♀ CM 58693, CM 58695).

Mops petersoni.—CAMEROUN: 25 km S, 3 km E Yaounde (3°38'N, 11°33'E), (1♂ CM 58688; 1♀ CM 58691).

Mops spurrelli.—CAMEROUN: 30 km N, 40 km E Obala (4°22'N, 11°58'E), (1♂ CM 58730); CAMEROUN: 25 km S, 3 km E Yaounde (3°38'N, 11°33'E), (2♂♂ CM 58731, CM 58786).

Mops thersites.—CAMEROUN: 30 km N, 40 km E Obala (4°22'N, 11°58'E), (1♂ CM 58737); CAMEROUN: 25 km S, 3 km E Yaounde (3°38'N, 11°33'E), (2♀♀ CM 58743, CM 58745); CAMEROUN: 7 km S, 8 km W Yaounde (3°48'N, 11°27'E), (2♂♂ CM 58739, CM 58741; 2♀♀ CM 58740, CM 58742).

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TRILOBITES FROM THE KEOKUK LIMESTONE (MISSISSIPPIAN) OF MISSOURI

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Abstract

A new species of the trilobite genus *Griffithides* Portlock, *G. salinensis,* new species, is described. *G. salinensis* is a rare component of the fauna of the Keokuk Limestone (Mississippian) of St Genevieve County, Missouri. It can be distinguished from other described species assigned to this genus by the posterior termination of the pygidial axis, which is upturned into a large node-like projection. The type specimens of this species were collected from just below the *Marginarugus magnus* bed of the Keokuk Limestone. In addition to *G. salinensis,* two specimens also recovered from the same bed are described and tentatively assigned to the genus *Waribole* Richter and Richter.

Introduction

The trilobite genus *Griffithides* Portlock is relatively poorly known from Carboniferous rocks of North America as compared to the many species recognized from correlative rocks of Europe. Of the three North American species recognized, only one, *G. bufo* Meek and Worthen, is known from more than just the type material. In contrast, specific diversity exhibited by this genus in Europe has prompted some authors (Hahn and Hahn, 1970, 1971; Hahn et al., 1983) to subdivide the genus

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into a number of subgenera. The recent recovery from the Keokuk Limestone of Missouri of a small number of specimens of *Griffithides,* which are notably dissimilar to previously recognized species, warrants the erection of a new species. The specimens of *Griffithides,* and two pygidia tentatively assigned to the genus *Waribole* were recovered from a light-gray lime grainstone in the Keokuk Limestone along Interstate 55 at Little Saline Creek, St. Genevieve County, Missouri. The specimens were recovered as accessories during field collections made for brachiopods by J. L. Carter and A. D. Kollar (Carnegie Museum of Natural History) from a bed just below the *Marginarugus magnus* bed or about in the middle of the Keokuk. The brachiopod fauna associated with these trilobites is dominated by *Productus crawfordsvillensis* Weller, *Imbrexia montonana* Miller, *Rhynchopora beecheri* Greger, and *Torynifer pseudolineatus* (Hall). The lithologic character of the strata, which yielded the trilobites, is similar to that in which other North American species of *Griffithides* have been found. Moreover, the specimens of *Waribole*? recovered from the Keokuk are similar to pygidia I have recovered from the lime grainstones of the Salem Limestone of southern Indiana. These specimens from the Salem are also found in association with a species of *Griffithides.* The consistent occurrence of these two trilobite genera together in particular lithologies may suggests a strong ecologic control on their distribution.

Terminology employed in this study follows that utilized by Harrington (1959).

SYSTEMATIC PALEONTOLOGY

Family Proetidae Salter
Subfamily Griffithidinae Hupé
Genus *Griffithides* Portlock

Distribution of North American species.—Present in the Keokuk Limestone (Osagean) of Missouri and Illinois, the Salem Limestone (Meramecian) of Indiana, and the Pitkin Limestone (Chesterian) of Oklahoma.

Diagnosis of North American representatives.—Cephalon parabolic in outline, moderately vaulted. Glabella pyriform with frontal lobe moderately to greatly expanded laterally and reaching the anterior margin of the cranidium. Lateral preoccipital lobes well-defined, subtrian-

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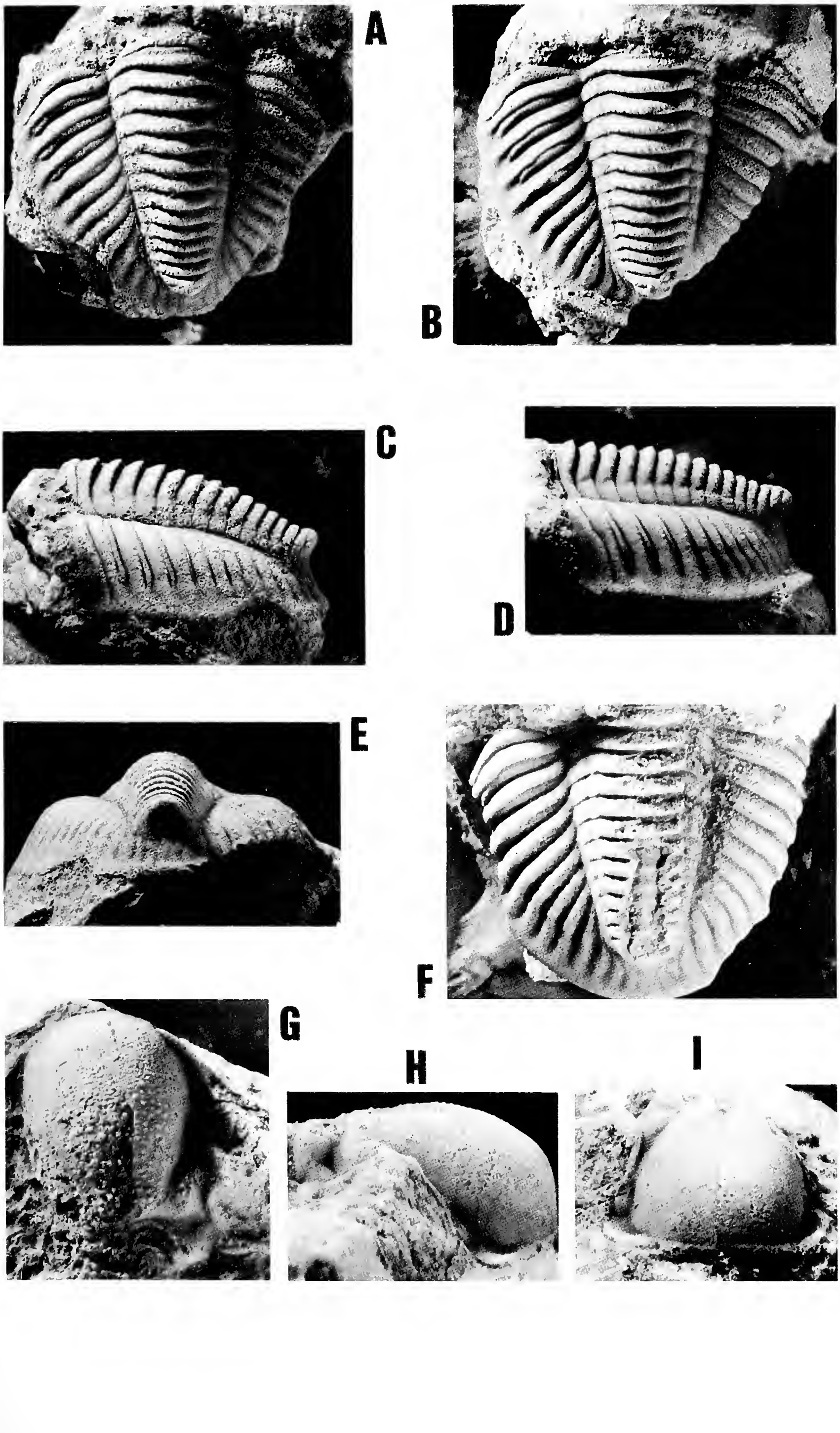
Fig. 1.—*Griffithides salinensis,* new species, A, C, E, holotype pygidium in dorsal, lateral, and posterior views, CMNH 34553, ×2; B, D, paratype pygidium in dorsal and lateral views, CMNH 34498, ×2; F, paratype pygidium, dorsal view, CMNH 34499, ×2.5; G, H, I, paratype cranidium in dorsal, lateral and anterior views, CMNH 34500, ×2.5.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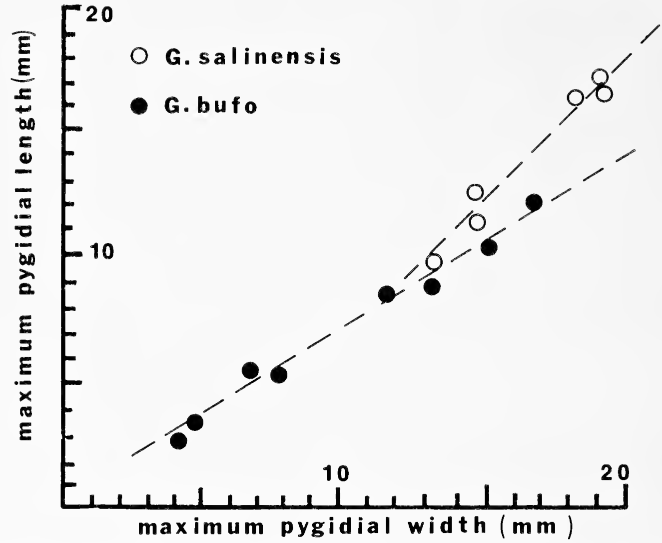

Fig. 2.—Bivariate plot of maximum pygidial width (W) vs maximum pygidial length (Z) for specimens of *Griffithides salinensis*, new species, and *G. bufo* Meek and Worthen.

gular, lp furrow narrow, deeply incised, widened anterolaterally. Palpebral lobes crescentic to semicircular in outline. Eyes of medium size, hemispherical in shape. Lateral border furrow well-defined and narrow, margin sharply rounded. Genal spines short, generally reaching to the third thoracic segment.

Thorax of nine segments, axial rings semicircular in transverse profile, ornamented by a row of small granules along the posterior margin. Pleurae sharply rounded at fulcrum, subangular at tip.

Pygidium semicircular to parabolic in outline, strongly vaulted, consisting of an axis composed of 11–15 rings and pleural fields of 9–14 ribs. Axis tapers posteriorly, does not reach posterior margin, strongly convex and steeply downsloping posteriorly. Pleural ribs extend nearly to the margin, with no well-defined border.

Discussion.—Although Hahn et al. (1983) were able to subdivide the Eurasian representatives of the genus *Griffithides* into three subgenera, no such division of North American species is possible. The main distinguishing features among North American species of *Griffithides* lie mainly in the shape (suboval versus parabolic) and structure (number of ribs and rings) of the pygidium. *Griffithides* can be distinguished from the contemporary trilobite genus *Paladin* by the presence of a well-developed pygidial border on the latter.

Table 1.—*Univariate measurements of select morphological characters of* Griffithides salinensis, *new species. For discussion and illustration of character definition see Shaw (1957).*

Character	N	Mean*	Range*
(W) pygidial width	7	16.2	12.7–19.6
(Z) pygidial length	7	13.4	10.1–16.8
(X) axial width (max.)	7	6.3	4.9–7.4
(Y) axial length	6	12.2	8.4–14.7
number of axial rings	6	15	14–15
number of axial ribs	5	14	13–14

* Measurements in millimeters.

Griffithides salinensis, new species

Figs. 1A–1I

Holotype.—CMNH 34553.

Paratypes.—CMNH 34498–34500.

Material.—10 incomplete pygidia and 1 partial cranidium.

Description.—Glabella pyriform with moderate lateral expansion to the frontal lobe. Frontal lobe strongly convex in transverse profile and extends to the anterior margin. In longitudinal profile glabella is nearly flat to mildly convex at the posterior terminus, becoming increasingly convex anteriorly, meeting the anterior margin vertically. Glabella covered by fine granules. Lateral preoccipital lobes subtriangular with granular ornament; lp furrow well-defined and of medium width, becoming broader toward the dorsal furrow. Palpebral lobes of medium size, semicircular in outline, inclined into the dorsal furrow at about 45° Facial sutures mildly divergent from α to β, rounded at β, wider at ω than α. Occipital lobe not preserved.

Thorax is unknown.

Pygidium parabolic in outline, moderately vaulted, .83 times as long as wide. Axis tapers posteriorly, .91 the total pygidial length, .39 the total pygidial (anterior) width, composed of 14 to 15 rings which are semicircular in transverse profile. Posteriormost axial ring is enlarged into a large node or nub that overhangs a slightly concave axial terminus. Each ring is slightly sinuous, being posteriorly bent across axis. A row of 12 fine granules ornament the posterior edge of each ring. Pleural fields strongly convex, made up of 13–14 posteriorly recurved ribs that extend nearly to the margin. The anteriormost three or four ribs exhibit a well-defined pleural furrow. A row of fine granules ornament each rib.

Discussion.—*G. salinensis,* new species, can readily be distinguished from other North American species of the genus by the upturned node-like termination of the pygidial axis, by the greater length to width ratio to the pygidium, and by the greater number of axial rings and pleural ribs. Only *G. bufo* Meek and Worthen has been recovered in sufficient number to allow any close comparison. Fig. 2 is a bivariate plot comparing the maximum pygidial widths with the maximum pygidial lengths for specimens of *G. salinensis* and *G. bufo.* There is a noticeable difference in the rectilinear trends exhibited by each species.

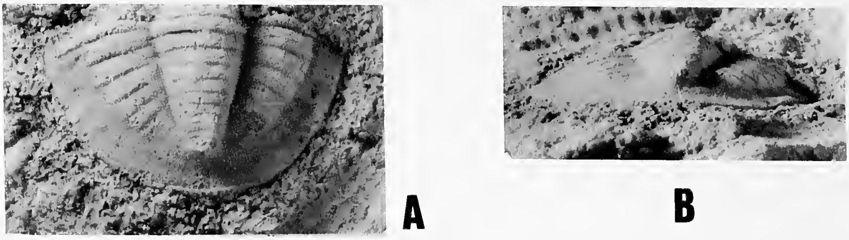

Fig. 3.—*Waribole*? sp. A, B, dorsal and posterior views of complete pygidium, CMNH 34501, ×.2.5.

The plot illustrates that *G. salinensis* possesses a greater length to width ratio than does *G. bufo* and is larger on the average. Unfortunately, insufficient numbers of *G. salinensis* are available at present to produce a reliable regression equation. *G. salinensis* differs from the poorly known *G. meramecensis* Shumard in that the latter exhibits fewer pygidial ribs and rings (12 and 13, respectively) and lacks the node-like termination of the axis. Both *G. meramecensis* and *G. salinensis* were recovered from the Keokuk Limestone of Missouri. The comparison presented above is based upon the drawing and description of *G. meramecensis* presented by Shumard (1855). Inasmuch as the location of the holotype is unknown, comparison must be based upon Shumard's description and drawing alone. *G. salinensis* differs from *G. pustulosus* Snider in that the pygidium of the former exhibits a parabolic outline and the prominent terminal node on the pygidial axis. All Eurasian species of *Griffithides* can be distinguished from *G. salinensis* by the terminal axial node on the pygidium.

Subfamily Cyrtosymbolinae Hupé

Genus ***Waribole*** Richter and Richter

Waribole? sp.

Fig. 3A, 3B

Material.—1 complete and 1 fragmented pygidium from the Keokuk Limestone. Illustrated specimen CMNH 34501.

Description.—Pygidium with low vaulting and relief, semicircular in outline with a length/width ratio of .65. Axis tapers posteriorly, is .85 the total pygidial length and .37 the maximum (anterior) pygidium width, composed of 11 rings and terminates, posteriorly, at inside margin of border. Pleural areas composed of six or perhaps seven ribs which become increasingly obsolete posteriorly. Each rib composed of two bands of approximately equal width. Border well-developed, smooth, and slightly concave to the margins, of nearly equal width all along pygidium.

Discussion.—The genus *Waribole* is most common in Late Devonian rocks and has a documented range into the earliest Carboniferous. The genus, to the best of my knowledge, has not been definitely documented from the stratigraphic interval of the Keokuk Limestone (that is, Visean). Moreover, *Waribole* has not previously been reported from North America. If these specimens are in fact not specimens of *Waribole,* then they belong to some very similar genus. At present insufficient specimens are available to make any further inference. The only other North American trilobite genus with pygidial characteristics somewhat similar to these two pygidia is *Richterella*; *Richterella,* however, exhibits a much greater vaulting to the pygidium and the pleural ribs lack the subdivision into anterior and posterior bands.

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RESULTS OF THE ALCOA FOUNDATION SURINAME EXPEDITIONS. X. PATTERNS OF CELLULAR DIVERGENCE AND EVOLUTION IN THE GASTRIC MUCOSA OF TWO GENERA OF PHYLLOSTOMID BATS, *TRACHOPS* AND *CHIRODERMA*

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Abstract

The fundic mucosa in *Trachops cirrhosus, Chiroderma trinitatum,* and *C. villosum* (Suborder Microchiroptera) was studied comparatively by transmission electron microscopy. *Trachops* is an animalivorous species that mainly feeds on Neotropical frogs, whereas both species of *Chiroderma* are frugivorous. In *Trachops,* two types of enteroendocrine cells (A and D cells) that possibly produce glucagon and somatostatin, respectively, were identified ultrastructurally. In *Chiroderma* examples of possible A, EC_n, D_l(H), and G cells were identified. The product in possible G-cells in *Chiroderma* ultrastructurally matched that found in the pylorus of another stenodermatine bat, *Ariteus flavescens,* which has been shown to exhibit gastrin-like immunoreactivity. In *Trachops*

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the pepsin-producing chief cells are restricted to the basal-most portion of the gastric gland and produce an electron-dense product, whereas in *Chiroderma* the chief cells occupy up to 75% of the gland and produce a pale product. In *Trachops* the parietal cells are less abundant and less active than in *Chiroderma* but mucous neck cells are far more abundant. The gastric pits are shallow in *Chiroderma,* whereas *Trachops* has deep gastric pits. The mucous secretory granules in the surface mucous cells in *Chiroderma* differ ultrastructurally from those in *Trachops.* Overall, the ultrastructure of gastric mucosa in *Trachops* resembles that found in *Phyllostomus* (animalivorous/omnivorous) and *Pteronotus* (insectivorous), whereas these features in *Chiroderma* resemble those of *Artibeus* (frugivorous). The general histology of the stomach of *Chiroderma* is similar to that of a megachiropteran, *Eidolon helvum,* suggesting that histological convergence has occurred in the evolution of the stomach of microchiropteran and megachiropteran fruit bats.

INTRODUCTION

Patterns of morphological evolution in bats are complex and undoubtedly constrained by many factors (Hill and Smith, 1984). Among these, dietary specialization appears to explain many chiropteran morphological features. Dental morphology, salivary gland structure, kidneys, gastric anatomy, relative brain size, jaws, and even length of forearm can be correlated with diet (Phillips, 1971; Phillips et al., 1977; Studier et al., 1983*a*; Eisenberg and Wilson, 1978; Findley and Wilson, 1982; Freeman, 1979, 1981). Consequently, bats represent an outstanding mammalian model against which hypotheses about the relationships among structure, function, and biological role of various anatomical features can be tested.

The digestive tract, and the stomach in particular, is especially interesting in bats because diet can be correlated with gross anatomy, musculature, histochemistry, and histology (for example, Park and Hall, 1951; Kolb, 1954; Schultz, 1965, 1970; Rouk and Glass, 1970; Hart, 1971; Forman, 1971, 1972; Forman et al., 1979; Kamiya and Pirlot, 1975; Ogunbiyi and Okon, 1976; Okon, 1977; Bhide, 1980; Yamada et al., 1984; Ishikawa et al., 1985). These correlations have been extended through recent studies in which we have demonstrated differences in 1) aspects of the ultrastructure of cell types, 2) possible presence or absence of certain entero-endocrine (endocrine-paracrine) cells, and 3) relative numbers of particular cell types (Phillips and Studholme, 1982; Phillips et al., 1984; Mennone et al., 1986). A variety of questions has been left unanswered by previous investigations. For example, we do not yet know exactly to what extent cellular and subcellular morphology differs in conjunction with diet or to what extent species with similar diets have similar cellular patterns, regardless of systematic associations.

For the present investigation we compared two genera of phyllostomid bats, *Trachops* (a phyllostomine) and *Chiroderma* (a stenodermatine), that represent probable extremes in feeding specialization. We chose *Trachops cirrhosus* because it has been characterized as an animalivorous species that feeds on small vertebrates, especially Neotropical frogs (Gardner, 1977; Tuttle and Ryan, 1981). As further evidence of feeding specialization, it has been shown that *Trachops* responds differentially to the vocal advertisements of edible and presumably non-edible (poisonous) anurans (Tuttle and Ryan, 1981) and has histologically unique accessory submandibular salivary glands that also might relate to its dietary habits (Phillips and Tandler, 1985; Phillips et al., in press). *Chiroderma trinitatum* and *C. villosum* are frugivores (Gardner, 1977), and Forman (1973) and Forman et al. (1979) have reported that the stomach of *Chiroderma villosum* has an unusually large fundic caecum making it "... perhaps the most extreme specialization for plant feeding ..." among the phyllostomids. Insofar as previous cellular comparisons are concerned, Phillips and Studholme (1982) demonstrated a significant ultrastructural difference in chief cells in the fundic mucosa of representative frugivorous and carnivorous (insectivorous and animalivorous) bats, including *Trachops* and *Chiroderma*. This ultrastructural difference was interpreted to mean that pepsinogen secretion is greatest in the frugivores.

The present investigation addressed the following questions. 1) How are dietary and structural specializations expressed at the cellular level in the gastric mucosa of *Trachops* and *Chiroderma*? 2) How do specializations in *Trachops* and *Chiroderma* compare with other microchiropterans for which data are available? 3) How do ultrastructural features of the gastric mucosa in *Chiroderma* and other frugivorous microchiropterans compare with those found in Old World frugivores of the Suborder Megachiroptera?

METHODS AND MATERIALS

Specimens of *Chiroderma trinitatum* (2 females; CM 77599, 77600), *Chiroderma villosum* (3 females; CM 76796, 76798, 77601), and *Trachops cirrhosus* (1 male, CM 63688; 1 female, CM 64048) were collected in the vicinity of Rudi Kappelvliegveld, Brokopondo, Suriname. All specimens have been deposited in the collections of the Section of Mammals, Carnegie Museum of Natural History (CM). The bats were captured in nets at night (1700–2400 h) while feeding. Subsequently, they were kept overnight without food until between 0900 and 1200 h when they were anesthetized with an intraperitoneal injection of 0.25 cc of sodium pentabarbitol (50 mg/ml). A polyethylene tube next was inserted into the stomach via the mouth and esophagus and approximately 1 cc of trialdehyde fixative (at ambient temperature) was injected into the digestive tract. After approximately eight minutes, an incision was made into the abdomen and the stomach removed and cut into 2 by 2 mm samples that included portions of the fundus. Only samples from the fundus (Fig. 1) were used for the present report.

The fixation protocol was developed specifically for field projects involving transmission electron microscopy (Forman and Phillips, in press; Phillips, 1985). The primary fixative (based on Kalt and Tandler, 1971) consisted of 3% glutaraldehyde, 1% paraformaldehyde, 0.5% acrolein, 2.5% dimethyl sulfoxide (DMSO), and 1 mM $CaCl_2$ in 0.05 M cacodylate buffer at pH 7.2 with 0.1 M sucrose. All tissues were stored in this primary fixative for approximately 20 h at ambient temperature (30–40°C). The fixative then was replaced with fresh buffer (0.05 M cacodylate buffer, pH 7.2, with 0.1 M sucrose); tissues were left in this solution, unrefrigerated, for ten days. When refrigeration was available, the tissues were placed in fresh buffer with 3% glutaraldehyde and stored at 4°C. For processing, the tissues were washed for one hour in 0.05 M cacodylate buffer (pH 7.2) with 0.1 M sucrose and post-fixed for one hour in 1% OsO_4 with cacodylate buffer and sucrose. Tissues then were dehydrated in an alcohol series and embedded in Epon 812. Thin sections were post-stained with uranyl acetate (saturated solution in 50% EtOH) and lead citrate (Reynolds, 1963) and examined and micrographed with a Philips 201 transmission electron microscope (TEM) operated at 60 Kv. Semithin (0.5 μm) sections were stained with toluidine blue for light microscopy.

Entero-endocrine cells in both genera were identified solely on an ultrastructural basis using Grube and Forssmann (1979) and Solcia et al. (1981) as guides. The ultrastructure of the acid-producing cells in our specimens was analyzed comparatively by using available experimental data as a guide to recognition of secretory state (Ito and Schofield, 1978; Schofield et al., 1979). Our descriptions thus are based on cells judged to be in the same state of activity in both species.

RESULTS

At the light microscopic (LM) level the fundic mucosa of *Trachops* and *Chiroderma* differed greatly (Fig. 1). In *Trachops* both surface mucous cells and chief cells were conspicuous because they contain toluidine blue stained secretory granules. In *Chiroderma* gastric pits either were very shallow or lacking and the basal half of each gastric gland was composed mostly of chief cells containing unstained granules. Transmission electron microscopic analysis revealed details of the various cell types, as described in the following paragraphs. At both the TEM and LM levels of comparison no noteworthy individual variation, other than the usual localized differences in fixation, was found among specimens of the same species.

Entero-endocrine (endocrine-paracrine) cells.—In *Trachops cirrhosus* only two types of entero-endocrine cells were distinguished. The most common was identified as an A-cell, present in nearly all gastric glands, positioned among the chief and parietal cells in the lower one-half of the gland (Fig. 1). These cells contained abundant spherical, electron-dense secretory granules (averaging 285 nm in diameter) with a narrow "halo" caused by an apparent space between the electron-dense material and the granule membrane (Fig. 2a). The cytoplasm contained scattered lamellar granular endoplasmic reticulum (GER), relatively few mitochondrial profiles, and lipid-like droplets (Fig. 2a). The A-cells frequently were juxtaposed to chief cells. The second cell type, identified as a D-cell, also was found within the most basal portion of the gastric gland, apparently often juxtaposed to A-cells. The D-cells were characterized by spherical secretory product (330 nm in diameter) with a finely granular appearance, exiguous GER, and few mitochondrial profiles (Fig. 2b)

In *Chiroderma,* four distinctive types of entero-endocrine cells were

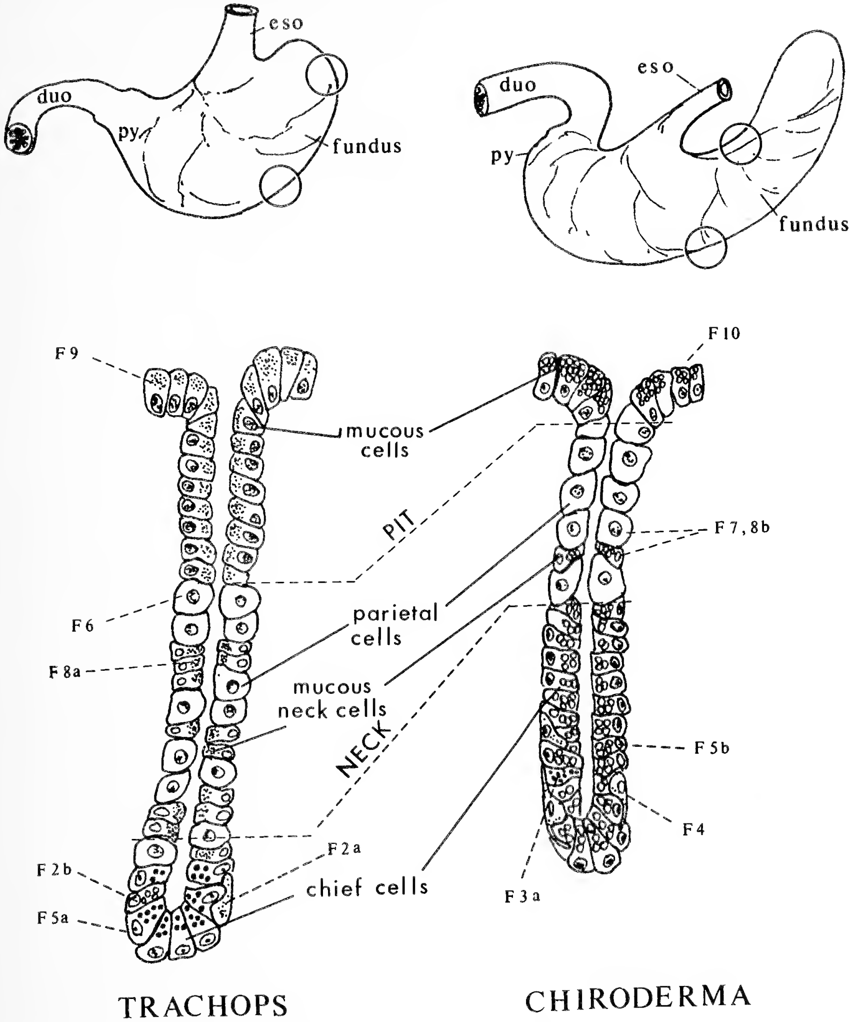

Fig. 1.—Diagrams of the gross anatomy of the stomachs and histology of the mucosa in *Trachops cirrhosus* and a representative of *Chiroderma* (*C. villosum*). Tissue samples used for electron microscopy were taken from areas enclosed by circles in the stomach diagrams. The mucosa diagrams illustrate the histology as well as the relative height of the glands and relative numbers of particular cell types. Examples of the ultrastructure of particular cell types can be found by using the "F" labels as a guide to illustrations. Abbreviations are: py, pylorus; duo, duodenum; eso, esophagus.

found in the lowermost portion of the gastric gland amongst the chief cells. One type contained highly irregular, somewhat granular secretory product (Fig. 3b) and corresponded morphologically to an EC_n cell. These cells tended to have a pale, leached appearance with abundant tubular smooth endoplasmic reticulum (SER) and little or no GER. The second cell type most closely resembled the D_1(H) cell (Grube and Forssmann, 1979); its cytoplasm contained small, spherical, electron-dense granules (approximately 160 nm in diameter), strands of GER, lipid-like droplets, and prominent Golgi complexes. The third type, which was by far the least common, corresponded to an A-cell in having abundant spherical electron-dense granules (Fig. 3a). The fourth type, which was common (possibly associated with each gastric gland), contained a mixture of granules most of which were small and contained a coarsely granular substance equivalent to that characteristic of gastrin-secreting G-cells (Fig. 4a, b). These cells were distinctive in that the cell body had elongate processes that extended among the chief cells so that cross-sectioned profiles were seen commonly (Fig. 4b). These elongate processes and the cell body itself were generally wedged in among the chief cells to the extent that chief cell secretory granules often intruded into the cytoplasm of the G-cell (Fig. 4a, b). This image was common and probably not an artifact because the granule membrane and cell membranes typically were intact (Fig. 4b). In the pro-

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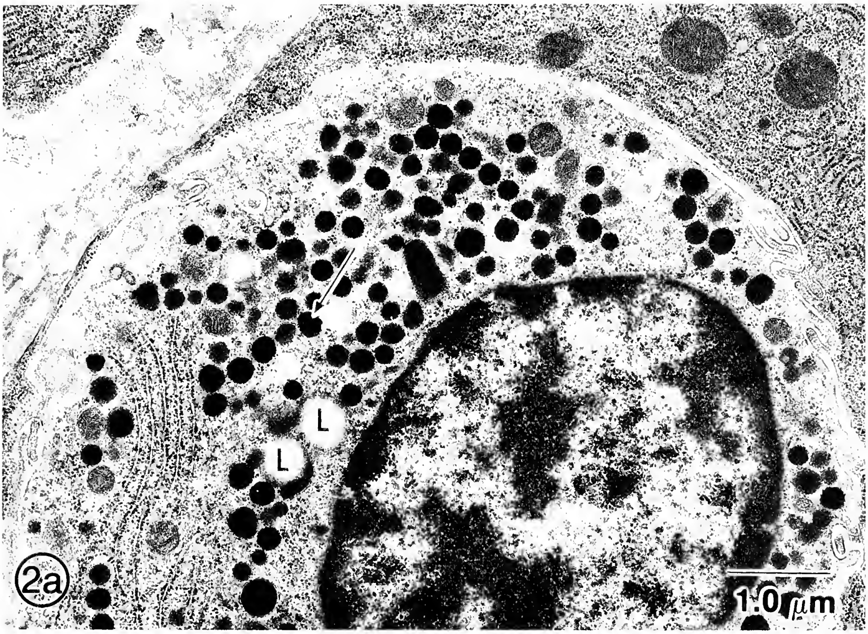
Fig. 2.—a: An A-cell positioned at the base of the fundic gland in *Trachops*. Note the spherical, electron-dense product (arrow) and lipid droplets (L) typical of these cells. *T. cirrhosus*, CM 63688. b: An example of a D-cell positioned among chief cells in *Trachops*. Note the typical secretory product (arrow) of these cells, which are thought to produce somatostatin. *T. cirrhosus*, CM 63688.

Fig. 3.—a: An example of an A-cell in *Chiroderma*. The mature secretory product (arrow) can be compared to an immature, electron-dense granule (img) associated with the Golgi complex. *C. villosum*, CM 77601. b: An EC_n-cell in *Chiroderma*; the granules (arrows) typically are elongate rather than spherical and possibly contain serotonin (5-HT). The cytoplasm of these cells often is pale and contains abundant tubular smooth endoplasmic reticulum (SER). A chief cell secretory granule (SG) also can be seen on the left. *C. villosum*, CM 76798.

Fig. 4.—a: A possible G-cell at the base of a fundic gland in *Chiroderma*. Note how the body of the cell is wedged among adjacent chief cells, whose secretory product (SG) intrudes into the G-cell cytoplasm. The cell and granule membranes (arrow) are intact, suggesting that this close relationship is not an artifact. bl, basal lamina. *C. villosum*, CM 76798. b: A cross-section through a G-cell process that extends between chief cells filled with product (SG). An arrow denotes an image suggestive of exocytosis; also note the tubular smooth endoplasmic reticulum (SER) and intact chief cell and granule membrane (MB). *C. villosum*, CM 76798.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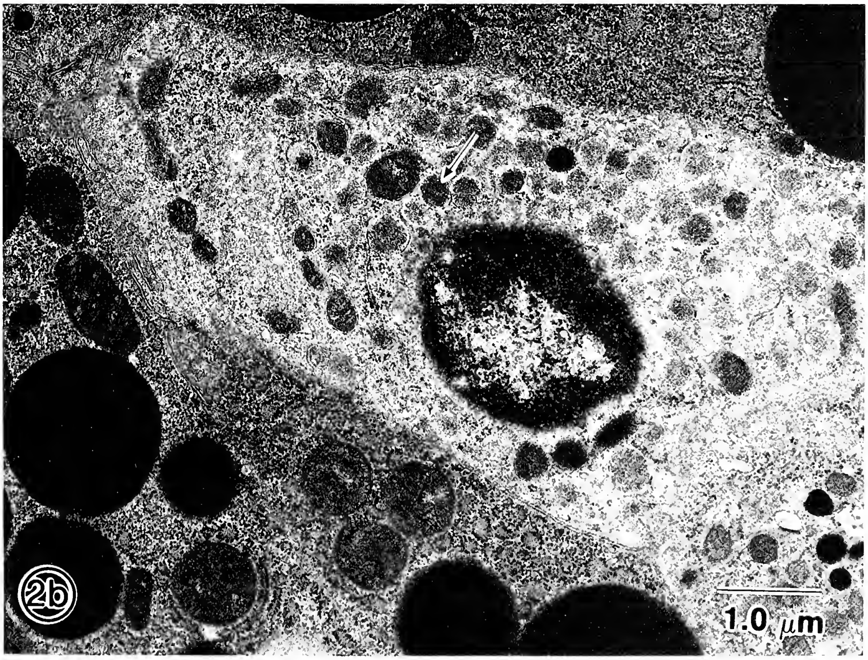
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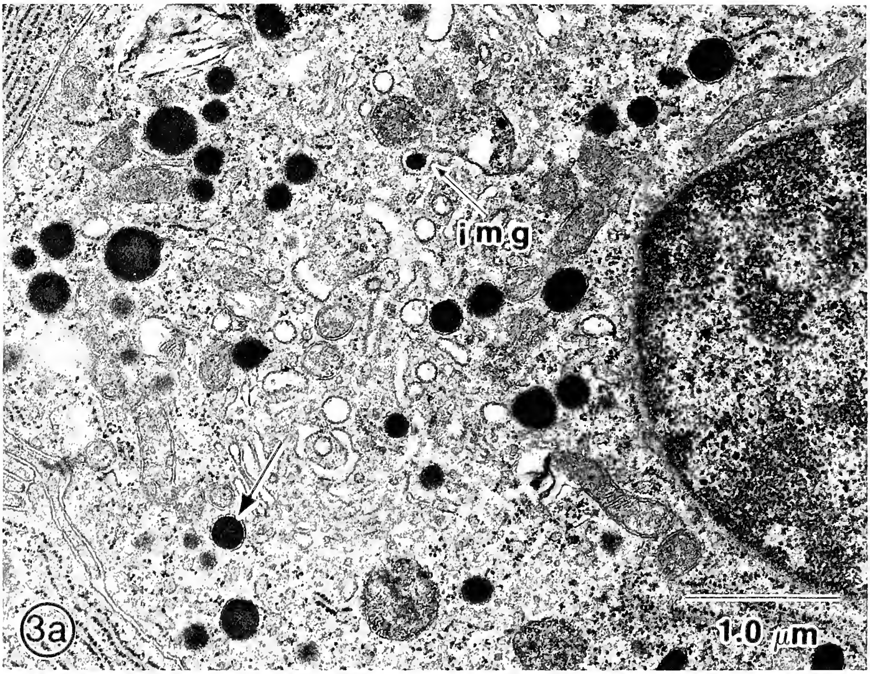
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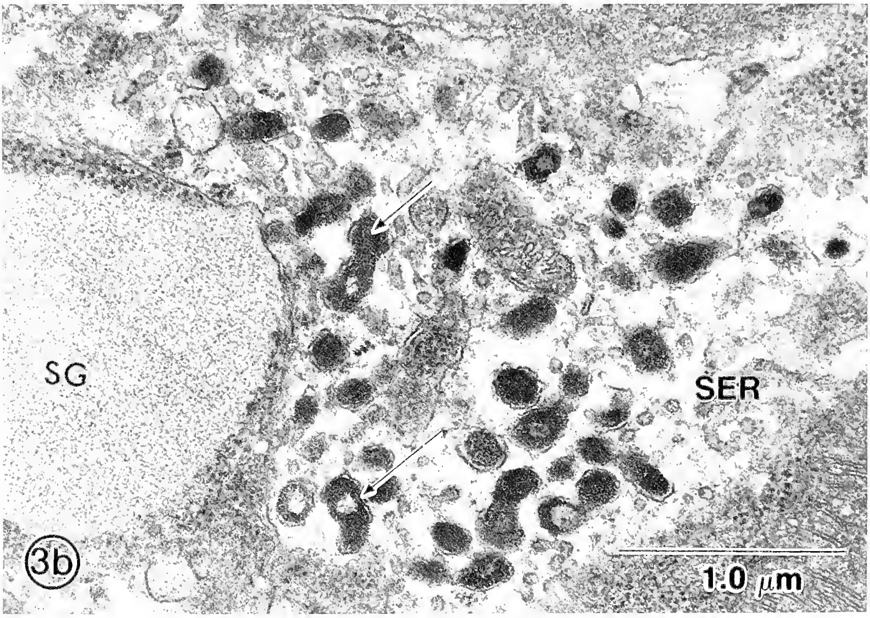
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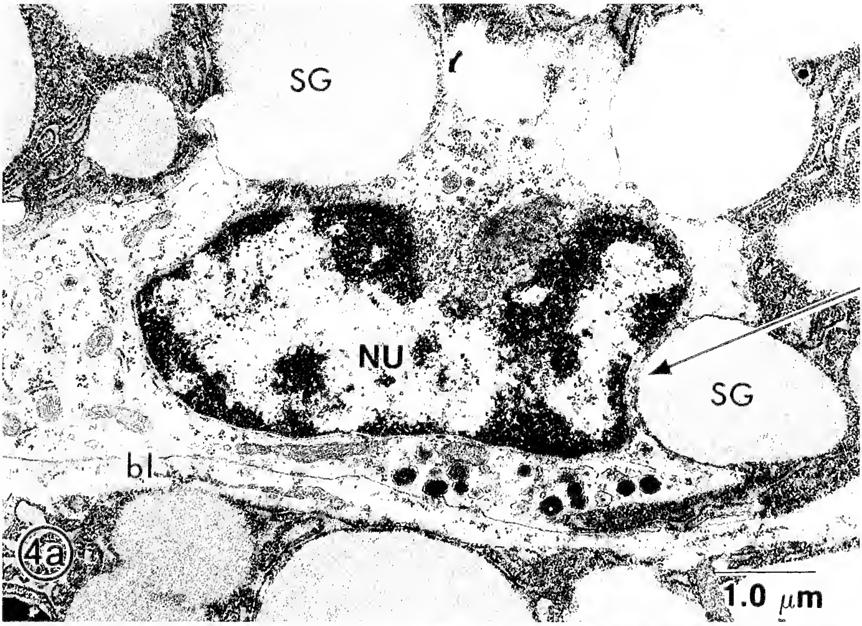
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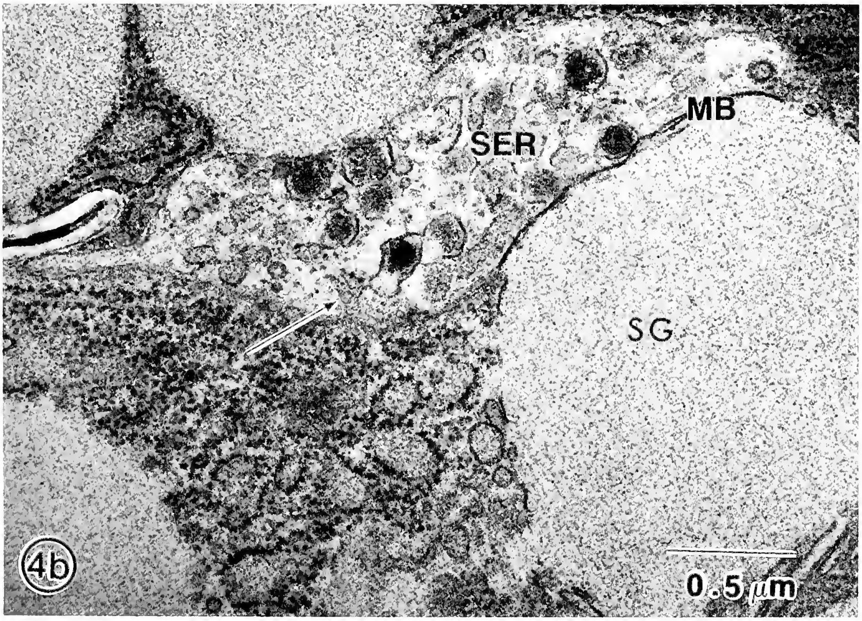
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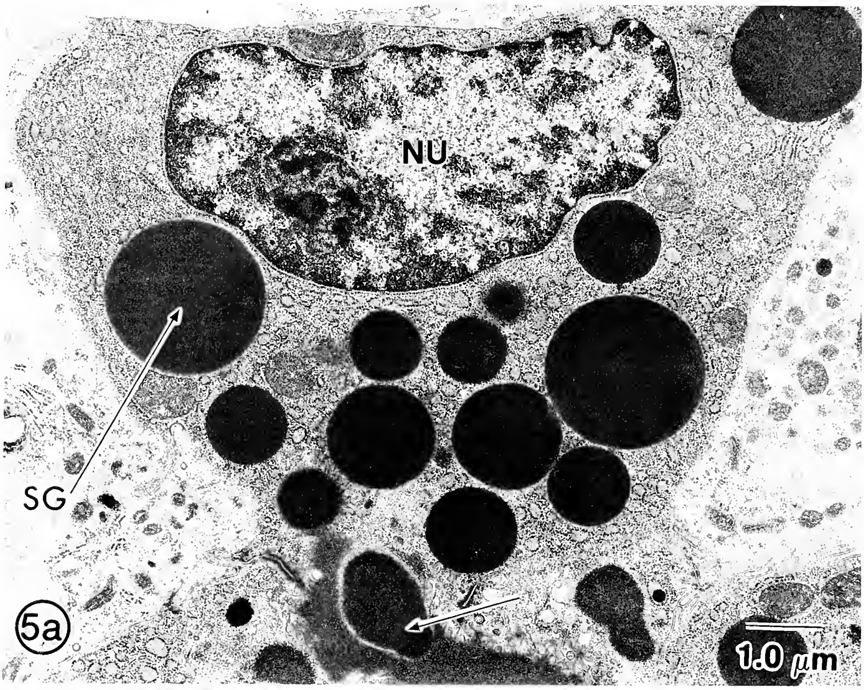
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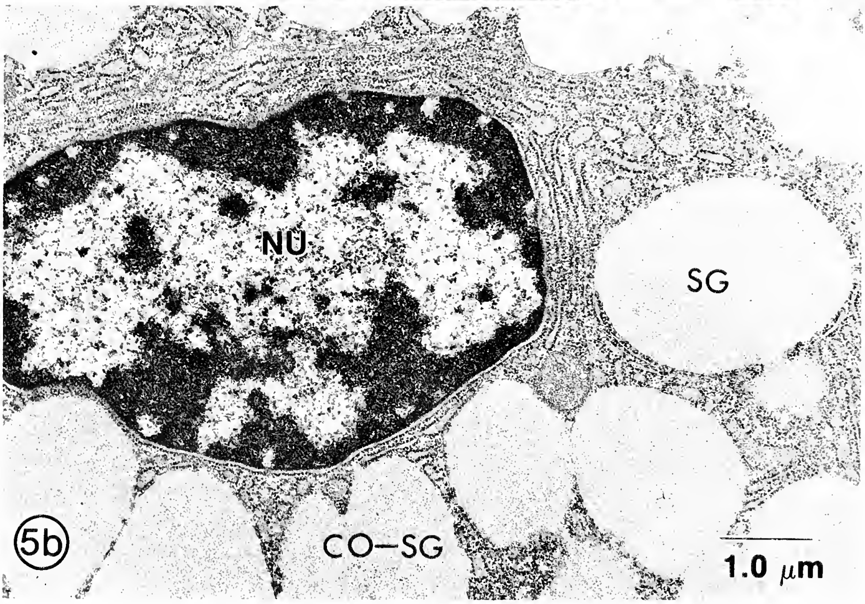
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cesses we found tubular smooth endoplasmic reticulum and images suggestive of exocytosis, suggesting that the G-cell granules might be released here (Fig. 4b).

Chief cells.—The gastric chief cells in *Trachops* were clustered at the base of the gastric gland (Fig. 1). The cells were pyramidal and contained spherical, electron-dense secretory product; the nucleus was irregular or ovoid and basally positioned; the GER profiles usually were swollen and spherical in appearance and the cisternae were filled with pale granular material (Fig. 5a). The Golgi complex was small and inconspicuous.

The chief cells in *Chiroderma* were extremely abundant, occupying at least half of each gland (Fig. 1). These cells differed dramatically from those in *Trachops* in that the abundant product did not stain with toluidine blue. Additionally, with the TEM the product was swollen, pale granules. Although many of the granules were in the form of individual spheres, others often had a coalesced appearance (Fig. 5b). The nucleus was basally positioned and usually irregular; lamellar GER and large Golgi complexes filled most of the remaining cytoplasm.

Parietal (oxyntic) cells.—The cytoplasm of parietal cells in *Trachops* was characterized by a modest number of profiles of intracellular canaliculi. The microvilli of these canaliculi were closely appressed and the intercellular spaces between them were filled with electron-dense product matching that found in the gland lumen (Fig. 6a, b). The cytoplasm of most parietal cells also contained large numbers of mitochondrial profiles and tubular and spherical vesicles (Fig. 6b). The parietal cells in our specimens of *Trachops* nearly always corresponded to an intermediate activity state (following Ito and Schofield, 1978).

In *Chiroderma,* the parietal cells could be placed into two categories: 1) an intermediate secretory stage, which was most common; and 2) an actively secreting stage, which was far less common (Fig. 7a, b). The ultrastructure of parietal cells in the intermediate stage differed from those in *Trachops* in the same stage in that these cells invariably had extensive, swollen-appearing intracellular canaliculi with thick, elongate microvilli (Fig. 7b). The cytoplasm of all parietal cells had abundant mitochondrial profiles and numerous vesicles, scattered GER profiles, and concentrations of lipofuscin granules (Fig. 7a, b). In active parietal cells, the intracellular canaliculi were greatly expanded and the

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Fig. 5.—a: Chief cell in *Trachops*; note the spherical electron-dense product (SG) and example of exocytosis (arrow) into the lumen. NU, nucleus. *T. cirrhosus,* CM 63688. b: Chief cells in *Chiroderma*; note the pale product (SG) and example of coalescing among secretory granules (CO-SG). NU, nucleus. *C. villosum,* CM 76798.

microvilli lining their borders were less compact (Fig. 7a). The cytoplasm of these cells contained few vesicles; instead, the Golgi complexes were the most prominent feature.

Mucous cells.—In *Trachops,* the mucous neck cells were scattered among the chief and parietal cells in the lower one-half of the gastric gland. The apex of each mucous neck cell bordered on the gland lumen. The nuclei were basally positioned and the apical cytoplasm contained secretory granules with pale, finely granular material and a distinctive electron-dense droplet occupying about one-fourth of the granule diameter (Fig. 8a).

The surface mucous cells and cells lining the gastric pits differed considerably from the mucous neck cells. The secretory product in these surface cells was more clearly defined (coalescing granules were not observed) and consisted of an electron-dense droplet set against a reticulated, dense substrate (Fig. 9). Some granule polymorphism was apparent; some of these cells also contained spherical or irregular, completely electron-dense granules located in the vicinity of the Golgi complex (Fig. 9).

The mucous neck cells in *Chiroderma* were relatively small and sparsely distributed and they primarily were positioned among parietal cells (Fig. 8b). The secretory product differed considerably from that in homologous cells in *Trachops.* The granules in *Chiroderma* consisted of a mixture of pale, flocculent material along with a coarser, fibrillar material and a small, peripheral electron-dense component (Fig. 8b). Gastric pits were nearly lacking in *Chiroderma.* The gastric surface consisted of mucous cells and exfoliating parietal cells with dark, dense

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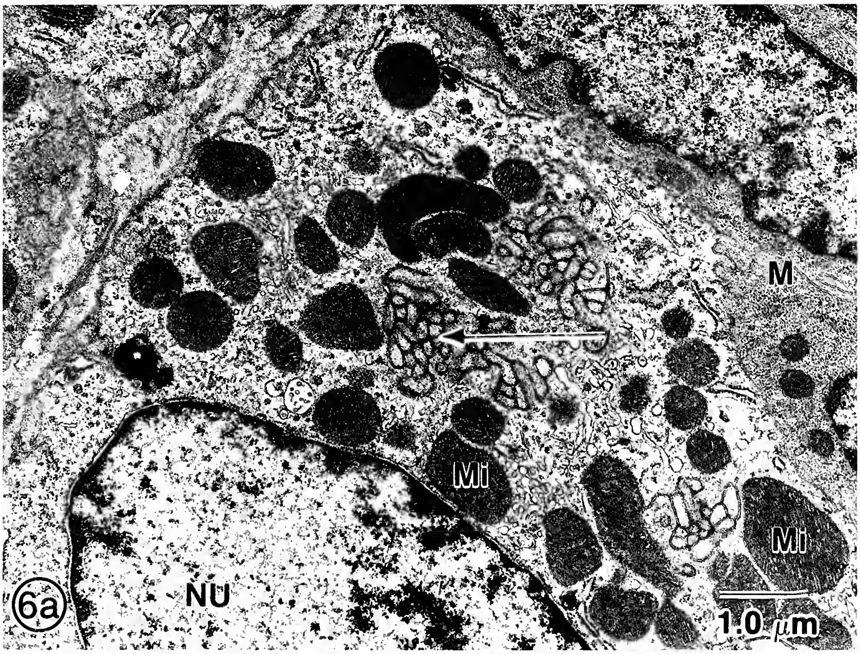
Fig. 6.—a: Parietal cell in *Trachops*; note the typical image of intracellular canaliculi in these cells in this species (arrow). NU, nucleus; Mi, mitochondria; M, mucous neck cell. *T. cirrhosus,* CM 63688. b: Parietal cell in *Trachops*; note the intracellular canaliculi (arrow) and tubular and spherical membrane profiles (V) in the cytoplasm. Abbreviations as above. *T. cirrhosus,* CM 63688.

Fig. 7.—a: Actively secreting parietal cell in *Chiroderma*; note the expanded intracellular canaliculus and cluster of lipofuscin granules (arrows). NU, nucleus; Mi, mitochondria; L, lumen. *C. villosum,* CM 76796. b: Inactive parietal cell in *Chiroderma*; note the lipofuscin granules (arrows) and compare the intracellular canaliculi (C) to those seen in *Trachops* parietal cells (Fig. 6). Abbreviations as above. *C. villosum,* CM 76796.

Fig. 8.—a: Mucous neck cells in *Trachops.* An immature granule (IMG) in association with the Golgi complex can be compared to mature mucous granules (MSG), which have an electron-dense droplet (arrow). *T. cirrhosus,* CM 63688. b: Mucous neck cell in *Chiroderma.* This cell is positioned near parietal cells (P) and is packed with mucous granules (MSG), which have an electron-dense droplet (arrows) but otherwise differ from those seen in *Trachops. C. villosum,* CM 76798.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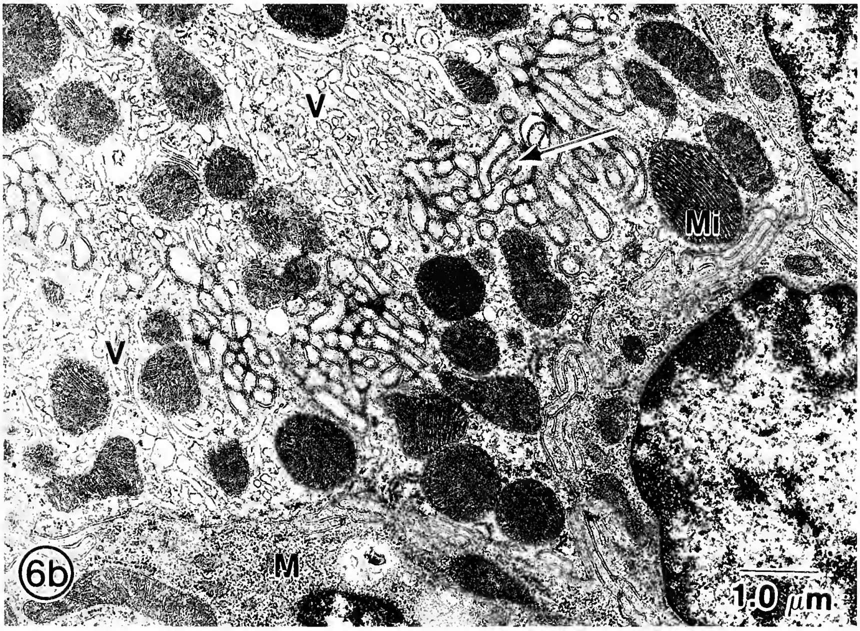
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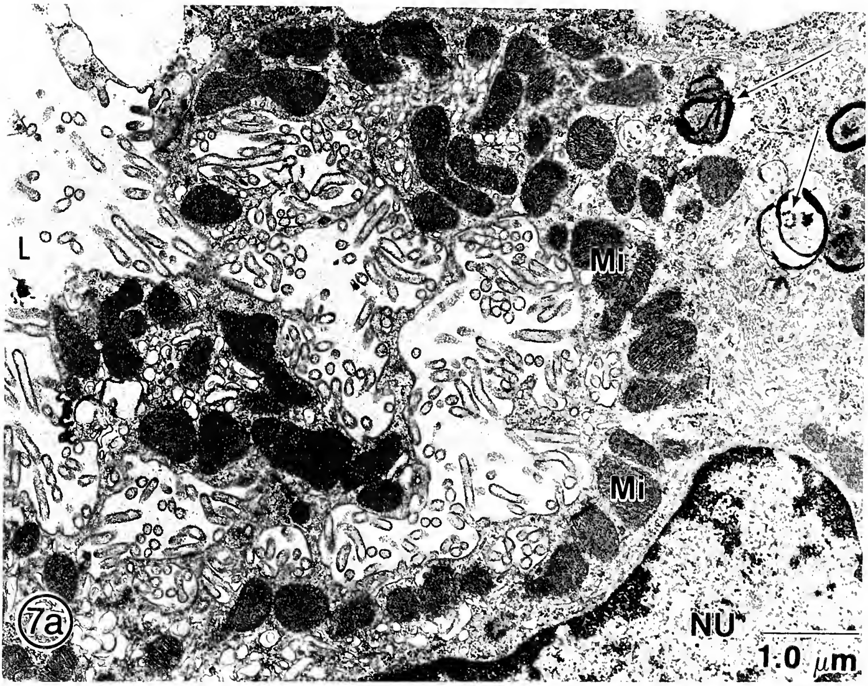
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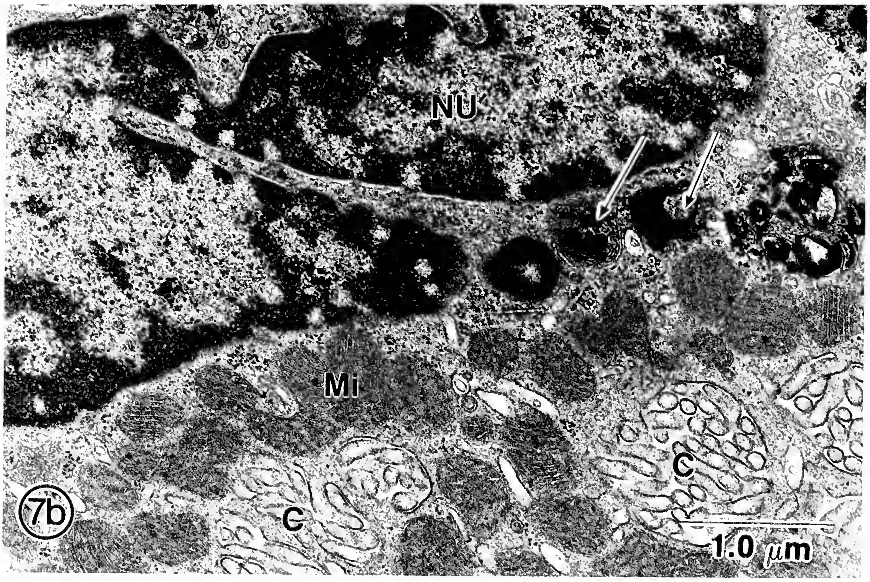
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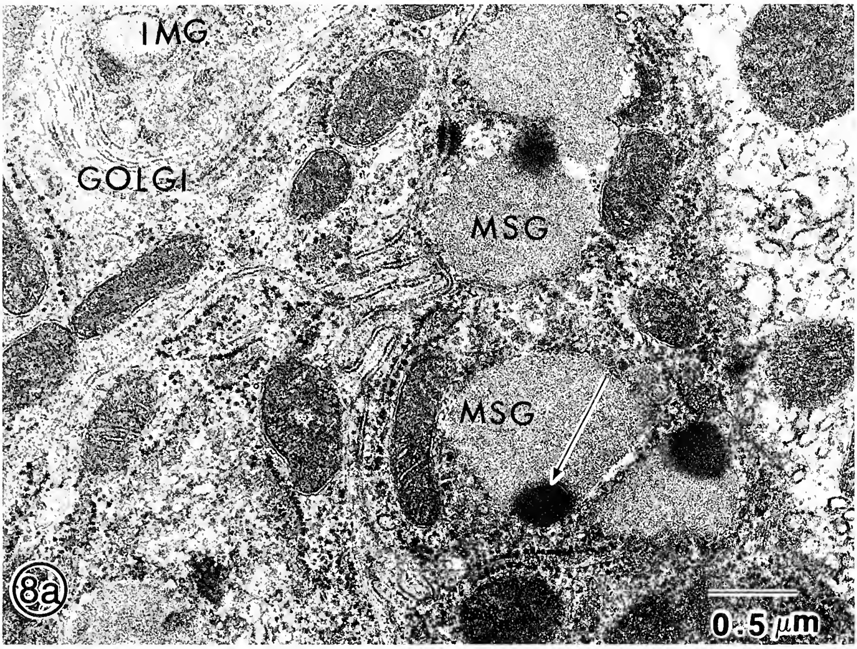
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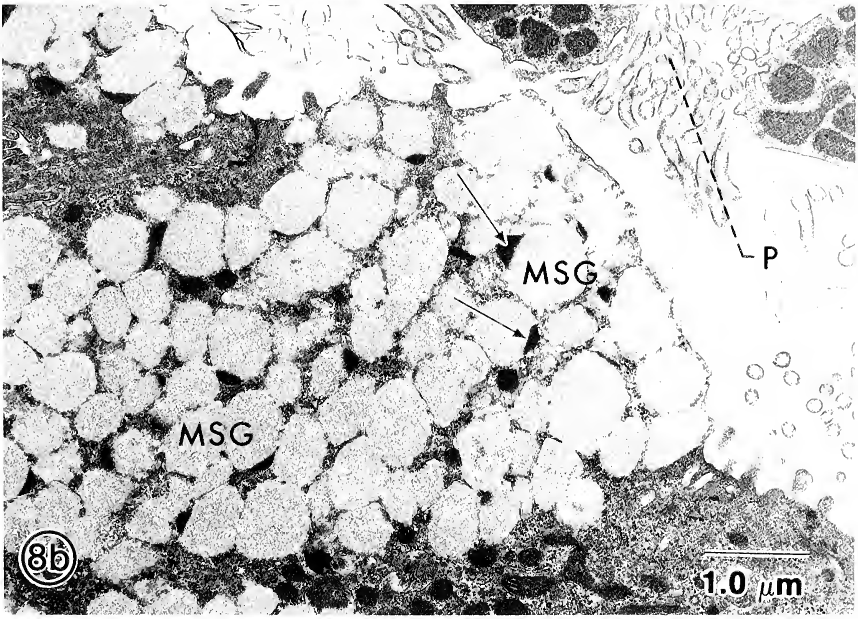
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cytoplasm. The surface mucous cells differed considerably from those in *Trachops* because the secretory product was pale and contained fibrillar material as well as a small, denser sphere at the margin of each granule (Fig. 10). Unlike the situation in *Trachops,* in *Chiroderma* the surface mucous cells and mucous neck cells appeared to produce only a single type of granule (Figs. 8b, 10).

DISCUSSION

Comparative transmission electron microscopy has been shown to be a useful addition to histological and histochemical techniques in the study of systematics and evolutionary biology of mammals (for example, Phillips et al., 1984; Feldman and Phillips, 1984; Tandler et al., 1986; Phillips et al., in press; Phillips and Tandler, in press). An analysis by TEM allows for interspecific comparisons of structure among cells that are thought to be homologous (following criteria of Rieger and Tyler, 1979) and in the same stage of differentiation. In making our comparisons of ultrastructure we recognized the fact that, in effect, we were comparing cells "fixed" at a moment in time and, thus, to some extent the molecular events and organization that we were viewing and comparing were aspects of functional state rather than genic differences that directly determine cell structure (Phillips et al., 1984). On the other hand, in making comparisons between regulated, polarized secretory cells in the two genera of bats, we were able to compare directly the ultrastructure of mature secretory granules containing gene products such as mucus, pepsinogen, and a variety of peptide hormones (Phillips and Tandler, in press). In our present investigation we found noteworthy ultrastructural differences among all cell types and many of their products as well as in the relative numbers of particular cell types in the fundic glands of two ecologically divergent species of bats (Table 1).

Entero-endocrine cells are important because they synthesize and secrete a wide variety of peptides as well as 5-hydroxytryptamine (serotonin) and these products can have a complex, and as yet not fully understood, controlling or modulating influence on the digestive tract (Pearse, 1969; Grube and Forssmann, 1979; Solcia et al., 1981). Indeed, although we use the terms "entero-endocrine" or "endocrine," at least some of these cells actually might be regarded as "endocrine-paracrine" cells. Our identification of entero-endocrine cells was based solely on

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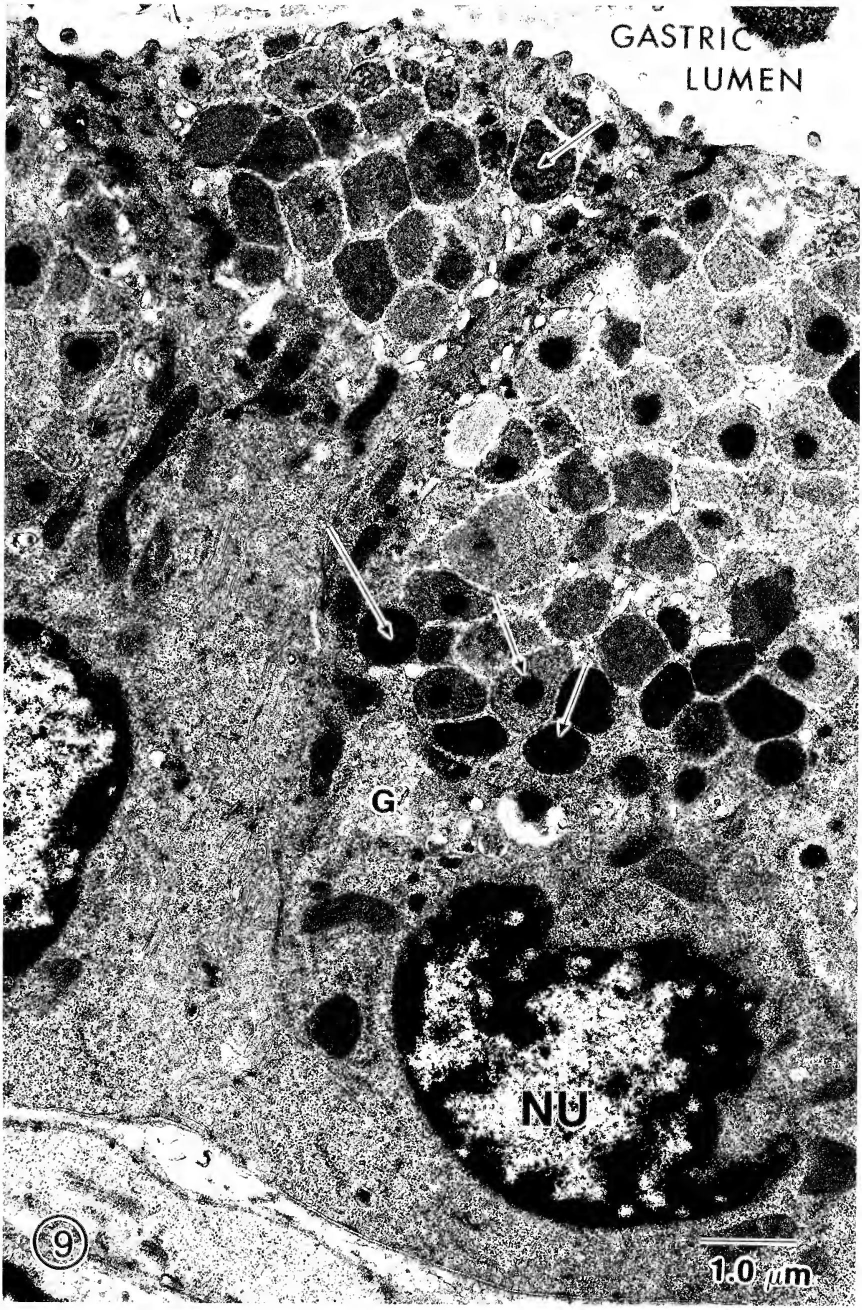
Fig. 9.—Surface mucous cells that line the surface of the stomach and the gastric pits in *Trachops*. Note the variety of product images in the cytoplasm (arrows). Those nearest to Golgi complexes (G) often are the most electron dense. NU, nucleus. *T. cirrhosus,* CM 63688.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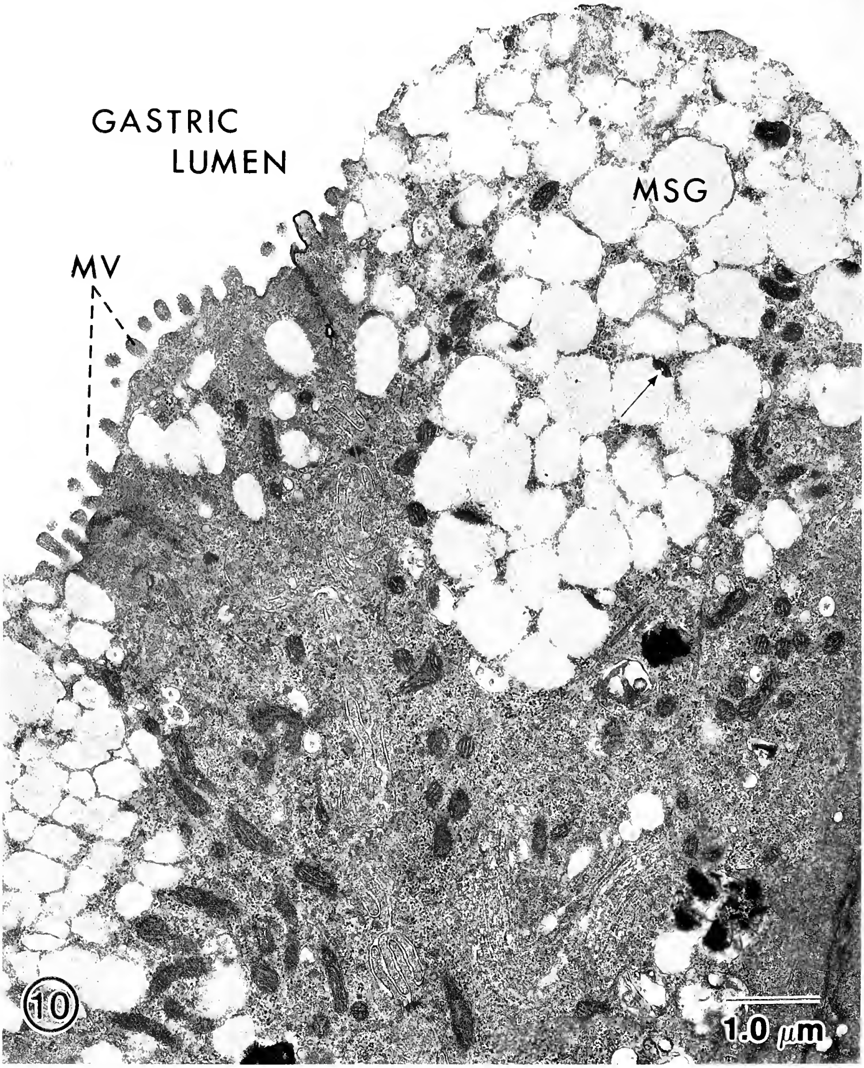

Fig. 10.—Surface mucous cells in *Chiroderma.* These cells are packed with secretory granules (MSG) that have an electron-dense droplet (arrow) and resemble those in mucous neck cells (Fig. 8b). Note the sparse microvilli (MV) on the apical surface of these mucous cells. *C. villosum,* CM 76798.

Table 1.—*A comparative summary of features of the fundic glands in* Trachops cirrhosus *and* Chiroderma trinitatum *and* C. villosum.

Feature	*Trachops*	*Chiroderma*	*Comments*
Entero-endocrine (=endocrine-paracrine) cells	A, glucagon D, somatostatin	A, glucagon EC_n, serotonin D_1, ? G, gastrin	See Figs. 2, 3, 4
Chief cells	Moderate numbers	Extremely abundant	Ultrastructural differences in secretory product; Figs. 1, 5
Parietal cells	Small in size, low average activity level in fasted animal	Extremely abundant, large in size; very high average activity level in fasted animal	Ultrastructural differences allow for comparisons of activity level; Figs. 6, 7
Mucous neck cells	Common	Scarce	Ultrastructural differences in secretory product; Fig. 8
Gastric pit and surface mucous cells	Abundant, with deep gastric pits	Very sparse, gastric pits nearly non-existent	Ultrastructural differences in secretory product; Figs. 1, 9, 10

ultrastructure; thus, we could only infer products from experimental literature. The following discussion of entero-endocrine cell products is therefore largely reliant on the accuracy of ultrastructural identification of particular cells; immunohistochemistry will be necessary for more precise identification.

In *Trachops* we identified A-cells (Fig. 2), which are thought to secrete glucagon (Moody et al., 1978; Unger et al., 1978) and D-cells, which secrete somatostatin (Hökfelt et al., 1975; Grube and Forssmann, 1979). Cells with essentially the same ultrastructure have been found in other species; A-cells have been described in *Pteronotus, Phyllostomus, Carollia,* and *Artibeus,* whereas D-cells have been found previously only in *Pteronotus* and *Phyllostomus* (Phillips et al., 1984). Yamada et al. (1984) have demonstrated both glucagon- and somatostatin-like immunoreactivity in endocrine cells in the fundic region of the stomach of the common vampire bat, *Desmodus rotundus,* so although ultrastructural data are lacking, this species also has both A- and D-cells. *Chiroderma* differed from *Trachops* in that A-cells were rare and in having EC_n-cells, G-cells, and D_1(H) cells, none of which was found in the *Trachops* material examined by us. However, it must be remembered that cell types that are scarce, or common but localized, could easily be overlooked in a TEM survey. Light microscopy of semithin

(0.5 μm) sections does not solve this problem because many endocrine cells cannot be detected and identified with light microscopy and routine staining.

The apparent presence of abundant glucagon- and somatostatin-producing entero-endocrine cells in *Trachops* is significant because these cells 1) also are found in other insectivorous, animalivorous, and sangivorous species (Phillips et al., 1984; Yamada et al., 1984), 2) are abundant, 3) are positioned among chief and parietal cells, and 4) because each of these products is known to inhibit gastric acid secretion (Konturek et al., 1975; Kusomoto et al., 1979; Stachura et al., 1981). Additionally, the physical proximity of A- and D-cells in *Trachops* resembles the situation in dogs, in which somatostatin apparently also inhibits, or limits, glucagon production (Kusomoto et al., 1979). In any case, the abundant presence of A- and D-cells in *Trachops* might correlate with the moderate number of generally inactive parietal cells, just as we found previously in both *Pteronotus* and *Phyllostomus* (Phillips et al., 1984). Likewise, the relative rarity of glucagon-producing cells and the possible absence or scarcity of somatostatin-producing cells in *Chiroderma* correlates with the extreme activity of the large and abundant parietal cells (Figs. 1, 7).

The presence of EC_n- and D_1-cells in *Chiroderma* (Fig. 3) cannot readily be related to any particular feature of the fundic gland. The EC_n-cells are thought to have endogenous serotonin (5-hydroxytryptamine), which also is found in enteric neurons (Grube and Forssmann, 1979; Gershon, 1981). The physiological roles of entero-endocrine cell serotonin possibly include inhibition of acid release along with stimulation of mucus. Some investigators also regard serotonin as an intrinsic neurotransmitter that modulates smooth muscle and affects blood flow (Gershon, 1981; Ormsbee and Fondacaro, 1985). Examples of an EC_n-type of cell also have been found in *Phyllostomus hastatus* so although we failed to find examples of EC_n-cells in our specimens of *Trachops,* their occurrence in *Chiroderma* suggests that they might be widespread in phyllostomid bats. This is further supported by Yamada et al. (1984) who reported that they found moderate numbers of serotonin-immunoreactive cells in the fundus of vampire bats.

The D_1-cells in *Chiroderma* have an ultrastructure that is indistinguishable from that found in D_1-cells in *Artibeus* (Phillips et al., 1984). Some authors have linked D_1-cells to production of vasoactive intestinal polypeptide (VIP) in the mammalian gut (for example, Grube and Forssmann, 1979), but others (for example, Larsson et al., 1979) have argued that the peptide produced by D_1 cells is not VIP but a similar molecule. Some workers now think that VIP in the digestive tract is found only in nerve fibers and nerve cell bodies (Baecker et al., 1983). Another possibility is that the D_1 cells in *Chiroderma* produce motilin or bombesin, or both, because these peptides also have been associated with cells that ultrastructurally fall into the D_1 cell group (Capella et al., 1978; Solcia et al., 1981). The product and physiological role of D_1 cells in *Chiroderma* and *Artibeus* thus is unknown at the present time.

The possible G-cells found by us at the base of fundic glands in *Chiroderma* are noteworthy for several reasons. Heretofore, gastrin-producing cells have not been identified in the fundic region of the mammalian stomach (Solcia et al., 1981) and Yamada et al. (1984) did not find any gastrin-like immunoreactivity in the fundus of vampire bats. Secondly, the gastrin peptide is known to stimulate gastric acid secretion (for example, Chew and Hersey, 1982), which is considerable in *Chiroderma,* if abundance, large size, and ultrastructure of parietal cells are reliable indicators of the level of acid secretion in the absence of quantitative data on gastric acid. Thirdly, the ultrastructure of the G-cells and their cytoplasmic granules is consistent with published descriptions of known G-cells in other mammals (Grube and Forssmann, 1979; Solcia et al., 1981) and with G-cells in the pylorus of *Ariteus flavescens,* which were identified by demonstration of gastrin-like immunoreactivity (Mennone et al., 1986). The apparent physical relationship between G-cells and chief cells in *Chiroderma* is another matter. It is not known with certainty that gastrin stimulates secretion of pepsinogen; instead, chief cells in mammals have been shown to have receptors to the peptides secretin and cholecystokinin (CCK) (Hersey et al., 1983, 1984). However, the ultrastructure of possible G-cells in *Chiroderma* differs substantially from the ultrastructure of either secretin or CCK-producing endocrine cells (Solcia et al., 1981) and thus would not be easily confused with either of these. Gastrin and CCK have been shown to share a common C-terminal portion of the molecule (Larsson and Rehfeld, 1977; Solcia et al., 1981) but in mammals they are produced by separate cells and appear to have separate functions. Indeed, it seems to be typical of entero-endocrine cells that their various products are stored in membrane-bound granules that have specific and consistent ultrastructural morphology and gastrin and CCK, regardless of their molecular similarities, are found in very different-looking granules (Phillips and Tandler, in press).

Available data on various types of entero-endocrine cells in *Trachops, Chiroderma, Phyllostomus, Carollia, Glossophaga, Artibeus, Ariteus, Erophylla, Desmodus,* and *Pteronotus* (Phillips et al., 1984; Yamada et al., 1984; Mennone et al., 1986) raise far more questions than answers. Some peptides (for example, glucagon, somatostatin, and gastrin) have been investigated to the extent that we can begin to relate physiological data from laboratory studies of other species to our findings in bats. However, most other peptides possibly produced in species-specific patterns of differential abundance in bats are far more difficult to integrate with other data because less is known about possible functions. The problem is compounded by the fact that some of these molecules are found in both enteric nerves and endocrine cells and may be functionally different in each (Hökfelt et al., 1975; Grossman, 1976; Schultzberg et al., 1980; Gershon, 1981; Miller, 1984). Nevertheless, these regulatory molecules probably have played a key role in the evolution of dietary diversity as seen in bats, and differential production of peptides or differential location of cells that produce some peptides might even contribute to or account for interspecific differences in histology of the chiropteran digestive tract (Mennone et al., 1986). Various peptides, and 5-HT as well, ultimately might provide a key to our understanding of the evolution of histological and functional diversity.

Parietal cell ultrastructure in *Chiroderma* closely resembles that of *Artibeus* and *Ametrida* (Phillips et al., 1984; Phillips, unpublished data) and, judging from experimental studies, is indicative of a high rate of HCl secretion, even in fasted animals (Ito and Schofield, 1978; Schofield et al., 1979; Black et al., 1980). This high rate of secretory activity may be further substantiated by the abundance of lipofuscin granules (Fig. 7) in *Chiroderma* parietal cells observed in all of our specimens. This type of lysosome has been correlated with degradation of byproducts of cellular metabolism and its presence in parietal cells suggests that cellular metabolism is occurring at a high rate (Toth, 1968; Fawcett, 1981).

Chief cells (which produce pepsinogen and rely on gastric acid for conversion to pepsin) also are extremely active in phyllostomid fruit bats, judging from the unusual ultrastructural appearance of the product (Fig. 5) in *Chiroderma, Artibeus,* and *Ametrida* (Phillips and Studholme, 1982; Phillips et al., 1984). This pattern may be a widespread occurrence in fruit bats because in *Eidolon helvum,* an African megachiropteran, an analysis of digestive enzymes demonstrated high pepsin content in both the stomach and lower esophagus (Ogunbiyi and Okon, 1976) and histological study has revealed abundant chief and parietal cells (Okon, 1977).

Differences among the mucus-producing cells in *Trachops* and *Chiroderma* were significant, but in keeping with previously reported patterns (Forman, 1972; Phillips et al., 1984). *Trachops* produces abundant mucus, whereas *Chiroderma* produces little mucus due to the limited number of mucous neck cells, the virtual absence of gastric pits lined with mucous cells, and the relative scarcity of typical mucous surface epithelial cells. In *Trachops,* the mucous cells ultrastructurally resembled those found in *Pteronotus* and *Phyllostomus* (particularly in the latter species) and differed from those in *Carollia* and *Artibeus* (Phillips et al., 1984) and *Chiroderma.* However, *Trachops* differed from its nearest studied relative (*Phyllostomus,* cf. Smith, 1976; Hood and Smith, 1982) in having relatively shallower gastric pits (hence fewer surface mucous cells) and in having a chemically different mucus in the surface cells. In *Phyllostomus,* the surface mucous cells exhibit toluidine blue metachromasia (Forman, 1972), suggesting the presence of a sulfonated compound (Spicer, 1963), whereas in *Trachops* the product is negative to toluidine blue staining. The significance of this chemical difference is unknown. It might represent a real interspecific difference but also could be the consequence of physiological state of the animals at time of sacrifice because Ohara et al. (1984) have demonstrated that histochemical changes in mucous glycoproteins can occur within hours in fasted laboratory rats. Although our bats all were handled the same way after capture, we have no way of knowing for certain whether they fed before being collected. On the other hand, intraspecific consistency among our specimens does seem indicative of a real interspecific difference.

The greatly reduced mucus-production in *Chiroderma* seems to be characteristic of Neotropical fruit bats (Forman, 1972, 1973). Although mucus often has been regarded as a major factor in the protection of the gastric epithelium, its relative scarcity in fruit bats with highly active parietal cells suggests otherwise. A recent study (Robert et al., 1984) that demonstrated a lack of correlation between the thickness of the mucus coat and protection of the stomach lining in laboratory rats helps to explain the fruit bat data. But how is the stomach protected in bats such as *Chiroderma* and *Artibeus*? One possibility is that the lining of the stomach is protected by salivary gland secretions (Studier et al., 1983*b*; Phillips et al., 1984). Other possibilities include surface-active phospholipids (Lichtenberger et al., 1983) and H^+ disposal by the surface cells through a Na^+/H^+ exchange system (Olender et al., 1984).

In summary, it seems reasonably clear that mucous production (amount and chemistry) in the fundus of the stomach in stenodermatine fruit bats differs substantially from that in phyllostomine animalivorous species. The mucus produced in fruit bats is less complex in the sense that mucous neck and surface cells are ultrastructurally the same, whereas in animalivorous species such as *Trachops* notable differences can be found when one compares the secretory granules in these cells. The biological significance of this intrafamilial divergence in mucous cells and in ultrastructure of mature product is unknown but the consistency of the pattern in the genera examined to date (Forman, 1972; Phillips et al., 1984) is noteworthy because when differences in the ultrastructure of an exocrine cell product can be correlated with systematics, a foundation is set for studying evolution at the cellular level (Tandler et al., 1986; Phillips and Tandler, in press).

To what extent do our ultrastructural data provide answers for our original question about the relationship among dietary and structural specialization and cellular features of the gastric mucosa? Although *Trachops cirrhosus* clearly represents an instance of behavioral evolution that includes specialized feeding on Neotropical frogs (Tuttle and Ryan, 1981), the gastric fundic mucosa at the cellular level is similar to that of *Phyllostomus hastatus* and *P. elongatus* (Phillips et al., 1984), which generally are regarded as "animalivorous" or "insectivorous" (Gardner, 1977). The only differences of note are the possible absence of EC_n-cells, the slightly shallower gastric pits, and the absence of toluidine blue positive components in the mucus in *Trachops.* The fundic mucosa of *Trachops* thus seems to be somewhat generalized even though these bats have adopted a specialized behavior and feeding strategy.

Chiroderma is very similar to *Artibeus* at the cellular level (Phillips et al., 1984). It differs significantly, however, in having a relatively greater abundance of chief cells (45–75% of each fundic gastric gland as compared to about 25%). Cellular differences in the gastric mucosae of different Neotropical fruit bats are interesting because they suggest the possibility of subtle differences in diet or in the assimilation of nutrients from a shared diet.

Lastly, how do *Chiroderma* and other previously studied phyllostomid fruit bats compare to the megachiropteran fruit bats? This question is significant because evolutionary convergence is virtually unstudied at the histological, histochemical, and ultrastructural levels. Available data support the theory that frugivory evolved independently in these bats (Kamiya and Pirlot, 1975; Smith, 1976) and some physiological studies suggest that the two groups might be different in the ways that they actually regulate their diets or dietary intake (Thomas, 1984). Furthermore, some data can be interpreted to show that megachiropteran and microchiropteran bats might have had separate origins altogether (Smith and Madkour, 1980). Given this, the general histological similarities in gastric mucosa of microchiropteran fruit bats of the genera *Chiroderma, Artibeus,* and *Ametrida* on the one hand (present study; Phillips and Studholme, 1982; Phillips et al., 1984) and the African megachiropteran, *Eidolon helvum,* on the other, are indeed remarkable. Judging from the published data of Ogunbiyi and Okon (1976) and Okon (1977), the microchiropteran fruit bats and *E. helvum* have the following features in common: 1) very shallow, almost nonexistent, gastric pits; 2) a scarcity of mucous neck cells; and 3) abundant, extremely active parietal and chief cells. The extent of histological convergence between the stenodermatines and megachiropterans as a group is less certain because the latter seem to be quite variable and published descriptions are not always adequate for comparisons. However, the stenodermatines do appear to share a variety of histological features with *Rousettus, Pteropus, Eonycteris,* and *Penthetor* (Kamiya and Pirlot, 1975; Bhide, 1980) and future ultrastructural comparisons will be of interest.

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AN INTERNATIONAL SURVEY OF THE POPULAR AND TECHNICAL LITERATURE OF MAMMALOGY

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Abstract

A questionnaire designed to assess the diversity and abundance of the technical, semitechnical, and popular literature of mammalogy was sent to curators in 161 mammal collections and museums in 74 countries; 104 responses were received from 55 nations. Results show a great disparity in the availability of the different types of literature among countries. Some nations have a very strong literature at all levels, while many are in great need of all types of literature. Countries that have a rich literature at the semitechnical and popular levels also have a strong foundation in the basic technical literature of mammalogy. A statistical analysis of various socioeconomic factors shows that per capita income (PCI) is strongly positively related to the availability of literature at all levels: increasing the PCI by $1000 per year results in a doubling of the available literature on mammalogy. The analysis suggests that only through international cooperative research on basic mammalogy can the PCI block be bypassed and the stage set for an increase in the popular literature of mammalogy.

An overview of the mammalogical literature is presented for each country queried. Responses of the curators are also given. Almost all respondents indicated a willingness to work in a cooperative manner with foreign scientists in producing semitechnical and popular literature in mammalogy.

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INTRODUCTION

Mammalogy is a diverse discipline, encompassing such areas as systematics, ecology, behavior, physiology, anatomy, and other fields of specialization. The trend in recent years has been away from basic systematic and survey research and toward more scientifically elegant and popular experimental and laboratory-oriented work. We believe that this is a very healthy and exciting pattern, particularly in the developed nations of the world. As Mares (1982, 1985, in press) has pointed out, one very important reason that modern theoretical/empirical research on mammals can be performed in developed countries is because the foundational research on mammal species was done decades ago by scores of mammalogists who constructed a framework upon which current research can be supported. It is no accident that most of the important research in state-of-the-art mammalogy is being performed by investigators living in countries that have a long and noble history of basic faunal research. In many cases, the organisms being examined by the current crop of new mammalogists have been studied in one form or another for more than a century.

An unfortunate correlate of the trend toward experimental research is the tendency by some investigators to view foundational systematic and survey research as being somehow less scientific and less inherently valuable than investigations that are *dernier cri.* This view obtains because in developed countries there is little work left to be done at the foundational level. Moreover, younger biologists, trained in the United States for example, are often quite parochial in their views of nature. This is not said in a condemnatory fashion, but is merely observational. Most young mammalogists in developed countries have only had dealings with very well-studied aspects of their natural environment. They have seldom been at a real loss for either taxonomic or ecological information on any vertebrate species with which they are familiar, and their view of nature reflects this familiarity. They tend to think of nature as a well-studied entity, believing that most of the foundational work was completed early in this century and viewing the research problems that remain to be done as exciting tests of theoretical questions. We believe that these views are consistent with an educational background in a country that is rich in the foundational literature of mammalogy. We suggest that these sanguine views of basic field biology are in error.

The literature of mammalogy is extremely diverse. Almost all countries of the world support one or more mammal collections or natural history museums that often help to contribute to the basic literature of the science of mammalogy (for example, Genoways and Schlitter, 1981; Hickman, 1981). Hickman (1981) surveyed the field guides that had been published to the mammal faunas of most countries of the world. However, in many cases the guides or papers cited by Hickman are quite old (that is, published in the mid-1800's or early 1900's), and/or are quite difficult to obtain. More important, as Mares (1985, in press) has argued, field guides and other popular literature owe their existence to the foundational literature of mammalogy, the taxonomic and geographic surveys that first clarify the faunal makeup of a country. It was clear from Hickman (1981), and from our own work in various countries, that there are pronounced differences in the availability of the mammal literature of the world. Some countries seem to have a particularly abundant literature, whereas others have, at best, a very scant literature on mammals. Moreover, we had not seen any reports examining the availability of both the popular literature on mammals and the technical literature that provides its foundational material. If, indeed, these two types of literature bear some relationship to each other, we might expect that few countries lacking a strong basic literature will show a pronounced level of development of popular literature on mammals.

Just exactly how extensive the foundational literature of mammalogy might be is not clear. No one, to our knowledge, has attempted a comprehensive assessment of the actual status of the world's mammalogical literature. We feel that information on the availability of such literature on a global scale will help point out potential areas requiring increased research efforts. Such a survey might also indicate that the world we inhabit is less biologically explored than many surmise.

In this paper, we present results of a survey of the literature of mammalogy that were obtained through the use of a questionnaire that was sent to most of the mammal collections of the world. A preliminary report on these data was given in Mares (1985); however, we herein present a much more complete literature survey based on many more responses than were included in the earlier report. These data present an overview of the popular and technical literature of mammalogy for many countries of the world. They include data from most countries that have a mammal collection of greater than 50 specimens, and offer some information on the availability of mammal literature for almost all countries of the world that have a mammal collection of even modest size. Taken together, these data give some indication of the current status of the world's mammal literature, including which countries have reached a high level of literature availability. They also show which countries need a cohesive plan of work to provide either the technical or popular literature, or both, that are required if the country's literature is to be brought up to acceptable levels.

MATERIALS AND METHODS

A questionnaire designed to assess the availability of various types of natural history literature (primarily that dealing with mammals) in different countries of the world was sent out in 1981. Respondents were asked to list available publications and indicate if these publications were available in the common language of the country. The following questions were used: 1) Is there a publication (in the style of a field guide) available that deals with the identification of the mammals of your region? 2) Is there a publication (technical survey) available to the museum specialist which is concerned with the mammals of your region? 3) Are there taxonomic keys available to the mammals of your region? 4) Are there any works available that deal with the collecting or preparation techniques of mammals? 5) Are there any publications available that deal with the operation or importance of natural history museums? 6) Would you judge the number of available children's books dealing with natural history topics to be many, few, or rare? 7) Please list three natural history or museum science subjects that you feel need attention in your particular geographic area. 8) Please list any projects underway that deal with any of the topics listed in the first seven questions. 9) Would you be interested in cooperative research with other museum specialists in preparing publications such as field guides, textbooks, etc., that deal with the fauna of your area? Names of museums, research organizations, collections, and personnel (curators and directors) were obtained from Genoways and Schlitter (1981). Museums or research organizations were queried if: (1) the collections were of a substantial size, or (2) they were the only major museum or collection in a particular country or region.

The countries queried are listed in alphabetical order and questionnaire responses are indicated where applicable. Countries which were not surveyed or which did not respond to the questionnaire are indicated by "*No response received*" before the list of literature citations. Responses given by the respondents are italicized. Additional literature citations, not given by respondents, were added to present a more complete overview of the literature availability for the countries listed and are not italicized. Topics were eliminated if the respondent(s) did not answer a question. Responses to research needed or projects underway which did not directly pertain to mammals or museum science were omitted. Under "Comments" we have either summarized as succinctly as possible, or reproduced verbatim, informal comments of respondents. In some cases we have added additional observations that we feel are particularly important to an understanding of the literature situation in any given country. Willingness of the respondent(s) to work in cooperation with specialists from other museums and institutions are denoted by WTC at the end of the comments if more than one-half of the respondents of a particular country answered positively. The absence of this designation indicates that a negative response was received or that this question was not answered. A concerted effort was made to verify all references given by the respondents. Those references which could not be verified and/or are partial references are denoted by an asterisk following the reference number.

Hickman's (1981) broad overview of field guides to national mammal faunas includes many old (pre-1940) natural history publications. We have tried not to duplicate works cited in Hickman (1981). Moreover, we have attempted to list only the more readily available recent literature.

Countries responding to the questionnaire were placed into one of six groups based upon the major geographic regions: Latin American, European, Middle Eastern, African, Asian, and Australian. Summaries of responses to each question are presented separately in tabular form (Tables 1–3).

Data on gross national product (GNP), per capita income estimates, population growth rates, population density, literacy, and the percent of the population living in urban areas were obtained from *The Global 2000 Report to the President* (Barney, 1982) and *The World Almanac* (Lane, 1983).

RESULTS

Survey of Responses

AFGHANISTAN: *No response received*; but see 261, 347, 409, 429, 430.

ALGERIA: *No response received*; but see 344, 401.

ANGOLA: *No response received*; but see 279, 401.

ARGENTINA: Museo Municipal de Ciencias Naturales "Lorenzo Scaglia." Guides: *None*; but see 447. Surveys: *496*; see also 113, 114, 115, 189, 273, 372, 387, 391, 475. Keys: *None*; but see 272. Technical manuals: *130**; see also 102. Museum science literature: *None.* Children's literature: *Rare.* Research needed: *Paleontology.* Projects underway: *None*; also, Mares et al., Mammals of Tucumán, Los Mamíferos de Salta. Comments: The recent field guide by Olrog and Lucero is already out of print, and was difficult to obtain even when it was still in print. Greenhall has written a key to the bats of Argentina and Pearson has written a key to the small mammals of Nahuel Huapi and Lanin National Parks. Both of these are published or in press. Most of the surveys published in Spanish are difficult to obtain, while those published in English are either poorly disseminated among the scientists in Argentina or are themselves difficult to obtain. Argentina illustrates a problem that will be encountered time and again during this survey, and that is the difficulty in obtaining publications that are published in obscure journals or materials that are unpublished and circulated among a few specialists. The literature of mammalogy in Argentina is quite poor, particularly for native students of the Argentine fauna.

AUSTRALIA: Arthur Rylah Institute for Environmental Research; Australian National Wildlife Collection; Central Australian Museum; Monash University; National Museum of Victoria; Queensland Museum; Queen Victoria Museum and Art Gallery; South Australian Museum; Taronga Zoo; Tasmanian Museum and Art Gallery; The Australian Museum. Guides: *29*, 218, 234, 300, 312, 313, 314, 389, 500, 663*; see also 85, 662. Surveys: *13, 40, 83, 84*, 234, 300, 389, 459, 500, 662, 663*; see also 41, 188, 215, 219, 238, 375, 576, 654, 676. Keys: *12, 39, 144, 300, 306, 337, 663.* Technical manuals: *There is no publication which is specifically oriented in this direction. The Tasmanian Museum and Art Gallery has a leaflet on collecting animals for the museum. Works published in North America and Europe are used.* Museum science literature: *483* gives a historical account of the beginnings of the National Museum of Victoria but does not cover the last 25 years. Several journals are used including:* Kalori, *of the Museums Association of Australia,* Museum, Museum News, Curator, *and* Museum Journal; see also 533. Children's literature: *Few to many.*

Research needed: *Studies on marine mammals; ecology, ethological and conservation studies on native vertebrates; animal population dynamics; handbooks and field keys; collection and preparation technique manuals; publications dealing with ecological and behavioral techniques for naturalists; museum science publications; field guide to cetaceans recorded in Australian waters; detailed surveys of the mammals of particular geographic regions.* Projects underway: *The zoology department of the University of Tasmania is publishing a Fauna of Tasmania Series; two field guides to Australian mammals are in preparation, one by J. W. Calaby and one by M. Archer; B. Marlow is preparing an identification manual (at a technical level) to all the terrestrial mammals of Australia.* Comments: Several respondents indicated that a large number of works are currently in preparation. Many indicated that no comprehensive keys are available to Australian mammals. Many referred to preparation/collection techniques manuals of the British Museum (Natural History). No publications are available which deal specifically with museum science and literature; some are included as part of a treatment of other topics, however. WTC.

AUSTRIA: Naturhistorishes Museum Wien; Oberösterreichisches Landesmuseum. Guides: *30**, *75**, *90.* Surveys: *65**, *411, 432, 670.* Keys: *30**, *75**, *432.* Technical manuals: *471 and later editions, 161.* Museum science literature: *None.* Children's literature: *Few.* Research needed: *A modern handbook on European mammals; a survey of Austrian mammals; a semipopular identification manual.* Projects underway: *All of the above are in preparation.* Comments: WTC.

BELGIUM: Institut Royal des Sciences Naturelles de Beligique; Laboratorium voor Algemende Dierkunde. Guides: *94.* Surveys: *192, this publication is not up to date, and is without notes concerning distributions*; see also 285. Keys: *575* only for Rodentia, Lagomorpha, and Insectivora.* Technical manuals: *285.* Museum science literature: *None.* Children's literature: *Many, but no original work—most are translations.* Research needed: *Mammal distributions; ecology of the Carnivora; studies on mammal protection.* Projects underway: *Mammal distributions.* Comments: WTC.

BELIZE: *No response received*; but see 231, 233, 273, 309, 336.

BOLIVIA: *No response received*; but see 27, 28, 113, 114, 115, 273, 666, 695. Comments: Research is currently underway by Sydney Anderson and various collaborators on the mammals of Bolivia. Literature on the mammals of Bolivia is particularly depauperate.

BOTSWANA: *No response received*; but see 401, 557, 558.

BRAZIL: Museu de Ciências Naturais; Museu Nacional; Museu Paraense "Emíio Goeldi"; Universidade Estadual Paulista. Guides: *651.* Surveys: *113, 114, 420, 641, 642*; see also 45, 46, 47, 115, 126, 273, 388, 419, 466, 476, 550, 584, 640, 643. Keys: *420, 641, 642, 651*; see also 472. Technical manuals: *A collection and preparation manual written by the Departamento de Zoologia was published by the Mus. Zool., Univ. São Paulo in 1967 (152).* Museum science literature: *None.* Children's literature: *None.* Research needed: *Keys to the mammals of southeastern Brazil.* Projects underway: *Chiroptera of southeastern Brazil; Chiroptera of Mato Grosso, Brasil; chave para determinação de quirópteros brasileiros (reformulation and actualization); guia para identificação de quiropteros do sul do Brasil (não existe verbas para impressão) (F. Silva).* Comments: Research is currently underway on mammals of the Cerrado by C. Alho and M. Mares. Brazil has an extremely complex fauna of mammals and has only been cursorily examined (474). One respondent, in referring to the availability of field guides for Brazil, noted that a field guide was published long ago but is not available today. This same respondent noted that many of the publications on Brazilian mammals are no longer available, even to specialists. WTC.

BURUNDI: *No response received*; but see 401, 639.

CAMEROON: *No response received*; but see 164, 165, 401.

CENTRAL AFRICAN REPUBLIC: *No response received*; but see 401, 528.

CHILE: Colección Particular de Fabian Jaksić y José Yañez; Instituto de Ecología y Evolución; Laboratorio de Citogenética; Museo de Zoología de la Universidad de Concepción. Guides: *412, 454.* Surveys: *383, 454*; see also 113, 114, 115, 154, 220, 273, 475, 477, 588. Keys: *382, 497*; see also 383, 454. Technical manuals: *None, although 230 has been used in the past.* Museum science literature: *None*; one respondent reported *There is something published by Museo Nacional de Historia Natural, Casilla 787, Santiago, Chile.* Another respondent suggested 154 as a source of information on museum science literature; see also 694. Children's literature: *None or rare.* Research needed: *Ecology; behavior; distribution and zoogeography; taxonomic studies; keys to Chilean mammals; field guide to Chilean mammals for country and particular regions; literature for the general public; preparation/collection technique manuals for the specialist and the general public.* Projects underway: *Miscellaneous projects dealing with particular species.* Comments: *A recent bibliography of references on terrestrial Chilean mammals is given in 464.* Additional information is given in 495. The research on Chilean mammals has increased significantly in recent years, although it has not been reflected in available publications on the topics of interest in this report. Mann's guide to mammals of Chile is difficult to obtain. WTC.

COLOMBIA: Instituto de Ciencias Naturales; Museo del Instituto de la Salle. Guides: *None.* Surveys: *62, 63, 268, 269, 270, 282**; see also

78, 113, 114, 115, 267, 273, 363. Keys: *62, 63*. Technical manuals: 202*. Museum science literature: *159*. Children's literature: *Few or rare*. Research needed: *Natural history studies of mammals; systematic studies on any of the various mammal groups (Rodentia, Ursidae, Cercopithecidae)*. Projects underway: *None*. Comments: Cabrera and Yepes, as well as Cabrera's systematic manual, are either extremely difficult to obtain and very expensive (the former) or out of print entirely (the latter). Many of the works cited for Colombia are old or are published in English. WTC.

CONGO: *No response received*; but see 401, 489.

COSTA RICA: *No response received*; but see 211, 231, 233, 309, 310, 323, 626. Comments: The basic information to form a field guide to the mammals of Costa Rica and, indeed, to produce many other types of basic mammalogical materials is available in diverse publications in English. Costa Rica's fauna is well-studied when compared with the fauna of most of Latin America. A key to the mammals of Costa Rica was written by Hooper but is generally unavailable. A key to the bats of Costa Rica (572) is also generally unavailable.

CZECHOSLOVAKIA: Insititute of Systematic Zoology; Institute of Vertebrate Zoology; National Museum; Západočeské Múzeum v Plzni. Guides: *24*, 185, 196*, 245, 465*. Surveys: *185, 239, 244, 245, 465*. Keys: *24*, 185, 245, 465*. Technical manuals: *583**. Museum science literature: *None*. Children's literature: *None to many*. Research needed: *A handbook and key to Czechoslovakian mammals*. Projects underway: *State research programs on nature conservation and on the fauna of Czechoslovakia; handbook of Czechoslovakian mammals; key to Czechoslovakian mammals*. Comments: One response indicated that a specialized museum science journal was available, "Musejni Práce." WTC.

DENMARK: Natural History Museum; Zoological Museum of the University. Guides: *373, 548*. Surveys: *139, 432*; see also 140. Keys: *Keys from a number of different sources and in a variety of languages are available to the specialist. Non-specialists can use handbooks and field guides for identification*. Technical manuals: *No special publication; techniques are given in a number of field guides for the general public (youth, teachers, sportsmen)*. Museum science literature: *None*. Children's literature: *Many*. Projects underway: *None*. Comments: *You always want an up-to-date, comprehensive, and confident treatment of the mammal region, but I think we have a fair picture of the Danish mammal fauna and new information is added every year. The same can be said for most countries in N.W. Europe*. In referring to the question on the availability of publications dealing with the operation and importance of natural history museums the following comments were made: *I can think of no special publications. Museums—including natural history museums—are part of the cultural tradition and depending on the actual financial situation in the country it may go up and down for the museum. In one period you may pay special attention to research, in the next to exhibition and other public relation (*sic*) e.g., in relation to nature conservation and management.* In reference to the question dealing with collecting or preparation techniques manuals, the following comments were made: *No special publication but techniques are mentioned in a number of field guides for youth, guides for teachers in biology, guides for sportsmen, 'do it yourself books,' etc. Generally, collecting and preparing a mammal should not be encouraged in countries in Western Europe and in many countries here mammals not considered game or pest species are totally protected.*

ECUADOR: *No response received*; but see 14, 51, 113, 114, 115, 273, 667.

EGYPT: Wassif's Collection. Guides: *453.* Surveys: *None*; see also 229, 287, 288, 289, 290, 453, 657, 658, 660. Keys: *525, 536, 537, 538, 539, 540, 541, 542, 659*; see also 401. Technical manuals: *None.* Museum science literature: *None.* Children's literature: *Few.* Research needed: *[Mammals of] the eastern and western deserts of Egypt; the Sinai.* Projects underway: *A study of the Western Desert of Egypt is currently underway and is scheduled to be published by the Desert Research Institute, Mataria, Cairo (in Arabic).* Comments: WTC.

EL SALVADOR: Museo de Historia Natural de El Salvador. Guides: *None.* Surveys: *106 (currently unavailable), 181*; see also 177, 178, 179, 180, 182, 231, 233, 309. Keys: *None*; see also 231, 233. Technical manuals: *25.* Museum science literature: *None.* Children's literature: *None.* Projects underway: *Mammals of the Monte Cristo National Park by Jim Hartman (in preparation); New Bats for El Salvador by V. Hellebuyck (in preparation).* Comments: There was also a comment indicating that publications dealing with preparation techniques of mammals are available at the museum library for these specialists. It was noted that these were not available for the general public. WTC.

ENGLAND: Booth Museum of Natural History; British Museum (Natural History). Guides: *93, 136, 137, 139, 141, 142, 359*; see also 392. Surveys: *136, 137, 139, 140, 141, 142, 359*; see also 42. Keys: *136, 137, 139, 359; a specialist key is available from Mrs. J. Coy,* Department of Environment, Faunal Remains Project, 63 University Road, Southampton SO9 5NH England. Technical manuals: *31, 379, 618**, *652*; see also 138. Museum science literature: *Various British Museum (Natural History) publications.* Children's literature: *Many.* Research needed: *A list of named collections, their content and location; curatorial codes and practices; a national inventory of collections.* Projects underway: *A Manual of Curatorship and a Code of Ethics are being developed by Museums Association, a museums professionals group; one or two keys to skeletal material are available from specialist museums groups in England.*

EQUATORIAL GUINEA: *No response received*; but see 380, 401.

ETHIOPIA: *No response received*; but see 143, 280, 355, 401, 690, 691, 692, 693.

FEDERAL REPUBLIC OF GERMANY: Coll. Pieper/Kiel; Landessammlungen für Naturkunde; Staatliches Museum für Naturkunde Stuttgart; Zoologische Staatssammlung München; Zoologisches Forschungsinstitut und Museum Alexander Koenig. Guides: *30*, 75*, 92, 195, 325*, 341.* Surveys: *325* (for Bavaria), 432.* Keys: *30*, 75*, 432.* Technical manuals: *148, 149, 471 (and later editions), some information given in field guides.* Museum science literature: *527 and several papers in* Natur und Museum. Children's literature: *Many.* Research needed: *Detailed distribution maps; studies of post-cranial osteology; survey of the mammals of Germany; a history of museum collections; type catalogues.* Projects underway: *None.* Comments: One respondent noted that there are several small papers dealing with the collection and preparation techniques of mammals that were issued for the public but are of questionable value. WTC.

FINLAND: Zoological Museum, University of Helsinki; Zoological Museum, University of Oulu. Guides: *547, 549.* Surveys: *547, 549, 552.* Keys: *549.* Technical manuals: *549, 552.* Museum science literature: *None.* Children's literature: *Few to many.* Research needed: *Zoogeography of the northern parts of Norway, Sweden, Finland, and Soviet Union; history of the distribution of mammals after the Ice Age; microtaxonomy of mammals today.* Projects underway: *None.* Comments: One respondent noted that most children's literature is translated from other languages. WTC.

FRANCE: Laboratoire de Zoologie, Mammiféres et Oiseaux; Musée Zoologique. Guides: *89, 519.* Surveys: *519*; see also 362, 506. Keys: Response affirmative, but none were listed. Technical manuals: *153, 356*.* Museum science literature: *80*, 214.* Children's literature: *Many.* Research needed: *Importance of natural history museums; an atlas of the fauna of France; inventory of the fauna of parks and reserves; an altitudinal distribution of the micromammals in the Vosges Mountain area; a precise list of distributions of the Chiroptera; status of a number of "pest" (hamster) and introduced species (raccoon, raccoon dog, nutria).* Projects underway: *Atlas of the distribution of mammals in France (by the Société Française pour l'Etude et la Protection des Mammiféres, S.F.E.P.M.).* Comments: WTC.

FRENCH GUIANA: *No response received*; but see 99, 113, 114, 115, 273, 668.

GERMAN DEMOCRATIC REPUBLIC: Staatliches Museum für Tierkunde Dresden; Zoologie der Sektion Biowissenschaften der Martin-Luther-Universitat. Guides: *30*, 75*, 194, 195, 707.* Surveys: *92, 664, 665*; see also 432. Keys: *30*, 75*, 92, 194, 195, 707.* Technical manuals: *471 (and later editions).* Museum science literature: *None.* Children's literature: *Many.* Research needed: *Operation of natural history museums.* Projects underway: *None.*

GHANA: University of Ghana. Guides: *77, 155, 247.* Surveys: *Numerous publications but no single one*; see also 401. Keys: *401.* Technical manuals: *Not generally available.* Museum science literature: *None.* Children's literature: *Few.* Research needed: *Guide to Ghanaian mammals; books on ecology and scientific method.* Projects underway: *None.* Comments: *There is no lingua franca in Ghana except perhaps English which is the language of literate people; few books are published in Ghanaian languages. Books are not generally available in Ghana anyway, especially under the present foreign exchange crisis.* The respondent noted further that *some books that could be used as children's books become available periodically. However, the supply of these materials is extremely erratic.* The respondent noted that *there is only a single copy of Meester and Setzer (1971–1977) available in the entire country and this new copy is incomplete.* WTC.

GREECE: *No response received*; but see 431, 449, 450, 706.

GUATEMALA: *No response received*; but see 210, 231, 233, 273, 309, 317, 585.

GUYANA: *No response received*; but see 113, 114, 115, 243, 273.

HONDURAS: *No response received*; but see 68, 197, 273.

HONG KONG: *No response received*; but see 509.

ICELAND: Náttẃrufraedistofun Íslands. Guides: *None.* Surveys: *162*, 223*, 517, 518, 612, 627*.* Keys: *None.* Technical manuals: *None.* Museum science literature: *None.* Children's literature: *Rare.* Research needed: *Natural history of whales and seals; natural history museum publications.* Projects underway: *None.*

INDIA: Central Arid Zone Research Institute; National Zoological Collection of India. Guides: *None.* Surveys: *60, 72, 167, 187, 381, 478, 479*; see also 96, 97, 98, 169, 328, 351, 482, 573, 574. Keys: *72, 166, 168, 478, 479, 681, 682, 683, 684, 685, 686, 687*; see also 163. Technical manuals: *71, 187.* Museum science literature: *None.* Children's literature: *None to rare.* Research needed: *A checklist of mammals; a field guide to the mammals of India; faunal works.* Projects underway: *Faunal work on the groups not covered by Pocock and Ellerman; an up-to-date checklist of Indian mammals is being prepared by the Zoological Survey of India.* Comments: 128 gives a review of research literature. First International Workshop on Management of Zoological Collections: Recent mammal collections in tropical environments sponsored by the Zoologcal Survey of India, Calcutta, and the Carnegie Museum of Natural History, Pittsburgh, USA, was held in Calcutta from 19–25 January 1984. The results of this workshop, which dealt almost entirely with museum topics, will be published in the near future. Two recent publications (423, 613) are available, which concern endangered and threatened animals of India. WTC.

INDONESIA: Museum Zoologicum Bogoriense. Guides: *399 (for Borneo)*. Surveys: *131, 357*. Keys: *399*. Technical manuals: *Use primarily publications of the British Museum (Natural History), American Museum of Natural History, and the Museum of Berlin*. Museum science literature: *None*. Children's literature: *Few*. Research needed: *Taxonomy and other information on the biology of mammals; research on methods of small pest control; research on zoonosis*. Projects underway: *Inventory studies of mammals in Indonesia; studies on the biology of murid rodents as pests on agricultural crops*. Comments: The respondent noted that there is no formal publication on mammal surveys for the Indonesian Archipelago other than for the island of Borneo. A bibliography of the mammals of Southeast Asia is given in 315. WTC.

IRAN: *No response received*; but see 100, 147, 360, 414.

IRAQ: Natural History Research Centre and Museum. Field guides: *None*. Surveys: *139, 169, 253, 254, 255, 262*; see also 19, 140, 251, 426, 522. Keys: *253, 254, 255*. Technical manuals: *255*. Museum science literature: *None*. Children's literature: *Few*. Research needed: *Field guide to Iraq's mammals; wildlife of Iraq including modern techniques*. Projects underway: *None*.

IRELAND: National Museum of Ireland, Dublin; Trinity College, Dublin. Guides: *88, 136, 435**. Surveys: *175, 176, 418*; see also 139, 140. Keys: *136, 422, 568*. Technical manuals: *31, 618*, 652*. Museum science literature: *None, but a publication by the Irish Museums Trust was due to be released in 1982*. Children's literature: *Few to many*. Research needed: *Museum maintenance; special techniques manuals; design and presentation of museum material; simple illustrated literature dealing with the common mammals; guides to specific areas of interest in the Natural History Museum*. Projects underway: *A book on extant Irish animals has recently been published by the Natural History Museum; a book on the history of the Natural History Museum is expected in the near future*. Comments: A book on Irish wild mammals was published as part of the Folens Irish Environmental Library Series. WTC.

ISRAEL: *No response received*; but see 10, 11, 43, 44, 74.

ITALY: Collezione Microteriologica di Longino Cantoli; Museo Civico di Storia Naturale; Museo Zoologico de "La Specola." Guides: *90, 699*. Surveys: *619, 620*; see also 117, 120. Keys: *619, 620, 699*. Technical manuals: *619, 620, 698**. Museum science literature: *None; al-*

though some visitors guides are available for a number of museums; see also 118, 119. Children's literature: *None to many.* Research needed: *Literature dealing with training people for collecting, preparing, and maintenance of natural history collections; publications concerned with the importance of natural history museums.* Projects underway: *Soricidae dell' ambiente bioclimatico mediterraneo (in press, Contoli); Gliridae, Arvicolidae, Muridae dell' ambiente bioclimatico mediterraneo (in press, Amori, Contoli, and Cristaldi).* Comments: One respondent noted that some Italian specialists have field guides currently in press to Italy's most important mammals. Comments from another respondent indicated that survey books having beautiful illustrations that can be used to explain mammalogy to local and national authorities as well as to common people are vitally needed in Italy, as are books that relate nature to the cultural and moral formation of children and to the general public. Moreover, the respondent felt that books dealing with collecting and preparation techniques are especially vital, as are materials that deal with the exhibition of mammalogical material.

JAMAICA: Institute of Jamaica. Guides: *None.* Surveys: *None*; see also 231, 233, 271. Keys: *473*; see also 231, 233. Technical manuals: *None.* Children's literature: *Few.* Research needed: *Study on the Jamaican cony,* Geocapromys brownii; *study of the manatee; natural history study of the mongoose.* Projects underway: *Studies on the manatee and cony (Natural Resources and Conservation Division, Dr. Patrick Fairbairn).*

JAPAN: Department of Oral Anatomy; Laboratory of Wildlife Resource Ecology; Natural History Museum; National Science Museum. Guides: *303, 304.* Surveys: *1, 303, 304, 349, 616**; see also 2, 448, 656, 696. Keys: *1, 303, 350*, 616*.* Technical manuals: *4*, 303.* Museum science literature: *None.* Children's literature: *Few to many.* Research needed: *Complete collections of representative animal faunas; zoogeographic studies; field guides and taxonomic keys to the mammal fauna of the Japanese islands.* Projects underway: *None.* Comments: WTC.

KENYA: National Museum of Kenya. Guides: *151, 155*; see also 135. Surveys: *17, 329, 330, 331, 332, 333*; see also 8, 252, 334, 335. Keys: *148, 401.* Technical manuals: *Field manual for museums (UNESCO).* Museum science literature: *None.* Children's literature: *Few.* Research needed: *Conservation of flora and fauna; ecology and population dynamics studies of mammals; general natural history studies of native species.* Projects underway: *None.* Comments: WTC.

KOREA: Natural History Museum. Guides: *680.* Surveys: *679**; see also 318, 319, 425. Keys: *679*.* Technical manuals; *None.* Museum science literature: *None.* Children's literature: *Rare.* Research needed: *Field guide geared toward the general public and for education*; *a* *monograph on the mammals of Korea; guide books in English.* Projects underway: *None.*

LEBANON: *No response received*; but see 43, 44, 366, 367.

LIBERIA: *No response received*; but see 346, 401.

LIBYA: *No response received*; but see 240, 293*, 401, 415, 486, 494, 535.

MADAGASCAR: *No response received*; but see 236, 469, 570*, 607.

MALAYSIA: Sarawak Museum. Guides: *54, 397*; see also 399. Surveys: *54, 397*; see also 55, 56, 146, 260, 396*, 398, 399, 400, 521, 624. Keys: *396**. Technical manuals: *None.* Museum science literature: *None.* Children's literature: *Few.* Research needed: *Field guide to the mammals of Malaysia; collection/preparation technique manuals; museum science literature.* Projects underway: *None.* Comments: An annotated bibliography of the mammals of Malaysia (116) and a bibliography of the land mammals of Southeast Asia (315) are available. WTC.

MEXICO: Escuela Nacional de Ciencias Biológicas; Universidad Nacional Autónoma de México. Guides: *365, 645, 647.* Surveys: *21, 26, 145, 212, 231, 232, 233, 292, 644*; see also 22, 23, 49, 52, 105, 125, 127, 201, 203, 273, 320, 321, 322, 323, 326, 364, 438, 491, 492, 529, 625, 661, 678. Keys: *231, 233, 648.* Technical manuals: *202*, 646,* Folleto de Divulgación, Instituto de Biología, varias ediciones en Español. Museum science literature; *None*; but see 50, 493. Children's literature: *Few to many.* Research needed: *Publications explaining the importance of scientific systematic collections; a brief history of the "Colección de mastozoología del Instituto de Biología, U.N.A.M."; locations of natural history specimens from Mexico that are housed outside of the country.* Projects underway: *Mamíferos de México, in preparation by Villa-R.* Comments: WTC.

MOÇAMBIQUE: *No response received*; but see 191, 563.

MOROCCO: Museum de l'Institut Scientifique. Guides: *456, 457, 520.* Surveys: *None*; but see 95, 401. Keys: *None.* Technical manuals: *None.* Museum science literature: *None.* Children's literature: *Rare.* Projects underway: *None.*

NAMIBIA: State Museum. Guides: *None.* Surveys: *401, 544*; see also 133, 286, 324, 507, 581. Keys: *170, 401, 503*; see also 134. Technical manuals: *None.* Museum science literature: *None.* Children's literature: *None to few.* Research needed: *Semi-popular literature on natural history and conservation of mammals; comprehensive study on the mammals of Namibia; field guides to small mammals in national parks; semi-popular literature in non-English languages.* Projects underway: *The mammals of Namibia (by C. G. Coetzee); check-list of mammals of Etosha National Park (by J. E. W. Dixon); taxonomic study of small mammals of southwest Africa/Namibia (by the State Museum).* Comments: One respondent pointed out the need for children's books and other popular material in the Ovambo language and other Bantu languages that are commonly used in Namibia. WTC.

NEPAL: *No response received*; but see 3, 217, 311, 401, 416, 417, 545, 577, 669.

NEW ZEALAND: Auckland Institute and Museum; Canterbury Museum; National Museum of New Zealand. Guides: *48, 199, 200, 480, 504*, 677*. Surveys: *48, 199, 200, 208, 677*. Keys: *200 (key to marine mammals)*. Technical manuals: *None; only general works on taxidermy; nothing specializing in mammals.* Museum science literature: *610*; we subscribe to English and American museum journals such as* Curator *and* Natural History. Children's literature: *Many.* Research needed: *Cetaceans; a guide to the fauna and flora of marine reserves.*

NICARAGUA: *No response received*; but see 53, 231, 233, 273, 309.

NIGER: *No response received*; but see 340, 401.

NIGERIA: D.C.D. Happold Collection of Mammals. Guides: *None.* Surveys: *510, 511, 512, 513*; see also 69, 246, 248, 249, 250, 299, 401. Keys: *511, 512, 513 (for selected species).* Technical manuals: *None.* Museum science literature: *None.* Children's literature: *None to rare.* Research needed: *Field guides at all levels for the vertebrates of Nigeria; conservation literature; general ecological principles in the tropics.* Projects underway: *Mammals of Nigeria by D.C.D. Happold (in preparation, about 400 pp., Oxford University Press).*

NORTHERN IRELAND: Ulster Museum and Botanic Gardens. Guides: *88, 142.* Surveys: *139*; see also 140. Keys: *136, 137.* Technical manuals: *379, 480*, 652.* Museum science literature: *None specifically for Northern Ireland, although three were listed for England.* Children's literature: *Many.* Research needed: *Archaeozoology and the history of the Irish fauna; osteology in natural history museums; a catalogue of the mammal collections in Britain and Ireland.* Projects underway: *None.* Comments: WTC.

NORWAY: *No response received*; but see 283, 284.

OMAN: *No response received*; but see 257.

PAKISTAN: *No response received*; but see 505, 546.

PANAMA: Museo de Ciencias Naturales. Guides: *171, 209, 233, 402.* Surveys: *None*; but see 231, 233, 241, 273, 309. Keys: *402*; see also 231, 233. Technical manuals: *None.* Museum science literature: *None.* Children's literature: *None.* Research needed: *Guides to preparation techniques; children's natural history books; keys to the mammals of Panama.* Projects underway: *None.* Comments: WTC.

PAPUA NEW GUINEA: Papua New Guinea National Museum and Art Gallery; University of Papua New Guinea. Guides: *103, 104, 275, 357, 406, 500, 590, 598, 601, 634, 655, 701, 703*; see also 702. Surveys: *121, 275, 276, 277, 294, 357, 368, 369, 378, 393, 394, 395, 403, 404*, 405, 407, 499, 521, 590, 591, 592, 593, 594, 595, 596, 597, 598, 599,* *600, 601, 602, 603, 604, 605, 606, 628, 629, 630, 632, 633, 634, 703, 704*; see also 160, 207, 631, 653. Keys: *295, 370, 404**, *702, 705.* Technical manuals: *652.* Museum science literature: *None.* Children's literature: *Few to none.* Research needed: *Handbook to New Guinea marsupials and monotremes; a guide to the collection and preservation of vertebrates; conservation of natural history specimens in the tropics; the role of museums in community education; the role of museum collections in scientific research.* Projects underway: *None.* Comments: WTC.

PARAGUAY: *No response received*; but see 70, 113, 114, 115, 273, 424, 671.

PEOPLE'S REPUBLIC OF CHINA: Department of Vertebrate Taxonomy and Faunology. Field guides: Surveys: *132*; see also 16, 18, 183, 498, 689, 700, 708. Keys: *None.* Technical manuals: *None.* Museum science literature: *None.* Children's literature: *Few.* Research needed: *An updated survey of the fauna of China.* Projects underway: *A synopsis of Chinese mammals with distributional maps.* Comments: WTC.

PERU: *No response received*; but see 113, 114, 115, 273, 343, 460, 461, 462, 463, 565, 566, 567, 609, 621, 623.

PHILIPPINES: *No response received*; but see 15, 59, 263, 315, 358, 487, 488, 523, 530, 608, 614.

POLAND: Mammals Research Institute. Guides: *484.* Surveys: *348*, 434*, 553**. Keys: *348*, 434*, 553**. Technical manuals: *433.* Museum science literature: *Przeglad Zoologiczny, the journal of the Polish Zoological Society contains articles on this subject.* Children's literature: *Many.* Research needed: *None.* Projects underway: *None.* Comments: WTC.

PORTUGAL: Museu Bocage; Museu e Laboratório Zoológico. Guides: *20, 150, 455.* Surveys: *139*; see also 140, 172, 377. Keys: *112, 150.* Technical manuals: *652.* Museum science literature: *Two publications by Almaça and one by Sacarrão are available; the journal* Museum *published by UNESCO is available.* Children's literature: *Rare to few.* Research needed: *Evolution; mammalogy; zoogeography.* Projects underway: *None.* Comments: One respondent noted that the Museum of Natural History was completely destroyed by fire in March 1978 with no specimens surviving the conflagration. WTC.

REPUBLICA DOMINICANA: Museo Nacional de Historia Natural. Guides: *None.* Surveys: *233, 636*; see also 231. Keys: *231, 473, 551, 571*; see also 233. Technical manuals: *None.* Museum science literature: *None.* Children's literature: *Few.* Research needed: *Ecology of the vertebrate fauna of the West Indies and the Caribbean; natural history, status and evolution of West Indian mammals.* Projects underway: *Murciélagos de la Repûblica Dominicana (J. A. Ottenwalder); status y explotación del manatí en la Republica Dominicana; habitat preference* *of the hutia* (Plagiodontia aedium); *natural history and systematics of* Solenodon; *marine mammals of the coast of the Dominican Republic; evolution and natural history of Capromyidae and fossil mammals (by C. A. Woods).*

REPUBLIC OF SOUTH AFRICA: Albany Museum; Department of Zoology, University of Cape Town; Jonkershoek Nature Conservation Station; Kaffrarian Museum; Transvaal Museum. Guides: *35, 155, 216, 503, 558.* Surveys: *170, 401, 503, 544, 562*; see also 307, 514, 515. Keys: *170, 401, 503, 562.* Technical manuals: *Minor publications are available.* Museum science literature: *Publications available, especially those published in SAMAB*; see also 675. Children's literature: *Rare to many.* Research needed: *Systematic and zoogeographic studies; multi-lingual children's literature on conservation and general natural history; techniques books on collection and preservation; a field guide to mammals of South Africa; general natural history publications aimed at the general public.* Projects underway: *Mammals of the Cape Province by Swanepoel; Mammals of Transvaal by Rautenbach was published in 1982; The Wildlife Society of Southern Africa is preparing a field guide to the eastern Cape Coast; Mammals of the Orange Free State by Lynch was published in 1983; Mammals of Natal by Pringle.* Comments: WTC.

ROMANIA: "Grigore Antipa" Museum of Natural History. Guides: *88.* Surveys: *122, 481.* Keys: *237*, 305.* Technical manuals: *428*, 458*.* Museum science literature: *157, 467*; three pre-1935 publications were written by Antipa on the importance of museums.* Children's literature: *Few*; for a summary of available literature see 157. Research needed: *Guide to the small mammals of Europe; establishment of general regulations for organizing and maintaining collections of small mammals; a manual which centralizes many of the methods (morphological, cytogenetic, etc.) used in the systematics of small mammals.* Projects underway: *An illustrated guide to the fauna of Romania.* Comments: WTC.

SAUDI ARABIA: *No response received*; but see 111, 253, 254, 255, 256, 427.

SCOTLAND: Aberdeen University; The Royal Scottish Museum. Guides: *108, 138, 141, 142, 359.* Surveys: *142, 501.* Keys: *108, 138, 139, 141, 142, 359.* Technical manuals: *31, 64, 568, 652.* Children's literature: *Many.* Research needed: *A guide to the Wildlife Protection Act of 1981; guides to the vertebrates of the eastern Mediterranean region.* Projects underway: *Conference is being held to discuss the implications of the Act of Parliament; the lack of field guides is known.* Comments: WTC.

SENEGAL: *No response received*; but see 76, 158, 291, 401.

SINGAPORE: Zoological Reference Collection. Guides: *258, 400, 624.*

Surveys: *131*; see also 398. Keys: *258, 259*, 400.* Technical manuals: *None.* Museum science literature: *None.* Children's literature: *None.* Projects underway: *None.* Comments: WTC.

SOMALI REPUBLIC: *No response received*; but see 193, 401.

SPAIN: Museu de Zoologia de Barcelona. Guides: *91*, 109*, 519.* Surveys: *432*; see also 638. Keys: *129, 436*.* Technical manuals: *9.* Museum science literature: *None.* Children's literature. *Few.* Projects underway: *None.* Comments: WTC.

SRI LANKA: *No response received*; but see 163, 166, 167, 278, 470.

SUDAN: *No response received*; but see 339, 342, 376, 401, 534.

SURINAME: *No response received*; but see 113, 114, 115, 205, 206, 273, 296, 297, 298, 672, 673.

SWITZERLAND: Naturhistorisches Museum Basel; Zoologisches Museum des Universität Zürich. Guides: *66, 92.* Surveys: *66, 432, 490.* Keys: *30*, 66, 75*, 92.* Technical manuals: *None printed in Switzerland, but several are available from Germany.* Museum science literature: *Birkhäusar-Verlag published the "Raritäten and curiositäten der natur, sammlungen der naturhistorischen museum Basel" in 1980.* Children's literature: *Few to many.* Research needed: *Natural history of Swiss mammals; importance of natural history museums; survey on distribution of mammals in Switzerland; a museum guide for children.* Projects underway: *A children's guide is in preparation by the Naturhistorisches Museum.* Comments: WTC.

TAIWAN: *No response received*; but see 308*, 316.

TANZANIA: College of African Wildlife Management; The Serengeti Research Institute. Guides: *155, 401.* Surveys: *None*; but see 235, 582. Keys: *None; keys are available to skulls of some selected mammal groups; some materials available on identification on mammalian teeth.* Technical manuals: *None.* Museum science literature: *None.* Children's literature: *None to few.* Research needed: *Keys to the mammals of the region; preparation manuals; guides to the importance of natural history museum.* Projects underway: *Studies on the ecology and behavior of the lion, cheetah, elephant, and mongoose.* Comments: WTC.

THAILAND: Division of Environmental Biology. Guides: *361.* Surveys: *None*; but see 101, 281. Keys: *361.* Technical manuals: *A preparation manual in Thai was published by the TISTR.* Museum science literature: *None*; see also 611. Children's literature: *Rare.* Research needed: *Mammals of southeast Asia; revisions of many southeast Asian bats and rodents.* Projects underway: *None.* Comments: A bibliography of the land mammals of Southeast Asia (315) is available. WTC.

THE NETHERLANDS: Rijkamuseum van Natuurlijke Histoire; Zoological Museum. Guides: *87, 107*, 302*, 374*.* Surveys: *301, 432, 519*; see also 86, 285, 485. Keys: *137, 139, 301, 432, 519.* Technical manuals: *285.* Museum science literature: *None.* Children's literature:

Many. Research needed: *Key to the identification of mammals in owl pellets; a distribution atlas of mammals; a modern and popular handbook on mammals.* Projects underway: *An owl pellet key is in preparation at the Rijksmuseum van Natuurlijke Historie, Leiden; an atlas project has just begun and will result from the collaboration of a large number of institutes, scientists, and amateurs.* Comments: WTC.

TRINIDAD AND TOBAGO: *No response received*; but see 124, 213, 231, 233, 502.

TURKEY: *No response received*; but see 173*, 174*, 421, 451, 452.

URUGUAY: Museo Nacional de Historia Natural de Montevideo. Guides: *None*; see also 186, 586. Surveys: *353, 688*; see also 113, 114, 115, 273. Keys: *None*; but see 354. Technical manuals: *None.* Museum science literature: *A few articles have been published in the Boletín del Museo Nacional de Historia Natural since 1973.* Children's literature: *None.* Research needed: *Ecology; ethology; biogeography.* Projects underway: *Catálogo sistemático de los vertebrados fósiles sudamericanos by A. Mones.* Comments: WTC.

USSR: Zoologica Museum of Moscow University. Guides: Publications available, but none listed. Surveys: Publications available, but none listed; see 5, 6, 7, 58, 190, 221, 222, 224, 225, 226, 227, 228, 264, 265, 266, 338, 410, 437, 440, 441, 442, 443, 444, 445, 446, 554, 555, 579, 580, 589, 615, 617, 637, 650. Keys: Publications available, but none listed; see 57, 73, 543, 578, 649, 697. Technical manuals: *None.* Museum science literature: *None.* Children's literature: *Many.*

VENEZUELA: *No response received*; but see 110, 113, 114, 115, 242, 273, 371, 439, 508, 526, 587. Comments: Although we received no response to the questionnaire, there are several types of ecological and systematic projects in mammalogy that are currently underway in the country. A key to the mammals of Venezuela was written by Handley but is generally unavailable.

VIETNAM: Laboratory of Zoology. Guides: *635.* Surveys: *81, 82*; see also 123, 516. Keys: *635.* Technical manuals: *153.* Museum science literature: *None.* Children's literature: *Few.* Projects underway: *The rodents of North Vietnam (in French) is in preparation; Key to the mammals of Vietnam by Tiên is in preparation and will be published in Vietnamese.* Comments: A bibliography of the land mammals of Southeast Asia (315) is available. WTC.

YEMEN: *No response given*; but see 524.

YUGOSLAVIA: Zoology Department Collection and Dr. Dulić's Collection. Guides: *198*.* Surveys: *156, 413**; see also 345, 468. Keys: *390, 413*.* Technical manuals: *Only booklets and papers dealing with preparation of animals in general including also the mammals. One very old one published in 1948 is a small introduction in preparation techniques in general. Author of this booklet is P. Alinger.* Museum

Table 1.—*The availability of field guides (fg), surveys (s), keys (k), and museum science literature (msl) within each geographic region. Percentages are given for each geographic region and are based on the total number of responses received from each region.*

Response		Latin American	European	African	Middle East	Asian	Australian
Available in the common language	fg	17%	90%	50%		62%	87%
	s	50%	86%	78%		62%	69%
	k	39%	83%	64%		69%	81%
	msl	17%	31%	7%		8%	25%
Available, but not in the common language	fg	11%	5%	21%	50%	8%	
	s	28%	7%	15%	50%	23%	
	k	11%	2%	7%	100%	23%	
	msl	5%	3%	7%		8%	
Unavailable	fg	72%	5%	29%	50%	30%	13%
	s	22%	7%	7%	50%	15%	25%
	k	59%	14%	29%		8%	19%
	msl	78%	64%	86%	100%	84%	75%
No response	fg						
	s						6%
	k						
	msl		2%				

science literature: *None.* Children's literature: *Few.* Research needed: *A good and comprehensive book on the mammalian fauna; compiled lists with distributional data; small monographs for different species or groups of species.* Projects underway: *Investigation of specific Yugoslavian mammal species.* Comments: The need for a manual on mammal preparation techniques was emphasized. WTC.

ZAIRE: Koninklijk Museum voor Midden-Afrika, Musée Royal de l'Afrique Centrale, Belgium. Guides: *155, 236.* Surveys: *531, 532*; see also 67, 79*. Keys: *401.* Technical manuals: *None.* Museum science literature: *204*; a list of West European museums with important collections of African small mammals was given in the supplement to the African Small Mammal Newsletter in July 1981. Children's literature: *Rare.* Research needed: *Importance of conservation of tropical forests; field guides and general natural history information of small mammals; conservation of mammals.* Projects underway: *None.*

ZAMBIA: *No response received*; but see 37, 38, 401.

ZIMBABWE: Museum of Zoology. Guides: *327, 556, 559, 674.* Surveys: *None*; but see 35, 36, 401, 561*, 563, 564, 674. Keys: *556, 559*; see also 184. Technical manuals: *None*; but see 33, 34, 560. Museum science literature: *None*; but see 32. Children's literature: *Few.* Research needed: *Translation of available literature into non-English languages; educational materials.* Projects underway: *None.*

Table 2.—*The availability of mammal collecting and preparation techniques manuals within each major geographic region. Percentages are given for each geographic region and are based on the total number of responses received from each region.*

Response	Latin American	European	African	Middle East	Asian	Australian
Available to the specialist in the common language	25%	50%	27%		29%	40%
Available to the general public in the common language	25%	37%	13%		14%	20%
Available to the specialist, but not in the common language	12%	4%	13%	50%	21%	
Available to the general public, but not in the common language		1%				
Generally unavailable	38%	8%	47%	50%	36%	40%

Literature Availability by Topic

An overview of the responses to each of the questions asked is given in Tables 1–3 for each geographic region. It must be kept in mind that there was often only a small number of responses for any particular country and these may not have been filled out with as much care as might have been desired. Nevertheless, additional library research on the availability of the literature of mammalogy for a country frequently was in accord with the impressions of the in-country specialists as indicated on the returned questionnaires.

The availability of field guides is shown to be quite spotty (Table 1), with Europe and the Australian region having such publications readi-

Table 3.—*The availability of natural history literature for children within each of the major geographic regions. Percentages are given for each geographic region and are based on the total number of responses received from each region.*

Response	Latin American	European	African	Middle East	Asian	Australian
Many in the common language	6%	62%	7%		8%	38%
Few in the common language	22%	24%	36%	100%	46%	56%
Rare in the common language	11%	2%	29%		15%	
Many, but not in the common language						
Few, but not in the common language			7%		8%	
Rare, but not in the common language			7%		8%	
None	61%	7%	14%		15%	6%
No response		5%				

ly available in the common language of the countries queried. In the Australian area, of course, this is English, but in Europe we found that most countries responding had access to field guides that were published in the common language of the country in question. Asia and Africa had a moderate rate of field guide availability and such books were primarily available in the common language of the country. Because of the frequency of having an official language (such as English, for example) listed for a country, however, there arises the problem of availability of such guides to the majority of people who may neither read nor speak the official language. More will be said about this problem when geographic regions are reviewed individually (below). The Middle East and especially Latin America are geographic regions that show a decided scarcity of field guides. Those few that are available are usually not published in the common language. Fully 72% of the respondents in Latin America reported that field guides to mammals are unavailable.

Mares (1982, 1985, in press) has discussed the importance of the technical literature of mammalogy as a basis for the popular literature. A review of the responses concerning the availability of technical literature (Table 1) indicates that such literature is generally more widely available (to the specialist) than is semi-technical literature on mammals. All geographic regions reported a fairly broad availability of technical literature on mammals, with Latin American responses reporting the lowest values. Generally, such literature is available in the common language of the country (except in the Middle East, where our sample size was quite small).

Taxonomic keys are vitally important to the diffusion of mammalogical information beyond a small coterie of specialists. It is keys that allow other biologists to identify their research materials with minimal effort. Such keys are also useful in instructional purposes and to people in government or other fields that need to have a correct determination made for a particular specimen. Most respondents (except for Latin Americans) indicated a fairly good availability of taxonomic keys for use by specialists and generally these were available in the common language of the country (Table 1).

One group of publications that proved to be quite scarce in all geographic regions is collecting and preparation manuals (Table 2). Even in such well-studied areas as Europe and Australia, only 50% or fewer of the respondents indicated the availabilty of such works to the specialist. These types of publications were even less readily available to the general public.

The types of mammalogical publications that turned out to be the least available on a worldwide scale were those that are concerned with the operation and importance of natural history museums (Table 1). The very low values for availability in any language indicate the general lack of literature in this area.

Children's literature on natural history was shown to be readily available only in Europe (Table 3). In most regions, fewer than 10% of the respondents reported that children's literature was readily available, while from 20–50% of them said such books were few.

Literature Availability by Region

Middle East.—Only two of five questionnaires sent to countries of the Middle East were returned, so it is not possible to speak in any detail about the status of the literature of this region. Each of the four countries surveyed has had foundational literature published on mammals, although most of this literature is available only in European languages. Nevertheless, although there are few guides to the mammals of these countries and apparently almost no museum literature or popular literature published in the native languages, a rather firm foundation for future workers has been established.

Latin America.—Eighteen of 32 questionnaires were returned from 10 countries. Unfortunately, this is not a large sample for such a vast region, but responses were received from Mexico, Central America, the Caribbean, and South America, giving a good geographical representation. In almost all literature areas surveyed, Latin America was ranked at the lowest levels. Most countries lack even the foundational literature, regardless of its language of publication. Few faunal surveys have been published for most countries, taxonomic keys and field guides are generally unavailable, museum literature is practically nonexistent, and children's literature is rare to unavailable. These trends are particularly pronounced for South America, as opposed to Central America, the Caribbean, and Mexico. Because of their proximity to North America, these regions have been fairly well-studied, especially Mexico, the Caribbean, Panama, and Costa Rica. Unfortunately, despite the availability of foundational literature (largely published in English), there are as yet relatively few publications available of the nature of field guides, children's books, and general museum publications. Indeed, even in Mexico, perhaps the best-studied of the Latin nations, semitechnical and popular publications are either uncommon or hard to obtain. For South America, the panorama is much less positive. There, even the foundational literature is lacking and, as has been argued by Mares (in press), without this most basic literature of mammalogy, the preparation of the literature needed to educate the general population is impossible. Among the South American countries, only Suriname, Venezuela, Uruguay, Chile, and Argentina have had an important portion of their foundational literature completed. Even in these few countries, however, the semitechnical and popular literature on mammals is largely unavailable.

Europe.—Forty-two of 66 questionnaires were returned from European collections, for a 64% response rate. Of the regions surveyed, Europe led in all categories of literature availability, reflecting a long history of nature study, museum collection formation, resident specialists on mammals, and so on. Generally, basic literature as well as the semitechnical and popular literature were available in the common language of each country.

Africa.—Fourteen of 23 (61%) African collections queried returned the questionnaires, with six responses coming from two countries, Namibia and the Republic of South Africa. Many African countries were thus not sampled due either to the fact that questionnaires were not returned or that a particular country had no collection-oriented mammalogist to be queried. There is little doubt that the inclusion of four responses from the Republic of South Africa skews the African data. Still, it is evident that the African area (excluding the Middle East) has a very poor literature base, particularly for works published in non-European languages. Although 50% of the respondents indicated the availability of field guides to the mammals of their particular country, published in the common language, this number is inflated. Many cited Dorst and Dandelot (1970), for example, which is limited to the larger mammals of Africa. Fully 86% of the respondents reported that technical publications were available in the common language of the country, and 83% said that taxonomic keys were readily available (Table 1), but again these are probably overestimations due to the fact that some well-surveyed countries responded (for example, Kenya, Republic of South Africa).

Australian region.—By and large, the Australian area supports a rich and varied literature at the technical, semitechnical, and popular levels. Field guides, technical publications, taxonomic keys, and collecting and preparation manuals were listed as readily available, as was children's literature.

In answer to the question requesting a listing of subject areas needing research, responses were understandably mixed. Topics suggested with regularity were surveys and technical publications on a country's fauna; taxonomic revisions; the production of both field guides and taxonomic keys; educational materials aimed at the general public and children that deal with museum/collection-related topics and natural history; theoretical and applied ecological research (including conservation); collecting and preparation technique manuals; and behavioral research.

Socioeconomic Factors

In any broad examination dealing with some facet of life in the diverse nations of the world, it is instructive to examine what country-wide phenomena might be related to the patterns that have been identified. We have shown that the world's literature on mammalogical subjects has an extremely spotty distribution. We might ask if there are any obvious measures of a country's socioeconomic profile that might be related to the availability of this type of literature. It takes no special understanding of economics or politics, for example, to see that those countries generally classified among the economically developed nations of the world (DC's) have a higher rate of literature availability than do those nations generally considered as being underdeveloped (UDC's).

We have examined some basic socioeconomic factors of each nation that responded to our questionnaire (Table 4). These data include information on Gross National Product (GNP), per capita income (PCI), the natural rate of population increase (r), percent literacy, population density, and the percent of the population that is urban. Utilizing the SPSS statistical package (SPSS Inc., 1983), we compared these data to an index of literature availability via multiple regression analysis and stepwise multiple regression analysis. In order to do this, it was necessary to score the responses from each country to each of the first six questions on the questionnaire (mean values were used in the case of multiple responses). Scores on each question varied from zero for an unavailability of literature to five for an abundance of literature. Scores for each question were summed to obtain the country's total score (scores may thus vary from zero to 30). Literature availability scores for those nations that responded fully to a questionnaire are given in Table 4.

When multiple regression analysis was run so that all independent variables (the socioeconomic data of Table 4) were examined for their effect on explaining the variance in the dependent variable (the literature availability scores of Table 4), two factors were shown to have statistical importance in explaining variance in literature availability: the rate of population increase, r, with $P = 0.04$; and the per capita income, with $P = 0.05$. The sign of the beta value for r was negative, whereas it was positive for the beta values of PCI (Table 5). This means that the greater the value for r, the lower the availability of literature, and the greater the PCI, the more literature that is available in a country. In this analysis, each variable was examined for its effect on the dependent variable, while all other variables were held constant.

In a separate stepwise multiple regression analysis, the single most

Table 4.—*Gross national product (GNP), per capita income, natural increase in population, percent literacy, population density, percent urban population, and the literature availability score given for most countries that responded to questionnaires. Countries are listed alphabetically within each region. The year in which the data were obtained is given in parentheses. Unnumbered countries lack sufficient data for regression analysis.*

Country (by region)	GNP (in billions of U.S. dollars)	Per capita income (in U.S. dollars)	Natural increase in population %	% Literacy	Population density (per sq. mi.)	% Pop. urban	Literature availability score
		Latin American					
1. Argentina	61.5 (78)	2331 (78)	1.6 (79)	94 (78)	25 (80)	72 (77)	9
2. Brazil	273 (80)	1523 (78)	2.3 (78)	75 (78)	36 (81)	63 (79)	7
3. Chile	19.8 (79)	1950 (79)	1.5 (78)	90 (78)	39 (81)	80 (78)	9
4. Colombia	30.6 (80)	1112 (81)	2.1 (78)	82 (78)	60 (81)	60 (73)	6
5. El Salvador	3.8 (80)	639 (78)	3.4 (77)	63 (78)	570 (81)	40 (78)	10
6. Jamaica	3.0 (81)	1340 (81)	1.2 (78)	86 (78)	502 (81)	37 (70)	5
7. Mexico	128 (80)	1800 (80)	3.3 (75)	74 (81)	95 (81)	65 (78)	20
8. Panama	3.2 (80)	1116 (78)	2.8 (75)	82 (78)	66 (81)	51 (79)	—
9. Republic Dominicana	6.7 (80)	1221 (80)	2.5 (78)	62 (81)	274 (81)	50 (79)	7
10. Uruguay	1.7 (80)	1710 (78)	0.6 (78)	94 (78)	42 (81)	83 (75)	6
		European					
11. Austria	76.3 (80)	9114 (79)	−0.1 (78)	99 (78)	232 (81)	52 (71)	19
12. Belgium	110.9 (79)	10,800 (79)	0.07 (78)	99 (80)	842 (81)	95 (76)	17
13. Czechoslovakia	77 (79)	3985 (76)	0.7 (78)	99 (81)	310 (81)	67 (74)	22
14. Denmark	66.4 (80)	12,956 (80)	0.2 (78)	99 (81)	308 (81)	67 (70)	20
15. England	445.9 (80)	7216 (79)	0.01 (77)	99 (81)	592 (81)	78 (73)	28
16. Federal Republic of Germany	824.6 (80)	9278 (78)	−0.3 (78)	99 (78)	642 (81)		25
17. Finland	41.3 (79)	6090 (78)	0.4 (78)	99 (78)	37 (81)	60 (80)	17
18. France	585 (80)	8980 (80)	0.4 (77)	99 (78)	252 (81)	73 (75)	20

Table 4.—*Continued.*

Country (by region)	GNP (in billions of U.S. dollars)	Per capita income (in U.S. dollars)	Natural increase in population %	% Literacy	Population density (per sq. mi.)	% Pop. urban	Literature availability score
19. German Democratic Republic	89.1 (79)	5340 (79)	0.0 (78)	99 (81)	413 (81)	75 (76)	23
20. Iceland	1.7 (80)	9000 (79)	1.2 (78)	100 (81)	6 (81)	87 (77)	5
21. Ireland	17.2 (80)	5000 (80)	1.1 (77)	98 (78)	122 (81)	52 (71)	19
22. Italy	394 (80)	6914 (80)	0.4 (77)	95 (78)	490 (81)		16
Northern Ireland						55 (73)	19
23. Poland	55.2 (79)	2500 (76)	1.0 (78)	98 (78)	296 (81)	57 (77)	16
24. Portugal	20.1 (79)	2000 (79)	0.9 (77)	72 (78)	281 (81)		20
25. Romania	67.5 (78)	3100 (78)	8.7 (79)	98 (78)	243 (81)	49 (77)	15
Scotland						70 (74)	23
26. Spain	201 (79)	5500 (79)	1.0 (77)	98 (78)	192 (81)		13
27. Switzerland	97.4 (79)	15,455 (79)	0.2 (78)	99 (78)	398 (81)	55 (709)	18
28. The Netherlands	139 (81)	9749 (81)	0.4 (78)	99 (78)	1003 (81)	88 (76)	—
29. USSR	1.5trl (80)	2600 (76)	0.9 (76)	99 (81)	31 (81)	62 (79)	17
30. Yugoslavia	69 (79)	3109 (79)	0.9 (78)	85 (78)	226 (81)	39 (71)	15
		Asian					
31. India	106.6 (79)	150 (77)	1.9 (78)	36 (78)	519 (81)	22 (79)	12
32. Indonesia	66.8 (80)	415 (81)	2.1 (78)	64 (81)	207 (81)	18 (74)	10
33. Japan	990 (80)	8460 (80)	1.0 (77)	99 (78)	811 (81)	76 (75)	17
34. Korea, South	59.2 (80)	1187 (78)	1.6 (78)	92 (78)	973 (81)	48 (75)	8
35. Malaysia	21.3 (80)	714 (75)	2.5 (78)	60 (78)	101 (81)	21 (70)	9
People's Republic of China	540 (80)	566 (80)	1.6 (78)	70 (78)	278 (81)		—

Table 4.—*Continued.*

Country (by region)	GNP (in billions of U.S. dollars)	Per capita income (in U.S. dollars)	Natural increase in population %	% Literacy	Population density (per sq. mi.)	% Pop. urban	Literature availability score
36. Singapore	9 (80)	4100 (80)	1.2 (78)	76 (78)	10,575 (81)		9
37. Thailand	21.8 (80)	444 (78)	2.3 (78)	84 (78)	227 (81)	13 (70)	8
38. Vietnam	7.6 (78)	150 (78)	2.2 (78)	78 (78)	414 (81)		8
		African					
39. Ghana	10.1 (79)	380 (79)	3.3 (78)	30 (78)	123 (81)	31 (74)	12
40. Kenya	6.0 (79)	337 (78)	4 (78)	40 (78)	73 (81)	10 (69)	12
41. Morocco	16 (81)	800 (81)	2.9 (78)	24 (78)	110 (81)	41 (78)	6
Namibia							
42. Nigeria	43 (78)	523 (78)	3.2 (78)	25 (78)	216 (81)		6
43. Republic of S. Africa	80.2 (80)	1296 (78)	2.1 (78)	55 (78)	62 (81)	48 (72)	20
44. Tanzania	4.6 (79)	253 (78)	2.9 (78)	60 (78)	48 (81)	13 (78)	8
Zaire							
45. Zimbabwe	3.4 (79)	8000[1] (79) 370[2] (79)	2.2 (78)	30 (78)	49 (81)	20 (79)	12
		Australian					
46. Australia	121.2 (80)	7720 (78)	1.2 (79)	99 (78)	5 (81)	86 (76)	23
47. New Zealand	23.4 (81)	7363 (81)	0.9 (77)	99 (78)	31 (81)	83 (76)	20
48. Papua New Guinea	2.3 (79)	480 (78)	2.7 (78)	32 (78)	17 (81)	13 (79)	19
		Middle East					
49. Egypt	18.9 (78)	448 (77)	2.7 (78)	44 (78)	116 (81)	44 (77)	11
50. Iraq	19 (77)	1561 (78)	3.4 (78)	30 (78)	76 (81)	66 (77)	9

[1] White Zimbabweans.

[2] Black Zimbabweans.

Table 5.—*Multiple regression analysis of the socioeconomic data versus the index of literature availability from Table 4 for countries that responded fully to the questionnaire. B = slope; SE B = standard error of B;* P *= level of significance; Beta is a standardized B.*

Variable	B	SE B	Beta	T	*P*
Urban population	−0.014	0.031	−0.063	−0.446	0.66
GNP	−0.004	0.003	0.187	1.529	0.13
Population density	0.49 ×10	0.49 × 10	−0.121	−1.017	0.32
PCI	0.55 × 10	0.27 × 10	0.349	1.975	0.05
Literacy	−0.054	0.048	−0.223	−1.128	0.26
r	−2.560	1.233	−0.475	−2.077	0.04
(Constant)	20.421	5.497		3.715	

important independent variable in explaining variance in the dependent variable was per capita income ($P < 0.0001$): all other independent variables were non-significant. In this analysis, $R^2 = 0.33$ and the beta value was 0.91×10^{-3}. Since only one independent variable was used, beta values can be used to show the effect of PCI on literature availability. We can see that if per capita income in a country were increased by $100/year, the availability of mammal literature would increase by almost 10%. Increasing PCI by $1000/year would essentially double the availability of literature in a particular society.

DISCUSSION

Clearly, there is a great need to increase the availability of all types of mammalogical literature throughout the world. In many places (for example, Latin America), even the foundational literature is lacking, thus making the development of a more broad-based and diverse literature more difficult. Many countries lack active mammalogists and do not support a working collection of mammals. In other countries, such collections, if they exist at all, are very poorly supported, ill-housed, and understaffed. Research, such as coordinated faunal surveys and basic taxonomic studies, is not encouraged. Given these conditions, the general mammalogical panorama is bleak and the foundational literature of mammalogy, that most basic literature that is the basis for more advanced topics such as ecology, physiology, behavior, and conservation, is unavailable. The questions that we asked of each curator covered both the basic literature as well as the more advanced and popular literature. It is consistent with the views of Mares (1985, in press) and with the points made earlier in this paper, that every country that reported a rich popular literature also reported a very broad basic literature. No country having a weak foundational literature reported an abundance of field guides, children's books, or other semitechnical or popular works. Very few countries reporting a strong foundational literature had a weak popular literature (exceptions are Ghana, Papua New Guinea, Portugal, Republic of South Africa, and Singapore). The close relationship between the foundational literature and the extremely important literature of the general public appears inescapable. It seems unlikely that a country could begin to publish popular faunal works on a large scale without first developing the infrastructure of mammalogy—the collections, the faunal surveys, and the taxonomic research.

We have shown that there is a great disparity in the way in which the literature of mammalogy is dispersed throughout the world. Literature availability does not appear to follow political ideologies, although there is a strong geographic component to the data. Holarctic countries generally have a strong literature in mammalogy—this literature is widely available in the common language of the country and includes both technical and popular literature. If a country is located north of 35°N latitude, it shows a strong literature at almost all levels. Countries south of this line, with notable exceptions (for example, the Australian region and some few African, Asian, and Latin American countries), lack a strong literature.

The response to the question dealing with suggested research topics supports our analysis as to the importance of the foundational literature. In countries having a rich literature, suggested research topics were often well-formulated and specific. Often they involved fine tuning of ongoing research efforts, or studies of sweeping scope that were synthetic in outlook. In countries having a poor literature, suggested topics involved the most basic types of research, taxonomic surveys, the construction of taxonomic keys, and so forth.

The analysis of the socioeconomic factors that might affect literature availability points out some interesting patterns. First, although some of the data items utilized may be intercorrelated, and even though all of these factors are the result of complex sociopolitical components, there are only two items of statistical significance that seem to affect literature availability, and these two items are themselves related. Per capita income and the rate of population increase would seem to be, a priori, inversely related. The faster a population is growing, the lower the rate of income per person. It is this latter statistic, PCI, that has such an important effect on literature availability. As per capita income increases, so does the literature of mammalogy become more diverse. We suspect that although we limited our analysis to literature on mammals, the same trends will be shown for all natural history literature. The higher the PCI, the greater the availability of literature on nature.

It is instructive to plot literature availability (as shown by the index) and PCI of countries (Fig. 1). There is a cluster of countries that have

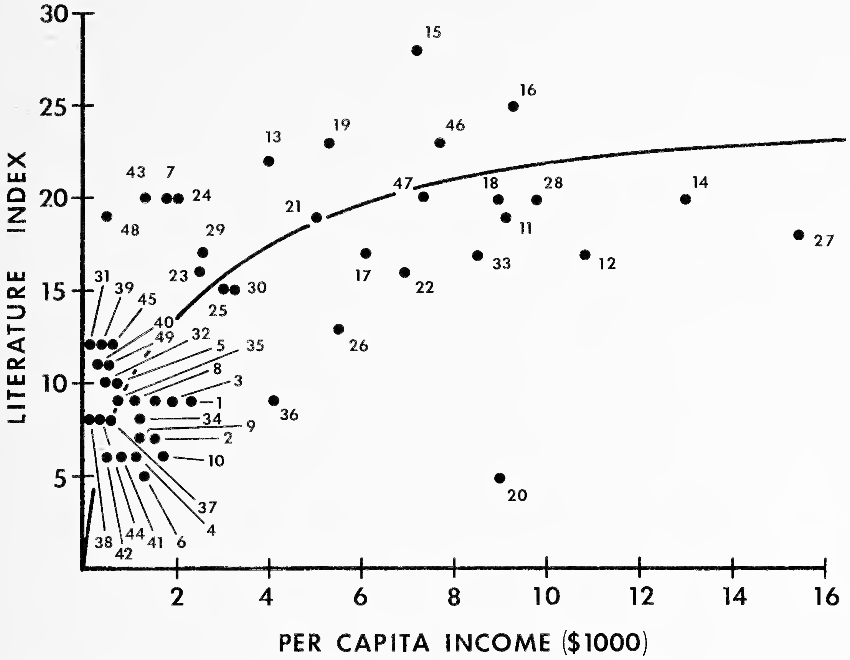

Fig. 1.—A plot of per capita income (PCI) versus an index of literature availability for the countries of the world that responded to the questionnaire. Numbers of countries refer to Table 4. The asymptotic curve (fitted by eye) shows that after a PCI of about $4000 per annum, literature availability reaches a relatively stable high level.

both a low per capita income and a low level of literature availability. With few exceptions, most countries that have a diverse literature on mammals have PCI's above $5000 US per year. Only about 11 countries show an anomalous relationship of PCI and literature availability. Several socialist nations (that is, Czechoslovakia, USSR, Poland, Romania, and Yugoslavia) show a rather abundant literature with relatively low PCI. Given the fact that PCI in a socialist nation is low due to the many social services that are covered through governmental programs, and because scientific education is strongly supported in these countries, it is not surprising that a higher level of literature availability is maintained with a lower PCI.

Singapore, a city/nation only since 1965, might be expected to support a poor literature, because few studies concern themselves with mammals of a densely populated urban area. Another country that deviates from the expected relationship, Iceland, is also easily explained. Although the country has a high PCI, it has a depauperate mammal fauna, thus detailed works on mammals are rare.

Several other nations that do not fit the observed pattern are the Republic of South Africa, where the PCI is quite low due to the inclusion of Black incomes in the overall PCI, while White incomes are quite high. The literature is primarily produced by and for Whites, thus the unusual location of the PCI versus literature value is easily explained.

Finally, Mexico, Portugal, and Papua New Guinea also seem to deviate from the general pattern. Mexico is well-studied due to its proximity to the United States, whose mammalogists have worked in Mexico for almost a century. Similarly, Papua New Guinea has had much of its fauna studied by colonial powers, such as England and Germany, as well as by Australians. Portugal, although having a low PCI at present (partially due to the fact that almost one-third of the labor force is composed of agricultural workers), has had a history of European research efforts on mammals in the recent past.

In general then, it appears that without a marked increase in per capita income, mammal literature will not increase. Obviously, this does not reflect a 1:1 relationship between PCI and literature availability. Apparently, scientific and educational resources in any country can only be allocated after basic societal needs are being met. PCI is a measure of how well such needs are being met, especially in a non-socialist society. If PCI is too low, few people are able to learn to read, to complete school, or to go into a complex field of study such as science. In countries with low PCI's, higher education will be a luxury, and research on mammals or other animal groups will be uncommon, because such studies are not usually viewed as being vital to the national interest. With few students, fewer professors, and a lack of support for natural history studies, literature availability will perforce be at minimal levels in these countries.

Can a country decide to reverse this pattern and produce the popular literature that is needed to educate the masses about the importance of their natural environment without increasing PCI? Our results suggest that this is not a simple task. The only exceptions to the perceived trend were in countries where PCI is a poor indicator of living standard (socialist countries) or where foundational research had been completed in the past due to historical accident (for example, Mexico). The PCI/literature relationship seems to be a strong one. Elevating the PCI clearly influences a multiplicity of societal factors in education, commerce, science, government, and so on. But there appears to be no ready mechanism whereby PCI can be bypassed with a resultant flowering of literature. The gradual elevation of the PCI (insofar as it reflects economic health) very likely leads to a society that has taken care of its basic economic needs and has developed the time and inclination to dedicate resources to what are, from the standpoint of the basic requirements of life, rather esoteric pursuits.

An important point in this analysis is that even though the best mechanism for increasing the availability of natural history literature is to raise the PCI, there is another way to elevate the overall level of literature in any country. Supporting basic research by scientists of any nation in a particular country will, ultimately, yield a significant amount of foundational literature. This literature will later be used by nationals of the country as building blocks for a more advanced and comprehensive national literature. Mexico is an excellent example of how a country with a long history of basic research by scientists from another nation, in this case the United States, is able to utilize the work of these foreign scientists to develop its own cadre of biologists and the diversity of its particular literature on nature, despite its low PCI. Papua New Guinea is another example of this same occurrence.

Our results lead us to be cautiously optimistic. If international cooperative research efforts on basic systematics, natural historical, and biogeographical research can be significantly increased, the foundational literature of each country can be established. The very positive response by almost all curators to the possibility of cooperative research/publication efforts indicates that the door to scientific interaction is open. Colleagues throughout the world are eager to participate with foreign scientists who might have expertise working with the fauna of a particular country. Together, these biologists can act to produce the keystone of the science of natural history, the foundational literature upon which all more advanced studies are based and upon which the popular literature of a country rests.

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CATALOG OF THE RECENT MARINE MAMMALS IN THE CARNEGIE MUSEUM OF NATURAL HISTORY

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Abstract

The Section of Mammals, Carnegie Museum of Museum of Natural History, houses 612 specimens of Recent marine mammals, including 34 cetaceans, 44 polar bears, six sea otters, 499 pinnipeds, and 29 manatees. Families represented in the Order Cetacea include Platanistidae, Physeteridae, Monodontidae, Delphinidae, Phocaenidae, and Balaenopteridae. Families represented in the Order Pinnipedia include Otariidae, Odobenidae, and Phocidae. The single family Trichechidae represents the Order Sirenia in the collection. For each specimen the following data are recorded: date collected, catalog number, sex, age or condylobasal length, nature of specimen, condition of specimen, and comments. The latter category gives information on the condition of the skin and skeletal material, and also explains the availability of the specimen.

Introduction

The Section of Mammals, Carnegie Museum of Natural History, currently holds 612 specimens of Recent marine mammals, including 34 cetaceans, 44 polar bears, six sea otters, 499 pinnipeds, and 29 manatees. The majority of the collection of marine mammals consists of specimens preserved as skulls or disarticulated skeletons. However,

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the collection also contains 151 skins and five fluid-preserved specimens as well as body mounts and articulated skeletons. The specimens are housed primarily in the fur vault and large osteological storage area of the Section of Mammals, but all mounted material is on display at this time in the public galleries of the Museum.

The primary purpose of this catalog is to make the availability of this material known to the scientific community. It is extremely difficult to obtain new specimens of any marine mammal because most species are considered to be threatened with extinction (Berger et al., 1979). All species are placed in at least Appendix II (Threatened) under the Convention on International Trade in Endangered Species and are protected under the various Marine Mammal Acts beginning as early as 1967. Therefore, it is necessary for researchers to make maximum use of the materials already stored in museum collections. Because specimens stored in this collection are essentially irreplaceable, none is available for study on loan. However, all qualified researchers are welcome to study any of the specimens at the collection facilities of the Section of Mammals.

All collection data files of the Section of Mammals have been computerized. This catalog presents selected data categories of which some are available on the computer file, but others have been specifically generated for this publication. Other categories of data are also available upon request in printout or machine-readable form. The format of this catalog is patterned after Napier's (1976, 1981, 1985) Catalogue of the Primates in the British Museum (Natural History) and the McLaren et al. (1984) Catalog of the Recent Scandentia and Primates in the Carnegie Museum of Natural History.

CLASSIFICATION

The collection of the Section of Mammals and this catalog follow G. G. Simpson's (1945) classification in the Principles of Classification and the Classification of Mammals through the level of subfamily. Below subfamily, specimens are arranged alphabetically by genus. Specimens stored in the osteological collection and the fur vault are then arranged numerically within the genus. This catalog is arranged alphabetically by genus, species, and in a few cases subspecies, so that researchers may easily see what is available for each taxon. Beyond this taxonomic arrangement all specimens are presented in numerical order. It is hoped that by arranging the catalog in this way that work by researchers in the collection will be facilitated.

Cetaceans in the collection have been examined and identified by C. W. Potter and G. S. Morgan. The *Odobenus* have been identified, and sexed in some cases, by Francis Fay. Hall (1980) has been used for identification of the Pinnipedia, but scientific names follow Honacki et al. (1982) except in the case of *Physeter catodon* (Schevill, 1986).

Explanation of Headings

Locality.—Collection localities appear as listed on the original skin and skull tags. Latitude and longitude were added to numerous localities as listed in the most recent edition of the Standard Names Gazetteer for localities outside of Canada (printed by the United States Board of Geographic Names). Gazetteer of Canada (printed by the Canadian Permanent Committee on Geographical Names) was used for referencing Canadian localities.

Of the 612 marine mammals, 31 were zoo specimens. In many cases, original localities are not known for these animals. To facilitate recognition of locality information pertaining to captive specimens, these data are followed by an asterisk.

Date of collection.—For wild taken specimens, this date refers to the day on which the animal was obtained. In nearly all cases for zoo specimens, the only date which is available is the day on which the animal died in captivity. In rare cases when more information is known about a particular captive specimen, those data will be shown under the "Comments" category.

Sex.—Three symbols are used for denoting sex: F, M, ? (undetermined by original collector). Where not denoted on the original tag, sex has sometimes been inferred based on the examination of adult skulls. This practice has not been used for the preparation of the current catalog, but in instances where such conclusions have been drawn previously, the appropriate symbol will be enclosed in brackets.

Age or condylobasal length.—During the preparation of this catalog, we were advised by R. L. Brownell to replace age with condylobasal length. Whenever possible this measurement was taken. If minor damage made precise measurement impossible, a rough measurement is shown in brackets. If skull damage was too severe to make this practical, or when only skins were available, a judgement based on tooth eruption, fusion of sutures, or pelage was sometimes possible. Additionally, original collectors' notes on specimen tags were sometimes utilized in an effort to provide potential researchers with an idea of whether a specimen was immature [Imm] or adult [Ad]. Immature specimens were recognized with most certainty. When satisfactory judgement was not possible, a question mark (?) appears in this category. In one series of *Phoca hispida hispida* specimens, collector J. K. Doutt noted age approximations (in years) as told to him by local Inuit hunters. These estimates have been included in brackets under this category, if measurements cannot be taken. When condylobasal length can be measured, these estimates appear in brackets under the "Comments" category.

Nature of specimen.—This category describes the type of preservation used for each specimen and corresponds to the two letter abbreviation system used on our computer file. The following list describes each type of preservation used in the marine mammal collection: SK = skull only; SO = skin only; SS = skin and skull; SB = skin, skull, and body skeleton; SN = complete skeleton; CO = cranium only; AL = alcoholic (preserved in 70% ethyl alcohol); BM = body mount; PS = partial skeleton. If peculiarities exist regarding availability of a specimen these are noted by an asterisk following the two letter code. There are two types of specimens that carry the asterisk: 1) specimens for which some of the parts are missing; 2) specimens on exhibit. These latter specimens are available for examination but work must be planned with the understanding that the specimens are in exhibit areas and are not housed with the remainder of the collection. For further explanations regarding the availability status of a specimen refer to the "Comments" category.

Condition of specimen and comments.—This category is designed to inform the reader of the usefulness of a specimen for systematics research. The term "Good" is used for all specimens and specimen parts, which are in useable condition for study. Damage to the skull is described so that measurability can be evaluated. All skins are either tanned or body mounts with the exception of a few newborn polar bears which have been prepared as conventional study skins. Captives are noted; missing parts and exhibit specimens are noted. Inuit age estimates of *Phoca hispida hispida* specimens are included here.

TAXONOMIC LIST

- Cetacea
  - Platanistidae
    - Iniinae
      - *Inia geoffrensis*
  - Physeteridae
    - Physeterinae
      - *Physeter catodon*
  - Monodontidae
    - *Delphinapterus leucas*
    - *Monodon monoceros*
  - Delphinidae
    - *Delphinus delphis*
    - *Sotalia fluviatilis*
    - *Tursiops truncatus*
  - Phocaenidae
    - *Phocaena phocaena*
  - Balaenopteridae
    - *Balaenoptera musculus*
- Carnivora
  - Ursidae
    - *Ursus maritimus*
  - Mustelidae
    - Lutrinae
      - *Enhydra lutris lutris*
- Pinnipedia
  - Otariidae
    - *Callorhinus ursinus*
    - *Eumetopias jubatus*
    - *Otaria byronia*
    - *Zalophus californicus*
  - Odobenidae
    - *Odobenus rosmarus divergens*
    - *Odobenus rosmarus rosmarus*
  - Phocidae
    - Phocinae
      - *Erignathus barbatus*
      - *Halichoerus grypus*
      - *Phoca fasciata*
      - *Phoca groenlandica groenlandica*
      - *Phoca hispida hispida*
      - *Phoca sibirica*
      - *Phoca vitulina concolor*
      - *Phoca vitulina mellonae*
      - *Phoca vitulina richardii*
      - *Phoca vitulina vitulina*
      - *Phoca vitulina*
      - *Phoca* species
    - Cystophorinae
      - *Cystophora cristata*
- Sirenia
  - Trichechidae
    - *Trichechus inunguis*
    - *Trichechus manatus latirostris*
    - *Trichechus senegalensis*

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Catalog of Marine Mammals

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Cetacea						
Plantanistidae						
Iniinae						
Inia geoffrensis						
Brazil: Amazonas; on Rio Yavari, near Benjamin Constant* 04°23′S; 69°59′W	6 Jun 1967	CM 60934	F	479.6	SB	Skull autopsied; skin tanned; zoo specimen
Brazil: Amazonas; on Rio Yavari, near Benjamin Constant* 04°23′S; 69°59′W	6 Jun 1967	CM 60935	?	[Imm]	SS	Skull fragmentary; skin tanned; zoo specimen
Brazil: Amazonas; on Rio Yavari, near Benjamin Constant* 04°23′S; 69°59′W	6 Jun 1967	CM 60936	F	468.3	SB	Skull autopsied; skin tanned; zoo specimen
Locality unknown*	6 Jan 1972	CM 60937	M	387.0	SN	Good, several loose teeth; zoo specimen, believed to have been collected with three previous specimens
Physeteridae						
Physeterinae						
Physeter catodon						
Locality unknown	1894	CM 21052	?	[Ad]	OT*	Lower jaw only, on exhibit
Monodontidae						
Delphinapterus leucas						
Canada: Quebec; mouth of Great Whale River	14 Aug 1935	CM 11274	?	?	SK	Skull fragmentary
Canada: Northwest Territories; South Belcher Islands	15 Jun 1938	CM 15511	M	?	SK	Skull fragmentary
Canada: Quebec; mouth of Nastapoka River 59°40′N; 76°45′W	31 Jul 1945	CM 23777	M	489.5	SK	Portions of skull wired together, most teeth loose or missing
Canada: Quebec; mouth of	31 Jul 1945	CM 23778	F	[Imm]	SK	Skull fragmentary

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Nastapoka River 59°40'N; 76°45'W						
Canada: Quebec; Great Whale River 55°15'N; 76°45'W	1 Aug 1945	CM 23779	F	?	SS	Skull fragmentary; tanned skin
Canada: Quebec; Great Whale River 55°15'N; 76°45'W	14 Aug 1945	CM 23780	?	?	SK	Skull fragmentary
Canada: Quebec; Great Whale River 55°15'N; 76°45'W	14 Aug 1945	CM 23781	?	485.9	SK	Good condition
Canada: Quebec; Hudson Bay	1945	CM 23785	?	?	SK	Skull fragmentary
Monodon monoceros						
Locality unknown	unknown	CM 20964	M	?	OT	Tusk only
Locality unknown	unknown	CM 20965	M	?	OT	Tusk only
Locality unknown	unknown	CM 20966	M	?	OT	Tusk only
Locality unknown	unknown	CM 20967	M	?	OT	Tusk only
Locality unknown	unknown	CM 20968	M	?	OT	Tusk only
Locality unknown	unknown	CM 20969	M	?	OT	Tusk only
Locality unknown	unknown	CM 20970	M	?	OT	Tusk only
DELPHINIDAE						
Species undetermined						
Locality unknown	unknown	CM 153	?	?	SK*	Dissected, on exhibit
United States: Florida; Palm Beach Co., Palm Beach	unknown	CM 1903	?	[160]	SK	Probably fetus
Delphinus delphis						
Locality unknown*	unknown	CM 1790	?	?	SN*	Good; mounted, on exhibit
Sotalia fluviatilis						
Locality unknown*	6 Jan 1972	CM 60938	F	[287]	SN	Rostrum damaged, old injury, CBL incomplete for normal animal; zoo specimen
Locality unknown*	Jul 1968	CM 60939	F	[331]	SB	Rostrum damaged, brittle; tanned skin; zoo specimen

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Locality unknown*	Jul 1968	CM 60940	F	[340]	SB	Skull autopsied; rostrum damaged; tanned skin; zoo specimen
Guyana: Bartica Dist.; in Cuyuni River, near Kartabo	11 Aug 1925	CM 60941	M	[Ad]	AL	Good; Williams, 1928
Guyana: Bartica Dist.; in Cuyuni River, near Kartabo	1967	CM 60942	?	[302]	SS	Skull brittle; rostrum damaged, tanned skin; zoo specimen
Tursiops truncatus						
United States: Florida; Dade Co., Miami Beach	Mar 1940	CM 19412	?	490	SK	Good; but pick-up with no teeth
PHOCAENIDAE						
Species undetermined						
Locality unknown	unknown	CM 1209	?	Fetus	AL	Good
Phocaena phocaena						
Baltic Sea coast	unknown	CM 1709	?	?	SN*	Good; mounted, on exhibit
Locality unknown*	unknown	CM 63097	?	307	SN	Good; zoo specimen
BALAENOPTERIDAE						
Species undetermined						
Locality unknown	unknown	CM 20971	?	?	OT	Bulla only
Balaenoptera musculus						
Locality unknown	unknown	CM 20972	?	?	OT	Bulla only
CARNIVORA						
URSIDAE						
Ursus maritimus						
Greenland: specific locality unknown	unknown	CM 1759	?	[Ad]	SK*	Good; on exhibit
USSR: Siberia; Wrangel Island	unknown	CM 2221	F	344.8	PS	Canines damaged; incisors, premolars missing
Locality unknown*	22 Nov 1915	CM 3222	M	[Imm]	SS	Zoo specimen; newborn
Canada: Quebec; Great Whale River	Aug 1915	CM 3393	?	280.7	SK	Several teeth broken or missing; left zygomatic arch broken

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; Great Whale River	Aug 1915	CM 3394	?	378.6	SK	Several teeth broken
Canada: Quebec; Great Whale River	Aug 1915	CM 3395	?	365.9	SK	Several teeth broken
Canada: Quebec; Great Whale River	Aug 1915	CM 3397	?	382.1	SK	Several teeth missing or broken
Canada: Quebec; Great Whale River	Aug 1915	CM 3398	?	312.4	SK	Good
Canada: Quebec; Great Whale River	Aug 1915	CM 3399	?	355.0	SK	Several teeth missing or broken
Locality unknown*	22 Nov 1916	CM 3934	?	[Imm]	SO	Skin stuffed; zoo specimen
Locality unknown*	7 Dec 1935	CM 10466	M	[Imm]	SS	Skull fragmentary; skin stuffed; zoo specimen
Locality unknown*	7 Dec 1935	CM 10467	M	[Imm]	SS	Skull fragmentary; skin stuffed; zoo specimen
Canada: Northwest Territories; James Bay, South Twin Island	31 Jul 1935	CM 10787	?	331.6	SK	Good
Canada: Northwest Territories; James Bay, South Twin Island	31 Jul 1935	CM 10788	?	368.0	OT	Skull and humerus; weathered
Canada: Northwest Territories; James Bay, South Twin Island	31 Jul 1935	CM 10789	?	307.1	OT	Skull and humerus; badly weathered
Canada: Northwest Territories; James Bay, South Twin Island	21 Jul 1935	CM 11285	F	316.7	SS	Good, but teeth have been lacquered; tanned skin
Canada: Northwest Territories; James Bay, South Twin Island	21 Jul 1935	CM 11286	M	205.1	SS*	Good; skin on exhibit

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; James Bay, South Twin Island	23 Jul 1935	CM 11287	M	356.2	SS	Braincase damaged; tanned skin
Canada: Northwest Territories; James Bay, North Twin Island	29 Jul 1935	CM 11288	M	372.0	SS	Good; tanned skin
Canada: Northwest Territories; James Bay, North Twin Island	30 Jul 1935	CM 11289	M	398.2	SS	Good; tanned skin
Canada: Northwest Territories; James Bay, Gray Goose Island	18 Aug 1935	CM 11290	M	390.0	SS	Good; tanned skin
Canada: Northwest Territories; James Bay, North Twin Island	29 Aug 1935	CM 11291	M	366.0	SS	Good; tanned skin
Locality unknown*	17 Sep 1936	CM 11413	F	290.2	SS	Good; tanned skin; zoo specimen
Canada: Northwest Territories; James Bay, Gray Goose Island	12 Aug 1936	CM 12042	M	338.6	SK	Good
Canada: Northwest Territories; James Bay, Bare Island	13 Aug 1936	CM 12044	M	[Imm]	SK	Braincase damaged
Canada: Northwest Territories; James Bay, Bare Island	13 Aug 1936	CM 12045	F	331.0	SS*	Good; skin on exhibit
Canada: Northwest Territories; James Bay, Bare Island	13 Aug 1936	CM 12046	M	357.8	SN	Good
Canada: Northwest Territories; Belcher Islands, Kugong Island 56°18′N; 79°50′W	Nov 1937	CM 15161	M	367.0	SK	Incisors damaged or missing; left bulla damaged
Canada: Northwest Territories; Walter Island	8 Sep 1938	CM 15162	F	325.4	SB	Good; tanned skin

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; Walter Island	8 Sep 1938	CM 15163	F	291.2	SS	Rostrum damaged; tanned skin
Locality unknown*	16 Jun 1940	CM 18743	M	344.9	SK	Several loose teeth; zoo specimen
Locality unknown*	17 May 1943	CM 21492	?	305.6	SK	Several loose teeth; zoo specimen
Canada: Quebec; Nastopoka Sound 56°45′N; 76°50′W	31 Jul 1945	CM 22925	?	317.3	CO	Pick-up, all teeth missing
Locality unknown*	19 Jan 1946	CM 30434	F	295.6	SK	Good; zoo specimen
Locality unknown*	12 Oct 1946	CM 30435	M	354.5	SK	Good; zoo specimen
Locality unknown*	13 Oct 1946	CM 30436	F	295.5	SS	Good; tanned skin; zoo specimen
Canada: Quebec; Great Whale River	9 Aug 1953	CM 39885	F	320.5	SS	Good; tanned skin
Canada: Quebec; Great Whale River	9 Aug 1953	CM 39886	?	203.8	SS	Good; tanned skin
Norway*	23 Mar 1967	CM 61407	M	389.1	SB	Good, but teeth missing and decayed; tanned skin; zoo specimen
Canada: Northwest Territories; Baffin Island, Eglinton Fjord 78°40′N; 69°50′W	24 Apr 1972	CM 61436	M	341.2	SK	Good
Canada: Northwest Territories; Baffin Island, Eglinton Fjord 78°40′N; 69°50′W	Nov 1971	CM 61437	?	378.0	SK	Zygomatic arches damaged
Canada: Northwest Territories; Baffin Island, near Clyde River	unknown	CM 61438	?	362.5	SK	Canines damaged
Canada: Northwest Territories; Baffin Island, near Ayr Lake 70°30′N; 69°30′W	13 Jan 1972	CM 61440	F	313.4	SK	Several teeth missing
Canada: Northwest Territories; Baffin Island, Home Bay 69°05′N; 67°W	13 Apr 1972	CM 61441	?	292.2	SK	Good

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
MUSTELIDAE						
LUTRINAE						
Enhydra lutris lutris						
United States: Alaska; Hinchinbrook Island	30 Jan 1965	CM 40574	M	126.8	SN	Good
United States: Alaska; Hinchinbrook Island	Spring 1965	CM 40575	M	133.7	SB	Good; tanned skin
United States: Alaska; Simeonof Island	21 Jul 1965	CM 40619	M	138.5	OT	Skull and baculum; good, molars very worn
United States: Alaska; specific locality unknown	1965	CM 61402	F	125.9	SB	Good; tanned skin
United States: Alaska; specific locality unknown	1965	CM 61403	F	98.1	SB	Basisphenoid broken; tanned skin
United States: Alaska; Aleutian Islands; Amchitka Island	Feb–Mar 1952	CM 94703	?	[Ad]	SO	Tanned skin; permanent loan from USNM
PINNIPEDIA						
OTARIIDAE						
Callorhinus ursinus						
United States: Alaska; Pribilof Islands	unknown	CM 135	?	[Imm]	SS	Skull fragmentary; tanned skin
United States: Alaska; Pribilof Islands	unknown	CM 136	?	[Imm]	SS	Skull fragmentary; tanned skin
Locality unknown	15 Oct 1900	CM 961	M	248.2	SN	Braincase damaged, teeth loose
Locality unknown	unknown	CM 963	?	[Imm]	SK	Skull fragmentary
United States: Alaska; Pribilof Islands, Polovina Rockery, St. Paul Island	8 Jul 1969	CM 59586	M	242.5	SS	Nasals damaged; tanned skin
Eumetopias jubatus						
Locality unknown	15 Oct 1900	CM 958	M	388.9/	SB*	Skin on exhibit; skeleton with skull

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
				374.7		in good condition—thought to be correct match; second skull with same number, braincase shot-damaged
Locality unknown	15 Oct 1900	CM 959	F	309.0	SN	Many loose teeth
Locality unknown	15 Oct 1900	CM 960	M	391.1	SK	Good
United States: California; San Mateo Co., Ano Nuevo Island	6 Jul 1906	CM 1484	M	?	PS*	Postcranial skeleton in good condition; skull missing
United States: California; San Mateo Co., Ano Nuevo Island	7 Jul 1906	CM 1485	F	?	PS*	Postcranial skeleton in good condition; skull missing
Locality unknown	15 Oct 1900	CM 21004	F	327.9	SK	Good
United States: Alaska; Aleutian Islands, Bogoslof Island 53°57′N; 168°04′W	26 Jun 1913	CM 21005	F	315.5	SK	Good
Otaria byronia						
Chile: Tierra del Fuego; Marinelleo Glacier, Ainsworth Harbor 54°S; 70°W	4 Mar 1939	CM 18094	?	229.1	SS	Skull has been lacquered; palatal region damaged; tanned skin
Chile: vicinity of Tropic of Capricorn, between Tocopilla and Antofagasta, Constitucion Bay	28 Mar 1939	CM 18095	?	296.3	CO	Pick-up, numerous missing teeth
Zalophus californicus						
Locality unknown*	unknown	CM 1444	M	207.1	SK	Skull very fragile, most teeth loose; zoo specimen
Locality unknown*	unknown	CM 1478	F	204.8	SN	Good; zoo specimen
Locality unknown*	Dec 1907	CM 1562	F	218.0	SB*	Most teeth loose; zoo specimen; skin missing

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
United States: California; Monterey Co., Pacific Grove, Mussel Point	4 Dec 1933	CM 8495	M	?	SO	Tanned skin
Locality unknown*	10 Jun 1941	CM 19535	F	204.9	SB	Good; zoo specimen
Locality unknown*	unknown	CM 21003	?	218.6	SK	Good, but most teeth loose; probably zoo specimen
Locality unknown*	26 Oct 1946	CM 30443	F	186.4	SS	Good; tanned skin; zoo specimen
Locality unknown*	unknown	CM 57378	F	231.1	SN	Good; zoo specimen
Locality unknown*	Oct 1970	CM 59580	F	215.8	SB	Good; tanned skin; zoo specimen
Locality unknown*	6 Jan 1972	CM 59640	F	180.8	SN	Good; zoo specimen
ODOBENIDAE						
Odobenus rosmarus divergens						
North Pacific: specific locality unknown	unknown	CM 20945	F	[Ad]	SK*	Skull with carved tusks, on exhibit
North Pacific: specific locality unknown	unknown	CM 20946	F	?	OT	Tusks only
North Pacific: specific locality unknown	unknown	CM 20947	M	?	OT	Tusks only
North Pacific: specific locality unknown	unknown	CM 20948	M	?	OT	Tusks only
North Pacific: specific locality unknown	unknown	CM 20949	M	?	OT	2 right tusks
Odobenus rosmarus rosmarus						
North Atlantic: specific locality unknown	unknown	CM 91	[F]	330	SK	Several loose teeth; limb bones present
North Atlantic: specific locality unknown	unknown	CM 92	[M]	[Ad]	SK	Skull fragmentary; limb bones present
North Atlantic: specific locality unknown	unknown	CM 93	?	[Imm]	SK	Skull fragmentary; limb bones present; calf or full term fetus
Canada: Quebec; Great Whale River	Aug 1915	CM 3400	[M]	334	SK	Braincase broken

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; Southampton Island, Prairie Point Floe	15 Apr 1930	CM 6668	F	149	SK	Good
Canada: Northwest Territories; Southampton Island, Bear Island Floe	15 Apr 1930	CM 6669	F	307	SK	Left zygomatic arch and palate damaged
Canada: Northwest Territories; Southampton Island, Walrus Island	22 Jul 1930	CM 6692	M	[Ad]	SK	Braincase damaged
Canada: Northwest Territories; Southampton Island, Bear Island	27 Jul 1930	CM 6696	F	[Ad]	SS	Braincase damaged; tanned skin
Canada: Ontario; Hannah Bay, Gull Point 51°28′N; 79°34′W	21 Sep 1935	CM 10823	M	[Ad]	CO	Pick-up, tusks removed
Canada: Northwest Territories; Belcher Islands, Kugong Island 56°18′N; 79°50′W	1 May 1938	CM 15317	F	301	SK	Old injury to left side of mandible
Canada: Northwest Territories; Belcher Islands, Kugong Island 56°18′N; 79°50′W	1 May 1938	CM 15318	M	[Imm]	SS	Skull fragmentary; tanned skin
Canada: Northwest Territories; Belcher Islands, Johnson Island 56°43′N; 79°32′W	May 1938	CM 15319	?	200	SK	Good; calf, about 6 months old
Canada: Northwest Territories; Belcher Islands, Kugong Island 56°18′N; 79°50′W	2 Jul 1938	CM 15320	M	[Ad]	SK	Braincase damaged
Canada: Northwest Territories; Belcher Islands, northwest of Kugong Island 56°18′N; 79°50′W	9 Jul 1938	CM 15321	M	324	SK	Left zygomatic and right bullar regions damaged

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; Belcher Islands, Kugong Island 56°18′N; 79°50′W	16 Jul 1938	CM 15322	M	332	SK	Right side of cranium damaged; left zygomatic arch broken; baculum saved
Canada: Northwest Territories; Belcher Islands, La Duke Island 56°06′N; 78°58′W	5 Aug 1938	CM 15323	M	318	SK	Good
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	18 Aug 1938	CM 15324	F	281	SS*	Good; skin mounted, on exhibit
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	18 Aug 1938	CM 15325	F	[Ad]	SS*	Skull fragmentary; skin mounted, on exhibit
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15326	M	353	SS*	Good; skin mounted, on exhibit; baculum saved
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15327	M	349	SK	Good
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15328	F	312	SK	Occipital region damaged
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15329	?	[Imm]	AL	Good
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15331	?	[Imm]	AL	Good
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15332	?	[Imm]	AL	Good

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15333	M	[Imm]	SS	Skull fragmentary; skin mounted; uncataloged adult female mixed with this specimen and 15334
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15334	M	[Imm]	SB	Good; skin mounted; uncataloged adult female skeleton mixed with this skeleton and 15333
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15335	[F]	[Ad]	SK	Braincase damaged
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15336	[F]	294	SK	Good
Canada: Northwest Territories; north end South Sleeper Islands 57°30′N; 79°45′W	19 Aug 1938	CM 15337	M	349	SK	Good
Canada: Northwest Territories; Belcher Islands 56°15′N; 79°15′W	unknown	CM 15338	M	?	OT	Several bacula, nothing else
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23309	M	291	SK	Right zygomatic arch damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	1945	CM 23310	[F]	293	SK	Interorbital region damaged
PHOCIDAE						
PHOCINAE						
Erignathus barbatus						
Canada: Ontario; Hannah Bay, Charlton Island 52°N; 79°30′W	17 Aug 1912	CM 2578	M	?	SK	Skull fragmentary; some limb bones present
Canada: Ontario; Hannah Bay, Charlton Island 52°N; 79°30′W	1 Sep 1912	CM 2584	M	[Ad]	SK	Nasals missing, both zygomatic arches and braincase damaged

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; Southampton Island, Native Point 63°44′N; 82°31′W	2 Feb 1930	CM 6545	M	122.2	SK	Good
Canada: Northwest Territories; Southampton Island, Native Point 63°44′N; 82°31′W	27 Mar 1930	CM 6636	?	[Imm]	SO	Tanned skin
Canada: Northwest Territories; Southampton Island, Walrus Island	22 Jul 1930	CM 6693	M	?	SK	Skull fragmentary
Canada: Northwest Territories; Southampton Island, Walrus Island	22 Jul 1930	CM 6694	F	?	SK	Skull fragmentary
Canada: Northwest Territories; Belcher Islands, Freshwater Lake	Mar 1936	CM 13160	?	[Imm]	SO	Tanned skin
Canada: Quebec; near mouth of Great Whale River	8 Jan 1938	CM 15307	M	[Imm]	SO	Tanned skin from trapper
Canada: Quebec; 5 mi below mouth of Great Whale River	28 Feb 1938	CM 15308	?	[Imm]	SO	Tanned skin from trapper
Canada: Northwest Territories; North Belcher Islands 56°50′N; 79°45′W	Mar 1938	CM 15309	?	[Imm]	SO	Skull fragmentary; tanned skin from trapper
Canada: Northwest Territories; near North Belcher Islands 56°50′N; 79°45′W	9 Jul 1938	CM 15310	M	190.7	SS	Left zygomatic arch damaged; tanned skin
Canada: Northwest Territories; Belcher Islands, SE side Tukarak Island 56°16′N; 78°45′W	12 Jul 1938	CM 15311	F	223.0	SK	Both zygomatic arches damaged, most teeth gone
Canada: Northwest Territories; Belcher Islands, east side	Jul 1938	CM 15312	M	222.7	SK	Both zygomatic arches damaged, most teeth loose

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Tukarak Island 56°16′N; 78°45′W						
Canada: Northwest Territories; Belcher Islands, northwest Kugong Island 56°18′N; 79°50′W	16 Jul 1938	CM 15313	M	221.3	SS	Good; tanned skin
Canada: Northwest Territories; Belcher Islands, Tukarak Island 56°16′N; 78°45′W	3 Aug 1938	CM 15314	?	210.2	PS	Pick-up; cranium and some skeletal parts
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	4 May 1938	CM 15315	F	[Ad]	SK	Braincase broken
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	4 May 1938	CM 15316	M	216.3	SK	Good
Canada: Northwest Territories; near Cape Jones, Long Island Sound 54°46′N; 79°15′W	Feb 1939	CM 17745	?	145.9	SS	Braincase damaged; tanned skin
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	3 Jun 1945	CM 23304	M	211.5	SK	Good
Canada: Quebec; vicinity of Cape Gertrude 59°25′N; 77°55′W	22 May 1945	CM 23305	M	224.9	SK	Good
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23306	?	212.2	SK	Good
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23307	?	194.8	SK	Left side of rostrum broken
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	6 Jul 1945	CM 23308	?	230.4	SK	Good, but all teeth gone

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Ontario; Albany Post of Hudson Bay Company	Sep 1945	CM 30445	?	?	SO	Tanned skin
Canada: Ontario; Albany Post of Hudson Bay Company	Oct 1945	CM 30446	?	[Imm]	SS	Braincase damaged; tanned skin
Canada: Ontario; Albany Post of Hudson Bay Company	Nov 1945	CM 30447	F	198.4	SS	Good; tanned skin
Halichoerus grypus						
North Atlantic: North Sea	unknown	CM 1773	?	[Ad]	SN*	Mounted, on exhibit
Phoca fasciata						
United States: Alaska; near Kotzebue 66°51′N; 162°40′W	Winter 1954–55	CM 39893	M	183.0	SS	Left zygomatic arch broken, several loose teeth; tanned skin
United States: Alaska; St. Lawrence Island, Gambell	10 Jun 1960	CM 40361	M	181.7	SS	Good; tanned skin
Phoca groenlandica groenlandica						
Canada: Quebec; La Tabatiere 50°50′N; 58°57′W	1938	CM 17680	?	209	CO	Zygomatic arches broken, several teeth missing
Canada: Quebec; La Tabatiere 50°50′N; 58°57′W	1938	CM 17681	?	192.2	CO	Good
Canada: Newfoundland; Labrador, Hamilton Inlet, Mud Lake 54°18′N; 57°42′W	12 Jul 1938	CM 17853	?	193.1	SK	Left bullar region damaged, numerous loose teeth; right upper tooth row shows old injury
Canada: Newfoundland; Labrador, Hamilton Inlet, Mud Lake 54°18′N; 57°42′W	12 Jul 1938	CM 17854	?	193.2	SK	Left zygomatic arch damaged, numerous loose teeth
Canada: Newfoundland; Labrador, Hamilton Inlet, Mud Lake 54°18′N; 57°42′W	12 Jul 1938	CM 17855	?	192.5	SK	Both zygomatic arches damaged, numerous loose teeth
Canada: Newfoundland; Labrador, Hamilton Inlet,	29 Aug 1939	CM 17856	?	178.9	SK	Right zygomatic arch damaged

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Northwest River, 54°18′N; 57°42′W						
Canada: Newfoundland; Labrador, Hamilton Inlet, Northwest River, 54°18′N; 57°42′W	29 Aug 1939	CM 17857	?	184.7	SK	Zygomatic arches broken; numerous loose teeth
Canada: Quebec; La Tabatiere 50°50′N; 58°57′W	7 Jan 1940	CM 18696	M	?	SO	Tanned skin
Canada: Quebec; La Tabatiere 50°50′N; 58°57′W	27 Dec 1939	CM 18697	M	?	SO	Tanned skin
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18700	?	183.2	SK	Left side of cranium damaged, most teeth loose
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18701	?	[Ad]	SK	Skull fragmentary
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18702	?	186.8	SK	Left side of mandible damaged
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18703	?	209.0	SK	Zygomatic arches broken; evidence of gum disease
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18704	?	187.5	SK	Right side of cranium damaged, left side of mandible broken
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18705	?	189.8	SK	Left side of cranium damaged, most teeth loose
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18706	?	[Imm]	SK	Rostrum broken

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18707	F	190.5	SK	Left side of cranium and mandible damaged
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18708	F	183.5	SK	Left side of mandible broken
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18709	F	193.2	SK	Many loose teeth
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18710	F	[Imm]	SK	Skull fragmentary
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18711	F	195.0	SK	Many loose teeth
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18712	F	181.0	SK	Zygomatic arches broken; many loose teeth
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18713	F	180.7	SK	Good
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18714	F	[Ad]	SK	Braincase broken
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18715	F	176.0	SK	Numerous teeth missing or broken
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18717	M	194.9	SK	Right zygomatic arch broken
Canada: Quebec; Gulf of St.	1939–40	CM 18718	M	[185]	SK	Parietal region broken

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Lawrence, La Tabatiere 50°50′N; 58°57′W						
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18719	M	188.6	SK	Zygomatic arches broken; mandible broken
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18720	M	198.2	SK	Numerous loose teeth
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18721	M	190.7	SK	Numerous loose teeth
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18722	M	191.0	SK	Numerous loose teeth
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18723	?	102.1	SK	Left bulla damaged; teeth not yet erupted
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18724	?	103.1	SK	Left zygomatic arch broken, teeth not erupted
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18725	?	106.8	SK	Basisphenoid gone; teeth not yet erupted
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18726	?	[Imm]	SK	Skull fragmentary
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18727	?	[Imm]	SK	Skull fragmentary
Canada: Quebec; Gulf of St.	1939–40	CM 18728	?	[Imm]	SK	Skull fragmentary

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Lawrence, La Tabatiere 50°50'N; 58°57'W						
Canada: Northwest Territories; Smith Island, Cape Smith 60°40'N; 78°30'W	Dec 1944	CM 23302	?	?	SO	Tanned skin
Phoca hispida hispida						
Canada: Quebec; Cape Jones 54°36'N; 79°47'W	30 Jul 1914	CM 3071	F	[131]	SK	Cranium damaged
Canada: Quebec; Great Whale River	25 Mar 1915	CM 3342	F	[106]	SK	Cranium damaged
Canada: Quebec; Great Whale River	5 Apr 1915	CM 3344	F	104.8	CO	Good
Canada: Quebec; Nastapoka River	14 Jun 1915	CM 3368	F	[Imm]	SK	Skull fragmentary
Canada: Quebec; Richmond Gulf 56°15'N; 76°20'W	10 Jul 1915	CM 3371	F	[Imm]	SK	Skull fragmentary
Canada: Quebec; south of Little Whale River	13 Jul 1915	CM 3372	F	144.6	SK	Cranium damaged
Canada: Northwest Territories; Southampton Island, Native Point 63°44'N; 82°31'W	2 Feb 1930	CM 6544	F	86.9	SS	Right zygomatic arch broken; stuffed skin
Canada: Northwest Territories; Southampton Island, Cape Kendall 63°36'N; 87°12'W	8 May 1930	CM 6676	F	158.8	SK	Good
Canada: Northwest Territories; Southampton Island, Cape Kendall 63°36'N; 87°12'W	12 May 1930	CM 6677	M	170.0	SK	Good
Canada: Quebec; Great Whale River	20 Jan 1936	CM 10727	?	[Imm]	SO	Stuffed skin
Canada: Quebec; Great Whale River	20 Jan 1936	CM 10728	?	[Imm]	SO	Stuffed skin

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; South Twin Island 53°07′N; 79°52′W	31 Jul 1935	CM 10819	?	?	SK	Skull fragmentary; pick-up
Canada: Northwest Territories; South Twin Island 53°07′N; 79°52′W	2 Aug 1935	CM 10820	?	?	SK	Skull fragmentary; pick-up
Canada: Quebec; Great Whale River	23 Aug 1935	CM 10821	?	?	SO	Trapper's tanned skin
Canada: Northwest Territories; Belcher Islands, Gateway to West from Eskimo Harbor 56°36′N; 79°12′W	24 Aug 1936	CM 12048	F	[Imm]	SS	Skull fragmentary; tanned skin
Canada: Northwest Territories; between Baker's Dozen and Belcher Islands	28 Aug 1936	CM 12049	?	?	SS	Skull fragmentary; tanned skin
Canada: Northwest Territories; between Baker's Dozen and Belcher Islands	28 Aug 1936	CM 12050	?	?	SS	Skull fragmentary; tanned skin
Canada: Quebec; Great Whale River	1936	CM 13157	M	133.0	SK	Good
Canada: Quebec; Great Whale River	1936	CM 13158	M	164.6	SK	Right bulla damaged
Canada: Quebec; Great Whale River	1936	CM 13159	M	167.2	SK	Left zygomatic arch damaged
Canada: Quebec; near mouth of Great Whale River	Jan 1938	CM 15222	F	[Imm]	SS	Skull fragmentary; tanned skin
Canada: Quebec; 5 mi below mouth of Great Whale River	Mar 1938	CM 15223	?	[Imm]	SO	Tanned skin
Canada: Quebec; 5 mi south of Great Whale River	28 Feb 1938	CM 15224	?	108.7	SS	Good; tanned skin

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; 5 mi below mouth of Great Whale River	28 Feb 1938	CM 15225	?	[Imm]	SO	Tanned skin
Canada: Quebec; 5 mi below mouth of Great Whale River	Mar 1938	CM 15226	?	[Imm]	SO	Tanned skin
Canada: Quebec; 5 mi below mouth of Great Whale River	Mar 1938	CM 15227	?	[Imm]	SO	Tanned skin
Canada: Northwest Territories; North Belcher Islands 56°50′N; 79°45′W	Mar 1938	CM 15228	?	[Imm]	SO	Trapper's tanned skin
Canada: Northwest Territories; North Belcher Islands 56°50′N; 79°45′W	Mar 1938	CM 15229	?	[Imm]	SO	Trapper's tanned skin
Canada: Northwest Territories; North Belcher Islands 56°50′N; 79°45′W	Mar 1938	CM 15230	?	[Imm]	SO	Trapper's tanned skin
Canada: Northwest Territories; North Belcher Islands 56°50′N; 79°45′W	Mar 1938	CM 15231	?	[Imm]	SO	Trapper's tanned skin
Canada: Northwest Territories; North Belcher Islands 56°50′N; 79°45′W	Mar 1938	CM 15232	?	[Imm]	SO	Trapper's tanned skin
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	16 Apr 1938	CM 15233	M	168.6	SK	Cross-section of canine saved; right zygomatic arch broken; [7 yrs old]
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Eskimo Harbor 56°36′N; 79°12′W	23 Apr 1938	CM 15234	?	[Imm]	SO	Tanned skin; [1 yr old]
Canada: Northwest Territories; Belcher Islands, southern	20 Apr 1938	CM 15235	?	141.4	SS	Good; tanned skin; cross-section of canine saved

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
end Flaherty Island 56°14′N; 79°17′W						
Canada: Northwest Territories; Belcher Islands, Wetalltok Bay 56°16′N; 78°45′W	25 Apr 1938	CM 15236	F	167.3	SK	Good; cross-section of canine saved; [7 yrs old]
Canada: Northwest Territories; Belcher Islands, Kugong Island 56°18′N; 79°50′W	25 Apr 1938	CM 15237	F	155.8	SS	Good; tanned skin; [2 yrs old]
Canada: Northwest Territories; Belcher Islands, Flaherty Island 56°36′N; 79°12′W	26 Apr 1938	CM 15238	F	[4 yrs]	SS	Skull fragmentary; tanned skin
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	27 Apr 1938	CM 15239	M	159.4	SK	Good; cross-section of canine saved; [5 yrs old]
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	Mar–Apr 1938	CM 15240	?	[Imm]	SO	Tanned skin
Canada: Northwest Territories; Belcher Islands, mouth of Wetalltok Bay 56°02′N; 79°14′W	29 Apr 1938	CM 15241	M	[Ad]	SS*	Cranium damaged; baculum saved; skin mounted, on exhibit
Canada: Northwest Territories; Belcher Islands, Kugong Island 56°18′N; 79°50′W	30 Apr 1938	CM 15242	M	147.7	SS	Cross-section of canine saved; left bulla damaged; [2 yrs old]; tanned skin
Canada: Northwest Territories; Belcher Islands, Wetalltok Bay 56°02′N; 78°14′W	4 May 1938	CM 15243	F	[Ad]	SS	Cross-section of canine saved; skull broken in two parts; tanned skin
Canada: Northwest Territories; Belcher Islands, Snape Island 55°45′N; 79°18′W	4 May 1938	CM 15244	F	157.5	SK	Good

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Gibson Peninsula 56°02′N; 78°10′W	24 Apr 1938	CM 15245	M	171.4	SS	Good; cross-section of canine saved; tanned skin
Canada: Northwest Territories; Belcher Islands 56°15′N; 79°15′W	May 1938	CM 15246	?	175.5	SK	Cross-section of canine saved; bullae gone
Canada: Northwest Territories; Belcher Islands, Kipalu Inlet 56°05′N; 79°06′W	6 May 1938	CM 15247	?	175.7	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Gushie Point 56°26′N; 78°56′W	7 May 1938	CM 15248	M	166.1	SK	Good; cross-section of canine saved; [7 yrs old]
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	6 May 1938	CM 15249	M	158.9	SB	Good; tanned skin; [4–5 yrs old]
Canada: Northwest Territories; Belcher Islands, near Wiegand Island 56°02′N; 79°14′W	7 May 1938	CM 15250	M	166.0	SS	Cross-section of canine saved; parietal region damaged; tanned skin
Canada: Northwest Territories; Belcher Islands, near Wiegand Island 56°02′N; 79°14′W	7 May 1938	CM 15251	M	156.1	SS*	Cross-section of canine saved; left side of skull damaged; skin used in exhibit
Canada: Northwest Territories; Belcher Islands, Kugong Island 56°18′N; 79°50′W	10 May 1938	CM 15252	M	[Imm]	SS	Cross-section of canine saved; cranium damaged; tanned skin; [1 yr old]
Canada: Northwest Territories; Belcher Islands, Kugong Island 56°18′N; 79°50′W	10 May 1938	CM 15253	F	167.1	SS	Cross-section of canine saved; good; tanned skin; [2 yrs old]

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Gushie Point 56°26′N; 78°56′W	14 May 1938	CM 15254	F	166.3	SK	Cross-section of canine saved; good
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Gushie Point 56°26′N; 78°56′W	16 May 1938	CM 15255	F	131.5	SK	Cross-section of canine saved; good
Canada: Northwest Territories; Belcher Islands, Johnson Island, 56°43′N; 79°32′W	16 May 1938	CM 15256	M	167.0	SK	Cross-section of canine saved; good; [7 yrs old]
Canada: Northwest Territories; Belcher Islands, Johnson Island, 56°43′N; 79°32′W	17 May 1938	CM 15257	M	156.1	SK	Cross-section of canine saved; good; [3 yrs old]
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Gushie Point 56°26′N; 78°56′W	24 May 1938	CM 15258	F	[150]	SK	Skull broken and glued; [4 yrs old]
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Gushie Point 56°26′N; 78°56′W	25 May 1938	CM 15259	?	152.5	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, east side of Tukarak Island 56°16′N; 78°45′W	May 1938	CM 15260	F	152.7	SK	Right zygomatic arch broken; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, east side of Tukarak Island 56°16′N; 78°45′W	May 1938	CM 15261	M	172.4	SK	Good; cross-section of canine saved

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; Belcher Islands, east side of Tukarak Island 56°16′N; 78°45′W	May 1938	CM 15262	F	178.4	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Gushie Point 56°26′N; 78°56′W	4 Jun 1938	CM 15263	F	138.9	SS	Cross-section of canine saved; cranium damaged; tanned skin; [1 yr old]
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Gushie Point 56°26′N; 78°56′W	4 Jun 1938	CM 15264	M	150.5	SK	Good; [2 yrs old]
Canada: Northwest Territories; Belcher Islands, Wetalltok Bay 56°02′N; 79°14′W	26 May 1938	CM 15265	F	163.7	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, Wetalltok Bay 56°02′N; 79°14′W	26 May 1938	CM 15266	F	166.2	SK	Good; cross-section of canine saved; [4 yrs old]
Canada: Northwest Territories; Belcher Islands, east side of Tukarak Island 56°02′N; 79°14′W	May 1938	CM 15267	M	178.7	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, east side of Tukarak Island 56°02′N; 79°14′W	May 1938	CM 15268	F	172.6	SK	Cross-section of canine saved; left zygomatic arch broken
Canada: Northwest Territories; Belcher Islands, east side of Tukarak Island 56°02′N; 79°14′W	May 1938	CM 15269	F	163.6	SK	Good; cross-section of canine saved

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; Belcher Islands, east side of Tukarak Island 56°02′N; 79°14′W	May 1938	CM 15270	F	169.3	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, east side of Tukarak Island 56°02′N; 79°14′W	May 1938	CM 15271	F	159.2	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, west side of Tukarak Island 56°16′N; 78°45′W	10 Jun 1938	CM 15272	M	?	SS	Skull fragmentary; baculum saved; tanned skin
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	May 1938	CM 15273	M	163.1	SK	Good; cross-section of canine and baculum saved
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	May 1938	CM 15274	M	156.3	SK	Good; cross-section of canine and baculum saved
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	May 1938	CM 15275	M	163.4	SK	Good; cross-section of canine and baculum saved
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	May 1938	CM 15276	F	175.0	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	May 1938	CM 15277	F	160.4	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	May 1938	CM 15278	F	160.8	SK	Good; cross-section of canine saved

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	May 1938	CM 15279	F	165.8	SK	Good; cross-section of canine saved; teeth all sheared off near gum line
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	May 1938	CM 15280	F	169.5	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	May 1938	CM 15281	F	174.9	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, Camsell Island 56°02′N; 78°41′W	May 1938	CM 15282	F	154.2	SK	Cross-section of canine saved; right zygomatic arch broken, skull glued in several places
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Gushie Point 56°26′N; 78°56′W	Jun 1938	CM 15283	?	167.6	SK	Good
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15284	M	154.7	SK	Good; cross-section of canine saved; [4 yrs old]
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15285	F	168.8	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15286	F	178.1	SK	Good; cross-section of canine saved; [4 yrs old]
Canada: Northwest Territories; Belcher Islands, vicinity of	Jun 1938	CM 15287	F	138.6	SK	Cross-section of canine saved; left side of skull damaged; [2 yrs old]

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Eskimo Harbor 56°36′N; 79°12′W						
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15288	F	167.0	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15289	M	177.0	SK	Good; cross-section of canine and baculum saved
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15290	F	165.4	SK	Good; cross-section of canine saved; [6 yrs old]
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15291	M	[155]	SK	Cross-section of canine and baculum saved; basioccipital region broken; [4 yrs old]
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15292	M	145.1	SK	Good; cross-section of canine and baculum saved; [2 yrs old]
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15293	M	157.7	SK	Good; baculum saved; [10 yrs old]
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15294	F	167.5	SK	Cross-section of canines saved; right zygomatic arch broken; [11 yrs old]

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15295	M	154.6	SK	Good; cross-section of canine and baculum saved; [7 yrs old]
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15296	F	171.3	SK	Good; cross-section of canine saved; [22 yrs old]
Canada: Northwest Territories; Belcher Islands, vicinity of Eskimo Harbor 56°36′N; 79°12′W	Jun 1938	CM 15297	F	156.0	SK	Cross-section of canine saved; braincase cracked; [7 yrs old]
Canada: Northwest Territories; Belcher Islands, Flaherty Island 56°14′N; 79°17′W	unknown	CM 15298	?	?	SK	Skull fragmentary
Canada: Northwest Territories; Belcher Islands, Flaherty Island 56°14′N; 79°17′W	unknown	CM 15299	?	?	SK	Skull fragmentary; pick-up
Canada: Northwest Territories; Belcher Islands, Tukarak Island 56°16′N; 78°45′W	6 Jul 1938	CM 15300	M	?	SB*	Skeleton missing; tanned skin
Canada: Northwest Territories; Belcher Islands, Gilmour Peninsula 56°18′N; 78°55′W	6 Jul 1938	CM 15301	F	?	SS	Skull fragmentary; tanned skin
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Gushie Point 56°26′N; 78°56′W	12 Jul 1938	CM 15302	F	?	SO	Tanned skin
Canada: Northwest Territories; Belcher Islands, Omarolluk	22 Jul 1938	CM 15303	M	139.0	SS	Zygomatic arches broken; left side of braincase damaged; left bulla sepa-

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Sound 56°03′N; 79°02′W						rate; cross-section of canine saved; tanned skin
Canada: Northwest Territories; Belcher Islands, Omarolluk Sound 56°03′N; 79°02′W	8 Aug 1938	CM 15304	M	?	SS	Skull missing; baculum saved; tanned skin
Canada: Northwest Territories; Belcher Islands, Kipalu Inlet 56°05′N; 79°06′W	9 May 1938	CM 15305	F	162.4	SK	Left bulla broken; cross-section of canine saved
Canada: Newfoundland; Labrador, Northwest River, 25 mi SW Traverspine	27 Aug 1939	CM 17850	?	144.2	SK	Skull brittle; zygomatic arches broken
Canada: Newfoundland; Labrador, Northwest River, Hamilton Inlet 25 mi SW Traverspine	27 Aug 1939	CM 17851	?	[Imm]	SK	Skull fragmentary
Canada: Newfoundland; Labrador, Northwest River, Hamilton Inlet	29 Aug 1939	CM 17852	?	180.4	CO	Zygomatic arches broken
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	29 Dec 1939	CM 18699	F	?	SO	Tanned skin
Canada: Quebec; within 125 mi Povungnituk Post 59°40′N; 77°30′W	6 Apr 1945	CM 23079	M	164.1	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; about 50 mi above mouth of Povungnituk River 60°15N; 76°W	7 May 1945	CM 23080	?	160.3	SK	Good; cross-section of canine saved
Canada: Quebec; near mouth of Povungnituk River 60°N; 77°15′W	7 May 1945	CM 23081	?	[Imm]	SK	Skull fragmentary

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; near mouth of Povungnituk River 60°N; 77°15′W	7 May 1945	CM 23082	?	149.4	SK	Good; cross-section of canine saved
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	April 1945	CM 23083	?	155.1	SK	Good
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	17 May 1945	CM 23084	M	154.7	SK	Good; cross-section of canine saved
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	17 May 1945	CM 23085	M	162.2	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	17 May 1945	CM 23086	M	157.9	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	17 May 1945	CM 23087	M	158.1	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	17 May 1945	CM 23088	M	151.4	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	17 May 1945	CM 23089	F	133.3	SK	Good
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	21 May 1945	CM 23090	M	171.5	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Cape Gertrude 59°25′N; 77°55′W	22 May 1945	CM 23091	M	162.9	SS	Right zygomatic arch broken; cross-section of canine and baculum saved; tanned skin

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	22 May 1945	CM 23092	M	172.3	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	22 May 1945	CM 23093	M	176.7	SK	Good; cross-section of canine saved
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	22 May 1945	CM 23094	M	164.8	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Mistake Bay 59°10′N; 78°15′W	22 May 1945	CM 23095	F	136.3	SS	Braincase damaged; cross-section of canine saved; tanned skin
Canada: Quebec; Cape Gertrude 59°25′N; 77°55′W	22 May 1945	CM 23096	M	165.8	SK	Good; cross-section of canine saved
Canada: Northwest Territories; Mistake Bay 59°10′N; 78°15′W	22 May 1945	CM 23097	F	[145]	SK	Braincase damaged
Canada: Northwest Territories; Mistake Bay 59°10′N; 78°15′W	22 May 1945	CM 23098	F	[150]	SK	Braincase damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	22 May 1945	CM 23099	M	152.6	SK	Good
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	22 May 1945	CM 23100	M	149.7	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	22 May 1945	CM 23101	F	156.0	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	22 May 1945	CM 23102	M	158.0	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	22 May 1945	CM 23103	F	153.2	SK	Most teeth loose; rostrum damaged

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	22 May 1945	CM 23104	M	161.6	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	22 May 1945	CM 23105	?	170.6	SK	Cross-section of canine saved; both zygomatic arches damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 May 1945	CM 23106	F	154.6	SK	Good; cross-section of canine saved; [3 yrs old]
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 May 1945	CM 23107	F	161.4	SK	Good; cross-section of canine saved; [4 yrs old]
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 May 1945	CM 23108	F	157.0	SK	Left zygomatic arch damaged; [4 yrs old]
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 May 1945	CM 23109	F	162.9	SK	Good; cross-section of canine saved; [3 yrs old]
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 May 1945	CM 23110	F	139.3	SK	Good; cross-section of canine saved; [2 yrs old]
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 May 1945	CM 23111	M	164.0	SK	Good; cross-section of canine and baculum saved; [4 yrs old]
Canada: Quebec; Povungnituk Post 59°40′N;77°30′W	27 May 1945	CM 23112	F	156.7	SS	Good; cross-section of canine and baculum saved; [3 yrs old]
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 May 1945	CM 23113	F	157.6	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 May 1945	CM 23114	F	159.9	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	30 May 1945	CM 23115	M	145.2	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	3 Jun 1945	CM 23116	M	[140]	SK	Braincase damaged; baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	3 Jun 1945	CM 23117	F	151.3	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	3 Jun 1945	CM 23118	F	161.5	SK	Good; cross-section of canine saved

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; Smith Island, Cape Smith 60°40′N; 78°30′W	12 Jun 1945	CM 23119	M	141.4	SS	Braincase cracked; cross-section of canine and baculum saved
Canada: Quebec; Smith Island, Cape Smith 60°40′N; 78°30′W	12 Jun 1945	CM 23120	F	?	SO	Tanned skin
Canada: Quebec; Smith Island, Cape Smith 60°40′N; 78°30′W	12 Jun 1945	CM 23121	M	167.0	SS	Good; cross-section of canine and baculum saved; tanned skin
Canada: Quebec; Smith Island, Cape Smith 60°40′N; 78°30′W	12 Jun 1945	CM 23122	?	159.1	SK	Skull brittle; cross-section of canine saved
Canada: Quebec; Smith Island, Cape Smith 60°40′N; 78°30′W	12 Jun 1945	CM 23123	?	154.2	SK	Left side of skull damaged; cross-section of canine saved
Canada: Quebec; Smith Island, Cape Smith 60°40′N; 78°30′W	12 Jun 1945	CM 23124	F	138.7	SS	Zygomatic arches damaged; cross-section of canine saved; tanned skin
Canada: Quebec; Smith Island, Cape Smith 60°40′N; 78°30′W	12 Jun 1945	CM 23125	M	166.2	SS	Left zygomatic arch and rostrum damaged; cross-section of canine and baculum saved; tanned skin
Canada: Quebec; Smith Island, Cape Smith 60°40′N; 78°30′W	12 Jun 1945	CM 23126	F	164.6	SS	Good; baculum saved; tanned skin
Canada: Quebec; Smith Island, Cape Smith 60°40′N; 78°30′W	12 Jun 1945	CM 23127	F	?	SO	Tanned skin
Canada: Quebec; near mouth of Kogaluk River 59°40′N; 77°25′W	14 Jun 1945	CM 23128	M	154.8	SK	Good; cross-section of canine and baculum saved

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; near mouth of Povungnituk River, Cape Anderson 60°05′N; 77°35′W	12 Jun 1945	CM 23129	F	?	SO	Tanned skin
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	5 Jun 1945	CM 23130	F	160.7	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	5 Jun 1945	CM 23131	M	165.1	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	5 Jun 1945	CM 23132	M	164.7	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; south of Kogaluk River 59°40′N; 77°25′W	5 Jun 1945	CM 23133	M	161.0	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; south of Kogaluk River 59°40′N; 77°25′W	5 Jun 1945	CM 23134	F	133.2	SK	Cross-section of canine saved; braincase cracked but measurable
Canada: Quebec; south of Kogaluk River 59°40′N; 77°25′W	5 Jun 1945	CM 23135	F	160.3	SK	Good; cross-section of canine saved
Canada: Quebec; south of Kogaluk River 59°40′N; 77°25′W	5 Jun 1945	CM 23136	M	172.1	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	5 Jun 1945	CM 23137	M	168.8	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	5 Jun 1945	CM 23138	M	161.6	SK	Cross-section of canine and baculum saved; braincase cracked
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	5 Jun 1945	CM 23139	M	154.0	CO	Left zygomatic arch damaged
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23140	?	136.6	SK	Good; cross-section of canine saved

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23141	?	161.7	SK	Good
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23142	?	156.3	SK	Cross-section of canine saved; palate damaged
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23143	?	146.8	SK	Good; cross-section of canine saved
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23144	?	156.9	SK	Good; cross-section of canine saved
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23145	?	155.1	SK	Good; cross-section of canine saved
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23146	?	172.2	SK	Good
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23147	M	157.7	SK	Cross-section of canine and baculum saved; left zygomatic arch broken
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23148	?	160.4	SK	Cross-section of canine saved; braincase cracked
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23149	M	163.6	SK	Good; numerous loose teeth
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23150	?	144.2	SK	Cross-section of canine saved; left side of skull damaged
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23151	?	154.1	SK	Cross-section of canine saved; left zygomatic arch damaged; right side of rostrum broken
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23152	?	170.4	SK	Good; cross-section of canine saved
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23153	M	173.4	SK	Cross-section of canine and baculum saved; basioccipital damaged
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23154	?	159.0	SK	Good; cross-section of canine saved
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23155	?	[Imm]	CO	Skull fragmentary

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23156	?	156.0	SK	Good; cross-section of canine saved
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	13 Jun 1945	CM 23157	?	153.7	SK	Cross-section of canine saved; right zygomatic arch broken
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23158	M	173.6	SS	Good; cross-section of canine and baculum saved; tanned skin
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23159	M	156.7	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23160	M	166.2	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23161	M	167.8	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23162	M	169.5	SK	Good; cross-section of canine and baculum saved; right bullar region damaged, several loose teeth
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23163	M	172.3	SK	Good; baculum saved; teeth all broken off
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23164	M	160.3	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23165	M	167.7	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23166	F	166.5	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23167	F	143.4	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23168	M	164.5	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	16 Jun 1945	CM 23169	F	[160]	SK	Rostrum broken
Canada: Quebec; Povungnituk Post 59°40′N: 77°30′W	16 Jun 1945	CM 23170	M	163.6	SK	Good; baculum saved

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	18 Jun 1945	CM 23171	M	176.6	SK	Cross-section of canine and baculum saved; basioccipital region broken
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	18 Jun 1945	CM 23172	F	157.3	SK	Cross-section of canine saved; left zygomatic arch broken
Canada: Quebec; near Magnet Point 60°25′N; 77°45′W	18 Jun 1945	CM 23173	F	157.1	SK	Good; cross-section of canine saved
Canada: Quebec; mouth of Kogaluk Bay 59°40′N; 77°25′W	23 Jun 1945	CM 23174	F	?	SO	Tanned skin
Canada: Quebec; mouth of Kogaluk Bay 59°40′N; 77°25′W	23 Jun 1945	CM 23175	F	168.3	SK	Good; cross-section of canine saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23176	M	172.0	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23177	M	156.0	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23178	M	152.9	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23179	M	[Imm]	SK	Rostrum fragmentary; baculum saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23180	F	156.0	SK	Good; cross-section of canine saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23181	F	159.3	SK	Good; cross-section of canine saved

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23182	F	152.0	SK	Good
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23183	F	153.3	SK	Good; cross-section of canine saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23184	F	147.6	SK	Good; cross-section of canine saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23185	F	158.3	SK	Good; cross-section of canine saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23186	F	143.7	SK	Good; cross-section of canine saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23187	F	144.9	SK	Good; cross-section of canine saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23188	F	161.8	SK	Good
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23189	F	152.0	SK	Right zygomatic arch broken; cross-section of canine saved
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23190	F	[Imm]	SK	Skull fragmentary
Canada: Quebec; mouth of Kogaluk River, near Kogaluk Bay 59°40′N; 77°10′W	Jun 1945	CM 23191	F	156.6	SK	Good; cross-section of canine saved

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; near mouth of Kogaluk River 59°40′N; 77°25′W	Jun 1945	CM 23192	F	164.3	SS	Good; tanned skin
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23194	?	165.2	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23195	?	159.8	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23196	?	134.8	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23197	?	167.0	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23198	M	158.4	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23199	?	162.6	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23200	?	160.1	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23201	?	149.8	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23202	F	152.1	SK	Cross-section of canine saved; left side of skull damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23203	M	170.6	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23204	M	154.3	SK	Cross-section of canine and baculum saved; braincase cracked; basisphenoid broken
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23205	M	[170]	SK	Skull fragmentary
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23206	?	[Imm]	SK	Skull fragmentary

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23207	M	161.3	SK	Rostrum damaged; numerous teeth missing; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	18 Jun 1945	CM 23208	M	168.8	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23209	F	170.7	SK	Good
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23210	M	161.7	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23211	M	168.5	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23212	M	159.1	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23213	F	148.9	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23214	F	177.8	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23215	F	152.5	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23216	F	170.3	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23217	?	164.7	SK	Good; cross-section of canine saved; numerous loose teeth
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23218	?	[170]	SK	Skull broken
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23219	M	160.1	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23220	M	153.7	SK	Cross-section of canine saved; braincase broken but measurable
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23221	?	154.2	SK	Cross-section of canine saved; right zygomatic arch broken

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23222	?	169.8	SK	Good
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23223	M	159.1	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23224	?	166.5	SK	Good; cross-section of canine saved; numerous loose teeth
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23225	?	165.5	SK	Good; cross-section of canine saved; numerous loose teeth
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23226	M	166.4	SK	Cross-section of canine and baculum saved; zygomatic arches broken
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23227	?	150.6	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23228	?	161.7	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23229	?	161.0	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23230	?	160.6	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23231	M	166.4	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23232	M	173.6	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23233	?	149.2	SK	Cross-section of canine saved; braincase damaged; numerous loose teeth
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23234	?	160.4	SK	Good
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23235	?	[Imm]	SK	Skull fragmentary
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23236	?	150.4	SK	Good; cross-section of canine saved; numerous loose teeth

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23237	?	160.4	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23238	?	153.9	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23239	?	157.7	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23240	?	164.8	SK	Good; cross-section of canine saved; parts of skull have been glued
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23241	?	165.1	SK	Good; cross-section of canine saved; numerous loose teeth
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	27 Jun 1945	CM 23242	?	162.9	SK	Good; cross-section of canine saved; numerous loose teeth
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23243	?	165.5	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23244	?	159.9	SK	Good
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23245	?	171.1	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23246	?	155.0	SK	Cross-section of canine saved; right zygomatic arch broken
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23247	?	166.5	SK	Cross-section of canine saved; rostrum damaged; nasals loose
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23248	?	157.1	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23249	?	154.5	SK	Cross-section of canine saved; right zygomatic arch broken
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23250	?	174.4	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23251	?	162.5	SK	Cross-section of canine saved; zygomatic arches broken

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23252	?	156.3	SK	Cross-section of canine saved; right side of skull damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23253	?	166.5	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23254	?	154.8	SK	Good
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23255	?	[155]	SK	Rostrum broken
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23256	?	161.7	SK	Cross-section of canine saved; braincase damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23257	M	163.6	SK	Cross-section of canine and baculum saved; left bulla damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23258	?	150.3	SK	Cross-section of canine saved; zygomatic arches damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23259	?	180.7	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23260	?	157.3	SK	Cross-section of canine saved; braincase cracked
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23261	M	143.7	SK	Cross-section of canine and baculum saved; left zygomatic arch and right side of rostrum damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23262	?	168.0	SK	Rostrum damaged; question whether both rami belong to this specimen
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23263	?	163.6	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23264	?	143.8	SK	Cross-section of canine saved; zygomatic arches broken; left bullar region damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23265	?	153.4	SK	Cross-section of canine saved; left zygomatic arch broken

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23266	?	156.8	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23267	?	158.6	SK	Good
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23268	?	164.4	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23269	M	159.3	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23270	?	155.5	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23271	M	159.8	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23272	M	154.5	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23273	M	165.6	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23274	M	159.7	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23275	?	152.5	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23276	?	152.5	SK	Good
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23277	M	170.7	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23278	?	171.3	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23279	?	162.0	SK	Cross-section of canine saved; left zygomatic arch broken
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23280	?	155.4	SK	Good; cross-section of canine saved

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23281	?	158.2	SK	Left bullar region damaged
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23282	?	166.7	SK	Good; cross-section of canine saved
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23283	M	154.4	SK	Cross-section of canine and baculum saved; right zygomatic arch broken; several loose teeth
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	28 Jun 1945	CM 23284	?	[Imm]	SK	Skull fragmentary
Canada: Quebec; mouth of Kogaluk River 59°40′N; 77°25′W	2 Jul 1945	CM 23285	F	161.1	SS	Cross-section of canine saved; right bullar region damaged; [3 yrs old]; tanned skin
Canada: Quebec; mouth of Kogaluk River 59°40′N; 77°25′W	2 Jul 1945	CM 23286	F	[Ad]	SS	Skull fragmentary; tanned skin
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	6 Jul 1945	CM 23287	?	[Ad]	SK	Skull fragmentary
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	6 Jul 1945	CM 23288	?	162.5	SK	Good; cross-section of canine saved
Canada: Quebec; 6 mi S of mouth Kogaluk River 59°40′N; 77°25′W	2 Jul 1945	CM 23289	?	159.9	SS	Good but skull may not match skin; cross-section of canine saved; tanned skin
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	1945	CM 23290	M	147.0	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	1945	CM 23291	M	156.9	SK	Good; cross-section of canine and baculum saved
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	1945	CM 23292	M	[Imm]	SK	Skull fragmentary; baculum saved

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	1945	CM 23293	?	[Imm]	SK	Skull fragmentary
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	1945	CM 23294	?	?	SO	Tanned skin
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	1945	CM 23295	?	?	SO	Tanned skin
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	1945	CM 23296	?	?	SO	Tanned skin
Canada: Quebec; vicinity of Povungnituk Post 59°40′N; 77°30′W	1945	CM 23297	?	?	SO	Tanned skin
Canada: Ontario; Moose River	Spring 1945	CM 23299	?	?	SO	Tanned skin
Canada: Quebec; Povungnituk Post 59°40′N; 77°30′W	1945	CM 23303	?	?	SO	Tanned skin
Canada: Ontario; Albany Post of Hudson Bay Company	May 1946	CM 30448	?	[130]	SS	Braincase damaged; tanned skin
Canada: Northwest Territories; Eglinton Fjord, Baffin Island 70°40′N; 69°50′W	22 Apr 1972	CM 66769	F	170.6	SK	Left side of rostrum and right side of braincase damaged
Canada: Northwest Territories; Eglinton Fjord, Baffin Island 70°40′N; 69°50′W	24 Apr 1972	CM 66770	M	[170]	SK	Rostrum fragmentary; baculum saved
Phoca sibirica						
USSR: Siberia; Lake Baikal	unknown	CM 61813	?	[130]	SK	Rostrum damaged; some loose teeth
Phoca vitulina concolor						
Canada: Northwest Territories;	20 Apr 1930	CM 6671	M	145.9	SK	Good

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Southampton Island, Bear Island Floe						
Canada: Northwest Territories; Belcher Islands, Freshwater Lake	11 Oct 1937	CM 13161	?	[Imm]	SS	Skull fragments saved; tanned skin
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Kasegalik Lake 55°58′N; 79°20′W	15 Jul 1937	CM 15217	F	?	SO	Tanned skin
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Kasegalik Lake 55°58′N; 79°20′W	30 Jun 1938	CM 15218	F	?	SB	Skull fragmentary; tanned skin
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Kasegalik Lake 55°58′N; 79°20′W	30 Jun 1938	CM 15219	F	[Imm]	SB	Skull fragmentary; tanned skin; young of CM 15218
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Kasegalik Lake 55°58′N; 79°20′W	30 Jun 1938	CM 15220	F	[Imm]	SB	Skull fragmentary; tanned skin
Canada: Northwest Territories; Belcher Islands, Flaherty Island, Kasegalik Lake 55°58′N; 79°20′W	19 Jun 1938	CM 15221	F	[Ad]	SS	Braincase broken; tanned skin; some limb bones saved
Canada: Quebec; La Tabatiere 50°50′N; 58°57′W	1 Jul 1939	CM 17679	M	?	SS	Skull fragmentary; tanned skin
Canada: Quebec; NE of Great Whale River, Seal Lake	1938–39	CM 17744	?	?	SO	Tanned skin
Canada: Newfoundland; Lab-	29 Jun 1939	CM 17848	?	156.8	SK	Good

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
rador, Straits of Bell Isle, Battle Harbor 52°16′N; 55°35′W						
Canada: Newfoundland; Labrador, Northwest River, Hamilton Inlet 54°18′N; 57°42′W	29 Aug 1939	CM 17849	?	154.4	SK	Rostrum damaged
Canada: Quebec; La Tabatiere 50°50′N; 58°57′W	23 Dec 1939	CM 18698	F	?	SO	Tanned skin
Canada: Quebec; Gulf of St. Lawrence, La Tabatiere 50°50′N; 58°57′W	1939–40	CM 18716	F	165.8	SK	Skull very fragile; right zygomatic arch and bullar region damaged
Canada: Northwest Territories; Belcher Islands 56°15′N; 79°15′W	Spring 1940	CM 18745	F	185.3	SS	Skull broken and glued in several places; tanned skin
Canada: Northwest Territories; Belcher Islands 56°15′N; 79°15′W	Spring 1940	CM 18746	M	?	SS	Skull fragmentary; tanned skin
Canada: Northwest Territories; Belcher Islands 56°15′N; 79°15′W	Spring 1940	CM 18747	M	[Imm]	SS	Skull fragmentary; tanned skin
Canada: Northwest Territories; Belcher Islands 56°15′N; 79°15′W	Spring 1940	CM 18748	F	150.1	SS	Good; tanned skin
Canada: Northwest Territories; Belcher Islands, Flaherty Island 56°58′N; 79°20′W	11 Aug 1940	CM 19445	F	[Ad]	SB	Skull fragmentary; tanned skin
Canada: Quebec; Rimouski Co., Trois Pistoles	28 Jun 1943	CM 21613	M	175.4	SK	Skull damaged and glued
Canada: Quebec; Rimouski Co., Trois Pistoles	28 Jun 1943	CM 21614	F	146.1	SK	Skull damaged and glued

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Phoca vitulina mellonae						
Canada: Quebec; Upper Seal Lake, 200 mi NE Great Whale River 56°N; 73°10′W	Summer 1937	CM 15211	F	?	SO	Trapper's tanned skin
Canada: Quebec; Upper Seal Lake, 200 mi NE Great Whale River 56°N; 73°10′W	Summer 1936	CM 15212	M	?	SO	Trapper's tanned skin
Canada: Quebec; Atchiguanipish River, Richmond Gulf, 125 mi NE Cairn Island 56°30′N; 74°30′W	22 Mar 1938	CM 15213	F	[Ad]	SB*	Skull broken and glued; postcranial skeleton missing, tanned skin
Canada: Quebec; Atchiguanipish River, Richmond Gulf, 125 mi NE Cairn Island 56°30′N; 74°30′W	22 Mar 1938	CM 15214	M	97.0	SB	Right bullar region broken; tanned skin; young of CM 15213
Canada: Quebec; Atchiguanipish River, Richmond Gulf, 125 mi NE Cairn Island 56°30′N; 74°30′W	23 Mar 1938	CM 15215	M	[184]	SB	Holotype: Doutt, 1942; tanned skin; skull broken and partially glued; locality on original tag differs from published locality which is Quebec; about 90 mi E Richmond Gulf, Lower Seal Lake 56°30′N; 74°30′W
Phoca vitulina richardii						
United States: Washington; Skagit Co., Laconner 48°22′N; 122°29′W	29 May 1940	CM 18738	F	194.7	SB	Good; tanned skin
United States: Washington; Skagit Co., Laconner 48°22′N; 122°29′W	29 May 1940	CM 18739	F	[Imm]	SN	Skull fragmentary; teeth just beginning to erupt
United States: Alaska; near Craig, Prince of Wales Island 55°40′N; 133°W	15 Apr 1965	CM 40582	?	?	SO	Tanned skin

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
United States: Alaska; Colville River	1958–59	CM 51985	M	214.6	SK	Both zygomatic arches broken; numerous loose teeth
United States: Alaska; Yakutat 59°29′N; 139°49′W	May–Jun 1954	CM 57626	?	187.7	SS	Good; tanned skin
United States: Alaska; Yakutat 59°29′N; 139°49′W	May–Jun 1954	CM 57627	?	179.2	SS	Tanned skin; left zygomatic arch damaged
United States: Alaska; Yakutat 59°29′N; 139°49′W	May–Jun 1954	CM 57628	?	189.6	SS	Good; tanned skin
United States: Alaska; Alexander Archipelago, Kuiu Island, Pillar Bay 56°40′N; 134°W	6 May 1967	CM 63102	M	[160]	SK	Skull fragmentary
Phoca vitulina vitulina						
North Atlantic: North Sea	unknown	CM 1741	F	[Ad]	SK*	On exhibit
North Atlantic: North Sea	unknown	CM 1744	?	[Ad]	SN*	Mounted, on exhibit
Phoca vitulina						
Locality unknown*	unknown	CM 57428	?	176.4	SN*	Good; postcranial skeleton missing; zoo specimen
Locality unknown*	18 Sep 1950	CM 61341	F	151.1	SB	Good; zoo specimen
***Phoca* species**						
Canada: Northwest Territories; Hudson Bay	unknown	CM 10822	?	[Imm]	SO	Mounted skin
Canada: Northwest Territories; Belcher Islands 56°15′N; 79°15′W	unknown	CM 15306	M	?	OT	4 bacula
CYSTOPHORINAE						
Cystophora cristata						
United States: Pennsylvania; Philadelphia Co., in Delaware River near Bristol	5 Sep 1951	CM 61355	F	177.0	SB	Good; tanned skin

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
SIRENIA						
TRICHECHIDAE						
Trichechus inunguis						
Brazil: Amazonas; on Rio Yavari, near Benjamin Constant* 04°23'S; 69°59'W	Oct 1970	CM 59579	M	[Imm]	SN	Braincase damaged; zoo specimen
Brazil: Amazonas; on Rio Yavari, near Benjamin Constant* 04°23'S; 69°59'W	16 Mar 1983	CM 79986	M	307	SN	Good; zoo specimen; originally collected June 1967
Trichechus manatus latirostris						
United States: Florida; Dade Co., Miami	about 1912	CM 17519	?	[307]	SK	Damaged to bullar region
United States: specific locality unknown	unknown	CM 18125	?	[313]	SN	Damaged to bullar region; most teeth missing
United States: specific locality unknown	unknown	CM 18126	?	357.5	SN	Damaged to bullar region
United States: Florida; Dade Co., Miami	unknown	CM 18752	?	[Ad]	BM*	Cast on exhibit
United States: Florida; Dade Co., Miami Harbor	22 Mar 1940	CM 19411	M	[315]	SN	Basisphenoid region destroyed
United States: Florida; specific locality unknown	1925	CM 21567	?	[Imm]	SN*	Cranium missing
United States: Florida; Brevard Co., west shore Indian River, Delespine 28°29'N; 80°46'W	23 Jan 1981	CM 77798	M	[Imm]	SN	Braincase broken
United States: Florida; Brevard Co., west shore Indian River, Delespine 28°29'N; 80°46'W	23 Jan 1981	CM 77799	M	[Imm]	SN	Braincase broken

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
United States: Florida; Brevard Co., west shore Indian River, Delespine 28°29′N; 80°46′W	4 Feb 1981	CM 77800	F	[Imm]	SN	Braincase broken
United States: Florida; Brevard Co., north bank of Barge Canal, near Sykes Creek, Merritt Island 28°24′N; 80°42′W	20 Aug 1980	CM 77801	F	347.1	SN	Good
United States: Florida; Brevard Co., Port Canaveral 28°24′N; 80°38′W	20 Aug 1980	CM 77802	F	[Ad]	SN	Braincase broken
United States: Florida; Brevard Co., Port Canaveral Lock 28°24′N; 80°37′W	15 Jun 1980	CM 77803	F	[Imm]	SN	Braincase broken
United States: Florida; Brevard Co., west shore Banana River, Surfside Estates 28°23′N; 80°40′W	30 Apr 1981	CM 77804	F	382.5	SN	Good
United States: Florida; Brevard Co., Banana River, Cocoa Beach 28°18′N; 80°37′W	9 Jul 1980	CM 77805	M	344.8	SN	Good
United States: Florida; Brevard Co., west shore Banana River, Merritt Island 28°14′N; 80°39′W	2 Sep 1980	CM 77806	F	[Ad]	SN	Braincase broken
United States: Florida; Brevard Co., north side Spoil Island, Indian River, Grant 27°55′N; 80°31′W	26 Mar 1980	CM 77807	M	[Imm]	SN	Braincase broken
United States: Florida; Brevard	26 Mar 1980	CM 77808	F	[Ad]	SN	Braincase broken

Catalog of Marine Mammals—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Co., west shore Indian River, 1 km N Sebastian River Bridge 27°52'N; 80°29'W						
United States: Florida; Brevard Co., north shore Sebastian Creek, 0.5 km W Hwy 1 Bridge 27°51'N; 80°29'W	17 May 1981	CM 77809	F	[Imm]	SN	Skull fragmentary
United States: Florida; Duval Co., north shore St. Johns River, Blount Island 30°23'N; 81°32'W	13 May 1981	CM 77810	M	347.2	SN	Good
United States: Florida; Duval Co., north shore St. Johns River, Jacksonville 30°19'N; 81°39'W	3 Feb 1981	CM 77811	M	352.3	SN	Good
United States: Florida; Duval Co., east shore St. Johns River, 1.5 km N Goodby Creek, Jacksonville 30°13'N; 81°37'W	3 Feb 1981	CM 77812	F	[Imm]	SN	Braincase broken
United States: Florida; Levy	3 Jul 1980	CM 77813	F	364.6	SN	Braincase damaged

CATALOG OF MARINE MAMMALS—*Continued.*

Locality	Date collected	Catalog number	Sex	CBL or age	Nature of specimen	Condition of specimen and comments
Co., west of mouth of East Pass, Suwanee River 29°17′N; 83°06′W						
United States: Florida; Levy Co., Inglis Lock, Florida Barge Canal, Inglis 29°01′N; 82°37′W	3 Nov 1980	CM 77814	F	[Ad]	SN	Braincase damaged
United States: Florida; Nassau Co., west bank Jolly River at confluence with St. Mary's River 30°43′N; 81°30′W	30 Jan 1981	CM 77815	F	[Imm]	SN	Braincase damaged
United States: Florida; Pinellas Co., 3.2 km E of west bank Old Tampa Bay, Clearwater 27°58′N; 82°40′W	17 Oct 1980	CM 77816	M	[Imm]	SN	Braincase damaged
United States: Florida; Putnam Co., east shore St. John's River, S San Mateo 29°36′N; 81°35′W	7 May 1981	CM 77817	M	382.9	SN	Good
Trichechus senegalensis						
Cameroun: 10 mi W Edea	1942	CM 42762	?	351.3	SK	Bullar regions damaged

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TAXONOMIC AND DISTRIBUTIONAL NOTES ON BATS FROM KENYA

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Abstract

Taxonomic and distributional comments are given for six species in three families of bats from Kenya. Two species (*Hipposideros camerunensis* and *Tadarida russata*) are reported from Kenya for the first time.

Introduction

During field work on the systematics of small mammals in Kenya from September to November 1985, a number of bats were collected

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Submitted 5 February 1986.

in various parts of Kenya. Some of these specimens add substantially to the knowledge of the distribution of bats in Kenya and East Africa while others were of taxonomic interest. This paper summarizes these data on six species of bats in three families.

MATERIALS AND METHODS

All specimens reported herein were captured with mist nets set in the normal manner. Cranial and forearm measurements were taken by means of dial calipers and are given in millimeters. All specimens are deposited in the Carnegie Museum of Natural History, Pittsburgh (CM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); and National Museums of Kenya, Nairobi (NMK). Coordinates for localities are listed only for the first reference to the locality.

ACCOUNT OF SPECIES

Family Hipposideridae

Hipposideros camerunensis Eisentraut, 1956

Hipposideros camerunensis Eisentraut, 1956. Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere, 84:526. Near Buea, Cameroun.

Records (1).—KENYA: Western Prov., Kakamega Dist., Kakamega Forest Station, 3-½ km E Kakamega (0°14′N, 34°52′E) (1 CM).

Measurements.—Selected measurements of an adult female, length of forearm, 74.3; condylocanine length, 24.9; zygomatic breadth, 15.7; alveolar length of maxillary toothrow, 9.3; and greatest crown breadth of upper molar toothrows, 11.1.

Remarks.—*Hipposideros camerunensis* is a rare, large forest species of *Hipposideros* resembling closely the more common *H. cyclops.* It has been reported from the type locality, Buea, Cameroun, and elsewhere only from Shabunda, eastern Zaire (2°42′S, 21°20′E) (Hill, 1963: 81). On 5 November a single adult female was taken in the bottom shelf of a mist net placed along a cleared trail in the Intermediate Evergreen Forest near the Forest Guest House at the Kakamega Forest Station. This specimen from the Kakamega Forest extends the range of this species about 900 kilometers to the northeast and is the first record of occurrence for Kenya. For a description of the capture area, see Zimmerman (1972).

In size, the Kenyan female agrees well with a series of Cameroun specimens in Carnegie Museum and with the measurements given by Hill (1963:80).

Hipposideros cyclops (Temminck, 1853)

Phyllorhina cyclops Temminck, 1853. Esquisses Zool. sur la Cote de Guine, p. 75. Boutry River, Ghana.

Records (2).—KENYA: Coastal Prov. Kwale Dist., Shimba Hills Nature Reserve, Makandara Picnic Site, 7 km S, 8 km W Kwale (4°15′S, 39°23′E) (2 CM).

Measurements.—Selected measurements of a male and female, respectively, length of forearm, 66.8, 63.7; condylocanine length, 27.1, 27.2; zygomatic breadth, 14.8, 15.2; alveolar length of maxillary toothrow, 8.4, 8.7; and greatest crown breadth of upper molar toothrows, 10.4, 10.6.

Remarks.—*Hipposideros cyclops* is known currently from two localities in western Kenya. Hayman (1935:48) reported this species from the Yala River and later Harrison (1961:290) listed Kaimosi. The species is not known from Tanzania.

On 14 October, two adult individuals of *H. cyclops* were captured in a mist net set in the cleared Makandara Picnic Site in the Shimba Hills Nature Reserve. The net was set parallel and adjacent to the forest edge. These two specimens extend the range of this species to extreme southeastern Kenya. The geographic range of this species probably reaches this region of Kenya along a corridor of forest blocks extending from southwestern Tanzania to northeastern Kenya. This species should be captured in appropriate forests in this Tanzanian corridor after careful and concentrated mist netting.

Family Vespertilionidae

Scotophilus nux Thomas, 1904

Scotophilus nux Thomas, 1904. Ann. Mag. Nat. Hist., (7) 4:355. Gambage, Ghana.

Records (4).—KENYA: Western Prov., Kakamega Dist., Kakamega Forest Station, 3½ km S, 12 km E Kakamega (2 CM, 1 MCZ, 1 NMK).

Measurements.—Selected external measurements of four females, length of forearm, 57.8, 57.6, 54.5, 55.3.

Remarks.—*Scotophilus nux* has been reported in Kenya only from 8 km SE Kakamega (Aggundey and Schlitter, 1984:138). The eight specimens from Kenya referred to by Robbins (1983:23) are from this locality. Both localities refer to the Kakamega Forest Station. Four additional specimens of this dark-brown colored forest species of *Scotophilus* were netted in the forest adjacent to the station and in the cleared areas around the station complex on 5 and 7 November. These specimens further verify the occurrence of this species in the forests of western Kenya. Specimens of *Scotophilus dinganii* were not taken together with *S. nux* at this locality, but the former species was taken in more heavily disturbed areas near the station complex and seems to be the most common species of *Scotophilus* taken in Kenya.

Kerivoula argentata argentata Tomes, 1861

Kerivoula argentata Tomes, 1861. Proc. Zool. Soc. London, 1861:32. Otjoro, Namibia.

Records (1).—KENYA: Coastal Prov., Kwale Dist., Shimba Hills Nature Reserve, 5 km S, 1 km W Kwale (4°13′S, 39°27′E) (1 CM).

Measurements.—Selected measurements of an adult male, length of forearm, 35.9; condylobasal length, 13.9; and alveolar length of maxillary toothrow, 5.9.

Remarks.—*Kerivoula argentata* occurs primarily in southern Africa and ranges northward as far as Kenya. Specimens of *Kerivoula* are seldom captured and there is a paucity of records for this species in eastern Africa. It has been reported from Liwale, in southern Tanzania (Harrison, 1958:95), an unspecified locality in Uganda (Kingdon, 1974: 304), and from Kibwezi, southeastern Kenya (Aggundey and Schlitter, 1984:139). A single adult male was taken on 12 October in a mist net set under the trees in the central clearing surrounding the bandas at the overnight facilities in Shimba Hills Nature Reserve. This specimen constitutes the second locality record of the species for Kenya and only the fourth for this region encompassing the northern part of the range of the species.

The Shimba Hills specimen exhibits the normal white-tipped orange-rufous dorsal coloration and the somewhat lighter colored ventral fur. Mensurally it fits within the size range of southern African examples of the species.

Family Molossidae

Tadarida* (*Chaerephon*) *russata (J. Allen, 1917)

Chaerephon russata J. Allen, 1917. Bull. Am. Mus. Nat. Hist., 37:458. Medje, Zaire.

Records (3).—Kenya: Rift Valley Prov., Naivasha Dist., Hell's Gate Canyon, 20 km S, 14 km W Naivasha (0°54′S, 36°19′E) (1 CM, 1 MCZ, 1 NMK).

Measurements.—Selected measurements of two males and one female, respectively, length of forearm, 45.4, 46.2, 46.2; condylobasal length, 18.0, 18.0, 17.1; zygomatic breadth, 11.2, 11.9, 11.2; alveolar length of maxillary toothrow, 7.2, 7.1, 6.7; and greatest crown breadth of upper molar toothrows, 9.0, 8.7, 8.3.

Remarks.—The taxonomic and distributional status of *Tadarida russata* was reviewed by Peterson (1971) and Fenton and Peterson (1972). This species is presently known from Ghana, Cameroun, and the type locality in northeastern Zaire (Fenton and Peterson, 1972:20). On 30 September, two adult males were captured in a mist net set across the floor of the northern end of Hell's Gate Canyon. On 3 October a single adult female was taken in a net set in the same area. These three specimens comprise the first record of the species for Kenya and extend the range of the species more than 1000 kilometers to the southeast.

The Kenyan specimens of this species agree in color of pelage with three Cameroun examples in Carnegie Museum. However, mensurally they appear to be appreciably larger than these examples and the measurements given in Fenton and Peterson (1972:21, 22). When more specimens from throughout the geographic range of this species become available, the Kenyan population may prove to be significantly larger and worthy of subspecific recognition.

Tadarida* (*Tadarida*) *fulminans (Thomas, 1903)

Nyctinomus fulminans Thomas, 1903. Ann. Mag. Nat. Hist., (7)12:501. Fianarantsoa, eastern Betsileo, Madagascar.

Records (1).—Kenya: Rift Valley Prov., Nakuru Dist., Njoro River, 3 km S, 3 km W Nakuru (0°19′S, 36°03′E) (1 CM).

Measurements.—Selected measurements of an adult male, length of forearm, 56.7; condylobasal length, 21.2; zygomatic breadth, 13.4; alveolar length of maxillary toothrow, 8.3; and greatest breadth of upper molar toothrow, 9.3.

Remarks.—The first record of occurrence for *Tadarida fulminans* in Kenya was a specimen from Nairobi reported by Harrison (1960:74). This species occurs primarily in southern Africa (Smithers, 1983) and reaches the northern extent of its range in Kenya. On 8 October a single adult male was captured in the gorge of the Njoro River southwest of Nakuru. The specimen was taken in a mist net set across shallow water and among trees on the steep bank of the watercourse.

ACKNOWLEDGMENTS

A research permit (CAB 13/001/11C38/17) allowing us to do field studies in Kenya was received from the Office of the President. We thank Mrs. C. A. Mwango and Miss L. A. Gwiyo and their staff for their efforts and courtesy in processing this permit on our behalf and the Secretary, National Council for Science and Technology, and his colleagues for approving our research project.

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RESULTS OF THE ALCOA FOUNDATION-SURINAME EXPEDITIONS. XI. BATS OF THE GENUS *MICRONYCTERIS* (MAMMALIA: CHIROPTERA) IN SURINAME

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Abstract

Of the 10 recognized species in the genus *Micronycteris,* seven species (*brachyotis, daviesi, hirsuta, megalotis, minuta, nicefori,* and *sylvestris*) have been reported to occur in Suriname. *Micronycteris daviesi* is easily distinguished from the other species by its large size (forearm over 50 mm) and massive dentition. The next largest species (forearm over 43 mm)—*M. hirsuta*—is distinguished by having the upper inner incisors separated at the base but in contact at the tip and having lower incisors that are high and wedged between canines so that the canines are in contact behind the incisors.

Micronycteris sylvestris has dorsal pelage that is tricolored. The upper incisors of this species are similar in length to the canines and the first upper premolar possesses accessory cusps.

The other four species form two species pairs. *Micronycteris megalotis* and *minuta* are the smallest members of the genus in Suriname. They can be distinguished from each other by the more deeply notched interauricular band in *minuta* and by the first upper premolar being smaller than the second premolar in *minuta* but of about equal size in *megalotis.*

Micronycteris brachyotis, which was not encountered during our work in Suriname, has short ears (less than 16 mm from notch) and lacks the faint gray line usually present on the lower back of specimens of *M. nicefori.* These species are also distinguished by

Submitted 24 April 1986.

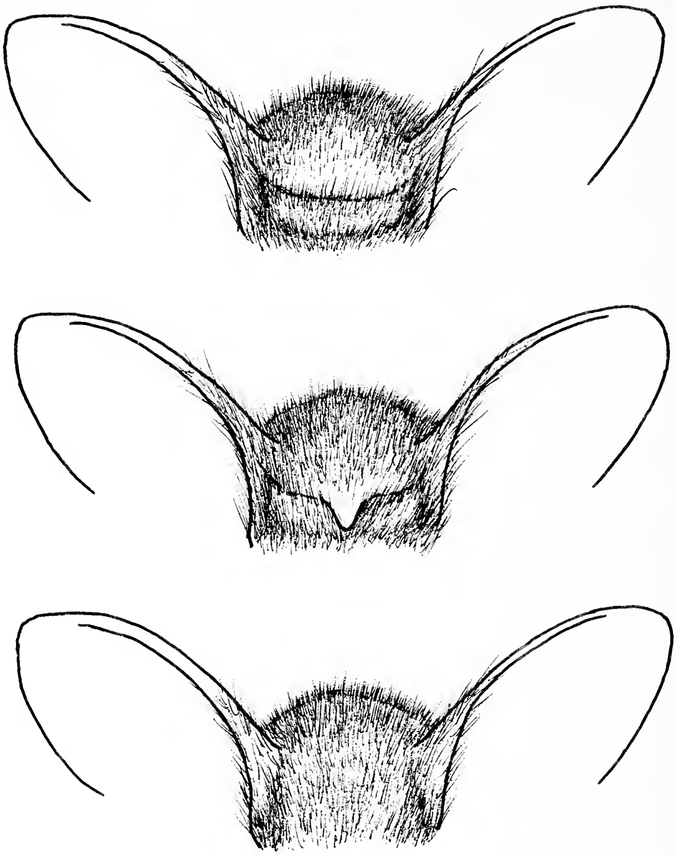

Fig. 1.—Stylistic representation of variation in the interauricular band of members of the genus *Micronycteris*. Upper, interauricular band complete (exemplified by *M. hirsuta*). Middle, interauricular band deeply notched in middle (*M. minuta*). Lower, interauricular band absent (*M. nicefori*). Not to scale.

their upper incisors, which are chisel-shaped and in line with the canines in *brachyotis*, but project forward and, therefore, are out of line with the canines in *nicefori*.

INTRODUCTION

The genus *Micronycteris* is a member of the subfamily Phyllostominae of the New World leaf-nosed bat family Phyllostomidae. *Micronycteris* is currently recognized as containing 10 small- to medium-sized species of bats. The genus was reviewed by Andersen (1906) and Sanborn (1949).

The genus is divided into six subgenera based primarily upon the work of Sanborn (1949). We suggest that this level of classification be carefully examined in the future because the genus seems oversplit at the subgeneric level. Andersen (1906) recognized seven species divided into two genera (*Micronycteris* and *Glyphonycteris*), whereas Sanborn (1949) recognized 10 species in one genus. Subsequent to Sanborn's work, one species (*platyceps*) was placed as a junior synonym of *brachyotis* (Goodwin and Greenhall, 1961) and another species, *daviesi,* was described in a separate genus (*Barticonycteris*; Hill, 1964), but was later placed into *Micronycteris* (Koopman and Cockrum, 1967).

During our field studies in Suriname, six species of the genus *Micronycteris* (*daviesi, hirsuta, megalotis, minuta, nicefori,* and *sylvestris*) were captured. Husson (1978) reported a seventh species (*brachyotis*) from the country. This means that only three of the currently recognized species of *Micronycteris* (*behni, pusilla,* and *schmidtorum*) have not been taken in Suriname. With this large number of species from this complex genus present in such a small geographic area, we have taken the opportunity to gain a better insight into the morphological and ecological relationships of species within the genus.

METHODS AND MATERIALS

Specimens were taken with mist nets and preserved as skins and skulls or in fluid. Field weights were taken with Pesola scales, accurate to 1 g. Measurements of forearm and cranial dimensions were taken with dial calipers accurate to 0.1 mm. Only adult specimens (phalangeal epiphyses completely fused) were measured in this study. Measurements were taken as described by Genoways and Williams (1984). Reproductive condition of the skin and skull specimens was determined by gross dissection in the field, whereas fluid preserved specimens were dissected in the laboratory. Specimens listed in each account were deposited in the Section of Mammals, Carnegie Museum of Natural History.

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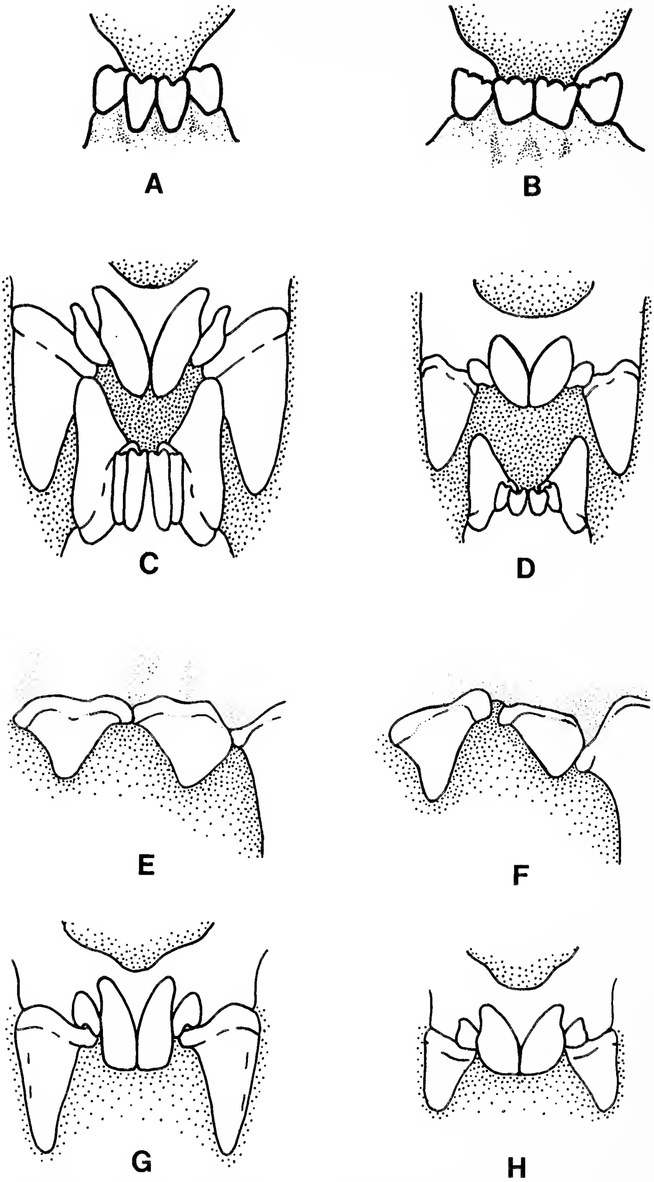

Fig. 2.—Dental characteristics of members of the genus *Micronycteris.* A, lower incisors bifid (exemplified by *M. megalotis*); B, lower incisors trifid (exemplified by *M. sylvestris*). C, upper and lower incisors of *M. hirsuta,* showing long, narrow lower incisors with unexpanded crowns and awl-shaped upper incisors; D, upper and lower incisors of *M. megalotis* showing short lower incisors with expanded crowns. E, upper premolars (P3,

KEY TO THE SPECIES OF *MICRONYCTERIS* IN SURINAME
(see also Medellin et al., 1985)

1. Interauricular band present (possibly notched or not as broad in the middle (Fig. 1A, B); lower incisors bifid (Fig. 2A) 2

1′. Interauricular band not present (Fig. 1C); lower incisors trifid (Fig. 2B) 4

2. Forearm less than 40; greatest length of skull less than 22; lower incisors with expanded crowns (Fig. 2D) 3

2′. Forearm greater than 40; skull more than 22; upper incisors awl-shaped; lower incisors long, narrow, and lacking expanded crown (Fig. 2C); $2n = 30$, $FN = 32$ ....*Micronycteris hirsuta*

3. Calcar longer than foot (claws included); length of interfemoral membrane more than twice the length of tail; band of skin between ears with shallow notch in middle; upper premolars (P3, P4) about the same height (Fig. 2E); $2n = 40$, $FN = 68$ .... *Micronycteris megalotis*

3′. Calcar shorter than foot (claws included); length of interfemoral membrane less than twice the length of tail; band of skin between ears deeply notched in middle (Fig. 1B); first upper premolar (P3) distinctly shorter than second upper premolar (P4) (Fig. 2F); $2n = 28$, $FN = 52$ .... *Micronycteris minuta*

4. First upper incisors similar to canines in length; first upper premolar (P3) having accessory cusps on lingual and posterior margins 5

4′. First upper incisors distinctly shorter and narrower than canines; first upper premolar (P3) lacking accessory cusps, only the main cusps present 6

5. Forearm less than 50; greatest length of skull less than 25; dorsal hair tricolored; two pairs of upper incisors; $2n = 22$, $FN = (40)$ .... *Micronycteris sylvestris*

5′. Forearm greater than 50; greatest length of skull more than 25; dorsal hair brownish throughout; sagittal crest straight; one pair of upper incisors; $2n = 28$, $FN = 52$ .. *Micronycteris daviesi*

6. Length of ear (to notch) less than 16; calcar about the same length as foot; first pair of upper incisors chisel-shaped (Fig. 2G) and in line with canines; second pair of upper incisors

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←

P4) of *M. megalotis* (anterior is to the right), note that premolars of about equal size; F, upper premolars of *M. minuta* (anterior is to the right), note that P3 is distinctly shorter than P4. G, chisel-shaped upper incisors of *M. brachyotis*; H, upper incisors of *M. nicefori* which are nearly as broad as they are tall.

bifid with elongated inner cusp; $2n = 32$, FN = 60 .... *Micronycteris brachyotis*

6′. Length of ear (to notch) greater than 16; calcar shorter than length of foot; faint gray line often present on lower back; first pair of upper incisors not chisel-shaped (Fig. 2H); upper incisors projected forward and out of line with canines; $2n = 28$, FN = 52 .... *Micronycteris nicefori*

GENERIC ACCOUNT

Micronycteris Gray, 1866

1866. *Micronycteris* Gray, Proc. Zool. Soc. London, p. 113, May.

1856. *Schizostoma* Gervais, Mammiferes *in* Castelnau Exped. dans les parties centrales de l'Amer. du Sud . . . pt. 7, p. 38. Type species, *Schizostoma minuta* Gervais. Preoccupied by *Schizostoma* Bronn, 1835, a genus of Mollusca.

1896. *Glyphonycteris* Thomas, Ann. Mag. Nat. Hist., ser. 6, 18:302, October. Type species, *Glyphonycteris sylvestris* Thomas.

1907. *Xenoctenes* Miller, Bull. U.S. Nat. Mus., 57:124, 29 June. Type species, *Schizostoma hirsutum* Peters.

1964. *Barticonycteris* Hill, Mammalia, 28:556, December. Type species, *Barticonycteris daviesi* Hill.

Type species.—*Phyllophora megalotis* Gray, 1842.

Diagnosis.—A genus of small- to medium-sized bats with a well-developed noseleaf and a tail extending only to the middle of the interfemoral membrane. In the subfamily Phyllostominae, the dental formula of i 2(1)/2, c 1/1, p 2/3, m 3/3 is shared only with the genera *Macrotus* and *Vampyrum*. The one species with only one pair of upper incisors is *M. daviesi*. Rostrum not as long as braincase; auditory bullae small; middle lower premolar approximately same size as last lower premolar.

Micronycteris (*Glyphonycteris*) *daviesi* (Hill, 1964)

Specimen examined (1).—SARAMACCA: Raleigh Falls, 1.

The species *M. daviesi* is easily distinguished from other members of the genus *Micronycteris* in Suriname by its large size (Table 1; Figs. 3A, 4A) and massive dentition. This species was originally described as the sole representative of the genus *Barticonycteris* by Hill (1964). Shortly thereafter, Koopman and Cockrum (1967) treated *Barticonycteris* as a synonym of *Micronycteris*. Most recent authors have followed this arrangement (see for example Jones and Carter, 1976), although LaVal (1977) and Hall (1981) are exceptions. Koopman (1978) treated *Barticonycteris* as a subgenus of *Micronycteris*, citing as his reasons that the characteristics of *Barticonycteris* "are simply those of *M.* (*Glyphonycteris*), the subgenus including *sylvestris* and *behni* carried one step further." Hill (1964) had earlier recognized that the closest relatives of *Barticonycteris* were members of *Glyphonycteris*. We agree with these assessments of the relationship of *daviesi* based upon our own studies, but we believe that the relationships of the taxon are represented best by placing it as a member of the subgenus *Glyphonycteris*.

Only one specimen of this rare species was taken during our work in Suriname (Fig. 5). It was an adult male taken on an island in the Coppername River that serves as the headquarters of the Raleigh Falls Nature Reserve. The bat was netted along a trail on the western side of the island, about 200 m northeast of the park headquarters and about 50 m from the river. Vegetation in the area consisted of near-mature lowland rainforest. Our specimen, weighing 18 and with testes measuring 3, was captured on 24 August at about 2000 hours following a short rainstorm. Sixteen other species of bats were taken in this area (Table 2).

Our specimen was found to have a $2n = 28$ and $FN = 52$. The X-chromosome was submetacentric, whereas the Y-chromosome was acrocentric (Honeycutt et al., 1980).

Micronycteris* (*Glyphonycteris*) *sylvestris (Thomas, 1896)

Specimens examined (14).—BROKOPONDO: Brownsberg Nature Park, 8 km S, 2 km W Brownsweg, 14.

Our specimens were the first of this species reported from Suriname (Williams and Genoways, 1980). This taxon can be recognized externally by having tricolored dorsal hair and ears that are about as broad as they are high. Cranially this species resembles *M. daviesi* with upper incisors about the same length as the canines (Figs. 3, 4). Currently *M. sylvestris* is considered to be monotypic (Jones and Carter, 1976), although not enough specimens have been available for a proper analysis of infraspecific variation.

Our 14 specimens were collected from a hollow tree in a mature tropical hardwood forest on the Brownsberg highlands (Fig. 5). The opening to the hollow was located about 3 m above the ground. Eight of the specimens were taken on 24 September and the other six on the following day. Four males weighed 6, 6, 7, and 7; each had testes that measured 3. Eight females had weights ranging from 7.5 to 11 with a mean of 9.3. None of these females evinced gross reproductive activity. Only 10 other species of bats were captured in nets set along trails near the hollow tree (Table 2).

The specimens of *M. sylvestris* from Suriname had a diploid number of 22 and a probable fundamental number of 36. The fundamental number could not be determined with certainty because only females were available for chromosomal analysis. It was supposed that the X-chromosome was biarmed (Honeycutt et al., 1980).

Table 1.—*Forearm and cranial measurements of six species of* Micronycteris *from Suriname.*

Catalog No.	Locality	Sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Mastoid breadth	Postorbital breadth	Length of maxillary toothrow	Breadth across upper molars
	Micronycteris daviesi									
CM 63573	Saramacca: Raleigh Falls	M	53.9	25.8	23.4	12.5	10.8	5.7	10.2	9.0
	Micronycteris hirsuta									
CM 68388	Para: Zanderij	F	44.4	23.6	20.4	11.2	10.2	4.9	8.9	7.1
	Micronycteris megalotis									
CM 63575	Brokopondo: 1½ km W Rudi Kappelvliegveld	M	32.9	18.3	15.7	8.6	8.3	3.9	6.4	5.1
CM 63574	Brokopondo: 1 km W Rudi Kappelvliegveld	M	33.5	17.7	15.4	8.8	8.3	4.1	6.6	5.5
CM 63578	Commewijne: Nieuwe Grond Plantation	M	35.9	19.3	16.4	9.1	8.7	4.0	7.1	5.9
CM 77109	Marowijne: Perica	M	35.3	19.6	16.8	9.4	8.8	4.2	7.4	6.3
CM 68390	Nickerie: Kayserberg airstrip	M	33.9	19.0	16.1	9.0	8.4	4.0	6.8	5.8
CM 63577	Brokopondo: 3 km W Rudi Kappelvleigveld	F	35.5	18.3	16.1	9.1	8.3	3.9	6.6	5.6
	Micronycteris minuta									
CM 63581	Brokopondo: 1 km N Rudi Kappelvliegveld	M	35.5	18.5	15.9	8.5	8.8	4.1	6.6	5.8
CM 63579	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	M	31.3	17.3	15.3	8.5	8.1	4.0	6.5	5.7
CM 76769	Marowijne: 3 km SW Albina	M	33.0	18.4	16.4	8.5	8.8	4.2	6.6	5.7
CM 63584	Saramacca: Voltzberg	M	33.7	18.7	16.6	8.5	8.6	4.1	6.8	5.8
CM 68391	Saramacca: Voltzberg	M	35.4	18.8	16.7	8.8	8.7	4.3	6.6	5.7
CM 63580	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	F	31.8	17.6	—	8.3	8.0	4.1	6.7	5.4
CM 63582	Commewijne: Nieuwe Grond Plantation	F	35.1	18.1	16.1	8.7	8.7	4.2	6.7	5.9
CM 52759	Marowijne: 10 km N, 24 km W Moengo	F	34.3	18.7	16.2	8.8	8.7	4.2	6.8	6.0
CM 63583	Saramacca: Voltzberg	F	34.3	18.5	16.2	8.6	8.8	4.1	6.4	5.8
CM 52760	Suriname: Powaka	F	35.2	18.8	16.2	8.8	8.7	4.2	6.6	5.9
	Micronycteris nicefori									
CM 52761	Marowijne: 10 km N, 24 km W Moengo	M	36.1	20.1	18.0	9.5	8.7	4.3	7.3	6.1
CM 76770	Marowijne: 3 km SW Albina	M	36.9	20.6	18.1	9.2	8.8	4.1	7.2	5.8
CM 76771	Marowijne: Perica	M	37.8	20.7	18.5	9.5	8.7	4.5	7.5	6.0
CM 68648	Nickerie: Kabalebo	M	36.8	20.8	18.5	9.2	8.6	4.4	7.4	6.2

Table 1.— *Continued.*

Catalog No.	Locality	Sex	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Mastoid breadth	Postorbital breadth	Length of maxillary toothrow	Breadth across upper molars
CM 68649	Nickerie: Kabalebo	M	35.3	20.2	18.0	9.4	8.6	4.0	7.1	6.0
CM 63585	Brokopondo: 1 km N Rudi Kappelvliegveld	F	37.3	20.3	18.1	9.1	8.5	3.9	7.1	6.1
CM 63586	Commewijne: Nieuwe Grond Plantation	F	38.6	20.3	18.0	9.2	8.5	3.9	7.2	6.2
CM 76772	Saramacca: Tafelberg, SE side of Arrowhead Basin	F	36.5	20.7	18.6	9.4	8.5	4.1	7.4	5.9
CM 52762	Suriname: Powaka	F	38.0	20.3	18.4	—	8.5	4.0	7.5	6.0
	Micronycteris sylvestris									
CM 63590	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	M	38.6	19.8	17.1	9.6	8.7	4.5	7.4	6.6
CM 63595	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	M	39.2	20.1	17.6	10.0	8.9	4.8	7.8	7.0
CM 63596	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	M	37.0	19.4	17.2	9.7	8.4	4.5	7.7	6.6
CM 63597	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	M	38.3	20.0	17.4	9.8	8.7	4.6	7.8	6.8
CM 63587	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	F	40.8	20.4	18.5	10.1	8.7	4.6	7.9	7.1
CM 63588	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	F	40.6	20.5	18.1	10.2	8.9	4.7	7.8	6.8
CM 63589	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	F	42.7	19.7	17.7	9.8	9.1	4.6	7.6	7.0
CM 63591	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	F	39.3	19.9	17.8	10.2	9.0	4.7	7.9	6.7
CM 63592	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	F	41.9	20.5	18.0	10.2	8.9	4.6	7.9	6.9
CM 63593	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	F	39.9	19.6	17.0	10.9	9.0	4.6	7.3	6.8
CM 63594	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	F	40.0	20.0	17.9	10.2	9.1	4.7	7.8	6.9
CM 63598	Brokopondo: Brownsberg Nature Park 8 km S, 2 km W Brownsweg	F	39.4	19.7	17.2	10.0	8.8	4.7	7.5	6.7

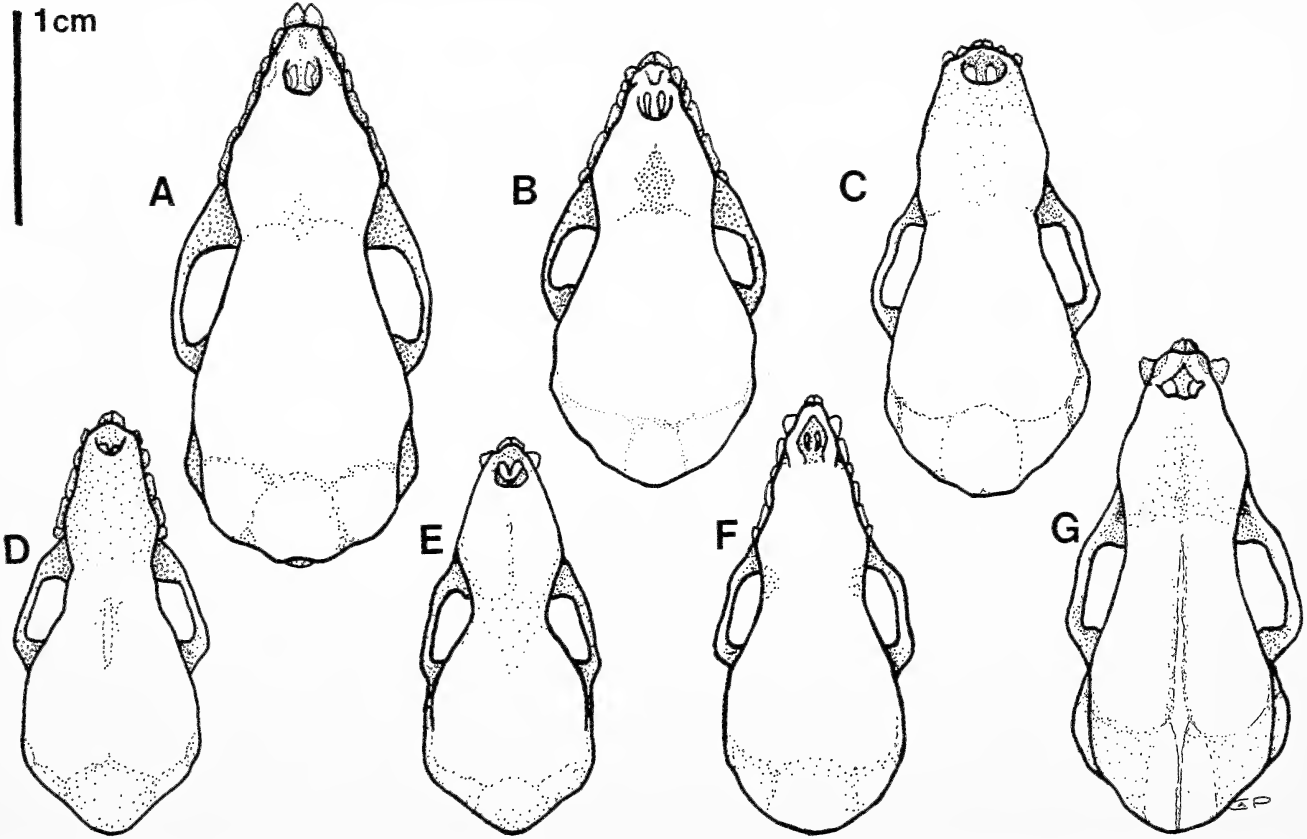


Fig. 3.—Dorsal view of the crania of the seven species of *Micronycteris* occurring in Suriname. A, *M. daviesi* (CM 63573); B, *M. sylvestris* (CM 63597); C, *M. brachyotis* (from Trinidad); D, *M. megalotis* (CM 68390); E, *M. minuta* (CM 63584); F, *M. nicefori* (CM 76771); G, *M. hirsuta* (CM 68388).

Micronycteris* (*Lampronycteris*) *brachyotis (Dobson, 1879)

Previous record.—BROKOPONDO: Gros (about 100 km S Paramaribo on railroad from Paramaribo to the interior) [5°06′N, 55°15′W] (Husson, 1978).

Husson (1978) first reported this species from Suriname based upon six males from Gros (Fig. 5). The specimens were taken from an old goldmine in a savannah area. We did not encounter this species during our work in Suriname.

Most of the characteristics of the specimens listed by Husson—forearm 40.2 to 42.9, no interauricular band, and second phalanx of third digit much longer than first—seem to match *M. brachyotis* closely; however, the Suriname specimens had the fourth metacarpal the shortest, whereas in *brachyotis* the fifth metacarpal is the shortest. The exact meaning of this difference must await further examination of these specimens.

Goodwin and Greenhall (1961) were the first to recognize that *M. platyceps,* described by Sanborn in 1949, was a junior synonym of the long described, but poorly known, *M. brachyotis.*

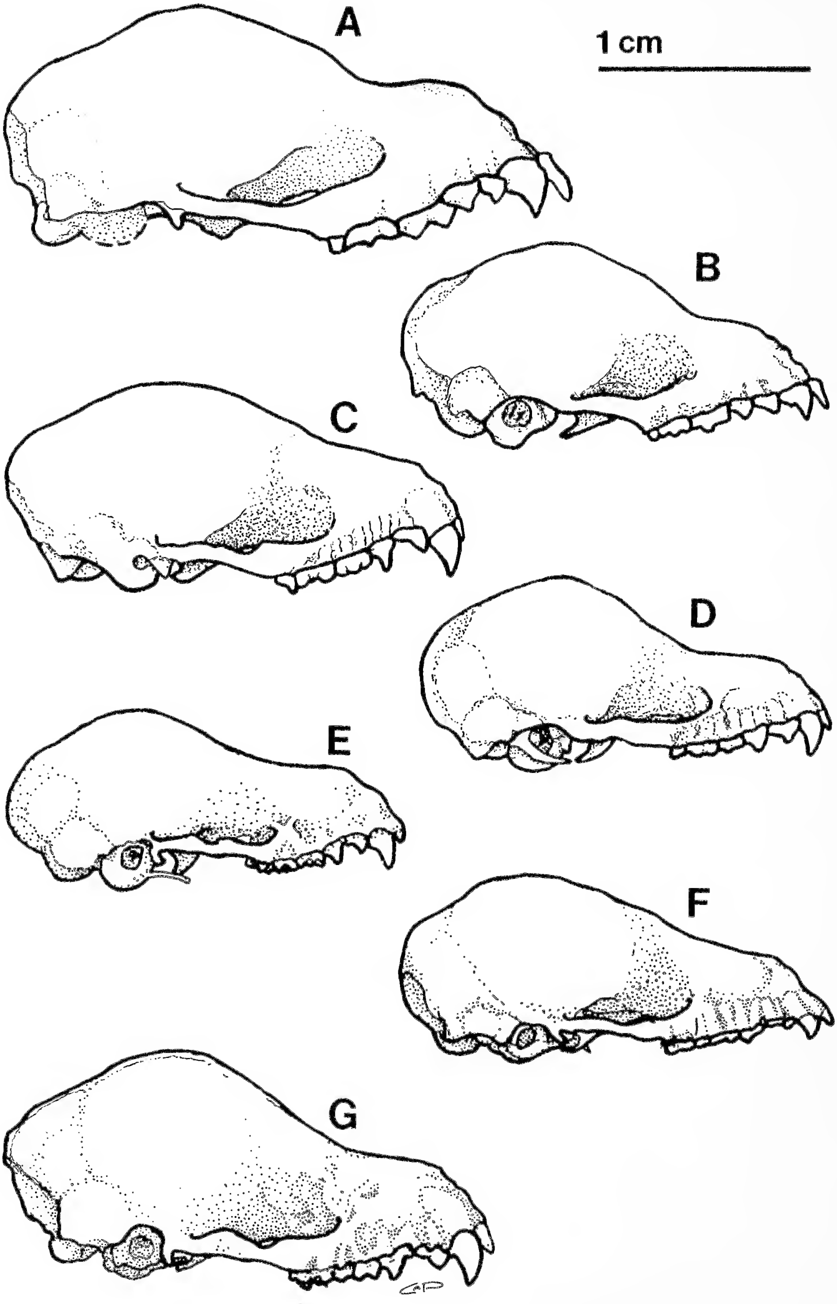
Micronycteris* (*Micronycteris*) *megalotis megalotis (Gray, 1842)

Specimens examined (12).—BROKOPONDO: 1 km N Rudi Kappelvliegveld, 1; 1½ km W Rudi Kappelvliegveld, 1; 3 km SW Rudi Kappelvliegveld, 2; Brownsberg Nature Park, 3 km S, 20 km W Afobakka, 1. COMMEWIJNE: Nieuwe Grond Plantation, 1. MAROWIJNE: Oelemarie, 1; Perica, 2. NICKERIE: Kayserberg airstrip, 2. PARA: Zanderij, 1.

Previous records (Husson, 1978).—SURINAME: Plantation Kwatta, near Rijweg; Paramaribo. No specific district or locality.

Among Surinamese representatives of the genus *Micronycteris, M. megalotis* is distinguished by the presence of an interauricular band which is only slightly notched, a broad interfemoral membrane, upper premolars (P3, P4) about the same size (Fig. 2E), and bifid lower incisors (Fig. 2A). The species is polytypic with the nominate subspecies occurring in Suriname and surrounding areas (Jones and Carter, 1976).

M. megalotis has been reported from localities in Suriname previously and these together with our records indicate that the species may be expected in most forested situations in the country (Fig. 6). Many of the capture sites were described by the collectors as being in mature tropical forest or lowland tropical rainforest. However, at the Nieuwe Grond Plantation a specimen was taken in a net set along an orchard path that was bordered on one side by a canal and on the other by alternating rows of citrus trees and secondary tropical vegetation. At Perica, the specimens were netted on the edge of secondary growth forest. *M. megalotis* was taken at more than half of its nine capture sites with six species (Table 2)—*Saccopteryx bilineata, S. leptura, Tonatia bidens, Carollia perspicillata, Rhinophylla pumilio,* and the larger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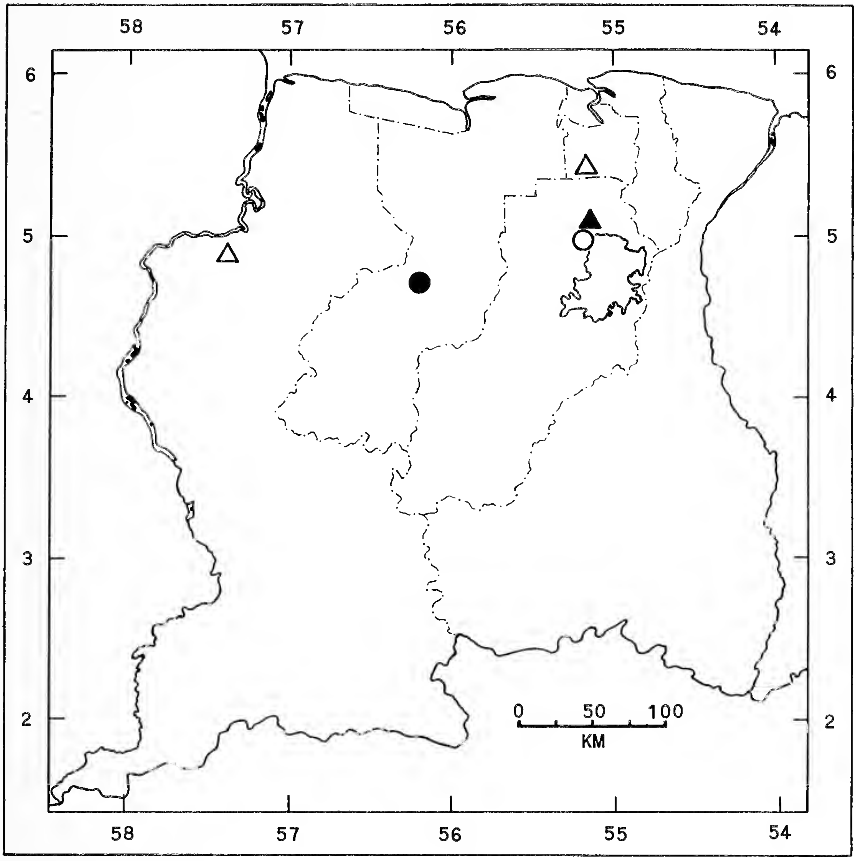

Fig. 5.—Map of the geographic distribution of four species of *Micronycteris* in Suriname. Closed circle, *M. daviesi*; open circle, *M. sylvestris*; closed triangle, *M. brachyotis*; open triangle, *M. hirsuta.*

species of *Artibeus.* It was also taken together with two other species of the genus—*minuta* and *nicefori*—although only at one and two sites, respectively.

Our 12 specimens consist of 10 males and two females. Testes measurements for the males are as follows (date of capture in parentheses):

←

Fig. 4.—Lateral view of the crania of the seven species of *Micronycteris* occurring in Suriname. A, *M. daviesi* (CM 63573); B, *M. sylvestris* (CM 63597); C, *M. brachyotis* (from Trinidad); D, *M. megalotis* (CM 68380); E, *M. minuta* (CM 63584); F, *M. nicefori* (CM 76771); G, *M. hirsuta* (CM 68388).

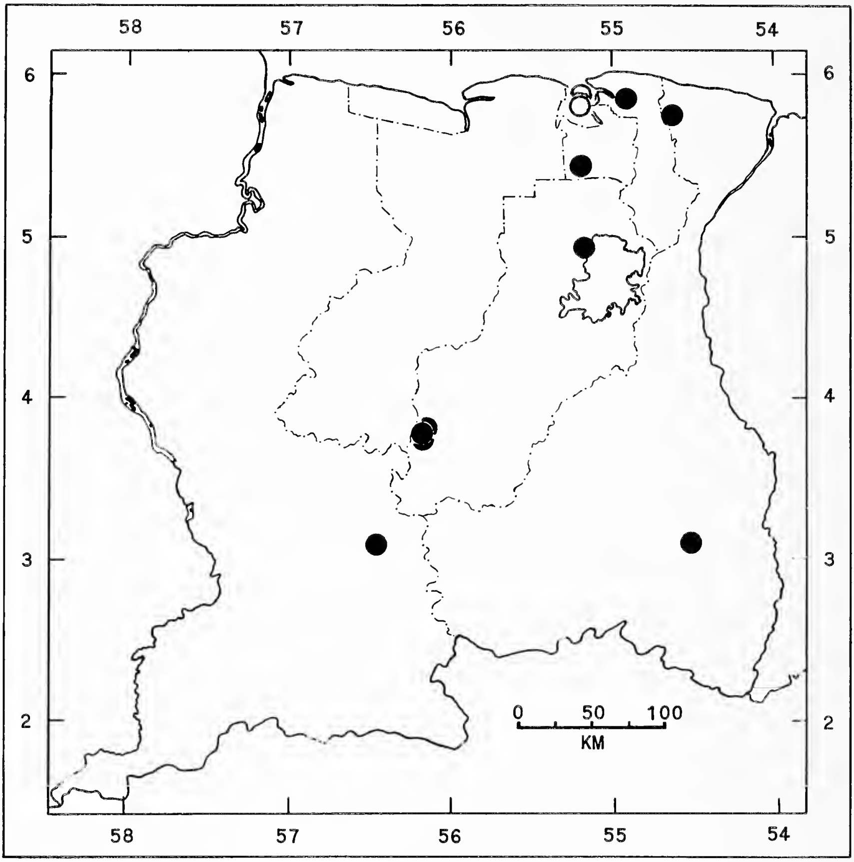

Fig. 6.—Map of the geographic distribution of *Micronycteris megalotis* in Suriname. Closed circles, specimens examined; open circles, previous records.

3, 3 (4 May); 3 (7 July); 2 (13 September); 2 (30 September); 2 (1 October); 2 (3 October); 3, 4.5 (24 October); 2.5 (23 November). A female taken on 1 October evinced no reproductive activity, whereas no data are available for the other female. Seven of the males had an average weight of 5.7 (range, 5–7) and the one female for which data are available weighed 6.

The karyotype of a male from Suriname had a $2n = 40$ and $FN = 68$. The X-chromosome was subtelocentric and the Y-chromosome was acrocentric (Honeycutt et al., 1980).

Micronycteris* (*Micronycteris*) *minuta (Gervais, 1856)

Specimens examined (15).—BROKOPONDO: 1 km N Rudi Kappelvliegveld, 1; Brownsberg Nature Park, 8 km S, 2 km W Brownsweg, 2. COMMEWIJNE: Nieuwe Grond Plan-

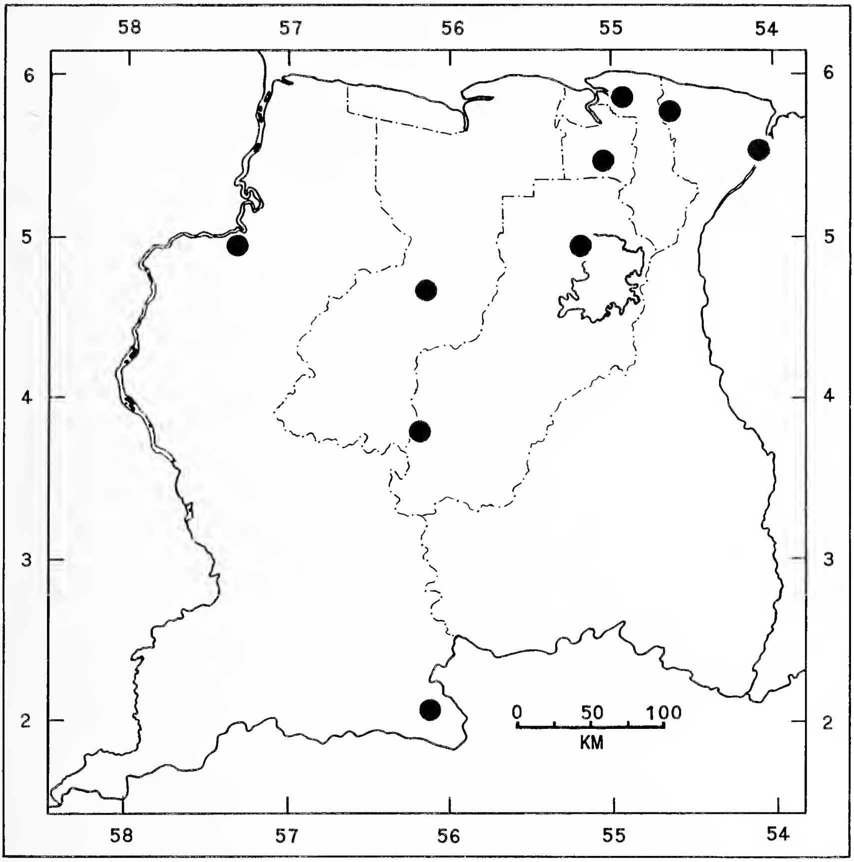

Fig. 7.—Map of the geographic distribution of *Micronycteris minuta* in Suriname.

tation, 1. MAROWIJNE: 3 km SW Albina, 1; 10 km N, 24 km W Moengo, 1. NICKERIE: Avanavero, 1; Sipaliwini airstrip, 4. SARAMACCA: Voltzberg, 3. SURINAME: Powaka, 1.

Prior to our work in Suriname (Genoways and Williams, 1979; Williams and Genoways, 1980) *M. minuta* was unknown from the country; however, we took the species in all major regions of the country (Fig. 7). In Suriname, *M. minuta* would most likely be confused with *M. megalotis*; however, *minuta* can be distinguished by the deeply notched interauricular band (Fig. 1) and a first upper premolar (P3) that is distinctly smaller than the second premolar (P4) (Fig. 2F). *M. minuta* has some individuals smaller than any individuals of *M. megalotis*, but the two species cannot be separated consistently on size alone (Table 1). *M. minuta* currently is considered to be monotypic (Jones and Carter, 1976). A comparison of our material with specimens from

Trinidad and Brazil deposited in the American Museum of Natural History revealed no notable differences; however, there may be slight karyotypic differences between specimens from Trinidad and Suriname (see discussion below).

Micronycteris minuta usually was netted in association with lowland rainforest. However, at several places such as 1 km N Rudi Kappelvliegveld, 10 km N, 24 km W Moengo, and Powaka, this species was taken in nets set in open areas along or near the forest. At the Nieuwe Grond Plantation, *M. minuta* was captured in a series of nets set through the lawns and gardens surrounding the plantation buildings. Nine species of bats were collected in association with *M. minuta* at more than half of the nine capture sites (Table 2). An interesting association is that between *M. nicefori* and *M. minuta,* which were taken together at five capture sites. *M. minuta* was also captured together with two other members of the genus (*megalotis* and *sylvestris*) at single localities.

Our 15 specimens consist of six males and nine females. Testes measurements for males were as follows (date of capture in parentheses): 3 (12 May); 2 (24 September); 2 (28 September); 3 (23 October); 2 (16 November). A female taken on 30 July was carrying a 13 mm fetus, and another was lactating on 24 September. Females netted on the following dates evinced no gross reproductive activity: 26 May; 6 August; 28 August; 12 September; 16 November (3 individuals). Four of the males had weights of 5, 5, 6, and 6 and three females weighed 5, 5, and 8.

The diploid number for this species in Suriname was 28 and the fundamental number was 52 (Baker et al., 1981). This karyotype differed slightly from that reported for the species from Trinidad (Baker, 1979). In the Suriname specimen, the smallest pair of autosomes was biarmed, whereas in the material from Trinidad this pair was acrocentric.

Micronycteris* (*Trinycteris*) *nicefori Sanborn, 1949

Specimens examined (31).—BROKOPONDO: 1 km N Rudi Kappelvliegveld, 1. COMMEWIJNE: Nieuwe Grond Plantation, 1. MAROWIJNE: 3 km SW Albina, 1; 10 km N, 24 km W Moengo, 1; Perica, 2. NICKERIE: Avanavero, 3; Kabalebo, 20. SARAMACCA: Tafelberg, SE side of Arrowhead Basin (3°54′N, 56°10′W), 600 m, 1. SURINAME: Powaka, 1.

This species had not been reported in Suriname before our work (Genoways and Williams, 1979; Williams and Genoways, 1980), but we found it to be widespread in the country (Fig. 8). *Micronycteris nicefori* is a medium-sized member of the genus (Table 1) that is most likely to be confused with *M. brachyotis. M. nicefori* can be distinguished by its upper incisors, which are shorter and narrower than the canines and project forward out of line with the canines (Fig. 2H), long

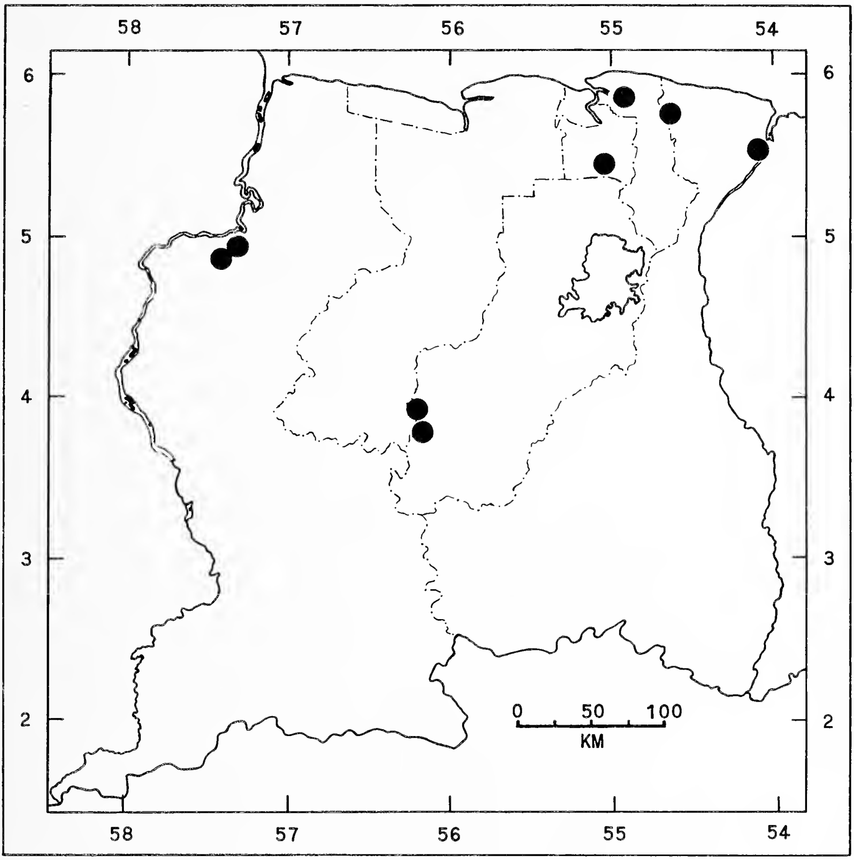

Fig. 8.—Map of the geographic distribution of *Micronycteris nicefori* in Suriname.

ears, and a faint gray line often present on the lower back. We compared our specimens with material from Trinidad and Colombia deposited in the American Museum of Natural History. We could detect no consistent differences in size or morphology, which supports the idea that this species is monotypic (Jones and Carter, 1976).

The large sample from Kabalebo is composed of all males. These individuals were captured in nets set along a newly cut trail, which passed through the moderate undergrowth of a secondary forest along a road, which eventually led into the larger trees of a mature rainforest. Elsewhere the species usually was collected in either secondary or primary lowland rainforest. The exceptions to this were in the highlands of Tafelberg where the typical vegetation was lower montane forest and at Nieuwe Grond Plantation where a single specimen was taken in nets set over the lawns and gardens surrounding the plantation headquarters. *M. nicefori* shows a high correlation with the distributions of only seven other species; five of these—*Lonchophylla thomasi, Carollia perspicillata, Rhinophylla pumilio, Sturnira lilium,* and *Artibeus* (large species)—were common, widespread species (Table 2). *Glossophaga soricina* was not a particularly common species in Suriname. The most interesting distributional correlation was with *M. minuta,* which was taken at five of the nine localities where *M. nicefori* was captured.

Length of testes of the 20 males from Kabalebo taken on 28 May averaged 3.5 (range, 3–4). Other males had the following testes lengths (date of capture in parentheses): 3, 4, 5 (26 May); 5 (6 August); 4 (23 October); 3 (24 October). None of the three females for which data are available evinced reproductive activity (netted on 30 July, 12 September, and 30 September). Two of the males weighed 7.3 and 8 and three females weighed 7, 8, and 8.5.

Surinamese specimens of *M. nicefori* had a $2n = 28$ and $FN = 52$. The X-chromosome was submetacentric and the Y-chromosome was acrocentric (Honeycutt et al., 1980; Baker et al., 1981).

Micronycteris* (*Xenoctenes*) *hirsuta (Peters, 1869)

Specimens examined (3).—NICKERIE: Kabalebo, 1. PARA: Zanderij, 2.

Micronycteris hirsuta is the sole member of the subgenus *Xenoctenes* (Figs. 3, 4). Miller (1907) originally gave this taxon generic status, but Sanborn (1949) reduced it to subgeneric level. The species *M. hirsuta* can be distinguished from other members of the genus in Suriname by the following characteristics: ears connected across the forehead by a low unnotched band (Fig. 1); upper inner incisors separated at base, but in contact near tip (Fig. 2C); upper outer incisors small; lower incisors high and wedged tightly between canines (Fig. 2C); lower canines in contact, or nearly so, behind incisors; and lower incisors bifid (Fig. 2C). The species is considered to be monotypic (Jones and Carter, 1976).

Our specimens were the first members of the species (Fig. 5) to be reported from Suriname (Genoways et al., 1981). The specimens from Zanderij, a reproductively inactive adult female and an immature female, were netted on 18 May. The specimen from Kabalebo was a reproductively inactive adult female. The area at Kabalebo was covered by mixed primary and secondary lowland rainforest, whereas the vicinity of Zanderij was secondary lowland forest associated with a rubber plantation. *M. hirsuta* was taken in association with 24 other species of bats (Table 2); however, only four species—*Phyllostomus elongatus,* *P. hastatus, Carollia perspicillata,* and large *Artibeus* species—were captured at both localities. All of these are common, widespread species in Suriname.

The specimens from Suriname had a $2n = 30$ and FN = 32 (Baker et al., 1981). This karyotype appears to be identical to the one found in Middle American populations of *M. hirsuta* but differs from that found on Trinidad where $2n = 28$ (Baker et al., 1973; Baker, 1979).

DISCUSSION

Seven of the 10 recognized species of *Micronycteris* are known from the small country of Suriname. As a general rule, specimens were taken in association with forested habitats, particularly mature lowland rainforest. However, there was a relatively low correlation between the occurrence of any one species of *Micronycteris* and any of the other species of the genus (Table 2). Only *M. minuta* and *M. nicefori* were taken together at more than half of their collecting sites. There are two possible explanations for this fact. First, there can be, and probably are, subtle differences in the microhabitat required by each of the species within the forest. The other factor affecting this correlation may be that the distribution of each species may be clumped around available roosting sites. We saw this phenomenon in at least two places in Suriname. At Brownsberg Nature Park, specimens of *M. sylvestris* were taken only from a hollow tree. At Kabalebo, a large number of male *M. nicefori* was captured only in one set of nets. If the occurrence of species of *Micronycteris* is clumped around available roost sites and individuals have relatively small home ranges, then there definitely should be a reduction in the places that species co-occur.

The seven species of *Micronycteris* from Suriname form a gradient in size starting with the small *M. minuta* and *M. megalotis* and progressing through the large *M. daviesi* at the opposite end of the scale. The small species really form a species pair based upon size, although *M. minuta* probably averages slightly smaller than *M. megalotis* for most characters. Between these extremes fall (beginning with the smallest) *M. nicefori, M. sylvestris,* and *M. brachyotis,* and finally *M. hirsuta. Micronycteris sylvestris* and *M. brachyotis* cannot be distinguished on size alone but there are numerous other useful characters to separate them. Size is not the only character needed to separate several of the species of *Micronycteris* in Suriname, but it is useful in narrowing the number of comparisons that need to be made.

We stated earlier that the genus *Micronycteris* seemed to be oversplit at the subgeneric level. The current arrangement was proposed by Sanborn (1949) based primarily upon characters of the wings and ears. Deviations from this arrangement have been suggested by Arnold et

Table 2.—*Species of bats taken in association with specimens of* Micronycteris *in Suriname. The numbers in each column represent numbers of localities.*

Species of bats	*M. daviesi*	*M. hirsuta*	*M. megalotis*	*M. minuta*	*M. nicefori*	*M. sylvestris*
No. of localities for which data are available	1	2	9	9	9	1
Saccopteryx bilineata	0	1	5	1	1	0
Saccopteryx canescens	0	0	2	0	0	0
Saccopteryx leptura	1	1	5	0	1	0
Cormura brevirostris	0	1	0	1	1	0
Pteronotus parnellii	1	1	3	4	3	1
Noctilio leporinus	0	0	0	1	1	0
Chrotopterus auritus	1	0	2	0	0	0
Micronycteris megalotis	0	0	—	1	2	0
Micronycteris minuta	0	0	1	—	5	1
Micronycteris nicefori	0	0	2	5	—	0
Micronycteris sylvestris	0	0	0	1	0	—
Tonatia bidens	0	0	5	1	2	0
Tonatia brasiliense	0	0	1	1	0	0
Tonatia carrikeri	0	1	0	2	0	0
Tonatia schulzi	0	0	2	0	1	0
Tonatia silvicola	0	1	1	3	2	1
Mimon crenulatum	0	0	1	1	1	0
Lonchorhina aurita	0	0	0	1	1	0
Phyllostomus discolor	1	1	2	1	0	1
Phyllostomus elongatus	1	2	4	6	3	1
Phyllostomus hastatus	1	2	3	5	3	0
Phyllostomus latifolius	0	0	1	2	0	1
Trachops cirrhosus	1	1	2	0	0	0
Anoura caudifer	0	0	3	0	2	0
Lonchophylla thomasi	1	1	4	7	6	1
Glossophaga soricina	0	0	2	4	5	0
Carollia brevicauda	1	0	0	1	0	0
Carollia perspicillata	1	2	7	5	6	0
Rhinophylla pumilio	1	1	5	6	5	1
Ametrida centurio	0	0	0	1	0	0
Sturnira lilium	1	1	4	6	6	0
Sturnira tildae	0	0	1	2	2	1
Artibeus cinereus	1	0	1	5	4	0
Artibeus concolor	0	0	1	1	1	0
Artibeus (large species)	1	2	7	9	8	1
Uroderma bilobatum	1	1	1	3	3	0
Chiroderma trinitatum	0	1	0	1	1	0
Vampyressa bidens	0	0	2	0	0	0
Vampyressa brocki	0	0	0	1	1	0
Vampyrops aurarius	0	0	0	0	1	0
Vampyrops brachycephalus	0	0	2	1	2	0
Vampyrops helleri	1	1	2	4	3	0
Vampyrodes caraccioli	0	0	0	1	1	0
Mesophylla macconnelli	0	1	1	2	3	0
Desmodus rotundus	0	1	0	1	0	0

Table 2.—*Continued.*

Species of bats	*M. daviesi*	*M. hirsuta*	*M. megalotis*	*M. minuta*	*M. nicefori*	*M. sylvestris*
Thyroptera tricolor	0	0	1	2	1	0
Natalus tumidirostris	0	0	0	1	0	0
Myotis nigricans	0	1	1	3	3	0
Eptesicus brasiliensis	0	1	4	1	3	0
Molossus ater	0	1	0	0	0	0
Molossus molossus	0	1	1	1	1	0
Total species (51)	16	24	36	41	35	10

al. (1983) based on electrophoretic studies. For phenotypic criteria a useful classification might be devised by using characters of the ears and the teeth at the front part of the dental arcade (canines and incisors). The genus can be split into two major groups—in the first the ears are connected by an interauricular band and the lower incisors are bifid, and in the second the ears are not connected by an interauricular band and the lower incisors are trifid. We suggest that future investigation of subgeneric classifications of this genus examine these groupings and any subgroupings within them.

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ANNOTATED CHECKLIST OF THE MAMMALS OF KENYA. II. INSECTIVORA AND MACROSCELIDEA

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Abstract

Four families of Insectivora (Tenrecidae, Chrysochloridae, Erinaceidae, Soricidae) and one of Macroscelidea (Macroscelididae) are known from Kenya. Of these families, only the Soricidae, with 31 species, and the Macroscelididae, with five species, are known from more than a single species. Records of occurrence are annotated by museum specimens or with references to the literature. *Suncus murinus* seems to be the only introduced species in the insectivore fauna of Kenya. Distributional records of insectivores in Kenya are poor as 13 species of the 39 reported are known from only a single locality in Kenya. A gazetteer of collecting localities is included.

Introduction

This is the second in a series of annotated checklists on Kenya mammals. The first checklist (Aggundey and Schlitter, 1984) covered the bats. This checklist includes the insectivoran orders Insectivora and Macroscelidea. Our treatment of this group follows Yates (1984). In this checklist we cover four Lipotyphlan families, namely the Tenrecidae, Chrysochloridae, Erinaceidae, and Soricidae, and a single Menotyphlan family, the Macroscelididae, of Kenya.

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In a series of papers, Dollman (1915*a,* 1915*b,* 1915*c,* 1915*d,* 1915*e,* 1915*f,* 1916) reviewed the African species of *Crocidura.* This review was followed by Hollister's (1918) review of Kenyan insectivores in the United States National Museum. In his massive checklist, Allen (1939) covered all of the species of Kenyan insectivores recognized at that time. This work is still important as a starting point in understanding the taxonomic relationships of these species. Since these early papers, there have been no subsequent reviews in a wider context of Kenyan insectivores except elephant shrews. Corbet and Neal (1965) and Corbet and Hanks (1968) reviewed the taxonomy and distribution of Kenyan species in their broader studies of elephant shrews. This second annotated checklist attempts to synthesize the pertinent literature on all of the insectivores known from Kenya. The taxonomy of many groups of insectivores, and particularly the family Soricidae in Africa, is still in a state of confusion. Undoubtedly many taxonomic changes and additional distributional records will be required before a satisfactory arrangement is possible.

We have followed the format from the first part of the series (Aggundey and Schlitter, 1984). Specimen records are included from the following museums with their accepted acronyms in parentheses.

Carnegie Museum of Natural History, Pittsburgh (CM)
National Museums of Kenya, Nairobi (NMK)
National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM)

As with the checklist on bats, we point out that the distributional records of this group are also undoubtedly incomplete. Nevertheless, it is our sincere hope that the information given will stimulate additional interest and research on the insectivores of Kenya.

ACKNOWLEDGMENTS

We were unable to spend as much time gathering distributional records from museum collections for this checklist as we were for the checklist on bats. Nevertheless, we would like to thank Charles O. Handley, Jr., for allowing us to record data at the Smithsonian Institution and for sending photocopies of numerous old and difficult to find articles. In Kenya, Mrs. Gooderis helped compile the list of the specimens of insectivores in the collection in Nairobi. R. Hutterer critically reviewed the manuscript. Winnie Woodland and Mary Ann Schmidt patiently and expertly typed numerous drafts of the manuscript. We thank them all for their important part in completing this checklist.

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CHECKLIST

Order Insectivora
Family Tenrecidae
Genus *Potamogale* Du Chaillu, 1860
Potamogale velox Du Chaillu, 1860

Potamogale velox Du Chaillu, 1860. Proc. Boston Soc. Nat. Hist., 7:361. Gabon.

Records.—4 km S Kakamega (Aggundey, 1977:368, NMK).

Family Chrysochloridae
Genus *Chrysochloris* Lacepede, 1799
Chrysochloris stuhlmanni fosteri (St. Leger, 1931)

Chlorotalpa fosteri St. Leger, 1931. Ann. Mag. Nat. Hist., (10)8:605, Dec. Mt. Elgon, 9300 ft, Uganda.

Records.—Mt. Elgon (NMK); Cherangani Hills (Duncan and Wrangham, 1971:149; Meester, 1974:3); southwest side Cherangani Hills, 6500 ft (Duncan and Wrangham, 1971:157); Labot, Cherangani Hills (Duncan and Wrangham, 1971:157).

Family Erinaceidae
Genus *Atelerix* Pomel, 1848
Atelerix albiventris (Wagner, 1841)

E(rinaceus) albiventris Wagner, 1841. Schreber's Saugethiere, Suppl., 2:22. Type locality unknown.

Erinaceus albiventris atratus Rhoads, 1896. Proc. Acad. Nat. Sci., Philadelphia, p. 544, 8 Dec. Lake Rudolf, Ngare Nocbor, Marsabit Dist., Kenya (ca. 2°45′N, 36°45′E).

Erinaceus hindei Thomas, 1910. Ann. Mag. Nat. Hist., (8)5:193, Feb. Kitui, 3500 ft, Kenya.

Erinaceus sotikae Heller, 1910. Smithsonian Misc. Coll., 56(15):1, 23 Dec. Southern Guaso Nyiro, Sotik Dist., Kenya.

Records.—Ngare Nocbor (Rhoads, 1896:544); Kitui (Peters, 1878:198; Anderson, 1895: 420; Thomas, 1910*a*:193); Southern Guaso Nyiro (Heller, 1910*b*:1; Hollister, 1918:26; J. Allen, 1922:16); Kapiti Plains (Hollister, 1918:26; J. Allen, 1922:16); Loita Plains (Hollister, 1918:26); Mt. Lololokwi (Hollister, 1918:26; J. Allen, 1922:16); Taveta (True, 1892:469, 480; Hollister, 1918:26); Ulukenia Hills (Hollister, 1918:26; J. Allen, 1922: 16); Upper Ura River (J. Allen, 1922:16); Lokori, Southern Turkana (NMK); Naivasha (NMK); Nairobi (Harmsen and Jabbal, 1968:158; Kingdon, 1974:32; Kock, 1978:116, NMK); Busia (CM); Voi (Allen and Lawrence, 1936:39); Lodwar (St. Leger, 1937:526); Olorgasailie (Toschi, 1949:28); River Kerio Suk (Ruxton, 1926:29); Narro Surra River (Kollmann, 1914:319); Machakos (Lonnberg, 1912*b*:48).

Family Soricidae
Genus *Crocidura* Wagler, 1832
Crocidura allex Osgood, 1910

Crocidura allex Osgood, 1910. Publ. Field Mus. Nat. Hist., Zool. Ser., 10(3):20, 7 Apr. Naivasha, Kenya.

Crocidura alpina Heller, 1910. Smithsonian Misc. Coll., 56(9):5, 22 July. West slope of Mt. Kenya, 10,000 ft, Kenya.

Records.—Naivasha Station (Osgood, 1910*b*:20; Hollister, 1918:67, USNM); West slope Mt. Kenya (Heller, 1910*a*:5; Hollister, 1918:68, USNM); Aberdare Range (Hollister, 1918:67, USNM); Oljoro O Nyon River (Hollister, 1918:67, USNM); Mau Forest (Toschi, 1947:12, NMK); Ngong (NMK); Loita (NMK); Amala River (NMK); Selangai (NMK); near Lake Olbollossat (Dollman, 1915*f*:513); Solai, 8000 ft (Dollman, 1915*f*: 514); Nanyuki (Southern and Hook, 1963:511); Mt. Kenya, 12,500 ft (Harmsen and Jabbal, 1968:160); north slope Mt. Kenya (Coe and Foster, 1972:8).

Remarks.—Heim de Balsac and Meester (1977:9) regard both *C. a. allex* and *C. a. alpina* as valid subspecies in Kenya.

Crocidura bottegi Thomas, 1898

Crocidura bottegi Thomas, 1898. Ann. Mus. Civ. Stor. Nat. Genova, (2):18, 677, 21 Feb. Between Badditu and Dime, northeast of Lake Rudolf, Ethiopia.

Records.—Marsabit (Heim de Balsac and Meester, 1977:10).

Crocidura elgonius Osgood, 1910

Crocidura bicolor elgonius Osgood, 1910. Ann. Mag. Nat. Hist., (8)5:369. Kirui's, southern foothills of Mount Elgon, 6000 ft, Kenya (restricted by Moreau et al., 1946:394).

Records.—Kirui's (Osgood, 1910*c*:369; Allen and Lawrence, 1936:44; Loveridge, 1937: 519); Kisumu (Hollister, 1918:65); Lukosa River (Hollister, 1918:65, USNM); Kapiti Plains (Hollister, 1918:65, USNM); Kaimosi (Hollister, 1918:65; Allen and Lawrence, 1936:44; Allen and Loveridge, 1942:159, NMK, USNM); Muguga (NMK); Lake Nakuru (Hutterer, 1983:225); Nairobi (Hutterer, 1983:225); Cherangani Hills (Ruxton, 1926: 29); Eldoret (Loveridge, 1923:698); Mt. Elgon (Granvik, 1924:9).

Remarks.—Both Heim de Balsac and Meester (1977) and Hutterer (1984) regard *C. elgonius* as a distinct species.

Crocidura fischeri Pagenstecher, 1885

Crocidura fischeri Pagenstecher, 1885. Jahrb. Wiss. Anst., Hamburg, 2:34, pl. 1, f. 1–3. Nguruman, Kenya.

Records.—Nguruman (Pagenstecher, 1885:34; Hutterer, 1986:26).

Remarks.—The type locality for the species was given by Pagenstecher (1885:34) as Nguruman with no other qualifier than Massailand. Neumann (1900) also visited Nguruman from 22–27 December 1893 and plots the locality on his map as slightly on the Tanzanian side of the border (which seems to be the same as the present border). He labels the locality on his map as "Nguruman (Bagasse)" which leads us to believe he was referring to a village near Lake Natron or "Nguruman Salz-See" from his map. Lake Natron seems to have been at a low level in 1893. Swynnerton and Hayman (1951:284) list the type locality of *Crocidura fischeri* as Nguruman, west of Lake Magadi, Kenya Colony [between 1°50′ and 2°S, 36°5′E; 2500 to 6000 feet]. This locality reaches from the Rift Valley floor to nearly up to the top of the eastern face of the Nguruman Escarpment. Hutterer (personal communication) has rechecked this type locality as part of a study (Hutterer, 1986) of *C. fischeri* and concluded that it is in Kenya based on Fischer's (1884, 1885) accounts of his explorations and especially the photographs and maps in these accounts. Fischer camped at the foot of a mountain range northwest of "Natron Swamp" or Lake Natron at 650 meters, near the foot of Mt. Sambo, where acacia steppe occurs and a flowing stream came down from the mountains. Mt. Sambo, although on the Tanzanian side of the border, is visible far in the background of a photograph of the campsite. It seems best to follow Swynnerton and Hayman (1951) and Hutterer (1986) in placing the type locality on the Kenyan side of the present border.

Crocidura flavescens nyansae Neumann, 1900

Crocidura flavescens nyansae Neumann, 1900. Zool. Jahrb., Syst., Geog., Biol., 13:544, 10 Oct. Fort Lubwa's in Ussoga, outlet of Victoria Nyanza, Uganda (restricted to Fort Thruston, 10 mi E Jinja, Busoga Dist., Uganda, by Moreau et al., 1946:396).
Crocidura kijabae J. A. Allen, 1909. Bull. Amer. Mus. Nat. Hist., 26:173. Kijabe, Kenya.

Records.—Kijabe (J. Allen, 1909:173); Elgeyo Forest (J. Allen, 1914:343); Aberdare Mountains, 11,000 ft (Dollman, 1915*b*:568; Hollister, 1918:43); Laikipia (Hollister, 1918:43); Mt. Kenya (Dollman, 1915*b*:568; Hollister, 1918:43); Mt. Umengo (Hollister, 1918:43); Naivasha Station (Hollister, 1918:43); Nakutishu River, Naivasha Plains (Hollister, 1918:43); Nyeri (Dollman, 1915*b*:568; Hollister, 1918:43); Kaimosi (Hollister, 1918:42; Allen and Lawrence, 1936:41); Kakamega (Hollister, 1918:42); Kisumu (Hollister, 1918:42); Sergoit Lake (Hollister, 1918:42); Jombeni (Dollman, 1915*b*:568); Mweru (Dollman, 1915*b*:568); Lake Olbollosat (Dollman, 1915*b*:568); Kirui's (Dollman, 1915*b*: 567); Londiani (Lonnberg, 1918:175); Lake Elmenteita (Osgood, 1936:221); Molo (Osgood, 1936:221); Mianzini (Thomas, 1891:182); Meru Country (Lonnberg, 1912*b*:52); Mt. Elgon (Granvik, 1924:8).

Crocidura fulvastra (Sundevall, 1843)

Sorex fulvaster Sundevall, 1843. Kongl. Svenska Vet.-Akad. Handl., Stockholm, p. 172, for 1842. Bahr-el-Abiad, Sudan.

Records.—North of Lokichokio (Hutterer, 1984:215).

Remarks.—This species includes *C. sericea* (Sundevall, 1843) as a synonym according to Hutterer (1984:211, 215).

Crocidura fumosa fumosa Thomas, 1904

Crocidura fumosa Thomas, 1904. Ann. Mag. Nat. Hist., (7)14:238, Sept. Western slope of Mt. Kenya, 2600 m, Kenya.
Crocidura alchemillae Heller, 1910. Roosevelt's African Game Trails, American ed., p. 480, London ed., p. 491. Summit of Aberdare range, Kenya.

Records.—Western slope of Mt. Kenya, 2600 m (Thomas, 1904:238; Dollman, 1915*e*: 369, 370); summit of Aberdare range (Heller, 1910*c*:480; Hollister, 1918:55); Kinangop (Kollmann, 1913:139); west side Mt. Kenya (Hollister, 1918:55, NMK); Fort Hall (Thomas, 1904:238; Kollmann, 1913:139; Hollister, 1918:55, NMK); Chyulu Hills (Osgood, 1910*b*: 21, NMK); Nairobi (NMK); Ngong (NMK); Chania River (NMK); Naro Moru (NMK);

Ol Arabel (NMK); Kikuyu (NMK); Thika (NMK); Nyeri (Hollister, 1918:55); Upper Nzoia River (Hollister, 1918:55); Mt. Elgon (Dollman, 1915*e*:369, 370); Jombeni Range (Dollman, 1915*e*:369, 370); Aberdare Mountains (Dollman, 1915*e*:369, 370); Machakos (Thomas, 1904:238; Kollmann, 1913:139); Nandi (Thomas, 1904:238; Kollmann, 1913: 139); Kakamega (Thomas, 1904:238; Kollmann, 1913:139); Donya Sabuk (Lonnberg, 1916:5); Juja Farm (Lonnberg, 1916:5); Nanyuki (Southern and Hook, 1963:512); Mt. Kenya (Southern and Hook, 1963:512; Duncan and Wrangham, 1971:161); Zebra Farm, Athi Plains (J. Allen, 1909:173); Lagari (Thomas, 1904:238); Blue Post (Lonnberg, 1912*b*: 53); Kagio (Lonnberg, 1912*b*:53); Embu (Lonnberg, 1912*b*:53); Kanyakeni (Lonnberg, 1912*b*:53); Meru (Lonnberg, 1912*b*:53); Mt. Kenya, 3800 m (Coe and Foster, 1972:8).

Remarks.—Lonnberg (1916:5) considered the series of 10 specimens from Donya Sabuk to approach *C. f. schistacea,* now considered a synonym of *C. luna.* It is doubtful that all of these listed records represent *C. fumosa* as the differences between *C. fumosa, C. luna,* and *C. zaodon* are subtle ones. Many of these records could prove to be *C. luna* upon reexamination.

Crocidura fuscomurina (Heuglin, 1865)

S.(orex) fusco murinus Heuglin, 1865. Leopoldina, 5:36, *in* Nova Acta Acad. Caes. Leop.-Carol., Dresden, June. Meshra-el-Req, Bahr-el-Ghazal Prov., Sudan.

Crocidura bicolor Bocage, 1889. Jorn. Sci. Math., Phys. e Nat., Lisboa, (2)1:29, March. "Gambos, dans l'interieur de Mossamedes," Angola.

Crocidura bicolor cuninghamei Thomas, 1904. Ann. Mag. Nat. Hist., (7)14:240, Sept. Vumba Island, 1 mi N Sagitu Island, Lake Victoria, Uganda.

Records.—Nairobi (Osgood, 1936:230).

Remarks.—Hutterer (1983) reviewed the taxonomy and distribution of *C. fuscomurina* but did not report any records from Kenya. His preliminary distribution map (Hutterer, 1983:224) included only records for which he had some degree of certainty of identification.

Crocidura hildegardeae Thomas, 1904

Crocidura hildegardeae Thomas, 1904. Ann. Mag. Nat. Hist., (7)14:240, Sept. Fort Hall, Kenya.

Crocidura lutreola Heller, 1912. Smithsonian Misc. Coll., 60(12):8, 4 Nov. Mt. Mbololo, Taita Hills, 5000 ft, Kenya.

Crocidura hildegardeae procera Heller, 1912. Smithsonian Misc. Coll., 60(12):10, 4 Nov. Mt. Lololokwi, 6000 ft, northern Guaso Nyiro, Kenya.

Crocidura ibeana Dollman, 1915. Ann. Mag. Nat. Hist., (8)15:514, May. Ann. Mag. Nat. Hist., (8)16:362, Oct. Olgerei River, Kenya.

Crocidura hildegardeae altae Heller, 1912. Smithsonian Misc. Coll., 60(12):9, 4 Nov. Mt. Garguez, Mathews Range, 6000 ft, Kenya.

Records.—Fort Hall (Thomas, 1904:240; Dollman, 1915*f*:508; Hollister, 1918:64, USNM); Mt. Garguez (Heller, 1912:9, 10; Hollister, 1918:65, USNM); Mt. Lololokwi (Heller, 1912:10; Hollister, 1918:64); Mt. Mbololo (Heller, 1912:8, 9; Hollister, 1918: 64; Allen and Lawrence, 1936:43, USNM); Olgerei River (Dollman, 1915*a*:514); Voi (Hollister, 1918:64, NMK); Ngong (NMK); Narosura River (Kollmann, 1914:319, NMK); Lemek Valley (NMK); Amala River (NMK); Nyeri (Hollister, 1918:64, NMK); Meru (Hollister, 1918:64, NMK); Amboseli (NMK); Engare Narok (Hollister, 1918:64, NMK);

Isiola River (Hollister, 1918:64); Kapiti Plains (Hollister, 1918:64); Mayo River, Laikipia (Hollister, 1918:64, USNM); Mt. Kenya (Hollister, 1918:64); Mt. Sagalla (Hollister, 1918: 64, USNM); Mt. Umengo (Heller, 1912:9; Hollister, 1918:64, USNM); Naivasha Station (Hollister, 1918:64, NMK); Ndi (Hollister, 1918:64, USNM); Oljoro O Nyon River (Hollister, 1918:64); Wambugu (Hollister, 1918:64); Taveta (Dollman, 1915*e*:379); Tsavo River (Dollman, 1915*e*:380); Mt. Elgon (Dollman, 1915*f*:508); Baringo (Dollman, 1915*f*:509); Kaimosi (Allen and Lawrence, 1936:43); Peccatoni (Allen and Lawrence, 1936:43); Wema (Allen and Lawrence, 1936:43); Kazere (Lonnberg, 1912*b*:54); Blue Post (Lonnberg, 1912*b*:54); Kutu (Lonnberg, 1912*b*:54).

Remarks.—We follow Demeter and Hutterer (1986) and Hutterer (personal communication) in recognizing *C. hildegardeae* for these Kenyan records rather than *C. gracilipes* Peters, 1870, an apparently distinct species.

Crocidura hirta Peters, 1852

Crocidura hirta Peters, 1852. Reise nach Mossambique, Saugeth., p. 78, pl. 18, f. 2. Tette, Mozambique (17°S).

Records.—None found.

Remarks.—Heim de Balsac and Meester (1977:17) list *C. h. velutina* Thomas, 1904 to occur in ". . . presumably also Kenya and southern Somalia."

Crocidura jacksoni Thomas, 1904

Crocidura jacksoni Thomas, 1904. Ann. Mag. Nat. Hist., (7)14:238, Sept. Ravine Station, Kenya.

Crocidura jacksoni amalae Dollman, 1915. Ann. Mag. Nat. Hist., (8)15:516, May; Ann. Mag. Nat. Hist., (8)16:376, Oct. 1915. Amala River, Nyanza Prov., Kenya (restricted by Moreau et al., 1946:396 to Amala River, 30 mi N Kenya-Tanzania border, 5500 ft, Kenya).

Records.—Ravine Station (Thomas, 1904:239); Amala River (Dollman, 1914*b*:309, 1915*a*:516, NMK); Isiola River (Hollister, 1918:60); Kaimosi (Hollister, 1918:60, USNM); Kapiti Plains (Hollister, 1918:60); Mtito Andei (Hollister, 1918:60, USNM); Neumann's Boma (Hollister, 1918:60); Southern Guaso Nyiro (Hollister, 1918:60); Ulukenia (Hollister, 1918:60); Voi (Hollister, 1918:60, Allen and Lawrence, 1936:43, USNM); Narosura River (Dollman, 1914*b*:309, NMK); Loita Plains (NMK); Ngong (NMK); Fort Hall (NMK); Tsavo River (Dollman, 1914*a*:88, NMK); Yala River (NMK); Sultan Hamud (NMK); Shimba Hills (NMK); Peccatoni (Allen and Lawrence, 1936:43); Golbanti (Allen and Lawrence, 1936:43); Zuwani (Dollman, 1914*a*:88); Lengototo (Dollman, 1914*b*:309).

Crocidura littoralis Heller, 1910

Crocidura littoralis Heller, 1910. Smithsonian Misc. Coll., 56(15):5, 23 Dec. Butiaba, east shore of Albert Nyanza, Uganda.

Records.—Kaimosi (Hollister, 1918:68; Dippenaar, 1980:129).

Remarks.—Hollister (1918:68) referred this series to *C. maurisca* but Dippenaar (1980:130) regards this species as known only by the holotype and that the specimens from Kaimosi are *C. littoralis.*

Crocidura luna Dollman, 1910

Crocidura luna Dollman, 1910. Ann. Mag. Nat. Hist., (8)5:175, Feb. Bunkeya River, Katanga, Zaire.
Crocidura fumosa schistacea Osgood, 1910. Publ. Field Mus. Nat. Hist., Zool. Ser., 10(3): 20, 7 April. Lukenya Mountain, Kenya.
Crocidura raineyi Heller, 1912. Smithsonian Misc. Coll., 60(12):7, 4 Nov. Mt. Gargues, Kenya.
Crocidura fumosa selina Dollman, 1915. Ann. Mag. Nat. Hist., (8)15:510, May; Ann. Mag. Nat. Hist., (8)16:371, Oct., 1915. Mabira Forest, Chagwe, Uganda.
Crocidura luna umbrosa Dollman, 1915. Ann. Mag. Nat. Hist., (8)15:514, May; Ann. Mag. Nat. Hist., (8)16:360, Oct., 1915. Machakos, 5400 ft, Kenya.

Records.—Lukenya Mountain (Osgood, 1910*b*:20); Mt. Gargues (Heller, 1912:7; Dollman, 1915*e*:373; Hollister, 1918:60); Machakos, 5400 ft (Dollman, 1915*a*:514, 1915*e*: 361); Ulukenia Hills (Hollister, 1918:59); Kapiti Plains (Hollister, 1918:59); Kaimosi (Hollister, 1918:59); Mt. Elgon (Rode, 1935:167).

Remarks.—Heim de Balsac and Meester (1977:18) list only *C. l. schistacea* occurring in Kenya and point out that *C. raineyi* could be a valid large subspecies. Hollister (1918:59) listed specimens from Kaimosi in western Kenya as *C. l. selina.*

Crocidura macarthuri St. Leger, 1934

Crocidura macarthuri St. Leger, 1934. Ann. Mag. Nat. Hist., (10)13:559, May. Merifano, 20 mi from mouth of Tana River, Kenya.

Records.—Merifano (St. Leger, 1934:559; Hutterer, 1986:28); 10 mi E Moyal, on Murri Road, 1500 m (Heim de Balsac and Meester, 1977:19; Hutterer, 1986:28); Ijara (Percy; et al., 1953*b*:11; Heim de Balsac and Meester, 1977:19; Hutterer, 1986:28); Rojewero Plains (Hutterer, 1986:28).

Crocidura macowi Dollman, 1915

Crocidura macowi Dollman, 1915. Ann. Mag. Nat. Hist., (8)15:515, May; Ann. Mag. Nat. Hist., (8)16:378, Oct. 1915. Mt. Nyiro, south of Lake Rudolf, Kenya.

Records.—Mt. Nyiro (Dollman, 1915*a*:515, 1915*e*:378).

Crocidura monax monax Thomas, 1910

Crocidura monax Thomas, 1910. Ann. Mag. Nat. Hist., (8)6:310, Sept. Rombo, Mt. Kilimanjaro, 6000 ft, Tanzania.

Records.—Amala River (Dollman, 1914*b*:309).

Crocidura nanilla Thomas, 1909

Crocidura nanilla Thomas, 1909. Ann. Mag. Nat. Hist., (8)4:99, Aug. Probably Entebbe, Uganda.
Crocidura denti St. Leger, 1932. Ann. Mag. Nat. Hist., (10)9:240, March. Koliokwell River, North Turkana Dist., Kenya (not *C. jacksoni denti* Dollman, 1915).
Crocidura rudolfi St. Leger, 1932. Ann. Mag. Nat. Hist., (10)10:487, Nov. (renaming of *C. denti* St. Leger, 1932).

Records.—Koliokwell River (St. Leger, 1932:241).

Remarks.—Heim de Balsac and Meester (1977:20) place *C. rudolfi* as a synonym of *C. nanilla.*

Crocidura parvipes Osgood, 1910

Crocidura parvipes Osgood, 1910. Publ. Field Mus. Nat. Hist., Zool. Ser., 10(3):19, 7 Apr. Voi, Kenya.
Crocidura parvipes nisa Hollister, 1916. Smithsonian Misc. Coll., 66(8):2, May. Kibabe, Kisumu, Kenya.

Records.—Eusso Nyiro Post (NMK); Voi (Osgood, 1910*b*:19; Hutterer, 1986:31); Kibabe (Hollister, 1916*b*:2; Hollister, 1918:47, USNM); Embu (NMK); Fort Hall (Hollister, 1918:47); Mt. Sagalla (Heller, 1912:9; Hollister, 1918:60; Heim de Balsac and Meester, 1977:12, USNM).

Remarks.—Three specimens of shrews from Mt. Sagalla are reported as *C. parvipes* by Heller (1912:9) but are referred to *C. jacksoni* by Hollister (1918:63). Heim de Balsac and Meester (1977:12) refer this record again to *C. cyanea parvipes.* Both *C. c. parvipes* and *C. c. nisa* are recognized as valid in Kenya by Heim de Balsac and Meester (1977: 12). Hutterer (1986:31) considered *C. parvipes* to be distinct from *C. cyanea.*

Crocidura ultima Dollman, 1915

Crocidura ultima Dollman, 1915. Ann. Mag. Nat. Hist., (8)15:517, May; Ann. Mag. Nat. Hist., (8)17:204, Feb., 1916. Jombeni Range, Nyeri Dist., 5000 ft, Kenya.

Records.—Jombeni Range, 5000 ft (Dollman, 1915*a*:517, 1916:205).

Remarks.—Heim de Balsac and Meester (1977:20) place *C. ultima* as a synonym of *C. monax,* but Dippenaar (1980:130) considers *C. ultima* to be a distinct species known only from the holotype.

Crocidura viaria (I. Geoffroy Saint-Hilaire, 1834)

Sorex viarus I. Geoffroy Saint-Hilaire, 1834. Voyage aux Indes-Orientales par C. Belanger, Zool., p. 127. Senegal (restricted by Hutterer, 1984:209, to region between Dakar and St. Louis).
Crocidura hindei Thomas, 1904. Ann. Mag. Nat. Hist., (7)14:237, Sept. Machakos, Kenya.
Crocidura suahelae Heller, 1912. Smithsonian Misc. Coll., 60(12):6, 4 Nov. Mazeras, Kenya.
Crocidura beta Dollman, 1915. Ann. Mag. Nat. Hist., (8)15:513, May; Ann. Mag. Nat. Hist., (8)16:78, July, 1915. Chania River, Kenya (restricted to Chania River, near Nyeri and Fort Hall, Kenya by Allen, 1939:31).

Records.—Machakos (Thomas, 1904:237; Hutterer, 1984:211); Mazeras (Heller, 1912: 6; Hollister, 1918:50, USNM); Chania River (Dollman, 1915*a*:513, 1915*c*:78); Changamwe (Hollister, 1918:50, UNSM); Juja Farm (Lonnberg, 1912*b*:54; Hollister, 1918: 46); Ulukenia Hills (Hollister, 1918:46); Nairobi (Loveridge, 1923:698, NMK); Kajiado (NMK); Potha (NMK); Ngatana (Allen and Lawrence, 1936:42); Mombasa (Hutterer, 1984:211); Karati (Thomas, 1904:237).

Remarks.—Hutterer (1984) placed *C. sericea* under *C. fulvastra* (Sundevall, 1843) but regarded *C. hindei* and *C. suahelae* as conspecific with *C. viaria.*

Crocidura voi Osgood, 1910

Crocidura voi Osgood, 1910. Publ. Field Mus. Nat. Hist., Zool. Ser., 10(3):18; 7 April. Voi, Kenya.

Crocidura percivali Dollman, 1915. Ann. Mag. Nat. Hist., (8)15:513, May; Ann. Mag. Nat. Hist., (8)16:126, Aug., 1915. Jombeni Range, Nyeri Dist., 3500 ft, Kenya.

Records.—Voi (Osgood, 1910*b*:18; Hutterer, 1986:30) Jombeni Range (Dollman, 1915*a*:513; Hutterer, 1986:30); Lakiundu River (Hollister, 1918:50); Mt. Suswa (Hutterer, 1986:30).

Remarks.—Hutterer (1986) recognized *Crocidura voi* as a distinct species, and included *C. butleri* from Sudan, *C. percivali* from Kenya, and *C. aridula* from Sudan as synonyms.

Crocidura xantippe Osgood, 1910

Crocidura xantippe Osgood, 1910. Publ. Field Mus. Nat. Hist., Zool. Ser., 10(3):19, 7 April. Voi, Kenya.

Records.—Voi (Osgood, 1910*b*:19; Dollman, 1915*e*:375; Heim de Balsac and Meester, 1977:25); Taveta (Dollman, 1915*e*:375); Nyiru (Heim de Balsac and Meester, 1977:25); Tsavo (Heim de Balsac and Meester, 1977:25).

Crocidura yankariensis Hutterer and Jenkins, 1980

Crocidura yankariensis Hutterer and Jenkins, 1980. Bull. British Mus. (Nat. Hist.), Zool., 39:305. Futuk, 16 km E Yankari Game Reserve boundary, Nigeria (9°50′N, 10°55′E).

Records.—West of Lake Rudolf, Kakuma, 50–60 mi NW Lodwar (Hayman, 1937:531; Hutterer and Jenkins, 1983:195).

Crocidura zaodon Osgood, 1910

Crocidura turba zaodon Osgood, 1910. Publ. Field Mus. Nat. Hist., Zool. Ser., 10(3):21, 7 Apr. Nairobi, Kenya.

Crocidura turba provocax Thomas, 1910. Ann. Mag. Nat. Hist., (8)6:112, July. Aberdare Mountains, 11,000 ft, Kenya.

Crocidura turba lakiundae Heller, 1912. Smithsonian Misc. Coll., 60(12):6, 4 Nov. Lakiundu River, near junction with Northern Guaso Nyiro, Kenya.

Crocidura turba kempi Dollman, 1915. Ann. Mag. Nat. Hist., (8)15:511, May; Ann. Mag. Nat. Hist., (8)16:134, Aug., 1915. Kirui's, southern foothills of Mount Elgon, 6000 ft, Kenya (restricted by Moreau et al., 1946:397).

Records.—Nairobi (Osgood, 1910*b*:21; Thomas, 1910*b*:113; Lonnberg, 1918:175, NMK); Aberdare Mountains, 11,000 ft (Thomas, 1910*b*:113; Dollman, 1915*a*:133; Hollister, 1918:54, NMK); Lakiundu River (Heller, 1912:6; Lonnberg, 1912*b*:54; Hollister, 1918:54); Kinangop (Kollmann, 1913:140); Kirui's, Mt. Elgon, 5000–6000 ft (Dollman, 1915*d*:134); Sirgoit Lake (Hollister, 1918:54); Sirgoit (Hollister, 1918:54); Kakamega (Hollister, 1918:54); Kibabe (Hollister, 1918:54); Naivasha Plains (Hollister, 1918:54); Mt. Kenia, west slope (Hollister, 1918:54); Isiola River, head (Heller, 1912:7; Hollister, 1918:54); Archer's Post (Heller, 1912:7; Hollister, 1918:54); Mt. Mbololo (Hollister, 1918:54); Mt. Umengo (Hollister, 1918:54); Nzoia River, Guas Ngishu plateau (Hollister, 1918:54); Mt. Sagalla (Hollister, 1918:54); Yala River (NMK); Nyeri (NMK); Kaimosi (Hollister, 1918:54; Allen and Lawrence, 1936:42, NMK); Kenna (NMK); Kericho (NMK); Maua (NMK); Mau Forest (Toschi, 1947:12, NMK); Kasigau (NMK); Kisumu (Hollister, 1918:54, NMK); Chania River (NMK); Amala River (Dollman, 1915*d*:132, NMK); Kabete (NMK); Fort Hall (Hollister, 1918:54, NMK); Laikipia plateau, 15 mi N Nyeri (Hollister, 1918:54); Lukosa River (Hollister, 1918:54); Northern Guaso Nyiro (Dollman, 1915*d*:132); Jombeni Range (Dollman, 1915*d*:132); Donya Sabuk (Lonnberg, 1916:6); Cherengani Hills (Ruxton, 1926:29); Zuwani Swamp (Dollman, 1914*a*:88); Nanyuki (Southern and Hook, 1963:512); Thomson's Falls (Southern and Hook, 1963:512); Mt. Kenya, 12,500 ft (Harmsen and Jabbal, 1968:159); Mt. Kenia, 2450 m (Lonnberg, 1912*b*: 54); Luazomela River (Lonnberg, 1912*b*:54); acacia steppe south of Guaso Nyeri (Lonnberg, 1912*b*:54).

Crocidura zaphiri simiolus Hollister, 1916

Crocidura simiolus Hollister, 1916. Smithsonian Misc. Coll., 66(8):3, May. Kisumu, Kenya.

Records.—Kisumu (Hollister, 1916*b*:3; Hollister, 1918:51); Kaimosi (Hollister, 1918: 51); Kibabe (Hollister, 1918:51).

Genus ***Suncus*** Hemprich and Ehrenberg, 1832

Suncus infinitesimus infinitesimus (Heller, 1912)

Pachyura infinitesima Heller, 1912. Smithsonian Misc. Coll., 60(12):5, 4 Nov. Rumruti, Laikipia Plateau, 7000 ft, Kenya.

Records.—Rumruti (Heller, 1912:5).

Suncus lixus aequatorius (Heller, 1912)

Pachyura lixus aequatoria Heller, 1912. Smithsonian Misc. Coll., 60(12):4, 4 Nov. Summit of Mt. Sagalla, 4000 ft, Taita Hills, Kenya.

Records.—Summit of Mt. Sagalla, 4000 ft (Heller, 1912:4; Hollister, 1918:41).

Suncus murinus (Linnaeus, 1766)

Sorex murina Linnaeus, 1766. Syst. Nat., 12th ed., 1:74. Java, Indonesia.

Records.—Lamu (Heller, 1912:5); Witu (Heller, 1912:5).

Remarks.—This introduced species probably has a more widespread distribution, especially along the coast, than these few records represent.

Genus ***Sylvisorex*** Thomas, 1904

Sylvisorex granti mundus Osgood, 1910

Sylvisorex mundus Osgood, 1910. Publ. Field Mus. Nat. Hist., Zool. Ser., 10:18, 7 Apr. Kijabe, Kenya.

Records.—Kijabe (Osgood, 1910*b*:18); west side Mt. Kenya, 7000, 8500, 10,000 ft (Hollister, 1918:39); Mt. Kenya (Duncan and Wrangham, 1971:161).

Remarks.—Two additional locality records, perhaps Mt. Elgon and Cherangani Hills, are plotted by Kingdon (1974:81). The former may be Butandiga, Uganda, reported by Allen and Lawrence (1936:41).

Sylvisorex megalura gemmeus Heller, 1910

Sylvisorex gemmeus Heller, 1910. Smithsonian Misc. Coll., 56(15):7, 23 Dec. Rhino Camp, Lado Enclave, Uganda.

Sylvisorex sorelloides Lonnberg, 1912. Ann. Mag. Nat. Hist., (8)9:67, Jan.; Kungl. Svenska Vet.-Akad. Handl., Stockholm, (2)48(5):51, pl. 3, f. 1, 1912. Steppe near Itiolu River, Northern Guaso Nyiro, Kenya.

Records.—Acacia steppe, near Itiolu River, south of Northern Guaso Nyiro (Lonnberg, 1912*a*:67, 1912*b*:51); Kaimosi (Hollister, 1918:39; Allen and Lawrence, 1936:41); Kirui (Allen and Lawrence, 1936:41).

Genus ***Myosorex*** Gray, 1838

Myosorex (Surdisorex) norae (Thomas, 1906)

Surdisorex norae Thomas, 1906. Ann. Mag. Nat. Hist., (7)18:223, Sept. East side of Aberdare Range, near Nyeri, Kenya.

Records.—East side of Aberdare Range, near Nyeri (Thomas, 1906:224); Aberdare Mountains, 10,000 to 11,000 ft (Hollister, 1918:37); Nr Kiandongoro Gate, Aberdare Mountains, 8400 ft (Duncan and Wrangham, 1971:160).

Myosorex (Surdisorex) polulus (Hollister, 1916)

Surdisorex polulus Hollister, 1916. Smithsonian Misc. Coll., 66(1):1, 10 Feb. West side of Mount Kenya, 10,700 ft, Kenya.

Records.—West side of Mt. Kenya, 10,700 ft (Hollister, 1916*a*:1); west side of Mt. Kenya, 9000 ft to 12,000 ft (Hollister, 1918:37); Mt. Kenya, 12,500 ft (Harmsen and Jabbal, 1968:160); Mt. Kenya, 3960 m (Coe and Foster, 1972:8); Naro Moru track, Mt. Kenya, 10,500 ft (Duncan and Wrangham, 1971:160).

Order Macroscelidea

Family Macroscelididae

Genus ***Petrodromus*** Peters, 1846

Petrodromus tetradactylus sangi Heller, 1912

Petrodromus sultani sangi Heller, 1912. Smithsonian Misc. Coll., 60(12):12. Mt. Mbololo, Taita Hills, 4000 ft, Kenya.

Records.—Mt. Mbololo, 4000 ft (Heller, 1912:12; Hollister, 1918:29; Allen and Lawrence, 1936:39; Loveridge, 1937:526); Voi (Corbet and Neal, 1965:68).

Remarks.—Corbet and Neal (1965:68) reported a skull in the Berlin Museum labelled "Kibwezi" but were uncertain if the record originated from the Chyulu Hills in Kenya or on Mt. Meru in Tanzania.

Petrodromus tetradactylus sultani Thomas, 1897

Petrodromus sultani Thomas, 1897. Proc. Zool. Soc. London, p. 435. Mombasa, Kenya.

Records.—River Mombaca (Guenther, 1881:164); Mombasa (Thomas, 1897:435; Neumann, 1900:541; Davis et al., 1968:844, CM, NMK); Mazeras (Heller, 1912:12; Hollister, 1918:29); Gede (Corbet and Neal, 1965:67, Rathbun, 1979:16, NMK); Msabaha (NMK); Sokoke Forest (CM, NMK); Watamu (NMK); Jilari (Corbet and Neal, 1965:67); Taveta (Thomas, 1910*c*:309; Corbet and Neal, 1965:68; Corbet and Hanks, 1968:70); Shimba Hills (Heller, 1912:13); Rabai Hills (Thomas, 1897:435); Mrima Hill, 30 mi SW Mombasa (Harmsen and Jabbal, 1968:158).

Genus *Rhynchocyon* Peters, 1847

Rhynchocyon chrysopygus Guenther, 1881

Rhynchocyon chrysopygus Guenther, 1881. Proc. Zool. Soc. London, p. 164, pl. 14. River Mombaca, Kenya [=Mombasa, Kenya, according to Moreau et al., 1946:392].

Records.—River Mombaca (Guenther, 1881:164); Gede (Corbet and Hanks, 1968:65; Rathbun, 1978:11, 1979:16, NMK); Mida (NMK); Msabaha (NMK); Sokoke Forest (Corbet and Hanks, 1968:65; Rathbun, 1978:12, CM, NMK); Takaunga (Corbet and Hanks, 1968:65); Arbagundi, Golana River (Corbet and Hanks, 1968:65); Malindi (Corbet and Hanks, 1968:65).

Remarks.—Moreau et al. (1946:392) restricted Guenther's type locality of River Mombaca to Mombasa, Kenya. Corbet and Hanks (1968:65) further qualify the type locality by suggesting a rather vague interpretation of Mombasa as the type locality. *R. chrysopygus* is presently known only from north of Mombasa. Rathbun (1979:9) reports observations at Kombeni River and Boni Forest.

Rhynchocyon petersi petersi Bocage, 1880

Rhynchocyon petersi Bocage, 1880. J. Sci. Math., Phys. Nat., Lisboa, (1)7:159, pl. 4, f. 2 ("Envoye de Zanzibar," restricted to mainland of East Africa, region opposite of Zanzibar, by Dollman, 1912:131).

Records.—Mazeras (Hollister, 1918:28); Rabai Hills (Corbet and Hanks, 1968:64); Shimba Hills (Corbet and Hanks, 1968:64).

Genus *Elephantulus* Thomas and Schwann, 1906

Elephantulus (*Elephantulus*) *rufescens* (Peters, 1878)

Macroscelides rufescens Peters, 1878. Monatsb. K. Preuss. Akad. Wiss., Berlin, p. 198, pl. 1, f. 3. Ndi, Kenya.

Macroscelides boranos Thomas, 1900. Proc. Zool. Soc. London, 1900:802. Mega, western Boran Galla, southeast of Lake Rudolf, Kenya.

Elephantulus dundasi Dollman, 1910. Ann. Mag. Nat. Hist., (8)5:95, Jan. Harich, near Lake Baringo, 3000 ft, Kenya.

Elephantulus phaeus Heller, 1910. Smithsonian Misc. Coll., 56(15):8, 23 Dec. Njoro O Solali, Sotik Dist., Kenya.

Elephantulus delicatus Dollman, 1911. Ann. Mag. Nat. Hist., (8)8:652. Orr Valley, Mt. Nyiro, Kenya.

Elephantulus pulcher rendilis Lonnberg, 1912. Kungl. Svenska Vet.-Akad. Handl., (2)48(5): 49, 26 June. Thera, below Chanler Falls, Northern Guaso Nyiro, Kenya.

Elephantulus rufescens mariakanae Heller, 1912. Smithsonian Misc. Coll., 60(12):10, 4 Nov. Mariakani, Kenya.

Records.—Ndi (Peters, 1878:199); Mega (Thomas, 1900:803); Njoro O Solali, Sotik (Heller, 1910*b*:8; Hollister, 1918:33); Harich (Dollman, 1910:96); Orr Valley, Mt. Nyiro (Dollman, 1911:653; Hollister, 1918:36); Thera (Lonnberg, 1912*b*:51); Mariakani (Heller, 1912:10; Hollister, 1918:33); Mtito Andei (Hollister, 1918:33); Voi (Hollister, 1918: 33; Allen and Lawrence, 1936:40; Corbet and Hanks, 1968:86, NMK); Kabalolot Hill, Sotik (Hollister, 1918:33); Lime Springs, Sotik (Hollister, 1918:33); Loita Plains (Hollister, 1918:33, NMK); Southern Guaso Nyiro (Hollister, 1918:35); Telik River, Sotik (Hollister, 1918:35); North Loroghi (Hollister, 1918:35); Nyama Nyango (Hollister, 1918: 35); Northern Guaso Nyiro River (Hollister, 1918:36); Longaya Water, Marsabit Road (Hollister, 1918:36); Archer's Post (Corbet and Hanks, 1968:86); Taveta (Thomas, 1910*c*: 309; Corbet and Hanks, 1968:86); Kithangaini (NMK); Kilungu (NMK); Kaimoni (NMK); Ngari Nyiro (NMK); Southern Kidong (NMK); Lemek (NMK); 11 mi N Entesekera (NMK); Emali (NMK); Sultan Hamud (NMK); Samburu (NMK); Lokori (NMK); Karuiru (NMK); Taru Desert (NMK); Golbanti (NMK); Kampi ya Samaki (NMK); Kanjangareng (NMK); Mt. Mbololo (Allen and Lawrence, 1936:40); Lodwar (St. Leger, 1937: 525); Wenje (Percy et al., 1953*a*:116, 118); River Kerio Suk (Ruxton, 1926:29); Baringo (Thomas, 1910*c*:310); Zuwani Swamp (Dollman, 1914*a*:88); Nanyuki (Southern and Hook, 1963:511); 12 mi NW Kerio River (Dollman 1914*b*:309); Kerio River (Lonnberg, 1918:175); below Chanler's Falls (Lonnberg, 1912*b*:51); Bushwackers (Rathbun, 1979: 16).

Elephantulus (Nasilio) brachyrhynchus (A. Smith, 1836)

Macroscelides brachyrhynchus A. Smith, 1836. Report of the Expedition for Exploring Central Africa, p. 42. Country between Lake Lakatoo and the Tropic.

Macroscelides delamerei Thomas, 1901. Ann. Mag. Nat. Hist., (7)8:155. Athi River, 6000 ft, Kenya.

Nasilio brachyrhynchus albiventer Osgood, 1910. Publ. Field Mus. Nat. Hist., Zool. Ser., 10(2):13. Lake Elementeita, Kenya.

Records.—Athi River (Thomas, 1901:155); Engare Narok River (Hollister, 1918:31, NMK); Loita Plains (Hollister, 1918:31, NMK); Southern Guaso Nyiro (Hollister, 1918: 31); Ulukenia Hills (Hollister, 1918:31); Bargunett River (Hollister, 1918:31); Engare Ndare River (Hollister, 1918:31); Lesiweru River, Meru Road (Hollister, 1918:31); Naivasha Station (Hollister, 1918:31, NMK); Nyuki River (Hollister, 1918:31); Olorgesailie (Toschi, 1949:27, NMK); Lemik Valley (NMK); Rumuruti (NMK); Wame Hill, Konza (NMK); Amala River (NMK); Voi (Allen and Lawrence, 1936:40); Narrosurra River (Kollmann, 1914:319); Suswa (Kollmann, 1914:319); Guasso Nyero (Kollmann, 1914: 319); Lengototo (Dollman, 1914*b*:309); Lake Elementeita (Osgood, 1910*a*:13).

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Locality names are listed in alphabetical order with variant names cross-referenced to the standard names. Standard names are taken from the second edition of the official standard names gazetteer for Kenya published in 1978 and approved by the United States Board on Geographic Names. Most of the entities can be identified and located on the 1978 version of the Kenya and Northern Tanzania Route Map published in English, French, and German by the Survey of Kenya.

Coordinates for locality names were taken mostly from the Kenyan gazetteer listed above. In addition, Loveridge (1937), Moreau et al. (1946), Chapin (1954), and Davis and Misonne (1964) were consulted together with place modifiers in the original references for published records. In the case of rivers, when no place modifiers were available for the published records or on the specimen labels, coordinates are given for the river mouth or confluence.

In a number of instances, more than one entity exists in Kenya for a place name. This generally does not cause a real problem but does in the case of the locality cited at Ewaso Ngiro and its variants, especially the older specimens labeled Guasso Nyiro. In this latter instance, we have given coordinates for both the southern and northern Ewaso Ngiro rivers in the gazetteer.

Aberdare Mountains	0°25′S, 36°38′E
Aberdare Range	0°25′S, 36°38′E

Amala River	1°02'S, 35°14'E
Amboseli	2°40'S, 37°17'E
Arbagundi	
Archer's Post	0°39'N, 37°41'E
Athi River	1°27'S, 36°59'E
Bargunett River [=Burguret River]	0°01'S, 36°56'E
Baringo [=Mukutan]	0°38'N, 36°16'E
Blue Post	
Burguret River	0°01'S, 36°56'E
Busia	0°28'N, 34°06'E
Chanler's Falls	0°47'N, 38°05'E
Changamwe	4°01'S, 39°38'E
Chania River	1°02'S, 37°04'E
Cherangani Hills	1°15'N, 35°27'E
Chyulu Hills	2°35'S, 37°50'E
Donya Sabuk [=ol Doinyo Sapuk]	1°06'S, 37°15'E
Eldoret	0°31'N, 35°17'E
Elgeyo Forest	0°46'N, 35°31'E
Emali	2°05'S, 37°28'E
Embu	0°32'S, 37°27'E
Engare Nanyuki	0°21'N, 36°55'E
Engare Narok	1°09'N, 36°35'E
Engare Ndare River [=Engare Ondare]	0°35'N, 37°23'E
Engare Ondare	0°35'N, 37°23'E
Eusso Nyiro Post [=Archer's Post]	0°39'N, 37°41'E
Entasekera	1°51'S, 35°51'E
Entesekera [=Entasekera]	1°51'S, 35°51'E
Ewaso Ngiro (Northern)	0°37'N, 36°55'E–0°28'N, 39°55'E
Ewaso Ngiro (Southern)	0°35'S, 35°47'E–2°04'S, 36°07'E
Fort Hall [=Muranga]	0°43'S, 37°09'E
Gede	3°18'S, 40°01'E
Golbanti	2°27'S, 40°12'E
Guasso Nyero [=Ewaso Ngiro]	
Guaso Nyiro River, Sotik District [=Ewaso Ngiro (Southern)]	
Harich [=Marich]	1°32'N, 35°27'E
Horr Valley	2°10'N, 36°55'E
Ijara	1°36'S, 40°31'E
Ilkaputiei	1°38'S, 37°00'E
Isiola River [=Isiolo River]	0°34'N, 37°35'E
Isiolo River	0°34'N, 37°35'E
Itiolu River [=Isiolo River]	0°34'N, 37°35'E
Jilari [=Jilore]	3°11'S, 39°54'E
Jilore	3°11'S, 39°54'E
Jombeni [=Nyambeni]	0°13'N, 57°52'E
Jombeni Range [=Nyambeni Range]	0°20'N, 37°57'E
Juja Farm	1°11'S, 37°07'E
Kabalolot Hill	ca. 1°00'S, 35°23'E
Kabete	1°16'S, 36°43'E
Kagio	0°40'S, 37°13'E
Kaimoni [=Kaumoni]	1°44'S, 37°35'E
Kaimosi	0°08'N, 34°51'E

Kajiado	1°51'S, 36°47'E
Kakamega	0°17'N, 34°45'E
Kakuma	3°43'N, 34°52'E
Kampi ya Samaki	0°36'N, 36°01'E
Kanyakeni [=Kanyekine]	0°08'S, 37°40'E
Kanyangareng	1°47'N, 35'08'E
Kanyekine	0°08'S, 37°40'E
Kapiti Plains [=Ilkaputiei]	1°38'S, 37°00'E
Kapsabet	0°12'N, 35°06'E
Karati	0°26'S, 37°27'E
Karuiro	0°37'S, 37°07'E
Karuiru [=Karuiro]	0°37'S, 37°07'E
Kasigau	3°50'S, 38°40'E
Kathera	0°03'S, 37°35'E
Kaumoni	1°44'S, 37°35'E
Kazere [=Kathera]	0°03'S, 37°35'E
Kenna [=Kinna]	0°19'N, 38°12'E
Kericho	0°22'S, 35°17'E
Kerio River	2°59'N, 36°34'E
Kibabe [=Kibabet]	0°11'N, 35°15'E
Kibabet	0°11'N, 35°15'E
Kijabe	0°56'S, 36°34'E
Kikuyu	1°15'S, 34°40'E
Kilungu	1°48'S, 37°22'E
Kinangop	0°44'S, 36°40'E
Kinna	0°19'N, 38°12'E
Kirui, Mt. Elgon [=Kirui's]	0°50'N, 34°40'E
Kirui's	0°50'N, 34°40'E
Kisumu	0°06'S, 34°45'E
Kithangaini	1°29'S, 37°23'E
Kitui	1°22'S, 38°01'E
Koliokwell River	
Kutu	0°34'S, 37°19'E
Lagari [=Lugari]	0°39'N, 34°53'E
Laikipia	0°25'N, 36°45'E
Laikipia Plateau	0°25'N, 36°08'E
Lake Elementeita [=Lake Elmenteita]	0°27'S, 36°15'E
Lake Elmenteita	0°27'S, 36°15'E
Lake Ilpolosat	0°09'S, 36°26'E
Lake Nakuru	0°22'S, 36°05'E
Lake Olbollosat [=Lake Ilpolosat]	0°09'S, 36°26'E
Lake Olbollossat [=Lake Ilpolosat]	0°09'S, 36°26'E
Lake Sergoi	0°42'N, 35°25'E
Lakiundu River [=Ngaramara River]	0°36'N, 37°37'E
Lamu	2°16'S, 40°54'E
Lemek	1°06'S, 35°23'E
Lemek Valley	1°09'S, 35°19'E
Lemik Valley [=Lemek Valley]	1°09'S, 35°19'E
Lengototo [=Lenkutoto]	1°39'S, 35°58'E
Lenkutoto	1°39'S, 35°58'E
Lesiweru River	
Lime Springs [=Maji Moto]	1°20'S, 35°42'E
Lodwar	3°07'N, 35°36'E

Loita	1°30′S, 35°41′E
Loita Plains	1°20′S, 35°32′E
Lokichokio	4°21′N, 34°21′E
Lokori	1°57′N, 36°01′E
Londiani	0°10′S, 35°36′E
Longaya Water	ca. 1°07′N, 37°38′E
Lorogi	1°00′N, 36°51′E
Luazomela River	0°29′N, 37°40′E
Lugari	0°39′N, 34°53′E
Lukenya	1°31′S, 36°58′E
Lukenya Hills	1°28′S, 37°03′E
Lukenya Mountain [=Lukenya Hills]	1°28′S, 37°03′E
Lukosa River	0°12′N, 34°56′E
Machakos	1°31′S, 37°16′E
Maji Moto	1°20′S, 35°42′E
Malindi	3°13′S, 40°07′E
Mariakani	3°52′S, 39°28′E
Marich	1°32′N, 35°27′E
Marsabit	2°20′N, 37°59′E
Mau Forest	0°20′S–0°40′S, 35°25′E–36°05′E
Maua	0°14′N, 37°56′E
Mayo River	0°10′S, 37°01′E
Mazeras	3°58′S, 39°33′E
Mega	
Merifano	2°19′S, 40°08′E
Meru	0°03′N, 37°39′E
Mianzini	ca. 0°55′S, 36°25′E
Mida	3°19′S, 39°58′E
Molo	0°15′S, 35°44′E
Mombasa	4°03′S, 39°40′E
Mt. Elgon	1°08′N, 34°33′E
Mt. Garguez [=Warges]	0°57′N, 37°24′E
Mount Lololokwi [=Ol Doinyo Sabachi]	0°50′N, 37°32′E
Mt. Kenia [=Mt. Kenya]	0°10′S, 37°20′E
Mt. Kenya	0°10′S, 37°20′E
Mt. Mbololo	3°17′S, 38°28′E
Mt. Nyiro [=Ol Doinyo Ngiro]	2°08′N, 36°51′E
Mt. Sagalla	3°27′S, 38°35′E
Mt. Umengo	ca. 3°18′S, 38°19′E
Moyale	3°32′N, 39°03′E
Mrima Hill	4°29′S, 39°16′E
Msabaha	3°16′S, 40°03′E
Mtito Andei	2°41′S, 38°10′E
Muguga	1°11′S, 36°39′E
Mukutan	0°38′N, 36°16′E
Muranga	0°43′S, 37°09′E
Mweru	0°40′S, 37°05′E
Nairobi	1°17′S, 36°49′E
Naivasha	0°43′S, 36°26′E
Naivasha Plains	0°41′S, 36°27′E
Naivasha Station	0°43′S, 36°26′E
Nakatishu River	0°33′S, 36°38′E

Nandi [=Kapsabet]	0°12′N, 35°06′E
Nanyuki	0°01′N, 37°04′E
Naro Moru	0°10′S, 37°01′E
Narosura River	1°33′S, 35°53′E
Narrosurra River [=Narosura River]	1°33′S, 35°53′E
Ndi	3°14′S, 38°30′E
Neumann's Boma [=Samburu Game Lodge]	0°34′N, 37°35′E
Ngari Nyiro [=Ewaso Ngiro]	
Ngaramara River	0°36′N, 37°37′E
Ngare Nocbor	ca. 2°45′N, 36°45′E
Ngatana	2°13′S, 40°11′E
Ngong	1°22′S, 36°39′E
Njoro O Solali	0°28′S, 35°04′E
North Laroghi [=Lorogi]	1°00′N, 36°51′E
Northern Guaso Nyiro [=Ewaso Ngiro]	0°37′N, 36°55′E–0°28′N, 39°55′E
Nyahururu	0°02′N, 36°22′E
Nyama Nyango [=Samburu Game Lodge]	0°34′N, 37°35′E
Nyambeni	0°13′N, 37°52′E
Nyambeni Range	0°20′N, 37°57′E
Nyeri	0°25′S, 36°57′E
Nyiru [=Ol Doinyo Ngiro]	2°08′N, 36°51′E
Nyuki River [=Engare Nanyuki]	0°21′N, 36°55′E
Nzoia River	0°03′N, 33°57′E
Ol Arabel	0°18′N, 36°18′E
Ol Doinyo Ngiro	2°08′N, 36°51′E
Ol Doinyo Sabachi	0°50′N, 37°32′E
Ol Doinyo Sapuk	1°08′S, 37°15′E
Olgerei River	1°43′S, 35°18′E
Olijoro O Nyon River	ca. 0°57′S, 35°55′E
Olorgasailie	1°34′S, 36°27′E
Orr Valley [=Horr Valley]	2°10′N, 36°55′E
Peccatoni	2°25′S, 40°43′E
Potha	1°34′S, 37°10′E
Rabai Hills	
Ravine Station	0°01′N, 35°43′E
River Kerio Suk	2°59′N, 36°07′E
River Mombaca [=Mombasa]	4°03′S, 39°40′E
Rojewero Plains	0°11′N, 38°10′E
Rumruti [=Rumuruti]	0°16′N, 36°32′E
Rumuruti	0°16′N, 36°32′E
Samburu	3°46′S, 39°17′E
Samburu Game Lodge	0°34′N, 37°35′E
Selengai	2°11′N, 37°10′E
Sera	1°01′N, 37°53′E
Sergoi	0°39′N, 35°23′E
Sergoit Lake [=Lake Sergoi]	0°42′N, 35°25′E
Shimba Hills	4°13′S, 39°25′E
Sirgoit [=Sergoi]	0°39′N, 35°23′E
Sirgoit Lake [=Lake Sergoi]	0°42′N, 35°25′E
Sokoke Forest	3°29′S, 39°50′E
Solai	0°01′N, 36°09′E
Southern Guaso Nyiro [=Ewaso Ngiro]	2°04′S, 36°07′E

Southern Kedong Valley	ca. 1°24'S, 36°27'E
Southern Kidong [=Southern Kedong Valley]	ca. 1°24'S, 36°27'E
Sultan Hamud	2°01'S, 37°22'E
Takaungu	3°41'S, 39°51'E
Talek River	1°26'S, 35°04'E
Taru Desert	3°45'S, 39°08'E
Taveta	3°24'S, 37°41'E
Telek River [=Talek River]	1°26'S, 35°04'E
Thera [=Sera]	1°01'N, 37°53'E
Thika	1°03'S, 37°05'E
Thomson's Falls [=Nyahururu]	0°02'N, 36°22'E
Tsavo	2°59'S, 38°28'E
Tsavo River	2°59'S, 38°31'E
Ulukenia [=Lukenya]	1°31'S, 36°58'E
Ulukenia Hills [=Lukenya Hills]	1°28'S, 37°03'E
Upper Nzoia River	ca. 0°53'N, 35°22'E
Upper Ura River	ca. 19°10'N, 37°59'E
Voi	3°23'S, 38°34'E
Wambugu	0°35'S, 37°02'E
Wame Hill [=Wami Hill]	1°39'S, 37°08'E
Wami Hill	1°39'S, 37°08'E
Warges	0°57'N, 37°24'E
Watamu	3°21'S, 40°01'E
Wema	2°13'S, 40°11'E
Wenje	1°47'S, 40°06'E
West Slope Mt. Kenya	0°10'S, 37°10'E
Witu	2°23'S, 40°26'E
Yala River	0°04'N, 34°09'E
Ziwani	3°23'S, 37°47'E
Ziwani Swamp	3°16'S, 37°47'E
Zuwani [=Ziwani]	3°23'S, 37°47'E
Zuwani Swamp [=Ziwani Swamp]	3°16'S, 37°47'E

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DEVONIAN AND MISSISSIPPIAN CONULARIIDS OF NORTH AMERICA. PART A. GENERAL DESCRIPTION AND *CONULARIA*

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Abstract

The systematics, morphology and paleoecology of the new phylum Conulariida proposed here, from the Devonian and Mississippian rocks of North America are reviewed in this two-part work. Conulariids are identified by an elongate, pyramidal exoskeleton comprising a framework of calcium phosphate rods, with or without spines and nodes, covered by an integument made of thin layers of calcium phosphate and protein. Conulariids were gregarious invertebrate animals that were attached to substrata by means of calcium phosphate or chitinous stalks. These animals were exclusively marine and limited to rocks of the Ordovician through the Triassic. Conulariids are found in all types of marine facies and most probably had either a pseudoplanktonic or a benthonic lifestyle.

Three valid genera of conulariids are recognized in the Devonian and Mississippian of North America. These are *Conularia* Miller *in* Sowerby, 1821, *Paraconularia* Sinclair, 1940*a* and *Reticulaconularia* Babcock and Feldmann, n. gen. The genus *Diconularia* Sinclair, 1952 is considered to be a junior synonym of *Conularia.* Prior to 1986, 69 species-level taxa of conulariids were described from the Devonian and Mississippian of North America. Herein, and in Part B, 28 species are recognized as valid. Eleven species are assigned to *Conularia* and are described in Part A.

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INTRODUCTION

Conulariids, members of an extinct phylum of invertebrates, have been described in the literature for a span of nearly 200 years. In that time, well over 400 species, subspecies or varieties, and over 40 genera have been named.

The purpose of this paper, and Part B of the same work, is to present taxonomic and morphologic information obtained from an examination of conulariids from Devonian and Mississippian strata of North America. Approximately 12% of all species-level conulariid taxa have been described based upon specimens collected from these rocks. Specimens described herein were collected only from the United States and Canada; conulariids are not known to have been collected in Mexico. This work involves: 1, studies of intraspecific and interspecific variation in morphology, ideally based upon large numbers of specimens; 2, studies of the stratigraphic and geographic distributions of species; and 3, analyses of conulariid anatomy, functional morphology and paleoecology, as the fossil record permits. Each taxon identified from Devonian or Mississippian rocks of North America is accompanied by a new, or in some cases, the first, illustration, and a description highlighting points of morphology now considered of greatest taxonomic value.

In the course of examining the Devonian and Mississippian forms, it became clear that it was necessary to revise the terminology related to morphology. In so doing, it was considered essential that conulariids from a much wider range of geological and stratigraphical occurrences had to be examined than those treated systematically herein. Thus, the detailed morphology and terms are intended to be applicable to all organisms referable to the Conulariida.

Part A of this work comprises a general description of the hard- and soft-part morphology of conulariids, occurrences and paleoecology of Devonian and Mississippian taxa of North America, a summary of the taxa treated both in this paper and in Part B, a key to the Devonian and Mississippian conulariid taxa of North America, and descriptions of species of that group which are referred to the genus *Conularia*. Part B of this work contains descriptions of species referable to the genera *Paraconularia* and *Reticulaconularia* n. gen. and specimens described in the literature as conulariids but which are here rejected from the phylum. Locality descriptions and measurements of selected specimens are included as appendices to Part B. Figures are numbered consecutively in both Parts A and B in order to avoid cross-reference confusion.

MORPHOLOGY

General.—When preserved in three dimensions, the exoskeleton of a conulariid generally has a four sided, bilaterally symmetrical, elongate pyramidal shape (Fig. 1.1). The profile may be modified by the development of one or more exoskeletal constrictions (Fig. 1.1). The exoskeleton, as preserved, generally ranges from 2 to 10 cm in length in full grown individuals. In a few species, however, the exoskeleton may attain a length in excess of 20 cm (Fletcher, 1938; Lamont, 1946; Sinclair, 1948; herein, Fig. 11.2). In nearly all instances, the conulariid exoskeleton diverges in width gradually and uniformly from a closed apical end to an open apertural end. The apical end may be closed either by a (morphological) apex (Fig. 1.1) or by an apical wall (Fig. 1.2). Presumed soft-parts consist of a single tubular structure that runs internally along the length of the exoskeleton and at least one globular body (Fig. 2.1).

Morphologic terms.—The literature on conulariid morphology includes important review papers by Slater (1907), Bouček and Ulrich (1929), Kiderlen (1937), Richardson (1942), Sinclair (1948, 1952), Moore and Harrington (1956*a*, 1956*b*) and Babcock and Feldmann (1986). Much misunderstanding of conulariid morphology has arisen from terms that have been improperly defined or undefined, from terms that are ambiguous and from terms that imply systematic affinities. Babcock and Feldmann (1986) proposed a set of morphological terms for conulariids that described morphological features without introducing unnecessary connotations of genetic affinities. Below is a list of morphological terms applied to conulariids, modified from Babcock and Feldmann (1986), together with terms here considered synonymous and which relate to the morphology of members of the phylum but are inappropriate in the light of advances made during this study.

ADAPERTURAL SPINE—long spine projecting from near the adapertural side of a rod, in the direction of the aperture.

ADAPICAL SPINE—short spine projecting from near the internal adapical side of a rod, in the direction of the apex.

ALIMENTARY TRACT—narrow, elongate, essentially tubular soft-part structure running the length of the central cavity. Synonyms: axial element, intestine.

ANGULATED CIRCULAR CURVE—style of rod articulation in which two abutting rods on a face form a broad arcuate, adapically concave ridge, interrupted by a slight adapertural point at the midline, and by gentle adapertural turns in the vicinity of the facial margins.

APERTURAL CONSTRICTION—exoskeletal constriction located nearest the aperture. Synonym: wrinkle.

APERTURE—opening at widest end of exoskeleton. Synonyms: base, mouth, opening.

APERTURAL TERMINATION—rounded or bluntly subtriangular extension of exoskeleton on each face at widest end of exoskeleton.

APEX (MORPHOLOGICAL APEX)—narrowest termination of exoskeleton, where the four faces join at a closed point. Synonyms: (biological) apex, summit. Compare with *hypothetical apex.*

APICAL ANGLE—hypothetical angle formed by one face of the exoskeleton; measured at the intersection of two lines each identified by tracing positions on the exoskeleton

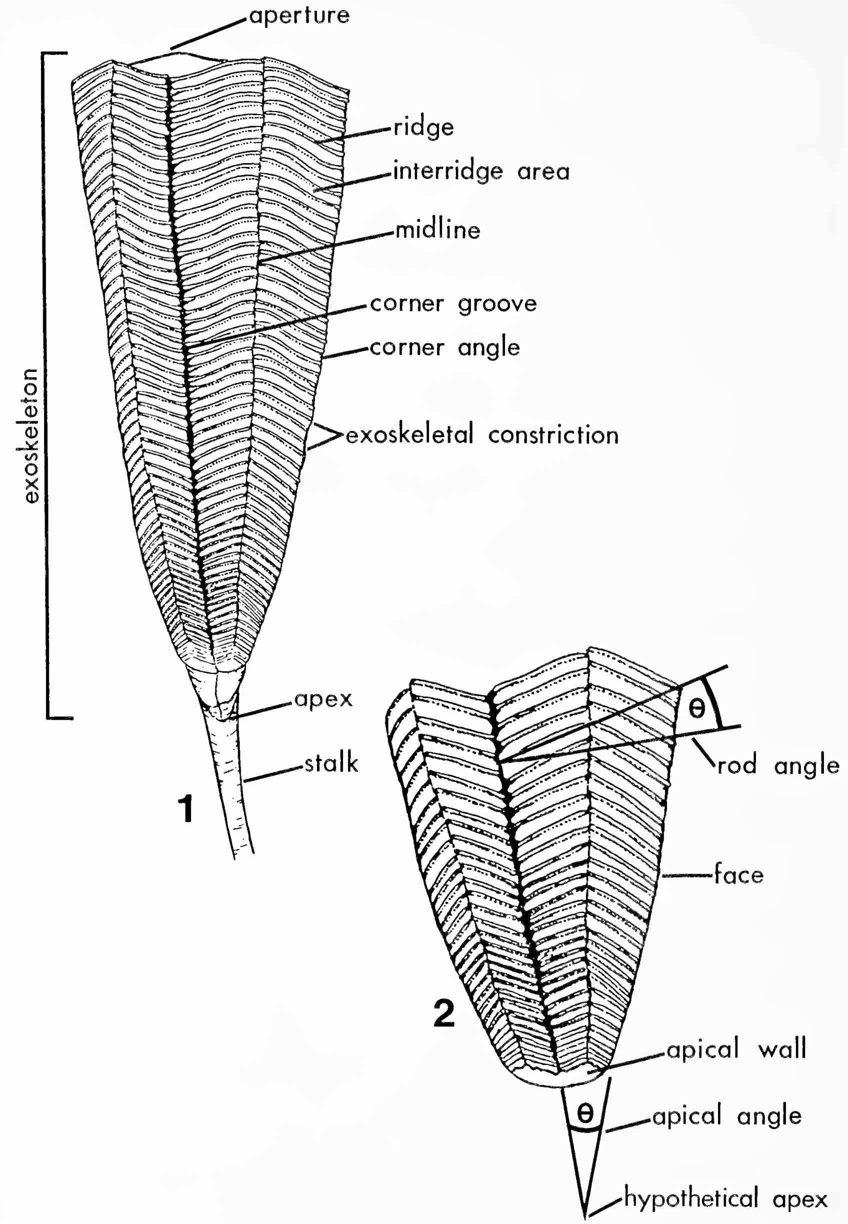


Fig. 1.—Conulariid morphology, exhibited by a generalized *Paraconularia*. 1.1; exoskeleton with stalk attached. 1.2; apical region with stalk removed. Morphological terms are explained in the text.

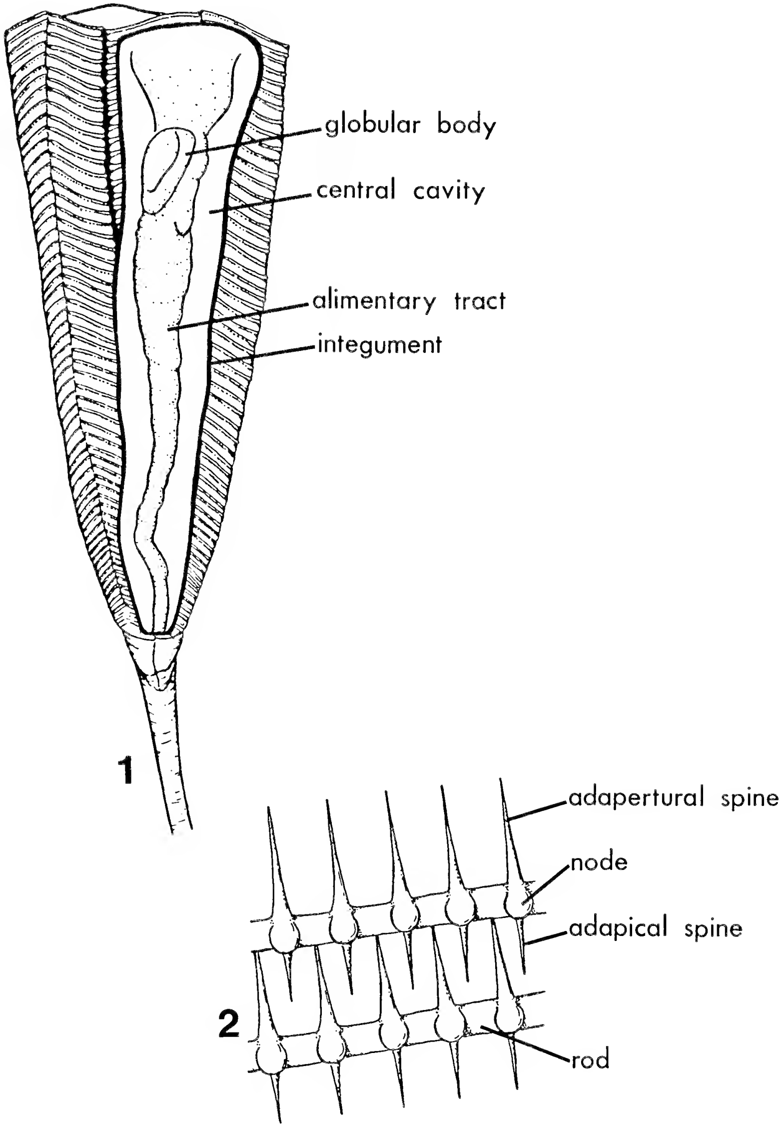


Fig. 2.—Conulariid morphology, exhibited by a generalized *Paraconularia*. 2.1; cutaway view of exoskeleton showing internal soft-parts. Structure of the soft-parts in the apertural region is problematic. 2.2; detailed view of two rods. Morphological terms are explained in the text.

tangential to the facial margins and defining the maximum angle of separation. Synonym: facial angle. See *major apical angle* and *minor apical angle.*

APICAL WALL—broadly rounded, adapically convex, portion of integument lacking rods which completely covers the apical end of the exoskeleton when the apex itself is missing. Synonyms: apical septum, apical diaphragm, basal limitation, diaphragm, internal partition, *Schott,* septum.

CENTRAL CAVITY—region located internal to the four faces of the exoskeleton. Synonym: body cavity.

CORNER ANGLE—longitudinal line in the marginal region of a face connecting points of greatest inflection of the rods. Synonym: shoulder.

CORNER GROOVE—longitudinal invagination of exoskeleton connecting points where pairs of rods from adjacent faces cross near the marginal terminations of those rods. Synonyms: angular furrow, articulating suture, edge, lateral channel, longitudinal channel, marginal furrow, marginal groove, side furrow.

EXOSKELETAL CONSTRICTION—depression, restricted in the longitudinal direction, traceable on all four faces of the exoskeleton in the same relative position. Compare with *apertural constriction.*

EXOSKELETON (SKELETON)—four sided pyramidal structure, open at the widest end and closed at the narrowest end, comprising rods joined by integument. Synonyms: periderm, pyramid, shell, test.

FACE—one of four sides of the exoskeleton crossed by ridges; it is delimited by the aperture, by the apex or the apertural wall and by two corner grooves. Synonyms: side, surface, wall. See *major face* and *minor face.*

GLOBULAR BODY—large internal soft-part structure, subovoid in outline, located near the aperture. Synonym: esophagus.

GOTHIC ARCH—style of rod articulation in which two adjacent rods on a face form ridges that meet at an obtuse, adapically concave angle at the midline and proceed away from the midline along lines subtly curved adapically.

HYPOTHETICAL APEX—point in space where two lines, traced along the mean direction of the corner angles; meet; the hypothetical apex may or may not coincide with the position of the (morphological) apex.

INFLECTED CIRCULAR CURVE—style of rod articulation in which two adjacent rods on a face form a broadly arcuate, adapically concave ridge except in the vicinity of the facial margins, where they turn gently adaperturally.

INFLECTED GOTHIC ARCH—style of rod articulation in which two adjacent rods on a face form ridges that meet at an obtuse, adapically concave angle at the midline and proceed away from the midline along lines subtly curved adapically except in the vicinity of the facial margins, where they turn gently adaperturally.

INTEGUMENT—multilayered, presumably flexible, structure composed of calcium phosphate and protein, within which rods and spines were embedded and held in position. Synonyms: periderm, test.

INTERRIDGE AREA—roughly transverse band of integument located between two facial ridges. Synonyms: intercostal space, interspace, transverse furrow, transverse sulcus, space.

INTERRIDGE CREST—raised area, usually a linear ridge, located in an interridge area and positioned at a right angle to a ridge; formed by integument covering an adapertural or adapical spine. Synonyms: bar, intercostal longitudinal striation, vertical striation, longitudinal bar, longitudinal striation.

INTERRIDGE FURROW—low area, usually linear, located in an interridge area, and between two interridge crests.

INTERROD AREA—open region located between two rods; exposed only when integument is absent.

MAJOR APICAL ANGLE—apical angle subtended by a major face.

MAJOR FACE—wider of two adjacent faces.

MARGIN (FACIAL MARGIN)—longitudinal edge of a face, or a line connecting points where two faces meet in a corner groove.

MIDLINE—longitudinal line connecting points where either two adjacent rods on a face meet, or central to the facial terminations of each pair of adjacent rods if the rods do not meet. The midline can be expressed as either a thin groove or a raised line if the integument is preserved. The midline seems to be pigmented in some specimens. Synonyms: central face furrow, central facial groove, facial groove, facial midline, longitudinal carina, median groove, median line, mesial furrow, mid-line, middle line, parietal line, septum, structural channel.

MINOR APICAL ANGLE—apical angle subtended by a minor face.

MINOR FACE—narrower of two adjacent faces.

NODE—minute, subcircular, raised surface on a rod or ridge. Synonyms: granule, papilla, tubercle, pustule, wart.

RIDGE (FACIAL RIDGE)—raised line crossing a face from a corner groove to the midline area, and formed by integument covering a rod. Synonyms: costa, crenulation, ornamental rib, plica, plication, rib, riblet, transverse line, transverse rib, transverse ridge, transverse striation.

ROD—narrow, elongate structure that is subcircular in cross section, composed of calcium phosphate, and embedded within the integument; it is thickened near the marginal termination, and tapers very gradually to a blunt point at the facial termination.

ROD ANGLE—angle subtended by a line connecting the two most distant points of a rod along a longitudinal line and a line constructed perpendicular to the facial margin at the point where that ridge intersects the corner angle. Synonym: angle at the midline.

ROD PAIR—two rods on a face whose distal ends meet, or approach closely, at the midline.

SKELETON—See *exoskeleton.*

SPINE—solid, narrow, short or elongate structure, projecting from, and whose axis is at a right angle to, a rod; tapers gradually to a sharp point distally. See *adapical spine* and *adapertural spine.*

STALK—elongate structure, possibly chitinous, phosphatic, or chitinophosphatic, which articulates proximally with a conulariid apex; distally, the structure seems to attach to a substratum of uncertain nature.

Abandoned morphological terms.—The following terms, previously used in connection with the description of conulariids, are here considered inappropriate for various reasons including: 1, the structures have been shown to be taphonomic in origin; 2, the structures were described from organisms which should be excluded from the phylum Conulariida; 3, the structures have been shown to be absent in conulariids; or 4, the structures were described from dubious fossil material.

ANUS.

APPENDIX.

APERTURAL LOBE. Synonyms: apertural flap, apertural lip, flap, laterales, lobe, lip, mouth flap.

ATTACHMENT DISC.

BODY WALL.

EYE LENS.

HINGE.

FEATHER EDGE.
KEEL.
LATERAL LINE. Synonym: longitudinal line, line near midline.
MOUTH PANEL.
NERVE CENTER.
NET-SHAPED EPITHELIUM.
ORNAMENTATION. Synonym: sculpture.
PLATE. Synonym: transverse plate.
SEPTUM: Synonyms: carina, internal longitudinal rib, internal rib, internal rod, internal septum, longitudinal septum.
SKIN-MUSCLE LINING.
URULA.
WALL OPENING.

Aperture.—The aperture (Fig. 1.1) appears to have been a simple opening at the larger termination of the pyramidal exoskeleton. This region has been the subject of much speculation. "Flaps" or "lappets," partially or wholly closing the apertural region, were first described by Miller (*in* Sowerby, 1821), and subsequently by Etheridge (1901), Laseron (1912), Richter and Richter (1930), Reed (1933), Kowalski (1935), Kiderlen (1937), Sinclair (1948), Moore and Harrington (1956*b*), Branisa (1965) and others. Kiderlen (1937), Termier and Termier (1949) and Moore and Harrington (1956*b*) proposed elaborate mechanisms for closure of the apertural region involving the infolding of a flexible exoskeleton. They assumed the line of flexure to be a straight line normal to the midline. In one mechanism of closure, the exoskeleton not only folded along a straight line perpendicular to a face, but also collapsed like a bellows in the vicinity of the corner angles (Moore and Harrington, 1956*b,* Fig. 43.1). Moore and Harrington (1956*b,* p. F57) suggested that, in order for a conulariid to have been so flexible in the apertural region, the line of flexure at the base of each "apertural flap" was chitinophosphatic, while the remainder of the exoskeleton was phosphatic. No chemical data were presented in support of this hypothesis.

Specimens exhibiting closed or partially restricted apertures are common. Over 200 such specimens were observed in the course of this study (for example, Figures 8.1, 10.1, 28.2). Among these, there is no evidence of a consistent line of flexure (for example, Fig. 7.1–7.2, 8.7–8.9, 10.2, 18.2, 22.2–22.3). Typically, the line along which a flap is developed is not straight. Instead, the line of flexure often mimics the style of rod articulation or seems to be arbitrary. No two adjacent faces on the same specimen necessarily fold inward at the same position. Within the same species, there is no consistency from individual to individual either in the placement of a line of flexure or in the mode of closure, as defined by Kiderlen (1937), Termier and Termier (1949) or Moore and Harrington (1956*b*). Furthermore, "apertural flaps" have been observed at multiple sites on single conulariid exoskeletons (Babcock and Feldmann, 1986, fig. 1E). Their presence at various places on the exoskeleton of different specimens indicates that they are taphonomic phenomena. Richter and Richter (1930), noted the extreme flexibility of the holotype of *Conularia tulipa* from the Hünsruckshiefer (Lower Devonian) of Germany. In their opinion, the conulariid exoskeleton was flexible enough to have collapsed under its own weight. Infoldings of exoskeleton commonly found in the apertural region, and less commonly elsewhere on a conulariid, are probably taphonomic structures resulting from collapse of the exoskeleton after death. The exoskeleton may not be quite as weak as suggested by Richter and Richter, but it is certainly not as rigid as a mollusk shell.

Apex.—The apical end of a conulariid may be: 1, a narrow, blunt point (Fig. 1.1); 2, truncated (Fig. 7.6); or 3, truncated, but having the end covered by a smooth, convex, imperforate apical wall (Fig. 1.2). The apex of a conulariid has been interpreted as a sharp point, as a bluntly rounded structure, as a smooth, imperforate wall, or as a smooth wall with a centrally located hole. Since the work of Kiderlen (1937), conulariids have been thought of as metazoans having a sharp point in the juvenile state. Presumably, the point was attached by an attachment disc to a hard substratum. Support for Kiderlen's argument was provided by supposed conulariids which were previously described by Ruedemann (1896*a,* 1896*b*). The specimens described by Ruedemann seem to be tubes of *Sphenothallus* (Feldmann et al., 1986). *Sphenothallus* has recently been shown to be unrelated to conulariids (Mason and Yochelson, 1985).

Apices of conulariids are exceedingly rare. The apices are not pointed as once interpreted, but are slightly rounded (Figs. 7.6, 16.6, 33.1–33.2). During life, most or all conulariids were attached by an elongate stalk (Figs. 1.1, 24.1–24.2, 32.5) to some substratum, during at least part of the life cycle. The apex was sheathed by the proximal portion of the stalk. Breakage at the proximal end of the stalk may possibly explain why so few conulariids are observed that have their apices intact.

Authentic conulariids with attachment discs have never been described. Small, round, black, and presumably chitinous or chitinophosphatic, bodies attached to bryozoans or brachiopods have been identified in various museum collections as conulariid attachment discs. Often, the presumed base of a tube is preserved connected to such a structure. Such tubes are circular or subcircular in cross section. These problematic fossils probably represent attachment devices of some type of organism, but a relationship to conulariids has not been demonstrated.

Smooth, imperforate apical walls have been noted by many authors

(Miller *in* Sowerby, 1821; Hall, 1876, 1879; Slater, 1907; Richter and Richter, 1930; Sinclair, 1948; Moore and Harrington, 1956*b*; Babcock and Feldmann, 1984, 1986, herein, Figs. 4.1, 10.4, 11.2, 14.1, 14.4, 15.4, 19.1). These structures have been termed septa, apical diaphragms or *Schotten.* None of these terms seems appropriate, either because of its genetic implications or because of an incomplete description of the morphology. Apical walls are single units of integument that cover the convergent end of a conulariid close to the apical terminus. An apical wall is not located at the apical terminus itself, but seems to be attached to the interior of the faces on the exoskeleton, slightly adaperturally of this region. The line of juncture of the apical wall with the remainder of the integument always seems to occur near the narrowest portion of an exoskeletal constriction. Apical walls appear to lack support from rods or other structures, and may be bowed slightly in the adapical direction. Multiple apical walls may be present in single individuals (Eichwald, 1860; Steinmann and Doderlein, 1890; Slater, 1907; Sinclair, 1948).

References to conulariids with centrally perforated apical walls include Slater (1907), Richardson (1942), and Swartz and Richardson (1945). A collapsed specimen of *Conularia congregata* exhibiting a subcircular structure located centrally on the apical wall is illustrated in Figure 4.1. This subcircular structure is interpreted as having resulted from the compression of a thin, flexible apical wall against the apical portion of some soft-part morphologic feature such as the alimentary tract.

The function of the apical wall may have been to seal off the portion of the central cavity in which the conulariid lived from the stalk and older, unused portions of the body. In specimens preserving apical walls, the most apicad portions of exoskeleton are not smooth (Figs. 11.2, 14.1). This indicates that conulariid exoskeletons like these may have been torn from their stalks by current forces. It is also possible that some few conulariids periodically may have shed unused portions of the exoskeleton (Babcock and Feldmann, 1984).

Apical angle.—An apical angle is measured at the intersection of two lines projected by tracing tangent lines along the trend of two adjacent corner grooves (Fig. 1.2). Apical angles are typically in the range of 8° to 26°.

The apical angle, as measured on a large segment of a specimen, may differ, by several degrees, from the apical angle as measured on a small section of the skeleton (see Appendix B in Part B). Small segments, particularly at exoskeletal constrictions and near the apex, usually yield somewhat larger apical angles than generalized apical angles, measured over a large segment of an exoskeleton.

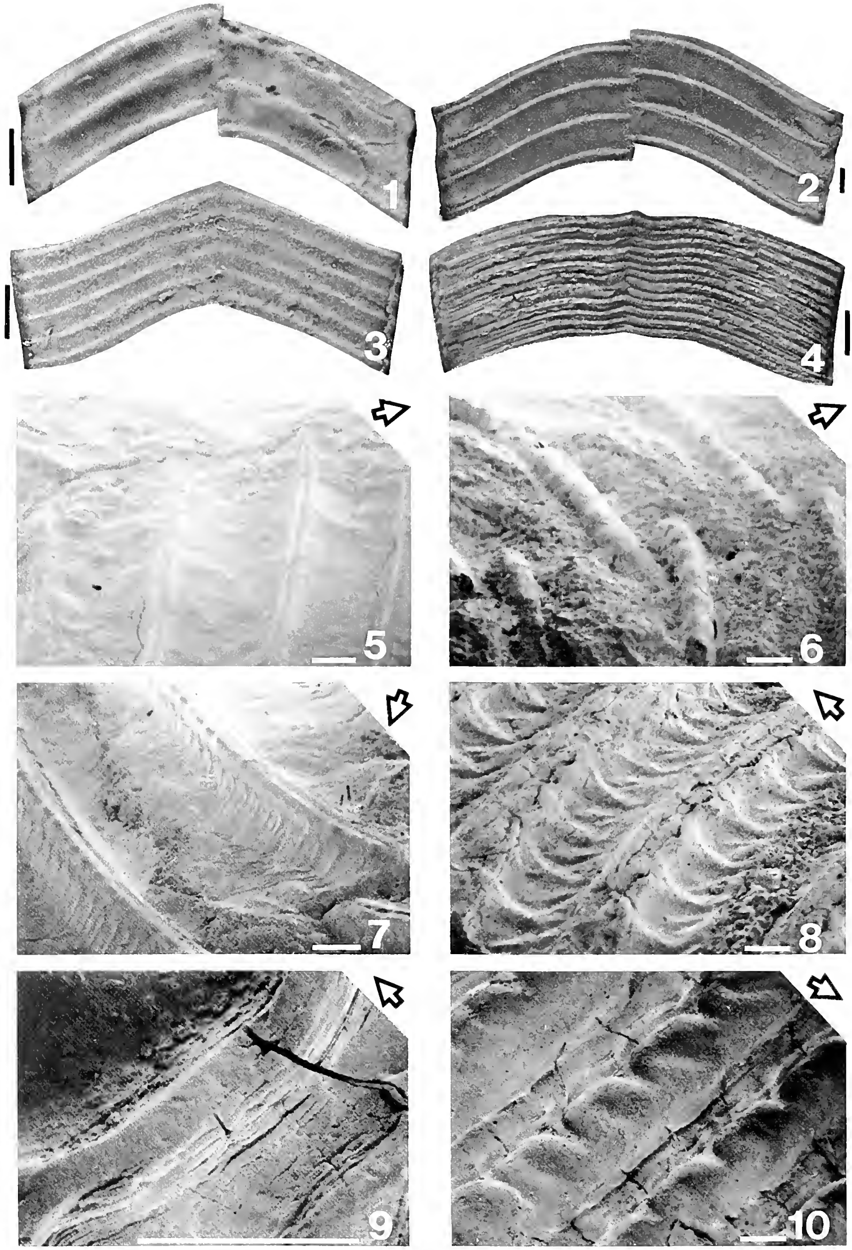
A difference in the acute apical angle between adjacent sides of a conulariid, mostly attributed to compression, has been noted by numerous authors, including Barrande (1867), Hall (1879), Slater (1907), Bouček (1939), and Sinclair (1948). Studies of compressed and presumably uncompressed materials indicate that opposite sides of a conulariid exoskeleton are paired (Babcock and Feldmann, 1984, 1986). In cross section, a conulariid is typically rectangular, if only slightly so (Figs. 30.4, 33.4). Each face subtends an apical angle equal to that of the face opposite it, but different from either adjacent face. This suggests that conulariids are bilaterally symmetrical, rather than tetramerally symmetrical, metazoans (Babcock and Feldmann, 1984, 1986). Rhomboid-shaped conulariids may exist, but most forms that are thought to have a rhomboidal cross section probably were described from subtly compressed specimens.

Faces.—In most cases, the four faces of the conulariid skeleton are essentially planar (Fig. 1.1). At least two forms, *Mesoconularia cahuanotensis,* from the Devonian of Bolivia (Branisa and Vanek, 1973) and *M. solitaria,* from the Silurian of Czechoslovakia (Sinclair, 1948), have faces that are markedly curved. In *Anaconularia anomala* from the Ordovician of Czechoslovakia, Kiderlen (1937) described a clockwise torsion of the exoskeleton, up to 40°. However, examination of eleven specimens referable to this taxon (GSC 85063–85073) indicates that these fossils, preserved in quartzite, are not twisted or compressed in a uniform fashion. Therefore, the "torsion" which Kiderlen observed may, in fact, be related to post-mortem diagenetic effects.

The two faces on a conulariid exoskeleton which subtend apical angles equal to each other, but smaller than the remaining two faces, are termed minor faces. Those two faces having larger apical angles are termed major faces.

Integument.—The thin walls, or faces, of the exoskeleton are made up of a multilayered calcium phosphate and protein integument (Ed Landing, personal communication, 1984; based upon electron microprobe analyses of specimens of *Paraconularia byblis* and *P. subulata* from locality 190). The precise number of layers and the extent to which this number is consistent from species to species has yet to be determined. In one example of *Conularia desiderata,* analyzed under the scanning electron microscope, at least thirty very thin, but discrete, layers of calcium phosphate were observed (Fig. 3.9). This stands in marked contrast to previous interpretations of the histology of the conulariid integument (for example, Sinclair, 1940*b,* 1948; Richardson, 1942), in which only two or three layers were observed through use of standard light microscopy.

Rods.—Rods (Fig. 2.2), embedded in the integument, are support structures which cross each face transversely; they are composed of calcium phosphate and are subcircular in cross section.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Each rod crosses one half of each face transversely until its distal end abuts with, or alternates with, the distal end of an adjacent rod. Proximally, rods of adjacent faces articulate in a corner groove. When covered by integument, a rod forms a thin ridge which traverses one half of each face of a conulariid skeleton.

A rod may be equipped with numerous spines (Fig. 2.2) which project adaperturally or adaperturally and adapically. When both types of spines are present, adapertural spines seem to be longer than adapical spines. The function of a spine was probably to provide a stronger framework to support the integument (Figs. 2.2, 3.8). Most conulariid species possess rods which have spines. Some, however, such as *Paraconularia planicostata* (for example, Fig. 3.1) and *P. subulata* (for example, Figs. 3.2, 3.6), have integument supported by rods alone.

Rods may or may not possess small nodes on the external side of the exoskeleton (Fig. 2.2). Nodes, if present, are arranged in a single row along a rod. These structures occur slightly adapically of each adapertural spine in all of the taxa reported herein (for example, Fig. 3.7). Thus, the number of adapertural spines and the number of nodes are equal. In *Paraconularia sorrocula,* the nodes seem to be fused with the adapertural spines, forming a single structure (Fig. 28.2).

The manner of rod articulation has long been used as a diagnostic character at the species level (Hall, 1859; Barrande, 1867; Holm, 1893). To delineate a "natural grouping" of the conulariids, Holm (1893) identified four species groups, based partially upon ridge characteristics. Richardson (1942) identified four modes of ridge arching among organisms which were then considered conulariids, presumably including

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Fig. 3.—3.1–3.4; rod articulation styles. 3.1; USNM 33785, *Paraconularia planicostata* (Dawson) showing gothic arch style; locality 165. 3.2; NYSM 3491, *P. subulata* (Hall) showing inflected circular curve style; locality 203. 3.3; AMNH 33018, *Conularia pyramidalis* Hall showing inflected gothic arch style; locality 117. 3.4; AMNH CU 282G, *C. elegantula* Meek showing angulated circular curve style; locality 174. 3.5–3.10; scanning electron micrographs; arrows point in apertural direction. 3.5; USNM 395833, *P. subulata* (Hall); view along midline showing integument draped loosely over rods; locality 190;. 3.6; USNM 395834, *P. subulata* (Hall), rods at midline, integument lacking; locality 72. 3.7; USNM 395830, *P. byblis* (White); integument closely draped over rods; locality 190. 3.8; USNM 395832, *C. desiderata* Hall, view of ridges, interridge crests and interridge furrows; rods have been broken away; locality 135. 3.9; USNM 395832, same specimen as in Fig. 3.8, *C. desiderata* Hall, ridge with rod removed, showing multilayered integument; locality 135. 3.10; USNM 395832, same specimen as in Fig. 3.8, *C. desiderata* Hall, view showing ridges with rods broken away, interridge crests and interridge furrows; locality 135. Bar scales equal 1 mm for Figs. 3.1–3.4 and 0.1 mm for Figs. 3.5–3.10.

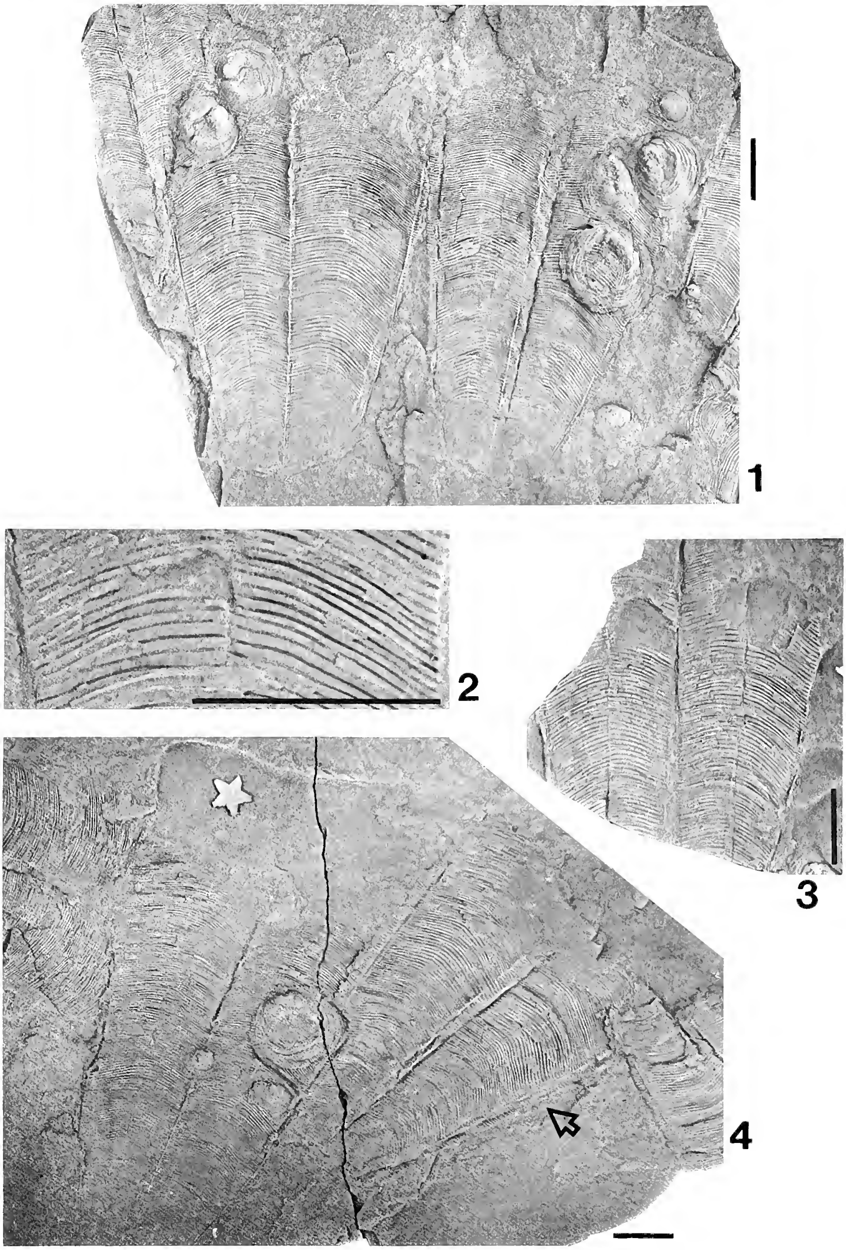

Fig. 4.—*Conularia congregata* Hall. 4.1; NYSM 3483, several paralectotypes from slab exhibiting lectotype and twelve paralectotypes, preserved in black shale. Note that shells

Sphenothallus, now considered a worm (Mason and Yochelson, 1985; Feldmann et al., 1986). Babcock and Feldmann (1986) recognized four modes of rod articulation which produce patterns of ridges useful as species-level taxonomic criteria. Their terminology for rod articulation patterns is followed herein; examples of each style are given in Figs. 3.1–3.4.

One additional feature of rod articulation at the midline is of interest for species-level determination of taxa. The two rods on a face which meet, or approach closely, at the midline are termed a rod pair. If the right rod of a rod pair is closest to the aperture when the specimen is examined with the aperture upward, the pattern of articulation is right superior (for example, Figs. 3.1, 3.2, 3.6). Conversely, if the left rod of a rod pair is closest to the aperture, the pattern is termed left superior (for example, Fig. 3.5). Some species can be distinguished from others, in part, by the relative proportions of right superior to left superior and to abutting rods on the major and minor faces.

An angle subtended by lines connecting the distal point of a rod with the point at which it joins the corner angle and a line projected across a face, perpendicular to the trend of the corner angle, from the point where a rod joins the corner angle, is termed a rod angle (Fig. 1.2). The description of a rod angle, combined with information on the style of rod articulation, is used herein as an effective way to help distinguish conulariid species. Rod angles generally vary across an exoskeleton within a few degrees. Notable changes in rod angles are often observed at the narrowest points of exoskeletal constrictions.

A complex of structures is produced on the external surface of the exoskeleton when the integument is draped over a framework of rods and spines. When integument covers a spine, an interridge crest is formed; when integument is draped between two adjacent spines, an interridge furrow is produced. A specimen preserved with the integument draped loosely over the rod and spine framework may appear to be of a different species than a specimen having integument diagenetically compressed close to the framework. It may also appear to be different from a specimen which lacks the integument altogether.

Midline.—A line, of variable distinctness, runs longitudinally down the middle of each face (Fig. 1.1). This line, termed the midline, may be a raised structure or a groove, and seems to be pigmented in some

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of the inarticulate brachiopod *Discina humilis* Hall are attached to the conulariid exoskeletons; locality 154. 4.2; NYSM 3484, detail of ridge structure as preserved in a counterpart specimen. 4.3; NYSM 3484, same specimen as in Fig. 4.2; locality 154. 4.4; NYSM 3483; lectotype and three paralectotypes exposed on same slab as specimens in Fig. 4.1; lectotype is indicated by an arrow. Bar scales represent 1 cm.

cases (Fig. 23.5). Wiman (1895), Knod (1908), and Liu (1981) have published hand-drawn figures of three separate structures radiating inward from the midlines of conulariids. Wiman (1895) described large T- or Y-shaped "septa," Liu (1981) figured elongate "septa" and Knod (1908) figured localized thickenings of integument. Among specimens examined from Devonian and Mississippian rocks of North America, there seems to be no evidence of an elongate, inwardly-directed structure associated with the midline. However, a thickening of the midline, on the internal side of the exoskeleton, has been observed on specimens of *Paraconularia ulrichana* from the Devonian of Bolivia. In some cases, there appears to be an invagination of the exoskeleton from the interior at the midline (Fig. 14.2).

Corner groove.—A corner groove (Fig. 1.1) is the facial invagination at a corner of the exoskeleton where two faces meet at right angles. An individual rod articulates proximally with an adjacent rod in a corner groove; rods on adjacent faces alternate in position along the corner groove. No evidence of localized thickenings of integument interior to the corner grooves, as described by Knod (1908), has been observed. The points of articulation of the rods in the corner grooves seem to be nodose swellings (Fig. 20.4).

Exoskeletal constriction.—An exoskeletal constriction (Fig. 1.1) is a slight depression in the conulariid exoskeleton which is identifiable at the same relative position on all faces. An exoskeletal constriction appears to be continuous about the four faces of the exoskeleton (for example, Figs. 5.3, 9.3–9.5, 10.1, 27.1–27.3). Trends of rod angles may change slightly (Figs. 8.3, 8.5), rods may converge (Figs. 8.5, 11.3) or an apical wall may be attached internally to the exoskeleton at the narrow end of such a structure (Figs. 11.2, 14.1). Exoskeletal constrictions may be indications that conulariids grew by the incremental addition of new integument and rods at the aperture. Because the apertural constriction, the last formed of the exoskeletal constrictions, is always located slightly adapically of the aperture (for example, Fig. 10.1), it is presumed that growth temporarily ceased near the widest portion of the exoskeleton, located between two adjacent exoskeletal constrictions.

"*Septa.*"—The term "septum" has been applied to three separate morphologic features in conulariids: 1, apical walls (for example, Miller *in* Sowerby, 1821; Slater, 1907); 2, ridges (Slater, 1907); and 3, T- or Y-shaped structures or unmodified elongate structures radiating inward from the faces at their midlines (Wiman, 1895; Kiderlen, 1897; Liu, 1981). None of these seems to be an appropriate application of the term. Most commonly, the word "septum" as applied to conulariids means large T- or Y-shaped structures of the exoskeleton that project inward from the midlines. These supposed hard-part structures were described in *Conularia loculata,* from the Silurian of Sweden by Wiman

(1895) and were thought by Kiderlen (1937) to be homologous to septa composed of endodermal tissue in living scyphomedusans. These structures have not been observed, at least not to such a marked extent, in any specimens other than those of Wiman. Wiman's material was illustrated only by drawings, and the specimens are now lost (W. A. Oliver, Jr., personal communication). Thus, Wiman's observations cannot be replicated.

The cross sectional view of a specimen of *Paraconularia subulata* illustrated in Fig. 33.4 exhibits a pattern of limonitic staining in the central cavity which roughly approximates Wiman's figures. The staining in this example is probably related to the preservation of incompletely decomposed internal viscera. It is suspected that Wiman and others may have been misled by some taphonomic feature such as this.

Soft-part morphology.—Much speculation has surrounded the study of the soft-parts of conulariids. Since the work of Kiderlen (1937), Knight (1937), Moore and Harrington (1956*a,* 1956*b*) and Werner (1966, 1967, 1969), conulariids have been interpreted as tentacled creatures. Support for such interpretation is weak, being based on a presumed homology of conulariids to medusoid cnidarians or upon a grouping of true medusoid cnidarians with the conulariids (Kiderlen, 1937; Knight, 1937; Moore and Harrington, 1956*a,* 1956*b*).

Remains of presumed conulariid soft-parts were independently described from European Devonian conulariids by Steul (1984) and from North American Mississippian conulariids by Babcock (1985*a*) and Babcock and Feldmann (1986). Babcock and Feldmann (1986), working only with exceptionally preserved three-dimensional specimens, identified a single elongate tube that extends the length of the central cavity and a large globular shaped structure near the aperture (Fig. 2.1). Steul's (1984) work, based upon x-ray analyses of collapsed specimens preserved in the Hunsruck Slate, revealed other structures which may be preserved soft-parts, though the evidence is ambiguous.

The tubular and globular internal structures (Figs. 30.2–30.6), presumably representing remains of organ systems, appear to be reduced in size compared to expected living organs and show no details of soft-part anatomy. These structures may be somewhat contracted masses of internal tissues. These structures may have been preserved, in outline at least, as altered remains of partially digested food matter and/or sediment left in the intestinal tract when the animals died. Other organs that were originally present in the North American studied specimens may have decayed.

OCCURRENCES AND PALEOECOLOGY

Conulariids have been reported exclusively from marine rocks ranging in age from the Late Precambrian to the Recent (Caster, 1957).

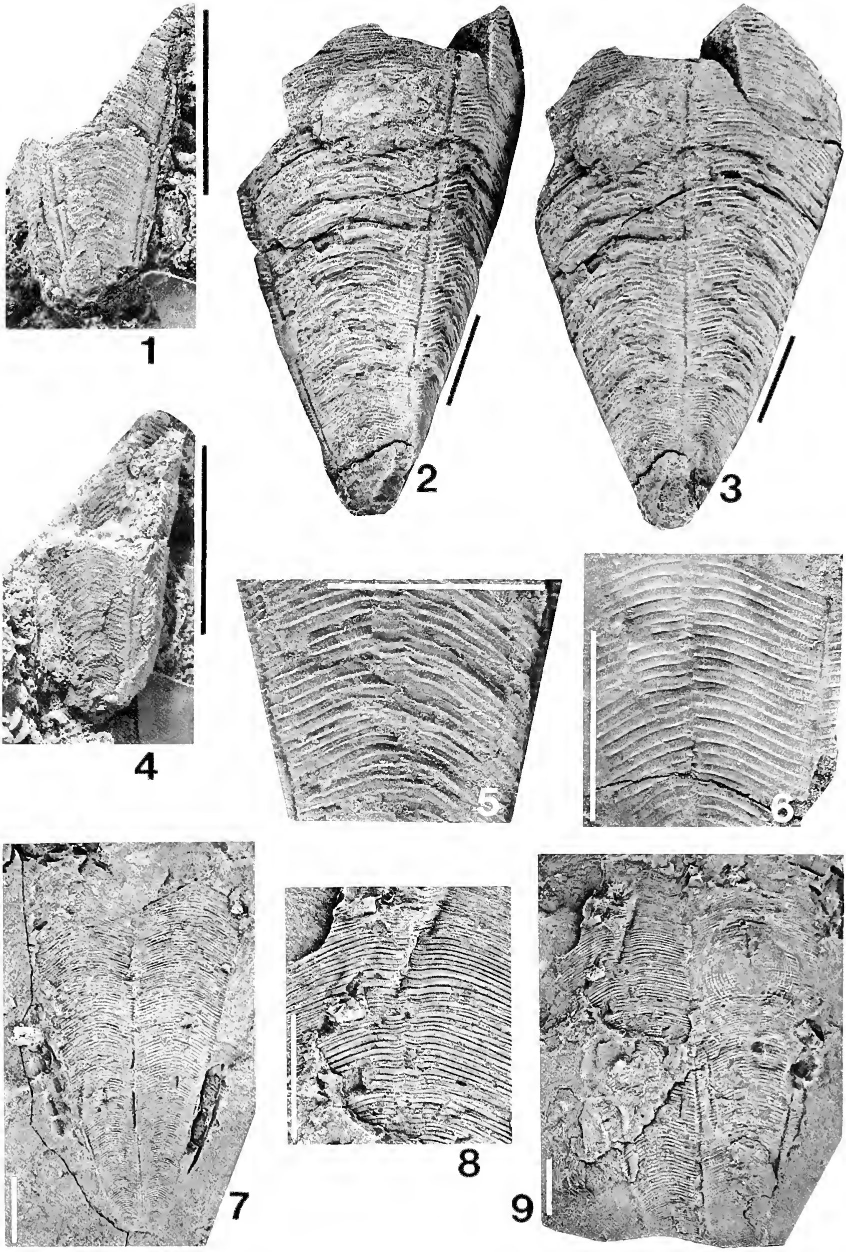

Fig. 5.—*Conularia desiderata* Hall. 5.1; AMNH 2697, holotype; major face, preserved in limestone; locality 121. 5.2; NYSM 3487, holotype of *C. continens* var. *rudis* Hall,

This range, however, includes a variety of taxa now referable to other groups. Occurrences here considered valid include specimens from Lower Ordovician (Sinclair, 1948) through Upper Triassic (Gou and Yang, 1985) rocks. While articulated conulariids are uncommon or rare in many instances, conulariids are, nonetheless, pervasive faunal elements in Middle Ordovician through Permian marine rocks. They are rare in the Lower Ordovician and in the Triassic. Some Paleozoic occurrences yield abundant conulariids.

Fossils identified as conulariids have been identified from all continents. However, the sole report of a conulariid from Antarctica (Cordini, 1955) has been received with skepticism and may represent plant material (Dalziel et al., 1981).

The conulariid skeleton, or exoskeleton, is composed of a calcium phosphate framework, made of rods, and usually having spines or nodes. The framework is set in an interlayered integument made of thin sheets of calcium phosphate and protein. Overall, the exoskeleton was probably fairly delicate, and upon death of the animal, was readily subject to collapse, occasional attachment of epibionts and decomposition accompanied by disarticulation (Feldmann and Babcock, 1986).

Most occurrences of articulated conulariids involve rapid burial and often, early diagenesis. For example, conulariids are abundant in the Meadville and Wooster members of the Cuyahoga Formation in northeastern and central Ohio. Specimens in these units are usually found in presumed tempestite beds or in siderite concretions. Specimens collected from tempestite beds often seem to be current aligned (Fig. 30.7). Specimens collected from siderite concretions, such as that illustrated in Fig. 10.4, are weakly current aligned, if at all. In the Cuyahoga Formation, concretions were probably produced through localized increases in pH and lowerings of eH, causing precipitation of iron carbonate. The onset of siderite precipitation probably occurred soon after burial of the animals.

Some occurrences of articulated conulariids involve "prefossilized" specimens, or ones which have undergone early diagenesis, and which have later been exhumed through bioturbation, winnowing of sediments by currents, or both. The specimens were later deposited in beds

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major face, preserved in siltstone; locality 132. 5.3; NYSM 3487, same specimen as in Fig. 5.2, corner view. 5.4; AMNH 2697, same specimen as in Fig. 5.1, minor face. 5.5; NYSM 3487, detail of minor face. 5.6; NYSM unnumbered, detail of specimen with integument draped loosely over rods; locality 124. 5.7; NYSM 3485, syntype of *C. continens* Hall, preserved in black shale. 5.8; NYSM 3486, syntype of *C. continens* Hall; detail of minor face; locality 125. 5.9; NYSM 3486, same specimen as in Fig. 5.8, nearly complete, flattened specimen. Bar scales represent 1 cm.

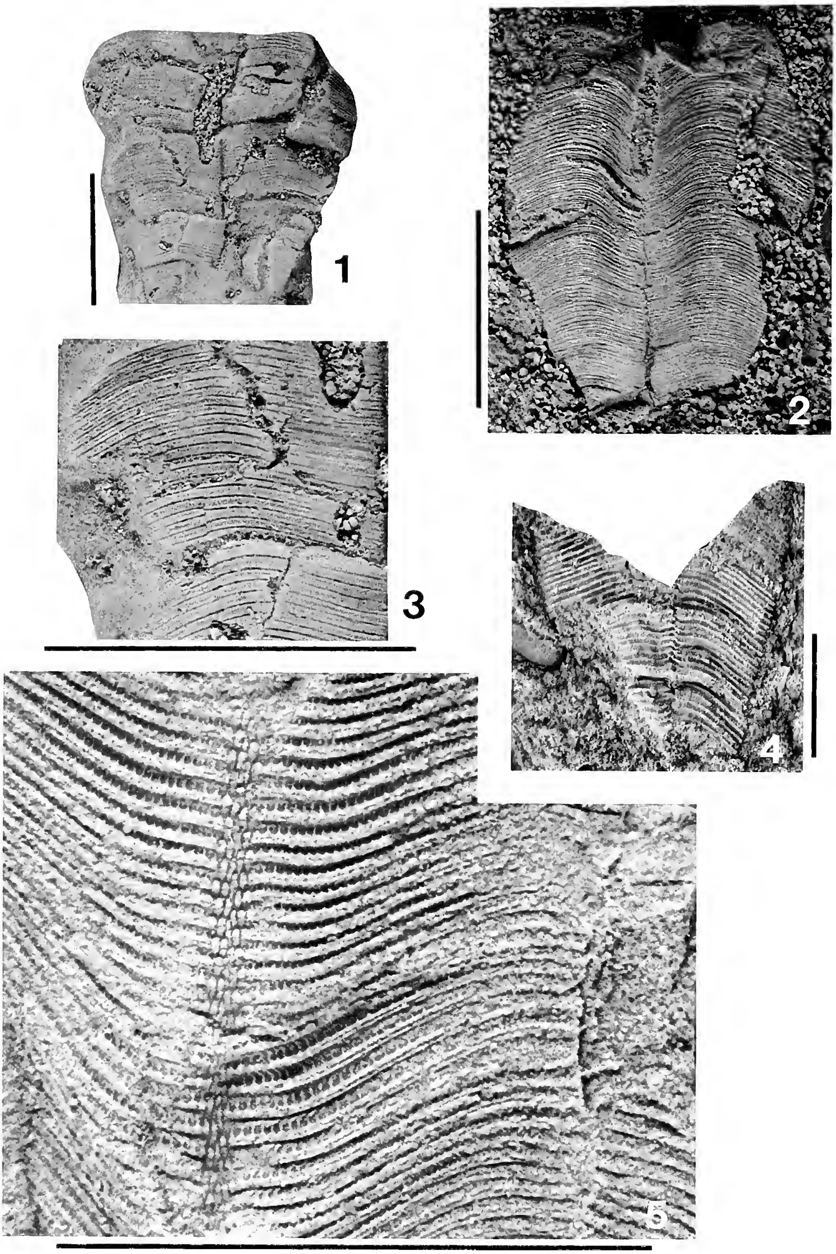

Fig. 6.—6.1–6.3; *Conularia delphiensis* (Maroney and Orr) preserved in phosphatic concretions at a stratigraphic discontinuity surface (Maroney and Orr, 1974). 6.1; IUPC

representing stratigraphic discontinuities (Maroney and Orr, 1974; Baird, 1981; Baird and Brett, 1981; herein, Figs. 6.1–6.3).

The general scarcity of articulated conulariid remains, at most localities, may be related to rapid disarticulation of the multielement skeleton, predation and scavenging, and the constancy of water movement near the sediment-water interface. The frequent occurrence of articulated conulariids in low diversity faunas (Ruedemann, 1934; Jux, 1960; Babcock and Feldmann, 1986; Feldmann and Babcock, 1986) may be largely a function of low biotic activity in these environments.

Many conulariids show indications that some breakdown of the exoskeleton has occurred, especially in the vicinity of the aperture (for example, Figs. 5.7, 7.5, 7.7), where the integument may be greatly reduced in thickness or lacking. In rare instances, poorly bioturbated stratigraphic units yield specimens of conulariids in which the integument is lacking over much of the exoskeleton and disarticulated rods have been displaced from their original positions (Fig. 21.4). In sediments that were probably well bioturbated, or sediments where water movement took place rather constantly, articulated conulariids are rare. It is possible that conulariid rods will be found in some Paleozoic and Mesozoic rock units that are sampled for microfossils by insoluble residue or other techniques. Disarticulated conulariid rods have been occasionally misidentified as fossil fish bones (Feldmann and Babcock, 1986).

Many species of conulariids seem to have been geographically widespread. For example, the Mississippian species, *Paraconularia chesterensis,* has a known geographic range from Alabama to British Columbia and, as with numerous other species, occurs in rocks of various lithologies. These lithologies include mudstones and wackestones (Chester Group of Illinois), gray shales (Borden Group of Indiana) and siderite concretions (Cuyahoga Formation of Ohio). The occurrence of this and other conulariid species in stratigraphic units of so vastly dissimilar lithologies and environments of deposition, and their wide geographic distribution, suggests that some species may have been planktonic or pseudoplanktonic at some point in the life cycle. The bilaterally symmetrical body plan (Babcock and Feldmann, 1984, 1986;

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14470-1, holotype; view of flattened specimen and detail of minor face; locality 23. 6.2; IUPC 14470-2, paratype; locality 23. 6.3; IUPC 14470-1, same specimen as in Fig. 6.1, detail of ?minor face. 6.4–6.5; *C. desiderata* Hall. 6.4; NYSM unnumbered, view of ?major face; locality 132. 6.5; USNM 395832, detail of specimen with most of integument removed, exposing broken rods and intact spines; locality 135. Bar scales in Figs. 6.1–6.4 represent 1 cm; bar scale in Fig. 6.5 represents 5 mm.

Steul, 1984), however, may be an indication that some species were weakly nektonic.

Conulariids are usually referred to as solitary animals. Clusters are rare, but a few have been figured by Slater (1907, Plate 2, fig. 1), Hall (1876, Plate 28, fig. 1; 1879 Plate 24, fig. 1), Sinclair (1944, Plate 2, fig. 5) and Babcock and Feldmann (1984, p. 17; Babcock and Feldmann, 1986, figs. 4A, 4C). In all these clusters, individual specimens are shown radiating about a central area. Apices are usually pointing inward in these aggregations (for example, Fig. 24.3). Occasionally, apices of such specimens are preserved intact (Fig. 24.1), yet in portions of a somewhat disaggregated cluster illustrated by Hall (1876, 1879), here illustrated in Figs. 4.1 and 4.4, the apices are missing, perhaps because of post-mortem decay. The apical walls are visible in some of these specimens.

A slab exhibiting numerous *P. chesterensis* from the Borden Group (Mississippian) of Indiana exhibits several small, black to reddish brown, tubular structures, circular in cross section, attached to, or very near the apices of, conulariids (Figs. 24.1, 24.3). Combined with discoveries of similar structures on conulariids from the Borden Formation (Mississippian) of Kentucky (Fig. 24.2) and from the Etherington Formation (Mississippian) of British Columbia (Fig. 32.5), these structures are interpreted as attachment stalks. The association of conulariids with plant remains, perhaps algae (for example, Fig. 28.7), indicates that some conulariids may have been pseudoplanktonic and were attached to, or entwined with, planktonic algae. Alternatively, the conulariids may have attached to plant remains which had previously settled to the ocean floor.

Cluster associations involving numerous specimens, usually comprising single species, serve to indicate that some, if not all, conulariids were gregarious, at least during some part of the life cycle. No evidence of budding or any other asexual reproductive style exists.

Regardless of whether the conulariids were planktonic, pseudoplanktonic, benthonic, or even nektonic, attached or free swimming, the soft-part organs in the region of the aperture of the exoskeleton probably functioned for filter feeding. There is no evidence for aggressive food gathering behavior.

The style of growth in conulariids was incremental, with addition of rods and spines taking place at the aperture. Growth lines, such as those seen on mollusks and brachiopods are not present. Exoskeletal constrictions, in exactly the same relative positions on all four faces, are possible evidences of incremental growth. Additional evidence of incremental growth at the aperture comes from some specimens showing healed injuries (for example, Figs. 20.1, 29.5). Along the exoskeletal constrictions of such examples, rods may be broken or the rod articulation patterns may be disrupted. This indicates two things: 1, that the positions of apertural terminations changed and correspond to the positions of apertural constrictions; and 2, that the apertural terminations were easily fragmented but healing could occur during a succeeding growth phase.

Development of multiple apical walls may also have been a function of an incremental growth pattern. When the internal cavity of an individual reached a certain volume, an apical wall was probably secreted adaperturally of the apical terminus. Apical walls are commonly preserved among specimens referable to the genus *Conularia* but are rarely found on specimens of *Paraconularia.* No specimens of *Reticulaconularia* have been observed with apical walls in place.

Epibionts on conulariids include orbiculoid brachiopods (Hall, 1876, 1879; Moore and Harrington, 1956*a*; Babcock and Feldmann, 1984, 1986; herein, Figs. 4.1, 4.4, 5.9, 13.1, 13.5, 16.4, 28.1–28.2), encrusting bryozoans (Finks, 1955; herein, Figs. 22.4–22.5) and edrioasteroid echinoderms (Barrande, 1867; Moore and Harrington, 1956*a*). Attachment of epizoans has been interpreted as either having occurred during the life of the conulariid (Finks, 1955; Moore and Harrington, 1956*a*) or as having occurred after the death of the conulariid (Baird, 1981; Babcock and Feldmann, 1986). In all the specimens examined in the course of this study, orbiculoids seem to have attached to the conulariids after they died and came to rest on the sediment surface. This is supported by the observation that orbiculoids are always found attached to only two faces of a conulariid (Figs. 4.1, 4.4). Presumably, these two faces were the only ones which projected above the sediment-water interface. A specimen is illustrated herein (Fig. 25.5) of a bryozoan encrusting a conulariid in the region of a corner groove. There is no sign of damage to the bryozoan on this specimen, indicating that encrustation by the bryozoan occurred after the death of the conulariid.

SYSTEMATIC PALEONTOLOGY

Summary of taxa.—A total of 69 trivial names have been applied to Devonian or Mississippian conulariids of North America prior to this paper. Of these, 54 taxa were published, and eight were described in unpublished manuscripts. Herein and in Part B, 28 species are recognized as valid, of which five are new. However, primary type specimens of 18 species were not available for study; therefore, the status of these taxa was not assessed fully. In Part B, one species is removed from the Conulariida. The conulariids described below and in Part B are divided among three genera, *Conularia, Paraconularia* and *Reticulaconularia,* n. gen. The genus *Diconularia* Sinclair, 1952 is regarded as a junior synonym of *Conularia* Miller *in* Sowerby, 1821 and the genus *Adesmoconularia* Driscoll, 1963 is considered to be a junior synonym of *Paraconularia* Sinclair, 1940*a*.

The list below summarizes all described species-level taxa of conulariids from North American Devonian and Mississippian rocks and indicates the status of each trivial name as currently recognized. Taxa are arranged alphabetically according to their presently recognized status. Junior synonyms and previously used combinations of each taxon are listed below each valid name.

- *Conularia congregata* Hall, 1876
- *Conularia delphiensis* (Maroney and Orr, 1974)
  - *Ctenoconularia delphiensis* Maroney and Orr, 1974
- *Conularia desiderata* Hall, 1861
  - *Conularia continens* Hall, 1876
  - *Conularia continens* var. *rudis* Hall, 1879
- *Conularia elegantula* Meek, 1871
- *Conularia milwaukeensis* Cleland, 1911
  - *Conularia congregata* var. *milwaukeensis* Cleland, 1911
- *Conularia multicostata* Meek and Worthen, 1865
  - *Conularia micronema* Meek, 1871
  - *Diconularia micronema* (Meek, 1871)
  - *Mesoconularia mcfarlani* Sinclair, [1948] MS
  - *Mesoconularia attica* Sinclair, [1948] MS
- *Conularia pyramidalis* Hall, 1859
  - *Conularia huntiana* Hall, 1859
  - *Conularia lata* Hall, 1859
- *Conularia subcarbonaria* Meek and Worthen, 1865
  - *Conularia intertexta* Miller, 1894
  - *Conularia spergenensis* Miller and Gurley, 1893
- *Conularia tuzoi* Clarke, 1907
  - *Conularia desiderata* var. *tuzoi* Clarke, 1907
- *Conularia ulsterensis* Howell, 1942
- *Conularia undulata* Conrad, 1841
  - *Conularia cayuga* Hall, 1876
  - *Conularia crebistria* Hall, 1876
- *Paraconularia alternistriata* (Shimer, 1926)
  - *Conularia alternistriata* Shimer, 1926
- *Paraconularia alpenensis* Babcock and Feldmann, n. sp.
- *Paraconularia blairi* (Miller and Gurley, 1893)
  - *Conularia blairi* Miller and Gurley, 1893
  - *Conularia sedaliensis* Miller and Gurley, 1896
  - *Paraconularia indiana* Sinclair, [1948] MS
- *Paraconularia byblis* (White, 1862)
  - *Adesmoconularia byblis* (White), 1862
  - *Conularia byblis* White, 1862
- *Paraconularia chagrinensis* Babcock and Feldmann, n. sp.
- *Paraconularia chesterensis* (Worthen, 1883)
  - *Conularia chesterensis* Worthen, 1883
- *Paraconularia missouriensis* (Swallow, 1860)
  - *Conularia missouriensis* Swallow, 1860

  Conularia gratiosa Miller and Gurley, 1893
  Conularia greenei Miller and Gurley, 1896
  Paraconularia sciotovillensis Driscoll, 1963
Paraconularia oklahomaensis Babcock and Feldmann, n. sp.
Paraconularia planicostata (Dawson, 1868)
  Conularia planicostata Dawson, 1868
Paraconularia recurvatus Babcock and Feldmann, n. sp.
Paraconularia salinensis (Whiteaves, 1891)
  Conularia salinensis Whiteaves, 1891
Paraconularia sorrocula (Beede, 1911)
  Conularia sorrocula Beede, 1911
Paraconularia subulata (Hall, 1858)
  Conularia subulata Hall, 1858
  Conularia victa White, 1862
  Conularia newberryi Winchell, 1865
  Conularia whitei Meek and Worthen, 1865
  Conularia sampsoni Miller, 1892
Paraconularia wellsvillia Babcock and Feldmann, n. sp.
Paraconularia yochelsoni Babcock and Feldmann, n. sp.
Reticulaconularia penouili (Clarke, 1907)
  Conularia penouili Clarke, 1907
  Conularia gaspesia Sinclair, 1942
Reticulaconularia sussexensis (Herpers, 1949)
  Conularia sussexensis Herpers, 1949

Whereabouts of Type Material Unknown

Climacoconus viata Swartz and Richardson *in* Richardson, [1942] MS
Conularia crawfordsvillensis Owen, 1862
Conularia gracilis Herrick, 1888
  (Name preoccupied by *C. gracile* Hall, 1847; changed to *C. herricki* by Miller, 1892.)
Conularia grandis Roemer, 1856
Conularia herricki Miller, 1892
Conularia jervisensis Shimer, 1905
Conularia latoides Swartz and Richardson *in* Richardson, [1942] MS
Conularia marionensis Swallow, 1860
Conularia missouriensis var. *hermansi* Calvin, 1890
Conularia molaris White, 1876
Conularia novascotica Hartt, *in* Dawson, 1868
Conularia osagensis Swallow, 1863
Conularia pyramidalis var. *parvinodis* Swartz and Richardson *in* Richardson, [1942] MS
Conularia siphunculophora Swartz and Richardson *in* Richardson, [1942] MS
Conularia triplicata Swallow, 1860
Conularia verneuilia Emmons, 1846
Paraconularia welleri Sinclair, [1948] MS

Non-Conulariid

Conularia tenuicostata Branson, 1938
  (Assigned, tentatively, to phylum Priapulida.)

Repositories.—Specimens are listed according to catalogue numbers with the repositories abbreviated as follows:

AMNH	American Museum of Natural History, New York, New York
AMNH CU	American Museum of Natural History, Columbia University Collection, New York, New York
BMS	Buffalo Museum of Science, Buffalo, New York
CM	Carnegie Museum of Natural History, Invertebrate Paleontology Collections, Pittsburgh, Pennsylvania
CMNH	Cleveland Museum of Natural History, Invertebrate Paleontology Collections, Cleveland, Ohio
FMNH P	Field Museum of Natural History, Paleontology Collection, Chicago, Illinois
FMNH PE	Field Museum of Natural History, Invertebrate Paleontology Collection, Chicago, Illinois
FMNH UC	Field Museum of Natural History, University of Chicago Collection from Walker Museum, Chicago, Illinois
GSC	Geological Survey of Canada, Ottawa, Ontario
ISGS	Illinois State Geological Survey, Illinois State Museum, Champaign-Urbana, Illinois
IUPC	Indiana University Paleontological Collection, Bloomington, Indiana
KSU	Department of Geology, Kent State University, Kent, Ohio
NJSM	New Jersey State Museum, Trenton, New Jersey
NYSM	New York State Museum and Science Service, Albany, New York
OC	Oberlin College Paleontological Collections, Oberlin, Ohio
PU	Department of Geology, Princeton University, Princeton, New Jersey
RM(MU)	Redpath Museum (McGill University), Montreal, Quebec
UCGM	University of Cincinnati Geological Museum, Cincinnati, Ohio
UIPC	University of Illinois, Department of Geology, Champaign-Urbana, Illinois
UK	University of Kentucky, Department of Geology, Lexington, Kentucky
UMC	University of Missouri–Columbia, Columbia, Missouri
UMMP	University of Michigan, Museum of Paleontology, Ann Arbor, Michigan
USNM	United States National Museum of Natural History, Washington, D.C.
WVU	West Virginia University, Department of Geology, Morgantown, West Virginia

Treatment of manuscript names.—One of the most influential papers regarding the systematics and morphology of conulariids is Sinclair (1948), an unpublished Ph.D. thesis. In it were proposed many new genus-level and species-level taxa. The undescribed genera identified by Sinclair were subsequently published (Sinclair, 1952); however, the majority of Sinclair's new species have never been formally described. Moreover, many of the species removed by Sinclair from *Conularia,* as used in the sense of a form-genus, and placed in different genera, have not been published in their revised state by Sinclair. Nevertheless, various authors have used Sinclair's combinations, often without reference to the authority for such usage.

It is our opinion that, because of the central importance of Sinclair's (1948) unpublished manuscript to the study of conulariid systematics, Sinclair's unpublished species-level names and his unpublished combinations should be included in the formal synonymies of the Devonian and Mississippian taxa discussed below. For the sake of completeness, we have also included in the present work the manuscript names of Swartz and Richardson *in* Richardson (1942). By including these unpublished names in synonymy though, we do not intend to suggest that these are available names. According to Article II(d)(ii) of the *International Code of Zoological Nomenclature, Third Edition* (International Commission of Zoological Nomenclature, 1985), "a previously unavailable name is not changed by its mere citation accompanied by a reference to the work in which the name was published but was not made available." Also, in Article 11(e), the *Code* states that a, "name first published as a junior synonym is not thereby made available unless prior to 1961 it has been treated as an available name . . ."

Phylum Conulariida Babcock and Feldmann, new phylum

Diagnosis.—Animals generally possessing a four sided, steeply pyramidal exoskeleton; bilaterally symmetrical; integument composed of calcium phosphate and protein, multilayered, moderately flexible; exoskeletal framework composed of calcium phosphatic rods arranged transversely across each side face; adjacent rods abut or alternate at midline of each face; rods of adjacent faces articulate in a groove at junction of two faces; apical end closed either by a blunt point; one or more smooth apical walls may be present internal to the exoskeleton and aperturad the apex; apex sheathed by a ?chitinous, phosphatic, or chitinophosphatic stalk; aperture simple and open. No internal hard-part structures known; internal soft-parts comprise an elongate tube extending most of the body length, in addition to one or more globular shaped structures, all of uncertain function.

Remarks.—Approximately 40 genera of organisms have, at one time or another, been grouped among the conulariids. Of these, six genera have been excluded from the phylum to date. Based upon new information on the architecture of the conulariid skeleton (Babcock and Feldmann, 1986), it seems that even more genera have been described than are warranted by fossil evidence. Upon further study, several other genera are likely to be excluded from the phylum Conulariida.

Organisms which are properly included within the phylum Conulariida must possess a bilaterally symmetrical exoskeleton composed of calcium phosphate rods and layered calcium phosphate and protein integument. Herein, genera of conulariids are defined upon: 1, the relative spacing of rods; 2, the relative proportion of rods that abut at the midline to those that alternate; 3, the apical angles; 4, the presence or absence of nodes and spines; and 5, the spacing of nodes and spines. Species are distinguished using the characters upon which generic distinctions are made as well as the following: 1, the patterns of rod articulation; and 2, the rod angles.

Descriptions of conulariids represented in the Devonian and Mississippian rocks of North America follow. After examination of specimens referred to the respective type species from Europe, Sinclair (1940*a*) proposed North American reference species. The following diagnoses of *Conularia* and *Paraconularia* are based largely upon specimens referable to the North American reference species. The new genus *Reticulaconularia* is based upon specimens from the Devonian of eastern North America.

Specimens of *Conularia* are recognizable by their closely spaced rods, by having more than 40% of the rods abutting at the midline, by having small apical angles and by having both nodes and spines which are closely spaced. Specimens referable to *Paraconularia* exhibit widely spaced rods, fewer than 40% of rods abutting at the midline and small apical angles. Nodes and spines may be present; if they are, they are closely spaced. Conulariids referable to *Reticulaconularia,* n. gen. have widely spaced rods which abut or alternate at the midline in proportions which are not well established yet. They also have large apical angles. Members of the genus *Reticulaconularia* are notable for the reticulate appearances of the external surfaces of the faces (Figs. 33.1–33.5, 34.1–34.2, 34.4), a product of nodes and spines which are widely spaced. It should be noted, however, that other conulariids, if preserved as external molds, may exhibit patterns similar to this "reticulate" appearance (for example, Figs. 8.5–8.6). Such specimens are best studied with latex casts.

Key to North American Devonian and Mississippian conulariids.—The following is a key to all species of Devonian and Mississippian conulariids from North America which are currently known. Some categories are ambiguous due to the lack of complete or well preserved specimens of some species, so it is not intended for use with specimens of different ages or of other areas of the world.

1. Faces have reticulate appearance 2
1. Faces do not have reticulate appearance 3
2. Inflected gothic arch rod articulation present ....
.... *Reticulaconularia sussexensis* (Herpers)
2. Inflected gothic arch rod articulation not present ....
.... *Reticulaconularia penouili* (Clarke)
3. Number of rods that abut at midline less than 40% 4
3. Number of rods that abut at midline greater than or equal to 40% 19
4. Gothic arch rod articulation present 5
4. Gothic arch rod articulation not present 9
5. Only gothic arch rod articulation present .. *Paraconularia alternistriata* (Shimer)
5. Gothic arch and another style of rod articulation present 6
6. Gothic arch and inflected circular curve rod articulation present ....
.... *Paraconularia oklahomaensis* Babcock and Feldmann, n. sp.
6. Gothic arch and inflected gothic arch rod articulation present 7

7. Rods/cm fewer than or equal to 11 .... *Paraconularia planicostata* (Dawson)
7. Rods/cm greater than 11 .... *Paraconularia yochelsoni* Babcock and Feldmann, n. sp.
8. Inflected gothic arch rod articulation present 9
8. Inflected gothic arch rod articulation not present 14
9. Only inflected gothic arch rod articulation present 10
9. Inflected gothic arch and another style of rod articulation present 11
10. Rods/cm fewer than 15 .... *Paraconularia chagrinensis* Babcock and Feldmann, n. sp.
10. Rods/cm greater than 15 .... *Paraconularia sorrocula* (Beede)
11. Rods/cm fewer than or equal to 12 12
11. Rods/cm greater than 12 13
12. Rods are slightly inflected at midline .. *Paraconularia blairi* (Miller and Gurley)
12. Rods are not inflected at midline .... *Paraconularia subulata* (Hall)
13. Number of rods that abut at midline fewer than 30% .... *Paraconularia salinensis* (Whiteaves)
13. Number of rods that abut at midline greater than or equal to 30% .... *Paraconularia byblis* (White)
14. Inflected circular curve rod articulation present; rods recurved near midline .. 15
14. Inflected circular curve rod articulation present; rods not recurved near midline .... *Paraconularia wellsvillia* Babcock and Feldmann, n. sp.
15. Rods/cm fewer than or equal to 12 17
15. Rods/cm greater than 12 16
16. Rods/cm fewer than 18 .. *Paraconularia alpenensis* Babcock and Feldmann, n. sp.
16. Rods/cm greater than or equal to 18 .... *Paraconularia recurvatus* Babcock and Feldmann, n. sp.
17. Rods/cm fewer than or equal to 7 .... *Paraconularia chesterensis* (Worthen)
17. Rods/cm greater than 7 .... *Paraconularia missouriensis* (Swallow)
18. Gothic arch rod articulation present .... *Conularia pyramidalis* (Hall)
18. Gothic arch rod articulation not present 19
19. Inflected gothic arch rod articulation present 20
19. Inflected gothic arch rod articulation not present 23
20. Rods/cm fewer than or equal to 30 21
20. Rods/cm greater than 30 22
21. Rods/cm fewer than or equal to 25 .... *Conularia milwaukeensis* Cleland
21. Rods/cm greater than 25 .... *Conularia multicostata* Meek and Worthen
22. Rods/cm fewer than or equal to 39 .... *Conularia tuzoi* Clarke
22. Rods/cm greater than 39 .... *Conularia ulsterensis* Howell
23. Angulated circular curve rod articulation present 24
23. Angulated circular curve rod articulation not present 27
24. Only angulated circular curve rod articulation present 25
24. Angulated circular curve and another style of rod articulation present 26
25. Rods/cm fewer than 34 .... *Conularia subcarbonaria* Meek and Worthen
25. Rods/cm greater than 34 .... *Conularia elegantula* Meek
26. Rod angle less than or equal to 17° .... *Conularia congregata* Hall
26. Rod angle greater than 17° .... *Conularia desiderata* Hall
27. Rods undulose .... *Conularia undulata* Conrad
27. Rods not undulose .... *Conularia delphiensis* (Maroney and Orr)

Genus *CONULARIA* Miller, *in* Sowerby, 1821

Type species.—Conularia quadrisulcata Sowerby, by original designation; Silurian of England. Holotype is lost. North American reference species, *fide* Sinclair (1940*a*): *Conularia niagarensis* Hall, 1852 (Silurian). Syntypes and plastosyntypes of *C. niagarensis*: AMNH 31625–31628; plastosyntype of AMNH 31625: FMNH UC 60850.

Diagnosis.—Conulariids with rods that are generally closely spaced, 9–84 rods/cm. Fewer than 60% of rods alternate at midline; more than 40% abut; two adjacent rods on a face form a single arc across the face. Apical angles small, 9–23°. Nodes, adapertural spines and adapical spines usually present and closely spaced, 1–7/mm.

CONULARIA CONGREGATA Hall, 1876
Figs. 4.1–4.4

Conularia congregata Hall, 1876, Pl. 28, fig. 1; Miller, 1877, p. 141; Bigsby, 1878, p. 418; Hall, 1879, p. 214–215, Pl. 34, fig. 1, Pl. 34A, figs. 9–11; Miller, 1889, p. 390; Harris, 1899, Pl. 8, fig. 59; Clarke and Ruedemann, 1903, p. 565; Moore and Harrington, 1956*b*, p. F61, fig. 46.2; Palmer and Brann, 1966, fig. 59; Babcock, 1985*b*, fig. 2; Babcock and Feldmann, 1986, fig. 4A.
Conularia s.l. *congregata* Hall. Sinclair, 1948, p. 286.
Conularia pyramidalis Hall. *Sensu* Babcock and Feldmann, 1984, p. 17.

Description.—Exoskeleton up to 11 cm in length. Major apical angle 17–18°; minor apical angle 12–14°. Rod articulation exclusively of inflected circular curve style. Rods almost always abut at midline; rod angle 9–13°. 16–21 rods/cm. 6–7 nodes/mm; 6–7 adapertural spines/mm; 6–7 adapical spines/mm; spines often not easily discernible. Apical wall may be present.

Occurrences.—Upper Devonian of New York; localities 149–150 and 152–160. Maillieux (1933), Markovski and Nalivken (1934) and Xu and Li (1979) reported *C. congregata* from Devonian rocks in Belgium, the U.S.S.R. and the People's Republic of China, respectively, but these occurrences have not been confirmed.

Types.—Lectotype and twelve paralectotypes on one slab, NYSM 3483. Remains of at least thirteen specimens are preserved on James Hall's slab of syntypes (Figs. 4.1, 4.4). From this syntypic suite, the best preserved of Hall's figured specimens (Fig. 4.4) is here chosen as the lectotype of *C. congregata*. The remaining ten specimens are considered paralectotypes. Counterparts of the paralectotype specimens shown in Fig. 4.1 are catalogued as FMNH unnumbered.

Remarks.—*Conularia congregata* Hall is most similar in morphology to *C. desiderata* Hall. The similarities lie in overall size, apical angle values, rod angle values and in the presence of inflected circular curve rod articulation. The differences between the two taxa are subtle. In specimens of *C. congregata*, few rods, generally fewer than 10%, alternate at the midline; also, rods show very little or no inflection toward the aperture near the midline. Among specimens referable to *C. desiderata*, as many as 15% of the rods may alternate at the midline; specimens also show a strong adapertural inflection of the rods at the midline. Some specimens, such as that illustrated in Fig. 5.6, appear to be intermediate in morphology between *C. desiderata* and *C. congregata.*

Conularia congregata may also be confused with *C. pyramidalis* Hall. *Conularia pyramidalis* differs from both *C. congregata* and *C. desiderata* is having inflected circular curve rod articulation in the apical region and inflected gothic arch rod articulation elsewhere. There is no evidence in *C. pyramidalis* that the rods inflect near the midline.

Material examined.—40 specimens; housed in the AMNH, BMS, FMNH, NYSM, USNM, and the private collection of Paul Zell.

CONULARIA DELPHIENSIS (Maroney and Orr, 1974)

Figs. 6.1–6.3

Conularia sp. Kindle, 1901, p. 737, Pl. 123, fig. 8.
Ctenoconularia delphiensis Maroney and Orr, 1974, p. 3–6, fig. 1A–F.

Description.—Exoskeleton up to 5.5 cm in length. Major apical angle and minor apical angle about 15°. Rod articulation inflected gothic arch style in apical region and inflected circular curve style elsewhere. Rods usually abut at midline; rod angle 10–11°. 26–42 rods/cm. 6–7 nodes/mm; adapertural spines and adapical spines not observed. Apical wall not observed.

Occurrence.—Upper Devonian of Indiana; localities 22–23.

Types.—Holotype, IUPC 14470-1; five paratypes, IUPC 14470-2 through 14470-6.

Remarks.—The six specimens which comprise the type suite of *C. delphiensis* are badly preserved. Although no spines were actually observed on any of the type specimens, all other morphologic features are consistent with species of the genus *Conularia* as defined herein. A specimen figured by Kindle (1901, pl. 123, fig. 8; USNM 62210), an apparent external mold of *C. delphiensis,* clearly shows that nodes are present, but spines are not evident. Spines may have been present in this taxon, but have not been observed because of the poor preservation of the specimens studied. A cross sectional view of an uncompressed specimen referable to this species has not been observed.

In their original description of *C. delphiensis,* Maroney and Orr (1974) did not indicate why they chose to include the species in the genus *Ctenoconularia* Sinclair, 1952. Moreover, they only compared this species to *Conularia congregata.* Sinclair (1952, p. 141) noted that the primary distinguishing characteristic of specimens referable to *Ctenoconularia* was "strikingly slender shells." This is certainly true in the type species, *Ctenoconularia obex* Sinclair. Judging from Sinclair's published figures (1952, figs. 56 A–C), the major and minor faces subtend angles of 4° and 3°, respectively. In other respects, specimens of *Ctenoconularia* are very similar to specimens of *Conularia.* "*Cten-*

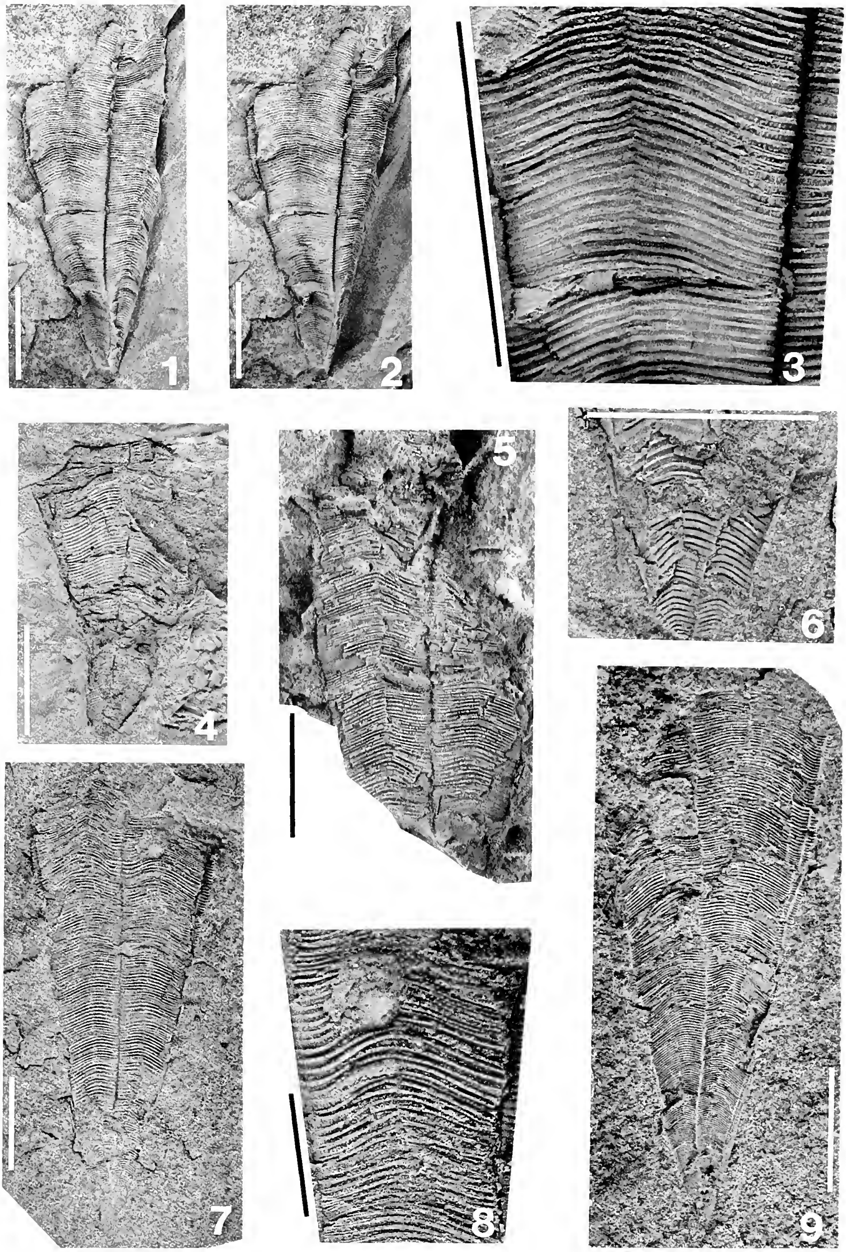

Fig. 7.—7.1–7.4; *Conularia elegantula* Meek. 7.1; AMNH CU 282G, holotype, corner view; locality 174. 7.2; AMNH CU 282G, same specimen as in Fig. 7.1, corner major

oconularia" *delphiensis,* which has apical angles of approximately 15°, seems to expand from the apex too rapidly to warrant inclusion in the genus *Ctenoconularia.*

Conularia delphiensis is similar in general morphology, including similarity of rod articulation styles, to only one Devonian species from North America, *C. milwaukeensis. Conularia delphiensis* differs, however, in having greater rods/cm values. Specimens here referred to *C. delphiensis* possess 26–42 rods/cm while specimens here referred to *C. milwaukeensis* have fewer than 30 rods/cm.

Material examined.—8 specimens; housed in the IUPC and the USNM.

CONULARIA DESIDERATA Hall, 1861

Figs. 3.8–3.10, 5.1–5.9, 6.4–6.5, 16.6

Conularia———? Hall, 1859, p. 480.

Conularia desiderata Hall, 1861, Pl. 72A, fig. 4; Richardson, 1942, p. 30–32, Pl. 4, figs. 7, 8; Babcock and Feldmann, 1986, figs. 1B, 1H.

Conularia continens Hall, 1876, Pl. 28, figs. 4–6; Miller, 1877, p. 141; Bigsby, 1878, p. 418; Hall, 1879, p. 212–214, Pl. 33, fig. 6, Pl. 34, figs. 3, 4, 6, Pl. 34A, fig. 6; Lesley, 1889, p. 143, fig.; Miller, 1889, p. 390; Clarke and Ruedemann, 1903, p. 565; Moore and Harrington, 1956*a,* fig. 25.1; Moore and Harrington, 1956*b,* p. F60, fig. 42.10a–b; Tasch, 1973, fig. 5.15H, Tasch, 1980, fig. 5.15H.

Conularia continens var. *rudis* Hall, 1879, p. 215–216, Pl. 34A, figs. 7–8; Miller, 1889, p. 390; Clarke and Ruedemann, 1903, p. 565; Grabau, 1906, p. 331.

Conularia s.l. *continens* Hall. Sinclair, 1948, p. 286.

Paraconularia desiderata (Hall). Sinclair, 1948, p. 185.

Conularia s.l. *rudis* Hall. Sinclair, 1948, p. 284.

Description.—Exoskeleton up to 10 cm in length. Major apical angle 14–27°; minor apical angle 14–18°. Rod articulation inflected circular curve in early stages to angulated circular curve in later stages. Rods almost always abut at midline; rod angle 7–17°. About 41 rods/cm in apical region; 14–27 rods/cm elsewhere. 3–4 nodes/mm; 3–4 adapertural spines/mm; 3–4 adapical spines/mm. Apical wall not observed.

Occurrences.—Lower and Middle Devonian rocks of New York and Pennsylvania; localities 121, 124–126, 132–135, 142, 144, 232, 235–236, and 239. *Conularia continens,* here referred to *C. desiderata,* has been reported from Devonian rocks in Ohio (Claypole, 1903) and in Indochina (Patte, 1926), but the specimens upon which these references were based were not studied. Woodward (1943) identified *C. continens*

←

face. 7.3; AMNH CU 282G, same specimen as in Fig. 7.1, detail of major face. 7.4; CMNH 44584, ?major face of flattened specimen; locality 175. 7.5–7.9; *C. milwaukeensis* Cleland. 7.5; USNM 85988, holotype; locality 255. 7.6; USNM 78212; detail of apical region. Note that no apical wall is present; locality 253. 7.7; MPM 20252, complete specimen; locality 253. 7.8; MPM 20252, same specimen as in Fig. 7.7, detail of major face. 7.9; MPM 22974; locality 253. Bar scales represent 1 cm.

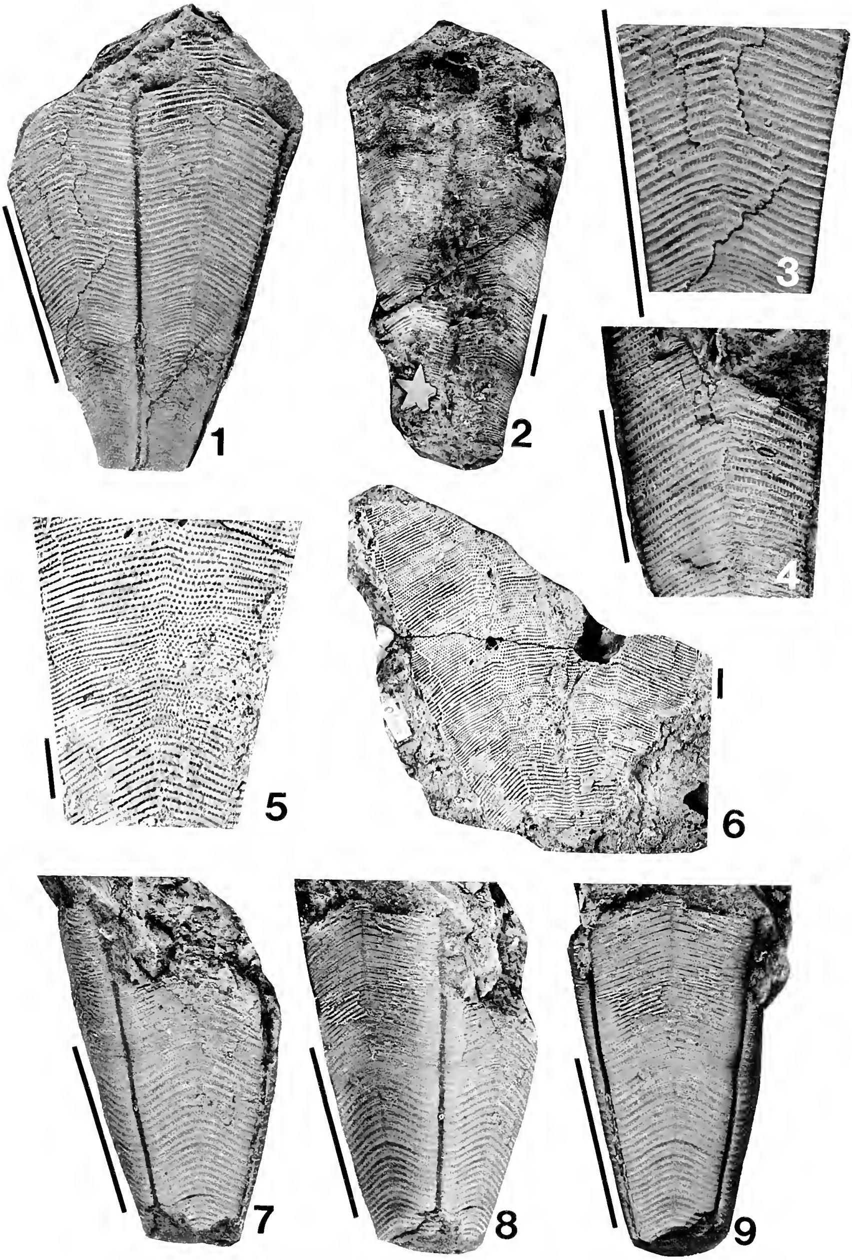

Fig. 8.—*Conularia pyramidalis* Hall. 8.1; AMNH 33017, lectotype; corner view of flattened specimen, preserved in calcareous shale; locality 117. 8.2; NYSM 3488, holotype of *C. huntiana* Hall, corner view, preserved in calcareous shale; locality 118. 8.3; AMNH

var. *rudis* (=*C. delphiensis*) in the Devonian of West Virginia, but Woodward's specimens were unavailable for study.

Types.—Holotype and plastoholotype of *C. delphiensis* Hall, AMNH 2697; two syntypes of *C. continens* Hall, NYSM 3485, NYSM 3486; holotype of *C. continens* var. *rudis* Hall, part and counterpart, NYSM 3487.

Remarks.—*Conularia desiderata* Hall is similar in appearance only to *C. pyramidalis* Hall. Both species have rod angles in the range of 14–27°. Also, specimens of both taxa possess rods which appear to be inflected at the midline. Features that are present in *C. desiderata,* but not present in *C. pyramidalis* include inflected circular curve to angulated circular curve rod articulation style and rod angles of 14–27°.

The syntypes of *C. continens* Hall differ morphologically from the holotype of *C. desiderata* Hall only in being flattened. The holotype of *C. continens* var. *rudis* differs from the holotype of *C. desiderata* in being larger and better preserved. The type specimens of each taxon have inflected gothic arch rod articulation in the region close to the apex and inflected circular curve rod articulation elsewhere. The major apical angle of the holotype of *C. desiderata,* measures 23°; the minor apical angle cannot be measured with certainty. The syntypes of *C. continens* have major apical angles of 16° and 19°. The major apical angle of the holotype of *C. continens* var. *rudis* is 27°. All of the type specimens have between 14 and 27 rods/cm and possess spines which are difficult to observe in most specimens. *Conularia continens* Hall. and *C. continens* var. *rudis* Hall are, therefore, here considered junior synonyms of *C. desiderata* Hall.

Material examined.—48 specimens; housed in the AMNH, BMS, GSC, NJSM, NYSM, USNM and the private collections of Larry Decina and Paul Zell.

CONULARIA ELEGANTULA Meek, 1871
Figs. 3.4, 7.1–7.4

Conularia elegantula Meek, 1871, p. 85–86; Meek, 1873, p. 228–229, Pl. 23, fig. 4; Miller, 1877, p. 141; Bigsby, 1878, p. 78; Whitfield, 1882, p. 242; Miller, 1889, p. 390; Babcock and Feldmann, 1986, fig. 2K.

Conularia s.l. *elegantula* Meek. Sinclair, 1948, p. 283.

←

33017, same specimen as in Fig. 8.1, detail of a minor face. 8.4; NYSM 3488, same specimen as in Fig. 8.2, detail of a minor face. 8.5; NYSM 3490, holotype of *C. lata* Hall, detail of major face; locality 122. 8.6; NYSM 3490, same specimen as in Fig. 8.5, entire specimen, preserved as an external mold in fine-grained sandstone. 8.7; AMNH 33018; paralectotype, preserved in three dimensions, major face; locality 117. 8.8; AMNH 33018, same specimen as in Fig. 8.7, corner view. 8.9; AMNH 33018, same specimen as in Fig. 8.7, minor face. Bar scales represent 1 cm.

Description.—Exoskeleton up to 7 cm in length. Major apical angle 20–30°; minor apical angle about 17°. Rod articulation uniformly of angulated circular curve style. 6 nodes/mm on rods. 6 adapertural spines/mm; 6 adapical spines/mm. Rods usually abut at midline; approximately 40% alternate left superior on major and minor faces; rod angle 3–13°. 32–39 rods/cm. Apical wall not observed.

Occurrences.—Middle Devonian of Ohio; localities 174–176.

Type.—Holotype, AMNH CU 282G.

Remarks.—*Conularia elegantula* Meek is similar to *C. pyramidalis* Hall in the values for rod angles, the number of nodes/mm on the rods and in the number of spines/mm. *Conularia elegantula* can be distinguished from *C. pyramidalis,* and, indeed, all other species of *Conularia* from the Devonian or Mississippian of North America by its rod articulation architecture, which seems to be uniformly of angulated circular curve style. Partial specimens of *C. desiderata* exhibiting rods from the apertural region can also be distinguished from specimens of *C. elegantula* by the curvature of the rods as they approach the corner angles. The rods of specimens of *C. elegantula* are noticeably more inflected in the apertural direction than are rods belonging to specimens of *C. desiderata.*

Material examined.—Three specimens; housed in the AMNH and the CMNH.

CONULARIA MILWAUKEENSIS Cleland, 1911
Figs. 7.5–7.9

Conularia congregata var. *milwaukeensis* Cleland, 1911, p. 130, pl. 26, figs. 4–7; Teller, 1911, p. 251.
Mesoconularia milwaukeensis (Cleland). Sinclair, 1948, p. 119.
Conularia congregata milwaukeensis Cleland. Munthe, 1980, p. 6.

Description.—Exoskeleton up to 5 cm in length. Major apical angle 12–15°; minor apical angle 11–14°. Rod articulation uniformly of inflected gothic arch style. Rods abut at midline; rod angle 5–18°. 18–24 rods/cm. 5–7 nodes/mm; 5–7 adapertural spines/mm; 5–7 adapical spines/mm. Apical walls not observed.

Occurrence.—Middle Devonian of Wisconsin; localities 253–255.

Types.—Holotype, USNM 85988; five paratypes, USNM 78212. Two paratypes, listed by Sinclair (1948) as MPM 244–245, could not be found.

Remarks.—*Conularia milwaukeensis* may be distinguished from similar appearing species such as *C. elegantula* Meek and *C. desiderata* Hall by having only inflected gothic arch style rod articulation and by attaining lengths of up to 5 cm, apparently without the addition of apical walls. *Conularia elegantula* has narrow apical angles like *C. milwaukeensis,* but its rod articulation style is exclusively angulated circular curve. Likewise, *C. desiderata* has narrow apical angles, but its rod articulation patterns include inflected circular curve style in the apical region and angulated circular curve style elsewhere.

None of the examined specimens of *C. milwaukeensis* preserves integument over the entire exoskeleton. Because of this, rods have obviously been moved slightly from their original positions, making the measurement of rod angles difficult. Also, because of the general lack of preserved integument in most specimens, there is no evidence that apical walls were developed in this species. Apical walls may have been a feature of this species, but simply have not been preserved in the samples studied.

Material examined.—37 specimens; housed in the GSC, MPM, and the USNM.

CONULARIA MULTICOSTATA Meek and Worthen, 1865

Figs. 9.1–9.5, 9.8, 10.1, 10.4, 12.1–12.5

Conularia multicostata Meek and Worthen, 1865, p. 252–253; Bigsby, 1878, p. 316; Miller, 1889, p. 390; Weller, 1898, p. 190; Babcock and Feldmann, 1986, figs. 1A, 1F.

Conularia micronema Meek, 1871, p. 84; Meek, 1875, p. 316, Pl. 18, figs. 1a–d; Miller, 1877, p. 141; Bigsby, 1878, p. 316; Herrick, 1888*a*, p. 94–95, Pl. 2, figs. 18–19; Herrick, 1888*b*, p. 49, Pl. 8, figs. 4–4a; Lesley, 1889, p. xv; Miller, 1889, p. 390, fig. 643; Herrick, 1893, Pl. 19, figs. 4–4a; Weller, 1898, p. 190; Grabau and Shimer, 1910, p. 13, figs. 1227c–f.

Mesoconularia multicostata (Meek and Worthen). Sinclair, 1948, p. 125.

Mesoconularia micronema (Meek). Sinclair, 1948, p. 124.

Mesoconularia mcfarlani Sinclair, [1948], p. 126–128, Pl. 16, figs. 3–5.

Mesoconularia attica Sinclair, [1948], p. 125–126, Pl. 9, fig. 2, Pl. 17, figs. 9–11.

Diconularia micronema (Meek). Sinclair, 1952, p. 138–139; Moore and Harrington, 1956*b*, p. F61, fig. 47.2.

Non Conularia trentonensis multicosta Ruedemann, 1912, p. 115–116; Ruedemann, 1930, p. 36; Goldring, 1935, p. 63.

Description.—Exoskeleton up to 25 cm in length. Major apical angle 20–24°; minor apical angle 18–22°. Rod articulation of inflected gothic arch style in apical and most other regions and of angulated circular curve style in apertural region of large specimens; rods exhibiting inflected circular curve style articulation are mildly recurved near the midline but they are angulated in the apertural direction at the midline. Rods abut at midline; rod angle 9–17°. 26–60 rods/cm. Nodes prominent; 2–3 nodes/mm; 2–3 adapertural spines/mm; 2–3 adapical spines/mm. Apical wall not observed.

Occurrences.—Lower Mississippian of Indiana, Kentucky and Ohio; localities 25, 71–73, 79–80, 193, 197–200, 205, 209, 214, 217–218, 223, 225, 227 and 228.

Types.—Holotype of *Conularia multicostata* Meek and Worthen is lost; plastoholotype, with small fragments of fossil adhering, USNM 50157. Holotype of *C. micronema* Meek is apparently lost (Sinclair, 1948, p. 124); neotype, AMNH 6713. Specimen intended by Sinclair (1948) to be holotype of *Mesoconularia mcfarlani,* UK 6089. Three


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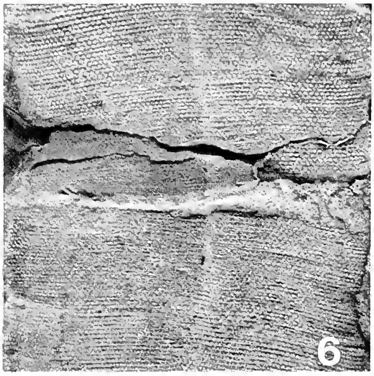
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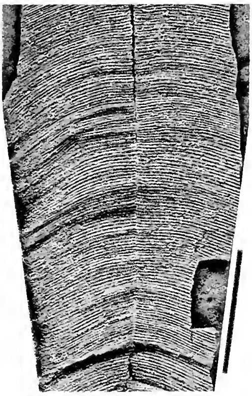
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specimens which Sinclair (1948) intended to designate as types of *M. attica,* CM 34533-34534, GSC 87204.

Remarks.—*Conularia multicostata* Meek and Worthen is most similar in morphology to *C. subcarbonaria* Meek and Worthen. Like *C. subcarbonaria, C. multicostata* has prominent nodes and can have more than 30 rods/cm. However, *C. multicostata* can be distinguished from this and all other species of *Conularia* by the combination of its very closely spaced rods, 26–60/cm, and its inflected gothic arch rod articulation in most places except the apertural region of large specimens. More importantly, though, the rods of specimens referred to *C. subcarbonaria* appear to be undulose. This is especially true for large individuals (for example, Figs. 11.2–11.3).

In the apertural region of specimens of *C. multicostata* which are large for the species, a unique form of angulated circular curve rod articulation is present. This rod articulation pattern involves slight recurvature beginning about ½ to ⅓ of the distance between the midline and the corner angle; at the midline, the rods are slightly angulated. Approximately 70% of specimens of *C. multicostata* are found to have well developed exoskeletal constrictions (for example, Figs. 9.3–9.5, 9.8, 10.1). These cannot be used as a species-level or genus-level taxonomic criterion, however, since well preserved exoskeletal constrictions have been observed in specimens belonging to nearly every taxon reported herein and in Part B. This species is notable because it shows good examples of this structure more frequently than any other known species of conulariid from the Devonian or Mississippian of North America.

According to Meek and Worthen (1865, p. 253), *C. multicostata* is unique among conulariids in that it possesses rods so closely spaced that "it is only under a good magnifier that the very minute crenulations can be seen." Later, Meek (1871, p. 84) described *C. micronema* as a

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Fig. 9.—9.1–9.5; *Conularia multicostata* Meek and Worthen. 9.1; USNM 50157, plastoholotype. Dark areas on photograph indicate areas where integument of the original specimen still adheres; locality 203. 9.2; UK 6089, specimen intended by Sinclair (1948) to be the holotype of *Mesoconularia mcfarlani* Sinclair, preserved in siderite concretion; probably minor face; locality 73. 9.3; AMNH 6713, specimen chosen by Sinclair (1942*b*) as neotype of *C. micronema* Meek, major face; locality 225. 9.4; AMNH 6713, same specimen as in Fig. 9.3, corner view. 9.5; AMNH 6713, same specimen as in Fig. 9.3, minor face. 9.6–9.7; *C. subcarbonaria* Meek and Worthen. 9.6; FMNH UC 6610, holotype of *C. intertexta* Miller; detailed view of exoskeleton, locality 28. 9.7; FMNH UC 6610, same specimen as in Fig. 9.6, view of entire specimen. 9.8; *C. multicostata* Meek and Worthen, AMNH 6713, same specimen as in Fig. 9.3, detailed view of minor face. Bar scales represent 1 cm.

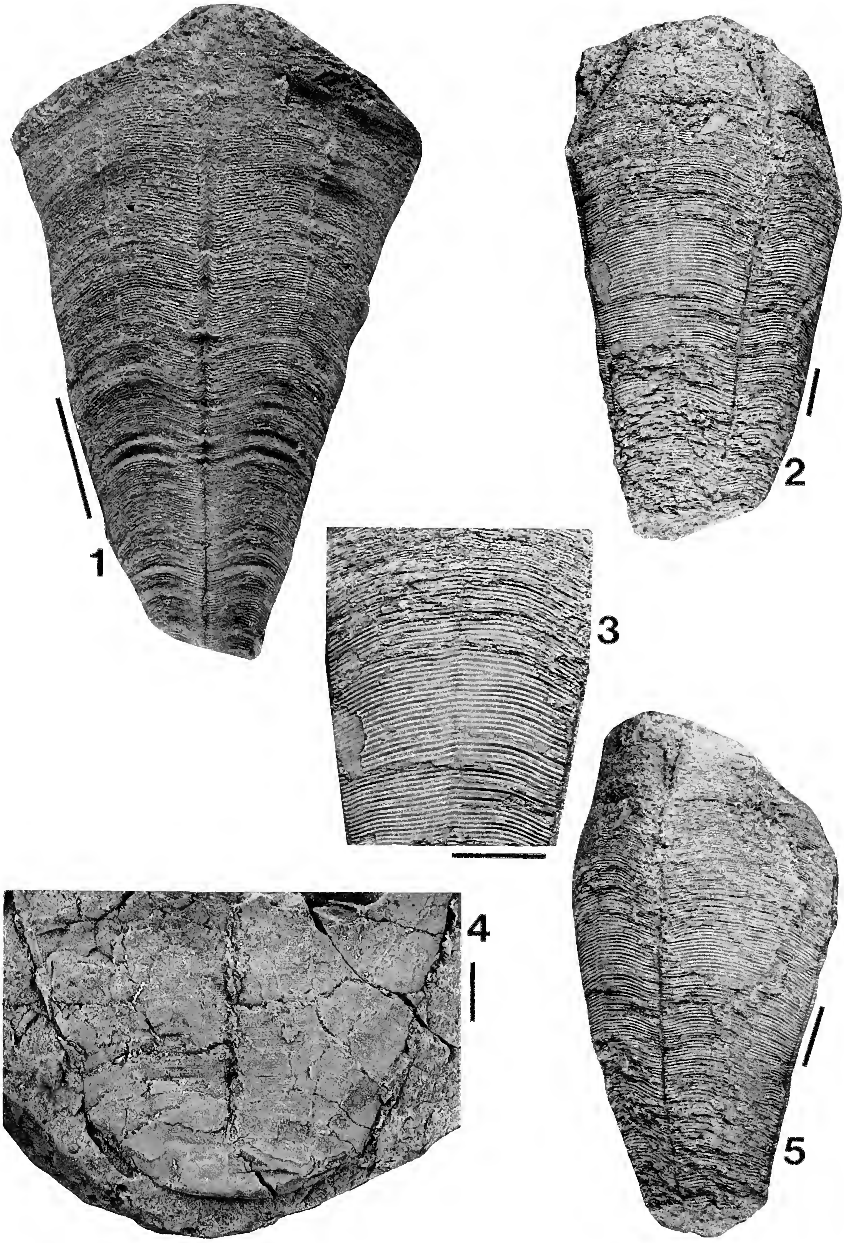

Fig. 10.—10.1–10.3; *Conularia multicostata* Meek and Worthen, 10.1; USNM 50128, corner view of specimen with pronounced exoskeletal constrictions; locality 225. 10.2–

conulariid distinct from all others because it possessed rods so closely spaced that "it requires the aid of a magnifier to see them distinctly." In all morphological respects, the two species are remarkably similar, assuming that AMNH 6713 is "typical" of the species *C. micronema* as suggested by Sinclair (1948, p. 142). *Conularia micronema* Meek is here considered a junior synonym of *C. multicostata* Meek and Worthen.

Two manuscript species, *Mesoconularia mcfarlani* Sinclair and *M. attica* Sinclair, are here placed in synonymy with *C. multicostata* for the reason that they have very closely spaced rods and nodes. Values for spacing of the rods and nodes are consistent with other specimens referred to *C. multicostata* (see Appendix B in part B). The specimen which Sinclair intended to designate the holotype of *M. mcfarlani* (Fig. 9.2) possesses an angulated circular curve style of rod articulation and is very similar in morphology to specimens from the Mississippian of Ohio which have been referred herein to *C. multicostata.* The same can be said for the three specimens (CM 34533–34534, GSC 87204) referred to as *M. attica* in Sinclair's (1948) unpublished thesis.

Conularia micronema was used by Sinclair (1952, p. 138) as the type species of the genus *Diconularia.* Sinclair (1952, p. 138–139) noted that *Diconularia* was a probable form-genus which differs from *Conularia* in routinely having closely spaced rods and an "accentuation of the pustules." *Conularia,* by contrast, was judged by Sinclair to exhibit these features only in gerontic specimens. The genus *Diconularia* is here included as a junior subjective synonym of *Conularia* because there does not appear to be any consistent pattern of differences between "*D.*" *micronema* and species included by Sinclair in the genus *Conularia.* Examples supporting this argument are given below.

Conularia niagarensis Hall, the North American reference species for the genus *Conularia* (Sinclair, 1940*a*), has large, well-pronounced nodes and rod spacing values in the range of about 12–24/cm. These characters closely resemble those of the "typical" specimen of "*D.*" *micronema,* AMNH 6713 (see Appendix B in Part B). The number of rods/cm exhibited in AMNH 6713, 28–32, is well within the limits of the genus *Conularia* as recognized herein. Species referable to *Conu-*

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10.3; *C. subcarbonaria* Meek and Worthen. 10.2; UIPC 10680, holotype, minor face, preserved in limestone; locality 13. 10.3; UIPC 10680, same specimen as in Fig. 10.2, detail of minor face. 10.4; *C. multicostata* Miller and Gurley, USNM 50647, apical region of specimen showing apical wall; locality 228. 10.5; *C. subcarbonaria* Meek and Worthen, UIPC 10680, same specimen as in Fig. 10.2, major face. Bar scales represent 1 cm.

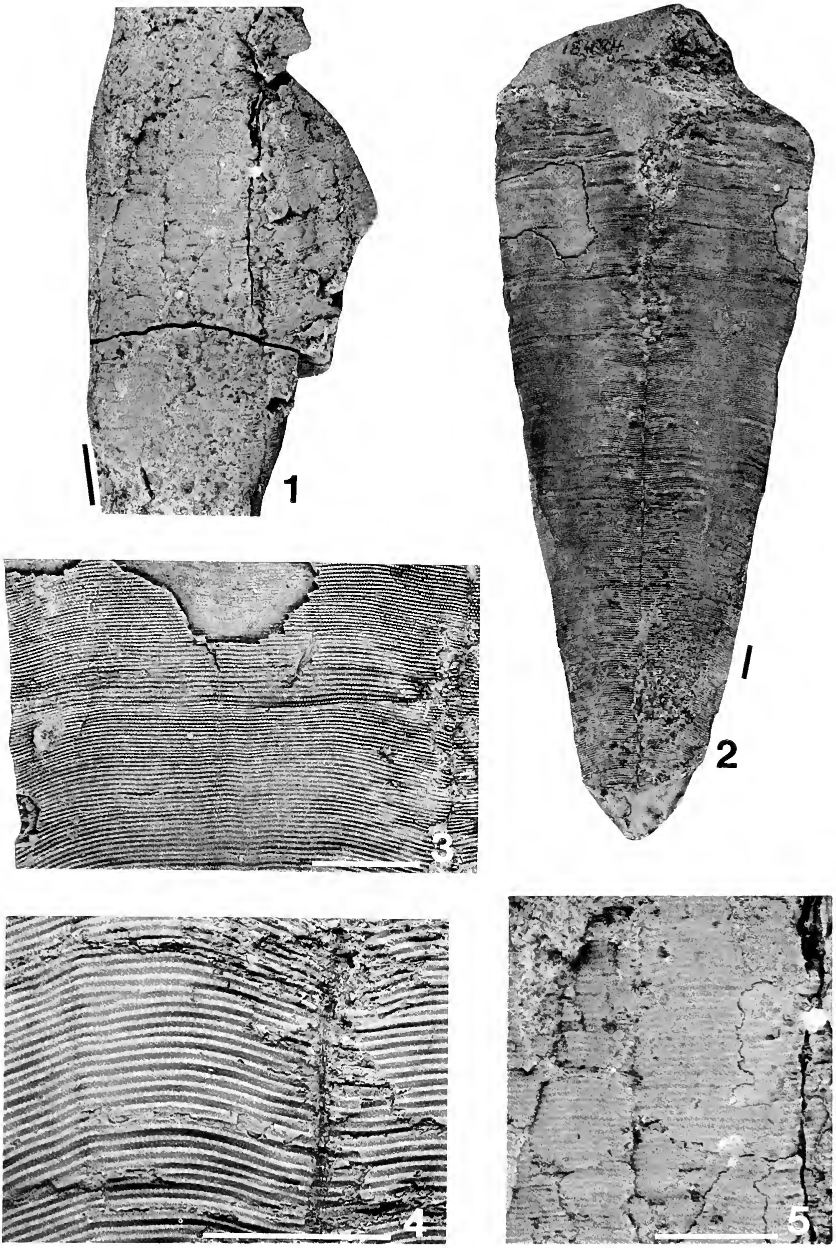

Fig. 11.—*Conularia subcarbonaria* Meek and Worthen. 11.1; FMNH UC 6289, badly weathered holotype of *C. spergenensis* Miller and Gurley, preserved in limestone; locality

laria from the Devonian and Mississippian of North America exhibit 9 to 84 rods/cm. Furthermore, no species of *Conularia* examined from Devonian or Mississippian age rocks of North America are known to consistently possess rods which are more closely spaced in large, presumably gerontic, individuals than in "average-sized" individuals.

Material examined.—67 specimens; housed in the AMNH, CM, CMNH, FMNH, GSC, and the USNM and the private collection of Ron Fisher.

CONULARIA PYRAMIDALIS Hall, 1859
Figs. 3.3, 8.1–8.9, 16.7

Conularia pyramidalis Hall, 1859, p. 347–348; Hall, 1861, Pl. 72A, figs. 1a–c; Miller, 1877, p. 141; Miller, 1889, p. 390; Whitfield and Hovey, 1899, p. 170–171; Richardson, 1942, p. 23–26, Pl. 3, figs. 4–9; Sinclair, 1948, p. 106; Babcock and Feldmann, 1986, fig. 2E.

Conularia huntiana Hall, 1859, p. 348; Hall, 1861, Pl. 72A, figs. 2a–b; Clarke and Ruedemann, 1903, p. 566; Grabau, 1906, p. 151, fig. 65; Grabau and Shimer, 1910, p. 13, fig. 1224; Sinclair, 1948, p. 106, Pl. 9, fig. 1.

Conularia lata Hall, 1859, p. 479–480, Pl. 70A, fig. 3, Pl. 91, fig. 1; Bigsby, 1878, p. 78; Miller, 1889, p. 390; Sinclair, 1948, p. 104.

Conularia huntana (*sic*) Hall. Miller, 1877, p. 141; Miller, 1889, p. 390.

Description.—Exoskeleton up to 20 cm in length. Major apical angle 17–23°; minor apical angle 16–17°. Rod articulation gothic arch style in apical region and inflected gothic arch elsewhere. Rods abut at midline; rod angle 5–22°. 7–17 rods/cm. 1–4 nodes/mm; 1–4 adapertural spines/mm; 1–4 adapical spines/mm. Apical wall not observed.

Occurrences.—Lower Devonian of New Jersey and New York; localities 114, 116–120 and 122.

Types.—Lectotype, designated herein from James Hall's syntypic suite of four specimens, AMNH 33018, smaller of two specimens bearing this number (Figs. 3.3, 8.1, 8.3); three paratypes, AMNH 33018, larger specimen, and AMNH 33019, two specimens. Holotype of *C. huntiana* Hall, NYSM 3488; holotype of *C. lata,* NYSM 3490, plastoholotype, GSC unnumbered.

Remarks.—*Conularia pyramidalis* Hall is similar in size and apical angles to *C. desiderata* Hall. Distinction between the two taxa is made on the basis of differences in rod angles, 9–14° for *C. pyramidalis* versus 13–17° for *C. desiderata.* Additionally, when complete enough speci-

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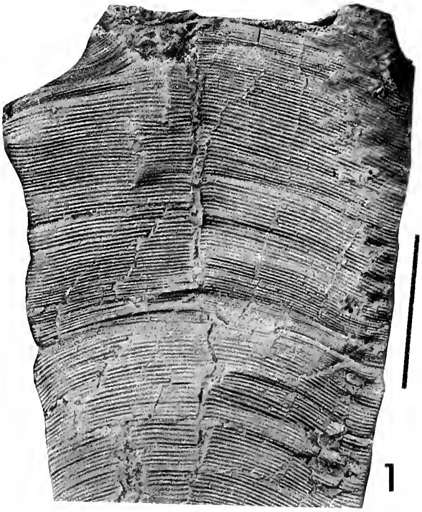
44. 11.2; FMNH UC 18494, larger of two specimens, flattened specimen with apical wall preserved, preserved in calcareous shale; locality 38. 11.3; FMNH UC 18494, same specimen as in Fig. 11.2, detail of major face. Note apparent convergence of rods at exoskeletal constriction. 11.4; UIPC 10680, same specimen as in Fig. 10.2, detail in region of corner groove; locality. 11.5; FMNH UC 6289, same specimen as in Figure 11.1, detail of exoskeleton. Bar scales represent 1 cm.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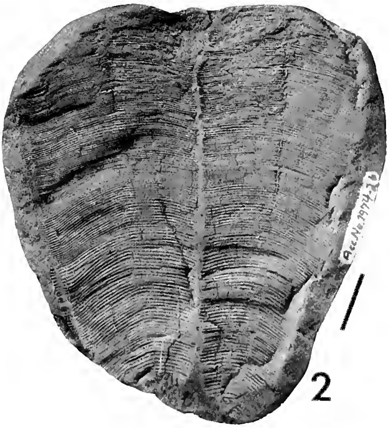
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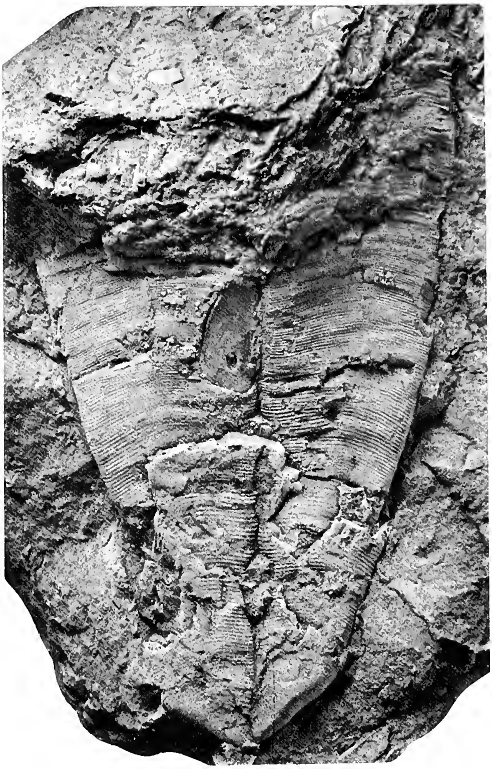
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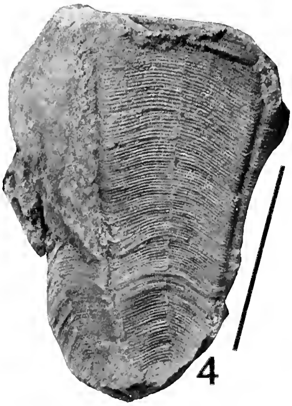
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mens are studied, distinction between these two species can be made on the basis of rod articulation style, gothic arch to inflected gothic arch for *C. pyramidalis,* compared to gothic arch to inflected circular curve for *C. desiderata.* Differences in rod articulation styles immediately serve to help distinguish *C. pyramidalis* Hall from *C. undulata* Conrad, though both may attain lengths greater than 15 cm. *Conularia pyramidalis* Hall is readily distinguished from *C. elegantula* Meek by having significantly fewer nodes and spines per unit space than are present in *C. pyramidalis.* The feature which immediately serves to distinguish *C. pyramidalis* from *C. multicostata* Meek and Worthen is the greater spacing between rods, 9–14/cm in *C. pyramidalis* and up to 32/cm in *C. multicostata. Conularia multicostata* and *C. subcarbonaria* Meek and Worthen have more prominent nodes on the rods than does *C. pyramidalis.*

Conularia huntiana Hall was distinguished from *C. pyramidalis* Hall (Hall, 1859, p. 348) by its greater length, its smaller apical angles, the greater convexity of its faces and differences in the appearance of ridges and spines. The apical angles of the lectotype of *C. pyramidalis* are 18° and 16°, and in the holotype of *C. huntiana,* the apical angles as measured are 13° and 11°. However, the holotype of *C. huntiana* is not compressed to the extent that the lectotype of *C. pyramidalis* is. Moreover, the lectotype of *C. pyramidalis* is a smaller specimen and presumably represents an earlier growth interval than does the holotype of *C. huntiana.* Therefore, a smaller set of apical angles is expected in *C. huntiana.* Differences in convexity of the faces between the two taxa is likely a result of differences in collapse of the exoskeletons after death of the animals and/or differences in compression of the exoskeletons. Differences in the appearance of the ridges and spines seem to be functions of preservation: most of the lectotype of *C. pyramidalis* is preserved as an internal mold, whereas the holotype of *C. huntiana* retains much integument. Where integument is present on the lectotype of *C. pyramidalis,* it is identical to that on the holotype of *C. huntiana* (compare Figs. 8.3 and 8.4). In both specimens, most of the rods are broken out, leaving a "double ridge" arrangement of the integument,

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Fig. 12.—*Conularia multicostata* Meek and Worthen. 12.1; GSC 87204, enlargement of a specimen intended by Sinclair (1948) to be a paratype of *Mesoconularia attica*; locality 193. 12.2; CMNH 4684, external mold of a flattened specimen preserved in a siderite concretion; locality 198. 12.3; CM 34533, specimen intended by Sinclair (1948) to be the holotype of *M. attica*; locality 193. Note that the apical wall is present. 12.4; FMNH UC 54014A, specimen figured by Herrick (1888*a*) as *C. micronema*; locality 228. 12.5; GSC 87204, same specimen as in Fig. 12.1, view of a collapsed specimen preserved in a siderite concretion; locality 193. Bar scales represent 1 cm.

marking the former positions of the margins of the rods within the integument.

Conularia lata Hall is included as a junior subjective synonym of *C. pyramidalis* largely because of qualitative similarities including nearly identical rod articulation styles. Also, values for apical angles and rod spacing are similar in the lectotype of *C. pyramidalis* and the sole specimen referred to *C. lata* by Hall, NYSM 3490. Major and minor apical angles for the lectotype of *C. pyramidalis* are 18° and 17°, respectively. For the holotype of *C. lata,* they are 23° and 17°. Rods/cm values for the lectotype of *C. pyramidalis* vary between 9 and 14 while those of the holotype of *C. lata* vary between 7 and 10. Values for rod angles and node spacing on the rods for both specimens are also well within the expected normal distribution for a species.

Material examined.—41 specimens; housed in the AMNH, CM, CMNH, FMNH, GSC, NJSM, NYSM, USNM, and the private collection of Paul Zell.

CONULARIA SUBCARBONARIA Meek and Worthen, 1865
Figs. 9.6–9.7, 10.2–10.3, 10.5, 11.1–11.5

Conularia subcarbonaria Meek and Worthen, 1865, p. 253; Meek and Worthen, 1873, p. 520–522, Pl. 19, figs. 4a–c; Miller, 1877, p. 141; Bigsby, 1878, p. 316; Miller, 1889, p. 390; Keyes, 1894, p. 218; Weller, 1898, p. 191–192.
Conularia intertexta Miller (*nomen nudum*), 1892*b,* p. 692.
Conularia intertexta Miller, 1894, p. 317, Pl. 10, fig. 4; Weller, 1898, p. 190.
Conularia spergenensis Miller and Gurley, 1893, p. 74–75, Pl. 8, fig. 2; Miller, 1897, p. 765; Weller, 1898, p. 191.
Mesoconularia subcarbonaria (Meek and Worthen). Sinclair, 1948, p. 123.
Mesoconularia intertexta (Miller). Sinclair, 1948, p. 123.
Diconularia micronema (Meek). *Sensu* Lane, 1973, p. 92–93, Pl. 8, figs. 2–3.

Description.—Exoskeleton up to 35 cm in length. Major apical angle 10–21°; minor apical angle 9–19°. Rods are undulose; rod articulation uniformly of angulated circular curve style. Rods abut at midline; rod angle 4–6°. 17–31 rods/cm. Nodes prominent; 3–5 nodes/mm on rods; no spines present. Apical wall may be present.

Occurrences.—Upper Devonian–Lower Mississippian of Illinois, Indiana, Iowa and Missouri; localities 8–9, 13, 20, 24, 27–28, 37–38, 42, 44–46, 48, 51, 61, 64, 67, and 101.

Types.—Holotype, UIPC 10680, plastoholotypes USNM 50158, FMNH UC unnumbered and GSC unnumbered. Holotype of *C. intertexta,* FMNH UC 6610, plastoholotypes, USNM 68130 and GSC unnumbered; holotype of *C. spergenensis,* FMNH UC 6289.

Remarks.—In the possession of prominent nodes along the rods, *C. subcarbonaria* Meek and Worthen resembles the Mississippian species, *C. multicostata* Meek and Worthen, and the Devonian species, *C. ulsterensis* Howell. These taxa are readily distinguished, however, on the basis of rod articulation style: *C. subcarbonaria* possesses angulated circular curve rod articulation in which the rods are undulose, particularly in large individuals. On the other hand, *C. multicostata* has both angulated circular curve and inflected gothic arch rod articulation and *C. ulsterensis* possesses only inflected gothic arch rod articulation. Additionally, *C. ulsterensis* is unique among the species of *Conularia* studied in having a rod spacing of 45–84 rods/cm in adult specimens.

Like the Devonian species, *C. undulata* Conrad, *C. subcarbonaria* possesses undulose rods. *Conularia subcarbonaria* can be distinguished from *C. undulata* in having more prominent nodes along the rods and by having rods which nearly always abut at the midline. The rods of *C. undulata* alternate at the midline in approximately 10% of the cases studied.

Conularia intertexta Miller is considered synonymous with *C. subcarbonaria* because of general qualitative similarities between the types of the two species and because of similarities in the value for number of rods/cm (see Appendix B in Part B). However, the holotype specimen (Figs. 9.6–9.7) of *C. intertexta* is very badly preserved, making any species-level assignment somewhat doubtful. One characteristic of the specimen is an apparently undulose set of rods. It is primarily because of its undulose rods that *C. intertexta* is here included in synonymy with *C. subcarbonaria.*

The holotype of *C. spergenensis* Miller and Gurley (Figs. 11.1, 11.5) is, like the holotype of *C. intertexta,* badly preserved. However, like the holotype of the latter taxon, *C. spergenensis* bears qualitative and quantitative similarities to *C. subcarbonaria,* most notably, undulose rods. It too is therefore considered to be a junior subjective synonym of *C. subcarbonaria.*

Material examined.—46 specimens; housed in the AMNH, FMNH, GSC, ISGS, IUPC, and the USNM.

CONULARIA TUZOI Clarke, 1907
Fig. 15.3

Conularia desiderata var. *tuzoi* Clarke, 1907, p. 181, fig.; Clarke, 1908, p. 144, Pl. 11, fig. 13; Dresser and Denis, 1944, p. 326.

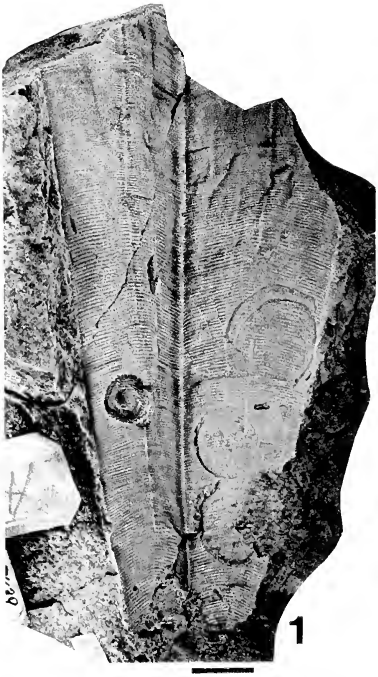
Conularia tuzoi Clarke. Sinclair, 1948, p. 105.

Description.—Description based only upon holotype. Exoskeleton 11.3 cm in length. Major apical angle approximately 10°; minor apical angle not observed. Rod articulation style unknown in vicinity of apex and of inflected gothic arch style elsewhere; rods are broadly inflected. Rods abut at midline; rod angle 9–10°. Nodes and spines not observed. Apical wall not observed.

Type.—Holotype, NYSM 9404.

Occurrence.—Lower Mississippian of Quebec; locality 244.

Remarks.—The holotype of *C. tuzoi* (Clarke) is badly preserved and no additional specimens are known. A cross sectional view is not pre-



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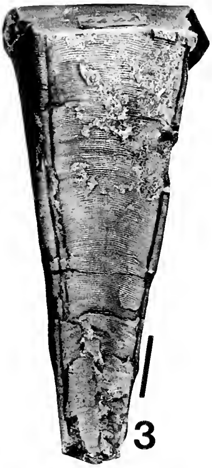

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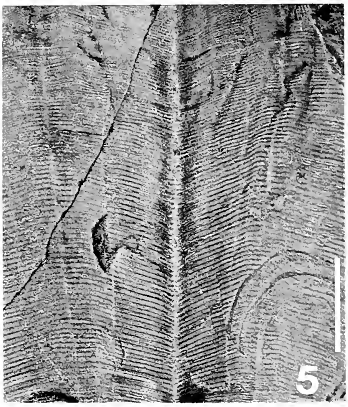

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Fig. 13.—*Conularia undulata* Conrad. 13.1; AMNH 41093, neotype, preserved as an external mold in siltstone. Note rounded marks produced by orbiculoid brachiopods

served on the holotype. This taxon appears to differ from other species of *Conularia* included in this paper in the possession of broadly rounded inflections where the rods are of inflected gothic arch style.

Material examined.—1 specimen, NYSM 9404.

CONULARIA ULSTERENSIS Howell, 1942
Figs. 15.4, 16.1–16.3, 16.5

Conularia ulsterensis Howell, 1942, p. 91, figs. 10–11; Goldring, 1943, p. 208.
Mesoconularia ulsterensis (Howell). Sinclair, 1948, p. 117.

Description.—Exoskeleton up to 3 cm in length. Major apical angle 14–19°; minor apical angle 10–15°. Rod articulation uniformly of inflected gothic arch style. Rods usually abut at midline; rod angle 11–15°. 45–84 rods/cm. Nodes prominent; 6–8 nodes /mm; 6–8 adapertural spines/mm; 6–8 adapical spines/mm. Apical wall not observed.

Types.—Holotype, PU 42071; two paratypes, PU 42072–42073.

Occurrences.—Lower Devonian of New York and Pennsylvania; localities 115, 231, 234 and 236. Specimens possibly referable to this taxon have also been found in the Lower Devonian of Quebec; locality 242.

Remarks.—This species is distinct in its possession of up to 84 rods/cm in adult specimens, the largest number recorded in the genus *Conularia.* It can also be distinguished by its prominent, closely spaced nodes. In this form, nodes are spaced as closely as 7/mm. Some specimens of *C. undulata* Conrad may have as many as 7 nodes/mm, but *C. undulata* has neither inflected gothic arch rod articulation throughout the exoskeleton nor prominent nodes.

The specimen of *C. ulsterensis* Howell illustrated in Fig. 16.2 is preserved as an internal mold. It is unusual in that it clearly shows that a longitudinal invagination existed along the integument internal to the midline.

Material examined.—7 specimens; housed in the CM, NJSM, and the NYSM.

CONULARIA UNDULATA Conrad, 1841
Figs. 13.1–13.5, 14.1–14.5, 15.1–15.2, 16.4

Conularia undulata Conrad, 1841, p. 57; Hall, 1861, p. 62–63; Bigsby, 1878, p. 62–63; Hall, 1876, Pl. 29, figs. 1–7; Hall, 1879, p. 208–209, Pl. 33, figs. 1–5, 7; Pl. 34A, figs. 1–4; Miller, 1889, p. 390; Whitfield and Hovey, 1901, p. 326–327; Grabau,

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that were previously attached to the conulariid exoskeleton; locality 145. 13.2; NYSM 3493, preserved in siltstone, major face; locality 145. 13.3; NYSM 3494, preserved in siltstone, major face; locality 145. 13.4; AMNH 41093, same specimen as in Fig. 13.1, detail of major face. 13.5; AMNH 41093, same specimen as in Fig. 13.4, detail in region of corner groove. Bar scales represent 1 cm.

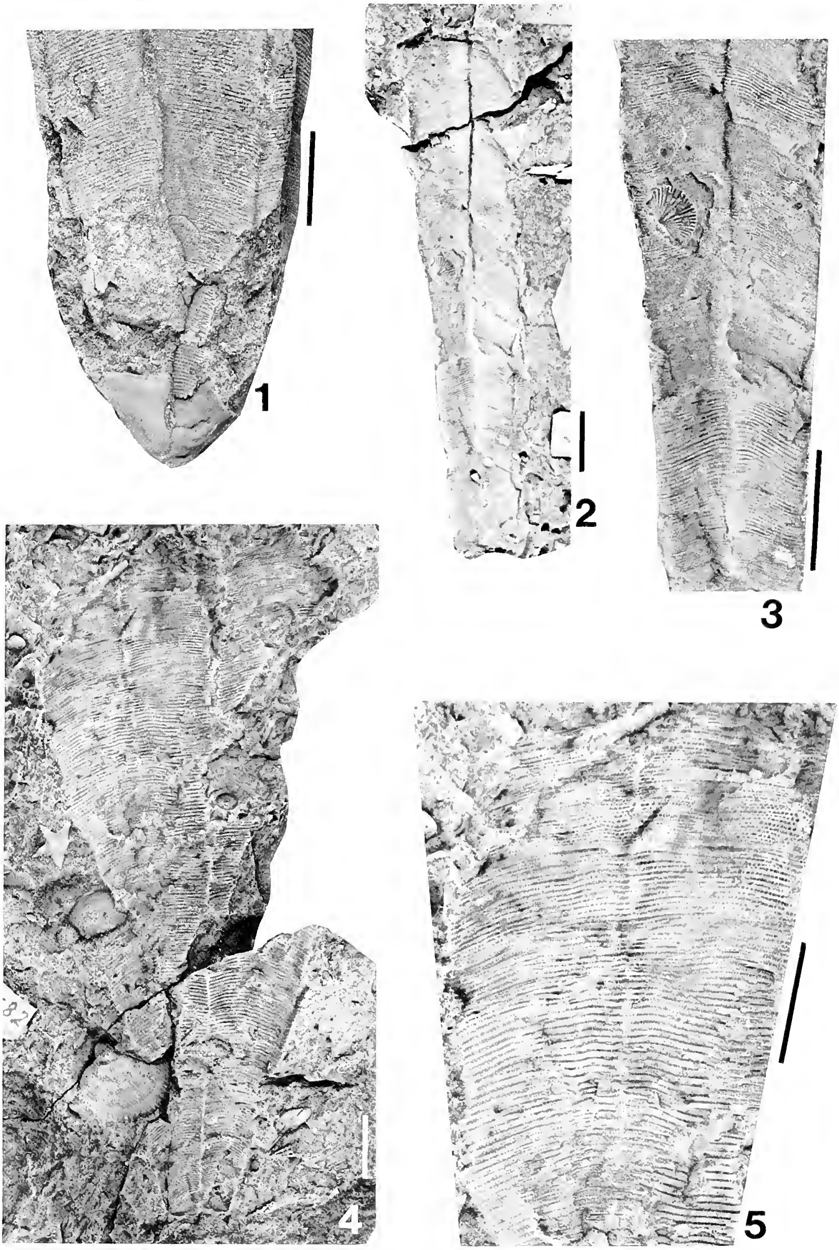

Fig. 14.—*Conularia undulata.* 14.1; AMNH 5439, specimen showing relation of apical wall to the remainder of the exoskeleton. Note flange for connection at adapertural end

1899, p. 284–285, fig. 219; Grabau and Shimer, 1910, p. 13, fig. 1225–1226; Moore and Harrington, 1956*b*, p. F60, fig. 25.2; Babcock and Feldmann, 1986, fig. 2I.

Conularia cayuga Hall, 1876, Pl. 28, figs. 2–3; Hall, 1879, p. 211–212, Pl. 34, figs. 2, 5; Miller, 1889, p. 390.

Conularia crebistria Hall, 1876, Pl. 29, figs. 8, 9.

Conularia crebistriata (*sic*) Hall, 1879, p. 210–211, Pl. 33, figs. 8–9, Pl. 34A, fig. 5; Miller, 1889, p. 390; Moore and Harrington, 1956*b*, p. F60, fig. 42.9.

Mesoconularia undulata (Conrad). Sinclair, 1948, p. 118.

Conularia s.l. *cayuga* Hall. Sinclair, 1948, p. 285.

Ctenoconularia crebistriata (*sic*) (Hall). Sinclair, 1948, p. 241, Pl. 6, figs. 10–11.

Ctenoconularia crebistria (Hall). Sinclair, 1952, p. 142.

Conularia sp. cf. *C. undulata* Conrad. Kasznica, 1986, p. 14–15, fig. 2.

Description.—Exoskeleton up to 15 cm in length. Major apical angle 10–18°; minor apical angle 8–15°. Rod articulation uniformly of inflected circular curve style; rods are undulose in the apertural ½. Rods usually abut at midline; rod angle 10–18° in apical region and 4–20° elsewhere. 17–32 rods/cm. 4 nodes/mm; 4 adapertural spines/mm; 4 adapical spines/mm. Apical wall may be present.

Types.—Neotype, AMNH 41093, plastoneotype, FMNH UC 694; James Hall's figured specimens, NYSM 3493, 3494, AMNH 5439. Holotype of *C. crebistria,* AMNH 5440, plastoholotype, FMNH UC 679; holotype of *C. cayuga,* NYSM 3482, plastoholotype, FMNH UC 685.

Occurrences.—Middle Devonian of Maine, Maryland, New York, Ontario, Pennsylvania, and Quebec; localities 90–91, 115, 128–129, 136–138, 140–141, 143, 145–148, 230, 236–238, and 241. Ulrich (1892) has indicated that *C. undulata* is present in the Devonian of Bolivia and Reed (1904) has cited this taxon in the Devonian of South Africa. These identifications are erroneous, and are described briefly below. They will also be described in greater detail elsewhere. Cordini (1955, p. 275, fig. 81) referred and figured some fossils found in Antarctica as *C.* cf. *C. undulata,* but these have been subsequently identified as plant remains (Dalziel et al., 1981).

Remarks.—Conrad's suite of syntypes is lost. However, judging from his description of *C. undulata* (Conrad, 1841, p. 57) it is clear that the species is based upon specimens now referable to either *C. undulata* or *C. pyramidalis* Hall. Hall's early figures and description of *C. undulata* (Hall, 1876, Plate 29, figs. 1–7, explanation of Plate 29; 1879, p. 208–209; Plate 33, figs. 1–5, 7, Plate 34A, figs. 1–4) have served as bases for all subsequent studies on the species. Therefore, it is appro-

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of apical wall; locality 145. 14.2; AMNH 5440, holotype of *C. crebistria* Hall, preserved in calcareous shale, minor face; locality 136. 14.3; AMNH 5440, same specimen as in Fig. 14.2, detail of minor face. 14.4; NYSM 3482; holotype of *C. cayuga* Hall, preserved in calcareous shale; locality 136. 14.5; NYSM 3482, same specimen as in Fig. 14.4, detailed view of minor face. Bar scales represent 1 cm.

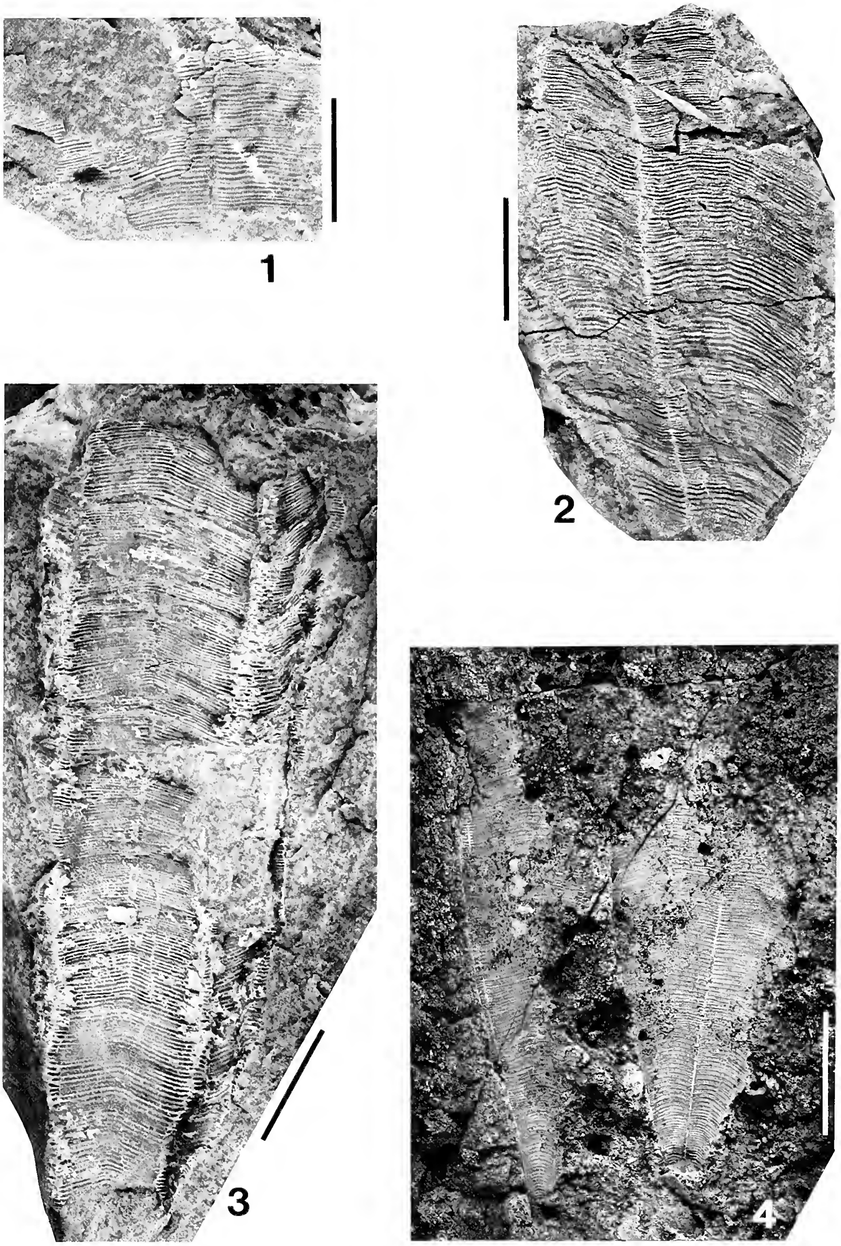

Fig. 15.—15.1–15.2; *Conularia* cf. *C. undulata* Conrad. 15.1; NYSM 9410, detail of exoskeleton; locality 241. 15.2; NYSM 9408, flattened and tectonically distorted specimen; locality 90. 15.3; *C. tuzoi* Clarke, NYSM 9404, holotype; locality 244. 15.4; NYSM

priate to select a neotype from among Hall's extant specimens. The specimen chosen, AMNH 41093, is the subject of one of the best known of Hall's figures of the taxon.

Two Devonian species are here considered junior subjective synonyms of *C. undulata* Conrad: *C. cayuga* Hall and *C. crebistria* Hall. *Conularia crebistria,* according to Hall (1879, p. 210) differed from *C. undulata* in being "more slender in its mode of growth" and in having more closely spaced rods. In terms of the arrangement of nodes and spines, the two were judged to be "precisely similar." The holotype of *C. crebistria,* AMNH 5440, is a badly preserved specimen exhibiting one face (Figs. 13.2–13.3). The apical angle cannot be determined because the specimen has been distorted and the corner grooves are not preserved on the surface of the slab. Like specimens of *C. undulata,* this specimen has inflected circular curve rod articulation. The rods are undulose in the vicinity of the aperture. The holotype of *C. crebistria* has rod spacing values ranging from 24 to 30 rods/cm and node spacing values of about 4 nodes/mm. No other values can be determined with confidence from this specimen. The equivalent values for the lectotype of *C. undulata* are 20–27 rods/cm and 6 nodes/mm. There seems to be no significant difference in the features exhibited in AMNH 5440 from other specimens here referred to *C. undulata.*

The holotype of *C. cayuga,* NYSM 3482, is a flattened specimen preserved as an external mold (Figs. 13.4–13.5). An apical wall is present. Hall (1879, p. 211–212) indicated that, in general, this specimen is "not dissimilar to *C. undulata.*" However, subtle differences, including "stronger" rods, wider spaced rods except in the apertural region and the presence of "striae" between adjacent rods (=spines) were used as key characters which served to distinguish this taxon from *C. undulata.* Spines, of course, are present in *C. undulata,* just as they are in the holotype of *C. cayuga.* The rods of NYSM 3482 have a spacing of 17–22/cm, well within the expected range of values for individuals of *C. undulata.* Other quantitative determinants, given in Appendix B in Part B, substantiate this conclusion. The rods are undulose except near the apical wall and are articulated in angulated circular curve style, similar to the neotype of *C. undulata.* The rods do not appear to be better pronounced than those shown in specimens referred to *C. undulata* which are preserved as external molds, including the neotype (Fig. 13.4). Thus, the holotype of *C. cayuga* is here referred to Conrad's species, *C. undulata.*

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9411, *C. ulsterensis* Howell, two specimens, one preserving an apical wall; locality 242. Bar scales represent 1 cm.

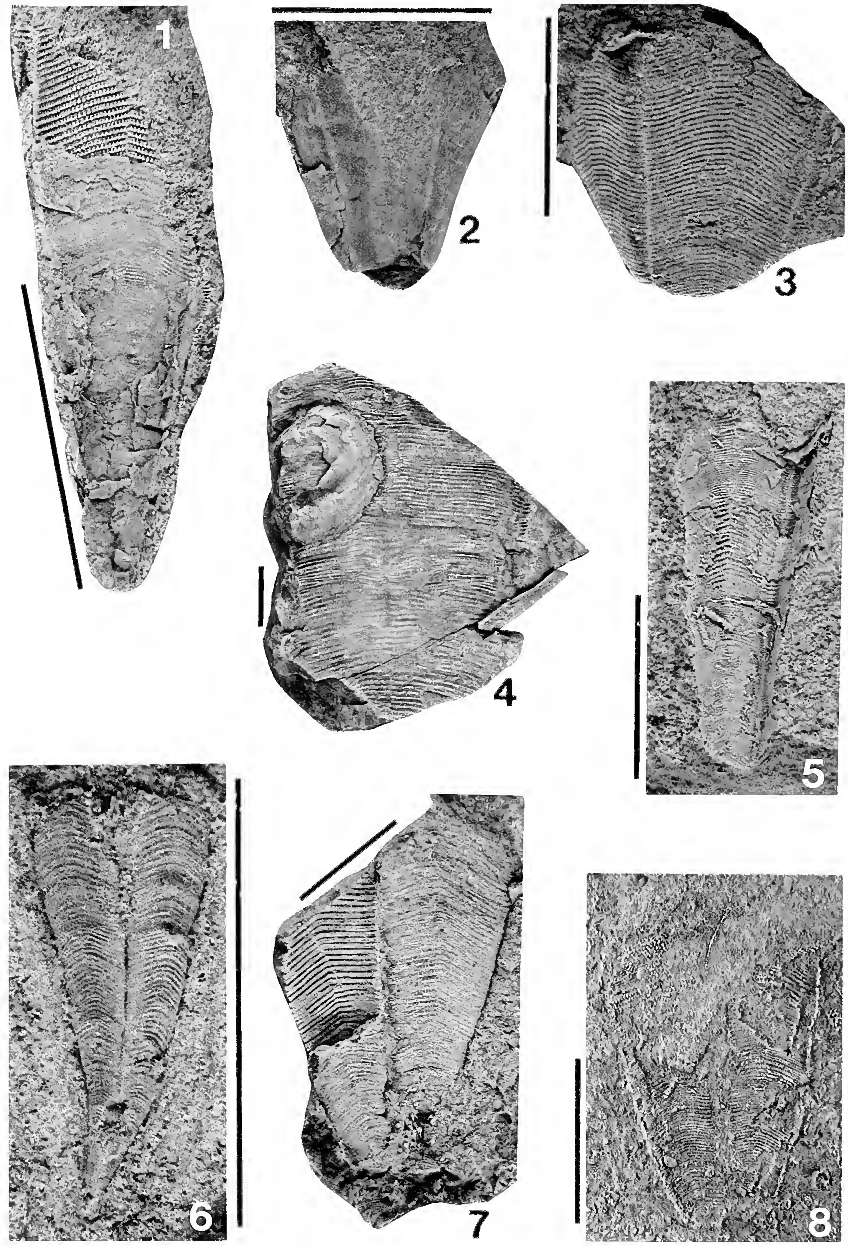

Fig. 16.—16.1–16.3; *Conularia ulsterensis* Howell. 16.1; PU 42071, holotype; locality 115. 16.2; PU 42072, paratype; internal mold showing longitudinal ridges at the midlines; locality 115. 16.3; NJSM 12843, external mold; locality 236. 16.4; CM 34520, *C. un-*

Sinclair (1948, p. 118) and Sinclair and Richardson (1954, p. 105) stated that the species *C. grandis* Roemer is synonymous with *C. undulata.* However, this cannot be substantiated here because the specimen upon which Roemer's description is based (Roemer, 1856, p. 436, Plate 3, figs. 21a–b) was not available for study. It is likely that the holotype of *C. grandis* is lost.

Conularia undulata is similar to *C. subcarbonaria* Meek and Worthen in the possession of an undulose mode of angulated circular curve style rod articulation. It differs from the latter form in having nodes on the rods which are not prominent. Moreover, the rods of *C. subcarbonaria* nearly always abut at the midline. In *C. undulata,* as many as 10% of the rods may alternate at the midline.

Two specimens from the Devonian of the Malvinokaffric Realm have been misidentified as *C. undulata.* The first (Ulrich, 1892, p. 31–33, Pl. 3, figs. 6a–b), which was collected in Bolivia, is referable to *C. albertensis* Reed, judging from Ulrich's well-executed figure. *Conularia albertensis* differs from *C. undulata* in having gothic arch rod articulation in the apical region and inflected gothic arch rod articulation elsewhere, whereas *C. undulata* has only inflected circular curve rod articulation. The second specimen from the Malvinokaffric Realm which was misidentified as *C. undulata* was described and figured by Reed (1904, p. 248–249, Pl. 31, figs. 1–1a). It was collected from the Bokkeveld beds of South Africa. A latex mold (UCGM 34720) of the specimen has been examined. It is referable to *C. quichua* Ulrich. *Conularia quichua* and *C. undulata* both have undulose rods, but *C. quichua* has rods articulated in gothic arch fashion in the apical region and in angulated circular curve style elsewhere.

Material examined.—43 specimens housed in the AMNH, CM, FMNH, GSC, NYSM, NJSM, USNM, and the private collections of Gordon Baird, Robert Linsley and Paul Zell.

***CONULARIA* sp.**

Fig. 16.8

Conularia cf. *huntiana* Hall. Merriam, 1973, p. 35, Pl. 12, figs. 18–20.

Occurrence.—Upper Devonian of Nevada; Locality 108.

Remarks.—Remains of at least six conulariid specimens from the Devonian of Nevada were figured and described by Merriam (1973,

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dulata Conrad, portion of specimen with orbiculoid brachiopod attached; locality 91. 16.5; *C. ulsterensis* Howell, CM 34528. 16.6; *C. desiderata* Hall, USNM 395827, juvenile, with apex intact; locality 142. 16.7; *C.* cf. *C. pyramidalis* Hall, GSC 2598; locality 241. 16.8; *C.* sp., USNM 159536; locality 108. Bar scales represent 1 cm.

p. 35, Plate 12, figs. 18–20). Merriam identified these specimens as *C.* cf. *huntiana.* The specimens (USNM 159536), one of which is figured herein (Fig. 16.8), are poorly preserved and cannot be assigned to a species at present.

The specimens in question possess an inflected circular curve rod articulation. The rods are slightly deflected adaperturally at the midline. This style of rod articulation is similar to that observed in specimens of *C. desiderata* Hall.

Material examined.—6 specimens; housed in the USNM.

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DEVONIAN AND MISSISSIPPIAN CONULARIIDS OF NORTH AMERICA. PART B. *PARACONULARIA, RETICULACONULARIA,* NEW GENUS, AND ORGANISMS REJECTED FROM CONULARIIDA

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Abstract

Descriptions of the species assigned to *Paraconularia* Sinclair, 1940 and *Reticulaconularia* Babcock and Feldmann, new genus, as well as organisms rejected from the Conulariida, are treated in Part B of this two-part work on the Devonian and Mississippian conulariids of North America. Fifteen species of *Paraconularia* are considered valid, of which five are new. The new taxa are *P. alpenensis, P. chagrinensis, P. oklahomaensis, P. wellsvillia,* and *P. yochelsoni. Adesmoconularia* Driscoll, 1963 is considered a junior synonym of *Paraconularia.* Two species are referable to *Reticulaconularia* Babcock and Feldmann, new genus; *Conularia penouili* is selected as the type species.

Introduction

This paper is the second, and final, part of "Devonian and Mississippian Conulariids of North America." This work contains descrip-

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tions of species referable to the genera *Paraconularia* and *Reticulaconularia* n. gen., as well as specimens described in the literature as conulariids but which are here rejected from the phylum. Locality descriptions and measurements of selected specimens are included as appendices A and B, respectively, herein. Figures are numbered consecutively in both Parts A and B in order to avoid cross-reference confusion.

Genus ***PARACONULARIA*** Sinclair, 1940

Type species.—*Conularia inequicostata* Koninck, 1883, designated by Sinclair (1940); Carboniferous of Belgium. Holotype: Musée Royal d'Histoire Naturelle de Belgique, Brussels, Belgium. North American reference species, *fide* Sinclair (1940): *Conularia blairi* Miller and Gurley, 1893 (Mississippian). Lectotype of *C. blairi*: UCGM 3985.

Diagnosis.—Conulariids with rods that are generally widely spaced, 4–35 rods/cm. More than 60% of rods alternate at midline; fewer than 40% abut. Apical angles small, 9–28°. Nodes, adapertural spines and adapical spines may or may not be present; if present, they are usually widely spaced, 2–6/mm.

PARACONULARIA ALPENENSIS
Babcock and Feldmann, new species
Figs. 17.1–17.3

Description.—Description based only upon holotype. Exoskeleton 3.6 cm in length. Major apical angle 21°; minor apical angle 16°. Rod articulation inflected circular curve style; rods are slightly recurved near midline in apertural region. Rods abut or alternate at midline; alternation pattern either right superior or left superior on major face, usually left superior on minor face; rod angle 9–10°. 14 rods/cm. Nodes not observed; spines absent. Apical wall not observed.

Occurrence.—Middle Devonian of Michigan; locality 92.

Type.—Holotype, GSC 85060.

Remarks.—This taxon is similar to *P. chesterensis* (Worthen), *P. missouriensis* (Swallow) and *P. recurvatus* Babcock and Feldmann, n. sp. in the possession of rods that are recurved near the midline. *Paraconularia alpenensis,* however, exhibits rods that are not recurved in the apical region, at least not in the holotype. None of the other three taxa possess this characteristic.

It is not known whether *P. alpenensis* possessed nodes on the rods. The holotype, and only known specimen, is weathered and lacks the external surfaces of all the rods which are present. No spines are present. The uniqueness of the rod articulation patterns are sufficient to distinguish this taxon from all other described taxa.

Material examined.—1 specimen, GSC 85060.

Etymology of trivial name.—Named for the Alpena Limestone, in which the holotype was found.

PARACONULARIA ALTERNISTRIATA (Shimer, 1926)
Figs. 17.5–17.6

Conularia alternistriata Shimer, 1926, p. 84, Pl. 4, figs. 11a–b.
Paraconularia alternistriata (Shimer). Sinclair, 1948, p. 190.

Description.—Description based only upon holotype. Length 1.9 cm. Major apical angle 11°; minor apical angle 10°. Rod articulation inflected gothic arch style; rods are almost imperceptibly inflected near the corner angles. Rods always alternate at midline; alternation pattern usually right superior on major face and usually left superior on minor face; rod angle 9–10°. 28 rods/cm (extrapolated). Nodes and spines absent. Apical wall not observed.

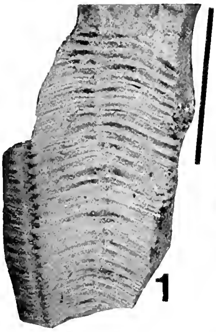
Occurrence.—Mississippian of Alberta; locality 4.

Type.—Holotype, GSC 5111.

Remarks.—*Paraconularia alternistriata* (Shimer) is similar in morphology to specimens of *P. yochelsoni* Babcock and Feldmann, n. sp. Both are of similar size, less than 3.5 cm in maximum length and both exhibit similar forms of rod articulation style. The rod articulation present on the holotype of *P. alternistriata* is here judged to be a form of inflected gothic arch style. The rods in this specimen are inflected so little, though, that the articulation could easily be confused for a gothic arch style articulation pattern. This may simply be a function of the small size of the holotype; a sample close to the aperture of a larger specimen may yield a rod articulation pattern more distinctly of an inflected gothic arch style. *Paraconularia yochelsoni* possesses rods which are clearly articulated in an inflected gothic arch style close to the apex and trending towards an inflected circular curve style near the aperture. *Paraconularia alternistriata* is further distinguished from *P. yochelsoni* in having a smaller apical angle, 10–11°, as compared to 15–20° in *P. yochelsoni* and, finally, in having greater rod spacing, 28 rods/cm as compared to 13–18 rods/cm.

The holotype, and only known specimen, of *P. alternistriata* exhibits longitudinal folds in the integument between adjacent rods suggesting that spines may have been present in this taxon. The folds are best developed near the corner angles. Their occurrence seems to be erratic and the spacing between adjacent folds is inconsistent. In all likelihood, these folds do not represent integument folded over spines but simply folds resulting from a contraction of the integument about the rods and, perhaps, some shearing of the exoskeleton due to compression. This phenomenon is relatively common among specimens of *Paraconularia,* having also been observed in *P. subulata* (Fig. 3.2) and *P. missouriensis* (Fig. 25.3).

Material examined.—1 specimen, GSC 5111.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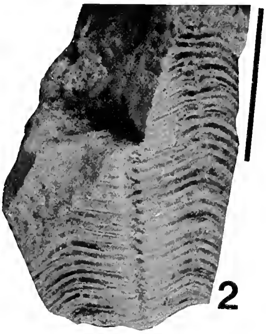
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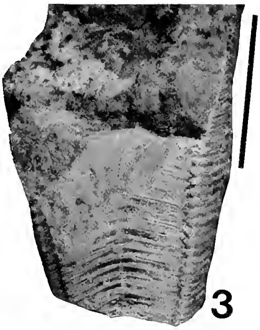
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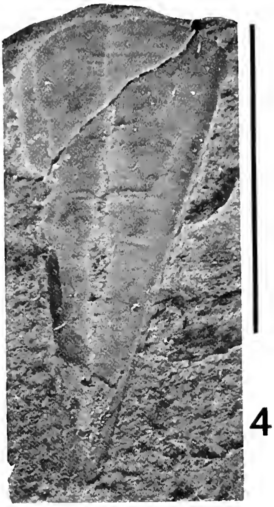
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PARACONULARIA BLAIRI (Miller and Gurley, 1893)
Figs. 18.1–18.5, 22.1–22.3

Conularia blairi Miller and Gurley, 1893, p. 73–74, pl. 7, figs. 14–15; Miller, 1897, p. 765; Weller, 1898, p. 189; Chappars, 1936, p. 16; Branson, 1938, p. 110, Pl. 14, figs. 7–8; Branson, 1944, p. 216.
Conularia sedaliensis Miller and Gurley, 1896, p. 28, Pl. 3, figs. 4–5; Miller, 1897, p. 765; Weller, 1898, p. 191; Chappars, 1936, p. 16.
Conularia (*Conularia*) *sedaliensis* Miller and Gurley. Bouček, 1939, p. A 121.
Conularia (*Paraconularia*) *blairi* (Miller and Gurley). Sinclair, 1940, p. 74.
Paraconularia blairi (Miller and Gurley). Sinclair, 1948, p. 197; Moore and Harrington, 1956, p. F65, fig. 50.2.
Paraconularia sedaliensis Miller and Gurley. Sinclair, 1948, p. 201.
Paraconularia indiana Sinclair, [1948], p. 195, Pl. 18, figs. 1–2.
Paraconularia cf. *newberryi* (Winchell). *Sensu* Sinclair, 1948, Pl. 13, figs. 1–3.
Paraconularia missouriensis (Swallow). *Sensu* Babcock and Feldmann, 1984, p. 16–17.

Description.—Exoskeleton up to 20 cm in length. Major apical angle 11–23°; minor apical angle 10–20°. Rod articulation inflected gothic arch style in apical region and inflected circular curve with a slight adapertural inflection at the midline elsewhere. Rods almost always alternate at midline; alternation pattern usually right superior on major and minor faces; rod angle 8–19°. 6–13 rods/cm. 2–3 nodes/mm; 2–3 adapertural spines/mm; adapical spines absent. Apical wall not observed.

Types.—Three syntypes of *C. blairi,* UCGM 3984–3986, of which UCGM 3986 (Fig. 18.5) is here designated the lectotype; UCGM 3984–3985 are here designated the lectotype; UCGM 3984–3985 are here considered paralectotypes. Four syntypes of *C. sedaliensis,* preserved in five pieces, UCGM 1393, 1399; specimen intended by Sinclair (1948) to be holotype of *P. indiana,* AMNH 25056.

Occurrences.—Lower Mississippian of Illinois, Indiana, Iowa, and Missouri; localities 11, 32, 35, 61, 94–98, 101, and 105. Laudon and Bowsher (1941) reported this taxon in the Mississippian of New Mexico, but their material was not available for study.

Remarks.—*Paraconularia blairi* (Miller and Gurley) is unique among species of *Paraconularia* in having rods that exhibit inflected circular

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Fig. 17.—17.1; *Paraconularia alpenensis* Babcock and Feldmann, n. sp., GSC 85060, holotype, minor face of specimen preserved in micrite; locality 92. 17.2; GSC 85060, same specimen as in Fig. 17.1, corner view. 17.3; GSC 85060, same specimen as in Fig. 17.1, major face. 17.4; USNM 173926, *Hyolithes* sp., crushed specimen of a hyolithid; locality 240. 17.5–17.6; *P. alternistriata* Shimer. 17.5; GSC 5111, holotype, major face; locality 4. 17.6; GSC 5111, same specimen as in Fig. 17.5, minor face. 17.7–17.8; *P. chesterensis* (Swallow). 17.7; GSC 85061, a collapsed specimen preserved in siltstone; locality 27. 17.8; GSC 85061, enlargement of same specimen as in Fig. 17.7. Note inconspicuous spines on the rods. Bar scales in Figs. 17.1–17.4 and 17.7–17.8 represent 1 cm; bar scales in Figs. 17.5 and 17.6 represent 5 mm.

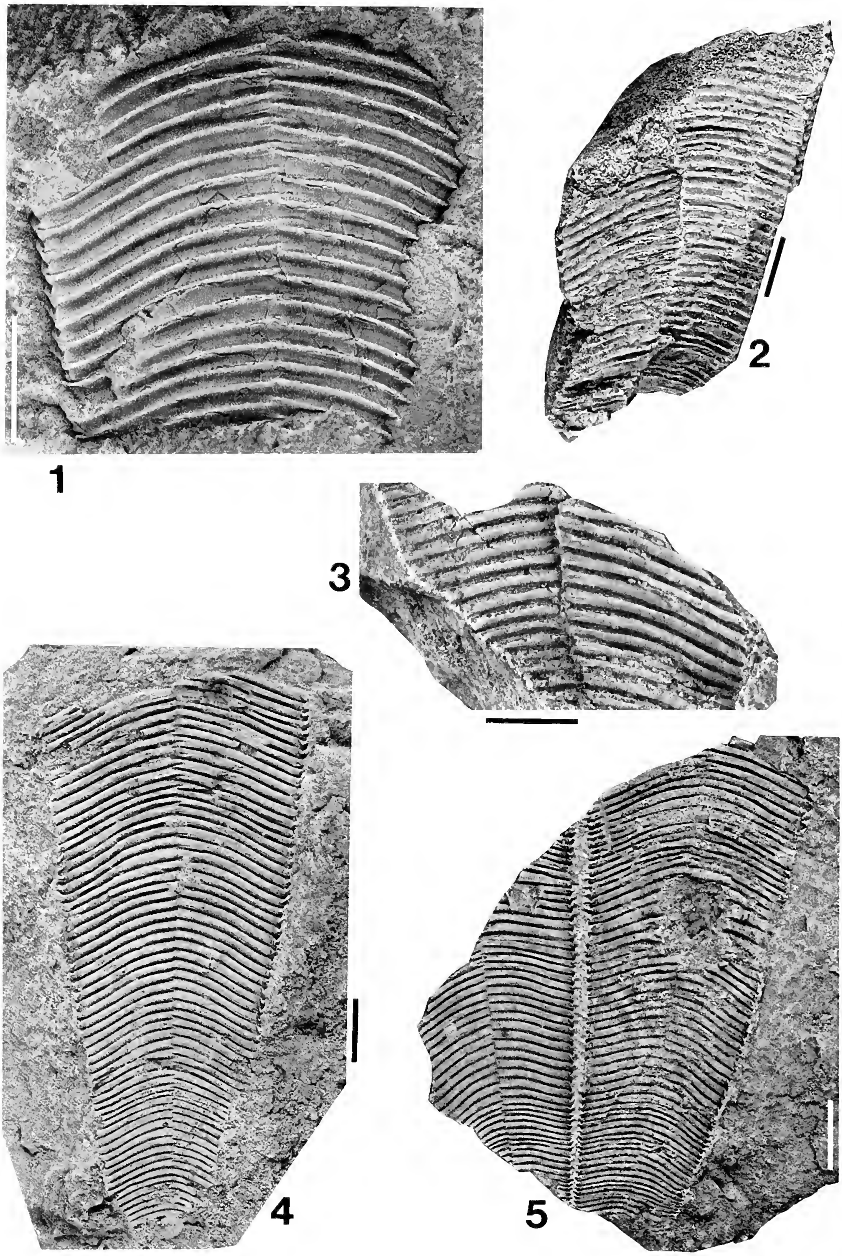

Fig. 18.—*Paraconularia blairi* (Miller and Gurley). 18.1; UMC 4270, detailed view of well preserved ?major face; locality 96. 18.2; UCGM 3985, syntype of *Conularia se-*

curve style rod articulation and which are slightly inflected at the midline. However, distinction between this species and *P. subulata* is often difficult, especially in small specimens that preserve only inflected gothic arch style rod articulation. Distinction between the two species can be made on these criteria: 1, *P. blairi* possesses distinct nodes on the rods, *P. subulata* usually does not; 2, *P. blairi* has a slight adapertural inflection of the rods near the midline except in the apical region, *P. subulata* does not; and 3, *P. blairi* possesses 6–13 rods/cm whereas *P. subulata* has 20–35 rods/cm.

Two species are here considered synonymous with *P. blairi*: *P. sedaliensis* (Miller and Gurley) and *P. indiana* Sinclair, MS. The type specimens of both are well enough preserved to compare all qualitative and quantitative features of taxonomic interest. Values obtained by measuring these specimens are given in Appendix B. In all respects, *P. sedaliensis* and *P. indiana* are indistinguishable from the lectotype and paralectotypes of *P. blairi.*

Material examined.—34 specimens; housed in the AMNH, FMNH, UCGM, UMC, and the USNM.

PARACONULARIA BYBLIS (White, 1862)
Figs. 3.7, 19.1–19.6, 23.2, 31.4

Conularia byblis White, 1862, p. 22; Miller, 1877, p. 141; Bigsby, 1878, p. 78; Herrick, 1888*a,* p. 95; Miller, 1889, p. 390; Weller, 1898, p. 189; Weller, 1900*a,* p. 118–119, Pl. 7, fig. 7; Weller, 1900*b,* p. 73; Grabau and Shimer, 1910, p. 14.
Conularia byblis White. Winchell, 1870, p. 257.
Conularia biblis (*sic*) White. Bigsby, 1878, p. 316.
Paraconularia byblis (White). Sinclair, 1948, p. 200–201; Babcock and Feldmann, 1986, figs. 1E, 2B.
Adesmoconularia byblis (White). Driscoll, 1963, p. 40–41, Pl. 3, figs. 1–7; Tasch, 1973, fig. 5.14 Ga–b; Tasch, 1980, fig. 5.14 Ga–b.
Conularia? sp. Driscoll, 1963, p. 41, Pl. 3, fig. 8.

Description.—Exoskeleton up to 7 cm in length. Major apical angle 18–26°; minor apical angle 10–19°. Rod articulation inflected gothic arch style in apical region and inflected circular curve style elsewhere; rods are strongly inflected adaperturally at midline; rod angle 12–18°. Rods generally abut at midline; 12–29 rods/cm. 1–2 nodes/mm; spines seem to be absent. Apical wall may be present.

Occurrences.—Lower Mississippian of Indiana, Iowa, Kentucky and Ohio; localities 29, 36, 39, 43, 50, 60, 62, 66, 71–72, 76, 77, 78, 81,

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daliensis Miller and Gurley; locality 98. 18.3; UCGM 3985, counterpart of specimen in Fig. 18.2. 18.4; UCGM 3984, paralectotype, ?minor face; locality 98. 18.5; UCGM 3986, lectotype, a flattened specimen preserved in micrite; locality 98. Bar scales represent 1 cm.


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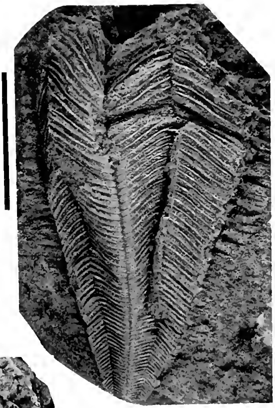
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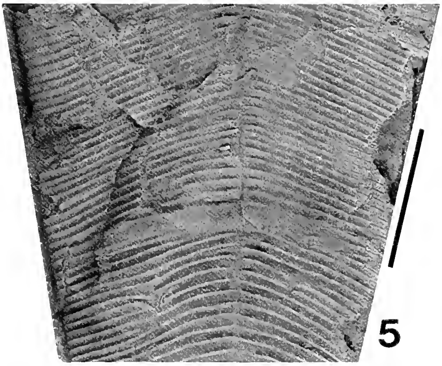
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185, 195, 210, and 223–224. A specimen referred with question to this species, UMMP 26735, is from Tennessee; locality 250.

Types.—Holotype, UMMP 2167.

Remarks.—*Paraconularia byblis* (White) is distinguished from all other species of *Paraconularia* by the combination of closely spaced rods, 12–29/cm, the lack of spines and by rod articulation involving an inflected gothic arch style in the apical region and an inflected circular curve style elsewhere. There does not seem to be a species present in the Devonian or Mississippian rocks of North America with which this taxon could be easily confused if well preserved specimens were available for study.

Driscoll (1963), designated *C. byblis* White as the type species of a new genus, *Adesmoconularia. Adesmoconularia,* by Driscoll's definition, is distinguished from *Calloconularia* Sinclair by a larger size and a lack of "swelling" of the interridge areas near the corner angles in *Adesmoconularia. Adesmoconularia* was deemed by Driscoll unlike *Paraconularia* Sinclair in the lack of nodes and by the presence of an apical wall in *Adesmoconularia.* To date, no other species have been referred to the genus *Adesmoconularia.*

Examination of the holotype of *Calloconularia strimplei* Sinclair (FMNH PE 142), the type species of the genus *Calloconularia,* reveals that there is no expansion of the interridge areas near the corner angles. Examination of the holotype of *Conularia byblis* White, type species of the genus *Adesmoconularia* Driscoll, shows that nodes are present on the rods, but they are very small and inconspicuous. The holotype appears to have been considerably weathered, rendering the nodes inconspicuous in most places on the specimen. Apical walls are present, but rare, in specimens of *Paraconularia.* According to Driscoll's diagnosis, then, size is the only criterion which distinguishes *Adesmoconularia* from *Calloconularia*; there is no distinction between *Adesmoconularia* and *Paraconularia.* Therefore, *Adesmoconularia* Driscoll, 1963 is here considered a junior synonym of *Paraconularia* Sinclair, 1940.

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Fig. 19.—*Paraconularia byblis* (White). 19.1; UMMP 2167, holotype, a weathered specimen preserved in micritic limestone, corner view; locality 62. 19.2; CMNH 4492, small specimen, preserved in shale and compressed along the faces and at the aperture; locality 219. 19.3; CMNH 2295, external mold preserving apical region; locality 195. 19.4; UMMP 2167, same specimen as in Fig. 19.1, minor face. 19.5; UMMP 2167, same specimen as in Fig. 19.1, detail of minor face. 19.6; CMNH 4691, ?major face of a specimen preserved in shale; locality 185. Bar scales represent 1 cm.

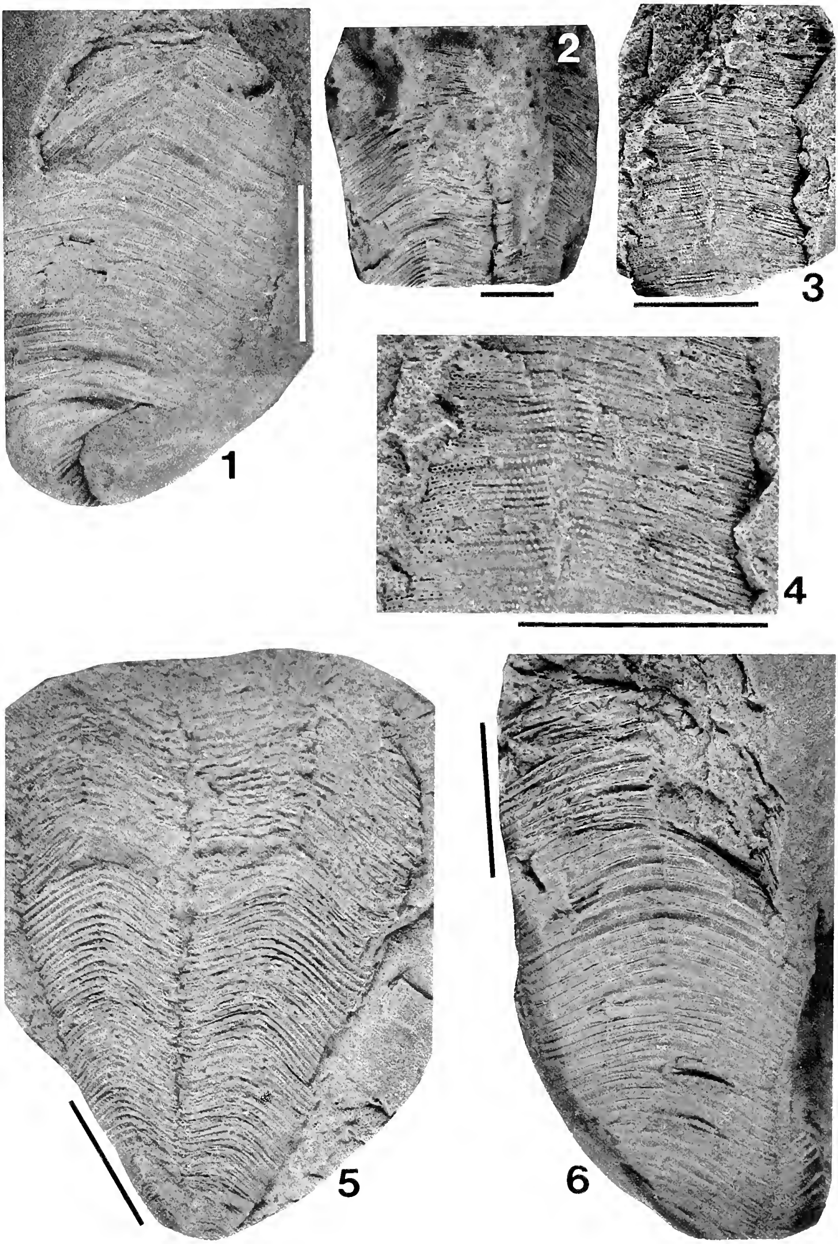

Fig. 20.—*Paraconularia chagrinensis* Babcock and Feldmann, n. sp. 20.1; CMNH 6717, paratype, preserved in a dark gray phosphatic concretion. Note apparent healed wound;

Material examined.—53 specimens; housed in the CM, CMNH, GSC, FMNH, UMMP, and the USNM.

PARACONULARIA CHAGRINENSIS
Babcock and Feldmann, new species
Figs. 20.1–20.6, 21.1, 21.2

Description.—Exoskeleton up to 9 cm in length. Major apical angle about 28°; minor apical angle 20–21°. Rod articulation exclusively of inflected gothic arch style. Rods usually alternate at midline; rods, if they alternate, usually alternate left superior on both major and minor faces; rod angle 9–12°. 16–20 rods/cm. 3–4 nodes/mm; nodes appear to be subtle in apical region and prominent in apertural region; 3–4 adapertural spines/mm; 3–4 adapical spines/mm. No apical wall observed.

Occurrences.—Upper Devonian of Ohio; localities 178–184.

Types.—Holotype, CMNH 6633; 12 paratypes, CMNH 1247, 1272, 1427, 1622, 1674, 1788, 1818, 4030, 4292, 6717, 6807–6808.

Remarks.—Among species of *Paraconularia,* only *P. chagrinensis* Babcock and Feldmann, n. sp. possesses the combination of wide apical angles, 20–28°, adapertural and adapical spines, as well as rod articulation which is exclusively of inflected gothic arch style. More striking, however, is the pattern of nodes on the rods. *Paraconularia chagrinensis* is the only conulariid observed which appears to have nodes which increase in size aperturally. Nodes are inconspicuous in the apical region, but are prominent in the apertural region. The increase in size of the nodes is not well shown in the holotype owing to the poor preservation of the apertural region of this individual. The pattern is well documented, however, in CMNH 6717 (Fig. 20.6).

When fragments of exoskeleton from the apertural region are found alone, as is the case with the specimen illustrated in Figs. 20.3–20.4, they are easily mistaken for species of *Conularia* such as *C. subcarbonaria* or *C. multicostata.* This dilemma can be resolved only when more complete material is found. Most conulariids from the small, presumably phosphatic, nodules found in the Upper Devonian Chagrin Shale of northeastern Ohio are preserved as fragmentary specimens, which renders generic identification difficult. To date, only *P. chagrinensis* has been identified from this unit.

One paratype, CMNH 6717, is noteworthy not only for demonstrating the unique pattern of the nodes, but also for exhibiting an apparent

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locality 179. 20.2; CMNH 1622, paratype; locality 184. 20.3; CMNH 1818, paratype; locality 181. 20.4; CMNH 1818, same specimen as in Fig. 20.3, detail showing nodes and spines. 20.5; CMNH 6633, holotype; locality 180. 20.6; CMNH 6717, same specimen as in Fig. 20.1, ?minor face. Note increase in size of nodes adaperturally. Bar scales represent 1 cm.

healed injury on one face (Fig. 20.1). On this specimen, rods in the apertural region have been truncated and their broken ends rounded slightly. Several rods have filled much of the region from where exoskeleton has been removed. These rods are oriented at a high angle to the rods which comprise the remainder of the exoskeleton and are complete with a midline distinct from the original midline on this face. A small gap is left between the most adapical portion of the injury and the most adapical rods which have filled the void. This region is filled with integument that lacks embedded rods.

Material examined.—13 specimens; housed in the CMNH.

Etymology of trivial name.—Named for the Chagrin Shale, currently the only known occurrence of this taxon.

PARACONULARIA CHESTERENSIS (Worthen, 1883)

Figs 17.7–17.8, 22.4–22.7, 23.1–23.4,
23.7, 24.1, 24.3, 32.5

Conularia chesterensis Worthen, 1883, p. 325; Miller, 1889, p. 390, Worthen, 1890, p. 134, Pl. 11, fig. 9a–b; Miller, 1897, p. 765; Weller, 1898, p. 189; Kent, 1982, p. 27.

Paraconularia chesterensis Worthen. Sinclair, 1948, p. 201–202; Babcock and Feldmann, 1986, fig. 4C.

Paraconularia newberryi (Winchell). *Sensu* Driscoll, 1963, Pl. 2, figs. 6–9.

Paraconularia crawfordsvillensis (Owen). *Sensu* Lane, 1973, p. 93–95, Pl. 8, fig. 1, Pl. 9, figs. 1–2.

Description.—Exoskeleton up to 20 cm in length. Major apical angle 14–21°; minor apical angle 10–18°. Rod articulation exclusively of inflected circular curve style, recurved near the midline. Rods alternate or abut at midline; rods, if they alternate, are not preferentially right superior or left superior on either the major or minor face; rod angle 8–12°. 8–20 rods/cm. 4–5 nodes/mm; adapertural spines appear to be absent in apical region, but small spines are sometimes present, 4–5/mm, in apertural region; adapical spines absent. Apical wall not observed.

Occurrences.—Upper Mississippian of Alabama, Kentucky, Illinois, Indiana, Iowa, Missouri, Nevada, Tennessee; localities 1, 10–12, 16–21, 33, 35–36, 38–41, 47, 49–59, 70, 84–89, 104, 110, and 251. Specimens referred questionably to this species have also been found in British Columbia and Utah; localities 7 and 352.

Types.—Holotype, ISGS 2489.

Remarks.—*Paraconularia chesterensis* (Worthen) is similar to *P. alpenensis* Babcock and Feldmann, n. sp., *P. missouriensis* (Swallow) and *P. recurvatus* Babcock and Feldmann, n. sp. in having rods that are recurved near the midline. Of these, *P. alpenensis* does not exhibit rods that are recurved in the apical region, and both *P. missouriensis* and *P. recurvatus* exhibit rods that are strongly recurved. The rods of *P. chesterensis* tend to be slightly recurved. A rod pair in this taxon often approximates the outline of a truncated pyramid (Figs. 22.4, 22.7).

In some cases, values for apical angles, rods/cm and rod angles may be similar for specimens of *P. chesterensis* and *P. missouriensis*. If rod articulation is also similar, distinction between the two may be made on the basis of the spacing between nodes. *Paraconularia chesterensis* possesses 4–5 nodes/mm and *P. missouriensis* possesses only 2–3 nodes/mm.

Specimens referable to *P. chesterensis* which have been observed with well-preserved spines are few in number. Moreover, it seems that spines are only produced in the apertural regions of those individuals that have them. When present, the spines are usually inconspicuous and seem to be directed only in the apertural direction (for example, Fig. 17.8). Many specimens referable to *P. chesterensis* (for example, Fig. 23.2), however, seem to have small ridges developed in the integument between ridges. These ridges resemble interridge crests. Such structures may indicate that adapertural, and perhaps even adapical, spines are produced in areas other than the apertural region in this taxon. No specimens exhibiting this have been observed to date. Thus, the observations that only adapertural spines are present in *P. chesterensis,* and when present, that they occur only in the apertural region, may be erroneous and owing to a lack of evidence to the contrary.

Material examined.—355 specimens; housed in the FMNH, GSC, ISGS, IUPC, and the USNM.

PARACONULARIA MISSOURIENSIS (Swallow, 1860)
Figs. 21.3, 25.1, 25.2–25.5, 26.1–26.2, 32.1

Conularia missouriensis Swallow, 1860, p. 657; Miller, 1877, p. 141; Bigsby, 1878, p. 316; Miller, 1889, p. 390; Keyes, 1894, Pl. 35, fig. 1a–b; Miller, 1897, p. 765; Weller, 1898, p. 190; Grabau and Shimer, 1910, p. 14; Branson, 1944, p. 246.

Conularia missouriensis Swallow?. Meek and Worthen, 1873, p. 541–542, Pl. 22, fig. 5; White, 1880, p. 513, Pl. 6, fig. 4; Walcott, 1884, p. 264, Pl. 23, fig. 4.

Paraconularia missouriensis (Swallow). Sinclair, 1948, p. 198–199.

Conularia gratiosa Miller and Gurley, 1893, p. 74, Pl. 8, fig. 1; Miller, 1897, p. 765; Weller, 1898, p. 190.

Conularia greenei Miller and Gurley, 1896, p. 27–28, Pl. 3, fig. 3; Miller, 1897, p. 765; Weller, 1898, p. 190, Cumings, 1906, p. 1367, Pl. 24, fig. 14.

Paraconularia greenei (Miller and Gurley). Sinclair, 1948, p. 194.

Paraconularia gratiosa (Miller and Gurley). Sinclair, 1948, p. 198.

Paraconularia sciotovillensis Driscoll, 1963, p. 37–40, Pl. 1, figs. 9–12; Tasch, 1973, fig. 5.16, Table 5.2; Tasch, 1980, fig. 5.16, Table 5.2.

Ctenoconularia? *greenei* (Miller and Gurley). Moore and Harrington, 1956, p. F65, fig. 51.4.

Conularia sp. Leary, 1985, Pl. 3, fig. 4.

Paraconularia cf. *P. missouriensis* (Swallow). Babcock, 1985*a*, p. 66–70, fig. 1A–B.

Description.—Exoskeleton up to 22 cm in length. Major apical angle 14–22°; minor apical angle 10–18°. Rod articulation inflected circular curve style, strongly recurved near the midline. Rods usually alternate at midline; if rods alternate, pattern is usually left superior; rod angle 6–17°. 4–10 rods/cm. 2–3 nodes/mm; 2–3 adapertural spines/mm; adapical spines absent. Apical wall not observed.

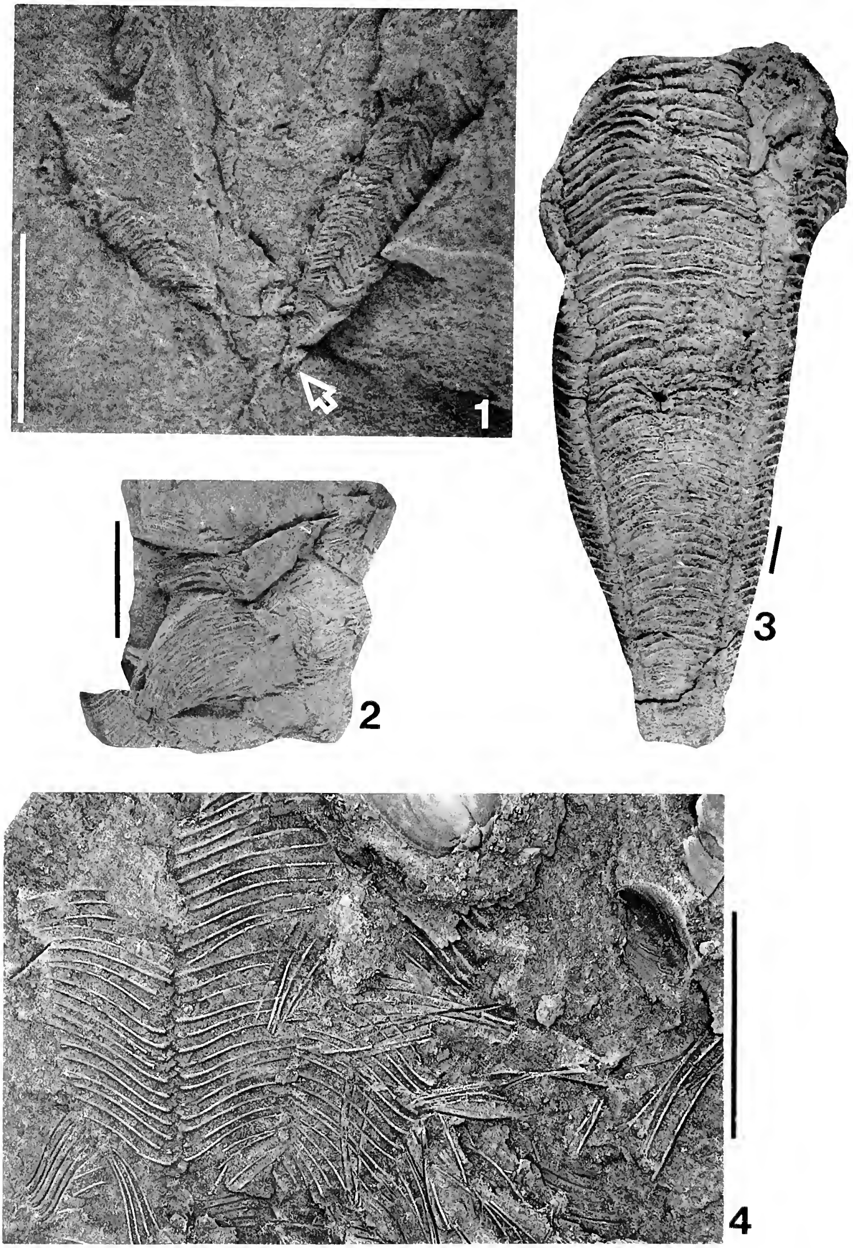

Fig. 21.—21.1; *Paraconularia chagrinensis* Babcock and Feldmann, n. sp., CMNH 1788, two small paratype specimens, presumably attached to the same object (obscured) and

Occurrences.—Lower Mississippian of Alberta, Illinois, Indiana, Iowa, Kentucky, Missouri, and Ohio; localities 2, 5, 14–15, 31, 39, 69, 83, 94, 100, 103, 223 and 226–227. A specimen referred with question to this species has been found in Alberta; locality 5.

Types.—Plaster cast of presumed holotype, FMNH UC 6639. Holotype of *C. gratiosa,* FMNH UC 6627, plastoholotype, USNM 67893; holotype of *C. greenei,* FMNH UC 6628, plastoholotype USNM 67880; holotype of *P. sciotovillensis,* UMMP 26740.

Remarks.—Considerable confusion has existed over the definition of *P. missouriensis* (Swallow). This confusion of nomenclature is related to at least two problems: 1, an ambiguous original definition of the species, a definition which may have incorporated characters now identified as belonging to at least two species; and 2, a loss of Swallow's original specimens. Swallow's type material was found in the "Carboniferous Limestone" of Cooper County, Missouri. This locality has yielded at least two conulariid species; herein, they are identified as *P. missouriensis* and *P. blairi.* It is possible, from Swallow's description (Swallow, 1860, p. 657), that specimens belonging to both forms were used in the formulation of the original definition of *P. missouriensis.*

Some early authors, most notably Meek and Worthen (1873) and Keyes (1894), used Swallow's indication that the faces of *P. missouriensis* were "marked by flexuous, high, sharp plications" as the primary determinative characteristic of the species. This concept of the species is followed herein. A plaster cast of a specimen, marked "holotype?" of *P. missouriensis* (FMNH UC 6639) is presumed to represent a cast of the holotype of this species.

Paraconularia missouriensis is similar to *P. chesterensis* (Worthen) in having an inflected circular curve style of rod articulation, with the rods being reflexed near the midline. The degree of reflexure, however, is greater in *P. missouriensis. Paraconularia missouriensis* can also be distinguished from *P. chesterensis* by having a greater number of nodes/mm on the rods, 4–5 nodes/mm as compared to 2–3 nodes/mm.

Other species of *Paraconularia* which have recurved rods include *P. alpenensis* Babcock and Feldmann, new species and *P. recurvatus* Bab-

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preserved in a phosphatic concretion. Arrow indicates a stalk; locality 184. 21.2; CMNH 4294, partially disarticulated paratype; locality 183. 21.3; *P. missouriensis* (Swallow), FMNH UC 1125, view of major face; locality 14. 21.4; *P. subulata* (Hall), USNM 395829, preserved in a very dark gray, organic-rich shale. Note that no integument is present and that rods are disarticulated. This specimen indicates that rods and integument are separate components of the conulariid exoskeleton. Two specimens of "*Lingula*" (=*Barroisella*?) are visible in this photograph; locality 189. Bar scales in Figs. 21.2–21.4 represent 1 cm; bar scale in Fig. 21.1 represents 5 mm.


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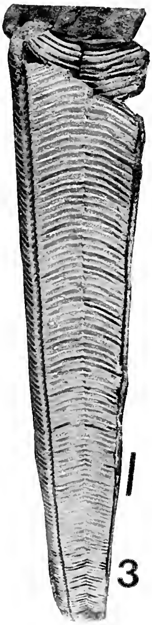
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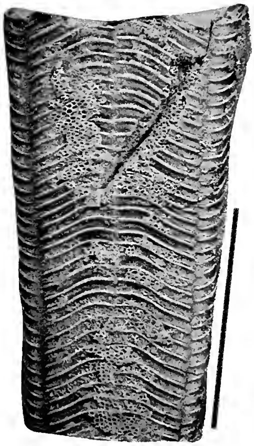
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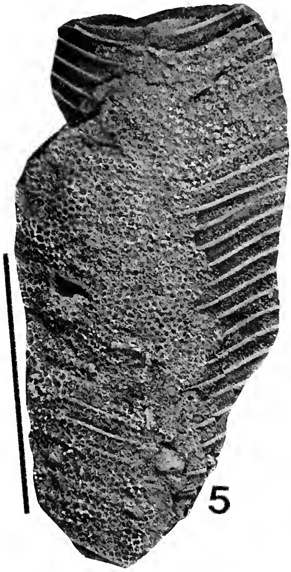
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cock and Feldmann, new species. Neither of these taxa have rod spacing values less than 14 rods/mm or adapical spines on the rods and are therefore easily distinguished from *P. missouriensis.* Moreover, *P. alpensis* possesses non-recurved rods in the apical region, unlike *P. missouriensis.*

The species *Conularia gratiosa* Miller and Gurley, *C. greenei* Miller and Gurley and *P. sciotovillensis* Driscoll are here included as junior synonyms of *C. missouriensis* because they all exhibit: 1, similar values for apical angles; 2, similar values for rod angles; 3, same rod articulation style, including right superior rods if the rods alternate at the midline; 4, similar values for rod spacing; 5, similar values for nodes/mm; and 6, presence of adapical spines. Comparative values are given in Appendix B.

Material examined.— 30 specimens; housed in the AMNH, FMNH, GSC, ISGS, and the USNM.

PARACONULARIA OKLAHOMAENSIS
Babcock and Feldmann, new species
Fig. 27.5

Description.—Description based only upon holotype. Exoskeleton 5.4 cm in length. Major apical angle 19°; minor apical angle 17°. Rod articulation of gothic arch style in apical end and of inflected circular curve style elsewhere. Rods usually abut at midline; if they alternate, pattern is usually right superior on major face and left superior on minor face; rod angle 12–13°. 24 rods/cm in apical region, 12 rods/cm elsewhere. Nodes and spines absent. Apical wall not observed.

Occurrence.—Upper Mississippian of Oklahoma; locality 229.

Type.—Holotype, USNM 409811.

Remarks.—*Paraconularia oklahomaensis* Babcock and Feldmann, n. sp. differs from all other described species of the genus in the combination of rod articulation pattern, frequent rod abuttment, spacing of rods, with 24 rods/cm in the apical region and 12 rods/cm elsewhere and the lack of nodes and spines on the rods.

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Fig. 22.—22.1–22.3; *Paraconularia blairi* (Miller and Gurley). 22.1; AMNH 25056, specimen intended by Sinclair (1948) to be holotype of *P. indiana* Sinclair, major face; locality 32. 22.2; AMNH 25056, same specimen as in Fig. 22.1, corner view. 22.3; AMNH 25056, same specimen as in Fig. 22.3, minor face. Note overturned apertural termination. 22.4–22.7; *P. chesterensis* (Worthen). 22.4; IUPC 17414, bryozoan-encrusted specimen; locality 1. 22.5; IUPC 17415, corner region of collapsed specimen that has been encrusted by bryozoans subsequent to collapse; locality unknown. 22.6; FMNH UC 23023; locality 38. 22.7; IUPC 11316; locality 57. Bar scales represent 1 cm.

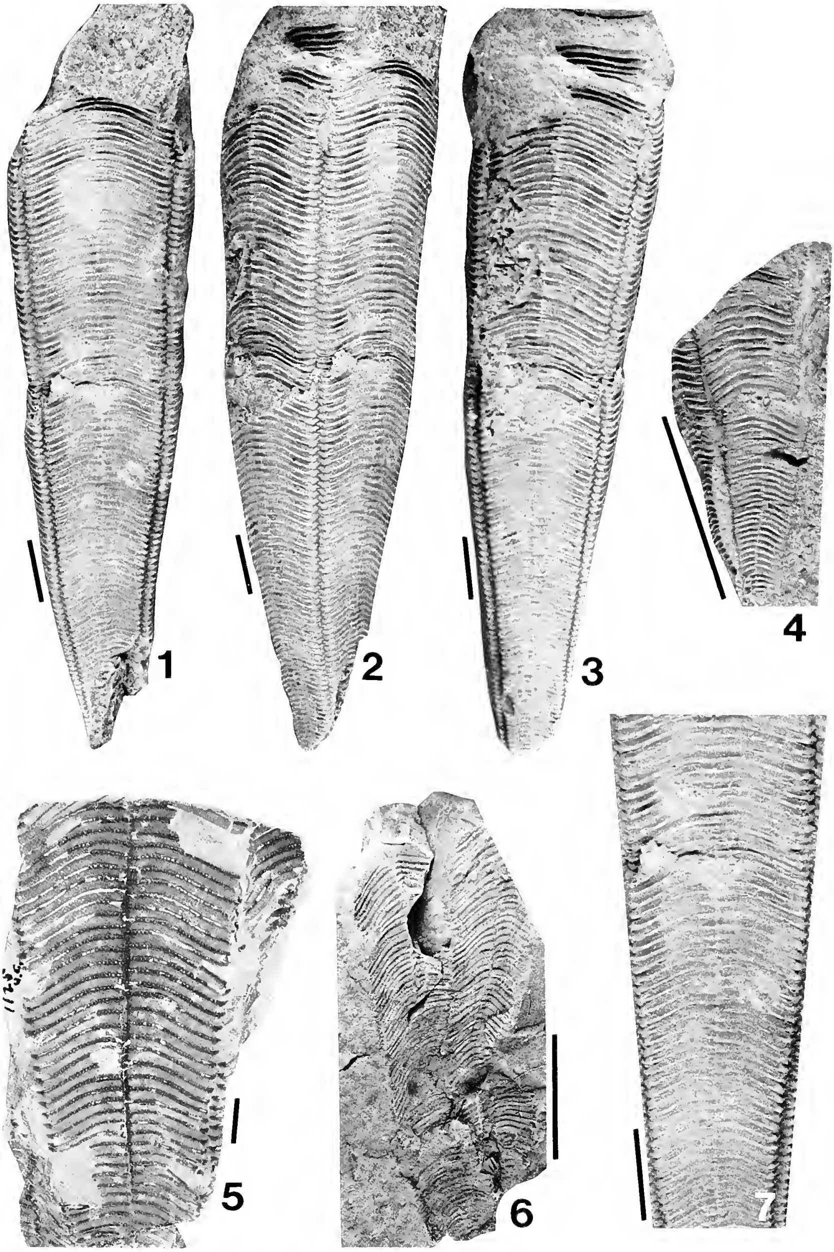

Fig. 23.—23.1–23.4; *Paraconularia chesterensis* (Worthen). 23.1; ISGS 2489, holotype, preserved in micritic to sparry limestone, minor face; locality 10. 23.2; ISGS 2489, same specimen as in Fig. 23.1, corner view. 23.3; ISGS 2489, same specimen as in Fig. 23.1,

This taxon is easily confused with *P. subulata* (Hall), which also lacks nodes and spines on the rods and has inflected gothic arch rod articulation in the apical region and inflected circular curve rod articulation elsewhere. The rods of *P. oklahomaensis,* however, are greatly inflected in the vicinity of the corner angles in the apical region and almost imperceptibly inflected elsewhere. In specimens of *P. subulata,* the pattern of relative inflexure of the rods is reversed. *Paraconularia oklahomaensis* is further distinguished from *P. subulata* in having 40–50% of the rods abutting at the midline whereas specimens referred to *P. subulata* seldom have more than 10% of the rods abutting.

Material examined.—1 specimens, USNM 409811.

Etymology of trivial name.—Named for the State of Oklahoma.

PARACONULARIA PLANICOSTATA (Dawson, 1868)
Figs. 3.1, 27.1–27.4, 27.6–27.8

Conularia planicostata Dawson, 1868, p. 307–308, fig. 117; Dawson, 1878, p. 307–308, fig. 117; Bigsby, 1878, p. 316; Dawson, 1883, p. 416; Lesley, 1889, p. 145, fig.; Beede, 1911, p. 174, 186; Bell, 1929, p. 98–100, Pl. 32, figs. 1–2; Bamber and Copeland, 1976, Pl. 15, fig. 3.

Conularia planocostata (*sic*) Dawson. Miller, 1877, p. 141; Miller, 1889, p. 390; Weller, 1898, p. 191.

Conularia quadrisulcata Miller *in* Sowerby. *Sensu* Dawson, 1889, p. 87, fig.

Conularia sorrocula Beede. *Sensu* Bell, 1929, p. 100, Pl. 32, figs. 3–3a.

Conularia cf. *tenuis* Slater. *Sensu* Bell, 1929, p. 100, Pl. 32, figs. 4–5.

Paraconularia planicostata (Dawson). Sinclair, 1948, p. 199–200; Babcock and Feldmann, 1984, p. 16–17; Babcock and Feldmann, 1986, fig. 2G.

Connularia (sic) *planicostata* Dawson. Alison and Carroll, 1972, p. 17.

Description.—Exoskeleton up to 8 cm in length. Major apical angle 21–25°; minor apical angle 18–22°. Rod articulation inflected gothic arch style in apical region and gothic arch style elsewhere. Rods abut or alternate at midline; if they alternate, rod pattern is usually right superior; rod angle 11–16°. 12–20 rods/cm. Nodes and spines absent. Apical wall not observed.

Occurrences.—Lower to Upper Mississippian of Nova Scotia and Quebec; localities 163–173 and 248.

Types.—Holotype, RM(MU) 2749, plastoholotype, GSC unnumbered.

Remarks.—*Paraconularia planicostata* (Dawson) is distinguished

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major face. 23.4; FMNH UC 25175; small specimen preserving apical region; locality 12. 23.5–23.6; *P. missouriensis* (Swallow). 23.5; FMNH UC 1125; specimen preserved in micrite showing darkened areas in the integument along the midline and surrounding the ridges. Darkened areas of integument in the vicinity of the midline have been interpreted by numerous authors as remains of original color markings. Specimen not coated with ammonium chloride; locality 14. 23.6; USNM 14425, original of Walcott (1884, Pl. 23, fig. 4), locality 110. 23.7; *P. chesterensis* (Worthen), ISGS 2489, same specimen as in Fig. 23.1, detail of minor face. Bar scales represent 1 cm.

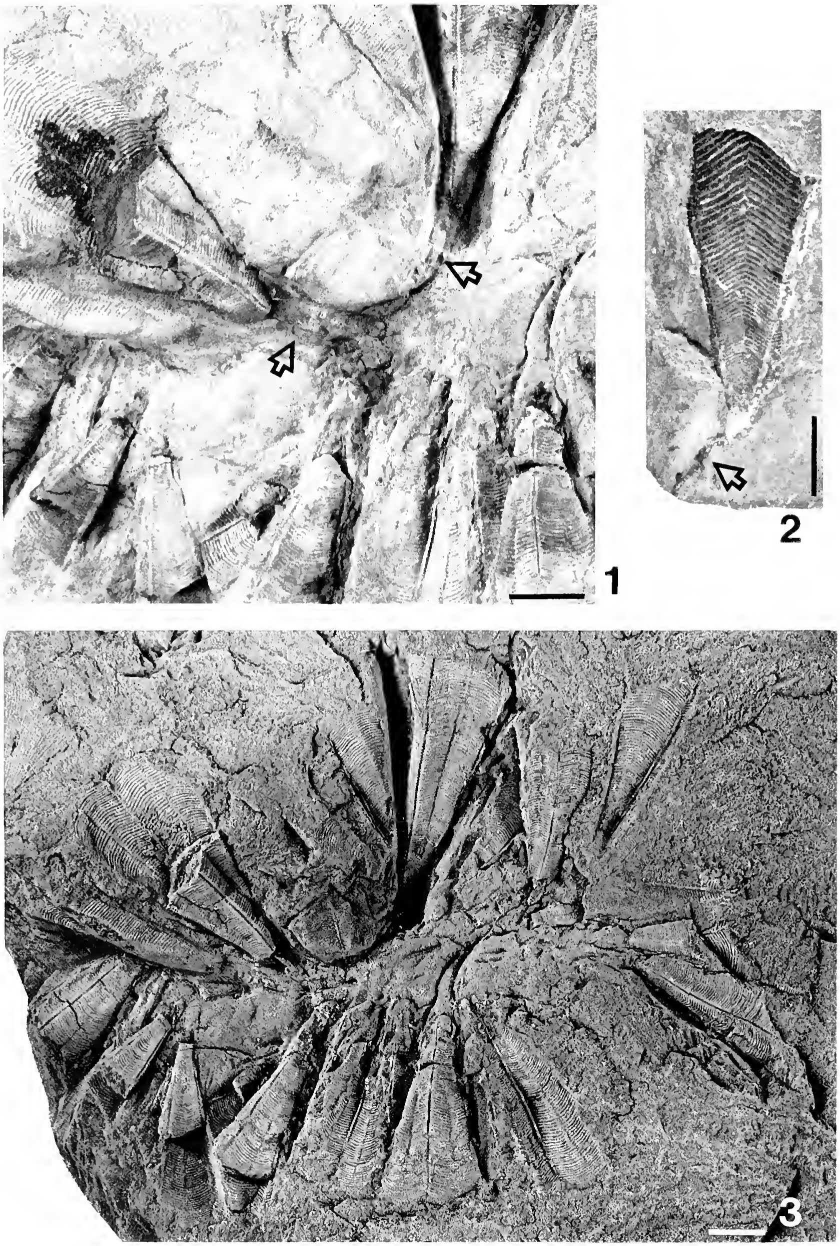

Fig. 24.—24.1; *Paraconularia chesterensis* (Worthen), USNM 50150, portion of large cluster of individuals preserved in siltstone and showing incomplete remains of stalks

from other members of the genus by the combination of: 1, its small size, generally less than 7.5 cm in length; 2, its inflected gothic arch and gothic arch rod articulation styles; 3, its very narrow apical angles, 8–14°; 4, its widely spaced rods, 12–20 rods/cm; and 5, its lack of nodes and spines. *Paraconularia planicostata* is particularly notable, and easily distinguished from all other taxa described herein because it possesses gothic arch rod articulation up to 7.5 cm from the hypothetical apex in the adapertural direction.

Dawson (1868, p. 308), in describing the species *Conularia planicostata,* compared the taxon to an apparent manuscript species, *C. novascotica* Hartt. Dawson considered this taxon, also from the Mississippian of Nova Scotia, to be a variety of *C. planicostata.* The intended holotype specimen of *C. novascotica* is lost, but based upon Hartt's scant description (*in* Dawson, 1868), it is likely to be an example of *P. planicostata* (Dawson).

Material examined.—30 specimens; housed in the CM, GSC, NYSM, RM(MU), and the USNM.

PARACONULARIA RECURVATUS
Babcock and Feldmann, new species
Figs. 32.3, 32.6

Description.—Exoskeleton up to 8 cm in length. Major apical angle about 16°; minor apical angle about 15°. Rod articulation exclusively of inflected circular curve style, greatly recurved near midline in apical region and slightly recurved near midline elsewhere. Rods abut or alternate at midline; if they alternate, pattern is usually left superior; rod angle 8–12°. 18–28 rods/cm. 2–3 nodes/mm; spines absent. Apical wall not observed.

Occurrence.—Upper Devonian of Nevada; locality 109.

Types.—Holotype, part and counterpart, USNM 409806. Three paratypes, USNM 409807–409809, all present on the same slab as the holotype. The paratype labelled as USNM 409808 is preserved as part and counterpart.

Remarks.—*Paraconularia recurvatus* Babcock and Feldmann, n. sp. is unique among members of this genus in having rods which are both closely spaced and which are recurved near the midline. Three other species of *Paraconularia* examined in this study have recurved rods, namely, *P. alpenensis* Babcock and Feldmann, n. sp., *P. chesterensis*

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(arrows), attached to possible plant matter. Specimen not coated with ammonium chloride; locality 27. 24.2; *Paraconularia byblis* (White), USNM 409800, specimen preserved in siderite concretion and showing a stalk (arrow); locality 71. Specimen not coated with ammonium chloride. 24.3; *P. chesterensis* (Worthen), USNM 50150, same specimen as in Fig. 24.1, view showing the complete aggregation of conulariids as exposed at the surface of the slab. Bar scales represent 1 cm.

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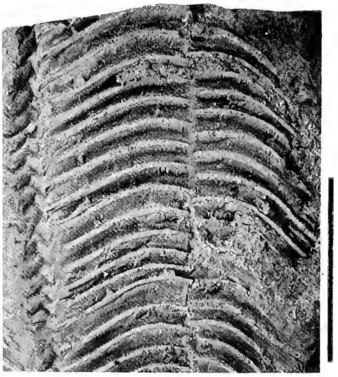

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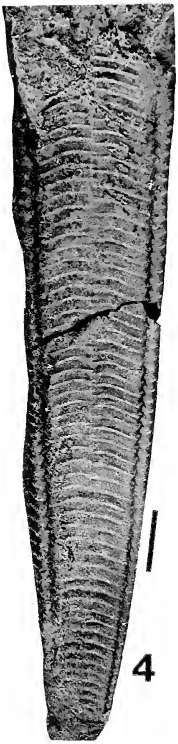

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(Worthen) and *P. missouriensis* (Swallow). *Paraconularia recurvatus* differs from all of these forms in rod spacing. Specimens in the type lot of *P. recurvatus* have 18–28 rods/cm while the holotype of *P. alpenensis* has 14 rods/cm, specimens of *P. chesterensis* have 8–25 rods/cm and specimens of *P. missouriensis* have 6–10 rods/cm.

In its overall appearance, it seems as though *P. recurvatus* could be mistakenly included in the genus *Conularia*. However, the lack of spines indicates that this species should be included in the genus *Paraconularia*. All quantitative data (Appendix B) further support this conclusion.

Material examined.—4 specimens; housed in the USNM.

PARACONULARIA SALINENSIS (Whiteaves, 1891)
Figs. 28.3, 28.5–28.6

Conularia salinensis Whiteaves, 1891, p. 244, Pl. 32, figs. 9–9a.
Conularia s.l. *salinensis* Whiteaves. Sinclair, 1948, p. 287.

Description.—Description based only upon holotype. Exoskeleton 3 cm in length. Major apical angle approximately 24°; minor apical angle 21°. Rod articulation inflected gothic arch style in apical region and inflected circular curve style elsewhere. Rods usually alternate at midline; if they alternate, pattern is usually right superior on major and minor faces; rod angle 13° in apical region, 8° elsewhere. 24 rods/cm. 3–4 nodes/mm; 3–4 prominent adapertural spines/mm; adapical spines absent. Apical wall not observed.

Occurrence.—Mississippian of Alberta; locality 3.

Type.—Holotype, GSC 4292.

Remarks.—This taxon can be distinguished from other species of *Paraconularia* by the combination of: 1, inflected gothic arch and inflected circular curve styles of rod articulation; 2, apical angles of 8–13°; 3, rod spacing of 24 rods/cm; 4, node spacing of 3–4 nodes/mm; and 5, prominent adapertural spines. *Paraconularia salinensis* (Whiteaves) does not seem to be easily confused with any other conulariid species described to date from the Devonian or Mississippian rocks of North America.

Material examined.—1 specimen, GSC 4292.

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Fig. 25.—*Paraconularia missouriensis* (Swallow). 25.1; FMNH UC 6639, plaster cast of presumed holotype specimen; locality 100. 25.2; ISGS 2619; oblique view of specimen with three inturned apertural terminations. The fourth apertural termination is broken off, but there is no indication of infolding. 25.3; UMMP 26740, holotype of *P. sciotovillensis* Driscoll, same specimen as in Fig. 26.1, detail of major face; locality 226. 25.4; FMNH UC 6628, holotype of *Conularia greenei* Miller and Gurley; minor face of a specimen preserved in micrite. 25.5; FMNH UC 6628, same specimen as in Fig. 25.4, corner view. Bar scales represent 1 cm.

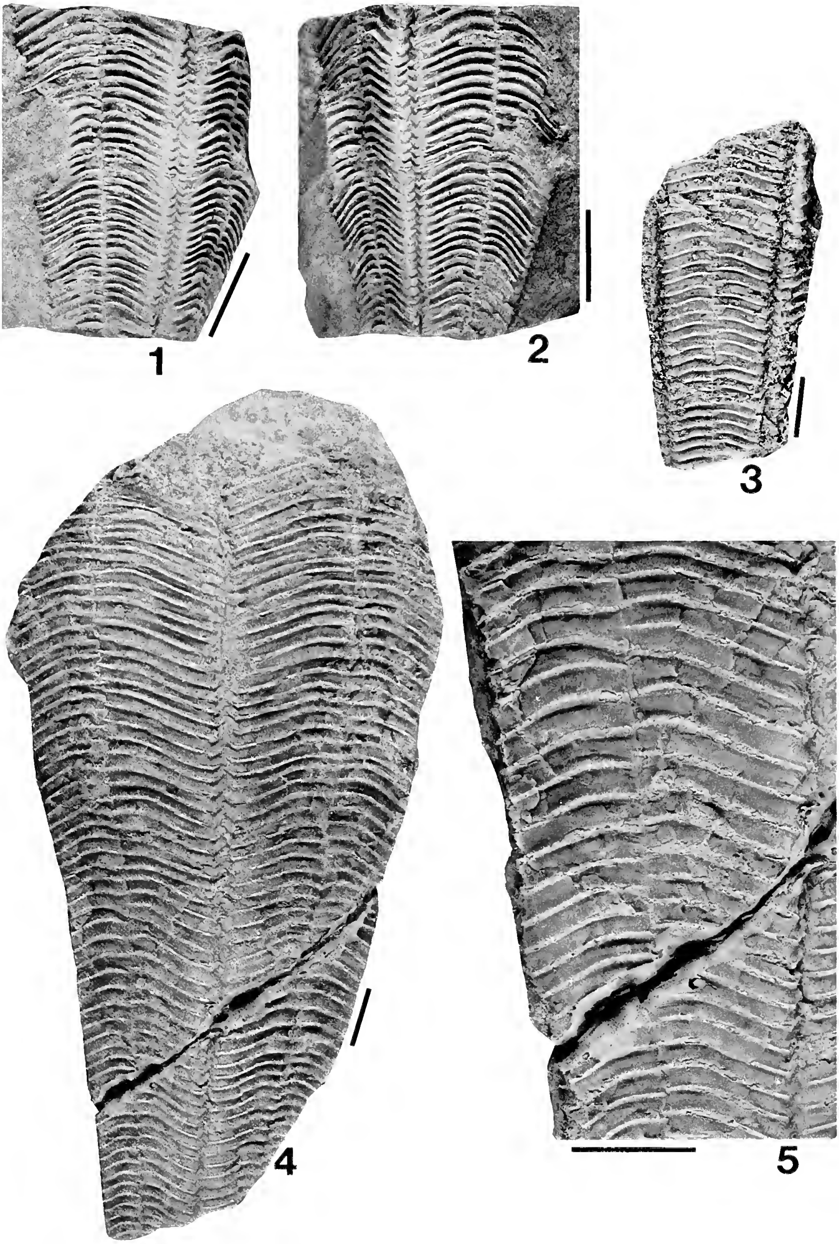

Fig. 26.—*Paraconularia missouriensis* (Swallow). 26.1; UMMP 26740, holotype of *P. sciotovillensis* Driscoll, minor face of a somewhat distorted individual preserved in a

PARACONULARIA SORROCULA (Beede, 1911)
Figs. 28.1–28.2

Conularia sorrocula Beede, 1911, p. 184, 186, 2 figs.
Paraconularia sorrocula Beede. Sinclair, 1948, p. 199.

Description.—Exoskeleton up to 3 cm in length. Major apical angle 19–24°; minor apical angle 17–22°. Rod articulation exclusively inflected gothic arch style with slight adapertural inflection at midline. Rods usually alternate at midline, less frequently they abut; rods, if they alternate, pattern is usually left superior on both major and minor faces; rod angle 11–14°. 18–20 rods/cm. Nodes elongate and appear to be continuous structures with adapertural spines; 5–6 nodes/mm; 5–6 adapertural spines/cm. Adapical spines absent. Apical wall not observed.

Occurrence.—Mississippian of Quebec; locality 247.

Type.—Holotype, part and counterpart, NYSM 9414.

Remarks.—*Paraconularia sorrocula* (Beede) is unique among North American Devonian or Mississippian examples of *Paraconularia* in the possession of only inflected gothic arch rod articulation. It is also the only conulariid species reported herein which has the nodes merged with the adapertural spines without a significant change at the junction of the two structures (Fig. 28.2). The nodes are not round or oblate in outline as in other species of *Paraconularia,* but are elongate.

The holotype of *P. sorrocula* is curved in the apertural region. This feature may have been present on the specimen in life, although this cannot be confirmed owing to the crushed nature of the fossil.

Material examined.—3 specimens; housed in the NYSM.

PARACONULARIA SUBULATA (Hall, 1858)
Figs. 3.2, 3.5–3.6, 21.4, 29.1–29.10, 30.1–30.8, 31.1–31.5, 33.4

Conularia subulata Hall, 1858, p. 32; Miller, 1877, p. 141; Bigsby, 1878, p. 316; Whitfield, 1882, p. 91, Pl. 8, fig. 3; Hall, 1883, p. 372–373, Pl. 31, fig. 3; Miller, 1889, p. 390; Lesley, 1889, p. 146, fig.; Lesley, 1895, p. 1690, fig.; Weller, 1898, p. 192; Whitfield and Hovey, 1901, p. 406–407; Cumings, 1906, p. 1366, Pl. 25, fig. 3.
Conularia victa White, 1862, p. 22–23; Miller, 1877, p. 141; Bigsby, 1878, p. 316; Miller, 1889, p. 390; Herrick, 1893, Pl. 19, fig. 3; Weller, 1898, p. 192.
Conularia newberryi Winchell, 1865, p. 130; Winchell, 1870, p. 258; Meek, 1875, p. 316–317, Pl. 18, fig. 2a–b; Miller, 1877, p. 141; Bigsby, 1878, p. 316; Hall, 1879, Pl. 34A, fig. 12; Herrick, 1888*a*, p. 93–94, Pl. 6, figs. 13, 17, Pl. 8, fig. 9; Herrick,

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siderite concretion; locality 226. 26.2; UMMP 26740, same specimen as in Fig. 26.1, major face. 26.3; AMNH 28692, minor face of a specimen preserved in sparry limestone; locality 30. 26.4; FMNH UC 6627, holotype of *Conularia gratiosa* Miller and Gurley, preserved in micritic limestone, corner view; locality 30. 25.5; FMNH UC 6627, same specimen as in Fig. 26.4, detailed view of a minor face. Bar scales represent 1 cm.


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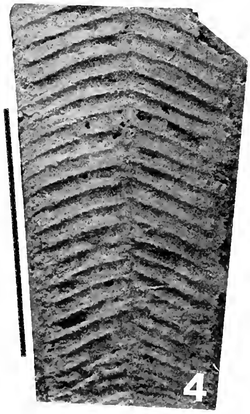
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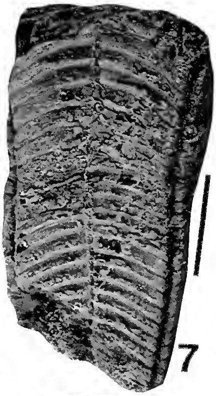
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1888*b*, Pl. 8, fig. 5, Pl. 10, figs. 27–28; Lesley, 1889, p. xv; Miller, 1889, p. 390; Herrick, 1893, Pl. 19, fig. 5; Miller, 1897, p. 765; Weller, 1898, p. 191; Clarke and Ruedemann, 1903, p. 566; Grabau and Shimer, 1910, p. 13, figs. 1227a–b; Tasch, 1973, fig. 5.16, Table 5.2; Tasch, 1980, fig. 5.16, Table 5.2.

Conularia whitei Meek and Worthen, 1865, p. 253–254; Bigsby, 1878, p. 316.

Conularia newberryi Winchell? Herrick, 1887, p. 146–147, Pl. 14, fig. 14.

Conularia victa White? Herrick, 1888*b*, p. 47–48, Pl. 8, fig. 3.

Conularia whitii (*sic*) Miller, 1889, p. 390; Weller, 1898, p. 192.

Conularia sampsoni Miller, 1892*a*, p. 690–691, Pl. 14, figs. 11–12; Miller, 1892*b*, p. 692; Holm, 1893, p. 125; Weller, 1898, p. 191; Branson, 1938, p. 110–111, Pl. 14, fig. 9; Branson, 1944, p. 216.

Paraconularia subulata (Hall). Sinclair, 1948, p. 198; Babcock and Feldmann, 1986, figs. 1C–D, 1G, 2F, 3A–C.

Paraconularia victa (White). Sinclair, 1948, p. 200.

Paraconularia newberryi (Winchell). Sinclair, 1948, p. 191–192; Driscoll, 1963, p. 34–37, Pl. 1, figs. 1–5, Pl. 2, figs. 1–4.

Paraconularia whitei (Meek and Worthen). Sinclair, 1948, p. 192.

Paraconularia sampsoni Miller. Sinclair, 1948, p. 197.

Paraconularia sp. Feldmann, Coogan and Heimlich, 1977, fig. 2.50A.

"*Conularia*" sp. Thompson, 1982, fig. 357.

Paraconularia cf. *P. missouriensis* (Swallow). *Sensu* Babcock, 1985*a*, figs. 1a–b.

Paraconularia missouriensis (Swallow). *Sensu* Babcock, 1985*a*, fig. 2.

Paraconularia cf. *P. subulata*. Babcock and Feldmann, 1986, fig. 2H.

Description.—Exoskeleton up to 17 cm in length. Major apical angle 17–22°; minor apical angle 12–18°. Rod articulation inflected gothic arch style in apertural region and inflected circular curve style elsewhere. Rods usually alternate at midline; if they alternate, pattern is usually right superior on major face and usually left superior on minor face; rod angle 15–18°. 20–35 rods/cm. Nodes absent or present; if present, they are inconspicuous, 2–3/mm; spines absent. Apical wall present.

Occurrences.—Lower Mississippian of Illinois, Indiana, Kentucky, Montana, Ohio; localities 16, 26, 29, 38, 39, 72, 75, 82, 106–107, 185–192, 194, 196–203, 205–208, 212–217, 220–222.

Types.—Lectotype, designated herein from James Hall's suite of three syntypes of *C. subulata*, AMNH 32403, smaller of two specimens bearing this number; two paratypes, AMNH 32403, larger of two specimens bearing this number, and AMNH 32404. Holotype of *C. victa*,

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Fig. 27.—27.1–27.4; *Paraconularia planicostata* (Dawson). 27.1; RM(MU) 2749, holotype; major face, locality 164. 27.2; RM(MU) 2749, same specimen as in Fig. 27.1, corner view. Note exoskeletal constrictions. 27.3; RM(MU) 2749, same specimen as in Fig. 27.1, minor face. 27.4; RM(MU) 2749, same specimen as in Fig. 27.1, detail of major face. 27.5; *P. oklahomaensis* Babcock and Feldmann, n. sp., USNM 409801, holotype, a flattened individual. 27.6–27.8; *P. planicostata* (Dawson). 27.6; CM 22667, major face; locality 168. 27.7; CM 22667, same specimen as in Fig. 27.6, minor face. 27.8; CM 22667, same specimen as in Fig. 27.6, corner view. Bar scales in Figs. 27.1–27.5 represent 1 cm; bar scales in Figs. 27-6–27.8 represent 5 mm.

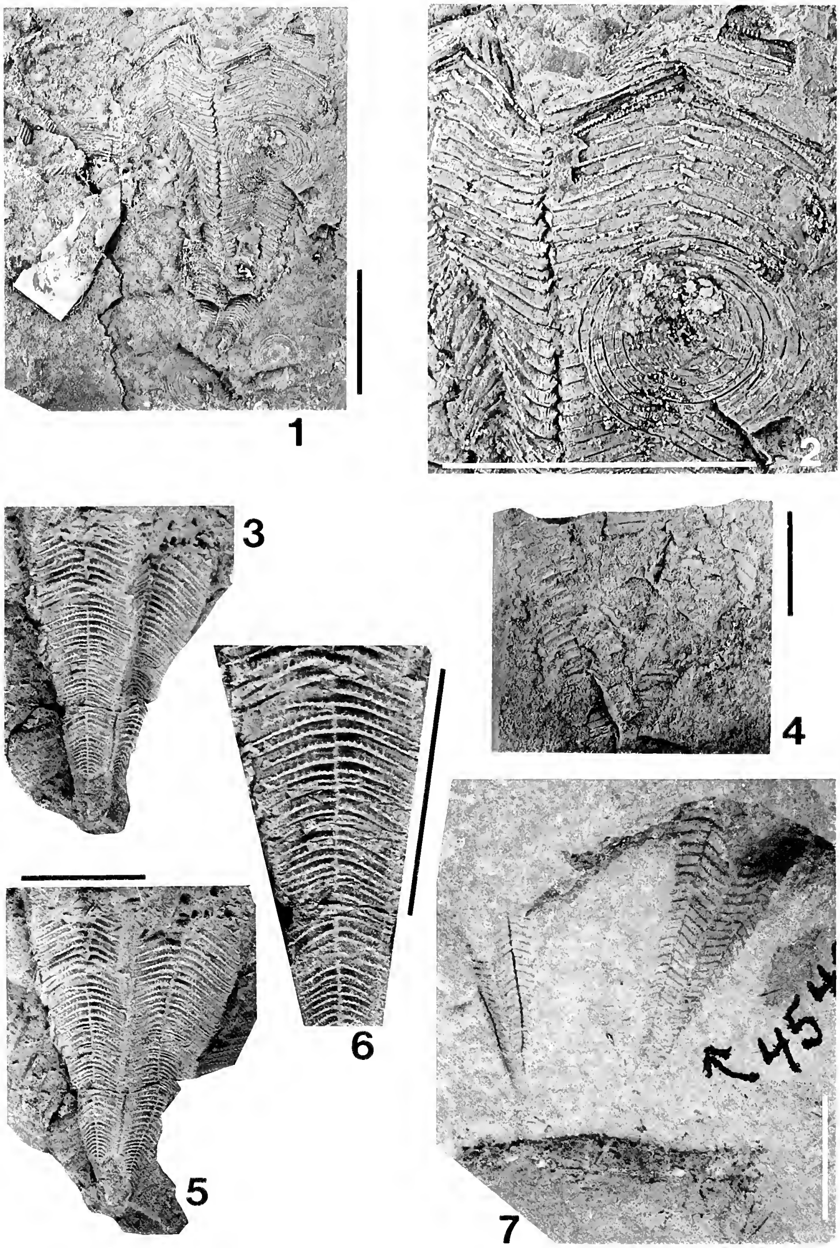

Fig. 28.—28.1–28.2; *Paraconularia sorrocula* (Beede). 28.1; NYSM 9414, slab showing two specimens, holotype to the right. Note orbiculoid brachiopods attached to, and

UMMP 2178, plastoholotype, GSC unnumbered; holotype of *C. newberryi,* UMMP 245; holotype of *C. whitei,* UIPC 10866; holotype of *C. sampsoni,* FMNH UC 6961, plastoholotype, USNM 68156.

Remarks.—Paraconularia subulata (Hall) is most similar in morphology to *P. oklahomaensis* Babcock and Feldmann, n. sp. Both taxa have inflected gothic arch rod articulation in the apical region and inflected circular curve rod articulation elsewhere. Also, specimens referable to both taxa may lack nodes and spines. Except for rod spacing values, the quantitative measures are also very similar. *Paraconularia subulata* has a rod spacing of about 20–35 rods/cm whereas the holotype of *P. oklahomaensis* has a value of 12–24 rods/cm. *Paraconularia subulata* differs most substantially from *P. oklahomaensis* in having very little inflection of the rods in the vicinity of the apex and in having a strong inflection of the rods elsewhere.

In addition to *P. oklahomaensis, P. blairi* (Miller and Gurley) bears close similarity to *P. subulata.* Both taxa have inflected gothic arch rod articulation adapically and inflected circular curve rod articulation adaperturally. Apical angles and rod angles are nearly equal in the two forms. *Paraconularia subulata* differs from *P. blairi* in its lack of nodes on the rods or in having inconspicuous nodes, in the lack of any adapertural inflection of the rods near the midline and in the possession of a greater number of rods/cm, 20–35 as compared to 6–8.

The species *P. victa* (White), *P. newberryi* (Winchell), *P. whitei* and *P. sampsoni* (Miller) are all included as junior synonyms of *P. subulata* because they are indistinguishable from the lectotype and paralectotypes of *P. subulata.* The type specimens of all these species bear subtle nodes on the rods; all have apical angles in the range of 12–22°; all have inflected gothic arch styles of rod articulation; all have 20–35 rods/cm; and all have rod angles of 15–18°. The holotype of *P. sampsoni* possibly could be construed as a juvenile of *P. blairi,* but the lack of rods which are slightly inflected at the midline makes assignment of this specimen to *P. subulata* more reasonable.

Paraconularia subulata is one of the most abundant conulariids in

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located near, the conulariids; locality 247. 28.2; NYSM 9414, same specimen as in Fig. 28.1, detail of holotype. 28.3; *P. salinensis* (Whiteaves), GSC 4292, holotype, minor face; locality 3. 28.4; *P.* sp., CM 34531, a collapsed and poorly preserved specimen in tan and dark red colored dolostone; locality 249. 28.5–28.6; *P. salinensis* (Whiteaves). 28.5; GSC 4292, same specimen as in Fig. 28.3, corner view. 28.6; GSC 4292, same specimen as in Fig. 28.3, detail of minor face. 28.7; *P. yochelsoni* Babcock and Feldmann, n. sp., external molds of two specimens attached to plant matter, holotype, UMMP 45499, to the right, paratype, UMMP 65509, to the left; locality 93. Specimen is not coated with ammonium chloride. Bar scales represent 1 cm.

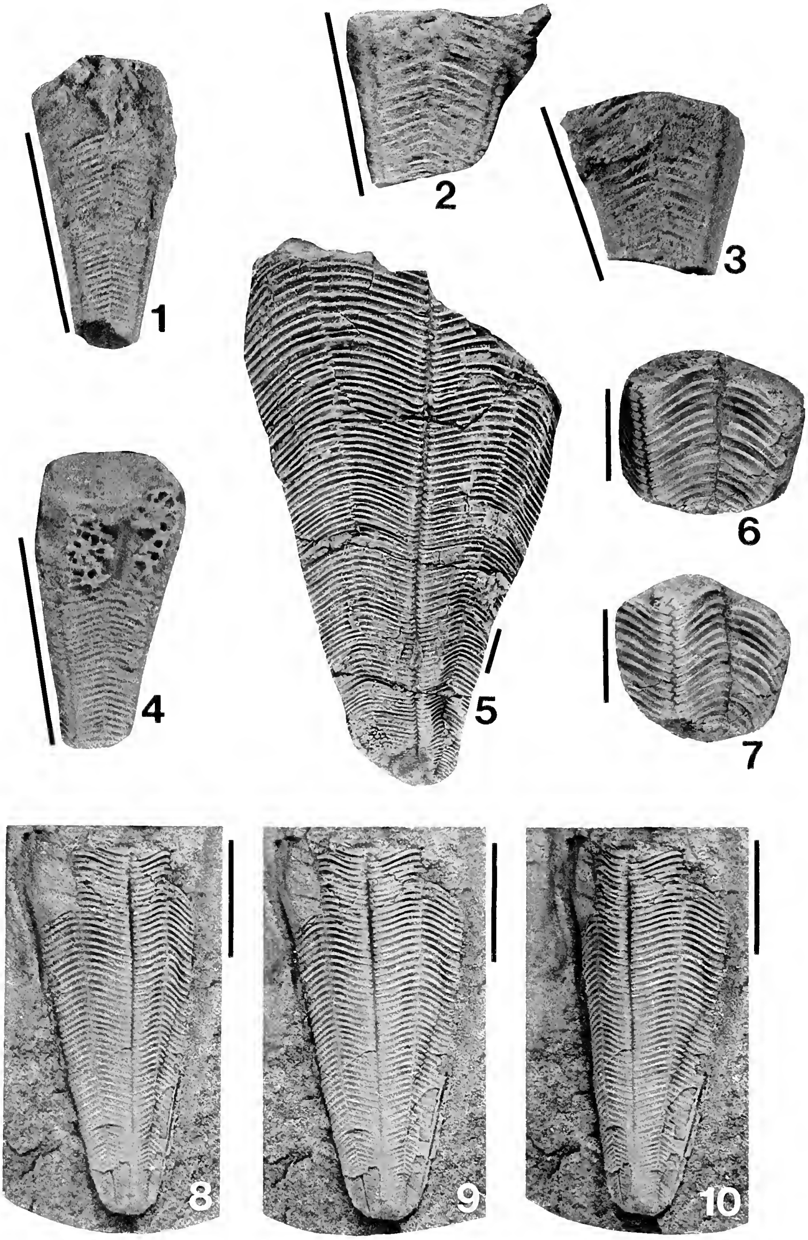

Fig. 29.—*Paraconularia subulata* (Hall). 29.1; AMNH 32404 (smaller of two specimens), lectotype, minor face; locality 16. 29.2; UMMP 245, holotype of *Conularia newberryi*

the Lower Mississippian of the North American midcontinent. It is often confused with other taxa, especially *P. missouriensis,* in museum collections. The reason for this confusion is not clear. Some specimens of this taxon, which superficially appear very similar to specimens of *P. blairi,* may have been confused with *P. missouriensis* because of ambiguity in Swallow's original description of the latter. It is likely that Swallow's description was based upon specimens now referable to both *P. missouriensis* and *P. blairi.*

Conulariids collected from the Bear Gulch Limestone of Montana (CM 34507–34527 and 35000) and from the Cameron Creek Shale of Montana (USNM 118731) are here assigned to *P. subulata* with little reservation. The specimens differ from the type series of *P. subulata* only in the uniform lack of nodes on the rods. However, samples of many specimens referable to *P. subulata* from Illinois, Ohio, and elsewhere indicate that nodes are frequently lacking in this taxon. Even when nodes are present on such specimens, they are subtle.

Material examined.—149 specimens; housed in the AMNH, CM, CMNH, FMNH, GSC, OC, UMMP, USNM, and the private collection of Ron Fisher.

PARACONULARIA WELLSVILLIA
Babcock and Feldmann, new species
Figs. 33.3, 33.6–33.8

Paraconularia sp. Babcock and Feldmann, 1986, fig. 2J.

Description.—Exoskeleton up to 13 cm in length. Major apical angle 14–18°; minor apical angle 12–15°. Rod articulation gothic arch style in apical region and inflected gothic arch style elsewhere; rods almost always alternate at the midline; if they alternate, pattern is usually left superior on major face and usually right superior on minor face; rod angle 26–31°. 4–5 rods/cm; 2–3 nodes/mm; 2–3 adapertural spines/mm; adapical spines appear not to be present. Apical wall not observed.

Occurrence.—Upper Devonian of New York; localities 161–162.

Types.—Holotype, CM 35001; 12 paratypes, CM 34538–34550.

Remarks.—*Paraconularia wellsvillia* Babcock and Feldmann, n. sp.

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Winchell, major face; locality 206. 29.3; UMMP 245, same specimen as in Fig. 29.2, minor face. 29.4; AMNH 32404 (smaller of two specimens), same specimen as in Fig. 29.1, major face. The pitted material attached to the specimen is glue. 29.5; CMNH 5988, corner view of large, partially compressed specimen. Note healed injury near top of minor face; locality 198. 29.6; UMMP 2178, holotype of *C. victa* White, ?minor face; locality 63. 29.7; UMMP 2178, same specimen as in Fig. 29.6, corner view. 29.8; FMNH UC 6961, holotype of *C. sampsoni* Miller, minor face; locality 94. 29.9; FMNH UC 6961, same specimen as in Fig. 29.8, corner view. 29.10; FMNH UC 6961, same specimen as in Fig. 29.8, major face. Bar scale in Fig. 29.5 represents 1 cm; bar scales in Figs. 29.1–29.4 and 29.6–29.10 represent 5 mm.


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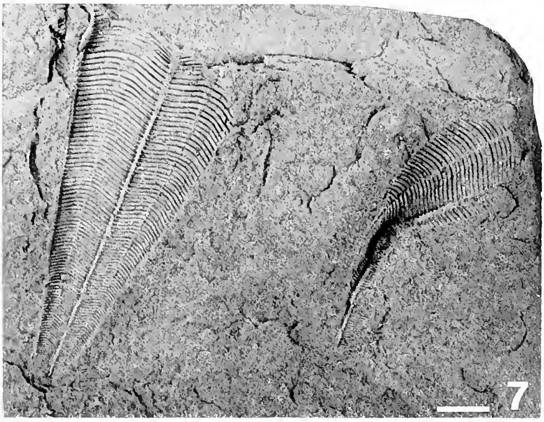
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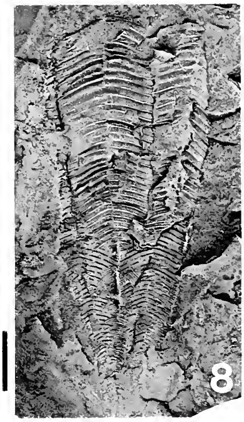
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is distinguished from all other species of *Paraconularia* known from the Devonian and Mississippian rocks of North America in having gothic arch rod articulation in the apical region and inflected gothic arch rod articulation elsewhere. Superficially, this taxon resembles *P. yochelsoni* in the general pattern of rod articulation near the aperture. *P. wellsvillia,* however, possesses nodes and adapertural spines whereas *P. yochelsoni* does not.

Of the 13 specimens examined and referred to *P. wellsvillia,* only the holotype, CM 35001, shows well preserved nodes and spines (Figs. 33.7–33.8). Others, such as the specimen illustrated in Fig. 33.6, seem to lack these structures. After examination of the holotype and 12 paratypes, it seems that two factors affect these profound preservational differences: 1, degree to which the integument is fit around the rods, nodes, and spines; and 2, type of lithology in which the specimen is preserved. The Wellsville Formation, from which all specimens in the type suite were collected, varies from a fine grained silty sandstone to a micaceous siltstone to a micaceous shale. Preservation of a conulariid tends to be better in a fine grained matrix.

The holotype of *P. wellsvillia* shows a wrinkling of the integument only partially related to the pattern of nodes and spines (Fig. 33.8). This wrinkling is also attributed, in part, to a tight fitting of the integument about the framework of the exoskeleton and slight displacement of the framework.

Material examined.—13 specimens; housed in the CM.

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Fig. 30.—*Paraconularia subulata* (Hall). 30.1; USNM 409802, minor face of specimen preserved in phosphatic concretion; locality 72. 30.2–30.3; USNM 395828, right and left halves of a specimen preserved in a phosphatic concretion and showing internal soft-parts; locality 72. 30.4; USNM 409802, same specimen as in Fig. 30.1, view from apical end showing rounded cross section of soft-parts (arrow). 30.5; USNM 409802, same specimen as in Fig. 30.1, x-ray photograph of specimen preserved in a phosphatic concretion. The photograph was obtained using a Hewlett-Packard Faxitron Series x-ray unit located in the Department of Anthropology, Kent State University. The specimen is in the same orientation as in Fig. 30.1. Presumed internal soft-parts appear as a single, elongate tube. 30.6; USNM 409803, specimen preserved in a phosphatic concretion with some of the exoskeleton broken away, revealing remains of limonite-coated internal soft-parts. 30.7; USNM 409804, two specimens preserved in same orientation in siltstone block. Sole marks on reverse side of slab parallel the orientation of the conulariids and indicate that these specimens have been current aligned; locality 220. 30.8; UIPC 10866, holotype of *Conularia whitei* Meek and Worthen preserved in siderite; locality 201. Bar scales in Figs. 30.1–30.3 and 30.5–30.8 represent 1 cm; bar scale in Fig. 30.4 represents 5 mm. Specimens in Figs. 30.2–30.4 and 30.6 have not been coated with ammonium chloride.


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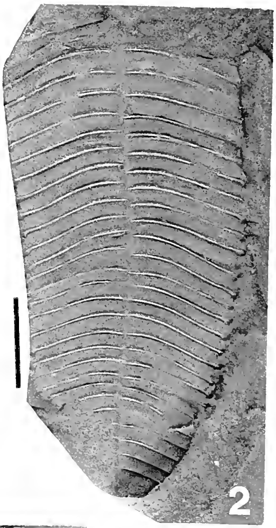
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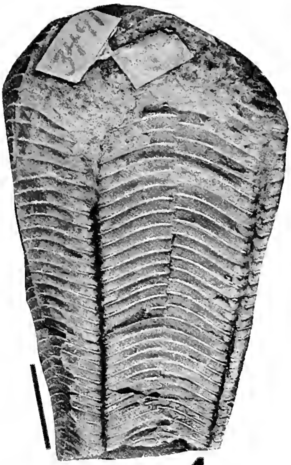
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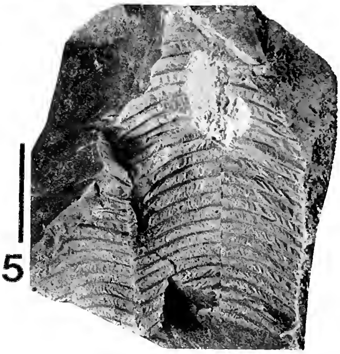
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Etymology of trivial name.—Named for the Wellsville Formation, from which the holotype specimen was collected.

PARACONULARIA YOCHELSONI
Babcock and Feldmann, new species
Figs. 28.7, 33.1–33.2, 33.5

Paraconularia newberryi (Winchell). *Sensu* Driscoll, 1963, p. 34–40, Pl. 1, figs. 6–8.

Description.—Exoskeleton up to 3.5 cm in length. Major apical angle 17–20°; minor apical angle approximately 18°. Rod articulation gothic arch style in earliest stages, inflected gothic arch style in later stages. Rods usually alternate at midline; if they alternate, pattern is usually right superior on both major and minor faces; rod angle 15–20°. 13–18 rods/cm. Nodes appear to be absent; spines absent. Apical wall present.

Occurrence.—Lower Mississippian of Michigan; locality 93.

Types.—Holotype, UMMP 45499; two paratypes, UMMP 65509 on the same slab as UMMP 45499, and UMMP 45500.

Remarks.—*Paraconularia yochelsoni* Babcock and Feldmann, n. sp. is only similar in morphology to *P. alternistriata* (Shimer). Both species seem to be less than 3.5 cm in maximum length, lack nodes on the rods and have rod articulation patterns which appear to be similar. *Paraconularia yochelsoni,* however, has larger apical angles, 15–20° as compared to 10–11°, and fewer rods/cm, 13–15 as compared to 28.

The holotype, UMMP 45499, and paratype, UMMP 65509, specimens of *P. yochelsoni,* are preserved as three dimensional specimens lacking the integument except along the midline. The midline may have been thickened in this taxon.

The holotype and paratype of *P. yochelsoni* are located on the same slab as a large portion of black, carbonaceous matter composed largely of densely packed, filamentous strands (Fig. 28.7). This material probably represents plant matter of some sort, perhaps a planktonic alga. The two conulariids appear to be attached to the presumed plant matter by stalks extending from their apices; only small traces of the stalks remain in place. The two conulariids on this slab are radiating away from the center of the dark mass.

Material examined.—3 specimens; housed in the UMMP.

Etymology of trivial name.—Named for Ellis L. Yochelson, a distinguished student of problematic fossils.

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Fig. 31.—*Paraconularia subulata* (Hall). 31.1; CM 34524, preserved in micrite; locality 106. 31.2; CM 35000, preserved in micrite; locality 106. 31.3; CM 34521, preserved in micrite, locality 106. 31.4; NYSM 3491, preserved in siderite; locality 203. Original of Hall's "*Conularia newberryi*" (1879, Pl. 34A, fig. 12). 31.5; USNM 118731; locality 107. Bar scales represent 1 cm.

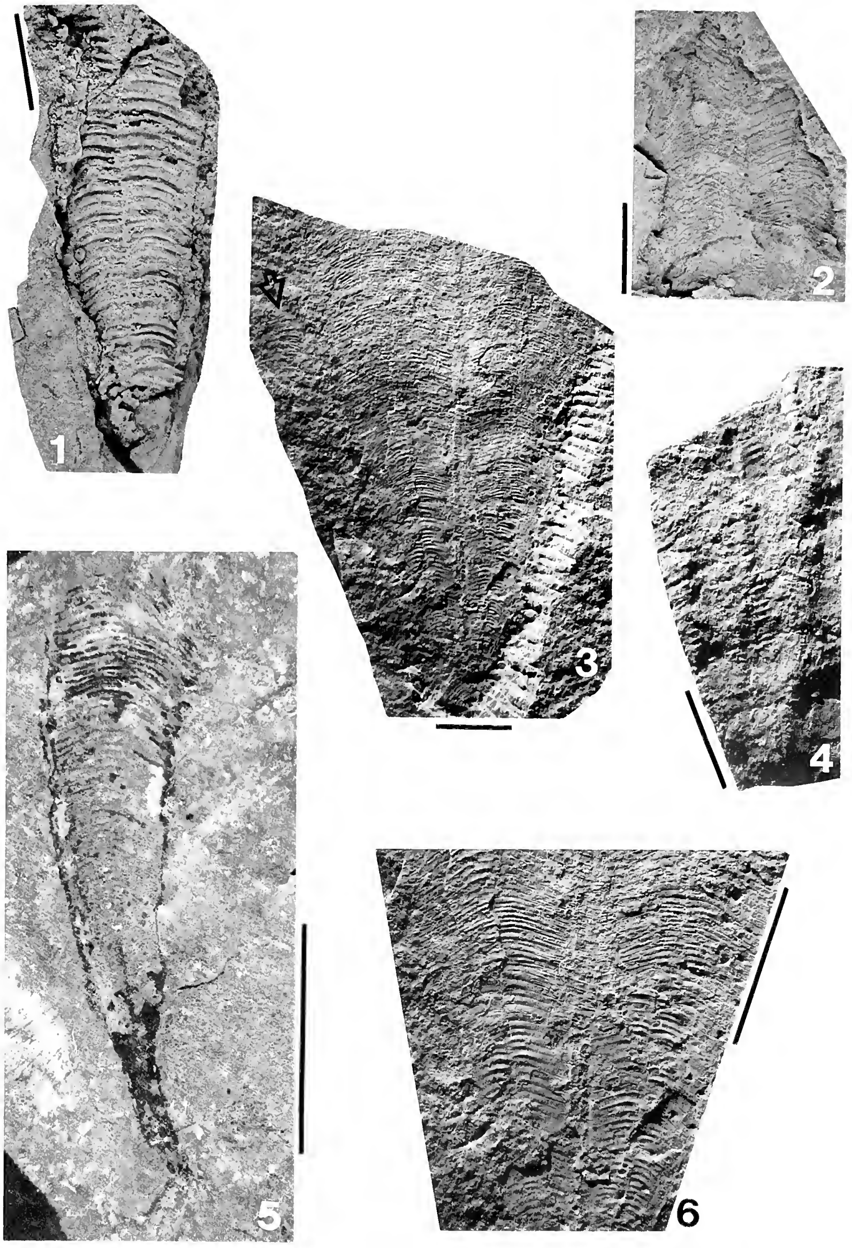

Fig. 32.—32.1; *Paraconularia missouriensis* (Swallow)?, GSC 85062; locality 5. 32.2; *P.* sp., USNM 409805, fragment of specimen lacking integument preserved in soft blue-

PARACONULARIA sp.
Fig. 28.4

Occurrence.—Upper Devonian-Lower Mississippian transition of South Dakota; locality 27.4.

Figured specimen.—CM 34531.

Remarks.—A single specimen of conulariid was collected from the Englewood Formation at Deadwood, South Dakota. It can be reliably identified only to the genus level.

The specimen is badly crushed and incomplete, making it possible to perform few qualitative or quantitative observations. The specimen in question possesses 7 rods/cm and lacks nodes and spines; it is therefore referred to the genus *Paraconularia.* The specimen seems to have a gothic arch style of rod articulation in the apical region and an inflected circular curve style elsewhere.

Species of *Paraconularia* examined in this work which may possess 7 rods/cm include *P. blairi* (Miller and Gurley) and *P. missouriensis* (Swallow); *P. chesterensis* (Worthen) can have as few as 8 rods/cm and *P. wellsvillia* Babcock and Feldmann, n. sp. has 4–5 rods/cm. Of these, CM 34531 appears to be most similar to *P. blairi* or *P. subulata* (Hall) in terms of rod articulation.

Material examined.—1 specimen, CM 34531.

RETICULACONULARIA Babcock and Feldmann, new genus

Diagnosis.—Conulariids with rods that are widely spaced, 12–39/cm. 30–80% of rods alternate at midline; 20–70% abut. Apical angles large, 22–59°. Nodes and adapertural spines present and widely spaced; adapical spines not known.

Type species.—*Conularia penouili* Clarke, 1907; Lower Devonian of Quebec. Holotype, NYSM 9412.

Remarks.—Species referable to *Reticulaconularia* differ from all other conulariids in having very large apical angles, 22–59° in the specimens measured in this study. The wide spacing between adjacent rods and between nodes, as well as between adapertural spines is also unique to species of this genus. In specimens retaining the external surface of the integument, this pattern of rods, nodes, and spines gives the exo-

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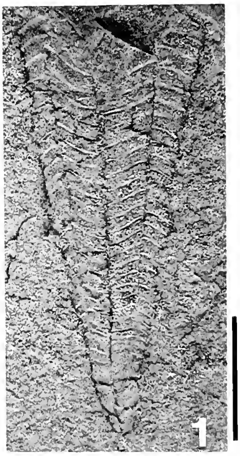
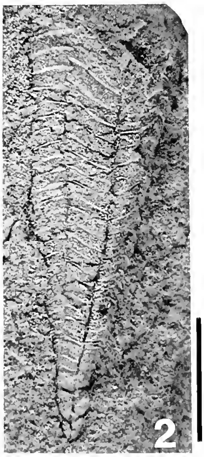
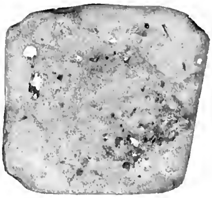
gray calcareous shale; locality 177. 32.3; *P. recurvatus* Babcock and Feldmann, n. sp., USNM 409806. Holotype to right; a paratype (USNM 409807) is indicated by arrow; locality 109. 32.4; *P. byblis* (White)?, UMMP 26735, a poorly preserved, collapsed specimen; locality 250. Original of Winchell (1871, p. 257). 32.5; *P. chesterensis* (Worthen)?, GSC 49383, a juvenile specimen with stalk preserved. Specimen not coated with ammonium chloride; locality 7. 32.6; *P. recurvatus* Babcock and Feldmann, n.sp., USNM 409806, same specimen as in Fig. 32.3, detail of holotype. Bar scales represent 1 cm.



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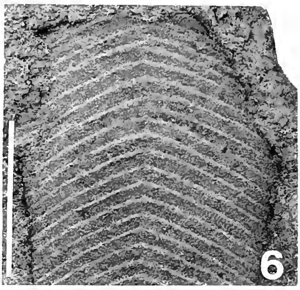

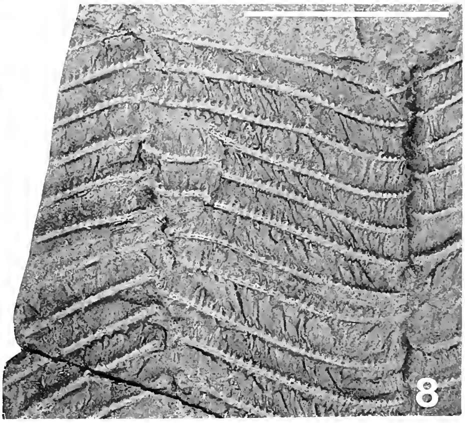

skeleton a somewhat reticulate pattern. The genus is named for this characteristic.

At present, three species of conulariids are referred with certainty to *Reticulaconularia*: *C. penouili* from the Lower Devonian of Quebec, *C. sussexensis* Herpers from the Lower Devonian of New Jersey, and *C. baini* Ulrich from the Devonian of Bolivia. This third species occurs outside the geographic limits of this paper; we and others will redescribe the taxon in a paper on the Devonian conulariids of Bolivia.

RETICULACONULARIA PENOUILI (Clarke, 1907)

Figs. 34.3–34.5; 35.3

Conularia penouili Clarke, 1907, p. 180–181, 2 figs.; Clarke, 1908, p. 144, Pl. 11, figs. 10–11.
Conularia gaspesia Sinclair, 1942, p. 158–160, fig.
Conularia s.l. *penouili* Clarke. Sinclair, 1948, p. 283.

Description.—Exoskeleton a curved pyramid, expanding slowly and non-uniformly from the apex. Exoskeleton up to 6.7 cm in length. Major apical angle approximately 59°; minor apical angle approximately 22–30°. Rod articulation of inflected circular curve style in apical ⅓, angulated circular curve style in middle ⅓, and inflected circular curve style in apertural ⅓. Rods usually alternate at midline; if they alternate, pattern is usually left superior on both major and minor faces; rod angle 0–8°. 12–21 rods/cm. 1–2 nodes/mm. 1–2 adapertural spines/cm; adapical spines probably not present. Interridge furrows broadly rounded into longitudinally oblong pits. Apical wall not observed.

Occurrence.—Lower Devonian of Quebec; localities 228 and 246.

Types.—Holotype, NYSM 9412; topotype of *Conularia gaspesia*, GSC 87242.

Remarks.—*Reticulaconularia penouili* (Clarke) is distinguished from *R. sussexensis* (Herpers) by the following features. First, *R. penouili* has 12–21 rods/cm and *R. sussexensis* has 11–14 rods/cm. Greater rod spacing in *R. penouili,* combined with wide spacing between the nodes and between the adapical spines has produced large, oblong, hollowed

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Fig. 33.—33.1–33.2, *Paraconularia yochelsoni* Babcock and Feldmann, n. sp. 33.1; UMMP 45499, holotype; corner view; locality 93. 33.2; UMMP 45499, same specimen as in Fig. 33.1, major face. 33.3; *P. wellsvillia* Babcock and Feldmann, n. sp., CM 34502, paratype, preserved in siltstone; ?minor face; locality 161. 33.4; *P. subulata* (Hall), KSU 1172, cross section showing weakly bilateral, four-sided nature of the exoskeleton. Specimen not coated with ammonium chloride; locality 216. 33.5; *P. yochelsoni* Babcock and Feldmann, n. sp, UMMP 45500, paratype; locality 93. 33.6–33.8; *P. wellsvillia* Babcock and Feldmann, n. sp. 33.6; CM 34503, detail of paratype preserved as an internal mold in siltstone and not exhibiting interrod ridges or interrod furrows; locality 162. 33.7; CM 35001, holotype, a collapsed specimen preserved in silty shale; locality 161. 33.8; CM 35001, same specimen as in Fig. 33.7, detail of a minor face. Bar scales represent 1 cm.

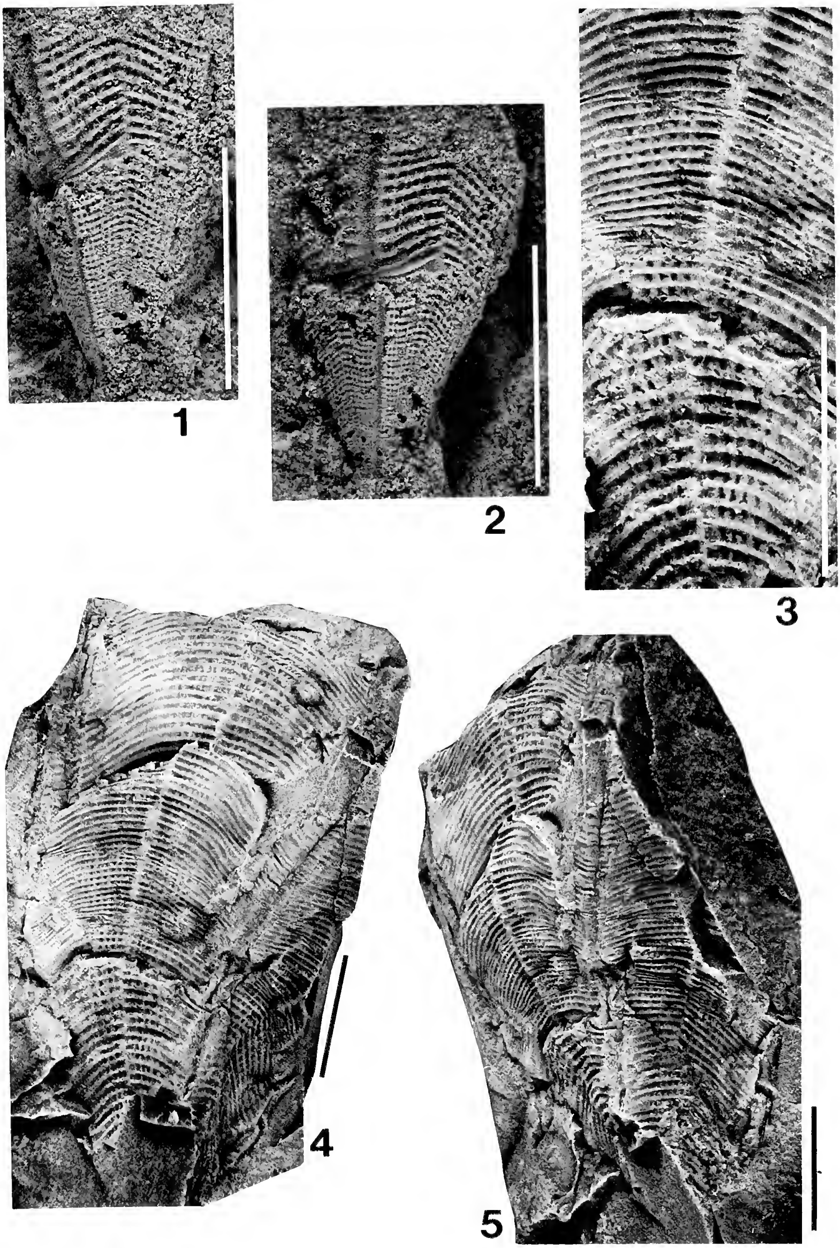

Fig. 34.—34.1–34.2; *Reticulaconularia sussexensis* (Herpers). 34.1; NJSM 10806, smaller of two specimens, major face of small specimen preserved in somewhat metamorphosed

out interridge furrows on the exterior surface of the exoskeleton. This feature is not exhibited, to this extent, on any other known species of conulariid.

Secondly, the values obtained for rod angles are consistently smaller for *R. penouili* than they are for *R. sussexensis,* 0–8° compared to 11–14°. *Reticulaconularia sussexensis* exhibits a greater number of rods which abut at the midline than does *R. penouili.* Up to 70% of rods abut in specimens of *R. sussexensis* while 20–30% of rods abut in the holotype of *R. penouili.* Unlike *R. sussexensis, R. penouili* shows an alternation between a circular curve style of rod articulation and an angulated circular curve style. *Reticulaconularia sussexensis* exhibits only an inflected gothic arch style of rod articulation. Finally, judging from the available sample, specimens of *R. sussexensis* seem to have a smaller maximum length than *R. penouili.* The maximum recorded hypothetical length of a specimen of *R. sussexensis* is about 2.5 cm. The hypothetical length of the holotype of *R. penouili* is 6.7 cm.

The holotype of *Conularia gaspesia* Sinclair, which was said to have been deposited in the RM(MU) (Sinclair, 1942, p. 160) apparently never was deposited in that museum (Ingrid Birker, written communication, 1985), and is now presumed to be lost. However, we have found, in the Sinclair collection housed in the GSC, a specimen labelled as *C. gaspesia* (GSC 87242; Fig. 35.3). The handwriting on a label accompanying the specimen is unmistakably that of G. Winston Sinclair. This specimen is of further value because a label glued to the specimen indicates that it was collected from Lower Devonian Grande Grève Limestone on the Gaspé Peninsula; thus, the specimen is a topotype.

This topotype specimen of *C. gaspesia,* GSC 87242, exhibits one well preserved face and has all of the salient morphological characteristics that the holotype of *R. penouili* posseses. Among the characteristics shown by the topotype of *C. gaspesia* are large, oblong, hollowed out interridge furrows, just as are present in the holotype of *R. penouili.* A good photograph of the holotype of *C. gaspesia* (Sinclair, 1940, fig.) shows these same features. Measurements taken on the topotype specimen are given in Appendix B. The only way in which GSC 87242 differs from the holotype of *R. penouili,* NYSM 9412, is that it is not

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siltstone; locality 112. 34.2; NJSM 10806, same specimen as in Fig. 34.1, corner view. Note prominent exoskeletal constriction. 34.3–34.5; *R. penouili* (Clarke). 34.3; NYSM 9412, holotype, detail of minor face; locality 246. 34.4; NYSM 9412, same specimen as in Fig. 34.3, minor face of specimen preserved in micrite. 34.5; NYSM 9412, same specimen as in Fig. 34.3, major face. Bar scales represent 1 cm.

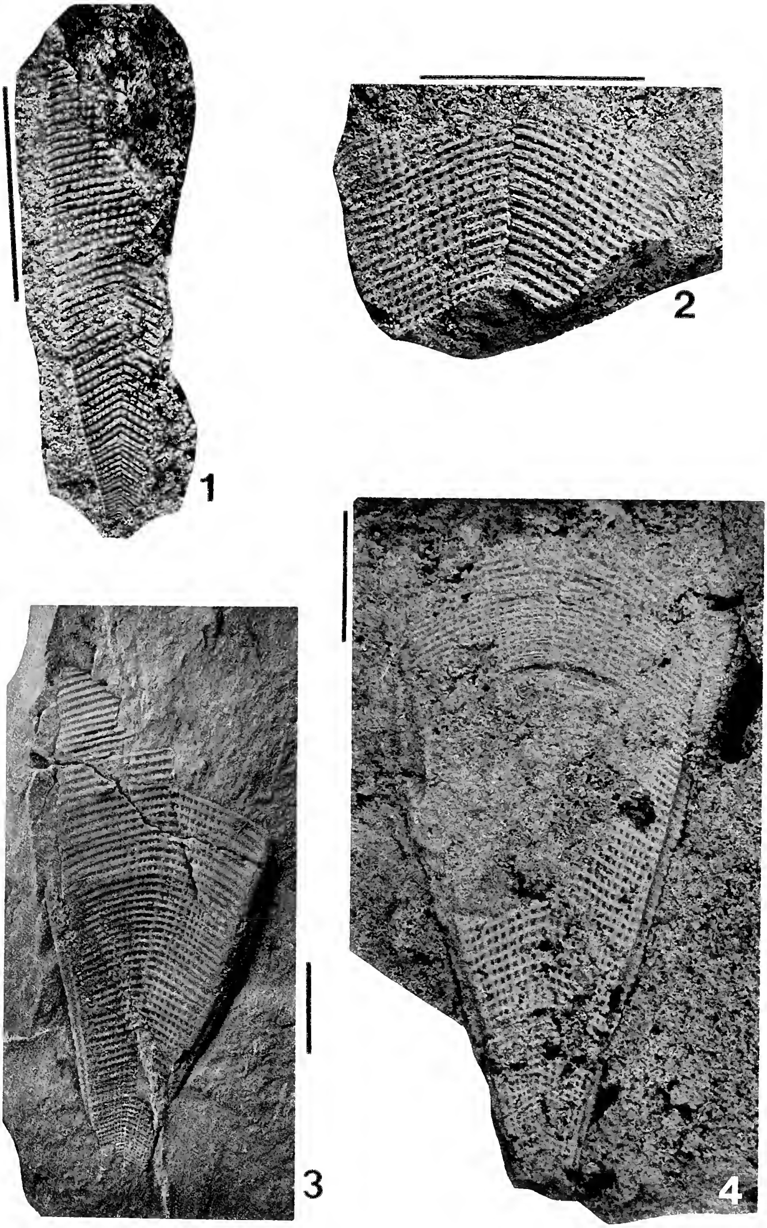

Fig. 35.—35.1–35.2. *Reticulaconularia sussexensis* (Herpers). 35.1; NJSM 10750, external mold of apical region of very small paratype specimen; locality 112. 35.2; NJSM 10751, largest of three specimens, paratype, preserved as an external mold; locality 112. 35.3; *R. penouili* (Clarke), GSC 87242, ?minor face of topotype of *Conularia gaspesia*

curved in the apical region. However, NYSM is a somewhat crushed or collapsed individual. One final interesting point is that both NYSM 9412 and GSC unassigned were collected from the Grande Grève Limestone on the Gaspé Peninsula. Based upon this topotype specimen of *C. gaspesia,* this taxon is here placed in synonymy with *R. penouili.*

Material examined.—2 specimens; housed in the GSC and the NYSM.

RETICULACONULARIA SUSSEXENSIS (Herpers, 1949)

Figs. 34.1–34.2, 35.1–35.2, 35.4

Conularia sussexensis Herpers, 1949, p. 1–7, Pl. 1, 2.
Conularia gaspesia Sinclair. *Sensu* Herpers, 1950, p. 619.

Description.—Exoskeleton up to 2.5 cm in length. Major apical angle 24–28°; minor apical angle 22–25°. Rod articulation uniformly of inflected gothic arch style. Rods usually abut at midline; if they alternate, they usually occur left superior on major face and right superior on minor face; rod angle 11–14°. Approximately 39 rods/cm (extrapolated) in apical region; 14–18 rods/cm elsewhere. 2 nodes/mm; 2 adapertural rods/mm; adapical spines absent. Apical wall not observed.

Types.—Holotype, NJSM 10749; four paratypes, NJSM 10750, NJSM 10751 (three specimens).

Occurrences.—Lower Devonian of New Jersey; localities 111, 112, 113.

Remarks.—The present samples of *R. sussexensis* (Herpers) differ from the holotype of *R. penouili* (Clarke) in that the former: 1, is of smaller size; 2, has no curvature to the exoskeleton; 3, has smaller apical angles, especially on the major face; 4, has a greater number of rods/cm; 5, has larger rod angles; 6, shows greater than 30% of the rods abutting at the midline; and 7, shows only an inflected gothic arch style of rod articulation. These differences are discussed more fully in the remarks accompanying the description of *R. penouili,* above.

Material examined.—10 specimens; housed in the NJSM.

ORGANISMS PREVIOUSLY ASSIGNED TO CONULARIIDA, HERE REJECTED FROM THE PHYLUM

Phylum Mollusca

Class Hyolitha

HYOLITHES sp.

Fig. 17.4

Conularia sp. Ellison, 1965, p. 48–49, Pl. 4, fig. 1.
Hyolithes sp. Babcock, 1985*b*, p. 14–16, fig. 1.

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Sinclair, preserved in micritic limestone; locality 242. 35.4; *R. sussexensis* (Herpers), NJSM 10749, ?major face of holotype, preserved in somewhat metamorphosed siltstone; locality 112. Bar scales represent 1 cm.

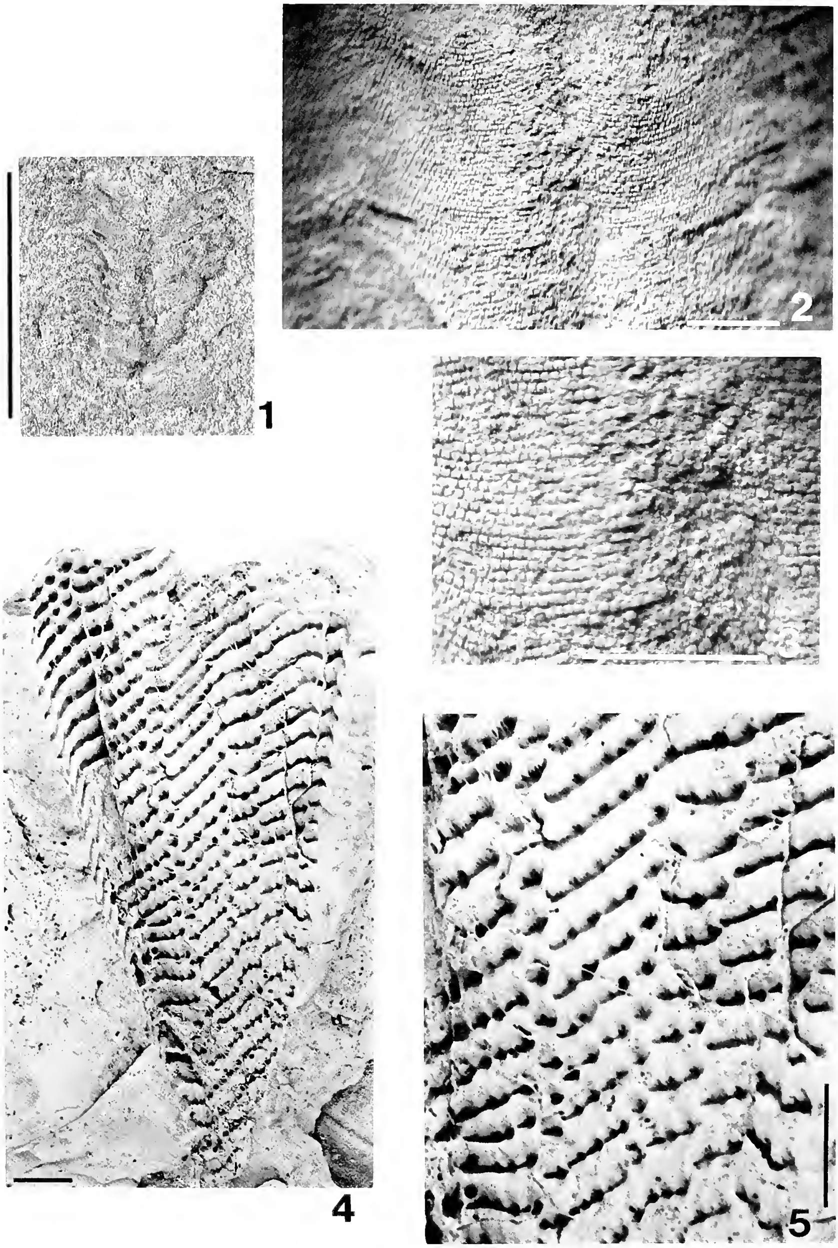

Fig. 36.—36.1–36.3; "*Conularia*" *tenuicostata* Branson, here interpreted to be a ?priapulid worm. 36.1; UMC 4271, holotype; locality 99. 36.2; UMC 4271, detail of same

Occurrence.—Middle Devonian of Pennsylvania; locality 240.

Figured specimen.—USNM 173928.

Remarks.—Ellison's figured specimen (1965, plate 4, fig. 1) is a small conical shell expanding slowly and uniformly from a bluntly rounded apex. The specimen possesses thin, closely spaced, raised lines, concentric about the apex. Crushing has produced a long, irregular line down the middle of the shell. A ligula, or an apertural extension of the shell on the dorsal side, is present, clearly indicating that the specimen is a hyolith, not a conulariid.

Phylum Priapulida?
Figs. 36.1–36.3

Conularia tenuicostata Branson, 1938, p. 111, Pl. 14, figs. 5–6; Branson, 1944, p. 216.
Mesoconularia tenuicostata (Branson). Sinclair, 1948, p. 128.

Occurrence.—Lower Mississippian of Missouri; locality 99.

Type.—Holotype, UMC 4271.

Remarks.—The holotype, and only known specimen of *Conularia tenuicostata* Branson, possesses tiny nodes or pustules arranged in closely spaced rows which appear to run essentially perpendicular to the long axis of the fossil. The rows of nodes or pustules are not supported by calcium phosphate rods. Additionally, the specimen is flattened and micrite replaced. This type of preservation is unlike that expected of an animal composed of calcium phosphate, such as a conulariid. Rather, the preservation is similar in appearance to the preservation of objects having a tough cuticle, such as *Plectodiscus discoideus* (Rauff), a chondrophorine cnidarian from the Hunsrück Slate (Devonian) of West Germany (Yochelson et al., 1983).

Branson's specimen possesses indiscrete ringlike segments delimited by thin, latitudinally arranged crests 0.5 to 0.7 mm apart. These segments are each covered with closely spaced, latitudinally arranged rows of minute papillae which are strikingly similar to the cuticle of living priapulid worms such as *Priapulus* and *Tubiluchus*. However, there is not enough of the holotype preserved to determine whether the animal possessed spines, a common feature of living priapulids. Thus, this fossil is referred to the phylum Priapulida with reservation.

The specimen in question preserves only a small portion of cuticle,

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specimen as in Fig. 36.1, showing ridges delimiting annular segments. 36.3; detail of same specimen as in Fig. 36.1, showing surface structure. 36.4–36.5; *Oracanthus* sp. 36.4; USNM 409810; locality 6. 36.5; USNM 409810; detail of specimen in Fig. 36.5, interpreted to be remains of fish spine. Bar scales in Figs. 36.1 and 36.4–36.5 represent 1 cm; bar scales in Figs. 36.2 and 36.3 represent 1 mm.

7.5 mm long and 8.1 mm wide. It is broken at its upper and lower margins, presumably between adjacent segments. This mode of preservation supports the interpretation that the specimen possessed a multielement covering, capable of readily fragmenting or tearing.

Phylum Chordata
Class Vertebrata
Order Pisces
ORACANTHUS sp.
Figs. 36.4–36.5

Conularia newberryi Winchell? *Sensu* McKee and Gutschick *in* McKee and Gutschick, 1969, p. 125–172.

Occurrence.—Lower Mississippian of Arizona; locality 5.

Figured specimen.—External mold preserved in dolostone and latex mold, USNM 409810.

Remarks.—This figured specimen mimics a conulariid in having nodose structures arranged in rows, crossing the surface transversely. The rows, however, are discontinuous, and form chevron-shaped patterns in some places. The rows seem to be composed of semidiscrete pits arranged in side-by-side fashion. As the specimen is an external mold, the "pits" would correspond to nodes. These is no evidence on the specimen of either a midline or a corner groove. The specimen is undulated near the left margin, however.

This specimen is here regarded as the spine of a gyracanthid shark. Michael E. Williams, of the Cleveland Museum of Natural History, has viewed this specimen and has noted that small portions of dentine adhere to it in places, confirming that it is a vertebrate fossil. It is his suggestion that this specimen be referred to the genus *Oracanthus*.

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APPENDIX A—LOCALITY INDEX

Collector, year of collection if known, description of locality, stratigraphic assignment and conulariid taxa present

ALABAMA

1 A. S. Horowitz. "Keyes site," Skyline, Alabama. Formation unknown; probably Chesterian Series. *Paraconularia chesterensis.*

ALBERTA

2 Anonymous. Near Banff, Alberta. Formation unknown and series unknown; Mississippian Subsystem. *Paraconularia missouriensis*?

3 R. G. McConnell, 1890. Athabasca River, La Saline, Alberta. Formation unknown; Chautauquan Series. *Paraconularia salinensis.*

4 H. W. Shimer, pre-1926. Lake Minnewanka, Alberta. Formation and series unknown; Mississippian Subsystem. *Paraconularia alternistriata.*

5 F. Beales. Upper part of Job Creek, western Alberta. Upper Rundle Formation, 345 m from the base of the formation; Chesterian Series. *Paraconularia missouriensis*?

ARIZONA

6 R. C. Gutschick and P.C.H., 1954. Top of mesa on point between Rock and Blye Canyons on 7BarV Ranch, WF Cattle Company, south of Peach Springs and Cherokee Point, Arizona. Chert in Member 2 of Redwall Limestone, about 53 m above base of Redwall Formation; ?Osagean Series. No conulariids collected; *Oracanthus* spine.

BRITISH COLUMBIA

7 D. Scott, 1962. Spur on northeast corner of Mt Hosmer, 14.5 km northeast of Fernee and 14.5 km southwest of Natal, British Columbia. Lower Etherington Member of the Rocky Mountain Formation of the Rundell Group; Chesterian Series. *Paraconularia chesterensis*?

ILLINOIS

8 Anonymous. Kinderhook, Pike County, Illinois. Kinderhook Group; Kinderhookian Series. *Conularia subcarbonaria.*

9 W. F. E. Gurley; Anonymous. Hamilton, Illinois. Keokuk Limestone; Osagean Series. *Conularia subcarbonaria.*

10 Anonymous. Chester, Randolph County, Illinois. Chester Limestone; Chesterian Series. *Paraconularia chesterensis.*

11 Sloss. Pike County, Illinois. Burlington Limestone; Osagean Series. *Paraconularia chesterensis, P. blairi.*

12 S. Weller, 1912. About 2.4 km south of Marigold, Illinois. "Lower Okaw, Marigold Oolite" (=Burlington Limestone?); Osagean Series. *Paraconularia chesterensis.*

13 W. F. E. Gurley; Anonymous. Hamilton, Illinois. Keokuk Limestone; Osagean Series. *Conularia subcarbonaria.*

14 W. F. E. Gurley. Madison County, Illinois. St. Louis Limestone; Meramecian series. *Paraconularia missouriensis.*

15 Anonymous. Warsaw, Madison County, Illinois. St. Louis Limestone; Meramecian Series. *Paraconularia missouriensis.*

16 Anonymous. Alton, Illinois. St. Louis Formation; Meramecian Series. *Paraconularia subulata, P. chesterensis.*

17 W. F. Gurley. Madison County, Illinois. St. Louis Limestone; Meramecian Series. *Paraconularia chesterensis.*

18 S. Weller, 1912. About 3.2 km east of Waterloo, Illinois, Illinois. Renault Limestone; Chesterian Series. *Paraconularia chesterensis.*

19 S. Weller, 1918. About 4 km southeast of Vienna, Illinois. Glen Dean Limestone; Chesterian Series. *Paraconularia chesterensis.*

20 A. S. Horowitz, 1966. Debris from slope below quarry in Mississippi River bluffs above Illinois State Highway 3 Bypass, SW¼, SW¼ Sec.29, T7S, R6W, Chester, Randolph County, Illinois, Chester 7.5′ Quadrangle. Menard Limestone; Chesterian Series. *Paraconularia chesterensis, Conularia* cf. *C. subcarbonaria.*

21 L. F. Rauchfrise; Anonymous. Pope County, Illinois. Chester Group; Chesterian Series. *Paraconularia chesterensis.*

INDIANA

22 E. M. Kindle. Delphi, Indiana. Sellersburg Formation; Chautauquan Series. *Conularia delphiensis.*

23 D. G. Maroney and R. W. Orr, pre-1974. Delphi Limestone Company Quarry, north side of U.S. Highway 421, northwest edge of Delphi, SW¼, SW¼ Sec. 19, T25N R2W, Carroll County, Indiana, Delphi 7.5′ Quadrangle. 0–10 cm thick phosphatic pebble bed at base of New Albany Shale; Chautauquan Series. *Conularia delphiensis.*

24 D. E. Hattin? Probably Indiana. Probably Harrodsburg Formation; Osagean Series. *Conularia subcarbonaria.*

25 D. E. Hattin. Hattin location S-776. Indiana. Borden Group; Meramecian Series. *Conularia multicostata.*

26 Anonymous. Curiosity Hollow, near Martinsville, Indiana. New Providence Formation; Osagean Series. *Paraconularia* cf. *P. subulata.*

27 Anonymous. Crawfordsville, Indiana. "Keokuk Group" (=Borden Group); Osagean Series. *Conularia subcarbonaria, Paraconularia chesterensis.*

28 W. F. E. Gurley. West Point, Indiana. "Keokuk Group" (=Borden Group); Osagean Series. *Conularia subcarbonaria.*

29 G. K. Greene; Washburn. New Albany, Indiana. "Knobstone Group" (=Borden Group); Osagean Series. *Paraconularia byblis, P. subulata.*

30 Anonymous. Spergen Hill, Indiana. St. Louis Limestone; Meramecian Series. *Paraconularia missouriensis.*

31 W. F. Gurley; Anonymous. Edwardsville, Indiana. "Keokuk Group" (=Borden Formation); Osagean Series. *Paraconularia missouriensis.*

32 Klippart. New Providence, Indiana. Carwood Member, Borden Formation; Osagean Series. *Paraconularia blairi.*

33 E. O. Ulrich. Crawfordsville, Indiana. Borden Formation ("Keokuk Group"); Osagean Series. *Paraconularia chesterensis.*

34 Anonymous. Near Providence, Indiana. Borden Formation; Osagean Series. *Paraconularia blairi.*

35 C. Rominger? Crawfordsville, Montgomery County, Indiana. Near middle of Borden Group; Osagean Series. *Paraconularia chesterensis.*

36 S. Makvrat. Bed of Gnaw Bone Creek just south of Indiana Highway 46, just east of Gnaw Bone, Indiana, Nashville 7.5′ Quadrangle. New Providence Shale according to collector; more likely Carwood or Locust Point Formation of Borden Group according to A. S. Horowitz (written communication, 1984); ?Osagean Series. *Paraconularia* cf. *P. byblis, P. chesterensis.*

37 R. Fields and J. Harris, 1981. Section on old Indiana Highway 37, SE¼, NW¼, NW¼ Sec.21, T9N, R1W, Monroe County, Indiana, Bloomington 7.5′ Quadrangle. Ramp Creek Member of Harrodsburg Limestone, 3–7 m above contact with Borden Group; ?Osagean Series. *Conularia subcarbonaria.*

38 J. Hall?; Washburn; Anonymous. Crawfordsville, Indiana. "Keokuk Group" (=Borden Group); Osagean Series. *Conularia subcarbonaria, Paraconularia chesterensis, P. subulata.*

39 W. F. E. Gurley; G. Robb, pre-1923. New Albany, Indiana. "Knob or Knobstone Shale" (=Borden Group?); Osagean Series. *Conularia multicostata, Paraconularia byblis, P. chesterensis, P. missouriensis, P. subulata.*

40 W. F. E. Gurley. West Point, Indiana. "Keokuk Group (=Borden Formation)"; Osagean Series. *Paraconularia chesterensis.*

41 R. L. Anstey et al., 1968. Bed of Indian Creek on O. C. Bennett or Ben Wilson property, approximately .8 km north of Indiana Highway 234, NE¼, NW ¼, SE¼ Sec. 8, T17N, R5W, Montgomery County, Indiana. ?Edwardsville Formation of Borden Group; Osagean Series. *Paraconularia* cf. *P. chesterensis.*

42 C. Rominger? Crawfordsville, Montgomery County, Indiana. Near middle of Borden Group; Osagean Series. *Conularia subcarbonaria.*

43 G. Campbell. Floyds Knob Hill, Highway 150, near center of NE¼ 28-25-6E (*sic*), 3.2 km northwest of New Albany, Indiana. Kenwood Formation; ?Osagean Series. *Paraconularia byblis.*

44 W. F. E. Gurley. Spergen Hill, Indiana. Probably St. Louis Limestone, though possibly Salem Limestone; Meramecian Series. *Conularia subcarbonaria.*

45 W. F. E. Gurley. Spergen Hill, Indiana. St. Louis Limestone or Salem Limestone; Meramecian Series. *Conularia subcarbonaria.*

46 Anonymous. Salem, Indiana. Salem Limestone; Meramecian Series. *Conularia subcarbonaria.*

47 A. S. Horowitz, N. G. Lane et al. Outcrop along west branch of Mosquito Creek, 0.48 km west and 0.24 km north of southeast corner of Sec. 25, T5S, R5E, approximately 4.5 km east of Laconia, Harrison County, Indiana; Laconia 7.5′ Quadrangle. Somerset Shale; Chesterian Series. *Paraconularia chesterensis.*

48 J. J. Galloway, 1949. Galloway location 1.40C, ravine beginning at railroad, 1.2 km northwest of Harrodsburg and running northwest 0.8 km to old Indiana Highway 7, SE¼, SW¼ Sec. 20, T7N R1W, Monroe County, Indiana, Clear Creek 7.5′ Quadrangle. Lower part of Harrodsburg Formation; Meramecian Series. *Conularia* cf. *C. subcarbonaria.*

49 J. J. Galloway, 1949. Galloway location 1.70A, old quarry, 4 km northwest of Dolan, Monroe County, Indiana. Site is probably an abandoned Quarry 2.4 km northwest of Dolan shown on Modesto 7.5′ Quadrangle topographic map; W½, SW¼, NW¼ Sec. 34, T10N R1W, approximately 0.4 km east of old Indiana Highway 37 (A.S. Horowitz, written communication, 1984). Lower part of Harrodsburg Formation; Meramecian Series. *Paraconularia chesterensis.*

50 D. E. Hattin, 1965. Roadcut on State Highway 46, east of Gnaw Bone, approxi-

mately N½, N½ Sec.25, T9N, R4E, Brown County, Indiana, Nashville 7.5′ Quadrangle. Carwood Formation of Borden Group; Chesterian Series. *Paraconularia* cf. *P. byblis, P. chesterensis.*

51 Anonymous. Spergen Hill, Indiana. Spergen Limestone; Meramecian Series. *Conularia subcarbonaria, Paraconularia chesterensis.*

52 Anonymous. Spergen Hill, Indiana? Spergen Hill Limestone?; Meramecian Series? *Paraconularia chesterensis.*

53 Anonymous. Hendricks County, Indiana. Formation unknown; probably Chesterian Series. *Paraconularia chesterensis.*

54 W. F. E. Gurley. Evansville, Indiana. "Chester Group"; Chesterian Series. *Paraconularia chesterensis.*

55 A. S. Brockley and T. G. Perry, 1954. Debris from Mulzer Brothers Quarry, SW¼, NE¼ Sec. 3, T2S, R2W, Crawford County, Indiana, Taswell 7.5′ Quadrangle. "Glen Dean Limestone" (=Lower Tar Springs Formation); Chesterian Series. *Paraconularia chesterensis.*

56 A. S. Horowitz. Spoil heaps from Mulzer Brother Quarry, north and south of county road, approximately 1.5 km south of junction of Indiana Highways 145 and 164 and approximately 4 km north of Eckerty and .4 km east of Indiana Highway 145, SW¼, SE¼ Sec.10, T2S, R2W, Crawford County, Indiana, Taswell 7.5′ Quadrangle. Glen Dean Limestone; Chesterian Series. *Paraconularia chesterensis.*

57 A. S. Horowitz et al., 1956–1982. Railroad cuts on west side of Baltimore and Ohio Railroad spur leading to National Gypsum Company quarry, near Shoals, SW¼, NE¼ Sec. 28, T3N R3W, Martin County, Indiana, Huron 7.5′ Quadrangle. "Golconda Formation" (=Indian Springs Member of the Big Clifty Formation); Chesterian Series. *Paraconularia chesterensis.*

58 A. C. Brookley and T. G. Perry, 1954. Debris from abandoned Lutgring Quarry, 9.6 km east of Branchville, NW¼, SW¼ Sec.18, T1S, R1W, Perry County, Indiana, Branchville 7.5′ Quadrangle. "Glen Dean Limestone" (=Lower Tar Springs Formation); Chesterian Series. *Paraconularia chesterensis.*

59 Haines. Washington County, Indiana. Formation unknown; probably Chesterian Series. *Paraconularia chesterensis.*

60 J. Below, 1965. Dam site 4.8–6.4 km north off Route 46, 4.8 km east of Gnaw Bone, Indiana. Borden Group; Osagian Series? *Paraconularia byblis.*

IOWA

61 W. F. Gurley. Le Grand, Iowa. Formation unknown; Kinderhookian Series. *Conularia subcarbonaria, Paraconularia blairi.*

62 C. A. White? Burlington, Iowa. English River Sandstone of the Kinderhook Group; Kinderhookian Series. *Paraconularia byblis.*

63 C. A. White? Burlington, Iowa. "Upper Division of the Burlington Limestone"; probably Osagian Series. *Paraconularia subulata.*

64 Anonymous. Iowa City, Iowa. Cedar Valley Limestone; Chautauquan Series. *Conularia subcarbonaria.*

65 Anonymous. Probably Iowa City area, Iowa. Probably Cedar Valley Limestone; Chautauquan Series. *Conularia subcarbonaria.*

66 Anonymous. Burlington, Iowa. Burlington Limestone; Osagean Series. *Paraconularia byblis.*

67 Fenton. Southwest of Waverly, Iowa. Cedar Valley Limestone, lower part; Osagean Series. *Conularia subcarbonaria.*

68 Anonymous. Burlington, Iowa. Burlington Limestone; Osagean Series. *Conularia subcarbonaria.*

69 Anonymous. Keokuk, Iowa. Keokuk Formation; Osagean Series. *Paraconularia missouriensis.*

70 S. Weller? Keokuk, Iowa. Keokuk Limestone, "bed 11"; Osagean Series. *Paraconularia chesterensis.*

KENTUCKY

71 C. E. Mason, 1984. Outcrops along Interstate 64, 8.2 km east of the junction with Kentucky Route 32, near Morehead, Rowan County, Kentucky. Float from lower few meters of Nancy Member of Borden Formation; Osagean Series. *Conularia multicostata, Paraconularia byblis.*

72 C. E. Mason, T. M. Stanley, and L. E. Babcock, 1984. Nancy Member of Borden Formation; phosphate pebble bed about 1 m above top of "dysaerobic fauna"; Osagean Series. Spillway to Cave Run Lake, Daniel Boone National Forest, Bath County, Kentucky, Salt Lake 7.5′ Quadrangle. *Conularia multicostata, Paraconularia byblis, P. subulata.*

73 Anonymous. Natural Bridge, Kentucky. Borden Formation, probably Nancy Member (*fide* F. R. Ettensohn, written communication, 1985); Osagean Series. *Conularia multicostata.*

74 Anonymous. Marion County, Kentucky. Borden Formation?; Osagean Series? *Paraconularia byblis.*

75 Anonymous. Lebanon, Kentucky. "Waverly Formation" (=Borden Group?); probably Osagean Series. *Paraconularia subulata.*

76 Anonymous. About 2.5 km east of Lebanon, Kentucky. New Providence Formation; Osagean Series. *Conularia subcarbonaria, Paraconularia byblis.*

77 T. W. Kammer. Kammer location 10885, St. Francis, Kentucky. Nancy Member of the Borden Formation; Osagean Series. *Paraconularia byblis.*

78 T. W. Kammer. Kenwood Hill, Louisville, Kentucky. New Providence Shale Member of the Borden Formation; Osagean Series. *Paraconularia byblis.*

79 Anonymous. Kentucky? Waverly Group equivalent?; Osagean Series? *Conularia multicostata.*

80 U. P. James. Boyle or Marion County, Kentucky. "Waverly Group" (=Borden Group?); probably Osagean Series. *Conularia multicostata.*

81 Anonymous. Knob just south of Louisville, Kentucky. New Providence Formation; ?Osagean Series. *Paraconularia byblis.*

82 G. Robb, pre-1923. Marion County, Kentucky. "Keokuk Formation, Knob Shale" (=Borden Formation?); Osagean Series. *Paraconularia subulata.*

83 Anonymous. Elizabethtown, Kentucky. St. Louis Limestone; Meramecian Series. *Paraconularia missouriensis.*

84 A. S. Horowitz. Pond north of Kentucky Highway 1576, about 2 miles east of Morrilla, Jackson County, Kentucky. Pennington Formation; Chesterian Series. *Paraconularia chesterensis.*

85 A. S. Horowitz. Near Colesburg, Hardin County, Kentucky. Somerset Shale Member of Salem Limestone; Meramecian Series. *Paraconularia chesterensis.*

86 S. Weller, 1920. 5.2 km south of Iola, Kentucky (GK 12). Glen Dean Limestone; Chesterian Series. *Paraconularia chesterensis.*

87 Anonymous. About 1.5 km west of Mongomery Switch, Caldwell County, Kentucky. Claystone bed of upper Chester Formation; Chesterian Series. *Paraconularia chesterensis.*

88 A. S. Horowitz, 1966, etc. Pond above road leading to Pearson Farm glade (road not on topographic map), near junction of road with Kentucky Highway 1576, approximately 3.0 km east of junction of Kentucky Highway 1576 and U.S. Highway

421, approximately 3 km east of Morrill, Jackson County, Kentucky, Big Hill 7.5′ Quadrangle. Lower part of Pennington Formation, just above top of Bangor Limestone; Chesterian Series. *Paraconularia chesterensis.*

89 A. S. Horowitz, 1969. Roy Norton Farm, glades on north, west and south slopes of tributaries on north side of Broad Run, 50–100 m south of Kentucky Highway 434, approximately 2.6 km west-southwest of Colesburg, Hardin County, Kentucky, Colesburg 7.5′ Quadrangle. Somerset Shale Member of the Salem Limestone; Chesterian Series. *Paraconularia chesterensis.*

MAINE

90 Anonymous. Presque Isle stream, Chapman Plantation, Maine. Chapman Sandstone; series unknown, Devonian System. *Conularia* cf. *C. undulata.*

MARYLAND

91 F. M. Swartz. West Maryland Railroad tracks, Corrigansville, Maryland. Upper part of the Shriver Chert; Ulsterian Series. *Conularia undulata.*

MICHIGAN

92 Anonymous. Alpena, Michigan. Alpena Limestone; Erian Series. *Paraconularia alpenensis.*

93 E. W. Hard. U.S. Gypsum Company Quarry, Sec. 27, T27N, R7E, near Alabaster, Michigan. Michigan Formation, gray gypsiferous limestone bed 1.3 m below 5.3 m thick bed of mottled white gypsum; Osagean Series. *Paraconularia yochelsoni.*

MISSOURI

94 Sampson; Faber. Sedalia, Missouri. Chouteau Limestone; Kinderhookian Series. *Paraconularia blairi, P. missouriensis.*

95 J. S. Williams, 1930? Easley, Missouri. Chouteau Limestone; Kinderhookian Series. *Paraconularia blairi.*

96 E. B. Branson. Providence, Missouri. Chouteau Limestone; Kinderhookian Series. *Paraconularia blairi.*

97 E. B. Branson, 1930. Providence, Missouri. Couteau Limestone; Kinderhookian Series. *Paraconularia blairi.*

98 Anonymous. Pettis County, Missouri. Chouteau Limestone; Kinderhookian Series. *Paraconularia blairi.*

99 E. B. Branson. Browns, Missouri. Chouteau Limestone; Kinderhookian Series. No conulariids identified; ?priapulid worm, "*Conularia*" *tenuicostata.*

100 W. F. E. Gurley. Boonville, Missouri. Keokuk Limestone; Osagean Series. *Paraconularia missouriensis.*

101 Anonymous. Carthage, Missouri. Formation unknown; Meramecian Series. *Conularia subcarbonaria.*

102 Van Horne. Foot of La Beaume Street, St. Louis, Missouri. St. Louis Limestone; Meramecian Series. *Paraconularia blairi, P. chesterensis.*

103 Anonymous. Kansas City, Missouri. "Coal Measures"; probably Osagean or Meramecian Series. *Paraconularia missouriensis.*

104 Anonymous. Carthage, Missouri. Keokuk Limestone; Osagean-Meramecian Series. *Paraconularia chesterensis.*

105 Anonymous. Little Rock, St. Genevieve County, Missouri. St. Louis Limestone; Meramecian Series. *Paraconularia blairi.*

MONTANA

106 R. Lund et al., 1978–1984. Potter's Creek Dome, approximately 50 km southeast of Lewistown, Fergus County, Montana. Bear Gulch Limestone of Heath Formation; Chesterian Series. *Paraconularia subulata.*

107 W. H. Easton? Delpine, Meagher County, Montana. Cameron Creek Shale of the Big Snowy Group; Chesterian Series. *Paraconularia subulata.*

NEVADA

108 Merriam. Simpson Park Range, Nevada. Rabbit Hill Limestone; Ulsterian Series. *Conularia* sp.

109 A. J. Boucot, 1984. West face of Red Hill, Eureka County, Nevada. "Fish bed" of the Denay Limestone; Senecan Series. *Conularia recurvatus.*

110 C. D. Walcott. Eureka District, Nevada. Formation and series unknown; probably Chesterian Series. *Paraconularia chesterensis.*

NEW JERSEY

111 D. Parris and K. Cruikshank, 1980. On Weider Road, near County Road 521, Montague Township, Sussex County, New Jersey. Esopus Formation; Ulsterian Series. *Reticulaconularia sussexensis.*

112 H. Herpers. Montague, Sussex County, New Jersey. Esopus Formation; Ulsterian Series. *Reticulaconularia sussexensis.*

113 H. Herpers, 1948. Millville, Montague Township, Sussex County, New Jersey. Esopus Formation; Ulsterian Series. *Reticulaconularia sussexensis.*

114 D. Parris, K. Cruikshank et al., 1984. 1.7 km southwest of Wallpack Centre, roadcut across from Batteli's Campground, Wallpack Township, Sussex County, New Jersey. Port Ewen Formation; Ulsterian Series. *Conularia pyramidalis.*

NEW YORK

115 R. M. Fulle. First Esopus outcrop south-southeast of Hurley, on left fork of road, about 1.6 km from Hurley, Ulster County, New York. Esopus Formation; Ulsterian Series. *Conularia ulsterensis.*

116 Anonymous. Schoharie, New York. New Scotland Limestone; Ulsterian Series. *Conularia pyramidalis.*

117 Anonymous. Clarkesville, Schoharie County, New York. "Lower Helderberg Group" (=New Scotland Limestone); Ulsterian Series. *Conularia pyramidalis.*

118 Anonymous. Probably Clarksville area, Schoharie County, New York. Helderberg Group?, possibly New Scotland Limestone; Ulsterian Series. *Conularia pyramidalis.*

119 Anonymous. NYSM locality 2969, near Helderberg, New York. Manlius Limestone; Ulsterian Series. *Conularia pyramidalis.*

120 Anonymous. Countryman's Hill, New Salem, New York. Coeymans Limestone or New Scotland Limestone; Ulsterian Series. *Conularia pyramidalis.*

121 Anonymous. Knox, Albany County, New York. Oriskany Sandstone; Ulsterian Series. *Conularia desiderata.*

122 Anonymous. Schoharie, New York. Oriskany Sandstone; Ulsterian Series. *Conularia pyramidalis.*

123 F. M. Swartz. Clarksville, New York. "Lower Helderberg Group," probably New Scotland Limestone; Ulsterian Series. *Conularia pyramidalis.*

124 Anonymous. NYSM location 2, about 2 km south of Bridgewater, New York. Marcellus Shale; Erian Series. *Conularia desiderata.*

125 Anonymous. Bridgewater, New York. Marcellus Shale; Erian Series. *Conularia desiderata.*

126. Anonymous. Probably from near Bridgewater, New York. Probably from Marcellus Shale; Erian Series. *Conularia desiderata.*

127 Anonymous. Vicinity of Hamilton, New York. Lower part of Hamilton Group; Erian Series. *Conularia desiderata.*

128 Anonymous. Morrisville, New York. Hamilton Group, probably Solsville Member of the Marcellus Formation; Erian Series. *Conularia undulata.*

129 Anonymous. About 1.2 km northwest of Solsville, Madison County, New York. Hamilton Group; Erian Series. *Conularia undulata.*

130 P. Zell, 1982. Swamp Road quarry, near Morrisville, New York, Morrisville 7.5′ Quadrangle. Marcellus Formation; Erian Series. *Conularia pyramidalis.*

131 L. E. Babcock, J. T. Hannibal, and R. M. Feldmann, 1984. Borrow pit on east side of Swamp Road, 4.2 km north of Morrisville, New York, Morrisville 7.5′ Quadrangle. Solsville Member of the Marcellus Formation; Erian Series. *Conularia pyramidalis.*

132 Anonymous. Schoharie County, New York. Hamilton Group, possibly Schoharie Formation; Erian Series. *Conularia desiderata.*

133 M. Kopf. 4 km east of Alexander, New York. Centerfield Limestone Member, Ludlowville Formation; Erian Series. *Conularia desiderata.*

134 I. H. Reimann. Spring Creek, Alden, New York. Ledyard Shale Member of Ludlowville Formation; Erian Series. *Conularia desiderata.*

135 G. J. Kloc, 1983. Lake Erie shore, south of the Wanakah Water Plant, Wanakah, Erie County, New York, N42°44′50″ W78°54′13″. *Nautilus* Bed of the Wanakah Shale Member of the Ludlowville Formation; Erian Series. *Conularia desiderata.*

136 Anonymous. Genesee Valley, New York. Hamilton Group; Erian Series. *Conularia undulata.*

137 Anonymous. Norton's Landing, Cayuga Lake, New York. Hamilton Group, possibly King Ferry Shale Member of the Ludlowville Formation; Erian Series. *Conularia undulata.*

138 Anonymous. NYSM location 428, Shurger's Glen, near Norton's Landing, Cayuga Lake, New York. Hamilton Group; Erian Series. *Conularia undulata.*

139 Anonymous. NYSM location 437, Shurger's Glen, near Norton's Landing, Cayuga Lake, New York. Hamilton Group; Erian Series. *Conularia* sp.

140 G. C. Baird, ca. 1980; L. E. Babcock, 1983. Banks and bed of Barnum Creek, below high falls 0.4 km west (upstream) from New York Route 89 overpass, Sheldrake Quadrangle, New York. Barnum Creek Bed of the King Ferry Shale Member of the Ludlowville Formation, approximately 10 m above top of the *Pleurodictyum* zone; Erian Series. *Conularia undulata.*

141 G. C. Baird, ca. 1980. Bed of Sheldrake Creek, below high falls 0.48 km northeast (downstream) from New York 89 overpass, Sheldrake Quadrangle, Seneca County, New York. 2 m below Barnum Creek Bed, in the King Ferry Shale Member of Ludlowville Formation; Erian Series. *Conularia undulata.*

142 G. A. Cooper, ca. 1930. Hamilton, New York, Cooper location 8Qa. Upper part of Pompey Formation; Erian Series. *Conularia desiderata.*

143 Anonymous. NYSM location 558, Norwich, Chenango County, New York. Hamilton Group; Erian Series. *Conularia undulata.*

144 Anonymous. NYSM location 611, Schoharie County, New York. Hamilton Group; Erian Series. *Conularia desiderata.*

145 Anonymous. Near Cazenovia, New York. Hamilton Group; Erian Series. *Conularia undulata.*

146 Anonymous. Cazenovia, New York. Hamilton Group, possibly Moscow Formation; Erian Series. *Conularia desiderata, C. undulata.*

147 P. Zell, 1983. Thompson Hill Road quarry, near Earlville, New York, Earlville 7.5′ Quadrangle. Moscow Formation; Erian Series. *Conularia undulata.*

148 R. M. Linsley; L. E. Babcock, J. T. Hannibal, and R. M. Feldmann, 1984. "Earlville trilobite quarry," off Morris Road, near Morrisville, New York, Earlville 7.5′ Quadrangle. Upper part of Moscow Formation; Erian Series. *Conularia undulata.*

149 Anonymous. Folsomdale, New York. Rhinestreet Shale; Senecan Series. *Conularia congregata?*

150 Anonymous. Ithaca, New York. Ithaca Formation; Senecan Series. *Conularia congregata.*

151 Anonymous. NYSM location 347, Ithaca, New York. "Chemung Group"; Senecan Series. *Conularia* sp.

152 Anonymous. NYSM location 390, west side of Cayuga Lake inlet, New York. Ithaca Shale; Senecan Series. *Conularia congregata.*

153 Anonymous. NYSM location 392, 1.5 km southeast of Ithaca, New York. Ithaca Group; Senecan Series. *Conularia congregata.*

154 J. W. Hall and G. B. Simpson, 1870. NYSM location 425, Ithaca, New York. Ithaca Shale, lower part of formation; Senecan Series. *Conularia congregata.*

155 Anonymous. NYSM location 514, Catskill Turnpike, 3–4.5 km east of Stamford, Delaware County, New York. Ithaca Group; Senecan Series. *Conularia congregata.*

156 J. W. Hall and C. Van Deloo, 1866. "Mr. Cornell's Quarry," 1.5 km northeast of Ithaca; also from Cemetary quarry and Cascadilla Creek, Ithaca, New York. Ithaca Shale; Senecan Series. *Conularia congregata.*

157 D. D. Luther, 1900. NYSM locality 2439, West Hill, near Naples, New York. "Naples Group"; Senecan Series. *Conularia congregata.*

158 Anonymous. South Hill, Ithaca, New York. Ithaca Shale; Senecan Series. *Conularia congregata.*

159 P. Zell, 1982–1983. Collins Hill Road quarry, near Sherburne, New York, Sherburne 7.5′ Quadrangle. Hamilton Group; formation unknown; probably Senecan Series. *Conularia congregata.*

160 L. E. Babcock, E. L. Yochelson, and W. T. Kirchgasser, 1982. Big Sister Creek, Angola, Erie County, New York. Float in Angola Shale; Chautauquan Series. *Conularia* cf. *C. congregata.*

161 E. B. Hall. E. B. Hall locality I, Wellsville, New York. Wellsville Formation; Chautauquan Series. *Paraconularia wellsvillia.*

162 E. B. Hall. E. B. Hall locality XVIII, Almond, New York. Wellsville Formation; Chautauquan Series. *Paraconularia wellsvillia.*

NOVA SCOTIA

163 Anonymous. Cape Breton, Nova Scotia. Lower Windsor Group; Osagian-Chesterian Series. *Paraconularia planicostata.*

164 W. Dawson. Irish Cove, Cape Breton, Nova Scotia. "Lower Carboniferous" limestone, probably Windsor Group; Osagian-Chesterian Series. *Paraconularia planicostata.*

165 Anonymous. Windsor, Nova Scotia. Lower Windsor Group; Osagian-Chesterian Series. *Paraconularia planicostata.*

166 D. G. Kelley, 1954. GSC location 24841, about 100 m east of corner of Route 5 and Buckwheat Road, Nyonza, Cape Breton Island, Nova Scotia. Lower Windsor Group; Osagian-Chesterian Series. *Paraconularia planicostata.*

167 D. G. Kelley, 1954. GSC location 24844, limestone at bridge on Lewis Mountain Road, 0.8 km from Route 19, Cape Breton Island, Nova Scotia. Lower? part of Windsor Group; Osagian-Chesterian Series. *Paraconularia planicostata.*

168 Anonymous. Nova Scotia. Lower Windsor Group; Osagian-Chesterian Series. *Paraconularia planicostata.*

169 Anonymous. Cape Breton, Nova Scotia. Windsor Group; Osagian-Chesterian Series. *Paraconularia planicostata.*

170 M. J. Copeland, 1962. Shore of Bros d'Or Lake, Irish Cove, Cape Breton, Nova Scotia. Windsor Group; Osagian-Chesterian Series. *Paraconularia planicostata.*

171 Anonymous. Brookfield, Colchester County, Nova Scotia. Lower Windsor Group; Osagian-Chesterian Series. *Paraconularia planicostata.*

172 Anonymous. Harts County, Nova Scotia. Basal Windsor Group; Osagian-Chesterian Series. *Paraconularia planicostata.*

173 Anonymous. Maxner Point, Nova Scotia. Probably lower part of Windsor Formation; Osagian-Chesterian Series. *Paraconularia planicostata.*

OHIO

174 Anonymous. Delaware, Ohio. "Corniferous Group," probably Delaware Limestone; Ulsterian Series. *Conularia elegantula.*

175 G. Meszaros, pre-1982. Rathbone, Ohio. Columbus Limestone; Ulsterian Series. *Conularia elegantula.*

176 Hyatt Brothers. Dublin, Franklin County, Ohio. Columbus or Delaware Limestone; Ulsterian Series. *Conularia elegantula.*

177 Anonymous. Quarry 4 km southeast of Sylvania, Ohio. Silica Shale; Erian Series. *Conularia* sp.

178 G. Meszaros, pre-1982. Leroy, Ohio. Chagrin Shale; Chautauquan Series. *Conularia multicostata, Paraconularia chagrinensis.*

179 E. Roeser, 1978. Float along Mill Creek, at and near Camp Koinonia, Lake and Ashtabula counties, Ohio, north and south of Ross Road bridge. Chagrin Shale; Chautauquan Series. *Paraconularia chagrinensis.*

180 D. Strock, 1985? Along Mill Creek, from Hidden Valley Park to the church camp, Lake County, Ohio. Chagrin Shale; Chautauquan Series. *Paraconularia chagrinensis.*

181 C. Talerico, 1984; L. E. Babcock et al., 1984. Float along Mill Creek, between Ross Road bridge and small dam upstream of Ross Road, Ashtabula County, New York. Chagrin Shale; Chautauquan Series. *Paraconularia chagrinensis.*

182 T. Stanley, 1984. Mill Creek, within 165 m downstream (north) of Ross Road bridge, Lake and Ashtabula counties, Ohio. Chagrin Shale; Chautauquan Series. *Paraconularia chagrinensis.*

183 M. E. Williams, 1981; S. McKenzie, pre-1982. Float along Mill Creek, Ashtabula County, Ohio. Chagrin Shale; Chautauquan Series. *Paraconularia chagrinensis.*

184 M. E. Williams, 1981; J. Hannibal et al., 1985. Stebbins Gulch, Holden Arboretum, Geauga County, Ohio. Contact between the Chagrin Shale and the Cleveland Shale Member of the Ohio Formation; Chautauquan Series. *Paraconularia chagrinensis.*

185 A. J. Weiss, 1984. Landfill on north side of Ohio Route 82, approximately 1.2 km west of I-77 interchange, Broadview Heights, Ohio. Cuyahoga Formation, Meadville Shale Member; Kinderhookian Series. *Paraconularia byblis, P. subulata.*

186 J. Hall? Alexander, Licking County, Ohio. "Berea Shale" (=Sunbury Shale Submember, Orangeville Member, Cuyahoga Formation); Kinderhookian Series. *Paraconularia subulata.*

187 Herrick? Alexander, Licking County, Ohio. "Berea Shale" (=Sunbury Submember of the Orangeville Member of the Cuyahoga Formation?); Kinderhookian Series. *Paraconularia subulata.*

188 L. E. Babcock, 1984. Sunbury Shale Submember of the Orangeville Member of the Cuyahoga Formation; 1–3 cm thick silty zone with abundant pyrite at Sunbury-

Berea Sandstone contact; Kinderhookian Series. Quarry Rock picnic area, north of Chagrin River, South Chagrin Reservation, east of Solon Road, Bentleyville, Cuyahoga County, Ohio. *Paraconularia subulata.*

189 M. Ciccarone, 1984. Sunbury Shale Submember of the Orangeville Member of the Cuyahoga Formation; Kinderhookian Series. Quarry Rock picnic area, north of Chagrin River, South Chagrin Reservation, east of Solon Road, Bentleyville, Cuyahoga County, Ohio. *Paraconularia subulata.*

190 L. E. Babcock, 1984. Sunbury Shale Submember of the Orangeville Member of the Cuyahoga Formation; approximately 1 m above the top of the Berea Sandstone; Kinderhookian Series. Quarry Rock picnic area, north of Chagrin River, South Chagrin Reservation, east of Solon Road, Bentleyville, Cuyahoga County, Ohio. *Paraconularia subulata.*

191 G. Meszaros, pre-1982. Weymouth, Ohio. Meadville Shale Member of Cuyahoga Formation; Kinderhookian Series. *Paraconularia subulata.*

192 J. Burke, W. J. Hlavin et al., 1967. North Branch of Rocky River near bridge at junction of Bagdad and Hood Roads, Bagdad, Ohio. Meadville Shale Member of Cuyahoga Formation; Kinderhookian Series. *Paraconularia subulata.*

193 Anonymous. Probably northeast Ohio. Probably Meadville Member of the Cuyahoga Formation; Kinderhookian Series? *Conularia multicostata.*

194 Anonymous. Voorhes Cemetary outcrop, west of Lodi, Ohio. Meadville Shale Member of Cuyahoga Formation; Kinderhookian Series. *Paraconularia subulata.*

195 R. W. Scott. Lodi, Medina County, Ohio. Cuyahoga Formation, probably Meadville Member; Kinderhookian Series. *Paraconularia byblis.*

196 G. Meszaros, pre-1982. Lodi, Ohio. Meadville Shale Member of the Cuyahoga Formation; Kinderhookian Series. *Conularia multicostata, Paraconularia subulata.*

197 R. Fisher. Creeks in and near Lodi, Medina County, Ohio. Meadville Member of the Cuyahoga Formation; Kinderhookian Series. *Conularia multicostata, Paraconularia subulata.*

198 R. Segedi et al., 1974. Streambed off Pawnee Road, about 200 m south of U.S. Route 224, Lodi, Medina County, Ohio. Meadville Shale Member of Cuyahoga Formation; Kinderhookian Series. *Conularia multicostata, Paraconularia subulata.*

199 R. Segedi. About 50 m east of bridge on Pawnee Road, just south of U.S. Route 224, Lodi, Medina County, Ohio. Float and *in situ* specimens from the Meadville Member of the Cuyahoga Formation; Kinderhookian Series. *Conularia multicostata, Paraconularia subulata.*

200 L. E. Babcock, 1985. West fork of East Branch of Black River, south of Route 224, near intersection with Pawnee Road, Homer Township, about 3 km west of center of Lodi, Medina County, Ohio, Lodi 7.5′ Quadrangle. Meadville Shale Member of Cuyahoga Formation; collected *in situ* in lowermost bed of siderite concretions upstream of Pawnee Road bridge; Kinderhookian Series. *Conularia multicostata, Paraconularia subulata.*

201 A. H. Worthen. Richfield, Ohio. "Kinderhook Formation" (=Cuyahoga Formation, probably Meadville Member); Kinderhookian Series. *Paraconularia subulata.*

202 Anonymous. NYSM location 110, Richfield, Summit County, Ohio. "Waverly Group" (probably Meadville Member of the Cuyahoga Formation); Kinderhookian Series. *Paraconularia subulata.*

203 Anonymous. Richfield, Ohio. Waverly Group, probably Meadville Member of the Cuyahoga Formation; Kinderhookian Series. *Paraconularia subulata.*

204 L. E. Babcock, 1984. Float in Meadville Member of the Cuyahoga Formation; Kinderhookian Series. Tributary to the Cuyahoga River, Furnace Run Metro Park, west off Route 21, about 1.5 km south of Summit County-Cuyahoga County boundary, Summit County, Ohio. *Paraconularia* cf. *P. byblis.*

205 Anonymous. Richfield, Ohio. "Waverly Group" (=Meadville Member of the Cuy-

ahoga Formation); Kinderhookian or Osagean Series. *Conularia multicostata, Paraconularia subulata.*

206 A. Winchell. Cuyahoga River gorge, Cuyahoga Falls, Summit County, Ohio. "Near top of the Waverly Group, water limestone below conglomerate" (=Cuyahoga Formation, possibly Meadville Member); Kinderhookian-Osagean Series. *Paraconularia subulata.*

207 J. Weiss, 1961. Gravel in Akron, Ohio area? Possibly Cuyahoga Formation; Kinderhookian or Osagian Series. *Paraconularia subulata.*

208 Anonymous. "Rocky River bed," probably Cuyahoga Formation; Kinderhookian or Osagean Series. Medina, Ohio. *Paraconularia subulata.*

209 Anonymous. Bagdad, Ohio. Probably Cuyahoga Formation; Kinderhookian or Osagean Series. *Conularia multicostata.*

210 C. L. Herrick. Near Lyon Falls, Richland County, Ohio. 18–24 m above "Conglomerate II": Osagean Series. *Paraconularia byblis.*

211 W. P. Cooper, 1890; Anonymous. Portsmouth, Ohio. Waverly Group, probably the Cuyahoga Formation; Osagean Series. *Paraconularia missouriensis.*

212 Anonymous. Wooster, Wayne County, Ohio. "Near the top of the Waverly Group" (=Wooster Member of the Cuyahoga Formation); Osagean Series. *Paraconularia subulata.*

213 Anonymous. Wooster, Wayne County, Ohio. Near top of Waverly Group, possibly the Wooster Member of Cuyahoga Formation; Osagean Series. *Paraconularia subulata.*

214 G. Meszaros, pre-1982. Wooster, Ohio. Cuyahoga Formation, Wooster Shale Member; Osagean Series. *Conularia multicostata, Paraconularia subulata.*

215 H. E. Wilson. 7.2 km south of Loudonville, Ashland County, Ohio. Probably Wooster Member, Cuyahoga Formation; Osagean Series. *Paraconularia subulata.*

216 F. Plutte, 1964. About 4.5 km south of Loudonville, Ashland County, Ohio. Wooster Member of the Cuyahoga Formation; Osagean Series. *Paraconularia subulata.*

217 L. E. Babcock, 1984. East facing borrow pit on west side of Route 3, 0.9 km north of junction with Route 97, just south of Loudonville, Ashland County, Ohio, Greer 7.5′ Quadrangle. Wooster Member of the Cuyahoga Formation; Osagean Series. *Conularia multicostata, Paraconularia subulata.*

218 J. Hall? Water works in Newark, Ohio. Waverly Group, "base of Division III"; probably Cuyahoga Formation; probably Osagean Series. *Conularia multicostata.*

219 G. Meszaros, pre-1982. Rushville, Ohio. Allensville Member of Logan Formation; Osagian Series. *Paraconularia byblis.*

220 Bowsher, Savage, and Allen, 1952. Approximately 300 m of elevation below Old Maid's Kitchen, in gully about 110 m west of Ohio Edison Dam on north side of Cuyahoga Gorge, Akron, Summit County, Ohio. Float in Meadville Shale Member of the Cuyahoga Formation; Kinderhookian Series. *Paraconularia subulata.*

221 Anonymous. Ohio. Possibly Cuyahoga Formation; Mississippian, possibly Osagean. *Conularia multicostata, Paraconularia subulata.*

222 Anonymous. Ohio. "Lower Waverly Group," Cuyahoga Formation; Osagean Series. *Paraconularia subulata.*

223 Stout and Girty, 1897. Dixon's Mill, on the Little Scioto River, about 5 km northeast of Sciotoville, Scioto County, Ohio. "Waverly Group," probably Wooster Member of Cuyahoga Formation; Osagian Series. *Conularia multicostata, Paraconularia byblis, P. missouriensis.*

224 Carman, Stout, and Carney. Sciotoville, Ohio. Upper part of Cuyahoga Formation, 16.5–23 m below base of the Logan Formation; Osagian Series. *Paraconularia byblis?, P. missouriensis.*

225 F. B. Meek; Anonymous. Sciotoville, Ohio. "Waverly Group," probably Cuyahoga Formation; Osagean Series. *Conularia multicostata.*

226 E. B. Andrews, 1869. Sciotoville, Ohio. Uppermost Cuyahoga Formation, Black

Hand Member or lowermost Logan Formation, Byer Member; Osagean Series. *Paraconularia missouriensis.*

227 G. Meszaros, pre-1982. Sciotoville, Ohio. Portsmouth Shale; Osagean Series. *Conularia multicostata, Paraconularia missouriensis.*

228 Cooper. James Hall's location 385, Moot's Run, Licking County, Ohio. Cuyahoga Formation, probably Wooster Member; Osagean Series. *Conularia multicostata.*

OKLAHOMA

229 G. A. Cooper et al., 1952. NE¼ Sec. 7 T22N R20E, 5.3 km south of Adair, Mayes County, Oklahoma. Fayetteville Formation; Chesterian Series. *Paraconularia oklahomaensis.*

ONTARIO

230 C. S. 9.6 km west of Cayuga, Ontario. Upper part of Oriskany Sandstone; Ulsterian Series. *Conularia undulata.*

PENNSYLVANIA

231 F. M. Swartz. Near Curtin, Pennsylvania. Shriver Chert; Ulsterian Series. *Conularia ulsterensis.*

232 F. M. Swartz. Intersection of Delaware and New York State Railroad, 0.8 km west of mill of Mimsruk Paper Company Experimental Mills, near Curtin, Pennsylvania. Shriver Chert; 1.05 m below Oriskany Shale; Ulsterian Series. *Conularia* cf. *C. desiderata.*

233 F. M. Swartz, 1937. Float on roadcut on road leading through gap east of Warfordsburg, Pennsylvania. Shriver Formation?; 0.3–1.7 m above conglomeratic sandstone at middle of Shriver-like beds; Ulsterian Series. *Conularia ulsterensis.*

234 F. M. Swartz, 1937. Roadcut along road leading through gap east of Waifordsburg, Pennsylvania. 0.3–1.5 m above conglomeratic sandstone at middle of Shriver-like beds; Ulsterian Series. *Conularia ulsterensis.*

235 F. M. Swartz. Road leading north from Schellsburg, Bedford County, Pennsylvania. Onondaga Shale; Erian Series. *Conularia* cf. *C. desiderata.*

236 S. Albright, 1981; B. White, 1983. Large roadcut on north side of Johnny Bee Road, about 0.2 km north of intersection with road to Dingmans Falls, Delaware Township, Pike County, Pennsylvania. Mahantango Formation, approximately Centerfield biostrome level; Erian Series. *Conularia desiderata, C. ulsterensis, C. undulata.*

237 D. Parris, 1982. Large roadcut on north side of Johnny Bee Road, about 0.2 km north of intersection with road to Dingmans Falls, Delaware Township, Pike County, Pennsylvania. Manhantango Formation; Erian Series. *Conularia undulata.*

238 L. Klensch and J. Valenti, 1981. Roadcut across from Bushkill Country Store, 2 km from U.S. Route 209, Lehman Township, Pike County, Pennsylvania. Mahantango Formation; Erian Series. *Conularia undulata.*

239 L. Decina, 1983. Roadcut on north side of Pennsylvania Route 895, approximately 0.8 km west of Auburn, Schuylkill County, Pennsylvania. Mahantango Formation; Erian Series. *Conularia desiderata.*

240 Anonymous. Huntingdon, Huntingdon County, Pennsylvania. Frame Shale Member of the Mahantango Formation; Erian Series. No conulariids collected; *Hyolithes* sp.

QUEBEC

241 R. B., 1862; Anonymous. Grande Grève, Gaspé, Quebec. Grand Grève Limestone; Ulsterian Series. *Conularia* cf. *C. desiderata, C.* cf. *C. undulata.*

242 Anonymous. High Falls, Dartmouth River, Gaspé Peninsula. Grande Grève Limestone; Ulsterian Series. *Reticulaconularia penouili.*

243 Anonymous. Little Gaspé, Quebec. Grande Grève Limestone; Ulsterian Series. *Conularia* cf. *C. desiderata.*

244 Anonymous. Percé Rock, Gaspé, Quebec. Grande Grève Limestone; Ulsterian Series. *Conularia tuzoi.*

245. Cape Barre, Quebec. "Cape Barre beds" (=Cape Bon Ami Formation); Ulsterian Series. *Conularia* cf. *C. desiderata.*

246 Anonymous. Gaspé Peninsula, Quebec. Float block of limestone, probably Grande Grève Limestone; Ulsterian Series. *Reticulaconularia penouili.*

247 J. W. Beede? Magdelen Islands, Quebec. Formation and series unknown; Mississippian Subsystem. *Paraconularia sorrocula.*

248 J. W. Beede? Cape le Tron, Grindstone Island, Magdelen Islands, Quebec. Formation and series unknown; Mississippian Subsystem. *Paraconularia planicostata.*

SOUTH DAKOTA

249 L. E. Babcock, 1984. "Slagpile section," overlooking bridge of Route 14A over Whitewood Creek, SW ¼ Sec. 13, T5N R3E, Deadwood, Lawrence County, South Dakota, Deadwood 7.5′ Quadrangle. Englewood Formation, dolostone about 20 cm above top of shale-dolostone transitional zone. *Paraconularia* sp.

TENNESSEE

250 J. M. Safford. Hickman County, Tennessee. "Waverly Group"; Kinderhookian or Osagean Series. *Paraconularia byblis*?

251 A. S. Horowitz, 1966, etc. Roadcuts on both sides of Interstate Highway 40, 8.3 km west of junction of Interstate Highway 40 and U.S. Highway 70 at Monterey, Putnam County, Tennessee, Monterey 7.5′ Quadrangle. Top of Pennington Formation; "Kinkaid level," zone of *Pterocrinus tridecibrachiatus* Gutschick, just below a quartz pebble conglomerate of the Pennsylvanian System; Chesterian Series. *Paraconularia chesterensis.*

UTAH

252 C. D. Walcott? Divide Bet, American Fork and Snake Creek, Wasatch Mountains, Utah, Kinderhookian or Osagean Series. *Paraconularia chesterensis*?

WISCONSIN

253 E. E. Teller. Milwaukee, Wisconsin. Probably Milwaukee Formation; Erian Series. *Conularia milwaukeensis.*

254 E. E. Teller? Estabrook Park, Milwaukee, Wisconsin. Lindwurm Member of the Milwaukee Formation; Erian Series. *Conularia milwaukeensis.*

255 E. E. Teller. Milwaukee Cement Quarry, Berthelet, Wisconsin. Milwaukee Formation; Erian Series. *Conularia milwaukeenensis.*

APPENDIX B—MEASUREMENTS

The following values are measurements of selected type and other conulariid specimens considered representative of each taxon treated herein and in Part A. Species are listed alphabetically according to species as they are recognized herein. Measurements are listed in columns across each page. In cases where replicate measurements have been taken at varying distances from the hypothetical apex, they are listed vertically under the appropriate columns. Terms are defined in the "Morphology" section. Abbreviations: L, length, cm; HL, hypothetical length, cm; AAMj, major apical angle, degrees; AAMn, minor apical angle, degrees; N, nodes/mm; RLAMj, ratio of right superior : left superior : abutting rods per ten on major face; RLAMn, ratio of right superior : left superior : abutting rods per ten on minor face; D, distance from hypothetical apex at apicad limit of measurement, applicable to values for R and RA; R, rods/cm; RA, rod angle, degrees; h, holotype; plh, plastoholotype; 1, lectotype; n, neotype; p, paratype; pl, paralectotype. Values given in parentheses are approximate; values followed by question marks are accurate, but it is not certain that they have been properly classified as pertaining to either the major or minor face.

Conularia congregata Hall

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
NYSM 3483 1	6.1	9.4	17	12	6	0:0:10	0:0:10	5.5	18	10
								8.0	16	13
NYSM 3483 pl	6.7	10.7	17	14	7	0:0:10	0:0:10	5.5	17	10
								8.5	21	9
NYSM 3483 pl	6.5	10.1	16	14	6	0:0:10	0:0:10	5.0	17	10
								8.5	20	12
NYSM 3483 pl	6.3	9.9	17	13	6	0:0:10	0:0:10	8.0	16	10

Conularia delphiensis (Maroney and Orr)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
IUPC 14470-1 h	2.0	(4.8)	—	—	6	1:1:8	1:1:8	6.0	36	10
IUPC 14470-2 p	2.1	(5.1)	—	—	—	1:0:9	0:1:9	4.5	36	11
IUPC 14470-4 p	2.7	(3.4)	15?	—	—	0:0:10	0:0:10	1.6	42	—
IUPC 14470-6 p	—	—	—	—	7	—	—	—	—	—

Conularia desiderata Hall

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
AMNH 2697 h	1.6	2.3	23	20?	—	0:10:0	0:10:0	3.5	27	15
NYSM 3487	5.8	6.4	27	22	3	1:8:2	1:9:0	5.0	17	12
								7.0	14	7
NYSM 3485	6.2	8.2	16	15	3	2:7:1	3:6:1	3.5	24	9
								6.5	20	10
USNM 395827	0.9	0.9	22	21	—	0:0:10	0:0:10	0.6	41	16

Conularia elegantula Meek

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
AMNH CU 282G h	3.9	6.7	20	17?	6	0:4:6	—	1.0	39	8
								4.0	37	13
CMNH 4584	2.7	3.2	(30?)	—	6	0:6:4?	—	3.5	32	3
CMNH 4648	3.1	(4.5)	—	—	5	—	—	(4.0)	(24)	—

Conularia milwaukeensis Cleland

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
USNM 85988 h	3.1	5.0	15	14	6	0:0:10	0:0:10	6.0	18	5
MPM 20252	4.9	6.0	12	11	6	0:0:10	0:0:10	4.0	21	16
MPM 22974	4.5	4.6	15	13	5	0:0:10	0:0:10	4.0	24	18
								6.0	18	8
								8.0	20	9

Conularia multicostata Meek and Worthen

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
USNM 50157 plh	2.8	6.7	20	18	—	0:0:10	0:0:10	4.5	32	16
UK 6089	6.3	8.5	—	11?	3	—	0:0:10?	9.5	52	12
AMNH 6713	6.5	9.3	23	22	2	0:0:10	0:0:10	5.0	40	17
								8.0	44	9
CM 34533	8.2	11.2	16	15	2	0:0:10	0:0:10	4.0	25	—
								5.5	29	12

Conularia pyramidalis Hall

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
AMNH 33017 1	2.3	3.3	18	17	3	0:0:10	0:0:10	3.0	14	11
								5.5	11	16
								7.5	9	9
NYSM 3490	11.8	19.2	23	17	1	0:0:10	0:0:10	8.0	7	22
								12.0	10	9
								15.0	10	5

Conularia subcarbonaria Meek and Worthen

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
UIPC 10680 h	8.6	11.9	21	19	4	0:0:10	0:0:10	8.0	18	4
FMNH UC 18494	24.5	33.5	10	9	4	0:0:10	0:0:10	18.0	27	5
								25.0	31	6
FMNH UC 6289	7.7	—	—	—	3	0:0:10	0:0:10	—	—	—
FMNH UC 6610	3.1	—	—	—	2	—	—	—	60	—

Conularia tuzoi Clarke

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
NYSM 9404 h	6.7	11.3	(10)	—	—	(0:0:10)	—	6.0	26	9
								9.0	36	10

Conularia ulsterensis Howell

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
PU 42071 h	1.8	2.5	18?	—	7	2:0:8?	—	4.5	45	13
CM 34528	1.9	3.2	17?	—	7	0:0:10?	—	2.2	60	12
								2.8	84	11
CM 34529	1.8	(2.8)	(18)	(15)	6	0:0:10	0:0:10	(2.0)	62	12

Conularia undulata Conrad

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
AMNH 41093 1	10.0	15.5	13	10	6	1:0:9	1:0:9	6.0	21	18
								10.0	20	11
								13.0	27	4
AMNH 5440	8.3	—		(8)	4	—	—	—	30	—
NYSM 3482	10.2	11.8	18	15	5	0:0:10	0:0:10	4.5	17	9
								9.5	24	10
CM 34532	7.5	(18.0)	21	14	5	0:0:10	0:0:10	18.0	32	9

Paraconularia alpenensis Babcock and Feldmann, new species

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
GSC 85060 h	1.5	3.6	21	16	—	2:2:6	4:2:4	3.0	14	9
								4.0	14	10

Paraconularia alternistriata (Shimer)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
GSC 5111 h	0.8	1.9	11	10	0	10:0:0	3:7:0	1.0	28	11

Paraconularia blairi (Miller and Gurley)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
UCGM 3986 1	7.4	11.2	(22)	20	3	6:4:0	3:5:2	5.5	11	8
								8.5	7	9
								11.0	9	15
UMC 4270	3.4	(11.5)	23?	—	3	7:2:1?	—	(16.0)	6	19
UCGM 3985	6.8	(16.0)	—	16	2	—	7:3:1	12.5	6	—
UCGM 3984 pl	9.2	15.5	—	18	3	—	5:4:1	8.0	8	15
								11.0	6	14
								14.0	6	15
AMNH 25056	13.0	19.0	11	10	2	8:1:1	2:6:2	7.0	13	9
								12.5	8	12
								16.0	7	17

Paraconularia byblis (White)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
UMMP 2167 h	6.7	10.0	22	(14)	1	1:4:6	—	6.5	15	12
CMNH 4691	2.8	3.8	26	—	1	1:7:2	—	2.5	28	13
USNM 409489	1.7	2.1	19	14	1	1:6:3	6:2:2	1.0	29	18

Paraconularia chagrinensis Babcock and Feldmann, new species

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
CMNH 6633 h	3.9	4.9	28	21	4	0:9:1	0:9:1	2.0	20	12
								3.0	18	9
								4.2	16	10
CMNH 1622 p	3.4	8.3	—	20?	—	0:7:3	0:8:2	5.0	16	9
CMNH 1818 p	2.0	—	—	—	4	—	—	—	—	—
CMNH 1674 p	4.5	(10.0)	—	—	3	—	—	—	—	—

Paraconularia chesterensis (Worthen)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
ISGS 2489 h	11.7	17.2	14	10	4	4:5:1	4:2:4	7.5	11	10
								10.0	10	9
								14.0	8	11
USNM 50156	2.7	3.9	21	17	5	4:3:3	8:2:2	1.0	25	8
								2.0	20	8
IUPC 17413	9.7	16.6	(14)	—	5	(4:5:1)	—	15.5	7	15
IUPC 11313	12.8	25.5	9	9	4	4:5:1	4:5:1	14.0	6	9
								20.0	5	9
								23.0	6	13
IUPC 6458	9.8	35.5	8	(7)	4	5:2:3	2:6:3	26.0	5	9
								30.0	4	11

Paraconularia missouriensis (Swallow)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
FMNH UC 6639 plh	11.0	14.6	19	—	—	1:9:0	—	6.5	6	9
								9.5	4	6

FMNH UC 6628	11.2	15.5	15	11	2	1:9:0	1:8:1	6.0	6	6
								13.0	5	10
FMNH UC 6627	12.8	19.5	14	11	3	2:8:0	3:7:0	10.0	6	11
								14.5	5	17
								19.0	5	11
AMNH 28692	5.7	13.8	—	10	—	—	9:1:0	10.0	6	8
UMMP 26740	3.6	6.4	21	15	2	3:5:2	4:4:2	4.0	10	9

Paraconularia oklahomaensis Babcock and Feldmann, new species

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
USNM 409801 h	4.4	5.4	19	17	0	4:1:5	2:4:4	2.0	24	12
								4.0	12	13

Paraconularia planicostata (Dawson)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
RM(MU) 2749 h	4.5	7.3	11?	9	0	6:3:1	5:4:1	3.5	19	12
								6.0	13	15
GSC 7715	3.3	4.9	18	14	0	5:4:2	5:3:2	3.0	14	15
GSC 24644	1.6	5.3	13	12	0	3:6:1	5:3:2	3.5	20	12

Paraconularia recurvatus Babcock and Feldmann, new species

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
USNM 409806 h	4.8	7.8	16	15	3	2:5:3	2:4:4	4.0	18	12
								6.0	(26)	8
USNM 409807 p	0.8	—	—	—	2	—	—	—	28	—
USNM 409808 p	1.1	2.6	16	—	3	3:6:1	3:5:2	1.5	26	8
USNM 409809 p	0.7	—	—	—	3	—	—	—	24	—

Paraconularia salinensis (Whiteaves)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
GSC 4292 h	2.6	3.0	(24)	21	4	7:2:1	5:3:2	1.0	24	13
								1.5	23	8

Paraconularia sorrocula (Beede)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
NYSM 9414 h	2.3	2.9	23	—	6	1:7:2	—	0.8	20	11
								1.2	19	14

Paraconularia subulata (Hall)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
AMNH 32404 1	0.6	0.8	21	18	4	5: 2:3	6:1:3	0.5	56	11
FMNH UC 6961	1.6	2.4	18	12	5	0:10:0	3:7:0	1.0	35	18
								1.5	35	11
UIPC 10866	6.6	7.8	—	12	4	—	7:1:2	5.0	8	22
UMMP 2178	0.9	(5.5)	—	—	4	—	—	—	24	(19)
UMMP 245	0.5	1.4	22	(20)	4	0:7:3	6:3:1	1.0	30	11
OC 8309	5.4	12.8	12	10	2	1:8:1	4:5:1	11.0	8	15

Paraconularia wellsvillia Babcock and Feldmann, new species

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
CM 35001 h	5.7	12.5	(14)	(13)	3	1:8:1	5:4:1	8.5	4	26
								10.0	5	31

CM 34502 p	5.8	(12.5)	(18)?	—	3	3:6:1?	—	7.5	9	(24)
								12.0	7	(18)

Paraconularia yochelsoni Babcock and Feldmann, new species

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
UMMP 45499 h	2.2	2.6	20	18	0	5:3:2	10:0:0	0.6	15	18
								1.5	14	17
UUMP 45500 p	2.6	3.1	17	—	0	6:1:2	—	0.6	18	15
								1.5	13	15
UMMP 65509 o	1.3	1.7	15	—	0	8:1:1	—	0.6	18	20

Reticulaconularia penouili (Clarke)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
NYSM 9412 h	4.6	6.7	59	(22)	2	2:5:3	3:5:2	3.0	14	4
								4.5	21	3
								6.0	14	0
GSC 87242	5.5	6.4	—	30?	2	—	5:4:1?	1.3	15	7
								3.3	12	8

Reticulaconularia sussexensis (Herpers)

SPECIMEN NO.	L	HL	AAMj	AAMn	N	RLAMj	RLAMn	D	R	RA
NJSM 10749 h	2.7	3.1	32	26	1	0:2:8	—	2.5	20	11
								3.5	36	8
NJSM 10750 p	1.5	1.8	(27)	24	2	1:2:7	2:1:7	0.6	39	14
								1.5	16	11

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FLORAL MORPHOLOGY AND VASCULAR ANATOMY OF *AMIANTHIUM MUSCAETOXICUM* (WALTER) A. GRAY (LILIACEAE-VERATREAE) WITH NOTES ON DISTRIBUTION AND TAXONOMY

Frederick H. Utech

Abstract

Presentation of pedicel to stigma vasculature of the monotypic *Amianthium muscaetoxicum* as a Veratrean example documents the perigyny, spiral insertion of floral parts and an apocarpous gynoecium which are encountered. Total floral vascularization is derived from three lower pedicel bundles. A spiral series of divisions and fusions in the upper pedicel produces three compound outer tepal and three inner tepal bundles. From the former, outer tepal medians, tepal laterals, stamen and dorsal bundles result, while from the latter, inner tepal medians, tepal laterals and stamen bundles result. Due to perigyny, their formation is above that at which the ventral and ovular supplies are established. The ventral supply is spirally derived from continuing bundles following the formation of the compound inner tepal bundles. Within each septal arm, a compound lateral is associated with a compound ventral and both undergo radial divisions. Opposing lateral and ventral products fuse as the perigynous condition ends and the three carpels are freed. Each carpel has two simple ventrals, two laterals and a dorsal in the upper perigynous zone and two fusion ventrals and a dorsal in the upper freed zone. Neither tepal glands nor nectaries occur in this species. Epidermal cells characterized by homogenous tannins occur in the pedicel, receptacle wall, abaxial tepal surfaces, filaments and freed carpels. Raphides commonly occur in cells along the lower margins of the inner tepals.

Introduction

Amianthium muscaetoxicum (Walter) A. Gray is a monotypic species of eastern North America with centers of distribution in both the Ozark-

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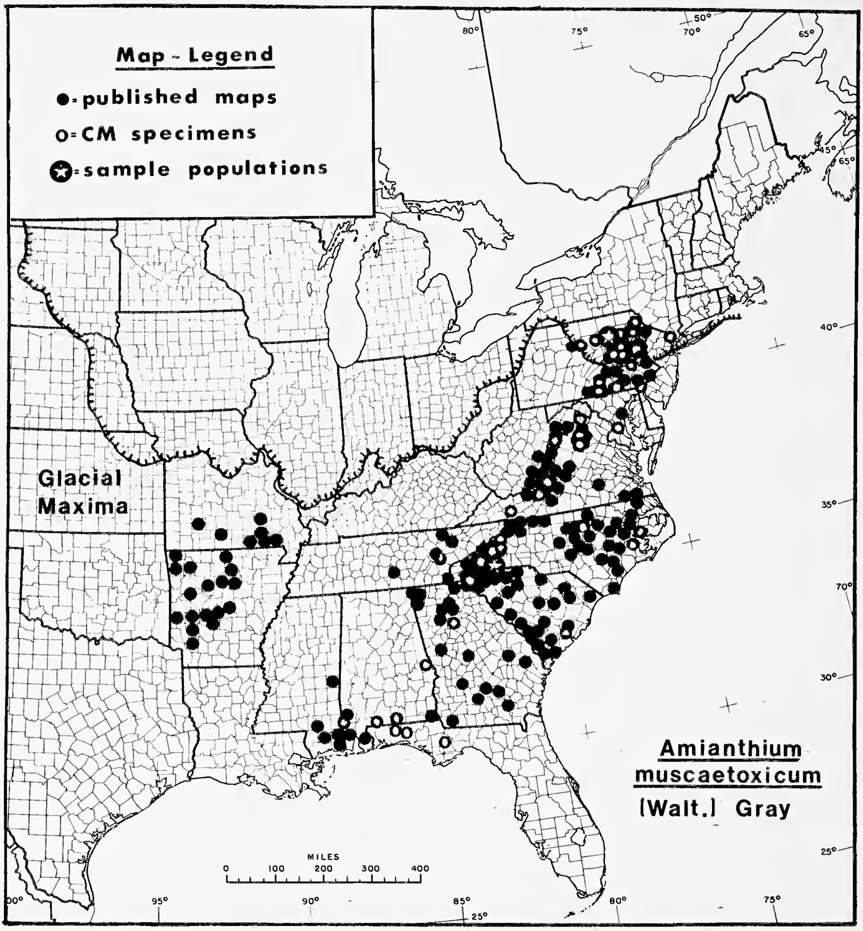


Fig. 1.—Distribution of *Amianthium muscaetoxicum* in eastern United States based on published maps (Steyermark, 1963; Radford et al., 1968; Johnson, 1969; Smith, 1978; Wherry et al., 1979) and collections at Carnegie Museum of Natural History (open circles). Johnson (1969) surveyed 46 herbaria in his southeastern United States treatment of the Liliaceae. Sampled populations are indicated by circled stars.

ian and Appalachian regions (Fig. 1). It occurs in mesic to dry wooded slopes and coastal plain savannas and pinelands. Familial and subfamilial names associated with *A. muscaetoxicum* have changed during the last century, but the tribal association with *Melanthium, Schoenocaulon, Stenanthium, Veratrum* and *Zigadenus* "sensu lato" (including *Toxicoscordion, Anticela, Tracyanthus* and *Oceanoros*) has remained. Bentham and Hooker (1883) included these six genera in the tribe

Veratreae, as did Engler (1889), Krause (1930), Melchior (1964), Thorne (1968), Takhtajan (1969), and Hutchinson (1934, 1959, 1973). Within this tribal grouping, two lines—the *Veratrum-Melanthium* and the *Zigadenus* lines—are generally recognized (Anderson, 1940; Preece, 1956; Zimmerman, 1958; Kupchan et al., 1961; Ambrose, 1975, 1980; Sterling, 1982). *Amianthium* and *Stenanthium* are generally placed somewhere between these two evolutionary lines. Engler (1889) initiated the association of the Veratreae with the subfamily Melanthioideae. This subfamily has been twice segregated as a separate family, the Melanthiaceae (Gates, 1918; Small, 1933; Dahlgren, 1980; Dahlgren and Clifford, 1982; Dahlgren and Rasmussen, 1983; Dahlgren et al., 1985) and the Colchicaceae (Baker, 1879).

Genera in the other tribes of the Englerian Melanthioideae share separate styles and septicidal capsules with the genera in the Veratreae, though the latter possesses unusual extrorse anthers with valvular dehiscence that open into peltate discs (Krause, 1930; Zimmerman, 1958; Kupchan et al., 1961) and usually many bitegmic, basitropic and campylotropous ovules per carpel (Sterling, 1982), except for *Amianthium* which has two, rarely four.

Amianthium of Asa Gray (1837) is a conserved generic name (Farr et al., 1979; Voss, 1983) and its monotypic species, *A. muscaetoxicum* (Walter) A. Gray (1837), has gone under various names since it was first described by Walter in 1788 as *Melanthium muscaetoxicum*. Later synonyms include: *Melanthium laetum* Solander in Aiton (1789), *Melanthium myoctonum* J. F. Gmelin (1796), *Helonias erythrosperma* Michaux (1803), *Helonias laeta* (Solander in Aiton) Kew-Gawler (Curtis, 1805), *Amiantanthus muscaetoxicum* (Walter) Kunth (1843), *Zigadenus muscaetoxicus* (Walter) Regel (1883), and *Chrosperma muscaetoxicum* (Walter) Kuntze (1891). Excluded species of *Amianthium* and their current status include: *A. nuttallii* A. Gray var. alpha (1837) (*Zigadenus nuttallii* A. Gray ex S. Watson), *A. nuttallii* A. Gray var. beta (1837) (*Z. paniculatus* (Nutt.) S. Watson), *A. angustifolium* A. Gray (1837) (*Z. densus* (Desr.) Fernald), *A. leimanthoides* A. Gray (1837) (*Z. leimanthoides* A. Gray), and *A. texanum* (Bush) Gates (1918) (*Z. leimanthoides* A. Gray).

Considerable biological information is implied in this species binomial. *Amianthium* is derived from the Greek *amianthos* for "unspotted" and *anthos* for "flower," an allusion to a major generic character, that is the lack of glands or nectaries on the perianth. The specific name, *muscaetoxicum,* translates literally as "fly poison." In 1883, a note in *Gardeners' Chronicle* "stated that the root, when bruised and mixed with honey, acts as a poison to flies." While the species is commonly known as "fly poison," it has also been known as "crow poison" and "swagger grass" (Muenscher, 1939, 1960). Several poisonous alkaloids are associated with the leaves and underground bulbs of the species and are reported to cause death in cattle and sheep (Pammel, 1911; Marsh et al., 1918; Muenscher, 1939, 1960; Kingsbury, 1964). Amianthine, a steroidal or modified steroidal alkamine alkaloid with a $C_{27}H_{41}O_2N$ formula, has been described from the roots and leaves of *A. muscaetoxicum* as well as jervine and two unidentified ester alkaloids (Neuss, 1953). The latter alkaloids were shown to be responsible for the high toxicity of the species (Neuss, 1953). Although numerous and highly poisonous alkaloids commonly occur throughout the tribe Veratreae, amianthine has only been reported in *Amianthium* (Kupchan et al., 1961; Willaman and Schubert, 1961; Hegnauer, 1963).

Two meiotic chromosome counts of $n = 16$ have been reported for *A. muscaetoxicum*: Ambrose (1975) from Bear Creek, Pennsylvania and Preece (1956) from Big Laurel Gap, Yancey County, North Carolina. Excluding various polyploid multiples, *Melanthium, Veratrum* and *Zigadenus* (=*Zygadenus*; Preece, 1956) all share $n = 16$ (Fedorov, 1969; Moore, 1973; Goldblatt, 1981). It is quite apparent that $x = 8$ is the basic number unifying the Veratreae.

In focusing on both the floral morphology and vascular anatomy of *A. muscaetoxicum* a comparative model of a Veratrean gynoecium will be established in this paper. Similar treatments for the other tribal members of the Veratreae, such as *Melanthium, Stenanthium, Veratrum* and *Zigadenus,* are in preparation and will continue the studies of Buxbaum (1925, 1927), Anderson (1940), El-Hamidi (1952), Ambrose (1975, 1980) and Sterling (1982) on the vascularization of the Veratrean carpel.

MATERIALS AND METHODS

Flowering and fruiting inflorescences of *Amianthium muscaetoxicum* were collected from two different populations—Pennsylvania: Clinton County, Mt. Tableland, ca. 4.5 mi E of Sinnemahoning, 20 July 1979, *Utech 79-241* (CM), and North Carolina: Macon County, ca. 3.5 mi N of Highlands, near Whiteside Mt., Nantahala National Forest, 28 July 1982, *Utech and Ohara 82-270* (CM). The collected materials were fixed in acetic-ethanol (1:3) for 10 h with subsequent storage in 70% ethanol. Standardized paraffin sectioning (14–16 microns) and staining (saffarin-methylene blue) techniques (Johansen, 1940; Sass, 1958) were used on samples (10 flowers and 10 young fruits of varying ages) from both populations. As an additional check on these serial sections, whole flowers and fruits were cleared and stained in a NaOH-1% fuchsin mixture (Fuchs, 1963).

Composite photomicrographs (Figs. 3–5, 7–8, 10) present the vascular floral anatomy and morphology of *A. muscaetoxicum,* whereas Figs. 6 and 9 are summary line diagrams for the species. No teleological implications are intended in the descriptive ascent and departure of the various floral bundles which are letter-coded for ease in comparison. This coding parallels that used in our previous liliaceous studies (Utech, 1978*a*–1978*e,* 1979*a,* 1979*b,* 1982, 1984; Utech and Kawano, 1975, 1976, 1980, 1981).

OBSERVATIONS

Amianthium muscaetoxicum is a glabrous, subscapose, perennial herb from a thick bulb (Fig. 2). At anthesis, the linear basal leaves are

Fig. 2.—Flowering individuals of *A. muscaetoxicum* in Macon County, North Carolina (*Utech and Ohara 82-270,* CM) (scale indicated).

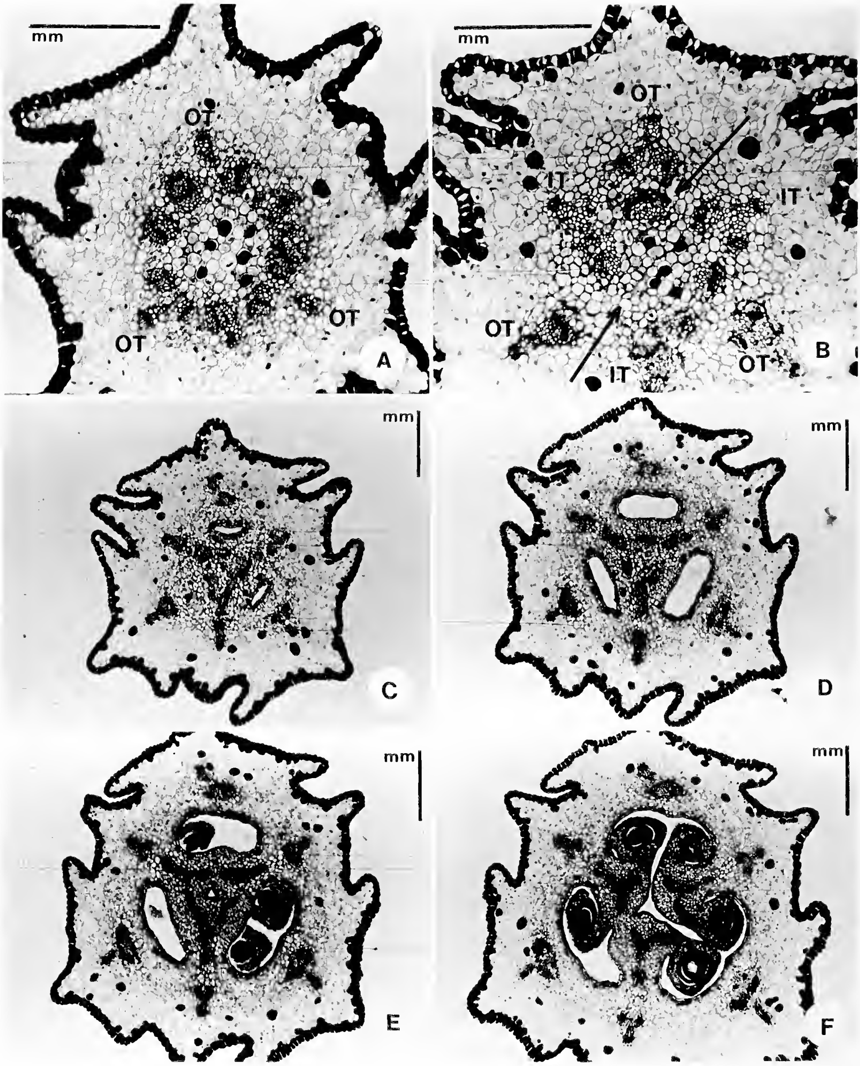


Fig. 3.—Cross-sections from the pedicel and lower receptalar areas of *A. muscaetoxicum* showing the spiral opening of the locules, the degree of perigyny and distribution of epidermal tannin cells. A. Mid-pedicel section showing the formation of three compound outer tepal (OT) bundles. B. Upper pedicel section showing formation of three compound inner tepal (IT) bundles and departure of compound OT bundles. Due to spiral bundle formation, a fusion bundle is opposite the upper OT bundle and a gap opposite the lower left OT bundle (arrows). C. Transition between upper pedicel and lower receptacle areas showing he opening of two locules, the departure of three IT bundles and the remaining central bundles which form the ventral supply. D. Lower receptacle area with perigyny

shorter than the stem. The few cauline leaves are progressively reduced and bract-like. The bracteate raceme is at first ovoid to conic, but at maturity it becomes cyclindric, measuring 4–14 cm long by 2–4 cm wide. Initially the flowers are white, but following anthesis the persistent tepals turn yellowish green or greenish purple and present a most striking color pattern.

The flowering pedicels are normally 7–17 mm long and ascending. In fruit, the pedicels are decidedly horizontal and much elongated. Internally, the fruiting and flowering pedicels have the same bundle number, though the vasculature in fruit is surrounded by a sclerenchymatous sheath. Lower flowering pedicel cross-sections are broadly triangular with three large, centrally arranged bundles. These three bundles establish the complete floral vasculature and are located on the radii which run from the middle of the "flat side" to the section's center. These three radii are designated the outer tepal (OT) radii. The three radii from the "corners" to the center are designated the inner tepal (IT) radii. Mid-pedicel cross-sections are characterized by broad fluting and ridges (Figs. 3 and 9) which continue through the perigynous zone.

The three lower pedicel bundles along OT radii undergo tri-parted, radial divisions with three resulting bundles from each division. These divisions occur at slightly different levels, that is they are not co-planar, but rather in a spiral pattern. Within each division a gap is created by the outward departure of a central bundle product. Three such central bundles, designated compound outer tepal (OT) bundles (dorsal-compound bundle; Sterling, 1982) depart along OT radii and remain free of other vasculature. Eventually they establish the dorsals (D), the outer tepal medians (OTM), the outer tepal laterals (OTL), and the outer stamen (OS) bundles (Figs. 6, 9A–D).

The two resulting lateral bundles which are opposite a gap following the tri-parted divisions fuse with similar adjacent laterals along the IT radii. These fusion bundles are formed in a spiral pattern and undergo a tri-parted division similar to that observed at a lower level among the three original bundles. The central bundles of this second set of divisions depart along the IT radii and establish the compound inner tepal (IT) bundles ("zwischenbundel"; Sterling, 1982).

←

evident and three open locules with formation of the central ventral supply. E. Mid-receptacle area showing the central hole and the ventral supply. F. Upper receptacle area showing the spiral septal arm formation within the perigynous zone, inter-locular connections and placental supply. Dorsal bundles are not established at this level (scale indicated).

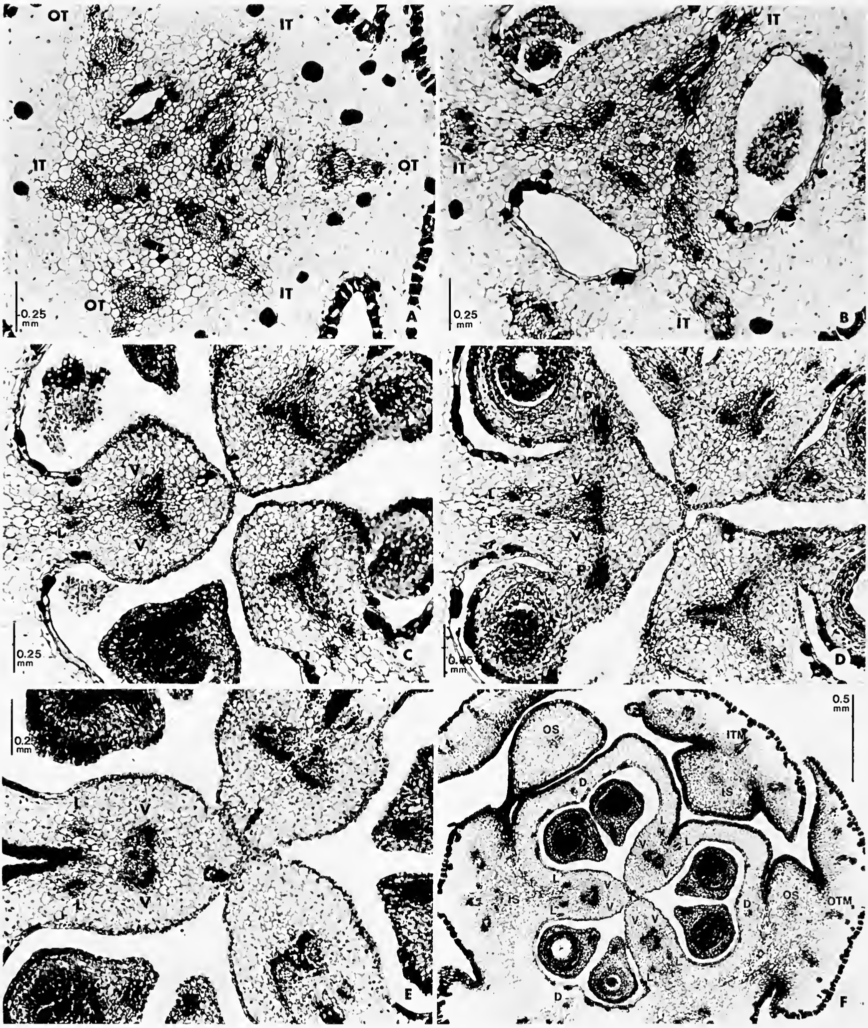


Fig. 4.—Cross-sections from the lower receptacle to upper perigynous areas of *A. muscaetoxicum.* A. Lower receptacle section showing the departure of compound OT and IT bundles, opening of two locules and formation of three bundles opposite IT bundles which establish the ventral supply. B. Section above A showing three open locules and the central hole. While three IT bundles depart, fusion and division occur among the remaining septal arm bundles. C. Section above B showing three freed septal arms between the inter-connected locules. Each septal arm has two laterals (L) and a compound ventral (V) from which placental bundles (P) arise. D. Section above C showing ovule supply via placental (P) bundles and the paired laterals and ventrals within the septal arms. E. Section above D showing the division of the compound ventral bundle (V) and the two laterals (L) within a septal arm. Papilloid nurse cells lining the inner septal arm

From the second set of tri-parted divisions, the two remaining lateral bundles fuse laterally with adjacent laterals, close the OT radii gaps formed when the compound OT bundles departed and eventually establish the total ventral supply (Fig. 6). These three fusion bundles undergo simple radial divisions in a spiral pattern. The two resulting products of this radial division fuse laterally with a similar adjacent lateral and form three fusion bundles along IT radii which close the gaps formed during the departure of the compound inner tepal (IT) bundles. Subsequent divisions among the compound OT and IT bundles will be discussed later. A given pedicel cross-section will usually show one bundle departing, another being formed and a gap in an area where a third will be formed.

The gynoecium and its associated vasculature can best be described in two parts: that in the lower perigynous zone and that in the upper freed zone. Ventral supply formation, locule opening and ovule placentation all occur within the lower perigynous zone (Figs. 3C–F; 4, 6). The dorsal bundles, on the other hand, which are derived from compound outer tepal (OT) bundles are established in the upper limits of the peripheral perigynous zone.

The ridged outline observed in the lower pedicel occurs up through the upper perigynous region where the tepals and stamens are freed (Figs. 3, 4F). Following the formation and departure of both the compound OT and IT bundles, a triangular vascular zone ("stele") remains in the central area (Figs. 3C–D, 4A–B). The three large bundles along IT radii establish the triangle's corners. These three complex fusion bundles which closed the gaps formed by the departure of compound IT bundles (Fig. 6) generally have two phloem caps or poles. Once these three corner bundles are established, the three locules which are perpendicular to OT radii open spirally.

With locular opening, each of the three compound bundles along IT radii undergoes a simple tangential division (Figs. 4B–C, 5A, C). Both resulting bundles are along the IT radii. The outermost division product has normally arranged xylem (adaxial) and phloem (abaxial), while the inner product has reversed conducting elements. Phloem strands frequently are observed to lag and may rarely and irregularly anastomose with other bundles (Fig. 5A–B).

←

margins are weakly appressed. F. Upper periygnous section showing the spiral arrangement of tepals, stamens and partially, freed carpels. Dorsals (D) are established at this level. Paired lateral (L) and ventral (V) products within septal arms are indicated as are outer tepal medians (otm), inner tepal medians (itm), outer stamen (os) and inner stamen (is) bundles. Epitepaly between an inner tepal and inner stamen is shown in the upper right (scale indicated).

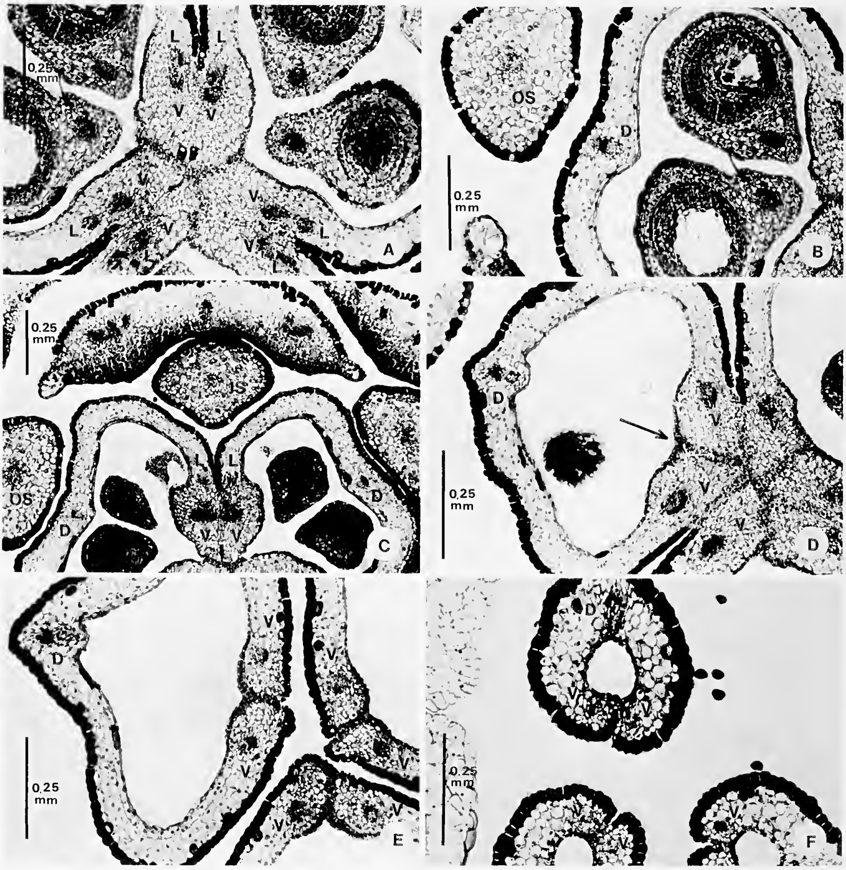


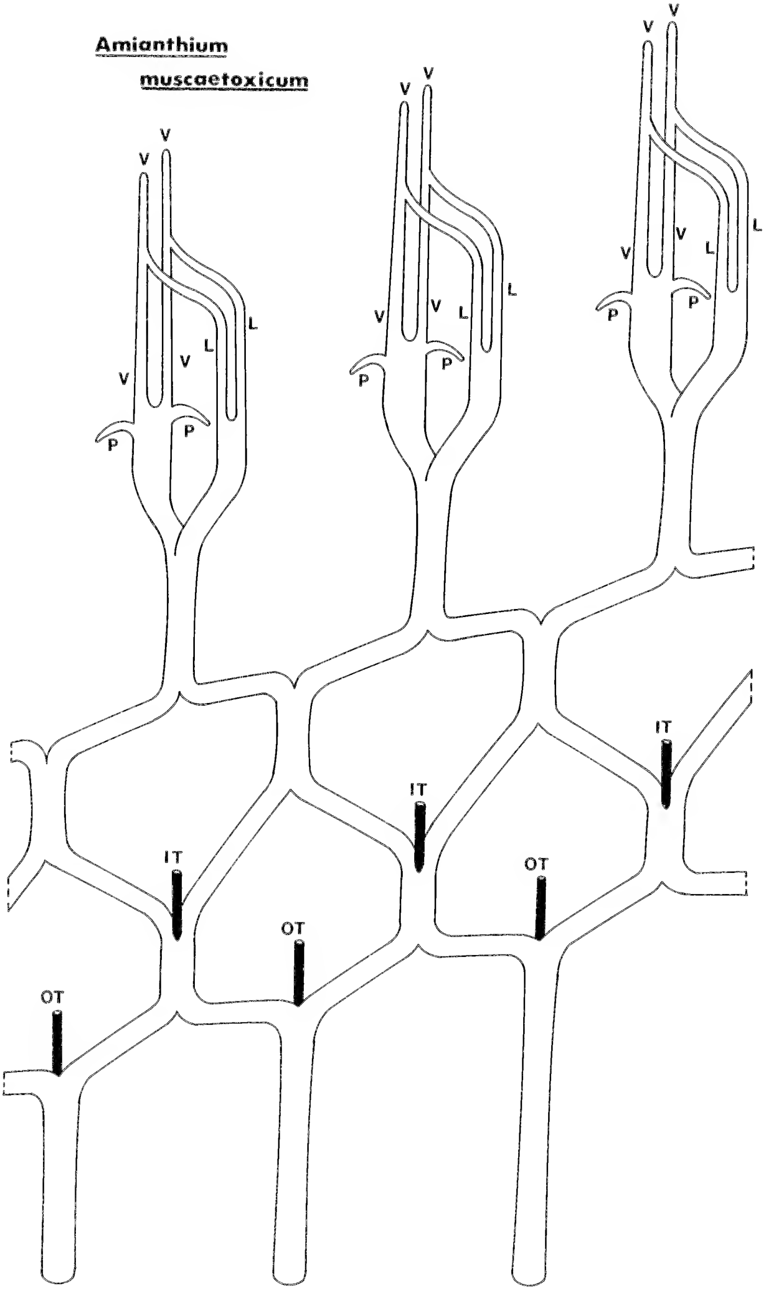
Fig. 5.—Cross-section of the middle to upper gynoecium of *A. muscaetoxicum*. A. Central zone showing three appressed septal arm tips and radial arm separation with paired lateral (L) and ventral (V) bundles. B. Section, same level as A, showing an outer stamen (OS) bundle and dorsal (D). An inner carpellary wall indentation, not a notch, is associated with each dorsal. C. Section above A showing the separated gynoecium and perianth. Within a septal arm, a given ventral and opposing lateral fuse to form a new, compound central in the same position as the lower, simple ventral. D. Section above C showing two compound ventrals (V) and dorsal (D) per carpel. The inner septal arm tips are further divided (arrow) compared with A. E. Section above D showing three free carpels each with a dorsal (D) and two ventrals (V). F. Stylar zone with the dorsal (D) and two ventrals (V) still present in each carpel (scale indicated).

The appearance at this level of a central opening or "hole" along the central floral axis (Figs. 3E, 4B) indicates inter-connection of the three locules will follow. Openings develop from this hole along the OT radii to each of the three locules (Fig. 3F). As openings inter-connect the three locules, three septal arms or wings are established along the IT radii. Within these septal arms further divisions occur among the paired ventral supply bundles. The outermost member of each septal bundle pair, that is the one with normally arranged conducting elements, divides radially and establishes two lateral bundles (L) (Figs. 4C–D, 5A, 6). (These bundles, here designated as laterals (L), could also be called septal axials.) The innermost member of each septal bundle pair, that is the one with reversed conducting elements, also undergoes a radial division which establish two placental (P) or ovule supplying bundles. The parental bundle which established the two placental (P) bundles also undergoes a radial division and establishes two ventral (V) bundles. Each septal arm at this level has a pair of laterals (L) with normally arranged conducting elements and a pair of ventrals (V) with reversed elements (Figs. 4C–F, 6).

Each locule has two, rarely four, bitegmic, basitropic, campylotropous ovules. The placental (P) bundles supplying these ovules depart quite horizontally. Usually one, rarely two, ellipsoidal, lustrous, dark reddish brown to black seeds are found in each carpel. The wingless seeds measure 1.5–2.0 mm wide by 4.5–6.0 mm long. Dehiscence begins in the upper stylar area and continues along the zones where the septal arms or margins meet (Fig. 5D–F).

The three dorsals (D) are the last carpellary vascular elements to be established and this occurs in the upper perigynous zone. The dorsals are associated with a zone of parenchyma cells which protrude as a locular indentation, not a notch (Figs. 4F, 5B, D–E, 7B). As the septal arms are subdivided along IT radii (Figs. 4E–F, 5A), the outer carpellary wall is freed from the perigynous zone. Septal arm subdivision follows the changing distribution of epidemal tannin cells which line the outer carpellary wall margins (Fig. 5A, C, D). Within each subdivided septal arm, two sets of vascular fusions occur. The two laterals (L) fuse with two opposite ventral bundles (V) which are along the same radii. The two resulting fusion bundles, here designated as ventrals (V), are in the same location as the two lower, simple ventrals (V) (Figs. 5A, C–D, 6). It should be noted that while the ventrals prior to fusion and after fusion are designated in the same way, there is a difference. The later ventral is a terminal fusion product. With the formation of these fusion ventrals (V), the three carpels are freed from one another (Fig. 5D–F) in what can best be described as an apocarpous condition. Each freed carpel has a dorsal (D) and two ventrals (V) which continue into the stylar zone (Fig. 5F). There is no terminal carpellary fusion between the ventrals or between the ventrals and the dorsal.

In most liliaceous species with a superior ovary, both the tepal and stamen vasculatures are well established before the locules open. This is not the case in *A. muscaetoxicum* (Figs. 3C–F, 9) and other members


Amianthium
muscaetoxicum
V
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of the Veratreae due to the basal perigynous condition. The six freed perianth parts, that is, the three outer and three inner tepals which are spirally inserted (Fig. 4F), are separate to their respective bases and spread widely. The inner tepals which measure 5–7 mm are slightly longer than the outer tepals. There are no glands or claws associated with these perianth parts as is frequently reported in *Melanthium* and *Veratrum.* The abaxial tepal surfaces of all six tepals are characterized by a single epidermal layer containing homogenous tannins (Fig. 8D). This epidermal tannin layer also occurs in the filaments and freed gynoecium. In addition to these tannin cells, there are randomly scattered tannin cells throughout the floral tissue. The adaxial tepal surfaces, on the other hand, lack these tannin cells and instead have papilloid cells (Fig. 8D). These papilloid cells occur from the basal regions of the freed tepals to the apices.

There are other differences between the inner and outer tepals (Figs. 7, 8). The inner tepals are differentiated from the outer in having a short vertical zone of enlarged cells along the basal tepal margins (Figs. 4F, 8B, C). These enlarged cells frequently contain long raphides. Epitepaly between the inner stamens and tepals is the rule (Figs. 4F, 8A, B). Epitepaly between the outer stamens and tepals occurs, but it is not as pronounced as the former.

Vascularization of the six tepals and six stamens occurs above the level at which the ovules are supplied (Figs. 3C–F, 4F, 7–9). This is due to the typical perigynous condition within the Veratreae. Six compound bundles, derived via fusion and established in the pedicel and lower receptacle levels, are ultimately responsible for the complete vascularization of the tepals and stamens (Figs. 6, 9). These compound bundles have been designated as the compound outer tepal (OT) and compound inner tepal (IT) bundles, respectively, for they are located along those respective radii. Insertion and departure of tepals and stamens follow a spiral pattern (Figs. 4F, 6, 9). A vascular description for one compound OT and IT bundle will illustrate the patterns for both sets since they are free from each other.

In the upper perigynous zone, a compound OT bundle appears triangular in cross-section (Figs. 7A, 9). Several complex subdivisions occur within the compound OT bundles which results in the formation

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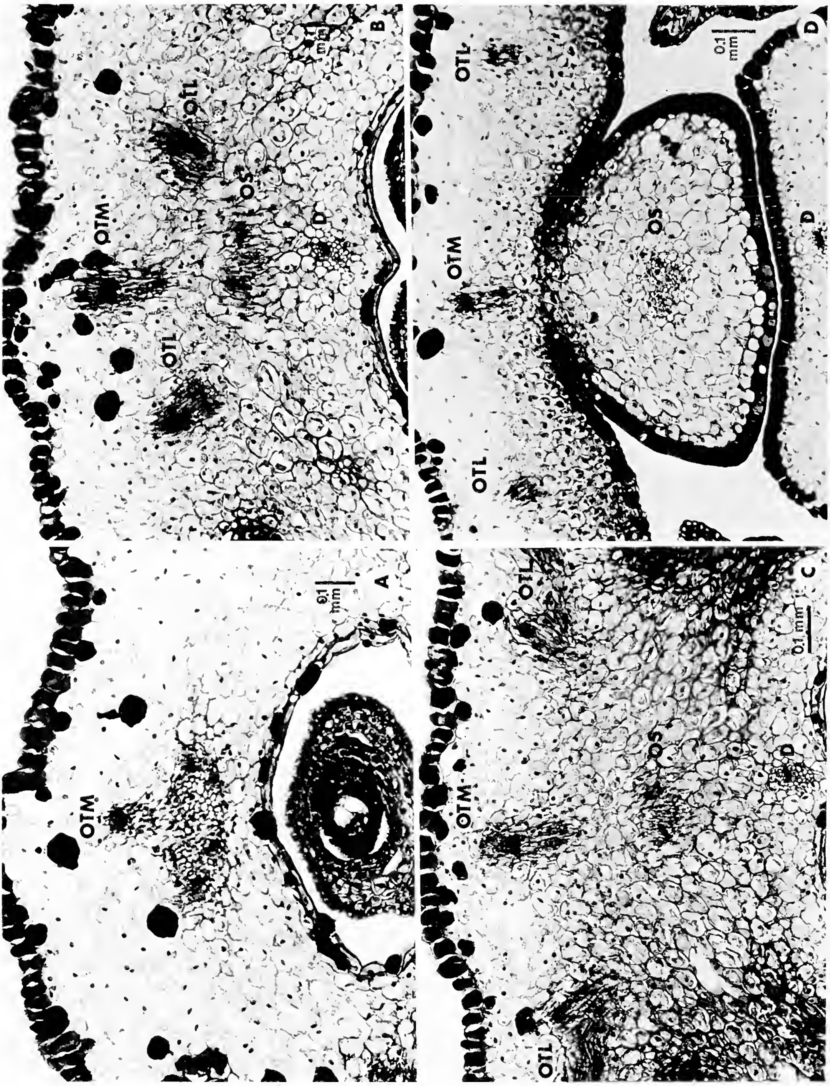
Fig. 6.—Roll-out longitudinal summary diagram for the floral vasculature of *A. muscaetoxicum.* A spiral pattern is indicated, in part, by the shifted levels at which the compound OT and IT bundles depart. Various text discussed bundles have been given the following code: L = lateral, V = ventral (simple and compound) and P = placental. Those bundles derived from the compound OT and IT bundles are not shown, see Figs. 7–9.


OTM
OTL
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OS
D
0.1 mm
B
OTM
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A
OTL
OTM
OS
D
OTL
0.1 mm
D
OTM
OTL
OS
D
0.1 mm
C

of an outer tepal median (OTM), two outer tepal laterals (OTL), an outer stamen bundle (OS) and a dorsal (D). The OTM is established first and has normally arranged xylem (adaxial) and phloem (abaxial) (Figs. 7A, 9B). The remaining product, after the departure of the OTM, undergoes a rapid and complex subdivision in which two OTLs, an OS and a D are established (Figs. 7, 9). The OTM, OS and D bundles all lie along the same radius. It should be noted that the outer tepal laterals are derived from the remaining product bundles, not the OTM. Basally each outer tepal receives three bundles, an OTM and two OTLs. The laterals undergo further radial divisions to establish additional laterals (Fig. 7C). In freed outer tepals, a seven bundled condition is typical, that is three OTLs + OTM + three OTLs.

The origin of the inner tepal median (ITM), the two inner tepal laterals (ITL), and an inner stamen bundle (IS) from a compound inner tepal bundle (IT) is similar to the outer series (Figs. 8, 9). The vascularization of the inner tepals and stamens is in a spiral pattern. The ITM, two ITLs and IS bundles have normally arranged xylem (adaxial) and phloem (abaxial). Basally each inner tepal is supplied with three bundles, an ITM and two ITLs. The laterals undergo further radial divisions, as in the outer series, to establish additional laterals (Fig. 8C). In freed inner tepals, a five bundled condition, rarely seven, is encountered, that is two ITLs + ITM + two ITLs. There is no fusion between the laterals or between laterals and medians in either tepal set. Tepal bundles follow a parallel course and end along tepal margins.

The six equal stamens are nearly as long as the inner tepals. The filament's epidermal layer contains tannins (Figs. 7D, 8C, 10A), while the anther walls do not. The basifixed, extrorse anthers have a valvular (lateral) dehiscence between the confluent thecae which open into a peltate disc (Fig. 10). The endothecium has wall thickenings or bands of the girdle type (Dahlgren and Clifford, 1982). This type of anther and mode of dehiscence is characteristic of the Veratreae.

The difference between outer and inner stamen vascularization which arose from compound OT and IT bundles, respectively, is that a dorsal

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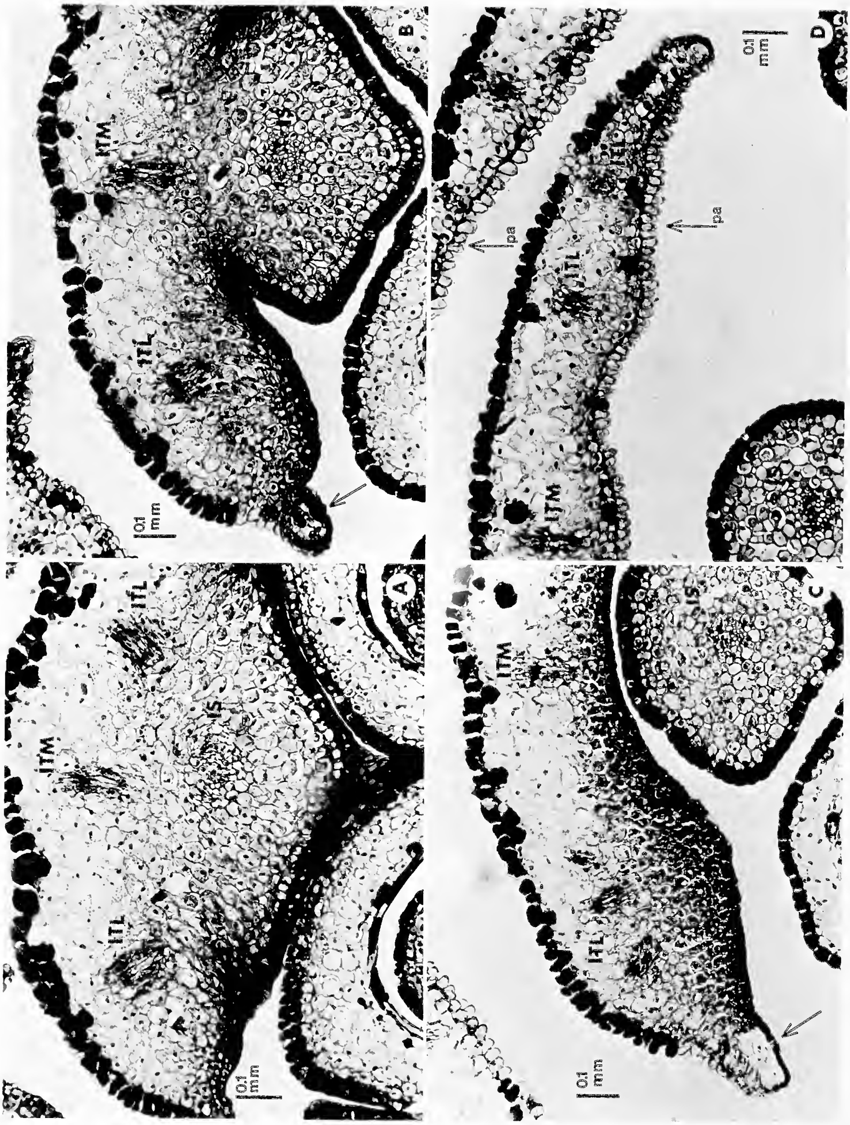
Fig. 7.—Vascularization of the outer tepals and stamens in *A. muscaetoxicum.* A. Mid-perigynous zone showing the departure of an outer tepal median (OTM) from a compound OT complex. B. Section above A showing the further division of the compound OT bundle into two outer tepal laterals (OTL) and an outer stamen (OS) bundle. The locular indentation associated with the dorsal (D) is evident. C. Upper perigynous section above B showing further division among the outer tepal laterals (OTL). D. Section above C showing the freed outer tepal and outer stamen (scale indicated).


ITM
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IS
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is associated with division of the OT parental bundle and there is no counterpart with the IT compound bundle (Figs. 7B–D, 8A–C, 9).

DISCUSSION AND CONCLUSIONS

In describing the vascular floral anatomy and carpel morphology within selected members of the liliaceous tribe Veratreae, Anderson (1940), El-Hamidi (1952), Ambrose (1975), Sterling (1982), and Utech in this report have noted characteristic similarities and differences between the flowers and fruits of *Amianthium muscaetoxicum* and the other members of the Veratreae. A common pattern of vascularization appears to be consistently observed within the tribe, while major differences which are frequently used to differentiate genera are reported. These anatomical and morphological characters include the presence or absence of sutural openings and a central carpellary hole at the lowermost level of ovular insertion, the degree of carpellary separation below the locular apex (an apocarpous tendency), the number of carpellary lateral or septal axial bundles and a hypogynous or perigynous versus epigynous condition at the lowermost level of ovular insertion. The floral vascular anatomy and carpel morphology of *A. muscaetoxicum* as reported here will serve as a case study of the continuous vascularization of a Veratrean gynoecium for further comparative work within the tribe.

The pedicel to stigma vasculature of *A. muscaetoxicum* is most unusual in that perigyny, spiral insertion of floral parts and apocarpous gynoecia are encountered. Through a complex series of divisions and fusions the complete floral vasculature is derived from three lower pedicel bundles. In the middle to upper pedicel a series of successive divisions and fusions in a spiral sequence produces three compound outer tepal (OT) bundles and three compound inner tepal (IT) bundles. From each compound OT bundle (dorsal-composite bundle; Sterling (1982)), an outer tepal median (OTM), several outer tepal laterals (OTL),

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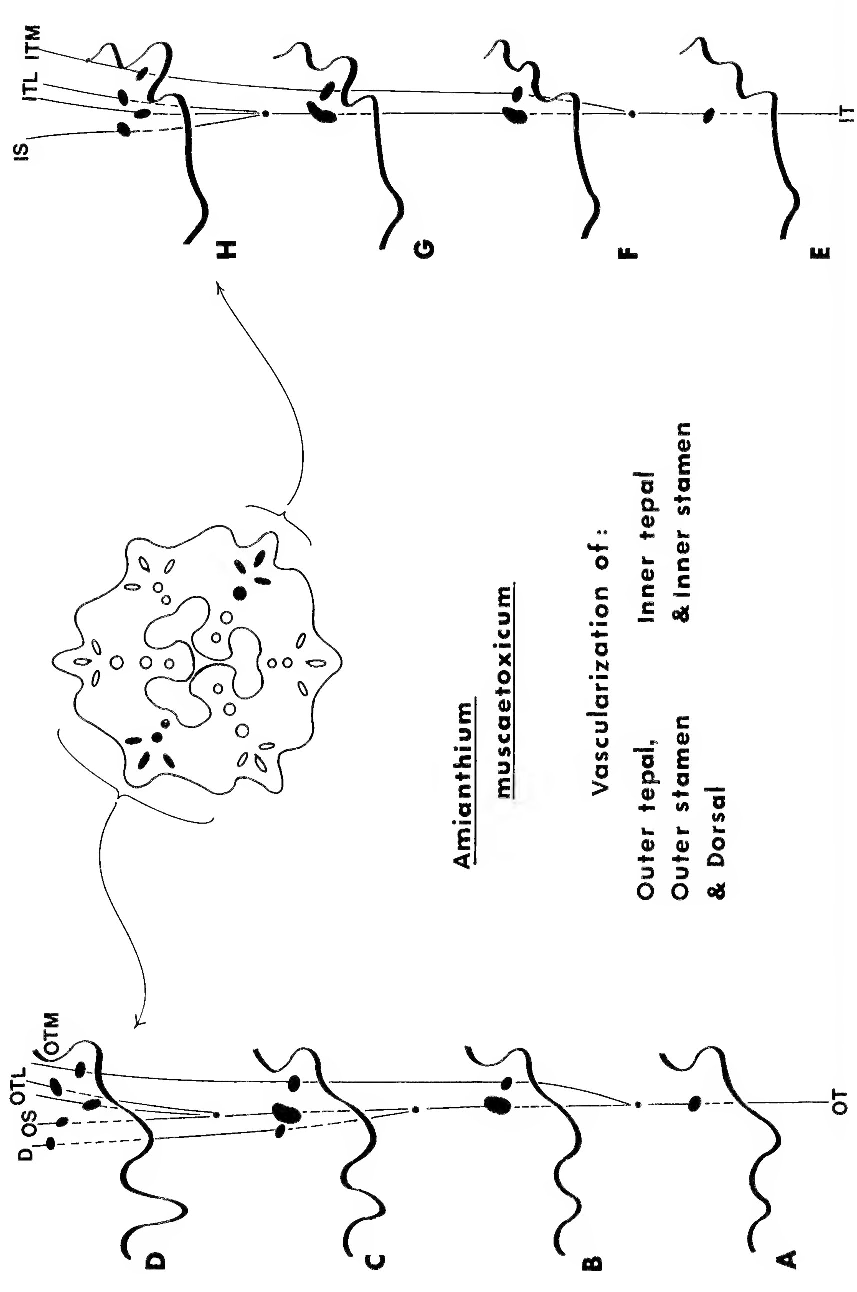
Fig. 8.—Vascularization of the inner tepals and stamens in *A. muscaetoxicum* with a tepal surface comparison. A. Epitepaly between an inner tepal and stamen is shown as an inner tepal median (ITM) is derived from a compound IT bundle. Subsequent division of the IT bundle establishes two inner tepal laterals (ITL) and inner stamen (IS) bundle. An epidermal tannin layer surrounds both the tepal and stamen. B. Section above A showing epitepaly as well as specialized cells which frequently contain raphides along the inner tepal margin (arrow). These cells are lacking in the outer tepals. C. Section above B showing a freed inner stamen and tepal with specialized cells (arrow). D. Section above C showing the difference in adaxial (tannins) and adaxial (pa = papilloid) tepal surfaces. These papilloid cells occur throughout both adaxial surfaces and extend to the tepal's tips (scale indicated).


Amianthium
muscaetoxicum
Vascularization of:
Outer tepal,
Outer stamen
& Dorsal
Inner tepal
& Inner stamen
A
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D
OS
OTL
OTM
OT
E
F
G
H
IS
ITL
ITM
IT

an outer stamen (OS) and a dorsal (D) result. Similarly, from each compound IT bundle ("zwischenbundel"; Sterling (1982)), an inner tepal median (ITM), and an inner stamen (IS) bundle result. Due to the perigynous condition, the formation of these tepal, stamen and dorsal bundles is at a level above that at which the ventral and ovular supplies are established.

The spiral origin of the ventral supply is via successive divisions and fusions of continuing lateral branches following the formation of the compound IT bundles. Within each of the three undivided septal arms, that is, the perigynous zone where the three locules are not interconnected, a lateral bundle (L) (compound septal axial bundle; Sterling (1982)) is associated with a ventral (V) (compound placental bundle; Sterling (1982)). The lateral bundle has normally arranged xylem and phloem while the ventral bundle has reversed conducting elements. There is a radial subdivision within each septal arm of both the ventral and lateral bundles. Each ventral bundle fuses with an opposite lateral bundle as the perigynous condition ends and the three carpels are freed.

It is noteworthy that at a lower level each carpel has five bundles, that is, a dorsal (D), two laterals (L) and two ventrals (V) while at a higher and freed carpellary level there is only a dorsal (D) and two fusion ventrals (V). Terminally, there is no fusion within a carpel between the dorsal and ventrals or between the ventrals. While the terminology varies, the above observations are similar to those of Sterling (1982). Anderson (1940) noted that the carpels in *Amianthium, Melanthium, Veratrum,* and *Zigadenus* were supplied by a dorsal, two laterals and two ventrals. The cross-section drawings of *Amianthium* by Ambrose (1975; fig. 32G–K) were described as having one dorsal and four ventrals. Simply counting carpellary bundles from selected cross-sections is not adequate for detailed comparative purposes, rather the continuity of the complete floral pattern including origins, fusions and divisions must be followed.

The combination of spirally inserted floral parts as well as their spirally derived vasculature coupled to both a perigynous and apocarpous gynoecium is most unusual among the "supposedly primitive lilies." Furthermore, there is a central carpellary hole associated with the gynoecial base. This central hole is internally continuous with the

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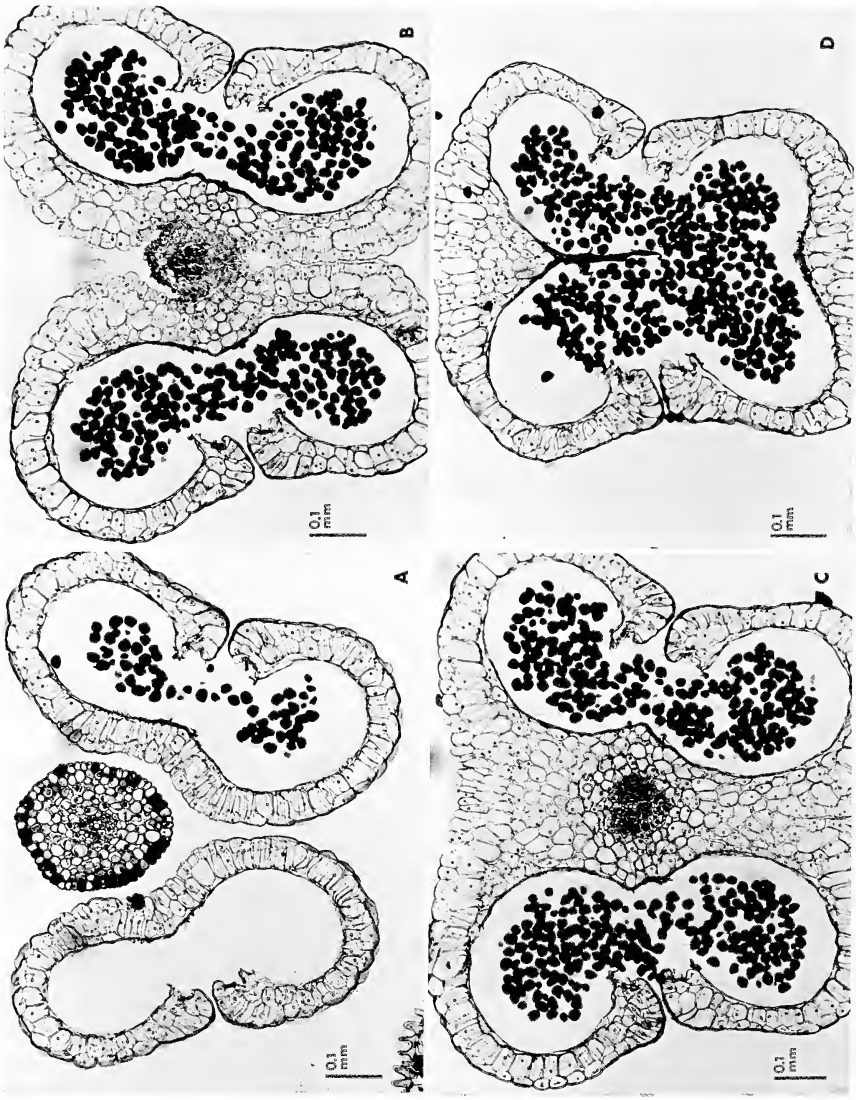
Fig. 9.—Line drawing showing cross-sections from the upper perigynous zone and the resulting vascularization from both a compound OT bundle (A–D) and a compound IT bundle (E–H). The outer tepal median (OTM), outer tepal laterals (OTL), outer stamen (OS) and dorsal (D) bundles are all derived from the compound OT bundle, while the inner tepal median (ITM), inner tepal laterals (ITL), and inner stamen (IS) bundles are derived from the compound IT bundle.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three locules and the open stylar canal. Such a central hole according to Sterling (1982) could be taken to represent a partially closed suture or a remnant of an open portion of the stylar canal. The three carpels are essentially free above the perigynous zone. The inner septal wing tips that form the stylar canal are weakly differentiated into papilloid nurse cells. In this inner zone, dehiscence occurs exposing the single, rarely two, wingless seeds of each carpel. Such inner septal margin separation is a variation of the typical septicidal capsule dehiscence where splitting occurs between two adjacent carpels along a common septal radius.

Neither tepal glands nor nectaries occur in *Amianthium* though they are commonly encountered throughout the Veratreae. The epidermal layers of both abaxial tepal surfaces as well as that of the pedicel, the complete perigynous zone, the filaments and the freed carpels are characterized by cells with homogenous tannins. However, the adaxial surfaces of both the inner and outer tepals have a generalized epidermis of small papilloid cells. Furthermore, as a possible defensive adaptation, raphides are observed in cells along the lower, outer margins of the inner tepals. Though there has been limited differentiation between the adaxial and abaxial tepal surfaces, they are not specialized as nectaries or glands. Travis (1984) observed that foraging beetles are the chief pollinators for *A. muscaetoxicum* and experimentally demonstrated that this species is nearly self-incompatible and the fecundity and fruit set levels are at least partly pollinator limited. Furthermore, only a small percentage of seeds from self-pollinated plants are viable.

ACKNOWLEDGEMENTS

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Fig. 10.—Cross-sections of an outer stamen in *A. muscaetoxicum*. A. Section through a filament with a tannin epidermal layer and two lower anther thecae which lack tannins. B. Section above A showing the central basifixed position of the filament. C. Section above B showing the central position of the outer stamen (OS) bundle. D. Upper anther zone section above C showing confluent thecae which open into a peltoid disc (scale indicated).

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