Bulletin OF THE Museum of Comparative Zoology

Volume 135
1966 – 1967

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS 02138 U.S.A.

CONTENTS

Bulletin OF THE
Museum of
Comparative
Zoology

The Postcranial Skeleton of the Giant Permian Pelycosaur *Cotylorhynchus romeri*

J. WILLIS STOVALL, LLEWELLYN I. PRICE, AND
ALFRED SHERWOOD ROMER

Museum of Comparative Zoology, Harvard University

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 135, NO. 1
SEPTEMBER 22, 1966

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN 1863–
BREVIORA 1952–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office

Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

THE POSTCRANIAL SKELETON OF THE GIANT PERMIAN PELYCOSAUR *COTYLORHYNCHUS ROMERI*

J. WILLIS STOVALL, LLEWELLYN I. PRICE, AND ALFRED SHERWOOD ROMER

Introductory note. In 1937 fragmentary remains of a gigantic new pelycosaur from the Oklahoma Permian were brought to the attention of Dr. Stovall of the University of Oklahoma, who shortly after published a preliminary account of the animal, as *Cotylorhynchus romeri*, aided by notes and drawings by Llewellyn I. Price and myself (Stovall, 1937). Subsequently, many additional specimens of this form were found; these were prepared under Dr. Stovall's direction, and studies and drawings were made of much of the material by Mr. Price. It was planned that the material be described in a joint paper by Stovall and Price, but owing to a variety of circumstances, this was never written. Nearly thirty years have passed, and except for a brief notice and figures of the skull in the "Review of the Pelycosauria" (Romer and Price, 1940: 419–421), no further account of *Cotylorhynchus* has appeared. Meanwhile Dr. Stovall has died, and Mr. Price is now resident in Brasil. Adding to the need for description is the fact that Dr. E. C. Olson has found additional remains of *Cotylorhynchus*, and a number of related forms have been discovered in a variety of localities and horizons in Texas and even in Russia (Olson, 1962: 24–47). In this situation, it has been agreed that I should publish a general account of the postcranial anatomy of *Cotylorhynchus*. But although I alone should be held responsible for any inaccuracies or misinterpretations that this paper may contain, I have felt that the paper should be considered as a joint effort, to give credit to Dr. Stovall for his work in the collection and supervision of preparation of the material, and to Mr. Price for his invaluable notes and drawings of the Oklahoma materials.

—Alfred Sherwood Romer

MATERIALS

Although a broad band of continental Permian beds extends across Oklahoma from the Kansas border to the Red River, relatively few vertebrates have been discovered in the Lower Permian of the state —quite in contrast to the situation to the south, in northern Texas. This relative paucity of finds appears to be due to the generally higher rainfall and consequent better vegetative covering in Oklahoma, and to the more level topography of Oklahoma, in contrast to the Texas area where the presence of a number of limestones and heavy sandstones makes for a more rugged topography and the development of potentially fossiliferous "breaks."

The discovery of abundant remains of a large new type of caseid pelycosaur, *Cotylorhynchus romeri*, was in consequence a major event in the history of paleontological work in Oklahoma. As noted in Stovall's paper (1937: 308), the first find of *Cotylorhynchus* material was made by Dr. W. S. Strain (then a graduate assistant at the

University of Oklahoma). The site lay in the Hennessey shales, 4¾ miles west of Navina, Logan County. The type specimen consisted of an incomplete skull and jaw, a front foot, and interclavicle. Shortly after, a nearly complete postcranial skeleton was found at about the same horizon, in the Hennessey Formation, but close to the city of Norman and hence some 50 miles or so from the region of the first discovery, and during the years 1937–1939 a very considerable number of further *Cotylorhynchus* specimens were collected in the Hennessey shales of the Norman district and prepared by laborers under Works Progress Administration funds. Most of this material is now in the Stovall Museum at Norman, but specimens were also obtained for the museums in Chicago, New York, Washington, and Cambridge. Preparation of the materials at Norman was carried out under the general direction of Dr. Stovall, and notes and figures on much of the material were made by Mr. Price. In the preparation of the present description, Romer has seen all this material, and has utilized Price's notes and figures in addition to his own observations. A word of caution must be given, however. Although preparation was carried out under Dr. Stovall's direction, it is not improbable that, with a considerable number of workers and with a number of specimens undergoing simultaneous preparation, a certain amount of inaccuracy may have occurred in the restoration and association of materials. Further, in the time that has since elapsed, some of the specimens have been moved several times for storage and re-cataloging and further chances of error have crept in.

The reptilian remains from the Hennessey shales of the Norman region appear, curiously, to pertain almost entirely to *Cotylorhynchus*, with very few remains of other reptiles and amphibians—a situation in strong contrast to the usual mixed assemblages generally present in typical Texas redbeds deposits. As far as can be seen, the *Cotylorhynchus* materials from the Norman area can be assigned to a single species as far as morphological characters are concerned.[1] There is however, considerable variation in size. In reptiles generally, early growth is rapid, followed by a slower if steady growth; the natural result is that the greater part of specimens recovered in the case of fossil forms should represent relatively young mature animals, with a small percentage of overly large specimens representing individuals which were exceptionally long-lived and consequently exceptionally large, and a small percentage of young and immature individuals. The present materials tend to show a rather greater size range than is common. As a rough index to size, I list the length (in mm) of major limb elements in a number of the better specimens (Table 1).

TABLE 1

Specimen No.	Humerus	Radius	Femur	Tibia
4-0-6	352	166+	311	—
4-0-2 (1249)	—	—	312	195
4-0-4	343	188	305	197
CNHM 272	327+	138+	308	127+
AMNH 7517	—	—	—	190
1250 (?)	232+	—	298	170
4-0-16	265	—	285	—
USNM	263	123+	251+	147+
MCZ 3416	246	—	239	135
4-0-13	197	115	—	—
4-0-3	191	110	—	—

These specimens are deposited in the following institutions: Chicago Natural History Museum (CNHM); American Museum of Natural History (AMNH); United States National Museum (USNM); Museum of Comparative Zoology, Harvard (MCZ). Other specimens (numbered) are in the University of Oklahoma collection.

As can be seen from this table, the first five specimens listed appear to be of relatively uniform large size. Below this there is a sharp drop to three specimens which are 20 per cent or so smaller than the first

---

[1] Dr. Olson informs me that there is a possible specific difference between the Norman material and the type from Navina.

group but appear to be essentially mature; below, with the MCZ specimen as a transition, there is a drop to small and seemingly immature specimens such as 4-0-3. Possibly there is a specific difference between the first and second groups. Equally possible, however, the contrast is a sexual one; in *Dimetrodon limbatus*, for example, there is a seemingly clear-cut size difference of 10 per cent between the sexes (Romer and Price, 1940: 341–342).

In typical Texas redbeds localities, fossil reptile remains are most commonly found in disarticulated condition, and when found articulated appear to have undergone deposition in a variety of poses. One gets the impression that this is the result of stream action, and that many of the "bone pockets" represent back eddies in streams in which cadavers brought downstream tended to collect (and decompose). But in the Hennessey shales of the Norman region, many of the specimens show clearly that the *Cotylorhynchus* individuals were generally buried in articulated and undisturbed fashion, right side up, with the limbs spread outward at the sides. This strongly suggests that we are here dealing with entombment of quite another sort. South African Permian pareiasaurs, equally large and clumsy herbivores, are typically preserved in similar fashion (Watson, 1913). There are two possible interpretations. Watson, in the case of the pareiasaurs, implies death from starvation, and suggests a covering of the cadavers *in situ* by loess-like materials. I would favor an alternative interpretation in both cases—that the animals were bogged down and entombed in swamps.

Study has been greatly handicapped by the nature of the specimens. Due in part, perhaps, to a rather spongy structure of the skeletal elements, and to the nature of the sediments in which they were embedded, much of the material has been subjected to crushing and distortion, with a consequent limitation of the accuracy with which restoration and illustration can be made. In great measure description and illustration of structures given here are based on a synthesis of a number of specimens. Wherever possible the illustrations are based on specific examples, although frequently with the addition from other individuals of details missing or obscured in the specimen primarily utilized.

It became apparent, even from the material described in Stovall's preliminary paper, that *Cotylorhynchus* was a giant relative of *Casea*, a small Clear Fork Texas pelycosaur described by Williston (Williston, 1910: 590–592; 1911: 111–131, etc.; Romer and Price, 1940: 412–419). Despite cranial differences, *Casea* and a number of other Texas pelycosaurs show such a large number of diagnostic postcranial similarities to *Edaphosaurus* that Romer (Romer and Price, 1940: 21, 366–378) felt justified in including these forms with *Edaphosaurus* in a common suborder Edaphosauria. As in *Casea*, the *Cotylorhynchus* postcranial skeleton agrees in almost every particular with the characteristics assigned to the Edaphosauria as a whole. In consequence, in the description which follows, comparisons are, in general, with *Casea* or other edaphosaurian types.

VERTEBRAL COLUMN

The general characteristics of the *Cotylorhynchus* vertebral column are almost exactly those cited in the "Review of the Pelycosauria" for the suborder Edaphosauria as a whole:

> "The number of presacral vertebrae is sometimes reduced. The dorsal vertebrae are moderately to greatly elongated; the cervicals are small in all dimensions. The dorsal centra are spool-shaped, with rounded bottoms, and lack any trace of ventral keel or lip. Intercentra are small. The dorsal transverse processes are moderately elongated and rise from a more antero-dorsal position on the arch than in other pelycosaurs. The zygapophysial surfaces are large, moderately tilted, and extend farther laterally than in sphenacodontids. The neural arches are not excavated above the diapophyses. . . . The atlas centrum reaches the ventral surface of the column."

Only a very few qualifications on this definition need be made to fit *Cotylorhynchus.* (1) It was stated that the presacral count is "sometimes" reduced. At the time this was written, the figure was known only in *Casea* where apparently 24 or 25 presacrals were present (Romer and Price, 1940: 417). It is now known that *Edaphosaurus boanerges* has likewise reduced the primitive pelycosaur number from 27 to 23 presacral vertebrae (Shuler and Witter, 1942). It is thus a reasonable inference that presacral reduction was general in the suborder, and reduction is present in *Cotylorhynchus.* (2) "Intercentra are small." Few are present in any *Edaphosaurus* material; only a single intercentrum was found in the *Casea* material (in the sacral region); none are known in *Cotylorhynchus* except for the atlas-axis. Small gaps between the ventral edges of the centra in all three genera suggest that tiny intercentra were present in cartilaginous form. (3) "The atlas centrum reaches the ventral surface of the column." This appears to be true of *Edaphosaurus,* and Williston (1911: pl. XIV) restores this centrum as reaching the ventral surface in *Casea.* As described below, however, it does not reach this surface in *Cotylorhynchus,* and Williston's material of *Casea* was obviously imperfect and open to misinterpretation.

The *Cotylorhynchus romeri* column includes definitely 25 and probably 26 presacral vertebrae, 3 sacrals, and about 55 caudals. It has proved difficult to determine the presacral count in *Cotylorhynchus.* There are several specimens in which dorsals, lumbars, and sacrals are present in well-connected series; generally, however, the cervicals are poorly preserved or absent. In 4-0-6, however, the cervicals are present. There are definitely 25 well-preserved presacral vertebrae, and apparently one further poorly preserved one. Several specimens show a sacrum of three vertebrae. The tail is preserved in but few cases. In the mounted slab of 4-0-2 (1249), a hind leg and tail, 43 caudals, the last apparently terminal, are present in seemingly articulated fashion. However, there is a suspiciously sharp drop in the size of centra following element 27, and a photograph of the specimen made during preparation shows that the last 16 vertebrae were not part of the block containing the main part of the material, although they may well pertain to the same individual. Measurements suggest that there is a gap here of about 10 vertebrae, to raise the probable total count to about 53. In the CNHM specimen, 37 caudals are present in articulation with the trunk; following a gap of about 23 cm in the slab there are eight further, much smaller, vertebrae, the last apparently terminal or sub-terminal. The gap is of such length as to suggest that 10 vertebrae are missing here, giving a probable total length of 55 vertebrae. This is a reasonable pelycosaurian number.

Dorsal vertebrae. Such a dorsal vertebra as, for example, vertebra 12 of 4-0-6 (Figs. 1C, 2C), exhibits a typical pelycosaurian and, further, edaphosaurian character. The centra are edaphosauroid—spool-shaped structures without any of the tendency seen in ophiacodontoids and sphenacodontoids for development of a ventral keel. The centrum, as in *Casea,* is relatively short and stout, its length, averaging about 60 mm in large individuals, being but about 1½ times the end height of 38–40 mm. The ventral surface is broad, essentially flattened, but slightly convex; at the margins of this area the sides curve upward sharply and, above this point, are slightly in-pinched. There is no visible suture between arch and centrum. On the sides of the centrum, at about the level where the base of the neural arch pedicel would be expected, there is a low longitudinal ridge, rounded at its summit, running lengthwise from a point well below the upper margin of the centrum anteriorly back to a somewhat higher position posteriorly. Above this point the upper part of the surface of the centrum and the lower lateral surface of the neural arch form a longitudinal depression extending length-

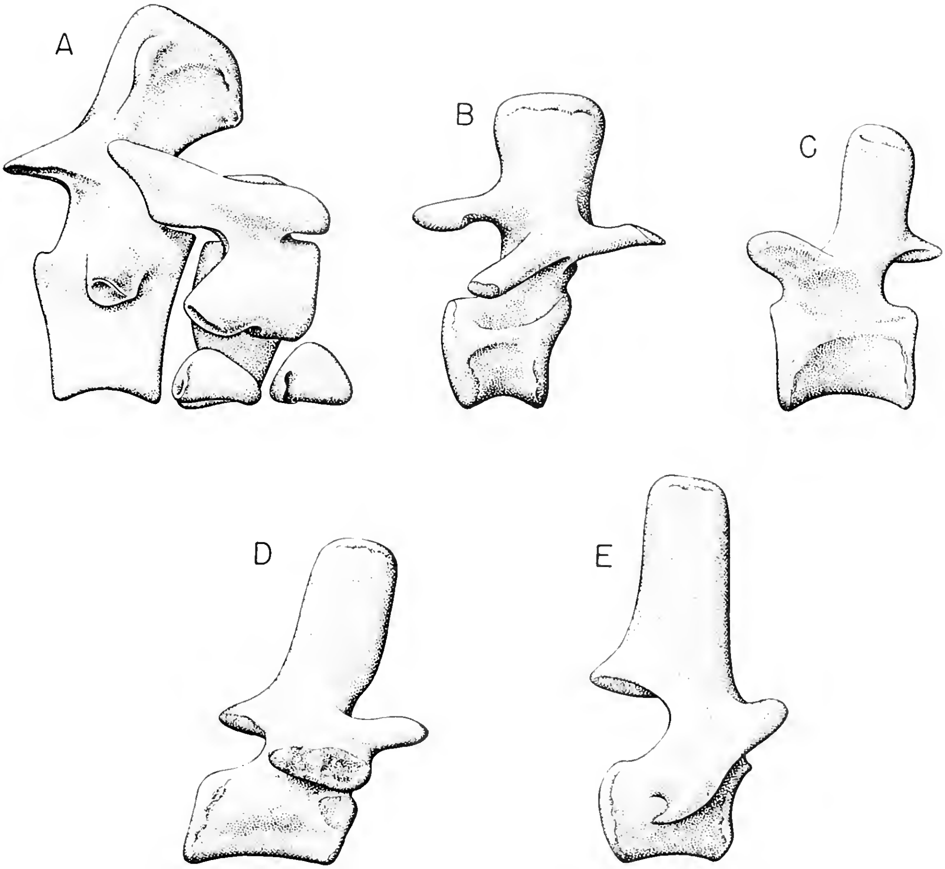


Fig. 1. Lateral views of representative vertebrae, in side view. *A*, atlas-axis, × $^2/_3$; *B*, vertebra 6, × $^1/_2$; *C*, vertebra 12, × $^1/_3$; *D*, vertebra 21, × $^1/_3$; *E*, proximal caudal, × $^1/_2$.

wise beneath the base of the transverse process.

The ends of the centrum are of a typical pelycosaurian nature—essentially circular in outline, with thickened edges. At either end this circle contains a cone-shaped depression for the notochord, the two cones connected by a small foramen. Both anteriorly and posteriorly the rim of the centrum is somewhat thickened laterally for the articulation of the capitulum, which was thus inter-central in position.

The transverse processes are highly developed in this region, extending outward on either side to a distance from the midline approximately equal to the vertebral length. In edaphosauroid fashion the transverse processes arise from a far anterior position on the neural arch, and their front margins extend almost directly outward from the level of the prezygapophyses. There is in this region no ventral expansion of the process, which is thin dorsoventrally but broad anteroposteriorly; there is thus no continuum in articular areas between capitulum and tuberculum. The transverse process here is directed almost straight laterally, with, however, a slight upward and forward tilt, rather than the downward slant of most pelycosaurs (*Casea* excepted). The base of the process is very broad, extending nearly the whole length of the vertebra.

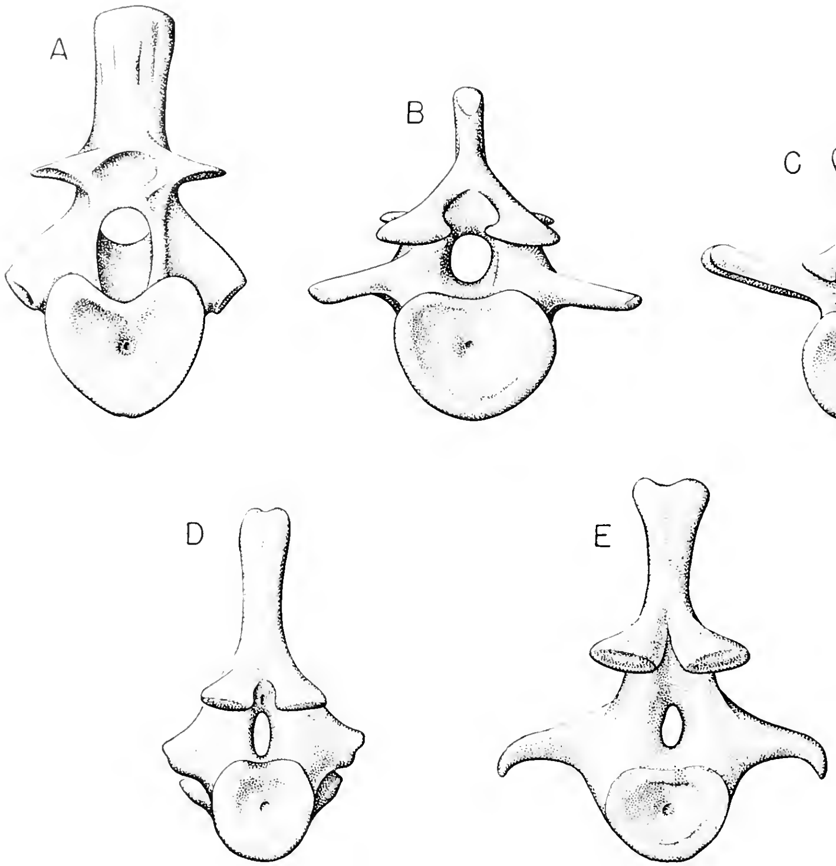


Fig. 2. Posterior views of the same vertebrae as those of Figure 1.

The broad articular surface for the tuberculum faces ventrally and only slightly laterally on the under surface of the process. Since the tuberculum is little raised, the proximal portion of the rib continues outward in the line of the transverse process. The zygapophyses are normally constructed, with a very slight median tilt of the articular surfaces. The neural arches, as in edaphosaurs generally, lack the lateral excavation seen in sphenacodontoids above the transverse processes. The neural spines, as in *Casea*, are slender transversely but long anteroposteriorly, and are low (although not as low, relatively, as in the last-named genus). In such mid-dorsals as are completely preserved the rugose end of the spine is expanded laterally on either side and indented medially, to give a somewhat bifurcate appearance, much as in, for example, some parts of the *Eryops* column.

Cervicals. Progressing forward through the anterior dorsals into the cervical series, the vertebrae are increasingly lightly built, as tends to be true of pelycosaurs generally, but more especially of edaphosauroids, such as *Cotylorhynchus*, in which the head is relatively small. The centra decrease steadily in diameter and length anteriorly, and the width tends to equal the length. In the 6th vertebra of 4-0-4, for example (Figs. 1B, 2B), the length is about 50 mm, the width about 45 mm. The flattened ventral surface of the centra persists into the cervical region. In the cervicals the transverse processes are shorter and lightly built, in correlation with the decreased size of the ribs. Anteriorly, the cleft in the summit of the neural spines disappears, although some distal expansion may persist; the spines become shorter and somewhat more rounded —ovoid—in section. Proceeding forward, the direction of the transverse processes gradually shifts. In a typical dorsal it points somewhat forward and upward, but in the cervicals the processes become somewhat ventrally and posteriorly directed, in correlation with the direction of the ribs in the relatively slender neck region. Even as far forward as vertebra 3, the capitular facet is high up on the rim of the centrum, showing little of the tendency to descend anteriorly, seen in most pelycosaurs. The cervical zygapophyses are, like the dorsals, widely separated and with essentially horizontal articular surfaces.

Atlas-axis. The atlas-axis complex is present and well preserved in 4-0-6, and is present also in 4-0-4 (Figs. 1A, 2A). A facet on the atlas neural arch indicates the presence in life of a proatlas. The atlas arch is bipartite and typically pelycosaurian, with a long posterior process articulating with the prezygapophysis of the axis and with a spur running farther back along the side of the axis neural arch. There is a short but distinct transverse process for rib attachment, turned strongly downward and backward. The atlantal intercentrum is highly developed for cranial articulation; laterally there is a distinct facet for the rib capitulum. As is well known, the atlas centrum is variable in development in pelycosaurs, reaching the ventral surface in *Dimetrodon*, for example, but excluded from this surface by the second intercentrum in *Ophiacodon*. The situation in *Cotylorhynchus* is not too clear. In both specimens in which the atlas-axis is preserved, there is a distinct ventral gap between intercentra 1 and 2, but the atlas centrum does not reach the surface here; possibly this gap may have been filled by a ventral cartilaginous continuation of the bone.

Intercentrum 2 is very well developed and bears a distinct rib facet. The axis centrum and arch are built in typically pelycosaurian—and especially edaphosaurian—fashion. The transverse process slants strongly downward and to a slight degree backward. The neural spine is, for an axis, rather short, but is stout, long anteroposteriorly, and expanded in a 3-pronged arrangement posteriorly toward the summit.

Posterior dorsals. Passing backward along the dorsal series, the vertebral centra increase somewhat in length to about vertebrae 17–19, beyond which a progressive reduction takes place so that beyond this point (as is also the case anteriorly) width exceeds length. In 4-0-4, for example, the length of vertebra 21 (Figs. 1D, 2D) is 51 mm, the breadth about 55 mm. An increase in central width, however, persists, width reaching its maximum in the sacral region, and the posterior dorsals are the most massive vertebrae in the column. In the more posterior presacrals the neural spines are increasingly long fore-and-aft and increasingly narrow in transverse diameter, although the arches are broadly expanded at the spine bases. In the posterior dorsal series the two members of each pair of prezygapophyses are joined by a horizontal ridge of bone bridging the space between them and forming a strengthening transverse element which crosses the front end of the vertebra between the ribs of either side. Progressing backward, the transverse processes are increasingly stout but decrease in length. In the last members of the series the processes are fused with the ribs. In the posterior vertebrae the area of attachment of the rib capitulum moves upward and backward to an oval area on the anterodorsal surface of the side of the centrum below the transverse process. Here, as in the transverse process, fusion with the rib takes place in the last few members of the dorsal series.

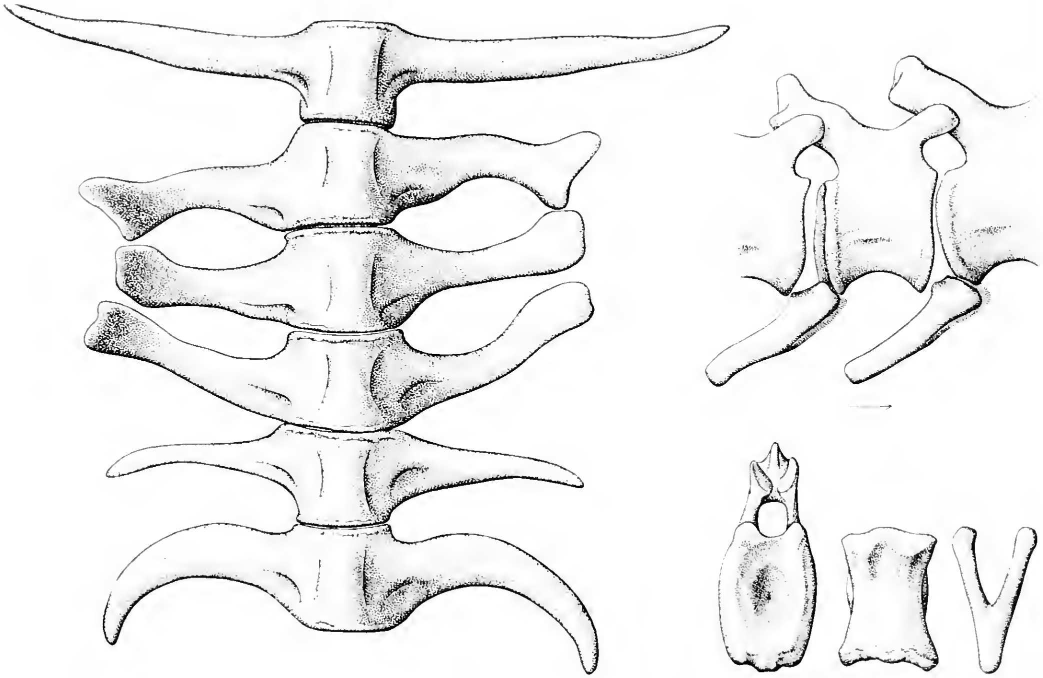


Fig. 3. *Left,* ventral view of last presacral, the three sacrals, and first two caudal vertebrae, × ¼. *Right, above,* lateral view of mid-caudal vertebrae, × ½. *Right, below,* posterior and ventral views of a mid-caudal vertebra and a mid-caudal chevron, × ½.

Sacrals (Fig. 3). Three sacral vertebrae are present, as noted in the description of the ribs. The centra are broad but appear to be shallow dorsoventrally (an effect perhaps due to crushing). In one specimen, at least, the centra of the first and second sacrals appear to be fused; whether the last two were fused is uncertain. On the first sacral the zygapophyses are still well separated, but on the third vertebra the two members of each pair are much closer together, a situation transitional to that in the tail. There appears to be no ossification of apposed zygapophyses. The transverse processes—firmly fused to the ribs—are short, but very stout, and are continuous with a large area on the centrum representing the capitular attachment. A depression which represents the point of junction of tubercular and capitular areas is seen in some specimens; it cannot be determined whether an arterial foramen perforates the structure. The neural spines of the first two sacrals are similar to those of the "lumbars"; that of sacral 3 is shorter fore-and-aft and less compressed from side to side.

Caudals (Figs. 1E, 2E, 3). The most anterior caudals resemble the last sacral closely. The breadth of the centrum is greater than the length or height; the rib attachment areas are short but greatly expanded, with a groove, presumably for an intersegmental artery, marking the line of distinction between tubercular and capitular components. More posteriorly, the transverse processes become greatly reduced in size (with a concomitant reduction in rib size), and process and rib have essentially disappeared by vertebra 12, although a slightly projecting ridge is present as far as vertebra 20. Meanwhile, the centra have begun a change in their proportions, so that by mid-length of the tail the length is considerably greater than the width and the

Fig. 4. *Above*, right ribs 1–8, seen from the posterior aspect, × ¼. *Below*, the heads of right and left ribs from the same mid-dorsal segment of a single individual, to show contrasts in post-mortem distortion, × ¼.

height also exceeds the width. The zygapophysial pairs have come to lie close to each other near the mid-line, and their articular surfaces have become sharply tilted to a plane close to the vertical. There is, further, a gradual reduction in height and stoutness of the neural spines, so that by the time the mid-caudals are reached, the spine is a low nubbin projecting a short distance above the postzygapophyses. The neural arch as a whole is much reduced, and in the most posterior part of the tail the material shows little evidence of any structure above the centra.

The first of the chevrons appears, in the CNHM specimen (No. 272), between the 3rd and 4th caudals; they continue back as far as vertebra 36, at least in one specimen. The first elements are stoutly built, with a length equal to two centra; as is normal, the length decreases posteriorly, although but slowly. In one specimen, as in pelycosaurs generally (and in *Casea*), there is, in the proximal elements, a basal intercentral component connecting the two arms of the chevron; but in the CNHM specimen not even the most proximal chevrons have a proper intercentrum, there being merely an enlargement of each of the two proximal ends of the chevron structure. Although both of the adjacent centra are bevelled for reception of a chevron, the centrum anterior to the chevron has the most obvious articulations; it bears ventrally a pair of well developed facets, each supported by a longitudinal ridge on the centrum. In the tail the bottom of the centrum shows a longitudinal depression, bounded on either side by these ridges.

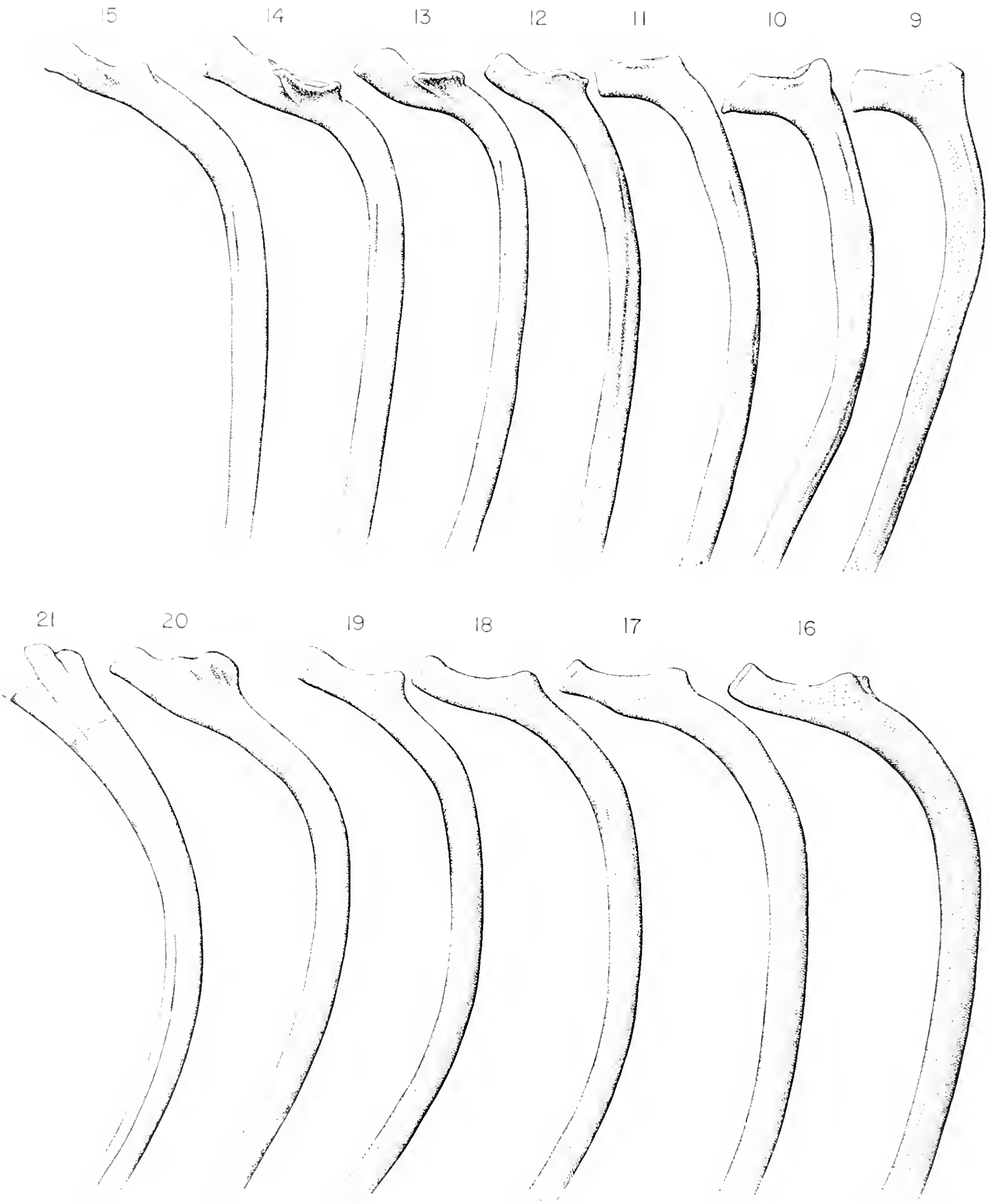


Fig. 5. The proximal part of right ribs 9–21, seen from the posterior aspect, × ¼.

RIBS

As in all known pelycosaurs, ribs were present on every vertebra from the atlas to and including the proximal caudals. For most parts of the series, specimens 4-0-6 and CNHM 272 furnish the best material.

Dorsal ribs (Fig. 5). In a typical dorsal rib the shaft extends outward (and in life somewhat upward) from the capitulum, the articular surface of which is an oval, narrow anteroposteriorly, occupying the entire head of the rib. The tuberculum in the mid-dorsals does not project to any marked degree from the shaft; it apposes to the transverse process a concave articular surface with an oval shape, broader distally, the length about twice the width.

The proximal end of the rib appears to run distally slightly upward to and past the tubercular region. Shortly beyond this point the rib curves markedly outward and downward to encase the flank. The degree of curvature in life is difficult to determine, due to variable post-mortem crushing and compression; see, for example, the marked contrast between the two members of a rib-pair from the same segment of a single individual shown in Figure 4. In most instances there is a considerable segment of the rib, lying beyond the point of proximal curvature, which is nearly straight; this includes about half the total rib length. This segment appears to have been directed diagonally outward and downward. Distally, beyond this straight section, the rib curves gradually inward toward the mid-line. Although seldom is a complete rib length preserved, it would appear that the greatest length of a rib (measured from the tuberculum) is about the length of 13 dorsal centra; two mid-dorsals of CNHM 272 measure 721 and 718 mm. In such dorsals as are completely preserved the distal end of the rib exhibits a cupped termination with which the cartilaginous section of the rib presumably articulated.

Despite the handicap noted as due to post-mortem distortion, articulation of ribs and vertebrae gives, on the average, a picture closely comparable to that given by Williston (1911: pl. XVII, fig. 1) for a *Casea* mid-dorsal, and shows the presence of a very broad, barrel-like trunk, with a probable transverse diameter of about 60 cm—i.e., about two feet.

Except for the rather flattened capitular region, typical dorsal ribs are essentially oval in section, and so tilted in life that the long axis of the oval slants downward and forward well over 45°, with the two major surfaces essentially anterior and posterior in position. The anterior margin is in all typical dorsals smoothly rounded. On the posterior surface a ridge develops at a point somewhat distal to the tuberculum and rather toward the ventral margin. This ridge extends outward along the straight lateral segment of the rib, gradually approaching the ventral margin of the rib and, decreasing in prominence, disappears at about the point where the median curvature begins.

There is little expansion of typical dorsal ribs at any region. The diameter of the rib is greatest a short distance distal to the tuberculum; beyond this region there is generally a very gradual decrease to a minimum of about two-thirds of the maximum.

Progressing anteriorly, from such a typical dorsal as that described, to rib 9, a series of gradual changes may be observed. The length decreases, rib 9 in 4-0-6, for example, being but 430 mm in length, i.e. about 60 per cent as long as the longest rib, and the ribs are more lightly built. In anterior dorsals, in contrast with mid-dorsals, the tuberculum projects markedly above the general outline of the dorsal rib margin, and, in contrast, the capitulum is sharply turned downward medially from the line of the shaft. There is here only a slight curvature beyond the tubercular region; when the rib is articulated with the vertebra, it is obvious that its shaft runs more directly downward than in the typical dorsals, indicating a narrowing of the body in the "chest" region, as the level of the shoulder girdle is approached. Distal to the straight descending portion of the shaft, there is a final segment curving somewhat inward. The total distance from the tuberculum to the beginning of the median curvature is little less than in rib 14, indicating that the "chest" is nearly as deep as the belly, although narrower.

The longitudinal ridge found on the posterior rib surface changes in position as one progresses forward. It has shifted upward, so that its proximal portion lies along the dorsal margin of the rib, and its distal end lies at about the middle of the posterior surface, rather than toward its ventral margin. It has, further, moved proximally, so that its proximal end has attained the distal margin of the tubercular projection, and its distal end extends only part-way down the vertical segment of the rib. Distally the anterior dorsal ribs remain sub-circular in section. Proximally, however, the posterior surface becomes much hollowed out, with the proximal part of the longitudinal ridge forming a very prominent projection dorsally. As far as can be determined in the usually crushed condition of the specimens, the most anterior dorsal ribs are somewhat expanded distally—notably rib 9 in 4-0-6.

Cervical ribs (Fig. 4). In the few previously known pelycosaurs in which the distal ends of the ribs have been well preserved, it appeared that rib 8 was stout distally and presumably had a sternal connection, establishing 7 as the probable number of non-sternal, i.e., cervical, ribs. In 4-0-6, however, rib 8, although elongate (with a length of about 360 mm) and resembling the dorsal rib following it in most regards, tapers to a point distally. It thus failed, obviously, to reach the sternum and must be considered technically to be a cervical.

In 4-0-6, remains of all the cervical ribs are present (but the third is poorly preserved). Although the rib-tips are incomplete, it is clear that all were slender and pointed distally. From rib 8 forward to rib 4 there is a sharp and steady diminution in length, and the preserved portions of the most anterior ribs indicate that these ribs were shorter still. In correlation with the wide separation of the two points of attachment to the vertebrae, tuberculum and capitulum are strongly divergent, giving a V-shape to the proximal part of the rib. The slender distal portions of the ribs appear to be somewhat compressed anteroposteriorly.

In the cervicals, as in the most anterior dorsals, the rib shaft runs straight distally from the tuberculum, indicating a narrow neck region; the tuberculum, as far as preserved in these ribs, retains the somewhat distinct character seen in the most anterior dorsals. On rib 8 the longitudinal ridge retains the character seen in the rib following for much of the proximal half of the shaft, forming a sharp dorsal margin of the rather thin rib, but it fails to reach the tuberculum. On rib 7, the ridge is present on the middle third of the shaft; on the more anterior ribs it has disappeared. It is in a sense replaced by a thin dorsal flange extending distally on rib 7 a short distance outward from the tuberculum, but not continuous distally with the typical dorsal ridge. This flange is present in reduced form on rib 6; more anteriorly, as far as can be seen from the material, no noticeable structures are present on the rib shafts. Ribs 6–8 appear to have lain beneath the scapula; these reduced flanges, presumably functioning for the origin of serratus musculature, contrast with the much greater flange development seen in many early tetrapods.

Posterior dorsal ribs (Fig. 6). Proceeding backward along the dorsal series, the posterior dorsal ribs as far as about rib 20 appear to be essentially similar to more anterior dorsals in character, and show little decrease in length; however, the proximal end of the longitudinal ridge described for the anterior dorsals retreats distally to a small extent in this region. Rib 20 becomes broader proximally; in the posterior ribs there is a gradual approximation of tubercular and capitular heads so that, from about rib 22 back, capitular and tubercular

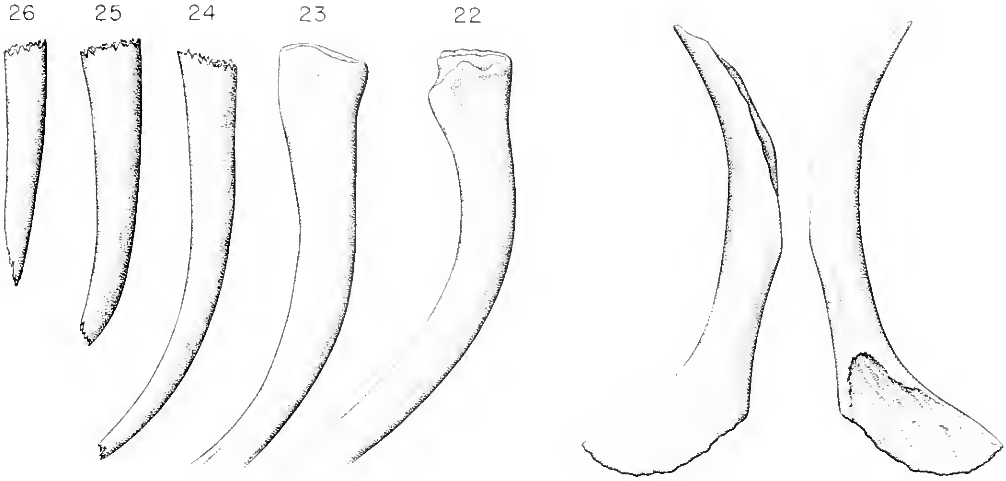


Fig. 6. *Left*, posterior presacral ribs of the right side, × ½. *Right*, left clavicle, external and internal views, × ¼.

areas are essentially fused into a single articular surface. A decrease in length of ribs is not marked until approximately rib 23, which is notably shorter than that preceding it (with a length in CNHM 272, as preserved, of 413 mm) and ribs 24–26 are increasingly short, the last being about 158 mm long in CNHM 272. As in pelycosaurs generally, the freedom of rib articulation with the vertebrae decreases posteriorly; the last 3 short ribs appear to be well fused and immovable and hence are to be considered as lumbars, and the next preceding may also have been immovable in life, although in 4-0-4 a suture between rib and vertebra was seen during preparation for the fourth presacral.

All the more posterior ribs tend to have shafts which are relatively broad and thin for most of their length; the last 5, however, definitely taper to a point distally, and thus lack a sternal connection, and the same may be true of rib 21. As far as segment 23 the ribs continue to be curved, turning downward and backward in life. Ribs 24–26, however, are nearly straight and directed laterally, their length being little more than that of the proximal nearly straight segment of rib 23. The breadth of the proximal part of the ribs increases posteriorly to a maximum in rib 24, which is very broad in proportion to its length.

Sacral ribs (Fig. 3). In correlation with the width of the trunk and pelvic region, the sacral ribs are longer than in sphenacodonts and ophiacodonts. Three sacral ribs are present. These are tightly fused to their vertebrae over a broad area; this includes the short transverse processes which arise from much of the lateral surface of the centra. No clear sutures are seen, but dorsally a rugose anteroposterior ridge marks the line of fusion of rib and transverse process. The rib head is deep dorsoventrally, as well as anteroposteriorly. Distinction between capitular and tubercular attachment is indicated by depressions on both anterior and posterior surfaces about half way down; these depressions have not been excavated, but may have been connected by a canal for the intervertebral artery.

The first sacral rib is short but stout. Beyond the head it contracts somewhat in width and extends outward horizontally and slightly posteriorly to terminate in a relatively thin expanded blade extending downward and apposed laterally to the inner face of the ilium. The second rib extends directly laterally; it is similar to the first but slightly less developed. The third rib

Fig. 7. *Left*, external, and *right*, internal views of the left scapulocoracoid. Broken lines on the internal view outline the portion preserved in No. 4-0-6. *Center*, dorsal, right lateral, and anterior views of the interclavicle. × 1/6.

is essentially accessory in nature; it is more slenderly built and curves forward to buttress the second rib as well as apposing the ilium with an only slightly expanded tip.

The first two sacral ribs are fairly comparable to those of *Casea*. In that genus, however, sacral rib 3 is well developed, and *Cotylorhynchus* here exhibits a condition which is less advanced. *Edaphosaurus* shows an intermediate condition in the development of sacral rib 3.

Caudal ribs. As in pelycosaurs generally, ribs are present in the proximal tail region. The first five show a fused attachment to transverse process and centrum with a pattern similar to that of the sacrals, although with a steadily diminishing attachment area; the heads are pierced anteroposteriorly by canals for the intervertebral artery. The first caudal is comparable to the third sacral in most regards, but it extends directly laterally, with a slight distal posterior curvature, to terminate in a pointed tip. Posterior to this, all the caudal ribs, as in pelycosaurs generally, continue to extend outward in a horizontal plane and to taper to distal extremities. In caudals 2–5 a backward curvature of the distal end is pronounced. These ribs show a steady decrease in length and stoutness. Rib 6 is notably shorter, with little development of a distal curved segment, and from this point back the caudal ribs, fused to the transverse processes, are laterally projecting, tapering, and pointed structures which decrease to small nubbins and disappear, except for low rugosities, beyond vertebra 11. In general the caudal ribs are comparable to those of *Casea*.

GIRDLES

Shoulder girdle. A nearly complete scapulocoracoid, as seen from the inner side, is present in 4-0-6, and the figure is based primarily on this specimen. The outer surface is not available in this specimen, but several others show this aspect. The scapular blade, incomplete in 4-0-6, is better preserved in other specimens; its exact height, however, is difficult to determine, due to the lack of distinctive features in this area. The blade in large specimens may have been somewhat more developed. In all available specimens the dorsal margin of the blade shows an unfinished surface, so that there may have been a considerable cartilaginous suprascapula. No sutures between the presumed three elements could be determined.

The scapulocoracoid (Fig. 7) is edaphosaurian in general character. It is short dorsoventrally, broad anteroposteriorly, with much the proportions of *Lupeosaurus* (*Casea*, presumably in relation to its smaller size, has a girdle of more slender build). The scapular blade is very short and broad, its breadth distally due to a backward flare of the posterior margin greater than is seen in any other pelycosaur. Below the point of clavicular attachment the margin of the scapula curves out widely anteriorly, to give great breadth to the lower part of the blade, as in *Edaphosaurus* and *Lupeosaurus*. In contrast to *Edaphosaurus* and *Lupeosaurus*, but in agreement with *Casea*, *Nitosaurus*, and *Mycterosaurus*, there is no supraglenoid foramen. There is, as in all pelycosaurs, a screw-shaped glenoid cavity; it is here, as in other edaphosaurians, remarkably deep anteriorly. Below its anterior end is the external opening of the supracoracoid foramen. Posteriorly, the coracoid region shows little development of a tubercle for origin of the coracoid head of the triceps. On the inner surface, the upper portion of the subcoracoscapular fossa is shallow, in correlation with the absence of a supraglenoid foramen.

No cleithrum is present in the available material. Much of the clavicles and the interclavicle are present in 4-0-6 and in the type (Figs. 6, 7). In contrast to *Edaphosaurus* and sphenacodonts, there is little ventral expansion of the clavicle (the clavicle of *Casea* is unknown). Its upper portion is well grooved posteriorly to clasp the anterior edge of the scapula. The blade of the interclavicle is unusually broad and short, and there is no development of the longitudinal ridge seen on the ventral surface of the shaft in most pelycosaurs. As preserved, the head turns sharply upward on the shaft, in contrast to the gentler curvature found in pelycosaurs generally, so that the surfaces apposed to the clavicles are essentially in a vertical plane. The head of the interclavicle is short and T-shaped, in contrast to the diamond-shaped head of many pelycosaurs, and is nearly completely occupied by the pair of crescent-shaped surfaces for the clavicles. These surfaces, which extend far laterally, are covered by rugose striations; the areas on the clavicles which meet them are similarly rugose, and set in distinctly below the general level of the "inner" surfaces of that bone. Obviously the contact between clavicles and interclavicle was an intimate one.

Pelvic girdle. Pelvic girdle material (Fig. 8) is relatively poorly represented. The *Cotylorhynchus* skeletons were nearly all buried with the dorsal surface upward; the ilia in consequence have been generally subject either to damage by crushing during entombment or to erosion prior to discovery, and this element is well preserved in only a few cases. The iliac blade is moderately high, as in sphenacodonts and other edaphosaurians, and in contrast to ophiacodonts, and agrees with other edaphosaurians in that (in contrast with sphenacodonts) there is little posterior elongation. There is a narrow but well-defined longitudinal area for muscle attachment at the top of the inner surface, above the areas for the sacral ribs. The first sacral appears to have been in contact with a depressed area at the anterior margin of the inner surface of the blade, the second presumably apposed to a flat area posterior to this; still farther posteriorly, a well-marked internal depression received the small distal end of the third sacral.

The acetabular region is of a typical pelycosaurian nature, with the usual primitive dorsal buttress. In most specimens sutures between the three pelvic elements are not clearly seen; in one specimen part of the sutures could be made out on the external surface, and in several instances lines of striae on the inner surface indicated the

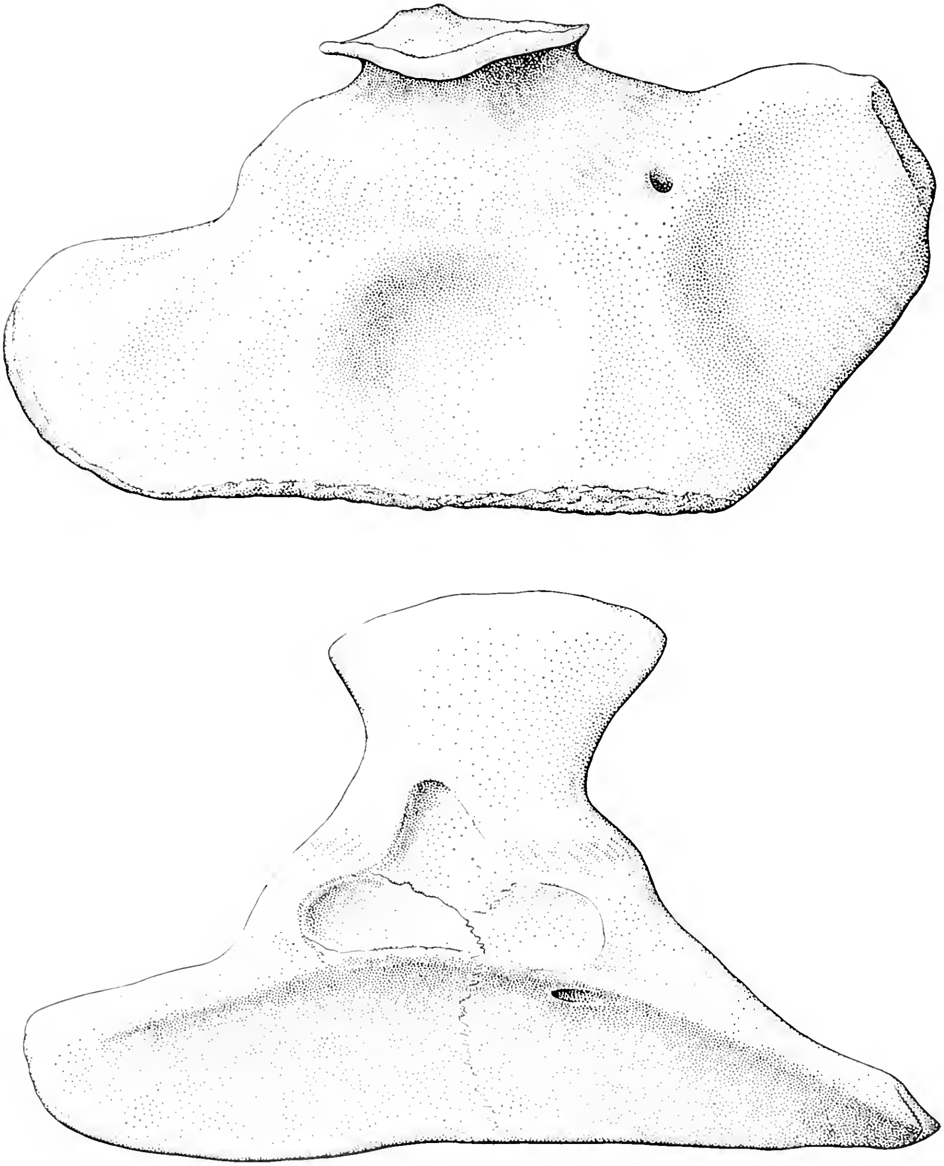


Fig. 8. Right pelvic girdle in dorsal and lateral views, × ⅓.

areas of fusion of ilium with pubis and ischium.

The puboischiadic plate is of very large size, with an anteroposterior length in 4-0-4, for example, of 380 mm, a depth below and internal to the base of the ilium of 112 mm and a breadth of the pubis, measured at right angles from the front end of the pubic symphysis, of 173 mm. There is but a slight indication in the material of the development of a pubic tubercle, such as is found in *Edaphosaurus*, *Nitosaurus*, and *Casea*. The great development of the puboischiadic plate is comparable to the type of structure seen in *Edaphosaurus* and *Casea*, and is associated with bodily breadth, present in the pelvic region as well as farther forward. The plate was strongly tilted outward at somewhat more than a 45° angle, so that it is not seen to any great degree in side view.

Internally, the puboischiadic plate exhibits, as in pelycosaurs generally, a gently hollowed out area, in which the bone is relatively thin, along the middle third of its length. Anterior and posterior to this, on pubis and ischium respectively, thickened bony areas—essentially supporting struts—descend from the iliac region to the symphysis. The presence of these thickened areas is reflected in the symphysis, which is thickened in both pubic and ischiadic regions, with a relatively thin intermediate zone. Anterior to the ridge descending the pubis is a very broad area of origin for puboischiofemoralis internus, which is but slightly turned outward from the general plane of the internal surface of the plate. Within this area is the usual internal opening of the obturator foramen which opens externally below the pubic portion of the acetabulum. There is a slight indication in certain specimens of a small area along the dorsal margin of the ischium for an ischiotrochantericus origin.

LIMB ELEMENTS

In almost all instances the limb elements have been crushed and flattened dorsoventrally, so that they are essentially two-dimensional—a situation making correct reconstruction difficult.

The major elements differ markedly from those of little *Casea*, and to a lesser extent from those of *Edaphosaurus* and *Lupeosaurus*, in the fact that they are very stoutly built. This is, of course, a feature associated with the large size and great weight of *Cotylorhynchus*. In most regards, however, they are not only typically pelycosaurian but show a number of distinctive edaphosauroid features. In few instances do we find all, or most, of the major limb elements present and well preserved in a single specimen. The pose was obviously that common to all pelycosaurs, with humerus and femur projecting nearly straight outward horizontally, and with the lower limb segment essentially vertical in position. Front and hind legs appear to be nearly equal in length, but with the humerus slightly shorter in overall length than the femur. In all pelycosaurs the lower limb is much shorter than the proximal segment, but this relative shortness is very marked in *Cotylorhynchus*. Here radius and tibia are only approximately 60 per cent as long as humerus and femur, respectively. In *Ophiacodon* the radius is about 77 per cent of the humeral length, the tibia about 83 per cent of the length of the femur; in *Dimetrodon* the comparable figures are 82 and 83 per cent. The *Cotylorhynchus* proportions, however, are comparable to those in other edaphosauroids; in *Edaphosaurus boanerges* we find figures of 62 and 57 per cent. Like other edaphosauroids, *Cotylorhynchus* was "low-slung."

Humerus (Fig. 9). The humerus is of the primitive tetrahedral type, although the shaft is stouter than in typical (and smaller) pelycosaurs. As figured, the "twist" of the ends on one another is extreme; this, however, appears to be due to crushing of the (none too well preserved) specimens upon which the drawing is based; specimen 4-0-3 shows the "twist" to have been one of approximately 90°. As is sphenacodonts and edaphosauroids generally, the proximal articular surface curves posteriorly well down onto the ventral surface of the head. In its very considerable proximo-distal breadth the entepicondyle is edaphosauroid. The entepicondylar foramen appears to have been unusually large.

The region of the ectepicondyle and the supinator process is imperfect in most specimens. In small specimens, such as University of Oklahoma specimens bearing the numbers 4-0-3 and 23–38, in which the distal end is well preserved, the supinator process is broad and close to the ectepicondyle but

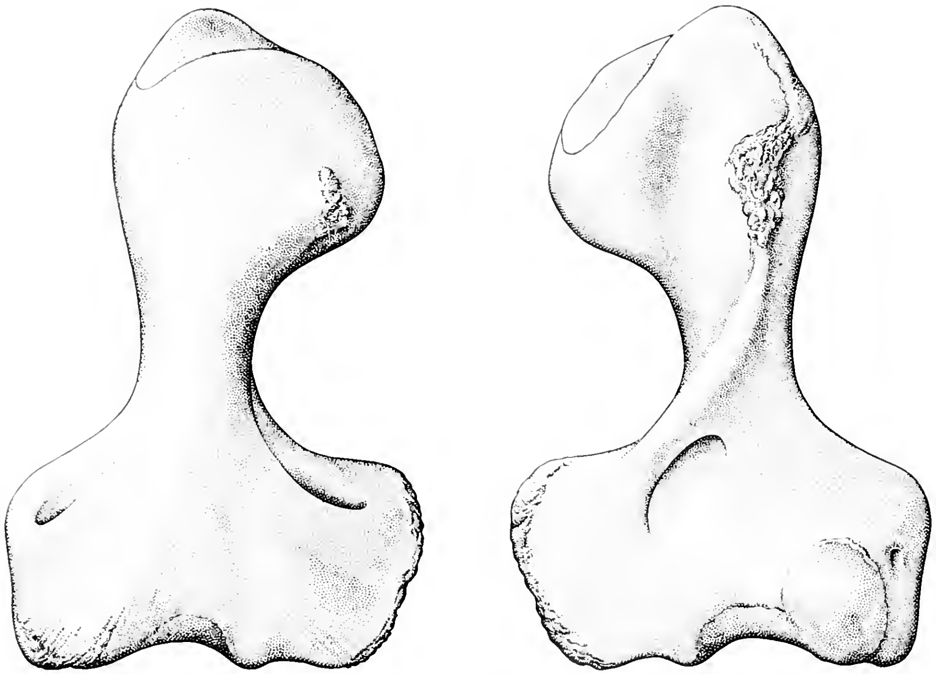


Fig. 9. Right humerus, viewed in dorsal and ventral aspects in the plane of the distal end, × 1/4.

separated from it by the notch typical of pelycosaurs. This separation, however, is obviously a growth stage only, for in 4-0-16 and a further University of Oklahoma specimen of uncertain number the notch is closed and an ectepicondylar foramen present. The foramen is otherwise found in pelycosaurs only in *Edaphosaurus*, and it is stated to be absent in *Casea*. In *Casea*, however, the gap between the tip of the supinator process and the ectepicondyle is small, and may well have been bridged in cartilage. It is obvious that the ectepicondylar foramen has developed more than once, in parallel fashion, in early reptiles; its presence here may perhaps be correlated with changes in limb mechanics and musculature, due to increased size, rather than attributed to inheritance from a basal edaphosauroid ancestor.

Radius (Fig. 10). The radius is preserved (although not too well preserved) in several instances. As noted above, it is short, with a length rather less than three-fifths that of the humerus. Although the effect is in all specimens accentuated by crushing, the bone was obviously relatively thin dorsoventrally, as in pelycosaurs generally. As in the case of other limb bones of *Cotylorhynchus*, the radius is broad in proportion to its length.

The proximal articular surface, where preserved, has the appearance of an oval, thin dorsoventrally; presumably it was subcircular in life. The dorsal (extensor) surface of the shaft is convex in section; the ventral surface apparently was flattened. A rugose area for ligament or muscle attachment is visible on the lateral edge of the dorsal surface just below the head of the bone. From the head the bone (when uncrushed) constricts to a somewhat thinner shaft. A short distance below the head, however, a ridge arises on the medial surface of the bone. Proximally it begins somewhat toward the ventral surface; it ex-

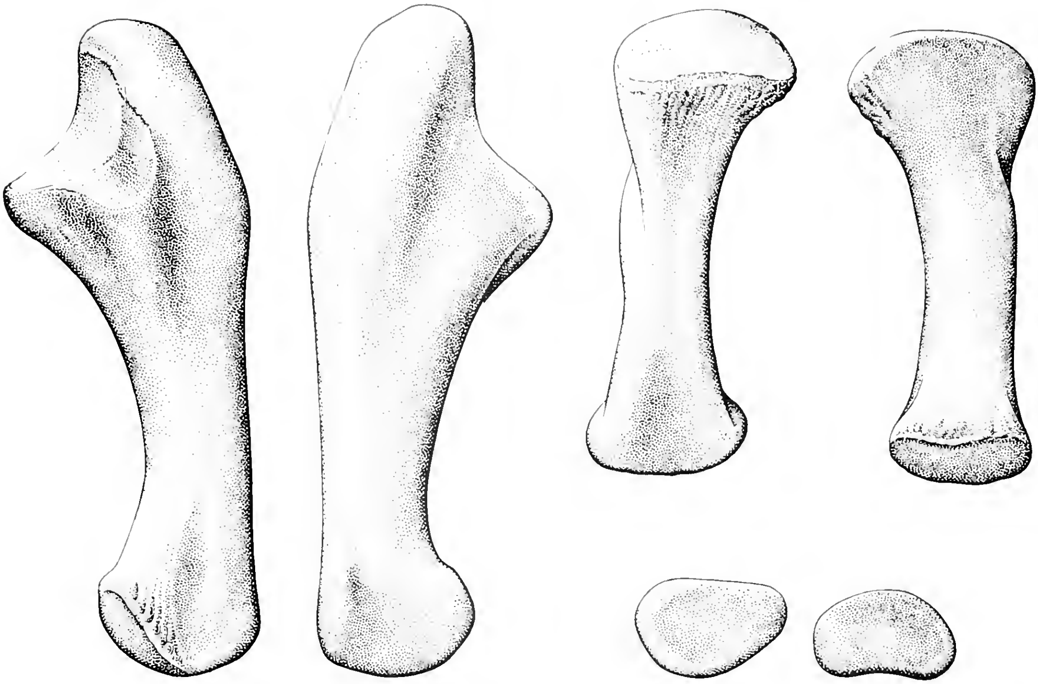


Fig. 10. *Left,* left ulna in extensor and flexor aspects. *Right,* comparable views of the radius. *Right, below,* proximal and distal surfaces of radius (dorsal aspect above). × 1/3.

pands, however, to attain the lateral margin and runs downward much of the length of the bone. Distally, the ridge is absorbed in a distal expansion of the bone leading toward the terminal articulation. As in pelycosaurs generally, the distal end of the bone is somewhat curved ventrally, so that the oval distal articular surface (for the radiale) faces somewhat ventrally as well as distally. The lateral margin of the shaft is also rather thin, but there is no development of a projecting ridge. Medioventrally there is an abrupt out-turning of the lateral margin above the articular surface.

Ulna (Fig. 10). The olecranon appears to have become well developed at a relatively early stage of growth, for it is nearly complete (although with a small unfinished terminal surface) in University of Oklahoma specimen N-7-37, a small specimen. As preserved, the head of the ulna is thin where seen, but this is presumably an effect due to crushing; very probably the head in life was as thick as in *Edaphosaurus.* As in the case of the radius, the bone is very short compared with the humerus. It is, further, exceedingly broad; the breadth of the distal end in one complete specimen measures about 40 per cent of the length of the bone as measured from the lower margin of the sigmoid notch; and the proximal width, across the notch, is about 50 per cent of the length. These figures are far in excess of those of other groups, in which the highest figures available to me are 29 per cent and 39 per cent for a specimen of *Ophiacodon.*

Femur (Fig. 11). The femur is typically edaphosaurian in nature, closely comparable in every major way to a well-preserved *Lupeosaurus* femur in the Harvard collection and likewise comparable, except for its stouter build, to the femora of *Casea* and *Edaphosaurus.* As in other edaphosaurs,

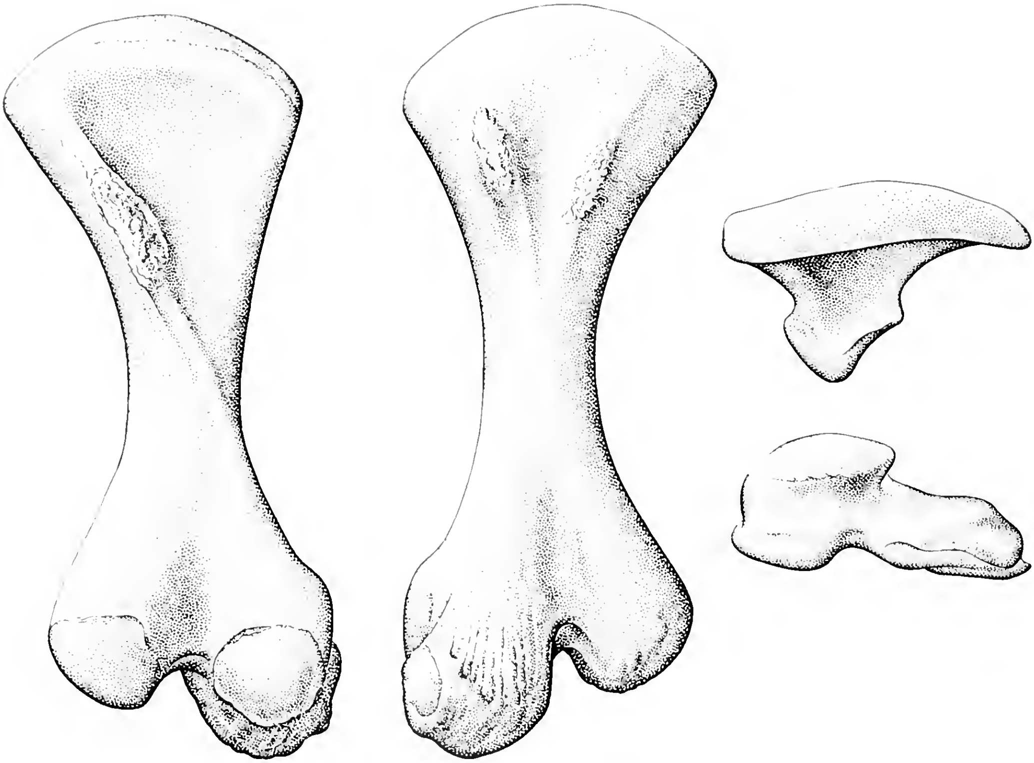


Fig. 11. Right femur, in ventral and dorsal views; at *right*, proximal and distal views (dorsal aspect above). × ⅓.

the curvature of the shaft characteristic of sphenacodonts is absent. Particularly characteristic is the ventral trochanteric system. There is a well-developed internal trochanter from which, in contrast to sphenacodonts and ophiacodonts, a ridge descends the under side of the shaft diagonally toward the external condyle. There is little indication of a distinct fourth trochanter along this ridge, and likewise little development of the posterior proximal branch of the Y-shaped ridge system, the intertrochanteric fossa thus being shallow posteriorly. In sphenacodonts, and to a lesser degree in some ophiacodonts, the proximal articular surface extends along the proximal portion of the posterior margin of the shaft; here, as in other edaphosaurs, this surface is confined to the proximal end of the bone. Proximally, on the dorsal surface of the shaft, there is sometimes seen, toward the posterior margin, a rugose area for muscle attachment. Unique is the presence at the anterior margin of a very distinct rugose ridge, about 25 mm long, likewise presumably for muscle attachment; this is clearly seen in two specimens. The external condyle, as in other edaphosauroids, projects very markedly beyond the internal (medial) one, and in a well developed specimen the tip of this condyle markedly overhangs the articular surface for the tibia below it, as it does in other edaphosauroid femora in which ossification is well advanced.

Tibia (Fig. 12). The tibia is, as noted earlier, relatively short, with a length only three-fifths or less that of the femur. As with other limb bones, the tibia is very broad, notably its head. The width of the head in one specimen is about 57 per cent

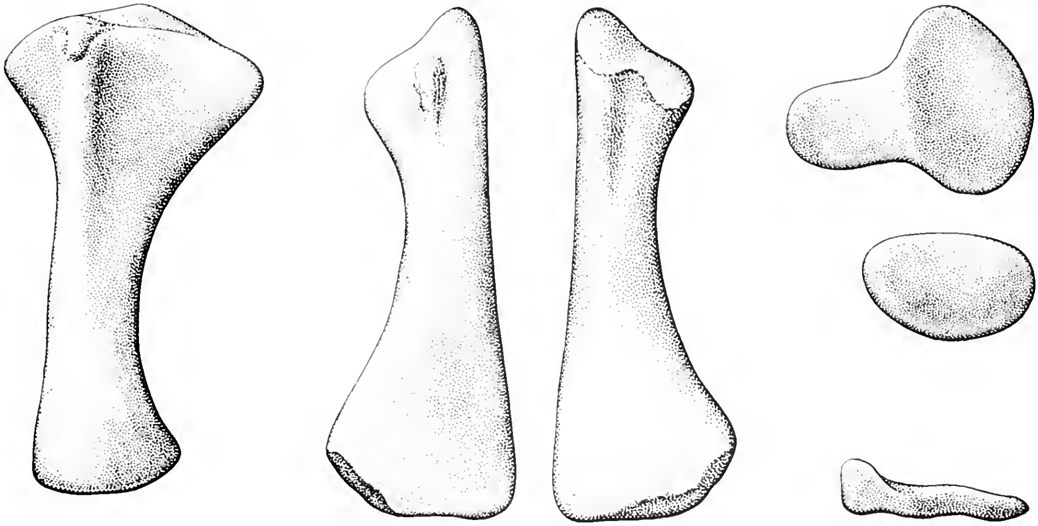


Fig. 12. *Left*, extensor aspect of right tibia; *center*, extensor and flexor aspects of right fibula; *right*, above, proximal and distal surfaces of tibia, and *below*, distal surface of fibula, extensor surface above. × 1/3.

the length of the bone, and the distal width nearly 33 per cent of the length. The closest approach to these proportions is in *Edaphosaurus*, in which these two figures approximate 50 per cent and 30 per cent. In all other known pelycosaurs the figures are much lower—*Dimetrodon limbatus*, for example, giving figures of 38 per cent and 22 per cent, *Ophiacodon* 37 per cent and 26 per cent. The two articular surfaces of the head are distinctly separated and set off from one another at a considerable angle. As in other ophiacodonts, the lateral femoral articular area is relatively narrow dorsoventrally. The cnemial crest is little developed. As in *Edaphosaurus*, and in contrast with most other non-edaphosaurian pelycosaurs, the distal articular surface curves strongly toward the lateral side of the bone.

Fibula (Fig. 12). As in the case of the tibia, the fibula is very short as compared with the femur, and is very broad distally. The mean breadth here in three specimens is 38 per cent of the length. This figure is comparable in *Edaphosaurus*, but pelycosaurs generally have a much slimmer fibula, with distal widths in *Dimetrodon* and *Ophiacodon*, for example, of 20 per cent and 29 per cent of the length.

FEET

Manus (Figs. 13, 14). As noted above, the specimens of *Cotylorhynchus* are not infrequently found in articulated fashion, and the feet are sometimes well preserved. We may note, for example, well preserved front feet in 4-0-1, 4-0-6 and 4-1-S2, hind feet in 4-0-10, 4-0-2 (1249), and both front and hind feet in the Chicago skeleton. Between the various specimens nearly all features of carpus, tarsus and digits are seen. As in the case of the major limb bones, the feet are broad and short, and thus differ considerably at first glance from those of most pelycosaurs. Study, however, shows that, apart from questions of proportions related to the size of the animals the feet are typically pelycosaurian and, despite the contrast in shape, resemble closely those of *Casea*.

The manus has the usual pelycosaur elements, including a pisiforme, two centralia and a series of five distal carpals. The

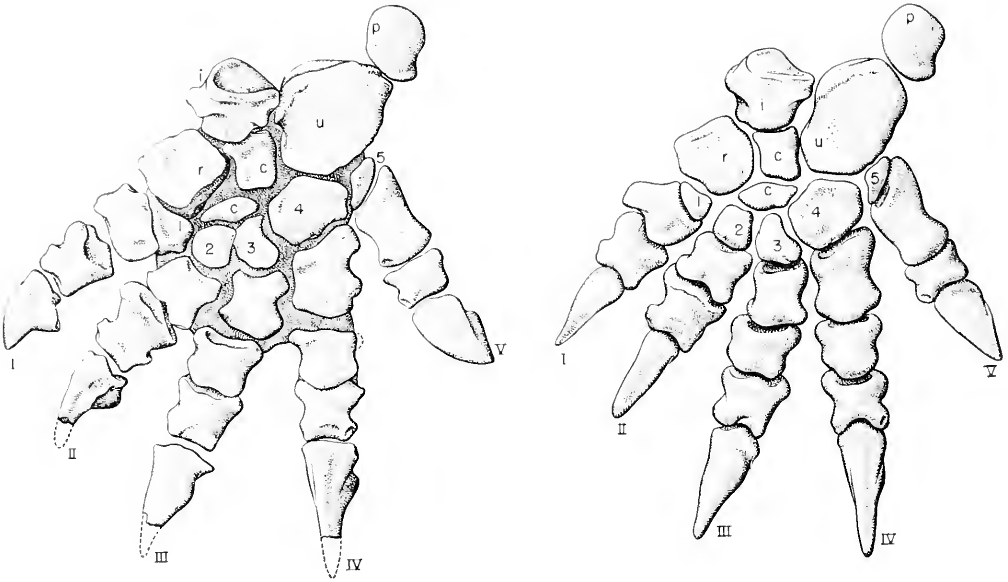


Fig. 13. *Left,* left manus of No. 4-0-6; *right,* restored left manus. × ¼. Abbreviations for Figs. 13–16: *a,* astragalus; *c,* centralia; *cal,* calcaneum; *F,* fibula; *i,* intermedium; *p,* pisiforme; *R,* radius; *r,* radiale; *T,* tibia; *U,* ulna; *u,* ulnare; 1–5, distal carpals or tarsals; *I–V,* digits.

radiale has a very deep, essentially square, proximal articular surface for the foot of the radius. The intermedium is short and broad, with well developed processes on both radial and ulnar sides at mid-height, and a broad proximal articular surface for the ulna. The ulnare is far shorter than in most pelycosaurs, but comparable in proportions to that of *Casea.* The proximal end is much less convex in outline than in most pelycosaurs; it forms a nearly continuous articular surface for the very broad ulna; this surface extends medially from a contact with the intermedium to a lateral facet for the pisiforme. This last element, as usual, is a thin plate. In 4-0-6 the bone is curved sharply toward the ventral surface at its outer margin; this may, however, be an effect of crushing. The medial or proximal centrale is again relatively short. The usual arterial gap is present between proximal centrale, intermedium and ulnare. The lateral centrale is not too well preserved; it is, as in pelycosaurs generally, a small element when viewed from the exterior surface, short proximodistally, broad mediolaterally. The articulated feet suggest that it was placed well in toward the center of the manus, with an unossified gap between radiale and distal carpal 1.

Distal carpal 1 appears to be essentially a simple rectangle in dorsal outline, short proximodistally but broad mediolaterally, covering the entire width of the head of metacarpal I. Element 2 is longer but less broad, its width less than the overall width of its metacarpal; its lateral border is straight, its proximal and medial borders a continuous curve. Element 3 is about as broad as 2, but longer proximodistally. As in pelycosaurs generally, 4 is by far the largest of the distal series, with a width double that of element 3 and a somewhat greater length proximodistally. Its proximal end has, as in pelycosaurs generally, two articular faces at somewhat of an angle to each other, a laterally tilted surface for apposition to the ulnare, a shorter medially tilted face for the proximal centrale. Distally the bone articulates broadly with the ex-

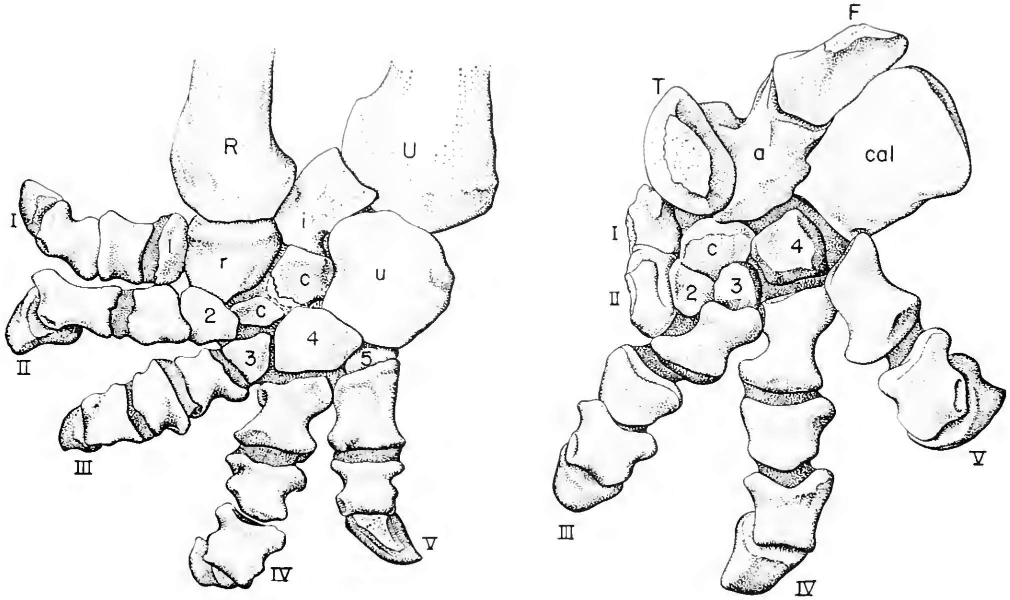


Fig. 14. *Left*, left manus of No. 4-1-S2; *right*, left pes of No. 4-0-10. × ⅓. Abbreviations as in Fig. 13.

panded head of metacarpal IV. Element 5 is narrow proximodistally but is expanded mediolaterally to meet the entire breadth of metacarpal V. Proximomedial and proximolateral surfaces meet element 4 and the ulnare, respectively.

In the metapodials (and in the phalanges) the shortness and breadth of the elements and the almost complete absence of a distinct shaft region give the foot a clumsy appearance. There is a steady increase in length from metacarpal I to metacarpal IV, and metacarpal V is, exceptionally, somewhat longer still. Metacarpal I appears to have a broad, flat head; in metacarpals II and III the proximal articular surface is a concave area not occupying the full width of the bone. In metacarpal IV the proximal articulation is a concavity, but a very broad one. In metacarpals II and III there is a pronounced expansion of the head toward the lateral side, and in IV this lateral extension is very pronounced. In metapodial V the proximal articulation does not appear to be cupped; it is tilted so that the outer margin is much more proximal than the medial.

The phalanges, like the metapodials, are short and massive in appearance. The nature and structure of the articulations of the elements is in general of a typically pelycosaurian type (Romer and Price, 1940: 167–169). From the massive build of the feet and the presumed herbivorous habits of the animal, one would expect the toes to terminate, like those of diadectids or pareiasaurs, in hoof-like structures. Instead, however, there are (as in *Casea*) long and powerful bony claw supports, suggesting that in life the animal did considerable digging for its food supply.

Pelycosaurs, in which good articulated feet are known, typically have a phalangeal formula in the manus of 2-3-4-5-3.[1] *Cotylorhynchus*, as is definitely proven by the material, has the surprisingly low formula of 2-2-3-3-2—even lower than in typical therapsids and rivalled for reduction among

---

[1] *Edaphosaurus*, formerly in doubt, is now known to have this formula also.

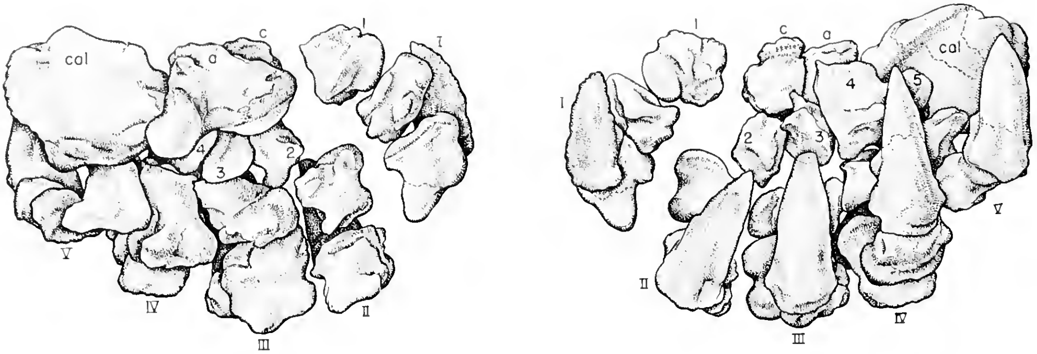


Fig. 15. Dorsal and ventral views of right pes of CNHM 272; the clawed toes are strongly flexed and bent under the tarsus. × 1/4. Abbreviations as in Fig. 13.

Paleozoic reptiles only by the pareiasaurs. In Williston's material of *Casea*, the manus was nearly complete but for the most part disarticulated. Williston, not expecting reduction, utilized the material available to give a manus with the typical reptilian formula (1911: fig. 13). To do this he was forced to assume that a number of elements were missing from the toes. However, new material described by Olson (1954) shows that the formula of the manus was 2-3-3-4-3—a definite reduction, although not as marked as in its giant relative. The series of elements present in Williston's specimen was, thus, actually nearly complete.

Pes (Figs. 14, 15, 16). Although the material of the hind foot is not as good as that of the manus, nearly all the structure can be clearly made out. There is a series of typical tarsal elements—astragalus and calcaneum proximally, and five distal tarsals; there is a lateral centrale, but whether a small medial centrale was present is uncertain. The proximal tarsal elements are relatively short, as compared with those of most other pelycosaurs except for the ophiacodonts; this presumably in relation to ponderous build. The astragalus appears to have had a relatively flat facet for the tibia. There is a typical arterial notch between artragalus and calcaneum.

As in the manus, the reduced phalangeal formula of 2-2-3-3-2 was present. Williston attempted to restore the foot of *Casea* with the primitive formula. But, as his description suggests, little of the material was actually articulated and it seems reasonable to believe that *Casea* had a reduced phalangeal formula in the pes similar to that in the manus; if so, Williston's foot material was nearly complete.

ABDOMINAL RIBS

In agreement, it would seem, with the fact that in the Edaphosauria generally the gastralia are little developed, no trace of abdominal ribs was discovered during preparation of the materials except in one instance. Here there were found numerous slender elements with tapering ends. The maximum length as preserved was 65 mm; the widths 3 to 5 mm. The material was not sufficient to determine their arrangement, although they were presumably arrayed in the usual series of V-shaped segments along the course of the abdomen.

RESTORATION

A lateral view of a restoration is shown in Figure 17, based on the series of larger specimens. The general appearance is comparable to that shown in restorations of its smaller relative, *Casea* (Williston, 1911: frontispiece; Romer and Price, 1940: fig. 71), except for the somewhat more massive build of *Cotylorhynchus* associated with its

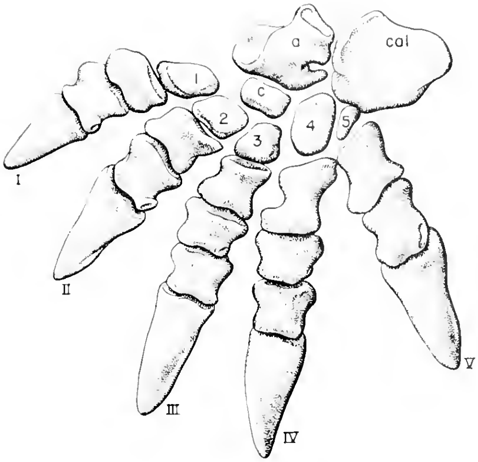


Fig. 16. Restored left pes, × 1/4. Abbreviations as in Fig. 13.

larger size, and the absurdly small size of the head. The lateral view does not, of course, give proper emphasis to the great breadth of the barrel-like trunk, commented on previously, and well shown in Williston's photograph of the mounted *Casea.* The build of *Cotylorhynchus* is in agreement with the portrait of a generalized edaphosaurian given by Romer and Price (1940: 377):

> "We find a tiny head armed with a powerful battery of blunt teeth, the trunk a large, broadly rounded barrel, the legs spread out broadly, but the lower segments so short that the belly cannot have been far clear of the ground. Such an animal was obviously not a carnivore, and, in the discussion of habits, we have already cited data supporting Williston's belief that these reptiles were herbivores. The enormous storage capacity of the abdomen further suggests that the food was probably of a bulky, watery nature, low in nutritive value, so that it was necessary for the animal to ingest large quantities. The curiously small head of the advanced edaphosaurs is matched among later plant-eating reptiles by the sauropods, whose food may have been of a comparable type."

Cotylorhynchus romeri exceeds in bulk any of the known pelycosaurs from the typical Texas Wichita and Clear Fork redbeds deposits, and is exceeded only by its presumed descendant, *C. hancocki* from the

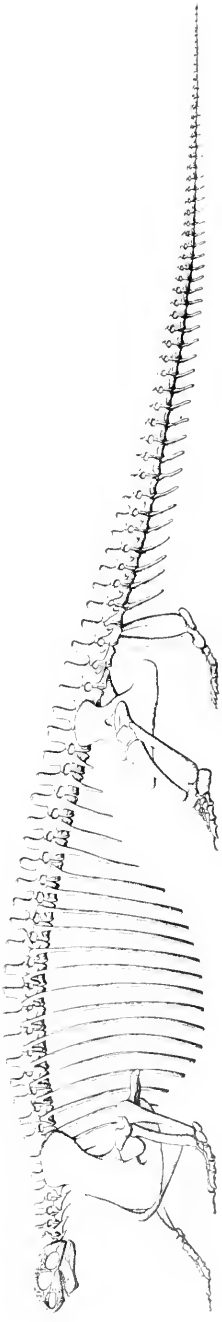


Fig. 17. Restoration of *Cotylorhynchus romeri*, 1/16 the size of a mature specimen.

San Angelo (Olson and Beerbower, 1953; Olson, 1962: 28–45). In the study of pelycosaurs generally, Romer (Romer and Price, 1940; Romer, 1948) used as an index to relative size—and weight—an "orthometric linear unit" based on the dimensions of dorsal vertebrae. At the time of publication of the "Review of the Pelycosauria" such information as was then available concerning *C. romeri* suggested that this unit was approximately 8.32, and this appears still to be a reasonable figure. Closest to *Cotylorhynchus romeri* among Wichita and Clear Fork pelycosaurs were the large terminal member of the *Ophiacodon* phylum, *O. major*, with an orthometric linear unit of 7.37, and the large terminal Clear Fork *Dimetrodon grandis*, at 7.61. Since the *Casea* unit is but 3.30, the average linear measurements of elements of *Cotylorhynchus* should be approximately two and one-half times that of *Casea*, and the weight more than 15 times as great. With an estimated weight of about 331 kg—roughly about one-third of a ton—*Cotylorhynchus* was the giant of its times.

RELATIONSHIPS

When *Casea* was first described it occupied an isolated position among pelycosaurs—so isolated, indeed, that Watson (1917: 173) suggested that it was not a pelycosaur at all. Possibly *Trichasaurus* (cf. Romer and Price, 1940: 422–423) is a relative, but until the discovery of *Cotylorhynchus* no further members of the family Caseidae were recognized. In recent years, however, Olson (1962: 24–47; and earlier papers) has added a number of new forms to the group from the middle and upper Clear Fork formations and the lower part of the Pease River group, including further species of *Casea* and *Cotylorhynchus*, and the new genera *Caseoides*, *Caseopsis*, and *Angelosaurus*; further, the caseids are now known to have ranged widely, for *Ennatosaurus* of the Russian Kazanian is clearly a caseid (as is possibly the poorly known *Phreatophasma*).

The caseids are the last major group of pelycosaurs to appear in the geological record. *Casea broilii*, the earliest acknowledged member of the family, only appears at about the Arroyo-Vale boundary in the Clear Fork group; other forms occur in the later Clear Fork formations and the roughly equivalent Hennessey of Oklahoma, or the still later Pease River group of Texas and the Russian Kazanian. Although some millions of years must be allowed for the development of caseid specializations, it is quite possible for the family to have evolved from some more generalized group during Wichita and early Clear Fork times. Until recently clues as to caseid ancestry were few. *Trichasaurus* of the Arroyo Formation and *Glaucosaurus* of the Clyde Formation of Texas were suggested by Romer and Price (1940: 421–423) as presumed edaphosauroids possibly related to the caseids. In the first-named genus the skull is unknown.[1] The second is represented only by a single small skull which is extremely short-faced and with an isodont dentition; this suggests possibilities of relationship to the caseid pedigree. As to a more remote ancestry, it was suggested by Romer (Romer, 1937; Romer and Price, 1940: 405–412) that *Mycterosaurus* and *Nitosaurus*, small early Permian pelycosaurs which seemed to be primitive in many ways but showed definite edaphosaurian characters in the postcranial skeleton, might represent the ancestral stock of the caseids and perhaps of the edaphosaurians as a whole.

In recent years several new finds have added somewhat to the picture. Vaughn (1958) has described as *Colobomycter* an imperfect skull from the Fort Sill quarry (an Arroyo equivalent in Oklahoma), and considers, reasonably, that its characters indicate that "it provides a good structural if not an actual ancestor for the family Caseidae." Fox (1962) has described as *Delo-*

---

[1] A toothplate provisionally referred to this genus (Romer and Price 1940: 423) is now known to pertain to the cotylosaur *Labidosaurikos*.

rhynchus three isolated maxillae from this same quarry; the bone itself is caseid-like, but the dentition is primitive and hence Fox classes it amongst the presumably ancestral Nitosauridae rather than placing it in the Caseidae. As noted by Langston (1965) there is little to distinguish *Delorhynchus* from its quarry-mate *Colobomycter*. Langston (1965) has recently described as *Oedaleops* a small pelycosaur from the New Mexican Permian represented by two skulls and other fragmentary material. As Langston points out, the *Oedaleops* skull is of a type quite surely expected in a caseid ancestor, but differs from proper members of that family in that, for example, the face is not as abbreviated and, most especially, the dentition is primitive; as proper for a primitive pelycosaur of any sort, the teeth are sharp-pointed and somewhat recurved and with a modest development of a maximum tooth size in the canine region, in one specimen, at least. As possibly attributable to *Oedaleops*, Langston describes a number of small postcranial elements found in the same quarry. Of these, the ilium, as Langston notes, is of a very primitive type, certainly not expected in a pre-caseid. Other elements, most notably the scapulocoracoid (lacking, significantly, the supraglenoid foramen), are comparable to those of *Nitosaurus* and caseids. They may well pertain to *Nitosaurus*.

Moreover, may not *Oedaleops* and *Nitosaurus*, contemporaries from the same region and horizon, be identical? Of *Oedaleops* we have no certain knowledge of postcranial material; of *Nitosaurus* we have no skull material except of maxilla. Langston briefly mentions this possibility but says that *Nitosaurus* "had longer jaws, a more slender dentary, considerably more teeth (subisodont in form) and a higher maxillary bone." But (1) we do not have a complete jaw in *Nitosaurus*; (2) the seeming slenderness of the *Nitosaurus* dentary is probably due to loss of the thin lower margin (cf. Romer and Price: fig. 70, and Langston: fig. 2a); (3) there is no evidence that *Nitosaurus* had more teeth than *Oedaleops*. In the latter genus the dentary is not known from associated material. In the two maxillae of *Oedaleops* found by Langston, the tooth counts appear to be 18 and 16; in the incomplete *Nitosaurus* maxilla 15 teeth and alveoli are present, and the total count was probably about 18. (4) There appears to be no significant difference in the height of the maxilla between *Oedaleops* and *Nitosaurus*—particularly if the obvious crushing undergone by the *Oedaleops* skull be taken into account.

The one possibly valid generic distinction lies in the greater isodonty of the maxillary dentition in *Oedaleops*. In the type there is a modest development of a "canine" pair at maxillary positions 2 and 3; in a second specimen the third tooth is large; in the *Nitosaurus* maxilla a maximum is not gained until we reach teeth 4 and 5. Considering the constant tooth replacement characteristic of reptiles and the consequent continual changes in the aspect of a dentition, this one feature seems hardly safe ground for generic distinction.[1]

Although the material of the genera discussed above is quite incomplete, in most instances, it appears that in this we have at least the beginnings of a phyletic series leading from such a primitive but edaphosauroid pelycosaur as *Mycterosaurus* upward toward the caseid condition. A complicating and confusing factor in the situation, however, was introduced by Watson (1954: 356) with his suggestion that *Eothyris* might be related to caseid ancestry. Both Vaughn and Langston have adopted this point of view, placing such forms as *Colobomycter* and *Oedaleops* in the Eothyrididae, and Langston goes to the extreme of excluding the Nitosauridae from any relationship to the Caseidae, despite the numerous and surely significant postcranial resemblances between the two.

The basic reason for considering *Eothyris*

---

[1] A subordinal distinction, actually, in Langston's chart, page 43.

as a possible relative of the caseids is, of course, the fact that *Eothyris*, like the caseids, is remarkably short-faced. This in itself is no more a valid reason for associating them than would be the association of the sphenacodont *Secodontosaurus* with the ophiacodont *Varanosaurus* because they are both extremely long-snouted. If the *Eothyris*-caseid relationship is to be substantiated, more positive reasons must be developed.

Langston (1965: 21) cites fourteen points in which *Oedaleops* and *Eothyris* are in partial or complete agreement. As he says, this seems to be, at first sight, an imposing list. Included, of course, is the fact that the face is short, not necessarily meaningful, and the fact, of no systematic value, that both are small. Correlated with small size, and hence likewise without other necessary significance, is the relatively large size of the orbits and of the pineal foramen. A number of other common features are such as are liable to be present in any relatively primitive pelycosaur, including: (1) relatively flat skull; (2) jaw articulation on a level with the toothrow, as in the Ophiacodontia, the primitive sphenacodont *Varanops*, and *Mycterosaurus*; (3) outward slope of cheek plates (contrasting with sphenacodonts); (4) a primitive long lacrimal; (5) normal relationship of roofing bones; (6) an unusually large supratemporal; (7) a long, tapering postorbital (as, for example, in the ophiacodont *Varanosaurus*, and the sphenacodont *Varanops*); (8) some indications in the tabular-supratemporal region of the otic notch of ancestral types; (9) a differentiated dentition, as in most pelycosaurs except *Edaphosaurus* and caseids.

The two genera, thus, are short-faced, small in size, and have both retained various primitive characters. Little remains of the original fourteen points which can be construed as positive indication of relationship. Langston cites "relative position of orbits and pineal opening," but there does not appear to be any unusual condition here in either case. With regard to "enlarged nares and obtuse rostrum," the nares in *Eothyris* do not appear to be any larger, proportionately, than in many other pelycosaurs, and the rostrum does not appear to be any more obtuse than in pelycosaurs generally. The *Eothyris* prefrontals are said to be "inflated" (i.e., somewhat expanded), but this does not seem significant.

There is thus little positive reason to associate *Eothyris* with caseid ancestry, and one very strong objection—the dentition. In all early pelycosaurs—indeed, in nearly all primitive tetrapods generally—there is a trend for the development of somewhat enlarged teeth near the front of the maxilla as an incipient "canine" region. In sphenacodonts and their therapsid descendants this trend is accentuated; in edaphosaurians—both *Edaphosaurus* and the caseids—there is an opposite trend toward isodonty. In such forms as *Oedaleops* there is but a mild, essentially primitive, development of a canine "maximum" such as might be expected in any relatively primitive pelycosaurs. In *Eothyris*, on the other hand, we find the greatest exaggeration of canine tusks to be found in any pelycosaur. In their dentition, *Eothyris* and the caseids have evolved in such diametrically opposite directions that it is difficult to believe that they are at all closely related.

But even if (as is not too probably the case) *Eothyris* should prove to be related to the caseids, it is dangerous to base hypotheses of broader relationships on the "family Eothyrididae," as has been done by Langston and, to a lesser degree, by Vaughn. As I have pointed out (Romer and Price, 1940: 247; Romer, 1956: 676), this family is a purely provisional one, set up to receive forms, presumably highly predaceous, which have marked canine development but are not members of the Sphenacodontia. Any unity the group might have is based on this dental feature—which is, of course, the one point in which all of them notably differ from the trend toward isodonty expected in caseid ancestors. There is no evidence that any form assigned to this family, other than *Eothyris*, was short-faced. Such postcranial material as can be associated with any of the genera included in this provisional family lacks any features indicative of caseid relationships, and such indications of systematic position as are shown by *Stereorhachis*, *Stereophallodon*, and *Baldwinonus* suggest the Ophiacodontia. With regard to *Eothyris*, the lack of postcranial data is a stumbling block.

On the assumption that the Ophiacodontia represent the basal stock of the Pelycosauria, it is a reasonable assumption that the caseids are of ultimate ophiacodontian derivation; but that any of the "eothyrids" are connecting links is very dubious.

Romer and Price (1940: 366–376) pointed out numerous skeletal features which *Edaphosaurus* and *Casea*, as two extremes, have in common, and advocated their being placed in a common suborder. There is, however, a seeming difficulty in assuming a common ancestry, because of chronological factors. The caseids seem quite surely to have specialized from primitive ancestors at a late date, for no form attributable to this stock is known earlier than fairly early Wichita times; on the other hand, *Edaphosaurus* had already evolved by the late Pennsylvanian. If both *Edaphosaurus* and the caseids evolved from essentially primitive edaphosaurians, such as the nitosaurs, this must have been, as Langston (1965: 58) notes, a very bradytelic group, and nitosaurs should have been in existence in the Pennsylvanian.

This appears to have been the case. It seems highly probable that *Petrolacosaurus*, from the Pennsylvanian Garnett shales of Kansas (Lane, 1945; Peabody, 1949, 1952), is a primitive edaphosauroid.

Lane, and Peabody at first, concluded that this small reptile was a pelycosaur. The latter author, however, impressed by cranial resemblances to *Prolacerta* (with which he was familiar), argued that *Petrolacosaurus* was an eosuchian—a primitive diapsid. There is no morphological proof, one way or another, of this suggestion. There was a lateral temporal opening, but the cheek is poorly preserved, and whether an additional upper opening was present cannot be determined. Apart from the possible but unproven diapsid nature of the temporal region, there is no reason to assign *Petrolacosaurus* to the Eosuchia. Peabody points out a number of common features of the skulls in *Petrolacosaurus* and *Prolacerta*, but these are essentially primitive characters which could have been inherited by both from captorhinomorph cotylosaurian ancestors. The time of appearance of *Petrolacosaurus* is one at which an eosuchian is hardly to be expected. There are no traces of any diapsid in the Lower Permian, and no sure evidence in the Middle Permian; the first certain diapsid is Upper Permian in age—a full period after *Petrolacosaurus*—and Watson (1957) has argued that diapsids were only then evolving from millerettid cotylosaur derivatives.

If, then, we abandon the possible but improbable suggestion that *Petrolacosaurus* was a precocious diapsid, all the features of this little reptile agree with the assumption that we are dealing with a pelycosaur, and several characters point strongly to the suggestion that it is a primitive edaphosaurian. The skull is primitive and generalized, as it is in such archaic ophiacodonts as *Clepsydrops* and *Varanosaurus*, such a sphenacodontian as *Varanops*, and such a nitosaurian as *Mycterosaurus*. Diagnostic features, however, can be found in the postcranial skeleton. (1) The postcervical vertebral centra are rounded ventrally as in ophiacodonts and edaphosaurs, in contrast to the keeled sphenacodonts. (2) In the carpus the ulnare is short, in contrast to advanced sphenacodonts and as in ophiacodonts and edaphosaurs (however, *Varanops* among the sphenacodonts also has a short ulnare). (3) In the tarsus there is a broad, highly developed, medial centrale forming the sole connection between astragalus and distal tarsals 1 and 2; edaphosaurs and sphenacodonts are similar, but ophiacodonts have two small centralia of subequal size in this position. (4) On the femur, the ventral system of trochanters and ridges is one found among pelycosaurs in edaphosaurs only (cf. Romer and Price, 1940: fig. 37). Distal to the internal trochanter an adductor crest slants diagonally across the bone towards the external trochanter. In sphenacodonts there is a pronounced fourth trochanter but no adductor crest; in ophiacodonts the crest descends the external margin of the bone. (5) Both Lane and Peabody ascribe to *Petrolacosaurus* a pelvis (University of Kansas no. 1425) which is very distinctively edaphosaurian. It is of a type strongly contrasting with that of any other reptilian group—most notably in the shovel-shaped iliac blade, tall but without a marked posterior projection. Were this pelvis definitely associated, *Petrolacosaurus* could be assigned to the Edaphosauria without hesitation. It was, however, found isolated, and since a specimen of *Edaphosaurus* has been found in the quarry, this pelvis may pertain to that genus. Several pelves with low, long ilia of ophiacodont type are also present in the material; but these, too, lack association, and may belong to an ophiacodont, also present in the Garnett material.

There are, thus, in the postcranial skeleton of *Petrolacosaurus* a number of features which strongly indicate that this genus belongs to a group of archaic edaphosaurians from which both *Edaphosaurus* and, at a much later time, the caseids may have arisen.

Preparation of material for this paper was aided by a grant (No. GB 500) from the National Science Foundation.

LITERATURE CITED

FOX, R. C. 1962. Two new pelycosaurs from the Lower Permian of Oklahoma. Univ. Kansas Publ. Mus. Nat. Hist., **12**: 297–307.

LANE, H. H. 1945. New mid-Pennsylvanian reptiles from Kansas. Trans. Kansas Acad. Sci., **47**: 381–396.

LANGSTON, W. 1965. *Oedaleops campi* (Reptilia: Pelycosauria). A new genus and species from the Lower Permian of New Mexico, and the family Eothyrididae. Bull. Texas Mem. Mus., **9**: 1–46.

OLSON, E. C. 1954. Fauna of the Vale and Choza. 7. Pelycosauria: family Caseidae. Fieldiana, Geology, **10**: 193–204.

———. 1962. Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R. Trans. Amer. Philos. Soc., (N.S.) **52** (part 2): 1–196.

OLSON, E. C. AND J. R. BEERBOWER, JR. 1953. The San Angelo Formation, Permian of Texas, and its vertebrates. Jour. Geol., **61**: 381–423.

PEABODY, F. E. 1949. Mid-Pennsylvanian pelycosaurs from Kansas. Bull. Geol. Soc. Amer., **60**: 1913.

———. 1952. *Petrolacosaurus kansensis* Lane, a Pennsylvanian reptile from Kansas. Univ. Kansas, Paleont. Contrib. Vertebrata, **1**: 1–41.

ROMER, A. S. 1937. New genera and species of pelycosaurian reptiles. Proc. New England Zool. Club, **16**: 89–96.

———. 1948. Relative growth in pelycosaurian reptiles. Robert Broom Commemorative Volume. Pp. 45–55.

———. 1956. Osteology of the reptiles. Chicago, Univ. Chicago Press, xxi + 772 pp.

ROMER, A. S. AND L. I. PRICE. 1940. Review of the Pelycosauria. Geol. Soc. Amer., Spec. Pap. No. **28**: 1–538.

SHULER, E. W. AND R. V. WITTER. 1942. The mounted skeleton of *Edaphosaurus boanerges* Romer at Southern Methodist University. Field and Laboratory, **10** (2): 140–144.

STOVALL, J. W. 1937. *Cotylorhynchus romeri*, a new genus and species of pelycosaurian reptile from Oklahoma. Amer. Jour. Sci., (5) **34**: 308–313.

VAUGHN, P. P. 1958. On a new pelycosaur from the Lower Permian of Oklahoma, and on the origin of the family Caseidae. Jour. Paleont., **32**: 981–991.

WATSON, D. M. S. 1913. The Beaufort Beds of the Karroo System of South Africa. Geol. Mag., (5) **10**: 388–393.

———. 1917. A sketch classification of the pre-Jurassic tetrapod vertebrates. Proc. Zool. Soc. London, 1917: 167–186.

———. 1954. On *Bolosaurus* and the origin and classification of reptiles. Bull. Mus. Comp. Zool., **111**: 295–449.

———. 1957. On *Millerosaurus* and the early history of the sauropsid reptiles. Philos. Trans. Roy. Soc. London, (B) **240**: 325–400.

WILLISTON, S. W. 1910. New Permian reptiles: rhachitomous vertebrae. Jour. Geol., **18**: 585–600.

———. 1911. American Permian vertebrates. Chicago, Univ. Chicago Press, 145 pp.

(*Received 27 September 1965.*)

Bulletin OF THE
Museum of
Comparative
Zoology

The Stromateoid Fishes: Systematics and a Classification

RICHARD L. HAEDRICH

Museum of Comparative Zoology, Cambridge, Massachusetts
Istituto di Biologia Generale, Università di Pisa, Italy

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 135, NUMBER 2
JANUARY 27, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office

Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

THE STROMATEOID FISHES: SYSTEMATICS AND A CLASSIFICATION[1]

RICHARD L. HAEDRICH[2]

TABLE OF CONTENTS

HISTORICAL INTRODUCTION

The Stromateoidei are a small suborder of the perciform fishes, characterized primarily by toothed saccular outgrowths in the gullet immediately behind the last gill arch. The stromateoids are all marine, pelagic, and widely distributed in the temperate and tropical oceans of the world. Most species are rare and infrequently seen, but a few form the basis of fisheries. Adult stromateoids range from less than a foot to over four feet in length.

Certain stromateoids were recognized in classical times. *Stromateus* was the name applied by the Greeks of Egypt to a fish probably from the Red Sea. The name, derived from the word for a brightly colored rug, may have referred to the fish's shape and coloration. Later, however, Rondelet (1554) used the name for a similar Mediterranean fish known in the contemporary Roman vernacular as *fiatola*. Linnaeus (1758) described the same fish as *Stromateus fiatola*.

The oceanic fish *pompilus* was sacred to the Greeks. As *pompilus* accompanied ships, it brought a calm sea (Gesner, 1560). *Pompilus* has been equated with *Centrolophus* (Günther, 1860), and Gesner's figure (1560:113) certainly is of this fish. Thompson (1947), however, presents evidence that *pompilus* is the pilot fish *Naucrates*. Cuvier

---

[1] This paper is based on a thesis presented to Harvard University in partial fulfillment of the requirements for the Ph.D. in Biology. Contribution No. 1685 from the Woods Hole Oceanographic Institution.

[2] Woods Hole Oceanographic Institution, and Museum of Comparative Zoology, Harvard University.

Bull. Mus. Comp. Zool., 135(2): 31–139, January, 1967

and Valenciennes (1833), citing Cetti's "Historia Naturale di Sardagni" (1777), suggested that *pompilus* might be a tuna. And while the subject of Ovid's heroic lines

> "Tuque comes ratium, tractique per aequora sulci
> Qui semper spumas sequeris, pompile, nitentes"

could well have been the centrolophid *Schedophilus ovalis*, it seems more likely that the poet is referring to *Coryphaena*, the dolphin. The classical name has been used in *Coryphaena pompilus* Linnaeus, 1758, an unrecognizable fish; in *Pompilus* Lowe, 1839, a synonym of *Centrolophus* Lacépède, 1803; and in *Pompilus* Minding, 1832, a synonym of *Naucrates* Rafinesque, 1810.

Identical figures of stromateoids were published by the Renaissance compilers Belon (1553), Rondelet (1554), Gesner (1560), and Aldrovandi (1613). Illustrations of clearly recognizable species appear in these works on the facing page with impossible monsters. Nonetheless, the information gathered by these men was to prove very useful to later authors, and was considered authoritative by many. Some of their work, for example, can be found almost word for word in Cuvier and Valenciennes (1833).

John Ray's studies (Willughby, 1686) are marked by their care and attention to detail. His anatomical work revealed for the first time the structure most characteristic of the stromateoid fishes, the peculiar pharyngeal sacs. Ray mistakenly believed that the sacs constituted a second stomach. Nonetheless, care that was not to reappear for several centuries is apparent in his description of the sacs of *Stromateus* (p. 156):

> "In palato duo oblonga ossicula aspera . . . Nam primo duos habet ventriculos; primum retro cor, prope ipsum os situm, quem echinum nun ab re dixeris: carnosus enim est, & apophysibus longis, asperis, crebris, pellis erinacei fere in modum intus consitur. (Appendices hae in sex radios divaricantur cylindriae supra centrum stellae erectae. D. Will.)"

During the first half of the nineteenth century a majority of the stromateoids were described and characterized reasonably well. The "Règne Animal" (Cuvier, 1817) and "Histoire Naturelle des Poissons" (Cuvier and Valenciennes, 1833) were especially valuable. Cuvier (1817) provided the basic arrangement which was expanded upon in the later "Histoire Naturelle."

Cuvier and Valenciennes (1833:381) added to Ray's description of the pharyngeal sacs of *Stromateus fiatola*:

> "A l'extérieur, cette partie présente la forme d'une bourse; les épines dont elle est armée sont de différent grosseur; les plus grandes sont un peu en forme fuseau; les petites garnissent les intervalles des grandes. Chacune de ces épines s'attache à la veloutée par sept ou huit ravines ou fibres disposées en étoile."

They continue later with their own observations on the sacs of *Stromateus candidus* (= *Pampus argenteus*) (p. 392):

> "Immédiatement après les os pharyngiens vient un oesophage en forme de sac ranflé et charnu, rond, un peu bilobé . . . garnies . . . de grosses épines osseuses . . ."

and of *Rhombus xanthurus* (= *Peprilus paru*) (p. 406):

> ". . . un oesophage charnu, armé intérieurement de dents osseuses coniques, les unes plus grandes, les autres plus petites . . ."

Cuvier and Valenciennes not only recognized this unique structure in "les Stromatées" but also described a similar structure in "les Centrolophes." Concerning *Centrolophus pompilus* (= *C. niger*) they wrote (p. 339):

> "Le pharynx du centrolophe présente une particularité remarquable, qui donne au commencement de leur oesophage un armure puissante. Entre les os pharyngiens . . . l'os supérieur du quatrième arceau porte plusiers appendices alongés et garnis de dents semblables . . . la partie latérale du pharynx a de profondes cannelures osseuses et dentées . . ."

They continue, observing that this seems to be:

> ". . . quelque analogie avec les épines dont le même cavité est armée dans les stromatées."

Here, for the first time, a relationship between the centrolophids and the stromateids was indicated.

Günther recognized a unifying character here and, in his Catalogue (1860:355), noted that in the Stromateina "tooth-like processes extend into the oesophagus." The "Catalogue" provided keys to the scombrid group Stromateina and to the two genera Günther included in it, *Stromateus* ("ventrals none in an adult state") and *Centrolophus* ("ventrals well developed"). The other groups in his family Scombridae were the Scombrina, Cyttina, Coryphaenina, and Nomeina, the last composed largely of stromateoids. The diagnostic pharyngeal sacs of the Nomeina remained to be discovered, for they were not mentioned in Günther's account.

Discussing the limits and arrangement of the scombroids, Gill (1862) corrected some of Günther's omissions. In doing so, however, he broke up the convenient group Nomeina, and added little to the classification. The Stromateina, though mentioned, were not defined.

"An Introduction to the Study of Fishes" (Günther, 1880) was essentially the same as the earlier "Catalogue" in its treatment of the stromateoids. Here, however, each group was given full family status as Stromateidae and Nomeidae. The close relationship of the two was still not indicated, and Günther continued to allocate a number of stromateoid genera to other families.

Although Günther's (1880) publication added almost nothing to the classification, it had an important incidental effect. Whether the cause was Günther's failure to have noticed Gill's earlier (1862) paper or whether it was his casual accounting cannot be said. At any rate, Günther's treatment of the stromateoids soon occasioned a vitriolic blast from Gill. In his "Notes on the Stromateidae," Gill (1884) united the forms scattered by Günther under the single family Stromateidae, still omitting *Nomeus* but including, albeit reservedly, *Psenes* and *Cubiceps*. The definition of the family noted "the gill-rakers of the upper segment of the last branchial arch enlarged and dentigerous or sacciform, and projecting backwards into the oesophagus" (p. 665). Gill furthermore recognized a basic dichotomy in the group by dividing the family into two subfamilies, the Stromateinae and the Centrolophinae:

> "These are distinguished by differences in the development of the vertebrae, the former [Stromateinae] having 14–15 abdominal and 17–21 caudal vertebrae, and the latter [Centrolophinae] 11 abdominal and 14 caudal vertebrae; these differences are supplemented by variations in the degree of complexity of the peculiar appendages representing and homologous with the gill-rakers of ordinary fishes, developed from the last branchial arch, and extending into the oesophagus (p. 654)."

He also observed that the Centrolophinae have normally persistent pelvic fins, while those of the Stromateinae are lost with growth. Gill considered the Centrolophinae to be the most generalized type; the Stromateinae he thought more specialized.

"Spolia Atlantica" of Lütken (1880) contained accounts of the genera *Psenes*, *Cubiceps*, *Stromateus*, and *Schedophilus*. The discussion of relationships was carefully done, and the listing of included species was especially good. Unfortunately, the work was in Danish, and has apparently been little used by subsequent investigators.

Fordice (1884) reviewed the American species of the Stromateidae. No mention was made of the pharyngeal sacs. Only two genera, *Stromateus* and *Leirus* (= *Schedophilus*) were mentioned, and, again, the division was based on the presence or absence of pelvic fins. Fordice provided keys and neat synonymies of most American stromateids. His paper was essentially an extension of the foundation laid down by Jordan and Gilbert's (1882) "Synopsis of the Fishes of North America," a work which erroneously reported (p. 448) for the Nomeidae, "No tooth-like processes in the oesophagus."

Relying heavily on the work of Gill, Jordan and Gilbert, and Fordice, Jordan and Evermann's (1896) "Fishes of North and Middle America" provided a synthesis of current thoughts on stromateoid classification. The Centrolophidae were considered a family apart from the Stromateidae, "differing in appearance and in the smaller number of vertebrae, although agreeing in the possession of teeth in the oesophagus" (p. 964). *Nomeus* and *Psenes*, in the family Nomeidae, remained distinct, and no mention of a relationship with the stromateids was made.

"Oceanic Ichthyology" (Goode and Bean, 1896) drew on Jordan and Gilbert, Gill, and Günther, for much of its information. An unexplained but correct innovation was the inclusion of *Icichthys* among the stromateoids. The treatment of the group was extremely casual; genera were shuffled into families more or less randomly without checking familial characters. The Nomeidae constituted almost the same unnatural group as set up by Günther (1860), with still no realization of its relationships. Goode and Bean's account confused, rather than improved, the stromateoid classification. Fortunately, it has been disregarded by most subsequent workers.

The first, and the only, world-wide revision of the stromateoids was that of Regan (1902). Regan gave the group its modern dimensions by adding the genera "*Nomeus*, *Cubiceps*, *Psenes*, *Bathyseriola*, and *Seriolella*, all of which have a toothed oesophagus exactly similar to that of a *Centrolophus*" (p. 117). His definition of the family was based largely on osteology, and made important contributions. His warnings of the pitfalls of allometry and of the unusual ubiquity of certain characters recognized a recurrent problem. Regan treated the group as one family, the Stromateidae, but disregarded the convenient subfamilial distinction made earlier by Gill (1884). Norman's much later "Draft Synopsis" (1957) differs from Regan only in this one respect, for Norman recognized two families based on the first couplet of Regan's key to genera, "ventral fins present" [Centrolophidae], or "ventral fins absent" [Stromateidae]. Citing correspondence with Boulenger, Regan suggested, for the first time, the affiliation of *Tetragonurus* to the stromateoids.

Boulenger was much impressed by one of Regan's diagnostic characters, the loose attachment of the pelvic bones to the pectoral arch in all stromateids. In his systematic account of the fishes for the "Cambridge Natural History" (1904), he removed the stromateids from the scombroids, where all previous workers had placed them, and ranked them among the Percesoces. Holt and Byrne (1903), using the same argument, also considered the stromateids to be allied with the Percesoces. Although in error with respect to the relationships of the group, their account of local British and Irish species was otherwise carefully done, and showed broad understanding.

Although the presence of teeth in saccular outgrowths in the gullet had long been used as a diagnostic character for the stromateoids, no one since John Ray had investigated the structure of this peculiar feature. Gilchrist (1922) examined teeth from the sacs of several South African stromateoids. He noted differences between species, but, although he recognized the value of the teeth in taxonomy, he did not indulge in systematic speculations. The sacs had previously been referred to as "oesophageal"; Gilchrist pointed out that they were "not strictly oesophageal, but . . . derived from . . . pharyngeal epithelium . . ." (p. 254). Later, in an incisive review, Barnard (1948) corrected some of Gilchrist's errors, and extended his work by examining more species and publishing more illustrations.

Bühler's (1930) monograph on the digestive system of the stromateoids pointed out, independently from Gilchrist, the pharyngeal origin of the toothed sacs. Bühler proposed the term "Rachensäche" [= pharyngeal sacs] to replace the misleading "oesophageal sacs" commonly in use. His work was done primarily with serial microscopic sections, allowing examination and description of great detail. It was a substantial contribution to understanding the origin, nature, and probable function of the teeth in the pharyngeal sacs. For details on any morphological aspect of the pharyngeal sacs, Bühler's work, or the recent detailed extension of this by Isokawa *et al.* (1965), should be consulted. Other parts of the digestive system were noted to change in rough correspondence with changes in the Rachensäche, and within Regan's (1902) framework Bühler proposed two subfamilies, the Lirinae, corresponding to Norman's (*vide supra*) Centrolophidae, and the Stromateinae, corresponding to Norman's Stromateidae.

The work of Gilchrist, Barnard, and Bühler offered sound characters for the stromateoid classification. But, because each study dealt with only a limited array of characters, the observations could not be properly or safely interpreted.

My work has dealt primarily with skeletal characters. I have looked at the soft anatomy only cursorily, and have found little of use except in a most general way. The study has involved only Recent fishes.

My conclusions are largely based on the presence or absence of pelvic fins, whether the dorsal fin is separated or continuous, the presence or absence of certain teeth, the number of vertebrae, the number of branchiostegal rays, and, in particular, the structure of the caudal region and the development of the papillae[1] in the pharyngeal sacs. The comparative morphology of these characters not only provides a reasonable separation of the suborder into five families, but also, because the characters change in a correlated fashion, it suggests the course of evolution in the stromateoids. In the trunk and caudal region the number of vertebrae increases, while the elements in the tail become fused and reduced, and the pelvic fins are lost. In the branchial region, the number of branchiostegals decreases, while the papillae of the pharyngeal sacs become increasingly more complex. The present geographical distributions of the different taxa support the conclusions based on anatomical evidence.

I propose for the stromateoids a hierarchy of five families and fourteen genera, as follows:

- Order Perciformes
- Suborder Stromateoidei
  - Family Centrolophidae
    - *Hyperoglyphe*
    - *Schedophilus*
    - *Centrolophus*
    - *Icichthys*
    - *Seriolella*
    - *Psenopsis*
  - Family Nomeidae
    - *Cubiceps*
    - *Nomeus*
    - *Psenes*
  - Family Ariommidae
    - *Ariomma*
  - Family Tetragonuridae
    - *Tetragonurus*
  - Family Stromateidae
    - *Stromateus*
    - *Peprilus*
    - *Pampus*

METHODS

Measurements were made point-to-point with a pair of fine-point dial calipers. A dissecting microscope with an eyepiece dial micrometer was used for a few very small specimens. Measurements routinely made were:

TOTAL LENGTH (TL), from the tip of the snout to the farthest tip of the caudal fin.

STANDARD LENGTH (SL), from the tip of the snout to the caudal fin base.

LENGTH OF HEAD, from the tip of the snout to the hindmost point on the opercular membrane, usually immediately above the pectoral fin.

LENGTH OF PECTORAL FIN, from the base of the uppermost ray to the farthest tip of the fin.

---

[1] This term implies the unit composed of a bony base with teeth seated upon it. It is adopted here in conformance with past usage (Bühler, 1930; Barnard, 1948).

Length of pelvic fin, from the base of the most anterior ray to the farthest tip of the fin.

Longest D_1 spine, from the base of the spine to its extremity.

Predorsal distance, from the tip of the snout to the base of the first element of the dorsal fin.

Preanal distance, from the tip of the snout to the base of the first element of the anal fin.

Maximum depth, the greatest depth of the body, exclusive of fleshy or scaly fin bases.

Depth of peduncle, the least depth of the caudal peduncle.

Snout, from the tip of the snout to the anterior margin of the orbit.

Eye diameter, the greatest distance between the fleshy margins of the eye.

Length upper jaw, from the symphysis of the premaxillaries to the hindmost point, often covered by the lacrimal bone, on the maxillary.

Interorbital width, the least distance between the bony rims over the eyes.

The measurements used for showing allometry were length of head, length of pectoral fin, length of pelvic fin, predorsal distance, preanal distance, and maximum depth. These were expressed as a percentage of standard length. This percentage was plotted against standard length following the method advocated by Parr (1956). The measurements of snout, eye diameter, length of upper jaw, and interorbital width were expressed as a percentage of length of head.

Counts were made with a fine needle, usually under low magnification on a dissecting microscope. For extremely small specimens, median finray counts were made more easily using transmitted, polarized light. Counts routinely made were:

D, total dorsal fin elements, spines indicated by Roman numerals, rays by Arabic. In some cases it was impossible to distinguish between spines and rays; these counts are followed by the expression "total elements." The last, double ray of both dorsal and anal fins was counted as one element.

A, total anal fin elements.

P, total pectoral fin elements, one side, spine not distinguished from rays.

Gill rakers, the total number of rakers on the first arch, one side. Expressed as number on upper limb plus one, if at angle, plus number on lower limb (e.g. 8 + 1 + 17).

Lateral line scales, the number of scales along the position normally occupied by the lateral line, one side, terminating at the caudal fin base. In many stromateoids the tubed scales end on the peduncle, but the count was nonetheless continued to the caudal base. Often the deciduous scales are lost and scale pockets must be counted. Lateral line scales is a difficult count and cannot be made on most specimens.

Counts less routinely made were:

Branchiostegal rays (BR), left side.

Vertebrae, number of precaudal vertebrae plus the number of caudal vertebrae, including the hypural plate (= 1). Almost all vertebral counts were made from radiographs. Determination of the first caudal vertebra is hence somewhat subjective. Where skeletal material has been used, the count is followed by the expression "skel."

All measurements and counts conform with the standards of Hubbs and Lagler (1958).

The osteology was studied primarily with radiographs and cleared-and-stained preparations. With the use of soft X-rays, specimens as small as 20 mm SL could be successfully radiographed.

Small fishes, usually no longer than 65 mm TL, were cleared and stained. Gill arches and the associated pharyngeal sacs were dissected from larger fish, usually around 190 mm TL, and were also cleared and stained. To remove the arches and sacs, cuts were made between the hyal and opercular series, the tongue and dentaries, and the last gill arch and pectoral girdle. The unit so freed was carefully disconnected from the base of the neurocranium,

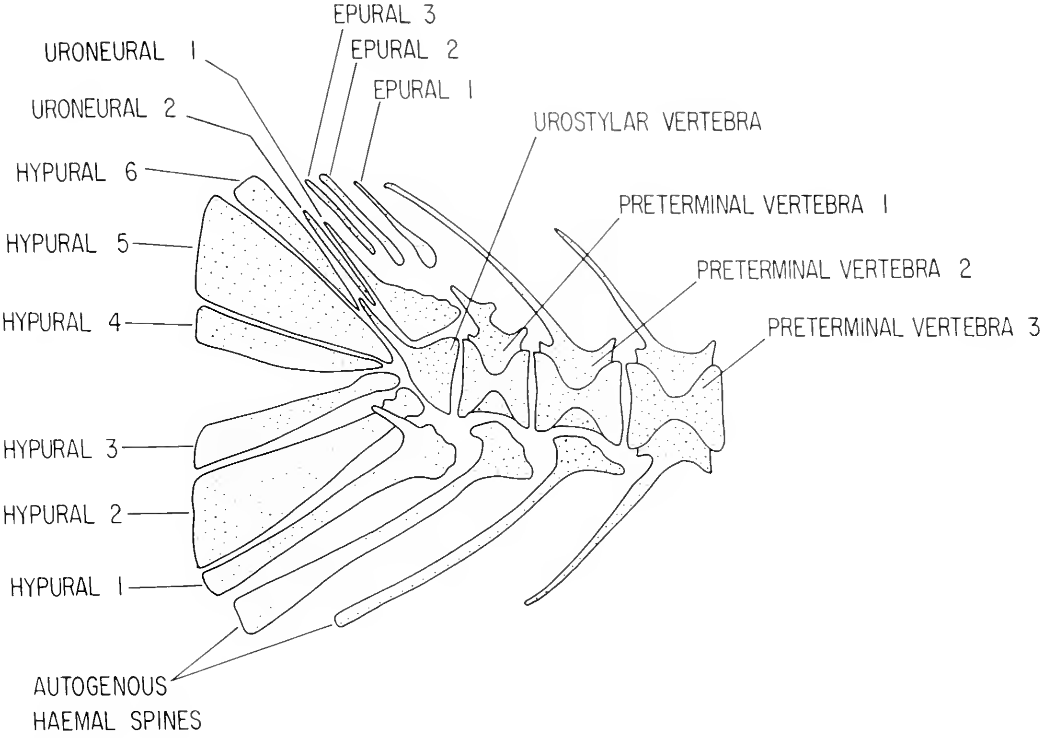


Figure 1. The bones of the caudal skeleton, schematic drawing of the basic centrolophid type.

and the pharyngeal sacs pulled forward from between the cleithra. The esophagus was cut behind the sacs, and the complete branchial apparatus removed. This was divided sagitally, and one half, usually the right, was cleared and stained. A more legible preparation was obtained if the gill filaments were stripped off prior to treatment. Teeth from the pharyngeal sacs were examined by macerating the sac in potassium hydroxide until the muscle was translucent, staining, and allowing the sac to disintegrate. Individual teeth could then be picked out and examined.

Excellent results were obtained following the clearing-and-staining method of Clothier (1950) modified from Hollister (1934). The entire clearing-and-staining procedure takes about two months.

A few complete skeletons were prepared, mostly from fresh specimens, by picking the meat carefully from the bones. Skulls were prepared by boiling the specimen until it fell apart. Only partial dissections were made in some cases. Whenever possible, skeletons in museum collections were examined. Scales were stained in alizarin, blotted dry, and mounted in balsam on slides.

Drawings of cleared-and-stained preparations were made through a Wild Dissecting Microscope with a camera lucida attachment. All caudal skeletons were drawn at 25 power, using transmitted light. Drawings of the branchial arches were made at 6 power, using transmitted light to draw the orientation of the bones, and reflected light to draw the arrangement and structure of the bases of the papillae. These drawings were redrafted on tracing paper and the final drawing was made with reference to the specimen through the 'scope without camera lucida. All anatomical drawings,

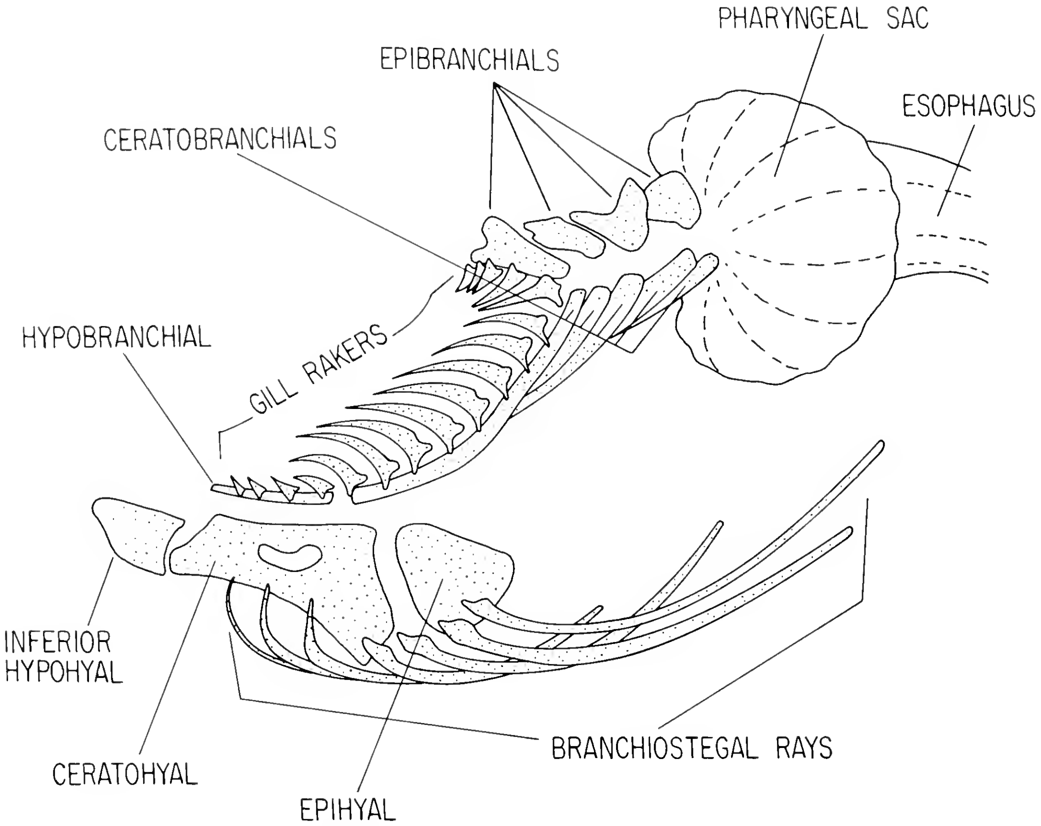


Figure 2. Elements of the branchial region, schematic drawing of the basic stromateoid type.

though made from specific preparations, are semi-diagrammatic.

The various elements in the drawings of the caudal skeleton are identified in Figure 1. Those of the branchial region are shown in Figure 2. Nomenclature of the caudal skeleton follows Gosline (1960, 1961); that of the head and branchial region follows Mead and Bradbury (1963).

MATERIAL

The specimens examined are arranged below under the classificatory scheme herein proposed. Museum and institutional names, in alphabetical order under each species, are abbreviated as follows:

ABE —Collection of Dr. T. Abe, Tokyo
AMS —Australian Museum, Sydney
ANSP —Academy of Natural Sciences of Philadelphia
BC —University of British Columbia, Vancouver
BCF —Bureau of Commercial Fisheries, Biological Laboratory, Washington, D. C.
BMNH —British Museum (Natural History), London
BOC —Bingham Oceanographic Collection, Yale University
CF —Danish Carlsberg Foundation, Charlottenlund Slot
CNHM —Chicago Natural History Museum
GTS —Guinean Trawling Survey
IIOE[1] —International Indian Ocean Expedition
MCZ —Museum of Comparative Zoology, Harvard University
MNHN —Muséum National d'Histoire Naturelle, Paris

---

[1] These specimens will ultimately be catalogued in the MCZ.

NRF —Nankai Regional Fisheries Research Laboratory, Kochi
NTU —Department of Zoology, Faculty of Science, Tokyo University
SAM —South African Museum
SIO —Scripps Institution of Oceanography
SU —Natural History Museum, Stanford University
USNM —United States National Museum, Washington, D. C.
WHOI[1]—Woods Hole Oceanographic Institution
ZMC —Zoological Museum, Copenhagen

The number of specimens, the range of standard lengths, and the locality appear in that order within the parentheses. Types are marked with an asterisk (*), the species name following within the parentheses. Specimens radiographed are marked with a dagger (†); specimens that have been cleared and stained are marked CS.

Hyperoglyphe

H. antarctica (Carmichael): †AMS IB. 3825 (1, 170 mm, near Sydney, N.S.W.). *† BMNH 1855. 9. 19. 2 (1, 108 mm, coasts of Australia, *Diagramma porosa* Richardson). †SAM 23592 (1, 105 mm, Cape Point, South Africa).

H. bythites (Ginsburg): CNHM 46408 (1, 12 mm, Ocean Spring, Miss.). *†USNM 157776 (1, 197 mm, off Pensacola, Fla., *Palinurichthys bythites* Ginsburg); *†USNM 157778 (1, 187 mm, Mississippi Delta, paratype *Palinurichthys bythites* Ginsburg). WHOI (1, 204 mm, OREGON sta. 3762); WHOI (1, 203 mm, OREGON sta. 4011); WHOI (7, 188–213 mm, OREGON sta. 4030).

H. japonica (Döderlein): ABE 58-258, 60-107 to 111, 60-113 to 116, 60-139, 60-225, 60-370, 60-709, 60-744, 60-775, 61-452, 61-458, 61-461 to 464, 61-500 to 511, 62-302, 62-303, 62-336 to 368, 63-435, 63-476, 63-447, 63-480, 63-541 to 544, 63-547, 63-668, 63-708, 63-728, 63-872 (35, 35–233 mm, Manazuru, Japan); ABE 64-2201 and 2202 (2, 400, 415 mm, Tokyo market); ABE 2236 (1, 695 mm, Tokyo market); ABE plankton collection (1, 20 mm, East China Sea). CNHM 59428 (1, 420 mm, Tokyo).

H. perciforma (Mitchill): †MCZ 36624 (2, 159, 209 mm, Woods Hole, Mass.). WHOI (47, 101–198 mm, 40°10′N 69°30′W, gill arch CS); WHOI (1, 50 mm, 38°37′N 69°24′W, CS).

Schedophilus

S. griseolineatus (Norman): †BMNH 1936. 8. 26. 1068–9 (2, 258, 258 mm, South Atlantic); *†BMNH 1936. 8. 26. 1070–1 (2, 193, 196 mm, South Atlantic, *Palinurichthys griseolineatus* Norman).

S. maculatus Günther: *†BMNH 48. 3. 16. 150 (1, 37 mm, China Seas, *S. maculatus* Günther).

S. huttoni (Waite): †ZMC (1, *ca.* 40 mm, 34°24′S 94°45′W).

S. marmoratus Kner and Steindachner: *†Hamburg Museum H464 (1, 37 mm, Südsee, *S. marmoratus* Kner and Steindachner). †ZMC (2, 28 and 46 mm, GALATHEA sta. 176).

S. medusophagus Cocco: *BMNH 60. 3. 18. 3 (1, *ca.* 405 mm, stuffed, Cornwall, *Centrolophus britannicus* Günther). †CF (7, 59–188 mm, North Atlantic). †USNM 163880 (1, 333 mm, Kitty Hawk). WHOI (19, 5.5–435 mm, North Atlantic, one CS).

S. ovalis (Cuvier and Valenciennes): *†BMNH 1860. 7. 17. 2–3 (2, 171, 186 mm, Madeira, *Leirus bennettii* Lowe). *MNHN 264. 4. 1. 2 (1, 299 mm, Nice, *Centrolophus ovalis* Cuvier and Valenciennes); *MNHN 264. 5. 1. 2 (1, 144 mm, Canary Islands, *Crius berthelotti* Valenciennes).

S. pemarco (Poll): BCF 928 (1, 95 mm, 4°31′S 10°53′E). †GTS (11, 103–217 mm, Gulf of Guinea, gill arch CS).

Centrolophus

C. niger Lacépède: *†BMNH 1862. 6. 14. 16 (1, 290 mm, Madeira, *Schedophilus elongatus* Johnson); BMNH 50. 9. 7. 3 (1, 385 mm, no locality); BMNH 55. 9. 19. 1461 (1, 124 mm, Hasler Coll.); BMNH 80. 12. 11. 1 (1, 183 mm, Falmouth); BMNH 1934. 8. 8. 67 (1, 362 mm, SW Ireland); BMNH 1934. 8. 8. 68–9 (2, 498, 560 mm, SW Ireland). †CF (2, 147, 204 mm, DANA sta. 4205, gill arch CS). MCZ 34246 (1, 443 mm, 42°10′N 66°45′W); MCZ 37983 (1, 284 mm, Provincetown); MCZ 37984 (1, 490 mm, Sable Island Bank). *†MNHN 264. 2. 2. 1 (1, 287 mm, Fécamp, *Centrolophus niger* Lacépède); *MNHN 264. 2. 2. 2, 264. 2. 2. 3 (3, 169–207 mm, Nice, *Centrolophus morio* Cuvier and Valenciennes); MNHN 264. 2. 2. 9 (1, 180 mm, Naples); *MNHN 264. 4. 2. 1 (1, 121 mm, Marseille, *Centrolophus valenciennesi* Moreau). †USNM 44440 (1, 189 mm, Dennis, Mass.); USNM 48367 (1, 39 mm, Naples); †USNM 48906 (1, 265 mm, North Truro, Mass.); USNM 49335 (1, 220 mm, Genoa). WHOI (1, 1065 mm, 40°13′N 65°45′W).

Icichthys

I. lockingtoni Jordan and Gilbert: ABE 63-526, 63-527, 63-529, 63-530, 63-548, 63-549, 63-555 (12, 72–173 mm, Manazuru, gill arch CS). BC 53-99A (1, 164 mm, Vancouver

Island); BC 59-652 (1, 132 mm, Vancouver Island). *SU 7442 (1, 65 mm, Monterey Bay, *Schedophilus heathi* Gilbert); SU 17346 (1, 42 mm, Seal Beach); SU 22955 (1, 41 mm, Catalina Island); SU 22971 (1, 26 mm, Monterey Bay); SU 41028 (8, 15–78 mm, Monterey Bay, CS). *†USNM 27397 (1, 159 mm, Point Reyes, *Icichthys lockingtoni*); *†USNM 89398 (3, 28–65 mm, Monterey Bay, *Centrolophus californicus* Hobbs). WHOI (2, 17, 83 mm, Monterey Bay, received through Giles Mead).

Seriolella

S. *brama* Günther: †AMS IA. 10170 (1, 233 mm, Sydney Harbour, New South Wales); †AMS I. 10333 (1, 152 mm, 40 miles W Kingston, South Australia). *BMNH (1, 298 mm, New Zealand, stuffed, *Neptomenus brama* Günther).

S. *punctata* (Bloch and Schneider): †AMS I. 10840 (1, 192 mm, Oyster Bay, Tasmania); †AMS I. 14747 (1, 220 mm, Portobello). *†BMNH 1869. 2. 24. 42–44 (3, 234–243 mm, Tasmania, *Neptomenus dobula* Günther). USNM 176915 (2, 190, 195 mm, Queensland, gill arch CS); †USNM 176968 (1, 149 mm, New South Wales); †USNM 177109 (2, 197, 203 mm, New South Wales).

S. *porosa* Guichenot: †USNM 176478 (1, 218 mm, Tictoc Bay, Chile); †USNM 176535 (1, 198 mm, Puerto Anchemo, Chile); †USNM 176593 (3, 197–203 mm, Auellon, Chile).

S. *violacea* Guichenot: †MCZ 17239 (2, 430, 445 mm, Callao, Peru). *SU 9590 (1, 262 mm, Callao, Peru, paratype *Neptomenus crassus* Starks). *†USNM 53465 (1, 265 mm, Callao, Peru, *Neptomenus crassus* Starks); †USNM 77513 (1, 130 mm, Mellendo, Peru); †USNM 77593 (1, 150 mm, Mellendo, Peru, gill arch CS); †USNM 77611 (1, 173 mm, Callao, Peru); †USNM 77625 (1, 213 mm, Callao, Peru). †ZMC (1, 87 mm, 14°S 77°W).

Psenopsis

P. *anomala* (Temminck and Schlegel); ABE 60-1232, 63-752, 63-1141 (3, 93–119 mm, Manazuru market); ABE 62-656 (1, 40 mm, Japan, CS); ABE 61-590 (1, 160 mm, Tsubaki); ABE 64-1223 to 1225 (25, 43–84 mm, 32°09′N 123°15′E); ABE 64-1972 to 1959 (8, 17–52 mm, Kozu); ABE 64-2014 to 2017, 64-2142 to 2144, 64-2148 to 2150 (14, 7.5–93 mm, off Misaki); ABE 64-2037 to 2039 (3, 30–42 mm, Amakusa Island); ABE, plankton collection (9, 7–28 mm, East China Sea); ABE (1, 150 mm, Tokyo market, gill arch CS). BC 56-29 (1, 136 mm, Tokyo market); BC 59-555 (1, 138 mm, Aberdeen market). CNHM 57288 (3, 91–124 mm, Kobe). †MCZ 1186 (2, 122, 143 mm, Kanagawa); MCZ 31150 (1, 125 mm, Yenosima). †USNM 6424 (1, 149 mm, Hong Kong); †USNM 49465, 71131, 151829 (3, 146–156 mm, Tokyo market); †USNM 59618 (1, 141 mm, Matsushima Bay); †USNM 177426 (2, 132, 142 mm, Taipei market).

P. *cyanea* Alcock: *†BMNH 1890. 11. 28. 9 (1, 120 mm, Ganjam Coast, India, *Bathyseriola cyanea* Alcock); †BMNH 1937. 6. 28. 1–8 (9, 103–110 mm, off Cananore).

Psenopsis sp.: †USNM 98818 (1, 132 mm, Maré Island, Dutch East Indies).

Cubiceps

C. *athenae* Haedrich: *†MCZ 42974 (1, 68 mm, 38°36′N 71°24′W, *Cubiceps athenae* Haedrich). *†USNM 198058 (1, 81 mm, 28°54′N 88°18′W, paratype *Cubiceps athenae* Haedrich). WHOI (1, 33 mm, 24°21′N 81°15′W, CS).

C. *caeruleus* Regan: *†BMNH 1913. 12. 4. 28–29 (2, 86, 95 mm, Three King's Isl., New Zealand, *Cubiceps caeruleus* Regan); BMNH 1926. 6. 30. 50 (1, 282 mm, Lord Howe Isl., Tasman Sea).

C. *capensis* (Smith): *BMNH (1, 905 mm, South Africa, *Atimostoma capensis* Smith, stuffed); †BMNH 1925. 10. 14. 1–4 (3, all *ca.* 160 mm, 70 mi. WNW Saldanha Bay, South Africa).

C. *carinatus* Nichols and Murphy: CNHM 61958 (5, 93–99 mm, 83°15′W 5°15′N); †CNHM 61939 (2, both 110 mm, 125 mi. SW Cape Mala, Panama). SIO 63-538 (1, 101 mm, 21°35′N 107°00′W); SIO 63-882, 63-888, 63-892 (4, 65–101 mm, Golfo de Tehuantepec); SIO 63-1027 (1, 91 mm, 13°33′N 95°59′W); SIO H 49–77 (1, 87 mm, off El Salvador); SIO H 52-351 (2, 90, 94 mm, 13°45′N 99°22′W). ZMC (1, 57 mm, 11°52′N 97°19′W); ZMC (2, 64, 71 mm, 12°14′N 97°46′W); ZMC (1, 70 mm, 12°38′N 98°14′W); ZMC (1, 72 mm, 13°00′N 98°41′W); ZMC (1, 71 mm, 13°41′N 97°34′W).

C. *gracilis* Lowe: †BMNH 63. 12. 12. 7–8 (2, 143, 150 mm, Madeira); BMNH 1960. 12. 19. 8 (1, 165 mm, 51°51′N 13°43′W). CF (5, 40–57 mm, DANA sta. 855); CF (2, 50, 59 mm, DANA sta. 856); CF (26, 5–35 mm, DANA sta. 939, one CS); CF (1, 69 mm, DANA sta. 1372); CF (1, *ca.* 70 mm, DANA sta. 1378); CF (1, 77 mm, DANA sta. 1380); CF (1, 43 mm, DANA sta. 4017, CS); CF (4, 43–76 mm, DANA sta. 4185); CF (18, 16–80 mm, DANA sta. 4192); CF (37, 11-61 mm, DANA sta. 4195);

CF (50, 10–58 mm, DANA sta. 4197). *MNHN 42-29 (1, 195 mm, Sète, *Trachelocirrhus mediterraneus* Doumet). WHOI (8, 20–51 mm, DELAWARE 63–4 sta. 3); WHOI 12, 25–51 mm, 39°27′N 27°35′W); †WHOI (1, 92 mm, DELAWARE 63–4 sta. 13); †WHOI (2, 75, 81 mm, DELAWARE 63–4 sta. 16).

C. longimanus Fowler: *ANSP 55058 (1, 42 mm, Durban, Natal, *Cubiceps longimanus* Fowler). HOE (1, 29 mm, ANTON BRUUN 6 sta. 338).

C. pauciradiatus Günther: ABE 57-347 (1, 120 mm, Manazuru, Japan); ABE 10832 (1, 80 mm, Kōchi, Japan). *ANSP 68380 (1, 124 mm, 40 mi. S Christmas Isl., Line Islands, *Cubiceps nesiotes* Fowler). *†BMNH 1870. 8. 31. 124 (1, 113 mm, Misol, Molucca Isl., *Cubiceps pauciradiatus* Günther). SIO 60-216 (1, 93 mm, 10°26′N 128°22′W).

C. squamiceps (Lloyd): ABE 57-348, 59-37, 61-843, 62-13, 62-106 (5, 84–154 mm, Manazuru, Japan); ABE 64-1348 (1, 264 mm, 6°15′N 164°10′W); ABE 10833 (1, 159 mm, Kōchi, Japan).

Nomeus

N. gronovii (Gmelin): ABE 64-1280 (1, 68 mm, Kushimoto, Japan); ABE plankton collections (5, 8–38 mm, Japan). BCF 1002 (1, 61 mm, 3°41′N 0°05′E); BCF 1003 (1, 40 mm, GERONIMO 4-155). BOC 602 (6, 17–101 mm, Key West Harbor); BOC 3361 (21, 10–118 mm, Atlantic Ocean); BOC 3515 (22, 13–149 mm, Gulf of Mexico); †BOC 3516 (8, 31–153 mm, Gulf of Mexico); BOC 3517 (14, 16–133 mm, 28°07′N 89°53′W); BOC 3518 (11, 13–114 mm, Atlantic Ocean). †CNHM (1, 225 mm, OREGON sta. 1178). HOE (4, 20–45 mm, 2°20′N 65°54′E); HOE (9, 12–41 mm, 8°00′S 65°00′E). †MCZ 35327 (2, 144, 154 mm, 39°27′N 70°38′W gill arch CS). *MNHN 264. 6. 2. 3 (3, largest *ca.* 42 mm, seas of Java, *Nomeus peronii* Cuvier and Valenciennes). SIO 60-263 (4, 22–40 mm, 5°18′N 160°05′W); SIO 61-84 (2, 20, 25 mm, 5°58′S 149°31′W); SIO 61-87 (1, 33 mm, 1°32′S 148°39′W); SIO 61-89 (3, 32–41 mm, 5°32′N 146°09′W). WHOI (2, 45, 66 mm, 17°00′N 65°05′W, CS).

Psenes

P. arafurensis Günther: ABE 60-101 (1, 72 mm, Manazuru, Japan); ABE 62-651 (1, 35 mm, Japan, CS); ABE 64-212 (1, 150 mm, Nagasaki); ABE 64-1767 (1, 92 mm, Komatsubara, Japan); ABE, plankton collection (2, 19, 37 mm, East China Seas). *†BMNH 1889. 7. 20. 55 (1, 30 mm, China Seas, *Psenes arafurensis* Günther). HOE (1, 25 mm, 2°20′S 64°54′E); HOE (1, 20 mm, 4°01′S 65°02′E). MCZ 41550 (5, 14–18 mm, 10°52′N 29°26′W). WHOI (1, 20 mm, 41°33′N 54°55′W).

P. benardi Rossignol and Blache: *MNHN 264. 9. 1. 1 (1, 63 mm, 3°38′S 9°22′E, *Psenes benardi* Rossignol and Blache); *MNHN 264. 9. 1. 2 (2, 63, 65 mm, 1°55′S 8°30′E, paratypes, *Psenes benardi* Rossignol and Blache).

P. cyanophrys Cuvier and Valenciennes: *† BMNH 1871. 7. 20. 156 (1, 111 mm, Manado, Philippines, *Cubiceps multiradiatus* Günther). CF (1, 28 mm, Dansk Vestindien sta. 132, CS). *†MNHN 264. 9. 2. 4 (1, 117 mm, New Ireland, Bismarck Archipelago, *Psenes cyanophrys* Cuvier and Valenciennes). CNHM 46409 (1, 80 mm, 25°N 89°W). WHOI (1, 38 mm, CRAWFORD 62, CS). †WHOI (2, 119, 128 mm, OREGON sta. 3715, gill arch CS).

P. maculatus Lütken: ABE 64-1226 (1, 20 mm, Japan); ABE plankton collection (1, 20 mm, East China Sea). CF (1, 48 mm, 15°31′N 18°05′W). †MCZ 41122 (1, 59 mm, 40°49′N 64°57′W). WHOI (1, 27 mm, 38°26′N 68°15′W); WHOI (1, 35 mm, 41°36′N 60°30′W). *†ZMC (2, 57 and 72 mm, 39°00′N 34°10′W, *P. maculatus* Lütken).

P. pellucidus Lütken: ABE 59-172, 60-102, 60-106, gill arch CS, 60-140 and 141, 61-21, 61-82 and 83, 61-459 (13, 72–147 mm, Manazuru, Japan); ABE 63-1064 (1, 89 mm, Tokyo market). †BCF 957 (1, 130 mm, 4°07′S 10°23′E). CF (1, 60 mm, 15°31′N 18°05′W); CF (1, 39 mm, ACENT PETERSEN sta. 769, CS). CNHM 5285 (1, 54 mm, Bermuda); †CNHM 49189 (1, 131 mm, Bermuda); *†CNHM 57097 (1, 193 mm, Okinawa, *Icticus ischanus* Jordan and Thompson). *†USNM 49745 (1, 67 mm, Newport, Rhode Island, *Psenes edwardsii* Eigenmann). SU 43310 (1, 93 mm, Bermuda). WHOI (1, 25 mm, 38°38′N 68°50′W). *†ZMC (1, 38 mm, Surabaya, *P. pellucidus* Lütken).

Ariomma

A. africana (Gilchrist and von Bonde): *† BMNH 1927. 12. 6. 45 (1, 166 mm, Agulhas Bank, South Africa, co-type, *Psenes africanus* Gilchrist and von Bonde).

A. bondi Fowler: *ANSP 52528 (1, 79 mm, Grenada, British West Indies, *Ariomma bondi* Fowler).

A. dollfusi (Chabanaud): *†BMNH 1931. 4. 16. 1 (1, 112 mm, Gulf of Suez, co-type, *Cubiceps dollfusi* Chabanaud).

A. evermanni Jordan and Snyder: *†USNM

57783 (1, 156 mm, Honolulu, Hawaii, *Ariomma evermanni* Jordan and Snyder).

A. indica (Day): BC 59-555 (1, 151 mm, Aberdeen market, Hong Kong). *†BMNH 1889. 2. 1. 3255–6 (2, 74, 90 mm, Madras, India, *Psenes indicus* Day). NTU 51941 to 51946 (6, 123–181 mm, near Hainan Island, gill arch CS).

A. lurida Jordan and Snyder: *SU 8441 (1, *ca.* 190 mm, Honolulu, Hawaii, paratype *Ariomma lurida* Jordan and Snyder). *†USNM 51400 (1, 166 mm, Honolulu, Hawaii, *Ariomma lurida* Jordan and Snyder); †USNM 109418 (1, 193 mm, Honolulu).

A. melana (Ginsburg): *†USNM 157779 (1, 154 mm, Mississippi Delta, *Cubiceps melanus* Ginsburg).

A. multisquamis (Marchal): *MNHN 264. 7. 2. 1 (type), 264. 7. 2. 2 (paratype) (2, 159, 147 mm, Ivory Coast, *Paracubiceps multisquamis* Marchal).

A. nigriargenteus (Ginsburg): *MCZ 37183 (1, 113 mm, Sandwich, Massachusetts, paratype *Cubiceps nigriargenteus* Ginsburg). *†USNM 151954 (1, 190 mm, off Cape Romain, South Carolina, *Cubiceps nigriargenteus* Ginsburg).

A. regulus (Poey): †USNM 197110 (2, 142, 150 mm, British Guiana). †WHOI (1, 136 mm, 29°59′N 87°06′W).

Ariomma sp. Western North Atlantic: MCZ 40259 (1, 116 mm, Provincetown, Massachusetts); MCZ 40498 (1, 115 mm, Provincetown, Massachusetts). SU 57297 (1, 86 mm, Bermuda). WHOI (3, 87–121 mm, OREGON sta. 3725); WHOI (2, 103, 109 mm, OREGON sta. 3733); WHOI (3, 122–134 mm, OREGON sta. 4014); WHOI (1, 143 mm, 9°03′N 81°22′W); WHOI (2, 141, 149 mm, 9°13′N 80°44′W); WHOI (3, 139–140 mm, 16°45′N 81°27′W); WHOI (3, 131–140 mm, 28°57′N 88°41′W); WHOI (2, 125, 133 mm, 29°07′N 88°34′W); WHOI (3, 130–140 mm, 28°54′N 88°51′W, gill arch CS); WHOI (1, 23 mm, CRAWFORD 62 sta. 29, CS); WHOI (1, 28 mm, 24°N 81°W, CS).

Ariomma sp. Japan: ABE 59-404, 59-408, 60-124, 60-144, 60-224, 60-478 and 479, 60-1611, 61-1188, 62-738, 62-955, 62-1387, 62-1628 (13, 99–226 mm, Manazuru, Japan). NRF 1441 (1, *ca.* 800 mm, Bonin Islands).

Tetragonurus

T. atlanticus Lowe: *†BMNH (1, 197 mm, Madeira, *Tetragonurus atlanticus* Lowe). MCZ 41726 (1, 21 mm, 39°47′N, 70°32′W, CS); MCZ 41791 (1, 66 mm, 39°41′N 69°54′W, CS). WHOI (2, 15, 20 mm, tropical Atlantic).

T. cuvieri Risso: CNHM 64218 (1, 340 mm, 46°51′N, 155°00′W, gill arch CS).

Stromateus

S. brasiliensis Fowler: *ANSP 11354 (1, 276 mm, Rio Grande do Sul, Brazil, *Stromateus brasiliensis* Fowler). †MCZ 4599 (3, 254–285 mm, Rio Grande do Sul, Brazil).

S. fiatola Linnaeus: †BMNH 87. 3. 2. 30 (1, 76 mm, Lower Congo). †GTS (6, 200–240 mm, 7°20′N 12°40′W). †MCZ 16729 (1, 257 mm, Mediterranean?). †SU 1537 (1, 44 mm, Palermo, Italy). †USNM (1, 177 mm, Fed. Fish. Serv. Nigeria, No. 4046).

S. stellatus Cuvier: †USNM Acc. No. 167496 (2, 230, 237 mm, 42°29′S 72°46′W). *MNHN 264. 11. 3. 1–2 (2, 144, 164 mm, Valparaiso, Chile, *Stromateus maculatus* Cuvier and Valenciennes). †USNM 176474 (3, 178–250 mm, Calbucco, Chile); †USNM 176494 (1, 193 mm, 41°52′S 73°53′W).

Peprilus

P. alepidotus (Linnaeus): †USNM 127352, 127353 (2, 122, 141 mm, Grand Terre, La.); †USNM 23215 (1, 130 mm, Bay Chaland, La.). WHOI (1, 39 mm, SILVER BAY sta. 4331, CS).

P. palometa (Jordan and Bollman): *†USNM 41136 (5, 53–61 mm, Perlas Isl; Panama, *Stromateus palometa* Jordan and Bollman; †USNM 50337 (2, 136, 169 mm, Panama).

P. paru (Linnaeus): †MCZ 4600 (1, 55 mm, Brazil); †MCZ 41064 (2, 48, 57 mm, Port-au-Prince, Haiti). *MNHN (1, 93 mm, Rio de Janeiro, *Seserinus xanthurus* Quoy and Gaimard).

P. simillimus (Ayres): †MCZ 26875 (1, 110 mm, San Diego, Calif.). †SU 48000 (1, 82 mm, Oceanside, California).

P. snyderi Gilbert and Starks: *†BMNH 1903. 5. 15. 190 (1, 217 mm, Panama, co-type *Peprilus snyderi* Gilbert and Starks). *†USNM 50448 (1, 189 mm, Panama, *Peprilus snyderi* Gilbert and Starks). †USNM 76796 (1, 178 mm, Panama City).

P. triacanthus (Peck): †ABE 64-1920, 1924, 1930 (3, 80–110 mm, Florida). †WHOI (7, 157–195 mm, SILVER BAY sta. 4104); †WHOI (4, 127–155 mm, 40°01′N 71°23′W); †WHOI (1, 120 mm, Woods Hole, gill arch CS); WHOI (1, 36 mm, BEAR 188 sta. 371, CS).

Pampus

P. argenteus (Euphrasen): †ABE 64-1231, 1233 (2, 105, 147 mm, Bangkok); †ABE 64-1929 (1, 133 mm, Hong Kong); †ABE 1936, 1937

(2, 48, 72 mm, off mouth of Shiota River, Ariake Sound, Kyushu, CS); †ABE 64-1964 (1, 156 mm, East China Sea); †ABE P 4347 (1, 92 mm, Sarawak, North Borneo). †HOE (6, 65–161 mm, Bombay). †USNM 44900 (1, 299 mm, Japan).

P. chinensis (Euphrasen): †ABE 64-1229 (1, 89 mm, Bangkok); †ABE P 2211, P 4319 (2, 77, 112 mm, Sarawak, North Borneo). †CNHM 15917 (1, 74 mm, Batavia, Java). †MCZ 16772 (1, 84 mm, Singapore).

P. echinogaster (Basilewsky): †ABE 64-902, 64-906, 64-909, 64-911, 64-926, 64-1192 (5, 165–207 mm, East China Sea); †ABE 64-1112 (1, 221 mm, Tokyo market); †ABE 1743 (1, *ca.* 180 mm, Tokyo market, gill arch CS); †ABE 64-1934 (1, 158 mm, south of Poi Toi Isl., Hong Kong). †CNHM 55810 (3, 81–106 mm, Chinnampo, Korea). †SU 22292 (3, 77–87, Chinnampo, Korea). †USNM 75941 (1, 236 mm, Japan?).

In addition to stromateoid fishes, the following non-stromateoids were examined:

Apolectidae

Apolectus [= *Parastromateus*] *niger* MCZ 15912 (3, Singapore).

Arripididae

Arripis trutta ZMC 74.P.475 (3, New Zealand).

Atherinidae

Menidia sp. WHOI (2, Morehead City).

Carangidae

Caranx hippos WHOI (1, Woods Hole). *Naucrates ductor* WHOI (1, ATLANTIS sta. 219). *Selar crumenopthalmus* WHOI (1, Woods Hole). *Trachinotus glaucus* WHOI (1, Trujillo, Honduras).

Coryphaenidae

Coryphaena equiselis WHOI (1, OREGON sta. 1297).

Ephippidae

Platax ocellatus MCZ 2748 (1, Manila).

Icosteidae

Icosteus aenigmaticus BC 63-98 (1, Alaska); BC 64-12 (1, Spiller Channel). MCZ 34915 (1, California). SU 1171 (1, Pacific Grove); SU 25640 (1, Monterey Bay). *USNM 27398 (1, Point Reyes); USNM 75159 (1, Pacific Grove).

Girellidae

Boops vulgaris MCZ 21706 (1, France). *Girella nigricans* MCZ 10775 (1, California).

Kuhliidae

Kuhlia malo MCZ 29367 (1, Papeete).

Kyphosidae

Kyphosus sectatrix WHOI (2, 32°08'N 67° 10'W). *Pimelepterus boscii* MCZ 2610 (1, Florida).

Monodactylidae

Monodactylus argenteus MCZ 34101 (1, Dar es Salaam).

Nematistiidae

Nematistius pectoralis BC 60-15 (1, Acapulco market).

Pomatomidae

Pomatomus saltatrix MCZ 16941 (5, New Jersey). WHOI (5, Woods Hole).

Scomberesocidae

Scomberesox saurus WHOI (1, 40°12'N 62° 54'W).

Scombridae

Auxis thazard WHOI (1, 41°16'N 57°37' W). *Scomber scomber* WHOI (1, Quisset, Mass.).

Scorpididae

Scorpis californiensis MCZ 4896 (2, California).

Theraponidae

Autisthes puta WHOI (2, Australia, received through James Moulton). *Pelates* sp. WHOI (2, Australia, received through James Moulton). *Therapon jarbua* MCZ 24823 (2, Java).

Zaproridae

Zaprora silenus BC 61-573 (1, Cross Sound, Alaska).

SYSTEMATIC SECTION

In the classification which follows, the suborder, the families, and the genera are characterized. Categories below the genus are not. In a number of cases, subgeneric division is certainly called for. This action is not taken here, but is reserved for critical treatment in a planned series of monographs. Likewise, the proper sorting of species is left for the future. As a preliminary step in clarifying the confusion which surrounds stromateoid classification, however, lists of nominal species are included under each genus. Species synonymies, whenever given, are to be considered tentative.

The synonymy of the suborder is fairly complete and is intended as a guide to most works, especially those of a faunistic nature, that include references to stromateoids. Distributional notes concerning single or very few species, however, have not been included. The synonymies of each family contain only major references. Family names have been used with such confusion in the past that complete synonymies would be essentially meaningless.

Included under each taxon are: synonymy, diagnosis or brief characterization, description, distribution (suborder, families), natural history (suborder, genera), relationships, and key to included taxa or list of nominal species. An asterisk (*) precedes the names of species of which I have seen the types.

Suborder STROMATEOIDEI

Stromatini. Rafinesque, 1810:39 (*Stromateus, Luvarus*).

Stromateini. Bonaparte, 1846:76 (*Stromateus, Peprilus, Luvarus, Kurtus*).

Stromatiniae. Swainson, 1839:177 (*Seserinus, Stromateus, Peprilus, Kurtus, Keris*).

Stromateina. Günther, 1860:397 (+ Nomeina p. 387, def., *Stromateus, Centrolophus, Gasterochisma, Nomeus, Cubiceps, Neptomenus, Platystethus, Ditrema*).

Stromateidae. Gill, 1884:665 (def., gen. synopsis, *Centrolophus, Schedophilus, Lirus, Stromateus, Stromateoides, Psenopsis*). Day, 1875:246 (+ Nomeidae, p. 237. descr.; India). Jordan and Gilbert, 1882:449 (key, descr.; North America). Fordice, 1884: 311 (key, synon.; America). Collett, 1896:26 (+ Nomeidae, p. 31. descr.; eastern Atlantic). Goode and Bean, 1896:213 (descr.; oceanic spp.). Regan, 1902: 117 (major revision, *Nomeus, Cubiceps, Psenes, Seriolella, Psenopsis, Centrolophus, Lirus, Stromateus, Peprilus, Stromateoides*). Holt and Byrne, 1903:71 (key, descr.; British Isles). Boulenger, 1904:643 (popular account). Smith, 1907:221 (key, descr.; North Carolina). Miranda-Ribeiro, 1915 (key, descr.; Brazil). Gilchrist, 1922:249 (papillae). Gilchrist and von Bonde, 1923:1 (descr.; South Africa). Meek and Hildebrand, 1925:407 (key, descr.; Panama). Bühler, 1930:62 (digestive system). Fowler, 1936:658 (key, descr.; West Africa). Fowler, 1941:152 (+ Nomeidae, list; Brazil). Fowler, 1944:78 (+ Centrolophidae, p. 79; Nomeidae, p. 80. descr.; Chile). Hildebrand, 1946:416 (descr.; Peru). Barnard, 1948:394 (descr., sacs and papillae; South Africa). Smith, 1949:302 (key, descr.; South Africa); 1949a:839 (revision; South Africa). Lozano y Rey, 1952:648 (descr.; Iberia). Mori, 1952:138 (+ Nomeidae, list; Korea). Bigelow and Schroeder, 1953:363 (+ Centrolophidae, p. 369, descr.; Gulf of Maine). Herre, 1953:258 (+ Nomeidae. list, synon.; Philippines). Tchang *et al.*, 1955:195 (descr.; Gulf of Pechili, Yellow Sea). Poll, 1959:125 (descr.; West Africa). Blache, 1962:70 (list; West Africa). Lowe, 1962:694 (list; British Guiana). Chu *et al.*, 1963:407 (descr.; East China Sea).

[Stromateidae.] Lütken, 1880:513, 521 (disc. gen., oceanic spp.). Günther 1889:10 (disc. gen., descr.; CHALLENGER). Nobre, 1935:332 (descr.; Portugal). Okada, Uchida, and Matsubara, 1935:123 (descr., ill.; Japan). Kamohara, 1940:173 (descr.; Japan).

Nomeiformes. Gregory, 1907:502 (relationships).

Stromateiformes. Jordan, 1923:182 (list, fam., gen.). Jordan, Evermann, and Clark, 1930: 226 (list, synon.; North America).

Centrolophidae. Fowler, 1928:138 (descr.; Pacific); 1931:325 (descr.; add. Pacific); 1934: 403 (descr.; add. Pacific); 1949:75 (descr.; add. Pacific). Norman, 1937:115 (+ Stromateidae, p. 118. descr.; Patagonia). Sanz-Echeverria, 1949:151 (otoliths). Tortonese, 1959:57 (revision; Gulf of Genoa).

Stromateoids. Gregory, 1933:306 (skull of *Rhombus* [= *Peprilus*]).

Stromateoidei. Berg, 1940:324 (def., fam. synopsis); 1955:247 (def., fam. synopsis). Bertin and Arambourg, 1958:2441 (fam., gen. synopsis). Munro, 1958: 117 (descr.; Australia). Duarte-Bello, 1959:119 (list; Cuba). Gosline and Brock, 1960:281 (descr.; Hawaii). Chu *et al.*, 1962:759 (descr.; South China Sea). Scott, 1962:142 (key, descr.; South Australia).

Stromateoidea. Blegvad and Løppenthin, 1944:178 (descr.; Iranian Gulf). Beaufort and Chapman, 1951:85 (descr.; Indo-Australian Archipelago). Norman, 1957:216 (fam., gen. synopsis, after Regan). Herald, 1961:243 (popular account). Marshall, 1964:398 (key, descr.; Eastern Australia).

Stromateoidae. Clemens and Wilby, 1961:230 (descr.; British Columbia).

Distinctive characters. There is no mistaking the "stromateoid look." Though the characters given in the diagnosis are the only ones that absolutely identify a member of the suborder, these fishes nonetheless have a physiognomy that nine times out of ten says "Stromateoid!" to an experienced ichthyologist. Once recognized, the stromateoid expression is not likely to be forgotten. It is a fat-nosed, wide-eyed, stuffed-up look, smug and at the same time apprehensive. Some stromateoids might even be accused of a certain prissiness.

The stromateoid look results from the expanded lacrimal bone all but covering the maxillary, the slightly underslung lower jaw shutting within the upper, the large centrally located eye rimmed with adipose tissue, and the protruding, inflated, naked, and pored snout and top of the head.

Diagnosis. Perciform fishes with toothed saccular outgrowths in the gullet immediately behind the last gill arch. Small teeth approximately uniserial in the jaws.

Description. Body slender to deep, compressed or rounded. Dorsal fin single or double; dorsal spines present, very weak in some species. One to three anal spines, never separated from the rays. Dorsal and anal fins coterminal. Pelvic fins present or absent. Rays in pectoral fin 16 to 25. Body scaled, snout and top of head naked. Scales usually thin, cycloid, deciduous, but very weakly ctenoid in some nomeids and *Schedophilus medusophagus*, and heavy, keeled, and adherent in *Tetragonurus*. Scales usually covering bases of median fins. Lateral line present, the scales with simple tubes, except no tubed scales in *Tetragonurus*. No bony scutes or keels associated with lateral line. Usually a well developed subdermal mucous canal system communicating to the surface through small pores liberally scattered over head and body. Eyes small to large, lateral, not entering into profile of head. Nostrils double, the anterior round, the posterior usually a vertical slit. Jaw teeth small, simple or minutely cusped, arranged more or less in a single series, close-set or spaced. Teeth on vomer, palatines, and basibranchials present or absent. No teeth on entopterygoid or metapterygoid. Small teeth usually present on inner edge of gill-rakers. Gills 4, a slit behind the fourth. Gill-rakers 10 to 20 on lower limb of first arch. Well developed pseudobranch usually present, but absent in *Pampus*; rudimentary gill-rakers under pseudobranch commonly present. Gill-membranes usually free from isthmus, but united in *Pampus*.

Skeleton never strongly ossified. Epiotic forked, orbitosphenoid absent, 15 principal branched rays in caudal fin. Pelvic fin, when present, with one spine, five rays. A bony bridge partially covering the anterior vertical canal of the ear. Opercular bones thin, denticulate or entire, never with strong spines, except moderate preopercular spines in *Schedophilus*. No bony stay for the preopercle. Five to seven branchiostegal rays. Lacrimal bone usually enlarged, often covering maxillary almost completely. Lacrimal absent in *Pampus*. Premaxillary scarcely if at all protractile. A slender supramaxillary present or absent. Pelvic bones not firmly attached to coracoid. Vertebrae 25, 26, or 29 to 60, including hypural. Caudal skeleton with two to six hypural elements, two or three epural elements, two autogenous haemal spines, except three in *Icichthys*, hypuropophysis present on first hypural. Sometimes two but usually three free interneurals ahead of dorsal fin, but six or more in *Icichthys*. Lower pharyngeal bones not united, partially supporting pharyngeal sacs. In the sacs, numerous simple teeth on irregularly-shaped or stellate bony bases [= papillae] seated in the muscular walls, arranged in longitudinal bands or not.

Distribution. All stromateoid fishes are marine. They are found in the three major oceans of the world on the high seas, over the continental shelves, and in large bays. Most species live in tropical and temperate waters, but a few occur in colder areas. No stromateoids have been reported from the Arctic Ocean, the Bering Sea, the Okhotsk Sea, the Baltic Sea, the Black Sea, and the Antarctic Ocean.

Natural history. The association between stromateoid fishes and medusae or siphonophores is widely known and well documented. Mansueti (1963) has reviewed the literature concerning this unusual association. His lists of all fish species involved is made up largely of stromateoids, and includes centrolophids, nomeids, tetragonurids, and stromateids. Only one ariommid has been reported from under a jellyfish, a 36-mm *Ariomma indica* taken in a 305-mm diameter ctenophore in Durban Bay, Natal (Fowler, 1934a).

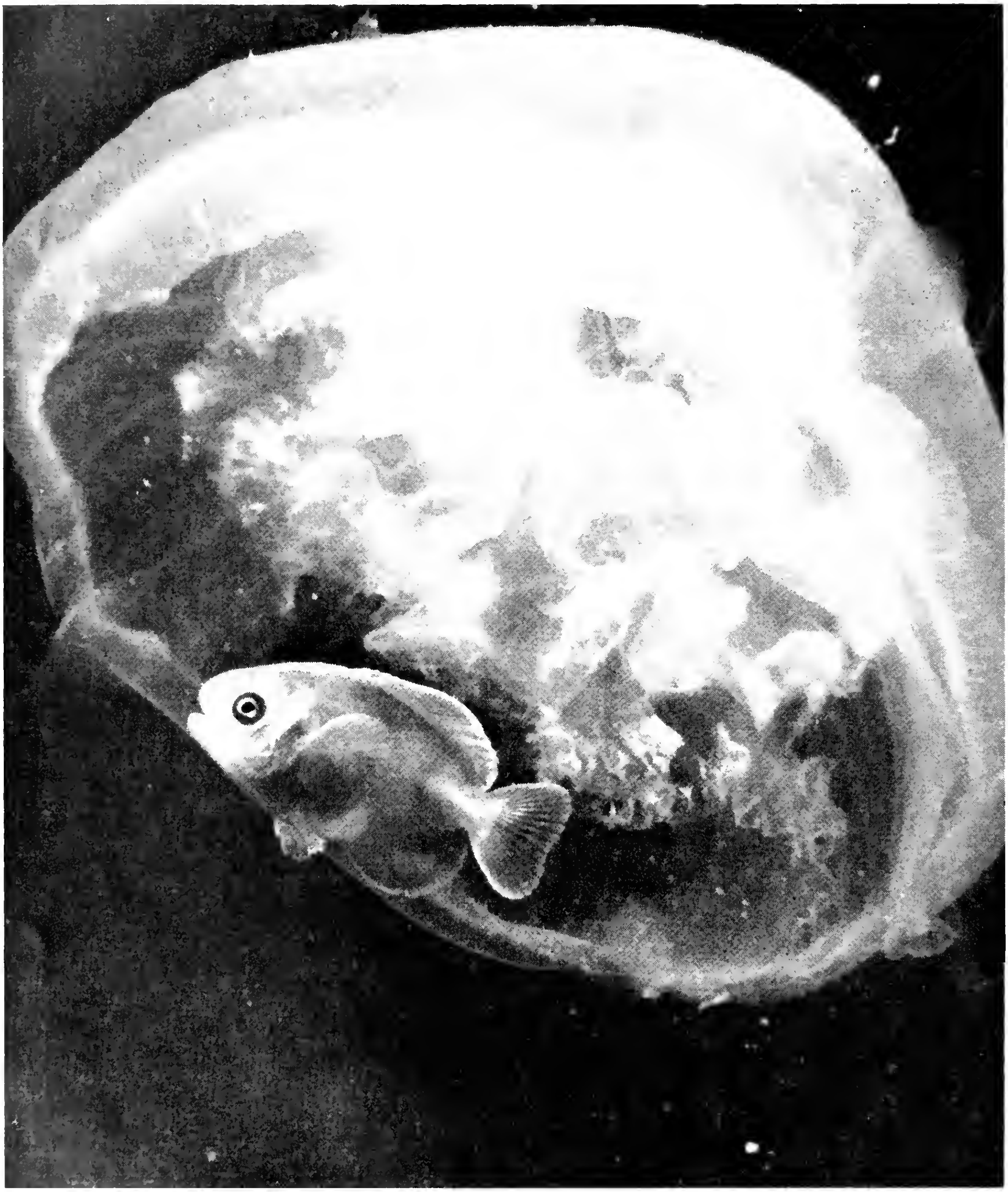


Plate 1. A young stromateoid, *Psenopsis anomala*, under a medusa. Iwago photo.

Young stromateoids are pelagic, and it is not surprising that it is the young stages that are found with jellyfishes. As they grow older, the fishes desert their surface-living host, and descend to deeper layers, the adult habitat. Stromateoids also hover beneath flotsam and *Sargassum* weed (Besednov, 1960). It is this characteristic

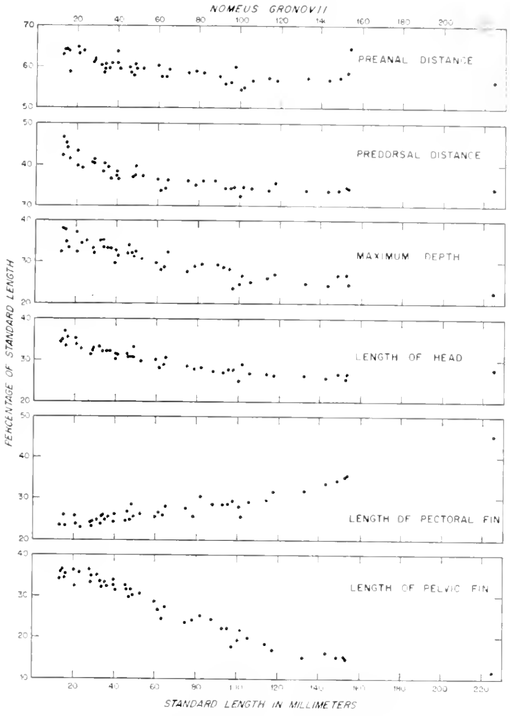


Figure 3. Scatter diagram of the allometric growth in the nomeid *Nomeus gronovii*.

habit which gives the barrelfish, *Hyperoglyphe*, its common name. Young stromateoids typically have a banded pattern, whereas adults tend to be plain. Undoubtedly, the banding is protective coloration for the fishes during that period of their lives when they live in the shifting shadows under a jellyfish.

Shelter is not all the jellyfish provide. Many stromateoids have been observed actively feeding on their hosts (*Schedophilus*, Maul, 1964; *Nomeus*, Kato, 1933; *Peprilus*, Mansueti, 1963, photo p. 63). The diagnostic pharyngeal sacs of stromateoids may have been perfected partially in response to this sort of diet. *Tetragonurus*, one of the most highly specialized stromateoids with great slicing teeth and a long pharyngeal sac, may feed almost entirely on soft-bodied medusae, ctenophores, and salps (Grey, 1955).

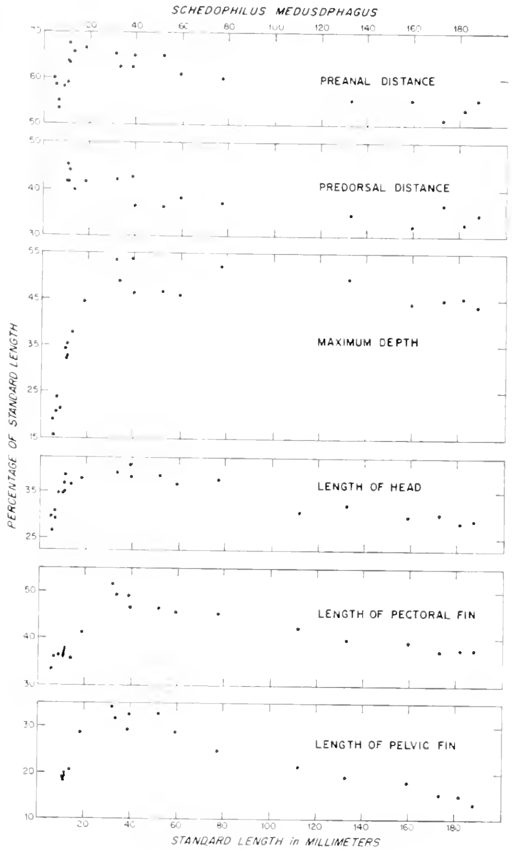


Figure 4. Scatter diagram of the early growth in the soft-spined centrolophid *Schedophilus medusophagus*, a fish which grows to 500 mm SL.

Stromateoids do show high resistance to the toxins of jellyfish (Lane, 1960; Maul, 1964) but they are by no means immune to it (Garman, 1896; Totton, 1960). Besides the relatively high resistance to the toxins, simple avoidance of the tentacles and the characteristic heavy coating of slime probably are important in allowing the fishes to swim with impunity under their hosts.

Because of the efficient shredding of food by the papillae, stomach contents of stromateoids are largely unidentifiable. Shredded transparent tissues, probably from jellyfish, ctenophores, and salps, predominated in stomachs examined. But I have also

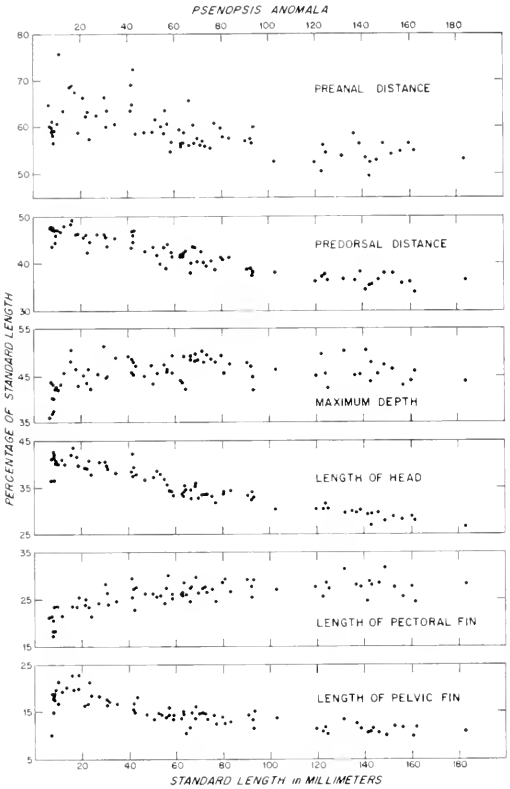


Figure 5. Scatter diagram of the growth in the hard-spined centrolophid *Psenopsis anomola.*

found remains of fishes, large crustaceans, and, rarely, squids.

With growth, marked changes occur. The fish are no longer in the immediate upper layers, but tend to live deeper in the water. The typically banded pattern of the young fish gives way to the plainer colors of the adult. The most pronounced changes are in relative proportions. Allometry is the rule among stromateoids. Generally, the relative length of the head, length of the pelvic fins, predorsal distance, and preanal distance increase rapidly, then decrease with growth. The relative length of the pectoral fin and the maximum depth may increase steadily, or increase and then decrease. Allometry is especially marked in nomeids (Fig. 3), most of which have a similar pattern of growth, and centrolophids (Figs. 4, 5). The growth curves given for *Tetragonurus* (Grey, 1955) are fairly regular, and rarely show a range of variation exceeding ten per cent. McKenney's (1961) curves for *Ariomma*, perhaps based on two species, likewise show regular and little variation. The pectoral fin of the stromateids may relatively lengthen or shorten with age and the fin lobes may be very long in the young, but the allometry is in general not remarkable in this family.

The largest stromateoids are the centrolophids, many of which reach three feet in length. A large *Centrolophus* or *Hyperoglyphe* will exceed four feet. A few nomeids attain two feet, but most are smaller. There is a diminutive species group in the family; its members rarely exceed six inches. Tetragonurids are said to reach two feet in length (Fitch, 1951). The largest reported ariommid was almost three feet long (Klunzinger, 1884), but most seem to be much smaller. A large stromateid barely exceeds 18 inches.

Stromateids, the subjects of substantial fisheries in the eastern United States, India, China, and Japan, and ariommids, with commercial potential but as yet unfished, are schooling fishes. The centrolophids *Psenopsis* and *Hyperoglyphe*, commercial fishes in Japan, and *Seriolella*, fished to a lesser extent in Peru, Chile, and Australia, are also found in shoals. Numerous young specimens of the more oceanic stromateoids are often taken by dipnet collecting, but data is too sparse, and large specimens too few, to know whether these fishes occur in schools or not.

Little is known of the breeding of stromateoids. The eggs are pelagic. Those of *Peprilus triacanthus* are described as buoyant, transparent, and containing a large oil globule (Bigelow and Schroeder, 1953). All species seem dioecious. There is some evidence that the sexes may be slightly dimorphic, with respect to color and/or relative proportions.

Relationships. The stromateoid fishes are a well-defined unit. Pharyngeal sacs are the diagnostic character. These are present in all species, and are readily apparent on dissection. A somewhat similar organ is found in *Dorosoma*, a clupeoid (Miller, 1964), and in *Trisotrophis*, a serranid (Katayama, 1959).

Within the group, there is a broad spectrum from primitive to highly advanced forms. Between existing families, there is evidence of phyletic relationships. The natural coherence of the group and the tendency toward direct internal lines from the generalized to the specialized condition, makes it unlikely that the stromateoids have given rise to other groups. *Tetragonurus*, a highly specialized form, is sometimes placed in a suborder of its own, in which case it would be considered a derived group. *Tetragonurus* is certainly far removed from the mainstream of stromateoid evolution, but its degree of divergence is probably not great enough to warrant subordinal recognition. It retains the characteristic sacs, and is here considered the sole genus of the stromateoid family Tetragonuridae.

Günther (1880) considered the stromateoids a subdivision of the scombroids. Little subsequent attention has been paid to the relationships of the suborder, with the exception of Boulenger (1904) and Holt and Byrne (1903) who found cause for including them in the Percesoces. General classifications have continued to place them near the Scombroidei. There is a close resemblance between some stromateoids and the carangids, a group standing near the base of the scombroid stem (Suzuki, 1962).

Freihofer's (1963) survey of patterns of the *ramus lateralis accessorius* (a facial nerve complex) in fishes indicated that the stromateoids might be related to entirely different groups. His pattern-10 teleosts are a novel assemblage, composed of stromateoids (centrolophids, nomeids, stromateids), pomatomids, kyphosids, scorpidids (excluding *Scorpis*), arripidids, girellids, theraponids, and kuhliids. The nematistiids have a reduced pattern 10.

The pattern of a nerve complex, because of its basically conservative nature, should be a strong taxonomic character in dealing with higher categories. The common pattern of the *ramus lateralis accessorius* in the above families is probably good cause for considering them a phylogenetic unit. But is there additional evidence for lumping these families together? The stromateoids, almost without exception, have a bony bridge across the inside of the anterior vertical canal of the ear. Because of its widespread occurrence in the diverse forms of the suborder, I consider this a conservative character, useful at higher categories. This bridge is also present, at least in some species and at some stage of growth, in pattern-10 families. The bridge is absent, however, in other perciform families examined (see Table 1 and Material examined, p. 43).

Many pattern-10 families have characteristics common to basal perciforms. Many have 25 vertebrae, seven branchiostegal rays, a suborbital shelf, and a caudal skeleton near to the basal perciform type with six hypurals and three epurals. In most, the shape of the body is of the most generalized type. The general impression is of an older group of fishes which have managed to remain successful without diverging too far from the basal stock.

The common *ramus lateralis accessorius* pattern and the bridge over the anterior vertical canal are strong evidence for considering that the relatively specialized stromateoids arose from somewhere in this relatively undifferentiated assemblage. Nonetheless, it is unlikely that the stromateoids are the descendents of any living pattern-10 family, all of which are specialized in some respect. With the present imperfect knowledge of the comparative osteology of these groups, the best that can be said is that all share a common heritage.

The fin spines of stromateoids are not remarkably developed, and the teeth are uniserial in the jaws. Pattern-10 families with moderate-to-weak fin spines and a major row of uniserial teeth (some have

TABLE 1. SELECTED CHARACTERS OF SOME TELEOSTEAN FAMILIES. + DENOTES PRESENCE; — ABSENCE.

	RLA PATTERN[1]	AVC BRIDGE	VERTEBRAE[2]	SUB-ORBITAL SHELF[3]	BRANCHIOSTEGAL RAYS[4]
Centrolophidae	10	+	25–60	+	7
Stromateidae	10	+	30–48	—	5–6
Nomeidae	10	+	30–42	*	6
Ariommidae	*	+	30–33	*	6
Tetragonuridae	*	+	43–58	*	5–6
Pomatomidae	10	+	26	+	7
Kyphosidae	10	+	25	—	7
Arripididae	10	+	25	+	7
Scorpididae	10	+	25	+	7
Girellidae	10	—	27	+	7
Theraponidae	10	±	25	+	6
Kuhliidae	10	+	25	—	6
Nematistiidae	reduced 10	—	*	*	*
Apolectidae	9	+	24	*	7
Carangidae	9	—	24–27	±	7
Scombridae	none	—	31–66	—	7
Coryphaenidae	*	—	30–33	—	7
Atherinidae	6	—	31–60	±	5–6
Monodactylidae	reduced 9	—	24	+	6
Ephippidae	9	—	24	+	6

* not examined

[1] From Freihofer 1963

[2] Largely from Regan 1913, and Bertin and Arambourg 1958

[3] From Smith and Bailey 1962

[4] Largely from Günther 1859, 1860, 1861

very reduced rows behind the major row) are the pomatomids, kyphosids, and scorpidids. These could be the groups most closely associated with the line leading to the stromateoids. The arripidids, girellids, theraponids, and kuhliids have teeth in bands and heavy fin spines.

There is a strong resemblance between the kyphosids and the centrolophids, the primitive stromateoids. In both, the general rule is 10 + 15 vertebrae, a caudal skeleton with six hypural and three epural elements, a perforate ceratohyal, an expanded lacrimal, and scaled fin bases. Behind the major row of uniserial teeth in *Kyphosus*, there are rows of small villiform teeth (Moore, 1962); there is only one row of teeth in centrolophids. The kyphosids, however, lack the subocular shelf found in some centrolophids.

The kyphosids are today one of the most primitive perciform families. They retain the teeth on the ectopterygoid and endopterygoid and the two foramina in the facial wall of the *pars jugularis*, conditions associated with the beryciform level. Patterson (1964) offers evidence for the derivation of the kyphosids, scorpidids, and monodactylids from the Cretaceous polymixioid *Berycopsis*. If this is the case, and if the stromateoids arose from near the kyphosid stem, a direct line can be drawn from the berycoid level to *Pampus*, one of the most advanced perciforms.

The carangids were probably derived from the Cretaceous dinopterygoid *Aipichthys* (Patterson, 1964). Their development,

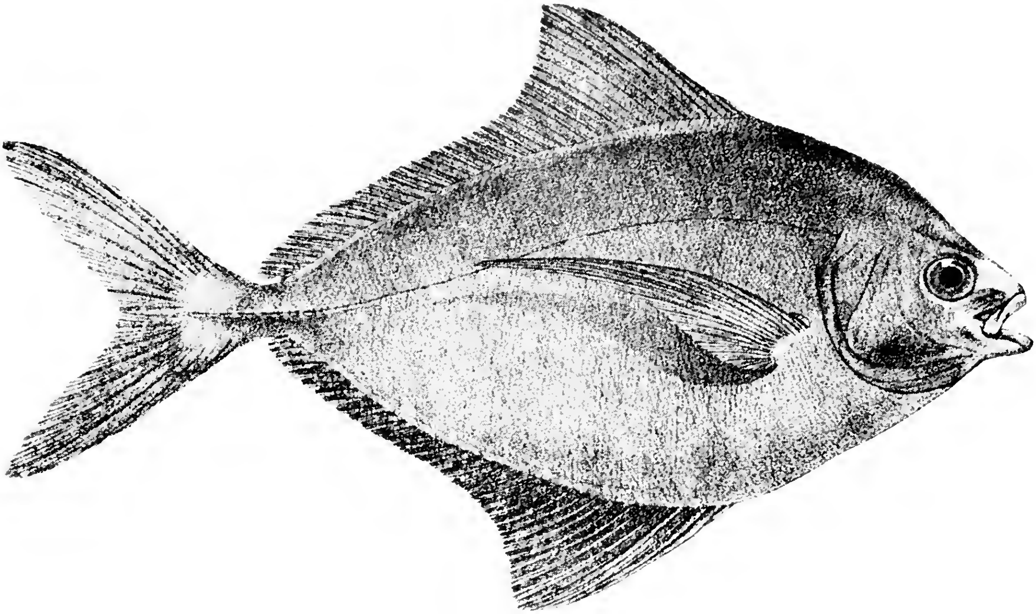


Figure 6. *Parastromateus niger*, drawing of a 15-inch specimen, from Day, 1875.

from beryciform to perciform level, has been independent of the line which produced the stromateoids. The resemblances between certain members of these two groups must therefore be considered an evolutionary convergence.

A problem remains in the genus *Parastromateus* (= *Apolectus*) (Fig. 6). Bloch (1795) described the sole representative of the genus as a species of *Stromateus*. The shape of the body and the small pelvics which are lost with age were good cause for this action. But *Parastromateus* lacks pharyngeal sacs and, because of this, Regan (1902) removed the genus from the stromateoids and placed it in the carangids. More extensive comparisons by Apsangikar (1953) supported the separation, but divergence from the carangids was noted and the new subfamily Parastromateinae of the Carangidae proposed. Suzuki (1962), in his great review of Japanese carangids, followed Jordan (1923) in considering *Parastromateus* the sole representative of a monotypic family.

Parastromateus is a pattern-9 teleost, as are the carangids (Freihofer, 1963), but has a bony bridge over the anterior vertical canal of the ear, as do the stromateoids. The only reason, other than the bony bridge, for relating *Parastromateus* to the stromateids is the similarity in body form. *Parastromateus*, however, has 10 + 14 vertebrae, while all stromateids have at least 13 + 17. Even if *Parastromateus* is related to the stromateids, the relationship is at most a very distant one.

Within the suborder Stromateoidei, there are three distinct groups, the primitive centrolophids, the intermediate nomeids with their specialized off-shoots the tetragonurids and the ariommids, and the advanced stromateids. The stromateids are an obvious derivative of the centrolophid line. The nomeids, an evolutionary grade above the centrolophids, have evolved parallel to the centrolophids, but from an earlier common ancestor. The probable relationships between the stromateoid families, discussed

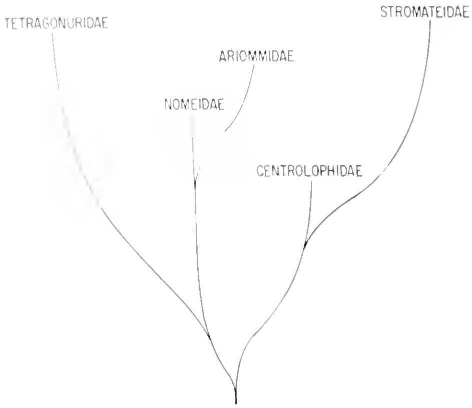


Figure 7. Dendrogram showing probable relationships of the five stromateoid families.

more fully in the family accounts, are expressed diagrammatically in Figure 7.

Fossils. The Cretaceous *Omosoma*, usually considered a stromateid (Arambourg, 1954) has been shown by Patterson (1964) to be a polymixioid, standing, interestingly enough, near *Berycopsis. Carangodes cephalus*, from the Monte Bolca beds of Austria, is well described and figured by Heckel (1856). Though it looks somewhat like some stromateoids and was considered a nomeid by Jordan (1923), the diagnostic characters are missing and it cannot be affiliated with this group with any certainty. *Aspidolepis* Geinitz 1868, based on a scale, was considered a stromateid by Jordan (1923). But the scales of the majority of stromateoids are in no way distinctive, and thus the possible relationships of this fossil genus cannot be determined. Two new fossil genera have been found by Bonde (1966) in the lower Eocene Mo-clay of Denmark.

Key to Stromateoid Families

1 (6). Two dorsal fins, distinctly, though scarcely, separated, the first usually with ten to twenty spines; if there are fewer than ten spines, the longest spine is about the same length as the longest dorsal finray. Pelvic fins always present. Vomer, palatines, and basibranchials toothed or not. 2

2 (5). The first dorsal fin with about ten long, slender spines, often folded into a groove, the longest spine nearly as long as, or longer than, the longest finray in the second dorsal. Anal finrays 14 to 30. Scales cycloid, thin, deciduous. Fleshy lateral keels on peduncle near caudal fin base absent or only slightly developed. Vertebrae 29 to 42. 3

3 (4). Vomer, palatines, and usually basibranchials with small, often almost indistinguishable, teeth. Caudal peduncle compressed, its least depth greater than 5 per cent of the standard length, without lateral keels. Usually more than fifteen rays in both the dorsal and anal fins. .... NOMEIDAE, p. 76

4 (3). Vomer, palatines, and basibranchials toothless. Caudal peduncle square in cross-section, its least depth less than 5 per cent of the standard length, with two low lateral keels on each side near caudal fin base. Fourteen or fifteen rays in both the dorsal and anal fins. .... ARIOMMIDAE, p. 88

5 (2). The first dorsal fin with ten to twenty short spines, the longest only half the length of the longest finray in the second dorsal. Anal finrays 10 to 16. Scales keeled, heavy, very adherent. Modified scales form two well developed lateral keels on each side of peduncle near caudal fin base. Vertebrae 43 to 58. .... TETRAGONURIDAE, p. 94

6 (1). A continuous dorsal fin, or two dorsal fins scarcely separated, the first with less than ten spines; if spines are present, the longest spine is less than half the length of the longest dorsal finray. Pelvic fins present or absent. Vomer, palatines, and basibranchials toothless. 7

7 (8). Pelvic fins always present. None or one to five weak spines, or five to nine stout spines precede dorsal finrays. Anal finrays 15 to 30. Median fins never falcate; their bases rarely the same length. Jaw teeth all conical, simple. Supramaxillary bone usually present, but hard to find in some. Seven branchiostegal rays. Vertebrae 25 to 30 or 50 to 60. .... CENTROLOPHIDAE, p. 53

8 (7). Pelvic fins never present in adults, rarely present in the young. No stout spines precede dorsal finrays, but, in some species, five to ten small blade-

like spines resembling the ends of free interneurals protrude ahead of the fin. Anal finrays 30 to 50. Median fins often falcate; their bases about equal in length. Jaw teeth laterally compressed, with three cusps. No supramaxillary bone. Five or six branchiostegal rays. Vertebrae 30 to 48. .... STROMATEIDAE, p. 98

Family CENTROLOPHIDAE

Type genus: *Centrolophus* Lacépède 1803

Centrolophes. Cuvier and Valenciennes, 1833:330 (descr.).

Centrolophinae. Gill, 1861:34 (list); 1862:127 (genera listed); 1884:666–667 (def., gen.). Jordan and Gilbert, 1882:450 (name, descr.).

Centrolophidae. Jordan and Evermann, 1896: 962 (descr.; North America). Jordan, 1923: 182 (in part, list). Norman, 1937:115 (descr., relationships; Chile). Tortonese, 1959:57 (in part, revision: Gulf of Genoa).

Lirinae. Bühler, 1930:62 (in part, morph., digestive system).

Nomeidae. Berg, 1940:323 (in part, dist.); 1955: 248 (part, dist.). Norman, 1957:503 (in part, def., genera listed).

Diagnosis. Stromateoid fishes with pelvic fins present in adults, continuous dorsal fin, toothless palate, seven branchiostegal rays, and six hypural bones in the tail. The papillae in the pharyngeal sacs with irregularly shaped bases, arranged in ten to twenty longitudinal bands.

Description. Body slender to deep, usually somewhat compressed. The rayed portion of the continuous dorsal fin preceded by six to eight short stout spines in *Hyperoglyphe*, *Seriolella*, and *Psenopsis*; none or one to five thin weak spines in *Centrolophus, Schedophilus*, and *Icichthys*. In the latter group and in *Psenopsis* the spines graduating to the rayed portion of the fin; in the others not. Three anal fin spines, not separated from the rays. Pelvic fins usually attached to the abdomen by a thin membrane and folding into a broad shallow groove. Head conspicuously naked, usually covered with small pores. Scales cycloid, but with minute cteni in *Schedophilus medusophagus*, and usually deciduous. Tubed scales of lateral line extending onto peduncle. Margin of preopercle usually moderately denticulate, but spinulose in most young stages and in *Schedophilus*. Opercle thin, with two flat, weak spines; the margin denticulate. Seven branchiostegal rays. Mouth large, maxillary extending at least to below eye. A nearly uniserial row of small conical teeth in the jaws; vomer, palatines, and basibranchials toothless. Supramaxillary bone present in most but absent in *Psenopsis.* Adipose tissue around eye usually not conspicuously developed. Vertebrae 25 or 26 in most species, except 50 to 60 in *Icichthys.* Caudal skeleton with six hypurals and usually three epurals, except two in *Icichthys.* Pharyngeal sacs with irregularly shaped papillae in ten to twenty longitudinal bands. Teeth seated directly on top of the bony base. Adults one to four feet in length, usually dark-colored and without conspicuous pattern.

Distribution. Centrolophids are pelagic, usually on the high seas and over the edge of the continental shelves, although *Psenopsis* and *Seriolella* occur in shallow water near the coast. Some are found in tropical waters, but the majority are fishes of temperate seas. The soft-spined centrolophids (*Centrolophus*, *Icichthys*, and *Schedophilus*) tend to be more oceanic than the hard-spined centrolophids (*Hyperoglyphe*, *Seriolella*, and *Psenopsis*). To some extent, the distributions of these two groups complement each other (Figs. 52, 53).

The distribution of the centrolophids is in part a relict distribution. *Centrolophus* is bipolar, found in the North Atlantic, South Africa, and Southern Australia and New Zealand. *Icichthys*, very similar in appearance to *Centrolophus*, is bipolar in the Pacific. In the waters from Australia to the coasts of Chile, the endemic genus *Seriolella* has evolved.

No centrolophids occur across the broad tropical Pacific or Indian Oceans.

Relationships. The Centrolophidae stand at the base of the line leading to the Stromateidae. Of all stromateoids, they are the least differentiated from the perciform ancestor. Most have 25 vertebrae, the well-known basic perciform number. Most have a supramaxillary bone. There are seven branchiostegal rays, and the caudal skeleton (Figs. 10, 12, 23) is of the basic perciform type (Gosline, 1961a). In this sense, the centrolophids can be considered the most primitive stromateoids.

The caudal skeleton of the nomeids, with hypurals 2 + 3 and 4 + 5 of the basic six fused, could easily have been derived from the centrolophids. The stellate papillae, also, and loss of one branchiostegal represent a grade above the centrolophid condition. But teeth are present on the vomer, palatines, and basibranchials of the nomeids, in general a primitive condition (Liem, 1963), and are absent in the centrolophids. This makes it unlikely that the former group has been derived from the latter. Rather, the two must represent approximately parallel lines, derived from an earlier form which had palatal dentition.

There is a fairly close and probably direct relationship between the advanced centrolophid genera *Seriolella* and *Psenopsis* and the stromateids *Stromateus* and *Peprilus*. Fishes in both these groups have well-ossified sclerotic bones, minute body pores, slender tapering branchiostegals, and extremely deciduous scales.

Key to Centrolophid Genera

1 (6). Spines of the dorsal fin weakly developed and all graduating to the dorsal rays. 2

2 (5). Weak denticulations on preopercular margin. Origin of dorsal fin usually well behind insertion of pectoral fins, but over pectoral insertion in very small specimens. Body elongate, maximum depth usually less than 30 per cent of the standard length. 3

3 (4). Total elements in anal fin 23 to 27. Scales small, very deciduous, preopercle and cheek naked. Scales in lateral line 160 to 230. Vertebrae 25. .... *Centrolophus*, p. 62. Fig. 13

4 (3). Total elements in anal fin 27 to 31. Scales moderate in size, not especially deciduous, present on preopercle and cheek. Scales in lateral line 100 to 130. Vertebrae 50 to 60. .... *Icichthys*, p. 65. Fig. 15

5 (2). Nine to fifteen small spines on preopercular margin. Origin of dorsal fin usually before insertion of pectoral fins, but over pectoral insertion in very large specimens. Body deep, maximum depth usually greater than 35 per cent of the standard length. .... *Schedophilus*, p. 58. Fig. 11

6 (1). Five to nine stout dorsal spines, shorter than and not graduating (graduating slightly in *Psenopsis*) to the dorsal rays. 7

7 (8). Dorsal finrays 19 to 25; anal finrays 14 to 21. Preopercular margin spinulose. Scales not especially deciduous. Lateral line arched anteriorly, straightening out over the anal fin. Adipose tissue around eye not well developed. Sclerotic bones not well ossified; golden iris appears as a complete ring. .. *Hyperoglyphe*, p. 54. Fig. 8

8 (7). Dorsal finrays 25 to 40; anal finrays 18 to 30. Preopercular margin entire or finely denticulate. Scales very deciduous. Lateral line follows dorsal profile. Adipose tissue around eye well developed. Sclerotic bones usually well ossified; golden iris appears divided by a vertical bar. 9

9 (10). Insertion of pelvic fins behind insertion of pectorals. Supramaxillary bone present. At least seven more dorsal finrays than anal finrays. Usually eight dorsal spines, the third, fourth, and fifth the longest. .... *Seriolella*, p. 69. Figs. 18, 19

10 (9). Insertion of pelvic fins before or just under insertion of pectorals. Supramaxillary bone absent. Number of dorsal finrays never exceeds number of anal finrays by more than five. Five to seven dorsal spines, increasing in length posteriorly. .... *Psenopsis*, p. 72. Fig. 21

Genus *HYPEROGLYPHE* Günther, 1859

Figure 8

Palinurus DeKay, 1842:118. (Type species: *Coryphaena perciformis* Mitchill, 1818:244, by monotypy. New York Harbor. Preoccupied by *Palinurus* Fabricius, 1798, Crustacea.)

Hyperoglyphe Günther, 1859 (June):337. (Type species: **Diagramma porosa* Richardson, 1845: 26, by monotypy. Coasts of Australia. A synonym of *Perca antarctica* Carmichael, 1818: 501.)

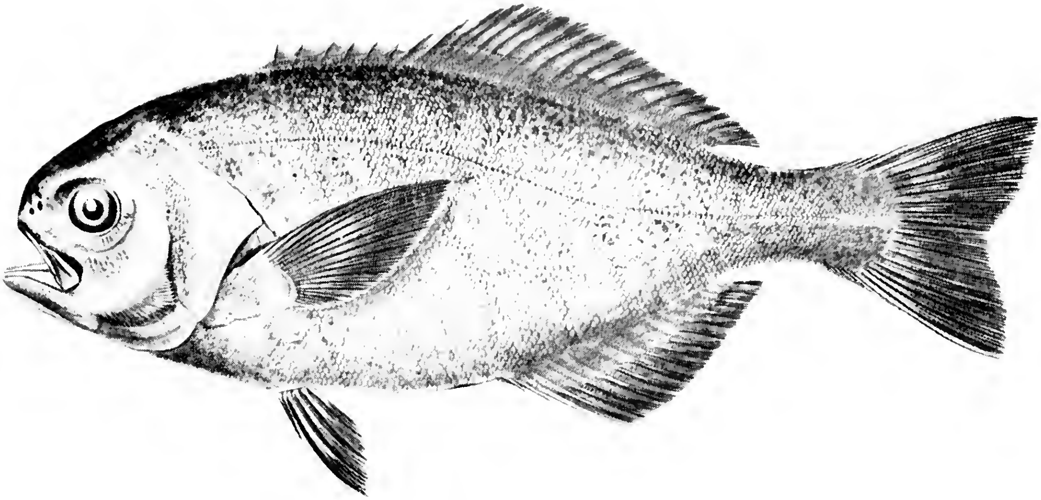


Figure 8. *Hyperoglyphe perciforma, drawing of on approximately 200-mm specimen, courtesy of the Smithsonian Institution.*

Palinurichthys Bleeker, 1859 (November):22. (Substitute name for *Palinurus* DeKay, and therefore taking the same type species, *Coryphaena perciformis* Mitchill, 1818:244.)

Palinurichthys Gill, 1860:20. (Substitute name, proposed independently from Bleeker, for *Palinurus* DeKay, and therefore taking the same type species, *Coryphaena perciformis* Mitchill, 1818:244.)

Pammelas Günther, 1860:485. (Substitute name for *Palinurus* DeKay, and therefore taking the same type species, *Coryphaena perciformis* Mitchill, 1818:244.)

Eurumetopos Morton, 1888:77. (Type species: *Eurumetopos johnstonii* Morton, 1888:77, by monotypy. Tasmania. A synonym of *Perca antarctica* Carmichael, 1818:501.)

Toledia Miranda-Ribeiro, 1915:5. (Type species: *Toledia macrophthalma* Miranda-Ribeiro, 1915:5, by monotypy. Macahé, Brazil.)

Ocyerius Jordan and Hubbs, 1925:226. (Type species: *Centrolophus japonicus* Döderlein *in* Steindachner and Döderlein, 1885:183, by original designation. Tokyo, Japan.)

The combination of less than 25 dorsal finrays, about eight short spines not increasing in length to the rays in the dorsal fin, toothless palate, pelvic insertion under pectoral fin base, supramaxillary bone present, and lateral line arched anteriorly straightening out over the anal fin, distinguishes *Hyperoglyphe* from all other stromateoid genera. The name, a feminine noun, is from the Greek ὑπὲρ, above, + γλυφὴ, groove, in reference to the deep longitudinal groove in the roof of the mouth.

Description. Body moderately deep, maximum depth around 30 to 35 per cent of the standard length; musculature firm. Caudal peduncle broad, of moderate length. Dorsal fin originating over or a little behind insertion of pectoral fins, continuous, six to eight short stout spines not graduating to the longer rays. The longest spine half the length of the longest ray. Anteriormost finrays the longest, those that follow shorter, 19 to 25 finrays in all. Anus at mid-body, in a slit. Anal fin originating a little behind middle of body, three spines precede the 15 to 20 rays. Pectoral fin rounded in the young, pointed in adult. Pelvic fins inserting under end of pectoral fin base, attached to abdomen by a small membrane and folding into a shallow groove. Caudal fin broad, emarginate to moderately forked in adult. Scales cycloid, moderate in size, somewhat deciduous, covering bases of median fins. Lateral line arched anteriorly, straightening out over middle of anal fin and extending onto peduncle. Skin moderately thick; extensive subdermal canal system communicating to the surface through small pores. Head around 33 per cent of the standard length, broad. Top of head not scaled, pores prominent, naked skin projecting backward over nape. Eye moderate to large, no adipose tissue. Nostrils located near tip of obtuse snout, large, the anterior round, the posterior a slit. Angle of gape extending below eye. Premaxillary not protractile. Lacrimal bone partially covering anterior portion of upper jaw when mouth is closed, end of maxillary remaining exposed. Supramaxillary present. Jaw teeth very small, pointed, uniserial, close-set; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin; opercle with two weak flat spines, scaled, margin very finely denticulate or entire; preopercle not scaled, striated, margin with numerous very small spinules. Angle of preopercle rounded, bulging backward slightly. Gill-rakers heavy, slightly longer than the filaments, finely toothed on inner edge, spaced, about 16 on lower limb of first arch. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal. Scapula visible. Vertebrae 10 + 15 = 25. Stomach a simple sac; intestine long. Pyloric caeca numerous, in a mass resembling a raspberry.

Base color green-grey or blue-grey to reddish brown. Back dark, sides and below lighter, sometimes silvery. Head dark, iris a golden ring, opercle often silvery. Median fins usually darker than the body. Color pattern irregularly striped, mottled, or clear, changeable in life. Inside of mouth and gill cavity light. Peritoneum light with minute dark speckles.

Natural history. Though *Hyperoglyphe* occurs throughout the world and is fished commercially in Japan, very little is known of its habits. The young commonly occur under flotsam, but usually not under jellyfish, in surface waters near the edge of the continental shelf. The larger adults form shoals in deep water, perhaps fairly near the bottom.

Figure 9. Branchial region of *Hyperoglyphe perciforma*, drawing of a cleared-and-stained preparation from a 173-mm SL specimen. Elements identified in Figure 2.

Small *H. perciforma* two to four inches long occur off the New England coasts under floating objects in great numbers during the summer. By fall, these fish have doubled or even tripled their size. With the approach of cold weather they disappear. Only recently has it been found that adult *H. perciforma* attain three feet in length, and live in deep water off the coast of west Florida (Schwartz, 1963). This discovery bears out an earlier suggestion by Merriman (1945) that the fish observed off New England were the young of a much larger bathypelagic species. In Japan, the large adults had been marketed long before the young were first discovered (Abe, 1955).

Bigelow and Schroeder (1953) reported small fishes and crustacean remains from stomachs of *Hyperoglyphe perciforma*. The fish may also feed occasionally on barnacles (Cornish, 1874; Holt and Byrne, 1903). At times *H. porosa* feeds heavily on the tunicate *Pyrosoma atlanticum* (Cowper, 1960).

Relationships. Hyperoglyphe is the central genus of the Centrolophidae. The mem-

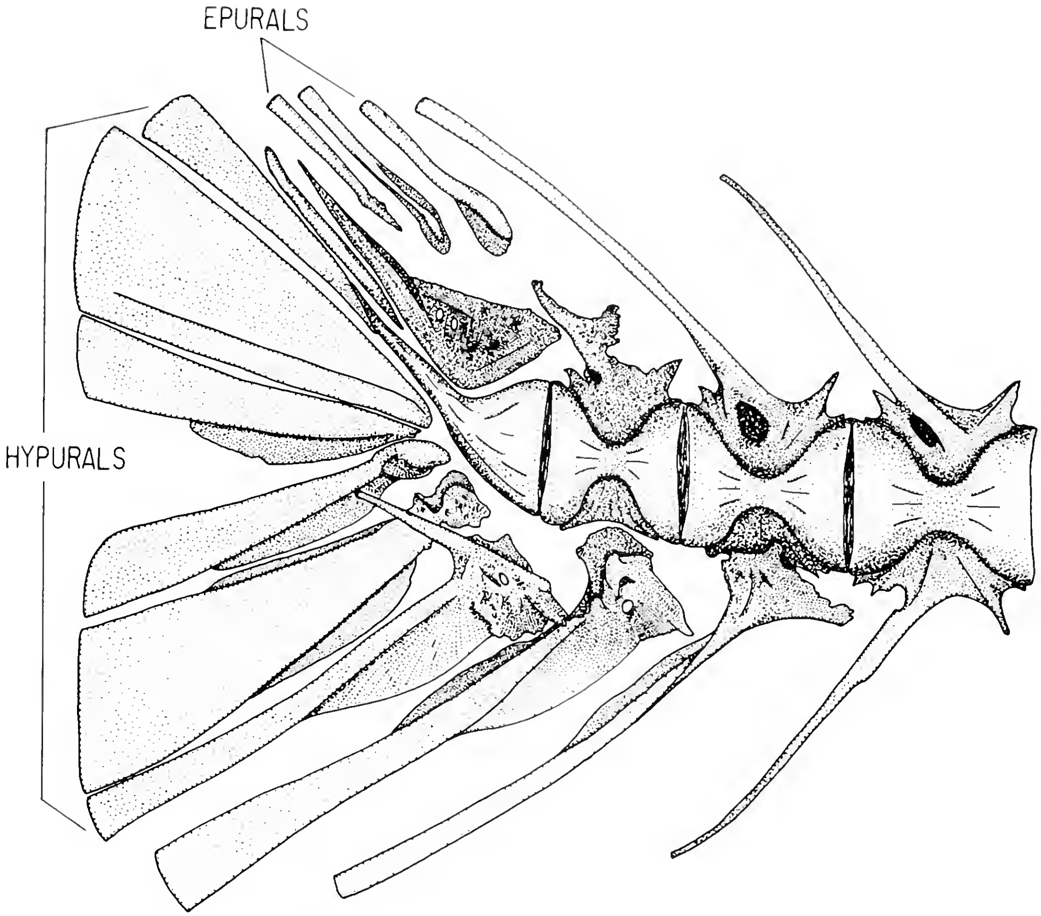


Figure 10. Caudal skeleton of *Hyperoglyphe perciforma*, drawing of a cleared-and-stained preparation from a 50-mm SL specimen. All elements identified in Figure 1.

bers of this genus are the most generalized fishes in the entire suborder, and are probably not unlike the ancestral form. The relatively low number of median finrays, the stout spines in the median fins, the seven blunt branchiostegal rays (Fig. 9), the 25 vertebrae, the spiny preopercle, and the large size attained, are all basal characters. The caudal skeleton (Fig. 10) is of the generalized perciform type.

Hyperoglyphe has given rise, on the one hand, to the more oceanic soft-spined centrolophids, through *Schedophilus* to *Centrolophus* and *Icichthys*. The major change has been the softening of the fin spines and of the tissues in general. On the other hand, *Hyperoglyphe* has given rise to the more coastal, advanced, hard-spined genera *Seriolella* and *Psenopsis*. The change in this direction has been one of slight refinement in the branchial region and a tendency toward fusion of elements in the caudal skeleton.

Species. *Hyperoglyphe* is a wide-ranging genus. The species are found in the slope water off the east coasts of the New World, in the Gulf of Mexico, near St. Helena and Tristan da Cunha, along the west coast of

Africa, in Australia–New Zealand, and in Japan.

There is little problem of synonymy, since the species are fairly distinct from one another. The changes that occur with growth, however, remain a stumbling block. The species in *Hyperoglyphe* are:

Hyperoglyphe antarctica (Carmichael, 1818) = *Perca antarctica* Carmichael. Tristan da Cunha, South Africa, southern Australia, and New Zealand, type locality Tristan da Cunha. D VIII, 19–21. A III 15–16. P 18–20. Gill-rakers 5 + 1 + 14. Vertebrae 10 + 15. This is the most primitive species in *Hyperoglyphe*, and stands nearer to the base of the stromateoid stem than any other fish. It attains a very large size. McCulloch (1914) reports a specimen 1072 mm long. The low median finray counts, large mouth, and a characteristic patch of scales on the otherwise naked occiput distinguish this species from all others. Synonyms are: **Diagramma porosa* Richardson, 1845, from Australia; *Eurumetopos johnstonii* Morton, 1888, from Tasmania; and *Seriolella amplus* Griffin, 1928, from Bay of Plenty, New Zealand.

Hyperoglyphe bythites (Ginsburg, 1954) = **Palinurichthys bythites* Ginsburg. Gulf of Mexico, type locality off Pensacola, Florida. D VII–VIII, 22–25. A III 16–17. P 20–21. Gill-rakers 6–7 + 1 + 15–16. Vertebrae 10 +15. Possibly a synonym of *H. macrophthalma* (Miranda-Ribeiro, 1915). This species has more dorsal finrays and a larger eye than *H. perciforma* (Mitchill, 1818).

Hyperoglyphe perciforma (Mitchill, 1818) = *Coryphaena perciformis* Mitchill. East coast of North America, Florida to Nova Scotia, type locality New York Harbor. D VII–VIII, 19–21. A III 15–17. P 20–22. Gill-rakers 5–7 + 1 + 15–17. Vertebrae 10 + 15 (skel.). This fish is the common "barrelfish" of the offings of New England. Young specimens have followed floating logs across the Atlantic to the British Isles (Holt and Byrne, 1903). *Pimelepterus cornubiensis* Cornish, 1874, is a synonym based on a specimen which floated to Cornwall in a box.

Hyperoglyphe japonica (Döderlein *in* Steindachner and Döderlein, 1885) = *Centrolophus japonicus* Döderlein. Seas of Japan, type locality Tokyo. D VIII, 22–24. A III 17–19. P 21–23. Gill-rakers 6–7 + 1 + 15–16. Vertebrae 10 + 15. This fish is the "medai" of Japanese fisheries literature. It is the subject of a small, deep, hand-line fishery. A probable synonym is **Lirus paucidens* Günther, 1889, based on three small specimens captured by the CHALLENGER somewhere between New Guinea and Japan.

Hyperoglyphe moselii (Cunningham, 1910) = *Leirus moselii* Cunningham. St. Helena, and coasts of Angola and South Africa, type locality St. Helena. D VI, 23–25. A III 19–20. P 20–22. Gill-rakers about 7 + 1 + 15. The type is described as having but one spine and 25 rays in the dorsal fin. The specimen is so large and heavy that I was unable to lift it and its container off the shelf in the British Museum, and hence did not get to examine it closely during my brief visit there. At such a large size, the first five spines in the dorsal may be buried in the skin, where Cunningham could have overlooked them. Probable synonyms are *Palinurichthys pringlei* Smith, 1949, and *Palinurichthys matthewsi* Smith, 1960, both from South Africa.

Hyperoglyphe macrophthalma (Miranda-Ribeiro, 1915) = *Toledia macrophthalma* Miranda-Ribeiro. Brazil, type locality Macahé. D VII, 26. A 20 (from Miranda-Ribeiro, 1915). Known from a single specimen 68 cm long. Possibly a synonym of *H. moselii* (Cunningham, 1910).

Genus *SCHEDOPHILUS* Cocco, 1839

Figure 11

Leirus Lowe, 1833:143. (Type species: **Leirus bennettii* Lowe, 1833:143, by monotypy. Madeira, Atlantic Ocean. Preoccupied by *Leirus* Dahl, 1823, Coleoptera. A junior synonym of **Centrolophus ovalis* Cuvier and Valenciennes, 1833:346.)

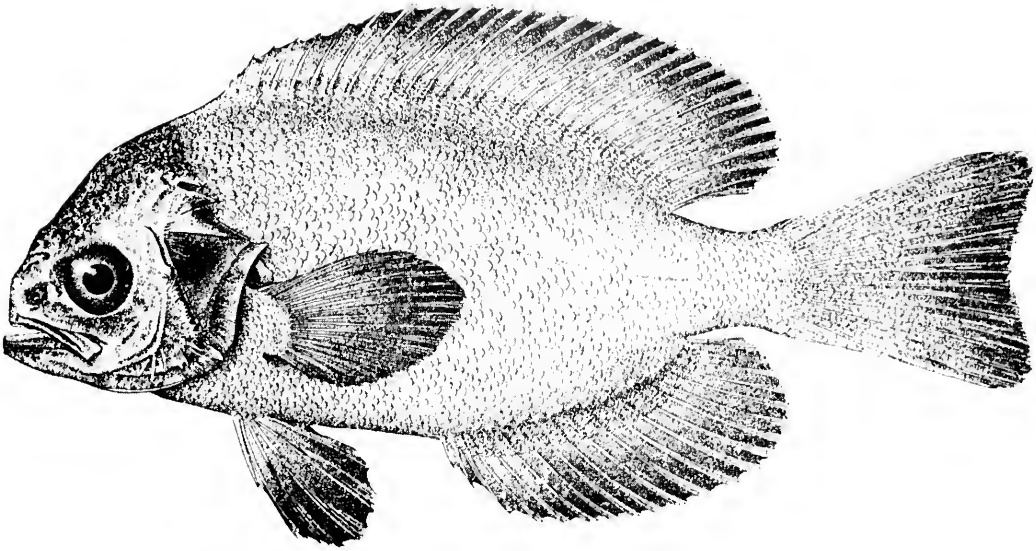


Figure 11. *Schedophilus pemarco*, drawing of a 245-mm specimen, from Poll, 1959.

Schedophilus Cocco, 1839[1]:57. (Type species: *Schedophilus medusophagus* Cocco, 1839:57, by monotypy. Messina.)

Mupus Cocco, 1840[1]:237. (Type species: *Mupus imperialis* Cocco, 1840:237, by monotypy. Messina. A synonym of **Centrolophus ovalis* Cuvier and Valenciennes, 1833:346.)

Lirus Agassiz, 1846:213. (Emendation of *Leirus* Lowe, 1833:143, and therefore taking the same type species, **Leirus bennettii* Lowe, 1833:143, a junior synonym of **Centrolophus ovalis* Cuvier and Valenciennes, 1833: 346.)

Crius Valenciennes, 1848:43. (Type species: **Crius bertheloti* Valenciennes, 1848:45, by original designation. Canary Islands, Atlantic Ocean. A synonym of **Centrolophus ovalis* Cuvier and Valenciennes, 1833:346.)

Hoplocoryphis Gill, 1862:127. (Type species: **Schedophilus maculatus* Günther, 1860:412, by original designation. Seas of China.)

Eucrotus T. H. Bean, 1912:123. (Type species: *Eucrotus ventralis* T. H. Bean, 1912:123, by monotypy. Bermuda, Atlantic Ocean.)

Tubbia Whitley, 1943:178. (Type species: *Tubbia tasmanica* Whitley, 1943:179, by original designation. Eastern Tasmania.)

The combination of deep body, broad deep head, large eye, continuous dorsal fin with weak spines graduating to the rays and originating before the pectoral insertion, toothless palate, and prominent spines on the preopercular margin distinguishes *Schedophilus* from all other stromateoid genera. The name, a masculine noun, is from the Greek σχεδία, raft, + φίλος, friend, in reference to the fish's common association with floating objects.

Description. Body deep, maximum depth generally greater than 35 per cent of the standard length; musculature soft. Peduncle fairly broad, short. Dorsal fin originating before (or over in very large specimens) insertion of pectoral fins, continuous, three to seven weak spines graduating to the 23 to 50 rays. Anus and genital pore at midbody, in a slit. Anal fin originating behind middle of body, three long weak spines preceding the 16 to 30 rays. Median fins with compressed fleshy bases. Pectoral fin rounded in the young, pointed in adult, relative length decreasing with growth. Pelvic fins inserting under end of pectoral fin base, reaching to anus in young and juveniles, attached to abdomen by a membrane and folding into a shallow groove; relative length of fin decreasing markedly

---

[1] Tortonese (1959) has clarified the confusion surrounding the publication dates of Cocco's names.

with growth. Caudal fin broad, forked. Scales small to moderate, cycloid, or with one or two minute cteni in young *Schedophilus medusophagus*, deciduous, covering fleshy bases of the median fins. Lateral line arched anteriorly, straightening out about mid-body and extending onto peduncle. Skin thin; extensive subdermal canal system communicating to the surface through small pores. Head soft, broad and deep, usually greater than 25 per cent of the standard length, not scaled, naked skin projecting slightly backward over the nape. Eye large, no adipose tissue. Nostrils located near tip of obtuse snout, anterior nostril round, the posterior a slit. Angle of gape extending below eye. Premaxillary not protractile. Lacrimal bone covering anterior portion of upper jaw when mouth is closed, end of maxillary remaining exposed. Slender supramaxillary present. Jaw teeth very small, pointed, uniserial, close-set; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin; opercle with two weak flat spines, scaled, margin denticulate; preopercle not scaled, margin set with nine to eighteen prominent spines, angle of preopercle rounded, bulging back slightly. Gill-rakers heavy, about half the length of the filaments, toothed on inner edge, spaced; 10 to 16 on lower limb of first arch; a few rudimentary rakers present under large pseudobranch. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal. Scapula visible. Vertebrae 10 + 15, 16 or 20 = 25, 26 or 30, or 12 + 17 = 29. Stomach a simple sac; intestine long. Pyloric caeca numerous, dendritic.

Base color brown, bluish, or silvery. Median fins, pectorals, and pelvics usually darker than the body. Color pattern irregularly striped, mottled, or clear. Young of some have dark vertical stripes.

Natural history. Most species in *Schedophilus* are oceanic, rare, and, consequently, little is known concerning their biology. The young of *S. medusophagus* occurs commonly with jellyfish. The fish may feed very largely on medusae, but will also take small crustaceans. At a length of about 200 mm, *S. medusophagus* deserts its coelenterate companion, and descends to deeper water.

Adult *Schedophilus* appear very different from the younger stages. The relative length of the paired fins is greatly decreased, the body is much more elongate, and the mottled or barred pattern, typical of juveniles, is gone.

Relationships. Schedophilus provides the link between the soft-spined and the hard-spined centrolophids. The range of variation in the genus is great, and the species grade from the one condition to the other. The caudal skeleton (Fig. 12) is most like that of *Centrolophus* and *Icichthys.* The pharyngeal sacs and teeth are intermediate between those of *Centrolophus* and *Hyperoglyphe. Schedophilus ovalis* has fairly stout spines ahead of the median fins; in *S. medusophagus* the spines are soft and flexible.

Schedophilus is derived from the central *Hyperoglyphe* stock. As it has moved into a more oceanic environment, the spines on the preopercle have become more pronounced, while the fin spines and the body in general have become softer.

Species. The species in *Schedophilus* are in general well differentiated. Almost all descriptions are based on young specimens. The large adults differ greatly in appearance from the young. Adults are so very rarely seen that only three have entered the literature, two of them assigned to other genera. Unfortunately, the species from the Australian region are very poorly known. Because of their isolated geographic distribution, critical examination of these species will doubtless provide much insight into the evolution of the soft-spined centrolophids.

The species in the genus are:

Schedophilus ovalis (Cuvier and Valenciennes, 1833) = **Centrolophus ovalis* Cuvier and Valenciennes. Eastern Atlantic Ocean from Spain to South Africa and Mediterranean Sea, type locality Nice. D

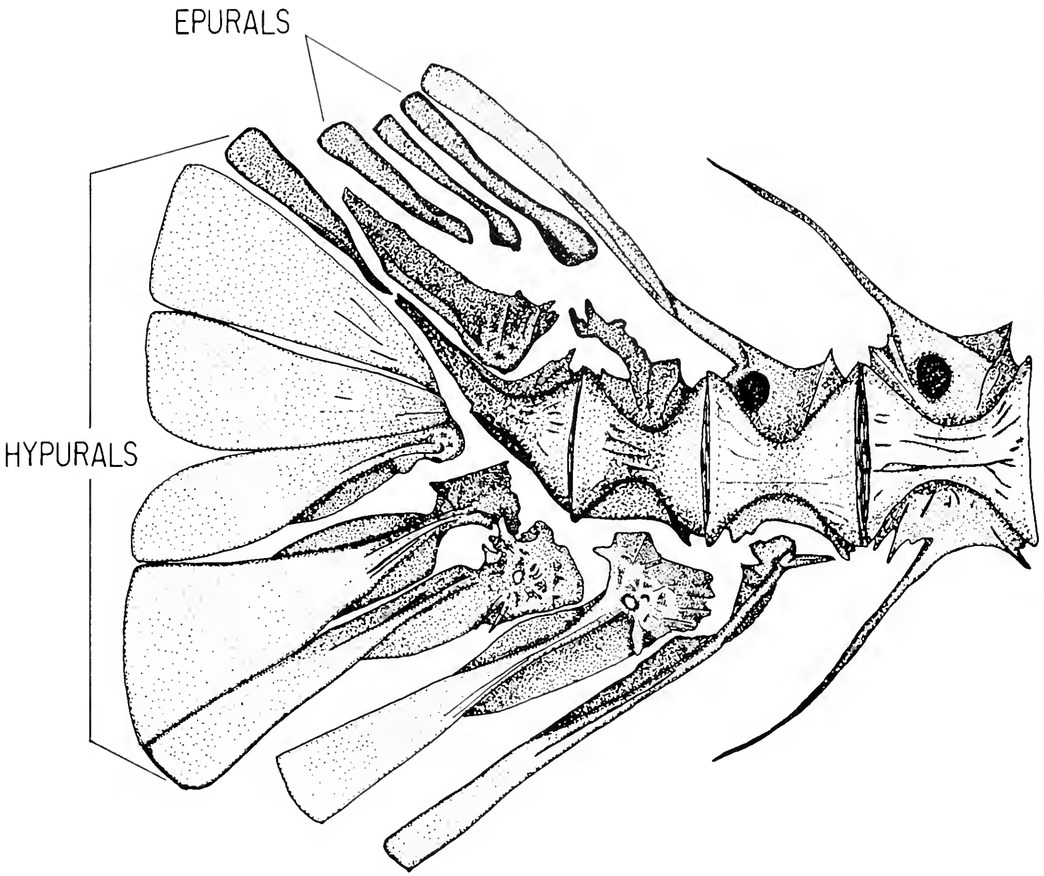


Figure 12. Caudal skeleton of *Schedophilus medusophagus*, drawing of a cleared-and-stained preparation from a 39-mm SL specimen. All elements identified in Figure 1.

VI–VIII, 30–32. A III 20–24. P 21–22. Gill-rakers around 6 + 1 + 16. Vertebrae 10 + 15. Silvery to greenish. Synonyms are: *Centrolophus crassus* Cuvier and Valenciennes, 1833, from west of the Azores; **Leirus bennettii* Lowe, 1833, from Madeira; *Mupus imperialis* Cocco, 1840, from the Mediterranean; **Crius bertheloti* Valenciennes, 1848, from the Canary Islands; *Centrolophus rotundicauda* Costa, 1866, from Naples; *Centrolophus porosissimus* Canestrini, 1865, and *Schedophilus botteri* Steindachner, 1868, from Barcelona.

Schedophilus medusophagus Cocco, 1839. Atlantic Ocean and western Mediterranean Sea, type locality Messina. D 44–50 (total elements). A 28–31 (total elements). P 18–21. Gill-rakers around 5 + 1 + 11. Vertebrae 10 + 15. Major preopercular spines usually about 12. Lateral line scales 160–230, increasing in number with growth. Brown, often mottled. The report of this species from the South Pacific (Günther, 1876), is undoubtedly that of a closely related form, *Schedophilus huttoni* (Waite, 1910). The adult of *S. medusophagus* has long been known under the name **Centrolophus britannicus* Günther, 1860a.

**Schedophilus maculatus* Günther, 1860. China Seas. D 36 (total elements). A 27 (total elements). P 19. Gill-rakers 5 + 1 + 13. Vertebrae 10 + 15. Major preopercular spines 13. This species is known only from the type, a 37-mm SL specimen that is soft and in poor condition.

**Schedophilus marmoratus* Kner and Steindachner, 1866. "Südsee," presumably near Australia. D 38 (total elements). A 27 (total elements). Vertebrae 12 + 17. This species is usually treated as a synonym of *S. maculatus* Günther, 1860. A probable synonym is *Hoplocoryphis physaliarum* Whitley, 1933, from New South Wales.

Schedophilus huttoni (Waite, 1910) = *Centrolophus huttoni* Waite. Seas of New Zealand, eastern Australia, and Tasmania, type locality Sumner, New Zealand. D 57 (total elements). A 38 (total elements). Gill-rakers 5 + 12. Vertebrae 10 + 20. Lateral line scales in the 776-mm holotype near 240. Brownish. As in *S. medusophagus*, the number of lateral line scales probably increases with age. A probable synonym is *Tubbia tasmanica* Whitley, 1943, from Tasmania, known only from a 10-cm specimen reported as having 144 scales in the lateral line.

Schedophilus ventralis (Bean, 1912) = *Eucrotus ventralis* Bean. Bermuda. D IV–VII, 31–34. A III 20–23. P 22. Gill-rakers around 5 + 1 + 16. Vertebrae 10 + 15. Major preopercular spines about 9. The type is apparently lost. This nominal species has been synonymized with *S. ovalis* (Cuvier and Valenciennes, 1833) by Fowler (1936).

Schedophilus griseolineatus (Norman, 1937) = **Palinurichthys griseolineatus* Norman. Southern Atlantic Ocean, type locality 49°00′S 61°58′W. D VII–VIII, 31–33. A III 20–21. P 19–21. Gill-rakers around 6 + 1 + 14. Vertebrae 10 + 16. Lateral line scales about 120. Major preopercular spines around 14. Blue-brown, horizontally striped. This species can be distinguished at once by the increased number of caudal vertebrae. The large specimens which Norman (1937) doubtfully referred to "*Palinurichthys caeruleus*" belong to this species.

Schedophilus pemarco (Poll, 1959) = *Palinurichthys pemarco* Poll. Gulf of Guinea, tropical Atlantic Ocean. D V–VII, 23–26. A III 16–18. P 19–22. Gill-rakers around 5 + 1 + 16. Vertebrae 10 + 15. Lateral line scales about 95. Major preopercular spines 15–19. Blue-brown, horizontally striped. The median finray counts in this species are lower than in any other.

Genus *CENTROLOPHUS* Lacépède, 1803

Figure 13

Centrolophus Lacépède, 1803:441. (Type species: *Perca nigra* Gmelin, 1788:132, by monotypy. "Rivers of Cornwall.")

Acentrolophus Nardo, 1827:28. (Substitute name for *Centrolophus* Lacépède, 1803, and therefore taking the same type species, *Perca nigra* Gmelin, 1788:132. *Centrolophus* deemed inapplicable.)

Gymnocephalus (*non* Bloch, 1793:24) Cocco, 1838:26. (Type species: *Gymnocephalus messinensis* Cocco, 1838:26, by monotypy. Messina. A synonym of *Perca nigra* Gmelin, 1788:132.) (*Vide* Jordan, 1923.)

Pompilus Lowe, 1839:81. (Type species: **Centrolophus morio* Cuvier and Valenciennes, 1833: 342, by absolute tautonymy, *C. pompilus* [= *P. pompilus*] Cuvier and Valenciennes, 1833: 334, considered a synonym. Madeira. A synonym of *Perca nigra* Gmelin, 1788:132. Preoccupied in *Pompilus* Schneider, 1784, Cephalopoda.)

Centrolophodes Gilchrist and von Bonde, 1923:2. (Type species: *Centrolophodes irwini* Gilchrist and von Bonde, 1923:3, by monotypy. South Africa. A synonym of *Perca nigra* Gmelin, 1788:132.)

The combination of elongate body, small head with prominent pores, continuous dorsal fin with very weak spines graduating to the rays, toothless palate, very small scales, and 160 to 230 scales in the lateral line, distinguishes *Centrolophus* from all other stromateoid genera. The name, a masculine noun, is from the Greek κέντρον, spine, + λοφος, crest of a helmet, probably in reference to the manner in which the dorsal fin rises from the back.

Description. Body elongate, maximum depth rarely exceeding 30 per cent of the standard length except in very small specimens; musculature firm. Peduncle broad,

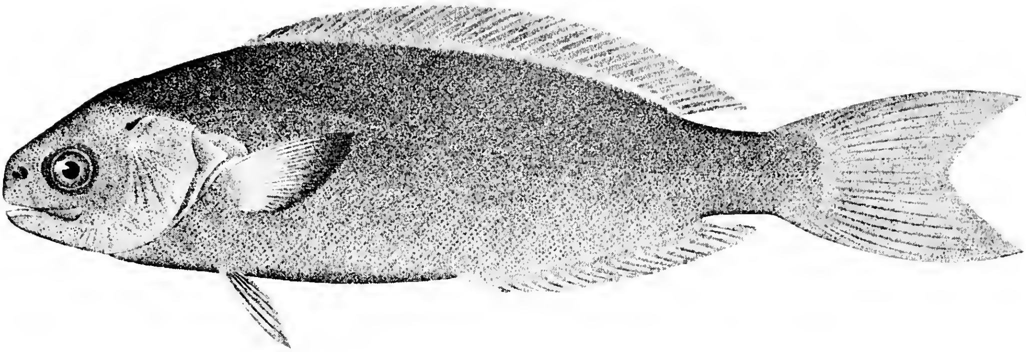


Figure 13. *Centralophus niger*, drawing of a 223-mm specimen, USNM 44440, courtesy of the Smithsonian Institution.

thick, long. Dorsal fin originating a little behind insertion of pectoral fins, continuous, about five very weak spines graduating to the 32 to 37 rays. Anus and genital pore at mid-body, in a slit. Anal fin originating a little behind middle of body, three weak spines precede the 20 to 23 rays. Pectoral fin rounded in the young, pointed in adult, relative length decreasing slightly with growth. Pelvic fins inserting under posterior portion of pectoral fin base, attached to the abdomen by a small membrane and folding into a shallow groove. Caudal fin broad, moderately forked. Very small cycloid scales, deciduous, covering fleshy bases of the median fins. Lateral line slightly arched anteriorly, straightening out about mid-body and extending onto peduncle; lateral line scales around 190. Skin fairly thick; extensive subdermal canal system communicating to the surface through small pores. Head usually less than 25 per cent of the standard length, not scaled, pores very prominent, naked skin not projecting backward over the nape. Eye of moderate size, no adipose tissue. Nostrils near tip of rounded snout, the anterior round, the posterior a slit. Angle of gape extending below eye. Premaxillary not protractile. Upper jaw covered completely by lacrimal bone when mouth is closed. Slender supramaxillary present. Jaw teeth small, pointed, uniserial, spaced, increasing in number with growth; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin, margins finely denticulate; opercle with two weak flat spines, scaled; angle of preopercle rounded, bulging back slightly; preopercle and cheek not scaled. Gill-rakers heavy, about half the length of the filaments, toothed on inner edge, spaced, about 13 on lower limb of first arch; rudimentary rakers present under large pseudobranch. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal. Scapula prominent. Vertebrae 10 + 15 = 25. Caudal skeleton with six hypurals and three epurals. Stomach a simple sac; intestine long. Pyloric caeca about 10, digitiform.

Base color brown. Range is from russet through chocolate to dark bluish. Median fins and pelvics darker than the body. No pattern, hardly any countershading in adults; young have three or four dark vertical stripes.

Natural history. Young *Centrolophus* have been taken under jellyfish (Collett, 1896) and swimming with *Mola* (Munro, 1958). Some described as "small" were found in the stomachs of bottom-living hake trawled west of the British Isles (Blacker, 1962). Presumably these *Centrolophus* had not been in association with pelagic medusae. While young fish are found near the surface, the large fish are taken at depth.

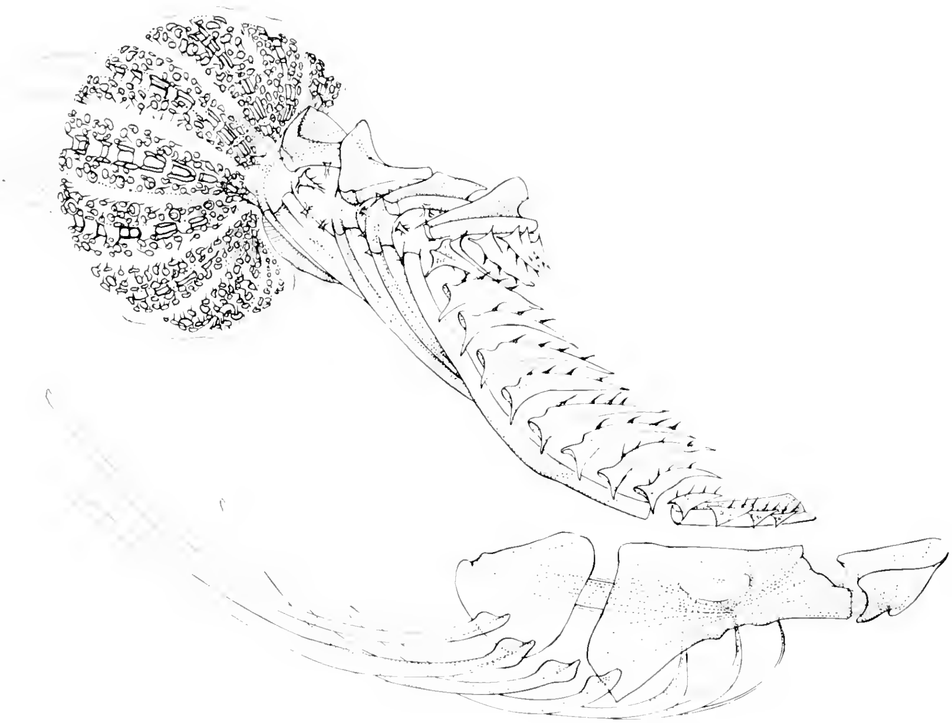


Figure 14. Branchial region of *Centrolophus niger*, drawing of a cleared-and-stained preparation from a 190-mm specimen. Elements identified in Figure 2.

In the North Atlantic, the adults seem widespread, but the young have been found only in the eastern Atlantic and Mediterranean areas. A spawned-out female, however, has been caught south of New England (Templeman and Haedrich, 1966).

The young are at first vertically banded, but by the time they are about 100 millimeters long they have become a uniform brown. Growth is very rapid; from December to May, five months, a Mediterranean specimen grew from 20 to 170 millimeters (Padoa, 1956). Growth is regular and the allometry is not marked. The number of jaw teeth does increase, however, from about 17 in a 150-millimeter specimen to near 100 in one of 1,200 millimeters.

Centrolophus is one of the largest stromateoids known. Specimens a meter or more in length have been taken in Australia (Mees, 1962), South Africa (Barnard, 1948), and the western North Atlantic.

Autumn spawning, from October into winter, is indicated by the occurrence of eggs and very small fish at this time in the Mediterranean (Padoa, 1956) and by the capture of a large, recently spawned-out female in December 1963 in the western North Atlantic. Fraser-Brunner (1935) noted dimorphism in the coloring of the sexes, the females said to be lighter than the males. This difference, however, is not always observed.

Lo Bianco (1909) observed young *Centrolophus* feeding on medusae, but Chabanaud and Tregouboff (1930) found that their aquarium specimen preferred small fish and plankton. It never attempted to eat the medusae which were present in the tank.

The large specimen from south of New England was taken on a long-line baited with squid. Fish and large crustacean remains occurred most often in stomachs examined, and, on one occasion, bits of potato and an onion were found.

As Nielsen (1963) has suggested, in reporting the seining of five near Skagen, *Centrolophus* may school. Blacker (1962) reports several hundredweight trawled off Ireland. Potentially a good fish with fine white meat, those offered experimentally in Milford Market found no sale (Blacker, 1962).

Relationships. Centrolophus is one of the most primitive stromateoids. The small pharyngeal sac with few rows of large papillae (Fig. 14), the heavy blunt-ended branchiostegal rays, and the large size attained, are all primitive characters. *Centrotrolophus* shows much affinity of form towards *Icichthys*, from which it differs mainly in having far fewer vertebrae.

Centrolophus, *Icichthys*, and *Schedophilus* are the soft-spined centrolophids. This group is in general a little more primitive than the hard-spined centrolophids, *Hyperoglyphe*, *Seriolella*, and *Psenopsis*. The soft-spined centrolophids usually have smaller sacs with fewer papillae, coarser jaw teeth, and attain a larger size than the hard-spined centrolophids.

Species. Centrolophus is known from the Australian region, from South Africa, and from the North Atlantic, where numerous species have been described. The counts of the Southern Hemisphere specimens, of which only a handful are known, overlap the range of those for the North Atlantic species. Some differences may exist in relative proportions, but these are only at certain stages of growth. Lacking comparative material, the safest course is to follow Waite (1910) and Mees (1962) in recognizing but one bipolar species:

**Centrolophus niger* (Gmelin, 1788) = *Perca nigra* Gmelin, 1788. North Atlantic, western Mediterranean Sea, Adriatic Sea, South Africa, southern Australia, and New Zealand, type locality "Rivers of Cornwall." D 37–41 (total elements). A III 20–23. P 19–22. Gill-rakers 5–6 + 1 + 12–15, usually 19 total. Vertebrae 10 + 15. The name *Centrolophus pompilus* (Linnaeus, 1758) is often used for this fish. Linnaeus's *Coryphaena pompilus*, however, is too poorly characterized, and differs too much in certain respects to be considered the same species. Gmelin's (1788) *Perca nigra* is the first available name. Synonyms from the North Atlantic are: *Centrolophus liparis* Risso, 1826, from Nice; *Acentrolophus maculosus* Nardo, 1827, from the Adriatic Sea; **Centrolophus pompilus* Cuvier and Valenciennes, 1833, from Marseille; **Centrolophus morio* Cuvier and Valenciennes, 1833 (ascribed to Lacépède), from the Mediterranean Sea; **Schedophilus elongatus* Johnson, 1862, from Madeira; and **Centrolophus valenciennesi* Moreau, 1881, from Marseille.

The two species described from the Southern Hemisphere, here considered synonyms of *niger*, are: *Centrolophus maoricus* Ogilby, 1893, Australia and New Zealand. Counts made on two specimens of this nominal species fell at the high end of the range for *C. niger*, as do the counts for one small specimen reported by Regan (1914).

Centrolophus irwini (Gilchrist and von Bonde, 1923) = *Centrolophodes irwini* Gilchrist and von Bonde. South Africa. The counts reported for the holotype likewise fall at the high end of the range for *C. niger*. *Mupus bifasciatus* Smith, 1961, based on two small specimens, is almost certainly the same fish. There is little cause to doubt that the South African and Australian forms belong to the same population.

Genus *ICICHTHYS* Jordan and Gilbert, 1880

Figure 15

Icichthys Jordan and Gilbert, 1880:305. (Type species: **Icichthys lockingtoni* Jordan and Gilbert, 1880:305, by original designation. Point Reyes, California.)

The combination of elongate soft body, continuous dorsal fin originating well be-

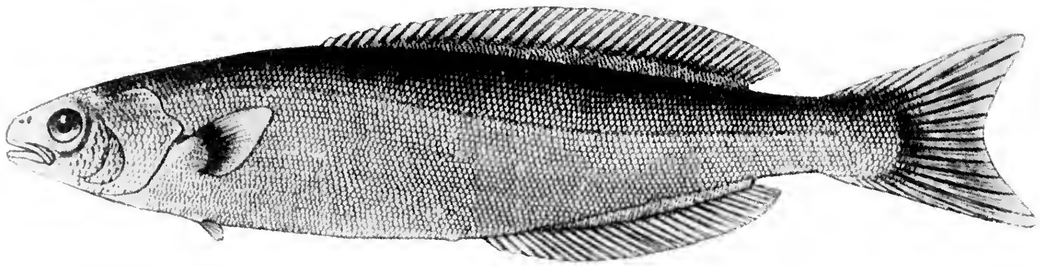


Figure 15. *Icichthys lockingtoni*, drawing of a 390-mm specimen, from Parin, 1958.

hind pectoral insertion, toothless palate, moderate scales covering opercles and cheek, 100 to 130 scales in the lateral line, and 50 to 60 vertebrae, distinguishes *Icichthys* from all other stromateoid genera. The name, a masculine noun, is from the Greek εἴκω, to yield, + ἰχθύς, fish, in reference to the fish's flexible soft body.

Description. Body elongate, maximum depth less than 25 per cent of the standard length except in small specimens; musculature soft. Peduncle broad, compressed, of moderate length. Dorsal fin originating well behind insertion of pectoral fins, continuous, a few very weak spines graduating to the rays, 39–43 elements in all. A mid-dorsal ridge preceding the fin. Anus at about mid-body. Anal fin originating slightly behind middle of body, three weak spines precede the rays, 27 to 32 elements in all. Median fins with compressed fleshy bases. Pectoral fin rounded, base fleshy. Pelvic fins small, inserting directly under insertion of pectoral fins, not attached to abdomen with a membrane, folding into an insignificant groove. Caudal fin broad, slightly rounded or emarginate. Moderate cycloid scales with prominent circuli, not especially deciduous, covering bases of median fins. Lateral line slightly arched anteriorly, straightening out over anterior part of anal fin and extending onto peduncle; lateral line scales around 120. Skin fairly thick; subdermal canal system not well developed, pores very small. Head around 25 per cent of the standard length, its profile sloping and the pores not prominent. Top of head not scaled, naked skin not projecting backward over the nape. Eye of moderate size, no adipose tissue. Nostrils near tip of truncate snout, both round. Angle of gape extending below eye. Premaxillary not protractile. Only upper margin of upper jaw covered by lacrimal bone when mouth is closed. Very slender supramaxillary present. Jaw teeth minute, pointed, uniserial, close-set; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin, both well scaled, margins with very fine spinules; opercle with two weak flat spines; angle of preopercle rounded, bulging backward. Cheek scaled. Gill-rakers heavy, a little shorter than the filaments, toothed on inner edge, spaced, about 10 on lower limb of first arch. Pseudobranch small. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal. Scapula not prominent. Vertebrae 50 to 60. Caudal skeleton with three autogenous haemal spines, six hypurals, and two or three epurals. Stomach a simple sac; intestine long. Pyloric caeca about 10, digitiform, slender.

Color in preservative tan to dark brown, the median fins and pelvics darker than the body. No pattern, slight countershading.

Natural history. Young *Icichthys* are commonly found swimming under or within medusae (Jordan, 1923a; Hobbs, 1929; Fitch, 1949), and sometimes appear in fair number off the California coast. Large adults have been taken by drift-nets (Parin,

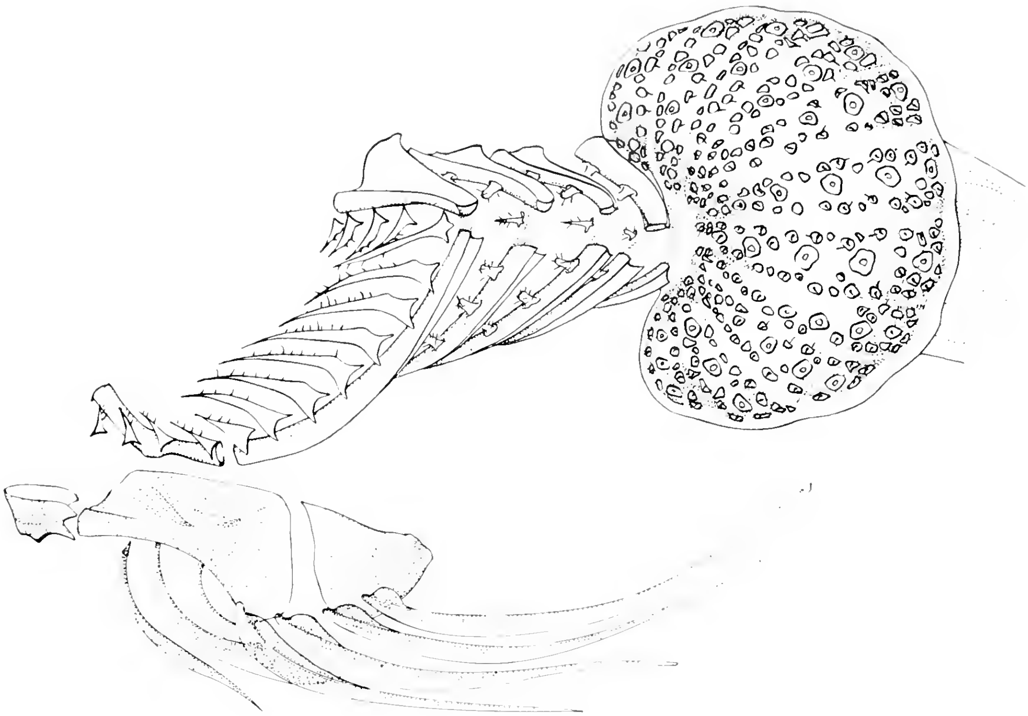


Figure 16. Branchial region of *Icichthys lockingtoni*, drawing of a cleared-and-stained preparation from a 173-mm specimen. Elements identified in Figure 2.

1958) and by deep trawl (Ueno, 1954), but are very rare. All recorded captures are from deep water. *Icichthys* is certainly oceanic, and, judging from its soft tissues, somber color, and rare occurrence, it may well live as an adult in the bathypelagic realms. Ueno's (1954) 362-mm SL specimen is the largest known.

Icichthys is found in cool waters. The appearance of twelve small specimens off the Cape of Manazuru, Japan, in the spring of 1963 corresponded with an unusual influx of *ca.* 15°C water in this normally warmer area (Abe, 1963).

Relationships. Externally, *Icichthys* very closely resembles *Centrolophus*, with which it has been synonymized by Parin (1958). However, in several respects—the scalation on the cheeks, the caudal skeleton, and the greatly increased number of vertebrae—*Icichthys* differs from *Centrolophus* enough to warrant generic recognition.

The structure of the pharyngeal sacs (Fig. 16, *cf.* Fig. 14) and the general appearance of *Icichthys* suggest a very close relationship with *Centrolophus*. *Icichthys* has lost an epural in the caudal skeleton (Fig. 17), and is almost certainly the derived form. But *Centrolophus*, having lost the cheek scales retained in *Icichthys*, cannot be the direct ancestor. Both must have branched from a common stem. It is perhaps significant that the ranges of the two genera complement each other nicely (Fig. 52).

Icichthys, a member of the most primitive group of stromateoids, has a very high number of vertebrae, an advanced condition. The number, between 50 and 60, is slightly more than twice the basic perciform number, 25, found in other centrolophids.

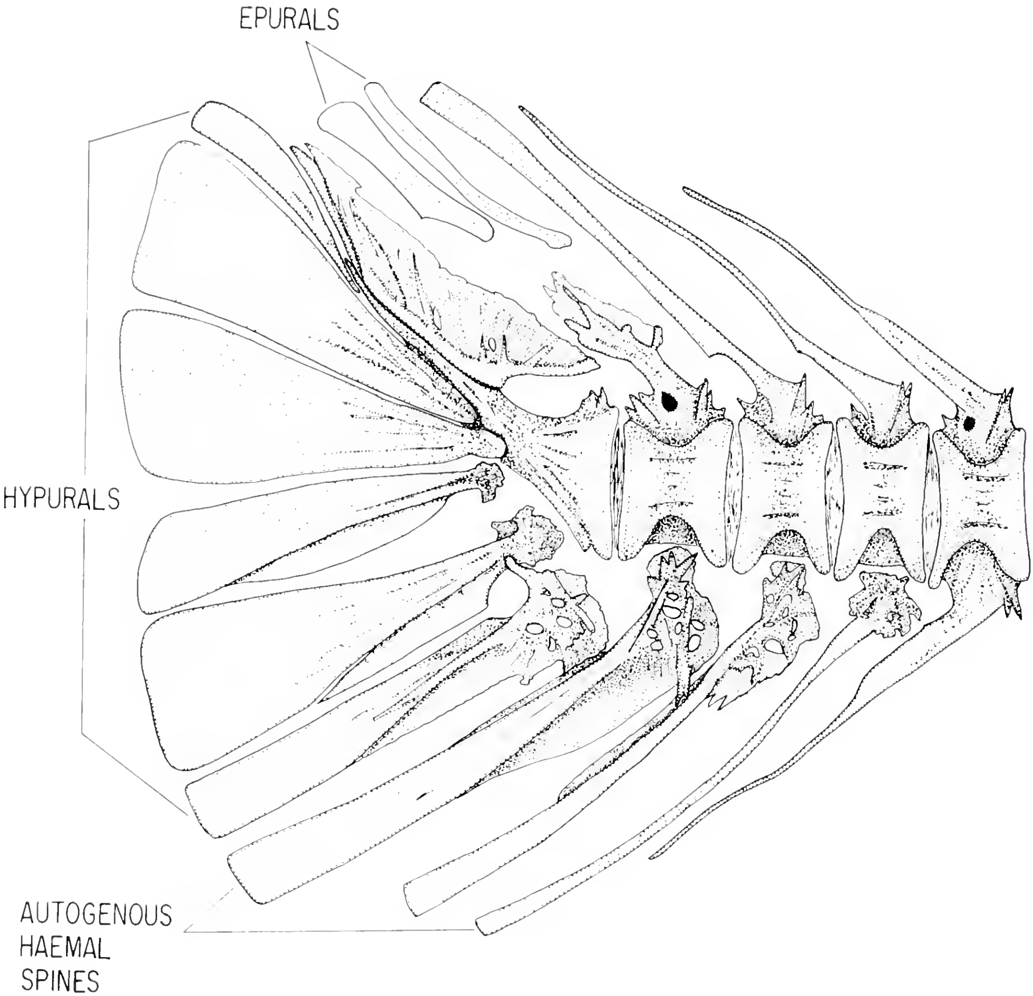


Figure 17. Caudal skeleton of *Icichthys lockingtoni*, drawing of a cleared-and-stained preparation from a 43-mm specimen, SU 41028. All elements identified in Figure 1.

The number of elements in the median fins is about the same as in *Centrolophus*, but there are more than twice the number of free interneurals ahead of the dorsal fin. The evidence is at least suggestive that *Icichthys* may have arisen by polyploidy; chromosome counts would be most instructive. The three autogenous haemal spines in the tail (Fig. 17), in contrast to the two of all other perciforms (Gosline, 1961a), are undoubtedly a by-product of the increased number of vertebrae.

Species. The genus is restricted to the cooler waters of the North Pacific and of New Zealand, from whence a new species is being described (Haedrich, in press). Abe (1963) reports more pyloric caeca and slightly fewer vertebrae for his Japanese specimens than are found in specimens from off California. Many more specimens will be needed to see whether these differences are significant. From knowledge of *Icichthys*' apparent bathypelagic habitat, it

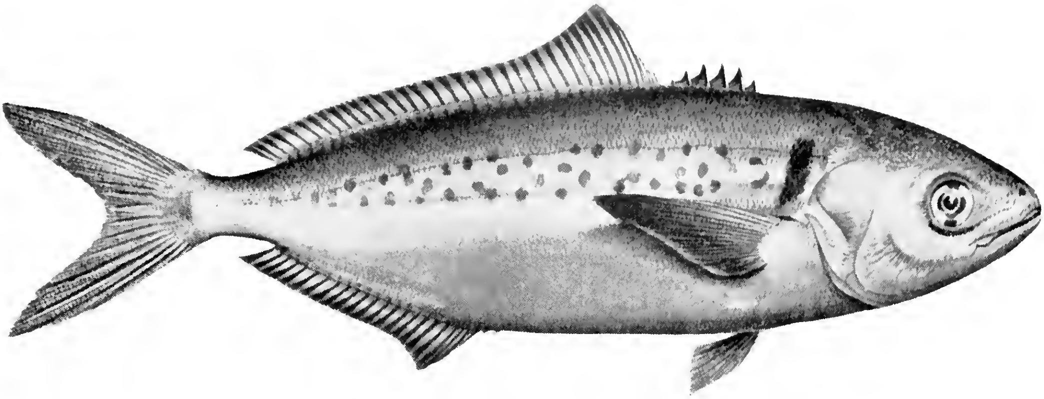


Figure 18. *Seriolella punctata*, an elongate species, drawing of an approximately 250-mm specimen, from McCulloch, 1911.

seems best for the time being to recognize but one North Pacific species:

**Icichthys lockingtoni* Jordan and Gilbert, 1880. California to Japan, type locality Point Reyes, California. D 39–43 (total elements). A 27–32 (total elements). P 18–21. Gill-rakers 4–6 + 1 + 11–13, usually 18 total. Vertebrae 56–60. Synonyms, both based on small specimens from the coast of California, are **Schedophilus heathi* Gilbert, 1904, and **Centrolophus californicus* Hobbs, 1929.

Genus *SERIOLELLA* Guichenot, 1848

Figures 18, 19

Seriolella Guichenot, 1848:238. (Type species: *Seriolella porosa* Guichenot, 1848:239, by subsequent designation of Jordan, 1923:238. Chile.)

Neptomenus Günther, 1860:389. (Type species: *Neptomenus brama* Günther, 1860:340, by original designation. New Zealand.)

The combination of at least seven more dorsal than anal finrays, short stout spines not increasing in length to the rays in the dorsal fin, toothless palate, pelvic insertion behind the pectoral insertion, supramaxillary bone present, and lateral line following the dorsal profile, distinguishes *Seriolella* from all other stromateoid genera. The name, a feminine noun, is the diminutive of *Seriola*, a carangid genus. Ultimately from the Latin *seria*, an oblong earthen vessel, it doubtless refers to the shape of the fish.

Description. Body moderately deep to elongate, maximum depth 25 to 40 per cent of the standard length, compressed but fairly thick; musculature firm. Peduncle stout. Two dorsal fins, the first originating over or slightly behind insertion of pectoral fins, with seven to nine short spines. Usually the third, fourth, and fifth spines are the longest, the longest spine less than half the length of the longest dorsal finray. Second dorsal with 25 to 40 finrays, the anteriormost the longest. Anal and genital pore slightly before or behind mid-body, in a slit. Anal fin originating at or behind mid-body, three spines increase in length to the 18 to 25 rays, the anteriormost finrays the longest. Number of dorsal finrays exceeds number of anal finrays by more than seven. Pectoral fins rounded in the young, long and falcate in the adult. Pelvic fins inserting just under end of or behind pectoral fin base, attached to the abdomen by a small membrane and folding into a shallow groove. Caudal fin broad and forked. Large cycloid scales, very deciduous, covering fleshy bases of the median fins. Lateral line moderately high, following dorsal profile and extending onto peduncle. Skin thin; main subdermal canal along inter-

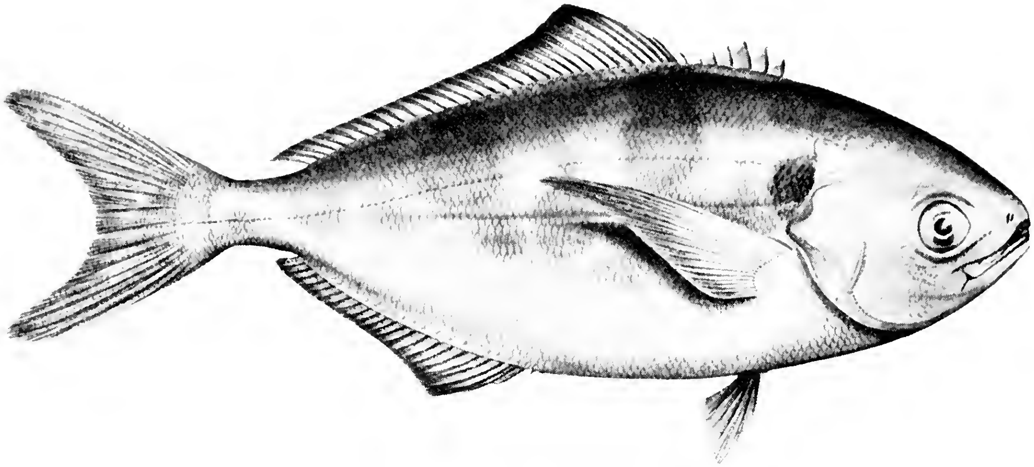


Figure 19. *Seriolella brama*, a deep-bodied species, drawing of an approximately 250-mm specimen, from McCulloch, 1911.

muscular septum and side branches usually visible, pores small. Head about 30 to 35 per cent of the standard length. Top of head naked, fine canal network and small pores usually visible, naked skin projecting backwards over the nape. Eye moderate to large. Adipose tissue around eye well developed and extending forward around the nostrils. Nostrils near tip of pointed or truncate snout, small, the anterior round, the posterior a vertical slit. Maxillary extending below eye but angle of gape before eye. Premaxillary not protractile. Lacrimal bone partially covering upper jaw when mouth is closed, ventral border of premaxillary and end of maxillary remaining exposed. Supramaxillary present. Jaw teeth small to minute, pointed, uniserial, close-set or slightly spaced, covered laterally by a membrane; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin, margins entire or finely denticulate; opercle with two weak flat spines, scaled, the scales covered by skin; preopercle not scaled, angle rounded, bulging backward. Cheek scaled, the scales covered by thick skin and not visible without dissection. Gill-rakers one-half to one-third the length of the filaments, toothed on inner edge, slightly spaced, 14 to 18 on lower limb of first arch; no rudimentary rakers under the small pseudobranch. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal, the tips of the branchiostegals pointed. Posterior border of scapula free from the body. Vertebrae 10 + 15, or 11 + 14 = 25. In the adult, hypurals 2 + 3 and 4 + 5 closely conjoined or even partially fused, three epurals. Sclerotic bones well ossified, subocular shelf present on second suborbital. Stomach a simple sac; intestine long. Pyloric caeca numerous and forming a dendritic mass.

Color in preservative brown or bluish, darker above than below, the sides sometimes with a silvery overlay. Usually a prominent dark blotch on the shoulder at the beginning of the lateral line; smaller spots often present on sides. Fins usually a little lighter than the body, but black-edged. Inside of mouth and gill cavity light.

Natural history. In contrast to most other centrolophids, the species of *Seriolella* are coastal fishes. Schools of them occur from 150 fathoms in towards the coasts, and some species even enter estuaries (Munro, 1958). Others live in kelp beds, apparently not deeper than 40 fathoms (Scott, 1962).

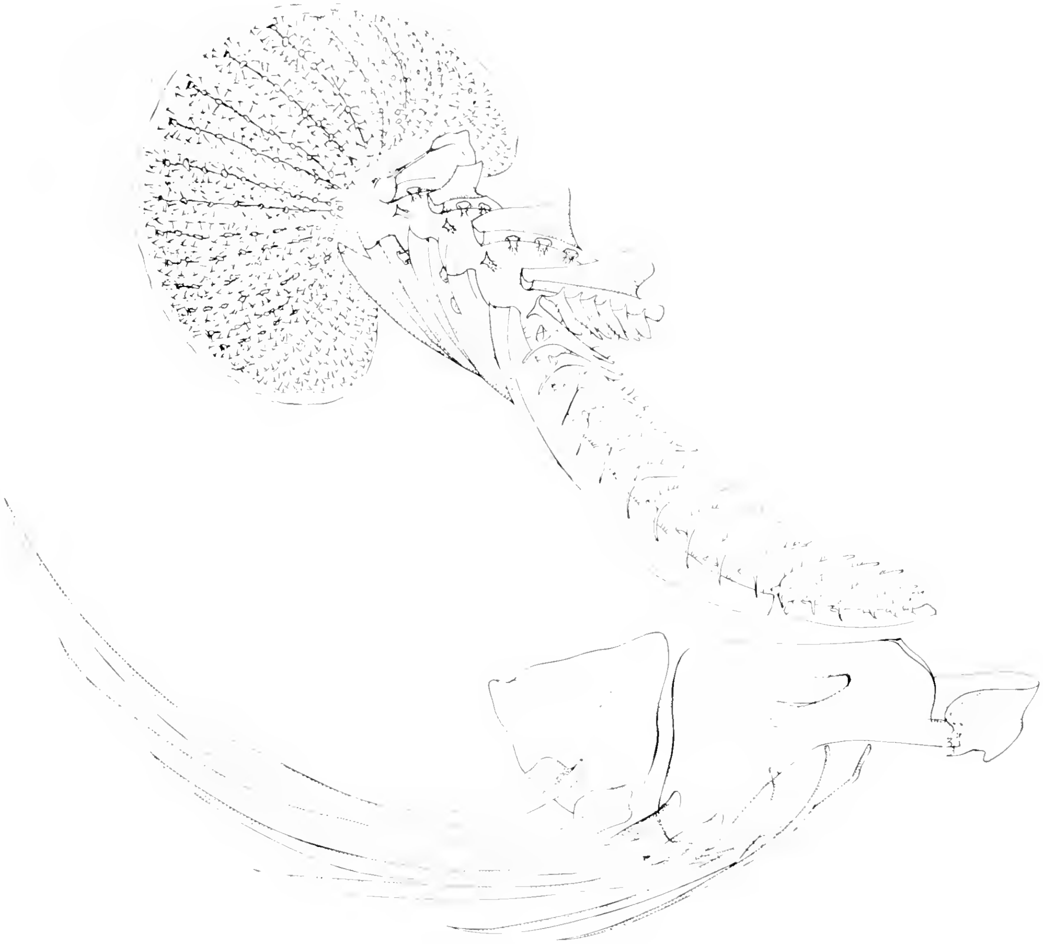


Figure 20. Branchial region of *Seriolella violacea*, drawing of a cleared-and-stained preparation from a 188-mm specimen, USNM 77593. Elements identified in Figure 2.

Nichols and Murphy (1922) report a young Peruvian specimen from under a jellyfish.

Seriolella is the subject of a modest fishery in Chile (Mann, 1953). In Peru, nine- or ten-inch specimens are at times so common that they are caught by jigging (Nichols and Murphy, 1922). These fish are occasionally taken by fishermen in Australia and New Zealand, but apparently are not sought-after commercial species there.

Relationships. Seriolella, with its probable off-shoot *Psenopsis*, represents the advanced condition among centrolophids. *Seriolella* is derived from a *Hyperoglyphe*-like stock, with which it shares the short stout spines in the dorsal fin and the fluted first haemal spine curving backward to meet the first interhaemal. The slender pointed branchiostegal rays (Fig. 20), the numerous bands of small papillae in the pharyngeal sacs, the well ossified sclerotic bones, and the partial fusion of hypurals 2 + 3 and 4 + 5 with growth are all advanced characters, and approach the nomeid grade. *S. violacea*, from Peru, comes near to bridging the gap between *Hyperoglyphe* and *Seriolella*.

Seriolella has given rise to *Psenopsis*. The pharyngeal sacs and caudal skeleton of both are very similar. Both genera have, in most species, well ossified sclerotic bones and a dark blotch on the shoulder. *Seriolella*, however, is closer to *Hyperoglyphe* in the possession of a supramaxillary, which has been lost in *Psenopsis*.

Species. *Seriolella* is restricted to the cool temperate waters of the Southern Hemisphere. About a dozen species have been described; the majority are known to me only from published descriptions. I have been able to examine only a few *Seriolella*, most of them from South America. The nominal species in the genus are:

Seriolella punctata (Bloch and Schneider, 1801) = *Scomber punctatus* Bloch and Schneider. Southern Australia, Tasmania, and New Zealand. Elongate. D VI–VII, 34–39. A III 21–24. P 19–22. Gill-rakers usually 6 + 1 + 14–15. Vertebrae 10 + 15. Synonyms are **Neptomenus dobula* Günther, 1869, from Tasmania, and *Neptomenus bilineatus* Hutton, 1872, from Wellington Harbor, New Zealand.

Seriolella violacea Guichenot, 1848. Chile and Peru, type locality Valparaiso. Moderately deep. D VII–VIII, 25–28. A III 18–20. P 21–22. Gill-rakers 5–7 + 1 + 16–18. Vertebrae 11 + 14. This fish is the "cojinoba" of Chilean fisheries literature (Mann, 1953). Synonyms are *Centrolophus peruanus* Steindachner, 1874, from Callao, Peru, and **Neptomenus crassus* Starks, 1906, also from Callao.

Seriolella porosa Guichenot, 1848. Chile and Peru, type locality Valparaiso. Elongate. D VI–VIII, 34–38. A III 22–23. P 19–21. Gill-rakers usually 6 + 1 + 14–15. Vertebrae 10 + 15. This species has the same counts as *S. punctata* (Bloch and Schneider, 1801), and was synonymized with *S. dobula* (Günther, 1869) [here considered = *S. punctata*] by Regan (1902). It is unlikely that an essentially coastal fish such as *Seriolella* would regularly cross the broad expanse of ocean between South America and Australia. With closer study *S. porosa*, *S. punctata*, and possibly *S. dobula* will probably prove distinct.

Seriolella brama (Günther, 1860) = *Neptomenus brama* Günther. Southern Australia and New Zealand, type locality New Zealand. Deep-bodied. D VI–VIII, 26–33. A III 21–23. P 20–21. Gill-rakers 7 + 1 + 16. Vertebrae 10 + 15. *Neptomenus travale* Castelnau, 1872, from New Zealand is a synonym.

Seriolella velaini Sauvage, 1879. Island of St. Paul, Indian Ocean. Moderately deep. D VIII, 27. A III 20. (From Regan, 1902.)

Seriolella christopherseni Sivertsen, 1945. Tristan da Cunha. Atlantic Ocean. D VI, 28. A III 20. Moderately deep. (From Sivertsen, 1945.)

Seriolella noel Whitley, 1958, is based on one battered specimen from Sydney, Australia, standard length 331 mm. The counts given are D X + 31?; A 2–30; P 14; gill-rakers 8 + 16; lateral line scales 95 + 8. The description is inadequate to tell even to what genus this fish belongs, but it is decidedly not a *Seriolella*. The ten dorsal spines indicate it may belong in the family Nomeidae.

Genus *PSENOPSIS* Gill, 1862

Figure 21

Psenopsis Gill, 1862:127. (Type species: *Trachinotus anomalus* Temminck and Schlegel, 1850: 107, by monotypy. Japan.)

Bathyseriola Alcock, 1890:202. (Type species: **Bathyseriola cyanea* Alcock, 1890:202, by monotypy. Ganjam Coast, India.)

The combination of dorsal and anal fin-rays in almost equal numbers, spines graduating to the rays, toothless palate, pelvic insertion directly under the pectoral insertion, broad forward scoop in the opercle below the second opercular spine, and no supramaxillary distinguishes *Psenopsis* from all other stromateoid genera. The name, a feminine noun, is from the Greek ψήνη, *Psenes* + ὄψις, appearance, drawing atten-

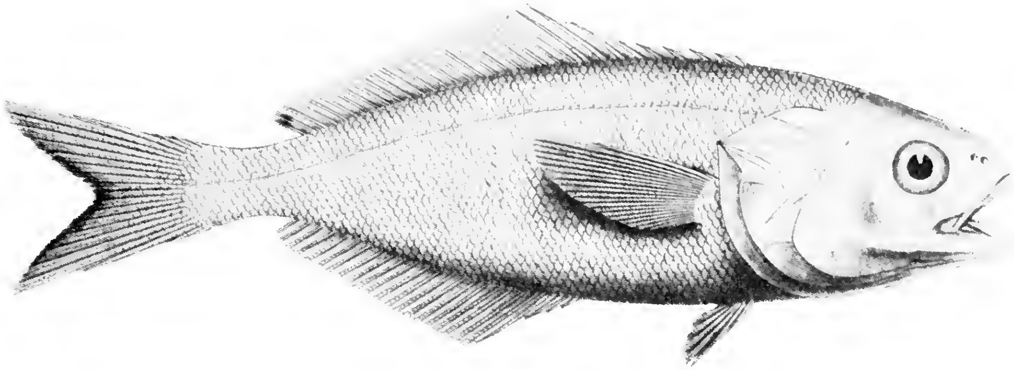


Figure 21. *Psenopsis cyanea*, an elongate species, drawing of a 139-mm specimen, BMNH 1890. 11. 28. 9, from Alcock, 1892.

tion to the superficial similarity between these two genera.

Description. Body moderately deep to deep, maximum depth 30 to 45 per cent of the standard length, compressed but fairly thick; musculature soft. Peduncle short, deep, and compressed. Dorsal fin originating over or slightly behind insertion of pectoral fins, continuous, with five to seven short spines increasing in length to the 27 to 32 rays. The last spine the longest, but less than half the length of the longest dorsal finray. Anal and genital pore well before or at mid-body, in a slit. Anal fin originating well before or slightly behind mid-body, three spines increase in length to the 22 to 29 rays. Number of dorsal finrays never exceeds number of anal finrays by more than five. Pectoral fins rounded in the young, usually produced in the adult. Pelvic fins inserting directly under origin of the pectoral fin, attached to the abdomen by a small membrane and folding into a groove which reaches to the anus. Caudal fin broad, slightly forked. Small cycloid scales, very deciduous, covering fleshy bases of the median fins. Lateral line moderately high, following dorsal profile and extending onto peduncle. Skin very thin; main subdermal canal along intermuscular septum and side branches clearly visible, canals particularly dense on back, pores very small. Head around 30 per cent of the standard length. Top of head naked, minute pores faintly visible, naked skin not projecting or projecting only slightly backwards over the nape. Eye moderate to large. Adipose tissue around eye developed and extending forward around the nostrils. Nostrils near tip of truncate snout, moderate in size, the anterior round, the posterior a slit. Maxillary extending below eye, angle of gape at anterior border of eye. Premaxillary not protractile. Upper jaw covered completely by lacrimal bone when mouth is closed. Supramaxillary absent. Jaw teeth minute, pointed, uniserial, close-set, covered laterally by a membrane; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin, not scaled, margins entire or finely denticulate; opercle with two weak flat spines; under the second spine the bone is Ƨ-shaped, the upper indentation reaching almost to the preopercle and covered with uncalcified membrane; angle of preopercle rounded, bulging backwards significantly, the margin scalloped in very small specimens. Gill-rakers about half the length of the filaments, toothed on inner edge, spaced, about 13 on lower limb of first arch; no rudimentary rakers under small pseudobranch. Seven branchiostegal rays, five on the ceratohyal, two on the epihyal, the tips of the branchi-

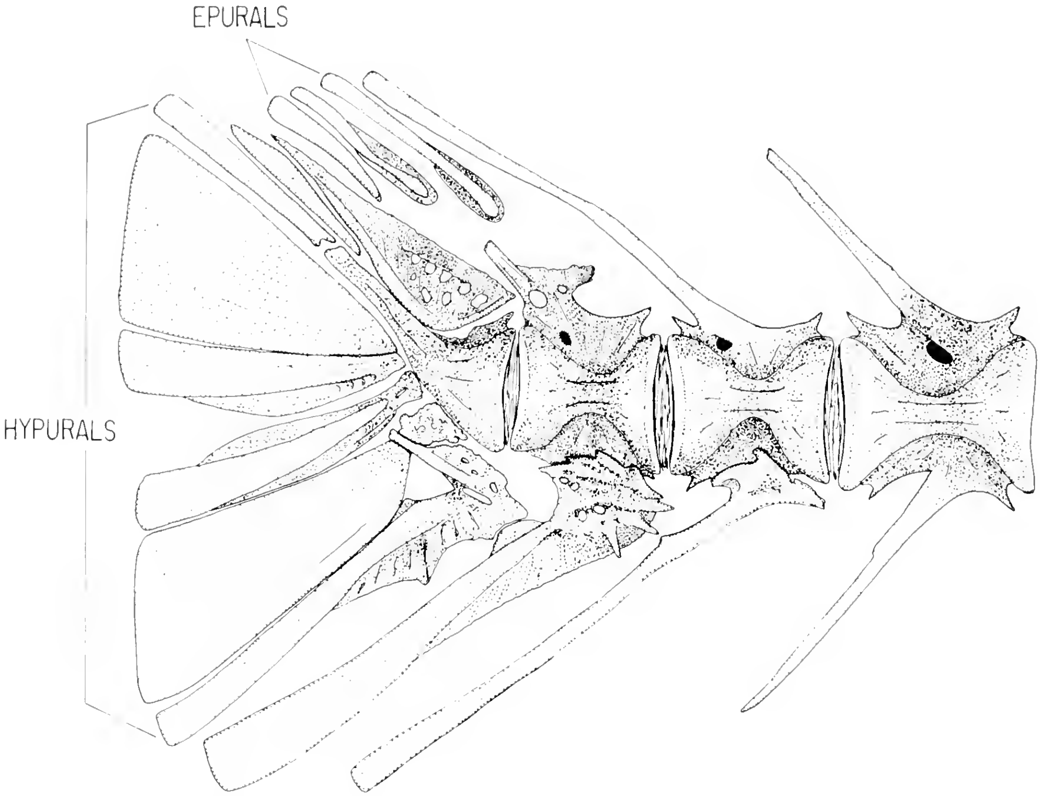


Figure 22. Caudal skeleton of *Psenopsis anomala*, drawing of a cleared-and-stained preparation from a 40-mm specimen, ABE 62-656. All elements identified in Figure 1.

ostegals pointed. Scapula visible. Vertebrae 10 + 15 = 25. In the adult, hypurals 2 + 3 and 4 + 5 closely conjoined, three epurals. Sclerotic bones well ossified, subocular shelf present on second suborbital. Stomach a simple sac; intestine long. Pyloric caeca very numerous, in a mass resembling a raspberry.

Color in preservative brown or bluish, deep-bodied form often with a silvery or whitish overlay. Deep-bodied form countershaded, others uniform. Usually a prominent black spot on shoulder at beginning of lateral line. Fins a little lighter than the body. Opercles and peritoneum silvery or blackish. Inside of mouth light, gill cavity dark.

Natural history. Though fished commercially in Japan, very little is known of the habits of these fishes. Young *Psenopsis* have been reported in association with medusae (Shojima, 1961). The adults of *P. anomala*, at least, live nearer the coasts and in shallower water than most centrolophids. Large schools are taken by nearshore trap nets in Japan. Adult specimens of *P. cyanea* were taken off Cananore in 1½ fathoms.

Psenopsis is one of the smaller centrolophids. Specimens of 180 mm SL are fully mature. Few exceed 200 mm.

Relationships. Psenopsis, with *Seriolella*, is the most evolutionarily advanced centrolophid. The slender tapering branchiostegal rays and the conjunction of hypurals 2 + 4 and 4 + 5 (Fig. 22) with growth

Figure 23. Branchial region of *Psenopsis anomala*, drawing of a cleared-and-stained preparation from a 150-mm specimen. Elements identified in Figure 2.

approach the nomeid grade. The pharyngeal sacs (Fig. 23) are larger, and there are more numerous bands of small papillae than are found in *Hyperoglyphe* or *Centrolophus*. The well ossified sclerotic bones, the absence of a supramaxillary bone, the smallish mouth, the deciduous scales, and the dorsal fin with only slightly more finrays than the anal suggest that *Psenopsis* may be near the base of the line leading to the Stromateidae. *Seriolella*, which retains the supramaxillary lost in *Psenopsis*, is its closest relative within the centrolophids.

Species. *Psenopsis* is an Indo-Pacific genus, found in India, Japan, northwest Australia, and the East Indies. There are four allopatric species, one of them undescribed. Little confusion has arisen regarding the identification of these fishes, and there are no problems of synonymy. The species are:

Psenopsis anomala (Temminck and Schlegel, 1850) = *Trachinotus anomalus* Temminck and Schlegel. China and southern Japan, type locality Tokyo. Deep-bodied. D V–VII, 27–32. A III 25–29. P 20–23. Gill-rakers usually 6 + 1 + 13, 12–15 on lower limb of first arch, 18–21 total. Vertebrae 10 + 15 (skel.). This species is the "ibodai" of Japanese fisheries literature, and is common from Hong Kong to Tokyo and into the Sea of Japan as far north as Hokkaido. It forms the basis of an important fishery. *P. shojimai* Ochiai and Mori,

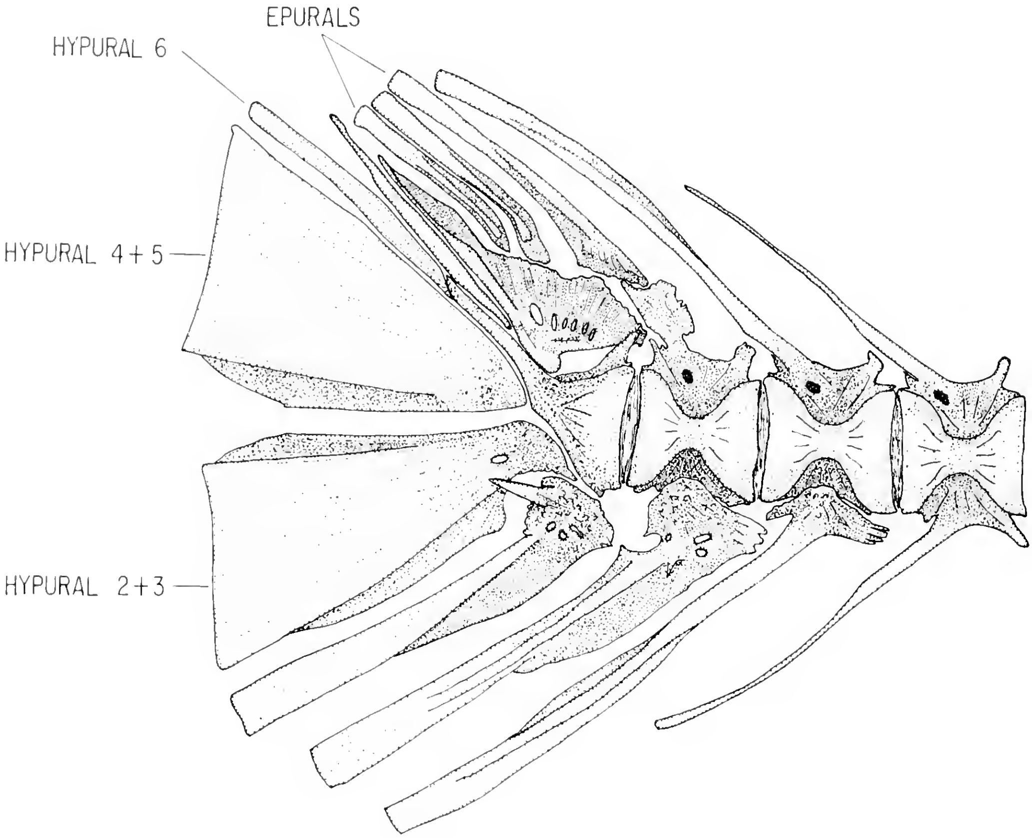


Figure 24. Caudal skeleton of *Nomeus gronovii*, drawing of a cleared-and-stained preparation from an 87-mm specimen. All elements identified in Figure 1.

1965, from the Sea of Japan is a probable synonym.

Psenopsis humerosa Munro, 1958. Dampier Archipelago, N. W. Australia. Deep-bodied. D VII, 28. A III 25. P 22. Gill-rakers 12 on lower limb of first arch (from Munro, 1958). Probably a good species, little differentiated from *P. anomala*.

Psenopsis cyanea (Alcock, 1890) = **Bathyseriola cyanea* Alcock, type locality, Ganjam Coast, India. Elongate. D VI, 25–26. A III 22–23. P 20. Gill-rakers 5 + 1 + 14. Vertebrae 10 + 15.

Family NOMEIDAE

Type genus: *Nomeus* Cuvier, 1817

Pasteurs. Cuvier and Valenciennes, 1833:242 (descr.).

Nomeina. Günther, 1860:387 (in part, def.).

Nomeidae. Günther, 1880:455 (in part, def.). Jordan and Gilbert, 1882:448 (descr.). Jordan and Evermann, 1896:948 (descr., North America). Jordan, 1923:183 (in part, list). Berg, 1940:323 (in part, dist.); 1955:249 (in part, dist.). Norman, 1957:503 (in part, def., genera listed).

Psenidae. Auctorum.

Diagnosis. Stromateoid fishes with pelvic fins present in adults, two dorsal fins, teeth on vomer and palatines, six branchiostegal rays, and four hypural and three epural bones in the tail. The papillae in the pharyngeal sacs with stellate bases, arranged in about five broad longitudinal bands.

Description. Body slender to deep, compressed. Two dorsal fins, the first with about ten slender spines folding into a

Figure 25. Bronchial region of *Nomeus gronovii*, drawing of a cleared-and-stained preparation from a 187-mm specimen, MCZ 35327. Elements identified in Figure 2.

groove, the longest spine at least as long as the longest ray of the second dorsal fin. One to three anal spines, not separated from the rays. Soft dorsal and anal fins approximately the same length. Bases of median fins sheathed by scales. Pelvic fins attached to the abdomen by a thin membrane, folding into a narrow groove, the fins greatly produced and expanded in young *Nomeus* and some *Psenes*. Scales small to very large, cycloid or with very small weak cteni, thin, extremely deciduous. Lateral line high, following dorsal profile and often not extending onto peduncle. Skin thin; subdermal mucous canal system well developed and visible in most; the main canal down the side of the body may be mistaken for a lateral line. Opercular and preopercular margins entire or finely denticulate. Opercle very thin, with two flat, weak spines. Six branchiostegal rays. Mouth small, maxillary rarely extending to below eye. Teeth small, conical, or cusped in some *Psenes*, approximately uniserial in the jaws, present on vomer, palatines, and basibranchials. Supramaxillary absent. Adipose tissue around eye only moderately developed in most. Vertebrae 30 to 38, 41, or 42. Caudal skeleton with four hypurals and three epurals. Pharyngeal sacs with papillae in upper and lower sections, papillae in five to seven broad longitudinal bands. Bases of the papillae stellate, teeth seated on top of a central stalk. Adults usually about a foot long, although a giant *Cubiceps* may exceed three feet. Silvery to bluish-brown, some with conspicuous striped or blotched pattern.

Distribution. Nomeids are oceanic fishes of tropical and subtropical waters. They occur in the Gulf of Mexico, the Caribbean Sea, the Atlantic Ocean, the western Mediterranean Sea, the Indian Ocean, and across the Pacific. Numerous in the waters of the Philippines and southern Japan, they do not seem to enter the shallow South China Sea (Fig. 54).

Relationships. From an evolutionary standpoint, the nomeids are a grade above the centrolophids. There are more vertebrae, fusions have occurred in the hypural fan (Fig. 24), a branchiostegal ray has been lost, and the papillae in the pharyngeal sacs have stellate bases (Fig. 25). Nomeids have teeth on the palate and basibranchials, however, which precludes their derivation from a centrolophid. Probably both families have a common ancestor, and development has been somewhat parallel. The palatal dentition, lost in the Centrolophidae, remains in nomeids. The Nomeidae have passed through the centrolophid stage without leaving living representatives at that level.

The Nomeidae have given rise to two other families, each with a single genus. The tetragonurids, a very highly specialized group, arose early, perhaps from the same line which produced *Psenes.* The similarity between the teeth of *Tetragonurus* and *Psenes pellucidus* is striking, but need not imply too close a relationship. The reappearance of characters in divergent lines of common ancestry is not an unusual phenomenon (Simpson, 1953), and seems widespread in stromateoids.

The ariommids may have been derived more recently. Superficially, they resemble nomeids very much, but the teeth on the palate have been lost, further fusions have taken place in the caudal skeleton, and the pharyngeal sacs are strikingly divergent. The species of the *Cubiceps pauciradiatus* group may share a common ancestor with the Ariommidae. These show a tendency toward the ariommid condition in the reduced palatal dentition, and share with them the very large, deciduous scales and the extremely slender (sometimes even absent) bridge over the anterior vertical canal in the ear.

Key to Nomeid Genera

1 (4). Body elongate, maximum depth usually less than 35 per cent of the standard length, greatest in small specimens. Origin of dorsal fin behind, or directly over in very small specimens, insertion of pectoral fins. 2

2 (3). Anal count I-III 14–25. Insertion of pelvic fins under end or behind base of pectoral fin. An oval patch of knoblike teeth on the tongue. Vertebrae 30 to 33. *Cubiceps*, p. 78. Fig. 26

3 (2). Anal count I-II 24–29. Insertion of pelvic fins before or under insertion of pectoral fin, possibly behind in very large specimens. No patch of teeth on the tongue. Vertebrae 41. .... *Nomeus*, p. 81. Fig. 27

4 (1). Body deep, maximum depth usually greater than 40 per cent of the standard length, but possibly less in very large specimens. Origin of dorsal fin before, or directly over in large specimens, insertion of pectoral fins. .... *Psenes*, p. 84. Fig. 28

Genus *CUBICEPS* Lowe, 1843

Figure 26

Cubiceps Lowe, 1843:82. (Type species: *Seriola*[1] *gracilis* Lowe, 1843:82, by subsequent designation of Jordan and Evermann, 1896:950. Madeira.)

Atimostoma A. Smith, 1849, plate XXIV. (Type species: *Atimostoma capensis* Smith, 1849, plate XXIV, by monotypy. South Africa.)

Navarchus Filippi and Verany, 1859:187. (Type species: *Navarchus sulcatus* Filippi and Verany, 1859:187, by monotypy. Mediterranean. A synonym of *Cubiceps gracilis* Lowe, 1843: 82.)

Trachelocirrhus Doumet, 1863:220. (Type species: *Trachelocirrhus mediterraneus* Doumet, 1863: 222, by monotypy. Sète, France. A synonym of *Cubiceps gracilis* Lowe, 1843:82.)

Mulichthys Lloyd, 1909:156. (Type species: *Mulichthys squamiceps* Lloyd, 1909:158, by monotypy. Arabian Sea.)

Mandelichthys Nichols and Murphy, 1944:247. (Subgenus. Type species: *Cubiceps carinatus* Nichols and Murphy, 1944:245, by monotypy. 180 miles SW of Cape Mala, Panama.)

---

[1] Lowe described his fish as a species in the genus *Seriola*, but noted (p. 82), "Still it is not unlikely that a comparison of the two fishes [*gracilis* and *S. bipinnulata* (Quoy and Gaimard)] may warrant . . . their separation from *Seriola* into a genus, which may be called *Cubiceps*."

The combination of elongate body, long winglike pectoral fins, insertion of pelvics behind pectoral fin base, scales on top of head, cheeks, and opercles, and a patch of teeth on the tongue distinguishes *Cubiceps* from all other stromateoid genera. The name, a masculine noun, is from the Greek *κύβος*, cube, + *κεφαλή*, head, in reference to the square profile of the fish's head.

Description. Body elongate, maximum depth 25 to 30 per cent of the standard length; musculature firm. Peduncle short, deep, and compressed. Two dorsal fins, scarcely divided. First dorsal originating behind insertion of pectoral fins, with about ten stiff spines folding into a groove, the longest spine longer than the longest ray of the second dorsal. Anterior rays of the second dorsal the longest, those that follow decreasing in length, 14 to 23 finrays in all. Anal and genital papillae behind mid-body, in a slit. Anal fin originating behind origin of second dorsal fin, one to three short spines preceding the rays. Anterior rays the longest, those that follow decreasing in length, 14 to 21 finrays in all. Pectoral fin pointed, becoming very long and winglike, the relative length increasing markedly with growth; base of the fin inclined at an angle of 45°. Pelvic fins inserting just under end of or behind pectoral fin base, attached to the abdomen by a small membrane and folding into a deep groove. Expanded coracoid often forming a conspicuous keel along mid-ventral line ahead of pelvics. Caudal fin forked, the lobes often folding over one another. Scales large, cycloid, very deciduous, covering bases of the median fins. Simple tubed scales of lateral line high, following dorsal profile and ending under last dorsal finray or extending onto peduncle. Skin thin; subdermal canals on flanks easily traced. Main canal may be confused with lateral line. Pores to surface small. Head around 32 per cent of the standard length. Top of snout naked, minute pores in naked skin. Scales extending forward on top of head almost to level of the nostrils. Eye large, bony supraorbital ridge pronounced. Adipose tissue around eye well developed, extending forward around the nostrils. Nostrils near tip of blunt snout, small, both round. Maxillary ending under anterior border of eye, angle of gape well before eye. Premaxillary not protractile. Lacrimal bone completely covering upper jaw when mouth is closed, ventral border of maxillary sometimes remaining exposed. Supramaxillary absent. Jaw teeth small, pointed, slightly recurved, usually spaced. Very small teeth usually present on vomer and in a single series on the palatines and basibranchials. An oval patch of low knoblike teeth on the glossohyal. Opercle and preopercle thin, scaled, margins entire or finely denticulate; opercle with two weak flat spines; angle of preopercle slightly rounded, not bulging backward. Cheeks scaled. Gillrakers slender, almost the length of the filaments, toothed on inner edge, fairly close set, 14 to 18 on lower limb of first arch; no rudimentary rakers under the large pseudobranch. Scapula prominent. Vertebrae 13 + 17 to 15 + 18 = 30 to 33. Sclerotic bones usually well ossified in adults. Stomach a simple sac; intestine of moderate length. Pyloric caeca very numerous, in a large dendritic mass.

Color in preservative either brownish, darker on the back than on the sides, or bluish above and silvery on the sides. First dorsal blackish, other fins usually the same color as the body, caudal dusky. Iris greyish, often with golden semicircles at anterior and posterior borders. Inside of mouth, gill cavity, and peritoneum dark.

Natural history. All the nomeids are oceanic. Most species are very rarely seen, and little is known of their habits.

Small *Cubiceps gracilis* are very numerous near the Azores, where they are taken in surface nets and from under medusae. By the time these fishes reach about 200 mm SL, they are mature. With the attainment of maturity growth does not stop, but

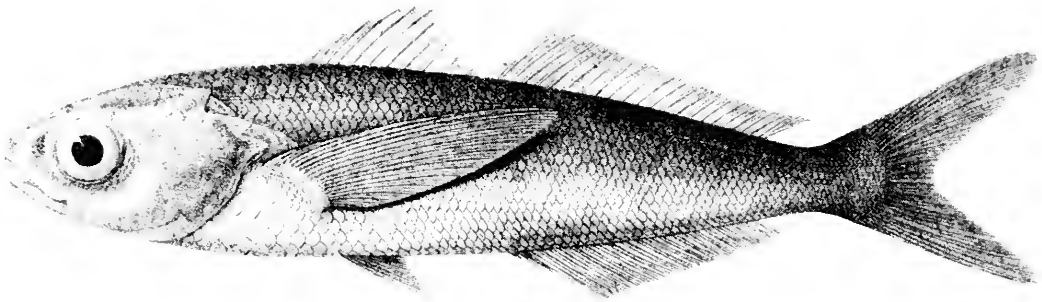


Figure 26. *Cubiceps gracilis*, drawing of a 164-mm specimen, from Günther, 1889.

continues significantly. Specimens near 800 mm SL have been reported from the Mediterranean (Ariola, 1912). With growth, the relative length of the pectoral fin increases markedly.

In the Philippines, *Cubiceps* is caught by using night-lights and lift-nets (Herre and Herald, 1950). Large specimens are taken occasionally by the near-shore winter long-line fishery for swordfish off southern Japan.

Relationships. *Cubiceps* occupies the central position in nomeid evolution. The two other nomeid genera, *Nomeus* and *Psenes*, are certainly derived from *Cubiceps.* In both derived genera the patch of teeth on the tongue has been lost, and there has been a tendency towards an increase in the number of vertebrae and finrays. The papillae in the pharyngeal sacs of *Cubiceps* are very similar to those of *Nomeus* (Fig. 25), but those of *Psenes* are in general smaller (Figs. 29, 30). The caudal skeletons of all three genera are almost identical (Fig. 24).

The Ariommidae have probably evolved from a *Cubiceps*, although the systematic position of the family is far from clear. The ariommids do share certain characters, however, with the fishes of the *Cubiceps pauciradiatus* group, as discussed on pages 77 and 90.

Cubiceps and the tetragonurids both have patches of teeth on the tongue. The jaw teeth, the pharyngeal sacs, and the scales, however, are very different in these two groups. It seems likely that the Tetragonuridae branched off very early from the nomeid stem, but their ancestor may have been a fish similar in many respects to the present-day *Cubiceps.*

Species. *Cubiceps* is found in the temperate and tropical waters of the Atlantic, Pacific, and Indian oceans. It also occurs in the western Mediterranean Sea, and the Gulf of Mexico and Caribbean Sea.

Much confusion surrounds the species of *Cubiceps.* The counts of all described are fairly close. Lacking sufficient comparative material, it is difficult to evaluate the small differences which do occur, for example in vertebral number. There seems to be a great differential in the size attained by the adult. The species of the *Cubiceps pauciradiatus* group may never exceed 200 mm SL (Haedrich, 1965), whereas fishes allied to *Cubiceps gracilis* are reported (Smith, 1849; Ariola, 1912; Abe, 1955a) to approach a meter in length.

The nominal species in the genus *Cubiceps* are:

Cubiceps gracilis (Lowe, 1843) = *Seriola gracilis* Lowe. Atlantic Ocean and western Mediterranean, type locality Madeira, perhaps a world-wide species. D IX–XI, I–II 20–22. A II–III 20–23. P 20–24. Gill-rakers 8–9 + 1 + 14–17. Vertebrae 15 + 18. Synonyms are: *Navarchus sulcatus* Filippi and Verany, 1859, from the Mediterranean; *Trachelocirrhus mediterraneus* Doumet, 1863, from Sète; *Cubiceps lowei* Osorio, 1909, from the Cape Verde Islands; and *Aphareus obtusirostris* Borodin, 1930, from the Azores.

Cubiceps capensis (A. Smith, 1849) = **Atimostoma capensis* Smith. Type locality South Africa. D IX–X, I–III 24–26. A II 22–23. P 16–18. Gill-rakers 8–9 + 1 + 16–17. Vertebrae 14 + 17. The stuffed type is about 900 mm SL. The margin of the opercle between the two flat opercular spines may be strongly serrate in this species. A probable synonym is *Cubiceps niger* Franca, 1957, from Angola.

**Cubiceps pauciradiatus* Günther, 1872. Central and western Pacific Ocean, type locality Misol Island. D X–XII, I 16–18. A I–II 14–17. P 18–19. Gill-rakers 8–9 + 1 + 16. This is a diminutive species, rarely exceeding 160 mm SL. Closely related forms are: **C. longimanus* Fowler, 1934a, *C. carinatus* Nichols and Murphy, 1944, and **C. athenae* Haedrich, 1965. **Cubiceps nesiotes* Fowler, 1938, from Christmas Island, Central Pacific, is a probable synonym.

Cubiceps squamiceps (Lloyd, 1909) = *Mulichthys squamiceps* Lloyd. South Africa to Japan, type locality Arabian Sea. D IX–XI, I–II 19–21. A II–III 18–21. P 18–20. Gill-rakers 8–9 + 1 + 16–17. This is a chunky-looking fish, with a very short peduncle and broad, winglike pectoral. **Cubiceps natalensis* Gilchrist and von Bonde, 1923, is probably a synonym.

**Cubiceps caeruleus* Regan, 1914a. Tasman Sea, type locality Three Kings Island. D X–XI, I–II 21–24. A II–III 21–24. P 19–21. Gill-rakers 7 + 1 + 16–17. Vertebrae 13 + 18. A few of the jaw teeth on the types are long and project like fangs. *Cubiceps baxteri* McCulloch, 1923, based on a damaged specimen 371 mm long, may be the adult.

**Cubiceps longimanus* Fowler, 1934. Western Indian Ocean, type locality Durban. D X–XI, I 15–16. A I–II 15. P 18–20. Gill-rakers 9 + 1 +14. All specimens known are less than 50 mm SL long.

Cubiceps carinatus Nichols and Murphy, 1944. Pacific Coast of Central America, type locality Gulf of Panama. D IX–X, I 14–16. A II 14–15. P 17–19. Gill-rakers 7–8 + 1 + 14–16. Vertebrae 13 + 17. This species has fewer median finrays than the closely related *C. pauciradiatus* Günther, 1872, from the Central and Western Pacific.

**Cubiceps athenae* Haedrich, 1965. East coast of North America. D X–XI, I 15–16. A II 14–15. P 18–19. Gill-rakers 8 + 1 + 16–17. Vertebrae 13 + 18.

Genus *NOMEUS* Cuvier, 1817

Figure 27

Nomeus Cuvier, 1817:315. (Type species: *Gobius gronovii* Gmelin, 1788:1205, by subsequent designation of Jordan and Gilbert, 1882:449.[1] Atlantic Ocean.)

The combination of elongate body, black fanlike pelvic fins with the full length of the trailing edge attached to the abdomen, insertion of the pelvics (usually) ahead of the pectorals, blotched and spotted pattern, and 41 vertebrae distinguishes *Nomeus* from all other stromateoid genera. The name, a masculine noun, is from the Greek *νομεὺς*, herdsman, a translation of the Dutch vernacular "Harder" (Marcgrave, 1648), probably in reference to the fishes' habit of following *Physalia*.

Description. Body elongate, maximum depth around 30 per cent of the standard length; musculature firm. Peduncle slightly tapered, compressed. Two dorsal fins, scarcely divided. First dorsal fin originating over or a little behind insertion of the pectoral fin, with about ten soft spines folding into a deep groove, the longest

---

[1] Cuvier and Valenciennes (1833:242) designated *Nomeus mauritii* Cuvier (1817:315) type for the genus. Cuvier's species, however, based on the "Harder" of Marcgrave (1648:153), appeared in name only, the description being later supplied by Cuvier and Valenciennes (1833:243). Under the International Code, a *nomen nudum* is unavailable as a type, and *Nomeus mauritii* Cuvier, 1817, is thus rejected. *Nomeus mauritii* (*non* Cuvier, 1817) Cuvier and Valenciennes, 1833, is a synonym of *Nomeus gronovii* (Gmelin, 1788).

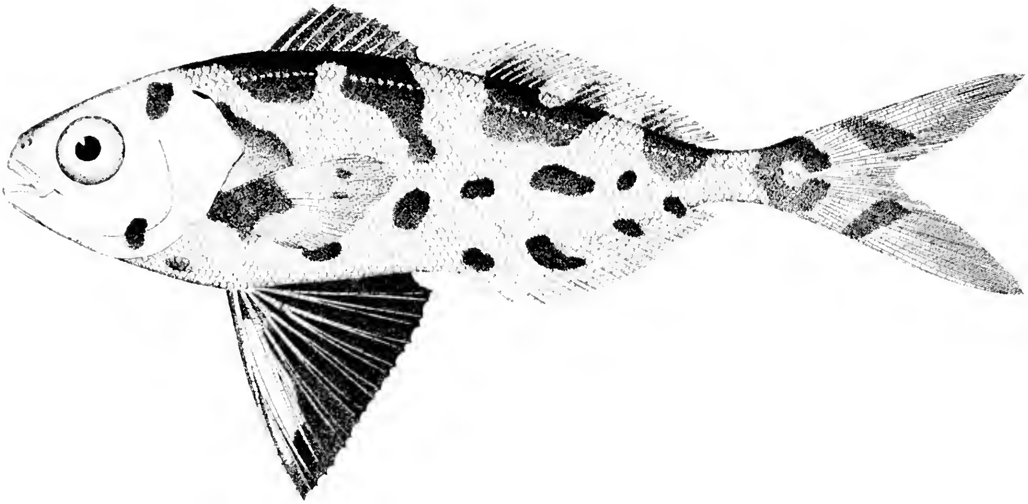


Figure 27. *Nomeus gronovii*, drawing of an approximately 40-mm specimen, courtesy of the Smithsonian Institution.

spine slightly longer than the longest ray of the second dorsal. Anterior rays of the second dorsal fin the longest, those that follow shorter, subequal, 24 to 28 finrays in all. Anal and genital papilla at mid-body, in a deep slit. Anal fin originating under or slightly behind origin of second dorsal fin, one or two weak spines preceding the rays. Anteriormost rays the longest, those that follow shorter, subequal. Pectoral fin rounded in the young, pointed, winglike, in the adult; the relative length increases markedly with growth. Pelvic fins inserting before, or in large specimens under, pectoral fin base, fan-shaped, innermost ray the longest, attached to the abdomen for its entire length by a strong membrane and folding into a deep groove which reaches to the anus. Relative length of the fin decreasing markedly with growth. Caudal fin deeply forked, lobes very long. Scales small, cycloid, very thin, deciduous, covering bases of median fins. Simple tubed scales of lateral line high, following dorsal profile and not appearing to extend onto peduncle. End of lateral line under last dorsal finray in most specimens (in the single large specimen known, the lateral line reaches the caudal base). Skin thin; subdermal canals on flanks easily traced. Main canal may be confused with lateral line. Pores to surface minute. Head around 30 per cent of the standard length. Top of snout naked, minute pores visible in naked skin. Scales extending forward over nape to level of anterior border of the eye. Interorbital space and top of snout covered with adipose tissue. Eye of moderate size, bony supraorbital ridge pronounced. Adipose tissue around eye very well developed, extending forward to cover the lacrimal and surrounding the nostrils. Nostrils on tip of truncate snout, small, the anterior round, the posterior a slit. Maxillary ends under, or before in large specimens, anterior border of the eye, angle of gape well before eye. Premaxillary not protractile. Lacrimal bone almost completely covering upper jaw when mouth is closed, ventral border of maxillary remaining exposed. Supramaxillary absent. Jaw teeth small, pointed, slightly recurved, spaced. Small recurved teeth present on vomer and in a single series on the palatines and basibranchials. No teeth on the glossohyal. Opercle and preopercle thin, scaled, margins very finely denticulate or entire; opercle with two weak hardly defined flat spines; angle of preopercle rounded, bulging backward in large specimens. Cheeks scaled. Gill-rakers slender, half the length of the filaments, toothed on inner edge, fairly close-set, about 16 on lower limb of first arch; sometimes a few rudimentary rakers under the large pseudobranch. Six branchiostegal rays, four on the ceratohyal, two on the epihyal. Scapula prominent. Vertebrae 15 + 26 = 41. In the single large specimen known, the sclerotic bones are well ossified. Stomach a simple sac; intestine of moderate length. Pyloric caeca numerous, in a small dendritic mass.

Color in life bright blue above, blotched and spotted with blue on the brilliant silvery sides. In preservative, the base color is tan, the blotches and spots appearing dark brown. Median fins with about three dark stripes. First dorsal and pelvics black, pectorals light. The single large specimen known is uniform dark brown. Eye usually greyish; in the large specimen the iris is golden, divided by a dark vertical bar. Inside of mouth, gill cavity, and peritoneum light.

Natural history. The association between *Nomeus* and *Physalia* is commonly cited as an example of commensalism, but actually very little is known about the true nature of the association or about the life histories of the animals involved. *Nomeus* has been observed eating *Physalia* (Kato, 1933) and *vice versa* (Garman, 1896). In comparison to other fishes, however, *Nomeus* is relatively immune to the toxin of the siphonophore (Lane, 1960).

The eggs and larvae of *Nomeus* are not known. Fishes of 10-mm SL have been taken from under *Physalia*, however, indicating that the association must form early in the fish's life. I have seen 150-mm SL specimens also taken with *Physalia*. These fishes appeared to be adults, but none were ripe. The largest known specimen of *Nomeus* was taken with a bottom trawl in the Caribbean Sea. This 225-mm specimen was apparently not in association with *Physalia*, was living fairly deep in the water, and was a uniform dark brown instead of blotched like smaller specimens. This fish appeared to be a mature male. Many young stromateoids live with jellyfishes, have a blotched or mottled color pattern, and both desert their coelenterate host and become uniformly colored with growth. The discovery of this large, dark *Nomeus* suggests that the familiar small, blotched *Nomeus* found under *Physalia* may only be the young form of a bigger fish which lives in the depths.

Relationships. Nomeus is derived from the central *Cubiceps* stock. It is very similar in appearance to *Cubiceps*. The differences between the two are slight, but sufficient to consider *Nomeus* a genus in its own right. In *Nomeus* the pelvic bones have become much shortened, the patch of teeth on the glossohyal has disappeared, the number of vertebrae and finrays has increased, and there are only two spines preceding the anal finrays.

Nomeus lives in a very specialized environment, under *Physalia*. The features which distinguish it from *Cubiceps* doubtless reflect the demands of this unusual habitat. Adapted to a particular way of life, *Nomeus* has given rise to no other forms.

Species. Nomeus is a wide-ranging genus, found in the temperate and tropical waters of all the major oceans. It does not occur, however, in the eastern Atlantic or the Mediterranean. I have examined specimens from the Atlantic Ocean, the Gulf of Mexico and Caribbean Sea, the Indian Ocean, and the central and western Pacific Ocean. The counts of all these are essentially the same. I cannot but conclude that in the genus *Nomeus* there is but one species:

Nomeus gronovii (Gmelin, 1788) = *Gobius gronovii* Gmelin. Temperate and tropical regions of the Atlantic, Pacific, and Indian Oceans, Gulf of Mexico and Caribbean Sea, type locality "American Ocean in the Torrid Zone." D IX–XII, 24–28. A I–II 24–29. P 21–23. Gill-rakers 8–9 + 1 + 15–18. Vertebrae 41. Synonyms are: *Eleotris mauritii*

Bloch and Schneider, 1801, from Mauritius; *Nomeus maculosus* Bennett, 1831, from the Atlantic coast of North Africa; *Nomeus maculatus* Valenciennes, 1836; *Nomeus oxyurus* Poey, 1861, from Cuba; and *Nomeus dyscritus* Whitley, 1931, from New South Wales. **Nomeus peronii* Cuvier and Valenciennes, 1833, from the seas of Java is known only from three specimens in very poor condition. It is hard to be certain that these fish belong to *Nomeus*, though they are almost surely nomeids. I was able to make counts on only one. The counts were D IX, 30; A 31 (total elements); P 21; gill-rakers 8 + 1 + 16. No subsequent material has appeared, and I consider **N. peronii* a synonym of *N. gronovii.*

Genus *PSENES* Cuvier and Valenciennes, 1833

Figure 28

Psenes Cuvier and Valenciennes, 1833:259. (Type species: **Psenes cyanophrys* Cuvier and Valenciennes, 1833:260, by original designation. New Ireland, western Pacific Ocean.)

Icticus Jordan and Thompson, 1914:242. (Type species: **Icticus ischanus* Jordan and Thompson, 1914:242, by original designation. Okinawa, western Pacific Ocean. A synonym of **Psenes pellucidus* Lütken, 1880:516.)

Papyrichthys J. L. B. Smith, 1934:90. (Type species: **Psenes pellucidus* Lütken, 1880:516, by original designation. Straits of Surabaja, Java.)

Thecopsenes Fowler, 1944a:63. (Type species: **Psenes chapmani* Fowler, 1906:119, by original designation. Cape Verde Islands, Atlantic Ocean. A synonym of **Psenes cyanophrys* Cuvier and Valenciennes, 1833:260.)

Caristioides Whitley, 1948:87. (Type species: *Caristioides amplipinnis* Whitley, 1948:88, by monotypy. Lord Howe Island, Tasman Sea. A synonym of **Psenes pellucidus* Lütken, 1880:516.)

Parapsenes J. L. B. Smith, 1949a:847. (Type species: *Psenes rotundus* Smith, 1949:307, by original designation. Dassen Island, South Africa.)

The combination of two dorsal fins, the first dorsal fin originating before or over the pectoral insertion, pelvic fins present, deep body, teeth on the palatines and basibranchials, and no teeth on the glossohyal distinguishes *Psenes* from all other stromateoid genera. The name, a feminine noun, is from the Greek ψήνη, the osprey *Pandion*, the allusion not evident. The authors of the name, Cuvier and Valenciennes (1833), may have been impressed by the resemblance of the "soureil bleu" on their little fish to the similar brow of the fish hawk.

Description. Body deep, maximum depth usually greater than 40 per cent of the standard length, but sometimes less in large specimens; musculature firm to soft and flabby. Regions at bases of median fins may be very compressed and translucent. Peduncle short, compressed, may be fairly slender. Two dorsal fins, scarcely divided. First dorsal fin originating before insertion of pectoral fins, with about ten soft spines folding into a deeper groove. Rays of the second dorsal fin nearly as long as the longest D_1 spine, all approximately the same length or decreasing in length posteriorly, 18 to 30 finrays in all. Anal papilla a little before mid-body, in a depression. Anal fin originating at mid-body, slightly behind origin of second dorsal fin, two or three weak spines preceding the 17 to 30 rays. Pectoral fin rounded or winglike; relative length of fin decreasing slightly or increasing markedly with growth. Pelvic fins inserting under posterior portion of pectoral fin base, attached to the abdomen by a small membrane and folding into a groove. Pelvics very long in the young of some, the relative length decreasing markedly with growth. Caudal fin deeply forked. Scales small to minute, with a few weak cteni, very thin, deciduous, covering bases of median fins. Simple tubed scales of lateral line high, following dorsal profile and ending under last dorsal finray or extending onto peduncle. Skin thin; main subdermal canals along intermuscular septum apparent, may be confused with lateral line, side branches not visible. Pores to surface minute or absent. Head around 30 per cent of the standard length. Top of snout naked, minute pores in naked skin. Scales extending forward on top of head almost to level

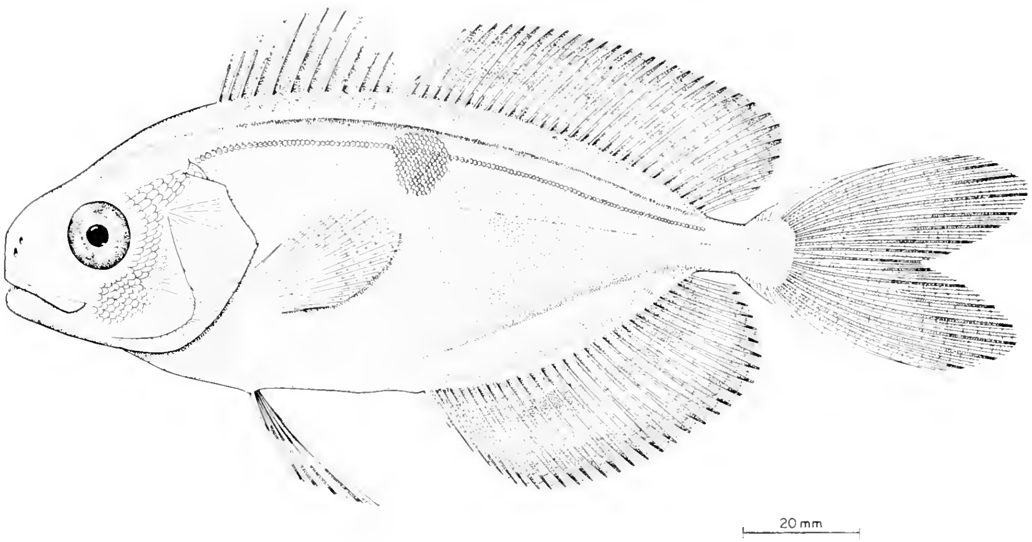


Figure 28. *Psenes pellucidus*, drawing of a 130-mm specimen by Margaret Bradbury.

of anterior border of the eye. Eye moderate to large. Adipose tissue around eye moderately developed. Nostrils near tip of truncate snout, small, the anterior one round, the posterior a slit. Maxillary ending under anterior portion of the eye. Premaxillary not protractile. Lacrimal bone almost completely covering upper jaw when mouth is closed, ventral border of maxillary remaining exposed. Supramaxillary absent. Teeth in both jaws uniserial, pointed; teeth in upper jaw small, slightly recurved, spaced; teeth in lower jaw larger, may be long and bladelike with small cusps, close-set. A few small recurved teeth in a patch on the head of the vomer and in a single series on each palatine and on the basibranchials. Opercle and preopercle thin, scaled, margins very finely denticulate or entire; opercle with two weak, hardly defined, flat spines; angle of preopercle rounded, projecting backward very slightly. Gill-rakers slender, a little shorter than the filaments, toothed on inner edge, moderately spaced, 14 to 19 on lower limb of first arch; sometimes a few rudimentary rakers under the long pseudobranch. Six branchiostegal rays, four on the ceratohyal, two on the epihyal. Scapula not prominent. Vertebrae 13 to 15 + 18 to 23 = 31 to 38, or 15 + 26 or 27 = 41 or 42. Stomach a simple sac; intestine very long. Pyloric caeca numerous, in a dendritic mass.

Color in preservative brown to yellowish, some species with a conspicuous, dark, blotched or longitudinally striped pattern. Median fins and pelvics often darker than the body. Region at bases of median fins translucent in *P. pellucidus*. Inside of mouth light brown, gill cavity usually darker. Peritoneum dark or light.

Natural history. The young of *Psenes* are fairly common in the surface layers on the high seas. They do not seem to associate with jellyfishes to any extent, but are very often dipnetted from under floating *Sargassum*. The larger adults, as with most other stromateoids, probably live deeper in the water. Most species in *Psenes* are strictly oceanic, and large specimens are rarely seen. Longley and Hildebrand (1941) report the remains of 120-mm *P. cyanophrys* from bird rookeries in the Tortugas. Other species found there included *Monacanthus*

Figure 29. Branchial region of *Psenes cyanophrys,* drawing of a cleared-and-stained preparation from a 128-mm specimen. Elements identified in Figure 2.

hispidus, Trachurops crumenopthalma, and *Caranx ruber,* all fishes commonly associated with floating Gulf weed.

In the Caribbean area, the monthly distribution of post-larval and juvenile *Psenes cyanophrys* suggested that spawning occurred from March through October (Legaspi, 1956). The young fish fed at first on copepods, but later a variety of foods—copepods, amphipods, chaetognaths, fish eggs and larvae—was taken (Lloyd, 1909; Legaspi, 1956). In large *P. pellucidus,* a sombre-colored probably mesopelagic species, I have found gonostomatids of the genus *Maurolicus.*

Relationships. Psenes, like *Nomeus,* is a derivative of the central *Cubiceps* stock. In *Psenes,* the number of median finrays and vertebrae has tended to increase, the first interhaemal has moved forward forming an abrupt angle with the haemal process of the first precaudal vertebra, the teeth on the glossohyal have disappeared, the toothbases in the pharyngeal sac have become smaller, and the body has become deeper. In the meso- or bathypelagic species the teeth are highly differentiated. Those in the lower jaw are long and knifelike, while those in the upper jaw are small and strongly recurved. In many species of

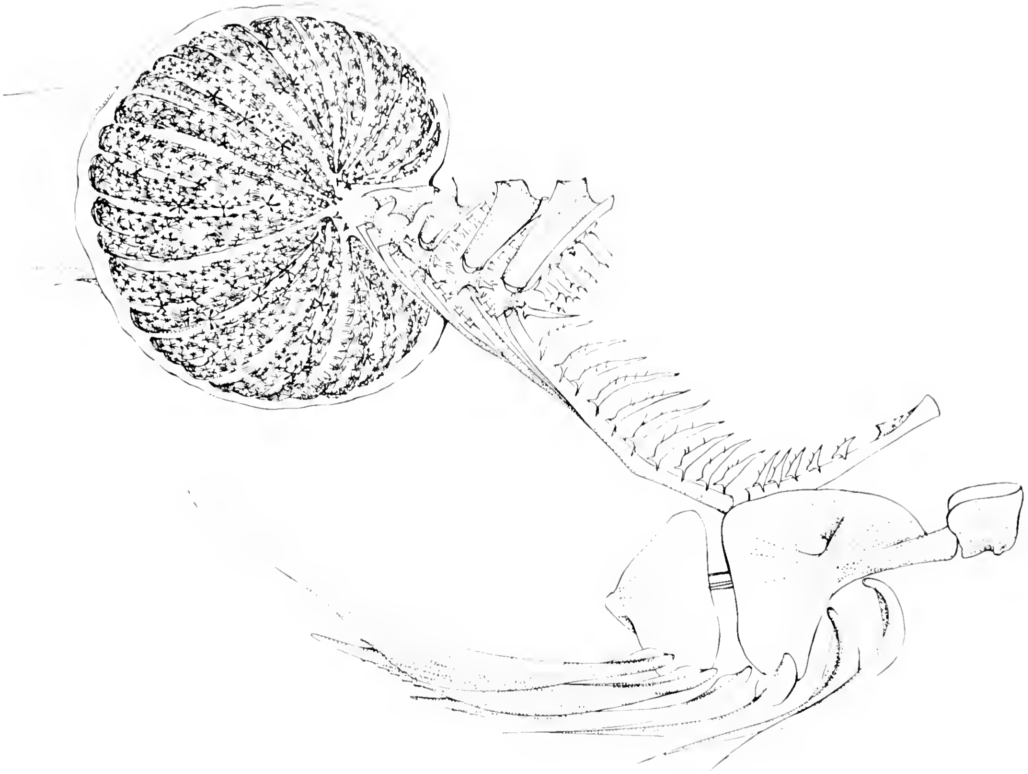


Figure 30. Branchial region of *Psenes pellucidus*, the type species for the nominal genus *Icticus*, drawing of a cleared-and-stained preparation from a 166-mm specimen, ABE 60-106. Elements identified in Figure 2.

Psenes, the teeth in the lower jaw are cusped.

Psenes has given rise to no other forms, although species such as *Psenes pellucidus*, which have entered the bathypelagic realm, seem to be diverging rapidly from the central bauplan. This fish has been described as a separate genus, *Icticus*. Were it not for the great similarity between the structure of the pharyngeal sacs of this nominal genus and *Psenes* (Figs. 29, 30), and for the presence of species intermediate in other characters, *Icticus* would stand as a genus derived from *Psenes*.

Species. *Psenes* is widespread in the temperate and tropical parts of the Atlantic, Pacific, and Indian oceans. There are numerous records of the genus from the Gulf of Mexico and the Caribbean, but none from the Mediterranean Sea.

As in *Cubiceps*, there is some confusion surrounding the species of *Psenes*. Most seem to be world-wide, with minor differences from ocean to ocean. Larger collections and more extensive series than those now available are necessary for proper comment on the significance of these differences.

The nominal species in the genus are:

**Psenes cyanophrys* Cuvier and Valenciennes, 1833. Atlantic, Pacific, and Indian oceans, type locality New Ireland. D IX–XI, 24–28. A III 24–28. P 17–20. Gill-rakers 8–9 + 1 + 19. Vertebrae 13 + 18. The counts recorded for specimens from the Gulf of Mexico (Legaspi, 1956) are modally higher than those of Pacific specimens. A very characteristic feature of this species is the numerous longitudinal streaks on the sides. According to Le Danois (1962), the following are synonyms: *Psenes javanicus* Cuvier and Valenciennes, 1833, from Java, *Psenes auratus* Cuvier and Valenciennes, 1833, from Guam, and *Psenes fuscus* Guichenot, 1866, from Madagascar. *Psenes leucurus* Cuvier and Valenciennes, the color of which is described by the authors (1833:265) as "jaunâtre, marbré de noirâtre et finement rayé de traits longitudinaux noirâtres," is also probably a synonym, but Le Danois (1962) does not agree. Other synonyms are: **Cubiceps multiradiatus* Günther, 1871, from Manado, Philippines; *Psenes chapmani* Fowler, 1906, from the Cape Verde Islands; *Psenes pacificus* Meek and Hildebrand, 1925, from the Bay of Panama; and *Psenes kamoharai* Abe, Kojima, and Kosakai, 1963, from Kyushu.

**Psenes pellucidus* Lütken, 1880. Atlantic, Pacific, and Indian oceans, type locality Surabaja Strait, Java Sea. D X–XI, I–II 27–32. A III 26–31. P 18–20. Gill-rakers 8–9 + 1 + 14–16. Vertebrae 15 + 26–27. This meso- or bathypelagic species is immediately recognizable by the soft, flabby musculature, the long knifelike teeth in the lower jaw, the sombre coloration, and the high vertebral and median finray counts. With growth, this species becomes quite slender. Synonyms are: **Psenes edwardsii* Eigenmann, 1902, from the Atlantic Ocean south of Rhode Island; **Icticus ischanus* Jordan and Thompson, 1914, from Okinawa; *Caristioides amplipinnis* Whitley, 1948, from Lord Howe Island, and *Cubiceps ismaelensis* Dieuzeide and Roland, 1955, from the coast of Algeria.

**Psenes maculatus* Lütken 1880. Atlantic, Pacific, and Indian oceans, type locality central Atlantic Ocean. D IX–XI, I 22–24. A III 21–23. P 20–21. Vertebrae 15 + 18–20. *Psenes nigrescens* Lloyd, 1909, from the Andaman Sea is a possible synonym.

**Psenes arafurensis* Günther, 1889. Atlantic, Pacific, and Indian oceans, type locality Arafura Sea. D X–XI, I–II 19–21. A III 20–21. P 18–20. Gill-rakers 7–9 + 1 + 15–16. Vertebrae 13 + 18. This species is very similar to **P. maculatus* Lütken, 1880, but the body is deeper at comparable sizes. The teeth in the lower jaws of both nominal species are like those of **P. pellucidus*. *P. rotundus* Smith, 1949, from South Africa is a probable synonym.

Psenes whiteleggii Waite, 1894. Coasts of New South Wales, type locality Maroubra Bay. D XI, I 19. A III 18. P 18. (From Waite, 1894.) *Psenes hillii* Ogilby, 1915, from Queensland is a probable synonym.

Psenes guttatus Fowler, 1934a. Coast of Natal. D XI, I 20. A III 18. Gill-rakers 7 + 18. (From Fowler, 1934a). This name appears as a *nomen nudum* in Fowler (1906). *Psenes stigmapleuron* Fowler, 1939, is a synonym. Perhaps a synonym of *P. whiteleggii* Waite, 1894.

**Psenes benardi* Rossignol and Blache, 1961. Gulf of Guinea. D XI, I 19–20. A III 21–22. P 19. Gill-rakers 9 + 1 + 16–17. **P. arafurensis* Günther, 1889, has a much deeper body, and is striped and mottled on the sides. *P. benardi* is uniform light brown. It is perhaps a synonym of *P. guttatus* Fowler, 1934a.

Family ARIOMMIDAE, new family
Type genus: *Ariomma* Jordan and Snyder, 1904

Diagnosis. Stromateoid fishes with pelvic fins present in adults, two dorsal fins, toothless palate, six branchiostegal rays, two hypural bones in the tail, and well ossified sclerotic bones. Bases of papillae in the pharyngeal sacs round; papillae not in bands and in upper halves of the sacs only.

Description. Body slender or deep, rounded to compressed. Peduncle slender, with two low fleshy lateral keels on each side. Two dorsal fins. The first dorsal with about ten slender spines folding into a groove. The longest spine twice the length of the longest ray of the second dorsal fin. Three anal spines, not separated from the rays. Soft dorsal and anal fins approxi-

Figure 31. Branchial region of *Ariomma* cf. *nigriargentea*, an elongate species, drawing of a cleared-and-stained preparation from a 140-mm specimen. Elements identified in Figure 2.

Figure 32. Branchial region of *Ariomma indica*, a deep-bodied species, drawing of a cleared-and-stained preparation from a 164-mm specimen, NTU 51942. Elements identified in Figure 2.

mately the same length, each with 14 or 15 finrays, the large basals protruding into the body profile. Bases of median fins not sheathed by scales. Pelvic fins attached to the abdomen by a thin membrane and folding into a groove. Scales large, cycloid, thin, extremely deciduous. Lateral line high, following dorsal profile and not extending onto peduncle; tubes in the lateral line scales sometimes branched. A branch of the lateral line extending forward over the eye in a bony tract. Skin thin; subdermal mucous canal system well developed. Opercular and preopercular margins entire or very finely denticulate. Opercle very thin, brittle, with two weak, ill-defined, flat spines. Six branchiostegal rays. Mouth small, maxillary barely extending to below eye. Teeth small, simple or three-cusped, uniserial in the jaws. Vomer, palatines, and basibranchials toothless. Supramaxillary bone absent. Eye large, adipose tissue well developed and covering the lacrimal bone. Sclerotic bones well ossified. Vertebrae 29 to 32. Caudal skeleton with two hypurals and three epurals. Pharyngeal sacs with papillae in the upper halves only. The papillae not in bands, their bases rounded with a stalk with teeth seated all along it arising off-center. Adults usually about a foot long, but in some species exceeding two feet. Silvery to blue-brownish, some species with conspicuous spotted or counter-shaded pattern.

Distribution. Ariommids apparently live near bottom in deep water of the subtropics and tropics. They occur along the east coast of North America, in the Gulf of Mexico and Caribbean Sea, along the coasts of West and South Africa, along Asian coasts from the Red Sea to Japan, and off Hawaii (Fig. 55).

Relationships. Ariomma, the single genus in the family, superficially appears to be a nomeid. The two dorsal fins, persistent pelvics, and six branchiostegal rays have been the cause for placement in this group close to *Cubiceps* (Psenidae of Jordan and Snyder, 1907; Nomeidae of Katayama, 1952). Some authors (Regan, 1914a; Jordan, 1923) have even considered *Ariomma* a synonym of *Cubiceps.* But the complete absence of teeth on the vomer, palatines, and basibranchials in *Ariomma* contrasts with the situation in the Nomeidae. The structure of the caudal skeleton (Fig. 33) and of the pharyngeal sacs (Figs. 31, 32) in *Ariomma* is unique among stromateoids, and divergent enough from any others to warrant separation at the family level. The unique

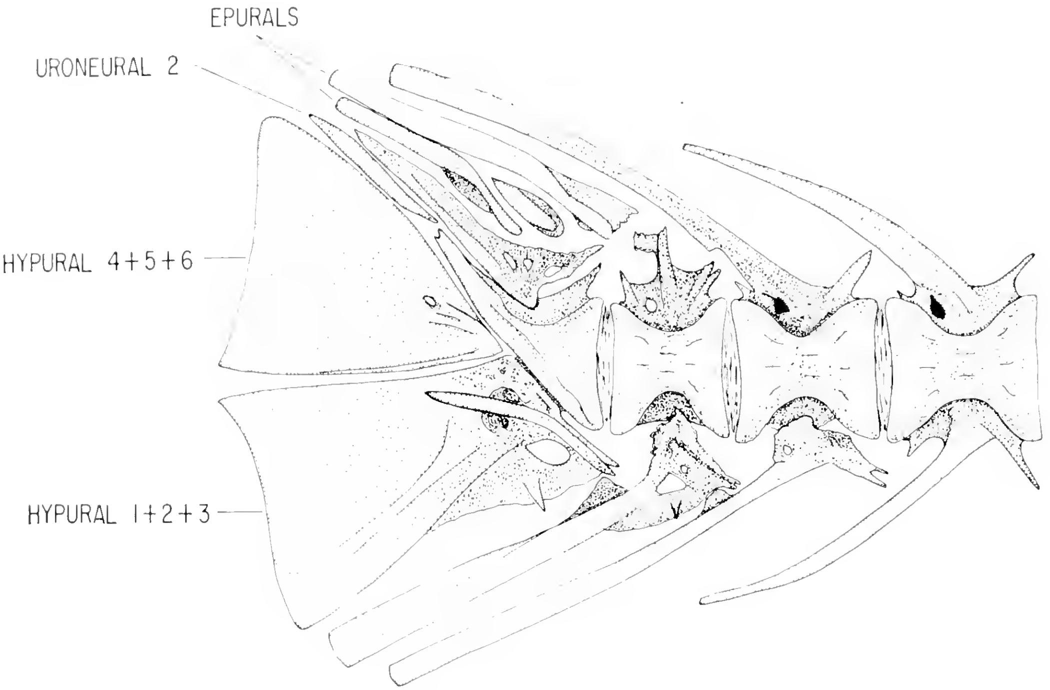


Figure 33. Caudal skeleton of *Ariomma* cf. *nigriargentea*, drawing of a cleared-and-stained preparation from a 28-mm specimen. All elements identified in Figure 1.

characters of the family, far from the condition of others in the suborder, are probably due to the shift the ariommids have made to an adaptive zone atypical for stromateoids (see below: *Natural history*, p. 93).

Ariomma presents a confusing array of characters which could suggest affinities with the centrolophids, the nomeids, or the stromateids. The well ossified sclerotic bones, minute body pores, and extremely deciduous scales are characters held in common with the advanced *Seriolella* group of the centrolophids and the diminutive *Cubiceps pauciradiatus* group of the nomeids and the stromateids. The teeth on the papillae occur all along the bony stalk, and the jaw teeth of *Ariomma indica* are cusped. Both characters are typical of stromateids. The general body shape is like *Seriolella*. The complete absence of palatal dentition suggests an affiliation with the line connecting the advanced centrolophids with the stromateids.

However, *Ariomma* has two distinct dorsal fins and very large scales, and the bony bridge over the anterior vertical canal of the ear is either very reduced or absent, all in marked contrast to the situation in centrolophids and stromateids. These conditions are found in the *Cubiceps pauciradiatus* group, nomeids which in addition have reduced palatal dentition. The Ariommidae are probably derived from somewhere in this line, and have lost the teeth on the palate and basibranchials.

Genus *ARIOMMA* Jordan and Snyder, 1904

Figures 34, 35

Ariomma Jordan and Snyder, 1904:942. (Type species: *Ariomma lurida* Jordan and Snyder, 1904:943, by original designation. Honolulu, Hawaii.)

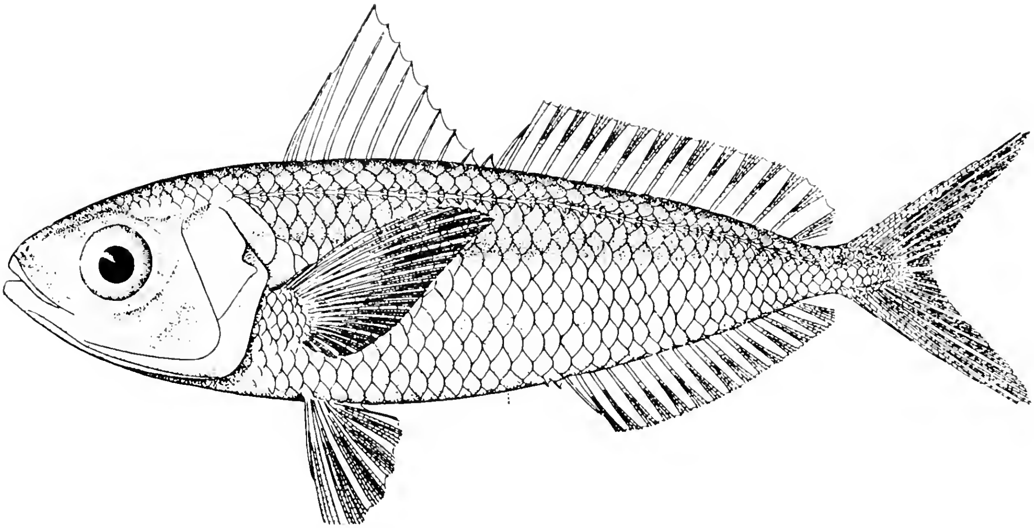


Figure 34. *Ariomma ledanoisi*, an elongate species, drawing of a 189-mm specimen, from Poll, 1959.

Paracubiceps Belloc, 1937:356. (Type species: *Paracubiceps ledanoisi* Belloc, 1937:356, by original designation. Coast of West Africa.)

The combination of slender caudal peduncle with lateral keels, deeply forked, stiff caudal fin, about fifteen dorsal and anal finrays with their basal elements pronounced and entering into the body profile, well-developed adipose tissue around the eye, two dorsal fins, and toothless palate distinguishes *Ariomma* from all other stromateoid genera. The name is a feminine noun of unknown derivation.

Description. Body either elongate, maximum depth about 25 per cent of the standard length, rounded, or deep, maximum depth 40 per cent of the standard length, compressed; musculature firm, often oily. Peduncle short, slender, square in cross-section, with two ill-defined, low, fleshy keels on each side at base of caudal fin. Two dorsal fins, scarcely separated. First dorsal originating directly over, or a little before, insertion of pectoral fin, with about ten long, brittle spines, folding into a deep groove. Second dorsal fin with 14 or 15 rays, each about half as long as the longest D_1 spine; the anterior rays a little longer than those which follow. Anal papilla a little behind mid-body, in a slit. Anal fin originating behind middle of body and behind origin of the second dorsal fin, two or three spines preceding the 14 to 15 rays; rays short, the anterior ones the longest. Rays of the median fins close-set anteriorly, becoming more widely spaced posteriorly. Basals of the finrays often projecting above the body profile. Pectoral fin rounded in the young, becoming pointed with growth; relative length decreasing slightly with growth of elongate form but increasing markedly with growth of deep-bodied form. Pelvic fins inserting under end or behind base of pectoral fin, attached to abdomen with a membrane and folding into a pronounced groove which reaches to the anus. Caudal fin stiff, deeply forked, rays on the leading edge stiff and spinelike. Scales large, cycloid, very thin, extremely deciduous, not covering bases of the median fins. Scales of the lateral line with branched tubes, located high on the body, following dorsal profile and not extending onto peduncle. A branch of the lateral line extend-

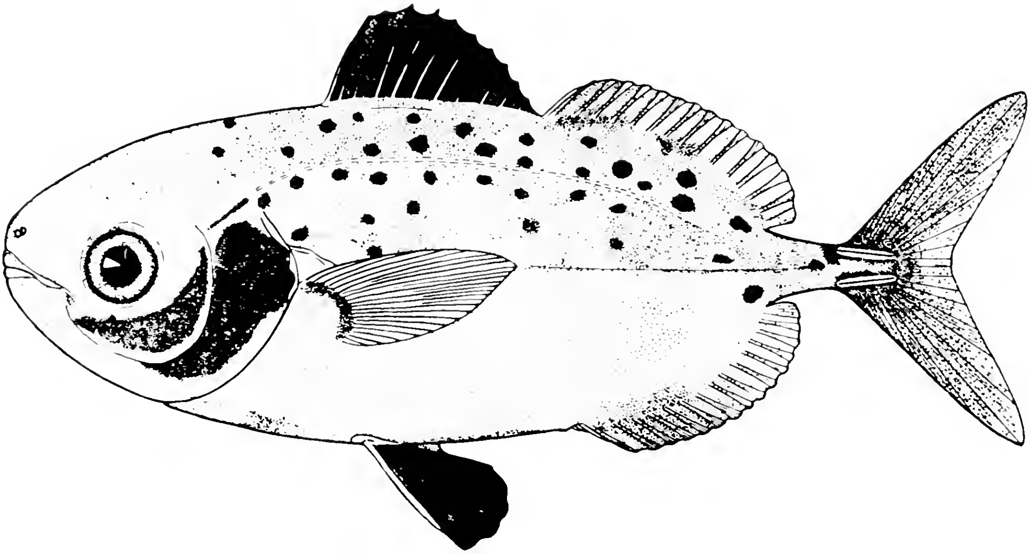


Figure 35. *Ariomma regulus*, a deep-bodied species, from McKenney, 1961.

ing forward over the eye in a bony tract from the head of the hyomandibular. Skin thin; main subdermal canal along intermuscular septum very apparent, may be confused with lateral line; side branches not as conspicuous, pores to surface seem to be wanting. Head around 30 per cent of the standard length. Top of snout naked, pores and subdermal canals barely visible. Scales extending forward over nape to level of anterior border of the eye. Eye large, bony supraorbital ridge pronounced. Adipose tissue around eye well developed, extending forward over the lacrimal and around the nostrils. Nostrils near tip of the obtuse snout, small, the anterior round, the posterior a slit. Maxillary scarcely reaching to under eye, angle of gape well before eye and nearer to tip of snout. Premaxillary not protractile. Lacrimal bone transparent, almost completely covering upper jaw when mouth is closed, the ventral border of the maxillary remaining exposed. Supramaxillary absent. Jaw teeth minute, covered basally with a membrane, usually pointed but three-cusped in a few deep-bodied forms, uniserial, close set or slightly spaced; vomer, palatines, and basibranchials toothless. Opercle and preopercle thin, brittle, margins very finely denticulate or entire; opercle rounded, with two weak, ill-defined, flat spines; angle of preopercle rounded and not bulging backward. Gill-rakers slender, half the length of the filaments, toothed on inner edge, fairly close set, about 19 on lower limb of first arch; no rudimentary rakers under the well-developed pseudobranch. Six branchiostegal rays, four on the ceratohyal, two on the epihyal. Scapula prominent. Vertebrae 12 to 14 + 17 or 18 = 29 to 32. Two hypurals and three epurals. Sclerotic bones well ossified. Stomach large, a simple sac; intestine very long. Pyloric caeca numerous, in a dendritic mass. Air bladder present, extending the length of the abdominal cavity.

Color in preservative brown, bluish, or silvery. First dorsal blackish, pelvic fins dark or clear, other fins usually light. Color pattern may be blue above, silvery below, the shades not intergrading, uniformly dark, or light with dark spots. Young have three to five dark vertical stripes. Opercles silvery or blackish. Iris usually golden, divided by a dark vertical bar. Mouth and gill cavity light or dark. Peritoneum silvery.

Natural history. Most stromateoids are pelagic, but *Ariomma* is a bottom or near-bottom fish of deep water. Very small *Ariomma* are pelagic, for they are taken in surface collections, but all large specimens reported have been taken in bottom trawls, usually at depths in excess of 100 meters (Lowe, 1962; McKenney, 1961; Poll, 1959). *Ariomma* apparently schools, for single net hauls contain numerous specimens (Poll, 1959).

The pharyngeal sacs, but not the stomachs, of most specimens dissected contained grit and mud, indicative of a bottom-feeding habit. This habit could account for the relatively high number of gill-rakers, around 30, found in *Ariomma*. The stomachs of specimens examined by Poll (1959) contained bits of crustaceans and unidentifiable meat. The thick adipose tissue on the head probably protects the eyes and nostrils as the fish scoops its prey from the sea floor.

Most *Ariomma* mature around 160 to 180 mm SL (*A. regula* [McKenney, 1961]; *A. ledanoisi* [Poll, 1959]; *A. indica*; *A. nigriargentea*), and probably do not grow much larger than this. Very large specimens are known from the Red Sea (800 mm, Klunzinger, 1884), Japan (356 mm SL, Abe, 1954), and Hawaii (635 mm, Fowler, 1923). The Japanese species, at least, does not seem to mature before reaching this size.

Species. The problem of delineating the species of *Ariomma* is one of the most perplexing in the entire suborder. Fourteen have been described, but all of these, from the Gulf of Mexico to Hawaii, have almost the same numbers of finrays and gill-rakers. Reports of lateral line scale counts vary slightly, but the scales are so deciduous in *Ariomma* that this information must be viewed with caution.

The species of *Ariomma*, with one intermediate exception, are either elongate, with the maximum depth less than 30 per cent of the standard length, or deep-bodied, with the maximum depth greater than 40 per cent of the standard length. It is possible that these two groups warrant subgeneric recognition, but, pending further study, this action is deferred.

The nominal species in *Ariomma* are:

Ariomma regulus (Poey, 1868) = *Psenes regulus* Poey. Gulf of Mexico to British Guiana, type locality Cuba. Deep-bodied. D XI, I 15. A III 15. P 21–24. Gill-rakers usually 7 + 1 + 15. (From McKenney, 1961.) Spotted. Teeth not cusped.

Ariomma indica (Day, 1870) = **Psenes indicus* Day. India to southern Japan, type locality Madras. Deep-bodied. D XI–XII, 14–15. A III 14–15. P 21–23. Gill-rakers usually 7 + 1 + 15. Vertebrae 12 or 13 + 18. The pectoral fin of this silvery species becomes produced, up to 35 per cent of the standard length, with growth. The teeth in the hind part of the lower jaw are three-cusped; the rest are simple. *Psenes extraneus* Herre, 1950, known from a single Philippine specimen, is very likely a synonym.

Ariomma brevimanus (Klunzinger, 1884) = *Cubiceps brevimanus* Klunzinger. Red Sea. Elongate, known from a single specimen 800 mm long. D XI, 15. A II 15. P 24. (From Klunzinger, 1884.)

**Ariomma lurida* Jordan and Snyder, 1904. Hawaii. Elongate. D XI–XII, 14–15. A III 13–14. P 20–21. Gill-rakers 9 + 1 + 20. Vertebrae 14 + 18. This species is distinguished from **A. evermanni* Jordan and Snyder, 1907, by the large eye, greater than 30 per cent of the length of the head, and fewer pectoral finrays.

**Ariomma evermanni* Jordan and Snyder, 1907. Hawaii. Elongate. D XI–XII, 15. A III 14. P 25. Gill-rakers 9 + 20. Vertebrae 13 + 18. Eye is less than 28 per cent of the length of the head. Attains a large size; *Cubiceps thompsoni* Fowler, 1923 (type 635 mm long), is a probable synonym.

Ariomma africana (Gilchrist and von Bonde, 1923) = **Psenes africanus* Gilchrist and von Bonde. South Africa. Deep-bodied. D IX–X, 15. A III 16. P 22. Gill-rakers 8

+ 1 + 16. Vertebrae 13 + 18. Very similar to *A. regulus* (Poey, 1868). Spotted. Teeth not cusped.

Ariomma dollfusi (Chabanaud, 1930) = **Cubiceps dollfusi* Chabanaud. Gulf of Suez. Intermediate, maximum depth of cotype 32 per cent of the standard length (112 mm). D XI–XII, 15. A III 15. P 22. Gill-rakers 7 + 1 + 14. Vertebrae 12 + 18. The teeth are said to be "comprimées . . . et crenelées" (Chabanaud, 1930:520), suggesting close relationship or synonymy with *A. indica* (Day, 1870).

**Ariomma bondi* Fowler, 1930. Grenada, British West Indies. Elongate, known from the holotype, 79 mm TL. D XI–XII, 14. A II 15. Gill-rakers 8 + 15. Lateral line scales 43. Dark above, light on sides. (From Fowler, 1930.) Possible synonyms are **A. nigriargentea* and/or **A. melana*, both of Ginsburg, 1954.

Ariomma ledanoisi (Belloc, 1937) = *Paracubiceps ledanoisi* Belloc. West equatorial Africa. Elongate. D XI–XII, 14–15. A III 14–15. P 20–22. Gill-rakers ? + ? + 16–17. (From Poll, 1959.)

Ariomma nigriargentea (Ginsburg, 1954) = **Cubiceps nigriargenteus* Ginsburg. Gulf of Mexico, Caribbean, and north to Cape Cod, type locality Cape Romain, South Carolina. Elongate. D XI–XII, 15–16. A III 15. P 21–22. Gill-rakers 9–10 + 17–19. (From Ginsburg, 1954.) Vertebrae 13 + 17. Said to differ from *A. melana* (Ginsburg, 1954) by the smaller scales (62 to 68 in lateral line), color (blue above, silvery below), less scalation on the head, and shorter maxillary. These characters, however, seem to intergrade.

Ariomma melana (Ginsburg, 1954) = **Cubiceps melanus* Ginsburg. Gulf of Mexico, Caribbean, and north to Cape Hatteras, type locality Mississippi Delta. Elongate. D XI–XII, 15. A III 14–15. P 21–22. Gill-rakers 9–11 + 18–20. Lateral line scales 39–56. (From Ginsburg, 1954.) Vertebrae apparently 15 + 16. Uniform dusky brown.

Ariomma multisquamis (Marchal, 1961) = **Paracubiceps multisquamis* Marchal. West equatorial Africa. Elongate. D XI–XII, 15–16. A III 14–16. P 21–23. (From Marchal, 1961.) Gill-rakers 9 + 1 + 18. Said to differ from *A. ledanoisi* (Belloc, 1937) by having more scales in the lateral line (61–63 *vs.* 36–40).

Family TETRAGONURIDAE

Type genus: *Tetragonurus* Risso, 1810

Tetragonuridae. Risso, 1826:382 (def.). Lütken, 1880:437 (disc., rel. to scombroids). Ramsay and Ogilby, 1888:9 (disc., rel. to Atherinidae). Regan, 1902:206 (rel. to Stromateidae). Boulenger, 1904:642 (popular account). Grey, 1955:1 (world-wide revision).

Tetragonurina. Günther, 1861:407 (def., rel. to Atherinidae).

Tetragonuroidei. Berg, 1940:323 (definition); 1955: 247 (definition). Smith, 1953:53 (review).

Diagnosis. Elongate stromateoid fishes with pelvic fins present in the adults, two dorsal fins, teeth on vomer and palatines, five or six branchiostegal rays, heavy adherent keeled scales, and four hypural and two epural bones in the tail. Papillae in the pharyngeal sacs with rounded bases, not in bands.

Description. Body slender, rounded. Peduncle thick, square in cross-section, with modified scales forming two prominent lateral keels on each side. Two dorsal fins, the first with 10 to 20 short spines, folding into a groove; the base of the fin as long as or longer than the base of the second dorsal. One anal spine, not separated from the rays. Soft dorsal and anal fins approximately the same length, with 10 to 17 fin-rays. Last ray of pelvic fin attached to abdomen for its entire length, fin folding into a depression. Scales moderate in size, ctenoid, with heavy longitudinal ridges, very adherent, arranged in a geodesic pattern around the body. Lateral line slightly arched forward, descending to run along middle of side and extending onto peduncle; no tubed scales. Skin thick; subdermal mucous canal system well developed, but barely visible. Opercular and preopercular margins entire or finely denticulate. Opercle thick, spines not apparent. Five or six

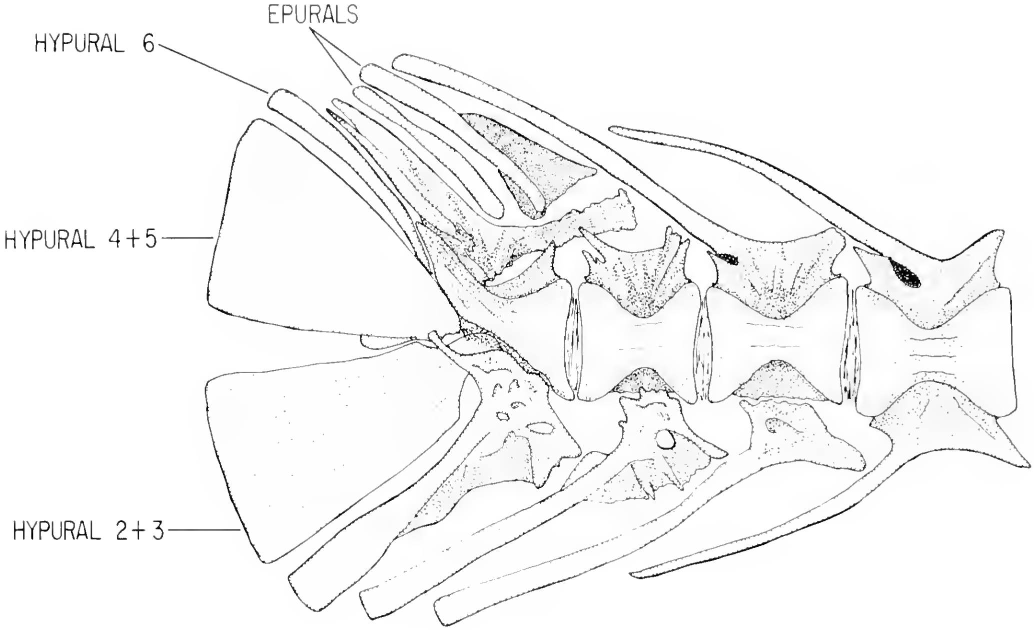


Figure 36. Caudal skeleton of *Tetragonurus atlanticus*, drawing of a cleared-and-stained preparation from a 66-mm specimen, MCZ 41791. All elements identified in Figure 1.

branchiostegal rays. Mouth large, maxillary extending below eye. Teeth moderate to large, simple and cusped, uniserial in the jaws. Vomer, palatines, basibranchials, and usually the tongue with teeth. Supramaxillary bone absent. Eye large, no adipose tissue. Sclerotic bones not well ossified. Vertebrae 43 to 58. Caudal skeleton with four hypurals and two epurals. Pharyngeal sacs with small papillae in upper and lower halves; bases of papillae not in bands, rounded, central stalk with a few teeth. Adults one to two feet in length. Uniform dark brown, with no pattern or countershading.

Distribution. The distribution of the Tetragonuridae largely parallels that of the nomeids (Fig. 54). Tetragonurids are oceanic fishes of tropical, subtropical, and temperate seas. None have been taken in the eastern Mediterranean Sea, the Red Sea, and the South and East China seas.

Relationships. Tetragonurus, the single genus in the family, has teeth on the vomer, palatines, and basibranchials. Thus, it is affiliated with the nomeid stock. The caudal skeleton (Fig. 36) is similar to that of the nomeids, but is advanced an evolutionary grade in having lost one of the epurals. The pharyngeal sacs (Fig. 37) and the heavy, keeled scales of *Tetragonurus*, however, are markedly different from the sacs and scales of the nomeids. The pharyngeal sacs are exceedingly elongate. The papillae are poorly ossified and are very reduced in size. The bases of the papillae are rounded, as they are in the Ariommidae, but there are less than six teeth seated on top of a short stalk. The fourth pharyngobranchial is very elongate and is fused to the third pharyngobranchial. This long bone is studded with teeth and extends well backward into the sac, where it no doubt aids both in shredding the food and in supporting the sacs. All nomeids have six branchi-

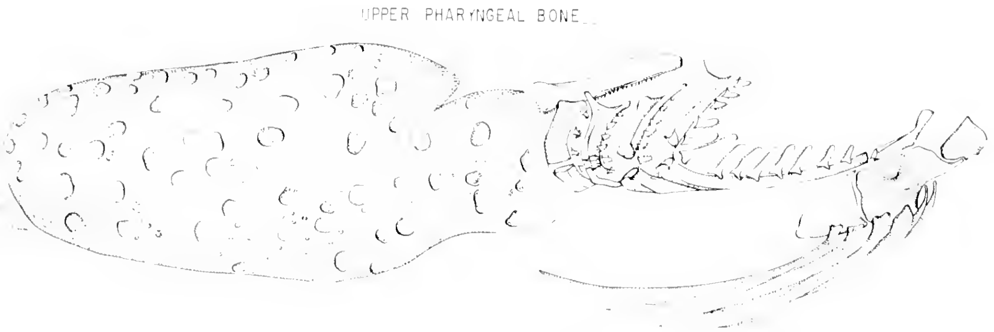


Figure 37. Branchial region of *Tetragonurus cuvieri*, drawing of a cleared-and-stained preparation from a 340-mm specimen, CNHM 64218. Elements identified in Figure 2. The upper pharyngeal bone is formed by the fusion of the third and fourth pharyngobranchials.

ostegal rays; tetragonurids have either six or five.

The highly differentiated jaw teeth of *Tetragonurus* are very similar to those of certain species in the genus *Psenes*. But *Tetragonurus* has teeth on the tongue, and cannot be derived from *Psenes*. It is very likely that *Tetragonurus* branched off fairly early from the nomeid stem and is derived from no living nomeid genus. The loss of an epural and a branchiostegal ray, the heavy keeled scales, the very elongate pharyngeal sacs with the reduced papillae, and the greatly increased number of vertebrae are quite divergent from the situation in nomeids, and together imply that evolution has proceeded independently in these two groups for some time.

The divergent characters of *Tetragonurus* are part of its adaptation to a very particular mode of life. *Tetragonurus* is certainly a derived form, and is probably quite unlike the ancestral nomeid. The central nomeid genus *Cubiceps*, like *Tetragonurus*, has teeth on the tongue. The nomeid stock from which *Tetragonurus* arose may have been in many respects similar to the present-day *Cubiceps*.

Genus *TETRAGONURUS* Risso, 1810

Figure 38

Tetragonurus Risso, 1810:347. (Type species: *Tetragonurus cuvieri* Risso, 1810:347, by monotypy. Mediterranean.)

Ctenodax Macleay, 1885:718. (Type species: *Ctenodax wilkinsoni* Macleay, 1885:718, by monotypy. Lord Howe Island, Tasman Sea. A synonym of **Tetragonurus atlanticus* Lowe, 1839:79.)

The combination of elongate body and peduncle, modified scales forming two keels on the peduncle, origin of first dorsal slightly to well behind pectoral insertion, base of first dorsal longer than base of second dorsal, heavy keeled scales, and peculiar lower jaw with heavy knifelike teeth distinguishes *Tetragonurus* from all other stromateoid genera. The name, a masculine noun, is from the Greek τετράγωνος, with four angles, + οὐρά, tail, in reference to the shape of the caudal peduncle.

Description. Body very elongate, maximum depth less than 20 per cent of the standard length, rounded; musculature firm. Peduncle long, thick, with modified scales forming two prominent keels at base of caudal fin. Two dorsal fins, scarcely divided. First dorsal originating slightly to well behind insertion of pectoral fins, with 10 to 21 stiff spines folding into a groove, the longest spine half the length of the longest ray of the second dorsal. Anterior rays of the second dorsal the longest, those that follow decreasing slightly in length, 10 to 17 finrays in all. Anus well behind midbody, in a depression. Anal fin originating slightly behind origin of second dorsal fin,

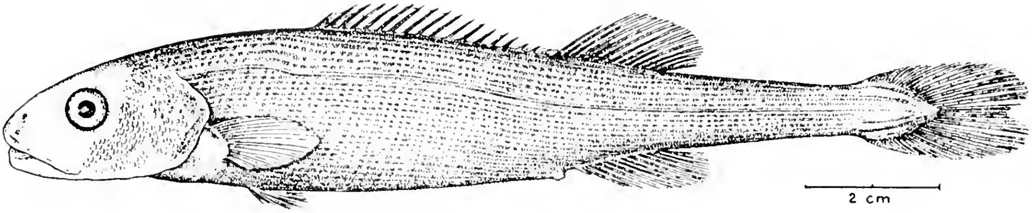


Figure 38. *Tetragonurus cuvieri*, drawing of a 129-mm specimen, from Grey, 1955.

one short spine preceding the rays. Anterior rays the longest, those that follow decreasing slightly in length, 9 to 15 finrays in all. Pectoral fin small, the central rays the longest. Pelvic fins small, inserting behind pectoral fin base and before origin of first dorsal, innermost ray attached to abdomen for its entire length. Caudal fin forked. Scales moderate in size, with heavy longitudinal keels, very adherent, following a geodesic pattern around the body. Very small scales on bases of median fins. Lateral line usually slightly arched anteriorly, descending to run along mid-lateral line of body and ending on peduncle at origin of keels; no tubed scales. Skin thick; subdermal canals cannot be traced. Pores to surface minute. Head 30 to 20 per cent of the standard length. Top of head and snout naked, small pores in naked skin. Scales extending forward over nape almost to level of posterior border of the eye. Eye large, with a series of grooves on the posterior rim. Nostrils toward top of blunt snout, large, well separated, the anterior round, the posterior a slit. Maxillary ending under eye, angle of gape well before eye. Premaxillary not protractile. Lacrimal bone covering most of upper jaw at all times, ventral border of maxillary remaining exposed. Lower jaw almost completely within upper jaw when mouth is closed. Supramaxillary absent. Teeth in upper jaw small, pointed, recurved, spaced. Teeth in lower jaw large, knifelike, close set, with small cusps, deeply embedded in the gum with only the tips showing. Strong recurved teeth present on head of vomer, and in a single series on shaft of vomer and palatines. Small teeth on basibranchials and, usually, profusely scattered on tongue. Tongue high-sided, depressed in center. Opercle and preopercle thin, fleshy, scaled, margins entire in adult, spinulose in the young; opercle with two very weak spines; angle of preopercle slightly rounded, not bulging backward. Cheeks scaled. Gill-rakers broad, fleshy, shorter than the filaments, toothed on inner edge, spaced, 8 to 14 on lower limb of first arch; rudimentary rakers often present under the large pseudobranch. Scapula not visible. Vertebrae 43 to 58. Sclerotic bones well ossified in adult. Stomach a simple sac; intestine long. Pyloric caeca numerous, in a large dendritic mass.

Color in preservative uniform brown, ranging from tan to almost black. Fins the same color as the body. Inside of mouth, gill cavity, and peritoneum dark.

Natural history. Young *Tetragonurus* have been found associated with medusae (Mansueti, 1963). There are also reports (Emery, 1882; Lo Bianco, 1909; Fitch, 1949) of young specimens found within salps, usually *Pyrosoma*. Mansueti (1963) felt that the association of *Tetragonurus* with jellyfishes was a chance occurrence, but, since jellyfish associations are commonly formed by other stromateoids, it is likely that the association is actively sought.

Tetragonurus probably feeds almost exclusively on coelenterates and ctenophores (Risso, 1826; Fitch, 1952). The large slicing teeth of the lower jaw and the peculiar boxlike jaw seem admirably suited for such a diet (Grey, 1955).

Risso (1826) reported that the flesh of *Tetragonurus* was poisonous, attributing this quality to the fish's diet of venomous jellyfishes of the genus *Stephanomie*. His report has been widely spread, but has only recently been reinvestigated. Fitch (1952) analyzed four California specimens and found them to be not poisonous. The possibility remains that *Tetragonurus* is poisonous only during certain seasons, for example at the time of spawning (Petit and Amar, 1946).

In the Atlantic, *Tetragonurus cuvieri* apparently spawns in spring and summer (Grey, 1955). Guiglia (1950) reports mature females of *T. cuvieri* taken throughout the year in the Mediterranean. *T. atlanticus* spawns during the fall in the eastern and northern Atlantic, but in winter and spring in the western Atlantic (Grey, 1955).

Tetragonurus is strictly oceanic (Grey, 1955). Although young specimens occur near the surface with jellyfish, the adults, judging from their somber coloration, probably are members of the meso- or bathypelagic faunas. *Tetragonurus* has been considered a rare fish (Fitch, 1949), but recent surveys in the North Pacific (Larkins, 1964) indicate that it is much more common than is usually thought, bearing out a prediction of Grey (1955).

Species. *Tetragonurus* has been ably treated by Marion Grey (1955), who recognized three species in the genus. As she has pointed out, each species varies widely, and further division may be justified when more specimens are available. The species are:

T. cuvieri Risso, 1810. Mediterranean Sea, Atlantic, Pacific oceans. D XV–XXI, 10–17. A I 10–15. P 14–21(?). Lateral line scales 97–114. Vertebrae 52–58. (From Grey, 1955.)

**T. atlanticus* Lowe, 1839. Atlantic, Pacific, Indian oceans. D XIV–XVII, 10–13. A I 9–12. P 14–18. Lateral line scales 83–95. Vertebrae 45–51. (From Grey, 1955.) *Ctenodax wilkinsoni* Macleay, 1885, is a synonym.

T. pacificus Abe, 1953. Pacific, Indian oceans. D X–XI, 10–12. A I 10–12. P 15–17. Lateral line scales 73–78. Vertebrae 40(?)–43. (From Grey, 1955.)

Family STROMATEIDAE
Type genus: *Stromateus* Linnaeus, 1758

Stromatées. Cuvier and Valenciennes, 1833:372 (in part, descr.).

Stromateina. Günther, 1860:397 (in part, def.). Gill, 1862:126 (genera listed).

Stromateinae. Gill, 1884:669 (def., gen.). Bühler, 1930:62 (digestive system).

Stromateidae. Jordan and Gilbert, 1882:449 (descr.). Jordan and Evermann, 1896:964 (descr., North America). Jordan, 1923:182 (list, + Pampidae). Berg, 1940:323 (dist.); 1955:248 (dist.).

Diagnosis. Deep-bodied stromateoid fishes with pelvic fins absent in the adults, continuous dorsal fin, toothless palate, four hypural and two or three epural bones in the tail, and well ossified sclerotic bones. The papillae in the pharyngeal sacs not in bands, in both the upper and lower halves of the sac; bases of the papillae stellate.

Description. Body deep, compressed. Single dorsal and anal fins, with none or one to ten flat, bladelike spines and three to five slender, graduated spines preceding the rays. Median fins about the same length, usually falcate; caudal fin deeply forked. Pectoral fin long and pointed. Pelvic fins present only in young *Stromateus*; absent in all others. Scales small, cycloid, extremely deciduous. Lateral line high, following dorsal profile, and extending onto the short peduncle. Opercular and preopercular margins entire. Opercle very thin, with two short, flat, weak spines. Gill membranes usually free from isthmus, but united in *Pampus*. Five or six branchiostegal rays. Mouth terminal to sub-terminal, small, angle of gape rarely reaching below eye. Teeth very small, laterally flattened, with three minute cusps, and uniserial in the jaws. Vomer, palatines, and basibranchials toothless. Supramaxillary absent. Eye fairly small; adipose tissue usually not well developed. Sclerotic bones well ossified. Vertebrae 30 to 48. Caudal skeleton with four hypurals and two epurals, except three epurals in *Stromateus fiatola*. Pharyngeal sacs with papillae in upper and lower halves, not in bands; bases of the papillae stellate, with teeth seated all along a central stalk. Adults usually about a foot in length. Silvery to blue, some with spots.

Distribution. Stromateids live over the continental shelves and in the bays of tropical, subtropical, and temperate waters. They are found on the east and west coasts of North and South America, from the Mediterranean Sea to South Africa, and from the Iranian Gulf to Japan (Fig. 56). None occur near oceanic islands, and none have reached Australia. *Stromateus*, in southern South America and western Africa, is the only genus that has representatives on both sides of an ocean. The genera are allopatric except for a small area of overlap between *Stromateus* and *Peprilus* in South America. All stromateids school, and many are important commercially.

Relationships. The Stromateidae are the current zenith in stromateoid evolution. The reduced number of branchiostegals and elements in the caudal skeleton (Figs. 42, 47), the absence of pelvic fins, the small mouth with cusped teeth, the broad stellate bases of the papillae in the pharyngeal sacs (Figs. 43, 46), and the deepened body are all advanced conditions.

The stromateids were derived from somewhere near the *Seriolella* group of the Centrolophidae, perhaps from a fish very like the deep-bodied *Psenopsis*. In *Stromateus fiatola* the presence of pelvic fins in the young and the three epurals recalls the centrolophid heritage.

The stromateids may have evolved only recently. Though the three genera are distinct, little speciation has occurred, but, in some cases, seems to be in an incipient stage. Almost-sibling species occur on either side of the Isthmus of Panama.

The stromateids are an end-point, and no other groups have been derived from them. But they are by no means an evolutionary deadend. *Pampus*, with its restricted gill-opening, elongate pharyngeal sac, and peculiar spines in some species, is diverging rapidly from the central stromateid bauplan and is widely successful along the coasts of southern Asia.

Key to Stromateid Genera

1 (4). Inter- and subopercles not united to the isthmus. End of maxillary before or at anterior border of eye. Cusps on teeth in lower jaw subequal, the teeth appearing truncate to the naked eye. Spine on end of pelvic bone present or absent. In small specimens (less than 80 mm SL) pelvic fins present or absent. Six branchiostegal rays. 2

2 (3). One to three flat, bladelike spines ahead of median fins. A small spine projecting posteroventrally from end of pelvic bone. Median fins falcate or not. Pelvic fins never present. 30 to 35 vertebrae. .... *Peprilus*, p. 103. Figs. 40, 41

3 (2). No flat, bladelike spines ahead of median fins. No spine at end of pelvic bone. Median fins never falcate. Pelvic fins absent in adult, but present in some small specimens. 40 to 48 vertebrae. .... *Stromateus*, p. 99. Fig. 39

4 (1). Inter- and subopercles broadly united to isthmus. End of maxillary under eye. Central cusp on teeth of lower jaw much larger than the other two cusps, which can hardly be seen without extreme magnification. No spine at end of pelvic bone. Pelvic fins never present. Five branchiostegal rays. .... *Pampus*, p. 108. Figs. 44, 45

Genus *STROMATEUS* Linnaeus, 1758

Figure 39

Stromateus Linnaeus, 1758:248. (Type species: *Stromateus fiatola* Linnaeus, 1758:248, by monotypy. Mediterranean.)

Chrysostromus Lacépède, 1802:697. (Type species: *Chrysostromus fiatoloides* Lacépède, 1802:697, by monotypy. Mediterranean. A synonym of *Stromateus fiatola* Linnaeus, 1758: 248.)

Fiatola Cuvier, 1817:342. (Type species: *Stromateus fiatola* Linnaeus, 1758:248, by monotypy. Mediterranean.)

Seserinus Cuvier, 1817:342. (Type species: "*Seserinus* Rondelet" [*Seserinus rondeleti*] Cuvier, 1817:343, by subsequent designation of Jor-

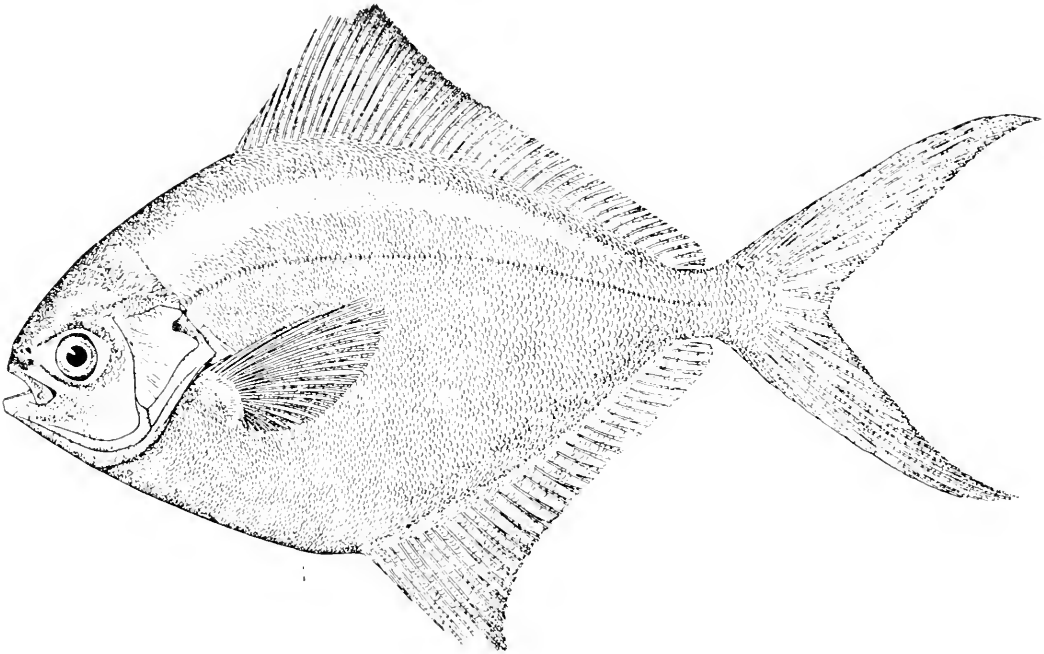


Figure 39. *Stromateus fiatola*, drawing of a 228-mm specimen, from Poll, 1959.

dan, 1923:106. Mediterranean. A synonym of *Stromateus fiatola* Linnaeus, 1758:248.)

Pterorhombus Fowler, 1906:118. (Subgenus. Type species: *Fiatola fasciata* Risso, 1826:289, by original designation. Mediterranean. A synonym of *Stromateus fiatola* Linnaeus, 1758: 248.)

The combination of deep body, small eye, moderate pectoral fin, no bladelike spines ahead of the median fins, no ventral spine on the pelvic bone, spotted body pattern, and (sometimes) pelvic fins in the young distinguishes *Stromateus* from all other stromateoid genera. The name, a masculine noun, is from the Greek *στρῶματευς*, a brightly colored quilt or bedding, probably in reference to the shape and pattern of the fish.

Description. Body deep, maximum depth generally greater than 40 per cent of the standard length, compressed; musculature firm. Peduncle very short, compressed. Dorsal fin continuous, originating over base of the pectoral fins, the anteriormost elements usually very small and buried in the skin, 44 to 53 elements in all. Anal papilla before mid-body, in a deep slit. Anal fin originating slightly before middle of body but behind dorsal origin, the small anteriormost elements buried in the skin, 35 to 47 elements in all. Anterior rays of the median fins produced, two to three times longer than the subequal rays of the posterior two-thirds of the fin, the lobes rounded and not falcate. No bladelike spines preceding median fins. Pectoral fin moderate in length, broad. Pelvic fins present in the young of at least some species, inserting under end of pectoral fin base, the fins lost in adult but with two dark flaps of skin sometimes indicating their former presence. Pelvic bone usually not visible on mid-line and lacking a ventral spine. Caudal fin stiff, deeply forked, the lobes very long. Scales small, cycloid, deciduous, minute scales covering all fins. Simple tubed scales of the lateral line moderately high, following dorsal profile and extending onto peduncle but not to caudal base. Skin moderately thick, subdermal canals not visible, pores to surface seem to be wanting. Head around 25 per cent of the standard length, very deep and broad. Top of head naked, small pores easily seen, naked skin underlain with numerous parallel canals projecting slightly backward over the nape. Eye small, adipose tissue around eye well developed and extending forward surrounding the nostrils. Nostrils moderate in size, the anterior round, the posterior a slit, located nearer to tip of blunt snout than to eye. Mouth broad. Maxillary scarcely reaching anterior border of the eye, angle of gape well before eye. Premaxillary not protractile. Lacrimal bone reduced, scarcely covering top of upper jaw when mouth is closed, end of maxillary exposed. Supramaxillary absent. Jaw teeth minute, uniserial, laterally flattened, with three subequal cusps, close set, covered laterally by a membrane; vomer, palatines, and basibranchials toothless. Gill membranes broadly united across the isthmus, divided from level of the back part of the eye. Opercle and preopercle thin, scaled, margins entire; opercle rounded, with two ill-defined, weak spines; angle of preopercle broadly rounded, projecting backward slightly. Cheek scaled. Gillrakers a little less than half the length of the filaments, diminishing in size anteriorly, not toothed, fairly close-set, about 12 on the lower limb of the first arch; no rudimentary rakers under the small pseudobranch. Six branchiostegal rays, four on the ceratohyal, two on the epihyal. Scapula not visible. Vertebrae slightly variable, usually 16 + 26 = 42 to 19 + 26 = 45. Sclerotic bones well ossified. Stomach a simple sac; intestine very long. Pyloric caeca numerous, in a long dendritic mass.

Color in preservative brown or bluish with a silvery or whitish overlay, dark above, lighter below. Back and sides with numerous dark spots. The young may have four or five dark vertical bands. Fins darker or lighter than the body; pectoral in some species blackish. Gill cavity, inside of mouth, and peritoneum light.

Natural history. The young of *Stromateus* commonly associate with medusae (Padoa, 1956), and Lo Bianco (1909) observed them eating jellyfish. Fish up to five inches in length have been reported in association (Smith, 1949a), but the majority probably desert their coelenterate host before reaching this size.

Poll (1959) found the adult common in depths from 12 to 50 meters off the coast of West Africa. I have examined adults taken by the Guinean Trawling Survey in 30 meters of water, and adults from Chile captured with a trammel net. Adult *Stromateus* may rarely descend to deeper water.

Small *Stromateus fiatola* have a vertically barred pattern and small pelvic fins. The bars and the pelvics are lost usually before the fish reaches 100 mm standard length. At this point, the young fish probably moves into the adult habitat. Whether or not the young of South American *Stromateus* have pelvic fins is unknown. Poll (1959) reports a *Stromateus fiatola* 500 mm long weighing 151 grams; this is probably near the maximum size attained.

In the Patagonian region, *Stromateus* moves shoreward to spawn in early summer (Hart, 1946). At this time the fishes form their maximum concentrations. Following spawning, they move offshore during the fall and winter, and become widely dispersed. In addition to inshore and offshore movement, Hart (1946) found evidence that *Stromateus* moves from lower to higher latitudes in the summer, and back in the winter.

Said to be a fish with "delicate flesh and fine flavour" (Gilchrist and von Bonde, 1923:11), *Stromateus* apparently does not receive the attention it deserves. Once described as numerous in the markets at Lima (Cuvier and Valenciennes, 1833), it is today the subject of only small local fisheries in parts of Chile and along the African coast.

Relationships. *Stromateus* contains the most primitive species of the family Stromateidae. *Stromateus fiatola*, the African species, has three epural elements in the caudal skeleton and, when young, has pelvic fins. These characters indicate the centrolophid heritage of the stromateids. In the South American species of *Stromateus*, there seem to be only two epural elements in the tail, and the young may lack pelvic fins.[1] This situation is typical of the stromateid grade.

Stromateus has a very high number of vertebrae, more than forty, an advanced condition. This high number may be a recently acquired characteristic of the genus. The number itself is variable, and, in a large proportion of cases, fusions of the centra occur in the caudal series. Centra with two or three neural and haemal spines appeared in four of the fourteen specimens radiographed. The variability and high incidence of fusions suggests a genetic instability perhaps correlated with recent acquisition.

Because of its high vertebral count, *Stromateus* cannot be the direct ancestor of either of the other two stromateid genera, both of which have lower counts. Rather, all three must share a common ancestor, a fish most like *Stromateus* but with a vertebral count somewhere near 13 + 17.

Species. Stromateus lives in temperate to tropical waters along the coasts of Mediterranean countries, West Africa, Argentina, and Chile. Though numerous species have been described, there seem to be no more than two, or possibly three, valid ones. Species are widespread along a coastline, but none jump ocean barriers. The species in the genus are:

Stromateus fiatola Linnaeus, 1758. Mediterranean, coast of West Africa south to Capetown, type locality Mediterranean Sea. D 48–51 (total elements). A 35–38 (total elements). P 22–24. Gill-rakers usually 3 + 1 + 11. Vertebrae 18–19 + 24–26. Specimens less than 100 mm SL have pelvic fins and vertical bars on the sides. The fins and the bars are gone in adults. The names of the Mediterranean *Fiatola fasciata* Risso, 1826, and *Seserinus microchirus* Cuvier and Valenciennes, 1833, are synonyms based on juveniles. Other synonyms are *Chrysostromus fiatoloides* Lacépède, 1802, from the Mediterranean and *Stromateus capensis* Pappe, 1866, from South Africa.

Stromateus stellatus Cuvier, 1829. Pacific coast of South America, Chile and rarely north to Lima, type locality coasts of Peru. D 44–53 (total elements). A 39–44 (total elements). P 19–24. Gill-rakers around 4 + 1 + 12. Vertebrae 16 + 26–27. **Stromateus maculatus* Cuvier and Valenciennes, 1833 (= *S. advectitius* Whitley, 1935), a junior synonym, is the name most often used for this fish. **S. maculatus* is also generally applied to the species of *Stromateus* which occurs along the Atlantic coast of South America. The two forms are very close in appearance but the Chilean form is a slenderer fish with a slightly longer head. The counts of the two overlap almost completely. The Atlantic form seems to breed near the northern limit of its range (Hart, 1946). Nothing is known concerning the breeding habits of the Pacific form, but the spawning area is probably well north of Tierra del Fuego. It seems unlikely that there is any gene exchange between the two populations, and I suspect that future study will show that sufficient difference exists to warrant recognition of both at the species level. The available name for the Atlantic population is:

**Stromateus brasiliensis* Fowler, 1906. Atlantic coast of South America, Tierra del Fuego north to Uruguay, type locality Rio Grande do Sul, Brazil. D 47–53 (total elements). A 44–47 (total elements). P 19–20. Gill-rakers around 3 + 1 + 12. Vertebrae 16–17 + 27–30. The bionomics and potential fishery for this fish are the subject of an excellent discussion by Hart (1946).

---

[1] I have seen no small *Stromateus* from South America, but the adults lack the two dark flaps of skin which bespeak the former presence of pelvics in adult African *Stromateus*.

Genus *PEPRILUS* Cuvier, 1829

Figures 40, 41

Rhombus Lacépède, 1800:60. (Type species: *Chaetodon alepidotus* Linnaeus, 1766:460, by monotypy. Charleston, South Carolina. Preoccupied by *Rhombus* Humphrey, 1797, Mollusca.)

Peprilus Cuvier, 1829:213. (Type species: *Sternoptyx gardenii* Bloch and Schneider, 1801: 494, by subsequent designation of Gill, 1862: 126. Charleston, South Carolina. A synonym of *Chaetodon alepidotus* Linnaeus, 1766:460.)

Poronotus Gill, 1861:35. (Type species: *Stromateus triacanthus* Peck, 1804:51, by monotypy. Piscataqua River, New Hampshire.)

Palometa Jordan and Evermann, 1896:966. (Subgenus. Type species: **Stromateus palometa* Jordan and Bollman, 1889:156, by original designation. Bay of Panama, Pacific Ocean.)

Simobrama Fowler, 1944b:2. (Type species: **Seserinus xanthurus* Quoy and Gaimard, 1824:384, by original designation. Rio de Janeiro. A synonym of *Stromateus paru* Linnaeus, 1758: 248.)

The combination of deep body, large eye, long pectoral fin, one to three bladelike spines ahead of the median fins, a ventral spine on the pelvic bone, and no pelvic fins, distinguishes *Peprilus* from all other stromateoid genera. The name, a masculine noun, is from the Greek *πεπρίλος*, one of Hesychian's many *ἰχθῦς ποίος*, unknown fish.

Description. Body deep, maximum depth 35 to 70 per cent of the standard length, highly compressed; musculature firm. Peduncle very short, compressed. Dorsal fin continuous, originating just behind insertion of the pectoral fin; one to three flat, bladelike spines, the first spine pointed on both ends, preceding the 30 to 40 finrays. Anteriormost rays of the median fins produced, the fins often falcate, the rays which follow much shorter, diminishing very slightly in length to the last ray, the shortest. Pectoral fins long, winglike, their bases slightly inclined. No pelvic fins. Pelvic bone visible on midline of body under the end of the pectoral fin base; a small spine on the end of the bone projecting posteroventrally through the skin. Tip of coracoid sometimes projecting slightly underneath the head at about level of margin of the preopercle. Caudal fin stiff, deeply forked, the lobes long and equal. Scales very small, cycloid, thin, very deciduous, extending onto all fins. Simple tubed scales of the lateral line moderately high, following dorsal profile and extending onto peduncle but not to caudal base. A branch of the lateral line extending upward from the head of the hyomandibular in a short, wide, bony tract. Skin very thin; main subdermal canal along intermuscular septum and side branches conspicuous, pores to surface very small. In some species, a row of large conspicuous pores in the back under the first half of the dorsal fin. Head around 25 per cent of the standard length. Top of head naked, pores clearly visible, naked skin underlain with numerous parallel canals projecting backward over the nape. Eye large. Adipose tissue around the eye developed, extending forward and surrounding the nostrils. Nostrils small, the anterior round, the posterior a slit, located near tip of the obtuse snout at level of top of the eye. End of maxillary barely reaching to below eye, angle of gape well before eye. Premaxillary not protractile. Lacrimal bone reduced, scarcely covering top of upper jaw when mouth is closed, end of maxillary exposed. Supramaxillary absent. Jaw teeth minute, uniserial, laterally compressed, with three subequal cusps, close set, covered laterally by a membrane. Vomer, palatines, and basibranchials toothless. Gill membranes united across the isthmus, divided from about level of the forward part of the eye. Opercle and preopercle thin, not scaled, preopercle finely striated, opercle smooth, margins entire; opercle with two ill-defined flat spines; angle of preopercle rounded, not projecting backward. Cheek not scaled. Gill-rakers a little more than half the length of the filaments, with fine teeth on the inner edge, the rakers close set, about 18 on the lower limb of the first arch; no rudimentary rakers under the small pseudobranch. Six branchiostegal rays, four on the ceratohyal, two on the epihyal. Scapula visible. Vertebrae variable, $13 + 17 = 30$ to $12 + 23 =$

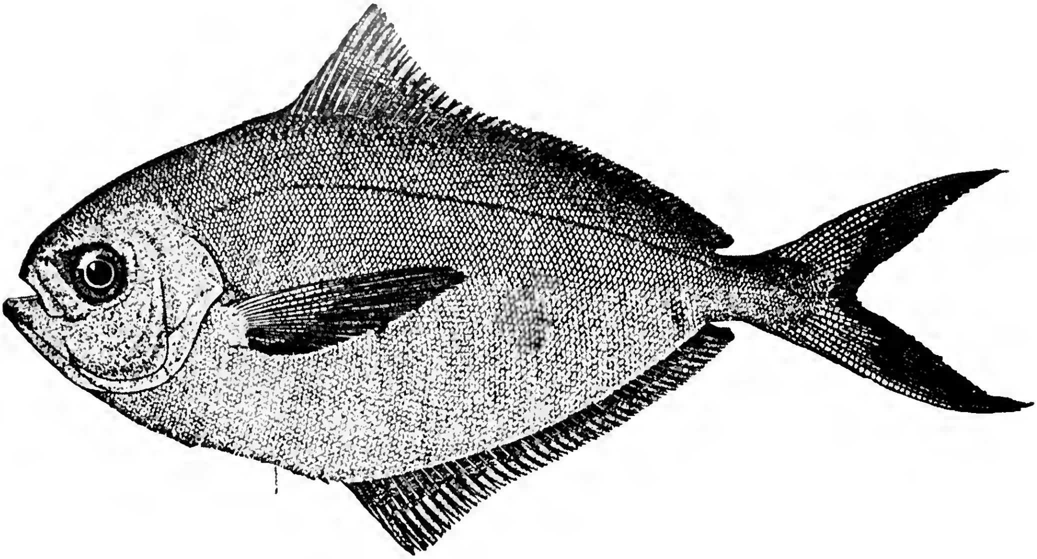


Figure 40. *Peprilus triacanthus*, drawing of a 7.5-inch specimen, courtesy of the Smithsonian Institution.

35. Sclerotic bones well ossified. Stomach a simple sac; intestine very long. Pyloric caeca very numerous, in a dendritic mass.

Color in preservative brownish, often with a silvery overlay, dark above, lighter below. Back and sides sometimes with spots. Median fins darker or lighter than the body; pectoral light. Gill cavity, inside of mouth, and peritoneum light.

Natural history. The species of *Peprilus* are prized for food wherever they occur. The biggest fishery is for *P. triacanthus*, which is found along the east coast of the United States. In some years, more than two million pounds of this species are landed in Massachusetts alone (Bigelow and Schroeder, 1953). Considering its commercial importance, surprisingly little is known of the habits of *Peprilus*. Almost all our knowledge of the natural history of the genus comes from a few general studies on *P. triacanthus*. The discussion here is based largely on the excellent review of Bigelow and Schroeder (1953).

Though young *P. triacanthus* are sometimes found with *Cyanea*, they do not seem to associate with medusae as actively as some other stromateoids. The small fishes are just as often observed swimming independently at the surface or clustered under floating Gulf weed. A much stronger association is formed by *P. alepidotus* with the sea nettle *Chrysaora* in Chesapeake Bay. *P. alepidotus* feeds actively on the medusa (Mansueti, 1963).

Peprilus triacanthus spawn in Massachusetts waters from summer into early fall. Spawning takes place a few miles offshore, but, except at this time, the adults are usually closer to shore in water less than 30 fathoms deep. The eggs are pelagic and, at a temperature of 65°F, hatch in less than two days. During their first summer, the young fish may grow to a length of three or four inches. They probably mature when about two years old at a length of seven inches. A large adult is no more than a foot long.

During the late fall, schools of *Peprilus triacanthus* apparently move offshore where they winter near bottom in about 100 fathoms. Though sometimes occurring as far

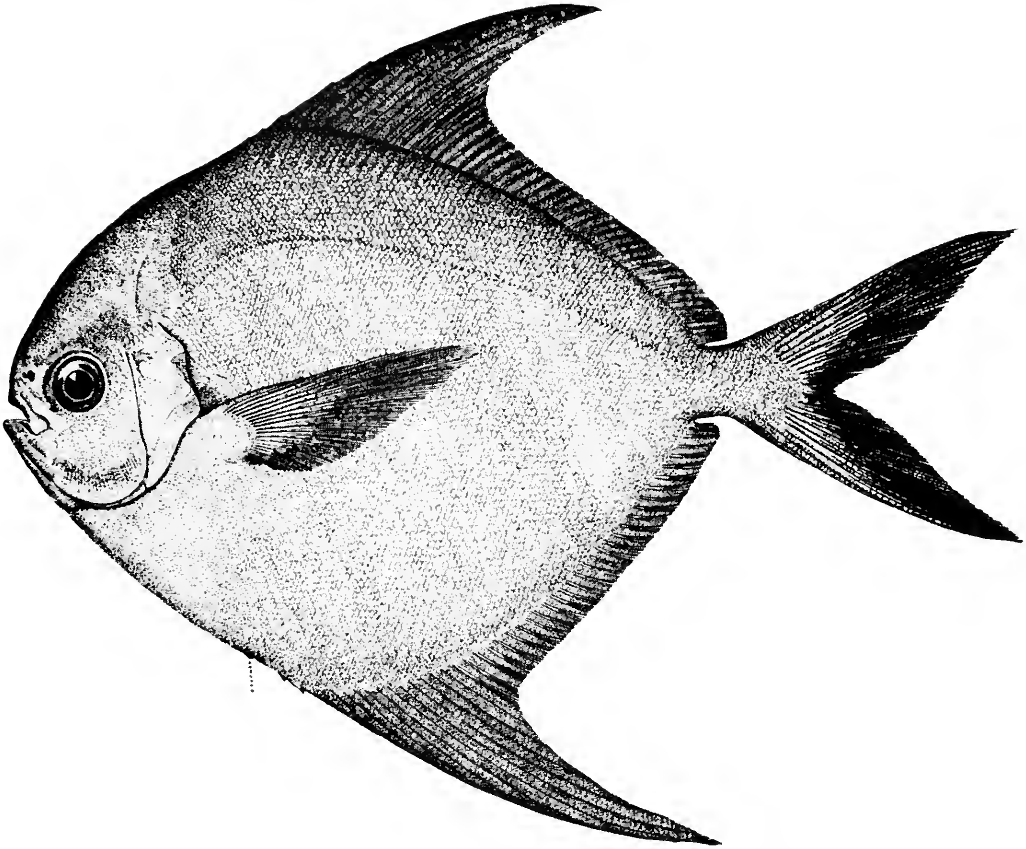


Figure 41. *Peprilus alepidotus*, drawing of a 7.5-inch specimen, courtesy of the Smithsonian Institution.

north as Newfoundland, *P. triacanthus*, like all members of the genus, is basically a warm water fish.

Relationships. Peprilus is more advanced than *Stromateus* in that all species lack pelvic fins and have only two epural elements in the caudal skeleton (Fig. 42). But it is more primitive than *Pampus* in having six instead of five branchiostegal rays and a shorter pharyngeal sac (Fig. 43; cf. Fig. 46). The few spines before the median fins in *Peprilus* are very similar in form to the more numerous spines of some *Pampus*, but the similarity is probably due to common heritage rather than to direct ancestry. It is unlikely that *Pampus* is derived from *Peprilus*. The most primitive species in *Pampus* has no spines before the median fins and shows no trace of the pelvic spine so characteristic of *Peprilus*. *Peprilus* is derived from a fish somewhat like *Stromateus*, but probably with fewer vertebrae.

Species. Peprilus is widespread, with a number of species along both the Atlantic and Pacific coasts of the New World north of the equator. One species is found as far south as Montevideo on the east coast of South America. *Peprilus* has been divided into several nominal genera, but the differences on which these are based—depth of body, fins falcate or not, certain pores well developed or not—are the differences between species, not genera. Osteologi-

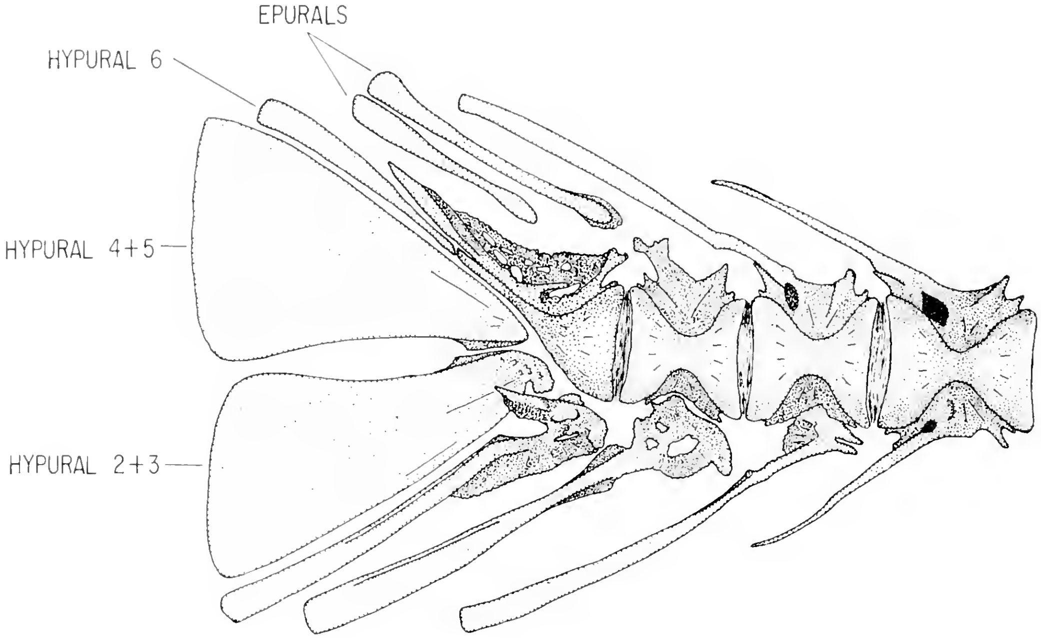


Figure 42. Caudal skeleton of *Peprilus triacanthus*, drawing of a cleared-and-stained preparation from a 36-mm specimen. All elements identified in Figure 1.

cally, all members of the nominal genera are very similar.

The species differ but little from one another. There is some question as to whether or not certain populations are to be regarded as full species or only as subspecies. The marked similarity between species, and therefore the doubt as to the rank to be accorded certain forms, is probably due to the fact that active speciation is occurring now in the genus. More variational studies and increased knowledge of the natural history are needed to resolve these questions.

The species in *Peprilus* are:

Peprilus paru (Linnaeus, 1758) = *Stromateus paru* Linnaeus. West Indies to Uruguay, type locality Jamaica. D III 38–44. A II 35–41. P 20–22. Vertebrae 13 + 17. This species is distinguished from the very closely related *P. alepidotus* (Linnaeus, 1766) by the lower counts and narrower pectoral fin (Hildebrand, MS). Synonyms are: **Seserinus xanthurus* Quoy and Gaimard, 1824, from Brazil; *Rhombus crenulatus* Cuvier and Valenciennes, 1833, from Cayenne; and *Rhombus orbicularis* Guichenot, 1866a, also from Cayenne.

Peprilus alepidotus (Linnaeus, 1766) = *Chaetodon alepidotus* Linnaeus. East coast of North America from Massachusetts to Florida and Gulf of Mexico, type locality Charleston, South Carolina. D III 43–49. A II 39–43. P 21. Vertebrae 13 + 17. This species is considered distinct from *P. paru* by Hildebrand (MS), although both are often lumped under this name. This is the "harvestfish" of the North American fisheries literature. *Stromateus longipinnis* Mitchill, 1815, from New York Bay, is a synonym.

Peprilus triacanthus (Peck, 1804) = *Stromateus triacanthus* Peck. East coast of North America from Newfoundland to Florida, type locality Piscataqua River, New Hampshire. D III 43–46. A II 37–43. P 19–21. Vertebrae around 13 + 19. This spe-

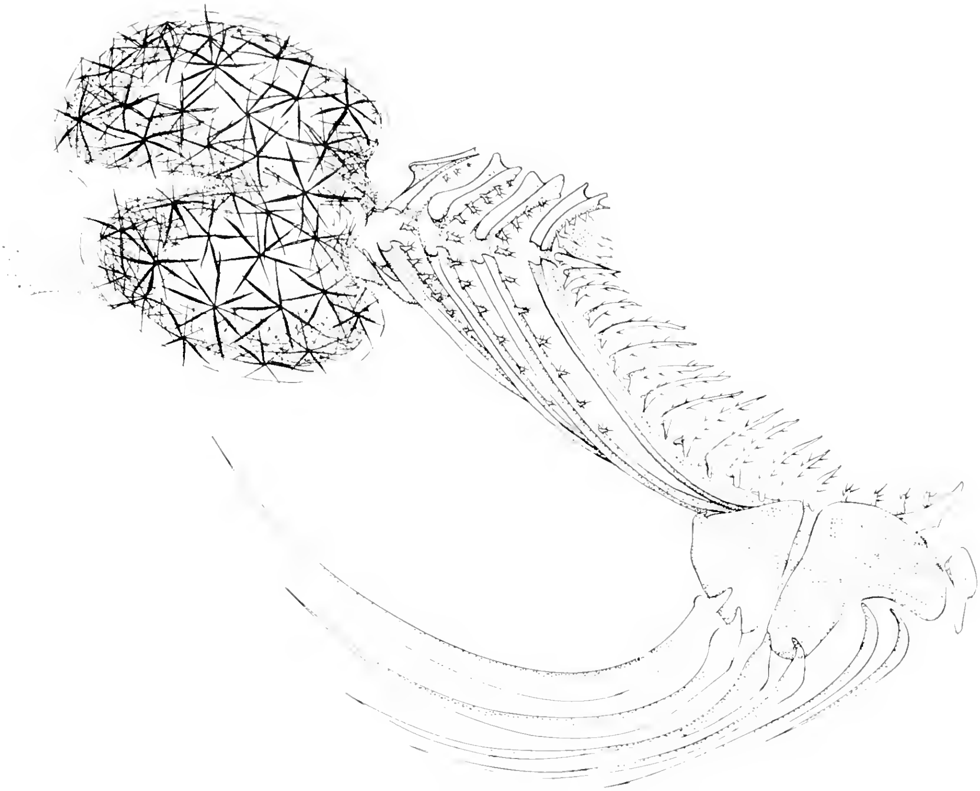


Figure 43. Branchial region of *Peprilus triacanthus*, drawing of a cleared-and-stained preparation from a 120-mm specimen. Elements identified in Figure 2.

cies is very close to *P. burti* Fowler, from which it is distinguished by a slightly higher vertebral count (Collette, 1963). These two forms have only recently diverged. This fish is usually known as *Poronotus triacanthus*, the "butterfish" of North American fisheries literature. *Stromateus cryptosus* Mitchill, 1815, from New York Bay, is a synonym.

Peprilus simillimus (Ayres, 1860) = *Poronotus simillimus* Ayres. West coast of North America, British Columbia to Baja California, type locality San Francisco. D III 45–47. A III 39–44. P 20–22. Vertebrae 13 + 17. This species is a member of the *P. triacanthus–burti* complex.

Peprilus medius (Peters, 1869) = *Stromateus medius* Peters. Known only from Mazatlán, Mexico, Pacific Coast. D III 42. A III 32. (From Fordice, 1884.) Possibly a synonym of *P. simillimus* (Ayres, 1860).

Peprilus palometa (Jordan and Bollman, 1889) = **Stromateus palometa* Jordan and Bollman. Pacific coasts of Panama and Colombia. D III 44–48. A II 43–46. P 22–23. Gill-rakers 5–6 + 1 + 15–16. Vertebrae 13 + 20–21. This deep-bodied fish with falcate median fins is a member of the Atlantic *P. alepidotus–paru* group.

**P. snyderi* Gilbert and Starks, 1904. Known only from Panama Bay. D III 41–47. A III 41–42. P 22–23. Gill-rakers 4 + 1 + 14. Vertebrae 13 + 23. This rarely seen species is distinguished from *P. palometa* (Jordan and Bollman, 1889) in having more vertebrae, a longer snout, and very short

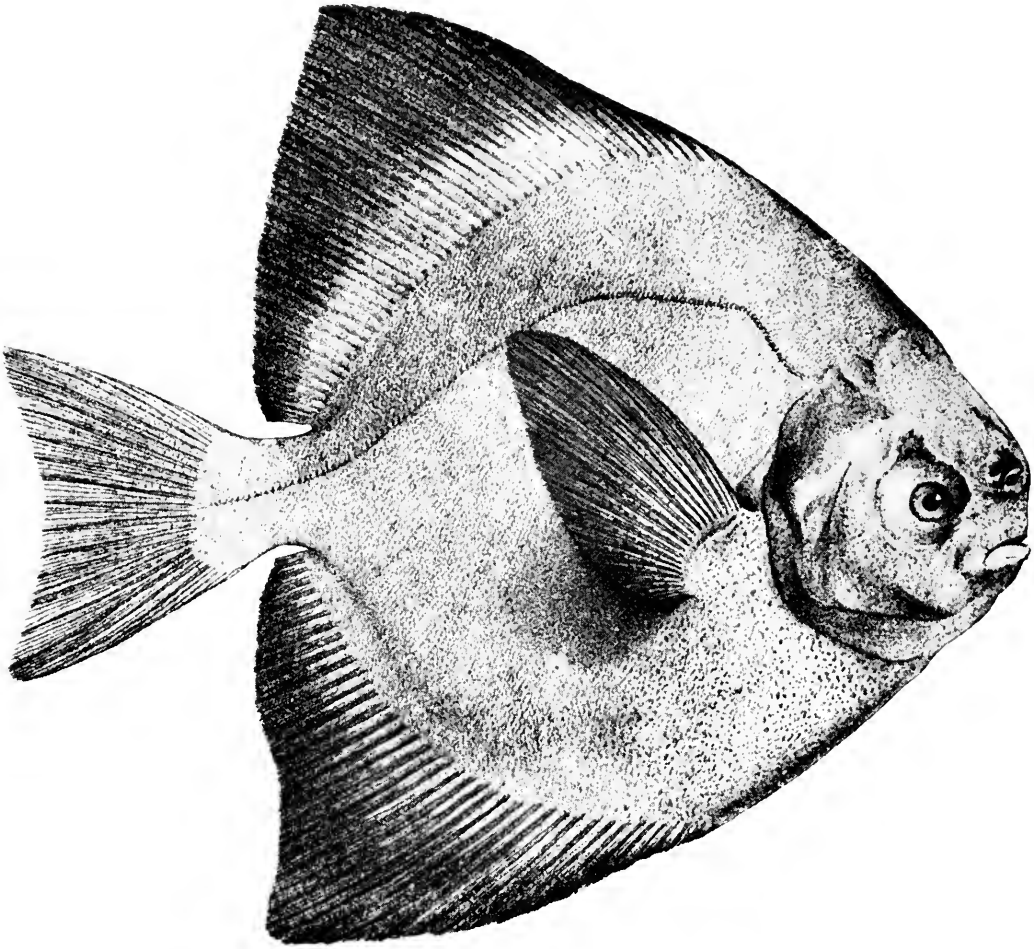


Figure 44. *Pampus chinensis*, a species lacking spines before the median fins, drawing of a 4-inch specimen, from Day, 1875.

lobes on the median fins. *P. snyderi* approaches *Stromateus* in the increased number of vertebrae and in the very reduced spines preceding the rays in the median fins. It may be very like the stromateid ancestral to *Peprilus* and *Stromateus*. Investigations of its systematic position, geographic distribution, and natural history should be very instructive.

Peprilus burti Fowler, 1944b. Gulf of Mexico, type locality Breton Island, Louisiana. D III 43–45. A III 40–41. P 20–21. (From Fowler, 1944b.) Vertebrae around 13 + 17 (Collette, 1963). This species is very close to *P. triacanthus* (Peck, 1804). Caldwell (1961) and Collette (1963) differ in their interpretation of its systematic status.

Genus *PAMPUS* Bonaparte, 1837

Figures 44, 45

Pampus Bonaparte, 1837:48. (Subgenus. Type species: *Stromateus candidus* Cuvier and Valenciennes, 1833:391, by subsequent designation of Jordan, 1923:187. Malabar Coast.

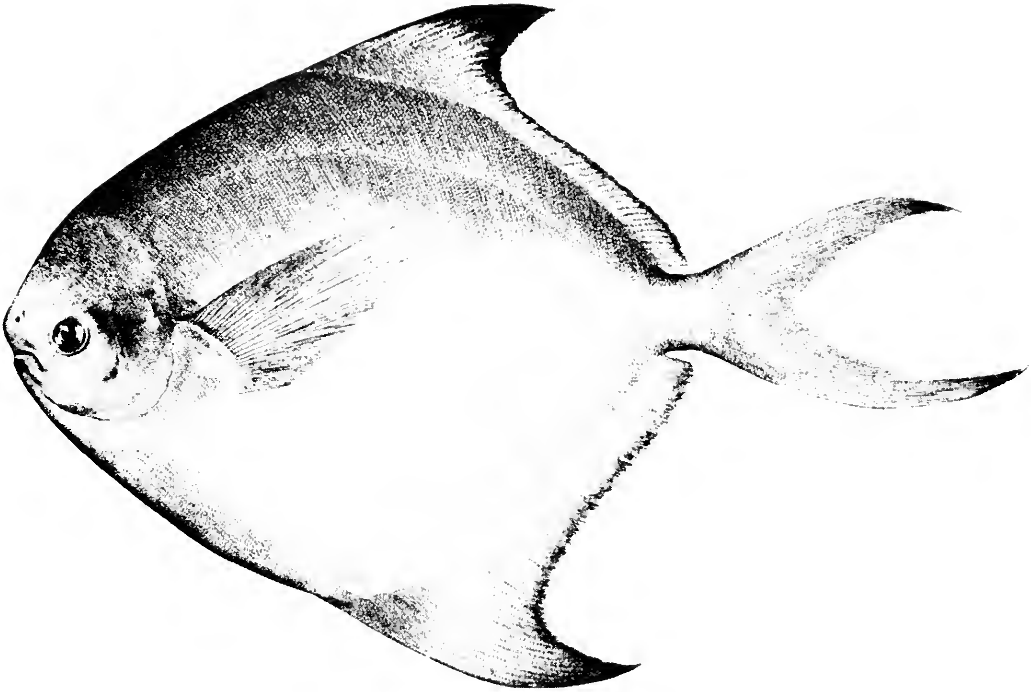


Figure 45. *Pampus argenteus*, a species with spines before the median fins, drawing of a 10.5-inch specimen, from Jordan and Metz, 1913.

A synonym of *Stromateus argenteus* Euphrasen, 1788:53.)

Stromateoides Bleeker, 1851:368. (Type species: *Stromateus cinereus* Bloch, 1793:90, by subsequent designation of Gill, 1862:126. A synonym of *Stromateus argenteus* Euphrasen, 1788:53.)

Chondroplites Gill, 1862:126. (Type species: *Stromateus atous* Cuvier and Valenciennes, 1833:389, by original designation. After Russell's "atoo-koia" (1803: plate 21), Vizagapatam. A synonym of *Stromateus chinensis* Euphrasen, 1788:54.)

The combination of deep body, no pelvic fins, fixed maxillary, and gill membranes broadly united to the isthmus distinguishes *Pampus* from all other stromateoid genera. The name, a masculine noun, is from the vernacular of the 19th century East Indian Spanish and Portuguese colonials, who generally used the term "pampus" (ultimately from "pampano") for any silvery, compressed fish.

Description. Body very deep, maximum depth greater than 60 per cent of the standard length, highly compressed; musculature firm. Peduncle very short, compressed. A continuous dorsal fin; both median fins preceded by either none or five to ten flat, bladelike spines, pointed on both ends, protruding but slightly and resembling the ends of free interneurals. In forms with bladelike spines, dorsal fin originating slightly behind end of pectoral fin base, the first spine generally over or slightly before the pectoral insertion; in forms lacking spines, dorsal fin originating over the pectoral fin base. Anal papilla well before midbody, in a slit. Anal fin originating at or before middle of body and only slightly behind origin of the soft dorsal. Anteriormost rays of the median fins produced, the fins often falcate, rays which follow shorter; in forms with bladelike spines, rays of the posterior two-thirds of the fin short and subequal, the anal fin lobe often extremely produced; in forms lacking spines, rays of the posterior two-thirds of the fin decreasing in length evenly to the last ray, the shortest. Pectoral fin long, winglike, the base of the fin inclined about 45°. No pelvic fins. Pelvic bone not visible on midline and lacking a ventral spine. Tip of coracoid often projecting slightly underneath head at about level of margin of preopercle. Caudal fin stiff, deeply forked, in forms with bladelike spines the ventral lobe often extremely produced. Scales very small, cycloid, thin, deciduous, extending onto bases of all fins. Simple tubed scales of the lateral line fairly high, following dorsal profile, and extending onto peduncle. Skin thin; main subdermal canal along intermuscular septum and side branches usually quite apparent, pores to surface seem wanting. Head around 25 per cent of the standard length, very deep and broad. Top of head naked, subdermal canals visible under naked skin but pores not visible, naked skin underlain with numerous parallel canals projecting backwards over the nape and along first part of lateral line. Eye small. Adipose tissue around eye developed and extending forward around the nostrils. Nostrils large, the anterior round, the posterior a long slit, located near tip of the inflated snout at level of the top of the eye, nasal capsules greatly expanded. Mouth subterminal, curved downward, small, maxillary scarcely reaching to below eye and angle of gape before eye. Premaxillary not protractile. Maxillary immobile, covered with skin and united to cheek. Lacrimal bone very much reduced. Supramaxillary absent. Jaw teeth minute, uniserial, flattened, with a large rounded central cusp and two shorter auxiliary cusps, close set, covered laterally by a membrane. Vomer, palatines, and basibranchials toothless. Gill membranes broadly united to the isthmus. Gill opening a straight slit, covered with a flap of skin. Gill-rakers small, about one-quarter the length of the filaments, not toothed, widely spaced. Pseudobranch absent. Five branchiostegal rays, three on the ceratohyal, two on the epihyal. Scapula not prominent. Vertebrae variable in species with bladelike spines, $14 + 20 = 34$ to $16 + 25 = 41$; in species without bladelike spines, vertebrae $14 + 19 = 33$. Dermal skeleton soft and spongy, but sclerotic bones well ossified; skeleton in general fibrous. Stomach a simple sac; intestine very long. Pyloric caeca numerous, in a small dendritic mass.

Color in life very silvery with a bluish cast on the back. Color in preservative brown or bluish with a silvery or whitish overlay. Median fins and caudal yellowish with dark borders. Head a little darker than the body, with fine speckling. Gill membranes and inside of mouth dark. Peritoneum silvery with black speckles.

Natural history. Pampus is the most sought after of all the stromateoid fishes. Throughout the Orient, it commands a good price wherever it appears. In India, where it is known as "pomfret," the 1962 landings totaled 25.7 thousand metric tons, more than four per cent of the total marine catch (FAO 1964). However, despite its commercial importance, virtually nothing is known of the life history of *Pampus.*

The young occur in shallow water along the coasts, and may even ascend estuaries (Day, 1875). The small mouths with cutting teeth and the long pharyngeal sacs suggest that soft-bodied coelenterates may figure largely in the diet. Most stomachs examined seemed to contain the shredded remains of these animals, but bits of fish were also found. Chopra (1960) found that a sudden appearance of numerous ctenophores and medusae in the waters off Bombay was accompanied by a marked increase in the local catch of *Pampus.*

Relationships. Pampus is the most advanced stromateid genus. The advanced characters are the reduction in the number of branchiostegal rays to five, the lengthening of the pharyngeal sac (Fig. 46), the restriction of the gill opening, the loss of the pseudobranch, and the development, in

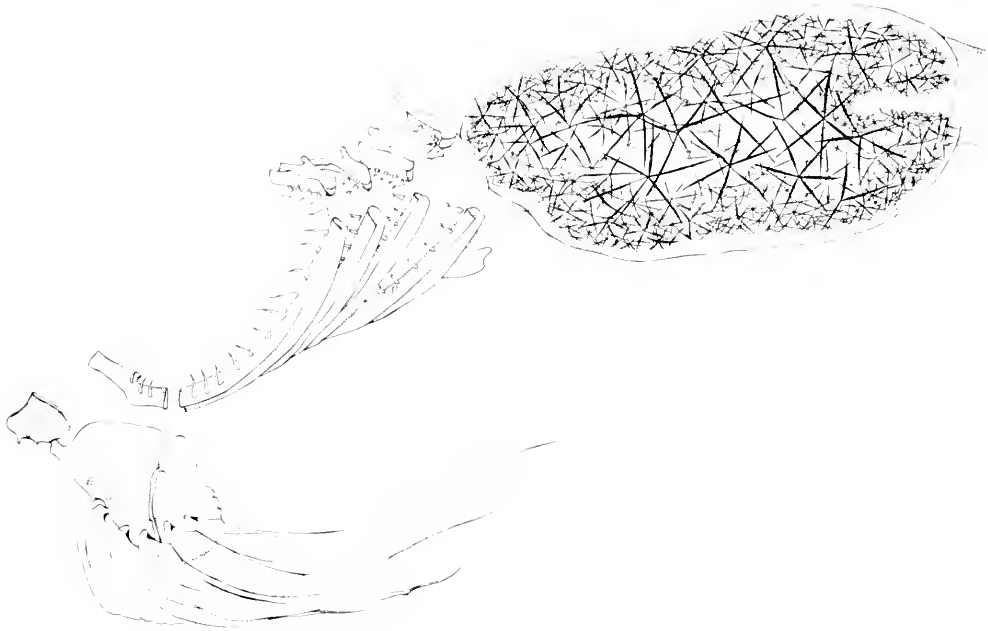


Figure 46. Branchial region of *Pampus echinogaster*, drawing of a cleared-and-stained preparation from a 180-mm specimen, ABE 1743. Elements identified in Figure 2.

some species, of flat, bladelike spines ahead of the median fins. The genus is derived from a fish very like *Stromateus*, but with fewer vertebrae. The most primitive species in *Pampus* has 14 + 19 vertebrae, but the more advanced may have as many as 16 + 25. All members of the genus have the typical stromateid caudal skeleton (Fig. 47).

Species. *Pampus* is widely distributed in tropical waters over the continental shelves from the Iranian Gulf to Japan. There are reports of specimens from Hawaii (Fowler, 1938) and from the Adriatic (Sòljan, 1948). No subsequent records have appeared from either place. The two localities are so far out of the established range of the genus that the records can only have been based on specimens brought from elsewhere.

Gill (1884) divided the genus *Stromateoides* (= *Pampus*) into two groups, which he apparently regarded as subgenera. The group *Stromateoides* had falcate fins and prominent dorsal and anal spines; the other group, *Chondroplites*, had neither. This dichotomy does exist in *Pampus*, but more work is needed to decide whether or not the distinction merits subgeneric recognition.

Numerous species have been described in the genus. The majority are probably synonyms. Published descriptions provide for the most part no clear-cut means of distinguishing species. At the present state of knowledge, only three can be recognized:

Pampus chinensis (Euphrasen, 1788) = *Stromateus chinensis* Euphrasen. India to China, type locality "Castellum Chinense Bocca Tigris." D 43–50 (total elements). A 39–42 (total elements). P 24–27. Vertebrae 14 + 19. This species lacks the peculiar flat spines before the median fins which are found in the other two species. The median fins are not falcate. The fin-rays gradually diminish in length posteriorly (Fig. 44). *P. chinensis*, the type for

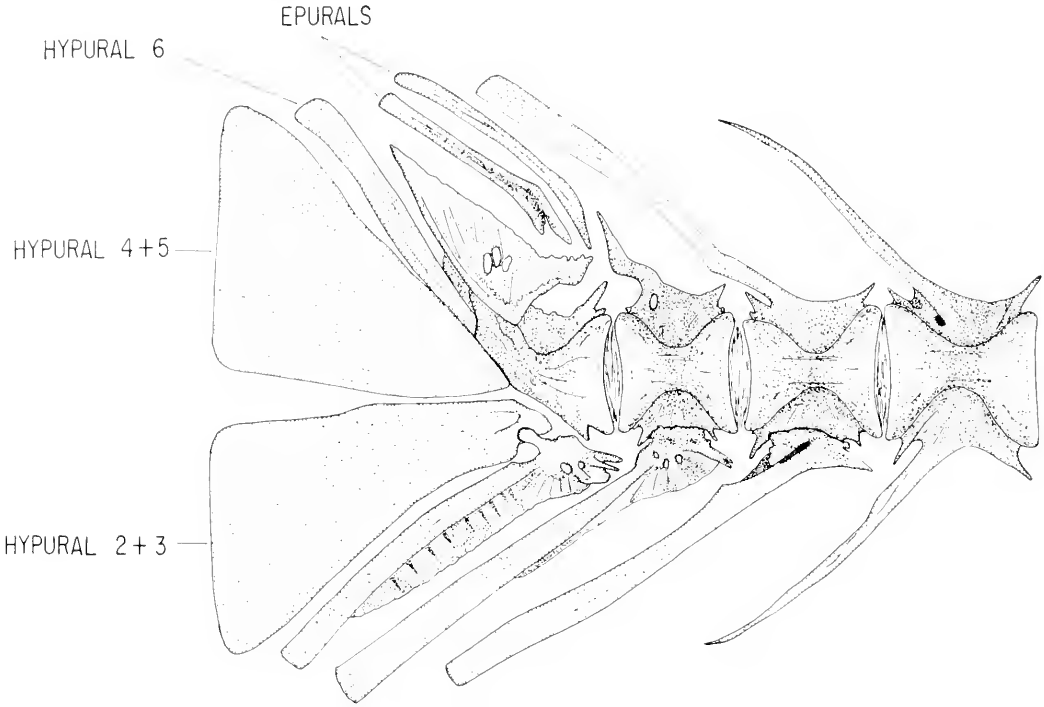


Figure 47. Caudal skeleton of *Pampus argenteus*, drawing of a cleared-and-stained preparation from a 48-mm specimen, ABE 1937. All elements identified in Figure 1.

Gill's (1884) genus *Chondroplites*, is certainly the most primitive species in *Pampus*. Synonyms are: *Stromateus albus* Cuvier and Valenciennes, 1833, from Pondichéry; *Stromateus atous* Cuvier and Valenciennes, 1833, from Vizagapatam; and *Stromateoides atokoia* Bleeker, 1852, from Malaysia. The trivial name is commonly written incorrectly *sinensis*.

Pampus argenteus (Euphrasen, 1788) = *Stromateus argenteus* Euphrasen. Iranian Gulf to Japan, type locality "Castellum Chinense Bocca Tigris." D V–X 38–43. A V–VII 34–43. P 24–27. Vertebrae 14–16 + 20–25. Falcate median fins, preceded by flat bicuspid spines, are characteristic of this species (Fig. 45). The species is apparently very wide ranging. Further study will no doubt show it to be composed of numerous subspecies or even species. This fish is the "pomfret" of Eastern fisheries literature, and is important commercially in India, China, and Japan. Probable synonyms are: *Stromateus cinereus* Bloch, 1793; *Stromateus candidus* Cuvier and Valenciennes, 1833, from Pondichéry; *Stromateus securifer* Cuvier and Valenciennes, 1833, from Bombay; *Stromateus griseus* Cuvier and Valenciennes, 1833, from Pondichéry; *Stromateus punctatissimus* Temminck and Schlegel, 1850, from Japan; and *Pampus simoprosopus* Fowler, 1934b, from Siam.

Pampus echinogaster (Basilewsky, 1855) = *Stromateus echinogaster* Basilewsky. China, Korea, and Japan, type locality China. D VIII–X 42–49. A V–VII 42–47. P 24–25. Vertebrae 14–15 + 24–26. This species has more median finrays than *P. argenteus*. Abe and Kosakai (1964) report that *P. echinogaster* has fewer, thicker pyloric caeca than *P. argenteus*, and 3–6 + 12–15 gill-rakers as opposed to 2–3 + 8–10 in *P. argenteus*. *Pampus lighti* Evermann and Shaw, 1927, from Nanking is a probable synonym.

EVOLUTIONARY TRENDS IN THE STROMATEOIDEI

Gosline (1959) and Liem (1963) have recently stressed the need for an understanding of functional morphology in connection with phylogenetic studies. Natural selection acts on efficiencies and abilities, and evolutionary change results. If function is understood, or at least taken cognizance of, an attempt can be made to evaluate observed differences in terms of efficiences and abilities. Within this framework, evolutionary trends can be discussed. Anatomy alone is insufficient; the way of life must also be taken into account.

The functional significance of many characters, however, is not known. It is hard to understand, for example, why selection should favor a fish with 15 principal branched rays in the caudal fin or with 25 vertebrae, yet these numbers have appeared in many independent phyletic lines. Studies of characters of this sort are, nonetheless, of much importance. The argument that the overall trends observed are real is made stronger when these characters change in step with characters for which the function is at least partially understood.

The trends in the evolution of the stromateoid fishes are discussed below, treating separately, as much as possible, groups of characters which can be considered anatomical units, i.e., caudal skeleton, branchial region, etc. Drawing on what little is known of the way of life of stromateoids, functional significance can be attached to changes in the teeth and jaws, the pharyngeal sacs, and the caudal skeleton. But the meaning of the changes in the size and shape of the body, the fin pattern, the branchial region, and the number of vertebrae cannot be easily interpreted. By and large, the discusion under each of these is necessarily brief and loaded with conjecture. Though each unit is treated separately, it must be remembered that they have evolved together. The organism responds as a whole to the environment, and the products of natural selection are all interdependent.

Attention should be drawn to the distinction between characters typical of a taxon and those typical of the grade of a taxon. In the first case, the characters are found in all members of the taxon. In essence, they are a part of the definition of that taxon. Grade refers to the "average" evolutionary status of the taxon *vis-a-vis* other taxa. The characters typical of a grade need not be found in all members of the taxon. In fact, because different parts of the animal respond to the environment at differing evolutionary rates, it is unlikely that these characters will be found in all. The use of grades provides a convenient way of discussing evolutionary trends without constantly itemizing the exceptions to the general picture. Thus, while 25 vertebrae characterize the centrolophid grade, not all members of the family Centrolophidae have 25 vertebrae. Most do have 25 but some have 26 and others have near 60.

Before proceeding to the discussion, let us briefly recall the more salient features of each of the five stromateoid families. The characters of the individual genera are presented in Table 2.

The Centrolophidae are one to four feet in length with moderately deep to elongate bodies. All have pelvic fins. Their mouths and the teeth in their jaws are fairly large. There are no teeth on the palate. The papillae in the round pharyngeal sacs have irregularly shaped bases. There are seven branchiostegal rays, a pseudobranch, and 25, 26, 29, 30, or 50 to 60 vertebrae. The caudal skeleton has six hypural and usually three epural elements. There are six genera: *Hyperoglyphe*, *Schedophilus*, *Centrolophus*, *Icichthys*, *Seriolella*, and *Psenopsis*.

The Nomeidae are six inches to over two feet in length with deep to elongate bodies. All have pelvic fins. Their mouths and the teeth in their jaws are small. The palatines and the vomer bear teeth. The papillae in

TABLE 2. CHARACTERS OF THE STROMATEOID GENERA. + DENOTES PRESENCE; — ABSENCE.

	BODY SHAPE	MAXIMUM LENGTH	PELVIC FINS	FORM OF TEETH	PALATAL DENTITION	BRANCHIOSTEGAL RAYS	VERTEBRAE	EPURALS + HYPURALS
Hyperoglyphe	moderate	4 feet	+	simple	—	7	25	3 + 6
Schedophilus	deep	3 feet	+	simple	—	7	25, 26, 29, 30	3 + 6
Centrolophus	elongate	4 feet	+	simple	—	7	25	3 + 6
Icichthys	elongate	3 feet	+	simple	—	7	50 to 60	2 + 6
Seriolella	moderate to elongate	3 feet	+	simple	—	7	25	3 + 6
Psenopsis	deep	1 foot	+	simple	—	7	25	3 + 6
Stromateus	deep	1 foot	— in adult	cusped	—	6	42–48	3 + 4
Peprilus	deep	1 foot	—	cusped	—	6	30–33	2 + 4
Pampus	very deep	18 inches	—	cusped	—	5	33–41	2 + 4
Cubiceps	elongate	3 feet	+	simple	+	6	30–33	3 + 4
Nomeus	elongate	1 foot	+	simple	+	6	41	3 + 4
Psenes	moderate to deep	1 foot	+	simple or cusped	+	6	30–42	3 + 4
Ariomma	deep to elongate	3 feet most <1 foot	+	simple or cusped	—	6	30–33	3 + 2
Tetragonurus	very elongate	2 feet	+	simple and cusped	+	5–6	43–58	2 + 4

the round pharyngeal sacs have stellate bases. There are six branchiostegal rays, a pseudobranch, and 30 to 38, 41 or 42 vertebrae. The caudal skeleton has four hypural and three epural elements. There are three genera: *Cubiceps*, *Nomeus*, and *Psenes*.

Most species of the Ariommidae are less than a foot long, although a few species attain more than twice that length. Their bodies are either deep or elongate. All have pelvic fins. Their mouths and the teeth in their jaws are very small. There are no teeth on the palate. The papillae in the elongate pharyngeal sacs have round bases. There are six branchiostegal rays, a small pseudobranch, and 30 to 33 vertebrae. The caudal skeleton has two hypural and three epural elements. There is one genus: *Ariomma*.

The Tetragonuridae are less than two feet long with very elongate bodies. All have small pelvic fins. Their mouths are fairly large. In the upper jaw, their teeth are small and recurved; in the lower jaw, they are large and knifelike. The palatines and the vomer bear teeth. The papillae in the very elongate pharyngeal sacs are much reduced and have small round bases. There are five or six branchiostegal rays, a pseudobranch, and 43 to 58 vertebrae. The caudal skeleton has four hypural and two epural elements. There is one genus: *Tetragonurus*.

The Stromateidae are usually no more than a foot long with deep bodies. None have pelvic fins when adult. Their mouths and the teeth in their jaws are very small. There are no teeth on the palate. The papillae in the round-to-elongate pharyngeal sacs have stellate bases. There are five or six branchiostegal rays, either a small pseudobranch or none at all, and 30 to 48 vertebrae. The caudal skeleton has four hypural and usually two epural elements. There are three genera: *Stromateus*, *Peprilus*, and *Pampus*.

There are two main lineages in the stromateoids (p. 51). One is composed of the Centrolophidae and their derivative, the Stromateidae. The other, a looser assemblage, is composed of the Nomeidae and their two derivatives, the Ariommidae and the Tetragonuridae (Fig. 7). The Centrolophidae and the Nomeidae are the basal stocks. Of these two, the Centrolophidae are in most respects the most primitive. Familial and generic relationships, to be touched upon only briefly here, have been discussed in the individual accounts of family and genus.

Figure 48 summarizes some of the major evolutionary trends in the stromateoid fishes. Each group is treated more or less as a grade in the diagram. The characters shown are relative size and shape of the body, fin pattern, presence or absence of palatal dentition, number of branchiostegal rays, vertebrae, epural plus hypural elements in the tail, and the shape of the papillae in the pharyngeal sacs. These are discussed in detail in the following accounts. The width of the arrow leading to each grade is proportional to the number of genera in that family.

Body (Fig. 48). The largest stromateoids are members of primitive centrolophid genera. McCulloch (1914) reports a 1,072-mm *Hyperoglyphe porosa* weighing 41 pounds from the Great Australian Bight, and I have seen an 1,195-mm *Centrolophus niger* taken south of New England on a long-line. The maximum depth in most centrolophids is within 25 to 30 per cent of the standard length and never exceeds 50 per cent. In the nomeids and in the ariommids, there are a few species whose maximum length approaches a meter but most are smaller. The maximum depth in these families is from about 25 to 40 per cent of the standard length. A large tetragonurid is 600 mm long (Fitch, 1951). These highly modified fishes are very slender, with the maximum depth usually less than 20 per cent of the standard length. The stromateids rarely exceed 450 mm in length, and mature when less than 200 mm long. These fishes are very deep bodied, the maximum depth ranging from 35 to over 70 per cent of the standard length.

The course of evolution in the form of the body has been one of diminution in size and of increase in depth. These two evolutionary tendencies are also displayed in other teleostean groups (Myers, 1958; Liem, 1963).

Fins (Fig. 48). Only one major change has occurred in the fin pattern of stromateoids—the loss of the pelvic fins at the stromateid grade. The presence of pelvics in young *Stromateus fiatola* and their subsequent loss in the adult are important clues in understanding the phylogeny of stromateids. There is a difference between the basic fin patterns of the two stromateoid lineages. Members of the nomeid line have two dorsal fins; members of the centrolophid line usually have but one.

The thoracic pelvic fins of perciform fishes are used in braking and turning (Harris, 1938). In deep-bodied fishes, however, the effectiveness of the fins for these purposes is probably greatly decreased due to the change in the hydrodynamic profile of the fish. In this situation, selective pressure may favor loss of the fins. This has apparently been the case in stromateids, and is also observed in *Parastromateus*, *Monodactylus*, *Psettus*, and a number of other unrelated deep-bodied teleosts.

In the great majority of stromateoids, the anterior rays of the median fins are no more than two or three times the length of the posterior rays. In the stromateids, however, the median fins have become falcate and the anterior rays are very much produced. In *Stromateus* this tendency is but little pronounced. The deeper-bodied species in *Peprilus* have very falcate fins. The anterior finrays of the anal fin in these species are

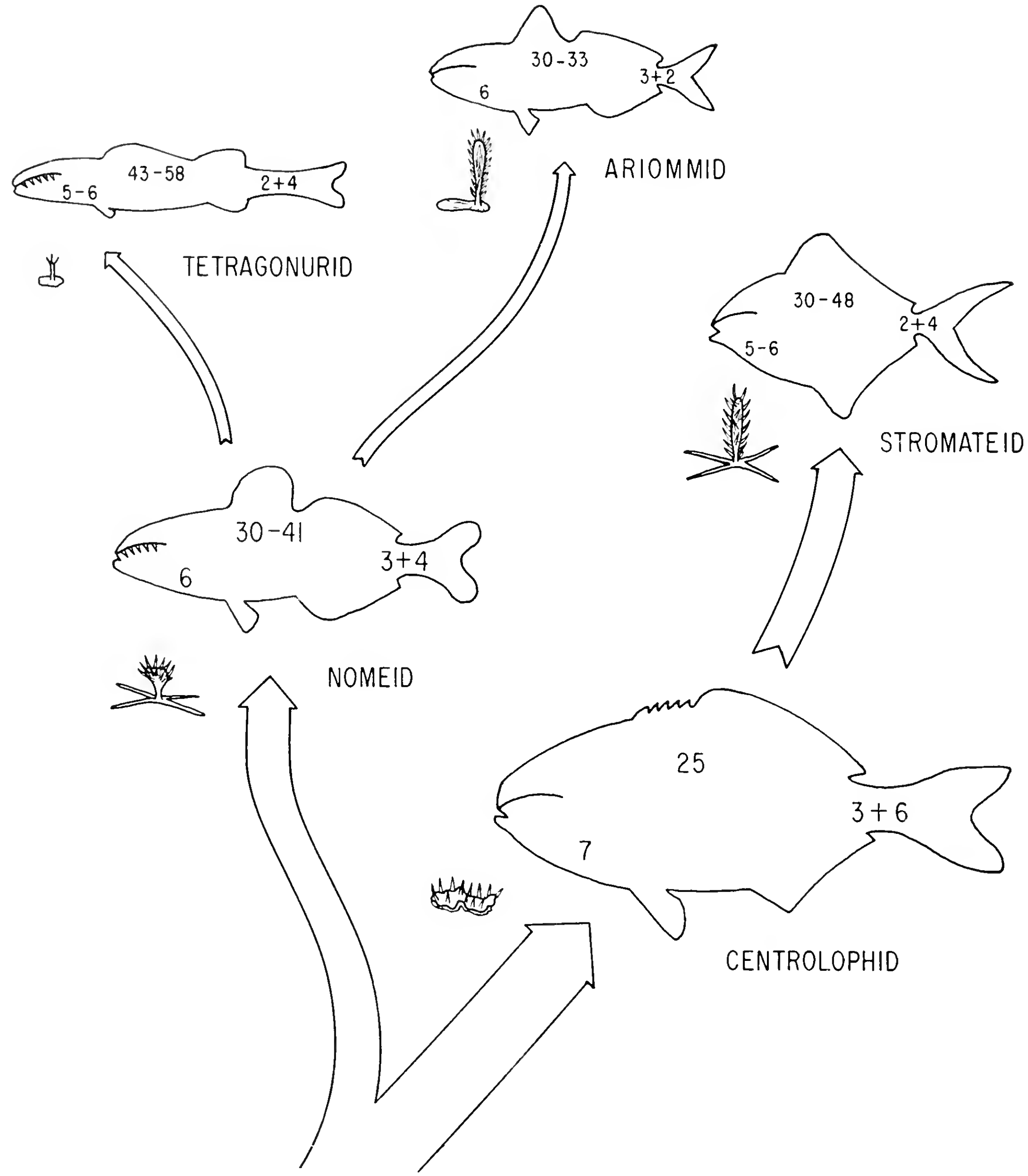


Figure 48. Evolutionary trends in the Stromateoidei, showing relative size and shape, fin pattern, and (within the outline from left to right) presence or absence of palatal dentition, and numbers of branchiostegals, vertebrae, and epurals + hypurals. Inset shows a papilla. Width of arrows proportional to number of genera in the family. See text.

seven or eight times longer than the posterior rays. In *Pampus* both the anterior rays of the anal fin and of the lower caudal lobe are produced, and those in the anal fin may be ten to 20 times longer than the posterior finrays. Lacking observations on living *Pampus*, it is difficult to know what advantage these elongate fins confer.

Teeth and jaws (Fig. 48). In most centrolophids the angle of the gape may be below the eye but in all other stromateoids the angle of the gape is before the eye. The ariommids and stromateids have the smallest mouths of all. In these two families even the end of the maxillary is before the eye. Centrolophids, with the exception of *Psenopsis*, have a small supramaxillary bone, but this is gone in all other stromateoids.

The presence of teeth on the palate is usually considered primitive (Liem, 1963). The palatine and vomerine teeth in the nomeids indicate that this group branched off early from the ancestral stock. Both the centrolophids, in most respects the most primitive of stromateoids, and their derivative, the stromateids, lack these teeth. Palatal dentition is well developed in the tetragonurids, which are derived from fish ancestral to the nomeids. The ariommids, which are probably derived directly from a nomeid, have lost these teeth.

In the majority of primitive centrolophids and in many nomeids, the jaw teeth are relatively large, strong, spaced, and often slightly recurved. The advanced centrolophids, stromateids, and ariommids have much smaller, close-set, straight teeth. The teeth of all stromateids and of some ariommids are laterally flattened and bear minute cusps. Tetragonurids and some species in the nomeid genus *Psenes* have two sorts of teeth in the jaws. Those in the upper jaw are conical, spaced, and recurved; those in the lower jaw are long, knifelike, very close set, and often bear very minute cusps.

The structure of the teeth and jaws is certainly a function of the diet. In stromateoids, which possess a masticatory organ in the pharyngeal sacs, the jaw teeth are primarily for catching and holding prey.

The diet of most centrolophids and nomeids is fairly diverse and often includes rather large animals. The strong, conical, slightly recurved teeth are ably suited to the catching and holding of fairly vigorous prey. The stromateids feed rather extensively on jellyfishes. Their smaller jaws and flattened, cusped teeth are more suited to slicing the tissues of coelenterates. With such animals, there is little need for catching and holding. Nonetheless, the tetragonurids, existing almost entirely on salps and coelenterates, have conical, recurved teeth in the upper jaw and on the palate which must hold the prey firmly while the long, knifelike teeth of the lower jaw slice off mouthfuls.

In the course of evolution, the jaws of stromateoids have become shorter and the supramaxillary bone is lost. The conical teeth have become flattened, cusped, smaller, and more closely set. In the nomeid lineage, the palatine dentition is lost. Changes in the dentition by and large reflect increasing specialization in the food habits.

Pharyngeal sacs (Figs. 49, 50). The sacs of centrolophids are higher than they are long, and the papillae are arranged in ten or more elongate patches (Fig. 49A). The bases of the papillae (Fig. 50A) are irregular in shape, with the teeth seated all over the inner face; the base is often humped up to fit over a ridge of muscle in the sac. In the nomeids, the sac is not so high in respect to its length, and the papillae are in about five longitudinal patches (Fig. 49B). The papillae are very different from those of the centrolophids. The bases (Fig. 50B) are stellate, and the teeth are concentrated near the end of a stalk. The sac in stromateids (Fig. 49C) is at least as long as it is high; in *Pampus* (Fig. 46) it is much longer. The papillae are in only two ill-defined patches in the top and bottom halves of the sac. As in the nomeids, the bases (Fig. 50C) are stellate, but they are in general larger, and the teeth are seated all along the long central stalk instead of only near the end. The sacs in both the ariommids (Fig. 49D) and the tetragonurids are longer than high, markedly so in the latter (Fig. 36). The large papillae of ariommids (Fig. 50D) have round bases, and the small teeth are seated all along the central stalk. The papillae are

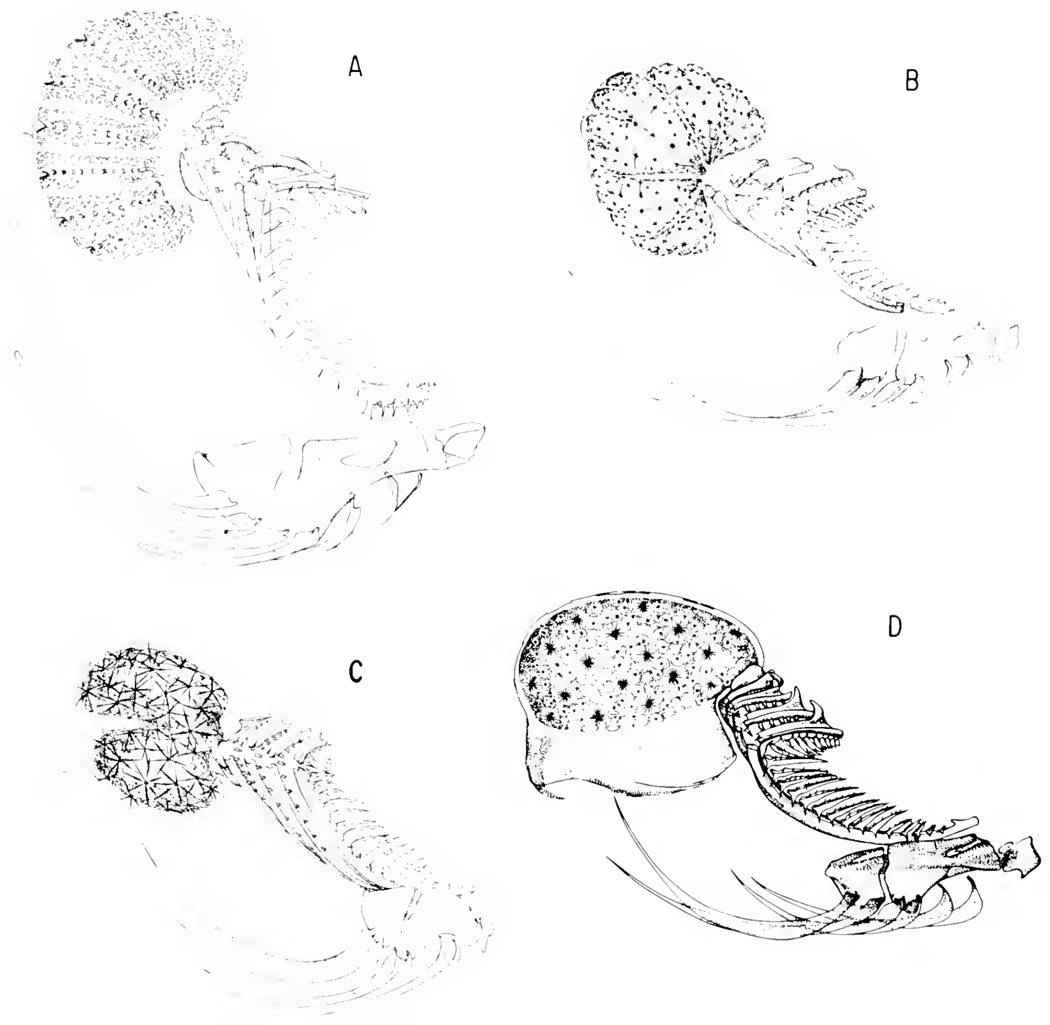


Figure 49. Comparison of branchial regions in four stromateoid families. A. Centrolophidae, *Hyperoglyphe*, from Figure 9. B. Nomeidae, *Nomeus*, from Figure 25. C. Stromateidae, *Peprilus*, from Figure 43. D. Ariommidae, *Ariomma*, from Figure 31. See text.

in a single patch, in the upper half of the sac only. In tetragonurids, the small papillae are widely separated and are not in bands. They are rounded, and there are a few weak teeth on the end of a short stalk.

The nomeids and the stromateids do not share a direct common ancestor. The nomeids are derived from a pre-centrolophid form and the stromateids are derived from an advanced centrolophid. Nonetheless, there is a great similarity in the stellate papillae found in both families (Fig. 50B, C), but this similarity is due to parallelism.

The centrolophid fishes are unspecialized in their diets. They feed on other fishes, on squids, on crustaceans, on jellyfishes and, sometimes but certainly not customarily, on garbage. The large sacs are capable of admitting fairly large objects. The crude papillae do shred the prey to some extent,

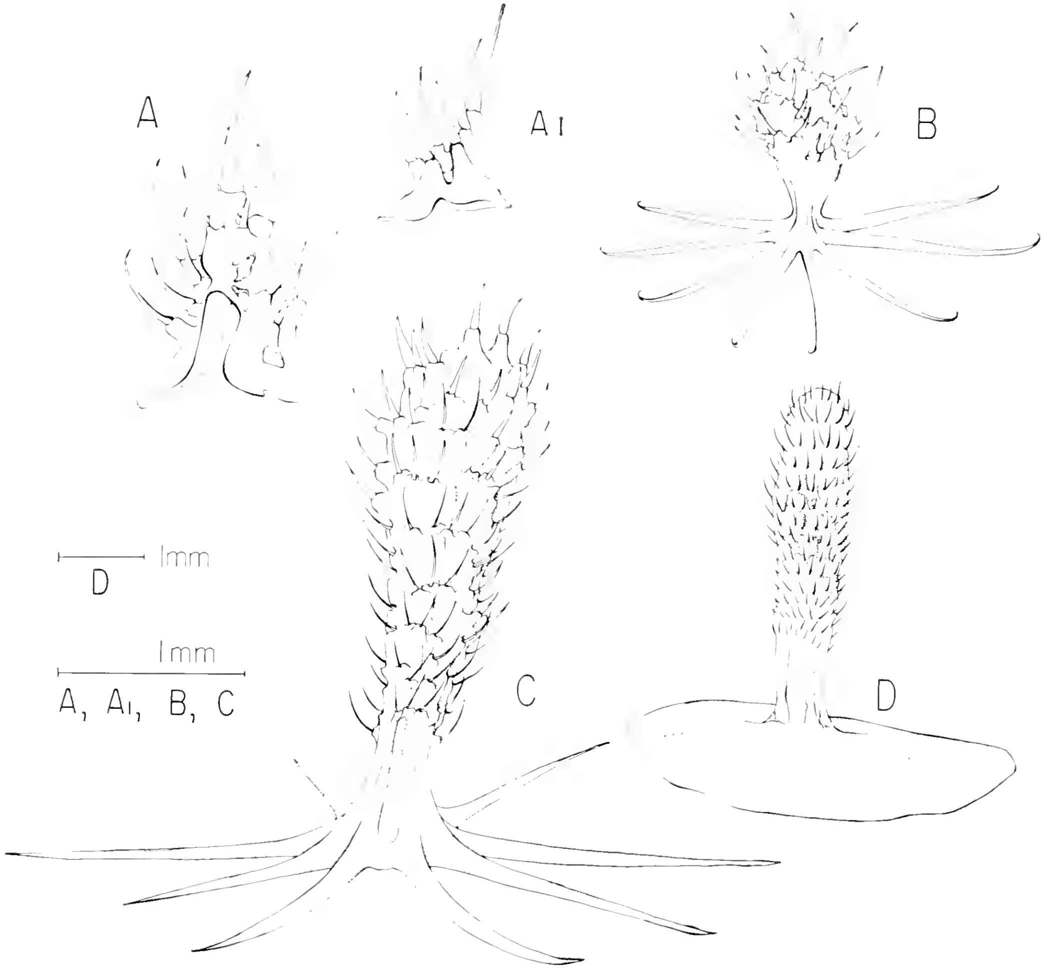


Figure 50. Comparison of papillae in the pharyngeal sacs of four stromateoid families. A. Centrolophidae, *Hyperaglyphe*, from preparation shown in Figure 9, large papilla. A_1. Same, small papilla. B. Nomeidae, *Nomeus*, from preparation shown in Figure 25. C. Stromateidae, *Peprilus*, from preparation shown in Figure 43. D. Ariommidae, *Ariomma*, from preparation shown in Figure 31. See text.

but never so much as to render stomach contents completely unrecognizable.

Little is known of the feeding habits of nomeids. Fish and jellyfish remains have been found in their stomachs. The fairly small sacs and the papillae with their stellate bases firmly seated in the muscular wall of the sac combine to make a good shredding organ, and stomach contents are often difficult to identify.

Stromateids may feed very largely on small crustaceans and medusae. The relatively smaller and more elongate sacs, the papillae with greatly extended bases, and the teeth ranged all along the central stalk of the papillae make a very efficient shredding organ, ably suited to rendering the rubbery tissues of medusae. The shredded stomach contents of stromateids are almost impossible to identify.

Too little is known of the natural history of ariommids to be able to understand the structure of the peculiar pharyngeal sacs found in this group. In almost every specimen examined, the sacs were filled with mud and silt. Is it possible they perform some sort of filtering function?

Tetragonurids may live largely on jellyfishes. The sacs of these fishes are very elongate, as might be expected, but the papillae are very reduced and are probably not very efficient shredders. The upper pharyngeal bones, however, are studded with teeth and extend very far backward into the sacs (Fig. 46). The pharyngeal bones are capable of considerable back-and-forth motion (Grey, 1955) and, in tetragonurids, may perform the shredding action for which the papillae do not seem suited.

The main changes that have occurred in the pharyngeal sacs of stromateoids have been elongation of the sac, reduction in the number of bands of papillae, and increase in complexity of the papillae. These changes are correlated with a change from more or less omnivorous feeding habits to increasing utilization of jellyfishes for food.

Branchial region (Figs. 48, 49). Seven, blunt-ended branchiostegals and a large ceratohyal fenestra are found at the centrolophid grade (Fig. 49A). The advanced centrolophids *Seriolella* and *Psenopsis* have pointed branchiostegals, and the first one is reduced in size (Figs. 20, 23). In nomeids (Fig. 49B) and ariommids (Fig. 49D) there are six tapering branchiostegals, and the ceratohyal fenestra is much smaller, or, in some species, closed. At the stromateid grade (Fig. 49C) there are six tapered branchiostegals and the ceratohyal fenestra is closed. The stromateid genus *Pampus*, perhaps the most advanced of stromateoids, has but five branchiostegal rays. Within the tetragonurids, the number of branchiostegals is either six or five.

A pseudobranch is present in all stromateoids with the exception of *Pampus*. Its loss may be correlated with the unification of the gill-covers to the isthmus. In most stromateoids, the pseudobranch is very well developed and the gill-covers are cleft well forward. In the stromateid genera *Stromateus* and *Peprilus* the pseudobranch is small and the gill-covers are united across, but not to, the isthmus. Finally, in *Pampus* the pseudobranch is gone and the gill-covers have become broadly united to the isthmus.

In the hyal series of stromateoids, two changes have occurred. The branchiostegal rays have become more slender and one ray is lost, and the ceratohyal fenestra becomes closed. The pseudobranch, well developed in most stromateoids, is lost in *Pampus*.

Axial skeleton (Fig. 48). Most centrolophids have 10 + 15 vertebrae, the well-known basic perciform number. The exceptions are in some *Schedophilus* with 10 + 16, 12 + 17, or 10 + 20, and *Icichthys* with a total of 50 to 60. In the nomeids both numbers have increased; there are 13 to 15 precaudal, and 17 to 23, 26, or 27 caudal vertebrae. The stromateids have 12 to 18 precaudal, and 19 to 27 caudal vertebrae, and within any one species the number may be quite variable. Ariommids, derived from a nomeid stock, usually have 12 or 13 + 17 or 18 vertebrae. The tetragonurids, also derived from the nomeids, have continued the increase, to a total of 43 to 58 vertebrae.

It is difficult to understand the selective pressures responsible for an increase in vertebral number. In *Nomeus*, however, the situation is reasonably clear. This genus has 41 vertebrae and is elongate in form. The high number of vertebrae allows the fish to move in a very sinuous manner, and to turn in a very small radius. The pelvic fins are also much enlarged and aid in the turning. This ability enables the fish to avoid more easily the stinging tentacles of the *Physalia* under which it lives.

In general, as the number of vertebrae has increased, the relative length of each individual vertebra has decreased. Fishes with an increased number of vertebrae have more neural and haemal spines than fishes with fewer vertebrae, and these are closer together. Hence there is a stronger frame

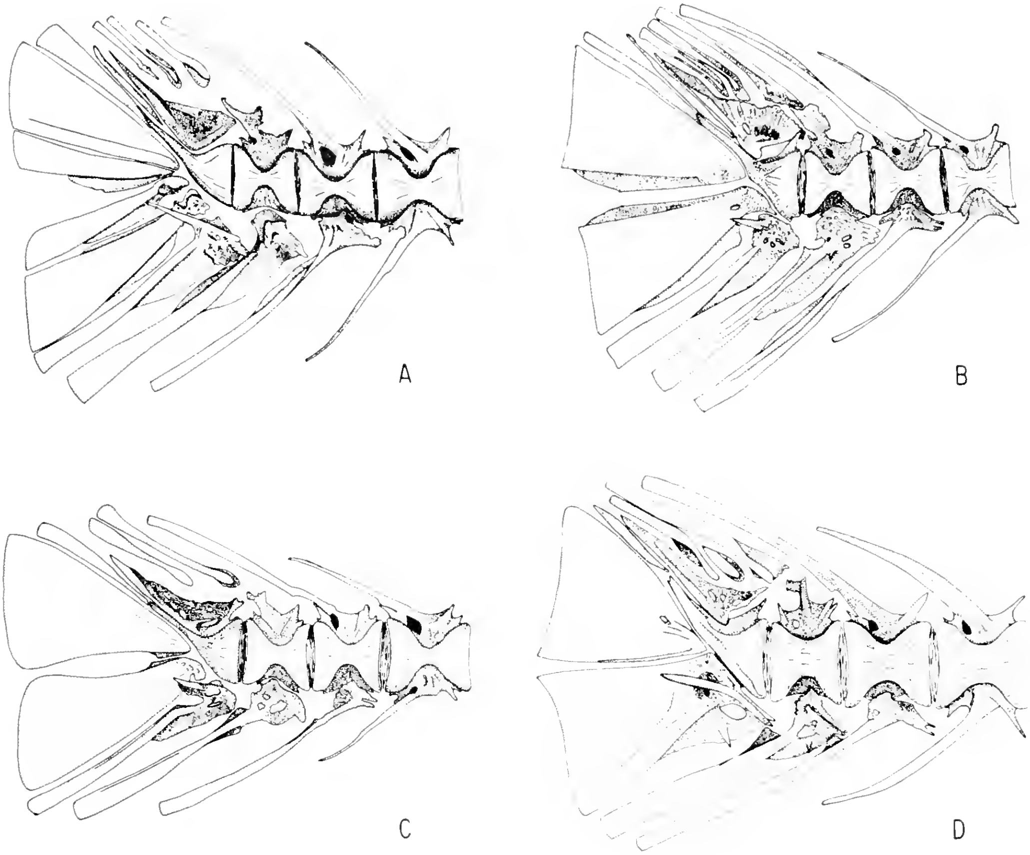


Figure 51. Comparison of caudal skeletons of four stromateoid families. A. Centrolophidae, *Hyperoglyphe*, from Figure 10. B. Nomeidae, *Nomeus*, from Figure 24. C. Stromateidae, *Peprilus*, from Figure 42. D. Ariommidae, *Ariomma*, from Figure 33. See text.

for attachment of the muscles. This probably has permitted, or even encouraged, the evolution of the deep, firm body characteristic of the stromateid grade.

With the increase in vertebral number, the number of median finrays increases as well. This, of course, might be expected, but need not necessarily follow. The ariommids and the tetragonurids, both with increased numbers of vertebrae, have very decreased numbers of median finrays. In *Psenes* and in the stromateids, the increased number of anal finrays has resulted in a forward swing of the first interhaemal so that it forms an abrupt angle with the haemal spine of the first precaudal vertebra. This tends to support and protect the belly of the fish. In the stromateids, the enlargement and extension of the pelvic bones, which bear no fins, and of the postcleithrum almost complete this trend towards support and, possibly, protection.

There has been a general tendency towards increase in the number of vertebrae in the evolution of the stromateoids. The number of caudal vertebrae has tended to increase the most, but the number of precaudal vertebrae has been affected as well. Secondary increase in the number of vertebrae from a basic number near 10 + 15 is of common occurrence in teleosts (Gregory, 1951; Liem, 1963). In many stromateoids, there has been a concomitant increase in the number of median finrays.

Caudal skeleton (Figs. 48, 51). The generalized perciform type of caudal skeleton with six hypurals and three epurals is typical of the centrolophid grade (Fig. 51A). With the fusion of hypurals 2 + 3 and 3 + 4, the number is reduced to four in the nomeids (Fig. 51B), stromateids (Fig. 51C), and tetragonurids. Three epurals are present in nomeids, but one of these is lost at the stromateid grade (Fig. 51C). In the ariommids (Fig. 51D), the fusion of hypurals 1 + 2 + 3 and 4 + 5 + 6 forms two solid blocks. In both the ariommids and some stromateids there is a tendency towards further fusion of hypural elements with the urostylar vertebrae. The ariommids have three epurals but the second one is very reduced in size, and is probably on its way to becoming lost. The tetragonurids have two epurals. Fusion of the uroneurals, both with each other and with the urostylar vertebrae, has occurred in several stromateoid genera.

Most of the centrolophid fishes spend at least the first part of their lives hovering quietly under floating objects. These fishes are able to hang almost motionless with a slight fanning of the pectorals and strong rotary motion of the caudal fin. This rotary motion is possible because of the numerous elements in the caudal skeleton. In the advanced centrolophids—fast-swimming, schooling fishes such as *Seriolella violacea*—partial fusions in the hypural series result in a more rigid tail.

Many of the nomeids are hovering fishes. At this grade, fusions in the hypural series tend to make the tail fairly stiff. This may be counteracted by the long, well-developed autogenous haemal spines, which may be moved laterally to produce a rotary motion in the fin. The long pectoral fins of nomeids, too, may aid their hovering. Observations on living fishes are, however, lacking, and are sorely needed.

The consolidated tail of stromateids allows for little rotary motion. These schooling fishes probably do not hover as much as nomeids or centrolophids but may swim fairly constantly. Specimens of *Peprilus triacanthus* observed in the Woods Hole Aquarium never remained still, but moved slowly forward, bouncing up and down with beats of their long, broad pectoral fins.

There are no observations of living ariommids or tetragonurids. From the structure of their caudal skeleton and fin, it can be assumed that the former at least are very strong, fast swimmers. Living near the bottom, they may not need to hover, but may cruise over the sea floor buoyed up by their well-developed air bladder.

The evolution of the caudal skeleton in stromateoids is marked by a reduction in the number of elements. In the hypural series, this reduction is accomplished by a series of fusions; in the epural series, an element is lost. The tendency toward consolidation and reduction of elements, ultimately resulting in a fused hypural plate, is a general phenomenon found in numerous perciform lineages (Gosline, 1961a). The changes in the stromateoid tail coincide approximately with a change from hovering to swimming fairly constantly in schools.

DISTRIBUTION OF THE STROMATEOIDEI

Distributional data for stromateoid fishes are at best scanty. Nonetheless, all available data tend to support the conclusions based on anatomical data, that is, that the centrolophids arose first, followed by the nomeids, tetragonurids, and, most recently, the stromateids and ariommids. Because of the scantiness of the data, the map figures accompanying this section must be considered approximate only. In general, the distributions have been extrapolated from a few records. Although I am fairly sure of the general picture presented, fine details of the distribution of stromateoids are lacking.

Centrolophidae. The major features of the centrolophid distribution are discontinuity, bipolarity, endemism, and sympatry of genera. The first three are found in the

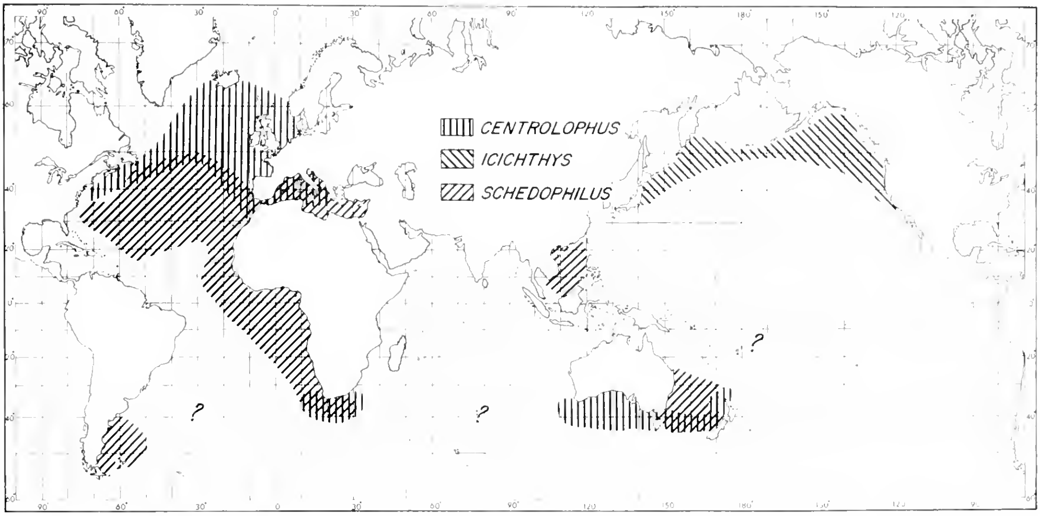


Figure 52. Distribution of the soft-spined Centrolophidae.

more primitive members of the family, the soft-spined centrolophids (Fig. 52). *Schedophilus* is found mainly in the Atlantic Ocean. The presence of two isolated populations, in the China seas and in the environs of the Tasman Sea, indicates that the former range of the genus was once much wider. The distribution of the two Pacific area populations of *Schedophilus* and the distribution of *Centrolophus* are bipolar, again indicative of a shrinking range. *Icichthys*, formerly considered an endemic element of the North Pacific fauna, has recently been found off New Zealand (Haedrich, in press), and is thus bipolar. *Icichthys* and *Centrolophus* probably share a common ancestor; the characteristics of each genus may well have developed in the isolation provided by an ancestral relict distribution. In the hard-spined centrolophids (Fig. 53), *Hyperoglyphe*, like *Schedophilus*, is bipolar in the Pacific but widespread in the Atlantic. The most primitive species in this genus, *H. antarctica*, is found only south of 30° S. *Seriolella*, a relatively advanced genus, is widespread in the higher latitudes of the Southern Hemisphere, where it is no doubt endemic. The most recently evolved centrolophid genus, *Psenopsis*, may be spreading out from the waters of the East Indian region. By and large, centrolophid species are oceanic or found near the edge of the continental shelf. Some species of the soft-spined centrolophids may even be meso- or bathypelagic. The advanced genera *Seriolella* and *Psenopsis*, however, commonly occur in shallow water, and some species may even enter estuaries. Some overlap with at least one other genus occurs within the ranges of all centrolophid genera. Four of the six genera occur in Australia and New Zealand.

Nomeidae. In the distribution of the nomeids (Fig. 54) there are no relicts, no bipolar species, and no regional endemism. For the most part, the three genera seem broadly sympatric, but records are too few to discuss the limits of each genus with precision. In the North Atlantic, however, *Nomeus* is found in the western parts, but has never been reported from Madeira, where its companion *Physalia* is common. *Cubiceps*, though it occurs in the western Atlantic, is much more common in the eastern portions and the Mediterranean. Most nomeid species are oceanic; a few species in *Psenes* seem to be mesopelagic. In general confined to more tropical waters, a

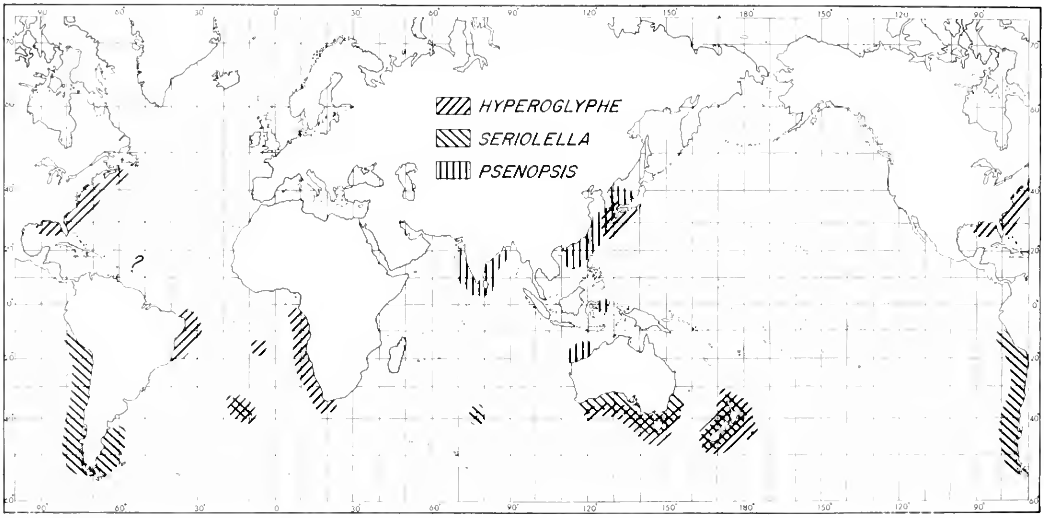


Figure 53. Distribution of the hard-spined Centrolophidae.

number of species, such as *Nomeus gronovii* and *Psenes cyanophrys*, are found in all oceans. All genera are found in Australia and New Zealand.

Tetragonuridae. The distribution of the tetragonurids is very poorly known. In general it seems to approximate the distribution of the nomeids (Fig. 54).

Ariommidae. The family Ariommidae, a nomeid derivative, is found mainly in tropical waters (Fig. 55). One deep-bodied species occurs off South Africa. All members of the single genus *Ariomma* seem to be engybenthic in deep water over continental shelves or near islands. The deep-bodied and elongate forms of *Ariomma* occur together in the New World, but tend to be allopatric elsewhere. Apparently there are no representatives on the west coast of Central America, although the genus is widespread throughout the Gulf of Mexico and the Caribbean, and elongate species occur in Hawaii. The latter are undoubtedly derived from Japanese forms. The most advanced species in the genus, *A. indica*, is a deep bodied silvery species with cusped teeth, found from the Gulf of Iran throughout the East Indian region to the East China Sea. No ariommids occur in Australia or New Zealand.

Stromateidae. The stromateid distribution is characterized by continuity, widespread species, restriction to continental shelves, a trans-Isthmian genus in the New World, and allopatry of genera. The distributions of each of the three genera (Fig. 56) are more or less continuous. In *Stromateus*, one species is found from the Mediterranean to South Africa. *Stromateus* is the only genus that has managed to cross an ocean. This has been accomplished across the shortest possible gap, from Africa to South America, and in the direction of the prevailing winds and currents. The advanced *Stromateus* of the east and west coasts of southern South America are very little differentiated from one another, and may be speciating at the present time. The genus *Peprilus*, apparently derived from *Stromateus* through a species such as the west coast *P. snyderi*, has spread on both coasts of North America and southward along the east coast of South America to Uruguay, where it occurs sympatrically with *Stromateus*. This is the only place where two stromateid genera are found to-

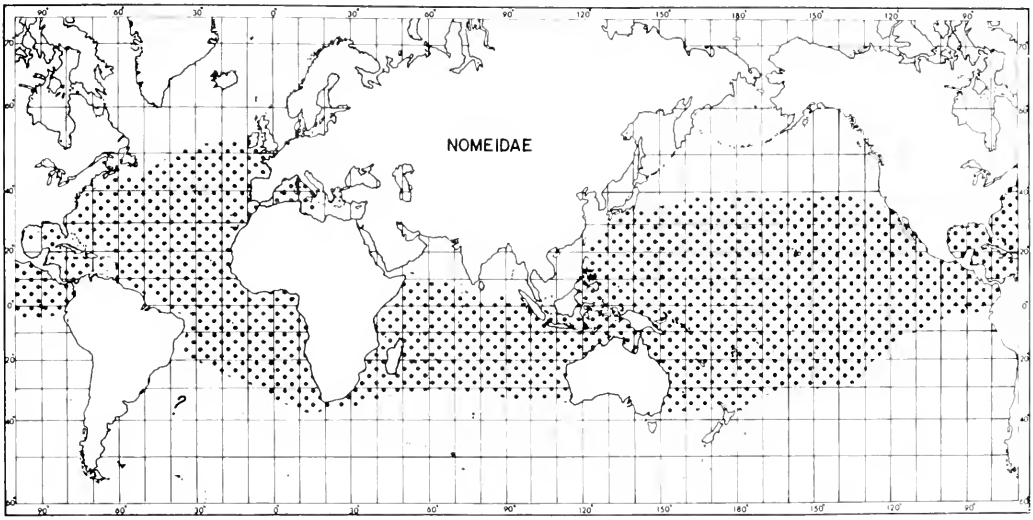


Figure 54. Distribution of the Nomeidae: *Cubiceps, Nomeus,* and *Psenes.*

gether. The most advanced stromateid genus, *Pampus*, occurs from the Gulf of Iran to Japan. Both an advanced species, *P. argenteus*, and a more primitive species, *P. chinensis*, occur through most of the East Indian region. No stromateids have crossed Wallace's line into Australia or New Zealand.

Discussion. The two most recently evolved families are the ariommids and the stromateids. In the ariommids, a single genus is widespread. Containing two incipient genera, one elongate and one deep-bodied, *Ariomma* has apparently had insufficient time for characteristics worthy of generic division to develop. Three genera have evolved in the stromateids, but in general each genus is restricted to a separate continental area. *Peprilus* has spread in a classical circular pattern, from Pacific South America across the Isthmus of Panama and south to Uruguay, to re-encounter the ancestral *Stromateus* stock. This small region in the western South Atlantic is the only area where stromateid genera occur sympatrically. Speciation is currently active in both families.

The ariommids and the stromateids, in contrast to the other stromateoid families, are restricted to near land. The ariommids live in deep water over the shelves and in the vicinity of Hawaii. The stromateids may prefer quite shallow water, and occur in large schools in wide embayments. Because of this relationship with the land, it is possible to examine and possibly date the emergence of the two families in the light of past tectonic activity.

The present stromateid distribution throughout Asia (but not the Red Sea), the Mediterranean, West Africa, and the New World is strongly suggestive of an ancestral Tethyan distribution. The stromateid ancestor could have been a member of the warm water shelf fauna which extended uninterrupted across this region in Tertiary times. In the Upper Eocene or Oligocene, the emergence of land in the Near East divided this fauna in two. The ancestral stromateid isolated in the East gave rise to *Pampus*; the form in the West was the central *Stromateus* stock. In the Pacific Panamanian region, separated from the southern stock of *Stromateus* by long coastlines unsuitable for stromateids, *Peprilus* evolved. Found today in both oceans, this genus must have been established be-

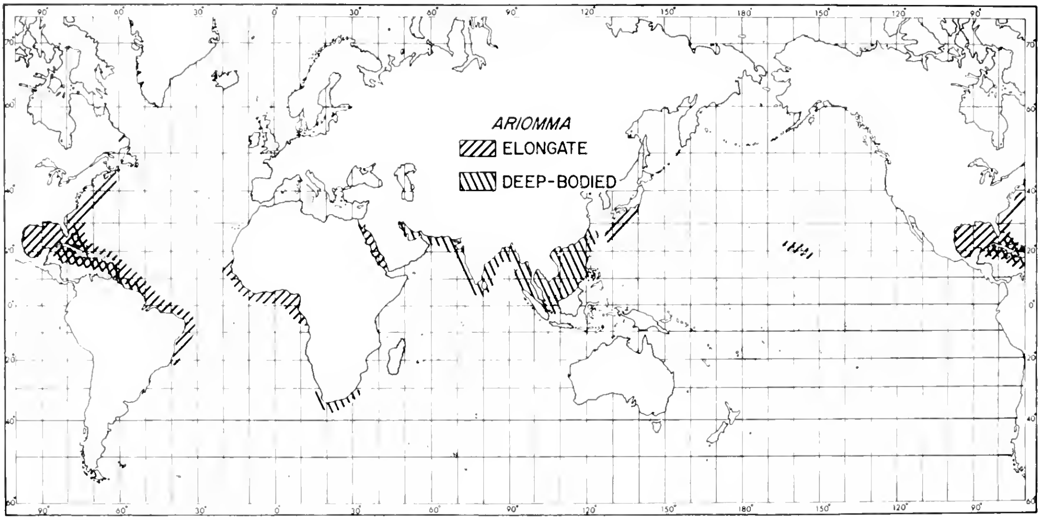


Figure 55. Distribution of the Ariommidae.

fore the emergence of the Isthmus of Panama in the lower Pliocene.

The ariommids are not so tightly bound to the coasts as the stromateids. Oceanic dispersal may be facilitated by pelagic juveniles, a few of which have been taken at Bermuda and in the tropical Central Atlantic. Widespread in the Gulf of Mexico and the Caribbean, no ariommids occur on the west coast of the New World. This suggests at least a late Pliocene dispersal. This fact, plus the remarkable homogeneity of the group and the structure of the pharyngeal sacs and the fused hypural fan, are strong evidence for considering the ariommids the most recently evolved stromateoid fishes.

The remaining stromateoid families, the centrolophids, nomeids, and tetragonurids, are by and large all oceanic. Changes in the configuration of the land would not have affected these fishes as they did the ariommids and stromateids. Since the major ocean basins have probably been a stable feature since well before the Cretaceous, the period of the great flowering of the teleosts, it is unlikely that tectonic activity has been an important isolating mechanism in the evolution of these groups.

The centrolophid distribution bears all the earmarks of an older group. Disjunct distributions, including bipolarity, are characteristic of an old group which has passed its peak. Another indication of the age of the centrolophids is their diversity. There are six genera in the family, and the species inhabit a wide range of environments. In Australia and New Zealand, where no stromateids occur, the advanced centrolophid genus *Seriolella* lives in shallow waters near the coast, the typical stromateid habitat. Numerous ebbs and flows have occurred in the distribution of the centrolophids, for numerous genera are found together. Lacking fossils, it is impossible to date the emergence of the centrolophids. Nonetheless, they certainly antedate the stromateids which had their beginnings in the mid-Tertiary. The centrolophids, then, probably arose in the early Tertiary, or perhaps even in the late Cretaceous.

The nomeids probably arose concurrently with, or perhaps a little after, the centrolophids. The genera occur together throughout the range of the family. Little specific differentiation seems to have developed, although the apparent commonness of circumtropical species in this group may only

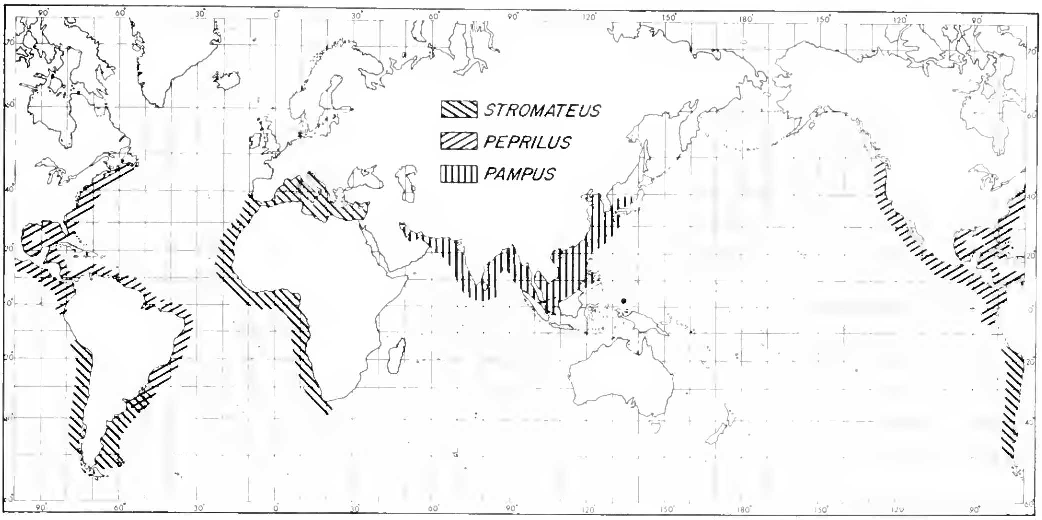


Figure 56. Distribution of the Stromateidae.

reflect the premium placed on a particular phenotype in the rigorous oceanic environment.

The great divergence from the nomeid condition of a derived family, the tetragonurids, suggests that they branched off at an early stage. The tetragonurids have become very specialized, and may be an evolutionary dead-end. There are apparently only three species in the single genus.

Two general features of the stromateoid distributions are of interest. The first is the tendency for the more primitive taxa to be found in higher latitudes. Included in this group are: *Centrolophus*, *Icichthys*, *Hyperoglyphe antarctica*, *Stromateus* in the New World, and, perhaps, the giant nomeid *Cubiceps capensis*. The Ariommidae and Stromateidae, both advanced, have not reached the Australian region. The second feature is that the most advanced or most recently evolved taxa have their centers of distribution in the East Indian region. Examples are the centrolophid genus *Psenopsis*, the stromateid genus *Pampus*, and the ariommid *Ariomma indica*.

ACKNOWLEDGEMENTS

In the course of this study I have been supported by an Emerson Fellowship from Harvard University and a Summer Fellowship and Predoctoral Fellowship from the Woods Hole Oceanographic Institution. The National Science Foundation sponsored my participation on Cruise 6 of the ANTON BRUUN, as a part of the U. S. Program in Biology, International Indian Ocean Expedition, and also permitted me to visit Japan under the joint U. S.–Japan Cooperative Program in Science (GF-147 to Harvard University). Funds from the Harvard Committee on Evolutionary Biology covered my visits to natural history museums in Washington, London, Paris, and Copenhagen. Incidental support has been derived from National Science Foundation Grant GB-543 to the Woods Hole Oceanographic Institution.

This study would not have been possible without the kind cooperation of numerous curators who have freely sent me specimens from far-flung collections. For these services my thanks go to Frank J. Talbot of the Australian Museum, Sydney; William J. Richards of the Bureau of Commercial Fisheries Biological Laboratory, Washington, D. C.; Alfred W. Ebeling of the Bingham Oceanographic Laboratory, Yale University; Frank Williams of the Guinean Trawling Survey, Lagos; M. J. Penrith of the South African Museum, Capetown; George S. Myers of the Natural History Museum, Stanford University; Richard H. Rosenblatt and Joseph F. Copp of the Scripps Institution of Oceanography, La Jolla; Werner Ladiges, Zoologisches Museum, Hamburg; and Jørgen G. Nielsen of the Zoological Museum, Copenhagen. On my visits to various institutions, which also supplied specimens for the study, I received the very best of treatment from James Tyler of the Academy of Natural Sciences of Philadelphia; C. C. Lindsey and Norman J. Wilimovsky of the University of British Columbia, Vancouver; P. H. Greenwood and A. C. Wheeler of the British Museum (Natural History), London; Loren P. Woods, Marion Grey, and Pearl Sonoda of the Chicago Museum of Natural History; M. Bauchot and M. Blanc of the Muséum National d'Histoire Naturelle, Paris; and Daniel M. Cohen, Bruce B. Collette, Robert H. Gibbs, Jr., Nathaniel Gramblin, and Leonard P. Schultz of the United States National Museum, Washington, D. C. Frank J. Mather, III of the Woods Hole Oceanographic Institution allowed me free access to collections made in connection with his pelagic fish studies and also examined the types of *Seriolella* in Paris. Especial thanks go to Erik Bertelsen of the Danish Carlsberg Foundation who provided the nucleus of specimens which initiated this study and who has encouraged it throughout, and to Tokiharu Abe who provided numerous Japanese specimens, who has increased my understanding through discussions, and who was to me a most gracious host during my stay in his country. Especial thanks also go to the staff of the Museum of Comparative Zoology—particularly Myvanwy M. Dick, Josie DeFalla, Elaine Kelley, and Charles Karnella—and to the staff of the Marine Biological Laboratory Library—particularly Jane Fessenden—for help cheerfully given.

I gratefully acknowledge the particular services rendered by a number of people, all friends and colleagues at the Woods Hole Oceanographic Institution. Louise Russell made the drawings of the gill arches and pharyngeal sacs. Clifford Hinton, Jr. made the final plates, and through discussion gave me much insight into the problems of photographic reproduction and of technical illustration. Barbara Jones, Martin Bartlett, and George Grice have been good listeners, and have lent assistance at many points. James Craddock has criticized parts of the manuscript, in particular the keys. And Jane Peterson has never faltered in her cheerful typing, retyping, and typing again of the manuscript.

Finally, I owe a special debt of thanks to two people who have discussed, criticized, and encouraged this work in all of its stages. The first of these is Richard H. Backus, Senior Scientist at the Woods Hole Oceanographic Institution. The second is Giles W. Mead, Curator of Fishes at the Museum of Comparative Zoology, my adviser at Harvard University, and the person who first introduced me to the stromateoid fishes.

SUMMARY

Known to the ancients, and investigated by such able ichthyologists as Günther, Gill, and Regan, the development of the stromateoid classification has a long history. Only recently, however, has sufficient material become available to clarify the confusion surrounding the systematics of these fishes.

The perciform suborder Stromateoidei is diagnosed by the possession of toothed pharyngeal sacs and small uniserial teeth in the jaws. Comparative study of the nature of the pelvic and dorsal fins, the tooth pattern, the number of vertebrae and branchiostegal rays, and, in particular, the structure of the caudal skeleton and the pharyngeal sacs suggests a separation of the suborder into five families and fourteen genera. These are: Centrolophidae—*Hyperoglyphe*, *Schedophilus*, *Centrolophus*, *Icichthys*, *Seriolella*, *Psenopsis*; Nomeidae—

Cubiceps, *Nomeus*, *Psenes*; Ariommidae (fam. nov.)—*Ariomma*; Tetragonuridae—*Tetragonurus*; and Stromateidae—*Stromateus*, *Peprilus*, *Pampus*. The Centrolophidae are the most primitive in the suborder, and have given rise directly to the Stromateidae. The Nomeidae have evolved parallel to the centrolophid–stromateid line, and have given rise to the Tetragonuridae and the Ariommidae.

Within the suborder, evolutionary trends from the generalized to the highly evolved condition are marked. The maximum size attained becomes smaller, and, in the stromateids, the relative depth of the body increases. The pelvic fins are lost. The mouth becomes smaller, the jaw teeth become cusped, and the palatine dentition may be lost. The pharyngeal sacs become more elongate and the structure of the papillae within them becomes more complex. The number of branchiostegal rays is reduced from seven to five. The pseudobranch is lost. The vertebrae increase in number from a basic 25. The number of elements in the caudal skeleton is reduced through losses and fusions.

The major features of the centrolophid distribution are discontinuity, bipolarity, endemism, and sympatry of genera. Four of the six genera occur in Australia and New Zealand. The three nomeid genera are broadly sympatric in temperate and tropical oceans, and there are no relicts, no bipolarity, and no regional endemism. The tetragonurid distribution is very poorly known, but is similar to that of the nomeids. The ariommids are found in deep water over the edge of the continental shelves from the east coast of the New World to Japan, and near Hawaii. The stromateid distribution is characterized by discontinuity, widespread species, restriction to continental shelves, and allopatry of genera. None occur in Australia and New Zealand. The distributional data support the conclusions based on comparative morphology.

The relationships and natural history of the stromateoid taxa are discussed. Synonymies, keys, and, under each genus, lists of nominal species are included.

LITERATURE CITED

Abe, Tokiharu. 1953. New, rare or uncommon fishes from Japanese waters. II. Records of rare fishes of the families Diretmidae, Luvaridae, and Tetragonuridae, with an appendix (description of a new species, *Tetragonurus pacificus*, from off the Solomon Islands). Jap. J. Ichthyol., **3**(1):39–47, 7 figs.

———. 1954. New, rare, or uncommon fishes from Japanese waters. V. Notes on the rare fishes of the suborders Stromateoidei and Tetragonuroidei (Berg). Jap. J. Ichthyol., **3**:222, 246, 255.

———. 1955. New, rare, or uncommon fishes from Japanese waters. V. Notes on the rare fishes of the suborders Stromateoidei and Tetragonuroidei (Berg). Jap. J. Ichthyol., **4**:113–118.

———. 1955a. Notes on the adult of *Cubiceps gracilis* from the western Pacific. J. Oceanogr. Soc. Japan, **11**(2):75–80.

———. 1963. Unusual occurrences of several species of boreal, amphipacific and bathypelagic fishes in Sagami Bay and adjoining waters during the first half of 1963, a coldwater season in southern Japan. Bull. Tokai Reg. Fish. Res. Lab., No. 37:27–35.

Abe, T., S. Kojima, and T. Kosakai. 1963. Description of a new nomeid fish from Japan. Jap. J. Ichthyol., **9**(1/2):31–35.

Abe, T., and Toshio Kosakai. 1964. Notes on an economically important but scientifically little-known silver pomfret, *Pampus echinogaster* (Pampidae, Teleostei). Jap. J. Ichthyol., **12**(1/2):29–31.

Agassiz, Louis. 1846. Nomenclatoris Zoologici. Index universalis continens nomina systematica classium, ordinum, familiarum et generum animalium omnium, tam viventium quam fossilium. Soloduri, Jent and Gassman, 393 pp.

Alcock, Alfred William. 1890. On the bathybial fishes collected in the Bay of Bengal during the season 1889–1890. Ann. Mag. Nat. Hist., Ser. 6, **6**:197–222.

———. 1892. Illustrations of the zoölogy of H. M. Indian marine surveying steamer "Investigator," under the command of Comm. A. Carpenter and Comm. R. F. Hoskyn. Part 1, Fishes, 7 pls. Calcutta.

Aldrovandi, Ulisse. 1613. De Piscibus libri V, et de Cetis liber unus. Bononiæ, fol., 765 pp.

Apsangikar, D. K. 1953. The systematic position of *Stromateus niger*. J. Univ. Bombay, N. S., **21**B(5):41–50, 32 figs.

Arambourg, Camille. 1954. Les poissons crétacés du Jebel Tselfat (Maroc). Not. Mém. Serv. Geol. Maroc., No. 118:1–185.

Ariola, V. 1912. Nuovo pesce abissale del Golfo di Genova (*Cubiceps capensis* (Smith)). Riv. Mens. Pesca, Pavia, **7**(14):185–192.

Ayres, William O. 1860. [On new fishes of the Californian coast.] Proc. Calif. Acad. Nat. Sci., 1st Ser., **2**:81–86.

Barnard, K. H. 1927. A monograph of the marine fishes of South Africa, Part II. Ann. S. Afr. Mus., **21**(2):419–1065.

———. 1948. Further notes on South African marine fishes. Ann. S. Afr. Mus., **36**:341–406, 4 pls.

Basilewsky, Stephanus. 1855. Ichthyographia Chinae Borealis. Nouv. Mém. Soc. Nat. Moscou, **10**:215–264, 9 pls.

Bean, Tarleton H. 1912. Description of new fishes of Bermuda. Proc. Biol. Soc. Washington, **25**:121–126.

Beaufort, L. F. de and W. M. Chapman. 1951. The fishes of the Indo-Australian Archipelago. IX. Percomorphi (concluded), Blennoidea. Leiden, E. J. Brill, xi + 484 pp., 89 figs.

Belloc, Gerard. 1937. Note sur un poisson comestible nouveau de la côte occidentale d'Afrique. (*Paracubiceps ledenoisi* nov. gen., nov. sp.). Rev. Trav. l'Office Pèches Marit., **10**(3):353–356. 4 figs.

Belon, Pierre. 1553. De Aquatilibus Libri ii. Cum eiconibus ad vivam ipsorum effigiem, quoad eius fieri potuit, expressis. Paris, 448 pp.

Bennett, Edward Turner. 1831. [Characters of new genera and species of fishes of the Atlantic coast of northern Africa presented by Capt. Belcher.] Proc. Zool. Soc. London, 1831:146–148.

Berg, Lev Semënovich. 1940. Classification of fishes both recent and fossil. Trav. Inst. Zool. Acad. Sci. U.R.S.S., Leningrad, **5**:87–517, 190 figs. [In Russian with complete English translation. Reprint 1947, Edwards Brothers, Ann Arbor.]

———. 1955. Classification of fishes and fish-like vertebrates, both living and fossil. Second edition. Trudy Zool. Inst. Akad. Sci. SSSR, **20**:1–286, figs. 1–263. [In Russian.]

Bertin, Louis, and Camille Arambourg. 1958. Super-ordre des Téléostéens *in* P. P. Grassé *et al.*, Traité de Zoologie, vol. 13. Paris. Masson et Cie. 2758 pp.

Besednov, L. N. 1960. Some data on the ichthyofauna of the Pacific Ocean driftwood. Trudy Inst. Okean. Akad. Nat. Sci. SSSR, **41**: 192–197. [In Russian.]

Bigelow, Henry Bryant and William C. Schroeder. 1953. Fishes of the Gulf of Maine. Fish. Bull. 74. Fish. Bull. U. S. Fish and Wildlife Serv., **53**:1–577.

Blache, J. 1962. Liste des poissons signalés dans l'Atlantique Tropico-Oriental Sud—du Cap des Palmes (4° Lat. N) à Mossamedes (15° Lat. S) (Province Guinéo-Equatoriale). Trav. Centre Ocean, de Point-Noire, O.R.S.T.O.M. 1962. Pp. 13–106.

Blacker, R. W. 1962. Rare fishes from the Atlantic Slope fishing grounds. Ann. Mag. Nat. Hist., Ser. 13, **5**:261–271.

Bleeker, Pieter. 1851. Over einige nieuwe geslachten en soorten van Makreelachtige visschen van den Indischen Archipel. Nat. Tijdschr. Neder.-Indië, **1**:341–372.

———. 1852. Bijdrage tot de kennis der Makreelachtige visschen van den Soenda-Molukschen Archipel. Verh. Batav. Genootsch., **24**: 1–93.

———. 1859. Enumeratio specierum piscium hucusque in Archipelago Indico observatarum. Act. Soc. Sci. Indo-Neerl., **6**:1–276.

Blegvad, J. and B. Løppenthin. 1944. Fishes of the Iranian Gulf. Danish scientific investigations in Iran, Part III:1–247, 10 pls.

Bloch, Marc Elieser. 1793. Naturgeschichte der Ausländischen Fische, Siebenter Theil. Berlin, J. Morino & Comp., 144 pp.

———. 1795. Naturgeschichte der Ausländischen Fische, Neunter Theil. Berlin, J. Morino & Comp., 192 pp.

Bloch, M. E. and J. G. Schneider. 1801. Systema ichthyologiae iconibus ex illustratum. Post obitum auctoris opus inchoatum absolvit, correxit, interpolavit Jo. Gottlob Schneider, Saxo. Berolini, 584 pp., 110 pls.

Bonaparte, Charles Lucien. 1837. Iconografia della fauna italica, per le quattro classi degli animali vertebrati. Tome III, part 2, Pesce. Roma.

———. 1846. Catalogo metodico dei pesci Europei. Napoli, 97 pp.

Bonde, Niels. 1966. The fishes of the Mo-Clay Formation (Lower Eocene). Medd. Dansk Geol. Foren., **16**:198–202.

Borodin, Nicholas. 1930. Some more new deep-sea fishes. Proc. New England Zool. Club, **11**:87–92.

Boulenger, George Albert. 1904. Teleostei (Systematic Part). The Cambridge Natural History, vol. 7:539–727, figs. 325–440. London, Macmillan & Co.

Bühler, Hermann. 1930. Die Verdauungsorgane der Stromateidae (Teleost). Zeitschr. Morphol. Ökolog. Tiere, **19**:59–115, 29 figs.

Caldwell, David K. 1961. Populations of the butterfish, *Poronotus triacanthus* (Peck), with systematic comments. Bull. S. Calif. Acad. Sci., **60**(1):19–31, 4 pls.

CANESTRINI, GIOVANNI. 1865. Sopra alcuni pesci poco noti o nuovi del Mediterraneo nota. Mem. R. Accad. Sci. Torino, Ser. 2, **21**:359–367, 2 pls.

CARMICHAEL, CAPT. DUGALD. 1818. Some account of the Island of Tristan da Cunha and of its natural productions. Trans. Linn. Soc. London, **12**:483–513.

CASTELNAU, FRANCIS L. 1872. Contributions to the ichthyology of Australia. Proc. Zool. Acclim. Soc. Victoria, **1**:29–247.

CETTI, FRANCESCO. 1777. Historia naturale di Sardagni. Pesci, pp. 71–208. Sassari.

CHABANAUD, P. 1930. Description d'un nouveau *Cubiceps* (Pisces Stromateidae) de la Mer Rouge. Bull. Mus. Hist. Nat. Paris, 2e Ser., **2**:519–523.

CHABANAUD, P. AND G. TREGOUBOFF. 1930. Observations morphologiques et biologiques sur un *Centrolophus niger* Gmelin, ayant veçu dans l'aquarium de Villefranche-sur-mer. Bull. Soc. Zool. France, **55**:479–484.

CHOPRA, SHASHI. 1960. A note on the sudden outburst of ctenophores and medusae in the waters off Bombay. Current Science, October 1960, **29**:392–393.

CHU, Y. T. *et al.* 1962. The fishes of South China Sea. Peking, xii + 1184 pp. [In Chinese.]

———. 1963. The fishes of East China Sea. Peking, xxviii + 642 pp. [In Chinese.]

CLEMENS, W. A. AND G. V. WILBY. 1961. Fishes of the Pacific Coast of Canada. Second Edition. Fish. Res. Bd. Canada, Bull. No. 68. 443 pp.

CLOTHIER, CHARLES R. 1950. A key to some southern California fishes based on vertebral characters. Calif. Fish. Bull., No. 79:1–83, 23 pls.

COCCO, ANASTASIO. 1838. Su di alcuni salmonidi del mare di Messina; lettera al Ch. D. Carlo Luciano Bonaparte. Nuovi Ann. Sci. Nat., Bologna, **2**:161–194.

———. 1839. Sopra un nuovo genere di pesci della famiglia de' Centrolofini e di una nuova specie di *Trachurus*. Innom. Messina, **3**(7): 56–59.

———. 1840. Su di alcuni nuovi pesci del mare di Messina. Maurolico, Messina, **4**:236–244.

COLLETT, ROBERT. 1896. Poissons provenants des campagnes du yacht l'Hirondelle (1885–88). Res. Camp. Sci. Monaco, Fasc. X, viii + 198 pp.

COLLETTE, BRUCE BADEN. 1963. The systematic status of the Gulf of Mexico butterfish, *Poronotus burti* (Fowler). Copeia, 1963(3):582–583.

CORNISH, THOMAS. 1874. *Pimelepterus Cornubiensis*, a supposed new fish, at Penzance. The Zoologist, Ser. 2, **9**:4255–4258.

COSTA, ORONZIO GABRIELE. 1866. Illustrazione di un centrolofo pescato nel Golfo di Napoli. Ann. Mus. Zool. Napoli, **6**:84–87.

COUCH, JONATHAN. 1863. A history of the fishes of the British Islands. Vol. II. London, Groombridge & Sons, iv + 265 pp., 63 pls.

COWPER, T. R. 1960. Occurrence of *Pyrosoma* on the continental slope. Nature, **187**:878–879.

CUNNINGHAM, J. T. 1910. On the marine fishes and invertebrates of St. Helena. With descriptions of new species of Hydrozoa and Porifera by R. Kirkpatrick. Proc. Zool. Soc. London, 1910:86–130. 3 pls.

CUVIER, GEORGES. 1817. Le regnè animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Edition I. Tome II, Poissons. Paris, 532 pp.

———. 1829. Le regnè animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Edition II. Tome II, Poissons. Paris, 406 pp.

CUVIER, GEORGES AND ACHILLE VALENCIENNES. 1833. Histoire naturelle des poissons. Tome IX. Paris, 512 pp.

DAHL, GEORGE. 1823. Coleoptera und Hymenoptera. Ein systematisches Verzeichniss, etc. Wien, 105 pp.

DAY, FRANCIS. 1870. On the fishes of the Andaman Islands. Proc. Zool. Soc. London, 1870:677–705.

———. 1875. The fishes of India, being a natural history of the fishes known to inhabit the seas and fresh waters of India, Burma, and Ceylon. Vol. I, Text, xx + 778 pp. Vol. II, Atlas, 198 pls.

DEKAY, JAMES ELLSWORTH. 1842. Zoology of New York, or the New York fauna. Comprising detailed descriptions of all the animals hitherto observed within the state borders. Class V. Fishes. Natural History of New York Geological Survey, Part I. Zoology. Albany, 415 pp., 79 pls.

DIEUZEIDE, R. AND J. ROLAND. 1955. Sur un Stromateidae nouveau du genre *Cubiceps*. Bull. Sta. Aquic. Pèche, Castiglione (N.S.), **7**: 341–368, 1 pl.

DOUMET, NAPOLEON. 1863. Description d'un nouveau genre de poissons de la Méditerranée. Rev. Mag. Zool., 2e serie, **15**:212–223, 1 pl.

DUARTE-BELLO, PEDRO PABLO. 1959. Catalogo de peces cubanos. Univ. Villaneuva Monografia **6**:1–208.

EIGENMANN, C. H. 1902. Description of a new oceanic fish found off southern New England. Bull. U. S. Fish Comm., **21**:35–37.

EMERY, CARLO. 1882. Contribuzioni all'Ittiologia. IV. Sulle candizimi di vita di giovani individui de *Tetragonurus cuvieri.* Mittheil. Zool. Stat. Neapel., **3**:281–282.

Euphrasen, Bengt Anders. 1788. Beskrifning på tremne fiskar. Vetensk. Akad. Nya Handl. Stockholm, **9**:51–55.

Evermann, B. W. and T. H. Shaw. 1927. Fishes from eastern China, with descriptions of new species. Proc. Calif. Acad. Sci., Ser. 4, **16**(4):97–122.

Fabricius, Johann Christian. 1798. Supplementum, J. C. Fabricii . . . Entomologia systematica emendata et aucta . . . adjectis synonymis, locis, observationibus, descriptionibus. Hafniæ, 572 pp.

FAO. 1964. Yearbook of fishery statistics. Catches and landings. Vol. 16. Food and Agriculture Organisation of the United Nations. Rome.

Filippi, Filippo de and J. B. Verany. 1859. Sopra alcuni pesci nuovi o poco noti del Mediterraneo. Mem. R. Accad. Sci. Torino, Ser. 2, **18**:187–199.

Fitch, John E. 1949. Some unusual occurrences of fish on the Pacific Coast. Calif. Fish and Game, **35**(1):41–49.

———. 1951. Notes on the squaretail, *Tetragonurus cuvieri.* Calif. Fish and Game, **37**(1):55–59.

———. 1952. Toxicity and taxonomic notes on the squaretail, *Tetragonurus cuvieri.* Calif. Fish and Game, **38**(2):251–252.

Fordice, Morton W. 1884. A review of the American species of Stromateidae. Proc. Acad. Nat. Sci. Philadelphia, 1884:311–317.

Fowler, Henry Weed. 1906. New, rare or little known scombroids, no. 3. Proc. Acad. Nat. Sci. Philadelphia, **58**:114–122, 3 figs.

———. 1923. New or little known Hawaiian fishes. Occ. Pap. Bernice P. Bishop Mus. Honolulu, **8**:375–392.

———. 1928. The fishes of Oceania. Mem. Bernice P. Bishop Mus. Honolulu, **10**:1–540, 49 pls.

———. 1930. The fishes obtained by Mr. James Bond at Grenada, British West Indies, in 1929. Proc. Acad. Nat. Sci. Philadelphia, **82**:269–277, 2 figs.

———. 1931. The fishes of Oceania—Supplement 1. Mem. Bernice P. Bishop Mus. Honolulu, **11**(5):311–381.

———. 1934. The fishes of Oceania—Supplement 2. Mem. Bernice P. Bishop Mus. Honolulu, **11**(6):383–466.

———. 1934a. Fishes obtained by Mr. H. W. Bell-Marley chiefly in Natal and Zululand in 1929 to 1932. Proc. Acad. Nat. Sci. Philadelphia, **86**:405–514, 53 figs.

———. 1934b. Zoological results of the third de Schauensee Siamese Expedition. Part I, Fishes. Proc. Acad. Nat. Sci. Philadelphia, **86**:67–163.

———. 1936. The marine fishes of West Africa, based on the collection of the American Museum Congo Expedition, 1909–1915. Part II. Bull. Amer. Mus. Nat. Hist., **80**(2): 609–1493.

———. 1938. The fishes of the George Vanderbilt South Pacific Expedition, 1937. Monogr. Acad. Nat. Sci. Philadelphia, **2**:1–349, 12 pls.

———. 1939. Ichthyological notes, No. 1. Notulae Naturae, No. 3:1–2.

———. 1941. A list of the fishes known from the coast of Brazil. Arquiv. Zool. Estad. São Paulo, **3**(6):115–184.

———. 1944. Fishes of Chile. Systematic catalog. Rev. Chil. Hist. Nat., **46**:15–116.

———. 1944a. Results of the fifth George Vanderbilt Expedition, 1941. The fishes. Monogr. Acad. Nat. Sci. Philadelphia, **6**:57–529, 20 pls.

———. 1944b. Description of a new genus and a new species of American stromateid fishes. Notulae Naturae, No. 142:1–4, 2 figs.

———. 1949. The fishes of Oceania—Supplement 3. Mem. Bernice P. Bishop Mus. Honolulu, **12**(2):35–186.

Franca, P. da. 1957. Contribução para o conhecimento dos Stromateidae de Angola. Anais, Jta. Invest. Ultramar, Lisboa, **12**(2): 7–26, 2 pls.

Fraser-Brunner, A. 1935. New or rare fishes from the Irish Atlantic slope. Proc. Roy. Irish Acad., **42B**:319–326, 5 figs.

Freihofer, Warren C. 1963. Patterns of the ramus lateralis accessorius and their systematic significance in teleostean fishes. Stanford Ichthyol. Bull., **8**(2):81–189.

Garman, Samuel F. 1896. Report on the fishes collected by the Bahama Expedition of the State University of Iowa, under Prof. C. C. Nutting in 1893. Bull. Lab. Nat. Sci. Univ. Iowa, **4**(1):76–93.

Geinitz, Hans Bruno. 1868. Die fossilen Fischschuppen aus dem Pläner-Kalke von Strehlen. Denkschr. Ges. Natur- und Heilk. Dresden, 1868:31–56, 4 pls.

Gesner, Conrad. 1560. Nomenclator aquatilium animantium. Icones animalium aquatilium in mari & dulcibus aquis degentium, plus quam DCC cum nomenclaturis singulorum Latinis, Grecis, Italicis, Hispanicis, Gallicis, Germanicis, Anglicis, alij'sq; interdum, per certos ordines digestae. 374 pp.

Gilbert, Charles Henry. 1904. Notes on fishes from the Pacific Coast of North America. Proc. Calif. Acad. Sci., Ser. 3, Zool., **3**:255–271.

Gilbert, C. H. and E. C. Starks. 1904. The fishes of Panama Bay. Mem. Calif. Acad. Sci., **4**:1–403, 33 pls.

Gilchrist, J. D. F. 1922. Note on the oesophageal teeth of the Stromateidae. Ann. Mag. Nat. Hist., Ser. 9, **9**:249–255.

Gilchrist, J. D. F. and C. von Bonde. 1923. The Stromateidae (Butter Fishes) collected by the S. S. "Pickle." Rep. Fish. Mar. Biol. Survey Union of S. Afr. Capetown. Rep. No. 3, Spec. Rep. No. 4:1–12.

Gill, Theodore Nicholas. 1860. Notes on the nomenclature of North American fishes. Proc. Acad. Nat. Sci. Philadelphia, **11**:20–21.

———. 1861. Catalogue of the fishes of the eastern coast of North America, from Greenland to Georgia. Proc. Acad. Nat. Sci. Philadelphia, **13** (supplement):1–63.

———. 1862. On the limits and arrangements of the family of scombroids. Proc. Acad. Nat. Sci. Philadelphia, **14**:125–127.

———. 1884. Notes on the Stromateidae. Proc. Amer. Phil. Soc., **21**(116):664–672.

Ginsburg, Isaac. 1954. Four new fishes and one little known species from the east coast of the United States including the Gulf of Mexico. J. Wash. Acad. Sci., **44**:256–264, 6 figs.

Gmelin, Johann Frederick. 1788. Caroli a Linné . . . Systema naturæ per regne triæ naturæ, secundum classes, ordines, genera, species, cum characteribus, differentis, synonymis, locis. Lipsiæ. Vol. 1:1–1516.

Goode, George Browne and Tarleton H. Bean. 1896. Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers BLAKE, ALBATROSS, and FISH HAWK in the northwestern Atlantic, with an atlas, containing 417 figures. Smithsonian Institution, United States National Museum, Special Bull. No. 2. Washington, Government Printing Office, xxxv + 553 pp.

Gosline, William A. 1959. Mode of life, functional morphology, and the classification of modern teleostean fishes. Syst. Zool., **8**:160–164.

———. 1960. Contributions toward a classification of modern isospondylous fishes. Bull. Brit. Mus. Nat. Hist., (Zoology), **6**(6):325–365, 15 figs.

———. 1961. Some osteological features of modern lower teleostean fishes. Smithsonian Misc. Coll., **142**(3):1–42, 6 figs.

———. 1961a. The perciform caudal skeleton. Copeia, 1961(3):265–270, 3 figs.

Gosline, W. A. and Vernon E. Brock. 1960. Handbook of Hawaiian fishes. Honolulu, University of Hawaii Press, ix + 372 pp.

Gregory, William K. 1907. The orders of teleostomous fishes. Ann. New York Acad. Sci., **17**:437–508.

———. 1933. Fish skulls: a study of the evolution of natural mechanisms. Trans. Amer. Phil. Soc., **23**:75–481, 302 figs.

———. 1951. Evolution Emerging. New York, Macmillan, 2 vols. 1013 pp.

Grey, Marion. 1955. The fishes of the genus *Tetragonurus* Risso. DANA-Report No. 41: 1–75, 16 figs.

Griffin, L. T. 1928. Studies in New Zealand fishes. Trans. Proc. New Zealand Inst. Wellington, **59**:374–388, 9 pls.

Günther, Albert. 1859. Catalogue of the acanthopterygian fishes in the collection of the British Museum. Volume First. London, Taylor and Francis, xxxi + 524 pp.

———. 1860. Catalogue of the acanthopterygian fishes in the collection of the British Museum. Volume Second. London, Taylor and Francis, xxi + 548 pp.

———. 1860a. On *Centrolophus britannicus*, a new British fish. Ann. Mag. Nat. Hist., Ser. 6, **3**:46–48.

———. 1861. Catalogue of the acanthopterygian fishes in the collection of the British Museum. Volume Third. London, Taylor and Francis, xxv + 586 pp.

———. 1869. Contribution to the ichthyology of Tasmania. Proc. Zool. Soc. London, 1869: 429.

———. 1871. Report on several collections of fishes recently obtained for the British Museum. Proc. Zool. Soc. London, 1871:652–675.

———. 1872. On some new species of reptiles and fishes collected by J. Brenchley, Esq. Ann. Mag. Nat. Hist., Ser. 4, **10**:418–426.

———. 1876. Andrew Garrett's Fische der Südsee, beschreiben und redigirt von A. C. L. G. Günther. Band II. J. Mus. Godeffrey, **4**: 129–260, 67 pls.

———. 1880. An introduction to the study of fishes. Edinburgh, Adam and Charles Black, 720 pp.

———. 1882. Description of a specimen of *Schedophilus medusophagus*, a fish new to the British fauna. Trans. Zool. Soc. London, **11**:223–224.

———. 1889. Report on the pelagic fishes collected by H.M.S. Challenger, during the years 1873–1876. Report on the scientific results of the voyage of H.M.S. Challenger. Zoology, **31**:1–47, plates I–VI.

Guichenot, Alphonse. 1848. Peces de Chile. *In*: Claudio Gay, Historia fisica y politica de Chile. Zoologica. Tomo Segundo. Paris and Santiago, pp. 137–370.

———. 1866. Catalogue des poissons de Madagascar de la collection du Musée de Paris.

avec la description de plusieurs espèces nouvelles. Mém. Soc. Sci. Nat. Cherbourg, **12**:129–148.

———. 1866a. Notice sur un nouvelle espèce de poissons appartenant au genre des rhombes du Muséum de Paris. Mém. Soc. Sci. Nat. Cherbourg, **12**:243–247.

Guiglia, D. 1950. Il *Tetragonurus cuvieri* Risso 1810 nel Golfo di Genova. Ann. Mus. Civ. Stor. Nat. Genova, **64**:158–169.

Haedrich, Richard L. 1965. *Cubiceps athenae*, a new nomeid fish from the western North Atlantic, and its systematic position among stromateoids. Copeia, 1965(4):501–505.

———. In press. The stromateoid fish genus *Icichthys*: notes and a new species. Vidensk. Medd. Dansk Naturh. Foren., **129**.

Harris, J. E. 1938. The role of the fins in the equilibrium of the swimming fish. II. The role of the pelvic fins. J. Exper. Biol., **15** (1):32–47.

Hart, T. John. 1946. Report on trawling surveys on the Patagonian continental shelf. Discovery Reports, **23**:223–408, 1 pl.

Heckel, Johann Jakob. 1856. Neue Beiträge zur Kenntnis der fossilen Fische Oesterreichs. Denkschr. Akad. Wiss. Wien, **11**:187–274, 15 pls.

Herald, Earl S. 1961. Living fishes of the world. Garden City, New York, Doubleday and Co., 304 pp.

Herre, A. W. C. T. 1950. Six additions to the Philippine fish fauna, including two new species. Philipp. J. Sci., **79**:341–346.

———. 1953. Check list of Philippine fishes. Res. Rep. U. S. Fish and Wildlife Service, No. 20:1–977.

Herre, A. W. C. T. and E. S. Herald. 1950. Noteworthy additions to the Philippine fish fauna, including two new species. Philipp. J. Sci., **79**:309–340, 12 figs.

Hildebrand, Samuel Frederick. 1946. Descriptive catalog of the shore fishes of Peru. Bull. U. S. Nat. Mus., No. 189:1–530, 95 figs.

———. MS. The marine fishes of Panama. [Partially completed revision of the earlier work by Meek and Hildebrand, 1925. Stromateidae section obtained from CNHM through Ira Rubinoff.]

Hobbs, Kenneth L. 1929. A new species of *Centrolophus* from Monterey Bay, California. J. Wash. Acad. Sci., **19**(20):460–462.

Hollister, Gloria. 1934. Clearing and dyeing fish for bone study. Zoologica, **12**:89–101, 4 figs.

Holt, E. W. L. and L. W. Byrne. 1903. On the British and Irish species of the family Stromateidae. Rep. Fish. Ireland for 1901, Part 2:70–76.

Hubbs, Carl Leavitt and Karl F. Lagler. 1958. Fishes of the Great Lakes region. Revised Edition. Cranbrook Institute of Science, Bulletin No. 26. Bloomfield Hills, Michigan, xi + 135 pp.

Humphrey, George. 1797. Museum Calonnianum. Specification of the various articles which compose the . . . Museum of Natural History collected by M. de Calonne in France, etc. Part I, 84 pp.

Hutton, Capt. Frederick Wollaston. 1872. Contributions to the ichthyology of New Zealand. Trans. Proc. New Zealand Inst., **5**:259–272.

Isokawa, Sohiti, K. Kubota, T. Kosakai, I. Satomura, M. Tsubouchi and A. Sera. 1965. Some contributions to study of esophageal sacs and teeth of fishes. J. Nihon Univ. Sch. Dent., **7**(3):103–111.

Johnson, James Yate. 1862. Description of some new genera and species of fishes obtained at Madeira. Proc. Zool. Soc. London, 1862:167–180.

Jordan, David Starr. 1923. A classification of fishes including families and genera as far as known. Stanford Univ. Pub., Univ. Ser., Biol. Sci., **3**(2):77–243. Reprint 1963, Stanford University Press.

———. 1923a. Note on *Icichthys lockingtoni* Jordan and Gilbert, a pelagic fish from California. Proc. U. S. Nat. Mus., **63**(2472):1–3, 1 pl.

Jordan, D. S. and Charles Harvey Bollman. 1889. Descriptions of new species of fishes collected at the Galapagos Islands and along the coast of the United States of Colombia, 1887–1888. Proc. U. S. Nat. Mus., **12**:149–183.

Jordan, D. S. and Barton Warren Evermann. 1896. The fishes of North and Middle America; a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. Bull. U. S. Nat. Mus., No. 47:1–1340. Reprint 1963, Smithsonian Institution.

Jordan, D. S., B. W. Evermann and H. W. Clark. 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Appendix X to the Report of the United States Commissioner of Fisheries for the fiscal year 1928. Reprint 1955, Washington, U. S. Govt. Printing Office, 670 pp.

Jordan, D. S. and Charles Henry Gilbert. 1880. Description of a new species of deep-water fish (*Icichthys lockingtoni*) from the coast of California. Proc. U. S. Nat. Mus., **3**:305–308.

———. 1882. Synopsis of the fishes of North America. Bull. U. S. Nat. Mus., No. 16:1–1018.

Jordan, D. S. and C. L. Hubbs. 1925. Records of fishes obtained by D. S. Jordan in Japan, 1922. Mem. Carnegie Mus. Pittsburgh, **10** (2):93–346, 7 pls.

Jordan, D. S. and C. W. Metz. 1913. A catalogue of the fishes known from the waters of Korea. Mem. Carnegie Mus. Pittsburgh, **6** (1):1–65, 10 pls.

Jordan, D. S. and J. O. Snyder. 1904. Notes on the collections of fishes from Oahu Island and Laysan Island, Hawaii, with descriptions of four new species. Proc. U. S. Nat Mus.. **27** (1377):939–948.

———. 1907. Notes on fishes of Hawaii, with descriptions of new species. Dept. Comm. Lab., Bull. Bur. Fish., **26**:205–218, 2 pls.

Jordan, D. S. and W. F. Thompson. 1914. Record of the fishes obtained in Japan in 1911. Mem. Carnegie Mus. Pittsburgh, **6**: 205–313.

Kamohara, Toshiji. 1940. Fauna Nipponica. Scombroidei (exclusive of Carangiformes). Vol. 15, fasc. 2, no. 5, 225 pp. [In Japanese.]

Katayama, Masao. 1952. A record of *Ariomma lurida* Jordan et Snyder from Japan, with notes on its systematic position. Jap. J. Ichthyol., **2**:31–34, 2 figs.

———. 1959. Studies on the serranid fishes of Japan (I). Bull. Fac. Educ., Yamaguchi Univ., **8**(2):103–181.

Kato, K. 1933. Is *Nomeus* a harmless inquilinus of *Physalia*? Proc. Imp. Acad. Japan, **9**(9): 537–538.

Klunzinger, Carl Benjamin. 1884. Die Fische des Roten Meeres. Eine kritische Revision mit Bestimmungs-Tabellen. Teil I. Acanthopteri veri Owen. Stuttgart, 133 pp.

Kner, Rudolf and Franz Steindachner. 1866. Neue Fische aus dem Museum der Herren Joh. C. Godeffroy & Sohn in Hamburg. Sitzungsber. Akad. Wiss. Wien, Abt. 1, **54** (8):356–395.

Lacépède, Bernhard Germain. 1800. Histoire naturelle des poissons. Vol. II. 372 pp.

———. 1802. Histoire naturelle des poissons. Vol. III. 378 pp.

———. 1803. Histoire naturelle des poissons. Vol. IV. 360 pp.

Lane, C. E. 1960. The Portuguese man-of-war. Sci. Amer., **202**(3):158–168, 9 figs.

Larkins, Herbert A. 1964. Some epipelagic fishes of the North Pacific Ocean, Bering Sea, and Gulf of Alaska. Trans. Amer. Fish. Soc., **93**(3):286–290.

Le Danois, Yseult. 1962. Catalogue des types de poissons du Muséum National d'Histoire Naturelle. (Nomeidae, Stromateidae, Apolectidae, Kurtidae.) Bull. Mus. Hist. Nat. Paris, 2^{e} Ser., **35**(3):228–234.

Le Gall, Jean. 1925. Un poisson peu commun: le *Centrolophus britannicus* Günther. Bull. Mus. Hist. Nat. Paris, 2^{e} Ser., **31**(1):288–295, 2 figs.

Legaspi, V. A. 1956. A contribution to the life history of the nomeid fish *Psenes cyanophrys*. Bull. Mar. Sci. Gulf & Carib., **6**:179–199.

Liem, Karel F. 1963. The comparative osteology and phylogeny of the Anabantoidei (Teleostei, Pisces). Illinois Biological Monographs: No. 30. Urbana, University of Illinois Press, v + 149 pp.

Linnaeus, Carl. 1758. Systema Naturae, ed. X, vol. I, 824 pp.

———. 1766. Systema Naturae, ed. XII, vol. I(1), 532 pp.

Lloyd, R. E. 1909. A description of the deep-sea fish caught by the R.I.M.S. ship "Investigator" since the year 1900, with supposed evidence of mutation in *Malthopsis*. Mem. Indian Mus. Calcutta, **2**:139–180, 7 pls.

Lo Bianco, Salvatore. 1909. Notizie biologiche riguardanti specialmente il period di maturità sessuale degli animali del Golfo di Napoli. Mittheil. Zool. Stat. Neapel, **19**(4):513–761.

Longley, William H. and Samuel F. Hildebrand. 1941. Systematic catalogue of the fishes of Tortugas, Florida, with observations on color, habits, and local distribution. Carnegie Inst. Washington Pub., No. 535:1–331, 34 pls.

Lowe, Richard Thomas. 1833. Characters of a new genus *Leirus* and of several species of fishes from Madeira. Proc. Zool. Soc. London, **1**:142–144.

———. 1839. A supplement to a synopsis of the fishes of Madeira. Proc. Zool. Soc. London, **7**:76–92.

———. 1843. Notices of fishes newly observed or discovered in Madeira during the years 1840, 1841, and 1842. Proc. Zool. Soc. London, **11**:81–95.

Lowe, Rosemary H. 1962. The fishes of the British Guiana continental shelf, Atlantic coast of South America, with notes on their natural history. J. Linn. Soc. London, Zool., **44**(301):669–700.

Lozano y Rey, Luis. 1952. Peces fisoclistos. Subserie toracicos. Segunda parte. Ordenes Escombriformes. Mem. Real Acad. Cien. Madrid. Ser. Cien. Nat., **14**:387–703.

Lütken, Chr. 1880. Spolia Atlantica. Bidrag til Kundskab om Formforandringer hos Fiske under deres Væxt og Udvikling, særligt hos nogle af Atlanterhavets Højsøfiske. Dansk. Vidensk. Selsk. Skr., (5)Nat. Math. Afd., 12 (6):409–613, 5 pls.

Macleay, William. 1885. A remarkable fish from Lord Howe Island. Proc. Linn. Soc. New South Wales, **10**:718–720.

Mann, Guillermo. 1953. Sobre le identidad de la "cojinoba" del norte y centro Chile. Invest. Zool. Chil., **2**(1):3.

Mansueti, Romeo J. 1963. Symbiotic behavior between small fishes and jellyfishes, with new data on that between the stromateid, *Peprilus alepidotus*, and the scyphomedusa, *Chrysaora quinquecirrha*. Copeia, 1963(1):40–80.

Marcgrave, George. 1648. Historiae rerum naturalium Brasiliæ libri viii. Liber iv, de Piscibus. Lugduni Batavorum et Amstelodami, 293 pp.

Marchal, E. 1961. Description d'une nouvelle espèce de *Paracubiceps* (Belloc), *Paracubiceps multisquamis* n. sp. (Poisson Téléostéen). Bull. Mus. Hist. Nat. Paris. 2^{e} Ser., **33**(5): 487–491, 2 figs.

Marshall, Tom C. 1964. Fishes of the Great Barrier Reef and coastal waters of Queensland. Sydney, Angus & Robertson, 566 pp.

Maul, G. E. 1964. Observations on young live *Mupus maculatus* (Günther) and *Mupus ovalis* (Valenciennes). Copeia, 1964(1):93–97.

McCulloch, Allen Riverstone. 1911. Report on the fishes obtained by the F.I.S. "Endeavor" on the coasts of New South Wales, Victoria, South Australia, and Tasmania. Part 1. Zoological results of the fishing experiments carried out by F.I.S. "Endeavor" 1909–10 under H. C. Dannevig, Commonwealth Director of Fisheries. Vol. I, Part I:1–87.

———. 1914. Report on some fishes obtained by the F.I.S. "Endeavor" on the coasts of Queensland, New South Wales, Victoria, Tasmania, South and South-Western Australia. Part 2. Zoological results of the fishing experiments carried on by F.I.S. "Endeavor" 1909–10 under H. C. Dannevig, Commonwealth of Fisheries. Vol. II, Part III:75–165.

———. 1923. Notes on fishes from Australia and Lord Howe Island. Rec. Aust. Mus., Sydney, **14**:1–7, 3 pls.

McKenney, Thomas W. 1961. Larval and adult stages of the stromateoid fish *Psenes regulus*, with comments on its classification. Bull. Mar. Sci. Gulf & Carib., **11**(2):210–236.

Mead, Giles W. and Margaret G. Bradbury. 1963. Names of bones. *In*: H. B. Bigelow and W. C. Schroeder, Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res., **1**(3):20–23.

Meek, Seth Eugene and Samuel Frederick Hildebrand. 1925. The marine fishes of Panama. Part II. Publ. Field Mus. Zool. Ser. (Chicago), **15**(226):331–707, 54 pls.

Mees, G. F. 1962. Additions to the fish fauna of Western Australia—3. Fish. Dept. W. Aust., Fish. Bull. No. 9, part 3:23–29.

Merriman, D. 1945. Notes on *Palinurichthys perciformis* and the evidence for its bathypelagic habitat. Trans. Conn. Acad. Arts Sci., **36**:837–848, 1 pl.

Miller, R. R. 1946. Distributional records for North American fishes, with nomenclatorial notes on the genus *Psenes*. J. Wash. Acad. Sci., **36**(6):206–212.

Miller, Robert V. 1964. The morphology and function of the pharyngeal organs in the clupeid *Dorosoma petense* (Günther). Chesapeake Science, **5**(4):194–199.

Minding, Julius. 1832. Lehrbuch der Naturgeschichte der Fische. Berlin, xii + 131 pp., 1 pl.

Miranda-Ribeiro, Alipio de. 1915. Fauna brasiliense, peixes. Tomo V. (Eleutherobranchios aspirophores.) Arch. Mus. Nac. Rio de Janeiro, **17**, about 600 pages, no continuous pagination.

Mitchill, Samuel Latham. 1815. The fishes of New York, described and arranged. Trans. Lit. Phil. Soc. New York, **1**:355–492.

———. 1818. [Supplement to "The fishes of New York . . ."] Amer. Month. Mag., **2**: 241–248.

Moore, Donald. 1962. Development, distribution, and comparison of rudderfishes *Kyphosus sectatrix* (Linnaeus) and *K. incisor* (Cuvier) in the western North Atlantic. Fish. Bull. 196, Fish. Bull. Fish & Wildlife Service, **61**: 451–480.

Moreau, Emile. 1881. Histoire naturelle des poissons de la France. Vol. 2. Paris, 572 pp., 220 figs.

Mori, Tamezo. 1952. Check list of the fishes of Korea. Mem. Hyogo Univ. Agric., Sasayama. Biol. Ser., **1**(3):1–228.

Morton, Alexander. 1888. Description of two new fishes. Pap. Proc. Roy. Soc. Tasmania for 1887:77–78, 1 fig.

Munro, Ian S. R. 1958. Handbook of Australian fishes. No. 29:117–120. Families Lepidopidae, Luvaridae, Centrolophidae, Nomeidae, Tetragonuridae. Australian Fisheries Newsletter, Nov. 1958:17–20.

Myers, George Sprague. 1958. Trends in the evolution of teleostean fishes. Stanford Ichthyol. Bull., **7**(3):27–30.

Nardo, Giovanni Domenico. 1827. Prodromus observationum et disquisitionum, Adriaticæ ichthyologiæ. Giorn. Fis. Chim. Stor. Nat. Pavia, **10**:22–40.

Nichols, John Treadwell and Robert Cushman Murphy. 1922. On a collection of marine fishes from Peru. Bull. Amer. Mus. Nat. Hist., **46**(9):501–516.

———. 1944. A collection of fishes from the

Panama Bight, Pacific Ocean. Bull. Amer. Mus. Nat. Hist., **83**(4):221–260.

NIELSEN, JØRGEN G. 1963. Marine fishes new or rare to the Danish fauna (from the period 1937–1961). Vidensk. Medd. Dansk Naturh. Foren., **125**:147–165.

NOBRE, AUGUSTO. 1935. Fauna marinha de Portugal. Vertebrados I. Descrição do peixes de Portugal. Porto, 547 pp., 77 pls.

NORMAN, JOHN ROXBROUGH. 1937. Coast fishes. Part II. The Patagonian region. Discovery Reports, **16**:1–150, 5 pls.

———. 1957. A draft synopsis of the orders, families and genera of the recent fishes and fish-like vertebrates (excluding Ostariophysi, Scleroparei, Ammodytidae and a few other families, notably Centrarchidae, Percidae, and Cichlidae) covering literature up to 1938, and, as far as it was available to the author, from 1939 to 1944. Brit. Mus. (Nat. Hist.), 649 pp. Unpublished manuscript.

OCHIAI, AKIRA AND KOICHIRO MORI. 1965. Studies on the Japanese butter fish referable to the genus *Psenopsis*. Bull. Misaki Mar. Biol. Inst., Kyoto Univ., No. 8:1–7.

OGILBY, JAMES DOUGLAS. 1893. Description of a new pelagic fish from New Zealand. Rec. Aust. Mus. Sydney, **2**(5):64–65.

———. 1915. On some new or little known Australian fishes. Mem. Queensland Mus. Brisbane, **3**:117–129.

OKADA, Y., K. UCHIDA AND K. MATSUBARA. 1935. Figures and descriptions of Japanese fishes. Tokyo, 425 pp., 166 pls. [In Japanese.]

OSORIO, BALTHAZAR. 1909. Contribução para o conhecimento da fauna bathypelagica visinha das costas de Portugal. Mem. Mus. Bocage, Lisboa, No. 1.

PADOA, EMANUELE. 1956. Centrolophidae, Nomeidae. *In*: Fauna e Flora Golfo di Napoli, Monogr. 38, part III:538–545.

PAPPE, CARL WILHELM LUDWIG. 1854. Synopsis of the edible fishes of the Cape of Good Hope. Capetown, 34 pp.

PARIN, N. V. 1958. Rare pelagic fishes of the northwest part of the Pacific Ocean. (*Taractes steindachneri*, *Palinurichthys japonicus*, and *Centrolophus lockingtoni*.) Voprosy Ikhtiol., **12**(11):162–170. [In Russian.]

PARR, ALBERT EIDE. 1956. On the original variates of taxonomy and their regressions upon size in fishes. Bull. Amer. Mus. Nat. Hist., **110**(5):369–398, 14 figs.

PATTERSON, COLIN. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. Phil. Trans. Roy. Soc. London. Ser. B. Biol. Sci. **247** (739):213–482.

PECK, WILLIAM D. 1804. Description of four remarkable fishes, taken near the Piscataqua in New Hampshire. Mem. Amer. Acad. Arts Sci., **2**(2):46–57.

PELLEGRIN, JACQUES. 1937. Le centrolophe oval, poisson comestible. Bull. Soc. Aq. Pêche, Paris, **44**:33–36.

PETERS, WILHELM CARL HARTWIG. 1869. Über neue oder weniger bekannte Fische des Berliner Zoologischen Museums. Monatsber. Akad. Wiss. Berlin, 1869:703–712.

PETIT, G. AND R. AMAR. 1946. Capture d'un *Tetragonurus cuvieri* Risso à Saint-Tropez (Var.). Bull. Mus. Hist. Nat. Marseille, **6**:34–39.

POEY, FELIPE. 1861. Memorias sobre la historia natural de la Isla de Cuba . . . Habana, vol. 2:337–442.

———. 1868. Synopsis piscium Cubensium. *In*: Repertorio fisico-natural de la Isla de Cuba . . . vol. 2:279–484. Habana. Barcina y Comp.

POLL, M. 1959. Poissons V—Téléostéens acanthoptérygiens (deuxième partie). Rés. Sci. Exped. Oceanogr. Belge Côte Afr. Atlant. Sud., vol. 4, 3B:1–417, 127 figs.

QUOY, J. R. C. AND J. P. GAIMARD. 1824. Voyage autour du monde des corvettes l' "Uranie" et le "Physicienne" pendant les années 1817–20. Zool., part II, Poissons. Paris, pp. 192–401.

RAFINESQUE-SCHMALTZ, C. S. 1810. Caratteri di alcuni nuovi generi e nuove specie de animale e piante della Sicilia. Palermo, 105 pp., 20 pls.

RAMSAY, E. P. AND J. D. OGILBY. 1888. On the genus *Tetragonurus* of Risso. Proc. Linn. Soc. New South Wales, Ser. 2, **3**(1):9–16.

REGAN, CHARLES TATE. 1902. A revision of the fishes of the family Stromateidae. Ann. Mag. Nat. Hist., Ser. 7, **10**:115–131, 194–207.

———. 1913. The classification of the percoid fishes. Ann. Mag. Nat. Hist., Ser. 8, **12**: 111–145.

———. 1914. British Antarctic ("Terra Nova") Expedition, 1910. Zoology I, Fishes, pp. 1–54.

———. 1914a. Diagnoses of new marine fishes collected by the British Antarctic ("Terra Nova") Expedition. Ann. Mag. Nat. Hist., Ser. 8, **13**:11–17.

RICHARDSON, SIR JOHN. 1845. Ichthyology. *In*: John Richardson and John E. Gray, The zoology of the voyage of H.M.S. "Erebus and Terror," under the command of Capt. Sir. J. C. Ross . . . during . . . 1839–43. London, viii + 139 pp., 60 pls.

RISSO, ANASTASE. 1810. Ichthyologie de Nice. Paris, F. Schoell, xxxvi + 388 pp., 51 pls.

———. 1826. Histoire naturelle des principales productions de l'Europe Meridionale, vol. III. Paris, 480 pp.

RONDELET, GULIELMUS. 1554. Libri de piscibus marinis, in quibus veræ piscium effigies expressæ sunt. Lugduni, fol., 620 pp.

ROSSIGNOL, M. AND J. BLACHE. 1961. Sur un poisson Stromateidae nouveau du Golfe de Guinée, *Psenes benardi* nov. sp. Bull. Mus. Hist. Nat. Paris, 2^e Ser., **33**(4):384–386, 1 fig.

RUSSELL, PATRICK. 1803. Descriptions and figures of two hundred fishes collected at Vizagapatam on the coast of Coromandel. Vol. 1. London, vii + 78 pp., 100 pls.

SANZ-ECHEVERRIA, J. 1949. Identificación de los peces de la familia Centrolophidae de España por medio de los otolitos. Real Soc. Esp. Hist. Nat., Tomo Extraordinaire: 151–156.

SAUVAGE, HENRI EMILE. 1879. Mémoire sur la faune ichthyologique de l'île Saint-Paul. Arch. Zool. Expéd. Gen. 1879–1880, **8**:1–46.

SCHNEIDER, JOHANN GOTTLOB. 1784. Sammlung vermischter Abhandlungen zur Aufklärung der Zoologie und der Handlungsgeschichte. Berlin, 348 pp., 1 pl.

SCHWARTZ, FRANK J. 1963. The barrelfish from Chesapeake Bay and the Middle Atlantic Bight, with comments on its zoogeography. Chesapeake Science, 4(3):147–149.

SCOTT, TREVOR D. 1962. The marine and freshwater fishes of South Australia. Adelaide, W. L. Hawes, Government Printer, 338 pp.

SHOJIMA, YOICHI. 1961. On the postlarvae and juveniles of a kind of butterfish, *Psenopsis* sp., accompanying the jellyfishes. Bull. Seikai Reg. Fish. Res. Lab., No. 21:67–74.

SIMPSON, GEORGE GAYLORD. 1953. The major features of evolution. New York, Columbia University Press, 434 pp.

SIVERTSEN, E. 1945. Fishes of Tristan da Cunha, with remarks on age and growth based on scale readings. Res. Norwegian Expedition to Tristan da Cunha 1937–38, Oslo, No. 12: 1–44, 8 pls.

SMITH, ANDREW. 1849. Illustrations from the zoology of South Africa; consisting chiefly of figures and descriptions of objects of natural history collected during an expedition into the interior of South Africa in 1834–36. Vol. IV, Fishes. 31 pls.

SMITH, C. LAVETT AND REEVE M. BAILEY. 1962. The subocular shelf of fishes. J. Morph., **110**(1):1–18.

SMITH, HUGH M. 1907. The fishes of North Carolina. North Carolina Geological and Economic Survey, Vol. II:1–453, 188 figs. Raleigh, E. M. Uzzell & Co.

SMITH, J. L. B. 1934. Marine fishes of seven genera new to South Africa. Trans. Roy. Soc. South Africa, 22:89–100.

———. 1949. The sea fishes of southern Africa. Capetown, Central News Agency, Ltd., South Africa, 550 pp. Rev. ed. 1953, 564 pp.

———. 1949a. The stromateid fishes of South Africa. Ann. Mag. Nat. Hist., Ser. 12, **2**: 839–851.

———. 1953. The genus *Tetragonurus* Risso, 1810. Ann. Mag. Nat. Hist. Ser. 12, **6**:53–66, 1 pl.

———. 1960. Two interesting fishes from South Africa. S. Afr. J. Sci., **56**:91–92, 1 fig.

———. 1961. A new stromateid fish from South Africa, and another new to that area. S. Afr. J. Sci., **57**:158–160.

SOLJAN, TONKO. 1948. Fauna et flora Adriatica. Vol. 1, Pisces. Split, Jugoslavia, 437 pp., 1350 figs.

STARKS, EDWIN CHAPIN. 1906. A collection of fishes made by P. O. Simons in Ecuador and Peru. Proc. U. S. Nat. Mus., **30**:761–800, 2 pls.

STEINDACHNER, FRANZ. 1868. Übersicht der Meeresfische an den Küsten Spanien's und Portugal's. Sitzungsber. Akad. Wiss. Wien, Abt. 1, **57**(3):351–424.

———. 1874. Ichthyologische Beiträge. Sitzungsber. Akad. Wiss. Wien, Abt. 1, **70**(32): 375–390, 1 pl.

STEINDACHNER, F. AND L. DÖDERLEIN. 1885. Beiträge zur Kenntniss der Fische Japans (III). Denkschr. K. Akad. Wiss. Wien, **49**: 171–212, 7 pls.

SUZUKI, KIJOSHI. 1962. Anatomical and taxonomical studies on the carangid fishes of Japan. Rep. Fac. Fish., Pref. Univ. Mie, **4** (2):43–233.

SWAINSON, WILLIAM. 1839. The natural history and classification of fishes, amphibians, and reptiles or monocardian animals. Vol. II. London, vi + 452 pp., 135 figs.

TCHANG, T. L. *et al.* 1955. The fishes of the Gulf of Pechili and Yellow Sea. Peking, 360 pp. [In Chinese.]

TEMMINCK, COENRAAD JACOB AND HERMANN SCHLEGEL. 1850. Pisces (last part). *In*: C. T. E. von Siebold, Fauna Japonica, sive descriptio animalium quae in itinere per Japoniam suscepto annis 1823–30 collegit, notis observationibus et adumbrationibus illustravit P. F. de Siebold. Lugduni Batavorum, pp. 270–324.

TEMPLEMAN, WILFRED AND RICHARD L. HAEDRICH. 1966. Distribution and comparisons of *Centrolophus niger* (Gmelin) and *Centrolophus britannicus* Günther, family Centrolophidae, from the North Atlantic. J. Fish. Res. Bd., Canada, **23**(8):1161–1185.

THOMPSON, D'ARCY WENTWORTH. 1947. A glossary of Greek fishes. London, Oxford University Press, vi + 302 pp.

TORTONESE, E. 1959. Revisione dei Centrolophidae (Pisces Perciformes) del Mare Ligure (1). Ann. Mus. Stor. Nat. Genova, **71**:57–82.

TOTTEN, A. K. 1960. Studies on *Physalia physalis* (L.). Part 1. Natural history and morphology. Discovery Reports, **30**:301–367, 18 pls.

UENO, T. 1954. First record of a strange bathypelagic species referable to the genus *Centrolophus* from Japanese waters, with remarks on the specific differentiation. Bull. Fac. Fish. Hokkaido, **5**:240–247.

VALENCIENNES, ACHILLE. 1836. Les poissons. *In*: G. Cuvier, Le règne animal . . . Edition III, Vol. 4, 392 pp.

———. 1848. Ichthyologie des îles Canaries, ou histoire naturelle des poissons, rapportés par MM. Webb et Berthelot. *In*: P. B. Webb and S. Berthelot, Histoire naturelle des îles Canaries, 1835–1850. Vol. 2, part 2, 109 pp.

WAITE, EDGAR RAVENSWOOD. 1894. New or rare fishes from Maroubra, N. S. W. Proc. Linn. Soc. New South Wales, Ser. 2, **9**:215–227.

———. 1910. Notes on New Zealand fishes. Trans. Proc. New Zealand Inst., Wellington, 1909, **42**:384–391.

WHITLEY, GILBERT P. 1931. New names for Australian fishes. Aust. Zool. Sydney, **6**:310–334.

———. 1933. Studies in ichthyology. No. 7. Rec. Aust. Mus. Sydney, **19**:60–112, 4 pls.

———. 1935. Studies in ichthyology. No. 9. Rec. Aust. Mus. Sydney, **19**(4):215–250.

———. 1943. Ichthyological notes and illustrations (part 2). Australian Zoologist, Sydney, **10**:167–187, 10 figs.

———. 1948. Studies in ichthyology. No. 13. Rec. Aust. Mus. Sydney, **22**(1):70–94.

———. 1958. Descriptions and records of fishes. Proc. Roy. Zool. Soc. New South Wales, 1956–57:28–51, 12 figs.

WILLUGHBY, FRANCIS. 1686. De historia piscium. Libri quatuor, jussu & sumptibus, Soc. Reg. Lond. ed. etc., Oxon., fol., 373 pp., 186 pls.

(Received 26 July 1965.)

Bulletin OF THE
Museum of
Comparative
Zoology

Morphology and Relationships of the Holocephali with Special Reference to the Venous System

BARBARA J. STAHL

~~Museum of Comparative Zoology,~~ Cambridge, Massachusetts
~~Istituto di Biologia Generale, Università di Pisa, Italy~~

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 135, NUMBER 3
JANUARY 27, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office

Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

MORPHOLOGY AND RELATIONSHIPS OF THE HOLOCEPHALI WITH SPECIAL REFERENCE TO THE VENOUS SYSTEM

BARBARA J. STAHL[1]

CONTENTS

INTRODUCTION

Although the evolutionary relationships of the Holocephali have been under consideration for years, no one theory of their descent has appeared so satisfactory that the question may be laid to rest. This paper is the result of the continuing search for progress in clarifying the position of these fishes. To this end an investigation of the venous system of *Chimaera colliei* Lay and Bennett (*Hydrolagus colliei*) has been undertaken, and a reassessment of the anatomy of the Holocephali has been made, taking into consideration both the structural arrangements revealed by the new dissection and current paleontological knowledge.

The problem of classifying the holocephalian fishes (the living genera of which are: *Chimaera*, *Callorhynchus*, *Rhinochimaera*, and *Harriotta*) has become more and more difficult as the understanding of the history of fishes has grown. In contrast to Linnaeus who set the Holocephali down in the same group with the sharks, rays, sturgeons, and lampreys because of their cartilaginous skeleton, modern scholars are giving much thought to the propriety of even including them with the elasmobranchs.

The day has passed, too, when an investigator could seek to solve the problem by focussing upon a single structure and suggesting that it indicates a probable evolutionary relationship. This point bears mention because the spotting of isolated similarities has generated several hypotheses, concerning the evolution of the Holocephali, which have proven untenable when an intensive examination is pressed. Based upon reasoning of this sort is the idea that the Holocephali might possibly be allied to the lungfishes through the common possession of autostyly and cutting toothplates. When the idea was tested by further study, it was

---

[1] St. Anselm College, Manchester, N.H.

shown that the nature of the palatoquadrate fusion was different, that the toothplates were surely not homologous structures, and that other anatomical characteristics were not alike. When paleontological evidence is considered, the probability of a relationship between the Holocephali and Dipnoi recedes still further. Despite the large amount of cartilage in the skeleton, lungfishes have definitely sprung from ancestral bony fishes, which sets them far from the holocephalians. The latter fishes arose probably from forms more nearly, though not necessarily very closely, allied with the ancestors of sharks than with the predecessors of the Osteichthyes. Assuming the truth of this statement, one can cast aside the hypotheses which link the Holocephali to fishes like *Latimeria* and *Polypterus* whose position as bony fish is well established, and also those which embed the holocephalians in the line of fishes leading to tetrapods.

Currently only two possibilities of holocephalian origin are receiving serious attention. One opinion holds that holocephalians are aberrant off-shoots from ancient cartilaginous fishes. Specifically, this school favors the idea that the Holocephali are descendants of the bradyodonts, an extinct group of presumed shark relatives distinguished by nonreplaceable teeth of a peculiar histological structure. Although no wealth of fossil material exists, paleontologists have speculated that at least some of the bradyodonts were autostylic, as are the Holocephali. A leading advocate of the bradyodont origin of the Holocephali, Moy-Thomas (1936) has studied one of the rare bradyodont fossils which consist of more than teeth and spines and found in it many resemblances to holocephalian design. This specimen, the cochliodont *Helodus simplex*, dates from Carboniferous times. If it is ancestral to the Jurassic chimaerids, one must assume that all the distinctive holocephalian characteristics which *Helodus* does not possess were evolved in the intervening years. Other bradyodonts such as *Menaspis* and *Oracanthus* have been discussed in relationship to the problems of holocephalian origin, but they have either possessed structures like the spines on the head of the former which makes one hesitate to place them in the direct ancestral line or they have been, like the latter, in too fragmentary a condition to allow a thorough comparison. In a recent paper, Patterson (1965) concludes that the bradyodonts are closely enough related to the Holocephali to be grouped with them in the class Holocephali, but abandons the idea that *Helodus* or any other bradyodont is ancestral to the holocephalian line.

The second possible source of the Holocephali is an older one. Amongst the ptyctodonts, a placoderm group, have been found several fossil forms that show characteristics which could be ancestral to those of holocephalians. The resemblances were recognized early (Pander, 1858), but neglected after the ptyctodonts were allied with the arthrodires, and after Moy-Thomas offered, in *Helodus*, a bradyodont ancestor for the holocephalians which had long been classified in a general category with sharks. The idea of a ptyctodont ancestor has returned to favor, however, as the magnitude of the differences between holocephalians and sharks has been revealed. It seems now most attractive to find a stock, traceable far back into the Devonian, which could be ancestral to the Holocephali. There are a number of fossils (in a more complete state than many of the cochliodont forms) which have been used as a basis for comparison with extinct and Recent chimaerids. Of these forms, students of holocephalian evolution cite most often *Rhamphodopsis*, *Ptyctodus*, and *Ctenurella*. The last is considered by Ørvig (1962) to show a remarkable number of similarities to the Holocephali. However, the ptyctodont–holocephalian relationship, while possible, is far from proved. There are still serious questions to be solved. One must suppose, for instance, if the relationship is a fact, that over the countless generations which separated the Devonian ptyctodonts from the Jurassic chimaerids the animals lost their distinctive pattern of dermal armor, their pectoral spines, and their internal bone. While changes of this nature are not impossible, there is no fossil evidence to prove that they did take place.

In trying to decide whether it is more likely that holocephalians originated from ptyctodonts than from a group closer to the shark line, one turns normally to the data available from embryological studies. In the case of the Holocephali, very little embryological work has been done. Since the holocephalian fishes lay their eggs, already fertilized and enclosed in a case, in deep water, the embryos are not often obtained. There have been only two studies made of embryonic forms: that of Schauinsland on *Callorhynchus* (1903) and that of Dean on *Chimaera* (1906). Although both studies were elegant pieces of work, a lack of certain stages resulted in the absence of observations of the fusion of the upper jaw and the step-by-step formation of the hyoid arch, for example. An understanding of these two points would shed great light upon the evolutionary question.

Besides the paleontological and embryological approaches, there is a third useful avenue of investigation. The contribution from the area of comparative anatomy cannot be omitted in assembling evidence which bears upon the problem. Although holocephalian fishes have been dissected numerous times, the work upon the anatomy of these fishes is not completed. In early anatomical investigations the dissector often placed his emphasis upon structures which are not the best keys to the evolutionary problem. There is no information available concerning some of the areas which are of great interest from the comparative point of view.

One such area, that of the venous system, has been completely untouched. Although there have been publications concerning the distinctive portions of the arterial pathway, there is nothing in the literature about the pattern of vessels returning blood to the heart. It was in the hope that the venous system would show special features which might serve as clues to a better understanding of holocephalian evolution that this study was undertaken.

MATERIALS AND METHODS

Since it was desirable to avoid describing as the general occurrence an anomalous vessel in a single fish, dissections were repeated until it appeared certain that a particular pattern was a normal and not an abnormal feature. The relatively large number of specimens available made this method possible. The first specimen to be dissected was a female *Chimaera colliei*, uninjected, which had been preserved in formalin and transferred to alcohol. A group of twelve specimens of *Chimaera colliei* were obtained fresh-frozen from Vancouver, B. C., through the kindness of Dr. Norman J. Wilimovsky. The procedure used with these animals was to defrost them, inject immediately with latex, preserve first in formalin, and after five days to transfer them in several steps to 70 per cent alcohol. The last six specimens of *Chimaera colliei*, four females and two males, were received already injected with latex through the kind efforts of Dr. Richard Snyder. For comparative purposes one specimen of *Callorhynchus* and one specimen of *Rhinochimaera* were examined.

Several methods of injection were tried. Because of the delicate nature of the vein-walls and the consequent similarity between veins and strands of connective tissue in some areas, nothing was interpreted as a vein unless it was observed filled with an injecting material or remnants of brown-colored agglutinated blood. In the first uninjected specimen described above, a carmine suspension was injected in area after area as the dissection proceeded. India ink was also tried. In the defrosted specimens, as noted, latex was used. Finally, to fill certain empty areas in the professionally injected specimens, ordinary poster paint was employed in its regular concentration and also in a slightly diluted form.

All these media were introduced through a glass-barreled syringe fitted with a number 23 needle inserted into an inch-and-a-half-long piece of polyethylene tubing, size 50. The tubing was tied into the vessel through which the injection was made.

The routes that were available for injection were limited. Injection via a sinus proved impractical, because the injecting apparatus could not be tied tightly to the delicate sinus-wall. Very fine veins disintegrated under the most careful handling. Only large veins of well-defined cylindrical shape were useful. Injecting through them was hampered only by the presence of valves which restricted the amount of injection material able to pass beyond into tributary vessels. In particular, this difficulty arose in getting material to pass from the common cardinal vein forward into the anterior cardinal sinus and also in filling the deep veins of the fins. Although various vessels were tried as the dissection advanced, for the initial attempt to fill as much of the venous system as possible, two veins were relied upon. To inject the hepatic portal system, the posterior dorsal intestinal vein was employed. To fill the systemic vessels, injection was made into the lateral cutaneous vein immediately posterior to the scapula. This vein could be uncovered easily over a considerable distance by removing the skin just below the lateral line. Injection was made through this vessel first in an anterior and then in a posterior direction.

DESCRIPTION OF THE VENOUS SYSTEM

The veins return blood to the two common cardinal vessels which lie medial to the anterior edge of the scapular process of the pectoral girdle and empty into the lateral corners of the sinus venosus. On either side, three veins meet at the point at which the last pharyngobranchial cartilage articulates with a facet of the scapula, to create the common cardinal of that side. These three are the anterior cardinal, the posterior cardinal, and the lateral cutaneous veins. The first comes from a forward direction, the second comes from the posterior region, and the third runs downward and slightly caudad to meet the other two. Into the upper end of the common cardinal, the inferior jugular vein opens. More ventrally, the brachial sinus opens into the common cardinal from the posterior side (Pl. 5, B, C).

Each of the major venous trunks will be described with its tributaries and the areas which they drain. So that the description may be more easily understood, the pattern of the venous system is presented first in concise, outline, form:

I. The Subcutaneous System
  Lateral cutaneous vein
    Caudal tributary
    Axial tributaries
      Pelvic anastomotic area
        Clasper veins
    Ventro-lateral tributary
    Postscapular tributary
      Dorso-lateral axial branch
      Dorsal fin branch
    Prescapular tributary
      Dorsal cephalic branch
    Anterior subcutaneous tributary
      Ventral cephalic branch
      Opercular branches
    Subscapular tributary
II. The Deep Veins
  A. Precardiac vessels
    Anterior cardinal sinus
      Inferior jugular vein
      Posterior cerebral vein
      Postorbital vein
        Hyoid tributary
        Orbital sinus
          Maxillo-facial vein
            Preorbital branch
            Deep labial branch
          Orbito-nasal vein
          Posterior palatal vein
          Superior adductor mandibular vein
          Anterior cerebral vein
            Posterior cerebral tributary
            Anterior cerebral tributary
            Ethmoidal vein
  B. Postcardiac vessels
    Brachial sinus
      Posterior brachial vein

      - Anterior brachial vein
  - Posterior cardinal sinus
    - Ventro-anterior parietal vein
    - Deep epaxial veins
    - Dorsal fin sinus
      - Medial dorsal vein
    - Anterior epaxial vein
    - Spino-basal vein
    - Esophageal veins
    - Anterior parietal veins
    - Veins of the reproductive tract
    - Renal veins
    - Femoral vein
      - Rectal tributary
      - Dorsal fin tributaries
      - Ventral fin tributaries
    - Hepatic veins
  - Renal portal veins
    - Caudal vein
    - Parietal veins
    - Ventro-posterior parietal vein
  - Hepatic portal vein
    - Intra-intestinal vein
      - Anterior dorsal intestinal tributaries
    - Anterior ventral intestinal vein
    - Mesenteric vein
      - Dorsal posterior intestinal vein
      - Ventral posterior intestinal vein
      - Auxiliary splenic veins
      - Lieno-pancreatic vein
      - Auxiliary pancreatic veins

The subcutaneous system is shown in Plate 1. The deeper veins are represented diagrammatically in Plates 2 and 3.

THE SUBCUTANEOUS VEINS

There is an extensive system of subcutaneous drainage (Pl. 1). The vessels which form it lie in the loose connective tissue under the skin. Although their pathways vary somewhat in different specimens, the basic pattern of flow is generally the same. Assigning names to the vessels of this system is a hazardous business because of the numerous anastomotic connections which are present, but there are several principal trunks which can be specifically distinguished.

The chief collecting trunk deserves the name *lateral cutaneous vein*, for it courses anteriorly, paralleling the lateral line. In the caudal region it is located about a half inch below the lateral line canal, but at the level of the base of the pelvic fin it bends dorsally somewhat and can be followed forward into the trunk region where it is to be found just ventral to the lateral line. At its anterior end it continues forward lateral to the muscle-covered dorsal extension of the scapular cartilage, bends medially around the anterior edge of this cartilage, and then runs ventrally for a short distance to form, with the anterior and posterior cardinals, the common cardinal vein. As it passes ventrally on the medial side of the scapula, it enlarges sufficiently to merit the name of *subscapular sinus*. Where it approaches the upper end of the common cardinal it is flanked by passing nerves, the anterior nerve trunk containing fibers of the cervical plexus which innervate the hypobranchial muscles, and the posterior trunk containing branches of the first through third spinal nerves. (There is also in the anterior trunk a small group of visceral vagus fibers.)

The lateral cutaneous vein, as the principal trunk of the subcutaneous system, has the firmest wall of any vein involved in the superficial drainage. The toughness of the wall is due primarily to an ensheathing layer of dense connective tissue. This vein receives many tributaries which will be described below, beginning with those bringing blood from the most posterior regions.

Although, in the caudal region, the lateral cutaneous runs forward a short distance ventral to the lateral line, there is another, smaller vein which accompanies the sensory canal. This *caudal tributary* turns ventrally to empty into the lateral cutaneous vein at the point along the length of the body which is on a level with the posterior limit of the pelvic fin attachment.

As the lateral cutaneous vein courses forward, it collects blood returning from the superficial regions of the axial musculature dorsal and ventral to it. The *axial tributaries* are arranged in an orderly but not a rigidly segmental pattern. The dorsal tributaries are relatively short and in the region of the trunk posterior to the dorsal fin spine have as their source a network of little veins which forms a narrow band dorsal to the lateral line and parallel to it. The ventral tributaries collect blood from a much greater area and in the pelvic region are considerably enlarged. There, they draw from an anastomotic network of veins. As part of that network, a vein can be seen running along the line of origin of the superficial levator muscle of the fin. The location of this line may be described as being about halfway between the lateral line above and the base of the pelvic fin below. Into this vein run tributaries from the levator muscle, from the axial muscle medial to the levator, and from the axial muscles which are posterior and ventral to the pelvic region. These tributaries have connections, also, with two veins which together encircle the base of the fin. One runs around the base laterally; the other runs around it medially, thus edging the anal region. These two vessels receive veins draining the fin web and the superficial muscles of the fin itself. In the male *Chimaera*, the veins of the clasper, which receive blood from the erectile tissue in the clasper tips, become superficial as they course proximally and empty into the venous ring at the fin base (Pl. 4, A). The chief *clasper veins* are two which appear on the ventral side of the clasper. One drains each prong, and they merge shortly before emptying at the posterior edge of the fin base.

From the anterior corner of the venous network in the pelvic region there flows forward a vessel of rather large size which gathers blood from the skin and superficial axial musculature ventral to the field served by the axial tributaries to the lateral cutaneous vein. This vessel meanders forward over a slightly wavy pathway, finally curving dorsally behind the pectoral region to empty into the lateral cutaneous trunk just before the latter turns inward around the anterior edge of the scapula. The name *ventro-lateral tributary* seems appropriate for this vein. In one specimen which had been injected with India ink, small veins were seen entering it from the posterior edge of the operculum dorsal to the gill opening and from the ventral part of the trunk immediately behind the opening from the gill chamber. The veins in this area were not injected successfully in any other specimen.

The lateral cutaneous trunk receives two sizable tributaries bearing blood from dorsal regions. The first one to be described begins lateral to the muscle-covered posterior tip of the scapular cartilage which is bound against the epaxial muscles at the base of the dorsal spine. This vein, called the *postscapular tributary*, receives blood from the *dorsal fin branch*, draining the web and muscles of the dorsal fin. Halfway along its course to the lateral cutaneous vein, the postscapular tributary receives the *dorso-lateral axial branch.* The latter vessel is a long one, running parallel but dorsal to the lateral cutaneous vein. It collects blood returning from the superficial epaxial muscles which lie dorsal to those drained by the axial tributaries of the main lateral trunk. Some of the branches which join the dorso-lateral axial branch can be seen to connect also with a median dorsal vessel whose blood flows eventually into the posterior cardinal sinus. These connections represent one of the few anastomoses between the subcutaneous and the deep venous drainage systems.

Far dorsally, near the base of the dorsal fin spine, there are prominent vessels which form an anastomosis between the postscapular vein and the second of the two sizable tributaries from the dorsal region. The second one, the *prescapular tributary*, courses ventrally just in front of the anterior edge of the scapula to join the lateral cutaneous vein at the point at which it turns medially to meet the common cardinal. Shortly before emptying into the lateral cutaneous, the prescapular tributary receives the *dorsal cephalic branch* carrying blood from the flattened triangular-shaped dorsal surface of the head. Atop the head, the dorsal cephalic branches of the left and right sides are connected through anastomosing venules. As it runs toward its meeting with the prescapular, the dorsal cephalic follows the posterior portion of the supraorbital sensory canal, collecting blood from fine venules which parallel the mucous canals above the eye. A small vein draining the skin immediately above the orbit may empty into the dorsal cephalic branch or may be connected to the tributary next to be described.

This tributary, called the *anterior subcutaneous*, empties into the lateral cutaneous vein at the same point at which the prescapular enters it. Approaching that point, it courses dorso-posteriorly, approximately paralleling the posterior quarter of the suborbital sensory canal. This vessel receives several *opercular branches* (some of which may anastomose with the ventrolateral tributary near its anterior end). It receives also a *ventral cephalic branch* which drains veins collecting forward and ventral of the orbit and fine venules which parallel the group of mucous canals anterior and ventral to the eye. The ventral cephalic branch may also receive blood from the region just posterior to the lower jaw, but in no specimen could the injection medium be made to penetrate that far forward.

The last tributary to the lateral cutaneous vein which remains to be mentioned is the *subscapular*. This one is really a small sinus, lying against the medial surface of the scapular cartilage. It receives venules from the cartilage itself and from two fine veins which follow the posterior border of the cartilage, one coming from a ventral and the other from a dorsal direction. The subscapular tributary is the last one to join the lateral cutaneous vein before it empties into the common cardinal vein.

THE DEEP VEINS

Precardiac Group

The return of blood from the deep portion of the body anterior to the heart takes place through the *anterior cardinal sinus*. This sinus is exposed by lifting the dorsal constrictor muscle which covers the gill area. As the connective tissue beneath the muscle is cleared away dorsal to the operculum, the scalpel falls into the sinus. The blood-space lies lateral to a muscle originating under the subocular shelf and inserting posteriorly upon the last pharyngobranchial cartilages. This muscle, the trapezius internus of Vetter (Vetter, 1878), covers a portion of the branchial branches of the vagus nerve. The latter are visible through the medial wall of the anterior cardinal sinus for a short part of their pathway ventral to the muscle-band. The sinus is situated dorso-laterally with respect to the efferent branchial arteries and entirely dorsal to the branchial skeleton.

Just as the anterior cardinal sinus, at its posterior end, curves slightly ventrad to join the common cardinal, it receives the *inferior jugular vein.* This vein, which enters the sinus from the ventral side, has so broad a mouth that it might be interpreted as opening partially into the common cardinal itself. The inferior jugular originates far anteriorly behind the lower jaw (Pl. 5, A). Although its main branch comes from within the hyoid "tongue" which protrudes from the floor of the mouth, branches also reach it from the thyroid gland, the ventro-medial fibers of the ventral constrictor muscle, and the anterior portion of the coracomandibularis. Veins from these sources were actually seen, but it is also possible that there exist venules which failed to be injected, draining all the tissues located posterior to the mid-ventral portion of the mandible.

About a centimeter behind the mandible, the inferior jugular vein turns medially and, running dorsal to the coracohyoideus muscle, almost meets its fellow of the opposite side. Without actually doing so, however, the vein turns posteriorly and takes a path lateral to the insertion points of the coracobranchial muscle fibers upon the branchial cartilages. The vein follows the coracobranchial insertion line, flaring widely from the ventral midline and curving dorsally as it does. This route leads the inferior jugular to the postero-ventral corner of the anterior cardinal sinus as described above. In its course along the inserting border of the coracobranchial, it receives blood from the lateral and medial sides of that muscle-sheet.

The drainage of the coracomandibularis and coracohyoideus muscles is only partly accounted for by the inferior jugular vein. Although no other veins in this area were injected, dissections suggest that there may be a deep vein immediately ventral to the ventral aorta which provides additional drainage (Pl. 4, B). From it blood may return through small veins in the dorsal pericardial wall to the common cardinal or possibly over a more ventral course to a pair of veins, to be described below, which run through a channel in each side of the pectoral girdle.

Farther forward than the entry-point of the inferior jugular the anterior cardinal sinus receives into its dorsal side the *posterior cerebral vein* (Pl. 6, A). This vessel collects blood from fine veins over the cerebellum and from membranes in the dorsal part of the cranial cavity. Since there is little likelihood, from the position of this vein, that it returns blood from any part of the cerebrum of *Chimaera*, the use of the term "cerebral" in naming the vessel is technically incorrect. The adjective has been retained merely as a convenience to indicate that this vessel is the posterior of two draining the brain region. There is a possibility that fine veins which connect with the posterior cerebral may also connect with the orbital sinus via an anastomosing vein that passes through the wall of the orbit with the trochlear nerve. The existence of a vein traveling with that nerve was not clearly demonstrable, however, and so is best left in question.

The posterior cerebral vein is formed as a median vessel in the dorsal portion of the cranial cavity over the medulla oblongata between the endolymphatic ducts. In addition to the blood from the brain and associated membranes, the posterior cerebral receives tributaries from the inner ear of each side. These veins pass through the wide opening by which the cavity of the inner ear communicates with that of the brain and hence do not pierce cartilage. Immediately posterior to the point of its formation, by the confluence of the small vessels described, the posterior cerebral vein widens, over the rear part of the medulla, to form a small sinus. Into the posterior end of this sinus run several little tributaries carrying blood forward from the spinal cord. The blood collected in the sinus leaves it through two veins which may be considered as paired posterior cerebrals, continuing from the median vessel. Each passes directly into a long, ventrally directed channel in the cartilage on its own side of the chondrocranium. Each channel, occupied solely by the paired portion of the posterior cerebral vein, terminates by passing dorsal to the vagus nerve (which is also traversing the cartilage at that point) and opening ventro-laterally, anterior to the foramen of the latter. The posterior cerebral vein runs forward close under the otic region of the chondrocranium and then turns laterally at the level of the posterior limit of the semicircular canals to join the anterior cardinal sinus.

At the anterior end of the anterior cardinal sinus, lies the opening of the *postorbital vein* (Pl. 6, A). This vein, which travels through the posterior wall of the subocular shelf, in a ventral direction, with the hyomandibular branch of the seventh nerve, forms a bridge between the orbital sinus and the anterior cardinal. As it enters the latter, dorsal nutrient veins from the gill septa were seen, in one specimen, to send a common stem dorsally to this blood channel. In no other specimen were these little veins detected.

The postorbital vein was examined with care, for it was expected that the hyoid sinus should open into it or nearby. However, no evidence was found in any specimen of the existence of a shark-like hyoid sinus. There was only a small vein, the *hyoid tributary* (Pl. 7, B), which could be traced ventrally to the dorsal tip of the ceratohyal cartilage and no further as a dissectable vessel. Posterior to the ceratohyal cartilage and anterior to the afferent branchial artery, in the position of the selachian hyoid sinus, it was possible to trace an uninjected vein in specimens with a favorable distribution of agglutinated blood. Although a connection with the above-described small vein was not clearly seen, it is possible that there was one and that this entire blood pathway is homologous to the selachian hyoid vessel.

In each dissection of the region ventroanterior to the postorbital vein, the subocular shelf and the cartilaginous bar which runs to the mandibular articulation were removed after examination of the bordering tissues. Beneath the cartilage and immediately dorsal to the skin of the roof of the mouth was a layer of loose connective tissue. The veins running through it were visible only when they remained filled with blood, as the injection mass never penetrated to them. They anastomosed with each other and one ran to join the postorbital as it emerged from beneath the subocular shelf (Pl. 7, B). It seems possible that the vessel traced from the postorbital vein to the tip of the ceratohyal may have connections with the veins of the connective tissue layer via a fine vessel which passes forward, dorsal to the ceratohyal, in company with the efferent pseudobranchial artery. This artery passes dorsally, pierces the chondrocranium, and splits into the cerebral and optic arteries. (In its dorsal course it runs along the posterior edge of the lymphomyeloid mass [Kolmer, 1923] dorsal to the skin of the palate.) Although it is difficult to discern, it is probable that a vein travels with the artery. Judging from the pathway of the artery, this vein might have connections to the network of veins in the connective tissue just described and to the orbital sinus as well. It is also possible that some drainage from the base of the brain might be carried to the orbital sinus or to the postorbital vein via the pathways which exist through the connective tissue.

The *orbital sinus* receives all the blood returning from the head except that which passes through the subcutaneous vessels, the inferior jugular, and the posterior cerebral veins. The sinus encircles the orbit medial to the nerves running through it. Intimately connected with this sinus is lymphomyeloid tissue. This tissue, which seems to be situated in the lateral edges of the blood-space, is present in such quantity at the ventro-anterior corner of the orbit that it bulges laterally in two sizable masses which are visible as soon as the skin is removed from that area. When the skin, connective tissues, and mucous canals[1] are removed from the head in front of and below the orbit, the largest tributary to the orbital sinus can be seen. This vessel, the *maxillo-facial vein*, coursing dorsally over the posterior palatoquadrate region and up over the subocular shelf, enters the ventral side of the orbital sinus anterior to the point at which the postorbital vein leaves it (Pl. 6, A). As the maxillo-facial vein approaches the sinus it assumes a position medial to the nerves which run out of the orbit. The vein carries blood from the deep portions of the overlying mucous canals, from the dermis of the upper lip and the area above it lateral to the labial cartilages, and from the muscles of the facial region which insert upon the labial cartilages and the lower jaw. As the maxillo-facial vein approaches the orbital sinus, it is joined by the *preorbital branch*, draining the muscle tissue anterior to the eye, and by small veins

---

[1] In the head region of *Chimaera* there are two groups of tubules lying under the skin which exude mucus through pores at their posterior ends. The dorsal set of six parallel tubules lies above the orbit and extends behind it. The ventral tubules, approximately the same in number and arrangement, cover an area of the face ventral to the eye and anterior to it.

which come from tissues lying just posterior to the maxillo-facial vein itself.

Since the maxillo-facial vein was nearly empty of blood in the frozen-and-thawed specimens and did not prove amenable to injection, its anatomy was studied in the fish which had been injected with latex and preserved immediately in formalin. In these animals the maxillo-facial vein was observed only upon the left side. The right side showed what appeared to be a large sub-surface pool of agglutinated blood—surely an artifact. Since the veins on the left were entirely empty, it is probable that the fresh-caught fish were stored right-side-downward, causing the blood to accumulate and to obliterate the vessels on that side. Although the vessels of the left side of the face were not filled with latex, it was possible to trace them by injecting poster-paint into the orbital sinus and expressing it into the facial veins by pressing gently upon the eye.

A small *deep labial branch* of the maxillo-facial vein brings blood from the lower lip and jaw, the upper jaw region medial to the labial cartilages, and the nasal capsule (Pl. 7, A).

There are two other veins which enter the orbital sinus from the ventral side, but both of them pierce the subocular cartilage to do it. The *orbito-nasal vein* passes through its own foramen. As it travels toward the foramen from the nasal region, it lies against the dorsal surface of the supra-palatal lymphomyeloid mass. Tracing this vein anteriorly, one finds that it can no longer be separated from the lymphomyeloid tissue where the anterior tip of the mass abuts the posterior side of the nasal capsule.

The second vein which reaches the orbital sinus by piercing the subocular shelf has already been mentioned. This is the vessel which accompanies the efferent pseudobranchial artery along the posterior edge of the lymphomyeloid mass and thence through its subocular foramen. The vein has been called the *posterior palatal vein* because its course lies over that area. Its relation to the suprapalatal lymphomyeloid tissue suggests that it plays a part in draining it. This vessel is never filled with the injection mass. Its presence is demonstrable only because of the blood left in it.

There are also veins which enter the orbital sinus in its antero-dorsal corner. To reach the orbital sinus at this point, the veins must traverse the posterior part of the ethmoid canal. The canal is a large, cartilage-roofed, median space dorsal to the portion of the cranial cavity occupied by the elongated telencephalon. It is separated from the brain cavity by a cartilaginous partition. The ethmoid canal, which is filled with lymphomyeloid material, encloses the ophthalmic nerves as they pass from the orbital region towards the snout. One of the veins which passes through the ethmoid canal on its way to the orbital sinus is the small *superior adductor mandibular vein.* It drains the most dorsal portion of the deep adductor muscle. Leaving the muscle, the vein passes inward through the wall of the ethmoid canal and joins the path of the superficial ophthalmic trunk, traveling with it through its foramen into the orbit.

A second vein, the *anterior cerebral,* enters the orbital sinus by passing through a foramen in the cartilage between the back of the ethmoid canal and the front edge of the orbit (Pl. 5, D). The foramen, which is medial to the departure-point of the ophthalmic profundus from the orbit, transmits only this vessel. The anterior cerebral vein brings blood back from the anterior end of the brain. It is formed as a median vessel within the cranial cavity by the union of a *posterior* and an *anterior cerebral tributary.* The posterior tributary runs from the tip of the long epiphysis (which extends forward to a position above the interorbital area) ventrad in a course which follows the curving posterior edge of the interorbital septum. The anterior cerebral tributary, which drains the telencephalic lobes, follows a dorsal pathway posteriorly through the cranial cavity to meet the posterior tributary just below the ventral edge of the interorbital septum. The anterior cerebral vein produced by the union of the two tributaries passes antero-dorsally through the edge of the interorbital partition and then through a short channel in the cartilage to enter the posterior end of the ethmoid canal. There it bifurcates. Each branch turns posteriorly to enter the orbital sinus on its own side. Just before it leaves the ethmoidal canal each portion of the bifurcated anterior cerebral vein receives an *ethmoidal vein.* The ethmoidal veins bring blood back through the ethmoid canal from the most rostral part of the snout. These vessels enter the anterior end of the canal through the same pair of foramina through which the superficial ophthalmic nerves issue.

THE DEEP VEINS

Postcardiac Group

Ventral to the confluence of the anterior cardinal, lateral cutaneous, and posterior cardinal trunks, there is an opening into the posterior side of the common cardinal vein from the *brachial sinus.* That sinus, which receives all the blood returning from the pectoral fin, lies behind the base of the fin in the angle between it and the body wall. There is an extension of the sinus ventrally along the posterior side of the pectoral girdle which meets its pair in the midline. The entrance of the brachial sinus into the common cardinal is edged by a sharp fold which acts as a valve. It is this valve, apparently, which prevents good injection of the pectoral veins.

The brachial sinus receives blood from two sources. The larger contributor is the *posterior brachial vein.* It borders the posterior edge of the muscle mass of the fin. In dorsal view it can be seen running along the posterior side of a deep levator of the fin (Pl. 5, B). Although neither Vetter (1878) nor Shann (1919) gives a specific name to this muscle, it can be recognized easily through its origin from the postero-medial surface of the scapula, its strap-like shape, and its insertion upon the metapterygial cartilage. The brachial nerves run from the body wall through the axial region toward the posterior brachial vein. Upon reaching it, they divide into dorsal and ventral branches, the former passing over the vein and the latter under it. The posterior brachial vein receives blood from the deep portions of the posterior half of the pectoral fin.

The second source of the blood collected by each brachial sinus is the *anterior brachial vein.* This vein emerges from a channel in the cartilage of the pectoral girdle to pour its contents into the sinus. The channel, which for most of its length contains the brachial artery as well as the anterior brachial vein, is a long one, piercing the cartilage in the coracoid region at a point close to the ventral midline and running dorsally through the girdle to open on the medial edge of the scapular process near the brachial sinus. Between its beginning in the coracoid area and its termination adjacent to the sinus, the channel opens to the surface twice more: there is a foramen facing ventro-laterally anterior to the articulation of the fin and another facing posteriorly dorsal to the base of the fin. Although the most ventral opening of the channel is sizable and set in the anterior side of the coracoid bar, no veins could be seen entering it from the coracomandibular muscle which originates from that surface of the girdle. Since the veins draining the muscle fibers in that area remained uninjected in every specimen, it is possible that such veins do exist but were not observed.

Between the entrance to the channel in the coracoid area and the ventro-lateral foramen mentioned above, the channel is filled with lymphomyeloid tissue like that in the head region. If the passage does carry a vein from the area of the hypobranchial musculature, the vessel would undoubtedly have connections with the vascular network of the lymphomyeloid substance. The first vein which appears certainly in the channel, however, is the tributary draining the deep, anterior ventral part of the fin. This vessel enters the passage through the ventro-lateral opening and follows the path of the channel dorsad. A tributary from the deep part of the anterior dorsal half of the fin enters the channel next, through the posterior foramen, and merges with the tributary from the ventral part of the fin to form the anterior brachial vein. It is this vein which leaves the channel at its dorsal termination to enter the brachial sinus.

Of the major trunks which empty into the common cardinal vein, the only one which remains to be described is the *posterior cardinal sinus.* Although this vessel is paired, there are numerous, sizable communications between the left and right sides, and posteriorly, at the origin of the trunk between the kidneys, there is a single median portion. There are four constant features concerning the anterior portion of this sinus which should be noted. Firstly, the entrance into the common cardinal of each side is cavernous. An injection mass introduced into the lateral cutaneous vein always descends and turns posteriorly into the posterior cardinal sinus rather than entering the smaller opening of the anterior cardinal. Just as the sinus approaches the common cardinal, the subclavian artery and two spinal nerve branches cross through it. Secondly, there seems to be a connection between the posterior cardinal and the brachial sinus. The connecting passage runs from the ventro-lateral edge of the posterior cardinal to the brachial sinus dorsal and posterior to its opening into the common cardinal. Thirdly, the left and right posterior cardinal sinuses extend ventro-laterally to meet each other in the ventral midline. This midline communication parallels that of the brachial sinuses and is separated from it by a sheet of connective tissue. It is to this part of the posterior cardinal sinus that the left and right *ventro-anterior parietal veins* bring blood from the deep anterior ventral and anterior ventro-lateral axial musculature. Fourthly, the sinus of each side extends dorso-medially as a blind pouch forward of its point of union with the anterior cardinal sinus. Thus, a cross-section made just in front of the anterior edge of the scapula shows the left and right pouches close to the midline above the branchial region and the anterior cardinal sinus of each side lying in a more ventro-lateral position.

Since the posterior cardinal sinus runs retroperitoneally against the dorsal body wall between the dorsal aorta and the more laterally placed kidney, the veins from the deep epaxial muscles surely empty into it. These fine *deep epaxial veins* were not injected and so remained invisible, but their presence may be predicated with safety.

Besides this drainage and that from superficial regions of the dorsal musculature via the subcutaneous system, there is one other route to be mentioned: between the left and right epaxial muscle groups in the trunk region can be found a *median dorsal vein* (Pl. 6, B). This vessel was injected successfully and seen to collect from the most dorsal parts of the musculature. Anastomoses existed between its tributary veins and those of the subcutaneous system. The median dorsal vein carries its blood forward to a median *dorsal fin sinus* set behind the base of the dorsal fin. This sinus has a single anterior opening on each side through which blood leaves it. These openings lead to the posterior cardinal sinuses. The blood returned from the median sinus by this route enters the posterior cardinal far forward, flowing into the blind pouch which extends anteriorly and dorsomedially into the anterior tip of the coelom.

Posterior to the opening of this sinus, on a line with the base of the dorsal spine, an *anterior epaxial vein* enters the posterior cardinal on each side, bearing blood from deep muscles forward of the dorsal fin. Medial to its point of entry is the cartilage plate which supports the dorsal spine. Against the side of this plate runs a vessel, the *spino-basal vein*, which connects the subcutaneous veins at the base of the fin-spine with the posterior cardinal sinus deep below.

The remaining tributaries to the posterior cardinal enter it more ventrally. There are several which come from the esophageal wall, leaving it as the gut tube makes its entry into the anterior end of the body cavity. In the region of the trunk anterior to the kidneys, *anterior parietal veins* on each side contribute blood from the most dorsal portions of the hypaxial musculature. The gonads and the ducts of the reproductive tract send their blood to the posterior cardinal, too. The blood from these structures seems to collect in sinuses between the double walls of the suspending dorsal mesentery. The sinus parallelling the oviduct of the mature female is quite spacious. There are veins running medially from it over the short distance to the posterior cardinal sinus. Around the anterior end of the functional kidney there is a wider communication between the two sinuses. The male fishes available for dissection were small and apparently not fully mature. The vas deferens was very fine and bound closely to the lateral border of the gland of Leydig (the transformed anterior end of the kidney). The venous drainage of the duct was invisible.

The *renal veins* run their usual short course, leaving the kidneys ventro-medially and entering the posterior cardinal sinus. Posterior to the entrance of all but a few of the renal veins the posterior cardinal sinus in *Chimaera* receives a vein which does not usually empty into it in cartilaginous fishes. That vessel, the large, firm-walled *femoral vein* (Pl. 7, C), is situated posterior to the femoral artery and, at the fin-base, is formed from *dorsal* and *ventral fin tributaries*, branches which come from the deep dorsal and ventral surfaces of the fin. Although the femoral vein is strong enough to withstand the injecting process, it proved impractical to use it as a route for injecting the deep veins of the pelvic fin because of a valve at its distal end which prevents backflow.

A short distance proximal to the fin-base, the femoral vein receives the *rectal tributary*. This vessel collects blood from a capillary network in the wall of the rectum and also, in the female, from the problematical glandular "seminal receptacle."

As the femoral vein runs toward the posterior cardinal sinus it passes the lateral edge of the kidney and turns ventral to it. There is, however, a small branch which leaves the femoral, passes over the lateral edge of the kidney to the dorsal side and connects with the renal portal vein. The connection, the iliac vein (Pl. 3), is a delicate one and possibly not uniformly present. Because of the small size of the vessel its functional significance is doubtful.

The last contributor to the posterior cardinal sinus is a strange one for any vertebrate. Without a doubt, the *hepatic veins* (Pl. 9, A and B) empty into this dorsal channel instead of passing forward through the transverse septum to enter the sinus venosus. Inspection of the posterior wall of the sinus venosus showed a pair of openings so reduced as to be incapable of carrying the entire blood-flow from the liver. When the liver was cut transversely through the small area which is bound to the back of the transverse septum, there were no sinuses to be seen in the interior of the tissue. In *Chimaera*, however, the anterior attachment of the liver to the back of the transverse septum is not the only bridge between that gland and surrounding tissues across which a hepatic vein might travel. The front portion of each lobe is attached dorsally to the underside of the posterior cardinal sinus and thus to the roof of the coelom. The line of attachment extends along the dorsal edge of the right lobe of the liver for about a third of its length and along that of the shorter left lobe for half of its length. When these areas of attachment were explored, it was found that hepatic veins of varying sizes passed through them, carrying blood from the liver directly to the posterior cardinal sinuses. The largest of these veins was one which drained the posterior two-thirds of the right lobe and entered the right posterior cardinal at a point immediately anterior to a mesentery strap extending from the midline, between the sinuses, to the tip of the pancreas. If the sinus wall is cut and deflected at that point, the dissector can look through a fenestrated membrane separating the sinus from the interior of the hepatic vein. This is the largest of all the hepatic veins and drains the entire free end of the large right lobe of the liver. For the most part, the branches feeding this hepatic vein lie dorsal to those from the hepatic portal vein which carry blood into the right lobe. Anterior to the point at which this large hepatic vein enters the posterior cardinal sinus, smaller hepatic veins enter the sinus separately. Although the left lobe of the liver is smaller, it is similarly drained. There are two main hepatic veins that leave it to enter the posterior cardinal sinus on the left side.

To conclude the description of the systemic venous drainage, one turns to the *renal portal veins* (Pl. 8, A). The blood entering the kidneys from the renal portal veins comes largely from the deep portions of the axial musculature. The muscles of the tail region send blood to the *caudal vein* which bifurcates behind the body cavity to become the left and right renal portal veins. These run forward along the dorsal surface of each kidney, medial to the mesonephric duct. At segmental intervals the renal portals receive veins from the body wall. The renal portals extend far forward, even beyond the region of the functional kidney, collecting the segmental *parietal veins* and finally dwindling to nothing about a centimeter behind the pectoral fin. At the level of the anterior edge of the pelvic girdle the renal portal receives the *ventro-posterior parietal vein*. This vessel can be seen through the peritoneum, lying parallel to the long axis of the body. It begins in the middle region of the trunk and carries blood posteriorly from the deep hypaxial muscles. Immediately anterior to the pelvic girdle it curves dorsally to join the renal portal. The only tributaries to the renal portal which do not return blood from axial musculature are the small veins from the posterior end of the mesovarium. For a short distance beyond the end of the oviducal sinus in the crowded posterior part of the body cavity, these vessels from the lower end of the oviduct enter segmental parietal veins as they are about to join the renal portal.

The Hepatic Portal System

Since the nature of the digestive tract and the arrangement in the body cavity of the associated glands are distinctive in chimaerid fishes, the pattern of the veins draining the system is also singular. Before trying to visualize the path of the vessels, one must understand several anatomical points. Firstly, there is no stomach in these animals. Instead of a long J-shaped structure there is a short continuation of the esophagus which reaches the beginning of the spiral intestine. Secondly, the spleen is not attached to the gut tube by mesenteries. The mesenteries are exceedingly reduced and the spleen is fairly free, bound only to the posterior end of the pancreas. When a fresh fish is opened, the pancreas and spleen appear to lie ventrally in the body cavity. Because the spleen has no relation to a stomach, the term "gastrosplenic" or "lieno-gastric" is not applicable to any vessel in the hepatic portal system. It is well to keep these facts in mind when pondering possible homologies between the vessels of chimaerid fishes and any others.

The *hepatic portal vein* is formed against the surface of the liver posterior to the base of the gall bladder by the confluence of the intra-intestinal, the anterior ventral intestinal, and the mesenteric veins (Pl. 8, B).

It runs immediately into the right lobe of the liver in one direction and, in the other, sends a large division along the posterior edge of the midventral portion of the liver. The blood carried in this vessel is distributed to the left lobe of the liver.

The first of the vessels which deliver blood to the hepatic portal, the *intra-intestinal vein*, drains the spiral valve and, as it emerges from the intestine wall, receives *anterior dorsal intestinal tributaries.* These vessels collect blood not only from the anterior wall of the spiral intestine but also from the posterior region of the esophagus which connects with it. These tributaries anastomose with others which converge to form the *anterior ventral intestinal vein* (Pl. 10, A). The intra-intestinal and the anterior ventral intestinal leave the intestine wall from points lying close against opposite sides of the bile duct. Running closely apposed to the duct, these vessels finally reach the hepatic portal vein.

The last of the vessels which contribute blood to the hepatic portal, the *mesenteric vein*, is formed by the confluence of the two posterior intestinal veins. The *posterior dorsal intestinal vein*, which drains the lower end of the intestine as far as the beginning of the rectum, receives tributaries which can be seen on the surface of the intestine wall. These tributaries anastomose with others which converge on the opposite side of the intestine to form the *posterior ventral intestinal vein* (Pl. 10, A). Both posterior intestinal veins leave the surface of the intestine to run free to a position against the side of the pancreas where they merge and are bound down. In their free portions, the dorsal and ventral veins have a different appearance: the ventral one is narrower and runs through a band of mesentery; the dorsal one is very wide in diameter and absolutely unconfined. At the point at which they merge and are tied to the pancreas, there is a thin mesentery strap which leaves to reach the dorsal midline behind the dorsal attachment of the liver.

The mesenteric vein, thus formed, receives several *auxiliary splenic veins* (the spleen is tied to the posterior end of the pancreas just behind the point where the two intestinals reach it) and then receives the relatively large *lieno-pancreatic vein.* The latter vessel travels through the length of the spleen and the portion of the pancreas which lies posterior to the origin of the mesenteric. After receiving the lieno-pancreatic vein, the mesenteric turns anteriorly and runs in company with the pancreatico-splenic artery, collecting from *auxiliary pancreatic veins* in its course. The mesenteric enters the hepatic portal in conjunction with the intra-intestinal vein (Pl. 10, B).

Additional Observations

One specimen of *Callorhynchus*, a small female, was examined after the dissections of *Chimaera colliei* were completed. It was found that the pattern of the confluence of the major venous trunks to form the common cardinal agreed with the findings in *Chimaera.* The hepatic veins were also found to enter the posterior cardinal sinus. An inspection of the posterior wall of the sinus venosus showed extremely small apertures that were similar to the reduced hepatic openings in *Chimaera.*

DISCUSSION OF THE SIGNIFICANCE OF THE CIRCULATORY SYSTEM TO THE PROBLEM OF HOLOCEPHALIAN RELATIONSHIPS

The venous system of the chimaerids bears a greater resemblance to that of sharks both in the structure of its vessels and their arrangement than it does to the system of any other group of extant fishes. There are certain deviations from the selachian plan, however, which are certainly clues to the separate evolution of the holocephalian line. A consideration of the significance of the venous system to the question of holocephalian relationships necessitates first, recognition of the resemblances, and then evaluation of the differences which exist.

The veins in both groups of animals, like those of all fishes, possess little muscular tissue. Their walls are therefore exceedingly delicate and difficult to differentiate from connective tissue in gross dissection. Even the main vessels may be opened by a chance touch of a scalpel tip. It is the combination of fragile walls and the presence of valves which gives rise in both holocephalians and selachians to the difficulties experienced in injection procedures. The lack of detailed description of the drainage of the head region stems directly from the inability of investigators to introduce substances into the veins which empty into the orbital sinuses. The valves, which are mere folds of the lining of the vein wall, seem to have a like distribution in chimaerids and sharks if non-penetration of injection media can be taken as a guide to their location. The dissector can see that the entrance into the common cardinal from the anterior cardinal is valved but that the opening from the posterior cardinal is not. This arrangement is also shown for *Heptanchus* by Daniel (1934).

The main venous channels in holocephalians as in sharks are sinuses. In both types of fishes the largest ones are held together from within by a network of connective tissue trabeculae. The position of these sinuses relative to each other is not distinctive in the Holocephali.

A great part of the basic arrangement of the venous system of selachians is duplicated in *Chimaera colliei.* The orbital sinus is the major collecting point for blood returning from the tissues of the head. As in *Heptanchus*, *Mustelus*, and *Scyllium*, it receives the orbito-nasal and anterior cerebral veins. Although Daniel (1934), Parker (1886), and O'Donoghue (1914), who investigated the three sharks named, respectively, do not describe in detail the specific structures drained by the orbito-nasal vein, the vessel in *Chimaera* is probably exactly comparable except that it receives blood from the palatal lymphomyeloid mass which the sharks do not possess. The anterior cerebral vein of *Chimaera* drains the same regions of the brain as the selachian vessel, although there is no reception of an ethmoidal vein in sharks, which lack an ethmoidal canal. The dissection of *Chimaera* revealed a maxillo-facial vein and two smaller vessels which also empty into the orbital sinus. That there are no comparable vessels shown for sharks is probably due to their having been uninjected and unreported rather than to their absence.

A postorbital channel exists in both holocephalians and sharks to carry blood from the orbital sinus to the anterior cardinal. Although its location relative to the two blood spaces it connects is the same in both types of fishes, its associations with skeletal and nervous elements are not identical. In *Chimaera* the postorbital vein passes through a foramen in the posterior corner of the orbit accompanied by the hyomandibular branch of the seventh nerve. In sharks, the vessel merely lies in a postorbital groove and the hyomandibular nerve, which never enters the orbit, does not share this anterior pathway. It seems likely that the postorbital veins of the two types of fish are homologous and that the different nervous and skeletal arrangements are due to the autostyly and forward compression of the cephalic structures in *Chimaera.* The presence of a foramen rather than a groove, for example, is due to the fusion with the cranium proper of an otic process extending from the jaw joint to the ear region. This cartilage provides the entire lateral wall of the foramen. The forward course of the hyomandibular nerve can be explained by the anterior displacement of the tissues it serves and by the absence of a spiracle and hyomandibular cartilage behind which it would normally pass.

The chimaerid anterior cardinal sinus carries blood over the gill region to the common cardinal in the shark-like manner, receiving in its course the posterior cerebral vein. The way in which the anterior cardinal and the other large veins of sharks meet to form the common cardinal vessel shows a degree of variation sufficient to preclude the interpretation of the holocephalian arrangement as worthy of special note. Even the connection of the lateral cutaneous vein via the subscapular sinus to this confluence of vessels has its prototype amongst the selachians.

In the postcardiac region the similarity of the selachian and holocephalian plan is still evident. The renal portal and posterior cardinal vessels are substantially the same in both groups. Although the hepatic portal system will receive special consideration below, it may also be generally described as more like that of sharks than that of other fishes. It is in the drainage of the pelvic fins, the ventral body wall, and the liver that significant differences do appear in the chimaerids.

The possession of a subcutaneous system of veins which run unaccompanied by arteries is a final point of likeness which should be mentioned. In sharks as well as chimaerids, the chief vessels in the network, the lateral cutaneous veins, receive segmental tributaries and finally lead to the subscapular sinuses. There are connections elsewhere with deeper vessels in the region of the dorsal and pelvic fins.

That the similarities between the venous systems of holocephalians and selachians do signify an evolutionary relationship is strongly suggested by the fact that their common pattern sets them off distinctly from the bony fishes. Neither ray-finned forms nor lungfishes show the development of spacious sinuses. Allen's (1905) excellent description and beautiful drawings of the circulatory system of the teleost, *Ophiodon*, reveal a complex arrangement of veins of small bore whose homology to vessels in cartilaginous fishes would be difficult to prove. In *Ophiodon*, fine facial vessels empty into a pair of jugular veins directly, since there are no orbital sinuses. The jugular veins, which carry blood posteriorly over the gill region, are thought by Van Gelderen (1938) not to be homologous to the anterior cardinals in the Chondrichthyes. The posterior cardinal vessels of *Ophiodon*, like those of cartilaginous fishes, receive blood from the renal capillaries, but in other bony fishes there may be direct connections with the caudal vein which never persist in sharks or chimaerids. No actinopterygians that have been investigated have subcutaneous veins except the Thunnidae (and here the veins are accompanied by arteries). As an adjunct to the venous system, teleosts have a well-developed set of lymphatics which all cartilaginous fishes (except possibly *Torpedo*) lack. A glance at the pattern of veins in dipnoans shows an even greater departure from the arrangement found in selachians and holocephalians, since there appear in the lungfishes vessels which are similar to those of amphibians.

Despite the broad similarities between the selachian and holocephalian venous systems there are points of apparent difference whose significance must be considered. A dissection of the hypobranchial region, for instance, does not reveal a pair of easily recognizable, shark-like inferior jugular veins. The area is laterally compressed and occupied by the massively developed hypobranchial muscles whose arrangement leaves no straight channel for these veins to follow. Beneath the muscles, and ventral to the ventral aorta, there exists a mass of loose connective tissue which probably does have fine veins draining blood posteriorly toward the sinus venosus. Allis, who made a preliminary sketch of this area in 1916,[2] drew a pair of veins here which he interpreted as inferior jugulars. Not finding a hyoid sinus in the usual location, he gave that name to a large vein which begins behind the mandible and

---

[2] This and other unpublished sketches of the anatomy of *Chimaera colliei* were given by the son of the late E. P. Allis to Dr. A. S. Romer and are in his library in the Museum of Comparative Zoology at Harvard University.

curves dorsally to enter the back corner of the anterior cardinal sinus. It seems more likely, however, that any veins lying deep and near the midline represent auxiliary drainage and that the more lateral, dorsally curving vessel is the inferior jugular vein of *Chimaera.* Although the curious position of this vein suggests that it might be a different vessel from that of sharks, its relation to the base of the gill arches is quite similar and its entry point into the anterior cardinal sinus near the union with the common cardinal is not very different from that shown by Parker (1886) for *Mustelus.* It seems that the inferior jugular vein has been shifted dorsally as the head became laterally compressed, and is not so different after all from that of sharks. It contrasts markedly with the inferior jugular of teleosts which is squeezed medially and in some forms, like *Ophiodon*, exists as a single median ventral vessel for most of its length.

The absence of a hyoid sinus in *Chimaera* may also be due to the relative reduction of the branchial apparatus. In contrast to the large channel which connects the anterior cardinal sinus with the inferior jugular vein in selachians, no major vein appears on either side of the ceratohyal cartilage. Examination with a dissecting scope showed in two specimens a fine vessel which lay anterior to the afferent branchial artery, but the vein was more easily traced along a pathway with the artery out upon the opercular flap than to a connection with the postorbital or anterior cardinal channels. If it is correct to assume that main vessels develop in the embryo as the result of dominance of particular pathways through the initial capillary net, then it is not surprising to find that chimaerids lack a shark-like hyoid sinus. In sharks, where the epihyal cartilage enlarges and develops a close association with the cranium, it is possible that a vein would appear behind it with a connection to the lateral head vein above. In *Chimaera*, where the epihyal never departs from its serial alignment with other parts of the visceral skeleton, the absence of a special hyoidean vein or sinus might be expected. If one follows this interpretation and accepts this assumption that the non-suspensory hyoid is primitive, it follows logically that the absence of a hyoid sinus may represent an original character rather than a secondary loss. If the holocephalians sprang from an ancestral stock which lacked a suspensory hyoid and a distinctive hyoid vein and then evolved the laterally compressed, short head of the extant animals, neither the space nor the stimulus for the development of a hyoid sinus would have existed.

In pointing out singularities in the precardiac drainage of *Chimaera*, one should not omit mention of the situation of the anterior cardinal sinus. Although it has generally the same location as the sinus in selachians, its route does show one variation: the vein passes lateral to a muscle which Vetter (1878) calls the trapezius internus. In sharks, the sinus lies medial to the entire levator (trapezius) series. Again, this difference could arise from a shift of the musculature rather than the development of a new vein, but it is also possible that there has been emphasis upon an alternate embryonic blood pathway in *Chimaera.* Leaving to one side the possibility of a mistake in the identification of the muscle (the fibers run posteriorly from the subocular shelf to insert upon the anterior edge of the scapula just beyond the last pharyngobranchials), it seems that either a shift in the arrangement of the muscles or the vein must be admitted. How great a significance should be attached to such an alteration remains an open question.

In the postcardiac part of the venous system of *Chimaera* there are differences from the selachian pattern that are more clear-cut if not easier to interpret. The lateral abdominal veins are absent, and the blood which they would have collected is differently distributed. From the pelvic fins and also from a rectal capillary network it is sent directly into the posterior end of the posterior cardinal sinus. A small part of the returning blood may even find its way to the renal portal by a fine connection from the femoral vein. Further forward, the blood from the deep part of the ventral body wall is collected by the ventro-posterior parietal vein which flows posteriorly to a confluence with the renal portal. Finally, the blood from the pectoral fins, instead of joining the flow from a lateral abdominal, enters the common cardinal vein alone. The drainage from the posterior half of the pectoral fin enters what may be more exactly described as a brachial sinus than a brachial vein at the base of the fin and is joined there by the blood from the anterior half of the fin which returns by a vein that passes through a channel in the pectoral girdle. There are two possible explanations for the derivation of this peculiar venous pattern. The first, which cannot be flatly dismissed, is that the ancestral stock of the Holocephali possessed this arrangement of vessels. The second and perhaps more probable suggestion is that the lack of lateral abdominals is secondary in chimaerids as it seems to be in the teleost fishes. The lateral abdominals and their homologues, the ventral abdominal and the umbilical veins, play too large a part in vertebrate development to allow one to dispose of them lightly. Their disappearance might be imagined to have required the longest possible evolutionary course. That these veins have not been described in cyclostomes complicates rather than solves the problem. If their absence represents a secondary loss, one has still no clue to the reason for their absence in holocephalians. If, on the other hand, the lack of lateral abdominals is a primitive vertebrate characteristic, which holocephalians are presumed to have retained, one must then question the homology between the lateral abdominals which selachians have developed and the ventral abdominal vein which appears in the first tetrapods.

The most distinctive feature of the venous drainage which might merit the same interpretation is the lack of hepatic sinuses opening into the sinus venosus. The anterior portion of the liver, just behind the transverse septum, is very thin, contains no sinuses, and seems to send no blood forward into the heart. The back wall of the sinus venosus, on the other hand, seems entire, but may have vestiges of hepatic openings. Since no injection material can be made to pass through, one might suppose that no passages exist. Slight indentations are visible, however, in a likely location, and a needle can be made to pass, after some probing, without seeming to pierce tissue. If traces of old entrances into the sinus venosus are present, they prove that the lack of hepatic sinuses in the usual location is secondary. Even if it is not certain that such openings are there, it would seem from the design of the hepatic drainage that a secondary arrangement has arisen. The liver is bound to the underside of the posterior cardinal sinus, in its forward portion, and sends to that channel one main vein, two or three other large ones, and several minor auxiliary vessels. In contrast to this pattern, the forward flow from liver to heart is characteristic of every other jawed vertebrate, embryo and adult. In the most deviant pattern, the hepatic sinuses of rays open into the common cardinal veins rather than into the more medial sinus venosus. If the holocephalian pattern were to be judged primitive, it would have to be supposed that it was the sole remaining example of a distinctive circulatory arrangement which existed in ancient times among ancestral vertebrates—a not too likely possibility. As in the case of the absence of the lateral abdominals, it seems more sensible to suggest that the liver drainage represents a great deviation from the usual vertebrate condition and may well have been the product of a long independent evolution.

The search for differences between selachians and holocephalians should be extended to the hepatic portal system, too, because the homologies between these vessels of sharks and chimaerids are not at once apparent. Upon close scrutiny it seems that the chimaerid veins are more simplified and abbreviated than those of sharks. All of the gastric veins are absent, of course, as are those which drain the spleen and run through mesentery. A short lienopancreatic vein and some small splenics join the vessel returning blood from the posterior regions of the intestine. Consequently, only one vein runs forward to join the intra-intestinal. The union of these two vessels and a smaller one from the anterior intestine and neighboring esophagus creates the hepatic portal. Although it is probable that the lack of mesenteries and the removal of the spleen from its usual place are secondary changes, it is not necessary to assume that the entire pattern of portal tributaries has been only recently evolved. The existence of two sizable branches draining the posterior intestine, an arrangement which has no counterpart in sharks, may not have arisen from any selachian forerunner. It would be tempting to add the lack of gastric veins as another possible preselachian character, because the absence of a stomach has been supposed to be a primitive arrangement; but it cannot be assumed definitely that the lack of a stomach and the minimal development of the spiral valve are primitive rather than degenerate developments. The hepatic portal system, one must conclude, does bear a resemblance to the selachian pattern but may be somewhat secondarily modified. Despite resemblances, on the one hand, and late modifications, on the other, however, it is not impossible that there might be some elements of an older independent pattern still included in the system.

The association of lymphomyeloid tissue with the venous system in the Holocephali is another characteristic which distinguishes these fishes from the shark group. Kolmer (1923), who studied this tissue in *Chimaera monstrosa*, describes it as consisting of a mass of lymphatic cells of varying sizes mixed with red blood cells in all stages of formation. These cells are supported by a network of fine connective tissue fibers which merge with the adventitia of the wide veins and small arteries that ramify within the mass. If the tissue found in the esophageal wall of sharks and rays is comparable to that which exists in a much expanded state in the chimaerids, one might predicate the presence of this material in the early placoderms. It may have been carried in several lines as a hemopoietic organ, its different location and extent in holocephalians and selachians indicating separate evolutionary pathways. It is harder to imagine that this tissue, which is widespread in sharks and batoids in its esophageal location, should disappear from that place and appear in the head and girdle regions of the Holocephali as they branched off from a shark stem. It is also possible that the tissue of the two groups, although it looks similar under the microscope, may not have a common origin. If that be the case, the hypothesis that chimaerids have been derived from early sharks would have another point against it.

A study of the remaining portions of the circulatory system reinforces the idea that holocephalians and sharks probably arose from placoderm stocks possessing some characters which both groups of fishes have carried to the present day. One has only to dissect the heart in each animal (cf., for example, Lankester, 1878, and Hyman, 1942: 329) to be convinced that chimaerids and sharks, while distinct lines, cannot be widely separated from each other on the evolutionary tree. The hearts of the two types of fishes are identical in their gross anatomy, and markedly distinct from the heart of lungfishes or that of ray-finned forms.[3] The only characteristic which distinguishes the chimaerid heart from the shark structure is its relatively small size

---

[3] Lankester (1878), besides describing the heart of *Chimaera*, makes a visibly futile attempt to point out homologies between its arrangement of valves and that in the heart of dipnoans.

(Fig. 4B). Although no measurements were made, it seems that the heart of *Chimaera* would have a smaller capacity than that of a shark of the same size. If one wishes to suppose that sharks and holocephalians have long traveled upon separate evolutionary paths, one must postulate that their type of heart represents the primitive gnathostome structure which has been retained in all cartilaginous fishes and highly modified in bony ones.

The one salient difference in the arterial pattern occurs in the head region. The Holocephali show a type of blood supply to the brain which differs from both selachians and bony fishes in that the pseudobranchial efferent alone reaches the cranial cavity (Allis, 1912). The hyoidean efferent, which feeds the internal carotid in elasmobranchs, forms in holocephalians only a commissure with no continuation running forward to the brain. Even if the investigator assumes that there were in the primitive state two pairs of efferent arteries which sent blood forward to the brain, and that in the Holocephali the more posterior pair has degenerated, he has not disposed of the entire problem posed by the cephalic arteries of the Holocephali. There is also an unusual mandibular artery for which to account. In sharks the lower jaw is supplied by a vessel which leaves the ventral end of the first efferent arterial loop (Hyman, 1942: 324); in holocephalians the mandibular artery runs ventrally from the efferent pseudobranchial, itself a more dorsal branch from the loop. The suggestion has been made by Allis (1912) that the holocephalian vessel, which follows the line of the jaw, represents the ventral portion of the afferent mandibular artery and that the retention of this vessel, which has generally disappeared in other vertebrates, is a primitive feature. If this supposed homology is correct, it would not be possible to derive the chimaerids from a shark group in which the mandibular afferent had already disappeared. However, Marples' (1936) discovery of a similar mandibular artery in *Squatina*, and his statement of the existence of the same type of vessel in *Polyodon* and certain teleosts, makes questionable Allis' interpretation and any evolutionary theories which might be based upon it.

The only other portion of the arterial system which deviates from the selachian pattern is the efferent branchial series of vessels. In contrast to the distinct loops created in selachians (Hyman, 1942: 324) by the union of well-formed pre- and posttrematic arteries, the poor development of the chimaerid pretrematic branches creates discontinuities in the posterior three collector loops. Allis (1912) believed that he saw four complete loops, but Allen (1905) and Parker (1886) failed to find any. Without doubt, the pretrematic vessels seem secondary to the posttrematic ones. In *Chimaera colliei*, the ventral ends of the pretrematics diminish in size and the distinct ventral commissures which close the loops were visible only in well-injected specimens. Again, two possible explanations present themselves: either the chimaerid situation represents an early step toward loop-formation or it is the result of a modification associated with the reduction of the gill arch apparatus and its concealment beneath the operculum. There is no way of deciding which theory is more probable.

In conclusion, then, one recognizes that the holocephalian circulatory system resembles that of selachians in numerous ways and yet differs from it distinctly in certain characteristics. In some of its nonselachian features the chimaerid system parallels the structure of bony fish while in others it is apparently unique.

Among the similarities to selachians can be listed the structure of the heart, the general design of the arterial system, the presence in the venous system of great sinuses, and the arrangement of the principal venous sinuses. Pursuing further similarities in the venous system, one must mention the existence of a pair of inferior jugular vessels which are more like the inferior jugulars of sharks than like those of other fishes, of similar renal portal systems, and of a hepatic portal system that is certainly closer to the type of system found in selachians than to that found in bony fish. Like the selachians, the holocephalians have a system of cutaneous veins and lack lymphatics. As a last point of similarity, even the valves in the chief vessels seem to be located at the same places.

Characters which distinguish the holocephalian circulatory system from that of sharks are found in both the arterial and venous pathways. It is perhaps significant that features of the arterial system which are unique to the Holocephali are all found in the head, a region which is as a whole very highly specialized. Although the incomplete collector loops and the absence of the anterior extension of the internal carotid arteries can be viewed as relatively small modifications of the selachian plan, the significance of the branching of the mandibular artery from the afferent pseudobranchial is not so easy to interpret.

In the venous system, the absence of lateral abdominal veins represents a great divergence from the selachian pattern and a resemblance to that of ray-finned fishes. With those vessels missing, the brachial veins empty into the common cardinals directly, as is the case in teleosts, and the femoral veins open into the posterior cardinal sinuses. The entrance into these sinuses of blood from the liver is surely a peculiarity developed in the holocephalian line, as such a route is unheard of in any other group of fishes. Whether the absence of a hyoid sinus is also to be interpreted as a secondary development or as a primary arrangement is not clear. The resolution of this question may depend upon the solution of the problem of the status of the hyoid arch with which the hyoid sinus is associated.

In surveying the circulatory system of the Holocephali, one receives the impression that the resemblance to the bony fish, which exists chiefly in the absence of the lateral abdominal veins, is fortuitous rather than representative of ancestral connections. Since the resemblance to the circulatory system of sharks is more general, the question seems to be whether the holocephalian system is a derivative of the selachian one or whether it has developed in its own path from a system which characterized a placoderm group ancestral to both holocephalians and selachians. An opinion as to which of these alternatives is the more probable could be more strongly supported if the structural arrangements of other systems were brought into evidence. Should they be found to contain characters too primitive to have been derived from the more specialized homologues of sharks, resolution in favor of descent from separate placoderm ancestors would be indicated. If the other systems seem entirely shark-like or differ from the shark pattern in minor ways only, a direct descent from some shark group cannot be ruled out. To extend the comparison between holocephalians and selachians beyond the confines of the circulatory system, then, a review of the nervous, skeletal, muscular, urogenital, and digestive systems is undertaken in the following pages. The study of these systems also provides a check upon the assumption made here that, although similarities between structures of holocephalians and actinopterygians do appear, there is little likelihood of an ancestral affiliation between the two groups.

DISCUSSION OF PHYLOGENETIC CLUES FROM OTHER ORGAN SYSTEMS

The Nervous System

In any study in which the relationships of the Holocephali are reviewed, the nervous system receives primary attention. Its gross anatomy has been studied in detail (Braus, 1898; Cole, 1896; Garman, 1904; Fürbringer, 1897; Nicol, 1950; Wilder, 1877), and microscopic work has been attempted in some areas (Kappers, 1911, 1912; Bäckstrom, 1924; Johnston, 1910;

Nicol, 1950). From the evidence presented in these papers, it seems that the holocephalian nervous system retains some characteristics that must surely be primitive but exhibits peculiarities which are generally interpreted as secondary phenomena.

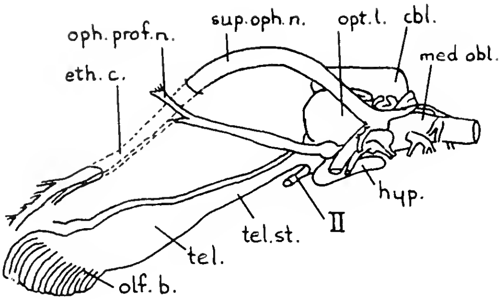


Fig. 1. *Chimaera colliei.* Brain, lateral view. *cbl.*, Cerebellum; *eth.c.*, ethmoid canal; *hyp.*, hypophysis; *med.obl.*, medulla oblongata; *olf.b.*, olfactory bulb; *oph.prof.n.*, ophthalmicus profundus nerve; *opt.l.*, optic lobe; *sup.oph.n.*, superficial ophthalmic nerve; *tel.*, telencephalon; *tel.st.*, telencephalic stalk; *II*, optic nerve. (After Garman.)

Although the form of the spinal cord is quite regularly shark-like, the brain is of an extraordinary nature. In its posterior portion it resembles closely the selachian organ, but the telencephalon is unique in the animal kingdom. In *Chimaera* and *Callorhynchus*, this anterior region of the brain extends forward as a long stalk beneath the interorbital septum. It widens finally into a subdivided telencephalic lobe just behind the olfactory bulbs associated with the nostrils. The uniqueness of the arrangement argues for its secondary development. Kappers and Carpentier (1911) have considered the elongation of the telencephalon and feel that it has taken place as a corollary to the enlargement of the eyes. Since the eyes have encroached upon the medial region normally occupied by the cerebral hemispheres, the forepart of the brain has been displaced. Rather than being compressed posteriorly, in the ancestors of the Holocephali, alone among all the animals that have developed enormous eyes, the telencephalon became displaced anteriorly. The result of the forward growth of the telencephalon has been the creation of long brainstalks through which regular connections with the diencephalon are maintained. *Rhinochimaera*, in which the eyes are smaller, the brainstalks not quite so elongated, and the olfactory tracts more selachian-like, may represent an earlier stage in the evolution of this curious arrangement.

Another characteristic of the telencephalon which lends itself to comment of a phylogenetic nature is the development of the pallium. Holmgren, who has studied forebrain morphology in lower vertebrates (1922), has investigated the pallial region in holocephalians, selachians, ganoids, teleosts, and lungfish. He points out that the selachian pallium is inverted to a greater degree than is the case in the other fishes. By inversion he means a rolling medially of both left and right edges of the embryonic neural plates, resulting in their contact dorsally if the two masses of tissue reach the midline as they do in selachians. Evagination of the more lateral portions of the developing forebrain wall gives rise to paired cerebral hemispheres. If nerve cells mass dorsally over the ependymal layer, the dorsal brain wall thickens and the dividing furrow between the hemispheres may be more or less obliterated. The developmental mode which occurs in the Holocephali, however, consists of a lateral rather than a dorsal concentration of nerve cells. The brain roof is then left relatively thin. In extreme manifestations of this latter tendency, the lateral brain walls grow exceedingly thick and may actually evert, leaving the roof to be covered by an expanded tela. This is the case in actinopterygians. A less extreme and perhaps more primitive version of the same condition is found in the lungfish *Ceratodus* (Holmgren and Horst, 1925). The dipnoan has a broad thin roof over the pallium but the moderately thick cerebral walls are not everted.

In holocephalians the laterally thickened pallium is inverted but never becomes continuous over the dorsal midline. There is always a small strip of ependyma bridging

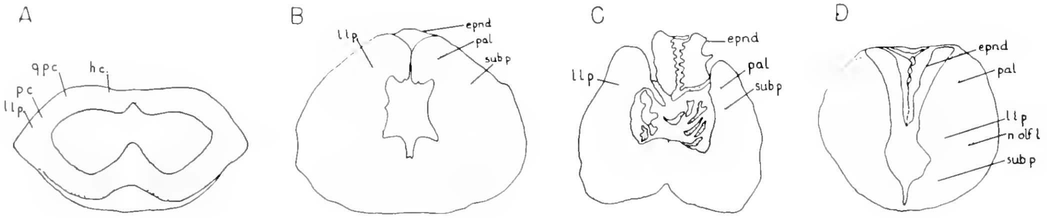


Fig. 2. Transverse section of the forebrain in A, *Acanthias*, B, *Chimaera*, C, *Pratopterus*, D, *Lepidosteus*, to show position of the pallium. *epnd.*, Ependyma; *g.p.c.*, general pallial cortex; *h.c.*, hippocampal lobe; *l.l.p.*, lateral limit of pallium; *n.olf.l.*, nucleus olfactorius lateralis; *pal.*, pallium; *p.c.*, pyriform cortex; *sub.p.*, subpallium. (After Holmgren.)

the dorsal gap. The pallium is evaginated to form two separate olfactory lobes which carry separate ventricles forward of the foramen of Munro. The pallium is rather small, being confined to the anterior, enlarged portion of the telencephalon. The brainstalks which connect the anterior enlargement with the remainder of the brain are composed entirely of subpallial tissue.

Kappers, who reviewed holocephalian brain structure in his compendium on the nervous system of vertebrates (1936), grouped the Holocephali with the lower actinopterygian fishes as intermediate between selachians and teleosts. He regarded the inversion of the pallium as carried over from the former and the eversion of the brainstalk walls as presaging the great pallial eversion of the latter. Holmgren disagrees with the conclusion of Kappers, however. He feels that eversion of the subpallial tissue of which the brainstalks consist cannot be regarded as an early stage of the pallial eversion seen in bony fish. In making his interpretation of the phylogenetic position of the Holocephali, Holmgren considers only the true pallium whose limits he has determined by histological study. He reasons that the holocephalian pallium resembles most nearly, in its degree of inversion and evagination, what must have been the type ancestral to that of extant cartilaginous and bony fishes. The development of greater inversion with resulting fusion across the dorsal midline would lead to the selachian condition, whereas the development of thicker and more widely separated walls would lead to the lungfish–lower actinopterygian–teleost sequence.

Observations upon the microscopic structure of the holocephalian brain have been more fragmentary, and no clear-cut indications of phylogenetic position arise from them. Kappers (1912) has mapped the arrangement of the motor nuclei in *Chimaera monstrosa* and he and several other workers have determined the course of some of the brain tracts in the chimaeroids (Kappers, 1911; Bäckstrom, 1924; Johnston, 1910). One example of the quandary to which these studies have led should suffice. The selachians, with which investigators have sought to compare the holocephalians, are characterized by three telencephalic tract decussations—one dorsal and two ventral. Since the left and right pallial masses of holocephalians do not fuse in the dorsal midline, the dorsal decussation is absent. It is not known whether the fibers which cross dorsally in selachians are channeled through the ventral commissures in holocephalians or whether these fibers are wholly or partially absent. In speaking of the ventral decussation, Bäckstrom goes on to say, "It is, however, possible that a number of fibre connections in this decussatio existing in *Chimaera* are lacking in selachians or vice versa" (Bäckstrom, 1924: 232).

The arrangement of the cranial nerves has also been examined by a worker with the phylogenetic question in mind. Cole, who has dissected these nerves in *Chimaera* in detail (1896; Cole and Dakin, 1906), was especially interested by the emergence from the brain and the distribution of nerves V, VII, and X. He points out that there is no trigemino-facial complex in *Chimaera* as there is in sharks. Nerve V emerges by two roots anterior to VII and underneath the buccal branch of the latter. It sends sensory and motor fibers to the usual destinations without ever mingling with portions of VII. Contact between these two cranial nerves is limited to a variable degree of binding together of their superficial ophthalmic branches. Nerve VII can be divided into a small motor portion and a larger lateral line component. Cole recognizes that the isolation of the lateral line fibers from the rest of the cranial nerve is also characteristic of other fishes and of amphibians which have a lateral line system and so has no special significance. The tenth cranial nerve of *Chimaera* is distinctive, though, in having its four parts in addition to the lateralis component (three branchial branches and one visceral) completely separate: each arises separately from the brain and each has its own ganglion. Cole dwelt upon the evidence of the primitive position of *Chimaera*, which the separation of the posterior cranial nerves suggests, and concluded: "The discrete nature of the fifth, seventh, and lateral line nerves makes *Chimaera* a very unique fish as regards its cranial nerves, and it is to be presumed that such a simple condition is more primitive than the more complex fusions and interminglings that obtain in other fishes. This separation may, however, be purely secondary, just as the form of the brain of *Chimaera* undoubtedly is, but on the other hand the vagus is also in a very simple and unfused condition in *Chimaera*, and the same may be said of its cranial nerves generally" (Cole and Dakin, 1906: 599).

While Cole was upholding the primitive position of *Chimaera* suggested by the arrangement of its cranial nerves, Fürbringer (1897) was concluding from his comparative study of the occipital nerves of selachians and holocephalians that the latter were farthest removed from the beginning of the evolutionary line. He had determined that the number of occipital nerves coming through foramina at the back of the skull ranged from five in notidanid sharks to one or none in rays. At first, after finding five such nerves in *Chimaera* and four in *Callorhynchus*, Fürbringer was ready to place these fish on a level with the notidanids. On closer observation, however, he noticed that only the first two resembled the occipital nerves of the selachians in appearance and in their course to the hypobranchial muscles. The remainder looked very much like the succeeding spinal nerves and, like the latter, sent fibers to the brachial plexus. Fürbringer distinguished these nerves as spino-occipital nerves, explaining that in the Holocephali two or three of the anterior vertebrae have been incorporated into the skull bringing their segmental nerves with them. Thus these spino-occipital nerves are not homologous to the posterior occipital nerves of simple selachians but are proof that the holocephalians belong to a "höhere, mehr specialisirte Abtheilung" (Fürbringer, 1897: 446).

The true spinal nerves of holocephalians bear a greater resemblance to those of selachians than to those of bony fishes in that the dorsal and ventral roots retain the large degree of independence which is characteristic of the former group. In *Chimaera*, one can see in each segment of the trunk two roots emerge, give off dorsal rami, and then, as ventral rami, gradually come together. The segmental nerve formed by their union soon divides, and the nerve continues its lateral course as a double-stranded structure. If the two strands represent the reseparation of dorsal and ventral root fibers, the holocephalians would then show a very limited association of dorsal and ventral root elements—an arrangement seemingly closer to the primitive state of complete separation than that shown even by selachians. At the level of the pelvic fin, Davidoff's dissections (1879) show a separation of the strands of the spinal nerves followed distally by a recombination involving the posterior strand in one segment and the anterior strand from the segment behind. In Davidoff's opinion, this arrangement as well as further connections between the first two nerves which supply the fin suggest the beginnings of a more complex pelvic plexus than is present in other fishes. The holocephalians' lack of a collector nerve in the pelvic region, according to Van der Horst (*in* Bolk, Vol. II, 1934), also sets them apart from selachians, dipnoans, and lower actinopterygians. The plexus at the level of the pectoral fin, however, resembles that of selachians and actinopterygians in being of a cervicobrachial nature. The holocephalians and these fishes are distinguished in this feature from the dipnoans which have, like tetrapods, two separate plexuses in this region. Assessing the various characteristics of the spinal nerves and the plexuses in which they are involved, one might conclude that the holocephalians may show the retention of a relatively primitive arrangement which has been modified to form a unique pattern in the pelvic region.

The last remaining part of the nervous system to be discussed, the autonomic division, has been described thoroughly by Nicol (1950). His study, it must be mentioned, was based only upon *Chimaera colliei*. Without attempting to repeat Nicol's description, one may say that he found a very close similarity between the autonomic systems of selachians and holocephalians and substantial contrasts between their type of system and that of bony fishes. For example, he notes that teleosts have well-ordered sympathetic chains connected to the spinal nerves by both gray and white rami. Although the dipnoans show a less well-developed pair of ganglionated chains, the presence of a delicate chain-structure differentiates even these fishes from the selachians and from *Chimaera*. In the cartilaginous forms there is a more or less segmental arrangement of sympathetic ganglia throughout the trunk (and an absence of ganglia in the tail); but these ganglia are haphazardly connected by a network of nerve fibers and communicate with the spinal nerves by white rami only. Since there are minor differences between the systems of selachians and *Chimaera*, Nicol is of the opinion that the chimaeroids split from the selachian line and have evolved in the final stages on a separate path.

A study of the sense organs produces little evidence which can be brought to bear upon the phylogenetic question. The olfactory, optic, and otic structures in holocephalians are similar to those of sharks, and there are no fossil remains of the first two types of sense receptors from which their hereditary history could be learned. The design of the inner ear in early vertebrates has been revealed through cranial casts, however, making comparisons possible. Stensiö's (1963) cast of the cavities in the cranium of the arthrodire *Kujdanowiaspis* shows a general arrangement of the labyrinth which still characterizes both holocephalian and selachian fishes. Even the endolymphatic duct appears, rising to open upon the dorsal surface of the head. The only point of difference between chimaerids and sharks, of which Stensiö speaks, concerns the structure of the utriculus. That of selachians is divided, while the utriculus of holocephalians is not. Stensiö thinks that the undivided state is more primitive and that the divided utriculus has appeared in certain orders of arthrodires and in elasmobranchs through parallel development. If Stensiö's speculation is correct, the ancestors of holocephalians and early sharks would have been separate but related stocks.

Both Stensiö (1947) and Holmgren (1942a) have included a study of the lateral line system of the Holocephali in their surveys of lateral line systems in fishes and amphibians. Although these authors disagree as to whether a general pattern of head canals can be defined, they state in concert that no explanation of the evolution of the holocephalian pattern is possible at this time. Holmgren finds it improbable that the holocephalian arrangement could be derived from that of selachians or vice versa. He suspects that the holocephalian system has been reduced from a more elaborate pattern although the absence of embryological studies prevents his speculating upon what the ancestral state might have been. He is forced to abandon the problem with the statement that the holocephalian head canals "could not be identified with lines in any other vertebrate" (Holmgren, 1942a: 21). Stensiö would have liked to have made a comparison between the head canals of holocephalians and those of ptyctodonts, but unfortunately the latter have not been preserved. The anatomy of the sensory canals of holocephalians reveals no more to the investigator than their arrangement. As Garman (1888, 1904) and Reese (1910) have shown, the sensory cells lie in open grooves in *Chimaera*, in slit tubules in *Rhinochimaera*, and in closed tubules in *Callorhynchus*. It is not possible to determine which of these arrangements is primitive or if any one of them is.

Although no single characteristic of the nervous system serves as a key to the evolutionary history of the Holocephali, it is possible to make a reasonable speculation based upon the group of anatomical features discussed above. The survey of the holocephalian nervous system has shown that no portion of it resembles that of any bony fish. Although the anterior extension of the telencephalon, the ramifications of the spinal nerves, and the pattern of the sensory canals are unique, the posterior parts of the brain, the sensory organs, and the autonomic nervous system are strikingly like the shark structures. In drawing conclusions based upon the nature of the nervous system, then, one must lay aside the possibility that the Holocephali might be allied to any line leading to bony fishes (despite Holmgren's view that the dipnoan pallium might be derived from the holocephalian type) and predicate, instead, some degree of relationship to the early sharks or their ancestors. If one agrees with the assumption that the partially inverted pallium is more primitive than the strongly inverted selachian structure and also with the interpretation of the cranial nerve arrangement as more primitive than that found in sharks, it follows that the Holocephali could not have evolved from early sharks in which the more complex selachian organization was already established. One is left with the hypothesis that the Holocephali have descended from an ancestral group separate from that of selachians but allied to it. This hypothesis allows, firstly, for the retention in holocephalians of the structures assumed to be primitive even though these elements are modified in sharks. Secondly, it provides an explanation for the presence of similar nervous structures in both types of cartilaginous fishes, since these elements may have been characteristic of the larger group to which both ancestral stocks belonged. Thirdly, the hypothesis suggests that the holocephalians developed along a separate line long enough to permit the evolution of the special structures which are unique to them. The alternative theory, that holocephalians are descended from an early shark group, with its corollary that the structures of the nervous system must all be derived by modification of the selachian plan, seems less likely than the above hypothesis which predicates no such close relationship between the two extant groups.

The Skeletal System

Extant holocephalians, like selachians, have a skeleton constructed entirely of cartilage, their only hard parts being isolated placoid scales and the large dorsal fin spine. In the Jurassic forms *Squaloraja* and *Myriacanthus*, however, the dermal elements are more extensive. The fact that there is a greater amount of hard tissue in extinct holocephalians than there is in modern ones gives added support to the idea that the cartilaginous skeleton characteristic of the Chondrichthyes is not the primitive vertebrate framework but a secondary development. Although this hypothesis does not disallow the possibility that the Holocephali split from the selachian line after the disappearance of bone, it invites one to speculate that the reduction to cartilage may have occurred in the two lines separately.

Comparative studies of the skeleton provide some evidence which can be used in trying to determine where the holocephalian and selachian fishes diverged, but one feels the lack of sufficient fossil data at every turn. Fossils of early sharks are not abundant and among those which have been studied, there is not one whose characteristics suggest that it might have served as an ancestor for the holocephalian line. Moy-Thomas (1936) has offered the cochliodont, *Helodus simplex*, as an ancestral type, but the bradyodonts are themselves distant from selachians. Watson (1938) and Ørvig (1962) have both suggested that the Holocephali have been derived from ptyctodonts, and thus they take the stand that holocephalians have never shared the selachians' evolutionary pathway. A review of the holocephalian skeleton can at best, then, only attempt to define the degree of similarity between it and that of selachians and can try to determine whether a relationship to ptyctodonts or cochliodonts is possible only where comparable structures have been preserved.

A review of the studies of the skull shows that relatively few workers have tackled the head skeleton in its entirety. Only Allis (1917, 1926), DeBeer and Moy-Thomas (1935), and Holmgren (1942b), have looked much beyond the labial cartilages. In making their more inclusive studies, they complain of the lack of data concerning embryonic development: literally nothing exists except the examination of a few embryos by Dean (1906) and Schauinsland (1903). It is a pity that the breeding places of these laboratory-shy fishes are not well-known, for a careful review of a series of embryos from the earliest stages would go far toward settling some of the questions which Allis, DeBeer, and Holmgren raise.

The first of these questions concerns the developmental interrelationships of the eyes and the cranial cavity. As has been mentioned before, Kappers felt that the depression of the telencephalic space occurred because of the dorsomedial expansion of the eyes. With this conclusion Holmgren would agree. Holmgren surmises from this point that the ancestors of the Holocephali must have been slightly flattened forms with rather dorsally placed eyes. Otherwise, Holmgren reasons, it would not be likely that expansion of the orbits would force the brain downward. It follows, in Holmgren's thinking, that even a more broad-headed cochliodont than *Helodus* would be a likely ancestor for the holocephalians.

In speaking of the structure of the cranial cavity, both Holmgren and Allis take issue with the opinion of DeBeer, Moy-Thomas, and Watson. The latter workers believe that the cranial cavity does not include the passage known as the ethmoid canal, through which the superficial ophthalmic nerves run forward after leaving the orbits. DeBeer and Moy-Thomas (1935) state that this canal is roofed over by a dorsal extension of the orbito-nasal lamina beyond the true cranial roof, and they present a series of drawings of hypothetical evolutionary stages from the uncovered to the covered condition of this supracranial space. In his publication of 1936 in which he presents the case for the descent of the Holocephali from the cochliodont *Helodus simplex*, Moy-Thomas stresses the fact that *Helodus* already shows a dorsally-flared orbito-nasal element.

Allis and Holmgren both hold that since the ethmoid canal is continuous with the cranial space, it is, therefore, a part of it. Allis (1926) suggests that the cranial space anterior to the orbits was cut off indirectly through the pressure of a mysterious embryonic "vesicle" which appears between the midbrain and the forebrain. As the forebrain is pressed downward, the trabeculae are squeezed outward, eventually rising up and inward to cut the cranial cavity in two. According to Allis' theory, the trabeculae form the floor of the ethmoid canal and the roof of the telencephalic enclosure. The floor under the telencephalon is composed of intertrabecular tissue with perhaps a contribution from the fused palatoquadrate.

Holmgren's interpretation is based more on anatomical examination and less upon flights of fancy. In his study of the heads of fishes (1942b), Holmgren presents photographs of six transverse sections through the orbital region of *Chimaera monstrosa* in which he points out a fine channel, running from the main cranial space forward over the interorbital septum to open into the ethmoid canal. He remarks that in *Rhinochimaera*, which seems to be the most primitive holocephalian, this channel is much wider, making even clearer the continuity of the two spaces. To explain the presence of a floor to the ethmoid canal which divides it from the telencephalic space beneath, he suggests that this cartilage may be a neomorph, citing its very late chondrification as shown by Schauinsland's study (1903) of a *Callorhynchus* embryo. He goes on to hypothesize that, as in some sharks, the superficial ophthalmic nerves of the ancestors of the Holocephali may have run in left and right preorbital canals whose lateral walls were formed by extensions of the supraorbital crest cartilages. Just as these nerves of *Pristiophorus* come inside the cranial space intermittently because of deficiencies in the walls medial to the preorbital canals, so in the Holocephali, through complete disappearance of the cranial walls in this area, the two preorbital canals may have merged with the anterior brain cavity. It is by such a change, according to Holmgren, that the superficial ophthalmic nerves may have come to run within what he considers to be the anterior part of the cranial cavity in the holocephalians. In disavowing the existence of an ethmoid canal as a unique holocephalian character, Holmgren removes one of the structures upon which DeBeer and Moy-Thomas leaned heavily in associating the Holocephali with the cochliodonts.

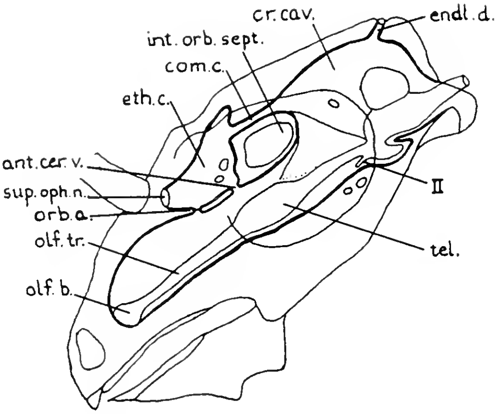


Fig. 3. *Rhinochimaera pacifica*. Neurocranium, lateral view. Cranial cavity with brain outlined. *ant.cer.v.*, Anterior cerebral vein; *com.c.*, communicating channel between cranial cavity and ethmoid canal; *cr.cav.*, cranial cavity; *endl.d.*, endolymphatic duct; *eth.c.*, ethmoid canal; *int.orb.-sept.*, interorbital septum; *olf.b.*, olfactory bulb; *olf.tr.*, olfactory tract; *orb.a.*, orbital artery; *sup.oph.n.*, superficial ophthalmic nerve; *tel.*, telencephalon; *II*, optic nerve. (After Holmgren.)

On the basis of what has been said about the interrelationship between the eyes and the cranial cavity, it becomes plausible to conclude that the chondrocranium probably surrounded a brain space of quite ordinary dimensions in the ancestors of the Holocephali and that the enlarging eyes pressing an interorbital septum between them gradually reduced the median cavity to its present divided condition. If this reasoning is correct, the Holocephali must have long been upon a separate evolutionary pathway, leading from a form like *Rhinochimaera* to one like *Callorhynchus* and finally to the chimaerids. This sequence of evolution is supported by the fact that the interorbital septum in *Chimaera* is even more extensive than that of *Callorhynchus* (Hubrecht, 1877). One would expect the area of the septum to be largest in the group which shows the greatest median expansion of the eyeball.

The otic region of the holocephalian braincase is short, the ear capsule being pressed close against the back of the orbit. Many selachians also show a relatively short otic portion of the skull. If, however, the selachians are descended from primitive forms with an elongate otic and occipital region as Romer believes (Romer, 1964) it becomes less probable that the holocephalian fishes diverged from early selachian stock. The alternative suggestion, that they diverged from the shark line after shortening of the otic region had occurred, places the origin of holocephalians very late, perhaps in the Permian or even in the Triassic period. If Dean (1904) is correct in his identification of *Menaspis*—a Permian form apparently not in the selachian line—as an early chimaerid, it would be better to seek a separate ancestral group for the Holocephali among the Devonian placoderms in which the posterior part of the skull was already short. Ørvig (1962) suggests the ptyctodonts as such a group. In particular, he describes the ptyctodont *Ctenurella* as possessing a short otic region set behind large orbits. Since the ethmoid region of *Ctenurella* slopes downward anterior to the eyes, the general form of the skull does bear a resemblance to that of the holocephalians. The holocephalians are unlike the selachians in having no cartilage wall separating the otic from the cranial cavity. Fossil remains are not sufficiently abundant to indicate whether the presence of a partition was primary, but Stensiö (1963) states that in the arthrodire *Kujdanowiaspis* the two cavities were separated by a thick wall. If the condition in *Kujdanowiaspis* was the general one in arthrodires as it is in modern selachians, one must assume that the confluence of the ear and brain cavities in the Holocephali is a secondary development. Although some teleosts show a confluence, it seems that in each group the modification arose separately.

Another characteristic of the posterior end of the braincase which is very probably secondary is the consolidation with the occipital region of two or three vertebral elements. Rays and also durophagous fishes (with disproportionate development of the head and shoulder region) show a fusion of skull and vertebral elements similar to that of the Holocephali. Such a modification has surely obscured the ancestral condition in both groups of fishes.

In comparing the braincase with that of sharks, Holmgren mentions particularly the location of foramina. The entryway into the orbit for the superficial ophthalmic nerve is separate from that of the other nerves in both groups, as Moy-Thomas also claims it to be in the cochliodont *Helodus*. The foramen for the entrance of the internal carotid artery, however, is farther forward in the Holocephali. The hypophysis grows ventrally into a depression that has an open passage in its floor in the Holocephali, and the notochord, which runs toward it in the base of the cranium, lies in a groove rather than being completely embedded in the cartilage as in sharks. The position of the notochord shows, in fact, not only a difference from that of sharks, but also a similarity to that of certain arthrodires described by Stensiö (1963). In his reconstruction of *Kujdanowiaspis* he shows the notochord lying in a groove on the dorsal surface of the cranial floor as it does in the holocephalians. This similarity to the arthrodires (if it proves to be general) and contrast to the selachians would favor the idea that the Holocephali have direct arthrodiran connections.

The holocephalians also differ from sharks, Recent and fossil, in the possession of a palatoquadrate cartilage which is fused with the chondrocranium rather than being suspended in amphistylic or hyostylic fashion. Since autostyly is known in extant fish only in dipnoans, the palatoquadrate in the Holocephali represents a remarkable departure from the piscine plan. DeBeer, Moy-Thomas, and Holmgren have each devoted attention to the holocephalian palatoquadrate, and, doubtless due to the scarcity of the embryonic material available to them, their opinions as to its nature are divided. DeBeer and Moy-Thomas (1935) see it as an elongate structure extending posteriorly to the mandibular joint by an otic process which fuses to the cranium against the ear capsule. Holmgren (1942b) recognizes the cartilaginous lamina between jaw-joint and ear region but is not so sure that it is truly a part of the palatoquadrate. It may be, he feels, a separate cartilage in the early embryo. If it is, then the Holocephali are characterized by a very short palatoquadrate element, and only fossil fishes having a short structure should be sought as possible ancestral stock. One might regard both the ptyctodonts and the cochliodont *Helodus* as having a short palatoquadrate if that element terminated at the jaw-joint and the extension to the otic region developed separately, as Holmgren believes it does in holocephalians.

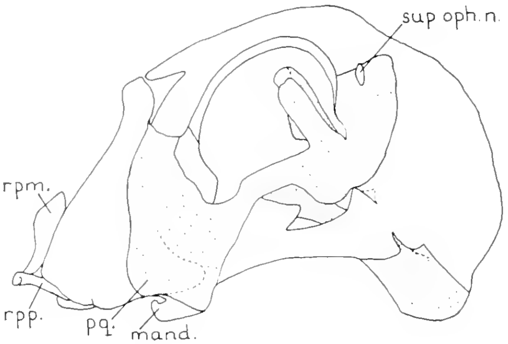


Fig. 4. *Callorhynchus antarcticus*. Skull of 60mm embryo, lateral view. True cartilage, stippled; precartilage, white. *mand.*, Mandible; *pq.*, palatoquadrate; *rpm.*, medial rostral process; *rpp.*, paired rostral processes; *sup.oph.n.*, superficial ophthalmic nerve. (After Schauinsland.)

Even though the complete fusion of the palatoquadrate to the chondrocranium seems so distinctive a feature, Holmgren minimizes the distance that this fusion puts between holocephalians and sharks. He points out that in shark embryos the palatoquadrate is connected to the trabeculae by a membrane, parts of which chondrify. One of the chondrifications attaches itself to the palatoquadrate as the orbital process; another fuses to the trabeculae to form the subocular shelf. He asks whether, if the entire membrane should chondrify, firmly uniting the palatoquadrate with the cranium, this process would be so far from what occurs in selachians. A glance at Schauinsland's (1903) illustration of the developing skull of the 65 mm *Callorhynchus* embryo, however, suggests that Holmgren's speculation here may be wide of the mark. At that stage, true cartilage already extends from the palatoquadrate area near the mandibular joint upwards to include the lower half of the orbit. The region in front of this smooth mass of cartilage, as well as that of the problematic extension to the otic capsule, is still in precartilaginous form. It seems that if the holostyly of the Holocephali was developed through further chondrification of a shark-like arrangement of the palatoquadrate and the trabecula, some indication of the separate nature of these elements should appear in this early stage before the palatoquadrate is developed completely. On the other hand, it is possible that the developmental step for which we are searching has been gradually abbreviated to the point of disappearance. Thus, there are two alternatives: either the separate palatoquadrate never existed even as an embryonic structure in fishes at the holocephalian level, or its development was suppressed later as the line evolved to the present day. Both of these answers imply an evolutionary path long separate from that which led to modern sharks.

It is not inconceivable that holocephalians might have inherited their autostyly from an earlier gnathostome group. That condition was evolved, according to Stensiö (1963) in several groups of arthrodires and apparently was not a rare occurrence. Ørvig admits, however, that in *Ctenurella* (the ptyctodont that he regards as being closely allied to the holocephalian line) the palatoquadrate was not fused to the neurocranium. Moy-Thomas, in advocating a cochliodont ancestor for the Holocephali, points to the autostylic suspension of the palatoquadrate of *Helodus* as an important similarity between that form and the holocephalians.

A second peculiarity of the visceral arch skeleton in holocephalians concerns the dorsal portions of the hyoid arch. As one might expect from the autostylic suspension of the palatoquadrate, no part of the second arch is enlarged as a hyomandibular. The epihyal and pharyngohyal resemble their serial homologues in the successive branchial arches. The question arises with regard to these elements of the hyoid arch as to whether their state is truly primitive or whether they have been reduced from a specialized, suspensory condition to mimic the simple arrangement of the posterior arches. Holmgren agrees with DeBeer and Moy-Thomas in regarding the non-suspensory condition of the hyoid arch as primitive. DeBeer and Moy-Thomas have examined the holocephalian hyoid arch in detail. In their opinion they have located all its parts, including the pharyngohyal, and judge it to be unmodified. They argue against the possibility that any portion of the hyoid could be fused to the cranium and so lost to view. To make this supposition, one would have to allow the migration of the cartilage dorsal to the lateral head vein, leaving all the other visceral cartilages properly ventral to it. Judging from the unanimity of opinion amongst these anatomists, then, it would appear that a non-suspensory hyoid is one of the primitive characteristics that the holocephalians have carried in their hereditary baggage from early gnathostome times. As an early gnathostome source for the non-suspensory hyoid arch, Watson would have offered the placoderms generally, since he believed them to be aphetohyoidean. Stensiö, however, is of the opinion that the early placoderms possessed a suspensory hyoid and that the hyomandibular was reduced to a non-suspensory bar in groups in which autostylism developed. It would not be feasible, according to Stensiö's interpretation, to seek a placoderm ancestor for the Holocephali if their hyoid arrangement is truly a primary one.

One would expect, in a fish with an elementary hyoid, to find a full gill slit anterior to the hyoid arch like that which Watson predicated for aphetohyoidean placoderms. Although a slit does appear in the embryo, it is dorsally placed and soon disappears. The space between the hyoid and the mandible is later crossed by three ligaments: not only is the spiracle absent, then, but the area has been completely rebuilt. It is probable that this change is a modification connected with the forward displacement of the visceral skeleton as a whole and, one might add, of the pectoral girdle behind it. The palatoquadrate is set far forward and fused to the cranium, as we have seen; the hyoid is close behind the mandible and firmly tied to it by the abovementioned ligaments; and the remaining five arches are crowded up under the posterior end of the cranium. The last two pharyngobranchials and epibranchials are squeezed to a fusion with each other, creating a small flat disc against which the scapula abuts. The entire gill apparatus is reduced and covered by an operculum. This arrangement of the visceral skeleton contrasts sharply with that of extant sharks which have five arches, or in the notidanids and *Chlamydoselachus* more than five, in an extensive pharyngeal region. Fossil forms with a short pharyngeal region (and branchial arches crowded forward beneath the posterior end of the braincase) did exist, and might be a more logical choice as a group ancestral to the Holocephali than the early sharks. The ptyctodonts have been figured by Watson (1938) and by Ørvig (1962) as having only a small branchial area, and Moy-Thomas (1936) describes the cochliodont *Helodus* as having the pectoral apparatus set close behind the head.

The possession of a single median rostral cartilage also distinguishes the Holocephali. In *Chimaera* the rostral cartilage is short; in *Callorhynchus* it is longer and bent ventrally; in *Rhinochimaera* it is longest and

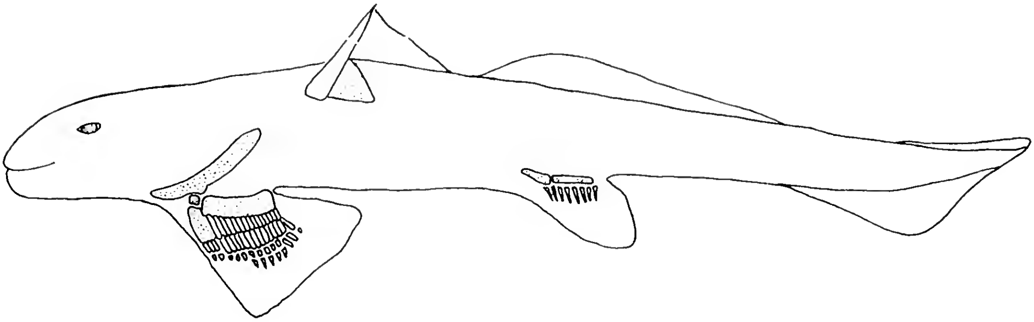


Fig. 5. *Helodus simplex*. Restoration of fish, lateral view. (After Moy-Thomas.)

extends directly forward. Garman (1904) believes that the longest cartilages are the most primitive. This supposition seems reasonable as *Rhinochimaera*, with the longest rostrum, also shows several other characters in what is apparently their earliest form. The fossil holocephalians *Squaloraja* and *Myriacanthus* show well developed rostral cartilages, the former exhibiting some calcification of the element. There, however, the trail ends mysteriously. *Ischyodus*, another extinct form, is figured by Dean (1895) as having a short, blunt head, and the earlier possible ancestors, the cochliodont *Helodus* and the ptyctodont *Rhamphodopsis*, are not known to have possessed rostral structures. *Ctenurella*, according to Ørvig, has a pair of rostral processes but not a medial one. It may be that such structures were not preserved, but in any case the rostral cartilages cannot now be used as Ariadne's thread to reach the light.

Holocephalians, like sharks, have paired labial cartilages. However, in their number and form the labial cartilages differ from the simple, slim bars—an upper and a lower one on each side—which meet at the angle of the jaw in selachians. At the mouth angle in holocephalians, on each side, there are two labial cartilages which meet, but the small superior maxillary element and the larger, flattened inferior maxillary are often fused in the adult. Against the anterior end of the lower jaw there may be a premandibular labial cartilage (it is absent in *Chimaera colliei*); beside the upper jaw there are always a large prelabial and a smaller premaxillary element.

The labial cartilages of the Holocephali were studied for two reasons. Comparative anatomists examined them hopefully as possible clues to the history of the descent of modern chimaeroids, and workers interested in the transition from agnathous to gnathous fish sought in them the remains of the premandibular visceral arches. Despite the descriptions given by Allis (1926), Dean (1906), Garman (1904), Holmgren (1942b), Hubrecht (1877), Luther (1909), and others, the significance of these cartilages has not been surely decided. Their early fossil record is dubious. Ørvig finds some in *Ctenurella* which he thinks resemble those of holocephalians rather than those of sharks. Holmgren suggests that they might be represented in three small elements in *Rhamphodopsis* which Watson (1938) had identified as parts of the hyoid arch. To the suggestion that these elements are modified premandibular arches there are at least two objections: firstly, they are lateral to, rather than medial to, the branchial arteries; and secondly, they show no close resemblance in number or design to visceral arches. Only their position against the upper and lower jaws argues for the assumption. Taking these objections into consideration, Luther (1909: 32) suggests that "Diese Stückchen stellen aller Wahrscheinlichkeit nach einer cäno-

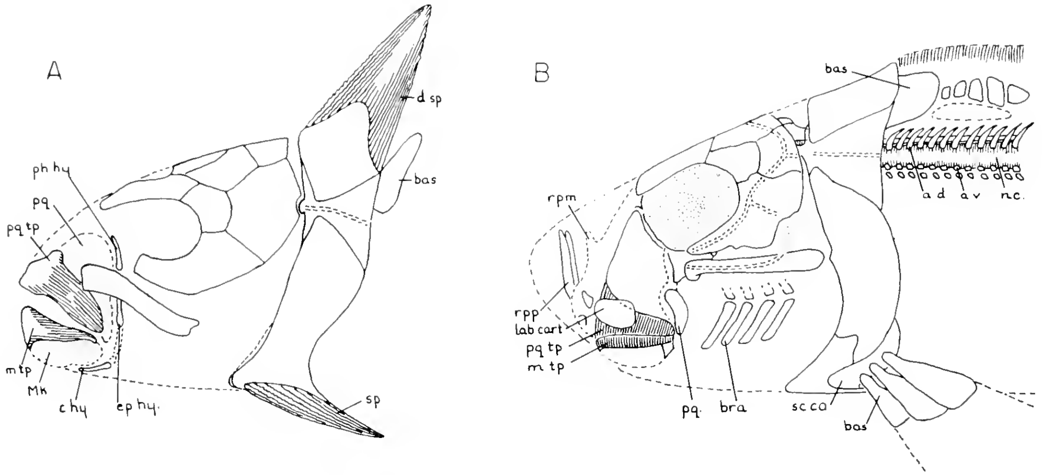


Fig. 6. Reconstruction of the head and shoulder girdle of two ptyctodonts; lateral view. A, *Rhamphodopsis trispinatus* Watson; B, *Ctenurella glodbachensis* Ørvig. *a.d.*, Dorsal arcualia; *a.v.*, ventral arcualia; *bas.*, basal; *bra.*, branchial arch; *c.hy.*, ceratohyal; *d.sp.*, dorsal spine; *ep.hy.*, epihyal; *lab.cart.*, labial cartilage; *Mk.*, Meckel's cartilage; *m.tp.*, mandibular toothplate; *n.c.*, notochord; *ph.hy.*, pharyngohyal; *pq.*, palatoquadrate; *pq.tp.*, upper toothplate; *rpm.*, medial rostral process; *rpp.*, paired rostral processes; *sc.co.*, scapulocoracoid ossification; *sp.*, spinale. (A after Watson; B after Ørvig.)

genetischen Erwerb dar, der speciellen mechanischen Bedürfnissen entsprang." All that can really be said with certainty is that the labial cartilages are quite different from those of sharks in their number and form, and in having muscles inserted upon them, and that their present condition implies a long, separate evolution.

The remainder of the axial skeleton is very much simpler to analyze than the skull, but no more directly indicative of the holocephalians' ancestry. The vertebral column presents certain distinctive characteristics which may be listed in a straightforward manner. Anteriorly, it is consolidated radically—not only are the first two or three vertebrae fused with the cranium, but the first seven elements posterior to the occipital articulation are broadly fused with each other to support the strong dorsal spine and an accompanying basal fin-cartilage. True centra are never present; in *Callorhynchus* the notochord is unconstricted; in *Rhinochimaera* and *Chimaera* cartilaginous rings develop within the notochordal sheath. Rabinerson (1925), who studied the comparative anatomy of the vertebrae of cartilaginous fishes, was of the opinion that the Holocephali were distinct from the selachians in the development of these elements. He recognized that the supra- and hypochordal arch elements of holocephalians bore a greater resemblance to those of selachians than to those of bony fish, but still he held that the similarity was due to convergence rather than to close relationship. Although the holocephalians have retained the primitively unconstricted notochord and in some forms surrounded it with a variable number of skeletal rings, they share with the selachians the tendency to develop arches and intercalary arches above and below it. If Rabinerson is correct in his opinion that the location of the foramina for the spinal nerves differs in holocephalians and in sharks and that the arch units in the two types of cartilaginous fishes have been laid down in a different arrangement, it would seem likely that the holocephalians and selachians evolved separately from a group in which only the general nature of the arch elements was defined.

Among the fossil forms which have been suggested as belonging at the base of the holocephalian line, only the ptyctodonts seem to show any vertebral structures which bear a special resemblance to holocephalian characters. Ørvig (1962) has stated that *Ctenurella* possessed a fusion of arch elements and an enlarged basal of the dorsal fin. Although Watson (1938) did not find a synarcual in *Rhamphodopsis*, he does figure an element which he believed to be the enlarged basal.

In reviewing the appendicular skeleton of the Holocephali, one is struck first by the fact that its general structure is similar to that of selachians and quite unlike that of bony fish. In both types of cartilaginous fishes the pectoral girdle takes the form of a large and firm U which embraces the body from the ventral side. Articulated with this girdle and with the smaller one in the pelvic region are basipterygia to which are attached jointed fin radials that extend halfway out upon the fin. The remainder of the fin is supported by dermal rays. On closer inspection of the holocephalian skeleton, however, distinctive features do appear. The pectoral girdle is extraordinarily massive and contains a pair of channels within it for the passage of blood vessels. Its scapular process extends extremely far dorsally. Whether the form of this girdle represents a modified selachian type or a different development is not possible to decide. Fossil evidence concerning the deep elements of the skeleton in the shoulder area is meager. Moy-Thomas believed that the pectoral girdle of the cochliodont *Helodus* retained separate left and right halves and if so would not have evinced the consolidation characteristic of the holocephalian structure. Neither Watson nor Ørvig describes the internal pectoral girdle of the ptyctodonts. Since the dermal armor of the shoulder was elaborate, however, one may speculate that inner, non-dermal, skeletal elements were not extensively developed.

The pelvic girdle differs from that of selachians in consisting of separate left and right halves. Although this arrangement characterizes the bony fishes, too, it may have been a common occurrence in early gnathostomes. Watson describes a pelvic girdle of this type in the ptyctodont *Rhamphodopsis* and Moy-Thomas also attributes such a structure to *Helodus*. The holocephalian girdle also contrasts with that of selachians in developing a strong dorsal process and foramina for the passage of nerves to the fin. One cannot seize upon these differences as demonstrating a significant separation of the holocephalian line, however, as Dean (1909) describes in *Cladoselache*, in the position of the pelvic girdle, a structure with separate left and right portions.

The pterygiophores of holocephalians and selachians, although similar in their general extent, do differ from each other. The basals of the former group are somewhat more compact, there being two rather than three in the pectoral fin and one rather than two in the pelvic fin. The radials in both forms are jointed, although those of holocephalians show a tendency to fuse at their proximal ends. Males of both groups bear pterygiophores modified as claspers. If one accepts *Cladoselache*, with its broad-based fins, long, unjointed radials, and probable lack of claspers, as typical of the ancestors of modern selachians, clearly one must derive the holocephalians from selachians later than *Cladoselache* in which the modern type of fin was already established or predicate a remarkable convergent evolution in the two groups. Again fossil data is too scanty to back either alternative convincingly. Both Watson and Ørvig claim that the ptyctodonts they have examined probably possessed claspers, and, considering the wide variety of clasper-designs among cartilaginous fishes shown by Leigh-Sharpe (1920 ff.), it is not impossible to imagine their having evolved from more than one source. There is no evidence of pterygiophores in ptyctodonts, although Watson speculates that the pelvic fins in *Rhamphodopsis* were probably narrow-based and freely movable.

The conclusion to which this review of the skeletal system leads is twofold. First, although the skull, vertebral column, and appendicular structures of holocephalians have distinctive features, there exists a sufficient similarity between the general plan of the holocephalian skeleton and that of selachians to suggest that the two groups are related in some way. Second, it seems obvious that the holocephalians have very little in common with the bony fishes. There are occasional similarities—the absence of a partition between the otic and cranial cavities and the existence of separate halves of the pelvic girdle—but no really firm basis exists for postulating a relationship between the two lines.

The nature of the relationship between holocephalians and selachians demands analysis. Certainly, the cartilaginous nature of the skeleton in both is a factor to be considered, but the possibility of its having been evolved separately removes the obligation to derive the holocephalians from an already established selachian line. It is not necessary to adhere to the improbable theory that the holocephalian braincase, with its downward-sloping ethmoid and short otic regions, was derived from the early selachian chondrocranium. If the non-suspensory hyoid is truly primitive, a non-selachian origin for it must be sought. If it is a secondary development, the feasibility of its dedifferentiation from the expanded selachian hyomandibular is still questionable. The palatoquadrate is also different in its proportions from the selachian structure if the point of articulation with the mandible marks its posterior limit. Its fusion to the braincase seems to have been an early event rather than a recent modification if its already cryptic embryonic development has any significance. Finally, labial cartilages are structures in the head which it is difficult to visualize as having been derived from their counterparts in selachians. Since the labial cartilages are regarded as vestigial in the latter group, it is not likely that they would have redeveloped to become the elaborate apparatus of the holocephalians. The median rostral cartilage is harder to assess. The structure is unique and may be a neomorph.

The postcranial skeleton of the Holocephali shows two features which are distinct from their selachian counterparts and difficult to imagine as having been derived from them. The circumchordal elements in chimaerids may be independent developments rather than merely reduced versions of selachian centra. The absence of any type of centra or ring-like structures around the notochord in *Callorhynchus* is possibly a primitive character. The same may be said of the separate halves of the pelvic girdle found in all holocephalians.

The Muscular System

The muscles of the Holocephali have been described by several investigators interested in evolutionary relationships among fishes. Maurer (1912) made a survey of trunk musculature, whereas Edgeworth (1935), Kesteven (1933), Shann (1919), and Vetter (1878) confined their attention to the muscles of the head and shoulder regions. Vetter provided the most exhaustive description of these muscles and assigned names to them. His paper is accompanied by a handsome set of drawings which are helpful in interpreting the text.

In surveying, first, the trunk musculature, one is forced to recognize the similarity of its structure in all fishes. The overriding demands of locomotion as performed by all but a relatively small number of specialized forms have been met by the visibly segmented, more or less zigzagged myotomes which run from the back of the skull and pectoral girdle to the caudal fin. Holocephalians share this general arrangement of the trunk muscles with other fishes but show one specialization which is apparent as soon as the skin is removed: the anterior portion of the ventral hypaxial musculature has become a non-segmented sheet which rises to the level of the lateral line, covering the more dorsal hypaxial bundles. This

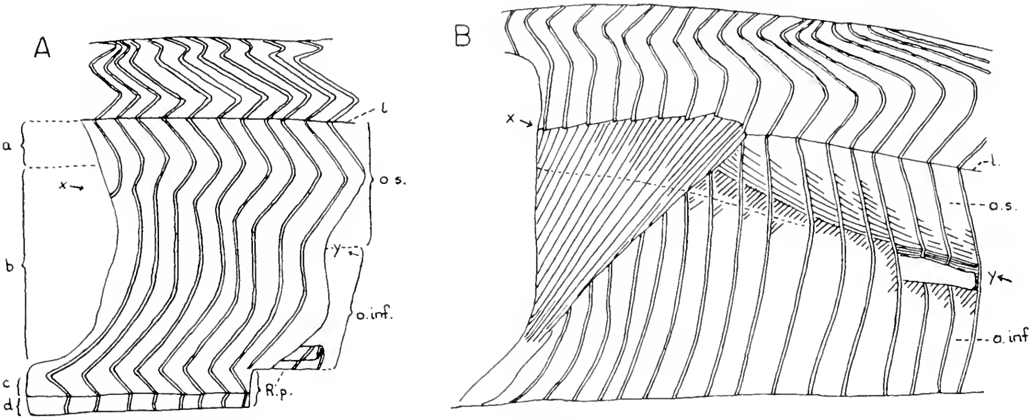


Fig. 7. Trunk musculature: anterior part, lateral view. A, *Chlamydoselachus anguinens*; B, *Chimaera monstrosa*. *a,b,c,d*, Divisions of hypaxial musculature; *l.*, lateral line; *o.inf.*, inferior oblique; *o.s.*, superior oblique; *R.p.*, rectus profundus; line *xy*, dorsal limit of inferior oblique. (After Maurer.)

sheet inserts, as one would expect, upon the pectoral girdle. Maurer (1912), who divides the hypaxial muscles into superior oblique, median oblique, and inferior oblique groups, regards the holocephalian sheet as being a modification of the inferior oblique portion. For Maurer, the state of the inferior oblique in the Holocephali represents a more highly evolved condition than exists in any other cartilaginous fish. In the arrangement which Maurer believes is primitive—that seen in *Chlamydoselache* and *Heptanchus*—there is a discontinuity between the inferior oblique and the median oblique (line x–y in his figures) which is set quite far ventrally, leaving much of the median oblique visible. In the course of evolution, the level of the discontinuity rises. The inferior oblique overlaps the median oblique and the latter is gradually reduced. Maurer relates this change to the growing dominance of the pectoral apparatus to which the inferior oblique is attached, and states that the Holocephali represent the extreme expression of this tendency. (He considers sharks but not batoids.) In Maurer's opinion, the Holocephali are also advanced in lacking a ventral rectus muscle of the sort that *Chlamydoselache* shows. That shark has the two most ventral muscle bundles (c and d in Maurer's figures) rolled medially to form a band bordering the midline. In the sharks, which Maurer regards as more highly developed, and in holocephalians this band does not appear. Throughout his paper, Maurer emphasizes the progression from primitive selachians to Holocephali. It is clear that he regards this progression as having taken place separately from the evolution of the bony fishes.

Shann (1924) noted that fibers of the trunk musculature of fishes are diverted to hold the pectoral girdle in place. Although Shann doubts that it is possible to draw homologies between the various shoulder muscles with absolute accuracy in every case, he does see a basic likeness between the muscles of holocephalians and elasmobranchs. Shann points out, however, that the shoulder muscles of the Holocephali show a far greater differentiation. In sharks, the scapular process is held firm by the antagonistic action of the hypaxial muscles and the cucullaris. The former insert upon the posterior border of the scapular cartilage and the latter upon its anterior edge. In holocephalians, however, both of these groups of muscles are subdivided into external and internal portions. The origin,

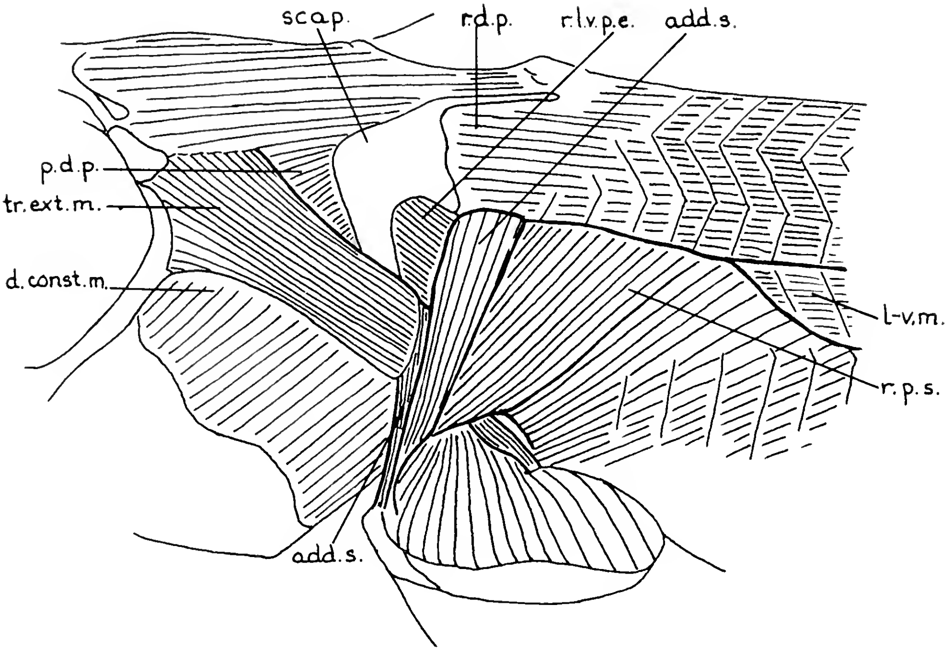


Fig. 8. *Chimaera colliei.* Muscles of the left pectoral region, lateral view. *add.s.*, Adductor superficialis; *d.const.m.*, dorsal constrictor muscle; *l-v.m.*, latero-ventral muscle; *p.d.p.*, protractor dorsalis pectoralis; *r.d.p.*, retractor dorsalis pectoralis; *r.l.v.p.e.*, retractor latero-ventralis pectoralis externus; *r.p.s.*, retractor pectoralis superior; *scap.*, scapula; *tr.ext.m.*, trapezius externus muscle.

insertion, and fiber direction of each differ slightly, clearly a more specialized arrangement. Since the scapular process of holocephalians rises above the level of the horizontal septum, there are also epaxial fibers which insert upon it. In sharks the epaxial muscles are not involved in the shoulder musculature.

In contrast to the more highly differentiated state of the holocephalian shoulder groups, the muscles which are associated with the coracoid region may be simpler than those of sharks. The bases of the coracobranchials are not fused into common coracoarcuals as they are in elasmobranchs. The coracohyoid muscles actually originate on the coracoid cartilage rather than on the fascia over the muscles anterior to it. These aspects of the hypobranchial musculature outweigh, in Shann's mind, the seemingly special, massive development of the coracomandibularis, and he emphasizes his impression that the Holocephali are in these structural arrangements more primitive than the sharks and rays.

From the musculature of the paired fins few inferences may be drawn concerning the relationships of the Holocephali. Again, in principle, the fin muscles of all fishes are much alike. To raise, depress, and twist the fins all that has proved necessary are a dorsal and a ventral muscle mass, some fibers of which are drawn into the fin over an oblique course. The holocephalians present but one modification of the general scheme. The proximal portion of the dorsal muscle mass associated with the pectoral fin is differentiated into discrete bands rather than existing as a simple sheet of parallel fibers. The most superficial band originates on fascia at the level of the lateral line and inserts upon the anterior edge of the fin through a small tendon. From the girdle another band of fibers extends to the front edge of the fin and another to the posterior edge. Between the latter band and the former two, which insert anteriorly, the deeper fibers which cover the fin-radials lie exposed. The distal fibers of the dorsal muscle mass are unmodified and resemble those of sharks. A dissection of the remaining fin muscles in either the pectoral or pelvic region shows that the superficial fibers originate upon fascia or upon parts of the girdle and insert upon connective tissue over the fin basals and radials in the usual way. The deeper fibers originate and insert upon the fin itself as they do in sharks.

The muscles associated with the anterior dorsal fin of holocephalians bear special mention. They consist of a proximal and a distal group of fibers on each side. The proximal muscle mass originates on the plate formed by the anterior vertebral fusion, inserts upon the base of the dorsal fin spine, and acts to elevate the spine. The distal fibers arise from the broad basal cartilage of the fin and insert at the base of the dermal fin rays, allowing the web of the fin to be drawn laterally. This combination of proximal and distal muscles, which is not found in any other cartilaginous fishes, may have been present among the ptyctodonts if Ørvig's interpretation of the skeletal elements of *Ctenurella* is correct. In *Ctenurella*, he finds a synarcual element beneath the dorsal fin and a basal piece which could have served as sites of origin for the proximal and distal fibers, respectively.

Much more has been written about the musculature of the head and pharyngeal region than about that of the trunk and fins. From Vetter's (1878) description of the branchial muscles of the Holocephali, one sees that the mandibular arch group resembles the selachian type, lacking the complex subdivision shown by that group in bony fishes. The adductor mass in holocephalians consists of a portion which is comparable to the quadrato-mandibularis of sharks and, anterior to it, a second part which is regarded as homologous to the selachian preorbitalis. In contrast to the relative size of these muscles in sharks, however, the posterior part of the adductor in holocephalians is smaller than the extensive preorbitalis. The preorbitalis has spread upward over the broad wall of cartilage created in front of the eye, by the fusion of the palatoquadrate cartilage to the neurocranium, and the development of the high cartilage wall in the ethmoid region. The levator and constrictor elements associated with the selachian mandibular arch are not present in holocephalians. The muscles which insert upon the holocephalian labial cartilages, however, appear in no other group of fishes.

The muscles of the hyoid and successive arches contrast sharply with those of sharks. The levator fibers in holocephalians are grouped in external and internal divisions, as was mentioned above, rather than existing as a unified cucullaris. The individual constrictor muscles of the posterior arches, identifiable in sharks, have disappeared. Only the hyoid constrictor remains, and this element is expanded to provide the musculature of the operculum. In the possession of a hyoid constrictor of this kind and in the reduction of the musculature associated with the branchial arches covered by the operculum, holocephalians bear a resemblance to the bony fishes. Kesteven (1942–1943), who accepted this resemblance as evidence of evolutionary relationship, was led into the construction of an evolutionary scheme which is untenable in the face of recent paleontological findings. It might be more correct to suppose that the similarities which do exist between holocephalians and bony fish have come about through convergence.

One could assume, then, that the holocephalian branchial musculature, with its distinctive specializations, developed in correlation with the crowding forward and the

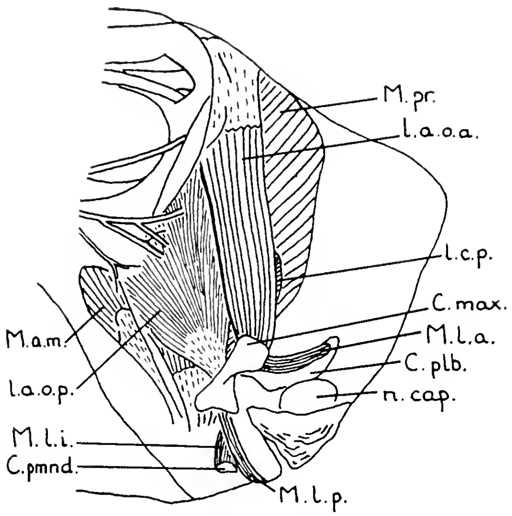


Fig. 9. *Chimaera monstrosa.* Muscles of the head, lateral view. *C.max.,* Maxillary cartilage; *C.plb.,* prelabial cartilage; *C.pmnd.,* premandibular cartilage; *l.a.o.a.,* levator anguli oris anterior; *l.a.o.p.,* levator anguli oris posterior; *l.c.p.,* levator of prelabial cartilage; *M.a.m.,* adductor mandibulae; *M.l.a.,* labialis anterior muscle; *M.l.i.,* labialis inferior muscle; *M.l.p.,* labialis posterior muscle; *M.pr.,* preorbitalis muscle; *n.cap.,* nasal capsule. (Adapted from Luther.)

fusions which took place within the visceral and cranial skeleton during the independent evolution of the Holocephali. As the gill arches became compressed under the occipital region and the extrabranchial cartilages spread to form an opercular cover, the branchial constrictor muscles gave way in favor of an expanded hyoid constrictor sheet. The branchial levators, adductors, and interbranchials all became reduced in accordance with the reduction and compression of the cartilages of the arches. Since the mandible is short in holocephalians and forms only a shallow curve, the ventral portion of the hyoid constrictor (which reaches the midline in sharks as the interhyoideus) apparently shifted the origin of its most anterior fibers forward to the connective tissue on the posterior ventral edge of the mandible. There being no division between the palatoquadrate and the ethmoid region of the cranium, the muscles innervated by the trigeminal nerve spread over the entire anterior region of the head. The divisions of this muscle which insert upon the labial cartilages would seem to be late developments. If the branchial muscles of the Holocephali evolved as suggested here, it would be logical to seek an ancestral stock in which the shortening of the head region had already begun. The ptyctodonts show such a condition and may thus be a better choice as ancestral material for the holocephalians than the longer-headed cochliodont *Helodus* or any early selachian.

In sum, then, one recognizes in the muscular system of the Holocephali a number of similarities to the system of sharks, many characteristics which are certainly specializations peculiar to the group, and certain features which are comparable to those of bony fishes. Among the holocephalian muscles, which show some resemblance to selachian counterparts, are the trunk and fin muscles, the hypobranchial muscles, and the adductor muscles of the mandibular arch group. Within each of these groups of muscles, however, some unique arrangement appears: the sheet-like, nonsegmented inferior oblique among the axial muscles; the special nature of the proximal pectoral extensors among the fin muscles; the great expansion of the preorbitalis in the mandibular arch group. Besides these peculiarities, the complexity of the shoulder musculature, the anterior dorsal fin muscles, and the muscles which insert upon the labial cartilages must be regarded as singular and non-selachian in nature. The sole resemblance of the holocephalians to the bony fish lies in the presence of an expanded hyoid constrictor and reduced musculature of the posterior branchial arches. In assessing this similarity as evidence of convergence rather than relationship, one may well be on solid ground. Estimating the significance of the similarities between holocephalians and selachians is more difficult, however. Since the musculature of the holocephalians shows no characteristics which are clearly more primitive than those of any shark—unless the absence of the common coracoarcuals be so considered—the possibility of its evolution from a generalized selachian pattern cannot be ruled out. On the other hand, the axial and branchial musculature shows many specializations which are closely allied to the design of the skeleton. If one considers the evolution of the muscular system in correlation with that of the skeleton, it seems more logical to suppose that it developed, as the skeleton seems to have done, from a more ancient root than the early selachian fishes. And if one leans toward the idea of descent from a ptyctodont rather than from a selachian group, it may be perhaps because it is easier to imagine building holocephalian musculature upon a ptyctodont frame, especially in the head region, than it is to derive it from shark-like origins.

The Urogenital System

Little research has been done on the urogenital system of the Holocephali. Studies of its development are lacking and the histology of its component organs has received only cursory attention (Burlend, 1910; Leydig, 1851). Its gross anatomy, which is known, is almost exactly like that of sharks and quite different from that of bony fishes.

A glance at the reproductive organs of the female holocephalian reveals an arrangement which is exactly like that of many selachians. Both ovaries, equally well developed, are set far forward in the body cavity. The oviducts run lateral to the ovaries to open with a common ostium in the extreme anterior end of the coelomic space. The shark-like nature of this arrangement is emphasized if one reviews the female genital system of other types of fishes: in almost all teleosts the oviduct is continuous with the ovary so that the eggs, which are produced in large numbers, are at no time free in the coelom. In a few forms like the trout, the ovary does release eggs into the body cavity, but the ostium of the oviduct may be located more posteriorly than it is in the cartilaginous fishes and the oviduct itself never shows the specialized areas characteristic of the oviducts in Chondrichthyes. In species which are descended from the earlier parts of the bony fish line (*Polypterus*, *Acipenser*, *Amia*, *Lepisosteus*), the ovary is unenclosed but is either more elongated or located more posteriorly. The oviduct in these forms differs in design from that in cartilaginous fishes. Admittedly, the position of the gonads and ducts in the female lungfish corresponds more nearly to that of the Holocephali. The lungfish ovary is much longer, however, and the oviducts are unspecialized and have separate ostia.

The specialized regions of the holocephalian oviduct resemble closely the selachian type. Prasad, who made a series of histological studies of such specialized areas, said, ". . . the nidamental glands of *Hydrolagus colliei* exhibit a structure very similar to that of a typical oviparous elasmobranch . . ." (Prasad, 1948: 57). One could say, in view of the similar reproductive habits of oviparous elasmobranchs and holocephalians, that their similarly specialized oviducts were a parallel development, but there is no evidence to disprove the idea that these fishes may have inherited both the habits and the structures from an earlier—even a very much earlier—common stock.

In searching for differences between sharks and holocephalians, one might seize upon the fact that adult female sharks have a cloaca whereas their holocephalian counterparts do not. However, the importance of this point diminishes when one sees that the young female holocephalian has at least a deep urogenital sinus which disappears as the uteri enlarge and press outward in the maturing animal. The one unique structure possessed by the female holocephalian is the so-called seminal vesicle. Hyrtl, who reported in 1850 on the indented blind sac which opens just posterior to the anus, thought that it functioned as a "Samentasche," but Burlend (1910) showed that it was glandular. Redeke (1898) saw in this sac a possible homologue of the digitiform gland of sharks: if the rectum of the holocephalian were pulled inward from the surface, drawing the "seminal receptacle" in with it, the latter structure would be in the same relation to the hindgut as the gland of the shark. It is probable that, whatever its mode of formation, the blind sac, which is not found in any other vertebrate, represents a minor specialization which has occurred in the later evolution of the Holocephali.

The reproductive system of the male holocephalian is as shark-like as that of the female. In both types of fishes the testis is connected by vasa efferentia to a highly coiled epididymis through which sperm are conducted to the more posterior and wider portion of the vas deferens. The vasa efferentia of the shark represent transformed anterior kidney tubules which lead into the embryonic Wolffian duct, and it is presumed that the efferent ductules of the Holocephali are homologous structures. The anterior part of the kidney in immature sharks and chimaerids has glomeruli in it, but these disappear during growth toward sexual maturity. The anterior part of the kidney transforms itself from an excretory to a secretory organ and is then known as Leydig's gland. In holocephalians, as in sharks, its secretion, which passes through short ducts to the epididymis and vas deferens, serves as a fluid matrix for the suspension of the sperm. The posterior portion of the kidney in both kinds of fishes remains excretory, sending urine through one or more ureters which empty into a urogenital sinus. In commenting upon the arrangement of pathways in the male system, Van Oordt says, "hinsichtlich, der Abführung der Spermien stimmen die Holocephalen mit den Selachiern überein" (Van Oordt, *in* Bolk, 1938, Vol. V: 750). In resembling the selachian system so closely, the male reproductive system of the holocephalians is markedly different from that of the bony fishes. In the latter group one finds either a duct for sperm which is separate from the original archinephric duct or the tendency to develop such an arrangement. Even in *Acipenser*, where the expression of this tendency is minimal, the urogenital system is distinguished from the selachian and holocephalian types by lacking a secretory portion derived from the anterior end of the kidney. No bony fish develops an accessory organ comparable to Leydig's gland.

Given the great degree of similarity between male selachians and holocephalians, investigators have tried to define the relatively small points of difference which do exist. It has been observed, for instance, that the number of vasa efferentia varies. In contrast to one in *Scyllium*, *Chimaera monstrosa* has five or six. Borcea (1906: 349), who made an extensive study of the urogenital system of elasmobranchs, considers that "le nombre des vaisseaux efférents est plus élevé et le canal longitudinal de l'epididyme est plus long chez les types les plus primitifs." In making this statement, Borcea had in mind the fact that the batoids are characterized by a few or only one vas efferens.

Another minor difference concerns the posterior region of the vas deferens which is enlarged to form an ampulla (Van den Broek's term) or a sperm vesicle (Burlend's term). In both sharks and chimaerids, the inner wall of this structure is thrown into folds which divide the lumen of the duct. In sharks like *Scyllium*, however, the partitions are as simple as septa in a mushroom cap, whereas the inner walls in a large section of the chimaerid ampulla run into one another in a more complex fashion, cutting up the space within the passage into interconnecting compartments. One feels, upon studying these septa, that their different design is less important than the fact of their presence in both holocephalians and selachians. The appearance of these structures is a remarkable point of similarity in two forms whose lines (in consideration of other organ systems) seem to have separated far back in time.

This same idea may be emphasized in the matter of the claspers of the male. Before describing the differences which exist between these structures in sharks and holocephalians, one must dwell a moment upon the fact that claspers, which are not a common vertebrate characteristic, do appear in a generally similar form in both of these groups of fishes. It would seem, at first, that the possession of such claspers is signal proof of the close relationship of sharks and holocephalians. The major obstacle to the acceptance of this idea lies in the fact that *Cladoselache*, a form apparently antecedent to modern sharks, shows no claspers. If it really had none, then the holocephalians must have developed their claspers independently. That they did so is not an impossible assumption. It appears that claspers may not be as peculiarly elasmobranchian a character as one would assume from a study of extant fishes. If Watson (1938) and Ørvig (1962) are correct in postulating the presence of claspers in *Rhamphodopsis* and *Ctenurella*, respectively, it may be that these structures were possessed by a number of placoderm groups. If that was the case, holocephalians and selachians might bear claspers inherited from separate ancestral stocks. In support of this hypothesis one might cite Ørvig's finding of a pair of dermal spines anterior to the pelvic girdle of *Ctenurella*. He believes that these spines may have been associated with anterior claspers, adjuncts to the reproductive system found in holocephalians but not in elasmobranchs.

The elaborate array of claspers characteristic of holocephalians sets these fishes apart from other cartilaginous forms. No other type of fish has either the aforementioned anterior claspers in front of the pelvic fins or the strange median frontal clasper or tenaculum set upon the dorsal surface of the head. In all extant holocephalians the anterior claspers are represented as small, gripping structures which are concealed in a pouch when not in use. Leigh-Sharpe (1922) believes that the prepubic processes found in *Squaloraja* supported anterior claspers in that Jurassic form. There are no reports of these structures in earlier fossils, however, except for Ørvig's mention of the spines in *Ctenurella*. Since Ørvig found no trace of a tenaculum in *Ctenurella*, the earliest form of that structure is known from *Squaloraja* and its contemporary, *Myriacanthus*. The tenaculum in those fishes was a long pointed protuberance. In living holocephalians, the tenaculum is smaller and rounded at its distal end.

In a lengthy series of papers Leigh-Sharpe (1920 ff.) presents a review of elasmobranch and holocephalian claspers. He describes the claspers of *Chimaera* and *Callorhynchus* as having two branches and suggests that these branches represent the ultimate and penultimate pelvic fin radials. He believes that claspers of this type are primitive. However, *Rhinochimaera*, which is thought to be the most primitive holocephalian in terms of its other systems, has an unbranched clasper more nearly like that of sharks. Leigh-Sharpe (1922) includes a drawing of a clearly preserved clasper of the fossil *Squaloraja* which shows a single but unusually broad structure terminated by a group of small, dermal hooks. Since the clasper of *Squaloraja* is unique in form, and since *Squaloraja* lived in Jurassic times when the holocephalian line was already established, one cannot be sure that the claspers of this fish give evidence of the original nature of the holocephalian structures.

In his classification of the cartilaginous fishes according to the type of clasper they show, Leigh-Sharpe sets the Holocephali amongst the primitive forms for still another reason. They have not developed the abdominal structures—a pair of muscular cavities called siphons—which play a role in sperm passage during the copulation of most elasmobranchs. Holocephalians do have a different sort of cavity, though, located in the proximal portion of the clasper.

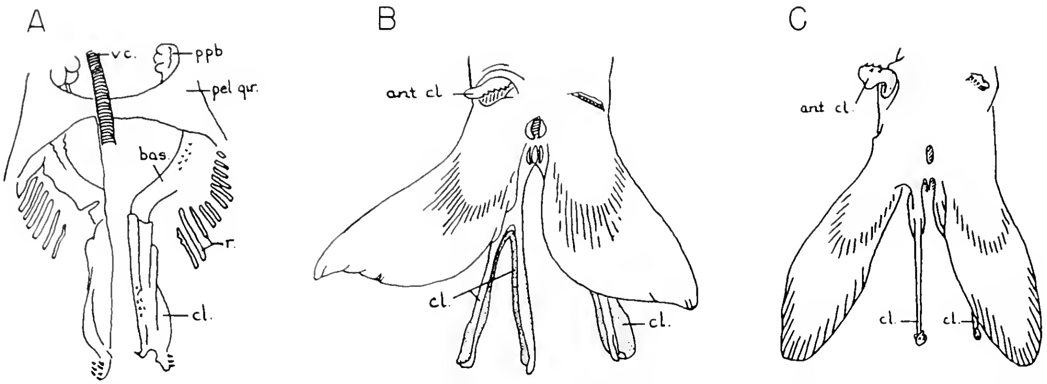


Fig. 10. Claspers of various holocephalian forms. A, *Squaloraja*; B, *Chimaera monstrosa*; C, *Rhinochimaera atlantica*. *ant. cl.*, Anterior clasper; *bas.*, basal; *cl.*, clasper; *pel.gir.*, pelvic girdle; *ppb.*, prepubic processes; *r.*, fin-rays; *v.c.*, vertebral column. (After Leigh-Sharpe.)

Leigh-Sharpe interprets this cavity as homologous to that of *Chlamydoselache* and so brackets these fishes together. Surely a common category for these forms stands on shaky ground. The Holocephali should probably be set apart even here if the presence of their curious frontal and anterior claspers is taken into consideration.

Although the kidneys have not been thoroughly examined histologically, their gross anatomy and their relationship to the genital organs have been well described (Burlend, 1910; Leydig, 1851). There is no doubt that these organs, too, are like those of elasmobranchs and quite different from those of other fishes. Unlike the kidneys of the cartilaginous forms, those of bony fishes never become closely involved with reproductive structures in the male and, in both sexes, are generally uniform in tubule-structure throughout their length, undergoing neither transformation nor degeneration at the anterior end as the animal reaches maturity. It is not necessary to lean entirely upon structural resemblances to predicate a possible relationship between the Holocephali and the Selachii either. The excretory systems of both groups bear the same distinctive functional earmark: the kidneys resorb urea selectively and maintain that substance in the bloodstream in unusually high concentration.

In adult holocephalians, as in sharks, urine is produced in the posterior regions of the kidney and drained by specially developed ureters. This arrangement contrasts with that of bony fish in which urine is produced throughout the entire kidney and is removed through the opisthonephric duct. In cartilaginous fish of the male sex the anterior kidney and the Wolffian duct become part of the reproductive system as was mentioned before. In females, despite there being no secondary use for the anterior region of the kidney, that portion degenerates and the Wolffian duct stretches forward and ends blindly. In the animals of both sexes the kidney gives some hint of its originally segmented nature. Especially in the anterior region traces of segmental divisions remain. The segmental blocks are particularly noticeable in the male, because ducts leave the gland of Leydig at segmental intervals.

Borcea (1906), in the study to which reference has already been made, is plainly of the opinion that the elasmobranchs represent the primitive vertebrates from which all the others have descended. Although most students of evolution no longer agree with that premise, they still admit the possibility that certain characteristics of cartilaginous fish may have been carried over from their primitive ancestors at the placoderm level. With this idea in mind and in consideration of the similarity of the urogenital systems in holocephalians and elasmobranchs, one may find interesting the following comment of Borcea: "C'est le groupe des Elasmobranches, qui nous montre la succession de ces trois stades (of the evolution of the vertebrate kidney) avec la plus grande netteté. D'une part, ils présentent l'état néphridioide . . . plus nettement que n'importe quel autre groupe de Vertébrés. D'autre part, ils sont parmi ceux-ci, les animaux les plus primitifs chez lesquels les glandes génitales entrent en relation avec le rein et son uretère primaire et alors la série des changements se montre d'une façon très manifeste. Chez les Elasmobranches la division de l'urètere primaire est tout à fait nette. Chez les plus primitifs d'entre eux ce n'est qu'à l'état adulte (en relation avec la maturité sexuelle), qu'on constate la modification du rein supérieur" (Borcea, 1906: 251).

Disregarding Borcea's use of the term "état néphridioide" which summons up an argument quite apart from the subject of this paper, one can still see in his statement reasons to support the thesis that the elasmobranch urogenital system is primitive rather than secondarily simplified. If the system is primitive, then there is an alternative to the theory that the holocephalians, whose urogenital organs seem shark-like, must therefore have diverged from the elasmobranchs relatively late. It is possible to speculate that, as evidence drawn from other structures suggests, the holocephalian and elasmobranch lines did split far back among their placoderm forebears, and that both groups of fish have carried to modern times the type of urogenital system which those early vertebrates possessed. That a system of this type may have become widespread in primitive gnathostomes generally is suggested by the development in all vertebrates except the bony fishes of an interrelationship between the testis and the kidney similar in principle to that which appears in the cartilaginous fishes. This idea is supported further by the emphasis, again in all vertebrates except bony fishes, upon the posterior portion of the kidney as the part chiefly responsible for excretory function.

To summarize the foregoing points, one may state that the urogenital system of the holocephalians resembles the selachian system closely. In the position of the gonads, the specialization of the accessory ducts, the nature of the kidney, the development of accessory ureters, and the possession of claspers on the pelvic fins of male animals, the two groups of cartilaginous fishes are remarkably alike. The type of urogenital system they share is distinct in all of these features from that of bony fishes. The kidneys of holocephalians and selachians are set apart from those of all other vertebrates by their ability to resorb urea selectively and return it to the circulating blood. The major point of difference between holocephalians and selachians lies in the possession by the former of claspers anterior to the pelvic fins and of a median tenaculum.

Although the remarkable similarity of the urogenital system of holocephalians to that of selachians could be cited as evidence of the evolution of the Holocephali from the selachian line, there appears to be an alternative to that hypothesis. Since it seems possible that the urogenital system of cartilaginous fishes is truly primitive and if so may have existed in a number of early gnathostome groups, holocephalians and selachians could have evolved from two separate ancestral stocks. Both types of cartilaginous fishes could have retained the urogenital system in its ancient form. This theory presumes that the holocephalian and selachian claspers were not derived from the same source. The possibility that ptyctodonts possessed claspers allows one to believe that there may have been more than one source of those structures at the placoderm level. The presence of anterior and frontal claspers in living and fossil holocephalians but not in selachians increases the probability of the existence of a separate placoderm ancestor for the holocephalians.

The Digestive System

The search of the digestive system for evidence of hereditary relationships turns up a profitable thread or two and also reveals several alleys which end blindly. As might be imagined, an investigation of the structure of the teeth gives rise to speculations based on firmer ground than does an examination of the digestive tract itself or its associated glands.

Holocephalians have three pairs of toothplates. The smallest, called vomerine plates, are located in the anterior portion of the upper jaw immediately in front of the larger palatine pair. The mandibular plates of the lower jaw are the largest, being equal in length to the other two combined. A comparison of the sections of these teeth figured by Brettnacher (1939) with those of cochliodonts shown by Nielsen (1932) suggests that the two tooth-types are not similar, as Moy-Thomas (1936) had maintained. A difference if it does exist, is important, because the structure of the toothplates was one of the main supports of the theory that the Holocephali are descended from bradyodonts. If the teeth of the two groups are truly unlike, and if the presence of holostylic jaw suspension in both groups is not as important a factor as Moy-Thomas thought it was, then the case for close relationship becomes very much weaker.

The discrepancies in tooth-type become apparent when descriptions of the internal structure of the teeth of each are set side by side. Eigil Nielsen (1952: 34) gives the now classic description of the bradyodont type: "This Bradyodont structural type is especially characterised by possessing a system of numerous, more or less parallel vascular canals ascending through the greater part of the crown, but ending blindly just below the tritoral surface. The ascending canals are lined with layers of dentine, and the dentine around each canal is separated from that around the other canals by a hard tissue, described as enamel by me in 1932."

The chimaerid toothplate has been examined, described, and figured by Bargmann (1933) and Brettnacher (1939). Their accounts of the histology of the toothplates agree, although the terminology that they use in their descriptions is not exactly the same. The outer surface of the crown of each plate as well as its embedded portion consists of a type of dentine which Brettnacher calls "Hüllendentin" and Bargmann calls "Manteldentin." In areas where epithelium comes in contact with the toothplate, there is a superficial layer of very hard material which, for Brettnacher, is true enamel, and for Bargmann merely a specially transformed part of the "Manteldentin." In the interior of the tooth, according to both men, there is a *meshwork* of dentin trabeculae rather than parallel dentinal tubules. Brettnacher gives these trabeculae the special name of "Balkendentin" (because they form supporting beams), although he does state that they are formed by an extension of the odontoblast layer which creates the "Hüllendentin." Bargmann uses the term "Manteldentin" to embrace the trabeculae as well as the peripheral layer. The spaces in the trabecular region are pulp channels which Bargmann says are slowly obliterated in the pressure-receiving parts of the plate by deposition of circumpulpar dentin.

Jacobshagen, who relies upon Brettnacher's work, has included the chimaerid toothplate in his review of the structure of selachian teeth (1941). As he presents his figures and comparative descriptions, one sees that there could be logic in his reasoning that the internal arrangement of the holocephalian plate is a primitive variant of the dentinal pattern still in existence in extant elasmobranchs. Both holocephalians and selachians show the outer "Hüllendentin" covering an inner trabecular meshwork. The categories that Jacobshagen establishes depend upon the thickness of the outer dentin layer and the amount and distribution of the inner "Balkendentin."

Jacobshagen does make a separate category for the toothplates of the Holocephali, not only because of their plate-like structure, but also because they contain a unique material which both Brettnacher and Bargmann describe. Brettnacher calls it "primary dentin" and Bargmann uses the old term "Kosmin" to refer to it. This substance is found within the pulp channels in several regions within each plate. Sometimes the Kosmin appears in pearl-like masses strung in rows; in some teeth the "pearls" seem coalesced to form an elongated bar. All the investigators who have discussed Kosmin regard it as an ancient vestige. Schauinsland thought it represented the remains of fused cylindrical teeth. Bargmann discards this idea, however, for the teeth of younger specimens show Kosmin in its undivided bar-like form. The rather periodic, pearl-like division, he feels, is a later manifestation. Bargmann has his own theory: he compares the structure of Kosmin to the structure of the surface knobs on *Cephalaspis* plates, and speculates that in the evolution of the Holocephali this early type of hard tissue may have sunk inward.

Brettnacher and Jacobshagen point out that dentin in general may have evolved from a relatively soft substance, penetrated by widely spaced, branching tubules to a much harder material with close-ranked parallel tubules. With this idea in mind they both consider that the dentin-tissue in the Holocephali is of the primitive type, the toothplate deriving its strength from the arrangement of the dentinal trabeculae rather than from the hardness of the dentin itself.

As these workers describe and discuss the structure of holocephalian toothplates, it seems less and less likely that these plates have much in common with cochliodont teeth. The latter consist of what Ørvig (1951) would classify as "tubular dentin" and in Nielsen's figures look singularly different from anything produced by the Holocephali. The "Balkendentin" which fills the chimaerid toothplate seems more akin to Ørvig's osteodentine in its arrangement and its apparent mode of development.

If it is not correct to associate holocephalian and cochliodont teeth with each other, one is free to seek other relationships. It seems not unreasonable to connect the chimaerid structure with that of ptyctodonts. Ptyctodont plates have been studied histologically most recently by Gross (1957) and Ørvig (1957). Gross found very little difference between the teeth of *Rhynchodus* and *Ptyctodus*, and his general description reveals a surface layer of dentin supported from within by dentinal trabeculae which formed a network. Against these internal trabeculae in tritoral areas, what Gross calls a secondary dentin was laid down. It would have been interesting if Gross had referred to the work of Brettnacher and Bargmann. Without such a reference one cannot be sure whether Gross considered the dentin material which he mentions equivalent or similar to that of the Holocephali. It is impossible from Gross' description, for instance, to tell whether he saw something like Kosmin. It appears that he did not.

Ørvig's description of *Paleomylus* is more puzzling. He states that the *Paleomylus* toothplate is much like those of *Ptyctodus* and *Rhynchodus*, and in the number of its tritoral columns even more like the Mesozoic and Cenozoic Holocephali. But he describes these tritoral columns as being separated by acellular bone, while in holocephalians they are separated by an interstitial substance "not unlike enamel." He refers to the chimaeroid columns as being of a peculiar tubular dentin *"sui generis."* Since describing the *Paleomylus* toothplate in 1957, however, Ørvig has revised his terminology. For hard tissues which grow inward toward the basal region of the toothplate, including tritoral columns, he has introduced the name "pleromic hard tissue." Although he does not mention *Paleomylus* specifically, in a forthcoming book he indicates similarities between the pleromic hard tissue of ptyctodont arthrodires and holocephalians. He emphasizes the difference in arrangement of the pleromic tissues of ptyctodonts and holocephalians, on the one hand, and of bradyodonts, on the other, by classifying the pleromic material of the former as columnar and of the latter as coronal.

Although it is usual to analyze the histological structure of teeth in an effort to derive evidence of phylogenetic significance, it might be well to keep in mind the possibility that convergent evolution could have brought about similar structure where no relationship exists. Radinsky (1961), who has found similar patterns in the dentin of bradyodonts, batoids, selachians, and dipnoans, is of the opinion that the internal structure of teeth may be adaptive and that classification should therefore not be based entirely upon it. Despite this consideration, however, the results of a comparison of cochliodont, holocephalian, and ptyctodont teeth seems useful. The difference between holocephalian teeth and those of cochliodonts, although the latter fishes were apparently durophagous, should be kept in mind. The resemblance between the structure of ptyctodont and holocephalian teeth may be significant in combination with other evidence.

One should not leave a discussion of chimaerid toothplates without mentioning the problem of their origin. Their plate-like structure is unusual and has dictated comparisons between the Holocephali and other vertebrates like Dipnoi that also possess plate-like formations in the mouth. These comparisons founder, however, upon one point. The plates of lungfish, the teeth of most cochliodonts, and the pavement dentition of rays, all can be shown to be compounded of units which arise first as separate entities. In holocephalians no amalgamation of individual denticles is demonstrable. Even in the early embryos which Schauinsland studied there were no indications of a fusion of teeth or tooth buds. It is possible that the Holocephali descended from forms whose teeth lost their discrete nature and that, as the group evolved, ontogenetic evidence of fusion was suppressed. Since it has not been demonstrated that all fossilized toothplates evolved through a compounding of individual units, however, it may be that holocephalian toothplates were derived from pre-existing integral structures. As antecedents of holocephalian toothplates, ptyctodont plates might be preferable to large cochliodont teeth produced through fusion.

In turning from the toothplates to the digestive tract, one reaches a series of structures whose evolutionary history is even harder to define. All the Holocephali show, beyond the mouth and pharynx, an esophagus which leads to the intestine directly, without the intervention of a differentiated stomach expansion. The obvious question—is the lack of a stomach a primitive or a degenerate character?—has found no sure answer. Since the stomachless condition is found in a number of unrelated fishes, one could argue that it represents a common type of degeneration which has occurred independently in several lines. On the other hand, the absence of a stomach in cyclostomes may be a remnant of the earliest vertebrate plan. At least one worker, Fahrenholz (1915), assumes that this is true in the case of the Holocephali. Since one answer seems as logical as the other, neither can be relied upon to carry much weight in the solution of the evolutionary problem.

The same may be said about the holocephalian spiral intestine. All the chimaerid fishes show an intraintestinal fold which takes one slow turn throughout the greatest part of the intestinal tube and then makes two and a half tighter turns at the posterior end. The edge of the fold is free in the loosely coiled forepart and caught up in the center of the corkscrew turns at the end. This arrangement seems to be a combination of the "gerollte" type which Jacobshagen (1915) described as existing in a few sharks and the "gedrehte" type which he declared to be much more common amongst the selachians. The peculiar nature of the spiral valve can be interpreted in either of two ways. Firstly, as Fee (1925) and Dean (1906) see it, the viscera of the chimaerid fishes, believed by them to be modified relatively late from sharks, have been crowded into a shortened body cavity. The stomach dilation fails to develop and "the intestinal valve, instead of undergoing the further spiral development of sharks, makes but a few turns (about four) . . ." (Fee, 1925: 179). The view of the valve arrangement as secondary, as set forth here, might be supported by Jacobshagen's contention that reduction in the intestinal fold always takes place from the anterior end. In fishes which bear a degenerate spiral valve or a vestigial one, the parts of it that remain are in the posterior region of the intestine. Secondly, the holocephalian valve might be held as primitive, especially in its histological structure. Evidence for this contention has been presented by Jacobshagen (1934), who has made a detailed comparative study of the spiral intestine in selachian, dipnoan, ganoid, and jawless fish. He points out that the valvular infolding in sharks includes only the mucosa and the muscularis mucosae. Since the ammocoetes larva shows inclusion of circular muscle as well, Jacobshagen suggests that the primitive fold was an indentation of the whole intestinal wall which lay within the enveloping serosa. Significantly, the holocephalians are the only fish that show portions of the main circular muscle of the intestine still included in the adult valvular fold. Of course, Jacobshagen's idea may be incorrect, and the inclusion of the muscle may not be a primitive condition in either animal.

As one advances to a consideration of the glands associated with the digestive tract, one finds less and less information available. Scammon, who has studied the selachian liver, reports in his account of it that "the histology of the adult elasmobranch liver was first briefly described by Leydig from observations on *Chimaera*" (Scammon, 1915: 245). Since Scammon does not even think to distinguish the holocephalian from the selachian organ, it is apparent that their characteristics must be very much alike. Scammon holds that the elasmobranch liver differs from that of other vertebrates by its unique type of lobulation, its accumulation of fat within the hepatic cells, and its comparatively slight development of the bile duct system. It is impossible to decide whether these characteristics are peculiar to the shark line or whether they arose deep within the placoderm stock.

The holocephalian pancreas has apparently not been studied. Siwe, writing in 1926, does not mention the chimaerid structure in his paper on the comparative anatomy of that gland. The only other glandular organ associated with the digestive tract of the Holocephali that has received attention is an intraparietal mass of tubules located at the posterior end of the spiral valve. Citterio (1932) discusses this gland, first described by Leydig, suggesting that it might be homologous to the digitiform gland of selachians and more primitive in its intraparietal location.

Another structure which may have a selachian homology is the mass of lymphomyeloid tissue dorsal to the skin of the palate. Extant sharks and rays have a pair of structures, similar in their histology, built into the sides of the esophagus (Fahrenholz, 1915). The tissue itself seems of a like construction in the Holocephali and the selachians: both show several different types of myeloid cells set in a fibrous stroma which is highly vascular. Kolmer (1923) who examined the tissue in *Chimaera monstrosa* regarded it as hemopoietic. Its distribution in the Holocephali is singular. There is none in the esophageal wall, but it exists in a large mass not only over the palate but also within each orbit and in the ethmoid canal. The tissue masses are connected by strands which run through foramina from one area to another. There seems to be a relatively small mass of it, isolated from the rest, within a pair of ventral channels in the pectoral girdle. Kolmer, impressed by the fact that much of this tissue was surrounded by cartilage, refers to it as "knockenmarkähnliche Gewebe." However, all of it seems to be external to the perichondrium. The presence of this tissue raises more questions than it answers. No one has dared to guess whether it is, in its present extent in the Holocephali, a specialization lately developed or another primitive vestige.

Conclusions from the nature of the digestive tract are difficult to draw. The Holocephali are extraordinary in the structure of their teeth, the lack of a stomach, the design of the intestinal valve, and the presence in association with the gut of unique masses of glandular and lymphomyeloid material. Examination of these characteristics, however, does not produce extensive evidence of value in solving the phylogenetic problem. Some clues may be gleaned, nevertheless. The greater resemblance between the internal structure of holocephalian and ptyctodont teeth than between those of holocephalians and cochliodonts suggests, if such similarities are at all significant, that there is more likelihood of a relationship between the Holocephali and the former than the latter group. The contrast between the integral structure of holocephalian toothplates and the tendency toward fusion of teeth which Moy-Thomas (1936) describes as being exhibited by the cochliodont *Helodus* makes it seem improbable that this type of cochliodont was ancestral to the Holocephali.

A hint of similarity to selachians lies in the likeness of the liver in the two groups of cartilaginous fishes. The affinities of the remaining soft parts of the digestive system of holocephalians defy analysis. It is impossible to determine whether the lack of a stomach and the minimal development of the spiral valve are primitive or secondary conditions. The evolution of the glandular mass at the posterior end of the intestine and of the lymphomyeloid matter in the pharyngeal region is equally obscure. One must admit, then, that little can be derived from an analysis of the digestive organs to reinforce either the theory of a selachian or a non-selachian origin of the Holocephali.

CONCLUSION

The study of the venous system of *Chimaera colliei* was undertaken in an attempt to clarify the evolutionary history of the Holocephali. The fishes of this group have been long regarded as an offshoot from the shark line and as such have been placed with selachians, bradyodonts, and batoids, in the class Chondrichthyes. The non-replacement of their toothplates resulted in their association with the bradyodonts, and through the work of Moy-Thomas (1936) the theory was established that they might have descended from a cochliodont of that group. Of late, however, Ørvig (1962) has argued that the Holocephali are more probably derived from a ptyctodont ancestor and so only distantly related to sharks.

In an effort to re-evaluate the position of the Holocephali, the anatomy of the venous system was examined for similarities and differences between it and that of other fishes. Undoubted resemblances to the selachian system were found in the presence and arrangement of sinuses and in the existence of a subcutaneous network of veins. The hepatic portal system, while not exactly like that of sharks, resembled the selachian system more nearly than that of bony fishes. The two main points of difference from selachians lay in the absence of lateral abdominal veins and the opening of the hepatic veins into the posterior cardinal sinuses. Further examination of the circulatory system brought forth no similarities to the bony fishes but a heart of the selachian type, and a unique arrangement of arteries in the head region. It was obvious from the study of the circulatory system that holocephalian structure agreed with that of bony fishes only in the lack of lateral abdominal veins, and that it bore a much greater resemblance to the selachian type. The peculiarities of holocephalian vessel arrangement gave no clue as to their derivation. It was impossible to determine whether they represented modifications from the selachian plan or whether they had been inherited from a non-selachian source.

A review of the holocephalian nervous, skeletal, muscular, urogenital, and digestive systems was made in the search for characteristics whose derivation could be more clearly interpreted. Since each system displayed distinct differences from the comparable system of bony fish, and the similarities to selachian structure were often marked, the degree and the implications of the resemblance to selachians became the focal problem.

A strong similarity between holocephalian and selachian structure allows the possibility of the origin of the former from the latter group but does not necessitate it. The possession of similar structures might also have occurred through their inheritance from a common ancestor at a lower level of the vertebrate line. In the case of a single structure, its presence may be the result of parallel evolution. The existence of characters which seem unlikely to be derived from selachian structures or of those which seem more primitive than their homologues in sharks might be less equivocal. If it can be shown that a structure is basically unlike its selachian counterpart or that it is not a secondary simplification of a form which exists in a more specialized state in sharks, one could conclude that the Holocephali should logically be traced back to placoderm stock by an independent line rather than to an early shark group.

The review of the nervous system revealed likenesses to selachians in the arrangement of the autonomic fibers and the anatomy of the sense organs and posterior regions of the brain. Although the unusual form of the telencephalon could have originated as a modification from the selachian plan, it does not appear likely that the structure of the pallium itself or the simple arrangement of the cranial nerves could have been so derived. It appears doubtful too, that the pattern of the sensory canals came from a selachian source.

The fact that the skeleton of both holocephalians and sharks is completely cartilaginous was once thought to be indicative of close relationship, but it has become apparent that that conclusion is not the only possible one. Since it seems, now, that a transition from bone to cartilage occurred in several vertebrate lines, one must allow that the cartilaginous skeletons of sharks and holocephalians may have developed independently. If one can look beyond the similarity of the skeletal material, holocephalians can be seen to have several skeletal characters that would be difficult to derive from early sharks. Their form of autostyly is distinctive. Although it appears that autostyly has developed several times among vertebrates, it is hard to believe that the arrangement in the Holocephali could be a modification of selachian structure. If it were, one would expect to find a longer palatoquadrate element rather than a short one with a process extending postero-dorsally in finger-like fashion to reach the otic region. Also, the hyoid would be expected to show some sign of its former involvement in the jaw suspension. In holocephalians it does not, being to all appearances exactly like the succeeding arches even in its dorsal part. In addition to the difference of the palatoquadrate and hyoid elements from the shark type, the presence of elaborate labial and rostral cartilages and the general proportions of the skull, with its short otic and steeply sloped ethmoid areas, distinguish holocephalians from early sharks.

A study of the muscular system produces less that is clearly significant. The similarity of the musculature of fishes generally and the difficulty of ascertaining homologies are obstacles to meaningful analysis. Peculiarities in holocephalian axial, appendicular, and branchial muscles are apparent, but there is nothing to indicate whether they were or were not derived from the selachian plan. There seems to be no sure ground for denying that they could have been.

The urogenital system of holocephalians resembles that of sharks very closely in the nature of kidneys, the gonads, the accessory ducts, and the interrelationship between those structures. Because that interrelationship is characteristic of most extant vertebrates (bony fish are the cardinal exception), it is possible to interpret the arrangement as one which was widespread among early gnathostomes and so obviate the necessity of deriving the holocephalian system from a specifically selachian source. If one is free to seek its forerunner in a wide variety of early vertebrate groups, one might consider the ptyctodonts as having had a system which could have been ancestral to the holocephalian type. Although no evidence of soft organs remains, it seems that ptyctodonts may have had, associated with the reproductive system, accessory claspers similar to those of holocephalians. No trace of those structures appears in any other fossil group.

The digestive system of the Holocephali is unlike that of selachians in its lack of a stomach and poor development of the spiral valve. Among the soft organs, the liver is the only structure which bears a striking resemblance to its selachian counterpart. While the evolutionary history of the soft parts of the digestive system is not clear, the holocephalian toothplates, which show no evidence of having developed through a fusion of separate teeth, seem not to be derived from any known shark structures.

The general conclusion to be drawn from this study is that, although similarities between holocephalians and selachians are numerous, holocephalians possess certain characteristics which suggest that these fishes evolved from other than a selachian stock. The existence in sharks and holocephalians of like structures does not contradict this hypothesis, since such structures may have been carried over from a common ancestor or developed convergently. Even the derivation of the Holocephali from the bradyodont sharks can be questioned. Although the cochliodont *Helodus* shows, according to Moy-Thomas, a number of similarities to holocephalians, the teeth of that fish show a tendency toward fusion of which there is no hint in the Holocephali. *Helodus* was apparently autostylic, as are the holocephalians, but autostyly has arisen repeatedly in vertebrate groups and cannot be considered as weighty evidence in favor of the holocephalian-cochliodont relationship. There is as good, or better, evidence in favor of a relationship between holocephalians and ptyctodonts. Although the ptyctodont palatoquadrate was not fused to the cranium, the toothplates appear to have been integral structures, and the body form, with the large, short head, was similar to that of holocephalians. If one will concede that the dermal skeleton of the ptyctodonts could have disappeared as the evolution of the group continued, then the presence of labial cartilages, rostral processes, anterior and pelvic claspers, a synarcual, and a dorsal fin supported by radials posterior to the dorsal spine, stand forth as a substantial and therefore possibly significant number of characteristics suggesting linkage between the ptyctodont and holocephalian lines.

In sum, one may assume from available evidence that holocephalians are not derived from selachians or bradyodonts but have evolved along an independent line. However, anatomical similarities between extant holocephalians and selachians which set both groups apart from the bony fishes suggest that these cartilaginous forms shared a common ancestor. This ancestral stock must have existed at the placoderm level or even earlier among unknown antecedent forms. Although the specific group of placoderms from which sharks originated is unknown, the ptyctodonts may represent the root of the holocephalian line.

ACKNOWLEDGMENTS

I want to express my gratitude to Dr. Alfred S. Romer of Harvard University for the guidance and encouragement that he has given me throughout my research and the preparation of this paper. I am indebted, also, to Dr. Richard Snyder of the University of Washington and to Dr. Norman J. Wilimovsky of the University of British Columbia through whose efforts I obtained the specimens of *Chimaera colliei* that I used. Instruction in the technique of latex-injection was given me by Dr. Richard Thorington who was, at the time, a graduate student at the Harvard Biological Laboratories. Mrs. Myvanwy Dick allowed me to preserve and store my fishes in the Fish Department of the Museum of Comparative Zoology and was kind enough to lend me a specimen of *Callorhynchus*. The list of people who answered my letters of inquiry is very long. I owe thanks especially to Dr. D. L. Gamble of Ward's and to Mr. Thomas E. Powell, Jr. of Carolina Biological Supply Company who sent advice about injecting frozen-and-thawed material. Lastly, I should like to thank Dr. David G. Stahl who encouraged me to undertake this work and whose patience and good will enabled me to finish it.

REFERENCES CITED

ALLEN, W. F. 1905. The blood vascular system of the Loricati, the mail-cheeked fishes. Proc. Washington Acad. Sci., **7**: 27–157.

ALLIS, E. P. 1912. The branchial, pseudobranchial, and carotid arteries in *Chimaera colliei*. Anat. Anz., **42**: 10–18.

———. 1916. The so-called mandibular artery and the persisting remnant of the mandibular aortic arch in the adult selachian. J. Morph., **27**: 99–118.

———. 1917. The prechordal portion of the chondrocranium of *Chimaera colliei*. Proc. Zool. Soc. London, 1917: 105–143.

———. 1926. On the homologies of the prechordal portions of the skull of the Holocephali. J. Anat., **60**: 335–340.

BÄCKSTROM, K. 1924. Contributions to the forebrain morphology in selachians. Acta Zool., **5**: 123–240.

BARGMANN, W. 1933. Die Zahnplatten von *Chimaera monstrosa*. Z. Zellforsch., **19**(3): 537–561.

BORCEA, J. 1906. Recherches sur le système urogenital des elasmobranches. Arch. Zool. (Paris), Sér. 4, **4**: 199–484.

BRAUS, H. 1898. Über die Innervation der paarigen Extremitäten bei Selachiern, Holocephalen, und Dipnoen. Ein Beitrag zur Gliedmassenfrage. Jena. Z. Med., **31**: 239–468.

BRETTNACHER, H. 1939. Aufbau und Struktur der Holocephalenzähne. Z. Mikr. Anat. Forsch., **46**: 584–616.

BURLEND, T. H. 1910. The urogenital organs of *Chimaera monstrosa*. Proc. Zool. Soc. London, 1910: 510–534.

CITTERIO, V. 1932. Richerche sul canale digerente di *Chimaera monstrosa*. Atti Soc. Ital. Milano, **71**: 93–118.

COLE, F. J. 1896. The cranial nerves of *Chimaera monstrosa*. Trans. Roy. Soc. Edinburgh, **38**: 49–56.

COLE, F. J. AND W. J. DAKIN. 1906. Further observations on the cranial nerves of *Chimaera*. Anat. Anz., **28**: 595–599.

DANIEL, J. R. 1934. The elasmobranch fishes. Berkeley, 334 pp.

DAVIDOFF, M. v. 1879. Beiträge zur vergleichenden Anatomie der hinteren Gliedmasse der Fische. I. Haie, *Chimaera* und Ganoidei chondrostei. Morph. Jahrb., **5**: 450–520.

DEAN, B. 1895. Fishes living and fossil. Macmillan, New York, 300 pp.

———. 1904. In the matter of the Permian fish *Menaspis*. Amer. Geol., **34**: 49–53.

———. 1906. Chimaeroid fishes and their development. Carnegie Inst. Washington, Pub. No. **32**, 172 pp.

———. 1909. Studies on fossil fishes (sharks, chimaeroids, arthrodires). Mem. Amer. Mus. Nat. Hist., **9**: 207–287.

DEBEER, G. R. AND J. A. MOY-THOMAS. 1935. On the skull of the Holocephali. Phil. Trans. Roy. Soc. London, B **224**: 287–312.

EDGEWORTH, F. H. 1935. The cranial muscles of vertebrates. Cambridge, 300 pp.

FAHRENHOLZ, C. 1915. Über die Verbreitung von Zahnbildungen und Sinnesorganen in Vorderdarm der Selachier und ihre phylogenetische Beurteilung. Jena. Z. Naturwiss., **53**: 389–444.

FEE, A. R. 1925. The histology of the colon and its contained spiral valve of the Pacific Coast dog-fish (*Squalus sucklii*) with an investigation of the phylogeny of the intestinal valve. Proc. Trans. Roy. Soc. Canada, Sect. V, **19**: 169–193.

FÜRBRINGER, M. 1897. Über die spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie. *In*: Festschr. 70 Geburtstage C. Gegenbaur, Leipzig, **3**: 349–788.

Garman, S. 1888. On the lateral canal system of the Selachia and Holocephalia. Bull. Mus. Comp. Zool., **17**: 57–119.

———. 1904. The chimaeroids, especially *Rhinochimaera* and its allies. Bull. Mus. Comp. Zool., **41**: 243–272.

Gross, W. 1957. Mundzähne und Hautzähne der Acanthodier und Arthrodiren. Paleontographica, **109**(A): 1–40.

Holmgren, N. 1922. Points of view concerning forebrain morphology in lower vertebrates. J. Comp. Neur., **34**: 391–440.

———. 1942a. General morphology of the lateral sensory line system of the head in fish. K. Svenska Vetenskaps-Acad. Handl., Ser. 3, **20**(1): 1–46.

———. 1942b. Studies on the head of fishes, an embryological, morphological, and phylogenetical study. 3: The phylogeny of elasmobranch fishes. Acta Zool., **23**: 129–261.

Holmgren, N. and C. J. van der Horst. 1925. Contributions to the morphology of the brain of *Ceratodus*. Acta Zool., **6**: 59–165.

Hubrecht, A. A. W. 1877. Beiträge zur Kenntniss des Kopfskeletts der Holocephalen. Niederl. Archiv. f. Zool., **3**: 255–276.

Hyman, L. H. 1942. Comparative vertebrate anatomy. 2nd ed., Chicago, 544 pp.

Hyrtl, J. 1853. Ueber weibliche Oviducte bei männlichen Chimaeren, und eine männliche Vesicula seminalis bei Weibchen. Sitzungsber. K. Akad. Wiss. (Vienna), **11**(5): 1078–1087.

Jacobshagen, E. 1915. Untersuchungen über das Darmsystem der Fische und Dipnoer. Jena. Z. Naturwiss., **53**: 445–556.

———. 1934. Das Problem des Spiraldarms. Morphol. Jahrb., **73**: 392–445.

———. 1941. Grundlinien einer vergleichenden Anatomie des Zahnbeines und der Zähne niederer Wirbeltiere. Z. Mikros. Anat. Forsch., **49**: 225–272.

Johnston, J. B. 1910. A note on the forebrain of *Chimaera*. Anat. Anz., **36**: 233–242.

Kappers, C. U. A. 1912. The arrangement of the motor nuclei in *Chimaera monstrosa* compared with other fishes. Proc. K. Akad. Wetensch., **14**: 1176–1180.

Kappers, C. U. A. and F. W. Carpentier. 1911. Das Gehirn von *Chimaera monstrosa*. Folia Neurobiologica, **5**: 127–160.

Kappers, C. U. A., G. C. Huber, and E. C. Crosby. 1936. The comparative anatomy of the nervous system of vertebrates. 3 Vols., New York, 1845 pp.

Kesteven, H. L. 1933. The anatomy of the head of *Callorhynchus antarcticus*. J. Anat., **67**: 443–474.

———. 1942–1943. The evolution of the skull and the cephalic muscles. Part I. The fishes. Mem. Aus. Mus., **8**: 1–132.

Kolmer, W. 1923. Über das Vorkommen eines knockenmarkähnlichen Gewebes bei einem Selachier (Knorpelmark bei *Chimaera monstrosa*). Anat. Anz., **56**: 529–534.

Lankester, E. R. 1878. On the hearts of *Ceratodus*, *Protopterus*, and *Chimaera*. Trans. Zool. Soc. London, **10**: 493–505.

Leigh-Sharpe, W. H. 1920–1926. The comparative morphology of the secondary sexual characters of elasmobranch fishes. J. Morph., **34**: 245–265; **35**: 359–380; **36**: 221–243; **39**: 558–577; **42**: 307–308.

Leydig, F. 1851. Zur Anatomie und Histologie der *Chimaera monstrosa*. Arch. Anat. Physiol., 1851: 241–271.

Luther, A. 1909. Beiträge zur Kenntnis von Musculatur und Skelett des Kopfes des Haies *Stegostoma tigrinum* Gm. und der Holocephalen. Acta Soc. Sci. Fennicae, **37**: 1–60.

Marples, B. J. 1936. The blood vascular system of the elasmobranch fish *Squatina squatina* (Linné). Trans. Roy. Soc. Edinburgh, **58**: 817–840.

Maurer, Fr. 1912. Die ventrale Rumpfmuskulatur der Fische. Jena. Z. Naturwiss., **49**: 1–118.

Moy-Thomas, J. A. 1936. On the structure and affinities of the Carboniferous cochliodont *Helodus simplex*. Geol. Mag., **73**: 488–503.

Nicol, J. A. C. 1950. The autonomic nervous system of the chimaeroid fish, *Hydrolagus colliei*. Quart. J. Micros. Sci., **91**: 379–400.

Nielsen, E. 1932. Permo-carboniferous fishes from East Greenland. Medd. om Grønland, **92**(3): 1–63.

———. 1952. On new or little-known Edestidae from the Permian and Triassic of East Greenland. Medd. om Grønland, **144**(5): 1–55.

O'Donoghue, C. H. 1914. Notes on the circulatory system of elasmobranchs, I. The venous system of the dogfish (*Scyllium canicula*). Proc. Zool. Soc. London, 1914: 435–455.

Ørvig, T. 1951. Histologic studies of placoderms and fossil elasmobranchs, I. The endoskeleton with remarks on the hard tissues of lower vertebrates in general. K. Svenska Vetenskap.-Akad., Ark. Zool., Ser. 2, **2**(2): 321–454.

———. 1957. Notes on some Paleozoic lower vertebrates from Spitzbergen and North America. Norsk Geol. Tidsskr., **37**(3–4): 285–353.

———. 1962. Y a-t-il une relation directe entre les arthrodires ptyctodontides et les holocéphales? Problèmes Actuels de la Paléontologie, Centre Nat. Recher. Sci., No. **104**: 49–61.

PANDER, C. H. 1858. Über die Ctenodipterinen des devonischen Systems. St. Petersburg, 65 pp.

PARKER, T. J. 1886. On the blood vessels of *Mustelus antarcticus*. Phil. Trans. Roy. Soc. London, Ser. B, **177**: 685–731.

PATTERSON, C. 1965. The phylogeny of the chimaeroids. Phil. Trans. Roy. Soc. London, Ser. B, **249**: 101–219.

PRASAD, R. R. 1948. Observation on the nidamental glands of *Hydrolagus colliei*, *Raja rhina* and *Platyrhinoidis triseriatus*. Copeia, No. **1**: 54–57.

RABINERSON, A. 1925. Beiträge zur vergleichenden Anatomie der Wirbelsäule der Knorpelfische. Anat. Anz., **59**: 433–454.

RADINSKY, L. 1961. Tooth histology as a taxonomic criterion for cartilaginous fishes. J. Morphol., **109**: 73–92.

REDEKE, H. C. 1898. Onderzoekingen betreffende het Urogenitaalsysteem der Selachiers en Holocephalen. Amsterdam, 85 pp.

REESE, A. M. 1910. The lateral line system of *Chimaera colliei*. J. Exp. Zool., **9**: 349–370.

ROMER, A. S. 1964. The braincase of the Paleozoic elasmobranch *Tamiobatis*. Bull. Mus. Comp. Zool., **131**(4): 89–105.

SCAMMON, R. E. 1915. The histogenesis of selachian liver. Amer. J. Anat., **17**: 245–315.

SCHAUINSLAND, H. H. 1903. Beiträge zur Entwicklungsgeschichte und Anatomie der Wirbeltiere, I., *Sphenodon*, *Callorhynchus*, *Chamaeleo*. Zoologica, **39**: 1–98.

SHANN, E. W. 1919. The comparative myology of the shoulder girdle and pectoral fin of fishes. Trans. Roy. Soc. Edinburgh, **52**: 531–570; continued in Proc. Zool. Soc. London, 1924: 195–215.

SIWE, S. A. 1926. Pancreasstudien. Morphol. Jahrb., **57**: 84–307.

STENSIÖ, E. 1947. The sensory lines and dermal bones of the cheek in fishes and amphibians. K. Svenska Vetenskaps.-Akad. Handl., Ser. 3, **24**(3): 1–195.

———. 1963. Anatomical studies on the arthrodiran head. Part 1. K. Svenska Vetenskaps.-Akad. Handl., **9**(2): 1–419.

VAN DEN BROEK, A. J. P. 1938. Gonaden und Ausführungsgänge. *In*: Bolk, L. et al., Handbuch der vergleichenden Anatomie der Wirbeltiere, Vol. 6: 1–154.

VAN GELDEREN, CHR. 1938. Venensystem, mit einem Anhang über den Dotter- und Plazentarkreislauf. *In*: Bolk, L. et al., Handbuch der vergleichenden Anatomie der Wirbeltiere, Vol. 6: 685–744.

VAN DER HORST, C. J. 1934. Spinalnerven. *In*: Bolk, L. et al., Handbuch der vergleichenden Anatomie der Wirbeltiere, Vol. 2: 505–540.

VAN OORDT, G. J. 1938. Besondere Morphologie der Harnorgane der Wirbeltiere. *In*: Bolk, L. et al., Handbuch der vergleichenden Anatomie der Wirbeltiere, Vol. 5: 727–836.

VETTER, B. 1878. Untersuchungen zur vergleichenden Anatomie der Kiemen- und Kiefermuskeln der Fische. II Teil. Jena. Z. Naturwiss., **12**: 431–550.

WATSON, D. M. S. 1938. A ptyctodont from the middle Old Red Sandstone of Scotland. Trans. Roy. Soc. Edinburgh, **59**(2): 397–410.

WILDER, B. 1877. On the brain of *Chimaera monstrosa*. Proc. Acad. Nat. Sci. Philadelphia, 1877: 219–250.

(*Received 27 September, 1965.*)

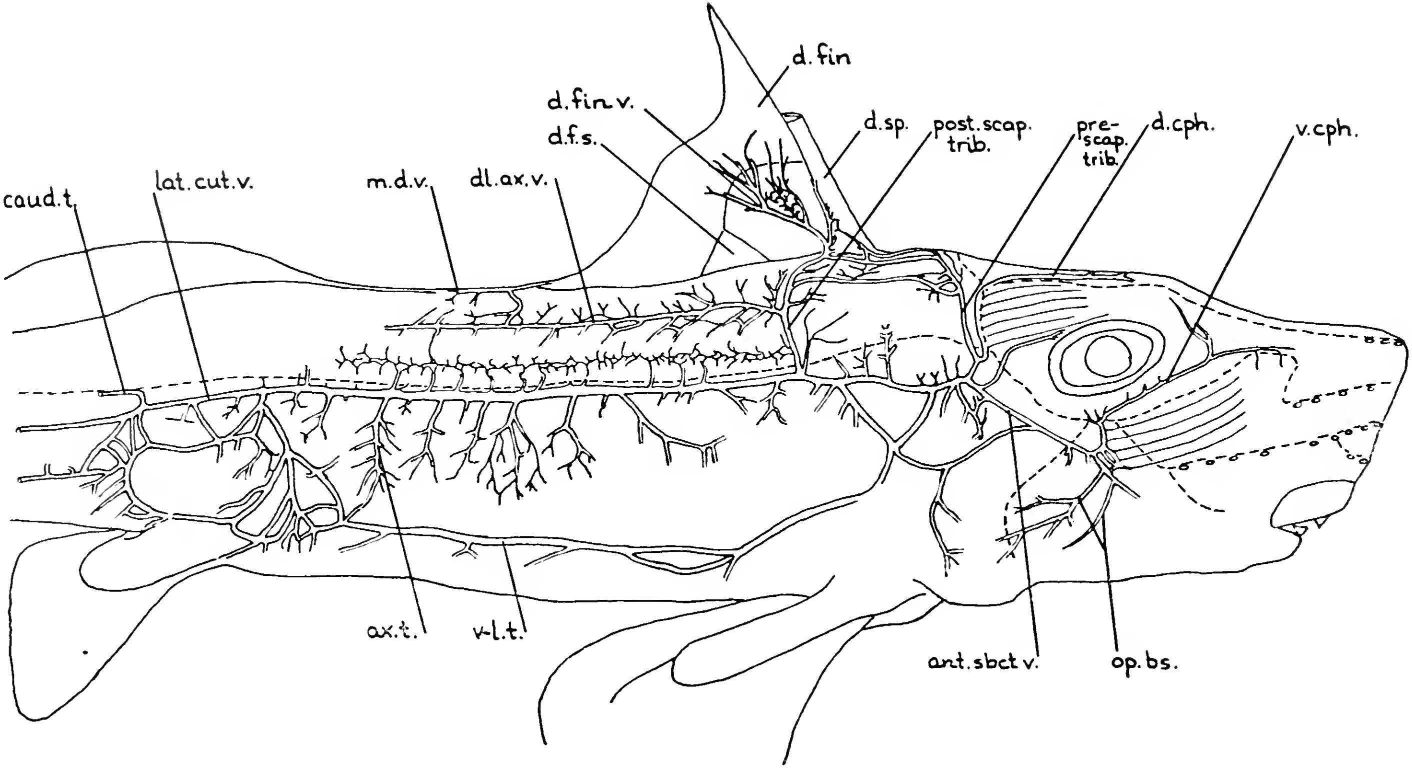


Plate 1. The subcutaneous veins of *Chimaera calliei*. Lateral view. × 0.5. *ant.sbct.v.*, Anterior subcutaneous vein; *ax.t.*, axial tributary; *caud.t.*, caudal tributary; *d.cph.*, dorsal cephalic branch; *d.fin*, dorsal fin; *d.fin v.*, dorsal fin vein; *d.f.s.*, dorsal fin sinus; *dl.ax.v.*, dorso-lateral axial vein; *d.sp.*, dorsal spine; *lat.cut.v.*, lateral cutaneous vein; *m.d.v.*, median dorsal vein; *op.bs.*, opercular branches; *post.scap.trib.*, postscapular tributary; *prescap.trib.*, prescapular tributary; *v.cph.*, ventral cephalic branch; *v-l.t.*, ventro-lateral tributary.

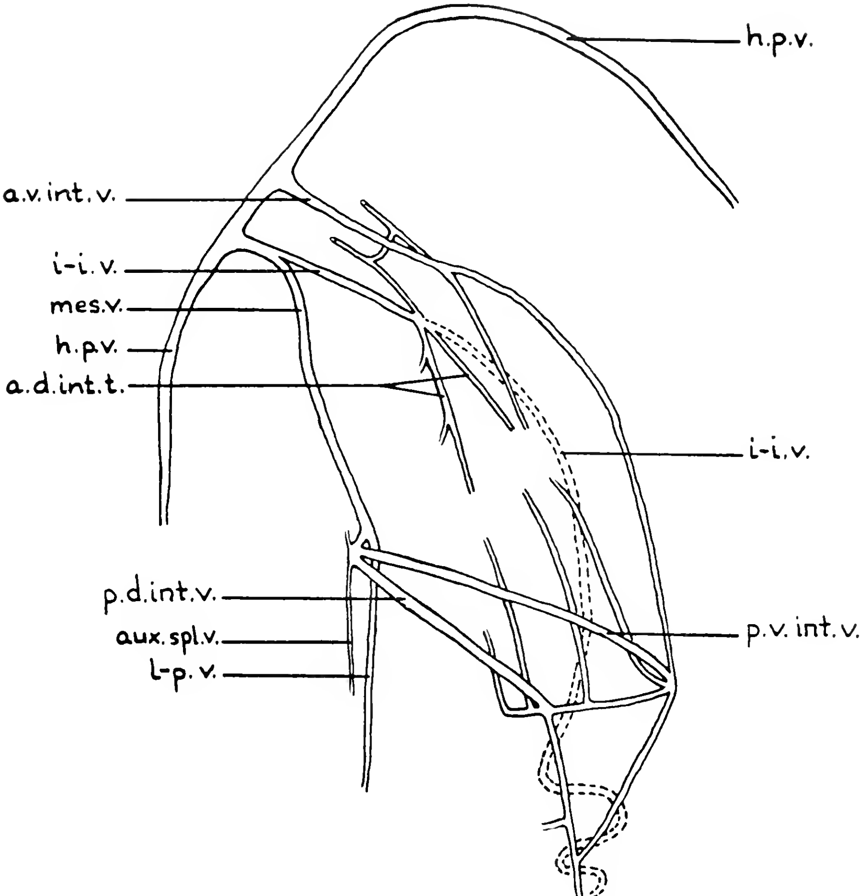


Plate 2. The hepatic portal system of *Chimaera colliei*. Diagrammatic view. × 0.75. *a.d.int.t.*, Anterior dorsal intestinal tributary; *aux. spl.v.*, auxiliary splenic vein; *a.v.int.v.*, anterior ventral intestinal vein; *h.p.v.*, hepatic portal vein; *i-i.v.*, intra-intestinal vein; *l-p.v.*, liena-pancreatic vein; *mes.v.*, mesenteric vein; *p.d.int.v.*, posterior dorsal intestinal vein; *p.v.int.v.*, posterior ventral intestinal vein.

Plate 3. The systemic and renal portal veins of *Chimaera colliei*. Diagrammatic view. × 0.5. *a.br.v.*, Anterior brachial vein; *ant.card.*, anterior cardinal sinus; *ant.cer.a.*, anterior tributary of the anterior cerebral vein; *ant.cer.p.*, posterior tributary of the anterior cerebral vein; *ant.sbct.v.*, anterior subcutaneous vein; *br.s.*, brachial sinus; *br.s.mid-v.ext.*, mid-ventral extension of brachial sinus; *caud.v.*, caudal vein; *eth.v.*, ethmoidal vein; *fem.v.*, femoral vein; *h.v.*, hepatic vein; *inf.jug.v.*, inferior jugular vein; *il.v.*, iliac vein; *lat.cut.v.*, lateral cutaneous vein; *m-f.v.*, maxillo-facial vein; *o-n.v.*, orbito-nasal vein; *orb.s.*, orbital sinus; *ov.s.*, oviducal sinus; *par.v.*, parietal vein; *p.br.v.*, posterior brachial vein; *post.card.*, posterior cardinal sinus; *post.card.mid-v.ext.*, mid-ventral extension of posterior cardinal sinus; *post.cer.v.*, posterior cerebral vein; *postorb.v.*, postorbital vein; *preorb.v.*, preorbital vein; *prescap.t.*, prescapular tributary; *rect.trib.*, rectal tributary; *rn.v.*, renal vein; *r.p.v.*, renal portal vein; *sbsc.s.*, subscapular sinus; *sbsc.trib.*, subscapular tributary; *s.v.*, sinus venosus; *v-a.par.v.*, ventro-anterior parietal vein; *v-p.par.v.*, ventro-posterior parietal vein.

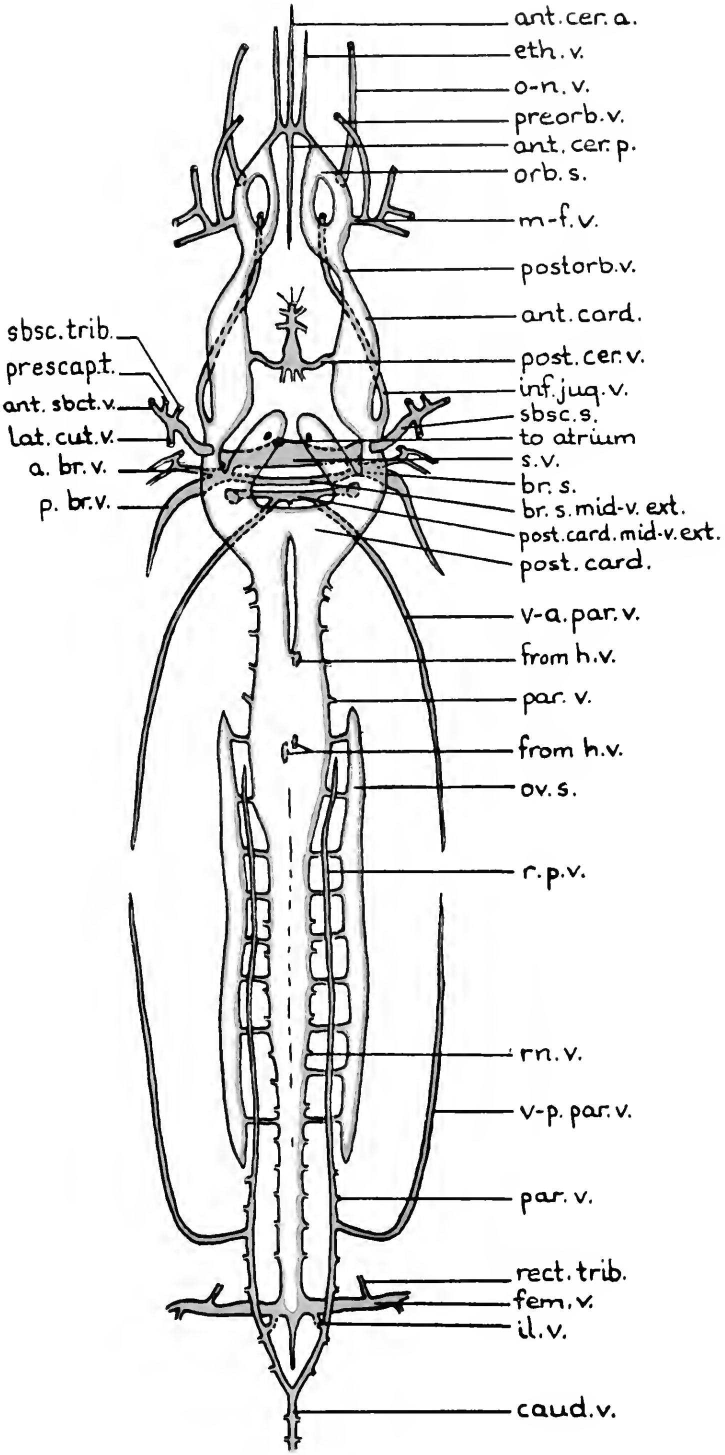

ant. cer. a.
eth. v.
o-n. v.
preorb. v.
ant. cer. p.
orb. s.
m-f. v.
postorb. v.
ant. card.
post. cer. v.
inf. jug. v.
sbsc. s.
to atrium
s. v.
br. s.
br. s. mid-v. ext.
post. card. mid-v. ext.
post. card.
v-a. par. v.
from h. v.
par. v.
from h. v.
ov. s.
r. p. v.
rn. v.
v-p. par. v.
par. v.
rect. trib.
fem. v.
il. v.
caud. v.
sbsc. trib.
prescap. t.
ant. sbct. v.
lat. cut. v.
a. br. v.
p. br. v.

Plate 4. A, The subcutaneous veins of the clasper and pelvic fin. Ventral view. × 1. B, The heart and vessels of the hypobranchial region. Ventral view. Coracomandibularis muscle and right half of pectoral girdle removed. × 1. *ab.p.*, Abdominal pore; *aff.brn.a.*, afferent branchial artery; *ant.cl.*, anterior clasper; *br.a.*, brachial artery; *br.n.*, brachial nerve; *br.s.*, brachial sinus; *c.a.*, conus arteriosus; *c-brn.m.*, coracobranchialis muscle; *c-h.m.*, coracohyoideus muscle; *cl.v.*, clasper vein; *c-m.m.*, coracomandibularis muscle; *com.card.*, common cardinal vein; *cor.c.*, coracoid cartilage; *hy.c.*, hyoid cartilage; *hyp.m.*, hypaxial muscle; *hypobrn.n.*, hypobranchial nerve; *inf.jug.v.*, inferior jugular vein; *mand.c.*, mandibular cartilage; *m.w.g.c.*, medial wall of gill chamber; *pect.f.*, pectoral fin; *post.card.*, posterior cardinal sinus; *sbct.v.pel.f.*, subcutaneous veins of pelvic fin; *s.v.*, sinus venosus; *trib.inf.jug.*, inferior jugular tributary; *v.a.*, ventral aorta; *x*, fine vein accompanying ventral aorta.

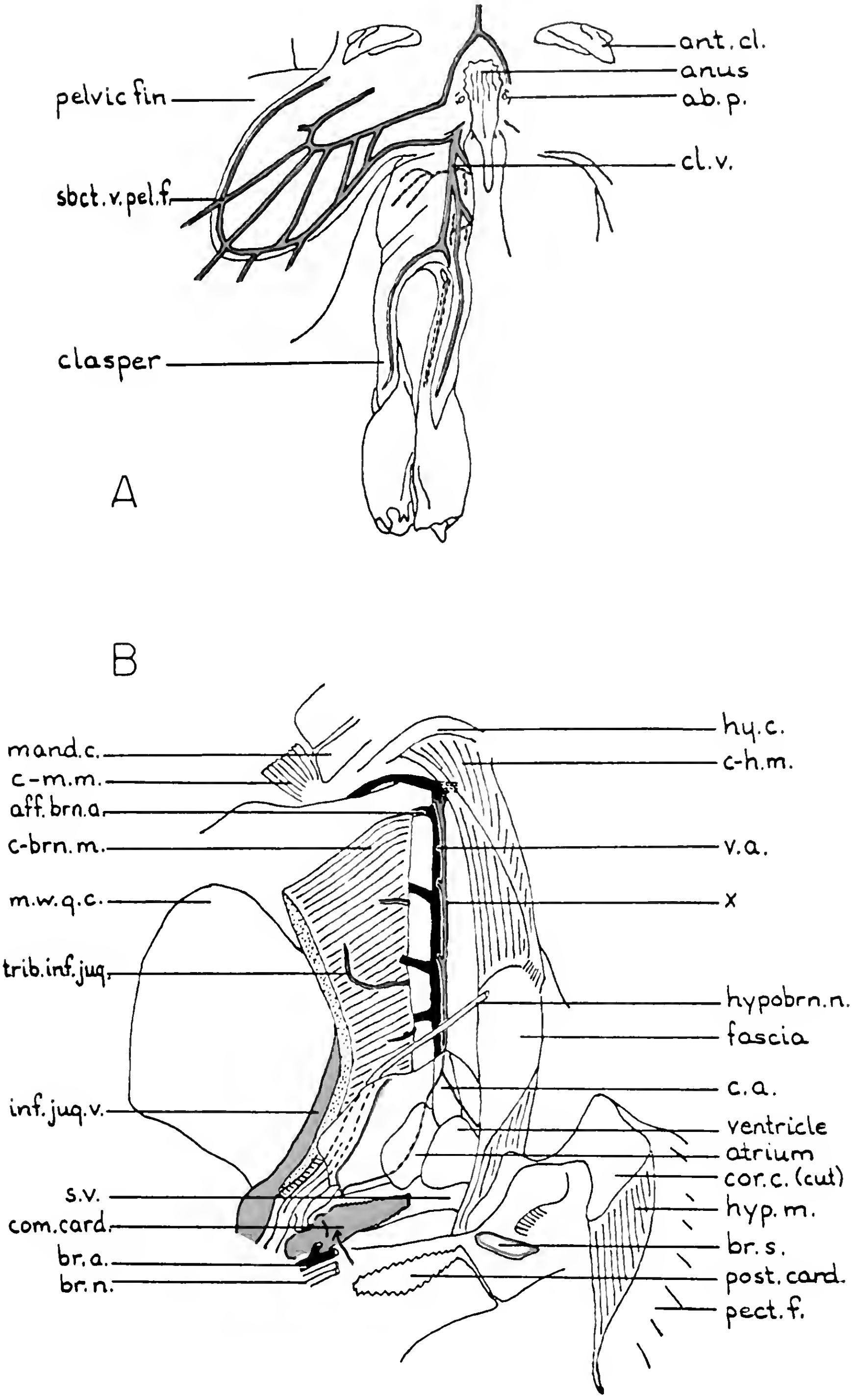

ant. cl.
pelvic fin
anus
ab. p.
cl. v.
sbct. v. pel. f.
clasper
A
B
mand. c.
c-m. m.
aff. brn. a.
c-brn. m.
m. w. q. c.
trib. inf. jug.
inf. jug. v.
s. v.
com. card.
br. a.
br. n.
hy. c.
c-h. m.
v. a.
x
hypobrn. n.
fascia
c. a.
ventricle
atrium
cor. c. (cut)
hyp. m.
br. s.
post. card.
pect. f.

Plate 5. A, Origin of right inferior jugular vein, showing drainage of tissues immediately posterior to mandible. Ventral view. Coracomandibularis muscle cut and deflected toward midline. × 1. B, The brachial veins. Postero-dorsal view of right pectoral fin, proximal region. × 1. C, The systemic veins entering the sinus venosus. Diagrammatic view. × 0.5. D, The anterior cerebral vein and its tributaries. Lateral view. Cartilage removed to show ethmoid and cranial cavities. × 1. *a.br.v.*, Anterior brachial vein; *ant.card.*, anterior cardinal sinus; *ant.cer.a.*, anterior tributary of the anterior cerebral vein; *ant.cer.p.*, posterior tributary of the anterior cerebral vein; *ant.cer.v.*, anterior cerebral vein; *ant.v.const.m.*, anterior ventral constrictor muscle; *a-v.*, antero-ventral; *br.a.*, brachial artery; *br.s.*, brachial sinus; *cart.*, cartilage; *cbl.*, cerebellum; *cer.a.*, cerebral artery; *c-m.m.*, coracomandibularis muscle; *com.card.*, common cardinal vein; *ent.orb.s.*, entrance to orbital sinus; *ep.*, epiphysis; *eth.v.*, ethmoidal vein; *hyp.m.*, hypaxial muscle; *inf.jug.v.*, inferior jugular vein; *int.hy.m.*, interhyoideus muscle; *int.orb.sept.*, interorbital septum; *lev.m.*, levator muscle; *lig.*, ligament; *lym.*, lymphomyeloid tissue; *mand.c.*, mandibular cartilage; *n.cap.*, nasal capsule; *nos.*, nostril; *o-n.v.*, orbito-nasal vein; *opt.a.*, optic artery; *opt.l.*, optic lobe; *p.br.v.*, posterior brachial vein; *pect.f.*, pectoral fin; *pect.gir.*, pectoral girdle; *post.card.*, posterior cardinal sinus; *psb.a.*, pseudobranchial artery; *sbsc.s.*, subscapular sinus; *scap.*, scapula; *sp.n.*, spinal nerve; *sup.oph.n.*, superficial ophthalmic nerve; *s.v.*, sinus venosus; *tel.*, telencephalon; *thy.gld.*, thyroid gland; *tr.int.m.*, trapezius internus muscle; *v.const.m.*, ventral constrictor muscle; *II*, optic nerve; *III*, oculomotor nerve; *IV*, trochlear nerve; *X*, vagus nerve.

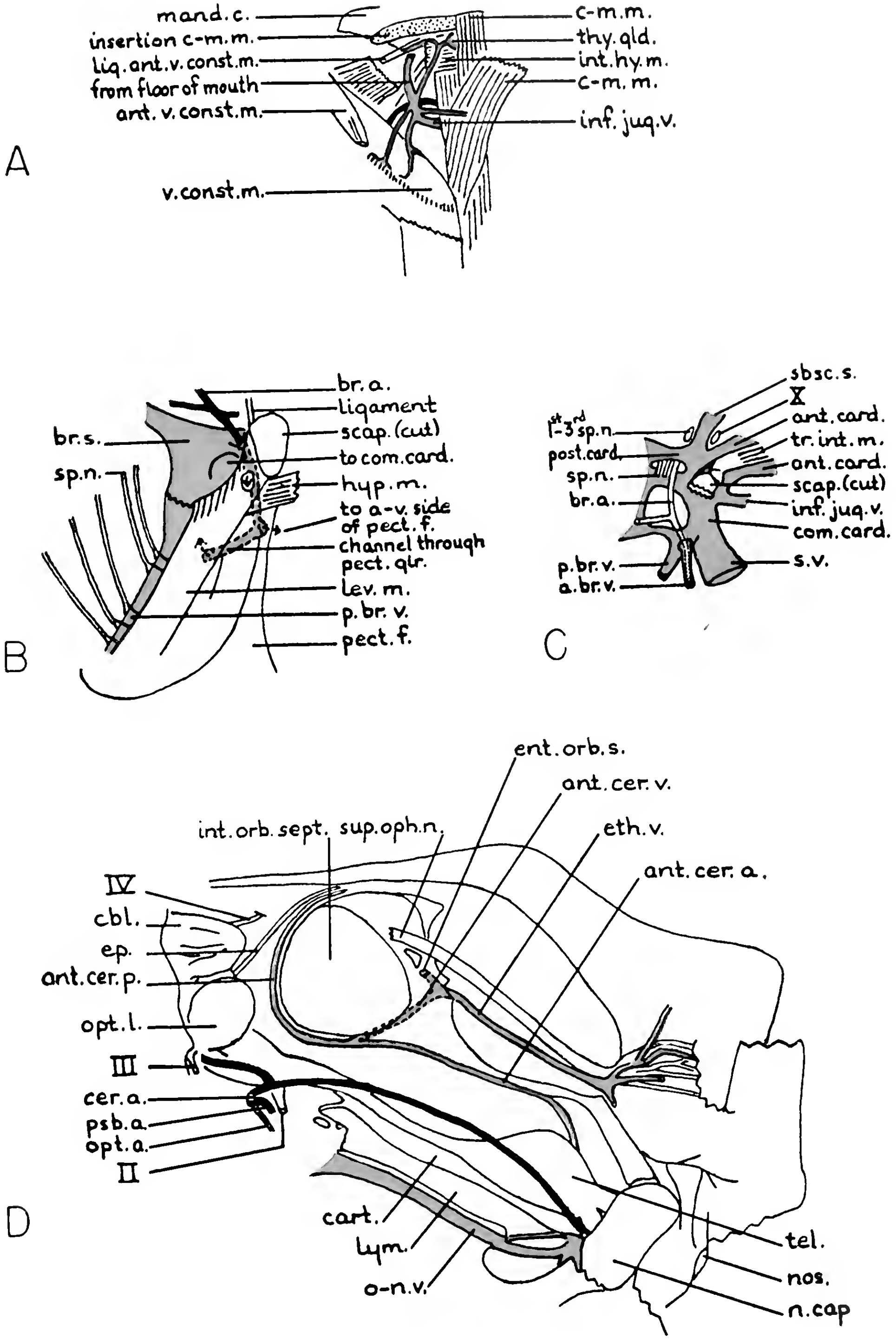

A
mand.c.
insertion c-m.m.
lig. ant. v. const.m.
from floor of mouth
ant. v. const.m.
v. const.m.
c-m.m.
thy. gld.
int. hy. m.
c-m. m.
inf. jug.v.
B
br. s.
sp.n.
br. a.
ligament
scap. (cut)
to com. card.
hyp. m.
to a-v. side of pect. f.
channel through pect. gir.
lev. m.
p. br. v.
pect. f.
C
1st-3rd sp.n.
post. card.
sp.n.
br. a.
p. br. v.
a. br. v.
sbsc. s.
X
ant. card.
tr. int. m.
ant. card.
scap. (cut)
inf. jug. v.
com. card.
s.v.
D
ent. orb. s.
ant. cer. v.
int. orb. sept.
sup. oph. n.
eth. v.
ant. cer. a.
IV
cbl.
ep.
ant. cer. p.
opt. l.
III
cer. a.
psb. a.
opt. a.
II
cart.
lym.
o-n.v.
tel.
nos.
n. cap

Plate 6. A, Systemic veins and related structures in the postero-dorsal region of the head. Lateral view. × 1. B, Veins draining dorsal region of trunk. Lateral view. Epaxial muscles cut and partially removed. Scapular cartilage cut and deflected ventrally. × 1. *a.ep.v.*, Anterior epaxial vein; *ant.card.*, anterior cardinal sinus; *a.v.s.c.*, anterior vertical semicircular canal; *brn.n.*, branchial nerve; *chcr.*, chondrocranium; *com.card.*, common cardinal vein; *d.const.m.*, dorsal constrictor muscle; *d.f.s.*, dorsal fin sinus; *d.sp.*, dorsal spine; *endl.d.*, endolymphatic duct; *ep.m.*, epaxial muscle; *lat.cut.v.*, lateral cutaneous vein; *lym.*, lymphomyeloid tissue; *m.d.v.*, median dorsal vein; *m-f.v.*, maxillo-facial vein; *ot.cap.*, otic capsule; *p.cbr.s.*, posterior cerebral sinus; *post.card.*, posterior cardinal sinus; *post.cer.v.*, posterior cerebral vein; *postorb.v.*, postorbital vein; *post.scap.trib.*, postscapular tributary; *sbsc.trib.*, subscapular tributary; *s-b.v.*, spino-basal vein; *scap.*, scapula; *sp.n.*, spinal nerve; *tr.int.m.*, trapezius internus muscle; *V*, trigeminal nerve; *VII*, facial nerve; *VII,hyo.*, hyomandibular branch of facial nerve; *IX*, glossopharyngeal nerve; *X*, vagus nerve.

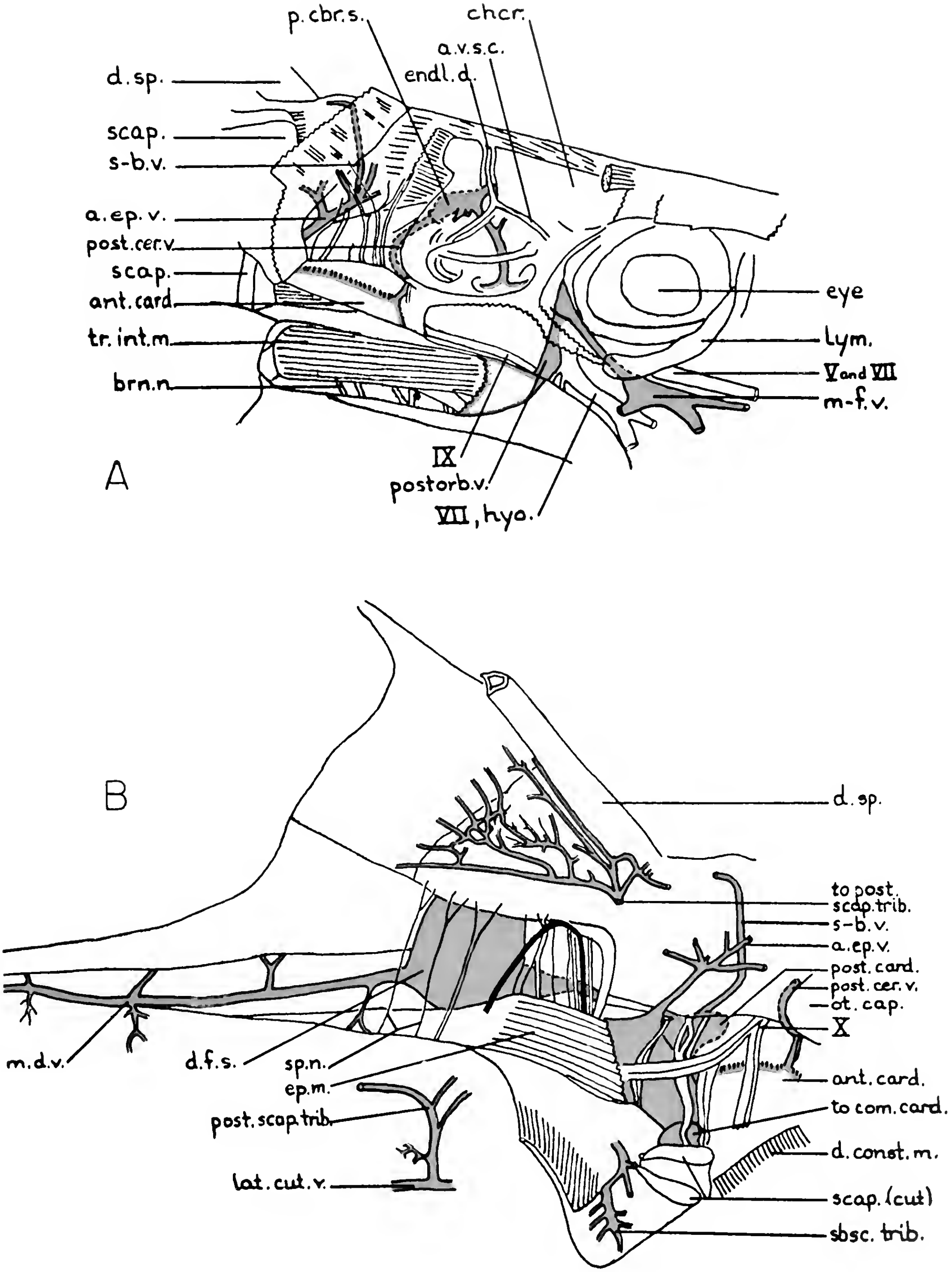
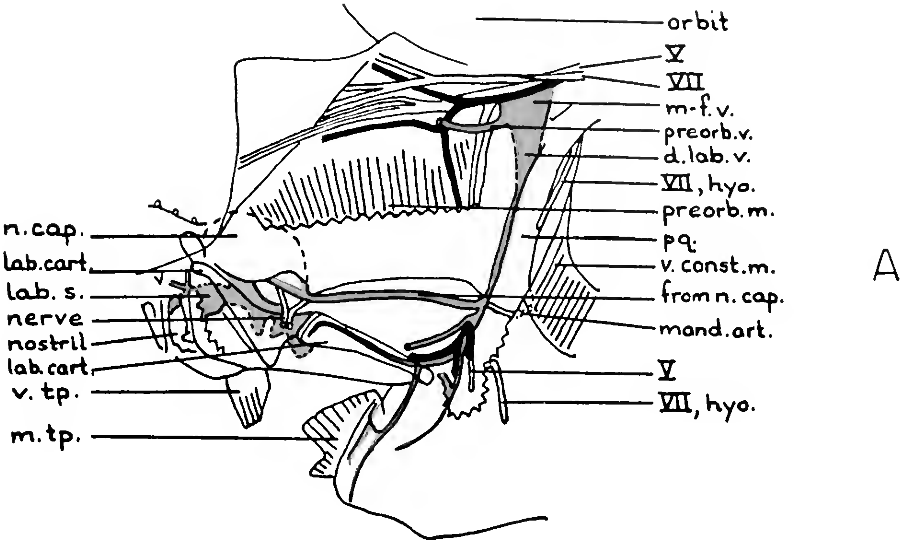
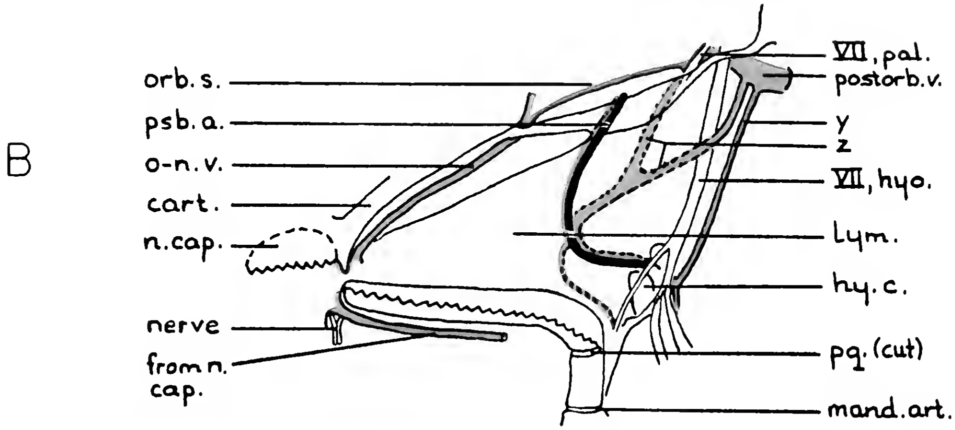

p. cbr. s.
ch. cr.
a. v. s. c.
endl. d.
d. sp.
scap.
s-b. v.
a. ep. v.
post. cer. v.
scap.
ant. card.
tr. int. m.
brn. n.
eye
lym.
V and VII
m-f. v.
IX
postorb. v.
VII, hyo.
A
B
d. sp.
to post. scap. trib.
s-b. v.
a. ep. v.
post. card.
post. cer. v.
ot. cap.
X
ant. card.
to com. card.
d. const. m.
scap. (cut)
sbsc. trib.
m. d. v.
d. f. s.
sp. n.
ep. m.
post. scap. trib.
lat. cut. v.

Plate 7. A, The maxillo-facial vein and its tributaries. Lateral view. Lower portion of adductor mandibulae muscle removed. × 1. B, Deep veins associated with lymphomyeloid tissue dorsal to mouth cavity. Lateral view. Palatoquadrate cartilage cut and partially removed. × 1. C, The femoral vein. Lateral view. Right side. × 0.75. *cart.*, Cartilage; *d.lab.v.*, deep labial vein; *eff.rn.v.*, efferent renal vein; *ex.ov.op.*, external oviducal opening; *fem.a.*, femoral artery; *fem.v.*, femoral vein; *hy.c.*, hyoid cartilage; *lab.cart.*, labial cartilage; *lab.s.*, labial sinus; *lym.*, lymphomyeloid tissue; *mand.art.*, mandibular articulation; *m-f.v.*, maxillo-facial vein; *m.tp.*, mandibular toothplate; *n.cap.*, nasal capsule; *o-n.v.*, orbito-nasal vein; *orb.s.*, orbital sinus; *ov.s.*, oviducal sinus; *pel.gir.*, pelvic girdle; *post.card.*, posterior cardinal sinus; *postorb.v.*, postorbital vein; *pq.*, palatoquadrate; *preorb.m.*, preorbitalis muscle; *preorb.v.*, preorbital vein; *psb.a.*, pseudobranchial artery; *rect.trib.*, rectal tributary; *r.p.v.*, renal portal vein; *sam.*, samentasche; *v.const.m.*, ventral constrictor muscle; *v.tp.*, vomerine toothplate; *y*, hyoid tributary; *z*, possible venous pathways; *V*, trigeminal nerve; *VII*, facial nerve; *VII,hya.*, hyomandibular branch of facial nerve; *VII,pal.*, palatine branch of facial nerve.


orbit
V
VII
m-f.v.
preorb.v.
d.lab.v.
VII, hyo.
preorb.m.
pq.
v. const.m.
from n. cap.
mand.art.
V
VII, hyo.
n.cap.
lab.cart.
lab. s.
nerve
nostril
lab.cart.
v. tp.
m.tp.
A


orb. s.
psb. a.
o-n. v.
cart.
n.cap.
nerve
from n. cap.
B
VII, pal.
postorb.v.
y
z
VII, hyo.
Lym.
hy.c.
pq. (cut)
mand.art.

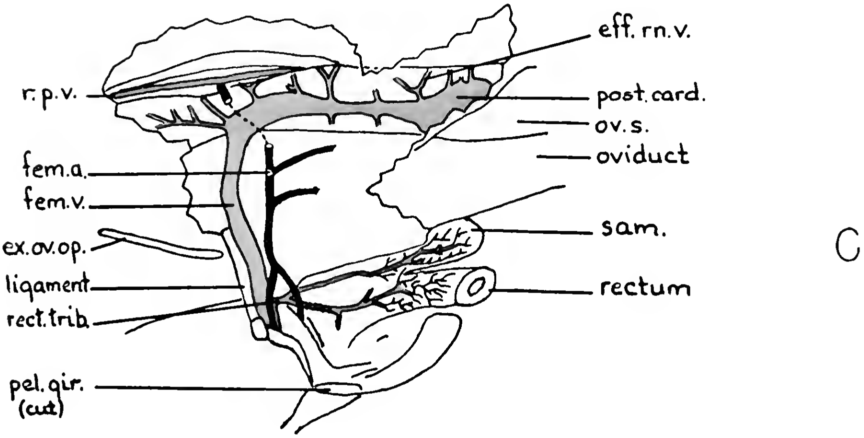

r.p.v.
fem.a.
fem.v.
ex.ov.op.
ligament
rect.trib.
pel.gir. (cut)
eff. rn.v.
post.card.
ov.s.
oviduct
sam.
rectum
C

Plate 8. A, The renal portal vein. Lateral view. Left side. × 1. B, The hepatic portal system. Dorsal view. × 1. *a.d.int.t.*, anterior dorsal intestinal tributary; *aff.rn.v.*, afferent renal vein; *a.v.int.v.*, anterior ventral intestinal vein; *b.d.*, bile duct; *esoph.*, esophagus; *fem.a.*, femoral artery; *fem.v.*, femoral vein; *g.b.*, gall bladder; *h.p.v.*, hepatic portal vein; *hyp.m.*, hypaxial muscle; *i-i.a.*, intra-intestinal artery; *i-i.v.*, intra-intestinal vein; *il.v.*, iliac vein; *k.*, kidney; *mes.*, mesentery; *mes.v.*, mesenteric vein; *ov.s.*, oviducal sinus; *pan.*, pancreas; *pan.d.*, pancreatic duct; *par.v.*, parietal vein; *p.d.int.v.*, posterior dorsal intestinal vein; *pel.gir.*, pelvic girdle; *p.mes.a.*, posterior mesenteric artery; *post.card.*, posterior cardinal sinus; *p.v.int.v.*, posterior ventral intestinal vein; *r.p.v.*, renal portal vein; *spl.*, spleen.

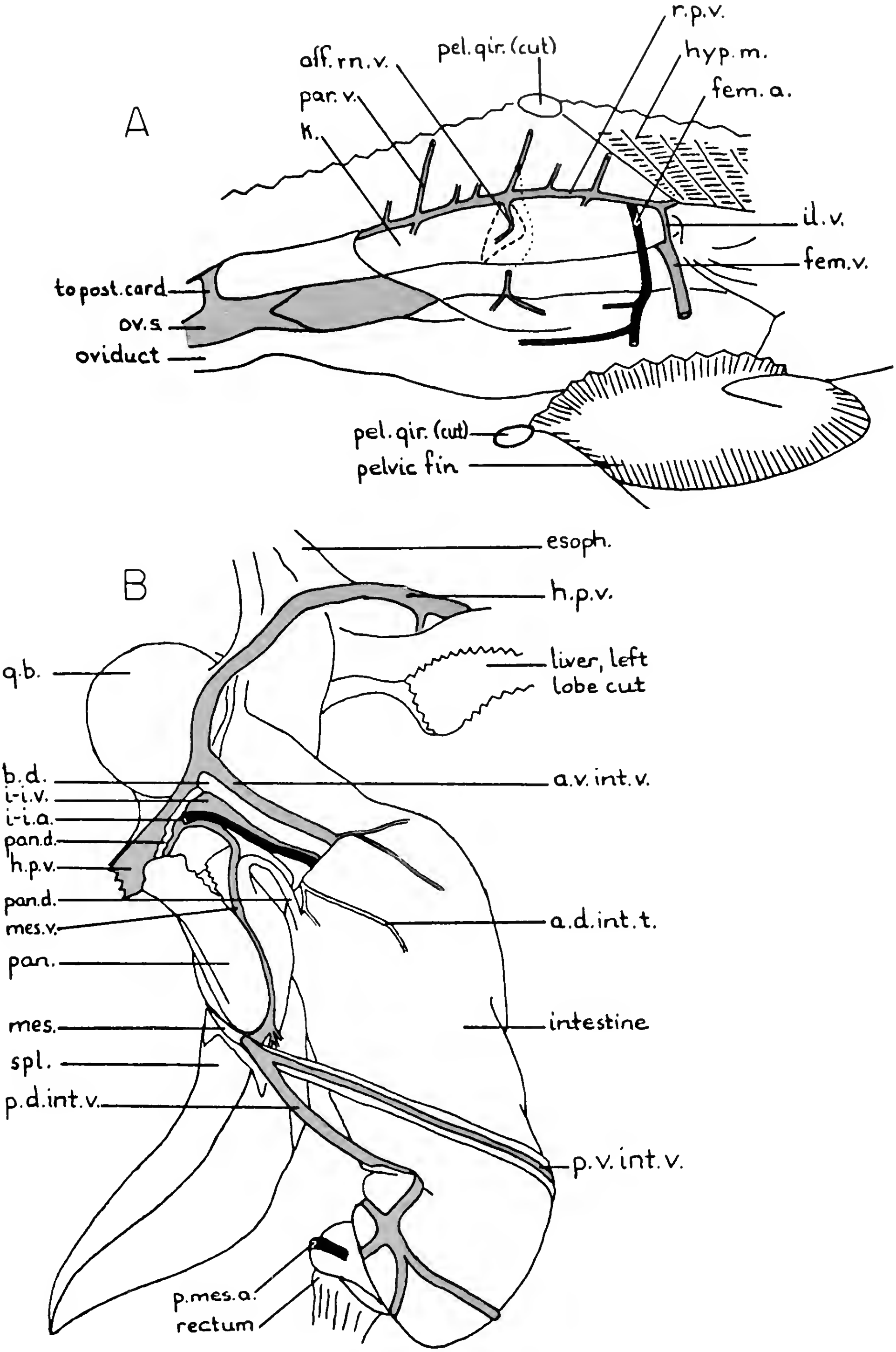

A
r.p.v.
pel.gir.(cut)
hyp.m.
aff.rn.v.
fem.a.
par.v.
k.
il.v.
fem.v.
to post.card.
ov.s.
oviduct
pel.gir.(cut)
pelvic fin
B
esoph.
h.p.v.
liver, left lobe cut
g.b.
b.d.
a.v.int.v.
i-i.v.
i-i.a.
pan.d.
h.p.v.
pan.d.
a.d.int.t.
mes.v.
pan.
intestine
mes.
spl.
p.d.int.v.
p.v.int.v.
p.mes.a.
rectum

Plate 9. A, Hepatic veins. Lateral view. Right side. × 1. B, Hepatic veins. Lateral view. Left side. × 1. *br.s.*, Brachial sinus; *epid.*, epididymis; *fen.mem.*, fenestrated membrane; *g.b.*, gall bladder; *h.p.v.*, hepatic portal vein; *h.v.*, hepatic vein; *L.gl.*, Leydig's gland; *mes.*, mesentery; *pect.gir.*, pectoral girdle; *post.card.*, posterior cardinal sinus; *sem.ves.*, seminal vesicle; *test.a.*, testicular artery; *t.s.*, transverse septum; *v.d.*, vas deferens.

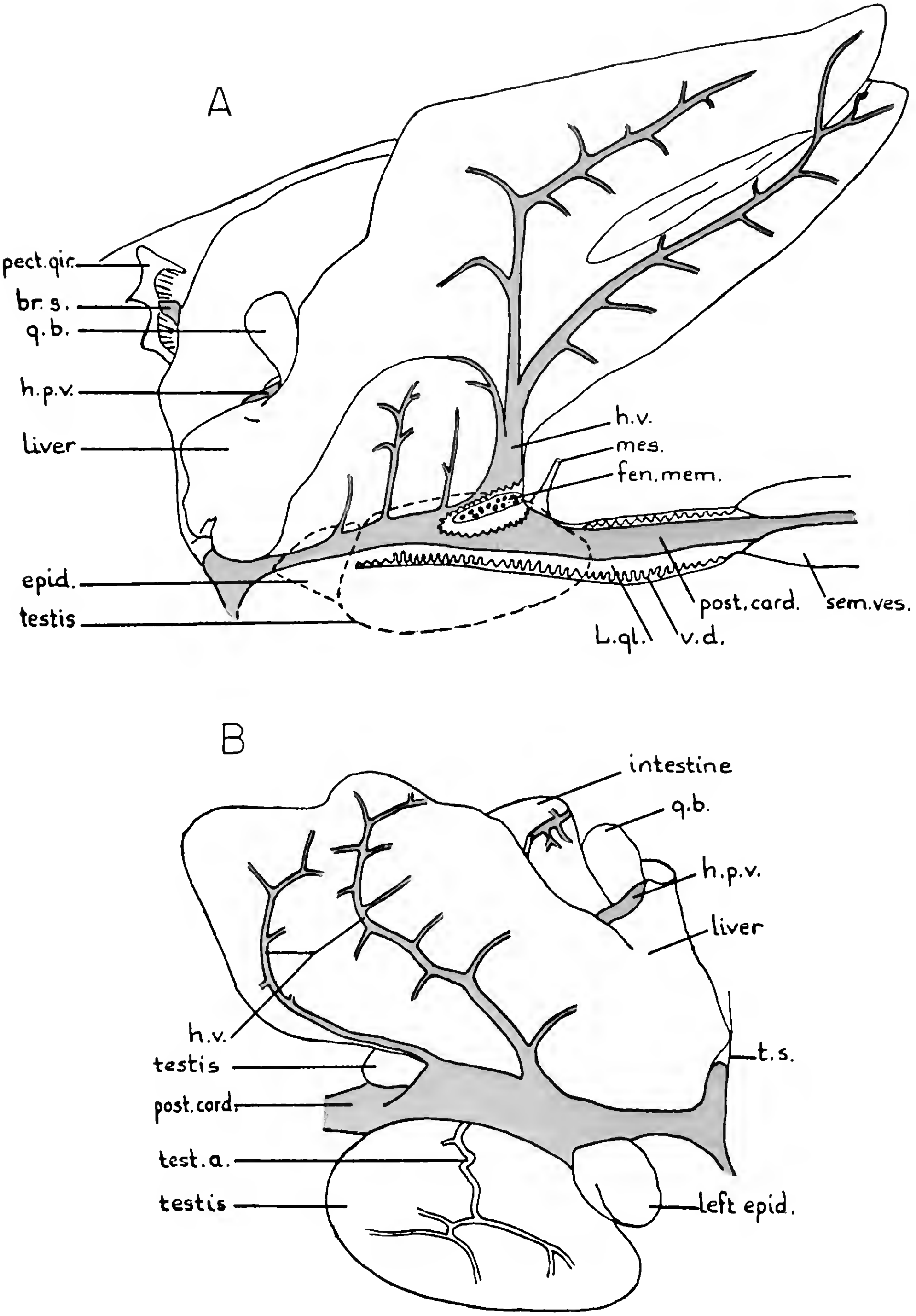
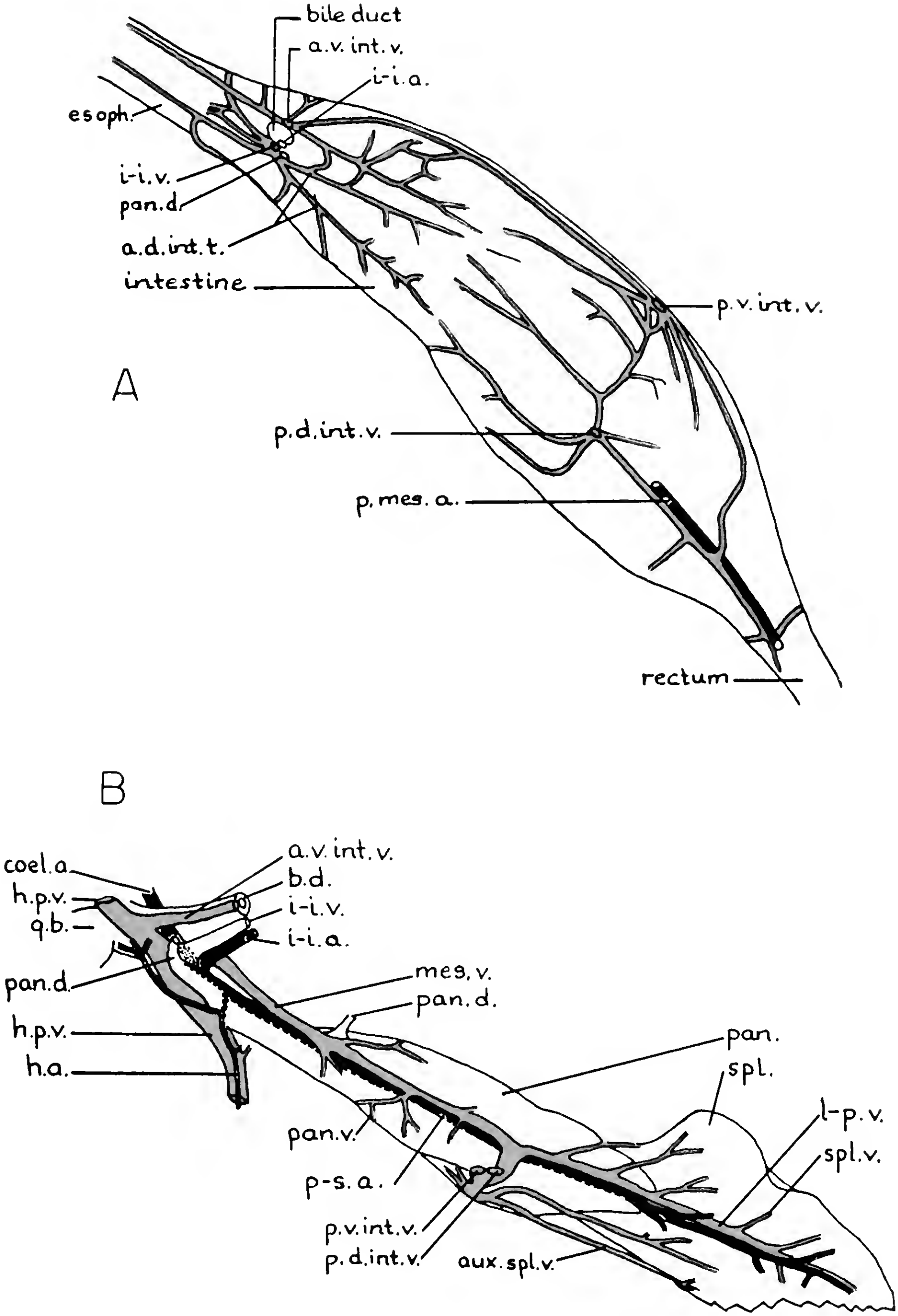

A
pect.gir.
br. s.
g. b.
h. p. v.
liver
epid.
testis
h.v.
mes.
fen.mem.
post.card.
sem.ves.
L.gl.
v.d.
B
intestine
g.b.
h.p.v.
liver
t.s.
left epid.
h.v.
testis
post.card.
test.a.
testis

Plate 10. A, The hepatic portal system: veins draining the intestine. ×1. B, The hepatic portal system: veins draining the pancreas and the spleen. × 1. *a.d.int.t.*, Anterior dorsal intestinal tributary; *aux.spl.v.*, auxiliary splenic vein; *a.v.int.v.*, anterior ventral intestinal vein; *b.d.*, bile duct; *cael.a.*, coeliac artery; *esoph.*, esophogus; *g.b.*, gall bladder; *h.a.*, hepatic artery; *h.p.v.*, hepatic portal vein; *i-i.a.*, intra-intestinal artery; *i-i.v.*, intra-intestinal vein; *l-p.v.*, lieno-pancreatic vein; *mes.v.*, mesenteric vein; *pan.*, pancreas; *pan.d.*, pancreatic duct; *pan.v.*, pancreatic vein; *p.d.int.v.*, posterior dorsal intestinal vein; *p.mes.a.*, posterior mesenteric artery; *p-s.a.*, pancreatico-splenic artery; *p.v.int.v.*, posterior ventral intestinal vein; *spl.*, spleen; *spl.v.*, splenic vein.


A
bile duct
a.v. int. v.
i-i. a.
esoph.
i-i. v.
pan. d.
a. d. int. t.
intestine
p. v. int. v.
p. d. int. v.
p. mes. a.
rectum
B
coel. a.
h. p. v.
g. b.
pan. d.
h. p. v.
h. a.
a. v. int. v.
b. d.
i-i. v.
i-i. a.
mes. v.
pan. d.
pan.
spl.
l-p. v.
spl. v.
pan. v.
p-s. a.
p. v. int. v.
p. d. int. v.
aux. spl. v.

Bulletin OF THE
Museum of
Comparative
Zoology

A Review of the Mesochrysinae and Nothochrysinae (Neuroptera: Chrysopidae)

PHILLIP A. ADAMS

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 135, NUMBER 4
FEBRUARY 24, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office

Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

A REVIEW OF THE MESOCHRYSINAE AND NOTHOCHRYSINAE (NEUROPTERA: CHRYSOPIDAE)

PHILLIP A. ADAMS[1]

ABSTRACT

In this preliminary subfamilial classification of the Chrysopidae, Mesochrysopidae is reduced to subfamilial rank. Keys to subfamilies and to genera of Nothochrysinae are presented. The Nothochrysinae, as newly constituted, is characterized by retention of jugum and frenulum, lack of alar tympanal organ, archaic pseudomedia (except in *Nothochrysa* and *Dyspetochrysa*) and little sclerotized prosternum. It includes *Paleochrysa, Archaeochrysa, Dyspetochrysa, Tribochrysa, Dictyochrysa, Triplochrysa, Hypochrysa, Kimochrysa, Pamochrysa, Pimachrysa,* and *Nothochrysa*. The living species of Nothochrysinae are cataloged, and the North American species described and illustrated.

New fossil taxa are: *Archaeochrysa*, new genus for *Paleochrysa creedi* Carpenter, *fracta* (Cockerell) and *paranervis* n. sp. (Florissant, Colo.); *Dyspetochrysa*, n. gen. for *Tribochrysa vetuscula* Scudder. New Recent species are: *Pimachrysa albicostales*, Baja Calif., and Arizona; *fusca, intermedia* and *nigra*, southern Calif.

INTRODUCTION

This study comprises the first section of a taxonomic revision of the North American Chrysopidae. The concept of the subfamily Nothochrysinae as herein employed is entirely new, necessitating a preliminary reclassification of the family.[2]

There appears no justification for retaining in a separate family the Mesozoic forms, which are placed in the family Mesochrysopidae. These already have achieved the alignment of the inner gradate veins which precedes the pseudomedia of the later forms. In addition, they show the fundamental chrysopid characteristics: many straight, unforked branches of Rs, which diverge from R at a wide angle; two regular gradate series; MP1 and MP2 few-branched, intersecting the wing margin near the base, so that most of the discal area is occupied by the R-Rs-MA system. These basic features of proportion, while difficult to define, readily separate the Chrysopidae from all other families.

The Apochrysinae, a distinctive and homogeneous group, has recently been revised by Kimmins (1952b). The Chrysopinae constitutes a receptacle for the remaining vast and various assemblage of forms, doubtless requiring subdivision when better understood.

All described genera of Mesochrysinae and Nothochrysinae are included in the keys, and all species have been cataloged. Descriptions and illustrations have been included for all living North American

---

[1] California State College, Fullerton.

[2] Although this paper was submitted for publication prior to the appearance of Tjeder's paper, 1966, it has been possible to include his new taxa. He delimits the Nothochrysinae (=Dictyochrysinae) similarly.

species, and for such fossil or Old World species as are of particular interest. I have not examined material of *Dictyochrysa* or *Triplochrysa*, which were reviewed by Kimmins (1952a).

It is interesting that the southwestern United States should have such a rich representation (two genera, six species) of this archaic group, which has changed but little since the Miocene (Adams, 1957). This concentration of these relics is rivaled by South Africa, with two genera and four species, and Australia and Tasmania, also with two genera and four species. Such a distribution contributes to the mounting evidence that the southwestern United States has served as an evolutionary refugium for the Neuroptera.

ACKNOWLEDGMENTS

Grateful acknowledgment is made of the help and encouragement of F. M. Carpenter and P. J. Darlington, Jr., of the Museum of Comparative Zoology (MCZ), Harvard. Ellis MacLeod, of the Biological Laboratories, Harvard, has made many valuable criticisms, and has given generously of his time during the preparation of the manuscript. D. E. Kimmins has kindly examined type material and has made useful suggestions. Material has also been made available through the courtesy of C. D. MacNeil, California Academy of Sciences (CAS), J. D. Powell, University of California, Berkeley, California Insect Survey (CIS), J. N. Belkin, University of California, Los Angeles (UCLA), P. R. Timberlake, University of California, Riverside (UCR), L. Stange, University of California, Davis (UCD), J. Lattin, Oregon State College (OSC), E. I. Sleeper, Long Beach State College, J. E. H. Martin, Entomology Research Branch, Canada Department of Agriculture, Ottawa (CNC), Hugo Rodeck, University of Colorado Museum, and Floyd Werner, University of Arizona.

Financial assistance has been provided through grants-in-aid from Sigma Xi-RESA, the American Academy of Arts and Sciences, and the University of California, Santa Barbara.

DISCUSSION OF CHARACTERS

The wing-coupling apparatus consists of a large jugal lobe on the fore wing, and a frenulum, bearing several long setae, on the hind wing; this is essentially the same apparatus as in Hemerobiidae, etc. The Chrysopinae may have a weak frenulum, but the jugal vein is thin, and there is no jugal lobe. Loss of the wing-coupling apparatus appears associated with narrowing and strengthening of the wing base, and is probably of great adaptive significance. A similiar modification has occurred in the evolution of the Myrmeleontidae and Ascalaphidae from an osmyloid ancestor (Adams, 1958), and in the Mantispidae.

In the Nothochrysinae, there is no obvious tympanal organ (Friedrich, 1953; Erhardt, 1916) in the base of R in the fore wing, and the stem of M is easily visible extending in a straight line adjacent to R. In the Chrysopinae, the tympanal organ forms a conspicuous bulge in R, at the point where Cu diverges; the base of M usually is coalesced with R, but if visible, makes a detour posteriorly around the tympanal organ. Probably this is an auditory organ (Adams, 1962).

In *Nobilinus* (Apochrysinae), the tympanal organ involves a large area between R and M, but is longer and does not form a bulge on the underside of R, as in Chrysopinae.

Another character, probably of great adaptive significance, is the pseudomedia, which differs fundamentally in the more primitive chrysopids, and in the Chrysopinae—Apochrysinae. In *Pimachrysa* (Figs. 1, 2), *Hypochrysa* (Fig. 5), and in most of the fossil genera, Psm is composed of crossveins alternating with the branches of Rs + MA, and is merely a basad extension of the inner gradate series. The course of the longitudinal veins and composition of the primitive pseudomedia is particularly clear in *Hypochrysa*. In the Chrysopinae

(Fig. 45), and Apochrysinae (Fig. 44), and in *Nothochrysa* (Fig. 3), Psm, at least basally, is composed of overlapping zigzagged branches of Rs and M, with no crossveins between them. (Some specimens of *N. fulviceps* show no overlap.) In a few genera of Chrysopinae, such as *Yumachrysa* and *Chrysopiella*, there is a transition from the primitive arrangement apically, with no overlap, to the more advanced arrangement basally, with overlapping veins.

Primitively, the longitudinal veins forked at the posterior wing margin, except for the anals in both wings, and CuP in the hind wing. This condition may be seen in the hind wing of *Archaeochrysa* (Figs. 40, 41). There is a tendency for the point of furcation to move proximally until it reaches the outer gradate crossveins; when this occurs, the pseudomedial cells appear each to give rise to two marginal veinlets. This process begins at the wing base, and proceeds apically; the sequence is best seen in the fore wing of *Archaeochrysa paranervis* (Fig. 40). Frequently the longitudinal veins fail to fork at all.

The pseudocubitus has evolved like the pseudomedia, by alignment of longitudinal veins and gradate crossveins. In the Nothochrysinae it usually is more strongly developed than Psm, especially in the fore wing. In the Chrysopinae, where the longitudinal veins may overlap at Psc, it is impossible to determine, in most cases, which marginal veinlets have arisen from which longitudinal veins. For this reason the overlap at Psc shown in Figures 44 and 45 is conjectural, although consistent with the tracheation of Psc in *Chrysopa signata* Walker, as demonstrated by Tillyard (1916).

Evolution of the basal Banksian cell of the hind wing has been described by Carpenter (1935). The archaic condition is exemplified by *Archaeochrysa*, where MP1 is connected to Rs + MA by the sectorial crossvein, which intersects MP1 in a Y-formation. More advanced genera exhibit slight basad migration of MF, and fusion of MP1 with Rs + MA. This evolutionary sequence can be seen by comparing Figures 41, 5, 4, and 2.

In Chrysopinae and Apochrysinae, the wing flexes along a line immediately anterior to Psm (dotted line, Figs. 44, 45). To facilitate this flexion in the fore wing, the first sectorial crossvein (first crossvein distal to the base of Rs + MA) and the branches of Rs + MA are interrupted or articulated at the point of intersection with the pseudomedia. In the Nothochrysinae, the sectorial crossvein is always interrupted, but the branches of Rs + MA never are so (except in *Nothochrysa*). Flexion along the pseudomedia is accomplished, in *Hypochrysa*, by folds traversing the crossveins of Psm (Fig. 5). In *Pimachrysa*, there appears to be no distinct line of flexion, except perhaps in *P. nigra* (Fig. 4). In this species the veins show no obvious weakening or articulation, but most specimens have a slight wrinkle in the membrane parallel and anterior to Psm. A similar line of flexion occurs between MA and MP in most other families of Neuroptera. In Chrysopidae, this line has been lost early in evolution; the pseudomedial fold is its functional, but not morphological, equivalent. As an interesting example of parallel evolution, the shape of the wing, and course of the pseudomedial fold in Chrysopinae is strikingly like that of the smaller Nymphidae (e.g. *Osmylops*, *Nesydrion*). In the *Nodita-Leucochrysa* complex (Chrysopinae), Psm curves up to join the outer gradate series; this evolutionary line has culminated in the Apochrysinae, of which the nymphid, *Myiodactylus*, is a counterpart.

Another striking feature of the Nothochrysinae is the near uniformity in thickness of most of the veins at the wing base. In Chrysopinae and Apochrysinae, R is expanded basally, and Cu is always inflated near the intersection with the first medial crossvein.

The Apochrysinae appear to be specialized derivatives of the *Nodita-Leucochrysa* complex (Chrysopinae). The closest resemblance is to forms such as *Gonzaga*, from which the less specialized Apochrysinae, such as *Synthochrysa* (Fig. 44), differ only in the loss of the basal subcostal crossvein, less distance between Psm and Psc, condition of MP2, and slight changes in the proportions of the wing.

In *Gonzaga* (Fig. 45), MP2 bends close to CuA, then up toward MP, thence down to CuA again, which it joins to form part of Psc. If MP2 were to shift posteriorly so that it joined CuA directly, eliminating the zig-zag, a configuration like that in the Apochrysinae would result. It may be noted that the second apparent medial crossvein of the Apochrysinae (Fig. 44) lies in exactly the same relationship to the first sectorial (sxv) and cubital crossveins as does the medial fork in *Gonzaga*. This is significant, since, if MP2 had instead moved anteriorly to coalesce with MP1, the apparent second medial crossvein would be expected to intersect CuA at the middle of the second cubital cell.

The degree of overlap of the branches of Rs + MA in Apochrysinae is the same as in Chrysopinae, and may be verified by matching branches of Rs + MA with the veinlets between Psm and Psc, working basally from the distal end of Psm. Such a count would not, of course, bear on the question of whether MP2 had disappeared by moving forward and coalescing with MP1, or whether it may have moved posteriorly and fused with CuA. But it precludes the possibility that the first median crossvein is MP2, as suggested by Kimmins (1952b), since in that case one would have to account for an extra crossvein between MP and CuA.

Investigation of male genitalic structures in a wide variety of neuropterous types has led me to believe that in the Planipennia, the ninth gonocoxites primitively articulate on the arms of the gonarcus. In the Chrysopidae, the "parameres" of most authors appear to be the gonocoxites and are referred to as such below.

Key to the Subfamilies of Chrysopidae

1. Media posterior 1 runs in an even curve to margin, not angulate at intersections with basal inner and outer gradate crossveins. These crossveins intersect MP at nearly a right angle, so that MP does not appear interrupted by either Psm or Psc (Mesozoic) .... Mesochrysopinae.
– Media posterior 1 usually definitely angulate at intersections with basal outer and inner gradates, so that it appears interrupted by a definite pseudocubitus, and (usually) a pseudomedia .... 2.
2. Jugal lobe of fore wing large; frenulum present on hind wing; tympanal organ of fore wing absent .... Nothochrysinae.
– Jugal lobe of fore wing and frenulum of hind wing reduced or absent; tympanal organ of fore wing present (reduced in Apochrysinae) .... 3.
3. In fore wing, basal subcostal crossvein and intramedian cell present; space between Psm and Psc relatively wide (Fig. 45) .... Chrysopinae.
– In fore wing, basal subcostal crossvein and intramedian cell absent; space between Psm and Psc relatively narrow (Fig. 44) .... Apochrysinae.

Subfamily MESOCHRYSOPINAE Handlirsch

Mesochrysopidae Handlirsch, 1908, Die fossilen Insekten: 612, pl. 48, fig. 14. Type: *Mesochrysopa* Handlirsch 1908.

Genus *MESOCHRYSOPA* Handlirsch

Mesochrysopa Handlirsch, 1908, Die fossilen Insekten: 612. Type (by monotypy): *Hageniotermes zitteli* Meunier, 1898.

Mesochrysopa zitteli Meunier

Hageniotermes zitteli Meunier, 1898, Arch. Mus. Teyl. (2) 6: 34, pl. 2, fig. 2 (reference from Handlirsch).

Mesochrysopa zitteli: Handlirsch, 1908, *loc. cit.* Tillyard, 1916, Proc. Linn. Soc. N.S. Wales 41: 245–248, text-fig. 8. Martynova, 1949, Trudy Paleontol. Inst., Akad. Nauk SSSR 20: 169. Adams, 1957, Psyche 63: 72.

Discussion. From the Jurassic limestone of Bavaria. A myrmeleontid appearance derives from the long slender wings, with Sc and R apparently fused apically, and with many branches of Rs. But the absence of pectinate branching of MP and CuA precludes relationship with the osmyloidmyrmeleontoid families. Although the inner and outer gradate series are somewhat irregular, the basal inner gradates are strongly inclined, forming a well-defined pseudomedia, which does not include MP. The multiplication and irregularity of veins is likely a function of the insect's large size (fore wing 36 mm long); the arrangement is essentially like that of the following genus.

Genus *MESYPOCHRYSA* Martynov

Mesypochrysa Martynov, 1927, Izvestia Akad. Nauk SSSR 21: 764. Type species (by monotypy): *Mesypochrysa latipennis* Martynov. Martynova, 1949, Trudy Paleontol. Inst. Akad. Nauk SSSR 20: 169.

Mesypochrysa latipennis Martynov

Mesypochrysa latipennis Martynov, 1927, Izvestia Akad. Nauk SSSR 21: 765, figs. 10–12 (hind wing and body structure). Martynova, 1949, Trudy Paleontol. Inst. Akad. Nauk SSSR 20: 169. Type from the Jurassic of Kara-tau (Turkestan), Paleontol. Inst. Acad. Sci. USSR, not examined.

Discussion. Martynov's figure (redrawn as Fig. 37) shows the body and hind wing in some detail. The course of MP is probably drawn too straight; one would expect slight zig-zagging at the intersection of the basal gradate crosswing. Probably two crossveins were present between the branches of MP, as in nearly all chrysopids.

This fossil is of particular interest in that the hind wing is exactly what one would postulate in the ancestor of *Archaeochrysa*. The basal Banksian cell is similar, but the inner crossvein is longer and more strongly inclined in *Mesypochrysa*. The basal branches of Rs + MA are only slightly zig-zagged, not strongly bent as in *Archaeochrysa*. It differs from more advanced chrysopids in the short, transverse pronotum.

Subfamily NOTHOCHRYSINAE Navás

Nothochrysinos Navás, 1910, Broteria 9: 38–59. Type: *Nothochrysa* McLachlan.

Nothochrysini Navás, 1913, Ann. Soc. Sci. Bruxelles 37: 303. Type: *Nothochrysa* McLachlan.

Dictyochrysinae Esben-Petersen, 1918, Ark. Zool. 11 (26): 26. Tjeder, 1966, p. 246. Type: *Dictyochrysa* Esben-Petersen. NEW SYNONYMY (subjective).

Description. Wing veins of nearly uniform diameter near base, tapering evenly apically; MP extends adjacent to R, but is not fused with it; no tympanal organ apparent on ventral side of R in fore wing; jugal lobe of fore wing conspicuously produced; Psm (except in *Nothochrysa* and *Dyspetochrysa*) composed of branches of Rs alternating with crossveins. Prosternal area largely membranous. Color rarely green.

Discussion. Navás (1910) based his tribal division of the Chrysopidae on relatively trivial venational characters. His tribe Nothochrysinos included all the forms which had the intramedian cell (the cell immediately distal to the fork of MP) either quadrangular, or absent. This resulted in the inclusion of *Nothochrysa* (most species of which belong in *Italochrysa*), *Leucochrysa*, and *Nesochrysa*. With the exception of three species of *Nothochrysa*, all of these are members of the Chrysopinae. *Hypochrysa* was placed in the "Chrysopinos."

There is some question as to the validity of Navás' 1910 names. The taxa were clearly designated as tribes and names properly constructed but for the colloquial plural endings. These names bore correct terminations in the 1913 paper, and have priority from that date at latest. While Navás' usage of the name makes it nomenclatorially available, the concept of the subfamily here proposed is entirely new.

The Tertiary genera differ from living forms in position of the basal subcostal crossvein only. Furthermore, *Kimochrysa africana* (Recent) has the crossvein as in the fossils. Two Tertiary chrysopids appear to have been described from Eurasia, both belonging to Recent genera (*Nothochrysa*, *Chrysopa*). Martynova (1949) reports having collected a series of wing imprints from the Miocene of Stavropol (North Caucasus), but these have not been described.

Nothochrysa is included here because of its many archaic features, not found in any member of the Chrysopinae. However, the development of the pseudomedia is more advanced than in any other nothochrysine (except *Dyspetochrysa*), and does not differ from that of the Chrysopinae. Sclerotization of the prosternum is intermediate between that of *Pimachrysa* and *Hypochrysa*, and Chrysopinae. These are both important evolutionary advances over the rest of the Nothochrysinae, and tribal separation might be advisable, but for the small number of genera involved.

Biology. Biological information on this subfamily is meagre. *Nothochrysa* (Killington, 1937; Toschi, 1966) and *Hypochrysa* (Principi, 1958) lay stalked eggs. The larvae of *Hypochrysa* (Brauer, 1867) and *Nothochrysa* (Killington, 1937; Toschi, 1966) have been described. Both *N. capitata* and *N. fulviceps* may occasionally carry trash, but have exceptionally small thoracic tubercles. There is some indication of preference by adults for ancient host-plants: *Nothochrysa fulviceps* associates with oak, and *N. capitata* with pine (Killington), *N. californica* with both conifers (W. Wade, pers. comm.) and oak. *Pimachrysa intermedia* feeds on willow pollen; other species of *Pimachrysa* have been taken in bait traps (*fusca, albicostales*) or on flowers (*nigra*, on *Ceanothus*) and may be pollen or nectar feeders.

In *Nothochrysa* and *Hypochrysa nobilis*, a pale mass of material is deposited on the dorsal surface of the female abdomen. This has been erroneously interpreted as a spermatophore (Killington, Principi). However, Toschi, 1966, has observed that in female specimens of *N. californica* bearing such a dorsal mass, the spermatophore is to be found internally in the bursa. In *Pimachrysa fusca*, and presumably the other species, a sac-like spermatophore (Fig. 21, sp) may often be found protruding from the gonocoxites ("gonapophyses laterales") which marginally bear hooked hairs, probably for its retention (Fig. 20).

Key to the Genera of Nothochrysinae

1\. Basal subcostal crossvein of fore wing arises distally to origin of Rs + MA, approximately opposite the medial fork (MF, Fig. 42); mostly fossil genera .... 2.
– Basal subcostal crossvein of fore wing arises basally to origin of Rs + Ma, or subcostal crossveins numerous; living genera .... 6.
2\. Innermost branch of Rs + MA coalesced with MP 1 + 2 .... *Dyspetochrysa* gen. n.
– Innermost branch of Rs + MA connected to MP 1 + 2 by a crossvein .... 3.
3\. In fore wing Rs + MA arises basally, nearer the first medial crossvein than to MF; in hind wing MP and Rs joined by a crossvein .... *Archaeochrysa* gen. n.
– In fore wing, Rs + MA arises more apically, nearer MF than to first medial crossvein; in hind wing MP coalesces with Rs for a short distance .... 4.
4\. Inner gradate series forms a smooth curve continuous with Psm .... 5.
– Apical inner gradate series closer to Rs + MA than is Psm, thus forming a broken curve, with basalmost inner gradate of apical series arising proximally to most distal inner gradate of basal series .... *Tribochrysa*.
5\. Subcosta and costa fused apically; living species .... 11.
– Subcosta and costa not coalesced; fossil species .... *Paleochrysa*.
6\. More than two series of gradates in both wings .... 7.
– Only two series of gradates in both wings .... 8.
7\. Three regular series of gradates .... *Triplochrysa*.
– Six or seven irregular series of gradates; discal area divided into a meshwork of polygonal cells .... *Dictyochrysa*.
8\. Proximal branch of Rs + MA usually coalesced for a short distance with MP 1; in living species, pseudomedial fold follows entire length of Psm in both wings .... *Nothochrysa*.
– Proximal branch of Rs + MA never coalesced with MP 1, so that Psm consists of alternating longitudinal veins and crossveins; pseudomedial fold intersects first sectorial crossvein above intramedial cell, and may cross some basal gradates of the Psm, but never extends the full length of Psm .... 9.
9\. Hooked hairs on ninth gonocoxites ("gonapophyses laterales") of female; basal crossveins of Psm not interrupted by pseudomedial fold .... *Pimachrysa*.

– No hooked hairs on ninth gonocoxite of female; basal crossveins of Psm interrupted by pseudomedial fold .... 10.

10\. In fore wing, 2A and 3A fused apically; male epiproct fused with ninth tergite, with ventral processes .... *Hypochrysa.*

– In fore wing, 2A and 3A connected by a crossvein; male ectoproct demarked from ninth tergite, with no ventral processes .... 11.

11\. Intramedian cell rhomboid, almost as high as long; fore pterostigma shorter than half wing width .... *Pamochrysa.*

– Intramedian cell about twice as long as high; fore pterostigma as long as two-thirds wing width .... *Kimochrysa.*

Genus *DICTYOCHRYSA* Esben-Petersen

Dictyochrysa Esben-Petersen, 1917, Proc. Linn. Soc. New South Wales 42: 214–215 (type, by original designation, *D. fulva* Esben-Petersen); 1918, Arkiv for Zool. 11(26): 1–37. Kimmins, 1952, Ann. Mag. Nat. Hist. (12)5: 70–72 (key to species).

Dictyochrysa fulva Esben-Petersen

D. fulva Esben-Petersen, 1917, Proc. Linn. Soc. N.S. Wales 42: 214–215, pl. 13, fig. 10. Holotype, from Queensland, Australia, Froggatt Collection, CSIRO, Canberra (not seen). Kimmins, 1952, Ann. Mag. Nat. Hist. (12)5: 71–72.

Dictyochrysa peterseni Kimmins

D. peterseni Kimmins, 1952, Ann. Mag. Nat. Hist. (12)5: 70–71, fig. 2 (wings, head, pronotum). Holotype, from Mt. Koscinsko, New South Wales, 6000 ft., 12 December 1931, R. J. Tillyard, coll. In Brit. Mus. (Nat. Hist.), not seen.

Additional distribution. Mt. Maria, Tasmania?

Dictyochrysa latifasciata Kimmins

D. latifasciata Kimmins, 1952, Ann. Mag. Nat. Hist. (12)5: 71–72, fig. 3 (male genitalia). Holotype male, from Mt. Wellington, S. Tasmania, 1300–2300 ft., 12–21 March 1913. Abdomen in balsam. Brit. Mus. (Nat. Hist.), not seen.

Genus *TRIPLOCHRYSA* Kimmins

Triplochrysa Kimmins, 1952, Ann. Mag. Nat. Hist. (12)5: 69–70 (type, by original designation, *T. pallida* Kimmins).

Triplochrysa pallida Kimmins

T. pallida Kimmins, 1952, *loc. cit.*, fig. 1 (wings). Holotype female, from Bunya Mt., Queensland, Australia, 27 January 1951, in Brit. Mus. (Nat. Hist.), not seen.

Genus *HYPOCHRYSA* Hagen

Hypochrysa Hagen, 1866, Stettiner Entomol. Zeit. 27: 377. Type species (by monotypy): *Chrysopa nobilis* Schneider.

Hypochrysa nobilis (Schneider)

Figures 5, 32, 33

Chrysopa elegans Burmeister, 1839, Handb. d. Entomol.: 981. Type locality "Harze," Saxesen collector, probably in the Zoological Museum, Univ. of Halle (not seen). This name has priority, but is a *nomen oblitum* under Rule 23b. Not to be confused with *Hemerobius elegans* Guerin 1838, which was transferred to *Chrysopa* by Schneider in 1851, and probably is a *Gonzaga*; this name is preoccupied by *Hemerobius elegans* Stephens 1836.

Chrysopa nobilis Schneider, 1851, Symb. ad Monogr. Gen. Chrysopae: 142–144, pl. 51. (Name replaces *elegans* Burmeister.)

Hypochrysa nobilis: Hagen, 1866, Stettiner Entomol. Zeit. 27: 377. Brauer, 1867, Verh. Zool.-Bot. Ges. Wien 17: 27–29, pl. 9, fig. 1 (larva). Navás, 1913, Insecta 28: 129–130, fig. 1; 1915, Arx. Inst. Cien., Barcelona 3(2): 88. Principi, 1956, Atti Acad. Sci. Inst. Bologna, Rend. (XI)3: 1–3, pl. 1 (Ethology, photographs of adult, egg, habitat); 1961, Mem. Mus. Civ. Stor. Nat. Verona 9: 109.

Description. Male ninth tergite fused with ectoprocts, not articulated with ninth sternite. Eighth and ninth sternites not fused, but moveable. Ectoprocts (Fig. 32, ect.) each posteroventrally bearing heavily sclerotized toothed process. Gonarcus flattened, heavily sclerotized, black; mediuncus bilobed; gonocoxites ("parameres") weakly sclerotized, dorsolateral to mediuncus lobes.

Distribution. Widespread in southern Europe.

Remark. *Hypochrysa argentina* Navás, 1911, is a *Chrysopa* (Tjeder, 1966).

Genus *KIMOCHRYSA* Tjeder

Kimochrysa Tjeder, 1966, S. African Anim. Life 12: 254. Type species (by original designation): *Kimochrysa impar* Tjeder.

Kimochrysa impar Tjeder

Kimochrysa impar Tjeder, *ibid.*: 256–259, figs. 820–834. Holotype male, Kleinmond, Cape Province, S. Africa, in the South African Museum, Cape Town (not seen).

Discussion. This is the only species of the Nothochrysinae with numerous subcostal veinlets in the fore wing. In the male, the ninth abdominal tergite is not hinged to the eighth and ninth sternites, and these sternites are completely fused.

Kimochrysa africana (Kimmins)

Hypochrysa africana Kimmins, 1937, Ann. Mag. Nat. Hist. (10) 19: 307–308, fig. Holotype female, from Worcester, Cape Province, S. Africa, in Brit. Mus. (Nat. Hist.) (not seen).

Kimochrysa africana: Tjeder, 1966, S. African Anim. Life 12: 259–261, figs. 835–838.

Kimochrysa raphidioides Tjeder

Figures 10, 29–31

Kimochrysa raphidioides Tjeder, 1966, *ibid.*: 261–262, figs. 839–844. Holotype female, from "Cap Drege" (abbreviation for "Cape of Good Hope, Drege, collector"), in the MCZ (examined).

Description. Head marked with dark as in Figure 10. Pronotum transverse, a thin transverse black line at outer edge of furrow, a short longitudinal line at posterior corner. Subcostal crossvein distal to origin of Rs + MA. Male ninth tergite hinged to ninth sternite (Fig. 31); fusion of eighth and ninth sternites demarked by internal sclerotized ridge. Gonocoxites (Figs. 29, 30, gcx) paddle-shaped.

Discussion. In addition to the type, a male with no data is also in the MCZ. This species is doubtfully distinct from *africana*, from which it differs only by the position of the subcostal crossvein (proximal to the origin of Rs + MA in *africana*), and by greater sclerotization of the spermatheca (which may be due to different degrees of maturity in the specimens). Tjeder differentiates these two species principally on the position of the second medial crossvein. But in *africana*, it varies in position from distal to proximal to the fork (Kimmins, pers. comm.). In the male of *raphidioides*, the crossvein intersects MP at the fork. In the specimen of *K. impar* figured by Tjeder, the second medial crossvein is proximal to the fork on one wing, and distal on the other.

The coloration of the two species is similar, although the frontal markings below the antennae are absent on the type of *africana*, and faint on the second specimen; the interantennal marks are faint on both specimens of *africana* (Kimmins, pers. comm.).

Genus *PAMOCHRYSA* Tjeder

Pamochrysa Tjeder, 1966, S. African Anim. Life 12: 248. Type species (by original designation): *Pamochrysa stellata* Tjeder.

Pamochrysa stellata Tjeder

Pamochrysa stellata Tjeder, *ibid.*: 250–253, figs. 797–815. Holotype male, from Cathedral Peak, Forestry Reserve, Indumeni River, Drakensberg, Natal, S. Africa, March 1959, in the Natal Museum, Pietermaritzburg, not seen.

Genus *NOTHOCHRYSA* McLachlan

Nothochrysa McLachlan, 1868, Monograph of the British Neuroptera-Planipennia. Trans. Entomol. Soc. London (1868): 195. Type species, *Chrysopa fulviceps* Stephens, designated by Banks, 1903, Trans. Amer. Entomol. Soc. 29: 142. Tjeder, 1941, Entomol. Tidskrift (1941): 30–31. Principi, 1946, Bol. Inst. Entomol. Univ. Bologna 15: 86.

Nathanica Navás, 1913, Trans. 2nd Intern. Congr. Entomol., Oxford, 1912, 2: 181 (type [by subsequent designation of Tjeder, 1941, *ibid.*]: *Hemerobius capitatus* Fabricius).

As McLachlan failed to designate a type for this genus, Banks' listing of *N. fulviceps* as type constitutes a valid type designation. Principi (1946) restricted *Nothochrysa* to include *fulviceps* and *capitata* only, erecting a new genus, *Italochrysa*, for *N. italica* Rossi. It appears that the great majority of Old World species formerly included in *Nothochrysa* belong instead to *Italochrysa*.

Description. Head wide, vertex low, eyes small, labrum emarginate. Antennae about as long as fore wing; scape about as long as wide, flagellar segments longer than wide. Prosternum small (Fig. 35). Tarsal claw either with basal enlargement (*fulviceps*) or simple (*capitata* and *californica*). Fore wing (Figs. 3, 43): basal subcostal crossvein opposite midpoint between first medial crossvein and medial fork. Rs originates basad of medial fork; two rows of gradates. Psm formed by overlapping longitudinal veins, may extend beyond basal inner gradates; pseudomedial fold present; MP2 parallels MP1, connected by a crossvein; second medial crossvein intersects MP2 midway between Mp and CuA. Psc parallels Psm; runs into outer gradate series. 1A forked apically; 2A and 3A simple. Jugal lobe prominent. Hind wing: frenulum well developed, MP coalescent with Rs for a moderate distance; two rows of gradates. Psm well developed, but longitudinal veins do not overlap (except basally in *fulviceps*); instead each intersects the next where it bends sharply apicad, so that the veins between Psm and Psc are exactly opposite the basal branches of Rs (a very conspicuous and characteristic feature). Pseudomedial fold present. Psc runs into outer gradate series.

Male: (Fig. 17) ninth abdominal tergite heavily sclerotized anteroventrally, with irregular margin; fused with ectoproct. Eighth sternite distinct or only weakly fused with ninth sternite. Cuticular gland openings present. Gonarcus (Figs. 18, 19) bears wide triangular mediuncus; gonocoxites small. Female: No hooked hairs on ninth gonocoxites; eighth sternum bilobed, lobes fitting into cuplike ninth valvulae ("diverticulos linguiformes" of Principi) so as to close the genital cavity anteriorly, as in Chrysopinae.

Key to the Recent Species of NOTHOCHRYSA

1. Pronotum membranous medially; Psm in fore wing extends beyond inner gradate series; head orange and black; North American .... *californica*.
– Pronotum sclerotized medially; Psm in fore wing runs into inner gradate series; head concolorous, orange or orange-brown; European .... 2.
2. Thorax with median pale band, tarsal claws with basal expansion; several marginal veinlets from Psc forked; large species (expanse 37–48 mm) .... *fulviceps*.
– Thorax orange-brown, no median band; tarsal claws simple; marginal veinlets from Psc rarely forked; smaller (expanse 27–36 mm) .... *capitata*.

Nothochrysa fulviceps (Stephens)

Chrysopa fulviceps Stephens, 1836, Illustr. Brit. Entomol. Mand., 6: 101. Types: 4 syntypes in the Brit. Mus. (Nat. Hist.), not seen.

Nothochrysa fulviceps: McLachlan, 1868, Trans. Entomol. Soc. London (1868): 207.

Nathanica fulviceps: Navás, 1913, Trans. 2nd Intern. Congr. Entomol., Oxford, 1912, 2: 181. Killington, 1937, Monogr. Brit. Neuropt. 2: 236–242, fig. 114 (male genit.), fig. 115 (female genit.), pl. 27, fig. 2 (wing), pl. 30, fig. 3 (larva).

Nathanica fulviceps var. *flavida* Navás, 1919, Bol. Soc. Entomol. España 2: 55.

Nothochrysa fulviceps: Tjeder, 1941, Entomol. Tidskrift (1941): 30–31.

Distribution. Europe.

Nothochrysa capitata (Fabricius)

Hemerobius capitatus Fabricius, 1793, Entomol. Syst. 2: 82. Type locality "Germania. Dom. de Paykull." Zool. Mus., Univ. of Kiel, not seen.

Chrysopa capitata: Curtis, 1834, Brit. Entomol. pl. 520.

Nothochrysa capitata: McLachlan, 1868, Trans. Entomol. Soc. London (1868): 207.

Nathanica capitata: Navás, 1913, Trans. 2nd Intern. Congr. Entomol., Oxford, 1912, 2: 181. Killington, 1937, Monogr. Brit. Neuropt. 2: 242–246, fig. 115c (female genit.), pl. 27, fig. 3 (wings); pl. 30, fig. 4 (larva).

Nothochrysa capitata: Tjeder, 1941, Entomol. Tidskrift (1941): 30.

Distribution. Europe.

Nothochrysa californica Banks

Figures 3, 8, 17, 18, 19, 22, 35

Nothochrysa californica Banks, 1892, Trans. Amer. Entomol. Soc. 19: 373. Male holotype from Los Angeles, Calif., MCZ No. 11406, examined. 1903, Trans. Amer. Entomol. Soc. 29: 142, pl. 2, fig. 3 (wing base); 1904, Cat. Neuropt. Insects U.S., Philadelphia: 26. MacGillivray, 1894, Canad. Entomol. (1894): 171. Smith, 1932, Ann. Entomol. Soc. Amer. 35: 582, pl. 1, fig. 5 (body and wings, color). Bickley and MacLeod, 1956, Proc. Entomol. Soc. Washington 58: 182–183.

Description. Head (Fig. 8): antennal sockets large, margins black. A black line extending down suture from antennal socket to anterior tentorial pit; black line connecting pits bent posteriorly in middle; dark mark on clypeus connected to this line laterally; black genal spot, near mandibular articulation. Vertex elevation slight; median and lateral stripes connected to circumantennal marks. Antennae black; scape wider than long. Palpi dark, pale at joints.

Pronotum divided by median longitudinal pale membranous area; lateral sclerites dark umbraceous, lateral margins pale. Alinotum dark, mesoprescutum with posterior pale band interrupted by black median longitudinal suture; mesoscutum pale anteriorly. Propleuron and sternum dark. Meso- and metapleura dark, pale posteriorly. Coxae dark, trochanters dark basally; femora with dorsal and ventral longitudinal dark stripes, confluent on hind femur. Tibiae pale with dark basal and apical marks; tarsi fuscous, dark apically. Claws lack basal tooth.

Fore wing (Fig. 3): veins black, except C, R, 3A and posterior marginal vein pale basally; sensory area posterior to apex of 3A and posterior marginal vein pale basally; sensory area posterior to apex of 3A, and jugal lobe, fuscous; stigma fuscous, spaces between apical subcostal crossveins ivory. MP1 desclerotized at intersection with basal sectorial crossvein; Psm continues beyond basal inner gradates. Hind wing: venation dark, R white to stigma; Rs and MP1 white basally; CuP white; stigma as in fore wing.

Abdomen: tergites black, narrowly pale apically; sternites may be pale both basally and apically. Female ninth tergite with pale spot posterolaterally; tenth tergite pale, callus cerci and posterior margin black. Eighth sternum (Fig. 22) bilobed. Dorsal postcopulatory mass white or creamy yellow. Male ninth sternum pale ventrally. Callus cerci fused to ninth tergum; ninth sternum partially coalescent with eighth (Fig. 17). Cuticular gland openings lacking on heavily sclerotized anteroventral area of ninth tergum, and tenth tergum. Mediuncus (Figs. 18, 19) broad, hoodlike; gonocoxites small, platelike.

Measurements (mm): Fore wing length 12.5–15. (13.5); width 4.5–5.5 (5.1); antenna 10–12 (11.2).

Distribution: CALIFORNIA: Alameda Co.: E. C. Van Dyke (USNM); Berkeley, 28-IV-12, ♀, J. C. Bridewell (USNM); Oakland, 17-IV-15, E. P. Van Duzee (MCZ); Hills back of Oakland, 30-IV-1911, ♂, 9-V-09, ♂, E. C. Van Dyke (CAS). Contra Costa Co.: Near Orinda, 21-IV-50, W. Wade (CNHM). Marin Co.: Mill Valley, 28-II-26, ♀, 6,7-III-26, 2 ♀, E. P. Van Duzee (CAS), 25-III-52, 2 ♂, 1 ♀, H. B. Leach (CAS), 8-V-56, E. S. Ross (CAS); Muir Woods, 23-IV-1911, ♀, E. C. Van Dyke (CAS); San Geronimo, 20-IV, O. Sacken (MCZ). Mendocino Co.: Caspar Lumber Camp, 12 mi. E. Fort Bragg, 20-VI-38, ♀, Van Dyke (CAS); Van Damme State Park, 18-V-47, ♂, H. Welsh (CAS); Yorkville, 1-V-24, ♀, E. P. Van Duzee (CAS). Santa Clara Co.: Stevens Cr. 16-III-41, ♀, E. S. Ross (CAS); Palo Alto, 27-V-92 (MCZ); Hills back of Palo Alto, 29-IV-1928, ♀, (CAS); Stanford Univ. 5-IV-04, ♀, (MCZ). San Mateo Co.: King's Mt., 5-VII-46, ♂, E. S. Ross (CAS).

OREGON: Benton Co.: Corvallis, 19-V-45, ♀, Marge Johnson (OSC); McDonald For., 5 mi. N. Corvallis, 26-V-56, ♀, J. R. Mori (OSC); Sulfur Spgs., 6 mi. N. Corvallis, 11-V-56, ♀, J. F. O'Brien (OSC); Rock Cr., 12 mi. W. Corvallis, 4-V-56, ♀, N. E. Johnson (OSC); 1 mi. N. Dawson, 2-V-62, 4 ♀, 1 ♂, W. Barnett, (OSC); 2 mi. S.E. Summit, 12-IV-57, ♂, J. Lattin (OSC).

WASHINGTON: Kittitas Co.: Easton, A. Koebele (USNM).

BRITISH COLUMBIA: Bowser, 5-IV-55, 20-VI-55, 1 ♂, 1 ♀, J. W. Brown (CNC); So. Pender Is., 30-V-50, on Douglas Fir, 1 ♀, (CNC); Vancouver, 31-V-31, on snow, 4700 ft., Seymour Mt., H. B. Leech (MCZ); Victoria, 4-V-18, W. B. Anderson (Smith, 1932).

Diagnosis. This species differs markedly from *N. fulviceps* and *capitata* in head coloration, in Psm extending beyond the basal inner gradates, and in the peculiar separation of the lateral pronotal sclerites by a median membranous area. It is retained in *Nothochrysa* because it shares with the other species the well developed Psm and Psc.

Discussion. The paucity of material from Oregon, Washington, and western Canada probably indicates less collecting activity, rather than scarcity. In the San Francisco Bay area it sometimes is locally fairly numerous. W. Wade (pers. comm.) collected eggs on conifers in the Orinda, California, area. D. Breedlove (pers. comm.) has noted adults abundantly on oak near Oakland, California. Throughout its range, it appears to be restricted to moist forest areas, not far from the coast. The type is probably mislabelled; in spite of intensive collecting around Los Angeles since 1892, no additional specimens have been taken.

Nothochrysa praeclara Statz

Figure 43

Nothochrysa praeclara Statz, 1936, Bechiana 93: 215–216, fig. 3 (photograph of fore wing), fig. 4 (drawing of fore wing). Holotype, from Rott am Siebengebirge, West Germany, mid-Tertiary, in the Los Angeles County Museum (examined).

This species, known from a single fore wing, differs from *capitata* only in having fewer overlapping veins in Psm. In all the specimens of *capitata* examined, at least four branches of Rs + MA coalesce with the next proximal vein at the Psm, whereas only one basal branch is so coalesced in *praeclara*. This may not be significant; in *fulviceps* the venation is very irregular, and some specimens show no overlap at all. *Praeclara* differs from *fulviceps* in smaller size (fore wing length 16.33 mm, 16 branches of Rs + MA).

Genus *PIMACHRYSA* Adams

Pimachrysa Adams, 1957, Psyche 63: 67–70. Type (by original designation): *P. grata* Adams.

Description. Vertex moderately elevated; anterior tentorial pits large; labrum barely emarginate. Antennal length variable: scape short, little swollen; apical flagellar segments more than twice as long as wide. Tarsal claws simple, without basal enlargement. Prosternum unsclerotized anteriorly to sternal pits (Fig. 34). Male with ninth tergite clearly separated from ectoproct; ninth sternite clearly demarked from eighth, posterior margin acute (Figs. 11, 14). Mediuncus slender, apex angulate (Figs. 12, 13, 15, 16). Cuticular gland openings present. Female with enlarged ninth gonocoxites bearing marginally a band of spoon-shaped setae (Figs. 20, 21). Eighth sternite (subgenital plate) and ninth valvulae lie on membrane of genital opening, so that it is permanently closed anteriorly. Spermatophore ovoid, protruding from gonocoxites.

Fore wing: costal area narrow; basal subcostal crossvein slightly basal to origin of Rs; Rs arising basally to cubital fork. MP2 not fusing with MP1, but turning to wing margin at apex of intramedian cell. Second mediocubital crossvein near MF, usually distal to it. Two gradate series, extending smoothly into Psm and Psc (except in *P. nigra*); no overlap of adjacent longitudinal veins on Psm or Psc. Pseudomedial fold undeveloped except for weak spot at intersection of first sectorial crossvein and MP1. Anals neither branched nor anastomosed. Jugal lobe prominent, with jugal vein.

Hind wing: frenulum present. Costal area narrow. Rs and MP merely touching, or fused for a short distance; basal Banksian cell large. Psm and Psc similar to those of fore wing. Anals neither forked nor anastomosed.

Discussion. This genus is most similar to *Hypochrysa*, but differs in having enlarged ninth gonocoxites, bearing modified hairs, probably serving to hold the spermatophore in place. In *Hypochrysa*, a postcopulatory mass is placed on the dorsal surface of the female abdomen, the second mediocubital crossvein is more basal and some anal veins are anastomosed; the eyes are smaller in relation to the remainder of the head, than in *Pimachrysa.*

Key to the Species of PIMACHRYSA

1. A slight break between inner gradates and Psm; only 1 or 2 branches of Rs forked marginally; color yellow-orange and black .... *P. nigra* sp. n.
– Inner gradates merge smoothly with Psm; nearly all branches of Rs forked marginally .... 2.
2. Head unmarked except for interantennal mark; body mostly pale yellow; stigma white .... *P. grata* Adams
– Head with dark marks on face and vertex; subcostal veinlets of stigma conspicuously dark-bordered; body gray-pruinose .... 3.
3. Discal veins of hind wing mostly black .... *P. intermedia* sp. n.
– Veins of hind wing (except Sc) all pale .... 4.
4. Costal veinlets of fore wing pale; in hind wing MP1 touches Rs + MA at one point only .... *P. albicostales* sp. n.
– Costal veinlets of fore wing black; in hind wing MP1 coalesced with Rs + MA as far as length of first radial crossvein .... *P. fusca* sp. n.

Pimachrysa grata Adams

Figures 9, 23

Pimachrysa grata Adams, 1957, Psyche 63: 67–70 (1956), figs. 1–5 (head and pronotum, genitalia, wings). Holotype female, from Madera Canyon, Santa Rita Mts., Arizona, 26 August 1949, at light. P. Adams, col. MCZ No. 29624, examined.

Description. Head (Fig. 9): straw yellow, marked with black; flagellum black. Pronotum ivory, with three fuscous stripes. Meso- and metanota yellow, scuta infuscate posterolaterally. Meso- and metapleurae bright yellow, with fuscous marks. Legs ivory, femora with wide apical fuscous band.

Wings (Adams, 1957, Fig. 1) more acute than in *fusca*; inner gradate series sinuous, so that in middle of series, the distance between inner and outer gradates equals half or less the distance from inner gradates to Rs. Second medial crossvein of fore wing basal to MF. Most marginal veinlets forked.

Fore wing: costa, subcosta and R white, stigma white; other veins fuscous except at wing base.

Abdomen (♀) short, slender, terminal segments greatly enlarged. Gonocoxites larger than in other species, with more hooked setae. Subgenital plate (Fig. 23) ligulate, with transverse ridge on ventral (anterior) surface. (The illustration, from Adams, 1957, shows a ventral view, with the distal margin uppermost. In the other species a posterior view is shown, with the distal margin below.)

Measurements (mm): Antennae 16; fore wing length 14.

Diagnosis. Immediately distinguishable from *fusca* by its pale body and venation.

The following three closely related species are grey with prominent stigmas, and look much alike.

Pimachrysa albicostales sp. n.

Figures 27, 28

Holotype. Male from Mexico; Baja Calif., 22 mi. N. of Punta Prieta, 9-XII-58, H. B. Leech, col., in the California Academy of Sciences. The specific name refers to the white costal veinlets.

Description. Eight or nine black spots on apical subcostal crossveins of fore wing, six or seven in hind wing. Intramedian cell of fore wing about four times as long as high, branches of Rs + MA more sharply inclined to Psm than in *fusca*, and cells between Rs and Psm longer. MP1 of hind wing merely touches Rs + MA, not coalesced over a long distance, as in *fusca.* Wing setae black; on dorsum of fore wing equal to length of longest costal veinlet.

Abdomen pale, tergites 2–8 with triangular dark marks (apices anterior); 9 with small mediodorsal dark rectangle, ectoprocts fuscous. Sternites light fuscous, paler medially; ninth dark-lineate basally, dark apically. Apical beak-like extension of ninth sternite longer than in *fusca.* Cuticular glands of basal segments sparser than in *fusca*. Gonarcus shorter, mediuncus (Figs. 27, 28) longer, spoon-shaped distally, with apical tooth.

Measurements (mm). Fore wing 10.0–11.3 (10.6).

Diagnosis. Head and thorax marked similarly to *fusca*, but paler. Wing veins colored as in *fusca*, but costal veinlets of fore wing pale. Membrane not brown in center of cells as in *fusca*.

Record (Paratype). ARIZONA, Tucson, Tumamoc Hill, week ending 5-XII-61, ♂, in ethylene glycol pollen trap, Sandra Ray Johnson, col. (MCZ, in alcohol).

Pimachrysa fusca sp. n.

Figures 1, 7, 11–13, 21, 24

Holotype. Male from L. Covington Flat, Joshua Tree Nat. Mon., Riverside Co., Calif., 19-III-61, E. L. Sleeper, col. In the California Academy of Sciences. The name refers to the dark appearance of this species.

Description. Head pale, marked with black (Fig. 7); scape pale with medial and lateral black stripes; pedicel and flagellum fuscous. Pronotum about as long as broad, lateral margins strongly deflexed; no transverse groove; pale ivory with fuscous median and marginal stripes; a short narrow longitudinal black stripe each side between the fuscous bands, connected to the median stripe posteriorly by a narrow transverse black band; black spot in posterolateral corner. Meso- and metanota with median and lateral fuscous stripes; mesoscutum pale near wing base, with black spots (areas devoid of microtrichia) on inner and outer margins of lateral stripe. Pleurae fuscous. Membrane anterior to prosternum pale. Legs pale, femora with dark preapical band; tibiae with dark bands at base, about two-fifths of distance to apex, and at apex. Tarsi fuscous.

Wing venation as in Figure 1. Fore wing: veins black except for C, apex of Sc, R, and bases of Cu and anals, white. Stigma pale, with 4–6 apical subcostal crossveins conspicuously black-bordered. Marginal area posterior to 3A black; membrane hyaline, usually brown-tinted in central portion of all cells. Intramedian cell about 3 times as long as high. Setae on upper surface black, long, stiff, sparse. Hind wing: veins, except Sc, all pale; posterior marginal black at intersections of marginal veinlets. MP1 coalesced with MA + Rs for a short distance. Macrotrichia about one-third length of those of fore wing.

Abdomen in male dark fuscous. Ninth sternite with a beak-like posterior projection, fused with eighth sternite medially (Fig. 11). Pores of cuticular glands sparse on apical segments, on ninth sternite confined to anterolateral area. Mediuncus (Figs. 12, 13) widened between attachment of membrane and apical tooth. Female abdomen mostly fuscous; ninth tergite pale laterally. Ninth gonocoxites (Fig. 21) not so large as in *P. grata*, and with fewer hooked setae. Eighth sternite (Fig. 24) with blunt, anterodorsally directed horn; a basal fragment present, shaped as a narrow transverse band. Ninth valvulae appear as slender rods. Spermatophore (Fig. 21, sp) ovoid, with cuplike apical indentation, and tubular process extending into genital opening.

Measurements (mm). Fore wing length 8.8–11.1 (10.3); maxillary palpus (apical three segments) 0.67–0.83 (0.73); scape 0.24–0.32 (0.28).

Diagnosis. In shape of head and wings, and in venation, this species is closer to *P. grata* than to *P. nigra*. It may be recognized by the gray-pruinose body, smoky wings, prominent dark pterostigma, dark costal veinlets of fore wings, and pale veins in the hind wing.

Records (Paratypes). CALIFORNIA: Riverside Co., Joshua Tree National Monument, L. Covington Flat #1, 19-III-61 ♂; #2, 5-III-61 ♀; #4, 25-XI-60 ♂, 5-XI-60; U. Covington Flat #1, 5-XI-60 ♂; Smithwater Wash #1, 25-XI-60 ♀, 4-III-61 ♀; all collected by E. L. Sleeper in molasses bait traps (Long Beach State College, MCZ, Adams Collection). Los Angeles Co.: Aliso Can. chapparal, 26-X-58 ♀, R. X. Schick (UCLA).

Pimachrysa intermedia sp. n.

Figures 2, 20, 25

Holotype. Female from Snow Creek, 1500′, White Water, Riverside Co., Calif., 8-III-1955, W. R. M. Mason, col. Canada Department of Agriculture, Ottawa. The name means intermediate.

Description. Head marked with black similarly to *fusca*, but dark border of antennal socket not connected to lateral vertex stripe, median vertex mark larger, and genae black-bordered posteriorly. Maxillary palpi and scape both shorter than in *fusca*. Pronotum longer than in *fusca*, pale, with lateral and median red-fuscous stripes, broader posteriorly; between these each side a brown stripe, extending to furrow (which is barely perceptible). Meso- and metanota dark; yellow spots laterally on prescuta and scuta. Propleura and cervical sclerites pale fuscous, prosternum dark-fuscous; membrane anterior to sternum pale, with median and lateral fuscous stripes, overlaid with a rufous transverse band. Meso- and metapleurae fuscous. Legs pale, femora with a broad preapical dark band; tibiae with thin dark band at about one-third distance from base to tip; fore and mid tibiae slightly infuscated, hind with two narrow dark stripes on ventral surface.

Wing venation as in Figure 2; few marginal veinlets forked. R (basal two-thirds) and 3A in both wings, and bases of 1A, 2A, and Cu in hind wing, pale; other veins all dark. Stigma white, with dark clouds on apical subcostal crossveins; membrane proximal to end of 3A in fore wing fuscous.

Abdomen fuscous, segments narrowly pale at anterior and posterior margins; muscle scars on tergites black, surrounded by pale areas. Female external genitalia similar to those of *fusca*; subgenital plate bears knob on basal margin, basal fragment much wider, and less sclerotized than in *fusca* (Fig. 25).

Measurements (mm). Fore wing 9.2; apical three segments, maxillary palpus, 0.49; scape 0.21.

Diagnosis and discussion. In the features by which this species differs from typical *fusca*—dark venation, smaller number of gradate cells, fewer forked marginal veinlets, short palpi, color and shape of pronotum—it grades toward *nigra*. Furthermore, it was taken geographically close to a *nigra* locality. It may be a unique hybrid individual, or a representative of an introgressed population.

Biology. The crop of the type is filled with *Salix* pollen (identified by D. Walkington, California State College, Fullerton).

Pimachrysa nigra sp. n.

Figures 6, 14–16, 26, 34

Holotype. Male from Gavilan, Riverside Co., Calif. 19-III-36, on *Ceanothus crassifolius*, Timberlake, col. (California Academy of Sciences). The name is descriptive of the dark coloration.

Description. Head long, eyes small; color shades from ivory anteriorly, to orange on vertex; dark-fuscous markings as in Figure 6; mark between antennae extending anteriorly to frontal suture, and broadly over antennal sockets and vertex. Maxillary palpi short, dark, pale at joints. Occipital foramen broadly dark-margined. Scape pale, broad medial and lateral dark stripes; pedicel and flagellum dark. Pronotum long, brown-fuscous with two narrow submedian pale stripes. Meso- and metanota dark, two disconnected yellow stripes. Propleurae, sternum, and cervical sclerites dark; rufous median area on membrane anterior to prosternum. Meso- and metapleurae dark. Legs dark; femora pale basally and apically; tibiae (especially metathoracic) paler exteriorly, with apical dark band.

Fore wing veins dark; bases of C, R, 3A, and marginal vein in jugal area, pale. Stigma black; conspicuous ivory spots on membrane, between apical subcostal crossveins. Hind wing similar, but R pale for two-thirds length.

Venation (Fig. 4): A break in alignment of inner gradates and Psm in both wings; weak pseudomedian fold in both wings (especially hind), but no definite articulations, as are found in *Nothochrysa*; usually only 1 or 2 branches of Rs forked marginally (3 and 4 in hind wings of one female).

Abdomen dark, segments narrowly pale-banded posteriorly. Male 8th and 9th sternites, and 9th tergite-ectoproct more strongly fused than in *fusca* (Fig. 14). Many cuticular gland openings, except on ectoproct. Margin of mediuncus between apical tooth and attachment of membrane, nearly straight (Figs. 15, 16). Female terminalia similar to those of *fusca*; 8th sternite (Fig. 26) preceded by broad basal fragment, ventrally with blunt horn. Ninth valvulae reduced to dotlike sclerites.

Measurements (mm). Fore wing 7.5–9.0 (8.0) long; apical three segments, maxillary palpi, 0.48–0.53 (0.51); antennae 7–8 (7.5).

Diagnosis. This small species may immediately be distinguished from all other species of *Pimachrysa* by its brown-black and orange markings. It strikingly resembles *Nothochrysa californica* Banks, for which it has been mistaken by several workers, including the writer. In shape of head, and condition of pseudomedia, it is closer to *Nothochrysa* than is any other species of *Pimachrysa*. However, these genera are structurally so different that the colorational resemblance is undoubtedly coincidental.

Records (Paratype). CALIFORNIA: Gavilan, 1-IV-38, ♀, on *Ceanothus crassifolius*, Timberlake, col. (MCZ). Pinnacles, San Benito Co., 23-III-40, R. L. Usinger, col. (CIS). Lebec, Kern Co., 1-IV-39, ♀, E. S. Ross (CAS).

DYSPETOCHRYSA gen. n.

Figure 42

Type species. Tribochrysa vetuscula Scudder. The feminine name means "difficult-chrysopid," referring to the intricacy resulting from the superimposition of fore and hind wings in the fossil.

Description. Basal subcostal crossvein distal to origin of Rs, opposite MF; Rs + MA originates far basal of MF. First sectorial crossvein intersects MP1 very near MF. Intramedian cell long. Proximal branch of Rs + MA coalesces with MP1, and second branch coalesces with proximal branch, so that basal portion of Psm contains no crossveins. Psc strongly developed, two marginal veinlets from third medial cell, basal one forked; at least four additional non-forked marginal veinlets from Psc. Hind wing with zig-zagged Psc.

Discussion. The fore wing base is similar to that of *Archaeochrysa*, except for the overlap of branches of Rs + MA forming Psm. It is most interesting that the wing should demonstrate such a generalized structure of Rs + MA and the intramedian cell, while having a pseudomedia which, at least basally, resembles that of *Nothochrysa*. In this regard, *Dyspetochrysa* is more advanced than all other Nothochrysinae, save *Nothochrysa* itself.

Dyspetochrysa vetuscula Scudder

Figure 42

Tribochrysa vetuscula Scudder, 1890, U. S. Geol. Geogr. Survey Terr., Rept., 13: 170, pl. 14, fig. 9. Holotype: Florissant, Colorado, Miocene; MCZ No. 245, tip of abdomen and distal half of fore wing missing; hind wing venation mostly not visible, examined.

Paleochrysa vetuscula: Cockerell, 1908, Canad. Entomol. 40: 90.

Paleochrysa stricta: Carpenter, 1935, J. Paleontol. 9: 263 (not Scudder).

Description. Head large, interocular width 1.0 mm, eye 0.5 mm. Scape short, flagellar segments 0.2 × 0.1 mm. Pronotum wide, anterior margin straight, corners slightly angulate; dark, a four-lobed pale central area; width 1.44 mm; length, extreme 1.0 mm, midline 0.7 mm. Costal area narrow, tallest cell 0.63 × 0.55 mm. Intramedian cell 0.35 × 1.5 mm, pseudomedial area as wide as pseudocubital area.

ARCHAEOCHRYSA gen. n.

Figures 40, 41, 46, 47

Type species. Paleochrysa creedei Carpenter. The feminine name means "old-chrysopid" referring to the archaic venation.

Description. Fore wing: Basal subcostal crossvein distal to origin of Rs + MA opposite MF. Rs + MA arises nearer to basal medial crossvein than to MF. Sectorial crossvein intersects MP1 slightly distally to MF. Proximal branch of Rs + MA not coalesced with MP1, but connected by a gradate crossvein; Psm strongly zig-zagged. Psc well developed.

Hind wing: Base of Rs + MA moderately long; not coalesced with MP1. Psm zig-zagged, with no overlap of veins. Psc poorly developed, strongly zig-zagged, so that the gradate series apparently extends to MP2; marginal veinlets from Psc all forked.

Pronotum broad, squarish; cervical sclerites and prosternum as in *Pimachrysa*. Terminal abdominal segments of male broad, short; ectoprocts forcipate (Fig. 46).

Discussion. This is the most archaic of the Miocene genera. It is unique in its lack of fusion of MP1 and Rs + MA in the hind wing. The unspecialized Psc of the hind wing is found elsewhere only in *Paleochrysa wickhami* Cockerell.

Archaeochrysa creedei (Carpenter)

Figures 41, 46, 47

Paleochrysa creedei Carpenter, 1935, J. Paleontol. 9: 265, fig. 3; 1938, Psyche 45: 108. Holotype: Creede, Colorado, Miocene, A. Caplan, coll.; MCZ No. 4316, examined.

Paleochrysa stricta: Carpenter, 1938, Psyche 45: 108, fig. 1.

Description. Costal area narrow, 0.25 mm wide, cells about as high as long. Ten branches of Rs + MA in fore wing, and 7–8 in hind wing. Gradate cells about twice as long as wide. Intramedian cell narrow, about 0.375 × 1.5 mm. Flagellar segments 0.13 × 0.21 mm. Pronotum (Fig. 47) squarish, anterior margin not clear; 0.94 mm wide, 0.91 mm (0.625 mm on midline) long. Ectoprocts (Fig. 46) lateral, forcipate; gonarcus small.

Discussion. The lateral margins of the conspicuous cervical sclerites apparently correspond to the pronotal margins in Carpenter's (1935) figure.

The prosternum apparently was unsclerotized. The basal Banksian cell is normal for *Archaeochrysa*; on the type, the proximal branch of Rs + MA is very indistinct, and was not shown by Carpenter, but is present on all the other specimens of this species.

Records. Creede, Colorado, Miocene; MCZ No. 4462–4471.

Archaeochrysa paranervis sp. n.

Figure 40

Paleochrysa vetuscula Cockerell, 1908, Canad. Entomol. 40: 90. (Erroneous identification.)

Paleochrysa stricta: Carpenter, 1935, J. Paleontol. 9: 263, fig. 1. (Erroneous identification.)

Holotype. Univ. Colo. Mus. No. 4419, Florissant, Colorado, Miocene, expedition 1907, examined. The name means "beside-vein," referring to the juxtaposition of the radial crossveins and the branches of the radial sector.

Description. Venation as in Figure 40; fore wing broad; costal area broad; Sc approaches C near stigmal base; 12 branches of Rs + MA, several branches opposite radial crossveins; longest gradate cell 2.5 times as long as broad. Fore wing length: 14.2 mm.

Diagnosis. Differs from *creedei* in the length and arrangement of branches of Rs, and in width of the costal space. This specimen was the basis for Carpenter's (1935) figure and redescription of *Paleochrysa stricta*.

Archaeochrysa fracta (Cockerell)

Paleochrysa fracta Cockerell, 1914, J. Geol. 22: 716, fig. 2. Holotype: Florissant, Colorado, Miocene, H. F. Wickham, col.; MCZ No. 4501 (formerly No. 3349), isolated fore wing, examined. Carpenter, 1935, J. Paleontol. 9: 264, fig. 7, p. 268.

Description. Costal area moderately wide, the cells 0.95 mm × 0.5 mm; veinlets inclined about 10°, 17 branches of Rs + MA, Rs hardly zig-zagged. Longest gradate cells 3.1 times as long as wide; intramedian cell 2.0 × 0.5 mm, acute proximally, distal crossvein oblique. 1A forked.

Diagnosis. This species differs from *creedei* in the shape of the subcostal area, more branches of Rs + MA, longer gradate cells, and forked 1A.

Carpenter's figure of this specimen was inadvertently transposed with that of *Tribochrysa firmata*, and appeared on page 268, as his Figure 7.

Genus *PALEOCHRYSA* Scudder

Figures 38, 39

Paleochrysa Scudder, 1890, U. S. Geol. Geogr. Survey Terr., Rept., 13: 166. Type species (by monotypy): *Paleochrysa stricta* Scudder. Cockerell, 1908, Canad. Entomol., 40: 90. Carpenter, 1935, J. Paleontol. 9: 262.

Lithochrysa Carpenter, 1935, J. Paleontol. 9: 265. Type species (by original designation) *Paleochrysa wickhami* Cockerell. NEW SYNONYMY.

Description. Basal subcostal crossvein distal to origin of Rs + MA; opposite MF. Rs + MA arises near MF; proximal branch of Rs + MA not coalesced with MP1, hence no overlapping veins in Psm. Gradate series run into Psm and Psc in an even curve in both wings. Psc of hind wing either regularly zig-zagged with forked marginal veinlets basally (*P. wickhami*), or with furcations more proximal, so zig-zagging is irregular, as in *Pimachrysa*, *Hypochrysa*, etc. (*P. stricta*).

Discussion. The type of *P. stricta* has all four wings superimposed, making interpretation excessively difficult. But the short distal stem of Rs + MA, in the fore wing and the coalescence of Rs + MA with MP1, forming a quadrangular Banksian cell in the hind wing, are clear; thus this species has the essential characteristics of *Lithochrysa* Carpenter. *Paleochrysa wickhami*, the type of *Lithochrysa*, does not differ from *stricta* in any important respect save the more archaic structures of Psc in the hind wing. The species of *Pimachrysa* show such variation in the site of furcation of the marginal veinlets (e.g., cf. Figs. 1 and 2) that I do not consider this difference in structure of Psc of sufficient importance to warrant maintaining a generic distinction.

Paleochrysa stricta Scudder

Figures 38, 39

Paleochrysa stricta Scudder, 1890, U. S. Geol. Geogr. Survey Terr., Rept., 13: 166, pl. 14, figs. 13, 14. Holotype: Florissant, Colorado, Miocene, S. H. Scudder; MCZ No. 242 a–b, examined.

(not) *Tribochrysa vetuscula*: Cockerell, 1908, Canad. Entomol. 40: 90. Carpenter, 1935, J. Paleontol., 9: 263.

Description. Costal area moderately wide, cells 0.69 mm long, 0.875 mm tall. Twelve branches of Rs + MA. Gradate cells 0.5 × 1.0 mm; intramedian cell 0.35 × 1.25 mm; 8 unbranched veinlets from Psc in fore wing. In hind wing, 5 unbranched veinlets from Psc to wing margin; CuA 3-branched, the distal branch with a marginal fork. Fore wing length, 16.0 mm, width 5.0 mm.

Paleochrysa wickhami (Cockerell)

Paleochrysa wickhami Cockerell, 1914, J. Geol. 22: 717, fig. 3. Holotype: Florissant, Colorado, Miocene, H. F. Wickham, col.; MCZ No. 4499, examined.

Lithochrysa wickhami: Carpenter, 1935, J. Paleontol., 9: 265, fig. 4.

Description. Costal area moderately broad, cells about 0.46 × 0.5 mm. Veinlets inclined about 15 degrees. Nine branches of Rs + MA in fore wing, and hind wing. Intramedian cell 0.313 × 0.88 mm. Gradate cells 5.25 × 0.75 mm. Costal space narrows abruptly before stigma, as in *Hypochrysa nobilis*; C and Sc may be coalesced for a short distance. Radius runs in a smooth curve at wing apex, not angulate near stigma as in *Hypochrysa*.

Eye fairly large (0.44 mm diam.). Pronotum rounded anteriorly, sides straight, parallel.

Paleochrysa concinnula Cockerell

Paleochrysa concinnula Cockerell, 1909, Canad. Entomol. 41: 218, fig. 5. Holotype: Florissant, Colorado, Miocene; Colo. Univ. Mus., not examined.

Lithochrysa concinnula: Carpenter, 1935, J. Paleontol. 9: 266, fig. 5.

Paleochrysa ferruginea Cockerell, *ibid.*: 218, fig. 6. Holotype: Florissant, Colorado, Miocene; Colo.

Univ. Mus., not examined. Carpenter, *loc. cit.*: 266–267.

Genus *TRIBOCHRYSA* Scudder

Tribochrysa Scudder, 1885, *in* Zittel-Barrois, Traité Paléont. 1: 777. Type species (by monotypy): *Tribochrysa inaequalis* Scudder. Scudder, 1890, U. S. Geol. Geogr. Surv. Terr., Rept. 13: 168.

Description. Eyes large (0.5 mm); scape large, flagellar segments 0.15 × 0.25 mm. Pronotum short, broad, margin arcuate. Subcostal crossvein obscured in all specimens. Rs + MA arises slightly basally to MF. No overlap of veins in Psm. Inner gradates in two series, so that the fourth gradate (numbered from base) is much closer to Rs than is the second or third. Psc well developed in fore wing. In hind wing, Rs + MA coalesces with MP1, and Psc is less well developed than in fore wing.

Discussion. The irregularity in the inner gradate series is a necessary precondition for separation from Psm, as has taken place in many Chrysopinae. It is, therefore, not surprising that several other taxa exhibit a similar, but less emphasized break in the inner gradate series [*Pimachrysa nigra* (Fig. 4), *Hypochrysa* (Fig. 5), *Nothochrysa californica* (Fig. 3)].

Tribochrysa inaequalis Scudder

Tribochrysa inaequalis Scudder, 1885, *in* Zittel-Barrois, Traité Paléont. 1: 777, fig. 982. Holotype: Florissant, Colorado, Miocene; MCZ No. 243, examined. Scudder, 1890, U. S. Geol. Geogr. Surv. Terr., Rept. 13: 170. Cockerell, 1908, Canad. Entomol. 40: 90. Carpenter, 1935, J. Paleontol. 9: 267, fig. 6.

Tribochrysa firmata Scudder

Tribochrysa firmata Scudder, 1890, U. S. Geol. Geogr. Surv. Terr., Rept. 13: 172, pl. 14, figs. 6, 7, 10, 11. Cotypes: Florissant, Colorado, Miocene; MCZ No. 241, No. 4127, examined. Carpenter, 1935, J. Paleontol. 9: 267, fig. 7.

LITERATURE CITED

Adams, P. A. 1957. A new genus and new species of Chrysopidae from the western United States, with remarks on the wing venation of the family. Psyche **63:** 67–74.

———. 1958. Studies in the Neuroptera, with special reference to wing structure and evolution in the Osmyloidea. Ph.D. thesis, Harvard University (unpubl.).

———. 1962. A stridulatory structure in Chrysopidae. Pan-Pac. Entomol. **38:** 178–180.

Brauer, A. 1867. Larve von *Hypochrysa nobilis* Heyd. Verhandl. Zool.-Bot. Ges. Wien **17:** 27–29, pl. 9, fig. 1.

Carpenter, F. M. 1935. Tertiary insects of the family Chrysopidae. J. Paleontol. **9:** 259–271.

Erhardt, E. 1916. Zur Kenntnis der Innervierung und der Sinnesorgane der Flügel von Insekten. Zool. Jahrb. (Anat.) **39:** 295–334, pls. 17–18.

Friedrich, H. 1953. Neuroptera. Bronns Klassen u. Ordnungen des Tierreichs, 5 Band, 3 Abt. XII Buch, Teil a. Leipzig. 148 pp.

Killington, F. J. 1937. A monograph of the British Neuroptera. Ray Society, London. 269 pp., 15 pls.

Kimmins, D. E. 1952a. Some new Australian Chrysopidae. Ann. Mag. Nat. Hist. (12) **5:** 68–81.

———. 1952b. A revision of the genera of the Apochrysinae (fam. Chrysopidae). Ann. Mag. Nat. Hist. (12) **5:** 929–944.

Martynova, O. 1949. Mesozoic lacewings (Neuroptera) and their bearing on concepts of phylogeny and systematics of the order. (In Russian.) Trudy Paleontol. Inst., Akad. Nauk SSSR **20:** 150–170.

Navás, L. 1910. Crisópidos nuevos. Broteria **9:** 38–59.

———. 1913. Les Chrysopides (Ins. Névr.) du Musée de Londres. Ann. Soc. Sci. Bruxelles **37:** 292–330; **38:** 73–114.

Principi, M. M. 1946. Contributi allo studio dei Neurotteri Italiani. IV. *Nothochrysa italica* Rossi. Boll. Ist. Entomol. Univ. Bologna **15:** 85–102.

———. 1958. Neurotteri dei Monti Sibillini. Mem. Mus. Civ. Storia Nat. Verona **6:** 175–189.

Scudder, S. H. 1890. The fossil insects of North America, with notes on some European species. II. The Tertiary insects. Rept. U. S. Geol. Geogr. Surv. Terr. **13:** 1–734, pls. 1–28.

Tillyard, R. J. 1916. Studies in Australian Neuroptera. No. 3. The wing-venation of the Chrysopidae. Proc. Linn. Soc. New South Wales **41** (2): 221–248, pls. X, X bis, XI.

Tjeder, Bo. 1941. Some remarks on the generic names of the British Neuroptera. Entomol. Tidskrift (1941): 24–31.

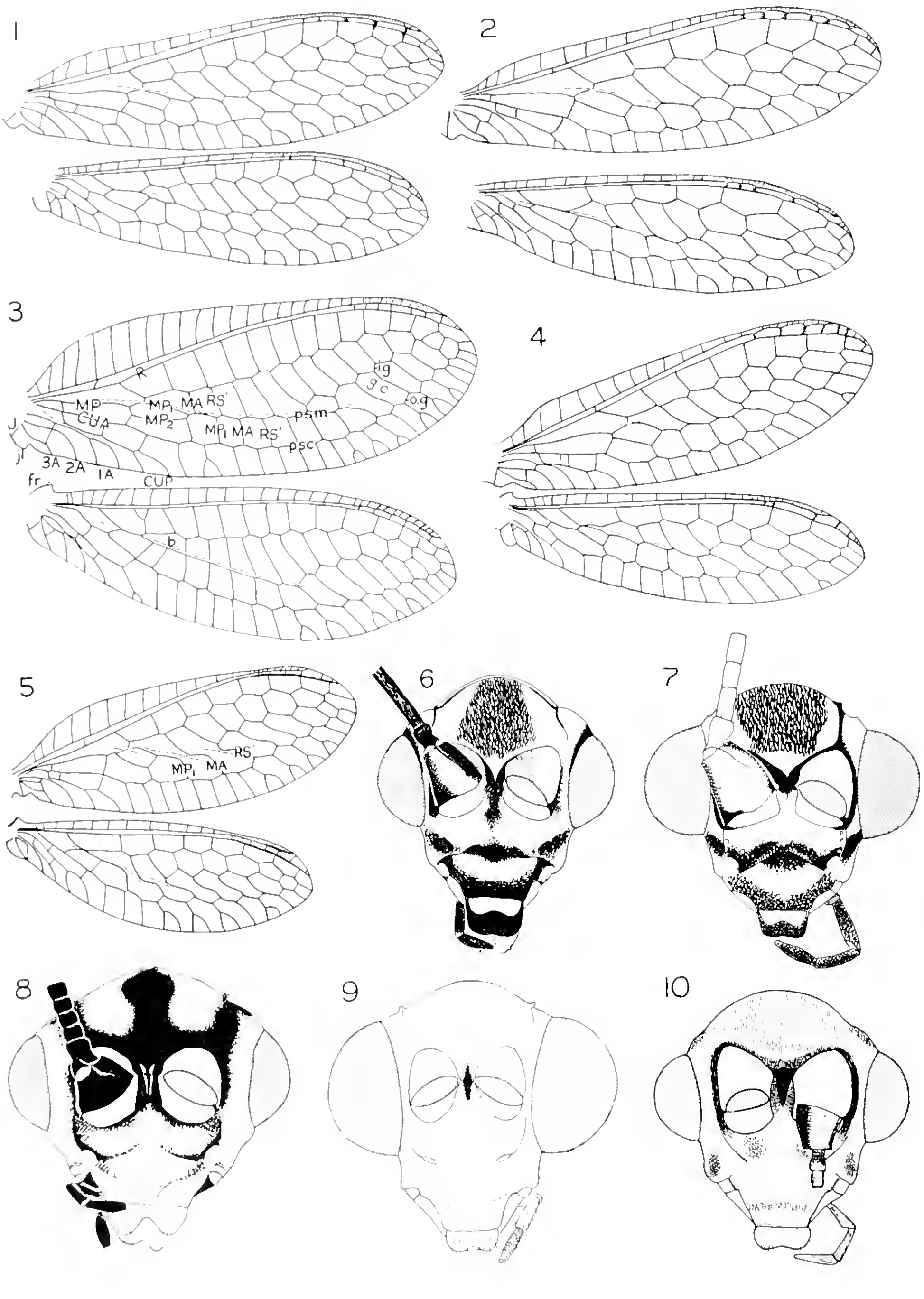
———. 1966. Neuroptera–Planipennia. The lacewings of Southern Africa. 5. Chrysopidae. South African Animal Life **12:** 228–534.

Toschi, C. A. 1966. The taxonomy, life histories, and mating behavior of the green lacewings of Strawberry Canyon. Hilgardia **36**: 391–435.

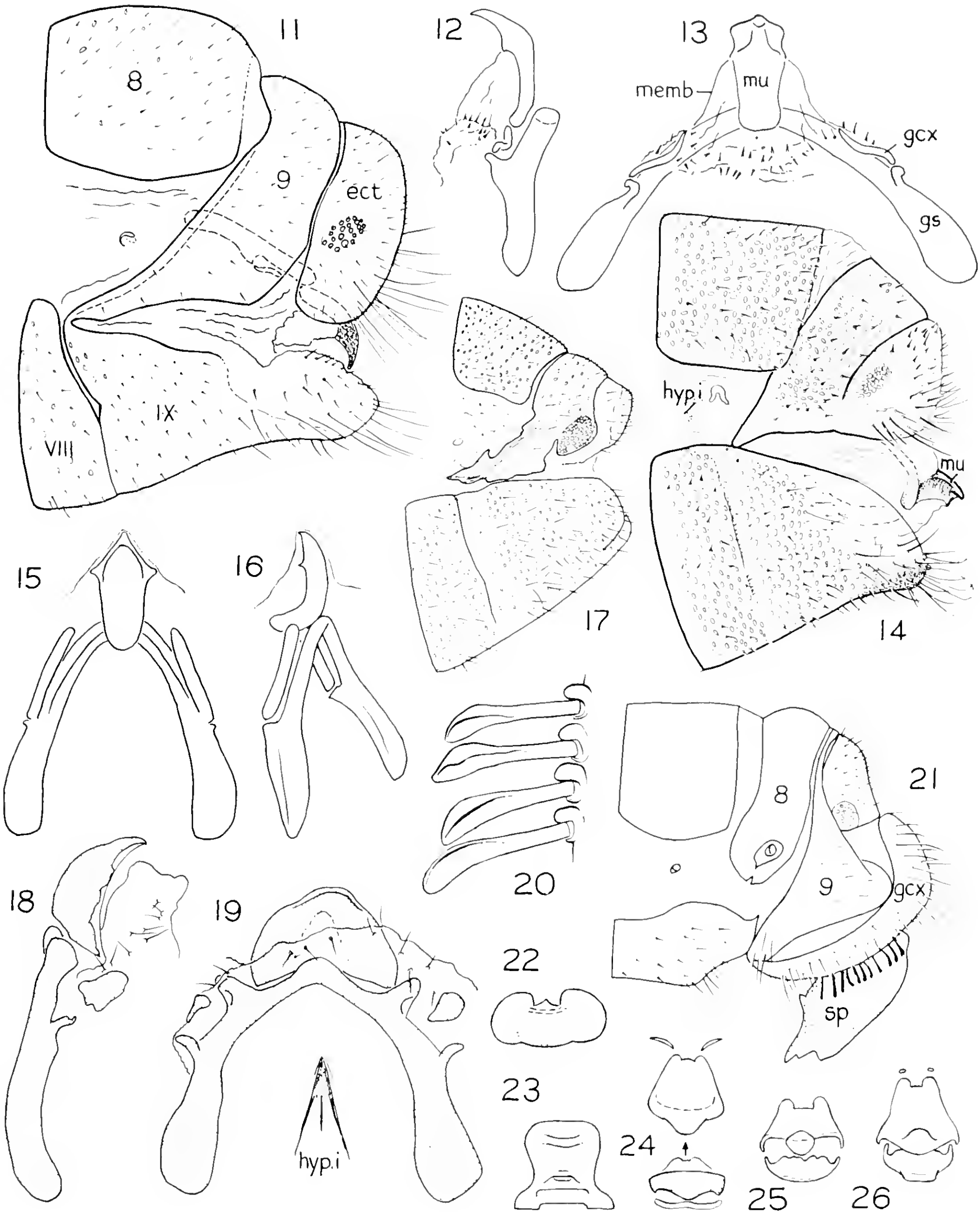
(Received 21 October 1965)

ABBREVIATIONS USED IN FIGURES

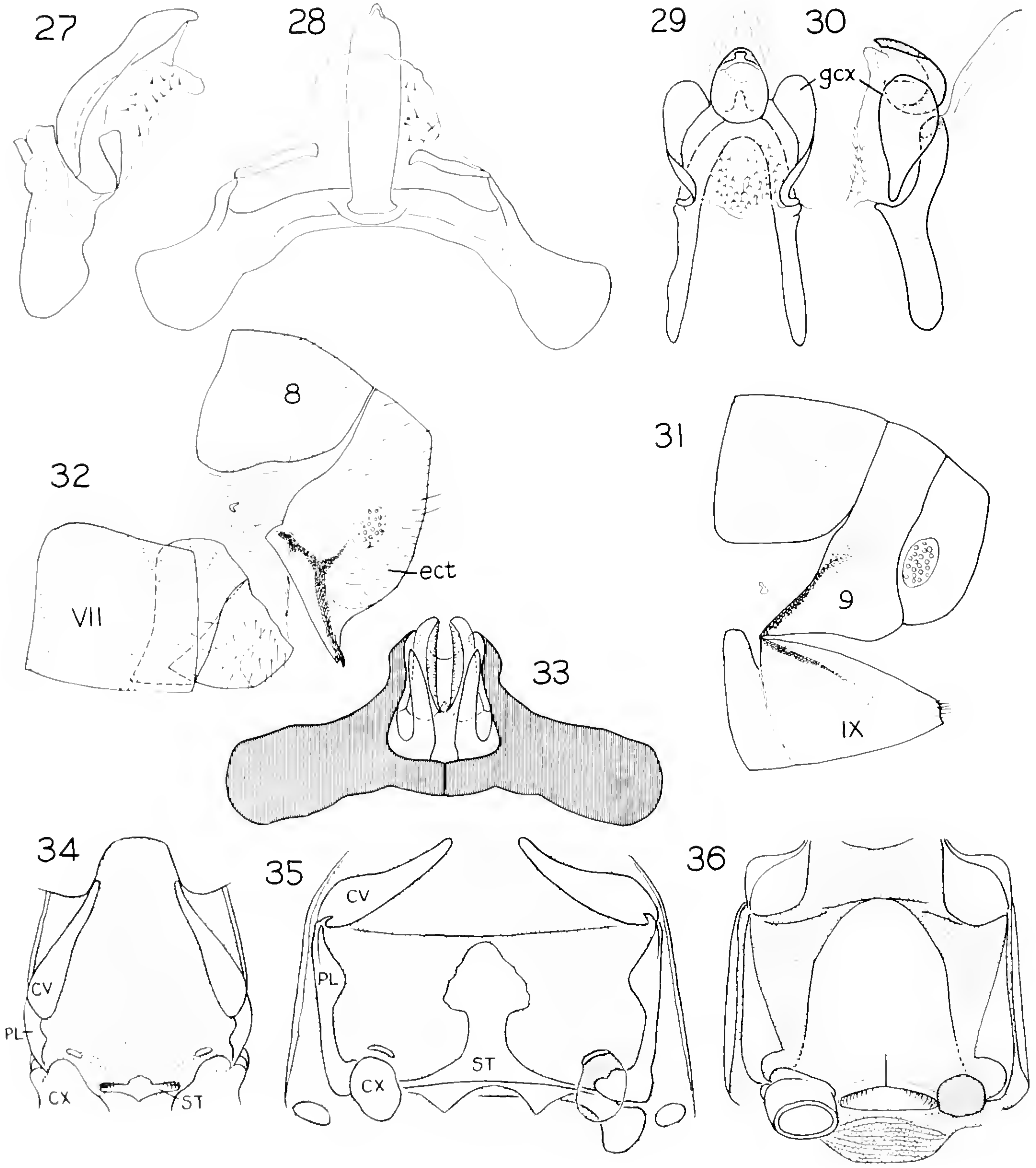
b—basal Banksian cell; CUA—cubitus anterior; CUP—cubitus posterior; CV—cervical sclerite; CX—coxa; ect—ectoproct; fr—frenulum; g.c.—gradate cell; gcx—♀, ninth gonocoxite (gonopophyses laterales), ♂, gonocoxites (= "parameres," "entoprocessus"); gs—gonarcus; hyp. i.—hypandrium internum; i.g.—inner gradate crossvein; im—intramedian cell; J—jugal vein, jl—jugal lobe; MA—the proximal branch of the fused media anterior and Rs, presumably media anterior; memb—membrane; MF—medial fork, fork of MP; MP—media posterior; mu—mediuncus; o.g.—outer gradate crossvein, PL—propleuron; pm—paramere; psc—pseudocubitus; psm—pseudomedia R—radius; RS'—proximal branch of radial sector; sp—spermatophore; ST—sternum; SXV—first sectorial crossvein; 1A, 2A, 3A—anal veins; 1m—first medial crossvein.



Wings: Fig. 1. *Pimachrysa fusca* sp. n. Fig. 2. *P. intermedia* sp. n. Fig. 3. *Nothochrysa californica.* Fig. 4. *P. nigra* sp. n. Fig. 5. *Hypochrysa nobilis.* Heads: Fig. 6. *P. nigra.* Fig. 7. *P. fusca.* Fig. 8. *N. californica.* Fig. 9. *P. grata.* Fig. 10. *K. raphidioides.*

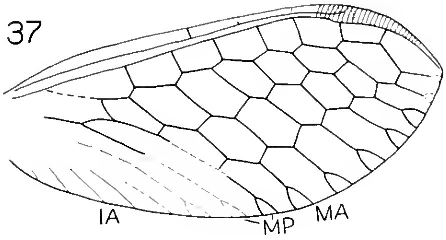


Figs. 11–13. *Pimachrysa fusca*. Fig. 11. Male abdomen, lateral view. Fig. 12. Gonarcus, lateral view. Fig. 13. Same, posterior view. Figs. 14–16. *P. nigra*. Fig. 14. Male abdomen, lateral view. Fig. 15. Gonarcus, posterior view. Fig. 16. Same, lateral view. Figs. 17–19. *Nothochrysa californica*. Fig. 17. Male abdomen, lateral view. Fig. 18. Gonarcus, lateral view. Fig. 19. Same, posterior view, and hypandrium internum. Fig. 20. *P. intermedia*, setae on margin of right ninth gonocoxite, lateral view. Fig. 21. *P. fusca*, female abdomen, with spermatophore. Figs. 22–26. Female eighth sternum or subgenital plate. Fig. 22. *N. californica*. Fig. 23. *P. grata*. Fig. 24. *P. fusca*, anterior view below, posteroventral above. Fig. 25. *P. intermedia*, anteroventral view. Fig. 26. *P. nigra*, anteroventral view.

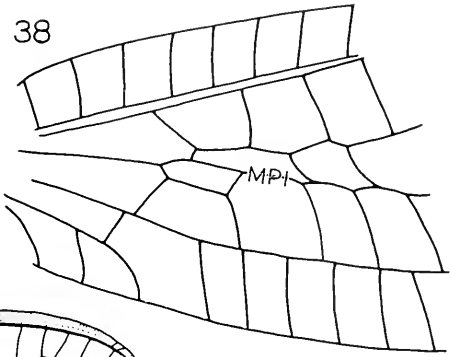


Figs. 27, 28. *Pimachrysa albicostales*, gonarcus, lateral and ventral views. Figs. 29–31. *Kimochrysa africana*. Fig. 29. Gonarcus, ventral view; Fig. 30. Same, lateral view. Fig. 31. Male abdomen, lateral view. Figs. 32, 33. *H. nobilis*. Fig. 32. Male abdomen, lateral view. Fig. 33. Gonarcus, dorsal view. Figs. 34–36. Prothorax, ventral view, membranous areas stippled. Fig. 34. *P. nigra*. Fig. 35. *N. californica*, left coxa removed to show sternal apophysis. Fig. 36. *Chrysopiella* sp. (Chrysopinae).

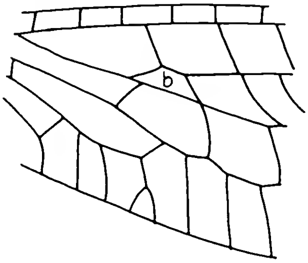
37



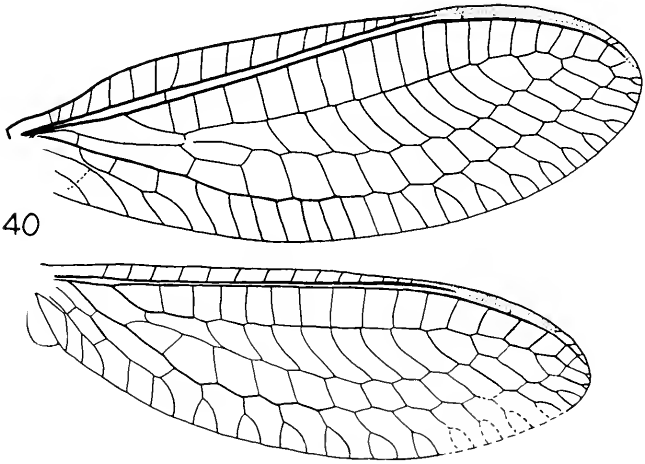
38



39



40



41

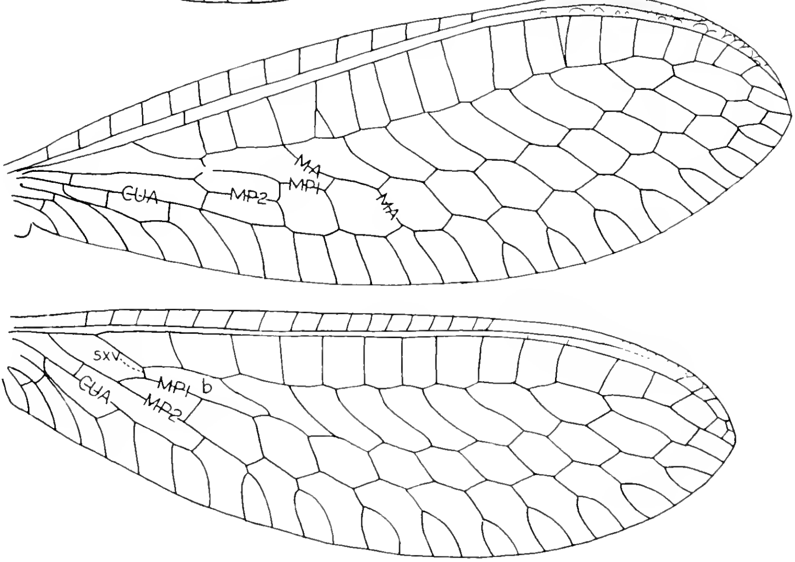
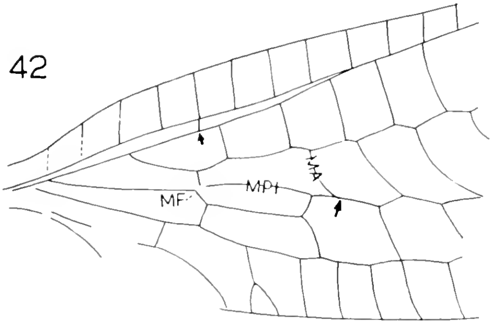
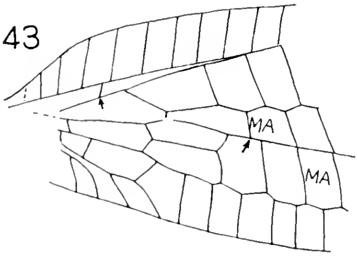


Fig. 37. *Mesypachrysa*, hind wing (after Martynov). Figs. 38, 39. *Paleachrysa stricta*, fore and hind wing bases. Fig. 40. *Archaeachrysa paranervis* type, wings. Fig. 41. *A. creedei*, wings (from type, and from MCZ specimens No. 4464 and No. 4462).

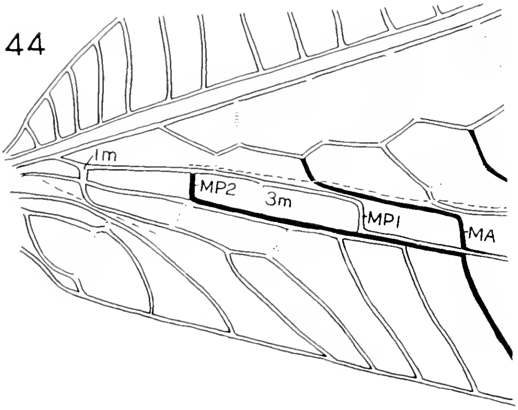
42



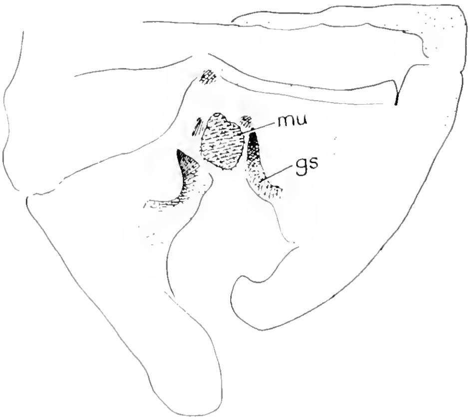
43



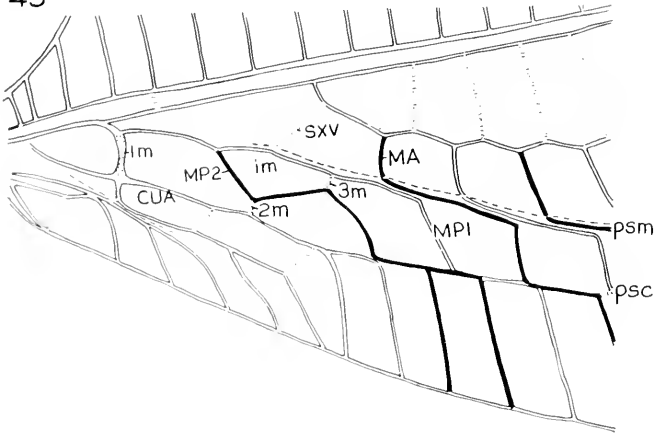
44



46



45



47

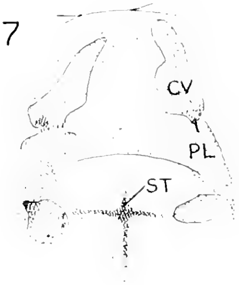


Fig. 42. *Dyspetochrysa vetuscula*, type, fore wing base; arrows indicate position of basal subcostal crossvein, and point of fusion of MP1 and MA. Fig. 43. *Nothochrysa praeclara*, fore wing base. Fig. 44. *Synthochrysa (Apochrysinae)*, fore wing base, showing overlap of veins at Psm, probable overlap at Psc and probable course of MP2 (modified from Kimmins, 1952b). Fig. 45. Gonzaga (Chrysopinae), fore wing base, showing overlap of veins at Psm, and course of MP2. Fig. 46. *Archaeochrysa creedei*, tip of male abdomen, showing forcipate gonarcus (from MCZ specimen No. 4466). Fig. 47. *A. creedei* type.

Bulletin OF THE
Museum of
Comparative
Zoology

Marine Nematodes of the East Coast of North America. I. Florida

WOLFGANG WIESER and [illegible]

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

[illegible] NUMBER 5
[illegible] 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoris 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

MARINE NEMATODES OF THE EAST COAST OF NORTH AMERICA. I. FLORIDA

WOLFGANG WIESER[1] AND BRUCE HOPPER[2]

CONTENTS

---

[1] Zoologisches Institut, Universität Wien, Wien, Austria.

[2] Nematology Section, Entomology Research Institute Research Branch, Canada Department of Agriculture, Ottawa.

Bull. Mus. Comp. Zool., 135(5): 239–344, April, 1967

ABSTRACT

A beginning is made on a series of papers in which the nematode fauna inhabiting the east coast of North America from Florida to Newfoundland is to be described. The present paper, dealing with 90 species, extends the number of species known from Florida to 118. One new genus, *Paratarvaia* within the Diplopeltidae, and 48 new species, are described, viz.: *Halalaimus meyersi, Bathylaimus arthropappus, Enoploides bisulcus, E. gryphus, Mesacanthoides fibulatus, M. psittacus, Metoncholaimus intermedius, M. simplex, M. scissus, Prooncholaimus hastatus, Viscosia oncholaimelloides, Illium libidinosum, Polygastrophora edax, Pomponema tesselatum, Longicyatholaimus annae, Xyzzors inglisi, Paracanthonchus platypus, Paracyatholaimus pesavis, Spirinia hamata, Chromaspirina inaurita, Metachromadora pulvinata, M. meridiana, Paradesmodora toreutes, Monoposthioides mayri, Paramicrolaimus lunatus, Hypodontolaimus interruptus, Chromadorella trilix, C. vanmeterae, Euchromadora pectinata, E. meadi, Atrochromadora denticulata, Sabatieria paradoxa, S. paracupida, Axonolaimus hexapilus, Odontophora variabilis, Paratarvaia seta, Terschellingia longispiculata, T. monohystera, Paramonhystera canicula, Steineria ampullacea, Theristus calx, T. ostentator, T. floridanus, T. erectus, T. galeatus, T. fistulatus, T. tortus,* and *T. xyaliformis.* The Halanonchinae n. subfam., with *Halanonchus* Cobb, 1920, *Rhabdocoma* Cobb, 1920, and *Cytolaimium* Cobb, 1920, is created within the Tripyloididae. The Halanonchinae, via *Trefusia*, is considered to link the Tripyloididae with the Oxystomatidae.

INTRODUCTION

The nematodes from the coasts of the American continents are poorly known, a fact that is regrettable since this group represents such an important component of the fauna of every marine habitat.

To improve this situation we decided to collect material towards a monograph on the marine nematodes inhabiting the east coast of North America. In order not to overburden this monograph with descriptions of new species and with taxonomic discussions, we shall publish the results of our investigation in a numbers of papers each dealing with a portion of coastline between Florida and Newfoundland. In each paper, descriptions and figures will be given for all the species found except for those in which agreement between our specimens and representations in the literature were considered very good. In addition, a list containing all species reported from the particular region will be included.

In the monograph, the information contained in the special reports will be condensed. Short descriptions and figures will be given of all species, together with keys to most of the genera and families of marine nematodes.

A portion of the material for this undertaking was collected separately by us on excursions to the eastern seaboard during the period 1958–1961, or it was sent to us by various colleagues whose cooperation we shall acknowledge in the relevant sections of this series. The bulk of the material, however, was collected by us between May 7 and June 8, 1963, on a trip in which we covered the area from southern Florida to Maine.

The following remarks should suffice to clarify our approach to the whole project:

Habitats.—At each location we tried to cover the important types of habitat that could be reached by manual sampling. Shallow water dredge or core sampling was carried out in Miami, Florida, Beaufort, North Carolina, Lewes, Delaware, and Woods Hole, Massachusetts. In addition we received shallow or deep water samples from various sources which we shall acknowledge later.

Methods.—In general, nematodes were extracted from the substrate utilizing a combination of the sieving and decanting processes. Live nematodes were relaxed in an oven maintained at 54°C prior to fixation in 2% formaldehyde. As the number of specimens recovered in most instances was considerable, only a representative fraction of the total was picked out and processed into dehydrated glycerine. The remainder of the material was also preserved and is being kept for reference in the Nematology Section, Entomology Research Institute, at Ottawa.

The dehydration process used was an adaptation of Seinhorst's methyl alcohol method (Seinhorst, 1959). The preserved specimens were placed in a B.P.I. watchglass containing 10% glycerine in methyl alcohol. The watchglass was then placed in an oven maintained at 54°C to hasten the evaporation of the methyl alcohol, a process which took less than 30 minutes. The watchglass containing the specimens was then transferred to a desiccator for 24–48 hours to insure complete dehydration of the glycerine prior to the construction of slides. Nearly all marine nematode species do well when subjected to this dehydration process. Sporadic distortion of varying intensity results with certain members of the Desmodoridae and a few isolated genera of other groups.

Systematics.—When we write the planned monograph we hope to be able to arrange the species and genera of marine nematodes into a more satisfactory classification than has been in use so far. For the special reports, however, we shall adhere to the old Filipjev-Micoletzky system as used by Schuurmans-Stekhoven (1935), with a few improvements suggested by Chitwood, in Chitwood and Chitwood (1950), and Chitwood (1951). We shall proceed only from the family downward, ignoring the position and status of higher systematic categories.

Descriptions.—We feel that too much weight has been attached in the past to the use of formulas in the descriptions of nematode species. Purely relative formulas like those suggested by de Man or by Cobb are of little value. Formulas in which absolute dimensions are used suggest a degree of precision in the construction of nematode species, which is fairly unrealistic. We shall, therefore, in our descriptions give as many absolute measurements as possible of body and organ dimensions but refrain from assembling them into formulas. Instead, we would like to stress the need for giving as precise a representation as possible of the morphology of the animal, especially of the structure of the male genital apparatus.

Various authors (i.e., Wieser, 1955, Chitwood, 1960, Inglis, 1962) have drawn attention to the necessity of the presence of a male specimen of a species as a prerequisite to a valid description of the species. Inglis (1962) goes as far as to state, ". . . I will not, in general, accept identifications based solely on females or larvae and I will insist on treating almost all species based originally on females or larvae alone as *species dubiae*." We are in complete sympathy with this view so far as the "larvae" are concerned. With regard to the female, however, we must support the concept with certain limitations. If such a rule were to be followed with no exceptions, some genera would receive little or no attention, e.g., *Ilium* in this paper. Males are scarce or unknown in certain groups, particularly the Plectoidea, and the advancement of our knowledge of these groups could be curtailed if Inglis' suggestion were adhered to without reservation. Therefore, we feel that the action suggested by Inglis might best be limited to those genera in which males are commonly known to occur.

In addition to species descriptions and figures, general discussions and keys will be supplied wherever necessary.

Florida collection.—The Florida coastline is one of the least known with respect to the nematode fauna of all the regions investigated. Only Cobb (1920, 1922), Chitwood (1951, 1956), and Hopper (1961a, 1966) have reported a few species, mainly from Miami and Key West. Our

Table 1. List of Collecting Sites in Florida

Sample No.	Date 1963	
M-1	May 16	Key Biscayne, Bear Cut area; about low water level; seaweeds scraped off mangrove roots. Canadian National Collection of Nematodes No. 4066.
M-2	Id.	Key Biscayne, Bear Cut area; shallow water (about 20 cm at low tide), close to submerged patch of *Thalassia* and *Syringodium*; fine sand and debris. C.N.C. of N. No. 4067.
M-3	Id.	Key Biscayne, Bear Cut area; flat around high-water level, with *Uca*; fine to medium sand, debris. C.N.C. of N. No. 4068.
M-4	May 17	Off Rickenbacker Causeway; very soft mud, stagnant water at low tide. C.N.C. of N. No. 4069.
M-5	Id.	Virginia Key; beach on grounds of Marine Institute; clean sand, mid-tide level. C.N.C. of N. No. 4070.
M-6	May 18	Everglades National Park, Florida Bay near Flamingo; clayish mud with a little sand; below low-tide level. C.N.C. of N. No. 4071.
M-7	Id.	Everglades National Park, Florida Bay near Flamingo; upper part of shore; sandy mud. C.N.C. of N. No. 4072.
M-8	May 20	Biscayne Bay, dredgings in *Thalassia* beds, about four meters deep; sand, shells and mud; several subsamples. C.N.C. of N. No. 4073.
L	May 21	Lauderdale-by-the-Sea; very exposed beach around mid-tide level; clean, coarse sand, shells. C.N.C. of N. No. 4074.
V	Id.	Vero Beach. Sheltered, muddy sand, with *Uca* and mangroves nearby. C.N.C. of N. No. 4075.

collection increases the total of species known to 118.

Most of our collecting was carried out in Biscayne Bay, in the vicinity of the Institute of Marine Science of the University of Miami, Virginia Key, Miami; additional collecting sites were in the Everglades, near Lauderdale-by-the-Sea, and near Vero Beach. A list of the collecting sites is given in Table 1, and a list of all the species found, together with the species reported in the literature, in Table 2.

SYSTEMATIC SECTION[1]

LEPTOSOMATIDAE

ANTICOMA Bastian, 1865

Type species.—*Anticoma eberthi* Bastian, 1865: 141, pl. 11, figs. 143–145.

In this genus it appears possible to distinguish two groups of species characterized by the position of the excretory pore and the length of the terminal excretory duct. The correlation between these two characters is fairly well established, although, due to a few insufficient descriptions, there remains some doubt as to its general applicability. The two groups (A and B) coincide, respectively, with group A and groups B + C in Wieser (1953). Filipjev (1927) had previously arranged the species of this genus in a similar manner.

Characteristics of Species of Anticoma *Group A*

Excretory pore situated between posterior cervical setae and nerve ring; terminal excretory duct short (never longer than the width of the excretory ampulla).

Key to Species of *Anticoma* Group A

1. Gubernaculum absent .... *A. dahli* Wieser, 1953
A. major Mawson, 1956
Gubernaculum present 2
2. Excretory pore a short distance behind cervical setae 3
Excretory pore about halfway between cervical setae and nerve ring 4

---

[1] Abbreviations used in this paper are as follows: a.b.d., anal body diameter; c.b.d., corresponding body diameter; L, length; Vu, vulva; w, width.

Excretory pore a short distance in front of nerve ring 6
3. Tail short .... *A. campbelli* Allgén, 1932
Tail long, filiform .. *A. filicauda* Mawson, 1956
4. Longer cephalic setae 24–25 μ = about one head diameter long .... *A. eberthi* Bastian, 1865
Cephalic setae less than 10 μ = one-half to two-thirds of head diameter long 5
5. Cuticularized portion of spicula (excluding velum) more or less parallel .... *A. lata* Cobb, 1898
Cuticularized portion of spicula strongly dilated near proximal end .... *A. columba* Wieser, 1953
Syn. *A. australis* Mawson, 1956
6. Supplement opening posterior to proximal end of spicula ...... *A. litoris* Chitwood, 1936
Supplement opening distinctly anterior to proximal end of spicula 7
7. Amphids one-third to one-fourth of cephalic diameter wide .... *A. trichura* Cobb, 1891
Amphids one-sixth of cephalic diameter wide 8
8. Tail short (4–5 a.b.d.) .... *A. insulaealbae* Filipjev, 1927
Tail long (8–10 a.b.d.) .... *A. tenuicaudata* Filipjev, 1946

Others. *A. typica* Cobb, 1891 is related to the above three species but too incompletely known for its position to be determined with certitude.

A. kerguelensis Mawson, 1958b is closely related to *A. lata*, perhaps even identical.

Characteristics of Species of ANTICOMA *Group B*

Excretory pore situated on a level with or in front of cervical setae; terminal excretory duct long (at least as long as the width of the excretory ampulla).

The species within this group will not be differentiated in this work. However, for the reader's convenience, a list of the recognizable species, including the most recent synonymy, is given:

A. acuminata (Eberth, 1863) (Syn.: *Odontobius acuminatus* Eberth, 1863; *Stenolaimus lepturus* Marion, 1870; *Anticoma limalis* Bastian, 1865 pt.; *A. tyrrhenica* de Man, 1878; *A. calveti* de Rouville, 1903; *A. pontica* Filipjev, 1918; *A. zosterae* Schulz, 1932; *A. similis* Cobb, 1898 [see Gerlach, 1962]; and *A. profunda* Micoletzky, 1930 [see Gerlach, 1962]); *A. pellucida* Bastian, 1865 (Syn. *A. limilis* Bastian, 1865 pt.); *A. subsimilis* Cobb, 1914 (see Mawson, 1958); *A. arctica* Steiner, 1916 (Syn. *A. procera* Micoletzky, 1930 [see Gerlach, 1962]); *A. minor* Filipjev, 1927; *A. murmanica* Filipjev, 1927; *A. extensa* Wieser, 1953; *A. stekhoveni* Wieser, 1953 (Syn. *A. acuminata* of Schuurmans-Stekhoven, 1950, nec Eberth, 1863); *A. wieseri* Mawson, 1958 (Syn. *A. stekhoveni* Mawson, 1956, nec Wieser, 1953).

Anticoma lata Cobb, 1898

Plate I, fig. 1, a–e

Anticoma lata Cobb, 1898: 384, 385.
Anticoma ditlevseni Micoletzky, 1930: 255–258, fig. 2.

L = 2.04–2.06 mm; w = 58 μ; esophagus 390–412 μ; tail 215–220 μ (♀, 6.5 a.b.d., ♂, 5.5 a.b.d.). Cephalic setae 4–4.5 + 3–3.5 μ. Buccal cavity conical. Amphids 3–4 μ wide, 11 μ behind anterior end. Cervical setae 33 μ behind anterior end. Excretory pore 115 μ from anterior end. Spinneret delicate and pointed, directed dorsally (always?). Spicula 61–70 μ, dorsal and ventral contours nearly parallel, velum present. Gubernaculum 21–24 μ. Supplement 56–70 μ in front of anus.

Representation in samples studied.—M-1, Key Biscayne.

Geographical distribution.—Australia (Cobb, 1898), Sunda Islands (Micoletzky, 1930), Maldives (Gerlach, 1962), Red Sea (Gerlach, 1958c).

Remarks.—The spicula are somewhat longer than reported by Micoletzky and by Gerlach (61–70 μ as against 40–47 μ), but our specimens seem to agree in all other points.

Anticoma trichura Cobb, 1898

Plate I, fig. 2, a–d

Anticoma trichura Cobb, 1898: 385, 386.

L = 3.01–3.04 mm; w = 49–52 μ; esophagus 390–445; tail in ♀, 530–565 μ (18 a.b.d.), in ♂, 460–480 μ (14 a.b.d.). Cephalic diameter 18–19 μ. Cephalic setae 15 + 8 μ.

TABLE 2. LIST OF FREE-LIVING NEMATODES REPORTED FROM THE COASTS OF FLORIDA (NUMBERS OF SPECIMENS FOUND ARE GIVEN IN PARENTHESES)[1]

Leptosomatidae	
Anticoma lata Cobb, 1898	M-1(6)
A. trichura Cobb, 1898	M-2(5)
Oxystomatidae	
Halalaimus cf. *fletcheri* Mawson, 1958	M-2
H. meyersi n. sp.	M-2(3)
H. pachydermatus (Cobb, 1920) Syn. *Tycnodora p.*	Cobb, 1920, Key West
Porocoma striata Cobb, 1920	Cobb, 1920, Biscayne Bay
Litinium aequale Cobb, 1920	Cobb, 1920, Miami
Tripyloididae	
Halanonchus macrurus Cobb, 1920	M-8(2), Cobb, 1920, Biscayne Bay
Cytolaimium exile Cobb, 1920	M-2(1), Cobb, 1920, Biscayne Bay
Bathylaimus australis Cobb, 1893	V(6)
B. arthropappus n. sp.	M-5(9)
Phanodermatidae	
Phanodermopsis longisetae Chitwood, 1936	V
Enoplidae	
Enoploides bisulcus n. sp.	M-2(13)
E. gryphus n. sp.	M-5(6)
Mesacanthoides fibulatus n. sp.	M-3(4)
M. psittacus n. sp.	L(3)
Ironidae	
Trissonchulus oceanus Cobb, 1920	Cobb, 1920, Miami
Oncholaimidae	
Anoplostoma heterurum (Cobb, 1914)	
Syn. *Oncholaimellus h.*	Chitwood, 1951, Ocala
A. viviparum (Bastian, 1865)	Hopper, 1961a, Panama City
Syn. *Symplocostoma v.*	
Oncholaimus dujardinii de Man, 1878	M-1(24)
Oncholaimium appendiculatum Cobb, 1930	M-1(1), M-2(1)
O. domesticum (Chitwood & Chitwood, 1938)	M-1(2)
Metoncholaimus intermedius n. sp.	M-5(23)
M. simplex n. sp.	M-5
M. scissus n. sp.	M-5
Prooncholaimus hastatus n. sp.	M-8(18)
Viscosia oncholaimelloides n. sp.	M-3(4), M-8(16)
V. papillata Chitwood, 1951	M-7(5), M-8(1), V(6)
V. macramphida Chitwood, 1951	M-2(8), M-8(23)
Enchelidiidae	
Eurystomina minutisculae Chitwood, 1951	M-1(4), M-7(1)
Illium exile Cobb, 1920	M-8(3)
I. libidinosum n. sp.	M-8(1)
Polygastrophora edax n. sp.	M-8(6), V(3)
Calyptronema cobbi Wieser, 1953	
Syn. *Catalaimus acuminatus* Cobb, 1920	Cobb, 1920, Biscayne Bay
Cyatholaimidae	
Pomponema tesselatum n. sp.	M-3(1)
Longicyatholaimus annae n. sp.	M-3(13), M-8(1)
Xyzzors inglisi n. sp.	V(5)
Paracanthonchus platypus n. sp.	M-8(5)
P. truncatus (Cobb, 1914)	Chitwood, 1951, Silver Springs
Syn. *Cyatholaimus t.*	
Paracyatholaimus pesavis n. sp.	M-6(3)
Halichoanolaimus quattuordecimpapillatus Chitwood, 1951	M-2(3), M-6(7), M-8(1)
H. duodecimpapillatus Timm, 1952	V
Neotonchus lutosus Wieser and Hopper, 1966	M-4(2)
Synonchium obtusum Cobb, 1920	Cobb, 1920, Miami

Desmodoridae	
Spirinia parasitifera (Bastian, 1865)	M-4(10), V(55)
S. hamata n. sp.	M-3(14)
Chromaspirina inaurita n. sp.	M-3(4)
Metachromadora pulvinata n. sp.	V(2)
M. onyxoides Chitwood, 1936	M-5(58)
M. meridiana n. sp.	M-2(1), V(103)
Paradesmodora toreutes n. sp.	M-3(7)
Desmodora quadripapillata (Daday, 1899)	
Syn. *Pseudochromadora q.*	M-2(1), M-3(1)
Xennella cephalata Cobb, 1920	Cobb, 1920, Key West
Leptonemella cincta Cobb, 1920	Cobb, 1920, Miami
Monoposthia mirabilis Schulz, 1932	M-2
Monoposthioides mayri n. sp.	M-3(9)
Microlaimidae	
Paramicrolaimus lunatus n. sp.	M-2(8)
Chromadoridae	
Hypodontolaimus interruptus n. sp.	M-1(3), M-3(2), M-5(17)
H. pandispiculatus Hopper, 1961	M-3(25), M-7(2)
Rhips ornata Cobb, 1920	M-5(29), Cobb, 1920, Miami, Key West
Actinonema pachydermata Cobb, 1920	Cobb, 1920, Key West
Chromadora macrolaimoides Steiner, 1915	M-1(30), M-4(9), M-5(1), M-7(1), M-8(3)
Timmia parva (Timm, 1952)	
Syn. *Parachromadora p.*	M-1(12), V(2)
Spilophorella paradoxa (de Man, 1888)	M-1(3), M-2(12), M-3(1), M-6(5), M-7(2), M-8(6)
Prochromadorella mediterranea (Micoletzky, 1922)	M-1(13)
Chromadorella filiformis (Bastian, 1865)	M-1(19)
C. trilix n. sp.	M-2(31)
C. vanmeterae n. sp.	M-2(14)
Euchromadora gaulica Inglis, 1962	M-1(38)
E. pectinata n. sp.	M-8(8)
E. meadi n. sp.	M-2(3), M-8(1)
Atrochromadora denticulata n. sp.	M-1(1), M-2(2)
Comesomatidae	
Mesonchium pellucidum (Cobb, 1920)	
Syn. *Pepsonema p.*	M-8(4)
M. poriferum Cobb, 1920	Cobb, 1920, Key West
Sabatieria paradoxa n. sp.	M-7(2), V
S. paracupida n. sp.	V
Laimella longicauda Cobb, 1920	Cobb, 1920, Biscayne Bay, Key West
Vannolaimus guttatus Cobb, 1920	Cobb, 1920, Biscayne Bay
Axonolaimidae	
Axonolaimus hexapilus n. sp.	M-5(3)
Odontophora variabilis n. sp.	V(11)
Parodontophora brevamphida (Timm, 1952)	V(5)
Aracolaimus punctatus (Cobb, 1920)	
Syn. *Coinonema p.*	Cobb, 1920, Biscayne Bay, Key West
Leptolaimidae	
Alaimella cincta Cobb, 1920	M-2(1), Cobb, 1920, Biscayne Bay
Cynura uniformis Cobb, 1920	Cobb, 1920, Miami
Haliplectus floridanus Cobb in Chitwood, 1956	Chitwood, 1956, Long Key
H. bickneri Chitwood, 1956	Chitwood, 1956, Atwood Grove, Ellenton
Camacolaimidae	
Camacolaimus prytherchi Chitwood, 1933	V(3)
Onchium ocellatum Cobb, 1920	Cobb, 1920, Key West
O. metocellatum Wieser, 1956	
Syn. *Onchulella ocellata* Cobb, 1920	Cobb, 1920, Biscayne Bay
Neurella simplex Cobb, 1920	Cobb, 1920, Key West

Ionema cobbi (Steiner, 1916)	
Syn. *Ionema ocellatum* Cobb, 1920	
Nemella ocellata Cobb, 1920	Cobb, 1920, Biscayne Bay
Diplopeltidae	
Paratarvaia seta n. gen., n. sp.	M-2
Didelta maculatum Cobb, 1920	M-8(1), Cobb, 1920, Key West
Linhomoeidae	
Terschellingia longicaudata de Man, 1907	M-4(1), M-6(13), M-7(89), M-8(1), V(9)
T. longispiculata n. sp.	M-7(24), M-8(1)
T. monohystera n. sp.	V(12)
Anticyathus tenuicaudatus Cobb, 1920	Cobb, 1920, Miami
Halinema spinosum Cobb, 1920	Cobb, 1920, Biscayne Bay
Paralinhomoeus fuscacephalum (Cobb, 1920)	
Syn. *Crystallonema f.*	Cobb, 1920, Miami
P. simile (Cobb, 1920)	
Syn. *Crystallonema s.*	Cobb, 1920, Miami
Linhomoella exilis Cobb, 1920	Cobb, 1920, Biscayne Bay
Monhysteridae	
Paramonhystera canicula n. sp.	M-1(1), M-3(6)
Steineria ampullacea n. sp.	V(1)
Theristus metaflevensis Gerlach, 1955	M-4(11)
T. calx n. sp.	M-4(3), V(33)
T. polychaetophilus Hopper, 1966	Hopper, 1966, Virginia Key
T. ostentator n. sp.	M-3(58)
T. floridanus n. sp.	M-2(5)
T. erectus n. sp.	M-2(3), M-3(83), M-4(1), V(2)
T. galeatus n. sp.	M-5(3)
T. oxyuroides (Schuurmans-Stekhoven, 1931)	M-2(1), M-4(19), M-5(1), M-8(1)
T. fistulatus n. sp.	M-3(2)
T. tortus n. sp.	M-2(5)
T. xyaliformis n. sp.	M-2(3)
Monhystera parva (Bastian, 1865)	M-1(7), M-7(1)
Scaptrella cincta Cobb, 1917	M-2(2)
Xenolaimus striatus Cobb, 1920	M-2(9), Cobb, 1920, Biscayne Bay
Desmoscolecidae	
Greeffiella dasyura Cobb, 1922	Cobb, 1922, Biscayne Bay

---

[1] The number of specimens indicated in this table represents only those that were present in the fraction of the total sample examined. In this manner the relative abundance of each species is somewhat suggested. In some cases, where a species was represented by only a few specimens, an effort was made to locate additional material from the preserved remainder of the sample. These additional specimens are not recorded in this table. Species for which the number of specimens is not indicated were not present in the original fraction examined. These were subsequently recovered from the remainder of the sample.

Amphids 5 μ wide = one-third of body diameter. Buccal cavity conical. Cervical setae 35 μ behind anterior end. Excretory pore 170 μ behind anterior end, i.e., 85% of distance anterior end to nerve ring. Spicula 59–63 μ, proximally bent, dorsal and ventral contours nearly parallel, with slight hump near proximal end. Velum present, smooth (not striated as figured by Gerlach, 1962). Gubernaculum about 20 μ. Supplement 55–60 μ in front of anus.

Representation in samples studied.—M-2, Key Biscayne.

Geographical distribution.—Australia (Cobb, 1898), Sunda Islands (Micoletzky, 1930), Maldives (Gerlach, 1962), Antarctic, Subantarctic (Mawson, 1958b, Allgén, 1959).

OXYSTOMATIDAE

HALALAIMUS de Man, 1888

Type species.—*Halalaimus gracilis* de Man, 1888: 3, 4, pl. 1, fig. 1.

A key to the species of this genus, excluding the subgenus *Pachyodora*, was given by Mawson (1958b).

There are three species which are set apart from the rest by the occurrence of a distinct circle of labial setae, i.e., *H. papil-*

lifer Gerlach, 1956, *H. fletcheri* Mawson, 1958, and *H. filicollis* Timm, 1961. In the first species the tail is rounded at the tip, in the latter two the tail is filiform and its tip is bifid. The Miami material contained one species which seems to correspond in all essential features with *H. fletcheri*, although the indistinctness of the amphids and the somewhat sketchy figures of the type leave room for doubt.

The second species in our material is closely related to *H. supercirrhatus* Gerlach, 1955, and *H. longisetosus* Hopper, 1963, but is distinguished by the much more elongated, filiform tail, the spicula which have a ventral hump, and the gubernaculum with its lateral guiding pieces. Examples of *H. longisetosus* have been recovered from the Charleston, South Carolina, samples, and its status will be clarified in the paper dealing with the specimens collected from that area.

Halalaimus (H.) cf. *fletcheri* Mawson, 1958
Plate II, fig. 3, a–c

Halalaimus (*H.*) cf. *fletcheri* Mawson, 1958: 332. fig. 13, a, b.

L = 2.6–2.37 mm; w = 26–35 μ; tail in ♂, 310 μ (18 a.b.d.), in ♀ 275 μ. Head at level of first cephalic setae about 4 μ wide and 6 μ high. Six labial setae, 2 μ long. Cephalic setae 6 μ long, arranged in two circles (6 + 4) about 4 μ apart. Amphids beginning about 10 μ from anterior end, indistinct, particularly the posterior end which appears to run into lateral alae. Its length in one specimen is probably 17 μ. Anterior portion of neck exceedingly drawn out, narrow for about two-thirds its length. Tail with bifid tip, each prong 10 μ long. Spicula 27 μ long, with velum. Gubernaculum strongly developed.

Representation in samples studied.—M-2, Key Biscayne.

Geographical distribution.—Macquarie Isl., Kerguelen Isl. (Mawson, 1958b).

Halalaimus (H.) meyersi new species
Plate II, fig. 4, a–c

L = 2.26–2.49 mm; w = 17 μ; Vu = 47%; tail in ♂, 540 μ. Head about 4.5 μ wide, 7 μ high. Cephalic setae 20 μ long, arranged in two circles (6 + 4). Cuticle finely striated. Amphids 38–40 μ long, beginning 20–30 μ from anterior end. Excretory pore 50 μ from anterior end, ampulla at base of amphids. Terminal excretory duct 8–10 μ long. Narrowed portion of neck about one-fourth its total length. Spicula 21 μ long, with ventral swelling at the end of its proximal third. Gubernaculum with lateral guiding pieces. Tail very thin, elongated, with narrow tip.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa Collection Number 4067, Type slide No. 60. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

Remarks.—This species is named in honor of Dr. Samuel P. Meyers, our Miami host.

TRIPYLOIDIDAE

HALANONCHINAE new subfamily

Type genus.—*Halanonchus* Cobb, 1920: 266.

Diagnosis.—Tripyloididae, with three large, well-separated lips, six labial papillae, and 10 cephalic setae in two circles, the anterior circle consisting of six jointed, mostly elongated setae; large, unarmed conical or cylindrical buccal cavity without partitions; spiral or tubular amphids; spicula short, bent; gubernaculum plate-shaped, simple, without apophysis; pre- and sometimes postanal supplements present in males.

Discussion.—In Cobb's paper of 1920 one finds the description of three closely related genera, the systematic position of which has been doubtful ever since. These genera are: 1) *Cytolaimium* [with the species *C. exile* Cobb, 1920, and *C. obtusicaudatum* Chitwood, 1936, the latter, according to Gerlach (1962), being a synonym of the former], 2) *Rhabdocoma* [with the species *R. americana* Cobb, 1920, *R. articulata* Gerlach, 1955, *R. brevicauda* Schuurmans-Stekhoven, 1950, *R. cylindricauda* Schuurmans-Stekhoven, 1950, *R. macrura* Cobb, 1920], and 3) *Halanonchus* (syn. *Latilaimus* Allgén, 1933) [with the species *H. macramphidus* Chitwood, 1936, and *H. macrurus* Cobb, 1920].

All three genera are characterized by a smooth cuticle, an arrangement of cephalic sense organs in three circles of 6 + 6 + 4, the second circle consisting of the longest and distinctly jointed setae, three large, deeply cut lips, a buccal cavity which is either conical or cylindrical, amphids which are either spiral with a single turn and a posterior break (*Cytolaimium*, *Rhabdocoma*), or more tubular or pocket-shaped with a circular opening (*Halanonchus*), simple spicula, plate-shaped, simple gubernacula, and the occurrence in males of many supplements, not only preanally but also postanally and even in the cervical region.

The number (though not the arrangement) of the cephalic setae, the deeply cut lips, the shape of the amphids (although the situation in *Halanonchus* is not quite clear), and the presence of a large buccal cavity suggest relationship with the Tripyloididae, to which family *Halanonchus* and *Rhabdocoma* have been referred by Filipjev (1934). On the other hand, as Schuurmans-Stekhoven (1950) and Gerlach (1955, 1962) have pointed out, both *Rhabdocoma* and *Cytolaimium* have a number of features in common with *Trefusia* de Man, 1893, which has no buccal cavity, pocket-shaped or spiral amphids and no supplements, and which so far has been considered an oxystomatid of somewhat uncertain position. Finally, Chitwood (1936, 1951) placed *Cytolaimium* and *Rhabdocoma* with the Monhysteridae.

We consider that by virtue of the deeply cut lips, the jointed setae, the large buccal cavity (particularly in *Halanonchus*), and the spiral amphids (in *Cytolaimium* and *Rhabdocoma*), the three genera mentioned belong to the family Tripyloididae. However, because of the simplicity of the buccal cavity, the arrangement of the cephalic setae in two circles (instead of one circle), and the different structure of the male genital armature, a distinct subfamily should be created for them, for which we propose the name Halanonchinae new subfamily, with *Halanonchus* Cobb as the type genus.

This new subfamily, via *Trefusia*, links the Tripyloididae with the Oxystomatidae and thus allows a more satisfactory placement of the former family which so far has occupied a rather isolated position either within the order Araeolaimoidea (Schuurmans-Stekhoven, 1935), or the superfamily Chromadoroidea (Chitwood, 1951).

Within the genus *Trefusia* and the subfamily Halanonchinae it seems as if a transition of the amphidial shape from spiral to pocket-shaped or tubular had taken place, thus stressing the intermediary position of this group of genera between the Oxystomatidae and the Tripyloididae. This is demonstrated not only by a comparison of *Halanonchus* with *Cytolaimium* and *Rhabdocoma*, but also by *Trefusia varians* Gerlach, 1955, in which the juveniles have spiral-shaped, and the adults tubular-shaped amphids not too different from the shape which we observed in *H. macrurus* (see below). Further proof of the intermediary position of the new subfamily might be the fact that *Rhabdocoma* is reported to have just one posterior ovary (as is the case in many oxystomatids), whereas *Cytolaimium* has two ovaries (like the Tripyloidinae).

HALANONCHUS Cobb, 1920

Type species.—*Halanonchus macrurus* Cobb, 1920: 266, fig. 51.

Halanonchus Cobb, 1920: 266.
Latilaimus Allgén, 1933: 90.

Halanonchus macrurus Cobb, 1920
Plate III, fig. 5, a–c

Halanonchus macrurus Cobb, 1920: 266, fig. 51.

L = 2.00 mm; w = 40 μ; esophagus = 265 μ. Head diameter (on level of 4 cephalic setae) 19 μ. Three large, deeply cut lips, on each lip 2 thin labial setae and, shortly behind, 2 larger, two-jointed cephalic setae, measuring 3–3.5 μ. Further behind, there are the four setae of the second cephalic circle, measuring about 5 μ and being non-jointed. There are many yellowish granules which are scattered throughout the epidermis of the body, although a certain arrangement into longitudinal rows can be discerned. The amphids give the impression of sawed-off and slightly bent pieces of tubing with an indistinct, more or less circular orifice; they are 8 μ long and situated 20 μ behind the anterior end. Cobb shows the amphids more pocket-shaped with a distinctly circular orifice. Each lip seems to be supported by a large oval structure which apparently was mistaken for the amphids by Allgén (1933) in his description of *Latilaimus zosterae*. In the cervical region one can distinguish 5–6 ventral bumps which might be papillae. The same organs have been observed in undescribed species of *Rhabdocoma* and *Halanonchus* by Gerlach (1962). Buccal cavity with strong walls, 20–22 μ long. Esophagus weakly dilated posteriorly, no bulb. A small triangular cardia is present. Spicula slender, 32 μ long, gubernaculum either absent or consisting of a thin lamella, lying parallel to the spicula. There are about 12 preanal supplements, the posterior six being more distinct than the more anterior ones. Tail 610 μ long, a.b.d. 28 μ.

Representation in samples studied.—M-8, Biscayne Bay.

Geographical distribution.—Biscayne Bay (Cobb, 1920).

CYTOLAIMIUM Cobb, 1920

Type species.—*Cytolaimium exile* Cobb, 1920: 251, fig. 31.

Cytolaimium exile Cobb, 1920

Plate III, fig. 6, a–d

Cytolaimium exile Cobb, 1920: 251, fig. 31.
Cytolaimium obtusicaudatum Chitwood, 1936: 13, fig. 3, J–L (cf. Gerlach, 1962).

L = 3.2 mm; w = 32 μ; diameter at base of esophagus 30 μ. Esophagus 250 μ long. Head diameter 20–25 μ. Head with six setose labial papillae, six segmented cephalic setae and four subcephalic setae. Cephalic setae in female 20 μ long, in male somewhat longer but distorted so as to render precise measurement impossible. Amphid 8 μ wide and located 20–23 μ from anterior end. Subcephalic setae 10 μ long in male, 5–6 μ in female and located 35 μ from anterior end. Body with several short (3–4 μ) cervical setae beginning 90 μ from anterior end and ceasing at nerve ring and with a few, very thin, somatic setae 10–15 μ in length. Female didelphic, amphidelphic, ovaries reflexed. Male diorchic, testes outstretched. Spicules 37 μ long, their chord 28 μ. Male preanally with 9 pairs of discoid supplements and 2 pairs of fleshy, setose papillae and postanally with 3 pairs of discoid supplements and 5 pairs of fleshy setose papillae. Tail length extremely variable, 15 μ long for one female, 420 μ for the other, and 740 μ for the male.

Representation in samples studied.—M-2, Key Biscayne.

Geographical distribution.—Biscayne Bay (Cobb, 1920), Beaufort, North Carolina (Chitwood, 1936), Maldives (Gerlach, 1962). 1962).

Remarks.—The data for our specimens (1 ♂, 2 ♀) lend support to the view of Gerlach (1962) that *C. obtusicaudatum* Chitwood, 1936, is a synonym of *C. exile* Cobb, 1920. The tail length in our three specimens ranged from 15 μ in one female to 740 μ in the male. In the specimens with shorter tails, the terminus appears abnormal and suggests the phenomenon of wound-healing as discussed for this species by Gerlach. Even in the case of the longest-tailed specimen there is the possibility of a missing portion, as no typical spinneret can be recognized.

The setose papillae associated with the male tail appear to be similar to the papillae seen on the discoid supplements, the only difference being the lack of the disc.

BATHYLAIMUS Cobb, 1893

Type species.—*Bathylaimus australis* Cobb, 1893: 409, 410, fig. 9, I–IV.

Our material contained two species of the genus *Bathylaimus*, one of which appears to be the type species, *B. australis* Cobb, 1893. The other represents an undescribed species closely related to *B. capacosus* Hopper, 1962, from which it can be distinguished by having the shorter of the submedian cephalic setae equal in length to the basal segment of the longer. In *B. capacosus* the shorter of the pair is approximately half as long as the basal segment of the longer.

Bathylaimus australis Cobb, 1893

Plate IV, fig. 7, a–e

Bathylaimus australis Cobb, 1893: 409–410, fig. 9, I–IV.

Bathylaimus assimilis de Man, 1922b: 119, 120, fig. 2–2e. NEW SYNONYMY.

L = ♂, 1.5–2.2 mm, ♀, 1.4 mm; w = 45–53 μ; diameter at base of esophagus 41–44 μ. Esophagus 270–370 μ. Vu = 51%. Tail 98–135 μ (3–3.5 a.b.d.). Head diameter 22–24 μ. Labial setae about 4 μ. Cephalic setae 20 + 9 μ, the longer set comprised of four segments. Cervical region bearing eight rows of somatic setae; those anterior to nerve ring being 5 μ long. Buccal cavity 37–39 μ long, bipartite (29–31 + 8–9 μ); without armature. Amphid 20 μ from anterior end, positioned over posterior half of the anterior portion of buccal cavity; internal amphidial pouch 5 μ wide, its orifice approximately 3 μ. Spicula 48–50 μ long, gubernaculum 50 μ long. Female tail without setae, male tail bearing setae as illustrated (Fig. 7, b, c).

Representation in samples studied.—V, Vero Beach.

Geographical distribution.—Cosmopolitan.

Remarks.—In considering the synonymization of *B. assimilis* de Man with *B. australis* Cobb, the following facts are pertinent. Wieser, 1956, separated the two species on the basis of different values for the lengths of both the buccal cavity and the spicula. According to the information presented by that author, *B. australis* has a buccal cavity of 33 μ and spicula of similar length, while in *B. assimilis* the figures were 50–55 μ and 45 μ, respectively. Further, Wieser states that: "*B. australis* and *B. assimilis* are very closely related and the differences in the length of both spicula and buccal cavity are the only ones I can find." An examination of the original description of *B. australis* shows that Cobb's animal had a buccal cavity of 50 μ and spicula of approximately 40 μ. These figures closely approach those presented by de Man in his original description of *B. assimilis* (buccal cavity 40–43 μ, spicula 37 μ). On this basis we consider *B. assimilis* de Man, 1922b, along with its synonyms, to be a junior synonym of *B. australis* Cobb, 1893.

B. setosicaudatus Timm, 1961, while extremely close to *B. australis*, can be separated by the fact that the spicular cephalization is reduced while that of *B. australis* is prominent. Also the spicula are uniformly bent in *B. setosicaudatus*, while in *B. australis* most of the curvature is limited to the mid region.

Bathylaimus arthropappus new species

Plate IV, fig. 8, a–f

L = 3.1–3.3 mm; w = ♂, 52–55 μ, ♀, 62 μ. Diameter at base of esophagus, ♂, 44–48 μ, ♀, 53 μ. Esophagus ♂, 687–750 μ, ♀, 820 μ, Vu = 56%. Tail ♂, 118–130 μ (3.4–3.7 a.b.d.), ♀, 220 μ (5.4 a.b.d.). Head diameter, 34–37 μ. Labial setae about 20 μ. Cephalic setae 47–52 + 18–19 μ. Both the labial setae and longer cephalic setae are segmented, with the former having three segments and the latter four. Cervical region bearing eight rows of somatic setae which are more or less arranged in circles. First circle, 6 μ long, near base of amphid. Second circle, 17 μ long, half the distance from the anterior end to the nerve ring. Third circle, 8 μ long, just anterior to nerve ring. Remaining two circles, 8–9 μ long, posterior to nerve ring, the last 70 μ posterior to nerve ring. Buccal cavity 28–35 μ long, without armature. Amphid in ♂, 12–13 μ, in ♀, 8 μ wide, located posterior to buccal cavity, 37–38 μ from anterior end. Spicula 50–57 μ long, proximally cephalated. Gubernaculum 50 μ long. Male tail bearing setae as illustrated (Fig. 8, f); subterminal setae 40–45 μ long. Four gland cells are associated with the spinneret apparatus in both sexes.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4070, Type slide No. 61. Type locality, M-5, Virginia Key.

Representation in samples studied.—M-5, Virginia Key.

Geographical distribution.—The species also occurs at Gulf Shores, Alabama (unpublished observation).

Remarks.—The region of the esophagus directly posterior to the buccal cavity is constructed in such a manner that, if the esophageal musculature were to exert a pull in this region, a cavity might arise which could be mistaken for a second compartment of the buccal cavity. This subject was also brought up in the description of *B. capacosus* Hopper, 1962.

PHANODERMATIDAE

PHANODERMOPSIS Ditlevsen, 1926

Type species.—*Phanodermopsis groenlandica* Ditlevsen, 1926: 13, 14, pl. 7, figs. 1, 2; pl. 8, fig. 5.

Our material contained typical representatives of *P. longisetae* Chitwood, 1936.

The following species have been described since a key to the species of this genus was given by Wieser (1953): *P. conicauda* Filipjev, 1946, and *P. ingrami* Mawson, 1958, belonging to Wieser's group A, and *P. obtusicauda* Filipjev, 1946, belonging to group B. *P. necta* Gerlach, 1957, does not appear to belong to this genus, since it has a well developed supplement and spicula as in *Phanoderma*. *P. suecica* Allgén, 1953, is a *species inquirenda*.

Mawson (1958a) raised the question of the position of this genus since Ditlevsen (1926) did not designate a type species. However, Filipjev (1927) in the appendix to his paper, established synonymy of his genus *Galeonema* with *Phanodermopsis* and designated *P. groenlandica* Ditlevsen as the type species.

Phanodermopsis longisetae Chitwood, 1936
Plate V, fig. 9 a–c

Phanodermopsis longisetae Chitwood, 1936: 209, 210, pl. 26, figs. 16–19.

L = 3.85 mm; w = 80 μ; tail 250 μ. Head diameter 15 μ, capsule weakly developed. Labial papillae distinct, conical. Cephalic setae 15 + 10 μ long. Amphids 6 μ wide = 40% of head diameter, 10 μ behind anterior end. Excretory pore 55 μ behind anterior end. Spicula 360 μ. Gubernaculum 56 μ. Caudal setae arranged in characteristic pattern, the setae being of two types: one fleshy and S-shaped, the other slender and straight or slightly curved.

Representation in samples studied.—V, Vero Beach.

Geographical distribution.—Beaufort, North Carolina (Chitwood, 1936).

ENOPLIDAE

ENOPLOIDES Saveljev, 1912

Type species.—*Enoploides typicus* Saveljev, 1912: 115.

In this genus, classification is possible only on the basis of the male genital armature. Consequently, we have to insist that all species known from juveniles or by females only are to be regarded as *species inquirendae*. This includes, in addition to the doubtful species mentioned by Wieser (1953), the following: *E. labiatus* Bütschli, 1874 [Synonymy of this species with *E. spiculohamatus* Schulz, 1932, cannot be proven in any way and should be abandoned, as advocated by Brunetti, 1950.], *E. tridentatus* Saveljev, 1912, *E. brevis*

Filipjev, 1918, *E. brattstromi*, *E. paralabiatus*, *E. reductus*, and *E. longicaudatus* all Wieser, 1953, *E. oligotricha* Mawson, 1956 (syn. *E. oligochaetus* Mawson, 1956), *E. pterognathus* Mawson, 1956, and *E. kerguelense* Mawson, 1958.

The remaining species can be separated into two groups, one with short spicula, the other with extremely long spicula. The former group comprises only two species, viz., *E. cirrhatus* Filipjev, 1918, and *E. tyrrhenicus* Brunetti, 1949 (cf. Gerlach, 1952), for which most likely a new genus or subgenus should be established.

The group with long spicula is very uniform. Since the gubernaculum represents one of the best distinguishing characters, the shape of this organ in all the species belonging to this group (except *E. typicus*, of which no figures were given) is shown in Text-figure 1. A number of species can be separated immediately by the shape of the gubernaculum, viz., *E. hirsutus* Filipjev, 1918, *E. brunettii* Gerlach, 1952, *E. rectis* Gerlach, 1957 (syn. *E. brunettii* var. *rectis*), and *E. harpax* Wieser, 1959. In the remaining species the gubernaculum is more or less S-shaped, although differences in shape between the species can be found. The species comprising this remaining group can be separated by use of the following key.

KEY TO SPECIES OF *ENOPLOIDES* POSSESSING S-SHAPED GUBERNACULA

1. Cephalic setae of equal length … *E. cephalophorus* (Ditlevsen, 1919)
   Cephalic setae of unequal length … 2
2. Longest cephalic setae about 1.2 head diameters long, shorter setae measuring $^1/_3$ of longer ones. Gubernaculum with characteristic ventral knob … *E. gryphus* n. sp.
   Longest cephalic setae measuring not more than one head diameter, shorter ones about $^1/_2$ that length. Gubernaculum rather smoothly S-shaped … 3
3. Tip of gubernaculum apparently 3-pronged: supplement measuring about half the corresponding body diameter (description and figures not quite clear) … *E. spiculohamatus* Schulz, 1932
   Tip of gubernaculum 2-pronged: supplement much shorter … 4
4. Distal end of spicula with mobile spine; mandibles 55–60 μ long … *E. amphioxi* Filipjev, 1918
   Distal end of spicula without mobile spine; mandibles 45 μ or less … 5
5. Spicula smooth, distal end pointed, then dilated; mandibles about 45 μ (extrapolated from Southern's figures and text) … *E. labrostriatus* (Southern, 1914)
   Spicula vertically striated, in their distal half with a diagonal break (Fig. 10, c); mandibles 30–35 μ long … *E. bisulcus* n. sp.

The type species, *E. typicus* Saveljev, 1912, is poorly known since no figures were given. It seems to differ from all other species by the small dimensions of its organs (cephalic setae only 8 μ long, buccal cavity only 9 μ deep!).

Enoploides bisulcus new species
Plate V, fig. 10, a–d

L = 3.5–4.2 mm; w = 115–120 μ; diameter at base of esophagus 95–105 μ. Esophagus 750–800 μ; nerve ring at 25%. Vu = 52.5%. Eggs 165 × 75 μ, one per uterus. Tail in ♂, 170–200 μ (4 a.b.d.), in ♀, 215–225 μ (3.7–4.5 a.b.d.), in juvenile 4.8 a.b.d. long. Head diameter 50–56 μ. Labial setae 25 μ. Cephalic setae 45–50 + 25–28 μ. Mandibles 30–35 μ long, deeply notched anteriorly, with strong apophyses and muscles that link them to the buccal capsule. Subventral teeth small, nearly parallel to mandibles and thus difficult to observe in lateral view. Their presence can best be ascertained in *en face* view. Dorsal tooth seemingly absent. Peribuccal portion of esophagus strongly developed, muscular. Spicula 420–475 μ, knobbed proximally, vertically striated throughout, with a diagonal break in their distal end that runs from dorsal to ventral, tip pointed. Gubernaculum S-shaped, its proximal end open, ill-defined; distal end forked. Supplement 20 μ long, 120–150 μ preanal. Tail with pair of fleshy, S-shaped spines and a number of setae. Setae in anal area and paired terminal setae, 17 μ long.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Ento-

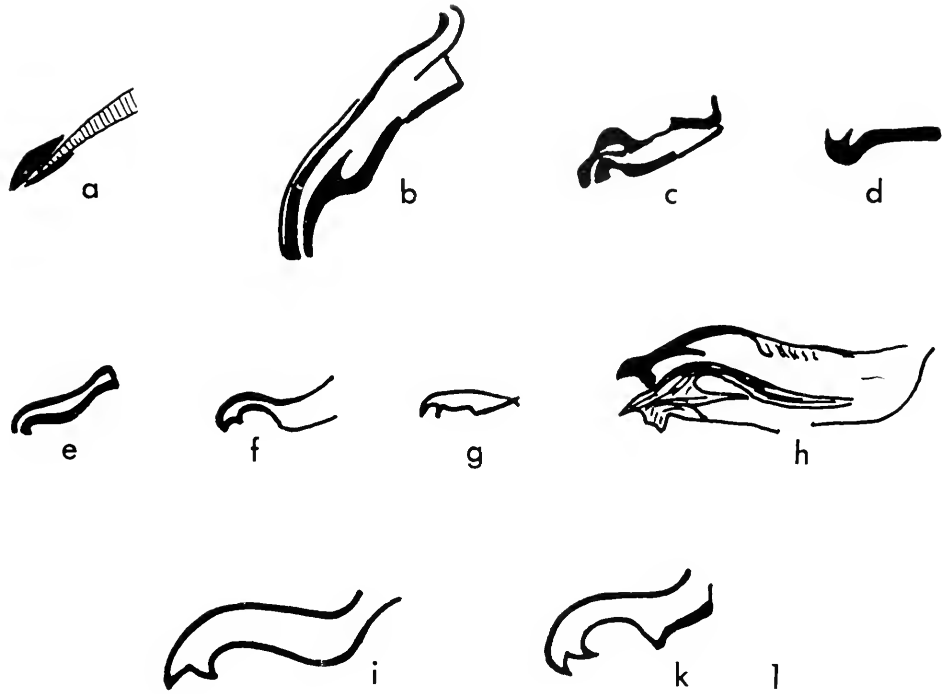


Figure 1. Gubernacula of several species of *Enoploides*. a—*E. hirsutus*; b—*E. brunettii*; c—*E. vectis*; d—*E. harpax*; e—*E. amphioxi*; f—*E. labrostriatus*; g—*E. cephalophorus*; h—*E. spiculohamatus*; i—*E. bisulcus*; k—*E. gryphus*. All gubernacula copied from original descriptions of respective species.

mology Research Institute, Ottawa, Collection Number 4067, Type slide No. 62. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

Enoploides gryphus new species

Plate III, fig. 11c; plate V, fig. 11 a, b

L = 3.0–3.7 mm; w = 85–100 μ; diameter at end of esophagus 70–85 μ. Esophagus 800–900 μ. Tail 190–240 μ; a.b.d. 45–60 μ. Head diameter 45–57 μ. Labial setae 28–32 μ. Cephalic setae 60–80 + 20–27 μ. Mandibles 26–28 μ. Apart from the dimensions, the structure of the buccal armature is the same as in *E. bisulcus*. Spicula 230–260 μ, 6–7 μ wide, knobbed proximally, vertically striated throughout, without break, tip pointed. Gubernaculum hook-shaped, with characteristic ventral knob. Supplement 80–110 μ preanal. Tail with pair of slender postanal spines (not S-shaped as in the foregoing species) and several setae. (Note: All the somatic and caudal setae on this species are shorter and more slender than on *E. bisulcus.*)

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4070, Type slide No. 63. Type locality, M-5, Virginia Key.

Representation in samples studied.—M-5, Virginia Key.

Remarks.—This species resembles the foregoing one in most respects. The main distinguishing features are the longer cephalic setae and the shorter spicular apparatus.

MESACANTHOIDES Wieser, 1953

Type species.—*Mesacanthoides sculptilis* Wieser, 1953: 86, fig. 46, a–d.

Through the addition of two new species this genus is becoming more heterogeneous as far as the male genital apparatus is concerned. However, its most characteristic feature, the shape and texture of the mandibles, suffices to separate it clearly from related genera. Classification is largely based on the genital armature (see Wieser, 1959). Consequently, *M. wieseri* Mawson, 1956, has to be considered a *species inquirenda*, although it appears to be closely related to *M. latignathus*.

Key to Species of *Mesacanthoides*

1. Gubernaculum reduced, no supplement . *M. latignathus* (Ditlevsen, 1919)
   Gubernaculum and supplement present 2
2. Supplement small, tubular 3
   Supplement very large, "wrench-like" .... *M. sculptilis* Wieser, 1953
3. Spicula more than two anal diameters long, tail filiform, with flagellum .... *M. fibulatus* n. sp.
   Spicula about one anal diameter long, tail plump or elongate, never filiform 4
4. Gubernaculum more or less plate-shaped; head with four circles of cephalic setae .... *M. caputmedusae* (Ditlevsen, 1919)
   Gubernaculum S-shaped; head with 2–3 circles of cephalic setae 5
5. Implantation of cephalic setae near middle of cephalic capsule; spicula strongly arcuate, tip pointed *M. sinuosus* Wieser, 1959
   Implantation of cephalic setae at posterior edge of cephalic capsule; spicula nearly straight, tip elaborately armed .... *M. psittacus* n. sp.

Mesacanthoides fibulatus new species
Plate VII, fig. 12 a–c

L = 4.3 mm; w = 75 μ. Esophagus = 675 μ. Tail = 350 μ. Head diameter 33 μ. Labial setae 10 μ. Longest cephalic setae 42 μ, setae of submedian pairs sticking together. One circle of subcephalic setae in male. Cephalic capsule deeply lobed. Cephalic organ present, in front of lateral cephalic seta. Mandibles 18 × 10 μ, solid as in *Enoploides* but with an additional transverse bar near the anterior end; moreover, the sclerotization is not uniform but gives a mottled impression. The tips of the claws are darker than the rest of the mandibles. Teeth well developed, about half as long as the mandibles. Stomodeal ring forming three "brackets" around the mandibles which serve as muscular attachments. Spicula 125–135 μ, about 4 anal diameters, cephalate proximally, with a break just before the distal sixth. Gubernaculum slightly S-shaped, 15 μ long. Supplement small, about 90 μ in front of anus. Tail at first conical, then abruptly attenuated and drawn out into an extremely long and whip-like flagellum, about five times the length of the spicula. In the circumanal region there are scattered setae.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4069, Type slide No. 64. Type locality, M-3, Key Biscayne.

Representation in samples studied.—M-3, Key Biscayne.

Mesacanthoides psittacus new species
Plate VI, fig. 13 a–e

L = 2.32 mm; w = 50 μ; esophagus = 540 μ; tail = 222 μ. Head diameter 35 μ. Lips plump, labial setae stout, 15 μ. Cephalic setae: lateral 62 μ, submedian 56 + 27 μ, implanted near posterior edge of cephalic capsule. The latter with straight edge, 17 μ high. Mandibles 19 × 11 μ, powerful, plump, of typical shape and texture, each claw with an oval apophysis on its "shoulder." Teeth well developed, about half as high as the mandibles. Spicula plump, nearly straight, 50 μ long, their tips broad, each with a three-pronged process on the caudal edge. Gubernaculum S-shaped, about 26 μ long, powerful. Supplement small, 90 μ in front of anus. Tail 5 anal body diameters long, with scattered setae.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4074, Type slide No. 65. Type locality, L, Lauderdale-by-the-Sea.

Representation in samples studied.—L, Lauderdale-by-the-Sea.

ONCHOLAIMIDAE

ONCHOLAIMUS Dujardin, 1845

Type species.—*Oncholaimus attenuatus* Dujardin, 1845: 236.

Keys to the species of *Oncholaimus* can be found in the works of Kreis (1934) and Wieser (1953).

Oncholaimus dujardinii de Man, 1878

Plate VII, fig. 14, a, b

Oncholaimus dujardinii de Man, 1878: 94, pl. 7, fig. 4, a–c.

L = 2.4–2.95 mm; w = 42–45 μ; esophagus 350 μ. Vu = 76%. Tail, in ♀, 67 μ long (2.6 a.b.d.). Head 18–20 μ wide, bearing 10 short, subequal cephalic setae, the longest 4 μ long. Buccal cavity 22–24 × 12 μ armed with 3 strong teeth of which the left subventral is the more prominent. Amphids in male 7–9 μ wide (= 37–45% of c.b.d.). Anterior end of esophagus with a pair of dark pigmented masses (cf. de Man, 1878). Excretory pore 45–50 μ behind anterior end. Renette cell prominent, 90–100 μ long, located approximately 200 μ posterior to base of esophagus. Spicula 27–31 μ long, proximally cephalated. Gubernaculum absent, although a dorsal thickening of the cloacal lining may give the impression of the presence of such a structure. The thickened area appears to be a point of attachment for muscles associated with the spicula. Male tail 40 μ long, ventrally curved; with 12–16 stout, circumcloacal setae. Distal extremity of male tail slightly enlarged and bearing two pairs of short, stout, subventral setae and a pair of slender, subdorsal setae.

Representation in samples studied.—M-1, Key Biscayne.

Geographical distribution.—Cosmopolitan.

Discussion.—While our species appears to be *O. dujardinii* de Man, 1878, there remains some doubt as to the identity of this species. Schuurmans-Stekhoven (1950) and Inglis (1962) reason that the typical *O. dujardinii* is devoid of a gubernaculum, whereas *O. dujardinii* de Man *sensu* Steiner, 1915 (and other authors) possesses such an organ and thus represents a different species. However, we are of the opinion that the dorsal thickening of the cloacal lining described in our specimens has been occasionally misinterpreted as a gubernaculum and we regard the questioned accounts of *O. dujardinii* as representing de Man's species.

ONCHOLAIMIUM Cobb, 1930

Type species.—*Oncholaimium appendiculatum* Cobb, 1930: 227, figs. 2, 3, 6, v, 8, 9.

A discussion of this genus, with a key to species, was given recently by Chitwood (1960). We feel that separation of this genus from *Oncholaimus* should be based mainly on the presence of a Demanian system and not so much on that of the *pre*anal papillae (not *post*anal, as erroneously stressed by Wieser [1953] and subsequent authors), as rudiments of preanal papillae can also be found in representatives of the latter genus as well as in other oncholaimid genera. This would suggest that the two short-spiculed species of *Metoncholaimus* described by Mawson, i.e., *M. brevispiculum* Mawson, 1957, and *M. thysanouraios* Mawson, 1958, actually ought to be referred to *Oncholaimium*. The diagnosis of Cobb (1930) has to be emended so as to include, in this genus, species in which the Demanian organ is provided with exit pores.

Both species found in Florida have been previously reported from the east coast of the United States.

Oncholaimium appendiculatum Cobb, 1930

Plate VIII, fig. 15, a–c

Oncholaimium appendiculatum Cobb, 1930: 227, figs. 2, 3, 6, v, 8, 9.

L = 2.27 mm; w = 44 μ; esophagus = 360 μ; nerve ring 280 μ behind anterior end. Head diameter 26 μ. Labial capsule lobed, conspicuous. Labial papillae conical. Cephalic setae 9 μ, equal. Buccal cavity 30 × 18 μ. Teeth 25 + 15–16 μ, the longest one reaching to about the level of implantation of the cephalic setae. Amphids 11 μ = 40% of c.b.d. wide. Scattered cervical setae. Excretory pore 30 μ in front of nerve ring. Spicula 65 μ (one tail length). No gubernaculum. Anal diameter 25 μ. One large, "prehensile" preanal papilla. Twenty-four to 26 circum- and postanal setae, about 13 μ long. Tail with small ventral papillae at the beginning of the distal third.

Representation in samples studied.—M-1, Key Biscayne.

Geographical distribution.—Woods Hole, Massachusetts, ? Beaufort, North Carolina (Pearse, Humm and Wharton, 1942).

Oncholaimium domesticum Chitwood and Chitwood, 1938

Plate VIII, fig. 16 a–d

Oncholaimium domesticum Chitwood and Chitwood, 1938.

Oncholaimium oxyuris var. *domesticus* Chitwood and Chitwood, 1938: 458, 459, fig. 1, f–h; nec Timm, 1952.

L = 3.3–3.4 mm; w = ♂, 65 μ, ♀, 85 μ; esophagus = 525–550 μ. Tail = 70 μ. Vu = 64%. Head diameter 37 μ. Labial capsule lobed, inconspicuous. Six labial papillae. Cephalic setae subequal, 8 μ. Buccal cavity 37–38 × 25–26 μ. Teeth 25 + 21 μ. Amphids 7–8 μ = 20% wide (both sexes). Excretory pore 70–75 μ behind buccal cavity. Demanian organ well developed, uvette about 400 μ posterior to vulva, 1–2 adanal openings on each side. Spicula 45 μ (one a.b.d.). No gubernaculum. Preanal papilla with two setae. Postanal papillae at the beginning of the distal third of the tail. Circumanal setae present. Tail 60–70 μ, with terminal swelling.

Representation in samples studied.—M-1, Key Biscayne.

Geographical distribution.—New York (Chitwood and Chitwood, 1938), California (Chitwood, 1960).

Remarks.—The characters distinguishing this species from *O. oxyure* (Ditlevsen, 1911) are the short teeth, the well-developed preanal papilla with setae and the stout spicula. The specimens described by Timm (1952) deviate in all these characteristics from *O. domesticum* and seem to be representatives of *O. oxyure*.

METONCHOLAIMUS Filipjev, 1918

Type species.—*Oncholaimus demani* Zur Strassen, 1894: 460, pl. 29, fig. 2.

A key to this genus was given recently by Chitwood (1960). We are of the opinion that, because of the shortness of their spicula, *M. brevispiculum* Mawson, 1957, and *M. thysanouraios* Mawson, 1958, belong to *Oncholaimium*. *M. haplotretos* Mawson, 1958, is considered as doubtful since only females are known.

Our material contained three new species, all of which are characterized by relatively short spicula (< 180 μ as against 250–750 μ in other species) and by the absence of a gubernaculum [which is also lacking in *M. albidus* (Bastian, 1865) but is present in all other species]. Moreover, *M. intermedius* and *M. simplex* are distinguished by short and plump tails, *M. simplex* by the presence of only one Demanian exit pore, *M. scissus* by two ventral papillae on the ♂ tail and by the slit-like openings of the Demanian organ. The relative position of osmosium and uvette serves as a further character distinguishing *M. simplex* and *M. intermedius*.

Metoncholaimus intermedius new species

Plate IX, fig. 17 a, d, e; Plate X, fig. 17 b, c

L = 2.2–2.7 mm; w = 38 μ; esophagus = 350–400 μ; Vu = 66–74%. Head diameter 26 μ. Labial papillae small but distinct. Labial capsule deeply lobed. Cephalic capsule weak. Cephalic setae 8 μ, subequal. Amphids 6 μ in ♀, 8–9 μ = 30–33% of c.b.d. in ♂. Buccal cavity 25–28 × 16–18 μ. Longest tooth 19–20 μ. Ventral gland 150–200 μ behind esophagus; excretory pore 80–90 μ behind anterior end. In some specimens large coelomocytes. Demanian organ well developed, uvette 325 μ behind vulva, osmosium anterior to uvette, two exit pores 70–100 μ preanal. Eggs 90 × 40 μ. Spicula 70–77 μ long, no gubernaculum. Preanal elevation with short, stout seta. Fourteen circumanal setae. One pair of postanal elevations with setae, near beginning of distal third of tail. Anal diameter 25 μ. Tail in ♀, 30 μ, in ♂ 48 μ long. Caudal glands 350, 490, and 560 μ preanal.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4070, Type slide No. 66. Type locality, M-5, Virginia Key.

Representation in samples studied.—M-5, Virginia Key.

Metoncholaimus simplex new species

Plate IX, fig. 18 a; Plate X, fig. 18 b–e

L = 1.95–2.32 mm; w = ♂, 40, ♀, 43–53 μ; esophagus = 330–360 μ; Vu = 63–70%. Head diameter 24–27 μ. Labial papillae small. Labial capsule indistinct. Cephalic capsule relatively (for this family) well developed. Cephalic setae 8–9 μ, subequal. Amphids 9 μ in ♀, 10 μ = 40% of c.b.d. in ♂. Buccal cavity 29–30 × 16–18 μ. Excretory pore 90–100 μ behind anterior end. Demanian organ well developed, uvette 360–430 μ posterior to vulva and 200–280 μ anterior to anus; osmosium *posterior* to uvette; one exit pore, opening on level of anus at dorsal side of body. Moniliform glands of varying grades of distinctness in different specimens. Eggs 107–120 × 40–45 μ. Spicula 120 μ long; no gubernaculum. Twelve to 14 circumanal setae and perhaps two preanal, indistinct pores. Tail conical, 37 μ long in ♂, 40–46 μ in ♀. Anal diameter 26 μ in ♂, 30–32 μ in ♀. In the single male a subterminal dorsal structure was seen on the tail which might represent the opening of two of the three caudal glands. In the female all caudal glands definitely open through the spinneret.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4070, Type slide No. 67. Type locality, M-5, Virginia Key.

Representation in samples studied.—M-5, Virginia Key.

Metoncholaimus scissus new species

Plate IX, fig. 19 a, b; Plate X, fig. 19 c

L = 4.3–4.5 mm; w = ♂, 64, ♀, 72 μ; diameter at base of esophagus ♂, 59, ♀, 69 μ. Esophagus 600–640 μ long. Vu = 65%. Head diameter 36–40 μ. Head with six small labial papillae. The nerves innervating the labial papillae and the points at which they pass through the cuticle are more prominent that the papillae themselves. Cephalic setae 13–15 μ, subequal. Amphid 10–11 μ wide. Buccal cavity 45–48 × 25–27 μ. Longest tooth 35–38 μ, shorter teeth 25–28 μ. Excretory pore 105–125 μ from anterior end. The most conspicuous structures of the Demanian organ are the moniliform glands. These glands are approximately 225 μ long and open to the exterior via 17 μ wide slits (not pores), which are located 157–172 μ preanal. Eggs 115–140 × 55–60 μ, six seen in the uterus of one specimen. Spicules 175–180 μ long. Dorsal wall of cloaca thickened, but not forming a distinct gubernaculum. Tail in ♀, 200–215 μ, in ♂, 220–230 μ long. Male with 5 pairs of circumanal setae, 6–7 pairs of subventral setae and two prominent ventral papillae.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4070, Type slide No. 68. Type locality, M-5, Virginia Key.

Representation in samples studied.—M-5, Virginia Key.

PROONCHOLAIMUS Micoletzky, 1924

Type species.—*Oncholaimus megastoma* Eberth, 1863: 26, pl. 1, figs. 18–20.

This genus is easily recognized by the large bubble-like cells ("Trabekula-Struktur," in German literature) that occur in the pseudocoelomic cavity between the longitudinal chords and the intestine. *P. armiger* Gerlach, 1955, does not possess these cells and is, therefore, of uncertain status. Moreover, since the spicular apparatus turns out to be of prime importance for classification, a number of species known only as females or juveniles have to be considered *species inquirendae*. These are: *P. keiensis*, *P. longisetosus*, and *P. obtusicaudatus*, all Kreis, 1932.

The remaining species form an extremely closely related group and are difficult to separate on the basis of existing information. We agree with Inglis (1962) that the shape of the distal end of the spicula might serve as an important taxonomic character, and use it as such in the differentiation of our species, although we realize that the data in the literature on which some of our conclusions are based probably are insufficient.

List of species of PROONCHOLAIMUS (*and their synonyms*)

P. megastoma (Eberth, 1863) [syn. *Oncholaimus megastoma* Eberth, 1863, *Prooncholaimus mediterraneus* Schuurmans-Stekhoven, 1943, nom. nov. for *P. megastoma* Micoletzky, 1924 nec Eberth, *P. megastoma* var. *neapolitanus* Micoletzky, 1924, *P. neapolitanus* (Micoletzky) Kreis, 1934]; *P. eberthi* (Filipjev, 1918) [Syn. *Metoncholaimus eberthi* Filipjev, 1918]; *P. ornatus* Kreis, 1932; *P. aransas* Chitwood, 1951; *P. banyulensis* Inglis, 1962; *P. hastatus* n. sp.

Our new species, *P. hastatus*, is most closely related to *P. banyulensis*, in that the distal extremity of the spicula possesses a distinct barb which is separated from the subterminal swelling of the spicula by a "handle." The two can be separated as follows:

Handle between subterminal swelling of spicula and barb very short; length of spicula 119–135 μ; tail with long terminal setae .... *P. banyulensis* Inglis, 1962

Handle between subterminal swelling and barb about the same length as the barb itself; length of spicula 90–95 μ; terminal setae very short .... *P. hastatus* n. sp.

Prooncholaimus hastatus new species

Plate XI, fig. 20 a–e

L = 2.10–2.53 mm; w = 80–100 μ; esophagus: ♂, 310–375 μ, ♀, 425 μ; tail: ♂, 120–150 μ, ♀, 175 μ; Vu = 73%. Head diameter 28 μ. Labial capsule well developed, lobed. Cephalic setae 5 μ, subequal. Amphid in ♂, 10–11 μ = 30% of c.b.d., in juvenile ♀ = 7 μ. Buccal cavity 40 × 21 μ, teeth 31 + 23 μ. Excretory pore on level of cephalic setae in adults. Esophagus with posterior pyriform swelling. Spicula 90–95 μ long, funnel-shaped proximally, distally with subterminal swelling, handle and well-developed barb. Gubernaculum 15 μ long, rather stout. There is an indication of a bursa and there are four pairs of adanal setae. More setae can be found anterior to the anus and subventrally along the tail. Anal body diameter 33 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4073, Type slide No. 69. Type locality, M-8, Biscayne Bay.

Representation in samples studied.—M-8, Biscayne Bay.

VISCOSIA de Man, 1880

Type species.—*Oncholaimus viscosus* Bastian, 1865: 136, pl. 11, figs. 131–133.

There is a group of species in this genus in which the cephalic setae are reduced to papillae or even to barely visible shallow pits in the cuticle. This morphological feature, in addition to the fact that in this genus the spicula offer hardly any distinguishing characters, renders classification particularly difficult. Stress has to be laid on size of amphids, shape of buccal cavity and teeth, arrangement of male circumanal organs like papillae and bursa, and shape of tail.

KEY TO SPECIES OF *VISCOSIA* HAVING CEPHALIC PAPILLAE

1\. Buccal cavity divided by strong cuticular ring into two chambers; one side of buccal cavity weakly cuticularized (resembling the condition in *Oncholaimellus*); ♂ amphids 60% of c.b.d.; pharyngeal valve about three times its own length behind buccal cavity .... *V. oncholaimelloides* n. sp.

Buccal cavity not divided by cuticular ring (at most a faint line can be seen); buccal wall well developed all around; amphids not more than 50% of c.b.d. wide; pharyngeal valve not more than its own length behind buccal cavity 2

2\. Male with bursa (or circumanal "alar membrane" *sensu* Chitwood, 1960, who was the first to point out the importance of this character) 3

Male without bursa 4

3\. Male amphids ⅓ of c.b.d.; walls of buccal cavity strongly cuticularized; ♂ tail 6 a.b.d. .... *V. papillata* Chitwood, 1951

Male amphids 40–45% of c.b.d.; walls of buccal cavity normally developed; ♂ tail 3.4–4.6 a.b.d. .... *V. papillatoides* Chitwood, 1960

4\. Male amphids at most 33% of c.b.d. wide .. 5

Male amphids 45–50% of c.b.d. wide 7

5\. Cephalic papillae distinct; long tooth not quite reaching to anterior end of buccal cavity; ♂ with 3 preanal and 3 postanal, small, setose papillae .... *V. keiensis* Kreis, 1932

Cephalic papillae indistinct, long tooth reaching to anterior end of buccal cavity; ♂ with not more than 1 preanal and 1 postanal papilla 6

6\. Male amphids 33% of c.b.d.; 1 preanal papilla; spicula open proximally .... *V. nuda* Kreis, 1932

Male amphids 25% of c.b.d.; 1 preanal and 1 postanal papilla; spicula knobbed .... *V. meridionalis* Kreis, 1932

7\. Cephalic papillae distinct; longest tooth not quite reaching to anterior end of buccal cavity 8

Cephalic papillae indistinct to seemingly absent; longest tooth reaching to anterior end of buccal cavity .... *V. carnleyensis* Kreis, 1932

8\. Male tail cylindrical, 5 a.b.d. long .... *V. nicaraguensis* (Gerlach, 1957) Syn. *V. papillata* var. *nicaraguensis* Gerlach, 1957

Male tail filiform, 8–13 a.b.d. long 9

9\. Male with only traces of circumanal papillae .... *V. glabra* (Bastian, 1865)

Male with 6 pairs of setose circumanal papillae .... *V. macramphida* Chitwood, 1951

Remarks.—The relationship of the two latter species is uncertain because no good figures of the male amphids in *V. glabra* have been published. However, the figures of female heads as given by De Coninck (1944) and Schuurmans-Stekhoven (1950) show the amphids to be ⅓ to ⅖ of the c.b.d. in width, or nearly as wide as the stoma, from which it may be concluded that the male amphids should be just as wide as those of *V. macramphida*. The only good difference we could find between the two species in question seems to be the size and arrangement of the genital papillae in the male. We consider this difference to be of specific value for the time being since figures of the male genital region in *V. glabra*, as given by two such excellent observers as de Man (1890) and Micoletzky (1924a), fail to show anything that can be compared with the distinct setose papillae that Chitwood (1951) and we (see below) found in *V. macramphida*.

Doubtful species are: *V. linstowi* (de Man, 1904), *V. pseudoglabra* Kreis, 1932, *V. dubiosa* Kreis, 1932, *V. fatigans* Filipjev, 1946, all of which are known only as juveniles or females, and *V. pellucida* (Cobb, 1898) nec Allgén, 1959, of which no figures were given. The statement in the key by Wieser (1953), copied from Kreis (1934), to the effect that in *V. linstowi* the excretory pore lies only two stomatal lengths from the anterior end, was based on an erroneous translation of de Man's text.

Viscosia oncholaimelloides new species
Plate XI, fig. 21 a–c

L = 1.95 mm; w = 22 μ; esophagus = 300 μ; tail: ♂, 140 μ. Head diameter 12–13 μ. Lips distinct; cephalic papillae distinct. Buccal cavity separated into two chambers by cuticular ring; anterior portion 5 μ, posterior portion 8–9 μ deep. The large subventral tooth is anchored to the buccal wall from the cuticular ring back to about the middle of the posterior chamber; from there on the buccal wall is weakly developed, resembling the condition in *Oncholaimellus*. The two smaller teeth are normally developed as in other species of *Viscosia* and not reduced as in *Oncholaimellus*. Large subventral tooth 10 μ long. Pharyngeal valve 7–8 μ behind buccal cavity. Scattered papillae in cervical region. Excretory pore just behind nerve ring, 165 μ behind anterior end. Male: spicula dagger-shaped, 17 μ long (1 a.b.d.). There are five pairs of circumanal papillae and one more pair of preanal and postanal papillae, respectively. Scattered papillae on tail.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4073, Type slide No. 70. Type locality, M-8, Biscayne Bay.

Representation in samples studied.—M-8, Biscayne Bay.

Viscosia papillata Chitwood, 1951
Plate XII, fig. 22 a–f

Viscosia papillata Chitwood, 1951: 627, fig. 1, k–n.

L = ♂, 1.18–1.24 mm, ♀, 1.04 mm; w = 39–47 μ; diameter at base of esophagus 39–40 μ. Esophagus 235–250 μ long. Tail 120–125 μ long. Vu = 67%. Head diameter 16 μ. Labial capsule well developed, cephalic papillae distinct. Amphid in male 6 μ, in female 5 μ wide, ⅛ of corresponding body diameter. Buccal cavity 21–22 μ deep, its walls particularly strong. Excretory pore 130–145 μ from anterior end, 15–20 μ behind nerve ring. Excretory cell 30 μ long, 40 μ behind base of esophagus. Spicula 24–25 μ long. Male with circumanal ala containing six pairs of papillae, the posterior pair the most prominent. In addition a pair of preanal setae is present.

Representation in samples studied.—M-7, Everglades National Park; V, Vero Beach.

Geographical distribution.—Copano Bay, Texas (Chitwood, 1951), Chesapeake Bay, Maryland (Timm, 1952).

Viscosia macramphida Chitwood, 1951
Plate XII, fig. 23, a–d

Viscosia macramphida Chitwood, 1951: 627, fig. 1, i–j.

L = 1.5–1.8 mm; w = 40 μ; diameter at base of esophagus 34–39 μ. Esophagus 260–305 μ long. Tail 180–195 μ long. Head diameter 13–16 μ. Labial capsule indistinct, cephalic papillae distinct. Amphid 7 μ wide. Buccal cavity 20–21 μ deep. Excretory pore 30 μ behind nerve ring. Spicula 23–25 μ long. Male with 4–5 pairs of setose papillae associated with circumanal ala as in *V. papillata*.

Representation in samples studied.—M-2, Key Biscayne; M-8, Biscayne Bay.

Geographical distribution.—Aransas Bay, Texas (Chitwood, 1951).

ENCHELIDIIDAE
EURYSTOMININAE
EURYSTOMINA Filipjev, 1918
Type species.—*Eurystoma spectabile* Marion, 1870: 20, 21, pl. E, figs. 1–1b.

This genus has been reviewed by Inglis (1962), who bases his classification almost entirely on the shape of the gubernaculum. While we agree that quite generally in marine nematodes more emphasis should be placed on the structure of the male genital armature, we feel this feature should not dominate to such an extent that other characters are ignored. Thus, Inglis considers *E. americana* Chitwood, 1936, and *E. minutisculae* Chitwood, *sensu* Timm, 1952, to be conspecific because of the similarity in the shape of their gubernacula, although (in Inglis' own words): "Chitwood reports only one row of denticles in the buccal cavity and the absence of ocelli while Timm, in describing his *E. minutisculae*, mentions three rows of denticles and ocelli." Moreover, it could be added, Chitwood shows an almost rectangularly bent spiculum, Timm a semicircular one, Chitwood a short terminal excretory duct, Timm a long one, Chitwood a tail provided with setae, Timm a naked one, etc. On the other hand, Inglis considers *E. americana* Chitwood, 1936, *not* to be conspecific with *E. americana* of Chitwood, 1951, because of a slight difference in shape between the two gubernacula in question, although all other characters in the two descriptions seem to agree.

This approach ignores the possibility of small variations in structural features and overrates differences taken from the illustrations of authors of different reliability.

Our material contained one species which is sufficiently close to *E. minutisculae* as described by Chitwood, 1951, and by Timm, 1952, to identify it with this species. The gubernacula of our male specimens are very similar to that figured by Timm, whereas the spicula more closely resemble Chitwood's figure. The heads of the specimens described by Chitwood, by Timm, and by us are so similar that it would seem unwarranted to refer them to different species, although we feel that Chitwood and not Timm was correct in the interpretation of the excretory gland.

Eurystomina minutisculae Chitwood, 1951
Plate XIII, fig. 24, a, b

Eurystomina minutisculae Chitwood, 1951: 629, fig. 3, d–g.

L = 3.1–3.3 mm; w = 45 μ; diameter at base of esophagus 40–45 μ. Esophagus 660–670 μ long. Tail 114–122 μ (3 a.b.d.) long. Head diameter 20 μ. Cephalic setae 9 + 5 μ. Buccal cavity 17–18 μ long, separated into two chambers by three rows of denticles. Amphid aperture transversely oval, displaced dorsally. Excretory pore on level of amphids; terminal excretory duct short. Ocelli 58 μ from anterior end. Gland-like structures (?) present in anterior neck region. Spicula 63–66 μ long, apophysis of gubernaculum 26–31 μ long. Supplements 70–75 μ and 130–155 μ preanal. Three pairs of preanal setae present, one subventral and longer that the two submedian pairs; cuticle in vicinity of anterior pair thickened.

Representation in samples studied.—M-1, Key Biscayne; M-7, Everglades National Park.

Geographical distribution.—Aransas Bay, Texas (Chitwood, 1951), Chesapeake Bay, Maryland (Timm, 1952), ? San Salvador (Gerlach, 1955: *E.* aff. *minutisculae*).

ENCHELIDIINAE
ILLIUM Cobb, 1920

Type species.—*Illium exile* Cobb, 1920: 261, 262, fig. 45.

In 1920 Cobb described a genus, *Illium*, which has never been found again until now. Our material contains two species of which one seems to be Cobb's *I. exile*, while the other is new. So far no males are known in this genus, for which reason we have to deviate from our rule and base the following two descriptions on females only. The shape of the buccal cavity is very much as in *Symplocostoma* or *Polygastrophora* except that there are no teeth. This might also be the reason for the weaker development of the cuticular rings surrounding the buccal cavity. Our two species are easily distinguished by the dimensions of head, amphids, and buccal cavity, as well as by the position of the amphidial "sensilla" with respect to the buccal cavity.

Illium exile Cobb, 1920
Plate XIII, fig. 25 a–d

Illium exile Cobb, 1920: 261, 262, fig. 45

L = 2.02–2.22 mm; w = 23–30 μ; esophagus = 438–492 μ; nerve ring = 240 μ behind anterior end; tail = 110–122 μ; Vu =60%. Head rounded, with six lips and, perhaps, minute labial papillae. There might be a second circle of cephalic papillae, but all these organs are extremely difficult to see. Buccal cavity consisting of vestibulum and two chambers, separated by two cuticular rings; the two chambers measure 7 μ in length, greatest width is 3 μ. Amphids consisting of opening, about 3 μ wide, pouch, duct and an unusual structure which we call "sensilla." There is no indication of an ocellus as assumed by Cobb. Distance of sensilla from anterior end = 12 μ, c.b.d. = 10 μ. Excretory pore a short distance behind nerve ring. Anal body diameter 17 μ.

Representation in samples studied.—M-8, Biscayne Bay.

Geographical distribution.—Jamaica (Cobb, 1920).

Illium libidinosum new species
Plate XIII, fig. 26, a, b

L = 2.28 mm; w = 70 μ; esophagus = 570 μ; nerve ring = 258 μ behind anterior end; tail = 200 μ; Vu = 60%. Head as in the foregoing species but much larger. Buccal cavity 10 × 5 μ, walls more curved than in the foregoing species. Amphids 5 μ wide, sensilla 15 μ behind anterior end, filled with fragments of a dense material. Excretory pore 25 μ behind nerve ring. Anal body diameter 33 μ.

Holotype specimen.—Female; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4073, Type slide No. 71. Type locality, M-8, Biscayne Bay.

Representation in samples studied.—M-8, Biscayne Bay.

POLYGASTROPHORA de Man, 1922
Type species.—*Polygastrophora attenuata* de Man, 1922a: 131, 132.

In this genus four species each possessing seven esophageal bulbs have been described, to which we shall add a fifth one. Of these five species, *P. tenuicollis* (Allgén, 1951) is best considered a *species inquirenda* as advocated by Chitwood (1960), and not a synonym of *P. heptabulba* as suggested by Wieser (1953). The remaining four species are separated mainly by the arrangement of their cephalic setae, but we are not so sure whether this character will turn out to be as stable as we assume at present.

List and Short Characterization of Valid POLYGASTROPHORA *spp. Possessing Seven Esophageal Bulbs*

P. maior Schulz, 1932: Submedian cephalic setae in both sexes very unequal in length (½ and ⅓ of c.b.d., respectively). Excretory pore 130–150 μ from anterior extremity. Spicula length = ⅘ of tail. Gubernaculum conical.

P. heptabulba Timm, 1952: Submedian cephalic setae reduced in ♂, one head diameter long and subequal in ♀. Excretory pore 44 μ behind anterior end. Spicula length = ½ of tail. Gubernaculum absent.

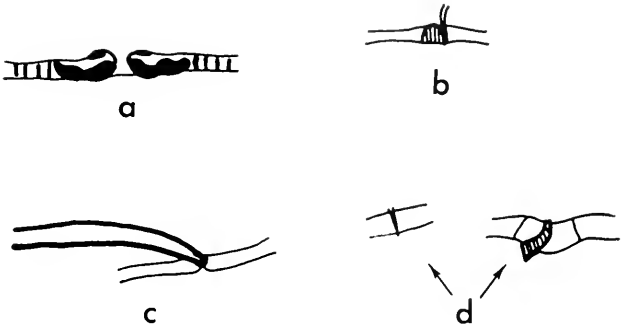
P. septembulba Gerlach, 1954: Submedian cephalic setae subequal (7–6 μ) in ♂, very unequal in ♀ (shorter ones about 2 μ). Excretory pore 41–52 μ from anterior end. Spicula length = ⅔ to ½ of tail. Gubernaculum absent (Gerlach, 1954) or small (Chitwood, 1960).

P. edax n. sp.: Submedian cephalic setae very unequal in length in both sexes (8–7 + 2 μ). Excretory pore 48–50 μ behind anterior end. Spicula length = ½ of tail. Gubernaculum plate-shaped.

Our new species *P. edax* is related to *P. septembulba* from which it can be distinguished by the characters presented in the above list.

Polygastrophora edax new species
Plate XIV, fig. 27, a–c

L = 2.65–2.90 mm; w = 105–110 μ; esophagus = 550–600 μ; tail: ♂, 175 μ, ♀, 165 μ (3.5–4 a.b.d.); Vu = 53%. Head diameter 10 μ. Mouth opening crenate. No labial papillae. Cephalic setae in ♂, 7 + 2 μ, in ♀, 8 + ?, indistinct. Amphids oval, 4.5 μ wide in ♂. Buccal cavity 14 × 7 μ, with two faint cuticular rings at about its middle and one strong basal band that is resolvable into elongated cuticular bodies. Refractory bodies (ocelli?) 18–20 μ behind anterior end. Excretory pore 48–50 μ behind anterior end, ampulla about 72 μ. Male: Spicula 80 μ, knobbed proximally. Gubernaculum faint, plate-shaped. Subventral circumanal setae and along the tail.



2

Figure 2. Types of preanal supplements in the Cyatholaimidae. a—*Pomponema* (type A); b—*Longicyatholaimus* (type B); c—*Paracanthonchus* (type C-1); d—*Paracyatholaimus* (type C-2, two forms).

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4075, Type slide No. 72. Type locality, V, Vero Beach.

Representation in samples studied.—V, Vero Beach.

CYATHOLAIMIDAE

CYATHOLAIMINAE

The genera within the subfamily Cyatholaiminae can be divided into two groups based on the presence or absence, in the male, of preanal supplements. In those genera in which the males possess preanal supplements, a further division is possible utilizing the structure and arrangement of these organs. Wieser (1954) presented a key to the genera of this subfamily, a key that still remains useful, but requiring several additions and emendations.

The genera with preanal supplements can be separated into the following three basic types (A, B, C) of which the last is subdivided into forms with "tuboid" supplements (C-1) and forms with "setose" supplements (C-2) (see Text-fig. 2).

Type A) Supplements large, complicated, consisting of several elements; cuticle between supplements lamellated. Genera included: *Pomponema* Cobb (syn. *Endolaimus* Filipjev), *Nummocephalus* Filipjev (syn. *Haustrifera* Wieser), *Craspodema* Gerlach (syn. *Kraspedonema* Gerlach) and *Anaxonchium* Cobb. Tentatively included is *Dispira* Cobb.

Type B) Supplements cup-shaped, large to minute, with narrow ducts leading to the cups. Genera included: *Longicyatholaimus* Micoletzky, *Xyzzors* Inglis, and *Biarmifer* Wieser.

Type C-1) Supplements tubular, large to medium. Genera included: *Paracanthonchus* Micoletzky, *Acanthonchus* Cobb, *Scuratiella* Ditlevsen and *Parascuratiella* Schuurmans-Stekhoven.

Type C-2) Supplements "setose," small. This type can probably be derived from type C-1, the "setose" papillae described by some authors most likely being minute tubuli with very narrow ducts. Genera included: *Paracyatholaimus* Micoletzky (in Text-fig. 2, represented by two forms), and *Paracyatholaimoides* Gerlach.

Those genera that definitely do not possess preanal supplements are: *Cyatholaimus* Bastian, *Xenocyatholaimus* Gerlach, *Metacyatholaimus* Schuurmans-Stekhoven, and *Phyllolaimus* Murphy.

Other genera are considered doubtful.

There are two main difficulties in classifying genera of this subfamily: first, separation of type C-1 from type C-2, since the difference between small tubuli of the *Paracanthonchus*-type and the so-called "setose papillae" of *Paracyatholaimus* may be only slight; second, deciding whether a species is devoid of supplements or possesses small, cup-shaped papillae of the type B. A case in point is *Longicyatholaimus*, in which species with and species without supplements have been described (see below).

The genus *Choniolaimus*, referred to this subfamily by many authors and included in his key by Wieser (1954), will have to be transferred to the Choanolaiminae since the redescription of the type species, *Ch. papillatus* Ditlevsen, by Gerlach (1964), and the description of *Ch. panicus* Gerlach, 1957, have made it clear that in this genus the buccal cavity is of a shape quite different from other cyatholaimids. Consequently, the species referred to *Choniolaimus* on the strength of their preanal supplements but with a typical cyatholaimid buccal cavity, i.e., *Ch. macrodentatus* Wieser, 1959, and *Ch. wieseri* Inglis, 1963, are to be transferred to *Longicyatholaimus* (see below, p. 265). *Cyatholaimus tautraensis* Allgén, referred to *Choniolaimus* by Wieser (1954) is better placed with *Nummocephalus* (see Gerlach, 1958b).

POMPONEMA Cobb, 1917

Type species.—*Pomponema mirabile* Cobb, 1917: 118, fig. 3.

This genus is characterized by the strong development of the buccal cavity, in which the vestibular ribs seem to function as particularly mobile clasping organs; the dorsal tooth is powerful and opposed either by two strong subventral teeth or by a great number of denticles. Further characteristics are the heterogeneous cuticular ornamentation, the lateral differentiation of the latter, and the peculiar male supplements. Closely related to *Pomponema* is the genus *Nummocephalus* Filipjev (syn. *Haustrifera* Wieser) which has less well developed vestibular ribs and teeth, and in which the cuticular markings are more uniformly dot-like. *Longicyatholaimus lineatus* Gerlach, 1952, which was referred to *Pomponema* by Wieser (1959), is perhaps better placed with *Nummocephalus*.

KEY TO SPECIES OF *POMPONEMA*

1. Lateral differentiation beginning on level with buccal cavity; in the cervical region the 2 longitudinal rows are half the c.b.d. apart ..... *P. multipapillatum* (Filipjev, 1922)
Lateral differentiation beginning approximately at end of esophagus; 2–4 longitudinal rows which are far less apart than half the c.b.d. 2
2. Cephalic setae in two circles, 4 + 6 ..... *P. segregatum* Wieser, 1959
Cephalic setae in one circle 3
3. Submedian pairs of cephalic setae very unequal in length. Dorsal tooth opposed by groups or rows of smaller teeth or denticles 4
Submedian pairs of cephalic setae subequal. Dorsal tooth opposed by two subventral teeth 5
4. Male amphids 6–6.5 turns, 50% of c.b.d. wide ..... *P. stomachor* Wieser, 1954
Male amphids 4.5 turns, 35% of c.b.d. wide ..... *P. polydonta* Murphy, 1963
5. Male amphids 6–6.5 turns, 90% of c.b.d. wide ..... *P. mirabile* Cobb, 1917
Male amphids 4.5 turns, 65% of c.b.d. wide ..... *P. tesselatum* n. sp.

Pomponema tesselatum new species

Plate XIV, fig. 28, a–d

L = 1.53 mm; w = 42 μ; esophagus = 360 μ. Head diameter 25 μ. Labial setae 14 μ. Cephalic setae 16 + 13 μ. Buccal cavity spacious, vestibulum protrusible, its ribs giving the appearance of prehensile clasping organs which are linked by joints to the buccal wall; dorsal tooth large, hollow, opposed by two similar though smaller subventral teeth. Amphids 19 μ = 68% of c.b.d. wide, describing 4.5 turns. Cuticular ornamentation complex and heterogeneous; in cervical region each annule at high focus with slit-like markings, at low focus of tesselated appearance; what are seen as dots in lateral view are actually short columns between the outer and the inner layer of the cuticle; these columns become rather thin from the mid-cervical region on, and the dots, consequently, smaller. There are two rows of dots per annule. A lateral differentiation in the form of four longitudinal rows of larger and more widely spaced dots begins at about the end of the esophagus. Many pores are arranged in more or less regular longitudinal rows all along the body. Spicula 45 μ, gubernaculum 36 μ, consisting of two portions, the distal one with lateral projections. There are 15 preanal supplements of characteristic shape. Between the supplements the cuticle gives a lamellated appearance. One preanal seta and many setae on the tail in four longitudinal rows. Tail 132 μ, a.b.d. 36 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4068, Type slide No. 73. Type locality, M-3, Key Biscayne.

Representation in samples studied.—M-3, Key Biscayne.

LONGICYATHOLAIMUS Micoletzky, 1924

Type species.—*Cyatholaimus longicaudatus* de Man, 1878: 111, 112, pl. 10, fig. 16, a–c.

This genus is characterized by the spicular apparatus, which is of a general shape found in some species of *Paracanthonchus* and *Paracyatholaimus*, in combination with the fact that the preanal supplements are never setose or tubular. In the type species, *L. longicaudatus* (de Man), indistinct papillae of type B (see above, p. 263 were apparently seen by de Man (1878) and by Kreis (1928) but not by Schuurmans-Stekhoven (1943). Since then other species have been described in which supplements were not mentioned. It would simplify matters if one were permitted to assume that in all these cases the small cup-shaped supplements were so indistinct as to have been overlooked, but the possibility that there exist species truly devoid of supplements must be considered. In such cases differentiation from other genera without supplements, particularly from *Cyatholaimus*, would have to be based on the shape of the spicular apparatus and, to a lesser extent, on the shape of the tail.

Further characteristics mentioned by Micoletzky are the lateral differentiation of the cuticular ornamentation and the long, filiform tail. However, species with fairly short, though always slender, tails have been described, which in other respects fit the generic diagnosis.

Classification of the species is rendered difficult by the uncertainty as to how the reputed absence of preanal supplements is to be judged. For the present, we shall accept this feature at its face value. This provides for an immediate separation of the species into two groups, Group A containing species described with supplements, and Group B, containing species in which no supplements were reported. The species contained within these groups are as follows:

Longicyatholaimus species group A: *L. longicaudatus* (de Man, 1878); *L. minor* (Cobb, 1898); *L. effilatus* (Schuurmans-Stekhoven, 1946); *L. stekhoveni* Wieser, 1954 (syn. *L. effilatus* Schuurmans-Stekhoven, 1950 nec 1946); *L. quadriseta* Wieser, 1954 nec 1959;[1] ***L. macrodentatus*** (Wieser, 1959) **new combination** (syn. *Choniolaimus macrodentatus*) and ***L. wieseri*** (Inglis, 1963) **new combination** (syn. *Choniolaimus wieseri*).

Longicyatholaimus species group B: *L. trichurus* (Cobb, 1898); *L. zosterae* Allgén, 1933; *L. choanolaimoides* (Schuurmans-Stekhoven, 1942); *L. continus* Filipjev, 1946; *L. dubius* Filipjev, 1946; *L. trichocauda* Gerlach, 1955, and *L. dayi* Inglis, 1963.

Species of doubtful status are: *L. heterurus* (Cobb, 1898); *L. tenuicaudatus* (Saveljev, 1912) and *L. filicaudatus* Schuurmans-Stekhoven, 1950.

As the species we found belongs to group A, a key to the species of this group is provided.

---

[1] Note: The species described as *L. quadriseta* Wieser by Wieser, 1959, is equipped with setose and not cup-shaped supplements. Since there are other differences from the type (smaller amphids, shape of gubernaculum) we consider *L. quadriseta* Wieser *sensu* Wieser, 1959, to be a different species and refer it to *Paracyatholaimus* under the name ***Paracyatholaimus pugettensis* new name** and **new combination.**

KEY TO SPECIES OF *LONGICYATHOLAIMUS* GROUP A

1. Lateral differentiation of cuticle in 4 longitudinal rows .... *L. minor* (Cobb, 1898)
   Lateral differentiation of cuticle irregular . 2
2. Posterior portion of tail filiform, much longer than conical portion .... *L. longicaudatus* (de Man, 1878)
   Posterior portion of tail cylindrical, not longer than conical portion 3
3. Gubernaculum distally truncate or notched; 3 preanal supplements .... *L. effilatus* (Schuurmans-Stekhoven, 1946) and *L. stekhoveni* Wieser, 1954
   Gubernaculum distally with well developed teeth or processes; 6–7 preanal supplements 4
4. Male amphids about 60% of c.b.d. wide; gubernaculum distally with three digitiform processes of rather unequal shape .... *L. wieseri* (Inglis, 1963) n. comb.
   Male amphids 30–40% of c.b.d. wide; gubernaculum distally with 3–4 equal-shaped teeth 5
5. Cephalic setae digitiform, 8–10 + 5–6 μ long. Preanal supplements 5 + 2, the 5 anterior ones regularly spaced; gubernaculum with 3 distal teeth .... *L. macrodentatus* (Wieser, 1959) n. comb.
   Cephalic setae conical, slender, subequal, 12 + 13 μ long; preanal supplements 4 + 2, the first one almost three times as far from the 2nd as the latter from the 3rd; gubernaculum with 4 distal teeth .... *L. annae n. sp.*

Longicyatholaimus annae new species
Plate XV, fig. 29, a–c

L = 1.96 mm; w = 70 μ; esophagus = 300 μ. Head diameter 33 μ. Labial papillae setose, stout, 4.5 μ long. Cephalic setae 13 + 9 μ. Buccal cavity deep, with one large dorsal tooth, two small subventral teeth and cuticular ridges. Amphids in ♂ 13 μ = 31% of c.b.d. wide, 4.5 turns. A group of dorsolateral cervical setae a short distance behind amphids. Cuticle with annules and homogeneous rows of dots; no lateral differentiation except on tail; there is one row of dots per annule in the anterior cervical region, but two rows can be found on the remainder of the body. Many pores arranged in more or less longitudinal rows. Spicula 70 μ, somewhat S-shaped, with velum in distal half, knobbed proximally. Gubernaculum 64 μ, stout, distally with 4 equal-sized teeth. There are 6 small but distinct cup-shaped preanal supplements, the anteriormost one at a distance of 210–230 μ preanally; the distance between the first and the second papillae is about as great as that between the latter and the anus. The two posteriormost papillae are more closely spaced than all the others. Tail 420 μ, a.b.d. 60 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4068, Type slide No. 74. Type locality, M-3, Key Biscayne.

Representation in samples studied.—M-3, Key Biscayne.

Remarks.—This species is named after Mrs. Ann Hopper, friendly hostess to wandering nematologists.

XYZZORS Inglis, 1963
Type species.—*Xyzzors fitzgeraldae* Inglis, 1963: 544–546, figs. 25–29.

According to Inglis (1963) *Xyzzors* is characterized by irregular lateral differentiation of the cuticle, cup-shaped preanal papillae, large and well-developed buccal armature and some structural peculiarities of the spicular apparatus. However, none of these characters separates *Xyzzors* unequivocally from *Longicyatholaimus*. The cuticle and the supplements are of the same type as found in the latter genus, the gubernaculum is somewhat larger than in most species of *Longicyatholaimus* but, e.g., *L. dubius* Filipjev, 1946, has a gubernaculum of exactly the same shape. Moreover, the figures given by Inglis do not justify his statement that "the spicules are much more elaborate than is usual in species of the Cyatholaimidae." The two features which could perhaps serve as characters distinguishing *Xyzzors* from *Longicyatholaimus* are the nearly conical tail and the buccal armature which indeed seems to be somewhat more elaborate than observed in the latter genus.

In our new species the spicular apparatus is simpler than in *X. fitzgeraldae* Inglis, and the proximal ends of the spicula are not doubled. There are 3 cup-like supplements followed posteriorly by two indistinct ducts, whereas Inglis reports 6 cup-like supplements. The amphids describe 4 turns in our species as against 6.75 in *X. fitzgeraldae*.

Xyzzors inglisi new species
Plate XV, fig. 30, a–c

L = 1.25 mm; w = 54 μ; esophagus = 240 μ. Head diameter 28 μ. Labial papillae stout. Cephalic setae 12 + 10 μ. Buccal cavity deep, with one large dorsal tooth, 2 pairs of subventral teeth and one conspicuous ridge that surrounds the ventral half of the buccal cavity. Amphids 16 μ = 48% of c.b.d. wide, 4 turns. Cuticle as in the foregoing species. Spicula 52 μ, with velum; proximally the inner edges are more strongly cuticularized, distally the outer edges. Gubernaculum 38 μ, distally expanded and dentate. There are 3 preanal supplements that consist of a cup-shaped portion (protruded in Fig. 30, b, c) and a duct leading to the latter. The distances are: 25 μ from anus to posterior papilla, 45 μ from this to the next one, 30 μ to the anteriormost one. Between the last papilla and the anus, two minute, indistinct ducts can be discerned. Tail conical, 108 μ, a.b.d. 44 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4075, Type slide No. 75. Type locality, V, Vero Beach.

Representation in samples studied.—V, Vero Beach.

PARACANTHONCHUS Micoletzky, 1924

Type species.—*Cyatholaimus caecus* Bastian *sensu* de Man, 1889b: 204–207, pl. 7, fig. 10, a–g.

The species of this genus were grouped by Wieser (1954) who used the shape of the gubernaculum as the main distinguishing feature. The shapes of gubernacula representing species belonging to groups A, B, and C, respectively, in Wieser's key, are shown in Text-figure 3. There are, however, species which do not fit readily into these three categories, for example, those that have a large gubernaculum subterminally dilated and tapering towards a pointed or spoon-shaped distal tip. This type of gubernaculum represents a transition between groups A or B and C, and is also shown in Text-figure 3. Species with such a gubernaculum are mainly *P. ruens* Wieser, 1954, and the new species to be described below, but *P. angulatus* (Schuurmans-Stekhoven, 1950), *P. batidus* Gerlach, 1957, and *P. mutatus* Wieser, 1959, come rather close.

P. platypus n. sp. is separated from its closest relative, *P. ruens* Wieser, 1954, mainly by the number, size, and arrangement of the preanal tubuli, and by the size of the spicular apparatus.

Paracanthonchus platypus new species
Plate XVI, fig. 31, a–c

L = 1.18–132 mm; w = 44–48 μ; esophagus 190 μ; tail: ♂, 135 μ, ♀, 105 μ; Vu = 48%. Head diameter 21–23 μ. Labial papillae conical. Cephalic setae 4 + 5 μ. A short cephalic capsule present. Buccal cavity with well-developed vestibular ribs and with medium-sized triangular tooth. Amphids in ♂, 11 μ = 40% of c.b.d., in ♀, 9 μ = 32% of c.b.d. wide. Excretory pore 27–32 μ behind anterior end. Ocelli 47–50 μ behind anterior end, with fibrils running from the pigment spot forward and backward, a bit reminiscent of the structures described for *Acanthonchus rostratus* by Murphy (1963), but a proper lens was not seen. Cuticular ornamentation homogeneous. Spicula 36 μ, gubernaculum 35 μ, spoon-shaped, with subterminal dilation and tapering towards the tip; there is a lateral projection. Preanally there are 4 tubuli, 22–23 μ long, one large spine (Fig. 31, c), and two subventral rows of slender setae. On the tail there are short setae and a characteristic ventral pair of long setae. Anal body diameter 43 μ.

Holotype specimen.—Male; Canadian Na-

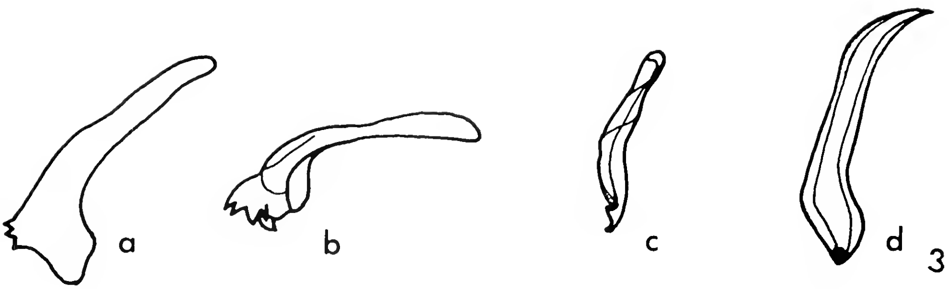


Figure 3. Types of gubernacula in *Paracanthonchus*. a—*P. strandensis* (after Schulz, 1932); b—*P. caecus* (after Timm, 1952); c—*P. cochlearis* (after Gerlach, 1957); d—*P. platypus* n. sp.

tional Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4073, Type slide No. 76. Type locality, M-8, Biscayne Bay.

Representation in samples studied.—M-8, Biscayne Bay.

PARACYATHOLAIMUS Micoletzky, 1921

Type species.—*Cyatholaimus dubiosus* Bütschli, 1874: 284, pl. 7, fig. 31, a, b.

This genus is characterized by the simple gubernaculum which is supposed to hardly expand distally, and in the diagnosis by Micoletzky (1924b) was described as being "ohne Dornen," and by the male supplements which Micoletzky called "Borstenpapillen." These supplements probably are not true setae but represent ducts of the *Paracanthonchus*-type with the lumina so narrow as to give the impression of setae.

Gerlach (1955) described a species, *P. paucipapillatus*, in which the gubernaculum expands distally to form a plate covered with rasp-like denticles. The supplements consist of strongly protruding conical papillae with cuticularized, narrow ducts. The first character links Gerlach's species to *Paracanthonchus*, the second character sets it apart from all other species of *Paracanthonchus* and *Paracyatholaimus* with the exception, perhaps, of *P. digitatus* Gerlach, 1957, in which similar supplements have been described and the gubernaculum is also rather strongly dentate. Our material contained representatives of what at first we held to be *P. paucipapillatus*. However, on closer examination we noted the following differences: 1) distal end of gubernaculum with distinct teeth, numbering from 4–8, rather than with a rasp-like field of denticles, 2) ducts of supplements more elaborate, and 3) buccal cavity with one large dorsal tooth and three small subventral teeth, whereas Gerlach speaks only of one dorsal tooth.

We consider these differences important enough to establish a new species, *P. pesavis* n. sp., named after the appearance of the distal end of the gubernaculum which resembles a spread bird's foot. This species and the two described by Gerlach mentioned above form a rather distinct group within the two genera *Paracanthonchus* and *Paracyatholaimus*.

Paracyatholaimus pesavis new species

Plate XVI, fig. 32, a–e

L = 1.08–1.17 mm; w = 35–44 μ; esophagus = 195–200 μ. Head diameter 18–20 μ. Labial papillae distinct. Cephalic setae 7–8 + 5–6 μ. Short cephalic capsule. Buccal cavity with one large pointed dorsal tooth and three small subventral teeth. Amphids 11 μ = 44% of c.b.d. wide, approximately 5 turns. Cuticular ornamentation with slight lateral differentiation in cervical and anal region. Spicula 29–31 μ, with velum. Gubernaculum 22–23 μ, expanding distally to a plate which in one specimen carried 8, in another 4 small teeth (Pl. XVI, fig. 32, c, d). There are two large conical papillae at a distance of 25–28 and 50–53 μ, respectively, from the anus. The papillae are penetrated by cuticularized ducts which show some distal elaborations; their openings are posteriorly directed. There is a very faint third papilla (10–13 μ in front of the anus) which might actually consist of two closely spaced minute tubuli as found in other species of *Paracyatholaimus.* Tail 80–100 μ long, narrowing abruptly in distal third; a.b.d. 35–40 μ. Spinneret 6–7 μ long.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4071, Type slide No. 77. Type locality, M-6, Everglades National Park.

Representation in samples studied.—M-6, Everglades National Park; V, Vero Beach.

Remarks.—The closely related species, *P. paucipapillatus,* was originally described from the Pacific coast of San Salvador, and later from the Congo estuary, and from Brazil (Gerlach, 1957a, b, c). The possibility that the Atlantic specimens are actually representatives of our new species is intriguing but remains to be proven.

HALICHOANOLAIMUS de Man, 1888

Type species.—*Spiliphera robusta* Bastian, 1865: 166, pl. 13, figs. 226, 227.

Our material contained two closely allied species which appear to represent *H. quattuordecimpapillatus* Chitwood, 1951, and *H. duodecimpapillatus* Timm, 1952. As neither author specifically stated the tail length for their respective species, it was necessary to make use of the de Man *c* value in identifying the two populations. The two species can be separated on the basis of the tail length as well as the shape of the spicules and gubernaculum. As the heads of both species are very similar, only one has been figured, *H. duodecimpapillatus.*

Halichoanolaimus quattuordecimpapillatus Chitwood 1951

Plate XVII, fig. 33, a–c

Halichoanolaimus quattuordecimpapillatus Chitwood, 1951: 639, fig. 7 c.

L = ♂, 1.7–2.0, ♀, 2.0–2.4 mm; w = ♂, 60–65, ♀, 70–90 μ; diameter at base of esophagus, ♂, 55–70, ♀, 70–83 μ. Vu = 43–45%. Esophagus in ♂, 270–300 μ, in ♀, 310–340 μ long. Excretory pore in ♂, 150–155 μ, in ♀, 162–180 μ from anterior end. Head 35–40 μ wide, with an internal circle of 6 labial papillae and an external circle of 10 cephalic papillae of which the laterodorsal and lateroventral pairs are setose. Amphid 15 μ wide, 16–19 μ from anterior end, spiral with 3.75–4 turns. Buccal cavity typical, containing 3 posterior apophyses, the anterior margins of which bear comb-like ribs and a medial, retrorse tooth. Spicules 88–90 μ long, weakly cephalated proximally and narrowing gradually distally. Gubernaculum paired, 40–45 μ long, with characteristic proximal cephalization (bottle-cap-opener). Male with 11–14 papilloid supplements. Tail initially truncate-conoid, then filiform, in ♂, 265–300 μ long, in ♀, 315–370 μ long. Spinneret 10–12 μ long. The male has a postanal ventral depression just prior to the filiform portion of the tail. The de Man *c* value for both sexes is 5.8–6.6.

Representation in samples studied.—M-2, Key Biscayne, Everglades National Park.

Geographical distribution.—Aransas Bay, Texas (Chitwood, 1951), Congo estuary, West Africa (Gerlach, 1957b), Cananeia, Brazil (Gerlach, 1957c).

Remarks.—An entire specimen of *Spilophorella paradoxa* was found within the gut of one female.

Halichoanolaimus duodecimpapillatus Timm, 1952

Plate XVII, fig. 34, a–d

Halichoanolaimus duodecimpapillatus Timm, 1952: 26–28, pl. 5, fig. 44.

L = ♂, 1.9–2.2, ♀, 2.1–2.5 mm; w = ♂,

68–72, ♀, 80–97 μ; diameter at base of esophagus, ♂, 62 μ, ♀, 65–87 μ. Vu = 40–47%. Esophagus in ♂, 250–280 μ, in ♀, 270–310 μ. Excretory pore 130–147 μ from anterior end. Head, cephalic sense organs and buccal cavity as described above for *H. quattuordecimpapillatus.* Spicules 90–100 μ long, proximal cephalization, broad and flat. Distally the spicules narrow more abruptly than in the foregoing species. Gubernaculum about 50 μ long, of characteristic shape. Male with 11–13 papilliod supplements. Tail elongate-conoid, then filiform, in ♂, 180–190 μ long, in ♀, 165–230 μ long. Spinneret 9–10 μ long. The de Man *c* value for the ♂ is 10.1–11.3 and for the ♀, 9.1–14.3.

Representation in samples studied.—V, Vero Beach.

Geographical distribution.—Chesapeake Bay, Maryland (Timm, 1952).

NEOTONCHINAE

NEOTONCHUS Cobb, 1933

Type species. *Neotonchus punctatus* Cobb, 1933: 87.

Comesa Gerlach, 1956: 94.

Neotonchus lutosus Wieser and Hopper, 1966

Plate XXVI, fig. 56, a–d

L = 0.87–1.02 mm; w = 42 μ; esophagus = 120 μ. Head diameter 20 μ. One circle of six minute labial papillae, one circle of six short cephalic setae, 3 μ long, and four submedian setae of about equal length. Scattered short cervical setae. Amphids 10 μ = 50% of c.b.d. wide, 4–4.2 turns. Cuticle with homogeneous punctation, the lateral dots somewhat larger and more widely spaced than the submedian ones. Buccal cavity 14 μ long, with one large hollow dorsal tooth and two small subventral teeth. Esophageal bulb pyriform, 30 × 25 μ, with two weak interruptions. Excretory pore 40 μ from anterior end. Spicula of shape typical for genus, bent at beginning of distal third, 29 μ long. Gubernaculum plate-shaped, dilated distally. One stiff preanal seta and 20 large, complicated supplements. Tail 75 μ long, a.b.d. 28 μ.

Representation in samples studied.—M-4, Rickenbacker Causeway.

Geographical distribution.—Restricted to above locality.

DESMODORIDAE

The Desmodoridae was first subdivided by Chitwood (1936). The original groupings, however, do not appear to be entirely satisfactory, especially with regard to their generic composition and systematic position. Uncertainties regarding the shape of amphids in the Stilbonematinae present further difficulties. A key position within the family is assumed by *Spirinia* (syn. *Spirina*) which not only links the Metachromadorinae with the Desmodorinae—perhaps via *Chromaspirina* (see Gerlach, 1963)—but also shows close affinities to the Microlaimidae and the Linhomoeidae (Wieser, 1954; Timm, 1962). The discussion of many genera belonging to the Desmodoridae by Gerlach (1951b, 1963b) has been a valuable aid in the classification of the family. The characters of each subfamily are briefly outlined below:

Brief Characterization of Subfamilies of Desmodoridae

A) Metachromadorinae (Chitwood, 1936): Cuticle always finely striated (striation sometimes so indistinct as to impart a smooth appearance to the cuticle); head not sharply set off from striation, non-rigid; striation always surrounding amphids; cuticle not tiled; esophageal bulb always present, either round or elongated; buccal cavity typically with well-developed armature, except in *Spirinia* where there are only minute teeth. (For further classification, see below.)

B) Richtersiinae Cobb, 1933: Cuticle striated, with many longitudinal rows of spines or hooks; head non-rigid; buccal cavity small or wide, unarmed; esophagus cylindrical, without bulb. With the genera: *Richtersia* Steiner, 1916 (syn. *Richtersiella* Kreis, 1929), and *Pteronium* Cobb, 1933.

C) Desmodorinae Micoletzky, 1924: Cuticle heavily annulated; head rigid, sharply set off from annulation; amphids not surrounded by annulation (exceptions are *Paradesmodora* and *Metadesmodora* in which the heavy annulation serves as distinguishing characters from the Metachromadorinae); amphids loop-shaped or spiral; cuticle not tiled (except, occasionally, on the head); esophageal bulb round or elongated; buccal cavity always armed with distinct teeth. (For further classification, see below.)

D) Stilbonematinae Chitwood, 1936: Cuticle striated or annulated, not tiled or longitudinally broken; buccal cavity shallow-conical or absent, unarmed or with minute teeth; head always well defined, amphids wholly outside striation, spiral-shaped, but apparently sometimes sunk into the cuticle so that only the slit-like opening is visible; esophageal bulb round to pyriform. With the genera: *Eubostrichus* Greeff, 1869 (syn. *Catanema* Cobb, 1920, ?*Laxus* Cobb, 1893), *Laxonema* Cobb, 1920, *Leptonemella* Cobb, 1920, *Stilbonema* Cobb, 1920, *Robbea* Gerlach, 1956, and *Squanema* Gerlach, 1963.

E) Ceramonematinae Cobb, 1933[1]: Cuticle heavily annulated, tiled or longitudinally broken by spined alae; head well set off from annulation; buccal cavity minute or absent, unarmed; amphids obscurely spiral to shepherd's crook; esophagus. With the genera: *Ceramonema* Cobb, 1920, *Xenella* Cobb, 1920, *Dasynemella* Cobb, 1933 (syn. *Dasynema* Cobb, 1920), *Pristionema* Cobb, 1933, *Pselionema* Cobb, 1933, *Dasynemoides* Chitwood, 1936, *Metadasynemella* de Coninck, 1942, and *Pterygonema* Gerlach, 1954.

F) Monoposthiinae Filipjev, 1934: Cuticle coarsely annulated, broken longitudinally by alae; head well set off from annulation, rigid; amphids circular, surrounded by annulation; buccal cavity well armed; esophageal bulb barrel-shaped. With the genera: *Monoposthia* de Man, 1889, *Nudora* Cobb, 1920, *Rhinema*, Cobb, 1920, and *Monoposthioides* Hopper, 1963.

KEY TO GENERA OF METACHROMADORINAE
(Based on classification of Gerlach, 1951)

1. Male supplements heavily cuticularized, large and tubular 2
   Male supplements indistinct or conical or consisting of narrow ducts, not large and tubular; only in *M. vivipara* and *M. quadribulba* are the supplements heavily cuticularized but not tubular 4
2. Supplements strongly S-shaped, heavily cuticularized 3
   Supplements faintly S-shaped, cuticularization light .... *Onyx* Cobb, 1891
3. Cephalic and subcephalic setae present .... *Sigmophora* Cobb, 1933
   Cephalic setae only present .... *Polysigma* Cobb, 1920
4. Teeth absent or minute .... *Spirinia* Gerlach, 1963
   Teeth well developed 5
5. Esophageal bulb weakly developed, round to pyriform; cuticular lining faint .... *Chromaspirina* Filipjev, 1918
   Esophageal bulb well developed, usually elongate, sometimes "barrel-shaped," rarely clavate and indistinctly set off from esophagus; cuticular lining usually distinct .... *Metachromadora* Filipjev, 1918

Pseudometachromadora Timm, 1952, is a genus of doubtful position. The esophagus is barely enlarged posteriorly, the cuticular striation is all but absent, the amphids are situated near the lips and the buccal cavity is cylindrical and strongly armed.

SPIRINIA Gerlach, 1963

Type species.—*Spira parasitifera* Bastian, 1865: 159, 160, pl. 13, figs. 201–203.

Spira Bastian, 1865, nec Brown, 1844, and *Spirina* Filipjev, 1918, nec Kayser, 1889.

Our material contained two species, one of which undoubtedly is *S. parasitifera* (Bastian, 1865). A redescription of this cosmopolitan species with discussion of its synonymy was recently given by Gerlach (1963b). Our second species is closely re-

---

[1] This subfamily may not belong to the Desmodoridae. Gerlach (1957) considers it related to the Axonolaimidae and the Halaphanolaimidae.

lated to *S. striaticaudata* (Timm, 1962) from which it can be distinguished by the hook-shaped proximal end of the spicula and the presence of small but distinct teeth in the conical buccal cavity. These two species are separated from all other members of the genus by the flagellate tail which in both sexes is much more distinctly and coarsely striated than the rest of the body. This is such a conspicuous and characteristic feature that we feel justified in establishing a new subgenus on it.

Spirinia (*S.*) *parasitifera* (Gerlach, 1963)

Plate XVII, fig. 35, a–e

Spirinia (*S.*) *parasitifera* (Bastian, 1865) Gerlach, 1963b: 67.

Spira parasitifera Bastian, 1865: 159–160, pl. 13, figs. 201–203; *Spirina parasitifera* auct.; *Spilophora oxycephala* Bütschli, 1874; *Spirina nidrosiensis* Allgén, 1933; *S. zosterae* Filipjev, 1918; and *S. rouvillei* Schuurmans-Stekhoven, 1950.

L = 1.57 mm; w = 55 μ; esophagus = 140 μ; nerve ring 77 μ from anterior end; tail = 140–155 μ. Head diameter 22 μ; cephalic setae 5 μ, on level of amphids. Cervical setae beginning at short distance behind amphids, rather scattered. Amphids 6 μ wide. Buccal cavity small, with 3 minute teeth. Esophageal bulb 40 × 36 μ. Spicula 50 μ, knobbed proximally, with velum, tail conical, a.b.d. 24–28 μ.

Representation in samples studied.—M-4, Rickenbacker Causeway, V, Vero Beach.

Geographical distribution.—Baltic, North Sea, North Atlantic, Black Sea, Mediterranean, Barents Sea, Indian Ocean (Maldives).

Spirinia (*Perspiria*) new subgenus

Type species.—*Spirinia* (*Perspiria*) *hamata* new species.

Differential diagnosis.—*Perspiria* n. subg. is distinguished from *Spirinia sensu stricto* by the more prominently striated and flagellate tail. In *Spirinia sensu stricto* the tail is conoid and the striations are fine—no coarser than those on the remainder of the body.

In addition to the new species described below, *Spirinia striaticaudata* (Timm, 1962) (syn. *Spirina striaticaudata*) is also included in the new subgenus.

Key to Species of *Spirinia* (*Perspiria*)

1. Stoma without teeth; proximal end of spicula knobbed, rounded .... *S.* (*P.*) *striaticaudata* (Timm, 1962)
   Stoma with minute teeth; proximal end of spicula hook-shaped .... *S.* (*P.*) *hamata* new species

Spirinia (*Perspiria*) *hamata* new species

Plate XVIII, fig. 36, a–c

L = 2.04 mm; esophagus = 160 μ. Head diameter 16–21 μ. Cephalic setae 4–5 μ. Very few short, scattered cervical setae. Amphids 5–6 μ. Buccal cavity small, with three minute teeth. Esophageal bulb 45 × 36 μ. Excretory pore between bulb and nerve ring. Cuticular striation distinct but weak. Spicula 37–43 μ, gubernaculum 16 μ. Tail 230–340 μ, from beginning of second fifth on coarsely striated, tip unstriated. Anal body diameter 32–43 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4068, Type slide No. 78. Type locality, M-3, Key Biscayne.

Representation in samples studied.—M-3, Key Biscayne.

CHROMASPIRINA Filipjev, 1918

Type species.—*Chromaspirina pontica* Filipjev, 1918: 229, 230–234, pl. 7, fig. 45, a–c.

Mesodorus Cobb, 1920: 325.

As previously suggested by Gerlach (1963b), this genus probably links the Metachromadorinae with the Desmodorinae. We do not agree, however, with Gerlach that the intermediate position of this genus is sufficient justification for merging the two subfamilies together. The position of *Chromaspirina* becomes less problematical if some of Gerlach's new combinations are returned to their former status. Thus we cannot accept the transfer of *Desmodora inflexa* Wieser, 1954, and *D. dimorpha* Hopper, 1961, to *Chromaspirina*. Both species are characterized by heavy annulation and a rigid head with the amphids situated outside the annulation (although in the latter species, admittedly, the position of the amphids with respect to the cuticular annulation is a bit doubtful) and thus most likely represent true members of *Desmodora*. The same would seem to apply to *D. rabosa* Gerlach, 1956, which was also tranferred to *Chromaspirina* by Gerlach. However, this species is known only from one female and thus remains doubtful.

Other doubtful species are *C. paucispira* Schuurmans-Stekhoven, 1950 (♀ only) and *C. robusta* Wieser, 1954 (juv. only). Two more species are known only as females, i.e., *C. crinita* Gerlach, 1952, and *C. pellita* Gerlach, 1954, but in their cases the pilosity of either head (*crinita*) or body (*pellita*) is probably sufficient to recognize them as good species. The following are regarded as good species of *Chromaspirina*: *C. cylindricollis* (Cobb, 1920) (syn. *Mesodorus cylindricollis*), *C. indica* Gerlach, 1963, *C. madagascariensis* Gerlach, 1953, *C. parapontica* Luc and De Coninck, 1959, *C. pontica* Filipjev, 1918, and *C. thieryi* De Coninck, 1943.

The conspecificity of *C. pontica* Filipjev *sensu* Gerlach, 1951, with Filipjev's species is questionable, as, in Gerlach's specimens, the cephalic setae are 9–11 μ long (as against 5 μ), the amphids are relatively larger, and the gubernaculum is shorter and of a somewhat different shape.

From the above mentioned species, *C. inaurita* n. sp., is separated by the indistinct cephalic papillae, the large and oval amphids which are about as long as the head is wide, the shape of the gubernaculum, and the presence of ventral papillae on the tail.

Chromaspirina inaurita new species
Plate XVIII, fig. 36, a–c

L = 1.18–1.35 mm; w = 29–35 μ; esophagus = 105–115 μ; tail: ♂, 90–95 μ, ♀, 90 μ; Vu = 49%. Eggs 30–33 × 60–70 μ. Head diameter 14 μ. Six minute cephalic papillae. Four cephalic setae, 5 μ long. In ♂ two (dorsal and ventral) subcephalic setae, in both sexes scattered short cervical setae. Amphids in ♂, 12–14 + 10–12 μ, loop-shaped, inner circle more heavily cuticularized, 6 × 5.5 μ, more narrowly coiled. Cuticular annulation distinct. Buccal cavity with three small teeth (these teeth are smaller than in most other species of *Chromaspirina* and stress the proximity of the genus to *Spirinia*). Esophageal bulb pyriform, 25 × 20 μ. Spicula 27–28 μ, with faint velum, hooked proximal end. Gubernaculum sickle-shaped, 15 μ. The preanal ventral cuticle is crenate over a long distance. Immediately in front of the anus there is a stout spine. On the tail there are four ventral supplements each accompanied by a pair of setae. Subventrally and subdorsally more setae can be seen. A.b.d. 23 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4068, Type slide No. 79. Type locality, M-3, Key Biscayne.

Representation in samples studied.—M-3, Key Biscayne.

METACHROMADORA Filipjev, 1918

Type species.—*Metachromadora macroutera* Filipjev, 1918: 218, 219–225, pl. 6, fig. 42a; pl. 7, fig. 42, b–h.

KEY TO SPECIES OF *METACHROMADORA*

1. Male supplements conical, each consisting of three (1 central, 2 lateral) cuticularized pieces .... subgenus *Chromadoropsis* Filipjev, 1918 2
   Male supplements indistinct or narrow ducts the openings of which are differentiated into button-shaped or conical bodies 3
2. Esophageal bulb, 2-sectioned .... *M. vivipara* (de Man, 1907) (syn. *Chromadora vivipara* de Man, 1907)
   Esophageal bulb, 4-sectioned .... *M. quadribulba* Gerlach, 1956
3. Somatic setae arranged in 10 dense longitudinal rows .... subgenus *Metonyx*

Chitwood, 1936 .... *M. horrida* Chitwood, 1936

Somatic setae not arranged in 10 dense longitudinal rows 4

4. Head with pronounced longitudinal striation .... subgenus *Metachromadora* Filipjev, 1918[1] 5

Head without pronounced longitudinal striation 6

5. Length 2.4–2.6 mm; male with 26–48 preanal supplements .... *M. macroutera* Filipjev, 1918

Length 1.0–1.4 mm; male with 12–14 preanal supplement .... *M. chandleri* (Chitwood, 1951) (syn. *Ichthyodesmodora chandleri* Chitwood, 1951, and *Metachromadora parasitifera* Timm, 1952)

6. Posterior portion of esophagus clavate; bulb not well set off, partitions absent or indistinct; cuticle smooth to indistinctly striated. (Subgenus doubtful, perhaps a new one to be established) 7

Posterior portion of esophagus bulbular; bulb well set off, partitions distinct; striations of cuticle distinct 9

7. Male without preanal supplements .... *M. spiralis* Gerlach, 1955

Male with distinct preanal supplements 8

8. Male with 3 knob-like preanal supplements .... *M. clavata* Gerlach, 1957

Male with 19–21 conoid preanal supplements .... *M. serrata* Gerlach, 1963

9. Posterior cephalic setae absent or stout and short; amphids (at least in male) on thick cuticularized plates; cuticle with lateral wings .... subgenus *Metachromadoroides* Timm, 1961 10

Posterior cephalic setae slender; amphids not on thick cuticularized plates 13

10. Esophageal bulb, 2-sectioned .... *M. remanei* Gerlach, 1951

Esophageal bulb, 3-sectioned 11

11. Male without preanal supplements and without ventral caudal "bumps" or "warts" .... *M. vulgaris* Timm, 1961

Male with 17–23 preanal supplements and with 2 ventral caudal "bumps" or "warts" 12

12. Cephalic setae present .... *M. pulvinata* new species

Cephalic setae absent .... *M. complexa* Timm, 1961

13. Lateral wings present .... subgenus *Neonyx* Cobb, 1933 14

Lateral wings absent .... subgenus *Bradylaimus* Schuurmans-Stekhoven, 1931 18

14. Circles of cephalic setae in typical arrangement (6 + 6 + 4) 15

Circles of cephalic setae in atypical arrangement, 6 + 6 + 8, through fusion with subcephalic setae (Cobb mentions this condition in rather vague fashion for *M. cancellata*) 17

15. Esophageal bulb, barrel-shaped; preanal supplements, 8; body shape, obese, de Man *a* value = ♂, 16–24, ♀, 9.5–11.5 .... *M. obesa* Chitwood, 1936

Esophageal bulb, elongate; preanal supplements, 12; body shape more slender, de Man *a* value = ♂, 33–44; ♀, 34 16

16. Subcephalic and cervical setae shorter than the longest cephalic setae .... *M. pseudocampycoma* Hopper, 1961

Subcephalic and cervical setae longer than the longest cephalic setae .... *M. campycoma* (Cobb, 1933) (doubtful species) (syn. *Neonyx campycoma* Cobb, 1933)

17. Buccal cavity with denticles .... *M. cancellata* (Cobb, 1933) (syn. *Neonyx cancellata* Cobb, 1933)

Buccal cavity without denticles .... *M. meridiana* new species

18. Esophageal bulb, 3-sectioned 19

Esophageal bulb, 2-sectioned 21

19. Buccal cavity with denticles; head with several circles of long subcephalic and cervical setae posterior to cephalic setae .... *M. setosa* Hopper, 1961

Buccal cavity without denticles; head with only a single circle of long subcephalic setae posterior to cephalic setae 20

20. Male with 9–10 preanal supplements .... *M. onyxoides* Chitwood, 1936

Male without supplements .... *M. asupplementa* (Crites, 1961)[2] (syn. *Neonyx asupplementa* Crites, 1961)

21. Esophageal bulb elongate, length more than twice width 22

Esophageal bulb ovate, length less than twice width 23

22. Amphid 7.5 μ wide, less than one-third c.b.d. .... *M. gerlachi* new name (syn. *M. onyxoides sensu* Gerlach, 1955, nec Chitwood, 1936)

Amphid 15 μ wide, more than two-thirds c.b.d. .... *M. spectans* Gerlach, 1957

23. Amphid 12 μ wide, more than one-half c.b.d. .... *M. pneumatica* Gerlach, 1954

Amphid 7–8 μ wide, about one-fourth c.b.d. .... *M. suecica* (Allgén, 1929) (syn. *Oistolaimus suecicus* Allgén, 1929)

---

[1] *M. cystoseirae* Filipjev, 1918, also belongs to this subgenus. However, it appears to have been described on the basis of a single female, and, as such, its systematic position is doubtful.

[2] Possibly a synonym of *M. onyxoides*.

Metachromadora (*Metachromadoroides*) *pulvinata* new species

Plate XIX, fig. 38, a–c

L = 1.72 (juv. ♀ = 1.11) mm; w = 95 (juv. ♀ = 65) μ; esophagus = 315 (juv. ♀ = 220) μ; tail: juv. ♀ = 80 μ; Vu 64%. Head diameter on level of amphids 40 μ. Lips cushion-like, demarcated from head by distinct groove. Labial papillae conical. Cephalic setae stout, 8 μ long in male. Short cervical setae. Somatic setae up to 18 μ in posterior part of body. Amphids in ♂, 22 × 18 μ, on cuticularized plates, ring-shaped, in ♀, 8 × 6 μ, loop-shaped. Cuticular striation distinct, reaching to base of lips. Lateral differentiation not very pronounced, beginning around end of esophagus, ending at some distance in front of anus. Buccal cavity strongly cuticularized, in ♂, 50 μ long, with large dorsal tooth, 2 small subventral teeth and an additional tooth at the bottom of the buccal cavity; vestibulum with ribs. Esophageal bulb tripartite, with heavy cuticular lining, about 105 × 62 μ. Spicula 55 μ long, 15 μ broad. Gubernaculum 27 μ. Preanally the ventral cuticle is extended and forms a striated membrane which is traversed by about 23 narrow ducts, each duct ending in a button-shaped body. Extended cuticle reaching 540 μ preanal. Immediately in front of anus one strong spine. Tail 110 μ = 2 a.b.d. long, in ♂ with two ventral, conical, cuticularized warts. Many long spines in longitudinal rows.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4075, Type slide No. 80. Type locality, V, Vero Beach.

Representation in samples studied.—V, Vero Beach.

Remarks.—The only other species in this subgenus with postanal ventral warts is *M. complexa* Timm, 1961, which, however, is devoid of cephalic setae.

Metachromadora (*Bradylaimus*) *onyxoides* Chitwood, 1936

Metachromadora (*Bradylaimus*) *onyxoides* Chitwood, 1936: 5, fig. 1, v–x.

Our specimens appear to be typical representatives of *M. onyxoides* as described by Chitwood (1936) and Hopper (1961a). The amphids in our male measured 7–8 μ.

Representation in samples studied.—M-5, Virginia Key.

Geographical distribution.—Beaufort, North Carolina (Chitwood, 1936), Gulf Shores, Alabama (Hopper, 1961a) and ? Pernambuco, Brazil (Gerlach, 1956).

Remarks.—Gerlach's (1955) identification of specimens from San Salvador as *M. onyxoides* is doubtful. In the table below some dimensions of our own specimens are compared with those of the animals described by Hopper (1961a) and by Gerlach (1955). It follows that Gerlach's specimens belong to a different species for which the name *M. gerlachi* new name is proposed.

	Present material (μ)	Hopper, 1961	Gerlach, 1955 (μ)
Length of first cephalic setae	2.5–3	"short"	6–7
Length of second cephalic setae	10	11 μ	15–17
Length of spicula	50	60 μ	27
Length of gubernaculum	35	40 μ	15
Esophageal bulb, length of partitions	25+25+25	20+25+25 μ	29+35

Metachromadora (*Bradylaimus*) *gerlachi* new name

Metachromadora onyxoides Chitwood *sensu* Gerlach, 1955.

Metachromadora (*Bradylaimus*) *gerlachi* new name is related to *M. onyxoides* Chitwood, 1936, from which it is distinguished by having a two-sectioned esophageal bulb, the bulb in *M. onyxoides* being three-sectioned.

Metachromadora (*Neonyx*) *meridiana* new species
Plate XIX, fig. 39, a–d

L = 0.95–1.05 mm; w = ♂, 47, ♀, 55–62 μ; esophagus 175–185 μ. Lips prominent. There are three distinct circles of cephalic sense organs: in front two circles, each composed of 6 conical, setose papillae, followed by one circle of 8 slender setae, each measuring 6–7 μ. It is assumed that this circle consists of the typical 4 cephalic plus 4 subcephalic setae. Close to the amphids there are two more subcephalic setae on each side of the body, measuring 8 μ. Cervical setae in the anterior region up to 10 μ, in posterior region up to 15 μ long. Amphids spiral, 7 μ = 30% of c.b.d. wide. Cuticular striation reaching to anterior end of amphids; lateral alae starting around middle of cervical region. Buccal cavity with rather thin walls, very strong dorsal tooth and small subventral projections. Esophageal bulb tripartite, with heavy cuticular lining, 60–70 × 28–32 μ in ♂, 80 × 35 μ in ♀. Eggs 70–75 × 40–50 μ. Spicules arcuate, 58 μ long, gubernaculum 29 μ long. Male with 9–10 thin preanal supplements, traversing the raised ventral cuticle. Tail 80–95 μ long. Female a.b.d. = 28 μ, male = 35 μ. Caudal setae on male tail arranged as illustrated in Plate XIX, figure 39c.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4075, Type slide No. 81. Type locality, V, Vero Beach.

Representation in samples studied.—V, Vero Beach.

Remarks.—At first we thought we had found *M. obesa*. However, Chitwood's original description is rather poor and all other authors who subsequently described this species (Timm, 1952; Hopper, 1961b; Crites, 1961) mention the typical arrangement of 6 short and 4 long cephalic setae, whereas in our specimens there is definitely a circle of 8 long cephalic setae.

DESMODORINAE

Key to Genera of Desmodorinae

1. Esophageal bulb elongate, tripartite 2
   Esophageal bulb round to pyriform 3
2. Head with large plates in posterior portion (head "jointed" or tiled) ....
   .... *Acanthopharyngoides* Chitwood, 1936[1]
   Head simple, without plates ....
   .... *Acanthopharynx* Marion, 1870
   syn. *Xanthodora* Cobb, 1920
3. Amphids half or completely surrounded by annulation 4
   Amphids not surrounded by annulation ....
   .... *Desmodora* de Man, 1889
   (see discussion by Gerlach, 1963b)
4. Amphids half surrounded by annulation, not situated on cuticularized plates ....
   Paradesmodora Schuurmans-Stekhoven, 1950
   Amphids completely surrounded by annulation, situated on cuticularized plates ....
   Metadesmodora Schuurmans-Stekhoven, 1942

PARADESMODORA Schuurmans-Stekhoven, 1950

Type species.—*Paradesmodora cephalata* Schuurmans-Stekhoven, 1950: 117, fig. 67, a–e.

This genus contains the following species: *P. campbelli* (Allgén, 1932) Gerlach, 1963 (syn. *Spirina campbelli*), *P. immersa* Wieser, 1954, *P. punctata* Gerlach, 1963, and *P. toreutes* n. sp. The type species, *P. cephalata* Schuurmans-Stekhoven, 1950, is known from a juvenile female only and is considered a *species inquirenda*.

Our new species can be distinguished from all other species of the genus by the shape and arrangement of male supplements, the hook-shaped spicula and the cuticular differentiations of the head.

Paradesmodora toreutes new species
Plate XX, fig. 40, a–f

L = 1.62 mm; w = 21 μ; esophagus = 114

---

[1] In this genus the cuticular annulation is not quite as pronounced as in other genera of this subfamily.

μ; head diameter 14 μ. Lips distinct, papillae minute. Cephalic setae 6 μ. Cuticle in posterior portion of (adult) head very much enlarged and forming plates which surround the anterior portions of the amphids. Amphids 6 μ = 40% of c.b.d. wide, one circular loop. There are a few short cervical setae. Cuticular annulation coarse. Esophageal bulb pyriform, 22 × 15 μ. Spicula semicircular, 20 μ, proximal end hooked. There are 10 preanal supplements each consisting of a ventral bump and a thickening of the cuticle. The row of supplements extends 220 μ preanally. Between two supplements there are 13–18 cuticular annules. Tail 95 μ long, a.b.d. 20 μ. Juvenile tail 7 a.b.d. long.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4068, Type slide No. 82. Type locality, M-3, Key Biscayne.

Representation in samples studied.—M-3, Key Biscayne.

DESMODORA de Man, 1889

Type species.—*Spilophora communis* Bütschli, 1874: 282, 283, pl. 5, fig. 27, a, b; pl. 7, fig. 27, c, d.

Gerlach (1963) has recently reviewed this genus, relegating several known genera to subgeneric rank (i.e., *Pseudochromadora*, *Xenodesmodora*, *Croconema*, *Bolbonema*, *Desmodorella* and *Zalonema*). Excellent discussions, with keys, for both the subgenera and the species within each sugenus are presented in Gerlach's paper.

Gerlach's (1963b, p. 84) discussion of *Xenodesmodora* makes synonymization of *Bla* Inglis, 1963, with the former subgenus inevitable. The type species, *Bla nini* Inglis, 1963, therefore, is transferred to the genus *Desmodora* and becomes ***Desmodora* (*Xenodesmodora*) *nini*** (Inglis, 1963) **new combination.**

The genus *Desmodora* was represented in our material, in samples M-2 and M-3 from Key Biscayne, by a single, well-known species, *Desmodora* (*Pseudochromadora*) *quadripapillata* (Daday, 1899) Gerlach, 1963 (synonyms *Pseudochromadora quadripapillata* Daday, 1899, *Micromicron cephalata* Cobb, 1920, and *M. luticola* Timm, 1952).

Pertinent measurements from a male specimen are as follows: L = 0.74 mm. Head diameter 14 μ. Amphids 6 μ. Spicula 28 μ.

Representation in samples studied.—M-2, Key Biscayne, M-3, Key Biscayne.

Geographical distribution.—New Guinea (Daday, 1899), Costa Rica (Cobb, 1920), Chesapeake Bay, Maryland (Timm, 1952), and Cananeia, Brazil (Gerlach, 1957).

MONOPOSTHIINAE

MONOPOSTHIA de Man, 1889

Type species.—*Spiliphora costata* Bastian, 1865: 166, 167, pl. 13, figs. 228, 229.

We prefer not to follow Gerlach (1963) in his synonymization of *Monoposthia* and *Nudora*. Thus in *Monoposthia* only species are retained in which the spicula are absent and the single gubernaculum is not conspicuously enlarged proximally. Within the genus there is a group of species characterized by the enlarged second annule. A key to this group reads as follows:

KEY TO SPECIES OF *MONOPOSTHIA*

1. Both first and second annule enlarged; amphids between the two annules .... *M. thorakista* Schulz, 1935
   Only second annule enlarged; amphids on this annule 2
2. Cuticle with 12 longitudinal rows of V-shaped markings .... *M. duodecimalata* Chitwood, 1936
   Cuticle with 6 longitudinal rows of V-shaped markings 3
3. Cephalic setae measuring less than ½ of head diameter; amphids $\frac{1}{3}$ of c.b.d. wide .... *M. mielcki* Steiner, 1916
   Cephalic setae approximately one head diameter long; amphids about $\frac{1}{6}$ of c.b.d. wide .... *M. mirabilis* Schulz, 1932
   syn. *M. longiseta* Allgén, 1935

Our material is representative of *M. mirabilis* Schulz, 1932, agreeing in all essential points with the excellent redescription given of this species by Luc and De

Coninck (1959). *M. ornata* Timm, 1952, described on the basis of one juvenile, is either a synonym of *M. mirabilis* or else a *species inquirenda.*

Monoposthia mirabilis Schulz, 1932
Plate XX, fig. 41, a, b

Monoposthia mirabilis Schulz, 1932: 380–382, fig. 26, a–g

Male.—L = 1.6 mm; w = 57 μ. Diameter at base of esophagus, 54 μ. Esophagus 210 μ long. Head diameter 19 μ, bearing six labial papillae and four, 19 μ long, cephalic setae. Cuticle with 6 longitudinal rows of V-like markings. Reversal of V's at mid-body. Body bearing 4 rows of somatic setae which carry on to the tail. Buccal cavity armed with dorsal tooth and opposed by a number of denticles. Gonad single, outstretched. Gubernaculum 38 μ long. Tail 110 μ long, a.b.d. 39 μ. A prominent double pair of fleshy papillae are positioned pre-anally, surrounded by a cuticularized ridge.

Representation in samples studied.—M-2, Key Biscayne.

Geographical distribution.—European Atlantic coasts, Mediterranean Sea (Gerlach, 1952).

MONOPOSTHIOIDES Hopper, 1963

Type species.—*Monoposthioides anonoposthia* Hopper, 1963: 850–852, figs. 11–18.

This genus is differentiated from *Monoposthia* by the shape of the gubernaculum ("spiculum" in the interpretation of other authors), the long spine attached to the latter, the presence of two testes and the absence of V-like markings in the anterior portion of the body.

Our specimens agree with this diagnosis except for the absence of the gubernacular spine. No trace of it could be detected in the four males examined. Further differences from the type, *M. anonoposthia*, are: the cephalic setae measure only about one head diameter as against 1.5, and in the gubernaculum it is the *dorsal* rather than the *ventral* arm of the proximal extension which is the longer. We thus consider our specimens to represent a new species which we call *M. mayri* n. sp. in honor of Dr. Ernst Mayr of the Museum of Comparative Zoology, Harvard University.

Monoposthioides mayri new species
Plate XX, fig. 42, a, b

L = ♂, 1.72, ♀, 1.4–1.5 mm; w = 40 μ; esophagus = 185 μ; Vu = 90–92%. Head diameter 16 μ. Lips distinct, with 6 setose papillae. Cephalic setae 17 μ. Cuticle with broad rings in the anterior cervical region whence they gradually become narrower. The second annule is even more enlarged than the adjacent ones and measures 7 μ in width. There are at least 12, probably 14, longitudinal rows of V-like markings which start about 50 μ from the anterior end. The reversal of the V's takes place in the male at 140 μ behind the posterior end of the esophageal bulb, in the female at 240–250 μ (in *M. anonoposthia* the V-shaped markings are reversed in the male at a point opposite the anterior margin of the bulb and in the female at a point approximately one and one-half tail lengths anterior to the anus). Buccal cavity cylindrical, measuring 22 μ from tip of tooth to base, with one large dorsal tooth and small subventral projections. Amphids more or less pocket-shaped and sunk into the cuticle, somewhat irregular in outline. Esophageal bulb 47 × 25 μ. Single gubernaculum 42 μ long, axe-like, proximal end 23 μ wide, gliding in an anal sheath as reported for *M. anonoposthia.* Tail: ♂, 140 μ, ♀, 100–105 μ long; a.b.d. = 30 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4067, Type slide No. 83. Type locality, M-3, Key Biscayne.

Representation in samples studied.—M-3, Key Biscayne.

MICROLAIMIDAE

PARAMICROLAIMUS Wieser, 1954

Type species.—*Paramicrolaimus primus* Wieser, 1954: 64, fig. 135, a–c.

In this genus the first circle of (6) cephalic sense organs is not papilloid but consists of slender setae which, in the three species so far described, are more than half as long as the (4) cephalic setae of the second circle. In our new species, the setae of the first circle are considerably shorter than those of the second. Thus the arrangement of cephalic organs is very much like that of several species of *Microlaimus.* However, further distinguishing features of *Paramicrolaimus* are the transversely oval amphids and the distinct preanal papillae in the male. The following species are known: *P. primus* Wieser, 1954 (♀ only!), *P. papillatus* (Gerlach, 1954) (syn. *Microlaimus papillatus*), *P. spirulifer* Wieser, 1959, and *P. lunatus* n. sp. In addition to the shorter cephalic setae, *P. lunatus* is characterized by the semicircular spicula.

Paramicrolaimus lunatus new species

Plate XXI, fig. 43, a–c

L = 1.2–1.3 mm; w = 29–33 μ. Head diameter 11–13 μ. Labial papillae distinct. First circle of cephalic setae short, at best 3 μ long. Second circle of cephalic setae, 7 μ long in ♂, 11 μ long in ♀. Amphids transversely oval, 10 μ wide (⅔ c.b.d.) in ♂, 8 μ wide (⅖ c.b.d.) in ♀; located 10–13 μ behind anterior end. Cuticular striation distinct, extending anteriorly only to base of cephalic setae. Buccal cavity wide, conical, with one large dorsal tooth, 2 subventral teeth and projections at the base. Esophagus 145–155 μ long, terminated by esophageal bulb 28 × 22 μ. The musculature of the esophageal bulb is indistinctly divided into two parts by a weak transverse break. Spicula 45 μ, regularly bent. Gubernaculum simple, 19 μ long. The male bears 5 prominent preanal supplements which appear to be tubular in structure. The cuticle in the area of each supplement is somewhat swollen. The 3rd and 4th preanal supplements are always closer together than are any of the remaining ones. Tail conical, 85–90 μ long, bearing 6 pairs of subventral setae; a.b.d. = 25–27 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4066, Type slide No. 84. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

CHROMADORIDAE

CHROMADORINAE

The genera in this subfamily are arranged as in Wieser (1954); that is, the primary division is into genera with hollow or with solid teeth. Within each of these two groups further separation is based on the structure of the cuticle (homogeneous or heterogeneous and with or without lateral differentiation).

HYPODONTOLAIMUS de Man, 1888

Type species.—*Spiliphera inaequalis* Bastian, 1865: 166, pl. 13, figs. 223–225.

Group A in Wieser's key (1954) contains species with very long somatic setae and up to now is represented by six species. Since classification of these species leans heavily on features of the spicular apparatus, *H. heymonsi* (Steiner, 1922), known from 1 ♀ only, is considered a *species inquirenda.* A key to the species reads as follows:

KEY TO SPECIES OF *HYPODONTOLAIMUS*
(Group A of Wieser, 1954)

1. Cephalic setae twice the head diameter. Pharyngeal bulb not very powerful, dorsal tooth weakly S-shaped, not pushed into ventral buccal wall. Indistinct preanal papillae present *H. setosus* (Bütschli, 1874)
   Cephalic setae measuring about 1 head diameter. Pharyngeal bulb powerful, dorsal tooth strongly S-shaped, pushed into ventral buccal wall. No preanal papillae 2
2. Distal portion of tail with *ventral* curvature. First circle of (6) cephalic sense organs

papilloid. Esophageal bulb indistinctly set off from esophagus .... *H. colesi* Inglis, 1962

Distal portion of tail with *dorsal* curvature. First circle of (6) cephalic sense organs setose. Esophageal bulb well set off 3

3\. Gubernaculum with hook-shaped apophysis .... *H. steineri* Wieser, 1954

Gubernaculum without apophysis 4

4\. Gubernaculum well developed, spoon-shaped, half the length of the spicula .... *H. schuurmansstekhoveni* Gerlach, 1951

Gubernaculum reduced to a short plate with thin lamella between the 2 spicula. Free portion of gubernaculum much shorter than half the length of the spicula 5

5\. Gubernacular lamella with dorsal extension. Spicula evenly curved, of nearly equal width throughout. Tail without break .... *H. solivagus* Hopper, 1963

Gubernacular lamella minute, without extension. Spicula tapering unevenly and of characteristic shape (see Fig. 44, d). Tail with distinct break in cuticle .... *H. interruptus* n. sp.

Group B of Wieser's key, comprising species without elongated somatic setae, includes a few species characterized by the possession of a double bulb. This group, which has been referred to as a distinct subgenus, *Ptycholaimellus* Cobb, 1920, by Gerlach (1955), is represented by the following 4 species:

H. carinatus (Cobb, 1920), distinguished by long cephalic setae but imperfectly known. The specimens described under this name by Timm (1952) almost certainly do not belong to *H. carinatus* but more likely to one of the following two species:

H. ponticus Filipjev, 1922. (For synonyms and description see Gerlach, 1951a.)

H. pandispiculatus Hopper, 1961. On the basis of our own material we can confirm Hopper's conclusion that this species is separated from *H. ponticus* by the shape of spicula and gubernaculum and by the shorter cephalic setae.

H. macrodentatus Timm, 1961, characterized by knob-like swellings at the base of the dorsal tooth, and by the shape of the spicula.

Hypodontolaimus (*H.*) *interruptus* new species

Plate XXI, fig. 44, a–d

L = 0.58–0.59 mm; w = 23–25 μ; esophagus = 95–100 μ. Head diameter 15 μ. Lips large. Cephalic setae: first circle of six = 2.5 μ, second circle of four = 15 μ. Cervical and somatic setae up to 35 μ long. The somatic setae are arranged in two sublateral rows on each side of the body. The same holds for the cervical setae but some submedian setae can also be seen. Cuticle annulated, with dots between the annules; lateral differentiation consisting of two longitudinal rows of larger dots and faint wings. Distance of longitudinal rows = 4 μ in mid-body, 5 μ in cervical region. Buccal cavity with powerful dorsal tooth. Pharyngeal bulb well developed. Esophageal bulb 20 × 16 μ. Amphids elliptical. Spicula 21 μ long, tapering unevenly, tip obliquely truncate. Gubernaculum reduced to a small plate with minute lamella between the spicula. Tail 85–87 μ long, with break in cuticle shortly before the middle; a.b.d. 22 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4070, Type slide No. 85. Type locality, M-5, Virginia Key.

Representation in samples studied.—M-5, Virginia Key.

Hypodontolaimus (*Ptycholaimellus*) *pandispiculatus* Hopper, 1961

Plate XXI, fig. 45, d, e; Plate XXII, fig. 45, a–c, f

Hypodontolaimus (*Ptycholaimellus*) *pandispiculatus* Hopper, 1961: 360, 361, figs. 1–4.

L = 1.14 mm; w = 28–30 μ; esophagus = 180 μ. Head diameter 15 μ. Cephalic setae (only second circle of four seen) 5–6 μ. Lips distinct. Cervical and somatic setae short, in two sublateral rows. Cuticular ornamentation typical; longitudinal rows of dots 5 μ apart in mid-body, 4 μ on level of esophageal bulb. Buccal cavity with medium-sized dorsal tooth and subventral projections. Pharyngeal bulb not very large. Esophageal bulb 40 × 28 μ, barrel-shaped, double, the anterior portion smaller than the posterior one. Excretory pore 22 μ behind anterior end. Spicula 35 μ long, with velum. *Two* gubernacula, 12 μ long, proximally expanded. Tail 110 μ long, a.b.d. 35 μ.

Representation in samples studied.—M-3, Key Biscayne.

Geographical distribution.—Gulf Shores, Alabama (Hopper, 1961).

Remarks.—Our specimens differ from the type in the more posterior position of the excretory pore, but there is agreement on all other essential points.

RHIPS Cobb, 1920

Type species.—*Rhips ornata* Cobb, 1920: 339, 340, fig. 118, a–c.

This genus comprises two species, *R. ornata* Cobb, 1920, and *R. longicauda* Timm, 1961, the latter being characterized by the elongated tail. We found Cobb's species in our material and shall give a figure of the head end, the spicular apparatus being well described in Cobb's original publication.

Rhips ornata Cobb, 1920

Plate XXII, fig. 46, a, b

Rhips ornata Cobb, 1920: 339, 340, fig. 118, a–c

L = 1.46 mm. Head diameter 12 μ. Lips distinct, with 6 setose labial papillae. Cephalic setae 5 + 3 μ, in two circles. Amphids 10 μ wide. Head with six triangular plates that probably serve as supports. Cuticular annules resolvable into basketwork-like structures in the cervical region, into elongated, more or less hexagonal structures in remainder of body. V-shaped lateral differentiations in posterior portion of body. A few cervical setae, measuring up to 15 μ. Buccal cavity with large dorsal tooth and two small subventral teeth. Spicula 43 + 28 μ long. Gubernaculum (lateral pieces) 19 μ. Tail 130 μ long, a.b.d. 23.

Representation in samples studied.—M-5, Virginia Key.

Geographical distribution.—Ocean Beach, Florida (Cobb, 1920), Brazil (Gerlach, 1957), and ? Campbell Islands (Allgén, 1932).

CHROMADORA Bastian, 1865

Type species.—*Chromadora nudicapitata* Bastian, 1865: 168, pl. 13, figs. 230–232.

This genus was discussed by Wieser (1954, 1955). We found what is probably *C. macrolaimoides* Steiner, 1915, as in our specimens the distal end of the gubernaculum seems to be more strongly expanded than that figured by Steiner or Chitwood (1951). However, this portion is weakly cuticularized and difficult to see. The species is characterized by the large esophageal bulb, the two small and rather faint preanal papillae, the weak curvature of the spicula and the long spinneret.

Chromadora macrolaimoides Steiner, 1915

Plate XXII, fig. 47

Chromadora macrolaimoides Steiner, 1915: 234–237, figs. 23–27; Wieser, 1955 (nec Steiner, 1922; Allgén, 1927).

Chromadorella macrolaimoides,—Filipjev, 1918; Chitwood, 1951.

Spicula 21 μ long, weakly curved, with velum. Gubernaculum 15 μ long, strongly expanded distally, edge slightly serrated. There are two preanal supplements, rather faint and of the usual cup-like shape but surrounded by an additional cuticular differentiation. The distance of the posterior supplement from the anus is 20 μ. Spinneret 6 μ long.

Representation in samples studied.—M-1, Key Biscayne, M-4, Rickenbacker Causeway.

Geographical distribution.—Sumatra (Steiner, 1915), Texas, Gulf Coast (Chitwood, 1951), and Japan (Wieser, 1955).

TIMMIA Hopper, 1961

Type species.—*Parachromadora parva* Timm, 1952: 24, 25, figs. 38, 39.

Parachromadora Timm, 1952, nec Micoletzky, 1914, nec Schulz, 1939.

This genus is distinguished from *Chro-*

madorina Filipjev, 1918, solely by the occurrence of a tubular supplement in addition to the usual preanal papillae in the male. Our material, from Vero Beach, contained representatives of the type species, *Timmia parva* (Timm, 1952) Hopper, 1961. In addition to the present locality, the species is known from Chesapeake Bay, Maryland (Timm, 1952), and Gulf Shores, Alabama (Hopper, 1961).

SPILOPHORELLA Filipjev, 1918

Type species.—*Spilophora paradoxa* de Man, 1888: 45–47, pl. 4, fig. 19.

We seem to have typical representatives of the cosmopolitan species, *Spilophorella paradoxa*, in our material.

Spilophorella paradoxa (de Man, 1888) Filipjev, 1918

Spilophora paradoxa de Man, 1888: 45–47, pl. 4, fig. 19.
Spilophorella paradoxa (de Man, 1888) Filipjev, 1918: 259.

L = 0.73–0.80 mm; w = 31 μ; esophagus = 145 μ; Vu = 44%. Head diameter 11 μ. Cephalic setae 5 μ. Esophageal bulb double, typical. Spicula 36–43 μ; gubernaculum 30–36 μ. Tail 120–130 μ long, spinneret 20–22 μ.

Representation in samples studied.—M-2, Key Biscayne, M-6, Everglades National Park.

Geographical distribution.—Cosmopolitan.

PROCHROMADORELLA Micoletzky, 1924

Type species.—*Chromadora neopolitana* de Man, 1878: 113, 114, pl. 9, fig. 17, a–c.

Prochromadorella mediterranea (Micoletzky, 1922)

Plate XXII, fig. 48, a–c; Plate XXIII, fig. 48, d, e

Chromadora mediterranea Micoletzky, 1922b; *Chromadorella pontica* Filipjev, 1922; and ? *Hypodontolaimus arabicus* Cobb, 1891.

L = 0.5–0.67 mm; w = 17–21 μ; esophagus = 100–105 μ; Vu = 46%. Head diameter 10–11 μ. Lips and labial papillae distinct. Cephalic setae in two circles, 6 short ones (about 1–1.5 μ), 4 longer ones (5 μ). A few cervical setae up to 10 μ, amongst which one characteristic circle of four sublateral pairs, two on each side, at about 20 μ from the anterior end. Cuticle typical, with at first dots, then elongated hexagonal bodies and rods between annules. Amphids faint though large, oval. Excretory pore on level of cephalic setae. Buccal cavity with three solid, subequal teeth. Esophagus enlarged posteriorly. Spicula semicircular, chord 18 μ long. Gubernaculum 10 μ, distally slightly expanded, with two or three teeth. Two faint preanal supplements 15 and 27 μ from anus, respectively. Tail in ♂, 75–100 μ (= 6–6.7 a.b.d.), in ♀, 110 μ (9 a.b.d.).

Representation in samples studied.—M-1, Key Biscayne.

Geographical distribution.—Mediterranean Sea, Black Sea, Red Sea (Gerlach, 1958), Bay of Bengal (Timm, 1961).

Remarks.—Our specimens are in perfect agreement with the type and with material from the Mediterranean.

CHROMADORELLA Filipjev, 1918

Type species.—*Chromadora filiformis* Bastian, 1865: 169, pl. 13, figs. 242–244.

Since our material contained three species, two of which are new, we shall provide a new key to the genus (see also Wieser, 1954).

KEY TO SPECIES OF *CHROMADORELLA*

1. Cuticular ornamentation always consisting of dots and rod-like markings 2
   Cuticular ornamentation in anterior cervical region consisting of solid bands with crenate contour, or of fused hexagonal bodies 5
2. Four longitudinal rows of dots on each side of body .... *C. circumflexa* Wieser, 1954
   Two longitudinal rows of dots on each side of body 3
3. Lateral differentiation beginning with cuticular annulation, there measuring ⅕ to ⅙ of c.b.d. ....

C. parapoecilosoma (Micoletzky, 1922)[1]
Lateral differentiation beginning a short distance behind cuticular annulation, there measuring not more than 1/10 of c.b.d. 4
4. Longitudinal rows 1/10 to 1/12 of c.b.d. apart; membrane present .... *C. membranata* Micoletzky, 1924
Longitudinal rows 1/6 to 1/8 of c.b.d. apart; membrane absent .... *C. filiformis* (Bastian, 1865)
5. Twelve preanal supplements 6
Five to 6 preanal supplements 7
6. Lateral differentiation irregular .... *C. edmondsoni* Wieser, 1959
Lateral differentiation two longitudinal rows, widely spaced in anterior cervical region .... *C. galeata* Wieser, 1959
7. Esophageal bulb distinctly set off, barrel-shaped, short. Spicula nearly semicircularly curved .... *C. parabolica* Wieser, 1954
Esophageal bulb not so well set off, more elongated. Spicula rectangularly bent 8
8. Three longitudinal rows, in anterior cervical region 1/10 of c.b.d. apart .... *C. trilix* n. sp.
Two longitudinal rows, in anterior cervical region 1/4 of c.b.d. apart *C. vanmeterae* n. sp.

We consider *C. mytilicola* Filipjev, 1918, as doubtful since only females are known.

Chromadorella filiformis (Bastian, 1865)
Plate XXIII, fig. 49, a, b; Plate XXIV, fig. 49, c, d

Chromadora filiformis Bastian, 1865; *Dichromadora tenuicauda* Schuurmans-Stekhoven, 1950; *Chromadorella filiformoides* Chitwood, 1951.

L = 0.77 mm; w = 26 μ; esophagus = 115 μ. Head diameter 14–15 μ. Lips distinct. Six short cephalic setae and 4 long ones, measuring 10–11 μ. Ocelli and pairs of cervical setae 20 μ behind anterior end (ocelli sometimes indistinct). Cuticle annulated, with transverse rows of dots between annules which become elongated in the posterior cervical region. Lateral differentiation through larger dots which arrange themselves into distinct longitudinal rows at about the level of the ocelli. Between esophageal bulb and anus the longitudinal rows are from 3.5–4.5 μ apart, that is, 1/6 to 1/8 of c.b.d. Buccal cavity with three solid, subequal teeth. Esophageal bulb elongated, 30–34 × 15–16 μ. Excretory pore on level of nerve ring, 60 μ behind anterior end. Spicula 5 μ wide, strongly curved; true length = 30 μ, chord = 22 μ. Gubernaculum 19 μ long, consisting of a piece between the two spicula and a caudal plate which distally ends in a three-pronged projection. There are 5 large preanal supplements. Tail 110 μ long, a.b.d. 25 μ.

Representation in samples studied.—M-1, Key Biscayne.

Geographical distribution.—Atlantic, Mediterranean, Black Sea, Red Sea, Sumatra, Japan, Sargasso Sea, Texas.

Remarks.—As has been noted in other species, the appearance of the ocelli in different specimens is variable, probably due to the action of the preserving fluid. Consequently, Chitwood's species, *C. filiformoides*, cannot be maintained.

A further fact that should be mentioned is that in our specimens the longitudinal rows of dots seem to be more widely spaced than indicated by de Man (1890) in his excellent description of European representatives of this species. Comparative data on this point would be desirable.

Chromadorella trilix new species
Plate XXIII, fig. 50, a–c; Plate XXIV, fig. 50, d, e

L = 0.95 mm; w = 28–30 μ; esophagus = 135 μ. Head diameter 13 μ. Lips distinct. Labial papillae and first circle of cephalic setae not seen. Four cephalic setae 5–6 μ long. Cuticular ornamentation consisting of solid bands with crenate contour in anterior cervical region which further posterior become resolved into rod-like markings. Lateral differentiation beginning with annulation, at first consisting of round markings, 1.5 μ apart, then of two rows of larger dots. About 30 μ behind the anterior end, one of the two longitudinal rows of dots moves into the middle of the lateral fields and is replaced sublaterally by a new row of dots.

---

[1] This species is not well known. There are doubts concerning the cuticular ornamentation since Micoletzky (1922) and Schuurmans-Stekhoven (1943) mention only dots and rod-like markings, whereas Wieser (1951) figures solid bands with crenate contour.

The result is a lateral differentiation consisting of three longitudinal rows which run to approximately the level of the anus where the middle row drops out. In midbody the outer rows are 3.5–4 μ apart. Buccal cavity with three solid, subequal teeth. Esophagus elongated, with three fairly distinct interruptions. Spicula 26 μ long. Gubernaculum expanded distally. Five large supplements, extending to 90 μ preanal. Tail 91 μ, a.b.d. 22 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4067, Type slide No. 86. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

Chromadorella vanmeterae new species
Plate XXIII, fig. 51, a–c; Plate XXIV, fig. 51, d, e

L = 1.25 mm; w = 35 μ; esophagus = 160 μ. Head diameter 20 μ. Head slightly swollen. Lips and labial papillae distinct. First circle of cephalic setae not seen, second circle of four setae, 5–6 μ. Cervical setae about 35 μ, behind anterior end, somatic setae along lateral fields. Cuticular ornamentation consisting of solid bands with crenate contour in anterior cervical region, resolving into elongated markings further posterior. Lateral differentiation by larger dots, forming two longitudinal rows, 4–6 μ apart. Buccal cavity typical. Esophageal bulb elongated, with distinct plasmatic interruptions. Spicula 31 μ long. Gubernaculum simple. Six preanal supplements, extending to 113 μ preanal. Tail 150 μ, a.b.d. 23 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4067, Type slide No. 87. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

Remarks.—This species is dedicated to Miss Nancy Van Meter who guided us safely to the muds of Florida Bay, Everglades National Park.

EUCHROMADORA de Man, 1886
Type species.—*Chromadora vulgaris* Bastian, 1865: 167, 168, pl. 13, figs. 233–235.

This genus is rather difficult because it seems to contain a great number of species distinguishable by subtle characters of the cuticle and the spicular apparatus. Most descriptions, however, are too vague to permit comparison on a sufficiently detailed level. We agree with Inglis (1962) that the highly developed cuticle possesses a number of features that could be used for taxonomic purposes. Probably the most suitable is the structure of the annules underlying the variously shaped blocks, rods, and "basketwork"-types of differentiations. These annules have, along the lateral line of the body, anterior or posterior projections which may be straight, notched, fenestrated, or even entirely separated from the annules, thus forming small cuticular pieces between the latter. All these differentiations may be specific but more comparative studies are required.

A grouping of the genus seems to be possible along the lines indicated by Wieser (1954). Thus, there is a group of species in which the dorsal tooth is relatively small, poorly cuticularized, forward pointing and not embedded in pharyngeal tissue. This group contains the following species: *E. amokurae* (Ditlevsen, 1921), (syn. *Spilophora amokurae* Ditlevsen, 1921); *E. arctica* Filipjev, 1946; *E. luederitzi* Steiner, 1918 (somewhat doubtful); and *E. mediterranea* Allgén, 1942. All other species referred to this group by Wieser (1954, group B) are insufficiently described and are considered *species inquirendae.*

In the second group, the dorsal tooth is large and heavily cuticularized, its base embedded in pharyngeal tissue. Two of the included species are characterized by a well-developed, oval bulb, distinctly set off from the esophagus, viz.: *E. loricata*

(Steiner, 1916) (synonyms: *Spilophora loricata* Steiner, 1916, *E. archaica* Steiner and Höppli, 1926), and *E. tyrrhenica* Brunetti, 1951.

The remaining species are difficult to separate. They are listed below, together with a short characterization of their distinguishing features, but the original descriptions should be consulted in each case.

E. vulgaris (Bastian, 1865)

Chromadora vulgaris Bastian, 1865; *E. tridentata* Allgén, 1929.

Spicula asymmetrical.

E. striata (Eberth, 1863)

Odontobius striatus Eberth, 1863, non *E. striata* of Chitwood, 1951 (= *E. gaulica*).

Spicula 70–90 μ, stout, central portion enlarged; lateral pieces of gubernaculum about 50% of spicula.

E. gaulica Inglis, 1962

E. striata of Chitwood, 1951, non Eberth, 1863; *E. chitwoodi* Coles, 1965.

Spicula 42–53 μ, proximal portion slender, proximal and "crinkled," distal portion enlarged; gubernaculum 50–66% of spicula.

E. parafricana Gerlach, 1958

Spicula 25–27 μ, stout; gubernaculum of even thickness, boomerang-shaped. Cephalic setae shorter than in above species.

E. pectinata n. sp. (See below, p. 286.)

Closely related to foregoing species. Spicula just as stout but more heavily cuticularized, 37–40 μ; gubernaculum sharply bent, with acute tip. Comb-like ridges in buccal cavity. Cephalic setae even shorter. Cuticular annules transversely split.

E. permutabilis Wieser, 1954

Spicula 104–133 μ. Tail plump (4 a.b.d. in ♀). Gubernaculum sharply curved distally.

E. tokiokai Wieser, 1955

Spicula 41–50 μ, slender throughout. Gubernaculum 66% of spicula, slightly curved distally.

E. meadi n. sp. (See below, p. 286.)

First circle of 6 cephalic setae elongated, second circle—at least in adults—absent. The absence of the second circle of cephalic setae distinguishes *E. meadi* from the remaining species of this group.

In addition to these species there are two more with unusually shaped spicular apparatus which might not belong to the genus at all, viz., *E. inflatispiculum* Schuurmans-Stekhoven, 1943, and *E. kryptospiculum* Allgén, 1951.

All the other species described are here considered as doubtful, or have been transferred to other genera by Wieser (1954).

Euchromadora gaulica Inglis, 1962
Plate XXIV, fig. 52, a; Plate XXV, fig. 52, b–d

Euchromadora gaulica Inglis, 1962: 260.
E. striata of Chitwood, 1951, non Eberth, 1863.
E. chitwoodi Coles, 1965 (NEW SYNONYMY).

L = 1.11–1.57 mm; w = 40–52 μ; esophagus = 245 μ; Vu = 50%. Head diameter 19 μ. First circle of six cephalic setae short, second circle of four, 7–9 μ. Cuticular ornamentation consisting, in front, of three transverse rows of dots, followed by the usual annules covered with hexagonal bodies which themselves are interconnected by a meshwork of lines. Further posterior, these bodies are more elongated and form a sort of grid that links the annules. The latter are solid and possess lateral projections ("lateral plates" of Inglis, 1962) which are directed anteriorly in the anterior half of the body, posteriorly in the posterior half. Each projection fits into a notch of the following annule, thus forming a series of joints. This condition has already been described by Steiner (1918). Occasionally the lateral projections are separated from the annules and then can be seen as cuticular pieces between the latter. Traces of pigment spots occur in the anterior cervical region. Buccal cavity with large dorsal tooth and several subventral and ventral denticles which form a comb-like ridge. Pharyngeal bulb well developed, esophageal bulb not set off, indistinct. Spicula 42–47 μ long, proximal end giving a "crinkled" impression, distal two-thirds dilated. Lateral plates of gubernaculum 25–28 μ long, proximal end straight or round depending on focus, distal end acute, with two minute subterminal denticles; dorsal plate 26–33 μ long, with lateral projections. Tail 135–150 μ long, a.b.d. 30 μ in ♂.

Representation in samples studied.—M-I, Key Biscayne.

Geographical distribution.—Texas, Gulf Coast (Chitwood, 1951), Mediterranean Sea (Inglis, 1962), coast of England (Coles, 1965).

Euchromadora pectinata new species

Plate XXIV, fig. 53, a; Plate XXV, fig. 53, b–d

L = 1.65–1.97 mm; w = 40–50 μ; esophagus = 258–290 μ; Vu = 48%. Head diameter 19 μ. Labial papillae indistinct. Cephalic setae: first circle of six, papillose; second circle of four, 3.5–4 μ. Cuticular ornamentation beginning, a short distance behind the cephalic setae, with two fused annules on which faint longitudinal striation can be seen, followed by single annules which, however, from about the middle of the cervical region to the middle of the tail, are transversely split. Consequently each annule consists—at least in the lateral portion of the body—of two parts of which the posterior one is the larger. This posterior part possesses the same lateral projections as described for the foregoing species, only less pronounced. Moreover, there are transverse "lacunae" on the annules of the mid-body. The differentiation superimposed upon the annules consists of the usual hexagonal blocks in the anterior cervical region, rod-like markings in the remainder of the body. These markings are thinner than in the foregoing species. The cuticle shows ventral or subventral differentiations in the vulvar region, in the anal region, and in males at a distance of 120 μ preanal and 70 μ postanal, respectively. Buccal cavity with medium-sized tooth, not as strongly cuticularized as in other species of this group, and a series of comb-like structures. Esophagus dilated, no true bulb. Spicula 6–7 μ wide, strongly cuticularized, without velum, 37–40 μ long. Lateral plates of gubernaculum 20–22 μ long, sharply bent distally and with acute tip. Tail in ♂, 160–180 μ long, a.b.d. 35 μ, in ♀, 200 μ long, a.b.d. 27 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4073, Type slide No. 88. Type locality, M-8, Biscayne Bay.

Representation in samples studied.—M-8, Biscayne Bay.

Euchromadora meadi new species

Plate XXIV, fig. 54, a, b; Plate XXV, fig. 54, c–f

L = 1.50 mm; w = 40 μ; esophagus = 200 μ. Head diameter 19 μ. Lips and labial papillae distinct. First circle of cephalic setae 2 μ, no second circle in adults. In juveniles four short setae could be seen immediately behind the first circle of six setae. Amphids fairly distinct, 12–13 μ wide. Cuticular ornamentation beginning with large annule, longitudinally striated, followed by narrower annules which are all solid and show no secondary development except the lateral projections described in the species above. Hexagonal blocks very thin even in anterior cervical region. Buccal cavity with large dorsal tooth and at least two subventral projections, no comb-like ridges. No distinct esophageal bulb. Spicula 45–47 μ long, slender, with velum. Lateral plates of gubernaculum 22–24 μ long, hammer-shaped; dorsal plate 18 μ long, with characteristic proximal projection. In the anal area the cuticular annules are weakly cuticularized subventrally to form a sort of "window." Tail 135 μ long, a.b.d. 35 μ, in juveniles 5–6 a.b.d. long.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4067, Type slide No. 89. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

ATROCHROMADORA Wieser, 1959

Type species.—*Spilophora parva* de Man, 1893: 89–91, pl. 5, fig. 5.

We found what appeared at first to be *A. parva* (de Man, 1893), but closer study revealed the following differences:

	parva	*denticulata*
Spacing of longitudinal rows (mid-body)	3.5 μ	6 μ
Length of spicula	17–18 μ	34 μ
Distal end of gubernaculum	straight	denticulated
Length of spinneret	12 μ = $\frac{1}{7}$ tail	7–8 μ = $\frac{1}{15}$ tail

Atrochromadora denticulata new species

Plate XXVI, fig. 55, a–f

L = 0.79–0.80 mm; w = 31–32 μ; esophagus = 96–109 μ; Vu = 46%. Head diameter 11 μ. Lips distinct, labial papillae and first circle of cephalic sense organs not seen. Cephalic setae 5–6 μ. Cervical setae as in *A. parva.* Amphids distinctly spiral, but small. Cuticular ornamentation beginning with transverse rows of dots, followed by annules. In the lateral region of the body a few dots or rod-like markings can be seen between the annules, particularly two longitudinal rows of larger dots, the spacing of which is 5–6 μ between cervical region and anus. Buccal cavity with three solid, subequal teeth. Esophageal bulb round. Excretory pore 37 μ in front of end of esophagus, ventral gland reaching to 48 μ behind the esophagus. Spicula nearly semicircular, 3 μ wide, 34 μ long. Gubernaculum 23 μ long, strongly dilated distally, with denticulated end plate. Tail 124–128 μ long, a.b.d. 28 μ in ♂, 20 μ in ♀. Spinneret 7–8 μ. In ♂ there is a slight ventral swelling, 45 μ postanally.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4067, Type slide No. 90. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

COMESOMATIDAE

MESONCHIUM Cobb, 1920

Type species.—*Mesonchium poriferum* Cobb, 1920: 294, 295, fig. 76.

Pepsonema Cobb, 1920: 295.

The following five species are known: *M. poriferum* Cobb, 1920; *M. pellucidum* (Cobb, 1920) syn. *Pepsonema pellucidum*; *M. nini* Inglis, 1961; *M. punctatum* Timm, 1961; *M. janetae* Inglis, 1963. They can be separated mainly by the shape of their spicula and by the pattern of their lateral cuticular differentiations. Moreover, *M. janetae* has shorter cephalic setae, and *M. nini* amphids with more turns than the rest of the species.

Our species agree with the description of *M. pellucidum* by Cobb (1920) except that in the posterior portion of the body we observed four longitudinal rows of dots, whereas Cobb states that near the tail "there are sometimes six or possibly eight rows." We cannot agree with Timm's (1961) synonymization of *M. pellucidum* with *M. poriferum* since in the two species the longitudinal rows are differently arranged, and in *M. pellucidum* the spicula are retrorsely barbed (a fact already mentioned by Cobb), whereas in *M. poriferum* they are acute distally. The description of *M. punctatum* Timm is confusing. In the text the presence of the usual number of four cephalic setae is mentioned, whereas the figure shows the head equipped with what seems to be eight or ten setae. In the text the amphids are said to describe 2.5 turns; in the figure they definitely have three turns. Even without these confusing discrepancies it would be difficult to give unequivocal reasons why *M. punctatum* and *M. poriferum* should be distinct species.

Mesonchium pellucidum (Cobb, 1920)
Plate XXVII, fig. 57, a–d

Pepsonema pellucidum Cobb, 1920: 295, 296, fig. 77.

L = 1.77–2.00 mm; w = 73–75 μ; esophagus = 250 μ; Vu = 47%. Head diameter 15 μ. Cephalic setae 12 μ. Amphids 10 μ, 2.5 turns. Buccal cavity cylindrical, 23 μ long, with three teeth. (The heads of our male specimens agree in every respect with Cobb's figures.) Cuticular differentiation: In both sexes there are four longitudinal rows of coarser dots, running from behind the amphids to behind the end of the esophagus. From there on the two outer rows gradually disappear and the whole lateral field is raised to form a lateral wing. In mid-body there are only two longitudinal rows of coarser dots. In the posterior portion of the body the wings are flattened again and the two outer rows of dots reappear. The spaces between the coarser dots are resolvable with difficulty into transverse rows of minute and closely spaced dots which are continuations of the usual transverse rows of dots into the lateral fields. Esophagus with a barrel-shaped posterior bulb and a small cardia. Ventral gland opposite end of esophagus, excretory pore behind nerve ring. Spicula 110 μ long, proximally cephalate, distally retrorsely barbed. Gubernaculum heavy, with 30 μ long apophysis. There are about 16 indistinct tubular supplements. Tail 200 μ long, a.b.d. 45–50 μ.

Representation in samples studied.—M-8, Biscayne Bay.

Geographical distribution.—Kingson, Jamaica (Cobb, 1920).

SABATIERIA de Rouville, 1903

Type species.—*Sabatieria cettensis* de Rouville, 1903: 11.

Two closely related, but distinct, species of *Sabatieria* were found in the sample from Vero Beach. Following the key given by Wieser, 1954, they belong to the group encompassing S. *cupida* Bresslau and Schuurmans-Stekhoven *in* Schuurmans-Stekhoven, 1935, S. *heterura* (Cobb, 1898), S. *rugosa* Schuurmans-Stekhoven, 1950, S. *similis* (Allgén, 1933), and S. *tenuicaudata* (Bastian, 1865).

The two new species, S. *paradoxa* and S. *paracupida*, can be separated from the above-mentioned related species by use of the following key.

KEY TO GROUP BASED ON MALE CHARACTERISTICS

1. Supplements 28–32 .... S. *tenuicaudata* (Bastian, 1865) (doubtful species)
   Supplements 15–22 2
2. Cephalic setae more than ⅔ of head diameter in length 3
   Cephalic setae less than ⅔ of head diameter in length 4
3. Spicules 46–50 μ long, 1.2 anal body diameters .... S. *cupida* Bresslau and Schuurmans-Stekhoven *in* Schuurmans-Stekhoven, 1935
   Spicules 63–68 μ long, 1.7–1.8 anal body diameters .... S. *paracupida* n. sp.
4. Spicules 1.6 or more anal body diameters in length 5
   Spicules 1.3 or less anal body diameters in length 6
5. Spicules 85 μ long, without proximal cephalation .... S. *heterura* (Cobb, 1898)
   Spicules 60–62 μ long, proximally distinctly cephalated .... S. *paradoxa* n. sp.
6. Amphid with 2.5 turns .... S. *rugosa* Schuurmans-Stekhoven, 1950
   Amphid with 2 turns .... S. *similis* (Allgén, 1933)

Sabatieria paradoxa new species
Plate XXVII, fig. 58, a–d

L = 1.46–1.66 mm; w = 42–44 μ. Diameter at base of esophagus 38–39 μ. Esophagus 135–140 μ. Tail 140–142 μ (4.0–4.1 a.b.d.). Head diameter 13 μ. Labial and cephalic papillae distinct. Cephalic setae 5–6 μ long, 38–46% of head diameter. Cervical setae, short, widely dispersed, somatic setae shorter and more widely spaced. Amphids spiral, with 2.25 turns; 7 μ wide (54% of head diameter). Lateral differentiation prominent, the transverse rows of punctations overlying the lateral chords being coarser and more widely spaced than on the remainder of the body. Spicules 60–62 μ long (1.7–1.8 a.b.d.), proximally cephalated, distally quite narrowed. Gubernaculum with lateral guiding pieces. Apophyses of gubernaculum 25–27 μ long. Preanal supplements minute, 17–19 in number. Caudal setae present, arranged as illustrated (Pl. XXVII, fig. 58, b).

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4075, Type slide No. 92. Type locality, V, Vero Beach.

Representation in samples studied.—M-7, Everglades National Park, V, Vero Beach.

Sabatieria paracupida new species

Plate XXVIII, fig. 59, a–c

L = 1.7–1.85 mm; w = 47–52 μ. Diameter at base of esophagus 44 μ. Esophagus 180–184 μ. Tail 148–150 μ (4 a.b.d.). Head diameter 13–14 μ. Labial and cephalic papillae distinct. Cephalic setae 10 μ long, 71–77% of head diameter. Cervical and somatic setae similar to preceding species. Amphids spiral, with 2.25 turns; 9 μ wide (64–70% of head diameter). Lateral differentiation as in preceding species. Spicules 63–68 μ long (1.7–1.8 a.b.d.), lacking proximal cephalation. Gubernaculum with lateral guiding pieces. Apophyses of gubernaculum 20 μ long. Preanal supplements minute, 19–22 in number. Caudal setae present, arranged as illustrated (Pl. XXVIII, fig. 59, c).

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4075, Type slide No. 93. Type locality, V, Vero Beach.

Representation in samples studied.—V, Vero Beach.

AXONOLAIMIDAE

AXONOLAIMUS de Man, 1889

Type species.—*Anoplostoma spinosum* Bütschli, 1874 *sensu* de Man, 1888: 19–21, pl. 2, fig. 11.

Axonolaimus hexapilus new species

Plate XXVIII, fig. 60, a–e

L = ♂, 1.8, ♀, 1.9 mm; w = ♂, 28, ♀, 35 μ; diameter at base of esophagus 28, 31 μ. Esophagus 172, 137 μ. Vu = 54%. Tail 128, 138 μ (4.3–4.6 a.b.d.). Head diameter 13, 14 μ. Head with six labial papillae and four cephalic setae (21–24 μ long). An additional 21–24 μ long seta is located about 5 μ behind each amphid. Amphid 12–13.5 μ long by 6–7 μ wide, slightly to distinctly open loop-shaped, 8 μ from anterior end. Buccal cavity 14–16 μ deep, of which the posterior conoid portion makes up about 10 μ. Anterior part of buccal cavity with six weak odontia. Esophagus clavate, 10 μ wide at base of buccal cavity, 12 μ at the nerve ring, expanding in the posterior ¼ to 20 μ at the base. Excretory pore slightly behind middle of conoid portion of the buccal cavity. Excretory pore ampulla 40 μ from head end, at level of "break" in esophageal musculature. Renette cell large, posterior to base of esophagus. Pseudocoelomocyte immediately behind renette cell. Cuticle finely striated. Somatic setae about 5 μ long.

Female didelphic, amphidelphic, ovaries outstretched; with two eggs observed in the posterior uterus (eggs 75–110 μ by 30 μ). Male diorchic, testes opposed, outstretched. Spicules 39 μ long. Gubernaculum short, with 12 μ long apophyses. Supplementary organs glandular, with minute exit pores. Male and female tail obtusely conoid. Caudal setae arranged as illustrated (Pl. XXVIII, fig. 60, c), those near terminus longer than the remainder. Spinneret three-lobed, the associated glands located in the tail.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4070, Type slide No. 94. Type locality, M-5, Virginia Key.

Representation in samples studied.—M-5, Virginia Key.

Remarks.—*A. hexapilus* n. sp. can be distinguished from all other *Axonolaimus* species by the presence of a long lateral seta associated near the base of each amphid. In possessing this character, along with the tri-lobed spinneret, this animal has some relationship to the monodelphic genus *Synodontium* Cobb, 1920.

ODONTOPHORA Bütschli, 1874

Type species.—*Odontophora marina* Bütschli, 1874: 285, pl. 3, fig. 13.

Odontophora variabilis new species

Plate XXVIII, fig. 61, a, b; Plate XXIX, fig. 61, c–e

L = 1.3–2.2; w = 36–50 μ; Vu = 53–56%. Diameter at base of esophagus 29–33 μ. Esophagus 112–135 μ long. Head diameter 11–15 μ. Head with cephalic papillae, 4 cephalic setae and 3 circles of subcephalic setae. Cephalic setae 14–17 μ long in ♂, 11–14 μ in ♀. First circle of subcephalic setae (paramphidial) 11–13 μ, second circle, 8–9 μ, third 4–5 μ long. The subcephalic setae all occur within the range of the buccal cavity. Cervical setae located 15–25 μ posterior to base of buccal cavity, the first circle the longest, 7–8 μ, the next two following closely and being progressively shorter. Amphid 8–10 μ long. Buccal cavity 23–25 μ long, the posterior conoid portion being 17 μ long. Buccal cavity with 6 odontia, the odontia with prominent apophyses to which are attached longitudinally directed muscles, an arrangement that undoubtedly serves to evert the odontia. Excretory pore at base of odontia. Eggs 100–110 μ long by 45 μ wide, two per uterus. Spicula sickle-shaped, 47–49 μ long, the chord being 32–33 μ. Gubernaculum with 12–13 μ long apophysis. Preanal supplements not observed. Tail length variable, 70–117 μ long. Male tail with numerous caudal setae and with terminal setae 17–18 μ long. Female tail with fewer caudal setae and devoid of terminal setae.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4075, Type slide No. 95. Type locality, V, Vero Beach.

Representation in samples studied.—V, Vero Beach.

Remarks.—The specific name *variabilis* serves to indicate the variation found within the specimens recovered from the single sample taken from the Vero Beach area. Body dimensions, such as total length, maximum width and tail length, are quite variable. Morphological structures, however, i.e., spicula, buccal cavity, amphid, distribution and size of cephalic and subcephalic setae, were conspicuously in close agreement. In particular, the shapes of the spicula were nearly identical despite the fact that the tails in the three male specimens observed measured 70 μ, 85 μ, and 117 μ in length.

O. variabilis, in possessing, in addition to the cephalic setae, three circles of subcephalic setae which could be interpreted as being arranged in four submedian rows, is related to *O. angustilaimoides* Chitwood, 1951, and perhaps may be that species. However, no mention is made of the presence of cervical setae in *O. angustilaimoides*, these being a prominent feature in *O. variabilis*. In addition, the size of the eggs and the number of eggs per uterus differs. Moreover, since no males have been described of *O. angustilaimoides*, this species is of doubtful status.

PARODONTOPHORA Timm, 1963

Type species.—*Pseudolella paragranulifera* Timm, 1952: 45, pl. 9, fig. 78.

Parodontophora brevamphida (Timm, 1952) Timm, 1963

Pseudolella brevamphida Timm, 1952: 44, 45, pl. 9, figs. 76, 77.

Parodontophora pacifica (Allgén) *sensu* Timm, 1963: 35, 36, fig. 1, g, h (NEW SYNONYMY).

L = 1.1–1.4 mm; w = 36–48 μ; Vu = 47–50%. Body bearing four rows of somatic setae, two on either side of each lateral chord. Anteriorly the somatic setae are about 4 μ long in the region of the nerve ring. At the vulva their length is reduced to less than 2 μ. Except for the anteriormost 14 μ, the cuticle is finely striated. One dorsal and two ventral setae are located in the region of the amphid. Amphid short shepherd's crook, with the ventral arm longer than the dorsal. Dorsal arm about 10 μ long, ventral arm 14–17 μ long. Amphid located on a level with and distinctly shorter than the 19 μ long posterior cylindrical portion of the stoma. Head rounded, with six lips, six labial papillae, and four 7–8 μ long, cephalic setae (75% of corresponding body diameter). There are no subcephalic setae. Anterior part of stoma with six prominent odontia, posteriorly cylindrical, 25–28 μ deep. Esophageal diameter increasing posteriorly; without basal bulb. Approximately 15 μ posterior to the base of the buccal cavity the tuboid esophageal marginal rays commence. Nerve ring encircling esophagus at approximately 65% of its length. Excretory pore not detected, the ampulla, however, located at the base of buccal cavity. Renette cell 65 μ long (40% of esophageal length), located posterior to base of esophagus. A prominent pseudocoelomocyte occurs immediately posterior to the renette cell.

Female didelphic, amphidelphic, ovaries outstretched. Eggs not observed. Male diorchic, testes opposed, outstretched. Spicules arcuate, 31–36 μ long (according to angle of view). Gubernaculum 8–10 μ long, arcuate. Male and female tail elongate-conoid, 135–155 μ long, the terminal ⅓ nearly cylindrical. Subterminal setae present on some specimens. Male with a short preanal seta and two subventral rows of 7–8 setae. Spinneret present, the gland cells located in the anterior portion of the tail.

Representation in samples studied.—V, Vero Beach.

Geographical distribution.—Chesapeake Bay, Maryland (Timm, 1952), Bay of Bengal (Timm, 1961), Arabian Sea at Karachi (Timm, 1962), Maldives (Gerlach, 1962).

Remarks.—At the present time considerable confusion exists in the taxa that have been identified as *P. pacifica* (Allgén, 1947) (syn. *Odontophora p.* Allgén). Gerlach (1962) considers a variety of species as synonyms of Allgén's species. In his list of synonyms, Gerlach lumps species in which the amphids are 18 μ long together with species in which the amphids are 80–150 μ long. This action seems a bit premature and is considered doubtful. Timm (1963) in creating the genus *Parodontophora* for species of *Odontophora* with parallel stomatal walls, intimates that *P. pacifica* might best be considered as a *species inquirenda*, validating *P. quadristicha* (Schuurmans-Stekhoven, 1950). We agree with Timm's statement and herein consider *P. pacifica* (Allgén, 1947) as a *species inquirenda*. However, in supporting such a move we do not feel that all subsequent *P. pacifica* descriptions refer to *P. quadristicha* and feel that *P. brevamphida* can be suitably differentiated from Schuurmans-Stekhoven's species.

For the present the following differences can be used to separate the two species under consideration:

P. quadristicha [syn. *O. pacifica* Allgén of Wieser, 1956] has amphids 24–32 μ long, a buccal cavity 40 μ long, and a renette cell 90–100 μ long (app. 50–55% of the esophageal length).

P. brevamphida [syn. *Pseudolella pacifica* (Allgén, 1947) of Timm, 1961, *Odontophora pacifica* Allgén of Gerlach, 1962, and *Parodontophora pacifica* (Allgén, 1947) of Timm, 1963] has amphids 12–18 μ long, a buccal cavity 25–31 μ long, and a renette cell 32–65 μ long (app. 30–40% of the esophageal length).

LEPTOLAIMIDAE

ALAIMELLA Cobb, 1920

Type species.—*Alaimella truncata* Cobb, 1920: 234, fig. 7b.

Alaimella cincta Cobb, 1920

Plate XXIX, fig. 63, a–c

Alaimella cincta Cobb, 1920: 233–234, fig. 7a.

Male.—L = 1.3 mm; w = 16 μ; diameter at base of esophagus 13 μ. Esophagus 250 μ long, with conoid cardia. Head 7 μ wide, bearing six papillae and four 12–13 μ long cephalic setae. Amphid 7 μ wide, with central raised "fleck." Cuticle coarsely annulated, the annules bearing prominent longitudinal markings. Spicules 27 μ long (chord 22 μ), proximally cephalated. Gubernaculum 9 μ long. Tail 100 μ long (7 a.b.d.), with at least one caudal seta.

Representation in samples studied.—M-2, Key Biscayne.

Geographical distribution.—Biscayne Bay, Florida (Cobb, 1920), Aransas Bay, Texas (Chitwood, 1951).

Remarks.—The central raised portion of the amphid in our specimens, while illustrated by Chitwood for his example, was not originally depicted by Cobb. This feature is somewhat suggestive of *A. truncata* Cobb, 1920. However, regarding the cuticle of *A. truncata*, Cobb states, "Secondary markings of the cuticle faint, if any." The Miami specimens, by manifesting prominent longitudinal markings, cannot be regarded as representative of *A. truncata* in view of this strong statement questioning the presence of such markings. Thus, even though the amphid on our specimens has a central fleck, we feel the remainder of the characters support our view.

CAMACOLAIMIDAE

CAMACOLAIMUS de Man, 1889

Type species.—*Camacolaimus tardus* de Man, 1889a: 8.

Camacolaimus prytherchi Chitwood, 1935

Plate XXIX, fig. 64, a–c

Camacolaimus prytherchi Chitwood, 1935: 49, 50, fig. 7, a–c.

L = ♂, 1.8, ♀, 1.9; w = ♂, 33, ♀, 39; diameter at base of esophagus 30–32 μ; esophagus 240–250 μ long. Vu = 54%. Tail 90–105 μ (3.1–3.4 a.b.d.). Head 13–14 μ wide, bearing six labial papillae and four, 8–10 μ long, cephalic setae. Somatic setae, short and thick, staggered in region overlying lateral chords, widespaced. Cuticle finely striated. Lateral surfaces with slight "bulges" anteriorly, progressively getting higher posteriorly until finally lateral alae are formed at a point approximately midway from vulva to anus, fading away quickly on the tail. Dorsal tooth and its base, 15 μ long. Esophagus divided into three distinct regions—corpus, isthmus, and swollen terminal region. Nerve ring encircling isthmus immediately behind the corpus. Terminal region gradually enlarged. Cardia 8 μ long and 12 μ wide. Spicules 53 μ long. Male tail with caudal alae and a pair of postanal setae.

Representation in samples studied.—V, Vero Beach.

Geographical distribution.—North Carolina (Chitwood, 1933); Chile (Wieser, 1956); Maldives (Gerlach, 1962).

Remarks.—An examination of the type specimen of *C. prytherchi* discloses the presence of both the caudal alae and the postanal setae. We wish to thank Mr. Curtis Sabrosky for making the specimens available for study.

DIPLOPELTIDAE

Some genera of this family have recently been transferred to the family Linhomoeidae by Gerlach (1963a). We postpone judgment on these changes until the material for our monograph is complete and shall adhere, in this paper, to the old classification.

PARATARVAIA new genus

Type species.—*Paratarvaia seta* n. sp.

Definition.—Diplopeltidae (or Linhomoeidae?). Head with 6 labial papillae and 10 cephalic setae in two circles, 6 + 4.

Amphid, double spiral, situated on punctated plaque. Esophagus cylindroid with small basal bulb, without valves. Cardia small. Female didelphic, amphidelphic. Male without supplements. Spicules arcuate, gubernaculum with medial piece, lateral guiding pieces and posteriorly directed apophyses.

Remarks.—*Paratarvaia* possesses characters that show affinity with both the Diplopeltidae (spiral amphid, amphid on plaque) and the Linhomoeidae (reduced buccal cavity and spicular apparatus as in *Terschellingia*, number of cephalic sensory organs). However, as we are going to postpone our judgment of the recent proposals by Gerlach (1963), we provisionally assign *Paratarvaia* to the Diplopeltidae. Within the Diplopeltidae *Paratarvaia* is related to both *Tarvaia* Allgén, 1934, and *Disconema* Filipjev, 1918. It is distinguished from *Tarvaia* by possessing 10 cephalic setae, as opposed to four. From *Disconema*, which lacks a plaque, *Paratarvaia* is separated by possessing a punctated plaque as well as by having the 10 cephalic setae separated into two circles of 6 and 4.

Paratarvaia seta new species

Plate XXX, fig. 65, a–c

L = 1.3–1.4 mm; w = 23–24 μ; width at base of esophagus 20–21 μ. Head 13 μ wide, bearing an internal circle of six setose labial papillae and a divided external circle of 10 (6 + 4) setae, 16 + 18 μ in length. Amphid a double spiral, 21–23 μ long and 16–17 μ wide, situated on a punctated plaque 25–27 μ long and 17 μ wide. In dorsal–ventral view the plaques are seen to be separated by a distance of 2–3 μ. Cuticle coarsely annulated, the annules about 1.5 μ wide just posterior to the amphids, about 2.0 μ at mid-body and about 1 μ wide on the tail. Body with fine somatic setae which extend onto the tail. Buccal cavity extremely reduced, with minute lips protruding from the head contour. Esophagus 165–170 μ long, cylindroid to a small, non-valvular, terminal bulb. Cardia present, flattened, not prominent. Excretory pore not observed. Vu = 54%, female with two opposed ovaries. Number of testes in male not determined. Spicules arcuate, 40 μ long (chord 25 μ). Gubernaculum complicated, bearing a medial piece between the spicules and two sigmoid lateral guiding pieces. Apophyses to gubernaculum 10 μ long. Male without supplements. Tail 150–180 μ long, the anterior ⅔ conoid, the remainder cylindroid to the slightly swollen terminus. Terminus with spinneret and two 8 μ long, terminal setae.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4067, Type slide No. 96. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

DIDELTA Cobb, 1920

Type species.—*Didelta maculatum* Cobb, 1920: 252, 253, fig. 33.

We found in our material one juvenile specimen which in every respect resembles Cobb's *Didelta maculatum*. Since Cobb's figure of the head is very good we supply only a figure of the tail of our single specimen.

Didelta maculatum Cobb, 1920

Plate XXX, fig. 66

Didelta maculatum Cobb, 1920: 252, 253, fig. 33.

Head diameter 23 μ. Cephalic setae 15 + 3 μ. Amphids (with plaque) 25 × 17 μ. Esophagus enlarged posteriorly, short cardia (25 μ long, 30 μ wide) present. Tail 410 μ, a.b.d. 37 μ. No spinneret or caudal glands.

Representation in samples studied.—M-8, Biscayne Bay.

Geographical distribution.—Off Key West, Florida (Cobb, 1920).

LINHOMOEIDAE

TERSCHELLINGIA de Man, 1888

Type species.—*Terschellingia communis* de Man, 1888: 12, pl. I, fig. 7.

The material from Florida contained

three species of *Terschellingia*. Excellent examples of *T. longicaudata* were found both in Biscayne Bay and in Florida Bay, with a variant found at Vero Beach. The distribution of the cervical setae in the specimens from the former habitats is exactly as depicted by de Man in his original figures of the species. The variant from Vero Beach has a slightly different arrangement of the cervical setae, viz., a reduction in number and a more posterior location of the first circle (compare Pl. XXX, figs. 67a, b, and 68a, b). These differences are stable within Florida habitats. Subsequent collections from South Carolina contain specimens, not only with the above two divergent patterns of cervical setae, but with intermediary distributions as well.

A second species, *T. monohystera* n. sp. is unique in that only the anterior ovary appears to be well developed, the posterior gonad being quite rudimentary. The third species, *T. longispiculata* n. sp., can be distinguished by the arrangement of the cephalic and cervical setae and also by the long spicules, which are about 2.5 anal body diameters in length.

Terschellingia longicaudata de Man, 1907 Plate XXX, figs. 67, a–c, 68, a, b; Plate XXXI, figs. 67, d, 68, c–e.

Terschellingia longicaudata de Man, 1907: 230.

L = 1.1–1.3 mm; w = 29–32 μ; diameter at base of esophagus 27–29 μ. Esophagus 90-125 μ; nerve ring at 50%. Head with four cephalic setae, 4–5 μ long. Cervical setae 4–5 μ long and arranged in distinctive patterns. The Biscayne Bay and Florida Bay specimens have two paramphidial pairs, two postamphidial pairs and a somewhat broken circle of eight situated about midway between the amphid and the nerve ring (Pl. XXX, fig. 67a). The Vero Beach specimens have a circle of four postamphidial, two sublateral and a dorsal–ventral pair (Pl. XXX, fig. 68a, b). Amphids circular, 7–8 μ wide. Terminal esophageal bulb 25 μ long and nearly of equal width. Cardia elongate, 14 μ long, 5 μ wide. Excretory pore located at a level slightly anterior to the anterior end of the esophageal bulb. Spicules 38–46 μ long (about 1.4–1.8 a.b.d), proximally cephalated. Apophyses of gubernaculum 10–12 μ long. Tail 325–365 μ long (about 14 a.b.d.).

Representation in samples studied.—M-4, Rickenbacker Causeway; M-6, M-7, Everglades National Park; M-8, Biscayne Bay; V, Vero Beach.

Geographical distribution.—Cosmopolitan.

Terschellingia monohystera new species Plate XXXI, fig. 69, a–f

L = 0.97–1.06 mm; w = 33–35 μ; Vu = 44%. Diameter at base of esophagus 31 μ. Esophagus 83–93 μ. Head diameter 13 μ. Head with four cephalic setae, 4 μ long. Four somatic setae occur in the cervical region. The anteriormost lies 8–12 μ behind the base of the amphid and is placed ventral to the lateral surface of the body. The three others are staggered dorsal and ventral in respect to the lateral surface. Amphid circular, 5 μ wide, 3–5 μ from anterior end; corresponding body diameter 14–15 μ. Female with only the anterior ovary developed and producing eggs (195 μ long), posterior branch rudimentary (70 μ long). Spicules 40 μ long (about 1.3 a.b.d.), without proximal cephalization. Apophyses of gubernaculum about 13 μ long. Tail 220–225 μ long (7.5–10 a.b.d.), of which the posterior half is filiform. Caudal setae arranged as illustrated (Pl. XXXI, fig. 69e).

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4075, Type slide No. 99. Type locality, V, Vero Beach.

Representation in samples studied.—V, Vero Beach.

Terschellingia longispiculata new species Plate XXXI, fig. 70, c, d; Plate XXXII, fig. 70, a, b

L = 2.2–2.3 mm; w = 63–65 μ; Vu = about

40%. Diameter at base of esophagus 55–57 μ. Esophagus with six cephalic papillae and four cephalic setae, 4–5 μ long. Two circles of prominent cervical setae present, four setae in each circle and all setae 4 μ long. The first circle occurs at the level of the posterior edge of the amphids. In addition to the prominent cervical setae, setae of lesser stature also occur in the anterior neck region. While these could be arranged in transverse circles of eight (sometimes incomplete), they could also be said to be arranged in eight longitudinal rows in which the prominent cervical setae might represent the anteriormost seta of each row. Amphid circular, 10 μ wide, 11–14 μ from anterior end; corresponding body diameter 33–36 μ. Terminal esophageal bulb 50 μ long and 42 μ wide. Spicules 122 μ long (about 2.5 a.b.d.); proximally cephalated. Apophyses of gubernaculum 25–30 μ long. Tail 435 μ long (about 10 a.b.d.). Caudal setae arranged as illustrated (Pl. XXXI, fig. 70, c).

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4072, Type slide No. 98. Type locality, M-7, Everglades National Park.

Representation in samples studied.—M-7, Everglades National Park, and M-8, Biscayne Bay.

MONHYSTERIDAE

MONHYSTERINAE

PARAMONHYSTERA Steiner, 1916

Type species.—*Monohystera (Paramonohystera) megacephala* Steiner, 1916: 639–641, pl. 32, fig. 37, a–f.

A key to the subgenera and species of *Paramonhystera* is provided by Wieser (1956). Following this author, the subgenus *Paramonhystera sensu stricto* contains the following species: *P. megacephala* Steiner, 1916, *P. micramphis* Schuurmans-Stekhoven, 1950, *P. biformis* Wieser, 1956, and *P. proteus* Wieser, 1956. Of these, *P. micramphis* is known from females and juveniles only and is considered a *species inquirenda*. Our new species, *P. canicula* n. sp., is distinguished from the remaining species by the long cephalic setae, the round amphids and the characteristic shape of the gubernaculum.

Paramonhystera canicula new species
Plate XXXII, fig. 71, a–d

L = 1.60 mm; w = 42 μ; esophagus = 250 μ. Head diameter 25 μ. Lips large, rounded, each with two labial setae 5 μ long. Cephalic setae 23 + 18 μ. Amphids with very faint contour, convex, in ♂, 14 μ = 52% of c.b.d. wide. Cervical and somatic setae in irregular longitudinal rows, the former 10–12 μ long. One short, asymmetrical (dorsolateral) seta between amphid and cephalic setae on each side of body. Cuticular annulation coarse. Spicula 135 μ long, knobbed proximally. Gubernaculum rather complicated, consisting of a proximal portion, cylindrical and 20 μ long, and a distal portion, 18 μ long, dilated, with ventrolateral projections, a deep notch and a serrated distal edge. Tail 175 μ long, a.b.d. 35 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4068. Type slide No. 100. Type locality, M-3, Key Biscayne.

Representation in samples studied.—M-3, Key Biscayne.

STEINERIA Micoletzky, 1922

Type species.—*Monohystera polychaeta* Steiner, 1915: 224–226, figs. 1–3 (new subsequent designation).

Monhystera setosissima Cobb, 1893, transferred to *Steineria* and regarded as the type species by Schuurmans-Stekhoven and De Coninck (1933: 10), is herein rejected as the type species of the genus *Steineria* on the grounds that it was not one of the included species brought to the subgenus *Steineria* when first established by Micoletzky (1922a: 168). This action is in accord with Article 69a (ii) of the International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology, London, July, 1958.

In this genus, two species with punctate cuticle have been known so far, i.e., S. *punctata* Gerlach, 1955, and S. *gerlachi* Wieser, 1959. From our Florida material a third species can be added that is rather closely related to S. *punctata* but can be separated on the following counts: subcephalic setae in eight groups of 5 and 4 (instead of 6 and 3), cephalic setae relatively longer, gubernaculum of different shape.

Steineria ampullacea new species

Plate XXXII, fig. 72, c; Plate XXXIII, fig. 72, a, b

L = 1.44 mm; w = 68 μ; esophagus = 210 μ. Head diameter 24 μ. Lips round, with small labial papillae. Cephalic setae jointed, 15 + 12 μ. Subcephalic setae in eight groups, the sublateral ones with 5 setae, measuring 20 + 27 + 30 + 40 + 62 μ, the submedian ones with 4 setae. Many cervical and somatic setae in eight longitudinal rows. Cuticle annulated, the annules resolvable into dots. Amphids 10 μ in ♂, 16 μ behind anterior end. Vestibulum of buccal cavity vertically striated which might be a characteristic separating this genus from *Theristus*, in which the supporting structures of the vestibulum give the impression of a more oblique striation. Excretory pore just posterior to nerve ring, the whole gland very short, its posterior end 30 μ anterior to the end of the esophagus. Spicula 55 μ long, gubernaculum with curved apophysis, 23 μ long. Tail 175 μ long, a.b.d. 55 μ, terminal setae 35 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4075, Type slide No. 101. Type locality, V, Vero Beach.

Representation in samples studied.—V, Vero Beach.

THERISTUS Bastian, 1865

Type species.—*Theristus acer* Bastian, 1865: 156, 157, pl. 13, figs. 187, 188.

Keys to the subgenera and their species are provided by Wieser, 1956. Species described subsequent to this work are considered in a more recent paper (Wieser, 1959).

Subgenus *Penzancia* de Man, 1889

Type species.—*Theristus velox* Bastian, 1865: 157, pl. 13, figs. 189–191.

The species of this subgenus may be separated into three groups according to the presence or absence of a gubernaculum and to the shape of the gubernaculum, as follows:

A) Gubernaculum with distal hook or triangular plate of characteristic shape (see Text-fig. 4):
T. bipunctatus (G. Schneider, 1906) (syn. *Monhystera bipunctata*); *T. flevensis* Schuurmans-Stekhoven, 1935 (syn. *Monhystera velox* Bütschli, 1874, de Man, 1922 nec Bastian [see Gerlach, 1951c]); *T. ambronensis* Schulz, 1935 (see Gerlach, 1951); *T. parambronensis* Timm, 1952; *T. macroflevensis* Gerlach, 1953; *T. metaflevensis* Gerlach, 1955; *T. borosi* Andrássy, 1958; and *T. calx* n. sp.

B) Gubernaculum conical or blunt:
T. inermis Gerlach, 1952; *T. parvulus* Timm, 1952 (doubtful species); *T. biarcospiculum* Timm, 1952; *T. tersus* Gerlach, 1954; *T. acribus* Gerlach, 1954; *T. megalaimoides* Wieser, 1956; and *T. stranus* Gerlach, 1957.

C) Gubernaculum absent:
T. megalaima Stewart, 1914 (doubtful species); *T. aculeatus* Schulz, 1935; *T. heteroscanicus* Wieser, 1955; and *T. hamatus* Gerlach, 1956.

All the other species listed by Wieser (1956) are here considered doubtful.

Group A, which was represented by two species in our material, is very homogeneous. The shape of the spicular apparatus (see

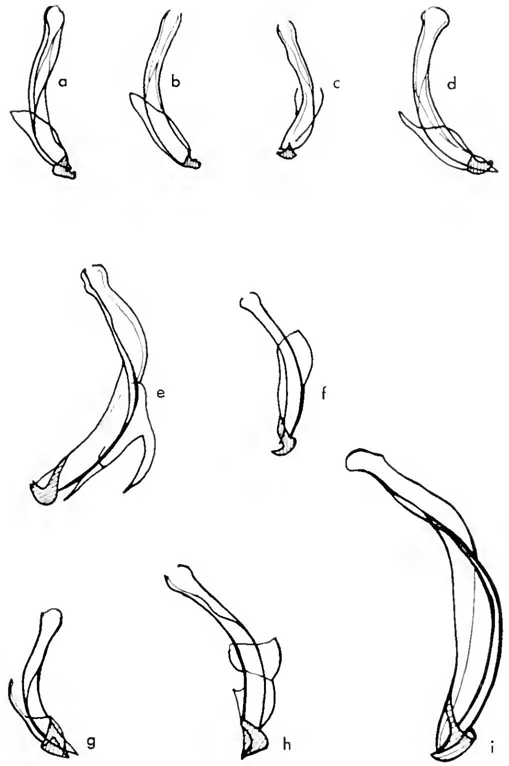


Figure 4. Spicular apparatus of species of *Theristus flevensis* group. a—*T. ambronensis* (after Gerlach, 1951); b—*T. flevensis* (after Gerlach, 1951); c—*T. bipunctatus* (after Skwarra, 1924); d—*T. macroflevensis* (after Gerlach, 1953); e—*T. borosi* (after Andrássy, 1958); f—*T. parambronensis* (after Timm, 1952); g—*T. metaflevensis* (after Gerlach, 1955); h—same species, present material; i—*T. calx* (present material).

Text-fig. 4) immediately separates *T. borosi* and *T. calx* from all other species. As for the remaining species, it could be argued that *T. flevensis*, *T. ambronensis*, and *T. bipunctatus* represent three subspecies of *T. flevensis*, characterized by the position of the vulva (65–72%), the more posterior position of the amphids, and the slight subterminal protuberance at the inner edge of the gubernacular hook (shown by Gerlach in 1951, but not in 1957). On the other hand, *T. metaflevensis* and *T. parambronensis* have the vulva at 83–87% and the gubernaculum ends distally either in a triangular plate or a smooth hook. However, the latter species is insufficiently described and the figure of the spicular apparatus is obviously rather stylized. *T. macroflevensis* is said to be characterized mainly by the long somatic setae. In other respects it links the *flevensis*-group with *metaflevensis* and *parambronensis*.

We have identified our second species with *T. metaflevensis* although we saw the gubernaculum to be slightly different from that described by Gerlach and found only *one* lateral seta instead of *three*. It is impossible at this time to judge the systematic value of these differences.

Theristus (*Penzancia*) *metaflevensis* Gerlach, 1955

Plate XXXIII, fig. 73

Theristus (*Penzancia*) *metaflevensis* Gerlach, 1955: 291–293, fig. 25, a–d

L = ♀, 1.36, ♂, 1.8 mm; w = 34–40 μ; esophagus = 230–275 μ; Vu = 83%. Head diameter ♀, 19, ♂, 26 μ. Cephalic setae 9 μ in female, 14 + 12 μ in male, only the usual ten setae seen, that is, no additional lateral setae. Amphids in male 7 μ wide, 19 μ behind anterior end, in female 6 μ and 13 μ, respectively. Spicula 53 μ long, typical. Gubernaculum rather large, distally with triangular plate in which a hook-shaped contour can be discerned. Tail in ♀, 170 μ, in ♂, 240 μ long; a.b.d. in the latter 42 μ.

Representation in samples studied.—M-4, Rickenbacker Causeway.

Geographical distribution.—San Salvador, Brazil (Gerlach, 1955).

Theristus (*Penzancia*) *calx* new species

Plate XXXIII, fig. 74, a, b

L = 3.25 mm; w = 70 μ; esophagus = 350 μ. Head diameter 31 μ. Six setose labial papillae, 10 cephalic setae, 16 + 13 μ. Amphids 7 μ = 20% of c.b.d. wide, 23 μ behind anterior end. No cervical setae. Spicula 118 μ long, of characteristic shape; the diagonal list that can be observed in all species of this group is here developed into a lateral plate connecting proximal and distal end of the spiculum. The gubernaculum is reduced except for the triangular plate that also in this species is very prominent. Tail 300 μ long; a.b.d. 60 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4069, Type slide No. 102. Type locality, M-4, Rickenbacker Causeway.

Representation in samples studied.—M-4, Rickenbacker Causeway.

Subgenus *Daptonema* Cobb, 1920
Type species.—*Daptonema fissendens* Cobb, 1920: 281, 282, fig. 66a.

In this subgenus there is a group of species distinguished by a characteristically shaped gubernaculum which gradually enlarges in its distal half, has a subterminal constriction and ends in a prominent hook (see Pl. XXXIV, fig. 75, e). Previously this group consisted of the following closely related species: *T. buetschlii* Bresslau and Schuurmans-Stekhoven, 1940; *T. buetschlioides* Chitwood, 1951, and *T. parabuetschlii* Timm, 1961. To this group we add a fourth species, *T. ostentator* n. sp., which is separated from the other three by the much larger male amphids, the shorter spicula, the longer cephalic setae and some other minor characters.

Theristus (Daptonema) ostentator new species
Plate XXXIII, fig. 75, a, b; Plate XXXIV, fig. 75, c–e

L = 1.76–1.77 mm; w = 30–32 μ; esophagus = 300–310 μ; Vu = 63%. Head diameter 20–23 μ. Lips large, with strongly developed framework (labial capsule). Labial setae 3 μ. Cephalic setae 20 + 15–16 μ, with additional lateral setae (1–3). Cervical setae short. Amphids, in male, 15 μ = 66% of c.b.d. wide, in female, 8 μ and 30%, respectively. Cuticular annulation coarse. Buccal cavity spacious, with cuticularized walls. Spicula 38–42 μ long, cephalate proximally. Gubernaculum 17–18 μ long, plate-shaped in its distal half, with subterminal constriction and terminal hook; there are also lateral projections. Tail in male, 130–155 μ long, a.b.d. 25–26 μ; in female, 175 μ long, a.b.d. 26 μ. Terminal setae, ♂, 20 μ long.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4068, Type slide No. 103. Type locality, M-3, Key Biscayne.

Representation in samples studied.—M-3, Key Biscayne.

Subgenus *Trichotheristus* Wieser, 1956
Type species.—*Steineria mirabilis* Schuurmans-Stekhoven and De Coninck, 1933: 10, 11, pl. 4, fig. 5; pl. 5, figs. 1–3.

Mesotheristus Wieser, 1956: 80, 91, NEW SYNONYMY.

We consider it inadvisable to base subgeneric division entirely on differences in the length of somatic setae and we therefore merge the two subgenera mentioned above. The important feature of this subgenus is the occurrence of long somatic setae. These setae may be confined to the anterior region of the body but they should *not* be confused with the single circle of eight groups of elongated cervical setae about on level with the amphids, characteristic of the subgenus *Pseudosteineria*.

Further classification of the subgenus may be based on the shape of the gubernaculum, the length and arrangement of the somatic setae, etc., as set out in the following key.

Key to Species of Subgenus *Trichotheristus*

1\. Gubernaculum without apophysis 2
Gubernaculum with apophysis 3
2\. Length of spicula 12.5 μ. Setae all over body .. *T. longisetosus* Schuurmans-Stekhoven and De Coninck, 1933
Length of spicula 64 μ. Setae in anterior half of cervical region only .... *T. circumscriptus* Wieser, 1959
3\. Apophysis large, set at an angle to the distal

shaft of the gubernaculum, pointing dorsocaudally 4

Apophysis small, in direct continuation of distal shaft, pointing dorsally 8

4. Somatic setae, at least in cervical region, measuring 2 c.b.d. or more 5

Somatic setae not surpassing one c.b.d. in length 7

5. Spicula strongly cephalate proximally, distally with large lateral hook. Longest setae in mid-cervical region .... *T. sanctimarteni* Timm, 1957

Spicula not cephalate, without lateral hook; longest setae in anterior cervical region 6

6. Distal half of spicula S-shaped. Additional circle of six subcephalic setae in ♂ .... *T. floridanus* n. sp.

Distal half of spicula more or less straight. No subcephalic setae .... *T. mirabilis* (Schuurmans-Stekhoven and De Coninck, 1933)

7. Cephalic setae 23–26 μ long, male amphids 13 μ wide, apophysis of gubernaculum rod-shaped .... *T. laxus* Wieser, 1956

Cephalic setae 13–16 μ, amphids 5–8 μ, apophysis of gubernaculum plate-shaped .... *T. setosus* (Bütschli, 1874); *T. hirtus* Gerlach, 1951 (for differences see Gerlach, 1951)

8. Somatic setae, at least in cervical region, measuring 1.5 c.b.d. or more 9

Somatic setae not surpassing one c.b.d. in length .... *T. erectus* n. sp.

9. Amphids distinctly spiral. Cephalic capsule well developed. One circle of four subcephalic setae in male .... *T. galeatus* n. sp.

Amphids circular. No cephalic capsule. No subcephalic setae 10

10. Lateral cephalic seta in ♂ elongated. Amphids 0.5 head diameters behind anterior end .... *T. heterus* Gerlach, 1957

Lateral cephalic seta not particularly elongated. Amphids 1.5 head diameters behind anterior end .... *T. setifer* Gerlach, 1952

Theristus (Trichotheristus) floridanus new species

Plate XXXIV, fig. 76, a–d

L = 1.50–1.57 mm; w = 50–60 μ; esophagus = 325–350 μ; Vu = 65%. Head diameter 20–23 μ. Lips round, labial papillae setose, short. Head with 12 cephalic setae, 20 + 16 μ long; in ♂ there is an additional circle of 6 subcephalic setae. Long and short somatic setae, the longest ones measuring 60–70 μ which is nearly 3 c.b.d. in the cervical region, about 1.2 c.b.d. in mid-body. Amphids in ♂, 7 μ, in ♀, 6 μ wide, 18–23 μ behind anterior end. Spicula 37 μ long, distal half S-shaped. Gubernaculum complicated, with plate-shaped apophysis, 10 μ long. Tail in ♂ 225 μ long = 5 a.b.d., in ♀ 250 μ long = 5.5 a.b.d. Terminal setae 60 μ long.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4067, Type slide No. 104. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

Theristus (Trichotheristus) erectus new species

Plate XXXIV, fig. 77, b; Plate XXXV, fig. 77, a, c, d

L = 1.3 mm; w = 55 μ; esophagus = 275 μ. Head diameter 16–24 μ. Lips round, labial papillae setose, short. Cephalic setae 10–17 + 8–15 μ long. Short and long somatic setae, the longest ones measuring 34 μ which is about one body diameter in the cervical region. There are four characteristic pairs of sublateral setae behind the amphids. Amphids in ♂ 6–7 μ = about 23% of c.b.d. in width, 16–22 μ behind anterior end. Cuticle with lateral alae (incisures?) which occur, for the most part, as two parallel refractive lines 7–8 μ apart (about $^1/_7$–$^1/_8$ c.b.d.). In the posterior neck and preanal regions, there frequently occurs a third refractive line between those normally present. Faint cuticular striations can be traced over the lateral alae. Spicula 35–38 μ long, proximal end cephalate, distal half slightly S-shaped, distal end with a lateral tooth. Gubernaculum 23 μ, with small, plate-shaped dorsal apophysis. Tail 200–210 μ long, a.b.d. 40 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4067, Type slide No. 105. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne, M-3, Key Biscayne, and M-4, Rickenbacker Causeway.

Remarks.—The closest relative of this species is *T. setosus* from which it can be separated by the small and dorsally directed apophysis of the gubernaculum.

Theristus (*Trichotheristus*) *galeatus* new species

Plate XXXV, fig. 78, a–c

L = 1.02 mm; w = 32 μ; esophagus = 205 μ. Head diameter 15 μ. Labial papillae setose, short. Cephalic setae jointed, 10 in number, 15 + 12 μ long. Male with 4 subcephalic setae. Short and long somatic setae, the longest ones measuring 65 μ which is about three times the c.b.d. in the cervical region. Cuticular annulation coarse, one annule 1.4 μ wide. The head seems to be strengthened by a cephalic capsule which consists of two portions, an anterior and a posterior one. Amphids spiral, 6 × 7 μ, 32–36 μ behind anterior end. Spicula 36 μ long, cephalate proximally, distally with a lateral tooth. Gubernaculum with dorsal apophysis and a distal three-pronged piece. In the postanal region there are indications of 'breaks' in the cuticular annulation. These breaks, however, seem to be rather irregular and are differently arranged in different specimens. Tail 170 μ long, a.b.d. 36 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4070, Type slide No. 106. Type locality, M-5, Virginia Key.

Representation in samples studied.—M-5, Virginia Key.

Subgenus *Cylindrotheristus* Wieser, 1956

Type species.—*Monohystera normandica* de Man, 1890: 169–171, pl. 3, figs. 1–1d.

This subgenus presents the greatest problems of classification, and, due to the insufficiency of many descriptions, no satisfactory treatment is possible at the present time. We follow Wieser (1956, 1959) and, on the basis of the shape of the gubernaculum, distinguish three groups of species, viz., A) gubernaculum without apophysis, B) with small dorsal apophysis, C) with distinct caudal apophysis. No new species have been described since Wieser's paper of 1959, but probably more of the species included in the grouping by Wieser have to be considered as *species inquirendae*, e.g., *T. longicaudatus* Filipjev, 1922, and *T. naviculivorus* Cobb, 1930.

Group A, species without gubernacular apophysis, contains a number of species in which the spicula in their distal fifth or sixth show a very characteristic outward bend. This additional curvature of the spicula appears to give, as it were, more room to the development of the distal portion of the gubernaculum which in these species shows some complex features that are difficult to analyze. The situation is illustrated by figures 79, c, and 80, c, d on Plate XXXVI in this paper. To this subgroup belong with certainty *T. kornoeensis* (Allgén, 1929) *sensu* Wieser, 1959, *T. oxyuroides* (Schuurmans-Stekhoven, 1931) and *T. fistulatus* n. sp., but it cannot be excluded that some more species described in the literature show the same differentiation of the spicular apparatus. *T. trecuspidatus* Wieser, 1959, displays the same characteristic but, by possessing a small dorsal apophysis of the gubernaculum, has been assigned to the next group.

Group B of this subgenus, comprising species with small dorsal gubernacular apophysis, is represented in our material by two well characterized new species, *T. tortus* n. sp., and *T. xyaliformis* n. sp.

Theristus (*Cylindrotheristus*) *oxyuroides* (Schuurmans-Stekhoven, 1931)

Plate XXXVI, fig. 79, a–c

Monhystera oxyuroides Schuurmans-Stekhoven, 1931: 655, 656, fig. 8, a–e.

L = 0.9 mm; w = 43 μ; esophagus = 140 μ. Head diameter 14 μ. Lips round, with short setose papillae. Twelve subequal cephalic setae, 9 μ long. Rows of short cervical and somatic setae. Amphids 7 μ wide, 12 μ behind anterior end. Spicula 28 μ long, sharply bent in middle and with an additional outward curvature in its distal sixth. Gubernaculum sleeve-like, without apophysis, distal half with curved pieces. Tail 160 μ long, a.b.d. 29 μ.

Representation in samples studied.—M-4, Rickenbacker Causeway.

Geographical distribution.—Baltic, North Sea, Zuiderzee; Chesapeake Bay, Maryland (Timm, 1952).

Remarks.—Our material contained what we consider to be fairly typical representatives of *T. oxyuroides* (Schuurmans-Stekhoven, 1931). The characteristic distal curvature of the spicula is apparent in Schuurmans-Stekhoven's original description, but both Gerlach (1951c) and Timm (1952), as far as one can infer from their figures, seem to hold that it is the gubernaculum and not the spicula that is curved distally. *T. kornoecensis* (Allgén, 1929) and *T. fistulatus* n. sp. can be separated from *T. oxyuroides* by the more backward position of the amphids and by differences in the finer structure of the spicular apparatus.

Theristus (*Cylindrotheristus*) *fistulatus* new species

Plate XXXVI, fig. 80, a–d

L = 0.86–1.04 mm; w = 30–36 μ; esophagus = 144–180 μ. Head diameter 15 μ. Lips round, bearing short setose papillae. Ten to 12 cephalic setae 13 + 11 μ long. Scattered cervical and somatic setae. Amphids 8–9 μ = 40–45 per cent of c.b.d. wide, 15–18 μ behind anterior end. Spicula 25–27 μ long, cephalate proximally, outwardly curved in its distal sixth. Gubernaculum sleeve-like, without apophysis, distally with curved, tubular piece. Tail 210–228 μ long, a.b.d. 23–26 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4068, Type slide No. 107. Type locality, M-3, Key Biscayne.

Representation in samples studied.—M-3, Key Biscayne.

Remarks.—*T. fistulatus* is characterized by the tubular element in the distal portion of the gubernaculum, whereas *T. kornoecensis* is equipped with two lateral projections at the distal tip of the gubernaculum.

Theristus (*Cylindrotheristus*) *tortus* new species

Plate XXXVI, fig. 81, a–d

L = 0.74–0.76 mm; w = 25–30 μ; esophagus = 168–192 μ. Head diameter 10–12 μ. Lips round, bearing short setose papillae. Ten to 12 cephalic setae, 10–12 + 7–9 μ long. No cervical or somatic setae. Amphids in ♀, 8 μ = 47% of c.b.d. wide, 24 μ behind anterior end, in ♂, 10 μ = 60% of c.b.d. wide, 23 μ behind anterior end. Thirteen to 15 cuticular annules between anterior end and amphids. Spicula slender, of even thickness, 27 μ long, cephalate proximally. Gubernaculum 15–16 μ long, with short dorsal apophysis, oblique grooves in distal half and two conspicuous, laterally pointing projections at its distal end. Tail in ♀, 175 μ, in ♂, 132–156 μ long, a.b.d. 20 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4067, Type slide No. 108. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

Remarks.—*T. tortus* n. sp. is distinguishable from all other species of this group by the large and posteriorly situated amphids, and by the shape of the gubernaculum. Its closest relative is *T. resimus* Wieser, 1959, which has a similar gubernaculum, although without the oblique grooves that occupy the anterior part of the gubernaculum in *T. tortus*.

Theristus (Cylindrotheristus) xyaliformis new species

Plate XXXVI, fig. 82, a–d

L = 0.63–0.73 mm; w = 21–22 μ; esophagus = 125–150 μ. Head round, diameter 6 μ. Labial papillae indistinct. Ten cephalic setae, subequal, 5 μ long. No cervical and somatic setae. Amphids 5 μ = 50% of c.b.d. wide, 20–22 μ behind anterior end, about 30 cuticular annules between anterior end and amphids. Buccal cavity unusually deep by enlargement of the "buccal ring." Spicula 19–20 μ long, cephalate proximally. Gubernaculum distally with small lateral projection, proximally with hook-shaped dorsally pointing apophysis. Tail 127–145 μ long, a.b.d. 16–19 μ.

Holotype specimen.—Male; Canadian National Collection of Nematodes, Entomology Research Institute, Ottawa, Collection Number 4067, Type slide No. 109. Type locality, M-2, Key Biscayne.

Representation in samples studied.—M-2, Key Biscayne.

Remarks.—In *T. xyaliformis* n. sp. the buccal cavity differs from that of all other species of *Theristus* by its elongation. The elongation has come about by the widening of the "buccal ring" which is in fact the prostome (in the sense of Osche, 1952), i.e., that part of the buccal cavity that lies between the base of the lips and the anterior end of the esophagus. Since the same type of elongation is a characteristic feature of the subfamily Xyalinae, *T. xyaliformis* can be considered to link this subfamily with the Monhysterinae. Moreover, *T. xyaliformis* is characterized by the far posteriorly situated amphids and by the hook-shaped apophysis of the gubernaculum.

MONHYSTERA Bastian, 1865

Type species.—*Monhystera stagnalis* Bastian, 1865: 97, pl. 9, figs. 9–11.

The proper status of our species is impossible to determine. It is undoubtedly closely related to *M. parva* (Bastian) but the differences of opinion concerning this species cannot be resolved at present. De Man (1888) figures the spicula of *M. parva* without any teeth or projections but subsequent authors all show the spicula in their proximal third or fourth to be equipped with a ventral projection (actually the point of attachment of the muscular "velum"). De Coninck and Schuurmans-Stekhoven (1933) claim that de Man overlooked this projection and consider *M. heteroparva* Micoletzky, 1924, to be a synonym. Timm (1952) rejected this claim and revived *M. heteroparva* as a valid species, to be separated from *M. parva* by the possession of this ventral tooth. Andrássy (1958) figured the spicular apparatus of *M. parva* not only with the proximal projection but also with a distal "nose" and hook. Our species closely agrees with Andrássy's description and figure and we tend to think that indeed many authors overlooked, or misinterpreted, either the proximal or the distal projection, or both, and that *M. parva* is a cosmopolitan species which needs to be restudied in its type habitat. We observed faint preanal supplements but again have our doubts whether this can be considered a real difference from previous descriptions.

Monhystera parva (Bastian, 1865)

Plate XXXVII, fig. 83, a–d

Tachyhodites parvus Bastian, 1865: 156, pl. 13, figs. 185, 186; *Monhystera parva* var. *meridiana* Micoletzky, 1922; *M. heteroparva* Micoletzky, 1924; *M. kossnensis* Paramonon, 1929; *M. antarctica* Cobb, 1914.

L = 0.58–0.72 mm; w = 18–22 μ; esophagus = 102–115 μ; Vu = 65%. Head diameter 8–10 μ. No labial papillae seen. Ten cephalic setae, 4 + 3 μ long. Amphids in ♂, 3.5 μ = 36% of c.b.d. wide, 10 μ behind anterior end. Two pairs of submedian cervical setae, 25 μ behind anterior end, excretory pore 37 μ, nerve ring 63 μ behind anterior end. Spicula 26–27 μ long, with proximal "handle" and projection on which the velum attaches, distally with a triangular cuticularized piece which forms a sort of recurved hook. Gubernacular apophysis 13 μ. About 15 indistinct preanal and two postanal supplements. In some specimens these supplements are hardly visible and appear only as darker and lighter portions of the cuticle. Tail 95–100 μ long, a.b.d. 16–18 μ.

Representation in samples studied.—M-1, Key Biscayne.

Geographical distribution.—Cosmopolitan.

XYALINAE

SCAPTRELLA Cobb, 1917

Type species.—*Scaptrella cincta* Cobb, 1917: 119, fig. 4.

Scaptrella cincta Cobb, 1917

Plate XXXVII, fig. 84, a–c

Scaptrella cincta Cobb, 1917: 119, fig. 4.

L = 1.7 mm; w = 41 μ; diameter at base of esophagus 33 μ. Esophagus 220 μ. Tail 360 μ. Head diameter 20 μ. Labial setae 6–7 μ long. Cephalic setae 12 (6 + 6), the lateral pairs 30 + 18 μ, the submedian 50 + 30 μ long. Amphid circular, with internal spiral, ♂, 10 μ, ♀, 8 μ wide. Buccal cavity cylindrical, 30 μ deep. Anteriorly armed with 6 jointed odontia. In addition, a blunt, weakly-sclerotized, dorsally-positioned onchium is present. Cuticle coarsely striated, about 3 μ wide in neck region and about 2 μ in mid-body. Somatic setae numerous, very fine, averaging 17 μ long on most of the body length. Tail with numerous caudal setae and a pair of 20 μ long terminal setae. Spicula 34 μ long, proximally cephalated. Gubernaculum with bidentated lateral guiding pieces.

Representation in samples studied.—M-2, Key Biscayne.

Geographical distribution.—Atlantic Coast from Massachusetts to North Carolina (according to Chitwood, 1951), Pernambuco, Brazil (Gerlach, 1956).

Remarks.—*Scaptrella cincta* is separated from *S. brevicaudata* Gerlach, 1952, by the longer and more filiform tail and by the longer cephalic setae.

XENOLAIMUS Cobb, 1920

Type species.—*Xenolaimus striatus* Cobb, 1920: 250, 251, fig. 30.

Xenolaimus striatus Cobb, 1920

Plate XXXVII, fig. 85, a–d

Xenolaimus striatus Cobb, 1920: 250, 251, fig. 30.

L = 1.06 mm; w = 33 μ; esophagus = 300 μ. Head diameter 16–17 μ. Lips 7 μ high, flap-like. Labial setae 5.5 μ long. Ten cephalic setae, the longer ones measuring 19 μ; the two setae of each submedian pair stick together. Buccal cavity wide and deep, with two weakly cuticularized teeth or cuticular folds projecting from the base of the mouth to the base of the lips. Amphids in an enlarged portion of the fifth cuticular annule. This enlargement about 6 μ. First cuticular annule wider than the following ones. The head, in the words of Cobb (1920: 250), "is protrusile and appears as if surrounded by a balustrade composed of the anterior annules of the cervical cuticle." Cuticular annulation coarse, with an unspecified number (12?) of longitudinal rows of V-shaped structures. Spicula asymmetrical, 28–30 + 32–34 μ long. Apophyses of gubernacula also asymmetrical, 17 + 21 μ long. Tail conical, 145 μ long, a.b.d. 27 μ.

Representation in samples studied.—M-2, Key Biscayne.

Geographical distribution.—Biscayne Bay, Florida (Cobb, 1920).

Remarks.—The present record represents the first time this species has been found since Cobb's original description. An unidentified example of *Xenolaimus* was recorded in a list of nematodes from the Gulf Coast of Florida by King, 1962 (*Xenolaimus* sp.).

ACKNOWLEDGMENTS

The collecting trip during the period from May 7 to June 8, 1963, was made possible through NSF grant GB 498 to one of us (W.W.). In this connection, we wish to thank Professor Ernst Mayr and Dr. Giles Mead of the Museum of Comparative Zoology of Harvard University for their support and encouragement. Particular thanks are due to Mr. R. H. Mulvey, Chief, Nematology Section, Entomology Research Institute, Canada Department of Agriculture, Ottawa, in whose Section the slides of our collections were mounted and who supported our project in many other ways. We wish to thank Mr. Curtis W. Sabrosky, U.S.D.A., Washington, for making available for study several type specimens from the United States National Museum. We are grateful to Dr. S. P. Meyers, of the Institute of Marine Science, University of Miami, Miami, Florida, who arranged for our stay at the Institute and, in addition, provided valuable assistance. Miss Nancy Van Meter served as an efficient guide to collecting sites in the Everglades National Park.

Many more people were very helpful to us during our trip and we shall acknowledge their hospitality and cooperation as we proceed with publication of our reports.

REFERENCES CITED

Allgén, C. A. 1927. Freilebende marine Nematoden von der Küste Tasmaniens. Zool. Anz., **73**: 197–217.

———. 1933. Freilebende Nematoden aus dem Trondheimsfjord. Capitata Zoologica, Deel **IV**, Afl. 2: 1–162.

———. 1959. Freeliving marine nematodes. Further results of the Swedish Antarctic Exped. 1901–1903, Stockholm. Zoology, **5**: 1–293.

Andrássy, I. 1958. Ergebnisse der zoologischen Aufsammlungen des ungarischen naturwissenschaftlichen Museums in Ägypten im Jahre 1957. Ann. Hist. Nat. Mus. Nat. Hung., **50**: 135–150.

Bastian, C. H. 1865. Monograph of the Anguillulidae or free nematoids, marine, land, and fresh-water; with descriptions of 100 new species. Proc. Linn. Soc. London, **25**: 73–184.

Brunetti, B. 1949. Contributo alla conoscenza dei Nematodi del M. Tirreno. II. Monit. Zool. Ital., **57**: 41–59.

———. 1950. Osservazioni critiche sul genere *Enoploides* Saveljev, 1912 (Nematoda, Enoplata). Monit. Zool. Ital., **58**: 45–48.

Bütschli, O. 1874. Zur Kenntnis der freilebenden Nematoden insbesondere der des Kieler Hafens. Abh. Senckenberg. Naturf. Ges., **9**: 237–292.

Chitwood, B. G. 1935. A new nematode, *Camacolaimus prytherchi*, n. sp. (Camacolaimidae). Proc. Helminthol. Soc. Washington, D.C., **2**: 49–50.

———. 1936. Some marine nematodes from North Carolina. Proc. Helminthol. Soc. Washington, D.C., **3**: 1–16.

———. 1951. North American marine nematodes. Texas J. Sci., **3**: 617–672.

———. 1956. A revision of the genus *Haliplectus* Cobb, 1913. Proc. Helminthol. Soc. Washington, D.C., **23**: 78–87.

———. 1960. A preliminary contribution on the marine nemas (Adenophorea) of northern California. Trans. Am. Microscop. Soc., **79**: 347–384.

Chitwood, B. G., and M. B. Chitwood. 1938. Notes on the "culture" of aquatic nematodes. J. Washington Acad. Sci., **28**: 455–460.

———. 1950. An introduction to nematology. Sect. 1. Monumental Printing Co., Baltimore, Md., pp. viii + 213.

Cobb, N. A. 1893. *Tricoma* and other nematode genera. Proc. Linn. Soc. N.S. Wales, **8**: 389–421.

———. 1898. Australian free-living marine nematodes. Proc. Linn. Soc. N.S. Wales, **23**: 383–407.

———. 1917. Notes on nemas. Contrib. Sci. Nematol., **5**: 117–128.

———. 1920. One hundred new nemas. Contrib. Sci. Nematol., **9**: 217–343.

———. 1922. *Greeffiella*. (*Trichoderma* Greef, 1869; not *Trichoderma* Steph., 1835). J. Washington Acad. Sci., **12**: 229–303.

———. 1930. The demanian vessels in nemas of the genus *Oncholaimus*; with notes on four new oncholaims. J. Washington Acad. Sci., **20**: 225–241.

———. 1933. New nemic genera and species, with taxonomic notes. Edited by Margaret V. Cobb. J. Parasitol., **20**: 81–94.

Coles, J. W. 1965. A critical review of the marine nematode genus *Euchromadora* de Man, 1886. Bull. Brit. Mus. (Nat. Hist.) Zool., **12**: 159–194.

De Coninck, L. A. 1944. Scientific results of Prof. Dr. P. Van Dye's Expedition in Iceland. XVI. Les Nématodes libres des eaux et des terres saumâtres. Biol. Jaarboek, Gent, **11**: 165–220.

De Coninck, L. A., and J. H. Schuurmans-Stekhoven. 1933. The free living marine nemas of the Belgian coast. Part II. With general remarks on the structure and the system of nemas. Mém. Mus. Hist. Nat. Belg., **58:** 1–163.

CRITES, J. L. 1961. Some free-living marine nematodes from the sand beaches of Piver's Island, North Carolina. J. Elisha Mitchell Sci. Soc., **77:** 75–80.

DITLEVSEN, H. 1911. Danish free-living nematodes. Vid. Medd. Naturh. Forening Kjøbenhavn (1912), **63:** 213–256.

———. 1926. Free-living nematodes. The Danish Ingolf Exp., **4:** 1–42.

EBERTH, G. 1863. Untersuchungen über Nematoden. Leipzig, 77 p.

FILIPJEV, I. N. 1918. (Free-living marine nematodes of the vicinity of Sevastopol. Part I.) (In Russian.) Tr. Osob. Zool. Lab. Sevastopol Biol. Stantsiya Ross. Akad. Nauk s., **2:** 1–352.

———. 1927. Les nématodes libres des mers septentrionales appartenant à la famille des Enoplidae. Arch. Naturgesch., **91**, A: 1–216.

———. 1934. The classification of the free-living nemas and their relation to the parasitic nemas. Smithsonian Inst., Misc. Collect., **89:** 1–63.

GERLACH, S. A. 1951a. Nematoden aus der Familie der Chromadoridae von den deutschen Küsten. Kieler Meeresforsch., **8:** 106–132.

———. 1951b. Revision der Metachromadoracea, einer Gruppe freilebender mariner Nematoden. Kieler Meeresforsch., **8:** 59–75.

———. 1951c. Freilebende Nematoden aus der Verwandtschaft der Gattung *Theristus*. Zool. Jahrb. (Syst.), **80:** 379–406.

———. 1952. Die Nematodenbesiedlung des Sandstrandes und des Küstengrundwassers an der italienischen Küste. I. Systematischer Teil. Archivio Zool. Italiano, **37:** 517–640.

———. 1954. Freilebende Nematoden aus der Lagoa de Freitas (Rio de Janeiro). Zool. Anz., **153:** 135–143.

———. 1955. Zur Kenntnis der freilebenden marinen Nematoden von San Salvador. Z. Wiss. Zool., **158:** 249–303.

———. 1956. Diagnosen neuer Nematoden aus der Kieler Bucht. Kieler Meeresforsch., **12:** 85–109.

———. 1957a. Marine Nematoden von der Kongomündung. Bull. Inst. Roy. Sci. Nat. Belgique, **33:** 1–16.

———. 1957b. Marine Nematoden aus dem Mangrove-Gebiet von Cananeia. (Brasilianische Meeres-Nematoden III.) Abhandl. Akad. Wiss. Lit. Mainz, Math.-Naturw. Kl. Jg. 1957, Nr., **5:** 131–176.

———. 1957c. Die Nematodenfauna des Sandstrandes an der Küste von Mittelbrasilien. (Brasilianische Meeres-Nematoden IV.) Mitt. Zool. Mus., Berlin, **33:** 411–459.

———. 1958a. Die Nematodenfauna der sublitoralen Region in der Kieler Bucht. Kieler Meeresforsch., **14:** 64–90.

———. 1958b. Deuxième contribution à la faune des nematodes des eaux interstitielles littorales de Madagascar. Mém. Inst. Sci. Madagascar, Sér. F, **2:** 343–365.

———. 1958c. Freilebenden Nematoden von den Korallenriffen des Roten Meeres. Kieler Meeresforsch., **14:** 241–246.

———. 1962. Freilebende Meeresnematoden von den Malediven. I. Kieler Meeresforsch., **18:** 81–108.

———. 1963a. Über freilebende Meeresnematoden. Revision der Linhomoeidae. Zool. Jahrb. (Syst.), **90:** 599–658.

———. 1963b. Freilebende Meeresnematoden von den Malediven II. Kieler Meeresforsch., **19:** 67–103.

———. 1964. Revision der Choniolaiminae und Selachinematinae (freilebende Meeresnematoden). Mitt. Hamburg. Zool. Mus. Int., **40:** 23–50.

HOPPER, B. E. 1961a. Marine nematodes from the coast line of the Gulf of Mexico. Can. J. Zool., **39:** 183–199.

———. 1961b. Marine nematodes from the coast line of the Gulf of Mexico, II. Can. J. Zool., **39:** 359–365.

———. 1962. Free-living marine nematodes of Rhode Island waters. Can. J. Zool., **40:** 41–52.

———. 1963. Marine nematodes from the coast line of the Gulf of Mexico. III. Additional species from Gulf Shores, Alabama. Can. J. Zool., **41:** 841–863.

———. 1966. *Theristus polychaetophilus* n. sp. (Nematoda), an external parasite of the spionid polychaete *Scolelepis* (*Scolelepis*) *squamata* (Müller, 1806). Can. J. Zool., **44:** 787–791.

INGLIS, W. G. 1962. Marine nematodes from Banyuls-sur-Mer: With a review of the genus *Eurystomina*. Bull. Brit. Museum (Nat. Hist.), Zool., **8:** 211–283.

———. 1963. New marine nematodes from off the coast of South Africa. Bull. Brit. Museum (Nat. Hist.) Zool., **10:** 531–552.

KING, C. E. 1962. Some aspects of the ecology of psammolittoral nematodes in the northeastern Gulf of Mexico. Ecology, **43:** 515–523.

KREIS, H. A. 1928. Weiterer Beitrag zur Kenntnis der freilebenden marinen Nematoden. Arch. Naturgesch., **92**, A: 1–29.

———. 1932. Papers from Dr. Th. Mortensen's Pacific expedition 1914–16. LXI. Freilebende marine Nematoden von den Sunda-Inseln. II. Oncholaiminae. Vidensk. Medd. Dansk Naturh. Foren. København, **93:** 23–69.

———. 1934. Oncholaiminae Filipjev, 1916.

Eine monographische Studie. Capita Zoologica, **4:** 270 pp.

Luc, M., and L. A. P. De Coninck. 1959. Travaux de la Station Biologique de Roscoff, LII. Nématodes libres marins de la région de Roscoff. Arch. Zool. Exp. Gen., **98:** 103–165.

Man, J. G. de. 1878. Contribution à la connaissance des nematodes du Golfe de Naples. Tijdschr. Ned. Dierk. Ver., **3:** 88–118.

———. 1888. Sur quelques nématodes libres de la Mer du Nord, nouveaux ou peu connus. Mém. Soc. Zool. France, **1:** 1–51.

———. 1889a. Espèces et genres nouveaux de nématodes libres de la Mer du Nord et de la Manche. Mém. Soc. Zool. France, **2:** 1–10.

———. 1889b. Troisième note sur les nématodes libres de la Mer du Nord de la Manche. Mém. Soc. Zool. France, **2:** 182–216.

———. 1890. Quatrième note sur les nématodes libres de la Mer du Nord et de la Manche. Mém. Soc. Zool. France, **3:** 169–194.

———. 1907. Sur quelques espèces nouvelles ou peu connues de nématodes libres vivant sur les côtes de la Zélande. Tijdschr. Ned. Dierk. Ver., **2:** 227–244.

———. 1922a. Neue freilebende Nematoden aus der Zuidersee. Tijdschr. Ned. Dierk. Ver., **18:** 124–134.

———. 1922b. Über einige marine Nematoden von der Küste von Walcheren, neu für die Eissenschaft und für unsere Fauna, unter welchen der sehr merkwürdige *Catalaimus Max Weberi* n. sp. Bijdr. Dierk. K. Zool. Genootsch. Natura Artis Magistra. Amsterdam, **22:** 117–124.

Marion, A. F. 1870. Recherches zoologiques et anatomiques sur des nématoides non parasites, marins. Ann. Sci. Nat., Paris, Zool., **13:** 1–100.

Mawson, P. M. 1958a. Free-living nematodes. Section 2: Additional Enoploidea from Antarctic stations. B.A.N.Z. Antarctic Res. Exp. 1929–1931, Rep. Ser. B, **6:** 291–305.

———. 1958b. Free-living nematodes. Section 3: Enoploidea from subantarctic stations. B.A.N.Z. Antarctic Res. Exp. 1929–1931, Rep. Ser. B, **6:** 307–358.

Micoletzky, H. 1922a. Die freilebenden Erd-Nematoden mit besonderer Berücksichtigung der Steiermark und der Bukowina, zugleich mit einer Revision sämtlicher nicht mariner, freilebender Nematoden in Form von Genus-Beschreibungen und Bestimmungsschlüsseln. Arch. Naturg., Berlin (1921), **87**, Abt. A, 1–650.

———. 1922b. Neue freilebende Nematoden aus Suez. Sitzungsber. Akad. Wiss. Wien, Math.-Naturw. Kl., **131:** 77–103.

———. 1924a. Weitere Beiträge zur Kenntnis freilebender Nematoden aus Suez. Sitzungsber. Akad. Wiss. Wien, Math.-Naturw. Kl., **132:** 225–262.

———. 1924b. Letzter Bericht über freilebende Nematoden aus Suez. Sitzungsber. Akad. Wiss. Wien, Math.-Naturw. Kl., **133:** 137–179.

———. 1930. Freilebende marine Nematoden von den Sunda-Inseln. I. Enoplidae (Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16, LIII). Vidensk. Medd. Dansk Naturh. Foren. København (1929–1930), **87:** 243–339.

Murphy, D. G. 1963. A note on the structure of nematode ocelli. Proc. Helminthol. Soc. Washington, D. C., **30:** 25–26.

Osche, G. 1952. Systematik und Phylogenie der Gattung *Rhabditis* (Nematoda). Zool. Jahrb. (Syst.), **81:** 190–280.

Pearse, A. S., H. J. Humm, and G. Walton. 1942. Ecology of sand beaches at Beaufort, North Carolina. Ecol. Monogr., **12:** 135–190.

Saveljev, S. 1912. Zur Kenntnis der freilebenden Nematoden des Kolafjords und des Relictensee Mogilnoje. Trans. Soc. Imp. Nat. St. Petersburg (Zoologie), **43:** 108–126.

Schuurmans-Stekhoven, J. H. 1931. Ökologische und morphologische Notizen über Zuiderseenematoden I. Die westliche Hälfte der Zuidersee. Morphol. Ökol., **20:** 613–678.

———. 1935. Nematoda errantia. *In* Grimpe and Wagler, Tierwelt der Nort- u. Ostsee. Lief., **28** V. b, 1–173.

———. 1942. The free living nematodes of the Mediterranean. III. The Balearic Islands. Zool. Mededeel. Rijksmus. Nat. Hist., Leiden, **23:** 229–262.

———. 1943. Freilebende marine Nematoden des Mittelmeeres. IV. Freilebende marine Nematoden der Fishereigründe bei Alexandrien. Zool. Jahrb. (Syst.), **76:** 323–380.

———. 1950. Mediterranean free-living marine nematodes. I. The Bay of Villefranche. Mém. Mus. Roy. Hist. Nat. Belg., **37:** 1–220.

Schuurmans-Stekhoven, J. H., and L. A. De Coninck. 1933. Diagnosis of new Belgian marine nemas. Bull. Mus. Roy. Hist. Nat. Belg., **9:** 1–15.

Seinhorst, J. W. 1959. A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. Nematologica, **4:** 67–69.

Skwarra, E. 1924. Ergänzung zur Kenntnis eines freilebenden Nematoden *Monohystera bipunctata* G. Schneider. Arch. Hydrobiol., **15:** 225–226.

Southern, R. 1914. Nemathelmia, Kinorhyncha and Chaetognatha. Proc. Roy. Irish Acad., **31:** sect. 3, Clare Island Surv., pt. 54, 80 pp.

Steiner, G. 1915. Freilebende marine Nematoden von der Küste Sumatras. Zool. Jahrb. (Syst.), **38:** 224–244.

———. 1916. Freilebende Nematoden aus der Barentssee. Zool. Jahrb. (Syst.), **39:** 511–676.

———. 1918. Neue und wenig bekannte Nematoden von der Westküste Afrikas. Zool. Anz., **50:** 4–18.

———. 1922. Beiträge zur Kenntnis mariner Nematoden. Zool. Jahrb. (Syst.), **44:** 1–68.

TIMM, R. W. 1952. A survey of the marine nematodes of Chesapeake Bay, Maryland. Chesapeake Biol. Lab., Solomons Islands, Maryland, Publ. No. **95:** 1–70.

———. 1961. The marine nematodes of the Bay of Bengal. Proc. Acad. Sci., Pakistan, **1:** 1–88.

———. 1962. Marine nematodes of the family Linhomoeidae from the Arabian Sea at Karachi. Can. J. Zool., **40:** 165–178.

———. 1963. Marine nematodes of the suborder Monhysterina from the Arabian Sea at Karachi. Proc. Helminthol. Soc. Washington, D. C., **30:** 34–49.

WIESER, W. 1951. Untersuchungen über die algenbewohnende Mikrofauna mariner Hartboden, I. Zur Ökologie und Systematik der Nematoden-fauna von Plymouth. Österr. Zool., Z., **3:** 425–480.

———. 1953. Free-living marine nematodes. I. Enoploidea. Chile Reports 10. Lunds Univ. Arsskr., N.F. Avd. 2, **49:** 1–155.

———. 1954. Free-living marine nematodes. II. Chromadoroidea. Chile Reports 17. Lunds Univ. Arsskr., N.F. Avd. 2, **50:** 1–148.

———. 1955. A collection of marine nematodes from Japan. Publ. Seto Marine Biol. Lab., **4:** 159–181.

———. 1956. Free-living marine nematodes. III. Axonolaimoidea and Monhysteroidea. Lunds Univ. Arsskr. Avd. 2, **52:** 1–115.

———. 1959. Free-living nematodes and other small invertebrates of Puget Sound beaches. Univ. Washington Publs. Biol., **19:** 1–179.

WIESER, W., AND B. E. HOPPER. 1966. The Neotonchinae, new subfamily (Cyatholaimidae: Nematoda) with an analysis of its genera, *Neotonchus* Cobb, 1933 and *Gomphionema* new genus. Can. J. Zool., **44:** 519–532.

ZUR STRASSEN, O. K. L. 1894. Über das röhrenförmige Organ von *Oncholaimus.* Zeitschr. Wissensch. Zool., **58:** 460–474.

(Received 12 January 1966)

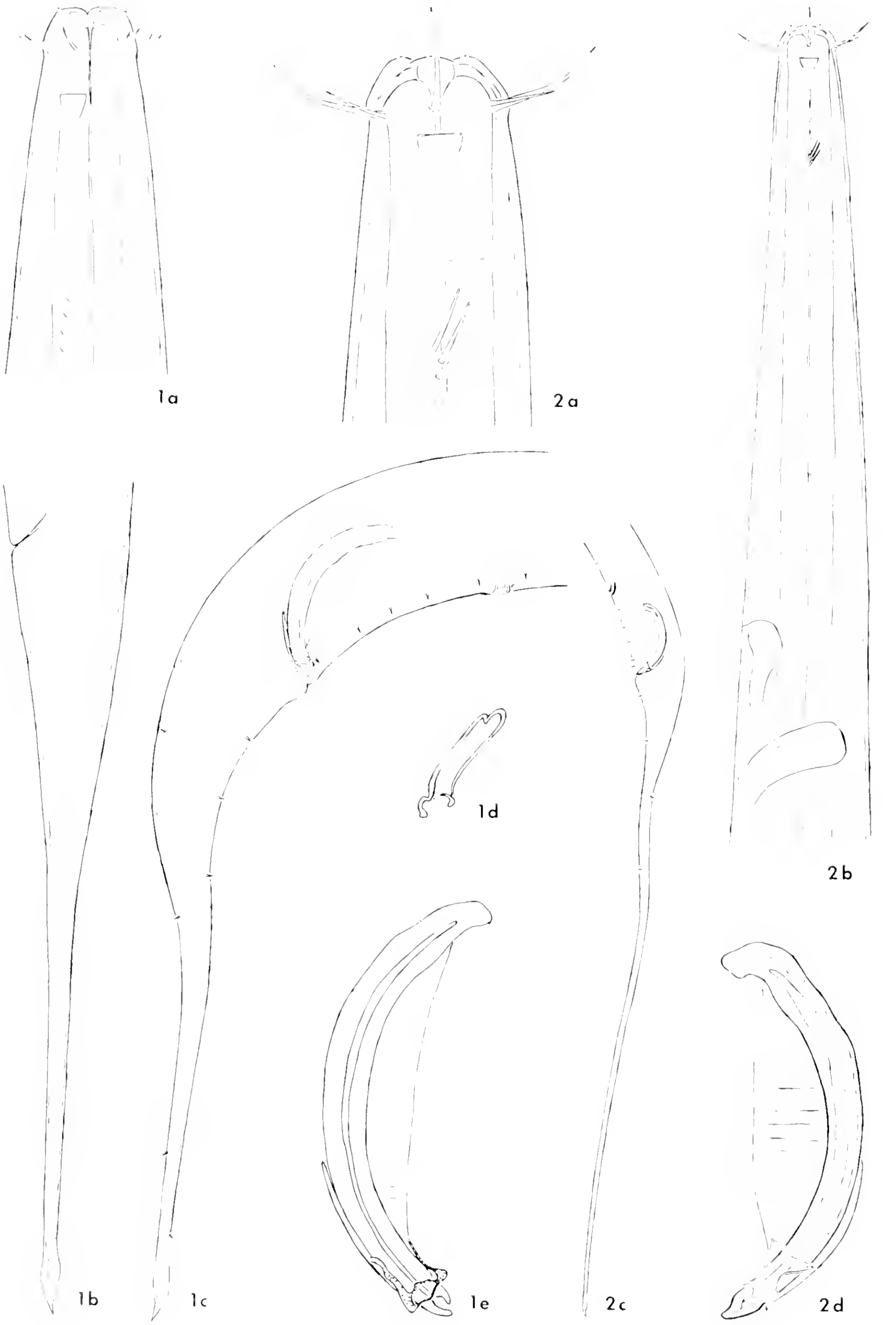


Plate I

Anticoma lata Fig. 1, a–e: a—anterior end of male; b—posterior end of female; c—posterior end of male; d—supplement; e—spicular apparatus. *Anticoma trichura* Fig. 2, a–d: a—anterior end of male; b—anterior neck region of male; c—posterior end of male; d—spicular apparatus.

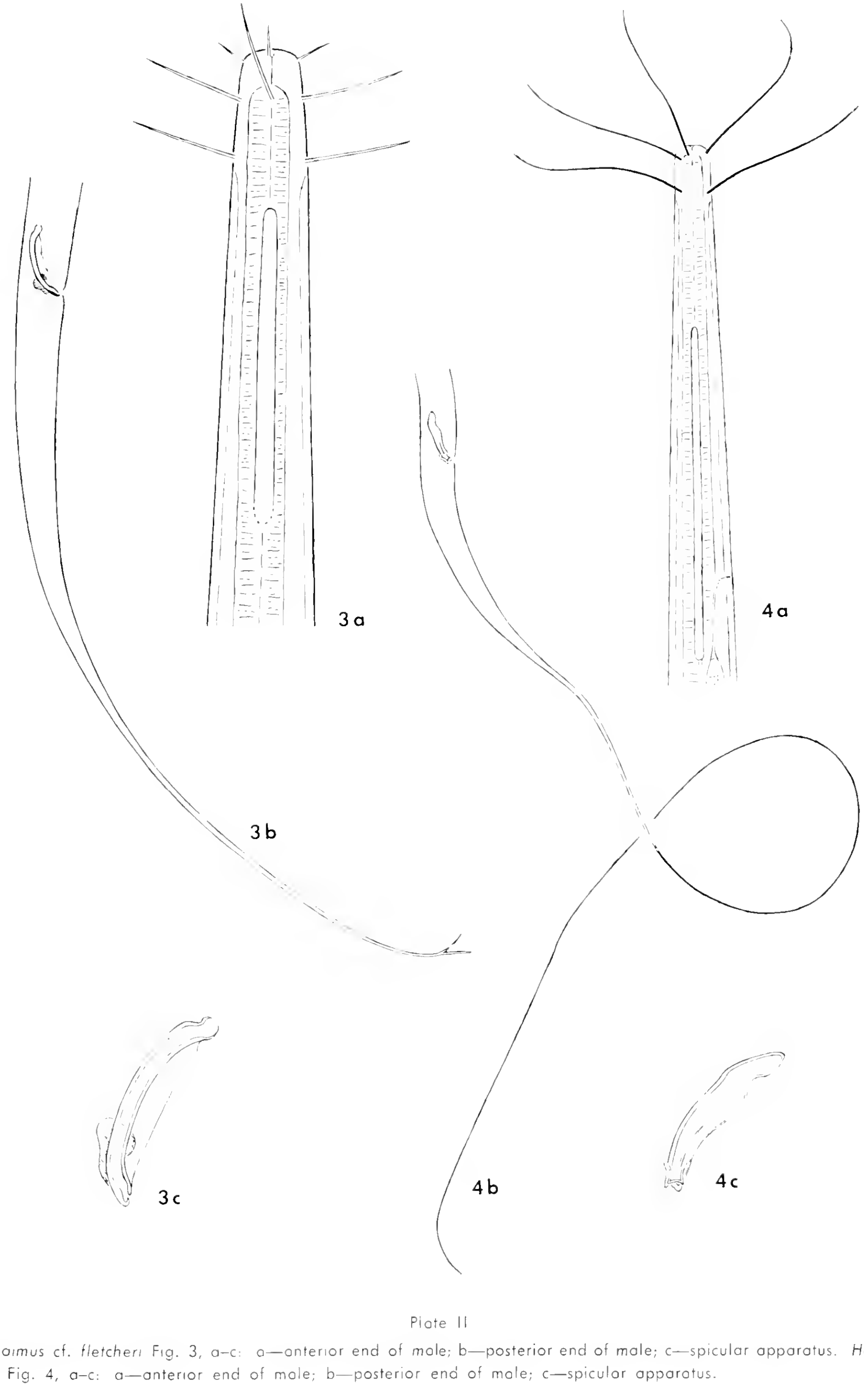
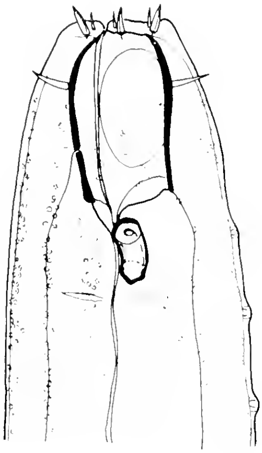
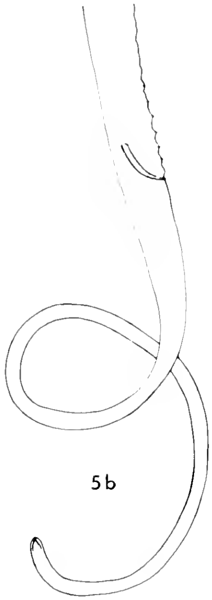
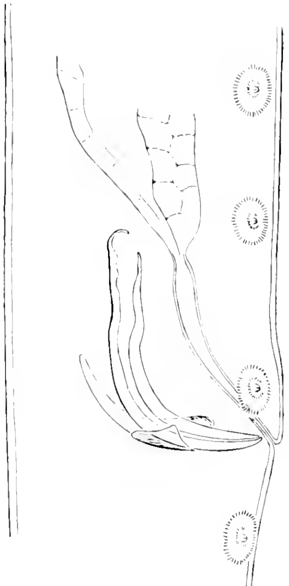


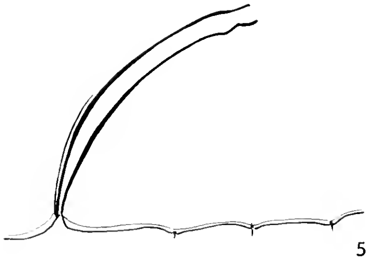
Plate II

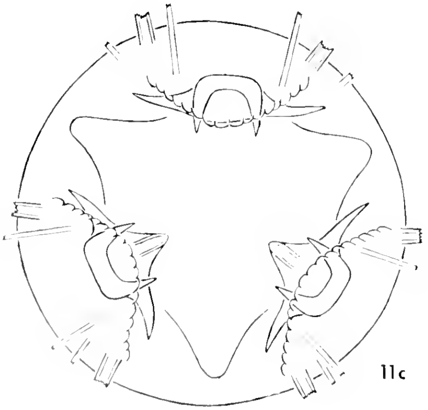
Halalaimus cf. *fletcheri* Fig. 3, a–c: a—anterior end of male; b—posterior end of male; c—spicular apparatus. *Halalaimus meyersi* Fig. 4, a–c: a—anterior end of male; b—posterior end of male; c—spicular apparatus.

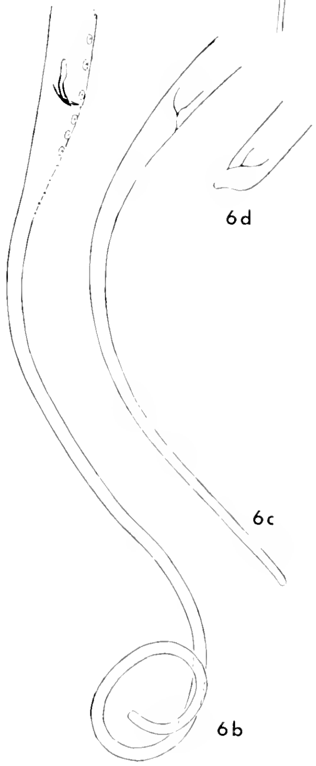

5a


5b


6a


5c


11c


6d

6c

6b

Plate III

Halanonchus macrurus Fig. 5, a–c: a—anterior end of male; b—posterior end of male; c—spicular apparatus. *Cytolaimium exile* Fig. 6, a–d: a—spicular apparatus; b–d—posterior ends of three different specimens. *Enaploides gryphus* Fig. 11, c: en face view.

Plate IV

Bathylaimus australis Fig. 7, a–e: a—anterior end of male; b—posterior end of male; c—posterior end of another male; d—posterior end of female; e—spicular apparatus. *Bathylaimus orthropappus* Fig. 8, a–f: a—anterior end of male, dorsoventral view; b—omphid of male; c—anterior end of male, lateral view; d—spicular apparatus and proximal spicular cephalization from two other specimens; e—posterior end of female; f—posterior end of male.

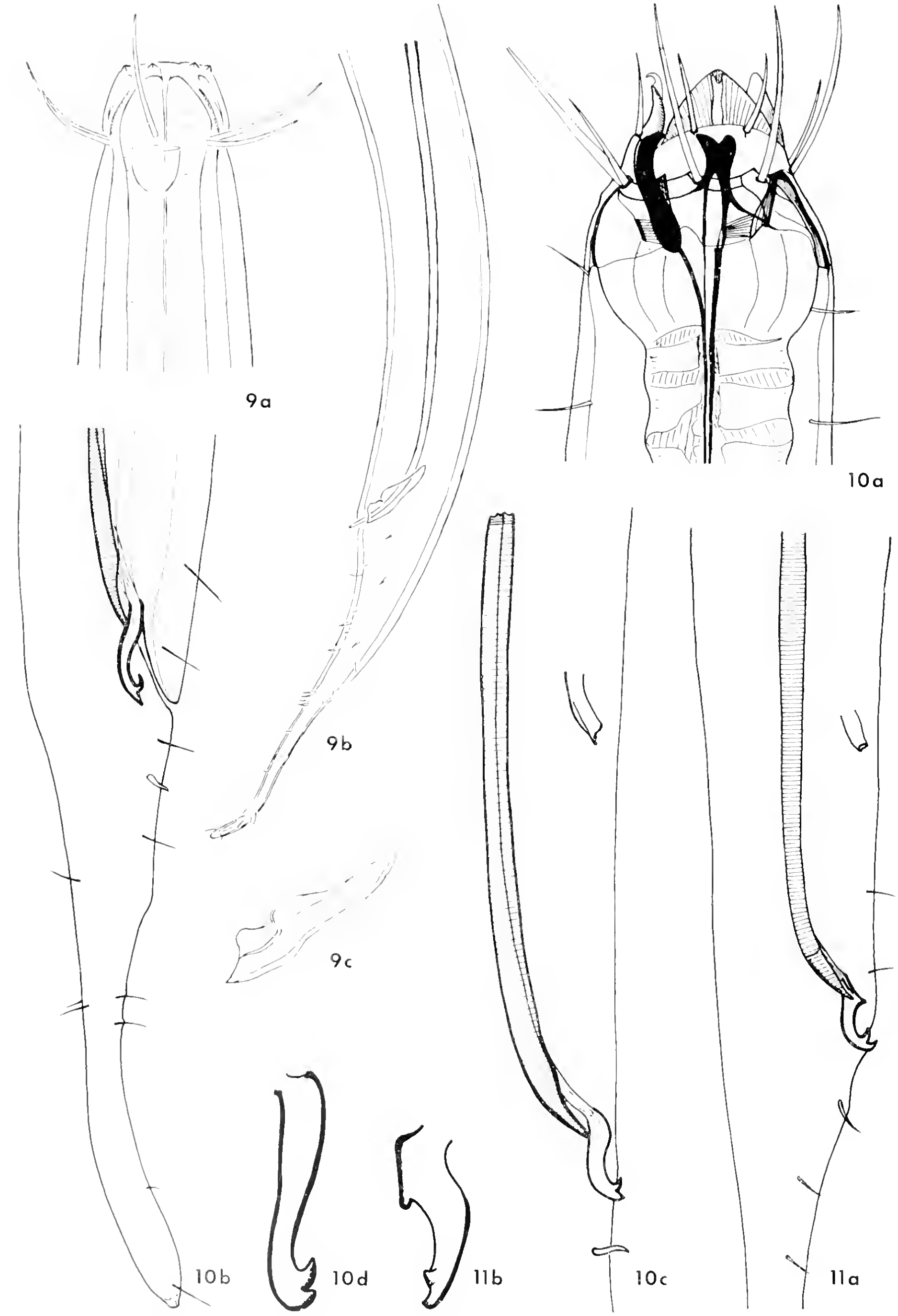


Plate V

Phanodermopsis longisetae Fig. 9, a–c: a—anterior end of male; b—posterior end of male; c—spicular apparatus. *Enoploides bisulcus* Fig. 10, a–d: a—anterior end of male; b—posterior end of male; c—spicular apparatus and supplement of another male; d—gubernaculum of third male in lateroventral view. *Enaplaides gryphus* Fig. 11, a, b: a—spicular apparatus; b—gubernaculum in lateroventral view.

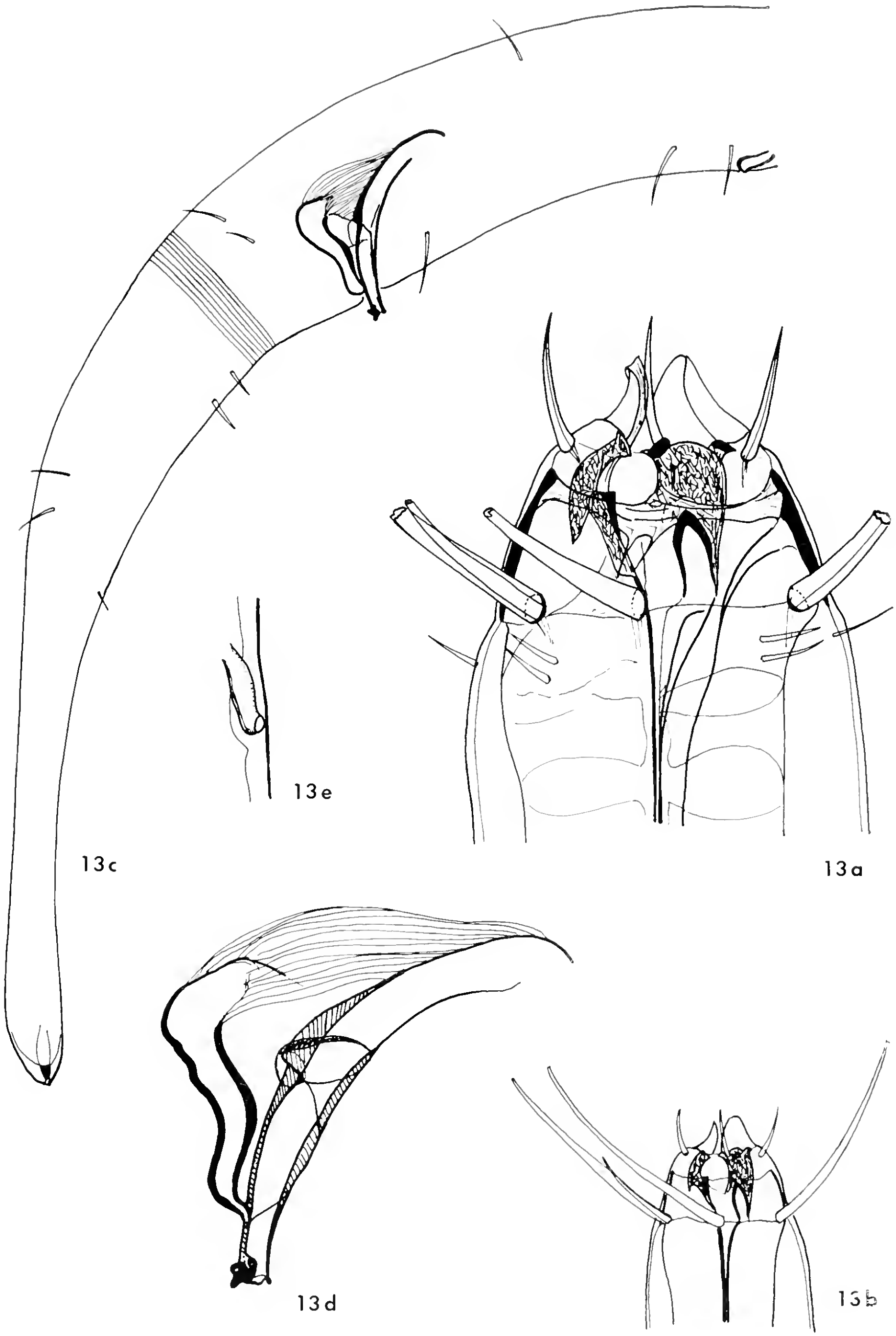


Plate VI

Mesacanthoides psittacus Fig. 13, a–e: a—anterior end of male (cephalic setae cut off); b—anterior end of same male; c—posterior end of male; d—spicular apparatus; e—supplement.

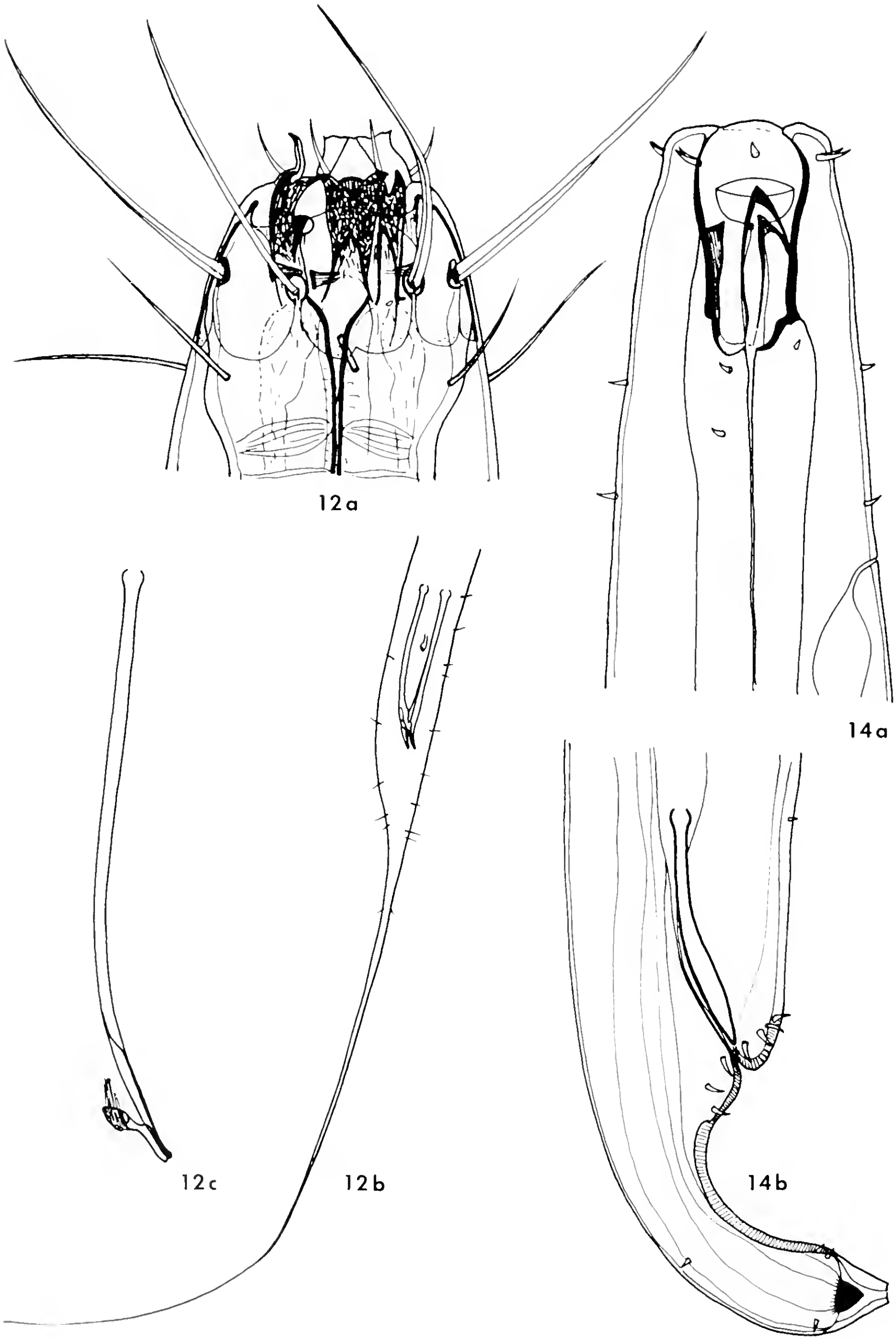


Plate VII

Mesacanthoides fibulatus Fig. 12, a–c: a—anterior end of male; b—posterior end of male; c—spicular apparatus. *Oncholaimus dujardinii* Fig. 14, a, b: a—anterior end of male; b—posterior end of male.

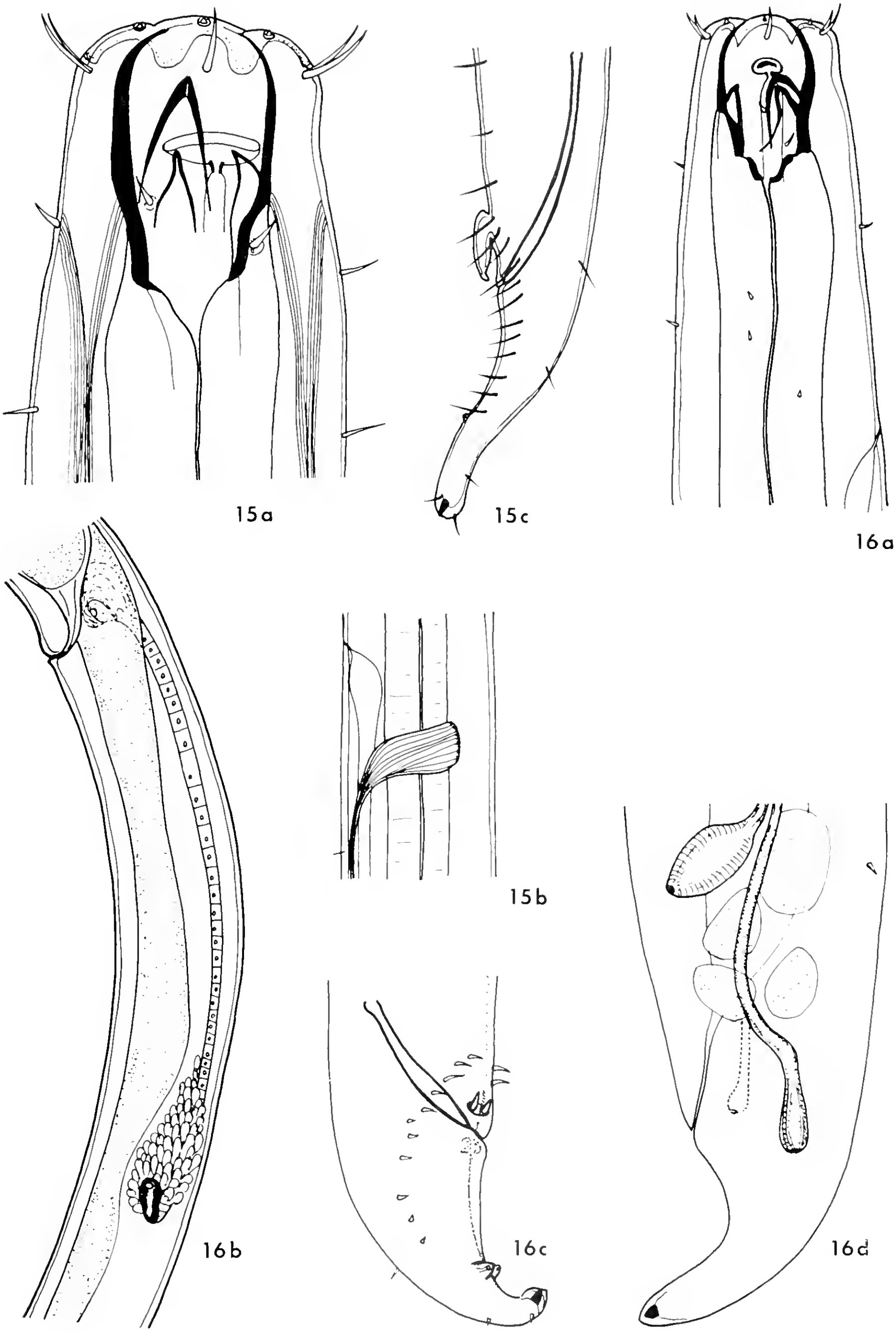


Plate VIII

Oncholaimium appendiculatum Fig. 15, a–c: a—anterior end of male; b—region of nerve ring; c—posterior end of male. *Oncholaimium domesticum* Fig. 16, a–d: a—anterior end of male; b—demanian organ, region of uvette; c—posterior end of male, lateroventral view to show pairedness of pre- and postanal papillae; d—posterior end of female.

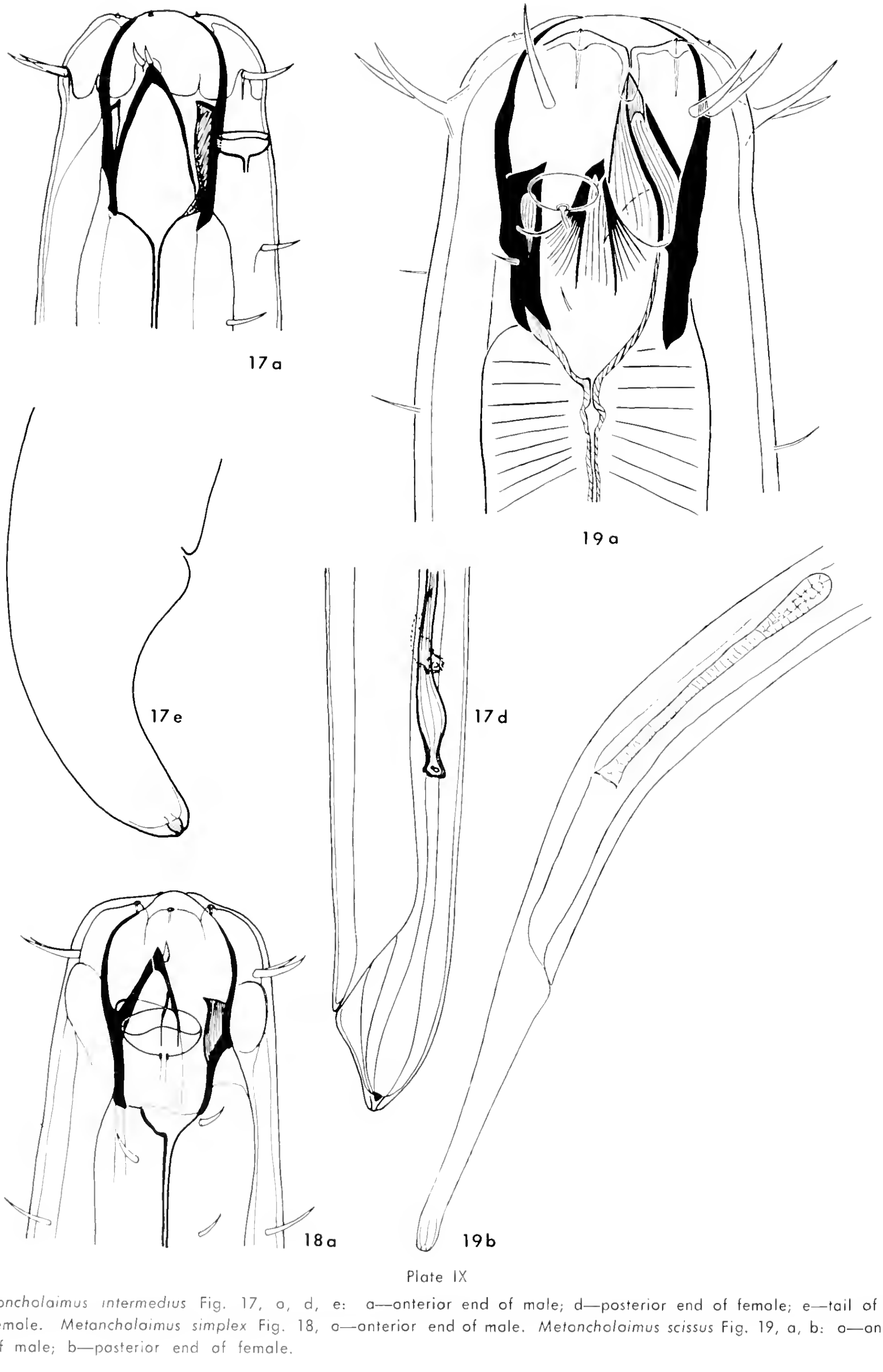


Plate IX

Metoncholaimus intermedius Fig. 17, a, d, e: a—anterior end of male; d—posterior end of female; e—tail of juvenile female. *Metancholaimus simplex* Fig. 18, a—anterior end of male. *Metoncholaimus scissus* Fig. 19, a, b: a—anterior end of male; b—posterior end of female.

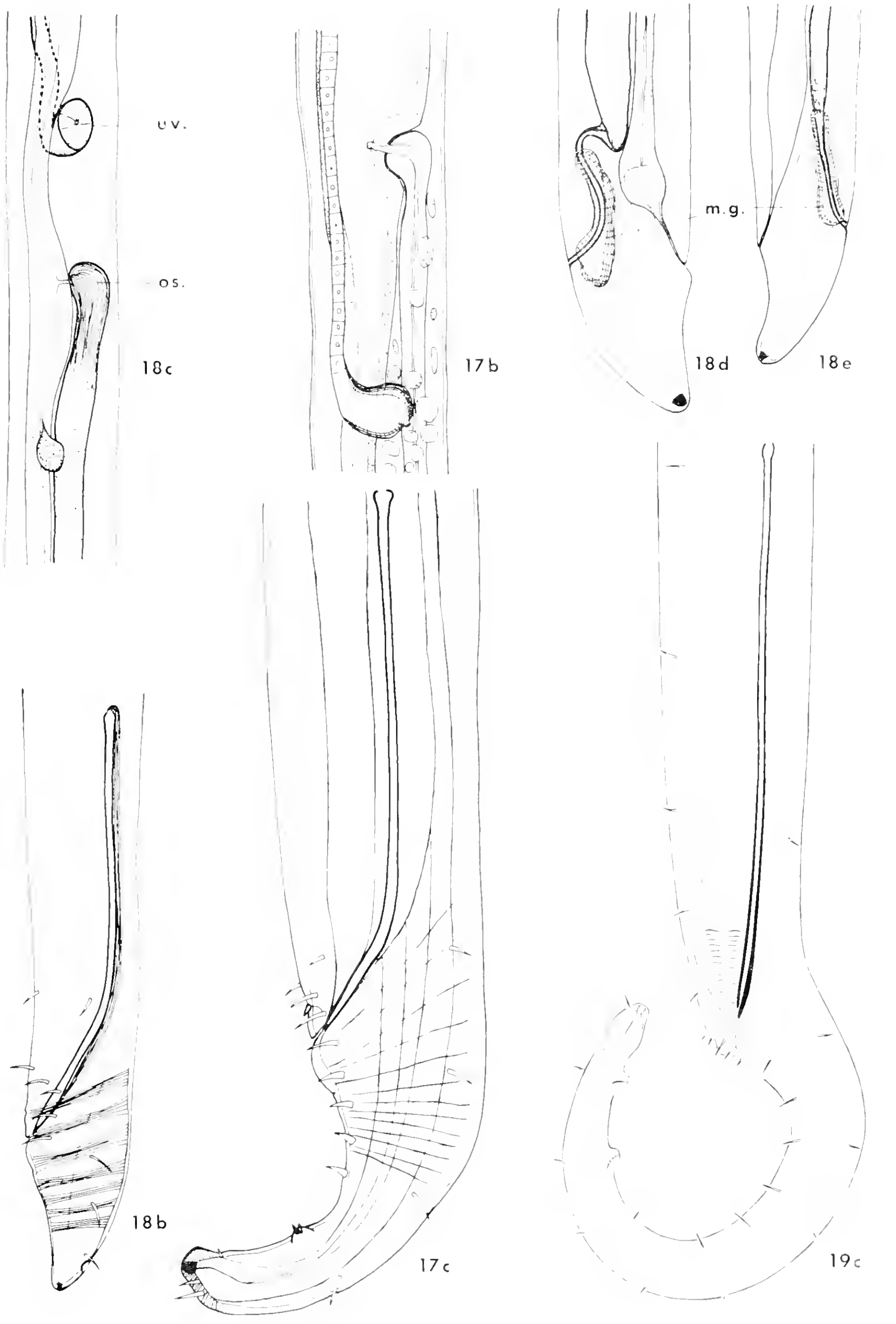


Plate X

Metoncholaimus intermedius Fig. 17, b, c: b—demanian organ, region of uvette and opening of enterine efferent into intestine; c—posterior end of male. *Metoncholaimus simplex* Fig. 18, b–e: b—posterior end of male; c—part of demanian organ (*uv.*, uvette; *os.*, osmosium); d, e—posterior ends of two females (*m.g.*, moniliform glands). *Metoncholaimus scissus* Fig. 19, c—posterior end of male.

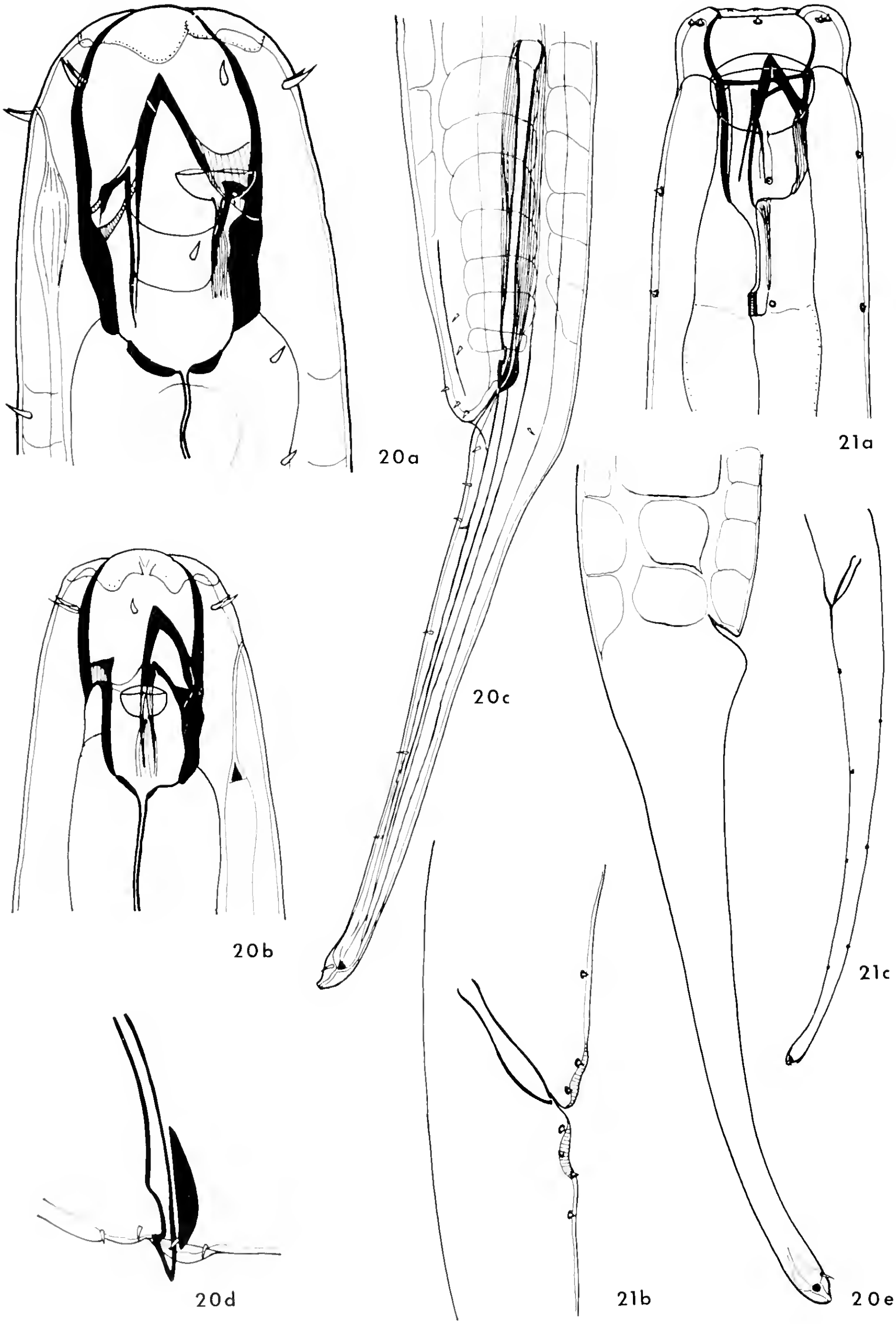


Plate XI

Prooncholaimus hastatus Fig. 20, a–e: a—anterior end of male; b—anterior end of young female; c—posterior end of male; d—distal portion of spiculum; e—posterior end of female. *Viscosia ancholaimelloides* Fig. 21, a–c: a—anterior end of male; b—anal region of male; c—posterior end of male.

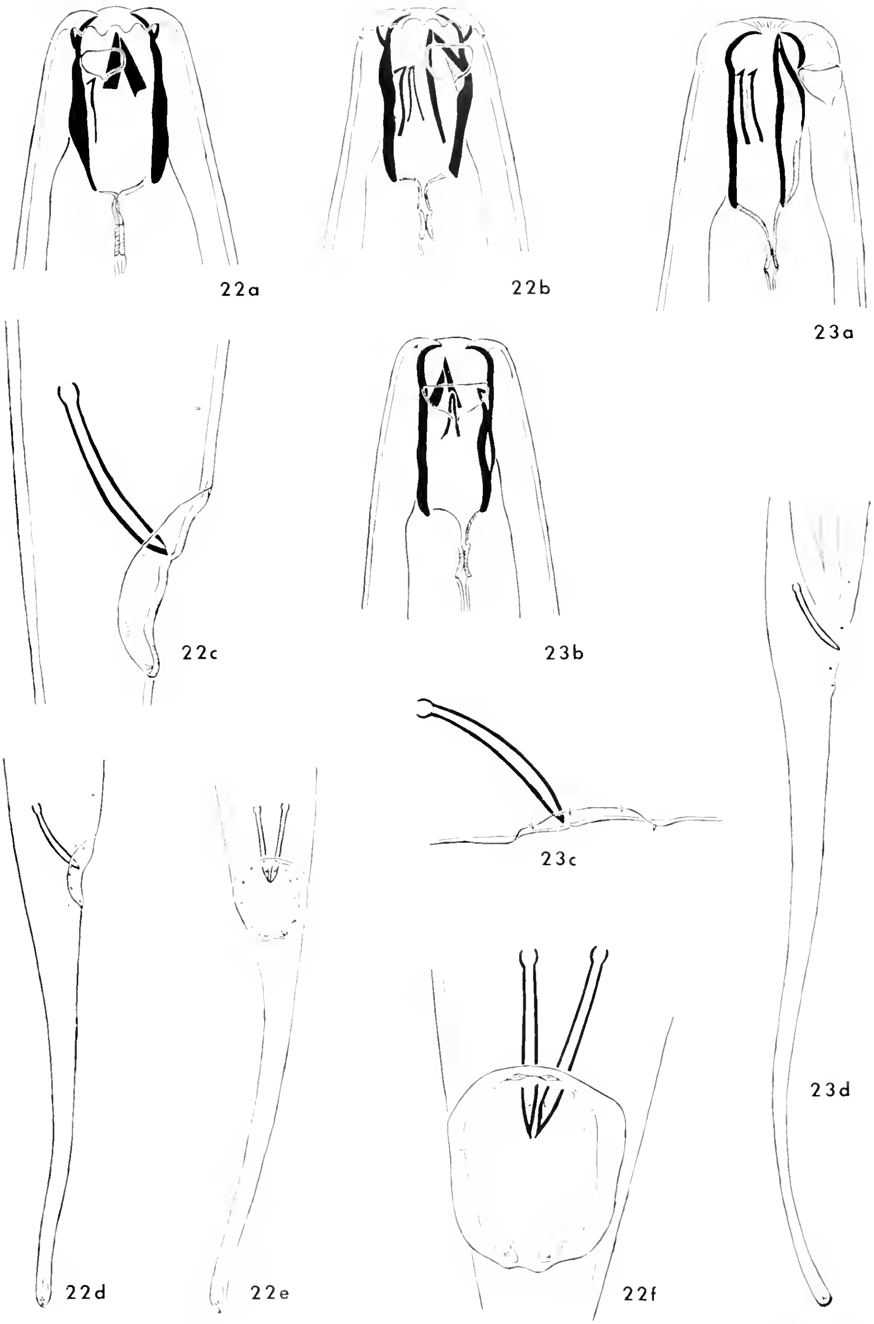


Plate XII

Viscosia papillata Fig. 22, a–f: a—anterior end of female; b—anterior end of male; c—spicular region, lateral view; d—posterior end of male; e—posterior end of male, ventral view; f—spicular region, ventral view. *Viscosia macramphida* Fig. 23, a–d: a, b—anterior ends of two males; c—spicular region; d—posterior end of male.

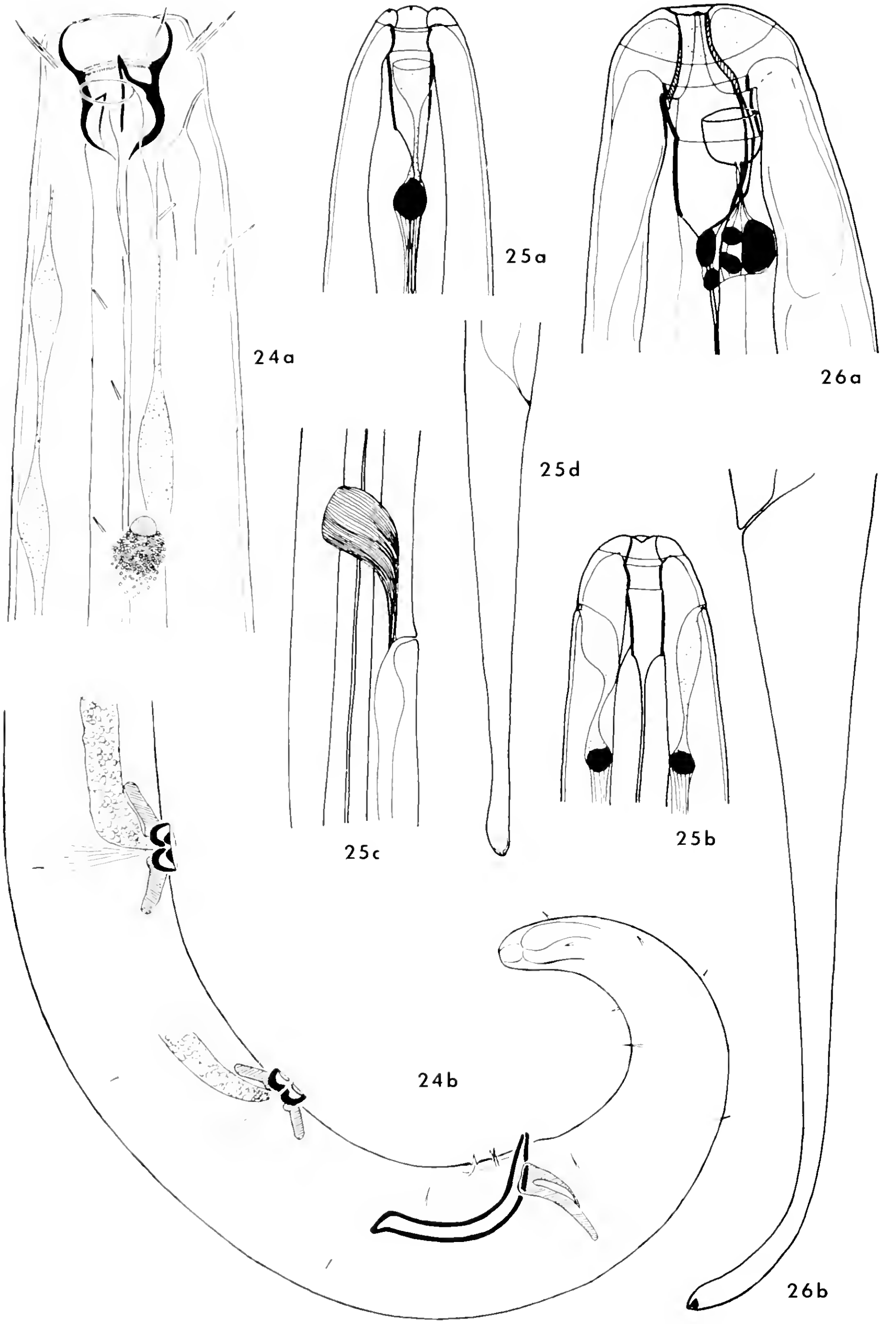


Plate XIII

Eurystomina minutisculae Fig. 24, a, b: a—anterior end of male; b—posterior end of male. *Illium exile* Fig. 25, a–d: a—anterior end of female, lateral view; b—anterior end of another female, dorsal view; c—region of nerve ring; d—posterior end of female. *Illium libidinosum* Fig. 26, a, b: a—anterior end of female; b—posterior end of female.

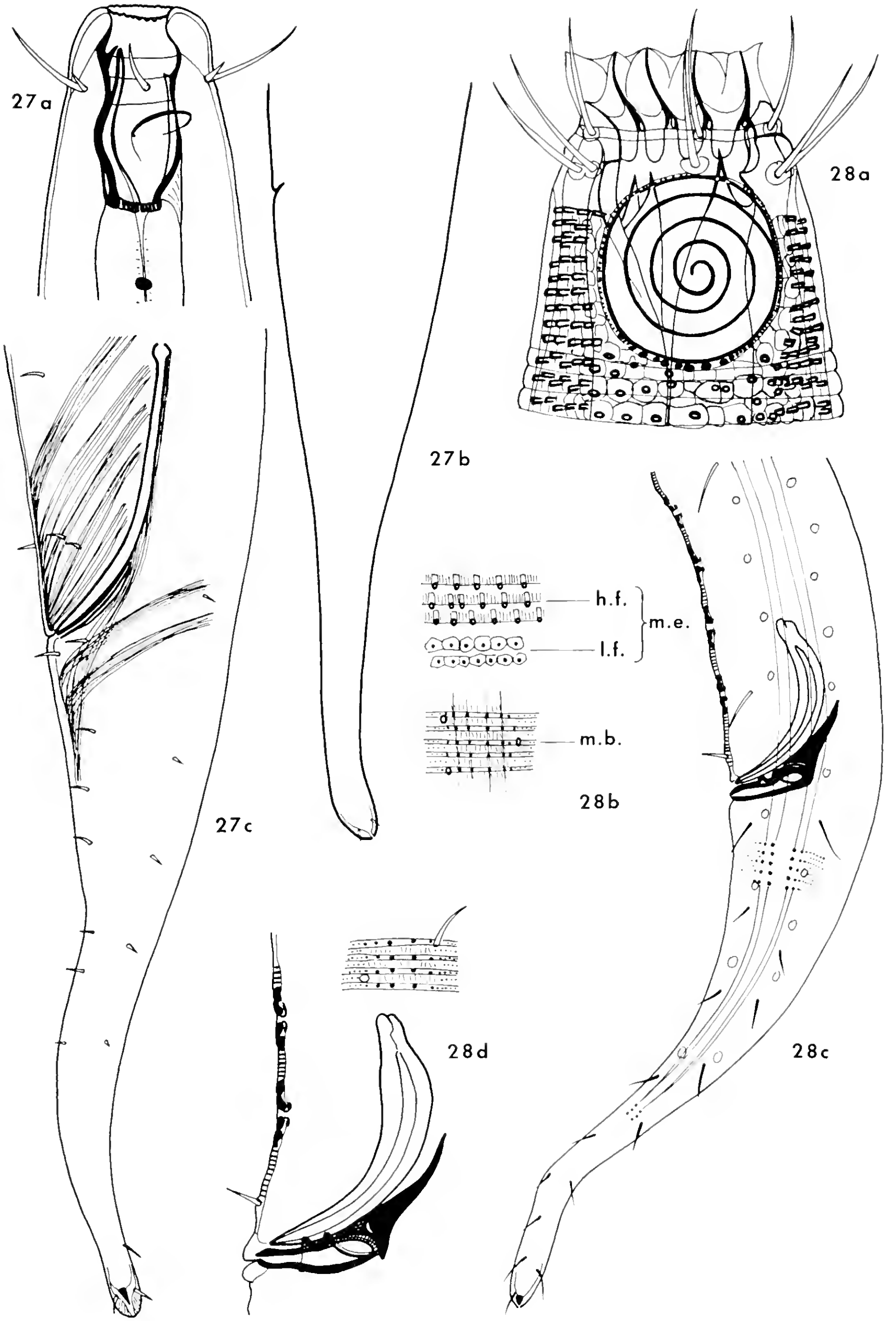


Plate XIV

Polygastrophora edax Fig. 27, a–c: a—anterior end of male; b—posterior end of female; c—posterior end of male. *Pomponema tesselatum* Fig. 28, a–d: a—anterior end of male; b—cuticular differentiation in lateral region (*h.f.*, high focus; *l.f.*, low focus; *m.e.*, mid-esophagus; *m.b.*, mid-body); c—posterior end of male; d—anal region of male.

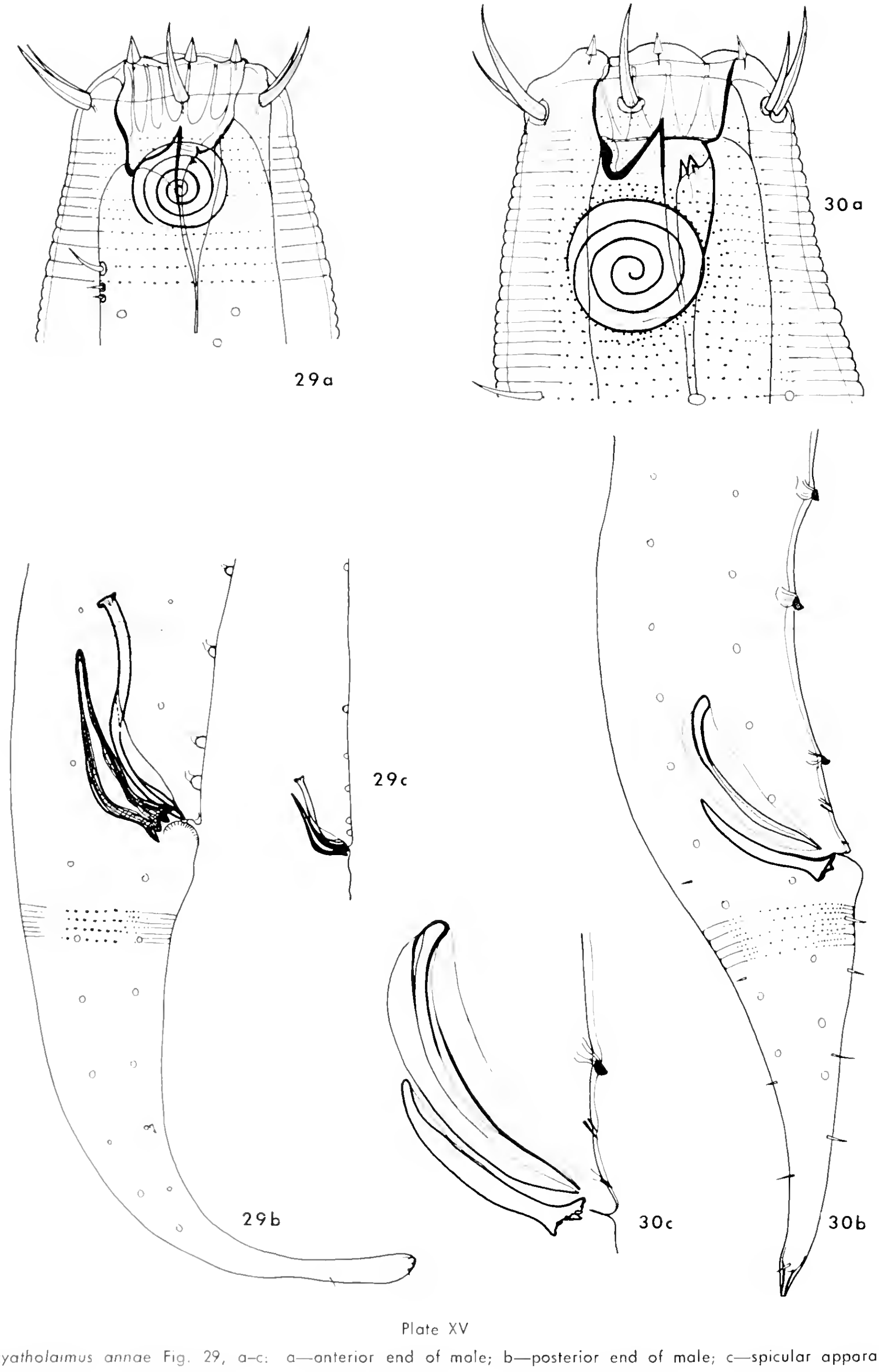


Plate XV

Longicyatholaimus annae Fig. 29, a–c: a—anterior end of male; b—posterior end of male; c—spicular apparatus and row of supplements. *Xyzzors inglisi* Fig. 30, a–c: a—anterior end of male; b—posterior end of male; c—spicular apparatus.

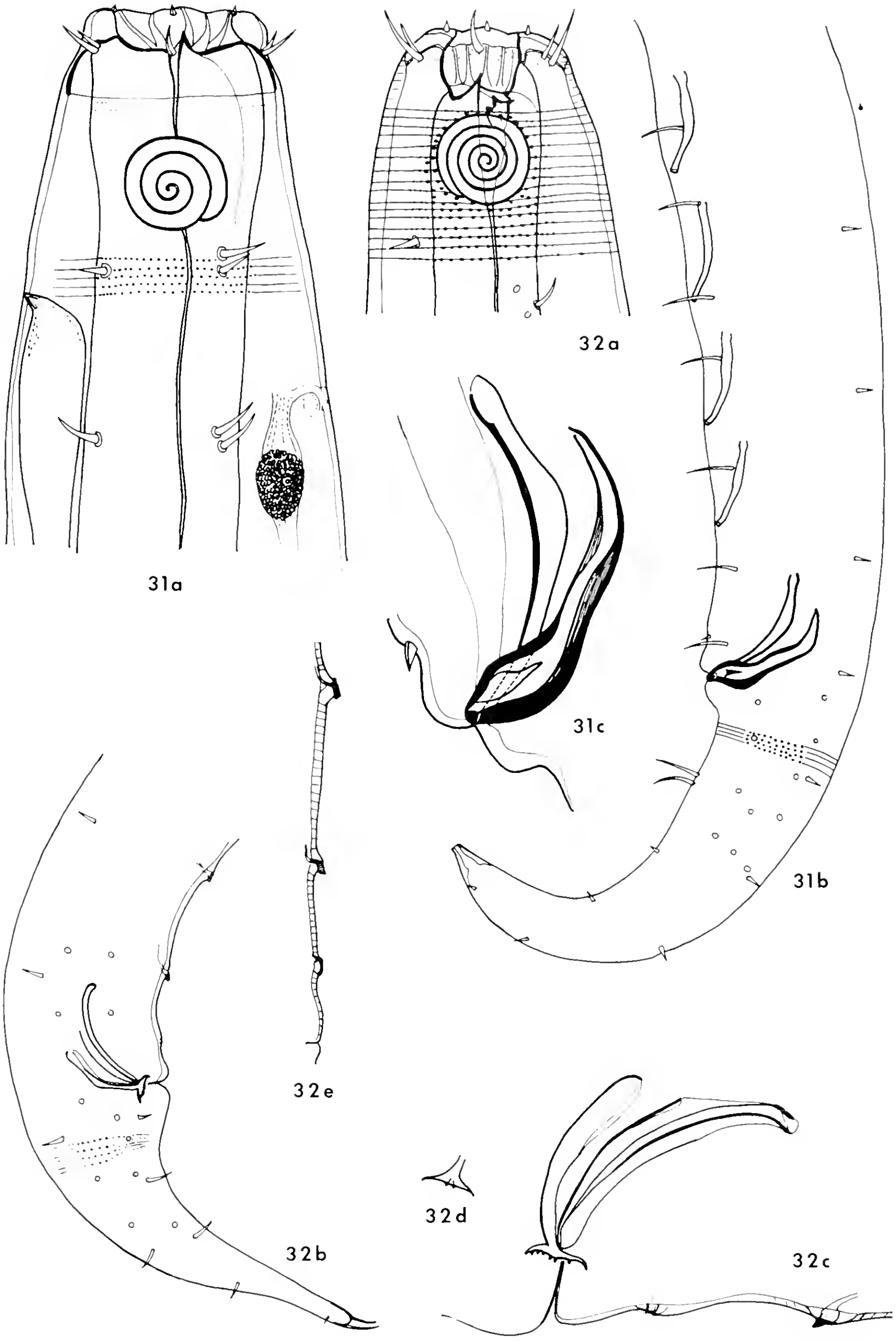


Plate XVI

Paracanthonchus platypus Fig. 31, a–c: a—anterior end of male; b—posterior end of female; c—spicular apparatus. *Paracyathalaimus pesavis* Fig. 32, a–e: a—anterior end of male; b—posterior end of male; c—spicular apparatus; d—distal end of gubernaculum of another male; e—row of supplements.

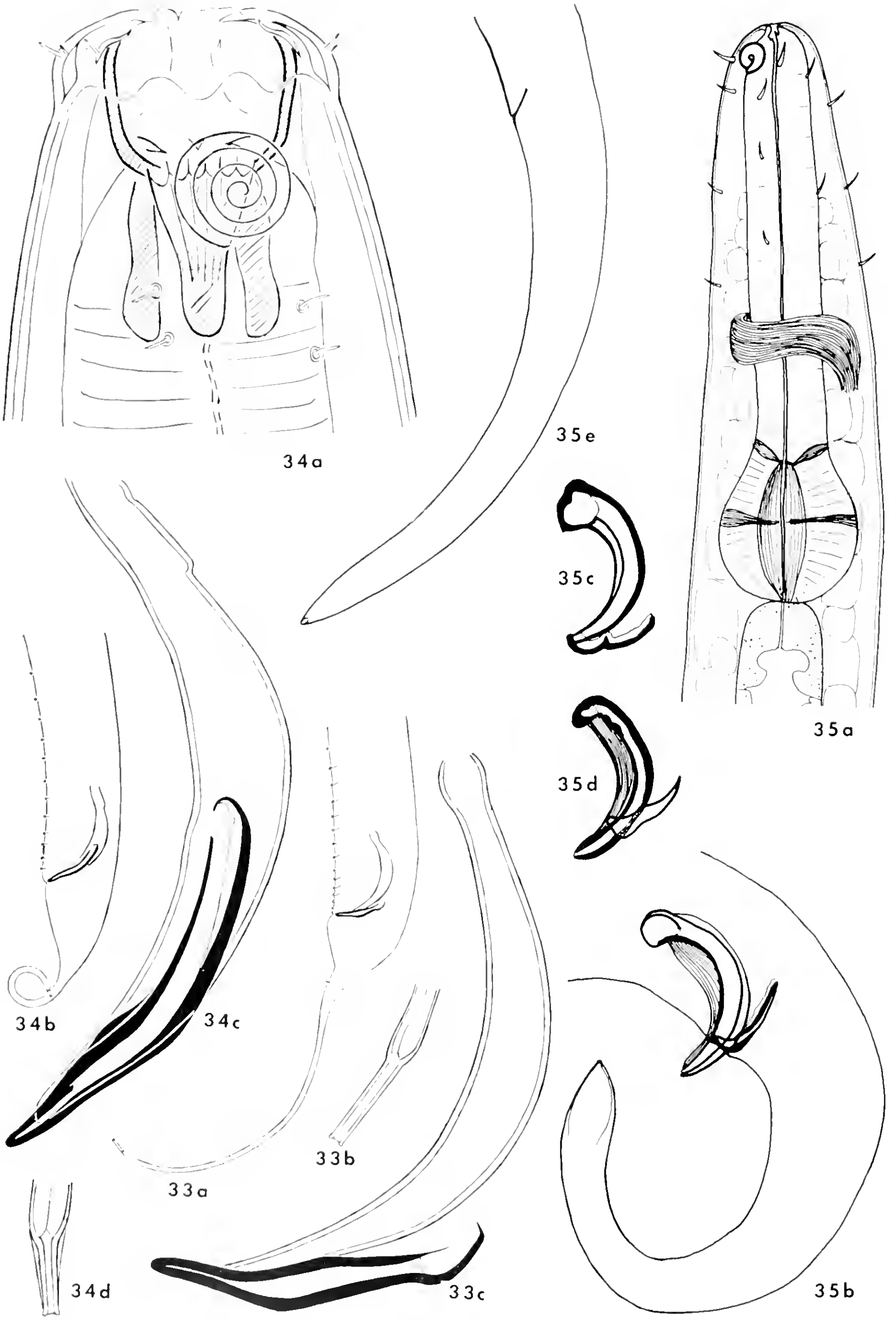


Plate XVII

Halichoanolaimus quattuordecimpapillatus Fig. 33, a–c: a—posterior end of male; b—spinneret; c—spicular apparatus. *Halichoanolaimus duodecimpapillatus* Fig. 34, a–d: a—anterior end of male; b—posterior end of male; c—spicular apparatus; d—spinneret. *Spirinia parasitifera* Fig. 35, a–e: a—anterior region of male; b—posterior end of male; c, d—spicular apparatus of two more males; e—posterior end of female.

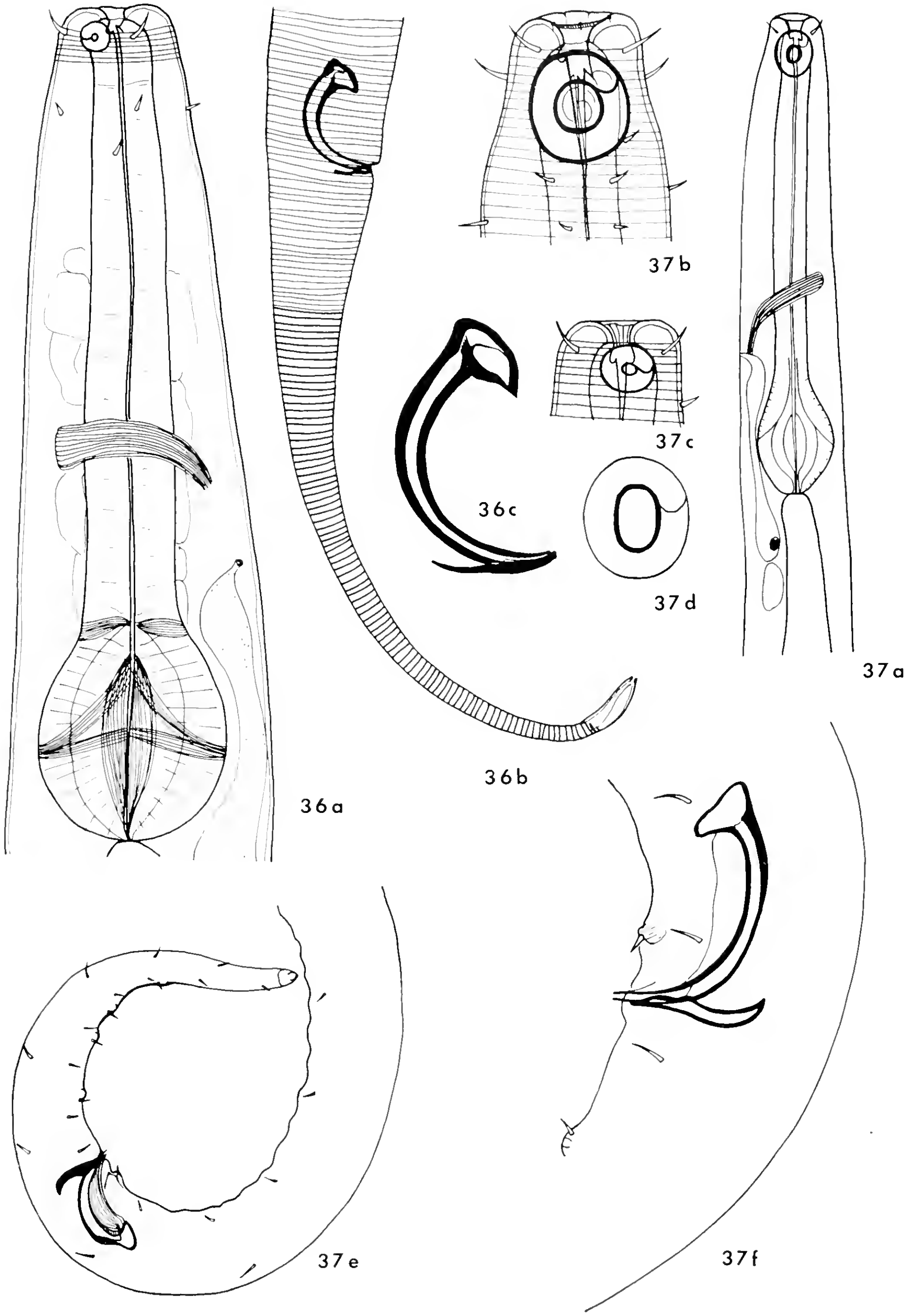


Plate XVIII

Spirinia hamata Fig. 36, a–c: a—anterior region of male; b—posterior end of male; c—spicular apparatus. *Chromaspirina inaurita* Fig. 37, a–f: a—anterior region of male; b—anterior end of male; c—anterior end of female; d—amphid of another male; e—posterior end of male; f—anal region.

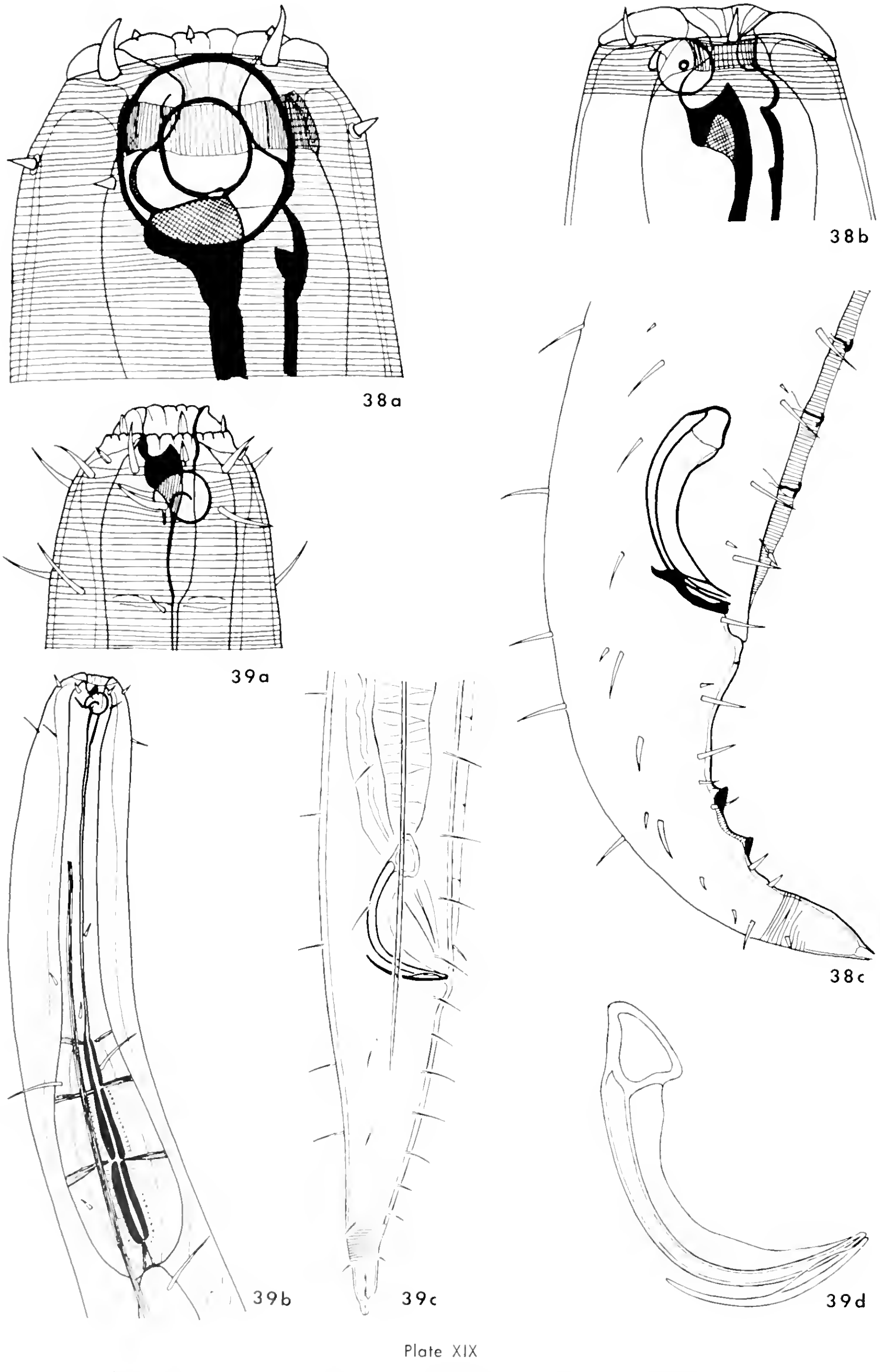


Plate XIX

Metachromadora pulvinata Fig. 38, a–c: a—anterior end of male; b—anterior end of juvenile; c—posterior end of male. *Metachromadora meridiana* Fig. 39, a–d: a—anterior end of male; b—anterior region of male; c—posterior end of male; d—spicular apparatus.

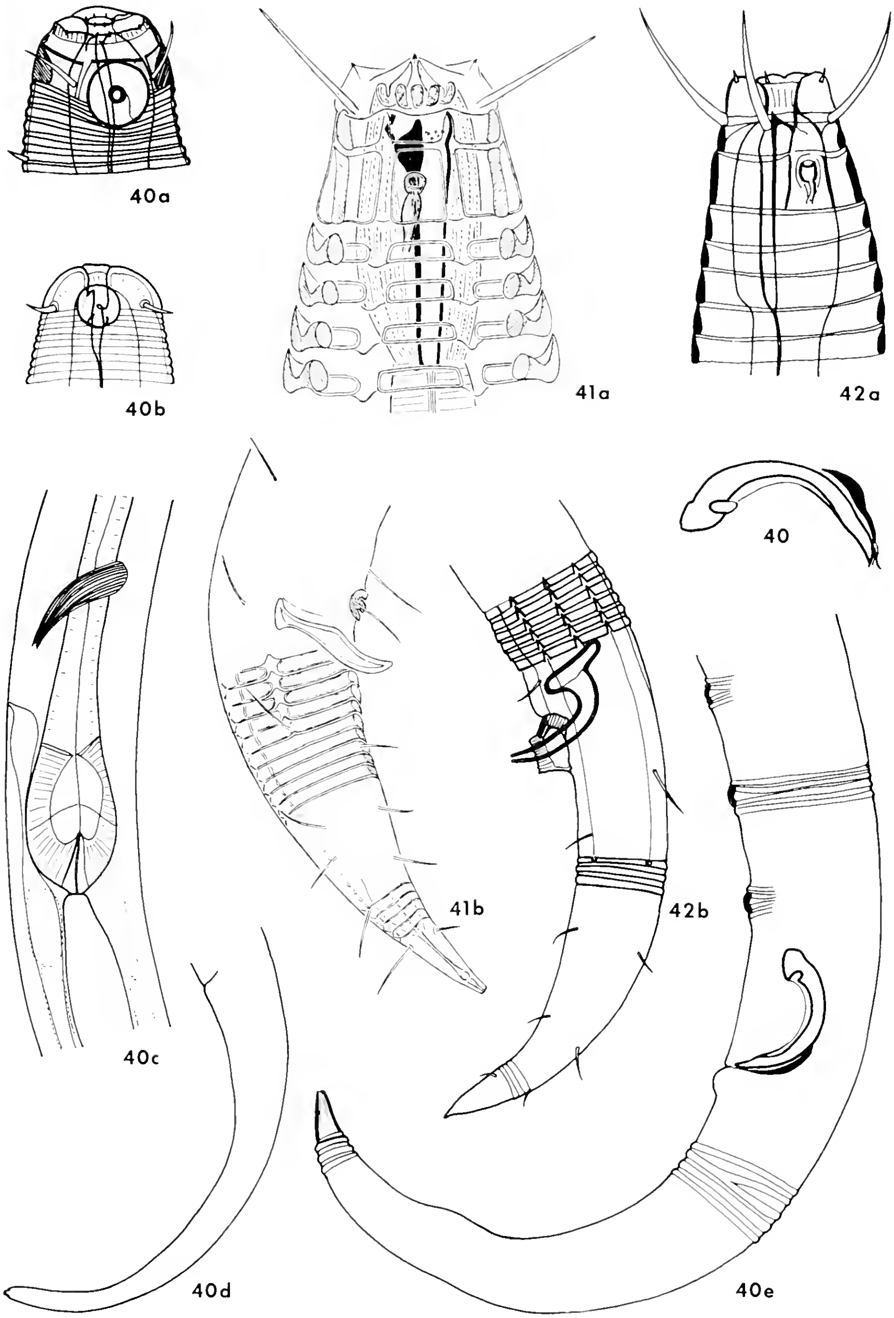


Plate XX

Paradesmodora toreutes Fig. 40, a–f: a—anterior end of male; b—anterior end of juvenile; c—region of esophageal bulb; d—tail of juvenile; e—posterior end of male; f—spicular apparatus. *Monoposthia mirabilis* Fig. 41, a, b: a—anterior end of male; b—posterior end of male. *Monoposthioides mayri* Fig. 42, a, b: a—anterior end of male; b—posterior end of male.

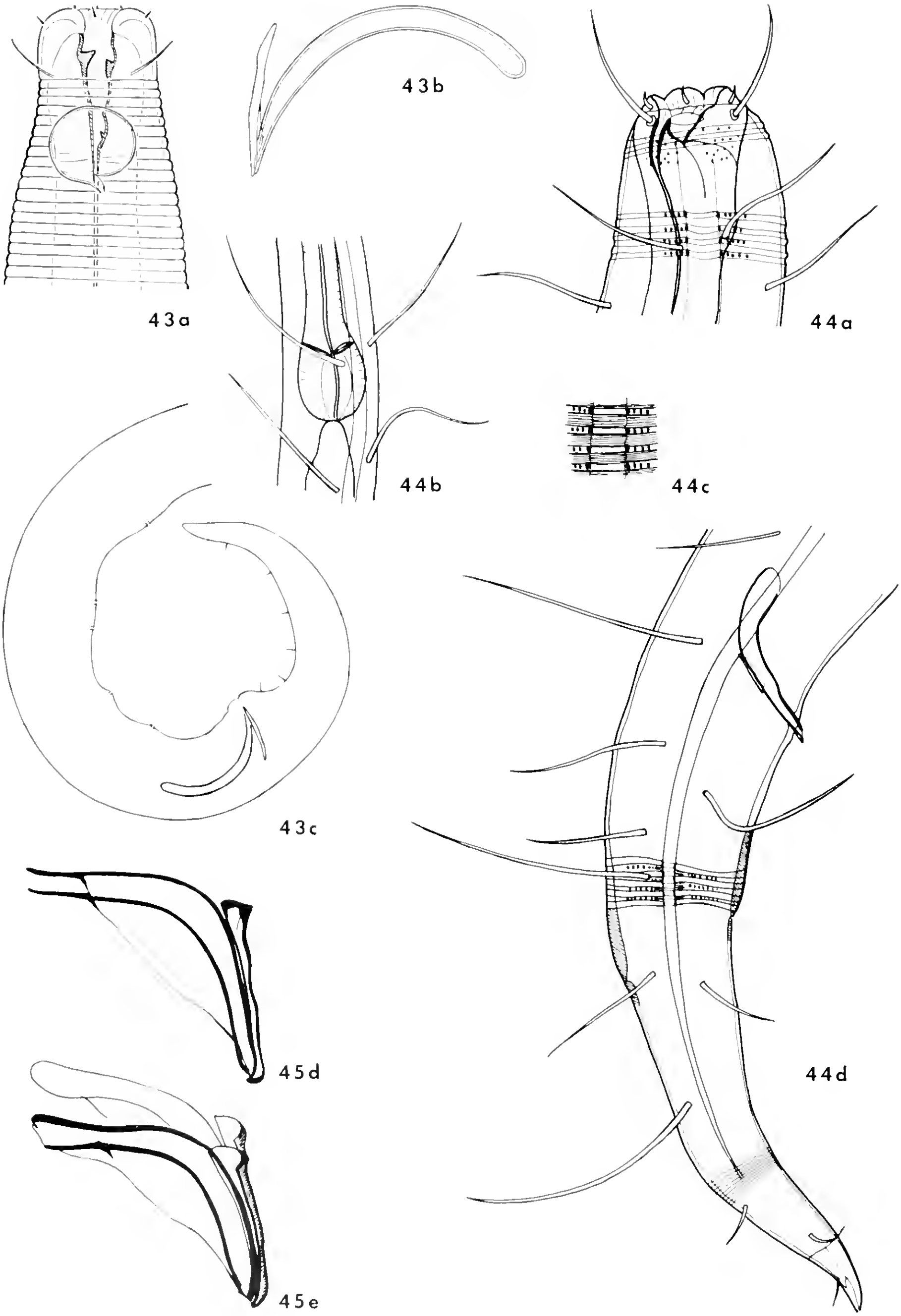


Plate XXI

Paramicrolaimus lunatus Fig. 43, a–c: a—anterior end of male; b—spicular apparatus; c—posterior end of male. *Hypodontolaimus interruptus* Fig. 44, a–d: a—anterior end of male; b—region of esophageal bulb; c—lateral differentiation of cuticle in mid-body; d—posterior end of male. *Hypodontolaimus pandispiculatus* Fig. 45, d, e: spicular apparatus of two males.

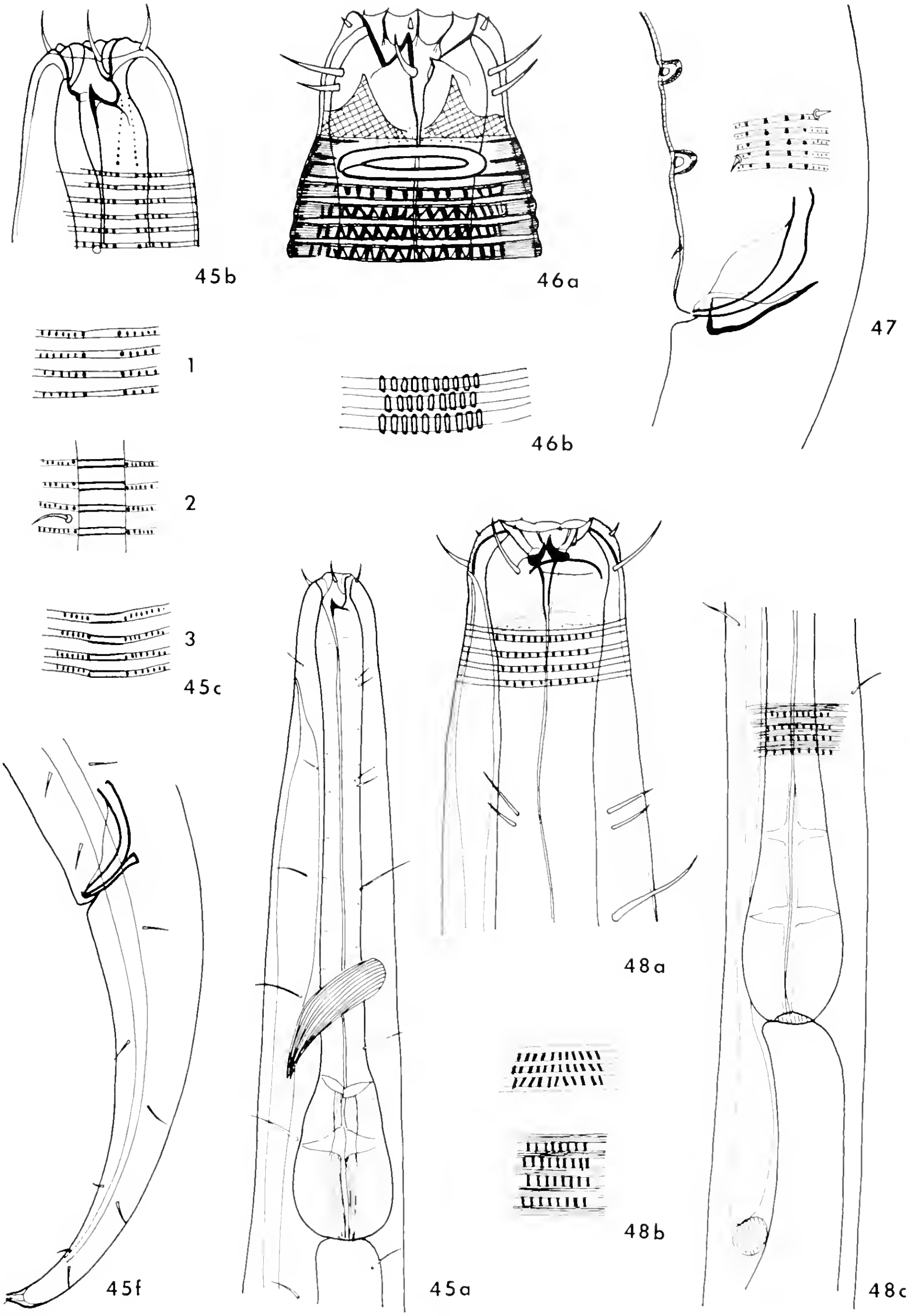


Plate XXII

Hypodontolaimus pandispiculatus Fig. 45, a–c, f: a—anterior end of male; b—anterior region of male; c—lateral differentiation of cuticle, 1: bulbar region, 2: mid-body, 3: anal region; f—posterior end of male. *Rhips ornata* Fig. 46, a, b: a—anterior end of male; b—cuticular differentiation in mid-esophagus region. *Chromadora macrolaimoides* Fig. 47: anal region of male. *Prochromadorella mediterranea* Fig. 48, a–c: a—anterior end of male; b—cuticular differentiation: mid-esophagus (above) and mid-body; c—region of esophageal bulb.

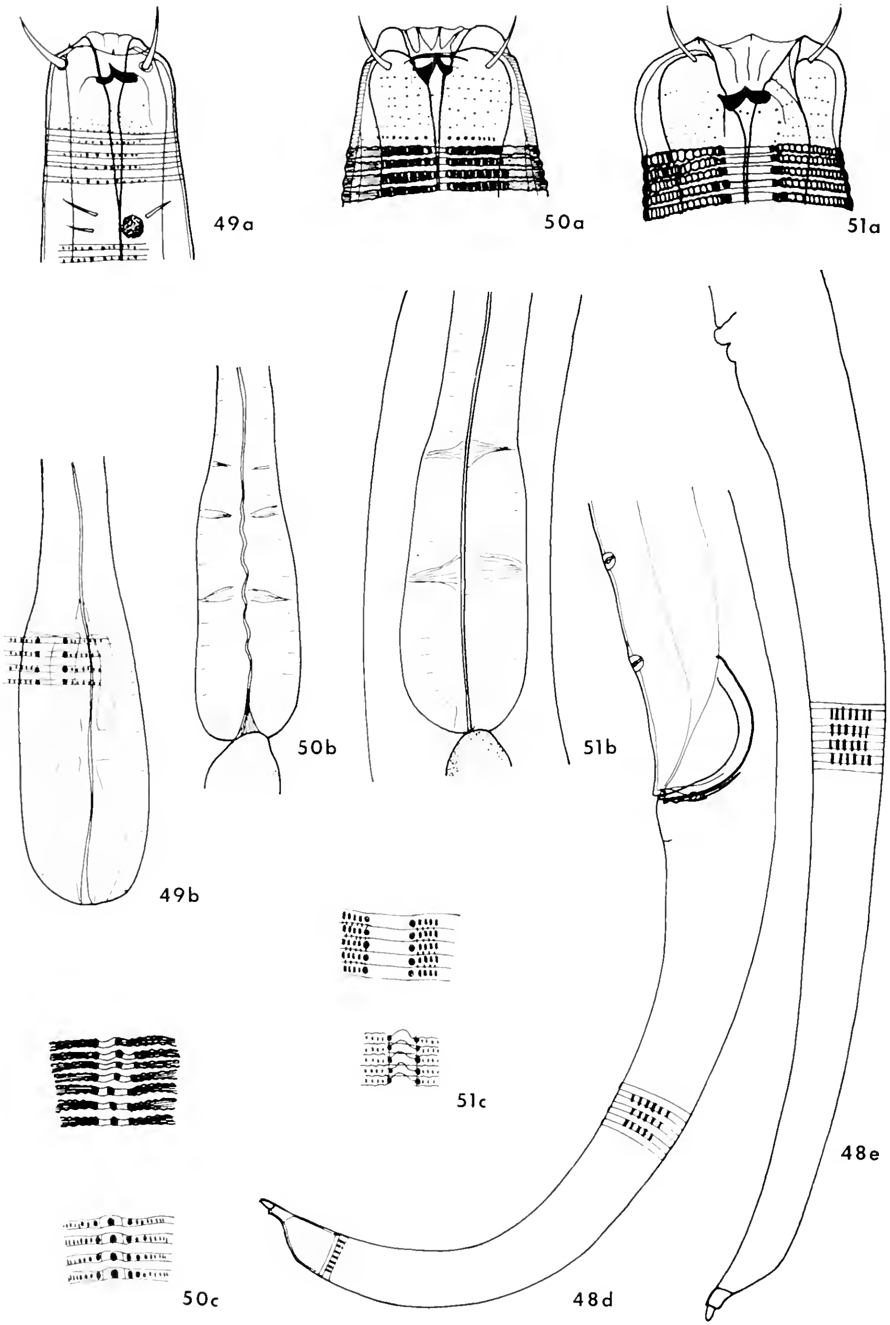


Plate XXIII

Prochromadorella mediterranea Fig. 48, d, e: d—posterior end of male; e—posterior end of female. *Chromadorella filiformis* Fig. 49, a, b: a—anterior end of male; b—esophageal bulb. *Chromadorella trilix* Fig. 50, a–c: a—anterior end of male; b—esophageal bulb; c—cuticular differentiation: anterior cervical region (above) and mid-esophagus. *Chromadorella vanmeterae* Fig. 51, a–c: a—anterior end of male; b—esophageal bulb; c—cuticular differentiation: posterior cervical region (above) and mid-body.

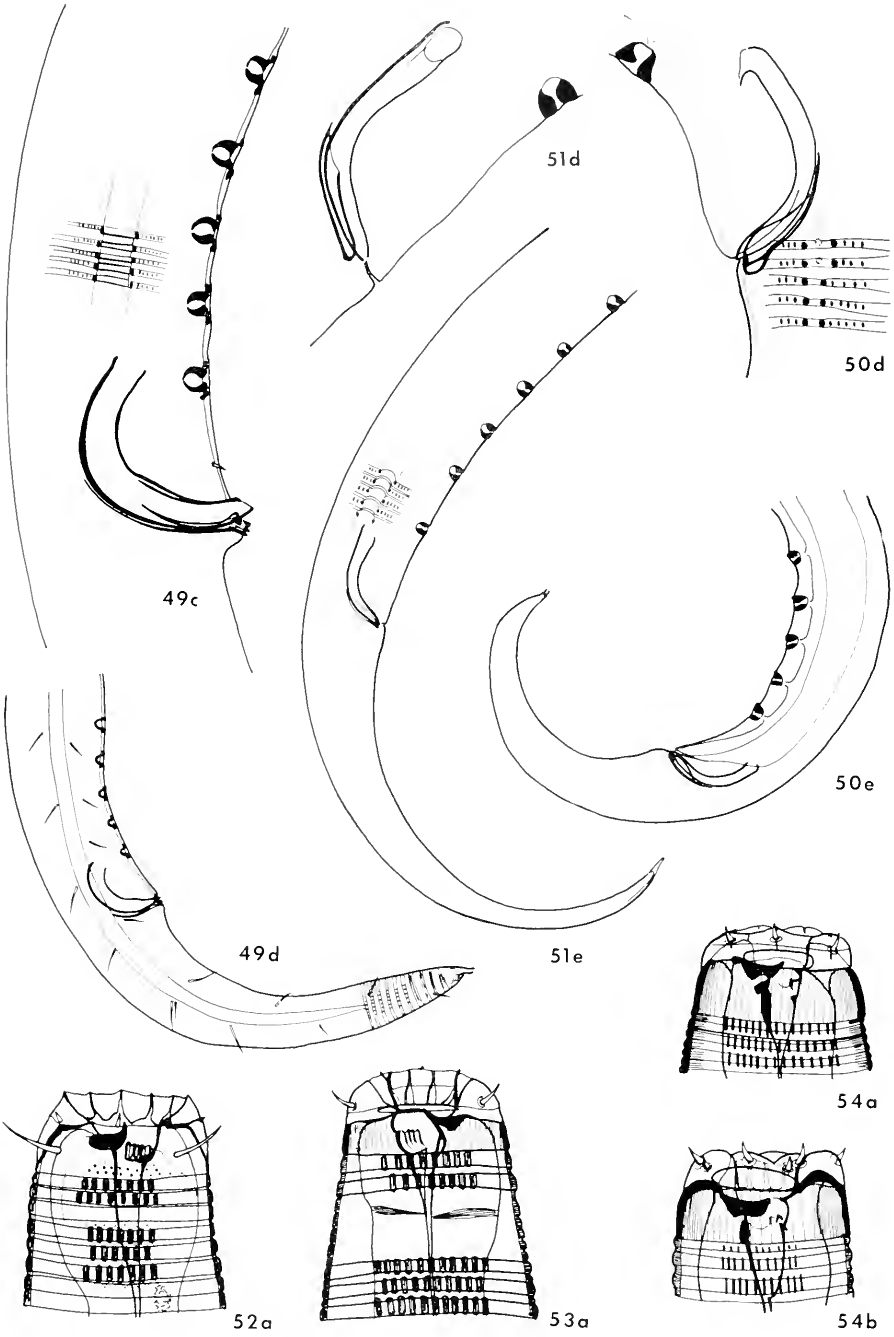


Plate XXIV

Chromadorella filiformis Fig. 49, c, d: c—oral region of male; d—posterior end of male. *Chromadorella trilex* Fig. 50, d, e: d—spicular apparatus; e—posterior end of male. *Chromadorella vanmeterae* Fig. 51, d, e: d—spicular apparatus; e—posterior end of male. *Euchromadora gaulica* Fig. 52, a—anterior end of male. *Euchromadora pectinata* Fig. 53, a—anterior end of male. *Euchromadora meadi* Fig. 54, a, b: a—anterior end of male; b—anterior end of juvenile.

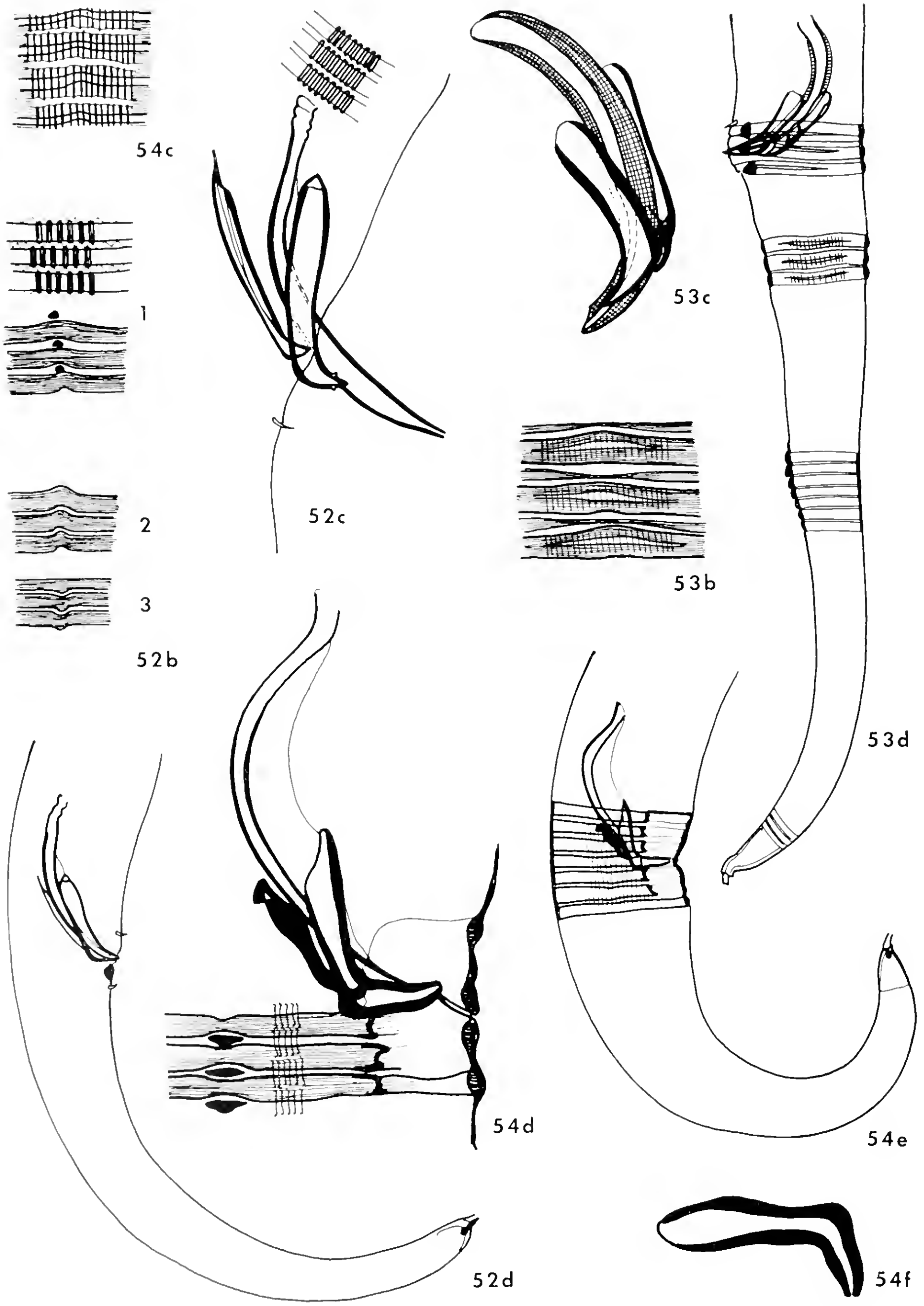


Plate XXV

Euchromadora gaulica Fig. 52, b–d: b—cuticular differentiation, 1: end of esophagus, high focus (above) and low focus, 2: mid-body, low focus, 3: anal region, low focus; c—spicular apparatus; d—posterior end of male. *Euchromadora pectinata* Fig. 53, b–d: b—cuticular differentiation, mid-body; c—spicular apparatus; d—posterior end of male. *Euchromadora meadi* Fig. 54, c–f: c—cuticular differentiation, end of esophagus; d—anal region of male; e—posterior end of male; f—gubernaculum of another male.

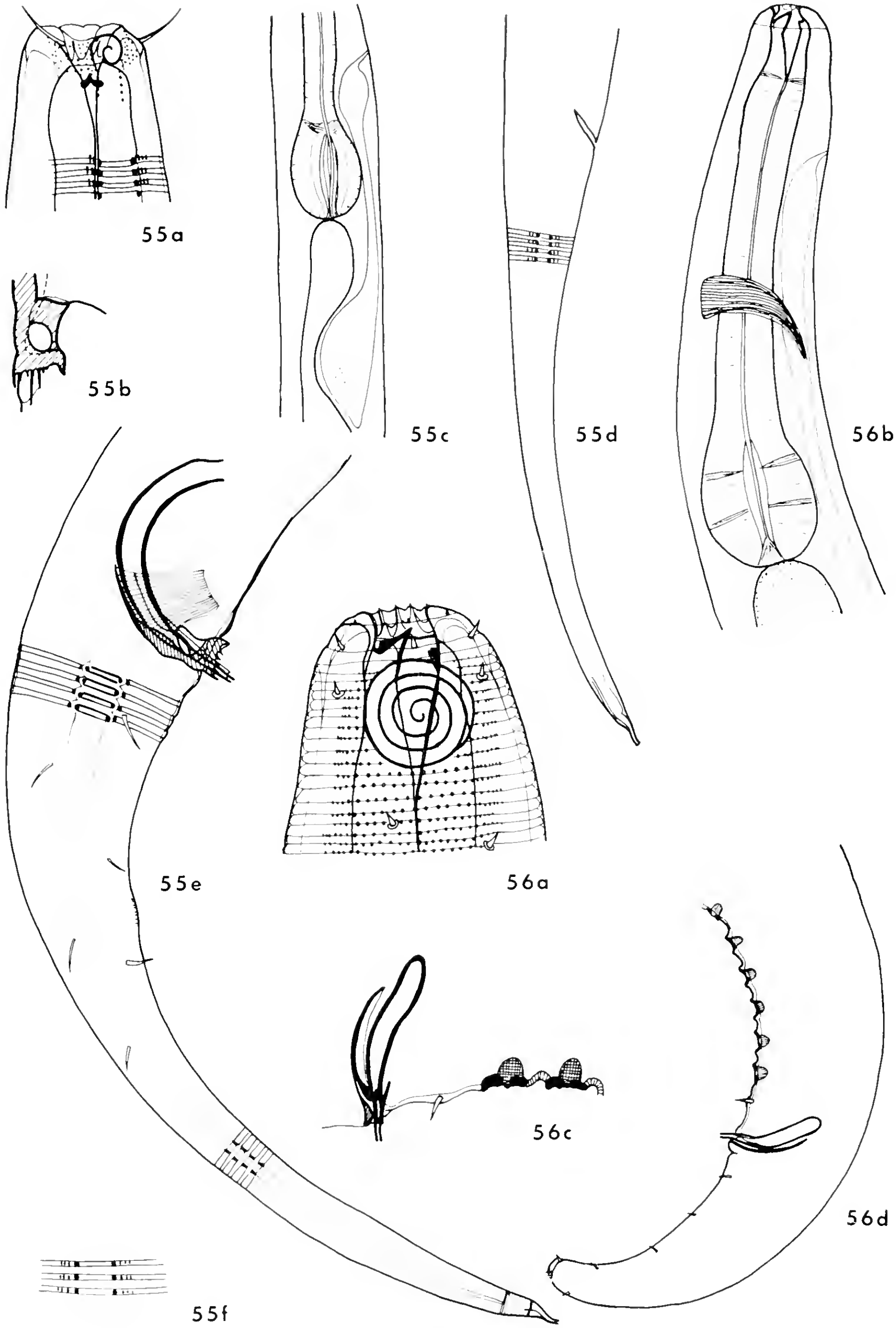


Plate XXVI

Atrochromadora denticulata Fig. 55, a–f: a—anterior end of male; b—distal end of spicular apparatus; c—region of esophageal bulb; d—tail of female; e—posterior end of male; f—cuticular differentiation, end of esophagus. *Neotonchus lutosus* Fig. 56, a–d: a—anterior end of male; b—anterior region of male; c—spicular apparatus; d—posterior end of male.

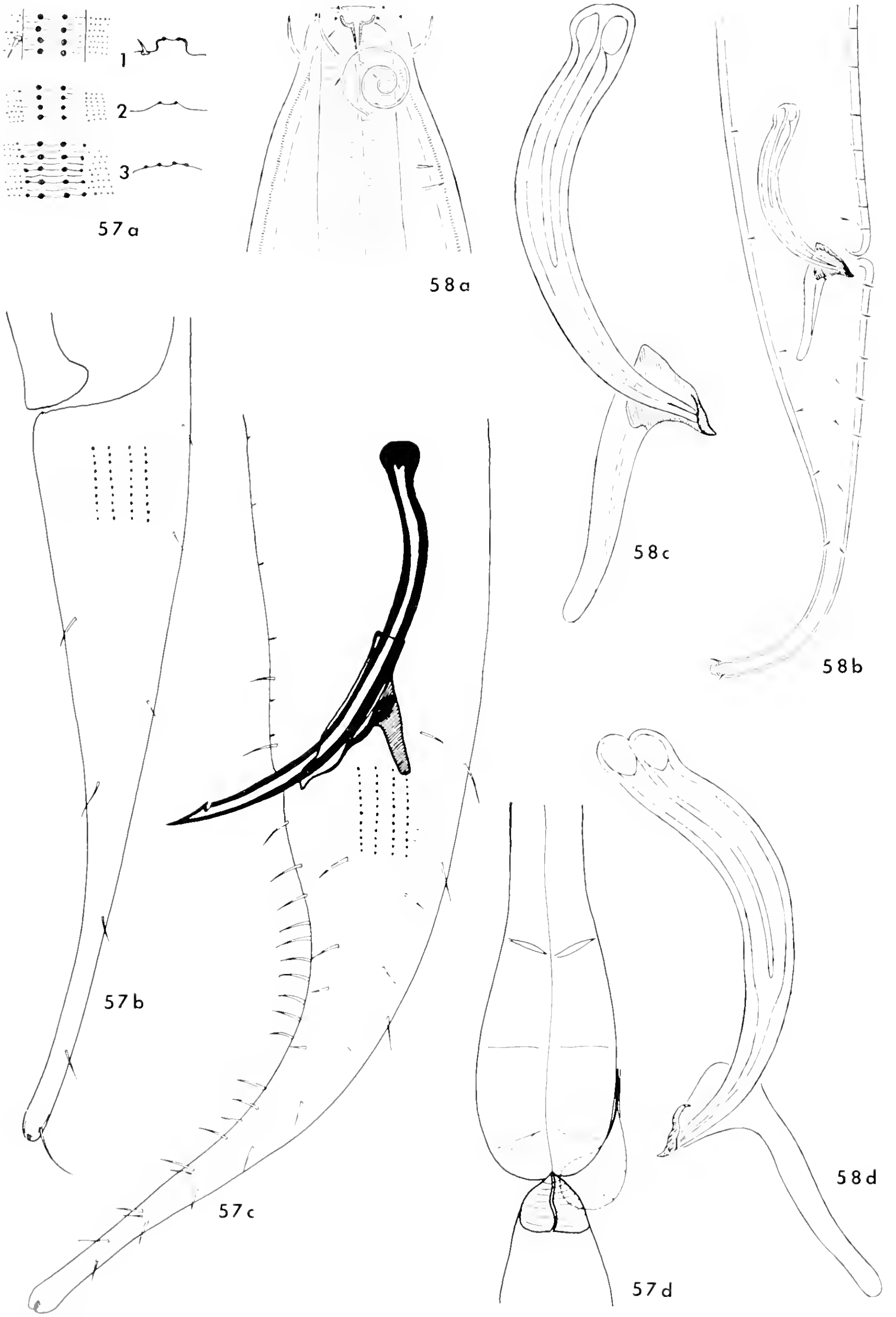
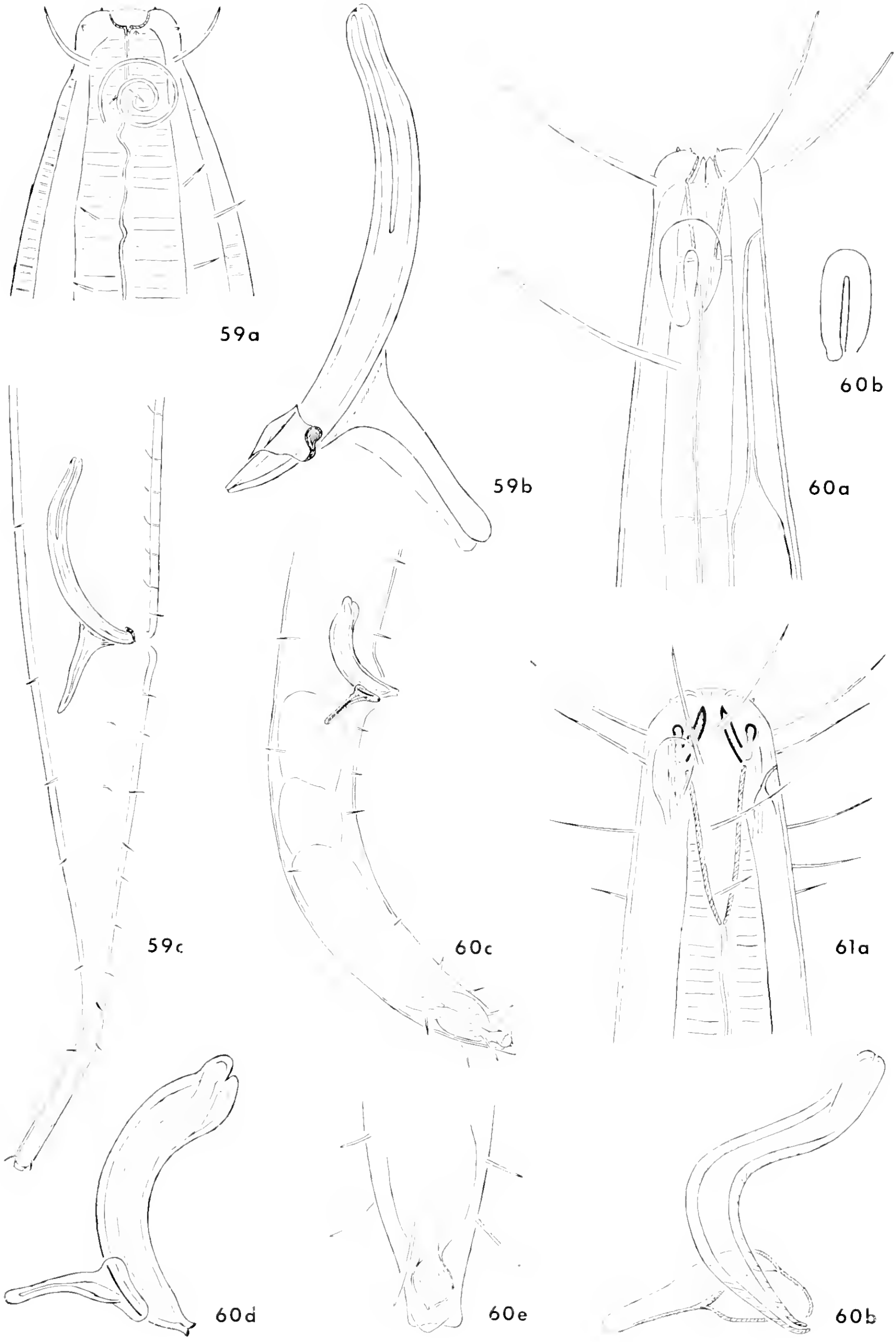


Plate XXVII

Mesonchium pellucidum Fig. 57, a–d: a—lateral differentiation of cuticle in lateral view and in cross section, 1: mid-body, 2: anal region of male, 3: anal region of female; b—tail of female; c—posterior end of male; d—esophageal bulb. *Sabatieria paradoxa* Fig. 58, a–d: a—anterior end of male; b—posterior end of male; c, d—spicular apparatus of two different males.



59a
59b
60b
60a
59c
60c
61a
60d
60e
60b

Plate XXVIII

Sabatieria paracupida Fig. 59, a–c: a—anterior end of male; b—spicular apparatus; c—posterior end of male. *Axonolaimus hexapilus* Fig. 60, a–e: a—anterior end of male; b—amphid of female; c—posterior end of male; d—spicular apparatus; e—tail terminus. *Odontophora variabilis* Fig. 61, a, b: a—anterior end of male; b—spicular apparatus (lower right, mislabeled 60b).

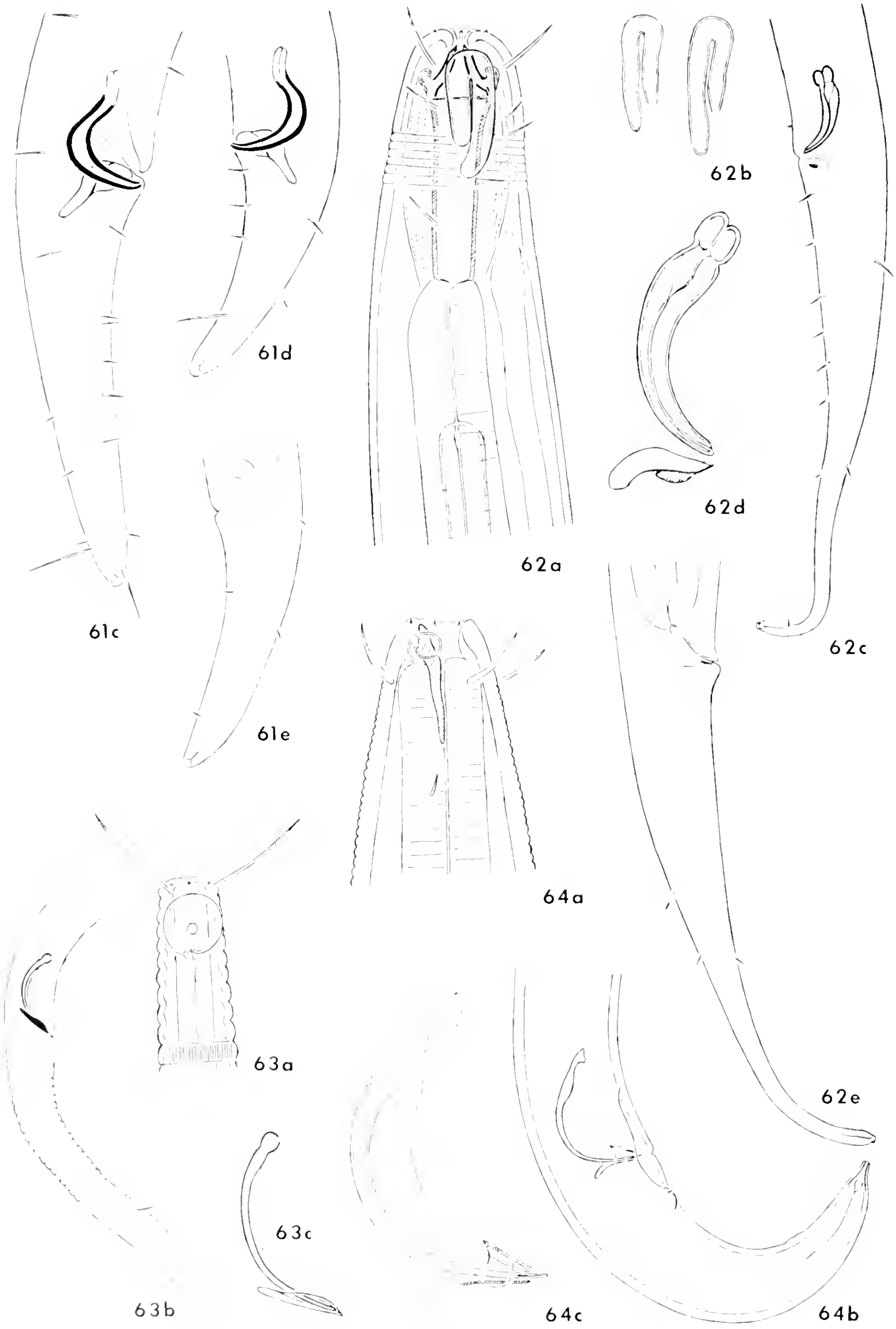


Plate XXIX

Odontophora variabilis Fig. 61, c–e: c, d—posterior ends of two males; e—posterior end of female. *Parodontophora brevamphida* Fig. 62, a–e: a—anterior end of male; b—amphids of two other specimens; c—posterior end of male; d—spicular apparatus; e—posterior end of female. *Alaimella cincta* Fig. 63, a–c: a—anterior end of male; b—posterior end of male; c—spicular apparatus. *Camacolaimus prytherchi* Fig. 64, a–c: a—anterior end of male; b—posterior end of male; c—spicular apparatus.

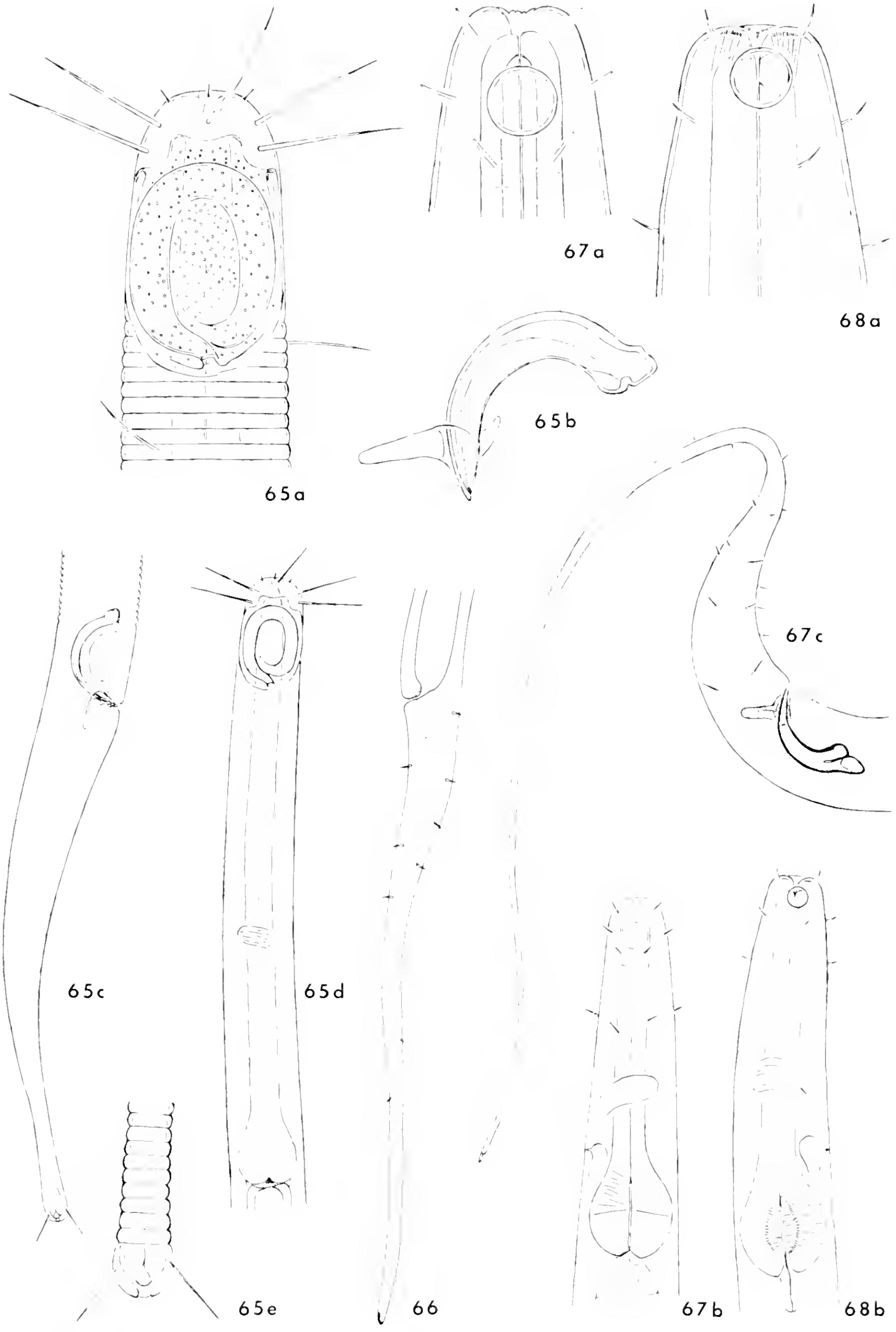


Plate XXX

Paratarvaia seta Fig. 65, a–e: a—anterior end of male; b—spicular apparatus; c—posterior end of male; d—anterior region of male; e—tail terminus. *Didelta maculatum* Fig. 66—posterior end of juvenile. *Terschellingia longicaudata* (Biscayne Bay-Florida Bay) Fig. 67, a–c: a—anterior end of male; b—anterior region of male; c—posterior end of male; (Vero Beach) Fig. 68, a, b: a—anterior end of male; b—anterior region of male.

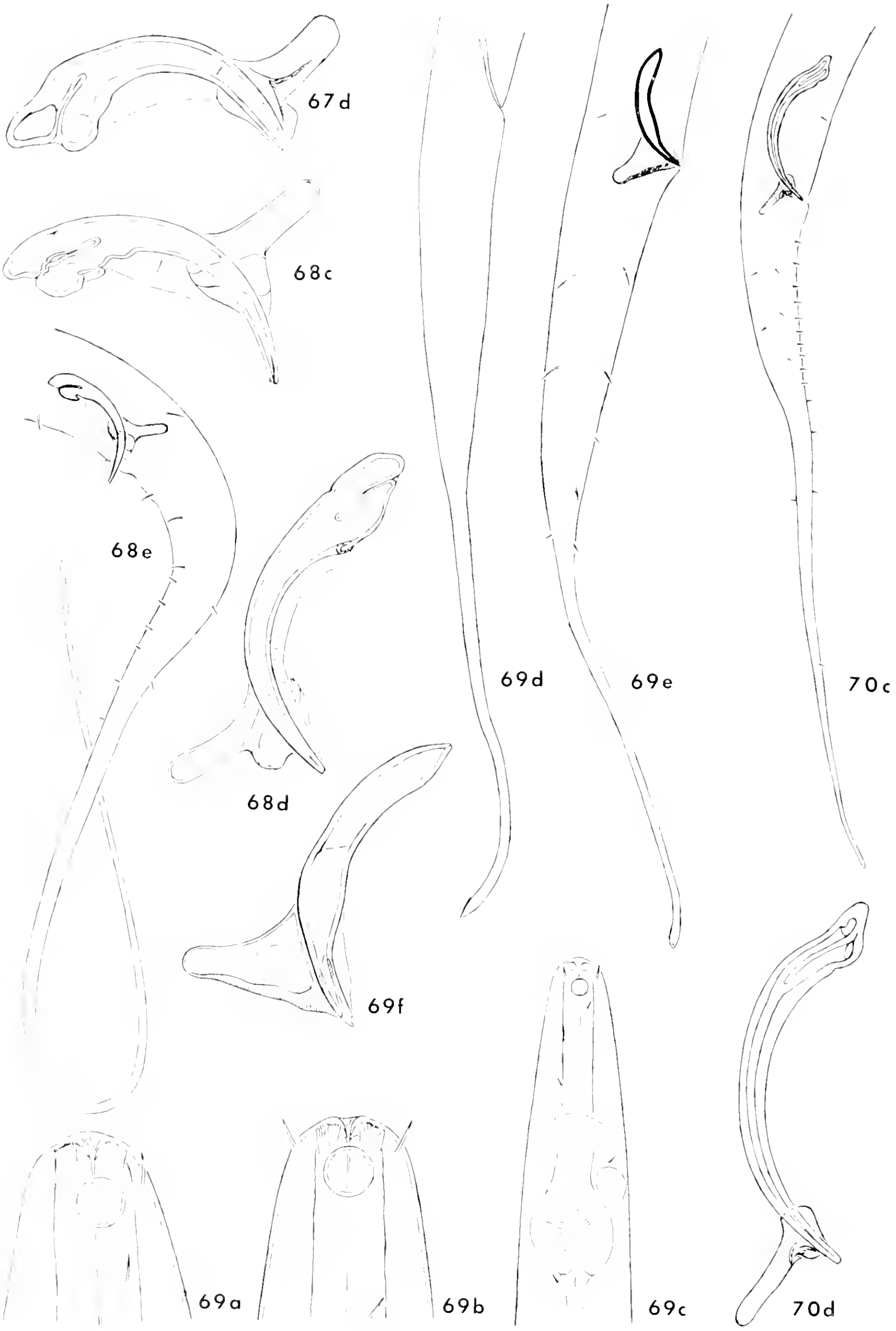


Plate XXXI

Terschellingia longicaudata (Biscayne Bay-Florida Bay) Fig. 67, d—spicular apparatus; (Vero Beach) Fig. 68, c–e: c, d—spicular apparatus of two males; e—posterior end of male. *Terschellingia monohystera* Fig. 69, a–f: a—anterior end of female; b—anterior end of male; c—anterior region of female; d—female tail; e—posterior end of male; f—spicular apparatus. *Terschellingia longispiculata* Fig. 70, c, d: posterior end of male; d—spicular apparatus.

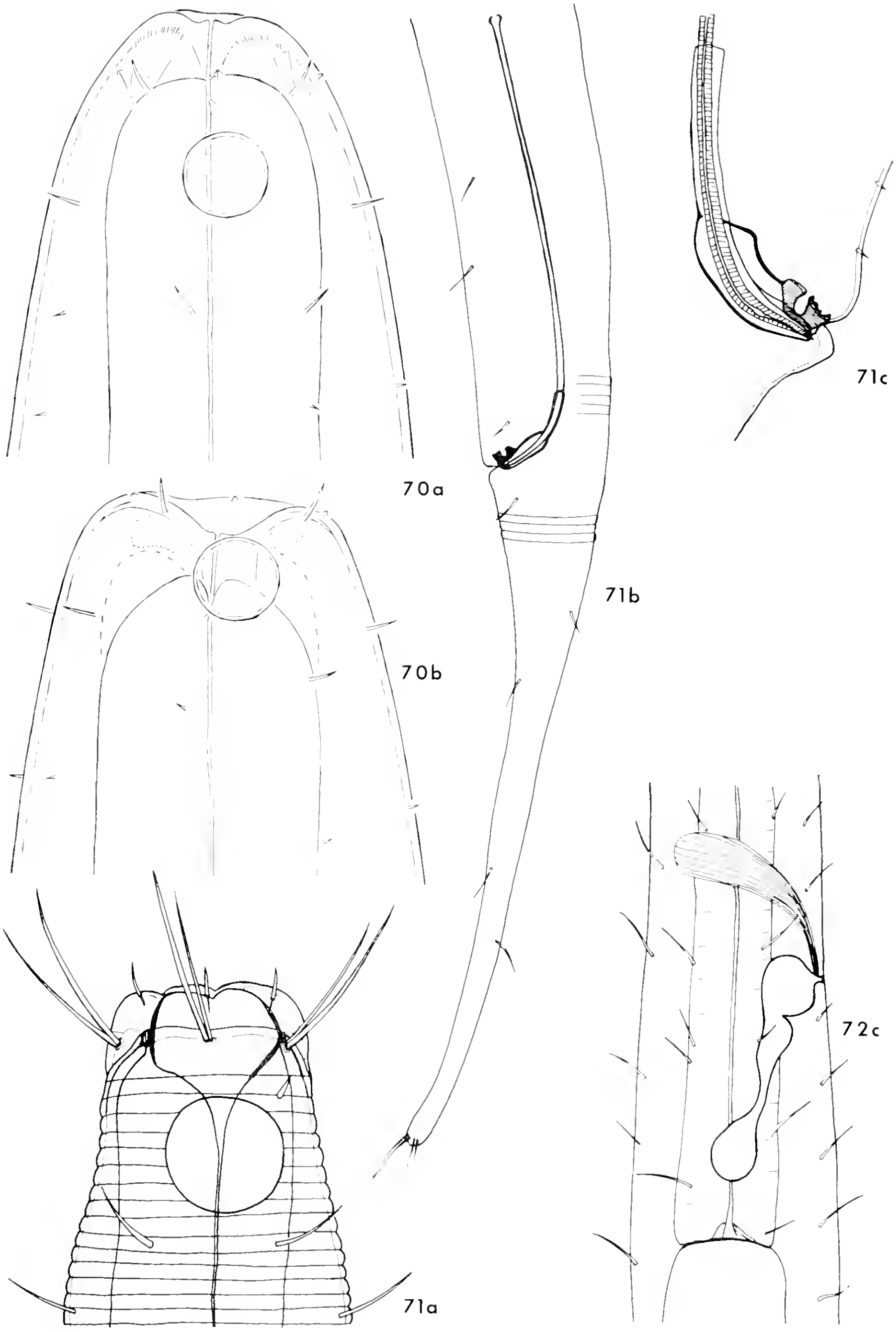


Plate XXXII

Terschellingia longispiculata Fig. 70, a, b: a—anterior end of female; b—anterior end of male. *Paramonhystera canicula* Fig. 71, a–c: a—anterior end of male; b—posterior end of male; c—distal portion of spicular apparatus. *Steineria ampullacea* Fig. 72, c—posterior esophageal region.

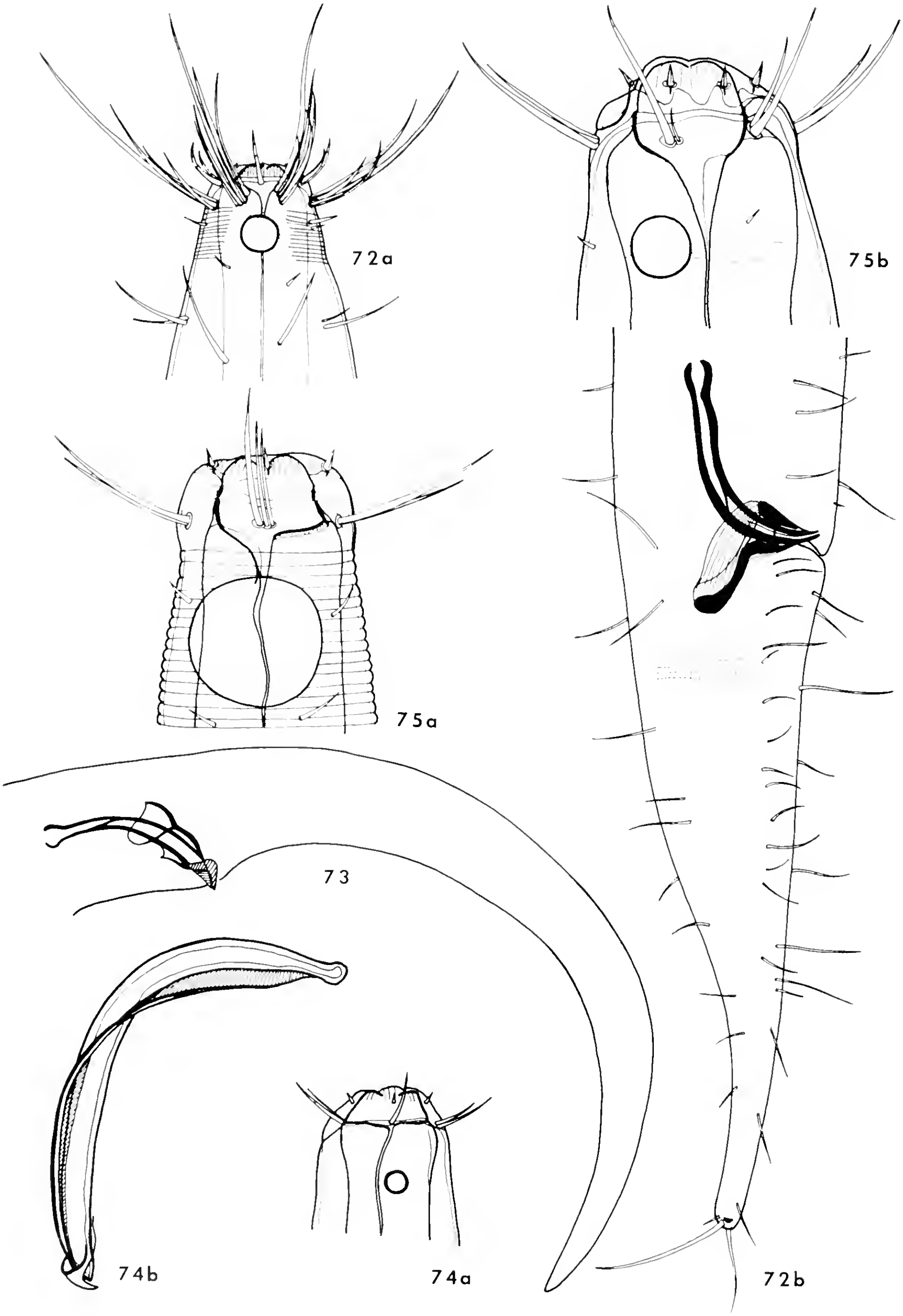


Plate XXXIII

Steineria ampullacea Fig. 72, a, b: a—anterior end of male; b—posterior end of male. *Theristus metaflevensis* Fig. 73—posterior end of male. *Theristus calx* Fig. 74, a, b: a—anterior end of male; b—spicular apparatus. *Theristus ostentator* Fig. 75, a, b: a—anterior end of male; b—anterior end of female.

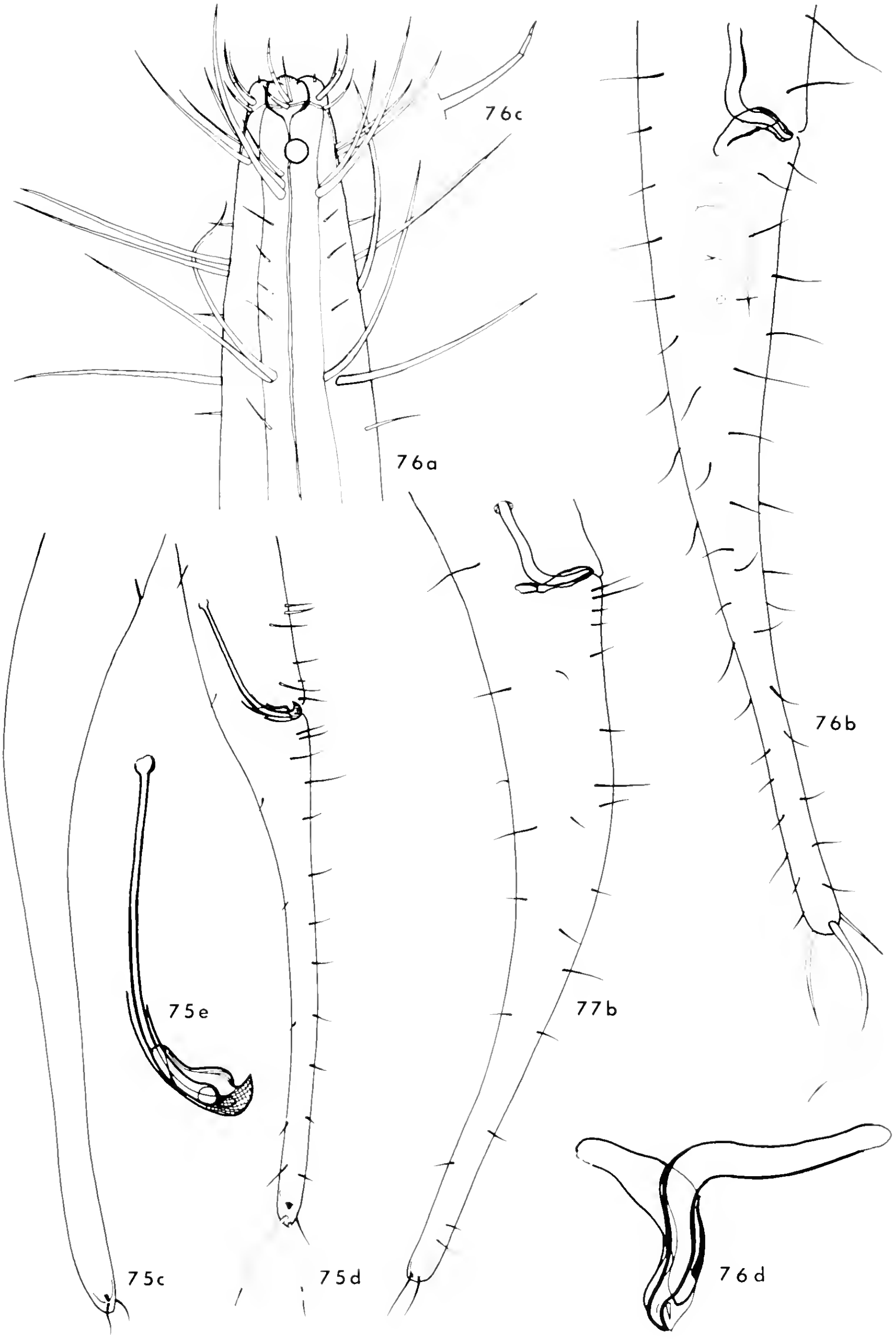


Plate XXXIV

Theristus ostentator Fig. 75, c–e: c—tail of female; d—posterior end of male; e—spicular apparatus. *Theristus floridanus* Fig. 76, a–d: a—anterior end of male; b—posterior end of male; c—cephalic seta; d—spicular apparatus. *Theristus erectus* Fig. 77, b—posterior end of male.

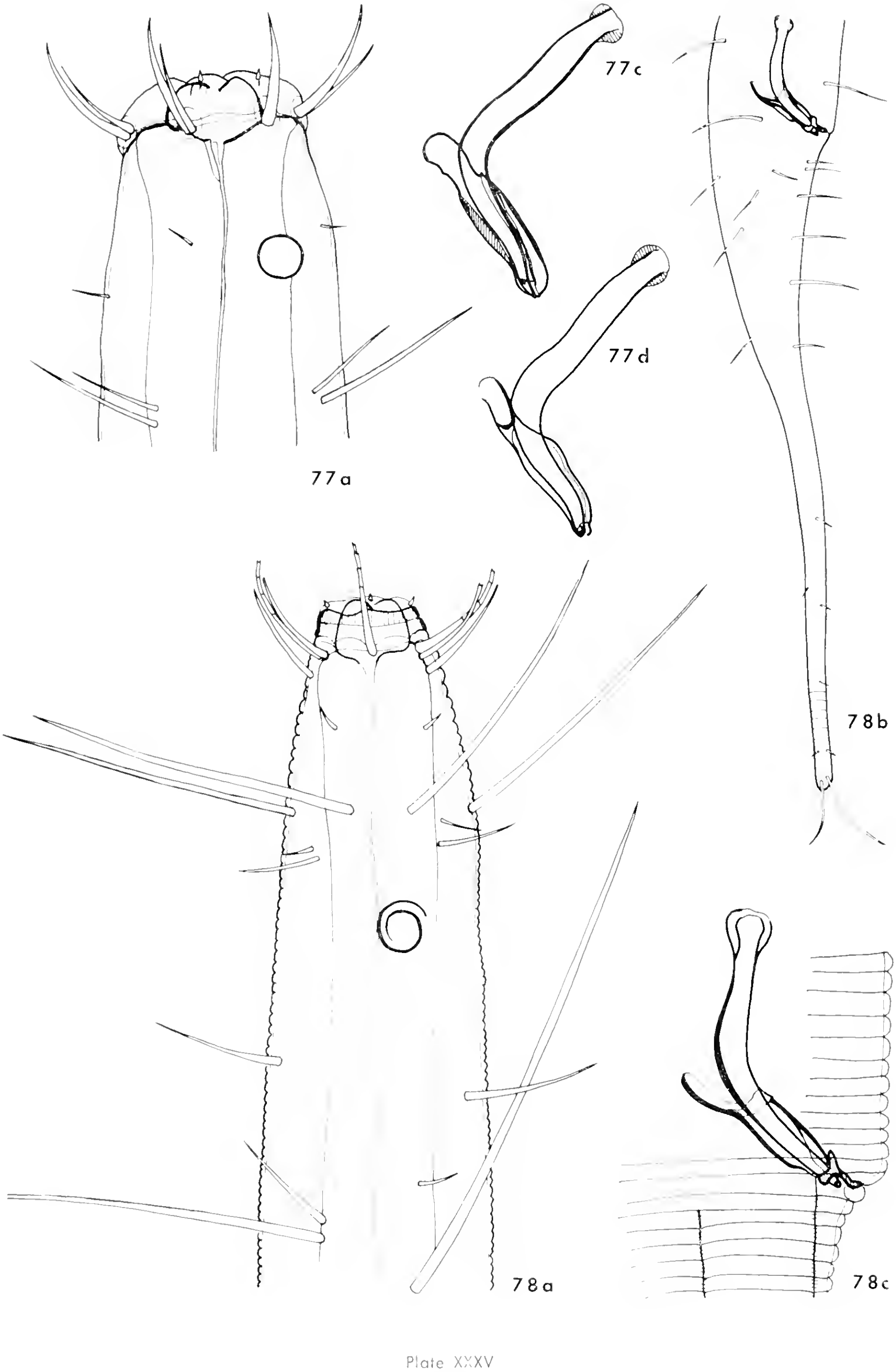


Plate XXXV

Theristus erectus Fig. 77, a, c, d: a—anterior end of male; c, d—spicular apparatus of two specimens. *Theristus galeatus* Fig. 78, a–c: a—anterior end of male; b—posterior end of male; c—anal region of male.

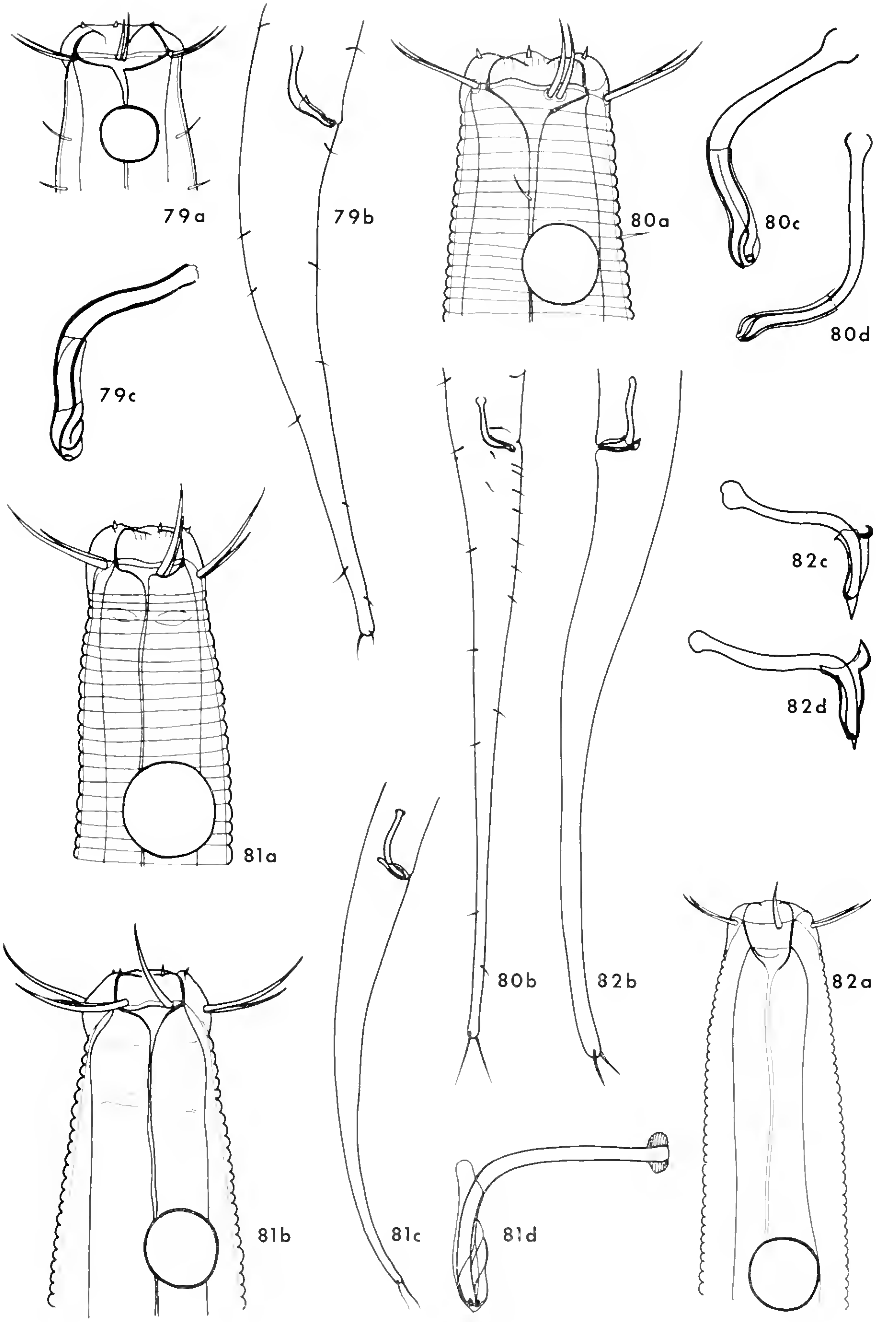


Plate XXXVI

Theristus oxyuroides Fig. 79, a–c: a—anterior end of male; b—posterior end of male; c—spicular apparatus. *Theristus fistulatus* Fig. 80, a–d: a—anterior end of male; b—posterior end of male; c, d—spicular apparatus of two specimens. *Theristus tortus* Fig. 81, a–d: a—anterior end of male; b—anterior end of female; c—posterior end of male; d—spicular apparatus. *Theristus xyaliformis* Fig. 82, a–d: a—anterior end of male; b—posterior end of male; c, d—spicular apparatus of two specimens.

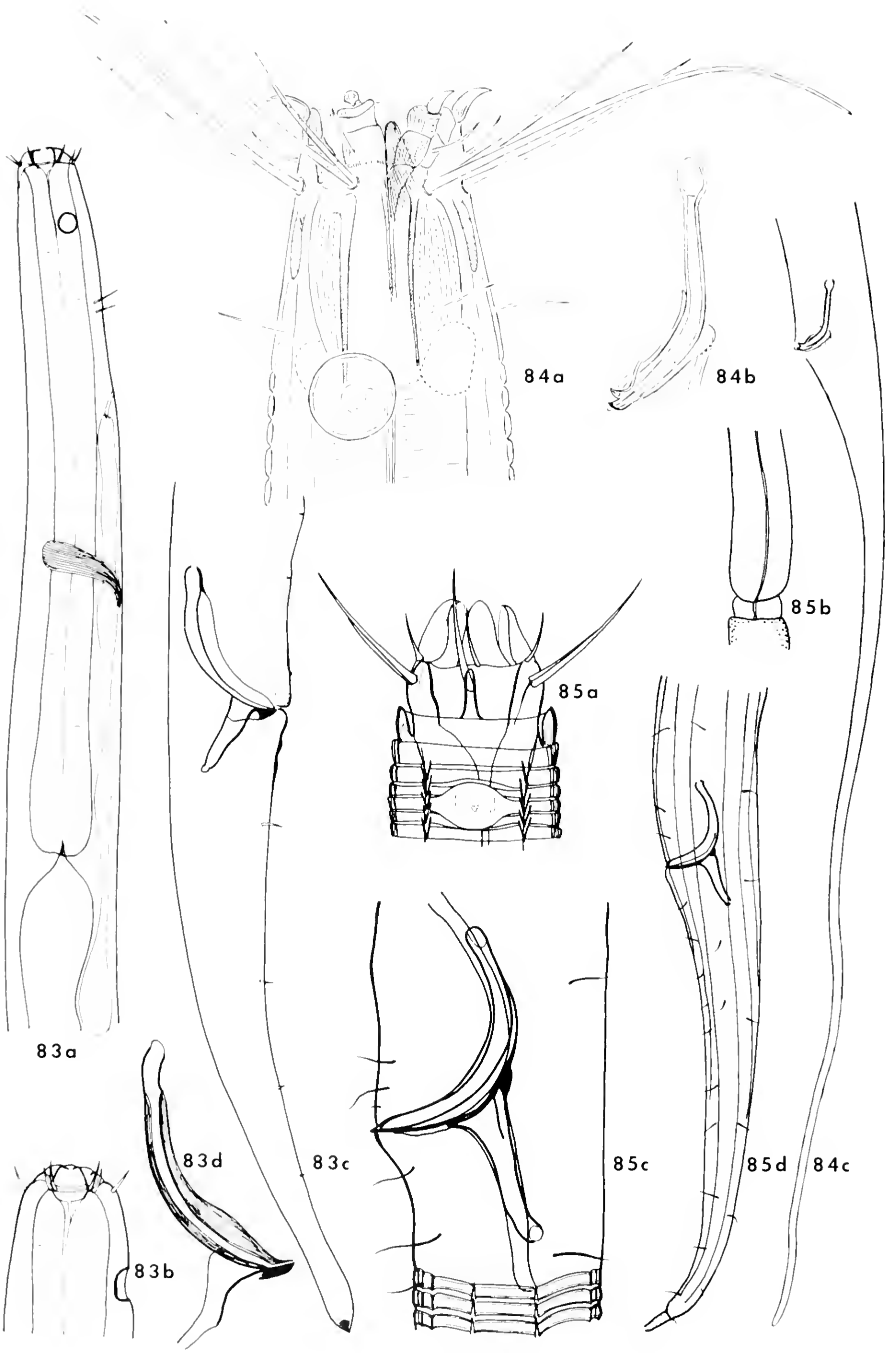


Plate XXXVII

Monhystera parva Fig. 83, a–d: a—esophageal region of male; b—anterior end of male; c—posterior end of male; d—spicular apparatus. *Scaptrella cincta* Fig. 84, a–c: a—anterior end of male; b—spicular apparatus; c—posterior end of male. *Xenolaimus striatus* Fig. 85, a–d: a—anterior end of male; b—posterior esophageal region; c—anal region of male; d—posterior end of male.

Bulletin OF THE
Museum of
Comparative
Zoology

The *Ameiva* (Lacertilia, Teiidae) of Hispaniola. III. *Ameiva taeniura* Cope

ALBERT SCHWARTZ

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 135, NUMBER 6
APRIL 24, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN 1863–
BREVIORA 1952–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

THE *AMEIVA* (LACERTILIA, TEIIDAE) OF HISPANIOLA.
III. *AMEIVA TAENIURA* COPE

ALBERT SCHWARTZ[1]

INTRODUCTION

Ameiva taeniura Cope was described in 1862 on the basis of an unknown number of syntypes from near Jérémie, Départment du Sud, Haiti. Barbour and Noble (1915: 433 *et seq.*) regarded *A. taeniura* as a synonym of *A. lineolata* Duméril and Bibron; the two species are very distinct in size, squamation and pattern, as Schmidt (1921a: 17) later demonstrated. Barbour and Noble examined 15 specimens of *A. taeniura*; with one exception, all were from various Haitian localities. Schmidt reported twelve specimens from the República Dominicana, and showed that the species was widespread throughout that republic. Mertens (1939:72–73) collected six specimens at three localities in the República Dominicana. Much more material was available to Cochran (1941:274), who noted the occurrence of the species at various Haitian and Dominican localities, as well as on the islets of Ile-à-Vache, Petite Cayemite and Grande Cayemite. Cochran had previously (1928:56 and 1934:179) described two other Hispaniolan *Ameiva*: *A. barbouri* from Ile de la Gonâve, and *A. rosamondae* from Isla Saona. These two species are correctly associated with *A. taeniura*, as Mertens (*loc. cit.*) has pointed out. Finally, Schmidt (1919:524) had described *Ameiva navassae* from Navassa Island between Hispaniola and Jamaica; later (1921b), he regarded *A. navassae* as being related to the Cuban *Ameiva auberi* Cocteau. In actuality, *A. navassae* is identical with *A. taeniura*; the precise status of this name is discussed in detail below.

Before proceeding, the status of the supposed syntypes of *A. taeniura* must be discussed. Barbour and Loveridge (1929:214) considered that three specimens in the Museum of Comparative Zoology at Harvard University (MCZ 3614) were the original syntypes. Examination of these specimens shows that, instead of their being *A. taeniura* from Hispaniola, they are specimens of *Ameiva thoracica* Cope from the Bahamas. Cope gave a detailed pattern description in his original work, and gave as well measurements on a single lizard, which was 3 inches in snout-vent length and 10 inches 6 lines in total length. None of the three supposed syntypes has a snout-vent length of 76 mm (=3 inches), the snout-vent lengths being 107, 92 and 70 mm. The pattern of these "syntypes" likewise does not agree with Cope's description. There is no question that MCZ 3614 does not contain the syntypes of *taeniura*; on the other hand, it is quite clear that Cope did indeed have specimens of the Hispaniolan lizard in hand when he wrote the original diagnosis.

There are three other specimens of *A. taeniura* in the Harvard collection (MCZ 3608, 3609 [2 specimens]) which were involved in the same loan to Cope that resulted in the confusion of the presumed syn-

---

[1] 10,000 S.W. 84 St., Miami, Florida 33143.

types. These lizards include two with snout-vent lengths of 75 and 77 mm, and thus quite close to the snout-vent length given by Cope. All agree also quite closely with Cope's pattern description. None, however, presently measures 267 mm (= 10 inches 6 lines) in total length. MCZ 3608, which has a snout-vent length of 75 mm, is the only specimen which currently has a tail (in two pieces), and a total length of about 240 mm is achieved when the specimen is assembled. It is possible that MCZ 3608 is one of the syntypes, and that Cope's total length measurement is in error, but I am reluctant to designate this lizard as a lectotype; it seems preferable to consider the original material, on which the name *A. taeniura* was based, as lost.

A. taeniura is now represented in collections by adequate series from the Tiburon Peninsula and the Península de Barahona; both of these regions pertain to the south island of Hispaniola (Williams, 1961). Despite intensive recent collecting in the República Dominicana, on the north island, *A. taeniura* remains rather poorly known in that republic. I have examined 406 specimens of *A. taeniura* from Hispaniola, Iles de Petite Cayemite and Grande Cayemite, Ile de la Gonâve, Ile-à-Vache, Isla Saona, and Isla Carenero in the Bahía de Samaná. Most of the material from the República Dominicana and much of the that from Haiti has been collected by Miss Patricia A. Heinlein and Messrs. Donald W. Buden, Ronald F. Klinikowski, David C. Leber, Dennis R. Paulson, Richard Thomas and the author, and is presently denoted as the Albert Schwartz Field Series (ASFS). To the above companions I wish to express my gratitude, and especially to Richard Thomas for visiting Isla Saona on my behalf. I have borrowed material from the following institutions and private collections: American Museum of Natural History (AMNH), Charles M. Bogert and George W. Foley; Carnegie Museum (CM), Neil D. Richmond and Clarence J. McCoy; Museum of Comparative Zoology (MCZ), Ernest E. Williams; Natur-Museum und Forschungs-Institut Senckenberg (SMF), Konrad Klemmer; University of Florida collections (UF), Walter Auffenberg; United States National Museum (USNM), Doris M. Cochran and James A. Peters; Peabody Museum at Yale University (YPM), Charles A. Reed; Donald W. Buden (DWB), and Richard Thomas (RT). I am grateful to the above for permission to study specimens in their care. The Harvard collections from the Tiburon Peninsula recently obtained with the aid of National Science Foundation grant GB2444 to Dr. Ernest Williams, have proved extremely pertinent and valuable, especially in defining the parameters of *A. taeniura* near the type locality. Paratypes of new forms have also been placed in the Museum of Natural History, University of Kansas (KU), and in the University of Illinois Museum of Natural History (UIMNH).

The main body of *A. taeniura* on the Hispaniolan mainland lies to the south of the Cul de Sac-Valle de Neiba plain. Not only is the species abundant in this region, but it also occupies three satellite islands (Ile-à-Vache, the Cayemites) associated with it. The species has not been taken on Isla Beata and Isla Alto Velo which are also associated with the south island of Hispaniola. On the north island, *A. taeniura* is known from the Llanos de Azua (where it appears to be quite rare), and from the region between Santo Domingo and Cabo Engaño (the eastern extremity of the island). There is an adequate series from the Península de Samaná (where the species appears to be abundant, although on two visits to the Península I have not seen it there). To the north in the República Dominicana, *A. taeniura* is known from the northern foothills of the Cordillera Central, from the Valle de Constanza region, Puerto Plata, and near Loma de Cabrera near the Dominico-Haitian border. In northern Haiti, there are specimens only from Plaisance and St. Michel de l'Atalaye; the species occurs as well near Trou Forban. The occurrence of *A. taeniura* on the north island satellites Isla Saona and Ile de la Gonâve (and on the islet Isla Carenero) has already been mentioned. The gaps in the distribution on the north island surely are not all real. However, collecting by ourselves and others in intermediate areas has not revealed the species.

Ameiva taeniura, in contrast to *A. lineolata* and *A. chrysolaema*, is a denizen of shady and mesic situations. It is common about Camp Perrin in southwestern Haiti and on Ile-à-Vache nearby. Large series from the Jérémie area attest to its abundance in that region. On the Península de Barahona, which, south of the Sierra de Baoruco, is extremely arid, *A. taeniura* occupies more shady stands of dry hardwood and *Acacia* forest; its interaction with *A. chrysolaema* near Laguna de Oviedo has already been discussed (Schwartz and Klinikowski, 1966). In the Llanos de Azua, the only two specimens secured were from a shady ravine; the remainder of the habitat was xeric thorn scrub. Mertens (1939) noted the occurrence of *A. taeniura* along the coast and even in the *Avicennia* zone at San Pedro de Macorís; the same situation occurs at Ile-à-Vache and near El Macao in the extreme eastern República Dominicana. Neither *A. chrysolaema* nor *A. lineolata* is so closely associated with shady and mesic situations as is *A. taeniura*; in increasing dependence upon this niche, the three species may be ranked as *lineolata-chrysolaema-taeniura* with *lineolata* the most confirmed denizen of hot and dry habitats.

The altitudinal range of *A. taeniura* is extensive. It occurs from sea level in many areas to elevations of 4250 feet (1296 meters) in the Cordillera Central in the República Dominicana, and 5600 feet (1707 meters) in the Montagne Noire in Haiti. No other Hispaniolan *Ameiva* (nor for that matter West Indian *Ameiva*) has such a broad altitudinal range. Doubtless its preference for more mesic and cool situations has allowed *A. taeniura* to ascend to these greater heights in the uplands.

There are 12 subspecies of *A. taeniura* discussed in the present paper; there is good evidence that this is not the complete roster of races on this species, but adequate material is lacking from the northern half of Haiti and the western and central portions of the República Dominicana. I have once again placed most emphasis on coloration and pattern—two features which vary geographically in a rational manner. Emphasizing these characters at the expense of scale counts demands that data on pigmentation and pattern must be taken on fresh specimens in the field. Without these data, some well-characterized races might be completely overlooked. In actuality, one must rely primarily on these two attributes in *A. taeniura*, since in most cases scale characters are extremely variable. For example, the range in number of rows of longitudinal ventrals for the entire sample of *A. taeniura* is 28 to 35; the range of this character in lizards from the Jérémie region alone is 29 to 34, and most other samples are comparable, usually merely lacking one or the other extreme, or both. Counts of fourth toe scales (both toes combined), femoral pores (both series combined), and scales in the fifteenth caudal verticil show somewhat more differentiation, but in hardly any case is there complete separation between subspecies on these counts.

The number of transverse rows of ventral plates has been used to characterize species of *Ameiva*. In *A. taeniura*, these rows are either 8 or 10, with only one population (southwestern shore of the Tiburon Peninsula) having a modal condition of 8. Any large sample (with the exception of 18 lizards from the Cordillera Central) includes both 8- and 10-row lizards. Thus even the number of transverse ventral rows is not constant in most cases. Although scale counts are given for all subspecies, they have in general been de-emphasized and must be used with discretion.

Ameiva taeniura may be defined as follows: 1) a moderate sized species of the genus *Ameiva* with snout-vent length to 102 mm in males and 103 in females; 2) dorsal

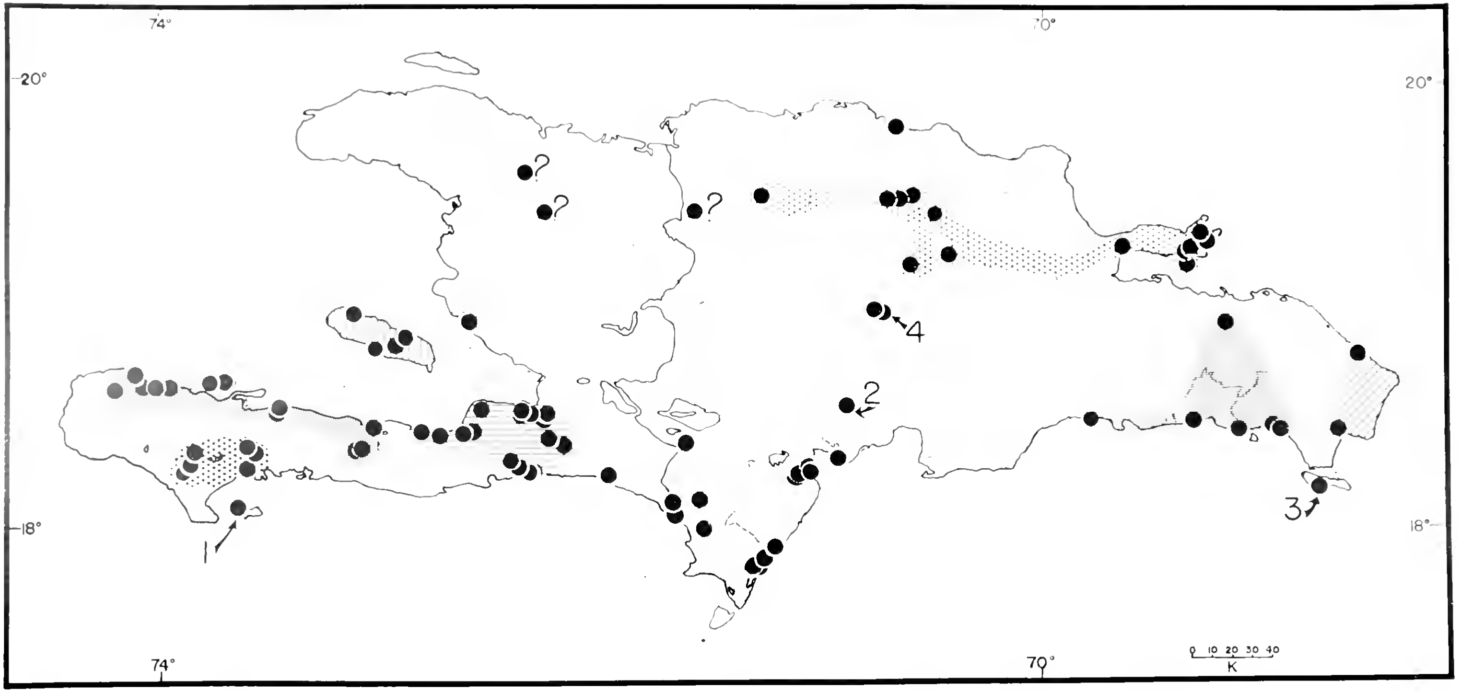


Fig. 1. Hispaniola, showing the known distribution of the subspecies of *Ameiva taeniura*, as follows: narrow vertical lines, *taeniura*; coarse stippling, *regnotrix*; wide horizontal lines, *varica*; fine stippling, *vulcanolis*; narrow horizontal lines, *tofacea*; diagonal lines, *vafra*; medium stippling, *ignobilis*; wide vertical lines, *barbouri*; 1) *aequorea*; 2) *azuae*; 3) *rosamondae*; 4) *algida*. The ranges of *tofacea* and *ignobilis* have been shaded to include localities which probably pertain to these races (see text for precise localities). Questioned localities in northwestern República Dominicana and northern Haiti are represented by specimens presently not assignable to subspecies. Lizards from Petite and Grande Cayemite are likewise not identified to race (see text for discussions).

caudal scales keeled and oblique; 3) ventrals in 8 or 10 transverse rows and in 28 to 35 longitudinal rows; 4) fourth toe subdigital scales from 61 to 91; 5) femoral pores 24 to 41; 6) fifteenth caudal verticil with 18 to 31 scales; 7) dorsal pattern consisting of either a) a series of five pale longitudinal lines on a dark back or, b) a median dorsal pale longitudinal zone, or c) a "combination" of the two conditions; and 8) hemipenis extending to about the sixth or seventh caudal verticil, sulcate surface naked; sulcus bifurcates slightly apically, the branches ending in two weakly bifid apical areas on each side; non-sulcate surface entirely flounced, the flounces extending around the organ onto the sulcate surface to near the sulcus itself; a small smooth triangular area on the non-sulcate side which divides the flounces for about one-half the length of the organ into two fields corresponding to the apical areas.

SYSTEMATIC ACCOUNT

Ameiva taeniura taeniura Cope, 1862

Ameiva taeniura Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, 14:63 (type locality—near Jérémie, Dépt. du Sud, Haiti)

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of moderate size (males to 88 mm, females to 76 mm, snout-vent length), usually 10 transverse rows of ventrals, low number of fourth toe subdigital scales and femoral pores, moderate number of scales in the fifteenth caudal verticil; dorsal pattern consisting of a dorsal zone bordered by one (paramedian) or two (paramedian and dorsolateral) pairs of pale longitudinal lines (the uppermost of which separating a fairly broad longitudinal dark zone between itself and the middorsal pale zone), lateral fields black with scattered pale (rusty in life?) dots, especially posteriorly; throat orange.

Distribution: The northern and western portions of the Tiburon Peninsula of Haiti from Marfranc east to Miragoâne and vicinity; inland, in the eastern portion of its range, to the vicinity of Fond des Nègres and St. Michel du Sud (Fig. 1).

Discussion: I have not seen living examples of *A. t. taeniura*, and thus am unable to treat the nominate subspecies in the same detailed manner as most of the other races. However, I have had the advantage of seeing a large body of freshly collected and well preserved material in the Museum of Comparative Zoology, and the following notes on pattern and coloration are drawn primarily from this recently taken material.

The dorsal pattern, although somewhat variable, shows the following situation. There is usually a broad middorsal pale longitudinal zone from the head onto the dorsal third of the tail. The basic pattern of Tiburon *taeniura* (as will be shown in the descriptions following) consists of a series of five pale longitudinal lines on a dark ground color. In *A. t. taeniura*, the median dorsal longitudinal zone embraces as many as the median and two paramedian longitudinal lines, so that the result is a longitudinal pale zone, bordered by a black longitudinal zone (the interspace between the original paramedian and dorsolateral light lines), which in turn is bordered by the dorsolateral light line. In many lizards, the extent of the dorsal pale zone is variable, so that the pale longitudinal paramedian lines may still be visible and not incorporated into the dorsal pale zone. The dorsolateral light lines are prominent, and begin above the eye and extend onto the proximal half of the tail, where they are wide and usually blue-green. On the head, the dorsolateral lines are rarely bordered medially by black. The lateral fields are black and extend from the temporal regions along the sides to the basal two-thirds of the tail. The lateral fields contain a few tiny pale spots (which probably were dull red or brick colored in life) especially posteriorly, and are bordered ventrally by a pale line which begins at the upper edge of the auricular opening and continues onto the basal quarter of the tail. This pale lateral line is regularly represented anterior to the auricular opening by one or two pale dots or dashes on the cheek between the eye and the ear. Below the lateral line the lower sides are dull grayish or brownish stippled with pale blue or blue-gray. The venter is blue-gray (presumably blue in life), and the tail is bright blue ventrally and distally, often with a median dorsal black zone (the continuation of the dark area between the dorsolateral pale body lines), a black lateral zone (the continuation of the lateral fields), and a ventrolateral dark line (the continuation of the dark area below the lateral line). These dark tail areas are separated by bold blue longitudinal lines and the blue underside of the tail. The throats are presently pale pinkish-orange, and I assume that in life they were bright orange. There is no striking sexual or ontogenetic difference in pattern, although juveniles have the dorsal pale lines more distinct than adults. In other races which I have seen in life, generally the orange throats of females are less brilliant than those of males.

The largest male (from Jérémie) measures 88 mm in snout-vent length, and the largest female (from Carrefour Sanon, near Jérémie) measures 76 mm. The longitudinal ventrals vary between 29 and 34 (mean 32.0) and these scales are most often arranged in 10 transverse rows (74.1 per cent), with 25.9 per cent having 8 transverse rows of ventrals. The fourth toe subdigital scales range from 65 to 82 (mean 73.2), and the femoral pores range from 24 to 35 (mean 29.3). The scales in the fifteenth caudal verticil vary between 23 and 29 (mean 25.8).

Of the two specimens from Fond des Nègres and St. Michel du Sud (USNM 72623 and AMNH 49721), the latter agrees well in pattern with *A. t. taeniura*. The individual from Fond des Nègres differs from all other *A. t. taeniura* in having the five dorsal lines well expressed, although the median one is fairly broad and expanded. I consider this individual as being a somewhat aberrant *A. t. taeniura*.

So many localities for *A. t. taeniura* can not be found on any map that it is difficult to state with certainty what the altitudinal limits of the race may be. There are specimens from sea level along the coast (10 mi. E Baradères, Petit Trou de Nippes, Roseaux) to about 600 feet (183 meters) at St. Michel du Sud and Fond des Nègres. Field notes (MCZ) by Francois Vuilleumier state that *Ameiva* "with blue tails" were regularly encountered but not collected on a trip between Lopino and Pourcine in the lower northern ranges of the Massif de la Hotte. Presumably the high elevation of the Massif de la Hotte to the south prevents *A. t. taeniura* from meeting the subspecies on the south coast.

Specimens examined: **Haiti**, *Dépt. du Sud*, Jérémie, 6 (MCZ 3608–09, 3 specimens; USNM 59240–42); Laye, nr. Jérémie (not mapped), 1 (MCZ 65070); Tiga, nr. Jérémie (not mapped), 1 (MCZ 65071); Carrefour Sanon, nr. Jérémie (not mapped), 18 (MCZ 65072–84, 69994–98); Perine, nr. Jérémie (not mapped), 2 (MCZ 65085–86); Bozor, nr. Jérémie (not mapped), 4 (MCZ 65087–89, 65113); Place Nègre, 2 (MCZ 65092–93); Paroty, nr. Jérémie (not mapped), 1 (MCZ 65094); Bozo, nr. Jérémie (not mapped), 5 (MCZ 69999–70003); La Source, nr. Jérémie (not mapped), 1 (MCZ 70004); Marfranc, 2 (MCZ 74547–48); Tessier, nr. Marfranc (not mapped), 4 (74556–59); Trou Bois on Jérémie road (not mapped), 5 (MCZ 74551–55); Roseaux, 4 (MCZ 74549–50, USNM 58245–46); 10 mi. (16 km) E Baradères, 4 (USNM 80767–70); Petit Trou de Nippes, 2 (USNM 80799–800); Miragoâne, 3 (USNM 77070–71, 72635); St. Michel du Sud, 1 (AMNH 48721); Fond des Nègres, 1 (USNM 72623); (the following localities, all "near Miragoâne," are unlocatable and unmapped and may be in either the *Département du Sud* or the *Département de l'Ouest*): Commune Aquin, 1 (MCZ 66302); Risque, 2 (MCZ 66303–04); Butète, 6 (MCZ 66305–06, CM 37926–29); Nan Carosse, 2 (MCZ 66307–08); Mingrette, 7 (MCZ 66309–10, 66314–15, CM 37930–32).

POPULATIONS ON THE ILES DE GRANDE AND PETITE CAYEMITE

This seems an appropriate place to discuss the small sample of *A. taeniura* from the islands of Grande and Petite Cayemite, which lie off the north coast of the Tiburon Peninsula between Jérémie and Baradères. The adjacent mainland of Haiti is occupied by *A. t. taeniura*.

There are two specimens (MCZ 25535–36) from Grande Cayemite and five (USNM 80819–23) from Petite Cayemite. The former consist of a male (snout-vent length 78 mm) and a female (75 mm), and the latter four males (snout-vent lengths 51 to 68 mm) and a female (67 mm). When treated as a group, the following scale counts are obtained: longitudinal ventrals in 30 to 33 rows (mean 31.9) and usually in 10 (one exception with 8) transverse rows. The fourth toe subdigital scales vary between 81 and 91 (mean 85.2), the femoral pores between 28 and 32 (mean 29.9), and there are from 26 to 30 (mean 28.4) scales in the fifteenth caudal verticil. The population(s) is thus very high (and almost completely separable from *A. t. taeniura*—with an overlap of only two scales) in number of fourth toe scales. In other counts they are comparable, although they average higher in both femoral pores and fifteenth verticil scales. In fact, no other population of *A. taeniura* approaches the very high number of fourth toe scales possessed by these Cayemite specimens.

Examination of the patterns shown by these specimens leaves much to be desired. The two specimens from Grande Cayemite are presently dark and have five bold pale dorsal lines with no trace of any middorsal pale zone. These two lizards are abundantly different from adjacent *A. t. taeniura*. The five specimens from Petite Cayemite present a different aspect, for all these lizards are patterned very much like the mainland specimens, with a pale middorsal zone bordered by a black zone. These Petite Cayemite specimens are presently not separable in pattern from those from the mainland. Thus, the Grande Cayemite specimens are different from *A. t. taeniura* in both pattern and fourth toe scales, whereas the Petite Cayemite individuals differ only in fourth toe scales and are comparable in pattern.

It is tempting to name the Cayemite lizards as a distinct race, which I have little doubt that they are. However, the anomalous pattern condition makes it imperative that additional material be secured before the above course is followed. It is possible that Petite Cayemite lizards might be best interpreted as intergrades or intermediates between *A. t. taeniura* and a distinct subspecies on Grande Cayemite, although of the two islands, the latter is closer to the mainland. Another possibility is that each has its own distinct subspecies; only fresh material will clarify the situation.

Ameiva taeniura regnatrix new subspecies[1]

Holotype: MCZ 81072, an adult male, from Camp Perrin, Dépt. du Sud, Haiti, one of a series collected 26 July 1962 by David C. Leber. Original number X2989.

Paratypes: MCZ 81073–75, same data as type; UF 21318–19, UIMNH 61602–03, same locality as type, 22 July 1962, native collector; ASFS X2667–70, X2686–88, X2701–04, same locality as type, 23 July 1962, native collector; ASFS X2818–22, same locality as type, 24 July 1962, native collector; CM 40555–58, same locality as type, 28 July 1962, native collector; AMNH 94233–34, Carrefour Canon, 500 feet (152 meters), Dépt. du Sud, Haiti, 1 August 1962, R. F. Klinikowski; AMNH 94232, 4 km NE Carrefour Canon, Dépt. du Sud, Haiti, 1 August 1962, D. C. Leber; KU 93303–04, Ravine Citronnier, 10 km N, 2 km E Cavaillon, Dépt. du Sud, Haiti, 6 August 1962, D. R. Paulson; UF 21320, 14 km N Cavaillon, 1800 feet (549 meters), Dépt. du Sud, Haiti, 6 August 1962, D. C. Leber; KU 93305–07,

---

[1] Latin, ruling; this is the only species of the genus known from its geographic range.

UIMNH 61604–06, Cavaillon, Dépt. du Sud, Haiti, 6 August 1962, native collector.

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of moderate size (males to 88 mm, females to 81 mm snout-vent length), regularly 8 transverse rows of ventrals, very low number of fourth toe subdigital scales, low number of femoral pores, and moderate number of scales in the fifteenth caudal verticil; dorsal pattern consisting of five dorsal, longitudinal, yellow to tan lines, the median and paramedian lines at times enclosed in a reddish brown middorsal zone (although these lines still maintain their distinctness if so included), lateral fields black and without included pale dots; throat orange.

Distribution: Extreme southwestern portion of the Tiburon Peninsula, from Carrefour Canon and Camp Perrin in the west, east to the vicinity of Cavaillon (Fig. 1).

Description of type: An adult male with the following measurements and counts: snout-vent length 83 mm, tail 204 mm; ventrals in 33 longitudinal and 8 transverse rows; fourth toe subdigital scales 38 and 34 (total 72); femoral pores 15 and 17 (total 32); 26 scales in the fifteenth caudal verticil. Dorsal ground color reddish brown in life, with a series of five longitudinal yellowish tan lines, the median and paramedian lines slightly wider than the dorsolateral lines and blending with the reddish brown head color on the occiput. A black longitudinal zone between the paramedian and dorsolateral lines beginning on the supraoculars, extending medially between the supraoculars and median head shields, and continuing onto the base of the tail, the dorsolateral lines the most prominent and extending onto the proximal three-quarters of the tail as dorsolateral pale yellowish lines. The paramedian lines extend onto the base of the tail where they fuse with one another at about the eighteenth dorsal caudal verticil. Lateral fields black, without included pale dots. Lateral pale line from the auricular opening to the groin, and then continuing behind the leg as a broad, blue ventrolateral caudal line. Throat vivid orange (pl. 2C12; all color designations from Maerz and Paul, 1950), this color extending onto chest; remainder of venter grayish orange extending onto underside of tail. Lower sides below yellow lateral line brown. Limbs vaguely marbled black and dark brown. A prominent yellow dash on the cheek and a yellow reversed C bordering the anterior edge of the auricular opening.

Variation: The series of 38 *A. t. regnatrix* has the following counts: longitudinal ventrals 28–33 (mean 31.3); rows of transverse ventrals 8 (94.7 per cent) or 10 (5.3 per cent); fourth toe scales 61–74 (mean 66.7); femoral pores 24–34 (mean 28.9); fifteenth verticil 23–28 (mean 24.8).

The coloration and pattern of *A. t. regnatrix* are fairly constant. The five dorsal longitudinal lines and the black lateral fields without included pale or red dots are regular features of the series. Some specimens have the median and paramedian dorsal lines widened, at times so much so as to form a dorsal pale zone. However, even in these cases the integrity of the longitudinal lines is quite clear. The extension of the black longitudinal zone onto the supraoculars and between them and the median head scales is a constant pattern feature. The underside of the tail in adults is orange-gray proximally and blue-gray distally; in juveniles the tail is vivid blue dorsally, whereas in adults only the more distal portion is blue, the proximal region being black with prominent tan to yellowish dorsal and dorsolateral lines.

Comparisons: The major scale difference between the races *taeniura* and *regnatrix* is that the former customarily has 10 transverse rows of ventrals, the latter 8. Although there is much overlap, the mean (66.7) of fourth toe scales in *regnatrix* is considerably lower than that (73.2) in *taeniura*.

In pattern the two are quite distinct. The middorsal zone of *taeniura* contrasts with the five-lined dorsum of *regnatrix*. *Taeni-*

ura regularly has some pale flecks in the black lateral fields, whereas *regnatrix* regularly lacks intrafield markings. The extension of the black longitudinal zones onto the head shields affords a rapid means of differentiating the two races.

Remarks: *A. t. regnatrix* occurs from sea level to elevations of 1800 feet (549 meters) in the Massif de la Hotte north of Cavaillon. At Camp Perrin, the lizards were abundant among rocks along the edges of cultivated fields. At Carrefour Canon they were collected along the edge of a canal in mesic coffee canopy forest, and 14 km N of Cavaillon they were encountered along the edge of *Coffea* in the uplands. The Ravine Citronnier locality is in xeric scrub, but is within the uplands of the Massif de la Hotte.

Ameiva taeniura aequorea[1] new subspecies

Holotype: MCZ 81086, an adult male, from western end, Ile-à-Vache, Dépt. du Sud, Haiti, one of a series collected 4 August 1962 by Ronald F. Klinikowski, David C. Leber, and Dennis R. Paulson. Original number X3416.

Paratypes: AMNH 94235–37, CM 40559–61, KU 93308–11, UF 21321–23, UIMNH 61607–09, same data as type; ASFS X3570–76, same locality as type, 6 August 1962, R. F. Klinikowski.

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of small size (males to 80 mm, females to 73 mm snout-vent length), regularly 10 transverse rows of ventrals, moderate number of fourth toe subdigital scales and scales in the fifteenth caudal verticil, and low number of femoral pores; dorsal pattern consisting of five longitudinal yellow dorsal lines, of which the median is often obsolescent or incomplete on the neck, on a black ground, lateral fields of black without or with very few tiny pale dots; throat dark orange.

Distribution: Ile-à-Vache, Haiti (Fig. 1).

Description of type: An adult male with the following measurements and counts: snout-vent length 80 mm, tail 146, distal two-thirds regenerated; ventrals in 33 longitudinal and 10 transverse rows; fourth toe subdigital scales 40 and 39 (total 79); femoral pores 15 and 13 (total 28); 21 scales in the fifteenth caudal verticil. Dorsal ground color black, with five longitudinal yellow lines which are distinctly orange anteriorly. The median line is obscure and broken on the neck, whereas the paramedian lines are somewhat brighter and the dorsolateral lines are boldly distinct. The longitudinal black stripe begins on the supraoculars and sends a short branch between the supraoculars and the median head scales. The lateral fields are black and have a very few tiny scattered pale dots. The paramedian lines extend onto the tail, where they join at about the twenty-third dorsal caudal verticil. The dorsolateral lines expand upon the base of the tail and continue (becoming progressively bluer) to the point of regeneration. There is an orange cheek spot and an orange preauricular spot. The lateral line begins at the auricular opening and continues to the groin; posterior to the hindlimb, the lateral line continues as a bold white ventrolateral tail stripe. The sides below the lateral line are black, somewhat stippled with gray. The throat, chest, and anterior half of venter were dark orange (pl. 1G12) in life, the remainder of the venter being duller grayish orange. The limbs are coarsely marbled black and tan. The underside of the tail is blue.

Variation: The series of 24 *A. t. aequorea* has the following counts: longitudinal ventrals 30–32 (mean 31.5); rows of transverse ventrals 10 (95.8 per cent) or 8 (4.2 per cent); fourth toe scales 65–83 (mean 76.6); femoral pores 26–31 (mean 28.3); fifteenth verticil 21–26 (mean 23.2).

The coloration and pattern of the paratypes are close to that of the type. No other specimen has any included pale dots in the black lateral fields, and indeed they are far from conspicuous in the type. The median pale dorsal line is always visible, regularly

---

[1] Latin, sea-girt, referring to Ile-à-Vache.

broken on the neck, and may be somewhat obscured by a tan clouding between the paramedian lines. Even in the latter case, the median line is visible. The throats, chests, and anterior portion of the venter are dark orange in males; females have the throats somewhat paler. The underside of the tail may be blue or gray. The limbs are heavily marbled with black and tan.

Comparisons: The most pertinent comparison is between *aequorea* and the adjacent *regnatrix*. The former has 10 transverse rows of ventrals and the latter 8. The much lower mean of fourth toe scales (66.7) in *regnatrix* differentiates the mainland race from *aequorea* (with a mean of 76.6). *Aequorea* also appears not to reach so large a size as *regnatrix*. The two are comparable in pattern, but the broken median line on the neck in *aequorea* will differentiate them. The dark orange throat and orange-tinted dorsal lines of *aequorea* differ from the brighter throat and yellow to tan lines of *regnatrix*. From *taeniura*, the Ile-à-Vache subspecies differs in lacking a middorsal pale zone and in lacking pale dots in the lateral fields. Both *aequorea* and *taeniura* have 10 transverse rows of ventrals. The northern race reaches a slightly larger size than *aequorea*.

Remarks: *A. t. aequorea* is close to *regnatrix* in pattern, and differs primarily in details of coloration and in number of transverse rows of ventrals. Its origin from *regnatrix* on the adjacent mainland is obvious. On Ile-à-Vache, *A. t. aequorea* was abundant in shady situations especially along the mangrove border, where the earth was cool even at midday. Many more lizards were observed than were collected.

Ameiva taeniura navassae Schmidt, 1919

Ameiva navassae Schmidt, 1919, Bull. Amer. Mus. Nat. Hist., 41(12):524 (type locality—Navassa Island).

It seems appropriate here to comment upon *Ameiva navassae* Schmidt. This species is known from a single specimen (AMNH 12607) collected by Rollo H. Beck on Navassa between 13 and 19 July 1917. It is an adult male, with the following measurements and counts: snout-vent length 85 mm; ventrals in 34 longitudinal and 10 transverse rows; fourth toe subdigital scales 43 and 42 (total 85); femoral pores 15 and 16 (total 31); scales in fifteenth caudal verticil 28. The dorsum is presently dark with four pale longitudinal lines and a median pale middorsal area; the dorsolateral pale lines extend anteriorly over the outer edge of the supraoculars and more or less onto the canthus. The lateral fields are black and without included pale dots. The lower sides are vaguely marbled with light and dark. The tail is regenerated for its distal half. Four dorsal pale lines extend onto the unregenerated portion of the tail and there is a broad pale ventrolateral line as well. Both fore- and hindlimbs are vaguely marbled with dark and light. There is a pale cheek spot and a pale preauricular spot. The top and sides of the head are dull tan, and the chin and throat are now pale, in contrast to the dull grayish blue of the venter.

There can be no doubt that *A. navassae* is related to *A. taeniura*, rather than to *A. auberi* from Cuba, as Schmidt (1921b:559) suggested. It may seem strange that Schmidt, who had collected *A. taeniura* in the República Dominicana (1921a), did not recognize the similarity of the two "species." This is, however, easily attributable to the fact that Dominican *A. taeniura* lack the lined pattern of the Tiburon races, which Schmidt had not observed.

A. navassae resembles most closely in details of pattern specimens of *A. t. regnatrix*. Thomas (1966) has commented on the possibility that the type specimen of *navassae* may have originated in the vicinity of Les Cayes (from which port Beck set out for Navassa; Wetmore and Swales, 1931:19) and later was mislabeled as having come from Navassa. This supposition reaches greater importance, for, should *regnatrix* and *navassae* be identical, the southwestern Tiburon race would then take the name *navassae*. The resemblance of *navassae* and *regnatrix* may be due to close relationship, since a Hispaniolan lizard arriving on Navassa might be most logically expected to have come from the tip of the Tiburon Peninsula, rather than elsewhere. The fact that no collector, either before or after Beck (see Thomas, 1966, for details), has taken another specimen of *Ameiva* on Navassa may be very significant, or it may be of no significance whatsoever, if the supposed destructive effects of the lighthouse-keeper's domestic animals can be blamed for the disappearance of some of the Navassan fauna.

In any event, from the very fact that I have not used the name *navassae* for the Camp Perrin-Cavaillon lizards, it is obvious that I am not convinced of the identity of *navassae* with *regnatrix*. The fourth toe scales in *navassae* number 85; no specimen from the Tiburon Peninsula itself nor from Ile-à-Vache (whence the type of *navassae* might have come) has so high a count (130 examined), the highest being a count of 83 for *aequorea*. The high count for *regnatrix* is 74. The *navassae* count of 85 is, however, included by the counts of Grande-Petite Cayemite lizards (81–91). However, since Beck is not known ever to have visited these islets, or even to have visited the north coast of the Tiburon, it does not seem likely that the type of *navassae* originated on the Cayemites. The 34 longitudinal rows of ventrals in *navassae* are greater in number than in any specimen of *regnatrix*, but are equalled or exceeded by three specimens of *taeniura*. *A. navassae* has 10 transverse rows of dorsals in contrast to 8 rows in *regnatrix*.

As Thomas (1966) has suggested, it is possible that *A. navassae* came from a local population of *A. t. regnatrix* which has as yet not been sampled, a population in which such high fourth toe counts do occur. I hesitate to say that no *Ameiva* occurred in the recent past on Navassa. What can be said is that *A. navassae* must be regarded as a subspecies of *A. taeniura*. whatever the history and provenance of the type and only specimen.

Ameiva taeniura varica[1] new subspecies

Holotype: MCZ 81076, an adult female, from Morne Calvaire, 1 mi. (1.6 km) SW Pétionville, 2300 feet (701 meters), Dépt. de l'Ouest, Haiti, taken 21 June 1962 by native collector. Original number X1299.

Paratypes: ASFS X1322, same data as type, 22 June 1962, R. F. Klinikowski; USNM 59220, Pétionville, Dépt. de l'Ouest, Haiti, 23 March 1917, J. B. Henderson and P. Bartsch; ASFS X2265–66, Belle Fontaine, north base of Morne la Visite, ± 3000 feet (915 meters), Dépt. de l'Ouest, Haiti, 13 July 1962, D. C. Leber; UIMNH 61610, Furcy, 5600 feet (1707 meters), Dépt. de l'Ouest, Haiti, 6 July 1962, E. Cyphale; ASFS X2351–52, Furcy, 5600 feet, Dépt. de l'Ouest, Haiti, 15 July 1962, native collector; MCZ 58016–17, Furcy, 5600 feet, Dépt. de l'Ouest, Haiti, 26 October 1950, A. Curtiss; MCZ 63606 (2 specimens), YPM 3657–58, Furcy, 5600 feet, Dépt. de l'Ouest, Haiti, May 1960, L. Whiteman; MCZ 65347, Furcy, 5600 feet, Dépt. de l'Ouest, (no date), A. Curtiss; AMNH 70144–45, Furcy, 5600 feet, Dépt. de l'Ouest, Haiti, September 1949, A. Curtiss.

Associated specimens: Haiti, *Dépt. de l'Ouest*, Petit Goâve, 1 (USNM 59244); 6.2 mi. (9.9 km) W Fauché, 1 (ASFS X2047); 1.3 mi. (2.1 km) NE Fauché, 2 (ASFS X2043–44); 5 km S Dufort, 1 MCZ 63339); Momance, 2 (MCZ 8637, 8643); Carrefour, 1 (MCZ 59503); Morne de Cayette, 1 (MCZ 63605); Diquini, 3 (MCZ 8691–92, 8695); Bas Cap Rouge, 5 (MCZ 65167–68, CM 37831–33); Marbial, 21 km NE Jacmel, 6 (MCZ 65163–66, CM 37829–30); 1 to 2 mi. (1.6 to 3.2 km) E Cayes Jacmel, 1 (AMNH 39899); halfway between Cayes Jacmel and Marigot, 2 (MCZ 58105, AMNH 49761).

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of moderate

---

[1] Latin, straddling, in reference to its occurrence on both sides of the Massif de la Selle.

size (males to 90 mm, females to 82 mm snout-vent length), usually 10 transverse rows of ventrals, low number of fourth toe subdigital scales, moderate number of femoral pores and scales in the fifteenth caudal verticil; dorsal pattern consisting of a broad pale to medium brown zone bordered by bright yellow dorsolateral lines, lateral fields black with scattered red to buffy dots; throat orange.

Distribution: The base of the Tiburon Peninsula, from Petit Goâve to Pétionville on the north, and into the uplands as far as Furcy and Belle Fontaine; on the south side of the Massif de la Selle from Bas Cap Rouge and Marbial near Jacmel, west to near Marigot (Fig. 1).

Description of type: An adult female with the following counts and measurements: snout-vent length 82 mm, tail broken; ventrals in 33 longitudinal and 8 transverse rows; fourth toe subdigital scales 36 and 37 (total 73); femoral pores 15 and 15 (total 30); 27 scales in the fifteenth caudal verticil. A pale brown dorsal band extending from the occiput onto the base of the tail, where it becomes gradually constricted and disappears on about the nineteenth dorsal caudal verticil; dorsal zone bordered laterally by bright yellow dorsolateral lines, and, in the region of the neck, some slightly darker longitudinal areas enclosed within the band adjacent to the dorsolateral lines. Lateral fields black with a few widely scattered red dots throughout their length, although the dots are more concentrated posteriorly. Lateral yellow line from auricular opening to groin, with orange cheek marking which is confluent with an orange auricular marking. Lateral line resumed behind hindlimb and, along with dorsolateral lines, continued onto tail. Lower sides flecked black and gray. Throat and lower labials orange (Maerz and Paul, 1950: pl. 1119), this color extending onto anterior abdomen; posterior venter gray, as also underside of tail. Limbs tannish, marbled with dark gray and black.

Variation: The series of 35 *A. t. varica* has the following counts: longitudinal ventrals 29–33 (mean 31.8); rows of transverse ventrals 10 (75.0 per cent) or 8 (25.0 per cent); fourth toe scales 64–80 (mean 71.5); femoral pores 26–35 (mean 30.8); fifteenth verticil 23–29 (mean 25.8).

A. t. varica is a somewhat variable race. Since it has a wide altitudinal range (from sea level to 5600 feet [1707 meters]), and since it occurs on both sides of the Massif de la Selle, such variation is not surprising. On the other hand, I am unable to distinguish specimens from the region between Petit Goâve and Momance, or from Marbial and Cayes Jacmel, from upland specimens from Pétionville and Furcy. Although most specimens resemble the type in having a broad brown, pale brown, or reddish brown middorsal zone, some (UIMNH 61610, for example) have buffy indications of the median and paramedian lines. Occasional individuals (CM 37830) lack dots in the black lateral fields. Others, rather than having the middorsal zone bordered directly by the dorsolateral yellow lines, have an interposed black stripe between the lines and the zone (MCZ 63605, for example). In this latter condition, the black lines stop on the neck and do not continue anteriorly onto the head. In fresh specimens the throats are orange, and the venters vary between dull orange and gray. The dorsolateral lines may be bright yellow, as in the type, buffy, or yellow anteriorly and grayish yellow posteriorly. The lower sides may be dotted with blue, and this color may occur also on the lateralmost ventral plates. The dots on the lateral fields vary from red to buffy, and there may be some red spotting on the lower sides. The hindlimbs may be flecked with dull red (brick).

Comparisons: *A. t. varica* may be differentiated from *regnatrix* in that the former has usually 10 transverse rows of ventrals, the latter regularly 8. From *regnatrix* and *aequorea*, *varica* differs in usually having prominent red dots in the lateral fields; although *taeniura* may have lateral dots, they are most often restricted to the posterior portion of the lateral fields. The lined dorsa of *aequorea* and *regnatrix* also distinguish these races from *varica*.

In size, *varica* is larger than *aequorea* and equal to *taeniura*; *varica* and *regnatrix* are about equal in size. In fourth toe scales, *varica* is most strongly different from *regnatrix* (means of 71.5 in the former, 66.7 in the latter).

Remarks: Both the altitudinal and geographic distributions of *A. t. varica* are extensive; the race occurs from sea level to 5600 feet (1707 meters) in the Morne l'Hôpital. Geographically, *varica* occurs on both sides of the Massif de la Selle, as high as about 1800 feet (549 meters) on the Plateau Cap Rouge and on the coast. I doubt that there is direct contact between the northern and southern populations, since the abrupt northern escarpment of the Massif de la Selle intervenes between these two regions. The way of contact must be devious. It is interesting that specimens of *varica* occur at the foot of the scarp at Belle Fontaine. Considering that the Massif de la Hotte in the west separates the races *taeniura* and *regnatrix*, it is surprising that apparently the Massif de la Selle does not act in the same manner in the east; on the other hand, there are no specimens of the western races from high elevations in the La Hotte (although this may well be an artifact of collecting). Specimens of *A. t. varica* have been taken in a wooded thicket in a mesic cultivated area (Morne Calvaire), from a river flood-plain in brush-covered rocks and in cultivated areas (Belle Fontaine), and along the inner margin of mangroves and on a rocky hillside near a *Musa* patch (Fauché).

The only subspecies which approaches *varica* closely on the west is *taeniura*; the closest localities for the two are Miragoâne (*taeniura*) and Petit Goâve (*varica*), which are separated by about 23 kilometers. Possibly some of the specimens from localities "near Miragoâne" would bridge this gap slightly. Specimens from the Miragoâne area show no approach to *varica*. The relationships between *varica* and the more northern and eastern subspecies will be discussed below.

Ameiva taeniura barbouri Cochran, 1928

Ameiva barbouri Cochran, 1928, Proc. Biol. Soc. Washington, 41:56 (type locality—La Source, Ile de la Gonâve).

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of large size (males to 100 mm, females to 74 mm snout-vent length), more often 10 transverse rows of ventrals (although the incidence of 8 rows is almost equal to that of 10), moderate number of fourth toe scales, very high number of femoral pores, and low number of scales in the fifteenth caudal verticil; dorsal pattern consisting of a broad median dorsal metallic tan zone bordered directly by black and undotted lateral fields without an intervening dorsolateral pale stripe; tail blue-green and unpatterned; throat orange.

Distribution: Ile de la Gonâve, and the adjacent mainland of Haiti in the vicinity of Trou Forban (Fig. 1).

Discussion: There are now available twenty-seven specimens of *A. t. barbouri* from Gonâve, and another from the mainland near Trou Forban. Coloration and pattern of two specimens from Etroits were recorded as: dorsal band metallic tan (Maerz and Paul, 1950: pl. 12D5), bordered directly by black and unspotted lateral fields. Sides grayish, not separated from lateral field by an intervening pale lateral line. Head rich tan. Throat orange (pl. 3B12), ventral ground color entirely blue (pl. 27E1). Tail blue-green (pl. 26J2), and without any pale or dark lines. Hands and feet pale blue, limbs clear gray, unspotted. The specimen from Trou Forban had a metallic tan back (pl. 14G8), grading to green on the base of the blue-green tail. The lateral field was completely black, the throat vivid orange (pl. 4B12), with the chest paler, fading to dull blue on the rest of the venter. The color description of the

Gonâve lizards and of that from Trou Forban are remarkably similar. It is possible that the mainland population may later be separated from that from Gonâve, but at present there is no reason for so doing.

There are only two females known, the larger with a snout-vent length of 74 mm; the largest male *barbouri* has a snout-vent length of 100 mm. The longitudinal ventrals vary between 30 and 34 (mean 32.7) and these scales are more often arranged in 10 transverse rows (51.9 per cent), with 48.1 per cent having 8 transverse rows of ventrals. The fourth toe subdigital scales range from 70 to 80 (mean 74.4), and the femoral pores range from 33 to 41 (mean 36.2). The scales in the fifteenth caudal verticil vary between 18 and 25 (mean 22.0). The Trou Forban male (not included in the above series) has a snout-vent length of 69 mm, 32 longitudinal and 8 transverse rows of ventrals, 76 fourth toe scales, 22 scales in the fifteenth verticil, and 18 femoral pores on the one uninjured leg.

Comparisons: The Gonâve race of *A. taeniura* requires no comparison with the mainland races to the south. The absence of any longitudinal lines on the back, the juxtaposed dorsal band and unspotted black lateral fields, and the unicolor and patternless tail will distinguish *barbouri* from the described races. The very high number of femoral pores (36.2 versus 28.3 to 30.8) is distinctive; there is no overlap in this count between *barbouri* and *aequorea*, and an overlap of only two or three scales between *barbouri* and *taeniura*, *regnatrix* and *varica*.

Remarks: The occurrence of *A. t. barbouri* on the mainland is suggestive of the relationships of the xeric littoral along the north shore of the Golfe de la Gonâve and the Ile de la Gonâve. The occurrence on this strip of such species as *Anolis brevirostris* and *Diploglossus curtissi* confirms the relationship of these two regions. Since both the anole and the galliwasp occur as well in the Cul de Sac plain, it is not completely unlikely that parts of this plain are (were) occupied by *A. t. barbouri*, although there is no evidence at present of such occurrence (see Discussion).

The record of *barbouri* from Trou Forban is one of three records of *A. taeniura* from north of the Cul de Sac plain in Haiti. To the south occurs the race *varica*, separated by some 68 kilometers airline. The other northern records for *A. taeniura* are Plaisance and St. Michel de L'Atalaye; the nearest of these localities is about 60 kilometers airline. None of the northern lizards is close to *barbouri*. The mainland distribution of *A. t. barbouri* is at present unknown.

On Gonâve, *A. t. barbouri* is widespread, being known from one northern and three more southern localities. The two specimens collected by us were taken on a rocky hillside at the foot of the central hills; the immediate area was xeric scrub with some large shade trees. At Trou Forban, the single lizard was taken on a rocky path into a moist depression with a dense stand of *Acacia* trees in an otherwise very arid area. The elevation at Nan Café on Gonâve is about 1260 feet (384 meters) an upper limit for the occurrence of *barbouri* on Gonâve.

Specimens examined: **Haiti**, *Ile de la Gonâve*, La Source, 2 (MCZ 25537–38, type and paratype); 1.5 mi. (2.4 km) SW Etroits, 2 (ASFS X2506–07); Nan Café, 20 (MCZ 61064–66, UF 12242 (2 specimens), UF 12243 (4 specimens), UF 12244, 12245, 12246 (4 specimens), YPM 3308–09, YPM 3311, YPM 3313–14); Pointe à Raquettes, 2 (YPM 3315–16); no other locality, 1 (USNM 80827); *Dépt. de l'Ouest*, 2.2 mi. (3.5 km) SW Trou Forban, 1 (ASFS X1926).

Ameiva taeniura vulcanalis[1] new subspecies

Holotype: MCZ 81077, an adult male, from 5 mi. (8 km) NE Oviedo, Pedernales Province, República Dominicana, one of a series taken 4 August 1963 by David C.

---

[1] Latin, belonging to Vulcan, in allusion to the vivid orange throat.

Leber and Richard Thomas. Original number V281.

Paratypes: ASFS V282–84, same data as type; ASFS X9959–60, RT 753, same locality as type, 30 July 1963, A. Schwartz, R. Thomas; RT 777, same locality as type, 7 August 1963; ASFS X9954, 13.1 mi. (21 km) SW Enriquillo, Pedernales Province, República Dominicana, 30 July 1963, A. Schwartz; ASFS X9410–15, 13.1 mi. (21 km) SW Enriquillo, Pedernales Province, República Dominicana, 22 July 1963, A. Schwartz, R. Thomas; DWB 296, 13.1 mi. (21 km) SW Enriquillo, Pedernales Province, República Dominicana, 7 December 1964, R. Thomas; UF 21324, 1.3 mi. (2.1 km) NW Oviedo, Pedernales Province, República Dominicana, 30 July 1963, R. Thomas; KU 93312, 3 km SW Enriquillo, Barahona Province, República Dominicana, 7 August 1963, R. Thomas.

Associated specimens: Haiti, *Dépt. de l'Ouest*, Tean, nr. Saltrou, 4 (MCZ 68576–79). República Dominicana, *Pedernales Province*, Pedernales, 9 (ASFS V2667, V2787–94); 8 km N Pedernales, 1 (ASFS V2602); 6 km NE Las Mercedes, 2600 feet (793 meters), 1 (ASFS V2648); 30 km NW Oviedo, 1 (MCZ 57731); *Barahona Province*, Barahona, 10 (AMNH 37203–06, 37208, MCZ 63192, 58020–22, ASFS X9749); 1 mi. (1.6 km) N Barahona, 1 (MCZ 43812); 4 km NW, 1 km SW Barahona, 1 (ASFS V201); 4 km NW, 2 km SW Barahona, 500 feet, 2 (ASFS V203–04); west side, Punta Martín García, 11 (ASFS V89–99); *Independencia Province*, 3 km WNW El Naranjo, 1000 feet (305 meters), 3 (ASFS X9946–48).

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of large size (males to 95 mm, females to 82 mm snout-vent length), usually 10 transverse rows of ventrals, low number of fourth toe subdigital scales, high number of femoral pores, and moderate number of scales in the fifteenth caudal verticil; dorsal pattern consisting of a broad pale (tan, gray, or greenish tan) zone, at times with remnants of the dorsolateral pale (lemon yellow to buffy) longitudinal lines, lateral fields black with many small orange flecks; throat fire orange.

Distribution: From the vicinity of Saltrou in extreme southeastern Haiti, east across the Península de Barahona (south of the Sierra de Baoruco) in the República Dominicana to Oviedo; thence northward along the coast to Barahona and west along the north flank of the Sierra de Baoruco to El Naranjo, and east around the Bahía de Neiba to Punta Martín García (Fig. 1).

Description of type: An adult male with the following counts and measurements: snout-vent length 90 mm, tail 224 mm; ventrals in 32 longitudinal and 8 transverse rows; fourth toe subdigital scales 37 and 37 (total 74); femoral pores 17 and 20 (total 37); 27 scales in the fifteenth caudal verticil. A broad tan middorsal zone from the occiput onto the basal quarter of the tail, this zone only very vaguely outlined with buffy, the lines not extending onto the head shields nor prominently onto the tail. Lateral fields obsolescent and gray on the temporal region, black between the limbs, heavily flecked with orange dots throughout their length, and becoming faint on the sides of the tail near the base. Lateral fields bordered below by a faint and obsolescent buffy line, which behind the hindlimbs forms a fairly prominent pale ventrolateral tail stripe. Pale cheek spot absent, preauricular spot present, buffy, and not conspicuous. Lower sides gray with indistinct dark mottling. Limbs tan, mottled with darker on the thighs. Throat and chest vivid fire orange, belly dull grayish blue. Tail greenish tan above, bluish green below.

Variation: The series of 57 *A. t. vulcanalis* has the following counts: longitudinal ventrals 31–35 (mean 32.3); rows of transverse ventrals 10 (80.3 per cent) or 8 (19.7 per cent); fourth toe scales 66–82 (mean 73.8); femoral pores 30–40 (mean 33.9); fifteenth verticil 24–30 (mean 26.7).

Despite its extensive range, *A. t. vulcanalis* is very constant in pattern, and most specimens resemble the description of the type. In precise shade of the dorsal zone, there is some variation, however; the range in color includes tan to greenish tan (Enriquillo), gray (Las Mercedes), tan with a faint greenish border or tan anteriorly and greenish posteriorly (Pedernales), and reddish tan anteriorly and grayish tan posteriorly (Punta Martín García). The lateral fields are black and almost always are heavily flecked with orange flecks, although occasional specimens (ASFS V93, for example) lack flecks completely. If there is a dorsolateral line separating the dorsal zone from the lateral field (this is not the usual condition), it is yellow. If there is a lateral stripe (and there often is not), it is cream. The throats and chests are always vivid flame orange, and the venters vary from whitish (Pedernales) to grayish blue (Enriquillo) or dull grayish orange (Punta Martín García). The head markings are always obsolete, the preauricular spot being the more persistent of the two. The tails are not prominently striped dorsally, and are greenish or tannish green dorsally, dark gray to black laterally, with a broad cream stripe ventrolaterally. The hindlimbs are dark, almost black, in many individuals, and the thighs are flecked with greenish or tan.

Comparisons: No other race thus far described has heavily flecked lateral fields and lacks dorsal stripes. *A. t. barbouri* superficially resembles *vulcanalis*, but in details the two subspecies are very different; the solid black lateral fields of the former blending into the dorsal metallic tan zone are distinct from the sharp-edged dorsal zone of *vulcanalis*. The unicolor tail of *barbouri* likewise distinguishes it from *vulcanalis*. The tan zonate dorsum of *vulcanalis* will distinguish it from the striped or brown or reddish brown dorsa of the western races.

Remarks: *A. t. vulcanalis* is an inhabitant of some of the more arid areas in Hispaniola, but in this region it occupies shady situations such as stands of deciduous trees, wooded mountain foothills, and shaded *Acacia* stands. Its interaction with *A. chrysolaema* at Oviedo has been described by Schwartz and Klinikowski (1966). Although several species of reptiles are restricted to the tip of the Península de Barahona by the Sierra de Baoruco and the virtually non-existent eastern coastal plain (and these restricted species include *A. chrysolaema* and *A. lineolata*, each of which has developed races both to the north and south of the Sierra de Baoruco in xeric habitats), such is not the case with *A. taeniura*, where *vulcanalis* occurs both to the north and south of the mountains. Undoubtedly, the eastern edge of the Sierra de Baoruco provides excellent mesic habitat for this lizard and this accounts for the continuity of the populations between Barahona and Oviedo. Also, *vulcanalis* has crossed the lower reaches of the Río Yaque del Sur. Near the mouth of this river, the Valle de Neiba is distinctly mesic, and this feature has presumably allowed *vulcanalis* to cross the otherwise xeric valley into the region of Punta Martín García. Although *A. t. vulcanalis* is not known to occur in the xeric regions of the Valle de Neiba, it does occur along the northern lower foothills of the Sierra de Baoruco as far west as El Naranjo. Since this locality is very close to the Dominico-Haitian border, *vulcanalis* is to be expected along the northern slopes of the Morne des Enfants Perdus in Haiti.

The highest elevation for *vulcanalis* is 2600 feet (793 meters) above Las Mercedes. The species is presumably absent from high elevations in the Sierra de Baoruco, since there has been much collecting in this range, especially in the Valle de Polo region. *A. t. vulcanalis* might be expected to occur at Forèt des Pins in Haiti, at 5800 feet (1768 meters) near the Dominico-Haitian border; it has not been taken there nor at intermediate or high elevations on the Dominican side of the boundary. It is interesting that of the four southern subspecies (*taeniura, regnatrix, varica, vulcanalis*) associated directly with mountainous areas, only *varica* occurs at very high elevations.

A. t. vulcanalis and *A. t. varica* approach one another along the southern coast of Haiti; the easternmost record of *varica* (halfway between Cayes Jacmel and Marigot) and the westernmost record for *vulcanalis* (Trou Roche near Saltrou) are separated by about 38 kilometers (Trou Roche cannot be precisely located). Between Marigot and Saltrou, the Morne Fortune forms a steep scarp adjacent to the ocean, and this may effectively separate *varica* and *vulcanalis*.

Ameiva taeniura azuae new subspecies

Holotype: MCZ 81078, a subadult male, from 22 km NW Azua, Azua Province, República Dominicana, taken 14 August 1963 by David C. Leber. Original number V459.

Paratype: ASFS V458, same data as type.

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of small (?) size (male 65 mm, female 70 mm snout-vent length), 10 transverse rows of ventrals, very high number of fourth toe subdigital scales, moderate number of femoral pores, and high number of scales in the fifteenth caudal verticil; dorsal pattern consisting of a broad brown dorsal zone, bordered by lemon yellow dorsolateral lines, black lateral fields with many large brick dots; throat black.

Distribution: Known only from the type locality in the Llanos de Azua, República Dominicana (Fig. 1).

Description of type: A subadult male with the following counts and measurements: snout-vent length 65 mm, tail 127 mm, distal half regenerated; ventrals in 34 longitudinal and 10 transverse rows; fourth toe subdigital scales 44 and 41 (total 85); femoral pores 16 and 15 (total 31); 31 scales in the fifteenth caudal verticil. A broad brown dorsal zone, bordered anteriorly by a pair of narrow dorsolateral lemon yellow lines, extending onto the unregenerated portion of the tail. Lateral fields black, continuous from temporal region onto sides of tail basally, and heavily spotted with large brick dots. Lateral line below lateral fields grayish yellow, fairly prominent. Cheek and auricular spots yellow and moderately prominent. Throat and chest black, infralabials and chin shields dull gray. Venter and underside of hindlimbs bronzy, underside of tail grayish blue. Limbs brown, somewhat marbled with darker gray or brown. Tail not striped dorsally, but with a pale ventrolateral stripe, the continuation of the lateral body stripe.

Variation: The only other specimen is a female with a snout-vent length of 70 mm, ventrals in 31 longitudinal and 10 transverse rows, 79 fourth toe scales, 31 femoral pores, and 30 scales in the fifteenth verticil. In coloration and pattern, the female is identical to the type, except that there are more brick dots in the lateral fields, and these dots are arranged into a series of about nine vertical bars in the posterior half of the fields. The throat of the female was dull gray rather than black; the ventral coloration was bronzy like that of the male.

Comparisons: No previously described race has a black throat, and *azuae* can be thus easily distinguished from all other subspecies. The high counts of fourth toe scales separate *azuae* from all other races; the only exception to this are those lizards from the Cayemites which have counts from 81 to 91. The high fifteenth verticil counts of *azuae* distinguish it from *taeniura*, *regnatrix*, *aequorea*, *varica* and *barbouri*. Additional specimens of *azuae* will doubtless bring about some overlap in these counts.

Remarks: Although *A. t. azuae* is known only from two specimens, it is eminently distinct. Of all the specimens of *A. t. vulcanalis*, its neighbor to the south, none has a black or gray throat—in fact the vivid flame orange throats of *vulcanalis* offer strong contrast to the black (and gray) throats of *azuae*. The closest approximation of *vulcanalis* (Punta Martín García) to the type locality of *azuae* is only about 23 kilometers airline. The specimens of *azuae* were taken in a moderately mesic ravine in

Acacia scrub. Although we collected extensively in the Llanos de Azua, often in mesic and shady areas, we did not encounter *A. taeniura* elsewhere. Surely the distribution of *A. t. azuae* is more extensive than the present record indicates. Schmidt (1921a: 17) reported Beck's taking of *A. taeniura* in "the interior of Azua Province"; whether this specimen is from the Llanos (and thus probably *azuae*) or is from the interior uplands (where much of Beck's collecting in this area was carried on; see Wetmore and Swales, 1931) is unknown. *A. t. azuae*, in addition to the Llanos de Azua, may occur as well in the Valle de San Juan.

Ameiva taeniura tofacea[1] new subspecies

Holotype: MCZ 81079, an adult male, from mouth of the Río Chavón, west side, La Romana Province, República Dominicana, one of a series taken 4 September 1963 by Ronald F. Klinikowski, Albert Schwartz and Richard Thomas. Original number V1065.

Paratypes: ASFS V1064, V1066–68, UIMNH 61611–13, same data as type; CM 40562–63, Río Cumayasa, 17 km W La Romana, La Romana Province, República Dominicana, 28 June 1963, D. C. Leber and R. Thomas; ASFS X9293, 8 km E La Romana, La Romana Province, República Dominicana, 19 July 1963, R. Thomas; AMNH 7567, San Pedro de Macorís, San Pedro de Macorís Province, República Dominicana (no date), G. K. Noble; SMF 25700, San Pedro de Macorís, San Pedro de Macorís Province, República Dominicana, 6 March 1939, R. Mertens; SMF 25553, Tres Ojos, Distrito Nacional, República Dominicana, 16 March 1939, R. Mertens.

Associated specimen: República Dominicana, *El Seibo Province*, "San Francisco Mountains, ± 2500 feet," 1 (USNM 35982).

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of large size (males to 96 mm, females to 83 mm snout-vent length), more often 10 than 8 transverse rows of ventrals (although the difference in incidence between the two categories is slight), and moderate number of fourth toe subdigital scales, femoral pores, and scales in the fifteenth caudal verticil; dorsal pattern consisting of a very pale greenish tan to sandy dorsal zone, bordered by yellow-green dorsolateral lines, lateral fields black with some scattered small brick dots; throat pale orange.

Distribution: Known from Tres Ojos east to the mouth of the Río Chavón; specimens reported by Cochran (1941: 274) from the city of Santo Domingo in the Distrito Nacional may be assignable to this subspecies. The single specimen from the "San Francisco Mountains, about 2500 feet" likewise seems close to *tofacea*, and extends the range of this race into the interior of eastern Hispaniola (Fig. 1).

Description of type: An adult male with the following counts and measurements: snout-vent length 77 mm, tail 143 mm; ventrals in 32 longitudinal and 8 transverse rows; fourth toe scales 36 on one leg, other leg damaged; femoral pores 14 and 13 (total 27); 23 scales in the fifteenth caudal verticil. A broad pale greenish tan dorsal zone, bounded by conspicuous yellow-green dorsolateral lines, and grading to greenish on sacrum and base of tail. Dorsolateral lines continue onto tail and are discernible to near tip. Head pale tannish brown, slightly darker than dorsal zone. Lateral fields black, bordered below by a yellow-green line, and with some scattered rusty flecks. Cheek and preauricular spots yellow, fairly prominent. Lower sides dark gray flecked with cream. Lateral pale stripe continues onto anterior face of thigh, and also resumes on tail as a broad ventrolateral pale stripe; sides of tail black, continuous with lateral fields. Both fore- and hindlimbs tan, much spotted with black. Throat and chest pale orange, remainder of venter pale bluish. Underside of tail pale blue.

Variation: The series of 15 specimens of *A. t. tofacea* has the following counts; lon-

---

[1] Latin, like sandstone, in allusion to the pale sandy dorsum.

gitudinal ventrals 31–33 (mean 32.1); rows of transverse ventrals 10 (53.3 per cent) or 8 (46.7 per cent); fourth toe scales 66–88 (mean 77.0); femoral pores 27–35 (mean 30.9); fifteenth verticil 21–29 (mean 24.2).

The paratypes agree closely with the type in coloration and pattern. The specimens from the Río Cumayasa were brown to greenish brown dorsally in life, with yellow-green dorsolateral lines and orange cheek and preauricular markings. The specimen from La Romana was bronzy tan above, with yellow dorsolateral lines. The lateral fields usually have some rusty flecks, although three juveniles lack this feature. The throats and chests are regularly pale orange; the ventral ground color varies from pale bluish to pale orange, and in the latter case, the lower sides are also dotted with orange. The underside of the tails varies from clayey gray to blue or blue-green.

Comparisons: From the four extreme western subspecies, *A. t. tofacea* differs in having a dorsal band bordered by dorsolateral stripes, rather than having a striped dorsum. *Tofacea* most closely resembles both *vulcanalis* and *azuae*, but may be distinguished from the latter in having a pale orange rather than a black or gray throat. The throat color of *vulcanalis* is brilliant orange, rather than pale orange. The heavily flecked lateral fields of *vulcanalis* differ from the more sparsely flecked fields of *tofacea*. The obsolete head markings of *vulcanalis* also will differentiate the two races. From *barbouri*, *tofacea* differs in having the dorsal zone bordered by the dorsolateral light lines, by having flecks in the lateral fields, and by having a patterned tail.

Remarks: *A. t. tofacea* occurs from the coast up to elevations of about 2500 feet (762 meters), if the elevation noted for the specimen from the "San Francisco Mountains" is correct. Since these mountains are presently not locatable on any map, I am not completely sure where they are; the major mountain range in extreme eastern Hispaniola is the Cordillera Oriental, whose maximum elevation is about 2300 feet (701 meters).

The specimen from La Romana was taken in xeric scrub but adjacent to a fence row of shade trees; the series from the Río Chavón was taken along the coast in shaded thorn-scrub and sea-grape. At the Río Cumayasa, on 28 July 1963, Richard Thomas collected five eggs under a large flat rock in the river valley; two of these eggs measured 18.9 × 13.6 mm and 18.8 × 11.5 mm. One was opened on the following day and contained a young *Ameiva*. This foetus (ASFS X9927) clearly shows the pattern characteristics of *A. t. tofacea*. As far as I am aware, the eggs of *A. taeniura* have never before been found in the field.

Ameiva taeniura vafra[1] new subspecies

Holotype: MCZ 81080, an adult female, from 0.5 mi. (0.8 km) NW Boca de Yuma, La Romana Province, República Dominicana, one of a series taken 30 August 1963 by Albert Schwartz and Richard Thomas. Original number V862.

Paratypes: ASFS V863–66, AMNH 94238–40, KU 93313–15, RT 798, same data as type.

Associated specimen: República Dominicana, *La Romana Province*, 0.7 mi. SE El Macao, 1 (ASFS X7878).

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of small size (males to 74 mm, females to 71 mm snout-vent length), usually 10 transverse rows of ventrals, moderate number of fourth toe subdigital scales, high number of femoral pores, and low number of scales in the fifteenth caudal verticil; dorsal pattern consisting of a rather narrow yellowish tan dorsal zone bordered by two indistinct yellow dorsolateral lines, lateral fields solid black; throat bright fire orange.

Distribution: Known only from two localities in extreme eastern Hispaniola, to the north and south of Cabo Engaño (Fig. 1).

---

[1] Latin, cunning, in allusion to their wariness.

Description of type: An adult female with the following counts and measurements: snout-vent length 71 mm, tail 158 mm; ventrals in 31 longitudinal and 10 transverse rows; fourth toe subdigital scales 41 and 41 (total 82); femoral pores 17 and 16 (total 33); 26 scales in the fifteenth caudal verticil. A broad yellowish tan dorsal zone bordered by a pair of dark yellow dorsolateral lines. Both dorsal zone and dorsolateral lines extend onto the tail, where the lines become pale blue and very wide, and continue down the length of the tail but are separated proximally by a black attenuated triangular figure. Lateral fields black, extending from the loreal region along the sides onto the lateral surface of the tail, bordered below by a yellow-orange line, and without any included flecking. Lateral line resumed behind hindlimbs to form a pale blue ventrolateral caudal line. Cheek and preauricular markings bold, yellow-orange. Lower sides gray, flecked with darker gray. Throat and most of venter vivid fire orange; underside of tail pale blue, upperside of tail greenish blue. Limbs marbled tan and dark brownish gray.

Variation: The series of 13 *A. t. vafra* has the following counts: longitudinal ventrals 31–33 (mean 31.7); rows of transverse ventrals 10 (84.6 per cent) or 8 (15.4 per cent); fourth toe scales 70–82 (mean 77.8); femoral pores 31–37 (mean 33.7); fifteenth verticil 20–26 (mean 22.5).

The series of paratopotypes requires no comment; they agree in detail with the type in coloration and pattern. The specimen from El Macao was described in life as having a tan dorsal zone with the edges a bit paler, but without definitive dorsolateral lines; the head was slightly orange. The lateral fields were solid black with a pale yellow lateral line. The lower sides were tan, flecked with pale yellow. The chin, throat, and subocular area were bright orange (Maerz and Paul, 1950: pl. 4D12). These notes agree fairly well with topotypical *vafra*, and I have little hesitancy in assigning the El Macao lizard to this taxon.

Comparisons: From its neighbor to the west, *A. t. tofacea*, *vafra* differs in smaller size (96 mm versus 74 mm in males) and apparently in having a higher number of femoral pores. The most diagnostic features are the vivid (versus pale) orange throats and solid black lateral fields of *vafra*. From the balance of the races, *vafra* differs in lacking a lined dorsum (as have the four Tiburon and Ile-à-Vache races), in having an orange throat (in contrast to black in *azuae*), and in smaller size and details of pattern and coloration from *vulcanalis*. *Vulcanalis* and *vafra* are virtually separable on the basis of number of scales in the fifteenth verticil; these scales are 24 to 30 in *vulcanalis* and 20 to 26 in *vafra*. From *barbouri*, *vafra* differs in smaller size, in having a patterned tail, and in having a dorsolateral line between the dorsal zone and the lateral fields.

Remarks: The distribution of *A. t. vafra* is apparently restricted to the more xeric coastal region of the Cabo Engaño area. The type series was collected along a roadside and in forest clearings on the limestone ridge which parallels the coast behind Boca de Yuma. The forest is rather mesic and extensive. At El Macao, the single individual was taken in a very mesic hammock woods adjacent to the ocean; several others were seen in a coastal *Cocos* grove nearby. The predilection of *A. taeniura* for shady and moist situations in otherwise arid regions is once more demonstrated.

A. t. vafra approaches *A. t. tofacea* by a distance of 32 kilometers airline (Río Chavón and Boca de Yuma). The area between these two points is presently virtually inaccessible.

Ameiva taeniura rosamondae Cochran, 1934

Ameiva rosamondae Cochran, 1934, Occ. Papers Boston Soc. Nat. Hist., 8:179 (type locality—Isla Saona).

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of large size (male to 101 mm snout-vent length, no adult females known), 10 transverse rows of ventrals, moderate number of fourth toe subdigital scales, high number of femoral pores, low number of scales in the fifteenth caudal verticil; dorsal pattern consisting of a narrow greenish gray dorsal zone, faint yellow-green dorsolateral lines, solid black lateral field, and a patterned tail; throat orange.

Distribution: Isla Saona, República Dominicana (Fig. 1).

Discussion: *A. t. rosamondae* is known from only two specimens, the type which is an adult male, and a subadult female collected by Richard Thomas. Color notes on the latter describe the details of pattern: top of head and anterior portion of dorsal zone tan, fading to greenish gray, and becoming green and then blue on tail; the tail has a charcoal wash down its median basal portion. The dorsolateral stripes are yellow-green, the lateral fields solid black bordered below by a pale green lateral stripe. The snout is orange; the mental region is pink, becoming orange on the throat and chest. The venter is grayish green (the anterior scales are edged with orange). The tail is greenish dorsally at the base and deep blue (pl. 36L6) for its distal three-quarters. The upper surface of the limbs is charcoal colored.

The new specimen agrees with the type in pattern. To the above description may be added that the dorsal zone is narrow and the lateral fields especially wide. The lateral fields continue boldly onto the sides of the tail as broad black bands; the lateral stripe forms a broad pale ventrolateral caudal stripe. The cheek and preauricular spots are present but obsolete. The sides below the lateral stripe are gray with black flecking.

Comparisons: Remarkably, in pattern *A. t. rosamondae* most closely resembles *A. t. barbouri* from Gonâve. The tan dorsum of the latter contrasts with the greenish gray dorsum of the former. The dorsal zone is much narrower in *rosamondae* than in *barbouri*, and the former has a patterned versus an unpatterned tail. From *A. t. vafra* on the adjacent mainland, *rosamondae* differs in being much larger (101 versus 74 mm in males), and in lacking obvious dorsolateral longitudinal lines. The tails of these two races are very similar in pattern and pigmentation. Comparison with the other subspecies is not necessary, since *rosamondae* is quickly distinguishable both from those subspecies with lined dorsa and those with zonate dorsa by its coloration and pattern.

Remarks: *A. t. rosamondae* is apparently uncommon on Isla Saona; Thomas saw no other individuals in his eight hours ashore there. It is really remarkable that the type of *rosamondae* (until now the only known specimen) is such a large individual; it ranks third among all specimens of *A. taeniura* I have examined.

Specimens examined: República Dominicana, *Isla Saona*, environs of Mano Juan, 1 (ASFS V3003); no precise locality, 1 (MCZ 37567—type).

Ameiva taeniura ignobilis[1] new subspecies

Holotype: MCZ 81081, an adult male, from 14.4 km E La Vega, La Vega Province, República Dominicana, one of a series taken 27 November 1964 by Richard Thomas. Original number V4204.

Paratypes: ASFS V4205–07, same data as type; ASFS V4270, 12 km NE Jarabacoa, 1400 feet (427 meters), La Vega Province, República Dominicana, 30 November 1964, native collector; ASFS V2925–27, 7 km W Santiago, Santiago Province, República Dominicana, 13 July 1964, R. Thomas; MCZ 58664, Santiago, Santiago Province, República Dominicana, (no date), Dr. Jiminez; SMF 26124, SMF 26251, SMF 26289, SMF 26317, Moca, Espaillat Province, República Dominicana, 10–16 April 1939, R. Mertens; MCZ 58667, Santiago and vicinity, Santiago

---

[1] Latin, obscure, ignoble, in allusion to the dark throat.

Province, República Dominicana, (no date), Dr. Jiménez; MCZ 57730, 3 km S Pena, Santiago Province, República Dominicana, 4 August 1958, C. E. Ray and A. S. Rand.

Associated specimens: República Dominicana, *Santiago Rodríguez Province*, 19 km SE Martín García, 600 feet (183 meters), 5 (ASFS V1253–57); *Puerto Plata Province*, Puerto Plata, 2 (MCZ 5441, AMNH 44845); *Samaná Province*, Samaná, 3 (AMNH 40984–85, MCZ 43700); 2 mi. from Samaná (not mapped), 1 (AMNH 42296); 1.5 mi. (2.4 km) from Samaná (not mapped), 4 (AMNH 42304–07); Rojo Cabo, 11 (AMNH 39346–53, 40254–56); Chico Puerto Francés (not mapped), 4 (AMNH 42300–03); 0.5 mi. (0.8 km) inland at Puerto Francés (not mapped), 3 (AMNH 42310–12); between Las Flechas and Clara (not mapped), 1 (AMNH 42297); Bahía del Rincón, 2 (AMNH 42298–99); Laguna, 1 (USNM 65018); Sánchez, 1 (CM 8137); "Samaná Peninsula," 1 (USNM 66765); Isla Carenero, 6 (AMNH 42274–79).

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of large size (males to 102 mm, females to 103 mm snout-vent length), usually 10 transverse rows of ventrals, moderate number of fourth toe subdigital scales, femoral pores, and scales in the fifteenth caudal verticil; dorsal pattern consisting of a broad brown dorsal zone, bordered by bright green or yellow-green dorsolateral lines, lateral fields black with large dull red flecks; throat black or gray.

Distribution: In the west, from south of Martín García and near La Vega, east to the tip of the Península de Samaná; apparently also on the north coast near Puerto Plata (Fig. 1).

Description of type: An adult male with the following counts and measurements: snout-vent length 87 mm, tail 201 mm; ventrals in 34 longitudinal and 10 transverse rows; fourth toe subdigital scales 35 and 33 (total 68); femoral pores 15 and 16 (total 31); 29 scales in the fifteenth caudal verticil. A broad deep brown dorsal zone, bordered by bright green dorsolateral lines, the dorsal zone continuing onto the tail where it gradually becomes checkerboarded and then inconspicuous; dorsolateral lines on tail faint. Lateral fields with faint orange, large, scattered spots. Lateral field begins on temporal region and continues onto basal portion of tail, where it is invaded by brown scales. Lateral field bordered below by a greenish yellow lateral line, which stops at the hindlimbs, and then continues onto the tail as a ventrolateral pale greenish gray line. Lower sides black mottled with reddish. Lower labials and tip of chin orange, throat black; chest dull gray, venter light gray. Underside of tail blue-black. Both fore- and hindlimbs heavily blotched brown and black. Cheek and preauricular spots orange, fairly prominent.

Variation: The series of 53 *A. t. ignobilis* has the following counts: longitudinal ventrals 30–34 (mean 32.3); rows of transverse ventrals 10 (82.7 per cent) or 8 (17.3 per cent); fourth toe scales 68–86 (mean 76.0); femoral pores 26–36 (mean 30.4); fifteenth verticil 23–30 (mean 26.0).

I am not certain that the large series of specimens from the Península de Samaná (38 lizards) is correctly associated with the lizards from the interior. This is partly due to the fact that I have never seen the Samaná lizards in life, despite three trips to the peninsula by myself and Richard Thomas. On the other hand, there are no scale differences between the two major samples, and I cannot at present determine any coloration or pattern differences. The Samaná lizards reach a larger size than do those from the interior, and in fact the largest female of any subspecies of *A. taeniura* is a Samaná lizard (USNM 65018). This female exceeds the largest female of any other races (*A. t. tofacea*, 83 mm) by 20 mm.

The dorsal band in western (interior) specimens of *A. t. ignobilis* is dark brown; it was noted in the specimen from Jarabacoa that the dorsal zone granules are green basally, so that when viewed from behind or above, the zone appears to be stippled with bright green. The dorsolateral lines are fairly conspicuous and vary from bright green to greenish yellow. The lateral fields are black, with rather large and scattered faint reddish to orange spots (although five young individuals with snout-vent lengths to 47 mm lacks dots). The cheek and preauricular markings may be orange or grayish yellow. The lateral stripes vary between greenish yellow and cream. The throat is always black or gray (in females or subadult males), although the labials may be bright orange. The venter is variable, having been recorded as yellowish gray or gray with an orange wash (Santiago), light gray (adult male) or orange (juveniles and females) (La Vega), pink (Jarabacoa), and bluish gray with faint orange posteriorly (Martín García). The upper surface of the tail is tan or brown proximally, usually with some checkerboarding, and black distally. One specimen (MCZ 57730) has the checkerboarding continued onto the posterior third of the dorsal zone.

A conspicuous pattern difference between these interior specimens and those from the Samaná is that the tails of Samaná lizards are prominently lined longitudinally, and lack the uniform coloration of the tails of interior individuals. I have little doubt that fresh Samaná specimens will be distinct from lizards from the interior region.

Comparisons: *A. t. ignobilis* requires comparison only with *A. t. azuae*; all other described races have orange rather than black throats. From *azuae*, *ignobilis* differs in much larger size (102 mm versus 65 mm), in having a dark brown rather than brown dorsal zone, and in not having so many dots in the lateral fields. The means of fourth toe scales are quite different (82.0 in *azuae*, 76.0 in *ignobilis*), but the counts on the two specimens of *azuae* are embraced by the counts of *ignobilis*.

Remarks: Additional specimens, presumably *ignobilis*, have been reported by Mertens (1939: 73) from the Río Mao near Monción, Santiago Rodríguez Province, and by Schmidt (1921a: 17) from the Río Gurabo and the Río Cana, probably also in Santiago Rodríguez Province, and from Villa Riva, Duarte Province. The latter record bridges the gap between the interior and Samaná localities.

The strange rarity of *A. taeniura* on the north coast of the República Dominicana deserves comment; there are but two specimens from this region, from Puerto Plata. During a lengthy stay at Sosúa in this area, and extensive travel along the north coast from Imbert to Gaspar Hernández, we encountered no *A. taeniura*. It is possible that specimens from along this north coast will differ considerably from material to the south and east.

In the interior, *A. t. ignobilis* occupies the foothills and northern slopes of the Cordillera Central to elevations of 1400 feet (427 meters). It occurs as well in the eastern (and more mesic) extremity of the Valle de Cibao near Santiago. The type and paratopotypes were collected in a plantain plantation near the Río Camú, and the specimens from Martín García were taken in woods along the edge of a stream. The specimen from Jarabacoa apparently came from pine forest.

Ameiva taeniura algida[1] new subspecies

Holotype: MCZ 81082, an adult male, from 1 mi. (1.6 km) WSW Constanza, 4000 feet (1220 meters), La Vega Province, República Dominicana, one of a series taken 2 July 1963 by native collector. Original number X8503.

Paratypes: ASFS X8502, X8504–06, same data as type; AMNH 94241–44, MCZ 81083–85, RT 683, same locality as type, 3 July 1963, native collector; ASFS X8653–54, UIMNH 61614–15, same locality as type, 4 July 1963, native collector; ASFS X8825, 6 km W Constanza, 4250 feet (1296 meters),

---

[1] Latin algida, cold, referring to the high elevation of this subspecies.

La Vega Province, República Dominicana, 9 July 1963, R. Thomas.

Diagnosis: A subspecies of *A. taeniura* characterized by a combination of moderate size (males to 92 mm, females to 76 mm snout-vent length), always 10 transverse rows of ventrals, moderate number of fourth toe subdigital scales and femoral pores, and high number of scales in the fifteenth caudal verticil; dorsal pattern consisting of a brown to reddish brown dorsal zone without dorsolateral light lines in adults (but present and yellow in juveniles), the dorsal zone heavily dotted with conspicuous yellow dots in males but not in females, lateral fields black to dark reddish brown flecked with brick or golden, lower sides heavily and boldly dotted with cream; throat and chest black.

Distribution: Known only from the vicinity of Constanza in the Cordillera Central, República Dominicana (Fig. 1).

Description of type: An adult male with the following counts and measurements: snout-vent length 91 mm, tail 79 mm, broken; ventrals in 32 longitudinal and 10 transverse rows; fourth toe subdigital scales 41 and 40 (total 81); femoral pores 16 and 16 (total 32); 26 scales in the fifteenth caudal verticil. A broad reddish brown dorsal zone, without indications of dorsolateral light lines, heavily dotted with yellow dots from the neck to the base of the tail, but more abundant and clear posteriorly; lateral field black, flecked with golden dots. Lateral line absent, the region between the lateral edges of the ventral plates and the lateral fields heavily sprinkled with creamy to golden dots. Temporal and preauricular markings absent. Upper surface of tail brown with some darker brown checkerboarding basally, and with no prominent longitudinal lines or dark lateral band, the underside of the tail dull grayish tan. Chin and snout bright orange, infralabials greenish yellow, throat and chest (including the first seven transverse rows of ventrals) black. Venter black, dotted with bright blue. Forelimbs marbled black and brown, hindlimbs blotched with reddish brown dorsally and spotted bright blue on their anterior faces.

Variation: The series of 18 *A. t. algida* has the following counts: longitudinal ventrals 31–33 (mean 32.0); rows of transverse ventrals always 10; fourth toe scales 67–86 (mean 74.6); femoral pores 27–38 (mean 31.2); fifteenth verticil 24–31 (mean 27.8).

Male *A. t. algida* agree with the description of the type; the dorsal zone may be brown or reddish brown, and the lateral fields vary between black and dark reddish brown, flecked in smaller males with brick and with golden in adults. The dorsal surface of the hindlimbs may be dotted with golden flecks. The four smallest males (snout-vent lengths to 73 mm) lack dorsal dotting. The females lack dotting, but have the dorsal zone, especially posteriorly, marbled with darker brown; the snout in females is pinkish, not orange. In females the lateral fields are black with many brick dots, and the lateral and dorsolateral lines vary between yellow and pale yellow-green. The throats are gray and the venter dull reddish orange. All adult males have black throats and chests, and in some specimens the black continues posteriorly to the center of the abdomen. The smallest male with a black throat has a snout-vent length of 65 mm, although two slightly larger males (66 and 73 mm) have only gray throats. In females, the cheek and preauricular spots are more clearly defined than in males.

Comparisons: *A. t. algida* requires comparison only with the two other black-throated races, *azuae* and *ignobilis*. All other subspecies have orange throats. From both *azuae* and *ignobilis*, *algida* differs in having a black chest (and at times part of the abdomen) and in having the dorsum in males dotted with bright yellow. The heavily dotted sides and obsolescent lateral line in adult males will also distinguish *algida* from the two other subspecies.

Remarks: *A. t. algida* is known only from a rather circumscribed area in the Cordillera Central at elevations of 4000 and 4250 feet (1220 and 1296 meters); undoubtedly it is more widespread than these data indicate. We spent two weeks at Constanza and saw only one lizard, which was collected by Richard Thomas late in a warm morning in a wooded but cut-over ravine. The natives who collected most of the specimens indicated that they had been taken in open areas near Constanza. Much of the slopes above the Valle de Constanza today is covered with mixed pine and deciduous shrubs and low trees; such a shaded habitat seems a very suitable situation for *A. taeniura*.

The only subspecies of *A. taeniura* adjacent to *algida* is *ignobilis*. The closest these two races are known to approach one another is about 37 kilometers, airline. The intervening area, however, is extremely rugged and dissected, and the two races may not be in direct contact.

NORTHWESTERN REPUBLICA DOMINICANA AND NORTHERN HAITI

There remain six other specimens, two from extreme western República Dominicana, and four from Haiti north of the Cul de Sac Plain, which require special comment. These are the only specimens of *A. taeniura* available from this region, and although they are suggestive, they are inadequate for systematic treatment.

1) ASFS V1168–69, 1 km S Loma de Cabrera, 900 feet (274 meters), Dajabón Province, República Dominicana. These are two males with the largest having a snout-vent length of 50 mm; they are both obviously young. In addition, the smaller is badly damaged. There is nothing distinctive about the scale counts. The throats were grayish orange in life (and thus not like either the adjacent *ignobilis* or *algida*), and the dorsal zones were olive, almost black, with the smaller having bright yellow dorsolateral lines. The lateral fields are black with red dots. The entire tail is very dark blue-black, with the dorsolateral pale lines very much reduced and almost absent. Quite obviously, these two lizards are not assignable to either *ignobilis* or *algida*. Their correct designation must await further material.

2) AMNH 49848, near Plaisance, Dépt. du Nord, Haiti. This is a large male with a snout-vent length of 87 mm. It is presently very discolored, but a dark median zone can be ascertained, and there appear to be dorsolateral lines. The lateral fields are flecked with pale. The entire venter is presently black, and presumably in life at least the throat (and chest) may have been black. The tail is patternless. This individual, separated from the nearest record of *ignobilis* by about 120 kilometers, airline, and from the Dajabon specimens noted above by about 85 kilometers, might be considered to be *ignobilis*. I prefer to consider it presently unidentifiable to subspecies.

3) USNM 74133–34, St. Michel de l'Atalaye, Dépt. de l'Artibonite, Haiti. These are two males with snout-vent length of 70 and 64 mm. The smaller has a black chest and throat, the larger has these regions gray. There is a broad dorsal zone with prominent pale dorsolateral lines. The lateral fields are heavily dotted with pale, and the lateral line is especially prominent. These two lizards might also be regarded as *ignobilis*, but they may well belong to the same taxon as the specimen from Plaisance (from which St. Michel is separated by only 28 kilometers). More material is badly needed from northern Haiti before any of these lizards can be evaluated properly.

4) USNM 75922, "Artibonite Valley," Haiti. I have commented elsewhere (Schwartz, 1966b) on the status of a specimen of *Leiocephalus melanochlorus* supposedly collected by J. S. C. Boswell in the Artibonite Valley; that lizard clearly came from the southwestern portion of the Tiburon Peninsula, probably in the vicinity of Les Cayes where Boswell is known to have collected. The *Ameiva*, although much discolored, is dorsally lined, and resembles (in

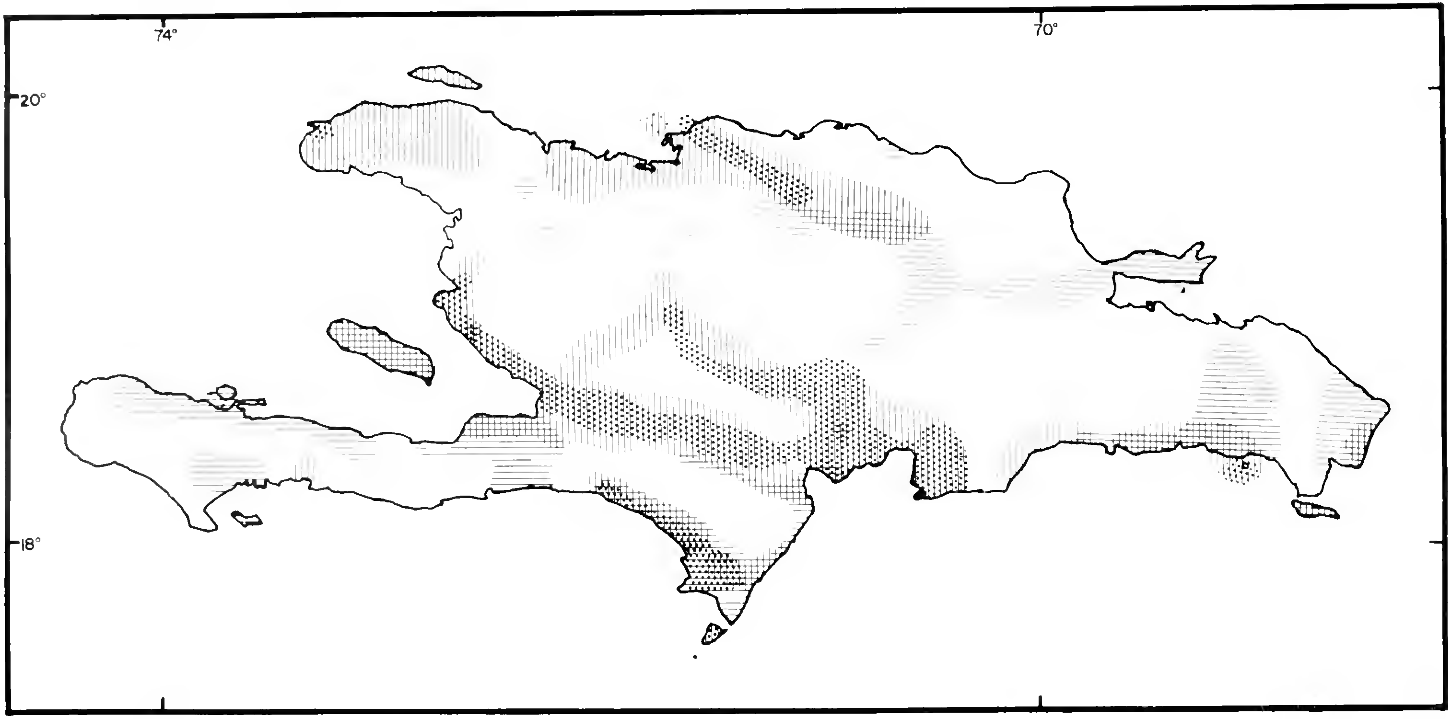


Fig. 2. Hispaniola, showing the combined known distributions of *Ameiva taeniura* (horizontal lines), *A. chrysolaema* (vertical lines) and *A. lineolata* (coarse stippling). Note general concordance of ranges of *lineolata* and *chrysolaema*, and rare sympatry between these two species and *A. taeniura*.

what details are discernible) specimens of *A. t. regnatrix*. Since there are no lined populations known from north of the Cul de Sac-Valle de Neiba plain, and since Boswell is known to have collected in the Les Cayes region, it seems likely that this *Ameiva* originated in that region and not in the Artibonite Valley. The closest record of *A. taeniura* to the Artibonite Valley itself is that of *A. t. barbouri*, a very distinctive subspecies. It is possible that there is a population of *A. taeniura* in the Artibonite Valley, but I consider it unlikely that this specimen originated there.

DISCUSSION

Ameiva taeniura, along with *Ameiva lineolata* and *Ameiva chrysolaema*, completes the roster of Hispaniolan teiids. The latter two species have been recently discussed (Schwartz, 1966a, Schwartz and Klinikowski, 1966) and the conclusion reached that both are north island (*sensu* Williams) species. Both *lineolata* and *chrysolaema* are confirmed inhabitants of xeric regions, the former somewhat more so than the latter. *A. lineolata* occurs on the south island only on the Península de Barahona (and Isla Beata), and *A. chrysolaema* occurs only east of a line drawn between Léogâne and Saltrou in Haiti (except for an isolated record at Aquin). Thus neither *lineolata* nor *chrysolaema* have extensive south island distributions. Reasons for suggesting that these two species are immigrants onto the south island have been discussed in the two papers mentioned above.

A. taeniura, on the other hand, occurs (in a general fashion) throughout much of the south island, and on Ile-à-Vache and the Cayemites. The peninsular races (*taeniura, regnatrix, varica*, and *aequorea*) share in a community of characters which include orange throats and lined dorsa. The eastern south island race *vulcanalis*, as well as all the north island races, have dorsa which show a dorsal zone. The races on Gonâve and Saona have this type of pattern also. It seems likely that *A. taeniura* is the south island *Ameiva* and that it was, prior to the invasion of *A. chrysolaema* and *A. lineolata*, the dominant and only ground lizard on this southern land mass.

Of the north island Dominican races (*azuae, tofacea, vafra, ignobilis*, and *algida*), two have orange throats (*tofacea, vafra*) and the balance have black throats. The orange-throated races are, I believe, derivatives of the eastern south island *vulcanalis*, which has successfully been able to cross the eastern (mesic) end of the arid Valle de Neiba (*vulcanalis* occurs today on the north island at Punta Martín García) and from this region has expanded to the east along the southern Dominican littoral as far as Cabo Engaño (and has reached Isla Saona as well). The current absence of records for *A. taeniura* between Punta Martín García and Santo Domingo may reflect only that the proper microhabitats in the intervening region have not been sampled; the fortuitous taking of *A. t. azuae* in the Llanos de Azua in a particularly favorable niche in an otherwise inhospitable (for *A. taeniura*) environment shows how isolated populations of this species might easily be overlooked. On the other hand, the gap between *vulcanalis* and *tofacea* may be real; since much of the intermediate area is today the hot and dry Llanos de Azua, it is possible that there may not be populations of *A. taeniura* throughout the entire region.

The origin of the northern black-throated races (*algida, ignobilis*) is difficult to determine. The situation in northern Haiti is presently completely unknown. As far as we now know, *tofacea* (orange-throated) and *ignobilis* (black-throated) approach one another most closely in the vicinity of the Bahía de Samaná (for the moment I am disregarding the approximation of black-throated *azuae* and orange-throated *vulcanalis* to the south). The possibility suggests itself that the black-throated forms represent a long isolated off-shoot from the south island stock which has become restricted to the more northern and (generally) interior regions of the north island. The scattered nature of the records for the black-throated subspecies suggests as well that these populations are in the process of becoming restricted in distribution, and what we see today are mere remnants of a formerly much more widespread range. In confirmation of this supposition is the finding of fossil *A. taeniura* (Etheridge, 1965:99) at Pedro Santana, San Rafael Province, República Dominicana, in an area where today the species is not known to occur. If we consider the black-throated races as being an old north island element, then *azuae* must be included, despite its proximity to orange-throated *vulcanalis.* The precise geographical relationships between the races *vulcanalis*, *azuae*, and *tofacea* in the Llanos de Azua and along the southern Dominican coast would be of extreme interest in clarifying the patterns of distribution of orange- and black-throated races in this area, but material is presently not available.

To sum up the above interpretations, I visualize *A. taeniura* as the south island Hispaniolan *Ameiva*; at some distant time, a stock of *A. taeniura* invaded the north island (either when the interisland strait was temporarily closed, or across the water gap) and evolved into the black-throated form of which *ignobilis*, *azuae*, and *algida* are now remnants. Secondly, *vulcanalis* from the south island later invaded the southern shore of the north island, and has since spread to the east and onto Isla Saona, and has developed two subspecies in the eastern portion of its range.

I have made no mention of *A. t. barbouri* in the above discussion. Its occurrence on the Hispaniolan mainland and on Ile de la Gonâve suggest that, rather than having evolved on Gonâve, this race has invaded Gonâve from the mainland. The Gonâve fauna includes such elements as *Diploglossus curtissi*, *Anolis brevirostris* and *Dromicus parvifrons alleni*; of these three forms, the galliwasp and the anole occur along the northern shore of the Golfe de la Gonâve and in the Haitian Cul de Sac Plain, and the snake has been shown to be strangely like some specimens of *D. p. protenus* from the Cul de Sac (Thomas and Schwartz, 1965). The Cul de Sacian affinities with Gonâve, and additionally with the adjacent mainland coast to the northwest, are rather striking. There would thus seem the possibility that *barbouri* represents a derivative from the (proto) *vulcanalis* stock which early crossed the Cul de Sac strait, and developed along the southern littoral of the north island. With the closure of the strait, the resulting arid plain was too xeric for *barbouri* (and this plain likely was rapidly colonized by *A. lineolata* and *A. chrysolaema*, as well as by *Leiocephalus semilineatus* and *L. schreibersi*—four species of ground dwelling lizards which bracket in size the intermediately-sized *barbouri*), and the race has become increasingly restricted in distribution to the shore of the Golfe de la Gonâve. At some time, *barbouri* has reached Gonâve, as have the other species noted above. Such a proposed history would be confirmed if *barbouri* were to be taken along the northern side of the Cul de Sac-Valle de Neiba plain in the foothills of the Montagnes du Trou d'Eau or the Sierra de Neiba; these particular areas have not been well collected. Casual observation of much of these foothill areas indicates that, compared with the ecological situations where *barbouri* was taken on Gonâve and at Trou Forban, they might well be very suitable for this subspecies.

As has been stated previously, *A. chrysolaema* and *A. lineolata* are both inhabitants of xeric environments, whereas *A. taeniura* prefers cool and shady habitats. Inspection of the map (Fig. 2) showing the known distributions of the three species on Hispaniola and its satellite islands, shows that the ranges of *A. chrysolaema* and *A. lineolata* correspond very closely. Only in occasional areas does *lineolata* occur without *chrysolaema*. *A. taeniura* overlaps *A. lineolata* in three major areas: the Península de Barahona, Trou Forban, and the Llanos de Azua.

In the latter two areas, the known distribution of *A. taeniura* is confined to but a single locality. *A. taeniura* and *A. chrysolaema* are somewhat more widely sympatric; known areas include the northeastern shore of the Tiburon Peninsula, portions of the Península de Barahona and the southern shore near Saltrou, the southeastern coast near Santo Domingo, the extreme eastern end of the island, the eastern end of the Valle de Cibao, and the islands of Gonâve and Saona. The three species are sympatric in only four areas: Trou Forban, Península de Barahona, Llanos de Azua, and Punta Martín García. In three of these regions of triple overlap, *A. taeniura* is distinctly the less common of the three species, and is restricted to the more mesic microsituations within the widespread arid macrosituation. In the fourth region (Península de Barahona), the same ecological arrangement of species occurs, but all three are widespread throughout the Península, with *lineolata* having the most restricted distribution. The more stringent ecological requirements of *lineolata* have doubtless brought this about; the eastern coast of the Península is more mesic and unsuitable for *lineolata*.

There are still wide areas in Hispaniola where *Ameiva* is unknown. Much of central Haiti is still *terra incognita* as far as the genus is concerned. At least *A. taeniura* (and possibly *A. chrysolaema*) should have wider distributions in this section. The same statement may be made concerning the extreme eastern and central República Dominicana. The status of *A. taeniura* along the north Dominican coast in the region of Puerto Plata and the interrelationships of the races *ignobilis*, *tofacea*, and *vafra*, on one hand, and of *vulcanalis*, *azuae* and *tofacea*, on the other, all require additional study.

Key to the subspecies of Hispaniolan *Ameiva*[1]

1. Size small (to 59 mm snout-vent length); 8 (occasionally 10) transverse and 26–33 longitudinal rows of ventrals; 14–21 scales in fifteenth caudal verticil; caudal scales smooth and oblique; dorsal pattern a series of boldly contrasting narrow black and white lines (*A. lineolata*) 2
Size larger; 8–12 transverse and 28–41 longitudinal rows of ventrals; 18–52 scales in fifteenth caudal verticil; caudal scales keeled, and straight or oblique; dorsal pattern never as described above 7
2. Usually 9 dorsal black lines at midbody 3
Usually 10 or 11 dorsal black lines at midbody 5
3. Snout and top of head black 4
Snout and top of head pale .... *A. l. semota*
4. Modal black stripe formula 7–9–7; throat creamy, not pale blue like balance of venter .... *A. l. privigna*
Modal black stripe formula 7–9–8; throat pale blue .... *A. l. beatensis*
5. Usually 11 dorsal black lines at midbody; snout clear pale sandy .... *A. l. perplicata*
Usually 10 dorsal black lines at midbody 6
6. Usually 7 black lines at level of sacrum; size smaller (to 55 mm snout-vent length); median black line broken on head or neck .... *A. l. meracula*
Usually 8 black lines at level of sacrum; size larger (to 59 mm snout-vent length); median black line entire or broken .... *A. l. lineolata*
7. Size large (to 160 mm snout-vent length); 10–12 transverse and 33–41 longitudinal rows of ventrals; 30–52 scales in fifteenth caudal verticil; caudal scales keeled and straight (*A. chrysolaema*) 8
Size moderate (to 103 mm snout-vent length); 8–10 (usually 10) transverse and 28–35 longitudinal rows of ventrals; 18–31 scales in fifteenth caudal verticil; caudal scales keeled and oblique (*A. taeniura*) 24
8. Ventrals modally in 10 transverse rows 9
Ventrals modally in 12 transverse rows 19
9. Dorsum patternless 10
Dorsum with pattern 12
10. Size large (to 137 mm snout-vent length); dorsum gray-green with indistinct gray-brown mottling in lateral field area; no

---

[1] This key depends in usefulness on having freshly taken specimens which still retain their original colors and patterns. Attempts to determine old badly faded or discolored specimens will meet with limited success, except in cases where scale counts or gross pattern are definitive.

black gular band ..... *A. c. richardthomasi*

Size smaller (to 126 mm snout-vent length); dorsum rusty brown, yellowish tan, grayish brown or olive; lateral fields absent or only vaguely indicated; black gular band present 11

11. Size small (to 111 mm snout-vent length); venter deep orange-red; lateral fields absent ..... *A. c. leberi*

Size larger (to 126 mm snout-vent length); venter some shade of blue to orange-gray; lateral fields absent or only indicated by a gray lateral stripe *A. c. bockeri*

12. Dorsal pattern consisting of pale blue spots on a tan to brown ground ..... *A. c. ficta*

Dorsal pattern not consisting of spots 13

13. Dorsum gray-green, heavily mottled with black; sides with black tigroid lateral markings ..... *A. c. richardthomasi*

Dorsum lined 14

14. Dorsal pattern of 5 pale lines on a very dark brown ground; pattern often highly modified to give complex longitudinal dorsal figures; sides with vertical tigroid markings ..... *A. c. woodi*

Dorsal pattern of 5 or more lines, each line often consisting of longitudinal series of pale dots; sides without tigroid markings 15

15. Dorsum tan to brown, with 6 or 7 dull pale lines; lateral fields brown and often without included pale dots; no black gular band ..... *A. c. defensor*

Dorsum seldom brown, with 5 to 10 lines; lateral fields black; black gular band present 16

16. 5–7 dorsal lines entire; dorsum brown ..... *A. c. alacris*

6–10 dorsal lines fragmented 17

17. Dorsum reddish brown; venter blue to solid black ..... *A. c. procax*

Dorsum gray, olive, to black; ventral coloration varying from gray to grayish orange, never black 18

18. Lateral fields prominent, outlined by pale longitudinal lines ..... *A. c. bockeri*

Lateral fields obscure, not outlined by pale longitudinal lines ..... *A. c. umbratilis*

19. Dorsum spotted or reticulate 20

Dorsum lined 21

20. Dorsum with discrete sky-blue spots on a black ground ..... *A. c. abbotti*

Dorsum with discrete or confluent (yielding a reticulum) yellow spots on a tan to blackish brown ground ..... *A. c. parvoris*

21. Dorsum with 5 wide black and confused longitudinal lines on a tannish gray to dark brown ground; lateral tigroid markings present and joined to the dorsal pattern; lateral fields absent ..... *A. c. jacta*

Dorsum with 5 to 7 pale lines; lateral fields present, no tigroid markings 22

22. Aspect faded; 6–7 dull buffy lines on reddish brown ground; lateral fields grayish brown; usually with black gular band reduced or absent ..... *A. c. secessa*

Aspect not faded; lateral fields black; black gular band present or absent 23

23. Size large (to 160 mm snout-vent length); dorsal pattern a series of 6 lemon yellow lines and/or linear series of dots on a dark brown to reddish brown ground; black gular band present ..... *A. c. chrysolaema*

Size smaller (to 132 mm snout-vent length); dorsal pattern a series of 5–7 pale yellow lines (at times modified into a clear tan middorsal zone) on a tan to brown ground; black gular band absent, or present but not extensive ..... *A. c. regularis*

24. Dorsum with a series of longitudinal lines and/or a middorsal zone accompanied by longitudinal lines; throat orange 25

Dorsum without a series of longitudinal lines but with a middorsal zone; throat orange or black (including gray) 29

25. Usually 10 transverse rows of ventrals 26

Eight transverse rows of ventrals ..... *A. t. regnatrix*

26. Total number of fourth toe scales 85 ..... *A. t. navassae*

Total number of fourth toe scales 83 or less 27

27. Dorsum with 5 longitudinal lines; lateral fields without dots ..... *A. t. aequorea*

Dorsum with a dorsal zone and associated longitudinal lines 28

28. Dorsum with a middorsal zone and one or two pairs of dorsolateral lines; lateral fields with only a few scattered pale dots, often only posteriorly ..... *A. t. taeniura*

Dorsum with a middorsal zone and one pair of dorsolateral lines; lateral fields with prominent and scattered pale (red to buffy) dots ..... *A. t. varica*

29. Throat orange 30

Throat (or throat and chest) black (including gray) 34

30. Dorsolateral lines completely absent; lateral fields immediately adjacent to dorsal zone; tail unlined ..... *A. t. barbouri*

Dorsolateral lines present or at least indicated 31

31. Throat pale orange; lateral fields sparsely flecked with rusty ..... *A. t. tofacea*

Throat orange, but not pale 32

32. Throat vivid fire orange; lateral fields heavily flecked with orange ..... *A. t. vulcanalis*

Throat orange; lateral fields without flecks 33

33. Dorsolateral lines distinct, yellow-green;

dorsal zone greenish gray .... *A. t. rosamondae*

Dorsolateral lines indistinct, yellow; dorsal zone yellowish tan .... *A. t. vafra*

34. Only throat black 35

Throat and chest black; dorsum in ♂'s heavily dotted with yellow, in ♀'s marbled with dark brown .... *A. t. algida*

35. Size small (to 70 mm snout-vent length); dorsolateral lines lemon yellow .... *A. t. azuae*

Size large (to 103 mm snout-vent length); dorsolateral lines green or yellow-green .... *A. t. ignobilis*

LITERATURE CITED

Barbour, Thomas and Arthur Loveridge. 1929. Typical reptiles and amphibians. Bull. Mus. Comp. Zool., **69** (10): 206–360.

Barbour, Thomas and G. K. Noble. 1915. A revision of the lizards of the genus *Ameiva*. Bull. Mus. Comp. Zool., **59** (6): 417–479.

Cochran, Doris M. 1928. The herpetological collections made in Haiti and its adjoining islands by Walter J. Eyerdam. Proc. Biol. Soc. Washington, **41**: 53–59.

———. 1934. Herpetological collections made in Hispaniola by the *Utowana* expedition, 1934. Occ. Papers Boston Soc. Nat. Hist., **8**: 163–188.

———. 1941. The herpetology of Hispaniola. Bull. U.S. Nat. Mus., **177**: i–vii, 1–398, 120 figs., 12 pls.

Etheridge, Richard. 1965. Fossil lizards from the Dominican Republic. Quart. Jour. Florida Acad. Sci., **28** (1): 83–105, 3 figs.

Maerz, A., and M. Rea Paul. 1950. A dictionary of color. New York, McGraw-Hill Book Co., pp. i–vii, 1–23, 137–208, 56 pls.

Mertens, Robert. 1939. Herpetologische Ergebnisse einer Reise nach der Insel Hispaniola, Westindien. Abh. Senckenberg. Naturf. Ges., **449**: 1–84, 10 pls.

Schmidt, Karl P. 1919. Descriptions of new amphibians and reptiles from Santo Domingo and Navassa. Bull. Amer. Mus. Nat. Hist., **41** (12): 519–525.

———. 1921a. Notes on the herpetology of Santo Domingo. Bull. Amer. Mus. Nat. Hist., **44** (2): 7–20, 12 figs.

———. 1921b. The herpetology of Navassa Island. Bull. Amer. Mus. Nat. Hist., **44** (18): 555–559, 2 pls., 5 figs.

Schwartz, Albert. 1966a. The *Ameiva* (Reptilia, Teiidae) of Hispaniola. I. *Ameiva lineolata* Duméril and Bibron. Carib. Jour. Sci., **5** (1, 2): 45–57, 4 figs.

———. 1966b. The *Leiocephalus* (Lacertilia, Iguanidae) of Hispaniola. I. *Leiocephalus melanochlorus* Cope. Jour. Ohio Herp. Soc., **5** (2): 39–48, 1 fig.

Schwartz, A. and Ronald F. Klinikowski. 1966. The *Ameiva* (Lacertilia, Teiidae) of Hispaniola. II. Geographic variation in *Ameiva chrysolaema* Cope. Bull. Mus. Comp. Zool., **133** (10): 425–487, 11 figs.

Thomas, Richard. 1966. A reassessment of the herpetofauna of Navassa Island. Jour. Ohio Herp. Soc., **5** (3): 73–89, 5 figs.

Thomas, R. and Albert Schwartz. 1965. Hispaniolan snakes of the genus *Dromicus* (Colubridae). Rev. Trop. Biol., **13** (1): 59–83, 10 figs.

Wetmore, Alexander, and Bradshaw H. Swales. 1931. The birds of Haiti and the Dominican Republic. Bull. U.S. Nat. Mus., **155**: i–iv, 1–483, 26 pls., 2 figs.

Williams, Ernest E. 1961. Notes on Hispaniolan herpetology. 3. The evolution and relationships of the *Anolis semilineatus* group. Breviora, Mus. Comp. Zool., No. **136**: 1–8, 1 map.

Bulletin OF THE
Museum of
Comparative
Zoology

New Cyclopoid Copepods Associated with Polychaete Annelids in Madagascar

ARTHUR G. HUMES and JU-SHEY HO

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 135, NUMBER 7
APRIL 24, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN 1863–
BREVIORA 1952–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Memoirs of the Boston Society of Natural History.

Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

NEW CYCLOPOID COPEPODS ASSOCIATED WITH POLYCHAETE ANNELIDS IN MADAGASCAR

ARTHUR G. HUMES[1,2] AND JU-SHEY HO[1]

INTRODUCTION

At Nosy Bé, in northwestern Madagascar, copepods are known to be associated with many different marine invertebrates, but as yet none has been described from polychaete annelids. This paper deals with six new cyclopoid copepods collected from polychaetes at Nosy Bé in 1960 and 1963–64.

All collections were made by A. G. Humes, those in 1960 during an expedition of the Academy of Natural Sciences of Philadelphia, and those in 1963–64 as part of the U.S. Program in Biology of the International Indian Ocean Expedition. Type material has been deposited in the large copepod collection of the United States National Museum. Other specimens of the new species (with the exception of *Nasomolgus leptus*) have been placed in the Museum of Comparative Zoology.

The study of the specimens has been aided by a grant (GB-1809) from the National Science Foundation of the United States.

All figures were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn.

The abbreviations used are: a_1 = first antenna, a_2 = second antenna, md = mandible, p = paragnath, mx_1 = first maxilla, mx_2 = second maxilla, mxpd = maxilliped, p_1 = leg 1.

We wish to thank Dr. Marian H. Pettibone of the United States National Museum for the identification of the polychaete hosts and to acknowledge with appreciation the assistance to the field work given by the staff of the Centre d'Océanographie et des Pèches at Nosy Bé. We are indebted to Dr. J. P. Harding and Miss P. D. Lofthouse of the British Museum (Natural History) who have examined for us the single type specimen of *Nasomolgus cristatus*.

The copepods described in this paper comprise the following:

1) from *Lepidonotus cristatus* (Grube)
   Cotylomolgus lepidonoti n. gen., n. sp.
2) from *Sabella fusca* (Grube)
   Pseudanthessius ferox n. sp.
3) from *Sabellastarte magnifica* (Shaw)
   Nasomolgus firmus n. sp.
   Nasomolgus leptus n. sp.
   Nasomolgus rudis n. sp.
   Nasomolgus parvulus n. sp.

SYSTEMATIC DESCRIPTION

CLAUSIDIIDAE Embleton, 1901

COTYLOMOLGUS[1] n. gen.

Body cyclopoid, elongated, moderately widened and rather flattened in the pro-

---

[1] Boston University, Boston, Massachusetts

[2] Associate in Marine Invertebrates, Museum of Comparative Zoology

[1] The generic name is a combination of κοτυλή = a small cup, alluding to the sucker on the second antenna, and μολγος = a sack made of leather.

Bull. Mus. Comp. Zool., 135(7): 377–414, April, 1967

some. Segment of leg 1 completely fused with the head. Urosome 5-segmented in the female, 6-segmented in the male. Caudal ramus with 6 setae. First antenna 6-segmented. Second antenna 4-segmented, with a large pedunculate sucker on the third segment. Mandible with 4 terminal elements (1 flattened recurved attenuated spine and 3 setae). Paragnath a spinulose lobe. First maxilla a small lobe with 4 elements. Second maxilla probably 2-segmented, with terminally a recurved spine and a long spiniform element. Maxilliped absent in the female, but well formed in the male, where it is 4-segmented (assuming that part of the terminal claw represents the fourth segment).

Legs 1 and 2 with 3-segmented rami. Leg 3 reduced to a single free segment. Leg 4 absent in both sexes. Leg 5 two-segmented in the female, the first segment with a single seta, the second segment armed with 4 setae, 3 of them long and spiniform, the other short and slender. Leg 5 in the male with a single free segment.

Other features as in the species described below.

Living on polychaete annelids.

Type and only known species: *Cotylomolgus lepidonoti* n. sp.

Gender masculine.

Cotylomolgus lepidonoti[1] n. sp.

Figs. 1–29

Type material.—10 females, 8 males, and 3 immature specimens from 5 *Lepidonotus cristatus* (Grube) under intertidal rocks at Antsakoabe, on the northern shore of Nosy Bé, Madagascar. Collected December 1, 1963. Holotype female, allotype, and 11 paratypes (6 females and 5 males) deposited in the United States National Museum, Washington; the remaining paratypes in the collection of A. G. Humes.

Other specimens (all from *Lepidonotus cristatus* collected intertidally at various localities on Nosy Bé).—1 female from 1 host, Ambatoloaka, September 2, 1960; 7 females and 6 males from 2 hosts, Antsakoabe, November 1, 1963; 6 females, 4 males, and 2 immature from 2 hosts, Navetsy, November 3, 1963; 2 females and 3 males from 4 hosts, Antsakoabe, February 16, 1964; 4 females and 4 males from 2 hosts, Antsakoabe, September 7, 1964; and 1 female and 1 male from 1 host, Befifika, October 7, 1964.

Female.—The body (Figs. 1 and 2), with a moderately broadened and somewhat flattened prosome, has a length (excluding the setae on the caudal rami) of 1.41 mm (1.29–1.50 mm) and a greatest width of 0.63 mm (0.59–0.72 mm), based on 8 specimens. The ratio of length to width of the prosome is 1.35 : 1. The segment of leg 1 is completely fused with the head. The epimeral areas of the metasomal segments are rounded posteriorly. These segments are separated by faintly striated intersegmental membranes.

The segment of leg 5 (Figs. 3 and 4) is wider than long, 101 × 257 μ, and bears the fifth legs ventrally on the posterolateral areas. Dorsally the segment bears posteriorly a transverse striated membrane, and ventrally between the insertions of the legs there are 2 patches of spinules arranged in somewhat irregular rows. The genital segment is wider than long, 141 × 177 μ in greatest dimensions, with the broadened anterior two-thirds separated abruptly from the narrowed posterior third (where the width is 130 μ). The posterior margin of the segment bears a striated membrane dorsally and ventrally and has delicate spinules laterally. The areas of attachment of the egg sacs are situated dorsolaterally in the middle of the segment. Each area (Fig. 5) bears 2 small setae about 7 μ in length and a small setiform projection. There are 3 postgenital segments, the first 2 bearing a posterior membrane dorsally and ventrally and lateral spinules as on the genital segment (though the membrane on the second postgenital segment is incomplete midventrally and is indented mid-

---

[1] The specific name *lepidonoti* is derived from the generic name of the host.

dorsally). The first postgenital segment is 75 × 120 μ, the second 49 × 114 μ, and the third 60 μ (greatest length) × 101 μ. The anal segment, on which the caudal rami are inserted dorsally, bears ventrally near the base of each ramus a patch of very small spinules.

The caudal ramus (Fig. 6) is elongated, 78 μ in length along its outer edge (70 μ along the inner edge) and 33 μ in width, or about 2.4 times longer than wide. The outer lateral seta is 45 μ long and naked. The pedicellate dorsal seta is 36 μ and naked. The outermost terminal seta (86 μ) and the innermost terminal seta (66 μ) are minutely spinulose. There is a single well developed long median terminal seta 314 μ in length and naked. From its outer basal area there arises a finely spinulose slender seta 53 μ in length. This seta has no apparent articulation; presumably it represents the outer of the 2 long terminal setae commonly found in poecilostomes which here has fused with the base of the inner long seta. On the proximal half of the dorsal surface of the ramus there are a few small spinules and on the distal ventral surface there is a patch of very small spinules. A small hair arises on the proximal outer margin of the ramus.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear scattered minute setules. The ratio of the length of the prosome to that of the urosome is 2 : 1.

The egg sacs are moderately elongated (Fig. 7), 593 × 246 μ, and contain numerous mostly hexagonal eggs about 55–60 μ in diameter.

The rostral area (Fig. 8) is not well developed and consists of a small lobe lying behind the prominent crescentic ridge between the bases of the first antennae.

The first antenna (Fig. 9) is 6-segmented. The lengths of the segments (measured along their posterior margins) are: 36 (30 μ along the anterior margin), 73, 48, 50, 42, and 32 μ respectively. The first segment bears 5 setae (the posteriormost with lateral hairs); the second bears 11 proximal setae and 3 anterodistal setae; the third 6 medioanterior setae, a single medioposterior seta, and 2 distal setae; the fourth 2 setae and one aesthete proximally and 2 setae distally; the fifth 2 setae and one aesthete distally; and the sixth 7 setae and one aesthete. The formula thus is: 5, 14 (11 + 3), 9 (6 + 1 + 2), 4 + 1 aesthete (2 and 1 aesthete + 2), 2 + 1 aesthete, and 7 + 1 aesthete. All the setae are delicately annulated and naked except for the single haired seta on segment 1.

The second antenna (Figs. 10 and 11) is 4-segmented and distinctly flexed, with the 3 short distal segments directed back toward the relatively elongated proximal segment. The first segment bears anterodistally a cluster of hairs. The second segment bears a row of spinules. The third segment bears a hyaline seta, a spine with its distal third formed like a crooked thumb and spinulose, and a large pedunculate sucker 56 μ in diameter, its cup having well sclerotized supporting rays and with its rim formed by a hyaline lamella ornamented with minute hairlike processes (spinules?). The fourth segment is longer and more slender than the preceding 2 and bears 2 setae on a subterminal expansion and 4 terminal setae, all of them annulated and naked.

The labrum (Fig. 12), held erect in alcoholized specimens, is linguiform in outline, with a small terminal indentation and 2 lateral hyaline lobes.

The mandible (Fig. 13) is a single elongated segment bearing 4 terminal elements: a recurved attenuated flattened spine with a few short lateral spinules, and 3 setae with lateral spinules. The paragnath (Fig. 14) is a rounded lobe bearing slender spinules and showing small circular markings in its cuticle. The first maxilla (Fig. 15) is a small segment armed with 4 elements: 1 seta on the anterior surface, and 3 terminal setae (2 large, the longer 33 μ in length, and 1 shorter and slender). Near the base of the seta on the anterior surface there is a group of surficial markings. The second maxilla (Figs. 16 and 17) probably consists of 2 segments, though the segmentation is obscure. The proximal portion (first segment?) bears a large ventral patch of small spinules arranged in irregular rows. The distal portion (second segment?) has surficial creases and folds, and bears 2 terminal elements: a greatly recurved spine having on its concave surface 2 relatively long hyaline spinules followed by 2 rows of minute spinules, and a long attenuated spiniform element not clearly articulated with the segment and bearing surficial punctations and a minute subterminal process. The maxilliped is absent.

The postoral area (Fig. 18) shows a number of sclerotized regions, with a transverse lobed area just posterior to the level of the second maxillae having a pair of irregular somewhat spherical sclerotizations. These 2 sclerotized pieces might be considered as remnants of maxillipeds, but since they are so far removed (see Fig. 8) from the usual position of maxillipeds in other poecilostomes they probably do not represent appendages. Posterior to the region shown in Figure 18 there is a balloonlike expansion (see Fig. 2) bearing 2 patches of small spinules arranged in irregular rows (Fig. 19).

As shown in a ventral view of the cephalosome (Fig. 8), the area between the bases of the first antennae is raised to form a crescentic ridge, and bears groups of small spinules. On either side, posterior to the bases of the antennae, the ventral wall of the cephalosome is raised to form a spinulose ridge that extends nearly to the posterolateral corners of the cephalosome. The rostrum and head appendages are thus surrounded by these ridges (except posteriorly). The ridges may aid (together with the 2 suckers on the second antennae) in adhesion to the host.

Legs 1 and 2 (Figs. 20 and 21) have 3-segmented rami. Leg 3 is reduced to a single segment. Leg 4 is absent. The spine and setal formula is as follows (the Arabic numerals indicating setae, there being no spines on the legs):

P 1 protopod 0-0; 1-0 exp 1-0; 1-1; 1,1,4
end 0-1; 0-1; 4
P 2 protopod 0-0; 1-0 exp 1-0; 1-1; 1,4
end 0-1; 0-1; 4
P 3 reduced, 1-0; 2
P 4 absent

Leg 1 (Fig. 20) shows a row of spinules on the outer distal area of the coxa, but there is no inner spine or seta on this segment. The intercoxal plate is broad and its distal edge is ornamented anteriorly and posteriorly with 2 groups of small spinules arranged in irregular rows. The basis has an outer haired seta and is ornamented on its anterior surface with a row of spinules between the insertions of the rami and with 3 or 4 rows of spinules medial to the insertion of the endopod; on the margin of the inner expansion of the basis there is a row of long hairs. The outer margins of the segments of both rami are well ornamented with spinules. Hairs occur along the inner margin of the first segment of the exopod and along the outer margins of the first and third segments of the endopod. The segments of the exopod bear slender annulated outer setae instead of the spines often seen in other poecilostomes. The inner margin of the third segment of the endopod shows an interruption of the sclerotization.

Leg 2 (Fig. 21) is in general similar to leg 1, but the several rows of spinules on the anterior surface of the basis medial to the insertion of the endopod are absent, the outer seta on the basis is smaller and naked, there is only 1 small annulated seta on the third segment of the exopod, and there is no interruption in the sclerotization of the inner margin of the third segment of the endopod.

Leg 3 (Fig. 22) consists of only a single elongated free segment, 58 × 22 μ, armed with 2 very unequal terminal setae, the inner 94 μ in length and bearing rows of very short spinules on its distal two-thirds, the outer 35 μ long, slender, and naked.

Near the insertions of the 2 setae there is a ventral patch of minute spinules. Close to the insertion of the free segment there is an outer naked seta 52 μ long arising from the body.

No trace could be found of leg 4.

Leg 5 (Fig. 23) is 2-segmented. The first segment is 88 × 73 μ, and bears an outer naked seta 52 μ long. On the dorsal surface of the segment there is a diagonal line from the base of the seta to the inner distal angle; on the ventral surface there are transverse rows of minute spinules near the distal margin. The second segment is 117 μ along the inner margin and 68 μ along the outer margin to the base of the first seta; its greatest diagonal length in 135 μ and its greatest width is 70 μ. The segment is armed with 2 outer lateral spiniform setae (99 and 112 μ long respectively) and 2 very unequal terminal setae, 1 slender and 55 μ, the other spiniform and 140 μ in length. All 4 setae bear extremely minute lateral spinules and are delicately annulated. Diagonal rows of minute spinules occur along the distal dorso-inner margin and extend around on the ventral surface to form a patch near the insertion of the innermost long seta. Another patch of minute spinules arranged in diagonal rows may occur (not in all specimens) on the ventral margin just proximal to the first outer seta.

Leg 6 is probably represented by the 2 small setae on the areas of attachment of the egg sacs (see Fig. 5).

The color in life in transmitted light is translucid to slightly opaque, the eye red, the egg sacs opaque gray.

Male.—The form of the body (Fig. 24) resembles that of the female. The length (without the setae on the caudal rami) is 1.06 mm (0.90–1.17 mm) and the greatest width is 0.46 mm (0.39–0.50 mm), based on 10 specimens. The ratio of length to width of the prosome is 1.4 : 1.

The segment of leg 5 (Figs. 25 and 26), measuring 81 × 172 μ, resembles that of the female. The genital segment is wider than long, 91 × 143 μ. The 4 postgenital segments are 55 × 107, 47 × 97, 33 × 92, and 40 × 86 μ from anterior to posterior.

The caudal ramus is like that of the female.

The surfaces of the prosome and urosome bear minute setules as in the opposite sex. The ratio of the length of the prosome to that of the urosome is about 1.8 : 1.

The rostral area, first antenna, second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla resemble those of the female. The maxilliped (Fig. 27) has a rather poorly defined basal segment. The large second segment bears 2 hyaline naked setae on its inner surface and a large patch of small blunt spinules arranged in longitudinal rows on its posterior surface. The third segment is small and unarmed. The fourth segment probably forms part of the short and rather stout terminal claw, which is 54 μ in length (measured along its axis) and bears near its base a slender naked annulated seta and a very small setule. On the concave surface of the claw there is proximally a minute hyaline process and more distally 2 parallel rows of minute denticles.

The postoral area and the cephalosome resemble generally those areas in the female.

Legs 1, 2, and 3 are like those in the female. Leg 4 is absent.

Leg 5 (Fig. 28) has a single free segment and is held against the sides of the genital segment in alcholic specimens (see Fig. 25) rather than diverging as in the female. The free segment is more elongated than in the female, 59 × 25 μ in greatest dimensions. The 4 setae measure from outer to inner 79, 95, 39, and 127 μ in length. There is a patch of small spinules on the ventral surface near the insertion of the longest seta. The group of spinules seen in the female on the ventral margin proximal to the first outer seta is absent here. The seta arising from the body near the free segment is 55 μ long and naked.

Leg 6 (Fig. 26) consists of a posterolateral flap on the ventral surface of the genital segment, ornamented with minute spinules but apparently lacking spines or setae.

The spermatophore (Fig. 29), attached to the female, is elongated, 234 × 68 μ, including the neck.

The color in life in transmitted light resembles that of the female.

Taxonomic position of the genus.—The new genus *Cotylomolgus* appears to be related to *Myzomolgus* Bocquet and Stock, 1957 (Clausidiidae), and to *Catinia* Bocquet and Stock, 1957 (Catiniidae), genera which live on sipunculid worms. As in these two genera, *Cotylomolgus* has the segment of leg 1 fused with the head, the urosome in the female is 5-segmented and in the male 6-segmented, the first antenna is 6-segmented, the second antenna is 4-segmented with a large sucker on the third segment, the first maxilla bears four elements, leg 5 in the female is 2-segmented and in the male has only a single free segment, and the maxilliped in the male is 4-segmented (assuming that the fourth segment forms part of the claw).

Cotylomolgus differs from *Myzomolgus* chiefly in lacking the maxilliped in the female, in the reduction of leg 3 and the absence of leg 4, and in the absence of an inner spine on the basis of leg 1.

The new genus differs from *Catinia* in having a well developed mandible with four terminal elements, in the reduction of leg 3 and the absence of leg 4, and in the absence of an inner spine on the basis of legs 1–3.

Cotylomolgus differs from both *Myzomolgus* and *Catinia* in certain features of legs 1–4, principally, the absence of an inner spine on the basis of legs 1 and 2, the reduction of the outer spines on the exopods of legs 1 and 2 to simple setae, the reduction of leg 3 to a single free segment, and the absence of leg 4.

The nature of the mandible in *Cotylomolgus*, with its four terminal elements, is more like that of *Myzomolgus* than that of *Catinia*. (Gooding, 1963, in an unpublished thesis, after examination of specimens of *Catinia plana* Bocquet and Stock, 1957, has shown that a pair of small, weakly cuticularized mandibles, bent midway almost at a right angle and apparently without major spines or setae, exists in that species.) Since the structure of the mandible in poecilostomes is characteristic within supraspecific groups and thus may be regarded as indicative of phylogenetic relationship, *Cotylomolgus* appears to be closer to *Myzomolgus* than to *Catinia*.

Bocquet and Stock (1957, p. 430) placed their new genus *Myzomolgus* in the Clausidiidae largely on the basis of the structure of the mouthparts, notably the mandible, the antennae, and the well developed thoracic legs. While *Cotylomolgus* shows a reduction of the legs, a feature which is characteristic of many of the genera in the Clausiidae, the form of its mandible is clausidiid rather than clausiid. We are led, therefore, to include provisionally the genus *Cotylomolgus* in the Clausidiidae, recognizing at the same time that there is a close relationship between the Clausidiidae and the Clausiidae and that the two families may actually represent a single category (see Wilson and Illg, 1955, p. 137).

LICHOMOLGIDAE Kossmann, 1877

PSEUDANTHESSIUS Claus, 1889

Pseudanthessius ferox[1] n. sp.

Figs. 30–59

Type material.—14 females, 5 males, and 5 immature specimens from 3 *Sabella fusca* (Grube), in 1 m, at Ambariobe, a small island between Nosy Bé and Nosy Komba, Madagascar. Collected October 4, 1964. Holotype female, allotype, and 14 paratypes (11 females and 3 males) deposited in the United States National Museum, Washington; the remaining paratypes (dissected) in the collection of A. G. Humes.

---

[1] The specific name *ferox* (from Latin = warlike, savage) alludes to the rather formidable appearance of the labrum.

Other specimens (all from *Sabella fusca*).—1 female and 2 males from 1 host, in 6–8 m, Ambariobe, December 27, 1963; 4 females, 10 males, and 12 immature specimens from 1 host, in 1 m, west of Pte. Mahatsinjo, Nosy Bé, March 27, 1964; and 4 females and 5 males from 1 host, in 2 m, Andraikarebe, Nosy Komba, October 9, 1964 (these specimens placed in the Museum of Comparative Zoology).

Female.—The body (Fig. 30) is rather elongated, with the prosome moderately broadened. The length (not including the setae on the caudal rami) is 1.73 mm (1.63–1.97 mm) and the greatest width is 0.71 mm (0.67–0.75 mm), based on 10 specimens. The ratio of length to width of the prosome is 1.67 : 1. The segment of leg 1 is separated from the head by a dorsal furrow. Near the level of the maxillipeds on each side of the cephalosome there is a slight notch, perhaps indicating the boundary of the maxillipedal segment. The epimeral areas of the metasomal segments are rather pointed posteriorly.

The segment of leg 5 (Fig. 31) is 104 μ long and bears a transverse sclerotized area 153 μ in width. (The exact width of the segment is difficult to determine, since the fifth legs are fused with it.) The genital segment (Figs. 31, 32, and 33) is 224 μ in length. In dorsal view the segment is widened in its anterior two-thirds (180 μ), then narrowed in its posterior third (130 μ). On the ventral surface of the anterior half there are 2 swollen areas, each about 112 × 68 μ. In lateral view these areas protrude conspicuously. These swellings were seen on all females examined. Their size, shape, position, and lack of a neck make it unlikely that they represent spermatophores. The areas of attachment of the egg sacs are located dorsolaterally at the level of the segmental constriction. Each area in dorsal view (Fig. 34) shows a pedicellate naked seta 37 μ long set upon a sclerotized base and 2 spinelike elements, one 22 μ long and naked, the other 14 μ and bearing a subterminal setuliform process. In lateral view (Fig. 35) the armature is more clearly visible. The 3 postgenital segments are 78 × 112, 62 × 95, and 90 × 91 μ from anterior to posterior.

The caudal ramus (Fig. 36) is elongated, 109 × 38 μ, or about 2.9 times longer than wide. The outer lateral seta is 92 μ long, the pedicellate dorsal seta 31 μ, the outermost terminal seta 81 μ, the innermost terminal seta 138 μ, and the 2 median terminal setae 360 μ (outer) and 560 μ (inner). All the setae except the 2 median terminal ones are finely annulated and all are naked except the innermost terminal 1 which bears an inner row of hairs near its base. The dorsal and ventral surfaces of the ramus bear scattered minute setules.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear minute setules. The ratio of the length of the prosome to that of the urosome is 1.45 : 1.

The egg sacs are elongated (Fig. 30), in one female measuring 952 × 190 μ, though there is some variation in length in different individuals, and contain numerous eggs, each about 60 μ in diameter.

The rostral area (Fig. 37) is undeveloped and represented by a crescentic line between the bases of the first antennae.

The first antenna (Fig. 38) is 7-segmented, but the third segment has on its ventral surface a small proximal sclerotized area suggesting an intercalary segment. The lengths of the segments (measured along their posterior non-setiferous margins) are: 15 (70 μ along the anterior margin), 75, 33, 51, 47, 33, and 24 μ, respectively. The formula for the armature is 4, 13, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All the setae are naked except 1 on segment 5 and 4 on segment 7 which are haired. One of the terminal setae on the last segment is longer (150 μ) and stronger than any of the others.

The second antenna (Fig. 39) is 4-segmented, with the formula 1, 1, 3, and 5 + II. The last segment, about 55 × 39 μ, bears terminally 2 strong unequal claws 72 and

36 μ long, a slender transversely divided seta, and a small seta near the insertion of the smaller claw; subterminally there are 3 setae, 1 short, the other 2 long. All the setae are naked, and those on the last 2 segments are slightly annulated.

The labrum (Fig. 40) has 2 medial rounded and rather hyaline lobes, external to which there are 2 large well sclerotized spikelike processes about 50 μ in length which extend ventrally to the mouthparts. The labrum lacks fine ornamentation.

The mandible (Fig. 41) has a small naked spinelike element on the convex side at the base of the blade. The blade is attenuated distally and bears a striated flange on the convex side and a row of spinules on the concave side. The paragnath (Fig. 40) is probably represented by a small unoramented rather hyaline lobe about 17 μ long located between the base of the mandible and the outer corner of the labrum. The first maxilla (Fig. 42) consists of a single segment armed with 4 setae, all of which are indistinctly articulated. The second maxilla (Fig. 43) is 2-segmented. The first segment is unarmed. The second segment bears the usual armature consisting of a small hyaline basal outer seta, a larger seta on the posterodorsal surface, and a long subterminal spinulose seta, and terminates in a moderately short lash with prominent dentiform spines proximally becoming slender spinules distally. The maxilliped (Fig. 44) has 3 segments: an elongated unarmed basal segment, a rather swollen second segment partially divided by surficial creases and bearing on the inner surface proximally a patch of spinules and distally 2 naked elements (1 spiniform and 1 setiform), and a small slender terminal segment bearing on its inner surface 2 naked elements (1 spiniform and 1 setiform) and terminating in a spiniform process (not articulated).

The postoral area (see Fig. 37) does not protrude ventrally. A sclerotized line connects the bases of the maxillipeds.

Legs 1–4 (Figs. 45, 47, 48, and 49) have 3-segmented rami, with the exception of the endopod of leg 4 which consists of a single segment. The spine and setal formula is as follows (the Arabic numerals representing setae, the Roman numerals spines):

P 1	protopod 0-1; 1-0	exp	I-0;	I-1;	III,I,4
		end	0-1;	0-1;	I,5
P 2	protopod 0-1; 1-0	exp	I-0;	I-1;	III,I,5
		end	0-1;	0-2;	II,I,3
P 3	protopod 0-1; 1-0	exp	I-0;	I-1;	III,I,5
		end	0-1;	0-2;	II,I,2
P 4	protopod 0-1; 1-0	exp	I-0;	I-1;	II,I,5
		end	II		

The inner seta on the coxa of legs 1–3 is long and feathered, but in leg 4 this seta is minute (12 μ long) and naked. In the first 3 legs the inner margin of the basis bears a row of hairs, but these hairs are absent in leg 4. In leg 1 (Fig. 45) the outer spines of the exopod have short blunt spinules along one side. Between the rami the basis (as in legs 2 and 3 also) forms a sharply pointed process (Fig. 46). In leg 2 (Fig. 47) the outer spines of the exopod have delicate spinulose lamellae. The terminal spine on the last segment of the endopod is 66 μ long, naked, somewhat irregular, and has a minutely pointed tip. Leg 3 (Fig. 48) is similar to leg 2, except for differences in the spine and setal formula. Leg 4 (Fig. 49) has a less prominent and more rounded process on the basis between the rami. The endopod is 1-segmented, though the restriction of the inner lateral hairs to the proximal portion and the interruption in the sclerotization suggest a division of the segment. The segment measures 115 × 57 μ in greatest dimensions. The outer margin of the endopod is somewhat irregular and on its distal half there are 3 groups of minute denticles borne on 3 marginal lobes. The 2 terminal spines are 44 μ (inner) and 29 μ (outer) in length. There is an anterior row of minute spinules near the insertions of these spines.

Leg 5 (Fig. 50) does not have a free segment and bears terminally a naked spine 37 μ and a naked seta 56 μ in length, and dorsally a seta 55 μ long with lateral hairs.

Leg 6 is probably represented by the armature on the area of attachment of the egg sacs (see Figs. 34 and 35).

The color in life in transmitted light is slightly opaque, the eye red, the egg sacs gray.

Male.—The form of the body (Fig. 51) resembles that of the female. The length (not including the setae on the caudal rami) is 1.41 mm (1.28–1.52 mm), and the greatest width is 0.46 mm (0.42–0.50 mm), based on 10 specimens (the allotype, 4 paratypes, and 5 specimens from Andraikarebe collected October 9, 1964). The epimeral areas of the segments of legs 2–4 are more rounded posteriorly than in the female. The ratio of length to width of the prosome is 1.66 : 1.

The segment of leg 5 is smaller than in the female, being only 52 × 96 μ, but otherwise similar. The genital segment (Fig. 52) is longer than wide, 161 × 146 μ, with gently arcuate lateral margins in dorsal view. The 4 postgenital segments are 77 × 90, 73 × 77, 50 × 64, and 64 × 64 μ from anterior to posterior.

The caudal ramus is like that of the female.

The surfaces of the prosome and urosome bear minute setules as in the female. The ratio of the length of the prosome to that of the urosome is about 1.15 : 1.

The rostral area and first antenna are like those in the female. The second antenna also resembles that of the female, but the slender transversely divided seta on the last segment next to the 2 claws is longer and more clawlike (Fig. 53). The labrum, mandible, paragnath, and first maxilla resemble those of the female. The second maxilla (Fig. 54) is much like that of the opposite sex, but the first segment appears to be a little more swollen and the terminal lash is relatively shorter. The maxilliped (Fig. 55) is 4-segmented (assuming that the fourth segment forms part of the claw). The first segment bears a prominent weakly sclerotized digitiform process on its distal inner corner. The second segment bears on its inner surface 2 setae (31 and 19 μ long) and a row of small spinules. The short third segment is unarmed. The slender claw (Fig. 56), 130 μ in length (measured along its axis), bears near its base a posterior seta 28 μ and an anterior seta 11 μ in length. The marginal lamella along the concave surface of the claw shows a minute interruption about midway, perhaps representing the distal boundary of the fourth segment. The tip of the claw has a very narrow lamella.

The postoral area resembles that of the female.

Leg 1 (Fig. 57) shows several differences from that of the female, especially in the endopod. The outer spines on the exopod are more slender and acutely pointed. The last 2 segments of the endopod are almost completely fused, the only evidence of the former articulation between them seen on the anterior surface where a line extends halfway across the ramus at the level of the spinous process. The distal part of the endopod is much modified, terminating in a sclerotized clawlike structure. There is a single short (10 μ) naked outer spine and 4 setae (1 naked, 20 μ long, with a narrow lamella, arising from the convex edge; 1 feathered, 32 μ long, arising on the posterior surface; and 2 feathered, 44 and 48 μ long, arising on the inner side). On the anterior surface between the spine and the first seta there is a sclerotized clawlike projection (for which no articulation could be seen). This projection may perhaps be derived from the outermost seta in the female. Two other small projections are located subterminally on the anterior surface. The presence of the clawlike structures and the curvature of the distal part of the endopod suggest a prehensile function. The formula for the endopod is 0-1; 0-1 . . . I,4.

Legs 2-5 resemble those of the female.

Leg 6 (Fig. 58) consists of a posterolateral flap on the ventral side of the genital segment, bearing 2 naked setae 27 and 44 μ in length and having a surficial spiniform projection 4.5 μ long.

The spermatophore (Fig. 59), as seen within the body of the male, is elongated, 151 × 62 μ, not including the short neck of 10 μ.

The color in life in transmitted light resembles that of the female.

Comparison with other species in the genus.—*Pseudanthessius ferox* may be readily distinguished from 13 of the 22 species in the genus listed by Stock, Humes, and Gooding (1963) on the basis of three recognition characters: the two spikelike processes on the labrum in both sexes, the process on the first segment of the male maxilliped, and the clawlike modification of the endopod of leg 1 in the male. These 13 species, which lack one or more of the three characters and thereby differ from *P. ferox*, are: *aestheticus* Stock, Humes, and Gooding, 1963; *assimilis* G. O. Sars, 1917; *deficiens* Stock, Humes, and Gooding, 1963; *latus* Illg, 1950; *liber* (Brady, 1880); *luculentus* Humes and Cressey, 1961; *mucronatus* Gurney, 1927; *nemertophilus* Gallien, 1935; *notabilis* Humes and Cressey, 1961; *pectinifer* Stock, Humes, and Gooding, 1963; *sauvagei* Canu, 1892; *thorelli* (Brady, 1880); and *tortuosus* Stock, Humes, and Gooding, 1963. *Pseudanthessius procurrens* Humes, 1966 from a cidarid echinoid in Madagascar lacks all three of the characters just mentioned and thus is easily separated from *P. ferox*.

Unfortunately, in the remaining 9 species no information is available regarding these three recognition characters, and other features must be used to separate them from *P. ferox*. Of these species, *liber, sensu* Sewell, 1949, has two long elements on the first segment of the first antenna; *dubius* G. O. Sars, 1918, has a 4-segmented urosome in the female; and the remaining 7 species (*concinnus* Thompson and A. Scott, 1903, *gracilis* Claus, 1889, *graciloides* Sewell, 1949, *obscurus* A. Scott, 1909, *spinifer* Lindberg, 1945, *tenuis* Nicholls, 1944, and *weberi* A. Scott, 1909) have slender setiform elements instead of strong claws on the last segment of the second antenna.

In addition to these differences, other features, such as the length to width ratio of the caudal rami, may be useful in separating many of the species from *P. ferox*. None of the known species of *Pseudanthessius* seems to be closely related to the new species from Madagascar.

NASOMOLGUS Sewell, 1949

This genus was established by Sewell on the basis of a new species, *Nasomolgus cristatus*, of which he found only a single female in debris at a depth of 38 m off the South Arabian coast. In describing the four new species which follow, we have been unable to compare at firsthand this type specimen (which is in the British Museum). However, Dr. J. P. Harding and Miss P. D. Lofthouse of the Museum staff have examined the permanent slide of *N. cristatus* and have supplied us with information on several critical points.

Nasomolgus firmus[1] n. sp.

Figs. 60–86

Type material.—28 females and 4 males from one sabellid polychaete, *Sabellastarte magnifica* (Shaw), in 2 m, at Ambariotelo, a small island between Nosy Bé and Nosy Komba, Madagascar. Collected May 15, 1964. Holotype female, allotype, and 20 paratypes (females) deposited in the United States National Museum, Washington; the remaining paratypes in the collection of A. G. Humes.

Other specimens (all from *Sabellastarte magnifica*).—14 females and 3 males from 2 hosts, under intertidal dead coral at Antsakoabe, on the northern shore of Nosy Bé, November 1, 1963 (of this collection 7 females and 2 males placed in the Museum of Comparative Zoology); 5 females and 3 males from one host, under intertidal rock at Antsakoabe, September 7, 1964.

---

[1] The specific name *firmus* (from Latin = firm, strong, robust) refers to the strong sclerotization of the body wall and appendages in this species.

Female.—The body (Fig. 60) is moderately broadened with a flattened prosome. The length (without the setae on the caudal rami) is 0.81 mm (0.78–0.84 mm) and the greatest width is 0.36 mm (0.33–0.38 mm), based on 10 specimens. The ratio of length to width of the prosome is 1.46 : 1. The segment of leg 1 is rather indistinctly set off from the head, and its lateral areas are rounded posteriorly. The epimeral areas of the segment of leg 2 are truncated, those of the segment of leg 3 are broadly rounded, and those of the small segment of leg 4 are rather truncated.

The segment of leg 5 (Fig. 61) is rather narrow, 36 × 68 μ, and bears the small fifth legs slightly ventrally a little posterior to the midlateral areas. There is a narrow weakly sclerotized intersegmental sclerite ventrally between the segment of leg 5 and the genital segment. The genital segment is longer than wide, and (as seen in dorsal view) is expanded in its anterior part to form 2 broadly rounded wings but is narrowed posteriorly where its sides are parallel. The length of the segment is 110 μ, the width at the expanded part 100 μ, and the width in the narrow posterior portion 58 μ. The areas of attachment of the egg sacs are situated dorsolaterally on the posterior halves of the expansions. Each area (Fig. 62) bears 2 small naked setae 20 μ and 10 μ in length. There are 3 postgenital segments, without posterior rows of spinules, the first 46 × 48 μ, the second 41 × 43 μ, and the third 44 × 42 μ.

The caudal ramus (Fig. 63) is moderately elongated, 39 μ along its outer edge, 35 μ along its inner edge, and 43 μ in greatest length (including the subconical terminal expansion). Its width proximal to the lateral seta is 18 μ, and distal to that seta 15.5 μ. Taking the greatest dimensions, the ratio of length to width is 2.9 : 1. The outer lateral seta, situated 21 μ from the base of the ramus, is 33 μ long. The pedicellate dorsal seta is 33 μ, the outermost terminal seta 40 μ, and the innermost terminal seta 39 μ. The 2 long median terminal setae, inserted between unornamented dorsal and ventral flaps, are 180 μ (outer) and 325 μ (inner), and do not show the basal "pegs" often seen in lichomolgids. The surfaces of the ramus are without ornamentation except for a setule and a refractile point dorsally.

The dorsal surface of the prosome is ornamented with minute setules and refractile points, and in addition the posterior half of the cephalosome shows dorsally a broad band of extremely fine transverse striations (visible only under very high magnification and not shown in Fig. 60). In dorsal view there are 2 internal longitudinal sclerotized bars (Fig. 60) extending posteriorly from the rostral area to nearly the middle of the cephalosome. (The dorsal surface of the cephalosome in this region is smooth, there being no crest such as Sewell described in *N. cristatus.*) The dorsal and ventral surfaces of the urosome bear relatively few minute setules and refractile points. The ratio of the length of the prosome to that of the urosome is 1.6 : 1.

The body wall (and, as will be seen below, the appendages) is strongly sclerotized, in contrast to the 3 species whose descriptions follow.

The egg sacs are slender (Fig. 64) and reach well beyond the ends of the caudal rami. Each sac is about 418 × 99 μ, and contains numerous eggs about 47 μ in diameter.

The rostral area (Fig. 65) projects slightly in front of the head. Posterior to it, on the ventral surface of the head between the insertions of the second antennae, there is a slight longitudinal ridge.

The first antenna (Fig. 66) is 7-segmented. The lengths of the segments (measured along their posterior non-setiferous margins) are: 13 (35 μ along the anterior edge), 57, 22, 28, 25, 17, and 13 μ respectively. The entire first antenna (without the terminal setae) is about 185 μ long. The formula is: 4, 13, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete.

All the setae are naked. The third segment shows ventrally a sclerotization suggesting an intercalary segment.

The second antenna (Fig. 67) is 4-segmented and rather robust. The first and second segments bear a single small inner seta. The short third segment bears 3 setae, one much larger than the other two. The fourth segment bears 7 elements: 3 proximal slender setae, another more distal slender seta, a slender clawlike seta, and 2 stout recurved claws. All the setae are naked. The entire second antenna is about 108 μ in length.

The labrum (Fig. 65) bears anterolaterally a pair of naked setae, each 44 μ in length, directed ventrally and somewhat anteriorly, and rather indistinctly articulated with the surface of the labrum. Near the extreme anterior end of the labrum, between these 2 setae, there is a somewhat triangular raised sclerotized area (rather similar to that described by Sewell in *N. cristatus*). Posteriorly the labrum is bifurcated to form 2 rounded lobes without ornamentation.

The mandible (Fig. 68) has a moderately elongated blade, with a row of small spinules along the concave outer margin and a fringe of large hyaline spiniform elements along the convex inner margin (the proximal spinelike element in this row being slightly more sclerotized and prominent that the succeeding ones). There are 2 sclerotized spiniform elements on the dorsal surface of the blade. The paragnath (Fig. 69) is a small lobe with hairs along its medial side. The first maxilla (Fig. 70) is a small lobe bearing 4 elements: terminally 2 long unilaterally barbed spines and a minute naked setule, subterminally a shorter naked spine. The second maxilla (Fig. 71) is 2-segmented, the first segment bearing a prominent sclerotized conical projection on its outer margin. The second segment bears proximally 2 slender naked inner setae and a minute outer setule; the segment is prolonged to form a short process bearing a row of about 8 outer spines graduated in length and becoming smaller distally. The maxilliped (Fig. 72) is 3-segmented and slender. The first segment is unarmed. The second segment bears 2 small inner naked setae. The clawlike third segment is very long (110 μ) and slender; proximally on the inner side there is a small naked seta and a minute setule. The distal half of the segment is more slender and less sclerotized than proximally and bears a row of short hairs along each side.

The postoral area (Fig. 65) shows a pair of sclerotizations extending medially from the bases of the maxillipeds, but not joining each other. There is a slightly projecting cordiform area just posterior to the mouth region. The area between the maxillipeds and the first pair of legs projects only slightly.

Legs 1–4 (Figs. 73, 74, 75, and 76) have 3-segmented rami except for the endopod of leg 4 which is 2-segmented. The spine and setal formula is as follows (the Roman numerals indicating spines, the Arabic numerals setae):

P 1	protopod	0-1; 1-0	exp	1-0;	1-1;	III,I,4
			end	0-1;	0-1;	I,5
P 2	protopod	0-1; 1-0	exp	I-0;	I-1;	III,I,5
			end	0-1;	0-2;	I,II,3
P 3	protopod	0-1; 1-0	exp	I-0;	I-1;	II,I,5
			end	0-1;	0-2;	II,2
P 4	protopod	0-1; 1-0	exp	I-0;	I-1;	II,I,5
			end	0-1;	2	

The inner seta on the coxa of legs 1–3 is long and feathered, but in leg 4 this seta is shorter (20 μ) and naked. A row of hairs occurs on the inner margin of the basis in all 4 legs. The spines on the exopods are recurved posteriorly, with the lateral fringe along their proximal sides more prominent than that on their distal margins. The outer spines on the exopod of leg 1 show small subterminal flagella; the terminal spine on this ramus has a straight tip, while in legs 2–4 the tip is reflexed. The outer spine on the last segment of the endopod of leg 1 is 7 μ in length. The endopod of leg 4 is elongated (Fig. 76). The first segment is 18 × 11 μ, having a row of hairs on the outer margin and bearing a long feathered inner distal seta 68 μ in length. The second segment measures 39 × 8 μ, having a row of hairs on both outer and inner margins and bearing 2 unequal terminal naked setae, the outer one 31 μ, the inner one 50 μ in length. In addition, there is an anterior row of minute spinules on the end of the segment near the insertions of the 2 setae.

Leg 5 (Fig. 77) has a very small quadrate free segment, 6 × 6 μ, bearing 2 terminal naked setae, the anterior 1 slender and 28 μ long, the posterior 1 much stouter and 44 μ long. The seta arising from the body wall adjacent to the segment is naked and 26 μ long.

Leg 6 is probably represented by the 2 setae near the attachment of the egg sacs (see Fig. 62).

The color in life in transmitted light is slightly opaque, the eye red, the egg sacs gray.

Male.—The body (Fig. 78) is more slender than in the female. The length (excluding the setae on the caudal rami) is 0.58 mm (0.52–0.63 mm) and the greatest width is 0.16 mm (0.14–0.18 mm), based on 10 specimens (the allotype, 3 paratypes, 3 specimens collected at Antsakoabe on November 1, 1963, and 3 collected at the same locality on September 7, 1964). The ratio of length to width of the prosome is 1.8 : 1. The segment of leg 1 is more distinctly separated from the head than in the female.

The segment of leg 5 (Fig. 79), 37 × 29 μ, resembles that of the female. The ventral intersegmental sclerite between the segment of leg 5 and the genital segment is not evident. The genital segment is longer than wide, 97 × 75 μ, with its lateral borders in dorsal view only slightly rounded. The 4 postgenital segments are 24 × 37, 29 × 34, 23 × 31, and 25 × 30 μ from anterior to posterior.

The caudal ramus (Fig. 80) resembles that of the female, but is relatively shorter, the greatest dimensions being 27 × 13 μ, or 2 times longer than wide. The 2 long terminal setae show basal "pegs."

The surfaces of the prosome and urosome bear scattered hairs and refractile points. The fine transverse striations seen on the dorsal posterior half of the cephalosome in the female are absent here. The ratio of the length of the prosome to that of the urosome is 1.25 : 1.

The rostral area and first antenna resemble those of the female. The second antenna (Fig. 81) is a little more slender than in the female. The first and second segments bear a small seta as in the female, but, in addition, the second segment is ornamented on its inner surface with 2 rows of minute spinules. The third segment bears 4 setae, 3 of them slender, the other larger and placed more distally, very near the base of the fourth segment. The fourth segment bears 7 elements: 3 slender outer setae, 2 setae near the bases of the claws, and 2 recurved claws, 1 slender, the other stout. The labrum, mandible, paragnath, and first maxilla resemble those of the female. The second maxilla (Fig. 82) has on the outer margin of its first segment groups of small spinules and a small process which is perhaps homologous to the prominent conical projection seen in the female. The maxilliped (Fig. 83) is slender and 4-segmented (assuming that the fourth segment forms part of the claw). The first segment shows on its inner edge a small knob and a rather pointed sclerotized process. The second segment has 2 small inner naked setae and 2 inner rows of small spinules. The small third segment is unarmed. The recurved claw, 58 μ in length (measured along its axis), bears proximally a posteromedial, minutely barbed seta 20 μ long and on its inner edge a slender naked setule 6 μ long and a small process. The posteroinner surface of the claw is covered with minute blunt spinules. At the tip of the claw there is a conspicuous lamella.

The postoral area resembles that of the female.

Legs 1–4 in general resemble those of

the female, having the same spine and setal formula. The outer distal corners of the first 2 segments of the endopods in legs 1–3 bear small spinelike processes not present in the female. The outer spine on the last segment of the endopod of leg 1 (Fig. 84) is 11 μ in length, a little longer than in the female.

Leg 5 is like that of the female.

Leg 6 (Fig. 85) consists of a posterolateral flap on the ventral surface of the genital segment, bearing 2 naked setae 17 and 28 μ long.

In 2 females spermatophores (Fig. 86) were attached in pairs. In both cases the 2 elongated spermatophores (86 × 31 μ without the neck) were joined in a common tube which led into the genital segment.

The color in life in transmitted light resembles that of the female.

Comparison with Nasomolgus cristatus.—*Nasomolgus firmus* seems to be close to *N. cristatus*, but shows several differences. In *N. firmus* the caudal ramus is a little longer (with a ratio of length to width of 2.9 : 1 instead of about 2.5 : 1), the lateral seta on the ramus is inserted halfway along the margin instead of at about the junction of the middle and distal thirds as in Sewell's species, the formula for the last segment of the endopod of leg 3 is II,2 instead of I,II,2, the two setae on the end of the last segment of the endopod of leg 4 have a ratio of 1 : 1.6 instead of about 1 : 2.2 as in Sewell's fig. 35E, and the outline of the genital segment in dorsal view is slightly different.

In both *N. cristatus* and *N. firmus* the labrum bears anteriorly a pair of prominent ventrally directed setae, there is a somewhat triangular sclerotized raised area near the front of the labrum at the posterior end of the rostral area, the maxilliped is 3-segmented with the last segment very long and slender, and the arrangement of the spines on the last segment of the exopod of leg 1 is III,I instead of II,I as in Sewell's formula (p. 125). Since it has been impossible to dissect the single type specimen of *N. cristatus*, the mouthparts cannot be compared in detail.

Nasomolgus leptus[1] n. sp.
Figs. 87–109

Type material.—4 females and 4 males from 2 *Sabellastarte magnifica* (Shaw), under intertidal dead coral at Antsakoabe, on the northern shore of Nosy Bé, Madagascar. Collected November 1, 1963. Holotype female, allotype, and 4 paratypes (2 females and 2 males) deposited in the United States National Museum, Washington; the remaining paratypes (both dissected) in the collection of A. G. Humes. (This species was collected in company with *N. firmus*, from the same 2 polychaetes.)

Female.—The body (Fig. 87) is elongated and rather slender, with the prosome not broadened and not as flattened as in the previous species. The length (not including the setae on the caudal rami) is 1.40 mm (1.37–1.44 mm) and the greatest width is 0.35 mm (0.31–0.39 mm), based on 4 specimens. The ratio of length to width of the prosome is 1.8 : 1. The segment of leg 1 is distinctly separated from the head. The epimeral areas of the metasomal segments resemble fairly closely those in the previous species.

The segment of leg 5 (Fig. 88) is 60 × 94 μ, with the small fifth legs borne as in *N. firmus*. A weakly developed intersegmental sclerite occurs ventrally between the segment of leg 5 and the genital segment. The genital segment is longer than wide, in dorsal view being broadly expanded laterally in its anterior half and constricted in its posterior half. The length of the segment is 174 μ, the width at the expansions 140 μ, and the width in the posterior part of the constricted area 73 μ (at this level the segment being slightly wider than more anteriorly). The areas of attachment of the egg sacs are placed

---

[1] The specific name *leptus* (from λεπτός = thin, slender) refers to the elongated slender form of the body in this species.

dorsolaterally on the posterior halves of the expansions. Each area (Fig. 89) carries 2 naked setae, 11 and 24 μ in length. The 3 postgenital segments, without posterior rows of spinules, are 96 × 60, 82 × 52, and 96 × 55 μ (the last segment being slightly expanded laterally in its posterior half where the width was measured).

The caudal ramus (Fig. 90) is very elongated and slender, 278 μ in length, 25 μ wide in its basal part and 19 μ wide at the level of the outer lateral seta. Taking the latter width, the ratio of length to width is 14.6 : 1. The outer lateral seta, located 177 μ from the base of the ramus, is 36 μ long. The pedicellate dorsal seta is 26 μ, the outermost terminal seta 40 μ, the innermost terminal seta 36 μ, and the 2 long median terminal setae are 143 μ (outer) and 260 μ (inner) and show weak basal "pegs." All the setae are naked. A minute setule 3 μ long occurs on the outer proximal margin of the ramus. The ramus is ornamented with a few minute hairs.

The dorsal surface of the prosome bears very few hairs and no refractile points. The dorsal and ventral surfaces of the urosome are very sparsely ornamented with hairs and refractile points. The urosome is longer than the prosome, the ratio being 1.2 : 1.

The egg sacs (Fig. 87) are elongated and slightly arcuate, reaching beyond the tips of the long caudal rami. Each sac is about 759 × 198 μ, and contains many eggs approximately 57 μ in diameter.

The rostral area (Fig. 91) does not project forward as in the previous species. Between the rostrum and the labrum there is a low longitudinal ridge (between the bases of the second antennae).

The first antenna (Fig. 92) is 7-segmented, the lengths of the segments (measured along their posterior non-setiferous margins) being: 18 (44 μ along the anterior margin), 94, 35, 45, 31, 18, and 14 μ respectively. The formula for the setae and aesthetes is the same as in *N. firmus*. All the setae are naked.

The second antenna (Fig. 93) is 4-segmented and fairly robust. Each of the first 2 segments bears a short distal inner seta with lamellate margins. The third segment bears 2 such setae plus a longer seta. The fourth segment carries 7 elements (including 2 stout recurved claws) much like those of *N. firmus*.

The labrum (Figs. 91 and 94) bears anterolaterally, as in the previous species, a pair of ventrally directed naked setae, each 55 μ in length. There is no triangular sclerotized area in front of the labrum, such as seen in *N. firmus*. Posteriorly, the edge of the labrum is deeply bilobed, with each lobe elongated, rounded, and unornamented, and with a short median process between the bases of the lobes.

The mandible (Fig. 95), paragnath, and first maxilla (Fig. 96) resemble those of *N. firmus*. The second maxilla (Fig. 97) is 2-segmented. The first segment has a broad sclerotized bulge on its outer margin and an interrupted crescentic row of spinules on its posterodorsal surface. The second segment is similar to that in the previous species, but the spines on the distal prolongation are more numerous and slender. The maxilliped is very similar to that of *N. firmus*, having the same general form and armature and with the slender clawlike segment 122 μ long.

The postoral area (Fig. 98) resembles generally that in the previous species and shows a weak line between the bases of the maxillipeds. The ventral surface between the bases of the maxillipeds and the first pair of legs is slightly protuberant.

Legs 1–4 (Figs. 99, 100, 101, and 102) resemble those of *N. firmus*, with the same spine and setal formula except for the endopod of leg 3 where the formula is 0-1; 0-2; I,II,2, the outer marginal spine on the last segment being retained. The terminal spine on the last segment of the exopods of all 4 legs is not reflexed at the tip. The outer spine on the last segment of the endopod of leg 1 is 14 μ in length. The endopod of leg 4 is elongated (Fig. 102). The first segment is 33 × 19 μ and bears a short feathered inner distal seta 22 μ long. The second segment is 74 × 13 μ and bears 2 terminal slightly barbed setae 44 μ (outer) and 77 μ (inner) in length. The ornamentation of the endopod resembles that of *N. firmus*. The inner coxal seta of leg 4 is short (13 μ) and naked.

Leg 5 (Fig. 103) resembles that in the previous species, with the small free segment 7 μ in anterior length, 6 μ in posterior length, and 8 μ in width at the middle.

Leg 6 is probably represented by the 2 setae near the attachment of the egg sacs (see Fig. 89).

The color in life in transmitted light is moderately translucid, the eye red, the egg sacs gray.

Male.—The body (Fig. 104) is more slender than that of the female. The length (excluding the setae on the caudal rami) is 0.94 mm (0.93–0.96 mm) and the greatest width is 0.19 mm (0.18–0.19 mm), based on 4 specimens. The ratio of length to width of the prosome is 2.1 : 1. The segment of leg 1 is less distinctly set off from the head than in the female.

The segment of leg 5, 40 × 58 μ, resembles that of the female. Ventrally between the segment of leg 5 and the genital segment there is no evident intersegmental sclerite. The genital segment (Fig. 105) is elongated, 151 × 50 μ, with its sides in dorsal view slightly rounded. The 4 postgenital segments are 57 × 46, 61 × 40, 47 × 34, and 57 × 33 μ from anterior to posterior.

The caudal ramus (see Fig. 105) is elongated, 135 × 16 μ, about 8.4 times longer than wide. It is a little less tapered distally than in the female, but bears similar armature.

The dorsal surface of the prosome seems to lack ornamentation. The dorsal and ventral surfaces of the urosome are unornamented except for a pair of hairs on the dorsal surface of the anal segment. As in the female, the urosome is longer than the prosome, the ratio being 1.3 : 1.

The rostral area and first antenna resemble those of the female. The second antenna (Fig. 106) is more slender than in the female. The arrangement of the spines and setae is the same as in the male of *N. firmus*, with 4 elements on the third segment instead of 3 as in the female. The 2 terminal claws are distinctly jointed. The slender clawlike seta on the last segment has a more blunt tip than in the female. The fine ornamentation, not present in the female, consists of a small patch of spinules on the inner proximal surface of the first segment and a long patch of small spinules on the inner surface of the second segment.

The labrum, mandible, paragnath, and first maxilla resemble those of the female. The second maxilla is also similar to that in the opposite sex, but the outer bulge on the first segment is much less prominent. The maxilliped (Fig. 107) resembles in general form that of *N. firmus*. The second segment has on its inner surface 2 small naked setae and 2 rows of spinules. The recurved claw, 68 μ in length (measured along its axis), shows a slight indication of division. Proximally the claw bears a posteromedial barbed seta 19 μ long and an adjacent inner naked setule 6 μ long. The concave surface of the claw bears a row of small spinules, instead of being covered with minute blunt spinules as in *N. firmus*.

The postoral area is similar to that in the previous species.

Legs 1–4 are like those of the female, with the same spine and setal formula. The outer distal spine on the last segment of the endopod of leg 1 is 16.5 μ in length, being slightly longer than in the female.

Leg 5 resembles that of the female.

Leg 6 (Fig. 108) consists of a posterolateral flap on the ventral surface of the genital segment, bearing 2 slender naked setae 26 and 31 μ in length.

The spermatophore (Fig. 109), seen only inside the body of a male, is elongated, 113 × 49 μ, not including the neck.

The color in life resembles that of the female.

Comparison with other species.—*Nasomolgus leptus* may readily be distinguished from *N. firmus* and *N. cristatus* by its greater length, by its more slender body form, and by the much more elongated caudal rami. It differs further from *N. firmus* in the nature of the protuberance on the first segment of the second maxilla in the female and in the ornamentation of the claw on the maxilliped in the male.

Nasomolgus rudis[1] n. sp.

Figs. 110–135

Type material.—10 females and 5 males from one *Sabellastarte magnifica* (Shaw), in 2 m, at Ambariotelo, a small island between Nosy Bé and Nosy Komba, Madagascar. Collected May 15, 1964. Holotype female, allotype, and 10 paratypes (8 females and 2 males) deposited in the United States National Museum, Washington; the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimens (all from *Sabellastarte magnifica*, but one host identification uncertain as indicated below).—10 females and 2 males from 2 hosts, under intertidal dead coral, Antsakoabe, on the northern shore of Nosy Bé, November 1, 1963; 11 females from 1 host (only the plume collected, but probably *S. magnifica*), in 14 m, Tany Kely, a small island south of Nosy Bé, December 23, 1963; 9 females and 1 male from 1 host, under intertidal rock, Antsakoabe, September 7, 1964 (these specimens placed in the Museum of Comparative Zoology); and 4 females from 1 host in 1 m, Ambariobe, near Ambariotelo, October 10, 1960.

Female.—The body (Fig. 110) is broadened in the prosomal region. The length (excluding the setae on the caudal rami) is 0.87 mm (0.77–0.97 mm) and the greatest width is 0.41 mm (0.36–0.46 mm), based on 10 specimens. The ratio of the length to the width of the prosome is 1.45 : 1. The segment of leg 1 is clearly set off from the head. The epimeral areas of the pedigerous segments are shaped much as in *N. leptus*.

The segment of leg 5 (Fig. 111) is 55 × 78 μ, with the fifth legs borne as in the 2 previous species. There is a small intersegmental sclerite ventrally between the segment of leg 5 and the genital segment. The genital segment is a little wider than long and in dorsal view is broadly expanded in its anterior two-thirds and constricted in its posterior third. The length of the segment is 99 μ, the width at the expansions 112 μ, and the width in the posterior part of the constricted area 58 μ. The areas of attachment of the egg sacs are situated dorsolaterally on the posterior halves of the expansions. Each area (Fig. 112) bears 2 naked setae 31 and 11 μ in length, a short inner spinous process, and an outer membranous expansion. The 3 postgenital segments, without posterior rows of spinules, are 32 × 52, 24 × 45, and 33 × 43 μ from anterior to posterior.

The caudal ramus (Fig. 113) is short, 25 μ along its inner margin, 27 μ along its outer margin, and 18 μ wide at the level of the outer lateral seta. The ratio of length to width is 1.44 : 1. The outer lateral seta, located 14 μ from the base of the ramus, is 56 μ long. The pedicellate dorsal seta is 33 μ, the outermost terminal seta 54 μ, the innermost terminal seta 72 μ, and the 2 long median terminal setae are 265 μ (outer) and 407 μ (inner) and are basally "pegged." All the setae are naked. Two minute hairs occur on the dorsal surface of the ramus.

The dorsal surface of the prosome is almost devoid of ornamentation, there being only a few hairs on the metasomal segments. The dorsal and ventral surfaces of the urosome have scattered hairs and refractile points. The prosome is much longer than the urosome, the ratio being 2.53 : 1.

The egg sacs are elongated, extending to the ends of the ramal setae. Each sac (Fig.

---

[1] The specific name *rudis* (from Latin = unaffected, simple) refers to the relatively uncomplicated external anatomy of this species.

114) is about 462 × 132 μ, with numerous eggs 44–47 μ in diameter.

The rostral area (Fig. 115) resembles generally that of *N. leptus*, and there is a low ridge between the bases of the second antennae as in that species.

The first antenna (Fig. 116) is much like that in *N. leptus*, with the same arrangement of setae and aesthetes. The lengths of the segments (measured along their posterior non-setiferous margins) are: 13 (38 μ along the anterior margin), 68, 26, 34, 27, 17, and 15 μ respectively. All the setae are naked.

The second antenna (Fig. 117) also resembles that of *N. leptus*, but the seta on the first segment is hyaline and lacks the lamellate margins.

The labrum (Figs. 115 and 118) resembles in general form that of the 2 previous species. Each of the 2 anterolateral and ventrally directed setae is 36 μ long and naked. The 2 posterior lobes are unornamented. There is no triangular sclerotized area near the front of the labrum, such as seen in *N. firmus*.

The mandible (Fig. 119), paragnath, and first maxilla (Fig. 120) are similar to those in the 2 previous species. The second maxilla (Fig. 121) resembles in general form that of *N. leptus*. There is a lightly sclerotized bulge on the outer margin of the first segment. Of the several spines on the distal end of the second segment the first spine is somewhat larger than the succeeding ones. The maxilliped (Fig. 122) resembles that in the 2 previous species, the slender terminal segment being 113 μ long.

The postoral area (Fig. 123) resembles that of *N. leptus*.

Legs 1–4 (Figs. 124, 125, 126, and 127) have the same spine and setal formula as in *N. leptus*, and closely resemble that species in their fine ornamentation. The outer spine on the last segment of the endopod of leg 1 is 10 μ long. The 3 spines on the last segment of the endopod of leg 2 are 12, 9, and 9 μ in length from distal to proximal; those on leg 3 are 16, 10, and 11 μ respectively. The inner coxal seta of leg 4 is 15 μ long and naked. The endopod of leg 4 is less elongated (Fig. 127) than in either of the 2 previous species. The first segment is 28 × 14 μ and bears a short feathered inner distal seta 29 μ long. The second segment is 47 × 12 μ and bears 2 terminal slightly barbed setae 32 μ (outer) and 66 μ (inner) in length. The fine ornamentation of the endopod is similar to that in the 2 previous species.

Leg 5 (Fig. 128) resembles that of *N. leptus*, with the segment having similar dimensions.

Leg 6 is probably represented by the 2 setae near the attachment of the egg sacs (see Fig. 112).

The color in life in transmitted light resembles that in the 2 previous species.

Male.—The body (Fig. 129) is much more slender than in the female. The length (excluding the setae on the caudal rami) is 0.52 mm (0.50–0.54 mm) and the greatest width is 0.15 mm (0.14–0.16 mm), based on 8 specimens (the allotype, 4 paratypes, 2 specimens collected at Antsakoabe on November 1, 1963, and one specimen collected at the same locality on September 7, 1964). The ratio of the length to the width of the prosome is 2.2 : 1. The separation between the segment of leg 1 and the head is rather weak.

The segment of leg 4, 28 × 44 μ, resembles that of the female. The ventral intersegmental sclerite between the segment of leg 5 and the genital segment is absent. The genital segment (Fig. 130) is elongated, 90 × 73 μ, with its sides in dorsal view nearly parallel. The 4 postgenital segments are 22 × 35, 22 × 33, 16 × 31, and 19 × 30 μ from anterior to posterior.

The caudal ramus (see Fig. 130) is relatively shorter than in the female. The length along the outer edge is 19 μ, along the inner edge 18 μ, and its width is 14 μ, or about 1.3 times longer than wide.

The dorsal surface of the prosome is unornamented. The dorsal and ventral surfaces of the urosome bear a few hairs and refractile points. As in the female, the prosome is longer than the urosome, the ratio being 1.54 : 1.

The rostral area resembles that of the female. The ridge seen between the bases of the second antennae in the female appears to be absent.

The first antenna is like that of the female. The second antenna (Fig. 131) has the same arrangement of spines, setae, and claws as in the preceding 2 species, with 4 elements on the third segment instead of 3 as in the female. The seta on the first segment has lamellate margins. The 2 large claws are distinctly jointed. The fine ornamentation is like that in *N. leptus.*

The labrum resembles that of the female, but the 2 large setae are situated more posteriorly. The mandible, paragnath, and first maxilla resemble those in the female. The second maxilla (Fig. 132) lacks the bulge on the outer margin of the first segment, but instead bears groups of small spinules; the spines along the distal end of the second segment are more numerous than in the opposite sex. The maxilliped (Fig. 133) resembles generally that of *N. leptus*, the recurved claw being 50 μ in length (measured along its axis).

The postoral area is like that of the female.

Legs 1–4 have the same spine and setal formula as in the female. The spines on the rami are somewhat longer and often straighter. The outer spine on the last segment of the endopod of leg 1 is 19 μ long. The 3 spines on the last segment of the endopod of leg 2 are 18, 13, and 9 μ long from distal to proximal; those on the last segment of the endopod of leg 3 are 21, 11, and 10 μ respectively. The second segment of the endopod of leg 4 is relatively a little shorter than in the female, being 31 × 10 μ.

Leg 5 resembles that of the female.

Leg 6 (Fig. 134) consists of a posterolateral flap on the ventral surface of the genital segment, bearing 2 slender naked setae both 22 μ long.

The spermatophore (Fig. 135), attached to the female, is elongated, 74 × 32 μ, not including the neck. Spermatophores may be attached singly or in pairs with a common stalk as seen in *N. firmus.*

The color in life resembles that of the female.

Comparison with other species.—*Nasomolgus rudis* may be separated from *N. cristatus*, *N. firmus*, and *N. leptus* by the length of the caudal rami. In addition, it may be distinguished from *N. firmus* in that its body wall is less strongly sclerotized, certain setae on the second antenna have lamellate margins, the first segment of the second maxilla in the female has a broad bulge rather than a prominent conical projection, the formula for the last segment of the endopod in leg 3 is I,II,2 rather than II,2, the inner distal seta on the first segment of the endopod in leg 4 is much shorter, and the ornamentation of the claw of the maxilliped of the male is less extensive. From *N. leptus* it may also be distinguished by the shorter second segment in the endopod of leg 4.

Nasomolgus parvulus[1] n. sp.

Figs. 136–142

Type material.—14 females from one *Sabellastarte magnifica* (Shaw), in 2 m, at Ambariotelo, a small island between Nosy Bé and Nosy Komba, Madagascar. Collected May 15, 1964. Holotype and 12 paratypic females deposited in the United States National Museum, Washington; the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimens (all from *Sabellastarte magnifica*).—2 females from 2 hosts, under intertidal dead coral, Antsakoabe, on the northern shore of Nosy Bé, November 1, 1963 (these specimens placed in the Museum of Comparative Zoology); 2 females from 1 host, under intertidal rock, Ant-

---

[1] The specific name *parvulus* (from Latin = very small) alludes to the small size of this species.

sakoabe, September 7, 1964; and 1 female from 1 host, in 1 m, Ambariobe, near Ambariotelo, October 10, 1960.

Female.—The body (Fig. 136) has a broad prosome. The length (not counting the setae on the caudal rami) is 0.57 mm (0.49–0.54 mm) and the greatest width is 0.23 mm (0.20–0.26 mm), based on 10 specimens. The ratio of the length to the width of the prosome is 1.35 : 1. The segment of leg 1 is separated from the head by a dorsal furrow. The epimeral areas of the pedigerous segments resemble those of *N. leptus* and *N. rudis.*

The segment of leg 5 is similar to that in *N. rudis.* Between this segment and the genital segment there is a small ventral intersegmental sclerite. The genital segment (Fig. 137) is a little wider than long and in dorsal view is broadly expanded in its anterior three-fourths and constricted in its posterior fourth. The length of the segment is 72 μ, the width in the expanded portion 83 μ, and the width in the constricted part 52 μ. The dorsolateral areas of attachment of the egg sacs are located a little more anteriorly than in *N. rudis.* Each area (Fig. 138) bears 2 naked setae 29 and 10 μ in length. The 3 postgenital segments, without posterior rows of spinules, are 25 × 41, 19 × 33, and 24 × 31 μ from anterior to posterior.

The caudal ramus (Fig. 139) is almost quadrate, 16 × 14 μ, the ratio of length to width being 1.14 : 1. The outer lateral seta is 35 μ long, the pedicellate dorsal seta 24 μ, the outermost terminal seta 40 μ, the innermost terminal seta 44 μ, and the 2 long median terminal setae are 133 μ (outer) and 237 μ (inner) and are basally "pegged." All the setae are naked. A minute hair is borne on the dorsal surface of the ramus.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear a few hairs. The prosome is longer than the urosome, the ratio being 2.0 : 1.

The egg sacs (see Fig. 136) are moderately elongated, 280 × 128 μ, and contain fewer eggs than in *N. leptus* or *N. rudis,* each egg being 44–50 μ in diameter.

The rostral area, first antenna, second antenna, labrum, mandible, paragnath, and first maxilla resemble those of *N. rudis.* The second maxilla (Fig. 140) lacks the bulge on the first segment seen in *N. rudis,* and the first spine in the row on the distal part of the second segment is less enlarged than in that species. The maxilliped and postoral area resemble those of *N. rudis.*

Legs 1–4 have the same spine and setal formula as in *N. leptus* and *N. rudis.* The outer distal corner of the first segment of the endopod of legs 1 and 2 lacks a spinous process. In leg 3 such a process is absent on both first and second segments of the endopod. The endopod of leg 4 (Fig. 141) resembles in general form that of *N. rudis.* The first segment is 17 × 9 μ and bears a short feathered inner distal seta 11 μ long. The second segment is 31 × 7 μ and carries 2 terminal slightly barbed setae 37 μ (outer) and 10 μ (inner) in length. The relationship between the lengths of these 2 terminal setae is about 4 : 1 rather than about 2 : 1 as in *N. rudis.* The fine ornamentation of the endopod is similar to that in the 3 previous species.

Leg 5 resembles that of *N. rudis.*

Leg 6 is represented by the 2 setae near the attachment of the egg sacs.

The spermatophore (Fig. 142), attached to the female in pairs, is 77 × 31 μ, not including the neck.

The color in life in transmitted light resembles that of the 3 previous species.

Male.—Unknown.

Comparison with other species.—Nasomolgus parvulus may be distinguished from all other species in the genus on the basis of its small size, its almost square caudal ramus, and the two very unequal terminal setae on the second segment of the endopod of leg 4. In addition, it differs from *N. firmus* in having a much more weakly sclerotized body wall, in the relative lengths of the prosome and urosome, in its stouter egg sac, in the absence of a prominent conical projection on the first segment of the second maxilla, and in the armature of the last segment of the endopod of leg 3. From *N. leptus* it is very easily distinguished by its much less elongated body, in having a shorter egg sac with fewer eggs, and in lacking the sclerotized bulge on the first segment of the second maxilla. It differs furthermore from *N. rudis* in the proportional lengths of the prosome and urosome, in its shorter egg sac with fewer eggs, and in the absence of an outer bulge on the first segment of the second maxilla.

REMARKS ON THE GENUS *NASOMOLGUS*

With the finding of these four new species of *Nasomolgus* living on a sabellid polychaete, it seems probable that members of this genus customarily live in association with annelids. One may conjecture that Sewell's specimen of *N. cristatus*, found in dredged debris, may have been dislodged from a polychaete host, but this is impossible to establish.

More than one species of *Nasomolgus* may live on a single polychaete. In two instances (collections at Ambariotelo, May 15, 1964, and at Antsakoabe, September 7, 1964) *N. firmus*, *N. leptus*, and *N. parvulus* occurred on a single *Sabellastarte magnifica*. In one case (collection at Antsakoabe, November 1, 1963) all four species of *Nasomolgus* were recovered from two hosts.

The exact region of the body where the copepods live is not known. It is possible that each species of copepod occupies a region separate from the others, but such a supposition can only be substantiated by careful observation of undisturbed living hosts.

Since the type species, *N. cristatus*, is now known to possess in common with the four new species from Madagascar certain fundamental characters (i.e., the pair of setae on the anterior part of the labrum, the 3-segmented maxilliped with a long slender last segment, and the number of spines [III,I] on the last segment of the exopod of leg 1) which were inadequately mentioned in Sewell's original description, a revision of the diagnosis of the genus *Nasomolgus* would be desirable. However, in view of the fact that we have been unable to make a firsthand study of the single specimen of *N. cristatus*, we are not attempting such a revision at present. There are certain features (especially the structure of the mouthparts) that would be necessary to clarify before undertaking a definitive revision. For the moment, the characteristics given by Sewell, together with the additions and corrections just mentioned, will serve to characterize the genus.

REFERENCES CITED

BOCQUET, C., AND J. H. STOCK. 1957. Copépodes parasites d'invertébrés des côtes de France. IVa. Le double parasitisme de *Sipunculus nudus* L. par *Myzomolgus stupendus* nov. gen., nov. sp., et *Catinia plana* nov. gen., nov. sp., copépodes cyclopoïdes très remarquables. Koninkl. Nederl. Akad. Wetensch. Amsterdam, Proc., Ser. C, **60**(3): 410–431.

BRADY, G. S. 1880. A monograph of the free and semi-parasitic Copepoda of the British Islands. Ray Society, London, **3**: 1–83.

CANU, E. 1892. Les Copépodes du Boulonnais, morphologie, embryologie, taxonomie. Trav. Lab. Zool. Mar. Wimereux-Ambleteuse (Pas-de-Calais), **6**: 1–354.

CLAUS, C. 1889. Über neue oder wenig bekannte halbparasitische Copepoden, insbesondere der Lichomolgiden- und Ascomyzontiden-Gruppe. Arb. Zool. Inst. Univ. Wien, **8**(3): 327–370.

GALLIEN, L. 1935. *Pseudanthessius nemertophilus* nov. sp., copépode commensal de *Lineus longissimus* Sowerby. Bull. Soc. Zool. France, **60**: 451–459.

GOODING, R. U. 1963 (unpublished). External morphology and classification of marine poecilostome copepods belonging to the families Clausidiidae, Clausiidae, Nereicolidae, Eunicicolidae, Synaptiphilidae, Catiniidae, Anomopsyllidae, and Echiurophilidae. Ph.D. Thesis, University of Washington, Seattle.

GURNEY, R. 1927. Zoological results of the Cambridge expedition to the Suez Canal, 1924. XXXIII. Report on the Crustacea:

Copepoda (littoral and semi-parasitic). Trans. Zool. Soc. London, **22**(4): 451–477.

Humes, A. G. 1966. *Pseudanthessius procurrens* n. sp., a cyclopoid copepod associated with a cidarid echinoid in Madagascar. Breviora, Mus. Comp. Zool., No. 246: 1–14.

Humes, A. G., and R. F. Cressey. 1961. Deux nouvelles espèces de *Pseudanthessius* (Copepoda, Cyclopoida) parasites des oursins à Madagascar. Mém. Inst. Sci. Madagascar, Sér. F, 1959, **3**: 67–82.

Illg, P. 1950. A new copepod, *Pseudanthessius latus* (Cyclopoida: Lichomolgidae) commensal with a marine flatworm. Jour. Washington Acad. Sci., **40**(4): 129–133.

Lindberg, K. 1945. Un nouveau copépode poecilostome de l'Inde de la famille des Lichomolgidae; *Pseudanthessius spinifer*, n. sp. Bull. Soc. Zool. France, **70**: 81–84.

Nicholls, A. G. 1944. Littoral Copepoda from South Australia (II). Calanoida, Cyclopoida, Notodelphyoida, Monstrilloida and Caligoida. Rec. So. Austral. Mus., **8**(1): 1–62.

Sars, G. O. 1917. An account of the Crustacea of Norway with short descriptions and figures of all the species. Vol. 6, Copepoda, Cyclopoida, pts. 11 and 12, Clausidiidae, Lichomolgidae (part), pp. 141–172. Bergen Museum, Bergen.

———. 1918. An account of the Crustacea of Norway with short descriptions and figures of all the species. Vol. 6, Copepoda, Cyclopoida, pts. 13 and 14, Lichomolgidae (concluded), Oncaeidae, Corycaeidae, Ergasilidae, Clausiidae, Eunicicolidae, Supplement, pp. 173–225. Bergen Museum, Bergen.

Scott, A. 1909. The Copepoda of the Siboga Expedition. Part I. Free-swimming, littoral and semi-parasitic Copepoda. Siboga Exped., **29**a: 1–323.

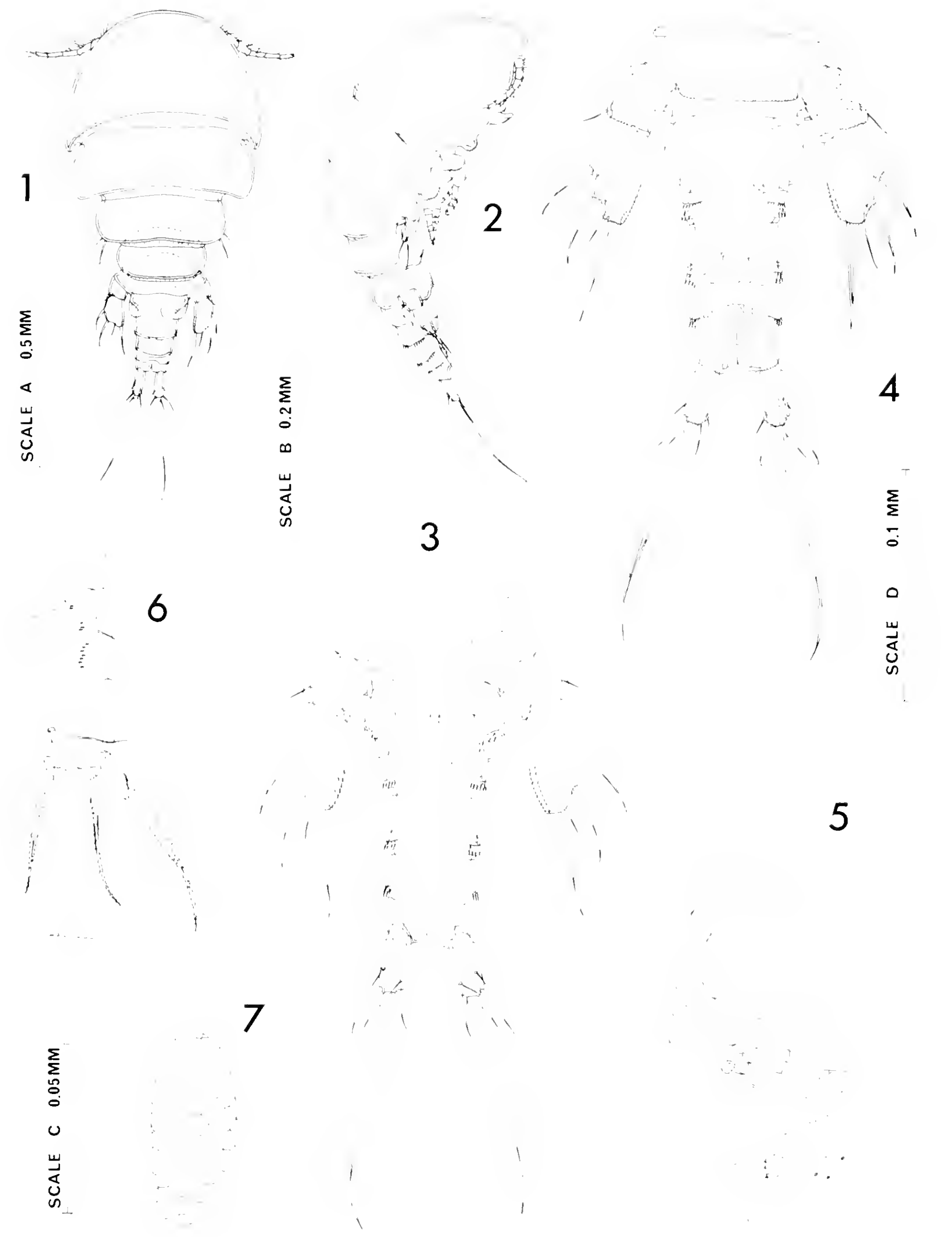
Sewell, R. B. S. 1949. The littoral and semiparasitic Cyclopoida, the Monstrilloida and Notodelphyoida. John Murray Exped. 1933–34, Sci. Repts., **9**(2): 17–199.

Stock, J. H., A. G. Humes, and R. U. Gooding. 1963. Copepoda associated with West Indian invertebrates IV. The genera *Octopicola, Pseudanthessius* and *Meomicola* (Cyclopoida, Lichomolgidae). Studies Fauna Curaçao and other Caribbean Is., **18**(77): 1–74.

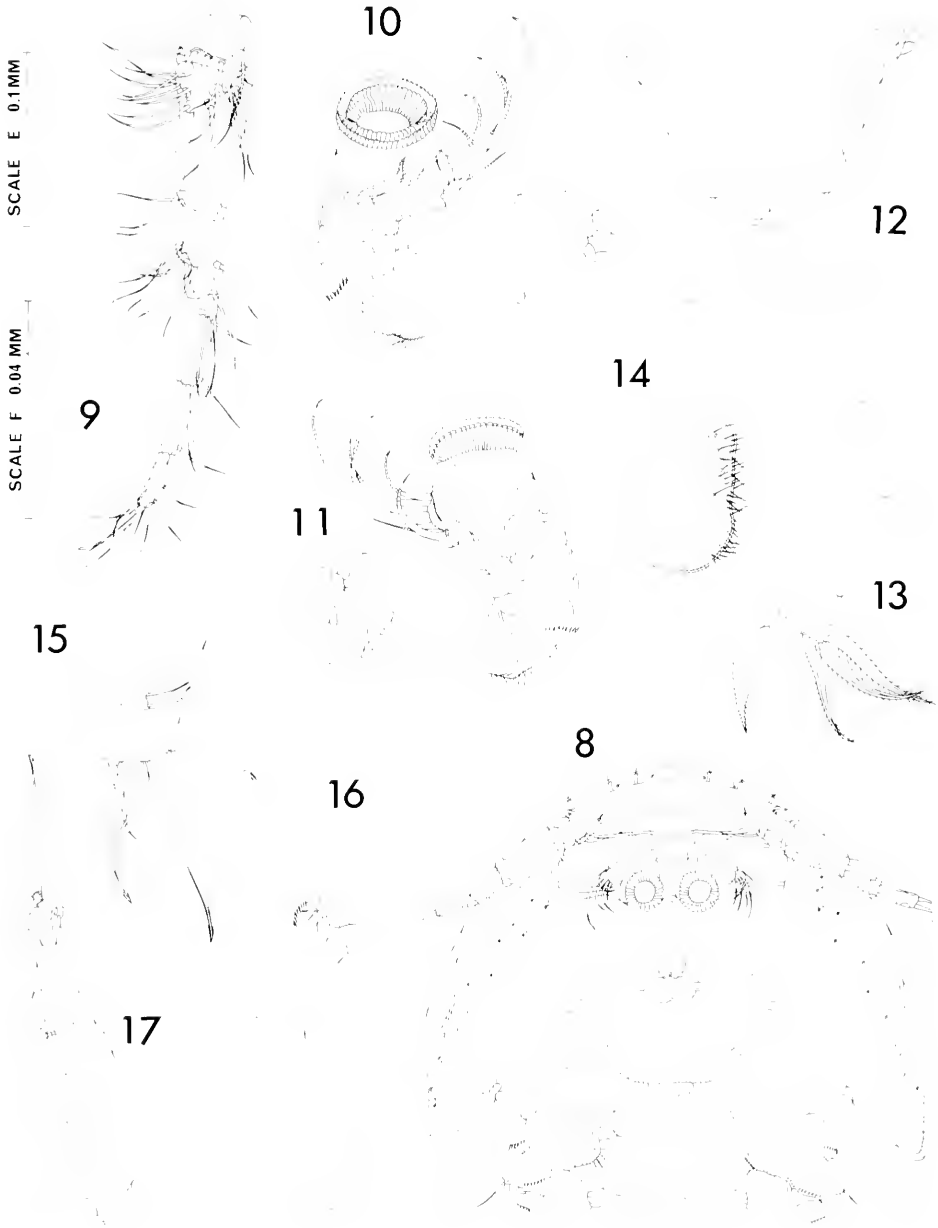
Thompson, I. C., and A. Scott. 1903. Report on the Copepoda collected by Professor Herdman, at Ceylon, in 1902. Rept. Govt. Ceylon Pearl Oyster Fish. Gulf of Manaar, pt. 1, Suppl. Rept. No. 7: 227–307.

Wilson, M. S., and P. L. Illg. 1955. The family Clausiidae (Copepoda, Cyclopoida). Proc. Biol. Soc. Washington, **68**: 129–142.

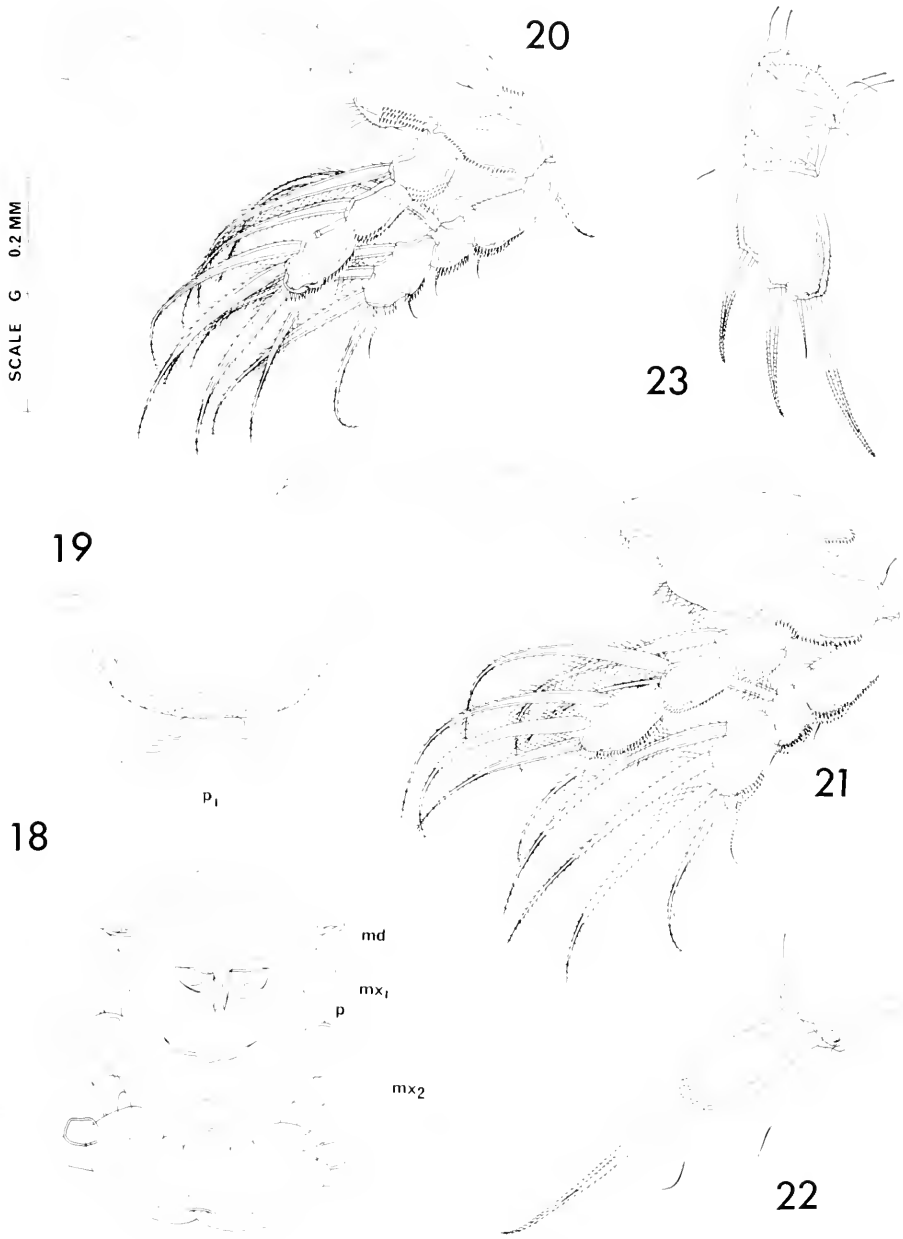
(Received December 10, 1965)



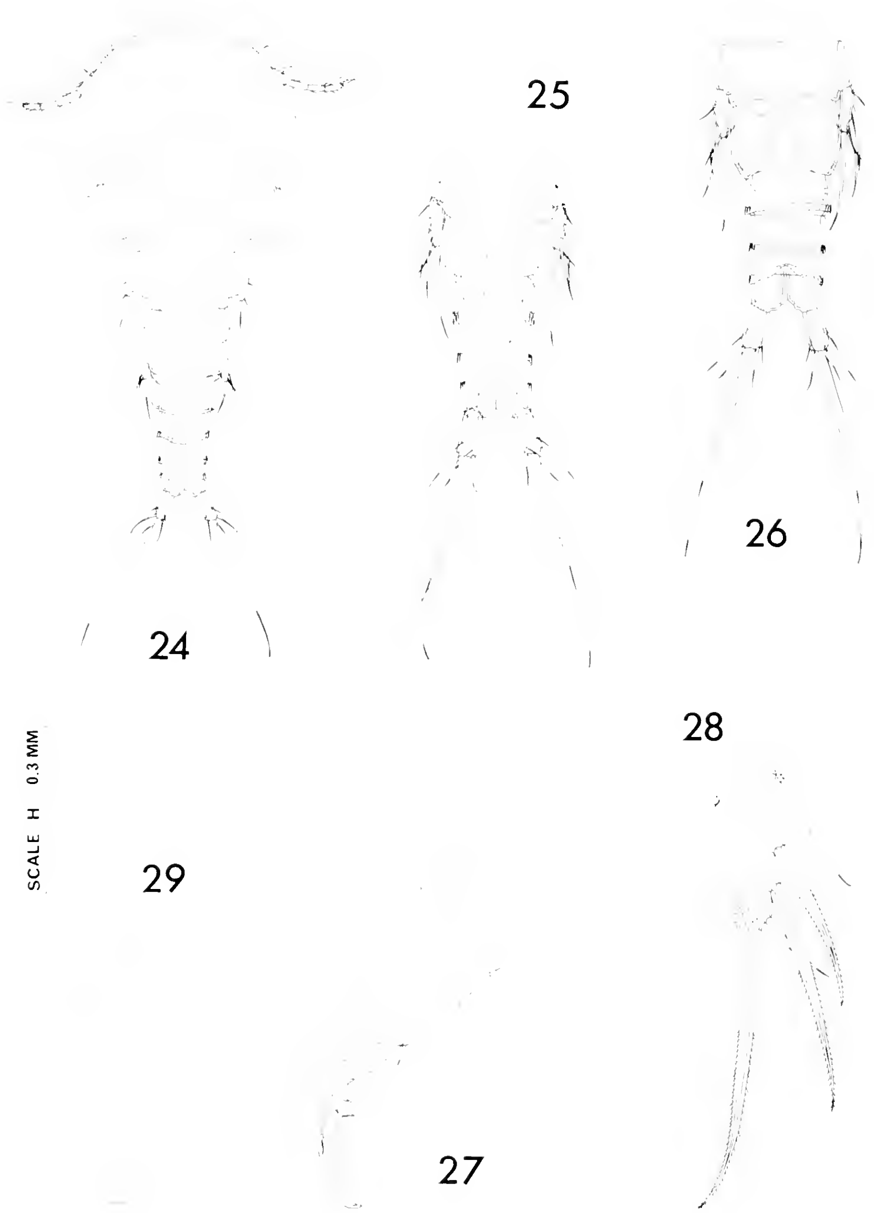
Figures 1–7. *Cotylamolgus lepidanoti* n. gen., n. sp., female. 1, dorsal (A); 2, lateral (A); 3, urosome, dorsal (B); 4, urosome, ventral (B); 5, area of attachment of egg sac, dorsal (C); 6, caudal ramus, dorsal (D); 7, egg sac, dorsal (A).



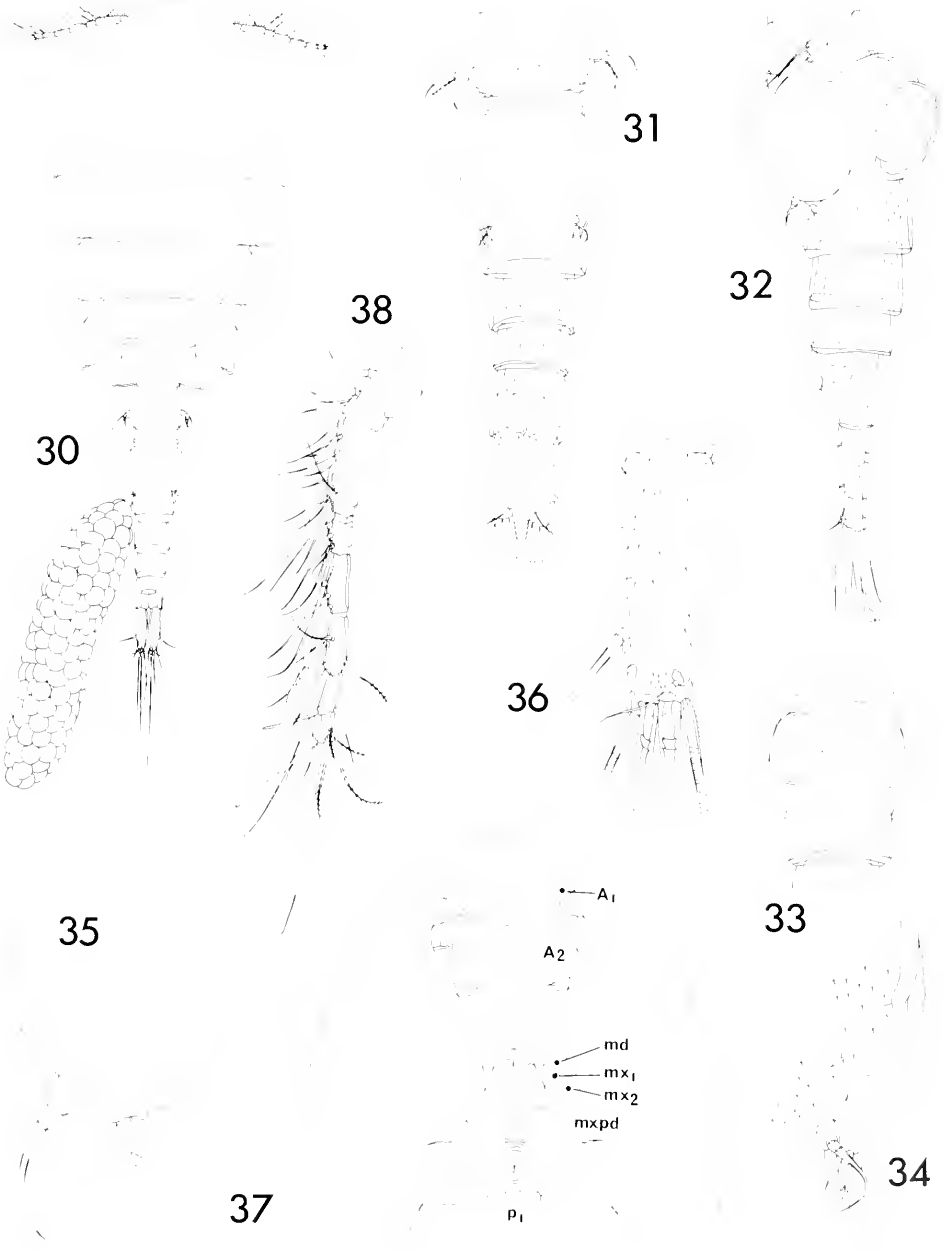
Figures 8–17. *Cotylomolgus lepidonoti* n. gen., n. sp., female (continued). 8, cephalosome, ventral (B); 9, first antenna, ventral (E); 10, second antenna, anterior (E); 11, second antenna, posterior (E); 12, labrum, anterior (C); 13, mandible, lateral (F); 14, paragnath, ventral (F); 15, first maxilla, anterior (F); 16, second maxilla, posterior (E); 17, second maxilla, ventral (E).



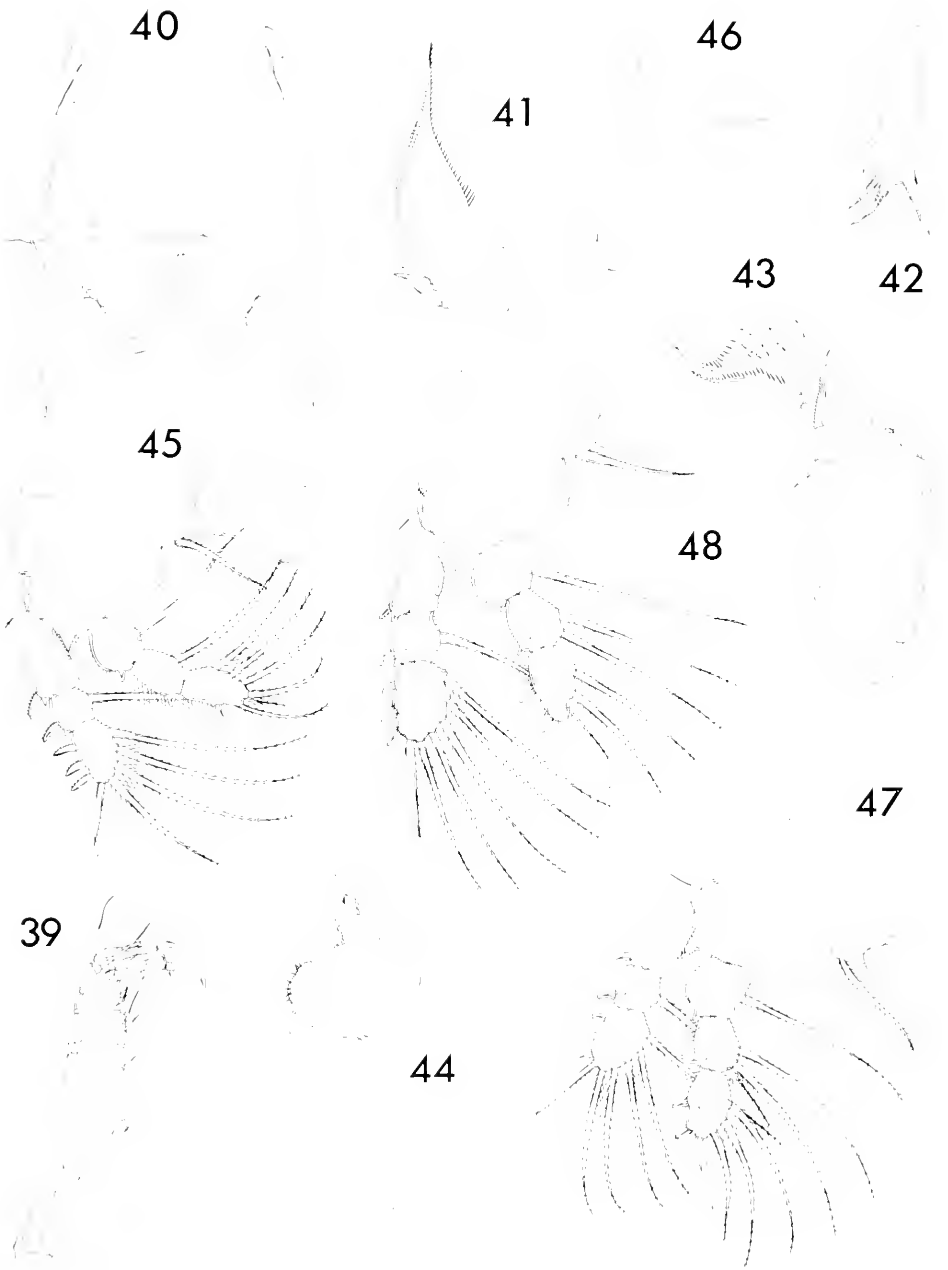
Figures 18–23. *Catylamolgus lepidonati* n. gen., n. sp., female (continued). 18, oral area posterior to labrum, ventral (C); 19, postoral protuberance between maxillipeds and leg 1, ventral (G); 20, leg 1 and intercoxal plate, anterior (E); 21, leg 2 and intercoxal plate, anterior (E); 22, leg 3, ventral (D); 23, leg 5, dorsal (G).



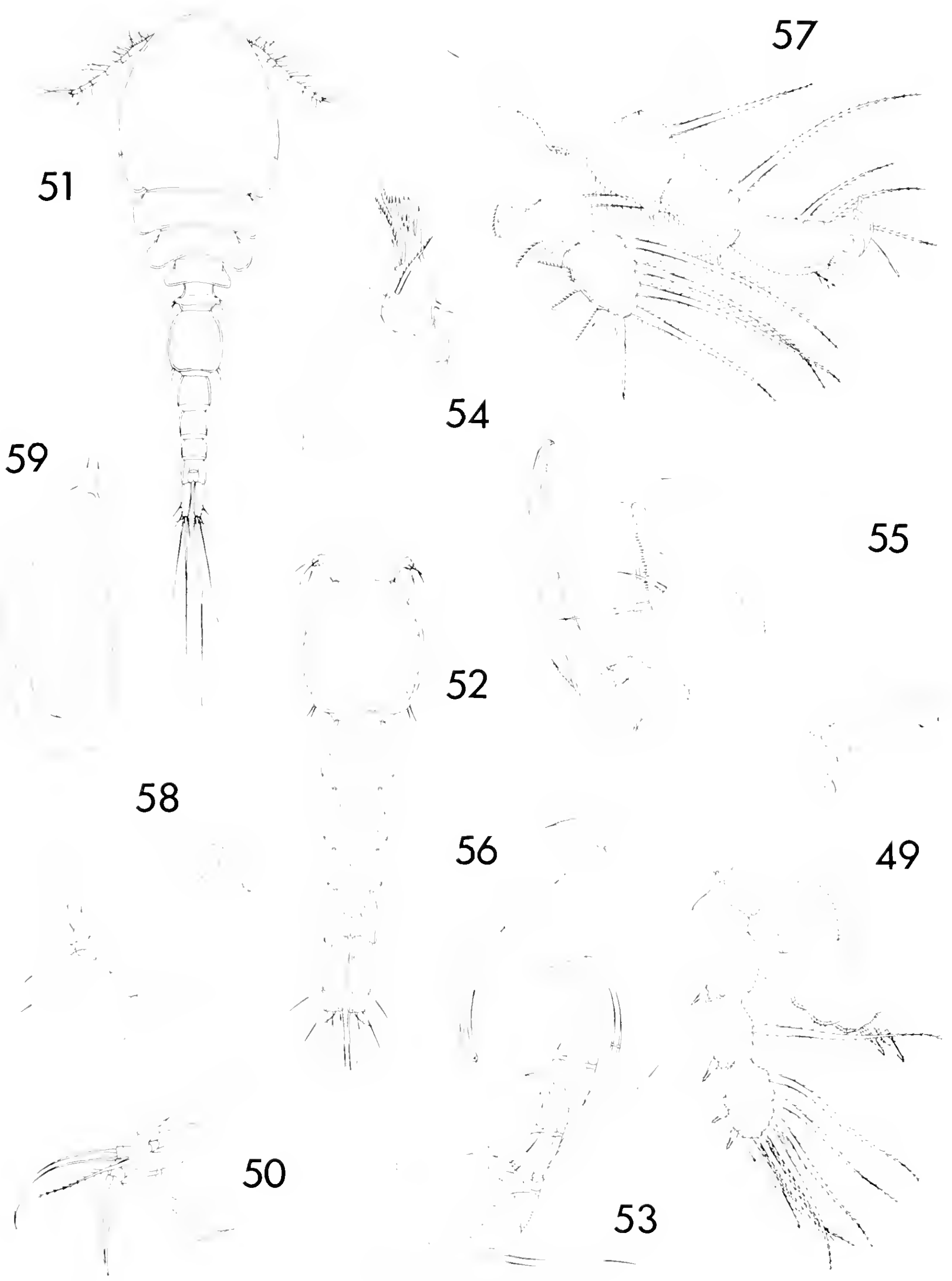
Figures 24–29. *Cotylomolgus lepidonoti* n. gen., n. sp., male. 24, dorsal (H); 25, urosome, dorsal (B); 26, urosome, ventral (B); 27, maxilliped, posterior (D); 28, leg 5, lateral (D); 29, spermatophore, ventral (G).



Figures 30–38. *Pseudanthessius ferax* n. sp., female. 30, dorsal (A); 31, urosome, dorsal (B); 32, urosome, lateral (B); 33, genital segment, ventral (B); 34, area of attachment of egg sac, dorsal (D); 35, enlargement of setae on egg sac attachment area, lateral (C); 36, caudal ramus, dorsal (D); 37, cephalosome, ventral (H); 38, first antenna, ventral (G).

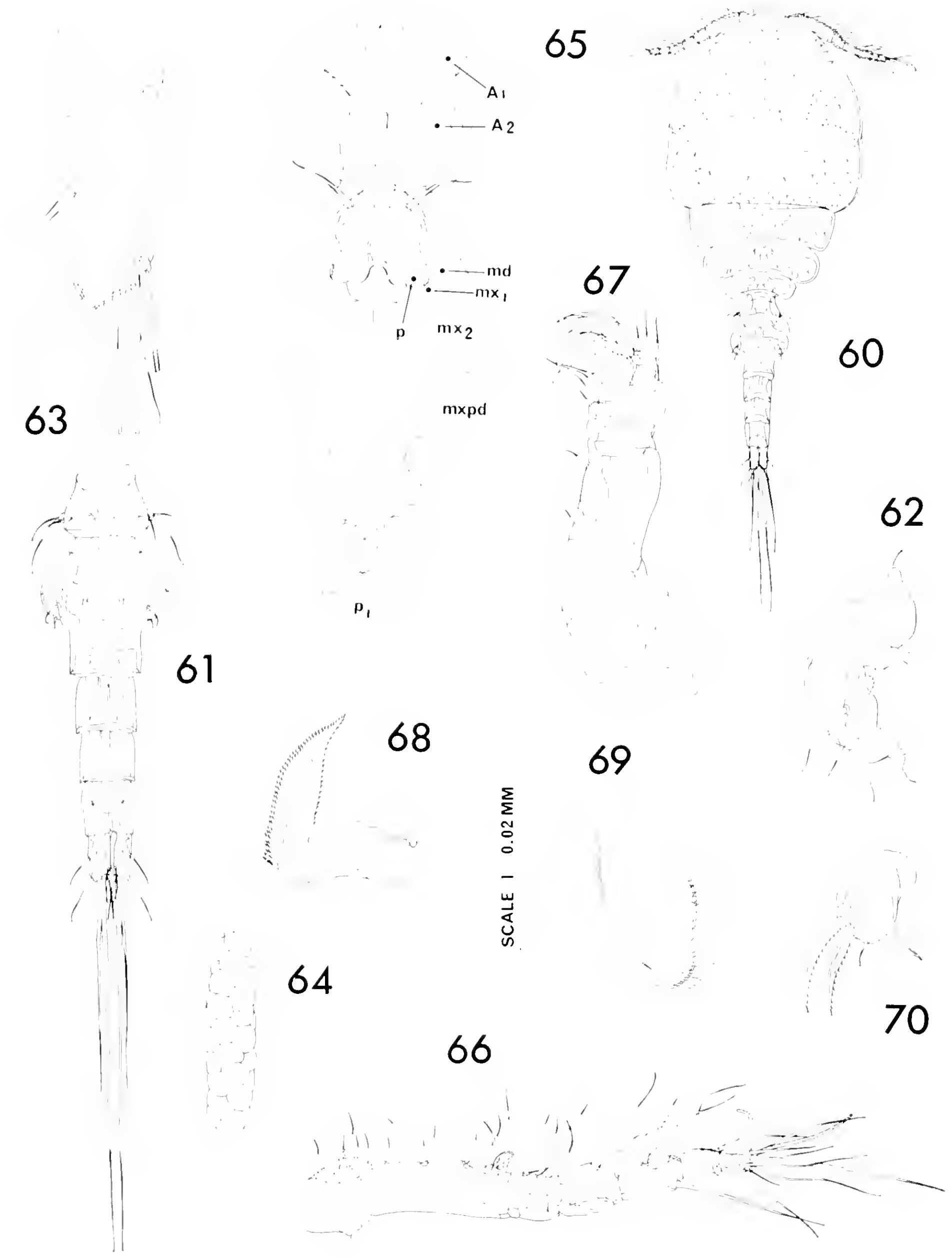


Figures 39–48. *Pseudanthessius ferox* n. sp., female (continued). 39, second antenna, anterior (G); 40, labrum, ventral (D); 41, mandible, anterior (D); 42, first maxilla, anterior (D); 43, second maxilla, posterodorsal (D); 44, maxilliped, anterior (D); 45, leg 1 and intercoxal plate, anterior (G); 46, angular lamella on basis of leg 1, anterior (C); 47, leg 2, anterior (G); 48, leg 3, anterior (G).



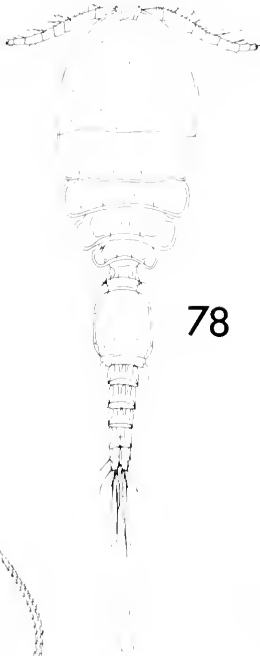
Figures 49–50. *Pseudanthessius ferox* n. sp., female (continued). 49, leg 4 and intercoxal plate, anterior (G); 50, leg 5, dorsal (D).

Figures 51–59. *Pseudanthessius ferox* n. sp., male. 51, dorsal (A); 52, urosome, dorsal (B); 53, last segment of second antenna, posterior (C); 54, second maxilla, posterodorsal (D); 55, maxilliped, anterior or dorsal (D); 56, claw of maxilliped, anterior or dorsal (D); 57, leg 1, anterior (D); 58, leg 6, ventral (D); 59, spermatophore inside male, ventral (E).

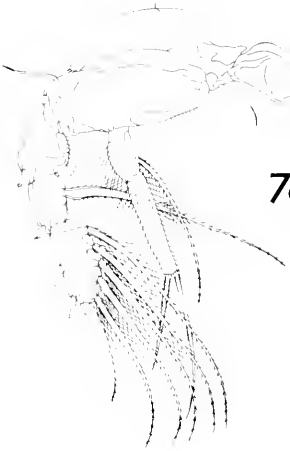


Figures 60–70. *Nasamolgus firmus* n. sp., female. 60, dorsal (H); 61, urosome, dorsal (G); 62, area of attachment of egg sac, dorsal (C); 63, caudal ramus, dorsal (F); 64, egg sac (H); 65, median part of cephalosome, ventral (E); 66, first antenna, ventral (D); 67, second antenna, anterior (C); 68, mandible, ventral (C); 69, paragnath, ventral (I); 70, first maxilla, anteroventral (F).


77

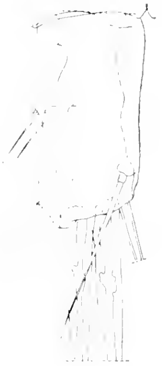

78


75


76


72


79


80


74


73


71

Figures 71–77. *Nasomolgus firmus* n. sp., female (continued). 71, second maxilla, posterodorsal (C); 72, maxilliped, anterior (C); 73, leg 1 and intercoxal plate, anterior (D); 74, leg 2, anterior (D); 75, leg 3, anterior (D); 76, leg 4 and intercoxal plate, anterior (D); 77, leg 5, dorsal (F).

Figures 78–80. *Nasomolgus firmus* n. sp., male. 78, dorsal (B); 79, urosome, dorsal (E); 80, caudal ramus, dorsal (I).


81

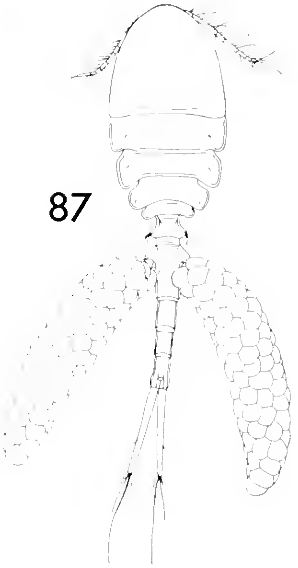

82

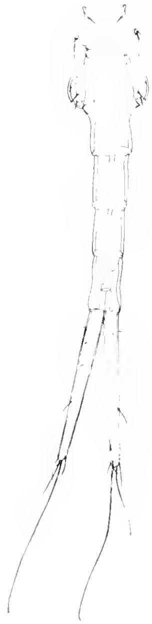

86


83


84

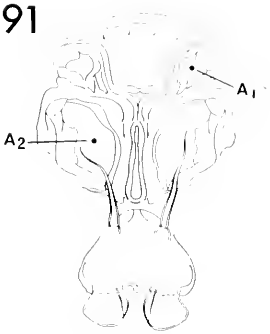

85


87


88

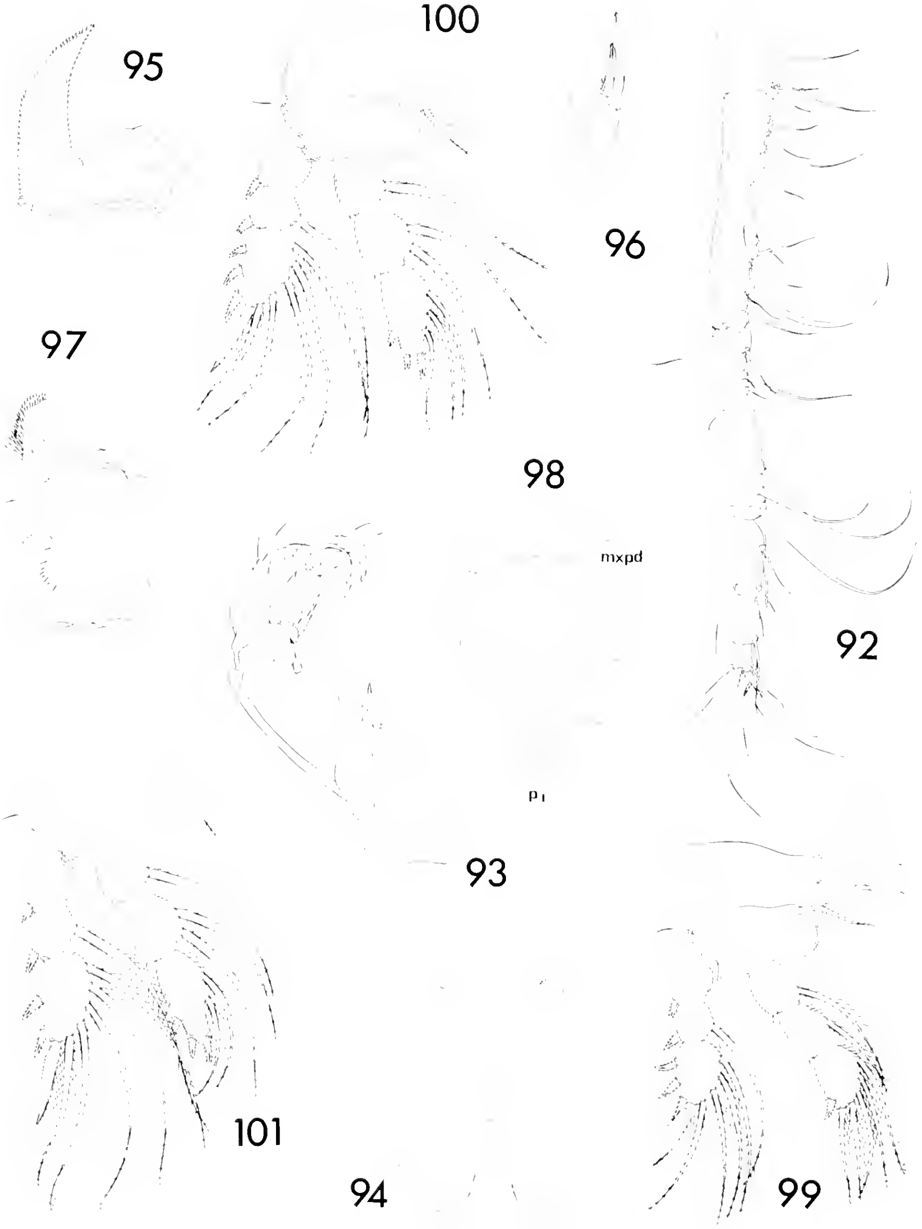

90


89

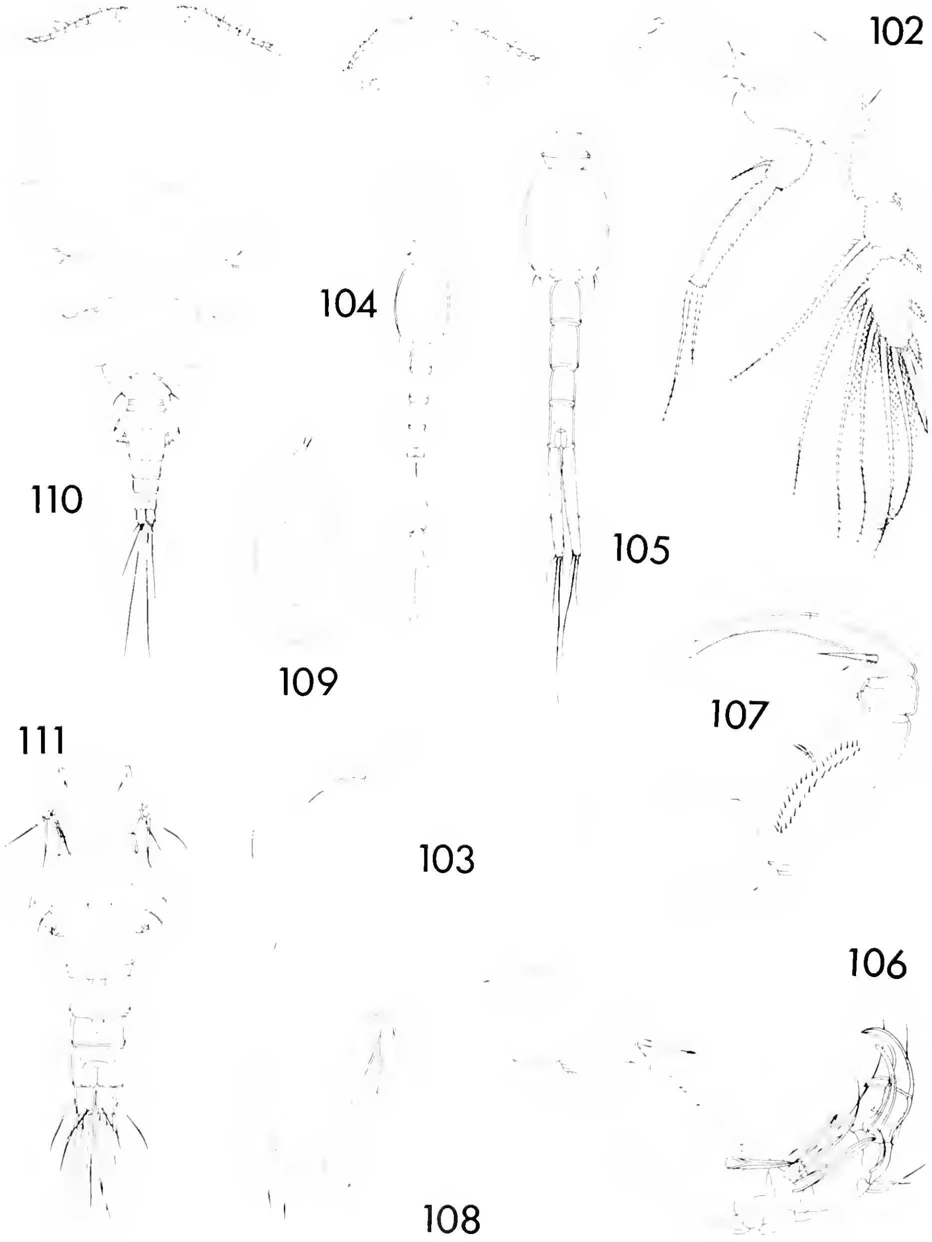

91

Figures 81–86. *Nasomolgus firmus* n. sp., male (continued). 81, second antenna, inner (C); 82, second maxilla, posterior (F); 83, maxilliped, posteromedial (C); 84, endopod of leg 1, anterior (C); 85, leg 6, ventral (F); 86, spermatophore, attached to female, ventral (D).

Figures 87–91. *Nasomolgus leptus* n. sp., female. 87, dorsal (A); 88, urosome, dorsal (H); 89, area of attachment of egg sac, dorsal (C); 90, caudal ramus, dorsal (G); 91, rostral area and labrum, with labral lobes erected ventrally and thus foreshortened in the drawing, ventral (E).



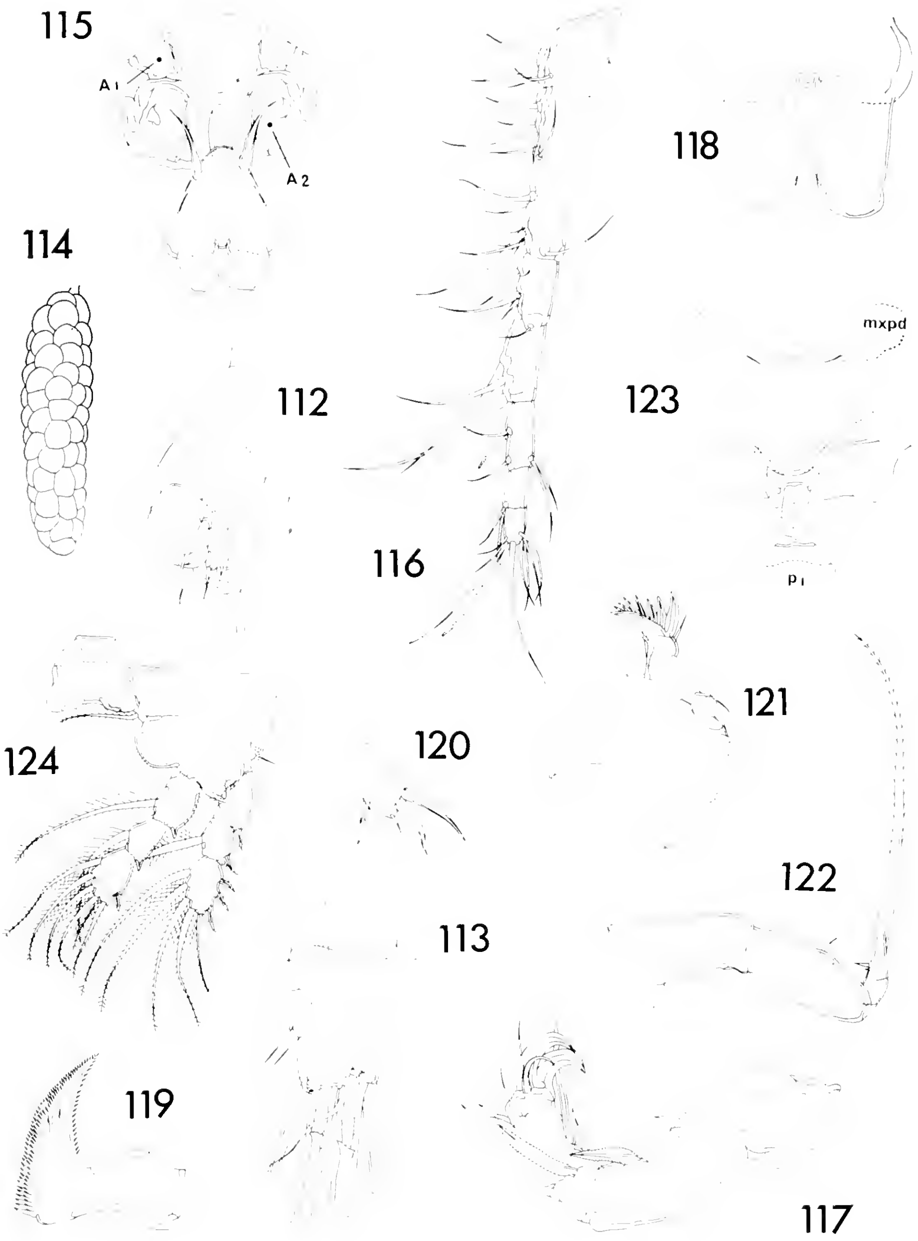
Figures 92–101. *Nasomalgus leptus* n. sp., female (continued). 92, first antenna, dorsal (D); 93, second antenna, posterior (D); 94, posterior part of labrum with bases of two setae, ventral (C); 95, mandible, ventral (C); 96, first maxilla, inner (C); 97, second maxilla, posterodorsal (C); 98, postoral area, ventral (E); 99, leg 1 and intercoxal plate, anterior (E); 100, leg 2, anterior (E); 101, leg 3, anterior (E).



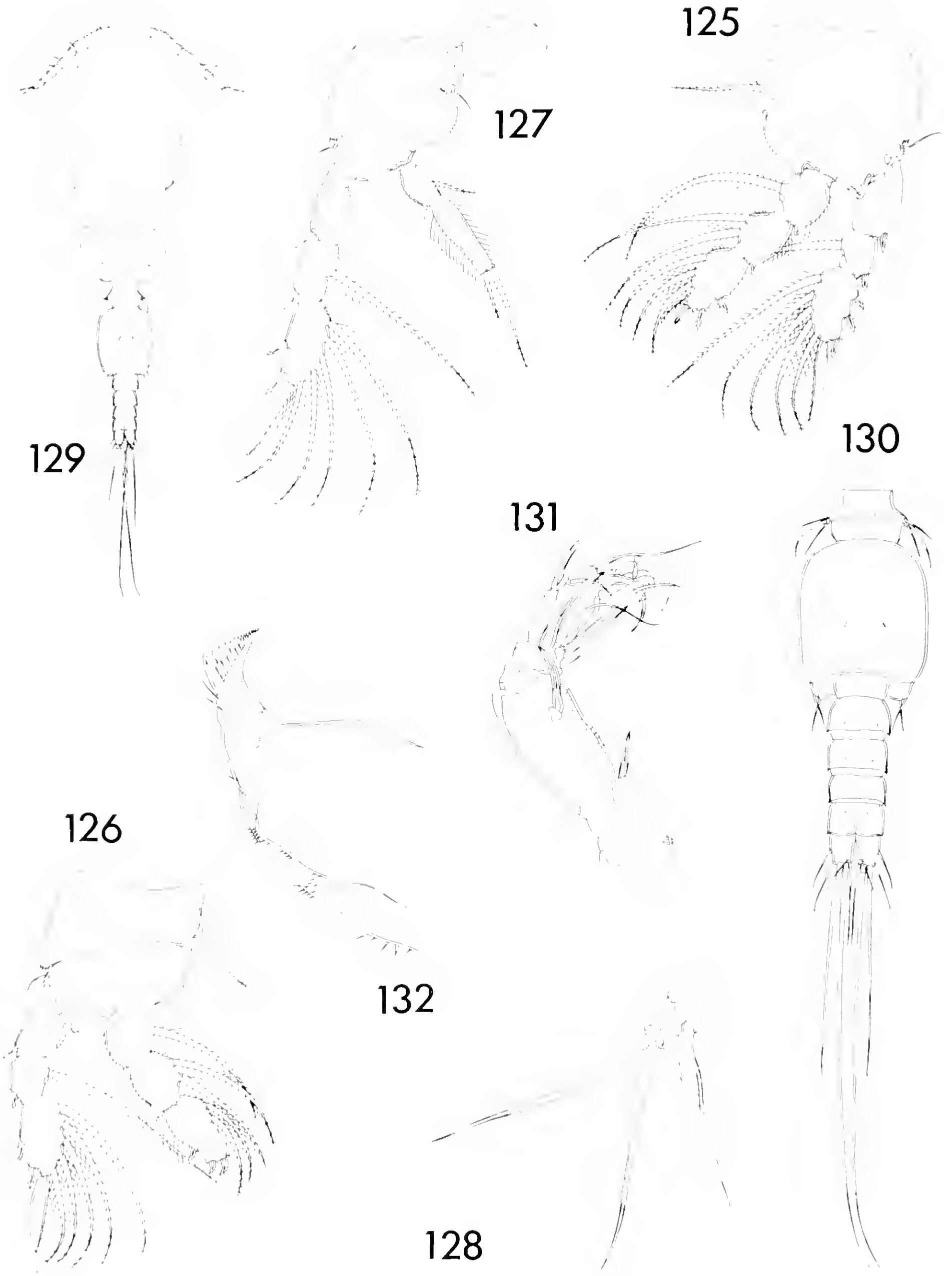
Figures 102–103. *Nasomolgus leptus* n. sp., female (continued). 102, leg 4 and intercoxal plate, anterior (E); 103, leg 5, dorsal (F).

Figures 104–109. *Nasomolgus leptus* n. sp., male. 104, dorsal (H); 105, urosome, dorsal (B); 106, second antenna, posterior (C); 107, maxilliped, posteromedial (C); 108, leg 6, ventral (C); 109, spermatophore, inside male, dorsal (E).

Figures 110–111. *Nasomolgus rudis* n. sp., female. 110, dorsal (H); 111, urosome, dorsal (G).



Figures 112–124. *Nasomalgus rudis* n. sp., female (continued). 112, area of attachment of egg sac, dorsal (C); 113, caudal ramus, dorsal (F); 114, egg sac, dorsal (H); 115, rostral area and labrum, with labral lobes erected ventrally and thus foreshortened in the drawing, ventral (E); 116, first antenna, dorsal (D); 117, second antenna, posterior (D); 118, posterior part of labrum, ventral (C); 119, mandible, dorsal (C); 120, first maxilla, ventral (C); 121, second maxilla, posterior (C); 122, maxilliped, posterior (C); 123, postoral area, ventral (E); 124, leg 1 and intercoxal plate, anterior (E).



Figures 125–128. *Nasomalgus rudis* n. sp., female (continued). 125, leg 2, anterior (E); 126, leg 3, anterior (E); 127, leg 4 and intercoxal plate, anterior (E); 128, leg 5, dorsal (F).

Figures 129–132. *Nasomalgus rudis* n. sp., male. 129, dorsal (B); 130, urosome, dorsal (E); 131, second antenna, posterior (C); 132, second maxilla, anterior (I).

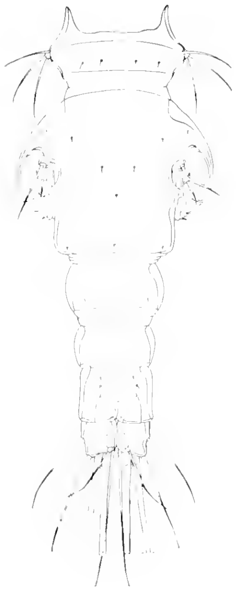

139


136

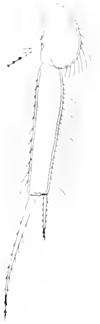

134


135


142


137


138


141


140


133

Figures 133–135. *Nasomolgus rudis* n. sp., male (continued). 133, maxilliped, posteromedial (C); 134, leg 6, ventral (F); 135, spermatophore, attached to female, dorsal (D).

Figures 136–142. *Nasomolgus parvulus* n. sp., female. 136, dorsal (H); 137, urosome, dorsal (D); 138, area of attachment of egg sac, dorsal (C); 139, caudal ramus, dorsal (I); 140, second maxilla, posterior (F); 141, endopod of leg 4, anterior (C); 142, spermatophores, attached to female, ventral (D).

Bulletin OF THE
Museum of
Comparative
Zoology

Proterochampsa barrionuevoi and the Early Evolution of the Crocodilia

WILLIAM D. SILL

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 135, NUMBER 8
APRIL 24, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN 1863–
BREVIORA 1952–
MEMOIRS 1864–1938
JOHNSONIA, Department of Mollusks, 1941–
OCCASIONAL PAPERS ON MOLLUSKS, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office
Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

PROTEROCHAMPSA BARRIONUEVOI AND THE EARLY EVOLUTION OF THE CROCODILIA

WILLIAM D. SILL

INTRODUCTION

During the months April through June of 1958 a joint expedition of the Museo Argentino de Ciencias Naturales and the Museum of Comparative Zoology explored continental deposits in the Province of Mendoza and San Juan in western Argentina. The last six weeks of the field season were spent in Triassic beds at Ischigualasto, a valley in the northeastern part of the province of San Juan. Fossils at this locality proved to be so abundant and so easily found that Romer (1962) has described it as a "paleontologist's dream." The crocodilians described in this paper were found there by Professor Bryan Patterson in the upper third of the Ischigualasto Formation, approximately 160 feet from the base. The formation consists of interbedded clays, shales, and some sandstone, characterized by the variegated green, white, brown, and red colors typical of so many fossil bearing continental deposits. As regards age, Frenguelli (1948) considered the formation to be upper Keuper; Romer (1960, 1962) states that it is certainly pre-Norian and probably pre-Carnian. Gomphodont cynodonts and rhynchosaurs were found in abundance in the formation in the same general area as the material here discussed.

The following year the Instituto Miguel Lillo of the Universidad de Tucumán sent two expeditions to the area. Under the direction of Dr. Osvaldo A. Reig a number of specimens were found, some of which have already been described (Reig, 1959; Casamiquela, 1960; Bonaparte, 1962, 1963). Reig (1959) published a preliminary account of the ancestral crocodilian discussed here, giving it the name *Proterochampsa barrionuevoi.*

The material discussed in this paper consists of one complete, well preserved skull (but with parts of the ventral area badly fractured), together with 13 articulated vertebrae and ribs, MCZ 3408, and one partial skull, MACN 18165 (Museo Argentino de Ciencias Naturales).

I am obliged to Arnold D. Lewis for preparation of the material, to Dr. Bernhard Kummel for the photography, to Dr. Edwin Colbert and The American Museum of Natural History for permission to examine *Protosuchus*, to Yale Peabody Museum for making available various mesosuchians for comparative study, and to Dr. K. A. Kermack of University College London for allowing me to examine the primitive crocodilian from Wales. The manuscript has been read by Professors Bryan Patterson, Ernest Williams, and Alfred Romer. To all of these people I express my sincere thanks. The expedition was supported in part by the National Science Foundation, and in part by Life Magazine.

MORPHOLOGY

THE SKULL

General remarks: The skull of *Proterochampsa* presents a remarkable combination of primitive thecodont, advanced crocodilian, and transitional characters. The dorsal surface resembles that of a modern crocodile in the highly sculptured surface, large dorsally placed orbits, small supratemporal fenestrae, and external nares near the midline of the snout. The skull is flat, relatively broad, and has a long snout. The sculpturing of the cranial table is noteworthy in that the rugose ridges usually follow a pattern, differing in this respect from the random pitted type of sculpturing found in later crocodiles. Most of the transitional characters are in the palatal region. The presence of relatively large antorbital fenestrae and of long curved teeth may be considered transitional or primitive. Sutures on the dorsal side of the skull are generally well preserved; on the underside, however, it is much more difficult to determine the bone pattern due to the fractured nature of the region.

The occipital face of the skull of *Proterochampsa* resembles that of a somewhat flattened version of a modern crocodile. Although the skull is 35 centimeters from the occipital condyle to the tip of the snout, it is only 4 centimeters high from the base of the occipital condyle to the top of the parietal. Of course, some allowance must be made for flattening and deformation in the process of fossilization, but the general aspect of length to depth remains the same (a modern crocodile of comparable size measured only 6 centimeters in depth from condyle to parietal).

The ventral portion of the skull is by no means as well preserved as the dorsal; fortunately, however, the position of the internal nares and the limits of the secondary palate are quite clear. The basisphenoid, the pterygoid flange and its tooth row, and the ectopterygoid relationships are clearly seen. The rest of the basicranial region is crushed and distorted. The interpretation presented here necessarily contains an element of the speculative.

Premaxilla. The premaxilla occupies the anterior end of the snout extending back from the "canine notch" toward the midline, forming an inverted V-shaped suture with the nasal and the maxilla. Ventrally, the premaxilla folds over and joins at the midline to form the anterior part of the secondary palate. The ventral suture of the maxilla and premaxilla is not visible, nor is it possible to verify the presence of an incisive foramen. The premaxilla bears six teeth. The shape and sutural relations of the dorsal side of this bone are very similar to those of a modern crocodile (see Plate V).

Maxilla. The maxilla extends posteriorly and laterally from the "canine notch," forms the anterior border of the antorbital fenestra, and joins the nasal medially and the jugal posteriorly. The maxilla in MCZ 3408 bears eleven teeth, and that of MACN 18165 at least twelve. Like the premaxilla, the sutural configuration of the maxilla is very much like that of modern crocodiles (see Plate V). Ventrally, the maxilla folds over to join with the premaxilla in the formation of the secondary palate. In this region there is no definite border delimiting the maxilla with relation to the internal nares and the palatine bones. There is, however, a slight difference in the color of the bone, which is symmetrical on both sides of the midline and has been taken as the probable boundary of the maxilla with the palatine. The maxillae are comparatively small ventrally, extending down from the posterolateral side of the upper jaw, meeting at the midline with the premaxillae, with a small process entering into the anterior border of the internal nares.

Nasal. The nasal bone of *Proterochampsa* forms a horizontal plate extending from an inverted V-shaped posterior border with the frontal and prefrontal to an anterior V-shaped suture with the premaxilla. A prominent, sculptured ridge runs longitudinally down the medial side of each nasal. Ventrally, the relationships are obscure, although it appears that there is a contact of the vomer with the nasal anterior to the internal naris. The nasal extends somewhat

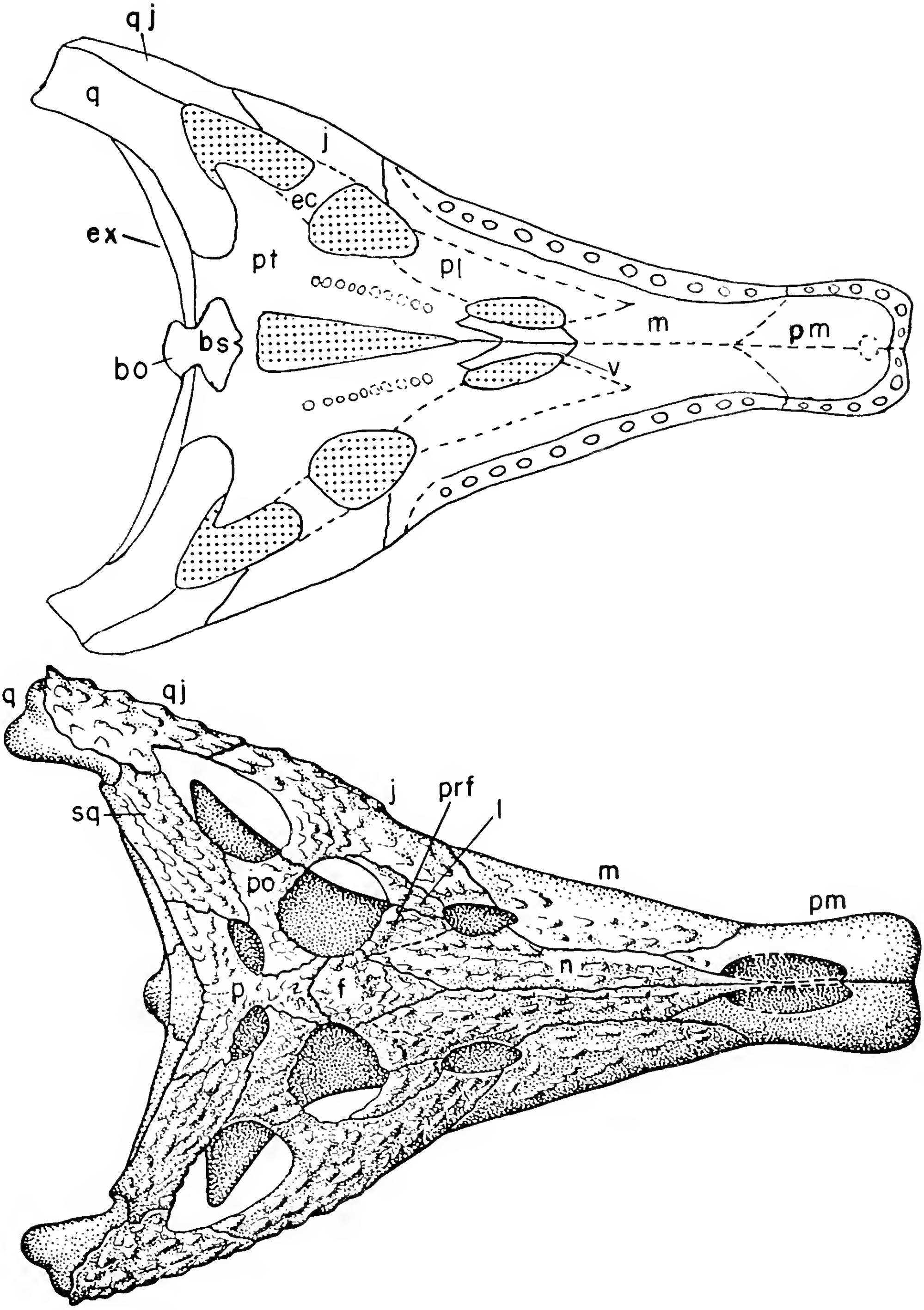


Fig. 1. Dorsal and ventral views of skull of *Proterochampsa barrionuevai*, MCZ 3408. × $\frac{1}{3}$. Abbreviations on page 436.

laterally at the antorbital fenestra, of which it forms the medial border.

Prefrontal. The suture of the prefrontal with the nasal is not clearly visible; it is inferred from the change in pattern of the bone and the orientation of the sculpturing in this area. The prefrontal stands out as a highly sculptured triangular bone forming the anteromedial border of the orbit and the posteromedial border of the antorbital fenestra. At the border with the lacrimal, the prefrontal is also marked by the strong sculptured crest extending around all but the lateral one-third of the orbit (see discussion of orbit below). The prefrontal is bordered medially by the nasal, anteriorly by the antorbital fenestra, laterally by the lacrimal, and posteriorly by the orbit and a small part of the frontal.

Lacrimal. The lacrimal of *Proterochampsa* is smaller than in later crocodiles. It is a triangular, lightly sculptured bone bordered by the jugal laterally, the prefrontal medially, the antorbital fenestra anteriorly, and the orbit posteriorly. It is distinctive in not having an orbital crest along its border with the orbit. The lacrimal inclines somewhat laterally; it is primitive in that it extends around a large part of the lateral margin of the orbit, but advanced as regards small size.

Frontal. The frontals are fused at the midline but there is still an indication of a suture between them. The sculpture pattern of the frontals is distinctive in consisting of transverse ridges forming peaks at the midline, slanting laterally, then sweeping up at the margin of the orbit to join in the orbital crest. The conjoined frontals have a triangular shape and look rather like an arrowhead pointing down the snout. They are bordered anteriorly by the nasals and the prefrontals, posteriorly by the parietals, and laterally by the orbits.

Parietal. The parietals are completely fused, with no trace at all of a suture separating them. They are slightly concave at the midline anterior to the supratemporal fenestrae, and slope upward posteriorly to form part of the occipital crest. Small ridges, not as prominent as those of the frontals, radiate out from the center of the fused parietals, becoming quite prominent posteriorly near the occipital crest. The parietals are roughly T-shaped, with the crossbar of the T forming part of the occipital crest. They are bordered posterolaterally by the squamosals, posteriorly by the supraoccipital and the exoccipitals, laterally by the postorbitals and anteriorly by the frontals. A very small lateral part enters the orbit, and the entire posterior border of the supratemporal fenestra is formed by the anterior edge of the crossbar portion of the bone.

Postorbital. The postorbital is a massive, heavily sculptured bone forming the greater part of the posterior margin of the orbit. It is bordered medially by the parietal, posteriorly by the squamosal, and laterally by the jugal. The postorbital participates in the formation of the orbit anteriorly, the supratemporal fenestra posteromedially, and forms the medial edge of the infratemporal fenestra laterally. Together with a medial extension of the jugal it forms the postorbital bar. Although the form of the bar is very similar to that of modern crocodiles, it remains entirely on the dorsal surface of the skull.

Squamosal. The squamosal forms the principal part of the occipital crest. It is a strong, massive bone with highly sculptured, very prominent ridges extending laterally along the occipital crest. Other ridges extend diagonally from the postorbital in front of the supratemporal fenestra and back across the squamosal to the lateral edge of the cranial table. Reig called special attention to this diagonal ridge; on the cast of the type specimen, which he kindly sent to the Museum of Comparative Zoology, this crest is much more prominent than on the specimens here described. The squamosal rests posteriorly on top of the exoccipital; laterally it meets the quadratojugal nearly horizontally, with strong sculpturing present on both bones. A small process of the squamosal extends down the lateral border of the exoccipital. Posterolaterally the quadrate sweeps up to form a steep, smooth suture directly underneath the squamosal. The squamosal forms a small part of the lateral border of the supratemporal fenestra and the largest part of the posterior border of the infratemporal fenestra. It is bordered by the parietal, exoccipital, quadrate, quadratojugal, and postorbital.

Jugal. The position of the jugal is quite different from that of the mesosuchians and eusuchians and much more like that of some of the early thecodonts. Unlike crocodiles in general, the jugal of *Proterochampsa* forms only a minor part of the orbit, being ventral to the lacrimal for most of the orbital area. The jugal extends forward from its border with the quadratojugal to form most of the lateral border of the infratemporal fenestra; it sends a process halfway up between the orbit and the infratemporal fenestra to meet the postorbital and to form the postorbital bar, which, as just described, is not displaced downward from the cranial surface (see Fig. 2). The jugal forms a small part of the lateral border of the orbit, meets the lacrimal and continues lateral to and beyond it to form the lateral border of the antorbital fenestra. The jugal is in general more lightly sculptured than most of the dorsal skull bones. Together with the lacrimal, it forms that part of the orbit which does not have a prominent raised crest. The part that forms the bar below the infratemporal fenestra is, however, quite massive and highly sculptured.

On the palate the sutures of the jugal are not fully discernible. However, the ectopterygoid can be seen extending from the jugal, and the suture with the quadratojugal can be seen. The border with the maxilla and the exact location of the suture with the ectopterygoid are not visible.

Quadratojugal. Like the jugal, the quadratojugal resembles that of its thecodont ancestors much more closely than it does

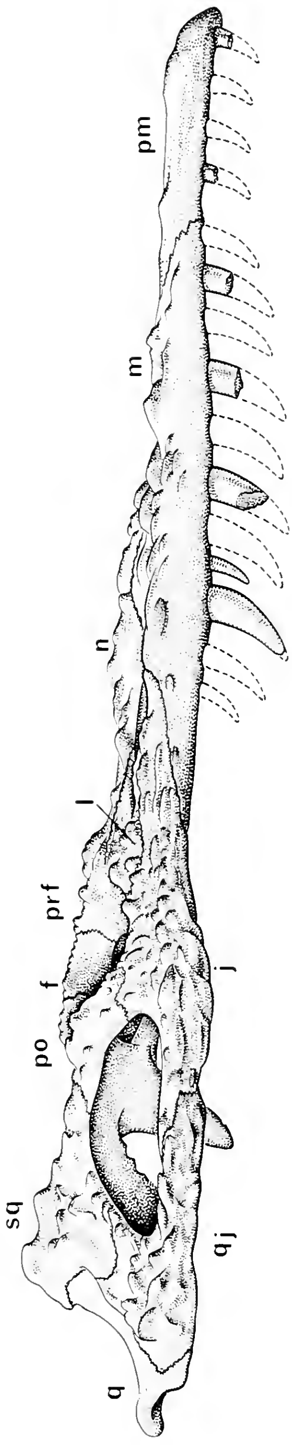


Fig. 2. Profile of *Proterochampsa barrionuevoi*, MCZ 3408. × 1/3.

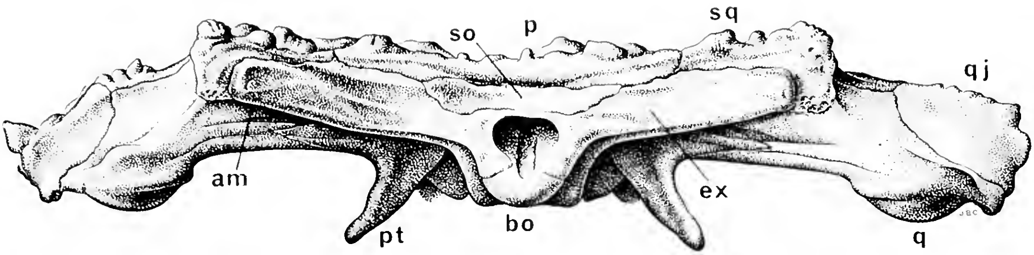


Fig. 3. Occipital view of *Proterochampsa barrionuevoi*, MCZ 3408. × ½.

that of later crocodiles. It is much larger than the modern crocodilian quadratojugal and forms the posterolateral corner of the dorsal surface of the skull. Anteriorly, it joins with the jugal, forms the posterolateral margin of the infratemporal fossa, and unites medially with the squamosal. Posteriorly and medially, the quadratojugal has a smooth face which joins with the quadrate.

On the palatal surface, the suture of the quadratojugal and the jugal runs diagonally forward. Its other ventral contact is with the quadrate, on which it sits like a cap with the lateral edge folded under. The dorsal and lateral parts of the bone are sculptured to about the same extent as the jugal, being more massive along the infratemporal bar. The posterior face of the bone is smooth and quite steeply inclined down to its junction with the quadrate.

Quadrate. In its posterior aspect the quadrate of *Proterochampsa* resembles that of advanced crocodilians in extending upward and medially with a smooth sloping face to join the exoccipital and the squamosal; it is not, however, overlain by the latter as in eusuchians. Further, it is quite unlike Recent crocodiles in having the external auditory meatus in the form of a groove going into the inner ear along the posterodorsal part of the quadrate, anterior to the exoccipital and underneath, but not enclosed by, the squamosal (see discussion of ear region below). The configuration of the articulating condyles of the quadrate is similar to that of some of the mesosuchian crocodiles [Teleosauridae, Libycosuchidae, and Metriorhynchidae (Kälin, 1955)] in the presence of two condyles, the medial larger than the lateral. This is in contrast, on the one hand, to the usual thecodont condition of only one condyle and, on the other, to the Recent crocodilians, which have two condyles but the lateral larger than the medial.

Ventrally, the posterior edge of the quadrate forms a vertical ridge running diagonally from the articulating surface medially to join the posterior border of the pterygoid. The lateral border, covered dorsally by the quadratojugal, remains horizontal and gives rise to the vertical ridge previously mentioned. In size, the quadrate is more like that of the thecodonts than of the crocodilians, but in shape it is transitional between the two.

Supraoccipital. The supraoccipital in *Proterochampsa* is a subtriangular, smooth bone lying vertically on the posterior face of the skull, just under the fused parietals, much as in the modern crocodiles. It is bordered dorsally by the parietals, laterally by the exoccipitals, and ventrally, just above the foramen magnum, by a thin expression of the exoccipital.

Exoccipital. The exoccipital forms all but the most ventral portion of the border of the foramen magnum; it extends outward to underlie the lateral part of the parietal and the posterior part of the squamosal. The small occipital process of the squamosal forms the lateral border of the exoccipital. Laterally and ventrally the exoccipital

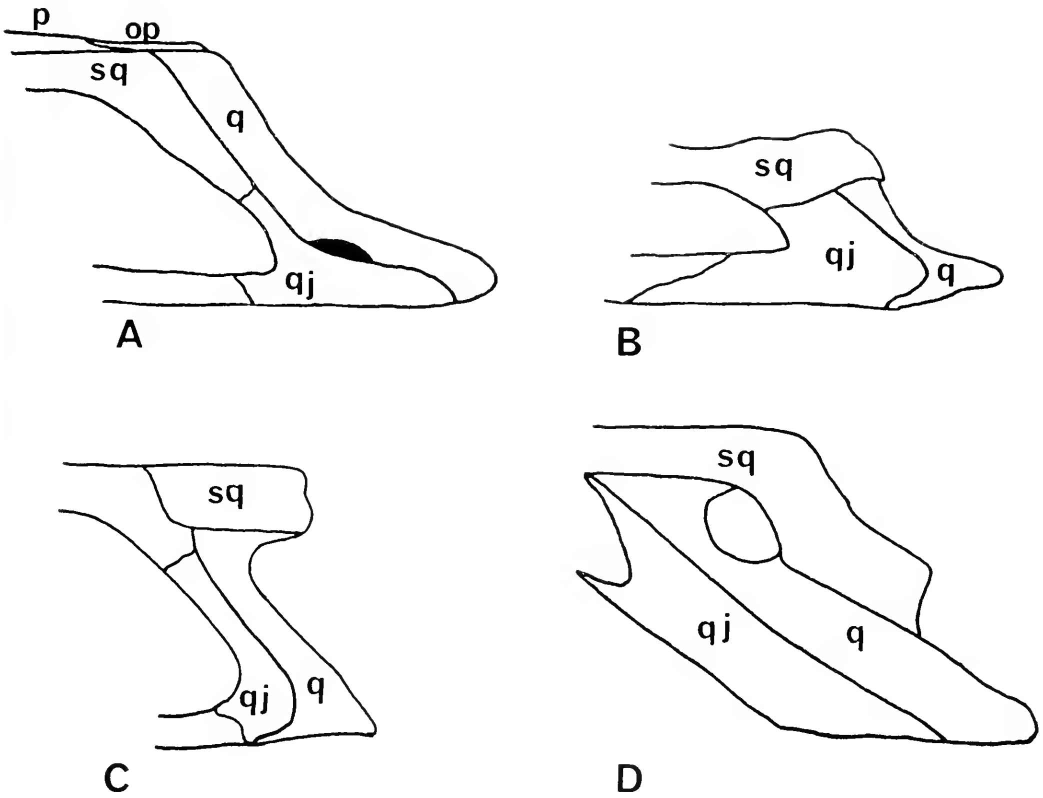


Fig. 4. External ear structure in A, *Chasmatosaurus* (proterosuchian thecodont); B, *Proterochampsa*; C, *Pelagosaurus* (mesosuchian crocodile); and D, *Crocodylus*.

joins with the quadrate. Ventrally, on the posterior face of the skull, it joins with the basioccipital.

Basioccipital. The basioccipital forms the entire occipital condyle and the most ventral border of the foramen magnum. Ventrally, it is fused completely with the basisphenoid, has a subrounded shape, resembling the thecodont rather than the eusuchian condition and is without the basioccipital processes common in mesosuchians.

Ear structure. Proterochampsa shows the beginning of the acquisition of the otic notch in crocodiles, and, with the mesosuchians, provides a phylogenetic sequence for the evolution of the unusual crocodilian ear structure (Fig. 4). In *Proterochampsa* there is a meatal groove running from the border of the quadrate and squamosal, passing anterior to the exoccipital and into the inner ear. Haughton (1924) mentions a similar groove in *Notochampsa*. In *Protosuchus* there is no evidence of either a groove or an otic notch.

In the earliest thecodonts, there is no indication of an otic notch (later thecodonts do possess one, although it is usually formed completely within the squamosal), and the quadrate is, as a rule, completely vertical.

In mesosuchians the otic notch is usually quite prominent, formed by the squamosal projecting out over the quadrate (see Fig. 4C). In modern crocodiles the squamosal has extended backward and downward onto the quadrate to close the otic notch and gain a broad posterior contact with the

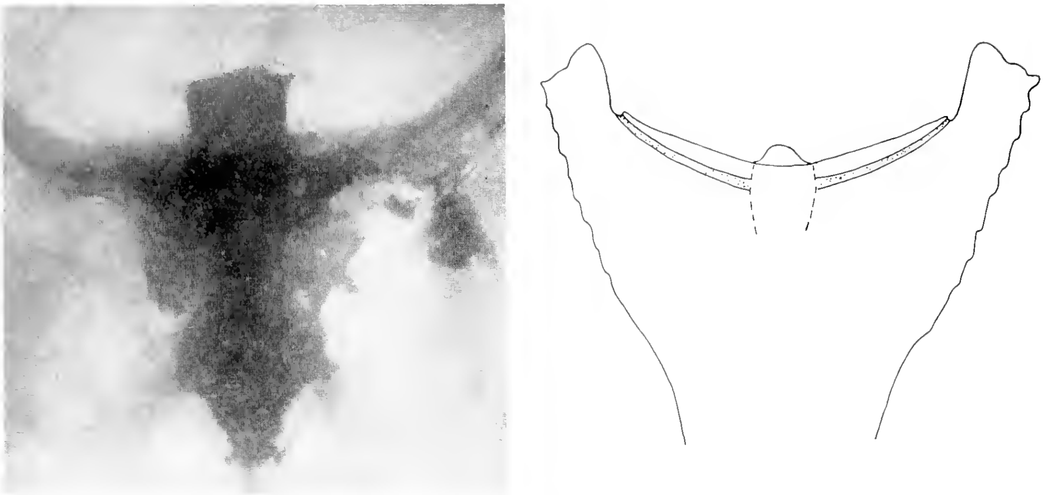


Fig. 5. Comparison of the external auditory meatus in *Crocodylus* (*left*) (X-ray, after Edinger, 1938), and *Proterochampsa* (*right*).

quadrate, forming, with the exoccipital, the deep pocket of the external and middle ear structures. This closing of the otic notch has been accompanied by a displacement of the tympanic cavity laterally from the braincase. This is already shown by some late Cretaceous mesosuchians of the family Notosuchidae (Kälin, 1955), in which the quadrate has become more posteriorly inclined (and the skull much more flattened). In this respect the quadrate of *Proterochampsa* resembles that of mesosuchians in both inclination and height.

Although the acquisition of the otic notch appears to follow the developmental sequence outlined above, it should be emphasized that this sequence is based more on external form than on a detailed comparative study of the osteology of the ear region of fossil crocodilians.

Dorsal openings of the skull. The external nares lie on either side of the midline, separated at least in part (and probably entirely) by the slender tip of the paired nasals. They are approximately five centimeters long, two and a half centimeters across, and oval shaped. They are completely enclosed by the premaxillae, except for the nasal process which separates them.

The antorbital fenestrae are oval-shaped openings, somewhat wider posteriorly than anteriorly. Like the external nares, they are completely dorsal. They are bordered by the maxilla, nasal, prefrontal, lacrimal, and jugal (as previously described).

The orbits of *Proterochampsa* are quite like those of modern crocodiles in being almost completely within the horizontal plane of the skull (there is a small lateral angle downward as in modern crocodiles). However, as in thecodonts and early crocodilians, the postorbital bar is still at the dorsal surface of the skull and the lacrimal bone plays an important part in the border of the orbit. The orbit is bordered by a very strong crest that extends around all but the anterolateral one-third of the circumference. Anteriorly, the crest stops at the lateral edge of the prefrontal part of the border to run down the prefrontal to the antorbital fenestra. Posteriorly, the encircling crest stops at the edge of the postorbital, halfway down the postorbital bar, and another crest goes off diagonally at the beginning of the postorbital bar across the postorbital and squamosal bones.

The supratemporal openings are considerably smaller than the infratemporal openings, as is the case in Recent Crocodilia. This condition is probably primitive and, as indicated by Colbert and Mook (1951), was lost in the mesosuchians and reacquired in the eusuchians. In *Proterochampsa* these openings are nearly horizontal, slanting slightly downward towards the orbits from the prominent crests of the parietal.

The infratemporal openings of *Proterochampsa* are much larger than those of Recent crocodiles, being about as large relative to the orbits as in thecodonts. In the latter, however, they are vertical, whereas in *Proterochampsa* they lie at about a 45° angle.

Secondary palate. The secondary palate of *Proterochampsa* is of great interest. As mentioned above, it consists of the premaxillae, the maxillae, and possibly a small part of the palatines. The premaxillae and the maxillae simply extend over to the midline, and the internal nares open at the posterior border of the maxillae. They are bordered laterally by the palatines and separated by the vomers. This arrangement provides an almost perfect transition between the thecodont type of palate and the mesosuchian, in which the internal nares have moved back to the posterior border of the palatines.

Palatine. The palatine bones cannot be clearly distinguished in the two skulls available for study. However, on the basis of a slight color and textural difference of the bone which follows the general osteological pattern of crocodiles and is symmetrical on both sides of the midline, the medial boundaries are tentatively placed at the lateral borders of the internal nares. If this is correct, the palatines, in addition to bordering the internal nares, form part of the anterolateral margins of the pterygoid fenestrae.

Vomer. The vomers diverge from the midline between the internal nares, emerge on the dorsal side of the secondary palate and extend posteriorly and laterally to reveal a V-shaped exposure of the pterygoids above and between them (Plate VII). The vomers form the medial border of the internal nares.

Pterygoid. The pterygoids are the largest of the basicranial elements, consisting of an anterior plate, a flange, and a posterior process from the base of the flange. In the available specimens the anterior part of the pterygoid is badly fractured, but a row of eight to twelve very small teeth is nevertheless visible extending from just behind the internal nares to the base of the pterygoid flange. At the midline the pterygoids are separated by an interpterygoid fenestra situated between the internal nares and the basisphenoid. Here the pterygoid border is formed by a prominent ridge extending from the vomer to the pterygoid flange. Laterally, the ectopterygoid joins the pterygoid at the anterior margin of the pterygoid flange. This flange in *Proterochampsa* is similar to that of modern Crocodilia in its flat, blade-like shape. It differs from that of Recent crocodiles in not being appreciably extended downward beyond the level of the jugal. The posterior edge of the flange curves medially and dorsally to meet the medial process of the quadrate.

Ectopterygoid. The ectopterygoid forms a bar between the pterygoid fenestra and the open area around the pterygoid flange (it is well preserved and is a simple straightforward bone). It is relatively short and is bordered medially by the pterygoid and laterally by the jugal.

Basisphenoid. The basisphenoid bears no resemblance at all to that of modern crocodiles. It is small, sub-rounded and completely fused with the basioccipital. On its anterior face are two flangelike processes with a median cleft between them (which may be the eustachian tube). Just behind these processes are two prominent openings assumed to be the carotid foramina. The area immediately around the basisphenoid is badly fractured, making its relationship with the pterygoid somewhat obscure. It appears, however, to be in contact with the posterior border of the pterygoid, slightly ventral to it.

Ventral openings of the skull. It is not possible to determine the size of the incisive foramen due to the mandible being pushed up into the skull and obscuring the anterior portion of the palate.

The internal nares are approximately five centimeters long by one and a half centimeters wide and extend slightly lateral from the midline, being bordered as previously described.

The interpterygoid fenestra is a triangular-shaped opening separating the pterygoids at the midline. It is seven centimeters long by three centimeters wide at its base.

The pterygoid fenestrae are oval-shaped openings. They are formed on the lateral side of the pterygoid and are approximately five and a half centimeters long by two centimeters wide. They are inclined slightly toward the midline and are narrower anteriorly than posteriorly.

MANDIBLE

The mandible is present in MCZ 3408, but is crushed up into the skull, leaving only the ventral surface visible. Although it is not possible to give a complete description of the jaw, there are some interesting features to be noted. The anterior part of the mandible is quite like that of *Crocodylus*, with a relatively narrow, oval-shaped ramus, the symphysis extending to about the fourth tooth, and not including the splenial. Posterior to the dentary, however, the mandible flares out to a broad articular surface at only a slight angle, with what is presumed to be the prearticular becoming quite thin laterally. The articular is, so far as can be determined, much larger than in other crocodiles or in thecodonts, forming the entire ventral surface of the articular region. A distinctive feature is the complete lack of a retroarticular process. The angular is relatively small, lying ventral to the articular and not extending beyond the maximum curvature of the angle. The adductor fossa is quite shallow and elongate, the floor apparently formed largely by the articular. A small elongate external fenestra is present; the articular participates in its posterior border.

This would appear to be a rather weak jaw for an aggressive carnivore, and, taking into account the relatively small number of teeth (17 total, with a third of these probably undergoing replacement at any one time), the mandible may be considered primitive or may indicate a specialized diet, perhaps fish or carrion.

DENTITION

There is a slight amount of dental differentiation in *Proterochampsa* as shown by the smaller alveoli at the anterior end of the snout. A slight constriction is present across the snout in the region of the premaxilla, which may have served to accommodate larger teeth in the lower jaw, but this is not a canine notch in the usual sense of the word. The maxillary tooth row is distinctive in extending back only as far as the anterior border of the orbit and containing only 11 teeth. About one-third of these appear to have been undergoing replacement, giving the animal only 8 or 9 operating maxillary teeth. The teeth are relatively long, slightly curved posteriorly, and slightly ovoid, the largest ones lying in the center of the maxilla, resembling those of the early mesosuchians. The mandibular teeth were not visible in either of the specimens examined.

The palatal teeth of *Proterochampsa* are extremely small, the largest being about two millimeters in diameter. They form a row along the length of the pterygoid, each row possessing from eight to twelve teeth. It is difficult to imagine these teeth functioning as either grasping or chewing mechanisms; they were probably vestigial. The palatal teeth do, however, provide a possible link to the primitive proterosuchid thecodonts.

VERTEBRAE AND RIBS

The postcranial material consists of 13

articulated vertebrae, and most of the associated ribs of MCZ 3408, which were found in series and in articulation with the skull. All except the first bear ribs.

Cervical vertebrae. There are seven or eight cervical vertebrae preserved in *Proterochampsa.* Except for the loss of the upper part of some of the neural spines, all are well preserved.

The atlas-axis complex is similar to that of crocodiles in general; the proatlas, if present, was not preserved. The atlas consists of the two sides of the neural arch surrounding what appears to be the odontoid process. The axis resembles the other cervical vertebrae, differing only in having a wider ventral keel, small, diagonally placed parapophyses and the characteristically larger neural spine. The rib of the axis is a normal rib, differing from the other cervical ribs only in articulating more anteriorly on the centrum. This is in contrast to the highly modified splint-like rib of the axis of modern crocodiles.

The remaining cervical vertebrae are rather lightly constructed with quite thin and comparatively long neural spines. The centra are strongly amphicoelous, slightly longer than high, oval in cross section but with prominent ventral keels. The neural arch lies relatively low on the centrum, with the diapophyses extending straight down the sides to just below the neurocentral suture. The diapophysis appears to angle slightly posteriorly in the more posterior cervicals. The base of the diapophysis is very strong, extending like an inverted triangle the entire length of each of the neural arches. The parapophysis is a small, flattened, oval-shaped process projecting outward from the base of the centrum just below, and slightly anterior to the diapophysis; that of the last two cervicals projects somewhat posteriorly. Unlike modern crocodiles, the capitular facets face straight outward instead of downward.

The anterior zygapophysis projects forward from the sub-triangular body of the neural arch as a blade-like process, with the articular surface facing dorsally and medially. In all of the cervicals it overhangs considerably the anterior edge of the centrum.

The posterior zygapophysis extends to the midline above the centrum (see Plate IX). It does not overhang the posterior face of the centrum. The articular facet lies just under the neural spine, facing downward and slightly outward. The articular surface of both zygapophyses is considerably more near the horizontal than that of modern crocodiles.

The neural spine is a narrow plate about twice the height of the centrum, arising from the posterior part of the neural arch just above the posterior zygapophysis and curving slightly backward. The neural spine becomes somewhat broader in the posterior cervical vertebrae.

Anterior dorsal vertebrae. Like the cervicals the dorsal vertebrae are strongly amphicoelous, with the centrum slightly longer than high. The transverse process projects out and down from the neural arch for a distance equaling the length of the centrum, reaching to about the level of the neuro-central suture. It is a relatively wide, blade-like process similar to that of modern crocodilians. The parapophysis, situated anteriorly and ventrally on the side of the centrum is very short and faces straight out, thus differing considerably from the more advanced crocodilian condition in which both heads of the rib articulate on the transverse process. The dorsal centra resemble those of the cervicals in being strongly keeled, but are more heavily constructed. The anterior zygapophysis is similar in general to that of the cervical vertebrae, although somewhat shorter and sturdier. The posterior zygapophysis is also very similar to that of the cervical, but somewhat stronger and has a more prominent median cleft. The neural spines of the dorsal vertebrae are wider and heavier than in the cervicals, and arise from the posterior edge of the neural arch.

Ribs. All the ribs preserved are bicipital and articulate dorsally and ventrally (not on the same level, as do those of modern crocodiles). The cervical ribs are well developed, differing only slightly from those of eusuchians. The first cervical rib is a slender, two-headed element attached to the normal diapophysis and to a very small parapophysis, which is nothing more than an articular facet facing laterally and anteriorly on the bottom of the centrum near the anterior edge. The remaining cervical ribs are relatively slender and project posteriorly. They become longer and sturdier posteriorly and thus grade into the size of the dorsal ribs. The articulation of the tuberculum with the diapophysis on the transverse process is considerably larger than in later crocodiles, occupying the entire face of the process. The capitulum articulates ventrally and slightly anteriorly to the tuberculum. These ribs possess what appear to be the beginnings of uncinate "bulges," located about one-third of the way down the rib body and bearing prominent ridges on the anterior edges of their dorsal surfaces.

DISCUSSION

HISTORICAL REVIEW

The affinities of primitive crocodilians are uncertain due to the small number of early forms so far known. In addition to the Middle Triassic *Proterochampsa*, these are: *Protosuchus* of North America, and *Notochampsa* and *Erythrochampsa* of South Africa. (A questionable crocodilian two centimeters long, without skull or limbs, was described by Young in 1951 from the Upper Triassic of China; also an undescribed crocodilian from the Upper Triassic of Wales has been reported by Kermack [1956].) Of these three, *Protosuchus* is known from a skeleton, the other two from much less complete material. All three are late Triassic or earliest Jurassic in age.

Notochampsa istedana was described by Broom (1904) from the impressions of the undersides of most of the roofing bones of a skull, most of the dorsal armor, a scapula, a coracoid, parts of a humerus, radius and ulna, part of a femur, and parts of a tibia and fibula. A second specimen from the same general area (Barkly East, Cape Province, South Africa) was named by him *Notochampsa longipes*. This specimen consisted of a well preserved pelvis, a femur, tibia and fibula, some foot bones, and part of the dorsal armor. Both specimens were found in the upper part of the Stormberg series. Broom placed the two species in the same genus on the basis of the similarity of the dorsal armor.

Haughton (1924) excluded *Notochampsa istedana* from the Crocodilia and grouped it with *Pedeticosaurus* in a family Notochampsidae, which he referred to the thecodont suborder Pseudosuchia. He considered the family to be intermediate between the aëtosaurian thecodonts and the crocodiles. The other species, *N. longipes*, he separated from *Notochampsa*, placing it within the Crocodilia but not in any family, giving the following reason (1924:369):

"If Broom's *N. longipes* is to be kept in the genus *Notochampsa* then the genus must be considered to be characterised by the possession of a skull differing from that of a true Crocodile and of a typically crocodilian pelvis. This is not impossible; but until more is known of these forms it would seem best to separate the two forms from one another, classing *istedana* as one of the higher Pseudosuchians and erecting, as above, a new genus *Erythrochampsa* for the more truly Crocodilian *Erythrochampsa longipes*." This explanation reflects the then current philosophy of graded rather than mosaic evolution and may not be justifiable.

The following year von Huene (1925) studied the material and came to the conclusion that both genera were pseudosuchian thecodonts, forming the end members of an evolutionary sequence leading towards the crocodiles from the pseudosuchians. The sequence he proposed consisted of the following forms: *Erpetosuchus*, *Aetosaurus*, *Stegomosuchus*, *Sphenosuchus*, *Pedeticosaurus*, *Notochampsa* and, finally, *Erythrochampsa*.

Broom returned to the subject of *Notochampsa* and *Erythrochampsa* in 1927. He reviewed the work of Haughton and of von Huene and agreed to the generic separation of *Notochampsa* and *Erythrochampsa*, but remained firm in his conviction that they are closely related and are true crocodiles. He modified the classifications of Haughton and von Huene by placing both genera in the Notochampsidae and referring the family to the order Crocodilia.

No further information regarding the ancestry of crocodiles appeared until 1933, when Brown reported the well preserved crocodilian from the Upper Triassic or Lower Jurassic rocks of Arizona, to which he gave the name *Protosuchus richardsoni*, erecting for it the family Protosuchidae. Unfortunately, as in the other early crocodiles, nothing is preserved of the palatal region of *Protosuchus*.

The following year (1934) Mook presented a classification of the Crocodilia in which the Protosuchidae was placed in a new suborder, the Protosuchia, and no mention at all was made of either *Notochampsa* or *Erythrochampsa* as members of the Crocodilia. Romer (1945) combined *Protosuchus*, *Notochampsa*, *Erythrochampsa* and, questionably, *Pedeticosaurus* in the family Notochampsidae. In 1951 Colbert and Mook published a thorough description of *Protosuchus*, and placed *Notochampsa* and *Erythrochampsa* in the suborder Protosuchia as members of the family Protosuchidae.

Kälin (1955) modified Colbert and Mook's classification by removing *Notochampsa* and *Erythrochampsa* from the Protosuchidae and reuniting them in the Notochampsidae. He recognized the suborder Protosuchia and referred the Notochampsidae to it. The current classification of ancestral crocodilians is as follows:

Protosuchia
Protosuchidae
Protosuchus
Notochampsidae
Notochampsa
Erythrochampsa

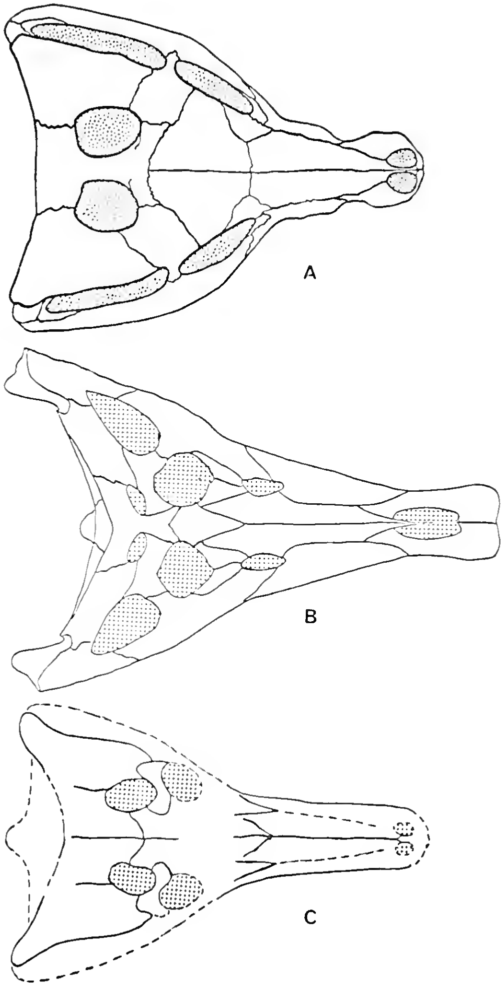


Fig. 6. Comparison of dorsal view of skull in A, *Protosuchus*; B, *Proterochampsa*; C, *Notochampsa*; not drawn to scale. (A, after Colbert and Mook; C, after Broom.)

The discovery of *Proterochampsa* requires a reappraisal.

THE AFFINITIES OF *PROTEROCHAMPSA*

In comparing *Proterochampsa* with these early crocodilians and with members of the

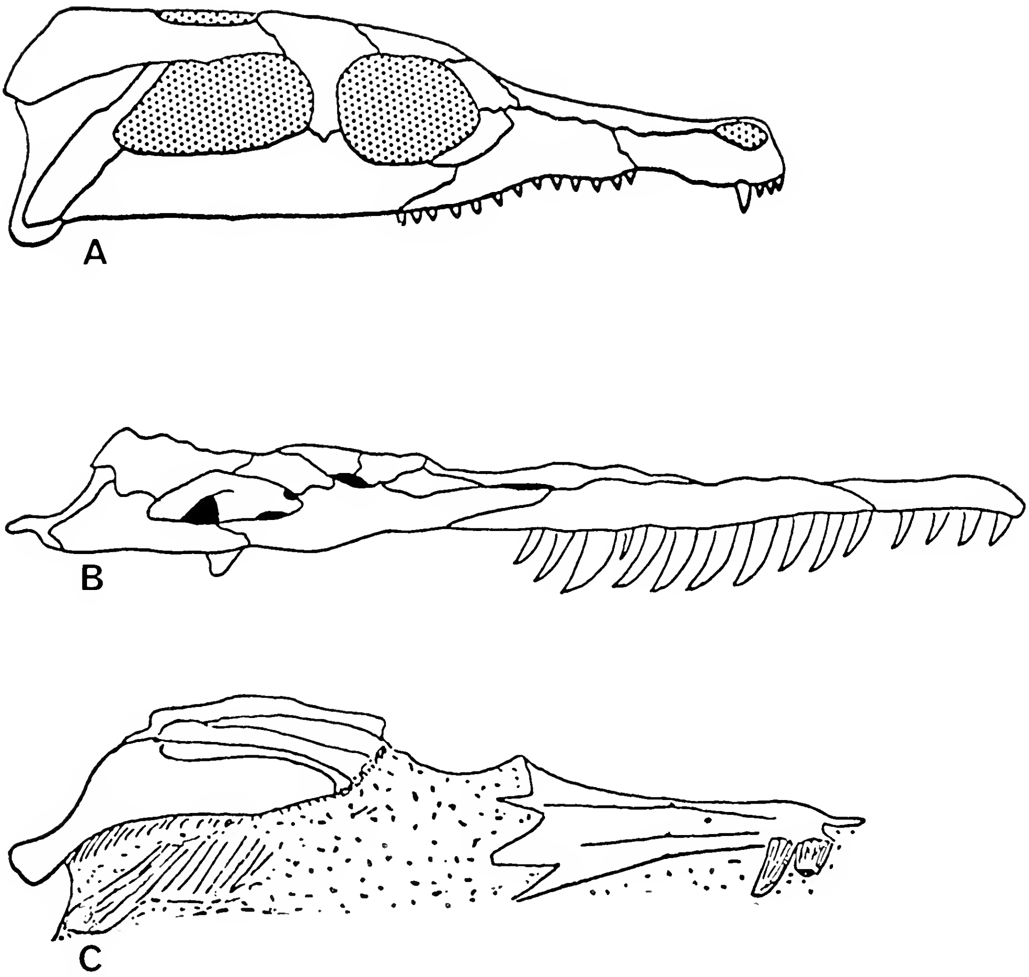


Fig. 7. Profile comparison of skulls of A, *Protosuchus;* B, *Proterochampsa;* C, *Notochampsa;* not drawn to scale. (A, after Colbert and Mook; C, after von Huene.)

Thecodontia, it becomes evident that *Proterochampsa* represents an excellent example of mosaic evolution and provides many of the characters expected in a transitional form. The snout and the dorsum of the skull generally are indistinguishable from those of a modern crocodile (except for the primitive antorbital fenestrae). On the other hand, the posterior part is remarkably like that of a primitive thecodont, except for its flatness and reduced supratemporal fenestrae. The palatal area is again quite like that of the primitive thecodonts except for the transitional features of the secondary palate and the development of the pterygoid flanges.

In trying to place *Proterochampsa* within the classification of the early Crocodilia we are faced as usual with the problems presented by inadequate material. Of *Proterochampsa* we have only the skull and a few vertebrae and ribs. *Protosuchus* is known from a skeleton, but the skull is imperfect, especially as regards the ventral surface; *Notochampsa* is represented by a very poor skull and some postcranial material; and *Erythrochampsa* is known only from postcranial elements. The main basis for relating *Protosuchus*, *Notochampsa*, and *Erythrochampsa* to each other has been the character of the postcranium: principally the similarities of the pectoral girdles of *Notochampsa* and *Protosuchus* and the pelvic girdles of *Erythrochampsa* and *Protosuchus*.

When the skull of *Proterochampsa* is compared with that of *Protosuchus* it is immediately apparent that they do not resemble one another sufficiently to be considered as members of the same phylogenetic line. The skull of *Protosuchus* is short relative to width and considerably deeper than either *Proterochampsa* or *Notochampsa* (see Figure 10). The orbits of *Protosuchus* are nearly on a vertical plane, facing outward and forward, while those of *Proterochampsa* are on a horizontal plane, facing upward. The snout of *Protosuchus* is short (less than half the total length of the skull) and lacks antorbital fenestrae, while that of *Proterochampsa* is long (over half the total skull length), and has prominent antorbital fenestrae. *Protosuchus* has a very lightly sculptured skull compared to the heavily sculptured skull of *Proterochampsa*. In *Protosuchus* the external nares are small, clearly separated, and at the very tip of the snout. Those of *Proterochampsa* are quite the opposite, being elongate, separated only by a thin nasal process and situated considerably back from the tip of the snout. In *Protosuchus* the squamosal is large and overlies the quadrate and quadratojugal completely; in *Proterochampsa* the squamosal is relatively small and overlies none of the quadratojugal and only a part of the quadrate.

The resemblances between the two forms are not impressive. Both have sculptured skulls (although different sculpturing), small supratemporal fenestrae, amphicoelous vertebrae, and a relatively small atlas. Both *Protosuchus* and *Proterochampsa* are crocodilians, but on the basis of skull morphology it would appear that *Proterochampsa* is closer to the main line of crocodilian evolution than is *Protosuchus*.

A much closer resemblance exists between *Proterochampsa* and *Notochampsa* as regards the skull. In *Notochampsa* this is relatively long compared to width (the snout occupies more than half the length of the skull), is relatively flat, and the orbits are in the horizontal plane, all of these features being in common with *Proterochampsa*. Both *Proterochampsa* and *Notochampsa* possess an auditory canal on the posterior face of the skull. Regarding the presence of antorbital fenestrae in *Notochampsa*, Broom says there are none, von Huene says there are, and Haughton was unable to decide; the specimen is too imperfect for a definite decision.

The skulls of *Notochampsa* and *Proterochampsa* quite evidently resemble each other more than either of them resembles *Protosuchus*. This presents the problem of the taxonomic position of *Proterochampsa* and indeed requires a re-evaluation of *Protosuchus* as an ancestral crocodile and of the role of the pseudosuchian thecodonts as possible ancestors.

Proterochampsa does not belong in the suborder Protosuchia on the basis of most taxonomic characters now used to define that group. The possibilities of phylogenetic placement then are the following: the suborder Protosuchia may be redefined as a group including all pre-Jurassic crocodilians without special regard to morphological similarities, and *Proterochampsa* placed in it; or *Proterochampsa*, *Notochampsa*, and *Erythrochampsa* may be grouped into a separate suborder leading to the Mesosuchia, and the Protosuchia retained as an aberrant lineage arising from the early crocodilian stock.

On the basis of skull comparison, it appears likely that *Protosuchus* is an aberrant offshoot from the line which gave rise to the Crocodilia, possessing some characters of both thecodonts and crocodiles. It may be argued that *Proterochampsa* cannot be legitimately compared to *Protosuchus* until

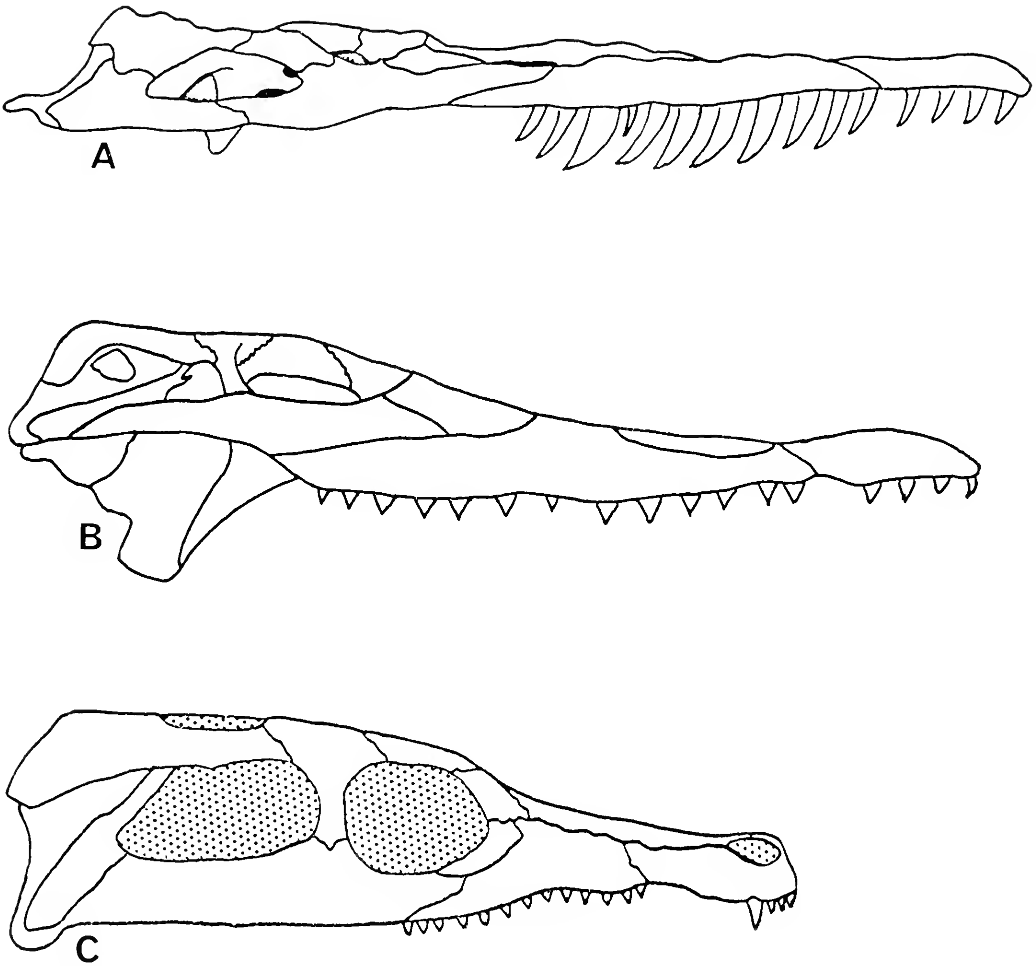


Fig. 8. Profile comparison of skulls of A, *Proterochampsa;* B, *Crocodylus;* C, *Protosuchus;* not drawn to scale.

something is known about the pectoral and pelvic girdles of the former. However, in this respect there are only three possibilities for the girdles of *Proterochampsa*: they may be the same as *Protosuchus*, more crocodilian, or less crocodilian. None of these possibilities alters the fact that *Protosuchus* has strayed considerably from the earlier line of more typical crocodilians represented by *Proterochampsa*.

If *Protosuchus* is regarded as representing an aberrant group, one not on the direct ancestral line leading to the mesosuchians, the possibility that *Proterochampsa* and *Notochampsa* actually belong within the suborder Mesosuchia must be examined.

The suborder Mesosuchia is defined as having a secondary palate formed by the premaxillae, the maxillae, and the palatines, the pubis excluded from the acetabulum, the postorbital bar at the dorsal surface of the skull, and the vertebrae amphicoelous or platycoelous. To redefine the suborder to include *Proterochampsa* and the Notochampsidae it would be necessary, so far, only to modify the definition with regard to the secondary palate. However, to redefine the Mesosuchia in this way would be to disrupt the classification of what appears to be a natural group, or at least a fairly uniform evolutionary grade. The acquisition of the secondary palate and internal nares of the Mesosuchia marks a significant phylogenetic stage, and is remarkably consistent throughout the nine families and thirty-seven genera of the suborder. In addition to the more primitive condition of the palate (at least in *Proterochampsa*), *Notochampsa* and *Proterochampsa* also possess a more primitive condition of the external auditory meatus, while the mesosuchians are consistent in the transitional nature of this character (see discussion of the ear). In general, the Mesosuchia presents the appearance of a well established group, greatly diversified, into which *Proterochampsa* and the Notochampsidae would fit less consistently than do any of the other families within this suborder. The remaining alternative is to place *Proterochampsa* and the Notochampsidae in a separate suborder, recognizing that the Notochampsidae are very poorly known and may later prove not to be that closely related to *Proterochampsa*. However, the elongate skull and dorsal orbits, particularly the latter, indicate that *Notochampsa* had acquired the aquatic habitus of the Crocodilia.

EARLY HISTORY OF THE CROCODILIA

The evolutionary trends within the Crocodilia only become relatively well documented after the late Jurassic, although specialized marine mesosuchians are known from the early and middle parts of this period. The early and middle Jurassic were probably times of great divergence within the order, but non-marine representatives are practically unknown, due to the lack of continental sediments of these ages. The primitive Triassic members of the order, as previously mentioned, are few in number and most of them are poorly preserved. Thus, there is a gap in knowledge from the late Triassic to the late Jurassic, coupled with a dearth of material from the earlier Triassic.

Protosuchus was the first reasonably well preserved early crocodilian found. Although not closely resembling later crocodiles, it possessed a number of crocodilian characters, especially in the postcranial skeleton. The strongly crocodilian coracoid and pubis, together with the more thecodont-like skull, suggested a pattern of gradual acquisition of crocodilian characters from a pseudosuchian ancestry. *Notochampsa* and *Erythrochampsa*, then as now, were too poorly known to contribute evidence of any great value. All of these forms were of very latest Triassic age, with *Protosuchus* considered as more or less the prototype of later crocodiles. Yet by the earliest Jurassic there existed good mesosuchian representatives; the order was by then well differentiated and was undergoing rapid radiation. This would leave very little time between the rather thecodont-like *Protosuchus* and the earliest mesosuchians. Although such rapid evolution and radiation as this view would imply might not be impossible it is rather unlikely.

The discovery of *Proterochampsa* changes all this, however, by demonstrating that a number of "modern" cranial characters of the Crocodilia were already in existence by the late Middle Triassic. The conclusion that the Crocodilia became differentiated relatively early in the history of the Thecodontia rather than being an "end product" of that group seems inescapable. *Proterochampsa* is certainly a crocodile, and at present is the best known representative of the primitive members of that group. It is of course possible that it is not the ancestor of the later crocodiles, but it appears to be closer to such an ancestor, at least morphologically, than any of the other presently known early forms.

This being so, the non-crocodilian features of *Protosuchus* might be explained in one of several ways: 1) the Crocodilia arose from a non-pseudosuchian group of aquatic

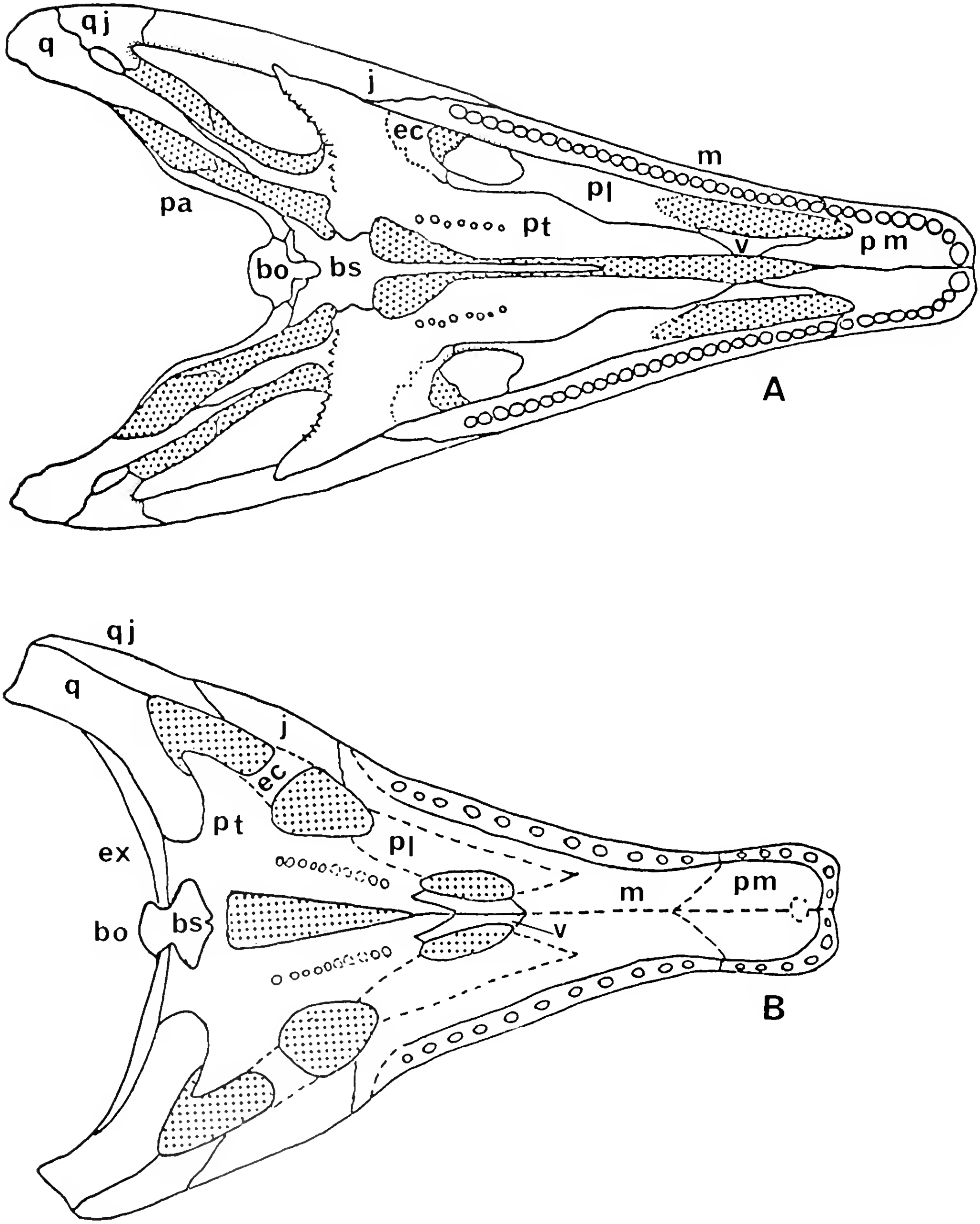


Fig. 9. Comparison of ventral view of skull in A, *Chasmatosaurus;* and B, *Proterachampsa.* × 1/3.

thecodonts, in which case the Protosuchia could be regarded as forms that secondarily became adapted for terrestrial life; 2) the Crocodilia arose from a primitive group of terrestrial thecodonts, possibly early pseudosuchians, in which case the Protosuchia could be regarded as having retained the primitive terrestrial features of the transitional group; 3) the Protosuchia were not true crocodilians and independently evolved crocodilian characters. Of these possibilities the last seems to be the least likely on present evidence, although the other two are almost equally uncertain. Any one of these possibilities, however, could explain the existence of groups that possessed a few good crocodilian characters but were more thecodont in habitus.

The primitive crocodilian recently discovered in the Triassic of Wales has been characterized by Dr. K. A. Kermack (pers. comm.) as a "crocodile trying to be a dinosaur." This description might be applied to some of the other archosaurs that appear to be in the "fringe area" of the Crocodilia, such as *Pedeticosaurus, Sphenosuchus, Platyognathus*, and perhaps *Hesperosuchus*. In this context *Protosuchus* might be considered as less successful in "becoming a dinosaur" than the sphenosuchians, and therefore as looking more like a typical crocodile.

The solution to the question of crocodilian origins naturally lies within the Thecodontia, but unfortunately this group is not well understood at present. Among early thecodonts, *Chasmatosaurus* somewhat resembles *Proterochampsa* in the palatal area. Although *Chasmatosaurus* is extremely primitive, it may nevertheless represent the group of thecodonts from which the Crocodilia arose.

CLASSIFICATION OF THE EARLIEST CROCODILIA

On the basis of this study it is proposed that the primitive, Triassic crocodilians be divided into two groups, the suborder Protosuchia, characterized by the Protosuchidae, and including, questionably, the sphenosuchid thecodonts, and a new suborder, the Archaeosuchia, for the Proterochampsidae and, provisionally, the Notochampsidae.

ARCHAEOSUCHIA new suborder

The Archaeosuchia may be defined as follows: Crocodilia with orbits in dorsal plane of skull, cranial table sculptured, snout long relative to width, palatines not participating in secondary palate, postorbital bar at surface of skull, auditory canal on posterior face of skull, vertebrae amphicoelous; pubis elongate, nearly or completely excluded from the acetabulum.

NOTOCHAMPSIDAE Haughton 1924

The family Notochampsidae, although erected in 1924, has never been defined. The following definition is proposed for it: premaxillae small, external nares divided, squamosals large, forming most of lateral border of cranial table, frontals not fused, participating in border of supratemporal fenestrae; coracoid enlarged, similar in shape to scapula. The type genus of the family is *Notochampsa*.

PROTEROCHAMPSIDAE new family

Proterochampsa differs from the notochampsids to a degree sufficient to warrant the erection of a family for its reception. This may be defined as follows: Archaeosuchia with external nares united at midline, premaxillae large, frontals small, fused, not participating in border of supratemporal fenestrae, squamosals small, limited to posterior border of skull. *Proterochampsa* is designated as the type genus of the family.

This would result in the following classification:

- PROTOSUCHIA Mook 1934
  - Protosuchidae Brown 1933
    - *Protosuchus* Brown 1933
- PROTOSUCHIA *incertae sedis*
  - Sphenosuchidae Haughton 1924
    - *Sphenosuchus* Haughton 1915
  - Sphenosuchidae *incertae sedis*
    - *Pedeticosaurus* Van Hoepen 1915
    - *Platyognathus* Young 1944
- ARCHAEOSUCHIA new suborder
  - Proterochampsidae new family
    - *Proterochampsa* Reig 1959

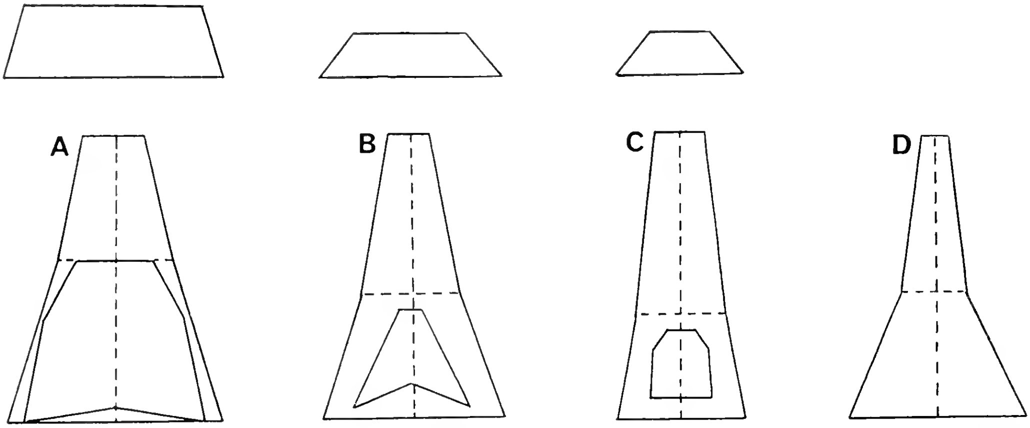


Fig. 10. Diagrammatic comparison of skull relationships of A, *Protosuchus*; B, *Proterochampsa*; C, *Crocodylus*; D, *Notochampsa*. Length of the skull is reduced to unity.

Notochampsidae Haughton 1924
Notochampsa Broom 1904
Erythrochampsa Haughton 1924

SUMMARY

Proterochampsa barrionuevoi represents a late Middle Triassic line of crocodilians showing many of the "progressive" features characteristic of later members of the order. The dorsum of the skull is almost identical with that of the modern *Crocodylus* except for the presence of an antorbital fenestra and the lateral position of the quadratojugal. Ventrally, a rudimentary secondary palate has evolved, consisting only of the premaxilla and the maxilla, while the very small pterygoid teeth and an interpterygoidal vacuity are retained. The posterior surface of the skull shows a meatal groove beginning at the ventral tip of the squamosal and passing anterior to the exoccipital. This is possibly the beginning of the reacquisition of an otic notch in the Crocodilia. The mandible is distinctive in the absence of a retroarticular process, the large size of the articular bone, and the slight angle. In general the jaw appears to have been a relatively weak structure. The marginal teeth are slightly ovoid, rather slender, and slightly curved posteriorly, fitting the typical thecodont pattern. The small number of these teeth (17) may be a primitive character or may indicate a specialized diet, perhaps fish or carrion. The pterygoid teeth are so small that it is difficult to believe they were of any great use. The skull of *Proterochampsa* shows an interesting combination of primitive, transitional, and advanced characters; it provides an excellent example of mosaic evolution.

The postcranium is represented only by the anterior vertebrae and ribs. The vertebrae are strongly amphicoeleous and have prominent keels. The ribs are all bicipital, with small uncinate processes present on those of the thoracic region.

The Crocodilia have long been considered an "end product" that arose from late Triassic thecodonts by the gradual acquisition of distinctive characters and an aquatic habitus. *Proterochampsa* provides evidence that the major features of crocodilian skull structure were in existence by the latter part of the Middle Triassic. A re-evaluation of the known primitive crocodilians suggests that there were apparently two lines of evolution during the Triassic. On one of these lines, crocodilian characters, most of which are shown in the skull of *Proterochampsa*, were evolved, while in the other, characterized by *Protosuchus*, the trend led away from the crocodilian way of life toward a more terrestrial habitat and acquisition of the necessary morphologic features for successful competition with its thecodont relatives.

On the basis of this study the family Proterochampsidae is proposed, and the primitive crocodilians are divided into two suborders, the Protosuchia, consisting of Protosuchidae and, questionably, the sphenosuchoidean thecodonts, and a new suborder, the Archaeosuchia, for the Proterochampsidae and, provisionally, the Notochampsidae.

RESUMEN

Proterochampsa barrionuevoi representa una línea de cocodrilos del Triásico medio que muestra muchos de los rasgos "progresivos" que caracterizan a los miembros más avanzados del orden. La superficie dorsal del cráneo es casi igual a la de *Crocodylus* de la actualidad, pero retiene los carácteres primitivos de las fosas anteorbitarias y de la posición lateral del cuadrado-yugal. Por el lado ventral, muestra un paladar secundario rudimentario formado por los premaxilares y los maxilares, y a la vez retiene los pequeños dientes pterigoideos y la fosa interpterigoidea que son mas bien características de los técodontes primitivos. La superficie posterior del cráneo posee un surco meatal que comienza en el punto ventral del escamoso y pasa por delante del exoccipital. Esto puede indicar el comienzo de la adquisición de la muesca ótica en el orden Crocodilia. La mandíbula se destaca por la falta del proceso retroarticular, por el tomaño grande del articular, y por la pequeñez del angulo. En general la mandíbula parece haber sido una estructura relativamente débil. Los dientes marginales son ligeramente ovoides, delgados, y algo recurvados hacia atrás, siendo su aspecto similar al de los técodontes. El pequeño numero de estos dientes (17) puede ser un carácter primitivo o quizás un indicio de una dieta especializada, que podría haber consistido en peces o carroña. Los dientes pterigoideos son tan reducidos que resulta difícil creer que fuesen de utilidad alguna. El cráneo de *Proterochampsa* muestra una combinación sumamente interesante de carácteres primitivos, transicionales, y avanzados, por lo que proporciona un excelente ejemplo de evolución mosaico.

La región post-craneana de *Proterochampsa* está unicamente representada por las vértebras y las costillas anteriores. Las vértebras son biconcavas y tienen quillas prominentes. Las costillas son todas bicipitales y las de la región torácica poseen pequeños procesos uncinados.

Tradicionalmente se ha considerado el orden Crocodilia como el "producto final" de una cepa de técodontes del Triásico superior, diferenciándose por la adquisición gradual de carácteres típicos y un habito acuático. *Proterochampsa* demuestra que los principales rasgos diagnósticos del orden Crocodilia ya existian en el Triásico medio. Una reevaluación de los cocodrilos primitivos conocidos hasta ahora sugiere la posibilidad de que durante el Triásico habia dos líneas de evolución. En una de estas líneas se desarrollaron los rasgos típicos del orden Crocodilia, la mayor parte de los cuales se ven en el cráneo de *Proterochampsa*. La otra línea, caracterizado por *Protosuchus*, se apartó del ambiente típico de los cocodrilos hacia una vida más terrestre, con la subsiguiente adquisición de los rasgos necesarios para competir con técodontes del mismo hábito.

Como resultado de este estudio se propone la creación de la familia Proterochampsidae y la división de los cocodrilos primitivos en dos subórdenes: Protosuchia, constituida por *Protosuchus* y, presuntamente, los técodontes esfenosucoideos, y un nuevo suborden, Archaeosuchia, para la Proterochampsidae y, provisionalmente, la Notochampsidae.

LITERATURE CITED

Bonaparte, J. F. 1962. Descripción del craneo y mandíbula de *Exaeretodon frenguellii*, Cabrera. Pub. Mus. Munic. Cienc. Nat. Trad. Mar del Plata, **1**: 135–202.

———. 1963. *Promastodonsaurus bellmani*, n. g. et n. sp., capitosaurido del Triásico Medio de Argentina. Ameghiniana, **3**: 67–77.

Broom, R. 1904. On a new crocodilian genus (*Notochampsa*) from the upper Stormberg beds of South Africa. Geol. Mag., Dec. 5, **1**: 582–584.

———. 1927. On *Sphenosuchus* and the origin of the crocodiles. Proc. Zool. Soc. London, 1927 (7): 359–370.

Brown, B. 1933. An ancestral crocodile. Amer. Mus. Novit., No. **638**: 1–4.

Casamiquela, R. M. 1960. Noticia preliminar sobre dos nuevos estagonolepoideos argentinos. Ameghiniana, **2**: 3–10.

Colbert, E. H. and C. C. Mook. 1951. The ancestral crocodilian *Protosuchus*. Bull. Amer. Mus. Nat. Hist., **97**: 149–180.

Edinger, T. 1938. Über Steinkerne von Hirn und Ohr-Höhlen der Mesosuchier *Goniopholis* und *Pholidosaurus* aus dem Buckeburger Wealden. Acta Zoologica, **19**: 467–504.

Frenguelli, J. 1948. Estratigrafía y edad del llamado Rético en la Argentina. Gaea, **8**: 159–309.

Haughton, S. H. 1915. A new thecodont from the Stormberg beds. Ann. South African Mus., **12** (3): 65–106.

———. 1924. The fauna and stratigraphy of the Stormberg series. Ann. South African Mus., **12** (8): 323–497.

Huene, F. von. 1925. Die Bedeutung der *Sphenosuchus*-Gruppe für den Ursprung der Krokodile. Zeitschr. Indukt. Abstammungs-und Vererbunglehre, **38**: 307–320.

Kälin, J. 1955. Crocodilia. *In*: Traité de Paléontologie, ed. J. Piveteau, vol. 5. Paris, Masson et Cie, pp. 695–787.

Kermack, K. A. 1956. An ancestral crocodile from South Wales. Proc. Linn. Soc. London, Session 166: 1–2.

Mook, C. C. 1934. The evolution and classification of the Crocodilia. Jour. Geol., **42**: 295–304.

Reig, O. A. 1959. Nuevos reptiles arcosaurios del Triasico de Ischigualasto. Rev. Asoc. Geol. Argentina, **13**: 257–270.

Romer, A. S. 1945. Vertebrate paleontology. Second edition. Chicago: University of Chicago Press, pp. 1–677.

———. 1960. Vertebrate-bearing continental Triassic strata in Mendoza region, Argentina. Bull. Geol. Soc. America, **71**: 1279–1294.

———. 1962. The fossiliferous Triassic deposits of Ischigualasto, Argentina. Breviora, Mus. Comp. Zool., No. **156**: 1–7.

Van Hoepen, E. C. N. 1915. Contributions to the knowledge of the reptiles of the Karroo Formation. Ann. Transvaal Mus., **5**: 83–87.

Young, C. C. 1944. On a supposed new pseudosuchian from the Upper Triassic saurischian-bearing red beds of Lufeng, Yunnan, China. Amer. Mus. Novit., No. **1264**: 1–4.

———. 1951. The Lufeng saurischian fauna in China. Paleont. Sinica, **134**: 19–95.

(*Received 4 January, 1966.*)

ABBREVIATIONS

am	auditory meatus
bo	basioccipital
bs	basisphenoid
ec	ectopterygoid
ex	exoccipital
f	frontal
j	jugal
l	lacrimal
m	maxilla
n	nasal
op	opisthotic
p	parietal
pa	paraoccipital
pl	palatine
pm	premaxilla
po	postorbital
prf	prefrontal
pt	pterygoid
q	quadrate
qj	quadratojugal
so	supraoccipital
sq	squamosal
v	vomer

TABLE I
TABLE OF MEASUREMENTS IN MILLIMETERS

	MCZ 3408	MACN 18165
Total length of the skull, from the posterior border of the quadrate to the end of the snout at the midline	395	440
Length of the skull from the occipital crest to the end of the snout at the midline	325	375
Length of the skull from the occipital condyle to the end of the snout	350	—
Width of skull between external borders of quadratojugals	270	—
Width of skull between external borders of the orbit	130	—
Maximum diameter of the orbit	45	45
Width between the lateral borders of the supratemporal fenestrae	84	—
Maximum diameter of the supratemporal fenestra	28	42
Maximum diameter of the antorbital fenestra	38	44
Maximum diameter of the infratemporal fenestra	71	89
Width between the medial borders of the infratemporal fenestrae	124	—
Distance between the supratemporal fenestrae	30	—
Distance between the orbits	41	—
Width of the skull between the antorbital fenestrae	58	—
Width of the snout at the anterior border of the antorbital fenestrae	108	109
Width of the snout at the "canine notch"	55	59
Length of the snout from the anterior border of the orbit to the tip of the premaxilla	238	280
Length of the snout from the anterior border of the antorbital fenestra to the tip of the snout	183	208
Distance from the anterior border of the internal nares to the tip of the premaxillae	—	184
Maximum diameter of each internal naris	—	13
Distance from the posterior border of the internal nares to the occipital condyle	144	—
Length of maxillary tooth row	155	207

TABLE II
COMPARISON OF CHARACTERS IN CROCODILES

P—primitive T—transitional A—advanced X—absent

CHARACTER	ARCHAEOSUCHIA	PROTOSUCHIA	MESOSUCHIA	EUSUCHIA
Development of secondary palate	P	?	T	A
Position of postorbital bar	P	P	T	A
Orientation of the orbits	A	P	A	A
Orientation of the external nares	A	P	A	A
Dental differentiation	P	P	T	A
Relative length of the snout	A	P	A	A
Presence of palatal teeth	P	?	A	A
Sculptured cranial table	A	P	A	A
Skull height	A	P	A	A
Antorbital fenestra	T	A	T	A
Auditory canal	P	X	T	A
Vertebral structure	P	P	T	A
Rib articulations	P	T	A	A

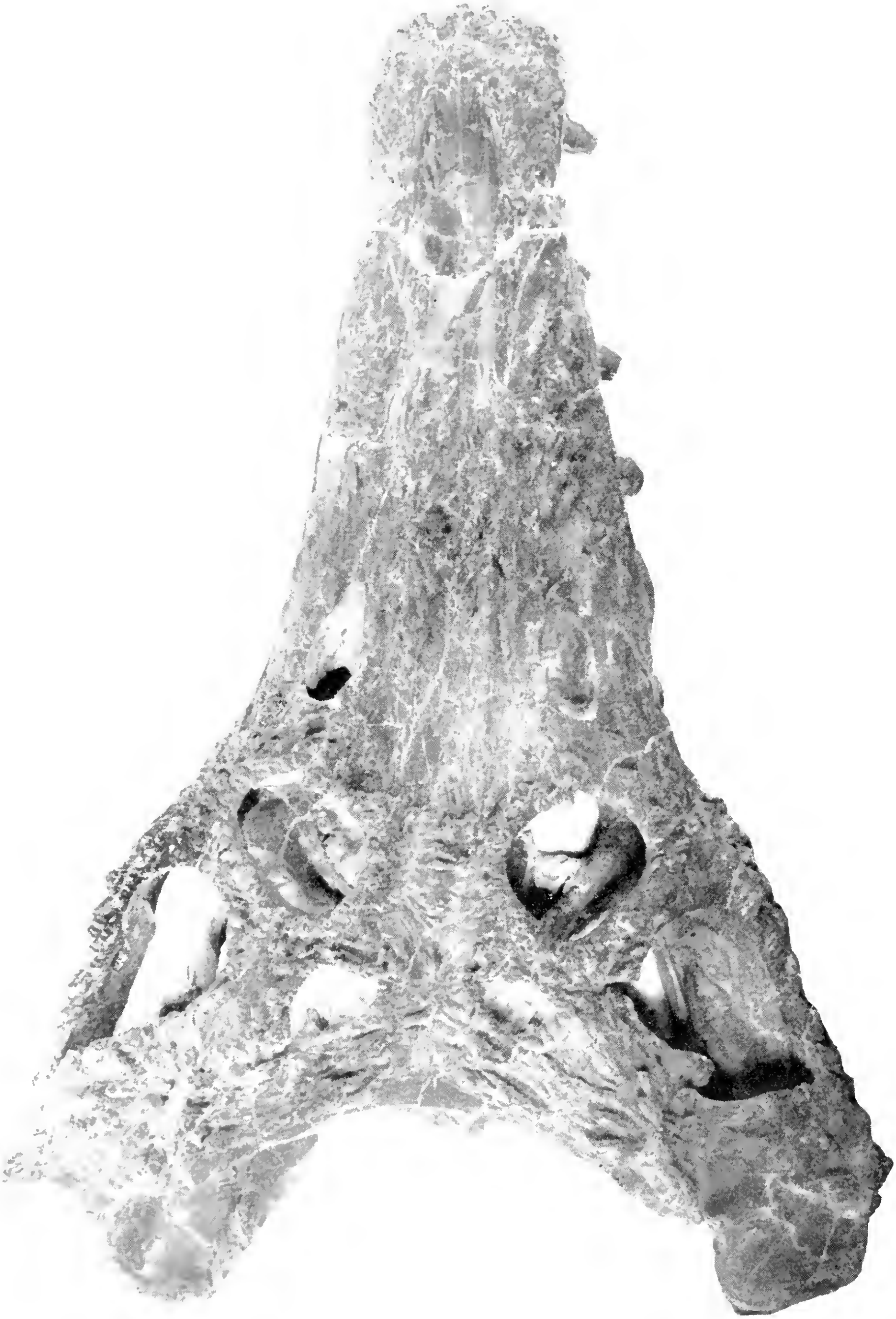


Plate I. Dorsal view of skull of *Proterochampsa barrionuevoi,* MCZ 3408. × 1/2 approx.

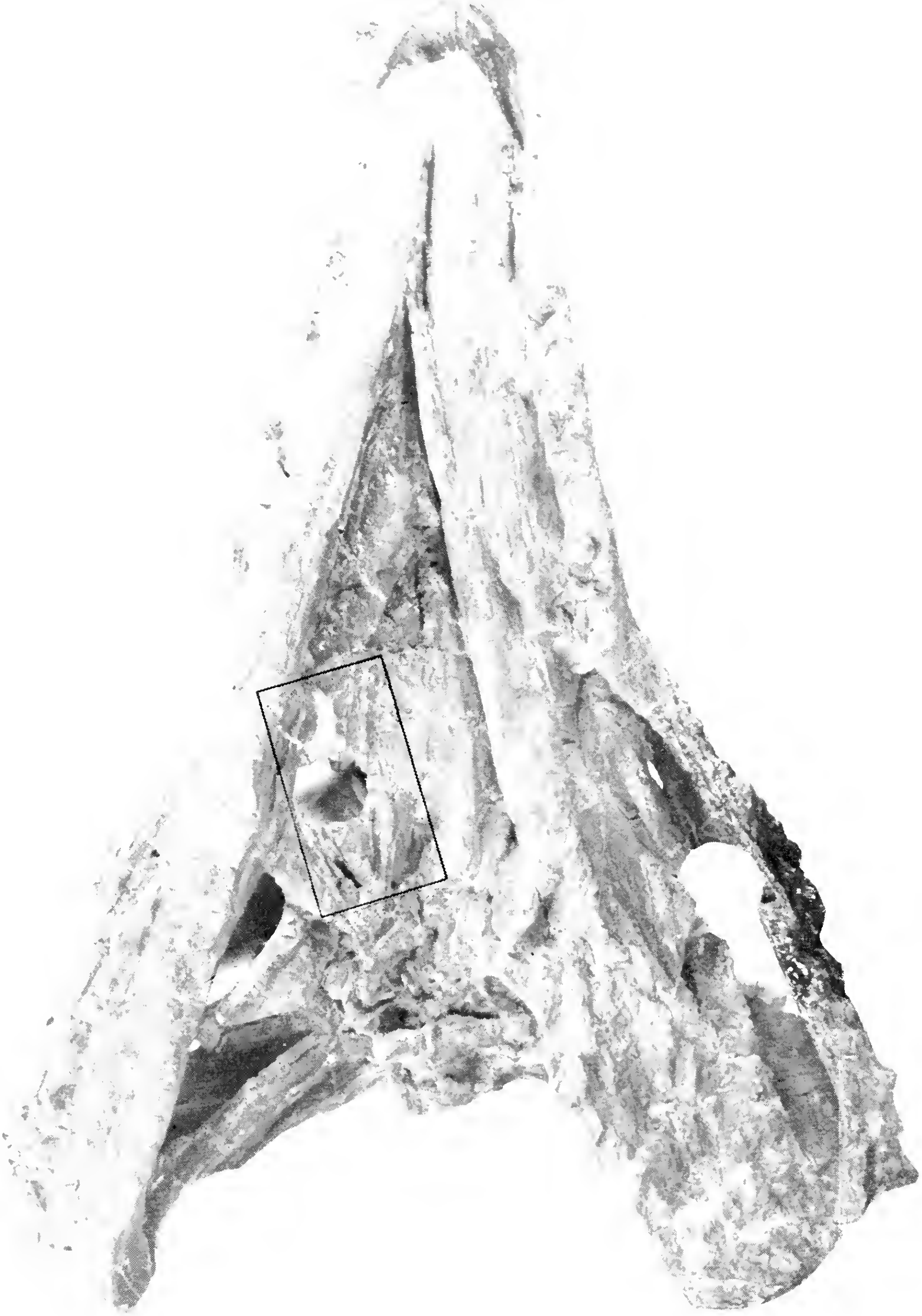


Plate II. Ventral view of skull of *Proterochampsa barrionuevoi*, MCZ 3408, showing mandible crushed into skull. × ½ approx.

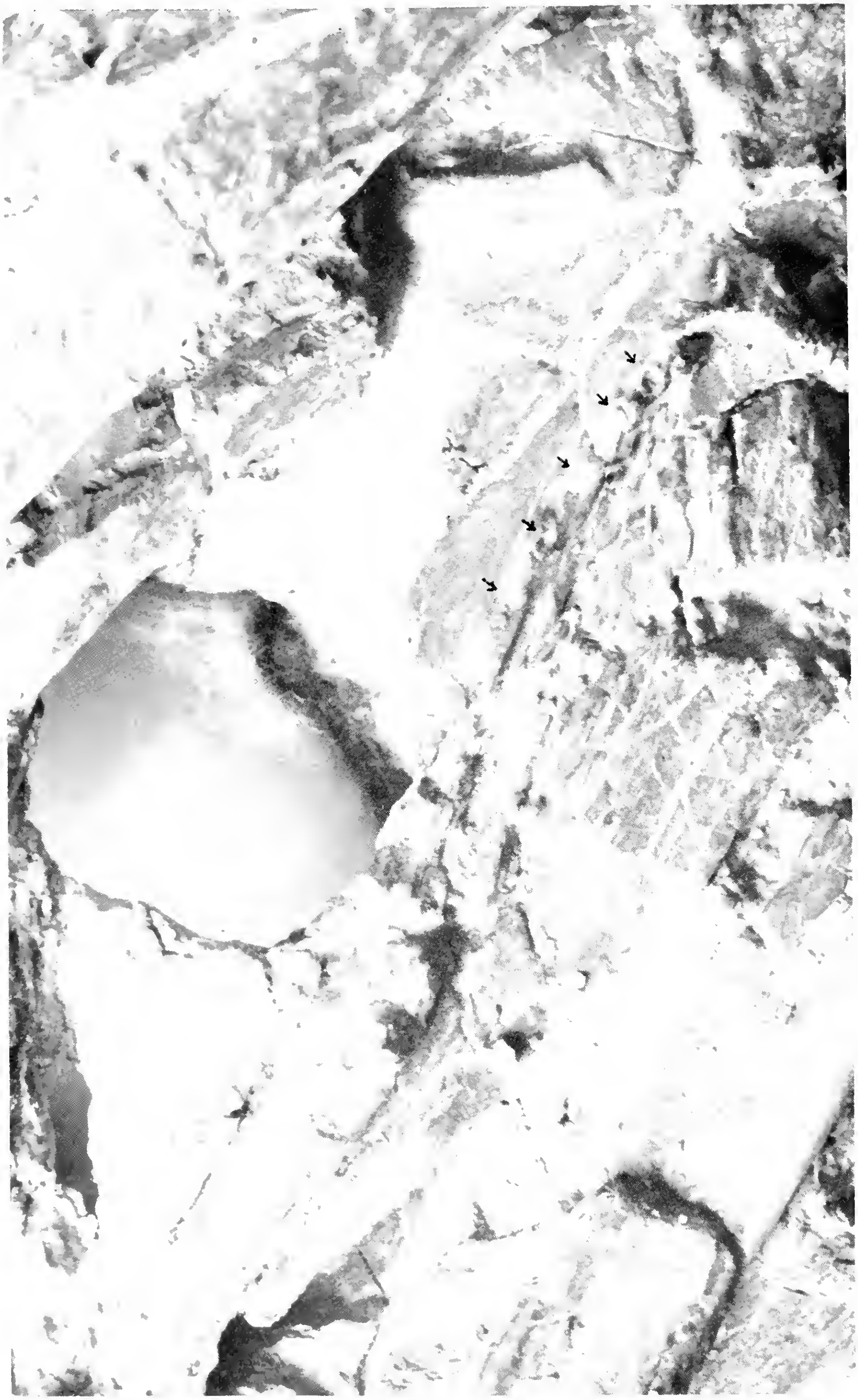


Plate III. Inset from Plate II; arrows show pterygoid teeth, MCZ 3408. × 2.

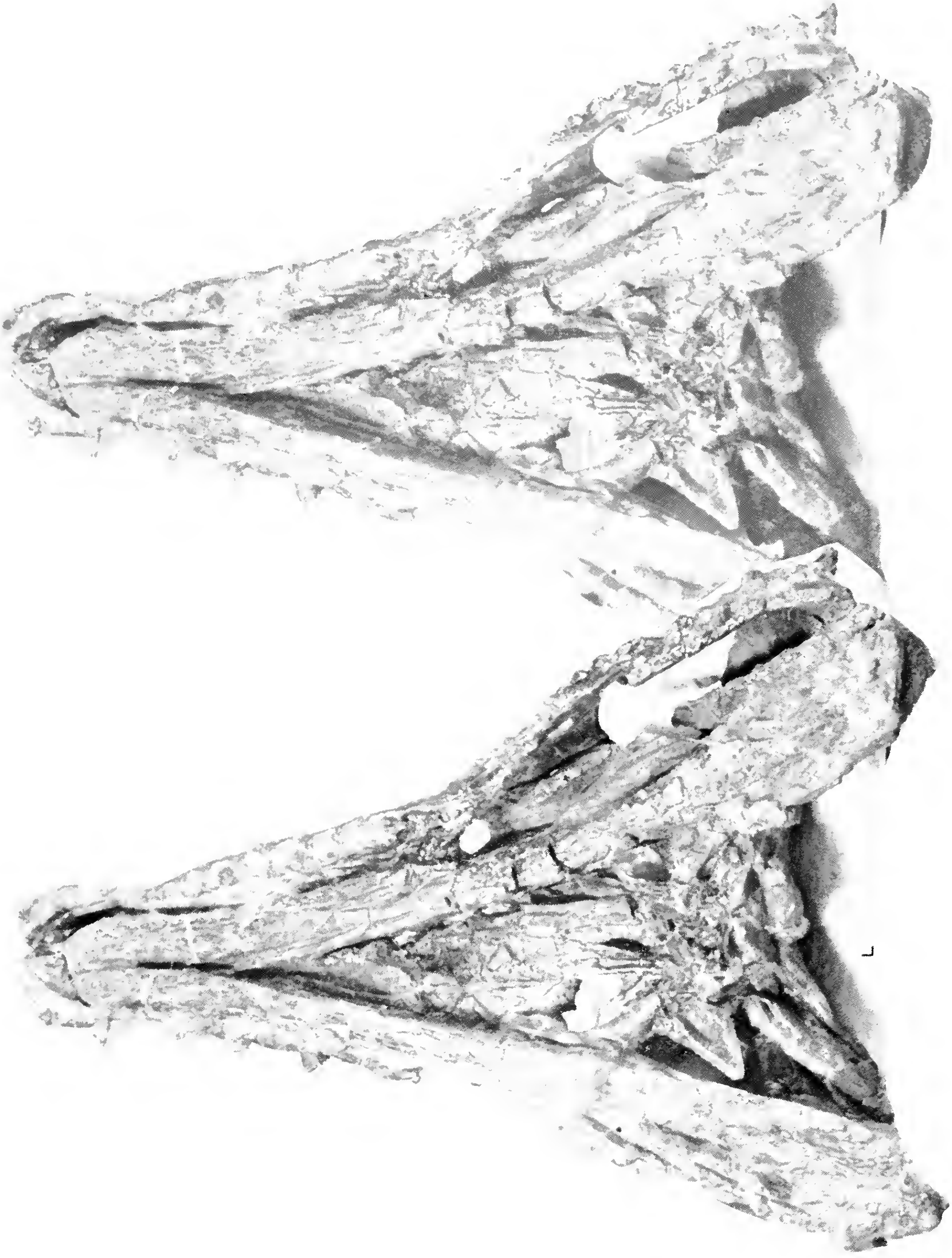
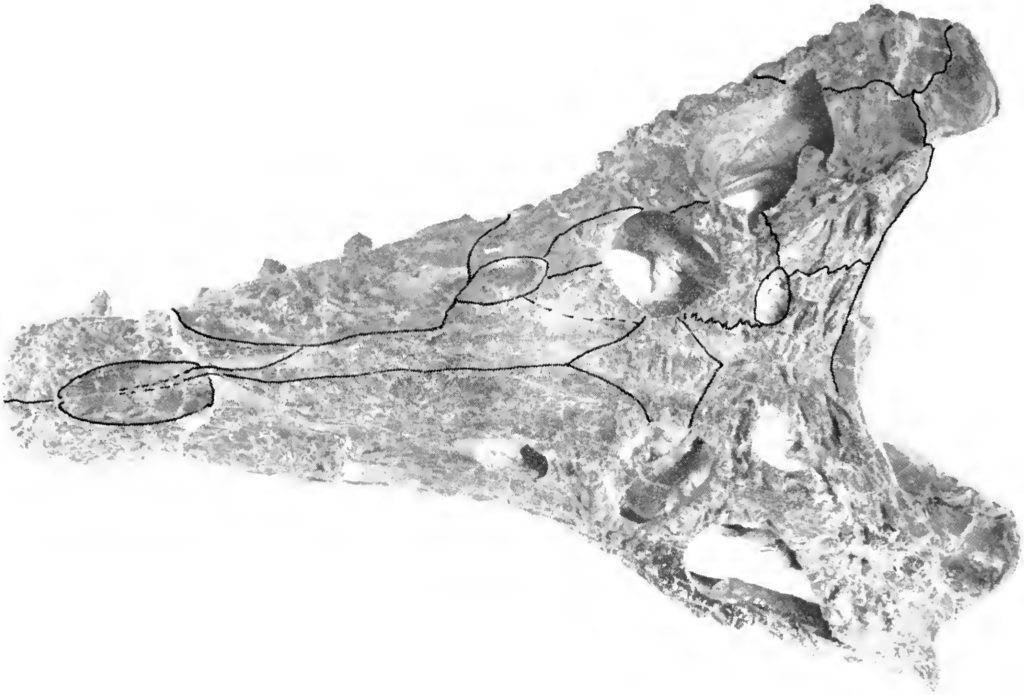


Plate IV. Ventral aspect of skull and mandible in stereoscopic view, MCZ 3408. × 1/3.



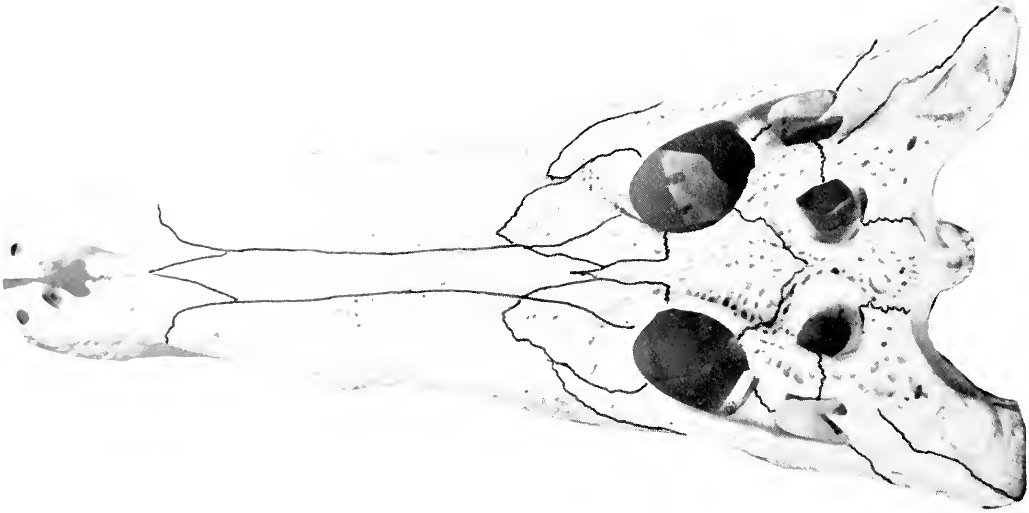


Plate V. Comparison of *Proterochampsa barrionuevoi*, MCZ 3408 (top), and *Crocodylus niloticus* (bottom), in dorsal view × 1/3.

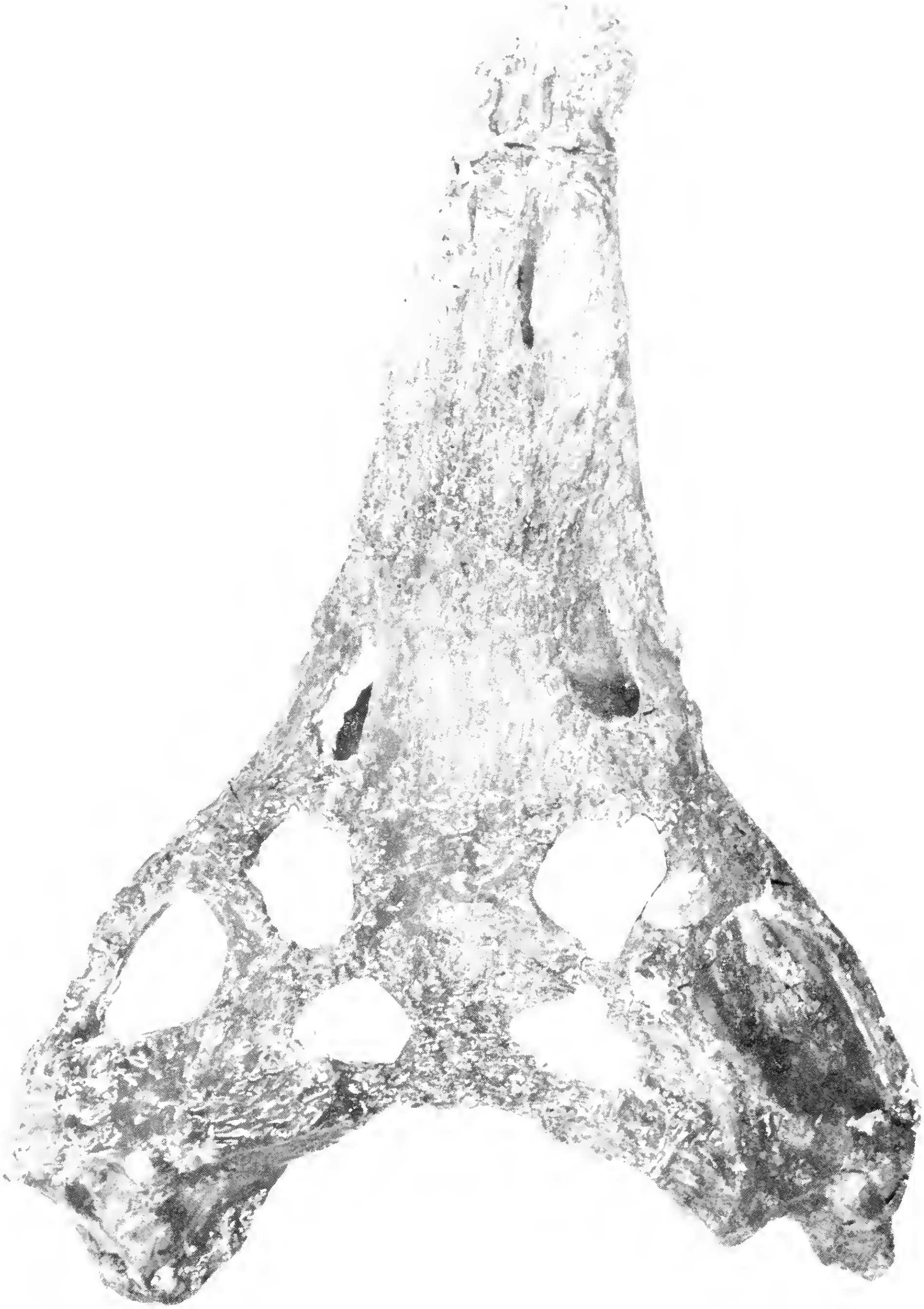


Plate VI. Dorsal view of *Proterochampsa barrionuevoi*, MACN 18165, partially restored. × 1/2 approx.

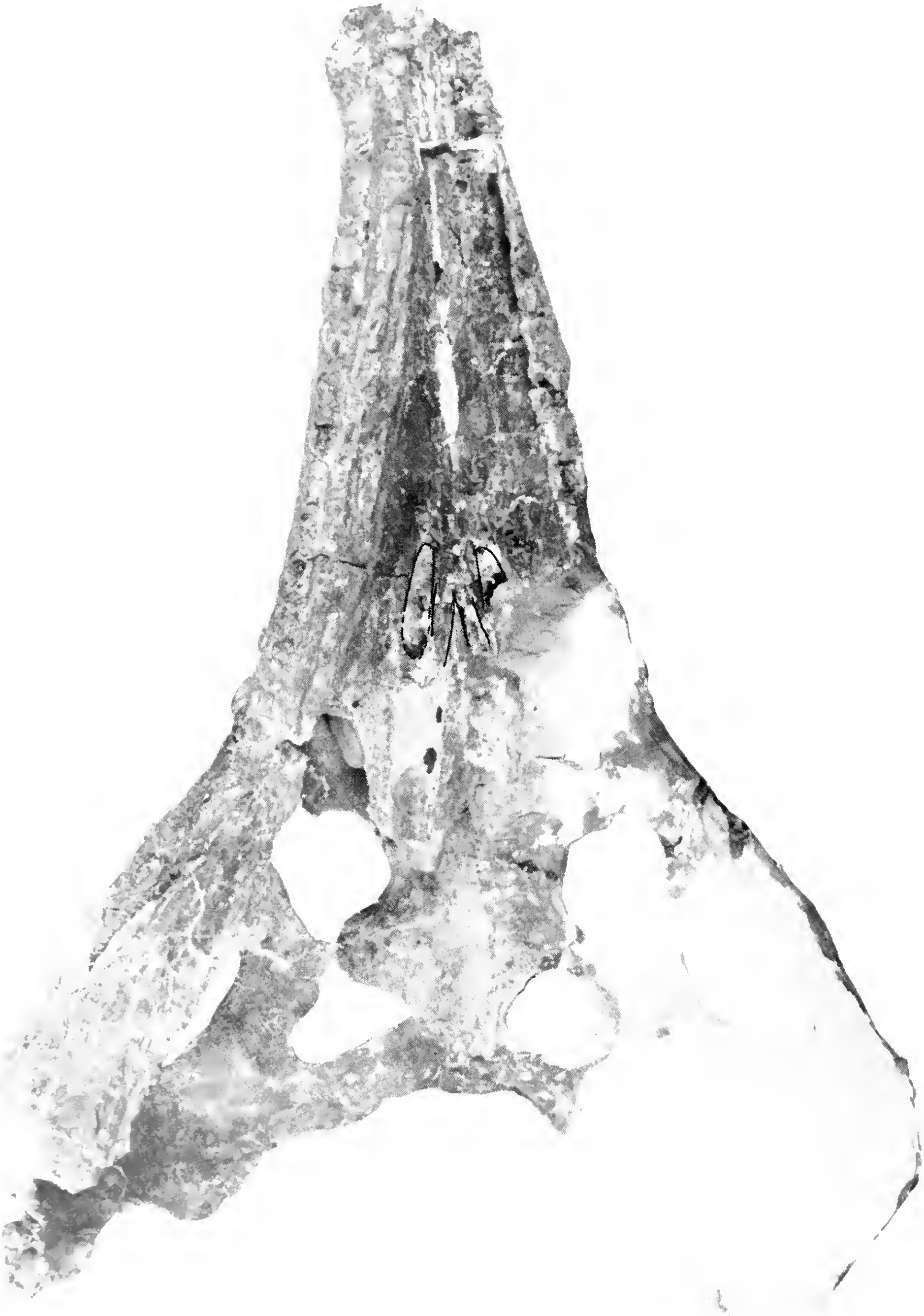


Plate VII. Ventral view of *Proterochampsa barrionuevoi*, MACN 18165, showing secondary palate and internal nares.

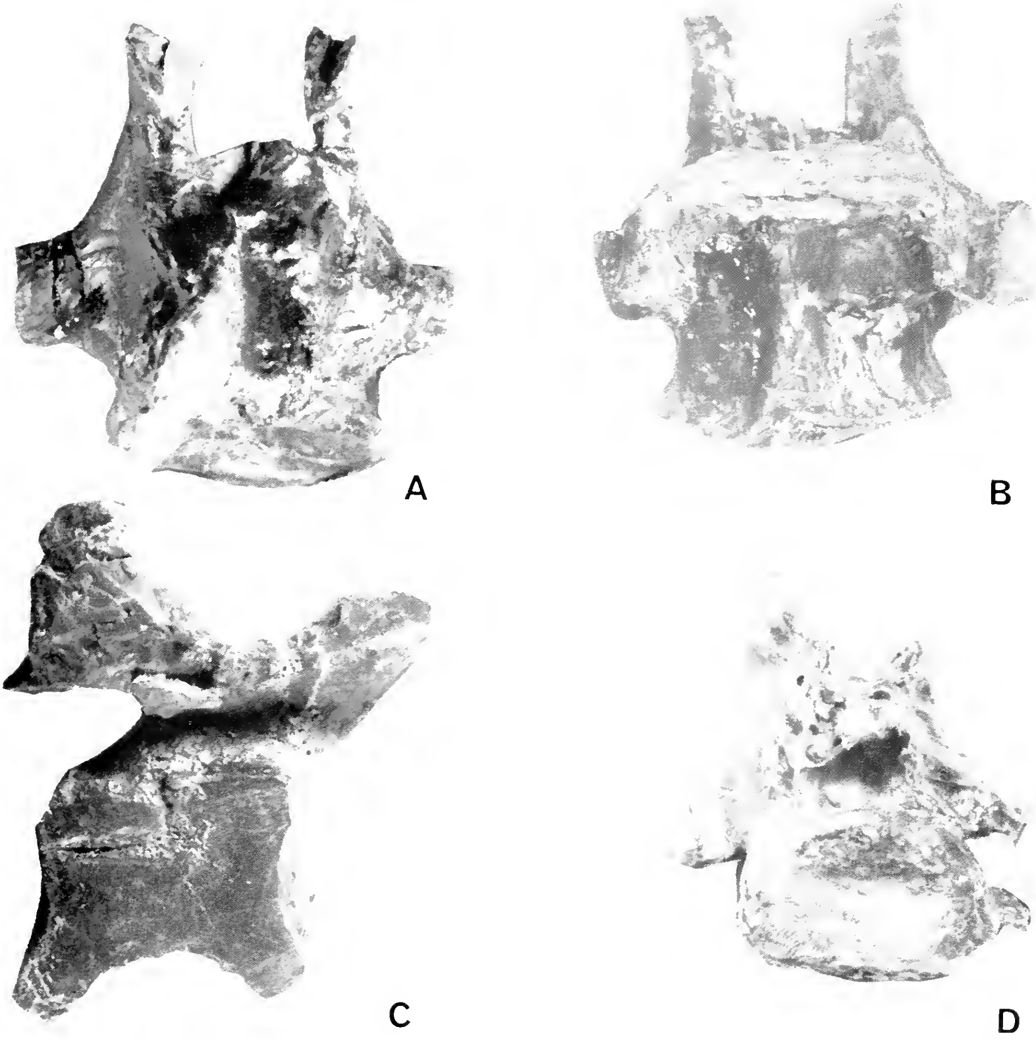


Plate VIII. A, B, D, Fourth cervical vertebra in dorsal, ventral, and anterior views, respectively. C, Longitudinal section of fifth cervical vertebra, MCZ 3408. × 2.

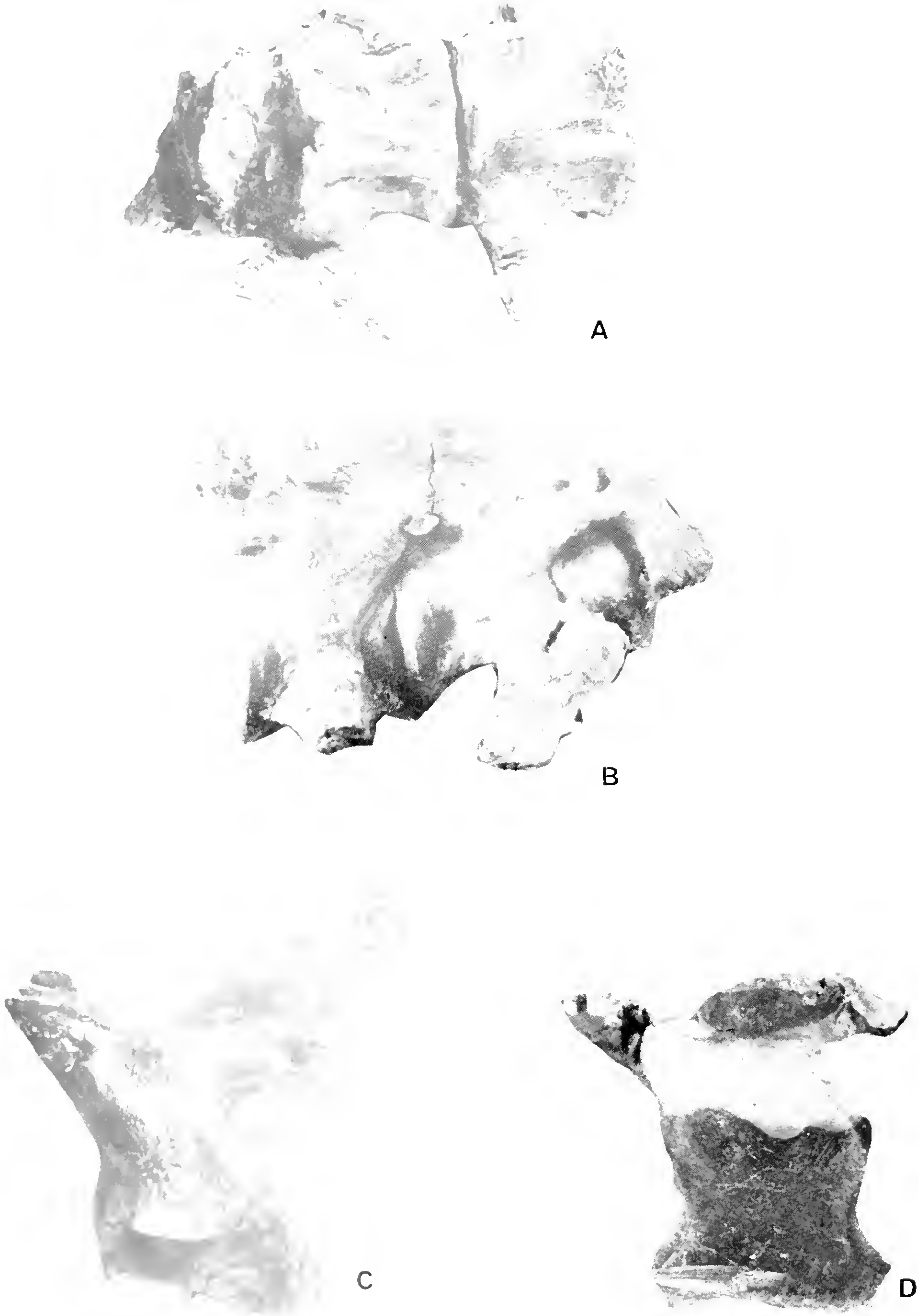


Plate IX A, Atlas, axis, and third cervical in ventral view, anterior end to the left. B, Side view of atlas, axis, and third cervical, anterior end to the right. C and D, Fifth cervical in side view and longitudinal section, MCZ 3408. × 2.

Bulletin OF THE
Museum of
Comparative
Zoology

Silicified Silurian Trilobites from Maine

H. B. WHITTINGTON AND K. S. W. CAMPBELL

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

VOLUME 135, NUMBER 9
JUNE 28, 1967

PUBLICATIONS ISSUED
OR DISTRIBUTED BY THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

Bulletin 1863–
Breviora 1952–
Memoirs 1864–1938
Johnsonia, Department of Mollusks, 1941–
Occasional Papers on Mollusks, 1945–

Other Publications.

Bigelow, H. B. and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P. and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B. and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

Publications Office

Museum of Comparative Zoology
Harvard University
Cambridge, Massachusetts 02138, U. S. A.

SILICIFIED SILURIAN TRILOBITES FROM MAINE

H. B. WHITTINGTON[1] AND K. S. W. CAMPBELL[2]

CONTENTS

INTRODUCTION AND ACKNOWLEDGMENTS

The trilobite exoskeletons described in this account are silicified, and so can be freed from the enclosing rock with acid. They are not only the best-preserved specimens known from Silurian rocks, but also the only ones which include a variety of growth stages. They provide a wealth of new information, and have enabled us to refine generic and familial definitions, as well as to make new suggestions regarding relationships to trilobites of older and younger systems. It is a fortunate if unexpected circumstance that such a fauna should be discovered in the strongly folded and slightly metamorphosed rocks of northwestern Maine. The very excellence of the preservation, however, militates against comparisons with less well-preserved and incomplete specimens. The study of Silurian trilobites, in North America as in other continents, has been neglected. There are no modern, critical accounts of the morphology and stratigraphical occurrence of trilobites from the type Silurian Series in Britain, nor from the classical regions of North America such as northern New York State and the central states. The fauna from Maine is peculiar in composition, lacking the illaenids, calymenids, cheirurids and lichids that typify earlier-described Silurian

---

[1] Sedgwick Museum, Cambridge, England.

[2] Australian National University, Canberra, A.C.T., Australia.

faunas, and rich in proetids and otarionids that are the least well-known elements in such North American faunas. All these factors combine to make it difficult to assess the age more precisely than Middle to Upper Silurian, and rule out meaningful consideration of faunal affinities.

Terms used in the systematic section are those defined by Harrington, Moore and Stubblefield (*in* Moore, 1959), glabella being used to include the occipital ring. In describing *Proetus*, the anterior subdivision of the axial ring is called the preannulus (Richter and Richter, 1956; cf. Moore, 1959, fig. 292). Other special terms and notations are explained in Figures 1, 7–10.

Blocks from Baker Pond were first collected by Professor Arthur J. Boucot in 1952, and subsequently prepared by Dr. A. R. Palmer, U.S. Geological Survey. Whittington is grateful to Dr. Palmer for inviting him to study this material, and to Professor Boucot for guiding him to the locality and helping to make a large additional collection in 1959. This material was prepared at the Museum of Comparative Zoology, and Campbell's visit in 1965 gave us the opportunity to study it. We express our thanks to the National Science Foundation, Grant GB-3577, for having made Campbell's visit possible, and for paying the costs of printing the plates; Grant GB-1807 provided technical assistance to Whittington. Text-figures have been drawn by Mr. Arnold Clapman. Mrs. Marjorie Korringa has prepared all the photographic prints, lettered the figures, and helped in many other ways. The major part of the collection, including all type and figured specimens, is deposited in the U.S. National Museum (abbreviated below as USNM).

Dr. David L. Bruton kindly gave us unpublished information on certain odontopleurid species, Dr. J. S. Jackson lent type specimens from the National Museum of Ireland, and Dr. A. Martinsson lent the type specimen of *Proetus concinnus* from the Palaeontological Institute, Uppsala, Sweden. We are also indebted to Mr. R. P. Tripp for discussing with us the new encrinurid genus and notation of glabellar tubercles, and to Dr. Robert R. Hessler for comments on certain morphological aspects of these trilobites, but we assume responsibility for interpretations expressed herein.

LOCALITY, CORRELATION, AND AGE OF THE FAUNA

The blocks of grey, silty limestone containing the trilobite fauna were selected from those lying on the central part of the east shore of Baker Pond, centre of Spencer Quadrangle, Somerset County, Maine. These limestones are different in appearance and fossil content from others that are present to the northeast and southwest, all included within the outcrop of the Hardwood Mountain Formation of Boucot (1961, pl. 34). Consideration of the regional geology (James B. Thompson, Jr., personal communication) suggests that the blocks cannot have been derived from the northwest, but that they came from a part of the formation now concealed by glacial deposits.

When dissolved in dilute hydrochloric acid the blocks yielded a residue of silicified trilobite exoskeletons, ostracode valves, rare bryozoans and brachiopods. The replacement of the trilobite exoskeletons preserves in remarkable detail the original surfaces. In large specimens the replacement is in the form of two layers, one at the original outer surface, the other at the original inner surface (e.g. Pl. 1, figs. 1–3; Pl. 10, fig. 11; Pl. 11, fig. 20; Pl. 13, fig. 17). These two layers, separated by a narrow space, are readily apparent in damaged specimens. In the smaller specimens a single layer replaces the entire thickness of the exoskeleton. Silt grains adhering to the surface are difficult or impossible to remove without damaging the specimen, and may be seen in many photographs (e.g. Pl. 1, figs. 5, 23, 24, 30, 31). Table 1 lists the trilobite fauna and gives a measure of its relative abundance. Dr. Jean M. Berdan (*in* Boucot, 1961, p. 181) named four ostracode genera from the formation. However, Dr. Berdan informs us (personal communication) that ostracodes from the silicified blocks are different from those obtained from other outcrops of the formation, and show some resemblance to ostracodes from the Henryhouse Formation, Oklahoma. Professor Boucot (personal communication) notes that the brachiopod fauna from the Baker Pond locality is rather different from that at other localities assigned to the Hardwood Mountain Formation. He concludes that the age is within the span of Wenlock to early Ludlow, and in terms of the North American sequence could be as old as the Waldron Shale. The trilobite fauna is dominated by proetids and otarionids, American Silurian species of which are poorly and incompletely known, and less common is the new encrinurid genus *Fragiscutum*. Encrinurids are not known to be present in rocks of Devonian age, so that the Silurian age of the fauna seems beyond question.

North American mid-continental Silurian trilobite faunas include illaenids, cheirurids, calymenids and lichids (cf. Weller, 1907; Raymond, 1916; Walter, 1927), but these families are not represented in the Baker Pond collection. Difficulties in correlation stem from this lack, and from the lack of recent work on Silurian trilobites. Campbell (in press) has studied trilobites of the Henryhouse Formation, Oklahoma, and while no one species is in common with the Baker Pond fauna, those of *Proetus*, *Fragiscutum* n. gen., and *Dalmanites* are alike. The Henryhouse Formation has not yielded otarionids, and only a poorly preserved free cheek of *Leonaspis*. The Baker Pond species of *Leonaspis* is compared to younger, Lower Devonian species, simply because these are the only well-known American species to which comparisons can be made. Species of *Leonaspis* are known to be long-ranging, and this single comparison cannot be taken to imply that the Baker Pond fauna is early Devonian in age. The balance of the evidence suggests that it is of about the same age as the Henryhouse—that is, near the Wenlock-Ludlow boundary. This age is consistent with comparisons between Baker Pond and Bohemian, British, and Swedish species made in the systematic section, and with age determinations based on brachiopods and ostracodes. Trilobites of Lower Silurian (Llandovery Series) age are not well known, but such comparisons as can be made do not suggest that the Baker Pond fauna is early Silurian.

SUMMARY OF MORPHOLOGICAL AND TAXONOMIC FINDINGS

The new morphological information, combined with data revealed by the growth stages, gives clues to relationships with older and younger groups. Some of the main points, elaborated in the systematic section, are:

1. Ordovician to Devonian proetids, typified here by *Proetus*, appear to be ancestral to Carboniferous genera like *Paladin*. A triangular rostral plate and the apparent absence of a sutural junction between the hypostome and the remainder of the cephalon characterise *Proetus*. In *Paladin*, however, the rostral plate is subquadrangular in outline and the hypostome is joined to the remainder of the cephalon by a suture.

2. *Otarion* (Ordovician to Devonian) also has a triangular rostral plate. Growth stages are remarkably like those of the Ordovician *Dimeropyge*, and suggest derivation from this older group. The supposed brachymetopid genus *Cordania* appears likely to be derived from otarionids.

3. Within the Proetacea, as presently conceived, there are thus two main phyletic lines, one leading through proetids to certain Carboniferous genera, the other being the dimeropygid-otarionid-brachymetopid line.

4. Three species of *Otarion* and one made the type of a new otarionid genus are described, based on cephala. Isolated

TABLE 1. TRILOBITE FAUNA OF THE HARDWOOD MOUNTAIN FORMATION AT BAKER POND, SOMERSET COUNTY, MAINE. INDICATION OF RELATIVE ABUNDANCE GIVEN BY TOTAL NUMBERS OF CRANIDIA OF ALL SIZES (INCLUDING FRAGMENTARY SPECIMENS) IN THE SAMPLE DISSOLVED.

Proetus pluteus n. sp.	150
Rhinotarion sentosum n. gen., n. sp.	8
Otarion instita n. sp.	148
Otarion plautum n. sp.	44
Otarion sp. ind.	38
Scutelluid gen. ind.	2
Fragiscutum rhytium n. gen., n. sp.	18
Dalmanites puticulifrons n. sp.	9
Xanionurus boucoti n. gen., n. sp.	8
Leonaspis cf. *williamsi* Whittington, 1956	10

segments and pygidia can only in a few cases be assigned to these species. Whether these are four distinct species, or whether one form may be a sexual dimorph of another, is an open question.

5. The type material of M'Coy's *Harpidella megalops* is redescribed, and it is concluded that the generic name is a subjective synonym of *Otarion*.

6. A new encrinurid genus is based on superbly-preserved material, including the first described developmental stages. These show that each ring of the pygidial axis represents a segment. Anterior bands of the thoracic pleurae are reduced to articulatory flanges, concealed in dorsal aspect. The pleural ribs of both thorax and pygidium are posterior bands. Canals, diminishing in diameter dorsally, traverse these bands and the axial rings, but appear not to open on either surface.

7. Incomplete developmental stages of *Dalmanites*, beginning with the late protaspis, reveal the remarkable similarity to similar stages of the ancestral Ordovician *Dalmanitina*.

8. Developmental stages of two odontopleurid species show the same major spine pattern as species of various Ordovician genera. One species, type of a new genus, appears to lie on a phyletic line between the Ordovician *Diacanthaspis* and the Devonian *Radiaspis*.

SYSTEMATIC PALEONTOLOGY

Superfamily PROETACEA Salter, 1864

Discussion. The discovery by Dr. W. T. Dean (personal communication) of a species of *Otarion* and a proetid from the Arenig of southern France shows the early separation between these two groups. A third group, the dimeropygids, is also present in the early Ordovician (Whittington, 1963: 45–50). *Phaseolops* from the Llanvirn of Newfoundland (Whittington, 1963: 36–40) is considered to be a proetid, and among other characters it exhibits a triangular rostral plate, though the axial rings of the thorax do not have the pre-annulus. In the later Ordovician and the Silurian, proetids and otarionids are more abundant and widespread. The present material of *Otarion* shows the characteristic triangular rostral plate, the narrow panderian notch situated close to the posterior margin of the segmental doublure, the absence of the pre-annulus, the characteristic long median spine of one thoracic segment, and a development of both cephalon and pygidium which recalls that of *Dimeropyge* (Whittington and Evitt, 1954). The species of *Proetus* described here reveal the triangular rostral plate, the typical pre-annulus of the segments, and the V-shaped panderian notch which is medially situated in the doublure of the segments. The hypostome is characteristic in shape but appears not to be attached at a hypostomal suture to the rostral plate and doublure of the free cheeks. The early developmental stages of *Proetus* differ from those of otarionids, notably in the absence of paired spines. A relationship between otarionids and dimeropygids is suggested not only by the development but also by many aspects of holaspid morphology, including the single median thoracic spine characteristic of many species.

Relationships between Silurian otarionids and proetids and Devonian and younger proetaceans present many problems. For example, the Lower Devonian genus *Cor-*

dania (Whittington, 1960) has an otarionid-like cephalon, a wide (tr.) sub-triangular rostral plate, and the thoracic segments lacking the pre-annulus, but the pygidium is unlike the otarionid pattern in that it is large and has some ten axial rings. In recent publications *Cordania* has been placed in the Brachymetopidae (Whittington, 1960; Amos, Campbell, and Goldring, 1960; Hessler, 1962a; Hahn, 1964), a Devonian-Carboniferous group embracing forms with the above characters, except that two of its Carboniferous members, *Brachymetopus* and *Australosutura* have a rostral plate that is not sub-triangular but extends close to the genal angle. We suggest that *Cordania* was derived from an otarionid rather than a proetid, but more information is needed before lines of descent of the Carboniferous Brachymetopidae can be discerned.

Silicified material of the Carboniferous genus *Paladin* (Whittington, 1954) shows that it is proetid-like in the shape and arrangement of the glabellar furrows, presence of the shallow panderian notch in the cephalic doublure, the form of the segments, nature of articulating arrangements, outline of the panderian notch on the thoracic segments, and the presence of the pre-annulus. On the other hand, however, the hypostome of *Paladin* has a wing process on the large anterior wing which appears to rest in a depression on the surface of the anterior boss, and there is a hypostomal suture linking it to the rostral plate and the doublure of the free cheeks. The rostral plate is transverse, subtrapezoidal in outline. The shape of the plate and mode of attachment of the hypostome distinguish *Paladin* from *Proetus* but the features in common indicate that *Paladin* and its allies may have been derived from the proetids.

Hessler (1962b; 1963; 1965) has described and discussed Lower Carboniferous trilobites which he refers to the Proetidae. His figures suggest that in species of *Griffithides* (1962b, pl. 176, figs. 12, 14) and possibly of *Phillipsia* (1963, pl. 61, figs. 3, 4) a pre-annulus is present on the first axial ring of the pygidium, while in other species he describes this ridge is not developed. Use of this thoracic and pygidial character, as well as ventral cephalic characters, may help to disentangle the relationships of Carboniferous and younger trilobites to each other and to different Devonian groups.

This discussion suggests that from early Ordovician onward there may have been two main phyletic lines within Proetacea—a proetid line leading to various Carboniferous groups, and a dimeropygid-otarionid line from which at least some brachymetopids may be derived.

Family PROETIDAE Salter, 1864
Subfamily PROETINAE Salter, 1864
Genus *PROETUS* Steininger, 1831
Proetus pluteus n. sp.

Plates 1, 2; Plate 3, figs. 6–8, 10, 13–16; Figs. 1–5, 6C.

Holotype. USNM 154457, cranidium and free cheek.

Description. Glabella widening from the posterior edge to a maximum width across midpoint of lateral occipital lobes, narrowing abruptly forward to the anterior margin of this lobe, less abruptly inside the palpebral lobes, to the well rounded frontal lobe. Axial furrow lightly impressed, except posteriorly; preglabellar and anterior border furrows confluent medially, deeper. Occipital furrow with an almost vertical anterior slope and more gentle posterior slope, the course gently convex forward medially, swinging forward and outward and deepening in front of the lateral lobe; latter moderately convex, extending back almost to posterior margin of ring, separated from ring by a furrow which becomes faint distally. Glabellar furrows may be faintly impressed on external surface and are indicated by smooth areas; shape and arrangement shown in Figure 1A (compare Pl. 1, fig. 8). On the inner surface the muscle areas may also appear faintly im-

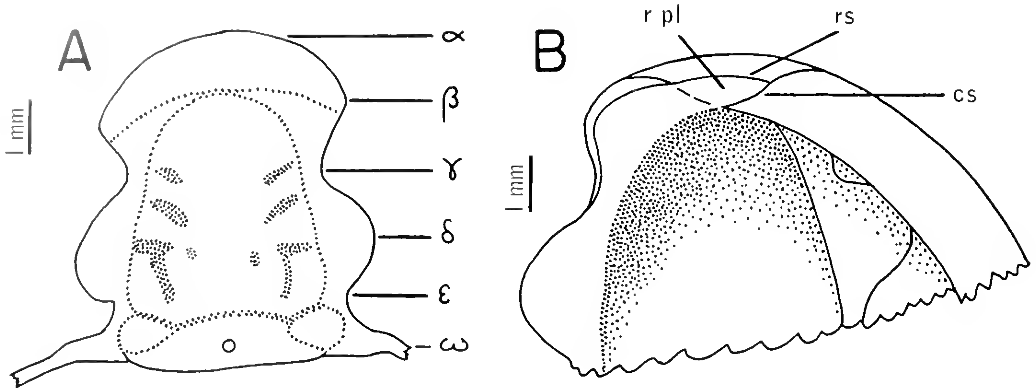


Figure 1. *Proetus pluteus* n. sp. A) Muscle areas of glabella and notation of points on facial suture (after Richter and Richter, 1940) based on original of Plate 1, figure 8. B) Restoration of rostral plate, based on originals of Plate 2, figure 2. Abbreviations: cs, connective suture; r pl, rostral plate; rs, rostral suture.

pressed, or the replacing silicification may be broken over these areas (Pl. 2, fig. 2).

Eye lobe elongate, gently convex eye surface steeply sloping, apparently smooth externally and internally—the preservation does not reveal any facets. Palpebral lobe flattened. Outside eye lobe, cheek curves down to borders; posterior border widening outward and curving posterolaterally into base of short, pointed fixigenal spine. Posterior border furrow moderately deep, curving out on to base of fixigenal spine; lateral and anterior borders broad and gently convex, separated from the cheek by a broad shallow border furrow. Doublure (Pl. 2, figs. 2, 3) of approximately same width as lateral and anterior borders, gently convex ventrally, the inner edge curved up beneath the groove formed by the border furrows. Beneath posterior border, doublure extends in to the fulcrum (Pl. 1, fig. 4); inside here, edge of exoskeleton has well-developed recess for articulating flange of first thoracic segment; occipital doublure very short (exs.) behind the lateral occipital lobes, but lengthening to about three-quarters length of occipital ring in midline. Shallow panderian notch in margin of lateral border in front of genal angle (Pl. 2, fig. 2). Course of sutures shown in Figure 1 (compare Pl. 2, fig. 2). Anterior branch runs inward and forward from β to α over edge of anterior border and continues inward across doublure as the connective suture, the two sutures meeting in the midline at the inner margin of the doublure. The rostral suture runs along the doublure a short distance in from the anterior margin, and thus isolates a triangular rostral plate. Isolated examples of this plate have not been found, but the outline of the doublure of the free cheek leaves no doubt as to its shape.

Hypostome with strongly convex central body partly subdivided by short, deep, backwardly-directed middle furrows into a large anterior and a small, crescentic posterior lobe; in midline at anterior margin of anterior lobe is a triangular, flattened or gently concave area (Pl. 1, fig. 13). Border furrows well defined except beside anterior wing; anterior border narrow, convex, the edge (which presumably faces forward and downward) having a deep slot along the median portion (Pl. 1, figs 13, 18). Crescentic posterior body gently inflated, especially at the tip where the oval macula is faintly defined by its convexity (Pl. 2, figs. 1, 4). Lateral border widening posteriorly, posterior border flattened and bearing a short, blunt spine at the posterolateral angle. Anterior wing consists of an upward and outwardly directed extension of the edge of the doublure, subtrapezoidal in outline, without a wing process; posterior wing small, subtriangular, directed upward and slightly inward; doublure between wings narrow, widest posterolaterally.

External surface of cephalon (Pl. 1, figs. 8, 11, 13, 14, 17, 18; Pl. 2, figs. 1, 4) inside borders bearing fine, evenly and closely spaced granules; these granules absent in the furrows and on the inner part of the palpebral lobe; posterior border apparently smooth along the crest; outer part of anterior and lateral borders and doublure bearing slightly irregular terrace lines running subparallel to the margin, these terrace lines continuing on to the genal spine. On hypostome, terrace lines on anterior lobe of middle body run subparallel to margins, fanning out anteriorly beside the flattened triangular area. Posterior lobe including macula apparently smooth; terrace lines along borders, subparallel to margins, becoming more widely spaced and curving on the outer surface of the wings.

Number of thoracic segments unknown. Ring subdivided by intra-annular furrow which curves forward distally and joins the more deeply-incised articulating furrow some distance in from the axial furrow; inner part of pleura flat, outer part steeply bent down; inner part relatively narrow (tr.) on anterior segments (Pl. 2, figs. 7, 8) and the outer part deflected backward. Pleural furrow runs diagonally out beyond fulcrum and along edge of broad facet. Doublure extends along posterior margin of outer part of pleura and beneath tip, with a broad, deep panderian notch (Pl. 2, fig. 25). The anterior edge of this notch is raised to form a stop during enrollment; in anterior segments this anterior part of the doublure is narrow and not raised (Pl. 2, fig 24). Articulation between anterior segments of the thorax, the cephalon, and the pygidium is facilitated by the ring process situated at the distal posterior margin of the axial ring, which fits into a socket on the anterior margin; in centre of this socket is the small axial process (Pl. 2, fig. 23) which fits into a corresponding axial socket. The inner anterior edge of the pleura is rounded, and fits into a groove on the posterior edge (Pl. 2, figs. 24, 25, 31). Doublure of ring similar in form to that beneath the occipital ring, medially extending forward as far as articulating furrow; anterior edge of articulating halfring with a deep slot along its whole width (Pl. 2, fig. 23).

Pygidium with axis ill-defined at tip; first ring stands markedly higher than succeeding seven or eight rings. Pleural regions with inner part adjacent to axis horizontal, outer part sloping steeply down to margin, no border furrow. Three or four pleural and interpleural furrows visible on pleural regions, dying out distally so that border is smooth, especially posteriorly (Pl. 2, figs. 26, 27). Broad, gently convex doublure extends inward for about one-third the width of the pleural regions.

External surface of rings and inner parts of pleurae of thorax and pygidium with fine granulation; terrace lines on pygidial doublure and around dorsal margin; branches from these lines curve forward and inward across the pleural region subparallel to the pleural and interpleural furrows (Pl. 2, fig. 26).

Variation and development of cranidium. Measurements of a size series of cranidia (Figs. 2, 3) show some aspects of the variability, and that this variability is continuous. A size series of cranidia (Pl. 1, figs. 5–7, 9, 10, 15, 16, 19–21, 23–31; Fig. 6c), ranging from a length (sag.) of 1.3 mm upward, shows the relatively minor changes that take place. Most noticeable is the change in longitudinal convexity—from a steep slope in front of the eye lobe to a lesser slope, combined with an increase in the inflation of the anterior border which gives a deeper border furrow.

Variation and development of pygidium. A series of specimens from transitory pygidia (Pl. 3, figs. 10, 13–16) to the small-

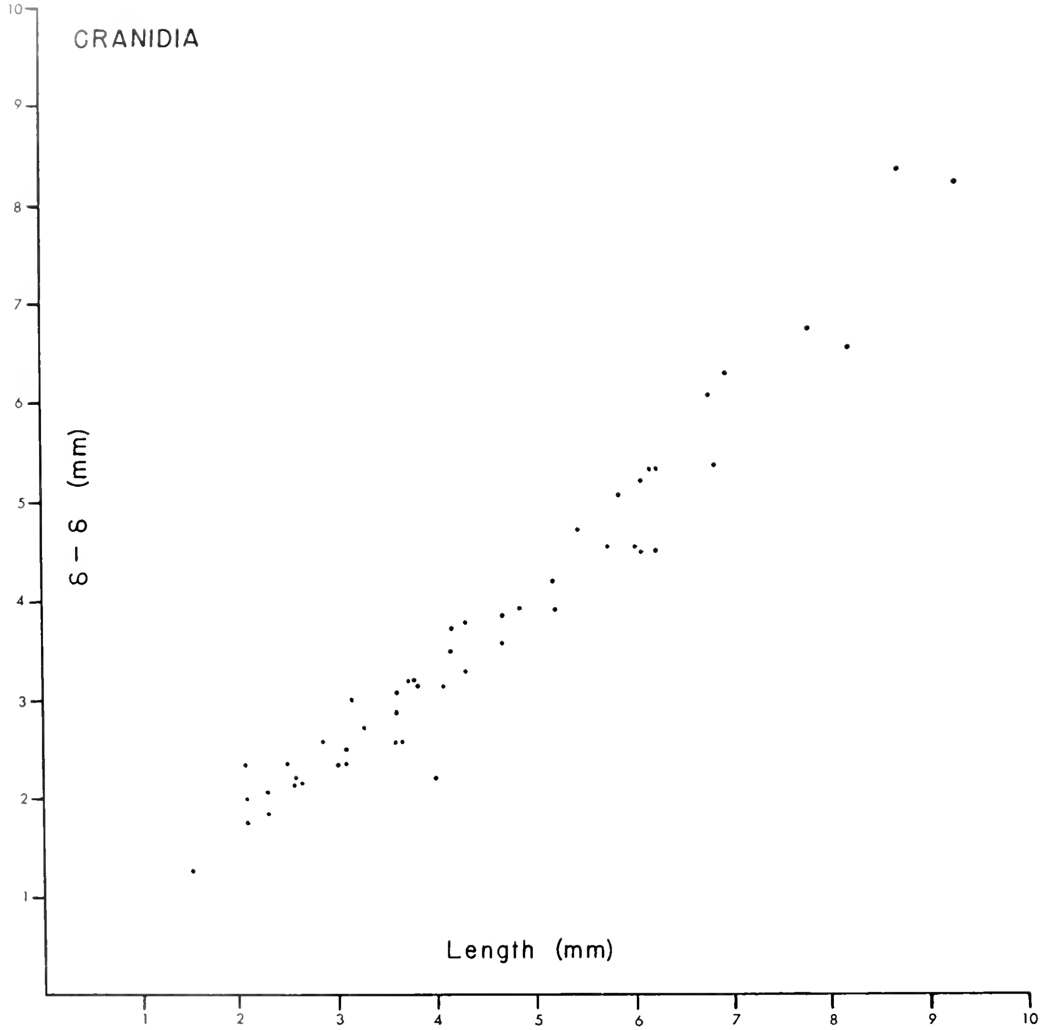


Figure 2. *Proetus pluteus* n. sp. Dimensions of 50 cranidia; length is sagittal; δ–δ is width across palpebral lobes at widest point. Measured cranidia include USNM 154458–60, 154464–6, 154475, 154478, figured specimens, remainder included under 154489.

est true pygidia (Pl. 3, figs. 6–8) to larger ones (Pl. 2, figs. 17, 20, 26–30) shows that there is little change in the series, apart from a tendency to become slightly broader. At a small size, the first ring stands higher than the others. The specimens are variable through a considerable size range, as shown in Figures 4, 5. There is no discontinuity within this variation and the material all appears to belong to one species.

Discussion. The present material, which is of dissociated exoskeletal parts except for one cephalon, is regarded as a single species because of the continuous range of variation. This range is wide, but the material is from a single locality.

Deep, smooth-edged slots run along the edge of the rostral suture of the cranidium

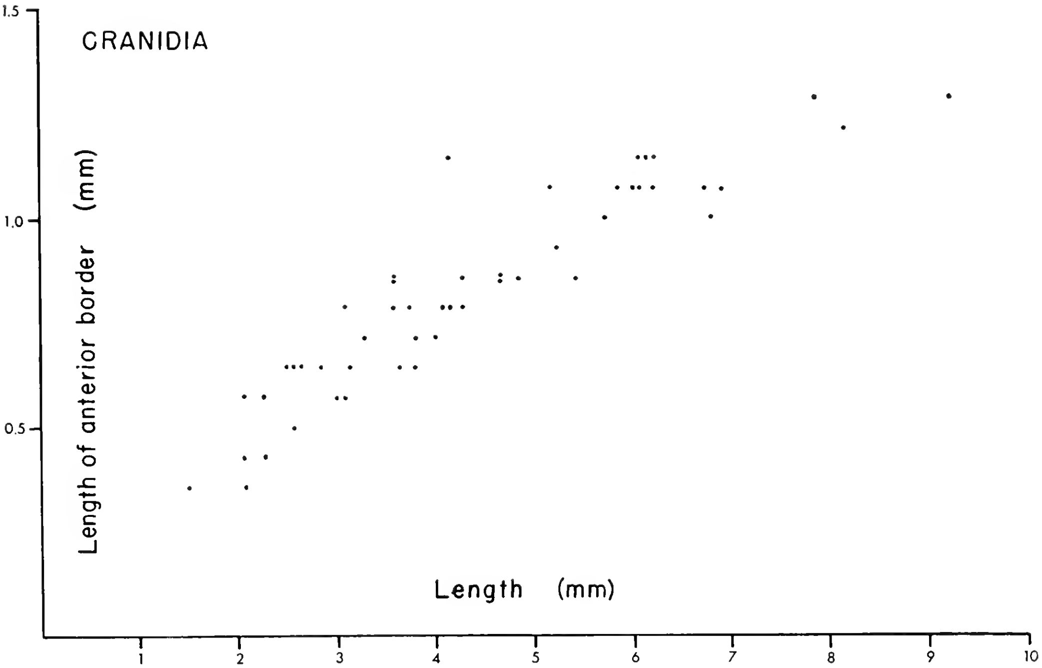


Figure 3. *Proetus pluteus* n. sp. Dimensions of 49 cranidia, both lengths sagittal. Measured specimens the same as Figure 2.

(Pl. 1, fig. 4; Pl. 2, fig. 2), around the edge of the articulating halfring of thoracic segments (Pl. 2, fig. 23) and the pygidium, and along the sutural margin of the hypostome (Pl. 1, fig. 13; Pl. 2, fig. 1). The smooth edges of the slots, and their consistent form in many specimens, argue against these features being the result of silicification, for example as being a gap between a silicified layer on the external and internal surfaces of the exoskeleton. Such double layering is seen (Pl. 1, figs. 1–3, 10), but where it is broken through at the edge of a specimen the margins of the two layers are not straight but ragged and irregular. It appears to us that the slots represent parts of the integument that were uncalcified in life. In the thorax, where such integument extended forward from the margin of the articulating halfring to the doublure of the ring in front, it must have been articulatory in function. Along the rostral suture it is not clear what the function of this uncalcified integument may have been. Between the cephalic doublure and the hypostome its function may have been articulatory, for not only is the sutural margin of the hypostome rounded and slotted (Pl. 2, fig. 1), but also the margin of the doublure of the cheek adjacent to the rostral plate (Pl. 2, fig. 3); these edges did not adjoin along flat surfaces. It is notable also that the margin of the anterior wing of the hypostome is thin and rounded, that the wing bears no wing process, and thus that there is no evidence of a close link between this wing and an anterior pit; indeed, there appears to be no anterior pit in this species. Thus the hypostome of *Proetus* was not rigidly fitted to the remainder of the cephalon, as it appears to be in, for example, *Fragiscutum* n. gen. (see below), and may have been movable.

So far as we are aware, the hypostome of a

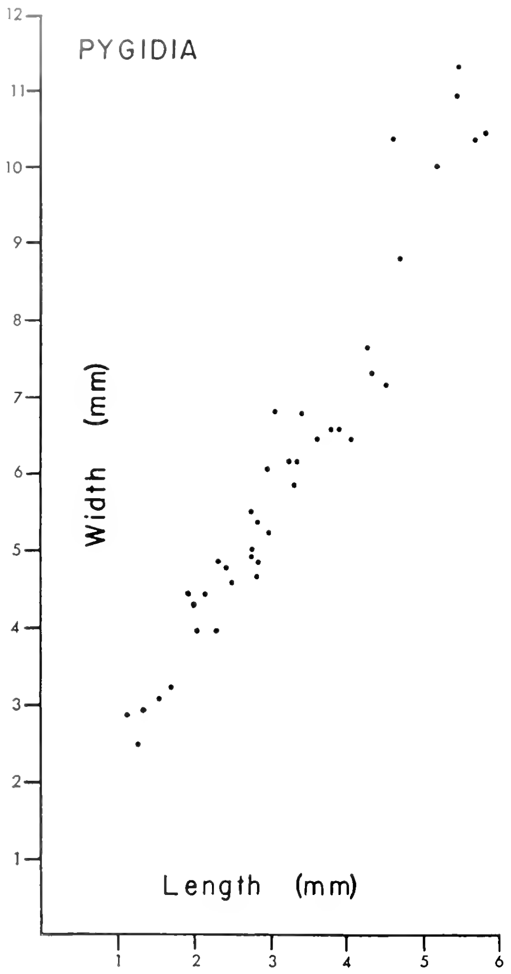


Figure 4. *Proetus pluteus* n. sp. Dimensions of 40 pygidia; length is sagittal (excluding articulating halfring); width is maximum. Measured pygidia include USNM 154482–5, figured specimens, remainder included under 154490.

proetid has not been found in place in any specimen. This evidence supports the view that there was no sutural link between the hypostome and the rest of the cephalon, but rather that the hypostome was kept in position by uncalcified integument and muscles, which decayed after death so that the hypostome was not retained in its original position. The attachment of the hypostome to the remainder of the cephalon has been discussed in *Dimeropyge* (Whittington and Evitt, 1954: 38–41, text-fig. 8), and in that genus there is no sutural junction between the inner edge of the doublure and the anterior margin of the hypostome. Other points of comparison between *Dimeropyge* and the present species are the doublure of the outer part of the pleurae, the panderian notch, and the form of the stop to enrollment, all of which appear to be similar (compare Plate 2, figure 25, with Whittington and Evitt, 1954, text-fig. 10).

New illustrations are given here of the type species of *Proetus*, *P. concinnus* (Pl. 3, figs. 4, 5, 9, 11, 12), from the Wenlock Series, Gotland, Sweden. The broken anterior border shows on the right side of the specimen the mould of the doublure, and on the left side the course of the anterior branch of the suture, which is continued by the connective suture to the midline at the inner edge of the doublure. The rostral plate was thus triangular in shape (cf. Lovén, 1845: 49, pl. 1, fig. 2b). The type species, *P. pluteus*, and a species from the Henryhouse Formation of Oklahoma being described by Campbell (in press), are exceedingly similar. These similarities include the detailed form of the cephalon (shape of the glabella, form of the muscle areas, position of the eye lobe, shape of the borders, and presence of a triangular rostral plate), and the form of the thoracic segments and pygidium. The latter lacks a clearly defined border and has the pleural furrows of the first one or two segments extending close to the margin. The fine granulation of the external surface of the glabella, the weak pitting on the free cheek inside the border, and the presence of terrace lines on the border (which on the pleural regions of the pygidium curve forward and inward) are characters common to all these species. These close similarities might well be used to limit the subgenus *Proetus* (*Proetus*) to a group of Middle and Upper Silurian species. The latter would probably include *P. fletcheri*, described by Reed (1901:11–14, pl. 1, figs. 5, 6) from the Wenlock Limestone of Britain, and *P. mořinensis*

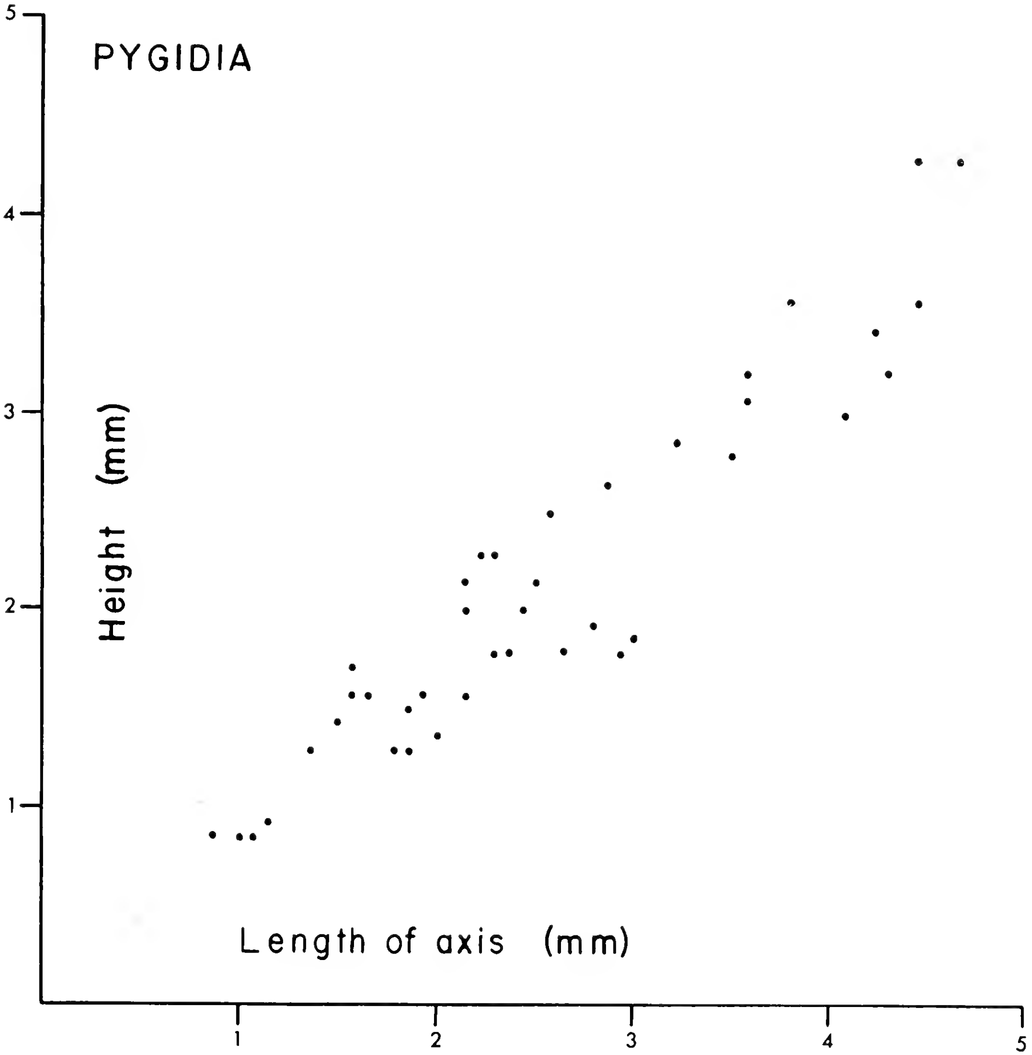


Figure 5. *Proetus pluteus* n. sp. Dimensions of 40 pygidia, length of axis is sagittal, height is maximum. Measured specimens the same as Figure 4.

Přibyl (1960: 204–206, pl. 2, figs. 1–5) from the Kopanina Shale, Lower Ludlow, of Bohemia. However, examination of specimens of *Proetus cuvieri*, from the Middle Devonian of the Eifel district of West Germany (Pl. 3, figs. 1–3; Richter and Richter, 1956), shows that this species is like the type *P. concinnus*. The rostral plate is not the relatively wide (tr.) and short (sag. and exs.) plate figured by Richter and Richter (1956, pl. 5, figs. 33b, c, d), but the doublure of the cephalon (the external mould is preserved in the original of Plate 3, figure 2) curls upward and inward so that the inner edge lies beneath the border furrow. The same specimen has the edge of the left connective suture preserved, and it runs inward and backward to meet the right suture at the inner margin of this doublure, isolating a rostral plate that is triangular in outline and sharply flexed in the longitudinal direction. The differences between holaspid *cuvieri* and *concinnus* are apparently in minor features—proportions of glabella, length of genal spine, presence of strong tubercles on the external surface of some specimens of *cuvieri*, and lack of incurved terrace lines on the pygidium of *cuvieri*. These do not seem to justify a subgeneric distinction between the Middle and Upper Silurian species and this Middle Devonian species.

From *P. concinnus* the new species may be distinguished by its less globose glabella, relatively longer (sag. and exs.) anterior border, shallower axial furrow between the palpebral lobe and the glabella, coarser granulation on the glabella, and shape and number of spines on the posterior border of the hypostome (Lindström, 1901, pl. 6, fig. 21).

Family OTARIONIDAE Richter and Richter, 1926

Discussion. The present material of *Otarion* and *Rhinotarion* n. gen. suggests that to the characters of this family given by Richter, Richter, and Schmidt (*in* Moore, 1959: O 403–404) may be added the convergence backward of the connective sutures to meet at the inner edge of the doublure, the absence of a panderian notch in the doublure of the cheek, the absence of the pre-annulus on the axis of the thorax, the extension of the median pleural furrow out close to the tip of the segment, and the narrow panderian notch situated close to the posterior edge of the segment. The hypostome (Richter, 1914; cf. Prantl and Přibyl, 1951: 443) is unlike that of proetids in having the middle furrow complete and a more prominent, crescentic, posterior lobe of the middle body on which the macula is not distinguishable. In addition, in the present examples, there is a tiny wing process and the anterior wing itself is smaller and differently shaped.

RHINOTARION n. gen.

Type species.—*Rhinotarion sentosum* n. sp.

Diagnosis. Differs from *Otarion* in that median part of anterior border is drawn forward into a projection; rostral suture traverses ventral side of projection close to outer margin, hence rostral plate is inverted "T" shape rather than triangular in outline.

Distribution. No other species that we would assign to this genus have been recorded. However, specimen 17729 in the collection of the Australian National University, from Unit 4 of the Dargile Beds, Locality 47, Parish Heathcote, Victoria, is almost certainly a member of the genus. The only reason for doubt is the poor preservation of the basal glabellar lobes.

Rhinotarion sentosum n. sp.

Plate 4; Plate 5, figures 1–6, 9–11, 13–16, 18.

Holotype. USNM 154211, cephalon and two segments.

Description. Glabella moderately convex, expanding forward to maximum width across basal glabellar lobes, slight but abrupt contraction at lateral furrows 1p, frontal portion rounded; maximum width slightly less than, or equal to, length (sag.). Occipital ring widest in midline, steep posterior slope and more gentle anterior slope to the deep occipital furrow; prominent, slightly backwardly-curved, blunt, median spine. Lateral furrow 1p situated slightly in front of mid-length, narrow and deep, directed inward and backward and reaching the occipital furrow, deepest close to axial furrow; basal lobe lachrymate in outline, moderately convex. Lateral furrow 2p situated opposite anterior margin of eye lobe, a smooth oval area situated a short distance in from the axial furrow. Convex cheek slopes steeply outward, cheeks joined by preglabellar field that is only slightly wider (sag. exs.) than the anterolateral border; borders defined by deep, well marked border furrows. Posterior border narrow (exs.) adjacent to occipital ring, widening rapidly outside the fulcrum and merging with the base of the genal spine. Lateral and anterolateral border with flattened upper surface which is outward sloping, maximum width of border anterolaterally; medially, borders drawn forward into a blunt, rounded projection, which is of width (tr.) similar to the width of the anterolateral border. Preglabellar field gently inflated. Genal spine long, curved and tapering. Eye lobe relatively large (exsagittal length greater than ⅓ sagittal length of glabella) and situated at highest point of inflated inner area of cheek; cheek slopes steeply in all directions downward from margin of eye lobe. Palpebral lobe curves inward and downward, without rim; eye surface convex externally, apparently smooth. Broad, low, eye ridge runs inward and forward to axial furrow opposite frontal glabellar lobe (Pl. 5, figs. 1, 4). Anterior branch of suture runs forward and slightly outward to border furrow, curves over border and runs inward along outer vertical slope to meet rostral suture at a very oblique angle; rostral suture runs along forward and downward facing surface of border close to the margin of the projection. Posterior branch of suture runs directly outward and backward across the cheek and posterior border, down the posterior slope of the latter and curves across the doublure beneath the base of the genal spine. At margins, surface of the border curves evenly around to inner ventral side, where exoskeleton is flexed up almost vertically and extended as the doublure close up to the impression of the border furrows. A shallow impression in the doublure immediately behind the anterior projection; latter is oval in transverse section. Connective sutures run inward and backward to inner margin of the doublure approximately in line (exs.) with the lateral margin of the anterior projection. Rostral plate (Pl. 4, figs. 10–12) is thus an inverted "T" shape, with the posterior edge indented and bent to slope sharply upward and inward. Doublure continues beneath genal angle without either vincular notch or panderian notch, and narrows rapidly inward to disappear at the fulcrum; along edge of exoskeleton inside fulcrum (Pl. 5, fig. 4) is a recess to accept the articulating flange of the first thoracic segment. External surface covered, except in furrows, by large rounded tubercles and smaller thornlike spines; these irregularly scattered but sparse on the upper, inner surface of the cephalic borders, absent distally on the genal spines, and few on the posterior border. On ventral facing surface of border and doublure are prominent terrace lines, these not extending on to the smooth underside of the genal spine. Glabellar furrows not extended ventrally as apodemes. Hypostome unknown.

Number of thoracic segments unknown. Certain isolated segments in the collection, including one with a long median spine (Pl. 5, figs. 9, 10, 13–16, 18), have a median tubercle and three additional pairs on the axial ring, and one to two tubercles scattered along the posterior pleural band, and a group at the posterolateral tip. In these respects they resemble the two segments attached to the holotype cephalon, and differ from isolated segments of type A (Pl. 8, figs. 13–15, 21) or type B (Pl. 9, figs. 1–3, 8), and hence are assigned to this species.

Convex axial ring with distal part curved slightly forward; anterior edge slopes gently to articulating furrow which rises sharply to the articulating halfring. Long median axial spine on one segment. Pleurae flexed down at fulcrum, subdivided by U-shaped pleural furrow which runs straight outward and slightly backward and extends close to the tip; convex posterior band the widest close to the axial furrow, anterior band widest distally. Anterior segment has outer part of pleurae bent slightly back, and facetted so that anterior band is cut off; subsequent segments have the pleurae transverse and parallel-sided, the tip rounded. Articulating ring process on posterior margin, axial socket immediately above it, on anterior margin corresponding ring socket and axial process; on inner part of pleura anterior articulating flange which fits into recess on posterior margin of segment in front; marked fulcral articulating process and socket. Doublure extends along posterior margin of outer part of pleurae and beneath tip, narrow, V-shaped panderian notch (Pl. 5, figs. 13, 18) close to posterior margin, anterior edge raised to form a stop during enrollment. Doublure not extended along anterior margin of outer part. Distal part of articulating furrow broadened and deepened, but not extended ventrally as an apodeme. External surface bearing a fine granulation in addition to the elongate tubercles described above.

Pygidium not known with certainty.

The original of Plate 5, figures 5, 6, appears to be the cranidium of a malformed individual of this species. The part of the glabella in front of the lateral lobes is relatively longer than in other specimens, the preglabellar field is absent medially, and the projection on the anterior border is smaller and upwardly directed. The tip of the projection is either broken (if so the break is remarkably even) or terminated by the rostral suture which runs up the sides and over the top of the tip.

Genus *OTARION* Zenker, 1833

Type species.—*Otarion diffractum* Zenker, 1833.

Synonym (subjective). *Harpidella* M'Coy, 1849.

Discussion. The type species of *Harpidella*, *H. megalops* (M'Coy, 1846), is redescribed below and reasons are given for regarding *Harpidella* as a synonym of *Otarion*.

Specimens from Maine referred to *Otarion* are distinguished from those of *Rhinotarion* in that the projection from the anterior border is absent. Cephala (excluding the hypostome) are readily divisible into two kinds, and a possible third. Only one example of the latter has a thoracic segment articulated with it, so that the segments, pygidia and their developmental stages, cannot readily be matched with these three types of cephala. The procedure adopted is to describe the two most abundant types of cephala as two distinct species, and the third as a possible but unnamed additional species. Then follow descriptions of a hypostome that probably belongs within this genus, segments, pygidia, and transitory pygidia. Whether or not two or three species are represented is problematical, and there is also the possibility that two of them are sexual dimorphs of one species, or even that one of them is a sexual dimorph of *Rhinotarion sentosum* n. gen., n. sp.

Developmental series of the cranidium and pygidium are described below. There is a remarkable similarity between the small cranidia and pygidia of *Otarion* and those of the Ordovician *Dimeropyge*, a greater similarity than that between small stages of *Otarion* and *Proetus* described here. The paired spines, present in *Otarion* but not in *Proetus* (Fig. 6), are the major feature in which *Otarion* resembles *Dimeropyge*. This resemblance in developmental stages may be taken to suggest a closer relationship between otarionids and dimeropygids than between otarionids and proetids.

Recent descriptions and diagnoses (Prantl and Přibyl, 1951; Richter, Richter, and Schmidt *in* Moore, 1959) do not give information on the rostral plate in this genus. A topotype specimen of the type species is here illustrated (Pl. 10, figs. 12, 14–16) for comparison with the Maine material, and it has been prepared to reveal the rostral plate (Pl. 10, fig. 15). The rostral suture runs parallel to the outer margin of the doublure, and is situated a short distance in from it. The anterior branch of the suture (Pl. 10, fig. 16) runs inward and forward over the edge of the border, and is continued inward across the doublure by the connective suture. The inner edge of the doublure is curled upward beneath the border furrow, but clearly the connective sutures are close together, or meet at the inner margin. The rostral plate is thus triangular in outline, and flexed in the longitudinal direction. The rostral plate in the Maine species (Pl. 5, fig. 26; Pl. 6, figs. 2, 9; Pl. 7, figs. 6, 7) is similar in shape.

Otarion megalops (M'Coy, 1846)

Plate 19, figures 1–14, 16.

Holotype. National Museum of Ireland, internal mould of incomplete cranidium (Pl. 19, figs. 1–4), from Boocaun, near Cong, County Galway, Eire. The strata at this locality are of Upper Llandovery age (Whittard, 1938: 101–102; Harper, 1949: 54).

Other material. Two topotype cranidia, and a cranidium from strata of the same age at Tonlegee, near Cong.

Description. The glabella is widest across the elongate-oval, inflated basal lobes, rounded anteriorly; lateral furrow 1p curving inward and backward, shallowing posteriorly before it merges with the broad occipital furrow; furrow 2p is a short, shallow depression running directly inward from the axial furrow. The cheek is highest posteriorly, the large palpebral lobe curving up from the summit (Pl. 19, figs. 12, 13); the line δ-δ runs across the basal glabellar lobe at about one-third the length. Inside the palpebral lobe the cheek is convex and descends steeply to the axial furrow. In front of the palpebral lobe the cheek descends at first steeply, then there is a break to a gentler slope before it curves steeply down to become vertical adjacent to the border furrow. The break in slope mentioned runs from immediately in front of the palpebral lobe, forward and inward to meet the axial furrow opposite the most anterior part of the glabella; this break in slope has been interpreted by M'Coy and later authors as an eye ridge. The preservation as internal moulds in medium-grained sandstones makes it uncertain that this change in slope is truly an eye ridge—no distinct ridge can be seen. Preglabellar field is convex, descending vertically, anterior border jutting forward. Anterior branches of sutures are straight and diverge forward, on the crest of the anterior border curving to run inward. The posterior branch runs backward and slightly outward, so that the posterior part of the fixed cheek (Pl. 19, figs. 1, 13, 16) is short (exs.) and narrow (tr.). Median occipital tubercle on posterior margin of occipital ring.

Discussion. The cranidium of M'Coy's species differs from that of the type species of *Otarion* (Pl. 10, figs. 12, 14, 16) in the presence of a distinct lateral furrow 2p, in the larger palpebral lobe which is situated farther back, in the relative narrowness (tr.) of the posterior part of the fixed cheek, and the relatively shorter (sag. and exs.) preglabellar field. These differences do not seem to be worthy of generic rank. The two new species and one indeterminate species of *Otarion*, described below, are like *megalops* in the presence of lateral glabellar furrow 2p, the size and position of the eye lobe, and the narrow (tr.) posterior part of the fixed cheek. A Middle Devonian species having a large eye lobe and probably of this type is *O. unguloides ranunculum* Erben, 1953. Přibyl (1960: 218–220, pl. 3, figs. 5, 6) has used *Harpidella* for Barrande's species *novella* and certain North American species. A cranidium of *O. novella* (MCZ 8552) from the Kopanina beds, Lower Ludlow, at Kopanina, shows that while lateral glabellar furrow 2p is present, and there is a distinct eye ridge, the palpebral lobe is small and similarly situated to that of *O. diffractum*, and the posterior part of the cheek is as wide as in the latter species. *O. novella* is thus intermediate between *diffractum* and *megalops*, and we consider *Harpidella* should not be used as Přibyl suggests. Re-investigation of many species is necessary as well as more complete material, before any subdivision of *Otarion* can be placed on a sound footing.

Otarion instita n. sp.

Plate 5, figure 24; Plate 6; Figure 6a.

Holotype. USNM 154220, cranidium with left free cheek.

Description. Glabella is subparallel-sided, bluntly rounded anteriorly, and moderately convex; occipital furrow deep and transverse behind median lobe, curving back behind basal lobe. Latter isolated by straight furrow 1p which runs from opposite midpoint of palpebral lobe diagonally inward and backward to occipital furrow; basal lobe convex, length (exs.) about one-quarter of sagittal length of glabella. Conspicuous smooth muscle area (Pl. 6, fig. 4) runs in from axial furrow along anterior side of furrow 1p for about half its length; similar but shorter (tr.) muscle area 2p runs directly inward from axial furrow in line with anterior end of eye lobe. Cheeks inside border furrows united by broad (sag. and exs.) preglabellar field which slopes gently forward and at its margin drops abruptly vertically to the inner edge of the border. Border broadest anteriorly and anterolaterally, flattened upper surface is horizontal anteriorly but outward sloping laterally. Posterior border narrow (exs.) between axial furrow and fulcrum, beyond here widening rapidly and merging with broad lateral border at genal angle; genal spine long, gently tapering and curved. Large eye lobe of length (exs.) approximately one-third sagittal length of cephalon; convex eye surface apparently smooth externally, but internal surface showing many minute facets (Pl. 5, fig. 24). Median pit in palpebral lobe. Anterior branches of suture moderately divergent, crossing border in line (exs.) with midpoint of palpebral lobe, posterior branch running straight outward and backward across border a short distance inside base of genal spine. Doublure flattened on under surface, extending inward to lateral and anterior border furrows, curved up at the inner edge so that this edge lies close beneath the furrow. Doublure extends inward beneath posterior border as far as fulcrum. Rostral suture runs along vertical face of anterior border; connective sutures converge backward to isolate a triangular rostral plate (Pl. 6, figs. 2, 9), the innermost portion of which is flexed upward and indented. External surface bearing closely-spaced tubercles on glabella except in furrows; large median occipital tubercle; similar tubercles along anterior portion, and steeply sloping edge of preglabellar field and anterior part of cheek; elsewhere, external surface apparently smooth, except for terrace lines on edge of border, genal spine and doublure.

Development. A size series of cranidia (Pl. 6, figs. 8, 9, 13–16, 18–24; Fig. 6a) has been picked out, the smallest example approximately 1 mm in length (sag.). In this specimen the glabella as well as the cranidium as a whole is more convex than in larger examples; the anterior border is relatively narrower (sag. and exs.) and less flattened on the upper surface; the basal glabellar lobe is present and of approximately the same relative size as in larger examples. Most striking are the spines, a median occipital, three pairs on the glabella (of which the posterior is the longest and thickest), a median pair on the preglabellar field and the anterior border, and accessory pairs on the fixed cheeks, palpebral lobe and borders. With increase in size there is a rapid reduction of these spines, and a loss of the symmetrical arrangement, followed by a gradual assumption of the pattern of the large examples. A size series of the free cheek is difficult to pick out, but small examples which probably belong (Pl. 6, fig. 17) bear many short spines which are rapidly reduced and disappear (Pl. 6, figs. 10–12).

The form of the small cranidia, and particularly the arrangement of paired spines, resembles that of small cranidia of the Ordovician *Dimeropyge* (Whittington and Evitt, 1954: 44–46; and compare Pl. 6, figs. 18, 19, 24 with Whittington and Evitt, 1954, pl. 3, figs. 16, 17, 21–26; pl. 22, figs. 1–10). In the Ordovician genus there is an increase in convexity of the cranidium during development, there is no basal glabellar lobe, the palpebral lobe is smaller, but the spines are reduced in size and lose the symmetrical arrangement, as in *Otarion*.

Otarion plautum n. sp.

Plate 7, figures 1–9, 11–15, 17–19, 23–25: Figure 6b.

Holotype. USNM 154231, cephalon lacking hypostome.

Description. Much less abundant than *O. instita* are cephala and cranidia of this type, distinguished by the glabella having a width across the base approximately equal to the length (sag.), the flatter transverse profile of both glabella and cephalon, the more divergent anterior branches of the suture, the narrower border anteriorly and anterolaterally, the stronger backward flexure of the posterior border outside the fulcrum, and the shorter, more rapidly-tapering genal spine. A faint eye ridge (Pl. 7, figs. 6, 8) runs inward and forward to the axial furrow. The doublure is narrow, forming with the border a tube-like structure, the rostral plate triangular (Pl. 7, figs. 6, 7) and relatively short (sag.). The external surface is tuberculate, and there is a slightly larger median occipital tubercle. Tubercles are irregularly but closely spaced on the glabella, fixed cheek inside the eye lobe, and preglabellar field.

A developmental series of cranidia has been picked out (Pl. 7, figs. 8, 11–14, 17–19, 23–25; Fig. 6b), which is distinguished from that of *O. instita* (Pl. 6, figs. 8, 9, 13–24) by the consistently steeper slope of the preglabellar area, as well as the more divergent anterior branches of the suture and the stronger backward flexure of the posterior border. The smallest example (Pl. 7, figs. 19, 24, 25) is extremely like that of *O. instita* (Pl. 6, figs. 18, 19, 24), and bearing spines of similar relative size and paired arrangement. The glabella is subparallel-sided and bluntly rounded anteriorly with a small, convex basal lobe. With increasing size there is a general reduction in convexity, and the glabella gradually assumes the broader, relatively shorter appearance. Spines are rapidly reduced and the irregular arrangement of tubercles assumed. As in the case of *O. instita*, attention is drawn to the similarity between this developmental series and that of *Dimeropyge* (Whittington and Evitt, 1954).

Otarion sp. ind.

Plate 5, figures 7, 8, 12, 17, 19–23, 25, 26.

Description. This type of cephalon is almost as abundant as that of *O. plautum*. It is intermediate between *O. instita* and *O. plautum* in the convexity of the cephalon, the outline of the glabella, and the width of the anterior border. The outline of the anterior margin is bluntly and obliquely angulate, as is the course of the anterior border furrow; these outlines are more angulate than those of *O. instita*, while those of *O. plautum* are rounded. On the other hand, the cephalon resembles that of *O. plautum* in having the short genal spines and stronger backward flexure of the outer part of the posterior border. Doublure is similar to that of the other species, and there is a triangular rostral plate (Pl. 5, fig. 26). No very complete developmental series of cranidia has been recognized, because of the obvious difficulty of picking out this intermediate type. The smallest cranidium that appears to belong to it (Pl. 5, figs. 22, 23) is of length (sag.) 1.5 mm. The external surface bears elongate, irregularly scattered tubercles and paired spines on the glabella, the posterior pair in line with the posterior part of the palpebral lobe being notably longer and thicker.

One specimen (Pl. 5, figs. 19, 25, 26) has the anterior thoracic segment linked to the cephalon. The axial ring bears a number of tubercles; the outer part of the pleural region is facetted so that only the posterior band extends to the tip, and bears on the external surface tubercles, including a small group at the tip.

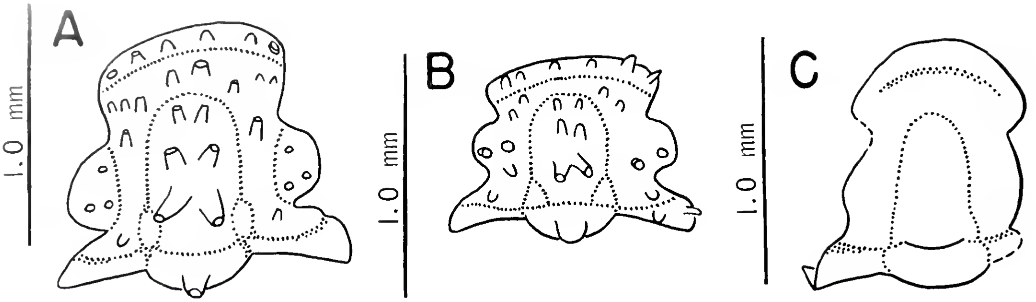


Figure 6. Smallest cranidia in size series showing some paired spines. A) *Otarion instita* n. sp. (original of Pl. 6, figs. 18, 19, 24). B) *Otarion plautum* n. sp. (original of Pl. 7, figs. 19, 24, 25). C) *Proetus pluteus* n. sp., USNM 154491, slightly smaller than original of Plate 1, figs. 23, 24, 30, 31.

Otarionid Hypostome
Plate 7, figures 10, 16, 20–22, 26, 27.

Description. The small number of specimens shows a variety of form—some relatively long (Pl. 7, figs. 10, 16), others relatively broader (Pl. 7, figs. 21, 22). In both types the anterior lobe of the middle body is moderately convex, separated by a complete middle furrow from the inflated, crescentic posterior lobe of the middle body. Macula not discernible. Shallow lateral and posterior border furrows, borders narrow, distinct shoulder at a point beyond the mid-length, short spine at posterolateral angle. Anterior wing triangular, directed upward and outward, tip rounded, on anterior margin near tip a small process directed forward. Doublure commences behind anterior wing and posterolaterally is of similar width to the border; posterior wing a pointed process directed upward and inward from the margin of the doublure beneath the shoulder.

Smaller examples are similar, the smallest (Pl. 7, fig. 20) distinguished by the relatively larger posterior lobe of the middle body, the relatively wider posterolateral border bearing a number of short spines, and the downwardly flexed anterior edge.

Otarionid hypostomes have rarely been found; the present examples are similar to that of the Middle Devonian *Otarion ceratophthalmus* portrayed by Richter (1914, text-fig. 1).

Otarionid Thoracic Segments and Pygidium, Type A
Plate 8, figures 1–6, 9, 10, 13–15, 19, 21–26.

Description. These are the most abundant types as isolated specimens, including segments with a median spine, and in three examples with several posterior segments articulated with a pygidium. The segments are typically otarionid, the narrow, shallow, pleural furrow running out almost to the tip before dying out. Inner part of pleura relatively narrow (tr.), with anterior flange and posterior recess; doublure commences outside this recess and runs along the posterior edge and beneath the tip of the outer part. Narrow panderian notch (Pl. 8, fig. 15) situated beneath posterior margin of pleural furrow, anterior edge raised to form a stop during enrollment. Pygidium transverse, broad axis extends back to inner margin of border and is bluntly rounded. Only first ring indicated by faint ring furrow. Pleural regions subdivided by first interpleural furrow, and one to three pleural furrows, the second and third extremely faint. Narrow border developed as a faint convexity without border furrow. Doublure is widest laterally, behind tip of axis becoming narrow and strongly convex (Pl. 8, fig. 10). External surface of both segments and pygidium finely granulate, the axial ring in larger examples (Pl. 8, figs.

13, 14, 23, 25) bearing numerous tubercles.

The tubercles on the axis and lack of tuberculation on the pleural regions suggest that these segments and pygidia may belong to either *Otarion instita* or *O. plautum*, their abundance indicating that they may belong to the former. The more posterior segments, particularly in the smallest example (Pl. 8, figs. 3, 6, 9) have the posterior tip bluntly pointed and directed backward. This may be a feature associated with small segments, for in the largest example the tips (Pl. 8, figs. 24, 25) are rounded on all segments; on the other hand, this may be a specific difference.

Otarionid Thoracic Segments and Pygidium, Type B

Plate 9, figures 1–14.

Description. These segments are differentiated chiefly by the external surface, which is tuberculate on the axial ring and the posterior bands, with a group of small, short spines projecting backward and outward from the posterolateral margin of the tip. In front of this group of spines the edge of the tip is slightly excavated, giving a characteristic scalloped outline (Pl. 9, figs. 1, 8). The occipital ring and posterior border of the cephalon of *Otarion* sp. ind. (Pl. 5, figs. 19, 25) bear scattered tubercles and short spines, as does the axial ring and posterior pleural band of the attached segment. The latter is strongly facetted, but the posterolateral tip appears to bear a few outwardly directed tiny spines. It appears that these segments may belong with this cephalon, and the axis is notably more convex than in type A.

No pygidium is known articulated with these segments; less abundant than those of type A are those placed here (Pl. 9, figs. 4–7, 9–14). Distinctive of the largest specimen (compare Pl. 9, figs. 4–7, with Pl. 8, figs. 1, 4, 10) is the slightly more prominent axis, the more triangular outline, the lack of any distinct border and the presence of the tubercles or short spines on axial rings and pleural regions. Three axial rings and a faint fourth ring are marked out by the first two ring furrows and bands of tubercles; on the pleural regions the first interpleural furrow and three pleural furrows may be distinguished, posteriorly as smooth bands between rows of tubercles. The doublure is similar to that of type A, narrow and convex behind the axis.

Otarionid Pygidium, Type C

Plate 8, figures 7, 8, 11, 12.

Description. One example of this distinctive pygidium is known, the outer part of the pleural regions steeply sloping and with a marked angle between outer and inner parts along the anterior margin. The doublure is of approximately constant width, and there is no border. The first axial ring is distinct, as is the first pleura, with a shallow pleural furrow. The general form and the external granulation suggest that this pygidium may belong with *Rhinotarion sentosum*, particularly if the angle between the inner and outer parts of the pleural regions is compared with that of the most posterior segment referred to this species (compare Pl. 8, figs. 7, 12, with Pl. 5, figs. 9, 14).

Otarionid Pygidium, Type D

Plate 8, figures 16, 17, 18, 20.

Description. This pygidium is quite like type A, but is distinguished by a more rapidly tapering axis, the less distinct ring and pleural furrows, and the lack of distinct narrowing of the doublure posteriorly.

Otarionid Transitory Pygidia

Plate 9, figures 15–27.

Description. Size series are known of some of the types of pygidia described above, and in addition there are transitory pygidia such as those shown in Plate 9, figures 15–26, which appear to form a series. The relatively narrow axis bears median spines on the rings, one of which is much stouter and longer than the others. This stout spine may be on the third axial ring (Pl. 9, figs. 15, 16, 19, 20, 23–25), or the first (Pl. 9, figs. 17, 21, 26), or be absent (Pl. 9, figs. 18, 22). It thus appears to progress forward, and its absence suggests that the segment bearing it has been released into the thorax. The pleural regions slope gently outward from the axis, more steeply distally. In larger specimens pleural and interpleural furrows are well-marked (Pl. 9, figs. 17, 21). At the distal change in slope there is a spine on the posterior band of each segment, and a second spine further inward (Pl. 9, fig. 17). These same rows of spines are present on the example lacking median axial spines (Pl. 9, figs. 18, 22). The external surface is granulate between the spines. The doublure is flat and of even width.

A different type of transitory pygidium, without prominent axial spines and with less conspicuous spines on the posterior bands of the pleurae, having well marked pleural and interpleural furrows, and with the ends of the segments extended into short backward pointing spines, is shown in Plate 9, figure 27. Possibly it is an earlier stage of type A, in which the posterolateral tip of the segment is also bluntly pointed in small examples (Pl. 8, figs. 3, 5, 6, 9).

Discussion. These transitory pygidia are considered to belong to *Otarion* because paired spines are also conspicuous in the early development of the cranidium of *Otarion*, and because of the presence of the median axial spine. It has not been possible to make any specific separations between them. The outline, the median axial spine and its progress forward, and the spines on the posterior pleural bands (most conspicuous distally) are points of strong resemblance between these transitory pygidia and those of the Ordovician *Dimeropyge* (Whittington and Evitt, 1954, pl. 3, figs. 13–15, 18–20; pl. 23, figs. 18–25).

Comparisons with other Silurian species

Few species have been described from Silurian rocks, and either the descriptions are old and inadequate or the more recently described specimens are fragmentary. Material in the Museum of Comparative Zoology, limited in quantity and vaguely localized, has enabled us to make the following comments:

Otarion sp., presumably *O. elegantula* Lovén, 1845, MCZ 8595, enrolled exoskeletons from Gotland, Sweden. Preglabellar field is short (sag. and exs.), steep, and the anterior border flat, but not as broad (sag. and exs.) as in *O. instita*. Cephalon appears to range in outline between that of *O. plautum* and *O.* sp. ind., but the flat border is distinctive. Thorax of 12 segments, and there is no median axial thoracic spine.

Otarion sp., from Wenlock Limestone, Dudley, England (Salter, 1853; Whittard, 1938: 102–103), MCZ 8597. The narrow preglabellar field and border are of length (sag.) about one-third that of the glabella, and the eye lobe is relatively small and high. The outline of the glabella resembles that of *O.* sp. ind., but the form of the cephalon is not the same. There are 11 thoracic segments, and a prominent median axial spine on the 6th segment.

Otarion christyi (Hall, 1879), MCZ 8596, cephala and complete exoskeletons from the Waldron Shale, Waldron, Indiana. Cephala range in outline and convexity between that of *O. plautum* and *O.* sp. ind., and like these forms, the eye lobe is relatively large. There are 12 thoracic segments, and no median axial spine. Of the three species discussed here, *O. christyi* is most like *O. plautum* and *O.* sp. ind. from Maine. Pending the redescription of adequate Waldron material, the Maine species are regarded as distinct.

Family SCUTELLUIDAE Richter and Richter, 1955

Scutelluid gen. ind.

Plate 10, figures 4, 6–8, 13.

Description. Two incomplete fragmentary cranidia only have been found, and

Table 2. Arrangement of glabellar tubercles in 11 specimens of *Fragiscutum rhytium*, listed in order of decreasing size, the arrangement expressed in the formula of Tripp (1957, 1962).

USNM 154272 (Pl. 11, fig. 2):	ii-1; II-1, 2; III-1, 3; iv-1; IV-0_*, 1, 2, 3; v-0, 1, 2; V-0_*, 1, 2, 3; VI-0.
USNM 154273 (Pl. 12, fig. 8):	II-0_*, 1, 2; III-0_*, 1, 2, 3; iv-0, 1; IV-0⁑, 1, 2, 3; V-0⁑, 1, 2, 3; VI-1, 2.
USNM 154275 (Pl. 12, fig. 1; Fig. 7b):	ii-1; II-1, 2; III-1, 3; iv-1, 2; IV-0, 1, 2, 3; v-0, 1, 2; V-0, 1, 2, 3; VI-1, 2.
USNM 154290:	ii-0; II-1, 2; III-1, 3; iv-1; IV-0, 1, 2, 3; v-0, 1; V-0, 1, 2, 3; VI-1, 2.
USNM 154291:	ii-0; II-1, 2; III-1, 3; iv-0⁑, 1, 2; IV-0, 1, 2, 3; V-0, 1, 2, 3; VI-1.
USNM 154277 (Pl. 12, fig. 4):	ii-0_*; II-1, 2; iii-0_*; III-1, 3; IV-0, 1, 2, 3; v-1, 2; V-0, 1, 2, 3; VI-1, 2.
USNM 154278 (Pl. 12, fig. 6):	II-1, 2; III-1, 3; iv-1; IV-0⁑, 1, 2, 3; v-1, 2; V-1, 2, 3.
USNM 154279 (Pl. 12, fig. 9):	ii-1; II-1, 2; III-1, 3; iv-0⁑, 1; IV-1, 2, 3; V-1, 2, 3.
USNM 154292:	ii-0; II-1, 2; III-1, 3; iv-0; IV-1, 2; v-0; V-0, 1, 2, 3; VI-0.
USNM 154280 (Pl. 12, fig. 15; Fig. 7a):	II-1, 2; III-1, 3; iv-1; IV-0_*, 1, 2, 3; v-1, 2; V-1, 2, 3; VI-1.
USNM 154281 (Pl. 12, fig. 18):	II-1, 2; III-1, 3; iv-0; IV-1, 2, 3; V-0⁑, 1, 2, 3.

both have a large, curved, backwardly-directed median occipital spine, and a small spine projecting back from the posterior margin of the palpebral lobe. The glabella expands forward and is moderately convex, reaching to the anterior margin where it merges with the anterior border. The palpebral lobe is placed far back and in line (exs.) with the outermost part of the glabella, the anterior branches of the suture divergent. Glabellar furrows cannot be distinguished. On the external surface there are terrace lines running concentrically on the anterior slope of the glabella.

Discussion. Species of several genera described by Šnajdr (1960) exhibit both the occipital and palpebral spines, and without information on the glabellar furrows it is not possible to be sure to which genus these specimens may belong. Species of *Kosovopeltis*, *Decoroscutellum*, and *Spiniscutellum* are present in the upper Silurian of Bohemia. Species of *Kosovopeltis* exhibit occipital and palpebral spines in the smaller specimens, but they are absent in the larger ones; species of *Decoroscutellum* commonly have two spines on the palpebral lobe, and species of *Spiniscutellum* have a wider anterior border than in the present specimens.

Family ENCRINURIDAE Angelin, 1854

FRAGISCUTUM n. gen.

Type species. *Fragiscutum rhytium* n. sp.

Diagnosis. Basic tubercle pattern (Table 2) includes: II-(1), 2; III-1, 3; iv-1; IV-(0), 1, (2), 3; V-(0), 1, 2, 3; VI-1; lateral glabellar lobe 1p reduced to a small lateral remnant, so that apodeme 1p lies almost in the same transverse line as the median part of the occipital furrow. True and "false" preglabellar furrows weak, "false" anterior border short (sag. and exs.) and with weak tuberculation. Extremely small fixigenal spine. Rostral plate trapezoidal, widest at hypostomal margin; hypostome with median lobe not extending beyond anterior margin, macula inconspicuous. Vincular furrow extends along anterolateral part of ventral surface of border. Granulation on borders, crests of large tubercles, and between the bases of these tubercles. Ten thoracic segments, none with a median axial spine. Axis of pygidium with less than 20 axial rings, weak median smooth band commencing behind second ring. Pleural region rounded posteriorly, where pleural bands curve inward.

Discussion. Various authors have distinguished groups of species within the genus *Encrinurus* (Reed, 1928; Rosenstein, 1941; Tripp, 1957, 1962), but while there is agreement between these authors that the groups center around certain species, the composition of particular groups has been disputed. Tripp used a combination of cephalic and pygidial, but not thoracic, characters in defining particular groups. We have followed his approach, and elected to give generic status to the new group. The "species-group" most closely allied to *Fragiscutum* is that of *Encrinurus variolaris* (Reed, 1928; Temple, 1956). Temple referred to this group as "advanced" and noted the reduction of the preglabellar furrow. Other characters which this group has in common with *Fragiscutum* are the absence of a median axial spine on the thorax, the rounded pygidial termination and the relative fewness of the axial rings of the pygidium. The *E. variolaris* group is distinguished from *Fragiscutum* by the pattern of tubercles on the glabella (Tripp, 1962, pl. 65, figs. 17–20), particularly in the presence of a distinct row I, the 11 thoracic segments and the absence of a median band on the pygidium.

Fragiscutum rhytium n. sp.

Plate 10, figure 11; Plates 11–13; Figures 7, 8.

Holotype. USNM 154272, incomplete exoskeleton.

Description. Occipital ring widest (sag.) medially. Lateral glabellar lobe 1p short (exs.) and limited to the lateral part of the glabella immediately in front of the outermost part of the occipital ring, so that furrow 1p and occipital furrow are united medially. Furrow 2p commences as a deep pit in the axial furrow and extends inward as a shallow depression, the furrows uniting medially to isolate a 2p glabellar ring. Furrow 3p, situated opposite the anterior margin of the eye lobe, is shallow and short. Curved apodemes, expanded distally, present at outer ends of occipital, 1p and 2p furrows (Pl. 11, fig. 3; Pl. 12, figs. 2, 3). Anterior margin of glabella (Pl. 12, fig. 5) faintly defined laterally by shallow preglabellar furrow which dies out medially. Axial furrow deep, wide and steep-sided, with a U-shaped cross-section on cranidium, continued on free cheek (Pl. 11, figs. 16, 18) as a much shallower depression which dies out toward the anterior margin. Anterior pit (Pl. 11, fig. 13) a deep depression immediately inside the margin of the cranidium. Highest point of cheek bearing the large eye lobe, the midpoint of which is situated in line with lateral glabellar lobe 3p. Posterior border furrow proximally as deep as axial furrow, shallowing distally where it curves forward inside the genal angle and continues as the shallow lateral border furrow (Pl. 11, fig. 1). Posterior border narrow and strongly convex in the inner part, outer part broader and less convex; tiny fixigenal spine in largest specimens (Pl. 10, fig. 11). Anterior border furrow shallow and ill-defined (Pl. 11, figs. 16, 18), running parallel to anterior margin and closer to this margin than to suture line. Anterior branch of suture runs forward and inward across cheek and axial furrow, curves around subparallel to preglabellar furrow, and makes an oblique angle with the short (tr.) rostral suture (Pl. 11, fig. 13). Posterior branch of suture runs outward and backward, curves over the border at the genal angle to reach the posterior margin immediately outside the tiny fixigenal spine, and crosses the doublure (Pl. 12, figs. 2, 3). Connective suture runs downward and slightly outward (Pl. 12, fig. 5), so that rostral plate was evidently trapezoidal in outline and widest at the anterior margin. Doublure of cephalon extends from immediately inside genal angle forward beneath the cheek border, and is widest posterolaterally where it extends inward as far as the border furrow. Anterolaterally the rolled margin is indented by a shallow vincular furrow (Pl. 12, fig. 3), which dies out before reaching a point in line with the axial furrow. Anteriorly, doublure is narrower where it is bounded by the hypostomal suture. On the free cheek (Pl. 11, fig. 19) this suture may be seen forming the inner edge of the doublure, running from the anteroventral margin inward to meet the inner margin of the doublure immediately beneath the anterior pit. From this posterior end of the hypostomal suture a flexure (Pl. 12, fig. 3) runs diagonally across the doublure of the free cheek.

Hypostome of width approximately equal to length (sag.), elongate-oval to diamond shaped in outline. Central body strongly inflated and with a pronounced, narrow anterior median lobe which projects forward below the anterior border furrow. Latter shallow, separated from the sutural margin by a narrow band. Shallow furrow at side of steep slope of median lobe runs backward and slightly outward to die out level with the anterior wing. Lateral border narrow and convex, border furrow deep and inflated middle body overhangs this border; posterior border widest medially, flattened, separated from the middle body by a shallow border furrow, and forming a flat posteriorly-directed projection. Macula (Pl. 11, fig. 21) a faint low swelling at posterolateral margin of the middle body. Anterior wing of hypostome (Pl. 11, figs. 6, 7, 12, 13) greater in height than the central body; outer tip of wing twisted and deflected outward and backward; inner, dorsal edge of wing deflected forward and produced into a slender process with a concave inner side which probably lies against the anterior pit of the cephalon; wing process does not extend as high as above mentioned process and lies outside it. Transverse slit-like pit in outer face of wing corresponds with this process; elongate boss on outer face of wing dorsad of pit. Posterior wing an inwardly and upwardly directed subrectangular projection, situated about halfway between the anterior wing and the rear of the central body; doublure wide between wings, behind posterior wing narrow, but widening beneath posterior border though it does not extend inward as far as the lateral or posterior border, except medially where there is a small cusp which extends forward almost to beneath the border furrow.

External surface, except in furrows, bearing large scattered tubercles. The arrangement of these on the glabella is shown in Figure 7, and in Table 2. Arrangement of tubercles on cheek and border is shown in the photographs; notable is the single row on the cranidium between the preglabellar furrow and the sutural margin, the median and faint additional tubercles present on the occipital ring, and low tubercles on the posterior border. A fine granulation is present on and between the tubercles (Pl. 11, fig. 20), on the ventrally facing part of the border, and on the hypostome. This granulation is not present in the deeper parts of the furrows.

Thorax of 10 segments; axis about one-third total width (tr.) at the fifth segment; axial furrows slightly impressed; axial rings with a faint elongate swelling distally. Inner part of pleura horizontal, outer part flexed steeply down; broad, convex pleural band is four times the width (exs.) of the narrow, flattened anterior flange, the two separated by a sharp change in slope rather than a pleural furrow. Lateral to the fulcrum, anterior flange expands to form a broad flattened facet; the pleural band tapers slightly, and is curved in an anteriorly concave arch, the tip extended as a

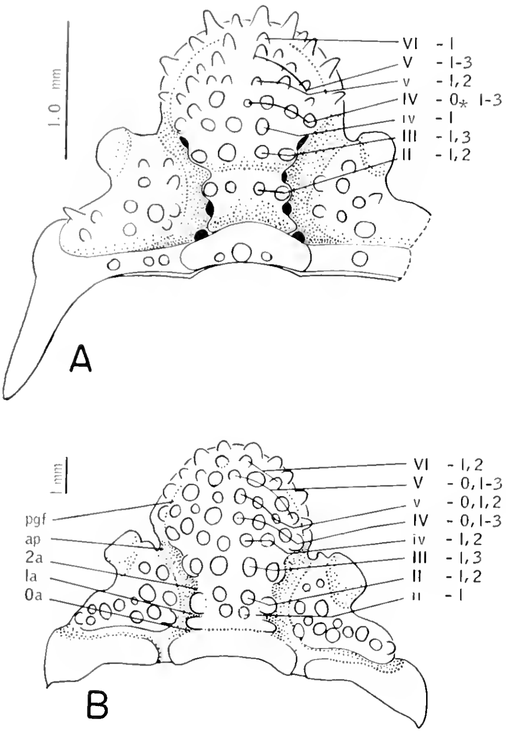


Figure 7. *Fragiscutum rhytium* n. gen., n. sp. Two cranidia showing notation (after Tripp, 1957, 1962) of glabellar tubercles. A) Original of Plate 12, figure 15. B) Original of Plate 12, figure 1. Abbreviatons: 0a, 1a, 2a, positions of occipital, first and second apodemes; ap, anterior pit; pgf, preglabellar furrow.

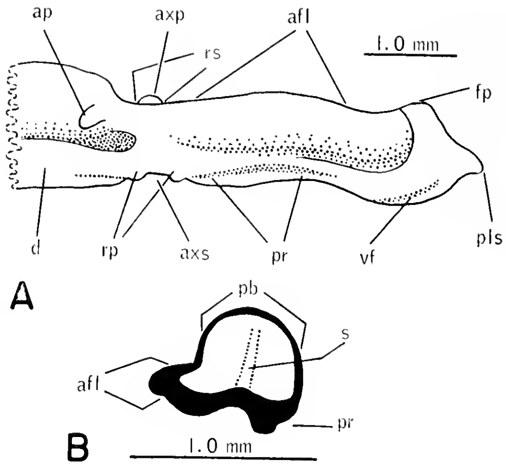


Figure 8. *Fragiscutum rhytium* n. gen., n. sp. A) Ventral view of part of a segment. Compare Plate 12, figures 13, 14, 17, 20. B) Section through inner part of pleura, in exsagittal plane. Solid black is replaced outer portion of exoskeleton. Abbreviations: afl, anterior flange; ap, apodeme; axp, axial articulating process; axs, axial articulating socket; d, doublure of axial ring; fp, projection at anterior margin of facet; pb, pleural band; pls, pleural spine; pr, posterior recess; rp, ring articulating process; rs, ring articulating socket; s, silicified lining of canal, appearing as a hollow cone (compare Pl. 13, fig. 17); vf, vincular furrow.

short, blunt spine. Apodeme (Pl. 11, fig. 3; Pl. 12, figs. 13, 17) is curved inward and downward, and situated a short distance in from the axial furrow. Ventral surface of pleura does not reflect dorsal surface (Fig. 8b); anterior half is convex downward, and there is a deep groove which curves outward just inside the narrow doublure; latter widens and extends across the pleura at the tip. The various structures that facilitate articulation between the segments and limit enrollment are shown in Figure 8a (compare Pl. 11, figs. 1–3; Pl. 12, figs. 13, 14, 17, 20). The downward-projecting ring process fits into a ring socket that surrounds the axial process. The anterior flange on the inner part of the pleura fits beneath the narrow posterior recess so that in dorsal aspect only the pleural bands are visible. Along the posterior edge of the outer part of the doublure is the vincular furrow, which receives the anterior edge of the pleural band of the succeeding segment. A limit to enrollment occurred when the outer parts of the pleural bands moved against each other and the thickened projections of the facets approached each other. Anterior two thoracic segments have outer parts of pleurae slightly shorter (tr.) than succeeding segments; posterior border of cephalon with structures for articulation corresponding to those along posterior margin of segment. Cross section of inner part of pleura of segment (Fig. 8b) shows exceptional thickness of exoskeleton in this region, and the exoskeleton of both the axial ring and outer part of the pleura must have been similarly thickened. As certain specimens show (Pl.

10, fig. 11; Pl. 13, fig. 17), along the transverse midline of the axial ring and pleura, the exoskeleton was partially traversed by canals, preserved in the silicified material as hollow cones extending from the inner toward the outer surface of the exoskeleton. These canals, however, did not open on either the inner or the outer surface of the exoskeleton, so far as the silicified specimens show (Pl. 12, fig. 20; Pl. 13, figs. 11, 14–17). Similar structures have been seen in specimens in which the exoskeleton is preserved as calcium carbonate (Campbell, in press), and when weathered the canals may be seen as perforations, but again they are apparently not visible on unweathered surfaces and it is uncertain whether or not they traversed the outermost layers of the exoskeleton.

Pygidium triangular in outline, width/length/height ratio approximately 5/4/2.5. Axis with flattened profile in cross section (similar to that of axial rings of thorax), larger specimens (Pl. 13, fig. 11) with 18 axial rings, ring furrows deeply incised laterally; behind second ring these furrows weaken so that a smooth median track runs posteriorly along the axis. Four or five large median axial tubercles, the first on ring 3 or 4, the second on ring 6 or 7, the third on ring 10 or 11, the fourth and fifth present close to the tip of the axis. Pleural regions curve steeply down, subdivided by deep furrows into eight pleural bands, the posterior pair curving inward distally and merging behind the tip of the axis; inside this pair there is a ninth pair and a faint median strip visible on larger specimens. The first five furrows extend to the margin, and the tips of the pleural bands project and are slightly expanded (Pl. 13, figs. 14, 15); behind here the pleural furrows die out before reaching the margin. Anterior margin of pygidium like that of anterior margin of segment, with anterior flange and facet, the latter crossed by a shallow (pleural?) furrow (Pl. 12, fig. 23; Pl. 13, fig. 15). Below tips of first five pleurae border of pygidium projects downward; behind here it is flattened on the ventral side; the projecting anterior part is shaped to fit inside the doublure of the cephalon during enrollment. There is a deep notch in the doublure beneath the tip of the axis; this notch received the projecting median lobe of the hypostome during enrollment.

External surface of thorax and pygidium granulated, except in the furrows. The granulation extends over the ventral-facing part of the pygidial border, but not on to the inward facing doublure. The median axial tubercles of the pygidium are present in both small and large specimens, but some specimens show no other tubercles on either axial rings or pleural bands. In some specimens four or five extremely faint tubercles may be recognized amid the granulation on the pleural bands; these are analogous to the very faint tubercles which may sometimes be recognized on the posterior border of the cephalon.

Development. Characteristic of the small exoskeleton is the spininess—the larger tubercles are elongated as blunt spines, and smaller tubercles as thorn-like spines. There is a curving fixigenal spine and the posterior bands of both thorax and pygidium are extended as spines. On the smallest cranidium (Pl. 12, figs. 12, 18; length 1.3 mm) the arrangement of tubercles on the glabella (Table 2) is like that in larger specimens, showing that the main outlines of this pattern are established at an early stage. Tubercles additional to the median are present on the occipital ring, and also on the posterior border and base of the fixigenal spine. The external surface of the free cheek (Pl. 12, fig. 11) also is spinose rather than tuberculate. The small hypostome (Pl. 11, figs. 11, 14, 15, 17) has the forward projection of the middle body less prominently developed, and the posterior border relatively narrower. This border bears a median posterior and three pairs of tiny spines on the margin. With increase in size the main changes in the cephalon are reduction of the spines to tubercles and a rapid relative reduction of the fixigenal spine beyond a length (sag.) of 1.5 mm (Pl. 12, figs. 1, 4, 6, 9, 15, 18).

The smallest transitory pygidium (Pl. 13, figs. 4, 9, 13) includes at least six segments, the axis tapering rapidly backward to the rounded tip, the third ring bearing a long upwardly and backwardly directed median spine and a shorter, more backwardly directed spine behind this, possibly on the fifth segment. The pleural regions curve down steeply and extend in a narrow band behind the tip of the axis; pleural bands are extended as spines, the longest on the first band directed backward, successive spines directed slightly inward. Each pleural band bears a prominent tubercle at about the mid-length, these tubercles forming a line that curves back subparallel to the axial furrow. Doublure narrow, curled under, narrowest medially where the margin is arched upward in posterior view, but lacking the median notch of large specimens (Pl. 13, fig. 14). The lack of a notch corresponds with the lower convexity of the median hypostomal lobe at this stage (Pl. 11, figs. 14, 17).

Larger transitory pygidia (Pl. 13, figs. 1–3, 5–8, 12) contain more segments, but are generally similar in form. Up to three median axial spines may be present, these spines apparently situated on every third ring. The border spines of the posterior pleural bands are relatively shorter but similarly directed. There may be two rows of tubercles on the pleural bands, and there is also a fine granulation on the rings and bands. As a small segment shows (Pl. 12, figs. 21, 22), these segments with a median axial spine and spines on the pleural band are released into the thorax during development. Apparently the median spines, as well as the additional tubercles on axial ring and pleural bands, are reduced and disappear in the larger stages; the same is true in the pygidium, though in rare specimens tubercles on the pleural bands may be distinguished. It seems probable that each of the five tubercles along the median axial band of the pygidium is also a reduced remnant of an axial spine. The median tubercles in the holaspid pygidium are not situated opposite every third ring as they appear to be in the transitory pygidia. This arrangement may result from the crowding of the rings in the axis, which evidently takes place at a developmental stage subsequent to that of these transitory pygidia.

Discussion. A second species of the new genus, from the Henryhouse Formation of Oklahoma, is being described by Campbell (in press). Other American Silurian species (e.g., Raymond, 1916; Best, 1961) are either unlike the present one or known only from such fragmentary material, including internal moulds, that comparisons are not possible.

Several authors (Rosenstein, 1941: 57, pl. 2, fig. 2; Temple, 1954; Tripp, 1962, pl. 67, figs. 2, 9b, 10; Whittard, 1938: 120, pl. 4, fig. 7) have described the hypostome of Silurian species of *Encrinurus* and the way in which it was attached to the remainder of the cephalon. The preservation of the present material shows clearly the form of the anterior wing of the hypostome (Pl. 11, fig. 7) and how it was related to the cranidium (Pl. 11, fig. 13). The anterior and posterior wings are joined in a single structure by a broad portion of the doublure; the anterior wing is the larger and is twisted so that its distal cross section is U-shaped, the open end of the 'U' facing anteriorly. From the inner surface projects the wing process, and there is a pit corresponding to this process on the outer, posterior surface. On the outer surface of the wing, inside this pit, there is an elongate projection from the surface of the wing—this apparently corresponds to the knob described by Temple. Inside this knob, the inner extremity of the wing is extended forward as a long flange, projecting directly anteriorly (Pl. 11, fig. 12). On the inner surface of the cranidium the axial furrow forms a broad prominent ridge, and just inside the sutural margin is the boss reflecting the anterior pit in the external surface. When the hypostome was in position, presumably the tip of the wing process was close to the backward-facing slope of the anterior boss. There does not appear to be a distinct pit in this backward-facing slope that received the tip of the wing process, similar to that seen for example in *Ceraurinella* (Whittington and Evitt, 1954, pl. 12, fig. 30). It is clear that the curved extremity of the wing is so shaped as to fit around close to the slopes of the axial furrow, the flange on the inner tip of the wing extending beside the steep inner slope of this furrow. When the hypostome was in place, with the relatively broad, flat surfaces along the hypostomal suture in contact with the rostral plate and free cheeks, the anterior wing wrapping around the anterior boss, it is difficult to imagine that any relative movement was possible between the hypostome and the cephalon.

In Whittington's (1965: 420–421) recent diagnosis of Encrinuridae, reference is made to anterior and posterior pleural bands of the thorax. In the present species, no pleural furrows and anterior bands are visible in the articulated thorax (Pl. 11, fig. 2; Pl. 13, fig. 17). What appears to be an anterior band in an isolated segment (Pl. 12, fig. 14) is a narrow strip, here termed the articulating flange, which fits beneath the posterior recess (Fig. 8) of the segment in front. The only pleural furrow visible is that on the facet of the pygidium (Pl. 12, fig. 23; Pl. 13, fig. 15). We have thus referred to pleural bands of thorax and pygidium, but the pleural furrow on the first segment of the pygidium makes clear that these bands are posterior bands and that the anterior band has been reduced. The position of the pleural furrow is at the foot of the slope of pleural band down to articulating flange. Tripp's (1962: 466) description of the thorax of *Encrinurus punctatus* suggests that the condition may be the same in that species. Other encrinurid species (Tripp, 1962, pl. 67, fig. 3; 1957, pl. 11, fig. 17; pl. 12, figs. 11, 16, 17) show clearly anterior bands and pleural furrows on both thorax and pygidium; i.e., in some species the anterior band is not so reduced as in *F. rhytium*. The transitory pygidia show an extremely narrow anterior band (or articulating flange) on only the first segment, not succeeding segments.

Family DALMANITIDAE Vogdes, 1890

Genus *DALMANITES* Barrande, 1852

Dalmanites puticulifrons n. sp.

Plates 14, 15; Plate 19, figures 15, 17.

Holotype. USNM 154302, cranidium, anterior border, and part of left free cheek.

Description. Cephalon of width about twice the length (sag.); longitudinal profile of glabella low, highest point at occipital ring, the profile descending gradually forward to the back of the anterior glabella lobe which is gently inflated; occipital ring more markedly convex, particularly transversely. Occipital furrow broad and well rounded medially, but narrowing rapidly into the deep, slot-like apodeme. Glabellar furrow 1p transverse, shallow adjacent to the axial furrow, deepening inward; furrow 2p directed inward and slightly forward, extremely shallow adjacent to the axial furrow but deepening at the apodeme; furrow 3p directed inward and backward, widest at the axial furrow, narrowing and deepening inward but not extended from the ventral surface as an apodeme. Occipital and 1p apodemes (Pl. 19, fig. 15) triangular in cross section proximally, distally becoming blade-like, and twisted so that the flat, blade-like portion is directed diagonally; apodeme 2p slimmer, blade-like, and not twisted. Median glabellar lobe narrower (tr.) than lateral lobes, anterior lobe diamond-shaped with a broad, shallow median pit in the posterior portion. Axial furrow shallow, curving inward at the anterior edge of the occipital ring, then running forward and slightly outward, rising and gradually shallowing to the mid-length of lateral lobe 3p, in front of here dropping into a broad, well-rounded furrow which curves around the extremity of the anterior lobe; preglabellar furrow shallow. Eye lobe situated in the inner corner of the cheek, the anterior margin abutting against the axial furrow, the posterior margin a short distance in front of the posterior border furrow. Palpebral lobe rises moderately steeply from the axial furrow, palpebral furrow much deeper in its anterior than its posterior half, the palpebral rim standing high above the crest of the lobe, flattened on the crest, with a narrow marginal band; the rim asymmetrical, the anterior part being the larger. Eye surface steeply sloping, facets large and arranged in diagonal lines (Pl. 19, fig. 15). Distinct furrow around the anterolateral margin of the eye lobe, on the outside of which is a low ridge, most prominent anteriorly; outside this ridge the cheek slopes gently outward and downward to the broad lateral border furrow. Lateral border with a flattened, outward-sloping upper surface, which is continuous with that of the anterior border; latter widest medially, forming a blunt projection (Pl. 14, fig. 1). Posterior border furrow sabre-like in outline with its anterior slope steeper than the posterior; posterior and lateral furrows do not merge at the genal angle, but the posterior border terminates slightly above and inside the shallow lateral furrow. Posterior border widening (exs.) rapidly outside the fulcrum, and running out into the base of the genal spine. Posterior branch of suture curves around the posterolateral margin of the eye and then runs straight out and slightly backward across the cheek to the margin; the points ϵ-ϵ and ω-ω are thus in the same transverse line. Anterior branch of suture runs forward in a sweeping curve a short distance outside the axial furrow and over the upper surface of the anterior border close to the inner edge, the two branches meeting in a smooth curve. Points β-β in line with the maximum width of the glabella across the anterior lobe.

Doublure of cephalon beneath lateral border of same width as border, wider anteriorly (Pl. 14, fig. 4). Beneath posterior border doublure extends from base of genal spine to fulcrum but not beneath inner part of border. At the inner margin the lateral doublure is bent sharply dorsad; this flexure dies out anteriorly and is absent along the hypostomal suture. Hypostome unknown.

External surface finely granulated (Pl. 19, fig. 17) except in axial, glabellar, and palpebral furrows and at base of median glabellar pit.

Three thoracic segments known, axial rings evenly arched transversely, longitudinally flattened; articulating furrow with slopes equally steep; axial furrow impressed only at the rear of each segment. Pleura having anterior band much higher than posterior band, with a vertical or slightly undercut posterior slope down to the pleural furrow; anterior slope of anterior band gentle, passing out beyond the fulcrum into the broad facet; faint articulating flange along anterior edge of pleura, dying away distally. Pleural furrow running in a slightly sigmoid course from inner anterior corner to the posterior border of the tip, dying out at a point directly above the inner edge of the doublure; furrow shallow and rounded near the axis, broader and with a flat base near the fulcrum, narrowing distally; posterior band of pleura with a gentle anterior slope throughout. Doublure extends along the posterior margin of segment halfway in to the fulcrum, but is not so extended along the anterior side.

Axis of pygidium with 12 complete rings and terminal portion, behind eighth ring axis tapers more gently and the ring furrows become shallower; in this differentiated posterior part of the axis the tip is rounded and prominent, the ring furrows are present only on the outer part, shallow and outwardly and slightly backwardly directed. Articulating halfring three-fifths the length of the remainder of the first segment; excavation in posterior margin of first axial ring of similar length (sag.), much smaller excavations in the posterior margin of the succeeding two rings. In longitudinal profile all except most posterior rings with a much steeper posterior than anterior slope. The outer quarter of the ring furrow is deep, and on the inner surface there is an apodeme on the inner part of this deepened region, the apodemes present on the articulating furrow and the next eight ring furrows (Pl. 14, fig. 14). Proximally the apodemes are triangular in section, the acute edge on the outer side, tapering to a blade-like tip directed downward and slightly forward. Pleural regions curving downward from the axial furrow to the narrow, flattened, and steeply sloping border on which pleurae are not marked. The first seven interpleural furrows sharply incised, the eighth indicated only by a smooth band in the granulation; pleural furrows narrow (exs.) adjacent to the axial furrow then widening rapidly and with a broad, flat floor extending out to the inner edge of the border; on all segments anterior slope steep, posterior slope much more gentle. Anterior band well rounded on all segments, each standing higher than the posterior band immediately in front of it, these posterior bands narrow and flattened. At posterior tip, border extended into a median spine which is flattened on the under surface (Pl. 14, figs. 15, 16). Doublure of about the same width as the border, the inner edge bent up vertically (Pl. 14, fig. 14).

External surface of thorax and pygidium (Pl. 14, fig. 12) bearing granules, which are present on the axial rings, in the articulating furrow and adjacent edge of the articulating halfring of the thorax, and are coarsest along the posterior margin of the ring; the rings of the pygidium are similar, but the ring furrow is smooth. The coarsest granulation on the pleural regions is on the crests of the anterior and posterior bands, with a finer granulation in the pleural furrows, on the facets, pygidial border and spine. An extremely narrow smooth strip on the anterior margin of the anterior pleural band. Doublure granulated along the outer portion, the granulation diminishing and disappearing inward.

Development. One protaspis (Pl. 15, figs. 5, 6, 10, 14, 17), lacking the free cheeks and hypostome, has the cephalic portion of length (sag.) 0.66 mm. The form is extremely like that of the protaspis from the Devonian described by Whittington (1956a: 105–106, pl. 24, figs. 1–5; text-fig. 1). Glabella shows a similar division into an extremely short (sag.) occipital ring with a prominent median tubercle, three glabellar rings of approximately equal length, and a wider anterior lobe which has the lateral portions faintly set off from the median region. On the preglabellar area there are two pairs of spines; the palpebral lobe is situated on the anterolateral margin of the shield, its position and the course of the sutures as in the Devonian example. The narrow posterior border is directed straight outward and turns vertically downward on the flank, where the specimen is broken. The protopygidium is also broken, but shows the convex axis, and apparently two segments, having backwardly directed spines on the outer part of the pleurae. The external surface of the fixed cheek is pitted (as in the Ordovician *Dalmanitina* protaspis of Temple, 1952, pl. 10, fig. 6), and there are paired granules on the cheek, including one halfway across the cheek, situated immediately in front of the posterior border furrow. Six conspicuous granules on the median occipital tubercle.

Cranidia of length 1.0 mm to 1.3 mm are meraspides (Pl. 15, figs. 7, 11, 15). The frontal lobe of the glabella is expanded and bent down more steeply with increasing size—the width becoming three-quarters the length (sag.) of the cranidium rather than less than half as in the protaspis. The palpebral lobe moves relatively backward as well as inward as shown by the position of the line δ-δ. In the protaspis this line runs just behind the anterior margin of the third glabellar ring, one-third the length (sag.) of the glabella from the anterior margin. In progressively larger specimens the line δ-δ moves to about the mid-length (Pl. 15, fig. 7) of the glabella, thence to a position about two-thirds the length (Pl. 15, fig. 1), where it crosses the second glabellar ring. Not only the frontal glabellar lobe but lobes 2p and 3p become relatively wider so that the axial furrows are strongly divergent forward (Pl. 15, figs. 1, 4), and glabellar furrow 3p ceases to be transverse, and becomes inclined to the transverse line. On the inner surface of the small cranidia there are rounded projections adjacent to the outer ends of the occipital furrow and glabellar furrows 1–3p, but strongly projecting apodemes are developed only in large cranidia.

In the original of Plate 15, figure 1 (5.2 mm in length [sag.]), granulation is present, the median occipital tubercle is almost completely reduced, and the pit is present in the frontal glabellar lobe.

The original of Plate 15, figures 9, 12, 13, 16, a transitory pygidium, shows the completely formed articulating halfring of the second segment beneath the first ring. The spines on the ends of the pleurae appear to be the combined tips of the anterior and posterior bands, which bands are more equal in width (exs.) than in larger stages. Scattered short spines are present on the axial rings and pleural bands, as well as granulation; short apodemes are present. A specimen of the same size (Pl. 15, fig. 8) does not have the articulating halfring of the second segment developed, and may be a small holaspid, but in dorsal aspect is very similar to the other example.

Discussion. Numerous American Silurian species of *Dalmanites* have been described (Delo, 1940: 37–52) but only ten of them are known from both cephalon and pygidium. The form of cephalon and pygidium, the depressed profile, the shape of the genal spines, shape of the posterior border and its relation to the lateral border furrow, and the relatively uniform nature of the granulation, ally this species with *D. limulurus* (Green, 1832) from the Rochester Shale. However, *D. puticulifrons* has a relatively larger eye lobe, no nodes at the extremities of the thoracic rings, deeper pleural furrows terminating at the rear edge of each thoracic segment, more numerous segments in the pygidium, a shorter terminal spine, and coarser granulation on the external surface.

A new species of *Dalmanites* being described by Campbell (in press), from the Henryhouse Formation of Oklahoma, has many features in common with *D. puticulifrons* and *D. limulurus*, the cephalon being very like that of *D. puticulifrons.* It may be distinguished by having a pygidium of different shape, with fewer rings and pleurae, and the granulation which varies more markedly in density and size on different parts of the cephalon. The British Silurian species *D. myops* (see Dean, 1960), from the Wenlock Series, belongs to the same species group and examination of specimens in the Museum of Comparative Zoology suggests that it is distinct from *D. puticulifrons* in having, among other characters, a shorter palpebral lobe, the facial suture lying in the preglabellar furrow, larger tubercles on the surface of the glabella, and differently shaped pleural furrows on both the thorax and pygidium.

According to Richter, Richter and Struve (*in* Moore, 1959: O 471–2), *Odontochile* differs from *Dalmanites* in that the anterior branches of the suture line are farther from the frontal glabellar lobe, in the number of spines on the margin of the hypostome and in the greater number of segments in the pygidium. The course of the anterior branches of the suture in *D. puticulifrons* is like that in *Odontochile*, but the hypostome is unknown. Delo (1940: 55) used number of segments in the pygidium as the main criterion in placing various American Devonian species in *Odontochile.* The value of this single character is open to question. Much more needs to be known of Silurian and Devonian dalmanitids before generic criteria can be clarified, and particularly the use of *Dalmanites* and *Odontochile.*

Family ODONTOPLEURIDAE Burmeister, 1843

Genus *LEONASPIS* R. and E. Richter, 1917

Leonaspis cf. *williamsi* Whittington, 1956

Plate 16, figures 1–14, 16–18, 20–22; Plate 17, figures 1–12, 16; Figure 9.

Description. The material is excellently preserved, and while it shows that there is individual variation (compare Pl. 16, figs. 1, 2, with Pl. 16, figs. 5, 6), it is not adequate to show the range of this variation. The exoskeletal parts are like, but apparently not identical with, those of the Lower Devonian species *Leonaspis tuberculatus* from New York and those of the species *L. williamsi* from Oklahoma (Whittington, 1956b: 507–510, pl. 57, pl. 58, figs. 1–4, 6, 7). The uncertainty regarding identity is partly because the New York and Oklahoma specimens are less perfectly preserved, and partly because the material from any one of the localities is limited. In these circumstances we have chosen to compare the Maine form to *williamsi,* as the better-known of previously described species. Some of the differences between the Maine specimens and those from the other localities are:

1) median occipital spine is longer than that of *williamsi,* not as long as that of *tuberculatus;*

2) eye lobe higher than that of *williamsi;* eye lobe of available specimens of *tuberculatus* is broken;

3) number of thoracic segments is unknown; *tuberculatus* has 9, *williamsi* has 8;

4) in such details as the number of tubercles on the anterior border of the cranidium, number of spines on the outer edge of the border of the free cheek and spacing of these spines, curvature and length of the posterior pleural spines of the thorax, and border spines of the pygidium, it is exactly like *williamsi.* The Maine specimens are unlike *tuberculatus* in the shorter genal spines and length of pleural thoracic spines. In *williamsi* (Whittington, 1956b, pl. 58, figs. 1, 2) there are five tubercles along the posterior border of the cephalon, several tubercles at the base of the posterior pleural spine, as well as two prominent tubercles on the pleural ridge of the pygidium. In the Maine specimens there are only two tubercles on the posterior border of the cranidium, large tubercles are lacking at the base of the posterior pleural spines, and only one tubercle is present on the pleural ridge of the pygidium.

These differences are in details, and it is difficult to assess their taxonomic significance.

The specimens from New York, Oklahoma and Maine (Pl. 17, figs. 5, 8–12) exhibit the anterior pleural spines, which are fused at the base and branch distally. The present material shows (Pl. 17, figs. 1, 2, 4) that on the first, and probably second, thoracic segments the anterolateral portion is beveled and facetted, so that on these segments there is only a short, rapidly tapering posterior pleural spine. The anterior pleural spine is not developed. More posterior segments of the thorax show the narrow doublure which lies immediately inside the base of the anterior pleural spine (Pl. 17, fig. 5). The anterior corner of this doublure projects forward as an articulating process; the posterior end shows a notch to receive the articulating process of the following segment, this notch lying beneath the base of the posterior pleural spine.

The two small cranidia (Pl. 16, figs. 7, 9, 10, 12–14) are the only known developmental stages of a species of this genus. In the smallest the palpebral lobe is far back, in line with the anterior edge of the occipital furrow, and the glabella has the specific outline. It also shows typical features of a small odontopleurid in that the rounded tubercles of the larger stages are represented by thorn-like spines, and the median occipital spine is much longer than in larger stages. The major spines (Fig. 9) are typical of the cranidium of

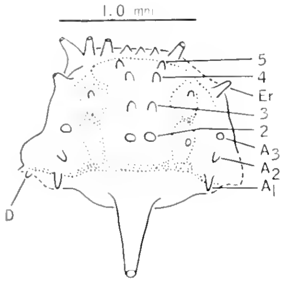


Figure 9. *Leonaspis* cf. *williamsi* Whittington, 1956. Major paired spines of a small cranidium, original of Plate 16, figures 12–14, lettered following Whittington, 1956c, text-fig. 1.

an early odontopleurid developmental stage. These include pairs 2 to 5 on the glabella, A_{1-3} on the fixed cheek, and the spine on the eye ridge (compare Whittington, 1956c, text-figs. 1, 6, 9, 22, for corresponding spines in developmental stages of other genera).

XANIONURUS n. gen.

Type species. *Xanionurus boucoti* n. sp.

Diagnosis. Differs from *Radiaspis* in that:

1) lateral glabellar lobes are not fused, but separated by deep 1p furrow;

2) there is a distinct, shallow occipital furrow and the occipital ring is relatively much shorter (sag.);

3) second axial ring of pygidium low, faintly divided by median longitudinal furrow and bearing pair of spines;

4) border of pygidium with 14 (not 16) spines, the posterior band of the anterior segment running into the base of the 5th (not the 6th) border spine;

5) besides the main paired spines on the glabella there are many additional spines and granules; similarly, on the cheek there are spines on the upper surface of the border, and many scattered spines and granules as on the pygidium. In *Radiaspis* the exoskeleton is smooth between the main spines.

Geological range. Upper Wenlock to Ludlow.

Discussion. Bruton (personal communication) points out that *Radiaspis* is like *Diacanthaspis* in lacking major border spines on the pygidium and in the radiating arrangement of the border spines. We agree with this, and add that the early developmental stages of the cranidium of the two genera appear to be similar, and the thoracic segments are alike. As in *Acidaspis* and *Dudleyaspis* there is a stout posterior sutural ridge in the new genus and a steeply inclined row of spines on the lower edge of the cheek border. However, *Xanionurus* lacks the characteristic inflation of the posterior band of the thoracic segments at the fulcrum, seen in these two genera, and the pygidia are unlike. It is possible that there is a line of descent from *Diacanthaspis* to *Xanionurus* to *Radiaspis,* independent of the possible line leading from *Primaspis* to *Acidaspis* and *Dudleyaspis* and of the line from *Primaspis* to *Leonaspis* and *Odontopleura.* If these views are correct they would suggest some modification of the phylogeny suggested by Whittington (1956c, text-fig. 3).

Xanionurus boucoti n. sp.

Plate 16, figures 15, 19; Plate 17, figures 13–15, 17–26; Plate 18, figures 1–9, 11–15; Figure 10.

Holotype. USNM 154449, incomplete cephalon.

Description. Glabella moderately convex transversely and longitudinally, widest at occipital ring, in front of lateral lobes 1p tapering forward to rounded anterior margin. Occipital ring about three times as wide as long (sag.), bearing a pair of curved posterodorsally directed spines which arise from the rear edge; much shorter median tubercle directed almost vertically, the tip exhibiting four small pits arranged at the corners of a square (Pl. 18, fig. 6). Occipital lobe poorly defined on inner surface, occipital furrow shallow, well rounded medially, distally passing into deep pit-like apodeme. Median glabellar lobe standing higher than lateral lobes, parallel-sided;

frontal lobe of similar width. Lateral lobes 1p and 2p oval in outline, independently convex, 1p one and one-half times longer than 2p, lateral furrow 1p diagonally directed and deepening adaxially into an apodemal pit; lateral furrow 2p similar in form. Third lateral lobes not developed. Axial furrow moderately deep. Cheek quarter-circle in outline, outward-sloping, eye lobe situated at highest point and in line with anterior part of lateral glabellar lobe 1p; prominent eye ridge curves inward and forward to shallow axial furrow opposite extremity of frontal glabellar lobe. Cheek inside eye inflated, shallow furrow runs along inner edge of eye ridge, posterior sutural ridge runs outward from eye lobe to curve back and merge with swollen base of librigenal spine. Anterior branch of suture runs along upper surface of eye ridge and over narrow anterior border in line with axial furrow; posterior branch of suture runs along sutural ridge to cross posterior border between spine B and base of librigenal spine. Posterior border widens rapidly distally, curving forward slightly to base of genal spine. Gently convex anterolateral border wider than anterior border, edge curled under and directed upward and inward as the narrow doublure. Outer margin of border bears 10 closely-spaced, downwardly and outwardly directed spines which diminish progressively in length anteriorly; marked gap between posterior spine and base of curved genal spine; shallow antennal notch immediately inside anterior spine. Rostral plate not known but rostral suture runs transversely along outer edge of anterior border; connective suture runs inward and upward across doublure (Pl. 18, fig. 2), hence rostral plate is short (sag. and exs.) and wide, trapezoidal in outline. Hypostome not known. Inner surface of cephalon shows short, blunt apodemes formed by inner end of deepest part of occipital furrow and lateral glabellar furrows 1p and 2p. Anterior pit not developed on outer surface, nor as apodeme on inner surface. External surface of cephalon bearing spines of various sizes, between which is a fine granulation. Three main pairs of spines (2–4; see Fig. 10) are visible on the frontomedian glabellar lobe, with pair 2a situated close together immediately in front of the occipital furrow. Spines A_{1-3} visible on inner part of cheek; prominent spine B on posterior border distally; row of 6 spines on crest of anterolateral border, the posterior situated above the base of the third-from-the-last downwardly directed border spine, and the anterior above the outer part of the rostral plate. Granulation is absent only from the deepest parts of furrows.

Number of thoracic segments unknown. Convex axial ring with pair of prominent sharp spines, articulating halfring long (sag.), equal in length to the ring; articulating furrow with anterior slope undercutting articulating halfring; apodemes blunt and short. Inner part of pleura extends out horizontally, divided by shallow pleural furrow into anterior band which is one-third the width (exs.) of the posterior band and lies below the convex posterior band. Two prominent spines on the posterior band (Pl. 17, figs. 15, 22, 25), the inner situated at about half the width (tr.), the outer situated at the fulcrum and directed upward and outward. Anterior pleural spine generally stubby, but becoming progressively longer (tr.) toward the rear, and directed outward and downward throughout; posterior pleural spine much more prominent and longer, directed downward and backward—the medial segments having this spine directed more steeply downward and more directly outward than in the more posterior segments, in which the posterior pleural spine is quite strongly curved (compare Pl. 17, figs. 15, 17, 18, 22, with Pl. 17, figs. 23–25). The first one or two segments (Pl. 17, figs. 13, 14) differ in that the pleura curves outward to end in a short, blunt, posterior pleural spine, the anterior pleural spine being merely a small projection; the segment is beveled to fit under the cephalon and as a consequence

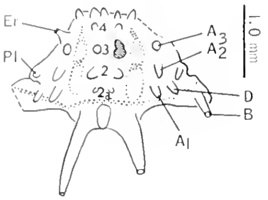


Figure 10. *Xanionurus boucoti* n. gen., n. sp. Major paired spines of small cranidium, original of Plate 18, figures 8, 9, 11, 12. Spines lettered as in Figure 9.

the outer spine on the posterior pleural band is not developed. External surface bearing granules of various sizes on axial rings, single row of granules along rear edge of articulating halfring; flattened strip behind posterior pleural band smooth; smooth areas on crest of posterior band between the spines and between the inner spine and the axial furrow; upper surfaces of both pleural spines smooth, apart from scattered granules on distal half of posterior spine; a band of elongate, sharp granules runs along the leading and trailing edges of both pleural spines, those on the posterior spine being larger; tubercles present along anterior band. The doublure is present only at the extremity of the segment, and there is a deep embayment for articulation between the doublure and upper surface on both anterior and posterior edges.

Pygidium (Pl. 17, figs. 19–21, 26), exclusive of spines, of width 3½ to 4 times length (sag.). Axis consisting of two segments; axial furrow shallow beside first ring but very deep beside second ring except at extreme tip, where it shallows. Articulating halfring like those of the segments; first axial ring prominent with one pair of spines. Second ring depressed below level of anterior ring and having a faint median longitudinal depression, the lateral parts bearing one pair of small, thorn-like spines. Pleural region subdivided by triangular depression of pleural furrow into a transverse anterior band and a diagonally directed pleural ridge; border convex and bearing seven pairs of border spines, none of which is more prominent than any other, directed more steeply downward anteriorly than posteriorly, the arrangement radial. Fifth border spine from anterior is opposite pleural ridge. Border curls under on ventral side to form a narrow doublure in which there is a distinct median embayment. Upper surface of border bearing spines as prominent as those on axial rings, situated at base of fourth to seventh border spines, that at the base of the fifth larger than the others. Elsewhere external surface granulate, except in deepest depressions, one or two larger spines on anterior band of first segment.

Development. Two small cranidia (Pl. 18, figs. 8, 9, 11–15; Fig. 10) show the relatively large paired spines typical of odontopleurid developmental stages. In outline, glabellar lobation, position of the palpebral lobe, as well as spine pattern, these cranidia are like those of the Ordovician *Diacanthaspis* (Whittington, 1956c, pl. 4, figs. 12–14). The long, curved occipital spines, general shape and spine pattern are also like those of the Ordovician *Apianurus* (Whittington, 1956c, pl. 19, figs. 14–16; text-fig. 22f), but the small spines are thick and straight in *Xanionurus* (not slim and curved as in *Apianurus*) and the posterior part of the fixed cheek is wider (tr.).

Discussion. Prantl and Vaněk (in Horný, Prantl, and Vaněk, 1958: 265–266, pl. 3, fig. 5) described an incomplete pygidium from the Upper Wenlock of Czechoslovakia which is like that of the present species in the number of pairs of border spines, relation of the fifth spine to the pleural ridge, and appearance of the second axial ring. They refer this species, *formosa*, with question to *Radiaspis*. Bruton (personal communication) has identified an entire specimen of this species (Pl. 18, fig. 10), flattened in shale. It is quite like the present one, differing in that the genal spine is relatively much longer (reaching back to the pygidium), the posterior pleural thoracic spines are longer, particularly on the anterior segments where they are directed slightly forward, the pygidial border spines are slimmer, the external surface appears to bear fewer and more scattered spines and to be granulated. We regard *formosa* as congeneric with our species and differing from the type species of *Radiaspis* in the characters given above in the generic diagnosis.

Transitory pygidium, undetermined
Plate 10, figures 1–3, 5, 9, 10.

Discussion. The two examples placed here may represent the same species, and are characterized by the axis tapering gently backward, the ring furrows deep distally, the pleural regions horizontal and subdivided by interpleural furrows, the pleural bands bearing prominent border spines which are outwardly and backwardly directed, more strongly backwardly directed posteriorly. The tip is bent down (Pl. 10, fig. 3), and the pleural border spines alternate in size, this latter feature particularly shown by the larger example (Pl. 10, figs. 1, 5). External surface of rings and pleural bands finely granulate, no larger tubercles or spines.

The shape of this pygidium, including the flat pleural regions and bent-down tip, is reminiscent of that of the cheirurid *Ceraurinella* (Whittington and Evitt, 1954, pl. 12, figs. 1–3, 9–11; pl. 28, figs. 1–14). The alternation in size of the pleural border spines distinguishes the present examples, as does the lack of a pleural furrow. No other cheirurid material has been identified among the present collection; the lack of paired axial or pleural spines appears to exclude this pygidium from odontopleurids, and the lack of a pleural furrow from the other groups.

REFERENCES

AMOS, A. J., K. S. W. CAMPBELL, AND R. GOLDRING. 1960. *Australosutura* gen. nov. (Trilobita) from the Carboniferous of Australia and Argentina. Palaeontology, **3**: 227–236, pls. 39–40.

BEST, R. V. 1961. Intraspecific variation in *Encrinurus ornatus*. Jour. Paleont., **35**: 1029–1040, pl. 124.

BOUCOT, A. J. 1961. Stratigraphy of the Moose River synclinorium, Maine. Bull. U.S. Geol. Surv., No. **1111-E**: 153–188, pl. 34.

CAMPBELL, K. S. W. (In press). Trilobites of the Henryhouse Formation, Oklahoma. Bull. Okla. Geol. Surv.

DEAN, W. T. 1960. The Silurian trilobite *Dalmanites myops* (König). Palaeontology, **2**: 280.

DELO, D. M. 1940. Phacopid trilobites of North America. Spec. Pap. Geol. Soc. Amer., No. **29**: 1–135, pls. 1–13.

ERBEN, H. K. 1953. Über einige Otarionidae (Tril.) aus dem Mittel-Devon der Eifel. Senckenbergiana, **34**: 73–80.

GREEN, J. 1832. A monograph of the trilobites of North America. Philadelphia. 94 p.

HAHN, G. 1964. Trilobiten der unteren *Pericyclus*—Stufe (Unterkarbon) aus dem Kohlenkalk Belgiens. Part 2. Senckenbergiana, **45**: 347–379.

HALL, J. 1879. The fauna of the Niagara Group, in central Indiana. New York State Mus., Ann. Rept. **28**: 98–203, pls. 3–34 [an earlier, incomplete edition in 1875].

HARPER, J. C. 1949. The Ordovician and Silurian rocks of Ireland. Proc. Liverpool Geol. Soc., **20**: 48–67.

HESSLER, R. R. 1962a. The Lower Mississippian genus *Proetides* (Tril.). Jour. Paleont., **36**: 811–816, pl. 119.

———. 1962b. Secondary segmentation in the thorax of trilobites. Jour. Paleont., **36**: 1305–1312, pl. 176.

———. 1963. Lower Mississippian trilobites of the family Proetidae in the United States, Part I. Jour. Paleont., **37**: 543–563, pls. 59–62.

———. 1965. Lower Mississippian trilobites of the family Proetidae in the United States, Part II. Jour. Paleont., **39**: 248–264, pls. 37–40.

HORNÝ, R., F. PRANTL, AND J. VANĚK. 1958. On the limit between the Wenlock and the Ludlow in the Barrandian. Sborník, Úst. Úst. Geol., **24**: 217–278, pls. 1–11 (Czech and English text, Russian summary).

LINDSTRÖM, G. 1901. Researches on the visual organs of the trilobites. Kongl. Svenska Vetenskaps-Akad. Handl., **34**(8): 1–86, pls. 1–6.

LOVÉN, S. L. 1845. Svenska Trilobiter. Öfv. Kongl. Vetenskaps-Akad. Förhandl., Stockholm. **2**(3): 46–56, pl. 1.

M'COY, F. 1846. A synopsis of the Silurian fossils of Ireland. Dublin. 72 p., 5 pls.

———. 1849. On the classification of some British fossil Crustacea, with notices of new forms in the University collection at Cambridge. Ann. Mag. Natur. Hist., Ser. 2, **4**:

161–179, 330–335, 392–414, 15 figs. (not numbered).

MOORE, R. C. (Editor). 1959. Treatise on invertebrate paleontology. Part O, Arthropoda I. Geol. Soc. America and Univ. Kansas. xix + 560 pp., 415 figs.

PRANTL, F., AND A. PŘIBYL. 1951. A revision of the Bohemian representatives of the family Otarionidae R. and E. Richter (Trilobitae). Stát. Geol. Úst. Českoslov. Repub., **17:** 353–512, pls. 1–5 (Czech and English text, Russian summary).

PŘIBYL, A. 1960. Neue Erkenntnisse über Mittelböhmische Trilobiten der superfamilie Proetacea. Sborník, Úst. Úst. Geol., **25:** 177–221, pls. 1–4 (Czech and German text).

RAYMOND, P. E. 1916. New and old Silurian trilobites from southeastern Wisconsin, with notes on the genera of the Illaenidae. Bull. Mus. Comp. Zool., **60:** 1–41, pls. 1–4.

REED, F. R. C. 1901. Woodwardian Museum notes: Salter's undescribed species. 2. Geol. Mag., N. S., Dec. 4, **8:** 5–14, pl. 1.

———. 1928. Notes on the family Encrinuridae. Geol. Mag., **65:** 51–77.

RICHTER, R. 1914. Über das Hypostom und einige Arten der Gattung *Cyphaspis*. Centralbl. Mineral., Geol., Paläont., Jahr. 1914: 306–317.

RICHTER, R. AND E. RICHTER. 1940. Die *Saukianda*-Stufe von Andalusien. Abh. Senckenb. Naturf. Gesell., **450:** 1–88, pls. 1–5.

———. 1956. Annular-teilung bei Trilobiten am Beispiel besonders von *Proetus* (*Pr.*) *cuvieri* und *prox*. Senck. Leth., **37:** 343–381, pls. 1–6.

ROSENSTEIN, E. 1941. Die *Encrinurus*-Arten des estländischen Silurs. Geol. Inst. Univ. Tartu, No. **62:** 49–80, pls. 1–4.

SALTER, J. W. 1853. Figures and descriptions illustrative of British organic remains. Mem. Geol. Surv. U. K., Dec. 7, pls. 1–10.

ŠNAJDR, M. 1960. Studie o čeledi Scutelluidae (Trilobitae). Rozpravy, Úst. Úst. Geol., **26:** 1–264, 37 pls., 61 figs. (Czech text, English summary).

TEMPLE, J. T. 1952. The ontogeny of the trilobite *Dalmanitina olini*. Geol. Mag., **89:** 251–262, pls. 9, 10.

———. 1954. The hypostome of *Encrinurus variolaris* and its relation to the cephalon. Geol. Mag., **91:** 315–318.

———. 1956. Notes on the Cheiruracea and Phacopacea. Geol. Mag., **93:** 418–430.

TRIPP, R. P. 1957. The trilobite *Encrinurus multisegmentatus* (Portlock) and allied Middle and Upper Ordovician species. Palaeontology, **1:** 60–72, pls. 11, 12.

———. 1962. The Silurian trilobite *Encrinurus punctatus* (Wahlenberg) and allied species. Palaeontology, **5:** 460–477, pls. 65–68.

WALTER, O. T. 1927. Trilobites of Iowa and some related Paleozoic forms. Iowa Geol. Surv., **31:** 173–400, pls. 10–27.

WELLER, S. 1907. The paleontology of the Niagaran Limestone in the Chicago area. The Trilobita. Chicago Acad. Sci., Bull. No. 4, (II): 163–281, pls. 16–25.

WHITTARD, W. F. 1938. The Upper Valentian trilobite fauna of Shropshire. Ann. Mag. Natur. Hist., Ser. 11, **1:** 85–140, pls. 2–5.

WHITTINGTON, H. B. 1954. Two silicified Carboniferous trilobites from West Texas. Smithson. Misc. Coll., **122:** 1–16, pls. 1–3.

———. 1956a. Beecher's supposed odontopleurid protaspis is a phacopid. Jour. Paleont., **30:** 104–109, pl. 24.

———. 1956b. Type and other species of Odontopleuridae (Trilobita). Jour. Paleont., **30:** 504–520, pls. 57–60.

———. 1956c. Silicified Middle Ordovician trilobites: the Odontopleuridae. Bull. Mus. Comp. Zool., **114:** 155–288, pls. 1–24, figs. 1–25.

———. 1960. *Cordania* and other trilobites from the Lower and Middle Devonian. Jour. Paleont., **34:** 405–420, pls. 51–54.

———. 1963. Middle Ordovician trilobites from Lower Head, western Newfoundland. Bull. Mus. Comp. Zool., **129:** 1–118, pls. 1–36, figs. 1–6.

———. 1965. Trilobites of the Ordovician Table Head Formation, western Newfoundland. Bull. Mus. Comp. Zool., **132:** 275–442, pls. 1–68.

WHITTINGTON, H. B., AND W. R. EVITT. 1954. Silicified Middle Ordovician trilobites. Mem. Geol. Soc. Amer., No. **59:** 1–137, pls. 1–33, 27 figs.

(Received 6 April 1966)

Explanation of Plates 1–19.

To make the photographs, the silicified specimens were mounted on insect pins with gum arabic; these pins have been blacked out, otherwise the photographs have not been retouched. Specimens preserved in limestone were coated with a dilute "opaque" to give a dull surface. All specimens have been given a light coating of ammonium chloride before being photographed. It is arbitrarily decided that the plane running through the posterior margin of the occipital or axial ring shall run in the dorsoventral direction, and views are described accordingly. Exterior views have been taken in the direction lying in the sagittal plane to give the fullest possible view of the exoskeletal surface. Oblique views have been taken in directions at an angle to the sagittal plane. The initials USNM refer to the U.S. National Museum, Washington, D.C., and the initials MCZ to the Museum of Comparative Zoology. These initials are followed by the catalogue numbers.

PLATE 1

Praetus pluteus n. sp.
Hardwood Mountain Formation, Silurian, Maine

Figure	
1–3	Holotype, cranidium and incomplete left free cheek, USNM 154457, dorsal, left lateral, anterior views, × 3.
4, 5	Cranidium, USNM 154458, showing complete doublure of posterior border on right side, ventral, dorsal views, × 4.5.
6, 7	Cranidium, USNM 154459, dorsal, left lateral views, × 3.
8	Part of cranidium, USNM 154475, oblique view, to show occipital lobe and smooth muscle areas (compare Fig. 1A), × 15.
9, 10	Cranidium, USNM 154460, dorsal, left lateral views, × 3.
11	Free cheek, USNM 154461, exterior view, × 4.5.
12	Free cheek, USNM 154463, exterior view, × 9.
13, 14, 17, 18	Hypostome, USNM 154470, anterior, posterior, exterior, left lateral views, × 4.5.
15, 16	Cranidium, USNM 154464, dorsal, left lateral views, × 4.5.
19, 20	Cranidium, USNM 154465, dorsal, left lateral views, × 6.
21, 28	Cranidium, USNM 154468, dorsal, right lateral views, × 9.
22	Free cheek, USNM 154462, exterior view, × 6.
23, 24, 30, 31	Cranidium, USNM 154469, anterior, ventral, right lateral, dorsal views, × 15.
25, 26	Cranidium, USNM 154466, dorsal, right lateral views, × 6.
27, 29	Cranidium, USNM 154467, dorsal, right lateral views, × 6.

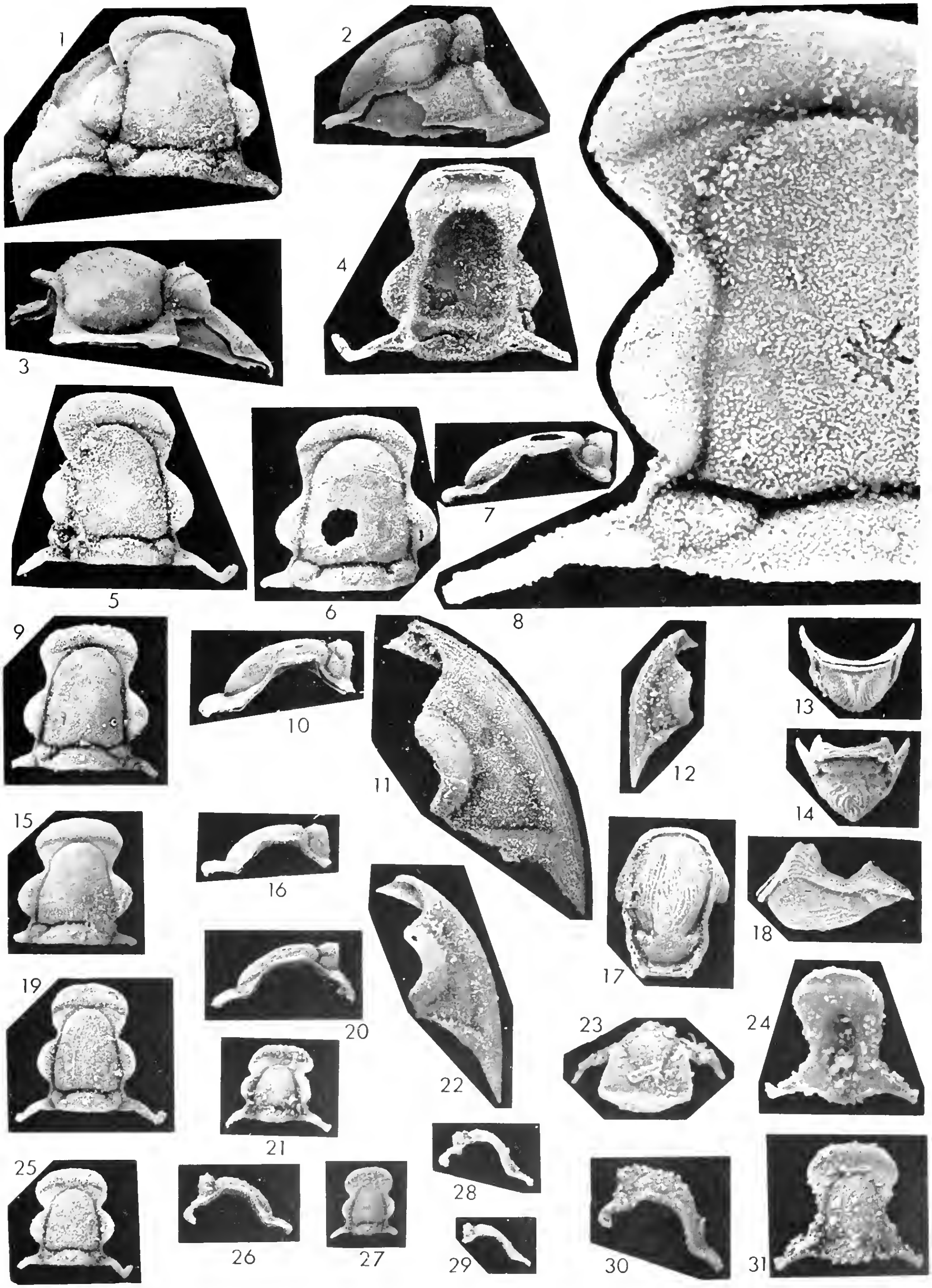

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31

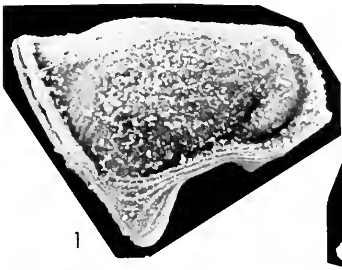
PLATE 1

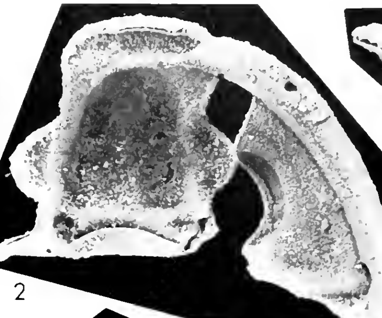
PLATE 2

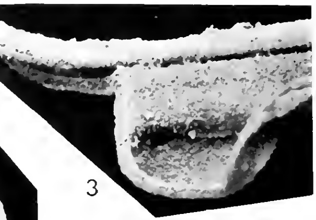
Praetus pluteus n. sp.

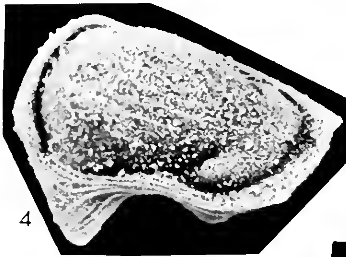
Hardwood Mountain Formation, Silurian, Maine

Figure	
1, 4–6, 16	Hypostome, USNM 154471, two oblique exterior views, × 9; oblique interior, right lateral, exterior views, × 4.5.
2	Cranidium (USNM 154478) and left free cheek (USNM 154476) placed close together, ventral view, to show doublure and course of connective suture (compare Fig. 1B), × 4.5. Portions of the muscle areas appear dark where the innermost silicified layer is broken.
3	Inner edge of doublure of free cheek, USNM 154476, showing that this edge is rounded and not a flattened hypostomal sutural margin. Oblique interior view, × 9.
7, 8, 24	Anterior segment, USNM 154479, dorsal, right lateral views, × 5; oblique interior view showing narrow doublure at tip, × 9.
9, 17, 20,	Small pygidium, USNM 154484, left lateral, dorsal, ventral views, × 6.
10, 14, 23, 25, 31, 32	Segment, USNM 154480: figs. 10, 14, 31, 32, left lateral, dorsal, posterior, anterior views, × 5; figs. 23, 25, oblique interior views, showing slot along anterior edge of articulating halfring and panderian opening, × 9.
11, 18, 19	Hypostome, USNM 154473, exterior, interior, right lateral views, × 6.
12, 13	Hypostome, USNM 154472, exterior, right lateral views, × 6.
15	Posterior segment, USNM 154481, dorsal view, × 5.
21, 22	Smallest hypostome, USNM 154474, exterior, left lateral views, × 15.
26, 30	Pygidium, USNM 154483: oblique exterior view, × 9; ventral view, × 4.5.
27–29	Pygidium, USNM 154482, dorsal, posterior, right lateral views, × 4.5.


1

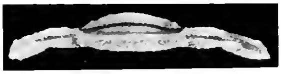

2


3


4


5

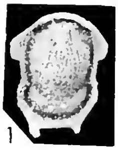

6


7

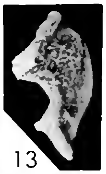

8

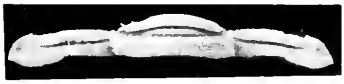

9


10


11


12


13


14


15


16


17

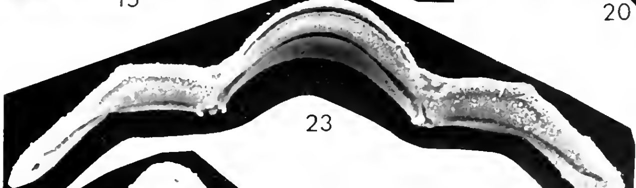

18

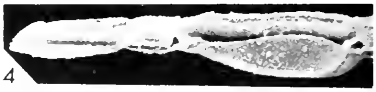

19

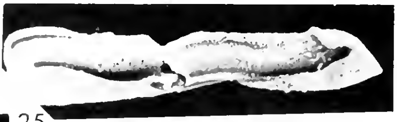

20


21

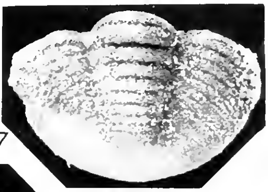

22

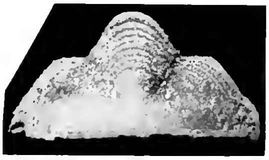

23

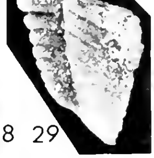

24

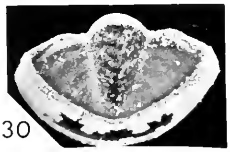

25


26


27


28


29


30


31


32

PLATE 2

PLATE 3

Proetus cuvieri Steininger, 1831

Eifel District, Middle Devonian, Western Germany

Figure	
1, 3	Incomplete cephalon with thoracic segments articulated, anteroventral, dorsal views, × 4.5. Schultze collection, MCZ 5924 2.
2	Incomplete cephalon, anterior view, × 6. Anterior border is broken off to reveal on left side of photograph mould of external surface of doublure, and in center the exoskeleton adjacent to the connective sutures. Schultze collection, MCZ 5924/1.

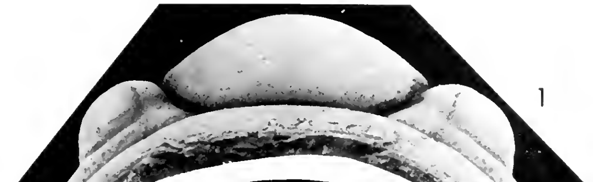
Proetus concinnus (Dalman, 1827)

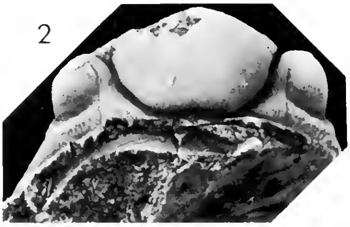
4, 5, 9, 11, 12	Holotype, incomplete partially enrolled individual, Mulde Beds, Wenlock Series, Djupvik, parish of Eksta, Gotland, Sweden. Pal. Instit. Uppsala G 733. Fig. 4, oblique view of cephalon photographed under alcohol, to show muscle areas as dark patches on glabella, × 6. Figs. 5, 11, 12, dorsal view of cephalon, dorsal view of pygidium, left lateral view, × 4.5. Fig. 9, anterior view of cephalon showing mould of doublure on right side and position of connective suture on left side, × 6.

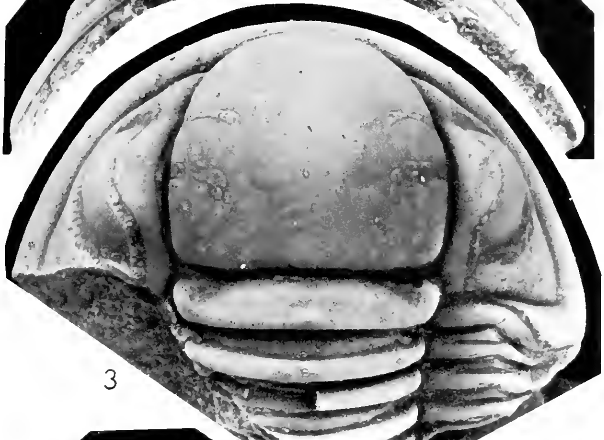
Proetus pluteus n. sp.

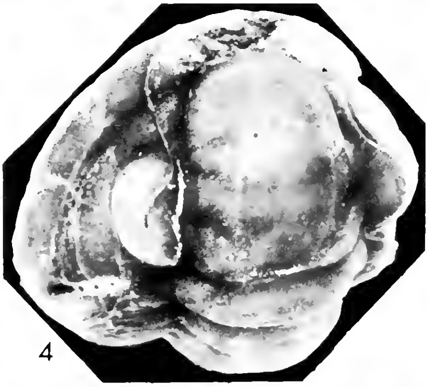
Hardwood Mountain Formation, Silurian, Maine

6, 10, 13	Transitory pygidium, USNM 154485, left lateral, ventral, dorsal views, × 15.
7, 8	Transitory pygidium, USNM 154486, dorsal, right lateral views, × 15.
14, 15	Transitory pygidium, USNM 154487, dorsal, ventral views, × 15.
16	Transitory pygidium, USNM 154488, dorsal view, × 30.

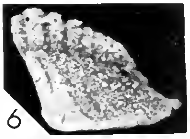

1

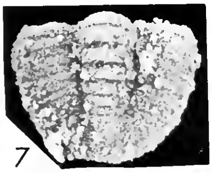

2


3

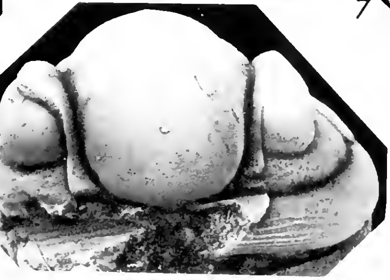

4


5

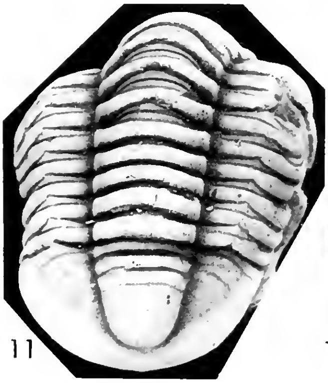

6

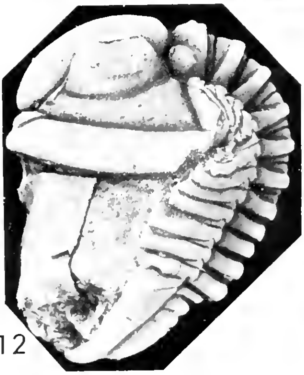

7


8

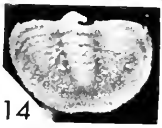

9

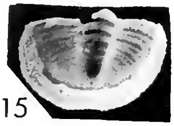

10


11


12


13


14


15

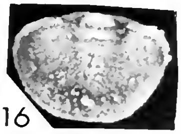

16

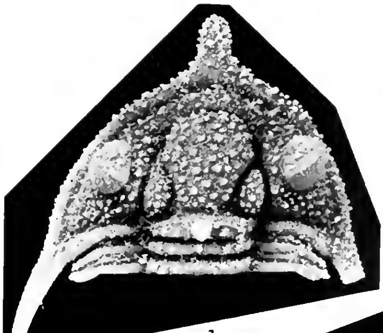
PLATE 3

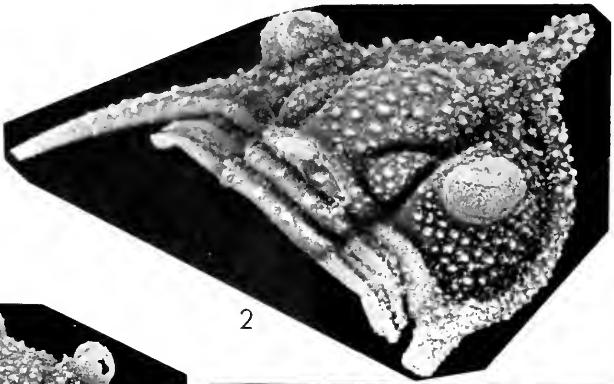
PLATE 4

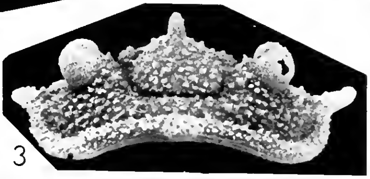
Rhinotarion sentosum n. gen., n. sp.

Hardwood Mountain Formation, Silurian, Maine

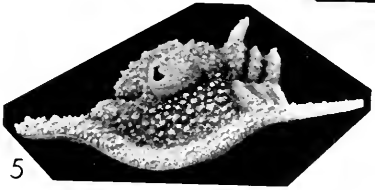
Figure	
1–7	Holotype, USNM 154211: figs. 1, 3, 4, 5, dorsal, anterior, posterior, left lateral views, × 6; figs. 2, 6, 7, two oblique exterior and a ventral view, × 9.
8, 9	Free cheek, USNM 154213, exterior, interior views, × 6.
10–12	Isolated rostral plate, USNM 154212, interior, exterior, oblique interior views, × 15.

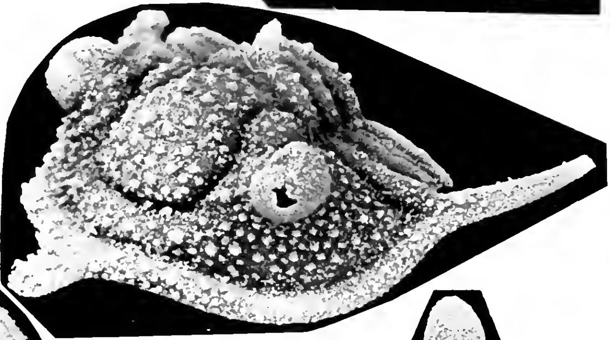

1

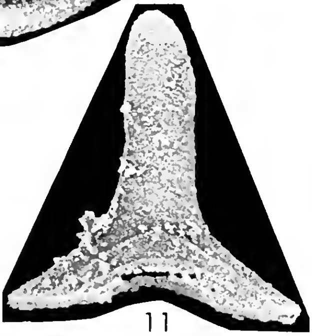

2

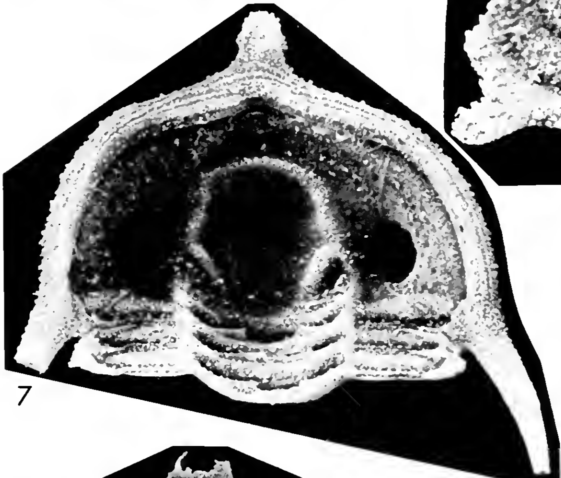

3

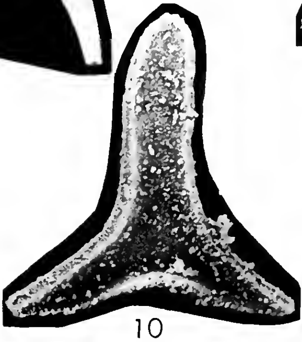

4

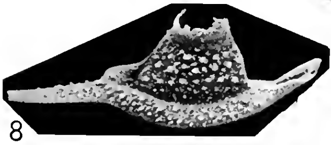

5

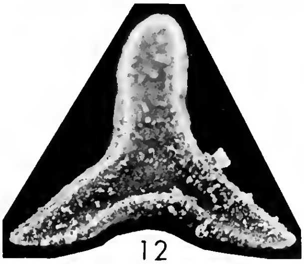

6


11


7


10


8


12

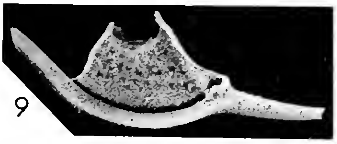

9

PLATE 4

PLATE 5

Rhinotarion sentosum n. gen., n. sp.
Hardwood Mountain Formation, Silurian, Maine

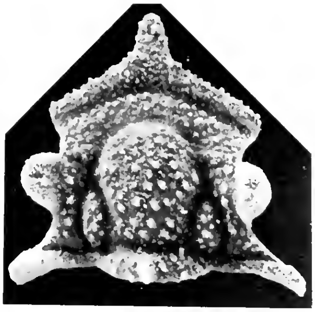
Figure	
1, 2, 4	Cranidium, USNM 154214, dorsal, oblique exterior, ventral views, × 9.
3	Free cheek, USNM 154215, exterior view, × 6.
5, 6	Malformed cranidium, USNM 154217, dorsal, right lateral views, × 6.
9, 10, 13, 14	Two segments articulated together, USNM 154218, dorsal, left lateral, oblique ventral, anterior views, × 9.
11	Small free cheek, USNM 154216, exterior view, × 15.
15, 16, 18	Segment with median axial spine, USNM 154219, dorsal, right lateral, oblique ventral views, × 9.

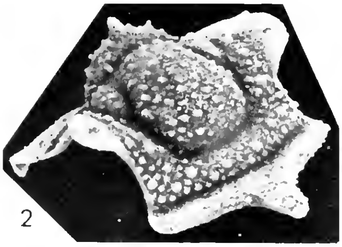
Otarion sp. ind.
Hardwood Mountain Formation, Silurian, Maine

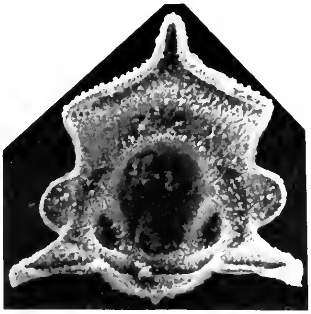
7, 8, 12, 17	Cranidium with right free cheek attached, USNM 154240, right lateral, anterior, dorsal, oblique views, × 6.
19, 25, 26	Cranidium with left free cheek and first thoracic segment attached, USNM 154241: fig. 19, oblique view showing outer part of segment, × 15; figs. 25, 26, dorsal, ventral views, × 9.
20, 21	Cranidium, USNM 154242, dorsal, left lateral views, × 6.
22, 23	Small cranidium, USNM 154243, dorsal, right lateral views, × 15.

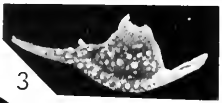
Otarion instita n. sp.
Hardwood Mountain Formation, Silurian, Maine

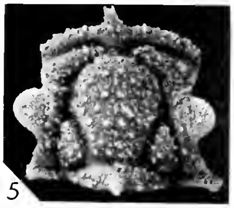
24	Interior view of eye surface (original of Pl. 6, figs. 7, 10) showing minute facets, × 30.

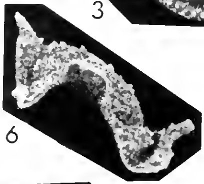

1

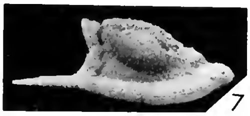

2


4


3

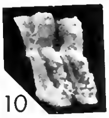

5

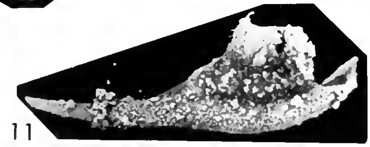

6

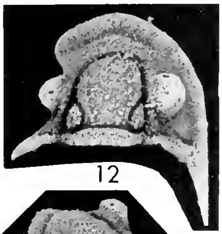

7


8

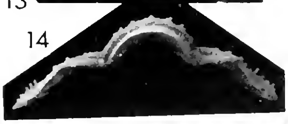

9

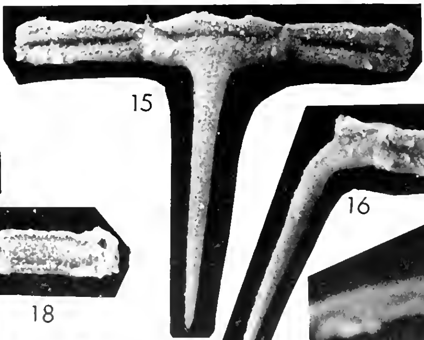

10


11

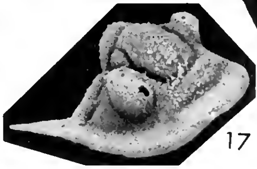

12

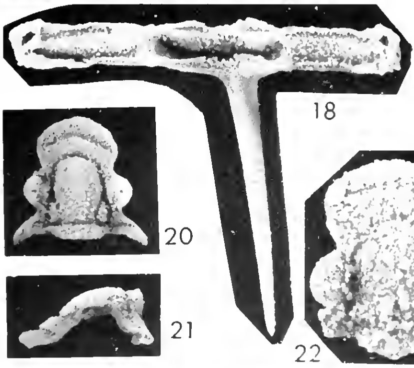

13

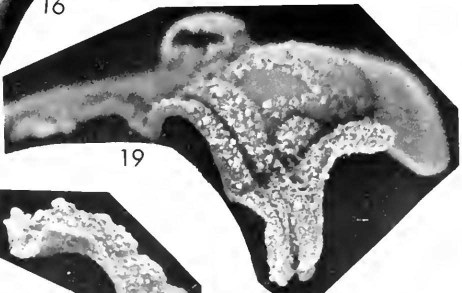

14

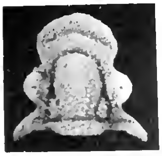

15

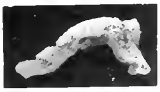

16

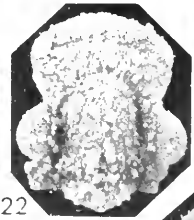

17

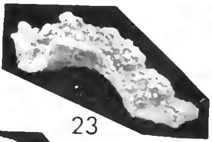

18

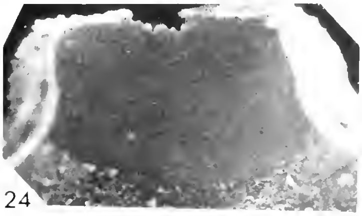

19

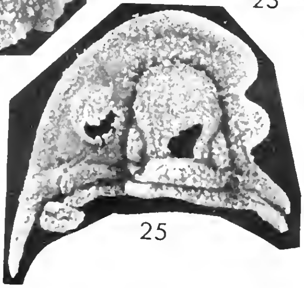

20


21


22


23


24


25

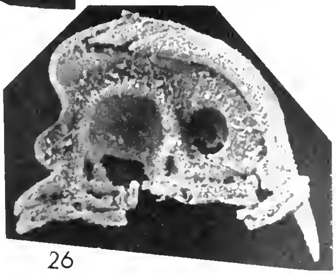

26

PLATE 5

PLATE 6

Otarion instita n. sp.

Hardwood Mountain Formation, Silurian, Maine

Figure	
1–5	Holotype, cranidium with left free cheek attached, USNM 154220: figs. 1, 2, 3, 5, anterior, oblique ventral, dorsal, left lateral views, × 6; fig. 4, oblique exterior view, × 8.
6	Cranidium, USNM 154221, dorsal view, × 6.
7, 10	Free cheek, USNM 154228, interior, exterior views, × 4.5.
8	Cranidium, USNM 154222, dorsal view, × 6.
9, 15, 16	Cranidium with rostral plate attached, USNM 154224: fig. 9, oblique ventral view, ×9; figs. 15, 16, dorsal, right lateral views, × 6.
11, 12	Free cheek, USNM 154229, interior, exterior views, × 15.
13, 14	Cranidium with left free cheek attached, USNM 154223, dorsal, left lateral views, × 6.
17	Small free cheek, USNM 154230, exterior view, × 30.
18, 19. 24	Smallest cranidium, USNM 154227, right lateral, dorsal, anterior views, × 30.
20, 21	Cranidium, USNM 154225, dorsal, right lateral views, × 9.
22, 23	Cranidium, USNM 154226, left lateral, dorsal views, × 15.

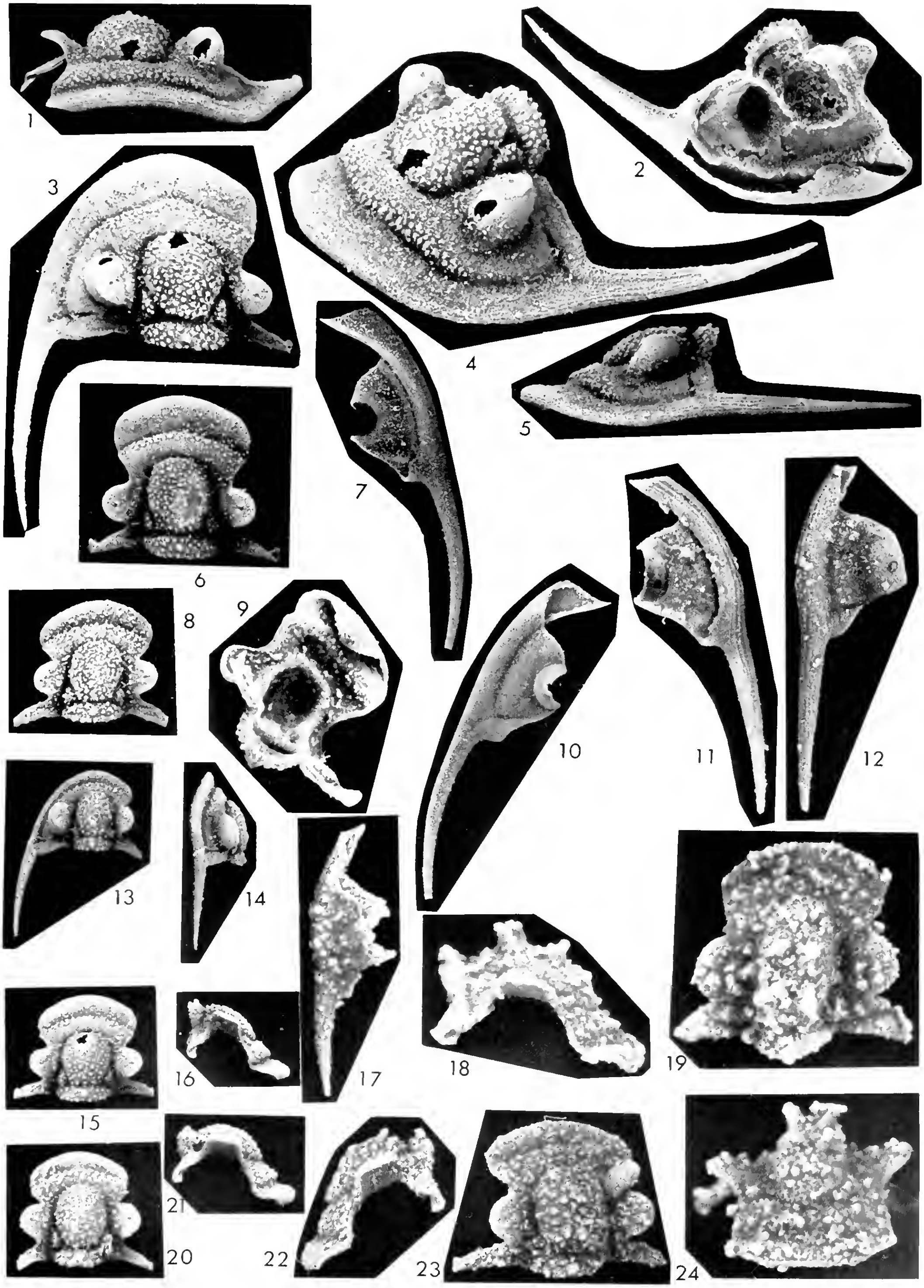


PLATE 6

PLATE 7

Otarion plautum n. sp.
Hardwood Mountain Formation, Silurian, Maine

Figure	
1, 2, 4, 6	Holotype cephalon lacking hypostome, USNM 154231: figs. 1, 2, 4, dorsal, left lateral, anterior views, × 9; fig. 6, oblique ventral view, × 10.
3, 5	Cranidium, USNM 154232, left lateral, dorsal views, × 9.
7	Cranidium with incomplete right free cheek and rostral plate, USNM 154233, ventral view, × 9.
8, 11, 12	Cranidium, USNM 154234: fig. 8, oblique exterior view showing smooth muscle areas, × 15; figs. 11, 12, dorsal, left lateral views, × 9.
9	Free cheek, USNM 154238, interior view, × 9.
13, 14	Cranidium, USNM 154235, dorsal, left lateral views, × 15.
15	Small free cheek, USNM 154239, exterior view, × 15.
17, 18, 23	Cranidium, USNM 154236, dorsal, left lateral, ventral views, × 15.
19, 24, 25	Cranidium, USNM 154237, left lateral, dorsal, anterior views, × 30.

Otarionid hypostome
Hardwood Mountain Formation, Silurian, Maine

10, 16	Left lateral, exterior views, × 15. USNM 154244.
20	Smallest example, exterior view, × 30. USNM 154247.
21, 22	Left lateral, exterior views, × 15. USNM 154245.
26, 27	Left lateral, exterior views, × 20. USNM 154246.

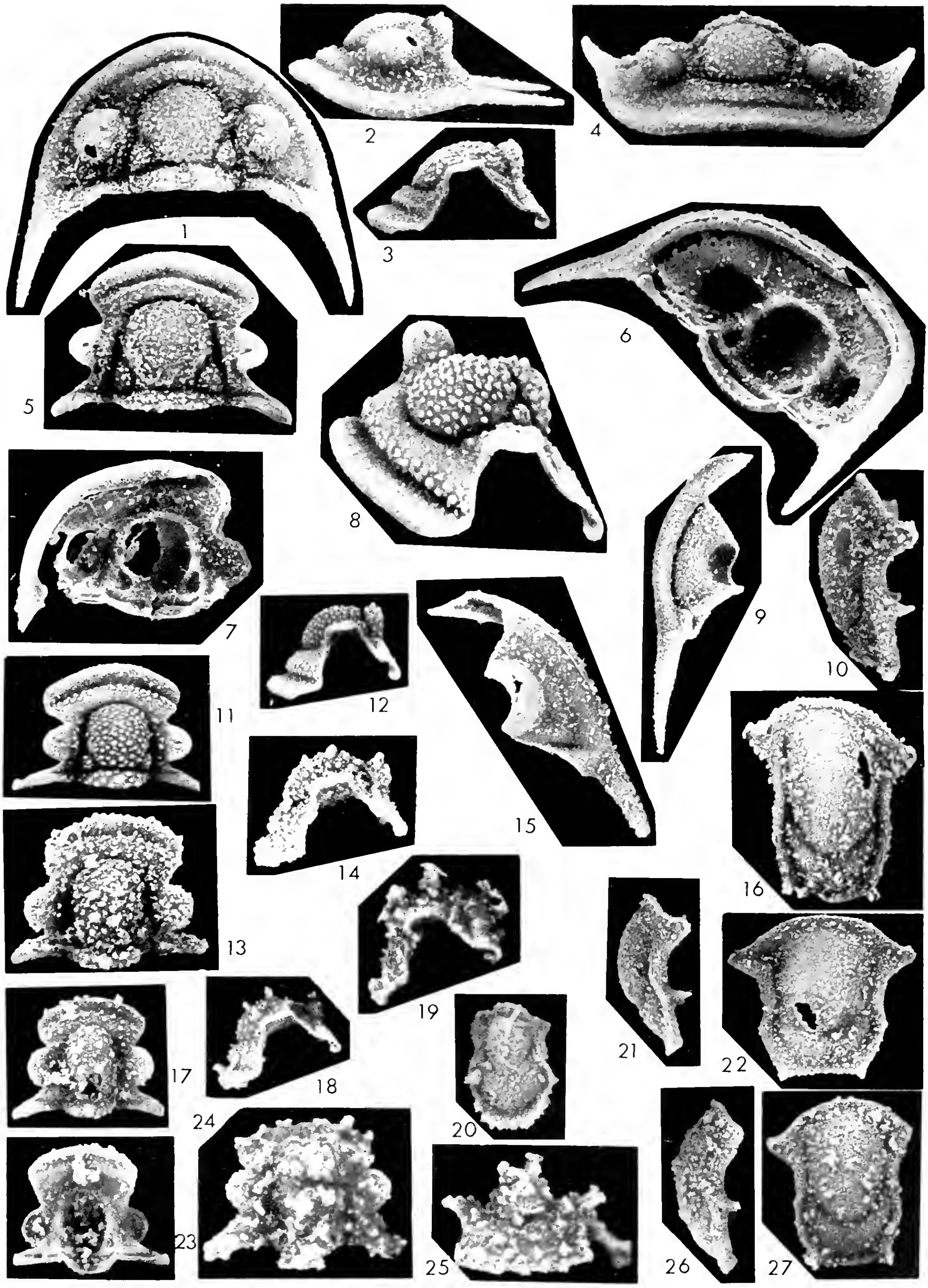


PLATE 7

PLATE 8

Otarionid Thoracic Segments and Pygidium, Type A
Hardwood Mountain Formation, Silurian, Maine

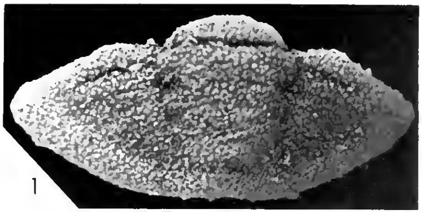
Figure	
1, 4, 10	Large pygidium, USNM 154248, dorsal, posterior, ventral views, × 15.
2	Small pygidium, USNM 154249, dorsal view, × 15.
3, 5, 6, 9	Three articulated segments and pygidium, USNM 154250, posterior, ventral, dorsal, left lateral views, × 15.
13, 15, 21	Segment with median axial spine, USNM 154253, dorsal, ventral, left lateral views, × 9.
14	Two segments, USNM 154254, dorsal view, × 4.5.
19, 22, 23, 26	Four segments and pygidium, USNM 154251, right lateral, posterior, two dorsal views, × 15.
24, 25	Five segments and pygidium, USNM 154252, two dorsal views, × 9.

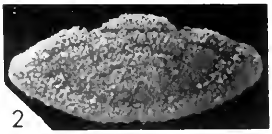
Otarionid Pygidium Type C
Hardwood Mountain Formation, Silurian, Maine

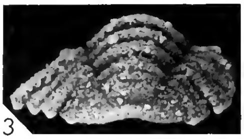
7, 8, 11, 12	Dorsal, right lateral, ventral, posterior views, × 15. USNM 154255.

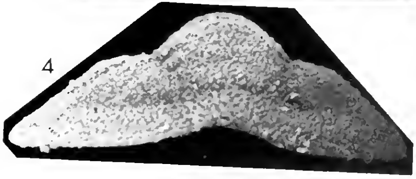
Otarionid Pygidium Type D
Hardwood Mountain Formation, Silurian, Maine

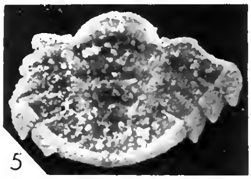
16, 17, 18, 20	Posterior, right lateral, dorsal, ventral views, × 15. USNM 154256.

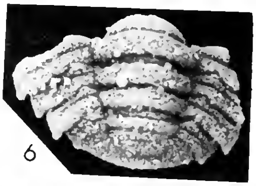

1

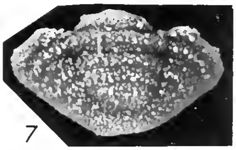

2

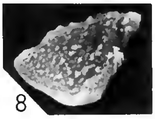

3

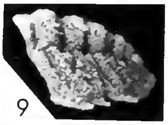

4

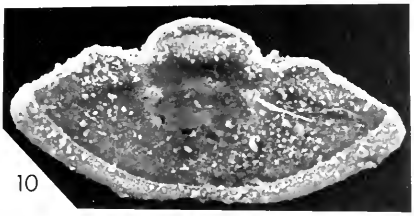

5

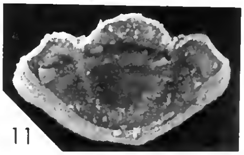

6

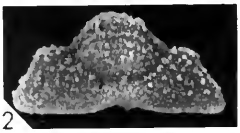

7

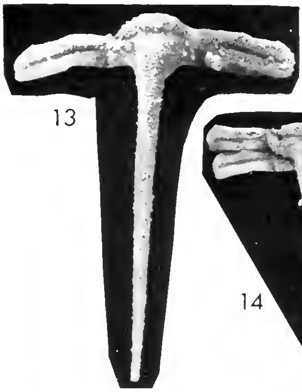

8


9


10

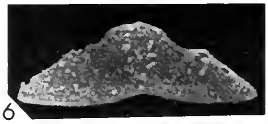

11

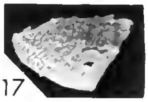

12

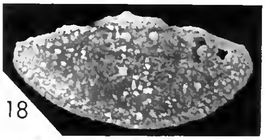

13

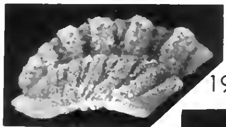

14

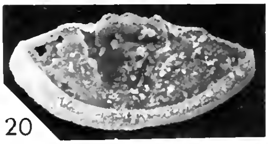

15


16

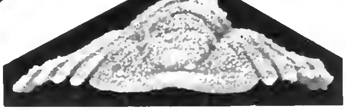

17

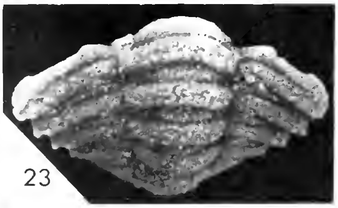

18


19

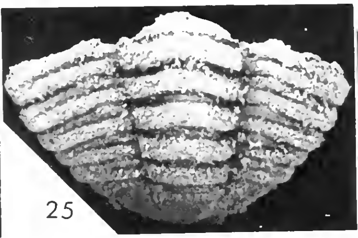

20


21


22


23


24


25


26

PLATE 8

PLATE 9

Otarionid Thoracic Segments and Pygidium Type B
Hardwood Mountain Formation, Silurian, Maine

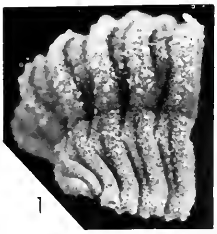
Figure	
1, 2	Six thoracic segments, USNM 154257, left lateral, dorsal views, × 15.
3, 8	Six thoracic segments, USNM 154258, dorsal, left lateral views, × 15.
4–7	Pygidium, USNM 154259, dorsal, right lateral, posterior views, × 30; ventral view, × 15.
9, 10, 12, 13	Pygidium, USNM 154260, dorsal, ventral, posterior, right lateral views, × 15.
11, 14	Pygidium, USNM 154261, dorsal, posterior views, × 30.

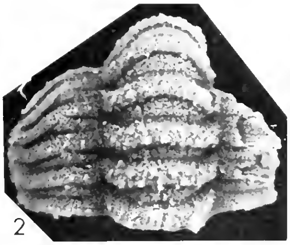
Otarionid Transitory Pygidium
Hardwood Mountain Formation, Silurian, Maine

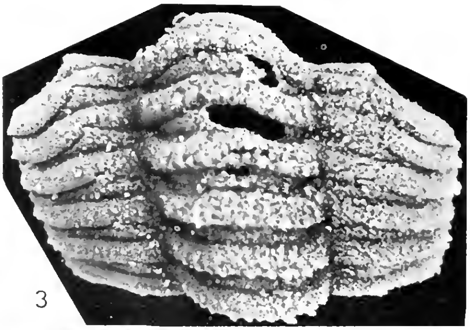
15, 16	USNM 154263, right lateral, dorsal views, × 30.
17, 21, 26	Specimen with major spine on first axial ring, USNM 154265, dorsal, ventral, posterior views, × 30.
18, 22	Specimen without major spine on axial rings, USNM 154266, dorsal, posterior views, × 30.
19, 20	Example with major spine on third axial ring, USNM 154262, dorsal, right lateral views, × 30.
23–25	Specimen with major spine on first and third axial rings, USNM 154264, dorsal, right lateral, ventral views, × 30.

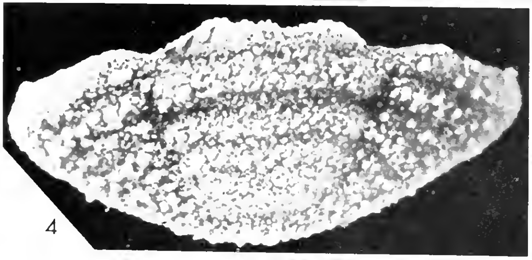
Otarionid Transitory Pygidium
Hardwood Mountain Formation, Silurian, Maine

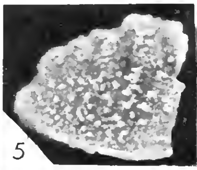
27	USNM 154267, dorsal view, × 30.

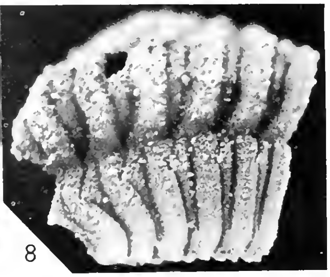

1

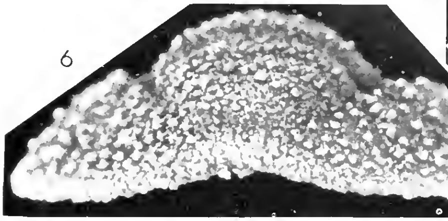

2

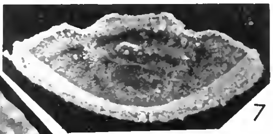

3

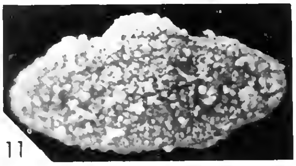

4

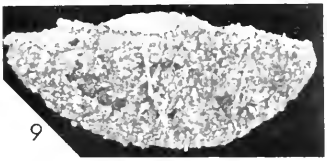

5

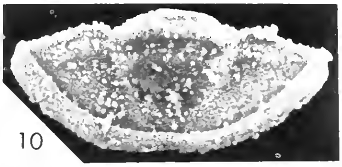

8

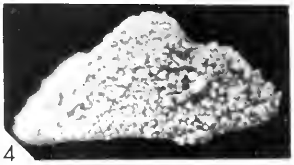

6

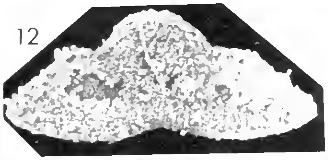

7

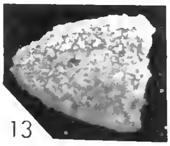

11

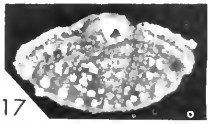

9

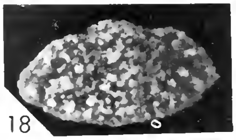

10

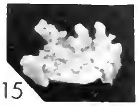

14

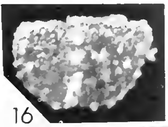

12

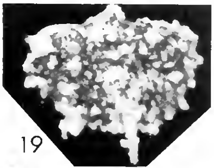

13

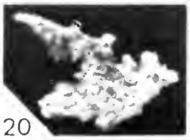

17

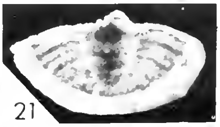

18

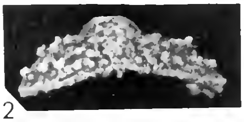

15

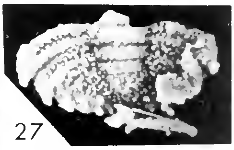

16

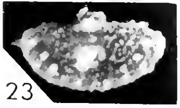

19

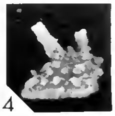

20

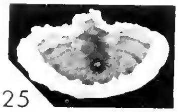

21


22


27


23


24


25


26

PLATE 9

PLATE 10

Unidentified Transitory Pygidium
Hardwood Mountain Formation, Silurian, Maine

Figure	
1–3, 5	USNM 154268, dorsal, ventral, left lateral, posterior views, × 30.
9, 10	USNM 154269, dorsal, posterior views, × 30.

Scutelluid gen. ind.
Hardwood Mountain Formation, Silurian, Maine

4, 6–8	Incomplete cranidium, USNM 154270, right lateral, ventral, dorsal, anterior views, × 6.
13	Incomplete cranidium, USNM 154271, dorsal view, × 15.

Fragiscutum rhytium n. gen., n. sp.
Hardwood Mountain Formation, Silurian, Maine

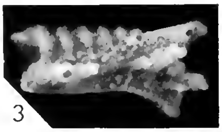
11	Holotype, USNM 154272, dorsal view of posterior margin of cephalon and the first five thoracic segments; on inner part of pleurae upper silicified layer is broken away, showing cones projecting up from midline of inner surface (cf. Fig. 8b), × 9.

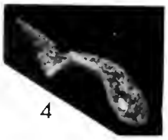
Otarion diffractum Zenker, 1833
Kopanina Beds, Ludlow, Upper Silurian, St. Ivan,
Czechoslovakia. Krantz Collection, MCZ 8542a.

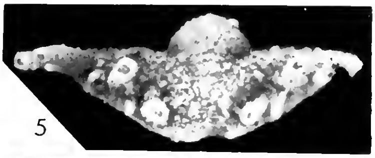
12, 14, 15, 16	Enrolled incomplete exoskeleton, figs. 12, 14, 16, dorsal, right lateral, anterior views, × 4.5; fig. 15, ventral view showing connective sutures and rostral suture, × 6.

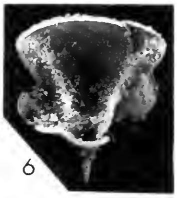

1


2

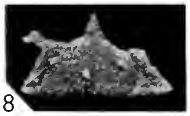

3

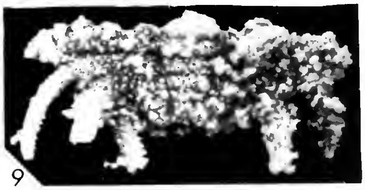

4

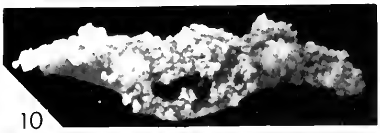

5

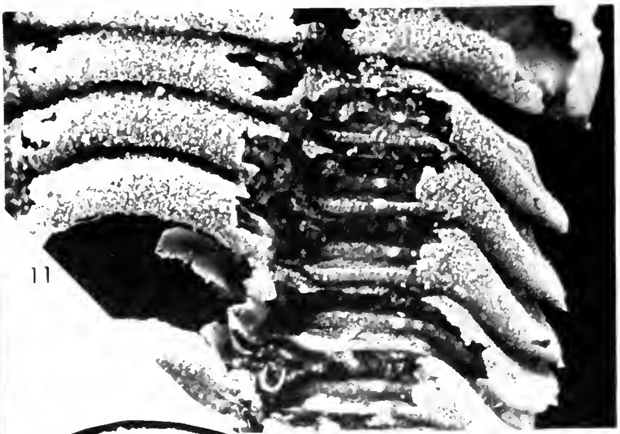

6

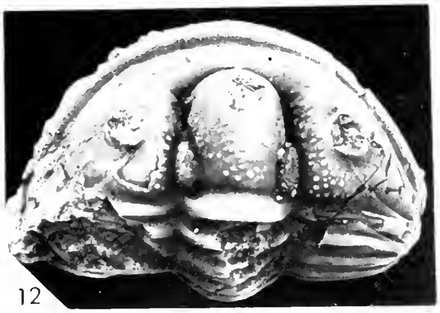

7

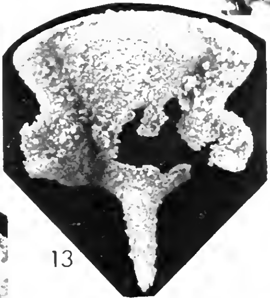

8

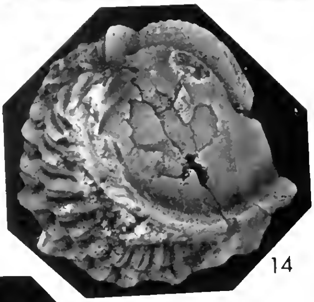

9

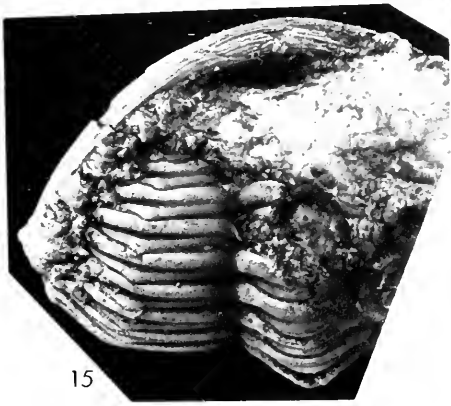

10


11


12


13


14


15

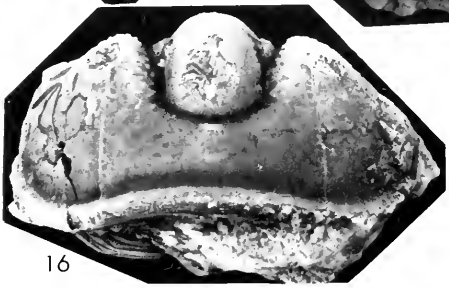
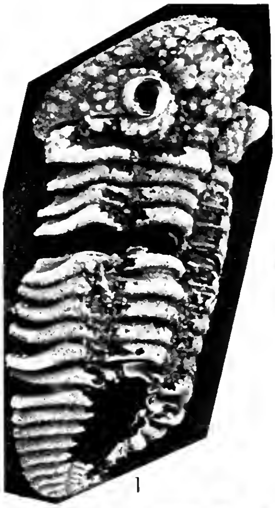

16

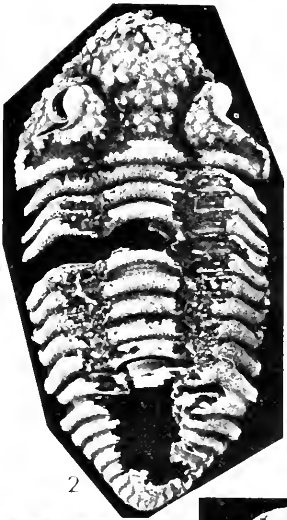
PLATE 10

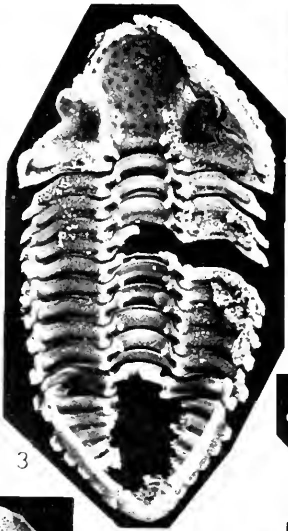
PLATE 11

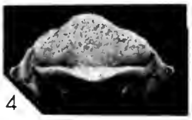
Fragiscutum rhytium n. gen., n. sp.
Hardwood Mountain Formation, Silurian, Maine

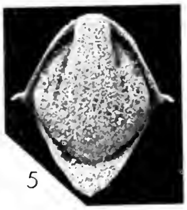
Figure	
1–3	Holotype, USNM 154272, oblique exterior, dorsal, ventral views, × 3.
4, 5	Hypostome, USNM 154282, posterior, exterior views, × 4.5.
6, 7, 12	Hypostome, USNM 154276; figs. 6, 12, anterior, interior views, × 4.5; fig. 7, oblique exterior view of right wings, × 15.
8–10	Hypostome, USNM 154285, exterior, posterior, right lateral views, × 6.
11, 15	Hypostome, USNM 154283, exterior, right lateral views, × 15.
13	Cranidium (USNM 154273) and hypostome (USNM 154276) in juxtaposition, oblique view, × 6.
14, 17	Smallest hypostome, USNM 154284, exterior, left lateral views, × 15.
16	Free cheek, USNM 154288, exterior view, × 6.
18, 19	Free cheek, USNM 154287, exterior, interior views, × 4.5.
20	Part of cephalon of holotype (USNM 154272), dorsal view to show granulation on and between tubercles, × 9.
21	Hypostome, USNM 154286, oblique view to show granulation and faintly-defined macula, × 9.


1

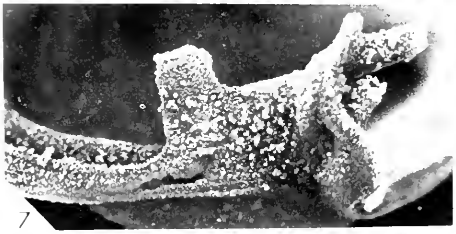

2

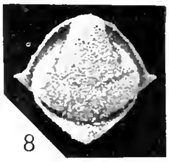

3


4


5

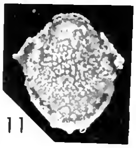

6


7

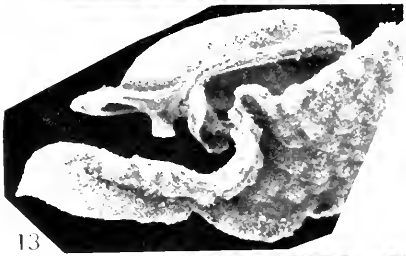

8

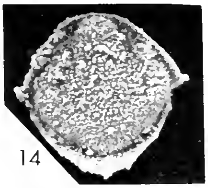

9


10

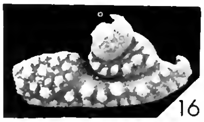

11


12


13

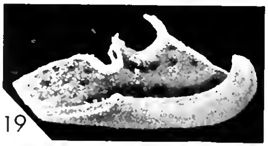

14


15


16


17


18


19


20

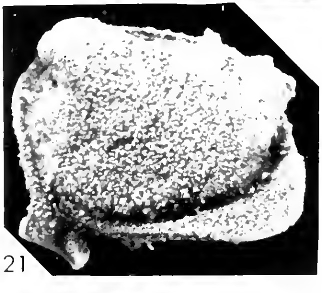
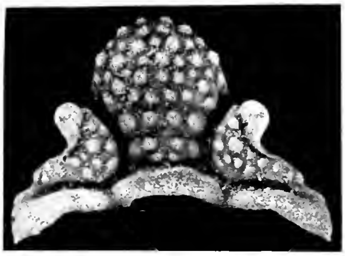

21

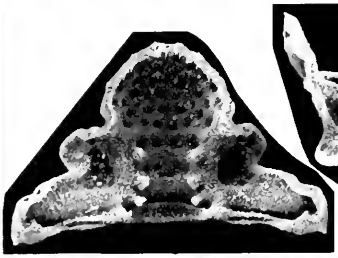
PLATE 11

PLATE 12

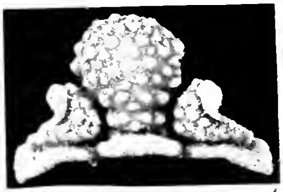
Fragiscutum rhytium n. gen., n. sp.
Hardwood Mountain Formation, Silurian, Maine

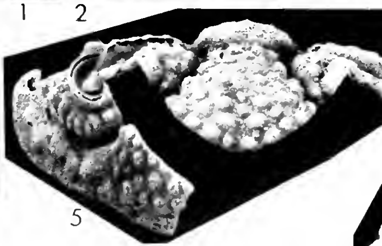
Figure	
1, 2	Cranidium, USNM 154275, dorsal (cf. Fig. 7b), ventral views, × 4.5.
3, 5, 8	Cranidium (USNM 154273) and free cheek (USNM 154274) in juxtaposition, oblique interior, anterior, dorsal views, × 4.5.
4	Cranidium, USNM 154277, dorsal view, × 4.5.
6	Cranidium, USNM 154278, dorsal view, × 6.
7, 9, 10	Cranidium, USNM 154279, right lateral, dorsal, ventral views, × 15.
11	Small free cheek, USNM 154289, exterior view, × 15.
12, 18	Cranidium, USNM 154281, anterior, dorsal views, × 15.
13, 14, 17, 20	Thoracic segment, USNM 154294, anterior, dorsal, posterior, ventral views, × 4.5.
15, 16, 19	Cranidium, USNM 154280, dorsal (cf. Fig. 7a), left lateral, anterior views, × 15.
21, 22	Small segment, USNM 154295, showing median axial spine and tubercles on pleural bands, posterior, dorsal views, × 15.
23	Pygidium, USNM 154296, right lateral view, × 4.5.

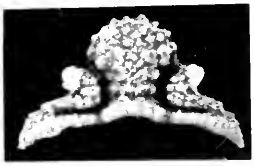

1

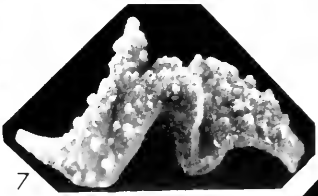

2

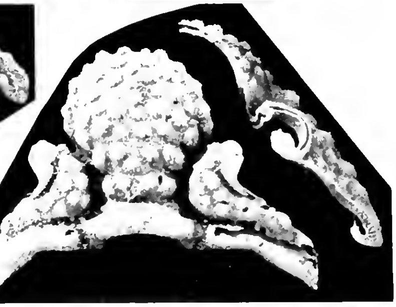

3

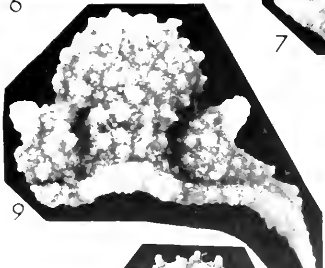

4

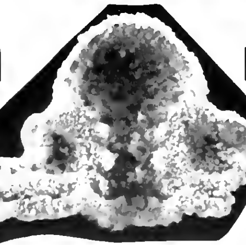

5

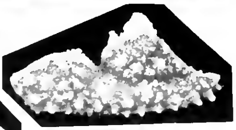

6

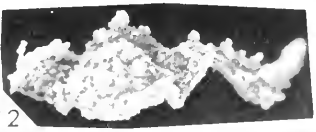

7

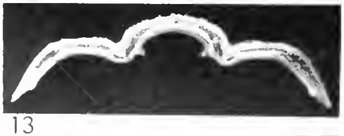

8


9

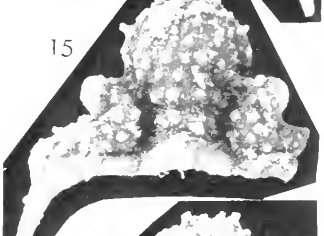

10

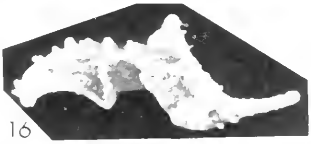

11

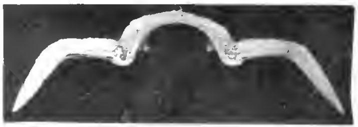

12


13


14


15

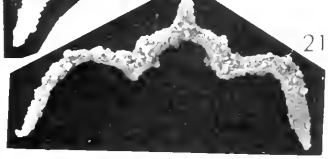

16

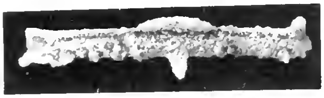

17


18


19


20


21


22

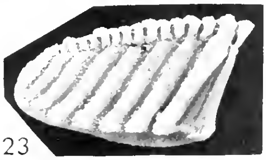

23

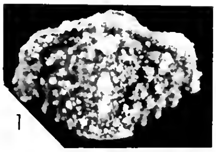
PLATE 12

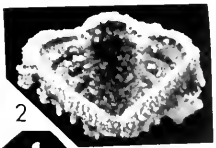
PLATE 13

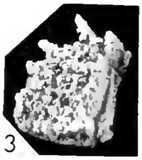
Fragiscutum rhytium n. gen., n. sp.

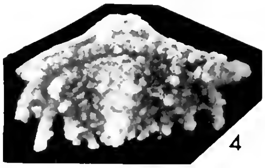
Hardwood Mountain Formation, Silurian, Maine

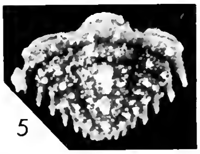
Figure	
1–3	Transitory pygidium, USNM 154298, dorsal, ventral, right lateral views, × 15.
4, 9, 13	Transitory pygidium, USNM 154301, dorsal, posterior, ventral views, × 30.
5–7	Transitory pygidium, USNM 154299, dorsal, posterior, right lateral views, × 15.
8, 12	Transitory pygidium, USNM 154300, dorsal, oblique views, × 30.
10, 11, 14, 15	Pygidium, USNM 154296, posterior, dorsal, ventral views, × 4.5; oblique view showing pleural ribs and outer part of first pleural furrow on facet, × 15.
16	Pygidium, USNM 154297, dorsal view, × 9.
17	Three thoracic segments, USNM 154293, dorsal view showing through broken outer silicified layer cones projecting upward from the lower layer, × 15.

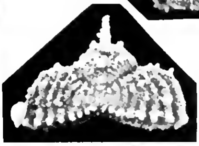

1


2

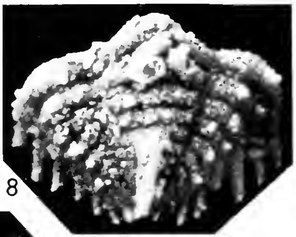

3

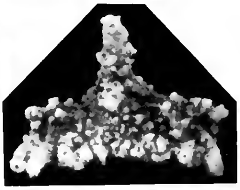

4

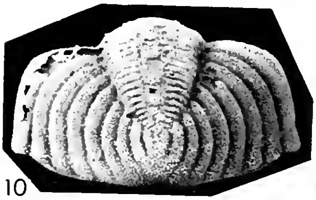

5

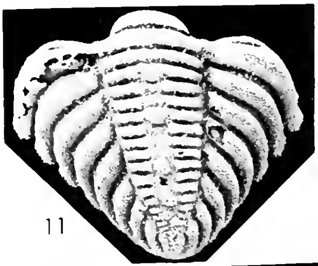

6

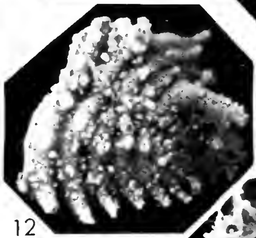

7

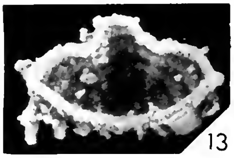

8

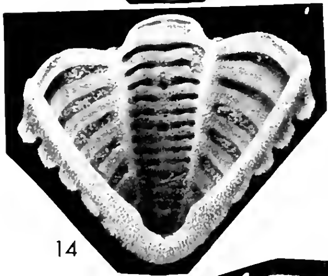

9

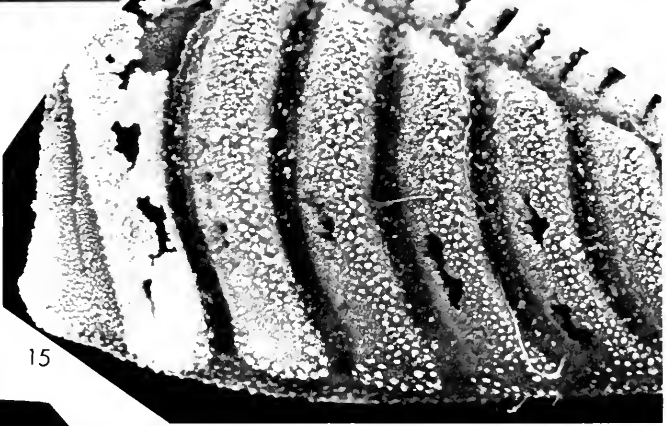

10

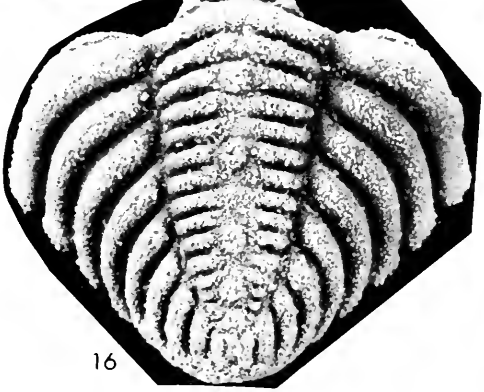

11


12


13


14


15


16


17

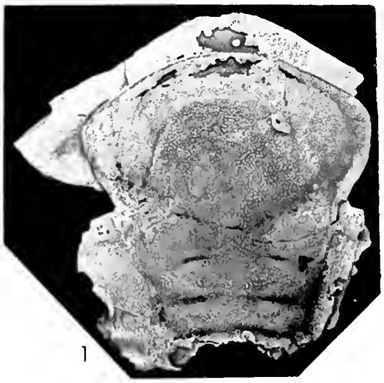
PLATE 13

PLATE 14

Dalmanites puticulifrans n. sp.

Hardwood Mountain Formation, Silurian, Maine

Figure	
1, 4	Holotype USNM 154302, incomplete cranidium with part of left free cheek and anterior border attached, dorsal, ventral views, × 2.
2, 3	Incomplete cranidium, USNM 154304, dorsal, right lateral views, × 1.
5	Latex cast of external mould of cranidium, USNM 154303, dorsal view, × 1.
6, 7	Cranidium, USNM 154305, dorsal, anterior views, × 1.
8, 14	Incomplete pygidium, USNM 154432, showing apodemes, ventral view, × 1; oblique view, × 3.
9–11, 13	Segment, USNM 154430, ventral, anterior, dorsal, right lateral views, × 1.7.
12	Pygidium, USNM 154431, dorsal view showing granulation, × 3.
15, 16	Incomplete pygidium, USNM 154433, showing terminal spine, dorsal, ventral views, × 4.5.



1

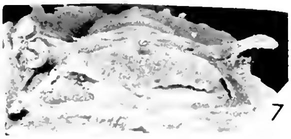
2

3

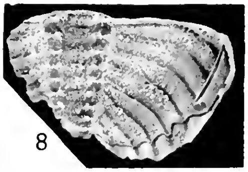
4

5

6

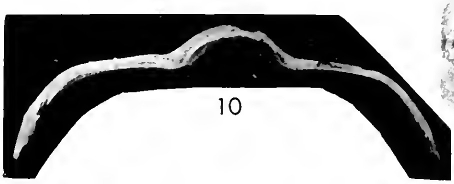


7

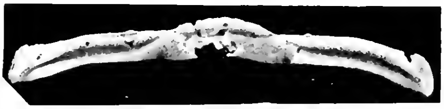


8

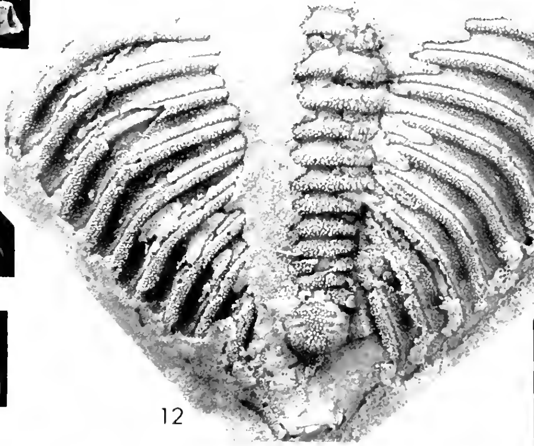
9



10

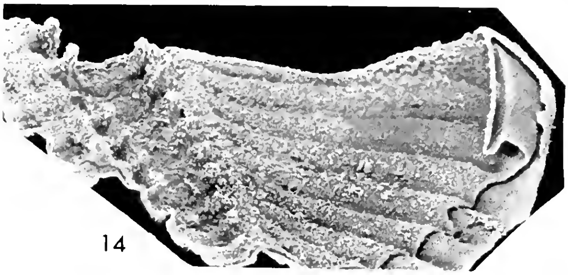


11



12

13



14

15

16

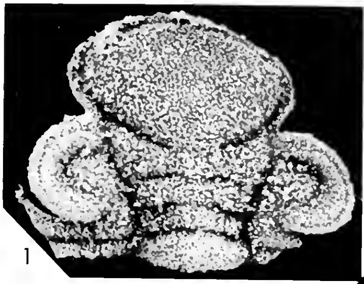
PLATE 14

PLATE 15

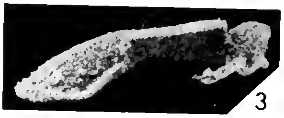
Dalmanites puticulifrons n. sp.

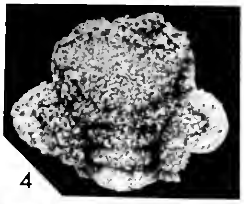
Hardwood Mountain Formation, Silurian, Maine

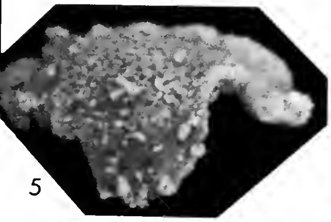
Figure	
1–3	Incomplete cranidium, USNM 154306, dorsal, anterior, left lateral views, × 6.
4	Incomplete cranidium, USNM 154307, dorsal view, × 9.
5, 6, 10, 14, 17	Incomplete protaspis, USNM 154310, right lateral, oblique exterior, anterior, dorsal, posterior views, × 50.
7	Incomplete cranidium, USNM 154308, dorsal view, × 30.
8	Transitory pygidium, USNM 154435, dorsal view, × 15.
9, 12, 13, 16	Transitory pygidium, USNM 154434, oblique exterior, left lateral, ventral, dorsal views, × 15.
11, 15	Incomplete cranidium, USNM 154309, dorsal, right lateral views, × 25.

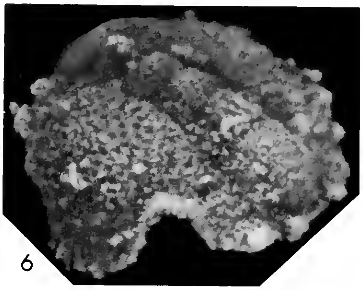

1

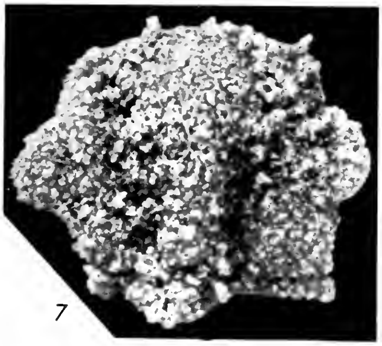

2


3

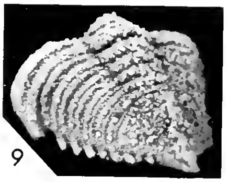

4

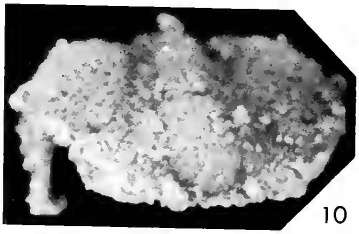

5

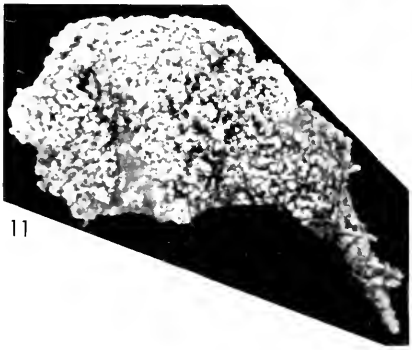

6

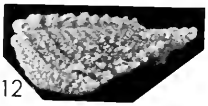

7

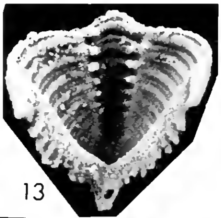

8

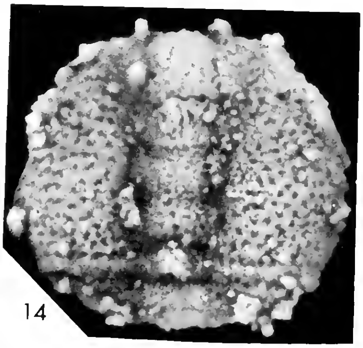

9

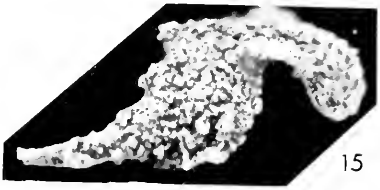

10

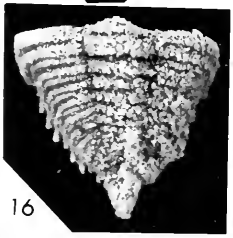

11


12


13


14


15


16

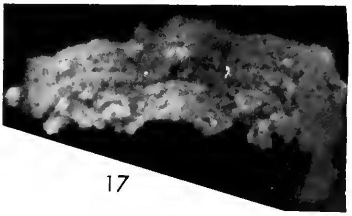

17

PLATE 15

PLATE 16

Leonaspis cf. *williamsi* Whittington, 1956

Hardwood Mountain Formation, Silurian, Maine

Figure	
1–4, 8, 20	Cranidium, USNM 154437, dorsal, anterior, right lateral, posterior, oblique exterior views, × 4.5; anterior view of part of cranidium to show external surface, ×15.
5, 6	Cranidium, USNM 154436, dorsal, anterior views, × 4.5.
7, 9, 10	Small cranidium, USNM 154438, left lateral, dorsal, anterior views, × 15.
11, 21, 22	Free cheek, USNM 154440, dorsal, exterior, interior views, × 4.5.
12–14	Small cranidium, USNM 154439, dorsal, anterior, left lateral views, × 15.
16–18	Hypostome, USNM 154441, silicified layer replacing external surface broken away except anteriorly, anterior, exterior, interior views, × 6.

Xanianurus baucati n. gen., n. sp.

Hardwood Mountain Formation, Silurian, Maine

15, 19	Cephalon lacking hypostome, USNM 154450, dorsal view, × 7.5; oblique exterior view, × 10.

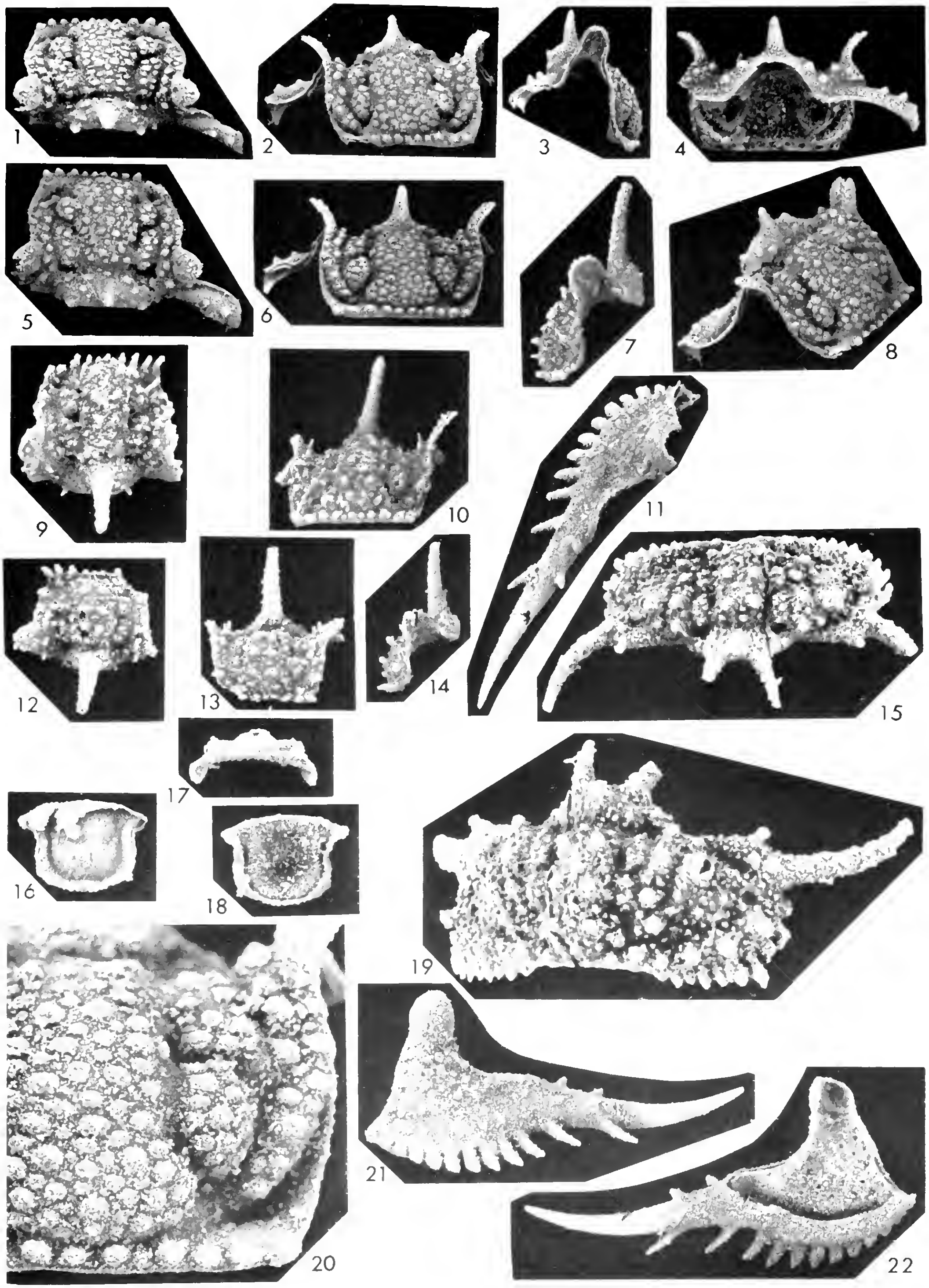


PLATE 16

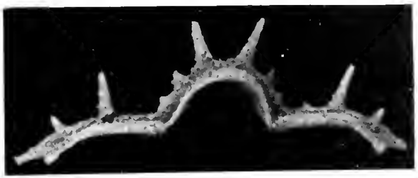
PLATE 17

Leonaspis cf. *williamsi* Whittington, 1956
Hardwood Mountain Formation, Silurian, Maine

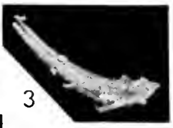
Figure	
1, 4	Anterior thoracic segment, USNM 154442, anterior, dorsal views, × 10.
2	Anterior thoracic segment, USNM 154443, ventral view, × 4.5.
3, 7, 16	Pygidium, USNM 154447, right lateral, ventral views, × 6; dorsal view, × 15.
5, 9, 11	Segment from posterior part of thorax, USNM 154445, oblique interior view, × 9; left lateral, dorsal views, × 4.5.
6	Incomplete pygidium, USNM 154448, dorsal view, × 6.
8, 10	Medial thoracic segment, USNM 154444, dorsal, anterior views, × 10.
12	Posterior thoracic segment, USNM 154446, dorsal view, × 10.

Xanionurus boucoti n. gen., n. sp.
Hardwood Mountain Formation, Silurian, Maine

13, 14	Anterior thoracic segment, USNM 154453, right lateral, dorsal views, × 15.
15, 17, 18, 22	Medial thoracic segment, USNM 154454, posterior, ventral, right lateral, anterior views, × 6.
19–21, 26	Pygidium, USNM 154456, right lateral, ventral, posterior views, × 4.5; dorsal view, × 9.
23–25	Posterior thoracic segment, USNM 154455, dorsal, left lateral, anterior views, × 9.


1


2


3


4

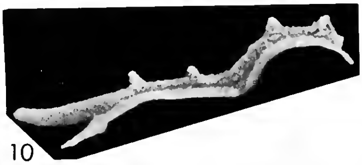

5


6

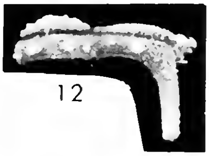

7

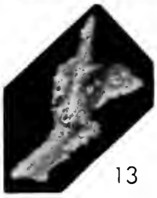

8

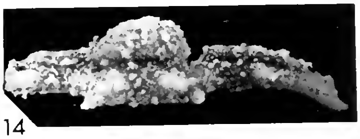

9


10

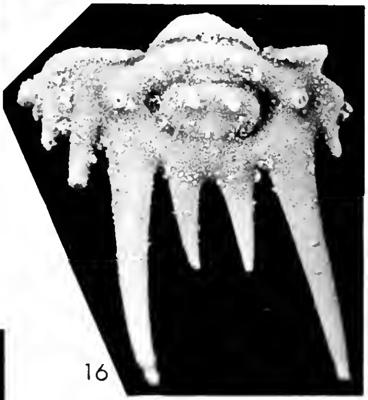

11


12


13


14

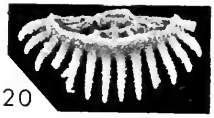

15


16

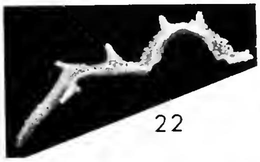

17

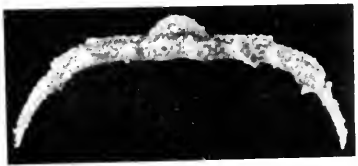

18

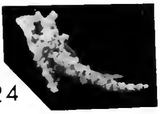

19


20


21


22


23


24


25

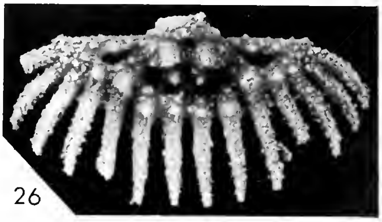

26

PLATE 17

PLATE 18

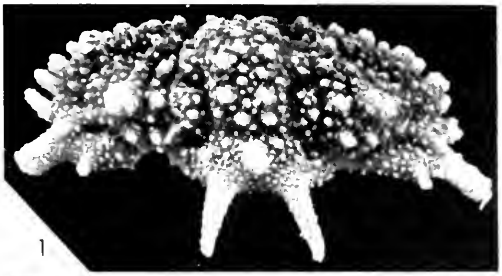
Xanionurus boucoti n. gen., n. sp.

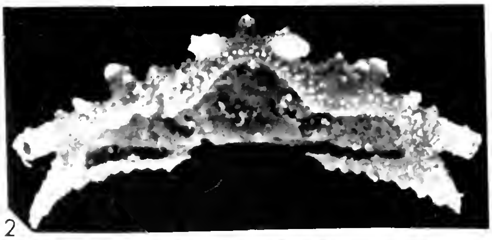
Hardwood Mountain Formation, Silurian, Maine

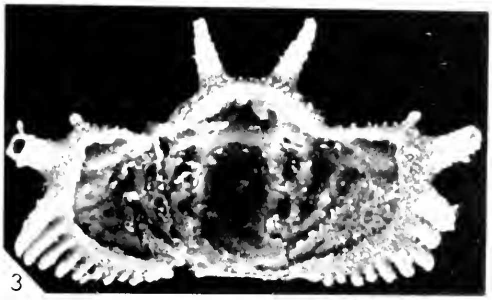
Figure	
1–6	Holotype cephalon lacking rostral plate and hypostome, USNM 154449, dorsal, posterior, ventral, anterior, left lateral views, × 10; occipital ring, paired spines and median spine, latter with pits at the tip, × 30.
7	Cephalon lacking rostral plate and hypostome (see Pl. 16, figs. 15, 19), USNM 154450, anterior view, × 7.5.
8, 9, 11, 12	Small cranidium, USNM 154451, dorsal, left lateral, anterior, oblique exterior views, × 15.
13–15	Smallest cranidium, USNM 154452, dorsal, right lateral, anterior views, × 15.

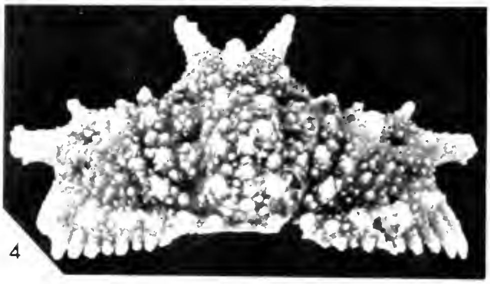
Xanionurus formosus (Prantl and Vaněk, 1958)

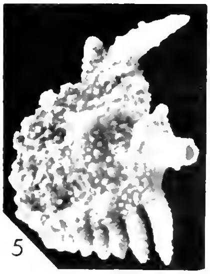
10	Incomplete extended exoskeleton, MCZ 4166, dorsal view, × 9. Loděnice, Liteň Beds (Upper Wenlock), Czechoslovakia.

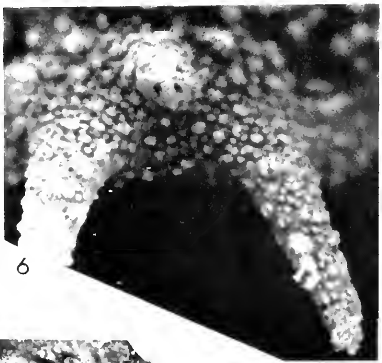

1

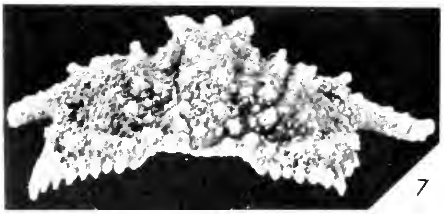

2

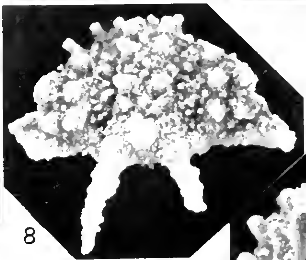

3

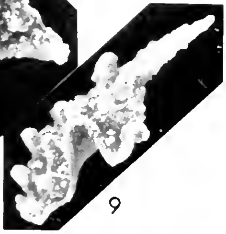

4

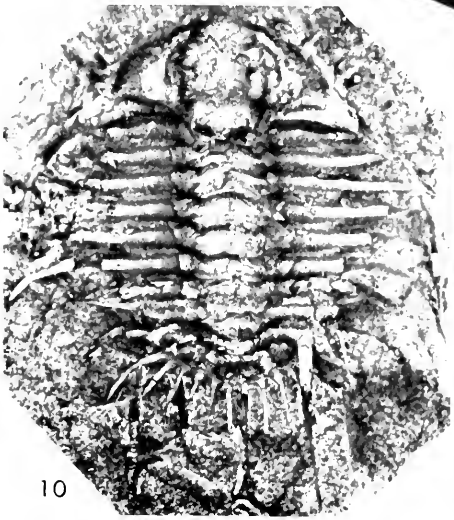

5

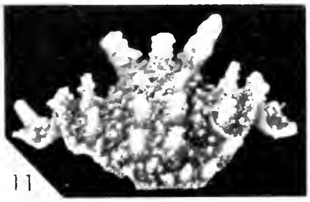

6

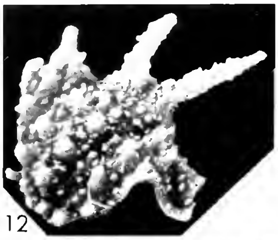

7


8


9


10


11


12


13


14


15

PLATE 18

PLATE 19

Otarion megalops (M'Coy, 1846)

Beds of presumed Upper Llandovery age, in the neighbourhood of Cong, County Galway, Eire. Griffith Collection, National Museum of Ireland.

Figure	
1–4	Holotype, internal mould of incomplete cranidium, original of M'Coy, 1846, pl. 4, fig. 5, from Boocaun, near Cong. Dorsal view, × 10; left lateral view, × 6; oblique exterior view, × 9; anterior view, × 6.
5, 8, 9	Topotype, internal mould of incomplete cranidium, dorsal, anterior, left lateral views, × 6.
6, 7, 10, 11	Topotype, internal mould of incomplete cranidium, left lateral, oblique exterior, dorsal, anterior views, × 6.
12–14, 16	Internal mould of cranidium, anterior, dorsal, left lateral, oblique exterior views, × 6. Tonlegee, near Cong.

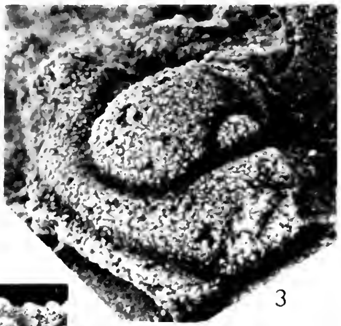
Dalmanites puticulifrons n. sp.

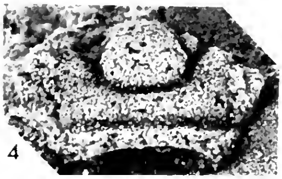
Hardwood Mountain Formation, Silurian, Maine

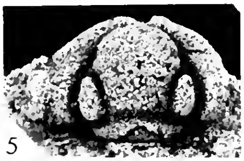
15	Interior of counterpart silicified exoskeleton of original of Plate 14, figure 5, interior view showing apodemes of occipital ring, 1p and 2p, facets of eye surface, × 3.
17	Exterior view of part of original of Plate 14, figure 6, showing granulation on external surface, × 4.5.


1

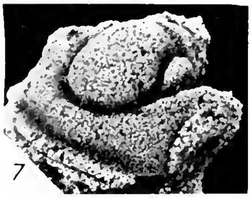

2


3


4

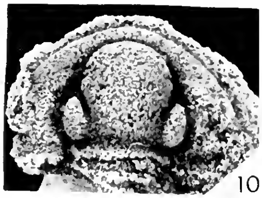

5


6

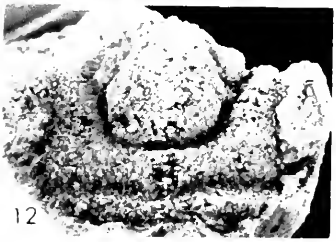

7

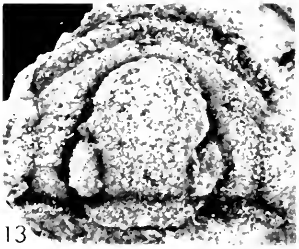

8


9


10

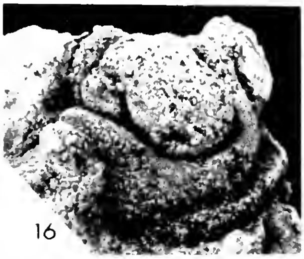

11


12


13


14


15


16

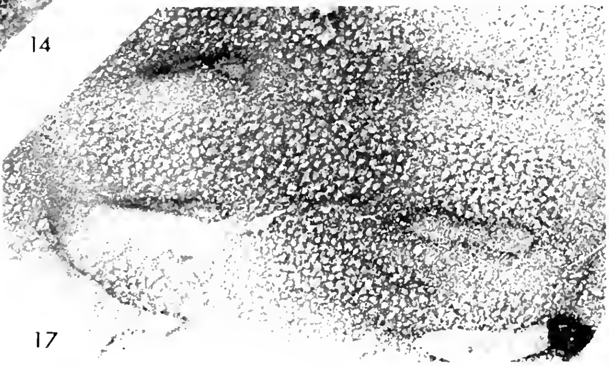

17

PLATE 19