POSTILLA
PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 128. 25 FEB. 1969

A NEW THEROPOD DINOSAUR FROM THE LOWER CRETACEOUS OF MONTANA

JOHN H. OSTROM

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

A NEW THEROPOD DINOSAUR FROM THE LOWER CRETACEOUS OF MONTANA

JOHN H. OSTROM

Peabody Museum of Natural History and Department of
Geology and Geophysics, Yale University

ABSTRACT

Deinonychus antirrhopus, a new genus and species of theropod dinosaur is described from the Cloverly Formation (Lower Cretaceous) of southern Montana. The species is characterized by a highly specialized pes bearing a very large, trenchant claw on digit II, a highly raptorial manus with a very mobile carpus, and a specialized caudal series with extremely long prezygapophyseal and chevron rods. The new species is closely related to *Dromaeosaurus albertensis,* which features similar specialization of the second pedal digit, and is referred to the family Dromaeosauridae (=Dromaeosaurinae Matthew and Brown, 1922). Other species with comparable pes structure that may be referred to this family are *Stenonychosaurus inequalis, Velociraptor mongoliensis* and *Saurornithoides mongoliensis.*

POSTILLA 128: 17 p. 25 FEBRUARY 1969.

INTRODUCTION

Late in August, 1964, Grant E. Meyer of the Peabody Museum staff and I discovered some fragmentary fossil remains of the species herein described in exposures of the Cloverly Formation (Early Cretaceous) near Bridger, Montana. Extensive quarrying operations during the next two summers recovered more than 1000 bones representing at least three individuals. This collection is the basis of a detailed analysis of the osteology, adaptations and affinities of this remarkable new dinosaurian species (Ostrom, in press).

During the course of the above study, this material was made available to Drs. Edwin H. Colbert of the American Museum of Natural History and Dale A. Russell of the National Museum of Canada, who were collaborating on a new study of *Dromaeosaurus albertensis* (Matthew and Brown, 1922) from the Oldman Formation of Alberta. This was particularly appropriate because it was evident to each of us that *Dromaeosaurus* was more closely related to the present species than to any other currently recognized taxon, and any new analysis of *Dromaeosaurus* would be incomplete without reference to and comparison with the new Yale specimens. At that time it was believed that my detailed analysis establishing this new species would be published well in advance of the study by Colbert and Russell. However, at this writing (December, 1968) a serious possibility exists that such cannot be accomplished. Accordingly, the present brief description of the new species is submitted in order that the name will be available.

Abbreviations used are as follows: AMNH — American Museum of Natural History; YPM — Peabody Museum, Yale University.

SYSTEMATICS

CLASS REPTILIA

ORDER SAURISCHIA

Suborder Theropoda Marsh, 1881

Family Dromaeosauridae (=Dromaeosaurinae Matthew and Brown, 1922)

DEFINITION: Small to moderate-sized theropods, lightly built and bipedal in posture. Fore limb not reduced. Manus long and slender with three functional digits. Digit III moderately divergent and carpus highly specialized with asymmetrical ginglymus on radiale. Hind limb long, pes of moderate length and functionally didactyl. Digit II modified as an offensive or predatory weapon with large, trenchant claw. Digits III and IV subequal and normal, digits I and V reduced. Eight to 9 cervical vertebrae, 13 to 14 dorsals and 3 to 4 sacrals. Caudal series of *Deinonychus* highly modified by extremely long prezygapophyseal and chevron processes which rendered the tail virtually inflexible throughout most of its length. Comparable caudal modifications are presumed, but not known, in other taxa referred to the family.

DISTRIBUTION: Late Aptian to Late Campanian or Early Maestrichtian, western interior of North America and central Mongolia.

Deinonychus, new genus

TYPE SPECIES: *Deinonychus antirrhopus,* new species.

DISTRIBUTION: Late Aptian, south central Montana.

DIAGNOSIS: Same as for the species, given below.

ETYMOLOGY: *Deinos* (Greek), terrible, and *onyx* (Greek; masculine), claw or talon.

Deinonychus antirrhopus, new species

TYPE: YPM 5205, a complete left pes and an incomplete right pes.

HYPODIGM: YPM 5201, 5202, and 5203, three series of articulated caudal vertebrae.

YPM 5204, part of the atlas, the axis, fourth and fifth cervicals and the fourth, sixth, seventh and ninth dorsals.

YPM 5206, nearly complete left and right manus.

YPM 5210, an incomplete skull and jaws (vomers, left and right quadratojugals, both squamosals, a left articular, left and right pterygoids, a right ectopterygoid, right surangular, left jugal, right angular, left dentary, and numerous teeth), the atlas, axis and seventh cervical, the first and tenth dorsals and an anterior (3rd or 4th) caudal.

YPM 5232, consists of the right maxilla, right and left nasals, right and left dentary, right and left (incomplete) premaxillae, right and left jugals, right squamosal, both postorbitals, right lachrymal, right and left articulars, left palatine, left angular and right quadratojugal.

YPM 5207, 5208, 5209, 5211-5231, 5233-5265, various isolated and fragmentary elements.

AMNH 3015, an incomplete skeleton, lacking the skull and jaws.

AMNH 3037, fragmentary bones from the manus and pes.

HORIZON: Cloverly Formation, lower part of Unit VII (=upper part of Himes member of Moberly, 1960) and upper part of Unit V (=Little Sheep mudstone member of Moberly, 1960), ranging from 50 to 100 feet below the Sykes Mountain Formation. (Units V and VII are defined in my report on the stratigraphy and paleontology of the Cloverly Formation [Ostrom, MS]).

LOCALITIES: YPM 64-75 — NE ¼ Sec. 17, T.7 S., R.24 E., Carbon County, Montana. AMNH 31-7 — NW ¼ Sec. 33, T.4 S., R.29 E., Big Horn County, Montana. AMNH 32-8 — NE ¼ Sec. 32, T.4 S., R.29 E., Big Horn County, Montana.

DIAGNOSIS: A small, bipedal theropod with moderately large head, moderately long and well developed hind limbs, fore limbs not reduced, manus long and slender. Pes of medium length with four digits, the fifth represented by a vestigial metatarsal. Digital formula of the pes 2-3-4-5-0. Digits III and IV equal in length and normal, digit II specialized and bearing a very large, trenchant and strongly recurved ungual, I reduced and directed backward. Pes functionally didactyl (III and IV). Distal end of metatarsal II deeply grooved, metatarsal III not greatly compressed proximally. Articular facets of II developed to permit unusual extension but very little flexion between first and second phalanges. Manus with three very long digits (formula 2-3-4), digits IV and V lost. Metacarpal I short and irregular in shape. Metacarpal III long, slender and divergent from II. Carpus consists of radiale and ulnare only. Radiale with well defined asymmetrical ginglymus proximally for articulation with radius. Humerus and radius-ulna not reduced. Skull with large, circular orbit and three antorbital fenestrae. Supraorbital rugosities on postorbital and lachrymal. Preorbital bar slender, in weak contact with thin, plate-like jugal. Quadratojugal very small, T-shaped and apparently not in contact with squamosal. Nasals long, narrow and unfused. Inferior premaxillary process forms lower margin of external naris. Pterygoid very long and slender, ectopterygoid complex and pocketed ventrally. Palatines expanded with subsidiary palatine fenestrae medially. Fifteen maxillary teeth, 4 asymmetrical, sub-incisiform, premaxillary teeth, 16 sub-isodont dentary teeth. All teeth with anterior and posterior serrations; denticles of posterior serrations nearly twice as large as denticles of anterior serrations on all teeth. Twenty-two or 23 presacral vertebrae, 3 or 4 sacrals and approximately 40 caudals. Cervical vertebrae of moderate length, massive, platycoelous and sharply angled. Dorsals short and platycoelous to amphiplatyan with well developed hyposphene-hypantrum and bearing short, stout neural spines. All presacrals with small but deep pleurocoels. Caudal vertebrae long and platycoelous. All caudals except the first 8 or 9 bear extremely long (up to 10 segments), rod-like, prezygapophyseal processes. Chevrons also elongated into long, paired, double, bony rods extending forward beneath the preceding 8 or 9 segments. Ischium with triangular obturator process. Pubis (if correctly identified) short and greatly expanded into a sub-circular, scoop-shaped element with a distinct obturator foramen.

ETYMOLOGY: *antirrhopus* (Greek; masculine), counterbalancing, in reference to the unusual adaptation of the caudal vertebrae.

DISCUSSION

The above diagnosis is based on the hypodigm and not on the type alone. The fossil remains recovered from the Yale site were closely associated, but largely disarticulated. The most notable exceptions are the three articulated caudal series (YPM 5201, 5202 and 5203), a complete left pes and a fragmentary right pes (YPM 5205), and a nearly complete left manus (YPM 5206). Because more than one individual is represented, it is impossible to establish definite individual associations of the disarticulated elements. Accordingly, the collections from this site have been catalogued as more than 50 separate entries, although in fact they may represent as few as three individuals. There is no doubt in my mind that these remains belong to a single species and I have thus based my diagnosis on the entire Yale sample, plus two fragmentary specimens in the American Museum collections (AMNH 3015 and 3037).

The most distinctive features of *Deinonychus* are the pes, carpus, manus and caudal vertebrae. Each of these structures indicate an animal of great agility and speed and a highly predaceous mode of life.

The pes is basically tridactyl in design (although a reduced hallux and a remnant of metatarsal V are present), but the foot functioned as a didactyl structure in locomotion (Fig. 1). The weight-bearing axis of the foot has been shifted from the normal theropod position at digit III to a position between digits III and IV. Metatarsal IV is distinctly shorter than III, but digits III and IV are equal in length, reflecting the fact that the weight was borne equally by these two digits.

The second digit is highly specialized for a non-locomotory, predatory function and quite probably did not contact the ground at all under normal circumstances. The ungual of the second digit is more than twice the size of the other unguals and is very strongly recurved and trenchant in contrast to the straighter and broader form of unguals III and IV (Fig. 2). Associated with this unusual sickle-like claw of digit II are several other peculiar specializations of the second digit. The distal joint is a very deeply grooved ginglymus that permitted considerable flexion of the ungual (note the very deep, parallel-sided articular facet of the ungual in Fig. 2a), but little extension. The joint between the proximal and penultimate phalanges, on the other hand, permitted no flexion, but allowed excessive (90° or more) extension (note the proximal "heel" or projection of the distal phalanx and the unusual elevation of the distal facet of the proximal phalanx in Fig. 3). This appears to be a unique adaptation for elevation of the sickle-like claw above the ground, perhaps to prevent its damage during normal locomotion. This joint, like the distal articulation, is an unusually deeply grooved ginglymus (Fig. 3).

The distal end of metatarsal II is also unusual in that it is deeply grooved, forming an asymmetrical ginglymus that had not been recognized before in any other theropod. It is evident from the deeply grooved form of all three joints that the second pedal digit of *Deinonychus* was adapted for flexion and extension in a narrowly restricted plane, and this seems to have been related to the unusual size and recurved, trenchant form of the claw.

The manus is of the usual tridactyl form characteristic of most theropod species. It differs from most, however, in its unusual length and the relative size and trenchant, raptorial form of the unguals (Figs 4 and 5). Digit III is unusual in its slender form and the fact that it apparently could be deflected away from the other digits, although it probably was not opposable in the usual sense.

The carpus consists of only two elements, ulnare and radiale; these were highly modified to produce precisely limited abduction-adduction and supination-pronation. The proximal facet of the radiale is a strongly asymmetrical ginglymus that permitted perhaps as much as 100° of abduction-adduction, and during the final phases of abduction approximately 35 to 45° of supination (Fig. 6). The proximal facet of the much smaller ulnare is a simple oval concavity that could have permitted rotation of the carpus and manus about the ulna long axis, as well as adduction-abduction or flexion and extension. These highly sophisticated movements of the wrist are entirely consistent with the raptorial design of the manus.

The caudal vertebrae of *Deinonychus* are remarkable in the extreme modification of the chevrons and prezygapophyses (Figs. 7 and 8). Posterior to the ninth or tenth caudal the chevrons are not blade-like ventral processes, but are flat, wedge-shaped elements pointing caudally. The anterolateral corners of these wedges are drawn out into long, double rods reaching lengths of eight to ten segments. These rods, ranging from approximately 2 mm to less than 0.2 mm in diameter, are preserved in bundles lying lateral to the lower half of the caudal centra. The prezygapophyses are correspondingly elongated into double rods extending forward as much as 10 segments. These are identical in size, shape and surface texture to the chevron rods and occupy a comparable position lateral to the neural arches. Both structures are present on all distal caudals; only the first eight or nine caudals lacked them. Both rod types probably developed by ossification of tendons associated with flexor and extensor muscles of the tail and appear to have been an adaptation for controlled stiffening of the tail. This feature seems best explained as an adaptation for balancing, a critical faculty in an obligatory biped.

I have placed *Deinonychus* in the Dromaeosauridae because of the almost identical form of the pes of *Deinonychus* and *Dromaeosaurus*. The latter is described in detail by Colbert and Russell (in press), and is not discussed further here. Other taxa that appear to be closely allied with *Deinonychus* on the basis of pes structure are: *Stenonychosaurus inequalis* Sternberg (1932), *Velociraptor mongoliensis* Osborn (1924), and *Saurornithoides mongoliensis* Osborn (1924). Accordingly, these are referred to the Dromaeosauridae. Further discussion of these assignments is included in my study of the osteology of *Deinonychus* that is now in press.

ACKNOWLEDGMENTS

I am grateful to Drs. Edwin H. Colbert and Dale A. Russell for many hours of stimulating discussion about *Deinonychus* and its allies. I also thank Dr. Colbert for permission to include the two American Museum specimens in this study and for providing Barnum Brown's field records pertaining to these specimens. The photographs were taken by A. H. Coleman and the manuscript was typed by Louise Holtzinger.

The discovery and collection of the Yale *Deinonychus* material was possible only because of grants from the National Science Foundation (GB-1015 and GB-3638), which are gratefully acknowledged.

LITERATURE CITED

Colbert, Edwin H., and Dale A. Russell. [In press]. The small Cretaceous dinosaur, *Dromaeosaurus*. Amer. Mus. Novitates.

Marsh, Othniel C. 1881. Principal characters of American Jurassic dinosaurs. Pt. V. Amer. Jour. Sci., Ser. 3, **21**: 417-423.

Matthew, William D., and Barnum Brown. 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. Bull. Amer. Mus. Nat. Hist. **46**: 367-385.

Moberly, Ralph, Jr. 1960. Morrison, Cloverly and Sykes Mountain Formations, northern Bighorn Basin, Wyoming and Montana. Bull. Geol. Soc. Amer. **71**: 1137-1176.

Osborn, Henry Fairfield. 1924. Three new Theropoda, *Protoceratops* zone, central Mongolia. Amer. Mus. Novitates, no. 144: 1-12.

Ostrom, John H. [In press]. Osteology of *Deinonychus antirrhopus,* an unusual theropod from the Lower Cretaceous of Montana. Bull. Peabody Mus. Nat. Hist.

———— [MS] [Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana.]

Sternberg, Charles M. 1932. Two new theropod dinosaurs from the Belly River Formation of Alberta. Canadian Field Naturalist 46: 99-105.

FIG. 1. Left pes of *Deinonychus antirrhopus,* YPM 5205 (type).

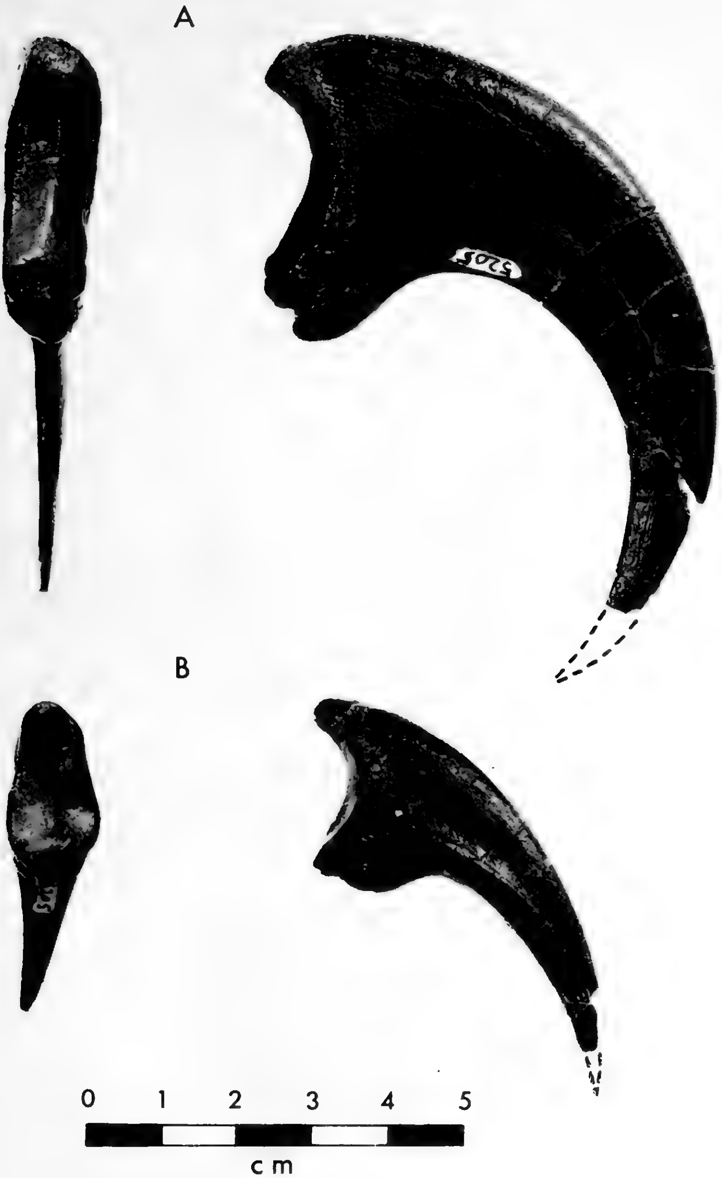


FIG. 2. Unguals of digits II (A) and III (B), left pes of *Deinonychus antirrhopus* (YPM 5205), in medial (right) and proximal (left) views. Notice the very long, narrow, parallel-sided articular facet of ungual II.

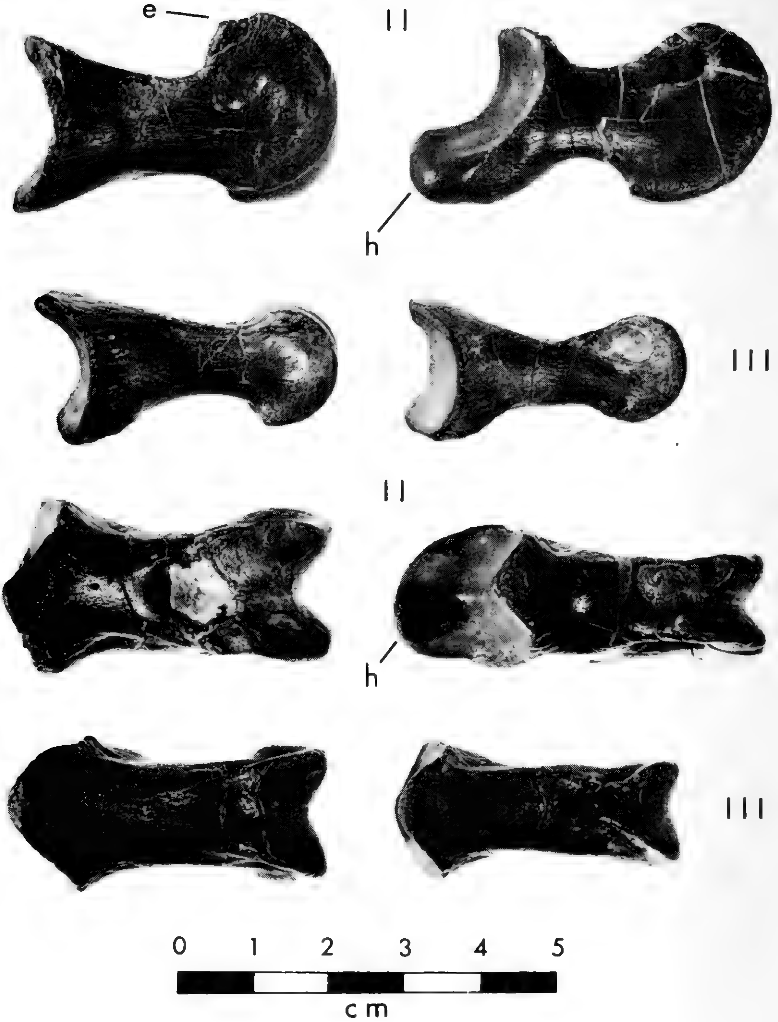


FIG. 3. Phalanges of digits II and III, left pes of *Deinonychus antirrhopus* (YPM 5205), in medial (above) and dorsal (below) views. Penultimate phalanx is on the right in all series, adjacent (proximal) phalanx is at left. Notice the prominent ventroproximal expansion or heel (h) of the distal phalanx of II, and the unusual elevation (e) of the distal facet of the adjacent phalanx. Together these restricted flexion, but permitted extreme extension (as shown in Fig. 1). Compare these features with those of the equivalent phalanges of digit III. Notice also in the dorsal views the deeper grooves of the ginglymoid facets of the second phalanges compared with the phalanges of III.

FIG. 4. Left manus of *Deinonychus antirrhopus* (YPM 5206) in palmar view.

FIG. 5. Left manus of *Deinonychus antirrhopus* (YPM 5206) in medial view. Notice the unusual size and raptorial form of the unguals.

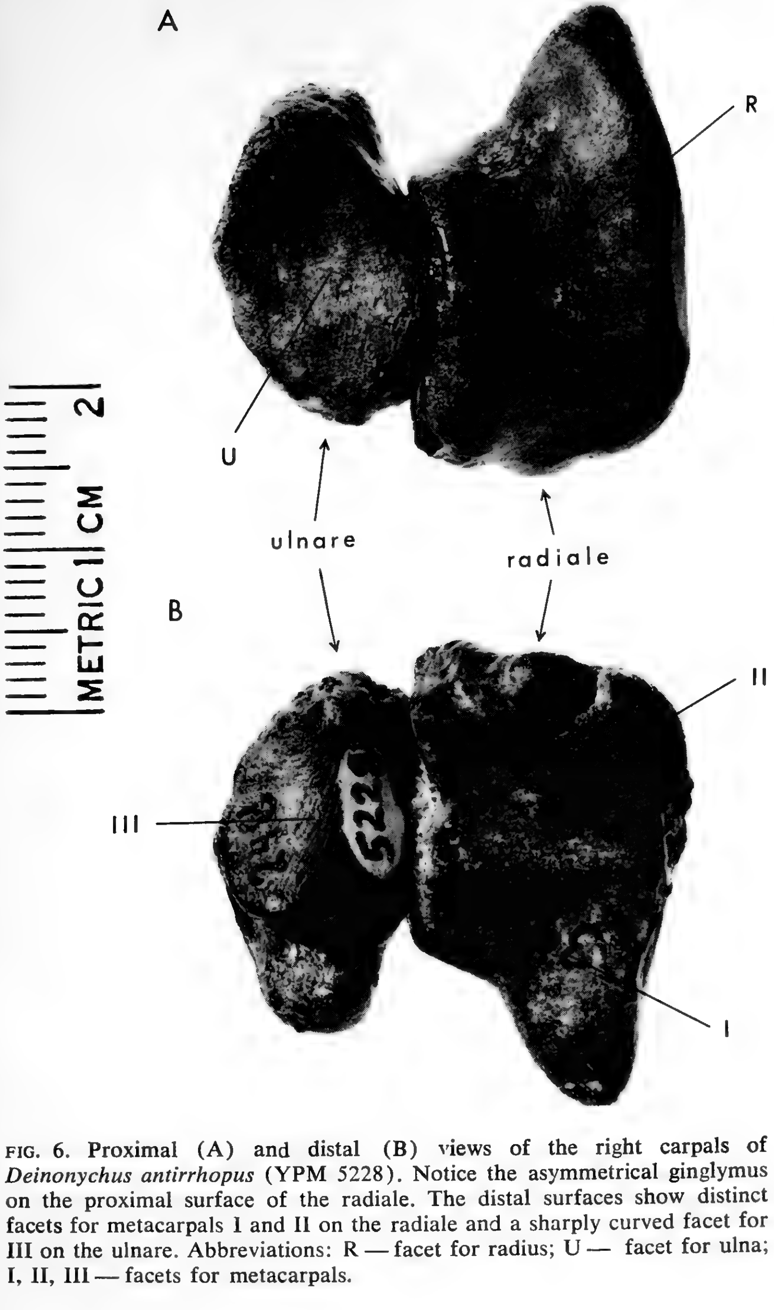


FIG. 6. Proximal (A) and distal (B) views of the right carpals of *Deinonychus antirrhopus* (YPM 5228). Notice the asymmetrical ginglymus on the proximal surface of the radiale. The distal surfaces show distinct facets for metacarpals I and II on the radiale and a sharply curved facet for III on the ulnare. Abbreviations: R — facet for radius; U — facet for ulna; I, II, III — facets for metacarpals.

FIG. 7. A nearly perfect caudal series of *Deinonychus antirrhopus* (YPM 5201). This series is nearly a meter in length, of which approximately 60 cm are shown here.

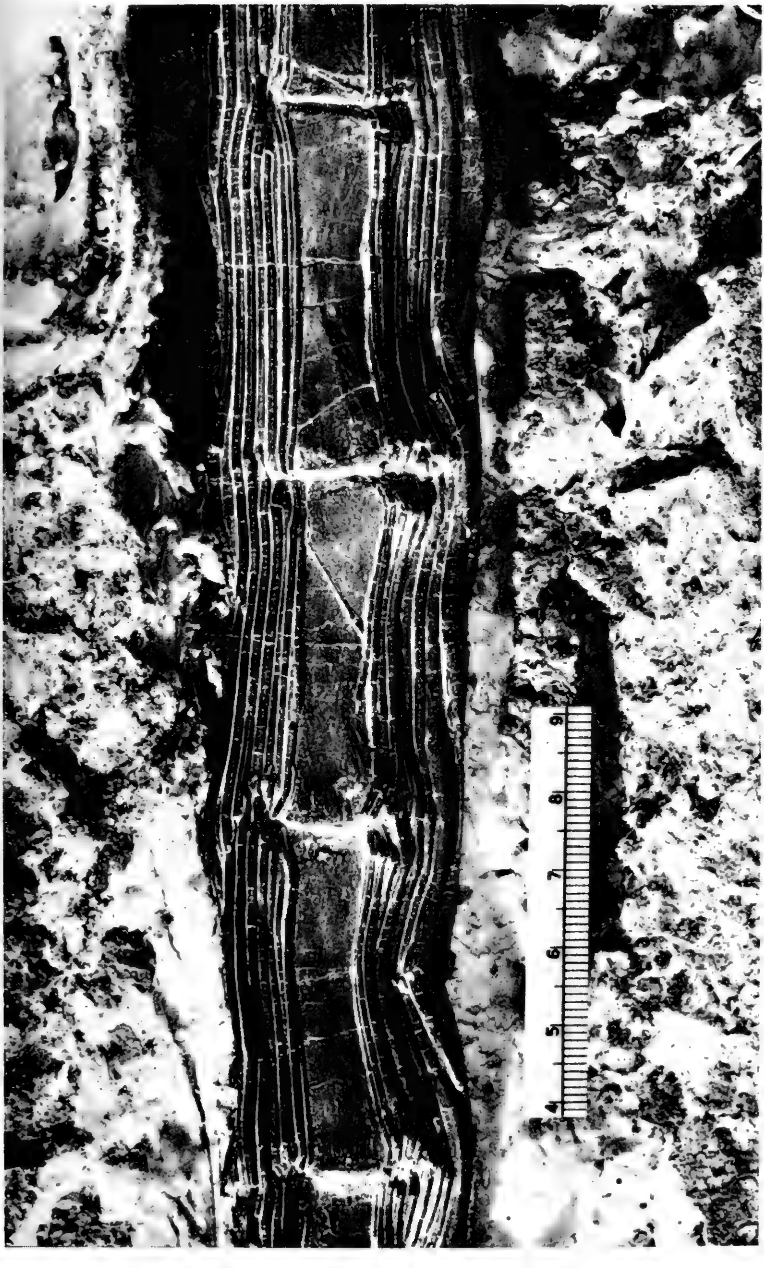


FIG. 8. Detailed photo of the same caudal series as Fig. 7 showing the prezygapophyseal rods above and the chevron rods below the centra. Approximately × 1.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

OMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

ILLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

THOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 129. 26 FEB. 1969

A NEW GENUS AND SPECIES OF TEIID LIZARD FROM BOLIVIA

THOMAS UZZELL

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

A NEW GENUS AND SPECIES OF TEIID LIZARD FROM BOLIVIA

THOMAS UZZELL

Department of Biology and Peabody Museum of Natural History, Yale University

ABSTRACT

Opipeuter xestus, new genus, new species, is placed in Group II of the family Teiidae (Squamata, Reptilia) because it has five clawed digits on all four feet, the nasals separated by a frontonasal, and the nostril pierced in the middle of the nasal scale. It differs from other known members of Group II in having the combination of total absence of keeled scales and a relatively enormous transparent disc in the lower eyelid. The arrangement of enlarged calcareous spines in the hemipenis distinguishes the new taxon; enlarged spines are present on the basal part of the median welt, and in a row on each side of the sulcus spermaticus. The affinities of the new taxon are not with *Prionodactylus,* although most specimens have been identified as *Prionodactylus bolivianus;* the affinities may be with *Euspondylus,* but are not clearly so. Known specimens come from several localities between 1000 and 3000 m above sea level in the headwaters of the Río Chapare on the eastern Andean slopes of central Bolivia.

***POSTILLA* 129: 15 p. 26 FEBRUARY 1969.**

INTRODUCTION

One of the frequently collected species of Boulenger's (1885) Group II of the Teiidae is regularly but incorrectly identified as *Prionodactylus bolivianus* Werner (1889). I have recently examined the holotype of *Prionodactylus bolivianus* in the Muséum National d'Histoire Naturelle in Paris and a second specimen identified by Werner as *P. bolivianus* in the Zoologische Staatssammlung in Munich. *P. bolivianus* is closely related to *P. okendeni* Boulenger (1906); both have the loreal in contact with the frontonasal and with one or more supralabials, an undivided frontonasal, a variable number (2 or 3) of median collar scales, and simple subdigital lamellae. While *P. bolivianus* agrees with the misidentified species in most of these features, the strong keeling on the dorsal scales, not mentioned by Werner but implied by his generic placement of *bolivianus,* readily distinguishes all *Prionodactylus* from the misidentified form, which has no keeled scales whatsoever.

The misidentified species appears to be unnamed. I here name it, but in so doing, am also obliged to consider its generic assignment. The new species, despite the fact that it has been identified as a member of the genus *Prionodactylus,* does not, in my opinion, belong to that genus. Alternatively, it could be placed in *Euspondylus.* Both *Euspondylus* and *Prionodactylus,* which I believe are only distantly related to each other, or the composite genus *Euspondylus* containing both groups of lizards, have included a wide variety of stocks of Group II of the Teiidae. I have examined members of most of the taxa in Group II, and I am gradually forming generic concepts for them. In my opinion, placing the new species in *Prionodactylus* is impossible, but placing it in *Euspondylus* would only add to the confusion in that overburdened genus. I therefore propose a new genus for the species, with full realization that the generic and specific characters are the same, and the conviction that if I or some other worker can convincingly place the new species in a previously recognized genus, such reassignment will be progress. It is my belief, however, that a new genus is warranted by the characters of the new form. Erecting a new genus draws attention to the distinctive characters of the new species, allows *Euspondylus* and *Prionodactylus* to begin to emerge as distinctive entities, and constrains the minds of herpetologists less than would placing the new species in *Euspondylus*.

For permission to examine material in collections in their charge, I thank Charles Bogert and Richard Zweifel, American Museum of Natural History (AMNH), Alice G. C. Grandison, British Museum (Natural History) (BMNH), Jean Guibé, Muséum National d'Histoire Naturelle, Walter Hellmich and Dieter Fuchs, Zoologische Staatssammlung, Munich (ZSM), James A. Peters, U.S. National Museum (USNM), Charles F. Walker, University of Michigan Museum of Zoology (UMMZ), and Ernest E. Williams, Museum of Comparative Zoology, Harvard University (MCZ). Travel was supported by the Peabody Museum, Yale University (YPM) and by a gift from Evan Commager. Mario Baudin helped me in determining many of the localities. The illustrations were done by Diane McClure, Jon Janosik, and A. H. Coleman.

CLASS REPTILIA

ORDER SQUAMATA

FAMILY TEIIDAE

Opipeuter, new genus

TYPE SPECIES. **Opipeuter xestus,** new species.

DESCRIPTION. Tongue with imbricate scalelike papillae. Snout moderate. Head scales without striations or rugosities; single frontonasal, frontal, and interparietal; paired prefrontals, frontoparietals, and parietals; a median occipital bordered by two laterals. Nostril pierced in a divided scale, the suture posterior to the nostril; nasals not in contact; loreal and frenoocular present, the former almost always in contact with supralabials; first superciliary expanded onto dorsal surface of head; a single long subocular. Eyelids well developed, the lower with a relatively enormous transparent circular disc without divisions. Ear opening small, tympanum deeply recessed, larger than ear opening. Gular crease weak; collar fold well developed. Gular scales flat, small, and nearly quadrangular anteriorly, flat, larger with rounded posterior margins posteriorly; collar scales 8-10, flat, about as wide as long, with rounded posterior edges. Limbs pentadactyl;

digits clawed. Scales along inner margin of palm between thumb and wrist slightly enlarged, but inner edge not produced. Underside of third and fourth toes with paired scales on proximal part, the inner scale not tuberculate. Dorsal scales smooth, in transverse rows, with rounded posterior edges. Lateral scales reduced in size, rounded in outline, smooth; ventral scales in transverse and longitudinal rows, smooth, posterior margins rounded. Femoral pores present in both sexes, usually fewer in females. Hemipenis with a cluster of enlarged spines on the basal part of the median welt, and with rows of enlarged spines along the edges of the sulcus spermaticus (Fig. 2).

DIAGNOSIS. The widely separated nasal scales, each surrounding a nostril, and the pentadactyl limbs with all digits clawed place *Opipeuter* in Group II of the Teiidae. The combination of smooth body scales and the large, nearly circular, undivided, transparent disc in the lower eyelid, distinguish *Opipeuter* from all other genera in Group II. In addition, I have examined hemipenes of about 20 genera and 50 species of this group of the family; the arrangement in *Opipeuter* is distinctive.

DERIVATION OF NAME. The name *Opipeuter* (masculine) is from the Greek όπῑπευτήρ, a gazer, in reference to the large transparent disc in the lower eyelid.

Opipeuter xestus, new species (Fig. 1)

HOLOTYPE. UMMZ 128835, an adult male collected in March, 1929, by F. B. Steinbach at Incachaca, Cochabamba, Bolivia, about 2200 m above sea level.

PARATOPOTYPES. UMMZ 69555 (4 specimens), 69559 (22), BMNH 1931.2.2.1-6, YPM 6575-6, F. B. Steinbach, March 1929; AMNH 38957-62, MCZ 49577, José Steinbach, 1920.

REFERRED MATERIAL. Bolivia, Cochabamba, Yungas de Cochabamba: UMMZ 69556 (7), BMNH 1931.2.2.7; Locotal (1600 m): UMMZ 69557; Paracti (1900 m): UMMZ 69558 (3); Yungas del Palmar: ZSM 5/1940; Monte Punco (3000 m): ZSM 5/1940; Bolivia: AMNH 22740-41; South America: USNM 59013.

Some of the localities listed above for typical material differ from the original catalog entries for them. The holotype and the paratypes, with the exceptions of AMNH 38957-62 and MCZ 49577 (*ex* AMNH 38956), were originally listed as Tucachaca. Charles F. Walker has informed me that the original label covering all of these specimens was incorrectly transcribed at the University of Michigan; evidence supporting this view has been patiently assembled by Mario Baudin; similarly, the specimens listed from Locotal were originally cataloged as from Sucotal, while those from Paracti were cataloged as from Toracti. BMNH 1931.2.2.7, while cataloged as from Yungas de Achabamba, was received from the University of Michigan Museum of Zoology, and was one of a series with similar data; I have therefore emended the locality to Yungas de Cochabamba.

DEFINITION. Distinguished by characters of the genus.

DESCRIPTION OF HOLOTYPE. Rostral in contact with first supralabial, nasal, and frontonasal. Frontonasal as wide as long. Two prefrontals forming short median suture. Frontal 1.5 times as long as broad. Paired frontoparietals in contact medially. Interparietal 1.75 times as long as broad, with parallel lateral margins. Parietals approximately as long as wide, each in contact medially with interparietal, anteriorly with frontoparietal, third supraocular, fifth superciliary, two temporal scales, and paramedian occipital scale. Nasal divided posterior to nostral, suture touching frontonasal

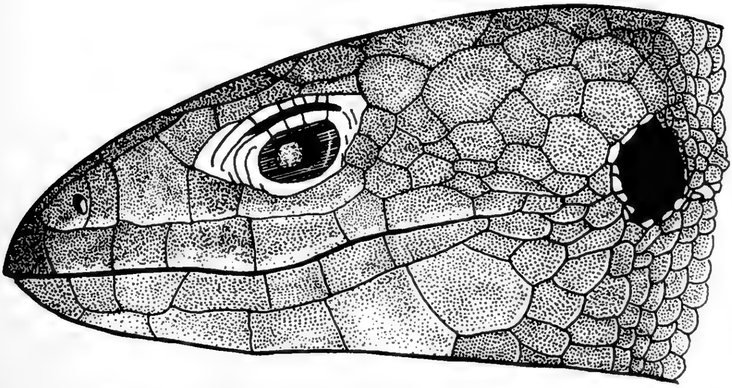


FIG. 1. Lateral head scales of the holotype (UMMZ 128835) of *Opipeuter xestus*, new species (× 8).

and first supralabial. Loreal touching prefrontal, second supralabial, and part of third. Beneath eye, a short frenoocular above third supralabial, and a long subocular touching third, fourth, and fifth supralabials. Six supralabials on each side; three supraoculars, first largest, third intermediate, second smallest; contact between first and third separating second from superciliary series on both sides. Superciliary series complete; large first superciliary expanded onto dorsal surface of head; three smaller scales adjacent to supraoculars; an enlarged fifth superciliary scale at hind margin of eye. Temporal scales flat, polygonal. Median occipital and paramedian occipital scales present. Disc in lower eyelid relatively large, occupying about ¾ diameter of eye itself. Ear opening taller than wide, about size of disc in lower eyelid; tympanum recessed within external auditory meatus. Mental followed by one unpaired chinshield 1.5 times as wide as long, and by four paired chinshields; first three chinshields in contact medially. The pregular scales (Ruibal 1952) smooth, polygonal, in irregular rows; anterior gulars small, roughly quadrilateral, with rounded posterior margins; posterior gulars larger with approximately same shape; gulars forming 8 rows anterior to collar; collar of 10 scales, rather larger than posterior gulars, largest scales median, all with rounded posterior edges.

Dorsal body scales smooth; on neck, wider than long, posteriorly, longer than wide; sides of dorsals subparallel except for median row; posterior margins rounded. Lateral scales smaller than dorsals or ventrals, forming wide band between them; laterals of same shape as dorsals, smooth, with rounded posterior margins. Ventral scales smooth, longer than wide anteriorly, wider than long at midbody, longer than wide posteriorly; edges subparallel, posterior margins rounded. Two large scales in anterior row of preanals, four large median and two minute lateral scales in posterior row; median preanals narrow, widening slightly from anterior to posterior; larger lateral posterior preanal scales almost as wide as long. Femoral pore series separated from preanal area by small scales; posterodistal edge of each femoral pore bounded by small scale. Scales on forelimb smooth; anteriorly and dorsally, larger; beneath, granular; subdigital lamellae simple, not divided; scales of palm granular; scales along margin between thumb and wrist not conspicuously enlarged. Scales of hind limb smooth; thigh with large rounded scales anteriorly, small granules posteriorly; shank with large rounded scales anteriorly and ventrally, with smaller scales dorsally; subdigital lamellae simple, divided, the separate parts not forming tubercles; scales of sole granular. Claws relatively robust. On tail, scales with essentially same shape above as dorsal scales; laterally, with similar shape but narrower; two median ventral rows somewhat wider than lateral rows adjacent to them.

Color and pattern obscure; a light line on two mid-dorsal rows bordered on either side by darker area; a thin, white line encircling tympanum, continuing posteriorly to collar, where broken, and on to above the arm insertion; ground color above dark gray drab; below light; each ventral scale with gray-black mark occupying most of scale area; steel gray area of mid- and posterior ventral scales surrounded by white borders and with melanin in them more diffuse; under surface of tail light; rest of tail dark except for suggestion of light line dorsally.

Snout to vent length 44 mm; tail tip regenerated; hind leg length 18 mm.

VARIATION. Most of the variation observed is given in Table 1. All but one of the specimens have 3-3 supraoculars; the exception has two supraoculars on the left; two individuals have an additional granule present on each side. Thirty-one individuals have the second supraocular on both sides excluded from the superciliary series by contact between the first and third supraoculars; 9 additional specimens have the second supraocular so excluded on one side. All but two specimens have a distinct median occipital; in one, the median occipital has a short longitudinal groove in its anterior end; another has two small scales, apparently representing a longitudinally divided median occipital. A loreal is present on all but one side of one individual; in this animal, a short vertical groove begins at the supralabials and indicates the outline of a loreal. The single loreal touches both frontonasal and supralabials in most individuals. In one, the loreal is divided into upper and lower scales on both sides; in six, it is divided on one side only; two additional individuals have one loreal semi-divided. Four individuals were recorded as having 10 longitudinal rows of ventral scales; the others were recorded as having 8 such rows, but at least 12 of these could have been recorded as 9 or 10. All but one of the specimens examined has the nasal divided on both sides; the exception has a groove ¾ of the way across the nasal beginning at the dorsal margin. The pattern of the division in the nasal varies considerably. Usually there is a groove vertically behind the nostril from the frontonasal to the first supralabial. In many individuals the dorsal end of the groove is shifted posteriorly along the dorsal margin of the nasal, or even down the posterior margin

TABLE 1. Variation in certain characters of *Opipeuter xestus*. Figures are ranges and (in parentheses) means.

Locality	Dorsal Scale Rows	Scales Around Midbody Region	Subdigital Lamellae		Total Femoral Pores	Transverse Rows of Ventrals
			4th toes	4th fingers		
Incachaca						
24 ♂♂	34-43 (39.0)	28-34 (30.7)	21-26[1] (23.8)	16-20[2] (17.8)	15-20 (17.1)	22-26 (24.4)
18 ♀♀	38-42 (39.9)	27-34[3] (30.7)	20-26[4] (23.2)	16-20[5] (18.0)	0-16 (3.0)	23-27 (25.2)
Cochabamba						
4 ♂♂	36-41 (38.0)	32-35 (33.0)	23-26[6] (24.0)	17-19 (17.9)	16-18 (16.7)	24-26 (25.3)
4 ♀♀	39-41 (40.0)	29-35 (31.0)	21-24 (22.5)	15-19 (17.4)	0-17 (7.8)	24-27 (25.5)
Paracti						
2 ♂♂	39-40	33-34	24[7]	16-18[7]	18-20	23-24
1 ♀	45	32	20-21	17-18	3	27
Locotal						
1 ♂	37	33	24	17-19	16	23
Monte Punco						
1 ♂	45	25	20-21	16-17	12	28
Palmar						
1 ♀	40	29	22-23	17	2	25
Miscellaneous						
1 ♂	35	30	22	17	18	26
2 ♀♀	38-40	30-33	20-22	14-16	2-20	26-27

[1] 45 digits; [2] 46 digits; [3] 17 females; [4] 31 digits; [5] 34 digits; [6] 7 digits; [7] 2 digits.

of the nasal so that only the posteroventral corner of the nasal shield is cut off. The long subocular is present in most individuals; in one it is divided on one side. This scale, together with the frenoocular, forms the complete lower margin of the eye opening. Usually the posterior end of the subocular lies over the fifth supralabial. Due to fusion or subdivision of labial scales, it may end over a fourth supralabial (1 side) or a sixth (3 sides).

The greatest variation noted was in coloration. In UMMZ 69558, in 6 specimens of UMMZ 69556, and in BMNH 1931.2.2.7, the general appearance of the lizard is much lighter than in the holotype or paratypes. This appears to be due to a reduced areal extent of the dark pigments, and a covering of them by a whitish pigment. The result is that the dark brown border of the grayish dorsal light line makes much greater contrast both with the light line and with the dull tan ground color lateral to the border, rather than getting lost in the generally dark dorsal color. The light line encircling the ear opening and continuing posteriorly along the side is wider and bordered above and below by dark brown. The venter is generally light, although many specimens show grayish spots caused by the blackish pigment showing through the whitish pigment that lies over it. It is highly probable that this variation is due to preservation of the darker individuals in formalin, the lighter ones in ethanol.

The largest male examined was 51 mm snout to vent; the largest female, 58 mm. Eight males 31 to 44 mm snout to vent with tail intact had tail over snout-vent length ratios of 1.8 to 2.0, mean 1.92; 4 females 46 to 50 mm snout to vent had ratios of 1.6 to 1.7, mean 1.67. Hind leg over snout-vent length ratios varied from 0.41 to 0.46 for small males (26 to 35 mm snout to vent), from 0.41 to 0.47 for longer ones (36 to 51 mm snout to vent). For females 42 to 55 mm snout to vent, this ratio varied from 0.38 to 0.43.

SEXUAL DIMORPHISM. The most conspicuous sexual dimorphism is in femoral pore number (Table 1). Although occasional females have pore counts of 13, 15, 17, or even 20, the great majority have 0, 2, or 4. In all females, however, the pores that are present are distal on the thigh rather than proximal; when the number in the series matches that found in males, the pore series reaches the proximal end of the thigh. There is variation in the number of preanal scales. Sixteen males were recorded as having 4 posterior preanal plates; one has 3, another 3 and 2 very small lateral scales. Thirteen have 4 large posterior preanals, plus 2 minute lateral slivers. One male has 5 posterior preanals, another 6; in these two, the outermost scale on each side is thin. Among the females, in contrast, counts of 6 were recorded for 15 individuals, although the outermost scales on each side in these is narrow. Eight other females have 4 posterior preanals plus a minute additional scale on each side. One count of 4 and two of 5 were also recorded.

HEMIPENIS OF OPIPEUTER XESTUS. The left hemipenis of one male from UMMZ 69559 was removed, washed overnight in distilled water, stained in a solution of alizarin red S in 0.5 percent KOH, and destained in distilled water. In order to insure rapid penetration of the dye, the hemipenis was slit along the sulcus spermaticus. After destaining, the hemipenis was completely opened on the ventral side by enlarging the slit in the sulcus. Photographs of various features are shown in Figs. 2 and 3.

It was possible to open the hemipenis for approximately half of its total length; the remaining part is largely made up of retractor muscle, and is not shown in Fig. 2. Within the basal half, there are two sets of flounces each with numerous members; each flounce contains numerous fine, calcareous spinules. These flounces form chevron-shaped folds in the inverted hemipenis, with the free ends on the median welt dorsally and adjacent to the sulcus spermaticus ventrally. The apices of the chevrons are basal. In the unopened and inverted hemipenis, each lateral flounce begins on the ventral side near the sulcus spermaticus, spirals diagonally toward the base around the lateral side of the space within the inverted hemipenis to form an angle dorsal to the lateral free edge of the median welt, after which each spirals distally around the lateral free edge of the dorsally placed median welt and end on its ventral side; each median flounce follows an essentially mirror-image

---

FIG. 2. Structure of the left hemipenis of *Opipeuter xestus* (UMMZ 69559). The inverted organ has been slit along the sulcus spermaticus. A. The basal part, showing general arrangement of flounces in the lateral (left) and medial (right) pockets, and locations of groups of enlarged teeth (× 17). B. Enlarged teeth on lateral wall of sulcus spermaticus (× 29). C. Enlarged teeth at base of median welt (× 29).


B
C
A

FIG. 3. Details of flounces and minute spines in the medial pocket of inverted left hemipenis of *Opipeuter xestus* (UMMZ 69559). The median welt has been folded back to show the apices of the chevron-shaped flounces (× 27).

course. When the hemipenis is slit and laid open along the ventral, sulcus-bearing side, the two sets of flounces line two distinct pockets. There are 21 medial and 19 lateral folds in the medial pocket (Fig. 3), and 15 medial and 19 lateral folds in the lateral pocket.

The spines do not continue across the apex of the flounce, although the flounces are continuous.

Basally, on the median welt, there are a series of enlarged spines. These form three rows, the most basal (scarcely visible in Fig. 2C) with four teeth, the middle with seven teeth, and the most distal (uppermost in Fig. 2C) with eight teeth.

On each side of the sulcus spermaticus there is a row of enlarged spines (Fig. 2A, B). There are three spines along the lateral edge of the sulcus, five along the medial edge.

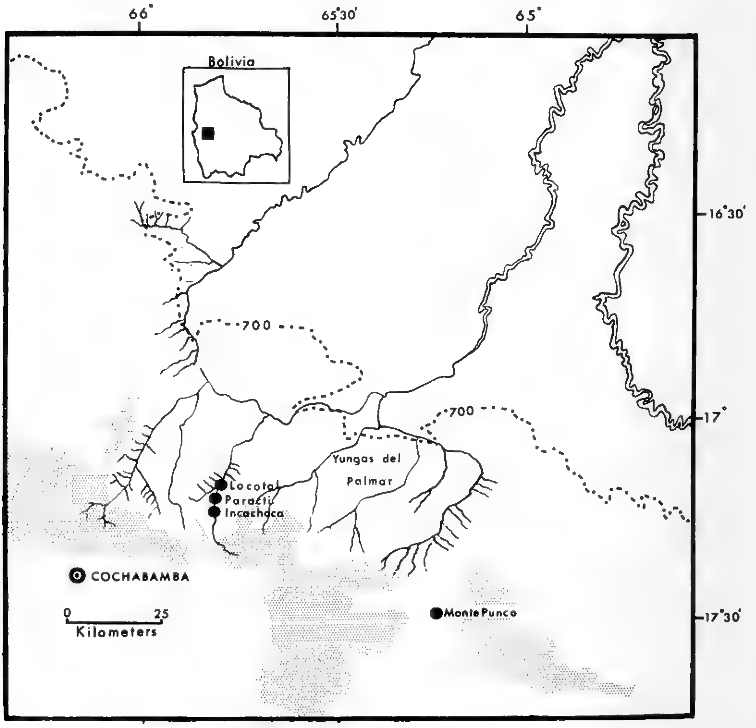
The most common arrangement of the flounces in the hemipenes of lizards of Group II of the Teiidae is a series of chevrons. Variation occurs in their continuity across the apices, across the median welt, in their number and in the number of spinules in them. Enlarged spines may occur at a variety of positions, either in the flounces or in separated groups. The groups of enlarged spines along the sulcus in combination with a group at the base of the median welt has not been observed outside of *Opipeuter*. A survey of these structures in Group II of the Teiidae is in preparation.

BIOLOGY. Nothing is known of the habits of *Opipeuter xestus*. Two leathery eggs, one in each oviduct, are present in each of three females; in all three, the right egg is located more anteriorly. Two other females each contain a single leathery egg, in both cases in the right oviduct.

The enlarged transparent eye disc represents an extreme expression of a widespread altitudinal and latitudinal gradient in teiid lizards of Group II. Northern populations, whether representing local populations of widespread species, restricted species, or even restricted genera, have the disc in the lower eyelid divided by vertical grooves into two to many segments. Usually when the disc is divided, the lens is translucent, although often, especially in populations from higher altitudes, the disc contains black pigment to varying degrees. Southern populations tend to have the disc an oval, undivided, translucent scale. *Opipeuter xestus,* with its large, almost circular, transparent, undivided disc, is extreme. The extent to which the eye is kept open or closed in life is not known, but the great specialization suggests that the lid must be closed most of the time.

RANGE. All of the specimens of *Opipeuter xestus* with detailed data were collected on the eastern Andean slopes of central Bolivia (map). Altitudes associated with the localities vary from 1600 to 3000 m above sea level.

DERIVATION OF NAME. The name *xestus* is derived from the Greek word for smooth, ζεστος.



Collection localities for *Opipeuter xestus* on the eastern Andean slopes of central Bolivia. Dotted line indicates 700 m; areas above 3500 m are shaded.

LITERATURE CITED

Boulenger, George Albert. 1885. Catalogue of the lizards in the British Museum (Natural History), **2**: xiii + 497 pp., 24 pls. Taylor and Francis, London.

——— 1906. Descriptions of new lizards in the British Museum. Ann. Mag. Nat. Hist. (7) **19**: 486-489.

Ruibal, Rodolfo. 1952. Revisionary studies of some South American Teiidae. Bull. Mus. Comp. Zool. Harvard Coll. **106** (11): 477-529.

Werner, Franz. 1899. Beschreibung neuer Reptilien und Batrachier. Zool. Anz. **22**: 479-484.

INFORMATION FOR AUTHORS

REVIEW	The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
STYLE	Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).
FORM	Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.
TITLE	Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
ABSTRACT	The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
OMENCLATURE	Follow the International Codes of Zoological and Botanical Nomenclature.
ILLUSTRATIONS	Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
FOOTNOTES	Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
TABLES	Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
REFERENCES	The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
THOR'S COPIES	Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
PROOF	Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
COPYRIGHT	Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 130.   18 MAR. 1969

KARYOLOGICAL HETEROGAMETY OF DEEP-SEA FISHES

T. R. CHEN

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

KARYOLOGICAL HETEROGAMETY OF DEEP-SEA FISHES

T. R. CHEN
Department of Biology
Yale University

ABSTRACT

Among 25 deep-sea fish species karyologically investigated, digamety is confirmed in 12. Observations were based on the consistent appearance of heteromorphic chromosome pairs, of asymmetrical and atypically behaving "sex" bivalents, and of two different chromosome counts from metaphase II. The occurrence of such digamety in other lower vertebrates is discussed. It occurs more frequently among teleostean fishes and other lower vertebrates than previously expected.

POSTILLA 130: 29 p.   18 MARCH 1969.

INTRODUCTION

Probable cytological digamety has been repoorted in several fishes before 1945 (Geiser, 1924; Foley, 1926; Vaupel, 1929; Ralston, 1933, 1934; Bennington, 1936; and Barigozzi, 1937). But its occurrence was questioned by Friedman and Gordon (1934), Makino (1934a, b), and Wickbom (1941, 1943), who doubted that atypical bivalency indicated heterogamety and denied any evidence of cytological sex differentiation. In the gwyniad *Coregonus lavaretus,* Svärdson (1945) discovered that most karyotypes of blastomeres from about half of the embryos examined included a supernumerary chromosome. But this chromosome was absent in testicular preparations from adult males. Consequently, he claimed that this fish was female heterogametic and that the supernumerary probably was the female-determining chromosome. In two specialized perciform fishes, *Mogrunda obscura* and *Cottus pollux,* Nogusa (1955, 1957) described possible XY male heterogamety from observations of heteromorphic and heteropycnotic bivalents. Lieder (1963) observed a non-paired chromosome "fragment" in the percid *Acerina cernua* and a satellited chromosome in the percid *Perca flaviatilis* and the freshwater eel *Anguilla anguilla,* and suggested that the "fragments" or "satelliteds" might be male-determining Y-chromosomes. He cautioned, however, that the partner of the satellited chromosome was probably not an X-chromosome but rather an autosomal homologue, indicating a "YO" sex type. Chen and Ebeling (1966) reported heteromorphic mitotic X and Y chromosomes and their presumed bivalent showing end-to-end chromatic association from all specimens of the deep-sea fish *Bathylagus wesethi* examined. Its heterogamety was further substantiated by the occurrence of two X's in tetraploid cells, probably from testicular supporting tissue, and by the occurrence of two dissimilar counts from secondary spermatocytes, one including, the other excluding this remarkably large chromosome. Moreover, by examining different somatic tissues (gill epithelium, spleen and kidney) as well as gonads, Chen and Ebeling (1968) reported cytological heterogamety in the mosquitofish *Gambusia affinis,* in which the female karyotype is characterized by a large metacentric, which, however, is absent in the male. We concluded that the mosquitofish is female-heterogametic of the WZ-ZZ sex type.

The cytology of deep-sea fishes, which are adapted to a remote, cold, dark, hyperbaric, relatively impoverished environment, has been little studied. Adaptation to such a stress condition may include various atypical cytological expressions (cf. Stebbins, 1966). The present paper reports the probable occurrence of cytologically expressed digamety among 25 selected deep-sea fishes.

Materials and Methods

Specimens were captured off the coast of southern California as far as Guadalupe Island, Mexico. Most tissues were first placed in 0.9 percent sodium citrate for about 20 minutes, then fixed in 1 : 3 acetic alcohol, and stored under refrigeration. A few live specimens of *Lampanyctus ritteri, Triphoturus mexicanus,* and *Bathylagus ochotensis* were injected intra-peritoneally with 0.05 percent colchicine. They were maintained for about two hours at 5°C, then killed and fixed. These colchicinized specimens provided many good metaphase plates. In total, about one thousand preparations from 114 specimens were examined or about 40 preparations from 2-10 specimens per species. Tissues for the squash preparations were mainly testicular; the only female tissues observed were ovarian metaphase plates from two halfgrown females of *Lampanyctus ritteri.* Occasionally kidney tissue provided good metaphase plates. Tissues were usually stained with aceto-orcein. Photomicrographs of the preparations were taken under both bright and phase-contrast optics.

Observations

The 25 deep-sea fish species are grouped according to their ordinal affinities: (1) the generalized salmoniform family Bathylagidae, (2) the related family of hatchetfishes, Sternoptychidae, (3) the evolutionarily intermediate myctophiform families of lanternfishes, Neoscopelidae and Myctophidae, and (4) the more specialized pre-percoid beryciform families Melamphaidae and Anoplogasteridae.

A). BATHYLAGIDAE. Bathylagids are typically mesopelagic (middepth) fishes, which live between 100 and about 1000 meters in the open ocean. This family includes but three or four deep-sea mesopelagic genera (Cohen, 1964). Cosmopolitan *Bathylagus* contains five Californian species, four of which were investigated (Figs. 1-10). Their diploid numbers range from 36 in *Bathylagus wesethi* to 64 in *B. stilbius*. Their male karyotype is unique in that its largest element, the presumed X chromosome, apparently comprises a considerable percentage of the total nuclear chromatin and lacks any homologue approaching it in size or morphology. Also, in all species but *wesethi,* it includes a series of very small chromosomes.

The presumed X is the largest metacentric chromosome in *B. wesethi, ochotensis,* and *milleri* but it is submetacentric in *stilbius* (Figs 1, 4-6). It is almost 1.5 times as long as the next largest chromosome in all but *ochotensis*. The presumed Y is acrocentric and is the smallest in *wesethi* but the next largest chromosome in the complements of *stilbius* and *ochotensis*. In *milleri,* which is the deepest-living species, it defies identification amongst the relatively large series of small dot-like chromosomes. In *wesethi* the sex bivalent, whose X and Y are associated end-to-end, appears satellited during metaphase I (cf. Chen and Ebeling, 1966, and Fig. 2). In metaphase II, two morphotypes, one with the "X" and the other without it, are readily identifiable (cf. Chen and Ebeling, 1966, and Fig. 3). Therefore, cytological male heterogamety is best demonstrated in this species. Although in the other species the karyotypes of secondary spermatocytes are unclear, their mitotic karyotypes and their presumed sex bivalent resemble those of *wesethi* (Figs. 7-10).

B). STERNOPTYCHIDAE. Hatchetfishes are small and common vertical migrators of the mesopelagic zone and like most such migrators have light organs, which are ventrally oriented. Four Californian species were studied. Their karyotypes are characterized by the presence of several chromosome pairs that are noticeably larger than the rest. Also, satellited pairs are relatively numerous, metacentric and submetacentric chromosomes dominate the complement, and heterochromatic bodies ("chromocenters") are distinctly expressed. Some of the larger chromosomes have many distinct heterochromatic bands throughout their length. In three species of *Argyropelecus,* sex chromosomes are not detectable. However, the diploid number of *Sternoptyx diaphana* is always 35 (Figs. 11, 12). The largest among five acrocentrics in the male complement is apparently unpaired. This may be the X of an XX-XO sex type and is the fifth largest pair in the complement. Among leptotene cells, an elongate deeply stained body, which morphologically resembles the unpaired "sex chromosome" from somatic cells, is presumably a heterochromatic sex element (Fig. 13) but is not observable, however, during later stages of meiosis. Occasionally, one to four other "chromocenters" occur simultaneously, but invariably they disappear earlier than the morphologically persistent "sex element." In metaphase I the presumed univalent X, which is morphologically indistinguishable from the mitotic X, is clearly observable (Fig. 14). In metaphase II two morphotypes are detectable (Fig. 15): one with 18 elements and the other with 17 elements and presumably lacking the X chromosome.

c). NEOSCOPELIDAE and MYCTOPHIDAE. Comprising more than 30 genera (Fraser-Brunner, 1949; Bolin, 1959, 1966), lanternfishes are the most speciose and among the most abundant of all deep-sea fishes. Species are often distinguished by differences in the patterns of light organs on the flanks and belly. Of about 25 species that occur off California, 11 were investigated cytologically (Figs. 16-29). Most karyotypes are 2n=48, with acrocentric chromosomes predominating. The chromosomes are subequal in length, excepting the presumed X and one or two pairs. The times of occurrence and disappearance of heterochromatic bodies during prophase I distinguish taxonomic groups within the Myctophidae.

In *Scopelengys,* the only Californian representative of the relatively primitive Neoscopelidae, an atypically behaving bivalent, whose univalents are associated end-to-end, always occurs at the periphery of the metaphase plate; it is probably composed of subequal sex chromosomes (Fig. 17). In *Symbolophorus californiensis* of the family Myctophidae, a "sex bivalent" occurs at the periphery of the metaphase I plate. It is formed of two submetacentrics associated end-to-end and lags behind the others during anaphase I when its four arms are clearly detectable (Figs. 19-21). In the mitotic complement the first and fourth largest chromosomes are submetacentric and probably constitute the sex chromosome pair. In the above two species, a heterochromatic "sex element" (cf. *Sternoptyx diaphana*) is clearly detectable in leptotene cells (Figs. 16 and 18). In *Lampanyctus ritteri* the diploid number is 47 in males but 48 in females (Figs. 22, 23). The largest chromosome in the male complement is submetacentric but two such elements are observable in females. Probably, therefore, this species is male heterogametic of the XX-XO sex type. The X-chromosome usually but not always forms a characteristic Y-shaped trivalent, probably with a particular autosomal bivalent (Fig. 24). In anaphase I (Fig. 25) and metaphase II (Fig. 26) counts clearly are n=24 with the X and n=23 without the X. This asymmetry is also observable in the specialized deep-living species *Parvilux ingens,* whose diploid number is 49 in males (Fig. 27). During metaphase I the presumed X, which behaves differently and forms either a V or ring, may appear chromatically associated at both poles (Fig. 28). In metaphase II, counts were n=25 with the X and 24 without the X (Fig. 29).

D). MELAMPHAIDAE and ANOPLOGASTERIDAE. These families generally live at greater depths than the previous species. Like many bathypelagic fishes, they lack light organs and probably do not undergo extensive diurnal vertical migrations (Ebeling, 1962). Five melamphaids and monotypic *Anoplogaster cornuta* were studied (Figs. 30-35). The complement is made up either of subequal chromosomes in most species or of many very small acrocentric chromosomes in others, e.g., *Poromitra crassiceps.* Generally, acrocentrics dominate the complements, which are unusually variable in number among the genera. The heterochromatic bodies ("chromocenters") are clearly observable during early prophase I.

A heteromorphic "sex bivalent" is detectable in *Melamphaes parvus* and *Scopeloberyx robustus* (Figs. 34-35). In *Scopelogadus mizolepis bispinosus* a large, "lampbrush-like" bivalent, which differs from all others in having broad sections between its narrowed ends, is observable during zygotene and pachytene (Fig. 32). This "sex bivalent" is observable until metaphase I, shows no chiasmata, and may be associated end-to-end (Fig. 33). In the mitotic complement a pair of relatively long chromosomes obviously differ in length and probably constitute the heteromorphic sex pair (Fig. 30).

DISCUSSION

Cytologically expressed digamety had previously been reasonably verified in only seven of 260 teleost fishes hitherto investigated (cf. Chen, 1967); however, the present results indicate that 12 of 25 deep-sea species have heteromorphic chromosome pairs, presumably of the XX-XY or XX-XO sex type. This disparity may be due primarily to technological difficulties in properly preparing slides for detailed study and to the generally small chromosome size of shallow-water fishes (Chen, 1967; Chen and Ebeling, 1968). Measuring five to six microns, however, most deep-sea fish chromosomes in mid-metaphase are two to three times as long as those of the shallow-water fishes which I and others have studied. Also the use of aceto-orcein has facilitated the present study because of its deep-staining affinity for chromatin. This allows examination of detailed chromosomal structures, which often are obscure in shallow-water fishes. Giemsa stains shallow-water fish chromatin very well, but is less effective than orcein for staining deep-sea fish chromatin.

Although in most deep-sea fishes, observations of sex chromosomes were made on testicular preparations only, abundant evidence substantiates the common occurrence of heteromorphic sex pairs: (1) these pairs are consistently observable among the tissues of different individuals, (2) males of some species have odd-numbered diploid counts, which were based on examination of at least three individuals from each species, (3) asymmetrical bivalents are always observable in metaphase I, and (4) the expected different haploid counts occur in MII in those species of the presumed XX-XO sex type. During metaphase I the atypically behaving "sex element" of *Scopelengys tristis* and *Parvilux ingens* always occurs outside the concentration of other bivalents in the metaphase plate. In *Scopelogadus m. bispinosus,* the only morphologically distinct chromosome during prophase I and metaphase I is probably the sex bivalent. In leptotene, a distinctly stained body, which is presumably of heterochromatic sex element and is easily distinguishable from "chromocenters," is observable in *Bathylagus milleri* (Fig. 10), *Sternoptyx diaphana, Scopelengys tristis, Symbolophorus californiensis,* and *Scopelogadus m. bispinosus* (Fig. 31).

The characteristic X of bathylagids is always distinctly longer than other chromosomes in the complement. This is substantiated in *Bathylagus wesethi,* whose two different types of metaphase II cells, one with and the other without this longest chromosome occur in equal frequency (Chen and Ebeling, 1966; and Chen, 1967). This strongly suggests that metaphase II cells without this element are not eliminated as zygotic lethals, i.e., that the chromosomal heteromorphy is an incident of isochromosomal fusion (Chen and Ebeling, 1966). Such a high frequency of deleterious cells would appear disadvantageous to this species and others in the family which have similar karyotypes. But, in fact, *Bathylagus stilbius,* whose karyotype is also characterized by the presence of a single distinctly hypertrophied chromosome in the complement, is one of the most abundant (i.e., most successful) mesopelagic deep-sea fishes in the eastern North Pacific Ocean. Therefore, it is most reasonable to assume that the large chromosome is the female-determining chromosome. The Y is interspecifically variable. It is the largest acrocentric chromosome in *Bathylagus ochotensis* but the smallest in *B. wesethi.*

Several investigators have suggested that intra-individual karyotypic polymorphism may commonly occur in shallow-water fishes (Ohno, Stenius, Faisst, and Zenzes, 1965; Ohno and Atkin, 1966; Beçak, Beçak, and Ohno, 1966).However, the intra- and inter-individual consistency of heteromorphic pairs observed in the present study seems unlikely to be the result of chromosomal interchanges. For example, not one bathylagid cell among about thirty specimens examined lacked the characteristic X chromosome. In the three hatchetfishes and lanternfishes of the presumed XX-XO sex type, the odd diploid counts in males were always based on more than 30 well spread metaphase plates. Also, the regular presence or absence of the large unpaired chromosome in secondary spermatocytes further substantiates their heterogamety.

Consequently, the occurrence of heteromorphic chromosome pairs may be much more widespread among teleosts than previously suspected. Also, the "Superorder" Teleostei is an evolutionarily diverse group, which has undergone extreme adaptive radiation. It is hardly conceivable that sex chromosomes remain primitively undifferentiated among its generalized and specialized species alike. Evidence of cytological digamety is accumulating in other lower vertebrates. For example, Nogusa (1957b) reported male heterogamey in the protochordate lancelet *Branchiostoma belcheri,* whose X is the largest and Y the smallest in the complement; Yosida (1957) observed it in the treefrog *Hyla arborea japonica;* and Gorman and Atkins (1966) and Gorman and Holzinger (1967) reported digamety in several species of the lizard *Anolis,* whose multiple sex-chromosome mechanism consists of $X_1X_1X_2X_2$ in females and X_1X_2Y in males.

ACKNOWLEDGMENT

I am grateful to: Dr. A. W. Ebeling (University of California at Santa Barbara), who advised me on collection methods, species identifications, and taxonomic relationships, for his most helpful assistance throughout the present work and also for reviewing the manuscript; Drs. F. H. Ruddle (Yale University), who also provided facilities in the later period of preparation of the manuscript, for reviewing the manuscript, C. L. Remington (Yale University) and S. Ohno (City of Hope Medical Center) for their stimulating discussions and valuable criticisms; and Mrs. A. W. Ebeling for her encouragement. My sincere gratitude goes to all personnel and organizations allowing my participation in cruises in the waters off southern California and Mexico from the General Motors R/V SWAN and the University of Southern California R/V VELERO.

This study was supported mainly through National Science Foundation grants in Systematic Biology, GB 1654 and 4277. The ship time for the collection of specimens was financed by NSF grants G-10691 to the University of Southern California, and GB 2867 and 2698 to the University of California at Santa Barbara. Further support was obtained from USPHS grant GM-9966-06.

LITERATURE CITED

Barigozzi, C. 1937. La gametogenesi e la sessualita di *Cyprinus carpio* var. specularis. Atti Soc. ital. Milano **76**: 88-104.

Beçak, W., M. L. Beçak, and S. Ohno. 1966. Intra-individual chromosomal polymorphism in green sunfish *(Lepomis cyanellus)* as evidence of somatic segregation. Cytogenetics **5**: 313-320.

Bennington, N. L. 1936. Germ cell origin and spermatogenesis in the Siamese fighting fish, *Betta splendens.* J. Morph. **60**: 103-125.

Bolin, R. L. 1959. Iniomi. Myctophidae from the "Michael Sars" North Atlantic deep-sea expedition 1910, p. 1-45. *In* Rept. Sci. Results "Michael Sars" N. Atlantic Deep-sea Expedition 1910, 4 (pt. 2, no. 7).

———— 1966. Interim account of family Myctophidae, p. 190-191. Interim account of family Neoscopelidae, p. 192-193. *In* Fishes of the western north Atlantic. Mem. Sears Foundation Mar. Res. **1** (5).

Chen, T. R. 1967. Comparative karyology of selected deep-sea and shallow-water teleost fishes. Ph.D. Dissertation, Yale University.

——— and A. W. Ebeling. 1966. Probable male heterogamety in the deep-sea fish *Bathylagus wesethi* (Teleostei: Bathylagidae). Chromosoma (Berlin) **18**: 88-96.

——— 1968. Karyological evidence of female heterogamety in the mosquitofish *Gambusia affinis* (Baird and Girard). Copeia, 1968 (1): 70-75.

Cohen, D. M. 1964. Suborder Argentinoidea, p.1-70. *In* Mem. Sears Foundation Mar. Res. **1** (4).

Ebeling, A. W. 1962. Melamphaidae I. Systematics and zoogeography of the species in the bathypelagic fish genus *Melamphaes* Günther. Dana Rept. **58**: 58 p.

Foley, J. O. 1926. The spermatogenesis of *Umbra limi* with special reference to the behavior of the spermatogonial chromosomes and the first maturation division. Biol. Bull. **50**: 117-147.

Fraser-Brunner, A. 1949. A classification of the fishes of the family Myctophidae. Proc. Zool. Soc. Lond., **118** (4): 1019-1106.

Friedman, B. and M. Gordon. 1934. Chromosome numbers in xiphophorin fishes. Amer. Nat. **68** (718): 446-455.

Geiser, S. W. 1924. Sex ratios and spermatogenesis in the top-minnow, *Gambusia holbrooki*. Biol. Bull. **47**: 175-212.

Gorman, G. C. and L. Atkins. 1966. Chromosomal heteromorphism in some male lizards of the genus *Anolis*. Amer. Nat. **100**: 579-583.

——— and T. Holzinger. 1967. New karyotypic data on 15 genera in the family *Inguanidae*, with a discussion of taxonomic and cytological implications. Cytogenetics **6**: 286-299.

Lieder, U. 1963. Über vermutiliche Gonosomen bei *Perca, Acerina* und *Anguilla* (Vertebrata, Pisces). Biol. Zbl. **82** (3): 296-302.

Makino, S. 1934a. The chromosomes of the sticklebacks, *Pungitius tymensis* (Nikol'sky) and *P. pungitius* (Linnaeus). Cytologia **5**: 155-168.

——— 1934b. Notes on the chromosomes of some fresh-water teleosts. Jap. J. Genet. **9** (2): 100-103.

Nogusa, S. 1955. Chromosome studies in Pisces. IV. The chromosomes of *Mogrunda obscura* (Gobiidae), with evidence of male heterogamety. Cytologia **22**: 11-18.

——— 1957a. Chromosome studies in Pisces. VI. The X-Y chromosomes found in *Cottus pollux* Günther (Cottidae). J. Fac. Sci. Hokkaido Univ., Ser. VI — Zool., **13**: 289-292.

——— 1957b. The chromosomes of the Japanese lancelet, *Branchiostoma belcheri* (Gray), with special reference to the sex-chromosomes. Annot. Zool. Jap. **28**: 249-255.

Ohno, S., and N. B. Atkin. 1966. Comparative DNA values and chromosome complements of eight species of fishes. Chromosoma (Berlin **18**: 455-466.

——— C. Stenius, E. Faisst, and M. T. Zenzes. 1965. Post-zygotic chromosomal rearrangements in rainbow trout (*Salmo irideus* Gibbons). Cytogenetics **4**: 117-129.

Ralston, E. M. 1933. The chromosomes of *Xiphophorus, Platypoecilus* and their hybrids during the maturation stages. Science **78**: 124-125.

——— 1934. A study of the chromosomes of *Xiphophorus, Platypoecilus* and *Xiphophorus* X *Platypoecilus* hybrids during spermatogenesis. J. Morph. **56**: 423-433.

Stebbins, G. L., Jr. 1966. Chromosomal variation and evolution. Science **152** (3728): 1463-1469.

Svärdson, G. 1945. Chromosome studies on Salmonidae. Rept. Swedish State Inst. Fresh-water Fish. Res. **23**: 151 p.

Vaupel, J. 1929. The spermatogenesis of *Lebistes reticulatus.* J. Morph. **47**:555-587.

Wickbom, T. 1941. The sex chromosomes of Cyprinodontidae and of teleosts in general with a list of new chromosome numbers of Cyprinodontidae. Arkiv für Zool. **33B** (10): 1-6.

——————— 1943. Cytological studies on the family Cyprinodontidae. Hereditas **29**: 1-24.

Yosida, T. H. 1957. Sex chromosomes of the tree frog, *Hyla arborea japonica.* J. Fac. Sci. Hokkaido Univ. **13**: 352-358.

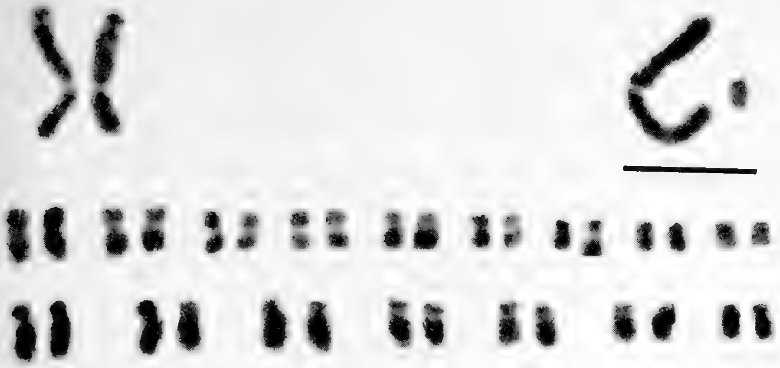
PLATES

(All figures reproduced at same scale: 10μ = 27 mm)

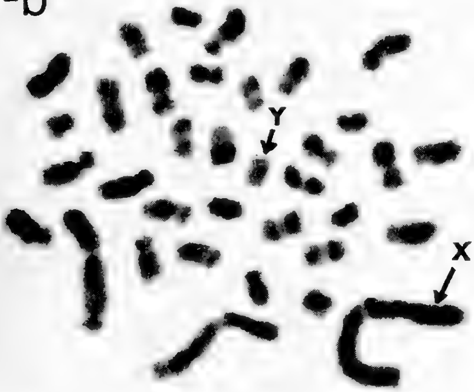
FIG. 1. Karyotype of *Bathylagus wesethi* (2n=36). a. Idiogram. b. Metaphase plate corresponding to a. Presumed X and Y chromosomes are underlined in the idiogram and indicated with arrows in the metaphase plates. (All figures follow same citation as mentioned here. All figures: reproduced at same scale: 10μ=27 mm)

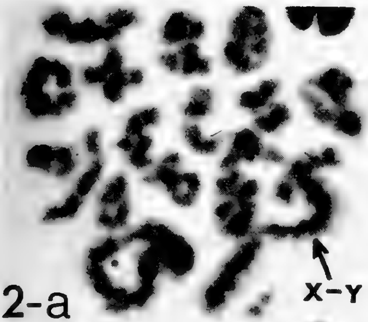
FIG. 2. Premetaphase I (a) and metaphase I (b) of *B. wesethi,* indicating the satellite-like "X-Y" bivalent (arrow).

1-a



1-b





2-a

2-b

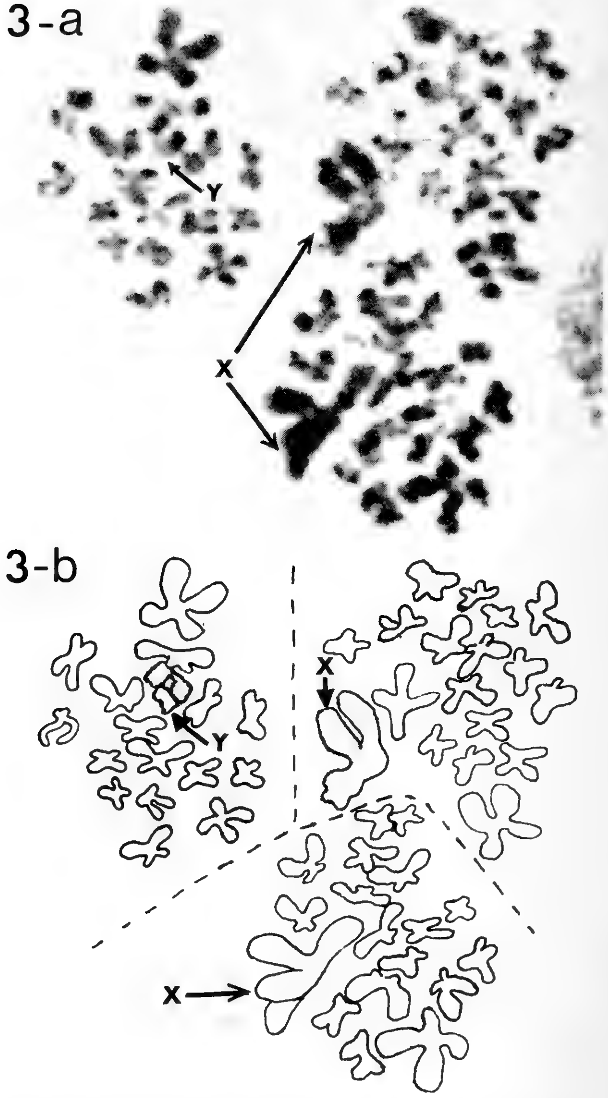


FIG. 3. Metaphase II of *Bathylagus wesethi.* N = 18 with the small "Y" (upper left) and with the large "X" (two cells at right).

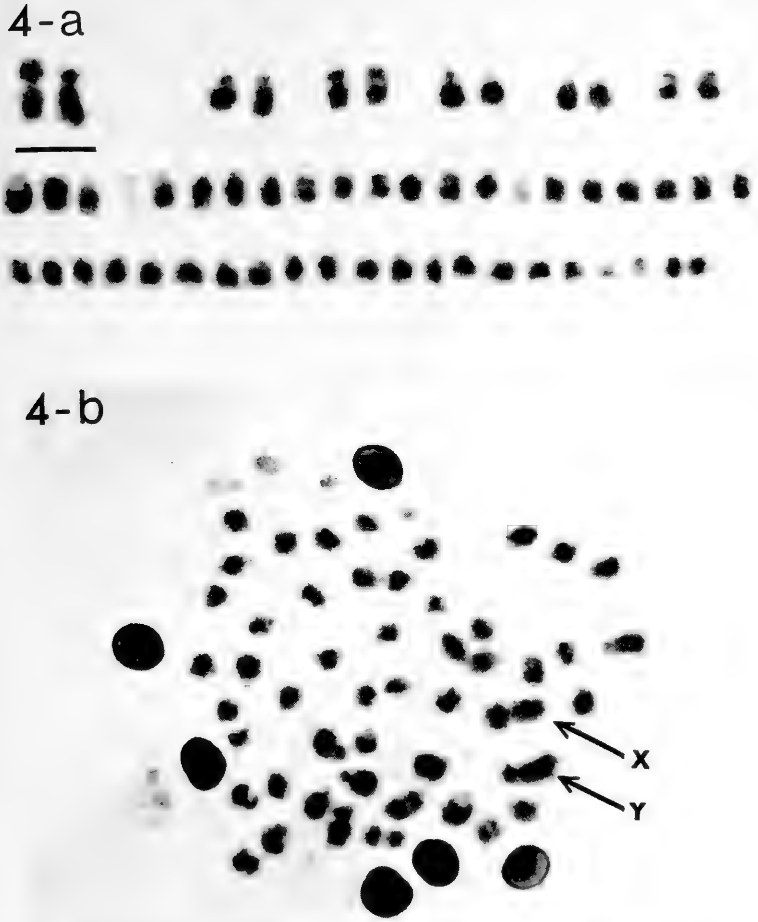


FIG. 4. Karyotype of *Bathylagus ochotensis* (2n=54). a. Idiogram. b. Metaphase plate corresponding to a.

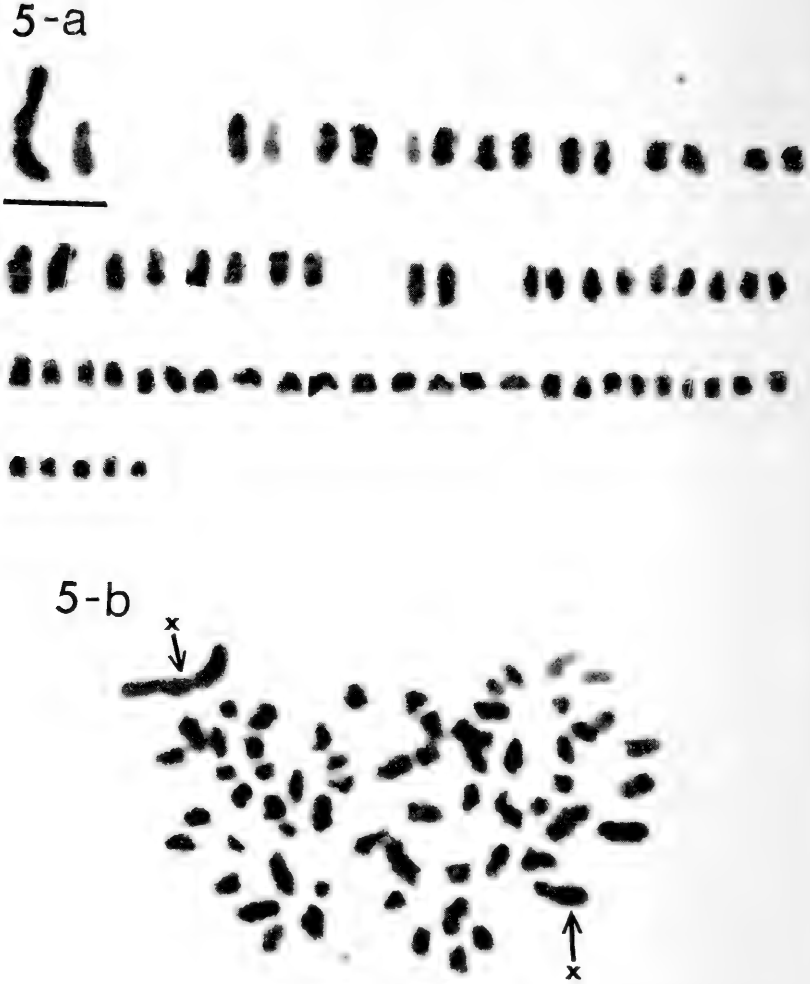


FIG. 5. Karyotype of *Bathylagus stilbius* (2n=64). a. Idiogram. Seven identifiable metacentric (M), 4 submetacentric (SM), and 1 acrocentric (A) pairs are placed separately. The rest are morphologically unidentifiable. b. Metaphase plate corresponding to a.

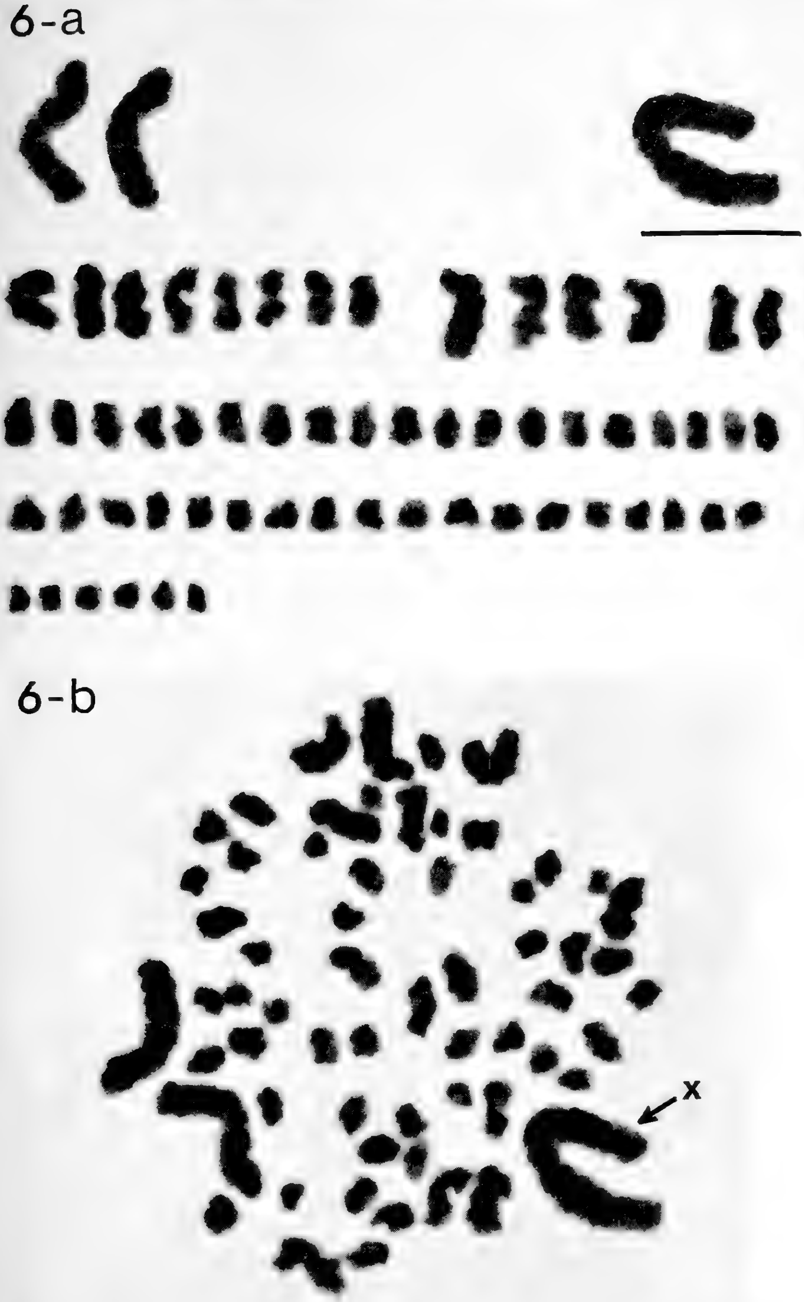
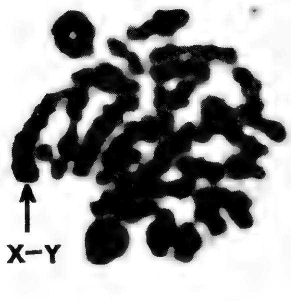


FIG. 6. Karyotype of *Bathylagus milleri* ($2n=60$). a. Idiogram. Morphologically identifiable autosomal pairs are placed separately. (cf. Fig. 5). b. Metaphase plate corresponding to a.

7

8



9

10

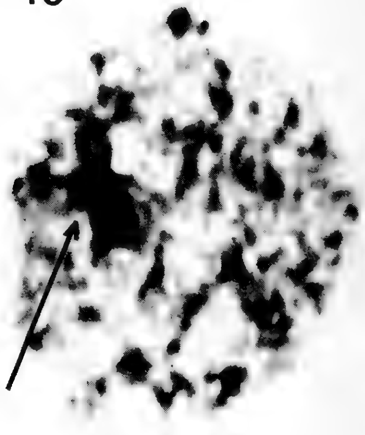


FIG. 7. Metaphase I of *Bathylagus ochotensis.*

FIG. 8. Metaphase I of *B. stilbius.*

FIG. 9. Metaphase I of *B. milleri.*

FIG. 10. Preleptotene of *B. milleri* showing the presumed heterochromatic sex element (arrow).

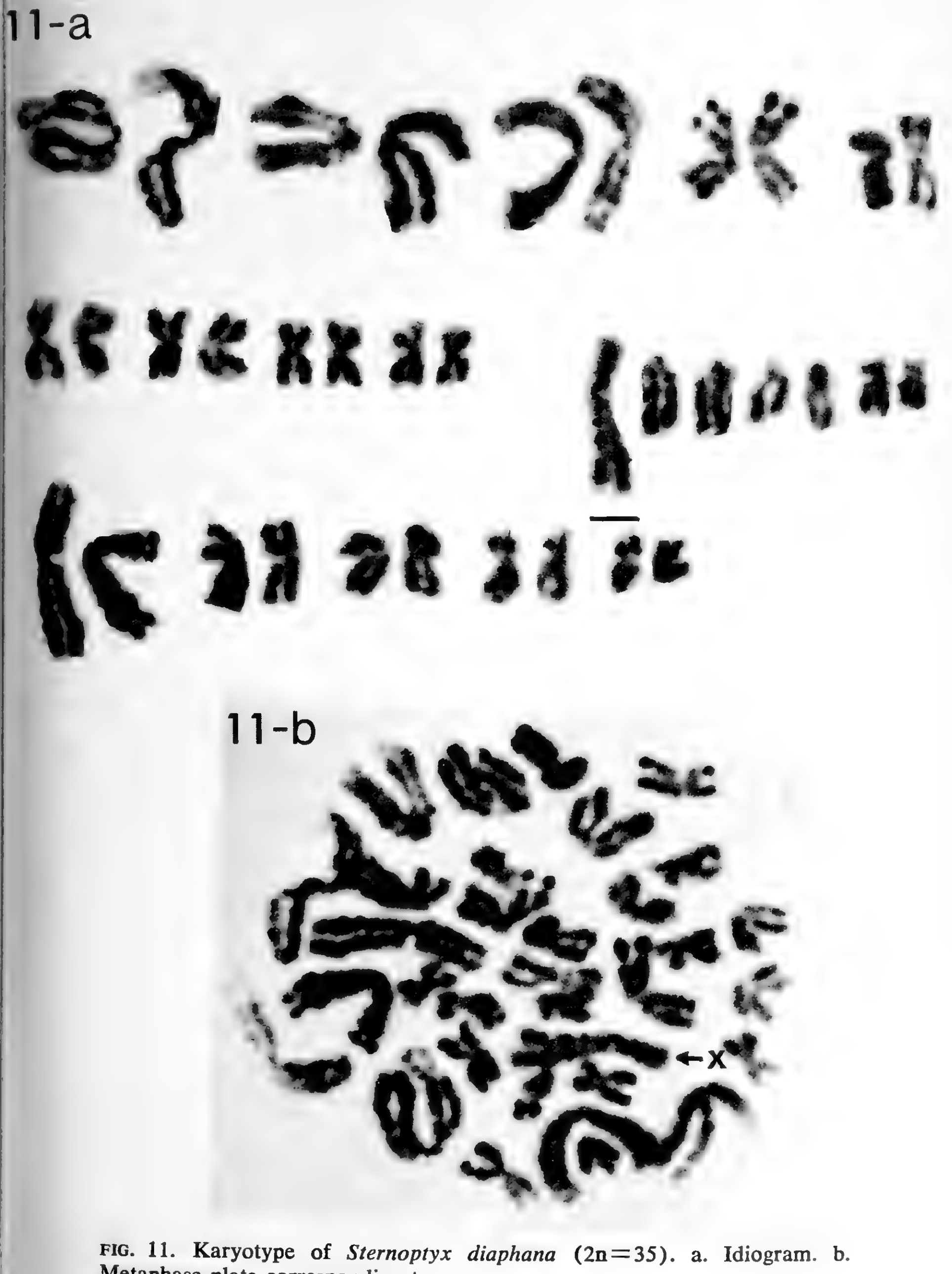
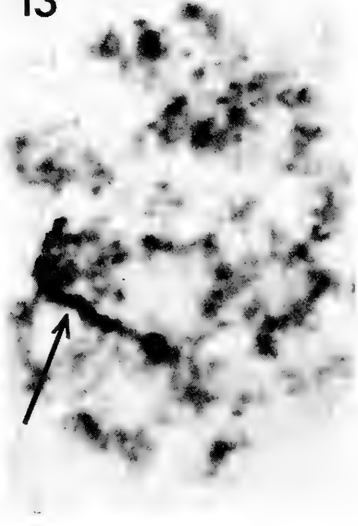


FIG. 11. Karyotype of *Sternoptyx diaphana* (2n=35). a. Idiogram. b. Metaphase plate corresponding to a.

12

13

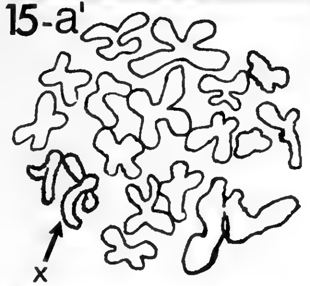


14

FIG. 12. Metaphase plate of *Sternoptyx diaphana.*

FIG. 13. Preleptotene of *Sternoptyx diaphana* showing the heterochromatic sex element (arrow).

FIG. 14. Metaphase I of *Sternoptyx diaphana* showing the univalent "X" (arrow).



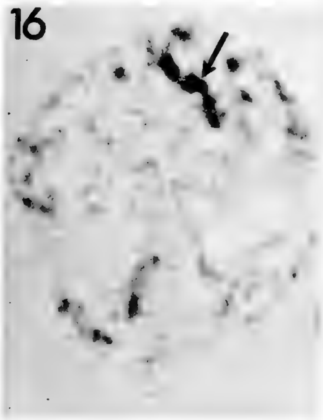
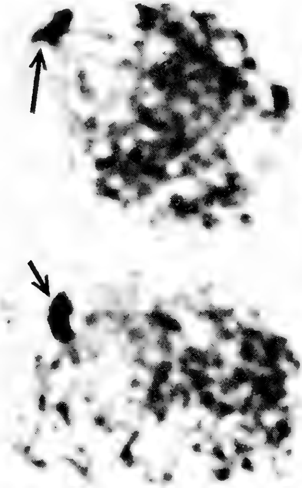


FIG. 15. Metaphase II of *Sternoptyx diaphana* showing 18 chromosomes (with the "X", a and a′) and 17 (without the "X", b).

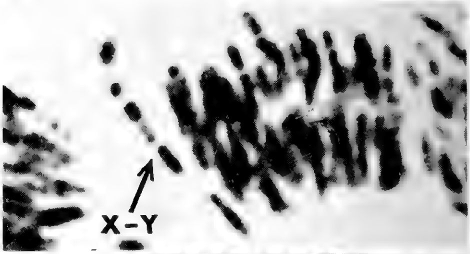
FIG. 16. Preleptotene of *Scopelengys tristis* showing the heterochromatic sex element (arrow).

FIG. 17. Metaphase I (sideview) of *Scopelengys tristis* (2n=48, n=24) showing atypically behaving presumed X-Y bivalent (arrows).

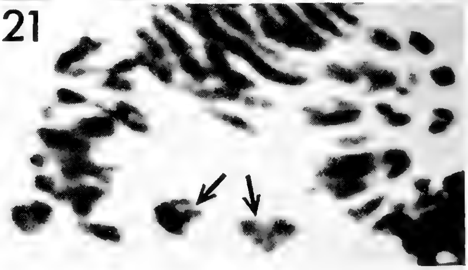
18



20



21



19

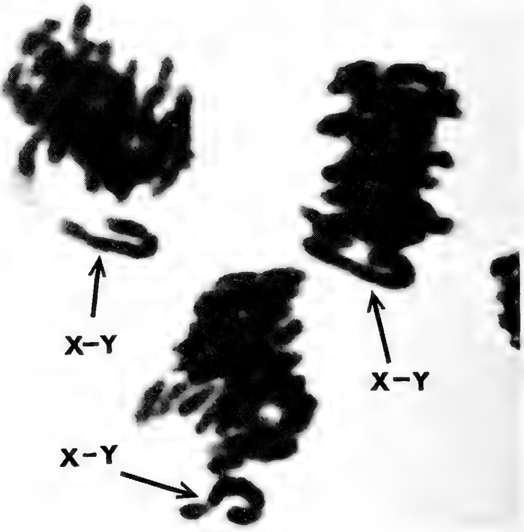


FIG. 18. Two leptotene cells of *Symbolophorus californiensis* (2n=48; n=24) showing the heterochromatic sex element (arrows).

FIG. 19. Metaphase I (sideviews) of *Symbolophorus californiensis* showing atypically behaving presumed sex bivalent (arrows).

FIG. 20. Early anaphase I of *Symbolophorus californiensis* showing the sex bivalent and its distinct heterochromatic bands (arrow).

FIG. 21. Anaphase I of *Symbolophorus californiensis* showing two lagging, presumed sex univalents (arrows).

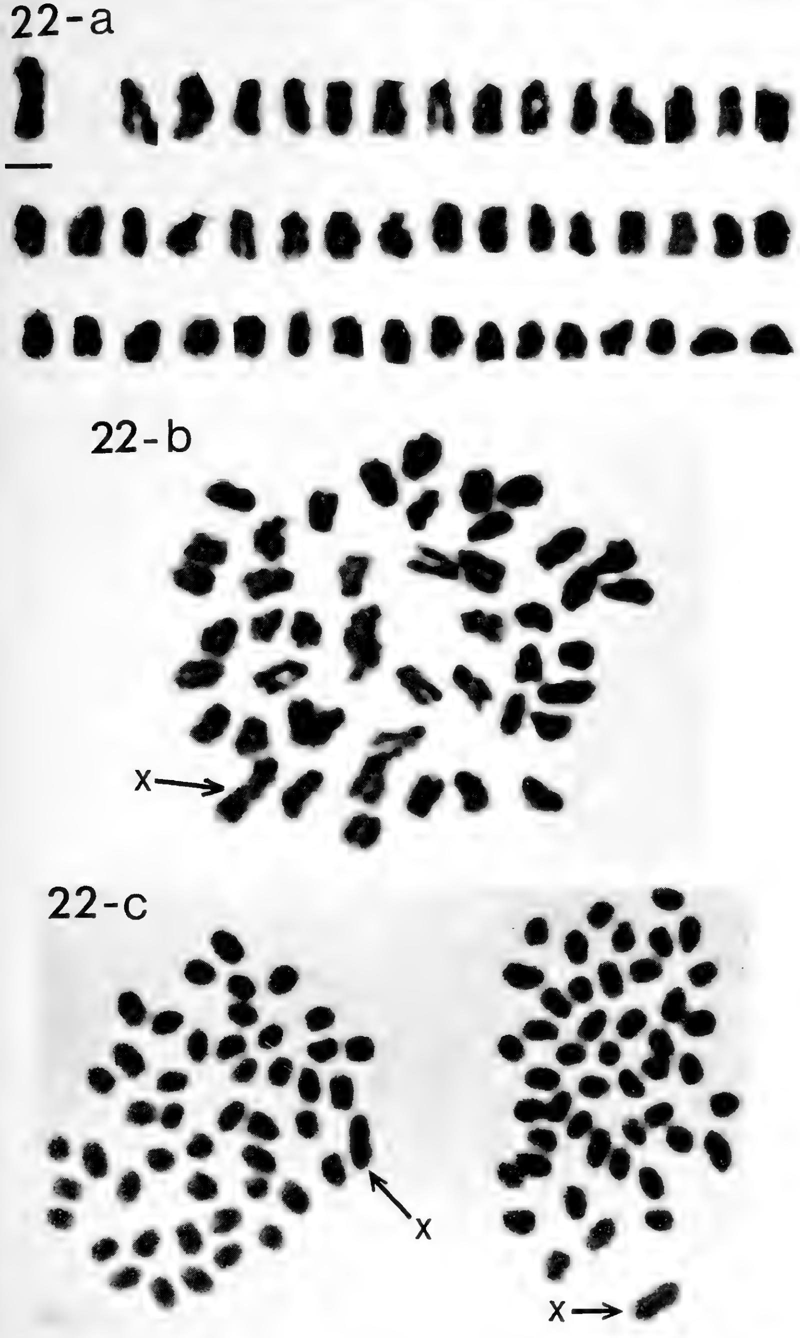
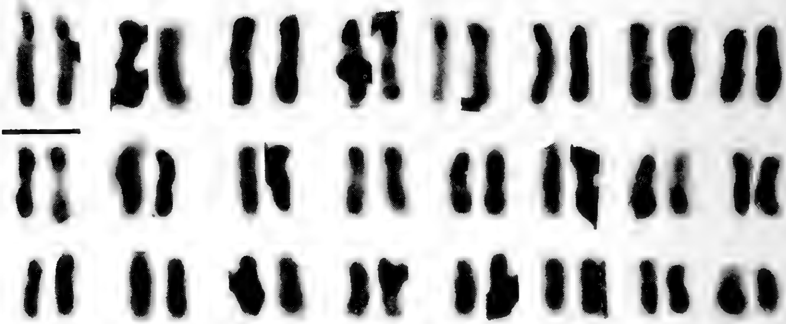
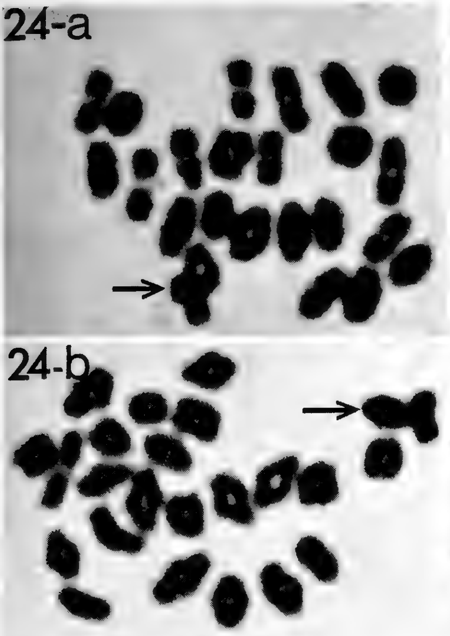


FIG. 22. Karyotype of male *Lampanyctus ritteri* ($2n = 47$). a. Idiogram. b. Metaphase plate corresponding to a. c. Two late metaphase plates.

23-a



23-b



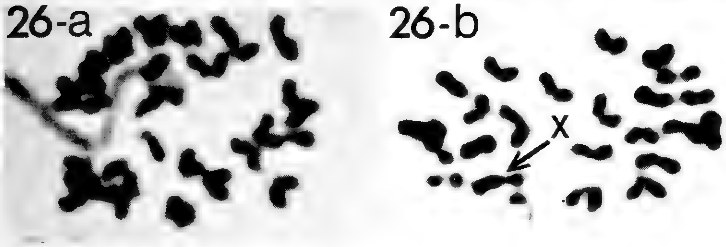


FIG. 23. Karyotype of female *Lampanyctus ritteri* (2n=48). a. Idiogram. b. Metaphase plates corresponding to a.

FIG. 24. Primary spermatocytes (MI) of *Lampanyctus ritteri* showing the "X"-autosome trivalent (a and b).

FIG. 25. Anaphase I of male *Lampanyctus ritteri* showing one (lower) with and the other (upper) without the "X" chromosome.

FIG. 26. Secondary spermatocytes (M II) of *Lampanyctus ritteri* showing: a, n=23 without, and b, n=24 with the "X".

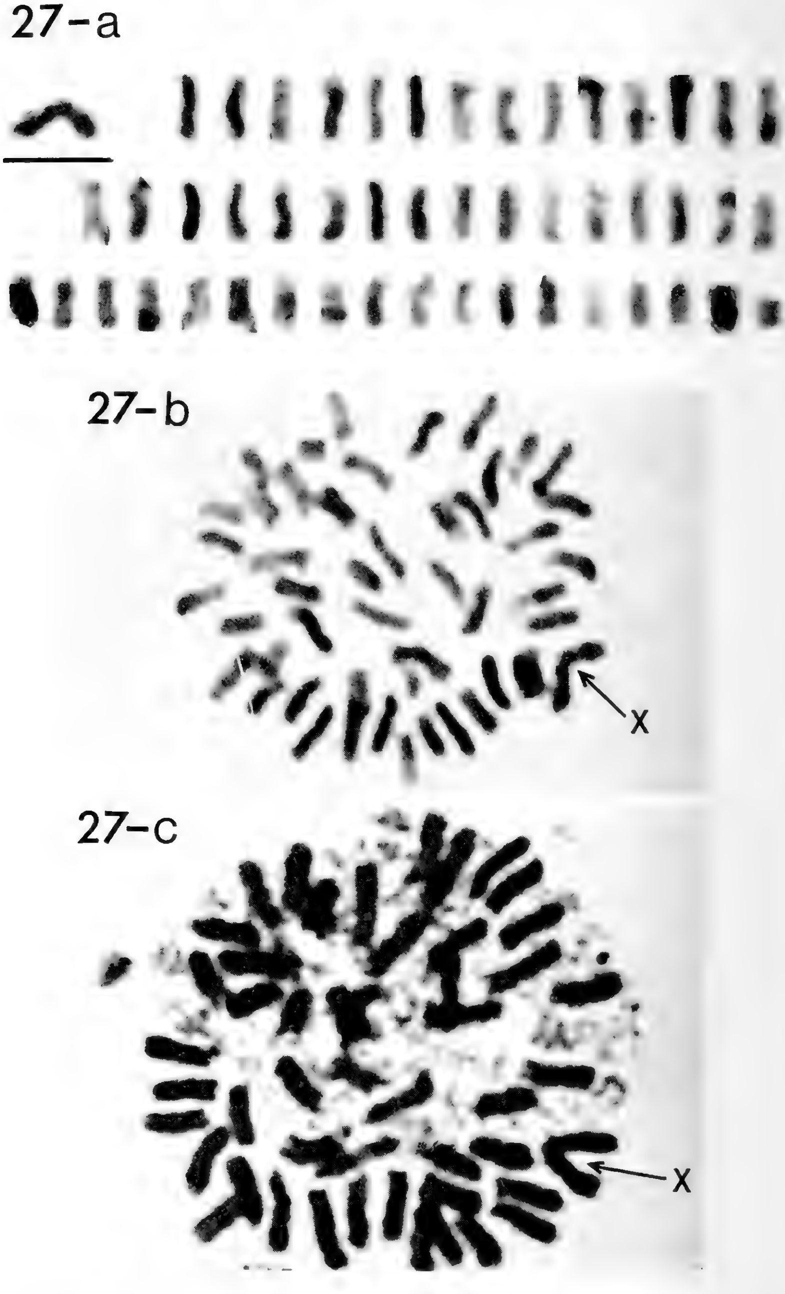
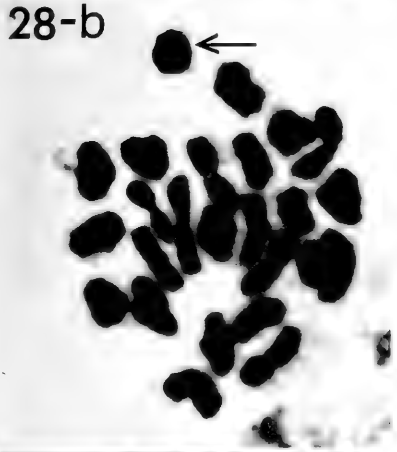
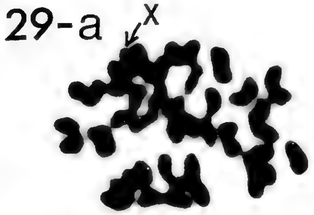
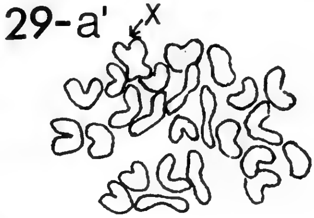


FIG. 27. Karyotype of *Parvilux ingens* (2n=49). a. Idiogram. b. Metaphase plate corresponding to a. c. Another metaphase plate showing the "X".







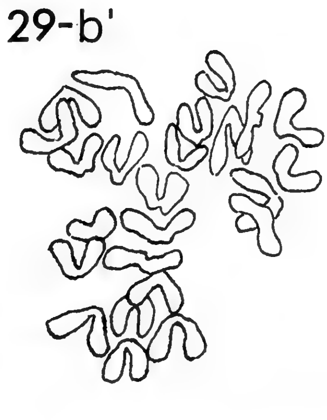
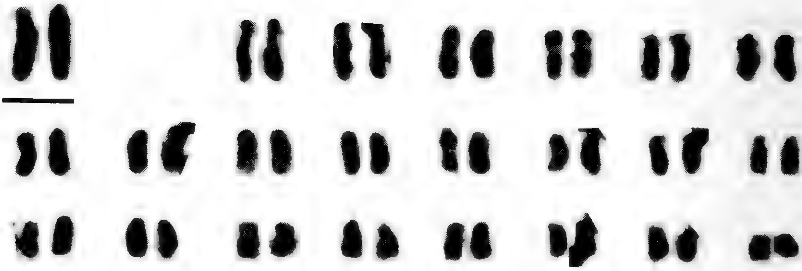


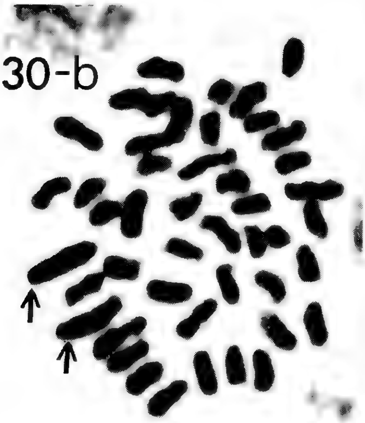
FIG. 28. Metaphase I of *Parvilux ingens* showing atypically behaving "X" univalent (a and b).

FIG. 29. Metaphase II of *Parvilux ingens*, (n=25, a and a′) with and the other (n=24, b and b′) without the "X".

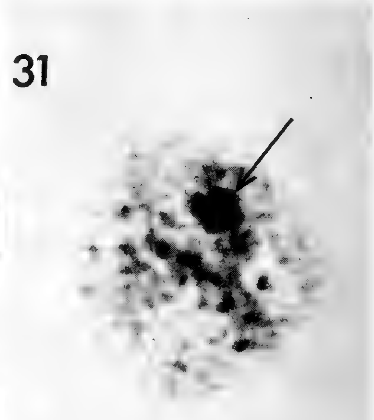
30-a



30-b



31



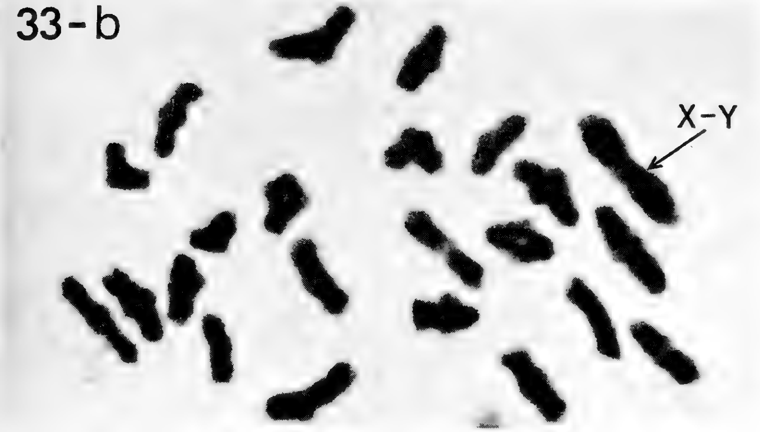
32

FIG. 30. Karyotype of *Scopelogadus mizolepis bispinosus* (2n=46). a. Idiogram. b. Metaphase plate corresponding to a.

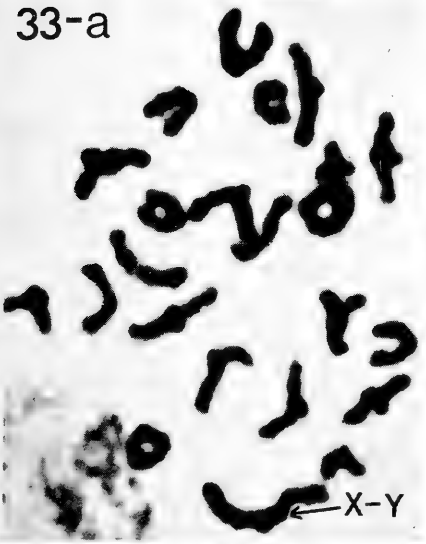
FIG. 31. Preleptotene of *S. m. bispinosus* showing the presumed heterochromatic sex element (arrow).

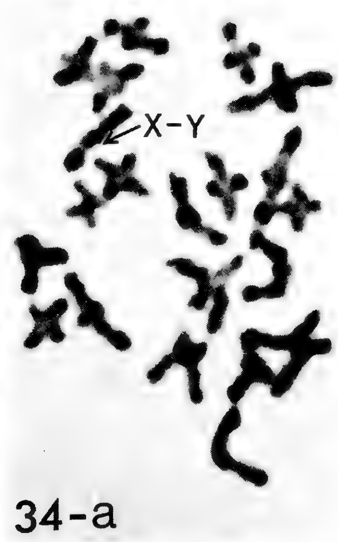
FIG. 32. Pachytene of *S. m. bispinosus* showing a lampbrush-like "X-Y" bivalent (arrow).

33-b



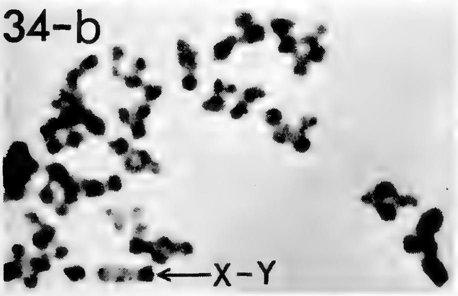
33-a

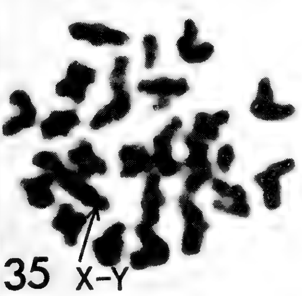




34-a

34-b





35

FIG. 33. Premetaphase I (a) and metaphase I (b) of *Scopelogadus mizolepis bispinosus.*

FIG. 34. Metaphase I (a and b) of *Scopeloberyx robustus* (2n=42, n=21) showing the heteromorphic "sex" bivalent (arrow).

FIG. 35. Metaphase I of *Melamphaes parvus* (2n=50, n=25) showing the heteromorphic "sex" bivalent (arrow).

INFORMATION FOR AUTHORS

REVIEW	The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
STYLE	Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).
FORM	Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.
TITLE	Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
ABSTRACT	The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
OMENCLATURE	Follow the International Codes of Zoological and Botanical Nomenclature.
LLUSTRATIONS	Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
FOOTNOTES	Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
TABLES	Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
REFERENCES	The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
HOR'S COPIES	Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
PROOF	Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
COPYRIGHT	Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 131. 15 MAY 1969

THE PELVIC MUSCULATURE OF THE DINOSAUR HYPSILOPHODON (REPTILIA: ORNITHISCHIA)

PETER M. GALTON

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

THE PELVIC MUSCULATURE OF THE DINOSAUR HYPSILOPHODON (REPTILIA: ORNITHISCHIA)

PETER M. GALTON
Peabody Museum of Natural History, Yale University

ABSTRACT

Evidence is provided to show that: 1) the prepubic process, diagnostic of an ornithischian, did not provide the main support for the abdomen; 2) the abdomen was large and extended ventral to the pelvic girdle with a strong M. rectus abdominis that was not functionally replaced by the lateral abdominal muscles; 3) either the M. pubo-tibialis or the ventral part of the M. pubo-ischio-femoralis internus originated on the lateral surface of the prepubic process. An important femoral protractor, the anterior part of the M. pubo-ischio-femoralis externus, had to be functionally replaced before the pubis changed position to lie close to the ischium in ornithischians and birds. This was accomplished by the development of a long anterior process to the ilium with the differentiation of a large M. ilio-tibialis 1. The lateral curvature of the anterior process of the ilium enabled it to clear the adjacent ribs and improved the mechanical position of part of the M. dorsalis trunci, the M. ilio-tibialis 1 and the dorsal part of the M. pubo-ischio-femoralis internus. A third dorsal muscle to the femur, the M. ilio-trochantericus, was differentiated in *Hypsilophodon.* The well-developed depression at the base of the fourth trochanter was the main insertion area of the M. caudi-femoralis longus. The large size of the fourth trochanter of the ornithopod femur lengthened the moment arm of the M. caudi-femoralis brevis during the initial part of femoral retraction; its pendant form resulted from stresses imposed by part of the M. gastrocnemius which originated on the tendon connecting the trochanter to the fibula.

POSTILLA 131: 64 p.   15 MAY 1969.

CONTENTS

INTRODUCTION

The first study of the pelvic musculature of an ornithopod dinosaur was by Dollo (1883) who discussed the muscles inserting on the femoral trochanters of *Iguanodon.* Subsequently Dollo (1888) suggested that the "trochanter creté" of *Iguanodon* was primitive for ornithopods. He regarded the pendant trochanter of *Hypsilophodon* and *Camptosaurus* as a secondary development but Nopcsa (1905), on the basis of the primitive nature of *Hypsilophodon,* argued that the reverse was the case. Gregory (1919 and *in* Romer, 1927b) made the first attempt to locate the area of attachment of all the pelvic muscles. Romer contributed several papers on the pelvic musculature of dinosaurs and related forms: 1923a (dinosaurs and birds), 1923b (alligator), 1923c (saurischian dinosaurs) and 1927a (chick). These studies were followed (1927b) by a detailed discussion of the pelvic muscles of ornithischians with a reconstruction of the pelvic musculature of the hypsilophodont *Thescelosaurus.* The pelvic musculature of the ceratopsian *Chasmosaurus* (Russell, 1935) and the hadrosaur *Anatosaurus* (Lull & Wright, 1942) has been briefly described but in both instances Romer's interpretations were followed. Janensch (1955) discussed the attachment areas in the region of the fourth trochanter of the femur of the hypsilophodont *Dysalotosaurus.*

Marsh (1878), using material of *Dryosaurus* (=*Laosaurus*) *altus* (YPM 1876), first showed that the complete ornithischian pubis consisted of an anteriorly directed prepubic process and a postpubic rod that lies close to the ischium. However, the presence of the latter was originally demonstrated by Huxley (1870) using a specimen of *Hypsilophodon* [BM(NH) 28707]. Although Dollo (1888), Nopcsa (1905), Romer (1927b) and Janensch (1955) referred to *Hypsilophodon,* the material has not been studied in detail with reference to the pelvic musculature. Most of the material is in the British Museum (Natural History), London and includes several articulated specimens, details of which are given in Galton (in press). The good specimens consisted of blocks with only some of the bone(s) exposed (see Hulke, 1882). I have prepared most of these in acetic acid so that the bones are completely free of matrix. Among these specimens is BM(NH) R193 (Figs. 4, 6-11, 13, 15) consisting of a pelvic region and partial hind limb. The figure of the pubis and ischium of *Hypsilophodon* given by Romer (1927b, fig. 7), was based mainly on the figure of this specimen given by Hulke (1882, pl. 66). The surface of the bones of the pelvic girdle and femur of this specimen is very well preserved so that the boundaries of several areas of muscle attachment can be located. These areas were identified using for the main part the descriptions and the reconstruction of the pelvic musculature of *Thescelosaurus* given by Romer (1927b) and information from living forms. In the process it was possible to compare the areas in these two genera that both belong to the family Hypsilophodontidae (for diagnosis see Romer, 1956). It also became apparent that there were several problems that needed discussion. These, together with certain functional considerations, are dealt with in the second half of this paper (see below, p. 21).

Pelvic Muscles of the Alligator and Birds

The reconstruction of the musculature of an extinct form should agree as far as possible with the musculature in the closest living relatives. Dinosaurs are classified in the subclass Archosauria, the only living order of which is the Crocodilia. Birds are archosaurian derivatives and, because the pubis lies close to the ischium, are particularly relevant to the musculature of any ornithischian. Consequently a brief summary of the pelvic musculature of the alligator and birds is given below. The following classification of the pelvic muscles of reptiles and birds has been adapted from Romer (1923b, 1927a, b, 1962).

Axial muscles

A. Dorsal

M. dorsalis trunci and caudae

B. Ventral

M. obliquus abdominis externus and internus,

M. transversus abdominis, M. rectus abdominis

M. ilio-caudalis and M. ischio-caudalis

Appendicular Muscles

- A. Dorsal
  - i) To the lower leg
    - a) M. triceps femoris — M. ilio-tibialis (including sartorius of birds), M. ambiens and M. femoro-tibialis
    - b) M. ilio-fibularis
  - ii) To the femur
    - a) M. pubo-ischio-femoralis internus of reptiles, M. ilio-femoralis internus of birds
    - b) M. ilio-femoralis of reptiles, M. ilio-femoralis externus and M. ilio-trochantericus of birds
- B. Ventral
  - i) To the lower leg
    - a) M. pubo-tibialis
    - b) M. pubo-ischio-tibialis
    - c) M. flexor tibialis internus of reptiles, M. ischio-flexorius of birds
    - d) M. flexor tibialis externus of reptiles, M. caudo-ilio-flexorius of birds
  - ii) To the femur
    - a) M. caudi-femoralis longus and brevis of reptiles, M. caudo-ilio-femoralis of birds
    - b) M. adductor femoralis of reptiles, M. pubo-ischio-femoralis of birds
    - c) M. pubo-ischio-femoralis externus of reptiles, M. obturator internus of birds
    - d) M. ischio-trochantericus of reptiles, M. ischio-femoralis of birds

In the following summary, unless indicated otherwise, information concerning the pelvic muscles of the alligator was taken from Romer (1923b) and for birds from Romer (1923b, 1927a, b). The areas of attachment and the lines of action of the individual muscles are shown for the alligator in Figures 1 and 2 and for an eight day old chick in Figure 3.

Dorsal Axial Musculature

The dorsal axial muscles in the alligator, lizards and *Sphenodon* lie lateral to the neural arches and dorsal to the transverse processes of the dorsal and caudal vertebrae. The M. dorsalis trunci has areas of insertion and the M. dorsalis caudae areas of origin on the inner surface of the dorsal part of the ilium. Further subdivision of this musclature is unnecessary in the present connection. The M. dorsalis trunci and caudae are completely separated by the ilia in birds.

Ventral Axial Musculature

In the alligator anteriorly the three lateral muscles originate from the lumbodorsal fascia. This fascia attaches to the surface of the M. dorsalis trunci, the tips of the transverse processes, the tip of the anterior process of the ilium and the surface of the M. pubo-ischio-femoralis internus. The M. obliquus abdominis externus passes posteroventrally and it has three insertion areas: by a tendon to the anterior edge of the acetabulum below the M. ambiens; on the posterodorsal end of the last abdominal rib, which is connected to the external edge of the pubis by a tendon; and on an aponeurosis lying above the main part of the M. rectus abdominis. The first insertion corresponds to the one on the lateral process of the pubis and the second to that on the pubo-ischiadic ligament in lizards (Snyder, 1954, fig. 21) and *Sphenodon* (Gregory & Camp, 1918, pl. 45, fig. A^2). The M. obliquus abdominis internus passes anteroventrally to insert on the posterior long rib and the anterior abdominal ribs. The M. transversus abdominis is the deepest muscle and it passes ventrally to insert on the deep surface of the M. rectus abdominis.

The three lateral abdominal muscles are slightly different in birds (George & Berger, 1966). The M. obliquus abdominis externus originates on the costal margin of the sternum and a midline raphe anteriorly or a fleshy contact with the muscle of the other side. It passes dorsally and slightly anteriorly or posteriorly depending on the genus to insert on an aponeurosis on the lateral surface of the ribs and on the ventral edge of the anterior part of the pubis. The M. obliquus abdominis internus originates from the last rib, passes posterodorsally and inserts by an aponeurosis on the distal third to two-thirds of the pubis. The origin of the M. transversus abdominis forms a ventral midline raphe that extends from the posterior margin of the sternum to the interpubic ligament. It inserts on the medial surface of the last two or three ribs and by an aponeurosis and/or by fleshy fibers on the ventral margin of the pubis. In ratites all three muscles insert on the whole of the ventral edge of the pubis (Gadow, 1880).

The M. rectus abdominis is large in the alligator as is the case in *Sphenodon* and lizards. It originates from the posterior edge of the sternum and the distal part of the long ribs. The more lateral part is interrupted by the gastralia and inserts on the last gastralia, which is connected to the pubis by membranous tissue ventrally and by a strong tendon laterally. The deeper fibers of the more medial part insert on the posterior edge of the pubis while the rest insert on the ventral surface of the M. ischio-caudalis. The M. rectus abdominis in birds originates from the posterior margin of the sternum and the last sternal rib; it inserts by an aponeurosis on the posterior part of the pubis and the interpubic ligament (George & Berger, 1966). In ratites the M. rectus abdominis inserts on the distal part of the pubis (Gadow, 1880).

Posteriorly the M. ilio-caudalis and M. ischio-caudalis (=M. ilio-ischio-caudalis; Romer, 1923b) are separated by the M. caudifemoralis in the alligator. The more dorsal M. ilio-caudalis originates on part of the dorsal edge of the ilium and inserts on the undersides of the transverse processes and centra of the caudal vertebrae. The M. ischio-caudalis originates on the posteroexternal angle of the ischium and inserts on the haemal arches of the tail. There are four posteroventral axial muscles in birds that control the movements of the very short tail. The details (George & Berger, 1966, p. 282), are unimportant because they are not relevant to the muscles in ornithischians.

Appendicular Muscles

The M. triceps femoris consists of three parts:

M. ilio-tibialis. This muscle originates along most of the dorsal margin of the ilium and is divided into two parts in lizards, three in crocodiles and five in birds. All these origins are tendinous except the most anterior one in birds which is fleshy. The insertion in all forms joins the tendon of the M. femoro-tibialis on the cnemial crest of the tibia.

M. ambiens in reptiles and birds has a tendinous origin just anterior to the acetabulum close to the ilio-pubic boundary and inserts on the tendon attaching to the cnemial crest. A second tendon crosses the knee to the fibular side in crocodiles and birds to join the external head of the M. gastrocnemius.

M. femoro-tibialis has a fleshy origin from much of the femoral shaft. In the alligator there are two parts but in birds there are several additional small heads. The tendinous insertion is on the cnemial crest of the tibia.

M. ilio-fibularis. This muscle in crocodiles and birds has a large fleshy origin on the postacetabular part of the ilium and is overlain by the M. pubo-tibialis. It inserts on the fibula and also on the external head of the M. gastrocnemius.

There are two dorsal muscles inserting on the femur in modern reptiles. The M. ilio-femoralis originates on the outer surface of the ilium and inserts on the posterior surface of the femoral shaft. The two parts of the M. pubo-ischio-femoralis internus primitively originate on the medial surface of the pubis. In the alligator they have a more dorsal origin. The main part originates on the ventral surfaces of the transverse processes of the last six dorsal vertebrae; it inserts on the dorsal surface of the proximal part of the femur. The more ventral part originates on the internal surface of the ilium and ischium and the ventral surfaces of the sacral ribs and passes ventrally to insert more anteroventrally on the femur.

There are three dorsal muscles inserting on the femur in birds that all originate on the outer surface of the ilium. The homologues of the two reptilian muscles are the M. ilio-femoralis externus and the more anterior M. ilio-femoralis internus. The muscle in between is the M. ilio-trochantericus that inserts in part on the greater trochanter.

The M. pubo-tibialis of primitive reptiles is lost in crocodiles and birds. The M. pubo-ischio-tibialis of lizards is a large ventral muscle (Snyder, 1954). It is reduced to a slip that originates on the lateral surface of the ischium below the acetabulum in the alligator. It is lost in birds.

The M. flexor-tibialis internus has three heads in the alligator. The first originates on the medial surface of the ischium near the posteroventral corner, the second on the outer surface posteroventral to the acetabulum and the third is on the posterior corner of the ilium. These three heads have a double tendon, one part inserting on the medial surface of the tibia and the other passing along the external head of the M. gastrocnemius. The only part in birds is the M. ischio-flexorius.

The M. flexor-tibialis externus arises from the posterior angle of the ilium in the alligator and from the tail in birds (M. caudo-ilio-flexorius). It inserts on the medial aspect of the head of the tibia.

The M. caudi-femoralis brevis originates on the posteroventral edge of the ilium and the sides of the centra of the last sacral and the first caudal vertebra in the alligator. It inserts on the dorsal surface of the fourth trochanter of the femur. The iliac portion is more important in birds.

The M. caudi-femoralis longus originates on the sides of the centra and the ventral surface of the transverse processes of caudal vertebrae 3 to 15 in the alligator. The thick tendon inserting on the fourth trochanter is connected to the head of the fibula by a thin tendon that is also present in lizards and birds.

M. adductor femoris has two heads that originate on the outer surface of the ischium. These two heads are separated by a portion of the M. pubo-ischio-femoralis externus in the alligator but not in birds. The insertion is a long and narrow area on the ventral side of the femur.

M. pubo-ischio-femoralis externus has three heads in the alligator. The first is on the ventrolateral surface of the pubis, the second on the dorsomedial surface of the pubis and the third on the outer surface of the ischium. The common tendon inserts on the posteroventral edge of the femur close to its head. This muscle has only one head in birds, the M. obturator internus, which originates on the ventral edge of the ischium and the dorsal edge of the pubis.

M. ischio-trochantericus of alligators is a small muscle which originates on the posterior part of the inner surface of the ischium. Its tendinous insertion is on the outer dorsal edge of the femur close to its head. This muscle originates on the outer surface of the distal part of the ischium and neighboring pelvic bones in birds.

THE PROBABLE AREAS OF ORIGIN AND INSERTION OF THE PELVIC MUSCLES IN HYPSILOPHODON

Romer (1927b) discussed the probable attachment areas of each pelvic muscle in ornithischians and gave a detailed reconstruction of these muscles for *Thescelosaurus* (Figs. 5, 16). His study has been used to interpret certain well-defined surface markings on BM(NH) R193 (Figs. 6-11, 13, 15), a specimen of *Hypsilophodon* that has an extremely well-preserved ilium, ischium, pubis and femur. The following section provides a summary of the evidence shown by this specimen but the reasons for certain of the interpretations are discussed in later sections. Data for other ornithischians are taken from Romer (1927b) unless otherwise indicated. Romer (1927b) applied avian names to several of the muscles of ornithischians. However, as ornithischians are reptiles I have not followed this practice unless there is good evidence that the muscle in *Hypsilophodon* resembled that of birds. When Romer (1927b) used the avian term this is given in parenthesis after the appropriate section heading (see also the classification of muscles given on p. 5).

A. AXIAL MUSCULATURE

Only the more superficial part of the dorsal axial musculature attached to the ilium (Figs. 4, 6). Part of the M. dorsalis trunci probably inserted on the medial surface of the anterior process, which is strengthened by a couple of longitudinal ridges. The square and rugose posterior edge of the ilium probably provided an area of origin for part of the M. dorsalis caudae.

The reconstruction of the ventral axial muscles anterior to the pelvic girdle must be rather tentative but I consider that the following is a reasonable approximation. The M. obliquus abdominis internus probably originated from the posterior edge of the sternum and by a midline raphe or a fleshy contact with the muscle of the other side. This muscle passed laterally and posterodorsally to insert on a dorsal fascia, similar to that in the alligator, and on the pubis. The M. transversus abdominis originated from a midline raphe and passed dorsolaterally to insert on the dorsal fascia and on the pubis. The M. obliquus abdominis externus originated from a midline raphe and from the lateral edge of the M. rectus abdominis and passed laterally and anterodorsally to insert on the pubis and on the dorsal fascia. The M. rectus abdominis originated from the posterior edge of the sternum and inserted on the distal part of the pubis and on the expanded distal end of the ischium.

The three lateral abdominal muscles probably inserted on the ventral edge of the pubis, as in birds. The insertion of the M. obliquus abdominis externus may have been restricted to the more anterior part of the pubis and that of the pars internus to the more posterior part as is the case in carinate birds (George & Berger, 1966). It would appear more likely that both these muscles, like the M. transversus abdominus, inserted along the whole of the ventral edge of the pubis (Fig. 6) as is the case in ratites (Gadow, 1880). It is possible that more distally the area of insertion of these three muscles was on the adjacent surface of the ischium. The problem of the abdominal musculature is discussed on page 21.

B. APPENDICULAR MUSCULATURE

The functional grouping of the limb muscles of *Hypsilophodon* is simplified because the action of the hind limbs was mainly anteroposterior.

1. Muscles that Extended the Tibia.

The three parts of the M. triceps femoris provided much of the propulsive force. The more anterior portion of the M. ilio-tibialis also raised the leg during forward movement and effected minor adduction and abduction. The insertion of all parts was presumably a tendinous one onto the cnemial crest of the tibia.

a) M. ilio-tibialis. This originated on the dorsal margin of the ilium. The dorsal edge of the ilium in lateral view (Fig. 6) has a definite bevel running from the posterior corner onto the anterior process. The complete bevel is visible in BM(NH) R196 and that part of it present in BM(NH) R193 has well-marked muscle scars. A separate portion, the M. ilio-tibialis 1 (the sartorius) was probably differentiated on the anterior process of the ilium as in birds. The posterior boundary of this portion is indicated by a rugose line running across the process in hadrosaurs and *Thescelosaurus* (Fig. 5); this is not present in *Hypsilophodon.*

b) M. ambiens. The origin on the pubis seems to be just anterior to the acetabulum. Romer (1927b) showed that this region varies in *Thescelosaurus* because a distinct bump is preserved in the type (Gilmore, 1915, fig. 17) that is lacking on specimens at the American Museum of Natural History. *Hypsilophodon* specimens BM(NH) R193, R195 and R196 show muscle scars on the dorsolateral edge of the prepubic process close to the acetabular region (Figs. 4, 6, 7) in the same position as the bump in *Thescelosaurus*. The main insertion was presumably on the cnemial crest of the tibia but, as in crocodiles and birds, there may also have been a tendon that crossed to the fibular side of the leg to insert on the external head of the M. gastrocnemius.

c) M. femoro-tibialis. Unlike the other two divisions of the M. triceps femoris there was no possibility of the M. femoro-tibialis functioning to protract the femur. Among archosaurs there was a general tendency for the M. femoro-tibialis to enlarge its area of insertion (Romer, 1923b, c; 1927b) so that it covered much of the femoral surface. Concerning *Thescelosaurus,* Romer (1927b, p. 261) wrote that "the femoro-tibialis origin, as is usually the case, is not well defined, but apparently includes a main area lying on the dorsal (anterior) surfaces of the femur, bounded externally by a ridge extending down from the 'lesser trochanter'. Probably a head originated on the ventral (posterior) surface external to the ridge, while a third (not seen in the figures) extended around the internal margin towards the ventral surface interior and anterior to the coccygeo-femoral insertion." These three divisions are referred to below as M. femoro-tibialis 1, 3 and 2 respectively and their areas of origin are clearly seen in the femur of *Hypsilophodon,* BM(NH) R193 (Figs. 8-10). It should be noted that the ridge below the lesser trochanter in *Thescelosaurus* is not equivalent to the groove in this position in *Hypsilophodon* but corresponds to the more posteriorly placed ridge.

M. femoro-tibialis 1. The area of insertion of this muscle is delimited by two longitudinal features on the femur. At the base of the lesser trochanter there is a well-defined shallow groove (Fig. 10C), with surface markings, which becomes wider close to the broken end of the bone. On the outer surface there is a strong and curved ridge (Figs. 8A, 9A, 10B) which commences level with the top of the fourth trochanter. Distally this ridge curves inward and widens to form a flat area with surface striations (Figs. 8A, 9A, 10A, B). The area bounded by these two features is convex and its anterior limit is marked by a series of rugose markings, which extend from the base of the lesser trochanter to the flatter area at the end of the ridge. There are few surface markings on this area but distally there is a diagonal system of low parallel ridges and grooves (Figs. 8A, 9A).

M. femoro-tibialis 2. The insertion area of this muscle is convex and is mainly bounded by the M. femoro-tibialis 1 and 3. The proximal extent of this muscle is not certain. There are some rugose markings, situated at the level of the lower part of the depression at the base of the fourth trochanter, which may mark the proximal limit (Figs. 8B, 9B, 10C, D). Alternatively, this muscle may have extended medial to the depression toward the base of the lesser trochanter.

M. femoro-tibialis 3. The area of insertion of this muscle is bounded externally by the sharp ridge mentioned above. Internally the proximal boundary is a faint line, formed by a series of small depressions, that extends from the proximal end of the ridge onto the base of the fourth trochanter. More distally on the trochanter this boundary continues as a rugose ridge (Figs. 8A, 9A, 10A) and then by an edge formed by the thickening of the trochanter (Fig. 10B). Distal to the trochanter the internal boundary is a line of small depressions extending from the distal end of the well-developed depression at the base of the fourth trochanter (Figs. 8B, 9B, 10D). The surface for the origin of this muscle is mostly concave but internally, in the region distal to the fourth trochanter, it is convex. A part of this muscle probably originated on the central area underneath the pendant part of the fourth trochanter (Figs. 8A, 9A, 10B) where there are surface markings.

d) M. pubo-tibialis. There is a well-defined area on the lateral surface of the prepubic process of *Hypsilophodon* on which the M. pubo-tibialis or the ventral part of the M. pubo-ischio-femoralis internus may have originated (see below, p. 28). The lateral area is best preserved in BM(NH) R193 (Figs. 4, 6, 7). The anterior part is also shown on BM(NH) R196 and the posterior part on BM(NH) R195 and R5829. The surface markings cease anteriorly close to the end of the process. Ventrally the area is delimited by a groove running along the corner of the process (Fig.

7). Posteriorly the surface of the prepubic process is concave, so that the area projects laterally (Fig. 11). Dorsally the markings continue to the rounded edge of the process. The surface markings are best developed posteriorly, where the area is wider, making an angle of about 45° to the long axis of the process (Figs. 6, 7). These same markings are present in BM(NH) R5829 but the area does not project laterally. Anteriorly, the area is narrower and the markings have no apparent direction. This part is the same in BM(NH) R196 where the markings stop a short distance from the end. If the M. pubo-tibialis was present, it would presumably have inserted on the medial surface of the tibial head.

The prepubic process of *Dryosaurus altus* (YPM 1876) has an area on the lateral surface similar to that in *Hypsilophodon*. Posteriorly the well-defined muscle scars are diagonally inclined and the area continues onto the dorsolaterally facing surface of the slightly flattened and expanded anterior part where the markings are longitudinal. The prepubic process of *Thescelosaurus* (AMNH 117) is similar to that of *Dryosaurus* but the posterior region is less well-defined and the markings less diagonally inclined. The markings on the prepubic process of most other ornithischians examined are, as Romer (1927b) noted, longitudinal striations. This is true for *Thescelosaurus neglectus* (NMC 8537, USNM 2210 and AMNH 6120), *Iguanodon atherfieldensis* [BM(NH) R5764] and the mounted skeletons of hadrosaurs and ceratopsians in the Peabody Museum of Yale University, United States National Museum, National Museum of Canada and the Royal Ontario Museum, Toronto. In some of the mounted hadrosaurs at the American Museum of Natural History (*Procheneosaurus,* AMNH 5461; *Saurolophus,* AMNH 5220; and *Corythosaurus,* AMNH 5240) the pattern is slightly different. In these specimens the striations radiate from the narrow part into the dorsoventrally expanded anterior part of the process. As a result the most dorsal and ventral striations are parallel to the appropriate edge of the process.

2. Muscles that Protracted the Femur.

a) M. ilio-femoralis(=M. ilio-femoralis externus; Romer, 1927b). Romer (1927b) concluded that the M. ilio-femoralis originated on the antitrochanter of the ilium of hadrosaurs. In

Thescelosaurus (Fig. 5) and *Hypsilophodon* (Fig. 6), in which the area of origin cannot be distinguished, the area shown on the ilium is comparable in position to that of the hadrosaurian antitrochanter. The insertion of the M. ilio-femoralis completely covered the lesser trochanter (Figs. 4, 10); it probably extended to the depression at the base on the anterior edge (Fig. 10C). This muscle helped to prevent disarticulation of the femur.

b) M. pubo-ischio-femoralis internus(=M. ilio-femoralis internus; Romer, 1927b). The ventral part of this muscle, rather than the M. pubo-tibialis, may have originated on the well-defined area on the lateral surface of the prepubic process (see p. 14, 28). A possible area of insertion for this part was on the femoral shaft proximal to the depression at the base of the fourth trochanter (Figs. 8B, 9B, 10D) and possibly also proximal to M. femoro-tibialis 2. On the ventral surface of the head and neck there is an area, with very strongly developed markings (Figs. 8B, 9B, 10C), which probably was not for this ventral part but for ligaments that held the head of the femur in the acetabulum.

3. Muscles that Flexed the Tibia.

a) M. ilio-fibularis. There is no indication of the area of origin of this muscle on the ilium in either *Thescelosaurus* or *Hypsilophodon*. Romer (1927b) concluded that it originated on the ilium posterior to the antitrochanter in hadrosaurs. The M. ilio-fibularis is shown in a comparable position in *Thescelosaurus* (Fig. 5) and *Hypsilophodon* (Fig. 6). The insertion was on the lateral surface of the fibula head. In BM(NH) R5830 there is a well-defined area with muscle scars on the posterior part of this surface which was probably for the M. ilio-fibularis (Fig. 4). This muscle, together with the other flexors, aided in retracting the femur.

b) M. flexor-tibialis internus(=M. ischio-flexorius; Romer, 1927b). Romer (1927b) showed that in *Thescelosaurus* the origin of this muscle was on a projection on the dorsal edge of the ischium just distal to the end of the obturator process (Fig. 5). There is no comparable projection in *Hypsilophodon* so its position in *Thescelosaurus* has been used in the reconstruction

(Fig. 6). A second head of the M. flexor-tibialis internus may have originated from the postacetabular part of the ilium as in the alligator but there is no evidence that this slip was present. The main insertion was presumably a tendinous one on the posterior part of the tibial head. A second tendon may have inserted on the external head of the M. gastrocnemius as in the alligator.

c) M. flexor-tibialis externus(=M. ilio-flexorius, Romer, 1927b). This muscle was probably present, but its area of origin has not been observed on the posterior part of the ilium of any ornithischian. The insertion was presumably on the posterior part of the tibial head.

d) M. pubo-ischio-tibialis. This muscle is reduced to a slip in the alligator and is lost in birds as was probably also the case in ornithischians.

4. Muscles that Retracted the Femur.

a) M. pubo-ischio-femoralis internus(=M. ilio-femoralis internus; Romer, 1927b). The more dorsal part of this muscle originated from the ventral surface of the transverse processes of the more posterior dorsal vertebrae. Romer (1927b) deduced that this muscle inserted on the greater trochanter in *Thescelosaurus* (Fig. 16). On the outer surface at the base of the greater trochanter in *Hypsilophodon,* there is a very prominent ridge that continues distally (Figs. 8A, 9A, 10B). Proximally, this ridge is sharp edged because it is the line of contact between two concave surfaces. More distally the anterior surface becomes convex and the posterior concave area cuts a distinct edge into this. The anterior concave area has strong longitudinal striations. The posterior area has only faint striations proximally but distally there are strongly developed and irregular markings on BM(NH) R193. In BM(NH) R2487 the posterior area is covered by longitudinal striations.

The two surfaces evidently formed an extension onto the shaft of the insertion area of two muscles that were attached to the greater trochanter. The M. pubo-ischio-femoralis internus probably inserted on the posterior area and the M. ilio-trochantericus on the anterior area (see p. 36).

b) M. ilio-trochantericus. The area of insertion of this muscle has just been discussed. Romer (1927b) deduced that in hadrosaurs the M. ilio-trochantericus originated from the lateral surface of the ilium anterior to the antitrochanter. The origin of this muscle is shown in a comparable position in *Thescelosaurus* (Fig. 5) and *Hypsilophodon* (Fig. 6). The M. ilio-trochantericus helped to prevent disarticulation of the femur.

c) M. caudi-femoralis longus and brevis(=M. coccygeofemoralis longus and brevis; Romer, 1927b). The M. caudifemoralis longus probably originated on the sides of the centra and the ventral surface of the transverse processes of the anterior third of the tail. Romer (1927b) pointed out that in many primitive ornithischians, including *Thescelosaurus,* the ilium has a broad brevis shelf from which the M. caudi-femoralis brevis originated. This muscle probably originated on the broad brevis shelf in *Hypsilophodon* (Figs. 4, 6) and, in addition, may have originated from the sides of the centra of the last sacral and the first caudal vertebra as in the alligator. Both of these muscles inserted on the fourth trochanter of the femur.

The outer surface of the fourth trochanter of *Hypsilophodon* continues the concave curve of the adjacent shaft (Fig. 10A). More distally on the outer surface there is a ridge extending to the tip of the trochanter (Figs. 8A, 9A, 10B). The position of this ridge relative to the distal edge of the trochanter varies—it is progressively farther away in the series BM(NH) R193, R195 and R196. Between this ridge and the dorsal edge there is a concave depression that proximally becomes indistinct as the ridge disappears. In BM(NH) R193 (Figs. 8A, 9A, 10A, B) this depression is rugose; it can be followed proximally where its boundary is formed by two series of small ridges that are parallel to the dorsal edge. The line of these ridges is continued onto the shaft of the femur as a faint line formed by a series of small depressions (Figs. 8A, 9A, 10A). In BM(NH) R195 there is a well-defined series of fine ridges running across this concave depression. In BM(NH) R196 the depression is less well defined and there are only faint insertion markings.

Distally the dorsal edge of the fourth trochanter is sharp because there is another concave area, with strongly developed insertion markings, on the inner side of the pendant portion of the trochanter (Figs. 8B, 9B, 10D). Proximally the dorsal edge is thickened on this side to form a strong ridge with very well-developed but irregular insertion markings (Figs. 8B, 9B, 10D). Internal to this ridge there is a smooth concave area that widens out distally between the strongly concave area on the pendant part of the trochanter and the depression on the shaft of the femur (Figs. 8B, 9B, 10D).

In BM(NH) R193 (Figs. 8B, 9B, 10D), R195 and R2477a the depression at the base of the fourth trochanter is deep with a well-defined edge anteriorly and distally. Proximally the depression merges with the shaft surface and posteriorly it merges with the smooth concave area below the dorsal ridge. The whole of the surface of this depression is rough with extremely well-developed insertion markings. In BM(NH) R196, R5829 and R5830 there is a well-defined area, with irregular and strong insertion markings, in the same position on the shaft but forming only a slight depression. Distally this area is slightly higher than the adjacent part of the femoral shaft. The remaining boundaries of this area can only be distinguished by the presence of insertion markings.

I consider that the main insertion of the M. caudi-femoralis longus was on the medial depression and that the pars brevis inserted on the lateral surface of the fourth trochanter. The anterior limit of M. caudi-femoralis brevis is indicated by the line approximately parallel to the edge of the trochanter (Figs. 8A, 9A, 10A). Consequently the pars brevis inserted on a marginal zone on the lateral surface that extends the complete length of the trochanter. Proximally the brevis may have extended slightly onto the shaft but no boundary is visible. The brevis probably wrapped round the edge of the trochanter to insert on the medial surface of the strong ridge (Figs. 8B, 9B, 10D). The medial depression on the pendant part of the fourth trochanter was for a tendon which extended to the head of the fibula (Figs. 4, 8B, 9B, 10D). The lateral surface of the base of the M. caudi-femoralis longus was closely applied to the adjacent structures (Figs. 8B, 9B, 10D): the unoccupied medial surface of the trochanter, the surface of the tendon to the knee and the medial surface of the brevis. The fourth trochanter and the depression at its base is discussed on page 38.

d) M. obturator internus(=M. pubo-ischio-femoralis externus, anterior part). Romer (1927b) thought that the posterior part of the M. pubo-ischio-femoralis externus had been lost in ornithischians and that it was replaced by the anterior part, which originated from ligaments connecting the postpubic rod and the ischium. There is no evidence to show whether or not the posterior part was lost in ornithischians but it is reasonable to conclude that it was as is the case in birds. In *Hypsilophodon* the postpubic rod has a sharp upper edge on which the puboischiadic ligament could have attached. Specimen BM(NH) R193 has surface markings running below the dorsal edge and passing below the obturator foramen (Figs. 6, 7) that were probably for the puboischiadic ligaments. Romer (1927b) stated that there is no sure indication of the area of origin of the M. obturator internus on the ischium of *Thescelosaurus* but that in hadrosaurs there is a ridge running lengthwise that marks its dorsal border. In *Hypsilophodon* the ischium of BM(NH) R193 has on its outer surface a definite ridge running along just below the middle of the shaft which marks the dorsal limit of the M. obturator internus (Figs. 6, 7). The lateral surface of the obturator process probably formed another surface for the origin of this muscle but no definite boundaries can be seen in this region or along the length of the blade. Romer (1927b) did not find any indication of the insertion area; he noted that it is on the ventral surface of the head in living forms. The femur of BM(NH) R193 of *Hypsilophodon* (Fig. 10A) has a small, faint circular rugose area that was possibly the area of insertion for the tendon of this muscle.

e) M. adductor femoralis. Romer (1927b) placed the origin of the two heads of this muscle on the shaft region of the ischium in *Thescelosaurus* (Fig. 5) where there is a series of rugose markings between the origin areas of the M. obturator internus and the M. ischio-trochantericus. In *Hypsilophodon* there is a longitudinal depression on the shaft of the ischium [BM(NH) R193, Figs. 6, 7 and BM(NH) R195] bounded by a slight ridge dorsally and ventally. Romer (1927b) noted that the insertion of the M. adductor femoralis is sometimes shown by a slight indication on a line from the fourth trochanter towards the outer condyle. This has not been located on the femora of *Hypsilophodon* unless it is represented by an area on the posterolateral part of the shaft in BM(NH) R193 (Figs. 8A, 9A, 10A, B). This area bears well-developed longitudinal striations and is separated by a sharp edge from the insertion area of M. femoro-tibialis 3.

f) M. ischio-trochantericus. In *Thescelosaurus* (Fig. 5) this muscle probably originated on the flattened upper surface internal to the dorsal edge of the ischium, which forms a prominent shelf below this muscle (Romer, 1927b). Romer noted that in all forms in which the position is determinable except *Camptosaurus* and *Protoiguanodon* there is no prominent shelf and the muscle originated from the outer surface. A rugose or ridged line running along most of the length of the ischium marks the ventral limit of this muscle in these forms.

In *Hypsilophodon* (Figs. 6, 7) the posterior part of the M. ischio-trochantericus probably originated on the flattened inner surface of the blade of the ischium as in *Thescelosaurus.* The dorsal margin of the shaft region does not form a distinct ledge and the muscle probably originated on its rounded margin, extending slightly onto the outer surface as far as the dorsal limit of the adductor muscles (Fig. 6). This dorsal margin shows very strongly developed markings in BM(NH) R195 and R196.

Romer (1927b) noted that the area of insertion of the M. ischio-trochantericus near the head of the femur is not visible. In his reconstruction of *Thescelosaurus* the insertion is shown very close to the head of the femur, behind the greater trochanter. In *Hypsilophodon* it probably inserted in the same region (Figs. 4, 8A, 9A, 10A).

Discussion

Several problems of an interpretational or functional nature became apparent while trying to identify the areas of muscular attachment described in the above section. The conclusions relevant to the identification of attachment areas were included but the reasons still need to be considered.

A. THE PUBIS

1. The Ornithischian Pubis and Abdominal Support.

The ornithischian pelvic girdle has a characteristic tetraradiate form (Figs. 5, 6) with the pubis forming an anteriorly directed "prepubic process" and a posterior "postpubic rod". The prepubic process is diagnostic of the order Ornithischia, one of the two orders of dinosaurs which were so successful during the Mesozoic era. The presence of a rod-like pubis close to the ischium occurs in only one other group, the Class Aves (Fig. 14D, E). Consequently it is important that the functional significance of the similarities and differences of the form of the pelvic girdle of ornithischians and birds be understood.

The prepubic process is generally regarded as a new structure with the postpubic rod as part of the normal reptilian pubis that, early in the history of the Ornithischia, came to lie close to the ischium. However, the postpubic rod had originally been regarded as a new development (Marsh, 1878, p. 451; more recently, Lebedinsky, 1913) but it is difficult to account for its development in terms of a muscle shifting its attachment area posteriorly. As Romer (1927b) maintained, a muscle involved in such a shift would probably have passed onto the adjacent anterior edge of the ischium. He thought it unlikely that a thin rod, lying close to the ischium, would have been formed because this is mechanically weaker. In addition, I consider that the implied evolutionary history of this "new" structure would be rather improbable because, after the lengthening of the rod until it was as long as the ischium in hypsilophodonts and camptosaurs, which on other characters are regarded as primitive Ornithopoda, it was then considerably shortened in the advanced Ornithopoda iguanodonts and hadrosaurs as well as in psittacosaurs and ceratopsians.

The pubis of birds has a postpubic rod similar to that of ornithischians and an anteriorly directly pectineal process (Figs. 3, 14D) for the M. ambiens. The pectineal process is best developed in ratites (Lebedinsky, 1914) but proportionally it is always minute in comparison with any prepubic process. The postpubic rod of birds clearly represents the original reptilian pubis because in the earliest bird known, the Jurassic *Archaeopteryx* (Fig. 14E), there is no pectineal process. In modern birds during embryonic development the pubis swings back to lie close to the ischium (Romer, 1927a). It seems likely, as Romer (1927b, 1956) believed, that the same thing occurred during the embryonic development of ornithischians.

In most reptiles the abdominal muscles insert on the anterior margin of the pubis and, if it is present, on the pubo-ischiadic ligament. As noted the postpubic rod probably represents the original reptilian pubis that, during the evolution of the Ornithischia, changed position to lie close to the ischium. Romer (1927b) pointed out that this change would have resulted in longer abdominal muscles under heavy pressure and without adequate support. He accounted for the development of the prepubic process of ornithischians as an adaptation to offset this weakness. Romer considered that a structure comparable to the processus lateralis of the Lacertilia lengthened and took over most of the obliquii muscles and possibly part of the rectus abdominis muscle. According to Romer the main part of the pubis could change position only *after* it had been released from its role of supporting the abdominal muscles. Romer (1927b, p. 246) suggested that the rotation provided the obturator muscle with a more advantageous position. Romer cited several points that he thought tended to confirm that the ornithischian prepubic process provided the main support for the abdomen: the direction of the prepubic process; its form, which in many types is a long thin blade; and when present, the muscle markings, which are longitudinal striations. Further evidence was obtained from a mounted skeleton of *Triceratops* in which the prepubic process was orientated so that its anterior end was in the plane of the ribs (Fig. 12). Romer (1927b, p. 244) pointed out that on the posterior border of the adjacent long dorsal rib there are "indications of a muscular or ligamentous attachment of considerable strength which matched in size and position the end of the prepubic process. This quite definitely seems to show that abdominal support was a major, although perhaps not the sole function of the process." Later, in discussing the musculature of *Thescelosaurus,* he argued (p. 260) that the M. rectus abdominis was probably not of great strength, "as suggested by the lack of any well-marked area for its insertion", and that the obliquii muscles had taken over the great part of the abdominal support. Romer followed W. K. Gregory in considering that there was a considerable constriction of the waist region, with little more than a flap of skin below the girdle, so that the thighs were not restricted.

2. The Pubis in Birds.

The pubis of birds lies close to the ischium and there is no prepubic process to provide support of the abdomen. Romer (1927b, 1956) considered that a prepubic process was unnecessary because of the shortness of the abdomen and the large sternum, which extends almost to the pelvic region. As a result the abdominal muscles have only a comparatively small space to cross. This is certainly the case in carinate birds that are extremely specialized for flying, but not in the earliest known bird, the Jurassic *Archaeopteryx.* In *Archaeopteryx* the pubis is directed backward and there is neither an anterior prepubic process nor a pectineal process (Fig. 14E). The abdominal area with 12 dorsal vertebrae (Heilmann, 1926, fig. 23; and in Romer, 1966, fig. 253) is proportionally almost as extensive as in ornithischians, which have 15 dorsal vertebrae. The sternum of *Archaeopteryx* could not have provided much support for the abdomen because, although broad, it is very short (Beer, 1954). It is therefore apparent that the short abdomen and the large sternum of birds developed *after* the pubis had changed position and, as a result, these features cannot be cited to explain the absence of a prepubic process in birds. *Archaeopteryx,* however, had at least 9 to 10 pairs of gastralia (Heilmann, 1926, fig. 7) which would have provided accessory support for the abdominal muscles.

Archaeopteryx was about the size of a large pigeon, which may reduce its relevance to the present inquiry, but the size of the early ornithischians in which the pubis shift occurred is not known. Gastralia are primitively present in reptiles of all groups and their occurrence in *Sphenodon, Archaeopteryx,* crocodiles, phytosaurs, thecodonts and some saurischians strongly suggests that they were present in primitive ornithischians. They have been reported only from *Stegoceras* (Gilmore, 1924a), but these may have belonged to a saurischian dinosaur. It must be concluded that gastralia were either cartilaginous or absent in most ornithischians. The possible absence of gastralia in most ornithischians does not necessarily mean that the prepubic process was essential for abdominal support because gastralia are also absent in ratites. The sternum of ratites is small and the abdominal muscles span a distance that is comparable to that in an ornithischian of the same height (see figure *Struthio* in Gadow & Selenka, 1891, pl. 5, fig. 1 and *Dinornis* in Romer, 1966, fig. 257). There is no accessory support provided by gastralia, a large sternum or a prepubic process yet some moas reached a height of 10-11 feet (Romer, 1966). An ornithopod of this height would have been at least 20 feet long. In addition there is no accessory support in any large mammal in which the ventral abdominal muscles are very long (see figures in Romer, 1966).

To summarize, *Archaeopteryx* shows that the pubis can lie close to the ischium without the development of a prepubic process, a large sternum or a short abdomen. Although gastralia were probably present in early ornithischians, their absence would be no problem because the ventral abdominal muscles of ratites and large mammals can span long distances without any accessory support. Consequently I consider that the basic assumption made by Romer (1927b) is incorrect. The arguments used to show that the obliquii muscles had functionally replaced the M. rectus abdominis as the principal supporter of the abdomen. will now be considered.

3. The Abdominal Muscles.

The mounted skeleton of *Triceratops* cited by Romer (1927b) is shown in Figure 12 (see also Osborn, 1933, for other views; for another mount see Erickson, 1966). The presence of a strongly developed ligamentous or muscular connection between the last dorsal rib and the prepubic process would certainly have braced and strengthened the side wall of the abdominal cavity. The high position of this process in *Triceratops,* like that in other ornithischians must, however, have limited its effectiveness in providing the main supporting point for the abdomen. According to Romer (1927b, fig. 17) for *Thescelosaurus* the M. obliquus abdominis passed posterodorsally to insert on the anterior end of the prepubic process (Fig. 5). Consequently in *Triceratops* the posterior limit of the effective abdominal cavity is marked by the last long dorsal rib (Fig. 12). This would give a short abdominal cavity and, as Romer noted, little more than a flap of skin below the pelvic girdle. This is a rather strange condition for herbivorous animals which in many cases reached a considerable size. Herbivorous mammals are characterized by a barrel-like rib cage and a large abdominal cavity to contain the greatly elongated intestine required to digest plants. The rib cage of *Triceratops* is certainly barrel-like as shown in Figure 12, in Osborn (1933) and even more clearly in Erickson (1966, pls. 1, 2) where the ventral part of the rib cage has been restored. It would seem more logical and provide a larger abdominal cavity if the principal muscles that supported the abdomen continued posteriorly and attached to the distal end of the ischium.

In marsupials there is a separate anterior part of the pubis, the epipubic bone, that is definitely important for abdominal support with the M. obliquus abdominis internus and externus inserting along its length (Elftman, 1929). In some marsupials, such as the wombat *Phascolomys* and especially the koala *Phascolartos* (Elftman, 1929, pls. 13, 14), the epipubic bone is very well developed and the abdomen large. In both these genera the epipubic bone is more ventrally directed so that the anterior end is proportionally much lower than that of the prepubic process of most ornithischians, e. g. *Hypsilophodon* (Fig. 4), *Thescelosaurus* (Fig. 5) and *Triceratops* (Fig. 12; for figures of other ornithischians see Colbert, 1961; Romer, 1966).

Romer (1927b) considered that the M. rectus abdominis was weak because there was no well-defined area for its insertion. In his reconstruction of *Thescelosaurus* Romer (1927b, fig. 16) showed the M. rectus abdominis attached only to the slender postpubic rod (Fig. 5). Although not specifically stated, it is apparent that Romer considered that the slender nature of the postpubic rod resulted from the reduction of the M. rectus abdominis. However, the slenderness may indicate that this muscle had transferred at least in part onto the ischium, a possibility that Romer (1927b, fig. 18) accepted for the M. obturator internus. Romer (1927b, p. 260) also noted that when the distal part of the pubis is lost, as in iguanodonts, hadrosaurs and ceratopsians, the M. rectus abdominis would have attached to the anterior border of the ischium below the termination of the pubis. Obviously such a transfer must have occurred *before* the postpubic rod could be lost so I consider that the M. rectus abdominis probably inserted on the ischium in hypsilophodonts and camptosaurs. The distal part of the ischium of *Hypsilophodon* (Fig. 13) and *Thescelosaurus* is expanded transversely. The anterior surface of the swollen distal end would have provided an adequate insertion area for a strong M. rectus abdominis. The adjacent part of the blade region probably formed an additional insertion area. This surface is covered by longitudinal striations in BM(NH) R193 and R5829 and it is unlikely that the M. obturator internus occupied the whole of this surface. I consider that the M. rectus abdominis of *Thescelosaurus* was not reduced and that it was a strong muscle that provided an important role in supporting the large abdomen. In addition it would have provided a ventral tie that would have helped in maintaining the curvature of the dorsal vertebral series.

It should be noted that Romer (1927b, figs. 16, 17) showed only two abdominal muscles in *Thescelosaurus:* the M. rectus abdominis passing posteriorly to insert on the whole of the ventral edge of the pubis and the M. obliquus abdominis passing posterodorsally to insert on the anterior end of the prepubic process (Fig. 5). He stressed that the former muscle had been functionally replaced by the latter but ventral to the pelvic girdle the reverse is the case with the M. rectus abdominis as the only muscle. The abdominal wall as reconstructed by Romer is rather unique and ill-adapted to support any viscera. In living amphibians, reptiles (except Chelonia), birds and mammals there is a ventral M. rectus abdominis and three lateral abdominal muscles that, though each is only a thin sheet, together form a strong abdominal wall as the fiber directions form a lattice work. Details of these muscles in the alligator and birds are given above (p. 7) and the reconstruction of these muscles in *Hypsilophodon* on page 11 and Figures 4 and 6.

From the similarity of the form of the postpubic rod the abdominal musculature of *Hypsilophodon* probably resembled that of birds rather than that of living reptiles. If the musculature resembled that of carinates (see p. 8 and George & Berger, 1966), then the M. obliquus abdominis externus probably inserted on the ventral surface of the prepubic process and the anterior part of the postpubic rod, the pars internus on the distal half of the postpubic rod and the M. transversus abdominis on all of the ventral edge of the pubis. With such an extensive abdomen it is more likely that the lateral abdominal muscles extended their area of insertion on the pubis so that they all inserted along the whole of the ventral edge of the pubis as in ratites (Gadow, 1880). In addition, it is possible that part of each muscle inserted on the laterally expanded distal part of the ischium. Consequently, I consider that the region below the pelvic girdle did not consist of "little more than a flap of skin." Even so, there was no problem as regards the free movement of the legs because the width of the sacrum, combined with the offset heads of the femora, provided plenty of space for a large and tapering abdominal cavity between the thighs. This is clearly shown in the posterior view of a mounted skeleton of *Camptosaurus* (Gilmore, 1912, pl. 60) and in figures of *Triceratops* mounts (Osborn, 1933; Erickson, 1966). The potential strain on the abdominal muscles, due to the posterior position of the pubis, was probably compensated for by an increase in the strength of all the abdominal muscles including the M. rectus abdominis. Apparently in the ornithopods part of this muscle and possibly the lateral abdominal muscles transferred to the adjacent surface of the ischium and, as a result, the postpubic rod became reduced in thickness (hypsilophodonts, camptosaurs). Subsequently this transfer was completed and the distal part was lost in iguanodonts, hadrosaurs, psittacosaurs and ceratopsians. It should be noted that the postpubic rod is thick and about the same length as the ischium in stegosaurs (Gilmore, 1914). Romer (1927b, p. 251) stated that he could not explain "on functional grounds the peculiar construction of the ischium and postpubis in this group. The broad surface presented by the two bones affords a large external area of origin for the obturator. But this can be but a minor factor." The position in stegosaurs probably indicates that the abdominal muscles had not shifted their insertion to the ischium to such an extent as had occurred in ornithopods.

4. The Question of Muscle Attachment to the Lateral Surface of the Prepubic Process of *Hypsilophodon*.

Romer (1923b, 1927b) concluded that the abdominal muscles, the M. ambiens and the anterior part of the M. pubo-ischio-femoralis externus were the only muscles on the pubis of saurischian and ornithischian dinosaurs. These muscles, together with the M. pubo-tibialis and the M. pubo-ischio-femoralis internus, will be considered in this section in an attempt to determine which muscle was attached to the well-defined area on the lateral surface of the prepubic process of *Hypsilophodon* (see above p. 14 and Figs. 4, 6, 7).

a) An abdominal muscle.

As suggested above (p. 27) all three lateral abdominal muscles inserted on the ventral surface of the prepubic process. The orientation of the muscle scars on the posterior part of the lateral area of BM(NH) R193 and R5829 are at about 45° to the long axis of the prepubic process. This indicates that the muscle concerned probably passed posteroventrally or anterodorsally. The M. obliquus abdominis externus may have had a posteroventral orientation so it could have occupied the lateral area. However, I think that this muscle was probably restricted to the ventral surface of the pubis. The extra insertion area for abdominal muscles on the prepubic process was probably a secondary result; certainly ratites and large herbivorous mammals manage to support their abdomen adequately without such a process.

In hypsilophodonts (Figs. 5, 6), *Psittacosaurus, Protoceratops* and *Leptoceratops* the prepubic process is rod-like (for figures of these and following genera, see Romer, 1927b, 1966; Colbert, 1961). In *Camptosaurus* and *Stegosaurus* the process is slightly expanded dorsoventrally. In *Iguanodon,* hadrosaurs and ceratopsians the anterior end is considerably expanded dorsoventrally, reaching its greatest extent in hadrosaurs and advanced ceratopsians (Fig. 12). Romer (1927b) correlated this with increased size and the resulting heavier strains on the obliquii muscles that supported the abdomen, because the expansion is in the plane of these muscles. However, this expansion may represent the increased size of a limb muscle, with particular emphasis on the longer fibers which originated on the more anterior part of the prepubic process. The ventral and the medial surfaces would still provide an insertion area for abdominal muscles. In most ornithischians where they are present the surface markings on the lateral surface of the prepubic process are longitudinal striations (see p. 15). Romer (1927b) cited this as evidence that the obliquii muscles inserted on this surface. However, in most of the ornithischians mentioned on page 15 the lateral surface of the anterior process of the ilium also has longitudinal striations. These were caused by the M. ilio-tibialis 1 and in hadrosaurs (Lull & Wright, 1942) and advanced ceratopsians (Fig. 12 and Lull, 1933) the prepubic process is similar but much larger than the anterior process of the ilium. The possibility that a limb muscle originated from the prepubic process must therefore be reconsidered.

b) M. pubo-ischio-femoralis externus.

In the alligator two heads of this muscle originate on the pubis and one on the ischium (Romer, 1923b); in saurischians probably one head was on each bone (Romer, 1923c). In birds there is no posterior part but the anterior part of the M. obturator internus swings back with the pubis during embryonic development to become secondarily associated with the ischium (Romer, 1927a, b). This probably occurred in *Hypsilophodon* so that the M. pubo-ischio-femoralis externus originated from the postpubic rod and ischium as a M. obturator internus. As Romer (1927b) pointed out, this muscle would have had to follow a devious route from the prepubic process to reach its normal area of insertion on the posterior surface of the femur.

c) M. ambiens.

There are insertion markings on the dorsolateral edge of the prepubic process in *Hypsilophodon* close to the acetabular region in BM(NH) R193 (Figs. 4, 6, 7), R195 and R196. These markings, which are completely separate from the well-defined lateral area (Figs. 4, 6, 7), correspond quite closely to the position of the bump for the M. ambiens in *Thescelosaurus* (see p. 13). It is considered unlikely that the M. ambiens also originated from the well-defined area on the lateral surface of the prepubic process of *Hypsilophodon.* Romer (1927b) noted that such an anterior origin would give the M. ambiens a very open angle quite unlike that found in any other group; its usual archosaurian course across the knee would appear to be impractical without interference with the tendon of the M. triceps femoris.

d) M. pubo-tibialis.

This muscle is absent in crocodiles and birds so Romer (1927b) concluded that it was also absent in ornithischians but the presence of the prepubic process itself could also be denied on these same grounds. In lizards the M. pubo-tibialis originates between the M. ambiens and the M. obliquii abdominis which is on the processus lateralis(Snyder, 1954). The origin of the M. pubo-tibialis is also adjacent to that of the M. ambiens in *Sphenodon* (Gregory & Camp, 1918). If the M. pubo-tibialis originated on the lateral area of the prepubic process of *Hypsilophodon,* it would have had the same spatial relationships with the M. ambiens and M. obliquii abdominis. The M. pubo-tibialis of *Sphenodon* (and lizards) extends to the medioproximal prominence of the tibia (Gregory & Camp, 1918). In hadrosaurs and ceratopsians especially, the form of the prepubic process resembles that of the anterior process of the ilium. It is possible that the M. pubo-tibialis originated on the prepubic process and inserted on the medial part of the tibial head while the M. ilio-tibialis, which originated more dorsally on the anterior process of the ilium, inserted on the cnemial crest (Fig. 4). Both muscles would have acted to raise the leg. This interpretation involves no change in muscle locations and, when the femur was no longer held laterally, the prepubic process was developed to give the M. pubo-tibialis a better leverage with an anteroposterior line of action. If the M. pubo-tibialis originated on the prepubic process of *Hypsilophodon,* then the absence of this process in birds could be related to the absence of a M. pubo-tibialis. However, the retention in *Hypsilophodon* of a muscle that has also been lost in crocodiles does pose certain problems. I consider that either this muscle or the one considered below probably originated on the lateral area of the prepubic process.

e) M. pubo-ischio-femoralis internus.

In its course from an origin on the centra of the posterior dorsal vertebrae to the greater trochanter of the femur this muscle passed dorsally, close to the prepubic process. Romer (1927b) stated that, despite this, it is improbable that it had any strong attachment to that element. There is a part of the M. pubo-ischio-femoralis internus, regarded by Romer (1927b) as a slip, that may have originated from the lateral area of the prepubic process. Romer (1927b, p. 255) noted that a part of the "ilio-femoralis internus may have followed the course normally taken by a portion of the primitive pubo-ischio-femoralis internus (and the ilio-femoralis of birds) and inserted farther down the femur towards the inner margin in the general position of the mammalian lesser trochanter. Rugosities for such an insertion have been located in specimens of *Corythosaurus, Triceratops,* and a few other forms, but they are generally rare and uniformly weak-appearing." The abdominal muscles inserted on the ventral surface of the prepubic process so in *Hypsilophodon* this ventral part would have passed laterally, from the dorsal centra over the prepubic process, and then ventrally to insert proximally on the shaft of the femur. This postulated course means that the ventral part of the M. pubo-ischio-femoralis internus *wrapped* around the prepubic process. It seems more likely that it actually originated on the lateral area on the prepubic process (Figs. 4, 6, 7). The line of action of this ventral part would have been more anteroposterior if it originated on the prepubic process rather than on the centra of the posterior dorsal vertebrae. Such an origin might account for the orientation of the muscle scars on the posterior part of this lateral area. According to Romer (1927b) the muscle scars on the femur for the insertion of this ventral part are generally rare and uniformly weak. This does not necessarily prove that the muscle itself was weak as several undoubtedly powerful muscles originated from the ilium in *Hypsilophodon* but, apart from the M. ilio-tibialis, the areas on which these muscles originated cannot be identified. There is a large area on the anteromedial surface of the femur above the area for M. femoro-tibialis 2 (Figs. 8B, 9B, 10E) on which this ventral portion could have inserted by a large but fleshy attachment. Consequently, it is possible that the ventral part of the M. pubo-ischio-femoralis internus originated on the lateral area on the prepubic process of *Hypsilophodon.*

5. The Pelvic Girdle of Ornithischians and Birds.

The anterior process of the ilium in *Archaeopteryx* (Fig. 14 E) and primitive ornithischians (Fig. 14C) is proportionally much longer than it is in primitive saurischians (Figs. 14A, B) while in crocodiles it is practically nonexistent (Fig. 1). The M. ilio-tibialis 1 (sartorius) probably originated from the complete length of this process and was the principal long femoral protractor that inserted on the tibia and extended the knee (Fig. 4). As a result of the much longer anterior process of the ilium in ornithischians and birds, this muscle was much larger and had a better mechanical position than in saurischians. In *Archaeopteryx* the anterior process of the ilium is deep (Fig. 14E) and covers the centra of the adjacent lumber vertebrae (Romer, 1966, fig. 253). As a result the M. pubo-ischio-femoralis internus of *Archaeopteryx* originated on the ilium as in modern birds. The ventral part of this muscle may have originated on the prepubic process of ornithischians, and, if this was the case, it would account for the absence of this process in birds (see above p. 16). This femoral protractor occupied a more lateral position in both *Archaeopteryx* and primitive ornithischians so that the line of action in both was fore and aft rather than more obliquely as in crocodiles and saurischians. However, it is possible that the prepubic process was for the M. pubo-tibialis, a muscle lost in birds, which would have supplemented the action of the M. ilio-tibialis 1 (see p. 14). This would also have been the case if the muscle on the prepubic process were the M. ambiens (see p. 13). Consequently the two femoral protractors in *Archaeopteryx* and primitive ornithischians probably occupied a position of better leverage than in saurischians and crocodiles. Saurischians probably possessed another anteriorly placed protractor, the M. pubo-ischio-femoralis externus (see Romer, 1923b, c), which originated from the pubis that was anteroventrally directed as in other reptiles (Fig. 14B). This muscle was probably large as in crocodiles (Figs. 1, 2) in which it is an important protractor of the femur.

It should be noted that when the pubis rotated backwards towards the ischium in birds and ornithischians the M. pubo-ischio-femoralis externus would have changed from a femoral protractor to a retractor. I suggest that the presumed greater development and improved mechanical position of the more anterodorsally situated protractors (the sartorius and possibly the ventral part of the M. pubo-ischio-femoralis internus) in *Archaeopteryx* and primitive ornithischians was necessary *before* the pubis could change position. Only when the M. pubo-ischio-femoralis externus was no longer essential as a femoral protractor could the pubis have come to lie close to the ischium.

As Romer (1927b) noted the pubis is directed ventrally rather than anteriorly in some primitive archosaurs. Thus in the thecodonts *Euparkeria* (Ewer, 1965), *Stagonolepis* (Walker, 1961) and *Saltoposuchus* the more distal part of the pubis is rod-like, ventrally directed and more or less perpendicular to the adjacent part of the vertebral column so the ventral part of the M. pubo-ischio-femoralis internus must have passed very close to the proximal part of the pubis to reach the femoral shaft. In the line of thecodonts leading to ornithischians, fibers of the ventral part of the M. pubo-ischio-femoralis internus probably attached to the proximal part of the pubis. The increased importance of these fibers with a more fore and aft action would have resulted in the formation of the prepubic process. When the M. ilio-tibialis 1 and possibly the ventral part of the M. pubo-ischio-femoralis internus were adequately developed the M. pubo-ischio-femoralis externus would no longer have been essential for protracting the femur. When this stage was reached, the pubis continued rotating backward to lie next to the ischium. In birds both muscles were on the ilium, but the result was the same with the pubis lying close to the ischium.

Depending on the degree of development of the M. ilio-tibialis 1 (as shown by the size of the anterior process of the ilium) it is possible that the prepubic process was quite small or even nonexistent when the pubis changed its position. In the latter case the attachment of the M. pubo-ischio-femoralis internus to the pubis would have occurred after this change occurred. I consider that the anterior process was probably quite long when the pubis rotated backward with quite a short prepubic process. If the muscle concerned was the M. pubo-tibialis then the prepubic process was probably moderately developed before the pubis changed position. It is probable that in ornithischians, as was certainly the case in birds, the development of a large anterior process of the ilium was the critical factor that enabled the pubis to lie close to the ischium.

The posterior position of the pubis in the ornithischian line would have provided a larger abdominal cavity which, as Nopcsa (1917) suggested, would be advantageous to an herbivorous animal. Romer (1927b) rejected this idea because it failed to explain why the same change occurred in birds. He related the backward shift of the pubis to a change in the position of the M. pubo-ischio-femoralis externus to form the M. obturator internus. However, this must have been a result rather than a cause. It is hard to visualize a selective force whose primary result was to convert a femoral protractor into a retractor. There would be a half-way stage when the muscle was neither but this would be no problem if other selective forces were acting. A backward extension of the effective abdominal cavity would also result in a posterior shift of the center of gravity nearer the acetabulum. This is advantageous to a bipedal animal and its importance was increased in birds in which, with the exception of *Archaeopteryx,* the tail is very short. The explanation may be even more general than this since in eutherian mammals, where the anterior part of the ilium is elongated, the anteroventral part of the pubis has been lost although it was present in earlier mammal-like reptiles. Consequently in these groups in which the femur moves anteroposteriorly in a vertical plane the emphasis has been on the more anterodorsally situated protractors. Ornithischians achieved a less perfect mechanical system than birds or mammals because one of the protractors was still on the pubis. However, the prepubic process is more anterodorsal than the pubis of other reptiles.

In ornithischians the more posterior position of part of the pubis (postpubic rod) probably resulted in the transformation of the anterior part of the M. pubo-ischio-femoralis externus from a protractor to a retractor. This anterior part became a M. obturator internus and replaced the posterior part as Romer (1927b) noted. This change in position of the pubis also affected the abdominal muscles. The lateral abdominal muscles extended their insertion along the complete ventral edge of the pubis. The lengthened M. rectus abdominis became stronger and, as in the example of living reptiles (except chelonians), remained the principal supporting muscle of the abdomen. When the pubis reached a position close to the ischium the M. rectus abdominis and the other abdominal muscles probably transferred to the adjacent surface of the ischium to a variable degree (see above p. 28).

B. THE ANTERIOR PROCESS OF THE ILIUM

The anterior process of the ilium of *Hypsilophodon* curves out laterally (Fig. 15). This outward curvature is a general feature of the ilium of ornithischians, as can be seen from the comparative illustrations given by Romer (1927b, figs. 2-5). There are several functional reasons for this lateral curvature: a) the outward curvature resulted in the anterior process clearing the ribs of the adjacent dorsal vertebrae; b) by curving outward the anterior process presented a larger surface, set at an angle to the longitudinal axis, for the insertion of part of the M. dorsalis trunci, so that the lateral extent of this muscle was increased; c) the outward curvature would have given the M. ilio-tibialis (sartorius, Fig. 4) a slightly improved mechanical position, as its line of action would be more anteroposterior (Fig. 15); and d) the anterior process overhung the dorsal surface of the M. pubo-ischio-femoralis internus that passed from the centra of the lumbar vertebrae to the greater trochanter of the femur (Fig. 4). As a result the ventral surface of the anterior process would have provided a potential surface of origin for this muscle. Such an origin probably did not occur in primitive ornithischians but, as Romer (1927b) suggested, it may have been important in many ceratopsians, stegosaurs and ankylosaurs.

C. THE FEMUR

1. The Greater Trochanter.

Romer correctly pointed out that the greater trochanter of saurischian (1923c) and ornithischian (1927b) femora is found almost precisely where the posteriorly inserting portion of the M. pubo-ischio-femoralis internus attached in primitive reptiles and crocodiles. Romer (1927b) concluded that in ornithischians the M. pubo-ischio-femoralis internus inserted on the greater trochanter, but he argued that the development of the antitrochanter on the ilium in hadrosaurs indicated that a second anterior femoral muscle had developed. This was the M. ilio-trochantericus, which probably originated on the surface of the ilium anterior to the antitrochanter in hadrosaurs. This origin closely resembles that of the M. ilio-trochantericus in birds, which inserts on the femur in a position similar to that of the greater trochanter of ornithischians. Thus it is reasonable to conclude that the hadrosaurian muscle inserted in the same region. Romer also (1927a, b) pointed out that the derivation and hence homology of the avian M. ilio-trochantericus is uncertain, because the evidence from development and comparative anatomy is inconclusive. The hadrosaurian muscle may have been derived from the M. pubo-ischio-femoralis internus, in which case an insertion on the greater trochanter would be expected. On the other hand, it might have been derived from the primitive M. ilio-femoralis, in which case an insertion on the lesser trochanter would be expected.

The ilium of hypsilophodonts does not provide any evidence concerning the differentiation of a M. ilio-trochantericus. Romer (1927b, p. 233) wrote that "from the point of view of the femur, however, a division into a more posterior ilio-femoralis and a more anterior ilio-trochantericus seems required (see Part V)." In Part V, when discussing the insertion of the M. ilio-trochantericus, Romer (1927b, p. 254) only said that the lesser trochanter, "when well developed, points upwards and, in most positions of the limb, markedly backward, very nearly at right angles with the direction necessarily taken by most fibers of the ilio-trochantericus. It seems improbable that the ilio-trochantericus inserted on the lesser trochanter." In his reconstruction of the musculature of *Thescelosaurus,* he showed the two muscles inserting on the greater trochanter (Fig. 16). The more posterior M. ilio-trochantericus is shown inserting on the fascia of the M. pubo-ischio-femoralis internus, the insertion of which covers the top of the greater trochanter. Romer (1927b) did not mention the presence of any insertion marks on the greater trochanter or in its immediate vicinity. Consequently, Romer did not provide any evidence to show that a M. ilio-trochantericus was differentiated in hypsilophodonts; the presence of this muscle was assumed by extrapolation from the ilium of hadrosaurs.

The lateral surface of the femoral shaft adjacent to the greater trochanter has two well-developed insertion areas that are separated by an "S" shaped ridge (Figs. 8A, 9A, 10B, see above, p. 17). This ridge was first figured by Hulke (1882, pl. 77) for BM(NH) R193 but its significance has not been commented upon. The ridge is present on all femora of *Hypsilophodon* in which this region is not damaged. This ridge is also visible on the femur of *Laosaurus minimus* (Gilmore, 1924b, pl. 2, fig. 4) and there are traces of it on the femur of *Dryosaurus altus* (YPM 1876). The origin of the M. pubo-ischio-femoralis internus was more anteriorly placed so it probably inserted on the anterior area while the M. ilio-trochantericus inserted on the posterior area (Figs. 4, 10B). The cleft between the proximal ends of the lesser and greater trochanters enabled the fascia of the M. pubo-ischio-femoralis internus to reach the inner area with less effect on the M. ilio-femoralis. This ridge at the base of the greater trochanter in *Hypsilophodon* supports Romer's assumption that a M. ilio-trochantericus inserted on the greater trochanter of hypsilophodonts. It also supports his suggestion that this muscle in ornithischians was derived from the M. pubo-ischio-femoralis internus rather than from the primitive M. ilio-femoralis. Romer (1962, table 2) lists the avian M. ilio-trochantericus and M. ilio-femoralis internus as homologous to the reptilian M. ilio-femoralis. If this is correct then the M. ilio-trochantericus of ornithischians and birds may not be homologous.

2. The Fourth Trochanter.

Dollo (1883, 1888) first pointed out that the fourth trochanter was the area of insertion for the well-developed caudi-femoralis muscles. Romer (1927b) merely noted that the size of the fourth trochanter furnished a rough guide to the size of these muscles. In his reconstruction of *Thescelosaurus* he showed the M. caudi-femoralis brevis inserting on the proximal part of the trochanter (Fig. 16). The M. caudi-femoralis longus is shown inserting more distally with a tendon passing from the pendant end of the trochanter. The muscle to which this tendon runs is not labeled in Romer's figure but from his text it is clear that it was the M. gastrocnemius (1927b, p. 257). Romer labeled a second muscle as the M. gastrocnemius so he recognized two divisions of the M. gastrocnemius. This omission of a label in Romer's figure appears to have misled Janensch (1955) who discussed this "problem". Janensch postulated a tendon in *Dysalotosaurus* that extended from one division of the M. gastrocnemius to a distinct facet on the lateral face of the pendant end of the fourth trochanter. He reconstructed the M. caudi-femoralis longus insertion on both sides of the fourth trochanter, but noted that the more proximal insertion of the M. caudi-femoralis brevis could not be definitely placed. He also drew attention to the well-developed depression near the base of the fourth trochanter in *Dysalotosaurus* and *Hypsilophodon*.

a) Possible functions for the depression at the base of the fourth trochanter.

1) To house a mucous gland.

Janensch (1955) thought that the depression near the base of the fourth trochanter in *Dysalotosaurus* and *Hypsilophodon* was too deep and extensive to have been the insertion area of a muscle. He postulated that the depression was for a mucous gland though, as he noted, the presence of such a structure is difficult to prove in fossil material. Janensch did not suggest why a mucous gland should have been housed in a depression on the femoral shaft or what function it would have served. However, such a position is much too deep for a characteristically epidermal structure. The depression is quite deep in some femora of *Hypsilophodon* but in others it is not (p. 19). In both types of femora an equivalent area is covered with surface markings of muscle attachments. Consequently this depression did not house a mucous gland but was the area of insertion of a muscle.

ii) Insertion area for part of the M. pubo-ischio-femoralis internus.

Janensch (1955) noted that on the femur of *Crocodilus niloticus,* dorsal to the wide depression on the fourth trochanter, there is another smaller depression that corresponds in position to the deep depression in *Dysalotosaurus.* He cited the figure of the alligator femur given by Romer (1923b, pl. 25) in which part of the M. pubo-ischio-femoralis internus is shown inserting on this region (Fig. 17). Romer (1927b) discussed this muscle (see above, p. 31) but, as Janensch (1955) noted, did not show it in the reconstruction of *Thescelosaurus.* Janensch considered that this muscle might have inserted on the deep depression on the femur of *Dysalotosaurus.*

iii) Insertion area for the M. caudi-femoralis.

The depression in *Hypsilophodon, Thescelosaurus* (Gilmore, 1915), *Camptosaurus leedsi* (Gilmore, 1909) and *Camptosaurus* (Gilmore, 1909), is partly on or close to the base of the fourth trochanter. This depression is further from the base in *Dryosaurus altus* (YPM 1876) and more markedly so in *Dysalotosaurus* where the depression is found quite anteriorly on the femoral shaft (see Janensch, 1955, pl. 15, fig. 2). Janensch (1955) recognized that the same muscle inserted on the depression is *Hypsilophodon, Camptosaurus* and *Dysalotosaurus* but, because it is separated by a wide space from the fourth trochanter in *Dysalotosaurus,* he considered that the depression was not for the M. caudi-femoralis. This depression is close to the fourth trochanter in *Iguanodon* (see Casier, 1960, pl. 10) and hadrosaurs (see Sternberg, 1924, pl. 4). I consider that the position of this depression in *Dryosaurus* and *Dysalotosaurus* is secondary and that it corresponds to the large depression at the base of the fourth trochanter on the alligator femur. Romer (1923b) showed the M. caudi-femoralis longus inserting on the depression at the base of the fourth trochanter in the alligator (Fig. 18). I checked the insertion areas of the M. caudi-femoralis longus and brevis in a *Gavialis gangeticus,* the only crocodilian that was available. The adjacent parts of the M. caudi-femoralis longus and brevis are closely spaced and when they are parted the fourth trochanter is seen between them. The M. caudi-femoralis longus inserts on the anterior surface of the trochanter, with an especially strong insertion on the depression at its base. The M. caudi-femoralis brevis inserts on the posterior surface of the trochanter. Because of the different postures of these reptiles the medial view (Fig. 10D) of the femur corresponds to the anterior view in the gavial and alligator (Fig. 17). I consider that the M. caudi-femoralis longus inserted into this depression in *Hypsilophodon* and *Dysalotosaurus* as it does in modern Crocodilia. The areas of the femur of *Hypsilophodon* [BM(NH) R193, Figs. 4, 8, 9, 10] on which the M. caudi-femoralis brevis and longus and the tendon from the knee region attached are described on page 31.

b) The function of the fourth trochanter.

A large fourth trochanter is characteristic of many dinosaurs, especially those that are bipedal, and its size is generally considered to reflect the degree of development of the caudi-femoralis muscles (Romer, 1927b; Lull & Wright, 1942; Ostrom, 1964). In crocodiles the caudi-femoralis muscle, which is the principal retractor of the femur (Snyder, 1962), is a very large muscle (see Haughton, 1865, fig. 20) but the fourth trochanter is small (Fig. 17). However, the pars longus, which forms the major part of the caudi-femoralis muscle, inserts mainly on the depression at the base of the fourth trochanter. It is possible that the size of the fourth trochanter of dinosaurs reflects the degree of development of the pars brevis rather than that of the longus or the caudi-femoralis musculature as a whole. The areas of origin and insertion of the M. caudi-femoralis brevis and longus were presumably similar in all bipedal ornithischians and like those of the alligator. The area of origin of the pars brevis was close to the head of the femur while that of the pars longus extended some way down the tail. The pars brevis inserted at the same level as the longus so its line of action was at a smaller angle to the femoral shaft (Fig. 4) and, as a result, its moment arm relative to the head of the femur was much shorter. In addition, when the femur was swung forward the moment arm of the pars brevis was shortened to a greater extent than that of the pars longus so it would have been reduced to zero sooner. Consequently the presence of a large fourth trochanter at right angles to the femoral shaft would have had a proportionally greater effect on the moment arm of the pars brevis. In normal positions of the femur the trochanter projected towards the area of origin of the pars longus and resulted in only a small increase in the moment arm of this part. Certainly an insertion on the depression on the femoral shaft would have been stronger than one on a projecting process. The moment arm of the pars longus of ornithopods is increased phylogenetically because the fourth trochanter is above the middle of the femur in hypsilophodonts, just below mid-femur length in camptosaurs and about two-thirds femur-length in iguanodonts and hadrosaurs. I consider that the function of the large fourth trochanter of dinosaurs was to increase the moment arm of the M. caudi-femoralis brevis during the initial part of femoral retraction. As the femur approached a vertical position the pars brevis became progressively less important while the moment arm of the pars brevis reached its maximum and its line of action became more perpendicular to the femoral shaft.

Nopcsa (1905) argued that the pendant fourth trochanter of hypsilophodonts and camptosaurs is primitive for ornithischians and that the "trochanter creté", considered by Dollo (1888) to be primitive, was a later development. However, Ostrom (personal communication) considers that the fourth trochanter of *Iguanodon* and hadrosaurs was also probably pendant. The functional significance of the pendant fourth trochanter is not certain. The space below the pendant part might have allowed a nerve, blood vessel or tendon to cross this part of the femur but there is no such structure in this region in crocodiles. In *Hypsilophodon* BM (NH) R193 (Figs. 8A, 9A, 10B) there are insertion markings on the distal surface, formed by the thick basal part of the trochanter, which were probably for part of M. femoro-tibialis 3 (see p. 14). Romer (1927b) noted that it is a general archosaurian tendency for the M. femoro-tibialis to increase in size. This origin on the fourth trochanter would have increased the moment arm of the fibers concerned, but I have not been able to find similar muscle scars on other ornithischian femora. I consider it unlikely that the origin of part of the M. pubo-tibialis 3 was the primary reason for the pendant form of the trochanter. A tendon of the M. caudi-femoralis longus muscle probably originated from the pendant part of the trochanter (Fig. 4) and passed to the knee region as Dollo (1888) first suggested. This tendon presumably inserted on the posterior aspect of the fibula head as it does in crocodiles, lizards and *Sphenodon* (Romer, 1923b; Snyder, 1954). The pendant form of the fourth trochanter may reflect stresses transmitted by this tendon if, as was possibly the case, a head of the M. gastrocnemius originated from the distal part (Figs. 4, 16). The moment arm of this head, or rather the part that originated from the tendon, would have been increased slightly. Consequently the pendant nature of the fourth trochanter may reflect stresses from the distal part of the leg rather than from the caudi-femoralis muscles.

SUMMARY

The reconstruction of the pelvic musculature of *Thescelosaurus* by Romer (1927b), with certain modifications, adequately accounts for the surface markings on the very well preserved pelvic girdle and femur of *Hypsilophodon* BM(NH) R193. Using data from living forms and functional considerations it is possible to place different degrees of confidence on the various possibilities that have been discussed.

Because the prepubic process is characteristic of ornithischian dinosaurs, it is important that its functional significance be understood. The suggestion by Romer (1927a, b, 1956) that this process provided a base for the obliquii muscles, which he considered had taken over the support of the abdomen from the M. rectus abdominis, was very neat. This theory accounted for a unique structure in terms of a new function and, apparently, explained why this process was not developed in birds. Unfortunately *Archaeopteryx* and ratites show that it was possible to have a backwardly directed pubis with long ventral abdominal muscles not supported by either a large sternum or a prepubic process. The pubis of birds had changed position to lie close to the ischium before the very large sternum and the short abdomen were evolved. The position in birds, together with the dorsal position of the prepubic process and the probable presence of

gastralia in early ornithischians at least, indicates that the primary function of the prepubic process was not abdominal support. Any potential weakening of the abdomen that resulted from the changed position of the ornithischian pubis was probably compensated for by an increase in size of all the abdominal muscles. The three lateral abdominal muscles, the fiber directions of which formed a grid-like arrangement, probably extended their area of insertion along the ventral surface of the whole length of the pubis and, in addition, possibly on to the blade-like distal part of the ischium. The latter also provided an additional insertion area for the strong M. rectus abdominis. The degree of transfer of the abdominal muscles on to the ischium occurred to a varying extent in different groups of ornithischians (see above, p. 28). The abdomen of ornithischians was probably large as in ratites and herbivorous mammals and was not just a flap of skin below the pelvic girdle as Romer (1927b) suggested.

I consider it unlikely that the muscle on the lateral surface of the prepubic process was an abdominal muscle or the M. ambiens (p. 28). The similarity in form of the prepubic process to that of the anterior process of the ornithischian ilium and the position of the M. pubo-tibialis in *Sphenodon* suggest that this might be the muscle concerned. Birds lack this muscle which would account for the absence of a prepubic process in that group. The presence of the ventral part of the M. pubo-ischio-femoralis internus on the prepubic process would also explain the absence of this process in birds where this muscle is on the ilium (M. iliofemoralis internus). The ventral part of this muscle probably originated on the prepubic process and did not wrap around the process as it would, if, as Romer (1927b) suggested, it originated on the centra of the dorsal vertebrae.

Although the postpubic rod of ornithischians probably represents the original reptilian pubis, as must be the case in birds, the functional reason for the change in position is not clear. Romer (1927b) suggested that it was related to a change in position of the anterior part of the M. pubo-ischio-femoralis which became the M. obturator internus. However, during the change in position of the pubis this muscle was converted from a femoral protractor into a retractor. I consider that the key factor in birds and ornithischians was the development of a very long anterior process to the ilium to provide a large M. ilio-tibialis 1. When the M. ilio-tibialis 1 (possibly with the ventral part of the M. pubo-ischio-femoralis externus or the M. pubo-tibialis in ornithischians) was adequate for femoral protraction, then the anterior part of the M. pubo-ischio-femoralis externus would not have been required for protraction so the pubis could change its position. In ornithischians, birds and mammals emphasis was on the more antero-dorsally situated femoral protractor with a more fore and aft line of action. The change in position of the ornithischian pubis would have enlarged the abdominal cavity which, as Nopcsa (1917) suggested, would have been an advantage to an herbivorous group. In addition, it would have shifted the center of gravity more posteriorly and this would have been an advantage to a bipedal animal.

The anterior process of the ilium curved laterally so that it cleared the adjacent ribs, provided both a larger area of insertion for part of the M. dorsalis trunci and a more fore and aft direction for the fibers of the M. ilio-tibialis 1. In addition the process overhung the M. pubo-ischio-femoralis internus and the ventral surface was an important area of origin for this muscle in stegosaurs, ankylosaurs and ceratopsians.

There are two distinct areas of muscle insertion near the base of the greater trochanter of the femora of *Hypsilophodon*. These indicate that a third dorsal muscle, analagous to the M. ilio-trochantericus of birds, was differentiated in hypsilophodonts as Romer (1927b) had postulated by extrapolation from the structure of the ilium in hadrosaurs. In some femora of *Hypsilophodon* the depression near the base of the fourth trochanter is well developed while in others it is not. In both cases the equivalent area has muscle insertion markings and, because the position of this depression is too deep for an epidermal structure, it is considered extremely unlikely that this depression housed a mucous gland as Janensch (1955) suggested. His second suggestion, that the depression was for the ventral part of the M. pubo-ischio-femoralis internus, is considered unlikely because this muscle in the alligator inserts on the shaft next to a comparable large depression. The M. caudi-femoralis longus inserts on the large depression in an alligator so it is reasonable to assume that this was also the case in *Hypsilophodon*. The degree of development of the fourth trochanter is probably not related to the size of the caudi-femoralis musculature as a whole. The function of the large fourth trochanter of bipedal dinosaurs was to lengthen the moment arm of the M. caudi-femoralis brevis during the first part of femoral retraction. The pendant form of the fourth trochanter of ornithopods may reflect the stresses from part of the M. gastrocnemius that attached to the tendon connecting the trochanter to the fibula.

ACKNOWLEDGEMENTS

Much of this paper is based on work done at the Zoology Department, King's College, University of London, England, made possible by a three year Research Studentship from the Department of Scientific and Industrial Research (subsequently the Natural Environment Research Council). I am especially grateful to Dr. C. B. Cox for all his advice and interest during the course of this work and to the British Museum (Natural History) for permission to borrow their unique material of *Hypsilophodon* and prepare it in acetic acid. The final paper has been much improved thanks to the criticisms and suggestions of Dr. J. H. Ostrom of Yale University. The manuscript was also read by Dr. A. W. Crompton, Mr. F. A. Jenkins, Jr. and Mr. R. T. B. Bakker, all of Yale University; Dr. G. E. Erickson of Brown University, Providence, R.I., and Dr. D. A. Russell of the National Museum of Canada, Ottawa; all of whose comments were much appreciated.

I am very grateful to people in the various museums for their help while studying the material under their care as cited in the text: to Dr. A. J. Charig of the British Museum (Natural History); Dr. E. H. Colbert of the American Museum of Natural History, who also kindly supplied the original for Figure 12; Drs. A. W. Crompton and J. H. Ostrom of the Peabody Museum of Yale University; Dr. A. G. Edmund of the Royal Ontario Museum, Ontario and Dr. D. A. Russell of the National Museum of Canada. Last but not least, my thanks must go to Dr. A. S. Romer of the Museum of Comparative Zoology, Harvard University who. as must be rather obvious by now, provided most of the information upon which this paper is based.

ABBREVIATIONS

Unless indicated to the contrary all figures show bones from the left side; Figures 4, 6, 7-11 and 13 have been printed in reverse.

The museum names have been abbreviated as follows:

AMNH	American Museum of Natural History, New York.
BM(NH)	British Museum (Natural History), London.
NMC	National Museum of Canada, Ottawa.
USNM	United States National Museum, Washington, D.C.
YPM	Peabody Museum, Yale University, New Haven.

The structures indicated in Figures, 5, 10, 13 and 15 are as follows:

acet — acetabulum
ant proc — anterior process
br sh — brevis shelf
gr troc — greater trochanter
les tro — lesser trochanter
obt proc — obturator process
po rod — postpubic rod
pre proc — prepubic process
4th troc — fourth trochanter

The muscles have been abbreviated as follows:

ACC — M. accessory obturator
ADD — M. adductor femoralis
AMB — M. ambiens
CA-FEM BR — M. caudi-femoralis brevis
CA-FEM L — M. caudi-femoralis longus
CA-IL-F — M. caudi-ilio-fibularis
DOR CA — M. dorsalis caudae
DOR T — M. dorsalis trunci
FEM-T 1, 2 & 3 — M. femoro-tibialis 1, 2 & 3
F T E — M. flexor tibialis externus
F T I — M. flexor tibialis internus
G — M. gastrocnemius
IL-CAUD — M. ilio-caudalis
IL-COST — M. ilio-costalis
IL-FEM — M. ilio-femoralis
IL-FEM EXT — M. ilio-femoralis externus
IL-FEM INT — M. ilio-femoralis internus

IL-FIB	— M. ilio-fibularis
IL-TIB 1 & 2	— M. ilio-tibialis 1 (sartorius) & 2
IL-TROC	— M. ilio-trochantericus
IS-CAUD	— M. ischio-caudalis
IS-FLEX	— M. ischio-flexorius
IS-TROC	— M. ischio-trochantericus
LIG	— ligaments for holding head in acetabulum
O A EXT	— M. obliquus abdominis externus
O A INT	— M. obliquus abdominis internus
OBL	— M. obliquus abdominis
OBT	— M. obturator internus (anterior part of P-I-F E)
P-I-F	— M. pubo-ischio-femoralis
P-I-F E	— M. pubo-ischio-femoralis externus
P-I-F INT 1	— dorsal part of M. pubo-ischio-femoralis internus
P-I-F INT 2	— ventral part of M. pubo-ischio-femoralis internus
P-TIB	— M. pubo-tibialis
R ABD	— M. rectus abdominis
TND	— tendon inserting on fibula
TR A	— M. transversus abdominis
TR P	— M. transversus perinei

LITERATURE CITED

Beer, G. de, 1954, *Archaeopteryx lithographica.* A study based on the British Museum specimen: London, British Museum (Natural History), 68 p.

Casier, E., 1960, Les iguanodons de Bernissart: Brussels, Inst. Roy. Sci. Nat. Belg., 134 p.

Colbert, E. H., 1961, Dinosaurs. Their discovery and their world: New York, Dutton, 300 p.

Dollo, L., 1883, Note sur la presence chez les oiseaux du "troisieme trochanter" des dinosauriens et sur la fonction de celui-ci: Mus. Roy. d'Hist. Nat. de Belg. Bull., v. 2, p. 13-18.

———— 1888, Sur la signification du "Trochanter pendant" des Dinosauriens: Sci. Fr. Belg. Bull., v. 19, p. 215-224.

Elftman, H. O., 1929, Functional adaptations of the pelvis in marsupials: Amer. Mus. Nat. Hist. Bull., v. 58, p. 189-232.

Erickson, B. R., 1966, Mounted skeleton of *Triceratops prorsus* in the Science Museum: Sci. Mus. St. Paul, Minn., Sci. Publn., (n.s.) v. 1, no. 1, p. 1-16.

Ewer, E. F., 1965, The anatomy of the Thecodont reptile *Euparkia capensis* Broom: Phil. Trans. (B), v. 248, p. 379-435.

Gadow, H., 1880, Zur vergleichenden Anatomie der Muskulatur des Beckens und der hinteren Gliedmasse der Ratiten: Jena, Fischer, 56 p.

Gadow, H. & Selenka, E., 1891, Vogel I. Anatomischer Theil. *In* Bronn, H. G., Klassen und Ordnugen des Thier-Reichs, in Wort und Bild. v. 6. Leipzig, Winter.

Galton, P. M., In press, On the anatomy of the ornithischischian dinosaur *Hypsilophodon foxii* from the Wealden (Lower Cretaceous) of the Isle of Wight, England: Brit. Mus. (Nat. Hist.) Bull., Geol.

George, J. C. & Berger, A. J., 1966, Avian myology: London, Academic Press, 500 p.

Gilmore, C. W., 1909, Osteology of the Jurassic reptile *Camptosaurus* with a revision of the species of the genus, and descriptions of two new species: U.S. Natl. Mus. Proc., v. 36, p. 197-332.

——— 1912, The mounted skeletons of *Camptosaurus* in the United States National Museum: U.S. Natl. Mus. Proc., v. 41, p. 587-696.

——— 1914, Osteology of the armoured Dinosauria in the United States National Museum, with special reference to the genus *Stegosaurus:* U.S. Natl. Mus. Bull., v. 89, p. 1-136.

——— 1915, Osteology of *Thescelosaurus,* an orthopodous dinosaur from the Lance Formation of Wyoming: U.S. Natl. Mus. Proc., v. 49, p. 591-616.

——— 1924a, On *Troodon validus* an orthopodous dinosaur from the Belly River Cretaceous of Alberta, Canada: Dep. Geol. Univ. Alberta Bull., v. 1, p. 1-43.

——— 1924b, A new species of *Laosaurus* an ornithischian dinosaur from the Cretaceous of Alberta: Roy. Soc. Can. Trans. (3), v. 18, sect. 4, p. 1-7.

Gregory, W. K., 1919, The pelvis of dinosaurs; a study of the relations between muscular stresses and skeletal form: Copeia, v. 69, p. 18-20.

Gregory, W. K. & Camp, C. L., 1918, Studies in comparative myology and osteology. No. III: Amer. Mus. Nat. Hist. Bull., v. 38, p. 447-563.

Haughton, S., 1865, On the muscular anatomy of the leg of the crocodile: Ann. Mag. Nat. Hist. (3), v. 16, p. 326-331.

Heilmann, G., 1926, The origin of birds: London, Witherby, 208 p.

Huene, F. von, 1926, Vollständige Osteologie eines Plateosauriden aus dem Schwäbischen Keuper: Geol. Paläont. Abhl., N.F., v. 15, p. 139-180.

Hulke, J. W., 1882, An attempt at a complete osteology of *Hypsilophodon foxii,* a British Wealden dinosaur: Phil. Trans. (B), v. 172, p. 1035-1052.

Huxley, T. H., 1870, On *Hypsilophodon foxii,* a new dinosaurian from the Wealden of the Isle of Wight. Geol. Soc. London Quart. Jour., v. 26, p. 3-12.

Janensch, W., 1955, Der Ornithopode *Dysalotosaurus* der Tendaguruschichten: Palaeontographica Suppl., v. 7 (3), p. 105-176.

Lebedinsky, N. G., 1913, Beitrage zur Morphologie und Entwicklungsgeschichte des Vogel Beckens: Zeit. Natur. Jena, v. 50, p. 647-774.

——— 1914, Über der Processus Pectinialis der Straussenbeckens und seine phylogenetische Bedeutung: Anat. Anz., v. 46, p. 84-89.

Lull, R. S., 1933, A revision of the Ceratopsia or horned dinosaurs: Peabody Museum, Yale Univ., Memoir, v. 3 (3), 135 p.

Lull, R. S. & Wright, N. E., 1942, Hadrosaurian dinosaurs of North America: Geol. Soc. Amer. Spec. Pap., v. 40, p. 1-242.

Marsh, O. C., 1878, Principal characters of American Jurassic dinosaurs: Am. Jour. Sci. (3), v. 16, p. 411-416.

Nopcsa, F. B., 1905, Notes on British dinosaurs I—*Hypsilophodon:* Geol. Mag. n.s. (5), v. 2, p. 203-208.

———— 1917, Über Dinosaurier 3. Über die Pubis der Orthopoden: Zentbl. Min. Geol. Palaont., v. 1917, p. 348-351.

Osborn, H. F., 1933, Mounted skeleton of *Triceratops elatus:* Amer. Mus. Novitates, no. 654, 14 p.

Ostrom, J. H., 1964, A reconsideration of the paleoecology of hadrosaurian dinosaurs: Am. Jour. Sci., v. 262, p. 975-997.

Romer, A. S., 1923a, The ilium in dinosaurs and birds: Amer. Mus. Nat. Hist. Bull., v. 48, p. 141-145.

———— 1923b, Crocodilian pelvic muscles and their avian and reptilian homologues: Amer. Mus. Nat. Hist. Bull., v. 48, p. 533-552.

———— 1923c, The pelvic musclature of saurischian dinosaurs: Amer. Mus. Nat. Hist. Bull., v. 48, p. 605-617.

———— 1927a, The development of the thigh musculature of the chick: Jour. Morph., v. 43, p. 347-385.

———— 1927b, The pelvic musculature of ornithischian dinosaurs: Acta. Zool., Stockh., v. 8, p. 225-275.

———— 1956, Osteology of the reptiles: Chicago, Univ. of Chicago Press, 772 p.

———— 1962, The vertebrate body (3rd edn.): Philadelphia, Saunders, p. 627.

———— 1966, Vertebrate paleontology (3rd edn.): Chicago, Univ. of Chicago Press, 468 p.

Russell, L. S., 1935, Musculature and functions in the Ceratopsia: Natl. Mus. Can. Bull., v. 77, p. 39-48.

Sternberg, C. M., 1924, A new species of hadrosaurian dinosaur from the Edmonton formation (Createaceous) of Alberta: Can. Dept. Mines Geol. Surv. v. 38, p. 13-26.

Synder, R. C., 1954, The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion: Amer. Jour. Anat., v. 95, p. 1-46.

———— 1962, Adaptations for bipedal locomotion of lizards: Amer. Zool., v. 2, p. 191-203.

Walker, A. D., 1961, Triassic reptiles from the Elgin area: *Stagonolepis, Dasynathus* and their allies: Phil. Trans. (B), v. 244, p. 103-204.

———— 1964, Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of the carnosaurs: Phil. Trans. (B), v. 248, p. 53-134.

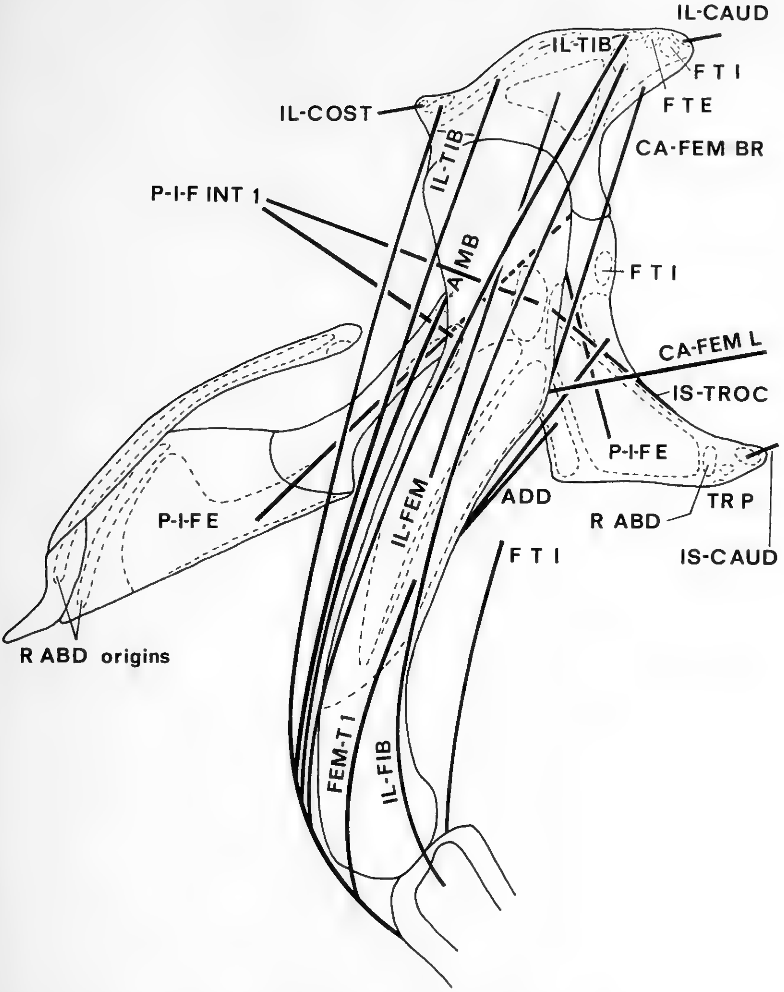


FIG. 1. Pelvic region of *Alligator mississipiensis* showing the areas of muscle attachment visible in lateral view and the lines of action of most of the muscles. Femur shown under the body in a position comparable to that of birds and dinosaurs. Data from Romer (1923b, pls. 19-25). Abbreviations on p. 46.

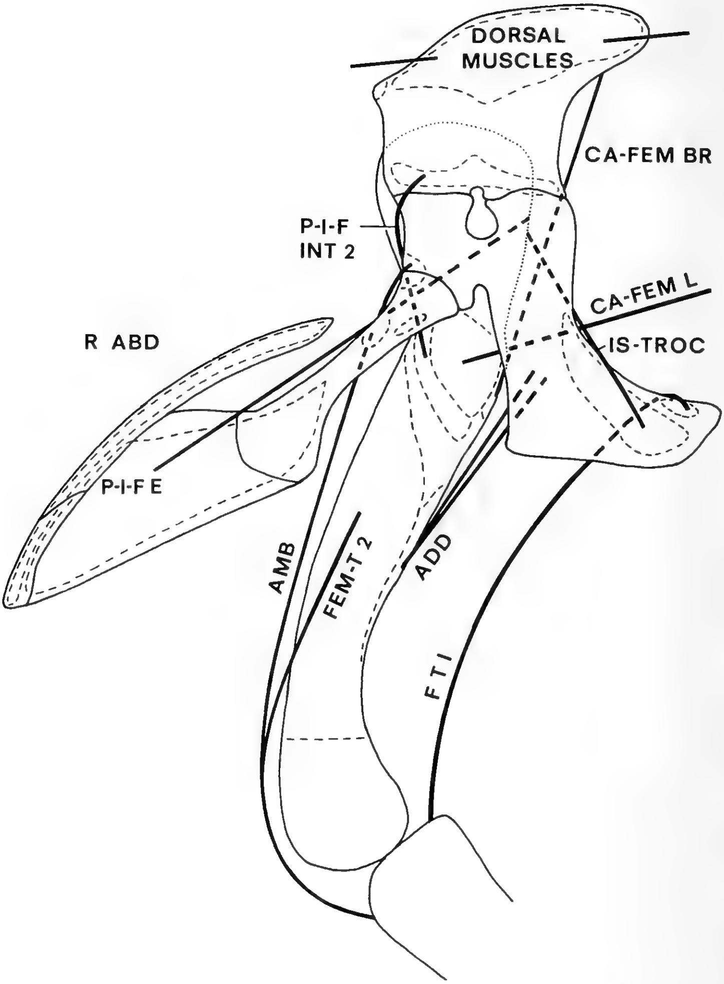


FIG. 2. Pelvic region of the alligator showing the line of action of the muscles whose area of attachment is visible in the medial view of the right side. Compare with Figure 1. Data from Romer (1923b, pls. 19-25). Abbreviations on p. 46.

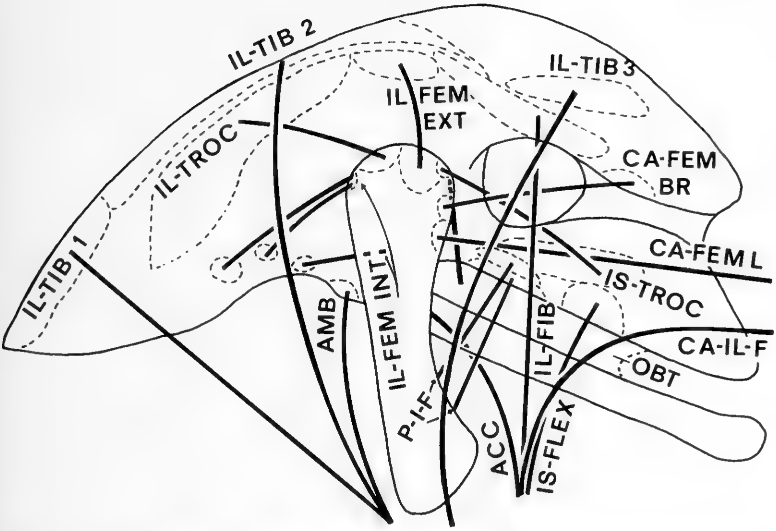


FIG. 3. Pelvic region of an eight day old chick to show attachment areas. Data from Romer (1927a, figs. 5, 5a, 5b; 1927b, fig. 1). Abbreviations on p. 46.

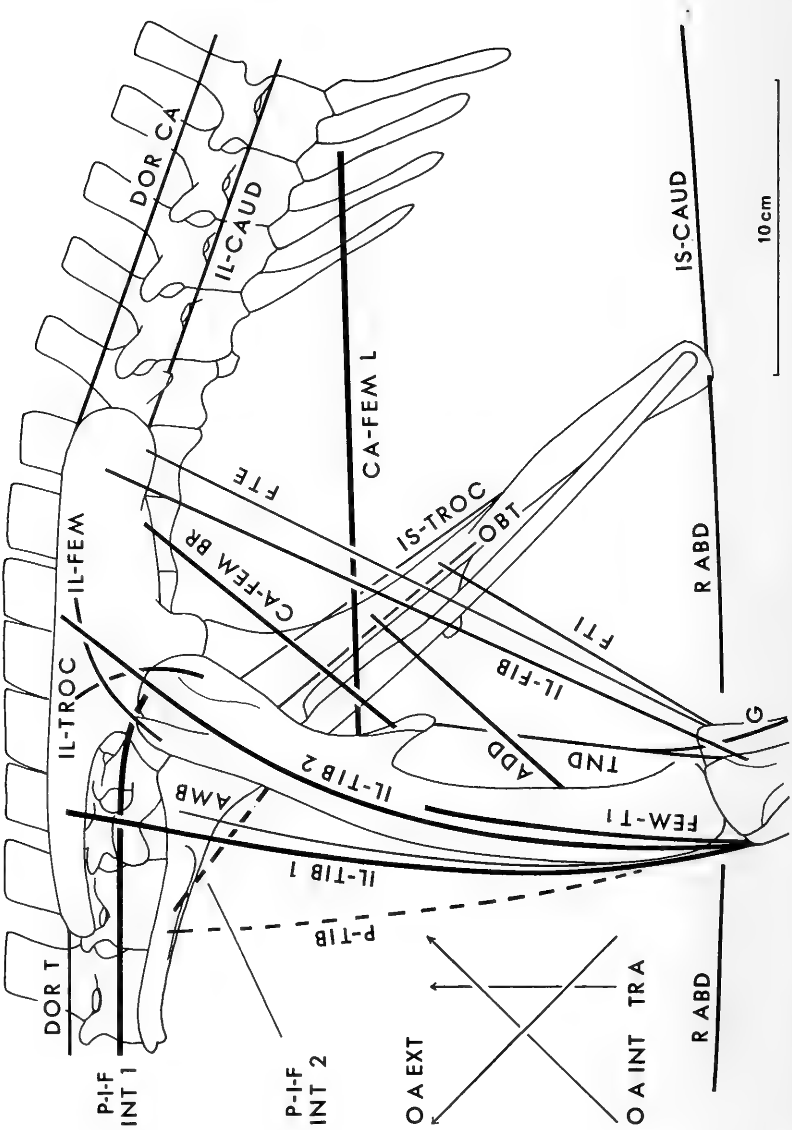


FIG. 4. Reconstruction of the pelvic region of *Hypsilophodon* showing the lines of action of the individual muscles. Data from BM(NH) R193, R196, R5830 and 28707. Abbreviations on p. 46.

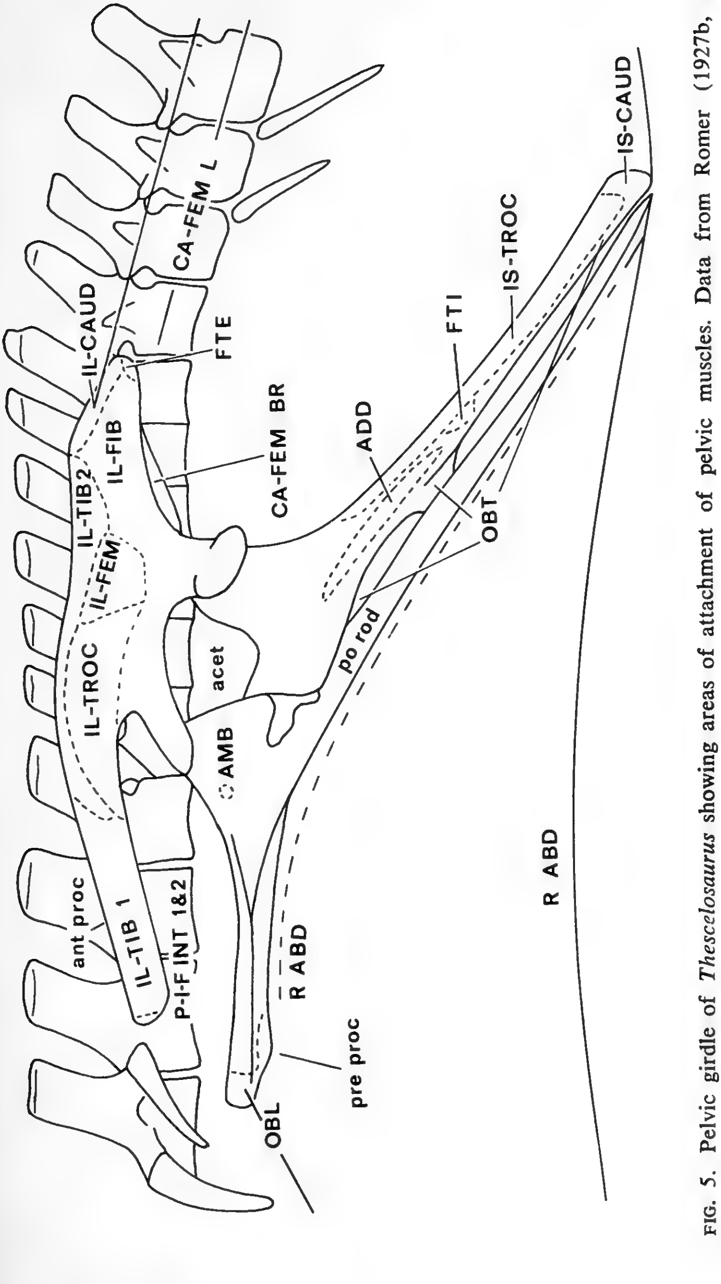


FIG. 5. Pelvic girdle of *Thescelosaurus* showing areas of attachment of pelvic muscles. Data from Romer (1927b, figs. 14-18). Abbreviations on p. 46.

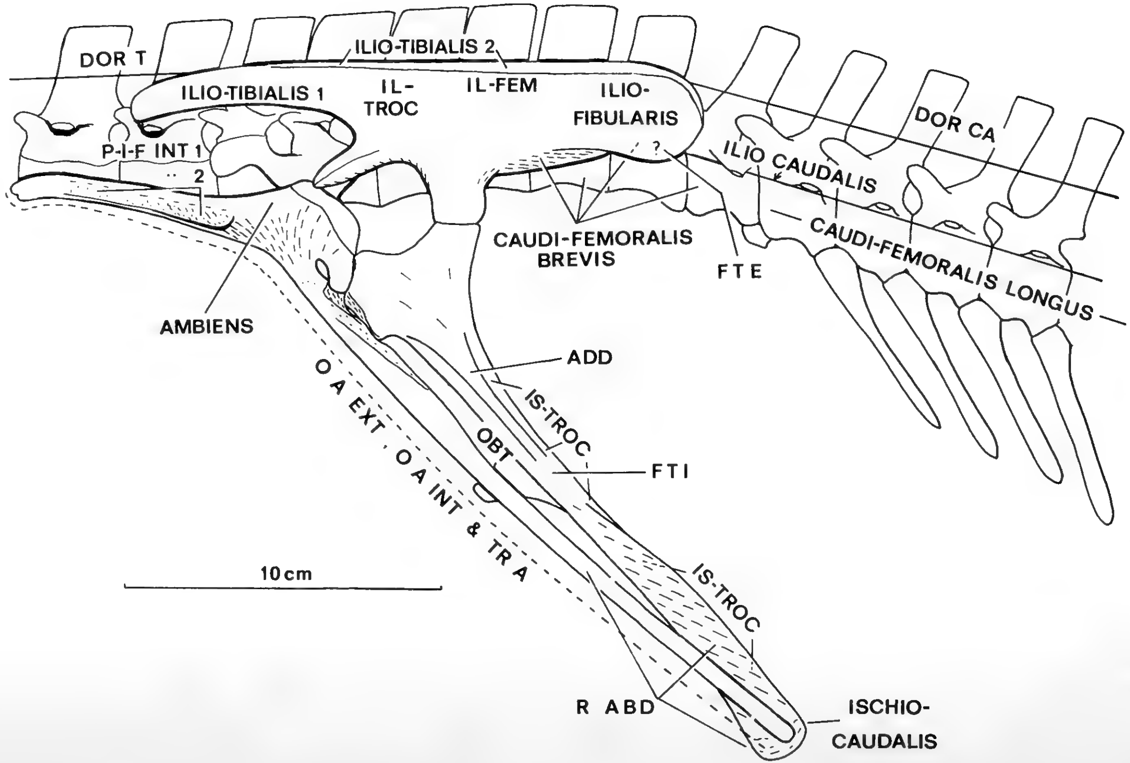


FIG. 6. Pelvic girdle of *Hypsilophodon*, BM(NH) R193, showing the areas of attachment of the individual muscles. Data also from BM(NH) R196 and 28707. Abbreviations on p. 46.

FIG. 7. Pubis and ischium of *Hypsilophodon,* BM(NH) R193. Compare with Figure 6. The scale is 10 cm.

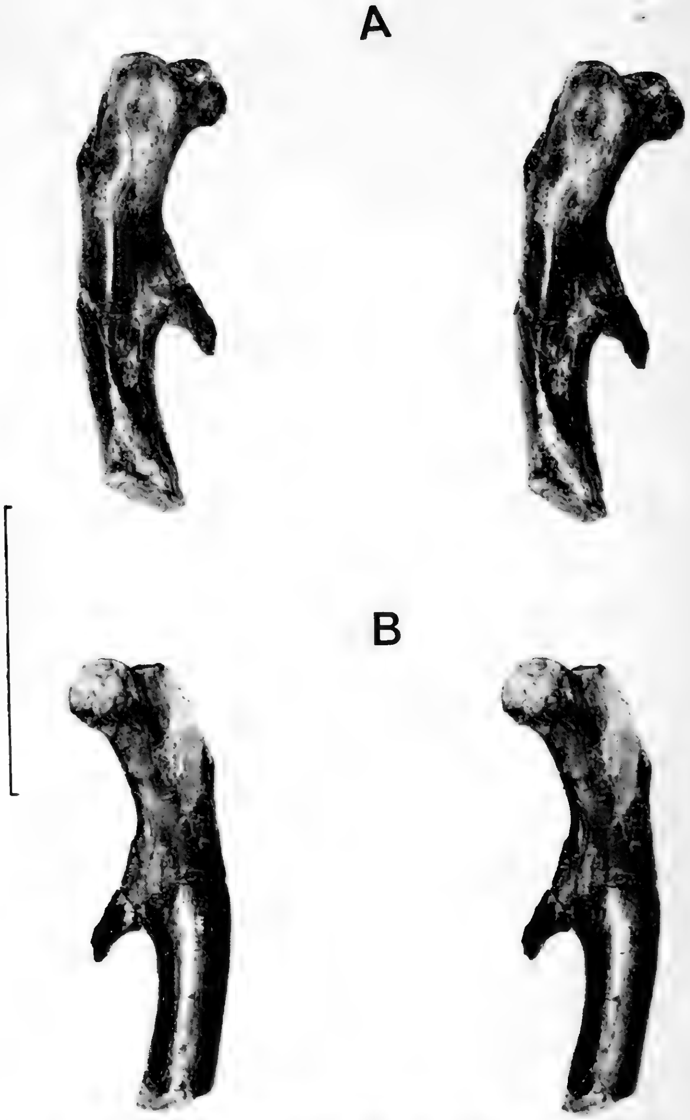


FIG. 8. Femur of *Hypsilophodon,* BM(NH) R193. A. Anteromedial view. B. Posterolateral view. Compare with Figure 9. The scale is 10 cm.

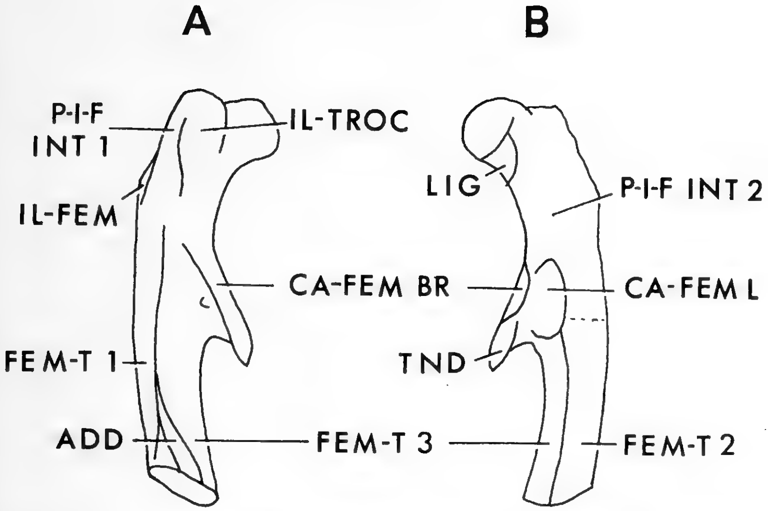


FIG. 9. Diagrams showing the attachment areas in the stereo-photographs of Figure 8, A and B. Abbreviations on p. 46.

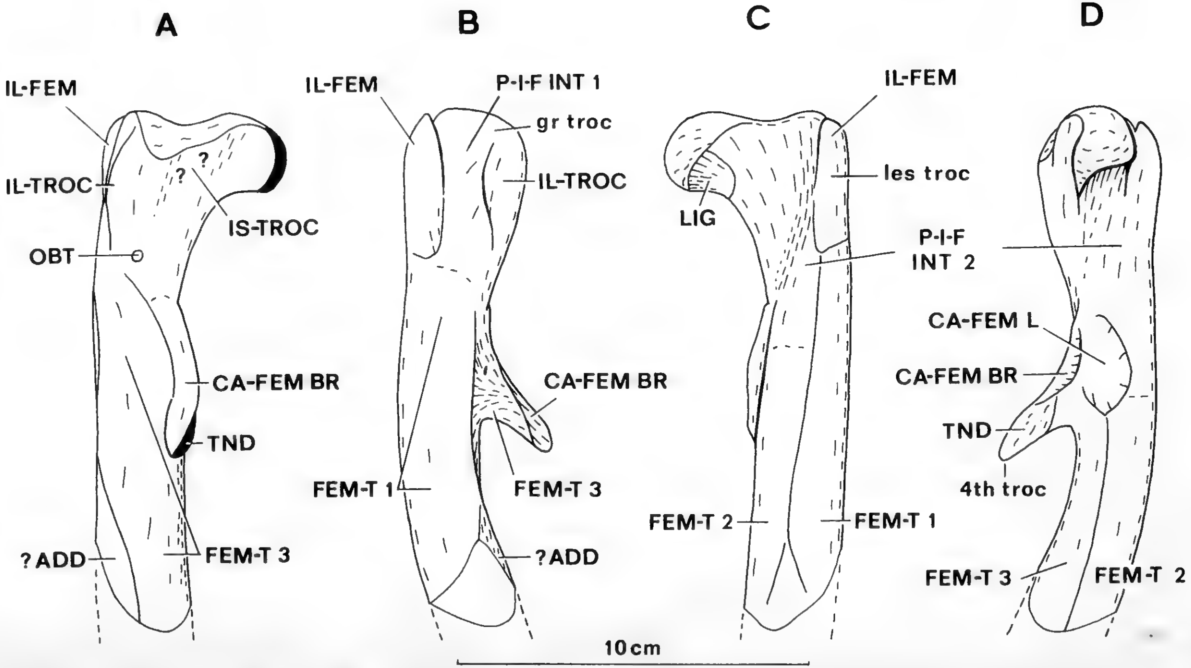


FIG. 10. Femur of *Hypsilophodon*, BM(NH) R193, showing the areas of attachment of the limb muscles. Data also from BM(NH) R196 and R5830. A. Posterior view, B. Lateral view, C. Anterior view, D. Medial view. Abbreviations on p. 46.

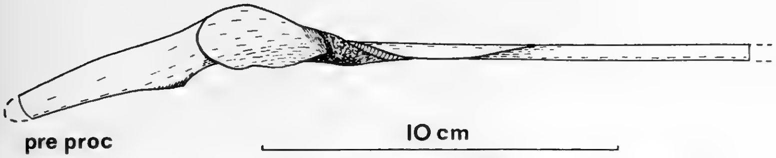


FIG. 11. Pubis of *Hypsilophodon* in dorsal view, BM(NH) R193.

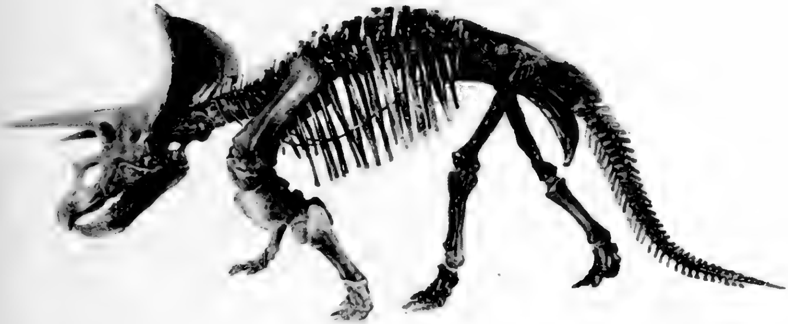


FIG. 12. Skeleton of ***Triceratops*** cf. ***elatus***, AMNH 5116, 5033, 5039, 5095. Original about 20′ or 6.2 meters. Courtesy of the American Museum of Natural History.

FIG. 13. Ischium of *Hypsilophodon* in ventral view, BM(NH) R193. Abbreviations on p. 46.

FIG. 14. Diagrams showing attachment areas of certain pelvic muscles in archosaurs.

A *Ornithosuchus* — Saurischia — Carnosauria (after Walker, 1964). The dotted part of the ilium represents a cartilaginous extension whose precise size and outline cannot be determined. As shown, it resembles *Tyrannosaurus.*

B *Plateosaurus* — Saurischia — Prosauropoda (after von Huene, 1926).

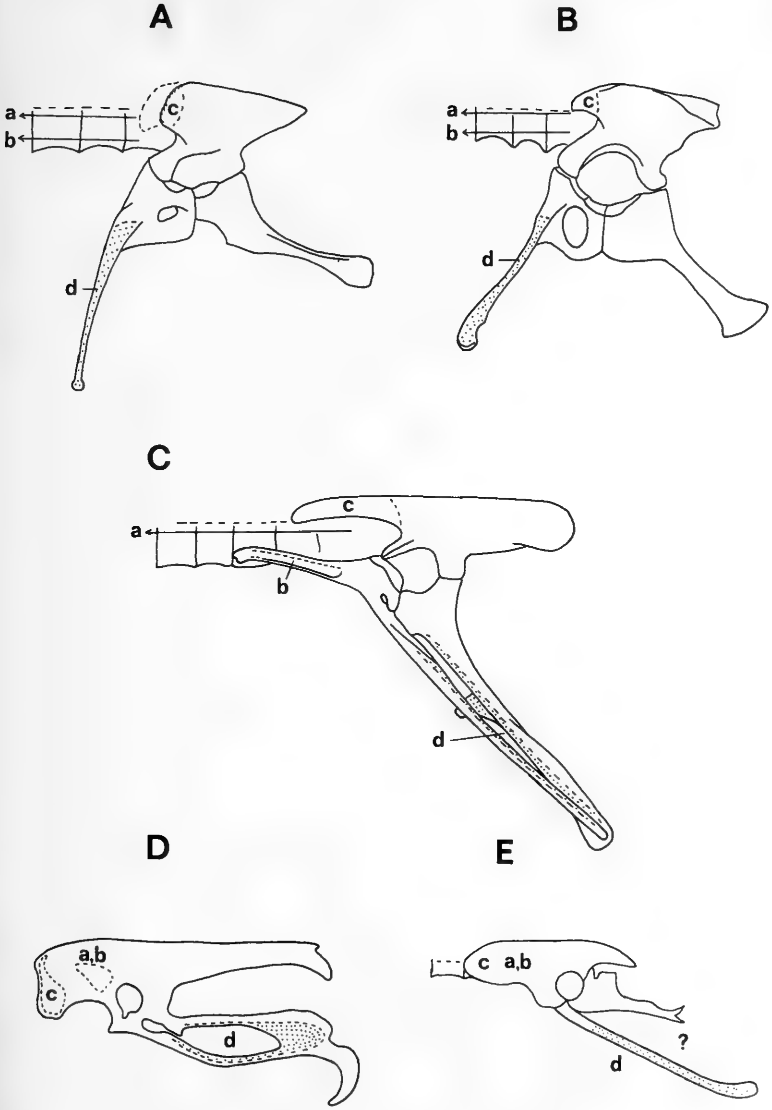
C *Hypsilophodon* — Ornithischia — Ornithopoda.

D *Struthio* — Aves — ratite (after Gregory & Camp, 1918, and Romer, 1923a).

E *Archaeopteryx* — Aves (after Heilmann, 1926) The question mark indicates the possibility of a cartilaginous extension to the ischium but its form is not known.

Abbreviations used in this figure:

a. dorsal part of M. pubo-ischio-femoralis internus. b. ventral part of the M. pubo-ischio-femoralis internus. In D and E these two parts form the M. ilio-femoralis internus. c. M. ilio-tibialis 1 (sartorius). d. anterior part of M. pubo-ischio-femoralis externus. In C-E this is the M. obturator internus that replaced the posterior part.


A
a
b
c
d
B
a
b
c
d
C
c
a
b
d
D
a,b
c
d
E
c
a,b
d
?

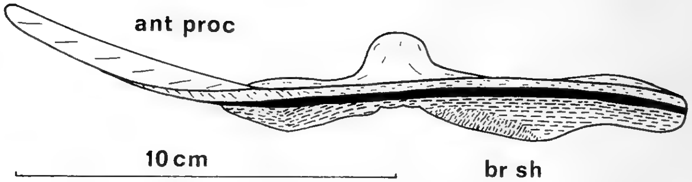


FIG. 15. Right ilium of *Hypsilophodon,* BM(NH) R193. Dorsal view. Abbreviations on p. 46.

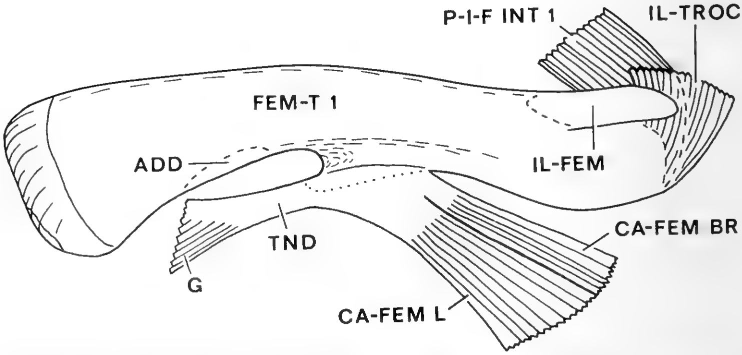


FIG. 16. Femur of *Thescelosaurus* showing areas of insertion of the pelvic muscles. Data from Romer (1927b, figs. 16-18). Abbreviations on p. 46.

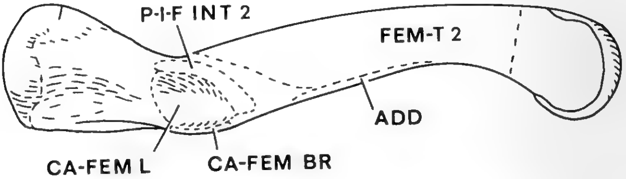


FIG. 17. Femur of *Alligator* showing areas of muscle attachment. Ventral view based on Romer (1923b, pl. 25). Abbreviations on p. 46.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

OMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

ILLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

THOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 132. 22 MAY 1969.

NEW SPECIES AND RECORDS OF SHALLOW WATER DEMOSPONGIAE FROM BARBADOS, WEST INDIES

GEORGE JOHN HECHTEL

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

NEW SPECIES AND RECORDS OF SHALLOW WATER DEMOSPONGIAE FROM BARBADOS WEST INDIES

GEORGE JOHN HECHTEL

Dept. of Biological Sciences
State University of New York at Stony Brook
Stony Brook, N.Y. 11790

ABSTRACT

Descriptions are given of eleven species of Demospongiae collected off Barbados, W.I. Five are new species and four are new records for this locality. New species are *Strongylophora dendyi, Coelosphaera raphidifera, Monanchora barbadensis, Bubaris ammosclera,* and *Timea stenosclera.*

POSTILLA 132: 38 p. 22 MAY 1969.

INTRODUCTION

The shallow water inshore sponges of Barbados were surveyed in June, 1966. The study was undertaken to provide additional descriptive information on the sponge fauna of the Lesser Antilles. An extensive faunal list is available only for Curaçao (Arndt, 1927). My study of Jamaican sponges (Hechtel, 1965) indicated the possible presence of a distinct southern Caribbean fauna, which might contain a strong West African element. Barbados was selected as a study site, since it has a marine station and a southeastern location in the island chain.

Previous records of Barbadian sponges are scattered in the literature. At least 34 species have been reported. The fauna includes one calcareous sponge (Burton, 1963, p. 367) and six hexactinellids (Stutchbury, 1842; Schmidt, 1880). Seven species of lithistid sponges are known from the island (Schmidt, 1879, 1880; identifications by Hartman, *in* Lewis, 1965). Non-lithistid Demospongiae have been recorded by Schmidt (1880), Weltner (1882), Carter (1883b), Topsent (1928), Uliczka (1929), and Hartman (identifications in Lewis, 1965). All species for which bathymetric information is available were collected at depths greater than 50 meters.

Collections for the present study were made by snorkeling from shore in water from 1–15 feet (about 1/3–5 meters) in depth. Specimens of 10 species were collected on corals and coral rubble immediately offshore from the Bellairs Research Institute. The station is located in St. James parish, on the west coast. An eleventh species, *Bubaris ammosclera,* was collected in 45–50 feet (about 14–15m) of water, 1/2 mile off the west coast, by Dr. I. G. Macintyre of the Dept. of Geological Sciences, McGill University. The specimens are deposited in the Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A. (abbreviated as YPM in the text).

Laboratory study methods have been summarized previously (Hechtel, 1965). In the data tables, ranges of spicule lengths are based on samples of 100 and ranges of megasclere widths on samples of 25 spicules, unless otherwise noted in parentheses. Means and standard deviations are calculated from random samples of 10 measurements. Other measurements are based on the scanning of sections and spicule strews.

The classification of de Laubenfels (1936b) is utilized in amended form. The family Adociidae is placed in the Haplosclerida (see Hechtel, 1965). The family Bubaridae is distinguished from the Axinellidae, as in Topsent (1928), and included in the order Clavaxinellida of Lévi (1956). Specimens are described in detail to facilitate future investigations at the Bellairs Institute. Zoogeographical studies also require detailed descriptions, since the limits of variation are poorly known for most species of sponges. For the benefit of investigators in the West Indies, each new species is compared not only with morphologically similar members of its genus, but with other tropical American species.

The study was supported by a 1966 summer research fellowship and grant-in-aid No. 31-0230A, both from the Research Foundation of the State University of New York. Field facilities were made available by Dr. John Lewis, Director of the Bellairs Institute. The study benefited from discussions with Dr. Willard D. Hartman of Yale University. Specimens were made available for comparisons through the kindness of Dr. Hartman, Dr. William K. Emerson, American Museum of Natural History, and Dr. Klaus Rützler, U.S. National Museum. Camera lucida drawings of spicules were prepared by Miss Martha Dimock. Mrs. Mary Buddenhagen and Mrs. Lillyan Yagman typed the final manuscript.

SPECIES LIST

Class DEMOSPONGIAE

Order HAPLOSCLERIDA

Haliclona erina de Laubenfels

Gelliodes ramosa (Carter)

Adocia carbonaria (Lamarck)

Strongylophora dendyi n. sp.

Order POECILOSCLERIDA

Coelosphaera raphidifera n. sp.
Agelas schmidtii Wilson
Monanchora barbadensis n. sp.

Order CLAVAXINELLIDA

Bubaris ammosclera n. sp.
Timea stenosclera n. sp.
Placospongia melobesioides Gray

Order CHORISTIDA

Chondrilla nucula Schmidt

ECOLOGY AND ZOOGEOGRAPHY

Sponges are known to be abundant in depths below 25 feet (about 8 m) near the Bellairs Institute (Lewis, 1965; personal communication). They are restricted in abundance and number in shallower water. The inshore collection has only two species *(Gelliodes ramosa, Agelas schmidtii)* in common with the 23 species collected by Lewis (1965) on shell debris in 50-100 meters. Encrusting sponges are certainly more numerous and diverse on coral rubble near the Kingston Cays, Jamaica (Hechtel, 1965, area H). Sponges could not be found in turtle grass beds along the coast of Christ Church parish, south of Bridgetown. They are abundant in numbers, if somewhat restricted in diversity, in similar beds near Port Royal and the Kingston Cays (Hechtel, 1965, areas D and J). Ramose and tubular sponges are common in 10-15 feet of water near the Cays (my area I, 1965), but are absent from the Barbadian study area.

Wave action may be interacting with an unstable substratum to restrict sponge settlement and survival. Inshore water is obviously laden with sediment. Lewis (1960) noted the paucity of corals in the Barbadian reef flat zone. He reported beach shifting at the landward limit of the zone in periods of heavy seas.

All of the observed sponges were encrusting in form. By contrast, Jamaican specimens of *Haliclona erina* often have tall oscular projections, and specimens of *Gelliodes ramosa* are typically elongate and cylindrical. In 50-150 meters, Barbadian specimens of *Agelas schmidtii* are elongate and tubular (Hartman, personal communication). Observational evidence indicates that many species of sponges are restricted to an encrusting form in wave-exposed habitats. Currents influence at least the direction of oscular chimneys, as was shown by Warburton (1960), using reaggregating specimens of *Microciona prolifera.*

The collection provides limited zoogeographical information. There is no evidence of affinities with West African sponges. Three of the previously known species are restricted, on present evidence, to tropical Atlantic American waters (*Haliclona erina, Gelliodes ramosa,* and *Agelas schmidtii*). *Chondrilla nucula* is circumtropical. Most records of *Placospongia melobesioides* are from the Indo-Pacific. *Adocia carbonaria* may be conspecific with Pacific sponges studied by Bergquist (1965, p. 158).

Three of the new species are morphologically similar to Indo-Pacific sponges. *Strongylophora dendyi* is very similar to *S. durissima* Dendy, from Ceylon. *Coelosphaera raphidifera* is similar to an Indonesian as well as a tropical American species. *Monanchora barbadensis* belongs to a genus that has been known previously only from the Indo-Pacific. Ekman (1953) noted faunal similarities between the West Indies and the Indo-Pacific on a generic level, using data from crabs and echinoderms. He suggested the similarities were due to an earlier connection between the regions provided by the Tethys Sea.

DESCRIPTIONS OF SPECIES

CLASS DEMOSPONGIAE Sollas

ORDER HAPLOSCLERIDA Topsent

FAMILY HALICLONIDAE de Laubenfels

GENUS *HALICLONA* Grant

Haliclona erina de Laubenfels, 1936a
Hechtel, 1965, p. 19.

MATERIAL. YPM 7740, two specimens on coral fragments; YPM 7754, a small specimen originally on a coral fragment with a specimen of *Agelas schmidtii* (YPM 7751). Occurs commonly.

SHAPE. Encrusting, about 0.5 cm in thickness, with some oscules raised 1–2 mm above the surrounding surface.

COLOR. The sponges are a dull dark green in life. They become pinkish-gray in alcohol.

CONSISTENCY. Compressible, but easily crumbled.

SURFACE. Even, smooth to the touch, but microhispid. The scattered, mostly flush oscules are 1–5 mm in diameter. Their rims are often jagged and irregular.

ECTOSOME. There is no skeletal specialization. Surface strips contain scattered spicules and severed endosomal tracts. The dermal membrane is pierced by oval to circular pores, separated by aspiculous bands about 10–20 μ in span. Typical pore sizes are 53×53, 63×53, 42×32, and 74×42 μ.

ENDOSOME. Microcavernous. A three- to five-sided subisodictyal network has one to several spicules on a side. In places, the skeleton contains slender spicule tracts, 20–40 μ in diameter. Most of the tracts run vertically near the surface. As seen in cross section, the ectosome is darkly pigmented and often pierced by terminal spicules of ascending tracts. Spongin is present at the network nodes. Some spicules, particularly thin ones, lie scattered in the mesh interstices. Typical sizes of the oval flagellated chambers are 35×24, 28×24, and 31×24 μ.

SPICULES. Oxeas, usually slightly curved, occasionally straight or strongly curved, rather uniform in diameter over most of their length. The points are typically gradually narrowed to hastate, but may be irregular, mucronate, or stair-stepped. A few spicules are styles, with or without a narrowed base. Spicule measurements are listed in Table 1.

TABLE I. *Haliclona erina* de Laubenfels – oxea measurements (μ).

Specimen	Length		Width	
	Range	Mean, SD	Range	Mean, SD
7740a	152-184	168±7	3.5-7.1	5.4±1.3
7740b	147-179	166±8	3.5-7.1	5.6±1.4
7754	147-189	172±5	3.5-7.1	5.4±1.3

DISCUSSION. The present specimens, which were collected in a more surf-exposed location, lack the pronounced volcanic oscular projections of Jamaican ones. They are similar to Jamaican specimens in architecture and spiculation. The flagellated chambers of Jamaican specimens are of similar size (for example, 35×16, 24×14 μ). De Laubenfels' Panamanian specimens (1936a, p. 457) are described as being amorphous to encrusting, as in the present case. The flagellated chambers of his material are of similar size (30 μ), but are described as spherical. The brilliant green coloration of his material differs from the dull green coloration of both Jamaican and Barbadian specimens.

FAMILY DESMACIDONIDAE Gray

GENUS *GELLIODES* Ridley

Gelliodes? ramosa (Carter, 1882)
Hartman, 1967, p. 20.

MATERIAL. YPM 7742, several specimens from coral and coral rubble; YPM 7748, an encrustation in the fork of a piece of coral rubble, which also bears a specimen of *Agelas schmidtii*. Occurs commonly.

SHAPE. Encrusting, about 0.5 cm in thickness.

COLOR. The sponges are dull blue to grayish purple in life. They become dull gray in alcohol.

CONSISTENCY. Slightly compressible, resilient, fibrous.

SURFACE. Rough to the touch, mostly even. The surface varies from microtuberculate to minutely conulose, with fiber tufts reaching nearly 1 mm in height. The scattered oscules are 0.5–3 mm in diameter. They may be flush with the surface or surrounded by irregular, slightly raised rims.

ECTOSOME. There is no dermal skeletal specialization. The membrane contains scattered debris, a few spicules, and fiber ends. The singly scattered dermal pores are 50–100 μ in diameter.

ENDOSOME. Microcavernous. A mostly pachychalinid fibroreticulation, with scattered spicules and loose spicule tracts in the interstices. The meshes are irregularly polygonal to rectangular, with parallel sides often several hundred microns apart. The fibers are 50–265 μ in diameter, with many visible to the unaided eye.

Some fibers, particularly thicker ones, are packed with spicules and coated by a thin spongin film. Smaller fibers intergrade with the loosely grouped spicule tracts of the interstices. Ascending fibers branch near the surface to end in tufts of varied size. Their terminal spicules often project slightly beyond the flesh. The small, oval flagellated chambers are about 30×20 μ.

SPICULES. Oxeas, usually slightly to considerably curved, occasionally straight, rarely stylote or strongylote. The shafts are rather uniform in diameter over most of their length. The points may be gradually narrowed, hastate, or stair-stepped. Spicule measurements are listed in Table II.

TABLE II. *Gelliodes ramosa* (Carter) – oxea measurements (μ).

Specimen	Length		Width	
	Range	Mean, SD	Range	Mean, SD
7748	189-242	223±11	4.7-8.2	7.8±0.8
7742a	179-273	231±19	5.9-11.8	8.9±1.7
7742b	200-273	235±17	7.1-9.4	8.2±0.4
7742c	179-263	230±15	5.9-10.6	8.7±1.0

DISCUSSION. The Barbadian specimens are similar in architecture, megasclere form, and megasclere size to Jamaican specimens (Hechtel, 1965, as *Gelliodes areolata*). They differ in having a dull blue color and an encrusting form (the latter perhaps due to strong wave action). Sigmas are lacking, as is the case for five of six Jamaican specimens. A Puerto Rican specimen, described as *Pachychalina areolata* by Wilson (1902), also lacks sigmas (Hechtel, 1955).

Hartman (*in* Lewis, 1965) recorded the species (as *Pachychalina areolata*) in depths of 50–150 meters off Barbados. *Pachychalina* Schmidt is similar to *Gelliodes* but lacks microscleres. It offers an alternative solution to the problem of generic placement posed by the variability of microsclere abundance in the species. Recently, Hartman (1967) placed Wilson's species into synonymy with *Gelliodes ramosa* (Carter, 1882), from Venezuela, after an examination of the holotype.

FAMILY ADOCIIDAE de Laubenfels

GENUS *ADOCIA* Gray

Adocia carbonaria (Lamarck, 1813)
Hechtel, 1965, p. 26.

MATERIAL. YPM 7746, two specimens growing on coral fragments, taken from *Porites* rubble. Minute specimens occur on several of the other coral fragments in the collection. Occurs commonly.

SHAPE. Encrusting, about 0.5–1 cm in thickness, with some of the oscules on volcano-shaped elevations, which reach 3 mm in height.

COLOR. Black, externally and internally, in life and when preserved in alcohol. The blue-black exudate characteristic of Jamaican specimens was noted at the time of collection. At first alcohol is darkly discolored by the sponge, but after several changes it merely becomes yellow.

CONSISTENCY. Brittle, but easily crumbled; only very slightly compressible.

SURFACE. Smooth to the touch and even, except for oscular elevations. The scattered oscules are flush to elevated in position, and 2–8 mm in diameter. The dermal membrane is conspicuous.

ECTOSOME. A subisodictyal, mostly unispicular, typically three- to five-sided network of oxeas, bound at nodes by spongin. In places the mesh includes several spicules on a side. The network encloses groups of 2–10 roughly circular dermal pores, 10–70 μ in diameter. Adjacent pores are separated by thin aspiculous bands, typically 2–5 μ in diameter. The spicules are often bordered (particularly at nodes) by small, dark, circular, pigmented cells 5 μ in diameter.

ENDOSOME. Microcavernous, with a confused to subisodictyal architecture. The mesh is variously composed of single spicules, loose groups of several spicules, and spicule tracts. Spongin is present at nodes and in small amounts along many of the tracts. The more compact spicule tracts are 55–105 μ in diameter, with parallel tracts frequently several hundred microns apart. Darkly pigmented cells are abundant.

SPICULES. Oxeas, slightly to strongly curved, rarely straight, nearly uniform in thickness over much of their length. The ends may be hastate, mucronate, stair-stepped, or blunt. A few spicules are stylote or strongylote, with narrowed ends. Spicule measurements are listed in Table III.

TABLE III. *Adocia carbonaria* (Lamarck) – oxea measurements (μ).

Specimen	Length		Width	
	Range	Mean, SD	Range	Mean, SD
7746a	194-236	214±7	5.9-9.4	8.2±1.3
7746b	194-247	215±10	5.9-10.6	9.2±1.3

DISCUSSION. The Barbadian specimens are similar to Jamaican ones in external and spicular characteristics. Spicule tracts are more prominent in the Barbadian examples. However, well-developed tracts are present in the holotype (Topsent, 1930, p. 26), specimens from Curaçao (Arndt, 1927, p. 152), and West Indian specimens (Carter, 1882, p. 277, 282).

GENUS *STRONGYLOPHORA* Dendy

Dendy's original generic diagnosis (1905) emphasized the presence of strongyles of varied size and smooth microxeas. None of the species attributed to the genus have sigmas, contrary to de Laubenfels' definition (1936b).

Strongylophora dendyi n. sp. (Figure 1)

HOLOTYPE. YPM 7747, one specimen, on a piece of coral rubble.

SHAPE. A small flat encrustation, 2–3 mm in thickness.

COLOR. In life, the sponge is cream to dull white. In alcohol, it is dull white.

CONSISTENCY. Soft, compressible, but easily crumbled.

SURFACE. Smooth to the touch, with an obvious dermal membrane. The oscules are scattered, flush with the surface, and 0.5–3 mm in diameter.

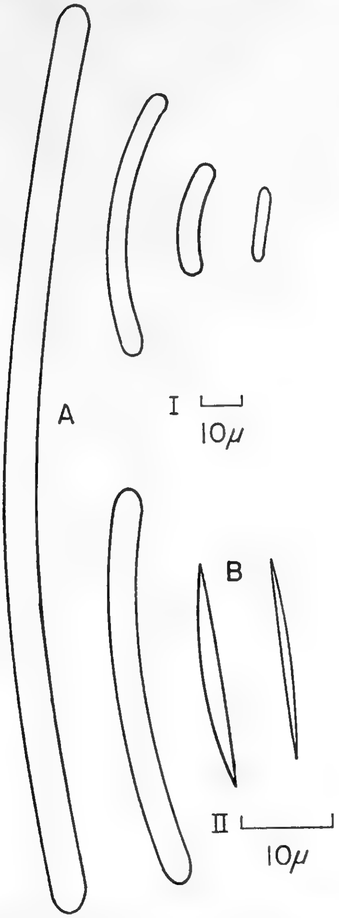


FIG. 1. Spicules of *Strongylophora dendyi* n. sp., YPM 7747. Holotype. A) Five strongyles of various sizes. B) Two microxeas. A: scale I. B: scale II.

ECTOSOME. A close-meshed, four- to five-sided reticulation. The skeletal network is composed typically of compact spicule tracts, but single spicules and loose spicule clusters are not infrequent. The tracts range in diameter from 20–55 μ. The maximum mesh span is typically 50–85 μ. Long robust strongyles form the bulk of the reticulation, but megascleres of all sizes are present, particularly at the skeletal nodes. Associated with the dermal reticulation are small projecting strongyles and numerous microxeas. The microxeas lie across or project from the reticulation, singly and in clumps.

ENDOSOME. An irregular, subisodictyal reticulation, with one to several spicules on a side. The mesh sides are composed largely of long and medium sized strongyles, but small ones are common at the skeletal nodes. Spongin is present at the nodes, and occasionally envelops a spicule. The mesh interstices contain thin developing strongyles, strongyles of small size, and an abundance of microxeas. In places dense bands of flesh, 30–105 μ in diameter, traverse the endosome. They contain numerous strongyles (mostly of small to medium size) and microxeas. Next to the substratum, strongyles of all sizes form a densely packed spicular mat.

SPICULES. Strongyles of varied size, and microxeas (Fig. 1). Spicule measurements are listed in Table IV.

TABLE IV. *Strongylophora dendyi* n.sp. – spicule measurements (μ) of holotype.

Spicule	Length		Width	
	Range	Mean, SD	Range	Mean, SD
Strongyle, large	158-242	205±22	4.7-8.2	6.8±1.4
Strongyle, medium	68-152 (50)	110±30	2.4-7.1	5.2±1.1
Strongyle, small	18-72 (50)	35±15	1.2-7.1	3.5±1.7
Microxea	18-28 (50)	22±3	1.2-1.7	1.4±0.2

A–strongyles, greatly varied in length. The smaller spicules are sausage-shaped, stout, and straight to slightly or considerably curved. They are rarely centrotylote. Medium-sized spicules are thin to robust, and slightly to considerably curved. The longer megascleres are robust and slightly curved. Intermediates are common between the three sizes.

B–microxeas, fusiform, straight to slightly curved or considerably bent, infrequently centrotylote, gradually pointed.

Some arcuate isochelas and oxyspherasters are present in spicule boils. In sections and dermal peels, almost all are associated with clumps of debris and obviously foreign spicules. They are considered to be foreign inclusions.

DISCUSSION. The smaller spicules of the Barbadian sponge are similar to those of the type species, *Strongylophora durissima* Dendy (1905), from the Indian Ocean. The latter species differs in having a largely unispicular dermal network and in having strongyles that become far more robust (up to 18–20 μ in diameter). Three tropical American species have been attributed to the genus. *S. amphioxa* de Laubenfels (1950) has peculiar stair-stepped oxeas interpreted by de Laubenfels as modified strongyles. The microscleres are thin, elongate, raphidiform oxeas. *S. rampa* de Laubenfels (1934) from deeper waters off Puerto Rico is a cylindrical sponge with elongate microxeas and strongyles of very uniform size (330–380 × 12–13 μ). *S. santa* de Laubenfels (1936a), from the Atlantic coast of Panama, differs from *S. dendyi* in being greenish-black, stony, and provided with large oxeas (215×5 μ).

Hartman (identifications *in* Lewis, 1965) recorded another Barbadian *Strongylophora* at depths of 50–100 meters. His specimens are not conspecific with mine, since they differ in strongyle form and in the larger size of their oxeote spicules (personal communication and examination of his slides).

ORDER POECILOSCLERIDA Topsent
FAMILY COELOSPHAERIDAE Dendy
GENUS *COELOSPHAERA* Thomson

Coelosphaera raphidifera n. sp. (Figure 2)

HOLOTYPE. YPM 7745, on a piece of coral.

SHAPE. A thin encrustation, from which closed fistules arise, particularly at the periphery. The base is several mm in thickness. The hollow thin-walled fistules are several mm wide and reach 2 cm in length. They occasionally have one or two short basal or apical branches.

COLOR. In life, the sponge is white with purplish-brown tinges. In alcohol, it becomes dull white to gray, except for the darkened apices of the fistules.

CONSISTENCY. The fistules are delicate and bendable. The base has a tough rind and crumbly endosome.

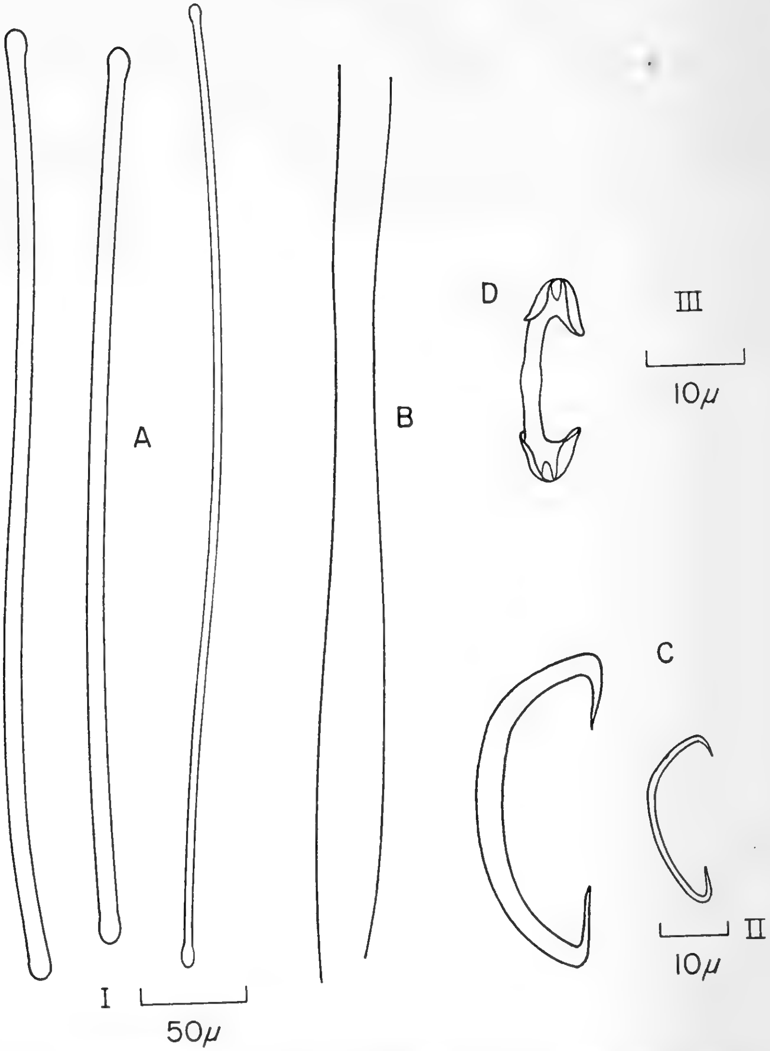


FIG. 2. Spicules of *Coelosphaera raphidifera* n. sp., YPM 7745. Holotype. A) Tylotes. B) Raphides. C) Sigmas of two sizes. D) Isochela. A, B: scale I. C: scale II. D: scale III.

SURFACE. Even, smooth to the touch, lipostomous.

ECTOSOME. The easily detachable dermal rind averages slightly less than 0.5 mm in thickness. Examination of dermal peels taken from the base suggests that the pore-bearing membrane contains scattered sigmas and singly scattered openings, about 35×25 μ. The membrane is underlain by a rind of thickly scattered tylotes, devoid of any distinct layering.

Fistule walls consist of a thick mat of tylotes, mostly oriented longitudinally or horizontally. The feltwork is devoid of microscleres, except for rare sigmas. In places the fistular cavities are partially occluded by cavernous tissue containing a varied number of sigmas (both sizes) and a few tylotes and isochelas.

ENDOSOME. Microcavernous. Tylotes are strewn loosely to thickly in the interior of the base. Although sometimes grouped into clusters, they never form compact tracts. The flesh contains numerous sigmas of both sizes and lesser numbers of isochelas and raphides. Most of the raphides are grouped into trichodragmata. Small sigmas are particularly common in the membranous regions around canals, where they occur in tangled masses.

SPICULES. Tylotes, sigmas, arcuate isochelas, and raphides. Spicule measurements are listed in Table V.

TABLE V. *Coelosphaera raphidifera* n. sp. – spicule measurements (μ) of holotype.

Spicule	Length		Width	
	Range	Mean, SD	Range	Mean, SD
Tylote	231-488	384±81	———	———
shaft	———	———	3.5-10.6	7.5±2.1
head	———	———	4.7-10.6	8.5±1.8
Sigma, large	42.4-61.2 (40)	49.6±4.9	1.2-3.2	———
Sigma, small	20.0-40.0	24.4±3.5	1.0-1.2	———
Isochela	19.9-28.2 (35)	24.7±2.3	0.7 (shaft)	———
Raphide	294-473 (35)	431±34	1	———

A–tylotes, long, thin, usually singly or doubly curved, less frequently nearly straight, with smooth oval heads. The heads are often no thicker than the middle region of the somewhat fusiform shafts.

B–raphides, largely in trichodragmata, often slightly undulating. The sheaves are 30–45 μ in diameter. Their presence makes it unlikely that the raphidiform spicules are early developmental stages of tylotes. (Thin tylotes with distinct heads are present in the endosome.)

C–sigmas, divided into two size classes, with a few intermediates.

D–isochelas, arcuate, but tending toward the palmate condition. The lateral teeth project freely from the shaft for up to one-third of their length.

DISCUSSION. The species is characterized by its spicule dimensions and the presence of trichodragmata, which are infrequent in the genus. It is distinguished from the closely related *Coelosphaera biclavata* (Priest, 1881, as *Polymastia*) from British Honduras by small differences in form, architecture, and spiculation. Priest's specimen is described as being a minute bulbous mass from which fistules project. The rind is extended inward at intervals by stout skeletal pillars (see his plate XXIII, fig. 4). The microsclere complement, if accurately described, differs from that of the present species in having two sizes of chelas and a single size of sigmas. In addition, the chelas (13 μ, 17 μ) and trichodragmata (254 μ) are smaller in size. De Laubenfels (1936b) erroneously transferred Priest's species to *Cornulella* Dendy (1921). *Cornulella lundbecki* Dendy, the type species, has a microsclere complement of isochelas, toxas, and microrhabds (plus a few sigmas, probably of foreign origin).

The Barbadian sponge is also similar in spiculation to the Indonesian *Coelosphaera fucoides* (Topsent, 1897). Topsent's material has chelas of larger maximum size and peculiar ramifying fistules. Little information is available on the internal structure of his species. The Barbadian sponge also has spicular similarities to the Pacific *Coelosphaera (Siderodermella) navicelligerum* (Ridley; see Ridley and Dendy, 1887), but it has no navicelliform chelas.

Two species of *Coelosphaera* have been recorded from tropical Atlantic America. *C. tunicata* Schmidt (1870, as *Desmacidon*) from Florida differs from *C. raphidifera* in having a single category of large sigmas and no raphides. Its "stumpf-stumpfe" megascleres may be strongyles. Topsent (1928, p. 224) was unable to locate the Floridian specimens at Strasbourg. He did locate Portuguese sponges that Schmidt (1870) regarded as aberrant specimens of *C. tunicata.* Topsent (1920, p. 17) identified them as *Hymedesmia filifera* (Schmidt), a species of the Myxillidae.

Coelosphaera fistula Little (1963) from Florida differs from *C. raphidifera* by the absence of raphides and in having distinctive unguiferate chelas, typically with four teeth at each end.

Xytopsene sigmatum de Laubenfels (1949; also see Little, 1963) from the Bahamas and Florida exhibits some similarities in spiculation to *Coelosphaera raphidifera.* It differs markedly in other respects, including the absence of a dermal rind and fistules.

FAMILY AGELASIDAE Verrill

GENUS *AGELAS* Duchassaing and Michelotti

Agelas schmidtii Wilson, 1902
Lewis, 1965, p. 1052, 1053, 1061.

MATERIAL. YPM 7741, two specimens, 7741a encrusting and 7741b with an oscular projection; YPM 7748, on a coral fragment along with a specimen of *Gelliodes ramosa;* YPM 7749; YPM 7751. All specimens were growing on coral rubble.

SHAPE. Mostly encrusting, with a maximum thickness of 0.5–1 cm; with or without oscular projections. YPM 7751 and 7741 b have single oscular projections (1 and 3 cm in height) arising marginally from an encrusting base. YPM 7749 is compressed, with an apical row of slightly elevated oscules, opening from a common central cloaca.

COLOR. In life, the exterior is light orange to reddish-orange while the interior is pale orange to yellow orange. In alcohol, the sponges become pale orange, pale brown, or drab with orange tinges.

CONSISTENCY. Tough but compressible.

SURFACE. Even to uneven. The surface varies considerably, within and between specimens. It is typically microtuberculate to conulose, but may also be smooth. Conules, when present, range from barely visible to 2–3 mm in height and tufted. Interconular ridges may also occur. The scattered oscules are 0.5–4 mm in diameter, with some apically placed on projections.

ECTOSOME. The aspiculous dermal membrane is pierced by the terminal spicules of ascending fibers. Foreign material may be abundant. No dermal pores can be distinguished.

ENDOSOME. Microcavernous. The skeleton is a three- to six-sided, irregularly polygonal fibroreticulation, with fibers 10–125 μ in diameter. Parallel fibers are 50 to several hundred microns or even greater than 1 mm apart. Although aspiculous intervals occur (rarely up to 1 mm in length), most of the fibers are echinated abundantly by singly scattered acanthostyles of all sizes. The spicules are embedded by their bases and usually project outward at approximately right angles to the fibers. Most of the echinators of horizontal fibers near the surface project toward the exterior. Fibers ascending to the conules are echinated and cored by acanthostyles. The coring spicules, mostly of considerable length, are grouped loosely to compactly in the fibers, often in a semi-plumose arrangement. The ascending fibers frequently branch near the surface. Their terminal spicules project slightly (if at all) beyond the protoplasmic surface. The flesh contains varied amounts of sand and spicular debris. Some spicules, particularly thin developing ones, apparently lie free in the flesh. Acanthoxeas, when present, occur in both the echinating and coring positions in low numbers.

SPICULES. Verticillately spined acanthostyles, with or without a few oxeote modifications, straight to slightly or considerably curved, with the shaft gradually tapering to a sharp point. Spines are almost completely confined to the whorls, with two to five visible in a row on spicules seen in profile. The spicule apices are often irregulary spined or devoid of spines. Larger spicules tend to have a higher number of whorls, a less prominent shaft spination, and more prominent basal spines. The correlation is far from absolute. In most spicules the spines are low and inconspicuous, ranging from 1.2–2.4 μ, although some spicules have spines as high as 4.7 μ. The spicule bases usually are covered with spines or stout blunt tubercles, up to 6 μ in length. Some spicules appear almost oxeote, due to the presence of a single large terminal tubercle. Spicule data are listed in Tables VI and VIII.

Three specimens have a low number of definite acanthoxeas. The oxeote spicules are slightly to considerably curved and gradually pointed. They lack any sort of localization in the sponge and are assumed to be extreme variants of the acanthostyles. Spicule data for acanthoxeas are listed in Tables VII and VIII.

TABLE VI. *Agelas schmidtii* Wilson – acanthostyle measurements (μ).

Specimen	± Raised Oscules	Length		Width	
		Range	Mean, SD	Range	Mean, SD
7741a	–	63-226	149±50	5.9-10.6	7.3±1.2
7741b	+	46-252	156±52	4.7-10.6	8.9±1.5
7748	–	53-252	122±48	4.7-10.6	8.0±2.1
7749	+	68-221	147±24	5.9-10.6	7.8±1.4
7751	+	74-336	180±70	4.7-11.8	9.6±2.3

TABLE VII. *Agelas schmidtii* Wilson – acanthoxea measurements (μ).

Specimen	± Raised Oscules	Length	Width
7741b	+	163-192±28-231 (10)	5.9-7.8±1.0-9.4 (10)
7748	–	179-222±41-299 (10)	5.9-8.0±1.6-10.6 (10)
7749	+	131-177±26-210 (10)	4.7-7.3±1.8-9.4 (10)

TABLE VIII. *Agelas schmidtii* Wilson – whorl counts.

Specimen	± Raised Oscules	Spicule	Whorls, range	Mean, SD
7741a	–	acanthostyle	8-16	11.2±1.1
7741b	+	acanthostyle	8-20	15.2±2.9
		acanthoxea	12-20	16.3±2.5
7748	–	acanthostyle	7-19	13.6±3.4
		acanthoxea	14-19	17.2±2.4
7749	+	acanthostyle	8-16	12.3±1.9
		acanthoxea	13-18	15.9±2.4
7751	+	acanthostyle	9-20	14.7±3.3

DISCUSSION. The five specimens are considered to be conspecific, despite differences in external form and spicule length. They are similar in skeletal architecture, spicule form, range of whorls per spicule, and spines per whorl.

The present material is considered tentatively to be conspecific with *Agelas schmidtii* Wilson (1902), originally described from St. Thomas. Wilson's type specimen (USNM 7683), which has been re-examined, is an elongate, microhispid, tubular, irregularly cylindrical sponge with several short projections. At present it is pale brown and compressible. A sample of 100 acanthostyles has a range of 67–234×3.5–7.1 μ, with 9–15, rarely to 21 whorls per spicule, and 2–3 visible spines per whorl. Most spicules are straight to slightly curved, but some of the more elongate ones are considerably curved. As in the present material, the correlation between spicule length and whorl number is only an approximate one. In smaller spicules the spines are usually prominent, thorn-shaped, and perpendicularly projecting to recurved. The spination is usually less prominent in the more elongate spicules.

The similarity in spiculation and architecture is offset partially by differences in external form. The presence of oscular projections in three of my five specimens, along with a central cloacal cavity in one of them, suggests the possibility of tubular growth in an environment less subject to wave action. The character of the surface approaches that of Wilson's type in my compressed specimen and the degree of conulation varies in the others.

Four species of *Agelas* have been recorded previously from Barbados. Hartman (identifications *in* Lewis, 1965) reported *A. schmidtii* from 50–150 meters. Lewis (p. 1052, 1053) described it as branching and red in life. Hartman's specimen (YPM 5880) is clearly conspecific with Wilson's, with similarities extending to external as well as anatomical features.

Lewis' samples from 50–150 meters also included specimens identified by Hartman as *Agelas dispar* Duchassaing and Michelotti (1864) and *A. sceptrum* (Lamarck, 1815; see Lamarck, 1836). The massive *A. dispar* is less similar in external form to the present material than is *A. schmidtii.* Burton and Rao (1932, p. 355) selected a neotype for *A. dispar,* but unfortunately gave neither a description nor geographical location for their specimen. The type specimen of *A. sceptrum* was restudied by Topsent (1933,

p. 33). It is a cylindrical sponge with small stout spicules that are typically 120×12 μ. *A. dispar* and *A. sceptrum* are now being revised by Dr. W. D. Hartman.

A. flabelliformis (Carter, 1883b, as *Ectyon*) was described from the "West Indies" and Barbados. It differs from the present material in having a flabellate form with pores restricted to groups on one surface. Its acanthostyles were only 127×12.7 μ in "average largest size."

Most of the other tropical American species of *Agelas* are poorly known. The common *Agelas sparsus* (Gray, 1867a) has smaller spicules than *A. schmidtii,* apparently all in the echinating position (Carter, 1871; de Laubenfels, 1936b).

FAMILY MYCALIDAE Lundbeck
GENUS MONANCHORA Carter

Monanchora barbadensis n. sp. (Figure 3)

HOLOTYPE. YPM 7750, on a coral fragment.

SHAPE. A small thin encrustation, less than 0.5 mm in maximum thickness.

COLOR. The sponge is bright red in life. It becomes brown in alcohol.

CONSISTENCY. Difficult to determine, due to the extreme thinness of the specimen.

SURFACE. Smooth, lipostomous, microtuberculate.

ECTOSOME. A thin membrane, in which openings cannot be detected. The membrane contains a few scattered thin megascleres and the projecting ends of endosomal skeletal spicules. Microscleres of both types are abundant.

ENDOSOME. Stout subtylostyles are implanted singly on the substratum. They are directed vertically upward with apices projecting slightly beyond the surface. A small amount of cementing spongin is present around the spicule bases. The thin subtylostyles are scattered and also partly clustered in loose groups, with bases at various levels and apices projecting slightly beyond the surface. The flesh contains debris and isochelas in varying abundance.

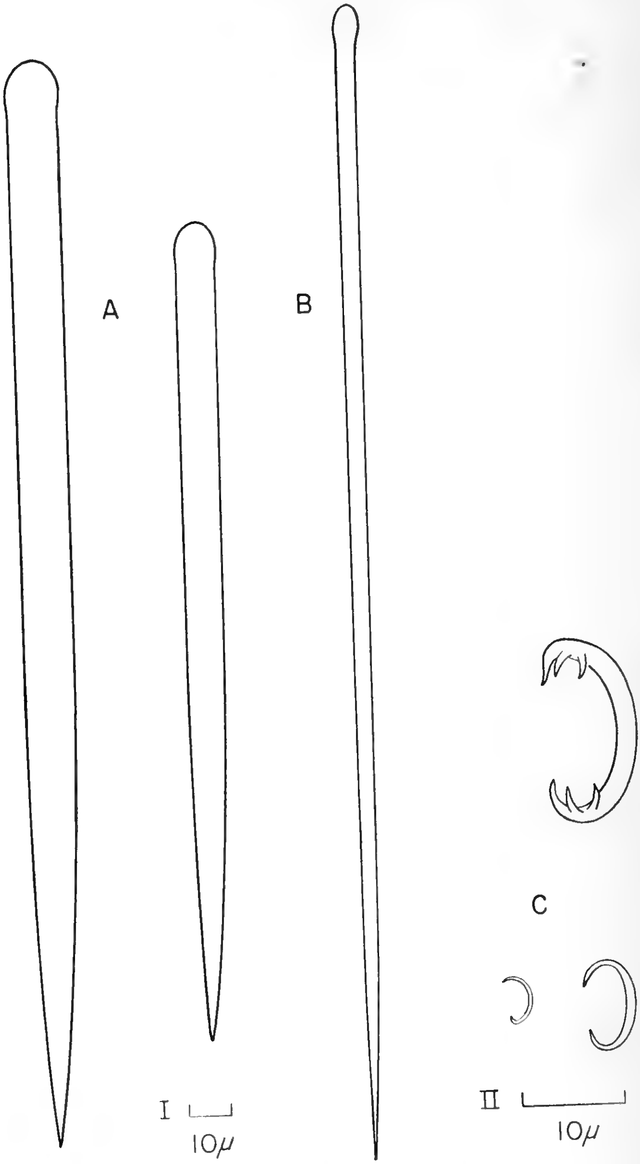


FIG. 3. Spicules of *Monanchora barbadensis* n. sp., YPM 7750. Holotype. A) Thick subtylostyles. B) Thin subtylostyle. C, D) Isochelas. A, B: scale I. C, D: scale II.

Chelas are more numerous near the surface and toward the substratum.

SPICULES. Stout and thin subtylostyles, and anchorate isochelas of two sizes (Fig. 3). Spicule measurements are listed in Table IX.

TABLE IX. *Monanchora barbadensis* n. sp. – spicule measurements (μ) of holotype.

Spicule	Length		Width	
	Range	Mean, SD	Range	Mean, SD
Subtylostyle, robust	142-273	189±27	———	———
shaft	———	———	4.7-9.4	6.6±1.4
head	———	———	5.9-10.6	8.0±0.7
Subtylostyle, thin	179-305	264±24	———	———
shaft	———	———	1.2-3.5	1.9±0.6
head	———	———	2.4-4.7	3.1±0.6
Isochelas, large	14.1-21.2 (50)	18.8±1.3	1.2-2.4 (shaft)	———
Isochelas, small	4.7-7.1 (25)	6.6±0.6	0.7 (shaft)	———

A–thick subtylostyles, rarely becoming styles, with rounded heads, without necks, and with gradually tapering shafts.

B–thin subtylostyles, usually straight, occasionally slightly curved, with narrow elongate heads, without necks, and with gradually tapering shafts.

C-anchorate isochelas, unguiferate, typically with five short, sharp teeth at each end, and strongly curved shafts. At each end, one tooth is in continuity with the shaft, while the two lateral teeth on each side share a common base. A few spicules seem to have only three teeth. The teeth are occasionally narrow and blunt-tipped.

D–small anchorate isochelas, unguiferate, c-shaped, and very thin. They are infrequent in sections and spicule strews, but are numerous in the dermal peels. Although teeth could not be seen on most, several spicules were clearly tridentate when viewed in situ under oil immersion.

Foreign spicules are present in the clumps of debris and in spicule strews. The most common are curved acanthostrongyles, 74–110×2.4–3.5 μ. They are in association with obviously foreign tylotes, palmate isochelas, and toxas, and probably represent the fragments of another sponge.

DISCUSSION. The present sponge is related to Indo-Pacific species placed in *Monanchora* Carter (1883a), *Folitispa* de Laubenfels (1936b), and *Neofolitispa* Bergquist (1965). Bergquist, regarding *Monanchora* as poorly known, established *Neofolitispa* for mycalids with unguiferate anchorate isochelas. At least for the present, *Neofolitispa* is regarded as a synonym of *Monanchora.* Bergquist emphasized the spatulate form of the anchorate isochelas in her redefinition of *Folitispa.* It should be noted that tooth form varies somewhat in the present material and also in *Monanchora unguiculata* (Dendy, 1921).

The type species of *Monanchora, M. clathrata* Carter (1883a) from Australia, has unguiferate anchorates with five elongate claw-shaped teeth at each end. Little information is available on the internal structure of the poorly preserved holotype, which may have had a polygonally reticulate surface. Carter found two categories of subtylostyles and a single category of chelas in his specimen. The maximum spicule dimensions are somewhat larger than in the present material, and the chelas have more narrow and elongate teeth.

Lévi (1961b) identified a Vietnamese sponge as *Monanchora clathrata.* His specimen differs from the holotype in having stylote megascleres and two categories of chelas. Bergquist (1965) considered Lévi's specimen to be conspecific with *Monanchora dianchora* de Laubenfels (1935). However, it may well represent a distinct species.

Bergquist (1965) recorded specimens from the Palau Archipelago as *Neofolitispa dianchora* (de Laubenfels). She considered her specimens to be conspecific with both *Monanchora dianchora* de Laubenfels and *Folitispa pingens* de Laubenfels (1954a). Her specimens and the holotype of *F. pingens* have plumose fibers and ectosomal spicule brushes. In both, the spicule complement includes a single category of megascleres and two sizes of isochelas. The Barbadian sponge differs from Bergquist's material in having two categories of megascleres and smaller-sized isochelas. According to de Laubenfels' description, *M. dianchora* has two partially distinct megasclere categories. The Barbadian sponge differs from his description of *M. dianchora* in form, architecture, and microsclere size.

Monanchora acuata (Lévi, 1958, as *Folitispa;* see also 1961a) from the Indian Ocean and Red Sea also has unguiferate chelas. It closely resembles the Barbadian sponge in architecture and spicule dimensions, but the large isochelas have no more than three teeth. Lévi's species lacks the plumose architecture of Bergquist's material.

Monanchora unguiculata (Dendy, 1921, as *Amphilectus*) differs from the present material in having a single megasclere category and chelas that are extremely variable in tooth development. Specimens attributed to the species by Lévi (1961a, as *Hymedesmia*) have two sizes of isochelas and acanthostyles of varied abundance.

Monanchora viridis (Kieschnick, 1898, as *Esperiopsis*) from Indonesia, with two sizes of isochelas, is distinguished by its robust tylostyles, fibrous architecture, and tubercular surface.

ORDER CLAVAXINELLIDA Lévi
FAMILY BUBARIDAE Topsent

The family was established by Topsent (1894, p. 20) and is used in the sense of Topsent, 1928. The family includes genera with monactinal megascleres, mostly projecting from a basal mat or axial column of diactinal megascleres. The latter are angulated, bent, undulating, or irregularly flexed. Microscleres, if present, are trichites.

GENUS *BUBARIS* Gray

Encrusting, massive, or ramose in form. The monactinal spicules are styles or tylostyles. The flexuous diactinal spicules are oxeas or strongyles. Two species have trichites (see Dendy, 1921).

Bubaris ammosclera n. sp. (Figure 4)

MATERIAL. Two specimens, YPM 7756 (holotype) and YPM 7757, collected by Dr. Ian Macintyre, of McGill University, in 45–50 feet (about 14–15m) of water, 1/2 mile off the west coast of Barbados.

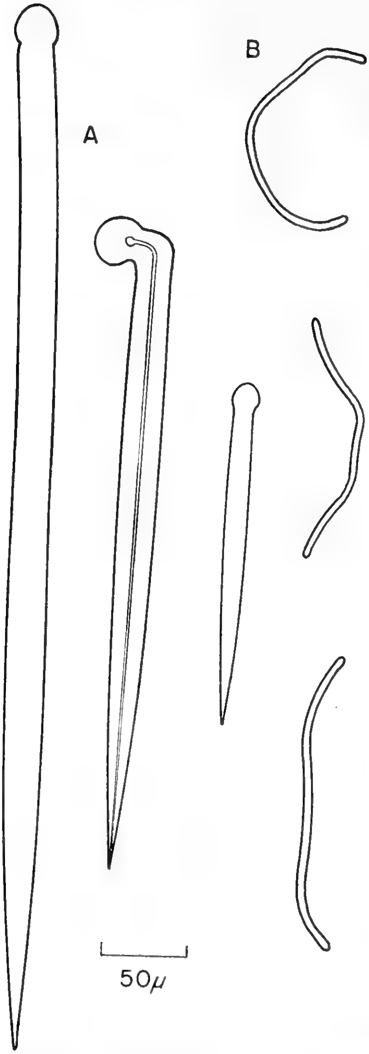


FIG. 4. Spicules of *Bubaris ammosclera* n. sp., YPM 7756. Holotype. A) Tylostyles. B) Contorted strongyles.

SHAPE. A thin film, less than 0.5 mm in thickness, extending over coral and continued as a mat binding clumps of fine to coarse calcareous sediment.

COLOR. In life and in alcohol, dull white and translucent.

CONSISTENCY. Soft, easily torn by forceps. Macintyre found the living sponge to be mucilaginous.

SURFACE. Even, hispid. A few scattered, flush oscules are present, 0.5–2 mm in diameter.

ECTOSOME. Many tylostyles pierce the surface. Dermal peels include tangentially scattered tylostyles and a very few flexuous strongyles. Some peels contain a considerable amount of fine debris and a few foreign spicules.

ENDOSOME. Some tylostyles are scattered in confusion, but many are implanted vertically by their bases on all sides of calcareous fragments. The strongyles, present in lesser numbers, are most frequent next to the debris.

SPICULES. Tylostyles and flexuous strongyles (Fig. 4). Spicule measurements are listed in Table X.

TABLE X. *Bubaris ammosclera* n. sp. – spicule measurements (μ).

Spicule	Length		Width	
	Range	Mean, SD	Range	Mean, SD
YPM 7756 (Holotype)				
Tylostyle	152-551	321±75	———	———
shaft	———	———	7.1-22.3	12.2±3.0
head	———	———	9.4-22.3	13.4±3.7
Strongyle	116-273 (50)	187±25	2.4-5.9	4.0±0.4
YPM 7757				
Tylostyle	116-583	275±100	———	———
shaft	———	———	4.7-22.3	14.1±4.5
head	———	———	7.1-22.3	15.5±4.7
Strongyle	68-294 (50)	159±26	2.4-5.9	3.8±0.6

A–tylostyles, straight to slightly curved, with prominent rounded or slightly trilobed heads, shafts rather uniform over most of their length, and with gradually tapering points. Most of the smaller tylostyles are straight. Curvature, when present, is particularly pronounced near the basal end. Some spicules are bent sharply just below the head (a condition found in many species of the Bubaridae). The heads are infrequently small, with the spicules approaching the stylote condition. A very few spicules are inflated subterminally and then often eccentrically. In most the head diameter slightly exceeds maximum shaft width, but in some larger spicules the reverse is true. Maximum shaft diameter occurs in midlength or slightly toward the apical end. The points are usually sharp, but occasionally narrowed and rounded.

B-strongyles, irregularly flexed, bent, or twisted, very uniform in diameter, with rounded, equally developed ends. The spicules range in form from elongate and only slightly irregular to grotesquely bent. The ends are always perfectly strongylote.

DISCUSSION. *Bubaris ammosclera* can be distinguished from other species of the genus by its tylostylote megascleres. The only other tropical American species of *Bubaris* is *B. mastophora* (Schmidt, 1870) from Florida, which differs further from *B. ammosclera* in having a lobate form and undulating oxeas. Specimens from the Azores attributed to *B. mastophora* by Topsent (1904) differ from the present material in having elongate strongyles with narrowed ends.

The peculiar habitus of the Barbadian sponge has been recorded for two other species of *Bubaris.* Topsent (1928) described Madeiran specimens of *B. vermiculata* (Bowerbank) as being "conglomérats faits de débris calcaires cimentés par l'éponge." Dendy (1921) described *B. salomonensis* as "spreading over a mass of calcareous debris."

Hartman (identification *in* Lewis, 1965) recorded another Barbadian *Bubaris* from 50 meters. It differs from the present species in the form of both styles and diactinal spicules (personal communication and examination of his slides.)

FAMILY SPIRASTRELLIDAE Ridley and Dendy

SUBFAMILY TIMEINAE Topsent

GENUS *TIMEA* Gray

Timea stenosclera n. sp. (Figure 5)

MATERIAL. YPM 7755 (holotype), on a small piece of coral.

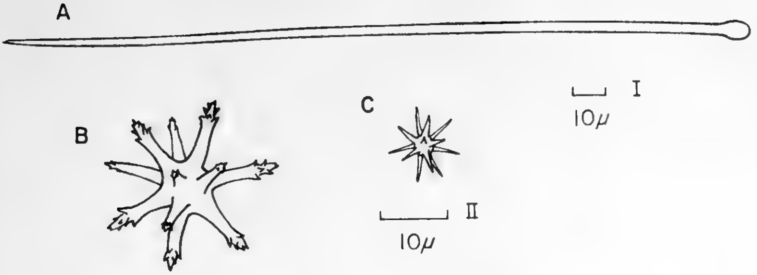


FIG. 5. Spicules of *Timea stenosclera* n. sp., YPM 7755. Holotype. A) Tylostyle. B) Large oxyspheraster with spined rays. C) Small euaster (oxyspheraster). A: scale I. B, C: scale II.

SHAPE. A small film-like encrustation, less than 0.5 mm in thickness.

COLOR. Orange in life, grayish-brown in alcohol.

CONSISTENCY. Difficult to determine, due to the extreme thinness of the specimen.

SURFACE. Smooth, lipostomous (in life as well as in preservative), microtuberculate.

ECTOSOME. There is little dermal specialization. The tylostyle bundles may project slightly. Euasters, abundant everywhere, are somewhat more frequent toward the surface. The singly scattered circular dermal pores are about 30 μ in diameter.

ENDOSOME. The interior is packed with euasters. Most of the tylostyles are grouped into loose clusters, with bases at various levels, and apices directed toward the surface.

SPICULES. Tylostyles and euasters (Fig. 5). The euasters are divided incompletely into two forms, large oxyspherasters and small euasters, without any obvious localization. Spicule measurements are listed in Table XI.

TABLE XI. *Timea stenosclera* n. sp. – spicule measurements (μ) of holotype.

Spicule	Length; aster diameter		Width	
	Range	Mean, SD	Range	Mean, SD
Tylostyle	173-252	210±25	———	———
shaft	———	———	1.7-2.4	2.1±0.3
head	———	———	3.5-4.7	3.6±0.2
Oxyspheraster	11.8-25.9 (100)	19.7±2.9	———	———
Euaster, small	4.7-11.8 (50)	9.2±2.3	———	———

A–tylostyles, slender, straight, (but with the head rarely at an angle to the shaft), gradually pointed, with an elongate although inconspicuous neck.

B–oxyspherasters, very abundant, with centrum diameter equal to or slightly less than ray length. The rays are thick (1.2–1.4 μ basally) usually conical, occasionally truncate or strongylote, and often distally roughened or spined.

C–euasters, oxy- to strongylospherastral in form, with a centrum diameter usually slightly less than ray length. The rays are very thin (0.7 μ or less basally), straight, smooth, and cylindrical or slightly conical. A few spicules are intermediate between categories B and C. In both categories, a very few spicules have a small, nearly inconspicuous centrum.

DISCUSSION. The Barbadian specimen is characterized by its short slender tylostyles and thin-rayed smaller euasters. The only other species of *Timea* with small tylostyles is *T. xena* de Laubenfels (1954b) from Hawaii, which differs from the present species in having only a single category of euasters.

The generic position of the species requires explanation. Most species of the subfamily Timeinae have a spiculation of tylostyles and one or more categories of euasters. Species lacking peculiarities of external appearance or euastral form should be placed in *Timea* Gray (1876a). De Laubenfels (1936b) established *Kotimea* for species with spherasters, which occur in *Timea stenosclera*. However, euastral form and the degree of centrum development vary within many species of the Timeinae, including *T. moorei* (Carter, 1880), the type species of *Kotimea*.

De Laubenfels (1936b, 1950) utilized *Halicometes* Topsent (1898) for species with two categories of euasters, as in *Timea stenosclera*. However, *Halicometes* is a member of the Stylocordylidae and cannot be utilized for species of the Timeinae. *Halicometes* was established for *Cometella stellata* Schmidt (1870), which has a tuberculate body mounted on a stalk. Schmidt described the spicule complement as including anisostrongyles, spherasters, and long-rayed euasters. At a later date (1880) Schmidt, partly on the basis of new material, transferred the species to *Tethya*. He gave it a new name, *Tethya cometes,* and listed *Cometella stellata* as a synonym. Sollas (1888) corrected Schmidt's nomenclature, calling the species *Tethya* (?) *stellata*. Topsent (1898) made *C. stellata* the type species of his new genus *Halicometes*. The genus, with a supposed spiculation of strongyles and spherasters, was placed in the family Stylocordylidae.

In a later paper (1920), Topsent described two specimens that Schmidt had deposited in the Strasbourg Museum under the name *Tethya cometes*. One specimen has smooth surface tubercles and the other has hispid ones. The latter thus resembles Schmidt's illustration (1870) of *Cometella stellata*. Topsent described the spicule complement of the Strasbourg sponges as including large skeletal anisostrongyles, peripheral styles, exotyles (in the stalk), spherasters (with centrum development varied between specimens), and chiasters (with a similar variation in centrum development). Topsent transferred the genus to the Tethyidae, but the presence of a stalk suggests that his original familial placement is more probable. Lévi (1964, p. 72-73) also regards *Halicometes* as being closely related to *Stylocordyla*. Assuming the identity of *Cometella stellata* and *Tethya cometes* (as intended by Schmidt), the diagnosis of *Halicometes* must be based on Topsent's description, making it a peculiar, monotypic genus without close relation to *Timea*.

The tropical Atlantic American fauna includes several species of *Timea* that resemble *T. stenosclera* in having two types of euaster. *T. perastra* (de Laubenfels, 1936b) from the Dry Tortugas, Florida, differs from the Barbadian species in having a cylindrical form and a euastral complement of tylasters and small chiasters. *T. parasitica* (Higgin, 1877) from Grenada, West Indies, differs from the present material in having large (508 μ)

subterminally inflated megascleres, and terminally spined chiasters as the smaller category of euaster.

Encrusting sponges from Bermuda (de Laubenfels, 1950) and Florida (Little, 1963) were identified as *Halicometes stellata* (Schmidt). They represent a species of *Timea,* with two categories of euaster, similar to *T. mixta* (Topsent, 1896; also see Topsent, 1900) from the Mediterranean and Cape Verde Islands. They differ from *T. stenosclera* in megasclere size, the absence of spination on their large spherasters, and the thick-rayed spinous form of their small euasters.

FAMILY PLACOSPONGIIDAE Gray
GENUS *PLACOSPONGIA* Gray

Placospongia melobesioides Gray, 1867b
Vosmaer and Vernhout, 1902, p. 1-17.

MATERIAL. YPM 7753, a small specimen on a coral fragment. The fragment was removed from a larger piece of rubble on which the holotype of *Coelosphaera raphidifera* (YPM 7745) was growing.

SHAPE. An encrustation, up to 3 mm in thickness, with an incipient projection, 7 mm high, at one edge.

COLOR. A dark brown cortex and yellowish endosome, in both the living and the preserved states.

CONSISTENCY. A hard cortex and tough endosome.

SURFACE. Covered by irregularly polygonal plates, up to 1 cm in span, with raised rims.

ECTOSOME. The cortex reaches 1 mm in thickness, with a thin spherule-rich ectochrote covering a dense selenastral rind.

ENDOSOME. The flesh is dense and fibrous, except for wide horizontal subcortical canals. Stout tylostyle bundles traverse the endosome, narrowing progressively, and penetrate the cortex. The bundles are 85–125 μ in width at the point of penetration. The tylostyles are placed at various levels within the bundles, with apices directed toward the surface. Larger sized megascleres are restricted to the endosome. The endosomal microsclere complement consists of numerous selenasters (both mature and developmental forms) and spherules. Many of the spherules are in irregular clusters, as noted by Lindgren (1898) and Vosmaer and Vernhout (1902).

SPICULES. Tylostyles, selenasters, and spherules. Spicule measurements are listed in Table XII.

TABLE XII. *Placospongia melobesioides* Gray – spicule measurements (μ) of YPM 7753.

Spicule	Length; aster diameter		Width	
	Range	Mean, SD	Range	Mean, SD
Tylostyle	252-845	577±97	——	——
shaft	——	——	4.7-12.9	7.5±1.8
head	——	——	5.9-14.1	10.4±1.6
Selenaster	40-63.5	55±4.3	25.9-56.4	45.2±4.3
Spherule	1.2-1.7	1.4±0.2	——	——

A–tylostyles, long, straight, gradually tapered, with conspicuous heads. The heads are usually rounded, sometimes oval, and infrequently subterminal. A very few spicules have a slight neck constriction. The apices, while narrow, are usually rounded.

B–selenasters, elliptical, with a hilum and a granular surface. Selenasters develop in the endosome from entirely spined rods, 16–22 μ in length. The intermediate stages are ovoid pincushions, about 22×12 μ (see also Vosmaer and Vernhout, 1902).

C–spherules.

D–spherasters, 12 and 13 μ. Only two examples were found in spicule strews.

DISCUSSION. *P. melobesioides* is a common Indo-Pacific species, recorded with some degree of certainty from tropical American waters only by Arndt (1927). Arndt's somewhat aberrant specimen had large spherules (6 μ) and a few oval microscleres. De Laubenfels (1936b) tentatively attributed a specimen from the Dry Tortugas, Florida, to *P. melobesioides.* His fragmentary material is unidentifiable since it lacks small microscleres (Little, 1963; Hechtel, 1965). Schmidt's record from Florida (1870) cannot be verified for the same reason (Arndt, 1927; Hechtel, 1965; Sollas, 1888).

ORDER CHORISTIDA Sollas
FAMILY CHONDRILLIDAE Gray
GENUS *CHONDRILLA* Schmidt

Chondrilla nucula Schmidt, 1862
Hechtel, 1965, p. 74; Rützler, 1965, p. 16

MATERIAL. YPM 7743, a specimen encrusting a *Porites* fragment, taken from *Porites* rubble.

SHAPE. A flat encrustation, about 2 mm in thickness.

COLOR. Dark brown externally, in life and in alcohol. The interior is cream in life, and drab to gray in alcohol.

CONSISTENCY. Tough.

SURFACE. Smooth. The oscules are small, flush, and scattered. Their diameter in life does not exceed 0.5 mm. The oscules contract strongly upon removal from water, giving the surface a lipostomous appearance.

ECTOSOME. A densely pigmented, richly spiculiferous region, about 100–160 μ in thickness. Dermal peels are pierced by singly scattered circular openings, which may be dermal pores. The openings, 85–160 μ apart, have diameters of 20–30 μ, and darkly pigmented rims about 10 μ in thickness. In one peel, a larger, possibly oscular opening is present, 105×42 μ, with an aspiculous pigmented rim 30–105 μ in span.

ENDOSOME. The ectosomal concentration of spherasters gradually diminishes toward the interior. In deeper parts of the sponge spherasters are largely restricted to canal linings and the basal layer of the endosome. Considerable areas (up to 400 μ in span) are devoid of spicules. Vertical canals, 30–135 μ in diameter, are prominent in the upper 1/2 – 1/3 of the dense endosome. They divide into smaller canals, often obliquely placed, which run toward the base of the sponge.

SPICULES. Spherasters, with a well-developed centrum and short conical rays, 14.1–37.6 μ (mean 26.8 ± 2.5 μ) in overall diameter. Rays are 1.2–6 μ in length. No long-rayed spherasters are present.

DISCUSSION. The present specimen differs from Jamaican ones by the absence of long-rayed spherasters. However, ray length varies considerably within and between specimens of the species (Hechtel, 1965).

LITERATURE CITED

Arndt, Walther. 1927. Kalk-und Kieselschämme von Curaçao. Bidr. Dierk. Amst. **25**:133-158.

Bergquist, P.R. 1965. The sponges of Micronesia. Part 1. The Palau Archipelago. Pacif. Sci. **XIX** (2): 123-204.

Burton, Maurice. 1963. A revision of the classification of the calcareous sponges. Br. Mus. (Nat. Hist.), Lond. 693 p.

Burton, Maurice and S. H. Rao. 1932. On the shallow-water marine sponges in the collection of the Indian Museum. Part 1. Rec. Indian Mus. **XXXIV**:299-356.

Carter, H. J. 1871. On two undescribed sponges and two Esperiadae from the West Indies; also on the nomenclature of the calcisponge *Clathrina* Gray. Ann. Mag. Nat. Hist. (4) 7:268-283.

——— 1880. Report on specimens dredged up from the Gulf of Manaar and presented to the Liverpool Free Museum by Capt. W. H. Cawne Warren. Ann. Mag. Nat. Hist. **(5)** 6:35-61, 129-156.

——— 1882. Some sponges from the West Indies and Acapulco in the Liverpool Free Museum described, with general and classificatory remarks. Ann. Mag. Nat. Hist. **(5)** 9:266-301, 346-368.

——— 1883a. New genus of sponges. Ann. Mag. Nat. Hist. **(5)** 11:369-370.

——— 1883b. Contributions to our knowledge of the Spongida. Ann. Mag. Nat. Hist. **(5)** 12:308-329.

De Laubenfels, M. W. 1934. New sponges from the Puerto Rican Deep. Smithson. Misc. Collns. **91**(17):1-28.

——— 1935. A collection of sponges from Puerto Galera, Mindoro, Philippine Islands. Philipp. J. Sci. **56**(3):327-336.

——— 1936a. A comparison of the shallow-water sponges near the Pacific end of the Panama Canal with those at the Caribbean end. Proc. U.S. Natn. Mus. **83**:441-466.

——— 1936b. A discussion of the sponge fauna of the Dry Tortugas in particular and the West Indies in general, with material for a revision of the families and orders of the Porifera. Pap. Tortugas Lab. **XXX**:1-225.

——— 1949. Sponges of the western Bahamas. Am. Mus. Novit. **1431**:1-25.

——— 1950. The Porifera of the Bermuda Archipelago. Trans. Zool. Soc. Lond. **27**(1):1-154.

——— 1954a. The sponges of the west-central Pacific. Ore. St. Monogr. Stud. Zool. **7**:1-306.

——— 1954b. Occurrence of sponges in an aquarium. Pacif. Sci. **VIII** (3):337-340.

Dendy, Arthur. 1905. Report on the sponges collected by Prof. Herdman, at Ceylon, in 1902. *In* W. A. Herdman, Report to the government of Ceylon on the pearl oyster fisheries of the Gulf of Manaar, with supplementary reports upon the marine biology of Ceylon by other naturalists. Publ. Roy. Soc. Lond. Suppl. **XVIII**:57-246.

——— 1921. Report on the Sigmatotetraxonida collected by H.M.S. Sealark in the Indian Ocean. Trans. Linn. Soc. Lond. **XVIII** (1):1-164.

Duchassaing de Fonbressin, P. and Giovanni Michelotti. 1864. Spongiaires de la mer caräibe. Natuurk. Verh. Mij. Haarlem **XXI**:1-124.

Ekman, Sven. 1953. Zoogeography of the sea. Sidgwick and Jackson, London. 417 p.

Gray, J. E. 1867a. Notes on the arrangement of sponges, with the description of some new genera. Proc. Zool. Soc. Lond., 1867:492-558.

——— 1867b. On *Placospongia,* a new generic form of Spongiadae, in the British Museum. Proc. Zool. Soc. Lond., 1867:127-129.

Hartman, W. D. 1965. Identifications *in* J. B. Lewis, The coral reefs and coral communities of Barbados, West Indies. Can. J. Zool. **38**:1133-1145.

——— 1967. Revision of *Neofibularia* (Porifera, Demospongiae), a genus of toxic sponges from the West Indies and Australia. **Postilla 113**:1-41.

Hechtel, G. J. 1965. A systematic study of the Demospongiae of Port Royal, Jamaica. Bull. Peabody Mus. Nat. Hist., Yale Univ., **20**:1-103.

Higgin, Thomas. 1877. Description of some sponges obtained during a cruise of the steam-yacht "Argo" in the Caribbean and neighbouring seas. Ann. Mag. Nat. Hist. **(4)** 19:291-299.

Kieschnick, O. 1898. Kieselschwämme von Amboina. *In* R. Semon, Zoologische forschungsreisen in Australien und dem Malayischen Archipel. **V**:545-582. Gustav Fisher, Jena.

Lamarck, J. B. 1813. Sur les polypiers empâtés. Annls. Mus. Hist. Nat. Paris **XX**:294-312, 370-386, 432-458.

——— 1815. Suite des polypiers empâtés. Mém. Mus. Hist. Nat. Paris **1**:69-80, 162-168, 331-340. (not seen).

——— 1836. Histoire naturelle des animaux sans vertèbres. Deuxième éd., (edited by G. Deshayes and H. Milne-Edwards). J. Baillière, Paris. 11 vols.

Lewis, J. B. 1960. The coral reefs and coral communities of Barbados, West Indies. Can. J. Zool. **38**:1133-1145.

——— 1965. A preliminary description of some marine benthic communities from Barbados, West Indies. Can. J. Zool. **43**:1049-1074.

Lévi, Claude. 1956. Étude des *Haliscara* de Roscoff. Embryologie et systématique des Démosponges. Archs. Zool. Exp. Gén. **93**(1):1-181.

——— 1958. Spongiaires de mer Rouge recueillis par la Calypso (1951-1952). Résult. Scient. Camp. "Calypso" **3**:1-46.

——— 1961a. Les Spongiaires de L'Ile Aldabra. Résult. Scient. Camp. "Calypso" **5**:3-32.

——— 1961b. Éponges intercoditales de Nha Trang (Viet Nam). Archs. Zool. Exp. Gén. **100**(2):127-148.

——— 1964. Spongiares des zones bathyale, abyssale, et hadale. Galathea Rep. **7**:63-112.

Lindgren, N. G. 1898. Beitrag zur Kenntniss der Spongienfauna des Malayischen Archipels und der chinesischen Meere. Zool. Jb., (Abt. Syst.) **XI**:283-378.

Little, F. J. 1963. The sponge fauna of the St. George's Sound, Apalachee Bay, and Panama City regions of the Florida Gulf Coast. Tulane Stud. Zool. **11**:31-71.

Priest, B. W. 1881. On an undescribed sponge of the genus *Polymastia,* from Honduras. J. Quekett Microsc. Club **VI**:302-304.

Ridley, S. O. and Arthur Dendy. 1887. Report on the Monaxonida collected by H.M.S. Challenger during the years 1873-1876. Rep. Challenger, Zool. **XX**:1-275.

Rützler, Klaus. 1965. Systematik und Oekologie der Poriferen aus Litoral-Schattengebieten der Nordadria. Z. Morph. Oekol. Tiere **55**:1-82.

Schmidt, E. O. 1870. Grundzüge einer Spongien-Fauna des Atlantischen gebietes. Leipzig. 88 p.

——— 1879. Die Spongien des Meerbusen von Mexico. I. p. 1-32. Gustav Fisher, Jena.

——— 1880. Die Spongien des Meerbusen von Mexico (und des Caraibischen Meeres). II. p. 33-90. Gustav Fisher, Jena.

Sollas, W. J. 1888. Report on the Tetractinellida collected by H.M.S. Challenger, during the years 1873-1876. Rep. Challenger, Zool **XXV**: 1-458.

Stutchbury, S. 1842. Description of a new sponge from Barbadoes. Ann. Mag. Nat. Hist. **IX**:504-506.

Topsent, Emile. 1894. Une réforme dans la classification des Halichondrina. Mém. Soc. Zool. Fr. **VII**:5-26.

——— 1896. Matériaux pour servir à l'étude de la faune des spongiaires de France. Mém. Soc. Zool. Fr. **IX**:113-133.

——— 1897. Spongiares de la Baie d'Amboine. Revue Suisse Zool. **IV**:421-487.

——— 1898. Introduction à l'étude monographique des Monaxonides de France. Classification des Hadromerina. Archs. Zool. Exp. Gén. (3) **VI**:91-113.

——— 1900. Étude monographique des spongiares de France. III. Monaxonida. (Hadromerina). Archs. Zool. Exp. Gén. (3) **VIII**:1-331.

——— 1904. Spongiares des Açores. Résult. Camp. Scient. Prince Albert 1 **XXV**:1-280.

——— 1920. Spongiares du Musée zoologique de Strasbourg. Monaxonides. Bull. Inst. Océanogr. Monaco. **381**:1-36.

——— 1928. Spongiares de L'Atlantique et de la Méditerranée provenant des croisières du Prince Albert 1er de Monaco. Résult. Camp. Scient. Prince Albert 1 **LXXIV**:1-376.

——— 1930. Éponges de Lamarck conservées au Muséum de Paris. Archs. Mus. Natn. Hist. Nat., Paris **(6)**5:1-56.

——— 1933. Éponges de Lamarck conservées au Muséum de Paris. 3. Archs. Mus. Natn. Hist. Nat., Paris **(6)**10:1-60.

Uliczka, E. 1929. Die tetraxonen Schwämme westindiens. *In* W. Kukenthal and R. Hartmeyer, Ergebnisse einer zoologischen forschungsreise nach West Indien. Zool. Jb., Suppl. **16**:35-62.

Vosmaer, G. C. and J. Vernhout. 1902. The Porifera of the Siboga-Expeditie. Siboga Exped. **VIA**:1-17.

Warburton, F. E. 1960. Influence of currents on form of sponges. Science, New York, **132**:89.

Weltner, W. 1882. Beiträge zur Kenntniss der Spongien. Freiburg. 62 p. (not seen).

Wilson, H. V. 1902. The sponges collected in Porto Rico in 1899 by the U.S. Fish. Comm. Steamer Fish Hawk. Bull. U.S. Fish. Comm. 1900, **20**(2):377-410.

INFORMATION FOR AUTHORS

REVIEW	The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
STYLE	Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).
FORM	Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.
TITLE	Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
ABSTRACT	The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
OMENCLATURE	Follow the International Codes of Zoological and Botanical Nomenclature.
LLUSTRATIONS	Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
FOOTNOTES	Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
TABLES	Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
REFERENCES	The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
HOR'S COPIES	Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
PROOF	Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
COPYRIGHT	Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 133. 9 JUNE 1969.

A PROBABLE PTERIDOSPERM WITH EREMOPTERID FOLIAGE FROM THE ALLEGHENY GROUP OF NORTHERN PENNSYLVANIA

T. DELEVORYAS

T. N. TAYLOR

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

A PROBABLE PTERIDOSPERM WITH EREMOPTERID FOLIAGE FROM THE ALLEGHENY GROUP OF NORTHERN PENNSYLVANIA

T. DELEVORYAS

Department of Biology and Peabody Museum of Natural History, Yale University, New Haven, Connecticut, 06520

T. N. TAYLOR

Department of Biological Sciences,
University of Illinois at Chicago Circle
Chicago, Illinois, 60680

ABSTRACT

Compressed fossilized foliage most comparable to that of *Eremopteris zamioides* (Bertrand) Kidston occurs in shale associated with coal in the Allegheny Group in northern Pennsylvania. In association with this foliage are abundant samaropsid seeds and small, apparently microsporangiate organs. Although close proximity of disconnected plant parts as fossils is not evidence in itself that these plant parts were originally connected, it is tempting to believe that these leaves, seeds, and microsporangia were parts of the same species. Furthermore, there have been a number of previous reports associating samaropsid seeds with *Eremopteris*. Additional frondlike structures with the same basic construction as the vegetative eremopterid leaves have been found; these offer information concerning the possible mode of attachment of the fertile organs.

POSTILLA 133: 14 p. 9 JUNE 1969.

INTRODUCTION

In his efforts to reconstruct plant life of the past, the paleobotanist is thwarted by the frequently fragmentary nature of plant remains in the rocks. It becomes essential to piece together these fragments into the proper whole by whatever valid means are available. Simple association of fragmentary plant parts in the fossil record cannot be used as definite proof that these parts were constituents of the same living plant. Obviously, the only conclusive proof involves organic connection or the demonstration that some peculiar or unique structural feature, such as that of the epidermis, is found in all the scattered parts. However, when associations occur with sufficient frequency, it is worth mentioning them and suggesting what the whole plant might have looked like if the pieces belong together.

Seward (1917, p. 170) figured a specimen of *Eremopteris artemisaefolia* (Sternberg) Schimper in close association with which are compressions of seedlike bodies referred to as *Samaropsis acuta* Kidson. This association was consistent enough for Seward to feel that the seeds were part of the plant that is known from these *Eremopteris* leaves. The seeds were flattened and bilaterally symmetrical, with two small distal hornlike projections.

Later Corsin (1928) described leaves like those of *Eremopteris zamioides* (Bertrand) Kidston from the Upper Westphalian of northern France. Associated with these fronds were fructifications that he assumed were part of the same plant that bore the leaves. Seeds, much like those figured by Seward (1917), were frequent, as were structures thought to be microsporangiate organs. These presumed microsporangia have small, radiating appendages, and look like small flowers. Parts of the foliage were also reported to have attached to them small, ovulelike structures in two rows along each pinna. These presumed ovulate structures, however, are immature and do not resemble the dispersed seeds. Corsin placed the entire assemblage into a new genus *"Pteridozamites"*, which he considered to be a pteridospermous plant.

Specimens of Carboniferous plants from Durham, England, in the Paleobotanical Collections of the Peabody Museum of Natural History include some *Eremopteris artemisaefolia*. On the same slabs, in close association with the leaf pieces, are bilaterally flattened seeds like those of *Samaropsis acuta* figured by Seward.

Thus, although nothing conclusive can be stated about the relationships of these vegetative and fertile plant parts, one is easily led to believe that very likely they belonged together, and that at least some species of *Eremopteris* were pteridospermous.

Description of New Material

Recent collections of Pennyslvanian plant compressions from northern Pennsylvania have further emphasized the possible relationship of platyspermic seeds and *Eremopteris* foliage. The material was collected in a strip mine about 4 km (2.5 miles) northwest of English Center, Lycoming County, Pennsylvania. The coal is thought to belong to the Allegheny Group and appears to be one of the easternmost outliers of that group in Pennsylvania. Plant fossils occur in a finely bedded gray shale that splits apart easily into thin sheets. Plant material is delicately preserved, although no cuticle appears to be present. Specimens are best examined submerged in xylene; photographs of the material included in this paper were taken in that fashion.

Common fossils at this site include *Sphenopteris obtusiloba* Brongniart and *S. spiniformis* Kidston, *Neuropteris heterophylla* Brongniart, *Lepidodendron obovatum* Sternberg, *Lepidostrobus* sp., and scattered *Lepidocarpon* megasporophylls.

Leaves of *Eremopteris* that closely resemble *E. zamioides* are extremely abundant. We believe that most of the specimens collected are entire leaves. They generally measure 14-20 cm in length; at the base of the rachis there seems to be a sharp line of abscission. Frequently, large numbers of these leaves are found closely aggregated, and all are extremely similar in general size and shape (Fig. 1). An alternative explanation of the abruptly truncated leaflike structures would be to regard them as pinnae of a much larger frond, the parts of which abscissed. Because most of the leaves found are the same size, and because it is difficult to visualize a pinnately constructed frond with pinnae identical throughout, we are inclined to regard these structures as entire fronds.

Pinnae are alternate to subopposite; the base of the rachis is generally naked, and lowest pinnae are smaller than the largest ones, which occur about half the distance up the rachis (Fig. 2). Largest pinnae may reach 5 cm in length. Pinnules are narrow

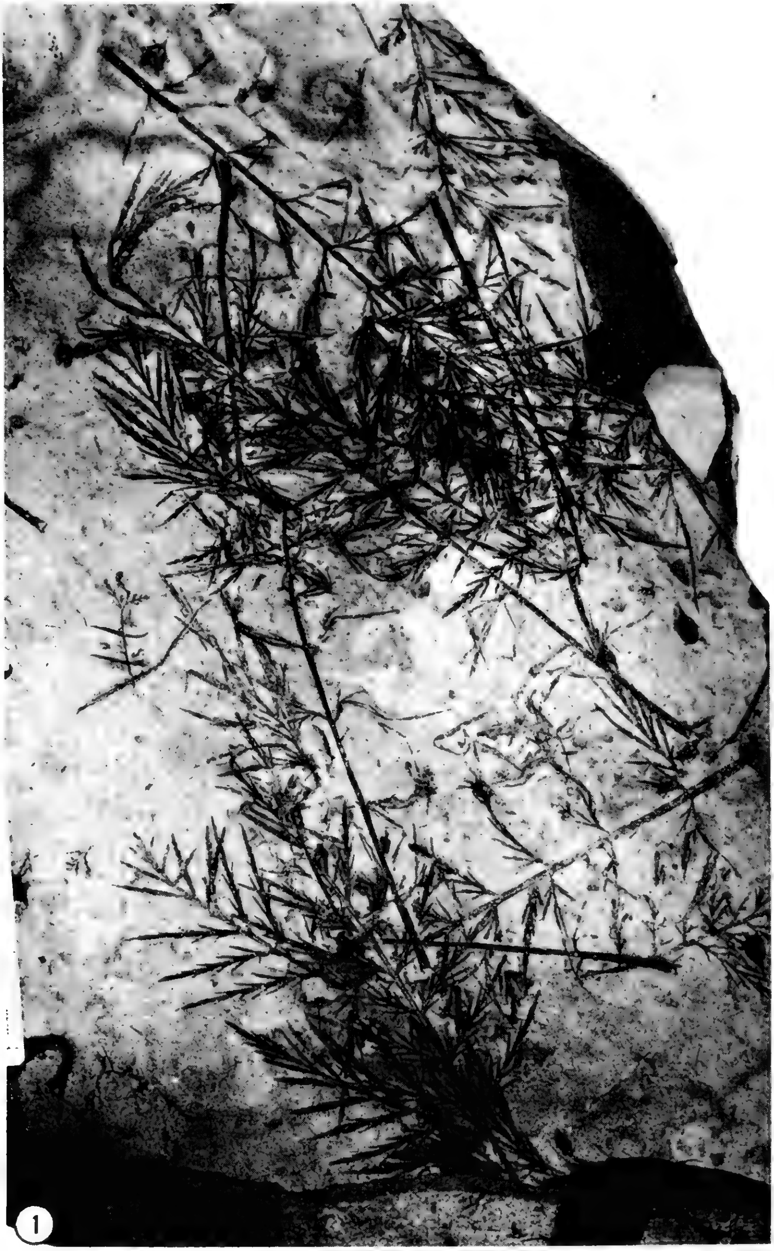


FIG. 1. *Eremopteris zamioides.* Slab with numerous leaves preserved. Intervals on scale at lower left are millimeters. YPM Paleobot. 1105. (Numbers refer to specimen numbers in the Paleobotanical Collections, Peabody Museum of Natural History)

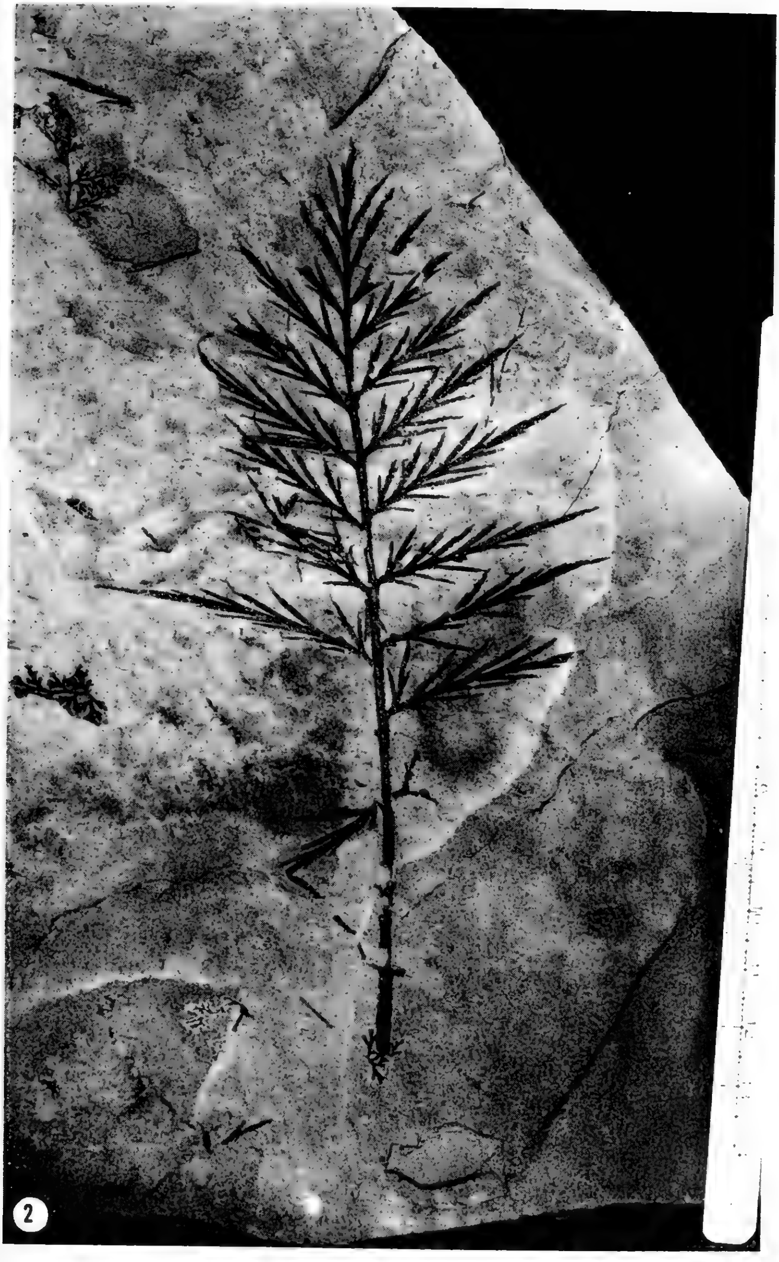


FIG. 2. *Eremopteris zamioides.* Nearly complete leaf. YPM Paleobot. 1106.

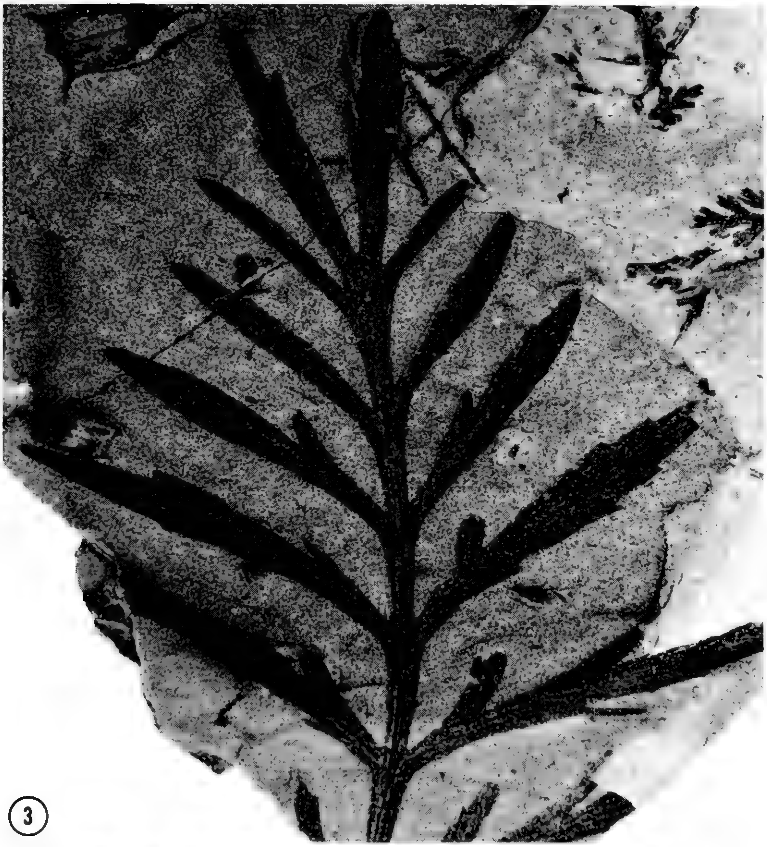
and incised; pinnae at the distal end of the frond may be entire or occasional ones may have some incising. Venation is the open dichotomous type characteristic of *Eremopteris,* with no apparent midvein in the pinnules (Fig. 3).

Seeds found in close proximity to the *Eremopteris* foliage are conspicuously flattened and bilateral, with two prominent distal spines (Figs. 4, 5). They are quite unlike *Samaropsis acuta* seeds and resemble somewhat the seeds called *Ptilocarpus bicornutus* by Lesquereux (1879, Pl. 85, fig. 51) and later (1880, p. 565) *Cardiocarpus bicornutus.* This seed material, described by Lesquereux as having coniferous affinities, originated in the shale above coal in Coshocton, Ohio. In many respects these seeds resemble the Lower Carboniferous genus *Lyrasperma* Long (1960) from Scotland.

Shape of the new seeds is highly variable, perhaps partly due to natural variation and partly to varying degrees of compression during fossilization. Furthermore, these different shapes may represent different ontogenetic stages. A central oval or elliptical portion, possibly representing the outline of the inner testa, is discernible on the compressed seeds. A flange, or wing, surrounds this central body, as in many species of *Samaropsis.* This wing, of course, could represent either a true flangelike extension of the integument, or it may simply be the flattened sarcotesta after compression. Proximally, the integument is extended into an acuminate process, the end of which represents the point of attachment. Length ranges from 10 to 15 mm, and width from 4 to 6 mm in the primary plane (not including the distance between the flaring distal projections). In many specimens a conspicuous line runs axially along each of the flat faces. These lines could represent vascular bundles, or they may reflect the fact that the integument may be composed of two symmetrical halves (as in *Lyrasperma*), with the lines on the flat faces representing sutures.

Generally the seeds are in the form of thin, carbonaceous films, but rarely a megaspore membrane is present. One such seed (Fig. 6) had split along the major plane of symmetry exposing the spore membrane.

Possible microsporangiate organs associated with the foliage and seeds are similar to those decribed by Corsin (1928) for his *"Pteridozamites"* material. They are always found detached, most



③

④

FIG. 3. *Eremopteris zamioides.* Terminal part of a leaf showing detail of venation. × 1.9. YPM Paleobot. 1107.

FIG. 4. Platyspermic seeds with distal hornlike projections and acuminate proximal region. × 1.3 YPM Paleobot. 1108.

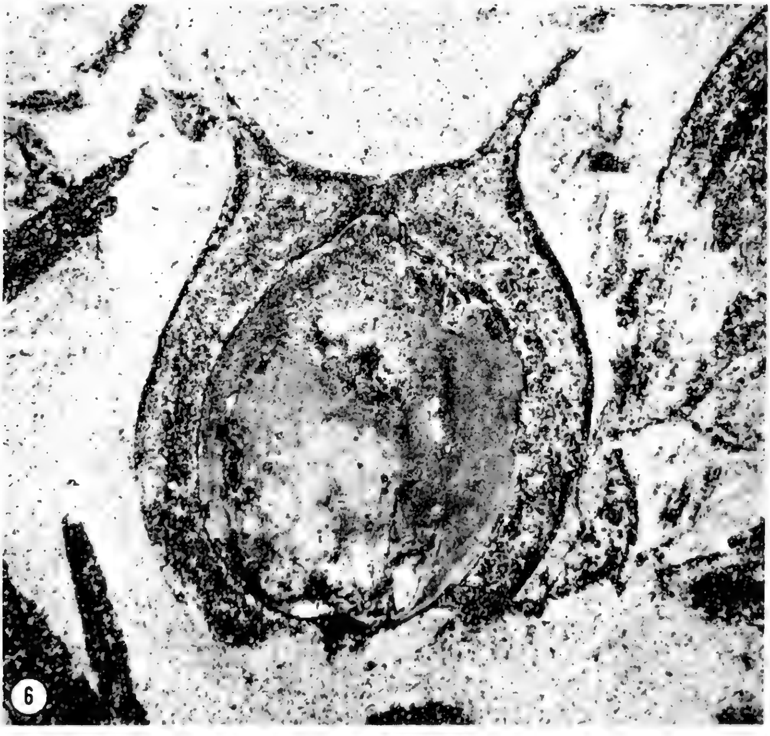


FIG. 5. Platyspermic seeds in close association with a frond of *Eremopteris zamioides*. × 1.3. YPM Paleobot. 1109.

FIG. 6. Seed split along the primary plane to reveal the central megaspore membrane. × 11.5. YPM Paleobot. 1110.

likely after having shed pollen, scattered over the bedding plane surfaces, generally in clusters. In their mature state they look somewhat flowerlike or star-shaped, probably the result of a capsulate structure having split open at the time of pollination (Fig. 7). Maceration of these presumed fructifications, unfortunately, yielded no pollen grains.

If the associated plant parts described above are, indeed, detached organs of the same plant, we should suggest possible means of attachment, and what the entire plant might have looked like. Obviously, if the plant was actually a pteridosperm, by definition the reproductive structures must have been borne on leaves. There is nothing about the eremopterid foliage described thus far that indicates the possible mode of attachment. Very significant, however, are additional foliar structures, again in close association with the other parts, that are generally smaller than the typical vegetative leaves, but that have the same kind of construction, that is, a main rachis with pinnately borne laterals, oppositely or suboppositely arranged. On these laterals (pinnae) are short stubby projections that seem to be abruptly truncated as if representing structures from which some other bodies had fallen off (Figs. 8, 9). It is on just such structures that the seeds and pollen-bearing organs could have been borne. Furthermore, there appear to be at least two sizes of these presumed fertile leaves; the larger (up to 13 cm in length) could conceivably have represented the megasporophylls, while the smaller (generally about 5 cm long) could be microsporophylls. It might be argued that these presumed fertile leaves are actually immature vegetative fronds, and that subsequent development would have resulted in differentiation into the more typical eremopterid frond form. In the same beds, however, are specimens that are obviously immature fronds (Fig. 10), and in spite of their relatively young age they are conspicuously different from the probable fertile leaves and actually have much in common with the fully mature adult vegetative leaves.

RECONSTRUCTION

From these various parts, it is tempting to envisage a pteridospermous plant, perhaps not too tall, with eremopterid foliage borne on the stem. We conclude that these plants were deciduous, dropping the leaves in their entirety, although not necessarily at seasonal intervals. In most plants with fernlike leaves the fronds generally wither and shrivel before falling from the stem. These eremopterid leaves, on the other hand, appear to be little distorted, nicely flattened, with an abrupt truncation at the base of the rachis. Thus, the lower part of the plant would be naked, with functional foliage at higher levels. Elsewhere on the plant there may have been modified leaves, with the same structural plan as that in the vegetative leaves, but much reduced and bearing either microsporangia or seeds. A possible reconstruction of such a plant is presented in Figure 11. It must be emphasized, however, that this drawing represents only one of the several possible, logical combinations of the various structures.

Nomenclature

If, indeed, all of these parts are thought to belong to the same kind of plant, a single specific name should be used for the entire assemblage. Corsin considered his diverse plant fragments to represent portions of a single species to which he applied the name *"Pteridozamites" zamioides* P. Bertrand. However, for a number of reasons, this move cannot be accepted. First, there is no generic diagnosis in Corsin's paper for *P. zamioides,* hence the generic name is invalid. A second reason for rejecting the combination *P. zamioides* P. Bertrand is that Bertrand did not institute the name. Third, Corsin had no more evidence than we do that all of these parts are pieces of the same plant. As mentioned above, one is tempted to believe that because of their constant association all the separate parts logically belong to the same plant, but more concrete evidence must be at hand to prove the connection. If our new material consisted of remains only of the parts described in this paper, then it would be more certain that these parts are all from the same kind of plant. There is an abundance of other remains, however, including sphenopterid leaves, so there is also the possibility that the seeds and microsporangia were borne on leaves of that type. For that reason we have not formally assigned all of the parts to one name.

Discussion

Since we are not willing to agree with Corsin's assigning the various isolated parts of his material to a single name on the

FIG. 7. Possible microsporangiate structures. ×3.3. YPM Paleobot. 1111.

FIG. 8. Possible microsporophyll, natural size. YPM Paleobot. 1112.

FIG. 9. Possible megasporophyll, natural size. YPM Paleobot. 1113.

FIG. 10. *Eremopteris zamioides.* Two immature vegetative fronds. Natural size. YPM Paleobot. 1114.

FIG. 11. Suggested reconstruction of a pteridospermous plant with eremopterid leaves and fertile structures such as those described in this paper.

grounds that the parts were not actually attached, we must justify our presumption in presenting the reconstruction in this paper. Certainly we are agreed that association in itself must be approached with caution. On the other hand, this is not the first time that the conspicuous association of platyspermic seeds with eremopterid foliage was noted. Reports by previous authors, together with this one, add up to evidence that cannot be dismissed lightly.

There is considerable precedent for the attachment of seeds to fernlike foliage in the Paleozoic. White's (1904) *Wardia fertilis* is an example of flattened seeds attached to foliage similar to that of *Adiantides. Emplectopteris triangularis* (Halle, 1927) is another example of platyspermic seeds borne on fernlike foliage, although in that case, seeds were borne on laminar surfaces. There are numerous other instances of seeds borne on foliage, but in most of the other reports, the seeds were radially symmetrical.

If such a plant as that suggested in our reconstruction did exist, what are its affinities? Platyspermic seeds are generally thought to be conifer-related, but the structure of eremopterid foliage is certainly far from a coniferophytic leaf morphology. Actually, bilaterally symmetrical seeds are an early type, having been reported by Long (1960) in the lower Carboniferous of Scotland. The fragments of axes on which are borne the various seeds with which Long worked are typically leafless, making it tempting to suspect that in some seed plants, at least, the seeds evolved *before* the appearance of leaves. If such is the case, it would be impossible to categorize these Mississippian plants as coniferophytes or pteridosperms. Eggert and Delevoryas (1960) suggested that bilateral symmetry of seeds need not be a reflection of natural affinities. *Conostoma* Williamson, a pteridosperm genus based on seeds with generally radial symmetry includes one species — *C. platyspermum* (Graham, 1934) — that is bilaterally flattened. Thus, platyspermic samaropsid seeds need not be considered uniquely coniferophytic, and their probable presence on eremopterid leaves need not be considered anomalous.

As work progresses on late Paleozoic and early Mesozoic pteridosperms, one cannot help but be impressed with the tremendous diversity of leaf types, seed structure, pollen-bearing organs, and vegetative anatomy. It is becoming increasingly obvious that the class Pteridospermopsida (or other nomenclatural equivalent) may ultimately be separated into a number of independent groups. Much parallel evolution of seed plants must have occurred during the Paleozoic, resulting in a number of groups of plants with fernlike foliage on which were borne seeds and pollen-bearing structures. The old class "Gymnospermae" has been shown to be an artificial assemblage (Arnold, 1948) with naked seeds being the only important feature in common. Similarly, we feel that before long the pteridosperms as they are now known cannot be held together as a natural entity solely by the character of seeds borne on fernlike foliage.

ACKNOWLEDGMENTS

We are grateful to Miss Ward Whittington for her rendition of Figure 11. Research for this project was supported by National Science Foundation grant GB-5911X to T. D. and grant GB-6834 to T. N. T.

LITERATURE CITED

Arnold, C. A. 1948. Classification of gymnosperms from the viewpoint of paleobotany. Bot. Gaz. **110**: 1-12.

Corsin, P. 1928. Sur les fructifications et la position systématique de *Sphenopteris zamioides* P. Bertrand. Ann. Soc. Geol. Nord **53**: 222-230.

Eggert, D. A., and Delevoryas, T. 1960. *Callospermarion* — a new seed genus from the Upper Pennsylvanian of Illinois. Phytomorphology **10**: 131-138.

Graham, R. 1934. Pennsylvanian flora of Illinois as revealed in coal balls. I. Bot. Gaz. **95**: 453-476.

Halle, T. G. 1927. Paleozoic plants from central Shansi. Geol. Surv. China, Palaeont. Sinica, Ser. A, **2** (Fasc. 1): 1-316.

Lesquereux, L. 1879. Atlas to the coal flora of Pennsylvania and of the Carboniferous Formation throughout the United States. Second Geol. Surv. Pennsylvania: Rept. of Progress. 18 p., 85 pls.

———— 1880. Description of the coal flora of the Carboniferous Formation in Pennsylvania and throughout the United States. Vol. **2**, p. 355-694. Second Geol. Surv. Penn.: Rept. of Progress.

Long, A. G. 1960. On the structure of *Samaropsis scotica* Calder (emended) and *Eurostoma angulare* gen. et sp. nov., petrified seeds from the Calciferous Sandstone series of Berwickshire. Trans. Roy. Soc. Edinburgh **64**: 261-280.

Seward, A. C. 1917. Fossil plants. Vol. **3**. Cambridge Univ. Press. 656 p.

White, D. W. 1904. The seeds of *Aneimites*. Smithsonian Misc. Coll. **47**: 322-331.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

MENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

LUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

HOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 134. 9 JUNE 1969.

COMMENTS ON THE AVIFAUNA OF TANZANIA, II

S. DILLON RIPLEY
GERD H. HEINRICH

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

COMMENTS ON THE AVIFAUNA OF TANZANIA, II

S. DILLON RIPLEY
Smithsonian Institution, Washington, D.C.

GERD H. HEINRICH
Dryden, Maine

ABSTRACT

Buccanodon olivaceum ulugurensis and *Viridubucco leucomystax meridionalis* (both Capitonidae), new subspecies, are described on the basis of morphological characters. Evidence is presented that *Dendropicos fuscescens* (Vieillot) and *Dendropicos lafresnayi* Malherbe (=*D. f. lafresnayi* Malherbe) are distinct taxa. The distribution of *Smithornis capensis* (Smith) is redefined based on an examination of a large series of specimens from eastern Africa. *Smithornis capensis meinertzhageni* van Someren, *S. c. suahelicus* Grote, *S. c. shimba* van Someren, and *S. c. chyulu* van Someren are reinstated as valid subspecies and a key to their identification is given. *Macrodipteryx longipennis* (Shaw) is recorded as new to Tanzania. New records of *Modulatrix stictigula stictigula* (Reichenow) from the Uzungwa Plateau show that this subspecies has a disjunct range in south-central Tanzania. Species and subspecies representing extensions of geographic range in Tanzania are *Caprimulgus poliocephalus* Rüppell, *Tricholaema lacrymosum lacrymosum* Cabanis and *T. l. ruahae* Neumann. Field data from specimens of *Alethe fulleborni* (Reichenow) reveal that the breeding season coincides with the rainy season, October to March. Call notes and behavior of this species, based on field observations, are also recorded.

POSTILLA 134: 21 p. 9 JUNE 1969.

INTRODUCTION

This paper discusses additional noteworthy material from the collection originally described in *Postilla* no. 96, 1966. The collection was procured by the junior author, his wife, and their son, Bernd Heinrich, for the Peabody Museum of Natural History in 1961-63 in Tanzania. For collecting stations, chronology and map see pages 1-3 of the earlier publication.

The following abbreviations are used to identify the institutions from which specimens were examined: AMNH—American Museum of Natural History, New York, N.Y.; YPM—Peabody Museum of Natural History, Yale University, New Haven, Conn.; and USNM—U.S. National Museum, Washington, D.C.

ANNOTATED LIST

Caprimulgus poliocephalus poliocephalus Rüppell

MATERIAL. 3 ♂ adults, YPM 79209-11, eastern and southern slopes of Mt. Meru, 1500-2000 m alt., northern Tanzania, 16 June — 17 July, 1962. 1 ♀ adult, YPM 79212, Livingstone Forest Reserve, 32 km southeast of Mbeya, 2600 m alt., southwestern Tanzania, 11 Nov. 1962.

MEASUREMENTS. Wing: males, 144-155 (149.3) mm; female, 150 mm. Weight: males, 39-47.5 g; female, 23 g.

RANGE IN EASTERN AFRICA. Ethiopia, southeastern Sudan and Kenya to northern Tanzania (Mackworth-Praed and Grant, 1952; White, 1965).

BREEDING. 16 June: 1 ♂ with gonads distinctly enlarged, Mt. Meru. 11 Nov.: 1 ♀ on nest with two eggs, Livingstone Forest Reserve.

HABITAT. The nest in the Livingstone Forest was found in a bare clearing between two patches of forest in a stand of scattered Eagle-ferns *(Pteridion).*

REMARKS. We are not able to distinguish the female from the far southwestern part of Tanzania from the series of males from Mt. Meru, except by the normal sexual dimorphism evident in the restriction of white on the two exterior rectrices to their apices.

Macrodipteryx longipennis (Shaw)

MATERIAL. 1 ♀ adult, YPM 79213, Ufipa Plateau, near Sumbawanga, 2200 m alt., southwestern Tanzania, 6 Dec. 1962. 1 ♂ juvenal, YPM 79214, near Mbeya, 2000 m alt., southwestern Tanzania, 24 Dec. 1962.

MEASUREMENTS. Wing: female adult, 172 mm; male juvenal, 184 mm. (This is the maximum length as recorded by Mackworth-Praed and Grant, 1952.)

RANGE IN EASTERN AFRICA. The Sudan, Eritrea and Ethiopia to Uganda and western Kenya; but in non-breeding season a migrant only to central Sudan from Darfur to Kassala and northern Ethiopia (Mackworth-Praed and Grant, 1952).

REMARKS. The above records are apparently new for Tanzania and extend the limits of the distribution by about 1000 km to the south.

Buccanodon olivaceum ulugurensis, new subspecies

HOLOTYPE. ♂ adult, YPM 79050, Uluguru Mts., eastern Tanzania, 16 Dec. 1961, collected by Gerd Heinrich, original field no. 31908.

MATERIAL. 2 ♂ adults, 1 ♀ adult, YPM 79215-17, Uluguru Mts., eastern Tanzania, 1500-1800 m alt., 29 Nov. — 14 Dec. 1961. 1 ♂ adult, USNM 325600, Uluguru Mts., 14 Sept. 1928.

MEASUREMENTS. Wing: males, 89-93 (91.8) mm; female, 89 mm. Weight: males, 53-58 g.

DESCRIPTION. Compared with 21 specimens of *Buccanodon olivaceum olivaceum* (Shelley) from eastern Kenya and Tanzania (YPM 79218-24 and USNM 519347-60), this new subspecies has the upperparts paler and more yellowish olive. The underparts lack the faint suffusion of gray on the chest. The sides of neck, flanks and ear coverts have a faint yellowish wash. The cap is also lighter and more brownish, less blackish, than is that of *B. o. olivaceum.* Compared with three specimens of *B. o. rungweensis* Benson from southwestern Tanzania (YPM 79225-27), *B. o. ulugurensis* lacks the decidedly gray throat and breast of the former subspecies, and the coloration of the upperparts is a more subdued, less intense olive green. We have not seen *B. o. belcheri* Sclater from Malawi and Mozambique, but the subspecific characters described by Mackworth-Praed and Grant (1952): ". . . whole head and neck to chest black, washed with bronze and green . . ." do not apply here. The measurements indicate that the new subspecies has a wing length similar to that of *B. o. olivaceum* and *B. o. rungweensis.* The wing is shorter, however, than that of *B. o. belcheri,* which, according to Mackworth-Praed and Grant (1952), is 94-97 mm.

RANGE. Known presently only from the Uluguru Mountains in eastern Tanzania.

ETYMOLOGY. The new subspecies' name is a Latinized word meaning "belonging to the Ulugurus."

Viridibucco leucomystax meridionalis, new subspecies

HOLOTYPE. ♂ adult, YPM 79051, Mdando Forest, Livingstone Mts., 48 km south of Njombe, southwestern Tanzania, 16 Oct. 1962, collected by Gerd Heinrich, original field no. 35526.

MATERIAL. 2 ♂ adults, 1 ♀ adult, YPM 79228-30, Mdando Forest, 48 km south of Njombe, southwestern Tanzania, Oct. 1962.

MEASUREMENTS. Wing: males, 55-57 (56) mm; female, 58 mm. Weight: males, 11-12.5 g; female: 14.5 g.

DESCRIPTION. Underside, particularly the belly and flanks, darker and grayer than that of *V. l. leucomystax* (Sharpe) and almost entirely lacking the light greenish tinge found in 17 examples of the nominate race from the mountains of northern and eastern Tanzania, i.e., Mt. Meru and the Paré, Uluguru and Usambara Mts. (YPM 79231-47).

RANGE. Presently known only from the Mdando Forest, Livingstone Mountains, southwestern Tanzania.

REMARKS. The Mdando Forest is an isolated patch of high mountain cloud-forest, covering the southern end of the Livingstone Mountains. It represents the most southern island of this type of habitat in Tanzania. Specimens of *Viridibucco leucomystax* (YPM

79248-51) collected farther north, in the Rungwe Mts. and Dabaga highlands, are somewhat intermediate between *V. l. meridionalis* and *V. l. leucomystax.*

ETYMOLOGY. The new subspecies name is a Latin word meaning "southern" and is proposed here to designate the particular location of the bird's habitat, which is the southernmost of its kind in Tanzania.

Tricholaema lacrymosum lacrymosum Cabanis

MATERIAL. 3 ♂ adults, 2 ♀ adults, 1 ♀ juvenal, YPM 79252-57, Morogoro, eastern Tanzania, 1 — 9 Feb. 1962. 2 ♂ adults, 3 ♀ juvenals, YPM 79258-62, Same, south of Paré Mts., northern Tanzania, 25-28 May 1962. 1 ♂ adult, YPM 79263, southern foot of Mt. Meru (near the Usa River), northern Tanzania, 12 June 1962.

MEASUREMENTS. Wing: Males, 68-70 (69) mm; females, 65-70 (68.1) mm. Weight: males, 25.5 — 27 g; females, 24.5-25.8 g.

RANGE IN EASTERN AFRICA. Southern Sudan, northern Uganda and Kenya (except southwestern), to east central Tanzania as far west as North Paré Mts. and Morogoro (Mackworth-Praed and Grant, 1952).

REMARKS. The localities from which our specimens were taken agree with the distribution of this subspecies as given above, except that we would extend the range slightly to the west in northeastern Tanzania to include Mt. Meru. Birds from that area are presently allocated to the subspecies *T. l. radcliffei* O. Grant, by these authors. Our specimen, however, agrees with the nominate subspecies in having drop-shaped black markings on the flanks, rather than the round ones that are diagnostic of *radcliffei.*

Tricholaema lacrymosum ruahae Neumann

MATERIAL. 2 ♂ adults, 1 ♀ adult, YPM 79264-66, Chimala (77 km east of Mbeya), southwestern Tanzania, 5 — 13 Jan. 1963. 4 ♂ adults, 4 ♀ adults, YPM 79267-74, Iringa, southcentral Tanzania, 22 Aug. — 2 Sept. 1962. 2 ♂ adults, 3 ♀ adults, YPM 79275-79, Lake Manyara, western slope of Rift Valley, northern Tanzania, 2 — 4 Aug. 1922.

MEASUREMENTS. Wing: males and females, 68-75 (69.1) mm. Weight: males, 25.5-27.5 g; females: 23-26 g.

RANGE IN EASTERN AFRICA. Tanzania from Ufipa, Kahama, Shinyanga, Mt. Gerui (Hanang), and Dodoma to the Rovuma River (Mackworth-Praed and Grant, 1952; White, 1965).

REMARKS. The range given here may be extended 325 km. to the north, based on our specimens from Lake Manyara.

THE TAXONOMIC HISTORY OF DENDROPICOS FUSCESCENS AND D. LAFRESNAYI

Few African birds are taxonomically so puzzling (and therefore so interesting) and have caused so many controversial opinions among taxonomists as the two woodpeckers *Dendropicos fuscescens* (Vieillot) and *Dendropicos lafresnayi* Malherbe. The two names stand as the oldest ones for two groups of numerous subspecies, at present all considered to represent one and the same species (*fuscescens* Vieillot), distributed over almost the entire African continent. *D. fuscescens* represents forms with clearly black or blackish, white-barred mantles. *D. lafresnayi* represents forms with dark olive-green mantles with only faintly indicated or obsolescent barring. A short review of only the most important steps in the taxonomic consideration of these two groups, arranged in historical sequence, reveals the following picture:

Friedmann (1930, p. 483): "The whole question of the distinction of *fuscescens* and *lafresnayi* is exceedingly involved. If it did not happen that two forms occurred side by side in various places in south and east Africa, the two might readily be considered one species . . . It is necessary to use two binomials for the present . . ."

Bannerman (1933, p. 441, footnote): "The *fuscescens* and *lafresnayi* groups may have to be united under the former name, as Dr. Chapin has suggested."

Lynes (1934, p. 68): "The case for two different species appears to be derived from the idea that somewhere in equatorial east and in south Africa two different colored aggregates are found on the same ground . . . I can see among the adults from the whole of the eastern side of the continent no evidence of there being more than the one species, viz. *fuscescens* . . . It looks not unlikely to be the same species *fuscescens,* which ranging westward from Kenya Colony with decreasingly barred, more mottled, back pattern, extends to west Africa, where the back pattern is practically a plain one and the form is *lafresnayi* . . ."

Someren (1939, p. 48-50) proves that the two groups are geographically widely interdigitated in east Africa, but are ecologically differentiated. He nevertheless concludes: "It appears reasonable that we are dealing with one species."

Chapin (1939, p. 579): "It has long been evident that *hartlaubi* and *lafresnayi* are not specifically distinct from *fuscescens,* and at last Admiral Lynes and Jack Vincent have arrived at this point of view . . . In southern and eastern Africa the back is boldly barred, toward the Congo this barring becomes weaker, and in Upper Guinea it practically disappears. The color of the back becomes greenish, too, in west Africa."

Peters (1948, p. 176) treats *lafresnayi* as a subspecies of *fuscescens.*

From then on the specific unity of *lafresnayi* and *fuscescens* is considered to be an established fact in ornithological literature, and White (1965) merely states that " there is much difference of opinion as to the number of forms worthy of recognition."

Dendropicos fuscescens hartlaubi Malherbe

MATERIAL. 3 ♂ adults, 2 ♀ adults, 1 ♀ juvenal, YPM 79280-85, Dar-es-Salaam, eastern Tanzania. 23 Oct. — 5 Nov. 1961. 1 ♂ adult, YPM 79286, Uluguru Mts., eastern Tanzania, 3 Jan. 1962. 1 ♂ adult, YPM no. 79287, Njombe, southwestern Tanzania, 19 Oct. 1962.

MEASUREMENTS. Wing: males, 85-88 (86) mm; females, 85-86 mm.

DESCRIPTION. One immature female from Dar-es-Salaam, 2 Nov. 1961, has the top of the head red, similar to the male. Lynes (1934) has already recorded several young females with the same plumage, mentioning that this may perhaps be the normal color of the young female. Mackworth-Praed and Grant (1952) do not record this plumage of the young female. Nevertheless, it is probably normal.

RANGE IN EASTERN AFRICA. Central and eastern Kenya to the Zambesi River, also Zanzibar Island (Mackworth-Praed and Grant, 1952). White (1965) includes Mozambique, Malawi, Zambia, Rhodesia, northern Botswana, Angola except northwest, Katanga to Kwango and Lualaba, Tanzania and southeast Kenya in the range of this form.

REMARKS. We are attributing the populations of almost the whole of Tanzania to the subspecies *hartlaubi* (described from Zanzibar) in accordance with Lynes (1934) and with Mackworth-Praed and Grant (1952). According to the latter authors, the range of this subspecies also comprises central and eastern Kenya. Our material indicates, however, that specimens from extreme northeastern Tanzania are well differentiated from *hartlaubi* in color as well as in size. They are consequently attributed to other subspecies as follows.

Dendropicos fuscescens hemprichi (Ehrenberg)

MATERIAL. ♀ adult, YPM 79288, Same, northeastern Tanzania, 26 May 1962. ♀ adult, YPM 79289, Mt. Meru (near Usa River) northern Tanzania, 17 June 1962. ♀ adult, YPM 79290, Mt. Meru (near Engare Namyuki) northern Tanzania, 19 July 1962. 2 ♂ adults,1 ♀ adult, USNM 519416-18, Sokoke Forest, eastern Kenya, 2-4 Dec. 1964.

MEASUREMENTS. Wing: 80-82 (81.3) mm. Weight: 21-27 g.

RANGE IN EASTERN AFRICA. Eritrea, central and southern Ethiopia and the Somalis to north-eastern Kenya, as far south as the Lorian Swamp (Mackworth-Praed and Grant, 1952). White (1965) lists range in Kenya as ". . . north Kenya west to Marsabit and south to Tana River."

REMARKS. The specimens listed above differ from *D. f. hartlaubi* by their distinctly smaller size and by a total lack of yellowish wash on underparts. In the specimens from Sokoke Forest the mantle is barred black and white and also lacks completely the yellowish wash characteristic of *hartlaubi;* the specimen from Same is identical with the ones from Sokoke Forest. In all four specimens from the latter area the innermost secondaries are conspicuously white-barred and the lesser and median wing coverts are apically conspicuously white-spotted, both characters also distinguish them at the first glance from *hartlaubi.* In the two birds from south and north of Mt. Meru the mantle shows a faint, scarcely perceptible, olive-yellowish tinge. They are thus intermediate between *D. f. hemprichi* and *D. f. massaicus* Neumann.

Dendropicos lafresnayi lepidus (Cabanis and Heine)

MATERIAL. 2 ♂ adults, 4 ♀ adults, USNM 519427-32, Kakamega Forest, 2100 m alt., western Kenya, 20-22 March, 7 June and 4-16 Dec. 1965. 2 ♂ adults, 1 ♀ adult, USNM 519419-21, Kiptogot Forest, northeast Mt. Elgon, 2600 m alt., western Kenya, 27-29 April, 1965. 3 ♂ adults, 2 ♀ adults, USNM 519422-26, nr. Kapenguria, W. Pokot, W. Cherangani Mts., 2300 m alt., western Kenya, 18 May-21 June 1965. 1 ♂ adult, 1 ♀ adult, 1 ♀ juvenal, YPM nos. 79291-93, eastern Usambara Mts., 500-1150 m alt., northeastern Tanzania, 28 March-13 April 1962.

MEASUREMENTS. Wing: 82-89 (85.5) mm. Weight: 20-31 g.

DESCRIPTION. All specimens listed above belong clearly to the green-backed group of subspecies, the mantle being olive-green with indistinct to obsolescent barring. They also differ from *Dendropicos fuscescens hemprichi* (Ehrenberg) by larger size, distinctly yellowish-green tinged chest and belly and by less extensive and not clear white but olive-tinged barring of innermost secondaries.

RANGE IN EASTERN AFRICA. Western Ethiopia, southern Sudan, Uganda and western Kenya (Mackworth-Praed and Grant, 1952). White (1965) includes Kenya only west of the Rift, and northeast Congo from Lake Albert to Kivu.

REMARKS. These new records from the eastern Usambara Mts. (near Amani; Ugambo and Muheza) extend the range of the green-backed forms far to the east, almost to the east coast of Africa. In addition, our new records of the smaller form with black-and-white-barred mantle, *D. f. hemprichi,* from semiarid regions, interspersed between the ranges of the green-backed ones, confirms the ecological separation of the two groups in East Africa, beyond a shadow of doubt. The question is only which conclusion and which taxonomic consequence should be drawn from this fact. Friedmann (1930) concluded that ". . . it is necessary to use two binomials . . .". Someren (1939), after having meticulously explained that the separation of the two groups of forms is ecological rather than geographical, concluded: "It appears reasonable that we are dealing with one species."

On the evidence that both groups of forms are transcontinental, but are ecologically differentiated in such a way that the one occurs only in dry or semiarid regions, the other in areas with denser and moister forests, we are convinced that *Dendropicos fuscescens* and *Dendropicos lafresnayi* should be considered distinct species. The case is a perfect parallel to the one of *Prodotiscus zambesiae* Shelley and *P. insignis* Cassin, as treated previously by Ripley and Heinrich (1966a), in which a green-backed form *(P. insignis)* and a non-green backed form *(P. zambesiae)* were ecologically separated and their ranges interdigitated where the two different habitats were interspersed. In the case of *Dendropicos* the two forms are each also geographically slightly differentiated. To treat all the green-backed together with the dorsally white-and-black-barred subspecies as subspecies of one and the same species would hide the underlying facts and confuse the issue. Geographical subspecies would be mixed on the same level with so-called ecological ones, the mere subspecific status of the latter being highly hypothetical and doubtful.

It should be added that the collection of the U.S. National Museum contains broad series of *Dendropicus fuscescens hemprichi* from many localities in the Ethiopian mountains, but not a single green-backed form from that area. On the other hand, *Dendropicos lafresnayi lepidus,* was clearly described (Cabanis and Heine, 1863, p. 118) as a green-backed form by the words "supra subflavido-olivaceo-virescens." The fact that in the Ethiopian mountains black-and-white-backed and green-backed forms are interspersed is proven beyond doubt by the material in the American Museum of Natural History, which contains numerous black-and-white-backed specimens from Ethiopia and a number of green-backed as well. In all probability, the separation of the two forms in Ethiopia is ecological, as is already noted above for east-central Africa. The mountains of Ethiopia would probably be the area where the problem of the two forms could best be studied and solved.

Campethera abingoni smithii Malherbe

MATERIAL. ♂ juvenal, 1 ♀ adult, YPM 79294-95, Chimala, southwestern Tanzania, 3 Jan. 1962 and 13 Jan. 1963. 1 ♀ adult, YPM 79296, Ufipa Plateau, southwestern Tanzania, 3 Dec. 1962. 1 ♀ adult, YPM 79297, Abercorn, Zambia, 14 Dec. 1962.

MEASUREMENTS. Wing: 115-120 (117) mm. Weight: ♀ adult 70 g.

REMARKS. Clancey (1965, 1967) wishes to change the name of this subspecies by making it an absolute synonym of the nominate form, *abingoni,* which he points out should have its type locality corrected from "Durban, Natal" to the Zeerust district of the western Transvaal. White (1967) disagrees, pointing out that the original description by Smith was somewhat equivocal, as in a footnote the describer mentioned having encountered this woodpecker at "Port Natal" (=Durban). For the time being we would prefer to adhere to the present tradition of having *C. a. smithii* Malherbe recognized as the form we are dealing with in southwest Tanzania, and typical *C. a. abingoni* (Smith) of the coastal area of Natal as the form ranging north through eastern Transvaal to Mozambique. In this particular case we would prefer to preserve the status quo, *mutatis mutandis.*

The specimens we collected differ strongly from *Campethera abingoni abingoni* by (1) the black color on throat and breast prevailing over the white (instead of white, streaked black), (2) lack of yellowish wash on chest and belly, and (3) darker and duller basic color of dorsal side, with less distinct green tinge. They should be attributed to the subspecies *C. a. smithii,* the range of which thus extends from Angola, Rhodesia and Zambia northward into southwestern Tanzania. This fact has already been published by Lynes (1934) but was ignored by Mackworth-Praed and Grant (1952), who include most of Tanganyika from Mt. Kilimanjaro, Kilosa, Pugu Hills and Ufipa

Plateau to Mozambique in the range of *C. abingoni abingoni.* Lynes (1934) has recorded *smithii* as far west as Iringa, and White (1965) lists "west Tanzania from Ufipa to Kigoma."

COMMENTS ON THE SUBSPECIES OF SMITHORNIS CAPENSIS

Mackworth-Praed and Grant (1952) acknowledge only two subspecies of *Smithornis capensis* (Smith) in East Africa (Kenya, Tanzania and Mozambique): *Smithornis capensis capensis* (Smith) to which they attribute a wide range from southeastern South Africa north to southeastern Kenya, and *S. c. medianus* Hartert and van Someren ranging over Kenya and Tanzania (except western and coastal areas) as far east as the Uluguru Mts. and as far south as fifty miles south of Dar-es-Salaam. The subspecies *meinertzhageni* van Someren 1919, *suahelicus* Grote 1926, *shimba* van Someren 1941, and *chyulu* van Someren 1941 have all been synonymized by these authors, although not by White (1961). Our series at hand from Kenya and Tanzania show that these two countries are inhabited by at least four, perhaps five, subspecies distinguished either by color or by size. These are *S. c. medianus, meinertzhageni, suahelicus,* and *shimba.* The subspecies *chyulu* has been tentatively maintained in the following key although its validity has been questioned by Peters (1948) and denied by Mackworth-Praed and Grant (1952) and Clancey (1963). Topotypes of this form from the Chyulu Mts., Kenya, have not been available to us for examination. Based on the material we have examined from coastal Tanzania and southeastern Kenya, we are unable to support the contention of Mackworth-Praed and Grant (1952) and White (1961) that the nominate subspecies *S. c. capensis* is the resident form in these areas. It is apparently restricted to South Africa and includes perhaps southern Mozambique, but is replaced in northern Mozambique and eastern Tanzania by a considerably smaller subspecies, *suahelicus.*

We propose to divide the east African populations of *Smithornis capensis* as follows:

Central Kenya and northern Tanzania at the foot of Mt. Meru and of Mt. Kilimanjaro (and perhaps also the area east of Mt. Meru), are inhabited by a large form, *Smithornis capensis medianus.* From the coastal belt of southeastern Kenya to the northern part of Mozambique, the large *medianus* is replaced by small forms with a wing length below 70 mm. Among these small forms the population of coastal southeastern Kenya appears to be well distinguished in color pattern and is called *shimba*. Specimens from eastern Tanzania south to about Beira, Mozambique, are tentatively united as *suahelicus*. A third, very distinct, small subspecies, equal in size to *shimba* and *suahelicus*, but quite different in color from the two, lives on the western fringes of the highlands of central Kenya, east of Lake Victoria. This is *meinertzhageni*. The range of this subspecies may extend to western Uganda (Toro District), although the only specimen (AMNH) examined from there has a wing a trifle larger than the average for that subspecies.

KEY TO EAST AFRICAN SUBSPECIES OF SMITHORNIS CAPENSIS

1. Size smaller. Wing 66-69 mm (in female black streaks on cap well discernable) 2

   Size larger. Wing 70-78 mm (in females black streaks on cap denser, often rendering cap predominantly blackish) . 4

2. Chest, breast (including sides) and flanks heavily, extensively and densely streaked black, extent of black color on these parts almost equal to extent of basic light color; mantle, shoulders and back dark-brown, heavily streaked and mottled with black; cheeks blackish . . . . *S. c. meinertzhageni*

   Chest, breast and flanks much more sparsely and more finely streaked black, extent of basic light color clearly prevailing over extent of black color; mantle, back and shoulders light brownish or brownish gray, sparsely and on shoulders indistinctly streaked with black, only area of white display feathers sometimes heavily mottled with black; cheeks grayish 3

3. Basic color of upper parts dark gray with only slight brownish tinge; area of display feathers fairly heavily mottled with black; streaks on underparts nearly equally long and very narrow, not at all widened from bases toward apices. . . . . *S. c. shimba*

   Basic color of upper parts generally lighter and often distinctly brown-tinged or olive; area of display feathers usually less heavily, often scarcely, mottled with black; streaks on underparts, particularly on middle of chest, usually less regular, tending to be more abbreviated and often slightly widened toward the ends. . . *S. c. suahelicus*

4. Basal half of ear coverts dirty white and forming a patch. . . . . *S. c. chyulu*
   Ear coverts differently colored 5

5. Sides of breast more or less markedly brownish-yellow or pale ochreous-tinged; basic color of upperparts distinctly brown or ferruginous. Streaks on underside fairly narrow and not very dense. . . . . *S. c. medianus*

   Basic color of sides of breast not brownish or ochreous tinged; basic color of upperparts in majority of specimens gray to dark olive . . . . *S. c. capensis*

Smithornis capensis medianus Hartert and van Someren

TYPE LOCALITY. Kyambu Forest, near Nairobi, Kenya.

MATERIAL. 1 ♂ adult, 1 ♀ adult, YPM 79299-300, Mt. Meru, near Usa River, 1500 m alt., northern Tanzania, 14-18 June 1962. 5 ♂ adults, 5 ♀ adults (AMNH), Kyambu Forest, Kenya. 3 ♂ adults, 2 ♀ adults (AMNH), foot of Mt. Kilimanjaro, northeastern Tanzania. (AMNH specimens examined but museum numbers not recorded by us.)

MEASUREMENTS. Wing: male, 72-77 (73.2) mm; female, 72-75 (74) mm. Weight: male (1), 27 g; female (1), 27.5 g.

DESCRIPTION. Distinguished in the first place by its considerable size in which character it agrees with the west African subspecies *S. c. albigularis* Hartert from Angola, which is similar also in color. Differs from *albigularis* by a more or less marked brownish-yellow tinge of the basic color on sides of breast, and by the upper parts being also more distinctly brown tinged. Differs from *camerunensis* Sharpe by less richly rufous upper side and sides of chest and by, on the average, narrower and less dense streaks on underside.

RANGE. Central Kenya and northern Tanzania at the foot of Mt. Meru and of Mt. Kilimanjaro (and perhaps also the area east of Mt. Meru).

Smithornis capensis meinertzhageni van Someren

TYPE LOCALITY. Lerundo, Kavirondo, Kenya.

MATERIAL. 7 ♂ adults, 3 ♀ adults, USNM 519643-52, Kakamega Forest, 1800 m alt., Kenya, 13-26 March, 14 June and 7-13 Dec. 1965.

MEASUREMENTS. Wing: males, 66-69 (68.1) mm; females, 67-68 (67.6) mm. Weight: males, 19-24 g, females, 20-21 g.

DESCRIPTION. Distinctive features of this subspecies are: small size, dark-brown basic color of upperside, very heavily and densely black-streaked breast, chest and flanks, and heavily black-marked white display feathers on back, with broad brown apical margins. Cheeks blackish: white between streaks on breast and flanks more or less distinctly gray-tinged, on sides of breast usually also with ochreous wash.

Differs from *S. c. medianus* markedly by minor size and darker brown basic color of upperside. The streaking on underside is denser and heavier than in all other subspecies.

RANGE. Western fringes of the highlands of western Kenya east of Lake Victoria.

BREEDING. 7-13 Dec.: 3 ♂ with testes enlarged; 2 ♂ and 1 ♀ with gonads moderately enlarged.

Smithornis capensis shimba van Someren

TYPE LOCALITY. Shimba Hills, Kenya.

MATERIALS. 3 ♂ adults, 1 ♀ adult, USNM 519638-41, Buda Forest, nr. Msambweni, Kenya, 21-24 Dec. 1964. 1 ♂ adult, USNM 519642, Muhaka Forest, nr. Ukunda, Kenya, 7 Dec. 1964.

MEASUREMENTS. Wing: males, 66-68 (67) mm; female, 67 mm. Weight: males, 17-23 g; female: 27 g.

DESCRIPTION. This subspecies of the coastal belt of southeastern Kenya agrees in small size with the population of eastern Tanzania and Mozambique, *S. c. suahelicus* and also with subspecies *S. c. meinertzhageni* from western Kenya. From the latter it differs strikingly by much sparser and much narrower streaking on ventral side and by scarcely brown-tinged upper parts. The difference from the birds from eastern Tanzania and Mozambique, treated below under the name *suahelicus,* is less marked. It is apparent mainly in the shape of the dark streaks on chest and breast and in the shade of the basic color of the dorsal side as described for *suahelicus.*

RANGE. Coastal area of southeastern Kenya.

BREEDING. 1 ♂ with testes enlarged, Muhaka Forest. 1 ♂ with testes enlarged; 1 ♀ with shelled egg and soft egg in oviduct, Buda Forest.

Smithornis capensis suahelicus Grote

TYPE LOCALITY. Pangani River at Magagoni, Tanzania.

MATERIALS. 1 ♂ adult, YPM 79301, Pugu Hills, 50 km south of Dar-es-Salaam, Tanzania, 20 Oct. 1961. 5 ♂ adults, 3 ♀ adults (AMNH), Mozambique.

MEASUREMENTS. Wing: males, 66-70 (67.4) mm; females, 67-68 (67.3) mm.

RANGE. Coastal areas of Tanzania south to about Beira, Mozambique (*vide* Clancey, 1963).

REMARKS. The specimen listed above and, in addition, a few others from eastern Tanzania, Uluguru and Uguru Mts., examined and measured (AMNH), are all small, with an average wing length below 70 mm. This character thus indicates clearly that the population from eastern Tanzania and at least parts of Mozambique are distinct from *S. c. medianus, albigularis* and *capensis.*

The name *suahelicus* is tentatively applied to this subspecies, because it is said in the original description of *suahelicus* (Grote, 1926, p. 17) that this form is "smaller than *medianus,*" and further that it is "near in size to *meinertzhageni.*" However, the type of *suahelicus* was not examined, and therefore the applicability of this name to the populations of eastern Tanzania and of northern Mozambique needs confirmation.

Specimens from these populations are equal in size and closely related in color to *S. c. shimba,* but differ as follows: streaks on breast on the average not quite as narrow, and often, particularly on median part of breast, not quite as long, here sometimes slightly approaching drop shape; basic color on dorsal side on the average distinctly browner. The latter applies mainly to Tanzania birds, while Mozambique birds appear to be on the average paler above, often close to pale olive-gray.

Modulatrix stictigula stictigula (Reichenow)

MATERIAL. 6 ♂ adults, 4 ♀ adults, YPM 79302-11, western Usambara Mts., near Lushoto and Shume, northern Tanzania, 16 Feb.-19 March 1962. 6 ♂ adults, 1 ♀ adult, YPM 79312-18, Uzungwa Plateau, Dabaga Mts., at Itanga, south central Tanzania, 15-22 Sept. 1962.

MEASUREMENTS. Wing: males, 76-82 (79.5) mm; females, 71-77 (73.7) mm. Weight: males, 29.5-35 g; females, 29-34 g.

RANGE IN EASTERN AFRICA. Eastern Tanzania from the Usambara to the Nguru Mountains (Mackworth-Praed and Grant, 1955).

BREEDING. 16 Feb.-19 March: 3 ♂ and 2 ♀ with gonads moderately enlarged, Usambara Mts. 15-22 Sept. 2 ♂ with testes slightly enlarged, Itanga.

REMARKS. In color Uzungwa birds from an area south of the Ulugurus are paler than *M. s. pressa* (Bangs and Loveridge), and should probably be kept with the form *stictigula,* thus creating a discontinuous distribution.

Modulatrix stictigula pressa (Bangs and Loveridge)

MATERIAL. 6 ♂ adults, 2 ♀ adults, YPM 79322-29, Rungwe Mts., 32 km south-southeast of Mbeya, southwestern Tanzania, 1-9 Nov. 1962. 5 ♂ adults, 1 ♂ juvenal, 3 ♀ adults, YPM 79330-38, Uluguru Mts., near Morogoro, eastern Tanzania, 27 Nov.-15 Dec. 1961. 3 ♀ adults, YPM 79339-41, Livingstone Mts., Mdando Forest, 48 km south of Njombe, southwestern Tanzania, 9-17 Oct. 1962.

MEASUREMENTS. Wing: males, 75-82 (78.4) mm; females, 71-79 (74.5) mm. Weight: males, 29.5-35 g; females, 29-34.5 g.

RANGE IN EASTERN AFRICA. Eastern to south-western Tanzania, from the Uluguru Mts., to Rungwe Mt., Njombe and Songea (Mackworth-Praed and Grant, 1955).

BREEDING. 1-9 Nov.: 4 ♂ and 1 ♀ with gonads enlarged, Rungwe Mts., 9-17 Oct.: 2 ♀ with ovaries slightly enlarged, Livingstone Mts.

REMARKS. The habits and distribution of *Modulatrix stictigula* agree closely with *Alethe fuelleborni* Reichenow. Both occur in the high mountain cloud forests of northern, eastern, central and southwestern Tanzania to Malawi, but neither of the two has so far been found on Mt. Meru and Mt. Kilimanjaro, nor on the highlands of Kenya.

The geographical variation of the two species shows a distinct parallel; the southern population of *Modulatrix stictigula,* around Lake Nyasa, being darker brown above (with denser and darker black spots on the throat), the northern population, on the Usambara Mts., having slightly lighter upperparts and paler and smaller spots on the throat.

The latter population represents the nominate subspecies *stictigula,* the former the subspecies *pressa.*

Alethe fulleborni fulleborni (Reichenow)

MATERIAL. 2 ♂ adults, 4 ♀ adults YPM 79342-47, Rungwe Mts., 20 km south-southeast of Mbeya, Tanzania, 28 Oct.-9 Nov. 1962. 5 ♂ adults, 2 ♀ adults, YPM 79348-54, Livingstone Mts., Mdando Forest, 30 km south of Njombe, Tanzania, 10-20 Oct. 1962.

MEASUREMENTS. Wing: males, 97-112 (105.3) mm; females, 96-103 (100) mm. Weight: males, 39.5-48.5 g; females, 44.5-47.5 g.

DESCRIPTION. This subspecies differs from *A. f. usambarae* Reichenow by the darker and warmer brown color of the upperparts and by smaller size. The sides of chest and breast are also more scaly in appearance, caused by the greyish apical margins on the otherwise white feathers.

RANGE IN EASTERN AFRICA. South-central and south-western Tanzania from Njombe to the Tukuyu district (Mackworth-Praed and Grant, 1955).

BREEDING. So far, according to Mackworth-Praed and Grant (1955) no definite breeding data have been recorded. However, a summary of all the records collected by the junior author in various months reveals clearly that the breeding season coincides, as in the other mountain thrushes, with the rainy season, October to March. This apparently applies to all localities within Tanzania. 28 Oct.-9 Nov.: 2 ♂ with testes enlarged; 3 ♀ with ovaries slightly enlarged, Rungwe Mts. 10-20 Oct.: 1 ♂ with testes enlarged; 1 ♂ and 3 ♀ with gonads moderately enlarged, Njombe.

HABITAT. This species inhabits only the evergreen mountain forests in altitudes between 1200 and 2600 m. Its distribution in Tanzania therefore is disconnected and confined to the scattered islands of cloud-forests covering the highest elevations of the country.

HABITS. The birds are extremely shy and elusive, staying always under cover of dense, low ground vegetation and never being seen more than a few feet above ground. Their movements on the ground are fast and vigorous. The flight is rapid and low. In common with all African mountain thrushes they like to feed on the armies of driver ants.

SONG. The song is composed of only two loud whistled notes, the first of which is slightly tremulous and a little deeper than the second. There is also a melodious, loud, one-syllabic call, repeated with moderate intervals for some time, and often answered by another bird at a distance. This call was confirmed beyond doubt as the voice of this species by direct observation at close range.

Alethe fulleborni usambarae Reichenow

MATERIAL. 2 ♂ adults, 4 ♀ adults, 1 ♂ juvenal, 2 ♀ juvenals, YPM 79355-63, western Usambara Mts. near Lushoto and Shume, northern Tanzania, 18 Feb.-22 March 1962. 5 ♂ adults, 1 ♀ adult, 1 ♂ juvenal, YPM 79364-70, eastern Usambara Mts., near Omain, northern Tanzania, 4-17 Apr. 1962. 3 ♂ adults, YPM 79371-73, Uluguru Mts., eastern Tanzania, 26 Nov.-14 Dec. 1961. 6 ♂ adults, 1 ♀ adult, YPM 79374-80, Uzungwa Plateau, Dabaga Mts. at Itanga, 30 km south-southeast of Iringa, south central Tanzania, 13-18 Sept. 1962.

MEASUREMENTS. (Northern and eastern specimens) Wing: males, 106-115 (110.2) mm; females, 104-116 (107.2) mm. Weight: males, 47.5-67 g; females 51-69 g. (Southern specimens) Wing: males, 101-111 (106.7) mm; female, 103 mm. Weight: males, 46-54 g; female, 50 g.

RANGE IN EASTERN AFRICA. Eastern Tanzania from the Usambara Mts. to the Uluguru Mts. and Mahenge (Mackworth-Praed and Grant, 1955).

BREEDING. 24 Feb.: 1 ♂ with testes enlarged; 1 ♀ with egg in oviduct, western Usambara Mts. 26 Nov.-14 Dec.: 3 ♂ with testes enlarged, Uluguru Mts. 13-18 Sept.: 2 ♂ with testes slightly enlarged, Itanga.

REMARKS. The population of the Uzungwa Plateau in south central Tanzania (a new locality) is similar in color but slightly smaller than populations of this subspecies collected farther north (see above).

LITERATURE CITED

Bannerman, D. A. 1933. Birds of tropical West Africa, vol. **3**. The Crown Agents for the Colonies, London. 487 p.

Cabanis, J., and F. Heine. 1863. Scansores, pt. 4. Mus. Heineanum, Halberstadt. 180 p.

Chapin, J. P. 1939. The birds of the Belgian Congo, part 2. Bull. Amer. Mus. Nat. Hist. **75**:632 p.

Clancey, P. A. 1963. Miscellaneous notes on African birds, XX. Durban Mus. Novit. **6**(19):231-264.

——— 1965. On the type-locality of *Campethera abingoni abingoni* (Smith), 1836. Bull. Brit. Orn. Club. **85**(4):64-65.

——— 1967. Critical comments on the subspecies of some birds from Zambia. Durban Mus. Novit. **8**(9):77-107.

Friedmann, H. 1930. Birds collected by the Childs Frick Expedition to Ethiopia and Kenya Colony. U.S. Nat. Mus. Bull. **153**:516 p.

Grote, H. 1926. Kurze Mitteilungen. Orn. Monatsb. **34**(1):17-18.

Lynes, H. 1934. Contribution to the ornithology of southern Tanganyika Territory. Journ. für Ornith., Sonderheft, **82**:1-147.

Mackworth-Praed, C. W., and C. H. B. Grant. 1952. African handbook of birds, Ser. 1. Longmans, Green and Co., London and New York. 836 p.

——— 1955. African handbook of birds, Ser. 1, **2**. Longmans, Green and Co., London and New York. 1099 p.

Peters, J. L. 1948. Check-list of birds of the world, vol. **6**. Harvard Univ. Press, Cambridge. 259 p.

Ripley, S. D., and G. H. Heinrich. 1966a. Additions to the avifauna of Northern Angola II. Postilla 95:1-29.

——— 1966b. Comments on the avifauna of Tanzania I. Postilla 96:1-45.

Someren, V. G. L. van. 1919. Bull. Brit. Orn. Club. **40**:24.

——— 1939. Report on the Coryndon Museum Expedition to the Chyulu Hills, part 2. Journ. East Afr. and Uganda Nat. Hist. Soc. **14**:15-129.

——— 1941. Bull. Brit. Orn. Club **62**:35.

White, C. M. N. 1961. A revised check list of African broadbills, pittas, larks, swallows, wagtails and pipits. The Government Printer, Lusaka. 84 p.

——— 1965. A revised check list of African non-passerine birds. The Government Printer, Lusaka. 102 p.

——— 1967. On the type locality of *Campethera a. abingoni* (Smith). Bull. Brit. Orn. Club **87**(4):66.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

OMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

ILLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

HOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 135. 11 JULY 1969.

THE STATUS OF THE GENERA ECPLEOPUS, ARTHROSEPS AND ASPIDOLAEMUS (SAURIA, TEIIDAE)

THOMAS UZZELL

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

THE STATUS OF THE GENERA ECPLEOPUS, ARTHROSEPS, AND ASPIDOLAEMUS (SAURIA, TEIIDAE)

THOMAS UZZELL

Department of Biology and Peabody Museum of Natural
History, Yale University

ABSTRACT

The genus *Ecpleopus* is diagnosed within Group II of the Teiidae by the elongate, keeled dorsal scales arranged in diagonal and transverse rows, smooth ventral scales in diagonal and transverse rows, first superciliary elongate, first supraocular in contact with the frontonasal and loreal, and superciliary series incomplete so that only first and fourth supraoculars are separated from the palpebrals.

The usual presence of plicae on the anterior part of the tongue suggests relationships with *Ptychoglossus* and *Alopoglossus,* which are distinctive within Group II because they have completely plicate tongues. *Leposoma* and *Arthrosaura* also appear to be related to *Ecpleopus.* The diagnostic characters of *Ecpleopus,* however, suggest that its relationships to these four genera are not especially close.

I consider *Arthroseps* a synonym of *Ecpleopus.* The genus is apparently monotypic. *Arthroseps werneri, A. fluminensis,* and *Alopoglossus gracilis* are junior synonyms of *Ecpleopus gaudichaudi. Aspidolaemus,* with *Ecpleopus (Aspidolaemus) affinis* as the only species, is recognized as a separate genus related to *Prionodactylus* and *Pholidobolus.*

Ecpleopus gaudichaudi is known from altitudes of less than 1000 m above sea level in eastern Brazil from Goyas south to Santa Catarina.

E. gaudichaudi, in contrast to most members of Group II, may mature only a single egg at a time.

POSTILLA 135: 23 p. 11 JULY 1969.

INTRODUCTION

One of the most poorly understood genera of Group II (Boulenger, 1885b) of the family Teiidae is *Ecpleopus,* described by Duméril and Bibron (1839) for their species *Ecpleopus gaudichaudi.* Peters (1862) enlarged the scope of *Ecpleopus,* including in it as subgenera *Ecpleopus* for *E. gaudichaudi, Aspidolaemus* for *E. affinis,* as well as *Pholidobolus, Oreosaurus, Euspondylus, Argalia, Xestosaurus,* and *Proctoporus.* Boulenger (1885b) modified Peters' concept of *Ecpleopus* by removing from it all the subgenera except *Ecpleopus* and *Aspidolaemus.* Since *Ecpleopus affinis* is a common species in museum collections, its characteristics, rather than those of the rarely collected *E. gaudichaudi,* have been the basis of most workers' concept of the genus *Ecpleopus.*

Recently I undertook to examine as many specimens as possible of *Ecpleopus gaudichaudi.* I now know 12 specimens that I consider to be this species; I have examined 10 of them; 2 have apparently been destroyed. Several specimens reported under this name were misidentified. Included in these 12 specimens are 4 holotypes, of which I have seen 3. Examination of these specimens bears out my conviction (Uzzell, 1959) that *Ecpleopus gaudichaudi* is very dissimilar to *Ecpleopus affinis.* It also indicates that the genus *Arthroseps* is a synonym of *Ecpleopus. Ecpleopus* has features that suggest affinities with *Arthrosaura,* with *Ptychoglossus* and *Alopoglossus,* and with *Leposoma.*

Abbreviations used:

BMNH — British Museum (Natural History), London
DZSP — Departamento de Zoologia, Secretaria da Agricultura, São Paulo
MNHN — Muséum National d'Histoire Naturelle, Paris
NHMB — Naturhistorisches Museum, Basel
NHMW — Naturhistorisches Museum, Wien
SMF — Senckenberg Museum, Frankfurt
UKMNH — University of Kansas, Museum of Natural History
UMMZ — University of Michigan, Museum of Zoology
ZSM — Zoologische Staatssammlung, Munich

Ecpleopus Duméril and Bibron

Ecpleopus Duméril and Bibron, 1839: 434.
Arthroseps Boulenger, 1898: 920. **New synonymy.**

DEFINITION. Tongue with imbricate scalelike papillae on middle and, sometimes, on posterior part; anteriorly usually with oblique folds[1]. Snout short, blunt. Head scales without striations and rugosities; single frontonasal, frontal, and interparietal; median occipital variable; paired prefrontals, frontoparietals, parietals and occipitals. Four supraoculars on each side, the second and third in contact with palpebrals. First superciliary elongate, not expanded onto dorsal surface of head. First supraocular elongate, narrowly in contact with loreal, relatively broadly in contact with frontonasal. Prefrontals and first supraocular subequal in length. Nasals not in contact; nostril in middle of nasal; a short suture posteriorly from nostril to hind margin of nasal. Loreal present, diagonally placed, separated from supralabial scales by contact between nasal and frenoocular. Eyelids developed, lower with relatively large translucent disc divided into two pieces by a vertical groove. Ear opening moderately large; tympanum only slightly recessed, not overhung by scales. One unpaired and three paired chinshields, the last pair not touching at midline; all chinshields in contact with labials. Gular crease weak; collar fold not well marked. Posterior median gular and collar scales shaped like ventrals.

Dorsal scales elongate, hexagonal, long pointed, strongly keeled, imbricate, the points overlapping the sutures between scales of next posterior row. Lateral scales similar. Ventral scales long, hexagonal, smooth, less sharply pointed than dorsals and laterals, imbricate, the points overlapping the sutures between scales of next posterior row. Scales mainly in complete rings around body, but dorsals somewhat shorter than ventrals. Caudal scales resembling body scales, keeled above and on sides, smooth below. A single series, usually with three scales, of elongate, smooth, preanals.

Limbs pentadactyl; digits clawed. Forefoot with enlarged platelike scales along inner margin of palm between thumb and wrist,

---

[1] The holotype of *Ecpleopus gaudichaudi* has papillae rather than plicae anteriorly.

the edges not produced. Upper tibial scales keeled. Underside of third and fourth digits of hind foot with paired scales proximally, the inner scale of each pair not tuberculate.

Usually one preanal pore on each side in both sexes; pore surrounded by a single scale.

Tail rounded in cross section.

Clear yellow below, brown above, with two light dorsolateral lines that approach each other on the neck.

Ecpleopus is readily recognized by the following suite of characters: dorsals keeled, forming diagonal and transverse rows; ventrals smooth, forming diagonal and transverse rows; first supraocular touching both loreal and undivided frontonasal; superciliary series incomplete, so that second and third supraoculars touch the palpebrals; tongue usually with plicae at anterior end.

REMARKS. Folds, or plicae, occur (as Ruibal, 1952, pointed out) on the posterior, notched part of the tongue of many teiid lizards. Folds on the middle and anterior parts of the tongue, however, are unusual. They have been observed in *Ptychoglossus* and *Alopoglossus,* in which the entire surface of the tongue is plicate[2]. The arrangement in *Ecpleopus* therefore appears to be structurally intermediate between the generally papillate condition and the completely plicate condition. Folds on the tongue have been reported in non-teiid genera. The tongue of *Takydromus* (Lacertidae) is completely plicate (Boulenger, 1885a). The pattern (de Rooij, 1915: fig. 1-5) strongly resembles that seen in *Alopoglossus* and *Ptychoglossus.* The lateral margin of the tongue of *Lacerta viridis,* as well as the posterior, notched part, has folds rather than plicae (Seiller, 1892).

Plicae similar to those in *Alopoglossus, Ptychoglossus,* and *Takydromus* apparently occur in *Tetradactylus,* one of the six genera of the Gerrhosauridae (Boulenger, 1885a).

Xantusiids and dibamids also have plicae on the posterior part of the tongue. The apices are directed forward in the xantusiids, but in *Dibamus* the plicae, instead of forming chevrons, form curves, with the convex side forward (de Rooij,1915: fig. 1-7).

Although the figure of the tongue of *Heloderma* and of *Lanthonotus* given by McDowell and Bogert (1954: figs. 29D, E)

---

[2] Werner (1910) reported folds on the tongue of *Perodactylus kraepelini.*

suggests that there are plicae on the anterior part of the tongue in these two genera, plicae are absent on the tongues of the individual of each genus that I have examined. Plicae thus appear to be confined to the families placed by Camp (1923) in the Scincomorpha, although very similar arrangements of folds are restricted to the Lacertoidea.

Regardless of the phylogeny of the Lacertilia that is accepted, plicate tongues have been developed or lost repeatedly within the Scincomorpha.

Ecpleopus gaudichaudi Duméril and Bibron (Fig. 1)

Ecpleopus gaudichaudi Duméril and Bibron, 1839: 436.
Arthroseps werneri Boulenger, 1898: 921, **New synonymy.**
Alopoglossus gracilis Werner, 1913: 13. **New synonymy.**
Arthroseps fluminensis Amaral, 1932: 67. **New synonymy.**

The characteristics of *E. gaudichaudi* are the same as those of the genus. Four features, the structure of the tongue, the nature of the feet, the hemipenis, and the coloration, merit additional comment.

TONGUE. The tongue of *E. gaudichaudi* is moderately long, with two relatively long smooth points anteriorly and a notch behind, giving the tongue an arrowheaded shape. The anterior part, just behind the smooth anterior points, and sometimes the posterior part around the notch are covered on the dorsal part with folds, or plicae, which form chevrons, the apex on the midline and anterior. On the middle and sometimes the posterior part, the tongue is covered dorsally by imbricate, rhomboidal, scalelike papillae. These can be viewed as formed by two sets of chevron-shaped divisions, one set with the apices forward, the other with the apices posteriorly directed. It is easy to imagine the transformation between papillae and plicae by the loss of the chevrons with posteriorly directed apices.

The presence of papillae on the middle and sometimes the posterior part of the tongue of all specimens of *E. gaudichaudi* examined and the usual presence of plicae at the anterior tip perhaps makes the absence of plicae at the anterior tip of the

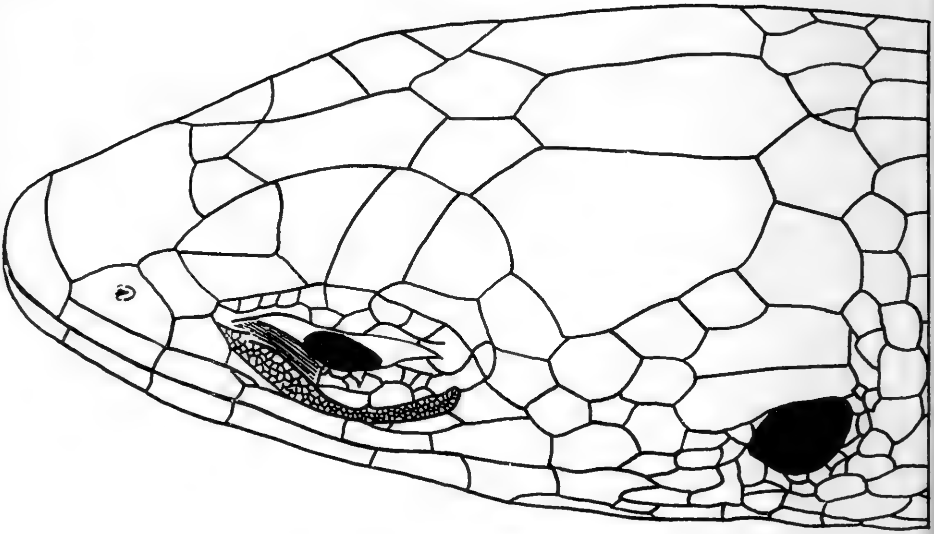


FIG. 1. Lateral view of the head of *Ecpleopus gaudichaudi* (SMF 11757) showing the contact between the palpebral series and the second and third supraoculars and the contact between the first superciliary and the loreal. ×14.

holotype of *E. gaudichaudi* more understandable. If subdivision of the folds to form papillae (or fusion of papillae to form plicae) is under genetic control such that it occurs in part of the tongue but not all, only a slight shift in timing or of developmental field would be required to produce a tongue with papillae at the anterior end as well as at the middle. The alternative arrangement, a completely plicate tongue, may also occur in some individuals of

E. gaudichaudi. Because of the rather generally papillate condition, I suspect that plicae represent the derived condition. I view their occurrence within Group II of the Teiidae as a single occurrence indicating affinity between *Ecpleopus* on the one hand and *Alopoglossus* and *Ptychoglossus* on the other.

FEET. The toes of *E. gaudichaudi* are short and slightly depressed (Fig. 2). On the ventral surface, the lamellae are divided. The digits of both feet appear to be joined together at the bases so that the palmar region seems to extend beyond the metapodial region of the foot. The claws are weak and curved. Although on the palm the thenar scales are moderately large, the medial edge is not produced into a free ridge. The inner member of each pair of subdigital lamellae at the base of the third and fourth toes is not swollen to produce a marked tubercle. Many of these features

FIG. 2. Underside of left forefoot of *Ecpleopus gaudichaudi* (SMF 11757). ×29.

of the feet vary among members of Group II of the Teiidae but their adaptive significance has not been investigated.

HEMIPENIS. I have examined the left hemipenis of UMMZ 79948 and UMMZ 115639. Each hemipenis was washed in distilled water, slit along the sulcus spermaticus, stained overnight in a dilute solution of alizarin red S in 0.5 percent KOH, and destained in distilled water.

Neither of the hemipenes examined shows any evidence of the calcareous spinules that occur in the hemipenes of many species of the genera of Group II of the Teiidae. The flounces in which the calcareous spinules are usually located are also absent. Description of the organ is therefore difficult; some features can be seen in Figure 3. The prominent fleshy fold in the middle of the organ is the median welt. It appears to extend into each of the lobes of the bilobate organ. The lobes themselves have the fleshy folds usually found in hemipenes of members of Group II.

FIG. 3. Structure of the left hemipenis of *Ecpleopus gaudichaudi* (UMMZ 115639). The inverted organ has been slit along the sulcus spermaticus. × 18.

COLORATION. Specimens of *Ecpleopus gaudichaudi* are generally brown above and clear yellow below. There are a pair of light dorsolateral lines 1-2 scales wide and dark bordered, on the posterior part of the head, on the shoulders and on the sacral regions. These light lines are usually broken on the head. There may thus be light patches on the outer edge of each parietal, a rounded light patch covering the posterolateral corner of each paramedian occipital scale as well as adjacent parts of adjacent scales, and a light crescent on the posterior part of the interparietal. Since the light spots on the paramedian occipital scales are closer to midline than the light spots on the parietals or dorsal scales, the pattern appears to consist of two dorsolateral light lines running from the head onto the shoulders, but pinched together at the neck.

The scales beneath the feet and hands are peppered with dark pigment. The labials are dark brown but light bordered. The tympanum is clear.

SPECIMENS OF ECPLEOPUS GAUDICHAUDI

Since so few specimens of *Ecpleopus gaudichaudi* are known and since several of these are lost or have no locality other than Brazil, I have tabulated the characteristics for each individual (Table 1). Invariant characters are included in the generic diagnosis.

1. Little need be added to the description of the holotype of *Ecpleopus gaudichaudi* (Duméril and Bibron 1839). The specimen (MNHN 7047) is an adult female with a single preanal pore on each side. The type locality is Brazil. Peters (1862) reported that the posterior maxillary teeth are biscuspid, but the second (posterior) cusp must be very small because I did not see it.

2. I have examined the holotype (BMNH 98.1.17.1, reregistered as 1946.8.2.4) of *Arthroseps werneri* Boulenger (1898). The specimen is a female collected by Franz Werner at Blumenau, Santa Catarina, Brazil (map). Except for the presence of plicae at the anterior tip of the tongue and the absence of a median occipital, the holotype of *A. werneri* agrees with the holotype of *E. gaudichaudi* in all characters that I consider taxonomically important. I therefore place *Arthroseps* in the synonymy of *Ecpleopus* (new synonymy), and *A. werneri* in the synonymy of *E. gaudichaudi* (new synonymy).

TABLE 1. Characteristics of 11 specimens of *Ecpleopus gaudichaudi.*

Museum	Specimen number	Snout-vent length	Tail/snout-vent length	Hind leg/snout-vent length	Dorsal scale rows	Ventral scale rows	Scales around midbody region	Total preanal pores	Median occipital	Subdigital lamellae	
										4th toe	4th finger
Males											
UMMZ	79948	38	—	0.32	31	19	37	2	present	15-14	9-9
UMMZ	115639	38	—	0.29	31	22	37	2	present	15-15	10-10
SMF	11757	31	1.6	0.32	31	18	32	2	present	13-13	7-7
Females											
DZSP	800[1]	39	—	0.23	30	19	29	2	present	—	—
DZSP	13320	40	—	0.32	32	20	36	0	present	15-15	7-9
DZSP	1966	38	—	0.26	32	19	33	2	present	11-	6-6
BMNH	98.1.17.1[2]	20	—	0.30	29	20	34	2	absent	—	—
—	—[3]	33	2.1	0.30	32[4]	18	34	0	present	—	—
MNHN	7047[5]	40	—	0.31	33	20	37	2	present	15-15	9-
MNHN	2828	—	—	—	33	21	37	0	—	15-15	11-11
NHMW	19160	36	—	0.31	32	21	38	2	absent	16-16	-9

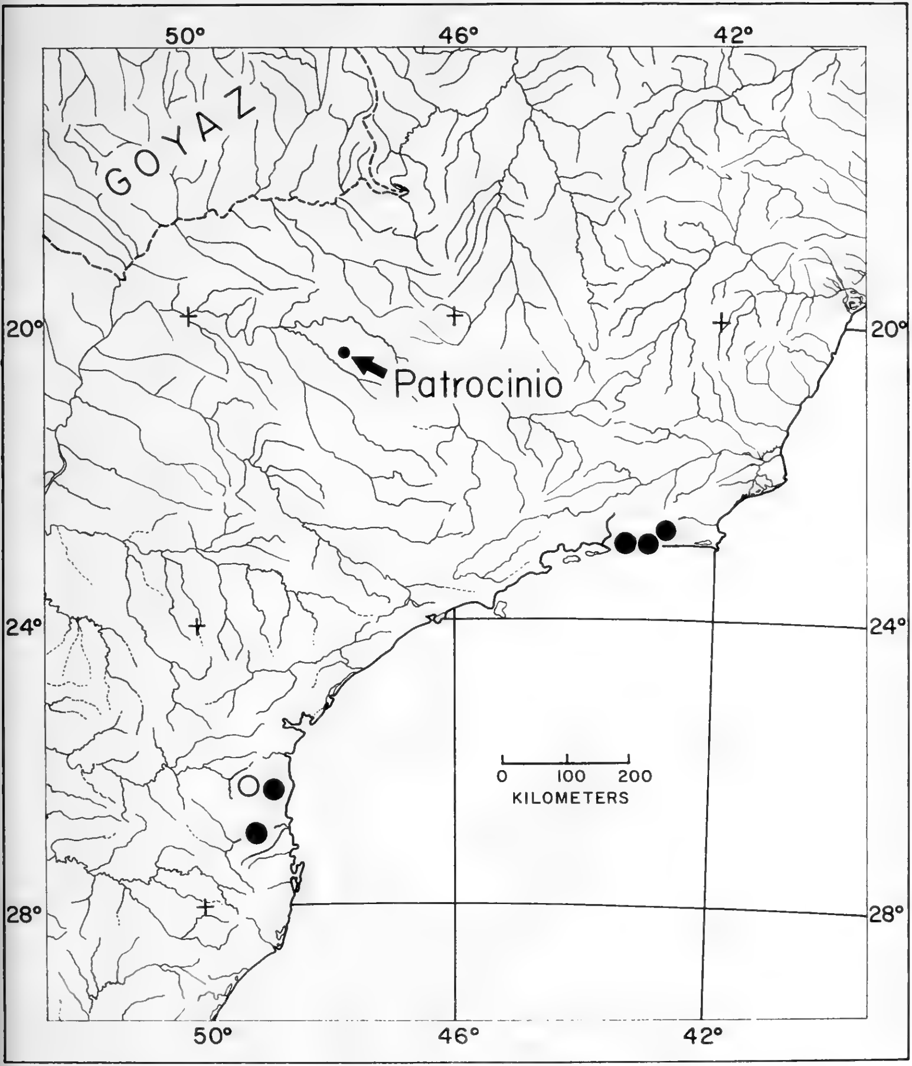
[1] Holotype of *Arthroseps fluminensis.*

[2] Holotype of *Arthroseps werneri.*

[3] Holotype of *Alopoglossus gracilis;* data from Werner (1913).

[4] To cloacal opening.

[5] Holotype of *Ecpleopus gaudichaudi.*



Southeastern Brazil from Goyas south to Santa Catarina, showing localities for *Ecpleopus gaudichaudi*. The open symbol represents the type locality for *Alopoglossus gracilis* Werner; solid symbols show localities for specimens examined when the localities were definite.

3. The holotype of *Alopoglossus gracilis* Werner (1913) was collected in the valley of the Rio Humboldt, a tributary of the Rio Itapocu in Santa Catarina, Brazil. It was apparently lost during World War II. Werner's generic placement of his species indicates that the tongue had conspicuous plicae. Characters in Table 1 show that *Alopoglossus gracilis* belongs with the other specimens referred to *Ecpleopus gaudichaudi.* Ruibal (1952) recorded specimens of *Alopoglossus* from the Pacific slopes of Ecuador and from the edges of the Amazonian basin from southern Peru north and east to British Guiana; these localities are enormously distant from the type locality of *Alopoglossus gracilis.* Since there seems little reason to expect members of the genus *Alopoglossus* in Santa Catarina, and since the morphological features of *A. gracilis* are so similar to those of *Ecpleopus gaudichaudi,* I consider *A. gracilis* a junior synonym of *E. gaudichaudi* (new synonymy).

4. Although Amaral (1932) stated that the holotype of *Arthroseps fluminensis* does not fit Boulenger's description of *A. werneri* in important features, he did not specify the differences. I have examined the holotype of *A. fluminensis* (DZSP 800), an adult female from the Serra de Macaé in Rio de Janeiro. I am unable to detect any important differences between it and the other specimens referred to *E. gaudichaudi.* I therefore consider *A. fluminensis* a junior synonym of *E. gaudichaudi* (new synonymy).

5. Localities and museum numbers for seven other specimens of *E. gaudichaudi* are given in the list of specimens examined. Specific localities are indicated on the map.

6. Tschudi's (1847) specimen from Brazil was soon lost (Peters, 1862). It adds nothing to our knowledge of this species.

BIOLOGY OF ECPLEOPUS GAUDICHAUDI

Virtually nothing is known about the ecology of *Ecpleopus gaudichaudi.* Its general similarity to *Leposoma* in body form and size suggest similarities in ecology. Specimens of *Leposoma* have been collected in damp leaves, under logs, in grassy marshes, under dead leaves along dried stream beds, and on leaves of forest floor (Ruibal, 1952). Both *Ecpleopus* and *Leposoma* are lowland animals, *Leposoma* occurring at altitudes of less than 600 m above sea level (Ruibal, 1952) and *Ecpleopus* at altitudes of up to perhaps 1000 m.

The holotype of *E. gaudichaudi* contains one egg with a wrinkled leathery shell. I estimated the egg to be 7 mm long and about 5 mm in diameter. The holotype of *A. fluminensis* contains a single enlarged ovum. Perhaps the normal clutch size for these small lizards is one rather than the two generally observed in species of Group II (Uzzell 1959, 1965, 1966; Fouquette 1968).

RANGE. The known range of *Ecpleopus gaudichaudi* is from Goyas on the north to Santa Catarina on the south (map). Most of the localities are in the immediate coastal drainages of southeastern Brazil, but the Goyas locality suggests that this genus, like *Placosoma* (Uzzell 1959, 1962) may have populations extending well to the north and west, perhaps being limited by the rainforest areas of the Amazon basin.

Specimens Examined

Brazil (no state given): MNHN 7047 (holotype of *Ecpleopus gaudichaudi*), MNHN 2828, NHMW 19160.
” Distrito Federal: Jacarepagua, Repressa da Convanca: UMMZ 115639.
” Goyas: UMMZ 79948.
” Rio de Janeiro: Grajáu: DZSP 13320.
” ” Serra de Macaé: DZSP 800 (holotype of *Arthroseps fluminensis*).
” Santa Catarina: Blumenau: BMNH 98. 1.17.1, recatalogued as 1946.8.2.4 (holotype of *Arthroseps werneri*).
” ” Joinville: SMF 11757.
” São Paulo: São Paulo: DZSP 1966.

Relationships of Ecpleopus

I first realized that *Ecpleopus* is related to *Alopoglossus* and *Ptychoglossus* when I discovered plicae on the anterior part of the tongue of two specimens (UMMZ 79948 and 115639). It was surprising not to find plicae at the tip of the tongue of the holotype of *E. gaudichaudi*. Nevertheless, the large number of features that these two specimens share with the holotype of *E. gaudichaudi* convinces me that they are conspecific with the holotype.

Ecpleopus also shares many features with *Leposoma*, which, as Ruibal (1952) observed, is very similar to *Alopoglossus*. These genera are also similar to *Arthrosaura*. The characters that the five genera share are few. Nevertheless, combinations of characters do offer support for the few distinctive characters of the group (Table 2).

In all five genera, the first supraocular is elongate. The long first superciliary is not expanded onto the dorsal surface of the head, but forms a suture with the first supraocular at the canthus rostralis. The loreal is separated from the labials in *Leposoma, Alopoglossus* and *Ecpleopus*. More importantly, except in *Arthrosaura,* the loreal is a relatively narrow, diagonally placed scale, with the upper end anterior to the lower. There is usually a single row of elongate preanal scales, although in some forms of two genera *(Leposoma, Arthrosaura)* the middle scale may be divided into anterior and posterior parts, and in *Arthrosaura,* all the preanal scales are relatively short.

There are usually three pairs of chinshields; the anterior pairs are in contact on the midline. The last chinshield is separated from the labials by small scales in some forms of all genera except *Arthrosaura* and *Ecpleopus*. Usually, the gular, collar, and ventral scales are shaped alike. *Arthrosaura* and one species of *Alopoglossus* have widened median gular scales. Some species of both *Arthrosaura* and *Ptychoglossus* have 3-3 supraoculars, but other species and the three other genera have 4-4 supraoculars.

I examined 28 characters that I believe are taxonomically significant to determine the overall similarity of the five genera considered. For 13 of the 28 characters, one state (marked by asterisks in Table 2) could be postulated to be primitive on the basis of nearly uniform distribution in other members of Group II (or, occasionally, in other groups) of the Teiidae. The remaining characters have states all of which can be found in genera of Group II other than the five considered here.

Five tabulations of shared character states are presented in Table 3. For phenetic comparisons, a genus with more than one character state was considered to share a state with each genus

TABLE 2. Characteristics of five genera of Group II.

	Arthrosaura	Ecpleopus	Leposoma	Alopoglossus	Ptychoglossus
Striae on Head Scales	absent*[1]	absent*	present[2]	present or absent*[3]	absent*
Superciliary Series	complete*	broken[4]	complete*	complete*	complete*
Supraocculars	3 or 4[5]	4	4	4	3 or 4[6]
Length of Parietal and Interparietal	equal	parietals shorter*	equal or parietals shorter*[7]	equal	equal
Interparietal Width	narrow*	narrow*	broad or narrow*[8]	narrow*	narrow*
Occipitals	absent	present	absent	absent	absent
Frontonasal-First Supraocular	separated*	in contact	separated*	separated*	separated*
Loreal and labials	in contact	separated.	separated	separated	usually in contact[6]

---

* Postulated primitive state (see text).

[1] Da Cunha (1967) reported striae on the head scales of *A. kockii;* they are absent on specimens I have examined (UKMNH 69812-14); the temporal scales are keeled in *A. kockii.*

[2] Absent on anterior head scales of some *L. rugiceps;* Ruibal 1952.

[3] Present on posterior head scales of *A. buckleyi;* Ruibal 1952.

[4] Second and third supraoculars touch palpebrals.

[5] 3 in *A. reticulata, A. versteegi,* and *A. amapaense;* 4 in *A. kockii;* da Cunha 1967.

[6] Species identifications in this genus are uncertain.

[7] Parietals and interparietal of equal length in *L. scincoides;* Ruibal 1952.

[8] Narrow in *L. scincoides;* Ruibal 1952.

TABLE 2. Characteristics of five genera of Group II. (Cont'd)

	Arthrosaura	Ecpleopus	Leposoma	Alopoglossus	Ptychoglossus
Last Chinshields	touching labials	touching labials	touching labials or not[9]	separated from or barely touching labials	separated from or barely touching labials
Gulars	smooth* two widened rows	smooth* no widened rows	keeled no widened rows	keeled two or no widened rows[10]	smooth* no widened rows
Dorsals	keeled parallel-sided	keeled parallel-sided	keeled leaf shaped or parallel-sided[11]	keeled leaf shaped	convex or keeled[6] parallel-sided
	long pointed	long pointed	mucronate	mucronate	truncate, bluntly hexagonal or long pointed[6]
Ventrals	smooth*	smooth*	keeled or smooth*[12]	keeled or smooth*[13]	smooth*
	longitudinal rows*	diagonal rows	longitudinal* or diagonal rows[14]	longitudinal rows*	Longitudinal rows*
	rounded posteriorly	long pointed	truncate, rounded mucronate or pointed[15]	truncate rounded or pointed[16]	rectangular*

---

[9] Labials touching chinshields in *L. scincoides;* Ruibal 1952.

[10] Widened in *A. buckleyi;* Ruibal 1952.

[11] Parallel-sided in *L. annectans* and *L. scincoides;* Ruibal 1952.

[12] Keeled or smooth in *L. rugiceps;* Ruibal 1952.

[13] Smooth in *A. festae* and *A. andeanus;* Ruibal 1952.

[14] In diagonal rows in *L. scincoides* and *L. annectens;* Ruibal 1952.

[15] Long pointed in *L. scincoides;* Peters 1862.

[16] Pointed in *A. copii* and *A. carinicaudatus;* rounded in *A. andeanus;* truncated in *A. festae;* pointed, rounded, or truncated in *A. buckleyi;* Ruibal 1952.

Preanal Scales	middle divided or not smooth*	middle not divided smooth*	middle divided or not[17] keeled	middle not divided smooth* or keeled[18]	middle not divided smooth*
Forelimbs	keeled	smooth	keeled	keeled	smooth
Thenar Scales	inner edge free	no free edge	inner edge free	inner edge free	inner edge free
Inner Lamellae under 4th Toe	swollen	not swollen	swollen	swollen	swollen
Preanal Pores	males	both sexes[19]	both sexes	males	males
Femoral Pores	males	absent	males	males	males
Tongue	papillate*	papillate*[20] or plicate anteriorly	papillate*	plicate	plicate
Maxillary Teeth	mostly tricuspid*	mostly unicuspid[21]	mostly tricuspid*	mostly bicuspid[22]	mostly bicuspid[22]
Tympanum	deeply recessed	moderately recessed	moderately recessed	deeply recessed	moderately or deeply recessed[6]
Hemipenis	numerous spinules in each flounce*	spines absent	two spines per flounce	spines absent	spines absent

---

[17] Not divided in *L. guianense;* Ruibal 1952.
[18] Weakly keeled in *A. carinicaudatum;* Ruibal 1952.
[19] Absent in some females.
[20] Papillate anteriorly in holotype of *E. gaudichaudi.*
[21] Hind cusp present but reduced (Peters 1862) or absent; anterior cusp absent.
[22] Hind cusp essentially lost.

TABLE 3. Numbers of characters for which pairs of genera share states.

		PHENETIC COMPARISONS			PHYLETIC ANALYSIS	
		All	Scored characters		Derived characters	
GENUS PAIR		characters	Shared	Variable	Shared	Invariant
Ecpleopus	— *Leposoma*	14	6	6	2	0
"	— *Ptychoglossus*	16	6	0	1	1
"	— *Arthrosaura*	12	6	1	0	0
"	— *Alopoglossus*	11	6	4	2	1
Leposoma	— *Ptychoglossus*	17	6	4	1	0
"	— *Arthrosaura*	18	9	5	2	0
"	— *Alopoglossus*	23	10	7	6	0
Ptychoglossus	— *Arthrosaura*	19	9	0	1	1
"	— *Alopoglossus*	23	10	3	4	4
Arthrosaura	— *Alopoglossus*	20	9	4	2	1

Data derived from Table 2. For phenetic comparisons, variable characters could be shared in each state observed; for phyletic analysis, only characters for which derived states were shared were counted.

that had at least one of those states; for phyletic analysis, only derived states were counted.

Using all 28 characters, *Ptychoglossus* and *Alopoglossus,* which share 23 states and *Alopoglossus* and *Leposoma,* which also share 23 states, are most alike. *Arthrosaura* shares 18 to 20 characters with these three genera.

When the number of primitive states retained by each genus is tabulated, *Arthrosaura* has 11 out of 13 and *Ptychoglossus* 9; *Leposoma* may show the primitive state for 8 characters, although interspecific variation may result in derived states for 4 of these; *Alopoglossus,* with between 7 and 4 primitive states, and *Ecpleopus,* with 7 or 6, appear to be more highly derived.

Phyletic comparisons based on derived character states presumably give better evidence of common descent than comparisons based on primitive characters, which may be retained in many independent phyletic lines. In such comparisons, *Leposoma* and *Alopoglossus* share the highest number (6 of 13) of derived states, followed by *Ptychoglossus* and *Alopoglossus* (4).

Since many of the derived character states occur variably within one or more of the genera compared, it is possible (if the genera themselves are valid)[3] that the ancestral stock that gave rise to them was heterozygous for many of the factors controlling the

---

[3] The number of features in which *Leposoma scincoides* differs from other *Leposoma* and resembles *Ecpleopus* is remarkable.

production of these states. Throckmorton (1962) presented careful arguments for such heterozygous inheritance in *Drosophila*. The presence of individuals or species with derived states for these intragenerically variable characters suggests descent from stocks that were heterozygous for controlling factors, but not common descent from derived stocks.

If variable characters are removed from consideration, only *Ptychoglossus* and *Alopoglossus* share any number of derived states (4); *Arthrosaura* shares one characteristic (short interparietal) with each of these two; *Ecpleopus* shares another (absence of hemipenial spines). In addition, *Alopoglossus* and *Ptychoglossus* share the completely plicate tongue and generally bicuspid teeth.

Although phenetically *Ecpleopus* seems almost equally close to all four other genera, sharing states for about half the characters with each, it shares the highest number of derived character states (2) with *Alopoglossus* and *Leposoma*. *Ecpleopus* is particularly close to *Leposoma scincoides*. On the other hand, the complete absence of hemipenial spines, the usually unicuspid teeth, and presence of plicae on the anterior part of the tongue of most individuals ally *Ecpleopus* most closely with *Ptychoglossus* and *Alopoglossus*.

The exact phylogenetic position of *Ecpleopus* remains unclear, but it is set off from its relatives by a series of features that are distinctive within the group.

SPECIMENS MISIDENTIFIED AS E. GAUDICHAUDI

I have examined MNHN 7048, supposedly the specimen reported by Guichenot (1855) as *Ecpleopus gaudichaudi*. The specimen is a female, 46 mm snout to vent. Scales have been rubbed off the top of the head except for the supraorbital region, the shoulders, and the tail. It is difficult to determine the identity of this specimen; clearly, however, it is not *Ecpleopus gaudichaudi*.

The dorsal body scales are quadrangular and only slightly imbricate: no keeling is perceivable, but perhaps the scales were weakly keeled at some time. The dorsal scales form transverse series only; laterally, the scales have the same shape, but there is a wide zone of intercalation of additional rows between the dorsal rows, which become narrower on the sides. The lateral scales adjacent to the ventral scales are very small and irregular, forming a fold along the sides of the body. The ventrals are square, in 12 longitudinal and 24 transverse rows. There are 41 scales around the midbody region. The anterior row of preanals has two scales; there are four elongate scales and two lateral slivers in the posterior row.

Few of the head scales can be described. There appear to be two moderately large supraoculars on each side; possibly (there is no evidence) a third small scale was present anterior to the two that can be seen. Contact with the palpebrals cannot be determined. The lower eyelid is too badly damaged to see a translucent disc if one was present. The nostril is present in the middle of a large nasal; there is no loreal, and the nasal extends in a point to the eye opening. There are five supralabials to and including the small supralabial under the posterior corner of the eye.

There are four pairs of chinshields, the anterior two of which are in contact across the midline; all are in contact with the labials. The gular crease is well developed, and the pregulars are rectangular and arranged in transverse rows; enlarged pregular scales are absent. The posterior gulars are rectangular and in seven transverse rows; the collar scales are elongate rectangles.

The subdigital lamellae on the third and fourth toes are divided proximally, but the inner scale of each pair is not tuberculate; the lamellae number about 20 under the fourth toe. Under the fourth finger, the lamellae are not divided, and number 12.

The tympanum is deeply recessed, and overhung by scales of the external opening.

There are no femoral pores.

The tongue is papillate throughout.

There are numerous characters that distinguish this specimen from *Ecpleopus gaudichaudi,* and, in fact, from all small teiids known from Patrocinio, Minas Geraes (map) or adjacent areas of Brazil, whence Guichenot's specimen supposedly came. Certain features, such as the arrangement of the nasal and absence of the loreal, suggest that this specimen belongs to some species of *Proctoporus* but I am unwilling to commit myself to this position. No member of the genus *Proctoporus* is known from any area of Brazil.

Other reports of *Ecpleopus gaudichaudi,* all from Ecuador, are based on misidentifications. Günther (1859) reported specimens of *Aspidolaemus affinis* as *Cercosaura gaudichaudi;* Boulenger (1885b) provided the correct specific name for these individuals. Boulenger (1882) reported specimens of *Pholidobolus montium* as *Cercosaura gaudichaudi,* but later (1885b) corrected the identification. Müller (1882) also reported a specimen (NHMB 3768) from Ecuador as *Ecpleopus gaudichaudi.* I have examined this specimen, and it is clearly referable to *Aspidolaemus affinis.*

RELATIONSHIPS OF ASPIDOLAEMUS AFFINIS

The second of the two species that Boulenger (1885) left in the genus *Ecpleopus* is only distantly related to *E. gaudichaudi.* The subgeneric name *Aspidolaemus* Peters, 1862, is available for this species.

Aspidolaemus affinis (Peters)

Ecpleopus (Aspidolaemus) affinis Peters, 1862: 199.

The relationships of this species are closer to *Pantodactylus, Prionodactylus,* and especially *Pholidobolus* than to *Ecpleopus gaudichaudi* (Uzzell, 1959). Among the many characters of this species that distinguish it from *Ecpleopus gaudichaudi* are the expanded first superciliary, the pigmented disc in the lower eyelid, the deeply recessed tympanum, the quadrangular to subhexagonal dorsal scales, the longitudinal rows of quadrangular ventral scales, and the calcareous spines in the hemipenis.

The relationships of *Aspidolaemus* with *Prionodactylus, Pantodactylus* and *Pholidobolus* are suggested by the two widened rows of gular scales, the longitudinal rows of ventral scales; the expanded first superciliary, and the relative shortness of the posterior preanals. The exact relationships of *Aspidolaemus* to these genera is not clear; it can be distinguished from all three by the complete absence of femoral pores and by the opaqueness of the disc in the lower eyelid. It can be distinguished from *Pholidobolus* (except for the curious *Pholidobolus anomalus* Müller, 1923) by the presence of prefrontals. It can be distinguished from *Prionodactylus* and *Pantodactylus* by the weakness of the keeling of the dorsal scales, which have several ridges.

ACKNOWLEDGMENTS

Many individuals have helped me with this study. For permission to examine material in collections in their charge, and for hospitality shown me while I was doing so, I thank Alice G. C. Grandison, British Museum (Nat. Hist.), Jean Guibé, Muséum National d'Histoire Naturelle, Walter Hellmich and Dieter Fuchs, Zoologische Staatssammlung, Munich, Robert Mertens, Senckenberg Museum, and Charles F. Walker, University of Michigan. Paulo Vanzolini, Secretaria da Agricultura, São Paulo, kindly lent me his institution's specimens of *Ecpleopus,* including the holotype of *Arthroseps fluminensis;* I especially welcomed this kindness. Material was sent for my examination by William E. Duellman (University of Kansas), Josef Eiselt (Naturhistorisches Museum, Wien), and E. Kramer (Naturhistorisches Museum, Basel); the use of this material is also much appreciated. Travel in Europe was made possible by the Peabody Museum and by a gift from Evan Commager.

LITERATURE CITED

Amaral, Afranio do. 1932. Estudos sobre lacertilios neotropicos I. Novos generos e especies de largatos do Brasil. Mem. Inst. Butantan **7**: 53-74, 55 figs.

Boulenger, George Albert. 1882. Account of the reptiles and batrachians collected by Mr. Edward Whymper in Ecuador in 1879-80. Ann. Mag. Nat. Hist. ser. 5, **9**: 457-467.

——— 1885a. Catalogue of the lizards in the collection of the British Museum, **I**. Taylor and Francis, London. 436 p., 32 pls.

——— 1885b. Catalogue of the lizards in the collection of the British Museum **II**. Taylor and Francis, London. 497 p., 24 pls.

——— 1898. Third report on additions to the lizard collection in the Natural History Museum. Proc. Zool. Soc. London, 1898: 912-921.

Burt, Charles E., and May Danheim Burt. 1931. South American lizards in the collection of The American Museum of Natural History. Bull. Amer. Mus. Nat. Hist. **61**(7): 227-395.

Camp, Charles Lewis. 1923. Classification of the lizards. Bull. Amer. Mus. Nat. Hist. **48**(11): 289-481.

da Cunha, Osvaldo Rodrigues. 1967. Lacertîlios da Amazônia. III: O gênero "Arthrosaura" Boulenger, 1885 (Lacertilia, Teiidae). Atas Simp. Biota Amazonica, **5** (Zoologia): 141-170.

Duméril, André M. C., and G. Bibron. 1839. Erpétologie général ou histoire naturelle complète des reptiles, **V**. Librairie Encyclopedique de Roret, Paris. 854 p.

Fouquette, M. J., Jr. 1968. Observations on the natural history of microteiid lizards from the Venezuelan Andes. Copeia 1968 (4): 881-884.

Guichenot, Alphonse. 1855. Reptiles, p. 1-95. *In* Francis de Castelnau, Animaux nouveaux ou rares recueillis pendant l'Expédition dans les Parties Centrales de l'Amérique du Sud . . . pendant les années 1843 á 1847, **2**. P. Bertrand, Paris.

Günther, Albert. 1859. List of the cold-blooded Vertebrata collected by Mr. Fraser in the Andes of western Ecuador. Proc. Zool. Soc. London, 1859: 89-93.

McDowell, Samuel Booker, Jr., and Charles M. Bogert. 1954. The systematic position of *Lanthonotus* and the affinities of the anguinomorphan lizards. Bull. Amer. Mus. Nat. Hist. **105** (1): 1-142, 16 pls.

Müller, F. 1882. Erster Nachtrag zum Katalog der herpetologischen Sammlung des Basler Museums. Verhandl. Natur. Gesell. Basel **7** (1): 120-165.

Müller, Lorenz. 1923. Neue oder seltene Reptilien und Batrachier der Zoologischen Sammlung des bayr.Staates. Zool. Anz. **57** (3-4): 49-61.

Peters, Wilhelm H. C. 1862. Über *Cercosaura* und die mit dieser Gattung verwandten Eidechsen aus Südamerica. Abh. Akad. Wiss. Berlin, 1862: 165-225, pls. 1-3.

Rooij, Nelly de. 1915. The reptiles of the Indo-Australian archipelago, I. Lacertilia, Chelonia, Emydosauria. E. J. Brill, Ltd., Leiden. 384 pp.

Ruibal, Rodolfo. 1952. Revisionary studies of some South American Teiidae. Bull. Mus. Comp. Zool. Harvard Coll. **106** (11): 477-529.

Seiller, Rudolf Freiherrn von. 1892. Die Zungendrüsen von *Lacerta*, p. 250-258, pls. 15, 16. *In* Festschrift zum siebenzigsten Geburtstage Rudolf Leuckarts. Leipzig.

Throckmorton, Lynn H. 1962. The problem of phylogeny in the genus *Drosophila*. Studies in Genetics **2**: 207-343.

Tschudi, J. J. von. 1847. Die familie der Ecpleopoda. Archiv für Naturgeschichte **13** (1): 41-60.

Uzzell, Thomas M., Jr. 1959. Teiid lizards of the genus *Placosoma*. Occ. Pap. Mus. Zool., Univ. Michigan, 606: 1-16.

———— 1962. Additional notes on teiid lizards of the genus *Placosoma*. Copeia 1962 (4): 833-835.

———— 1965. Teiid lizards of the genus *Echinosaura*. Copeia 1965 (1): 82-89.

———— 1966. Teiid lizards of the genus *Neusticurus* (Reptilia, Sauria). Bull. Amer. Mus. Nat. Hist. **132** (5): 277-328.

Werner, Franz. 1910. Über neue oder seltene Reptilien des Naturhistorischen Museums in Hamburg. Mitt. Naturhist. Mus. Hamburg, **27**: 1-46.

———— 1913. Neue oder seltene Reptilien und Frösche des Naturhistorischen Museums in Hamburg. Jahr. Hamburg Wiss. Anst. **30**, Beiheft 2: 1-51.

INFORMATION FOR AUTHORS

REVIEW	The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
STYLE	Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).
FORM	Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.
TITLE	Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
ABSTRACT	The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
NOMENCLATURE	Follow the International Codes of Zoological and Botanical Nomenclature.
ILLUSTRATIONS	Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
FOOTNOTES	Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
TABLES	Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
REFERENCES	The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
THOR'S COPIES	Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
PROOF	Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
COPYRIGHT	Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 136. 26 AUGUST 1969.

NEW SPECIES AND SYNONYMY IN THE GENUS MELEOMA (NEUROPTERA, CHRYSOPIDAE), WITH A DISCUSSION OF GENITALIC HOMOLOGIES

PHILLIP A. ADAMS

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

NEW SPECIES AND SYNONYMY IN THE GENUS MELEOMA (NEUROPTERA, CHRYSOPIDAE), WITH A DISCUSSION OF GENITALIC HOMOLOGIES

PHILLIP A. ADAMS*

Department of Biology and Peabody Museum of Natural History, Yale University

ABSTRACT

Three new species of *Meleoma* are described, *carapana* from Mexico, *poolei* from Venezuela, and *festivata* from Colombia. *M. dolicharthra* (Navás) (=*M. cavifrons* Banks, new synonymy) is redescribed; *M. tezcucana* (Banks) (from *Chrysopa*) new combination, is recorded from Arizona. The pseudopenis of Chrysopidae is homologous to the mediuncus; the secondary mediuncus of *Meleoma* derives from fused gonocoxite dorsal horns as found in *M. poolei,* members of *Chrysopa* s. str., and the *Chrysopa lineaticornis* group.

---

* Present address: Dept. of Biology, Calif. State College, Fullerton, Calif., 92631.

POSTILLA 136: 18 p. 26 AUGUST 1969.

INTRODUCTION

Two of the new species described below represent the first records of this genus from South America. *Meleoma* is a highly specialized derivative of *Chrysopa,* in which the majority of species show secondary sexual dimorphism or possess a stridulatory mechanism which is unique for Neuroptera. The two new South American species appear to be transitional between *Chrysopa* and *Meleoma,* both in male genitalic characters and in structure of the male frontal pit and horn; they are therefore of significance both toward understanding evolutionary trends and in interpreting genitalic homologies in *Meleoma.*

Tjeder (1966) recognizes several subgenera of *Chrysopa,* based upon male genitalic characters. In some cases, it is not possible to assign females to these subgenera without having associated males of the same species. Similarly, it would not be possible to assign females of some species to *Meleoma,* unless the associated males were known. Therefore the suggestion put forth by MacLeod (personal communication) that *Meleoma* be considered a subgenus of *Chrysopa* has considerable merit. On the other hand, I regard the specializations of the male genitalia, together with the very unusual modifications of the male head, or wing veins, and the stridulatory apparatus, as sufficiently important to warrant continuing the traditional generic separation from *Chrysopa.*

ABBREVIATIONS

ac—acumen; bg—bursal gland; coll.g.—colleterial gland; dh—dorsal horn; fc—fertilization canal; gcx—gonocoxite; gs— gonarcus; gsac—gonosaccus (sclerotized sac beneath mediuncus); hy.i. —hypandrium internum; mu—mediuncus; ovd—oviduct; psm—pseudomedia; Rs—radial sector; sb—sclerotized band connecting mediuncus and gonarcus; smu—secondary mediuncus; sp—spermatheca; 8S—eighth sternite; 8T—eighth tergite; 10S—tenth sternite, or subanale.

Meleoma carapana, sp. n.

Figures 1-7

DESCRIPTION OF HOLOTYPE. Head (Figs. 1, 2): maxillary palpi black-spotted exteriorly; clypeus and vertex yellow-green, clypeus black-bordered, vertex with two faint reddish stripes. Ocular border and genae paler, brown genal spot barely distinct. Clypeus angulate anteriorly, with median ridge; frons elevated, with two prominent tufts of hairs bent posteriorly and laterally. Shallow transverse depression below antennae, with oval median aperture to seta-lined cavity; below each antenna, a small oval setose sclerite, below the horn a larger oval plate bearing short, spinose microtrichia. Frontal horn hardly extends beyond antennal articulation, squarely truncate, with two lateral and one median hair tufts, and two shallow dorsal oval depressions. Vertex low. Scapes long, straight, somewhat bulbous apically. Flagellum unmodified. Pronotum with red spot on each anterior corner, and a very thin anterior median red line; sides straight, anterior margin curved, sulcus lies 1/5 of length anteriorly to posterior margin, preceded by a prominent transverse ridge; a few pale setae laterally, bare medially. Body and legs green, no median pale stripe.

Forewing: longitudinal veins green, costal veinlets pale anteriorly, those near wing base dark for most of their length; transverse veins and branches of Rs dark at ends, gradates entirely dark, a few marginal veinlets dark at the forks. Hindwing: veins green except several costal veinlets and anterior ends of radials, dark. Setae pale, short, sparse. In forewing, entire radial system slightly inflated, especially the radial crossveins under the stigmal base, at their posterior ends. Forewing costals 22, 25; radials 14, 13, free branches of Rs 8, 9; inner gradates 7, 7; outer gradates 7, 8; seven apparent crossveins in pseudomedial space beyond intramedian cell. Length/width of third gradate cell from wing base 3.8; height of costal area/width of longest costal cell 1.74; width of radial area/height of costal area 1.34.

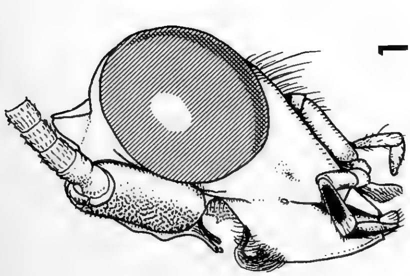
Genitalia. Ninth tergite and ectoprocts inflated dorsally, blunt apically, setae on posterior surface medially directed (Figs. 3, 4). Secondary mediuncus broad-based, apex slender, down-curved, with blunt dorsal spine (Figs. 4, 5). True mediuncus, or "pseudopenis" (mu) narrow basally, broadly paddlelike apically, upcurved. Gonocoxites (gcx) form sides of bowl-shaped depression. Membranous ventral sac bears long setae dorsally; ventral and lateral surfaces bluntly microspinose. Transverse arch a small papilla ("acumen", Fig. 4, ac); tenth sternite a small transverse oval. Gonapsis as in Fig. 7 (right); hypandrium internum with large comes attached near gonopore.

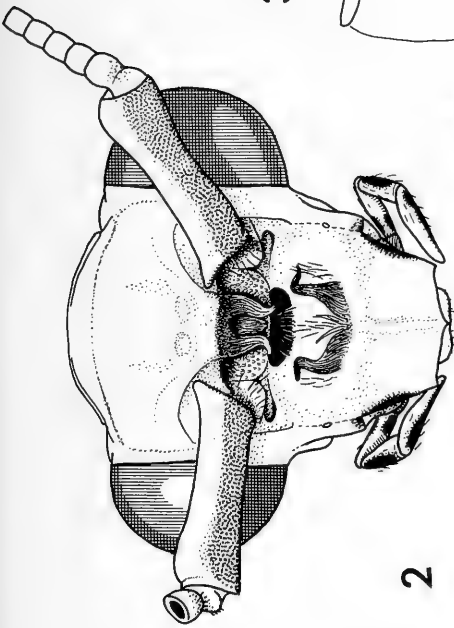
MEASUREMENTS. Forewing length 15.5 mm, width 4.8 mm; pronotal length/width ratio 1.06; antenna about 9 mm.

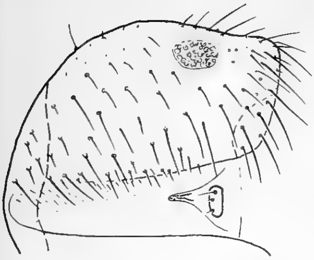
HOLOTYPE. Male, 3 miles east of Carapan, Michoacán, México. 10 July 1963, F. D. Parker and L. A. Stange, leg. Peabody Museum of Natural History. (No other specimens seen.)

DISCUSSION. This species is related to *Meleoma hageni* Banks. *M. hageni* differs in having a larger cavity, extending nearly the full width of the face, a longer frontal horn, with shorter setae, and scapes (about 2/3 as long as in *M. carapana*), each with prominent round anterobasal bulge, stouter flagellum, and black genal stripe. The mediuncus of *M. hageni is* more slender, with two small, dorsal, winglike projections instead of a median horn, and the pseudopensis is upcurved and slender, with a pointed tip. The wings are similar, but in *Meleoma hageni,* the basal costal veinlets are black only at their bases (for most of their length in *M. carapana*). The marginal fork of psm is 2.9 times longer than wide in *hageni,* and 1.8 times in *carapana; hageni* has longer setae on the veins. The pronotum of male *hageni* has a dense covering of very short, fine setae; in *carapana* it is bare, except for a few pale marginal setae.

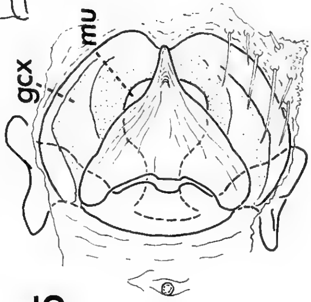
FIGS. 1-7, *Meleoma carapana,* n. sp., holotype (male). 1-2) head, extent of red scape marks indicated by stipple; 3) right ectoproct and 10th sternite, apical view; 4) abdominal apex, lateral; 5) genital armature, dorsal; 6) 8th and ninth sternites, ventral; 7) hypandrium internum (left) and gonapsis (right) (same scale as Fig. 5).


1

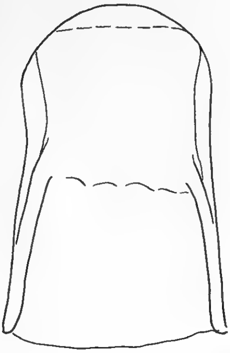

2

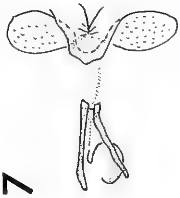

3

4



5


6


7

Meleoma dolicharthra (Navas), n. comb.

Figures 8-10, 12

Chrysopa dolicharthra Navás, 1914, Ann. Soc. sci. Bruxelles 38: 96. Holotype ♂, "Capetillo, Guatemala, G. C. Champion, Godman-Salvin Collection, 1913—214," Brit. Mus. (Nat. Hist.).

Meleoma dolicharthra Kimmins, 1940, Ann. Mag. Nat. Hist. (11)5: 448; Banks, 1945, Psyche 52: 172.

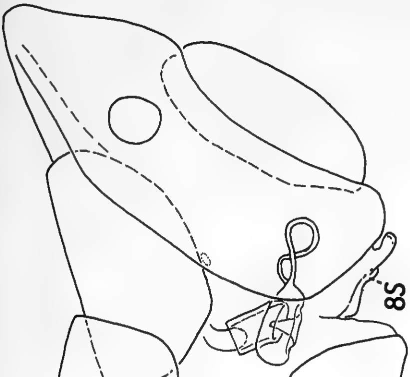
Meleoma cavifrons Banks, 1950, Psyche 57: 46. *New synonymy.* Holotype ♂, "Pinecrest, Tuolumne Co., Calif., VII-10-48 (P. H. Arnaud, Jr.), MCZ No. 28350," Mus. Comp. Zool.

DESCRIPTION. Interantennal horn bifid, and densely setose apically (Fig. 9). Median horn slender with hook-like apical expansion, and lateral hair-tufts (Fig. 8). Facial cavity wide, with deep lateral pits. Frons inflated, bearing a few short hairs beneath frontal horns. Scape slender (in the figure, the right antenna has been drawn as if rotated upward, to show a frontal view; in the type of *dolicharthra,* both scapes point anteriad). Anterior clypeal margin angulate, with small median ridge. Abdominal apex similar to that of *carapana* (Fig. 4). Secondary mediuncus broad, with slight dorsal ridge, lateral margins downcurved; true mediuncus or "pseudopenis" upcurved, apex spatulate (Fig. 10, 12).

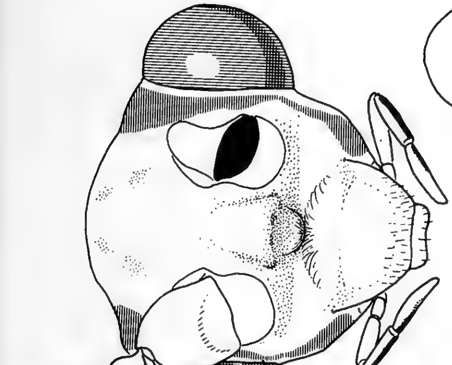
REMARKS. The synonymy of *Meleoma cavifrons* and *M. dolicharthra* was discovered during preparation of the description of *M. carapana.* Since no adequate description of either *M. dolicharthra* or *M. cavifrons* has previously appeared, drawings of the more important diagnostic features of the type of *dolicharthra* have been included. A fuller redescription will be given by Tauber (in press).

FIGS. 8-10, 12, *Meleoma dolicharthra,* holotype (male). 8-9) head; 10) genital armature, lateral, sclerites stippled; 12) same, dorsolateral, showing partially sclerotized sac beneath pseudopenis.

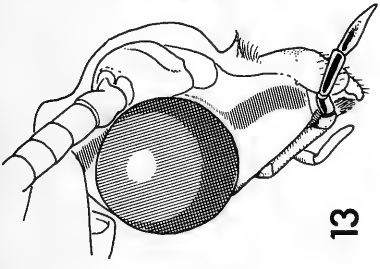
FIG. 11, *Meleoma tezcucana,* female; 8th sternite, ventral.



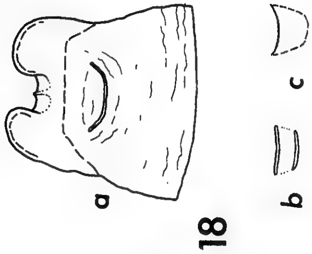
15



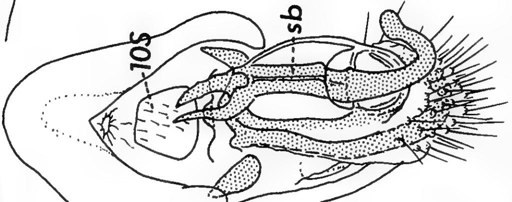
14



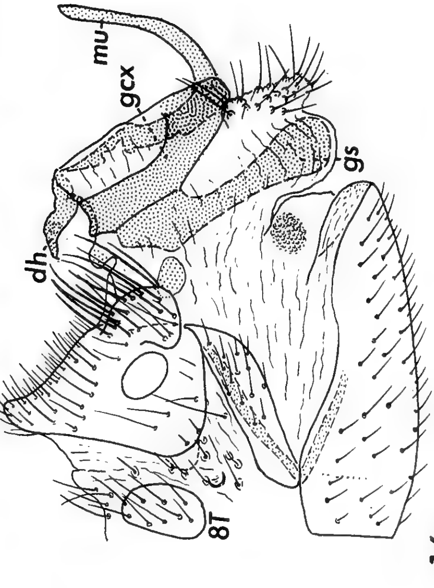
13



18



17



16

Meleoma tezcucana (Banks), n. comb.

Figure 11

Chrysopa tezcucana Banks, 1948, Psyche 55: 157-158, Fig. 7, 11, 28, 31.

TYPES. Holotype: female, "Lomas de Chapultepec, Mexico City, 8-VIII-40, [leg.] A. Dampf, Mex. M.C.Z. Type #27993." In the Museum of Comparative Zoology. The abdomen, which is dry, in a vial on the pin beneath the specimen, was not dissected. Paratypes in the Mus. Comp. Zool.: female, "Cuernavaca, Mor., 1240 m, 26-IV-32, #2540," (Morelos, México; the number is probably an A. Dampf field number); "Mexico City, No. 437, A. Dampf, Mex." (D. F., México, no date).

OTHER SPECIMENS. In the Peabody Museum of Natural History, there are two specimens from the United States: a male from Carr Canyon, Huachuca Mts., Cochise Co., Ariz., 28 Feb. 1964, leg. R. F. Sternitzky; a female from Sierra Vista, Cochise Co., Ariz., 16 June 1964, leg. R. F. Sternitzky. Both of the Yale specimens have dark-bordered gradate veins.

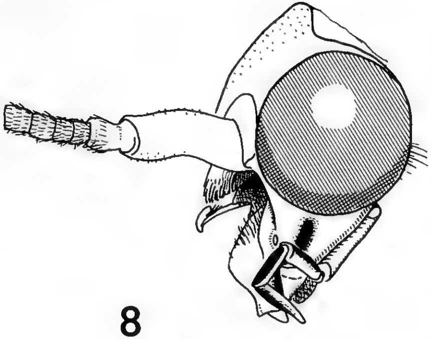
REMARKS. The eighth sternite of the Arizona female has a well-developed pocket, and the anterior margin is not distinctly delimited (Fig. 11). A complete redescription of this species will appear in Tauber's forthcoming revision of *Meleoma.*

Meleoma poolei, sp. n.

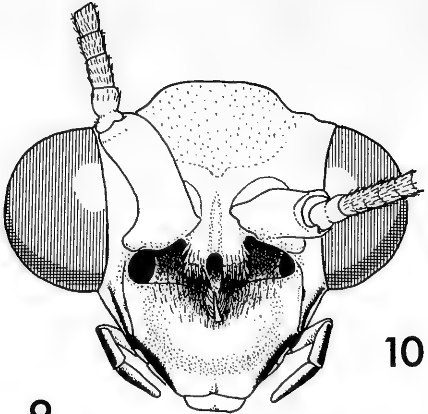
Figures 13-18

DESCRIPTION. Face (Figs. 13, 14) green, vertex ochre-yellow medially, pale laterally; clypeus unmarked, or red laterally; red

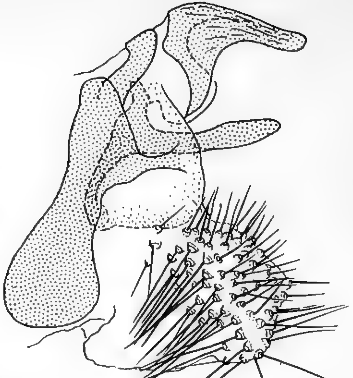
FIGS. 13-18, *Meleoma poolei* n. sp.: 13-14) male head, grey tone indicates red markings; 15) female abdomen, lateral, spermatheca shown *in situ;* 16) (holotype) male abdomen, lateral, gonarcus arms extended farther than natural to show shape of parts, transverse arch and heavily sclerotized portions of gonarcus and its appendages, stippled; 17) same, apical view; 18) female 8th sternite, ventral, a—pocket area, with single lip, b—pocket area, showing two lips, c—same, fully developed pocket present.



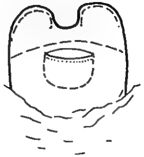
8



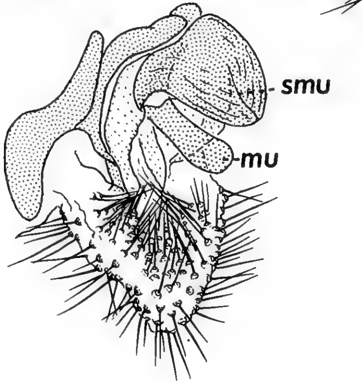
9



10



11



12

genal stripe sometimes confluent with lateral red stripes on frons, extending to vertex. Usually, two small red vertex spots. Male: labrum emarginate; clypeus very slightly convex; lower face flat. sloping upward across middle of frons, so that antennal bases lie on large bulge separated by distance equal to scape width. No interantennal horn, but a low, nearly quadrangular bulge, bearing a ligulate group of partially fused setae on transverse anterior ridge. Antennae pale, scapes subglobose, flagellum slender, basal segments slightly inflated. Female face little modified, scapes separated by 0.9 scape width; flagellum less inflated than in male, basal segments as long as wide. Maxillary palps black-lineate exteriorly.

Pronotum about as long as wide, anterior margin rounded laterally, deep sulcus at one half length. Thorax green dorsally with broad white or yellow median stripe. On pronotum, pale stripe is bordered laterally with broad red stripes, extending to sulcus; two smaller spots on posterior border. Pink spots on mesoprescutum and mesoscutum, bordering median stripe. Pleura and sterna white. Abdomen narrowly green laterally, with ivory median stripe irregularly bordered laterally with red.

Wing veins pale green; in forewing, transverse veinlets and crossveins red at ends, gradates red, cubital crossveins red. Marginal veinlets red at the forkings. Forewing slender, costals 22-(24.3)-27; radials 12-(12.6)-15, free branches of Rs 8-(♀ 9.6, ♂ 9.3)-10, inner gradates 7-(7.7)-9, outer gradates 8-(♀ 8.7, ♂ 8.3)-10, apparent pseudomedial crossveins beyond intramedian cell 7. Gradate series subparallel, inner series about halfway between Rs and outer series. Wing setae dark, curved, as long as about 0.4 width of gradate cells.

Male genitalia. Eighth tergite (Fig. 16, 8T) represented by two lateral plates. Ninth tergite and ectoprocts pointed dorsally, bearing rounded apical lobes, posterior margin with dense series of medially curved bristles. Callus cerci prominent, green in dried material. Gonarcus bears two dorsally directed hooks (Fig. 16, 17, dh); true mediuncus or "pseudopenis" (mu) clearly connected to gonarcus, arising from bowl-shaped depression with transverse partition; gonocoxites ("parameres") connected to bowl. Ventral sac with slender setae, membrane not spinose. Transverse arch represented by oval lateral plates and weakly sclerotized median papilla. Tenth sternite very large, setose. Gonapsis consists of lateral oval fields of short, spinose microtrichia, not sclerotized medially. Hypandrium internum with large comes, similar to that of *carapana* (Fig. 7, left), but not lying so near the genital opening.

Female genitalia. Abdomen (Fig. 15) very sharply acute; eighth sternite (Fig. 18) with one or two sclerotized lips on membrane, or small pocket, small median tooth on posterior margin, weakly sclerotized anteriorly to intersegmental fold.

MEASUREMENTS (mm, for females N=10, for males N=3, means in parenthesis). Forewing length ♀ 15.5-(16.1)-16.5, ♂ 15.0-(15.3)-15.5; width ♀ 5.2-(5.3)-5.5, ♂ 4.7-(4.8)-5.0; pronotal length/width, ♀ (1.06), ♂ (1.13); length/width, third gradate cell from base of forewing, ♀ (2.35), ♂ (1.88); height of costal area/width of longest costal cell, ♀ (2.36), ♂ (2.47); height of radial area/height of costal area, ♀ (1.1), ♂ (1.2); antenna length (estimated) 10-12.

TYPES. Holotype: male, Rancho Grande, 7 km N. of Maracay, Aragua Prov., Venezuela, 25 June 1967, leg. R. W. Poole, 1100 m, at mercury vapor lamp; Peabody Mus. Nat. Hist. Paratypes (same locality and year): males: June 18 (Mus. Comp. Zool.), June 20 (Beard Coll.), July 7 (Adams Coll.); females: June 9 (1, Peabody Mus. Nat. Hist.), June 12 (1, E. MacLeod Coll.), June 25 (3—2, Mus. Comp. Zool., 1, Peabody Mus. Nat. Hist), July 5 (1, P. Adams Coll.), July 7 (1, Beard Coll.), July 8 (5—3, Beard Coll., 1, U. S. Nat. Mus., 1, Univ. Central de Venezuela, Maracay), August 3 (2, Beard Coll.), August 5 (1, C. Tauber Coll.).

REMARKS. Until the discovery of this species, the southernmost record for *Meleoma* was Costa Rica (Tauber, in press). The species is named for the collector, R. W. Poole; all of the material formerly was in the collection of Robert Beard.

Meleoma festivata, sp. n.

Figures 19-26

DESCRIPTION. Head (Figs. 20, 21) pale, lower face greenish, vertex orange, red stripes between vertex and eye, and on genae. Antennae pale, scapes yellow above. Maxillary palpus thinly black-lineate exteriorly. Low median elevation anterior to antennae, bearing small tuft of setae apically; clypeus little elevated, frons slightly depressed posterior to frontoclypeal suture, surface porose anteriorly. Flagellum inflated and rigid basally, with short pale setae.

Thorax (Fig. 19) and abdomen green laterally, with median stripe ivory except yellow on pronotum, meso- and metascutella. Red marks on cervical sclerite near opening of scent glands, anterolateral border of pronotum, and elsewhere on thorax as indicated by dark shading in Fig. 19; abdominal ivory stripe red-bordered. Anterior pronotal margin probably rounded in life; corners angulate in dried material; sulcus moderately deep, preceded by narrow ridge.

Wing setae sparse, moderately long, decumbent. Venation pale; on forewing all crossveins wholly red except costals, apical radials, "pseudomedials" dark at ends; 2a-3a pale. Marginal veinlets red at forks. No inflation of Rs in male. Forewing costal area broad, anterior margin strongly convex; postcubital area broad. Forewing costal veinlets 24-25; radial crossveins 12; free branches of Rs+MA 8; inner gradates 5, outer gradates 7; 7 apparent crossveins beyond intramedian cell. Gradate series parallel except 2 basal inner gradates aligned.

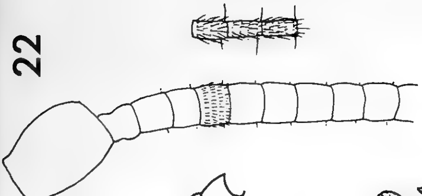
Hind wing pointed, postapical margin convex; veins pale, subcostals and radials faintly red at ends; outer gradates 6, inner gradates 4.

Male genitalia. Ectoprocts similar to those of *poolei*. Tenth sternite a narrow transverse band, close to gonarcus; transverse arch absent. Dorsal horns of gonocoxites flat, truncate, tips bent medially. Mediuncus bent more than that of *poolei*, arising from well-developed membranous pocket. Eversible setose lobe larger than in *poolei*.

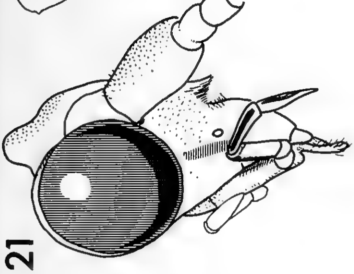
Female genitalia externally like those of *poolei*. Eighth sternite lacks median tooth of marginal notch; flask-shaped cavity opens

FIGS. 19-26, *Meleoma festivata*, n. sp.: 19) male head and thorax, dorsal; darkest shading indicates red, even gray tone indicates green, and stipple indicates yellow or orange; 20-21) male head, left antenna omitted to show facial detail; 22) male right antenna, dorsal, base and segments near tip; 23) female 8th sternite, ventral; 24) female reproductive system, left lateral; 25-26) male genital armature.

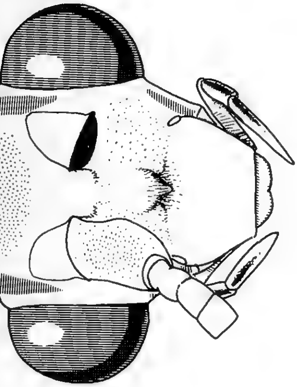
FIG. 27. "MacLeod's *Meleoma*" (Tauber, in press), secondary mediuncus, showing double structure basally.



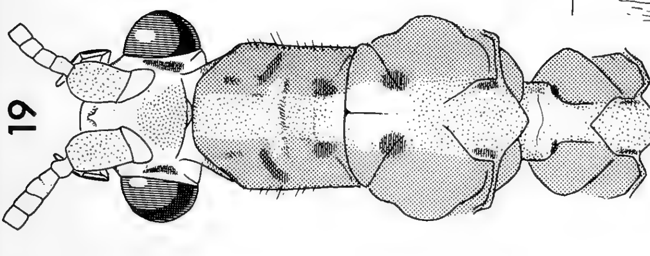
22



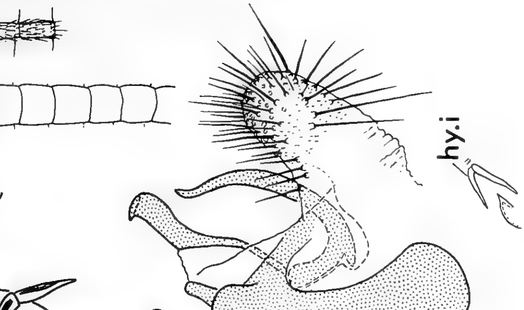
21



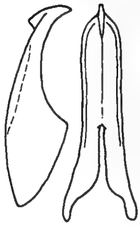
20



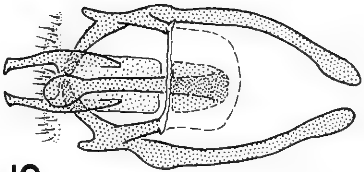
19



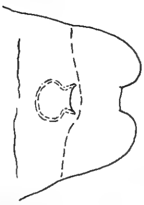
26



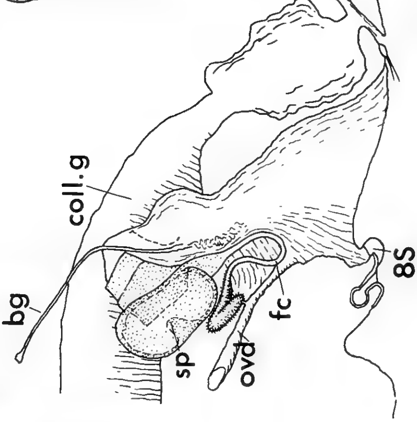
27



25



23



24

ventrally. Spermatheca with smaller ventral invagination; bursal gland ducts slender, bursa small; colleterial gland duct with flattened posterior chamber receiving two lateral ducts.

MEASUREMENTS. Male forewing length 12.8 mm, width 4.5 mm, length/width of third gradate cell from wing base 3.6; height of costal area/width of longest costal cell 2.7; width of radial area/height of costal area 1.04.

TYPES. Holotype: male, La Estrella (Antioquia), Valley of Medellín, Colombia, 1700-2000 m, at light, 8 May 1962, leg. Rev. B. Schneble; Mus. Comp. Zool. No. 31776. Allotype: female, same locality, 5 May 1962, E. G. MacLeod Collection.

DISCUSSION. This species is very similar to *poolei,* but *poolei* lacks the orange vertex mark, and the pronotum has a single stripe on each side anteriorly to sulcus. The face of *festivata* is flatter, the scale-like frontal hair tuft is smaller, and the frontal depression traverses the face in almost a straight line between the tentorial pits. The nearly flat faces of these two species, with scattered (glandular?) pores and small median hair tuft, undoubtedly represents the primitive condition, from which the deeper cavity of species such as *M. dolicharthra* has been derived. In *M. dolicharthra,* the female inserts her mouthparts into the frontal cavity during courtship (Tauber, 1966); presumably she ingests secretions which have accumulated within the cavity. In *M. festivata* and *M. poolei,* the median hair tuft may act as a wick, accumulating similar secretions.

The dorsal horns of the gonocoxites and 10th sternite of the male of *M. festivata* are distinctive. *M. festivata* resembles the other species of *Meleoma* more than does *M. poolei* in having a more loosely hinged mediuncus, lying in a better developed membranous pocket.

The gut structure and contents provide a clue to the feeding habits of these two species: the female *festivata* crop contained moth scales, but no pollen, as did one *poolei* crop. Another female *poolei* crop contained fungal fruiting bodies, and a few large, spheoroidal pollen grains. If these species visit sap fluxes on tree trunks, these contents would largely be explained.

In both these species, the apex of the crop diverticulum is elaborately ruffled. In *poolei* the proventriculus is normal, while in *festivata,* a slender cylindrical middle segment allows passage of only small particles to the hind gut. Probably both species are primarily liquid feeders, with the other materials being ingested accidentally.

Discussion of Genitalic Homologies in Chrysopidae

In the most primitive subfamily, Nothochrysinae, the male genitalic apparatus is far simpler than in *Meleoma* (Chrysopinae), consisting of an arched gonarcus, loosely hinged mediuncus, and a pair of gonocoxites articulated laterally on the gonarcus (Adams, 1967). This arrangement is clearly comparable to that in the other families of the Planipennia, is widespread in the Chrysopinae, and in all probability represents the primitive condition for Chrysopidae. Despite apparently great divergence, the genitalia of the higher chrysopids can be derived from this ground-plan.

In the Chrysopidae, the mediuncus may be either rigidly attached to the gonarcus ("mediuncus" of Tjeder), or loosely hinged ("arcessus" of Tjeder); if quite distant from the gonarcus, and of a thin, rodlike shape, it is termed a "pseudopenis" by Tjeder. The pseudopenis is ordinarily connected to the gonarcus by a flexible sclerotized band (e.g., in *Chrysopa bimaculata,* Fig. 19, sb). As Tjeder (1966) states, the pseudopenis is not present if there is an arcessus, and vice versa. There appears to be little question but that the terms "mediuncus", "arcessus," and "pseudopenis" refer to different conditions of the same morphological structure. The equivalence of the mediuncus and pseudopenis has been pointed out previously (MacLeod and Adams, 1968).

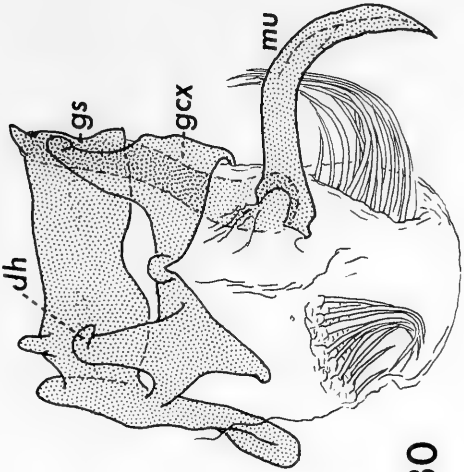
In contrast to the usual condition in Chrysopinae, all species of *Meleoma* but *poolei* and *festivata* appear to have both a mediuncus and a pseudopenis; this necessitates a secondary origin for one or the other of these structures in *Meleoma.* In *M. poolei,* the morphological identity of the pseudopenis is indicated by the sclerotized band connecting it to the gonarcus (Fig. 17, sb). This band is double, with an apparently unsclerotized median line. In most chrysopids, if the mediuncus is closely associated with the gonarcus, both the dorsal surface of the mediuncus and the flexible hinge, show a similar double structure, lightly sclerotized medially (Fig. 27). The "pseudopenis" of *M. poolei,* like that of other genera of chrysopids, appears equivalent to the mediuncus, but it includes an elongated hinge, so that the base lies remote from the gonarcus.

M. poolei is the only species of *Meleoma* with two dorsal horns on the gonarcus. The other species of *Meleoma* have, in addition to the true mediuncus ("pseudopenis"), a mediuncus-like structure that is attached to the gonarcus; according to my interpretation, the latter must be regarded as secondarily derived, presumably from the fusion of processes such as the dorsal horns of *M. poolei.* In *Meleoma,* the gonocoxites are not clearly delimited from the gonarcus, but form supports for a bowl-shaped depression lying below the "pseudopenis"; probably the dorsal horns of *M. poolei* are also part of the gonocoxites. The general configuration of the male terminalia in *M. poolei* resembles that in *Chrysopa* s. str. (Fig. 30, dh), in which the dorsally directed horns are more discernably part of the gonocoxites. Similar horns, in the *Chrysopa lineaticornis* group, also are apparently gonocoxite derivatives; frequently, as in *C. bimaculata,* the gonocoxites are closely approximated on the midline (Fig. 29). In the related *C. claveri* Navás, medial fusion is complete, so that a plate without obvious suture is interposed between the gonarcus and pseudopenis. The gonarcus-mediuncus-gonocoxite complex in this species group bears an unusual variety of horns and other processes. Considering the extreme plasticity shown by these structures, it does not seem unreasonable to conclude that the mediuncus of *Meleoma* has originated from medial fusion of the gonocoxites and their dorsal horns. This interpretation is supported by the tendency of the secondary mediuncus of *Meleoma* to show a bilobed condition basally (Fig. 27).

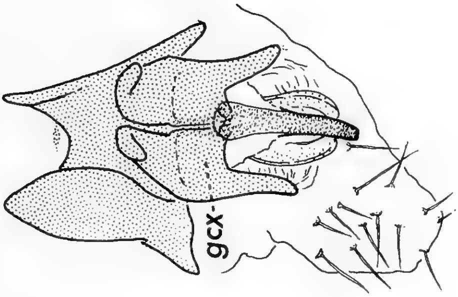
If terminology of genitalic structures is to be based upon morphological homology, a new term is required for the mediuncus-like lobe of *Meleoma; secondary mediuncus* is proposed.

FIGS. 28-29. *Chrysopa bimaculata,* internal male genital armature; 28) lateral view; 29) dorsolateral view.

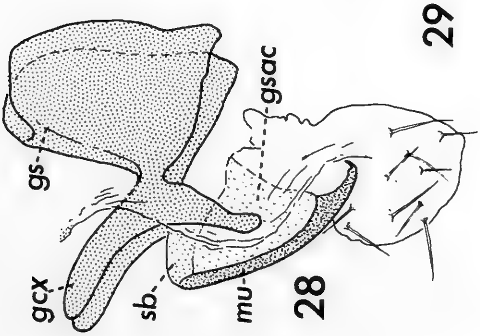
FIG. 30 *Chrysopa oculata,* internal male genital armature, mediuncus turned to right, setal tufts partially expanded basally.



30



29



28

ACKNOWLEDGEMENTS

I am indebted to Dr. Lionel Stange, Instituto Miguel Lillo, Universidad de Tucumán, Mr. Robert Beard, Cornell University, Dr. D. E. Kimmins, British Museum (Natural History), Dr. Howard E. Evans, Museum of Comparative Zoology, Harvard University, Dr. O. S. Flint, Jr., U. S. National Museum, and Dr. Ellis MacLeod, University of Illinois, for making available the material used in this study. Dr. C. L. Remington, Yale University, and Dr. Ellis MacLeod have offered helpful suggestions. Time and facilities have been made available through my appointment as Visiting Associate Curator of Insects at the Peabody Museum of Natural History, Yale University.

REFERENCES CITED

Adams, P. A. 1967. A review of the Mesochrysinae and Nothochrysinae (Neuroptera: Chrysopidae). Bull. Mus. Comp. Zool., Harvard Univ., 135: 215-238.

MacLeod, E. G. and P. A. Adams. 1968. A review of the taxonomy and morphology of the Berothidae, with the description of a new subfamily from Chile (Neuroptera). Psyche 74: 237-265.

Tauber, C. A. [C. A. Toschi] (In press). Biology and systematics of the genus *Meleoma* (Neuroptera: Chrysopidae). Univ. Calif. Publ. Entomol. (Ph.D. thesis, University of California, Berkeley, 1968.)

Tjeder, B. 1966. Neuroptera-Planipennia. The lace-wings of South Africa. 5. Family Chrysopidae. South African Animal Life 12: 228-534.

Toschi, C. A. 1966. The taxonomy, life histories, and mating behavior of the green lace-wings of Srawberry Canyon (Neuroptera: Chrysopidae). Hilgardia 36: 391-433.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

NOMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

ILLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

THOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 137. 29 SEPT. 1969

NEW GENERA AND SPECIES OF CORALLINE SPONGES (PORIFERA) FROM JAMAICA

WILLARD D. HARTMAN

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

NEW GENERA AND SPECIES OF CORALLINE SPONGES (PORIFERA) FROM JAMAICA

WILLARD D. HARTMAN

Department of Biology and Peabody Museum of Natural History, Yale University, New Haven, Conn., 06520

(Received 10 June 1969)

ABSTRACT

Three new genera including four new species of coralline sponges from Jamaica are described. The sponges are characterized by a compound skeleton of aragonite, siliceous spicules and organic fibrous elements and are related to *Astrosclera, Merlia* and *Ceratoporella.*

POSTILLA 137: 39 p. 29 SEPT. 1969.

INTRODUCTION

The rediscovery of *Ceratoporella nicholsoni* (Hickson, 1911) in Jamaican waters reported by Hartman and Goreau (1966) has been followed by the finding of four additional species of sponges with a compound skeleton of aragonite, siliceous spicules and an organic fibrous material. These coralline sponges occur in the same general habitat of the fore-reef slope environment (Goreau and Hartman, 1963) on the northern coast of Jamaica as does *Ceratoporella.* Together with *Astrosclera* Lister (1900) and *Merlia* Kirkpatrick (1908), the entire complex comprises a group of sponges with certain affinities with the class Demospongiae but with a notable difference in the presence of a basal mass of aragonite intrinsic to the sponges. It is the purpose of this paper to describe these four new species of Jamaican coralline sponges. Their affinities to other sponges are uncertain, and no higher categories are suggested at this time.

Stromatospongia, gen. nov.

TYPE-SPECIES. *Stromatospongia vermicola,* sp. nov.

DIAGNOSIS. Coralline sponges in which an aragonitic basal mass, varying in thickness from 3 mm to 4 cm, is associated with the calcareous tubes of serpulid worms. The surface of the aragonite is ornamented with lamellate or branched processes 0.8 to 2.0 mm high. The siliceous spicules are acanthostyles secreted in the superficial sponge tissue and later entrapped in argonite as the basal calcareous mass grows upward. Often the siliceous spicules protrude from the processes that arise from the surface of the basal calcareous material. This arrangement seems to come about through the fact that the heads of the spicules are joined together by a loose network of fibrous organic material that also serves as a matrix for the calcareous skeleton.

The living tissue of the sponges forms a thin veneer that fills in the irregular spaces between the processes of the calcareous skeleton. Its structural and functional organization is comparable to that of most sponges of the Class Demospongiae. Dermal pores perforate the surface of the tissue and open into vestibular cavities leading into incurrent canals that in turn communicate with excurrent channels by way of choanocyte chambers. The excurrent channels course to the surface and are there visible in living specimens as obvious varicosities along the length of which oscules open. The oscules may be localized at the center of stellate regions of convergence of excurrent channels, and these may leave faint depressions in the surface of the aragonite.

REMARKS. The generic name, feminine in gender, is derived from *stromato*—(Greek), anything spread out + *spongia* (Greek), sponge.

Stromatospongia vermicola, sp. nov.

DIAGNOSIS. An encrusting species that always grows in association with masses of tubes of a serpulid worm. Basal calcareous mass seldom exceeding 3 mm in height above the substrate; the surface of the aragonite is ornamented with multibranched processes. Siliceous acanthostyles present with mean lengths of 165 to 187μ (range of means of three specimens) and mean widths of 6.2 to 8.0μ (range of means of three specimens). The oscules may open anywhere along the length of the superficial excurrent channels. Living sponge tissue apricot to light salmon pink.

DESCRIPTION. *The calcareous skeleton.* As this species spreads over its substrate it lays down a thin layer of aragonite, usually less than 3 mm in height. The sponge occurs inevitably in association with certain serpulid worm tubes, but how this relationship begins in the life of any particular sponge is unclear. Perhaps the young sponges overgrow serpulid tubes initially. Later additional serpulids overgrow the sponge only to be overgrown by the sponge on which more serpulids settle and so on. The calcareous sponge skeleton often extends into the interior of the serpulid tubes. The eventual result of this interaction between the sponge and serpulid tubes is the formation of massive associations of calcareous matter from two sources measuring up to 40 cm in diameter and up to 10 cm in height (Fig. 1).

The surface of the aragonite laid down by the sponge is marked (Figs. 13, 17) by numerous upright, multibranched processes, 1.5

FIG. 1. *Stromatospongia vermicola* sp. nov. Holotype. YPM No. 6376. Runaway Bay, Jamaica; 31-37 m. Entire specimen, ×0.75.

to 2.0 mm high, ornamented with low rounded bosses or spines 25 to 65μ in height. The skeletal surface of *S. vermicola* is, therefore, not provided with regularly arranged pits in which the sponge tissue is organized into units as in *Ceratoporella nicholsoni* (Hartman and Goreau, in press); instead, the living tissue extends down into irregular spaces left between the branching terminal processes of the calcareous skeleton.

The aragonitic skeleton of *S. vermicola* is made up of sclerodermites (Fig. 21). Crystals of aragonite radiate in all directions from centers of calcification that are usually located around spicule heads. Secondary deposits of aragonite filling spaces at the base of some of the surface processes are apparent here and there in ground thin sections. This species spreads out laterally at a quite rapid rate, but the calcareous base grows slowly in thickness. The aragonite of *S. vermicola* has a faint pinkish-brown tint when viewed under the microscope.

Siliceous and organic skeletal elements. The range of means (with standard error) of the length of the siliceous acanthostyles of three specimens (100 measurements per specimen) is 165 (±7.0) to 187 (±7.7)μ and the overall range in length is 75 to

519μ. In width the means (with standard error) of three specimens (100 measurements per specimen) range from 6.2 (±0.15) to 8.0 (±0.18)μ, and the overall range in width is 3.3 to 13.0μ. The spicules (Fig. 2) bear several rounded or flattened, sometimes bifurcating, knobs on the head and whorls of spines on the shaft. The whorls of spines tend to be closer together at the head end. Typically the first whorl is recurved toward the pointed end of the spicule; then follow one or two whorls with straight spines. The remaining whorls of spines are recurved toward the head end. The spicules become overgrown by aragonite as the basal calcareous mass is built up, and they often protrude from the calcareous processes at the surface. Many of those embedded in aragonite are partially eroded (Fig. 21). The head of each of the spicules, including those embedded in aragonite, is surrounded by a mass of organic material continuous with sheet-like expansions of the same substance that serves as an organic matrix for the calcareous skeleton.

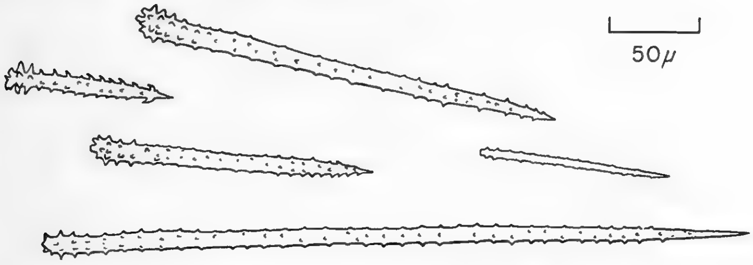


FIG. 2. *Stromatospongia vermicola* sp. nov. Siliceous spicules.

Living tissues of the sponge. The living tissues, varying from apricot (Maerz and Paul, 1950, Pl. 10, F-7) to light salmon pink (ibid., Pl. 10, A-7), form a thin veneer over the surface of the aragonite and extend downward between the branched processes that ornament the surface of the basal calcareous mass. The epidermis is supported above extensive vestibular cavities by means of vertical tracts of spicules and is perforated by ostia, 50 × 50 to 75 × 100μ in major diameters (Fig. 3). Vertical incurrent channels lead from the base of the subdermal cavities into the choanosome where they subdivide and open into spheroidal, eurypylous choanocyte chambers, 16 to 20μ in diameter (Fig. 25).

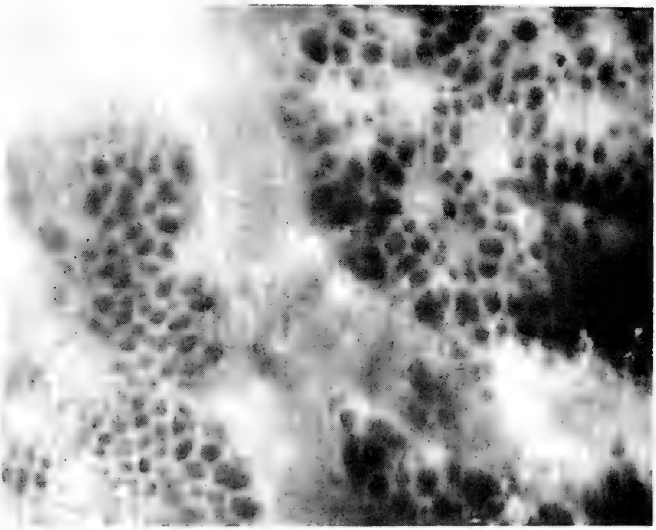


FIG. 3. *Stromatospongia vermicola* sp. nov. Portion of surface of living specimen showing ostia and a branching excurrent channel. Photographed in laboratory. ×40.

The excurrent channels run to the surface where they are apparent in living specimens as dilated tubes (Fig. 29) that may converge upon oscular areas where one to three oscules open to the exterior, or the oscules may open out anywhere along the length of the channels. The oscules are elliptical in outline and vary in diameters from $170 \times 500\mu$ to $500 \times 750\mu$; the dilated exhalant channels on the surface of the sponge vary from 0.9 to 1.2 mm in width.

Egg cells, $40 \times 25\mu$ in major diameters and with nuclei 12μ in diameter and nucleoli 4μ in diameter, are rare in sections. Several ellipsoidal cleaving embryos, probably at the 32-cell stage, and measuring $44 \times 33\mu$ in major axes, are present in sections. Although fully developed larvae have not yet been found, the available evidence suggests that this species incubates its larvae.

SYMBIONTS. The association between *S. vermicola* and the unidentified species of serpulid polychaete appears obligatory with respect to the sponge. Whether or not the serpulid occurs independent of the sponge is unknown.

Branching filamentous organisms are occasionally seen in the organic matrix in decalcified thin sections of *S. vermicola.* The irregular course taken by the filaments and their anastomoses suggest that the organisms are most probably Chlorophyta, but it is possible that they are Cyanophyta.

RANGE AND HABITAT. Known at present only from the northern coast of Jamaica where it occurs from Maria Buena Bay, Trelawny Parish, eastward to Salt Gut, St. Mary Parish. It is especially common in the fore-reef slope environment of Runaway Bay and Discovery Bay at depths of 10 to 95 m. The sponge occurs on rock walls or on the reverse sides of large reef corals, always in deep shade. Its maximum size is reached below 60 to 70 m; above 30 m, individuals are quite small.

HOLOTYPE. Peabody Museum, Yale University (YPM) No. 6376 (Fig. 1). Runaway Bay, Jamaica; 31-37 m. Collected by T.F. Goreau, March 31, 1965.

Repositories of paratypical material: United States National Museum, Smithsonian Institution, Washington, D.C.; British Museum (Natural History), London; Institute of Jamaica, Kingston. About 20 lots of specimens from Runaway Bay and Discovery Bay, Jamaica, were studied.

COMPARISON WITH OTHER SPECIES OF STROMATOSPONGIA. *S. vermicola* may be distinguished from the following species by its habit of growing in association with tangled masses of serpulid tubes on which it deposits a thin layer of aragonite. The upright, branched processes of the calcareous skeleton are higher and less closely spaced than those of the other species of the genus, and the siliceous spicules are somewhat shorter and stouter. Its apricot to light salmon pink color in life is distinctive.

REMARKS. The specific name is derived from *vermis* (Latin), worm + —*colus* (Latin), inhabiting.

Stromatospongia norae, sp. nov.

DIAGNOSIS. A species that takes the form of rounded, mammillate masses extensions of which encrust the tubes of serpulid worms that tend to grow away from the central mass of the sponge.

The basal mass of aragonite may reach a height of 4 cm above the substrate; the surface of the calcareous skeleton is ornamented with upright lamellate processes. Siliceous acanthostyles present with mean lengths of 195 (±10.6)μ to 215 (±9.5)μ (range of means of three specimens) and mean widths of 5.5 (±0.11)μ to 6.1 (±0.16)μ (range of means of three specimens). The oscules open to the exterior where a group of excurrent channels converge. Faint impressions of the stellate patterns so formed by the excurrent channels may occasionally be seen on the surface of the basal aragonitic mass. The living sponge tissue varies in color from cream to ecru biege.

DESCRIPTION. *The calcareous skeleton.* The aragonitic skeleton of this species has a basic rounded, mammillate form (Fig. 4), but cornuate processes are frequently present representing serpulid worm tubes that become associated with and encrusted by the sponge and grow out away from its central mass (Fig. 5). The largest specimens known at present are 7 cm across in the case of the mammillate form and 20 cm in greatest length for the cornuate form.

Closely set, short, lamellate processes, up to 0.8 mm high, seldom exceeding 1 mm in length, and terminating in low, rounded bosses, arise from the surface of the basal aragonitic mass (Figs. 14, 18). In some areas of the surface several such lamellae run parallel to one another and thus mark off furrows into which the living tissue extends. On other areas the lamellae are shorter and are arranged irregularly, leaving depressions of varying shapes. In fine structure the aragonite resembles that of *S. vermicola* with sclerodermite units (Fig. 22) formed of crystals radiating from centers of calcification which are frequently the organic material that surrounds the heads of entrapped siliceous spicules.

Siliceous and organic skeletal elements. The siliceous acanthostyles (Fig. 6) are similar in form to those of *S. vermicola* but are somewhat longer and thinner. The range of means (with standard error) of the length in three specimens (50 measurements per specimen) is 195 (±10.6) to 215 (±9.5)μ and the overall range in length is 75 to 519μ. In width the means (with standard error) of three specimens (50 measurements per specimen) range from 5.5 (±0.11) to 6.1 (±0.16)μ and the overall range in width is 2.7 to 9.1μ. The heads of the spicules bear several rounded

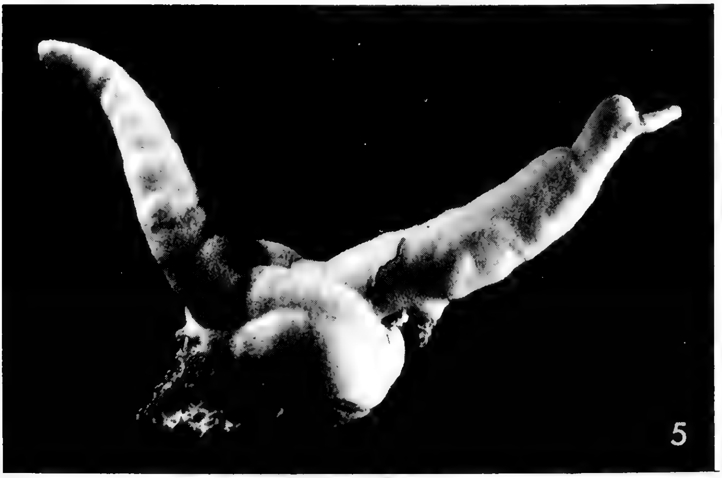
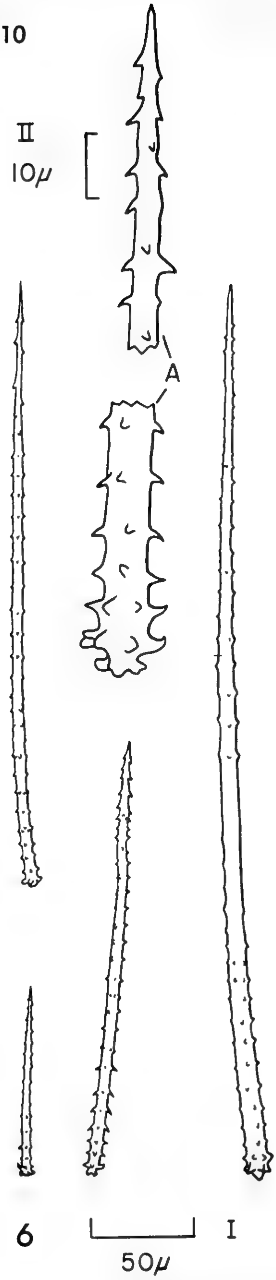


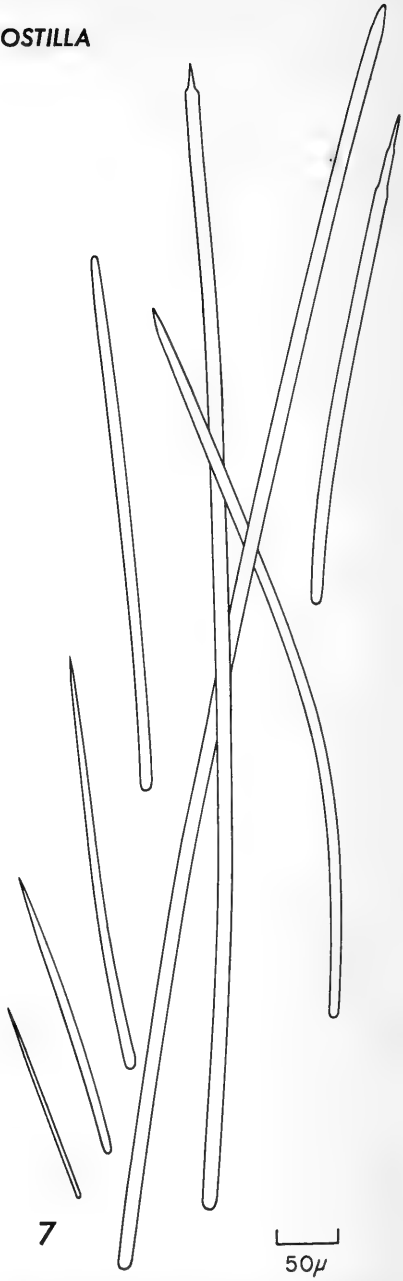
FIG. 4. *Stromatospongia norae* sp. nov. Holotype. YPM No. 7770. Runaway Bay, Jamaica; 26-28 m. Mammillate specimen, × 1.1.

FIG. 5. *Stromatospongia norae* sp. nov. Paratype. YPM No. 6463. Runaway Bay, Jamaica; 34 m. Cornuate specimen, × 1.5. Photo by Fritz Goro.

or somewhat flattened, often bifurcating knobs, and the shaft is ornamented with whorls of spines. The first one or two rows of spines at the rounded end of the spicule are recurved toward the pointed end, the next one or two rows are straight and the remaining whorls are made up of spines recurved toward the head



6



7

FIG. 6. *Stromatospongia norae* sp. nov. Siliceous spicules. Scale II refers to spicule A.

FIG. 7. *Hispidopetra miniana* sp. nov. Siliceous spicules.

end of the spicule. The spicules are embedded in aragonite as the calcareous skeleton grows upward and some of them become partially eroded. An organic material surrounds the heads of the acanthostyles and a sheetlike matrix may be observed in decalcified thin sections.

Living tissues of the sponge. These vary in color from cream (Maerz and Paul, 1950, Pl. 9, D-2) to ecru biege (ibid., Pl. 11, E-4, "maple"). Ostia, 62 to 186μ in diameter, circular to elliptical in outline and distributed quite evenly over the surface of the epidermis, lead into vestibular cavities from which vertical incurrent canals lead to the tissue masses that fill the spaces between the surface lamellate processes of aragonite. Spheroidal choanocyte chambers (Fig. 26), 15 to 17μ in diameter, join the incurrent and excurrent canals and the latter pass to the surface where they characteristically form radiating patterns (Fig. 30) as they converge upon the elliptical oscules, 350 × 500μ in major axes. The excurrent channels may leave faint, depressed stellate patterns on the surface of the calcareous skeleton in some specimens.

SYMBIONTS. Every specimen examined during the preparation of this description is associated with at least one serpulid worm tube which it has encrusted, suggesting an obligatory relationship. These worm tubes tend to grow out away from the central mass of the sponge as though attempting to escape complete overgrowth by the sponge. In *S. vermicola,* however, the serpulid tubes attach in entirety to the sponge surface and will eventually be completely covered by an aragonitic deposit secreted by the sponge.

Multibranching cavities, 1μ in width, representing the galleries of a boring organism, are common throughout the calcareous skeleton of *S. norae.* In some instances they are filled with the dried remains of chlorophyll-bearing cells and may have been formed by a species of endolithic Chlorophyta or Cyanophyta.

RANGE AND HABITAT. Known at present only from the North Coast of Jamaica where it ranges from Maria Buena Bay, Trelawny Parish, eastward to Salt Gut, St. Mary Parish. It is moderately common in the fore-reef slope environment of Runaway Bay and Discovery Bay at depths of 8 to 85 m, but chiefly above 35 m. It lives on the sides and ceilings of deep caverns and sub-reef tunnels where little light penetrates.

HOLOTYPE. YPM No. 7770 (Fig. 4). Runaway Bay, Jamaica. 26-28 m. Collected by T. F. Goreau, March 8, 1968.

Repositories of paratypical material: United States National Museum; British Museum (Natural History); Institute of Jamaica. Eight lots of specimens from Runaway Bay and Discovery Bay were studied.

COMPARISON WITH STROMATOSPONGIA VERMICOLA. *S. norae* deposits a thicker basal layer of aragonite than its congener, and the surface processes of the calcareous skeleton are lamellate in form, shorter and more closely spaced. Its siliceous spicules are somewhat longer and thinner. The color of the living tissues of the sponge vary from cream to ecru biege.

REMARKS. The specific name is given in honor of Mrs. Nora I. Goreau who has assisted greatly in studies of the histology of the coralline sponges.

Hispidopetra, gen. nov.

TYPE SPECIES: *Hispidopetra miniana,* sp. nov.

DIAGNOSIS. Coralline sponges varying in form from encrustations to dome-shaped or irregular masses up to 15 cm in diameter and at least 3 cm high. The surface of the aragonitic basal mass is covered with numerous conspicuous processes, variable in shape and up to 7 mm high. The processes are covered with rounded spines, up to 50μ high, from which protrude numerous partially embedded, smooth, stylote, siliceous spicules, slightly curved and varying greatly in length.

The living tissues vary in color from carmine to vermilion and are similar to those of *Stromatospongia* in general organization. Lophocytelike cells frequently occur.

REMARKS. The generic name, feminine in gender, is derived from *hispidus* (Latin), bristly + *petra* (Latin), rock.

Hispidopetra miniana, sp. nov.

DIAGNOSIS. An encrusting to massive species reaching 15 cm in diameter and 3 cm in height; the surface of the calcareous skeleton is ornamented with processes up to 7 mm in height and of variable shape. Siliceous smooth styles present with mean lengths of 269 (±6.9) to 301 (±10.8)μ (range of means of three specimens) and mean widths of 5.4 (±0.11) to 7.4 (±0.16)μ (range of means of three specimens). Oscules open anywhere along the length of the superficial excurrent channels. Living sponge tissue varies in color from carmine to vermilion.

DESCRIPTION. *The calcareous skeleton.* This species is encrusting in early life (Fig. 9) and grows into dome-shaped or irregular masses (Fig. 8) up to 15 cm in diameter and 3 cm high. The surface of the aragonitic skeleton bears numerous processes, obvious to the naked eye, arborescent, lamellate or knoblike in form and up to 7 mm high. In some young, encrusting specimens the processes are chiefly arborescent and in others they are knoblike; but in larger specimens the processes are variable in shape. The processes are covered with rounded spines, 25 to 50μ high, and the pointed ends of numerous long stylote siliceous spicules protrude from these (Figs. 15, 19). Serpulid worm tubes, bearing a keel 3 to 4 mm high, invariably overgrow older specimens, and the sponge overgrows them in turn, often giving the keel the aspect of a cockscomb.

The aragonitic skeleton of *Hispidopetra miniana* is similar to that of *Stromatospongia* in fine structure. Sclerodermites (Fig. 23), comprising crystals of aragonite radiating in all directions from centers of calcification, are the basic units of the skeleton. The centers of calcification are frequently located around the heads of siliceous spicules. The aragonite of this species has a pinkish-brown tint in thin sections when viewed under the microscope.

Siliceous and organic skeletal elements. The siliceous spicules (Fig. 7) are smooth, slightly curved styles varying greatly in length. The range of means (with standard error) of the length of the styles of three specimens (100 measurements per specimen) is 269 (±6.9) to 301 (±10.8)μ and the overall range in length is 125 to 818μ. In width the means (with standard error) of three specimens (100 measurements per specimen) range from 5.4

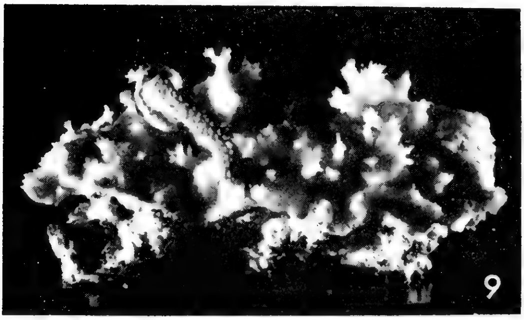


FIG. 8. *Hispidopetra miniana* sp. nov. Holotype. YPM No. 6843. Discovery Bay, Jamaica; 55-57 m. Entire specimen, ×1.25.

FIG. 9. *Hispidopetra miniana* sp. nov. Paratype. YPM No. 6459. Runaway Bay, Jamaica, 25-28 m. ×1.95. Photo by Fritz Goro.

(±0.11) to 7.4 (±0.16)μ, and the overall range in width is 1.3 to 10.4μ.

The rounded ends of the spicules are enclosed in an organic material. A fibril-bearing flocculent substance serves as a matrix for the aragonitic basal mass. Both the siliceous spicules and the organic skeletal materials are enclosed within the calcareous skeleton as the sponge increases in size. Some of the siliceous spicules, but fewer than in *Stromatospongia,* show evidence of erosion after entrapment in the aragonite.

Living tissues of the sponge. In most specimens the living tissue of *Hispidopetra miniana* varies from carmine (Maerz and Paul, 1950, near Pl. 2, L-5) to vermilion (near Pl. 2, L-12). Often the color decreases in intensity toward the base of the sponge. An occasional specimen is light pinkish-orange (near Pl. 2, D-10).

A thin, diaphanous, unpigmented exopinacoderm, often pierced by spicules, stretches between the tips of the vertical calcareous processes of the basal mass and is thus separated from the mesohyl and choanosome by extensive cavities of the incurrent and excurrent water-conducting systems. Ostia, 50 to 100μ in diameter in living specimens, are usually rather sparsely distributed but occur occasionally in groups of 50 or more. The extensive incurrent cavities beneath the exopinacoderm lead into wide incurrent canals that subdivide repeatedly and eventually communicate with eurypylous choanocyte chambers (Fig. 27), 16 to 18μ in diameter. A complicated network of low excurrent canals, 0.5 to 0.6 mm across in expanded sponges in the laboratory, runs above the exopinacoderm (Fig. 31). Oscules, circular to elliptical in outline and ranging up to 1.0 × 1.5 mm in diameter, open from these canals at any point and not only at sites of anastomoses.

Large ovoid to pear-shaped cells, 10 × 20μ in major diameters, with nucleolate nuclei, 6μ in diameter, and with processes that may extend over 30μ beyond the cell body, occur clustered at the base of the tissue where it is in contact with the calcareous skeleton. The processes are fibrillar in nature, and the cells may therefore be compared with the lophocytes described from many other sponges. The cell bodies are filled wih large granules and occasionally bear food vacuoles. It is possible, in view of their localization in the sponge, that these cells not only secrete elements of the organic matrix but also may function as calcoblasts.

SYMBIONTS. Serpulid worms grow on the surface of the calcareous skeleton of all older specimens of *Hispidopetra miniana.*

In living specimens the processes of the calcareous skeleton are bright green. The organisms responsible for the color are recognizable in ground thin sections of the skeleton where the tips of the processes are filled with a tangle of filaments of two sizes, 1.0μ and 0.4μ respectively. It is probable that these organisms are boring Chlorophyta, although some of the filaments bear a resemblance to those described by Duncan (1877, pl. 7, fig. 39-44) as boring fungi.

RANGE AND HABITAT. Known from the northern coast of Jamaica where it ranges from Maria Buena Bay, Trelawny Parish, eastward to Salt Gut, St. Mary Parish. It is common locally in the fore-reef slope environment of Runaway Bay and Discovery Bay at depths of 10 to 95 m and is restricted in these areas almost entirely to overhanging surfaces in caves, crevices and under ledges. The species increases in abundance and size of individuals with depth.

This species is also known from the southern coast of Jamaica where two specimens were dredged in 40 m south of Great Pedro Bay by R/V *Gosnold.*

HOLOTYPE. YPM No. 6853 (Fig. 8). Discovery Bay, Jamaica; 55-57 m. Collected by Roma Chapman, July 20, 1966.

Repositories of paratypical material: United States National Museum; British Museum (Natural History); Institute of Jamaica. Ten lots of specimens from Runaway Bay and Discovery Bay, Jamaica, were studied.

COMPARISON WITH OTHER CORALLINE SPONGES. *Hispidopetra miniana* is readily distinguished from other Jamaican coralline sponges by its carmine to vermilion color in life and its long, smooth stylote siliceous spicules. The surface processes of the aragonitic basal skeleton are more prominent (up to 7 mm in height) than in any other known species and are often marked by protruding siliceous spicules.

REMARKS. The specific name is the Latin word for vermilion.

Goreauiella, gen. nov.

TYPE SPECIES. *Goreauiella auriculata,* sp. nov.

DIAGNOSIS. Coralline sponges with an auriculate or saucer-like form, living attached to the substrate by a broad peduncle. Individuals vary up to 16 cm in diameter and 3 mm in thickness. The surface of the aragonite is covered with delicate arborescent processes, up to 1 mm or more in height, and is marked by raised, branching patterns that run to the edge of the skeleton. Siliceous spicules in the form of short acanthostrongyles or truncate acanthostyles are present and become embedded secondarily in the aragonitic basal mass.

The living tissue forms a thin veneer that fills in the intricate spaces between the surface processes of the aragonitic skeleton. The organization of the tissue is similar to that described for *Stromatospongia* except that in this form all the oscules open at the edge of the sponge and the excurrent canals at the surface run toward the peripheral oscules.

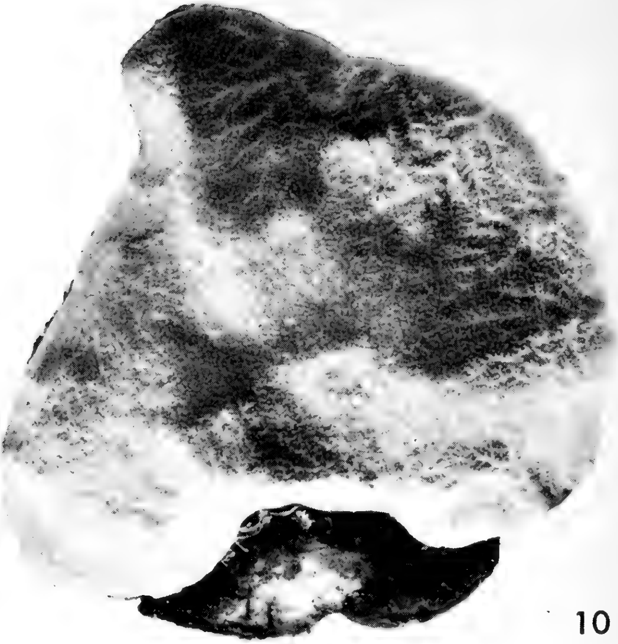
REMARKS. The genus, feminine in gender, is named in honor of Dr. Thomas F. Goreau, who discovered the remarkable fauna of coralline sponges on the Jamaican reefs.

Goreauiella auriculata, sp. nov.

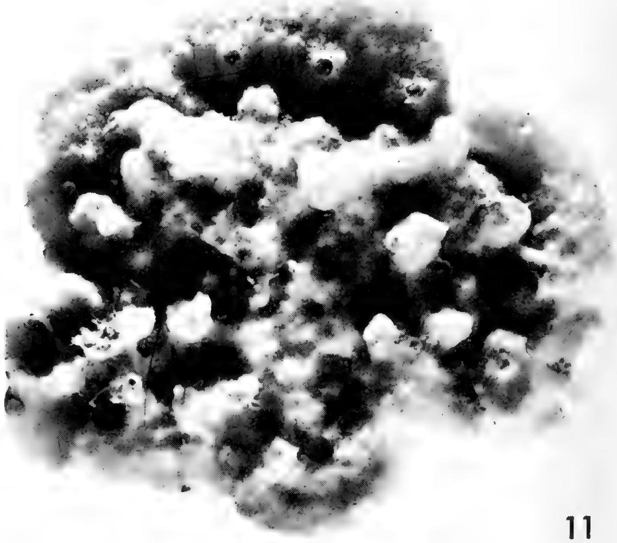
DIAGNOSIS. With the skeletal characters of the genus. Living tissue, various shades of light yellow, with a pattern of organization as described above.

DESCRIPTION. *The calcareous skeleton.* The aragonitic basal mass has an auriculate or shallow dishlike shape (Fig. 10), with the edges upturned or curled downward, and is attached to the substrate by a broad peduncle. Individual sponges range up to 16 cm in longer diameter, but the calcareous skeleton is very thin, seldom exceeding 3 mm. Numerous, closely set, delicate, arborescent calcareous processes (Figs. 16, 20), from 0.5 to 1.1 mm in height, arise from the surface of the calcareous skeleton; the processes are covered with rounded spines, 12 to 40μ high. When viewed with the unaided eye the surface of the calcareous skeleton of most specimens reveals raised multibranching patterns resembling the delta systems of rivers (Fig. 10) and draining to the very edge of the skeleton. Under a dissecting microscope it is apparent that these raised areas result from an increased height of the arborescent processes that cover the surface.

As in the other coralline sponges described, the basic units of



10



11

FIG. 10. *Goreauiella auriculata* sp. nov. Holotype. YPM No. 6858. Runaway Bay, Jamaica, 25 m. Entire specimen, × 1.4.

FIG. 11. *Goreauiella auriculata* sp. nov. Paratype. YPM No. 7773. Runaway Bay, Jamaica, 26-28 m. Entire specimen with upright processes induced by presence of commensal zoanthideans. × 1.3.

the calcareous skeleton are sclerodermites (Fig. 24) made up of crystals of aragonite radiating out from centers of calcification. The aragonite is colorless in this species when ground thin sections are examined microscopically.

Siliceous and organic skeletal elements. The siliceous spicules (Fig. 12) are relatively short rods of equal diameter throughout, straight, slightly curved or with a pronounced curve; each is ornamented with whorls of spines that vary greatly in size and orientation. Typically one end of the spicule is provided with rounded knobs or a whorl of spines recurved toward the opposite end; there follow one to three whorls of spines recurved in the same direction. Then one or two whorls of straight spines occur followed by many whorls of spines recurved toward the end with blunt knobs. The tip of the spicule is provided with a whorl of straight or recurved spines. The orientation of the spines is thus reminiscent of that in *Stromatospongia vermicola* and *norae,* although the spicules of these species are stylote and lack the terminal whorl of spines. In *Goreauiella auriculata* the spines vary in length from less than 1μ to 5μ. The spicules become embedded in aragonite as the calcareous base builds up, and some of them show evidence of erosion as in the other coralline sponges described above. Mean values for length and width measurements

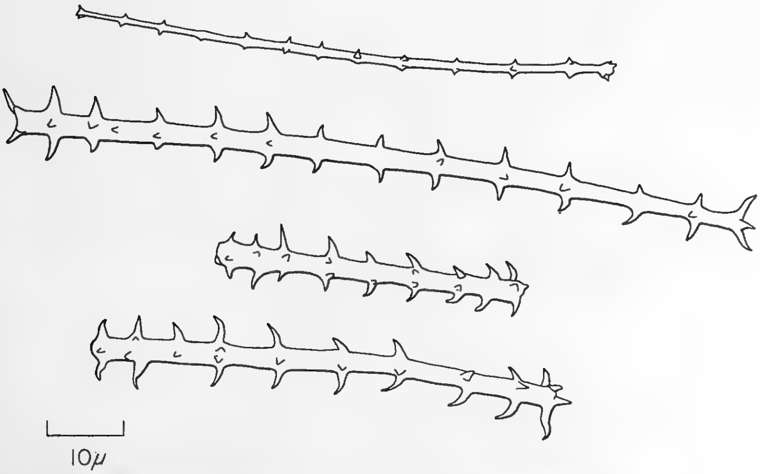


FIG. 12. *Goreauiella auriculata* sp. nov. Siliceous spicules.

(with standard errors) of spicules of three specimens (50 spicules measured per specimen) are 60 (±1.5) to 68 (±2.3)μ by 2.3 (±0.06) to 2.7 (±0.08)μ. Overall ranges in length are 35 to 124μ, and in width, 1.3 to 3.9μ.

That end of each spicule that bears blunt knobs is always enclosed in an organic material, suggesting that the end in question corresponds to the rounded end of the styles in *Stromatospongia* and *Hispidopetra.* A fibril-bearing flocculent material remains as a matrix after decalcification.

Living tissues of the sponge. The color of the living tissue of *Goreauiella auriculata* varies from straw yellow (Maerz and Paul, 1950, Pl. 10, F-2) to chrome lemon (Pl. 9, K-2) or yellowish-gray. Ostia, 50 to 150μ in diameter in the living sponge, are evenly distributed over the exopinacoderm between the branching excurrent canals. The ostia lead into vestibular cavities lying beneath the exopinacoderm and these in turn lead into wide incurrent canals which, after branching, open into eurypylous choanocyte chambers (Fig. 28), 14 × 15 to 18 × 26μ in major diameters. The oscules, with diameters of approximately 300μ, open out along the edge of the sponge where their positions are marked by indentations in the periphery of the calcareous skeleton. The excurrent canals (Fig. 32) are transparent, dotted with fine white spots and receive short side branches from the adjacent tissues as they run along the surface of the sponge. The systems of branching excurrent canals lie directly above the raised branching patterns of the calcareous skeleton described above, suggesting that the flow of water in the former influences the deposition of aragonite beneath each canal.

SYMBIONTS. Orange-tan zoanthideans occasionally grow with *Goreauiella auriculata.* The polyps often induce the formation of processes of the calcareous skeleton (Fig. 11) reaching heights of one cm and widths up to 6 mm. The zoanthideans, distributed over the surface of the sponge at intervals of 6 to 8 mm, sit in depressions in the calcareous skeleton. Whether or not the polyps are interconnected by stolons is unknown.

Boring algae, probably Chlorophyta but possibly Cyanophyta, with filaments 1.2μ in width, are commonly present in the calcareous processes of the skeleton.

RANGE AND HABITAT. Found on the northern coast of Jamaica from Maria Buena Bay, Trelawny Parish eastward to Salt Gut, St. Mary Parish. It is common in the fore-reef slope environment of Runaway Bay and Discovery Bay at depths of 8 to more than 70 meters. It is most abundant in narrow passages in the reef framework and occurs also in larger caves; in both habitats the sponges are found attached to the ceiling of the cavities and are suspended with the tissue side down.

HOLOTYPE. YPM No. 6858 (Fig. 10). Runaway Bay, Jamaica; 25 m. Collected by T. F. Goreau, March 8, 1968.

Repositories of paratypical material: United States National Museum; British Museum (Natural History); Institute of Jamaica. Eighteen specimens from Runaway Bay and Discovery Bay, Jamaica, were studied.

COMPARISON WITH OTHER CORALLINE SPONGES. *Goreauiella auriculata* is distinguished by its auriculate external form and yellowish color in life. The siliceous spicules are short, truncate acanthostyles with a terminal whorl of spines. The delicate arborescent processes of the aragonitic basal skeleton and the raised, branching patterns running to the edge of the skeleton are additional distinctive features of this species.

REMARKS. The specific name is derived from *auricula* (Latin), diminutive of *auris,* ear.

ACKNOWLEDGMENTS

I am deeply grateful to Thomas F. Goreau, University of the West Indies, Kingston, Jamaica, and the State University of New York at Stony Brook, who entrusted the description of these remarkable sponges to me. He and his diving associates, Eileen A. Graham, Roma Chapman, Paul Chapman, Judith Lang and the late R. S. Jackson collected the specimens upon which this study is based. Nora I. Goreau and Aimorn Stewart assisted in the histological work. T. F. Goreau and Fritz Goro kindly made available to me the photographs accredited to them. I am also indebted to A. H. Coleman and Diane M. Barker who assisted in the photography and to my wife, Shirley G. Hartman, who prepared the drawings.

This study was supported in part by National Science Foundation grant GB-7343.

LITERATURE CITED

Duncan, P. M. 1877. On some thallophytes parasitic within recent Madreporaria. Proc. roy. Soc. London **25**: 238-257.

Goreau, T. F., and W. D. Hartman. 1963. Boring sponges as controlling factors in the formation and maintenance of coral reefs, p. 25-54. *In* R. F. Sognnaes[ed.] Mechanisms of hard tissue destruction. AAAS Publ. 75. Washington, D. C.

Hartman, W. D., and T. F. Goreau. 1966. *Ceratoporella,* a living sponge with stromatoporoid affinities. Amer. Zool. **6**: 563-564.

Hartman, W. D., and T. F. Goreau. [In press.] Jamaican coralline sponges: their morphology, ecology and fossil relatives. *In* W. G. Fry [ed.] Biology of the Porifera. Symp. zool. Soc. London, no. 25. Academic Press, London.

Hickson, S. J. 1911. On *Ceratopora,* the type of a new family of Alcyonaria. Proc. roy. Soc. London (B) **84**: 195-200.

Kirkpatrick, Randolph. 1908. On two new genera of recent pharetronid sponges. Ann. Mag. nat. Hist., ser. 8, **2**: 503-514.

Lister, J. J. 1900. *Astrosclera willeyana,* the type of a new family of sponges, p. 459-482. *In* Arthur Willey, Zoological Results, vol. 4.

Maerz, A., and M. R. Paul, 1950. A dictionary of color. McGraw-Hill Book Co., Inc., New York. 2nd ed. 208 p.

FIG. 13. *Stromatospongia vermicola* sp. nov. Enlarged view of processes on surface of aragonitic basal skeleton, living tissues removed. YPM No. 6379. Discovery Bay, Jamaica; 71 m. × 10.

FIG. 14. *Stromatospongia norae* sp. nov. Enlarged view of processes on surface of aragonitic basal skeleton, living tissues removed. YPM No. 6463. Runaway Bay, Jamaica; 34 m. × 10.

13

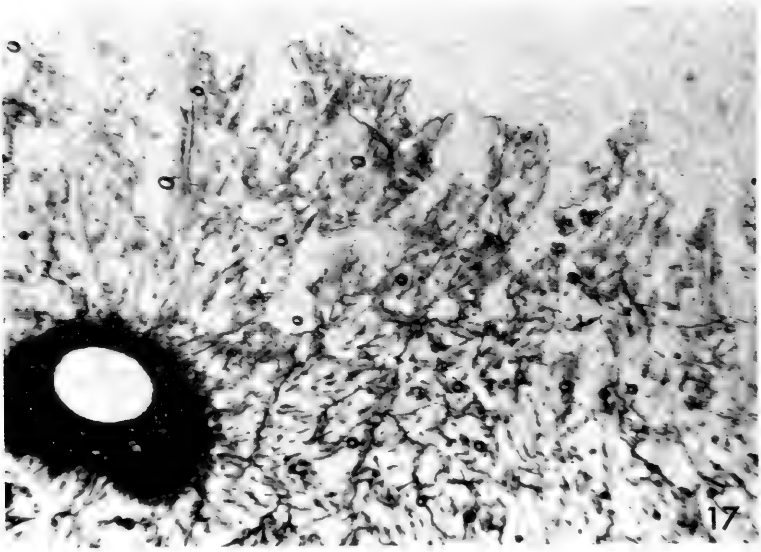
14

FIG. 15. *Hispidopetra miniana* sp. nov. Enlarged view of processes on surface of aragonitic basal skeleton, living tissues removed. Numerous siliceous spicules hispidate the processes. YPM No. 6460. Runaway Bay, Jamaica; 38 m. × 10.

FIG. 16. *Goreauiella auriculata* sp. nov. Enlarged view of processes on surface of aragonitic basal skeleton, living tissues removed. Lighter bands represent lines of somewhat higher processes that are formed beneath excurrent channels on surface. YPM No. 6465. Runaway Bay, Jamaica; 28 m. × 10.

15

16



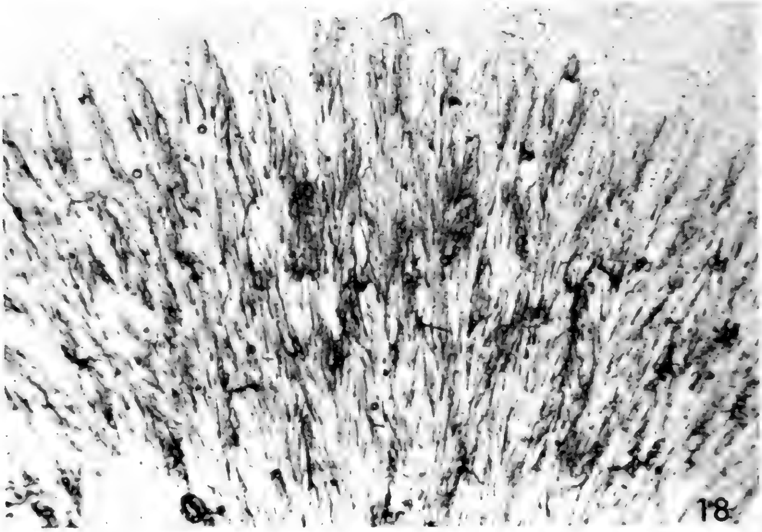
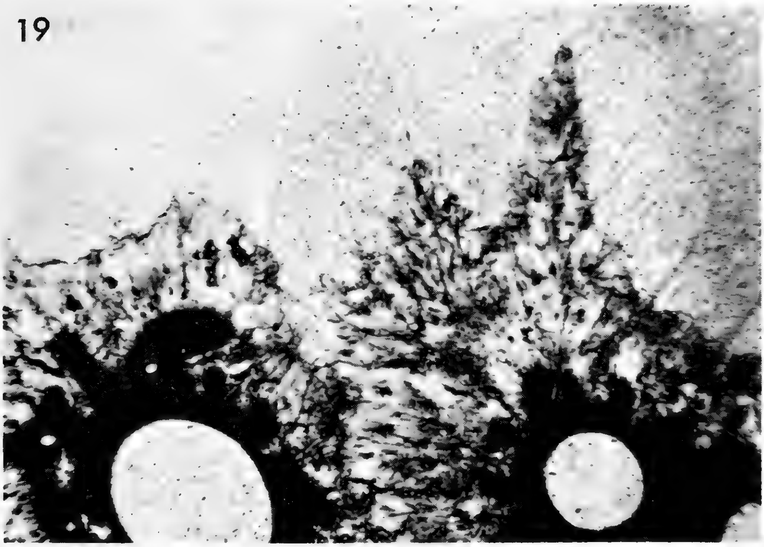
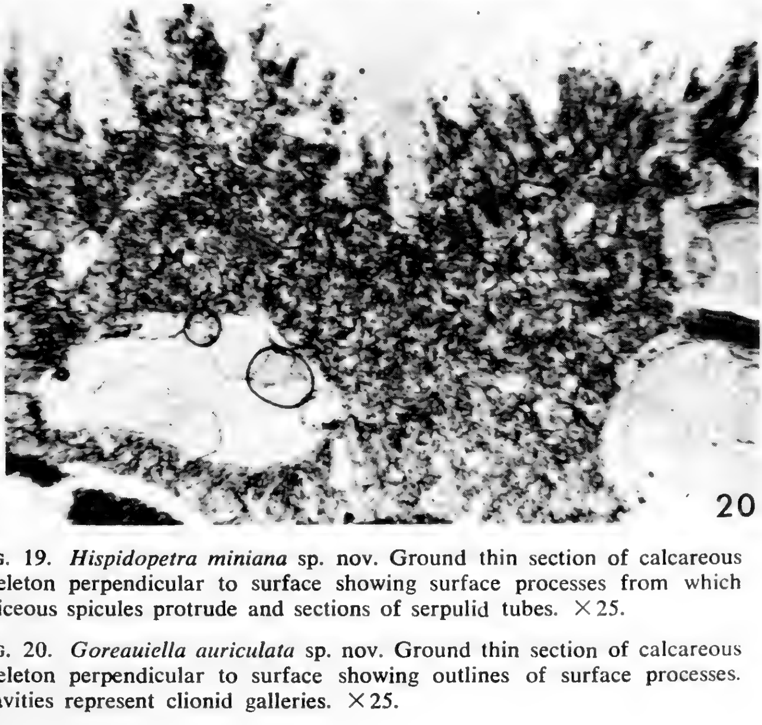


FIG. 17. *Stromatospongia vermicola* sp. nov. Ground thin section of calcareous skeleton perpendicular to surface showing surface processes, siliceous spicules embedded in aragonite and section of serpulid tube. ×25.

FIG. 18. *Stromatospongia norae* sp. nov. Ground thin section of calcareous skeleton perpendicular to surface showing surface processes and siliceous spicules embedded in aragonite. ×25.

19





20

FIG. 19. *Hispidopetra miniana* sp. nov. Ground thin section of calcareous skeleton perpendicular to surface showing surface processes from which siliceous spicules protrude and sections of serpulid tubes. ×25.

FIG. 20. *Goreauiella auriculata* sp. nov. Ground thin section of calcareous skeleton perpendicular to surface showing outlines of surface processes. Cavities represent clionid galleries. ×25.

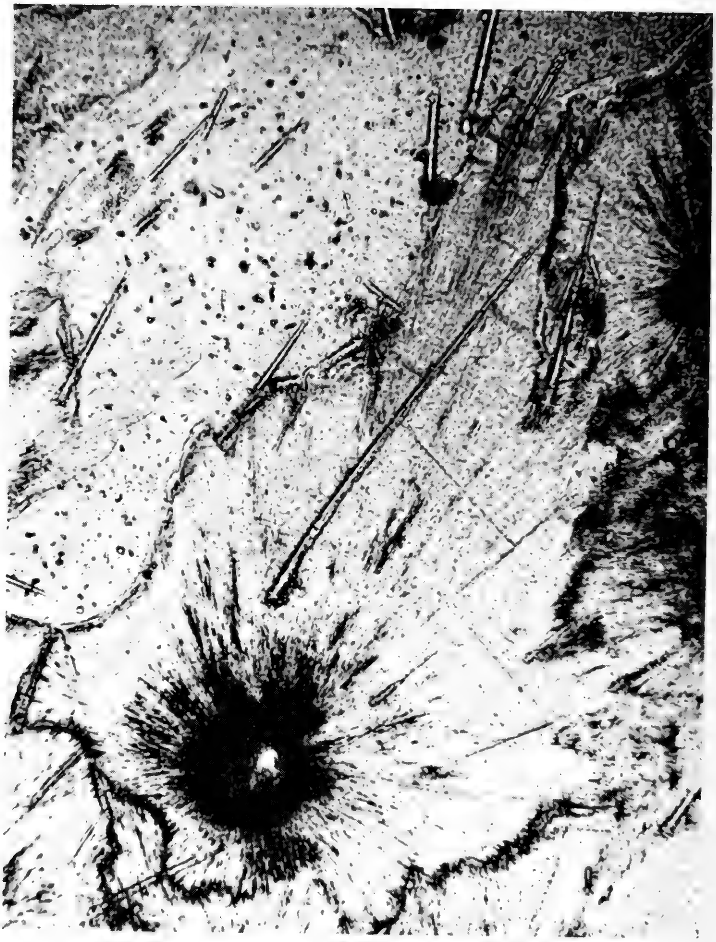


FIG. 21. *Stromatospongia vermicola* sp. nov. Ground thin section of calcareous skeleton showing sclerodermite surrounding serpulid tube. Note partially eroded siliceous spicule. YPM No. 6377. Discovery Bay, Jamaica; 71 m. × 132.

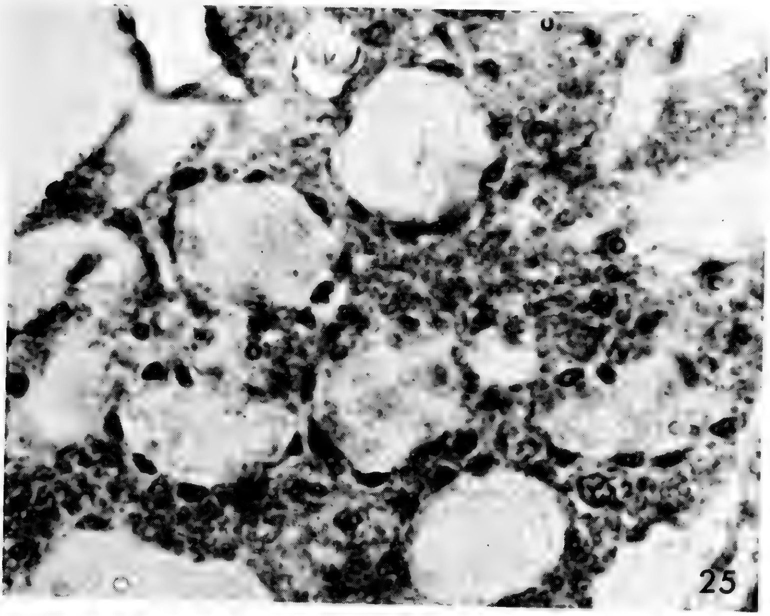
FIG. 22. *Stromatospongia norae* sp. nov. Ground thin section of calcareous skeleton showing sclerodermite and siliceous spicules embedded in aragonite. YPM No. 7770. Runaway Bay, Jamaica; 26-28 m. × 132.

FIG. 23. *Hispidopetra miniana* sp. nov. Ground thin section of calcareous skeleton showing sclerodermite. YPM No. 6460. Runaway Bay, Jamaica; 38 m. ×132.

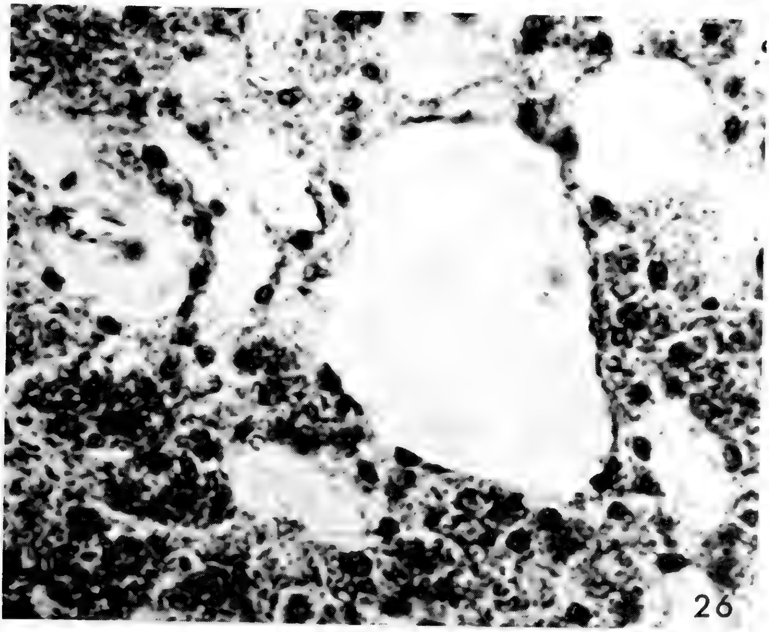
FIG. 24. *Goreauiella auriculata* sp. nov. Ground thin section of calcareous skeleton showing sclerodermites. YPM No. 6464. Runaway Bay, Jamaica; 25 m. × 132.

FIG. 25. *Stromatospongia vermicola* sp. nov. Decalcified thin section showing choanocyte chambers. Hematoxylin and eosin; 7μ section. × 1538.

FIG. 26. *Stromatospongia norae* sp. nov. Decalcified thin section showing choanocyte chambers. Mallory's phosphotungstic acid hematoxylin; 7μ section. × 1538.



25

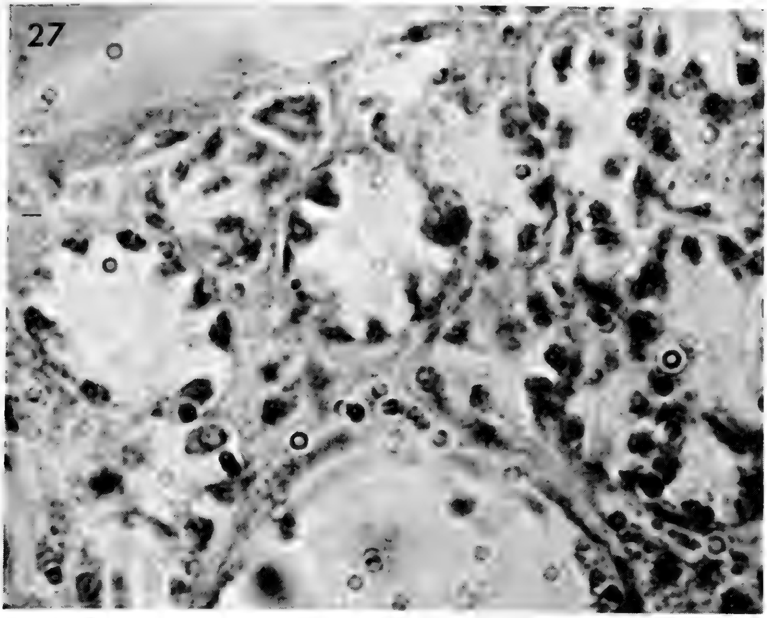


26

FIG. 27. *Hispidopetra miniana* sp. nov. Decalcified thin section showing choanocyte chambers. Hematoxylin and modified Mallory trichrome: 7μ section. × 1538.

FIG. 28. *Goreauiella auriculata* sp. nov. Decalcified thin section showing choanocyte chambers. Hematoxylin and modified Mallory trichrome; 8μ section. ×1538.

27



28

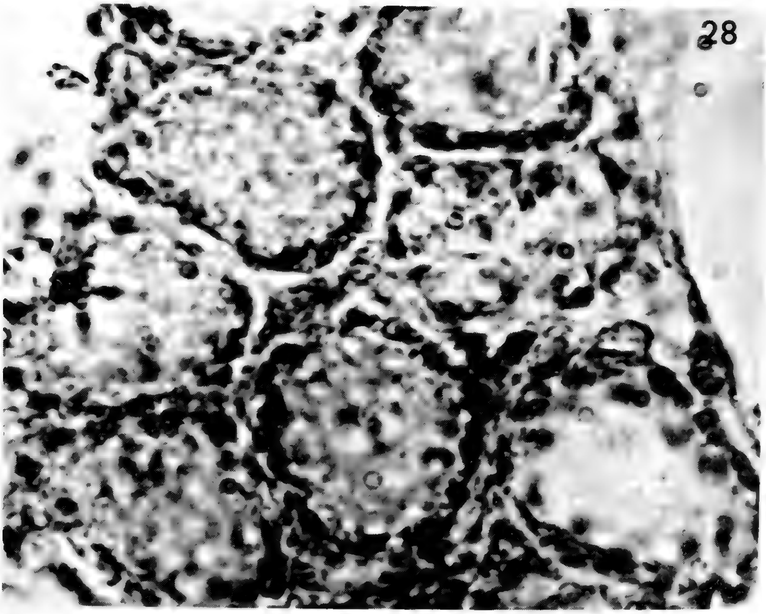


FIG. 29. *Stromatospongia vermicola* sp. nov. Surface view of living specimen *in situ* showing expanded excurrent channels. Oscule opens out at center of stellate pattern of channels at right top. Small dark dots represent incurrent openings from the vestibular cavity into the choanosome of the sponge. Runaway Bay, Jamaica, 40 m. ×7. Photo by T. F. Goreau.

FIG. 30. *Stromatospongia norae* sp. nov. Surface view of living specimen *in situ* showing stellate patterns of excurrent channels converging upon oscules. Dark spots represent incurrent openings from the vestibular cavity into the choanosome of the sponge. Runaway Bay, Jamaica; 25 m. ×7. Photo by T. F. Goreau.

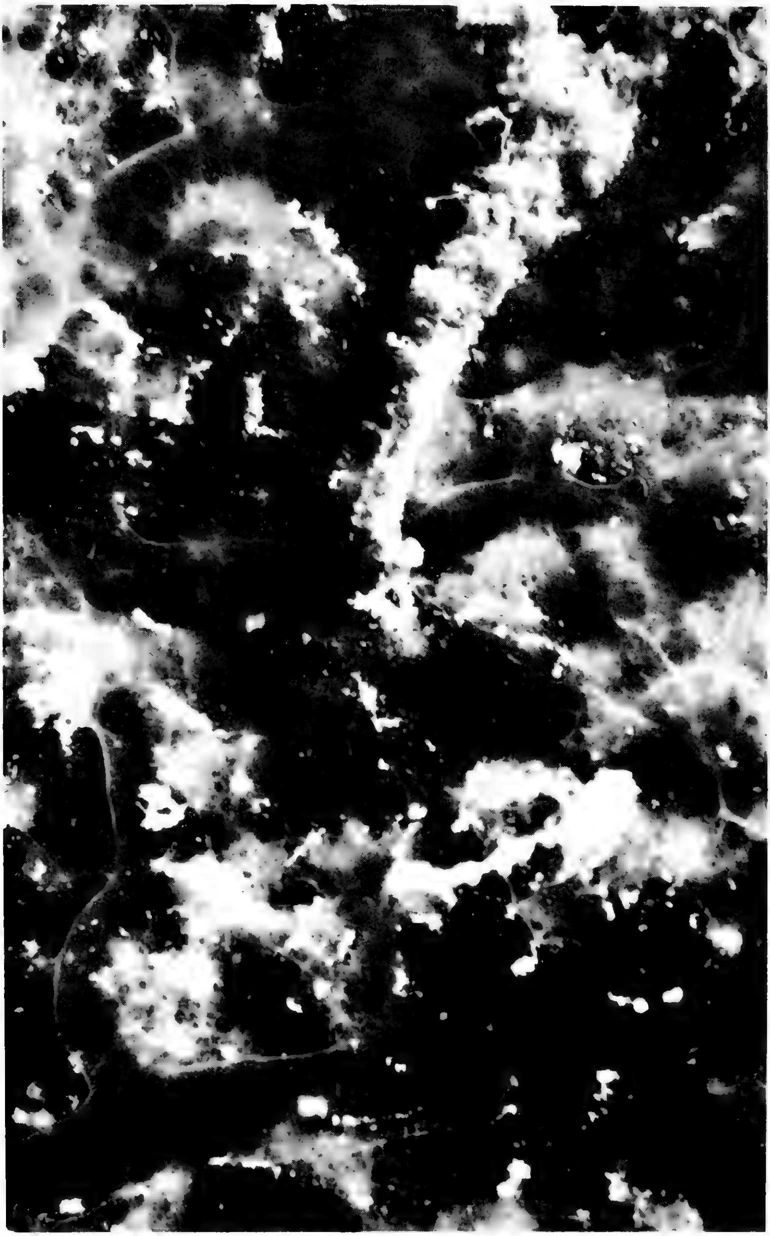


FIG. 31. *Hispidopetra miniana* sp. nov. Surface view of living specimen *in situ* showing excurrent channels. Small dark spots represent incurrent openings from vestibular cavity into the choanosome of the sponge. Runaway Bay, Jamaica; 34 m. ×7. Photo by T. F. Goreau.

FIG. 32. *Goreauiella auriculata* sp. nov. Surface view of living specimen in *situ* showing dilated excurrent channels. Small dark spots represent incurrent openings from vestibular cavity into the choanosome of the sponge. Runaway Bay, Jamaica; 25 m. ×7. Photo by T. F. Goreau.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

OMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

LLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

THOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 138. 1 OCTOBER 1969

GIGANTOPITHECUS (PONGIDAE, HOMINOIDEA) A NEW SPECIES FROM NORTH INDIA

E. L. SIMONS
S. R. K. CHOPRA

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

GIGANTOPITHECUS (PONGIDAE, HOMINOIDEA) A NEW SPECIES FROM NORTH INDIA

E. L. SIMONS
Peabody Museum of Natural History and Department of Geology and Geophysics, Yale University

S. R. K. CHOPRA
Department of Anthropology, Panjab University, Chandigarh, India

ABSTRACT

A nearly complete mandible of *Gigantopithecus* representing a new species, *Gigantopithecus bilaspurensis,* is described. The specimen lacks incisors, left P_4 and the posterior portions of both rami. Even so, it is the most complete Pre-Pleistocene hominoid mandible ever found in the Indian subcontinent. Found in the Dhok Pathan beds northwest of Haritalyangar, India, it is of middle Pliocene age. It is also the most complete higher primate mandible of its age known from any site in the world.

In various ways the new specimen resembles species of *Australopithecus, Ramapithecus* and *Dryopithecus* more than does the specialized Chinese Pleistocene species *Gigantopithecus blacki.* In consequence of these resemblances the new Indian find tends to strengthen the close phyletic relationships already suggested by some, on the basis of other finds, for these four genera. It is suggested that in all probability *Gigantopithecus* is derived from a species of *Dryopithecus* and not from *Apidium* via *Oreopithecus* — a position which before this new discovery in India remained a possibility. Thus the new find further demonstrates that *Gigantopithecus,* although well off the line of direct human ancestry, has definite resemblances in the biomechanics of its jaws and teeth to unquestioned Hominidae. Differences in details of this functional system suggest that these features of *Gigantopithecus* may have arisen in parallel with the similar mandibular and dental mechanics of *Ramapithecus* and *Australopithecus.*

***POSTILLA* 138: 18 p. 1 OCTOBER 1969.**

HORIZON AND LOCALITY

Upper levels of the Dhok Pathan zone, ?middle Pliocene, north of Haritalyangar, Himachal Pradesh, India.

NATURE OF THE FIND

The specimen, found originally in three associated parts, was identified by G. E. Meyer, co-investigator of the project, in April 1968.[1] The find described here is the first reported scientific result of the joint Chandigarh-Yale research program in search of early hominids and related apes in North India. This description is intended to provide a preliminary statement on the find which will be dealt with in greater detail at a later date. The specimen consists of both horizontal rami of the mandible joined at the symphysis and complete to the base of the ascending ramus on both sides (see Fig. 1). All teeth are preserved intact except that the incisors, left P_4, and anterolateral half of the right canine are broken away. This is the most complete primate fossil ever found in the Miocene/Pliocene sediments of India and one of the most complete Tertiary fossil hominoid specimens ever found in Eurasia.[2]

SYSTEMATICS

CLASS MAMMALIA
ORDER PRIMATES
SUBORDER ANTHROPOIDEA
SUPERFAMILY HOMINOIDEA
FAMILY PONGIDAE
SUBFAMILY DRYOPITHECINAE
GENUS *GIGANTOPITHECUS* Koenigswald 1935

---

[1] The authors also wish to acknowledge the services of the remainder of the field staff present at the time of discovery: S. J. Boyer, S. S. Kaul, D. Powers, G. C. Thoron, L. S. Sidhu and P. Singh.

[2] Although of much greater age and from a different geographical area than the three Chinese mandibles of *Gigantopithecus blacki,* this mandible, for convenience of discussion, will be referred to below as *Gigantopithecus* mandible IV.

TYPE SPECIES. *Gigantopithecus blacki* Koenigswald (1935, p. 874).

INCLUDED SPECIES. *G. blacki, G. bilaspurensis* sp. nov.

DISTRIBUTION. South China: Hei-Dong or Black Cave, Tahsin District; teeth of uncertain provenance from Chinese drug stores (possibly from the cooperatives of Nanning, Kwangsi, and Canton, Kwangtung); caves 1, 2, Liucheng, Kwangsi. India: Dhok Pathan zone, Himachal Pradesh.

GENERIC DIAGNOSIS (modified from Simons and Pilbeam 1965, p. 134-5). Largest genus of dryopithecine.[3] Exhibits markedly reduced lower incisors and somewhat reduced and low-crowned canines. Simian shelf typically shorter (front to back), relative to absolute mandibular size, than in most modern apes; cross-section similar to that of *Australopithecus robustus*. Greatest length of symphyseal section shorter (in both presumed male and female *Gigantopithecus*), relative to an absolute size index combining length of P_3 — M_3 and depth and breadth of mandible at M_2, than is typical of gorillas including *G. g. beringei* both male and female. Mandible deeper and more robust, relative to tooth size, than in any other ape and typically increasing in vertical height of horizontal ramus posteriorly. Incisors crowded between canines, vertically emplaced and with as small a bicanine breadth, relative to the length of cheek-teeth (P_3 — M_3), as in *A. robustus*. Lower canine crowns comparatively reduced and vertically implanted rather than flaring out laterally as is typical of a majority of Recent apes, i.e. in hominids canine roots are typically more than twice the length of unworn crown. Lower premolars only slightly heteromorphic with distinct internal cusps (metaconids) on P_3 as well as P_4 and with relative reduction of anterolateral face of P_3 correlative with distinct shortening and size reduction of upper canine compared to other apes. Molars absolutely larger than in any other extinct hominoid genus; larger than in most gorillas.

---

[3] Hominid placement of this genus as advocated by Koenigswald (1952) Weidenreich (1945), Dart (1960) and Woo (1962), among others, is not impossible, but placement among Pongidae, following Remane (1950, 1960) and Simons and Pilbeam (1965), is continued here pending more complete fossil finds of this animal and of early hominids.

Gigantopithecus bilaspurensis[4] sp. nov.
Figures 1-4

TYPE. Chandigarh-Yale Project No. 359/68, both horizontal rami of mandible joined at symphysis containing left C, P_3, $M_{1\text{-}3}$ and posterior half right C, $P_{3\text{-}4}$, $M_{1\text{-}3}$. Horizontal rami are broken off just posterior to third molars.

DISTRIBUTION. North India, early or middle Pliocene.

HYPODIGM. Type only.

SPECIFIC DIAGNOSIS. Mandible smaller in absolute size than smallest known *G. blacki,* but showing relatively even smaller anterior teeth. Teeth preserved (C through M_3) are little worn and lack characteristic polycuspidation of unworn *G. blacki* teeth. In this cusp simplicity these teeth resemble some *Dryopithecus,* for instance most *D. sivalensis* and *D. indicus.* Unlike *G. blacki* molars or the large molar of *D. indicus* from Alipur, India, GSI D-175[5]; lower molar protoconid distinctly smaller than metaconid, and apices of lower molar cusps more laterally placed— such a distinction also separates most *Dryopithecus* from *Ramapithecus.* Teeth much less hypsodont than *G. blacki.* Resembles *Ramapithecus punjabicus, G. blacki,* and most hominids in having lingually and labially expanded cheek tooth occlusal faces so that sides of teeth are oriented in a more nearly vertical plane, not rounded out as in most *Dryopithecus* species and *G. blacki.* Molars not strongly divided into trigonid and talonid portions by a lingual indentation between metaconid and entoconid as is typical of *G. blacki.*

DISCUSSION

SIZE. The new mandible represents a very large primate species. Although it is somewhat smaller than the geologically younger Chinese Pleistocene species of *Gigantopithecus,* the Himachal

---

[4] Named from its provenance in the former Hill State of Bilaspur; Himachal Pradesh, India and in honor of H.H. Sir Anand Chand, Maharajah of Bilaspur.

[5] This specimen is the type of *D. gigantius* Pilgrim, 1915, which was later proposed as type of a distinct genus and species *Indopithecus gigantius* (Koenigswald, 1949). Hooijer (1951), however, challenged the propriety of establishing a distinct genus on two unassociated teeth.

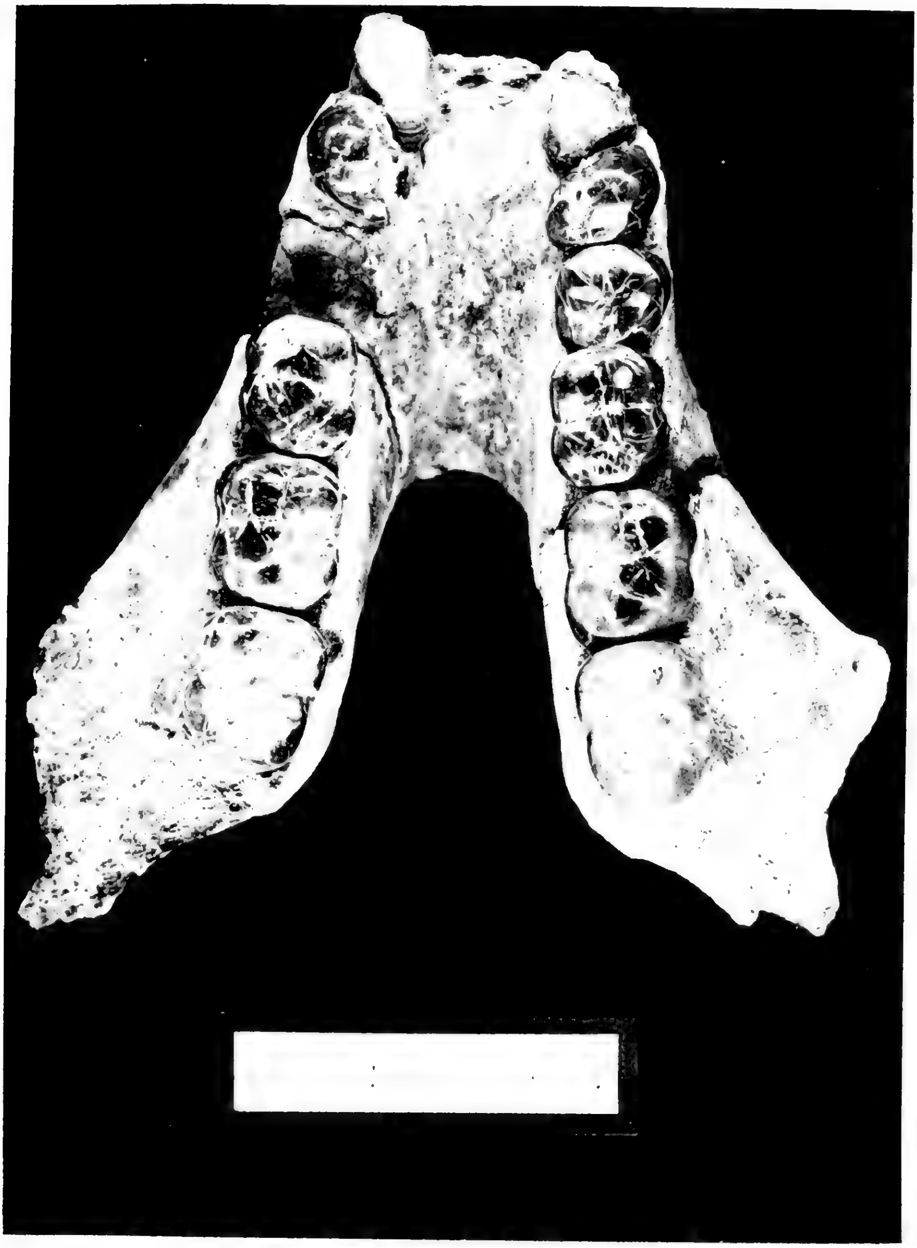


FIGURE 1. Occlusal view of the teeth and mandible of the type specimen of *Gigantopithecus bilaspurensis,* X1.

Pradesh specimen has larger premolars and molars than are typical of most hominoids. Ever since Remane's report (1921) it has been clear that variation in the absolute size of cheek-teeth among given hominoid species is great. Even so these are very large. The general robustness of the horizontal rami of the mandibles under premolars and molars is well above the range for living *G. gorilla,* including *G. g. beringei.* The contrast between the mandibles of *G. blacki* and *G. bilaspurensis* and those of living apes may be seen by comparing *Gigantopithecus* (Fig. 2) with male and female members of the largest living race of apes, the mountain gorilla, *G. g. beringei.* The male mountain gorilla, AMNH 115609 of this figure, in most cheek-tooth measurements is above the 95% confidence limits calculated by Pilbeam (in press) for a sample of 20 *G. g. gorilla* males. In these measurements it is also above the upper ranges for *Gorilla* given by Remane (1960). The M_{1-3} length is greater than in a gorilla with exceptionally large teeth described by Schultz (1964). There must then be few if any gorilla mandibles of larger size. Even so it is clear from Figure 2 that the horizontal rami of all four *Gigantopithecus* are both absolutely and relatively deeper than those of the living ape with cheek-teeth of approximately the same size.

Another major difference between *Gigantopithecus* and the three largest ape species relates to the marked reduction in size of the front teeth in *G. blacki* and *G. bilaspurensis* when compared to *Gorilla g. beringei.* The frequent spacing out of incisors and lateral flare of canines often seen in male gorillas is wholly different from the crowded incisors and vertically implanted canines of the presumed male of *Gigantopithecus.* Distinct differences also exist in this region between female *G. g. beringei* and the type of *G. bilaspurensis,* a probable female. The same distinctions from female *Gorilla* are to be seen in mandible I from the South Chinese Pleistocene site in Kwangsi, which has been assumed by Woo (1962) and others to be female. From Table 1 it is clear that although measurements of the incisors and canines of *Gigantopithecus* are near the minima for gorillas, the lengths and breadths of cheek-teeth of *Gigantopithecus* are close to or exceed the maxima known for *Gorilla.*

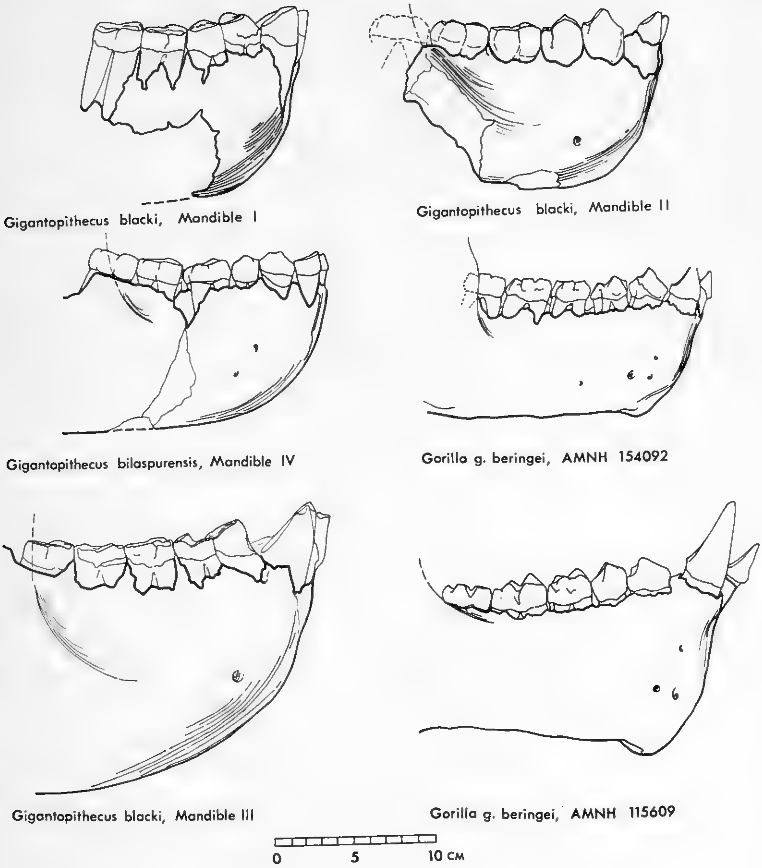


FIGURE 2. The four mandibles of *Gigantopithecus* compared with specimens of the largest living ape, *Gorilla gorilla beringei*. The male mountain gorilla, AMNH 115609, has the longest molars on record for a gorilla.

TABLE 1[6]. Measurements comparing the four *Gigantopithecus* lower dentitions with minima and maxima of *Gorilla* males.

	Teeth							
	I_1	I_2	C	P_3	P_4	M_1	M_2	M_3
Anteroposterior length								
Gorilla (minima)	7.2	7.8	12.6	14.8	9.8	13.0	14.6	14.7
Gorilla (maxima)	9.4	11.1	18.0	20.4	13.5	18.3	21.0	22.0
Gigantopithecus I	6.0	7.7	11.5	15.1	14.2	17.7	18.6	—
Gigantopithecus II	—	7.2	—	16.4	16.3	20.1	21.3	—
Gigantopithecus III	—	8.0	13.1	16.5	17.0	18.9	21.2	21.4
Gigantopithecus IV	—	—	9.3	11.8	13.1	17.0	19.1	19.6
Labiolingual breadth								
Gorilla (minima)	8.7	9.9	14.2	9.2	11.5	11.7	13.2	13.0
Gorilla (maxima)	11.0	13.2	24.0	14.8	17.0	16.2	17.8	18.7
Gigantopithecus I	8.7	9.5	15.4	15.0	16.1	16.7	17.4	—
Gigantopithecus II	—	10.0	—	16.0	17.8	17.2	18.9	—
Gigantopithecus III	—	10.0	15.0	16.9	18.0	18.5	21.0	18.8
Gigantopithecus IV	—	—	16.0	14.6	14.5	14.2	16.0	16.2

DENTITION

INCISORS. Although the incisors of *G. bilaspurensis* are missing, the breadth across these four teeth can be measured because the mesiolabial corner of the left canine bears a wear facet formed by interstitial attrition with the distal border of I_2. This attrition indicates the degree of crowding in the front teeth, a feature also noted by Woo (1962) for all three Chinese Pleistocene mandibles. The position of this facet also shows that in life the lateral incisor was appressed to the mesiolabial face of the canine and situated so that the outer face of this incisor projected well forward of a line drawn between the anterior faces of the lower canines. Such an orientation of the left lateral incisor is preserved in Chinese mandible I as well as in the *Gigantopithecus* mandible III right lateral incisor, see Woo, 1962, plate IX. This establishes that the incisors of *Gigantopithecus* formed a compressed anterior-facing

---

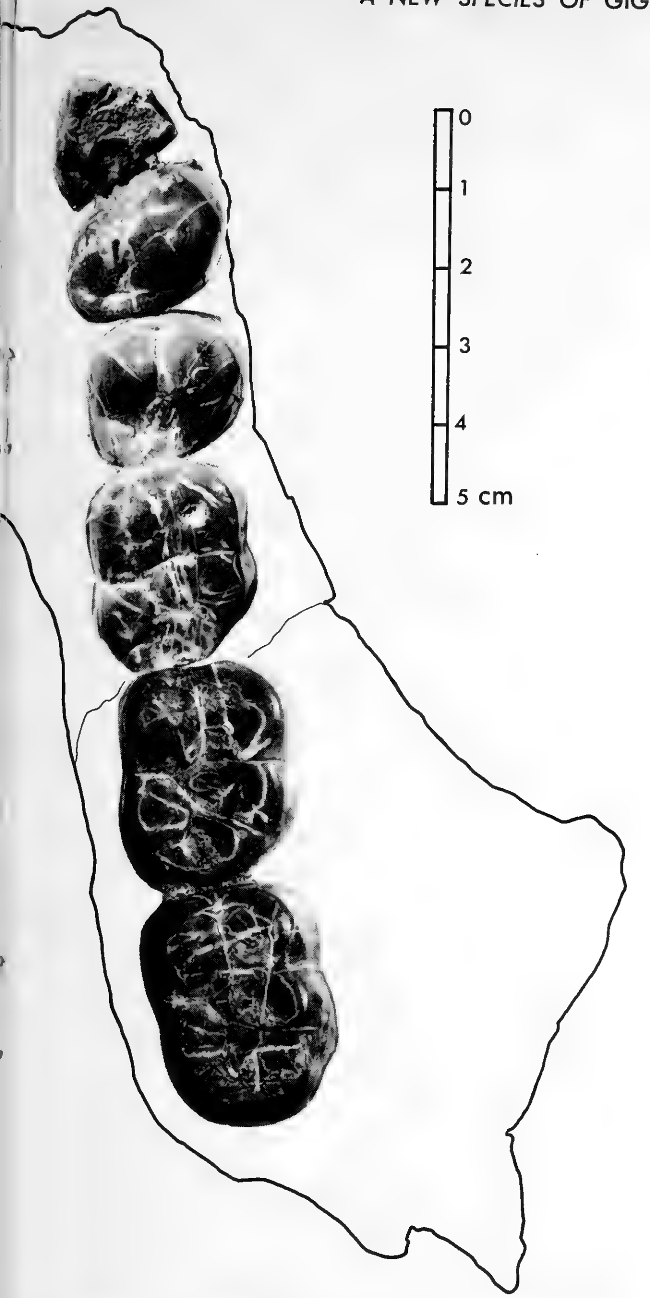
[6] Measurements of *Gorilla* from Schultz (1964) after Remane (1960), with addition of new molar length maxima from AMNH 115609.

arc. At least after some wear, in *G. bilaspurensis* there was no longer a gap between the crowns of I_2 and C as is typical of *G. g. beringei* and most other modern pongids even when these teeth are in contact at the base. The *Gigantopithecus* mandible I shows that a continuous plane of wear has truncated the six front teeth so that the outer, or leading edges of the occlusal faces of these six front teeth form a continuous row. The same arrangement of incisors and canines appears to have been true of *Gigantopithecus* mandible IV.

Relative to the extreme robustness of the horizontal ramus of the mandible and the large size of the cheek-teeth, the incisors of *Gigantopithecus* are unlike all other pongids in their relatively small size and closely compressed condition. The narrow breadth of the four incisors correlates with a remarkably constricted space between the canines and premolars above the planum alveolare.

CANINES. As was previously evident from the canines in mandibles I and III as well as isolated canine teeth described by Koenigswald (1952) and by Woo (1962) the canine is more reduced in this genus (relative to size of mandible and cheek-teeth) than in any other ape. In consequence the canines would have barely overlapped when unworn upper and lower dentitions were in occlusion, as seen in female *G. g. beringei,* Fig. 2. Nevertheless, after eruption of the full adult dentition, the course of wear is subsequently rather different in *G. g. berengei* females and both male and female *Gigantopithecus.* In *Gigantopithecus* the whole top of the canine crown appears to have been worn off early in the life of the individual. This phenomenon, which would permit greater transverse movement of the anterior dentition during mastication, is best demonstrated in the mandible under consideration (*Gigantopithecus* IV). This specimen is of much younger dental age than are either of the two Chinese *Gigantopithecus* mandibles whose canines are preserved, and the molars are so little worn that only on the protoconid of the first molars has the enamel been significantly penetrated, yet the canine is already completely truncated, see Fig. 3. Viewed directly from above, the canine of *Gigantopithecus* IV, *G. bilaspurensis,* is roughly ovoid, with the long axis of the tooth situated at an angle of about 45° to the sagittal plane of the mandible. Recently Leakey (1968) has argued that possession of an anteroposteriorly compressed canine of this

FIGURE 3. Composite of individual close-up photographs of the teeth



Gigantopithecus bilaspurensis superimposed on the outline of the mandible.

sort is a hominid feature. Admittedly the canine in the African apes is usually "pear-shaped" ("triangular" in Leakey's terms) in cross-section at the base of the enamel with the larger bulge located anterolaterally, but an ovoid, parallel-sided canine cross-section is not rare among Pongidae, and indeed is a regular occurrence in the Orangutan. One final observation of some significance is that the canines of modern female apes do not wear down in the manner seen in *G. bilaspurensis.* The plane of wear on lower canines of great apes (whether heavily worn or not) slopes steeply downward typically at angles of from 50° to 75° relative to the plane of the long axis of the tooth row. In *G. bilaspurensis* this angle is much lower at about 18°. In *G. blacki* these angles are somewhat higher than in *G. bilaspurensis* but are lower than is typical in modern apes or *Dryopithecus. Gigantopithecus* mandible I, a probable female, has an angle of 29° and in the old male *G. blacki* (III) this angle is 46° (left C).

PREMOLARS. P_3. The anterior premolar of *G. bilaspurensis* is remarkable for an ape in that the tooth does not exhibit an anterolateral exension for sectorial or sharpening action against the posterior wear facet of the upper canine. This is to be expected in a form in which the absolute size of canines has been relatively reduced. Consequently P_3 is not much larger than P_4 but in such females this tooth nevertheless retains an anterolateral boss against which the back of the upper canine shears. In *Gorilla* of the dental age of *G. bilaspurensis* a wear facet on the anterolateral boss of P_3 is usually detectable. Another difference between the P_3 of *Gigantopithecus* and that of most apes is that the inner, metaconid cusp is well-developed. This is most clearly seen in P_3 of mandibles II and IV and gives the premolars a bicusped, hominid look. This could be taken as a special indication of affinities with hominids but since small metaconids do occur on P_3 in at least some *Dryopithecus,* as well as *Oreopithecus,* the secondary enlargement of the cusp could have taken place in this line independent of a similar development among hominid ancestors. Such a parallelism may have occurred because in both lineages there could have been a similar reorganization of function and relative proportions in the anterior dentition, particularly P_3, consequent to canine and incisor reduction. This tooth is reminiscent of *Dryopithecus* in outline and general proportions but differs from *Dryopithecus* and species of the three genera of great apes as well in having an extremely low, flattened metaconid and protoconid lacking all but the slightest expression of the ridges or crenulations which radiate from the apices of these cusps in most unworn hominoid premolars. Although one could maintain that such crenulations might have been somewhat obscured by wear on the crown, had they ever been present, some evidence of this character would probably remain in the talonid basin. In addition to these differences the trigonid portion of P_4 is greatly expanded while the talonid is much reduced over what is typical of apes. In *Gorilla* there is often a well-developed posterointernal cusp of P_4. In *G. bilaspurensis* the heel of this tooth is hardly more than a cingulum. Moreover this tooth differs markedly from *G. blacki* and from *Gorilla* in the extreme lowness of the trigonid.

MOLARS. M_1 — M_3. As is typical in *Aegyptopithecus* and early *Dryopithecus,* the molars of *G. bilaspurensis* increase in size posteriorly, both in breadth and length. This is apparently a primitive character among Pongidae. In *G. blacki* the M_3 of mandible III is distinctly narrower than M_2. Although the M_1 in mandible III is barely longer than M_2, interstitial wear has undoubtedly shortened lengths of M_1 and M_2 which would render Woo's published measurements somewhat doubtful (see Table 1). In mandible I, M_2 is barely larger than M_1, which does not suggest a posterior size increase in molars. Nevertheless the sample of *Gigantopithecus* jaws is too small for one to be sure that the two species of *Gigantopithecus* differed consistently in the degree of molar size-increase posteriorly.

A particularly distinctive feature of the molars of *G. bilaspurensis* is the extraordinary flatness of their occlusal surfaces which is most closely paralleled elsewhere among Anthropoidea by hominids and perhaps *Pongo.* These teeth lack the deeply incised crenulations and polycuspidation of molars and premolars seen in newly erupted teeth of *G. blacki* (mandible II and isolated unworn teeth). In *G. bilaspurensis* all the molar cusps are delineated on the occlusal face by shallow grooves, but even before wear the apices of the cusps could not have risen to an extent in any way similar to cusp height in most apes (other than some *Pongo*) because the enamel has only been perforated by wear on the protoconid and hypoconid of both M_1's. Considering the length and breadth of these molars, molar crown height is extremely low, resembling Hominidae and not *G. blacki,* which as Weidenreich (1945) and Koenigswald (1952, p. 318) have pointed out shows incipient hypsodonty. Thus the molar breadth-height indices for the two species of *Gigantopithecus* are at nearly opposite extremes among Hominoidea (see Table 2).

TABLE 2. Mean molar breadth-height indices for samples of various hominoid species, arranged in ascending order of magnitude.

Pongo pygmaeus	41.3[7]
Gigantopithecus bilaspurensis	46.5
Gorilla gorilla	54.3
Homo erectus	ca. 55.0
Pan troglodytes	58.8
Homo sapiens	61.2
Gigantopithecus blacki	73.6

In view of the fact that nearly all *Dryopithecus* species tend to show lower cusps than do the modern great apes, the brachyodonty of Pliocene *G. bilaspurensis* is a feature which it shares with earlier apes of the Miocene epoch.

THE PHYLETIC POSITION OF GIGANTOPITHECUS

There have been two primary views among earlier workers as to the affinities of *Gigantopithecus.* These are: 1) that it is an aberrant pongid with some distinctive dental features which either: a) adapt it to a novel manner of feeding, or b) are due to allometric changes related to its large absolute size; and 2) that the genus should be placed in Hominidae, either: a) ancestral to later hominids, or b) as an extinct side branch of Hominidae which existed in South East Asia as an apparent contemporary of *Australopithecus* and/or *Homo.* The uncertain age of the *Stegodon*—*Ailuropoda* fauna of South China in which *G. blacki* occurs, is discussed by Kahlke (1961).

---

[7] All values from Weidenreich (1945) apart from those of *Gigantopithecus* (*G. blacki* value from Koenigswald, 1952).

Of these choices 2a has been generally abandoned. Without going into the whole history of study in this short paper the alternative views of authors can be tabulated as follows:

In Hominidae	In Pongidae
Weidenreich (1945)	Koenigswald (1935)
Koenigswald (1949, 1952, 1958)	Pei and Woo (1956)
Heberer (1959 a and b)	Pei and Li (1959)
Dart (1960)	Remane (1950, 1960)
Woo (1962)	Ti-Cheng (1962)
	Simons and Pilbeam (1965)

This study of *G. bilaspurensis* makes it seem probable that *Gigantopithecus* represents a side branch of Asian apes which achieved a dental mechanism approximating to some extent that of hominids. These functional similarities, however, are not as close to *Australopithecus* and *Homo* as are those of *Ramapithecus,* and the latter remains the best candidate for ancestral relationship to *Australopithecus.* Figure 4 gives evidence that the symphyseal cross-section can no longer be considered a descriminent between apes and hominids. The symphyseal cross-sections of Figure 4 do not clearly separate *Gigantopithecus* and *Gorilla* and are also similar to such sections of *Australopithecus* and *Dryopithecus* mandibles. Both *G. bilaspurensis* and *Ramapithecus punjabicus* show morphological ties with *Dryopithecus,* particulary with *D. indicus* which has rather flat cheek teeth. Evidence is thus accumulating that both these genera arose from an early species of *Dryopithecus.* The latter in turn is apparently derived from Oligocene *Aegyptopithecus.*

Simons (1960) suggested that the possibility of a relationship between *Oreopithecus* and *Gigantopithecus* should be examined. This was mainly because of the common possession in these two forms of extremely deep mandibles relative to tooth size, and particularly polycuspidate molars with distinct centroconids in both *Oreopithecus bambolii* and *G. blacki.* In addition, the molar trigonids and talonids of *G. blacki* are clearly separated by a vertical interior and exterior groove into fairly distinct trigonid and talonid lobes much as is the case in *Oreopithecus.* It is now evident that polycuspidation and central pinching of the molars of *Gigantopithecus* must have been late developments in this line

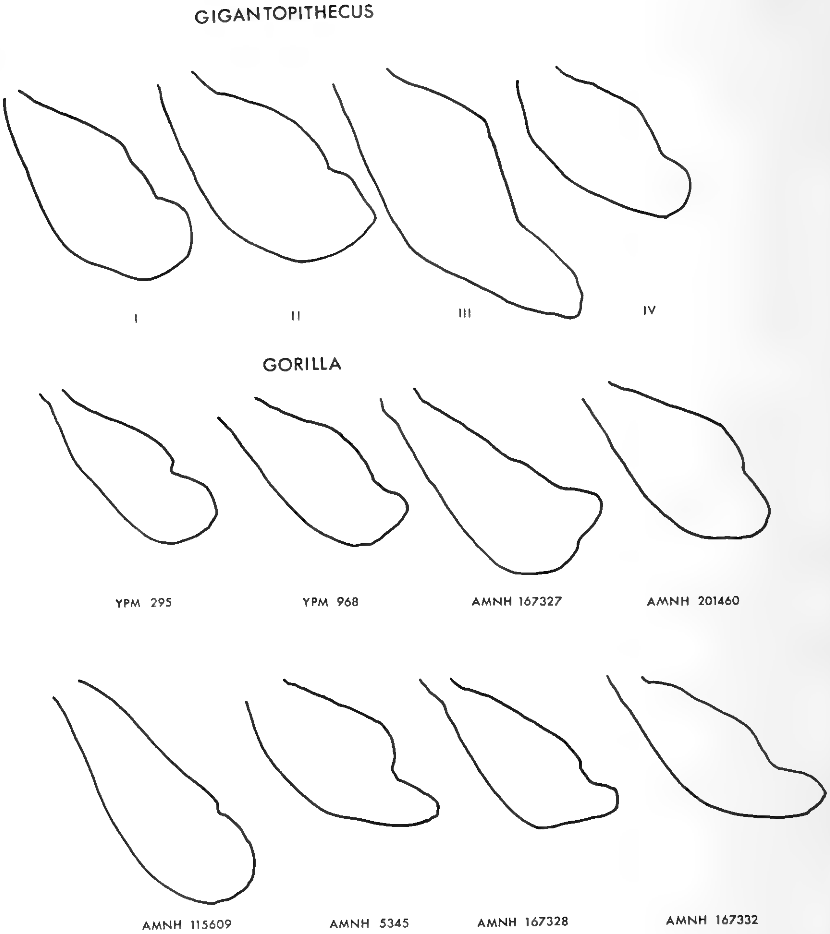


FIGURE 4. Symphyseal cross-sections of the four *Gigantopithecus* mandibles (top row) compared with those of eight large gorillas (second and third rows) showing close correspondence in outline of this section. *Australopithecus robustus* has similar sections.

since they are absent in *G. bilaspurensis*. Other late developments were the acquisition of a high index of hypsodonty and a relatively deeper mandible in *G. blacki*.

Thus this new and much older species of *Gigantopithecus, G. bilaspurensis,* does not indicate a derivation of *Gigantopithecus* from *Oreopithecus,* but from *Dryopithecus.*

In sum, it would appear that *Gigantopithecus* represents a divergent branch of the Pongidae with distinctive dental specializations which perhaps fitted it for foraging in open country. It may have been derived from earlier rather gorilla-like forest dwelling ancestors such as *D. indicus.*

ACKNOWLEDGEMENTS

We wish to express our sincere thanks to V.K.R.K. Rao, Minister of Education, Government of India, and H. R. H. Anand Chand M. P., inaugurators of our co-operative project; to the Vice-Chancellor of Panjab University, Mr. Suraj Bhan, for his help in initiating the work; to the Smithsonian Foreign Currency Program (Grant No. 37); and the National Science Foundation (Grant No. G.S. 1817) for providing the funds which have made our research program possible. The photographs were prepared by Mr. Baldev Singh, photographer of the Department of Anthropology, Panjab University and the figures by Mrs. Susan Weeks, Division of Vertebrate Paleontology, Peabody Museum. The senior author would like to acknowledge a brief discussion regarding the text of this paper with the junior author, and the assistance while preparing the manuscript of Ian Tattersall and David R. Pilbeam of the Peabody Museum.

LITERATURE CITED

Dart, R. A. 1960. The status of *Gigantopithecus*. Anthrop. Anz. **24**: 139-145.

Heberer, G. 1959a. The descent of man and the present fossil record. Cold Spring Harbor Symp. Quant. Biol. **24**: 235-244.

———— 1959b. Ein neurer Unterkiefer des chinesischen "Riesenaffenmenschen" gefunden. Kosmos **55**.

Hooijer, D. A. 1951. Questions relating to a new large anthropoid ape from the Mio-Pliocene of the Siwaliks. Amer. J. Phys. Anthrop. **9**: 79-95.

Kahlke, H. D. 1961. On the complex of the *Stegodon — Ailuropoda* fauna of South China and the chronological position of *Gigantopithecus blacki* v. Koenigswald. Vertebrata Palasiatica **2**: 83-108.

Koenigswald, G. H. R. von. 1935. Eine fossile Säugetierfauna mit *Simia* aus Südchine. Kon. ned. Akad. Wetensch. Amsterdam. **38**: 872-879.

——— 1949. Bemerkungen in *"Dryopithecus" giganteus* Pilgrim. Ecl. geol. Helv. **42**: 515-519.

——— 1952. *Gigantopithecus blacki* von Koenigswald, a giant fossil hominoid from the Pleistocene of Southern China. Anthrop. Pap. Amer. Mus. Nat. Hist. **43**: 292-325.

——— 1958. *Gigantopithecus* and *Australopithecus*. The Leech **28**: 101-105.

Leakey, L. S. B. 1968. Lower dentition of *Kenyapithecus africanus*. Nature **217** (5131): 827-830.

Pei, W-C, and Y-H. Li. 1959. Discovery of a third mandible of *Gigantopithecus* in Liu-Cheng, Kwangsi, South China. Vertebrata Palasiatica **2**: 193-200.

Pei, W-C and Woo, J-K. 1956. New materials of *Gigantopithecus* teeth from South China. Acta Palaeont. Sinica **4**: 477-490.

Pilbeam, D. R. (in press). Tertiary Pongidae of East Africa. Peabody Mus. Nat. Hist., Yale University, Bull. **31**.

Pilgrim, G. E. 1915. New Siwalik primates and their bearing on questions of the evolution of man and the Anthropoidea. Rec. Geol. Surv. India. **45**(1):1-74.

Remane, A. 1921. Beiträge zur morphologie des anthropoidengebissen. Arch. Natgesch., A. **11**: 1-179.

——— 1950. Bemerkungen über *Gigantopithecus blacki*. *In* H. Weinert, Über die neuen Vor-und Frühmenschenfunde aus Afrika, Java, China und Frankreich. Z. Morph. Anthrop. **42**: 113-148.

——— 1960. Die Stellung von *Gigantopithecus*. Anthrop. Anz. **24** (2-3):146-159.

Schultz, A. H. 1964. A gorilla with exceptionally large teeth and supernumerary premolars. Folia Primat. **2**: 149-160.

Simons, E. L. 1960. New fossil primates: a review of the past decade. Amer. Sci., **48**(2): 179-192.

Simons, E. L. and D. R. Pilbeam. 1965. Preliminary revision of the Dryopithecinae (Pongidae, Anthropoidea). Folia Primat. **3**: 81-152.

Ti-Cheng, T. 1962. The Taxonomic Position of *Gigantopithecus* in Primates. Vertebrata Palasiatica **6**: 375-383.

Weidenreich, F. 1945. Giant early man from Java and South China. Anthrop. Pap. Amer. Mus. Nat. Hist. **40**: 1-134.

Woo, J.-K. 1962. The mandibles and dentition of *Gigantopithecus*. Palaeont. Sinica 146, N.S., D. No. **11**: 1-94.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

NOMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

ILLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

THOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 139. 20 NOV. 1969

OCCLUSION IN DOCODON (MAMMALIA, DOCODONTA)

FARISH A. JENKINS, JR.

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

OCCLUSION IN DOCODON (MAMMALIA, DOCODONTA)

FARISH A. JENKINS, JR.

Department of Anatomy, College of Physicians and Surgeons,
Columbia University, New York, N.Y. 10032

ABSTRACT

The pattern of molar occlusion in the Late Jurassic mammal genus *Docodon* was determined by "mapping" the wear facets on all known upper and lower dentitions. The coincidence of lower and upper molar wear is evidence that the proposed occlusal pattern is correct. The lingual halves of the upper molars occlude in the lower intermolar basins formed by the adjacent halves of lower molars. The buccal halves of upper molars pass buccally to the lower molar row. The disposition of opposing cusps and crests, and the verticality of most wear facets, reveals that molar function was primarily shearing rather than crushing. The vertical crenelations (or ribs and furrows) on the molar crowns are interpreted as accessory shearing edges.

POSTILLA 139: 24 p.   20 NOVEMBER 1969.

INTRODUCTION

The genus *Docodon* is one of the Mesozoic mammalian genera named by Marsh (1880 and later papers) from material collected at Como Bluff, Wyoming. The order Docodonta (to which *Docodon* belongs) is known chiefly from the dentition and on this evidence is generally considered to be too specialized to have been closely related to therian ancestors. This paper provides a functional evaluation of occlusion in *Docodon,* and presents other conclusions on cusp homology and molar function. Previous accounts and diagrams of molar occlusion in *Docodon* (Simpson, 1929: 71; 1933: 145; Patterson, 1956: 73; Butler, 1961: 123; Vandebroek, 1961: 281) differ in detail and leave considerable doubt as to the precise occlusal relationship of upper and lower molars. The descriptions of *Docodon* molars given by Simpson (1929), Butler (1939) and Patterson (1956) obviate the necessity of redescribing the molars. A representative upper and lower molar are here fully illustrated for the first time (Figs. 5-14). Certain questions of taxonomy and cusp nomenclature will be discussed as they relate to the reconstruction of the occlusal pattern.

MATERIALS

All available specimens of *Docodon* were studied. These specimens are housed in the Peabody Museum of Natural History, Yale University (YPM), the U. S. National Museum (USNM) and the American Museum of Natural History (AMNH). *Docodon* is known from only two localities, both in the Morrison Formation: the "Old Quarry" at Garden Park, Fremont County, Colorado, and Quarries 9 and 1 at Como Bluff, Albany County, Wyoming. The Garden Park material consists of two specimens, USNM 21863 and USNM 2717, which on the basis of present knowledge cannot be assigned to any species known from Quarry 9. A single lower jaw (AMNH 3002) was recovered from Quarry 1 at Como Bluff; the remaining 58 specimens come from Quarry 9.

TAXONOMIC CONSIDERATIONS

Five species of *Docodon* were recognized by Simpson (1929). Of these, four are based on partial or nearly complete mandibles: *D. victor* (Marsh 1880), *D. striatus* Marsh 1881, *D. crassus*

(Marsh 1887) and *D. affinis* (Marsh 1887). The fifth species, *D. superus* Simpson, 1929, is a conventional species for all upper dentitions of this genus.

No associated upper and lower dentition of *Docodon* is yet known and no criteria have been recognized by which species based on lower dentitions can be confidently related to any upper dentitions. Partly for these reasons and partly on account of the lack of variation in available material did Simpson (1929) place all upper dentitions of *Docodon* in a separate species. The unsatisfactory state of knowledge of *Docodon* species may tend to cast doubt on any reconstruction of the occlusion. Furthermore, of the 23 specimens of lower dentitions that are sufficiently well preserved to be utilized in this study, only five (including the four type specimens) could be identified to species; the other fragmentary specimens could only be referred to *Docodon* sp. because the species diagnoses are based on more or less complete mandibles with most of the alveoli if not nearly all of the teeth present. There are reasons to believe, however, that there are actually fewer species. Simpson (1929: 86-87) pointed out that the only difference between the type specimens of *D. striatus* and *D. victor* lay in the molar number, the former having seven and the latter eight, and that this difference could well be due to the immaturity of the type of *D. striatus*. Inasmuch as the type is the only assigned specimen of the species, and complete lower dentitions are so few, it is also possible that *Docodon* molars varied in number within a species. Although Simpson recognized this possibility as the most plausible, he nonetheless deemed it "best to retain Marsh's species provisionally" (1929: 87). A strong case has yet to be made for this species distinction, and the present study of all material failed to reveal any taxonomically significant differences.

Similar arguments may be made for synonymizing both *Docodon crassus* with *D. affinis* and *D. striatus*. The principal features that distinguish *D. crassus* from *D. affinis* and *D. striatus* (P_3, M_6, and a shorter and more shallow jaw) are probably due to the immature condition of the types. Characteristics that separate them from each other are based on the relative sizes of P_3, P_4, and the canines, and on minor differences in the premolar external cingula. Referring to *D. crassus* and *D. affinis,* Simpson (1929: 89) wrote: "They do have some slight differences from the other species now referred to this genus, but these are so unimportant, and even doubtful, that their real validity can only be tested by a still larger series of specimens than is now available. It is probable that *Docodon* includes more than one species, and perhaps as many as four or five but one must hesitate to vouch for the necessary validity of all the present established species."

A taxonomic revision awaits new and more complete material and is not the purpose of this paper. The four species based on lower dentitions and the one conventional species created for upper dentitions, although nominally separate, may in fact be regarded as one for purposes of determining the occlusal pattern and function of the dentition as presently known. No important variations in molar cusp pattern or crown morphology were detected during the present study of *Docodon* material. Observed differences in wear facet development are slight and are apparently the result of variable degree of wear or of minor variations in occlusion, neither of which is admissible as a taxonomic character.

Cusp Homology and Molar Morphology

CUSP HOMOLOGY. Simpson (1929), Butler (1939) and Patterson (1956) designated the largest buccal cusp on *Docodon* upper and lower molars as the paracone and protoconid, respectively. These cusps almost certainly represent the primary cusps of reptilian ancestry. Crompton and Jenkins (1968) employed the letters *A* and *a* in referring to these cusps; this approach facilitated comparisons among non-therian teeth without employing terminology usually used for therian teeth. However, it is clear from that study and from those of other workers that the paracone and protoconid of docodonts are homologous with the similarly named cusps of therians.

The homology of other cusps is not so easily established. Simpson's (1929) and Butler's (1939) descriptions use a tribosphenic terminology, in keeping with the then current belief that docodonts were aberrant pantotheres. Gidley (1906) was the first to propose that the docodont dentition was derived from an evolutionary lineage apart from that leading to the tribosphenic pattern. Later, Patterson (1956) presented a concrete outline of docodont-eozostrodont (=morganucodont) relationships. Subsequently, Crompton and Jenkins (1968) documented Patterson's proposed phylogeny in more detail, using wear-facet evolution and the dental structure of the docodont *Haldanodon*[1] as evidence.

The argument that only the docodont protoconid and paracone have homologues among therian dentitions, as claimed by Patterson (1956), is based on the supposition that the common ancestor of docodonts and therians had a haplodont dentition. However, Crompton and Jenkins (1968) pointed out that cynodonts, which were the precursors of most Triassic and later Mezozoic mammals, already had a tricuspid dentition. Furthermore, Crompton and Jenkins hypothesized that the common ancestor of both therians and docodonts may have been an early eozostrodontid with a molar pattern like that of *Eozostrodon.* Thus, if both docodonts and therians are derived from an ancestor with a basically tricuspid dentition, more than one cusp on each upper and lower molar may be homologous.

The evolution of the docodont molar from the eozostrodont molar involved two basic modifications: (1) lingual expansion of both upper and lower molar crowns, and (2) loss of one primary cusp on each lower and upper molar. The lingual expansion involved new or otherwise displaced cusps that cannot be compared with any cusps in the tribosphenic lineage. Modification of the buccal aspect of the molars is not so great. As Patterson first noted, loss of the cusps immediately posterior to the protoconid (cusp *c,* Fig. 1) and anterior to the paracone (cusp *a,* Fig. 1)[2] transforms an eozostrodontid pattern into a docodont pattern. Two cusps of the original cynodont tricuspid pattern remain: on the lower molar, the protoconid and the cusp anterior to it (cusp *a*), and on the upper molar, the paracone and the cusp posterior to it (cusp *c*). Inasmuch as the tricuspid molar pattern is basic to both therian and non-therian (i.e., triconodont, docodont) dentitions, then it is probable that lower cusp *a* is the paraconid and upper cusp *c* is the metacone. However, use of these terms seems unwarranted at present because they connote derivation from a tribosphenic pattern. As an alternative, Patterson's (1956) terminology

[1] *Haldanodon* is a *nomen nudum* because Kühne (1968) failed to designate any species for this genus. Anticipating that this taxonomic problem will be resolved, I use this name for the Kimmeridgean docodonts from Portugal described by Kühne (1968).

[2] Crompton and Jenkins (1968) referred to upper cusp *a* as cusp *B*.

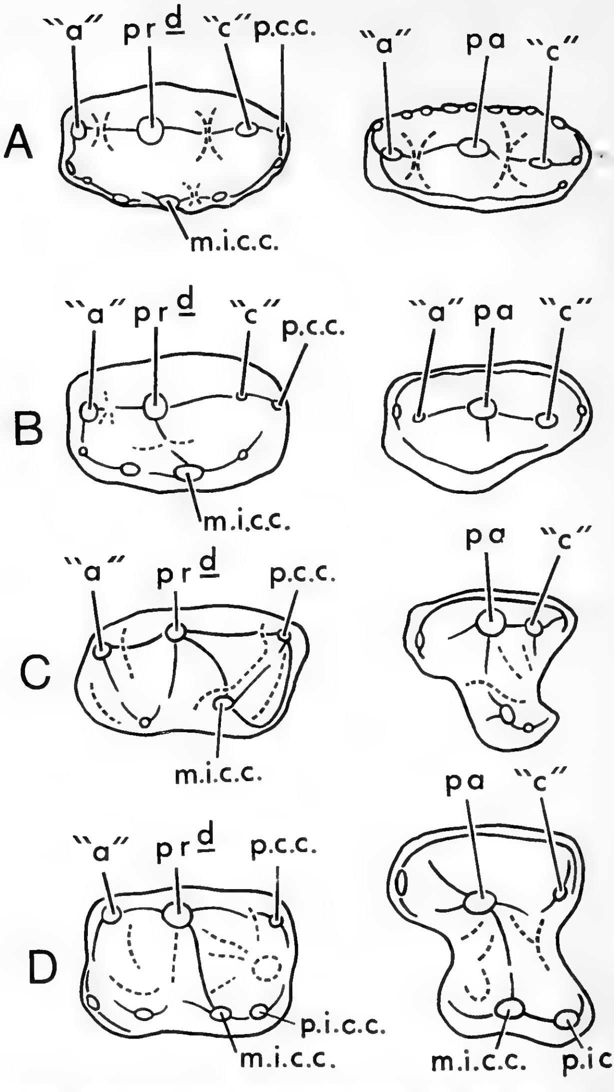


FIG. 1. Molar evolution and cusp homologies in the teeth of Triassic eozostrodontids and Jurassic docodonts. A) *Eozostrodon,* from the Rhaetic; after Crompton and Jenkins, 1968. B) Hypothetical Early or Middle Jurassic docodont. C) *Haldanodon,* from sediments of Kimmeridgean age, Portugal; after Kühne, 1968. D) *Docodon,* from the Late Jurassic Morrison Formation. On the left are lower molars, on the right, upper molars. Anterior is to the left; lingual aspect toward the bottom of the page. Not drawn to scale. Abbreviations: "a"—cusp *a;* a.c.c.—anterior cingulum cusp; a.i.c.c.—antero-internal cingulum cusp; "c"—cusp *c;* d.c.—distal cuspule; m.i.c.c.—main internal cingulum cusp; pa—paracone; p.c.c.—posterior cingulum cusp; p.i.c.c.—postero-internal cingulum cusp; prd—protoconid.

is available; in the interest of providing designations that are free from the tribosphenic context, and to avoid erecting a new terminology, Patterson's terminology is used in this paper.

MOLAR MORPHOLOGY. The rectangular lower molars progressively increase in crown length and width from M_1 to M_5 (Fig. 2B). M_6 is slightly smaller in both dimensions than the preceding molar, and its nearly rectangular shape contrasts to all other molars in which the posterior width is somewhat greater than the anterior width. These minor differences aside, the pattern and relative proportions of the cusps remain so constant throughout the molar series that the details of a single molar may be taken as representative (Figs. 5-9). The maximum lengths and widths in millimeters of the molars of the holotype of *Docodon victor,* YPM 11826, are respectively: M_1, 1.64, 1.18; M_2, 2.02, 1.22; M_3, 2.14, 1.47; M_4, 2.18, 1.51; M_5, 2.22, 1.64; M_6, 1.96, 1.47. M_{78} are missing and are unknown in any specimen. These measurements and those for the upper molars given below differ slightly from the tooth lengths given by Simpson (1929: 92, 97) for the same specimens because of the additional preparation undertaken during the present study.

In occlusal view, the upper molars have an hour-glass outline, the long axis of which is set transversely in the maxilla (Fig. 2A). The lingual half of each molar is offset posteriorly from the buccal half, so that the long axis is actually obliquely transverse. Molars increase in length and width from M^1 to M^3 and thereafter decrease in both dimensions. As in the lower molar series, differences between upper molars are either proportional or are due to differential wear; the details of one molar may be taken as representative (Figs. 10-14). The maximum lengths and widths in millimeters of the molars of the holotype of *Docodon superus* (YPM 10647) are respectively: M^1, 1.76, 1.89; M^2, 2.02, 2.14; M^3, 2.14, 2.44; M^4, 2.02, 2.39; M^5, 1.68, 2.18.

Adjacent molars, both upper and lower, form a series of ridges and basins. Individual ridges are confined to a particular molar crown, whereas the basins are formed between two adjacent molars. In lower molars, one ridge runs longitudinally from front to back (cusp *a,* protoconid, p.c.c.) (Figs. 1D, 5). Another ridge transverses obliquely across the center (protoconid, m.i.c.c., p.i.c.c. in Figs. 1D, 5). These two ridges define anterior and posterior half-basins which, on every lower molar, are completely

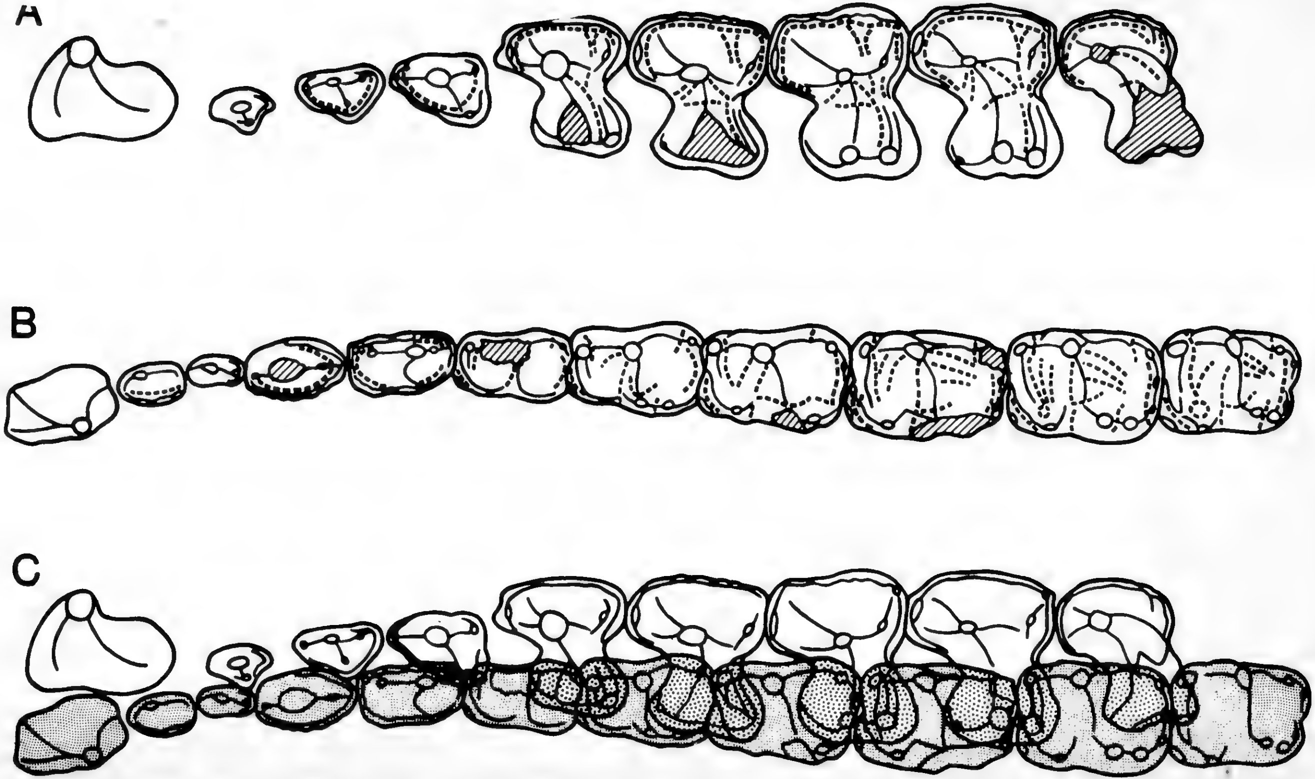


FIG. 2. Diagrammatic reconstructions of the dentition in *Docodon* in occlusal view. A) Upper right dentition (C^1 P^{1-3} M^{1-5}) based on *D. superus*, YPM 10647 and YPM 13769. B) Lower right dentition (C_1 P_{1-4} M_{1-6}) based on *D. victor*, YPM 11826. C) Occlusal reconstruction. Oblique hatching indicates damaged areas. Approximately ×10.

separated by the ridge from the protoconid to the middle internal cingulum cusp (m.i.c.c.). The anterior half-basin of one molar joins with the posterior half-basin of the preceding molar to form a large intermolar basin into which an upper molar occludes (Fig. 3, bottom). The upper molar is similarly arranged. A prominent ridge connecting the paracone and m.i.c.c. divides an anterior half-basin from a posterior half-basin (Fig. 1D). Adjacent half-basins form large intermolar basins; unlike the lower intermolar basins, however, the "floor" of these basins is not continuous (Fig. 2A).

OCCLUSION

The precise occlusal pattern in *Docodon* will remain uncertain until an associated upper and lower dentition are recovered. Without such complete material, it is nevertheless possible to approximate closely the occlusal pattern by carefully mapping the distribution of wear facets. More than 50 available specimens, representing single molars to nearly complete dentitions, provided the opportunity to determine the typical pattern of each facet.

Wear facets are designated by numbers (1-13 on lower molars, 14-21 on upper molars, Figs. 5-14). Areas of wear that are commonly represented by two or more confluent but differently oriented facets are given additional letter designations (e.g., la, lb, etc.). The total pattern of facets is complex. Such a pattern could be produced only by rather specific facet-to-facet relationships; these are tabulated in Table 1. Facets that appear to have no opposing feature represent either normal abrasion of cusp apices (9a, 10, 14, 16a, 21) or very slight (and often uneven) wear on a cusp shoulder (15, 16b, 16c) as a result of the cusp apex penetrating abrasive food.

The facet-to-facet relationship given in Table 1 has been used to reconstruct the occlusion of a complete molar series (Fig. 2C). The details of molar occlusion are best illustrated in buccal, lingual, anterior and posterior views (Fig. 4). In buccal view (Fig. 4C-D), the buccal half of an upper molar shears past the protoconid-cusp *a* ridge. The lingual half of an upper molar occludes in the intermolar basin formed by two adjacent lower molars (Fig. 4A-B). However, the maximum anteroposterior length of the lingual half of an upper molar (*x* in Fig. 4A) is less

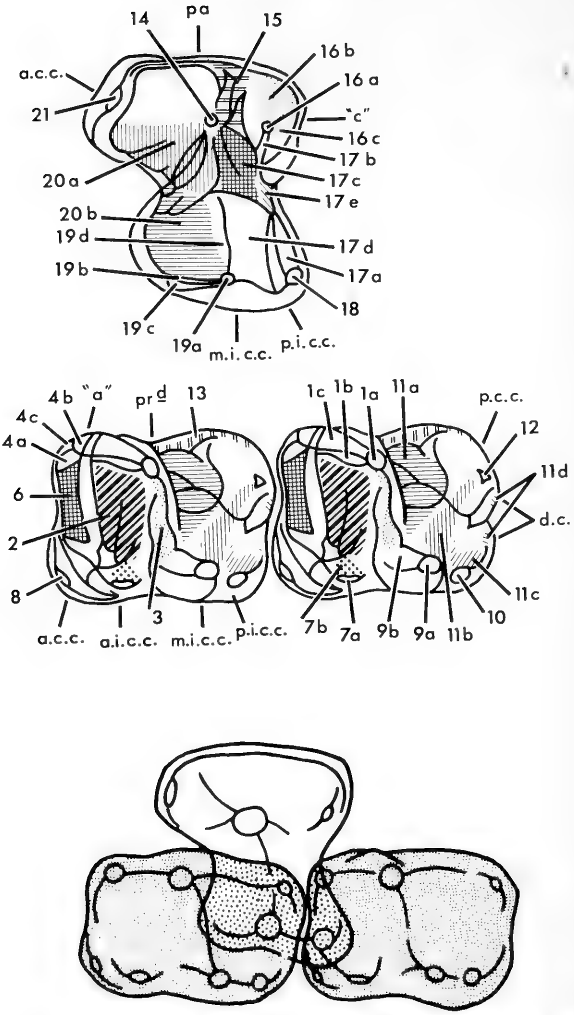


FIG. 3. Above, diagrammatic occlusal view of an upper and two lower molars to show the distribution of wear facets. Below, for comparison, the same molars in the approximate occlusal relationship required to produce the observed wear facets. See Table 1 for details of facet apposition.

than 3/4 the length of the lower intermolar basin (y in Fig. 4A). In actual distance on representative specimens, $y - x$ is estimated to be about 0.5 mm. Therefore, this amount of movement of the lower dentition relative to the upper dentition may have been

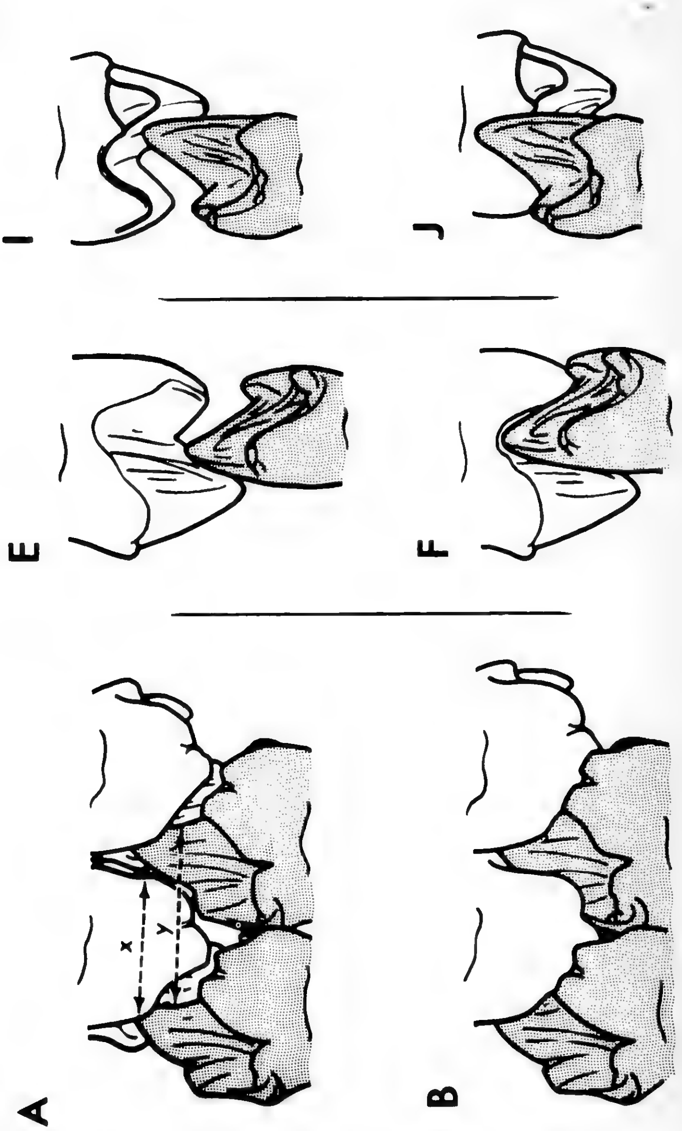
TABLE 1. The reconstructed facet-to-facet relationships between typical lower and upper molars in *Docodon* sp.

Lower molar	Upper molar
1a	20b
1b, c	17b, c, e
2	17a
3	17a, 19b
4a, b, c	17b, c, d, e
5	17d
6	17a
17a, b	18
8	19a (18 in heavy wear)
9b	18
11a	19b, 20b
11b, c	19a, c
11d	19a, d
12 (variably developed)	19d
13	20a

Facets not directly associated with opposing facets: 9a, 10, 14, 16a and 21 represent a flattening abrasion of cusp apices by food and are apparently not formed by opposition with any other particular facets; 15, 16b and c are variably developed and represent slight wear around the apices of the paracone and upper cusp *c*.

possible. The relative proportions of certain facets also are evidence of anteroposterior movement. For example, only facet 17a is situated to appose facets 2 and 6; yet 17a is much narrower anteroposteriorly than 2 and 6, and therefore 2 and 6 must have moved anteroposteriorly relative to 17a to have produced the observed wear.

In anterior view (Fig. 4E-F), the lingual half of an upper molar is seen to shear down the posterior face of a protoconid at the same time as the paracone passes buccal to, and slightly behind, the protoconid. In active occlusion, the lingual, posterior and buccal aspects of the protoconid are in snug contact with an upper molar half-basin (Fig. 4F). The buccal half of the preceding upper molar shears across the buccal aspect of the protoconid and lower cusp *a* (Fig. 4G-H). In active occlusion, the anterior aspect of the protoconid and the entirety of lower cusp *a* contact the posterior half-basin of the preceding upper molar (Fig. 4H; the posterior half-basin of an upper molar is depicted in Fig. 4I).


I
J
E
F
A
B
x
y

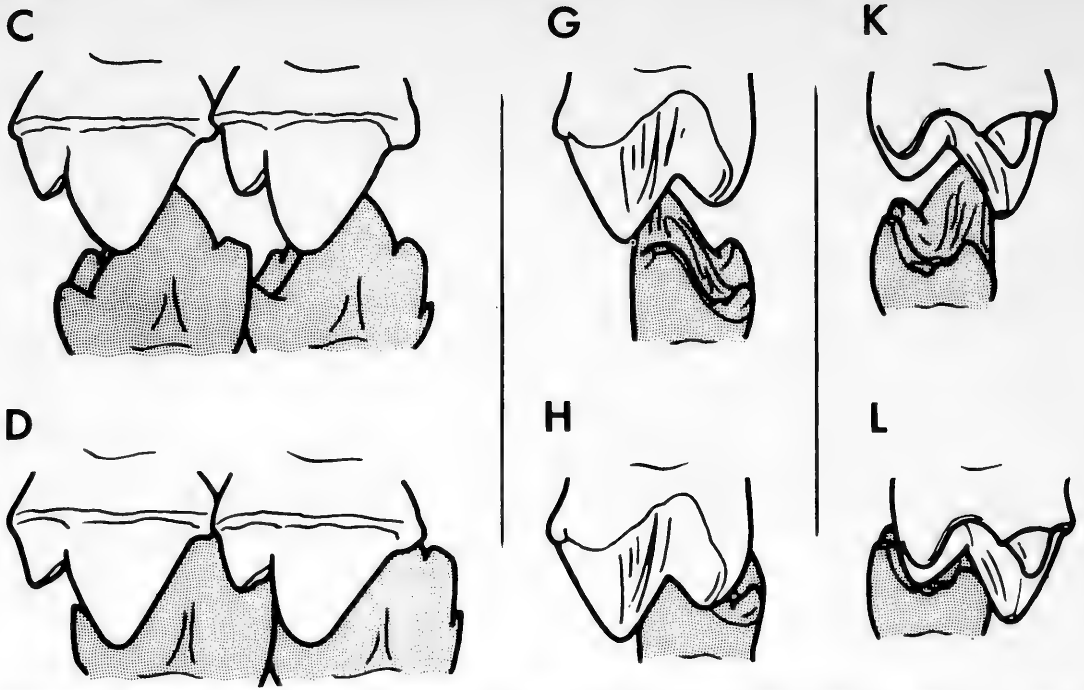


FIG. 4. Diagrammatic views of *Docodon* molars entering occlusion. A-B) Lingual view of M^{2-3} and M_{3-4}; *x*, anteroposterior distance between upper molar facets that wear against lower molar facets separated by distance *y*. Thus the distance *x* minus *y* is an approximation of the amount of anteroposterior movement. C-D) Buccal view of the same. E-F) Anterior view of M^3 and M_3. G-H) Anterior view of M^2 and M_3. I-J) Posterior view of M^2 and M_3. K-L) Posterior view of M^3 and M_3.

In posterior view, the shear of an upper molar anterior and posterior to the buccal aspect of the protoconid is again evident (Fig. 4 I-J, K-L). In Fig. 4 I-J, the upper postero-internal cingulum cusp (p.i.c.c.) may be seen passing into the anterior half-basin of a lower molar. Likewise, in Fig. 4 K-L, the upper middle internal cingulum cusp (m.i.c.c.) passes into the posterior half-basin. Simultaneously, the crest between the paracone and upper m.i.c.c. shears against the posterior face of the protoconid.

FUNCTION

PREVIOUS OPINIONS. Simpson (1929: 85) briefly characterized the occlusal relationship in *Docodon* as "a premature and ill-fated effort toward the production of broad-crowned crushing or grinding teeth from the more ancient piercing insectivorous type". Later, Simpson (1933: 145) more explicitly expressed his opinion of the molar function in a discussion of the docodonts as a family within the order Pantotheria (a taxonomic assessment now abandoned by Simpson, 1959: 407, and other workers): "... the teeth have become quadrate, rather than triangular, the cusps are in general somewhat blunter and heavier, the shearing crests have disappeared as such, supplementary cusps have arisen, and the talonids have become relatively much larger and are well basined. There is conclusive structural evidence that these are related to the other pantotheres and merely represent a rather superficial specialization, but functionally they are very different. In the docodonts occlusion involves almost exclusively opposition [*vide infra*] . . . They may be considered as somewhat more durophagous than other pantotheres, but a more probable analogy seems to be with later forms, e.g., many bunodont primates, which are frugivorous-omnivorous. This end has been obtained in a way differing structurally from any later development."

Simpson (1933) also outlined four "general principles" or modes of occlusion: alternation, opposition, shearing and grinding. Opposing occlusion, the mode Simpson believed to have been employed by docodonts to the practical exclusion of any other, is achieved either by opposing "positive elements (cusps, crests) into negative elements (basins, valleys) . . . or positive elements against other positive elements". Simpson's discussion makes clear his opinion that occlusion in *Docodon* was of the former type. In a later paper (1936: 946-947), he further noted that "opposition is also associated principally with orthal motion, but is generally also accompanied by some freedom of motion in a horizontal plane, propalinal or ectental . . . The function is in part grasping . . . but as a distinct type is primarily that of crushing". In the same paper (p. 952) he reiterated his view that the docodonts ". . . have emphasized opposition almost to the exclusion of shearing and alternation. . . ." Patterson (1956: 77), in his revised diagnosis for the order Docodonta which was originally proposed by Kretzoi (1946), concurred with Simpson, describing the molars as opposing and crushing.

INTERPRETATION OF THE PRESENT STUDY. The claim that *Docodon* molars are crushing teeth is apparently based on the relatively broad crowns (especially of the upper molars), the robust, often blunt cusps, the large, talonid-like basins, and the apparent lack of shearing crests. If its molars were specialized for crushing, *Docodon* would differ from other Mesozoic mammals in which shearing is the principal mode of occlusal action. Moreover, the occlusal diagram of *Docodon* (Fig. 2C) shows that a relatively large area of the upper molar crown overlaps, or opposes, the lower molar crown. This fact would appear to support the claim that *Docodon* molars crush and do not shear.

A complete evaluation of molar function in *Docodon* must take into account more than general morphology and a two-dimensional occlusal diagram. Three features of the *Docodon* dentition are pertinent to a functional interpretation: 1) the inclination of the prominent crests between cusps, 2) the orientation and relative size of wear facets, and 3) the distribution of crenelations (ribs and furrows) on the larger wear facets.

(1) Crests. The functional importance of crests that interconnect or otherwise define cusps has been widely recognized and has been recently re-emphasized by Mills (1966). Crests function as cutting or shearing blades. Their shearing efficiency is increased by an obliquity of the edge which is analogous in principle to a guillotine, as Mills has pointed out. In the *Docodon* dentition, oblique crests are prominent features. On lower molars (Figs. 5, 6 and 7) a substantial crest runs from the protoconid to the poste-

rior cingulum cusp (p.c.c.) and from the protoconid to the middle internal cingulum cusp (m.i.c.c.). Both crests are major sites of shear; wear facets are developed on both sides of each crest. Perhaps to a lesser extent the crest from the protoconid to cusp *a* (Figs. 6 and 7) is also a shearing crest. On upper molars (Figs. 10 and 12) the most prominent crest runs transversely across the crown from the paracone to the middle internal cingulum cusp (m.i.c.c.) (Figs. 10 and 12). Other crests descend anteriorly and posteriorly both from the paracone and middle internal cingulum cusp. The best defined of these descends anteriorly from m.i.c.c. and bears facets 19c and 19b (Fig. 12). This crest, together with the crest from the paracone to the m.i.c.c., bypasses a similar crest from the protoconid to the lower m.i.c.c. (Fig. 4E-F) and generates a major transverse shear. There is little doubt that these and other crests on *Docodon* molars are related to a cutting rather than a crushing mode.

(2) Facets. The orientation and relative sizes of molar facets are another indication of dental function in *Docodon.* The following graphical technique was used to obtain an estimate of the verticality and areal extent of facets. Each of the major facets was photographed in two views: one view perpendicular, the other view parallel to the plane of the wear facet. Tracing the facet on an enlarged perpendicular view with a planimeter yielded an estimate of the size of the facet. An enlarged parallel view yielded the orientation of the facet relative to a horizontal plane. On both upper and lower molars over 80% of the total facet area is oriented within 30° of the vertical — well within the range expected of shearing surfaces. Thus, as upper and lower molars occlude, the majority of wear facets are established by the shearing action of bypassing cusps and crests and not by contact of surfaces perpendicular to jaw movement. This interpretation assumes that mandibular movement in docodonts was primarily orthal. Such a supposition is reasonable. On better preserved mandibles a coronoid boss is evidence of transverse processes of the pterygoid that would restrict lateral movement. A small amount of anteroposterior movement is indicated by the wear facet relationships (see above). However, there is no evidence that a large amount of propalinal movement was involved. Instead, it seems likely that the lingual half of an upper molar may have occluded in two

slightly different positions — one just anterior to the other. If the lower intermolar basin was exactly the size of the lingual half of the upper molar, impacted food might block the full shearing stroke. To prevent this, the lower intermolar basin is slightly larger than the lingual half of the upper molar.

(3) Crenelations. A third aspect of the *Docodon* dentition is the presence of crenelations or ribs and furrows on the occlusal surface of the crown (Figs. 7-9, 12-14). These features were briefly mentioned by Marsh (1887), Butler (1939) and Patterson (1956); Simpson (1929: 91-92) described them in some detail but neither he nor any other author offered a functional explanation of them. Crenelations are most prominently developed on the larger facets (e.g., facets 2, 11a, 17c, 20a). These facets are produced by the shearing action of cusps or crests bypassing in close apposition. If these surfaces were simple flat facets, no additional shearing effect could be generated after a cusp or crest, acting as a blade, passed its counterpart on the opposing tooth. An appropriate analogy is a pair of scissors in which the cutting effect is exclusively confined to the point at which each blade

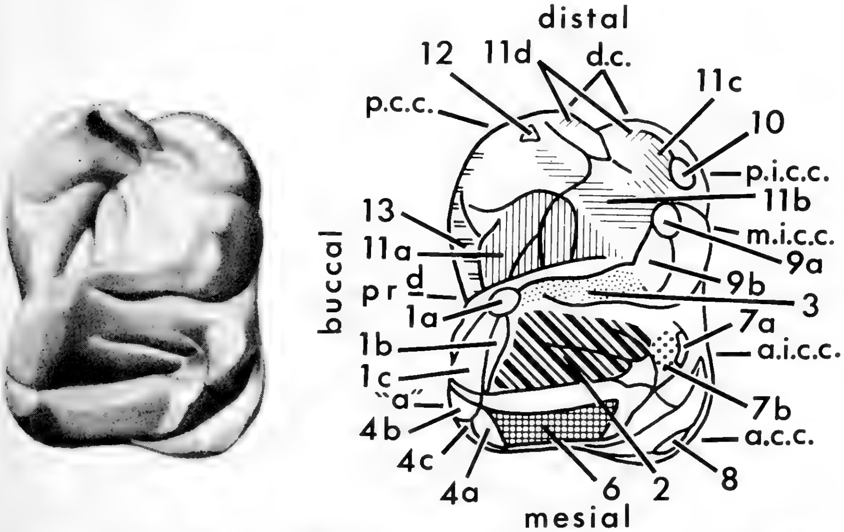


FIG. 5. Crown view of M_6 of *Docodon victor* (YPM 11826). ×23.5. See text and Table 1 for details of facets 1a through 21 in this figure and in Figs. 6-14, and see Fig. 1 for abbreviations.

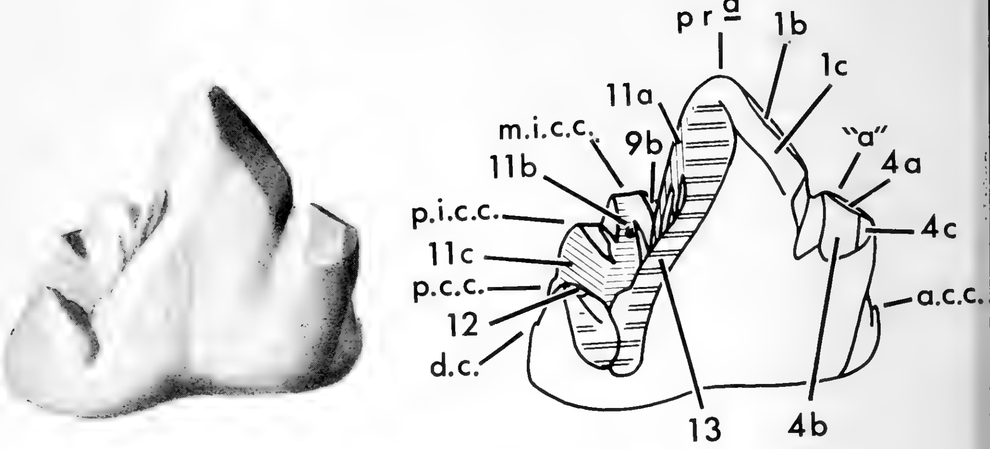


FIG. 6. Buccal view of M_6 of *Docodon victor* (YPM 11826). ×23.5.

passes the other. Material between the flat sides of two scissors blades cannot be cut. Crenelations in *Docodon* circumvent this problem by acting as secondary shearing edges after primary shearing edges (cusps, crests) have bypassed their counterparts. Two factors account for this additional shearing effect. First, the force per unit area of occlusal surface is concentrated on the

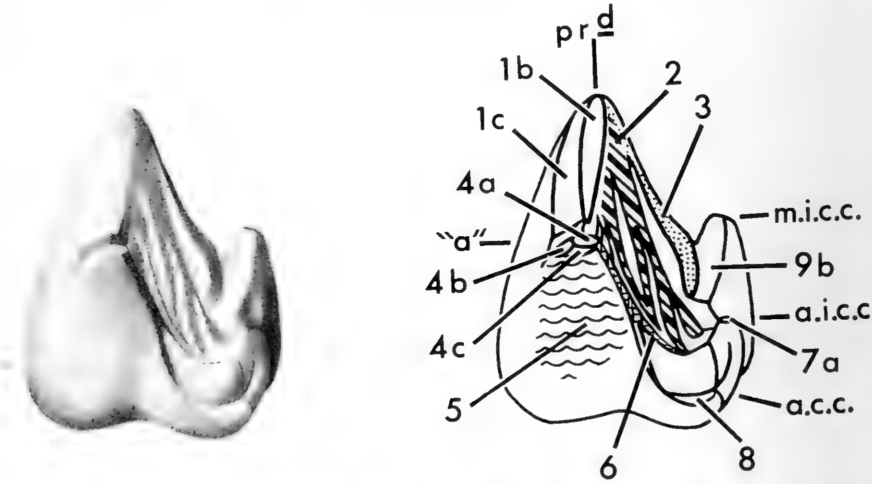


FIG. 7. Anterior view of M_6 of *Docodon victor* (YPM 11826). ×23.5.

linear crenelations by the recessing of the surfaces between them. Second, the beveling of the tops of the crenelations produces sharp edges (Fig. 15). Food brought to bear against these edges will tend to be sliced by these edges, although the cutting action here is in no measure as complete as between the major crests and cusps.

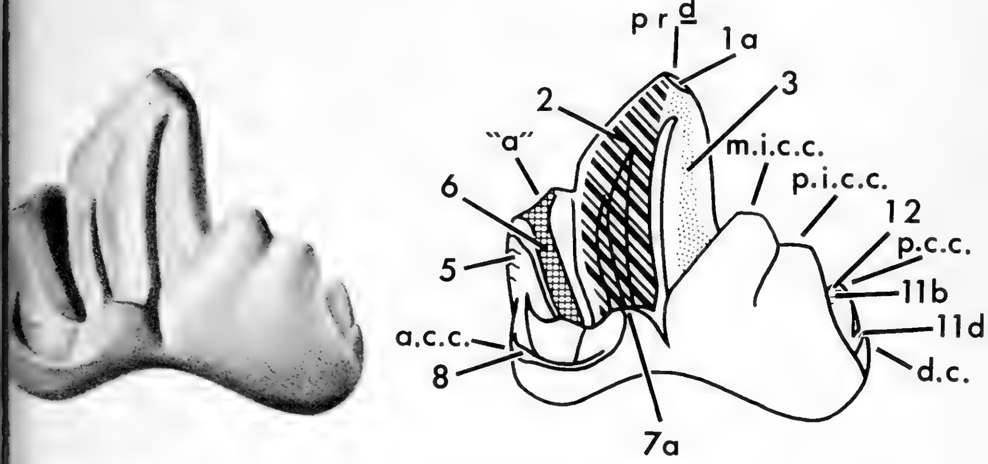


FIG. 8. Lingual view of M_6 of *Docodon victor* (YPM 11826). ×23.5.

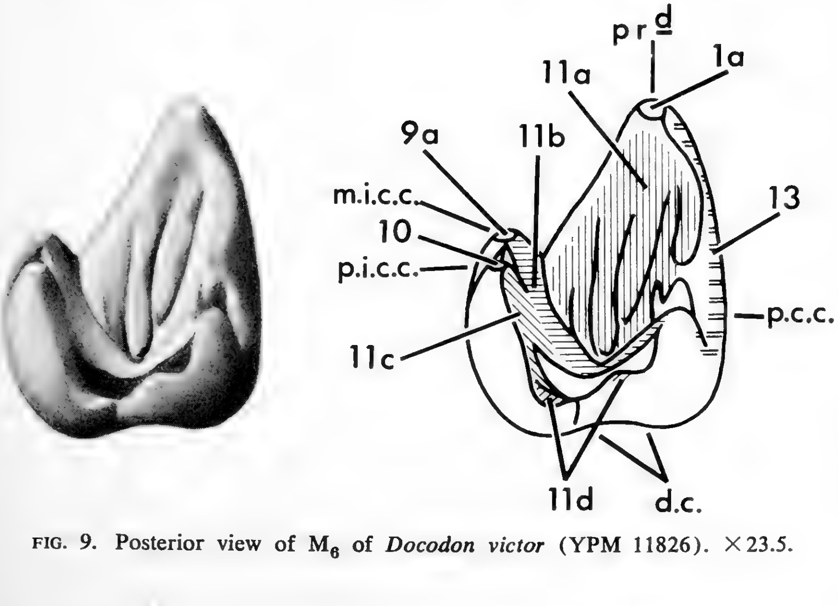


FIG. 9. Posterior view of M_6 of *Docodon victor* (YPM 11826). ×23.5.

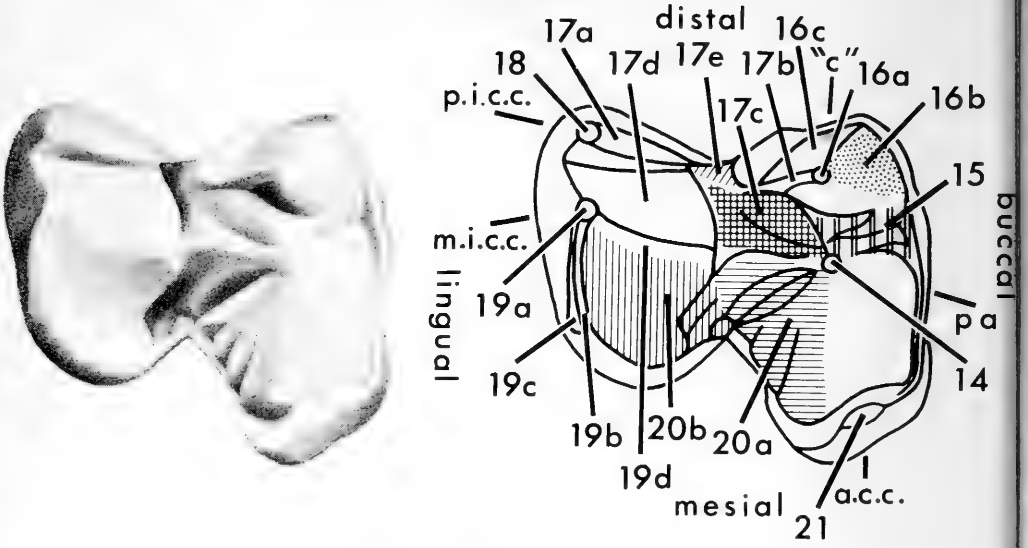


FIG. 10. Crown view of M^3 of *Docodon superus* (YPM 10647). ×21.5.

Discussion

On the basis of the morphology of the molar crowns, the orientation of wear facets, and the presence of accessory shearing crenelations, the dentition of *Docodon* is more appropriately characterized as functionally shearing rather than crushing. I doubt that opposing and crushing (in the sense of Simpson, 1933) is an efficient method of masticating most types of plant and animal food. In molluscivorous species, for example, crushing dentitions are obviously required to break into shells. Aside from such specialized diets involving very hard and brittle material, all other food sources involve material that is pliable to some degree. The most efficient method to reduce pliable material for ingestion and digestion would appear to be fragmentation by shearing. Thus shearing is probably the most important functional principle in the majority of mammalian dentitions. The diversity of molar form among mammals represents not so much a diversity of functional modes, but a diversity in the manner in which a shearing mode can be specifically adapted to various types of food.

The evolution of the *Eozostrodon* — *Haldanodon* — *Docodon* lineage, as interpreted by Crompton and Jenkins (1968), represented an adaptive shift from a simple longitudinal shear to a

FIG. 11. Buccal view of M^3 of *Docodon superus* (YPM 10647). ×21.5.

complex pattern of both longitudinal and transverse shear. The *Docodon* lineage exploited the expansion of lingual cingula to produce additional shearing surfaces. These surfaces represent a proportionately larger total occlusal area than could be developed by the simple longitudinal shear of *Eozostrodon* and related eozostrodontids. This development is perhaps related to the increase in molar number of *Docodon* over that in eozostrodontids. In the latter, the amount of shearing surface was more or less proportional to molar length. In docodonts, however, with the lingual expansion of the molar crowns and the addition of transverse

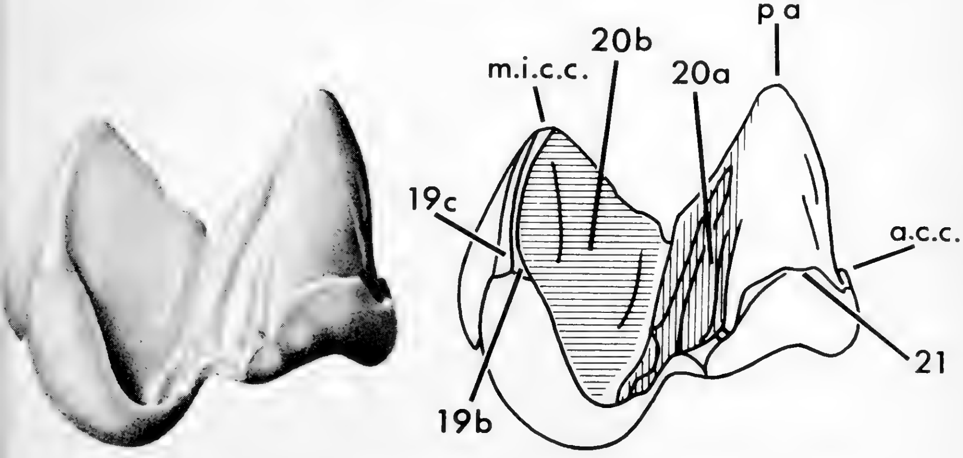


FIG. 12. Anterior view of M^3 of *Docodon superus* (YPM 10647). ×21.5.

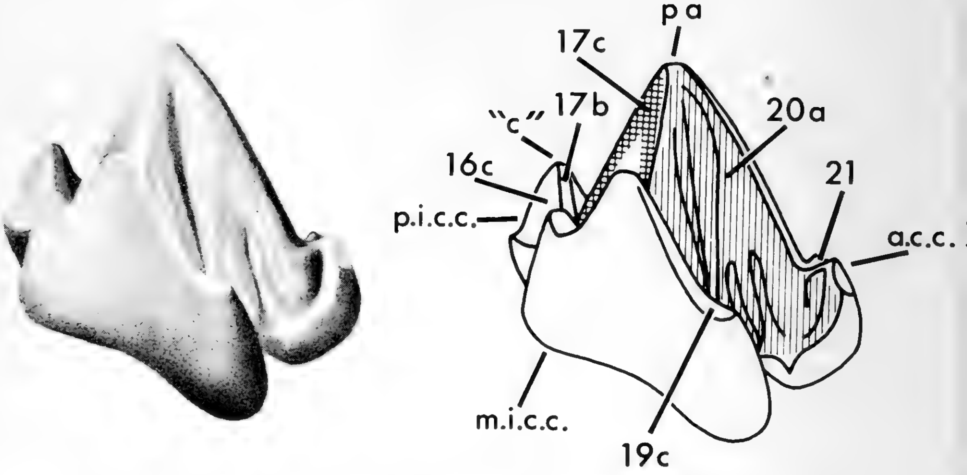


FIG. 13. Lingual view of M^3 of *Docodon superus* (YPM 10647). ×21.5.

shearing surfaces, the amount of shearing surface was less dependent on molar length. Thus the *Eozostrodon* — *Docodon* lineage appears to have increased the total molar shearing surface by both increasing the number of molars and by expanding the shearing features on each molar.

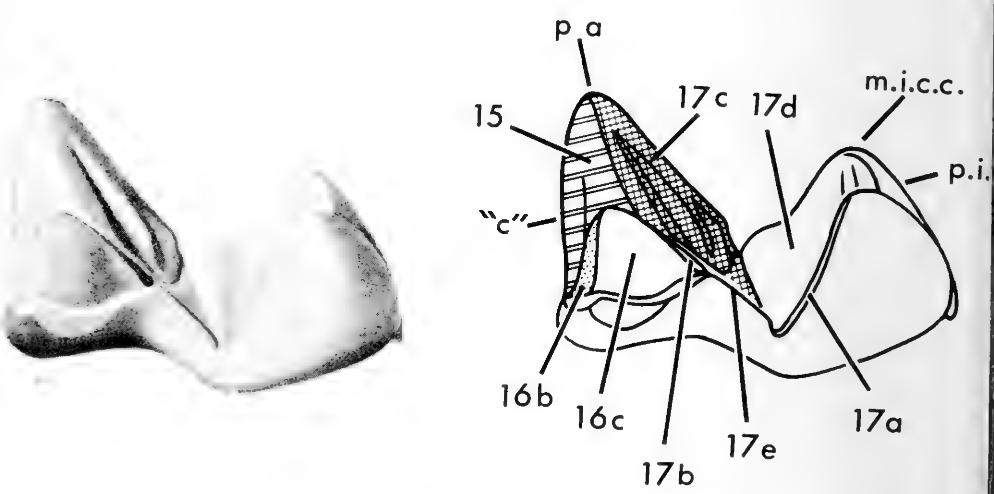


FIG. 14. Posterior view of M^3 of *Docodon superus* (YPM 10647). ×21.5.

FIG. 15. Stereoscopic photographs of M_5 of *Docodon victor* (YPM 11826) in posterior view to show the sharp ridges resulting from the beveling of the vertical crenelations. The buccal aspect of the postero-internal cingulum cusp has been lost.

ACKNOWLEDGEMENTS

I am very much indebted to Dr. A. W. Crompton for initiating and collaborating with me on the early phases of this study, and particularly for his reviews of the manuscript at various stages. Dr. James A. Hopson also contributed to this study through discussions and a review of the preliminary results. Mr. Carl R. Wester, Jr., executed the figures with his usual meticulous care. I express my sincere thanks to Dr. C. Lewis Gazin, United States National Museum, for permitting me to study the docodonts in his department. Dr. Malcolm C. McKenna of the American Museum of Natural History kindly loaned me the single docodont specimen belonging to that institution. Dr. R. G. Every took the stereoscopic photographs in Fig. 15.

LITERATURE CITED

Butler, P. M. 1939. The teeth of the Jurassic mammals. Proc. Zool. Soc. Lond. **109**: 329-356.

——— 1961. Relationships between upper and lower molar patterns. Internat. Colloq. on the Evolution of Mammals. Kon. Vlaamse Acad. Wetensch. Lett. Sch. Kunsten België (Brussels) Part **I**: 117-126.

Crompton A. W., and F. A. Jenkins, Jr. 1968. Molar occlusion in Late Triassic mammals. Biol. Rev. **43**: 427-458.

Gidley, J. W. 1906. Evidence bearing on tooth-cusp development. Proc. Wash. Acad. Sci. **8**: 91-106.

Kretzoi, M. 1946. On Docodonta, a new order of Jurassic mammals. Annals Hist.-Nat. Mus. Natn. Hung. **39**: 108-111.

Kühne, W. G. 1968. Kimeridge mammals and their bearing on the phylogeny of the Mammalia, p. 109-123. *In* Ellen T. Drake (ed.), Evolution and environment: a symposium presented on the occasion of the one hundredth anniversary of the foundation of Peabody Museum of Natural History at Yale University. Yale University Press, New Haven.

Marsh, O. C. 1880. Notice of Jurassic mammals representing two new orders. Amer. J. Sci., 3rd Ser., **20**: 235-239.

——— 1881. New Jurassic mammals. Amer. J. Sci., 3rd Ser., **21**: 511-513.

——— 1887. American Jurassic mammals. Amer. J. Sci., 3rd Ser., **33**: 327-348.

Mills, J. R. E. 1966. The functional occlusion of the teeth of Insectivora. J. Linn. Soc. (Zool.) **47**: 1-25.

Patterson, B. 1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. Fieldiana, Geol., **13**: 1-105.

Simpson, G. G. 1929. American Mesozoic Mammalia. Mem. Peabody Mus. Yale Univ. 3. 235 p.

——— 1933. Paleobiology of Jurassic mammals. Paleobiologica **5**: 127-158.

——— 1936. Studies of the earliest mammal dentitions. Dent. Cosmos **78**: 791-800, 940-953.

——— 1959. Mesozoic mammals and the polyphyletic origin of mammals. Evolution **13**: 405-414.

Vandebroek, G. 1961. The comparative anatomy of the teeth of lower and non-specialized mammals. Internat. Colloq. on the Evolution of Mammals. Kon. Vlaamse Acad. Wetensch. Lett. Sch. Kunsten België (Brussels) Part **I**: 215-320; Part **II**: 1-181.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

NOMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

ILLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

UTHOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 140. 3 DEC. 1969

THE ANATOMY AND INTERNAL ARCHITECTURE OF THE MUSCLES OF MASTICATION IN DIDELPHIS MARSUPIALIS

KAREN HIIEMAE

FARISH A. JENKINS, JR.

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

THE ANATOMY AND INTERNAL ARCHITECTURE OF THE MUSCLES OF MASTICATION IN DIDELPHIS MARSUPIALIS

KAREN HIIEMAE

Department of Biology, Yale University

Unit of Anatomy in Relation to Dentistry, Anatomy Department, Guy's Hospital Medical School, London

FARISH A. JENKINS, JR.

Department of Anatomy, College of Physicians and Surgeons, Columbia University

ABSTRACT

The anatomy and internal architecture of the jaw musculature in *Didelphis marsupialis,* the American opossum, was studied using a combination of dissection and thick sectioning techniques. Since the purpose of this investigation was to provide detailed anatomical information as a basis for subsequent functional studies of jaw activity, all muscles associated with normal feeding and ancillary oral behaviour are described. These muscles are the temporal, masseter, pterygoids, digastric, mylohyoid, the remaining suprahyoid muscles and part of the extrinsic tongue musculature.

In mammals, the jaw muscles medial to the superficial masseter are classically regarded as the temporal, masseter and zygomatico-mandibular; however, no structural justification for such a division can be found in *Didelphis.* With the exception of the outermost layer of the adductor mass which is differentiated as a discrete superficial masseter, the temporal and masseteric part of the adductor musculature is a single unit converging from an extensive origin on bone and fascia to insert onto the coronoid process or its associated tendon. This musculature is described as consisting of three parts: an external adductor originating from the temporal fascia, the zygomatic arch and the masseteric fascia and inserting onto the external surface of the coronoid process, its tendon and the ramus of the lower jaw; an internal adductor originating primarily from the wall of the cranium and inserting onto the inner surface of the coronoid process; and a posterior adductor, the fibers of which pass anteriorly from the cranium posterior to the temporo-mandibular joint to insert onto the posterior border of the coronoid process and the most posterior part of its tendon. The fibers in each part have a different orientation but are not

POSTILLA 140: 49 p. 3 DECEMBER 1969.

separated into discrete muscles. This division is for descriptive purposes only and no homologies are implied with the similarly named muscles of reptiles.

The superficial masseter is a large, fan-shaped muscle extending from a tendinous origin on the maxilla to the inferior surface of the inflected mandibular angle where it has a thick, fleshy insertion.

The remainder of the adductor musculature in the opossum consists of a very small external and a thick internal pterygoid muscle. The former inserts into the articular capsule of the temporo-mandibular joint as well as into the condylar neck. The latter has a long, almost linear cranial origin extending posteriorly from the palate toward the temporo-mandibular joint. The fibers pass inferolaterally to insert on the upper surface of the inflected angle.

The anatomy of the suprahyoid muscles in the opossum is essentially the same as in eutherian mammals. All the muscles gain part, if not all, of their attachment to the hyoid through a thick, crescentic tendon formed by the fusion of the central tendons of both digastrics.

No definite conclusions can be drawn as to the exact function of these muscles on the anatomical evidence alone. However, their position, internal architecture and relative size are suggestive: the external and internal adductors probably have the dual function of suspending the lower jaw from the cranium and adducting the jaw against resistance. The nearly horizontal orientation of much of the posterior adductor is evidence that it can, in addition, act as an effective retractor, with the superficial masseter as its antagonist. In addition to protracting the mandible, the superficial masseter may have a role in producing lateral movement in conjunction with the pterygoids or the adductors. Finally, the suprahyoid musculature in *Didelphis* probably functions, as in other mammals, to control the movement of the hyoid apparatus, the larynx and epiglottis, and the lower jaw relative to the hyoid. In addition, the mylohyoid, geniohyoid and genioglossus have an important action in elevating and depressing the floor of the mouth and the tongue.

INTRODUCTION

Didelphis marsupialis belongs to an ancient family of marsupials that first appeared in Late Cretaceous time (Clemens, 1968). An understanding of both the anatomy and function of its jaw musculature may aid in interpreting this system in Mesozoic mammals and in reconstructing the basic plan from which the jaw musculature of Eutheria differentiated. The primary purpose of this paper is to provide a full description of the anatomy and internal architecture of the jaw musculature in *Didelphis* as a basis for later consideration of its functional and evolutionary contexts.

The group of muscles innervated by the fifth cranial nerve, the trigeminal, and often referred to as "the muscles of mastication", constitutes the greater part of the jaw musculature in mammals. These muscles are the M. temporalis (temporal), the M. massetericus (masseter, normally divided into two parts, the M. massetericus superficialis or superficial masseter and the M. massetericus profundus or deep masseter), the M. pterygoideus internus (internal or medial pterygoid), the M. pterygoideus externus (external or lateral pterygoid) and two smaller muscles, the M. mylohyoideus (mylohyoid) and the anterior belly of the M. digastricus (digastric). For practical purposes the whole digastric is regarded as a muscle of mastication. All these muscles act in the initiation and control of the movements of the lower jaw and so are responsible for most masticatory activity involving mandibular movement. However, the mechanisms of ingestion, mastication and deglutition are also dependent on other ("accessory") muscles of mastication. These can be broadly divided into two groups. The first includes the M. geniohyoideus (geniohyoid), the M. genioglossus (genioglossus), the M. buccinatorius (buccinator) and the M. orbicularis oris (orbicularis oris). All these muscles are attached to one or both jaws. The second group, the remaining supra- and infrahyoid muscles, have a less direct action but are particularly important in deglutition because they control the position of the hyoid complex and its attached soft tissues. Since this paper is primarily concerned with the functional anatomy of the jaw musculature, only the muscles of the first group are included in this account.

Although frequent references to *Didelphis* are found in the comparative anatomical literature and particularly where the phylogeny of jaw musculature is discussed (Dobson, 1882; Adams, 1919; Edgeworth, 1935; Fox, 1964; Barghusen, 1968), the only available general description of this region in the opossum was published by Coues in 1872. This account, although comprehensive in its coverage, includes little detail on the attachments and internal structure of the muscles. More recently, Turnbull (in press) has prepared an account of the jaw muscles in *Didelphis* as a part of a general functional survey of jaw muscles in mammals.

Some explanation of the approach used in this study is necessary as it differs from that commonly adopted by anatomists. Fiedler (1952) and Frick (1957) regarded the jaw musculature in mammals as a single unit (M. adductor mandibulae) as did Adams (1919) and Lubosch (1938) although the latter two excluded the digastric. However, the musculature is rarely described as such despite Fiedler's and Frick's assertion that any division between the temporal, masseter and the pterygoids is both arbitrary and artificial. If Fiedler and Frick could be described as belonging to the "lumping" school, using Simpson's (1945) neologism, then many classical anatomists are "splitters". For example, the masseter has been described as having as many as four layers (Allen, 1880) one of which is often separately designated as the M. zygomatico-mandibularis (Parsons, 1899; Fiedler, 1952; Becht, 1954; Schumacher and Rehmer, 1962). The criteria on which these authors base this division of the masseter into "layers" or "parts" are rarely stated or justified. The large mass of muscle tissue extending from the zygomatic arch to the masseteric fossa on the lateral surface of the coronoid process and ramus of the mandible often seems to have been divided into a variable number of elements on the basis of vague fascial planes, intramuscular neurovascular bundles or on the arbitrary delineation of limits of origin or insertion. However, the deeper fibers of the masseter are often continuous with and adherent to those of the temporal (Allen, 1880; Parsons, 1896; Tullberg, 1899; Toldt, 1905; Adams, 1919; Becht, 1954) making separation difficult. While the recognition of parts within muscles or even within muscle masses may be valuable in purely anatomical or phylogenetic terms, it does not facilitate functional studies unless this division reflects changes in fiber orientation and therefore differences in action. In this respect description of the gross anatomy and internal architecture of the jaw musculature of *Didelphis marsupialis* constitutes a problem.

In *Didelphis* a large compact mass of muscle homologous with the temporal and masseter of other mammals fills the temporal fossa and ensheathes the coronoid process. This mass has a complex internal architecture but contains no natural divisions to justify recognition of separately named muscles. Such a muscle is difficult to describe, particularly in view of its complicated internal architecture. In this account the mass is called the adductor complex. Description of the internal architecture of the adductor complex is here facilitated by the use of the terms "posterior", "internal" and "external adductor"; these terms are intended solely in reference to parts of the adductor complex which have a characteristic fiber orientation. No homologies with the similarly named jaw muscles of reptiles are implied.

The large mass of muscle ensheathing the coronoid process of the lower jaw and taking origin from the lateral margin, roof and medial wall of the temporal fossa in mammals has been variously divided. The simplest and most usual division is into a M. temporalis and a M. massetericus which broadly correspond with the internal and external adductor musculature of mammal-like reptiles (Barghusen, 1968). Some authors (Parsons, 1898; Fiedler, 1952; and Davis, 1964, among others) recognize a third basic element, the M. zygomatico-mandibularis, described by Becht (1954) as "an independent member of the group with a history of its own." Within this basic division, further elements are sometimes recognized. The temporal is usually divided into deep and superficial parts separated in the plane of the coronoid process by its tendinous extension into the body of the muscle (Davis, 1964). Becht (1954) describes a separate anterior temporal muscle in Carnivora originating in the orbits and varying in size according to the development of the postorbital ligament. In addition, a pars suprazygomaticus, passing horizontally forward over the zygomatic arch to insert into the anterior border of the coronoid process, is recognized by many authors. The divisions of the masseter are even more complicated. It is variously described as consisting of two, three or four layers depending on whether or not the author recognizes a separate M. zygomatico-mandibularis. The most external of these layers may or may not be regarded as a separate muscle, the superficial masseter, although its great development in the Rodentia has made this recognition usual in that group (Parsons, 1894, 1896). Sicher (1944) and Davis (1964) describe a distinct superficial masseter in several genera of bears and the giant panda, and Miller *et al.* (1964) describe a superficial layer of the masseter in the dog, as does Allen (1880). Many authors regard the deeper element as a single deep masseter but if the zygomatico-mandibular is also recognized, the deeper element is automatically divided into two layers. According to Becht (1954), who does distinguish the zygomatico-mandibular, the deep masseter consists of two layers in Rodentia and three in the "Ruminantia". Even if the deepest layer is not elevated to the status of a separate muscle, the deep masseter is still reported as having two layers in many mammals including the dog (Miller *et al.,* 1964).

The plethora of terms, not all of which have been detailed above, used to describe the jaw musculature in mammals is not applicable to *Didelphis* where no real division exists. If *Didelphis* is a relatively generalized survivor of a Cretaceous marsupial radiation, then the anatomy of the jaw adductors may substantially represent the basic arrangement in early mammals. Moreover, if Adams (1919) is justified in stating that the anatomy of the muscles of mastication in mammals has remained remarkably uniform overall with only minor adaptive changes, then there are no reasonable grounds for maintaining or adding to the existing complex nomenclature.

MATERIALS AND METHODS

The anatomy of the jaw musculature of *Didelphis marsupialis* was examined by dissection of fresh, unfixed heads as well as heads fixed in 12% Formal-saline. The internal architecture of the muscles was studied by sectioning frozen heads with a band saw in either coronal, horizontal or sagittal planes; the sections were then stored in 10% Formal-saline before examination under a dissecting microscope. This method revealed the precise distribution and orientation of internal tendons and muscle fibers.

OBSERVATIONS

The greater part of the jaw musculature is confined within the area of the temporal fossa (Figs. 1, 2, 4, and Appendix 1). This musculature consists of three major components: the adductor complex (broadly corresponding to the temporal and deep masseter of Eutheria), the superficial masseter and the pterygoids. The temporal and masseteric fascia, an intrinsic although nonmuscular part of the system, are described first in view of their intimate relation to the adductor musculature.

THE TEMPORAL AND MASSETERIC FASCIA

The superficial surface of the adductor musculature both above and below the zygomatic arch is covered by a well-defined layer of fascia. Variable in thickness, it extends over the entire lateral surface of the head from the nuchal and sagittal crests above to the lower border of the mandible below. This fascia is divided into two parts by the zygomatic arch; in mammals the upper is normally termed the temporal fascia and the lower, the masseteric fascia. Although the underlying musculature in *Didelphis* is not distinguished by these names in this paper, the terms temporal and masseteric are retained in reference to the fascia in the comparable position to that in mammals.

The Temporal Fascia

The temporal fascia extends from the sagittal and nuchal crests to the zygomatic arch where it fuses with the periosteum. Anteriorly the fascia terminates as a thick band of fibrous tissue connecting the postorbital processes of the frontal and jugal bones, thus defining the posterior superficial margin of the orbit. A thin, inferior extension of this band separates the anterior wall of the adductor musculature from the orbital tissues. With the exception of its anterior border, the temporal fascia is attached to bone at all its margins.

Much of the temporal fascia is very dense, completely aponeurotic and extremely difficult to separate from the underlying muscle fibers that take origin from it. In its lower part (along the upper border of the zygomatic arch and over a small area adjacent to the postorbital process of the frontal) the fascia is an important origin for adductor muscle fibers. The fact that a substantial proportion of the adductor musculature takes origin from the fascia is correlated with the relatively large size of the muscle and the relatively small area available for its attachment. The temporal fascia is a functional replacement of the original bony roof of the temporal fenestra but has the advantage of accommodating the expansion of the musculature accompanying contraction.

The Masseteric Fascia

The temporal fascia continues inferiorly as the masseteric fascia. Attached above to the periosteum of the outer surface of the zygomatic arch, it passes inferiorly over the adductor musculature and over the superficial masseter to merge with the connective tissue covering the digastric and suprahyoid muscles at the lower border of the jaw. With the exception of the upper one third, which overlies the adductor musculature, the fascia is neither thick nor aponeurotic. Anteriorly its border merges with the periosteum of the maxilla immediately in front of the tendinous origin of the superficial masseter and with the fascia surrounding the buccinator. Below the buccinator, the fascia continues toward the lower border of the jaw but is less distinct and fades out close to the anterior free border of the superifical masseter behind and below the last molar. Posteriorly, in the region of the temporo-mandibular joint, the fascia blends with the joint capsule over its lateral surface.

The greater part of the masseteric fascia represents the thin layer of connective tissue normally covering muscles. In its thick and predominantly aponeurotic upper third, the fascia provides an attachment for the lower external fibers of the adductor musculature and is difficult to separate from them.

THE ADDUCTOR COMPLEX

The adductor complex has a multiple origin from both bone and fascia which can be divided into medial, lateral, superior and inferior areas relative to the temporal fossa.

The medial origin covers the lateral wall of the cranium (Fig. 4A, C) extending from the posterior margin of the orbit to the nuchal crest behind, and from the sagittal crest above to the alisphenoid and the root of the zygomatic process of the squamosal below (Appendix II).

The lateral origin of the adductor complex can be divided into three areas. The largest of these is the entire medial surface of the zygomatic arch from immediately behind its postorbital process to the point at which its squamosal element curves medially to join the cranium. The second area is on the inferior border of the zygomatic arch and extends from the jugo-maxillary suture to the posterior tip of the jugal. This area faces slightly outward as well as downward (Fig. 3). Finally, fibers take origin from the masseteric fascia as it extends ventrally toward the upper border of the superficial masseter.

The superior origin is from the lateral half of the temporal fascia and from a triangular area overlying the postorbital constriction of the cranium.

The inferior origin is the smallest and most clearly delimited. It corresponds exactly with the upper surface of the zygomatic process of the squamosal and with the superior surface of the bone overlying the temporo-mandibular joint.

The areas of insertion of the adductor complex are on the coronoid process and mandibular ramus (Fig. 4A, B). The medial insertion extends downward over the entire inner surface of the coronoid process as far as a near horizontal line connecting the alveolus of the last molar, the upper border of the inferior dental foramen, and the junction of the posterior border of the coronoid process with the condylar neck. The lateral insertion is only slightly more extensive. It covers the lateral surface of the coronoid process and the masseteric fossa on the ramus of the mandible and continues posteriorly onto the outer, slightly forward-facing surface of the condylar process below the sigmoid notch (Fig. 4A). In addition, many fibers originating from the posterosuperior area of the lateral wall of the braincase insert on the aponeurotic continuation of the coronoid process. This is a tendon of insertion, the "planum tendineum temporalis" or tendo m. temporalis (Davis, 1964), extending upward within the body of the muscle to a point approximately level with the base of the sagittal crest, and extending posteriorly almost to the nuchal crest. In its shape this tendinous sheet corresponds to a continuation both posteriorly and superiorly of the recurved upper portion of the coronoid process.

The Internal Architecture of the Adductor Complex

The adductor complex can be regarded as consisting of three basic parts on the basis of fiber orientation: an internal adductor, an external adductor and a posterior adductor. The first two are also more or less demarcated by the sites of origin of their fibers; the delineation of the posterior adductor on this criterion alone is somewhat arbitrary. However, the internal architecture of the of the muscle mass as shown in Figures 8, 9 and 10 demonstrates the basically dissimilar orientation of the posterior fibers as compared with the internal and external adductor groups.

The Internal Adductor

This part broadly corresponds to the deep temporal of other authors and includes, in its anterior part, a small element of the superficial temporal. Almost all its fibers pass laterally and inferiorly from their origin on the lateral wall of the cranium anterior to the temporo-mandibular joint (IA, Fig. 4A, C) to insert either into the medial surface of the internal tendon or onto the medial surface of the coronoid process (Fig. 4A, B). The orientation of these fibers (in the parasagittal plane) as they pass to their insertion is not uniform. Fibers originating anterior to the coronoid process pass slightly posteriorly, those arising in the central area pass vertically downward, and those behind the process pass slightly forward to their insertion. (For a detailed account see Appendix II). In some but not all specimens, the organization of the most superior fibers included in the internal adductor is complicated by a mesh of internal tendon plates (Fig. 8C). Short fibers insert into these plates which then insert into the internal tendon, giving this part of the muscle a multipennate structure.

The External Adductor

In many respects the internal architecture of the external adductor is a mirror image of the fiber pattern of the internal adductor. The external adductor takes origin from the temporal fascia (but not its aponeurotic area posterosuperior to the orbit), the zygomatic arch and the masseteric fascia. All external adductor fibers pass medially and more or less inferiorly to insert onto the coronoid process or the internal tendon. Those fibers originating from the temporal fascia are arranged in substantially the same pattern as those of the internal adductor except that their course is, in general, shorter and nearer the horizontal. Anteriorly, fibers of the external and internal adductors form the muscular posterior wall of the orbit and here the two muscles have about the same bulk (Figs. 8D, 9A, B). Occasionally small tendon plates are found in the posterosuperior part of the external adductor and serve as both origin and insertion for the muscle fibers (Figs. 8C right, 10E).

A gradual change in the orientation of the external adductor occurs between the fibers from superior and inferior limits of the muscle (Fig. 8). The majority of fibers which arise from the temporal fascia above the zygomatic arch, pass inferomedially with a slight anterior inclination. The block of fibers attached to the medial surface of the zygomatic arch pass directly inferomedially to their insertion into the masseteric fossa (Fig. 8C, D) as do most of those originating from its inferior border. However, the fibers attached to the posterior third of the inferior border of the zygomatic arch pass posteriorly as a thick band to attach to the condylar process and lower border of the mandible just anterior to the temporo-mandibular joint (Figs. 6, 8B left). The most external fibers, originating from the masseteric fascia, also have a slightly posterior as well as inferomedial orientation. The external and internal adductors almost fuse anteriorly where they form the dense, muscular posterior wall of the orbit (Figs. 9A, B, 10B, C). Such separation as is anatomically recognizable is provided by a small tendon extending the coronoid process anteriorly and fusing, in part, with the postorbital fascial wall.

The architectural differences between the external and internal adductors relate to the more extensive insertion of the external adductor and to its two small internal tendons. These tendons could be used to demarcate a zygomatico-mandibular or two layers of a deep masseter, although neither extends completely through the muscle. The larger and the better developed of these tendons extends inferiorly from its origin at the junction of the medial and inferior surfaces of the central part of the zygomatic arch

(Fig. 8C). The other tendon is less distinct; it projects laterally and superiorly from the sharp lower border of the masseteric fossa below and anterior to the condylar process (Figs. 8C right, 9C). As the superficial fibers of the external adductor insert by means of this tendon, it separates the outer surface of the adductor from the deep surface of the superficial masseter in this area.

The Posterior Adductor

The posterior adductor has its main axis in the horizontal rather than in the vertical plane. Unlike the other parts of the adductor complex, the posterior area of insertion of the adductor is much smaller than its origin so that its fibers converge on their insertion. The bulk of the posterior adductor takes origin from the posterosuperior area of the temporal fossa and the adjacent parts of the sagittal and nuchal crests. These fibers pass outward, forward, and either downward or horizontally to converge on the internal tendon or the posterior border of the coronoid process (including the sides of its recurved tip). There are two small slips of this muscle, the suprazygomatic and the fibers originating from the bony roof of the joint, which pass horizontally forward (see Appendix II).

As is shown in Figures 8A and 10E, the internal architecture of the major part of the posterior adductor is, in some specimens, complicated by a dense mesh of internal tendon and aponeuroses. The posteroexternal fibers are more clearly organized and pass predominantly anteroinferiorly to insert into the internal tendon of the coronoid process. Near the anterior margin of the posterior adductor, above the joint, the fibers run more evenly anteroinferiorly to attach to the tendon and so to the coronoid process (Fig. 8B right).

The posterior adductor is not divisible into true "superficial" and "deep" parts. Although the coronoid process and its extension tendon separate the insertion of the muscle into outer and inner areas, this division does not completely divide the muscle. The fiber orientation of this muscle mass suggests that it is a single functional unit and one basically different from either the internal or external adductors.

Discussion

The question arises as to whether a relatively undifferentiated muscle mass such as the adductor complex in *Didelphis* can exhibit the same type and range of movement as a group of recognizably separate muscles. Anatomical evidence alone cannot provide an answer but the internal structure of the adductor complex is suggestive. Although there are no distinct anatomical boundaries to distinguish the internal, external and posterior adductors, the substantial shift in fiber orientation is indicative of a basic difference in their effect on contraction.

The adductor musculature functions to maintain the integrity of the jaw apparatus and to initiate and control movements of the lower jaw. The first is achieved in conjunction with tendons and ligaments and particularly of the joint capsule. However, the major factor in regulating the position of the lower jaw is the activity of the tonic musculature. The anterior temporal and the deep masseter were found to suspend the lower jaw from the cranium in the rat (Hiiemäe, 1966) and to be in large part responsible for the stability of the system. As can be readily seen in the coronal sections in Figure 8, the external and internal adductors in *Didelphis* also "sling" the mandible between them by ensheathing almost the entire mandibular ramus and the coronoid process in muscle.

The most important phasic action of the adductor complex is elevation or adduction of the lower jaw. In addition, since both internal and external adductors have a substantial transverse component, contraction of the external adductor of one side with relaxation of the other could produce lateral movement. This action is unlikely to be the main mechanism for producing lateral jaw movement in *Didelphis* although such an action may be synergistic.

The precise function of the posterior adductor is less readily elucidated on purely anatomical grounds. In many mammals, including man, the analogous musculature is regarded as primarily a mandibular retractor and elevator and in addition as a synergist in the production of lateral movements (Kawamura, 1964; Hiiemäe, 1966). Mandibular elevation and retraction are very probably functions of the posterior adductor in *Didelphis* also. In addition, the posterior adductor in *Didelphis* has a small transverse component which may be capable of pulling the coronoid process of the same side posteromedially, so moving the lower jaw toward the contralateral side. Such an action could be of considerable importance in the production of "Bennett movements"[1], if they occur.

THE SUPERFICIAL MASSETER

Phylogenetically the superficial masseter is derived from the adductor complex (Barghusen, 1968), and in *Didelphis* it is sufficiently differentiated from the external adductor to justify its recognition as a separate muscle. However, some intermingling of fibers is found and in many specimens the separation of the upper part of the deep surface of the superficial muscle from the outer surface of the adductor is somewhat arbitrary. Nevertheless, the two are different functional entities in view of their fiber length and orientation.

The superficial masseter is a fan-shaped, unipennate muscle (Fig. 5) with an effective length some three times that of the external adductor and with a long axis near the horizontal. It takes origin as a thick but slightly flattened tendon from a small prominence on the maxilla immediately below and in front of the lower border of the jugo-maxillary suture. This tendon passes posteroinferiorly and after a short course broadens out into a triangular aponeurosis. The upper border of the aponeurotic area more or less coincides with the upper border of the muscle and is almost straight, passing posteriorly toward the external auditory meatus and fading out on the superficial surface of the muscle below the temporo-mandibular joint. The lower border is very much shorter; it passes more sharply downward, exposing muscle fibers anterior to it (Fig. 5) and again fades out on the outer surface of the muscle. This aponeurosis serves as the origin for the superficial masseter which arises from its deep surface and fans out to wrap around the lower border of the jaw. The muscle inserts on the expanded lower surface of the jaw and onto the fascial layer separating the internal pterygoid from the superficial masseter. A few fibers, however, take origin from the tendon or even from

---

[1] Bennett (1908) stated that the mandibular condyle in man would, in certain circumstances, be translated laterally (or medially) across the glenoid fossa. Any such linear movement is known as a Bennett movement.

the maxilla and pass directly downward to insert on the medial surface of the lower border of the mandible where they are closely related to the insertion of the anterior belly of the digastric. These fibers are clearly seen in Figures 5 and 13. This part of the muscle overlies, but does not attach to, the convex, smooth area separating the masseteric fossa and the lower border of the jaw. It appears that this area functions as a pulley around which the superficial masseter contracts.

The bulk of the fibers insert into the broad medial expansion of the lower border of the jaw and the inflected angle (Fig. 4A, B, D). A few fibers insert into the fascial layer linking the medial border of the condylar process with the angle and so pass around the joint immediately external to the lower part of the joint capsule. A number of the most superficial fibers insert onto the fascial plane formed by the fusion of the fascia covering the internal pterygoid and the superficial masseter, which is itself attached to the extreme medial edge of the angular process. As the muscle approaches its insertion it becomes extremely thick and gives a rounded appearance to the angular region of the jaw.

Discussion

By virtue of its nearly horizontal orientation the superficial masseter probably functions as a protractor of the lower jaw and therefore could act as an antagonist to the posterior adductor. However, the superficial masseter also wraps around the lower border of the jaw and the inflected angle. This relationship indicates the possibility that the superficial masseter rotates the jaw about its long axis (i.e., moves the lower border laterally and dorsally). Conversely, it is possible that the torque of the superficial masseter is balanced by an opposing torque of the pterygoids. Experimental data, rather than anatomical evidence, is necessary to solve this problem.

THE PTERYGOID COMPLEX

The two muscles which form the mammalian pterygoid complex, the internal pterygoid (M. pterygoideus internus or medialis) and the external pterygoid (M. pterygoideus externus or lateralis) have probably had quite different phylogenetic histories. Crompton (1963) has shown that the former, together with the M. tensor tympani, is derived from the anterior pterygoid musculature of reptiles, while the external pterygoid developed from a slip which separated from the deep surface of the medial part of the reptilian adductor mass.

The Internal Pterygoid

The internal pterygoid is a thick, short muscle that appears almost trapezoid in shape when viewed from the interomedial aspect (Fig. 11). It originates from a long, approximately triangular area on the cranium (Figs. 4A, 8B, C) below the lower border of the origin of the internal adductor and is separated from it by the first and second divisions of the trigeminal nerve. The triangle has its base anteriorly on the palatine bone behind the sphenopalatine foramen and extends onto the pterygoid and its wide transverse process (Figs. 4A, 8C left). The remaining area of origin is much narrower and extends posteriorly from the pterygoid process along a ridge of the alisphenoid.

In contrast, the area of insertion is large. The limit of its attachment is along the condylar notch to immediately above the inferior dental foramen and from there down onto the medial surface of the lower jaw. The superior limit of its attachment is along a line extending from the base of the condylar process to immediately below the inferior dental foramen; from there the line passes down to the lower border of the ramus where the inflected angle narrows to become a rounded margin (Fig. 4B). From this line the insertion extends inferiorly and medially over the entire surface of the angle and the angular process as well as the adjacent area of the fascia linking the angular and coronoid processes. In addition, some fibers insert into the common fascial plane shared by the internal pterygoid and the superficial masseter. It should be noted, however, that anteriorly the attachments of the two larger muscles diverge, leaving a small area of bone for the attachment of the mylohyoid (Fig. 11).

The fibers of the internal pterygoid pass downward, laterally and posteriorly to their insertion. Those fibers originating on the palatine or pterygoid process insert near the anterior limit of the inflected angle and those originating posteriorly from the alisphenoid insert onto the angular process. In fact the muscle has a partly fibrous, partly tendinous origin. The thick, free anterior border of the internal pterygoid is fleshy but posteriorly the deeper fibers (superficial in Figs. 11 & 12) take origin from an aponeurosis extending over the upper and posterior quarters of the muscle surface (Fig. 10C). In this area, the origin of the muscle is never entirely aponeurotic; some fibers take origin from the alisphenoid but the considerable bulk of the internal pterygoid can be partly attributed to the additional area for fiber attachment afforded by the tendon. In addition to this aponeurosis, the body of the muscle is more or less divided along its length by an internal tendon of variable extent and position (Figs. 8B, C, 9D, 10C). As the orientation of the muscle fibers superficial and deep to the tendon is essentially the same, it seems likely that the tendon serves as an internal area of origin and insertion rather than dividing the muscle into two different functional units.

The External Pterygoid

This muscle, barely more than a slip, originates from a small area on the alisphenoid above and behind the foramen rotundum (Fig. 4D). It then passes posteriorly, laterally and slightly downward to insert into a small depression on the superomedial surface of the condylar process and into the capsule of the squamodentary joint (Figs. 4B, 10B). When dissected from the inferomedial approach (Fig. 12) it is seen as a thin, rounded fasciculus with a thin aponeurosis on its (deep) surface. Removal of this deep belly exposes a second, thinner, fasciculus partly separated from the first. The larger belly inserts into the condylar process and the smaller into the joint capsule.

Discussion

While the anatomical relations of the internal pterygoid can be clearly seen (Figs. 8B, C, 9C, D, E, 10C, E), the functional relationships of the muscle to the superficial masseter is not clear. Although the two occupy similar positions in *Didelphis* and in eutherian mammals, the inversion of the angular process must alter their functional relationships. First, the actual length of the superficial masseter in *Didelphis* is thereby increased and that of part of the internal pterygoid reduced. Second, part of the attachment of the internal pterygoid is moved medially. On contraction this muscle will tend to invert the lower border of the mandible (as well as pull it medially and forward) and is thus capable of inducing a rotation of the mandible about its long axis. It has already been suggested that the superficial masseter might be capable of producing lateral movement of the mandible coupled with a similar type of rotation. Whether or not this is the case, it remains likely that the two muscles act as mutual antagonists and also probably as synergists, i.e., the internal pterygoid of one side acting in concert with the contralateral superficial masseter.

In *Didelphis,* the external pterygoid may initiate mandibular depression by rotating the condyle forward, thus tilting the lower jaw downward. It also may act with the internal pterygoid in producing lateral jaw movement. Positive experimental confirmation of these actions is not yet available; however, its very small size suggests that no powerful action can be produced by its contraction and that its role in the generation of mandibular movement is probably supplementary to that of the other muscles. The position of both internal and external pterygoids in mammals has led to the suggestion that they both act primarily to produce lateral movement of the lower jaw. Whether or not this is their principal function in *Didelphis* is not known, but the development of the "marsupial flange" and the consequent alteration of the position of the internal pterygoid must reflect some functional difference.

THE SUPRAHYOID MUSCULATURE

There are three important muscles linked to the hyoid apparatus and functioning as muscles of mastication: the M. digastricus (digastric), the M. mylohyoideus (mylohyoid) and the M. geniohyoideus (geniohyoid). In addition, two muscles of the tongue, the M. genioglossus (genioglossus) and the M. hyoglossus (hyoglossus) can be included in this group as they are attached to the lower jaw and the hyoid, respectively, and are functionally associated with the other accessory muscles.

The Digastric

As in most, but not all, mammals the digastric in *Didelphis* is formed of two fleshy bellies linked by a central tendon. This tendon, arising as an aponeurosis on the deep surface of the posterior belly, forms part of the "expansion aponeurotique de digastrique" described by du Châine (1914). Du Châine demonstrated a tendinous arcade, formed largely by the paired central tendons of the digastric but with contributions from the mylohyoid and geniohyoid, which serves as a common attachment for all these muscles and is itself attached to the hyoid bone. In effect, the major suprahyoid muscles have a common insertion into the median expansion of the central tendons of the paired digastric. This arcade is well developed in *Didelphis* as a narrow, almost crescentic band of tendon, convex anteriorly, which crosses the midline in front of the trachea and arches posteriorly toward the angles of the lower jaw at each side.

The posterior belly of the digastric in *Didelphis* has a fleshy origin from the paraoccipital process and is closely related to the cranial attachments of the M. styloglossus and M. stylohyoideus. As it passes anteriorly it lies in a gutter between the fibers of the superficial masseter laterally and the internal pterygoid dorsomedially and in fact overlies the common fascial insertion of these muscles. At about the level of the angular process the posterior belly begins to change from an entirely fleshy mass of ovoid cross-section into a narrow, tendinous band. The fibers of the posterior belly insert either into the aponeurosis on its deep surface, which forms the most posterior extension of the central tendon, or directly into that tendon.

The anterior belly of the digastric has a long origin from the central tendon and a long linear insertion into the lower jaw (Fig. 4B, D). It is a thin sheet of muscle, broadly triangular in shape with its origin and insertion forming the base and one side of the triangle (Fig. 13), the other side being its long medial free border. The fibers of the anterior belly run directly anteroposteriorly so that the more lateral the fiber, the shorter its course. The medial fibers pass anteriorly for a considerable distance to attach to the jaw just below the first molar. The medial edge of the anterior belly is bound down to the underlying mylohyoid and to its pair on the other side by a fairly dense layer of fascia.

The digastric in *Didelphis* is similar to that of most mammals and in all probability serves the same functions.

The Mylohyoid

The mylohyoid, like the digastric, is a paired muscle but is fused in the midline to form a single functional unit. It is a thin sheet arching downward and medially from one half of the lower jaw, across the midline and up to its attachment on the other. The bony insertion of this muscle is linear and lies on the medial aspect of the lower border of the jaw (Fig. 4B, D). The posterior fibers of the mylohyoid take origin from a narrow area of bone below the inferior dental foramen and on the medial surface of the inflected angle between the insertion of the internal pterygoid and the superficial masseter. At the level of the anterior border of the internal pterygoid, the attachment of the mylohyoid curves upward (dorsally) and then passes anteriorly. Over the anterior half of its length the attachment of the mylohyoid is closely related to the insertion of the anterior belly of the digastric (Fig. 4B) but is always separated from it by smooth bone. The anterior limit of mylohyoid origin is at approximately the level of the first molar.

There is no obvious central raphe in the mylohyoid of *Didelphis*. The majority of fibers seem to pass directly across the midline. Not all, however, have a straight course; those originating near the inferior dental foramen pass slightly anteriorly as well as medially. Over the central third of the posterior border, the mylohyoid is attached to the tendinous arcade and so gains insertion into the hyoid apparatus. The short anterior border of the mylohyoid is bound down by fascia.

The Geniohyoid

This muscle is the largest of the supra-hyoid group. A powerful, unipennate muscle, the geniohyoid originates from the inferior lip of the genial depressison on each half of the lower jaw and immediately behind the symphysis as a tough but flattened tendon. This passes posteriorly for a short distance and then is continued as the thick, rounded fleshy belly which inserts into the deep part of the tendinous arcade and into the hyoid bone itself. There is no constriction of the belly of the geniohyoid as it approaches its insertion. The muscles of the right and left sides are in contact medially but do not fuse. Throughout its length the belly of the geniohyoid is covered superficially by the mylohyoid. The geniohyoid in turn covers the genioglossus (Fig. 14).

Discussion

The digastric, mylohyoid and geniohyoid are regarded as accessory muscles of mastication for two reasons. First, they control (with the assistance of the remaining supra-and infra-hyoid muscles) the position of the hyoid bone and its associated structures in relation to the cranium and the lower jaw. In swallowing, the hyoid moves upward carrying the larynx with it so that the epiglottis can effectively seal the airway. On completion of deglutition, the hyoid apparatus drops or is pulled back. The stylohyoid and the posterior belly of the digastric suspend the hyoid from the cranium; the mylohyoid, geniohyoid and the anterior belly of the digastric control its position in relation to the lower jaw and the infra-hyoid muscles connect it with the sternum and the scapula. Second, the anterior belly of the digastric, the mylohyoid and the geniohyoid can all lift the floor of the mouth and so act as elevators of the tongue. The mylohyoid, in view of its orientation, is probably the most effective of the group in this respect; however, their common tendinous insertion coupled with their close fascial connections means that all three muscles are likely to be involved.

The Genioglossus

This muscle is one of the larger extrinsic muscles of the tongue and has an important action in controlling its shape and position. Taking origin as a fleshy bundle from the genial depression, it passes posteriorly beneath the geniohyoid as a progressively widening band, fading out in front of the hyoid apparatus. Its most superficial fibers curve upward to their insertion into the dorsum of the tongue (Fig. 14). Viewed in sagittal section (Fig. 10D) the genioglossus can be seen as a broad fan of muscle fibers passing posterosuperiorly into the body of the tongue from their origin on the lower jaw. The genioglossus can pull the tongue bodily forward or can depress its middle or posterior thirds.

The Hyoglossus

Like the genioglossus, the hyoglossus is a large muscle. It originates as a fleshy mass from the hyoid bone deep to the insertion of the geniohyoid and then passes forward, laterally and upward around the posterior part of the genioglossus (Fig. 14) to insert as a fan of fibers into the lateral part of the body of the tongue in its posterior two-thirds. This muscle acts to retract the tongue, or, like the genioglossus, to alter its shape.

Discussion

The tongue is an extremely mobile organ and has an essential role in ingestion, mastication and deglutition. These two muscles, together with the styloglossus and its intrinsic musculature, are responsible for movement of the tongue and for producing the local changes in shape essential to efficient mastication.

THE FACIAL MUSCULATURE

In addition to the muscles which initiate and control mandibular movement, there are other smaller muscles which function in normal feeding activity. The most important of these is the buccinator (M. buccinatorius) which, with the orbicularis oris (M. orbicularis oris), forms the body of the lips and the cheek. The opossum, like many mammals, has very short functional lips. The angle of the mouth is approximately level with the second molar; at this point the labial sulcus has considerable depth but this diminishes anteriorly until the sulcus is eliminated just in front of the third premolar. The mobile length of the lips is therefore about one third the length of the tooth row; the remainder is closely tied down to the underlying bone and to the rhinarium. It seems unnecessary to recognize both a buccinator and orbicularis oris in *Didelphis*. A thick, well-defined muscle homologous with the buccinator of other mammals is present and this fades out in the anterior premolar region, leaving only traces of muscle in the lip surrounding the anterior teeth.

Buccinator

The buccinator in *Didelphis* is a thick muscle, basically crescentic in shape with the "horns" pointing anteriorly and the "body" lying across the angle of the mouth and forming the cheek posteriorly (Figs. 5, 6 and 13). The attachments are to soft tissue, to fascia and to bone. The inner, labial attachment is anterior to the angle of the mouth, merging with the soft tissue of the lip and gradually fading out anterior to the second premolar. The outer border is attached to the maxilla just above the last premolar and the first and second molars, as the muscle sweeps round to its midpoint, where the attachment leaves bone (Fig. 4A). The fibers regain a bony attachment parallel to the upper along the body of the lower jaw below the cheek teeth. This edge can best be described as "rolled" (Fig. 13). The muscle is at its thickest near the angle of the mouth where there is a somewhat tendinous raphe. As it passes upward and forward or downward and forward, the fibers sweep round and then turn under to reach their attachment. At the angle of the mouth the muscle is covered by the fascia overlying the anterior part of the superficial masseter and its tendon.

Discussion

The function of the buccinator in man and in those mammals in which this muscle has been examined is one of food control. Contraction of the buccinator serves to assist the tongue in repositioning the material on the occlusal surfaces of the cheek teeth. It is worth noting that *Didelphis* frequently drops the lower jaw through an arc of thirty degrees or more. When this occurs the buccinator is under considerable tension and stands out within the cheek. Indeed, the full depth of the labial sulcus becomes clearly visible only in these circumstances as the cheek pulls away from the teeth.

CONCLUSIONS

The conclusions of this study, in addition to the basic descriptive text, are as follows:

Previous descriptions of the muscles of mastication in *Didelphis* have failed to appreciate the undifferentiated nature of the adductor musculature within the infratemporal fossa. This muscle mass has been variously subdivided into separately named muscles. In fact, there is no evidence for such subdivision, although for *descriptive purposes* only the terms "internal", "external" and "posterior" adductors are convenient in reference to major parts of this single muscle muscle mass which have distinctive fiber orientations.

The anatomy of the superficial masseter in *Didelphis* is unlike that of its homologue in the eutherian carnivores. In the latter group this muscle usually inserts onto the small angular process of the lower jaw and in some cases into a common raphe with the internal pterygoid (Becht, 1954). The arrangement in *Didelphis* differs due to the medial inflection of the angular process. The nature of the superior attachment of the superficial masseter also differs. In the carnivores this muscle takes origin from the inferolateral surface of the zygomatic arch as a wide fibrous band and is, therefore, a rectangular muscle with an upward and forward inclination. In *Didelphis* the superficial masseter originates from a narrow tendon attached to a boss on the maxilla just below and anterior to the zygomatic process of that bone. The muscle then fans out to become a powerful unipennate fleshy belly with a nearly horizontal line of action. The superficial masseter is the only part of the adductor mass to have achieved anatomical and, apparently, functional separation.

We are cautious about the possible paleobiological significance of the arrangement of adductor musculature in *Didelphis*. We are aware, on the one hand, that *Didelphis* is one of the most generalized of living marsupials; its dentition is basically similar to that of Late Cretaceous marsupials, although Clemens (1968) has demonstrated certain distinct dental differences. On the other hand, there is as yet no direct evidence that *Didelphis* retains the basic adductor pattern of Late Cretaceous marsupials. With reservations, therefore, some speculative remarks may be made. The basic pattern of mammalian jaw musculature was established in advanced cynodonts (Crompton, 1963; Barghusen, 1968). At this phylogenetic stage, the adductor musculature had attained a position and relative size comparable with the temporal and masseter of mammals. Assuming that the adductor muscle pattern of *Didelphis* retains the basic pattern of Late Cretaceous marsupials, it would appear that an advanced degree of morphological differentiation of the adductors was a comparatively late event in therian phylogeny. However, fiber groupings characterized by distinct orientation are present in *Didelphis* and this condition probably simulates the first stage in the development of the differentiated jaw muscles of eutherians.

ACKNOWLEDGMENTS

We appreciate the contributions of others to the preparation of this paper. Our thanks are due in particular to Professors H. J. J. Blackwood and A. W. Crompton for reading the manuscript and for much helpful discussion; to Dr. W. Turnbull of the Field Museum, Chicago, for the loan of dissection notes and for part of the text of a forthcoming paper; to Messrs. R. Bauer, R. Morrill and D. Allen for the patient trapping and subsequent care of our colony of *Didelphis;* to Miss Margaret Newton and Miss Rosina Miles for assistance in the preparation of the manuscript and lastly to Miss Jennifer Middleton for Figures 1-7 and 11-14.

This work has been made possible by N.I.H. grant No. 1 RO1 DEO 02648-01 DEN.

APPENDIX I

THE ANATOMY OF THE DIDELPHIS SKULL AS RELATED TO THE JAW MUSCULATURE

As can be seen in Figures 1, 2 and 3, the actual cranium of *Didelphis* is small both absolutely, reflecting the limited cerebral development of the opossum, and relatively when compared with the snout. The extent to which the facial bones dominate the skull is partly attributable to the long tooth row which, in the figured specimen, approximates 69% of the total skull length. In order to accommodate the molar series, the maxilla has an extensive posterior extension which completes the floor of the orbit (Figs. 1, 2). The corresponding length of the mandibular tooth row coupled with the posterolateral position of the jaw joint (Figs. 2, 3) result in a relatively long lower jaw. With such a small cranium and a large lower jaw, the available area for bony origin of the adductor musculature is disproportionately small. However, the development of nuchal and sagittal crests as well as the deep zygomatic arch compensate for the limited surface area of the cranium.

The greater part of the adductor musculature in *Didelphis* takes origin from the bony surfaces limiting the temporal fossa. In the absence of a postorbital bar the fossa is delimited anteriorly by the postorbital processes of the frontal and the jugal above (Fig. 2) and by the posterior extension of the maxilla and the alveolus of the third molar below (Figs. 1, 3). The fossae of both sides share a common superior border, the sagittal crest. This is formed by the frontals, the parietals and the fused postparietals and supraoccipitals. The latter also contributes, with the squamosal, to the nuchal crest which delimits the temporal fossa posteriorly. Strictly speaking, the fossa has no inferior border but the origin of the adductor musculature extends downward to include the thin triangular pterygoid processes and the lower limit of the wing of the alisphenoid. Posteriorly, the inferior border of the temporal fossa is formed by the squamosal root of the zygomatic arch which continues anteriorly to form the lateral wall of the fossa.

The zygomatic arch of *Didelphis* is a very deep and robust bar of bone, formed by the zygomatic process of the squmosal, the jugal and the zygomatic process of the maxilla. The latter makes a very limited contribution to the outer, lateral surface of the arch anteriorly but on its medial surface extends backward as far as the postorbital process and forms the lateral wall of the orbit. The zygomatic arch of *Didelphis* not only curves outward and backward from its anterior root but also outward and downward. The extreme lateral margin of the skull is formed by the inferior rather than the superior border of the arch (Figs. 1, 2). The width of the temporal fossa is greatest at the level of the postorbital constriction of the cranium and the pterygoid processes (Figs. 1, 3). The widening of the fossa is also more or less coincident with the anterior border of the coronoid process of the lower jaw. Posteriorly, the zygomatic arch changes orientation as it curves medially toward the cranium. At the level of the squamosoalisphenoidal suture the lower border curves medially through a right angle to become the anterior border of the squamosal root of the zygomatic arch. The superior margin curves more gently medially to merge with the body of the squamosal (Fig. 1) and to continue toward the nuchal crest as a thick ridge of bone above the external auditory meatus (Fig. 2). This "twisting" of the arch brings the originally external surface into a downward-facing position as the glenoid fossa. The internal surface forms an upward and forward-facing bony floor to the posterior part of the temporal fossa (Fig. 1).

The oval articular fossa is largely formed by the squamosal but with a small contribution from the jugal near its anterolateral margin. Its long axis is transverse to that of the skull. In its short axis the fossa is shallowly concave. A robust postglenoid process extends downward and slightly posteriorly (Fig. 2).

In its general form the mandible of *Didelphis* closely resembles that of some eutherian carnivores. There are large coronoid and angular processes; the latter is inflected medially, a marsupial specialization. The lower border of the mandibular ramus widens posteriorly, giving it an elongated triangular shape (Fig. 3) and providing a large area for muscle attachment. Above its expanded lower border the mandibular ramus is excavated on its lateral surface by a well-developed masseteric fossa and on its inner medial surface by a pterygoid fossa. The former extends from the lower border of the lateral surface of the ramus to the apex of the coronoid process and posteriorly to the condylar process. The pterygoid fossa, much smaller, extends from the medial margin of the inflected angle to the lingula. The lateral margin of the lower border of the mandibular is smoothly curved from the level of the second molar to below the middle of the masseteric fossa (Figs. 2, 3). Posteriorly, this smoothly curved margin merges with the inferior surface of the inflected angle. The masseteric fossa is closely related anteriorly to the thickened border of the coronoid process which arises inferolateral to the first molar and extends upward for about two-thirds of the length of the process to fade out at the junction of its anterior and superior borders. The posterior border of the fossa which forms the sigmoid notch with the short condylar process is very much thinner.

In lateral view (Fig. 2), the stout condylar process is continuous with the lower border of the mandible. The short condylar neck expands into the transversely orientated condyle which is more sharply convex in its anteroposterior (short) axis than in its transverse (long) axis. Much of the articular surface is flat. The articular condyle is on a level slightly above the occlusal plane.

In the articulated skull the lower jaw bisects the temporal fossa at an angle of approximately 15° to the long axis of the skull (Fig. 1). The coronoid process, which in lateral view (Fig. 2) projects above the upper border of the zygomatic arch, lies almost equidistant from the arch and the outer wall of the braincase when the mandible is in centric position.

APPENDIX II

The Anatomy and Internal Architecture of the Adductor Complex

The adductor complex has four main areas of origin: medial, lateral, superior and inferior. The first is the most extensive. Anteriorly, the medial origin is limited by a slight ridge on the frontal bone which passes posteroinferiorly to the fronto-alisphenoidal suture above the ethmoidal foramen. Passing above the optic-orbital fissure and the anterior alar foramen, the ridge continues (although less well-marked) posteriorly as the inferior margin across the wing of the alisphenoid. The ridge terminates at the anterior root of the zygomatic process of the squamosal. Like the anterior and anteroinferior margins, the superior and posterior limits of the medial origin are continous. The superior extends from the postorbital process of the frontal as a slightly marked ridge curving medially towards the midline (Figs. 1, 4C). It then passes along the top of the sagittal crest to the junction of the sagittal and nuchal crests. The posterior border corresponds with the tip of the nuchal crest until its junction with the posterior root of the zygomatic process. The margin then runs anteriorly along the dorsal surface of the zygomatic process to the alisphenoid where it joins the slight ridge marking the inferior border of the area of attachment. The lateral wall of the braincase enclosed by these margins is concave anteriorly and convex posteriorly (Figs. 1, 2).

The Internal Architecture of the Adductor Complex

THE INTERNAL ADDUCTOR. The internal adductor is of fairly simple structure. As can be seen from Figures 8, 9 and 10, its fibers pass laterally and more or less inferiorly to their insertion on the medial surface of the coronoid process. However, the orientation of these fibers in the parasagittal plane is not uniform. Those taking origin from the anterior part of the medial wall of the fossa and from the small fascial area above pass inferiorly, laterally and slightly posteriorly. They insert either into a small tendinous area in front of and continuous with the anterior border of the coronoid process (Fig. 9B) or onto the anterior border of the process itself (Figs. 8D, 9C, D). Fibers originating from the medial wall of the fossa at the level of the postorbital constriction of the cranium pass almost directly laterally and inferiorly (Fig. 8C left) to insert on the entire medial surface of the coronoid process (Fig. 4B). The most posterior fibers taking origin from the wall of the cranium just anterior to the squamo-dentary joint pass laterally, inferiorly and anteriorly to their insertion on the posterior part of the medial surface of the coronoid process (Figs. 8B left, 10B).

The course of fibers originating from the medial wall of the fossa above its maximum convexity is slightly different. In general, they are all orientated anteriorly and pass more horizontally and laterally than do the deeper and inferior fibers (Figs. 8B left, C). They insert into either the apex of the coronoid process or into the internal tendon. Anteriorly, the fibers originating from the dorsum of the cranium just behind the postorbital process of the frontal form the upper anterior part of the muscular postorbital wall and have a complicated course. Instead of inserting into the medial surface of the coronoid process near its anterior edge, they pass over this edge and insert onto the lateral surface of the process.

THE EXTERNAL ADDUCTOR. The fibers of the external adductor pass more or less directly inferiorly and medially to their insertion. However, there is a variable degree of antero- or posteromedial inclination depending upon the site of fiber origin. Anteriorly, for example, fibers originating from the fascia near the upper border of the zygomatic arch pass slightly posteriorly as well as medially before inserting into the central part of the masseteric fossa (Fig. 9B). As the fibers elongate towards the anterior and inferior parts of the muscle mass, their direction changes from the near horizontal to the near vertical (Figs. 8, 9). The part of the adductor originating from the medial surface of the zygomatic arch has no significant change in fiber orientation; it inserts into the inferior part of the masseteric fossa. The fibers passing to the anterior of the coronoid process are almost vertical (Fig. 8D left). There is, however, a more marked change in orientation of the fibers which take origin from the inferior border of the zygomatic arch. Just in front of the squamo-dentary joint, a band of fibers passes inferomedially to link the inferior border of the zygomatic arch and the concave posteroinferior area of the masseteric fossa (Fig. 8B left, C right). This band is continued anteriorly as fibers originating from the expanded lower border of the zygomatic arch (Fig. 8D left). These gradually fade out as the lower border of the mandible narrows anteriorly and curves inferiorly, thus increasing the vertical distance between the arch and the lower border of the masseteric fossa. In general, the outermost layers of fibers, which originate from the masseteric fascia below the arch, parallel the deeper group but are inclined slightly posteriorly (Fig. 10A).

THE POSTERIOR ADDUCTOR. The internal architecture of the posterior adductor is basically simple, as can be seen from Figures 8, 9 and 10. Two small blocks of muscle are worth further comment.

The suprazygomatic slip is a thin band of fibers passing almost horizontally on the external surface of the adductor immediately above the posterior root of the zygomatic arch. They insert into the posterior border of the coronoid process immediately below its apex. Removal of this slip exposes fibers of the posterior adductor passing horizontally and in some cases even upwards to insert into the internal tendon.

The inferior limit of the origin of the posterior adductor, the "roof" of the squamo-dentary joint, provides attachment for a thick band of fibers without internal tendons. Enclosed on three sides by bone (Fig. 8A right), these fibers pass horizontally forward to insert onto both the medial and lateral surfaces of the posterior part of the coronoid process as well as its posterior border below the recurved apex. This small block of muscle is closely related to the external pterygoid which passes superolaterally to its insertion on the condylar neck immediately below.

LITERATURE CITED

Adams, L. A. 1919. A memoir on the phylogeny of the jaw muscles in recent and fossil vertebrates. Ann. N. Y. Acad. Sci. **28**: 51-166.

Allen, H. 1880. On the temporal and masseter muscles of mammals. Proc. Acad. Nat. Sci. Philad. **1880**: 385-396.

Barghusen, H. R. 1968. The lower jaw of cynodonts (Reptilia, Therapsida) and the evolutionary origin of mammal-like adductor musculature. Postilla **116**: 1-49.

Becht, G. 1954. Comparative biologic-anatomical researches on mastication in some mammals. I and II. Proc. K. Ned. Akad. Wet., Series C, **56**: 508-527.

Bennett, N. G. 1908. A contribution to the study of movements of the mandible. Proc. R. Soc. Med. **1**: 79-85.

Clemens, W. A. 1968. Origin and early evolution of marsupials. Evolution **22**: 1-18.

Coues, E. 1872. The osteology and myology of *Didelphys virginiana.* Mem. Boston Soc. Nat. Hist. **2**: 41-154.

Crompton, A. W. 1963. On the lower jaw of *Diarthrognathus* and the origin of the mammalian lower jaw. Proc. Zool. Soc. Lond. **140**: 697-753.

Davis, D. D. 1964. The giant panda: a morphological study of evolutionary mechanisms. Fieldiana, Zool. **3**: 1-339.

Dobson, G. E. 1882. On the digastric muscle, its modifications and functions. Trans. Linn. Soc. Lond., (Zool.), 2nd Ser., **2**: 259-267.

du Châine, J. 1914. Le digastrique (abaisseur de la mandible des mammifères). J. Anat. Physiol., Paris, **50**: 248-319, 393-417,

Edgeworth, F. H. 1935. The cranial muscles of vertebrates. Cambridge University Press, Cambridge. 493 p.

Fiedler, W. 1952. Zur Gliederung der Kaumuskulatur bei den Säugetieren. Verhandl. Anat. Ges. **50**: 354-361.

Fox, R. C. 1964. The adductor muscles of the jaw in some primitive reptiles. U. Kans. Publs. Mus. Nat. Hist. **15**: 657-680.

Frick, H. 1957. Über die Trigeminusmuskulatur und die tiefe Facialmuskulatur von *Orycteropus aethiopicus.* Z. Anat. Entwgesch. **116**: 202-217.

Hiiemäe, K. M. 1966. The development, structure and function of the mandibular joint in the rat. Ph. D. Thesis, unpubl., Univ. Lond.

Kawamura, Y. 1964. Recent concepts of the physiology of mastication, p. 77-109. *In* P. H. Staple [ed.], Advances in Oral Biology. Vol. I. Academic Press, New York.

Lubosch, W. 1938. Muskeln des Kopfes: Viscerale Muskulatur (Fortsetzung). D. Säugetiere, p. 1065-1105. *In* Bolk, Göppert, Kallius and Lubosch [eds.], Handbuch der vergleichenden Anatomie der Wirbeltiere 5. Urban and Schwarzenberg, Berlin and Vienna.

Miller, M. E., G. C. Christensen and H. E. Evans. 1964. Anatomy of the dog. W. B. Saunders Co., Phil. 941 p.

Parsons, F. G. 1892. Some points on the myology of rodents. J. Anat. Physiol., Lond., **26**: x-xiii.

——————— 1896. Myology of rodents. Part II. Proc. Zool. Soc. Lond. **1896**: 159-192.

——————— 1898. The muscles of mammals with special relation to human myology. J. Anat. Physiol., Lond., **32**: 428-450.

———— 1899. The joints of mammals compared with those of man. J. Anat. Physiol., Lond., **34**: 41-68.

Schumacher, G. H. and H. Rehmer. 1962. Über einege Unterschiede am Kauapparat bei Lagomorphen und Rodentia. Anat. Anz. **111**: 103-122.

Scott, J. M. 1955. Growth changes in the glenoid fossa. Dent. Practnr. Dent. Rec. **6**: 117-120.

Sicher, H. 1944. Masticatory apparatus in the giant panda and the bears. Field Mus. Nat. Hist., Zool. Ser., **29**: 61-73.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist. **85**: 1-350.

Toldt, C. 1904, 1905. Der Winkelfortsatz der Unterkiefer beim Menschen und bei Säugetieren und die Beziehungen der Kaumuskulatur zu demselben. Sber. Acad. Wiss. Wein., Abt. 2, **113**: 43-108; Abt. 3, **114**: 315-376.

Tullberg, T. 1899. Uber das System der Nagethiere: eine phylogenetische Studie. Nova Acta R. Soc. Scient. Upsal., Ser. 3, **18**: 1-514.

Turnbull, W. D. [in press]. The mammalian masticatory apparatus. Fieldiana, Geol.

FIGURE SECTION

The following abbreviations refer to Figures 4, 8, 9 and 10.

MUSCLES

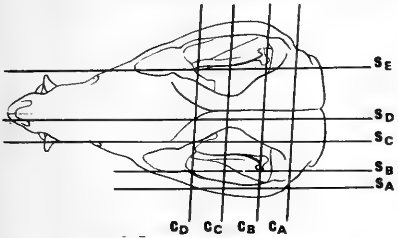
External adductor, EA; Internal adductor, IA; Posterior adductor, PA; Superficial masseter, SM; Internal pterygoid, IP; External pterygoid, EP; Digastric, posterior belly, Dpb; anterior belly, Dab; Mylohyoid, Mh; Geniohyoid, Gh; Genioglossus, Gg; Hyoglossus, Hh; Buccinator, B.

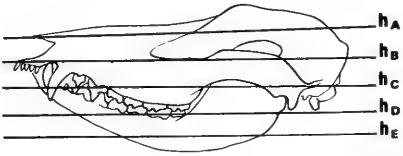
FASCIA AND TENDONS

Temporal fascia, Tf; Masseteric fascia, Mf; Adductor tendon, At; Internal tendon, It (of either external adductor or internal pterygoid as shown); Tendon of superficial masseter, Smt.

Figures 8, 9 and 10

Serial coronal ($C_{A\text{-}D}$), horizontal ($H_{A\text{-}E}$), and sagittal ($S_{A\text{-}E}$) sections of the heads of adult *Didelphis* to show the internal architecture of the masticatory musculature at various levels. The orientation and labeling of each section is shown in the key diagram.





The following symbols are used:

▨	Bone
‒ ‒	Thick fascia
—	Internal tendons
●	Fibers cut transversely
—•	Fibers cut longitudinally
╱●	Fibers cut obliquely, the "head" represents the cut surface, the "tail" shows the direction and approximate angle of the fiber.

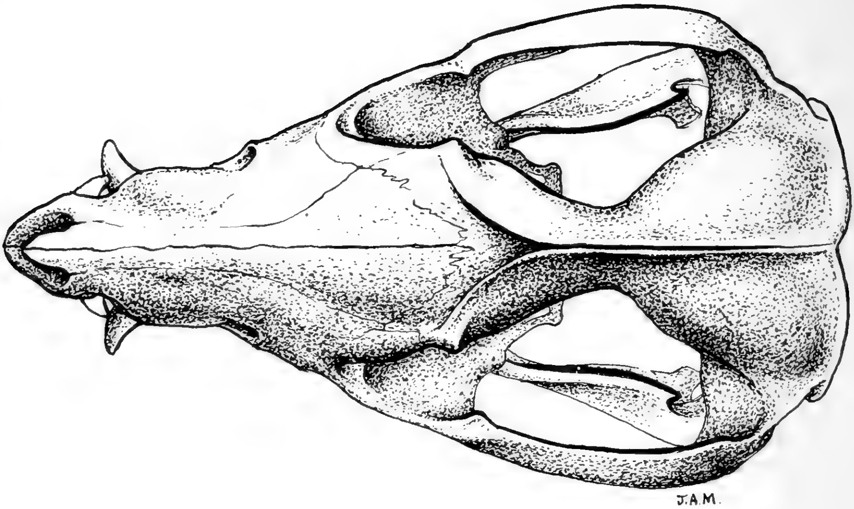


FIG. 1. *Didelphis marsupialis:* dorsal view of the articulated skull and lower jaw. Young adult, actual size.

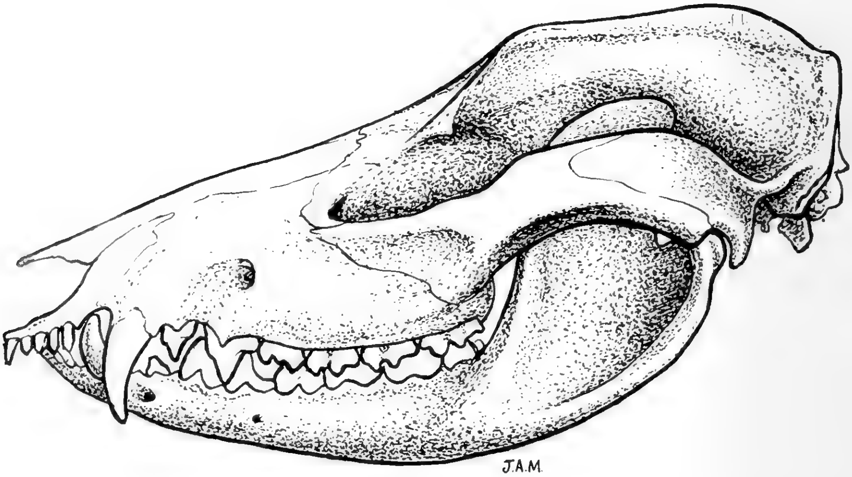


FIG. 2. *Didelphis marsupialis:* lateral view of articulated skull and lower jaw. Actual size.

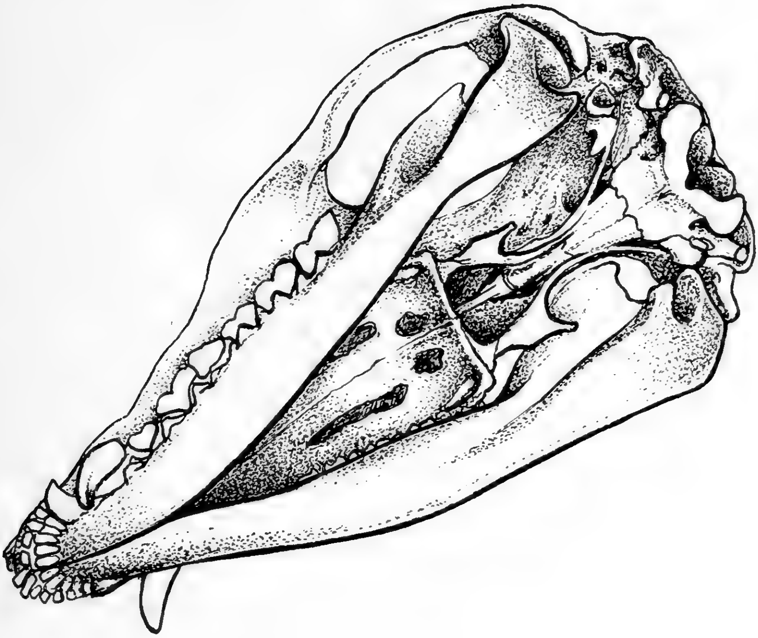


FIG. 3. *Didelphis marsupialis:* inferolateral view of articulated skull and lower jaw to show the position of the squamo-dentary joint and the inflected angle of the lower jaw. Actual size.

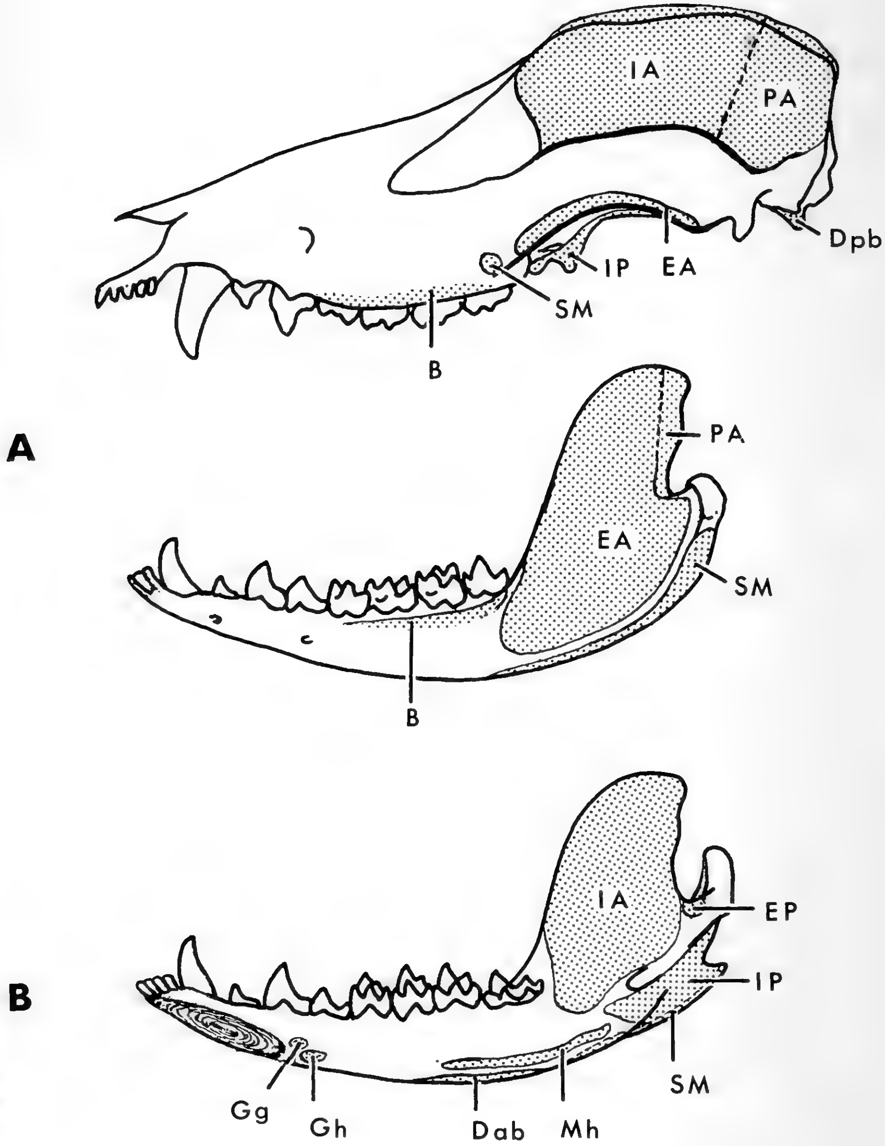


FIG. 4. The bony attachments of the masticatory muscles in *Didelphis:* A) lateral view of the skull and lower jaw; B) medial view of the lower jaw; C) dorsal view of the articulated skull and jaw; D) inferolateral view of the articulated skull and lower jaw.

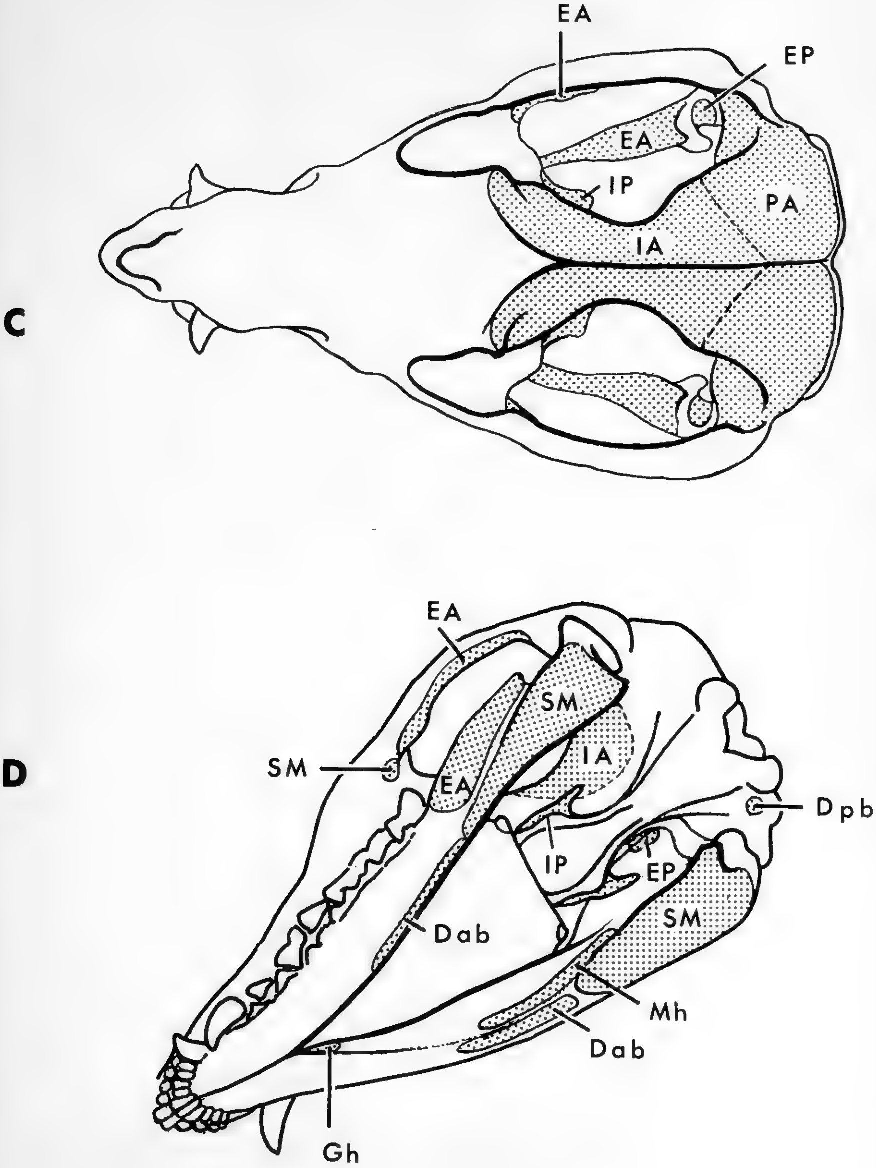


FIG. 4. cont.

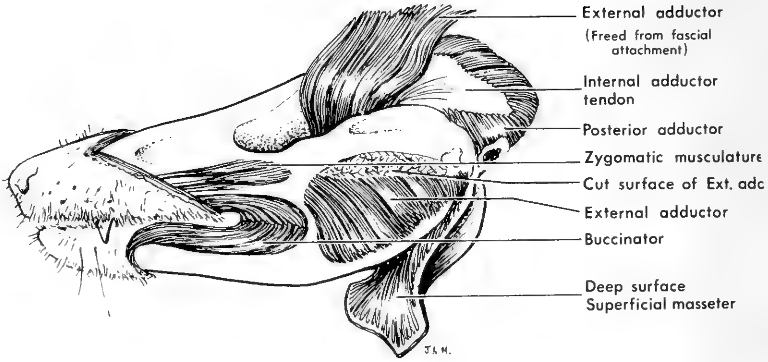


FIG. 5. Lateral view of a *Didelphis* head after removal of the skin and dermal musculature to expose the temporal and masseteric fascia, the underlying adductors and the superficial masseter.

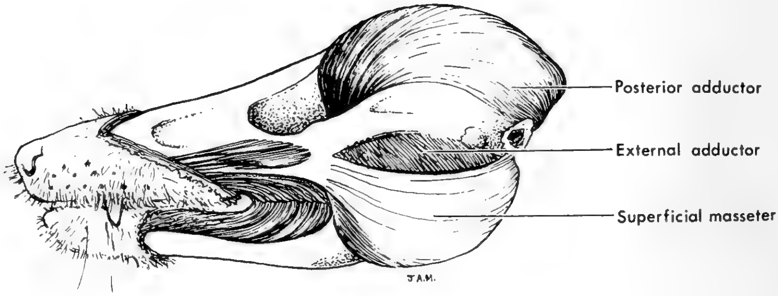


FIG. 6. Lateral view of a dissected head of *Didelphis* after reflection of the external adductor, exposing the internal tendon continuous with the coronoid process. Reflection of the superficial masseter shows the position of the lower part of the external adductor.

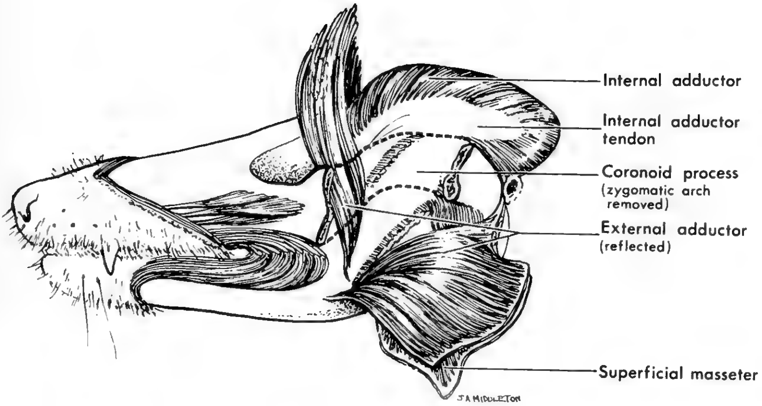


FIG. 7. Lateral view of the head of a dissected specimen of *Didelphis* to show the relationships of the coronoid process, the internal tendon and the adductors.

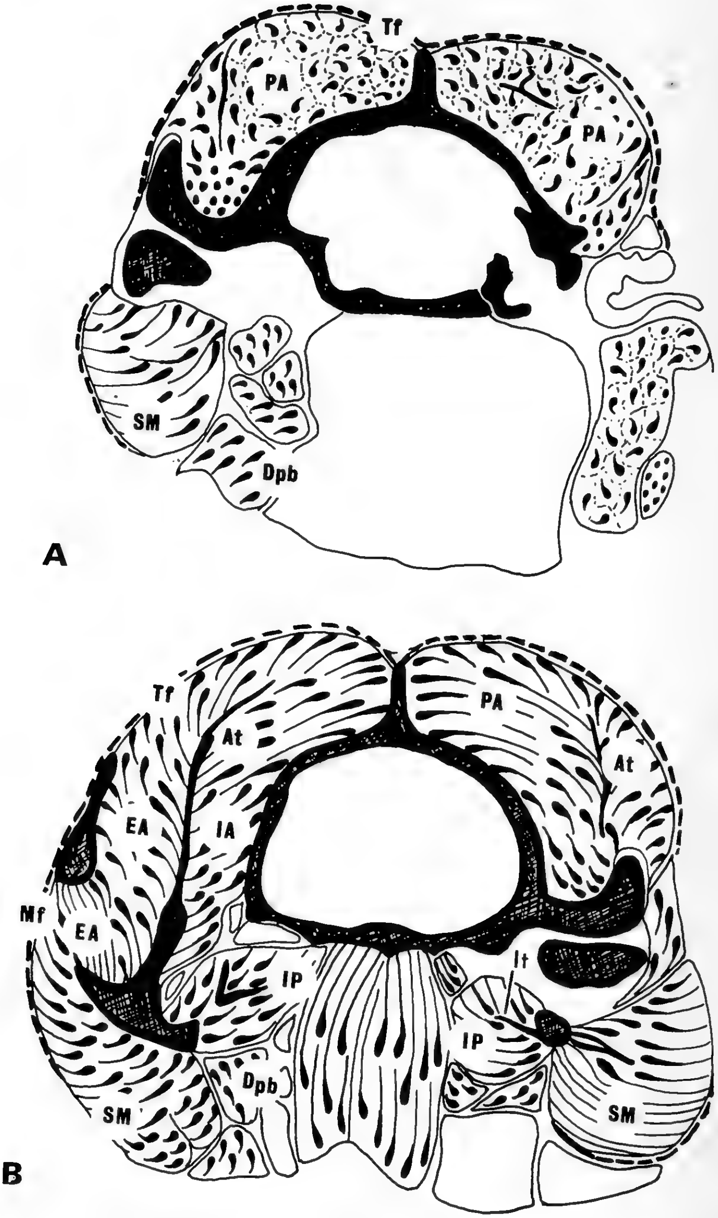


FIG. 8. Coronal sections of a head of *Didelphis*. The posterior surface of each section is figured. The left hand side of each section is in a plane slightly anterior to the right hand side. For position of sections, see p. 33.

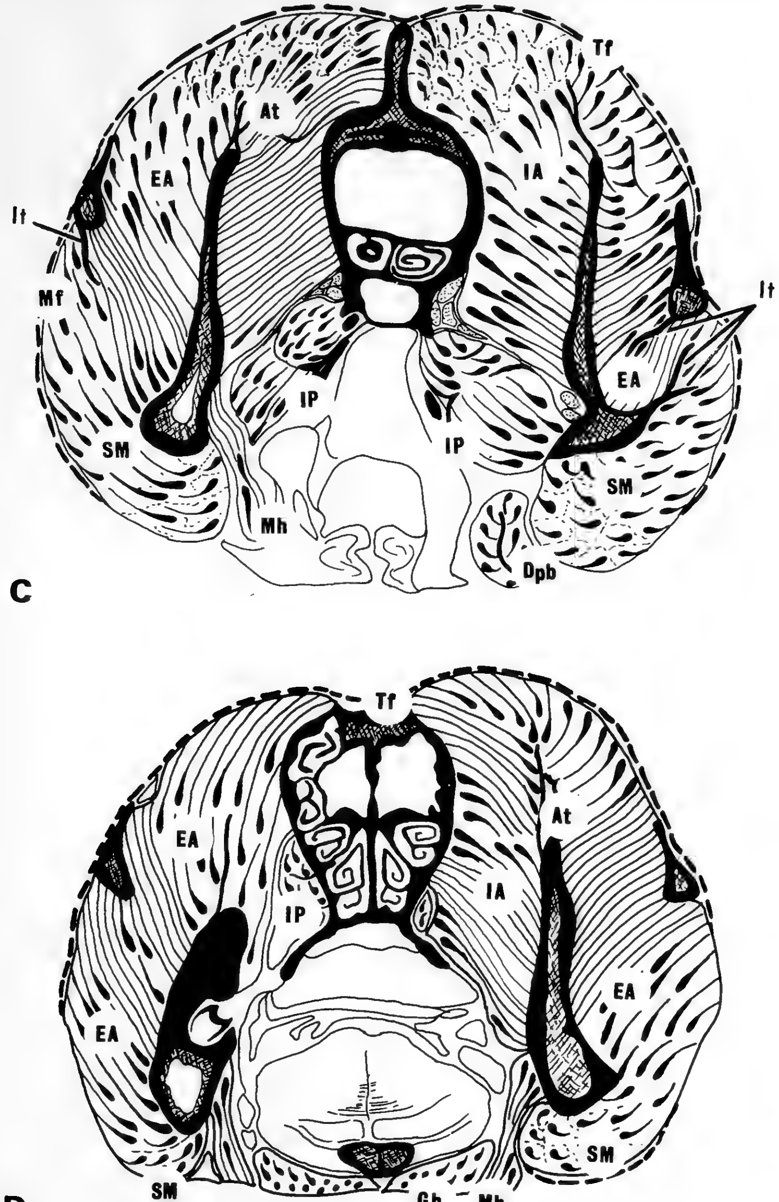

Tf
At
EA
IA
It
Mf
It
EA
IP
IP
SM
SM
Mh
Dpb
C
Tf
EA
At
IP
IA
EA
EA
SM
SM
Gh
Mh
D

FIG. 8. cont.

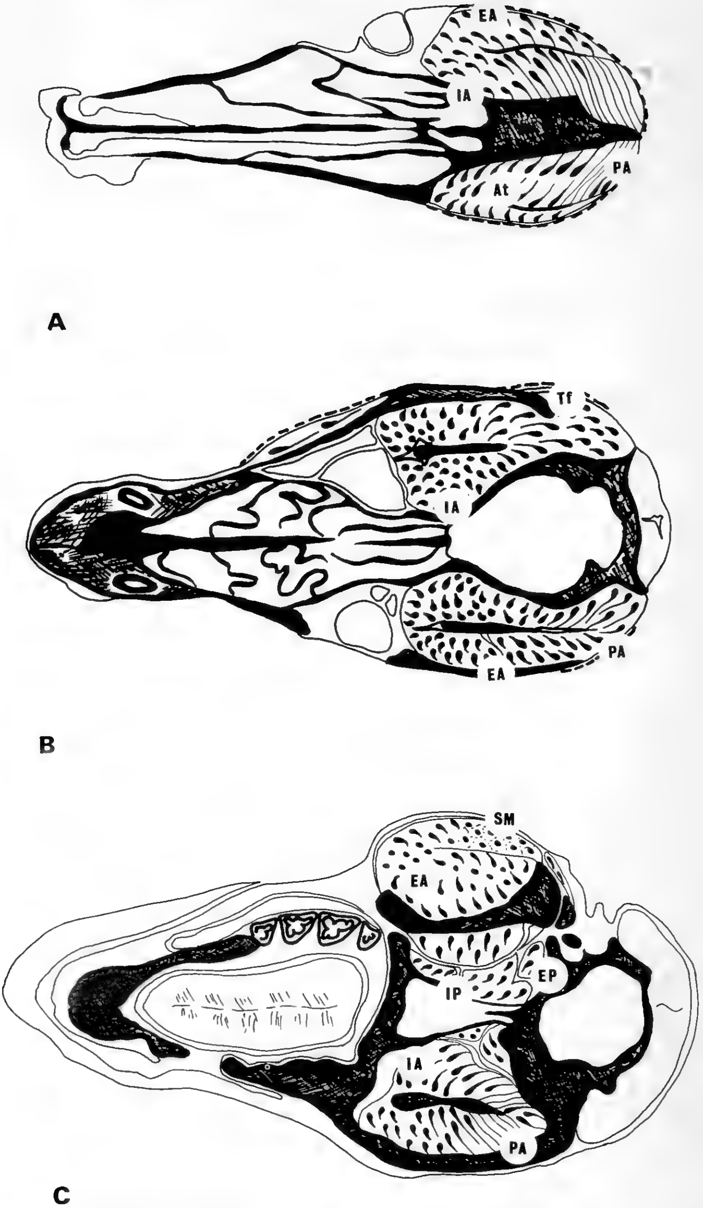


FIG. 9. Horizontal sections of a head of *Didelphis* viewed from below. The upper half of each section is in a plane slightly ventral to the lower. For position of sections, see p. 33.

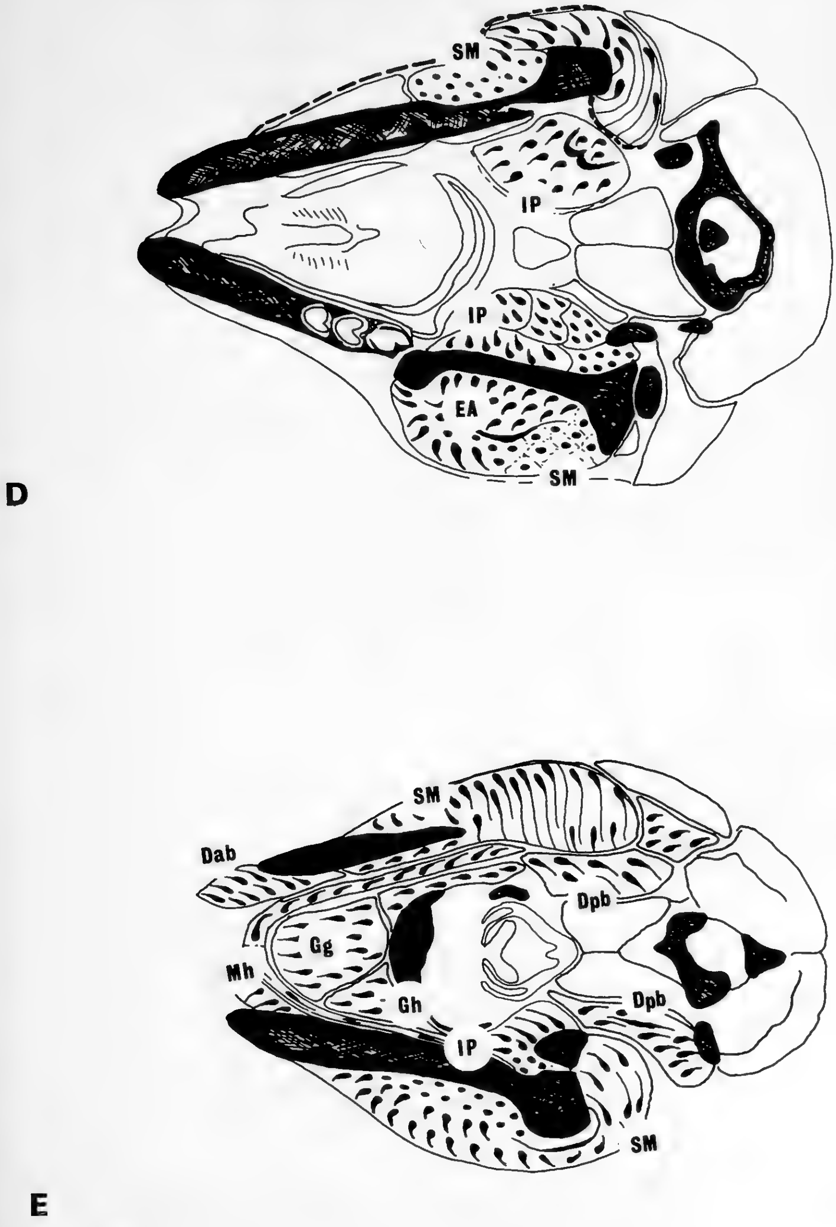


FIG. 9. cont.

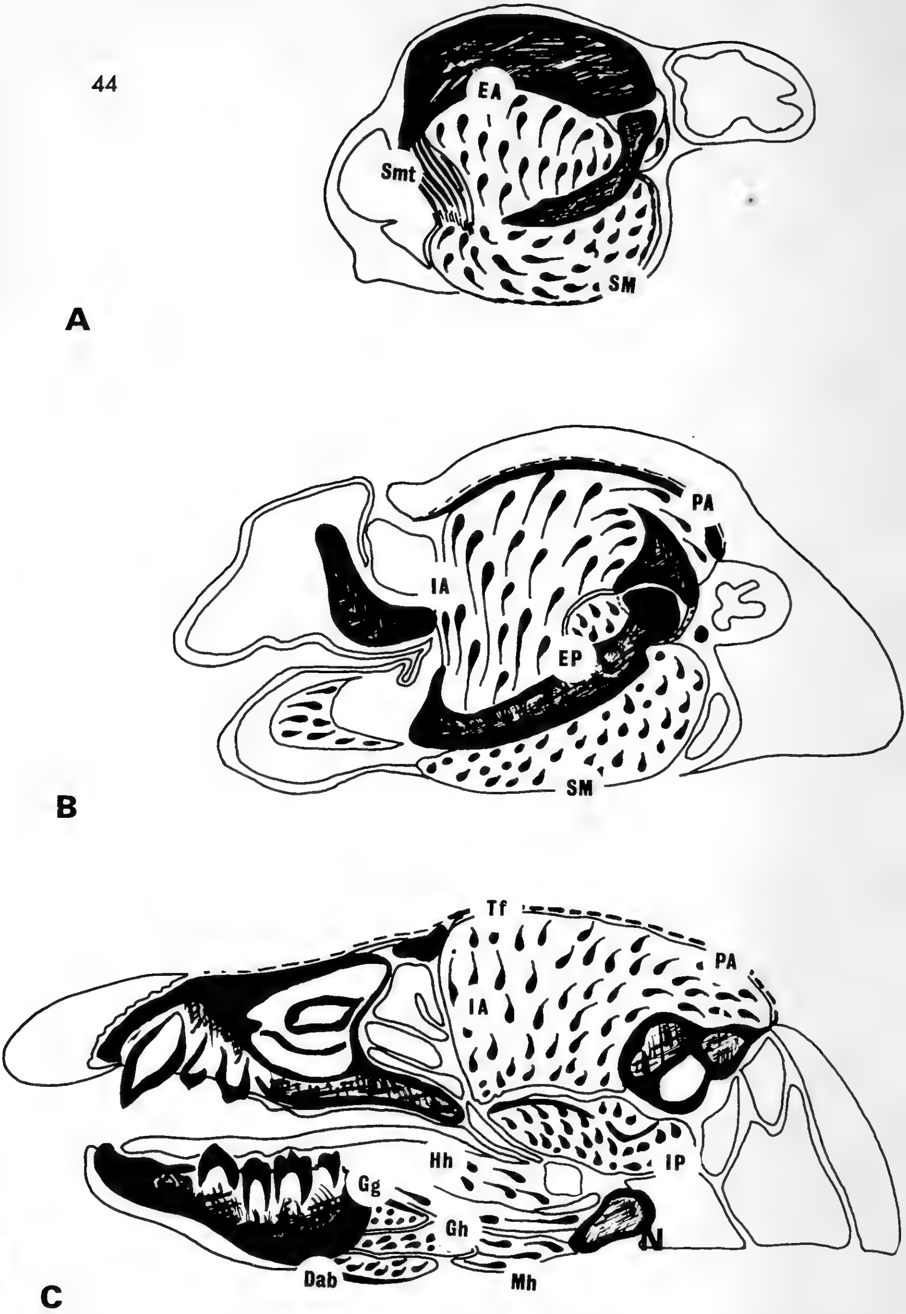


FIG. 10. Sagittal sections of a head of *Didelphis*. Sections A-D show the outer (lateral) surface of each section, section E the inner (medial) surface of a section from the other side of the head. For position of sections, see p. 33.

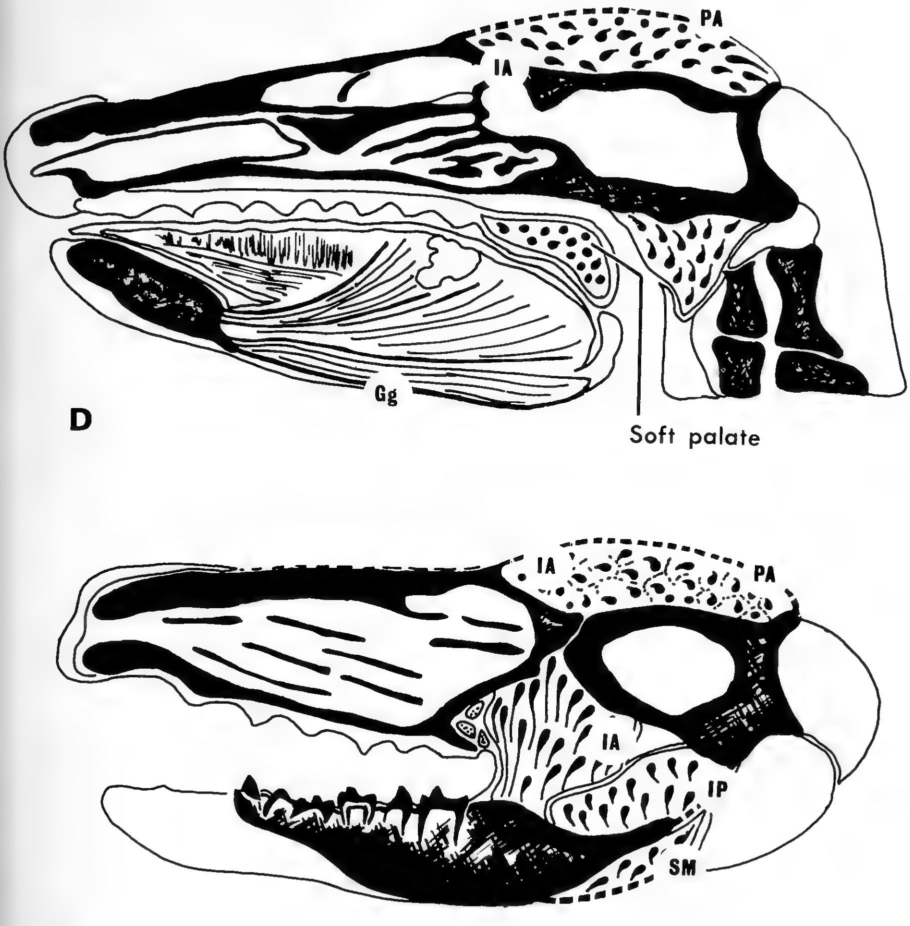


FIG. 10. cont.

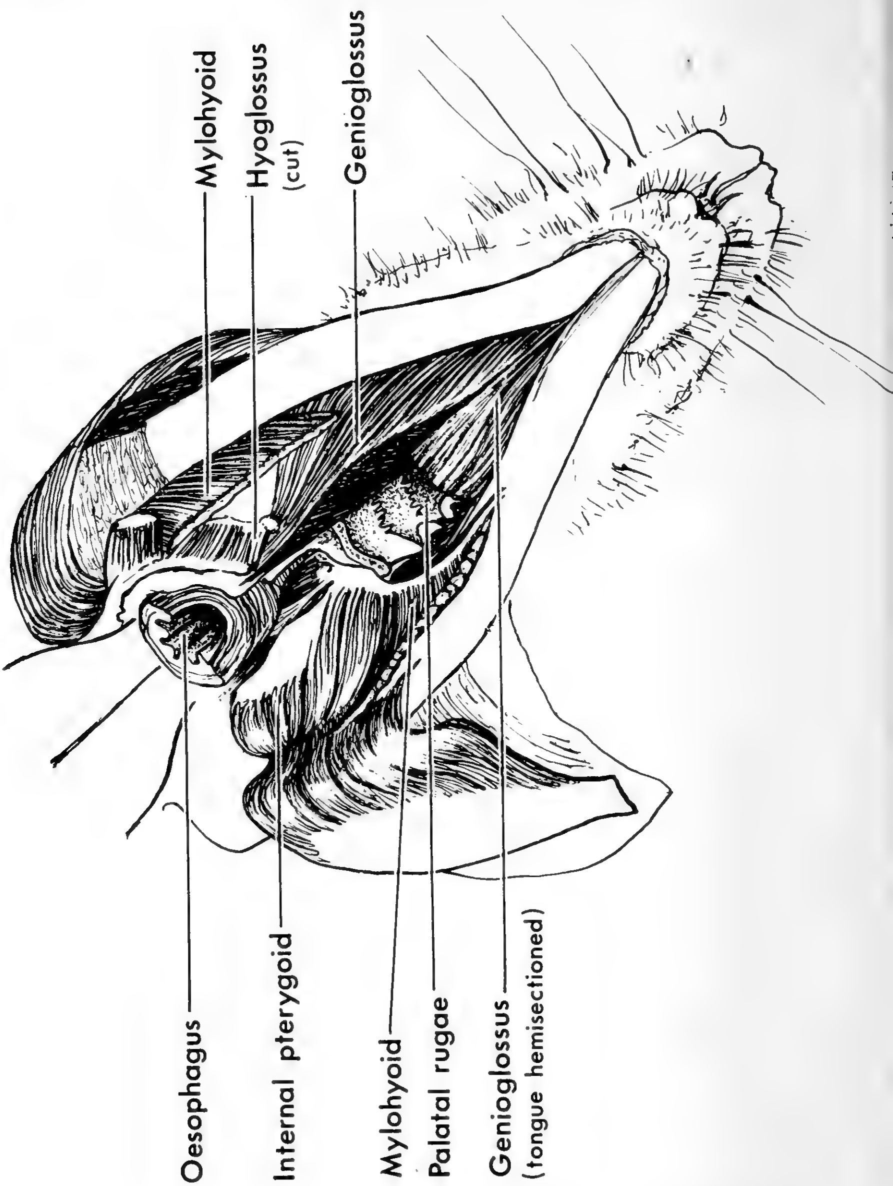


FIG. 11. Ventral view of a head of *Didelphis* after removal of the suprahyoid musculature to show the relationships of the superficial masseter, the internal pterygoid, and the mylohyoid.

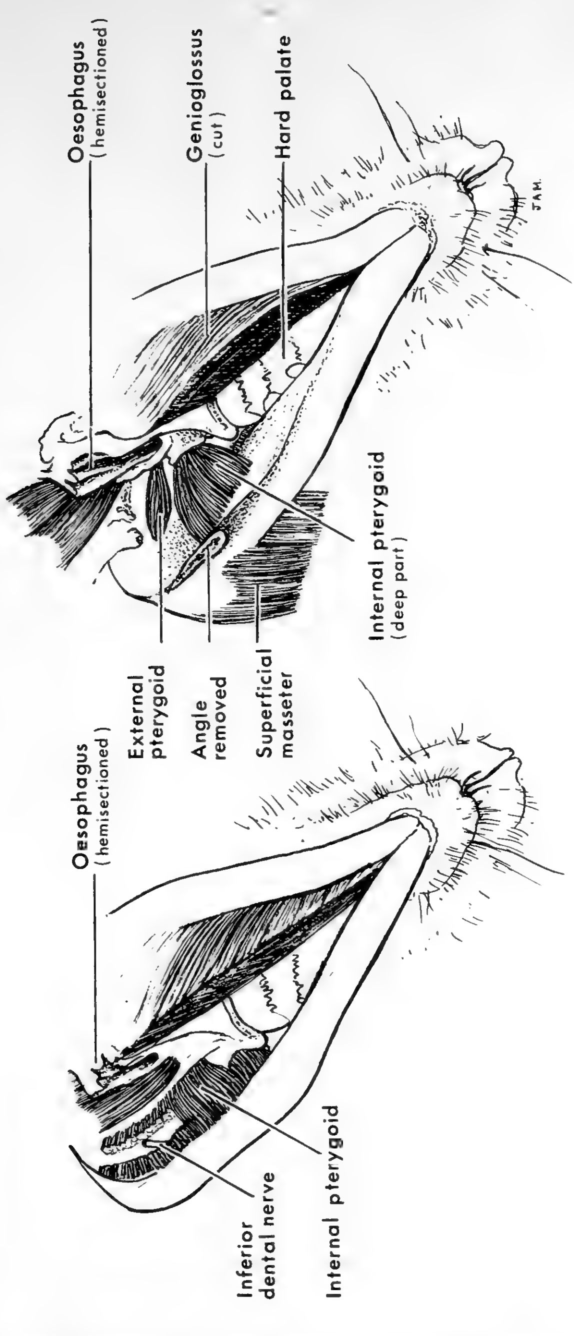


FIG. 12. Ventral views of the head after removal of: a) the posterosuperficial part of the internal pterygoid to show its relation to the inferior dental nerve, and b) after removal of the greater part of the internal to expose the external pterygoid.

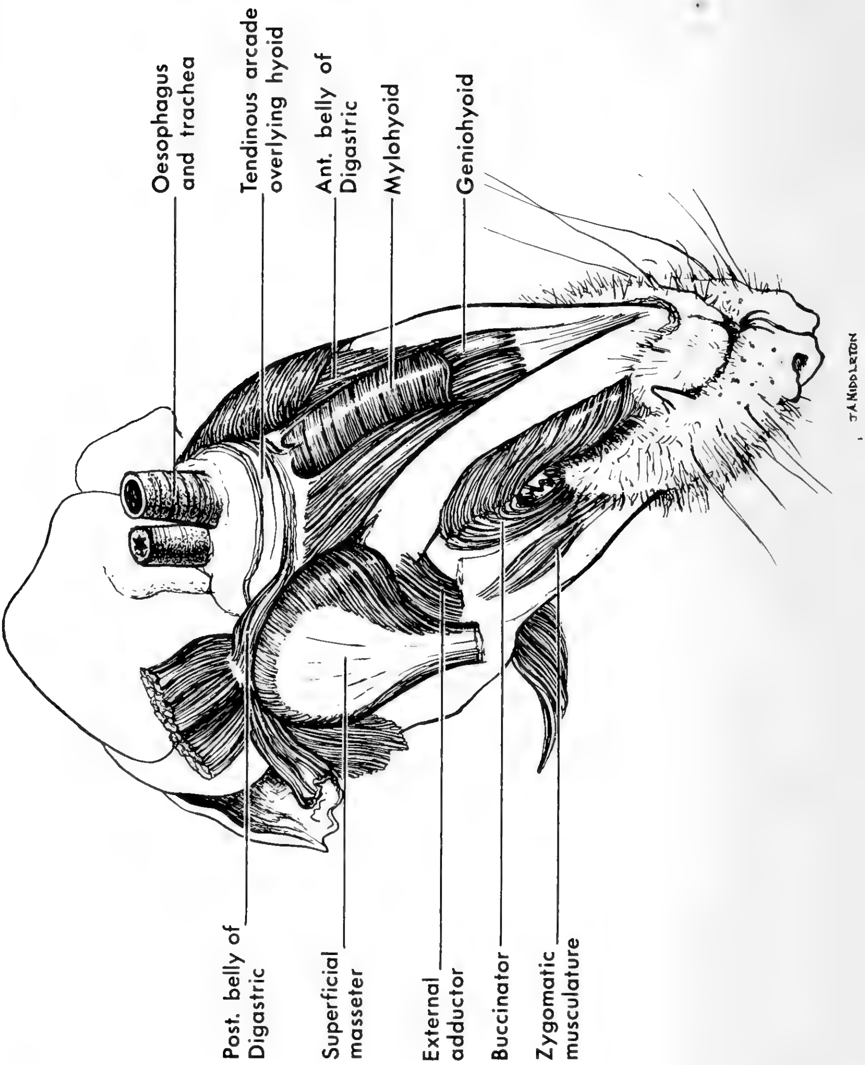


FIG. 13. Ventral view of the head, after removal of the skin and superficial fascia, to show the relationships of the suprahyoid muscles.

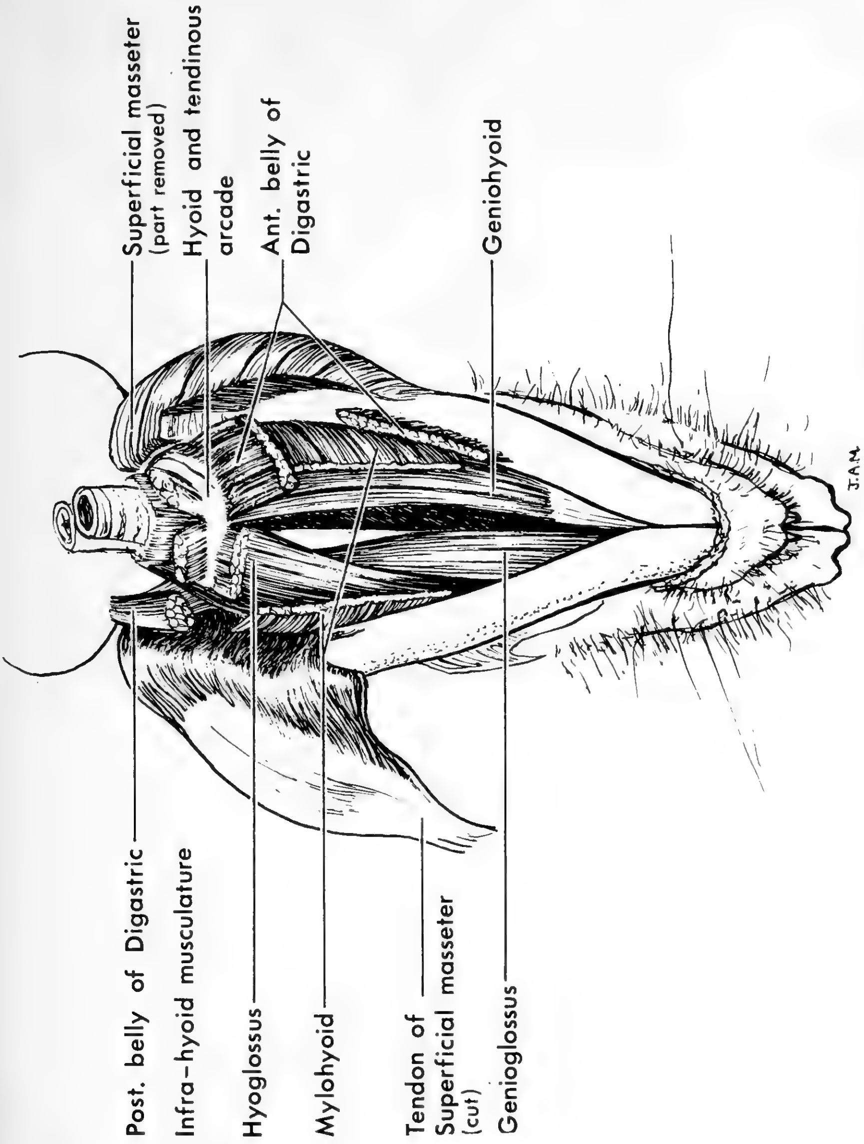


FIG. 14. Ventral view of the head, after removal of parts of the digastric and mylohyoid, to show the arrangement of the hyoid and tongue musculature.

INFORMATION FOR AUTHORS

REVIEW	The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
STYLE	Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).
FORM	Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.
TITLE	Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
ABSTRACT	The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
OMENCLATURE	Follow the International Codes of Zoological and Botanical Nomenclature.
ILLUSTRATIONS	Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
FOOTNOTES	Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
TABLES	Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
REFERENCES	The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
THOR'S COPIES	Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
PROOF	Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
COPYRIGHT	Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 141. 26 DEC. 1969

A NEW GENUS AND SPECIES OF OSMYLIDAE (NEUROPTERA) FROM CHILE AND ARGENTINA, WITH A DISCUSSION OF PLANIPENNIAN GENITALIC HOMOLOGIES

PHILLIP A. ADAMS

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

A NEW GENUS AND SPECIES OF OSMYLIDAE (NEUROPTERA) FROM CHILE AND ARGENTINA, WITH A DISCUSSION OF PLANIPENNIAN GENITALIC HOMOLOGIES

PHILLIP A. ADAMS

Department of Biology and Peabody Museum of Natural History, Yale University*

ABSTRACT

Phymatosmylus, a new genus of Stenosmylinae, is proposed for the new species *Phymatosmylus caprorum.* The genus is morphologically primitive in the position of the medial fork of the forewing, and in the partially free eighth abdominal tergite of the male. Osmylid female genitalia are prepared for examination by the customary clearing in KOH and staining in chlorazol black E, but removal of the internal structures from the abdomen, following cutting around the genital opening, makes details more visible than when examined *in situ,* as previously. The male gonarcus-mediuncus complex of Planipennia is probably derived from fused parameres, as in some Sialodea, and the articulation of the gonocoxites has shifted from the ninth tergite to the ends of the gonarcus.

*Present address: Department of Biology, California State College, Fullerton, California 92631.

POSTILLA 141: 11 p. 26 DECEMBER 1969.

INTRODUCTION

The subfamilies Stenosmylinae and Kempyninae of the neuropteran family Osmylidae (see systematic list at end of paper) are restricted to South America, Australia, New Zealand and Tasmania. The only previously known New World example of the Stenosmylinae is *Isostenosmylus* and of the Kempyninae, *Kempynus falcatus* Navás. Aside from the protosmyline *Paryphosmylus ornatus* Krüger, the only other described Recent osmylid from the New World is the highly aberrant *Gumilla* Navás, which is too poorly known for meaningful discussion. *Narodona* Navás, from Mexico, is probably an ithonid, judging from the illustrations. Carpenter (1943) has discussed the relationships of the fossil species from the Florissant shales of Colorado; they belong to the Protosmylinae and the Kempyninae.

In the course of examining the Neuroptera in the collection of the Peabody Museum, I have been able to study a series of a previously undescribed species from Chile belonging to a new genus of the Stenosmylinae. Additional material from Argentina has been made available by Ellis MacLeod.

The osmylid subfamilies Stenosmylinae and Kempyninae have been revised by Kimmins (1940); his figures may be consulted, where reference is made to features of genera related to the new genus described below.

In this group of osmylids, many features of the male genitalia may be discerned in dried material, as they are usually carried in an exposed position. However, due to shriveling of the soft, membranous structures, the appearance of the genitalia may be markedly different from that of material properly cleared and expanded in KOH and observed in glycerine. The gradual transition from sclerite to membrane on mediuncus, gonarcus, and gonocoxites can only be suggested in a drawing. In Figures 2, 3, and 4, an attempt has been made to indicate, by stipple, areas which stain heavily with chlorazol black E.

Previously, taxonomists have illustrated only the most readily observed portions of the female system, the spermathecae and their ducts. A study of several osmylid genera indicates that the remainder of the female reproductive system also has characters useful in systematics. As with male material, the abdomen is prepared for study by heating in 10% KOH solution, washing, and staining in chlorazol black E. Removal from the abdomen is accomplished by cutting the membrane surrounding the gonopore and gently drawing the ducts out anteriorly, with forceps. It is virtually impossible to see the details of the delicate ducts and sacs *in situ.* The internal system may be dehydrated and permanently mounted on a slide, or reinserted into the abdomen after examination. This method of removal does no damage to the abdominal exoskeleton.

Phymatosmylus, new genus

DESCRIPTION. In forewing (Fig. 1A), MP forks halfway from base to apex; CuA bends sharply posteriad, anteriorly pectinate; 2A fuses with 1A opposite fused portion of RS+MA. In hindwing, basal piece of MA sinuate, joining R before origin of RS+MA, or absent. Proximal nygma of forewing opposite or slightly beyond divergence of RS and MA. Distal nygmata highly irregular; in male forewing, usually one or two, sometimes three, between proximal branch of RS and MA, sometimes one between last two branches of RS, and a few, usually small, between MA and MP. In hindwing, one distal nygma between last branch of RS and MA; one or two between last two branches of RS. All veins of male forewing thickened and filled with granular substance; in female, bases of Cu and 1A slightly thickened. In forewing, most crossveins with single dorsal seta, borne on swelling at midpoint. Fore coxa of female with two irregular rows of pedestalled setae (Fig. 8); arolium bilobed.

TYPE. The type is the only known species, *Phymatosmylus caprorum.* The name is derived from the Greek *phyma, phymatos,* a swelling, referring to the enlarged veins of the male forewing, plus - *osmylus.*

DISCUSSION. *Phymatosmylus* is placed in the Stenosmylinae because of the thickened veins and the partial fusion of the eighth and ninth abdominal tergites of the male. Both the structure of the media in the forewing and the structure of the male abdomen appear transitional between the Stencsmylinae and the Kempyninae. In Osmylidae, the primitive position of the medial fork

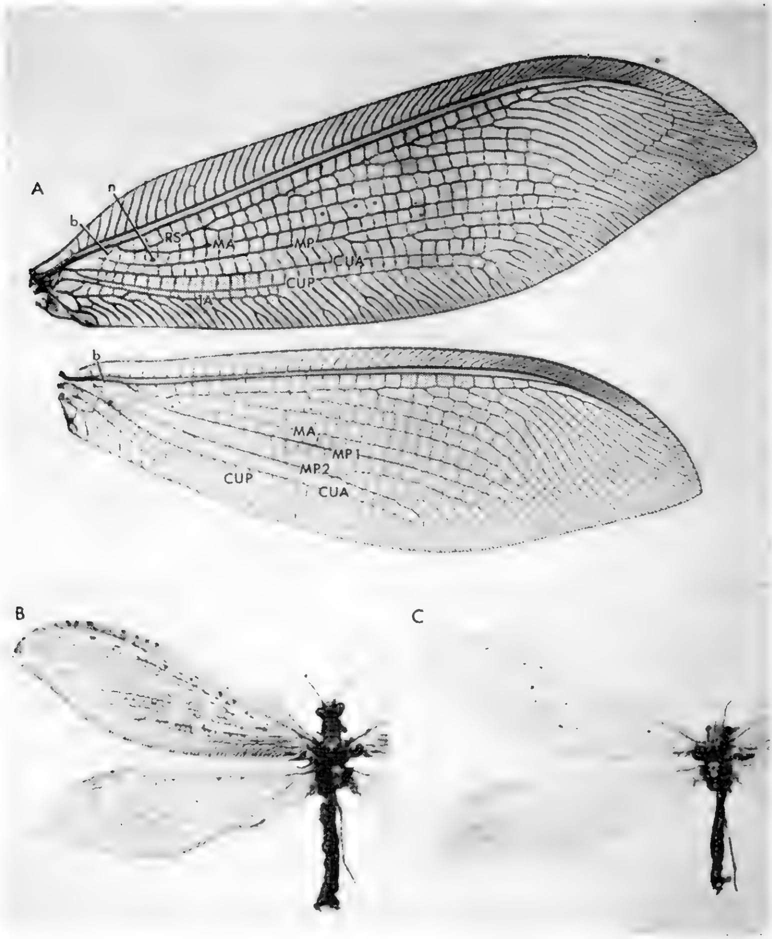


FIG. 1. *Phymatosmylus caprorum.* A) Wings of a lightly pigmented male, showing venation and thickening of veins in forewing. B) Heavily pigmented female. C) Moderately pigmented female.

Abbreviations: b — basal piece of MA, CuA — cubitus anterior, CuP — cubitus posterior, MA — media anterior, MP — media posterior, n — nygma, RS — radial sector, 1A, 2A — first and second anal veins.

in the forewing is near the base, as seen in fossil material (e.g., *Sogjuta* O. Martynova, Triassic) and in the Recent Protosmylinae. *Phymatosmylus* has this fork in an intermediate position; in other Stenosmylinae, it lies near the wing apex. In *Oedosmylus* and *Isostenosmylus,* CuA2 curves abruptly posteriad at the level of the medial fork, and usually is anteriorly pectinate. *Stenosmylus* and *Stenolysmus* are more specialized in that MP2 has fused with CuA; the location of the medial fork in these genera is marked only by an oblique crossvein, as in the forewing of the Myrmeleontidae. Thickened forewing veins also occur in *Oedosmylus,* but in the female rather than in the male (Kimmins, 1940).

The partially free eighth abdominal tergite in the male is more generalized than in the remainder of the Stenosmylinae, where the eighth and ninth tergites are completely fused.

The female reproductive system of *Phymatosmylus* (Fig. 6) differs from that of *Plethosmylus* (Osmylinae) only in minor details. In the closely related genus *Isostenosmylus* (Stenosmylinae), which is more specialized in male genitalic characters and wing venation, the female reproductive system differs significantly from that of *Phymatosmylus:* the genital opening is located at the bottom of a large genital atrium; the copulatory bursa is expanded into a sac posteriorly to the attachment of the spermathecal canals; the slender dorso-median duct is absent; the oviduct is expanded laterally to form large folds enveloping the sides of the copulatory bursa, so that the spermathecal ducts arise from the bottom of a depression; the proximal connection of the fertilization canal is not apparent, and the canal extends much farther anteriad along the oviduct; a prominent duct joins the oviduct opposite the distal end of the fertilization canal. Most of these features of *Isostenosmylus* appear to be specializations, but too few genera of osmylids have been examined to state this with assurance. These differences, however, are sufficiently fundamental to demonstrate the potential utility of the female system as a source of taxonomic characters.

Phymatosmylus caprorum, new species

DESCRIPTION. Head and antennae yellow, a brown spot at anterior mandibular articulation; ocelli black-bordered medially; vertex scars pale, variable in shape, usually large medial square and thick lateral band. Pronotum subrectangular, viewed from above, width slightly greater than length, yellow, bordered with lateral fuscous stripe; a thin median fuscous line on anterior half; setae long, pale except on lateral stripes. Meso- and metanota fuscous-mottled laterally, with broad median yellow stripe. Pleurae and legs pale, spurs short, hind basitarsus as long as next three tarsomeres. Abdomen pale, tergites 1-7 fuscous; thin ventral fuscous line. Male with fused ninth tergite and ectoproct shiny, yellow. Gonarcus, gonocoxites and tenth sternite pale; tenth sternite setose (Figs. 2-4). Gonarcus and gonocoxites suspended from apical margin of ninth tergite. Mediuncus lobes membranous laterally, sclerotized medially, shaped as in Figures 2 and 3; extended prominently in dried specimens. An irregular, weakly sclerotized gonapsis anterior to gonopore, shaped similarly to hypandrium internum (Fig. 4, gps). A lightly sclerotized, setaless ring surrounds anus. Female eighth sternite concave, with anterior median hook, projecting angle at anterior margin of eighth tergite, lateral setose spatulate process opposite eighth spiracle (Fig. 7). Eighth gonocoxite narrowed medially, with rounded disclike apical lobes (Figs. 5, 7). Ninth tergite and gonocoxites pale, a black stripe on gonocoxite; setae on abdominal apex pale. Female genital opening single (Fig. 5, go); slender colleterial gland reservoir opens into copulatory bursa posteriorly, lined with microtrichia (Fig. 6). Thin duct, probably from bursal gland, joins copulatory bursa dorsally. Spermathecae spheroidal, ducts enter sclerotized anterior lobe of bursa; below this a short fertilization canal of typical externally microvillose appearance joins bursa at base of oviduct.

Wing venation as in Figure 1A. Color varies from uniform light brown to pale with veins and membrane fuscous-mottled. In heavily marked individuals (Fig. 1B), on the forewing pale spots appear on basal subcostal area, scattered over disc; a pale line directed toward wing apex, and a row of small spots on posterior margin. Hind wing patterned similarly, but paler. Nygmata dark brown or black.

MEASUREMENTS. Chilean specimens: forewing length, ♂ 20-(21.3)-23 mm (N=7), ♀ 22-(22.5)-24 mm (N=6), antenna 7.4-8.4 mm (N=4). Argentine specimens: forewing length 25-26 mm (N=3), antenna length 6.5-6.8 mm (N=2).

HOLOTYPE. Male, Las Cabras, "S. of Chillan vulcain", 36°49′S-71°26′W, Nuble Province, Chile, elev. 1480 m, 10-23 Dec. 1954, Luis E. Peña, leg. Peabody Museum of Natural History.

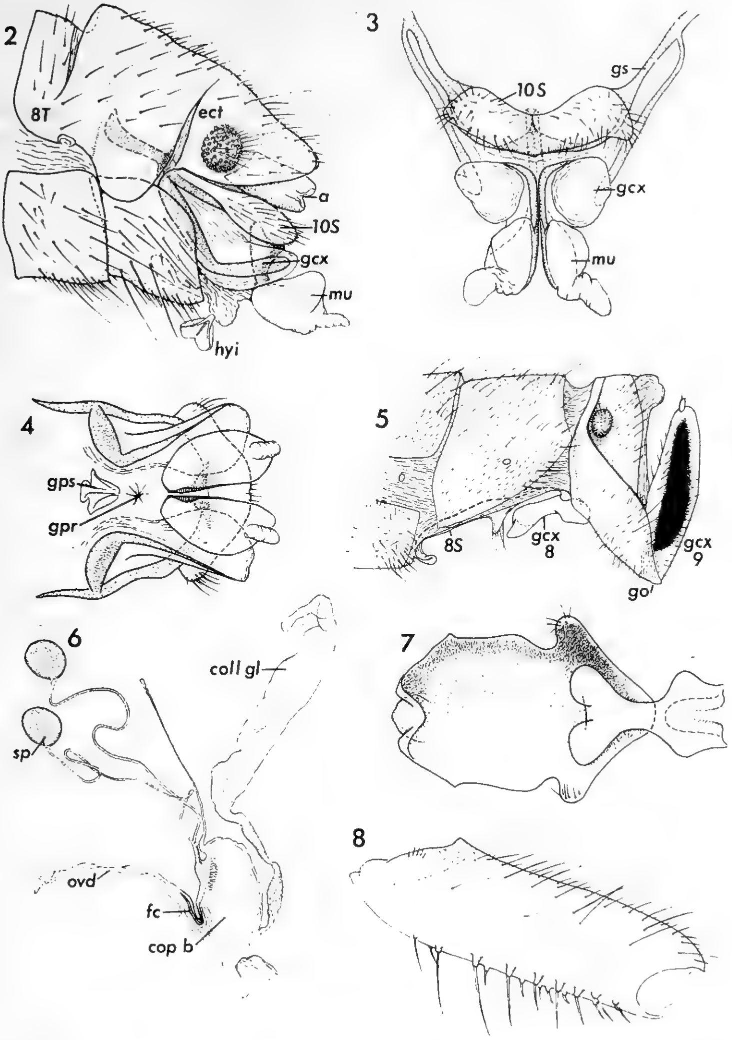


FIG. 2. male abdominal apex, lateral view. FIG. 3, gonarcus and gonocoxites, posterior view. FIG. 4, same, ventral. FIG. 5, female abdomen, lateral view; fine dotted lines show location of spermathecae. FIG. 6, female genital system, cleared specimen. FIG. 7, female 8th sternite and gonocoxite, ventral. FIG. 8, female left fore coxa, lateral, showing pedestaled setae.

Abbreviations: a — anus, coll gl — colleterial gland, cop b — copulatory bursa, ect — ectoproct, fc — fertilization canal, gcx — gonocoxite, go — genital opening, gpr — gonopore, gps — gonapsis, gs — gonarcus, hyi — hypandrium internum, mu — mediuncus, ovd — oviduct, sp — spermatheca, 8S — eighth sternite, 8T— eighth tergite, 10S — tenth sternite.

PARATYPES. Same data as holotype, seven males, seven females. One ♂, one ♀ in Museum of Comparative Zoology, Harvard, one ♂, one ♀ in British Museum (Natural History), one ♂, one ♀ in Adams collection, remainder in Peabody Museum. Additional paratypes: Las Trancas, Cord. Chillán, Nuble Prov., Chile, 21-30 Nov. 1964 (2 ♂), 1-10 Dec. 1964 (2 ♀), L. E. Peña, leg., Adams collection; Alto de Vilches, Cordillera, [35°37′ S, 70° 21′ W] Talca Prov., Chile. 21-23 Nov. 1964 (♂), leg. L. E. Peña. Lagi Currhué, 1000 m. [39°52′ S, 71°28′ W], Neuquén, Argentina, 26 Dec. 1954 (♀), Adams collection, purchase ex F. H. Walz; Pucará, Parque Nac. Lanín. Argentina, 30 Nov. 1959 (♀), Adams collection, purchase ex F. H. Walz, Feb. 1951 (♀), leg. S. S. Schajovskoy, MacLeod collection; Lago Hermoso, Parque Nac. Lanín, Neuquén, Argentina, Nov. 1949 (♀), Dec. 1949 (♂), leg. S. S. Schajovskoy. Material from the Adams collection was not available for study when the foregoing description was written.

DISTRIBUTION. This species appears confined to moist montane areas. The specimens from Argentina were collected in the lake region of Neuquén. Probably the Andes do not constitute an important distributional barrier in this area, since several passes exist at 1200 meters elevation. The gap of approximately 300 kilometers between the Nuble localities, on the west slope of the Andes, and the Neuquén localities may be an artifact of collecting.

Homologies of Planipennian Male Genitalia

The terminology used here differs from that of Tjeder, Kimmins, and other recent workers in several respects, but is consistent with my previous usage (e.g., MacLeod and Adams, 1968). The tenth sternite is often present in the Planipennia; it is nearly always setose, and in archaic forms it may be associated with the gonarcus (e.g., Psychopsidae, Acker, 1960, figs. 74-79, "sternite 11"). As Kimmins (1940) has pointed out, the tenth sternum of this subfamily is the most archaic to be found among the Planipennia. Along its ventral border extends the gonarcus, which may be a derivative of part of the tenth sternum, as Kimmins suggested.

Another interpretation, which I consider more probable, is that the entire gonarcus-mediuncus complex has arisen from the fused parameres of Sialodea and Raphidiodea. The bilobed or bipartite structure of the planipennian mediuncus is apparent in most cases; even when the mediuncus is a single structure, it is ordinarily lightly sclerotized medially. Occasionally, the gonarcus similarly shows evidence of a paired origin (*Oliarces,* Acker, 1960, fig. 52, "coxopodite 9"). Among the Sialodea, the parameres may be approximated at the midline (some species of *Sialis*) or show medial fusion and a pair of lobes (*Corydalus*), or occur as a bilobed medial process (*Neohermes, Chauliodes*). Thus, among the Sialodea, a gonarcus-like structure is commonly found, from which it is reasonable to consider that the planipennian gonarcus has been derived.

In the Sialodea and Raphidiodea there is a difference in texture of the parameres and gonocoxites that offers a helpful guide to homologies: the parameres are never setose (in Sialodea, they are smooth, and in Raphidiodea, minutely spinose); in contrast, the gonocoxites, or claspers, are nearly always setose. Primitively, the gonocoxites articulate on the ninth tergite, but they are occasionally attached laterally to the fused parameres (*Neohermes*).

In Planipennia, the articulation of the gonocoxites shifts to the gonarcus, but the setose condition is usually retained. Their structure is often still clasper-like (e.g., *Myiodactylus,* see Acker, 1960, fig. 152, "paramere", and Psychopsidae, figs. 50-60, "paramere"). In *Phymatosmylus,* the primitive attachment of the gonocoxites to the ninth tergite has persisted, in addition to the more advanced articulation with the gonarcus.

Probable stages in the evolution of the mediuncus-gonarcus complex and gonocoxites may be summarized as follows:

1. A pair of plates (volsellae or parameres) lie laterally to the phallus (as in *Agulla,* Raphidiodea); these may be united dorsally to the phallus (*Raphidia ophiopsis* L.). Gonocoxites articulate on the ninth tergite.

2. A pair of plates dorsal to the genital opening, usually approximated on the midline, each of which may bear a submedian process (Sialodea: *Sialis*).

3. Paramere plates fused medially to form a transverse band dorsal to the genital opening; usually with a pair of submedian processes. Gonocoxites may be articulated to the ninth tergite

(Sialodea: *Corydalus*) or appear as setose lateral lobes of the transverse band (Sialodea: *Neohermes*).

4. Paramere plates fused medially to form a transverse band (gonarcus) which bears a pair of movable, closely approximated submedian processes (mediuncus lobes); gonocoxites articulated laterally on the gonarcus (Planipennia: *Dilar, Sisyra,* and Osmylidae).

5. Mediuncus lobes fused, often bifid apically or showing median suture; gonocoxites laterally articulated on gonarcus (most Planipennia).

According to this interpretation, the gonocoxite corresponds to the "paramere" or the "entoprocessus" of Tjeder's (1957) terminology, and the true parameres to his combined "gonarcus" and "mediuncus". But the gonarcus and mediuncus bear very little resemblance to primitive parameres, and two separate terms are needed for them. Furthermore, use of the term paramere in this unusual sense would inevitably result in confusion. Therefore there appears to be strong justification for retention of Tjeder's terms, gonarcus and mediuncus. The gonocoxites may as well be referred to as such, thus making it possible to avoid applying the rather ambiguous term paramere to any planipennian structure.

Acker (1960) has generally identified the gonarcus as the "ninth coxopodite", the mediuncus as the fused "styli", and the ninth gonocoxites as "parameres"; in the osmylid *Porismus,* however, the mediuncus lobes are identified as "parameres" and the gonocoxites as "styli".

The small gonapsis-like structure has not been previously noted in osmylids; however, I have also found it in *Porismus* and *Kempynus.*

ACKNOWLEDGMENTS

Ellis G. MacLeod has kindly lent material from his collection, and contributed many useful comments; C. L. Remington has generously assisted during the progress of this study, and has made many helpful suggestions. Their aid is gratefully acknowledged. Thanks are also due to Luis E. Peña, the collector of the Chilean material, who is accomplishing so much toward achieving a better knowledge of the insect fauna of his country.

SYSTEMATIC LIST

Order Neuroptera
  Suborder Raphidiodea
    Agulla, Raphidia ophiopsis L.
  Suborder Sialodea
    Sialis, Neohermes, Chauliodes, Corydalus
  Suborder Planipennia
    Osmylidae
      Osmylinae: *Plethosmylus*
      Protosmylinae: *Paryphosmylus ornatus* Krüger
      Stenosmylinae: *Isostenosmylus, Oedosmylus, Stenosmylus, Stenolysmus, Phymatosmylus caprorum* Adams
      Kempyninae: *Kempynus falcatus* Navás
      Porisminae: *Porismus*
      Incertae sedis: *Gumilla*
    Ithonidae: *Narodona* (?), *Oliarces*
    Nymphidae: *Myiodactylus*
    Psychopsidae
    Dilaridae: *Dilar*
    Sisyridae: *Sisyra*

REFERENCES CITED

Acker, T. S. 1960. The comparative morphology of the male terminalia of Neuroptera (Insecta). Microentomology **24** : 25-84.

Carpenter, F. M. 1943. Osmylidae of the Florissant shales, Colorado. Am. J. Sci. **241** : 753-760.

Kimmins, D. E. 1940. A revision of the osmylid subfamilies Stenosmylinae and Kalosmylinae (Neuroptera). Novit. Zool. **42** : 165-201, pl. 5-8.

MacLeod, E. G., and P. A. Adams. 1968. A review of the taxonomy and morphology of the Berothidae, with the description of a new subfamily from Chile (Neuroptera). Psyche **74**: 237-265.

Navás, L. 1912. Insectos neurópteros nuevos ó poco conocidos. Mem. R. Acad. Cienc. Artes Barcelona (3) **10**: 135-202.

Tjeder, B. 1957. Neuroptera-Planipennia. The lace-wings of South Africa. I. Introduction and Families Coniopterygidae, Sisyridae, and Osmylidae. S. African Animal Life **4** : 95-188.

INFORMATION FOR AUTHORS

REVIEW	The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
STYLE	Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).
FORM	Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.
TITLE	Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
ABSTRACT	The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
NOMENCLATURE	Follow the International Codes of Zoological and Botanical Nomenclature.
ILLUSTRATIONS	Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
FOOTNOTES	Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
TABLES	Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
REFERENCES	The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
THOR'S COPIES	Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
PROOF	Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
COPYRIGHT	Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 142. 30 JAN. 1970

TEIID LIZARDS OF THE GENUS PROCTOPORUS FROM BOLIVIA AND PERU.

THOMAS UZZELL

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

TEIID LIZARDS OF THE GENUS PROCTOPORUS FROM BOLIVIA AND PERU

THOMAS UZZELL

Department of Biology and Peabody Museum of Natural
History, Yale University

ABSTRACT

Four species [*P. pachyurus* Tschudi, *P. bolivianus* Werner, *P. guentheri* (Boettger), *P. ventrimaculatus* Boulenger] occur in Bolivia and Peru. The first three (the *P. pachyurus* group) have an undivided translucent disc in the lower eyelid, a median occipital, two or three supraoculars, and squarish pregulars not forming chevrons. This group resembles *P. striatus* (Peters) in the last character, but differs from it in the first three. *P. pachyurus* (17 examined) and *P. bolivianus* (158) occur at about 2500-3800 m above sea level on the eastern Andean slopes, the former in central Peru, the latter in southern Peru and northern Bolivia. *P. guentheri* (30) occurs parapatrically at lower elevations (1000-2516 m). Although the hemipenes of *P. bolivianus* and *P. guentheri* resemble each other rather than that of *P. pachyurus,* in most respects *P. bolivianus* and *P. pachyurus* are more similar to each other. Specimens of *P. bolivianus* from the upper reaches of the Río Urubamba differ from those from the lower Río Urubamba valley in size, ventral coloration, presence of a loreal, and number of anterior supralabials. A small sample from Cuzco resembles those from the lower Río Urubamba valley in absence of a loreal and in femoral pore number, but resembles specimens from the

POSTILLA 142: 39 p. 30 JANUARY 1970.

upper valley in size and some aspects of coloration. *P. ventrimaculatus* (2; northern Peru, 2200-2700 m) has a divided eye disc, an enormous first superciliary resembling a supraocular, a small first supraocular touching the palpebrals, and a smaller second supraocular separated from the palpebrals by a superciliary. The relationships of *P. ventrimaculatus* may be with *P. striatus.* The name *P. petersi* (Boettger) is placed in the synonymy of *P. unicolor* (Gray). *P. bolivianus* is removed from the synonymy of *P. guentheri* and is used for the taxon formerly called *P. petersi; P. lacertus* (Stejneger), *P. longicaudatus* Andersson, and *P. obesus* Barbour and Noble are synonyms. *P. ocellifer* (Boulenger) and *P. anomalus* (Barbour and Noble) are placed in the synonymy of *P. guentheri.*

INTRODUCTION

More than ten years ago I examined most of the Peruvian and Bolivian lizards of the genus *Proctoporus* in North American museums. At that time, I was unable to decide to which population of these the name *Proctoporus petersi* applied. A recent opportunity to examine the holotype of *Proctoporus petersi* has, however, removed my doubts, and the imminent publication of a checklist of South American reptiles, being edited by James Peters, provides some urgency for recording new information on the taxonomy of these animals.

The specimens examined include two groups and four species. One group contains *Proctoporus ventrimaculatus*. I have examined two specimens of this form, both from northern Peru; I am uncertain about its affinities. The other group, with three species in Bolivia and southern Peru, is related to *Proctoporus striatus* of Colombia. These three southern species may be distinguished as a separate subgroup on the basis of the undivided transparent disc in the lower eyelid. Such an undivided disc occurs frequently in southern populations of many species of lizards in Boulenger's (1885) Group II of the family Teiidae, and does not indicate that the members of the subgroup are more closely related to each other than to *P. striatus*. The subgroup is purely a matter of my convenience.

KEY TO SPECIES OF PROCTOPORUS IN PERU AND BOLIVIA

The four species of the genus *Proctoporus* that I presently recognize in Peru and Bolivia can be distinguished by the following key.

1a. Dorsal scales 49 or more . . . . *P. pachyurus*
b. Dorsal scales 47 or fewer 2
2a. A pair of enlarged pregular scales in contact on midline behind the second pair of chinshields; belly clear yellow; conspicuous ocelli in males, 29-35 dorsal scales . . . . *P. guentheri*
b. No pair of enlarged pregulars; ventral scales uniformly dark or at least heavily spotted on lateral rows 3
3a. Supraoculars 2-2 or 3-3, separated from palpebral scales by a complete superciliary series . . . . *P. bolivianus*

b. Supraoculars 2, the first in contact with palpebrals and preceded by an enormous first superciliary (or, supraoculars 3, the middle in broad contact with the palpebrals) .... *P. ventrimaculatus*

PROCTOPORUS PACHYURUS GROUP

DEFINITION. A continuous narrow zone of granules separating the ventral and lateral scales. Males with or without ocelli in pattern. Two or three supraoculars, all separated from upper palpebrals by superciliary series; first superciliary expanded onto dorsal surface of head or not. Translucent disc in lower eyelid composed of single scale. Median occipital almost always present. Pregulars (Ruibal, 1952: 478) variable, but usually not forming chevrons with apices forward; many pregulars quadrangular; pregulars and gulars separated by granular row. Limbs not or scarcely overlapping when adpressed. Tibial scales weakly keeled. Thenar scales, especially in *P. guentheri,* with weakly produced edge. Females with or without femoral pores; when present, fewer than in males; males with femoral pores; no preanal pores in either sex.

Lizards of the *P. pachyurus* group can be identified by the narrow zone of granules separating the lateral and ventral scales and by the undivided disc in the lower eyelid. The median occipital is absent in five specimens, although in six others it is replaced by two small scales and in one, it is partly fused to an occipital[1]; when series are available, presence of a median occipital is apparently a reliable feature to distinguish the *P. pachyurus* group from the *P. luctuosus* group (Uzzell, 1958).

RELATIONSHIPS. The relationships of the *P. pachyurus* group are with *Proctoporus striatus.* This is especially suggested by the arrangement of the pregular scales, the complete superciliary series, and the narrow zone of small scales just lateral to the ventral scales. *P. striatus* differs from members of the *P. pachyurus* group in having more (4-5) supraoculars, longer legs, a divided disc in the lower eyelid, and usually no median occipital (although Burt and Burt, 1931, reported variation in this character). *Proc-*

---

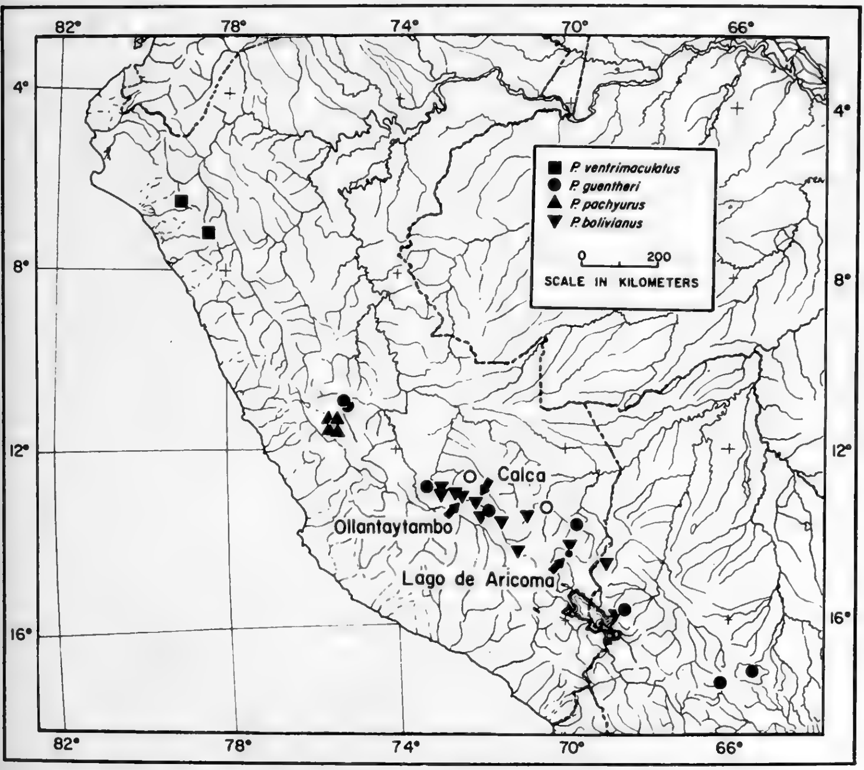
[1] One individual lacks an interparietal, therefore presence or absence of a median occipital is a meaningless distinction.

toporus hypostictus is perhaps related to *P. striatus* and the *P. pachyurus* group, although it shares many features with the *P. luctuosus* group (Uzzell, 1958).

Proctoporus pachyurus Tschudi

Proctoporus pachyurus Tschudi, 1845, Archiv für Naturgeschichte 11:161.

Tschudi (1845) described this species on the basis of two specimens that he collected in the valley of the Río Chanchamayo in eastern Peru. This river, located in Junín, joins the Río Paucartambo and gives rise to the Río Perené. The two syntypes,



Collection localities for four species of *Proctoporus* in Peru and Bolivia. Open symbols represent published records. Localities for *P. guentheri* are generally at lower altitudes than those for *P. pachyurus* and *P. bolivianus.* Arrows point to towns mentioned in text.

which are in the Musée d'Histoire Naturelle in Neuchâtel, Switzerland, were examined and described in detail by Peters (1862). I have recently examined one of these, and can add only that it, the specimen figured by Peters, is a female. Recent specimens of this species are from the valley of the Río Tarma, which flows into the the Río Chanchamayo (map). One of these had previously been reported by Griffin (1917).

VARIATION. Data on 10 males and 7 females are presented in Table 1. All of the specimens have an undivided disc in the lower eyelid, and a loreal that touches both the supralabials and frontonasal. A complete superciliary series separating the supraoculars from the palpebral scales occurs on 33 of 34 sides; in SMF 65286, the left second supraocular touches the palpebrals. A median occipital is present in 13 specimens; in the other 4 the corresponding area is occupied by 2 small scales. One specimen (SMF 65287) has no interparietal, and the parietals touch behind the very elongate frontoparietals. Counting only those longitudinal series that are continuous for at least 3 ventral scales, there are 12 longitudinal rows of ventrals in 8, 11 rows in 8[2]; enlarged ventrals across the belly number 12-14. The males have 24 (5 specimens), 25 (3) or 26 (2) transverse rows of ventral scales; 3 recently collected females have 26 transverse rows of ventrals; 1 has 25; the syntype examined and 2 others have 24. Thirteen specimens have 3-3 supraoculars; in four of these the second supraocular on each side is excluded from contact with the superciliaries. Two males and two females, including the syntype examined, each have 2-2. In all specimens, the first supraocular is the largest. The first superciliary is expanded onto the dorsal surface of the head in all specimens.

The dorsal scales are convex but smooth, or weakly keeled or striate. The lateral scales are separated from the ventrals by a granular row. The gular scales are usually in 7 or 8 rows, the pregulars in 5 or 6 at midline.

COLORATION. Specimens of *P. pachyurus* are basically gray-brown above and below, although somewhat lighter below than above. The ventral scales are each marked by diffuse dark pigment, and

[2] One individual was not scored.

TABLE 1. Variation in specimens of *Proctoporus pachyurus.* Figures represent ranges and (in parentheses) means

	Total femoral pores	Dorsal scale rows	Subdigital lamellae		Scales around midbody region	Hind leg
			4th finger	4th toe		Snout-vent length
Acobamba 2 ♂♂	18-19 (18.5)	52-59 (55.5)	11-13 (12.2)	19-20 (19.5)	43 (43.0)	.35 (.350)
Tarma 6 ♂♂	16-21 (18.0)	51-55 (53.2)	12-14[1] (13.3)	20-22[2] (20.8)	40-44 (41.4)	.33-.39 (.355)
Tarmatambo 2 ♂♂	18-19 (18.5)	49-55 (52.0)	11-12 (11.5)	20-21 (20.5)	40-44 (42.0)	.34-.35 (.345)
Acobamba 3 ♀♀	8-9 (8.3)	54-55 (54.7)	13-14 (13.5)	19-21 (19.8)	41-43 (42.3)	.29-.32 (.311)
Huanuquillo 1 ♀	6	55	—	—	—	.37
Tarma 2 ♀♀	4-8 (6.0)	54-56 (55.0)	11-14 (12.5)	18-21 (19.5)	40-44 (42.0)	.33 (.330)
Syntype 1 ♀	5	54	—	—	—	.29

[1] 8 digits; [2] 7 digits

especially in younger specimens, this dark pigment tends to form ventral lines, one on each row of ventral or subcaudal scales.

Adults are more uniform above than the young. In the young there tend to be light dorsolateral lines bounded below by darker brown; these lines extend from the hind corner of the eye to the end of the body and onto the tail. They may be retained in adult females. There is usually a mid-dorsal dark stripe on the shoulder region. A bright white line passes from the middle of the lower border of the eye to the tympanum. There is a row of light spots along the upper side of the body between the limb insertions and below the dorsolateral light lines.

LENGTH. Both the largest male and the largest female (a syntype) examined are 58 mm snout to vent. Two males and one female with intact tails have tail over snout-vent length ratios of 1.4 to 1.9 (mean 1.76).

SEXUAL DIMORPHISM. The greatest dimorphism is in femoral pore number (Table 1). The preanal scale number is also dimorphic. Six females have six posterior preanals, while one has four plus two lateral slivers. Seven males have four posterior preanals, two have five, the median a small triangular wedge; and one has six. The pattern may also show some dimorphism, mature males being more uniform above.

BIOLOGY. Nothing is known about the biology of *Proctoporus pachyurus.*

RANGE. Although *P. pachyurus* is not known to occur sympatrically with other members of the genus, *P. guentheri* also occurs in the valley of the Río Chanchamayo (map). In this valley, the localities for *P. guentheri* are downstream from and lower (1000-1500 m above sea level) than the exact localities for *P. pachyurus* (2900-3800 m).

SPECIMENS EXAMINED. Peru: Junín: valley of Río Chanchamayo, MN unnumbered, syntype of *Proctoporus pachyurus;* Tarma, Tarma (3000 m) CM 1043, FMNH 134384-90; Huanuquillo (3800 m): FMNH 134391; Tarma, between Acobamba and Palcamayo (2900 m) SMF 65284-88; Tarmatambo (3300 m) AMNH 88323 (2 specimens).

Proctoporus bolivianus Werner

Proctoporus bolivianus Werner, 1910, Mitt. Naturh. Mus. Hamburg 27 (pt. 2): 30.
Oreosaurus lacertus Stejneger, 1913, Proc. U.S. Nat. Mus. 45: 546.
Proctoporus longicaudatus Andersson, 1914, Arkiv f. Zool. 9 (3): 6.
Proctoporus obesus Barbour and Noble, 1921, Proc. U.S. Nat. 58(2352): 616.

Proctoporus bolivianus was described from a single female with a body length of 48 mm collected at Sorata, La Paz, Bolivia, at about 2615 m above sea level (Werner, 1910). Dr. Erna Mohr has informed me that the holotype, formerly in the collection of the Zoologisches Museum in Hamburg, was lost during World War II.

Although Burt and Burt (1931) placed *P. bolivianus* in the synonymy of *P. guentheri,* several characters in the original description of *P. bolivianus* convince me that it is not conspecific with *P. guentheri.* These characteristics are, however, found among the other specimens that I have referred to *P. bolivianus.* Among the characters that I consider significant are the absence of large scales behind the second pair of chinshields (present in all but one of 30 specimens of *P. guentheri* examined), the larger number (26) of transverse rows of ventral scales (17 to 20 in *P. guentheri*), and the larger number (between 37 and 45, according to Werner's key) of dorsals (29 to 35 in *P. guentheri*). Werner's count of scales around the midbody region (28) is low for both species, but did not include the small granules between the dorsal and ventral scales.

VARIATION. Variation in several characters of the specimens of *Proctoporus bolivianus* examined is presented in Tables 2 through 5.

There is considerable geographic variation in this species. I have examined 158 specimens (89 males, 69 females) that I refer to *P. bolivianus,* but I am not convinced that I understand their relationships. I have examined series from several localities in the middle and upper Urubamba valley, and two series from near Limbani in the Río Madre de Dios drainage. The latter is separated by a very high divide from the upper Río Urubamba valley. My knowledge of this species in Bolivia depends on the descrip-

TABLE 2. Variation is several scale counts for males of *Proctoporus bolivianus.* Figures are ranges and (in parentheses) means; for larger samples the standard deviation times Student's t for 95% confidence limits is also indicated

	Ventral scale rows	Dorsal scale rows	Scales around midbody region	Total femoral pores	Subdigital lamellae 4th toe	Subdigital lamellae 4th finger
Cuzco, 20 mi. S 1 ♂	24	42	37	12	18 (18.0)	11 (11.0)
Cuzco – A 37 ♂♂	22-26 (23.9±2.2)	37-44 (40.4±4.0)	34-41 (36.8±3.4)	9-12 (10.7±1.8)	14-19^{1} (16.2±2.1)	9-13^{2} (10.5±1.5)
Cuzco – B 3 ♂♂	23 (23.0)	36-40 (38.3)	37-40 (38.3)	15 (15.0)	15-19 (17.3)	10-12 (10.8)
Calca 27 ♂♂	21-25^{3} (23.3±2.4)	36-43^{3} (40.8±3.7)	38-43^{3} (40.6±3.4)	10-14 (11.9±1.9)	15-22^{4} (18.3±2.7)	10-14^{5} (11.5±1.7)
Ollantaytambo 1 ♂	22	44	41	14	21 (21.0)	13-14 (13.5)
Torontoy 1 ♂	23	41	42	13	18-20 (19.0)	13-14 (13.5)
Tinccochaca 2 ♂♂	20-21 (20.5)	34-37 (35.5)	35-38 (36.5)	11-12 (11.5)	16-18 (17.0)	11-12 (11.5)
Marcapata 2 ♂♂	21-23 (22.0)	41-44 (42.5)	39-41 (40.0)	10-12 (11.0)	19-22 (20.2)	12-14 (13.0)
Limbani 13 ♂♂	22-25 (23.2±1.9)	37-41 (38.9±3.0)	34-41 (37.3±3.9)	10-13 (11.1±2.3)	14-19^{6} (16.9±2.2)	9-12^{7} (10.6±1.6)
Pelechuco 1 ♂	23	41	37	15	16-17 (16.5)	10-11 (10.5)

[1] 69 digits; [2] 72 digits; [3] 26 males; [4] 52 digits; [5] 50 digits; [6] 28 digits; [7] 27 digits

TABLE 3. Variation in several scale counts for females of *Proctoporus bolivianus*. Figures are ranges and (in parentheses) means; for larger samples the standard deviation times Student's t for 95% confidence limits is also indicated

	Ventral scale rows	Dorsal scale rows	Scales around midbody region	Total femoral pores	Subdigital lamellae	
					4th toe	4th finger
Sicuani 1 ♀	22	39	42	4	18-19 (18.5)	10-12 (11.0)
Cuzco – A 28 ♀♀	22-27[1] (24.2±2.5)	39-47[1] (41.7±3.4)	33-38[1] (36.3±2.7)	2-4[1] (2.6±1.8)	14-18[2] (16.3±1.6)	9-12[3] (10.8±1.5)
Cuzco – B 2 ♀♀	24 (24.0)	40-42 (41.0)	38 (38.0)	0-1 (0.5)	17-18 (17.7)	11-13 (11.5)
Calca 21 ♀♀	22-26 (24.1±2.1)	40-45 (42.7±2.5)	38-45 (40.6±3.9)	0-4 (2.8±2.2)	17-20[4] (18.3±1.5)	10-13[5] (11.4±1.3)
Ollantaytambo 2 ♀♀	23-26 (24.5)	41-45 (43.0)	39-41 (40.0)	0 (0)	19-21 (20.0)	12-14 (12.7)
Torontoy 1 ♀	23	41	41	4[6]	20 (20.0)	12-13 (12.5)
Ñusta Hispana, Tinccochaca 3 ♀♀	20-21 (20.7)	37-40 (39.0)	39-40 (39.7)	2-8[6] (4.7)	17-20[7] (18.4)	11-14 (12.3)
Marcapata 2 ♀♀	22-24 (23.0)	38-43 (40.5)	41-43 (42.0)	0 (0)	18-19 (18.5)	11-13 (12.0)
Limbani 9 ♀♀	22-24 (23.1±1.8)	36-41 (39.0±4.1)	35-41 (37.1±4.3)	0-1 (0.2±1.0)	14-19[8] (16.7±2.9)	9-11[8] (10.1±1.6)

[1] 26 females; [2] 50 digits; [3] 51 digits; [4] 41 digits; [5] 42 digits; [6] females with counts of 2 and 4 have pores distal on thighs; [7] 5 digits; [8] 18 digits

TABLE 4. Body length and frequencies of certain states for several characters in males of *Proctoporus bolivianus*. Frequencies are given as sides with state/sides examined

	Maximum body length (mm)	Loreal present[1]	2 supra-oculars[2]	3 supralabials anterior to angle[3]
Cuzco, 20 mi. S 1 ♂	40	2/2[4]	2/2	0/2
Cuzco-A 37 ♂♂	47	72/74	60/74[5]	58/74[6]
Cuzco-B 3 ♂♂	47	0/6[7]	6/6	0/6
Calca 27 ♂♂	48	54/54	54/54	38/54
Ollantaytambo 1 ♂	44	0/2	2/2	0/2
Torontoy 1 ♂	58	0/2[8]	0/2	0/2
Tinccochaca 2 ♂♂	49	0/4	4/4	0/4
Marcapata 2 ♂♂	58	1/4[9]	0/4	1/4[10]
Limbani 13 ♂♂	56	2/26[11]	6/26	24/26
Pelechuco 1 ♂	54	0/2	2/2	2/2

[1] states observed: present, partly delimited, absent; [2] states observed: 2, 3; [3] states observed: 3 or 4 unless noted; [4] loreal touches labials; [5] one additional side with irregular 3 could be counted as 2; [6] 2 additional sides with irregular minute 4 could be counted as 3; [7] partly delimited on both sides in two specimens; [8] partly delimited on both sides; [9] loreal irregular on one side, partly delimited on another; [10] counts include an irregular 4 and an irregular 5; [11] loreal separated from labials

tion of *P. bolivianus* and on examination of the holotype of *P. longicaudatus*.

The specimens from the upper part of the Urubamba valley (map: Calca and south) are rather different from those from the middle part (Ollantaytambo and north). The scalation characteristics that most suggest this difference are included in Tables 4 and 5, and include the greater frequency of a loreal and the higher number of individuals with three supralabials anterior to the posteroventral angle of the subocular (Fig. 1) in the specimens from Calca and south. Specimens from Calca and south also average considerably shorter in body length. Although the sample sizes

TABLE 5. Body length and frequencies of certain states for several characters in females of *Proctoporus bolivianus.* Frequencies are given as sides with state/sides examined

	Maximum body length (mm)	Loreal present[1]	2 supra-oculars[2]	3 supralabials anterior to angle[3]
Sicuani 1 ♀	34	2/2	2/2	0/2
Cuzco-A 28 ♀ ♀	48	56/56	46/56	54/56
Cuzco-B 2 ♀ ♀	31	0/4	4/4	0/4
Calca 21 ♀ ♀	47	42/42	42/42	31/42
Ollantaytambo 2 ♀ ♀	54	0/4	2/4	0/4
Torontoy 1 ♀	59	2/2	1/2	0/2
Ñusta Hispana, Tinccochaca 3 ♀ ♀	53	0/6	6/6	0/6
Marcapata 2 ♀ ♀	52	0/4	0/4	2/4
Limbani 9 ♀ ♀	54	0/18	8/18	18/18

[1] states observed: present, partly delimited, absent; [2] states observed: 2, 3; [3] states observed: 3, 4

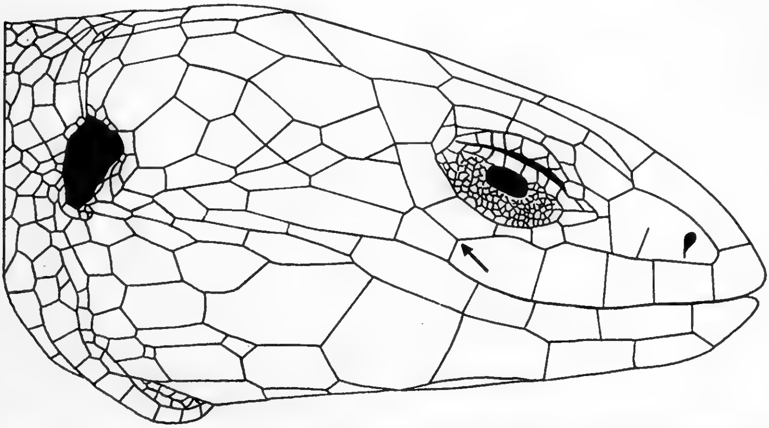


FIG. 1. Scales on the side of the head of *Proctoporus bolivianus* (FMNH 81373). The arrow on the fourth supralabial points toward the posteroventral angle of the subocular. This angle marks the point anterior to which supralabials were counted. × 11.

from Ollantaytambo and north are small, in two out of three samples the largest female is larger than the largest female from Calca and south; the largest male in all three samples is larger than the largest male from Calca and south[3].

Perhaps the most striking difference, however, is coloration. Analysis is complicated by the darkening of coloration with increasing size, especially on the ventral surfaces. Nevertheless, specimens from the region from Calca south are much lighter in coloration than those from Ollantaytambo north. The dorsal coloration of the upper Urubamba valley specimens is a chocolate brown with moderately well-defined dorsolateral light lines. Occasional males show some indication of ocelli along the sides. Ventrally, these animals have a clear gray-white midventral area, with dark brown pigment encroaching on it from the sides. The chin tends to be especially light. The tail is lighter above than the body, darker below than the midventral area. Often there is a thin, irregular dark line around the rostral, across the nostrils and the edges of the eyelids, across the parietals, and continuing posteriorly as a very irregular dark lateral border to whatever dorsolateral light line exists.

Among the specimens reportedly from near Cuzco, there is considerable variation. Differential characters are given in Table 6. The local relief in this region is so great that it is entirely possible that the variation observed is entirely microgeographic. In certain features (femoral pore number, absence of loreal, uniformity of supraocular counts of 2-2, and absence of a fourth anterior supralabial), one of the samples (Cuzco-B, consisting of FMNH 34096-34100) resembles specimens of *P. bolivianus* from Ollantaytambo and north more than the other sample (Cuzco-A, the 63 specimens of FMNH 40427 and ZSM 174/1938). In size, however, Cuzco-B certainly belongs with the populations from Calca south rather than from Ollantaytambo north.

The specimens from near Limbani are rather similar to those from the middle Urubamba valley (Ollantaytambo and north). They are larger (Tables 4 and 5) and tend to lack a loreal. In ventral coloration, especially, they resemble the middle Urubamba valley specimens; adult males are dark lead black below, although

---

[3] The male holotype of *Proctoporus obesus,* approximately 78 mm snout-to vent, is omitted from the Ñusta-Hispana-Tinccochaca sample in Table 4.

TABLE 6. Comparisons of two samples of *Proctoporus bolivianus* from near Cuzco. A: FMNH 40427 (63) and ZSM 174/1938. B: FMNH 34096-34100. ZSM 174/1938 has 12 femoral pores, a loreal on each side, 2-2 supraoculars, and 4-4 anterior supralabials

	Sample size	Total femoral pores[1]	Loreal present[2]	Two supraoculars[2]	Three anterior labials[2]
♂♂					
Cuzco – A	36	9-12 (10.6)	70/72	58/72[3]	56/72[4]
Cuzco – B	3	15(15.0)	0/6[5]	6/6	0/6
♀♀					
Cuzco – A	28	2-4 (2.6)	56/56	46/56	54/56
Cuzco – B	2	0-1 (0.5)	0/4	4/4	0/4

[1] range and mean; [2] sides with state/sides examined; [3] one additional side with an irregular third supraocular could be counted as 2; [4] two additional sides with an irregular, minute fourth supralabial could be counted as 3; [5] loreal partly delimited on both sides in two specimens

there may be a few light dots at the posterolateral corners of the ventral scales or in the middle of the scale itself in the lateral rows of ventrals. The lateral scales may also have dot-like pigmentless areas arranged somewhat in rows. The dorsal surface is uniformly dark, and dorsolateral light lines are almost invisible. The snout, however, is somewhat lighter, with the chinshields and lower labials lighter gray, the supralabials and the other head scales anterior to and including the parietals and interparietal somewhat browner. This difference is not due to loss of epidermal layers.

On the other hand, the specimens from near Limbani tend to have three supralabials anterior to the posteroventral angle of the subocular (Fig. 1), and thus resemble the specimens from the upper Urubamba valley.

The single individual that I have examined from Bolivia, the holotype of *P. longicaudatus,* is an adult male 54 mm snout to vent. Although it is in the size range of the dark individuals from near Limbani and from the middle Urubamba valley, it differs in being rather light, even more so than most of the specimens from the upper Urubamba valley. Unfortunately, specimens of *P. bolivianus* from Bolivia are very scarce in collections; one of the two of which I know (the holotype of *P. bolivianus*) has been destroyed.

It seems highly probable that the population referred to *P. bolivianus* in the upper Urubamba valley could be recognized either as a distinct subspecies of *P. bolivianus* or as a distinct species. The sample labeled Cuzco-B could be interpreted as showing occurrence of a population with dark venter, no loreal, four labials anterior to the posteroventral angle of the last subocular, and numerous femoral pores, features typical of populations from Ollantaytambo north and elsewhere in the range of *P. bolivianus,* sympatrically with the populations in the upper Urubamba valley. I do not now name the upper Urubamba valley population. Except for Cuzco-B, the characteristics of samples along the Río Urubamba suggest changing frequencies of states as one moves from headwaters downstream. On the other hand, the characters by which the upper Urubamba valley specimens and by which the dark form from the middle Urubamba valley and the Limbani region differ from the populations that occur near the type locality of *P. bolivianus* are not clear. When more Bolivian material becomes available, recognition of the upper Urubamba valley population may seem in order. In my opinion, it is probably conspecific with *P. bolivianus.*

In addition to the features in Tables 2 through 5, certain other data were recorded on most individuals examined. The first superciliary may or may not be expanded onto the dorsal surface of the head. This character shows high correlation with the number of supraocular scales: when there are two, the superciliary is expanded dorsally; when there are three, the extra supraocular scale is usually anterior, and occupies the space that would be filled by a dorsal expansion of the first superciliary. In a small percentage of cases, the first superciliary is expanded even though three supraoculars are present. A median occipital is absent in two animals (Limbani); in another specimen, it is replaced by two small scales (Cuzco-A). The number of longitudinal ventral scale rows varies geographically, with 10 in most specimens from near Limbani and in the middle Urubamba valley, and 12 in the upper Urubamba valley.

Since body size shows important geographic variation, the largest male and largest female are listed for each population separately (Tables 4 and 5). Thirty-one males (21 to 58, mean 34.6 mm snout to vent) with tails intact have tail over snout-vent length ratios of 0.82 to 2.21 (mean, 1.57). Twenty-three females (20 to 54, mean 33.4 mm snout to vent), 1.00 to 1.94 (mean 1.65).

REMARKS. Four names are available for populations here referred to *P. bolivianus.* Characteristics of four holotypes are compared in Table 7. I am confident that all four names belong to a closely related group of individuals.

Oreosaurus lacertus. The holotype, USNM 49551, was collected at Tinccochaca, Cuzco, Peru (Stejneger, 1913). This locality (Bingham, 1916) is in the valley of the Río Vilcabamba, a small tributary that enters the Río Urubamba near 13° S latitude. The elevation here is approximately 2800 m. I have examined the holotype and three paratypes (USNM 49549, MCZ 12085, 12087). Certain additional data on the holotype are given in Table 7. Variational data on the paratypes are included in Tables 2 through 5.

The holotype of *Oreosaurus lacertus* has a continuous row of granular scales separating the ventral scales from those on the

TABLE 7. Characteristics of four holotypes in the synonymy of *Proctoporus bolivianus*

	Proctoporus bolivianus[1]	*Oreosaurus lacertus*	*Proctoporus longicaudatus*	*Proctoporus obesus*
Sex	♀	♂	♂	♂
Snout-vent length (mm)	48	49	54	78[2]
Dorsal scales	(37-45)	37	41	44[2]
Ventral scales	10 x 26	11 x 20	10 x 23	11x19[2]
Scales around midbody region	28[3]	38	37	40
Loreal	present	absent	absent	present[4]
Total femoral pores	0	12	15	8
Supraocular scales	3-3[5]	2-2	2-2	3-3
Pairs of chinshields in contact	2	2	2	3
Median occipital	present	present	present	present
First superciliary	not expanded[6]	expanded	expanded	not expanded
Ventral coloration	yellowish white	uniformly dark	each ventral with diffuse dark mark	dull cream
Labials to angle	—	4-4	3-3	4-4

[1] data from Werner (1910); [2] estimated; [3] not including lateral granules; [4] loreal separated from labials; [5] possibly the anteriormost was a dorsally expanded first superciliary; [6] an assumption based on a supraocular count of 3-3

sides of the body, and thus differs from members of the *Proctoporus luctuosus* group, which includes the type of the genus *Oreosaurus* (Uzzell, 1958).

Although *P. lacertus* has not been recognized as a distinct species for many years (Burt and Burt, 1931), the present allocation of the name is new. The name *lacertus* is, however, available for the large, dark population from near Limbani and from the middle Urubamba valley, if it becomes important to distinguish this population nomenclatorially.

Proctoporus obesus. This species was described (Barbour and Noble, 1921) from Ñusta Hispana, Cuzco, Peru. The locality is a monolith about one half mile from Rosapata (Bingham, 1913) in the valley of the Río Vilcabamba, a small tributary that enters the Río Urubamba at about 13° S latitude. The elevation in this region varies dramatically over short distances, but is probably about 2700 m at the valley floor.

I have examined the holotype of *Proctoporus obesus* (USNM 60748). Although E. C. Erdis is listed as the collector, it was almost certainly collected by a native. The head and body are separated and the skin has drawn back on each piece. There is at least one straight cut, as though a machete had been used on the animal. The neck is tightly constricted, suggesting that the body was not severed when the animal was captured, and that the animal was carried for some distance hanging by a thin noose around the neck. For these reasons, counting the scales is difficult, and many of the counts in Table 7 are estimates.

This individual differs from most of the specimens referred to *P. bolivianus* in its greater size and robustness. The scales are quite smooth, and the coloration is remarkably light for a member of this species, although under the microscope some mottling of the scales is apparent. The superciliary series on the right side is broken so that a corner of the second supraocular touches the palpebrals. The equivalent corner of the left second supraocular very nearly touches the palpebrals. There are four supralabials anterior to the posteroventral angle of the subocular and eight femoral pores; a loreal is present but separated from the labials.

There is enough room within my concept of *P. bolivianus* to include the holotype of *P. obesus,* even though other specimens from Ñusta Hispana and from nearby at Tinccochaca look rather different (Tables 4 and 7).

The name *Proctoporus obesus* has long resided in synonymy (Burt and Burt, 1931) but the present allocation is new.

Proctoporus longicaudatus. The holotype (NRS 3224) was collected by Neils Holmgrem and Erland Nordenskiöld at Pelechuco, La Paz, Bolivia, about 3567 m above sea level (Andersson, 1914). I have examined the holotype, and most of my observations are incorporated in Tables 2, 4, and 7.

Although this specimen is geographically closest to the type locality of *P. bolivianus,* the two holotypes differ in that the holotype of *P. longicaudatus* has no loreal and has two supraoculars on both sides. Both characters vary in one or more series referred to *P. bolivianus.*

The name *Proctoporus longicaudatus* has long been recognized as a junior synonym for the species to which it is referred, but the present allocation is new.

SEXUAL DIMORPHISM. The most striking sexual dimorphism is in femoral pore number (Tables 2 and 3). Coloration also is slightly dimorphic, females never being as dark, within their populations, as males. In certain populations, males have weakly developed ocelli. The number of posterior preanal scales also varies sexually; in a subsample of 23 males, counts include 4 (2 specimens), 5 (3), 6 (17), and 7 (1); in a subsample of 21 females, counts include 5 (2 specimens), 6 (12), 7 (5), and 8 (2).

BIOLOGY. Virtually nothing is known about the biology of *Proctoporus bolivianus.* The specimens from near Calca (FMNH 34101, 34119-22, 34137, 34333-35) were found under stones, as was the holotype of *P. longicaudatus.* One female contained one leathery egg in each oviduct.

RANGE. Specimens referred to *Proctoporus bolivianus* are known from the Urubamba and Madre de Dios drainages of the eastern Andes of central and southern Peru and northern Bolivia (map). Altitudes associated with specific localities vary from 2500 to 3600 m. No other species of *Proctoporus* is known to be sympatric with *P. bolivianus,* but *P. guentheri* occurs throughout all of the area inhabited by *P. bolivianus* at lower altitudes (825 to 2516 or perhaps 3362 m).

SPECIMENS EXAMINED. Bolivia: La Paz: Pelechuco (3567 m) NRS 3224 (holotype of *Proctoporus longicaudatus*).

Peru: Cuzco: Fort Sacsahuama (3600 m) FMNH 34096-100; Hacienda Urco, near Calca (2850 m) FMNH 34101 (22 specimens), 34119-22, 34137 (19), 34333-35; Cuzco (3362 m) FMNH 40427 (63), 40428, ZSM 174/1938; 20 mi S of Cuzco (3000 m) CAS 84753; Ñusta Hispana (2700 m) USNM 60699-700, 60748 (holotype of *Proctoporus obesus*); Ollantaytambo (2800 m) USNM 49549 (paratype of *Oreosaurus lacertus*), 60719, 60746, Sicuani (3515 m) AMNH 38823; Tinccochaca (2800 m) USNM 49551 (holotype of *Oreosaurus lacertus*), MCZ 12085, 12087 (paratypes of *O. lacertus*); Torontoy (2500 m) USNM 60726-27; Puno: Limbani (3200 m) BMNH 1901.8.2.28-29, 1904.10.26.91, 1907.5.7.1, FMNH 39360 (7), 40426 (11); Marcapata (3260 m) FMNH 83171-74.

Proctoporus guentheri (Boettger)

Oreosaurus guentheri Boettger, 1891, Zool. Anz., 14:345
Oreosaurus ocellifer Boulenger, 1902, Ann. Mag. Nat. Hist., Ser. 7, 10: 400. **New synonymy.**
Oreosaurus anomalus Barbour and Noble, 1921, Proc. U.S. Nat. Mus. 58: 614. **New synonymy.**

Oreosaurus guentheri was described from an adult male collected by Ernesto Guenther in the vicinity of Sorata, La Paz, Bolivia (Boettger, 1891). The elevation at this locality is about 2516 m. The holotype, formerly in the Lubeck Museum, was destroyed during World War II (G. von Studnitz, personal communication, 1960).

Many characteristics of the holotype of *P. guentheri* are listed in Table 9. These, together with the 9 rows of pregular and gular scales and the three posterior preanal scales identify it as belonging with the other specimens that I here refer to *P. guentheri*.

I have examined 30 specimens (14 males, 16 females) of this species, including two holotypes. The specimens come from central and southern Peru and northern and central Bolivia; they thus encompass all three type localities for proposed names for this species. Although geographic variation is apparent in the series examined (Table 8), the following features characterize the

TABLE 8. Variation in specimens of *Proctoporus guentheri*

	Dorsal scale rows	Scale rows around midbody	Transverse rows of ventrals	Total femoral pores	Subdigital lamellae 4th finger	Subdigital lamellae 4th toe	Hind leg / Snout-vent length
Perene Valley 9 ♂♂	29-33 (30.4)	30-40 (35.1)	17-18 (17.8)	14-16 (14.7)	7-9 (8.1)	13-15 (14.0)	.29-.37 (.320)
10 ♀♀	30-33 (31.2)	30-40 (34.4)	17-19 (18.2)	0-6 (1.8)	7-9 (8.4)	13-16 (14.4)	.26-.39[1] (.320)
Holotype of *O. anomalus* ♂	30	40	18	15	10-11 (10.5)	15-16 (15.5)	.33
"Juliaca" ♂	31	30	19	12	8 (8.0)	12[2]	.31
♀	31	32	19	4	7-8 (7.5)	13-14 (13.5)	.27
Cuzco ♂	33	37	20	19	9[2]	15-16 (15.5)	.32
Holotype of *O. ocellifer* ♂	29	30	19	15	—	—	.34
Santo Domingo ♂	32	33	18	12	7-8 (7.5)	13 (13.0)	.30
♀	32	35	19	9	8 (8.0)	12-14 (13.0)	.28
Holotype of *O. guentheri*[3] ♂	35	30	20	15	—	—	.37
Cochabamba 2 ♀♀	34-35 (34.5)	41-43 (42.0)	19-20 (19.5)	2-4 (3.0)	8-10 (9.0)	15-16 (15.3)	.34-.36 (.350)
Palmar 2 ♀♀	33-35 (34.0)	36-38 (37.0)	20 (20.0)	4-7 (5.5)	9-10 (9.5)	14-16 (14.7)	.32-.34 (.331)

[1] 9 females; [2] 1 digit; [3] data from Boettger (1891)

TABLE 9. Characteristics of three holotypes in the synonymy of *Proctoporus guentheri*

	Oreosaurus guentheri[1]	*Oreosaurus ocellifer*	*Oreosaurus anomalus*
Sex	♂	♂	♂
Snout-vent length	32	35	37
Supraoculars	3-3	3-3	3-3
Loreal	present[2]	absent	absent[3]
Median occipital	present	present	present
Pairs of chinshields in contact	3[4]	2[5]	2[5]
Rows of pregulars plus gulars	9	8	9
Scales around midbody region	30	30	40
Dorsal scale rows	35	29	30
Ventral scales	8 x 20	8 x 19	10 x 18
Total femoral pores	15	15	15
Ocelli	9-11	7-8	8-12
Light dorsolateral stripe	—	present	present
Belly pigmentation	uniform yellow	uniform yellow	uniform yellow

[1] data from Boettger (1891); [2] separated from supralabials; [3] partly indicated on left side; [4] I interpret the posteriormost pair as enlarged pregulars (Fig. 2); [5] followed by a pair of enlarged pregulars (Fig. 2)

species. There are usually 3-3 supraoculars and the first superciliary is usually not expanded onto the dorsal surface of the head; BMNH 1902.11.28.4, however, has 2-2 supraoculars and an expanded first superciliary. There is a large pair of pregulars (Fig. 2) filling the space behind the second pair of chinshields and between the third, except in ZSM 173/1938. The superciliary series is complete except for one side in ZSM 173/1938. All individuals have an undivided translucent disc in the lower eyelid. Only two individuals (AMNH 23209, ZSM 43/1950) lack a median occipital, but a third (ZSM 165/1954) has the median and left paramedian occipitals fused, and a fourth (also ZSM 43/1950) has two small scales in this area. Other characters that distinguish *P. guentheri* from Peruvian and Bolivian congeners (*P. pachyurus* and *P. bolivianus*) include the lower number of dorsal scales (29-35) and of transverse ventral scale rows (17-20). Specimens of *P. guentheri* have large, flat scales on the under side of the lower forelimb.

VARIATION. Data on the specimens examined are included in Table 8. In general, Bolivian specimens have more transverse rows of dorsal and ventral scales, more scale rows around the midbody region, more subdigital lamellae, and more longitudinal rows of ventral scales than Peruvian specimens.

The loreal is variably present in *Proctoporus guentheri.* It is absent in 18 of the specimens from the Perené valley; one female (FMNH 45475) has both a loreal and a frenoocular on both sides. On the left side in the holotype of *Oreosaurus anomalus,* a loreal is completely delimited from the frenoocular and partly delimited from the nasal by a short diagonal groove from the frenoocular. The specimens from "Juliaca", from Cuzco, from Santo Domingo, and the holotype of *O. ocellifer* have no loreal. The holotype of *O. guentheri* has both a loreal and a frenoocular on both sides. One of the specimens from Yungas del Palmar (ZSM 43/1950) has no loreal, but the other three females from Bolivia have the

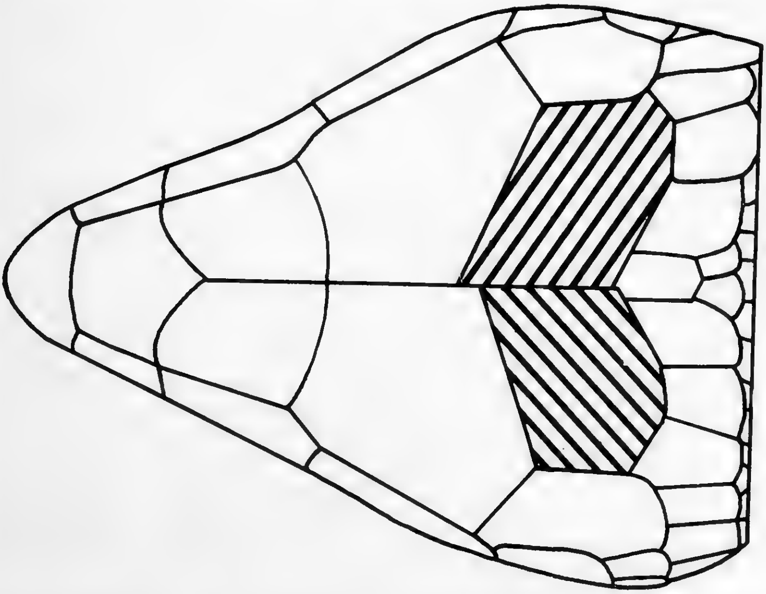


FIG. 2. Scales on the underside of the head of *Proctoporus guentheri* (AMNH 23223). The enlarged pregular scales are barred. × 10.

loreal partly marked just as in the holotype of *O. anomalus.* The frequency of partly delimited loreals in Bolivian specimens makes the occasional occurrence of a completely delimited loreal, as in the holotype of *O. guentheri,* seem rather likely to occur.

In general, the specimens of *P. guentheri* have two rows of small pregular scales, at least at the middle of the throat. They have 6-9, (mean 6.9) rows of gular scales before the collar.

COLORATION. In males from the Río Perené area, the belly is yellow cream, with a few dark brown flecks on the extreme posterior part. The throat and chin are the same, with numerous minute brown flecks. The tail is moderately flecked below with dark brown on yellow cream; the flecking is lighter along the lateral seams, forming light lines. The dorsum has a yellow cream ground color, very heavily flecked with brown, giving a warm brown appearance. In some specimens, the flecking tends to form a linear series of dots, but the pattern is not lined mid-dorsally. The dorsolateral flecking is arranged to form light, dark-bordered lines that are well developed only on the shoulder and above the hindlimb insertions. Below this light line there is a series of ocelli, the dark border of which is as wide as a dorsal scale length, the white spot of which has a diameter about three fourths a dorsal scale width. This series has one ocellus anterior to the forelimb insertion, usually one just above the forelimb insertion, numbers about 8-11 per side, and may extend as many as two behind the hindlimb insertion. A light line on the tail extends posteriorly from the level of the hindlimb insertion. Below this there is a dark line, and below this, the flecking of the underside of the tail.

The light dorsolateral line extends onto the head to the posterior end of the superciliary series. Usually there is a dark line below the canthus rostralis; occasionally there is a faint suggestion of a light line on the canthus. The lips are flecked with light areas, occasionally with a suggestion of a light line from the posterior corner of the eye to the rictus oris.

Females from the Río Perené are similar, but have poorly defined ocelli.

The young are like the females, but the pattern on the dorsum and sides is more nearly linear, with light dorsolateral and paravertebral lines, a dark median line, and dark borders to the dorsolateral light lines. There is a row of light dots between the legs just above ventral scales.

Specimens of *P. guentheri* from Bolivia resemble northern ones, but generally the dorsal and lateral surfaces are darker brown. The single female with well-developed ocelli (ZSM 43/1950) is from Bolivia.

LENGTH. The largest male examined is 40 mm snout to vent; the largest female 47 mm. Three small females (snout-vent lengths 22-25 mm) have tail over snout-vent length ratios of 1.7; two larger females (35 and 37 mm snout to vent) have ratios of 1.7 and 2.0 respectively. A small male (22 mm snout to vent) has a tail over snout-vent length ratio of 1.8; two larger males (35 and 40 mm snout to vent) have ratios of 1.8 and 1.9, respectively.

SEXUAL DIMORPHISM. The conspicuously dimorphic features are the number of posterior preanal scales, the number of femoral pores (Table 8) and the development of lateral ocelli. ZSM 43/1950, an adult female 47 mm snout to vent, has seven well-developed ocelli along each side, but this is very unusual. The number of femoral pores in males varies from 12 to 19; in females, from 0 to 9. BMNH 1902.11.28.5 has three medial pores and one distal one on the right side, four medial pores and one distal one on the left. If the intervening scales on each side also had pores, this female would have a total of about 17 pores.

Thirteen Peruvian males have the following counts of posterior preanal scales: 2: eight individuals; 3: four; 5: one (ZSM 173/1938). The holotype of *P. guentheri,* the only Bolivian male for which I have data, had three posterior preanals. Ten Peruvian females have counts of three four times; one of these has only a narrow posterior median wedge; two additional females have three plus a lateral sliver on each side. Five occurs three times, and another female has five with the median scale semidivided by a groove at the posterior end. All four Bolivian females have five posterior preanals.

REMARKS. Although all of the synonyms of *P. guentheri* were described in the genus *Oreosaurus,* the species has a narrow groove of granular scales along the side of the body (Uzzell, 1958, Fig. 1-C) and thus does not belong to the *Proctoporus luctuosus* group which includes the type species of *Oreosaurus.*

Characteristics of three holotypes in the synonymy of *P. guentheri* are given in Table 9.

I have examined the holotype of *Oreosaurus ocellifer* Boulenger (BMNH 1902.5.29.183, reregistered as 1946.8.31.22). It is an adult male collected by G. Okenden in the valley of the Río Marcapata, Cuzco, of southeastern Peru (Boulenger, 1902). This locality is about 300 km northwest of the type locality of *P. guentheri*. The slight differences between the holotypes of *Oreosaurus ocellifer* and *O. guentheri* are largely those expected on the basis of the geographic variation in this species. The holotype has the enlarged pregulars that occur in most *P. guentheri* (Boulenger called them chinshields). I therefore consider *P. ocellifer* a junior synonym of *P. guentheri* (new synonymy).

The holotype of *Oreosaurus anomalus,* USNM 60704, was collected by Edmund Heller near San Fernando in the valley of the Río San Miguel, Cuzco, Peru (Barbour and Noble, 1921). The elevation here is about 1900 m. I have examined the holotype; the only way in which it differs from other individuals of *P. guentheri* is in the presence of very regular supranasal scales. It is conceivable that supranasal scales characterize a population of *Proctoporus* in the Urubamba valley, but much more likely this individual is anomalous, as the name suggests. Certainly it is conspecific with *P. guentheri*. I therefore consider the name *P. anomalus* a junior synonym of *P. guentheri* (new synonymy).

Although *P. bolivianus* Werner (1910) was placed in the synonymy of *P. guentheri* by Burt and Burt (1931), I believe that *P. bolivianus* is a different species (see discussion of *P. bolivianus*).

The specimens (AMNH 1703, 7414) supposedly from about 4500 m above sea level near Lake Aracona, Juliaca, Peru, resemble the specimens from Peru more than the specimens from Bolivia. Lake Aracona is vastly higher than other localities for *P. guentheri*. The American Museum material supposedly from this region collected by H. H. Keays seem to include several specimens with erroneous localities. Dunn (1942) reported that Harvey Bassler suggested that American Museum material labeled Juliaca was sent from there by a member of the Inca Mining Company (apparently Keays), but was probably collected near the mine at Santo Domingo, at about 1200 m above sea level.

The specimen from Cuzco (ZSM 173/1938) is from a higher altitude than others of this species (3362 m). I believe that this elevation is above the actual range of the species. The specimen has several unusual features (absence of enlarged pregular scales [Fig. 2], high number of femoral pores, and relatively massive head) that suggest local differentiation in this area. These unusual features do not occur in the holotype of *Oreosaurus anomalus,* geographically the closest specimen.

BIOLOGY. Little is known about the biology of this species. Three females have each contained a single leathery egg; the dimensions are such (4.5 x 7 mm, more or less) that I doubt that more than a single egg enlarges at one time. A similar interpretation has been made for *Ecpleopus gaudichaudi* (Uzzell, 1969b). Most members of Group II of the Teiidae lay two eggs (Uzzell, 1959, 1965, 1966, 1969a; Fouquette, 1968).

RANGE. Localities for specimens of *Proctoporus guentheri* examined are in central and southern Peru and central Bolivia on the eastern slopes of the Andes; elevations associated with specimens that I have examined, except for the doubtful pair from Juliaca, vary from 1000 to perhaps 3362 m above sea level. In the northern part of its range, *P. guentheri* occurs in the same drainage as *P. pachyurus,* but apparently at lower altitudes. In the central and southern part of its range, it occurs in the same drainages as *P. bolivianus,* but again at lower altitudes.

Charles F. Walker (personal communication) has examined a specimen of *P. guentheri* (NRS 3225) from Linguapata, (Carabaya), Puno, Peru, at 825 m above sea level.

SPECIMENS EXAMINED. Bolivia: Cochabamba (2516 m): ZSM 165/1954 (2 specimens); Yungas del Palmar: ZSM 43/1950 (2).

Peru: Cuzco: (3362 m): ZSM 173/1938; Marcapata Valley: BMNH 1902.5.29.183, reregistered as 1946.8.31.22 (holotype of *Oreosaurus ocellifer*); San Fernando, Río San Miguel (1900 m): USNM 60704 (holotype of *Oreosaurus anomalus*); Junín (Tarma): Chanchamayo (1000-1500 m): AMNH 23161; FMNH 45475; La Merced (1000-1500 m): AMNH 23203, -05, -07, -10, -13, -18-23, -28; MCZ 49578-9; UMMZ 121443-44; ZSM 290/1929 Puno (Carabaya): Santo Domingo (1862 m): BMNH 1902.11.28.4-5; Juliaca, Lake Aracona (= Lago de Aricoma): AMNH 1703, 7414.

THE HEMIPENIS OF SPECIES OF THE PROCTOPORUS PACHYURUS GROUP

Hemipenes were removed from one individual of each species of the *Proctoporus pachyurus* group. They were prepared for examination by slitting them along the sulcus spermaticus, washing them over night in distilled water, staining them in a dilute solution of alizarin red S in 0.5 percent KOH, and destaining them in distilled water.

The hemipenis of *P. pachyurus* (SMF 65285, left organ; Fig. 3) is unusual in several features. It differs from the hemipenes of the other two species of the *P. pachyurus* group in lacking spines on the basal part of the median welt (Fig. 3A), and in having the spinous areas of the flounces much reduced (Fig. 3B). In the lateral pocket, there are seven lateral flounces with spines, and six with spines on the median welt; in the medial pocket, seven lateral and seven medial flounces have spines. The spines in any flounce with spines are largest near the center of the row, and decrease in size toward either end of the spine row. There is considerable variation in the length of the spiny row in each flounce. The flounces in each pocket are chevron shaped, and continuous across the apices of the chevron, which is basal and dorsal to the free edge of the median welt. The distal end of the hemipenis is arranged so that when everted, there would be two lobes. The lobes bear a series of fleshy folds.

The hemipenis of *P. bolivianus* (FMNH 81372, left organ; Fig. 4) differs from that of *P. pachyurus* in having nearly completely spinous flounces. As in *P. pachyurus,* the flounces are chevron-shaped, with the apices of the chevrons basal and dorsal to the free edge of the median welt. In the lateral pocket, there are 14 flounces on the lateral wall, 11 on the medial wall; in the medial pocket, there are 11 on the medial wall, 14 on the lateral, so that the two pockets form mirror images of each other. The extra flounces on the lateral walls appear to continue across the basal part of the median welt as four rows of very irregular spines (the basalmost row has but a single tooth, Fig. 4C). Although the flounces are continuous across the apices of the chevrons, there is a small gap separating the tooth rows (Fig. 4B). As in *P. pachyurus,* the hemipenis is bilobate distally when everted, and each lobe bears a series of fleshy folds.

The hemipenis of *P. guentheri* (ZSM 290/1929, left organ;

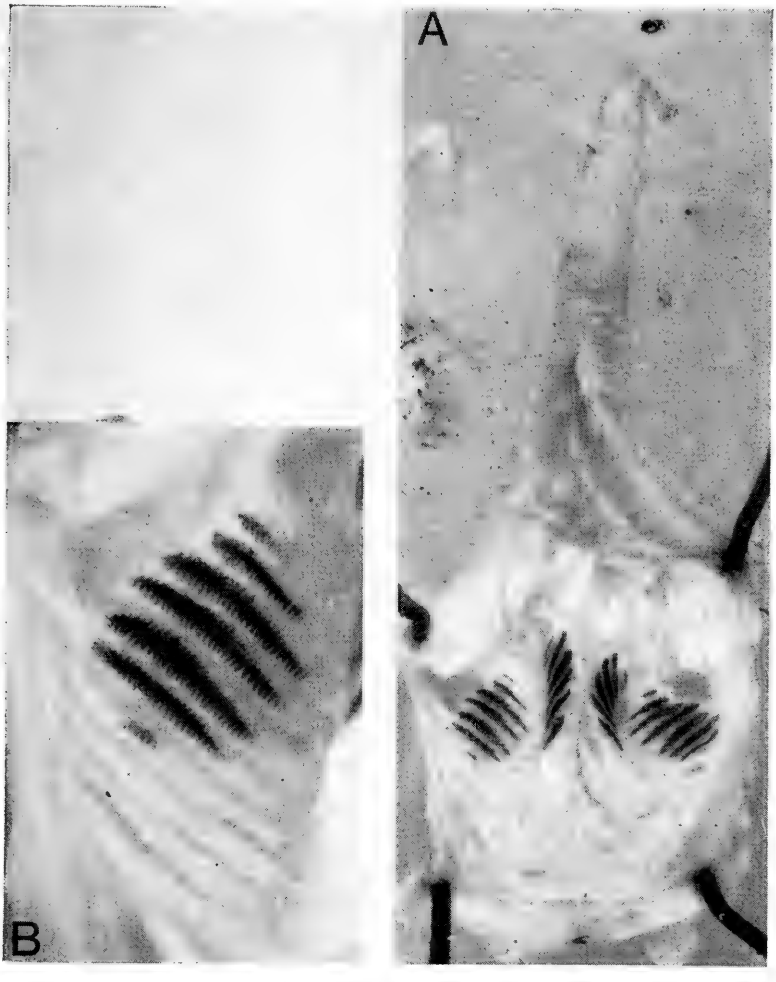


FIG. 3. Structure of the left hemipenis of *Proctoporus pachyurus* (SMF 65285). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ showing general arrangement of flounces in the lateral (left) and medial (right) pockets. There are no enlarged teeth. × 14. B) Details of teeth in lateral wall of lateral pocket; additional flounces without teeth are also shown. × 42.

Fig. 5) is rather similar to that of *P. bolivianus*. There are 19 lateral and 14 medial flounces in the lateral pocket, 14 medial and 19 lateral flounces in the medial pocket. The arrangement of flounces thus is a mirror image in the two pockets. One distal

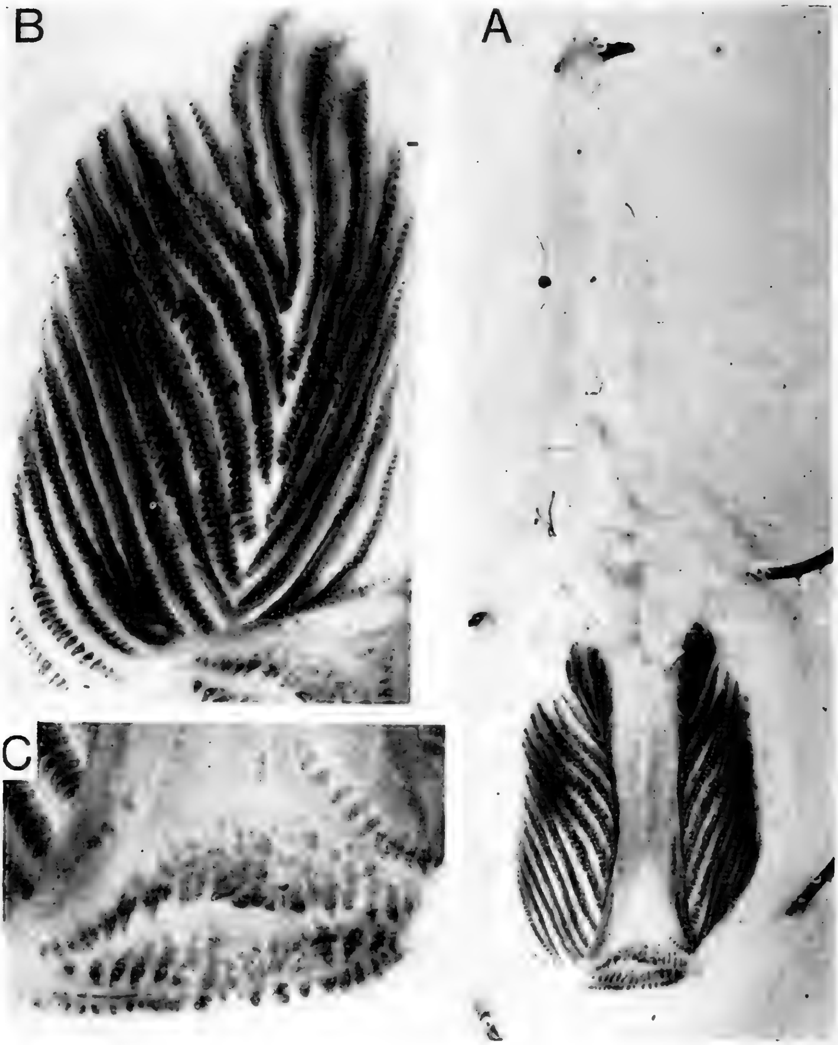


FIG. 4. Structure of the left hemipenis of *Proctoporus bolivianus* (FMNH 81372). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ, showing general arrangement of flounces into lateral (left) and medial (right) pockets, and location of teeth at base of median welt. × 10. B) Details of flounces and teeth in lateral pocket. The median welt has been folded back to show the apices of the chevron-shaped flounces. × 16 C) Details of the irregular teeth at the base of the median welt. × 26.

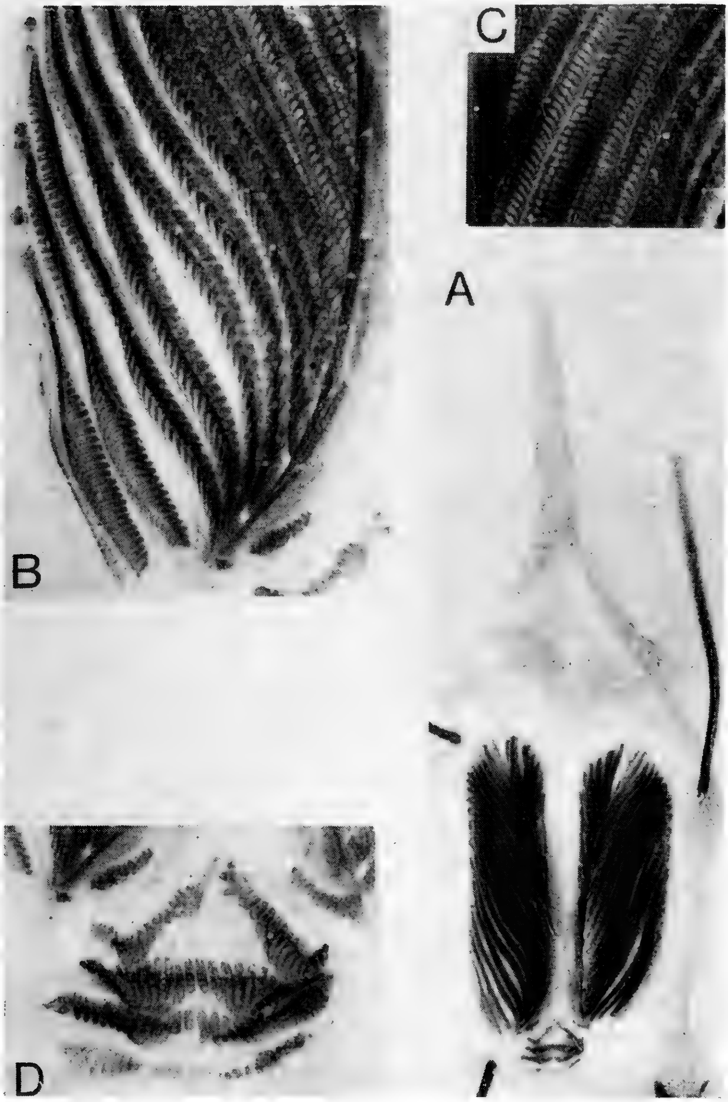


FIG. 5. Structure of the left hemipenis of *Proctoporus guentheri* (ZSM 290/1929). The inverted organ has been slit along the sulcus spermaticus. A) The entire organ, showing general arrangement of flounces in the lateral (left) and medial (right) pockets, and the teeth at the base of the median welt. × 9. B) Details of teeth in the basal part of the lateral pocket. × 30.C) Details of teeth in the middle part of the medial pocket. × 30. D) Details of teeth at the base of the median welt. × 30.

flounce and four basal flounces from the lateral wall of each pocket do not continue onto the medial wall, but the remaining 14 form chevrons, the apices basal and dorsal to the free edge of the median welt. There are four rows of teeth across the basal part of the median welt (Fig. 5D); the distalmost of these could be considered an additional median flounce of each pocket. The teeth in the flounces appear to be rather uniform in size along the flounces, although at the extreme ends of the flounces, they become reduced in size (Fig. 5B, C). The everted organ is bilobate and bears fleshy folds at the distal end of each lobe.

It is not known to what extent the differences between the arrangements of spines reflect interspecies differences and to what extent they reflect individual variation.

Relationships within the Proctoporus pachyurus Group

The distributions suggest that *P. pachyurus* and *P. bolivianus,* which are allopatric and which both occur at higher altitudes than *P. guentheri,* are more closely related to each other than either is to *P. guentheri.* The morphological data generally support this relationship. Thus, *P. pachyurus* and *P. bolivianus* share large body size (some populations of *P. bolivianus* are small), a high number of transverse rows of ventral scales, and a high number of longitudinal rows of ventral scales. The scales under the lower forelimb are large and flat in *P. guentheri;* they are relatively smaller in *P. pachyurus* and *P. bolivianus.* The enlarged pregular scales that are present in most specimens of *P. guentheri* examined are absent in *P. pachyurus* and *P. bolivianus.* Populations of *P. guentheri* are uniformly clear yellow below, and have conspicuous ocelli, at least in males; both *P. pachyurus* and *P. bolivianus* have at least some dark pigment superimposed on the ventral ground color; ocelli, when present, are not conspicuous. Externally, the relationship of *P. bolivianus* to *P. pachyurus* is so close that it seems necessary to point out again that the two species can be distinguished by the number of dorsal scale rows. On the other hand, the structure of the hemipenis marks *P. pachyurus* off as a quite distinct species, although individual variation in the structure of the hemipenis has not been studied.

PROCTOPORUS PETERSI (BOETTGER)

Ecpleopus (Oreosaurus) petersi Boettger, 1878, Ber. Offen. Ver. f. Natur. 17-18:9.

I consider *Proctoporus petersi* a junior synonym of *P. unicolor* (Gray).

Proctoporus petersi was described (Boettger, 1878) from an adult male (SMF 11763) that the Senckenberg Museum obtained in 1849 as an exchange from the museum in Milano. The type locality given by Boettger—Province of Pará in northern Brazil—has long been considered doubtful (Burt and Burt, 1933).

Recently I examined this specimen in the Senckenberg Museum. Although I have comparatively little to add to the description given by Boettger, the following five points are, I believe, critical for correct placement of this name. There are 3-3 supraoculars, of which the middle on each side is in contact with the palpebrals. There are 8-8 lamellae under the fourth fingers, 12-13 under the fourth toes. The transparent disc in the lower eyelid is divided into 3-4 pieces by vertical grooves. The innermost femoral pores, contrary to Boettger's figure, are preanal, and are separated by two rather than four small scales. The pregulars immediately behind the paired chinshields are elongate, rather than squarish or wider than long. This set of characters readily distinguishes the holotype of *Proctoporus petersi* from *Proctoporus bolivianus,* the form to which the name is usually applied. Each of these characters, on the other hand, occurs as a regular feature of *Proctoporus unicolor* (Gray), from the higher altitudes of Ecuador. I therefore place *Proctoporus petersi* in the synonymy of *P. unicolor* (new synonymy), although the name is perhaps available should local geographic variation in *P. unicolor* warrant recognition of subspecies.

The history of the application of this name seems easily explained. Neither Boettger nor Wilhelm Peters, to whom Boettger showed the holotype, knew *Proctoporus unicolor* except from Gray's original description. Boulenger (1885), in his catalog of the lizards in the British Museum, left the species *petersi* in the genus *Oreosaurus;* it is readily distinguished from the other lizards that Boulenger placed there. Finally, the two characters figured by Boettger that might have insured its correct placement (the arrangement of the femoral pores and of the superciliary series) are both incorrect in Boettger's drawing. Although Boettger provided a great deal of information on the holotype of *P. petersi,* none of the counts of scales (dorsals, ventrals, scales around midbody region) and, in fact, almost no feature mentioned by Boettger, will distinguish *P. unicolor* from *P. bolivianus,* although I believe that they represent distinct genera.

PROCTOPORUS VENTRIMACULATUS BOULENGER

Proctoporus ventrimaculatus Boulenger, 1900, Ann. Mag. Nat. Hist. Ser. 7, 6:185.

The holotype of *Proctoporus ventrimaculatus* (BMNH 1900.3.30. 17, reregistered as 1946.8.2.34) was collected by P. O. Simons near Cajamarca (Cajamarca), Peru, about 2700 m above sea level (Boulenger, 1900). I have examined the holotype and another specimen (MCZ 18807) that I consider to be *P. ventrimaculatus.* The second specimen comes from Huambos (or Huamboo), Cajamarca (Chota), Peru, some 100 km to the NNW of the type locality (map), and about 2200 m above sea level. Both specimens are females. Certain of their characters are compared in Table 10.

The arrangement of the pregular scales of *P. ventrimaculatus* in three transverse rows of rectangular scales gives the throat considerable similarity to that of *P. pachyurus* or *P. striatus.* On the other hand, the arrangement of the dorsal head scales is quite distinctive. Above the eye, there are three large scales. The posteriormost is separated from the palpebral scales by one elongate posterior superciliary. I consider the anteriormost to be an enlarged superciliary, although Boulenger (1900) considered it to be a supraocular. If it is a supraocular, it is not separated from the palpebral scales by a superciliary. The middle scale I consider to be the first of two supraoculars. Boulenger considered it to be the second of three supraoculars. Regardless, it is not separated from the palpebral scales by superciliary scales. These three scales are illustrated in Fig. 6.

The loreal of MCZ 18807 is a small scale separated from the supralabials by contact between the very large nasal and the rather small frenoocular. The holotype has no loreal. Under the posterior corner of the eye in MCZ 18807, there is a large infralabial

TABLE 10. Characteristics of two specimens of *Proctoporus ventrimaculatus*

	Snout-vent length (mm)	Femoral pores	Dorsal scale rows	Scales around midbody region	Rows of ventrals		Median occipital	Loreal	Subdigital lamellae	
					longitudinal	transverse			4th finger	4th toe
BMNH 1900.3.30.17	34	3-3	32	33	22	10	P	A	9-9	14-15
MCZ 18807	35	2-2	33	34	21	12	A	P	8-8	12-13

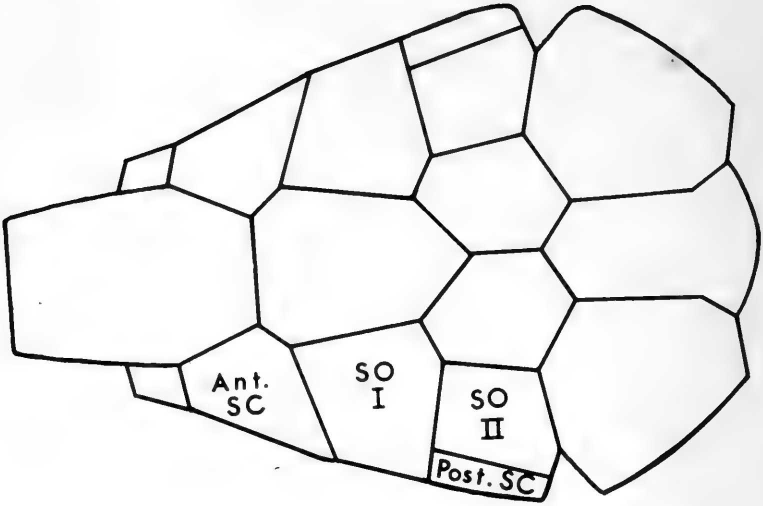


FIG. 6. Scales on the top of the head of *Proctoporus ventrimaculatus* (MCZ 18807). Ant. SC - anterior superciliary; Post. SC - posterior superciliary; So I and SO II - first and second supraoculars. × 13.

that reaches the lip line in a point between the third and the very small fourth labials. This scale is not enlarged in the holotype.

The ventral and lateral scales of *P. ventrimaculatus* meet in a narrow granular zone with little or no intercalation of the dorsal and ventral rows; the arrangement is thus like that in *P. striatus* and that figured for *P. guentheri* (Uzzell, 1958: Fig. 1-C). The preanal scales number five in the posterior row in the holotype, six in MCZ 18807. The innermost pores are femoral, not preanal.

The tibial scales are smooth. The scales above and beneath the forearm are smooth rather than striate; those below the forearm are relatively small. There is no enlarged scale on the upper surface of the upper arm. The limbs are relatively short, not overlapping when adpressed; the hind limb is about 29 percent of the snout-vent length. The thenar scales of the palm and the inner scales of the basal pairs of subdigital lamellae on the fourth toes are not conspicuously enlarged.

The eye disc is clear and divided into three parts. The anterior and posterior parts are smaller in the holotype than in MCZ 18807.

The two specimens differ somewhat in coloration. The holotype is rather uniform dark above. The ventral scales have large black spots on a light background. MCZ 18807 is also generally dark above and below, but with light, dark-bordered dorsolateral lines from the posterior corner of the eye to the tip of the tail. There is a suggestion of a dark mid-dorsal line at the shoulders. The venter is very dark, the scales having only light posterior margins.

Nothing is known about geographical variation or sexual dimorphism in this species.

REMARKS. The arrangement of the pregular scales into transverse rows of quadrangular scales suggests that *P. ventrimaculatus* is related to *P. striatus* and members of the *P. pachyurus* group. The arrangement of supraoculars is very distinctive, however, and I am uncertain that *P. ventrimaculatus* is closely related to *P. striatus* or *P. pachyurus,* although I see no other obvious relatives for the species. Both *Proctoporus unicolor* and its relatives and *Proctoporus columbianus* and its relatives regularly have the superciliary series incomplete and one or more supraoculars touching the palpebral scales. Both of these groups, however, have the pregular scales arranged in chevrons, the apices forward. A whole series of other characters also distinguishes *P. unicolor* and its relatives from *P. ventrimaculatus.*

Much of the detail included for this species is to distinguish *P. ventrimaculatus* from AMNH 18310, a specimen related, I believe (Uzzell, 1958) to *Proctoporus striatus.*

Nothing is known of the biology of *P. ventrimaculatus.*

No other species of *Proctoporus* are known from northern Peru. Huambos is on the divide between Marañón and Pacific drainages; Cajamarca is in the headwater drainage of the Río Cajamarca, which flows into the Río Marañón (map).

ABBREVIATIONS

AMNH	—	American Museum of Natural History, New York
BMNH	—	British Museum (Natural History), London
CAS	—	California Academy of Sciences, San Francisco
CM	—	Carnegie Museum, Pittsburgh
FMNH	—	Field Museum of Natural History, Chicago
MCZ	—	Museum of Comparative Zoology, Harvard University
MN	—	Musée d'Histoire Naturelle, Neuchâtel
NRS	—	Naturhistoriska Riksmuseet, Stockholm

SMF — Senckenberg Museum, Frankfurt
USNM — United States National Museum, Washington
UMMZ — University of Michigan Museum of Zoology
ZSM — Zoologische Staatssammlung, Munich

ACKNOWLEDGMENTS

Many people have helped me in this project by providing me with access to specimens in collections in their charge, and often by hospitality while I visited their institutions. For their kindness I thank Charles Bogert and Richard Zweifel, The American Museum of Natural History, Alice G. C. Grandison, British Museum (Natural History), Alan Leviton, California Academy of Sciences, C. J. McCoy, Carnegie Museum, Robert Inger and Hymen Marx, Field Museum of Natural History, Ernest Williams, Museum of Comparative Zoology, Harvard University, Fritz Gehringer, Musée d'Histoire Naturelle, Neuchâtel, Konrad Klemmer and Robert Mertens, Senckenberg Museum, Frankfurt, James A. Peters, United States National Museum, Charles F. Walker, University of Michigan Museum of Zoology, and Heinz Wermuth and Dieter Fuchs, Zoologische Staatssammlung, Munich. Greta Casteegley, Naturhistoriska Riksmuseet, Stockholm kindly sent the holotype of *Proctoporus longicaudatus* for me to examine. Travel in Europe was supported by the Peabody Museum, Yale University and by a gift from Evan Commager. The illustrations were prepared by Diane McClure, Alfonso Coleman, and Rosanne Rowen.

LITERATURE CITED

Andersson, Lars Gabriel. 1914. A new *Telmatobius* and new teiidoid lizards from South America. Arkiv f. Zoologi 9 (3): 1-12.

Barbour, Thomas, and G. K. Noble. 1921. Amphibians and reptiles from southern Peru collected by the Peruvian Expedition of 1914-1915 under the auspices of Yale University and the National Geographic Society. Proc. U.S. Nat. Mus. 58 (2352): 609-620.

Bingham, Hiram. 1913. In the wonderland of Peru. The work accomplished by the Peruvian Expedition of 1912, under the auspices of Yale University and the National Geographic Society. Nat. Geog. Mag. 24 (4): 387-573.

————. 1916. Further explorations in the land of the Incas. The Peruvian Expedition of 1915 of the National Geographic Society and Yale University. Nat. Geog. Mag. 29 (5): 431-473.

Boettger, Oskar. 1878. Studien Über neue oder wenig bekannte Eidechsen I. Ber. Offen. Ver. f. Natur. 17-18: 1-12.

——— 1891. Reptilien und Batrachier aus Bolivia. Zool. Anz. 14: 343-347.

Boulenger, George Albert. 1885. Catalogue of the lizards in the British Museum (Natural History) II. 24 pls. Taylor and Francis, London. 497 p.

——— 1900. Descriptions of new batrachians and reptiles collected by Mr. P. O. Simons in Peru. Ann. Mag. Nat. Hist., Ser. 7, 6: 181-186.

——— 1902. Descriptions of new batrachians and reptiles from the Andes if Peru and Bolivia. Ann. Mag. Nat. Hist., Ser. 7, 10: 394-402.

Burt, Charles E., and May Danheim Burt. 1931. South American lizards in the collection of The American Museum of Natural History. Bull. Amer. Mus. Nat. Hist. 61 (7): 227-395.

——— 1933. A preliminary check list of the lizards of South America. Trans. Acad. Sci. St. Louis. 28 (1 & 2): 1-104.

Dunn, Emmett Reid. 1942. The American caecilians. Bull. Mus. Zool. Harvard Univ. 91 (6): 439-540.

Fouquette, M. J., Jr. 1968. Observations on the natural history of microteiid lizards from the Venezuelan Andes. Copeia 1968 (4): 881-884.

Griffin, Lawrence Edmonds. 1917. A list of the South American lizards of the Carnegie Museum, with descriptions of four new species. Ann. Carnegie Mus. 11 (1 & 2): 304-320.

Peters, Wilhelm. 1862. Über *Cercosaura* und die mit dieser Gattung verwandten Eidechsen aus Südamerica. Abh. Akad. Wiss. Berlin, 1862: 165-225, pls. 1-3.

Ruibal, Rodolfo. 1952. Revisionary studies of some South American Teiidae. Bull. Mus. Comp. Zool. Harvard Coll. 106 (11): 477-529.

Stejneger, Leonhard. 1913. Results of the Yale Peruvian expedition of 1911. Batrachians and reptiles. Proc. U. S. Nat. Mus: 45 (1992): 541-547.

Tschudi, J. J. von. 1845. Reptilium conspectus quae in Republica Peruana reperiunter et pleraque observata vel collecta sunt in itinere a Dr. J. J. de Tschudi. Archiv für Naturgeschichte 11 (1): 150-170.

Uzzell, Thomas. 1958. Teiid lizards related to *Proctoporus luctuosus,* with the description of a new species from Venezuela. Occ. Pap. Mus. Zool., Univ. Michigan 597: 1-15.

——— 1959. Teiid lizards of the genus *Placosoma.* Occ. Pap. Mus. Zool., Univ. Michigan 606: 1-16.

——— 1965. Teiid lizards of the genus *Echinosaura.* Copeia 1965 (1): 82-89.

——— 1966. Teiid lizards of the genus *Neusticurus* (Reptilia, Sauria). Bull. Amer. Mus. Nat. Hist. 132 (5): 277-328:

——— 1969a. A new genus and species of teiid lizard from Bolivia. Postilla 129: 1-15.

——— 1969b. The status of the genera *Ecpleopus, Arthroseps,* and *Aspidolaemus* (Sauria, Teiidae). Postilla 135:1-23.

Werner, Franz. 1910. Über neue oder seltene Reptilien des Naturhistorischen Museums in Hamburg. II. Eidechsen. Mitt. Naturhist. Mus. Hamburg 27: 1-46.

INFORMATION FOR AUTHORS

REVIEW	The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
STYLE	Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).
FORM	Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.
TITLE	Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
ABSTRACT	The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
OMENCLATURE	Follow the International Codes of Zoological and Botanical Nomenclature.
LLUSTRATIONS	Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
FOOTNOTES	Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
TABLES	Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
REFERENCES	The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
HOR'S COPIES	Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
PROOF	Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
COPYRIGHT	Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 143. 10 MARCH 1970

SHARPNESS OF TEETH IN MAN AND OTHER PRIMATES

R. G. EVERY

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Jeanne E. Remington and Nancy A. Ahlstrom

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

SHARPNESS OF TEETH IN MAN AND OTHER PRIMATES

R. G. EVERY

Centre for the Study of Conflict, 25 Clifton Terrace, Sumner, Christchurch 8, New Zealand, and Dept. of Zoology, University of Canterbury, Christchurch 1, N.Z.

(Received June 1968)

Abstract

Analyses of wear characteristics on the teeth of a young adult male baboon, a male native human from New Guinea and a male Caucasian from New Zealand are made, and their inseparable relationship to behavior emphasized. These characteristics provide evidence of the evolution of precise anatomical and innate behavioral tooth-grinding mechanisms specific to the production of sharp teeth. Although the teeth on eruption have some degree of morphological sharpness, the tooth-grinding behavior perfects this sharpness and subsequently maintains it throughout the functional life of the teeth. The male baboon, used here as broadly representative of man's non-hominid relatives and ancestors, has a specialized, sickle-like, vertically oriented upper canine, sharpened specifically as a slashing weapon. The lower anterior premolars are the honing tools which grind against the upper canines in a motion opposite to that of the masticatory stroke. These premolars are noticeably specialized for this tooth-to-tooth grinding action by their enlarged buccal crown-faces, thickened enamel gingival extensions, and by paired roots placed perpendicular to the "whetstone" faces.

In contrast, man's short-canine condition has evolved to provide a specialized, horizontally sharp shearing device. The continuous rows of even, constantly sharpened teeth, vertically oriented and firmly anchored in jaws which provide greater force at the biting teeth, give man the capacity for powerful, lethal,

POSTILLA 143: 30 p. 10 MARCH 1970.

"segmentive" biting. Thus man's dentition is seen not as "generalized", and certainly not as "regressed" or "weakened", but as highly specialized. The significance of the short-canine condition (currently regarded as a diagnostic feature of hominids) is not that man has become biologically defenseless, but that the hominid dental mechanism has harnessed attritional wear to provide a more stable and durably functional weapon.

It is concluded that tooth-sharpening and related phenomena are evidence of innate behavior related to a specialized, viable, biological weapon in *Homo sapiens,* and because this weapon — the teeth — is the primary one and has been overlooked it emphasizes a corollary: intraspecies use of the teeth is strictly controlled by genetical determinants, whereas such control of the secondary weapon — the hand — is slight.

INTRODUCTION

The prime evolutionary advantage of mammalian and especially primate teeth — their sharpness — has previously received little discussion in the literature. The special morphology of these teeth, and the fact that they are composed of enamel and dentine (the hardest and most durable of biological substances) gives them the capacity to penetrate and divide exogenous materials. Because the initial morphological sharpness of unworn teeth is so advantageous, mechanisms to perfect and maintain this sharpness through progressive wear are further advantageous and have evolved as important characteristics of mammals (with very few specialized exceptions, e.g., the toothless anteater and baleen whale).

The fossil record suggests that in the evolution of the hominid dental system leading up to *Homo sapiens* there was a period of rapid transition in such mechanisms. Apparently with a few million years, at the most, there was a switch from the pongid condition of vertically sharp upper canines to the condition seen in recent hominids of horizontally sharp teeth. As continuous rows of short, even teeth assumed the role of weapons, the weapon-like action of the dentition changed from slash to bite. Moreover, the process of precise attrition-sharpening, (*thegosis*, see below) was extended to include all upper and lower incisors and canines. This was a considerable addition to the premolar-plus-molar, horizontal shearing blades which emerging hominids already possessed. Incision, furthermore, was profoundly improved by the significant addition of a unique feature — antero-posterior (retrusive) shearing; it was no longer a simple vertical (orthal) action in the canine-incisor region, such as that seen in the non-hominid anthropoids today.

In previous reports that introduced my tooth-sharpening hypothesis (Every, 1960, 1965), figures were not presented. In the present paper, figures are included and the major arguments of the hypothesis are discussed; special attention is given to considerations of dynamic spatial relationships among dental structures. Furthermore, it is emphasized that these anatomical considerations can be understood only in the light of corresponding ethological considerations, of which they are an integral part. Tooth-sharpening and related phenomena give a new dimension to the study of mammals (particularly). Out of the immense amount of detail already emerging, this paper concentrates on that related to *Homo sapiens,* his hominid ancestors and anthropoid relatives.

FUNCTIONAL ANATOMICAL CONSIDERATIONS

NON-HOMINID ANTHROPOIDEA

The baboon (*Papio*) shows an extreme specialization for vertical sharpness of the canine and is therefore chosen to illustrate functional anatomical adaptations in cercopithecoids (Figs. 1-3).

Important features of the baboon upper canine are as follows (Fig. 1):

1. Facet striated by wear from *attrition*[1] (the discrete wear from the forceful grinding of the surface of one tooth against that of its opposite, i.e., tooth-to-tooth contact wear). See also Figure 4 and discussion.

2. The absence of wear from *abrasion* (the diffuse wear from friction of exogenous material). Compare with Figure 4.

3. The thin enamel coating on the palatal surface (indistinctly shown on the mesial side of the facet, and on the less extensively worn gingival third of the crown).

4. The relatively thick enamel coating on the labial surface (indistinctly shown by the strip of enamel which forms the distal edge — the cutting edge — of the crown).

---

[1] The basic material of this paper was first prepared as the legend and discussion of five illustrations (here figured 1-5) and submitted for publication in 1964 along with the article "The teeth as weapons; their influence on behaviour" (Every, 1965). At that time I used "attrition" and "abrasion", terms I had differentiated and given specific meaning (Every, 1960). Hitherto in the literature these terms were used synonymously. Since then, however, I have used a new term, *thegosis* (from the Greek, *thego,* to whet, sharpen). My argument for the use of *thegosis* as more appropriate to an evolutionary adaptive phenomenon, and taking precedence over *bruxism* (a term poisoned by a current definition of mal-adaption, pathology and myth) is developed in another paper, in preparation. Since numbers of scientists are already familiar with my term *thegosis* I shall, therefore, use it in the remainder of this paper.

5. The concavity of the vertical cutting (distal) edge; it tends to a sickle-like formation. The distal edge is also concave when viewed directly from behind. This is because the palatal surface itself is distinctly concave, and this extends the length of the crown. The reflected light in this unretouched photograph, therefore, comes from the apical part of the facet only.

6. The continuity of the concavity of the thegosis-facet. This extends vertically from the gingival border of the facet to the apex of the crown. There is no rounding-over (convexity) at the apex. The tooth is thus ground to a sharp spike.

7. The continuity of the thegosis-facet in the mesiodistal (horizontal) aspect. There is no rounding-over at the distal edge of the crown, the blade of which is thus ground to a fine edge.

An examination of the origin of the attrition-facet of the upper canine reveals specializations characteristic of non-hominid catarrhines; these facets are adapted for producing and maintaining sharpness of the weapon. The grinder (the cutting tool, the hone or whetstone) is the lower anterior premolar, P_3 (Fig. 3). Its morphological and structural characteristics make it possible to identify this tooth as a specialized sharpening tool. Moreover, this is its major function. It is not in any way specialized for shearing or sectioning, as is widely believed. The buccal surface of the crown of P_3 is an elongated area of thick enamel which is continuous from apex to gingival extension and which forms a hard grinding surface relatively unyielding to wear. In all other teeth of *Papio* (except the lower canine at its tubercle – see below) there is a gradual thinning of enamel towards the gingival edge. Thin enamel extends over the whole of the palatal surface of the upper canine, a feature which allows it to yield easily to grinding against P_3, and the underlying dentine, when exposed, yields even more readily.

Specialization of this sharpening tool is further evidenced by its roots: it has two; the distolingual is heavier than the mesiobuccal, and the line in which they are placed is at right angles to the crown's grinding surface. Such precise arrangements are clearly to withstand the force of the laterally directed sharpening action.

Lower anterior premolar root formations, concomitants of the

FIG. 1. Palatal surface of upper right canine tooth: young adult male baboon. This view is inverted so that the direction of its cutting (distal) edge faces in the same direction (left) as in Figs. 2 and 3.

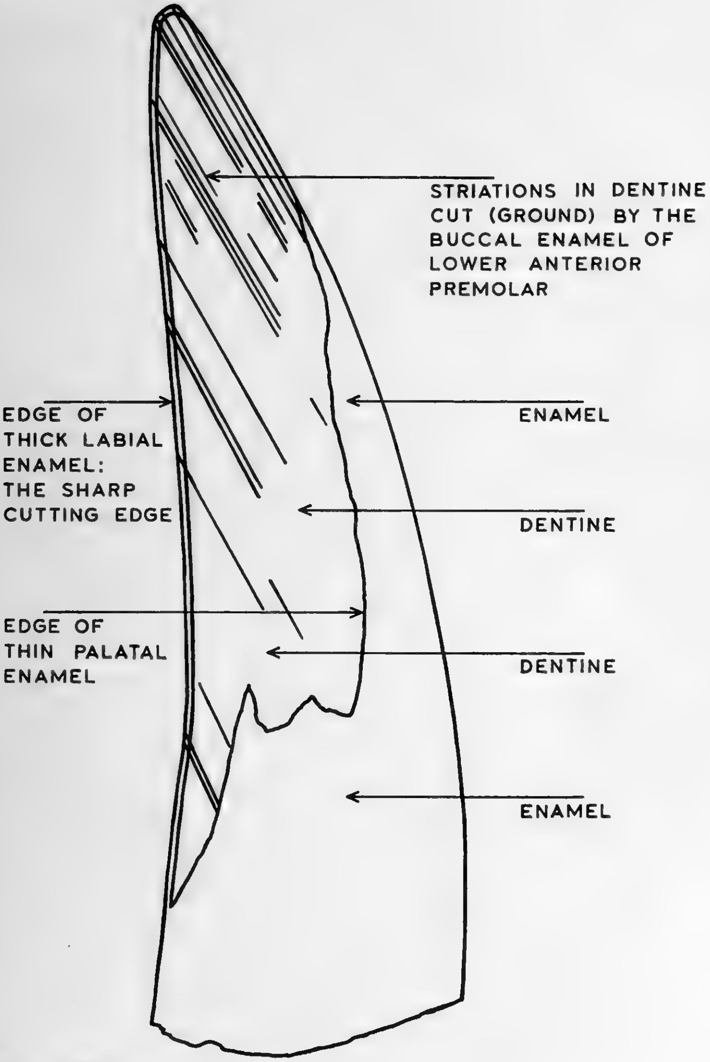


FIG. 1. (cont.)

vertically bladed upper canines, reappear with significant frequency in *Homo sapiens* (Tomes, 1923), strongly to suggest an origin from long canined ancestors. Earlier hominids, the *Australopithecus,* show this even more distinctly, as they do the

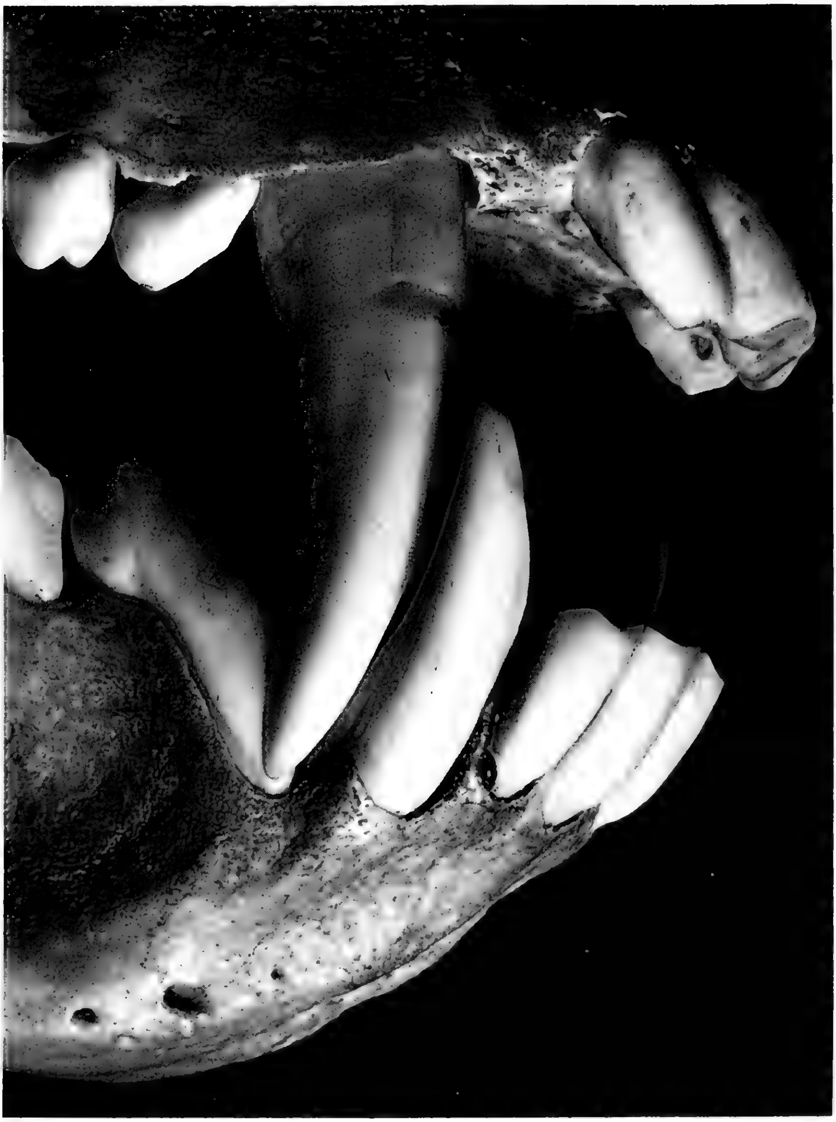


FIG. 2. Terminal phase of premolar grinding the canine in young adult male baboon.

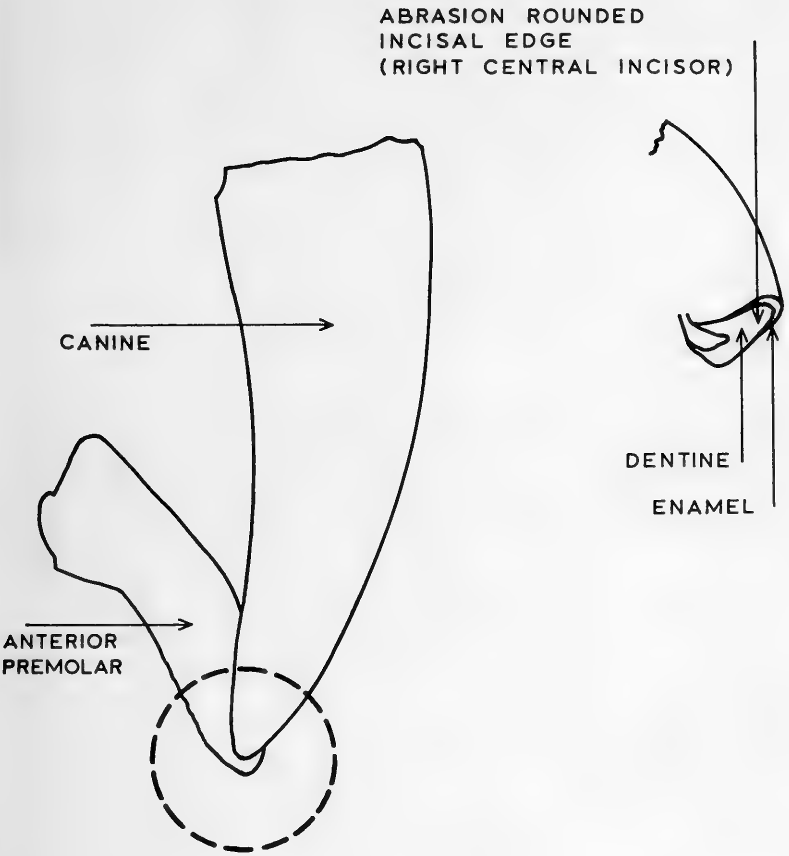


Fig. 2. (cont.)

feature of a distogingival tubercle on the lower canine. The report of these (overt) features (Robinson, 1956) does not, however, relate their concomitance (see below).

Contrary to current understanding, the motion of the mandible in this tooth-to-tooth wearing action is not as it is in mastication. The masticatory stroke, in the terminal phase of the masticatory cycle, is an approximation of the teeth, in a medial, i.e., buccal to lingual (ectal) movement; it terminates in central position. In contrast, the sharpening movement starts with the teeth in central

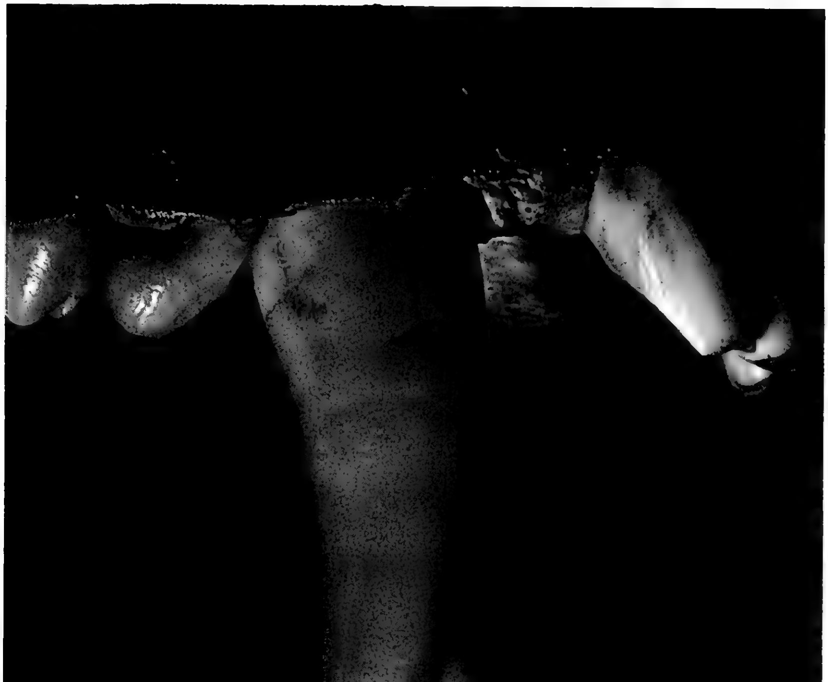


FIG. 3. Beginning phase of canine grinding canine in young male adult baboon.

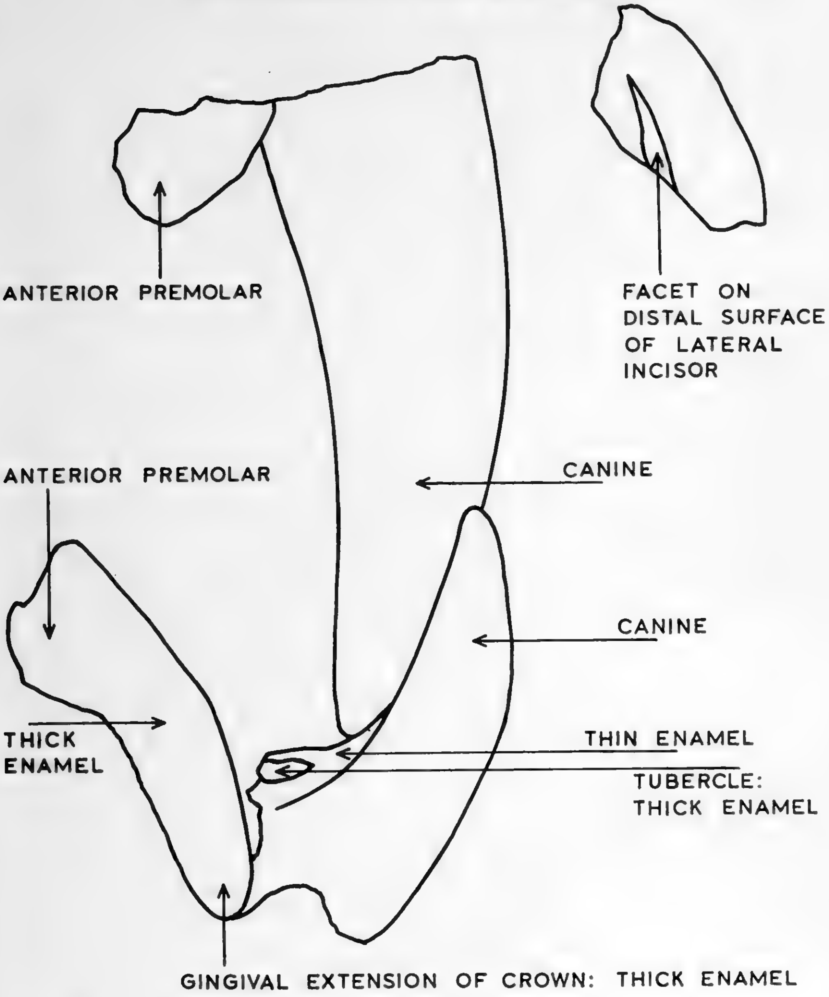


FIG. 3. (cont.)

occlusion. The mandible is extended laterally, i.e., from lingual to buccal (ental) movement, and is concurrently depressed. This is effected by action of the external pterygoid muscle on one side alone, in combination with the depressor muscles (chiefly the digastric) of the mandible (Every, 1965). The strokes are rapid, and the sound produced by such grinding in many animals has frequently been heard but has been recorded merely as tooth-chattering (e.g., van Hooff, 1962); it has, moreover, been interpreted solely as an action deriving from tension and perhaps as a signal — nothing more.

The audibility of tooth-grinding (chattering) and the lack of any such sound in masticatory tooth-to-tooth contact is consistent with the proposition that man's teeth seldom, if ever, meet in masticatory or incisive action; they meet when swallowing, but even then too lightly to produce significant wear (Jankelson, Hoffman, and Hendron, 1953; Yurkstas and Emerson, 1954; Anderson, 1955). Attrition (thegosis) does not occur during chewing and swallowing because masticatory and incisive strokes are terminated, presumably by proprioceptive reflex, just short of contact between opposing teeth. The division of exogenous material is achieved as the teeth approximate; should the teeth make contact no further advantage would be achieved, and the production of uncontrolled wear would be a serious disadvantage.

The presence of the tubercle situated distogingivally on the baboon lower canine tooth (Fig. 3) provides a further example of morphological, structural, and behavioral specialization which has evolved as a result of the advantages of the sharpening process. The previously unexplained function of the tubercle can now be understood as a specialization to protect the apex of the upper canine in the terminal phase of the grinding stroke. Fig. 2 depicts this position. At the critical phase, where the apex of the canine is poised precariously on the gingival extension of the premolar crown, the hazard of maintaining the necessary grinding pressure without rounding over, and thus blunting the apex, is eliminated by the presence of the tubercle. This tubercle contacts the upper canine tooth higher (gingivally) on its crown, an arrangement which (with further mandibular action) allows the apex to disconnect from the grinder without change of direction and thus without damage. The tubercle supports the lateral pressure at the termination of the grinding stroke, and as a result, possesses a thicker coat of enamel than the remainder of the lower canine crown in this area.

Further sharpening of baboon canine apices is effected by grinding the lower canine apex against the apex of the upper. The beginning of this action (shown in Fig. 3) appears to require a shift from lateral (extrusive) action of the mandible to retrusive action but with the mandible still held in a lateral position. It is possible, however, that no change of action is necessary and that the two can occur independently. Retrusion is limited by the postglenoid tubercle of the temporomandibular joint. There is, nonetheless, sufficient freedom in the baboon's temporomandibular joint (only slight movement is necessary) to allow some forceful contact with the distal surface of the upper canine, and thus effect a mutual sharpening of each apex[2].

The apex of the lower canine is further sharpened by yet another action of the mandible which grinds it against the distal surface (shown in Fig. 3) of the upper lateral incisor. This action, which affects the mesiolingual surface of the lower canine, is concurrent with the beginning of the major weapon-sharpening action on the opposite (contralateral) side of the mouth.

In the baboon, as in many non-hominid Anthropoidea, the enamel of the upper canine's anterior surface is grooved to form two vertical columns. The corresponding (anterior) and the opposing (distal) surfaces of the lower canine are not grooved; moreover, both the ground (distal and lingual) surfaces have only a thin coat of enamel. This arrangement favors sharpening of the lower canine apex, yet maintains the continuity of buccal and mesial enamel on the upper canine. This is vital to its piercing and cutting efficiency. Although the apices of both canines are sharpened, it is the upper canine, with its acute blade sharpness, (entirely absent in the lower canine), which is the dominant weapon. The action of the upper canine in the baboon (reflected in the strong nuchal musculature; Every, 1965) is in slashing in a downward, backward, and inward direction. Even when biting, this distally sharpened blade, shaped as a sickle (see No. 5 above) and oriented posteriorly, remains exposed; it is the crown's mesial surface which is covered by the overlapping lower canine. The upper canine serves as an efficient weapon rather than as a grasping organ[3].

---

[2] The postglenoid tubercle is, significantly, absent in many mammals, particularly the rodents and lagomorphs. Its absence in the pig is part of this animal's specialized temporomandibular joint which permits retrolateral mandibular action — an adaptation for sharpening the lower canine tusk.

[3] This is in marked contrast to the typical carnivore condition where canines, aided by a large diastema, double in function as weapons and grasping tools, and although their rounded distal surfaces may show vertical ridges, these are slight and do not impair the vital — for a carnivore — grasping advantage of the relatively blunt, hook-shaped walls.

FIG. 4. Upper left molars of a male human native of New Guinea.

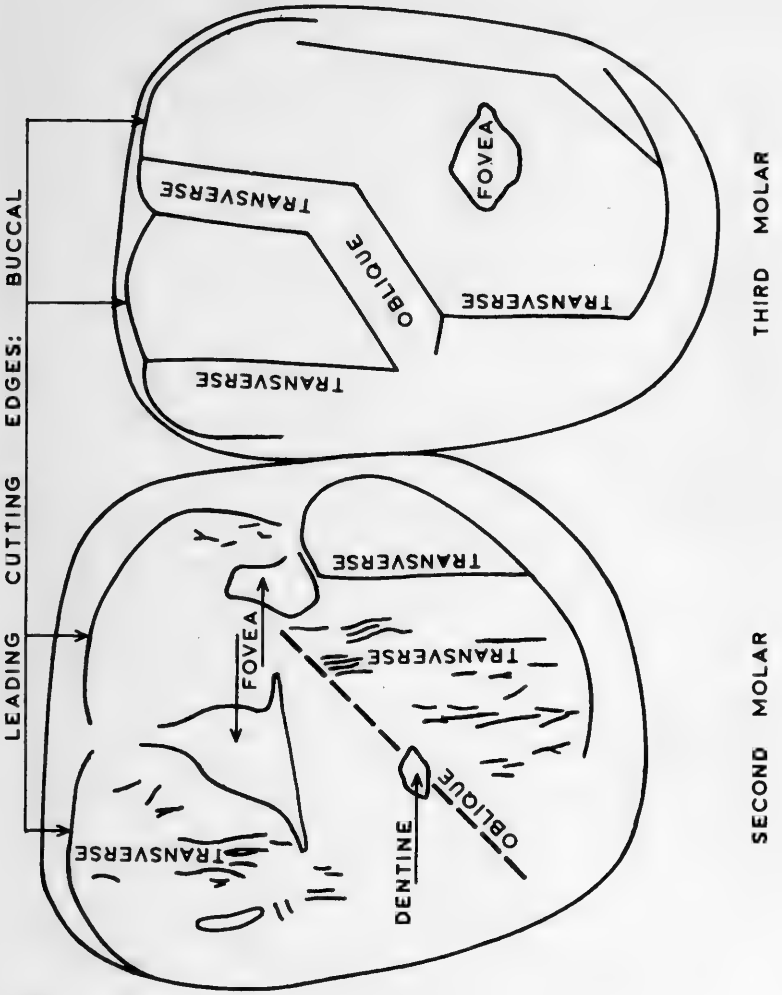


Fig. 4. (cont.)

HOMINIDS

Figure 4 shows some of the features of wear and sharpening processes in the molars of *Homo sapiens*. The third molar, with six to eight years' less use than the second molar, shows a clear picture of wear principally from the tooth-to-tooth contact wear of thegosis. This wear is the result of two discrete mandibular movements which have produced two equally discrete sets of facets (some of these are high-lighted in the photographs); the facets form ridges and grooves which meet at distinct boundaries. The transverse boundaries (vertical in the photograph) are formed by a left lateral (extrusive) thegosis action. In this action the mandible rotates about an axis at the left postglenoid tubercle (see discussion of Fig. 5, below), i.e., about a point posterior to the mandibular condyle on the same (ipsilateral) side as the teeth in the figure. This movement is in exact opposition to that of the masticatory stroke in its terminal phase, and therefore must occur apart from mastication. The oblique boundaries are formed by a lateral mandibular movement, i.e., the mandible rotates about an axis at the postglenoid tubercle on the opposite (contralateral) side. As this movement is beyond the terminal phase of a masticatory stroke, the oblique facets are also fashioned apart from mastication.

Wear from abrasion (in this instance, the friction of food) is predominant in the second molar because it has had from six to eight years' more use than the third molar; there is, however, a small thegosis-facet on the remnant of the distal surface of the distopalatal cusp (hypocone). Mesial to this distal thegosis-facet, with its discrete transverse ridge, are irregular, but still transversely oriented, lines. These are the result of friction scouring by exogenous material. In contrast to the thegosis-facet, the more heavily abraded remainder of the occlusal surface of this second molar has no precise occlusal conformity with an antagonist.

Three other key features are to be seen on this second molar:

a) The prominent sharp edge to the buccal cusps, from which the chewing table slopes down to the less prominent palatal cusps (the incline is more apparent in a mesial or distal view). This buccal edge is (relative to the movement of the lower molars) the leading (cutting) edge of the upper molar; it forms a crest on the tooth's vertical, relatively flat, buccal surface. In the lower molars the corresponding leading edge and vertical, relatively flat, surface is lingual.

b) The worn concavity of the palatal aspect of the buccal cusps. This feature, which helps to maintain the sharpness of the leading edge, is formed as a result of specializations in the temporo-

mandibular joint, in the mandibular symphysis, and in the proportions of the basal skull, maxillae, and mandible.
c) The remnant of the oblique ridge connecting the distobuccal cusp with the mesiopalatal cusp. Midway along the palatal section of this ridge is a small area of exposed dentine. With progressive wear from the friction of masticatory action other areas of dentine are exposed and gradually increase in size, and because dentine is a softer substance these areas become hollowed out. This phenomenon is characteristic of most mammals and provides a most important adaptive feature in allowing additional enamel cutting edges to appear (i.e., around the boundaries of the abraded dentine), thus maintaining – even enhancing – the sharpness of the tooth throughout its life.

Figure 5 shows some of the features of wear and sharpening processes on the incisors and canines of *Homo sapiens*. The principle reason for inclusion of this figure is to demonstrate the incorrectness of the hypothesis that states that excessive tooth wear in civilized man is the result of a "heavy bite". This hypothesis also often includes the proposition that heavy wear may have atavistic components, occurring more frequently in culturally primitive races (the traditional example given is the Australian aborigine).

Heavy wear is most often accounted for (e.g., Zuckerman, 1958) by assuming that use (age) wears hominid teeth down from their tips, and that they become flat and blunt as a result. Fig. 5, however, clearly shows a picture of wear which is dominated by thegosis, with the remaining loss of tooth substance resulting from decay, abrasion, and erosion. There is also evidence that thegosis occurs on distinctly separate occasions from incision and mastication, i.e., in the absence of exogenous material. Furthermore, it is possible to determine that the mandibular stroke producing thegosis is both oblique to the incisive stroke, and extrusive. Its action is in contrast to that of the terminal phase of incision, which is directly retrusive. This is shown by:

1) The thegosis ridges on the right (left side of the picture) canine, and (indistinctly) on the right central incisor. These thegosis ridges form arcs which are concentric with the transverse ridges on molars situated on the same side (ipsilateral),

FIG. 5. Three remaining incisors, two canines, and one premolar from the upper jaw of a Caucasian male New Zealander.

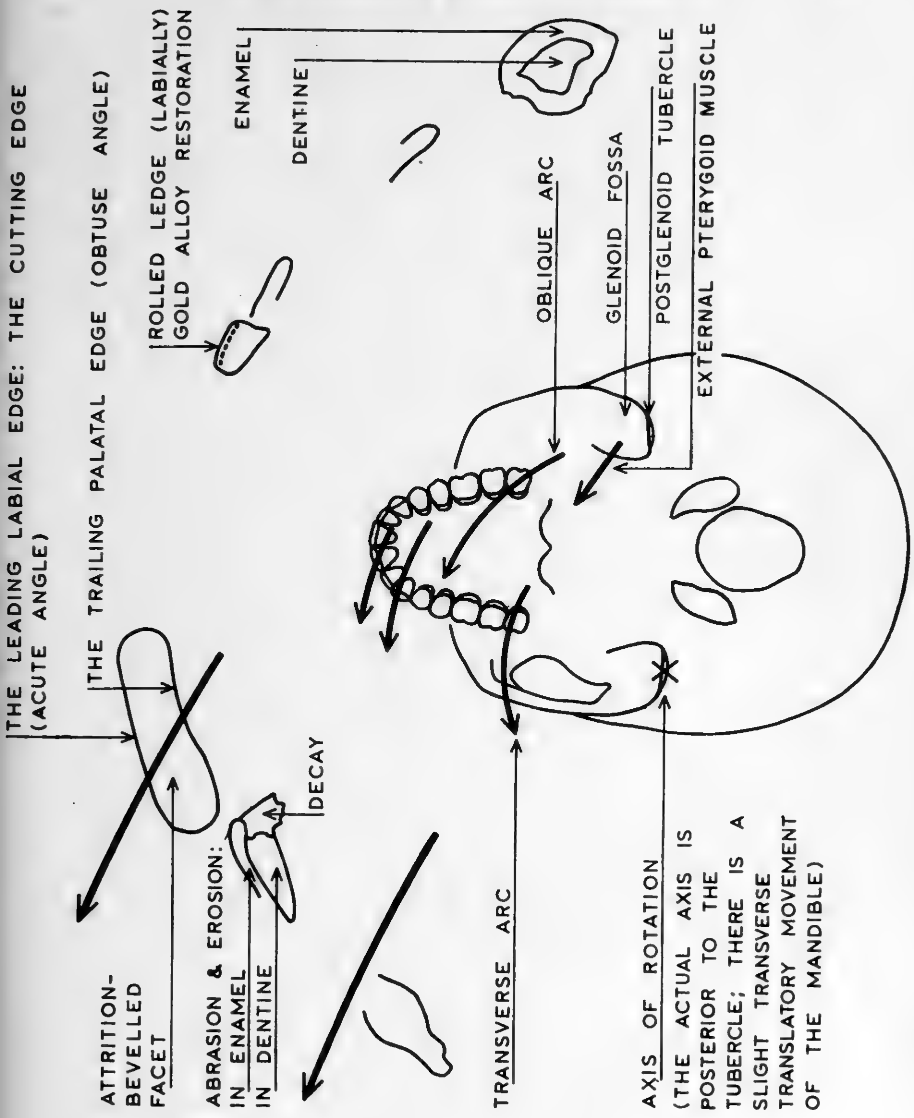


FIG. 5. (cont.)

and with the oblique ridges on the opposite (contralateral) side of the dental arch.

2) The gold-alloy restoration of the mesial incisal angle of the left lateral incisor which has the appearance of being repeatedly

beaten. The wear on all the anterior teeth shows that their occlusal relations to the lower anterior teeth are now relatively edge-to-edge; there is evidence of an overjet but no overbite. If the current notion were true — that normal wear on anterior teeth is a result of incision — this action would be expected to produce a palatal rolling over of the malleable alloy, since the terminal phase of incision is a retrusive mandibular stroke (particularly in this edge-to-edge specimen where there is no overbite). But the alloy is rolled to a labially projecting ledge. It has been hammered over to produce a ledge, as in a rivet. This can only have occurred under an action of forceful occlusion — an action distinct from and incompatible with incision or mastication (Every, 1965).

3) The flat incisal facet on the right central incisor. Especially when there is a normal incisor overbite and overjet relationship, this characteristic flat formation can be caused only by a mandibular movement which extensively crosses over the two rows (upper and lower) of anterior teeth. That is, the row of lower anterior teeth must cross over, and become diagonally related to, the row of upper anterior teeth. This is actually achieved by extensions of the same movement which grinds facets on the molars. (See evidence outlined in discussion of Fig. 4.)

4) The angle that a typical upper incisal facet makes with the vertical labial surface is about 76°. (Although this is not apparent in the figure, the incisal facet is inclined palatally). The fallacy that these teeth wear blunt is exposed by noting that the flat facet is the bevel to the sharp, leading, labial edge. In the lower teeth, the sharp, leading, cutting edge is the lingual boundary of the incisal facet. In contrast to man, the baboon's incisors (see Figs. 2 and 3) are more likely to wear blunt; but this is an abrasive bluntness: the baboon cannot grind bevelled facets on its incisal edge — any possible crossing over of occluding upper and lower rows of anterior teeth is prevented by the baboon's long canines and jaw proportions. Furthermore, relative to the pongid condition and, by inference, that of the hominid's long-canine-toothed ancestors, the lingual enamel which forms the sharp cutting edge of lower incisors and canines is thickened. Although the corresponding sharp edges of upper incisors and canines are labial, the palatal enamel of these teeth is also thickened. This, however, is to the advantage of the stage of wear when dentine

becomes exposed and hollowed out by abrasive wear (see discussion of Fig. 4). When this occurs the thickened palatal enamel provides an additional cutting edge, and is also subject to thegosis. This feature, of course, correspondingly occurs, but in the reverse relationship, in the lower teeth; the new cutting edge, which appears when dentine is exposed, forms a crest on the labial enamel[4].

Discussion

When man fabricated his first stone chisels, he found an optimum angle of bevel which was advantageous in cutting and durability. He had probably learned much from his use of other animals' teeth as chisels. In his use of either stone or teeth he would not have directly applied the flat bevel in the cutting stroke. Yet this inefficient action is imagined by some to occur in the functioning of man's own teeth; the flat facet on incisors of *Homo sapiens* is called the "incisal edge", whereas the real incisal edge is the boundary of the facet (the *edge* of the bevel), not its flat surface.

Hundreds of millions of years before man fabricated a functioning blade — a blade which, when blunted by use, was resharpened — natural selection had achieved numerous specializations for the maintenance and function of sharp teeth. It is a commonplace that, failure to discern a specific function for an anatomical feature does not imply that it is truly functionless. The "functionless" lateral incisors of the lagomorphs, for example, actually serve as specialized sharpeners; this is their dominant, if not exclusive, function (Every, 1967). By a stroke of the mandible at right angles to the incisive stroke an extremely fine "razor-edge" to the lower central incisor is honed[5]. The precision of this action in lagomorphs becomes even more apparent when it is seen that

---

[4] This system of consecutive blades oriented relatively in a horizontal plane is seen more specifically in the selenodont molars of herbivores. Selenodont teeth only come into full function when dentine is exposed and hollowed out and the precise shearing blades (not rough, grinding surfaces) are brought into accurate alignment by thegosis — a genetically programmed behavior as in most other mammals. A characteristic selenodont molar then presents pairs of four consecutive, sickle-like blades, and each of the eight blades is precisely oriented to face the direct line of the masticatory stroke.

[5] The leading edge of the lower central incisor of lagomorphs and rodents in particular, and of most mammals in general, is labial.

the striations of the remainder of the extensive bevel are cut by the twin gouges which crest the incisal edge of the labial surface of the upper central incisor. This action involves a forceful protrusive mandibular stroke. Thus the two sets of striations on each bevel of the lower incisors are at right angles to each other and cannot have been caused either by grasping or by cutting of exogenous material. In marked contrast to this wear on the lower incisors is the characteristic wear from abrasion on the upper incisors, which likewise contributes to sharpening. (A detailed analysis of this will be presented in a later paper.)

The significance of all this to man is that it clarifies not only human dental morphology but also his innate tooth-sharpening behavior. It is important to emphasize that, for an animal to kill, two basic components must exist: a) the anatomical weapon, and b) the physiological mechanisms to activate it. These two components, though separate conceptually, are in functional terms inseparable. Aggressive behavior is unlikely to evolve, i.e., become genetically programmed, when there is no biological weapon. Learned improvements in aggressive behavior, moreover, are still less likely to occur in such a case.

In this light the hypothesis that the earliest hominid was biologically defenseless, and that improvements in the brain and hand produced aggressive behavior and cultural weapons "in compensation", is unconvincing.

The important part played by teeth in the evolution of most mammals is generally recognized, and particularly in the evolution of the hominids the teeth are considered to have played a vital part. But, paradoxically, this part is considered to be a negative one — the weapon is thought to have disappeared. In the light of the phenomenon of thegosis, however, these erroneous notions can now be discounted. The clarification of man's evolution concerns not only the evolution of his biologically inheritable features but also the evolution of his culture, which he does not inherit but acquires.

These subsequently learned cultural improvements in killing, however, today so occupy our attention that we tend to be oblivious of any unlearned components which may be programming our behavior. Any suggestion that innate aggression is a component of human behavior we tend to regard as objectionable, as "animal" and "inhuman". And, at best, when its existence is recognized, we hopefully believe that we may effect its control by avoidance, redirection, and sublimation.

It seems that the phenomenal success of our (learned) cultural achievements has caused us to fail to perceive the importance of precultural improvements in learning as facilitating genetical programming of behaviors. The increased capacity to learn is, of course, a biological improvement. The cultural improvement (particularly the overwhelming advantage of the accumulation of experience through the capacity to speak) is merely an extension of the same advantage. It is as if learning were the leaven to the dough: leaven does not constitute the food; it merely improves the food and enhances its ultimate utilization.

Interpretations of these hitherto unsuspected phenomena require reappraisals of both the palaeontological and the recent record of reptilian and mammalian life. In the case of man, the reappraisal includes not only aspects of his morphological characteristics, of his behavior and social organization (of those aspects which are genetically determined), but also of his culture — the feature which distinguishes him from other animals.

Furthermore, these interpretations are antithetical to many current ideas of the selective forces which produced man. They suggest, not merely a modification, but a reversal of ideas, particularly related to man's aggression. Certain notions, such as those aptly stated by Washburn (1960), become untenable: "The skull of the man-ape has transferred to its hands the functions of seizing and pulling, and this has been attended by a reduction of its incisors. Small canines and incisors are biological symbols of a changed way of life; their primitive functions are replaced by hand and tool."

Such misinterpretations of the relative grasping capacities of the dentition of higher primates can be disproved in the light of phenomena already well documented. For example: the assumption that there had been a transfer, in the "man-ape", of functions of seizing and pulling (to hands from teeth), suggests that no such transfer had occurred in the ape itself; yet I have seen no report of anyone having observed an ape transporting its young by its teeth, let alone supporting its own weight by grasping with its teeth; nor any report of any ape seizing and grasping an adversary, or a struggling prey, by its teeth. In contrast, the seizing and pulling capacity of man is demonstrated by his capacity to seize and hold an adversary by his teeth, and by the circus performer's act where the force from the combined weights of two individuals, plus the centrifugal force from their swinging as a pendulum, is supported by the strength of one dentition.

Such a capacity is made possible in man by the improved leverage of his jaws as a result of the shortening of the snout. It is a feature which has allowed the reduction in the size of the "masticatory" muscles without loss of force available at the teeth (Every, 1965).

The grasping capacity of the sub-human primate dentition is impaired, furthermore, by the acute sharpness of the distal edges of the upper canine teeth. These canines do not double in function as grasping tools as do the carnivore's; they are specialized as slashing weapons, and are more formidable than the carnivore's, which are poorly adapted for slashing. The grasping function of a carnivore's canine teeth, however, is enhanced by the bluntness of the walls of their crowns and by diastemata posterior to, and thus exposing, their bluntness. Although the slashing advantage is to the detriment of grasping, this is of little consequence to a primate; the arboreal ancestors of all primates show no evidence of their teeth having had dominant grasping functions.

Washburn's statement quoted above that the transference of functions had been "attended by a reduction of [the man-ape's] incisors" suggests that there is a correlation between these factors, i.e., large incisors are advantageous for seizing and pulling. Yet the dentitions of characteristic carnivores, specialized for seizing and pulling, have minute incisors, relatively a fraction of the size of those of any anthropoid, including man.

Until the tooth-sharpening hypothesis first appeared (Every, 1960), there was, apparently, no suggestion that the hominid's short canine teeth gave direct evolutionary advantage *per se* to their possessor. On the contrary, evolutionary theorists widely and confidently held that the canines had "regressed" and had become "weak and inefficient". Moreover, they believed that, in use, the canines "wore down from their tips" and soon become "flat and blunt" — as did the hominid incisors, premolars, and molars (e.g., Zuckerman, 1958; Leakey, 1960; Le Gros Clark, 1962). This was taken as evidence that biological progress in early hominids had occurred in other features, particularly in the brain and in the use of the hand, and that these morphological and cortical adaptations were "necessary" to offset the disadvantages of short, small, and weak teeth. This theory suggests that *Ramapithecus,* and certainly the earliest *Australopithecus,* must have had sufficient intelligence to use tools, if not to make them. It also suggests that this capacity must have been developed sufficiently to compensate for the absence of dental weapons during millions of years of what must on this theory have been extremely precarious existence. It is clear, however, that during the Pleistocene there was no lack of sizable predators. Early hominids were not fast runners; they had, as a result of bipedalism, a reduced climbing capacity, a low procreative rate, a reduced sense of smell and hearing, probably a lengthening period and increasing intensity of infant dependence, a small brain, no capacity to transmit accumulated experience by speech, and a comparatively limited capacity to transmit any experience by signals. In addition, evolutionary theorists widely held that the teeth were inefficient, not only as weapons, but also as tools of mastication, incision, and grasping. Despite all these disadvantages and hazards, early hominids were not overwhelmed; they managed to survive the long and critical epoch unprotected by the intelligence which is concomitant with a capacity for true speech, and supposedly unprotected by an effective biological weapon. This supposed achievement was made the more remarkable by the absence of one other significant and fundamental advantage which a biological weapon gave and still gives today. This advantage, moreover, is one which no artificial weapon presents or can ever present. It is that a biological weapon is built in; it cannot be dropped, mislaid, or lost, nor can its possessor be dispossessed, or taken by surprise "unarmed"; in an emergency it is always immediately available.

Conclusions

The evidence for the hypothesis of man's biological killing capacity can be studied in three aspects:

1. The anatomical weapon, i.e., the biological instrument of killing.

2. The permanent (inflexible) genetical determinants of killing behavior.
3. The transient (flexible) learned adjustments to the genetically programmed behavior.

The simple but fundamental hypotheses of tooth-sharpness and tooth-sharpening processes (thegosis) throw further light on the evolutionary events leading to man. The evidence suggests that in hominid evolution there was no period of defenselessness; the increased number of attrition-sharpened teeth, introducing the new and specialized feature of anterior shearing blades with a capacity for "segmentive biting"[6] (Every, 1965), was defensively, predatorily, and aggressively advantageous. It was especially advantageous when coupled with an increasing capacity to know and to signal when and where not to use the primary biological weapon.

The origin of the short canine by paedomorphic novelty is generally accepted (e.g., Koestler, 1966). Also accepted is the significance to evolutionary processes of paedomorphic novelty, which is not so much the initial event itself but that selection, here (operating on a more plastic, less committed stage) allows a sudden advance in a new direction. It is this sudden (now gerontomorphic) advance which, in the hominid short-canine condition, evolutionists have overlooked.

Once this process advanced to the stage where the relatively sudden appearance of a chin altered the shape of the oral cavity and the face, these prior advantages permitted the evolution of the further, and overwhelming, advantage of a capacity to speak (Every, 1965).

But along with this overwhelming advance in the capacity to learn came an inevitable disruption of the biologically balanced (unlearned) controls: the physiological reactions evoking and attenuating agonistic behavior. This disruption clearly resulted from two principal causes:

1. The introduction of the exogenous (artificial) weapon immediately gave lethality to the secondary, and fundamentally non-lethal, weapon — the hand. Being non-lethal (except by

---

[6] I use this term (Every, 1965) to describe the separation and removal (in one action) of a large chunk of material.

accident) the hand is subject to relatively scant intraspecies (ritualized) control of its use, whereas the lethal primary weapon — the teeth — has its intraspecies use strictly controlled. That this control of agonistic behavior should be built in, i.e., automatic, stereotyped, species-specific (universal) and unlearned, is clearly advantageous. For, in agonistic behavior, especially when the weapon is sexually dimorphic (Every, 1965) in the adult, there is no margin of time allowance for learning: uncontrolled, random, trial-and-error actions of a built-in lethal instrument would rapidly lead to chaos. And if the species were to survive there would need to be strong selective pressure against learning the controls. This feature accounts for the restricted use of the primary weapon today, i.e., it is restricted in frequency of occurrence, force of bite, and selection of site; seldom are teeth used, seldom is a bite segmentive, and it is almost unknown for it to be sited at the fatally vulnerable neck.

2. The introduction of the exogenous weapon immediately extended the distance from the attacker in which the adversary could be injured. With sophistication of the weapon and progression of the distance this concomitantly and progressively dilutes the efficacy of the biological perceptions (seeing, hearing, touching, smelling, tasting) through which the controls are instrumented. Today, a kill can be made in circumstances devoid of direct biological perception. There is, as a result, almost complete disruption of the biologically balanced controls. The evoker, inevitably and tragically, is favored.

Genetical determinants of an animal's behavior can be considered permanent in the sense that they evolve in relation to permanent, or even relatively permanent, environmental features such as seasons; tides, bisexual reproduction, prey-food, and so on. Even less consistent but reasonably cyclic features such as droughts and famine can, in this sense, qualify as "permanent". When this permanency, i.e., inflexibility, is applied in the consideration of innate controls of killing behavior, whether it be predation, defense from predation, or intraspecies decimation in caged (e.g., overpopulation) circumstances, it is clear that especially for the higher animal, the capacity to learn is crucial. Because of the ever present non-permanent (i.e., transient) environmental circumstance, learning allows adjustment to the timing and the movement of the innate sequence, and thus facilitates its consummation. In this view the capacity to learn is an inherent concomitant of the unlearned determinant of behavior — not a replacement.

Direct and comparative morphological studies of man's dentition, together with dental[7], psychological[8], psychosomatic[9], vertebrate paleontological[10], and paleoanthropological[11] studies of the conditions which evoke his sharpening behavior, suggest that man sharpens his teeth as weapons; he does not directly sharpen his teeth as tools of mastication or grasping. His teeth are adequately maintained as sharp tools in the normal frequency of their preparation as weapons.

The tooth-sharpening phenomenon uniquely presents a discrete entity of innate behavior in man which appears to be unclouded by argument that it could be learned. It, moreover, elucidates unlearned determinants of man's agonistic behavior, and strongly suggests that a partial measure of the (pre-cultural) biologically

[7] Experimental studies in loss (other than by caries and accident) of tooth substances; force and direction of mandibular action; i.e., using and devising techniques of conservative restoration, periodontia, therapeutic splinting and orthodontic appliance, full and partial prosthesis (allowing unique control of nocturnal action). (Every, 1939, 1949, 1960, 1965; Craddock and Johnston, 1961; Reed, 1968).

[8] Communication by facial expression, particularly (innate) signals and their auditory concomitants. Communication by olfaction. Relationship of (innate) unlearned and (cultural) learned determinants of behavior. Behavioral and morphological changes permitting the evolution of the capacity to speak. Pain thresholds in fight and flight. Use of tooth-sharpening as a marker of stress. (Every, 1960, 1965; Hughes, 1969).

[9] Oral symptoms of repression. Presentation of the *Syndrome of extreme mandibular movements*. Experimental therapy. (Every, 1946, 1960; Craddock and Johnston, 1961).

[10] The reptilian-mammalian transition. Mesozoic mammalian dentition, particularly in respect to the origin of the talonid and protocone, the contact point, the transition of cusp-interdigitation to cusp-apposition and opposing-convexities of shearing blades, and the significance to sharpness of differentially hard tooth-substances. Post-Mesozoic radiation. (Every, "Reinterpreting the dentitions of *Amphitherium* and *Peramus*," paper read at the Symposium of Vertebrate Palaeontology and Comparative Anatomy, London, 1967).

[11] The transition from vertically sharp slashing blades to horizontally sharp shearing blades. Evolutionary advantages of the hominid short-canine condition. Relationship of changes in the dentition to brain enlargement. (Every, 1965, and paper cited in Footnote 10).

balanced controls is restorable. But this only when man's (flexible) culture is made to harmonize with his (inflexible) biology.

ACKNOWLEDGMENTS

Dr. Elwyn L. Simons (Peabody Museum of National History, Yale University) has given much assistance in the preparation of this manuscript, for which I am deeply grateful. Others also deserve my sincere gratitude; they gave facilities, access to collections and clinical material, discussion, service, encouragement and support. Too numerous to mention individually, they are spread out among universities, museums, hospitals, miscellaneous institutions, private practices, and private individuals, in New Zealand, Australia, Germany, England and the U.S.A. To Professor Dr. Walter G. Kühne, Geologisch Paläontologisches Institut, Freie Universität, Berlin; Dr. Fraser McDonald, Medical Superintendent and Director Research Unit, Kingseat Psychiatric Hospital, Papakura, New Zealand; Dr. Ronald Singer, Dept. of Anatomy, University of Chicago, and Dr. Albert A. Dahlberg, Dept. of Anthropology and Zoller Memorial Dental Clinic, University of Chicago, I give special thanks for the additional assistance of short-term posts in their departments. The whole basis of this work was formulated in a psychiatrically oriented private dental practice in Christchurch, N. Z. In the final stages, crucial financial support, most of it anonymous, was given by private well-wishers. For this I am extremely grateful. Part of the preparation for publication was later supported by grants from the Canterbury Medical Research Foundation, N.Z.; The Golden Kiwi Lottery Committee for the Promotion of Medical Research, N.Z.; and The Explorers Club, New York, U.S.A.

LITERATURE CITED

Anderson, D. J. 1955. Physiology of mastication. Dent. Pract. **5**: 389-394.

Craddock, F. W., and J. W. Johnston. 1961. A new explanation of facial pain. N.Z. Dent. J. **57**: 153-161.

Every, R. G. 1939. Contact points. N.Z. Dent. J. **35**: 287-291.

__________ 1946. The problem of the thumb-sucker. N.Z. Dent. J. **42**: 178-183.

__________ 1949. The elimination of destructive forces in replacing teeth with partial dentures. N.Z. Dent. J. **45:** 207-214.

__________ 1960. The significance of extreme mandibular movements. Lancet **2:** 37-39.

__________ 1965. The teeth as weapons; their influence on behaviour. Lancet **1:** 685-688.

Hughes, R. N. 1969. Social facilitation of locomotion and exploration in rats. Br. J. Psychol. **60:** 385-388.

Jankelson, B., G. M. Hoffman, and G. A. Hendron. 1953. Physiology of the stomatognathic system. J. Am. Dent. Assn. **46:** 375-386.

Koestler, Arthur. 1966. Biological and mental evolution — an exercise in analogy, p. 95-107. *In* Knowledge among men. Simon and Schuster, Washington, D.C.

Leakey, L. S. B. 1960. Finding the world's earliest man. Nat. Geog. **118:** 240-435.

Le Gros Clark, W. E. 1962. The antecedents of man, 2nd ed., University Press, Edinburgh. 388 p.

Reed, J. W. 1968. A new design for a partial lower denture. N.Z. Dent. J. **64:** 23-26.

Robinson, J. T. 1956. The dentition of the Australopithecinae. Transvaal Museum (Pretoria) Memoir **9.** 178 p.

Tomes, C. S. 1923. A manual of dental anatomy, human and comparative, 8th ed. J. and A. Churchill, London. 547 p.

Washburn, S. L. 1960. Tools and human evolution. Sci. Am. **203:** 3-15.

Yurkstas, A. A., and W. H. Emerson. 1954. Study of tooth contact during mastication with artificial dentures. J. Pros. Dent. **4:** 169-174.

van Hooff, J. A. R. A. M. 1962. Facial expression in higher primates, p. 97-125. *In* Evolutionary aspects of animal communication. Symp. Zool. Soc. Lond. **8.**

Zuckerman, S. 1958. Correlation of change in the evolution of higher primates, p. 300-352. *In* Huxley, Julian, A. C. Hardy, and E. B. Ford [eds.] Evolution as a process. George Allen and Unwin, London.

INFORMATION FOR AUTHORS

REVIEW	The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
STYLE	Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).
FORM	Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.
TITLE	Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
ABSTRACT	The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
OMENCLATURE	Follow the International Codes of Zoological and Botanical Nomenclature.
LLUSTRATIONS	Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
FOOTNOTES	Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
TABLES	Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
REFERENCES	The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
THOR'S COPIES	Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
PROOF	Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
COPYRIGHT	Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 144 27 APRIL 1970

THE TAXONOMIC STATUS OF QUILL WORMS, GENUS HYALINOECIA (POLYCHAETA: ONUPHIDAE), FROM THE NORTH AMERICAN ATLANTIC CONTINENTAL SLOPE

CHARLOTTE P. MANGUM
WILLIAM R. RHODES

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

THE TAXONOMIC STATUS OF QUILL WORMS, GENUS HYALINOECIA (POLYCHAETA: ONUPHIDAE), FROM THE NORTH AMERICAN ATLANTIC CONTINENTAL SLOPE

CHARLOTTE P. MANGUM
WILLIAM R. RHODES

Department of Biology
College of William and Mary

ABSTRACT

Morphological characters of quill worms from the North American continental slope have been compared with those of *Hyalinoecia tubicola* (O. F. Müller) from the English Channel. The results indicate consistent and exclusive differences in worms of the same size. We suggest that *Hyalinoecia artifex* Verrill be reinstated for North American quill worms, as originally intended.

POSTILLA 144: 13 p. 27 APRIL 1970.

Introduction

Quill worms of the onuphid genus *Hyalinoecia* are often dredged in great numbers from 400–1500 meters depth on the continental slope of the northwestern Atlantic Ocean. These worms were originally described as *H. artifex* by Verrill (1880, 1885a, 1885b), who remarked upon the close relationship with the European *H. tubicola* (O. F. Müller). The primary difference clearly stated by Verrill (1880) is larger size, although his full description (Verrill, 1885b) includes a number of morphological characters that do not agree with those of *H. tubicola*.

Probably unaware of Verrill's findings, Ehlers (1887) described a North American collection of extremely small (less than 21.5 mm long) worms as *Onuphis gracilis,* explicitly noting the resemblance to both *H. tubicola* and the West Indian *H. varians* Baird. Quite a few characters, notably the condition of the occipital antennae, the anterior setae and the absence of so-called "Augenflecke" on the largest specimen, do not agree with *H. tubicola.*

Augener (1906) noted the existence of differences between European and American worms, particularly the absence of "eyes" and the location of gills, but nevertheless synonomized both *H. artifex* Verrill and *O. gracilis* Ehlers with *H. tubicola* (O. F. Müller). He believed that the differences could be attributed to size.

Since Verrill's discovery of a North American quill worm, other animals identified as *H. tubicola* have been dredged from all of the world's major seas except the Antarctic Ocean. The species is often cited as an example of the cosmopolitan fauna of the deep sea (Ekman, 1953). The concept of a single faunal assemblage comprised largely of cosmopolitan species inhabiting the depths of oceans throughout the world is currently being questioned due to the elucidation of distinct faunas in different regions (Sanders, Hessler and Hampson, 1965). Nonetheless, there remains a sizable group of species such as *H. tubicola* that have been so widely reported that they are considered cosmopolitan. We have investigated American and European representatives of this species in hopes of clarifying the basis of morphological differences noted by earlier workers. Diagnoses of morphological, physiological and molecular characters will be presented in evidence. This paper is restricted to a morphological comparison of three populations, one European and two North American.

All animals in our own collections were removed from their tubes prior to preservation in 70% ethyl alcohol. This precaution not only facilitates preservation but also prevents autotomy of the tail region and distortion of the body. We made no special effort to insure against bias for size; the measurements given are intended to portray the samples on which our results are based, not the natural populations. The error is probably not large, but small worms are easily overlooked in shipboard sorting, and a few of the largest were discarded from the European sample because they did not fit the mailing containers.

RESULTS

European worms

Hyalinoecia tubicola (O. F. Müller, 1776)

Hyalinoecia tubicola Quatrefages, 1865; Grube, 1878; Langerhans, 1880; Fauvel, 1923; Støp-Bowitz, 1948.

More than 300 specimens were collected by R/V *Sula* of the Marine Biological Association of the United Kingdom in the summer of 1967. The worms originated from depths of 44 to 55 meters in the English Channel (50° 15–17′ N, 4° 20–30′ W). Excluding tentacles and terminal cirri, the size range of the animals was 35–130 mm (Fig. 1A). The quill-like tubes of the species, a few cm longer than their inhabitants, were described by Watson (1903).

DESCRIPTION OF MATERIAL COLLECTED. Prostomium bulbous, bearing five occipital antennae with annulate (3–4 rings) ceratophores, and two stout, short frontal antennae without ceratophores. Three dorsomedial occipital antennae of equal length, twice as long as more lateral pair (Fig. 166i in Fauvel, 1923), and extending posteriorly as far as setigerous segment XVI. Two dark pigment spots (often designated “eyes” in the literature) occurring lateral to the bases of the dorsomedial paired occipital antennae. Ventrally two large globose palps forming the upper border of the mouth.

Buccal segment dorsally forming an achaetous ring at the base of the prostomium. Mouth located ventrally, with reniform lower lip and two protruding wing-shaped mandibles. Four pairs and one unpaired dark maxillae (Fig. 88 in McIntosh, 1885). Maxillae I hooked forceps. Right maxilla II typically with 13–14 teeth (range

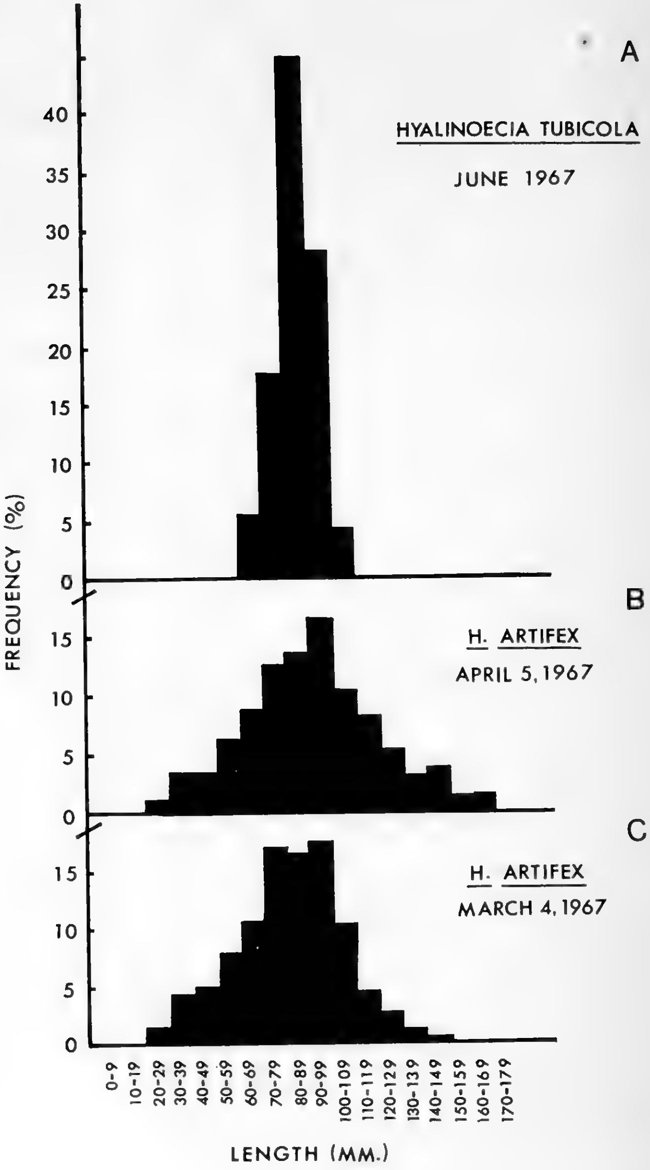


FIG. 1. Size distribution in sample of quill worms. A. English Channel. B. and C. North American continental slope (420–480 m).

10–15); left maxilla II with 12 (11–14) teeth. Right maxilla III absent; left maxilla III with 13 (12–14). Right maxilla IV with 10 (10–11); left with 13 (12–14). Each right and left maxilla V with 1 tooth only.

Setigerous segment I smooth dorsally, longer than succeeding segment. Parapodia enlarged, directed anteroventrally. Dorsal parapodial cirri about same size as on segment II; ventral cirri slightly larger than on II. Presetal lobe somewhat fan-shaped (enlarged distally) covering the bases of typically 3 (2–6) stout tridentate acicula (Fig. 2A). Postsetal lobe cirriform, about one-half as large as on setiger II.

Setigerous segment II shorter than I. Parapodia smaller, more conical and directed ventrally. Presetal lobe spatulate, covering bases of 2–4 bilimbate capillary setae (Fig. 2D in Claparède, 1868) which are noticeably stouter than in succeeding segments, 2–4 stout tridentate acicula and a small clump of pectinate setae. Postsetal lobe more closely applied to fascicle, less conical, and more lobulate than on I.

Setigerous segment III closely resembling II though slightly smaller. Dorsal and ventral parapodial cirri slightly smaller than on II, beginning posterior gradation in size. Limbate capillary setae

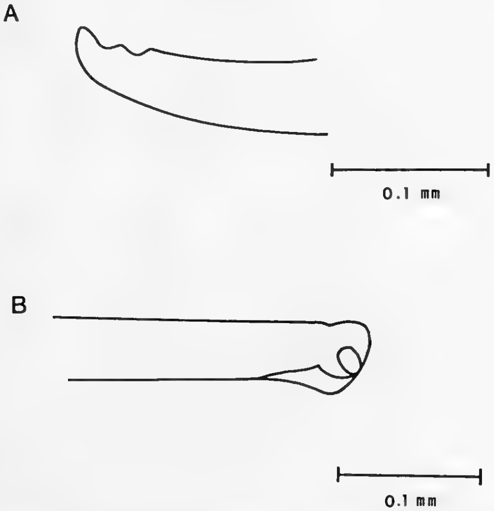


FIG. 2. *Hyalinoecia tubicola* (O. F. Müller). English Channel. A. Tridentate aciculum from setiger I. B. Hooded bidentate aciculum from branchial region.

up to 11; clump of pectinate setae in dorsal portion of fascicle. Emergent acicula lacking.

Setigerous segment IV with several pectinate setae (Fig. 166n in Fauvel, 1923) as well as limbate capillaries. Ventral cirrus short, globose, becoming a flattened cushion by setiger V and persisting as such for rest of body length. Presetal lobe diminishing to rudimentary lip on branchial segments. Postsetal lobe diminishing to rudimentary lobe, then disappearing by setiger XXXV.

Branchiae flattened, beginning typically at setiger XXIV (XXIII to XXV) and subsequently increasing in length up to or more than two-thirds the body width. Dorsal parapodial cirri simultaneously decreasing to a fine filament about one-tenth the length of the branchial filaments.

Number of limbate setae increasing to maximum of 14 per fascicle between setigers IX to XXV. Single hooded bidentate aciculum (Fig. 2B) appearing in the middle of the fascicles at about setiger XXV (XX to XXVIII), increasing to typically 2–3 (up to 5) more posteriorly. Hooded bidentate aciculum notched immediately proximal to teeth, which are directed at acute angle to main axis of seta (Fig. 2B). Number of limbate capillary setae decreasing to 9 or less per fascicle in the midbranchial region. Pectinate setae present on all but setiger I. Three stout, tapered, hooded acicula present internally in all parapodia but typically not emerging.

Posterior region becoming flattened, ending in large pygidium with two fragile terminal cirri. Last few segments without branchiae but with dorsal cirri and all setae types (in reduced numbers).

Material deposited in the Peabody Museum, Yale University, YPM No. 2694.

North American worms

Hyalinoecia artifex Verrill 1880

Hyalinoecia artifex Verrill, 1885a; Verrill, 1885b.
Onuphis (Paronuphis) gracilis Ehlers, 1887.
Hyalinoecia tubicola Augener, 1906; Hartman, 1944; Pettibone, 1963.

We have collected thousands of specimens from the Atlantic continental slope at 420–480 meters depth, 34° 16′ N, 75° 48′ W. The collections were made on cruises on R/V *Eastward* of the

Duke University Marine Laboratory in the period 1965–68. The description below summarizes our examination of several hundred worms ranging in length from 15 to 180 mm (Figs. 1B and 1C). The morphology is stable after the worms reach a length of approximately 20 mm, but quite plastic in smaller animals. The description pertains to worms exceeding 20 mm; a few notes on juvenile specimens follow at the end.

DESCRIPTION OF MATERIAL COLLECTED. Prostomium bulbous (Fig. 3A), bearing five occipital antennae with annulate (3–4 rings) ceratophores and two short, stout, frontal antennae without cerato-

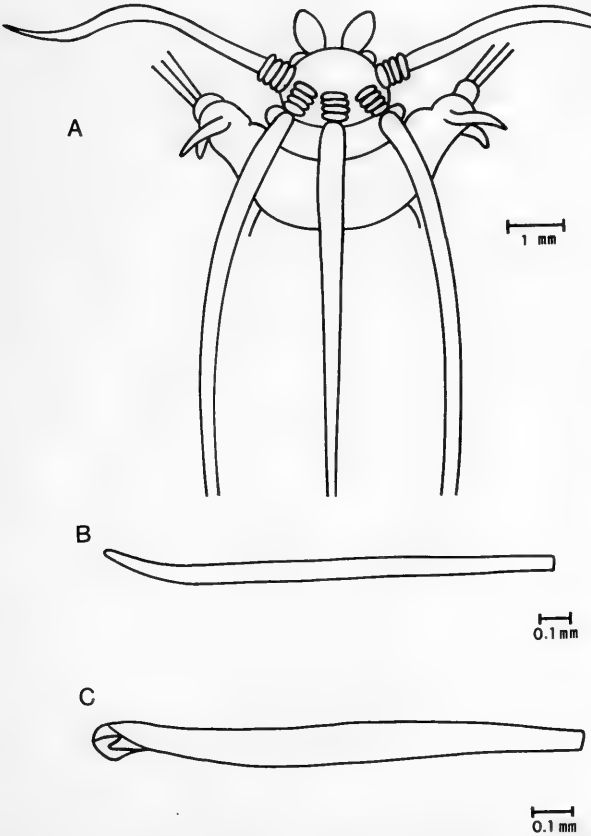


FIG. 3. *Hyalinoecia artifex* Verrill, continental slope (420–480 m). A. Anterior region, dorsal view. B. Blunt aciculum from setiger I. C. Hooded bidentate aciculum from branchial region.

phores. Three dorsomedial antennae of equal length, about 3–4 times the length of the more lateral pair (Fig. 178 in Verrill, 1885b) and extending as far posteriorly as setiger XXX. Prostomium of adult worms invariably without dark pigment spots (see notes on juvenile specimens below). Ventrally two large globose palps forming upper border of mouth.

Buccal segment dorsally forming achaetous collar at base of the prostomium. Mouth located ventrally, with reniform lower lip and two protruding wing-shaped mandibles. Four pairs and one unpaired maxillae; Maxillae I hooked forceps; right maxilla II with 13 (10–15) teeth; left with 14 (11–16). Right maxilla III absent and left with 13 (11–15) teeth. Right maxilla IV with 12 (9–14) and left with 10 (8–12). Each maxilla V with 1 tooth only.

Setigerous segment I smooth dorsally, longer than succeeding segment. Parapodia enlarged, directed anteroventrally. Dorsal and ventral parapodial cirri smaller than on setiger II. Presetal lobe somewhat fan-shaped (enlarged distally) covering bases of 3–4 stout, smooth-tipped acicula (Fig. 3B). Postsetal lobe cirriform, about one-half as large as on setiger II.

Setigerous segment II slightly shorter than I. Parapodia smaller and more conical than on I, directed ventrally. Dorsal and ventral cirri larger than on I. Presetal lobe spatulate, covering bases of 3–4 stout acicula, 3–4 stout mono- and bilimbate capillary and small clump of pectinate setae. Postsetal lobe closely applied to fascicle.

Setigerous segment III slightly smaller than II. Dorsal cirri longer than on II; ventral parapodial cirri smaller than on I, beginning to diminish and becoming very small in mid-branchial region (see below). Presetal lobe a small tongue, beginning to diminish. Postsetal lobe similar to that on II, but beginning to diminish. Limbate capillary setae up to 10; clump of pectinate setae in dorsal portion of fascicle. Emergent acicula lacking.

Setigerous segment IV with slightly smaller parapodia than III; parapodia diminishing to roughly constant size by VII. Pectinate setae present, as well as limbate capillaries. Ventral cirrus short, globose, becoming a flattened cushion by VII. Presetal lobe grading to rudimentary lip by setiger X and persisting as such posteriorly. Postsetal lobe beginning gradation to rudimentary lobe by setiger L.

Branchiae simple, flattened, beginning typically at setiger XXIX (XXVI to XXXIII); length up to but not exceeding two-thirds of body width. Dorsal parapodial cirrus decreasing to fine filament at base of branchiae and about one-eighth the length of the branchial filament; dorsal cirrus becoming somewhat larger again in postbranchial region.

Maximum number of limbate setae about 16, occurring between setigers XV and XL. Single hooded bidentate aciculum appearing in center of fascicle between setigers XXIV and XLV, increasing to 2 (uncommonly 3) in more posterior segments; hooded acicula not notched, with teeth directed parallel to main axis (Fig. 3C). Number of limbate capillary setae decreasing to maximum of 12 in midbranchial region. Pectinate setae present on all but setiger I. Three stout, tapered, hooded acicula present internally on all parapodia but typically not emerging.

Posterior region becoming flattened, ending in small pygidium with two fragile terminal cirri. Last few setigerous segments without branchiae but with dorsal cirri and setae (reduced numbers). Maximum segment number about 200.

Material deposited in the Peabody Museum, Yale University, YPM No. 2695.

We have also examined forty individuals from the same population between 12 and 25 mm in length. The two smallest specimens (12 mm) show striking morphological deviations from larger members of the species (greater than 20–25 mm). Most striking is the enlarged condition of dorsolateral antennae (Fig. 4) and the very short condition of other occipital antennae. Many of the remaining small worms (12–25 mm) show a transitional condition for this character. Another interesting deviation found in the smallest worms is the absence of demarcation between the buccal segment and the first setiger. Two somewhat larger specimens of the forty examined had distinct prostomial pigment spots very much like those found on all specimens of *H. tubicola*. Comparing the morphological characters of these very small worms with those attributed by Ehlers (1887; see Fig. 6) to North American worms, we believe that he described as *Onuphis gracilis* an intermediate condition between juvenile and adult forms of *H. artifex* Verrill.

Hyalinoecia sp.

Finally, we have examined 50 specimens obtained by Dr. Gilbert Rowe at 33° 59′ N, 75° 46′ W. This station is very close to the

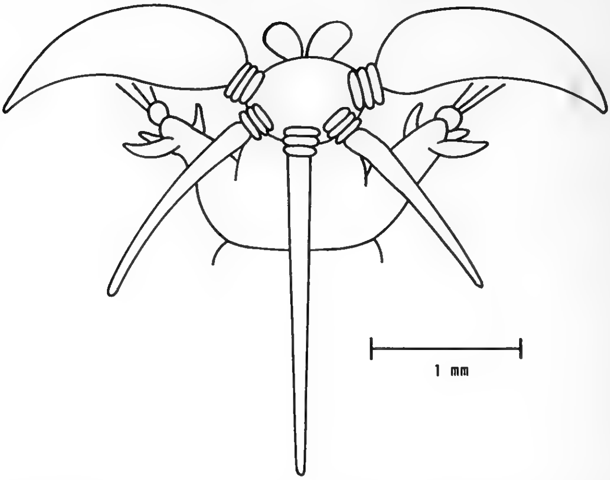


FIG. 4. *Hyalinoecia artifex* Verrill, continental slope (420–480 m). Anterior region of a worm 12 mm in total length, dorsal view.

previous one on the Atlantic continental slope, but at the considerably greater depth of 1125–1350 meters. The taxonomic status is particularly interesting because horizontal belts of quill worms are found at the two depths but not in between (Rowe, 1968).

DESCRIPTION OF MATERIAL COLLECTED. Prostomium bulbous, bearing five occipital antennae with annulate (3–4 rings) ceratophores, and two stout, short, frontal antennae without ceratophores. Three dorsomedial occipital antennae 3–4 times the length of the lateral pair. Unpaired median antenna extending as far as setiger XXVI; paired dorsomedial antennae extending as far as segment XIX. Single median antenna consistently longer. Prostomium without dark pigment spots. Ventrally two large globose palps forming the upper border of mouth.

Buccal segment dorsally forming an achaetous ring around base of prostomium. Mouth located ventrally with reniform lower lip and two protruding wing-shaped mandibles. Four pairs and one unpaired dark maxillae. Maxillae I hooked forceps. Right and left maxillae II with 12 (10–14) teeth. Right maxilla III absent; left with 8 (6–10) teeth. Right maxilla IV with 8 (6–13) teeth; left with 8 (6–11). Both right and left maxillae V without teeth, rudimentary.

Setigerous segment I very large, longer than succeeding segment. Parapodia enlarged, directed anteroventrally. Dorsal and ventral cirri about same as on segment II. Presetal lobe fan-shaped (enlarged distally), covering bases of 2–4 stout, tapering acicula. Postsetal lobe small (one-half the size as on II), cirriform.

Setigerous segment II about two-thirds the length of I; parapodia smaller, more conical and directed ventrally. Dorsal and ventral cirri about the same size as on I. Presetal lobe somewhat spatulate covering bases of about 8 stout limbate and several pectinate setae. Postsetal lobe considerably larger than on I, more conical. Setiger III about three-fourths the length of II. Setiger IV about three-fourths the length of III, slightly larger than other body segments of the anterior and mid-regions.

Branchiae simple, flattened, beginning typically on setiger XX (XIX to XXII). Branchiae less than two-thirds width of body.

Limbate setae increasing to about 24 per fascicle in prebranchial segments. Emergent bidentate acicula appearing about setiger XXVIII, and increasing to two in posterior segments. Hooded acicula resembling those of *H. artifex*. Three stout, tapered, hooded acicula present internally on all parapodia but typically not emerging. Posterior region missing. Pectinate setae present in all but setiger I.

Material deposited in the Peabody Museum, Yale University, YPM No. 2696.

DISCUSSION

Shallow-water North American quill worms differ from their European relatives by the following morphological characters: 1) allometry of dorsomedial occipital antennae relative to lateral occipital antennae as well as to body segments; 2) allometry of median occipital antenna relative to paired dorsomedial antennae; 3) virtually complete absence of prostomial pigment spots; 4) adentate condition of acicula on anterior setigers; 5) morphology and smaller number of hooded bidentate acicula in branchial and mid-regions; 6) more posterior position of branchiae; 7) larger numbers of capillary and pectinate setae; 8) allometry of pygidium relative to body; 9) allometry of dorsal cirri relative to branchial filaments in mid-region.

North American worms differ from their European relatives by a number of other characters, the importance of which is difficult to assess. Some of these differences may arise from handling or method of preservation; others, although undoubtedly natural, are of minor significance. The differences include: 1) allometry of frontal antennae; 2) disappearance of postsetal lobe on different setigers; 3) number of teeth on maxillae; 4) allometry of dorsal and ventral parapodial cirri on first and second setigerous segments; 5) larger mean size and segment number. It should be emphasized that these differences occur in worms of the *same overall size.*

The two North American populations also consistently differ from one another in: 1) number of limbate setae per fascicle; 2) allometry of occipital antennae relative to one another and to the body; 3) appearance of gills on different segments; and 4) rudimentary condition of maxillae V. While the absence of posterior ends prevents a quantitative size comparison, the lower slope specimens are approximately the same diameter. There are additional differences that we believe attributable to preservation of the lower slope specimens without prior removal from the tube. Because of the poor preservation and the absence of complete specimens from the greater depth, we do not consider our morphological comparison adequate. It is included here to call attention to possible morphological divergence correlated with the interesting ecological separation.

In conclusion, the differences between North American and European worms that were noted by Augener (1906) do exist; moreover, there are additional morphological differences. Contrary to the conclusion of Augener (1906), the differences are consistently found in worms of the same size. Since the synonomization is not supported by either evidence or well-founded argument, it seems reasonable to recognize Verrill's (1880) species *Hyalinoecia artifex* as distinct from the European form *H. tubicola* (O. F. Müller).

ACKNOWLEDGMENTS

This work was supported by research grants NSF GB-5563 and GB-6884 from the National Science Foundation. We are grateful to Drs. Meredith L. Jones and J. L. Simon for their criticisms of the manuscript.

LITERATURE CITED

Augener, H. 1906. Westindische Polycheten. Bull. Mus. Comp. Zool. **43**: 91–196.

Clàparede, E. 1868. Les annélides chétopodes du Golfe de Naples. Mém. Soc. Phys. **19**: 313–584.

Ehlers, E. 1887. Report on the annelids of the dredging expedition of the U.S. coast survey steamer *Blake*. Mem. Mus. Comp. Zool. **15**: 1–335.

Ekman, S. 1953. Zoogeography of the sea. Sidgwick and Jackson, Ltd. London, 417 p.

Fauvel, P. 1923. Faune de France. 5. Polychètes errantes. 488 p.

Grube, A. E. 1878. Systematische Untersuchungen über die Familie Eunicea. Jahresber. Schles. Gesell. f. Vaterland Kult. **55**: 79–104.

Hartman, O. 1944. New England Annelida. Part 2. Bull. Amer. Mus. Nat. Hist. **82**: 327–344.

Langerhans, P. 1880. Die Wurmfauna von Madiera. Zeits. wiss. Zool. **33**: 267–316.

McIntosh, W. C. 1885. Report on the Annelida, Polychaeta collected by H. M. S. *Challenger* during the years 1873–76. Challenger Reports **12**. 554 p.

Müller, O. F. 1776. Zoologiae Danicae prodromus, seu animalium Daniae et Norvegiae. 274 p.

Pettibone, M. H. 1963. Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. U.S. Nat. Mus. Bull. **227**. 356 p.

Quatrefages, A. de. 1865. Histoire naturelle des annéles marins et d'eau douce. Annélides et géphyriens. Libr. Encycl. de Rôret I. 588 p.

Rowe, G. T. [MS.] Distribution patterns in populations of large, deep-sea benthic invertebrates off North Carolina. Ph.D. dissertation, unpubl. 1968, Duke University, Durham, North Carolina. 296 p.

Sanders, H. L., R. R. Hessler and G. R. Hampson. 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head—Bermuda transect. Deep-Sea Res. **12**: 847–867.

Støp-Bowitz, C. 1948. Polychaeta from the *Michael Sars* North Atlantic deep-sea expedition, 1910. Rep. Sci. Results *Michael Sars* North Atlantic Deep-Sea Exped. 1910. **5** (8). 91 p.

Verrill, A. E. 1880. Notice of recent additions to the marine Invertebrata, of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. (Pt. II). Proc. U.S. Nat. Mus. **3**: 356–405.

——— 1885a. Results of the explorations made by the steamer *Albatross* off the northern coast of the United States in 1883. Rep. U.S. Fish Comm. for 1883: 503–699.

——— 1885b. Notice of recent additions to the marine Invertebrata of the northeastern coast of America, with descriptions of new genera and species and critical remarks on others. (Pt. V). Proc. U.S. Nat. Mus. **8**: 424–448.

Watson, A. T. 1903. Observations on the habits of the Onuphidae (Polychaeta), and on the internal structures with which they fortify their homes. Proc. Trans. Liverpool Biol. Soc. **17**: 303–318.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

OMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

ILLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

THOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 145. 25 MAY 1970

GENERIC STATUS OF THE INOCERAMUS? TEGULATUS SPECIES GROUP (BIVALVIA) OF THE LATEST CRETACEOUS OF NORTH AMERICA AND EUROPE

IAN G. SPEDEN

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Nancy A. Ahlstrom, Elizabeth G. Weinman, Elise K. Kenney.

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

GENERIC STATUS OF THE INOCERAMUS? TEGULATUS SPECIES GROUP (BIVALVIA) OF THE LATEST CRETACEOUS OF NORTH AMERICA AND EUROPE

IAN G. SPEDEN

New Zealand Geological Survey, Lower Hutt, New Zealand

(Received February 3, 1969)

ABSTRACT

Five named species of the latest Cretaceous *Inoceramus*? *tegulatus* species group are, on present information, considered valid: two from North America, *fibrosus* (Meek and Hayden) and *argenteus* Conrad; three from Europe, *tegulatus* Hagenow, *caucasicus* Dobrov and *dobrovi* Jeletzky. The morphology of the ligament area and the pattern of muscle scars differentiate the species from *Inoceramus,* and *Tenuipteria* Stephenson is the valid generic name for the broad taxon encompassing the five species.

The five species can be divided into two lineages: a lineage of equivalved species (*tegulatus, fibrosus, caucasicus*) and a lineage of inequivalved species (*argenteus, dobrovi*). The equivalved species occur in the uppermost Late Campanian, Early Maestrichtian and lowermost Late Maestrichtian, and the inequivalved species appear to be restricted to the Late Maestrichtian.

Tenuipteria fibrosa and *argentea* are redescribed and illustrated, a neotype for *argentea* is designated, and a lectotype for *T. tegulata* is designated.

POSTILLA 145: 45 p. 25 MAY 1970.

INTRODUCTION

Externally similar species of *Inoceramus*?, characterized by relatively strong concentric and radial plicae, occur in the latest Campanian and Maestrichtian of Europe and North America. These species are included by authors in a single species group, that of *Inoceramus*? *tegulatus* Hagenow (Jeletzky and Clemens, 1965). The stratigraphic range in regions of Europe and North America of the five species here accepted as valid is given in Figures 1 and 2.

Species included in this group are frequently referred to in biostratigraphic studies and in discussions of inter-regional correlations among North America, Western Europe and Russia (Dobrov, 1951; Seitz, 1959; Jeletzky, 1962). However, because of a lack of knowledge of internal morphology, the generic position of *I.*? *fibrosus* (Meek and Hayden) and the other species has been uncertain (Jeletzky, 1962, p. 1014; Jeletzky and Clemens, 1965).

Well-preserved specimens of *I.*? *fibrosus* from the Mobridge Member of the Pierre Shale and the overlying Fox Hills Formation in the type area of the latter in north-central South Dakota, Western Interior of the United States (Waage, 1961, 1968), provide for the first time full details of the hinge morphology and musculation of the species. These data, together with similar data for two other members of the species group, *I.*? *tegulatus* Hagenow from Europe and *Tenuipteria argentea* (Conrad; Stephenson, 1955) from the Owl Creek Formation, Gulf Coast, North America, permit a reevaluation of the generic status of these species.

Abbreviations used in the text and plate captions are:

MMH	— Mineralogisk-Geologiske Institut, Copenhagen, type specimen number
NZGS–WM	— New Zealand Geological Survey, World Mollusca Collection
UMMP	— University of Michigan Museum of Paleontology
USGS	— United States Geological Survey
USNM	— United States National Museum
YPM	— Peabody Museum of Natural History, Yale University, type specimen number
YPM–A	— Peabody Museum of Natural History, Yale University, collection number

ACKNOWLEDGEMENTS

Comparison of the species of the *Inoceramus*? *tegulatus* species group was facilitated through the loan of specimens, provision of information and discussions by the following persons whose assistance is appreciated and gratefully acknowledged: Dr. Erle G. Kauffman, United States National Museum; Prof. K. M. Waage, Peabody Museum of Natural History, Yale University; Dr. J. A. Jeletzky, Geological Survey of Canada; Dr. L. B. Kellum, Museum of Paleontology, University of Michigan; Dr. Tové Birkelund, Mineralogisk Museum, Universitetets Mineralogisk-Geologiske Institut, Copenhagen; and Prof. Dr. O. Seitz and Dr. F. Schmid, Niedersächsisches Landesamt für Bodenforschung, Hannover. S. N. Beatus took most of the photographs for the plates. Drs. A. Wodzicki and G. A. Challis, New Zealand Geological Survey, kindly translated parts of Polish and Russian papers.

Drs. Kauffman, Waage, Birkelund, and G. R. Stevens and C. A. Fleming, New Zealand Geological Survey, read the manuscript and made valuable suggestions.

Specimens of *Inoceramus*? *fibrosa* were collected and described as part of a dissertation for the degree of Doctor of Philosophy at Yale University while the author was on leave from the New Zealand Geological Survey under a New Zealand Department of Scientific and Industrial Research National Research Fellowship.

THE INOCERAMUS? TEGULATUS HAGENOW SPECIES GROUP

NORTH AMERICAN SPECIES

Two groups of thin-shelled *Inoceramus*? with weak to moderately strong radial and concentric ornament have been recognized in latest Cretaceous sequences of the United States: (a) Equivalved or possibly subequivalved species with moderately inflated and weakly projecting, anteriorly situated umbones. (b) Inequivalved species with a strongly inflated left valve possessing a projecting, swollen umbone and a flattish right valve with a very slightly projecting umbone.

Three names have been given to species classified in the equivalved group. All are known only from the Western Interior.

1. *Inoceramus fibrosus* (Meek and Hayden, 1856a). Lectotype,

by subsequent designation of Meek (1876, Pl. 17, fig. 17a), USNM 460, a steinkern of a right valve, oblique length 34.7 mm. Type locality: Forks of the Cheyenne River, South Dakota. Stratigraphic position: Pierre Shale, Early Maestrichtian.

2. *Inoceramus whitii* Toepelman (1922, p. 63). Location of type material unknown (see Cobban, in Jeletzky and Clemens, 1965, p. 958). Type locality: White River Badlands, South Dakota. Stratigraphic position: from the "transitional beds between the Pierre and Fox Hills" (Toepelman, 1922, p. 63), Early Maestrichtian.

Jeletzky (Jeletzky and Clemens, 1965) thought that this interval might be equivalent to part of the Mobridge Member, at the top of the Pierre Shale, in the Missouri Valley succession, but it could in part be equivalent to even older Pierre Shale units (Waage, 1961, 1968).

3. *Inoceramus cobbani* Kellum (1964, p. 1006; = *radiatus* Kellum, 1962, *non* Heine, 1929). Holotype, the original (and only) specimen of Kellum (1962, Pl. 3, fig. 17), UMMP 37433, a left valve, length 22.9 mm. Type locality: 1924/K–6, Old Woman Creek, Niobrara County, Wyoming. Stratigraphic position: Fox Hills Sandstone, Maestrichtian.

In addition to these three named "species" Cobban (1964, p. A136) has recognized a stratigraphic succession of four forms, each with a different pattern of ornament:

> . . . an early form with weak radial and concentric folds, a later form (typical form) in which radial folds dominate over the concentric ones, and a still later form in which radial and concentric sculpture is of about equal strength, and a final form in which the concentric sculpture dominates.

The typical form of *I.*? *fibrosus* is rhomboidal in shape, has strong radial plicae and corresponds to the second group of Cobban (1964). *Inoceramus cobbani* Kellum is characterized by extremely weak radial ornament and stronger concentric plicae, and could be classed in Cobban's group four.

Jeletzky, in one of his important studies of the North American species of the *I.*? *tegulatus* species group (Jeletzky and Clemens, 1965, p. 958), noted that "representatives of *I. whitii* always occur in association and appear to intergrade with the more typical representatives of *Inoceramus*? *tegulatus*" (= *fibrosus,* according to Jeletzky). He considered *whitii* to be an extreme morphological variant of the one "polytypic species". Jeletzky also placed *cobbani* (= *radiatus)* in synonymy with *whitii.*

Populations of *I.*? *fibrosus* from all biostratigraphic zones of the Fox Hills Formation in its type area are extremely variable in shape and ornament. Individual specimens from populations of *fibrosus* match exactly the specimen of *cobbani* figured by Kellum (1962, Pl. 3, fig. 17). The same applies to *whitii* which, on the basis of Toepelman's description, is indistinguishable from the Fox Hills species. Specimens with strong radial ornament (*fibrosus* sensu stricto) occur in populations from all stratigraphic zones in the Fox Hills Formation but are more common in the underlying Mobridge Member of the Pierre Shale.

Future detailed statistically based studies on adequate samples from various horizons may prove the existence of successive subspecies. Until this type of study is undertaken the information available suggests that only one morphologically variable species, for which the name *fibrosus* has priority, should be recognized in the uppermost Cretaceous of the Western Interior of the United States and Canada. This procedure is accepted for the purpose of this paper.

Two species of inequivalved, radially plicate *Inoceramus*? have been described from the Maestrichtian of the Gulf Coast of the United States (Fig. 2).

1. *Inoceramus argenteus* Conrad (1858, p. 329). Type specimen lost (Stephenson, 1955, p. 111; Richards, 1968). Type locality: Owl Creek, Tippah County, Mississippi. Stratigraphic position: Owl Creek Formation, Maestrichtian.
2. *Inoceramus costellatus* Conrad (1858, p. 329). Other data as for *I. argenteus.*

Stephenson (1955, p. 111) synonymized *costellatus* under *argenteus* but did not discuss the reasons for this step. As Conrad described *argenteus* first on page 329, Stephenson probably used the argument of page priority. Conrad's (1858) illustrations do not permit positive conspecific identity of the two specimens. The figure of *argenteus* is poor and shows an incomplete left valve apparently marked only by fine concentric plicae. His figure of *costellatus* (1858, Pl. 34, fig. 12) is good and shows an inequivalved specimen with strong radial and concentric plicae on the right valve. Conrad recorded the presence of an inoceramid hinge on the specimen. Consequently it would have been better to select *costellatus* as the valid name of the species.

Stephenson (1955) separated *argenteus* from *Inoceramus,* largely on the basis of its possession of a narrow ligament area bearing only a few (5 to 6) shallow ligament pits of irregular width, spacing and impression, and made it the type species of a new genus *Tenuipteria.* The status of this taxon is discussed in a later section.

EUROPEAN SPECIES

Three species and eight varieties of small, thin-shelled *Inoceramus* closely resembling *I.? tegulatus* Hagenow and *fibrosus* (Meek and Hayden) have been named from latest Cretaceous sequences of an area extending from Western Europe to the Caucasus.

1. *Inoceramus tegulatus* Hagenow (1842, p. 559). Lectotype, here designated, the original of Wolansky (1932, Pl. 5, fig. 6), an almost complete left valve in the original collection studied by von Hagenow, in the Geological-Paleontological Institute, University of Griefswald, East Germany. Type locality: Rügen Island, East Germany. Stratigraphic position: Mukronatenkreide, Lower Maestrichtian (Wolansky, 1932; Nestler, 1965).

2. Inoceramus *caucasicus* Dobrov (1951, p. 167). Holotype, by original designation, specimen no. 12 of Dobrov (1951, Pl. 2, fig. 2), bivalved, height 35 mm, length of ligament area 17 mm. Type locality: Dobrun Zolka River, Northern Caucasus. Stratigraphic position: Maestrichtian (Mst. s_1). (Specimen in the Geological Cabinet of Moscow State University.)

3. *Inoceramus dobrovi* Jeletzky (Jeletzky and Clemens, 1965, p. 956). Holotype, by original designation of Jeletzky (Jeletzky and Clemens, 1965, p. 956), the original of Dobrov (1951, Pl. 2, figs. la-c), a complete bivalved specimen, length 37 mm, height 30 mm. Type locality: Darya River, Northern Caucasus. Stratigraphic position: Maestrichtian (Mst. s_2). (Specimen in the Geological Cabinet of Moscow State University.)

Dobrov (1951) also proposed eight new varieties, three under his concept of *tegulatus* Hagenow and five under his concept of *caucasicus* Dobrov, namely:

I. tegulatus Hagenow var. *gibbera* Dobrov
I. tegulatus Hagenow var. *undulato-sulcata* Dobrov
I. tegulatus Hagenow var. *curta* Dobrov

I. caucasicus Dobrov var. *monilifera* Dobrov
I. caucasicus Dobrov var. *cabardinica* Dobrov
I. caucasicus Dobrov var. *fluctuosa* Dobrov
I. caucasicus Dobrov var. *fistulata* Dobrov
I. caucasicus Dobrov var. *ravni* Dobrov

Hagenow (1842, p. 559) did not illustrate any of his specimens of *tegulatus*. A translation of his brief description follows:

> 6) *I. tegulatus n.* The present very damaged 10 examples allow only a general comparison to the former similar species [refers to *I. mytiloides* Mantell, a species described directly before], and both valves appear to be symmetrical and moderately strongly inflated. Just as in the case of *I. mytiloides* growth ridges are crossed by 14 to 18 radiating furrows which have a sharper base, among which 3–4 are always more prominently impressed. The generally equally broad and flat raised intervals resemble a row of overhanging flat roof-tiles with a somewhat convex front margin.

The last part of the first sentence of Hagenow's description makes it almost certain that he was studying an equivalved species. This interpretation is supported by Wolansky's (1932, p. 28–29) revision of the original collection of von Hagenow. Her statement (p. 29) "Der Angabe ödums, dass die rechte Klappe kleiner sei als die linke und keinen vorspringenden Wirbel besitze, kann ich nicht folgen, da mir auch solche Schalen mit kräftig ausgeprägtem Wirbel vorliegen" indicates a similar degree of projection of the umbones of both valves. Although Wolansky says the right valve has a strongly projecting umbone, her illustrations (Pl. 4, fig. 4; Pl. 5, figs. 5, 6), while not good, especially for the left valve, clearly show, as noted by Jeletzky (Jeletzky and Clemens, 1965, p. 956), that Hagenow's species is equivalved and has similar moderately inflated and slightly projecting umbones on each valve. Wolansky (p. 34) synonymized in *tegulatus* the specimens classified as *mytiloides* by von Hagenow.

Prior to Wolansky's (1932) restudy of Hagenow's original collection, Ødum (1922, p. 10) examined specimens from the "White Chalk of Denmark" and defined *I. tegulatus* Hagenow:

> The main characteristics of *Inoceramus tegulatus* are as follows: the long anterodorsal angle, the considerable difference in convexity of the right and left valves, the radial ribs and the small ear formed by the long anterodorsal angle. To these

> features may be added the absence of small pits in the ligament area. (Translation by New Zealand Department of Internal Affairs.)

In his detailed description Ødum stressed the inequivalveness and the presence of a strongly inflated and projecting umbone on the left valve and a small very weakly projecting umbone on the right valve. The few specimens and illustrations available to the writer suggest that the umbone of the right valve is less prominent than that on Hagenow's specimens (see also Jeletzky, in Jeletzky and Clemens, 1965, p. 956).

Seitz (1959, p. 123–124) was the first to point out the existence of two concepts for *I. tegulatus*: an equivalved "Avicula-like" *I. tegulatus* Hagenow (see Pl. 2, figs. 1–3) and an inequivalved "Pholadomya-like" *I. tegulatus* Hagenow of Ødum (see Pl. 2, figs. 4–6). Jeletzky (Jeletzky and Clemens, 1965) later fully documented the differences between the two species and renamed Ødum's species concept as *I. dobrovi* Jeletzky, but he selected the holotype for his new species from a suite of Caucasian specimens described and illustrated by Dobrov (1951).

Seitz also considered there to be a possible difference in ornament between *tegulatus* Hagenow and *dobrovi* Jeletzky. Specimens of the two species sent to the writer by Dr. Tové Birkelund tend to confirm Seitz' observation. *I. dobrovi* appears to have consistently finer and more regular concentric plicae and more regular radial plicae that are restricted to the anterior half of the valve, whereas the broad posterior wing has regular concentric growth lamellae only. As stressed by Seitz (1959, p. 124), additional well-preserved and accurately identified specimens are required to clarify the apparent differences in ornament and to document more adequately other possible morphological differences, especially of the form of the anterior ear of the left valve and of the ligament area of *I. dobrovi.*

Differences in the prominence of the umbone and the form of the anterior ear of valves figured by Ødum (1922) and my knowledge of these features on the North American *I.*? *fibrosus* led me to suspect that Ødum may have studied specimens of both *tegulatus* Hagenow and *dobrovi* Jeletzky. My suspicion was confirmed independently by the observations of Birkelund, who commented (letter of January 15, 1966):

> In Ødum's paper both *I.*? *tegulatus* v. Hag. (fig. 4, 5, 6) from the Lower Maastrichtian and *I.*? *dobrovi* Jeletzky (fig. 1, 2, 3, 7)

> from the Upper Maastrichtian are figured. Ødum (1922) did not mention any differences between the specimens he examined from the Lower and Upper Maastrichtian of Denmark and Jeletzky (in his 1965 paper) did not realize that Ødum figured both the so-called *I.*? *dobrovi* and the real *I.*? *tegulatus* v. Hag.

The nonrecognition by Jeletzky of the mixture of species studied by Ødum does not affect in any way Jeletzky's conclusions of the validity of the two species.

The third European spècies, *I. caucasicus* Dobrov, was named by Dobrov during his study of the *I. tegulatus* species group in the uppermost Cretaceous of the Caucasus. Dobrov recognized two species: *I. caucasicus* in the upper Lower and lower Upper Maestrichtian (Mst. s_1; upper marl) and *I. tegulatus* Hagenow in the upper Upper Maestrichtian (Mst. s_2; limestone). Dobrov's text and illustrations prove conclusively that he followed Ødum's concept of *I. tegulatus,* and I agree with Jeletzky (in Jeletzky and Clemens, 1965) in accepting the *I. tegulatus* Hagenow of Dobrov as conspecific with *I. dobrovi* Jeletzky.

The varieties of *I. tegulatus* and *dobrovi* proposed by Dobrov (1951), some of which apparently occur together, are here believed to be extreme morphological variants of their respective species. *Inoceramus caucasicus* Dobrov includes specimens with strong concentrics but with very weak radials (holotype of *caucasicus*) to those with very strong radial plicae (*caucasicus* var. *fistulosa*). The latter closely resemble the holotype of *I.*? *fibrosus*. Specimens of *I. dobrovi* Jeletzky (= the *tegulatus* of Dobrov) show a comparable range of ornament, i.e., weak radials (*tegulatus* var. *gibbera* of Dobrov) to strong radials (*tegulatus* var. *undulato-sulcata* of Dobrov).

To summarize: As in North America, two species occur in the latest Cretaceous: an equivalved species with moderately inflated and projecting umbones, distinct anterior ears, and similar ornament on each valve (*I.*? *tegulatus* Hagenow), and an inequivalved species with a strongly inflated and projecting umbone on the left valve and an almost flat right valve on which the umbone barely projects above the dorsal margin (*I.*? *dobrovi* Jeletzky).

The problems of whether *I.*? *caucasicus* and *I.*? *tegulatus* are synonymous or distinct subspecies and the status of the varieties of Dobrov require a statistical study of stratigraphically located samples of adequate numbers of specimens, as suggested above for the North American *I.*? *fibrosus*. The holotype of *caucasicus* has strong concentrics and weak radials, whereas the lectotype of *tegulatus* has strong radial and concentric plicae. Evidence of successive populations dominated by different ornament types would favor the possibility of different subspecies or species.

Because of past confusion in the concept of the species, specimens recorded in the literature as *I. tegulatus* should be reexamined to determine whether they are *tegulatus* (sensu stricto) or *dobrovi.*

GENERIC POSITION OF THE SPECIES OF THE INOCERAMUS? TEGULATUS SPECIES GROUP

The generic position of the species of the *I.? tegulatus* species group has been uncertain from the date they were proposed, in part because of the pteriid-like shape and presence of a distinct anterior ear, largely because of our lack of knowledge of the internal morphology of the species. *Inoceramus*? *fibrosus* has been classified in *Avicula* Lamarck, *Pholadomya* G. B. Sowerby, *Pinna* Linnaeus, *Pteria* Scopoli, *Pseudoptera* Meek, *Inoceramus* J. Sowerby, *Actinoceramus* Meek, and *Tardinacara* Elias (nomen nudum) — *Inoceramus* being the most frequently used (see Jeletzky, 1962). *Inoceramus*? *tegulatus* Hagenow has been placed under *Inoceramus* and *Spyridoceramus* Heinz (1932).

Inoceramus? *fibrosus* (Meek and Hayden) from the type area of the Fox Hills Formation has a ligament area that is longitudinally striated, with a few irregular depressions crossing the area under the umbone, but lacking the regular incised ligament pits characteristic of *Inoceramus* (Pl. 1, figs. 1, 3). The specimens also bear a distinctive pattern of muscle scars. The true *tegulatus* Hagenow of Ødum (1922, figs. 4–6; Pl. 2, fig. 2) has a similar ligament area, but some specimens (Ødum, fig. 6) have small, faint, irregular pits along part of the ligament area similar to but less distinct and regular than those on the ligament area of species of the *I. barabini* group from the Pierre Shale (see p. 31). Dr. Birkelund (letter of February 7, 1966) has informed me that Ødum's specimen with the ligament pits is "stratigraphically older than the specimens from Alborg" which have no pits. Consequently, the degree of impression and regularity of the pits probably degenerated during the late Campanian-early Maestrichtian.

Although the musculation of *tegulatus* Hagenow is unknown, and although some doubt may exist as to the degree to which weak ligament pits are present on the ligament area, the similarity of the ligament areas and of external morphology make it reasonably certain that *fibrosus* and *tegulatus* are congeneric. The ligament area and musculation of *caucasicus* were not observed by Dobrov. However, because of its close external similarity and approximate time equivalence with *tegulatus,* I tentatively accept *caucasicus* as congeneric with *fibrosus* and *tegulatus.*

The musculation of the inequivalved species *argenteus* Stephenson and *dobrovi* are unknown. The ligament area of *argenteus* has two to six shallow irregular pits as described by Stephenson (1955); that of *dobrovi* is unknown. Except for the inequivalveness, and the presence of irregular weak pits crossing the ligament area, *argenteus* is closely similar to *tegulatus* and *fibrosus* and is here considered congeneric with them under the broad generic diagnosis given below. Because of its close external similarity to, and approximate stratigraphic equivalence with *argenteus, dobrovi* is here tentatively considered congeneric with *argenteus.*

The lack of incised regular ligament pits crossing the full width of the ligament area and the presence of a distinctive pattern of muscle scars clearly separate the *tegulatus* species group from *Inoceramus* J. Sowerby, as defined by the type species *I. cuvierii* J. Sowerby (1814) (Cox, 1955).

Three names are available for the generic taxon to include *tegulatus* Hagenow, *fibrosus* (Meek and Hayden), *argenteus* Conrad, and probably the other two species also: *Tardinacara* Elias (1931, opp. p. 58, p. 122, 130), *Spyridoceramus* Heinz (1932, p. 19) and *Tenuipteria* Stephenson (1955).

Tardinacara was proposed by Elias (1931, p. 130) in the form " . . . *Inoceramus fibrosus* Meek & Hayden (*Tardinacara* [*Pseudoptera*] *fibrosa* of the writer) . . . " and was not accompanied by a diagnosis or use of the words new genus or type. As stated by Jeletsky (in Jeletzky and Clemens, 1965, p. 955) it is a nomen nudum.

Spyridoceramus Heinz was proposed as follows:

> "*Spyridoceramus* nov. gen.
> Genotyp: *Inoceramus tegulatus* HAG.
> Die systematische Stellung dieser Gattung ist noch ungewiss."

There was no diagnosis, discussion or illustration, and it is not certain which concept of *I. tegulatus* Hagenow, the equivalved or inequivalved, was meant by Heinz. As Ødum's (1922) description was relatively recent and superior to earlier descriptions, Heinz may have accepted the concept of an inequivalved *I. tegulatus* Hagenow (= *I.*? *dobrovi*).

Heinz' name *Spyridoceramus* is invalid (Article 12, International Code of Zoological Nomenclature, adopted by the 15th International Zoological Congress with later minor amendments (Stoll et al., 1964)), as has been recognized by Vokes (1967, p. 171), even though Heinz selected a type species and obeyed the rules operative prior to 1931. Other workers have accepted (Aliev, 1958) or validated (Seitz, 1961) names proposed by Heinz (1932). However, as recommended by the International Commission of Zoological Nomenclature (1950, Bull. Zool. Nomenclature, v. 14, p. 563, paragraph 48), the validation of nomina nuda or invalid names may cause confusion and should be avoided.

Tenuipteria Stephenson 1955 is a valid name and is here applied to the five species discussed above. A diagnosis and discussion of my concept of the genus is given in the systematic section of this paper.

ADDENDUM. In the recently published Part N, Mollusca 6, Bivalvia, of the *Treatise on Invertebrate Paleontology* (R. C. Moore, ed., Geological Society of America and University of Kansas Press, 1969), a copy of which was received while this paper was in galley proof, the generic taxon *Spyridoceramus* Cox, new genus, was validated (p. N320) by the late Dr. L. R. Cox, who noted that "*Inoceramus argenteus* Conrad is the North American representative of this genus" and placed the genus in the Inoceramidae. On page N310 Cox accepted the genus *Tenuipteria* Stephenson, 1955, with *Inoceramus argenteus* as type species, and classed it in the Bakevelliidae.

If *argenteus* and *tegulatus* are considered conspecific, as clearly held by Dr. Cox and by myself in this paper, *Tenuipteria* has priority and is the valid name for the generic taxon. Future studies may permit the application of the name *Spyridoceramus* to an equivalved generic or subgeneric taxon.

BIOSTRATIGRAPHY AND CORRELATION

EUROPE

In Europe the species of *Tenuipteria* are recorded from the latest Campanian and Maestrichtian of the Russian Platform, northern

Poland, northern East and West Germany, Sweden and Denmark. The species are restricted to the Boreal Province (Jeletzky, 1948, 1951; Naidin, 1954; Kongiel, 1962).

Biostratigraphic subdivision of the latest Campanian and Maestrichtian of Europe has been based on many phyla and classes of organisms. Up to seven zones have been recognized in the Maestrichtian (Troelsen, 1937; see Birkelund, 1957, table 4). Belemnoids are of primary importance for zonation, and two (Naidin, 1952; Maslakova, 1959; Moskvin, 1962), three (Kongiel, 1962), four (Birkelund, 1957; Jeletzky, 1951) or five (Jeletzky, 1958, 1962; Naidin, 1960) zones are accepted.

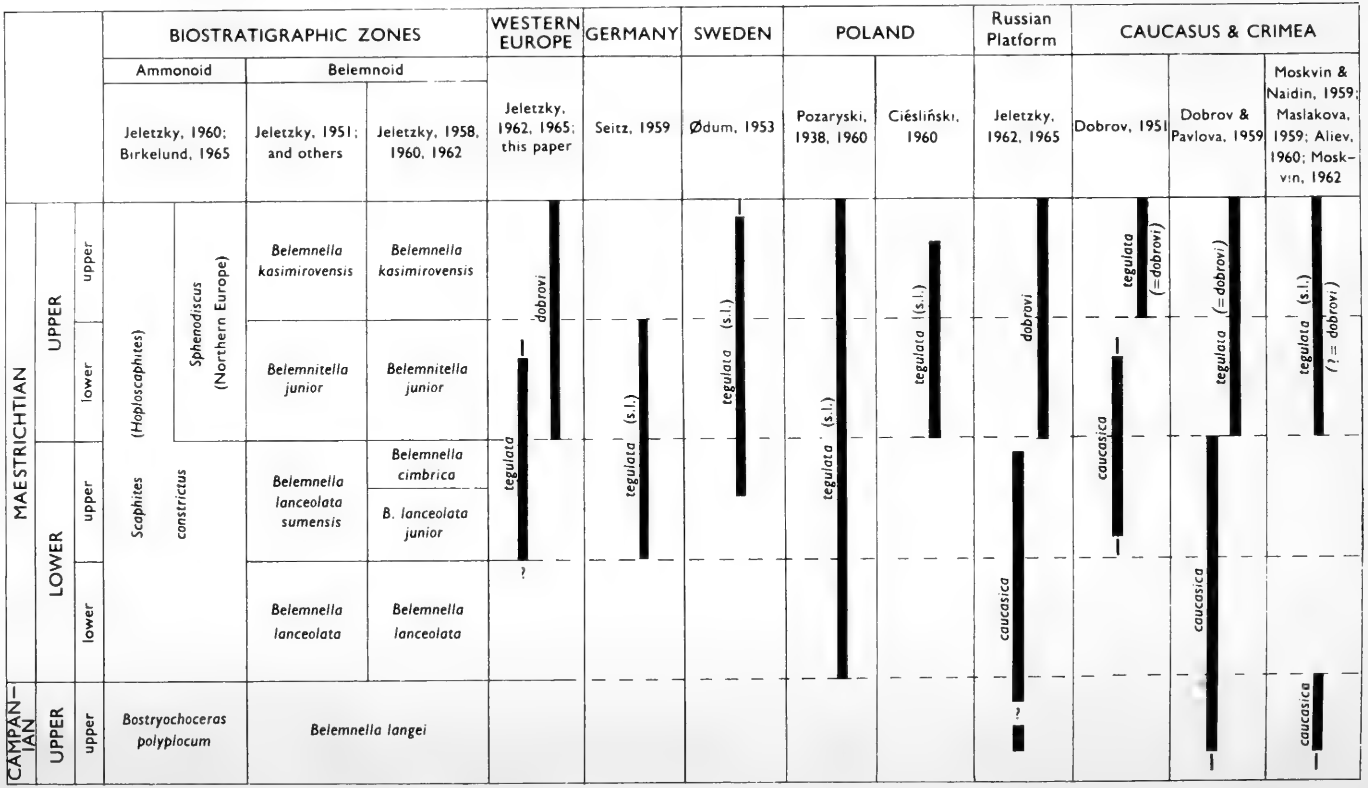
The controversy over the identification and nomenclature of belemnoid species important for the zonation of the European Maestrichtian (Kongiel, 1962, p. 23; Birkelund, 1965, p. 153), the diversity of proposed zonations, and the overlapping range zones of many belemnoid species (Kongiel, 1962, tables 6, 7; Birkelund, 1957, table 4) raise doubt as to the validity of the standard zonation and proposed correlations between sections (see also Wood, 1967), and are perhaps responsible for the difficulties encountered in deciding the position of the Campanian-Maestrichtian boundary (Birkelund, 1957) and of boundaries within the Maestrichtian (Ebensberger, 1962, p. 9). As most workers have employed a fourfold subdivision of the Maestrichtian, it is here accepted as a framework to which can be related the ranges of the European species of the *Tenuipteria tegulata* species group.

The stratigraphic range of the species of *Tenuipteria* in important areas is given in Figure 1. For four reasons this table should be interpreted with caution:

Firstly, *caucasica* Dobrov is treated as distinct from *tegulata* Hagenow, although future systematic work may show them to be conspecific.

Secondly, in the absence of illustrations the specific status of specimens listed as *tegulata* by many authors is uncertain. These records are treated as *tegulata* (sensu lato) but may include equivalved *tegulata* or *caucasica* and/or the inequivalved *dobrovi*.

Thirdly, the belemnoid zones of Northwest Europe and Russia are taken as approximately time equivalent. This is probably only partly true, for in Russia Jeletzky (1958; 1962, p. 1013) considers the zone of *Belemnella kasimirovensis* to include some of the "latest lower Maestrichtian" and the zone of *Belemnella lanceolata* to extend down into the uppermost Campanian.


BIOSTRATIGRAPHIC ZONES
Ammonoid
Belemnoid
Jeletzky, 1960; Birkelund, 1965
Jeletzky, 1951; and others
Jeletzky, 1958, 1960, 1962
WESTERN EUROPE
Jeletzky, 1962, 1965; this paper
GERMANY
Seitz, 1959
SWEDEN
Ødum, 1953
POLAND
Pozaryski, 1938, 1960
Ciésliński, 1960
Russian Platform
Jeletzky, 1962, 1965
CAUCASUS & CRIMEA
Dobrov, 1951
Dobrov & Pavlova, 1959
Moskvin & Naidin, 1959; Maslakova, 1959; Aliev, 1960; Moskvin, 1962
MAESTRICHTIAN
UPPER
upper
lower
LOWER
upper
lower
CAMPAN-IAN
UPPER
upper
Scaphites (Hoploscaphites)
Sphenodiscus (Northern Europe)
constrictus
Bostrychoceras polyplocum
Belemnella kasimirovensis
Belemnitella junior
Belemnella lanceolata sumensis
Belemnella lanceolata
Belemnella kasimirovensis
Belemnitella junior
Belemnella cimbrica
B. lanceolata junior
Belemnella lanceolata
Belemnella langei
dobrovi
tegulata
?
tegulata (s.l.)
tegulata (s.l.)
tegulata (s.l.)
tegulata (s.l.)
dobrovi
caucasica
?
tegulata (=dobrovi)
caucasica
tegulata (=dobrovi)
caucasica
tegulata (s.l.) (? = dobrovi)
caucasica

Fourthly, in relating the threefold belemnoid zonation of the Lower Maestrichtian to the twofold zonation, the zone of *B. lanceolata* is taken to be equivalent to the Lower Lower Maestrichtian and the other two zones to the Upper Lower Maestrichtian. This does not correspond to the proportions shown by Jeletzky in tables accompanying his papers of 1958, 1960 and 1962.

Figure 1 suggests three patterns:

1. In both Northwest Europe and Russia older equivalved species (*tegulata-caucasica;* upper Campanian to lowermost Upper Maetrichtian) are followed by a younger inequivalved species (*dobrovi;* Upper Maestrichtian).
2. The equivalved species appears earlier in Russia *(caucasica),* in the zone of *Bostrychoceras polyplocum* (Maslakova, 1959), than in Europe (*tegulata;* Seitz, 1959), whereas the inequivalved species appears to have similar stratigraphic ranges in both regions.
3. The equivalved *tegulata* may extend into younger rocks in Northwest Europe than the equivalent *caucasica* in Russia, where *caucasica* probably did not continue to the top of the Lower Maestrichtian (Jeletzky, 1960, p. 1013; Dobrov and Pavlova, 1959). However, it should be noted that Dobrov (1951) originally recorded *caucasica* in the uppermost Lower Maestrichtian (Mst. i_2) and lowermost Upper Maestrichtian (Mst. s_1).

Dr. Friedrich Schmid (letter of September 27, 1966) has recently collected a poorly preserved specimen identified as *I. tegulatus* from the beds outcropping at Hemmoor at some 50 to 60 meters above the "Tonband" (Schmid, 1955, fig. 1). If the specimen is an equivalved *tegulata* Hagenow, this discovery represents a significant increase in the upward stratigraphic range of the species and places it well within the lower Upper Maestrichtian zone of *Belemnitella junior.*

If further systematic and biostratigraphic studies support these patterns, then the equivalved species (as *caucasica*) may have evolved on the Russian Platform, spreading later to Northwest Europe, and possibly becoming morphologically distinct (as *tegulata)* in the process. In this case the inequivalved *dobrovi* possibly also evolved on the Russian Platform but spread more rapidly to Northwest Europe.

FIG. 1. Stratigraphic distribution of the species of the *Tenuipteria tegulata* species group in the Upper Cretaceous of Europe. Note: *T. tegulata* (sensu lato) may include equivalved (*tegulata, caucasica*) and/or the inequivalved (*dobrovi*) species.

NORTH AMERICA

In North America species of *Tenuipteria* are recorded from the Maestrichtian of the Gulf Coast and the Western Interior of the United States and Canada. Until recently the epicontinental uppermost Cretaceous sea of the Western Interior was considered to open to the south (and doubtfully to the north) (Reeside, 1957; Hattin, 1967). Gill and Cobban (1966) and Birkelund (1965, fig. 125) have shown that the sea also opened to the north into the boreal ocean.

Two faunal provinces can be recognized. There is a Western Interior province, including central Canada, with faunas dominated by baculitid and scaphitid ammonoids and bivalves; this province has affinities with the Boreal Province (Birkelund, 1965). And there is a Gulf Coast province with faunas characterized by different families and species of bivalves, a more diverse gastropod fauna (Sohl, 1964) and sparse cephalopods. Because of the incomplete systematic coverage of phyla in one or both regions, documentation of the definitive characteristics of the provinces is at present inadequate.

Biostratigraphic zonation of the upper Campanian and Maestrichtian of the Western Interior is based principally on baculitid and scaphitid ammonoids (Cobban and Reeside, 1952; Jeletzky, 1962; Gill and Cobban, 1966), although zonation of the upper part of the section equivalent to the Fox Hills Formation is hampered by a lack of systematic work on the scaphite ammonoids (Waage, 1968). The Gulf Coast sequence is zoned at a grosser level by oysters (Sohl and Kauffman, 1964), gastropods (Sohl, 1960, 1964), and other molluscs (Stephenson et al., 1942). Cephalopods are uncommon and of limited importance. Zonation of the Western Interior and Gulf Coast sequences is complicated by the occurrence of nonmarine beds at the top of the Cretaceous and by stratigraphic breaks, respectively. Consequently, the range of species and zones based on marine organisms is likely to be incomplete.

Correlation of North American sequences is given in Figure 2. Correlation between the Western Interior and the Gulf Coast is complicated by a paucity of common taxa (Waage, 1968) and depends largely on the work of Jeletzky (1960), who argues that the *Scaphites (Discoscaphites) nebrascensis* zone of Fox Hills Formation in its type area is approximately isochronous with the *S. (D.) conradi* zone of the Prairie Bluff Chalk. Because of the close similarity of their faunas, correlation between the Western Interior and south-central Canada is good.

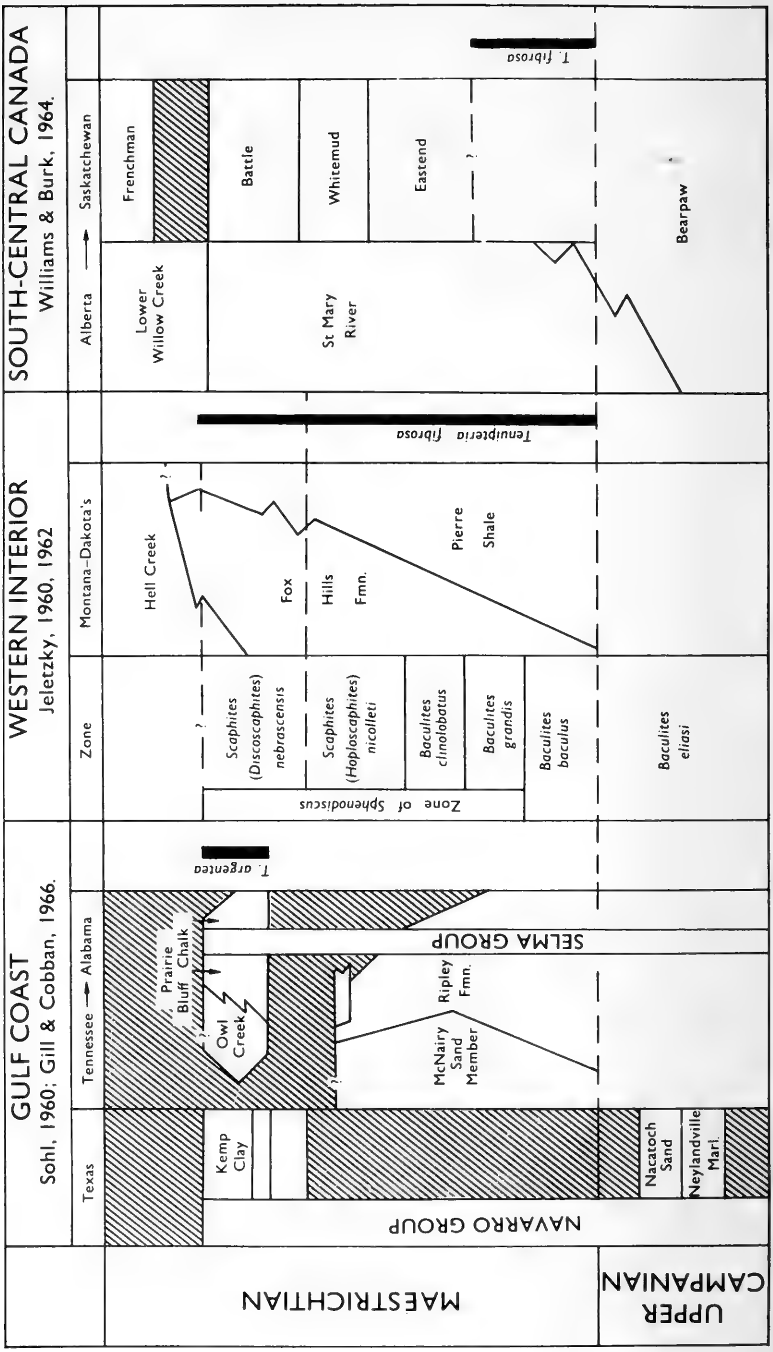
Figure 2 also shows the stratigraphic range of the North American species of *Tenuipteria*. The short range zone of *T. fibrosa* in south-central Canada is undoubtedly due to the change from marine to nonmarine deposition.

Tenuipteria argentea is known only from the Owl Creek and Prairie Bluff formations of northern Mississippi and southeastern Missouri. As these formations have unconformable lower and upper limits, the stratigraphic range of the species may have been much longer, a view supported by Sohl (1964, p. 155) who considers that a "moderate part of the Maestrichtian is missing." No radially ribbed, equivalved, mytiloid-shaped *Inoceramus* with relatively weak plicae which resembles *T. fibrosa* has been reported from the older units of the Navarro Group. A large subcircular right valve from the Nacatoch Sand, recorded as *"I. vanuxemi* Meek & Hayden?" by Stephenson (1941, Pl. 13, fig. 3), has strong, widely spaced, narrow concentric plicae, and fine, weak radial plicae. As the left valve holotype (Meek, 1876, Pl. 14, figs. 2a,b) and right valves studied by Meek (1876, p. 57) lack radial plicae, Stephenson's specimen should be reevaluated.

In contrast to the situation in Europe, no succession of an equivalved species followed by an inequivalved species has been recognized in any one region of North America. This may be largely due to the incompleteness of sequences and the onset of nonmarine deposition. If, as proposed by Jeletzky (1960), the Fox Hills Formation in its type area and the Prairie Bluff Chalk are correlatives, then *argentea* and *fibrosa* could have overlapping ranges much as *tegulata* and *dobrovi* overlap in the lower part of the Upper Maestrichtian *Belemnitella junior* zone of Northwest Europe (fig. 1).

CORRELATION BETWEEN THE LATEST CRETACEOUS OF EUROPE AND NORTH AMERICA

Correlations between the latest Cretaceous sequences of Europe and North America have been based on scaphitid and sphenodiscid ammonoids, belemnoids, and the bivalve genus *"Inoceramus"* (Seitz, 1959; Jeletzky, 1960, 1962; Birkelund, 1965; Waage, 1968). Only Cobban and Reeside (1952) and Jeletzky (1960, 1962) have proposed correlations at the intrastage level.


GULF COAST
Sohl, 1960; Gill & Cobban, 1966.
Texas
Tennessee → Alabama
Kemp Clay
Nacatoch Sand
Neylandville Marl
NAVARRO GROUP
Owl Creek
Prairie Bluff Chalk
McNairy Sand Member
Ripley Fmn.
SELMA GROUP
T. argentea
WESTERN INTERIOR
Jeletzky, 1960, 1962
Zone
Montana–Dakota's
Scaphites (Discoscaphites) nebrascensis
Scaphites (Hoploscaphites) nicolleti
Baculites clinolobatus
Baculites grandis
Baculites baculus
Baculites eliasi
Zone of Sphenodiscus
Hell Creek
Fox Hills Fmn.
Pierre Shale
Tenuipteria fibrosa
SOUTH-CENTRAL CANADA
Williams & Burk, 1964.
Alberta → Saskatchewan
Lower Willow Creek
St Mary River
Frenchman
Battle
Whitemud
Eastend
Bearpaw
T. fibrosa
MAESTRICHTIAN
UPPER CAMPANIAN
?

Cobban and Reeside (1952, p. 1026) did not document their statement that "the Fox Hills fauna corresponds to the upper Maestrichtian fauna of the European sequence". They seem to have accepted the correlation given by Stephenson and Reeside (1938, fig. 3). Jeletzky argued that the *S.* (*Discoscaphites*) *nebrascensis* zone of the type Fox Hills Formation and its equivalents in Texas and northern Mexico are Upper Lower Maestrichtian (upper part of the *Belemnella cimbrica* zone) (1960, fig. 2), and the *Triceratops* beds are of late Maestrichtian age (equal to part or all of the *Belemnitella junior* and *Belemnella kasimirovensis* zones of northern Europe). The possibility of a basal Upper Maestrichtian age for the uppermost marine Cretaceous of the Western Interior was not excluded by Jeletzky. In fact, in his text-figures (1962, text-figs. 1, 2) he extended the youngest Fox Hills Formation well into the range zone of *Belemnitella junior* (lower Upper Maestrichtian).

Considerable doubt exists as to the position of the base of the Maestrichtian Stage in the Western Interior sequences. Most workers follow Jeletzky (in Cobban and Reeside, 1952, p. 1026–1027) in tentatively placing the lower boundary of the stage at the base of the zone of *Baculites baculus*. On the evidence of the ammonites the boundary could be placed either at the base of the *B. baculus* zone or possibly within or at the top of the zone. Jeletzky favored the first alternative, emphasizing the appearance of certain European Lower Maestrichtian scaphitid species even though late Campanian European species are also present in the zone of *B. baculus* and other typical European Lower Maestrichtian species appear high in or above the *B. baculus* zone. Doubt about the stratigraphic ranges of many of the North American ammonoid species, and lack of documentation that the North American and European species discussed by Jeletzky are conspecific (Birkelund, 1965; Waage, 1968) increase the uncertainties of the proposed correlations between the regions.

Similarly, the position of the boundary between the Lower and Upper Maestrichtian in the Western Interior is uncertain. Most workers accept Jeletzky's (1962, p. 1008) selection of the upper limit as the top of the range zone of *Discoscaphites nebrascensis*.

Jeletzky (1960, 1962) placed a lot of weight for an upper Lower Maestrichtian age for the type Fox Hills Formation on his discovery

FIG. 2. Stratigraphic distribution of the species of the *Tenuipteria tegulata* species group in the Upper Cretaceous of North America.

at Hemmoor of an ammonoid fragment which he identified as *S.* (*H.*) *nicolleti*. Both Birkelund (1965) and Waage (1968) consider the fragment indeterminable. Waage goes further in showing it to be morphologically distinct from the true *nicolleti* of the Western Interior. After an analysis of the belemnoids, scaphitids and sphenodiscids, Waage concludes that an inadequate knowledge of the systematics, biostratigraphy, paleoecology and paleogeography of these taxa in both Europe and North America prevents refined correlations between the two regions. Of the cephalopods he emphasizes the potential value of hoploscaphitid ammonoids for correlation at the intrastage level (see also Birkelund, 1966).

The stratigraphic distribution of the species of *Tenuipteria* in Europe and North America tends to support Jeletzky's correlations. The equivalved species appear about the same time, latest Campanian, in both regions—at least in Russia and south-central Canada if the specimen of *fibrosa* from some 80 feet below the Belanger Sandstone Member of the Bearpaw Formation (Furnival, 1946, p. 62), and hence probably below the zone of *Baculites baculus,* is correctly identified. The absence of an inequivalved species of *Tenuipteria* in the Western Interior of the United States and Canada, together with the lack of other index taxa, counts against the presence of Upper Maestrichtian marine beds. Likewise, the occurrence of the inequivalved *T. argentea* in the Prairie Bluff Chalk of the Gulf Coast is compatible with a correlation with the latest Lower Maestrichtian and earliest Upper Maestrichtian.

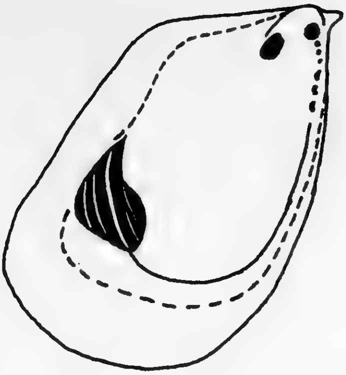
However, the present inadequate knowledge of the systematics, biostratigraphy and paleogeography of the species of *Tenuipteria,* coupled with the uncertain status of European latest Cretaceous biostratigraphy, negates the possibility of precise correlations. Theoretically, the species need not have isochronous range zones in Europe

FIG. 3. Muscle scar and pallial line impressions for inoceramid species from the uppermost Cretaceous of the Western Interior of the United States.

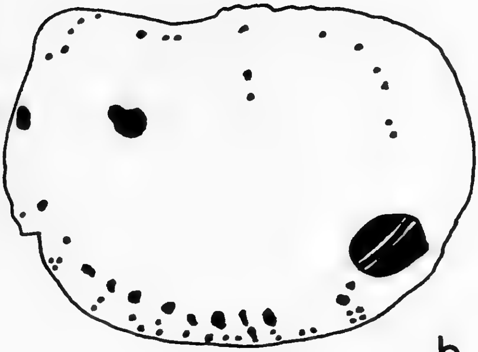
3a. *Tenuipteria fibrosa* (Meek and Hayden). YPM 24037, drawn from the original of Plate 1, figure 5. The dashed line indicates the position of edge of the inner shell layer.

3b. *"Inoceramus" barabini* Morton. YPM 24052, Pierre Shale, Converse County, Wyoming, C. E. Beecher and J. B. Hatcher, collectors.

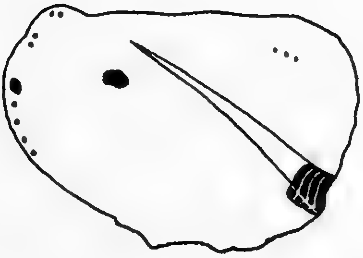
3c. *"Endocostea" typica* Whitfield. YPM 24053, Pierre Shale, Converse County, Wyoming.



a



b



c

and North America. Assuming that *caucasica* and *tegulatus* are conspecific, and that the correlations are correct, the nonisochroneity of some range zones would be well documented by the appearance of *caucasica* in Russia before the entry of *tegulatus* in Western Europe —a difference equivalent to the range zone of *Belemnitella lanceolata* (Fig. 1). Even if species are able to spread geographically in a geologically insignificant time interval, the evolution of a species in a region may involve at least half a million years (Gill and Cobban, 1966), and the migration and establishment of a species may be prevented by environmental, biological (Briggs, 1967), geological or hydrographic factors. For example, the later appearance of an equivalved species of *Tenuipteria* in Western Europe may be due largely to environmental control. Until detailed systematic and biostratigraphic studies are completed these arguments tend to be semantic.

Possibly the best evidence for the correlation of the Western Interior sequence comes from the assessment of biostratigraphy and potassium-argon ages prepared by Gill and Cobban (1966, p. 34–37). These authors demonstrate that the base of the *Baculites baculus* Range Zone, which is correlated with the base of the Lower Maestrichtian, is at about 70 million years, and that the *Discoscaphites nebrascensis* Range Zone is older than 66 ± 2 million years and estimated to be about 68 million years. Although these dates give a reasonably good fix for the Western Interior sequence and tend to place the youngest marine Cretaceous of the Western Interior in the latest Lower Maestrichtian, correlation with the European stages remains dependent on classical biostratigraphic methods. Refined correlation is not possible until radiometric ages are available for European sequences.

SYSTEMATIC DESCRIPTIONS

Tenuipteria Stephenson 1955 Emend.

SYNONYMY.

Tardinacara Elias, 1931, opp. p. 58, p. 122, 130 (nomen nudum).
Spyridoceramus Heinz, 1932, p. 19 (invalid, no diagnosis).

TYPE SPECIES. By original designation of Stephenson (1955, p. 110), *Inoceramus argenteus* Conrad (1958, p. 329), Owl Creek Formation, Maestrichtian, Gulf Coast, North America.

DIAGNOSIS. Thin-shelled inoceramid characterized by radial and concentric plicae, a distinct small anterior auricle and a narrow ligament area, concave in cross section, longitudinally striated, either lacking ligament pits *(fibrosa,* the stratigraphically younger *tegulata)* or with faint, broad, irregular, weakly impressed pits (stratigraphically older *tegulata, argentea).* Muscle scars consist of a posteroventrally situated large adductor scar and two anterodorsal byssal-pedal scars which are joined by a pallial line of discrete scars anterodorsally but fused ventrally *(fibrosa).*

EMENDED DESCRIPTION. Equivalved or inequivalved, when the left valve is the more strongly inflated, small to medium sized with a distinct anterior ear, usually delimited from the main disc of the shell, and a flattened, rounded, posterior dorsal margin. Umbones anterior, moderately projecting on equivalved species, strongly projecting on the left valve but only slightly projecting on the right valve of inequivalved species. Shell ornamented by radial and concentric plicae of variable strength and numbers, usually regular and tending to produce a distinctive "tile-like" pattern, but sometimes with the radial plicae stronger than the concentric, or vice versa. Along the crest and ventral flank of the concentric plicae are concentric lamellae which are dominant on the posterodorsal flank where the plicae are subdued or absent. Shell thin, of two layers: a thicker, outer prismatic shell layer which may project well beyond the margin of a thinner, inner nacreous shell layer *(fibrosa, tegulata).*

DISCUSSION. The above diagnosis has been made broad to include species of similar external ornament and shape, but either equivalved or inequivalved, and having a range of ligament area and musculation characteristics. In the diagnosis and description species names in parentheses are given after those features where the morphology is known from less than three species.

Species included in my broad concept of *Tenuipteria* are

Tenuipteria tegulata (Hagenow, 1842)
T. fibrosa (Meek and Hayden, 1856a)
T.? caucasica (Dobrov, 1951)
T. argentea (Conrad, 1858)
T.? dobrovi (Jeletzky and Clemens, 1965)

As discussed above, *fibrosa* and *caucasica* might be conspecific with *tegulata* and *dobrovi* with *argentea*. Because of lack of knowledge of the morphology of their ligament areas, *caucasica* and *dobrovi* are tentatively classed in the genus.

All species included in *Tenuipteria* differ from *Inoceramus* in one or a combination of the internal morphological characteristics.

Future work may show that the equivalved species with a few very weak or no ligament pits and a partly continuous pallial line (*Tenuipteria tegulata, fibrosa, ?caucasica*) should be separated subgenerically or generically from the inequivalved species with irregular, weak ligament pits, strongly inflated umbone and the correlated smaller anterior ear and convex anterodorsal margin on the left valve (*argentea, ?dobrovi*).

The Turonian genus *Didymotis* Gerhardt (1897) has a smooth ligament area lacking pits (Imlay, 1955) and superficially resembles *Tenuipteria* in shape, ornament and possession of a thin shell. However, the equivalved species of *Didymotis* are oval in shape, have inconspicuous subcentral umbones and a long, straight dorsal margin, and lack the distinctive regular "tile-like" ornament of *Tenuipteria*. On *Didymotis* irregular, closely spaced, concentric plicae dominate the few weak, widely spaced, radial plicae that occur only on the main disc of each valve (Gerhardt, 1897, Pl. 5, figs. 3a,b). The morphological differences between the genera, and the reasonable assumption of derivation from different inoceramid stocks at different times warrant their treatment as separate taxa. The resemblance of *Didymotis* to *Tenuipteria* is undoubtedly due to convergence, perhaps dependent on the adoption of a similar mode of life.

Tenuipteria fibrosa (Meek and Hayden)

(Plate 1, figs. 1–6; Fig. 3a)

Avicula? *fibrosa* Meek and Hayden, 1856a, p. 86–87.

Pholadomya fibrosa (Meek and Hayden). Meek and Hayden, 1856b, p. 283.

Pinna fibrosa (Meek and Hayden). Meek, 1864, p. 9.

Avicula (*Pseudoptera*) *fibrosa* (Meek and Hayden). Meek, 1873, p. 489.

Pteria (*Pseudoptera*) *fibrosa* (Meek and Hayden). Meek, 1876, p.

36–37, Pl. 17, figs. 17a–d. Whitfield, 1880, p. 386, Pl. 7, fig. 5. Whiteaves, 1885, p. 32, Pl. 4, fig. 1.

Inoceramus (*Actinoceramus*) *whitii* Toepelman, 1922, p. 63.

Inoceramus (Actinoceramus) fibrosus (Meek and Hayden). Dobbin and Reeside, 1929, p. 20.

Tardinacara (*Pseudoptera*) *fibrosa* (Meek and Hayden). Elias, 1931, opp. p. 58, p. 124, p. 130. Searight, 1934, p. 4.

Inoceramus (*Actinoceramus*) *fibrosa* (Meek and Hayden). Russell, 1940, p. 88.

Inoceramus fibrosus (Meek and Hayden). Landes, 1940, p. 136–137. Cobban and Reeside, 1952, p. 1020, and correlation chart. Jeletzky, 1962, p. 1011–1014, Pl. 141, figs. 4–7. Seitz, 1959, p. 123–124 (? synonymous with *I. tegulatus* Hagenow (1842, p. 559)).

Inoceramus radiatus Kellum, 1962, p. 57, Pl. 5, fig. 17 (*non* Heine, 1929, p. 105, Pl. 18, figs. 68, 69).

Inoceramus cobbani Kellum, 1964, p. 1006 (new name for *I. radiatus* Kellum).

Inoceramus? *tegulatus* Hagenow, 1842 (*non* Ødum, 1922). Jeletzky, in Jeletzky and Clemens, 1965, p. 957.

Tenuipteria fibrosa (Meek and Hayden). Speden, 1970, Pl. 8, figs. 11–18; Pl. 9, figs. 1–16.

DESCRIPTION. Specimens 5 to 55 mm long, equivalved, inequilateral, maximum inflation about mid-height close to anterior margin. Shape extremely variable, submytiloid to subquadrangular, and rarely almost oval. Height, anterior length and width are, respectively, 83 to 100, 8 to 15 and 12 to 27 percent of the length of the outline of the inner shell layer. Dorsal margin straight, posterodorsal margin rounded, and the angle subtended at the umbone by the dorsal margin and the line joining the posteroventral extremity is about 40 to 50 degrees. Umbones prosogyrous, sited near the anterior end of the straight dorsal margin, not prominent, project only slightly above the dorsal margin. Anterior auricle distinct, always present, relatively small but of variable size, delimited from the moderately to strongly inflexed anterodorsal margin by a narrow groove of variable prominence. When the anterodorsal margin is strongly inturned the associated groove is deep, and there is a distinct byssal notch and gape where the groove meets the margin. Otherwise, the byssal notch and gape are small or indefinite.

PLATE 1

Tenuipteria fibrosa (Meek and Hayden)

1. YPM 24644; ligament area of a left valve. Note the lack of ligament pits. YPM A–1140, Locality 115, *Protocardia-Oxytoma* Assemblage Zone, Little Eagle lithofacies, Trail City Member, Fox Hills Formation. X1.5.

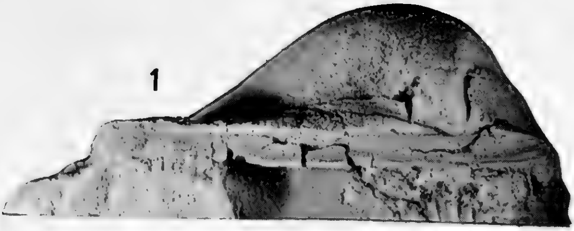
2,3. YPM 24033; the divergence of the outer prismatic layer from the inner layer dorsally and strong concentric plicae (2), and the striated ligament area which lacks ligament pits.
YPM A–992, Locality 231, Lower *nicolleti* Assemblage Zone, Little Eagle lithofacies, Trail City Member, Fox Hills Formation. Fig. 2 X1, Fig. 3 X2.

4. YPM 24039; right valve steinkern with equally strong radial and concentric plicae.
YPM A–336, Locality 32, Mobridge Member, Pierre Shale. X1.

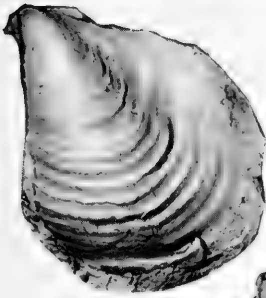
5. YPM 24037; right valve steinkern with a posteroventrally situated adductor scar and two anterior byssal-pedal scars on either side of an umbonal fracture. The specimen on which Figure 3a is based.
YPM A–350, Locality 39, *Cucullaea* Assemblage Zone, Timber Lake Member, Fox Hills Formation. X6.

6. YPM 24028; left valve steinkern with strong radial plicae.
YPM A–336, Locality 32, Mobridge Member, Pierre Shale. X2.

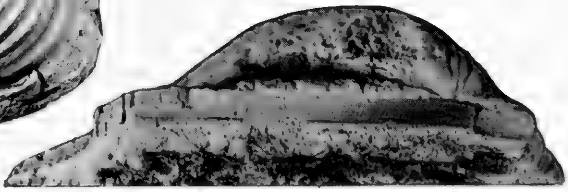
1



2

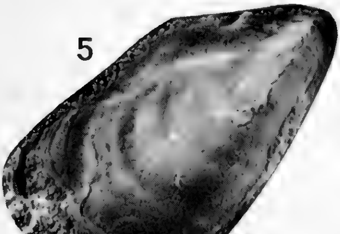


3



4

5



6

Ornament extremely variable, consisting of concentric and radial plicae usually of equal size and regular and giving a distinctive "tile-like" pattern, but sometimes with stronger radial or concentric plicae. Radial plicae appear at about 5 to 20 mm from the tip of the umbone and are absent only rarely on specimens longer than 20 mm. Radial plicae absent from the posterodorsal flank of the valve where the concentric plicae also weaken and concentric lamellae dominate. A concentric lamella occurs along the crest or along the dorsal part of the ventral flank of each concentric plica. Specimens greater than 30 mm in height have about 15 to 30 radial plicae, which are usually slightly wider than the interspaces, and about 20 to 35 concentric plicae. Some specimens have irregular broad undulations bearing three to four of the regular concentric plicae.

Ligament area extends the length of the dorsal margin, inclined at 30 to 40 degrees to the commissural plane, generally strong concave and almost semicircular in cross-section, or more rarely L-shaped with a wider, slightly concave dorsal limb and a flat ventral limb inclined at 60 to 80 degrees to the commissural plane. Surface of ligament area marked by fine longitudinal striae separated by much wider shallow grooves; striae stronger on the dorsal part of the ligament area, often weak or absent on the ventral part. Ligament area lacks impressed pits, but rare specimens show traces of faint shallow undulations. In the vicinity of the umbones the dorsal margin usually strongly overhangs the ligament area.

Posterior adductor scar large, elliptical to pear-shaped, tapering posterodorsally where deeply impressed at extremity, anterior margin with an indentation of variable prominence, situated at posteroventral extremity of inner shell layer close to its junction with outer shell layer; rarely preserved. In the umbonal cavity are two anterodorsal scars (pedal-byssal retractors), a small oval impression anterior to the line of maximum inflation and a slightly larger subrectangular scar posterior to the line of maximum inflation. Pallial line on inner shell layer close to junction with outer shell layer, consisting of a narrow continuous band with irregularly spaced swellings from the posterior adductor to above mid-height of shell, then continuing as a series of four to eight small discrete oval or linear impressions. Above the anterior pedal-byssal scar and close to the dorsal margin are sometimes seen three to five scars.

Calcitostracum very thin and fragile, observed maximum thickness 0.7 mm, rarely exceeds 0.5 mm, composed of a thick, outer prismatic layer and a thin, inner pearly nacreous layer one quarter to one sixth of the thickness of the outer layer. Outer layer extends considerably beyond the inner layer, forming a broad flange. Internal surface of the umbonal cavity is marked by fine irregular striae which approximately parallel the growth axis. Many specimens have a faint ridge along a line extending from the dorsal margin posterior to the umbone to the anterodorsal end of the posterior adductor.

TYPE SPECIMEN. Lectotype of *Avicula*? *fibrosa* Meek and Hayden, by subsequent designation of Meek (1876, Pl. 17, fig. 17a), USNM 460, a steinkern of a right valve, oblique length 34.7 mm. Type locality: Forks of the Cheyenne River, South Dakota. Stratigraphic position: Pierre Shale, Early Maestrichtian, Upper Cretaceous.

OCCURRENCE. In the Western Interior of the United States *T. fibrosa* occurs in the Pierre Shale and Fox Hills Formation and ranges from the *Baculites baculus* zone through to the top of the Timber Lake Member of the Fox Hills Formation. In the type area of the Fox Hills Formation it is common only in the Lower and Upper *nicolleti* assemblage zones (Waage, 1961). In south-central Canada it is known only from the upper part of the Bearpaw Formation (Jeletzky, 1962, p. 1012; and see Furnival, 1946, p. 62).

DISCUSSION. The description given above is based on specimens from the Mobridge Member, Pierre Shale, and the Fox Hills Formation in its type area. The reader is referred to Speden (1970) for additional illustrations of specimens of *fibrosa* and data on occurrence. No account is taken of the morphological variation described for other samples by Cobban (1964).

Important features of the morphology of *T. fibrosa* are discussed below:

a) *Shape*. The variation in shape is marked. A striking feature of complete specimens is that the outline of the outer shell layer does not parallel the outline of the inner shell layer. This divergence is most marked along the posterior and posteroventral margins, while the dorsal margin of the ligament area diverges from the dorsal margin of the inner shell layer by angles of 10 to 25 degrees (Pl. 1, fig. 2). The outline of steinkerns is usually defined by the margin of the inner shell layer, and all too frequently the thin outer shell layer breaks off along its junction with the inner layer. Consequently, the shape based on steinkerns, or even shelled specimens, may be false. *Tenuipteria fibrosa* tends to be more oval than is indicated by the typical mytiloid steinkerns.

Because of the wide variation in shape shown by *fibrosa,* and the nonparallelism of the outlines of the outer and inner shell layers, only gross measurements are given in the above description.

b) *Ornament.* The Fox Hills "populations" are characterized by extremely variable ornament. Normally, the radial and concentric plicae are of almost equal strength, although the concentric ornament is commonly stronger than the finer and more regular radial plicae. Specimens with strong radial sulci, which closely resemble the lectotype, are present in many collections from all assemblage zones but are more common in the Mobridge Member of the Pierre Shale along the Moreau River (YPM A-336). The radial plicae are very weak on some small specimens, particularly those in collections from the Timber Lake Member, Fox Hills Formation. However, this weakness may be related to the factor of size.

The pattern of ornament shown by the Fox Hills "populations" covers the third and fourth "forms" of Cobban (1964, i.e. those with "concentric and radial sculpture . . . of about equal strength, and a final form in which the concentric sculpture dominates". It should be stressed that the individual specimens may have very strong or very weak radial plicae. The range of variation of ornament in a single collection at a locality prevents positive placing in either of Cobban's "forms", at least until they are more fully documented.

Ornament studies ideally should be based on external moulds or the original shell surface and not on steinkerns, which are often all that a paleontologist has to study. In the case of the Fox Hills samples the narrow radial plicae are notably more subdued on the steinkern than on the external mould or shell surface

c) *Ligament area.* The ligament area is basically smooth and lacks the incised, transverse, rectangular ligament pits characteristic of the genus *Inoceramus.* Rare specimens show traces of faint shallow undulations on the floor of the ligament area. These, however, are irregular and cannot be compared with the ligament pits of *Inoceramus.* Ødum (1922) records the presence of similar faint undulations on his specimens of *T. tegulata* from the White Chalk of Denmark and shows the presence of small ligament pits on the dorsal half of the ligament area of a specimen from Møens Klint (1922, fig. 6). According to Birkelund (letter of February 2, 1966), the specimen with ligament pits from Møens Klint is stratigraphically older than the specimens from Aalborg which lack pits.

Small but distinct pits occur on the dorsal part of the ligament area of specimens of *Inoceramus* cf. *barabini* Morton (YPM 24452, 24055), labeled as from Converse County, Wyoming, Pierre Shale (Campanian), C. E. Beecher and J. B. Hatcher, collectors, held in the Division of Invertebrate Paleontology, Peabody Museum of Natural History, Yale University. On these specimens the pits are smaller and less definite toward and under the umbones (Speden, 1970). Derivation of the *fibrosa* type of pitless ligament area by degeneration from a typical *Inoceramus* ligament area with pits is suggested by these observations.

d) *Musculation.* Musculation is rarely described for species of *Inoceramus,* largely because of the lack of impression of the scars into the thin shell and the poor preservation of specimens. The adductor scar of *fibrosa* is also hard to find for the above reasons, and also because it is sited so close to the posteroventral margin of the inner shell layer, a portion of the shell often broken or not collected.

A search of the literature indicates that the musculation of species classed in *Inoceramus* consists characteristically of a pallial line of discrete scars and a posterior adductor scar sited in a submedial position (see Jones and Gryc, 1960, p. 159). Kauffman (1965) has recently recognized three types of muscle scar patterns in Cretaceous species of *Inoceramus.* One category includes that of *T. fibrosa* as described above. Other Upper Cretaceous *"Inoceramus"* species have a musculation pattern similar to that of *fibrosa,* but with a pallial line consisting solely of discrete scars and generally with small scars extending in a line across the posterodorsal part of the shell. A specimen (YPM 24052) of the *"Inoceramus" barabini* complex and two specimens (YPM 24053) labeled *"Endocostea typica* Whitf.", all from "Converse County, Wyoming, Pierre Shale", C. E. Beecher and J. B. Hatcher, collectors, have this type of pattern (Figs. 3b,c; see also Speden, 1970).

Species of recent isognomiid genera *(Isognomon, Melina)* have a very similar pattern of muscle scars, with two small byssal-pedal scars in an anterodorsal position, but the large adductor scar is usually in a more subcentral position on the inner shell layer and is joined to the anterior of the two anterodorsal scars by a line of discrete small pallial scars. The possession of similar musculation patterns supports the close relationship between the isognomiid and inoceramid stocks postulated on stratigraphic and other morphological grounds by many workers (Cox, 1940; Hayami, 1960). In the case of *fibrosa* the resemblance is probably secondary and due to convergence through the adoption by an inoceramid stock of an epifaunal mode of life similar to that of *Isognomon.*

COMPARISONS. Seitz (1959) suspected that *T. tegulata* Hagenow (not of Ødum) might be synonymous with *T. caucasica* Dobrov and *T. fibrosa* Meek and Hayden, but he stressed the need for further study of better preserved and more abundant specimens before his proposed synonymies could be accepted as valid. Jeletzky (1962), using the concept of *tegulata* Hagenow as an inequivalved species, synonymized *caucasica* Dobrov with *fibrosa* Meek and Hayden. In 1965 Jeletzky (Jeletzky and Clemens, 1965) accepted *tegulata* Hagenow as being an equivalved, morphologically variable species and synonymized *fibrosa* and *caucasica* under *tegulata* Hagenow.

Seitz considered that *T. fibrosa* differs from *T. tegulata* Hagenow in having growth lamellae which are convex ventrally across the raised nodular radial plicae, whereas they are convex dorsally on *T. tegulata*. On specimens of *fibrosa* from the Fox Hills Formation, South Dakota, the growth lamellae and striae may be concave or convex dorsally across the raised radial plicae, and an individual lamella may have both orientations along its length On most specimens the second order concentric costate ornament has a straight or slightly convex ventral trace. Only on specimens where a very nodular pattern is produced by strong radial and concentric plicae do the lamellae have a convex dorsal trace. The growth lamellae on specimens of *T. dobrovi* available to me have an irregular trace, while a specimen of *T. tegulata* (the original of Ødum, 1922, fig. 5) does not show clearly the concentric lamellate ornament across the radial plicae on the main disc of the valve. On the posterodorsal flank the lamellae are irregularly undulating. Although the difference between *tegulata* Hagenow and *fibrosa* noted by Seitz is unlikely to be of specific rank, additional data on the consistency of orientation of the trace of these lamellae across the radial plicae are required to confirm my opinion.

The few specimens and illustrations of *tegulata* Hagenow and *caucasica* available to the writer indicate, as suggested by Seitz (1959) and Jeletzky and Clemens (1965), that the three equivalved species *tegulata, fibrosa* and *caucasica* might be synonymous. The three "species" include forms with a wide variation of shape and similar ornament. Specimens of *fibrosa* greater than 30 mm in height have about 15 to 30 radial raised plicae and about 20 to 35 concentric plicae (see p. 28). Ødum's (1922, fig. 5) specimen of *tegulata* Hagenow has an indefinite number of radial plicae and about 25 concentric plicae, while those of *caucasica* figured by Dobrov (1951) have about 10 to 30 radial and 20 to 35 concentric plicae.

Cobban (1964), in his recognition of his ornament groups, has emphasized the variation in strength of radial and concentric plicae.

Our present knowledge is insufficient to permit the synonymizing of the three species. Detailed studies are required of the stratigraphic and biogeographic variation of adequate samples of the European species such as are being undertaken by Cobban (1964) for the North American *T. fibrosa.*

Tenuipteria argentea (Conrad)

(Plate 2, fig. 7; Plate 3, figs. 1–6)

Inoceramus argenteus Conrad, 1858, p. 329, Pl. 34, fig. 16.
Inoceramus costellatus Conrad, 1858, p. 329, Pl. 34, fig. 12.
Inoceramus argenteus Conrad. Stephenson and Monroe, 1940, p. 280, Pl. 10, figs. 8, 9.
Tenuipteria argentea (Conrad). Stephenson, 1955, p. 111, Pl. 16, figs. 4–9.

REDESCRIPTON. Species of moderate size, specimens from about 10 to 65 mm long, inequilateral, inequivalved, umbones prosogyrous.

Right valve slightly to moderately inflated, the umbone barely projecting above the dorsal margin, the anterior auricle small and distinct. Left valve strongly inflated with a prominent umbone projecting above the dorsal margin, anterior auricle small. Posterodorsal margin of each valve rounded.

Valves ornamented by radial plicae, strongest on the right valve, which divide by gemmation on the center of the disc, become wider ventrally and are separated by narrower interspaces Radial plicae number about 25 to 30 on the left valve (N = 4) and 26 to 33 on the right valve (N = 4). Posterodorsal third of the shell and the anterodorsal margin lack radial plicae. Radial plicae crossed by regular weak concentric plicae which are accentuated by a prominent growth

PLATE 2

Tenuipteria tegulata (Hagenow)

1, 2, 3. MMH 1816; the original of Ødum, 1922, fig. 5, a left valve steinkern with shell dorsally showing anterior ear, slightly projecting umbone, and a longitudinally striated ligament area which lacks ligament pits. Aalborg, Lower Maestrichtian. (Plaster cast NZGS–WM 8956). Figs. 1, 2 X3; Fig. 3 X1.

Tenuipteria dobrovi (Jeletzky)

4. MMH 1814; poorly preserved left valve, the original of Ødum, 1922, figs. 1, 2. "Dania" at Mariager, Upper Maestrichtian. (Plastic cast NZGS–WM 8957). X1.

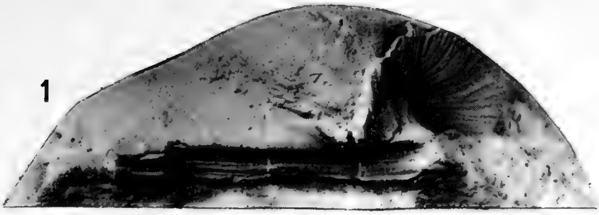
5. MMH collection 1965/694; left valve steinkern. Limhamn, Scania, Sweden, Upper Maestrichtian. X1.

6. MMH collection 1965/693; left valve steinkern. Limhamn, Scania, Sweden, Upper Maestrichtian. (Plaster casts NZGS–WM 9238). X1.

Tenuipteria argentea (Conrad)

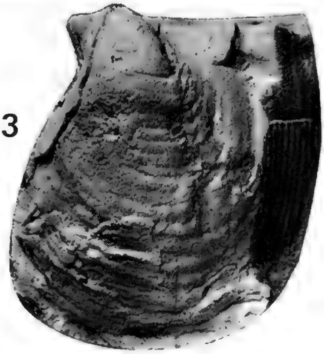
7. USNM Cat. No. 159947; left valve, incomplete. Topotype, USGS Locality 707, USNM 20661, Owl Creek, Mississippi, Maestrichtian. X2.

1



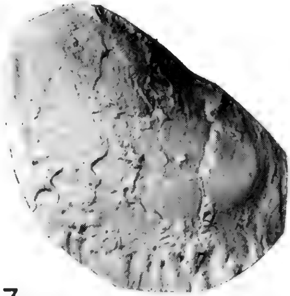
2

3

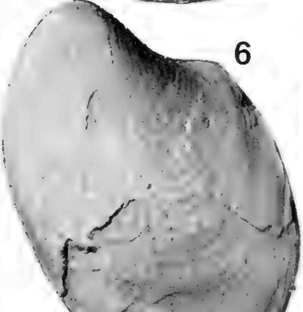


4

5



6



7

PLATE 3

Tenuipteria argentea (Conrad)

1. USNM Cat. No. 159948; an incomplete bivalved specimen. X1.5.

2. USNM Cat. No. 159949; right valve showing lack of radial plicae on the posterior flank. X1.5.

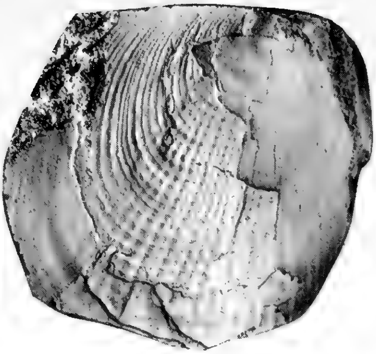
3. USNM Cat. No. 159947; left valve ligament area showing weak ligament pits. X2.

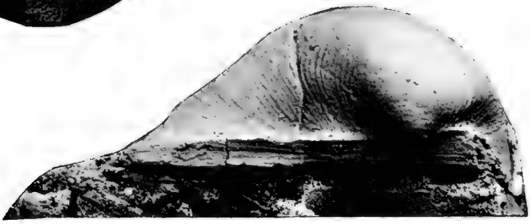
4. USNM Cat. No. 159948; left valve of specimen of Figure 1. X1.5.

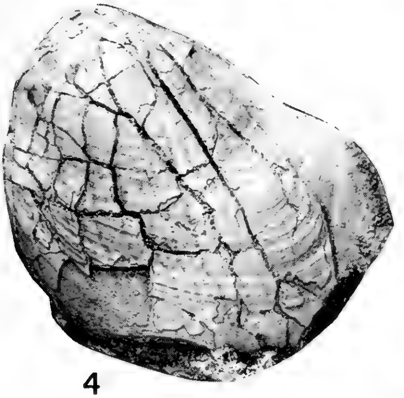
5, 6. USNM Cat. No. 159950; right valve showing ornament and ligament area with more strongly incised ligament pits and distinct anterior auricle. Fig. 5 X1.5; Fig. 6 X3.

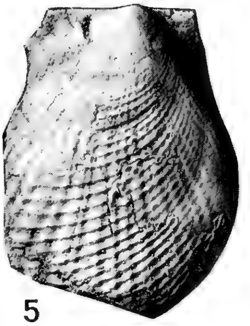
All specimens are topotypes from USGS Locality 707, USNM collection 20661, Owl Creek, Mississippi, Owl Creek Formation, Maestrichtian.

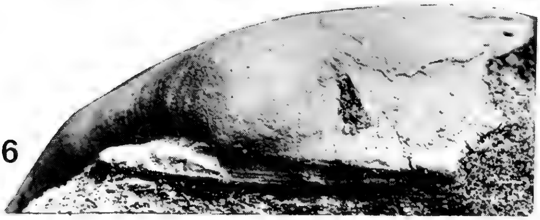

1


2


3


4


5


6

lamella developed along the crest of each plica. Concentric plicae closely spaced on umbonal 10 mm of shell, on the dorsal flanks and along the ventral margins of adult specimens, but number about one per millimeter on the main disc of the shell. The intersection of radial and concentric plicae produces a distinctive tile-like pattern of shallow rectangular depressions.

Ligament area more or less flat, bearing two to five shallow subrectangular or subtrigonal ligament pits; that under the umbone the largest, and sometimes consisting of two fused pits. Pits and interspaces crossed by fine striae extending the length of the ligament area. Ligament area of the right valve inclined at about 20 to 30 degrees to the plane of the commissure, and that of the left valve inclined at about 60 to 80 degrees

Muscle scars unknown. Shell very thin; shell of the main disc attaining a maximum thickness of about 0.5 mm, consisting of a thick, inner nacreous lamellar layer (0.4 mm) and a very thin, outer prismatic layer (0.1 mm).

TYPE SPECIMEN. Neotype, USNM 124102, here designated, a topotypic left valve shell showing the ligament area, the original of Plate 16, figure 6 of Stephenson (1955), USGS 6464. Type locality: Owl Creek, three miles northeast of Ripley, Tippah County, Mississippi (E ½ Sec. 7, T.4 S, R.4 E). Stratigraphic position: Owl Creek Formation, Maestrichtian.

Stephenson (1955) presumed that the holotype was lost, and this was confirmed subsequently by Richards (1968). Conrad (1858) did not record the number of species he studied, but apparently no syntypes are present in the collection of the Academy of Natural Sciences, Philadelphia. Consequently, one of the topotypic specimens studied by Stephenson when he established the genus is selected as a neotype.

DISCUSSION. The above redescription is based on the examination of about 60 specimens, mostly incomplete and slightly crushed, in collections held by the United States National Museum, catalogue numbers USGS 6875 (N=6), USNM 20612 (N=22) and USNM 20661 (N=31), kindly forwarded to the writer by the courtesy of Dr. Erle G. Kauffman.

Measurements taken from the best specimens in these collections are given in Table 1. Because the measurements are based on the outline of the inner shell layer they should be accepted with caution.

TABLE 1. Measurements of specimens (in mm) of *Tenuipteria argentea* (Conrad).

No.	Valve	Length	Height	Half width	Anterior length	Length of dorsal margin	DUPM*
USNM 20661	right	17	32	7.0	4.6	—	—
”	left	29	30	14.0	3.0	18	4.5
”	left	65	62	14.0	15.0	41	—
”	left	15	13	2.0	2.5	12	—
”	right	27	26	7.0	4.0	18	—
”	right	25	25	6.0	5.0	22	—
20612	left	39	42	18.5	6.0	28	6.5
”	right	40	41	10.0	6.0	—	—
USGS 6875	right	31	28	5.0	6.0	24	—
”	right	49	45	7.0	9.0	33	—

*Distance the umbone of the left valve projects above the dorsal margin of the ligament area.

COMPARISONS. Dobrov (1951, p. 164) was the first to suggest the presence in the latest Cretaceous of North America of the inequivalved group of "*Inoceramus tegulatus*". *Tenuipteria dobrovi* Jeletzky (1965) externally closely resembles *T. argentea* in having a strongly inflated left valve and a flattish right valve, with both valves ornamented by regular to subregular radial and concentric plicae and concentric lamellae.

Examination of specimens of *Tenuipteria argentea* in three collections held by the United States National Museum, Washington (catalogue numbers USGS 6875 and USNM 20612 and 20661), three left valves of *T. dobrovi* from the late Maestrichtian of Denmark, and illustrations indicates that the valves of these species are very similar in size and shape. Each species has left valves with height to length ratios of about one. *Tenuipteria argentea* has height to length and half width to length ratios for left valves of 0.87 to 1.14 ($N = 5$) and 0.22 to 0.47 ($N = 3$), respectively; for *T.? dobrovi* the ratios are 1.00 to 1.20 ($N = 3$) and 0.23 to 0.34 ($N = 4$), respectively. Because of the inadequate numbers of specimens these values can be taken only as an indication of similarity.

On both *T. argentea* and *dobrovi* the radial plicae are most distinct on the central and anterior part of the valve and are weak or lacking on the broad posterior ear. Replicas of two left valves of *dobrovi* from the Maestrichtian of Denmark, NZGS–WM 8957 (the original of Ødum, 1922, figs. 1, 2; height = 46 mm; Pl. 2, fig. 4) and NZGS–WM (height 43 mm; Pl. 2, fig. 6), have 17 and 23 radial plicae and about 37 and 29 concentric plicae, respectively. Photographs of a left and a right valve of *argentea* figured by Stephenson (1966, Pl. 16, figs. 4, 6) suggest the presence of about 18 radial plicae; the concentric plicae could not be counted. Topotypes of *argentea* from Owl Creek, Mississippi, in collection Cat. No. 20661 held by the U.S. National Museum, have 25 to 30 radial plicae on the left valve (N = 4) and 26 to 33 on the right valve (N = 4). These valves, which are 20 to 41 mm high, have about one concentric plica per millimeter on the main disc, i.e. about 25 to 45 per valve.

The close external similarity of *T. dobrovi* and *argentea* suggests that they may be conspecific and congeneric. However, the ligament area of *dobrovi* has not been described or illustrated. Until the internal morphology of *dobrovi* and the external morphology of both species are more fully known, the synonymy of the two species is uncertain though possible.

LITERATURE CITED

Aliev, M. M., 1958, Inotseramy melovykh otlozhenii SSSR: Akad. Nauk Azerbaidzhanskoi SSSR Izv., 1957, no. 3, p. 47–61. (Reprinted in Internat. Geol. Cong., 20th, Mexico 1956, sec. 7, Paleontologia, taxonomia y evolución, p. 123–137 [1958]).

Aliev, R. A. 1960, K Paleontologicheskoy Kharakteristike Verkhnego Mela Yugo-Vostochnogo Kavkaza [The paleontological characteristics of the Upper Cretaceous in South-east Caucasus]: Akad. Nauk SSSR Doklady, v. 131(2), p. 378–379. (Am. Geol. Inst. translation, 1961, p. 295–296a).

Birkelund, Tové, 1957, Upper Cretaceous belemnites from Denmark: Kgl. Danske Vidensk. Selsk., Biol. Skr., v. 9, no. 1, 69 p., 6 pls.

——— 1965, Ammonites from the Upper Cretaceous of West Greenland: Meddelelser om Grönland, v. 179, no. 7, 192 p., 48 pls.

——— 1966, Die Entwicklung der jüngsten Scaphiten und ihre stratigraphische Bedeutung Gebiet: Deutsche geol. Gesell. Ber. [Berlin], Wiss. A, Geologie Paläontologie, v. 11, no. 6, p. 737–744.

Briggs, J. C., 1967, Dispersal of tropical marine shore animals: Coriolis parameters or competition: Nature, v. 216, no. 5113, p. 350.

Cieslinski, Stefan, 1960, Biostratygrafia i zasieg form przewodrich górnej kredy W Polsce [Biostratigraphy and extent of index forms in the Upper Cretaceous of Poland]: Kwartalnik geologiczny [Warsaw], v. 4, no. 2, p. 432–441. (English summary)

Cobban, W. A., 1964, Evolution of two Upper Cretaceous mollusks, *in* U.S. Geol. Survey Mem., Paleontologia Indica, ser. 9, v. 3, pt. 3, 157 p.,

——— and Reeside, J. B., Jr., 1952, Correlation of the Cretaceous formations of the western interior of the United States: Geol. Soc. America Bull., v. 63, p. 1011–1043.

Conrad, T. A., 1858, Observations on a group of Cretaceous Fossil Shells, found in Tippah County, Miss., with descriptions of fifty-six new species: Acad. Nat. Sci. Philadelphia Jour., ser. 2, v. 3, p. 323–336, pls. 34, 35.

Cox, L. R., 1940, The Jurassic lamellibranch fauna of Kuchh (Cutch): India Geol. Survey Mem., Paleontologia Indica, ser. 9, v. 3, pt. 3, 157 p., 10 pls.

——— 1955, Proposed determination of the nominal species to be accepted as the type species of the genus "*Inoceramus*" Sowerby (J.), 1814 (Class Pelecypoda) and proposed addition of that name to the "Official list of generic names in Zoology": Zool. Nomenclature Bull., v. 11, p. 239–245.

Dobbin, C. E., and Reeside, J. B., Jr., 1929, The contact of the Fox Hills and Lance formations: U.S. Geol. Survey Prof. Paper 158, p. 9–25.

Dobrov, S. A., 1951, Gruppa *Inoceramus caucasicus* sp. n.—*Inoceramus tegulatus* Hag. na severnam kavhaze: Pamiati Akademika A. D. Arkhangels'kogo Voprosy Litologii i Stratigrafii SSR, Moscow, Press Acad. Sci. SSSR, p. 163–172, 2 pls.

——— and Pavlova, M. M., 1959, Inoceramy, *in* Moskvin, M. M., ed., Atlas verkhnemelovai fauny severnogo Kavkaza i Kryma: Moscow, State Sci.-Tech. Press Oil and Mining-Fuel Literature, p. 130–165, pls. 1–23.

Ebensberger, Hans, 1962, Stratigraphische und mikropaläontologische Untersuchungen in der Aachener Oberkreide, besonders der Maastricht-Stufe: Palaeontographica, v. 120, Abt. A, p. 1–120, 12 pls.

Elias, M. K., 1931, The geology of Wallace County, Kansas: Kansas Geol. Survey Bull. 18, 254 p.

Furnival, G. M., 1946, Cypress Lake map-area, Saskatchewan: Canada Geol. Survey Mem. 242, 161 p.

Gerhardt, K., 1897, Beitrage zur kenntniss der Kreideformation in Columbien: Neues Jahrb. Mineralogie, Geologie, Paläontologie, Beilage-Bande 11, p. 118–208.

Gill, J. R., and Cobban, W. A., 1966, The Red Bird section of the Upper Cretaceous Pierre Shale in Wyoming: U.S. Geol. Survey Prof. Paper 393–A, 73 p.

Hagenow, F. von, 1842, Monographie der Rügen'schen Kreide-Versteinerungen. III. Abtheilung: Mollusken: Neues Jahrb., Mineralogie, Geognosie, Geologie, Petrefakten-Kunde, Jahrg. 1842, p. 528–575, 9 pls.

Hattin, D. E., 1967, Stratigraphic and paleoecologic significance of macroinvertebrate fossils in the Dakota Formation (Upper Cretaceous) of Kansas, *in* Teichurt, C. and Yochelson, E. L., eds., Essays on paleontology and stratigraphy: Lawrence, Univ. Kansas Press, p. 571–589.

Hayami, Itaru, 1960, Jurassic inoceramids in Japan: Tokyo Univ., Fac. Sci., Jour., sec. 2, v. 12, pt. 2, p. 277–328.

Heine, Friedrich, 1929, Die Inoceramen des Mittelwestfälischen Emschers und Unteren Untersenons: Preuss. geol. Landesanstalt Abh., n.s. 120, 124 p., 20 pls.

Heinz, Rudolph, 1932, Aus der neuen Systematik der Inoceramen. Beiträge zur Kenntnis der Inoceramen 14: Mineralog.-Geol. Staatsinst. Hamburg Mitt. 13, p. 1–26.

Imlay, R. W., 1955, Stratigraphic and geographic range of the Late Cretaceous pelecypod *Didymotis:* Jour. Paleontology, v. 29, p. 548–550.

Jeletzky, J. A., 1948, Zur Kenntnis der Oberkreide der Dnjepr-Donez-Senke und zum Vergleich der russischen borealen Oberkreide mit derjenigen Polens und Nordwesteuropas: Geol. fören. Stockholm Förh., v. 70, no. 4, p. 583–602.

——— 1951, Die stratigraphie und Belemnitenfauna des Obercampanan und Maastricht Westfalens, Nordwestdeutschlands und Dänemarks sowie einige allgemeine Gliederungs — Probleme der jüngeren borealen Oberkreide Eurasiens: Beihefte Geol. Jahrb. [Hannover], no. 1, 142 p.

——— 1958, Die jüngere Oberkreide (Oberconiac bis Maastricht) Südwestrusslands und ihr Vergleich mit der Nordwest = und Westeuropas: Beihefte Geol. Jahrb. [Hannover] no. 33, 157 p.

——— 1960, Youngest marine rocks in western interior of North America and the age of the Triceratops-beds, with remarks on comparable dinosaur-bearing beds outside North America: Internat. Geol. Cong., 21st, Copenhagen 1960, Rept., part 5, p. 25–40.

——— 1962, The allegedly Danian dinosaur-bearing rocks of the globe and the problem of the Mesozoic-Cenozoic boundary: Jour. Paleontology, v. 36, p. 1005–1018.

——— and Clemens, W. A., 1965, Comments on Cretaceous Eutheria, Lance *Scaphites,* and *Inoceramus*? ex *gr. tegulatus:* Jour. Paleontology, v. 39, p. 952–959.

Jones, D. L., and Gryc, George, 1960, Upper Cretaceous pelecypods of the genus *Inoceramus* from northern Alaska: U.S. Geol. Survey Prof. Paper 334–E, p. 149–165.

Kauffman, E. G., 1965, Taxonomic, ecologic, and evolutionary significance of interior shell morphology in the Inoceramidae (Mesozoic Bivalvia): Geol. Soc. America Spec. Paper 87, Abstracts for 1965, p. 86 [1966].

Kellum, L. B., 1962, Upper Cretaceous Mollusca from Niobrara County, Wyoming: Michigan Acad. Sci., Arts, Letters, Papers 1961, v. 47, p. 37–81.

——— 1964, *Inoceramus cobbani,* new name for *Inoceramus radiatus* Kellum, 1962: Jour. Paleontology, v. 38, p. 1006.

Kongiel, Roman, 1962, On belemnites from Maastrichtian, Campanian and Santonian sediments of the Middle Vistula valley (Central Poland): Museum Ziemi Prace, Prace Paleozoologiczne [Warsaw], no. 5, 148 p., 21 pls.

Landes, R. W., 1940, Geology of the southern Alberta Plains. Part 2. Paleontology of the marine formations of the Montana Group: Canada Geol. Survey Mem. 221, p. 129–217, pls. 1–8.

Maslakova, N. I., 1959, The Upper Cretaceous deposits of the Rocky Region of the Crimea: Moskovskoe Obschestvo Ispytatelei Prirody Bull., n.s., Otdel Geologisckii, v. 34, no. 4, p. 67–76. (English summary)

Meek, F. B., 1864, Check list of the invertebrate fossils of North America. Cretaceous Formation. Notes and explanations: Smithsonian Misc. Colln., v. 7, p. 1–26, 31–38.

——— 1873, Preliminary paleontological report, consisting of lists and descriptions of fossils, with remarks on the ages of the rocks in which they were found, etc.: U.S. Geol. Survey Terr., 6th Ann. Rept., 1872, p. 429–518.

——— 1876, A report on the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri country: U.S. Geol. Survey Terr. Rept. v. 9, 629 p., 44 pls.

——— and Hayden, F. V., 1856a, Descriptions of twenty-eight new species of Acephala and one gasteropod, from the Cretaceous formations of Nebraska Territory: Acad. Nat. Sci. Philadelphia Proc., v. 8, p. 81–87.

——— 1856b, Descriptions of new fossil species of Mollusca collected by Dr. F. V. Hayden, in Nebraska Territory; together with a complete catalogue of all the remains of Invertebrata hitherto described and identified from the Cretaceous and Tertiary formations of that region: Acad. Nat. Sci. Philadelphia Proc., v. 8, p. 265–286.

Moskvin, M. M., 1962, [Upper Cretaceous sediments of the North Caucasus and Subcaucasia]: Acta Geol. Polonica, v. 12, p. 159–199. (English summary, p. 191–199)

——— and Naidin, D. P., 1959, Stratigraphie du Crétacé Supérieur de la plate-forme russe, de la Crimée et du Caucase du Nord: Cong. Soc. Savantes Paris, 84th Cong., Dijon, Comptes rendus, Colloque sur le Crétacé Supérieur Français, p. 497–522.

Naidin, D. P., 1952, Wierchniemielowyje belemnity Zapadnoj Ukrainy: Moskovskoe Geol.-Rasw. Inst. Ordzonikidze Trudy, v. 37. (In Russian)

——— 1954, Niekotoryje osobiennosti rasprostranienija u predielach Jewropy wierchniemielowych belemnitow: Moskovskoe Obschestvo Ispytatelei Prirody Bull., n.s., Otdel Geologisckii, v. 29, no. 3, p. 19–28.

——— 1960, The stratigraphy of the upper Cretaceous of the Russian platform: Stockholm Contr. Geol., v. 6, p. 39–61.

Nestler, Helmut, 1965, Die Rekonstruktion des Lebensraumes der Rügener Schreibkreide-Fauna (Unter-Maastricht) mit Hilfe der Paläoökologie und Paläobiologie: Geologie, Jahrg. 14, Beih. 49, 147 p.

Ødum, Hilmar, 1922, *Inoceramus tegulatus* v. Hag. det danske Skrivekridt: Dansk. geol. Fören. Medd., v. 6, no. 10, p. 1–13. (English summary)

——— 1953, Die Geologiska Resultaten Fran Borrningarna vid Höllviken. Del 5: The macro-fossils of the Upper Cretaceous: Sveriges geol. undersökning, ser. C, Arsb. 46, no. 3, 37 p., 4 pls.

Pozaryski, W., 1938, Stratygrafia senonuw przelomie Wisly Rachowem i Pulawami (Senonsstratigraphie im Durchbruch der Weichsel zwischen Rachów und Palawy in Mittelpolen): Geol. Inst. Pologne, Warsaw, Bull. 6, 94 p.

——— 1960, An outline of stratigraphy and palaeogeography of the Cretaceous in the Polish Lowland: Geol. Inst. Pologne, Warsaw, Pub., v. 30, part 2, p. 377–440. (English summary, p. 430–440).

Reeside, J. B., Jr., 1957, Paleoecology of the Cretaceous seas of the western interior of the United States, *in* Hedgpeth, J. W., ed., Treatise on marine ecology and paleoecology: Geol. Soc. America Mem. 67, v. 2, p. 505–541.

Richards, H. G., 1968, Catalogue of invertebrate fossil types at the Academy of Natural Sciences of Philadelphia: Acad. Nat. Sci. Philadelphia Spec. Pub. 8, 222 p.

Russell, L. S., 1940, Geology of the southern Alberta Plains. Part 1. Stratigraphy and structure: Canada Geol. Survey Mem. 221, p. 1–128.

Schmid, Friedrich, 1955, Die bisherigen Untersuchungen über das Unter/Obermaastricht — Grenzprofil von Hemmoor (Niederelbe), seine Schichtfolge und leitformen: Geol. Staatsinst. Hamburg Mitt. 24, p. 75–86.

Searight, W. V., 1934, The Stoneville coal area: South Dakota Geol. Survey Rept. Inv. 22, 20 p.

Seitz, Otto, 1959, Vergleichende Stratigraphie der Oberkreide in Deutschland und in Nordamerika mit Hilfe der Inoceramen: Internat. Geol. Cong., 20th, Mexico 1956, El Sistema Cretácico, Symposium, v. 1, p. 113–129.

——— 1961, Die Inoceramen des Santon von Nordwestdeutschland, I Teil. (Die Untergattungen *Platyceramus, Cladioceramus* und *Cordiceramus*): Beih. Geol. Jahrb., v. 46, 186, p., 15 pls.

Sohl, N. F., 1960, Archeogastropoda, Mesogastropoda and stratigraphy of the Ripley, Owl Creek, and Prairie Bluff formations: U.S. Geol. Survey Prof. Paper 331–A, p. 1–151.

——— 1964, Neogastropoda, Opisthobranchia and Basommatophora from the Ripley, Owl Creek, and Prairie Bluff formations: U.S. Geol. Survey Prof. Paper 331–B, p. 153–334.

——— and Kauffman, E. G., 1964, Giant Upper Cretaceous oysters from the Gulf Coast and Caribbean: U.S. Geol. Survey Prof. Paper 483–H, p. H1–H22.

Sowerby, J., 1814, Anonymous notice: Annals Philosophy, v. 4, p. 448.

Speden, I. G., 1970, The type Fox Hills Formation, Cretaceous (Maestrichtian), South Dakota. Part 2, Systematics of the Bivalvia: Peabody Mus. Nat. History, Yale Univ., Bull. 33 (in press).

Stephenson, L. W., 1941, The larger invertebrate fossils of the Navarro group of Texas exclusive of corals and crustaceans and exclusive of the fauna of the Escondido formation: Texas Univ. Pub. 4101, 641 p., 95 pls.

——— 1955, Owl Creek (Upper Cretaceous) fossils from Crowleys Ridge, southeastern Missouri: U.S. Geol. Survey Prof. Paper 274–E, p. 97–140.

——— and Monroe, W. H. 1940, The Upper Cretaceous deposits (Mississippi): Mississippi State Geol. Survey Bull. 40, 296 p., 15 pls.

——— and Reeside, J. B., Jr., 1938, Comparison of Upper Cretaceous deposits of Gulf region and Western Interior region: Am. Assoc. Petroleum Geologists Bull., v. 22, p. 1629–1638.

———, King, P. B., Monroe, W. H., and Imlay, R. W., 1942, Correlation of the outcropping Cretaceous formations of the Atlantic and Gulf Coastal Plain and Trans-Pecos Texas: Geol. Soc. America Bull., v. 53, p. 435–448.

Stoll, N. R. et al., 1964, International code of zoological nomenclature adopted by the XI International Congress of Zoology: London, Internat. Trust for Zoological Nomenclature, 176 p.

Toepelman, W. C., 1922, The paleontology of the area, *in* Ward, Freeman, The geology of a portion of the Badlands: South Dakota Geol. Nat. History Survey Bull. 11, p. 62–73.

Troelsen, J. C., 1937, Om den stratigrafiske inddeling af skrivekridtet i Danmark: Dansk. geol. Fören. Medd., v. 9, p. 260–263.

Vokes, H. E., 1967, Genera of the Bivalvia: A systematic and bibliographic catalogue: Am. Paleontology Bull., v. 51, no. 232.

Waage, K. M., 1961, The Fox Hills Formation in its type area, central South Dakota, *in* Symposium on Late Cretaceous rocks: Wyoming Geol. Assoc. Guidebook 16th Ann. Field Conference, p. 229–240.

——— 1968, The type Fox Hills Formation (Maestrichtian), South Dakota. Part 1. Stratigraphy and paleoenvironments: Peabody Mus. Nat. History, Yale Univ., Bull. 27, 175 p.

Whiteaves, J. F., 1885, Report on the Invertebrata of the Laramie and Cretaceous rocks of the vicinity of the Bow and Belly rivers and adjacent localities in the Northwest Territory: Canada Geol. Survey, Nat. History Survey, Contr. Canadian Paleontology, v. 1, p. 1–89, 11 pls.

Whitfield, R. P., 1880, Paleontological report on the fossils collected by the United States Geological and Geographical Survey of the Black Hills, *in* Newton, Henry, and Jenney, W. P., Report on the geology and resources of the Black Hills of Dakota: Washington, Govt. Printing Office, p. 329–468, pls. 1–16.

Williams, G. D., and Burk, C. F., 1964, Upper Cretaceous, *in* McCrossan, R. G., Glaister, R. P., et al., Geological history of Western Canada: Alberta Soc. Petroleum Geologists, Calgary, p. 169–189.

Wolansky, Dora, 1932, Die Cephalopoden und Lamellibranchiaten der Ober-Kreide Pommerns: Univ. Griefswald Geol.-Paläont. Inst. Abh., v. 9, 72 p.

Wood, C. J., 1967, Some new observations on the Maastrichtian Stage in the British Isles: Geol. Survey Great Britain Bull., no. 27, p. 271–288.

INFORMATION FOR AUTHORS

REVIEW	The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
STYLE	Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).
FORM	Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.
TITLE	Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
ABSTRACT	The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
NOMENCLATURE	Follow the International Codes of Zoological and Botanical Nomenclature.
ILLUSTRATIONS	Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
FOOTNOTES	Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
TABLES	Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
REFERENCES	The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
THOR'S COPIES	Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
PROOF	Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
COPYRIGHT	Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 146 18 AUGUST 1970

MORPHOLOGICAL VARIATION IN GAMMARUS MINUS SAY (AMPHIPODA, GAMMARIDAE), WITH EMPHASIS ON SUBTERRANEAN FORMS

JOHN R. HOLSINGER
DAVID C. CULVER

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Nancy A. Ahlstrom, Elizabeth G. Weinman, Elise K. Kenney.

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection*. All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

MORPHOLOGICAL VARIATION IN GAMMARUS MINUS SAY (AMPHIPODA, GAMMARIDAE), WITH EMPHASIS ON SUBTERRANEAN FORMS

JOHN R. HOLSINGER

Department of Biology, Old Dominion University,
Norfolk, Virginia 23508

DAVID C. CULVER

Department of Biology, University of Chicago,
Chicago, Illinois 60637

(Received November 26, 1969)

ABSTRACT

Gammarus minus Say is a common amphipod species in springs and caves of limestone areas of the eastern and middle-eastern United States. Samples of populations from the central Appalachians were examined closely and morphological variation between spring and cave populations was analyzed. This species occurs in three morphological forms: a spring form, an intermediate cave form and an extreme cave form. The latter form was termed variety *tenuipes* by some earlier workers but has no nomenclatural validity. In contrast to the spring form, the cave forms show a reduction in eye structure, a change in pigmentation of the integument and a proportionate increase in the length of some of the appendages. It is concluded that *G. minus* is an extremely vagile and highly variable species that can occupy a variety of habitats, ranging from surface springs to small or large cave systems in certain karst areas.

POSTILLA 146: 24 p. 18 AUGUST 1970.

INTRODUCTION

Gammarus minus Say is a common inhabitant of springs, small spring-fed streams and cave streams in the eastern United States but is most often encountered in springs developed in limestone areas. This species was originally described by Say (1818), but subsequent references to it were few. Shoemaker (1940) carefully redescribed *G. minus* and gave a thorough literature review of the species up until that time. In the same treatment, Shoemaker (1940) synonymized *G. propinquus* Hay and *G. purpurascens* Hay with *G. minus* and designated a variety which he called *tenuipes*. Hubricht (1943) added numerous new locality records for this species and discussed the variety *tenuipes*. The species was again treated systematically by Bousfield (1958), who confirmed the earlier synonymies of Shoemaker and suggested that the variety *tenuipes* might be a distinct troglobitic (obligatory cavernicole) species. More recently, Minckley and Cole (1963) analyzed the morphological variation in several populations of *G. minus* from spring-fed streams in north-central Kentucky and compared the ecology and morphology of these populations with sympatric populations of *G. bousfieldi* Cole and Minckley. Finally, this species was compared biogeographically with some other members of the family Gammaridae in a paper on the biogeography of freshwater amphipods of the southern and central Appalachians by Holsinger (1969).

Both Shoemaker (1940) and Hubricht (1943) treated the morphological variation in *G. minus* as it related to cave populations in terms of "varieties." Presumably, Shoemaker and Hubricht used the term "variety" to signify a unified morphological group that apparently had become restricted to subterranean waters. Whether these workers were using the variety *tenuipes* to express genetic difference or to express the extreme variation of a plastic phenotype, or both, cannot be determined. Nevertheless, Shoemaker (1940) formally designated several cave populations of *G. minus* from Greenbrier County, West Virginia as a taxonomic variety under the name *tenuipes*. This name was later used by Hubricht (1943) and Bousfield (1958), but not necessarily in a nomenclatural sense.

Although Shoemaker described *tenuipes* as a "variety," he designated a type and created a trinomen. However, it was not clear whether he intended this taxon to be a subspecies or an infrasubspecific group. *The International Code of Zoological Nomenclature* (Stoll et al., 1964, Article 45) allows a certain amount of freedom in dealing with "varieties" and "forms" proposed prior to 1961. Therefore, based on our interpretation of the Code, the variety *tenuipes* is considered to be of infrasubspecific rank and should not be accorded taxonomic validity.

While Shoemaker (1940) recognized a single variety *(tenuipes)* of *G. minus,* Hubricht (1943) went further and divided the species into three varieties or forms, but he did not treat them in a nomenclatural manner. The three varieties recognized by Hubricht were: a brown spring form with well-developed eyes and short antennae; a bluish intermediate cave form with slightly reduced eyes and long antennae; and a bluish fragile-bodied cave form with greatly reduced eyes and long antennae (i.e., *tenuipes).*

To facilitate discussion in this paper, three morphological groups, approximately equal to those described by Hubricht (1943), will be assigned Roman numerals and designated as follows: *"tenuipes"* Form I, intermediate cave Form II, and spring Form III.

The objectives of this study were: 1) to quantify and describe the morphological variation in central Appalachian populations of *G. minus* with particular reference to subterranean populations; 2) to clarify the morphological status of the three forms of *G. minus;* and 3) to demonstrate that the subterranean "variety" *tenuipes* is an ecophenotype or extreme morphological variant of the more common and widespread spring form.

During the course of this study we critically examined 222 collections of *G. minus* from 179 different localities in the Appalachian region. A breakdown of the locality data follows: three caves, four springs and one spring-run in three counties of northern Alabama; one spring in one county of northwestern Georgia; seven springs and two spring-runs in five counties of southern Indiana; three caves and five springs in five counties of central and eastern Kentucky; two caves, five springs and one spring-run in three counties of central Maryland; five caves, nine springs and three spring-runs in eight counties of central and southern Pennsylvania; three caves, six springs and seven spring-runs in nine counties of central and eastern Tennessee; nine caves, 30 springs and one spring-run in 16 counties of northern and western Virginia; 46 caves, 24 springs and two spring-runs in eight counties in eastern West Virginia. In addition to the above, samples were examined in less detail of *G. minus* from

40 localities in southern Indiana, Kentucky, southern Ohio and central Tennessee. The present study, therefore, is based primarily on the first 222 samples mentioned above.

DISTRIBUTION AND ECOLOGY

As presently understood, the range of *G. minus* s. str. extends from eastern and central Pennsylvania southwestward to northwestern Georgia and northern Alabama and westward to central Tennessee, western Kentucky and south-central Indiana. This species is almost exclusively restricted to areas underlain by carbonate rocks. *G. minus* may also range from southwestern Illinois across southern Missouri and northern Arkansas to the extreme northeastern corner of Oklahoma (Hubricht and Mackin, 1940; Mackin, 1941; Hubricht, 1943; Hubricht, 1959; Minckley and Cole, 1963). However, further critical examination of material from this area, especially from the Ozark Plateau region, is needed before definite determinations can be made. The middle-western material tentatively referable to *G. minus (G. minus* s. lat.) is being studied currently by G. A. Cole *(in litt.).*

Throughout the eastern range of *G. minus,* the sympatric or syntopic occurrence of this species with any other species of *Gammarus* is extremely rare; the only notable exception is the sympatric association of *G. minus* and *G. bousfieldi* in Doe Run in Meade Co., Kentucky (Minckley and Cole, 1963). A similar situation of mutually exclusive ranges occurs in England, where overlapping ranges of species of freshwater *Gammarus* are uncommon (Hynes, 1955). This situation does not hold true, however, for the western Illinois-eastern Missouri area where there are overlapping ranges of four species of *Gammarus: G. troglophilus, G. acherondytes, G. pseudolimnaeus* and *G. minus* (s. lat.). Species pairs of *Gammarus* in this area may consist of *G. troglophilus/G. acherondytes* (restricted to Monroe and St. Clair Counties, Illinois), *G. minus* (s. lat.)/*G. pseudolimnaeus,* and occasionally *G. minus* (s. lat.)/*G. troglophilus.* The association of *G. minus* (s. lat.) with *G. pseudolimnaeus* in southern Illinois springs is rather common. Character displacement may influence the slight but subtle differences noted for populations of *G. minus* (s. lat.) from southwestern Illinois and farther west, which have so far complicated the specific assignment of this material. The possibility that character displacement sometimes occurs when *G. minus* exists syntopically with other species of *Gammarus* should be investigated in greater detail. Minckley and Cole (1963) studied this possibility for *G. minus*/*G. bousfieldi* in Doe Run, Kentucky, but the evidence for character displacement in *G. minus* in this particular association was unclear and obscured by other factors (see Discussion and Conclusions section).

G. minus is generally limited in habitat to cave streams, springs and small spring-runs. Larger streams, ponds and even cave pools are seldom inhabited by this species. For example, Spring Creek in Greenbrier County, West Virginia is a large stream, principally derived from spring water. The springs that feed this creek contain large populations of *G. minus* but the creek itself does not. *G. minus* probably is excluded from larger streams by a number of ecological factors such as temperature differences, pO_2, available food, predation, cover and flow rate.

It is possible that spring forms of *G. minus* (Form III) disperse by washing downstream during late winter and spring flooding and subsequently migrate back upstream to the same or a different spring when the water level and flow rate return to normal. We observed a part of this postulated dispersal procedure during February 1967 in Pocahontas County, West Virginia. A large population of *G. minus* III occurs in a spring resurgence at the entrance to Overholts Blowing Cave. Observations throughout most of the year revealed that this population is limited to a narrow band extending downstream only a short distance from the cave entrance. However, during a late winter thaw in February 1967, we observed a number of individuals more than one-half mile downstream from the spring. Some of these individuals presumably migrate upstream later and re-populate the spring. Unfortunately, we have no quantitative data to indicate how many individuals are washed downstream during periods of high water or flooding or how many individuals subsequently migrate back upstream to a given spring. There are studies on upstream movement in amphipods which point out that not all species are able to migrate. In a paper on upstream movements of *Gammarus* in Doe Run, Kentucky, Minckley (1964) pointed out that *G. bousfieldi* could migrate *en masse* upstream, while the upstream movement of *G. minus* was much less obvious. Perhaps, on the contrary, there is no appreciable upstream movement by *G. minus* to springs after flooding and the ability of this species to maintain itself in springs and headwaters depends on its high reproductive rate. The question has not yet been answered satisfactorily by either our own or Minckley's observations, and an investigation on this aspect of the animal's ecology might provide some interesting data. Nevertheless, Minckley (1963) did point out that very short upstream movements of *Gammarus* of one to two feet per day would assist in maintaining populations in headwaters and springs.

G. minus I is represented by populations in two well separated karst areas of the central Appalachian region of Virginia and West Virginia: the Great Savannah karst of south-central Greenbrier County, West Virginia in the Greenbrier Valley (New-Kanawha River drainage); and the Maiden Springs karst of southwestern Tazewell County, Virginia in the headwater region of the Clinch River (upper Tennessee River drainage). These two karst areas are separated by about 76 airline miles and several prominent mountains and ridges typical for this part of the Appalachians. Populations of *G. minus* (Forms II and III) occur in caves and springs located between and on the sides of these two areas.

G. minus I occurs in areas of extensive cave and karst development further characterized by integrated subsurface drainage. Therefore, we assume that limited dispersal by this species from one cave stream to another can take place through the underground conduits hypothesized to exist between caves in these areas. In the Great Savannah karst, which we have examined most carefully, *G. minus* I is the most common amphipod species in most cave streams. It is much more common than two other amphipods, *Stygonectes emarginatus* and *S. spinatus,* with which it is sometimes associated. Although common in cave streams, *G. minus* I is seldom encountered in rimstone pools located above streams or out of reach of potential flooding by streams. Over 100 rimstone pools were examined in Greenbrier Valley caves and only two of these contained specimens (a total of four) of *G. minus*. In marked contrast are the two troglobitic species of *Stygonectes* which were encountered in rimstone and other kinds of drip pools nearly 20 percent of the time and are apparently able to disperse interstitially by phreatic and vadose routes other than streams (Holsinger, 1967, 1969).

In comparison with *G. minus* I, *G. minus* II is found over a much wider part of the central Appalachians and is known primarily from caves in Greenbrier, Monroe, Mercer, Randolph, Tucker and Pocahontas Counties in West Virginia; Giles and Tazewell Counties in Virginia; and Fayette County in Pennsylvania. With a few exceptions, this form is comparatively less abundant in cave streams than *G. minus* I, and usually occurs in caves representative of small to medium-sized subterranean drainage systems. On the other hand, this form is occasionally found in large cave systems such as Bone-Norman and Friars Hole in Greenbrier County and is rather common in caves of the well-developed karst of southern Pocahontas County (such as Swago Creek and Hillsboro areas).

Specimens of Form II also have been collected from caves on the periphery of the Great Savannah karst (viz., Grapevine and Fullers Caves) and of the Maiden Springs karst (viz., Lost Mill Caves). In the caves of Tucker, Randolph and Pocahontas Counties this form is more common (although often not very abundant) than any other amphipod species of this region. In some of these caves it is the only amphipod species recorded.

Of further ecological significance is the almost complete absence of *G. minus* from the cave streams of southwestern Virginia (especially in Lee, Scott and Russell Counties), eastern Tennessee, northwestern Georgia and northern Alabama. Some of the karst, caves and subterranean drainage complexes of this part of the Appalachians are developed to an extent comparable with those of Greenbrier and Tazewell Counties; yet, despite the common occurrence of *G. minus* in springs of this region and intensive collecting over a ten year period, this species is rarely found in these caves. The same situation is generally true of the caves of the adjacent Interior Low plateau region of southern Indiana, Kentucky and central Tennessee where some of the most extensive subterranean drainage systems in the world exist. A partial reason for the scarcity of *G. minus* in cave streams of these regions is probably its inability to compete successfully with troglobitic species of *Crangonyx, C. antennatus* and *C. packardii* (s. lat.). These two species of *Crangonyx* are distributed over an area extending from southwestern Virginia southwestward to Georgia, across northern Alabama, and north through central Tennessee, central Kentucky and into southern Indiana.

In the upper Tennessee River drainage basin, especially in the

Powell valley of southwestern Virginia, a concentrated investigation of caves has revealed that *C. antennatus* is a very common species that inhabits both drip pools and small streams (Holsinger, 1969). The cave-stream macrohabitat of this species appears to be similar to that of *G. minus* (I and II) of other areas. *C. packardii* (s. lat.) occupies essentially the same kind of habitat in some of the Interior Low plateau caves, especially those of central Kentucky and southern Indiana. The vagility of these two species of *Crangonyx,* combined with their ability to populate, often in large numbers, both pools and small streams, is probably indicative of their adaptive success and may be the major reason for the near exclusion of *G. minus* from caves of the same areas.

ANALYSIS OF VARIATION

A few minor structural variations were noted that apply to *G. minus* in general but not to any one morphological form. We will comment on these first. Minckley and Cole (1963) studied morphological variation in several populations of *G. minus* from northern Kentucky and observed differences in the amount of setation of the first four coxal plates and peduncular segments of the first antenna, occasional absence of calceoli on the second antenna of the male and minor size differences in sexually mature individuals. In general our studies revealed similar variation. In particular, we found that calceoli were occasionally absent on the second antenna of the male but were usually present in larger males. Like Minckley and Cole (1963), we examined the setal formula given by Bousfield (1958) i.e., peduncular segments 1, 2 and 3 with 1, 3–5 and 1 ventral groups of setae respectively, and found occasional but slight variation.

Finally, our observations revealed that the number of accessory flagellar segments of the first antenna may range up to 5 or 6 in some of the larger males. A slight range variation in number of accessory flagellar segments (from 3 to 6) also was recorded by Minckley and Cole (1963) but the differences between populations were not significant. In his diagnosis of *G. minus,* Bousfield (1958) gave a range of only 3 to 4 accessory flagellar segments, but his observations apparently were based on a small number of specimens.

We will next examine in detail those characters found by some earlier workers to differ among the three forms of *G. minus*. Shoemaker (1940) listed six characters diagnostic of his variety *tenuipes*: a) slender gnathopods and pereopods, especially the second joint of the last three pereopods; b) lateral lobes of the head with rounded corners; c) reduced number of spines on the urosome in some specimens; d) eyes greatly reduced and occasionally almost absent; e) inner ramus of the third uropod proportionately longer; and f) weaker and more delicate appearance of the whole animal. Hubricht (1943) stated the Forms I and II had longer antennae and a bluish color, whereas Form III had shorter antennae and a brownish color.

In order to properly analyze the validity of the "diagnostic" characters given above, we assigned all populations studied in detail to one of the three groups based on habitat. These included: 1) the large, well-integrated cave systems in Greenbrier and Tazewell Countries; 2) other caves, excluding those listed in (1); and 3) springs, including resurgences at cave entrances. Thus, in general, Habitats 1, 2 and 3 should correspond to *G. minus* I, II and III populations, respectively.

As will be seen below, a division into habitat groups is essential because any mixed population can be separated into groups based on morphology alone. This, however, does not reflect any biological phenomenon except that populations differ.

The amount of degeneration of the compound eye is undoubtedly the most striking difference among populations from the three habitat groups. The various stages of eye degeneration are shown in Figure 1; the extremes between individuals from Habitats 1 and 3 are shown in Figures 2 and 3. In most specimens from Habitat 1 the amount of eye degeneration has reached the extreme shown in Figure 3, and there are no discernible eye facets remaining. Occasionally, however, a specimen was found in Habitat 1 with a few facets completely formed. Moreover, a few specimens were found in Habitat 2 populations with as much eye degeneration as those from Habitat 1 populations.

The populations from Habitats 2 and 3 can be separated on the basis of the number of well-formed facets in the compound eye. By using specimens from various localities the following data were obtained:

Springs (Habitat 3): N = 87, median = 28, range = 14 to 42

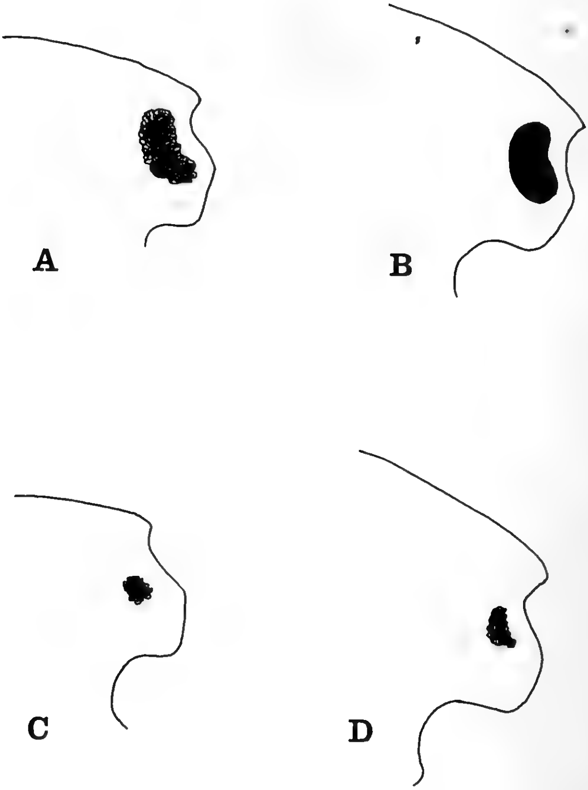


FIG. 1. Structure of the compound eye in mature males (11.00 mm) from four different populations of *Gammarus minus.* A) Tawneys Cave, Giles County, Virginia (Form II); B) spring in Washington County, Maryland (Form III); C) the Hole Cave, Greenbrier County, West Virginia (Form I); D) Bowens Cave, Tazewell County, Virginia (Form I).

FIG. 2. Head region of *Gammarus minus* (8.00 mm male) from Fort Spring, Greenbrier County, West Virginia. Upper, enlargement of compound eye showing individual facets.

FIG. 3. Anterior region of *Gammarus minus* (12.00 mm male) from Benedicts Cave, Greenbrier County, West Virginia. Upper, enlargement of compound eye showing loss of individual facets.

Caves (Habitat 2): $N = 62$, median $= 15$, range $= 0$ to 33. The medians are significantly different ($P > 0.99$) using the distribution-free Mann-Whitney U test.

Many cases of asymmetry were noted in the amount of eye degeneration in individuals from all three habitat groups. One particularly striking example was a specimen from Coffmans Cave in Greenbrier County which had approximately 20 countable facets in one eye and none in the other. Despite slight variation and asymmetry noted above, differences in the amount of compound eye degeneration were more clear-cut than any other character investigated. A careful examination of numerous specimens did not support Shoemaker's contentions that the interantennal lobes of the head are more rounded in Form I animals or that the number of dorsal spines on the urosome is reduced.

Hubricht (1943) pointed out that spring populations are brownish in color and that cave populations are bluish. Although this observation is generally true, there is sometimes a greater variation in color than implied; spring forms tend to be brownish to brownish-green and occasionally brownish-red, while cave forms may vary from bluish to dull gray, and rarely, to almost colorless. For instance, the population from Linwood Cave (Habitat 2) Pocahontas County is especially light in color with some individuals almost colorless, but morphologically this population is intermediate between Forms II and III. Explanations for the reduction and/or loss of integumentary pigment in cave crustaceans are still incomplete, although a number of experimental studies have been published on this subject (Baldwin and Beatty, 1942; Beatty, 1942, 1949; Anders, 1956; Maguire, 1961). The integumentary pigment of amphipods is made up of various carotenoid-protein complexes; these animals are unable to synthesize the carotenoids and, therefore, must obtain them from the environment (Beatty, 1949; Maguire, 1961 and papers cited therein). Apparently pigmentation in many of the troglobitic forms is genetically controlled; hence exposure of these animals to environmental carotenoids does not cause integumentary pigment to reappear (Vandel, 1964). Trogloxenes and troglophiles vary in their coloration from surface to cave, so availability of usable carotenoid-containing foods may affect the development of carotenoid-based pigments in their integument (Maguire, 1961). Thus spring forms of *G. minus* with apparently easy access to usable carotenoids in the form of abundant vegetable matter are brownish to brownish-green, while cave populations with apparently limited access to usable carotenoids undergo a reduction in pigmentation and are bluish to gray. If a difference in the availability of dietary carotenoids is the major factor in the development of pigment in *G. minus,* then any concomitant genetic influence on pigment production would be masked and very difficult to discern.

Both Shoemaker (1940) and Hubricht (1943) pointed out that *G. minus* I had proportionately longer and more slender appendages and hence a more fragile appearance than Form III, but it is probably the proportionately longer pereopods and antennae that give *G. minus* I the overall appearance of having a more delicate body and more slender appendages. These subjective observations are more apparent than real. Shoemaker (1940) also stated that the second joints (or bases) of the last three pereopods were more narrow than in the surface forms, but this is rare. The widths of the pereopod bases differ only slightly among representatives of the habitat groups as seen in Figure 4.

Some real differences among the three morphological groups in the proportionate lengths of certain appendages compared to body lengths suggests a trend toward allometry in the cave forms. To investigate the significance of these differences we made numerous measurements and treated the resulting data statistically.

Tables 1 and 2 give data for ratios of pereopod 7, uropod 3 and antenna 1 to total length for mature males from a variety of spring and cave populations. The ratios among the three habitat groups were statistically significant (Mann-Whitney U test) with two exceptions: a) uropod 3/total length is not significantly different in springs and caves (Habitat 2); b) pereopod 7/total length is only marginally significant ($P < 0.10$) in springs and caves (Habitat 2).

A general regression equation for appendage growth is $Y = aX^b + c$, where: Y is the dependent variable, i.e., antenna 1, pereopod 7 and uropod 3; b is the coefficient of allometry which equals 1 when no allometry occurs; X is the independent variable, i.e., total length; a is the slope of the regression line; c is the intercept on the ordinate. From this regression there are four ways in which the different ratios of dependent variable to independent variable might arise:

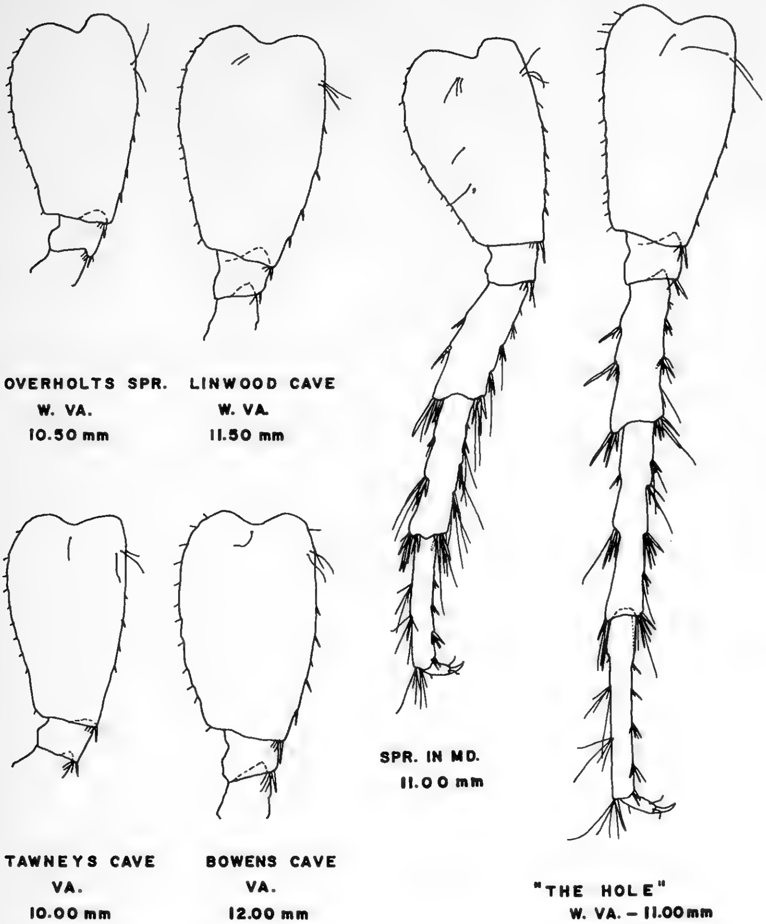


FIG. 4. Variation in structure of pereopod 7 in mature males from the indicated localities. Note difference in length but general similarity in structure of the pereopods of the males from the spring in Maryland (Form III) and the cave in West Virginia (Form I). Note also the slight variation in the shape and armature of the bases of the pereopods of males from different populations.

TABLE 1. Variation in the ratio of length of three different appendages (antenna 1, pereopod 7 and uropod 3) to length of body in mature males of 12 populations of *Gammarus minus.*

Cave Localities	Sample size	Mean length (mm)	Antenna 1/body	Mean ratios Pereopod 7/body	Uropod 3/body
Higginbothams, Greenbrier Co., W.Va.	5	11.9	0.698	0.485	0.217
Buckeye Creek, Greenbrier Co., W.Va.	5	10.9	0.652	0.461	0.192
Grapevine, Greenbrier Co., W.Va.	5	11.8	0.655	0.489	0.187
Linwood, Pocahontas Co., W.Va.	5	12.3	0.590	0.426	0.175
Cave Hollow, Tucker Co., W.Va.	5	10.8	0.625	0.452	0.180
Benedicts, Greenbrier Co., W.Va.*	5	10.8	0.750	0.513	0.223
Ludington, Greenbrier Co., W.Va.*	5	10.4	0.674	0.485	0.188
McClungs, Greenbrier Co., W.Va.*	8	11.3	0.720	0.523	0.207
The Hole, Greenbrier Co., W.Va.*	12	12.3	0.707	0.494	0.200
Greenbrier, Greenbrier Co., W.Va.*	20	12.0	0.647	0.482	0.209
Hugh Young, Tazewell Co., Va.*	7	11.0	0.749	0.485	0.226
Bowens, Tazewell Co., Va.*	11	11.9	0.793	0.493	0.226

*Indicates Habitat 1 cave; the remaining populations are from Habitat 2 caves.

TABLE 2. Variation in the ratio of length of three different appendages to body length in mature males of 11 spring populations of *Gammarus minus.*

Spring Localities	Sample size	Mean length (mm)	Antenna 1/body	Mean of ratios Pereopod 7/body	Uropod 3/body
Washington Co., Maryland	20	11.8	0.529	0.426	0.183
Smulton Spr., Centre Co., Pa.	10	10.1	0.576	0.449	0.188
Lancaster Co., Pa.	10	11.6	0.515	0.432	0.185
Tazewell Co., Va.	10	10.3	0.572	0.443	0.189
Maiden Spr., Tazewell Co., Va.	5	9.1	0.556	0.416	0.175
Spr. at Van, Lee Co., Va.	6	8.7	0.602	0.486	0.195
Windfields Spr., Bath Co., Va.	18	11.8	0.569	0.432	0.185
Sweet Sprs., Monroe Co., W.Va.	10	8.6	0.579	0.424	0.178
Overholt Spr., Pocahontas Co., W.Va.	11	9.6	0.613	0.452	0.190
Cold Spr., Monroe Co., W.Va.	10	9.7	0.586	0.443	0.191
Spr. on Mill Run, Tucker Co., W.Va.	10	11.2	0.570	0.459	0.166

1) Different ratios may reflect different coefficients of allometry. In particular, when b is less that 1 the dependent variable is increasing with a decreasing rate, and when b is greater than 1, the dependent variable is increasing with an increasing rate.

2) a, b and c may be the same for all groups, but when $c \neq O$, changing the size of the independent variable, i.e., total length, will change the ratio.

3) Different ratios may reflect different slopes of the linear $(b = 1)$ regression line.

4) Different ratios may reflect different intercepts.

In practice, solving for b in the above equation involves taking the logs of both sides which causes c to disappear. In order to find c by the usual methods, b must be considered to be equal to 1. Moreover, we will only consider a when b is assumed to be equal to 1. First, we will consider those dependent variables that show allometric growth. Those that do not show any allometry will be considered in terms of the last three possibilities listed above by using the equation $Y = aX + c$.

TABLE 3. The results of a test for allometry between the three habitat groups of *Gammarus minus*.

Independent variable	Dependent variable	Habitat†	b*
total length	pereopod 7	3 (springs)	0.96 ± 0.08
"	"	2 (caves)	0.86 ± 0.33
"	"	1 (large caves)	0.98 ± 0.16
"	uropod 3	3 (springs)	0.87 ± 0.11
"	"	2 (caves)	0.81 ± 0.62
"	"	1 (large caves)	1.10 ± 0.22
"	antenna 1	3 (springs)	0.79 ± 0.12
"	"	Fort Spring (3)	1.01 ± 0.12
"	"	2 (caves)	0.81 ± 0.31
"	"	Coffmans Cave (2)	0.92 ± 0.12
"	"	1 (large caves)	0.83 ± 0.14
"	"	Benedict Cave (1)	0.83 ± 0.14
outer ramus of third uropod	inner ramus of third uropod	Fort Spring (3)	1.27 ± 0.09
		Coffmans Cave (2)	1.15 ± 0.10
		Benedict Cave (1)	1.15 ± 0.09

†Those habitats labeled 1, 2 and 3 were calculated using only mature males. For Fort Spring, Coffmans Cave and Benedicts Cave, all sizes and both sexes were used.

*If b is not significantly different from 1.0 there is no evidence for allometry.

The results of the analysis of allometry are given in Table 3. The only clear case of positive allometry where *b* is greater than 1 occurs in the regression of the inner ramus of the third uropod against the outer ramus of the third uropod, but not in the regression of body length and uropod 3. However, positive allometry occurs in all three habitat groups, not just in the Habitat 1 populations. There is a tendency for antenna 1 to display slightly negative allometry in all three habitat groups. Therefore, we can conclude that there are no differences in allometry which could explain differences in the appendage to body length ratios.

If all the populations are on the same regression line, then the total lengths of the cave populations must be greater than the spring populations, and the intercept *c* must be less than one or vice versa. Random samples from three populations in Greenbrier County were measured for total length. These populations were from Benedicts Cave (Habitat 1), Coffmans Cave (Habitat 2) and Fort Spring (Habitat 3). A Mann-Whitney U test was used to test for significant differences. The Benedicts Cave population was significantly larger ($P > 0.99$) than Coffmans Cave population; the latter, in turn, was significantly larger than the Fort Spring population ($P > 0.99$). This relationship also holds true if only mature males are considered. If the mean lengths of mature males from springs (Table 2) are compared with mean lengths of mature males from caves of either Habitat 1 or 2, the differences are significant ($P > 0.95$ by the Mann-Whitney U test), but differences between the two cave habitat groups are not significant. These results indicate that as we go from spring forms to cave forms the total length (independent variable) increases, thus effectively moving up the regression line. However, when we consider the actual intercepts of the regression lines (see Table 4) very few of them have negative intercepts. Only in the comparison of the inner and outer rami of the third uropod are all of the intercepts of the three groups negative, and this particular ratio is complicated by allometry.

There is no significant pattern toward a higher slope or higher intercept in cave populations as shown in Table 4. However, the slopes of the Habitat 1 populations tend to be higher for pereopod 7, uropod 3 and antenna 1. A pattern in the intercepts is much less clear.

This pattern may not hold true for spring populations in general. The problem can be seen by comparing the antenna 1 regression of

TABLE 4. Analysis of the changes in intercept and slope of linear regression where $Y = aX + c$.

Independent variable	Dependent variable	Habitat*	a	c
total length	pereopod 7	3 (springs)	0.43 ± 0.04	1.73
"	"	2 (caves)	0.39 ± 0.16	8.33
"	"	1 (large caves)	0.48 ± 0.08	2.15
"	uropod 3	3 (springs)	0.16 ± 0.02	2.39
"	"	2 (caves)	0.16 ± 0.11	3.02
"	"	1 (large caves)	0.22 ± 0.05	—1.34
"	antenna 1	3 (springs)	0.44 ± 0.06	13.10
"	"	Fort Spring (3)	0.58 ± 0.06	—2.30
"	"	2 (caves)	0.35 ± 0.22	33.82
"	"	Coffmans Cave (2)	0.56 ± 0.07	5.50
"	"	3 (large caves)	0.59 ± 0.18	11.90
"	"	Benedict Cave (1)	0.45 ± 0.08	7.60
outer ramus of third uropod	inner ramus of third uropod	Fort Spring (3)	0.73 ± 0.04	—4.20
		Coffman Cave (2)	0.67 ± 0.05	—2.90
		Benedict Cave (1)	0.63 ± 0.04	—2.50

*Those habitats labeled 1, 2 and 3 were calculated using only mature males. For Fort Spring, Coffmans Cave and Benedicts Cave, all sizes and both sexes were used.

all spring populations with the Fort Spring population, Habitat 2 populations with the Coffmans Cave population and Habitat 1 populations with the Benedicts Cave population. Although expected, there is little correspondence between these pairs. This is due in part to the fact that only mature males were used for the first member of each pair, therefore resulting in the large standard errors seen in Table 4.

It is also possible to spot check for differences in slope in the regression by comparing the ratios of various appendages to total length from two populations with approximately the same range in total lengths. This minimizes the disturbing influences of allometry and the differences due to different intercepts. The results of these comparisons are shown in Table 5, and, as indicated by these data, one almost always finds a significant difference whenever populations from mixed habitats are compared. Whenever two like populations are compared, there are significant differences between these pairs about one-third of the time.

TABLE 5. Mann-Whitney U test on the ratios of lengths of antenna 1, pereopod 7 and uropod 3 to total length for a variety of population pairs of *Gammarus minus*.

Population pair and habitat group	Antenna 1	Uropod 3	Pereopod 7
Spr., Washington Co., Md. (3) *The Hole Cave, W.Va. (1)	<.001	<.001	<.001
*McClungs Cave, W.Va. (1) Spr., Tucker Co., W.Va. (3)	<.001	<.001	<.001
*The Hole Cave, W.Va. (1) Spr., Bath Co., Va. (3)	<.001	<.001	<.010
*Bowens Cave, Va. (1) Spr., Bath Co., Va. (3)	<.001	<.001	<.0001
*Higginbothams Cave, W.Va. (2) Spr., Bath Co., Va. (3)	<.001	<.001	<.001
*Grapevine Cave, W.Va. (2) Spr., Bath Co., Va. (3)	<.001	<.005	N.S.
*Grapevine Cave, W.Va. (2) Spr., Washington Co., Md. (3)	<.001	<.025	N.S.
*Spr., Bath Co., Va. (3) Spr., Washington Co., Md. (3)	<.001	N.S.	N.S.
*The Hole Cave, W.Va. (1) Greenbrier Caverns, W.Va. (1)	<.005	N.S.	<.050
*Spr., Lee Co., Va. (3) Spr., Monroe Co., W.Va. (3)	N.S.	<.001	N.S.
Grapevine Cave, W.Va. (2) Higginbothams Cave, W.Va. (2)	N.S.	N.S.	N.S.
Cave Hollow Cave, W.Va. (2) Buckeye Creek Cave, W.Va. (2)	N.S.	N.S.	N.S.
*Ludington Cave, W.Va. (1) Benedicts Cave, W.Va. (1)	<.050	N.S.	<.005

*Indicates the population with higher ratios.

DISCUSSION AND CONCLUSIONS

On the basis of the observations and analyses given above, we have concluded that *G. minus* is a single, highly variable species. The careful examination of a number of diagnostic characters did not reveal a single character that would unequivocally divide this species into separate taxa. The former recognition of a separate and distinct variety *tenuipes* probably resulted from the failure of earlier workers to examine sufficient material from a wide variety of habitats.

As already pointed out, Minckley and Cole (1963) found measurable variations in populations of *G. minus* from northern Kentucky. When associated with *G. bousfieldi* in Doe Run, *G. minus* differed from the "typical" spring populations and the possibility of character displacement was implied. Morphological variation noted for Doe Run populations associated with beds of *Fissidens* (an aquatic moss) resulted from their association with the moss, since the same variation was noted in *G. minus* whether *G. bousfieldi* was present or absent (Minckley and Cole, 1963). Similarly, some of the variation we observed within populations from the various habitat groups (see Tables 1, 2 and 5) might also have been affected by variation in the nature of the habitat. The springs observed varied: some are fast-flowing like the Overholts Blowing Cave resurgence; some are small, seepage types while others are large, pond-like springs with considerable vegetation (such as Fort Spring). According to Houston (1960), differences in current velocity affect the size at maturity of *Gammarus pulex*. Similarly, current velocity may also affect the size at maturity of *G. minus* in both caves and springs, since flow rate in both kinds of habitats is often variable. Other environmental parameters of cave streams such as temperature, quantity of washed-in food and chemistry, are also variable and are often influenced by seasonal changes on the surface.

One question still largely unresolved is why populations of *G. minus* I are restricted to certain caves in two very specific areas. Are certain caves able to select out these extreme types while others are not? We cannot satisfactorily answer this question, especially in view of the fact that *G. minus* II occasionally occurs in large cave systems (such as Bone Norman Cave) and some of the *G. minus* II populations occupy caves immediately adjacent to or even hydrologically related to caves with Form I populations. It should be noted, however, that *G. minus* I does not inhabit smaller, semi-isolated caves and that the two areas inhabited by *G. minus* I contain large, well-integrated drainage systems. Bowens and Hugh Young Caves, although small in terms of human traverse, are a part of a large, underground drainage complex believed to resurge through Maiden Springs in Tazewell County. The most accessible part of this complex is Fallen Rock Cave which contains five or more miles of traversable passages. In terms of traversable size, however, some of the Great Savannah caves in Greenbrier County are considerably larger. Greenbrier Caverns, for example, has at least 18 miles of explorable passages. It would appear, then, that a large subterranean drainage system is a necessary prerequisite for the development of Form I morphology. Undoubtedly, selection is playing a role here, but exactly how it operates is not clear.

The variation in *G. minus* may be genetic or ecophenotypic, or influenced by both effects. It is apparent that the *G. minus* I morphology is composed of the extremes present in both *G. minus* II and III populations that are being selected for by certain, as yet undetermined, factors of the subterranean environment. Depending on circumstances, the same morphological change may be ecophenotypic or genetic; processes similar to those shown by Waddington's (1956) classical experiment on genetic assimilation of environmentally induced change in *Drosophila melanogaster* may explain some variation in *G. minus*.

If the three forms of *G. minus* are components of a single, variable species, one must accept the potential for gene exchange between population extremes. The opportunities for gene exchange are probably as great, or even greater, between certain spring and cave populations than they are between widely distributed spring populations. Almost any spring population is semi-isolated and such populations are best regarded as geographic isolates in the sense of Mayr (1963). If we consider physical barriers and drainage patterns in karst areas, migration from a spring into a cave or vice versa is easier to envision than migration from one spring to another. The latter event usually would be limited to the rather circuitous routes of surface streams, while the former could take place more directly. One means by which dispersal might occur between springs has already been suggested, but at best this method is limited and difficult to conceive of as a common event. Environmental conditions, rather than isolation, might play a more significant role in determining the form in a given habitat.

One of the problems encountered with *G. minus* in the central Appalachians was somewhat similar to that which Christiansen and Culver (1968) found in the cave collembolan *Pseudosinella hirsuta*. With this species, there was a striking parallelism and convergence in morphology in geographically isolated, highly cave-adapted populations. We found a similar situation with *G. minus* in two well-separated and isolated karst areas with similar habitats. The *tenuipes* form may be a convergent ecotype (see Dobzhansky, 1951) which occurs only under special environmental conditions and in the presence of proper genetic variants.

The present study is preliminary and it is obvious that there are a number of uninvestigated aspects pertinent to the overall problem which would provide interesting topics for future studies.

ACKNOWLEDGMENTS

A part of this study was supported by grants to Holsinger from the National Speleological Society Research Advisory Committee and the Old Dominion University Educational Foundation and by a grant to Culver from the Cave Research Foundation. We are grateful to the West Virginia Association for Cave Studies, Inc. (WVACS) for providing field assistance in Greenbrier County, and to Dr. Thomas E. Bowman for providing specimens from the Smithsonian Institution (United States National Museum). We thank the following persons for their assistance in the field and/or for their contribution of specimens: Roger Baroody, William Biggers, John and Martha Cooper, Richard Franz, Ronald Larue, Charles Maus, David Newson, John Rutherford and Paul Starr. We are also indebted to a number of landowners who kindly allowed us to visit caves on their property.

LITERATURE CITED

Anders, Fritz. 1956. Über Ausbildung und Vererbung der Körperfarbe bei *Gammarus pulex* ssp. *subterraneus* (Schneider), einer normalweise pigmentlosen Höhlenform des gemeinen Bachflohkrebses. Zeit. indukt. Abstammungs-u.Vererbungslehre, **87**: 567–579.

Baldwin, E. and R. A. Beatty. 1942. The pigmentation of cavernicolous animals I. The pigments of some isopod Crustacea. J. Exp. Biol., **18**: 136–143.

Beatty, R. A. 1942. The pigmentation of cavernicolous animals II. Carotenoid pigments in the cave environment. J. Exp. Biol., **18**: 144–152.

——— 1949. The pigmentation of cavernicolous animals III. The carotenoid pigments of some amphipod Crustacea. J. Exp. Biol., **26**: 125–130.

Bousfield, E. L. 1958. Fresh-water amphipod crustaceans of glaciated North America. Can. Field-Natur., **72(2)**: 55–113.

Christiansen, K. A. and D. C. Culver. 1968. Geographic variation and evolution in *Pseudosinella hirsuta*. Evolution, **22**: 237–255.

Dobzhansky, Theodosius. 1951. Genetics and the origin of species. Columbia Univ. Press, New York, 364 p.

Holsinger, J. R. 1967. Systematics, speciation, and distribution of the subterranean amphipod genus *Stygonectes* (Gammaridae). U.S. Nat. Mus. Bull., 259, 176 p.

——— 1969. Biogeography of the freshwater amphipod crustaceans (Gammaridae) of the central and southern Appalachians pp. 19–50. *In* P. C. Holt [ed.] The distributional history of the biota of the southern Appalachians. Part I: Invertebrates. Virginia Polytechnic Inst. Press, Blacksburg, Va.

Houston, K. 1960. Size of *Gammarus pulex* in fast- and slow-running streams. Report Dauntsey's School Nat. Hist. Soc., 1959–1961, pp. 11–13.

Hubricht, L. 1943. Studies on the Nearctic freshwater Amphipoda. III: Notes on the freshwater Amphipoda of eastern United States with description of ten new species. Amer. Midl. Nat., **29**: 683–712.

——— 1959. Malacostraca (Amphipoda), pp. 876–878. *In* W. T. Edmondson [ed.] Ward and Whipple's freshwater biology. John Wiley and Sons, New York.

Hubricht, L. and J. G. Mackin. 1940. Descriptions of nine new species of fresh-water amphipod crustaceans with notes and new localities for other species. Amer. Midl. Nat., **23**: 187–218.

Hynes, H. B. N. 1955. Distribution of some fresh-water Amphipoda in Britain. Verh. int. Ver. Limnol., **12**: 620–628.

Mackin, J. G. 1941. A key to the species of Amphipoda of Oklahoma. Proc. Oklahoma Acad. Sci., **21**: 29–30.

Maquire, B. 1961. Regressive evolution in cave animals and its mechanism. Texas J. Sci., **13**: 363–370.

Minckley, W. L. 1964. Upstream movements of *Gammarus* (Amphipoda) in Doe Run, Meade County, Kentucky. Ecology, **45(1)**: 195–197.

Minckley, W. L. and G. A. Cole. 1963. Ecological and morphological studies on gammarid amphipods *(Gammarus* spp.) in spring-fed streams of northern Kentucky. Occasional Papers of the C. C. Adams Center for Ecol. Stud., **10**: 1–35.

Mayr, E. 1963. Animal species and evolution. Belknap Press, Cambridge, Mass., 797 p.

Say, T. 1818. An account of the Crustacea of the United States. J. Acad. Natur. Sci. Philadelphia, **1**: 374–401.

Shoemaker, C. R. 1940. Notes on the amphipod *Gammarus minus* Say and description of a new variety, *Gammarus minus* var. *tenuipes*. J. Washington Acad. Sci., **30**: 388–394.

Stoll, N. R. (Chairman), R. Ph. Dollfus, J. Forest, N. D. Riley, C. W. Sabrosky, C. W. Wright, R. V. Melville (Sec'y.) 1964. International code of zoological nomenclature. International Trust for Zoological Nomenclature, London, 176 p.

Vandel, A. 1964. Biospéologie. Gauthier-Villars, Paris, 619 p.

Waddington, C. H. 1956. Genetic assimilation of the bithorax phenotype. Evolution, **10**: 1–13.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

OMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

ILLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

THOR'S COPIES Each author receives 50 free copies of his *Postilla*. Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 147 10 JULY 1970

NOTOGONEUS OSCULUS COPE, AN EOCENE FISH FROM WYOMING (GONORYNCHIFORMES, GONORYNCHIDAE)

PHILIP L. PERKINS

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Nancy A. Ahlstrom, Elizabeth G. Weinman, Elise K. Kenney.

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* special publications, and available back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection.* All except *Discovery* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

Erratum

Perkins, Philip L. 1970. Notogoneus osculus Cope, an Eocene fish from Wyoming (gonor~~h~~ynchiformes, Gonorynchidae), Postilla 147, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

****

Page 18. The second entry under "Literature Cited" should read·

Cope, E.D. 1885. On two new forms of polydont and gonorhychid fishes from the Eocene of the Rocky Mountains. Mem. Nat. Acad. Sci. 3· 161-165.

NOTOGONEUS OSCULUS COPE, AN EOCENE FISH FROM WYOMING (GONORYNCHIFORMES, GONORYNCHIDAE)

PHILIP L. PERKINS

Department of Biology and Peabody Museum of
Natural History, Yale University

ABSTRACT

The gonorynchid fish *Notogoneus osculus* Cope is reexamined on the basis of newly prepared material. It is similar to the Recent genus *Gonorynchus* in possessing a cephalic rib, in the construction of the pelvic girdle, the suspensorium, coalesced frontals and the mandibular elements. Gonorynchid evolution from the Eocene on has been very conservative, and it is probable that the mechanics of the protrusible jaws in all genera of the family has remained unchanged from the Upper Cretaceous to the Recent.

POSTILLA 147: 18p. 10 JULY 1970.

INTRODUCTION

The gonorynchiform fish consist of five Recent and nine extinct genera, of which only one Recent genus *(Chanos)* has a fossil record. These fish, and the somewhat more primitive salmoniformes are first recorded from the Lower Cretaceous, and thus it would seem that the protacanthopterygian fishes originated shortly before, in the Late Jurassic. The suborder Gonorynchoidei is first noted in the Upper Cretaceous *(Charitosomus),* after which there is a gap until the Lower Eocene when the cosmopolitan genus *Notogoneus* appears. *Notogoneus* disappears in the Oligocene, and the only Recent record of this family is the marine genus *Gonorynchus*. The suborder Chanoidei includes three families, two of which (Kneriidae, Phractolaemidae) lack a fossil record and are further restricted to fresh water. The third family, Chanidae, has six genera; the one surviving genus, *Chanos,* is a marine form.

Greenwood et al. (1966, p. 374–380) have discussed in some detail the differences and similarities between the gonorynchiformes and the salmoniformes, clupeoids, albuloids and ostariophysians. Although they demonstrated that the gonorynchiformes share numerous characters with these other groups, they concluded that: 1) the gonorynchiformes are a natural assemblage and 2) these fishes and the ostariophysians were probably derived from a common group near the salmoniformes. Closeness to the ostariophysians is indicated by the beginning of a divided swim bladder, although *Gonorynchus* lacks one, by similarities in the caudal fin skeleton and by unusual cephalic ribs in the vicinity of the first three vertebrae.

Within the gonorynchiformes, Greenwood et al. concluded that the Recent genera *Chanos, Kneria, Cromeria* and *Phractolaemus* are closer to each other than is *Gonorynchus,* and consequently, *Gonorynchus* is placed in a separate suborder (Gonorynchoidei, with one family, Gonorynchidae) from the other extant forms.

The members of the family Gonorynchidae are the most aberrant fishes in the order discussed here. As such, study of any particular genus would not be expected to illuminate the course of ostariophysian evolution significantly. However, a study of the skeletal changes within the gonorynchids might be expected to indicate the rate of evolution in that group. Of the two extinct genera of gonorynchid fishes, *Charitosomus* and *Notogoneus,* the latter is the best known genus in terms of well-preserved material. Recent preparation of two unusual specimens (YPM 5772, 14124) afforded an opportunity to make a preliminary comparative study of *Notogoneus* and to compare it with the surviving genus *Gonorynchus*. It was felt such work might indicate whether or not the family Gonorynchidae had attained essentially "modern" skeletal characters by the Eocene. The results of this work suggest that by the Eocene, and quite probably earlier, the gross skeletal evolution of the gonorynchids had practically ceased, and that whatever changes occurred thereafter were limited to the soft parts and physiology.

The family Gonorynchidae is represented today by the genus *Gonorynchus* which contains six species with a reported distribution in the seas surrounding New Zealand, Australia and Japan. The fossil record of this family indicates that the long, fusiform body and rather highly specialized feeding parts of the mouth of these fishes have changed little from Late Cretaceous times to the present. Presumably, these fishes have been well adapted to a bottom-dwelling existence during this time span, and it is probable that they all possessed a barbel suspended from the lower border of the maxilla.

The genus *Notogoneus* contains the following species: *N. janeti* Priem, Lower Oligocene, France; *N. longiceps* (Meyer), Upper Oligocene, Germany; *N. osculus* Cope, Eocene, North America; *N. squamosseus* (Blainville), Lower Oligocene, France and *N. cuvieri* (Agassiz), Upper Eocene, France.

The material upon which this study is based includes five specimens of *Notogoneus osculus* (YPM 5772, 14124; AMNH 3900, 2504, 1340), and two specimens of *Gonorynchus gonorynchus* (Linné) kindly sent to me by Dr. Tokiharu Abe.

Descriptions and Comparisons

A. cranial material

The bones of the skull of *Notogoneus osculus* (YPM 5772) have been somewhat disarticulated (Fig. 1); however, they are exceptionally well shown in the prepared specimen. Five skull bones merit special attention. The first is the operculum. Both opercula are present: the right operculum is articulated with the suboper-

FIG. 1. *Notogoneus osculus* (YPM 5772). X 1.

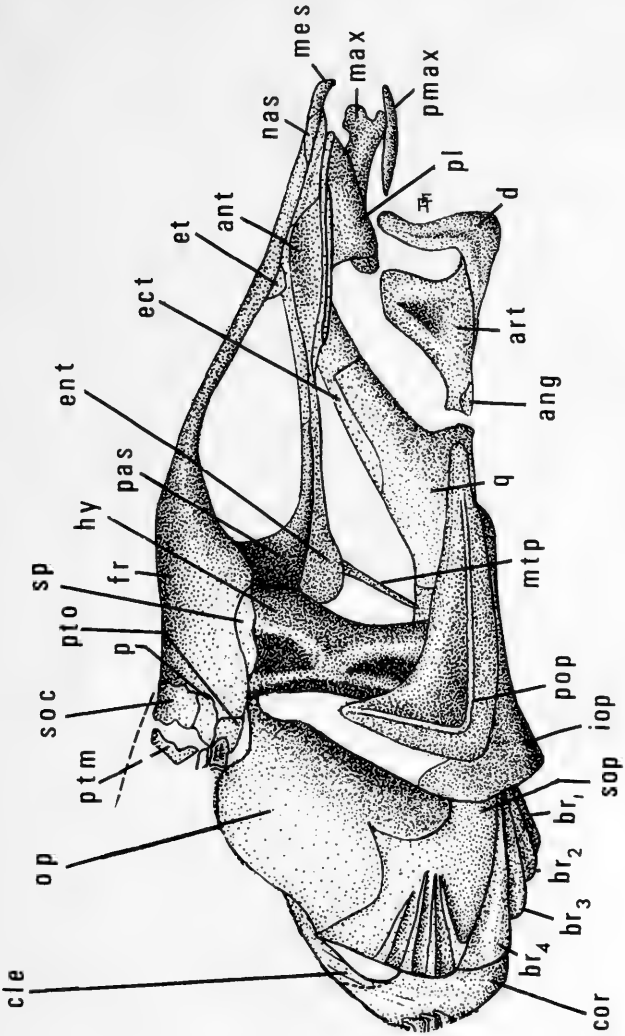


FIG. 2. *Notogoneus osculus.* Composite of YPM 5772 and AMNH 1340, 3900. Abbreviations at end of text X 1.

culum and slightly overlaps the posterior border of the hyomandibula. It has been rotated about from its natural position, hence the restoration (Fig. 2) places it and the suboperculum approximately 15° anteriorly about an axis formed by the opercular condyle on the hyomandibula. The left operculum (Fig. 3) is represented in its entirety. It has a rugose surface with numerous pits, though not highly sculptured. The anterior crescentic blade articulates with the posterior border of the hyomandibula and with the posteromedial border of the preoperculum.

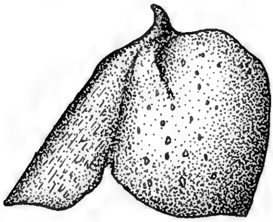


FIG. 3. *Notogoneus osculus* (YPM 5772). Left operculum, lateral view. X 1.

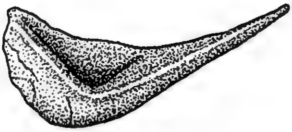


FIG. 4. *Notogoneus osculus* (YPM 5772). Right preoperculum, lateral view. X 1.

The opercula of the two specimens of *Gonorynchus* observed are only slightly different from that of *Notogoneus:* the anterior falcate blade of the latter extends somewhat more toward the hyomandibula and lacks the prominent preopercular groove seen in *Gonorynchus.*

The preoperculum (Fig. 4) of *Notogoneus* has a less robust horizontal limb than that of *Gonorynchus,* but it resembles the preoperculum in the latter fish in outline and size relative to the other cranial bones. The anterior part of the preopercular canal approaching the quadratoarticular joint is quite prominent (Fig. 1), but the vertical portion of the canal is lacking. The suboperculum (Fig. 5) has four large clefts on the posterior border. All reach over half the distance across the bone. A small cleft, probably a fracture, is dorsal to the others. In Figure 2, the suboperculum is depicted as having participated in the ventrolateral aspect of the opercular apparatus to a much greater degree than it does in *Gonorynchus.*

In the various species of *Notogoneus* currently recognized, all except *N. longiceps* have four clefts in the suboperculum (Woodward, 1901; Signeux, 1961). In an illustration of Whitfield (1890, fig. 3) of *Procatostomus constablei (=Notogoneus osculus,* AMNH 3900) there are seven clefts shown on the suboperculum; in fact there are

FIG. 5. *Notogoneus osculus* (YPM 5772). Right suboperculum, lateral view. X 1.

FIG. 6. *Notogoneus osculus* (YPM 5772). Mesethmoid with nasals, dorsal view. X 1.

only four, since the remainder are fractures in the bone. Chabanaud (1931, fig. 6) gives another inaccurate restoration of the right suboperculum based on Whitfield's specimen.

One major difference noted in the relative placement of the suboperculum with respect to the operculum is that in *Notogoneus* the former bone accounts for nearly one-half of the opercular shield, while in *Gonorynchus* (Ridewood, 1905; Monod, 1963) the suboperculum occupies approximately one-third of the same area. Both bones are closely apposed in all specimens of *Notogoneus* examined (except YPM 14124) and would have moved about the operculohyomandibular condyle during dilation and contraction in the same manner as that of the modern form. One curiosity is the absence of the preopercular channel in *Notogoneus*. This channel accepts the posterior border of the preoperculum and the interoperculum when the opercular series is constricted, and the lack of this mechanism implies that the fascia enveloping the external surfaces of the opercular apparatus must have restrained the preoperculum at about the position that it appears in Ridewood's (1905) figure of *Gonorynchus*. Figure 1 of this paper shows the operculum and suboperculum rotated somewhat dorsally and posteriorly; the posterodorsal border of the operculum reaches nearly to the level of the pterotic.

The mesethmoid has undergone perhaps the greatest modification of any of the endochondral bones. While that of the Recent form closely resembles a fleur-de-lis without the median blade, the mesethmoid of *Notogoneus* (Fig. 6) is more nearly triangular in outline. In YPM 5772 it has become dissociated from the frontal, but both nasals remain attached.

In all specimens of *Notogoneus* seen, the frontal (Fig. 7) was crushed inward during preservation. The lack of a midline suture is repeated in the Recent forms as well. Because of post-mortem damage to the frontal, it has lost whatever dorsoventral convexity it may have originally possessed; it has been restored in Figure 2 with a dorsally directed convexity over the orbits much as in Ridewood (1905, pl. 16, fig. 5). In his illustration of the skull of *Gonorynchus greyi,* Ridewood seems to have overemphasized the convexity of the frontal, because an X-ray plate made of *G. gonorynchus* in the Peabody Museum indicates that the skull in lateral view resembles a spear point, with the posterior portion of the frontal rising somewhat higher than the dorsal border of the

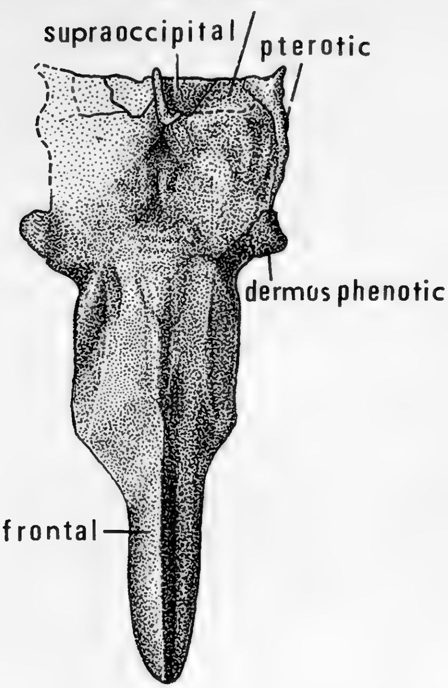
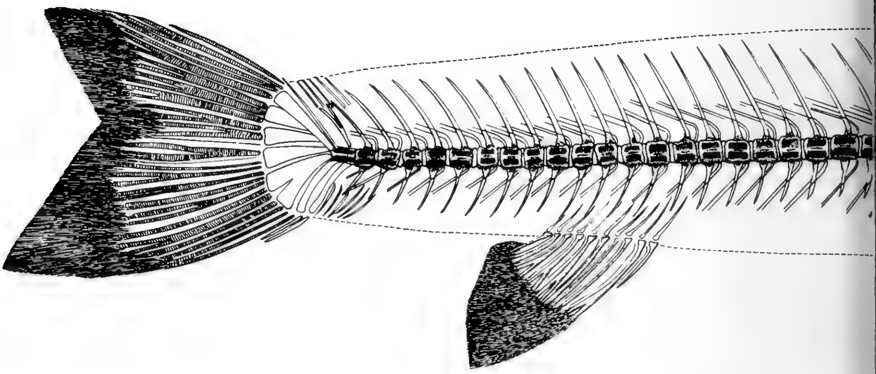


FIG. 7. *Notogoneus osculus* (YPM 5772). Frontal, dorsal view. X 1.

orbits. Monod (1963, fig. 3) correctly gave this outline in *G. gonorynchus;* however, the occipital portion of his illustration is far too short. The postorbital part of the skull of *N. osculus* is nearly equal to the length of the preorbital part. Hussakof (1908, fig. 43) incorrectly showed a midline suture on the frontal, a mistake that undoubtably arose because all three specimens used by him in his reconstruction are broken down the midline. As Gregory remarked (1933, p. 175–76) in his discussion of the functional analysis of the skull of *Gonorynchus,* "The length and narrowness of the interorbital bridge and bony rostrum would perhaps be a source of weakness if these very long frontals were not coalesced in the mid-line."

In addition to the frontal itself, the right lateral ethmoid, a por-



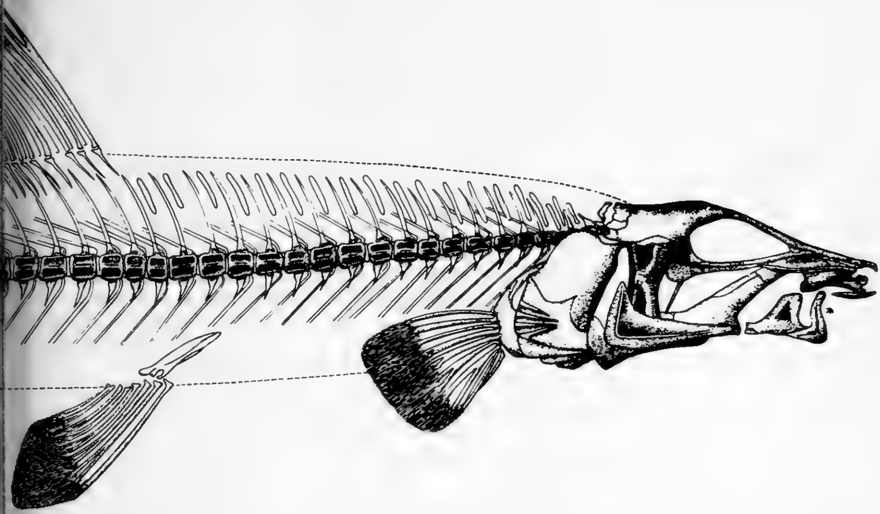


FIG. 8. *Notogoneus osculus*. Composite of YPM 5772, 14124 and AMNH 1340, 3900. X 2/5.

tion of the left parietal, the left pterotic and left sphenotic are clearly identifiable in YPM 5772. A small lateral ridge, probably the left dermosphenotic, is present.

The hyomandibula of *Notogoneus* is vertical and it presumably articulates with the cranium at two points as in *Gonorynchus* (Ridewood, p. 365). However, Monod (1963, p. 260) stated that the articulation runs along the entire dorsal surface of the bone. There is little indication in YPM 5772 as to its precise articulation, for the cranial bones medial to the hyomandibula have been badly crushed. Its external shape has changed little during the Tertiary, and it is likely that the small anterior and large posterior heads performed the same functions in the Eocene as they do today. The thick vertical ridges seen in *Gonorynchus* are wanting in our specimens of *Notogoneus*; possibly these have been broken off. The right hyomandibula (Fig. 1) is positioned correctly with respect to the operculum. The left hyomandibula lies, disarticulated, above the frontal.

The small angular, the larger overlying articular and the dentary are well preserved in all specimens examined, and Woodward has shown them in plate XVIII (1896). The ascending processes of the articular and the dentary are very slightly higher than those of *Gonorynchus* proportionally and are almost identical in shape. The maxilla (Fig. 1) is partially overlain by other bones, but it has a characteristic blunt, triradiate head (Woodward, 1896). The premaxilla was not observed in any specimens, but the antorbital was present in AMNH 2504 as a small, leaf-shaped bone containing the suborbital canal. This element is relatively the same size as that in the living form. The entopterygoid (Fig. 2) bore no teeth at its posterior end.

The interoperculum is difficult to distinguish from some other bones in that area. It has been restored (Fig. 2) as extending from the anteroventral base of the quadrate to the posteroventral end of the suboperculum. Possibly this includes part of the coracoid; however, Ridewood pointed out that the gonorynchids did not have a precoracoid process, hence the interoperculum may not have extended this far back. The hyoid apparatus cannot be observed and there is only one branchiostegal apparent.

The two dentaries are well exposed in AMNH 1340. The mesial surface of the horizontal ramus of the right dentary in that specimen shows a small groove running parallel to the dorsal surface of the bone. Presumably this channel served as the insertion for the "Meckelian muscle" as suggested by Monod (1963, fig. 87). No evidence of the sesamoid articular (Ridewood, 1905) was found.

The palatoquadrate arch has nearly the same form in both modern and fossil fishes. X-ray plates of preserved specimens of *G. gonorynchus* show that when the mandible is fully depressed, the angle through which the lower jaw moves is about 25°. The maxilla and premaxilla appear to move as a unit, rotating about their ligamentous attachment to the prevomer through an angle of about 45°. Labial muscles and fascia curtain the lateral gape while the maxilla performs a similar function to that in the mouth of higher teleosts today. Figure 2 shows the lower jaw to be about half open.

Le Danois (Monod, 1963, p. 311–12) partly dissected the mandibular musculature of *G. gonorynchus* and found that the mandibular adductors have three heads. The largest of these is inserted on the medial face of the ascending process of the articular, while the other two are inserted on the posterolateral and dorsal surfaces of the same bone. The great obliquity of the suspensorium and the relatively long distance between the articular and the hyomandibula would indicate that the power derived from these small muscles would not by themselves be a significant factor in the rapid closure of the mouth. However, a double-headed set of labial muscles arising on the coronoid process of the dentary, and a large internal mandibular quadrate muscle which inserts on the posterodorsal surface of the coronoid process and attaches to the quadrate would provide the requisite power for rapid closure of the mouth. Undoubtedly, the mechanics of depression and closure of the lower jaw are the same in both *Notogoneus* and *Gonorynchus*.

B. POSTCRANIAL MATERIAL

Very little of the immediate postcranial skeleton was observed in any of the specimens of *Notogoneus*. The upraised flange along the posterior border of the operculum and suboperculum in YPM 5772 does not, however, seem to belong to the opercular series, but presumably is a remnant of the coracoid. This ridge commences approximately 0.5 cm anterodorsal to the pectoral fin, continues up along the posterior border of the suboperculum and the operculum, and then appears to approach the remnant of the posttemporal bone. The coracoid, in reconstruction, appears just below and behind the suboperculum.

The left cleithrum is exposed in YPM 5772 (Fig. 1). It lies immediately below the left preoperculum with its mesial side facing out. At the proximal end, forming an obtuse angle with the main body of the bone is the articular surface that faces the opposing cleithrum. As in the modern form, the mesial side is deeply excavated. Although Chabanaud (1931, p. 512) found remnants of the hyper- and mesocoracoid, I did not see any traces of these bones, or of the hypocoracoid in any of the specimens of *Notogoneus* examined. Also missing are the actinosts supporting the dermal rays of the pectoral fin. However, the first dermal ray has at its proximal end a small cap-shaped head protruding at a right angle to the axis of the ray. It has been suggested by Monod (1963, p. 264) that this may have resulted from the fusion of two lepidotrichia. In *Gonorynchus* this head articulates directly with the hypercoracoid. The remaining dermal rays all have similar talon-shaped processes at their proximal ends.

The pelvic girdle of *Notogoneus* (Fig. 8) exhibits practically no differences from that of *Gonorynchus;* it is composed of two lanceolate splints to which the dermal rays of the pelvic fin attach directly. As in the Recent form, the proximal heads of the rays have a small talon that articulates with the cartilaginous distal end of the pelvic bone.

The anal, caudal and dorsal fins are very similar in construction in both the Eocene and Recent forms. The branching dermal rays are commonly preceded by one or more spiniform rays, but the fin ray supports at the distal ends of the pterygiophores (axonosts, mesonosts and baseosts) are not apparent in the fossil fish. An unusual feature seen in the unpaired fins in *Notogoneus,* but not in *Gonorynchus,* is the presence of small thin splint-like rays, one of which precedes each of the branching rays. Presumably, these small bones gave support to the lower half of the fin; they do not extend out past the branching portion of their sister dermal rays. Because of their extreme narrowness and the fact that they did not articulate with a pterygiophore, it seems unlikely that they had any radial muscles attached to their lateral surfaces. Instead, they were probably held in position by the external fascia of the fin itself.

The caudal fin of *Notogoneus* differs from that of *Gonorynchus* (Gosline, 1960, fig. 8) only in possessing more dermal rays. Caudal skeleton evolution in the Gonorynchidae has been extremely conservative. The penultimate vertebra has both a neural and haemal spine, while the terminal half-centrum supports a uroneural and six hypurals. Hypurals 2 and 3 are fused, and there is a marked separation between hypurals 2–3 and 4. The epural in Gosline's figure 8 was not observed in *Notogoneus,* although further examination of specimens may show this bone to be present. The number of branched fin rays is commonly 21 or 22.

The vertebrae of *Notogoneus* are unfortunately rather poorly preserved. Numerous workers have remarked on the robust parapophyses of *Gonorynchus;* by contrast, those of *Notogoneus* are commonly small and do not protrude markedly laterad to the hourglass-shaped centra. The centra are amphicoelous with a small constricted tunnel for the notochord. Horizontal trabeculae traverse the lateral surfaces of the centra while the dorsal and ventral areas are indented for the reception of the neural and haemal spines. The haemal spines increase in length gradually from anterior to posterior, while the neural spines maintain relatively the same length along the entire vertebral axis. Interneurals are present commencing from the second vertebra and ceasing at the level of the anterior border of the dorsal fin.

The restoration of the intermuscular bones in *Notogoneus* is difficult since all are disarticulated from their associated vertebrae. Monod's excellent work (1963, fig. 56) with these bones in *Gonorynchus* suggests that most of the same ones are probably present in *Notogoneus,* although only those labeled *a* (epineurals), *b* (dorsal ribs) and *c* (pleural ribs) are anywhere near their points of attachment. There are other scattered elements observable in the fossil material; presumably these are the bones labeled *d* by Monod (epipleural ribs).

A curious feature mentioned by Greenwood et al. (1966) is the construction of the three anterior vertebrae and the posterior "ledge" of the exoccipital in *Gonorynchus*. Each of the first three vertebrae is not only different from each other, but is also different from all the remaining ones. They do not bear true ribs or epineurals. The third vertebra has a rib inserted into a pit in the centrum rather than on the parapophysis. An examination of all available material was inconclusive, because the first two to five vertebrae are usually dislocated during post-mortem burial. However, in AMNH 1340, a cephalic rib (?) resembling exactly those illustrated by Monod (1963, figs. 74, 75) and Greenwood et al. (1966, fig. 8) is found apparently articulated to the fourth vertebra. There seems to be little question that this is in fact the same rib-like bone described by Monod and by Greenwood; its placement on the fourth vertebra was perhaps a result of post-mortem dislocation. If so, this rib and the bones of the skull have changed remarkably little since the Early Eocene.

CONCLUSION

The indistinctness of a number of cranial bones makes a detailed study of the functional morphology of the skull impracticable at this time. It is not possible to identify the metapterygoid, symplectic, ectopterygoid or parasphenoid. The nature and size of these bones could significantly influence the effectiveness of the masticatory apparatus. The lack of exoccipitals and basioccipitals in fossil specimens makes it difficult to compare the articulation of the vertebral column and the cranium of *Notogoneus* with that of *Gonorynchus*. However, it is not difficult to reconstruct the cranium, since most of the major bones (frontal, opercular apparatus and mandibular elements) are present. By comparing YPM 5772 with those specimens illustrated in the works of Woodward (1896, 1901) and of Cope (1885b), and utilizing the information in Monod and Ridewood, we made a reconstruction of the articulated skull given in Figure 2. The cranial outline is quite similar to Monod's illustration (1963, fig. 3). This similarity reflects my belief that Gregory's conclusion (1933, p. 179) that the skull ". . . as a whole seems relatively less elongate and depressed than in the recent genus" is not borne out by the fossil material. Whatever differences there may be between the sizes of the bones of the recent forms and those that were not identifiable in the fossil specimens, it does not seem likely that there would be a great deal of change, relatively, in the skull shape. In particular, the pterygoids, the parasphenoid and the convexity of the frontal would have the greatest effect on skull shape. Since the hyomandibula is very similar to that of the living species, and since the preoperculum and the mandibular elements seem to have about the same relative length as in the modern forms, it is highly likely that the remaining bones (pterygoids and parasphenoid) would maintain the same relative sizes and shapes. Unless the gape of the mouth in the fossil specimens differed greatly from that of the recent ones (i.e., considerably wider) or unless the convexity of the frontal also differed significantly, then we are practically forced to conclude that the skull shape has changed very little during the last sixty million years. It is interesting to note that in an illustration of Woodward (1896) as well as in YPM 14124, in which there appears to be little distortion, the gape of the mouth is about the same as that in Gregory's reconstruction of the skull of *Gonorynchus* (fig. 66); that is, the maxilla and anterior border of the ascending process of the dentary meet at nearly the same angle.

Given that the major difference between *Gonorynchus* and *Notogoneus* involves the possession of a toothed entopterygoid and hyoid in the former, it would be profitable to study the skull of the European Upper Cretaceous genus *Charitosomus* in detail. Illustrations of this fish (Woodward, 1896) indicate that the major cranial and jaw elements are very similar to those in *Gonorynchus*. Woodward (1901) has noted teeth on the hyoid apparatus as well as on the entopterygoid of *Charitosomus*. Most probably, the hyoid teeth occur on the 2nd basibranchial, as in *Gonorynchus*. X-ray studies of the masticatory habits of a living *Gonorynchus* coupled with a careful reconstruction of *Charitosomus* may well suggest the precise masticatory behavior of *Charitosomus* since the morphology of the jaws in both genera is practically the same. The lack of these denticulate structures in *Notogoneus,* while not resulting in any major restructuring of the jaw bones, does suggest a change in food preference. Consequently, there must have been special ecological conditions favoring *Notogoneus* from the Early Eocene to the Late Oligocene, when that genus apparently became extinct.

ACKNOWLEDGMENTS

I wish to thank Dr. Bobb Schaeffer of the American Museum of Natural History for the loan of specimens of *Notogoneus osculus,* and Dr. Tokiharu Abe of the Zoological Institute of the University of Tokyo for the specimens of *Gonorynchus gonorynchus*. The illustrations were made by Miss Diane McClure of the Peabody Museum.

ABBREVIATIONS USED IN ILLUSTRATIONS

ang	Angular	mtp	Metapterygoid
ant	Antorbital	nas	Nasal
art	Articular	op	Operculum
$br_{1,2}$	Branchiostegal rays	p	Parietal
cle	Cleithrum	pas	Parasphenoid
cor	Coracoid	pl	Palatine
d	Dentary	pop	Preoperculum
ect	Ectopterygoid	pmax	Premaxilla
ent	Entopterygoid	ptm	Posttemporal
et	Lateral ethmoid	pto	Pterotic
fr	Frontal	q	Quadrate
hy	Hyomandibula	soc	Supraoccipital
iop	Interoperculum	sop	Suboperculum
max	Maxilla	sp	Sphenotic
mes	Mesethmoid		

YPM–Peabody Museum, Yale University
AMNH–American Museum of Natural History

LITERATURE CITED

Chabanaud, P. 1931. Affinités morphologiques, répartition stratigraphique et géographique des poissons fossiles et actuels de la famille des Gonorhynchidés avec la description de deux genres nouveaux et d'une espèce nouvelle. Bull. Soc. Géol. Fr. **(5) 1**: 497–517.

——— 1885b. On two new forms of polydont and gonorhynchid fishes from the Eocene of the Rocky Mountains. Mem. Nat. Acad. Sci. **3**: 161–165.

Gosline, W. A. 1960. Contribution toward a classification of modern isospondylous fishes. Bull. Brit. Mus. (Nat. Hist.), Zool. **6 (6)**: 325–365.

Greenwood, P. H., D. E. Rosen, S. H. Weitzmann and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Amer. Mus. Nat. Hist. **131 (4)**: 341–455.

Gregory, W. K. 1933. Fish skulls: a study of the mechanism of natural evolution. Trans. Amer. Phil. Soc. **23 (2)**: 75–481.

Hussakof, L. 1908. Catalogue of types and figured specimens of fossil vertebrates in the American Museum of Natural History. Pt. I, Fishes. Bull. Amer. Mus. Nat. Hist. **25**: 1–103.

Monod, T. 1963. Sur quelques points de l'anatomie de *Gonorhynchus gonorhynchus* (Linné 1766) Mem. L'Inst. Fr. D'Af. Noire. **68**: 255–310.

Ridewood, W. G. 1905. On the skull of *Gonorhynchus greyi*. Ann. Mag. Nat. Hist. **(7) 15**: 361–372.

Signeux, J. 1961. Sur quelques fossiles du basin parisien. Bull. Soc. Géol. Fr. **(7) 3**: 417–423.

Whitfield, R. P. 1890. Observations on a fossil fish from the Eocene beds of Wyoming. Bull. Amer. Mus. Nat. Hist. **3**: 117–120.

Woodward, A. S. 1896. Extinct fishes of the teleostean family Gonorhynchidae. Proc. Zool. Soc. Lond. 500–504.

——— 1901. Catalogue of fossil fishes in the British Museum. Vol. 4. London. 636 p.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

OMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

LLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

THOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 148 21 DECEMBER 1970

A REVIEW OF THE NEW WORLD DILARIDAE

PHILLIP A. ADAMS

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Zelda Edelson, Elizabeth G. Weinman, Elise K. Kenney.

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* and special publications. *Postilla* and the *Bulletin* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

Inquiries regarding back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection,* should be directed to:

Walter J. Johnson, Inc.
111 Fifth Avenue
New York, N.Y. 10003.

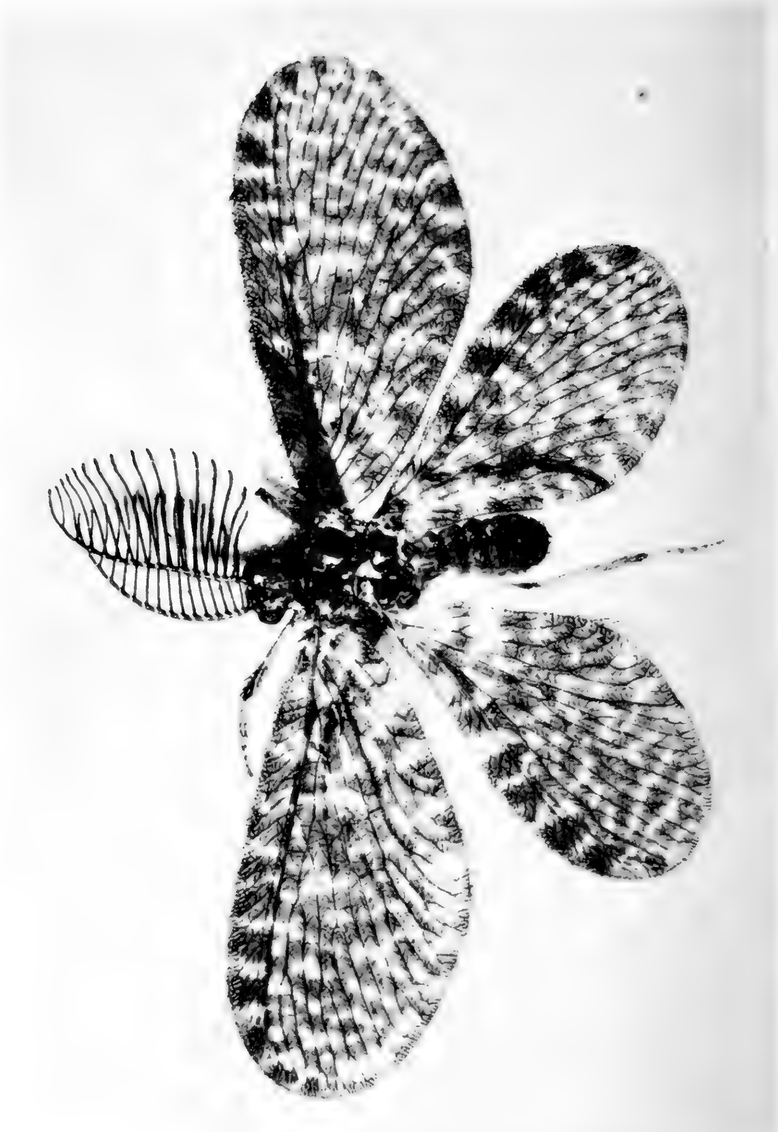


FIG. 1. *Nallachius limai*, n. sp., male, showing pectinate antennae characteristic of this genus.

A REVIEW OF THE NEW WORLD DILARIDAE

PHILLIP A. ADAMS

Department of Biology, California State College, Fullerton,
California 92631

(Received February 25, 1970)

ABSTRACT

Nallachiinae differs from Dilarinae in having non-homologous claspers and in structure of the vein, media anterior. *Neonallachius* Nakahara is referred to Dilarinae; *Nulema* Navás and *Neodilar* Carpenter are synonymized with *Nallachius*. No known exceptions remain to an exclusively Old World distribution for Dilarinae and a New World distribution for Nallachiinae. All New World species are listed; *Nallachius americanus, N. pulchellus, N. prestoni* and *N. loxanus* are illustrated, and the range of *N. americanus* is extended to Venezuela. New species are *Nallachius phantomellus, N. limai, N. ovalis* and *N. dicolor,* all from Brazil.

POSTILLA 148: 30 p. 21 DECEMBER 1970.

INTRODUCTION

This review of the New World dilarids, all members of the subfamily Nallachiinae, has been prompted by the discovery of specimens of four new species of this family from Brazil, in the Peabody Museum of Natural History. Since Navás' (1914) treatment of the Dilaridae, Carpenter (1940, 1947) has contributed importantly to an understanding of the New World fauna. However, males and females have been associated previously in only three species of Nallachiinae. The new material is of special interest in exhibiting more extreme sexual dimorphism in color and wing shape than had previously been known to occur in this family. In addition, examination of a large number of species has made possible evaluation of the utility of genitalic characters. Available type specimens have been examined, but considerations of time have prevented the general amassing of material that would have made a full-fledged revision possible.

ABBREVIATIONS

b—basal piece of MA; CuA—cubitus anterior; CuP—cubitus posterior; dl—dorsal lobe of ectoproct; dp—digitiform process of ectoproct; ect—ectoproct; gs—gonarcus; hy i—hypandrium internum; MA—media anterior; ml—median lobe of aedeagus; MP—media posterior; mu—mediuncus; R—radius; RS—radial sector; xv—crossvein; 8S, 8T—eight abdominal sternite and tergite; 9S, 9T—ninth abdominal sternite and tergite.

ACKNOWLEDGMENTS

Ellis G. MacLeod of the University of Illinois, Urbana, and the late Robert G. Beard, Cornell University, have been generous with the loan of specimens, and have offered helpful comments. Dr. D. E. Kimmins, British Museum (Natural History), Dr. S. Kelner-Pillault, Paris Museum, and Dr. Howard Evans, Museum of Comparative Zoology, Harvard University, have also graciously lent material for study. Most of this study was completed during my appointment as Visiting Associate Curator of Insects, Peabody Museum of Natural History, and was greatly facilitated by the assistance of Dr. Charles L. Remington. To all of these people I am most grateful.

METHODS OF STUDY

Male genitalia were cleared in KOH, stained with chlorazol black E and transferred to glycerine. The gonarcus and gonocoxites were partially separated from the tergites and sternites for more detailed examination. Because of the small size of this material, care was taken that the internal armature retain a connection to the remainder of the abdomen to prevent its loss during manipulation and transfer to the storage vial. The ectoprocts were positioned for drawing in the view most suited for showing the shape of the dorsal lobes and dorsal processes. In some cases this is a dorsolateral view; for a dorsal view, the abdomen was flattened under a glass chip. Examination with a compound microscope is essential. Drawings were produced with the aid of a camera lucida.

The female abdomen was similarly cleared and stained. I have not been able to see any important interspecific characters internally. The dorsal setiferous tubercles may have a distinctive shape, but these differences are so subtle that they are virtually valueless for use in taxonomy. Length of the ovipositor is the most useful feature; this was obtained by measuring a camera lucida drawing with dividers. A rough estimate of the ovipositor length relative to abdominal length may be obtained by flexing the ovipositor along the dorsum of the abdomen and noting upon which tergite the apex falls.

The photographs were made by Mr. A. H. Coleman and, with the exception of Figure 1, are all reproduced at the same scale.

SUBFAMILIAL CLASSIFICATION OF DILARIDAE

Two subfamilies of the Dilaridae, Nallachiinae (Nallachini Navás) in the New World and Dilarinae (Dilarini Navás) in the Old World, have generally been recognized, but the differences between them have not previously been clearly stated. According to Navás (1914), the two are separated as follows:

> Espèces de l'ancien Continent. Champ sous-costal assez large, avec plusieurs veinules; toujours plus de quatre veinules entre le radius et son secteur; quelques veinules sur toute l'étendue des ailes, parfois disposées en gradin .... 1. Tribus Dilarini Navás.
>
> Espèces américaines. Champ sous-costal étroit, sans veinules ou à peu près; moins de quatre veinules entre le radius et son secteur; très peu de veinules discales .... 2. Tribus Nallachini Navás.

Of these characters, only the geographical one now appears reliable. The width of the subcostal field is variable and may be quite broad in Nallachiinae. The number of "veinules" or crossveins between radius and radial sector is rarely more than three in *Nallachius*, but in the left forewing of the female allotype of *N. limai* there are nine radial crossveins. Usually Nallachiinae have fewer discal crossveins than have Dilarinae.

Carpenter (1947) considered size to constitute an important difference between Dilarinae and Nallachiinae: "The former are relatively large, with a wing expanse of 20 mm. or more, whereas the Nallachini have a wing expanse of less than 10 mm." This criterion no longer holds, especially with the larger females of Nallachiinae, as the following wingspreads demonstrate: *N. pulchellus,* an Arizona specimen in the Cornell University Collection, 18.3 mm; *N. ovalis,* 18.7 mm; *N. championi* (from original description), 22.5 mm. Carpenter mentions having noted genitalic and venational differences, but an account of these has unfortunately never been published.

An important character is the structure of the anterior media. The basal piece of MA usually joins the radial system near the wing base in the forewing of both subfamilies. In Dilarinae, the distal portion of MA diverges from R proximally to the base of RS, so that MA appears as a separate vein (Fig. 2B). *Rexavius marmoratus,* a dilarine, has MA as a free vein connected to R by a crossvein (Fig. 2A). Carpenter (1940) calls attention to a similar condition in *Dilar corcyracus* Navás; I have not seen this species. These are the only cases of which I am aware, in the forewings of modern insects, where a free MA is present. In Nallachiinae, MA is fused with RS basally, so that it appears as the proximal branch of that vein (Fig. 2C). In the hindwing of Dilarinae, the basal piece of MA typically is sinuous, joining RS distal to the separation of R and RS; whereas in the hindwing of Nallachiinae, the basal piece of MA is usually fused with R proximally to the origin of RS+MA or may be absent. The distal part of MA appears as a branch of RS in both subfamilies.

In male Dilarinae, several apical flagellar segments may lack elongate lateral processes, while Nallachiinae usually have only one or two, but never more than three, such "unarmed" segments.

The most significant difference between these two subfamilies concerns the male terminalia. In the few Dilarinae where the genitalia are known, the ectoprocts are reduced and their clasping function is transferred to the modified ninth tergite (Acker, 1960; Aspöck and Aspöck, 1967). The internal apparatus consists of a gonarcus with laterally articulated gonocoxites and two submedially articulated mediuncus lobes. The arrangement of the internal armature thus closely resembles that of the Osmylidae (Adams, 1970). In the Nallachiinae, the ectoprocts are normally developed, often with a pair of modified dorsal lobes abutting on a modified ninth tergite (Fig. 9). In addition to possessing gonocoxites and mediuncus lobes similar to those of the Dilarinae, a median sclerite (Fig. 9C, *ml)* is present, articulated on the gonarcus. The gonopore is located immediately beneath this median sclerite, resulting in a configuration closely resembling that of coniopterygids such as *Coniopteryx* (see Tjeder, 1957, figs. 93, 94). The proximity of the median sclerite to the gonopore indicates that the former may be a remnant of an

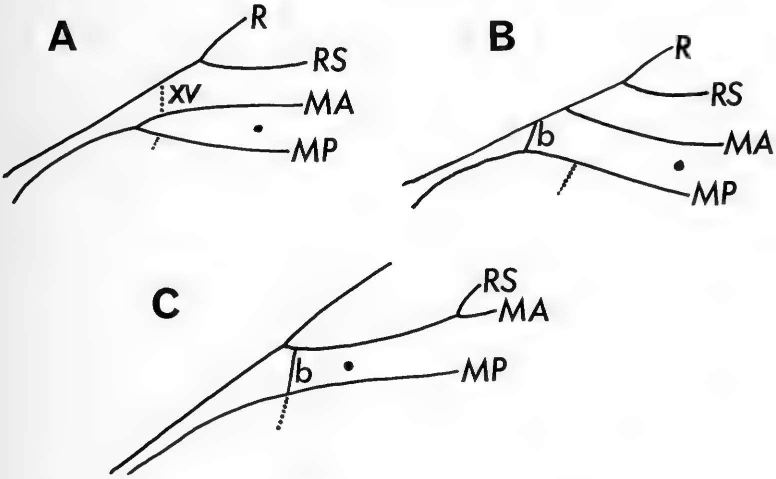


FIG. 2. Evolution of media anterior in the forewing of Dilaridae: A) Media anterior (MA) is a free branch of media, connected only by a crossvein to the radial system *(Rexavius marmoratus* Banks, type); B) MA bends upward to contact R, as in most Dilarinae; C) MA appears as a branch of RS, as in Nallachiinae.

aedeagus, as considered to be by Carpenter (1947). Since I have not observed a comparable structure in Raphidiodea or Sialodea, I suspect that it may be a specialized, rather than a primitive feature. For the time being, it appears preferable to refer to this structure by the morphologically neutral term, "median lobe." Acker (1960) mistakenly identified the median lobe as the hypandrium internum (his "tenth sternite") overlooking the presence of the inconspicuous true hypandriun internum lying on the wall of the gonoduct near the gonopore (Fig. 4C, *hy i).*

In summary, male terminalia of the two subfamilies appear to differ in having non-homologous claspers and a median process present in Nallachiinae but absent in Dilarinae. Until the genitalia of the Dilariinae have been more extensively explored, the reliability of these differences cannot be assessed with assurance.

GEOGRAPHIC DISTRIBUTION

Exceptions to the formerly neat geographical restriction of the Dilarinae to the Old World, and Nallachiinae to the New World are seemingly provided by *Neodilar* Carpenter, a supposed New World dilarine, and *Neonallachius* Nakahara, a supposed Old World nallachiine.

Carpenter referred *Neodilar* to the Dilarinae principally because of its large size (wing expanse 25 mm) and the extensive secondary branching of the veins. As noted above, size is not a reliable criterion; indeed the wing spread of female *Neodilar* exceeds that of female *Nallachius championi* (Navás) by only 2.5 mm. The secondary branching consists of inward extension of the marginal twiggings; this probably does not represent a fundamental change in venational pattern but only a response to increased size. Similarly broad wings and increased secondary branching are demonstrated to a somewhat lesser extent by *Nallachius limai,* a probable close relative. Most importantly, in *Neodilar* MA does not diverge directly from R in the forewing as in most dilarines, but coalesces basally with RS as in *Nallachius;* the basal piece of MA is absent from both anterior and posterior wings of *Neodilar,* as is often the case in Nallachiinae. Furthermore, *Neodilar hermosa* has fewer discal crossveins than do most dilarines. The coloration and details of body proportion are similar to those of most Nallachiinae. The emarginate black labrum resembles that of *Nallachius limai,* which also has a closely similar wing shape and venational pattern. Certainly then there is no basis for assigning *Neodilar* to the Dilarinae. Moreover, I have been unable to discover any reason for separating *Neodilar* from *Nallachius.*

Neonallachius Nakahara, 1963, is more problematical. This tiny insect (forewing 3 mm) is smaller than any *Nallachius* I have seen, including an *N. americana* from Puerto Rico, in the Cornell University Collection which has a 3.6 mm forewing. Its venation is so reduced as to indicate nothing concerning its taxonomic position. The antennal flagellum, however, bears only relatively short projections, and these are entirely absent on the five apical segments. Both of these features are common in Dilarinae but unknown in Nallachiinae. It is difficult to make much of the male genitalia, as figured by Nakahara (1963). In the lateral view of the abdominal apex, there is no callus cerci shown, nor is a separate ninth tergite shown in addition to the claspers. Apparently the claspers correspond to the ninth tergite, as in other Dilarinae. The figure of the "tenth sternite" (=gonarcus, etc.) shows a pair of gonocoxites laterally and a bilobed median process which probably represents fused mediuncus lobes. All known Nallachiinae have separated mediuncus lobes in addition to the median structure. The only described features of *Neonallachius* possibly consistent with assignment to the Nallachiinae are the small size and correlated aberrant reduced wing venation, but these conditions could as well have been attained in a dilarine. Until evidence is produced to the contrary, genitalic and antennal structure adduce assignment of *Neonallachius* to the Dilarinae.

The earlier generalization therefore still seems valid, that the Dilarinae are restricted to the Old World and the Nallachiinae to the New World.

SUBFAMILY NALLACHIINAE NAVÁS

Nallachini Navás, 1914, Gen. Insectorum 156: 11.

Nallachiini Carpenter, 1947, Psyche 54: 100.

This taxon has previously been treated as a tribe. I consider the genitalic characters sufficiently distinct from those of Dilarinae to warrant subfamilial separation. The sole included genus is *Nallachius*.

Nallachius Navás

Nallachius Navás, 1909, Mem. R. Acad. Cienc. Barcelona 7: 665; 1914, Gen. Insect. 156: 11; Carpenter, 1940, Proc. Amer. Acad. Arts Sci. 74: 272–275; 1947, Psyche 54: 100–109. Type: *Dilar prestoni* McLachlan, designated by Navás, 1914.

Nulema Navás, 1914, Gen. Insect. 156: 12. Type, by original designation, *N. championi* Navás 1914. **New synonymy** (subjective).

Neodilar Carpenter, 1947, Psyche 54: 107. Type, by original designation, *Dilar hermosa* Banks. **New synonymy** (subjective).

DESCRIPTION. Male antennae monopectinate, female antennae filiform. Vertex and dorsum of thorax and abdomen with conspicuous setiferous tubercles. Basal piece of MA in forewing appears as crossvein between MP and R before origin of RS+MA, sometimes absent. In hindwing, basal piece of MA is sinuous, joining RS after separation of RS from R, often weakly developed or absent. MP2 coalesced with CuA in several species, usually free. Ninth tergite normal; ectoprocts with a series of medial lobes, usually a dorsal lobe and a digitiform process. Gonarcus arcuate with narrow dorsal shelf; gonocoxite variously developed, articulated on gonarcus. Mediuncus lobes separate, elongate, articulated on base of slender sclerotized median lobe; beneath median lobe lies the gonopore.

DISCUSSION OF SYNONYMY

According to Navás, *Nulema* differs from *Nallachius* in having two unarmed flagellar segments rather than one, in having numerous (16) very long flagellar processes and in lacking discal crossveins in the apical half of the wing. The number of unarmed flagellar segments varies; most species of *Nallachius* have only one, but the type of *N. ovalis* has two on the left side and one on the right; *N. americanus* may have three. The number and length of the flagellar processes vary; the large number in *Nulema championi* is probably a correlate of its size and is equalled by *Nallachius limai.* The number of discal crossveins is also variable; *Nallachius americanus* alone of the species I have examined lacks these in the apical half of the wing, thus resembling *Nulema.*

None of the characters used by Navás serves generically to differentiate *Nulema championi* from the other species of *Nallachius.* Mr. D. E. Kimmins has been kind enough to examine the male type; the genitalia have not been cleared, but the form of the ectoproct is like that of *N. prestoni,* the type species of *Nallachius.* Inasmuch as the ectoproct furnishes the most distinctive taxonomic characters in the *Nallachiinae, Nulema* must be considered a synonym of *Nallachius.*

Neodilar Carpenter, 1947, is based upon *Dilar hermosa* Banks, 1913, known from a single female. The only differences from *Nallachius* are the larger size, more extensive branching of veins and broader wings. If one considers the range of diversity now known for *Nallachius,* continued recognition of *Neodilar* appears unjustified. The possibility remains, however, that the male may prove distinctive; consequently the synonymy must be regarded as provisional.

BIOLOGY AND GEOGRAPHIC DISTRIBUTION

MacLeod and Spiegler (1961) have reviewed what is known of the biology of *Nallachius americanus,* the only member of the genus whose immature stages are known. Most larvae were taken under "tightly adherent bark of erect, recently dead trees," *Quercus* and *Liriodendron.* Two were found in older, more-decayed wood, and two adult females were taken on the stump of a much-decayed, crumbling Virginia Pine. In the laboratory they successfully fed the larvae a variety of soft, disabled insect larvae and eggs.

N. americanus appears to be non-specific in its requirements for kind or condition of wood or kind of prey and is the most wide-ranging species, occurring widely in the Eastern deciduous forests of the United States, in Puerto Rico and in Venezuela. *N. pulchellus* also shows a wide range, being known from Cuba and southern

Arizona; probably it will appear in Central America when more collecting is done there. The other species are all known from single localities, including two nearby localities for *N. limai,* but very possibly will also prove to have extensive distributions. Greatest diversity occurs in the area of Paraguay and southeastern Brazil where seven species are known. Guatemala, Colombia, Ecuador and Argentina have one species each. In Latin America, all the localities are hilly or mountainous; there are no known species from the Amazon basin. This may merely reflect collecting intensity.

Emergence time seems to be during the summer. In the northern hemisphere, most records occur from May to August; the single September record is from Woodville, Texas. Southern hemisphere records are mostly for October through January, with one record for September and one for March.

TAXONOMIC CHARACTERS

Wing venation in Nallachiinae is highly variable with respect to number of vein branches and position of forks, and to number and location of crossveins. More useful are characters dealing with proportion, such as overall shape of the wing and the relative areas occupied by the various major veins. Width of the costal area and presence of forking of costal veinlets are especially critical. Coalescence of MP2 with CuA occurs in several member species: *N. loxanus, N. pupillus, N. americanus, N. hermosus.* Of these, only *N. americanus* is known from more than a single specimen; I have not seen any examples that lack this feature, nor have I seen any examples of fusion of these veins among other species where series have been available. However, in view of the excessive venational variation exhibited by these insects, this character should probably be regarded with suspicion. Females are generally somewhat larger with more slender, paler wings.

In the male terminalia, the most important differences are in the shape of the posterior border of the ninth abdominal tergite and in development of a pair of dorsomedial ectoproct lobes which I term the dorsal lobe and the digitiform process. Shape of the gonocoxite and the relative lengths of the mediuncus lobes and the median lobe of the gonarcus may also be distinctive. In the *pulchellus* group especially *(vide infra),* differences are extremely subtle; between the species pairs *N. ovalis* and *N. dicolor, N. prestoni* and *N. reductus,* I was unable to discern any differences whatever in the male genitalia.

The species of this genus comprise several indistinctly differentiated subgroups:

A. The *pulchellus* group. Venation varied, MP2 not coalesced with CuA in forewing, wings usually elongate, subtriangular. Labrum pale, dorsal lobe of ectoproct well-developed, digitiform process ordinarily with small blunt medial spine. 1. *N. phantomellus,* 2. *N. pulchellus,* 3. *N. reductus,* 4. *N. prestoni,* 5. *N. dicolor,* 6. *N. ovalis,* 7. *N. championi.*

B. The *limai* group. Wings broad, rounded, much secondary branching of longitudinal veins. In *N. hermosus,* MP2 briefly coalesced with CuA. Labrum dark. Genitalia as in *N. pulchellus* group. 8. *N. limai,* 9. *N. hermosus* (male unknown).

C. The *americanus* group. MP2 fused with CuA in forewing; digitiform process reduced, dorsal lobe of ectoproct not clearly developed. 10. *N. americanus,* 11. *N. loxanus,* 12. *N. pupillus* (male unknown).

D. Incertae sedis. 12. *N. bruchi.*

KEY TO THE SPECIES OF NALLACHIUS (MALES)

1. In forewing, MP2 fused with CuA, costal veinlets simple (Fig. 14) 2
In forewing, MP2 not fused with CuA, some costal veinlets occasionally forked 4

2. Wing apex rounded, nearly symmetrical about long axis (Paraguay) .... *N. pupillus* Navás
Wing apex plainly asymmetrical, posterior margin angulate 3

3. More than 2 radial crossveins in forewing; several crossveins between branches of RS in both wings, genitalia as in Fig. 14 .... *N. loxanus* Navás
Only 2 radial crossveins in forewing, no crossveins between branches of RS in either wing; genitalia as in Fig. 13. North America, and south to Venezuela .... *N. americanus* (McLachlan)

4. Male antennae with 16 elongate processes .... *N. championi* (Navás).
   Male antennae with 14 or less elongate processes 5

5. Labrum black, wings rounded .... *N. limai* n. sp.
   Labrum pale, wings more elongate 6

6. Dorsal lobe of ectoproct inflated, costal veinlets simple ....*N. pulchellus* Banks
   Dorsal lobe of ectoproct flat 7

7. Dorsal lobes of ectoprocts approximated on midline 8
   Dorsal lobes of ectoprocts widely separated in middle 9

8. Costal area wider, most distal costal veinlets forked .... *N. ovalis,* n. sp.
   Costal area narrow, most costal veinlets simple .... *N. dicolor,* n. sp.

9. Subcosta nearly straight, costal area narrow, many costal veinlets forked .... *N. prestoni* (McLachlan)
   Subcosta curved posteriad at stigma, costal area wider, few costal veinlets forked .... *N. reductus* Carpenter

The description of *N. bruchi* Navás is insufficient for inclusion of that species in the key. The male of *N. hermosus* is unknown; this large species has MP2 fused with CuA, forked costal veinlets, black labrum. I have not seen *N. championi*.

Nallachius phantomellus, new species

Figures 3, 4

DESCRIPTION. Male antennae white, fragile, crumpled in dried material, slightly longer than head and thorax, ten elongate processes. Labrum pale, flat, deeply incised. Head, legs and body yellowish white, setae entirely pale. Wings pale (Figs. 3A, B), two broad irregular transverse pale brown bands of which the apical is more prominent. Anterior margin straight, costal space narrow, subcostal

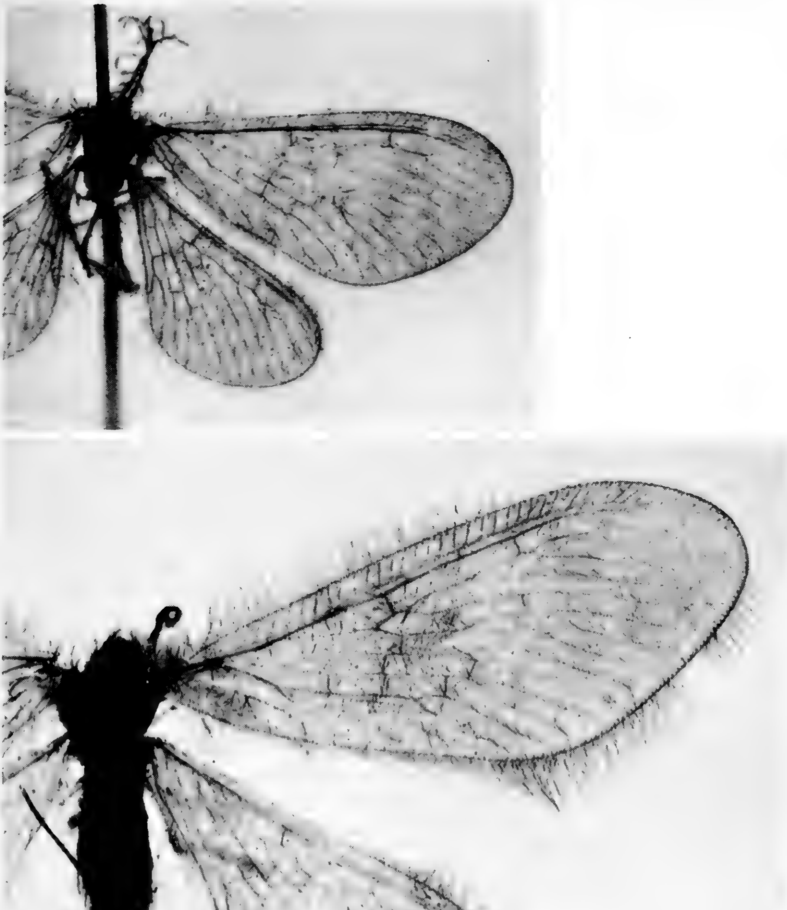


FIG. 3. *Nallachius phantomellus,* n. sp., male above, female below.

veinlets unbranched in male, a few branched in female. Two radial crossveins, five unforked branches of RS; MA deeply forked. Male genitalia (Fig. 4) similar exteriorly to those of *N. dicolor,* but digitiforms process more cylindrical, bearing a slender hook on medial surface. Gonocoxites shorter than in *N. dicolor,* lateral edge angulate so that shape resembles scimitar, with tip bent dorsally. Mediuncus lobes short, spatulate, hardly bent ventrad, with prominent lateral projections. Median process ends at level of these lateral projections.

MEASUREMENTS (mm). Forewing length: male 4.6, 4.7; female 9.2, 8.5, 7.5.

TYPES. Holotype male, Rio Caragualà, Brazil, 21°48′S–52°27′W, 400 m, March 1963, leg. Fritz Plaumann, Peabody Mus. Nat. Hist. (Yale). Allotype and paratypes, same data, one male, three females, Peabody Museum.

REMARKS. This species is immediately recognizable by the pallid coloration, the extremely narrow costal space, especially in the hind wing, and the male genitalia.

Nallachius pulchellus (Banks)

Figure 5

Dilar (Nallachius) pulchellus Banks, 1938, Rev. de Ent., Rio de Janeiro 9: 289.

Nallachius pulchellus Carpenter, 1940, Proc. Amer. Acad. Arts Sci. 74: 274; 1947, Psyche 54: 104. Stange, 1961, Pan-Pac. Ent. 37: 144.

REDESCRIPTION. The male of this species is readily distinguished by the bladder-shaped dorsal ectoproct lobes and the incised margin of the ninth tergite (Fig. 5). The gonocoxites are slender, unspecialized apically, and the mediuncus lobes downcurved, bluntly rounded apically, with lateral projections on surface of adjoining membrane. The labrum is pale, flat, with undulating margin.

TYPE. Male, Central Soledad (near Cienfuegos) Cuba, 4 May, 1930, leg. P. J. Darlington, Mus. Comp. Zool. No. 22681 (examined).

Additional material: previously recorded from the Santa Rita and Huachuca Mts., Arizona. New record, Onion Saddle Rd., .7 mi. SE. E. Turkey Cr., Chiricahua Mts., Cochise Co., Ariz., on knoll, 6500 ft., 13 July, 1969, at u.v. light, leg. R. G. Beard.

Nallachius reductus Carpenter

Figure 7

Nallachius reductus Carpenter, 1947, Psyche 54: 104–106.

TYPE. Ilalyria, Paraguay, October, leg. F. Schade, male, MCZ 27664 (examined). Carpenter's citation of the type locality as "Ualyaia" was no doubt due to misinterpretation of Banks' rather unclear script on the locality label. I have been unable to ascertain the position of this locality.

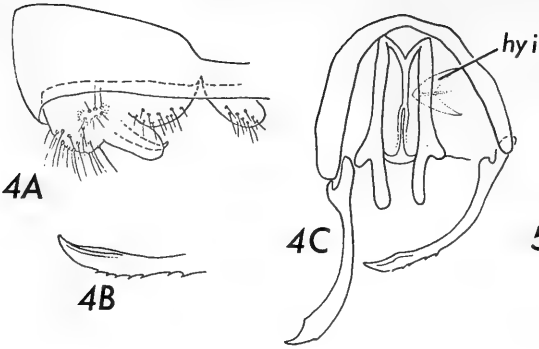
REMARKS. Carpenter's figure shows a space between the dorsal lobe and the digitiform lobe of the ectoproct, but I have not been able to observe this (Fig. 7). The digitiform process bears no medial hook. The gonocoxites are slender, with a short hook apically. The genitalia are like those of *N. prestoni,* which *N. reductus* resembles closely. In *N. reductus,* fewer costal veinlets are forked than in *N. prestoni,* the forewing is more pointed and the costal area of the hind wing is much broader.

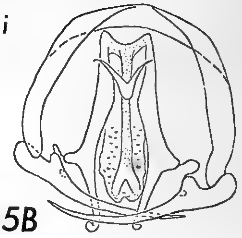
Nallachius prestoni (McLachlan)

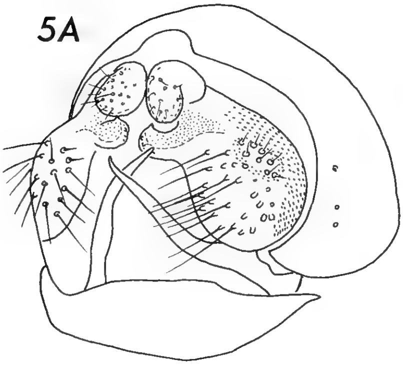
Figure 6

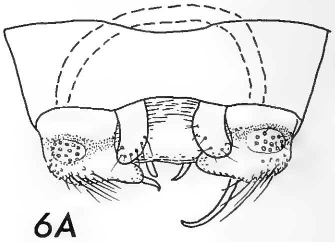
Dilar prestoni McLachlan, 1880, Ent. Mo. Mag. 17: 39.

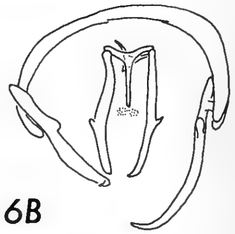
Nallachius prestoni, Navás, 1909, Mem. Acad. Cienc. Barcelona 7: 667; 1911, Ann. Soc. sci. Bruxelles 35: 221; 1914. Genera Insectorum 156: 11; 1930, Rev. Chilena Hist. Nat. 34: 63. Carpenter, 1940, Proc. Amer. Acad. Arts Sci. 74: 273; 1947, Psyche 54: 102–103, fig. 1.











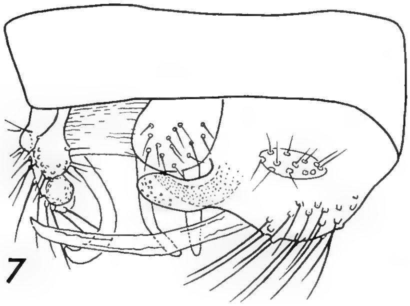


FIG. 4. *Nallachius phantomellus,* n. sp.: A) abdominal apex, dorsal; B) apex of gonocoxite, lateral; C) internal genital armature, dorsal, same scale as 4A.

FIG. 5. *Nallachius pulchellus:* A) abdominal apex of holotype, posterolateral; B) internal genital armature, ventral (Arizona).

FIG. 6. *Nallachius prestoni,* holotype: A) abdominal apex, dorsal; B) internal genital armature, dorsal.

FIG. 7. *Nallachius reductus,* holotype, abdominal apex, dorsolateral.

TYPE. "Rio, Preston 11/72. McLachlan Coll. B. M. 1936–674. Dilar Prestoni M. L." Abdomen in balsam.

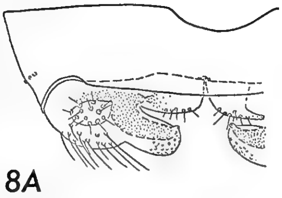
REMARKS. The venation of this species is accurately figured by Carpenter (1947). The dorsal lobes of the ectoprocts are widely spaced, and the gonocoxites are slender with no blade-like expansion (Fig. 6B). I can see no differences between the genitalia of this species and those of *N. reductus* Carpenter. However, the wings are of a markedly different shape in these two species, as Carpenter's figures clearly show, so they undoubtedly are distinct. In general appearance, *N. prestoni* is much like *N. dicolor,* but the genitalia differ.

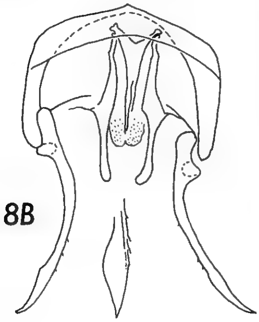
Nallachius ovalis, new species

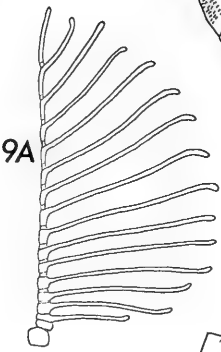
Figure 11

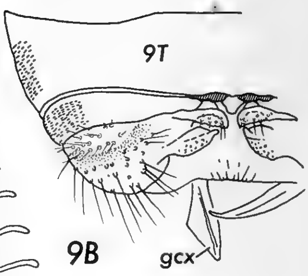
DESCRIPTION. Male antennae moderately crumpled when dry, 8–9 projections, unarmed distal flagellar segments two in type, one in paratype. Labrum pale, margin slightly emarginate, surface concave. Head pale, frons and vertex brown, vertex tubercles paler. Thoracic dorsum brown, mesoscutum pale medially, pleurae and legs pale. Male forewing broad, rounded, costal veinlets inclined, spaced about one-fourth their length apart, mostly forked on distal half of wing. Two radial crossveins, RS five-branched, the last shallowly forked. MP2 and CuA1 not coalesced. 1A runs at an angle to wing margin, without long pectinate series of marginal veinlets as in *N. dicolor.* Hind wing also broad, basal piece of MA weakly developed, fuses with R before origin of RS+MA. Wings colored similarly to those of *N. dicolor,* but dark spots larger, especially on anterior margin, and a greater area of the wing is pale. Female wing more slender and paler than that of male, with about six dark spots on costal area of forewing; remainder of wing surface almost uniformly covered with grey tessellated pattern. Male genitalia as in *N. dicolor.* In female, ovipositor long, extends to fourth tergite when flexed forward.

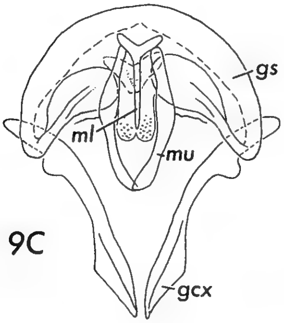
MEASUREMENTS (mm). Forewing length, male 5.5; female 7.3–7.5; ovipositor 2.8–3.2.











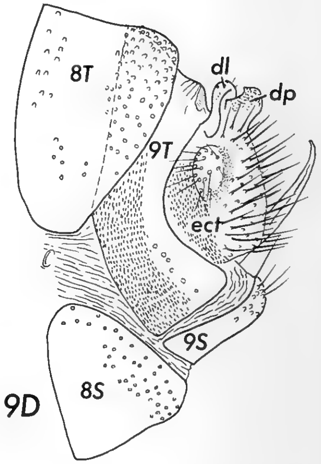


FIG. 8. *Nallachius dicolor:* A) abdominal apex, dorsal; B) internal genital armature, dorsal.

FIG. 9. *Nallachius limai,* n. sp.: A) male antenna; B) abdominal apex, dorsal; C) internal genital armature, dorsal; D) abdominal apex, lateral. Setal bases shown by small circles; dashes on 9T and ectoproct indicate pore fields, present on all known species.

TYPES. Holotype male, Nova Teutonia, Santa Catarina, Brazil, 27°11′5–52°23′W, 300–500 m, Oct. 1963, leg. Fritz Plaumann, Peabody Mus. Nat. Hist. (Yale). Allotype, female, same data, 5 Dec. 1965 or 1966, E. G. MacLeod Coll.

PARATYPES, same data: male, Oct. 1966, E. G. MacLeod Coll.; female, Oct. 1963, Peabody Museum.

REMARKS. Resembles *N. dicolor,* but wing is darker and broader, so that costal veinlets are spaced less than twice their length apart. In the forewing, 1A runs at an angle to margin, not parallel to it as in *N. dicolor*. The ovipositor of *N. ovalis* is longer, extending to the middle of the fourth tergite when bent forward.

Nallachius dicolor, new species

Figures 8, 10

DESCRIPTION. Male antennae flexible, crumpled in dry material, either one or two terminal segments of flagellum without long processes; eight, nine or sometimes ten processes present. Labrum pale, weakly emaginate, anterior surface concavely angulate. Head fuscous; anterior vertex tubercle larger than two posterior tubercles, which nearly touch on midline. Body fuscous, paler beneath.

Male wings (Fig. 10, top) with membrane mostly brown; about six pale spots in costal area of forewing; smaller pale spots scattered uniformly over surface. Wing triangular, costal space narrow; costal veinlets more than half their length apart, few forked. RS with four or five branches, the last forked. MP2 not coalesced with CuA in forewing. Basal piece of MA not developed in hindwing.

Female wings (Fig. 10, bottom) more slender and paler than those of male; about six large brown spots in costal area, smaller spots scattered over wing surface, denser basally.

Male genitalia. Posterior margin of ninth tergite unmodified, dorsal lobes of ectoprocts small, flat, approximated on midline; digitiform lobe with stout hook protruding near apex (Fig. 8A). Gonocoxites lancet-shaped, curved outward; mediuncus lobes slender-ligulate apically; median process wide basally, apex bilobed, projecting beyond lateral processes of mediuncus lobes (Fig. 8B).

FIG. 10. *Nallachius dicolor,* n. sp., male above, female below.

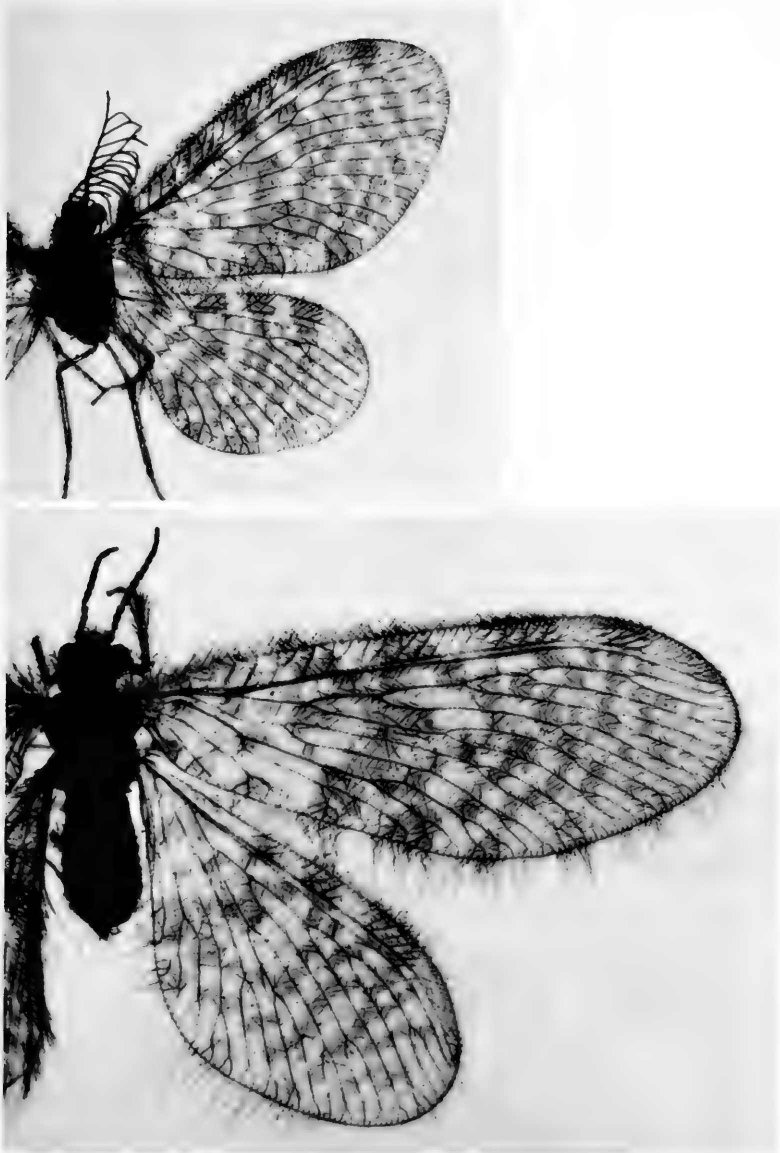


FIG. 11. *Nallachius ovalis*, n. sp., male above, female below.

Ovipositor extends to middle of sixth tergite when flexed anteriorly.

MEASUREMENTS (mm). Male forewing length 4.3–(5.0)–5.2 (n=11); female forewing length 5.1–(6.6)–7.9(n=8), ovipositor length, 1.65–(1.98)–2.2.

TYPES. Holotype male, Nova Teutonia, Santa Catarina, Brazil, 27°11′S, 52°23′W, 17 Oct. 1956, leg. F. Plaumann, Peabody Mus. Nat. Hist. (Yale). Paratype males, same locality, 1 Sept. 1948, 16 Nov. 1949, 18 Sept. 1956, 29 Sept. 1956, 12 Oct. 1956, 7 Dec. 1956, 19 Jan. 1957, 18 Oct. 1957, Peabody Museum. Allotype, same locality, 6 Oct. 1944, Peabody Museum; paratype females same locality, 12 Oct. 1944, 31 Sept. 1956, 1 Oct. 1956, 22 Oct. 1956, 29 Nov. 1956, 3 Oct. 1957, 19 Oct. 1959. Peabody Museum.

REMARKS. The name of this species is derived from the remarkable sexual dimorphism in wing color. Although similar in appearance to *N. dicolor, N. prestoni* differs in the following ways: 1A does not extend so far toward the wing apex, it has a flat labrum, the dorsal ectoproct lobes are separated medially, and it lacks the lancet-like expansion of the gonocoxites.

Nallachius championi (Navás), new combination

Nulema championi Navás, 1914, Gen. Insect. 156: 12.

LECTOTYPE. Male, Guatemala, Cerro Zunil, [14°44′N, 91°27′W] 4–5,000 ft., leg. Champion, Brit. Mus. Nat. Hist. (not seen). A pair of specimens, male and female, is in the British Museum. Navás did not designate either as type, so I now designate the male as **lectotype.**

REMARKS. As pointed out above, there appears to be no significant difference between *Nallachius* and *Nulema*. D. E. Kimmins has examined the male type; the ectoprocts are formed as in the *pulchellus* or *limai* group (personal communication). The wings of both sexes are illustrated by Navás. This is a large species (wing expanse of female, 22.5 mm; of male, 16 mm) with distinctive wing markings.

Nallachius limai, new species

Figures 1, 9, 12

Nulema sp., Lima, 1943, Insetos do Brasil 4:80, figs. 52, 53 (male).

Nallachius (?) *prestoni,* Lima, 1943, not McLachlan 1880, Insetos do Brasil 4:82, figs. 54, 55 (female). Carpenter, 1947, Psyche 54: 103. Gurney, 1947, Psyche 54: 148.

DESCRIPTION. Male antennae (Figs. 1, 9A) about as long as head and body, 14–16 segments with stiff branches which curl only slightly at ends. Labrum black, margin incised, anterior surface flat. Head pale, frons and vertex broadly fuscous, vertex tubercles pale, anterior tubercle about same size as posterior tubercles. Thorax and abdomen fuscous.

Wings. Male wings (Fig. 12, top) rounded, broader and darker than those of female, the anterior margin of forewing convex, costal space broad, many subcostal veinlets branched. Radial crossveins, 3–5, RS with 5–6 main branches; posterior two branches of RS and MA, also branched. CuA not fused with MP2 in either wing. Male hindwing rounded, costal space broad, costals mostly forked, 2–3 radial crossveins, basal piece of MA indistinct distally. Wing membrane white, a group of about 8 large dark spots on costal area, remainder of wings uniformly covered with confluent spots and transverse streaks so that about 2/3 of wing surface is dark.

Female wings (Fig. 12, bottom) much more elongated than in male, costal margin nearly straight in middle; in forewing, 6–7 radial crossveins, RS with four main branches of which the posterior two and the MA are deeply branched.

Male genitalia. Apical margin of ninth tergite with dark submedian sclerites and median ventrad projection (Fig. 9B). Dorsal lobe *(dl)* of ectoproct cupped with anterior tooth contacting sclerotized area of ninth tergite; digitiform process *(dp)* flattened, posterior margin angulate, apical tooth prominent (Fig. 9D). Gonocoxite blades (Fig. 9C) lancet-shaped, mediuncus lobes apically downcurved and angulate, median lobe bifid apically, gonarcus curved, its upper surface membranous with indistinctly sclerotized plates arising from posterolateral corners.

FIG. 12. *Nallachius limai*, n. sp., male above, female below.

MEASUREMENTS (mm). Male forewing length 6.6, 6.2, antennae 2.94, female forewing length 8.9.

TYPES. Holotype: Male, Nova Teutonia, Brazil, 27°11′S–52°23′W, 300–500 m., Dec. 1968, leg. Fritz Plaumann, Peabody Mus. Nat. Hist. (Yale). Paratypes, same locality: Male, Terias deva, 2 Jan. 1966, Peabody Museum; male, Nov. 1966, E. G. MacLeod Coll.: female, 1 Nov. 1966, E. G. MacLeod Coll. Additional paratype: Male, Neu Bremen, Santa Catarina, Brazil, 8 Mar. 1937, leg. Fritz Hoffman, Cornell Univ.

REMARKS. The male is easily recognized by the broadly rounded wings, the unusually large stiff antennae and the distinctive genitalia. The female differs from *ovalis, dicolor* and *pulchellus* in having a wider costal space, branched subcostals, rounder wing tips and black labrum. In the broad, rounded wings, wide costal area, numerous forkings of longitudinal veins, and black labrum, this species resembles *Nallachius hermosus* (Banks).

Lima (1943) probably concluded that the male of this species was a *Nulema* because of the numerous antennal processes. A photograph of the female is captioned by him as *N.* (?) *prestoni;* his failure to associate the two sexes is understandable in view of the highly dimorphic wing shape.

Nallachius hermosus (Banks), new combination

Dilar (Nallachius) hermosa Banks, 1913, Trans. Amer. Entomol. Soc. 39: 220.

Neodilar hermosa, Carpenter, 1947, Psyche 54: 108–109, fig. 5 (wings).

REDESCRIPTION. Labrum deeply emarginate, thin, dark-pigmented. Wingspread of female 25 mm; extensive secondary branching of MP produces a bulge in hind margin of both wings. MP2 briefly anastomosed with CuA. Body color yellow, wings pale, brown-tessellated. Male unknown.

TYPE. Pacho, E. Cordilleras, Colombia, elev. 6600 ft., Oct., leg. Fassl, female (examined).

REMARKS. In shape and color of labrum, and complexity of venation, this species most closely resembles *N. limai.*

Nallachius americanus (McLachlan)

Figure 13

Dilar americana McLachlan, 1880, Entomol. Mo. Mag. 18: 55. Banks, 1905, Trans. Amer. Entomol. Soc. 32: 24.

Nallachius americanus, Navás, 1909, Mem. Real Acad. Cienc. Artes Barcelona 7: 669; 1914, Gen. Insect. 156: 11. Carpenter, 1940, Proc. Amer. Acad. Arts Sci. 74: 273–274; 1947, Psyche 54: 106–107, fig. 4. Gurney, 1947, Psyche 54: 147–169 (photo of wing; larva). Stange, 1961, Pan–Pac. Entomol. 37: 144. MacLeod and Spiegler, 1961, Proc. Entomol. Soc. Washington 63: 281–286 (development).

REDESCRIPTION. Carpenter has illustrated the wing venation (1947) and male genitalia (1940). The ninth abdominal tergite may bear a triangular projection on its posterior border (Fig. 13C). The ecto-

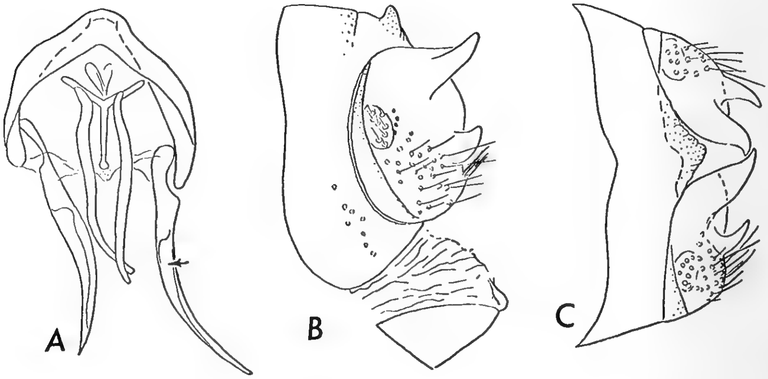


FIG. 13. *Nallachius americanus:* A) internal genital armature, dorsal, showing slender gonocoxites with groove (arrow); B) abdominal apex, lateral, showing widely spaced marginal hooks and unusual configuration of ectoproct; C) abdominal apex, dorsal, showing median projection of ninth tergite (stippled).

procts are highly distinctive, with prominent angular-margined dorsal lobes, widely separated from the ligulate lobe which probably corresponds with the digitiform process of the other species. In most specimens except those from Michigan, ventrally to this ligulate lobe is a small, dorsally directed hook with an apical tuft of setae. The gonocoxites are slender, pointed, with a deep longitudinal depression (Fig. 13A); the median process is unusually short.

TYPE. Bee Spring, Kentucky, June, 1874, leg. Sanborn, female, MCZ No. 10434.

DISTRIBUTION. This is the most wide-ranging species of *Nallachius*, previously recorded from Michigan, Kentucky, Virginia, Maryland, Texas and Puerto Rico. I have seen a male from Archbold Biol. Station, Lake Placid, Highlands Co., Florida, 30 March 1959, leg. J. G. Francelemont, Cornell Univ. The following material is the southernmost record for the species: Rancho Grande, 7 km. N. of Maracay, Aragua Province, Venezuela, 1100 m., Aug. 15, 1967, at mercury vapor light, leg. R. W. Poole, 2 males, R. Beard Coll.

Nallachius loxanus Navás

Figure 14

Nallachius loxanus Navás, 1911; Ann. Soc. sci. Bruxelles 25: 219; Carpenter 1947, Psyche 54: 107.

REDESCRIPTION. Labrum pale, incised medially; anterior vertex scar well separated from posterior scars and twice their diameter; head light brown, vertex scar paler. Antennae missing. Thorax light brown, paler medially, pronotal tubercles pale. Wings pale with uniformly distributed small light brown spots, the diameter of each about the same as intervein distance; pale spaces between them also approximately equal to intervein distance. Right wing venation as in Fig. 14D. MP2 is fused with CuA in both forewings. Left forewing: four radial crossveins, seven branches of RS+MA; hindwing: six branches of RS+MA.

Male genitalia (Fig. 14A, B, C). Posterior margin of ninth tergite angulate. Ectoproct subtriangular, with spatulate digitiform process, posterior to which is a shallow depression; dorsal lobe absent. Gonocoxites slender, no apical expansion, mediuncus lobes also slender, tips rounded.

HOLOTYPE. Male, "Museum Paris, Equateur, Loja, A. Poujade, 1904." "Nallachius loxanus Nav.," (in Navás' hand). "H. & U. Aspöck vid. 1967."

MEASUREMENT. Forewing length 6.7 mm.

REMARKS. The male genitalia most nearly resemble those of *N. americanus* (Fig. 13) in shape of ninth tergite and specialization in

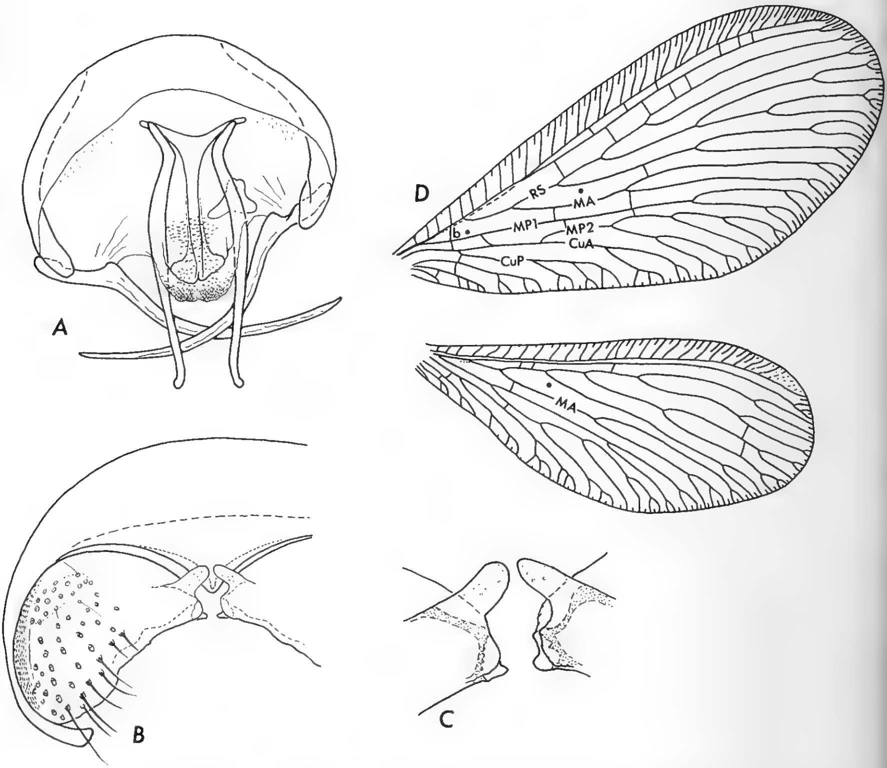


FIG. 14. *Nallachius loxanus:* A) internal genital armature, dorsal; B) abdominal apex, dorsal; C) apices of ectoprocts more enlarged; D) wing venation, forewing reconstructed from a composite drawing.

the area of dorsal lobe and digitiform process. Fusion of MP2 and CuA in the forewing also occurs in *N. americanus;* it appears probable that these species are related.

The species is known only by the type, of which the right forewing had been broken off at the base and reattached with acetate cement, causing some longitudinal folding and obscuring of the base. Consequently, Fig. 14D is a composite of camera lucida drawings from several aspects, with the anterior half of the extreme base taken from the left wing.

Nallachius pupillus (Navás), new combination

Nulema pupillus Navás 1930, Rev. Chilena Hist. Natural 34: 62–63, fig. 11.

TYPE. Male, "Paraguay, San Bernardino" [25°16′S, 57°16′W, ca. 700 ft. elev.] "36.1, H. Fiebrig."

REMARKS. The unique type of this species was in the Hamburg Museum and presumably has been destroyed. Navás' drawing shows an oval forewing; MP2 is fused with CuA. Small size (forewing length 4.2 mm) is correlated with reduced venation; only three branches of RS, in addition to MA, are indicated. The only apparent reason for originally referring this species to *Nulema* is the lack of discal crossveins beyond the middle of the wing; the antennae have only a single unarmed segment instead of two, as is supposedly characteristic of *Nulema.*

Nallachius bruchi Navás

Nallachius bruchi Navás, 1923, Arxius l'Inst. Cienc. Barcelona 7: 195. Carpenter, 1947, Psyche 54: 104.

The type, a female from Alta Gracia, Córdoba, Argentina, was deposited in the Navás collection. No illustration is given and the description is inadequate to permit inclusion of this species in the key. Probably MP2 has not anastomosed with CuA ("procubito prope basim furcato"), and a series of five gradate crossveins is present.

REFERENCES CITED

Acker, T. S. 1960. The comparative morphology of the male terminalia of Neuroptera (Insecta). Microentomology 24: 25–84.

Adams, P. A. 1970. A new genus and species of Osmylidae (Neuroptera) from South America, with a discussion of genitalic homologies. Postilla (Peabody Mus. Nat. Hist., Yale Univ.) 141: 11 p.

Aspöck, H. and U. Aspöck. 1967. Neue Dilariden aus Asien (Neuroptera, Planipennia). Ent. Nachrbl. (Wien) 14: 56–59.

Banks, N. 1913. Synopses and descriptions of exotic Neuroptera. Trans. Amer. Entomol. Soc. 39: 201–242, pl. 23–26.

——— 1938. New West Indian Neuropteroid insects. Rev. de Entomologia Rio de Janeiro, 9: 285–304.

Carpenter, F. M. 1940. A revision of the nearctic Hemerobiidae, Berothidae, Sisyridae, Polystoechotidae and Dilaridae (Neuroptera). Proc. Amer. Acad. Arts Sci. 74: 193–280.

——— 1947. Taxonomic notes on the Dilaridae (Neuroptera). Psyche 54: 100–109.

Gurney, A. B. 1947. Notes on Dilaridae and Berothidae, with special reference to the immature states of the nearctic genera (Neuroptera). Psyche 54: 145–169.

Lima, A. da Costa. 1943. Órdem Neuroptera. Insetos do Brasil 4: 73–108.

McLachlan, R. 1880. Occurrence of the neuropterous genus *Dilar* in South America. Entomol. Mo. Mag. 17: 39.

MacLeod, E. G. and P. E. Spiegler. 1961. Notes on the larval habitat and developmental peculiarities of *Nallachius americanus* (McLachlan) (Neuroptera: Dilaridae). Proc. Entomol. Soc. Washington 63: 281–286.

Nakahara, W. 1963. A remarkable new dilarid from India (Neuroptera). Kontyû 31: 77–78.

Navás, L. 1909. Monografía de la familia de los Diláridos (Ins. Neur.). Mem. R. Acad. Cienc. Art. Barcelona 7: 619–671, 2 pl.

——— 1911. *Dilaride* (Ins. Névr.) nouveau. Ann. Soc. sci. Bruxelles 35: 219–221.

——— 1914. Neuroptera. Fam. Dilaridae. Genera Insect. 156: 14p., 2 pl.

——— 1923. Estudis sobre Neuròpters (Insectes). Arx. Inst. Cienc. Barcelona 7: 179–196.

——— 1930. Insectos neotrópicos. Rev. Chilena Hist. Nat. 34: 62–75.

Stange, L. A. 1961. New records for the genus *Nallachius* Navás (Neuroptera: Dilaridae). Pan-Pac. Entomol. 37: 144.

Tjeder, B. 1957. Neuroptera-Planipennia 1. Introduction and Families Coniopterygidae, Sisyridae, and Osmylidae. S. African Animal Life 4: 95–188.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

OMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

ILLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

THOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA
PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 149 28 DECEMBER 1970

INTRACRANIAL MOVEMENT IN THE COELACANTH LATIMERIA CHALUMNAE SMITH (OSTEICHTHYES, CROSSOPTERYGII)

KEITH STEWART THOMSON

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Zelda Edelson, Elizabeth G. Weinman, Elise K. Kenney.

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* and special publications. *Postilla* and the *Bulletin* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

Inquiries regarding back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection,* should be directed to:

Walter J. Johnson, Inc.
111 Fifth Avenue
New York, N.Y. 10003.

INTRACRANIAL MOVEMENT IN THE COELACANTH LATIMERIA CHALUMNAE SMITH (OSTEICHTHYES, CROSSOPTERYGII)

KEITH STEWART THOMSON

Department of Biology and Peabody Museum of Natural
History, Yale University, New Haven, Connecticut 06520

(Received May 18, 1970)

ABSTRACT

The intracranial kinesis of the coelacanth fish *Latimeria chalumnae* Smith was studied from motion picture records of manipulation of the skull of a "fresh" dead specimen. Frame-by-frame analysis provided data on the relationships between change in angle of the gape and the angle at the intracranial joint. The length relationships of the subcephalic and geniocoracoid muscles during the mouth-opening sequence were noted. The data suggest that anterior movement of the shoulder girdle is an important feature of the intracranial mechanism and that such movement allows the geniocoracoid to contract essentially isometrically when the gape is opened. The possible function of cranial kinesis is discussed.

POSTILLA 149: 12 p. 28 DECEMBER 1970.

INTRODUCTION

For many years one of the most interesting aspects of the morphology of the Coelacanthini, and their close relatives the wholly fossil Rhipidistia, has been the special mechanism of intracranial kinesis, a major feature of which is the division of the braincase into halves with the "intracranial joint" between them. The anterior functional unit of the skull (anterior braincase, cheek, palate and lower jaws) is movably attached to the posterior unit (posterior braincase, gill apparatus and trunk). The structure and probable mode of action of the skull in these fishes have been discussed by several workers (see Thomson, 1967, 1969 for reviews of these subjects), but no worker has yet been able to study this system in live specimens of *Latimeria chalumnae* Smith, the only extant crossopterygian. While the possible adaptive role of intracranial kinesis in crossopterygians (and indeed other vertebrates) has often been debated, the situation is still far from clear. Presumably the special advantages of such a system must lie in part in the mode of opening and closing the gape, the special orientation of the gape, the extent of gape opening and the mode and force of gape closure.

According to most authorities (see review by Thomson, 1967), the principal muscle involved in the crucial dorsal flexure of the intracranial joint of crossopterygians is the paired M. geniocoracoideus lying on either side of the ventral midline. This is also the principal mandibular retractor (Millot and Anthony, 1958). It has been supposed that by virtue of the mechanical arrangement of the various skull parts, the action of this muscle in retracting the mandibles and rotating them ventrally around the quadrate joint includes translation of the ventrally and posteriorly directed forces into a force pushing the palate and anterior portion of the braincase forward and upward. During this process (Fig. 1), again by virtue of the shape and arrangement of the palate, the mandibles are actually projected considerably forward. At first sight, therefore, it would seem that the length of the geniocoracoideus muscles would in fact increase during this process (Fig. 1) rather than remain constant or decrease as one would expect if their contraction is the prime mover in this process. Closure of the gape is a more complicated process. There is a special paired subcephalic muscle (see Millot and Anthony, 1958) that lies along the ventral surface of the endocranium and is responsible for "adduction" of the anterior unit of the braincase (ventral

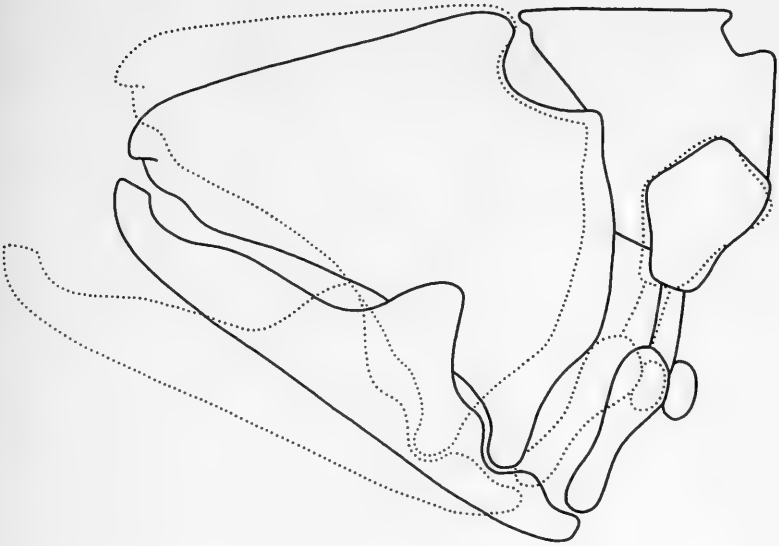


FIG. 1. *Latimeria chalumnae.* Outline drawings of the braincase, palate, hyoid arch and lower jaw showing the relative positions of the skull components when the gape is closed (solid lines) and when the gape is opened and the intracranial joint flexed dorsally (dotted lines). Redrawn from Thomson, 1969.

rotation at the intracranial joint). The gape itself is closed by the large mandibular adductors, both the origins and insertions of which lie wholly within the anterior skull unit. The anterior skull unit may also be retracted by the musculature associated with the ventral hyoid skeleton. This paper examines the length relationships of the geniocoracoideus and subcephalic muscles (see Fig. 2) during intracranial kinesis in *Latimeria chalumnae* with the hope of further elucidating their roles in this complex process.

In the absence of live material and in the face of many logistic difficulties before live material of this large rare fish can be worked within a laboratory situation, we based the present study on observations made upon a specimen preserved fresh by freezing immediately after capture. The specimen [YPM 1482 (Yale Peabody Museum); see

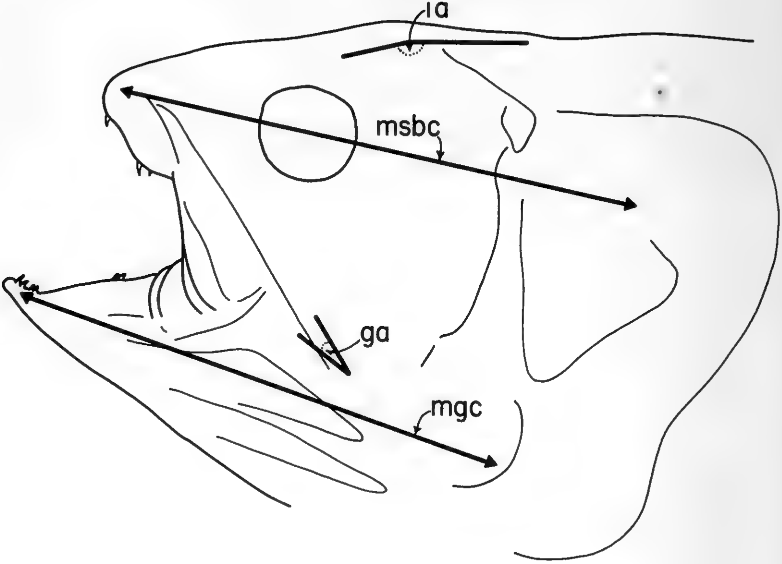


FIG. 2. *Latimeria chalumnae.* Outline drawing made from motion picture record of dead specimen showing dimensions and angles measured. Specimen YPM 1482, Fish Collection, Yale Peabody Museum of Natural History; total length 107 cm, fresh weight 15.87 kg, (ga = angle of gape; ia = angle at intracranial joint; mgc = estimate of length of M. geniocoracoideus; msbc = estimate of length of M. subcephalicus).

Thomson, 1966a, b] was thawed in the laboratory and the skull carefully manipulated to observe the sequence of movements involved in opening the gape. It was not felt that the process of gape closure could be simulated with any degree of accuracy because there is no way of predicting the sequence of operation of the separate subcephalic and adductor mandibulae systems (see below). The sequence of movements during opening of the gape and accompanying dorsal flexure at the intracranial joint was recorded in motion pictures for subsequent frame-by frame analysis, a series of markers having been attached to the head of the fish. From drawings made from the film while projected (Fig. 2), measurements were made of the distances between origin and insertion of the geniocoracoideus and subcephalic muscle systems. These measurements are used in the following analysis as an estimate of the lengths of these muscles during opening of the gape. The dimensions of the specimen are indicated in Figure 2.

RELATIONSHIP BETWEEN THE ANGLE OF THE INTRACRANIAL JOINT AND THE ANGLE OF THE GAPE

From the film record it was seen that opening of the gape (depression of the mandibles) was accompanied by simultaneous dorsal rotation (extension) at the intracranial joint. The relationship between the two angles is shown in Figure 3, and it will be noted that the curve has a sigmoid shape. Certain points have to be noted, here, however. In manipulation of the skull it was seen that in the "inert" position, with the gape closed, the intracranial joint was bent slightly downward. Apparently, in life this did not occur and the slight sagging of the anterior portion of the skull in our specimen was probably due to a general lack of muscle tonus and notochordal elasticity. If so, it may well be that in life the initial phases of mandibular depression (perhaps 0° to 5°) occurred without change in the angle of the

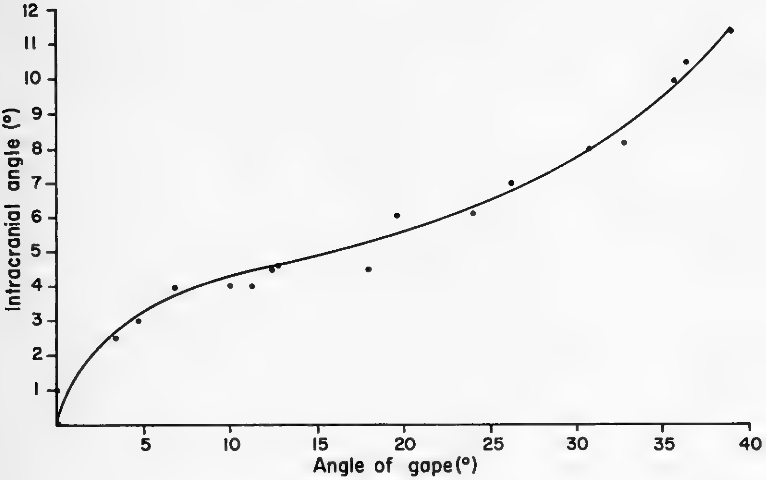


FIG. 3. *Latimeria chalumnae.* Graph showing probable relationship between angle of gape and angle of intracranial joint during the sequence of opening the mouth.

intracranial joint. It is also possible that, during the sequence of manipulation, in attempting to simulate the forward thrusting of the mandibles this action was overemphasized. The final part of the graph (Fig. 3) is therefore slightly suspect (gape opening between 35° and 40°).

LENGTH RELATIONSHIPS OF M. GENIOCORACOIDEUS

From motion picture analysis, the length relationships of M. geniocoracoideus are somewhat puzzling. As Figure 4A shows, when the angle of the gape increases, the distance between the origin and insertion of the geniocoracoideus increases in a regular manner. Figure 4B shows, however, that the initial phases of dorsal intracranial extension are not correlated with a change in length of this muscle until the

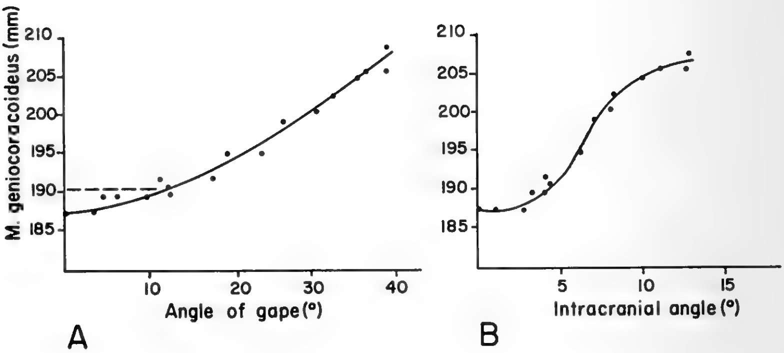


FIG. 4. *Latimeria chalumnae*. Graph showing probable relationship between change in length of M. geniocoracoideus and (A) angle of gape and (B) angle at intracranial joint during sequence of mouth opening ("resting length" 187 mm).

intracranial joint has been moved through about 3° (20% of total flexure). The graph of the total relationship is a sigmoid curve. During opening of the mouth, M. geniocoracoideus increases in length by about 12%. This therefore seems to document the paradox that the muscle that is assumed to be the main mandibular retractor and the prime mover in dorsal rotation at the intracranial joint may actually increase in length in the process of opening the mouth. It is indeed difficult to visualize how a muscle with this type of relationship could activate this system. There are several possibilities for resolution of this dilemma: 1) It is possible that the point of insertion of the muscle onto the shoulder girdle is moved forward during the sequence (by action of the axial musculature), thus allowing net shortening of the muscle. 2) It is possible that, as noted previously, the anterior skull unit is normally held at a slightly extended (dorsal) angle during the initial part of gape opening. If this were the case, then at this time retraction of the mandibles would not have been accompanied by movement at the intracranial joint. In Figure 5, a reconstruction

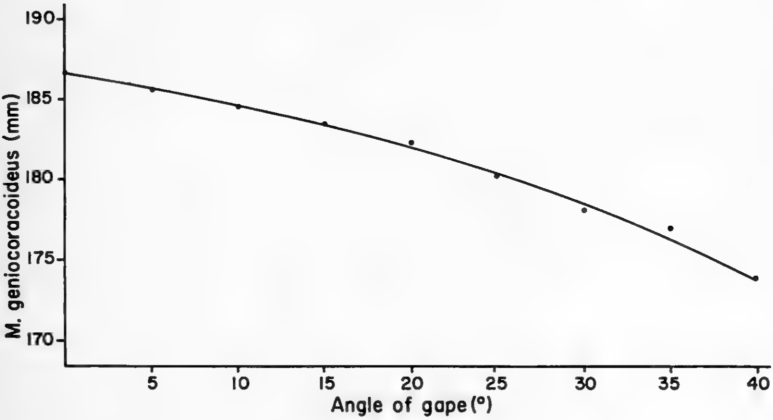


FIG. 5. *Latimeria chalumnae.* Estimated relationship between change in length of M. geniocoracoideus and angle of gape when there is no movement at the intracranial joint (from graphical reconstructions).

is given of the relationship between geniocoracoid length and gape angle in a sequence of mandibular retraction without intracranial movement (made from a graphical reconstruction, this is presumably impossible in life). In this case, the muscle shows a steady decrease in length (approximately 7%). Given the imperfection of our techniques, it seems reasonable to suggest that during the early phases of opening the mouth, M. geniocoracoideus was contracting isometrically (Fig. 4A, dotted line). This does not, however, resolve the paradox of increase in length of this muscle during the later stages of mouth opening. 3) A third factor that may be involved is the contraction of other muscles, such as the MM. sternohyoideus. This has been discounted as a factor in mandibular retraction by Millot and Anthony (1958) and Thomson (1967) but it is worth raising the possibility that some other muscle system is involved in the later phases of gape opening. Having mentioned these three possibilities, I should observe that the first of these seems to me the most plausible.

In my 1967 study of crossopterygian intracranial kinesis, I suggested that flexure of the intracranial joint might be possible without opening of the gape in coelacanths (but not Rhipidistia). This might be associated with respiratory movements of the head (see also Thomson, 1969). Figure 6 shows the length relationships of M. geniocoracoideus under such conditions (from a graphical reconstruction). It will be seen again that the length relationships strongly indicate that anterior movement of the shoulder girdle would be necessary in order for M. geniocoracoideus to maintain a constant length or to contract during this sequence. Indeed, I suggest that these data provide firm evidence supporting the postulation of such a movement. The data also indicate that a minimum forward movement of the coracoid through 12% of the resting length of the muscle (21 mm in this fish) would be necessary to achieve isometric contraction of the M. geniocoracoideus in normal opening of the gape.

LENGTH RELATIONSHIPS OF THE SUBCEPHALIC MUSCLE

The probable relationships of this muscle were estimated from the change in length of the straight-line distance between the origin and insertion of this muscle during mouth opening. In fact, this muscle has a considerable tendinous insertion at the front of the palate. As shown in Figure 7, the relationships between the overall length and

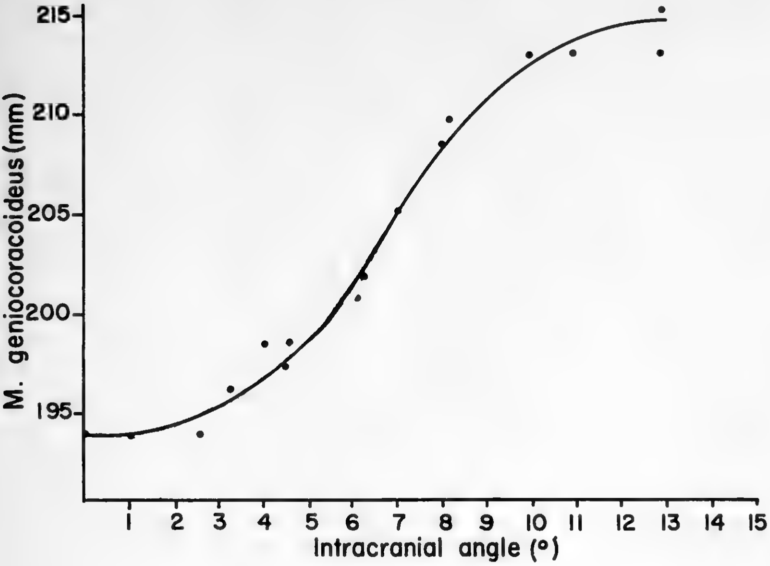


FIG. 6. *Latimeria chalumnae.* Estimated relationship between change in length of M. geniocoracoideus and angle at intracranial joint when there is no depression of the mandibles (from graphical reconstructions).

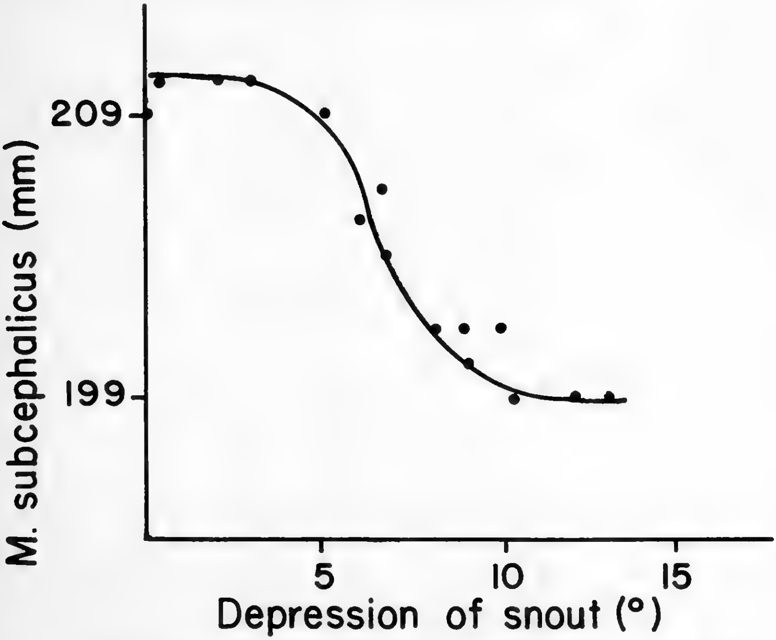


FIG. 7. *Latimeria chalumnae.* Graph showing probable relationship between change in length of M. subcephalicus and angle at intracranial joint, during depression of the snout ("resting length" 200 mm).

the angle of the intracranial joint are complicated. Due to the configuration of the skull, the changes in length describe a sigmoid curve. However, it must be noted that the total change in length of the muscle-tendon combination is in fact only some 5.5% of the resting length which presumably indicates that contraction is virtually isometric when the snout is being depressed. Since the sequence of separate activation of the subcephalic muscles in depressing the snout and the mandibular adductors cannot be determined from dead material, the relationship between change in the intracranial angle and the angle of the gape in closing the mouth cannot be measured.

DISCUSSION

A surprisingly large number of vertebrates, from the Paleozoic arthrodires (see, for example Miles, 1969) to the lizards and snakes, possesses a system whereby the skull or some part of it can be elevated as the mandibles are depressed. In the Actinopterygii perhaps an analagous system is the protrusion of the upper jaws, which may also be accompanied by a raising of the head (see Schaeffer and Rosen, 1961; Alexander, 1968). In many of these animals, structures of the trunk play an important role in dorsal extension of the head. This movement may involve axial muscles, inserted on the occipital region, or the shoulder girdle to which muscles of the branchial apparatus and jaws are attached. In the Crossopterygii, living and fossil, intracranial kinesis, operating around a joint in the mid-part of the braincase, is a unique system and of considerable interest. Because we know so little about the biology of crossopterygians, even the living species *Latimeria chalumnae,* one is hesitant to try to draw general conclusions from so imperfect a set of data and methods as those presented here. Nonetheless, there seems to be some support here for the intuitively acceptable conclusion that the operation of intracranial kinesis during opening of the gape must be accompanied by a forward rotation of the ventral coracoid region of the shoulder girdle by the muscles of the trunk. If this is not the case, then an extremely puzzling situation exists with respect to the mode of action of the geniocoracoideus muscles that seem to be the prime agents in opening the gape and elevating the snout.

Unfortunately this study has not shed light on the mode of action of the subcephalic muscles and the adaptive role of depression of the anterior skull unit in closure of the mouth. If the subcephalic muscles are brought into play during the early phases of gape closure, their role might be to provide an immediate rapid downward and backward movement of the palatal dental battery, ensnaring the prey from above while the mandibles are as yet in an early stage of adduction. This would have the interesting effect of reducing the absolute upward movement of the mandibles at this point. However, it would have no effect on the movement of the mandibles relative either to the palate or to the prey since all three are functionally part of the same anterior skull unit during this time. Similarly, this would not reduce the force of mandibular adduction. The combined movement of the anterior skull unit is also rearward during this process, having the effect of bringing the prey further into the gullet. The alternative hypothesis, i.e., that contraction of the subcephalics does not occur until later in the sequence of gape closure, is also acceptable in terms of the estimates made here of the length relationships of the subcephalic muscles. However it is difficult to see what advantage such a system might have, except possibly with respect to forcing the prey down into the gullet once it had been assaulted by the mandibles. The intracranial kinesis may also be used alone in respiratory movements but in this case it is necessary to find some kind of compensatory action, probably movement of the shoulder girdle, to allow appropriate contraction of the geniocoracoideus muscles.

One of the interesting features to the author of making such a study as this is that it is in some sense predictive. One can only hope that before too long such a study may be followed by direct observation of the feeding mechanism of a live coelacanth.

ACKNOWLEDGEMENT

The study was supported by a grant from the National Science Foundation (GB 7573X). I am grateful to Philip L. Perkins for criticism of the manuscript. The illustrations were prepared by Rosanne Rowen.

LITERATURE CITED

Alexander, R. McN. 1968. Animal mechanics. Sidgwick and Jackson, London. 346 p.

Miles, R. S. 1969. Features of placoderm diversification and the evolution of the arthrodire feeding mechanism. Trans. Roy. Soc. Edinburgh. 68: 123–170.

Millot, J. and J. Anthony. 1958. Anatomie de *Latimeria chalumnae*. Vol. I. Squellette, muscles et formations se soutien. Centre de la Recherche Scientifique, Paris.

Schaeffer, B. and D. E. Rosen. 1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. Amer. Zool. 1: 187–204.

Thomson, K. S. 1966a. Intracranial mobility in the coelacanth. Science 153: 999–1000.

——— 1966b. Mobility of the skull and fins in the coelacanth *(Latimeria chalumnae* Smith) Amer. Zool. 6: 565–566. (Abstr.)

——— 1967. Mechanisms of intracranial kinetics in fossil rhipidistian fishes (Crossopterygii) and their relatives. J. Linn. Soc. (Zool.) 46: 223–253.

——— 1969. The biology of the lobe-finned fishes. Biol. Rev. 44: 91–154.

INFORMATION FOR AUTHORS

REVIEW The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.

STYLE Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).

FORM Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.

TITLE Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.

ABSTRACT The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.

OMENCLATURE Follow the International Codes of Zoological and Botanical Nomenclature.

ILLUSTRATIONS Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.

FOOTNOTES Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.

TABLES Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.

REFERENCES The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.

THOR'S COPIES Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.

PROOF Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.

COPYRIGHT Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

NUMBER 150 22 JANUARY 1971

A NEW TRIASSIC CYCAD AND ITS PHYLETIC IMPLICATIONS

T. DELEVORYAS
R. C. HOPE

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Zelda Edelson, Elizabeth G. Weinman, Elise K. Kenney.

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* and special publications. *Postilla* and the *Bulletin* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

Inquiries regarding back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection,* should be directed to:

Walter J. Johnson, Inc.
111 Fifth Avenue
New York, N.Y. 10003.

A NEW TRIASSIC CYCAD AND ITS PHYLETIC IMPLICATIONS

T. DELEVORYAS

Department of Biology and Peabody Museum of Natural
History, Yale University, New Haven, Connecticut 06520

R. C. HOPE

Department of Geology, Campbell College,
Buie's Creek, North Carolina 27506

ABSTRACT

Upper Triassic beds in North Carolina yield excellently preserved compressions of ferns, cycadophytes and conifers. Among the cycadophyte remains are leaves comparable to those of the genus *Pseudoctenis* attached to a slender, elongated stem fragment. Other stem remains show bases of petioles with a similar arrangement. Cuticular analysis of laminae, rachises and stem surfaces suggests the existence of a member of the Cycadales with loosely arranged pinnately compound fronds on a slender stem, with cataphylls and terminal cones. Although Cycadales probably originated before the Triassic, the growth habit of only a very small number of Triassic members is known. This discovery is significant in allowing the reconstruction of one of the oldest members of the order and presents evidence that its growth habit is unlike that of later Cycadales. The slender stem and loosely spaced compound leaves point to a pteridosperm ancestry.

Dedicated to Professor Chester A. Arnold in the year of his official retirement as Professor of Botany at the University of Michigan, and in honor of his distinguished service to the fields of morphology and paleobotany.

POSTILLA 150: 21 p. 22 JANUARY 1971.

INTRODUCTION

The Cycadales represent an order of vascular plants with a number of unsolved evolutionary problems. The group is an old one and has been extensively studied; yet questions concerning its origin and subsequent evolution remain unanswered. Recent papers (Taylor, 1969; Mamay, 1969) suggest that the order first appeared during late Paleozoic times. Taylor presents as evidence a Pennsylvanian pollen cone that has certain cycadalean features; however, just as noteworthy are structures more characteristic of conifers (Taylor, 1970). Mamay described two types of fragmentary megasporophylls from the Permian, one of which resembles *Spermopteris* Cridland and Morris (1960). Although fossil remains of possible Cycadales in the upper Paleozoic are scanty, the existence in the Triassic Period of members of the order with structural features identical with those of modern genera would tend to support the suggestion that the order had become established before the onset of the Mesozoic.

As is so frequently the case, many of our efforts to understand the morphology and evolution of fossil plant groups are hampered by the fragmentary nature of the fossil remains with no accurate means of understanding how the pieces had fit together in life. With continuing paleobotanical investigations, however, it is becoming increasingly possible to present reconstructions of extinct plants. With this new knowledge of the whole plant, we are in a progressively better position to discuss biological problems involving these plants and some aspects of evolution of the plants in question.

Recently discovered Upper Triassic deposits (Hope and Patterson, 1969) with well-preserved plant remains in Chatham County, North Carolina, have yielded an abundance of cycadophyte fossils. In fact, cycadophytes are the single most important element in the flora, with ferns second and conifers next. Occurrence of persistent cuticular remains on foliar and cauline structures is inconsistent, but fortunately the fronds of cycadophytes typically have well-preserved cuticle. Thus it is possible to recognize the existence of both principal orders of cycadophytes, the Cycadales (Nilssoniales) and Cycadeoidales (Bennettitales). Of the cycadophyte fronds, *Otozamites* (Cycadeoidales) is the most abundant. The next most commonly occurring leaves are comparable to those of the genus *Pseudoctenis* (Cycadales). The latter are commonly found in association with stem fragments, and in one instance actual attachment was observed.

By cuticular analysis it is possible to correlate the separate leaf and stem fragments and to determine that the same kind of plant was involved. Attached to the stem fragment with a leaf is a structure resembling a pollen cone.

Whereas these leaves, if they had been found isolated, would have been included within the genus *Pseudoctenis,* they resemble no known species of the genus. Furthermore, demonstration of attachment of leaves, stems and cones as parts of a plant in the Cycadales warrants the establishment of a new genus for all of these parts, reserving *Pseudoctenis* for isolated leaves only. It is conceivable that the various species of *Pseudoctenis* could belong to different genera of plants.

SYSTEMATIC DESCRIPTION

CLASS CYCADOPHYTA

ORDER CYCADALES

FAMILY CYCADACEAE

Leptocycas, gen. nov.

TYPE SPECIES. **Leptocycas gracilis,** sp. nov.

GENERIC DIAGNOSIS. Same as for the type species, see below.

Leptocycas gracilis, gen. et sp. nov.

(Figs. 1–12)

DIAGNOSIS. Stems slender, 3 to 5 cm wide, bearing terminal crown of loosely arranged, pinnately compound leaves of the *Pseudoctenis* type, with persistent bases of petioles a little farther down, and devoid of foliar structures at lower levels. Cataphylls intermixed with leaves, cones borne terminally.

Cuticle of pinnae, rachises and stems with straight epidermal cell walls and haplocheilic stomata tending to be oriented parallel with veins; dorsal wall of guard cell thickened into a flangelike structure; pole of guard cell extending beyond the dorsal thickening.

Pinnae decurrent, with parallel venation, attached to rachis laterally and broadly, but the base of pinna tilted with respect to rachis axis; distal edge of pinna closer to the ventral surface of the leaf than proximal edge.

STRATIGRAPHIC OCCURRENCE. Pekin Formation, Upper Newark Group, Upper Triassic.

HOLOTYPE. YPM Paleobot. 1148.

DESCRIPTION. *Leaves.* The fronds, comparable to those usually assigned to the genus *Pseudoctenis,* are petiolate, with pinnately arranged, linear leaflets (Figs. 1, 4, 5). An entire frond has not been found, but one fragment measured 21 cm long (Fig. 4). This fragment has no petiole, but the fact that other pieces of fronds with proximal portions preserved indicate that the petiole may be as long as 10 cm (Fig. 5) is evidence that the entire frond may have exceeded 30 cm in length. Pinnae average about 4.5 cm long and about 3.5 mm wide. Venation is only barely discernible, and no anastomoses were observed. Attachment of the pinna base to the rachis is not parallel with the rachial axis, but rather, the pinna is slightly tilted, with the distal edge of the pinna closer to the ventral surface of the leaf than the proximal edge. As a result, pinnae are not parallel with bedding planes, and splitting of the shale often does not expose the entire pinna, but only a thin strip of it, and the width of the pinna appears narrower than it actually is. Pinnae are decurrent along the rachis. There seems to be no relationship of pinna position on both sides of the rachis; pinnae generally appear to be alternate, although in some instances they are opposite.

Epidermis. Cuticle was removed from the shale matrix mechanically, either with a needle or a brush, placed in Schulze's reagent until it became translucent, washed, and then placed in a very dilute solution of ammonium hydroxide for a short time. After another washing, the cuticle fragments were carried through an alcohol-xylene series and mounted in one of a number of synthetic resins. Epidermal cells have smooth walls, with stomata arranged parallel to the pinna veins and only on the lower side. Stomata are characteristically cycadalean (see Greguss, 1968) with haplocheilic guard cell ontogeny (Figs. 6–11). The guard cells are sunken, elongated and somewhat boat-shaped, with the poles bent toward the surface of the leaf. The dorsal thickening on each guard cell flares outward (away from the stomatal opening), and the thickening on the two adjacent guard cells are such that two pairs of projections overlap the guard cells, with the poles of the guard cells extending beyond. This configuration is identical to that in a number of cycad genera (Greguss, 1968); Pant and Nautiyal, 1963).

Stems. Consistently frequent association of compressed stem fragments (Fig. 3) with the *Pseudoctenis*-like leaves suggests that leaves and stems are parts of the same kinds of plants. More definite evidence, however, is the one stem fragment with an attached leaf (Fig. 1). These stem fragments are slender (3 to 5 cm wide) and, instead of closely spaced persistent leaf bases so characteristic of many cycads, the stems bear loosely spaced, slender leaf bases (Fig. 3). The stem surface has coarse wrinkles, but the epidermis itself appears fairly smooth. Stomata are present in the cuticle of stems (Figs. 7, 9) and petiole bases (Fig. 11) as well as on parts of laminae of the leaves (Figs. 6, 8, 10). In fact, the precise correspondence of stomatal and epidermal configurations on pinnae, petioles and stem fragments makes it convincing that all of these parts, even though connection is not always evident, are portions of the same kind of plant.

Near the apex of the stem fragment with the attached leaf are some cataphylls, about 3 cm long, 5 mm wide at the base, and tapering to a point. These appear to have been coriaceous and thick, and must have dropped off, along with the expanded leaves, lower down on the stem.

Attached to the stem apex is a structure resembling a cycad pollen cone (Figs. 1, 2). It is bent downward, measures about 6 cm long and 1.5 cm thick, and has only fair preservation. Neither cuticular remains nor pollen grains could be retrieved from it.

Reconstruction. The various parts of this cycad suggest a plant such as that figured in the reconstruction (Fig. 12). The stem was slender, devoid of leaf bases below, with a surface that was somewhat wrinkled but that had a smooth epidermis, at least in the upper portion. At higher levels there were persistent leaf bases rather loosely arranged. A crown of leaves was borne at the apex, and cones, when present, were borne terminally. It cannot be ascertained whether the cone actually terminated the stem, or whether it represented a branch produced close to the stem apex. It is not possible, either, to determine whether these plants were dioecious, as are all living cycads, or monoecious.

DISCUSSION

This discovery of cycad remains is of interest for a number of reasons. First, even though parts of cycads are abundant in Mesozoic deposits and the group was an extremely important one in Mesozoic floras, stem remains are rare. Florin's (1933) familiar reconstruction of *Bjuvia simplex* showing a rather massive, erect stem was not based on actual stem remains. Similarly, Harris' (1961) reconstruction of the Jurassic plant bearing leaves of *Nilssonia tenuinervis,* pollen cones of *Androstrobus wonnacotti* and seed cones of *Beania mamayi* was not based on any stem fossils. Harris admitted, however, that there were other, indirect pieces of evidence for assuming a stem of that kind. Archangelsky and Brett (1963) reported a new genus, *Michelilloa,* from the Triassic of Argentina. They compared this plant with the modern *Dioon spinulosum* on the basis of anatomical structures. Jain (1962) described a stem fragment, *Fascisvarioxylon mehtae,* that he considered to be a cycad. However, even with these reports of fossil material purported to belong to the Cycadales, there exists no accurate reconstruction of a Mesozoic cycad with parts known from the actual fossil record. In restorations of Mesozoic dioramas that include plant communities, members of the Cycadales are shown looking like modern genera, with no basis for this type of habit.

One of us (Delevoryas, 1968) presented a survey of all known cycadeoids in an attempt to detect the most commonly occurring body form among members of the Cycadeoidales. The usual picture of cycadeoids is of a plant with a squat, fleshy stem with closely spaced persistent leaf bases which, along with thick ramental scales, formed a dense armor on the trunk surface. It appears, however, that this concept has arisen primarily because the genus *Cycadeoidea,* which this description best fits, is the best known. In reality, most cycadeoids seem to have had slender stems, often branched, and leaf bases did not necessarily persist over the entire stem surface.

A paper by Harris (1969) adds further evidence that cycadeoids were often slender, branched plants. In that work he presents a partial restoration of a plant, *Bucklandia pustulosa,* that was previously known from stem remains assigned to that taxon, leaves called *Ptilophyllum pecten,* and cones known as *Williamsonia leckenbyi.* This restoration fits precisely into the concept of the body form postulated by Delevoryas as the typical one for Mesozoic cycadeoids.

Bucklandia dichotoma, recently described by Sharma (1969) from the Middle Jurassic of India, is another example of a cycadeoidalean stem from the Mesozoic that is slender and branched.

Although fewer members of the Cycadales are preserved as fossils, on the basis of what is known about the stems of fossil members of the order, as well as other pieces of indirect evidence, we would suggest the same kind of habit for most Mesozoic members of the order. Harris, when he presented his tentative reconstruction of *Beania,* apparently felt the same way, at least about that plant. The remains of *Leptocycas* from North Carolina are good evidence to reinforce the idea that early Cycadales had slender stems, and that the more "typical" form, with squat, fleshy stems is most likely a derivative and not the primitive form.

If the habit of Mesozoic Cycadales was, indeed, in the form of a slender, probably branched, plant, with leaves not arranged in a crowded fashion, it would be easier to visualize the late Paleozoic pteridosperms as the likely ancestors. Stem structure and anatomy, as well as compound leaves and seed features are all held in common between the seed ferns and the Cycadales. Furthermore, the occurrence of reproductive structures on leaves tends to hold the two groups together. Mamay (1969) believes that the primitive Cycadales had entire leaves, and that the divided leaf came later. He points out that in all of the known fossil sporophylls the lamina is undivided. Although we have no evidence to dispute this suggestion, and admit that it could be correct, we feel that there is really little difference between an entire cycadophyte leaf and a pinnately compound one, and that it may be premature to conclude that the primitive megasporophyll was consistently entire. We await discovery of additional late Paleozoic and early Mesozoic cycads to provide the definitive answer.

ACKNOWLEDGMENTS

Thanks are extended to Carl Wester for his elegant reconstruction in Figure 12. This paper profited from discussions with R. E. Gould concerning fossil Cycadales. We are grateful to the authorities of the Boren Clay Products Company, especially to E. L. Rummage, for their cooperation in making it possible to collect material from their quarry. Russ Patterson, Sanford, North Carolina, was extremely helpful with his enthusiasm in the field. Research for this project was supported by National Science Foundation Grant GB 20999X to T. D. and by a research grant from Campbell College to R. C. H.

Literature Cited

Archangelsky, S., and Brett, D. W. 1963. Studies on Triassic fossil plants from Argentina. II. *Michelilloa waltonii* nov. gen. et spec. from the Ischigualasto Formation. Ann. Bot. n.s. 27: 147–154.

Cridland, A. A., and Morris, J. E. 1960. *Spermopteris,* a new genus of pteridosperms from the Upper Pennsylvanian series of Kansas. Amer. J. Bot. 47: 855–859.

Delevoryas, T. 1968. Some aspects of cycadeoid evolution. J. Linnaean Soc. (Bot.) 61: 137–146.

Florin, R. 1933. Studien über die Cycadales des Mesozoikums. Kungl. Svensk. Vetensk. Akad. Handl., ser. 3, 12(5): 1–134.

Greguss, P. 1968. Xylotomy of the living cycads. Akadémiai Kiadó, Budapest. 260 p.

Harris, T. M. 1961. The fossil cycads. Palaeontology 4: 313–323.

——— 1969. The Yorkshire Jurassic flora III. Bennettitales. British Mus. (Nat. Hist.) Pub. No. 675: 1–186.

Hope, R. C., and Patterson, O. F. III. 1969. Triassic flora from the Deep River Basin, North Carolina. North Carolina Dep. Conserv. Dev., Div. Mineral Res. Spec. Pub. 2: 1–12.

Jain, K. P. 1962. *Fascisvarioxylon mehtae* gen. et sp. nov., a new petrified cycadean wood from the Rajmahal Hills, Bihar, India. Palaeobotanist 11: 138–142.

Mamay, S. H. 1969. Cycads: fossil evidence of late Paleozoic origin. Science 164: 295–296.

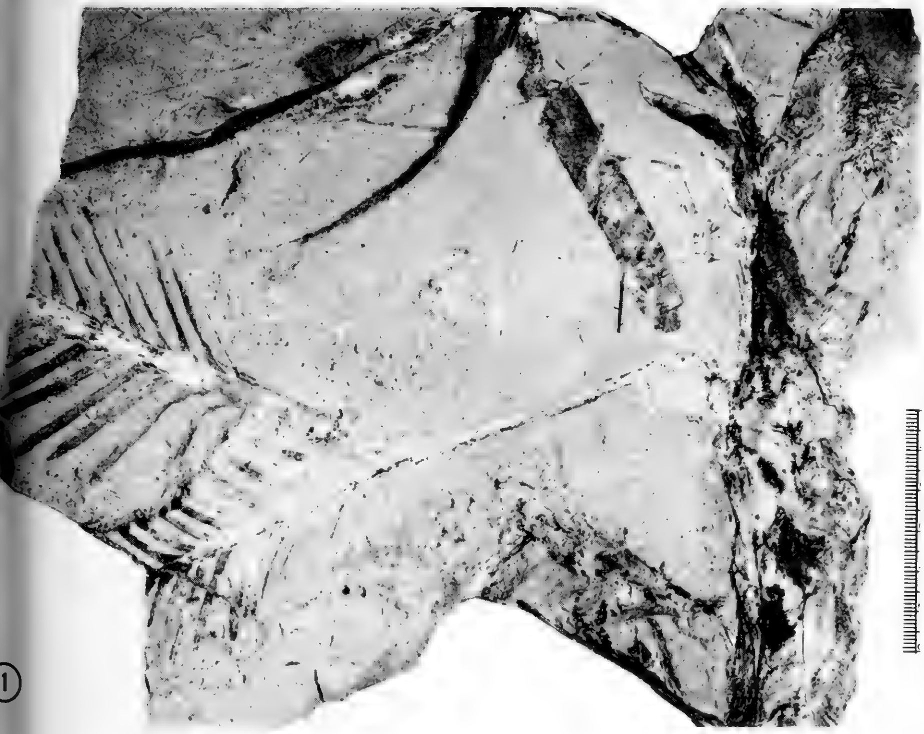
Pant, D. D., and Nautiyal, D. D. 1963. Cuticle and epidermis of recent Cycadales. Leaves, sporangia and seeds. Senck. Biol. 44: 257–348.

Sharma, B. D. 1969. *Bucklandia dichotoma* sp. nov. from the Middle Jurassic of Rajmahal Hills, India. Ameghiniana 6: 303–308.

Taylor, T. N. 1969. Cycads: evidence from the Upper Pennsylvanian. Science 164: 294–295.

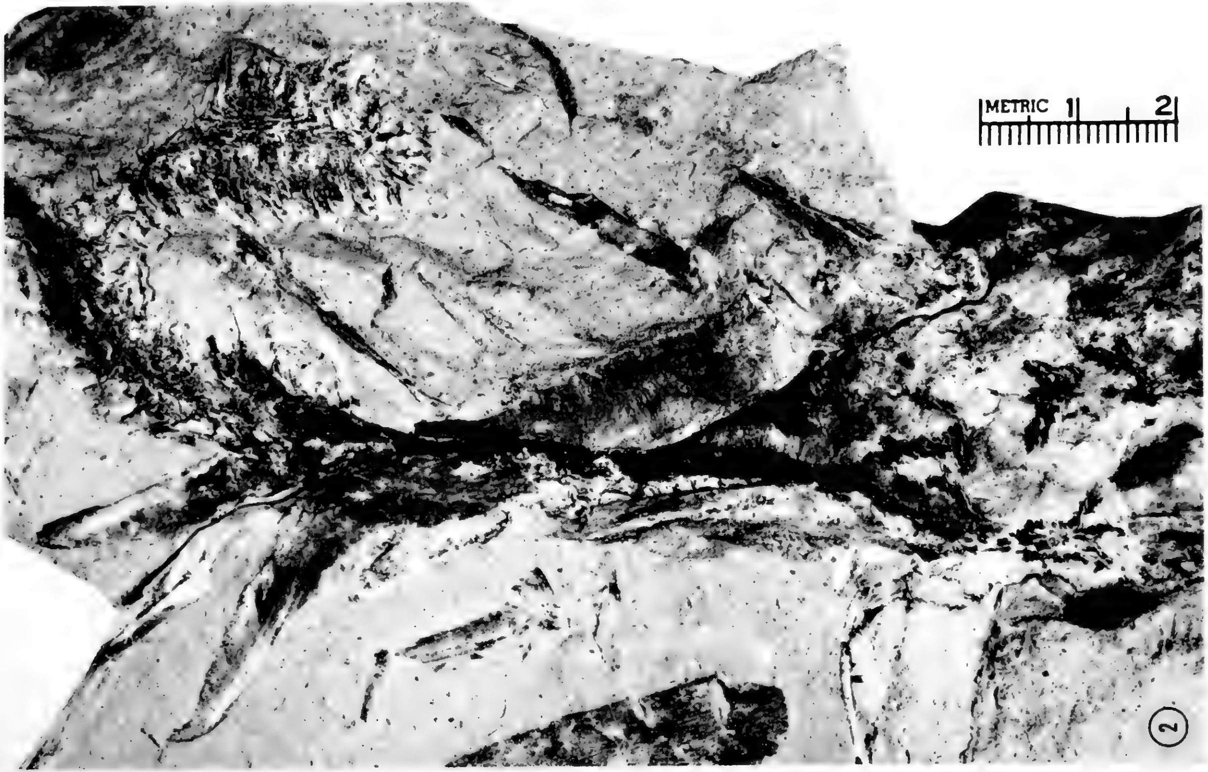
——— 1970. *Lasiostrobus* gen. nov., a staminate strobilus of gymnosperm affinity from the Pennsylvanian of North America. Amer. J. Bot. 57: 670–690.

FIG. 1. *Leptocycas gracilis*. Holotype, consisting of a stem fragment, one attached leaf, cataphylls and a cone. YPM Paleobot. 1148.



①

FIG. 2. *Leptocycas gracilis.* Distal part of holotype with details of petiole base (lower left), cataphylls and terminal cone. YPM Paleobot. 1148.



②

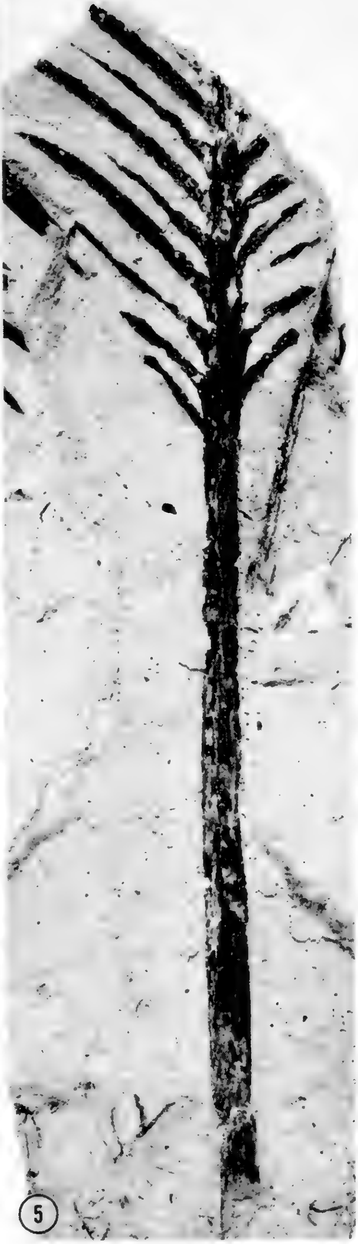
FIG. 3. *Leptocycas gracilis*. Stem fragment with persistent petiole bases. YPM Paleobot. 1149.

③

FIG. 4. *Leptocycas gracilis*. Portion of a leaf. ×0.77. YPM Paleobot. 1150.

FIG. 5. *Leptocycas gracilis*. Basal portion of a leaf. ×0.88. YPM Paleobot. 1151.

④

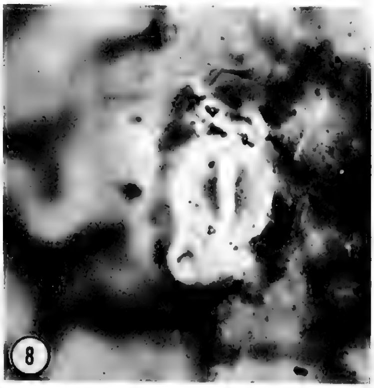


⑤

FIGS. 6–11. *Leptocycas gracilis.* Cuticular preparations from various parts of the plant. FIG. 6. From leaf epidermis of holotype. YPM Paleobot. 1148. FIG. 7. From epidermis of stem. YPM Paleobot. 1149. FIG. 8. From epidermis of isolated leaf. YPM Paleobot. 1152. FIG. 9. From epidermis of stem. YPM Paleobot. 1153. FIG. 10. From epidermis of isolated leaf. YPM Paleobot. 1154. FIG. 11. From epidermis of petiole of stem fragment with persistent leaf bases. YPM Paleobot. 1155. All figures ×590.

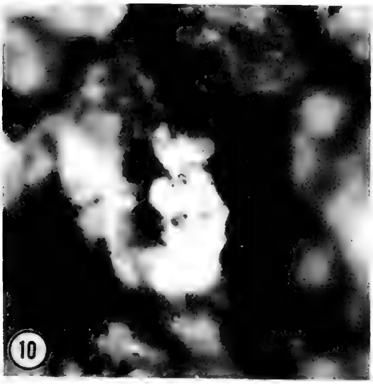
⑥

⑦

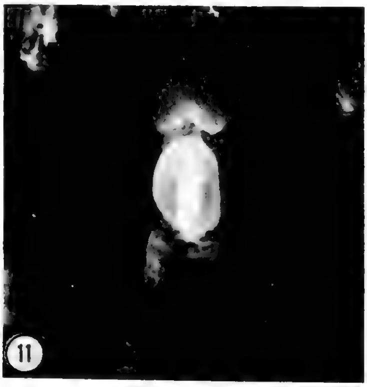


⑧

⑨



⑩



⑪

FIG. 12. *Leptocycas gracilis*. Suggested reconstruction of a plant about 1.5 m tall.

INFORMATION FOR AUTHORS

REVIEW	The Publications Committee of the Peabody Museum of Natural History reviews and approves manuscripts for publication. Papers will be published in approximately the order in which they are accepted; delays may result if manuscript or illustrations are not in proper form. To facilitate review, the original and one carbon or xerox copy of the typescript and figures should be submitted. The author should keep a copy.
STYLE	Authors of biological papers should follow the *Style Manual for Biological Journals,* Second Edition (Amer. Inst. Biol. Sci.). Authors of paleontological manuscripts may choose to follow the *Suggestions to Authors of the Reports of the U.S. Geological Survey,* Fifth Edition (U.S. Govt. Printing Office).
FORM	Maximum size is 80 printed pages including illustrations (= about 100 manuscript pages including illustrations). Manuscripts must be typewritten, with wide margins, on one side of good quality 8½ x 11″ paper. *Double space everything. Do not underline anything except genera and species.* The editors reserve the right to adjust style and form for conformity.
TITLE	Should be precise and short. Title should include pertinent key words which will facilitate computerized listings. Names of new taxa are not to be given in the title.
ABSTRACT	The paper must begin with an abstract. Authors must submit completed BioAbstract forms; these can be obtained from the *Postilla* editors in advance of submission of the manuscripts.
OMENCLATURE	Follow the International Codes of Zoological and Botanical Nomenclature.
ILLUSTRATIONS	Must be planned for reduction to 4 x 6½″ (to allow for running head and two-line caption). If illustration must go sideways on page, reduction should be to 3¾ x 6¾″. All illustrations should be called "Figures" and numbered in arabic, with letters for parts within one page. It is the author's responsibility to see that illustrations are properly lettered and mounted. Captions should be typed double-spaced on a separate page.
FOOTNOTES	Should not be used, with rare exceptions. If unavoidable, type double-spaced on a separate page.
TABLES	Should be numbered in arabic. Each must be typed on a separate page. Horizontal rules should be drawn lightly in pencil; vertical rules must not be used. Tables are expensive to set and correct; cost may be lowered and errors prevented if author submits tables typed with electric typewriter for photographic reproduction.
REFERENCES	The style manuals mentioned above must be followed for form and for abbreviations of periodicals. Double space.
THOR'S COPIES	Each author receives 50 free copies of his *Postilla.* Additional copies may be ordered at cost by author when he returns galley proof. All copies have covers.
PROOF	Author receives galley proof and manuscript for checking printer's errors, but extensive revision cannot be made on the galley proof. Corrected galley proof and manuscript must be returned to editors within seven days.
COPYRIGHT	Any issue of *Postilla* will be copyrighted by Peabody Museum of Natural History only if its author specifically requests it.

POSTILLA

PEABODY MUSEUM
YALE UNIVERSITY

INDEX

NUMBERS 101 — 150

MAY 1966 — JANUARY 1971

POSTILLA

Published by the Peabody Museum of Natural History, Yale University

Postilla includes results of original research on systematic, evolutionary, morphological, and ecological biology, including paleontology. Syntheses and other theoretical papers based on research are also welcomed. *Postilla* is intended primarily for papers by the staff of the Peabody Museum or on research using material in this Museum.

Editors: Zelda Edelson, Elizabeth G. Weinman, Elise K. Kenney.

Postilla is published at frequent but irregular intervals. Manuscripts, orders for publications, and all correspondence concerning publications should be directed to:

Publications Office
Peabody Museum of Natural History
New Haven, Conn., 06520, U.S.A.

Lists of the publications of the Museum are available from the above office. These include *Postilla, Bulletin, Discovery,* and special publications. *Postilla* and the *Bulletin* are available in exchange for relevant publications of other scientific institutions anywhere in the world.

Inquiries regarding back numbers of the discontinued journal, *Bulletin of the Bingham Oceanographic Collection,* should be directed to:

Walter J. Johnson, Inc.
111 Fifth Avenue
New York, N.Y. 10003.

TITLES

101. The Meteorite and Tektite Collections of Yale University. Karl K. Turekian. May, 1966.
102. Two Prehistoric Archeological Sites in Egyptian Nubia. W. E. Wendt. September, 1966.
103. A New Species of Clathriid Sponge from the San Juan Archipelago. Tracy L. Simpson. November, 1966.
104. Two New Species of *Clymenella* (Polychaeta: Maldanidae) from Brazil. Charlotte P. Mangum. December, 1966.
105. Variation in the Sternal Notches of Suboscine Passeriform Birds. Mary A. Heimerdinger and Peter L. Ames. February, 1967.
106. A New Genus and Species of Marine Dipnoan Fish, from the Upper Devonian of Canada. Keith Stewart Thomson. February, 1967.
107. A Revised List of Brazilian Scleractinian Corals and Description of a New Species. Jacques Laborel. April, 1967.
108. Environmental Factors Influencing the Distribution of *Barbatia domingensis* (Mollusca, Bivalvia) on the Bermuda Platform. Sara S. Bretsky. June, 1967.
109. Functional Morphology of the Masticatory Apparatus of Two Dicynodonts (Reptilia, Therapsida). A. W. Crompton and Nicholas Hotton III. August, 1967.
110. Revision of *Syncyclonema* (Upper Cretaceous) and Comparison with Other Small Pectinid Bivalves and *Entolium*. Ian G. Speden. September, 1967.
111. A Fossil *Colobus* Skull from the Sudan (Primates, Cercopithecidae). Elwyn L. Simons. October, 1967.
112. A Reappraisal of the North American Species of the Siluro-Devonian Trilobite Genus *Scotiella*. J. H. Shergold. November, 1967.

113. Revision of *Neofibularia* (Porifera, Demospongiae), a Genus of Toxic Sponges from the West Indies and Australia. Willard D. Hartman. November, 1967.
114. The Anatomy and Systematic Position of the Antpipits *Conopophaga* and *Corythopis*. Peter Peter L. Ames, Mary A. Heimerdinger and Stuart L. Warter. January, 1968.
115. A Didelphid (Marsupialia) from the Early Eocene of Colorado. George Gaylord Simpson. February, 1968.
116. The Lower Jaw of Cynodonts (Reptilia, Therapsida) and the Evolutionary Origin of Mammal-like Adductor Jaw Musculature. Herbert R. Barghusen. March, 1968.
117. A ?Diapsid (Reptilia) Parietal from the Lower Permian of Oklahoma. Robert L. Carroll. March, 1968.
118. Avian Anatomical Specimens in the Peabody Museum of Natural History, Yale University. Peter L. Ames and Eleanor H. Stickney. March, 1968.
119. A New Sibling *Papilio* from the Rocky Mountains, with Genetic and Biological Notes (Insecta, Lepidoptera). Charles L. Remington. May, 1968.
120. Ectoproct and Entoproct Type Material. Frank J. S. Maturo, Jr. and Thomas J. M. Schopf. July, 1968.
121. A New Dinocephalian from the Cisuralian Region (Reptilia, Therapsida; Upper Permian). P. K. Tchudinov. July, 1968.
122. Lung Ventilation in Dipnoan Fishes. Keith Stewart Thomson. August, 1968.
123. A Mandible of *Indraloris* (Primates, Lorisidae) from the Miocene of India. Ian Tattersall, August, 1968.
124. A New Devonian Fish (Crossopterygii: Rhipidistia) Considered in Relation to the Origin of the Amphibia. Keith Stewart Thomson. September, 1968.
125. The Relationships of the "Wren-thrush", *Zeledonia coronata* Ridgway. Charles G. Sibley. September, 1968.
126. Morphology and Systematics of the Northern Dvina Cynodonts (Reptilia, Therapsida; Upper Permian). L. P. Tatarinov. November, 1968.
127. Vertebral Structure in Rhipidistia (Osteichthyes, Crossopterygii) with Description of a New Permian Genus. Keith Stewart Thomson and Peter Paul Vaughn. December, 1968.
128. A New Theropod Dinosaur from the Lower Cretaceous of Montana. John H. Ostrom. February, 1969.

129. A New Genus and Species of Teiid Lizard from Bolivia. Thomas Uzzell. February, 1969.
130. Karyological Heterogamety of Deep-sea Fishes. T. R. Chen. March, 1969.
131. The Pelvic Musculature of the Dinosaur *Hypsilophodon* (Reptilia: Ornithischia). Peter M. Galton. May, 1969.
132. New Species and Records of Shallow Water Demospongiae from Barbados, West Indies. George John Hechtel. May, 1969.
133. A Probable Pteridosperm with Eremopterid Foliage from the Allegheny Group of Northern Pennsylvania. T. Delevoryas and T. N. Taylor. June, 1969.
134. Comments on the Avifauna of Tanzania, II. S. Dillon Ripley and Gerd H. Heinrich. June, 1969.
135. The Status of the Genera *Ecpleopus, Arthroseps* and *Aspidolaemus* (Sauria, Teiidae). Thomas Uzzell. July, 1969.
136. New Species and Synonymy in the Genus *Meleoma* (Neuroptera, Chrysopidae), with a Discussion of Genitalic Homologies. Phillip A. Adams. August, 1969.
137. New Genera and Species of Coralline Sponges (Porifera) from Jamaica. Willard D. Hartman. September, 1969.
138. *Gigantopithecus* (Pongidae, Hominoidea) a New Species from North India. E. L. Simons and S. R. K. Chopra. October, 1969.
139. Occlusion in *Docodon* (Mammalia, Docodonta). Farish A. Jenkins, Jr. November, 1969.
140. The Anatomy and Internal Architecture of the Muscles of Mastication in *Didelphis marsupialis*. Karen Hiiemäe and Farish A. Jenkins, Jr. December, 1969.
141. A New Genus and Species of Osmylidae (Neuroptera) from Chile and Argentina, with a Discussion of Planipennian Genitalic Homologies. Phillip A. Adams. December, 1969.
142. Teiid Lizards of the Genus *Proctoporus* from Bolivia and Peru. Thomas Uzzell. January, 1970.
143. Sharpness of Teeth in Man and Other Primates. R. G. Every. March, 1970.
144. The Taxonomic Status of Quill Worms, Genus *Hyalinoecia* (Polychaeta: Onuphidae) from the North American Atlantic Continental Slope. Charlotte P. Mangum and William R. Rhodes. April, 1970.

145. Generic Status of the *Inoceramus*? *tegulatus* Species Group (Bivalvia) of the Latest Cretaceous of North America and Europe. Ian G. Speden. May, 1970.
146. Morphological Variation in *Gammarus minus* Say (Amphipoda, Gammaridae), with Emphasis on Subterranean Forms. John R. Holsinger and David C. Culver. August, 1970.
147. *Notogoneus osculus* Cope, an Eocene Fish from Wyoming (Gonorynchiformes, Gonorynchidae). Philip L. Perkins. July, 1970.
148. A Review of the New World Dilaridae. Phillip A. Adams. December, 1970.
149. Intracranial Movement in the Coelacanth *Latimeria chalumnae* Smith (Osteichthyes, Crossopterygii). Keith Stewart Thomson. December, 1970.
150. A New Triassic Cycad and Its Phyletic Implications. T. Delevoryas and R. C. Hope. January, 1971.

AUTHORS

Adams, Phillip A., *136, 141, 148*
Ames, Peter L. and Mary A. Heimerdinger, *105*
Ames, Peter L. and Eleanor H. Stickney, *118*
Ames, Peter L., Mary A. Heimerdinger, and Stuart L. Warter, *114*
Barghusen, Herbert R., *116*
Bretsky, Sara S., *108*
Carroll, Robert L. *117*
Chen, T. R., *130*
Chopra, S. R. K. and E. L. Simons, *138*
Crompton, A. W. and Nicholas Hotton III, *109*
Culver, David C. and John R. Holsinger, *146*
Delevoryas, T. and R. C. Hope, *150*
Delevoryas, T. and T. N. Taylor, *133*
Every, R. G., *143*
Galton, Peter M., *131*

NEW FAMILY

NEW GENERA

NEW SPECIES

NEW SUBSPECIES

Buccanodon olivaceum ulugurensis, 134: 3
Mussismilia hispida hispida, 107: 8
Neofibularia nolitangere nolitangere, 113: 10
Neofibularia nolitangere oxeata, 113: 11
Viridibucco leucomystax meridionalis, 134: 4

NEW COMBINATIONS

Kloucekia (Kloucekia) obsoleta (Ulrich and Delo 1940), *112:* 11
Meleoma dolicharthra (Navás), *136:* 6
Meleoma tezcucana (Banks), *136:* 8
Nallachius championi (Navás), *148:* 22
Nallachius hermosus (Banks), *148:* 25
Nallachius pupillus (Navás), *148:* 29
Scotiella conservatrix (McLearn 1924), *112:* 4