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The Macristiidae, a Ctenothrissiform Family Based on Juvenile and Larval Scopelomorph Fishes

BY DONN ERIC ROSEN¹

INTRODUCTION

The generic term *Macristium* was created by Regan in 1903 to include a hitherto undescribed form from the Azores, *Macristium chavesi*. The genus was defined by Regan as, "Allied to *Bathysaurus*, Günth., which it resembles in the position of the fins and the number of rays, but with the mouth only moderately wide, the dentition weaker, the maxillary dilated posteriorly, the fin-rays much prolonged, and the ventrals still more anterior in position." He had but a single specimen that was 110 mm. in standard length. Regan (1911) re-examined this specimen and then commented that "it has been a good deal damaged, and in the absence of precise information I should judge that it may have been washed ashore. The snout and end of the lower jaw are injured and the praemaxillaries have been lost; one of the pectoral fins is complete, but none of the other fins has even a single ray entire.

"Originally I believed that *Macristium* was related to *Bathysaurus*, Günth., which it resembles in the position of the fins and the number of rays. I am now of the opinion that this resemblance is misleading, for I think that in all probability the praemaxillaries would not exclude the

¹ Chairman and Curator, Department of Ichthyology, the American Museum of Natural History.

maxillaries from the gape. In any case, *Macristium* must be made the type of a distinct family, Macristiidae, probably related to the Alepocephalidae." Regan's account also included an excellent figure of the specimen, fin ray, branchiostegal and myotome counts, and an expanded description of the specimen's superficial morphology.

The type of *Macristium chavesi* is now lost.

Based on Regan's published taxonomic recommendation, Berg (1940) placed the Macristiidae in his order Clupeiformes, suborder Clupeoidei, superfamily Alepocephaloidea. He commented only that the systematic position of the family is uncertain.

Marshall (1961) reported on a larval fish of 33 mm. in standard length from the Bay of Biscay. He identified it as a young *Macristium chavesi*, although it differed from Regan's specimen in dorsal, anal, pectoral, pelvic, branchiostegal and myotome counts, as well as in some features of the head that may or may not be attributable to its larval state. Using the meager data from his and Regan's specimens, Marshall reopened the question of macristiid relationship. He considered and rejected, as did Regan, the possibility of a *Macristium-Bathysaurus* linkage, and, in general, concluded that a *Macristium*-myctophoid relationship of any kind is improbable. Marshall proposed instead a relationship of *Macristium* with the Cretaceous Ctenothrissidae, based entirely on some superficial similarities of fin pattern and upper jaw structure. He failed to demonstrate in any convincing manner, however, that the similarities are more than spurious. Indeed, examination of Marshall's and Regan's figures of *Macristium* and of Smith Woodward's (1903) and Patterson's (1964) reconstructions of various ctenothrissids reveals only that the pelvic fins are elongate in both groups and that the dorsal is greatly elongate in *Macristium* and only slightly enlarged in ctenothrissids. The other fins and the upper jaw bones in the two groups are more different than they are similar.

Berry and Robins (1967) in describing a second macristiid, *Macristiella perlucens*, thought it unlikely that the macristiids are related to the ctenothrissids.

The genesis of the present review of macristiid relationships is the identification of an additional *Macristium*-like larva taken in mid-Atlantic by the Woods Hole Oceanographic Institution's vessel, "R. V. Chain." This specimen, 20 mm. in standard length, was called to my attention and sent to me for study by Dr. Richard L. Haedrich of the Woods Hole Oceanographic Institution's staff.

The larva in question is shown in figure 1. It was taken on June 16, 1965 at a depth of 100 to 140 meters, latitude 19° 52' N., longitude 69°

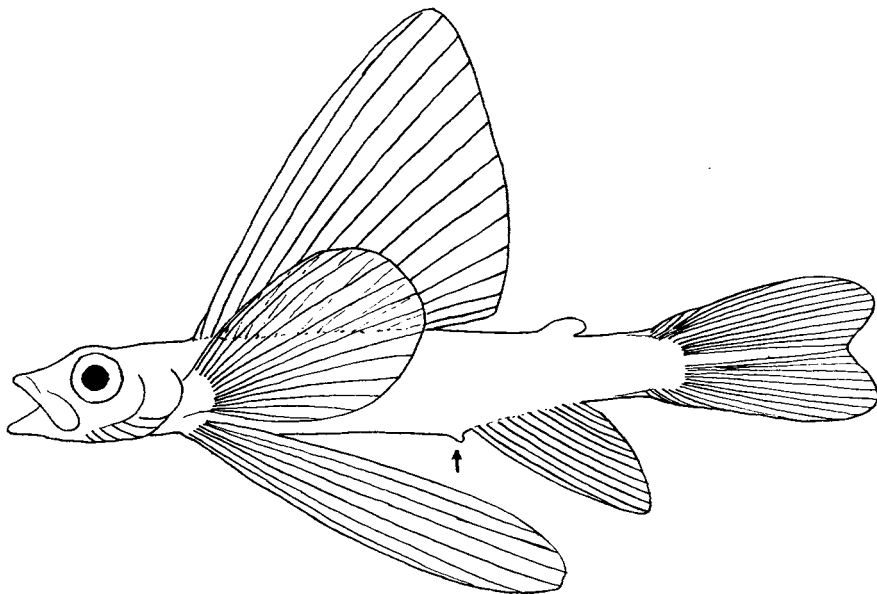


FIG. 1 Semidiagrammatic reconstruction of a larval fish of 20 mm. in standard length taken by the "R. V. Chain" (A.M.N.H. No. 21896). The body was somewhat twisted and all fins, except the adipose, were damaged to some extent. Fin size reconstructed on basis of longest, apparently intact, ray. Arrow indicates vent.

46' W. to latitude 19° 51' N., longitude 69° 56' W. The reason for its suspected identification as another *Macristium* is evident in the comparison of the "Chain" specimen (fig. 1) with Marshall's "Discovery" specimen (fig. 2), although the latter was somewhat larger (33 mm. in standard length). Differences between the two specimens, as drawn, are doubtless due to a combination of factors such as size, condition of the specimen, and method and style of reconstruction and drawing of the damaged fins. Some of the differences concern metamerism and are undoubtedly real. Table 1 compares attributes of the "Chain" specimen with those of Marshall's and Regan's specimens. In dorsal, anal, pectoral, pelvic, and myotome counts, the three specimens are similar. The "Chain" and "Discovery" specimens exactly agree in anal fin ray counts (13), and the "Chain" and Azores specimens agree in pelvic and branchiostegal counts (8 for both). All specimens agree in principal caudal fin ray counts (19). Body proportions are similar in all (figs. 1-3). The "Chain" specimen differs from the other two mainly in having the pelvic fins very slightly more advanced in position, and in having a definite

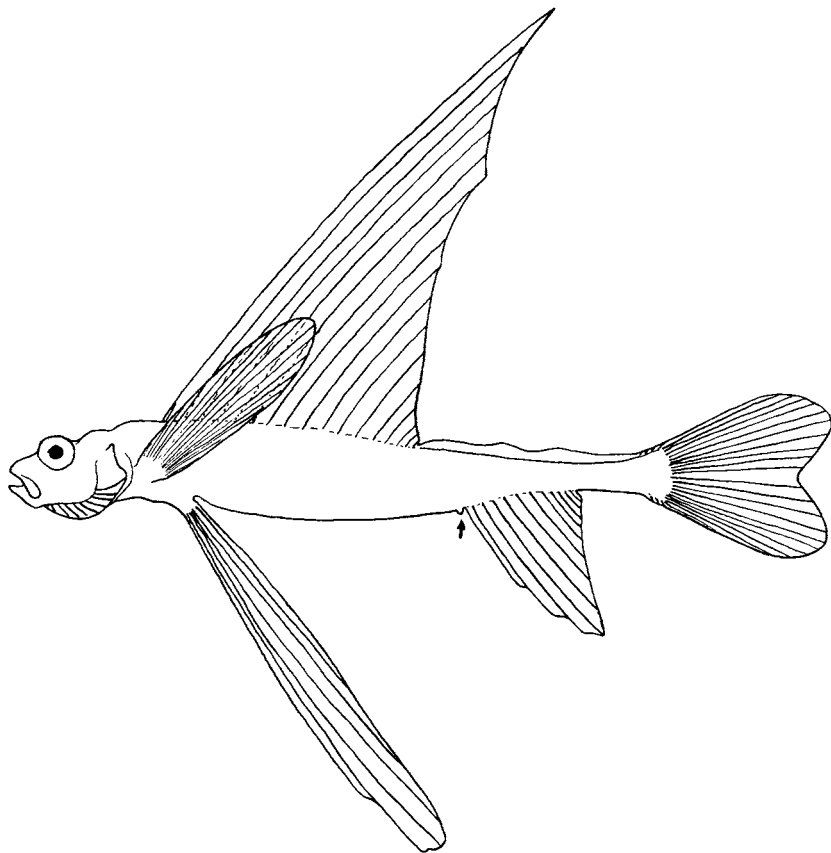


FIG. 2. A fish of 33 mm. in standard length, identified by Marshall (1961) as a larval *Macristium chavesi*. After Marshall (1961), simplified. Arrow indicates vent.

adipose fin. Whether an adipose was present in the "Discovery" and Azores specimens is problematical. The Azores specimen was first seen in an exceedingly battered condition evidently with many parts of the body and fins destroyed or missing, and Marshall illustrated the "Discovery" specimen as having a hyaline fold from the dorsal fin terminus to the upper caudal fin origin which might have been an early development or remains of an adipose. The adipose in the "Chain" specimen is exceedingly delicate and difficult to see without strong oblique lighting and very high magnification.

Especially because of the presence of an adipose fin together with the

TABLE 1
THE FOUR "MACRISTHID" SPECIMENS COMPARED WITH NINE SCOPELOMORPH FAMILIES

	Dorsal	Fin Rays		Pelvic	No. Vertebrae	No. Branchiostegals	No. Supramaxillae	Position of Anus	Adipose Fin
		Anal	Pectoral						
"Chain" specimen	16	13	15	8	ca. 60 ^a	8	1	Near anal	Present
"Discovery" specimen ^b	17	13	15	7	ca. 61 ^a	10	0	Near anal	Absent
" <i>Macristium chavesi</i> " ^c	18	13	16	8	ca. 62 ^a	8	?	Near anal	Absent
" <i>Macristiella perlucens</i> " ^d	12	13	15	8	ca. 69 ^a	16	0	Near pelvics	Present
Aulopidae ^e	14-21	9-13	11-14	9	41-53	16	2	Near anal	Present
Bathypteroidae ^f	11-15	8-13	8-16	8-9	49-60	11-13	1	Variable	Present or absent
Bathysauridae ^g	15-18	11-14	15-17	8	50-63	8-13	0	Near anal	Present ^h or absent
Chlorophthalmidae ⁱ	9-13	7-11	15-17	8-9	38-49	8	1	Midway between anal and pelvics	Present
Harpadontidae ^j	14	14	12	9	?	17-25	0	Near anal	Present
Ipnopidae ^k	8-13	9-19	9-16	7-8	51-80	8-17	1	Near pelvics	Absent
Neoscopelidae ^l	12-14	9-15	14-16	8	?	8-11	1	Near anal	Present
Scopelosauridae ^m	9-14	16-21	10-15	9	45-66	8-10	1	Near pelvics	Present
Synodontidae ⁿ	9-14	8-16	10-14	8-9	44-58	11-18	0	Near anal	Present

^a Vertebral number estimated from myotome counts.

^b Data from Marshall (1961).

^c Data from Regan (1911).

^d Data from Berry and Robins (1967).

^e Data from Mead (1966a).

^f Data from Mead (1966c).

^g Data from Mead (1966b).

^h Present in *Bathysaurus mollis*, absent in *B. ferox*.

ⁱ Data from Mead (1966e) and Okada and Sano (1960).

^j Data from Günther (1887) and Norman (a draft synopsis of the orders, families and genera of Recent fishes and fishlike vertebrates).

^k Data from Nielsen (1966) and Mead (1966d).

^l Data from Miller (1947).

^m Data from Marshall (1966).

ⁿ Data from Anderson, Gehringer, and Berry (1966).

advanced, neoteleostean¹ arrangement of the paired fins just behind the head, the "Chain" specimen seemed to show relationships to the Scopelomorpha. The premise that the "Chain" specimen might therefore be a larval scopelomorph led to a secondary premise that all the forms so far assigned to the Macristiidae might also be larval scopelomorphs. The "Chain" specimen, although small, is rather well ossified and could therefore be stained with alizarin dye, and the well-formed but unossified cartilages, with methylene blue.

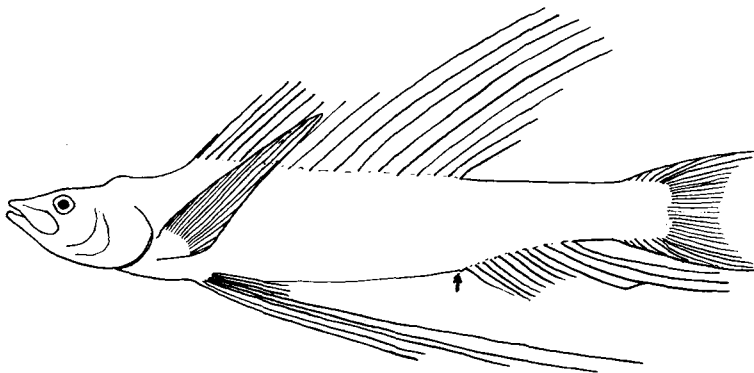


FIG. 3. *Macristium chavesi*, of 110 mm. in standard length. After Regan (1911), simplified. Arrow indicates vent.

ACKNOWLEDGMENTS

I especially thank Dr. Richard L. Haedrich, Woods Hole Oceanographic Institution, for calling to my attention and sending to me for unrestricted use the larval specimen that forms the basis of the present study. I am greatly indebted also to Dr. Giles Mead, Museum of Comparative Zoology, for essential confirmation and identification of the relationships of some of the comparative material, and for an illuminating conversation on mytrophoid fishes. To Dr. Gareth J. Nelson, the American Museum of Natural History, I am grateful for needed advice on the structure of the pharyngobranchial apparatus; to Dr. Colin Patterson, British Museum (Natural History), my sincere thanks for reading and helpfully commenting on the typescript. The work was supported, in

¹ The term "neoteleostean" was introduced by Rosen and Patterson (1969) to embrace the Scopelomorpha (containing only the mytrophiforms), the Paracanthopterygii, and the Acanthopterygii.

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INSTITUTIONAL ABBREVIATION

A.M.N.H., the American Museum of Natural History

ANATOMICAL ABBREVIATIONS

ant, antorbital	lac, lacrimal
art, articular	lat, lateral ethmoid
artmx, articular process of maxilla	mx, maxilla
artpmx, articular process of premaxilla	na, neural arch
asc, ascending process of premaxilla	nas, nasal
bb, basibranchial	no, notochord
bhyl, basihyal	nsp, neural spine
brstg, branchiostegal ray	op, opercular
cbr, ceratobranchial	pa, parietal
chyl, ceratohyal	pal, autopalatine
cl, cleithrum	pal-quad, palatoquadrate cartilage
co, coracoid	pasph, parasphenoid
dbb, dermal basibranchial	phbr, pharyngobranchial
dbhyl, basihyal toothplate	phyp, parhypural
dn, dentary	pmx, premaxilla
dpal, dermopalatine	pmxp, postmaxillary process of premaxilla
dphbr, upper pharyngeal toothplate	pop, preopercular
dsph, dermosphenotic	pt, posttemporal
ebr, epibranchial	pter, pterotic
ect, ectopterygoid	quad, quadrate
end, endopterygoid	rcart, rostral cartilage
ep, epural	ret, retroarticular
eth, ethmoid block	scl, supracleithrum
fr, frontal	smx, supramaxilla
hb, hyoid bar	soc, supraoccipital
hbr, hypobranchial	sop, subopercular
hhyl, hypohyal	sph, autosphenotic
hsp, hemal spine	sym, symplectic
hyo, hyomandibular	un, uroneural
hyp, hypural	up, uncinat process
ihyl, interhyal	vo, vomer
iop, interopercular	

ANATOMY AND RELATIONSHIPS OF THE MACRISTIIDS

Various osteological features directly support the hypothesis that the "Chain" specimen is a larval neoteleostean fish. These features concern the structure and support of the upper jaw, the form of the hyoid and branchiostegal apparatus, and the organization of the epibranchials and

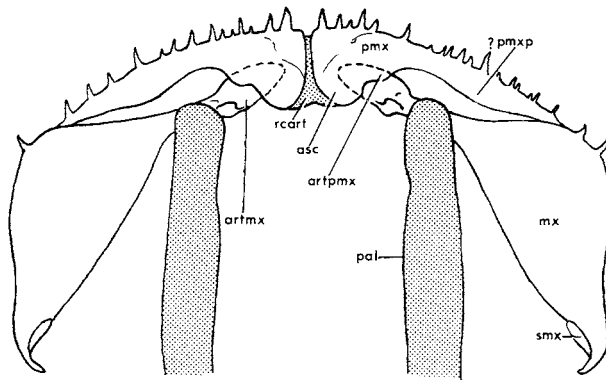


FIG. 4. Dorsal view of the upper jaw of the "Chain" larva. Stippled areas represent cartilage.

pharyngobranchials. The upper jaw (figs. 4, 5) shows the presence of an incipient premaxillary ascending process that overlies and is adherent to a rostral cartilage, an incipient premaxillary articular process, and a slight elevation midway along the alveolar arm of the premaxillary that may be an incipient postmaxillary process. The head of the maxilla is differentiated and bears a long tongue-like process that is seated under

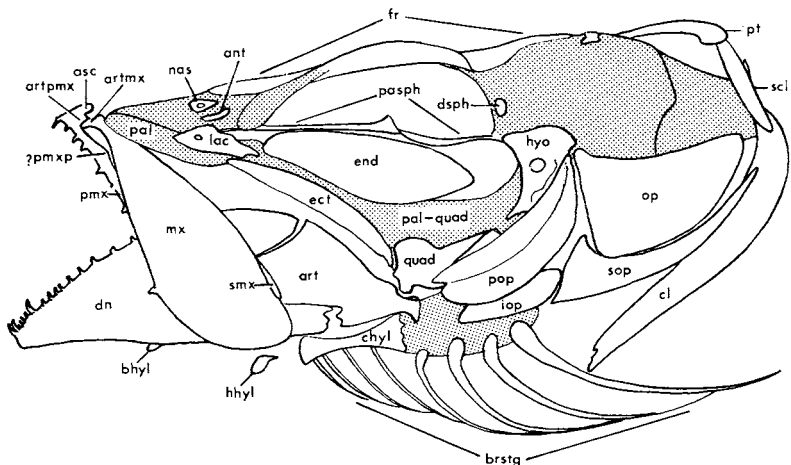


FIG. 5. Lateral view of the syncranium of the "Chain" larva. Stippled areas represent cartilage.

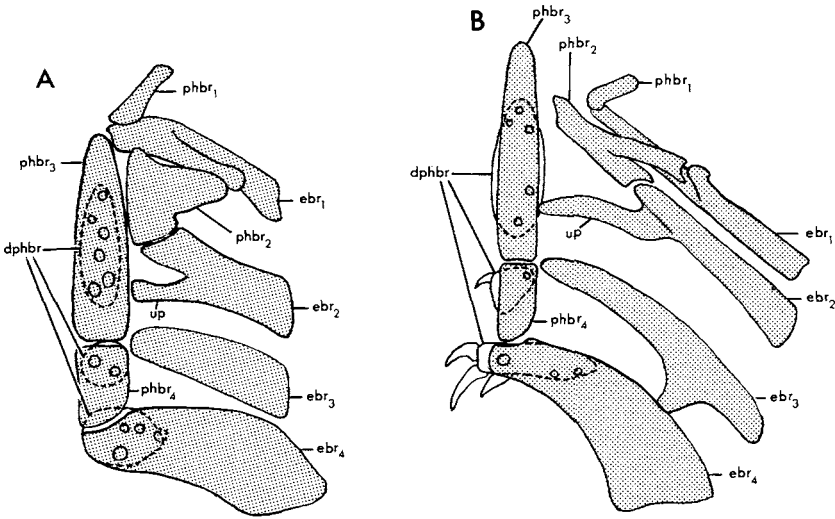


FIG. 6. Epibranchial and pharyngobranchial elements. A. "Chain" larva. B. Chlorophthalmid larva. All elements, except for the toothplates, which are seen through the epibranchials and pharyngobranchials, cartilaginous.

the premaxillary articular, and the lateral part of the premaxillary ascending, processes. The autopalatine is large and overlaps the maxilla subdistally in such a way that the maxilla can rotate forward and back on this palatine hinge. All of these features are characteristic of the neoteleostean upper jaw as defined by Rosen and Patterson (1969, pp. 458-459). The hyoid and branchiostegal apparatus, although incompletely ossified, shows distinct similarities to an advanced neoteleostean pattern, in which the four, hairlike anterior branchiostegals are attached to the inner surface of the slender anterior part of the hyoid bar (the anterior ceratohyal) and the larger, bladelike posterior branchiostegals are attached to the outer surface of the expanded posterior part of the bar (the posterior ceratohyal). This specialized condition of the hyoid apparatus was discussed by Hubbs (1919) and illustrated and further documented by McAllister (1968). The final decisively neoteleostean feature present in the "Chain" specimen involves the epibranchials and pharyngobranchials (fig. 6A). The neoteleostean pattern includes an enlarged third pharyngobranchial which, in growing forward, laterally displaces the much smaller first and second pharyngobranchials. In some neoteleosteans the third pharyngobranchial is not only the largest element but also the most anterior in extent. Correlated with the lateral

displacement of the first and second pharyngobranchials in scopelomorphs is the development along the posterior edge of the second epi-branchial of a greatly elongate accessory arm (uncinate process, of Harrington, 1955) by means of which the second epibranchial maintains its secondary articulation with the third pharyngobranchial. These neoteleostean patterns, Nelson (1969, p. 528), differ from the several more primitive teleostean patterns in which the pharyngobranchials are arranged in an anteroposteriorly graded series, in which the epi-branchials articulate only with their respective pharyngobranchials, or in which the accessory arms for secondary articulations are always short and feebly developed. Although there are a number of other distinctive teleostean patterns, none becomes specialized in exactly the neoteleostean manner as described above (see Nelson, 1967, figs. 1-5, 8; 1968a, fig. 6; 1968b, figs. 2-6, 8-10; 1969, plate 82, figs. 3-5). The upper pharyngeal dentition, which constitutes the only ossified material in this region of the gill arches in the "Chain" specimen, also conforms to a generalized neoteleostean pattern, as defined by Nelson (1969); in this arrangement a principal toothplate is on the enlarged third pharyngobranchial, a small toothplate occurs on the anterior part of the fourth pharyngobranchial, and a fairly large, somewhat ovoid toothplate oriented at a right angle to the plane of the other two overlaps the posterior edge of the fourth pharyngobranchial and extends laterally onto the fourth epibranchial. Among neoteleosteans, this latter toothplate is so far known to be confined to the Scopelomorpha (Nelson, 1969, p. 490).

Another striking attribute of the hyobranchial apparatus in the "Chain" specimen is the development of a row of recurved, conical, and somewhat fanglike teeth along the forward edge of the dermal basihyal (fig. 7). Marshall (1961) noted that in the "Discovery" specimen the "spatulate tongue is armed with a transverse row of 3 pointed, retrorse teeth, which emerge fairly close to the anterior border of this organ," and Regan (1911) noted the presence on the basihyal of his *Macristium chavesi* of small, acutely pointed teeth. Regarding the only other specimen assigned to the Macristiidae, *Macristiella perlucens*, an apparently larval form of 28.5 mm. in standard length, Berry and Robins (1967) commented that the basihyal was equipped with "one median tooth and two lateral teeth on each side in a transverse row." Their drawing of these teeth (their fig. 3) shows six in a transverse row, approximately as in the "Chain" specimen. These observations naturally raise the question as to what form and distribution basihyal teeth might take in other fishes. Such an arrangement of basihyal teeth, however, is thus far un-

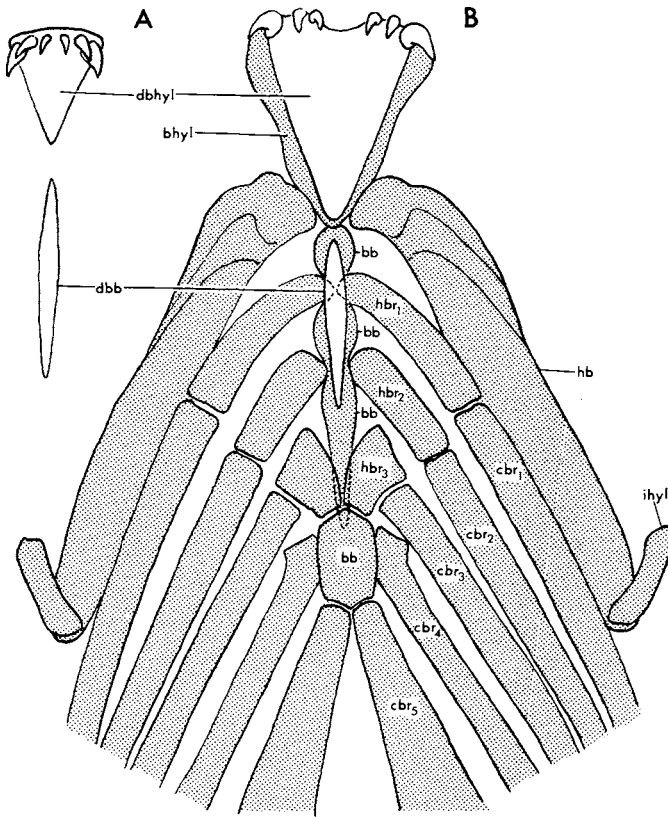


FIG. 7. Hyobranchial elements. A. Ossified basihyal toothplate and dermal basi-branchial in the "Chain" larva. B. Cartilaginous ventral hyobranchial elements and ossified basihyal toothplate and dermal basi-branchial in a chlorophthalmid larva.

known in any adult fish, teleostean or otherwise (see Nelson, 1969). The only known approximation of this pattern is in the argentinid, *Glossanodon* (Cohen, 1964), but in the argentinids, these basihyal teeth form on a dermal basihyal of generally greatly elongate and otherwise distinctive shape (Nelson, 1970).

Proceeding with the now reasonable inference that the "Chain" specimen is a larval neoteleostean of some sort, and with the hypotheses that it may be a scopelomorph and that its distinctive basihyal dentition may be characteristic of larval scopelomorphs, the "Chain" specimen was compared with a small juvenile or larval chlorophthalmid also of 20 mm.

standard length (fig. 8). The results of this comparison are summarized in the accompanying series of figures (figs. 4-7, 9-11). Among the many congruences between the "Chain" specimen and the larval chlorophthalmid is the notable similarity in the form of the basibranchial, basihyal, and basihyal dentition, the principal difference in this dentition being the separation in the chlorophthalmid of the transverse row of six teeth into two series of three teeth on each side of a shallow notch (fig. 7B). The over-all similarities between the two specimens are listed in table 2. There are a number of reasons, however, why the "Chain" specimen

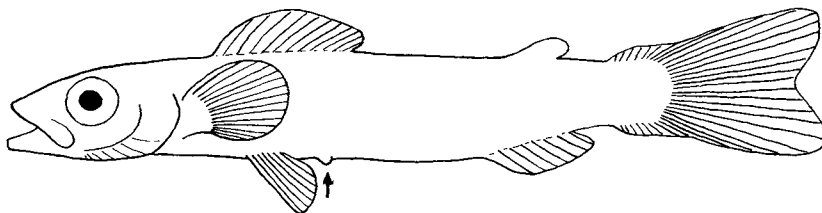


FIG. 8. Larval chlorophthalmid of 20 mm. in standard length from the Straits of Messina (A.M.N.H. No. 14241). Provisionally identified as *Chlorophthalmus agassizi* Bonaparte. Semidiagrammatic. Arrow indicates vent.

is not a chlorophthalmid, the chief reasons being the height of the fins and the number of fin rays, the length of the skull roof and the form of the ethmoid region, the number of myotomes, and the position of the anus (see figs. 1, 8, 9, and table 1).

The morphological evidence, which supports the hypothesis that the "Chain" specimen is a scopelomorph of some sort, seems also to exclude the possibility that the larva may be a paracanthopterygian or acanthopterygian. This specimen seems to be certainly excluded from the Paracanthopterygii on the grounds that its caudal skeleton has three epurals, rather than two, and that the last full neural spine is in the position of the third, rather than the second, preural centrum. The latter point may be deduced from the fact that the last hemal spine before the parhypural is directly under a neural arch with no spine and that that hemal spine is invariably on the second preural centrum in all known fully formed teleostean caudal skeletons. The "Chain" specimen also lacks the levator maxillae superioris muscle characteristic of the paracanthopterygian upper jaw, but that lack could sensibly be interpreted as a larval feature. The structure of the caudal skeleton seems not to allow that latitude of argument, especially since one of the three epurals lies

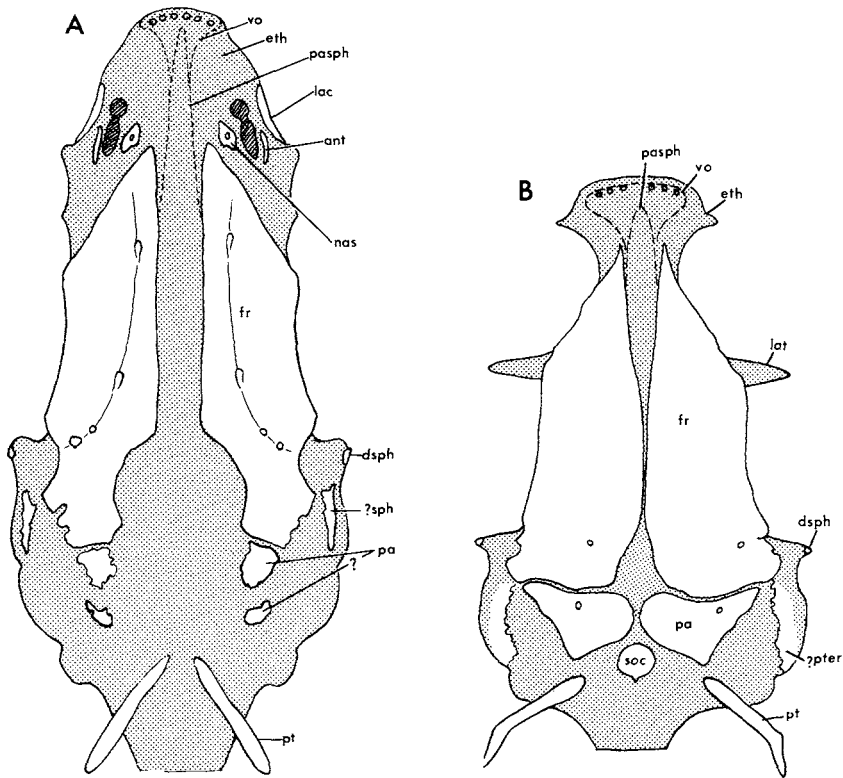


FIG. 9. Dorsicrania. A. "Chain" larva. B. Chlorophthalmid larva. Stippled areas represent cartilage. Anterior part of parasphenoid and vomer shown underneath ethmoid cartilage.

directly over the arch of the presumptive second preural centrum. The probable exclusion of the "Chain" specimen from the Acanthopterygii is predicated on the observation that none of the more primitive acanthopterygians combines the adipose fin and high vertebral number present in this larva. Among neoteleosteans, the adipose fin is restricted to the Scopelomorpha and Paracanthopterygii.

The presence of a few maxillary teeth in the "Chain" specimen may be noted as an argument for excluding this fish from the Scopelomorpha, since no living adult scopelomorph has such teeth. Berry (1964) has shown, however, that in the genus *Scopelosaurus* maxillary teeth are initially present, from a body size of 10 to 23 mm. in standard length, and that these teeth are lost when the animal reaches a 29 mm. stage.

The loss of maxillary teeth corresponds to the increase in length and complexity of the developing premaxillary bone.

There is, thus, no reason that the writer can advance for excluding the "Chain" specimen (fig. 1) from the Scopelomorpha, and one may infer, therefore, that the "Discovery" specimen (fig. 2) described by Marshall (1961) is also a scopelomorph. The fin and body proportions of Regan's *Macristium chavesi* (fig. 3) indicate similar affinities, as do the fins and basihyal teeth of Berry and Robins's *Macristiella perlucens* (fig. 12).

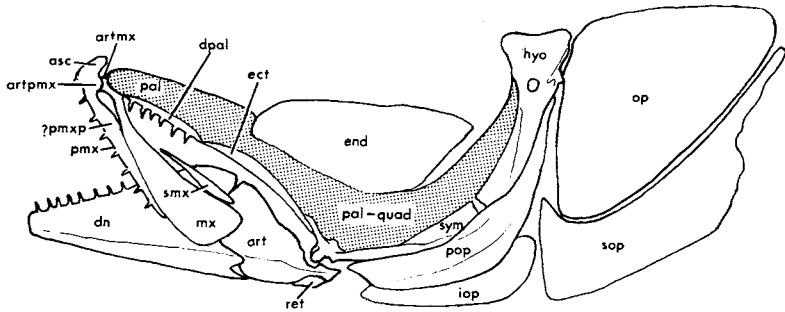


FIG. 10. Jaws, jaw suspension, and opercular apparatus in chlorophthalmid larva. Stippled areas represent cartilage. Compare with figure 5.

If all of the macristiids are, in fact, larval or juvenile scopelomorphs, to which groups of the Scopelomorpha might they belong? Before attempting to answer this question the distinct possibility must be recognized that the three presently known "Macristium"-like animals each represent a different species, so that the "macristiids" may include four species of two basic types: those with 8 to 10 branchiostegals, elongate dorsal, anal, pectoral, and pelvic fins, 60 to 62 vertebrae, and the vent near the anal fin (the "Macristium" type), and those with 16 branchiostegals, elongate pectoral and pelvic fins, 69 vertebrae, and the vent near the pelvic fins (the "Macristiella" type). Furthermore, an exact answer to the question of the taxonomic allocation of these larval and juvenile forms must depend ultimately on an exact knowledge of the early life history of representatives of each of the main groups of scopelomorphs. Clearly, then, exactness of taxonomic allocation is not now possible, and one must be content with a series of approximations. For reasons of extreme specialization, fin arrangement, or low fin ray counts, a number of scopelomorph families may be ruled out as having pertinence to the question at hand, and these families are: Paralepididae, Mycto-

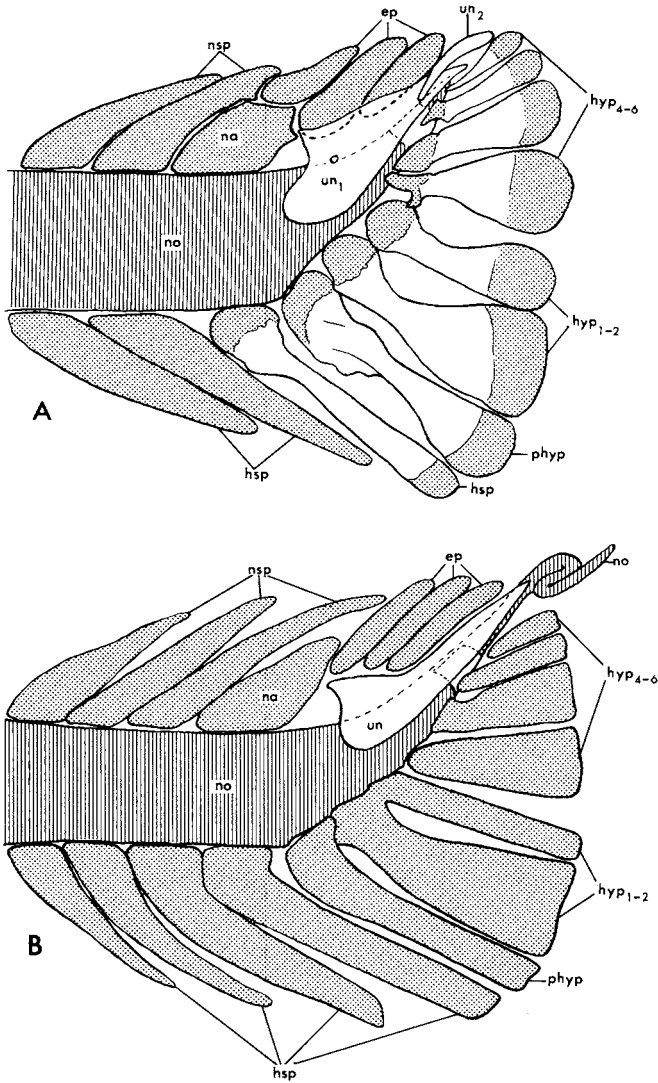


FIG. 11. Caudal skeletons. A. "Chain" larva. B. Chlorophthalmid larva. Hatched area represents notochord, stippled areas cartilage.

phidae, Omosudidae, Evermannellidae, Alepisauridae, Anotopteridae, and Scopelarchidae. The remaining nine scopelomorph groups are compared, in table 1, with the four "macristiid" individuals. In this

comparison, the first three "*Macristium*" types, in fin ray counts, number of body segments, number of branchiostegals and supramaxillae, position of the anus, and development of an adipose fin, most closely match the Bathysauridae. Bathysaurids also are noted for their enlarged dorsal, anal, pectoral, and pelvic fins which, at least in *Bathysaurus mollis*, are known to be relatively longer in the smaller specimens (see Günther, 1887, pl. 46, figs. B, B'). In addition, bathysaurids grow to be as long as 2 feet, so that even Regan's 110 mm. specimen from the Azores would be an extremely small juvenile, if a bathysaurid. The "Chain" specimen has a single extremely small and delicate supramaxilla on each jaw and this bone is not known to occur in the other "*Macristium*," or in bathysaurids, but the supramaxillae are greatly reduced in most scopelomorphs and are present or absent within some groups, and little, if anything, is known of the osteology of the Bathysauridae. The over-all similarity of the three "*Macristium*" to the bathysaurids is great, and it was with this group that Regan (1903) had first compared his specimen from the Azores. The "*Macristiella*" type of larva (fig. 12). on the other hand, is a very different kind of fish, most closely approximating the Ipnopidae in the tabulated characters, and differing substantially from the ipnopids only in having an adipose fin. The adipose of "*Macristiella*," however, is not a clearly differentiated structure as in the "Chain" specimen, but is part of a hyaline dorsal fold that extends between the dorsal fin terminus and the upper caudal fin base, as in the "Discovery" specimen. The "*Macristiella*" larva also has in common with most ipnopids relatively large pectoral and pelvic fins and a relatively small eye (*cf.* the eye in the "Chain" and "Discovery" specimens which are large enough to enter the dorsal profile as in bathysaurids).

Although other scopelomorph groups include species with one or more of the "macristiid" features, for example, the enlarged fins in harpaxodontids, bathypteroids, and aulopids (fig. 13), there is a poor match of at least one, and usually more than one, of the other characters. Moreover, synodontid, myctophid, and, to a lesser extent, chlorophthalmid and paralepidid, larvae are known and the known larvae differ significantly from the "macristiid" specimens. Provisionally, then, the "macristiids" may be regarded as scopelomorph larvae and juveniles belonging or related to the Bathysauridae and Ipnopidae.

CLASSIFICATION OF THE CTENOTHRISOID FISHES

With the allocation of the "Macristiidae" provisionally resolved, the relationships of the Cretaceous Ctenothrissoidei, now coextensive with the order Ctenothrissiformes, may be examined. The relevance of the

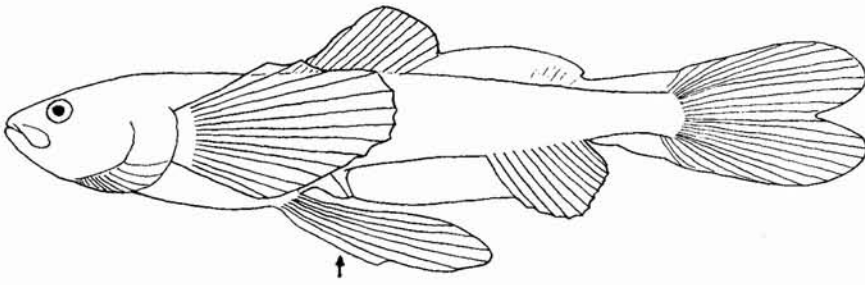


FIG. 12. *Macristiella perlucens* Berry and Robins, a larval fish of 28.5 mm. standard length. After Berry and Robins (1967), simplified. Arrow indicates vent.

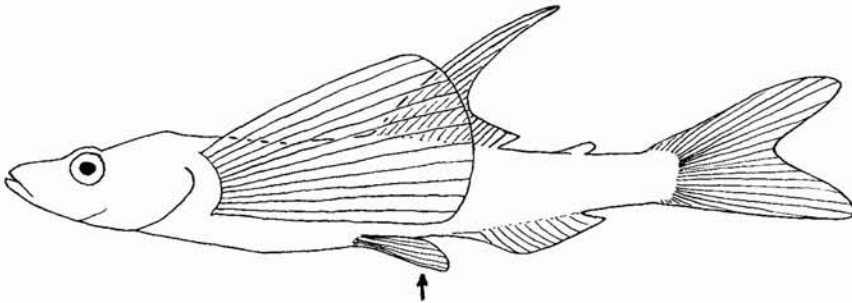


FIG. 13. Larva of *Aulopus filamentosus* Cloquet, of approximately 35 mm. in standard length. After Sanzo (1915), simplified. Arrow indicates vent.

ctenothrissoids to the Acanthopterygii has been extensively documented (Patterson, 1964, 1967, 1968) and commented on by Rosen and Patterson (1969), as follows: "The ctenothrissoids resemble the acanthopterygians in the absence of an adipose fin, the structure of the upper jaw, which is not unlike that of some Cretaceous berycoids. . . , the perforate ceratohyal (imperforate in all myctophoids), the subthoracic or thoracic pelvics, and the presence of procurrent caudal spines (as in all berycoids, but among myctophoids only in the Myctophidae). For these reasons we feel inclined to reject the hypothesis that ctenothrissoids are merely myctophoids, and place them on the acanthopterygian side of the divergence from the common ancestor of myctophoids and acanthopterygians. This conclusion may be modified if Marshall (1961) was correct in relating the living *Macristium* (Macristiidae) to the ctenothrissoids, and if Berry and Robins (1967) were right in placing their new genus *Macristiella* in the Macristiidae, for this fish . . . has an adipose

fin and has 16 branchiostegals, many more than *Macristium* (10) and ctenothrissoids (nine). . . . No conclusions on the macristiids can be drawn until adult specimens are available." Well, adult specimens probably are available, but in the unexpected guise of scopelomorphs such as the bathysaurids and ipnopids or related forms. It is now possible, therefore, to adopt the hypothesis that ctenothrissoids are acanthopterygians. The similarity of the ctenothrissoids (including the Ctenothrissidae and Aulolepididae) to the Cretaceous trachichthyid berycoids of the genus *Gnathoberyx* (Patterson, 1967) in body and fin form, and particularly in the structure of the upper jaw, suggests that they may be most closely related to these beryciforms. Patterson (1964) also reported the presence in *Ctenothrissa* of a narrow subocular shelf on the infraorbital bones, and regarding this shelf commented (1967) that the presence of a similar shelf in the Cretaceous beryciforms on the first and anterior part of the second infraorbitals "is powerful additional evidence for close relationship between the Ctenothrissiformes and the ancestral Beryciformes." The relatively more primitive skull roof of ctenothrissoids, in which no distinct supratemporal fossa is present [although the presence of a decided supratemporal ridge (Patterson, 1964, figs. 2, 3, 5) retrospectively seems to have forecast the development of such a fossa], and the very small premaxilla of some species, would identify the ctenothrissoids as the most primitive and generalized true acanthopterygians known.

Regarding the phylogenetic integrity of the Ctenothrissoidei, Rosen, and Patterson (1969) noted that "There seem to be no specialized features common to the three known genera of ctenothrissoids [*Ctenothrissa*, *Aulolepis*, *Pateroperca*] which will enable one to characterize them as a monophyletic group, whereas the differences between *Aulolepis* and *Ctenothrissa*, both well-known genera, coupled with the different type of caudal skeleton in the poorly known *Pateroperca*, suggest considerable diversity in the group." Moreover, Goody (1969) described an additional ctenothrissoid, *Pattersonichthys delicata*, that differs from all others known in the skull roof, the upper jaw, and fin size and shape, and that is without clearly defined relationships to the Ctenothrissidae or Aulolepididae. In these uncertain circumstances, any attempt to classify the ctenothrissoids without first establishing their possible relationships to one another and to the beryciforms would be a futile exercise. Finally, the composition of the Beryciformes, which was questioned by Patterson (1964, pp. 459-460) and considerably reorganized with additions and subtractions by Rosen and Patterson (1969), must itself be firmly resolved before much progress can be made in ctenothrissoid classification. The

TABLE 2
ANATOMICAL CONGRUENCES BETWEEN THE "CHAIN" "MACRISTIID" LARVA
AND A CHLOROPHTHALMID LARVA

	"Chain" Larva	Chlorophthalmid Larva
Fins		
Dorsal	Originating over pectoral base	Originating just behind pectoral base
Adipose	Present	Present
Pectoral	High on side	Same
Pelvic	Thoracic	Subthoracic
Skull		
Suboperculum	Forming most of gill cover margin	Forming almost entire gill cover margin
Parietals	Present	Present
Vomer	With transverse row of six teeth	With transverse row of six teeth divided into two rows of three each
Endopterygoid	Extensive, filling floor of orbit	Same
Premaxillary	With definite ascending and articular processes	Same
Maxillary	Expanded proximally, oblanceolate; with one small, sliver-like supra-maxillary	Expanded proximally, with squarish proximal end; with one elongate and posteriorly slightly expanded supramaxillary
Hyoid apparatus	4 slender branchiostegals on inner surface of anterior part of hyoid bar, 4 bladelike branchiostegals on outer surface of posterior part of hyoid bar	Same
Gill basket	A triangular basihyal with 6 teeth in transverse row distally; a single slender dermal basibranchial; epibranchials and pharyngobranchials and upper pharyngeal teeth of neoteleostean type (see text)	A triangular basihyal slightly indented anteriorly with a transverse row of 6 teeth divided into two series; a single slender dermal basibranchial; epibranchials and pharyngobranchials and upper pharyngeal teeth of neoteleostean type (see text)
Caudal skeleton		
Hypurals	Two lower and four upper	Same
Epurals	Three in number, the first lying over the arch of the second preural centrum	Three in number, all lying posterior to the arch of the second preural centrum
Uroneurals	A large expanded uroneural lying under last two epurals; with a small, slender, posterior element	A large expanded uroneural lying under all three epurals; no second uroneural
Preural elements	A spineless neural arch in position of second preural centrum; first full arch and spine in position of third preural centrum (see text)	Same

only taxonomic action that seems possible at this time is to recommend the transfer of the Ctenothrissiformes from the Protacanthopterygii to the Acanthopterygii adjoining the Beryciformes.

SUMMARY

A new *Macristium*-like larval fish is compared with published accounts of specimens previously assigned to the Macristiidae and with known myctophoid larvae. It is concluded that the new *Macristium*-like larva and all of the macristiids are myctophoids, and it is hypothesized that together they represent larval and juvenile bathysaurids and ipnopids or forms closely related to these families. The implications of that conclusion for ctenothrissiform classification are discussed.

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