

THE CERATIOID FISHES OF THE GENUS *THAUMATICHTHYS*

OSTEOLOGY, RELATIONSHIPS, DISTRIBUTION AND BIOLOGY

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ABSTRACT

On the basis of a total of 26 specimens of the genus *Thaumatichthys*, ranging from larvae to adults, a general description of the genus is presented, including the osteology, dentition, jaw mechanism and illicium and esca structures of the females and a description of the previously unknown male. The genera *Amacrodon* Regan & Trewavas and *Galathea-thauma* Bruun are synonymized with *Thaumatichthys* Smith & Radcliffe and it is concluded that the

known specimens of this genus represent three species: *T. pagidostomus* Smith & Radcliffe, *T. binghami* Parr, and *T. axeli* (Bruun).

The relationships of *Thaumatichthys* to other genera of Ceratioidei is discussed mainly on basis of a comparative study of a representative of the genus *Lasiognathus* Regan. Diagnosis of the family and keys to its genera and the species of *Thaumatichthys* are provided.

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I. INTRODUCTION

In a bottom haul with a herring otter trawl at 3570 m depth in the east Pacific, the Galathea Expedition caught a fish which the leader of the expedition, Dr. Anton F. Bruun, in the popular report on the cruise (Bruun 1953, 1956) declared "unquestionably the strangest catch of the Galathea Expedition, and

altogether one of the oddest creatures in the teeming variety of the fish world" (cf. Pl. 1). Besides data on the catch, he provided a painting of the nearly 450 mm long fish, gave a short general description of the specimen, and named it *Galathea-thauma axeli*, a new genus and species of deep-sea angler fishes

(Ceratioidea). Bruun made preparations for a scientific publication to replace this preliminary note but, due to his untimely death in 1961, it was not finished.

Bruun was aware that the most outstanding character of this fish, the position of the light organ (esca) in the roof of the mouth instead of on top of the head and the extreme development of the upper jaw and its teeth, was not quite unique among ceratioids. He wrote (Bruun 1956) "We found that a small specimen, eight centimetres long, of a similar type, had been taken by an American expedition in 1908, in Indonesia in 1385 metres of water ..." This first representative of this kind of ceratioid was described by Smith and Radcliffe (1912). It was a most curious fish which they rightly named "the trap-mouthed wonderfish": *Thaumatichthys pagidostomus*. Having the first dorsal fin ray transformed into a lure and lacking pelvic fins, it could be referred to the pediculate fishes of the suborder Ceratioidei. However, in several features it differed to such an extent from the then known species that they placed it in a separate new family, the Thaumatichthyidae. Among other things it was distinguished by the greatly expanded and depressed head, with enormously developed movable premaxillaries which carried long hooked teeth and were anteriorly widely separated, only connected by membranous skin. Furthermore, the bulb of illicium projected from the underside of this membrane just inside the mouth.

The next specimen referred to *Thaumatichthys* was described by Parr (1927). It was caught in a midwater trawl fished with 8000 feet of wire in the western North Atlantic. The specimen differed from the type of *T. pagidostomus* in size (39 versus 59 mm s.l. (standard length)), in development of eyes and teeth, and, according to the description, in number of dorsal fin rays. It was made the type of a new species *T. binghami* Parr, 1927. Regan and Trewavas (1932) placed this species in a separate new genus, *Amacrodon*, solely based on the absence of the pair of very long hooked premaxillary teeth found in the type of *T. pagidostomus*. Parr (1934) accepted this separation when, without description, he reported a second specimen of "*Amacrodon binghami*" caught in the same area as the type specimen.

Bertelsen (1951) tentatively referred to *Thaumatichthys pagidostomus* four larval specimens (4.4 to 24 mm in total length) from the Dana Expeditions, on basis of osteological characters and number of dorsal fin rays.

Finally, Brewer (1973) reported, from off the

Pacific coast of Mexico, a catch of a specimen, 22 mm s.l., which he referred to *T. pagidostomus*.

Including the *Galathea* specimen, the total number of hitherto recorded specimens of this group is thus nine, assigned to three species and genera.

When, after Anton Bruun's death, the senior author of this paper (E.B.) took over the study of the *Galathea* specimen, and had the opportunity to compare it with the recorded specimens of *Thaumatichthys* and *Amacrodon*, it became evident that the differences on which the separation in genera were based could be ascribed to differences in age and that they, consequently, all should be referred to *Thaumatichthys* Smith & Radcliffe, 1912. Study of a new specimen obtained by the other author (P.S.) confirmed this, but added to the difficulties in separating the species. More material was needed to be able to judge ontogenetic and individual variation, and partly for this reason publication was postponed. Meanwhile, increased effort in deep-sea research in recent years has resulted in the collection of a considerable number of specimens of this genus, which have kindly been made available for this study.

Including the previously known 9 specimens, the study material consists of 26 specimens, representing stages from larvae of 3 mm s.l. to adults of about 365 mm s.l. Most of the specimens are females. Besides three larval males described by Bertelsen (1951), only a single adolescent male has been obtained. After the study was completed information on 6 additional females was received. Of this total of 32 specimens, 25 were caught in the Caribbean and adjacent Atlantic waters, and only 5, including the type of *T. pagidostomus*, the *Galathea* specimen, and 2 larvae, are from the Indo-Pacific. From this material we have concluded that three species comprise the genus *Thaumatichthys*: *T. pagidostomus*, *T. binghami*, and *T. axeli*.

Acknowledgments

We are most grateful to the following persons and institutions for loans and gifts of specimens:

Richard C. Robins and John C. Staiger, University of Miami, Marine Laboratory (UMML); Harvey R. Bullis, National Marine Fisheries Service, Pascagola (specimens now in USNM); Richard H. Rosenblatt and Carl L. Hubbs, Scripps Institution of Oceanography (SIO); Robert J. Lavenberg,

Natural History Museum of Los Angeles County (LACM); Cara Cashman, Department of Oceanography, Texas University; and G.E. Maul, Museu Municipal do Funchal, Madeira. Many thanks are due to colleagues at the U.S. National Museum, Bingham Oceanographical Collection and University

of Miami, Marine Laboratory for hospitality and assistance during visits to these institutions. For helpful discussions we are indebted to Theodore W. Pietsch, Museum of Comparative Zoology, Harvard University, and Jørgen Nielsen, Zoological Museum, University of Copenhagen.

II. GENERAL DESCRIPTION OF THE GENUS *THAUMATICHTHYS*

A. FEMALES

The most characteristic external features of metamorphosed female *Thaumatichtys* are 1) the broad and depressed head and anterior part of body; 2) the development of the premaxillaries which carry long hooked teeth and are extended far beyond the short lower jaw; furthermore, they are anteriorly widely separated from each other, and are hinged to the skull in such a way that they can be turned up and down; 3) the position of illicium which emerges anteriorly in the roof of the mouth from the ventral side of the membrane which connects the premaxillaries; 4) the presence of a denticle on esca; 5) the position of the tiny eyes close to the corner of the mouth. In shape of head and position of illicium and eyes, *Thaumatichtys* differs from all other ceratioids, and only *Lasiognathus* has similarly developed premaxillaries and denticles on the esca.

The posterior part of the body is somewhat more slender than in most other female ceratioids, and the dorsal fin is relatively well developed. The skin is black or dark brown and carries on the lower part of the head and body numerous small spines.

In the following account those features which may be relevant to the understanding of the relationships, ontogeny, and biology of the members of this genus will be described in more detail.

1. Osteology

The following description is based (A) on an alizarin stained juvenile female of *T. binghami* ZMUC P921948 69.9 mm s.l. Comparative observations (B) were made on the adult holotype of *T. axeli*, 365 mm s.l. which is nearly completely skinned. On some of the other specimens, including the types of *T. pagidostomus* and *T. binghami*, observations were made on X-ray photographs and on superficial bones, either through the skin or through incisions in this.

Finally, comparisons were made with the alizarin stained larval male described by Bertelsen (1951). Except for ontogenetic differences, the skeletons of the examined specimens were extremely alike in nearly all details.

Cranium (Fig. 1). A. The skull is short and very flat. In percent of its length, from anterior margin of vomer to posterior margin of epiotics, the greatest depth is hardly 20, greatest width at sphenotics and pterotics 75, width of vomer 58 and smallest interorbital width 28. The ethmoid cartilage is a triangular solid plate, covering the anterior part of the parasphenoid and the broad vomer, and dorsally bordered and partly covered by the slender anterior parts of the frontals and the lateral ethmoids. Anteriorly it forms in each side semi-spherical swellings which protrude between the lateral wings of vomer and the expanded heads of the lateral ethmoids, and articulate laterally with the palatines and maxillaries, and anteriorly with the prolonged articular process of the premaxillaries (cf. Figs 2 and 17). No symphyseal cartilage of the upper jaw could be observed, and no supraethmoid ossification (= the mesethmoid of Regan & Trewavas 1932, Bertelsen 1951, and others - cf. Pietsch 1972) is developed.

Each of the lateral ethmoids consists of a broad cup-shaped head which is rigidly attached to the ethmoid cartilage, and a relatively slender conical shaft which at its posterior thicker end is ankylosed ventrolaterally on the anterior part of the frontals.

The vomer is broad, about 75% of the greatest width of the skull. Its anterior margin is medially concave, and its ventral surface is smooth and toothless.

The frontals are widely separated and anteriorly narrowly pointed without a notch at the base of the lateral ethmoids. The parietals are small, triangular or nearly drop-shaped, with the posterior end drawn out into a slender point and overlapping the

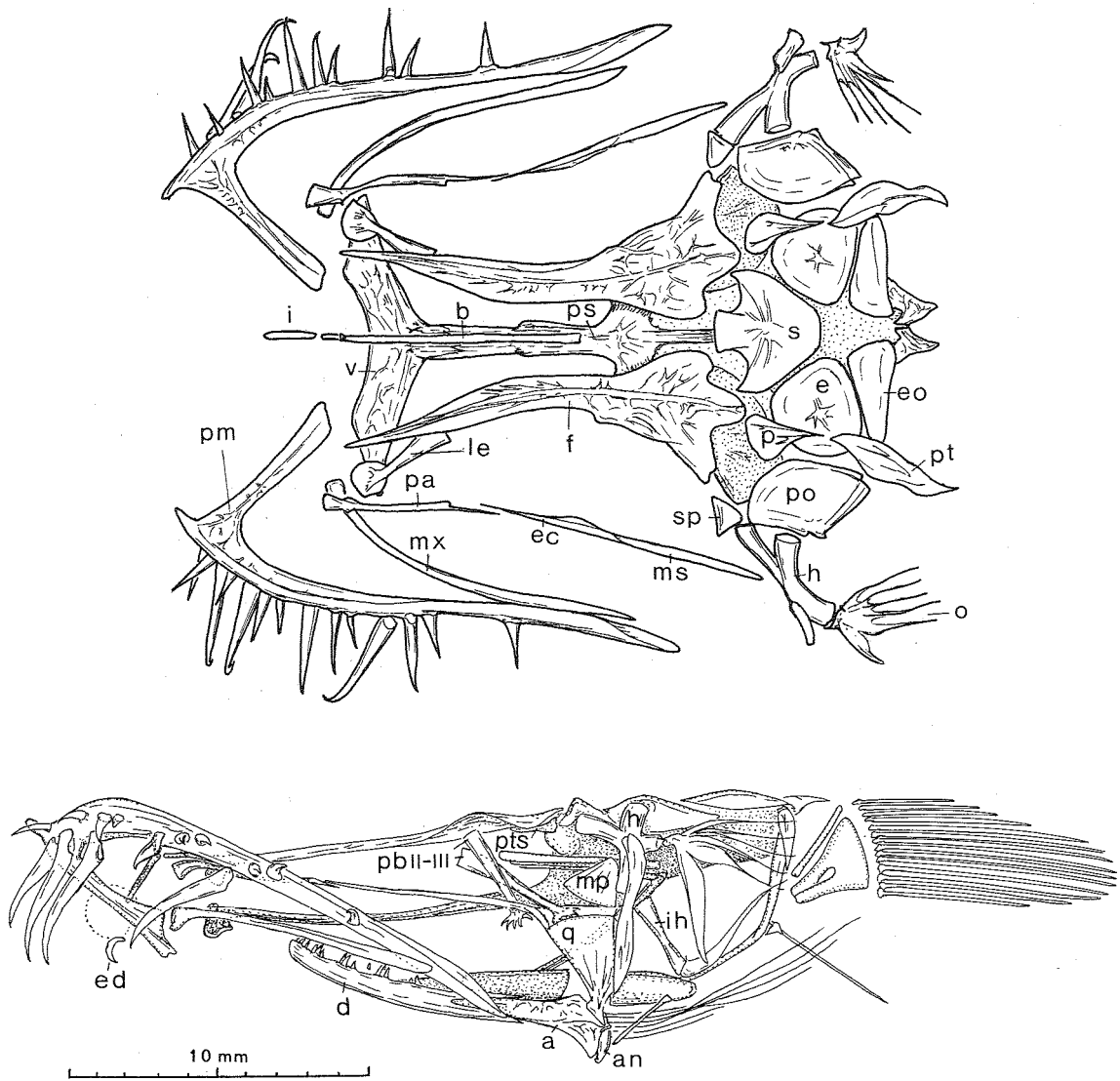


Fig. 1. Skeleton of head of *Thaumataichthys binghami* 69.9 mm (ZMUC P 921948) in dorsal and lateral view. (a: articular, an: angular, b: pterygiophore of illicium, d: dentary, e: epiotic, ec: ectopterygoid, ed: denticle of esca, eo: exoccipital, f: frontal, h: hyomandibular, i: illicium, ih: interhyal, le: lateralethmoid, mp: metapterygoid, ms: mesopterygoid, mx: maxillary, o: operculum, p: parietal, pa: palatine, pb II-III: pharyngobranchials, ps: parasphenoid, pm: premaxillary, po: prootic, pt: posttemporal, pts: pterosphenoid, q: quadrate, s: supraoccipital, sp: sphenotic, v: vomer).

epiotics. Small pterosphenoids are present. The conical sphenotics are very small, while the pterotics, epiotics, supraoccipital and exoccipitals are well developed. The epiotics do not meet behind the supraoccipital.

As no dissection of the specimen was made, the bones forming the floor and lower sides of the skull, prootics, exoccipitals, basioccipital, and posterior part of parasphenoid were not studied in detail.

B. As far as could be observed without staining of the 22.6 mm female larva (LACM 31107, Fig. 15), its head skeleton was quite similar to that of the 18.5 mm larval male, showing that at this stage no sexual dimorphism in the osteology had developed except for the presence of a small upward directed illicium on the snout of the female and the presence of two tiny denticlelike ossifications at the tip of the basal bone and the base of the illicium of the male (Ber-

telsen 1951). The frontal bones of the larvae are much broader than those of the metamorphosed specimens. They meet medially, carry wide lateral laminae above the well developed eyes, and are anteriorly notched at the base of the lateral ethmoids. Furthermore, the vomer of the larval male carries four well developed teeth. (Their possible presence in the unstained female larvae could not be ascertained). Like in the stained 69.9 mm specimen, no supraethmoid is developed; the sphenotics are very small, the parietals are posteriorly pointed, and each of the posttemporals has a posterior long saillike extension. The skull of the large adult specimens differs in the normal way from the larvae and juveniles in the stronger ossification of the bones which overlap or are strongly connected in irregular sutures; the epiotics meet behind the supraoccipital. In the 365 mm holotype of *T. axeli* a small supraethmoid could be observed as an almost circular bony plate medially on the large ethmoid cartilage (Fig. 2).

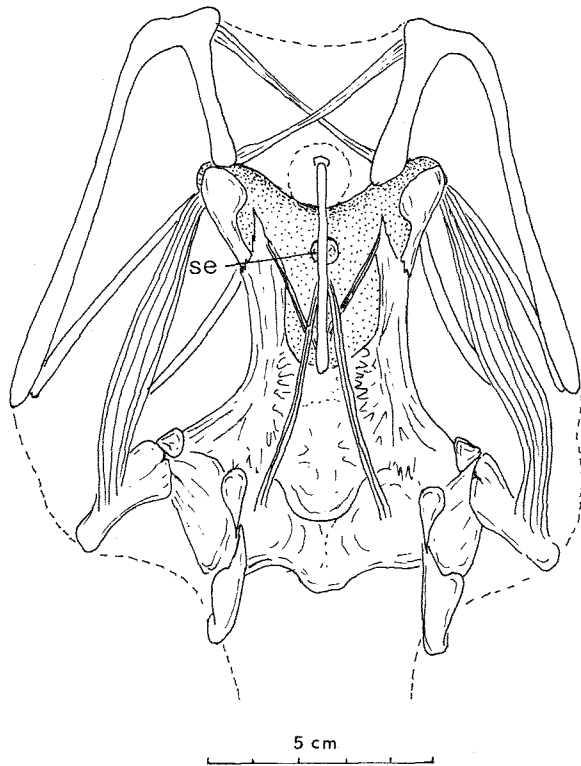


Fig. 2. Skeleton of head of *Thaumatoichthys axeli*, holotype, 365 mm. (Ethmoid cartilage dotted; se: supraethmoid).

Mandibular arch. A. The premaxillaries are very long and strongly ossified bones which are situated in a very forward position on the head. They are slightly S-curved and carry series of more or less long, hooked teeth (cf. p. 15).

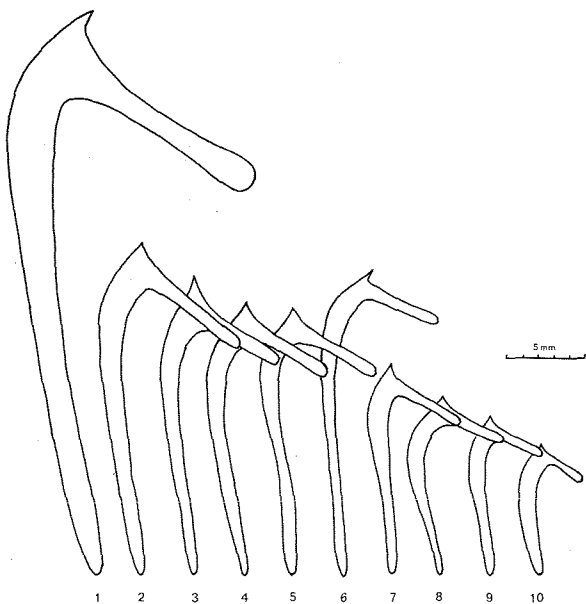


Fig. 3. Left premaxillary of *Thaumatoichthys binghami* (1,2, 4,5, and 7-10), *T. axeli* (3), and *T. pagidostomus* (6), arranged according to standard length of specimens: 1) 145.5 mm, 2) 87.1 mm, 3) 85.2 mm, 4) 73.1 mm, 5) 69.9 mm, 6) 60.0 mm, 7) 57.2 mm, 8) 51.5 mm, 9) 45.0 mm, 10) 40.0 mm.

Each has at the anterior end a short, slightly upturned spine representing the ascending process, and behind this an extremely long, mediocaudally directed, articular process. The heads of the premaxillaries and their processes are widely separated. They lack a symphyseal cartilage and are connected only by membranous tissue, and more indirectly by a pair of elastic bands connecting each ascending process with the anterior end of the maxillary and palatine of the opposite side (Figs 2 and 17). For further details on the premaxillaries, cf. the section on jaw mechanism (p. 29).

The maxillaries are thin, slender bones, each with a small, nearly undivided head attached by ligaments to the head of the palatine and the proximal end of the elastic band mentioned above.

In ventral view the lower jaw forms a nearly exact half-circle. In lateral view its length is only about half of the total length between the angular spine and the tip of the premaxillary. The dentaries are relatively weakly developed and lack a symphyseal spine. As in the premaxillaries, the teeth are arranged in regular series (cf. p. 18). A labial cartilage (cf. Pietsch 1972) is present posteriorly,

connecting the dentary with the premaxillary and maxillary. The articular carries a very small spine behind the articulation with the quadrate.

B. In the larvae the premaxillaries do not extend beyond the lower jaw, their heads meet, and each has an ascending process which is as long or longer than the articular process. The length and shape of premaxillaries were examined in a number of specimens representing all three species (Fig. 3 and App. Table 1, p. 38). In the larval stages its length is 11-15% s.l., in the 36.5 mm juvenile holotype of *T. binghami* it has increased to 18% s.l., and in all the larger (40 to 293 mm s.l.) specimens of this species it ranges from 23.4 to 26.3% s.l.

The premaxillary lengths of the two specimens of *T. axeli* fall within the upper end of this range (25.6% and 26.5% s.l.). In the holotype of *T. pagidostomus* it is distinctly longer, being 32.8% s.l. As shown in Fig. 3, it furthermore differs in shape from the others, being anteriorly more curved and

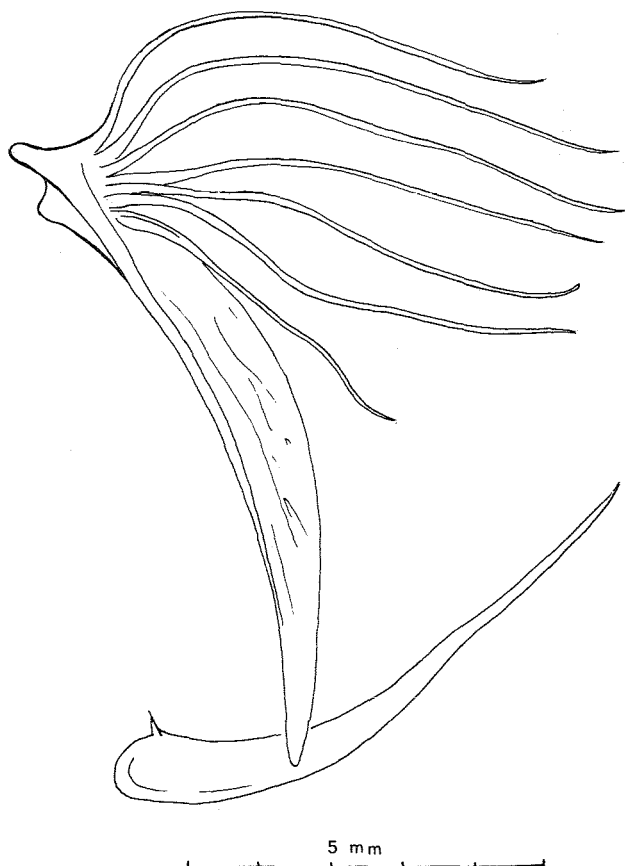


Fig. 4. Opercular bones of *Thaumatchthys binghami*, 142.5 mm (ZMUC P 921950).

having a sharper, more medial directed anterior spine. The change in number and length of teeth with increase in the size of specimens will be described in a separate section below.

Palatine arch. A. The triangular metapterygoids are well developed, while the palatines, meso- and ectopterygoids are very thin and elongated.

Hyoid arch. A. In connection with the small depth of the head and the great width between angles of the lower jaw, the hyomandibular-symplectic-quadrate arch is directed outwards, forming an acute angle with the horizontal plane.

The hyomandibular has a double head and a well developed posterior process articulating with the operculum. The symplectic is thin and slender. The interhyal and quadrate are well developed, the latter with a small oblique, ventrocaudally directed spine. Epihyals, ceratohyals, dorsal and ventral hypohyals are well developed. The ceratohyal is long and carries six branchiostegal rays, the first two well spaced medially on the bone, while the last four are closely set on its posterior, broader end.

Opercular bones (Figs 4 and 5A). A. The preoperculum is a narrow, oblong bone, closely connected with the lower arm of the hyomandibular, the symplectic, and the posterior upper part of the quadrate.

In the stained specimen the operculum is divided into six radiating branches. The lowermost branch is separated from the five upper branches by a wide notch, and has a broad, posterior, membranous flange. Similar, but smaller flanges are present at the base of the upper branches which distally taper into slender rays. The suboperculum is long, posteriorly tapering into a very slender backwardly curved tip. The anterior end is truncated and carries dorsally a tiny, anteriorly directed spine. The interoperculum is long and narrow, with a small posterior flange at its upper end.

B. The shape of operculum and suboperculum could be observed in a number of specimens. It was found that the branching of the operculum exhibited variation. The larval male (Bertelsen 1951) has a total number of nine radiating branches, of which the two behind the strong lowermost branch are ventrally directed and partly enclosed in its membranous posterior flange. The upper six branches are closely set and separated from the lower ones by a broad notch. In the 22.6 mm female larva

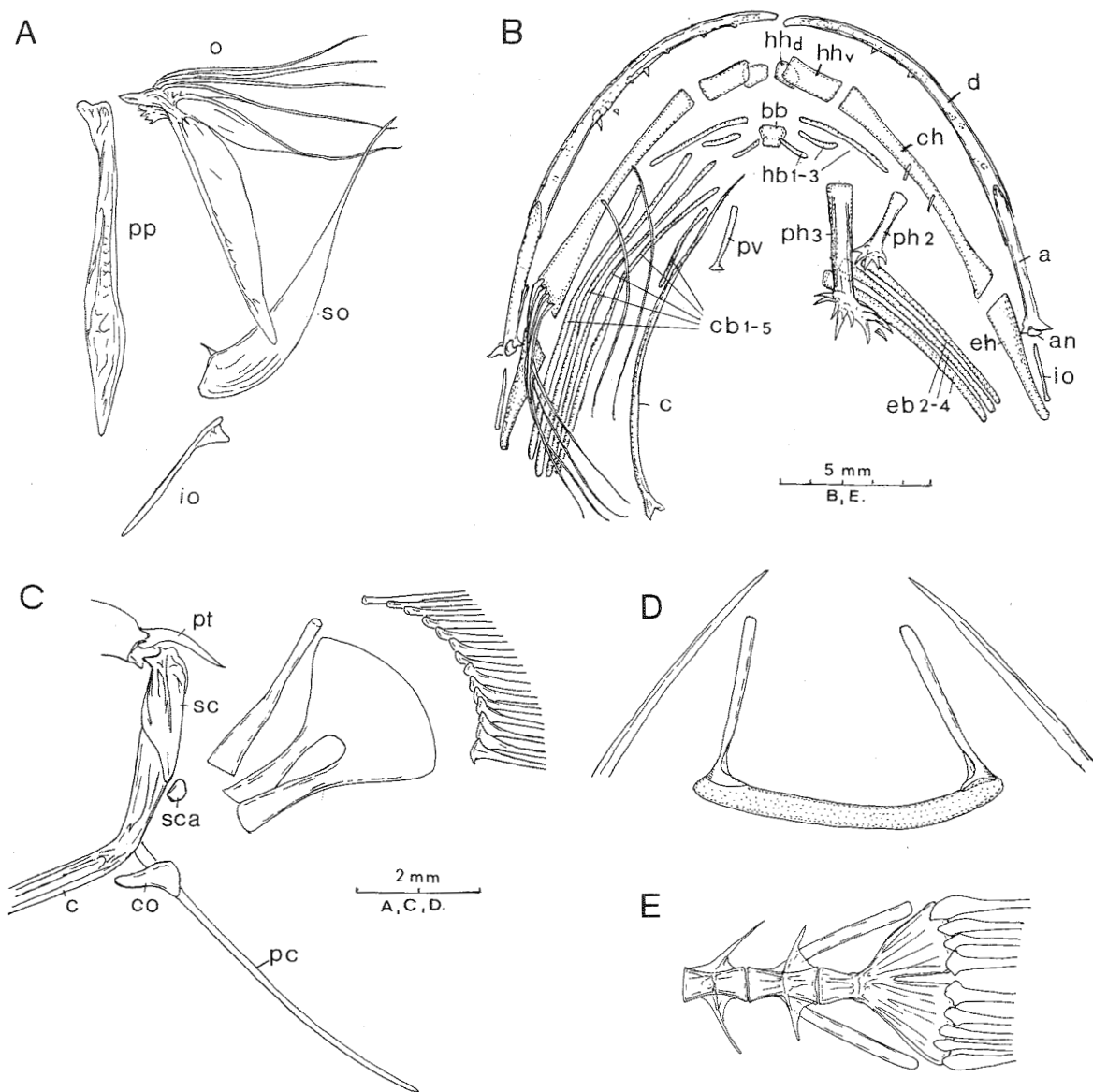


Fig. 5. Skeleton of *Thaumataichthys binghami*, 69.9 mm (ZMUC P 921948). A, opercular bones (io: interopercle, o: opercle, pp: preopercle, so: subopercle); B, branchial arches and adjacent bones (a: articular, an: angular, bb: basibranchial, c: cleithrum, cb 1-5: ceratobranchials, ch: ceratohyal, d: dentary, eb: epibranchials, eh: epihyal, hb 1-3: hypobranchials, hh-d and hh-v: dorsal and ventral hypohyal, ph 2-3: pharyngobranchials, pv: pelvic bone); C, skeleton of pectoral girdle and fin (c: cleithrum, co: coracoid, pc: postcleithrum, pt: posttemporal, sc: supracleithrum, sca: scapula); D, pelvic bones; E, caudal skeleton.

there is a total of 13 radiating ribs, of which the six uppermost ones are well developed free rays while the following six are less distinct and more or less enclosed in the posterior flange of the strong lowermost branch. In the 36.5 mm type of *T. binghami* there are six free upper rays, while no distinct ribs or rays are present in the broad flange of the lower branch. In the 40 mm *T. binghami* only four distinct

upper rays could be observed. The 142.5 mm *T. binghami* (Fig. 4) has seven upper rays, of which the base of the lowermost is fused with the flange of the strong lower branch. The branching of the operculum in *T. pagidostomus* and *T. axeli* seems to fall within this variation, but in each of the three specimens the fragile branches have been broken, and less developed rays or ribs have been lost.

There are five or six upper rays present in the type of *T. pagidostomus*, six in the type of *T. axeli*, and five in the 85.2 mm specimen of this species.

The suboperculum tends to become more slender and relatively longer with increasing size of the specimens. The small anterodorsal spine is present in all the examined specimens including the holotype of *T. pagidostomus* and both specimens of *T. axeli*.

Branchial arches (Fig. 5B). A. The very large third pharyngobranchial carries 10 recurved teeth and the somewhat smaller second pharyngobranchial 6 teeth.

B. Like the teeth in the jaws, the number and length of teeth on the pharyngobranchials increase with increasing size of the specimens from respectively 4 and 5 in the 2nd and 3rd pharyngobranchials in the 45.0 mm specimens to 15-17 and 24-25 in the holotype of *T. axeli* (cf. App. Table 1).

No first epibranchial and first pharyngobranchial could be observed. The remaining epibranchials II to IV, and the anterior four ceratobranchials are long and thin. The 5th ceratobranchial is only about one-third of the length of the others. None of them carries tooth plates. Three hypobranchials and a single basibranchial ossification are present.

Pectoral girdle (Fig. 5C). A. The posttemporals are narrow, blade-shaped bones pointed at both ends; the anterior ends overlap the epiotics, while the posterior ends protrude freely as sail-like extensions of the roof of the skull. The supracleithrum and the upper descending part of cleithrum are relatively short and robust, while the lower anteriorly directed part of cleithrum is very long and thin. The ventroposteriorly directed postcleithrum is slender and slightly curved upwards.

The coracoid is small and no ossification of the scapula could be observed. There are three pectoral radials. The uppermost first radial is a simple, slightly conical rod without expansion of its thin distal end, while the two lower radials are widely expanded distally and fused.

B. The larval male has three well separated pectoral radials, the lowermost two of about the same size and somewhat larger than the uppermost. As described above, the expanded distal ends of the two lowermost radials are fused in the 69.9 mm specimen (Fig. 5C). In the 142.5 mm *T. binghami* this fusion is nearly complete, only a short narrow split remains of their separation (Fig. 6A), and in

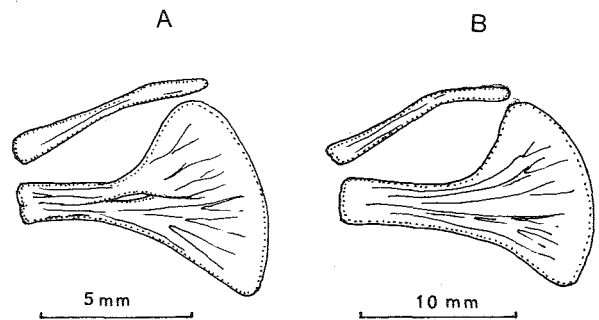


Fig. 6. Pectoral radials. A, *Thaumatchthys binghami*, 142.5 mm (ZMUC P 921950); B, the holotype of *T. axeli*, 365 mm.

the 293.5 mm *T. binghami* and the 365 mm holotype of *T. axeli* the fusion is complete (Fig. 6B).

Pelvic bones (Fig. 5D). A. The pelvic bones are small, slender rods with slightly expanded distal ends. They are widely separated and their posterior ends are connected with a long, slightly curved band of cartilage.

Illicial apparatus (Fig. 1). A. The pterygiophore (the basal bone of illicium) is relatively short (14.3% s.l.) and completely hidden by the skin of the head. The illicium bone is very short (3.2% s.l.) and downward directed behind the crossing elastic bands in the membranous tissue connecting the premaxillaries. The esca carries a curved denticle, pointed at both ends. The rudiment of the second cephalic ray is situated close to the anterior end of the basal bone. (For further details cf. p. 19).

Fin rays. A. In the stained specimen there are seven dorsal rays carried by the same number of pterygiophores, four anal rays carried by three pterygiophores, nine (2 + 4 + 3) caudal rays carried by a single hypural plate, deeply notched between the bases of the upper four and lower five caudal rays (Fig. 5E). The neural and haemal spine of the last free vertebra (the second preural centrum) are greatly enlarged. Each of the pectoral fins has 15 rays.

B. There is little variation in number of fin rays in the examined specimens, and no significant differences between the three species of *Thaumatchthys* were found. All specimens examined have four anal rays and nine caudal rays. The following variation in ray counts was noted. The single specimen of *T. pagidostomus* has 7 dorsal rays and 15 and 16 pec-

toral rays. The two specimens of *T. axeli* have 6-7 dorsal rays and 14-16 pectoral rays. The 17 specimens of *T. binghami* have 6-7 dorsal rays and 14-16 pectoral rays. The five larvae not assigned to species have 6-7 dorsal rays and 14-15 pectoral rays. Parr (1927) reported the holotype of *T. binghami* to have four dorsal fin rays; however, the anterior two rays are almost completely hidden by the skin and the correct count is six.

2. Dentition of jaws

As the previous separation into species and even genera of the known species of *Thaumatichthys* was based on differences in their development of the premaxillary teeth, a detailed examination is required of the individual, ontogenetic and specific variation in this character. For this purpose the premaxillary (in most cases the left) of each specimen was drawn, the length of each tooth was measured and its position in the pattern of series was determined. The results are summarized in Fig. 8 and Tables 1 and 2.

The two female larvae, 6.3 and 22.6 mm, have relatively short, conical, slightly curved teeth arranged in a double series, about 8-12 in each premaxillary and about 8-10 in each dentary. No trace of these larval teeth could be observed in the smallest metamorphosed specimens of 36.5 and 40.0 mm s.l. (BOC 2015 and 3713), in which all the teeth in the jaws are in early stages of development and have soft, unossified bases (Fig. 7A).

The premaxillary teeth of all of the metamorphosed specimens are arranged in a very distinctive pattern consisting of six overlapping, oblique longitudinal series (Figs 7 and 8). The first tooth of each of the six series are spaced along the edge of the jaw in the young specimens. The second tooth of each series develops slightly in front, ventromedial to the first tooth of the following series, the third in front and inside the second tooth of the following series, etc., forming in this way oblique transverse series sectioning the longitudinal series. In each series, the longitudinal as well as the transverse, the teeth increase in length in both the caudad and mediad directions. The teeth are slender, conical, and more or less recurved. The larger teeth of series II to IV are especially strongly hooked.

The last developing teeth of each series are placed inside the edge of the jaw, and until they have reached their full length and are ossified at the bases

they tend to be depressed towards the roof of the mouth. As will appear from the diagramme (Fig. 8) such teeth frequently terminate the oblique, longitudinal series and are found only in this position in the tooth patterns. When fully developed, they are raised and become depressibly hinged to the edge of the premaxillary bone, and with increasing age and growth of the bone they are gradually displaced upwards on the side of this. In later stages they become fixed, and finally the oldest and smallest teeth of each series lose function, become covered by skin, and may be more or less imbedded in the jaw bone or disappear completely.

In the two largest specimens of *T. binghami*, 225 and 293.5 mm s.l. where at least some of the series appear to be complete, the number and position of missing teeth can be extrapolated. In the 365 mm holotype of *T. axeli*, a greater number is missing. By comparison of the length of teeth with those in the corresponding series of the smaller specimen of *T. axeli* and the series of *T. binghami*, the best agreement is obtained if it is assumed that the anterior-most tooth of the best represented series in the *T. axeli* holotype (series III to V in the right jaw) represents tooth number 2 (cf. Fig. 8u-v).

As will appear from the figures and the summary in Table 1, there is an increase in number of teeth with increasing length of fish within the observed size range of specimens, i.e., from 10 to 15 in each premaxillary of the specimens less than 60 mm; 14 to 22 in specimens between 60 and 100 mm, 24 to 31 in the two specimens between 100 and 150 mm, 37 to 46 in the two specimens of 225 to 293 mm, and 54 to 55 in the 365 mm specimen if the 10 to 11 assumed lost teeth are included. Variation occurs; in some specimens the teeth are further developed than in others of similar length. For example, the 225 mm UMML 30958 with 45 teeth is in this respect ahead of the 293.5 mm USNM 214571 with 37 and 38 teeth in each side of the jaw.

In the number of premaxillary teeth and their distribution in each series, neither the holotype of *T. pagidostomus* nor the smaller specimens of *T. axeli* differ significantly from *T. binghami* of equal size. Similarly, the largest of the known *Thaumatichthys* specimens, the holotype of *T. axeli*, is in this respect in good accordance with the observed developmental series.

In the first fully developed teeth (I 1, and the first 3 to 5 of series II-VI) the variation in length of corresponding teeth is relatively small in the best represented species (*T. binghami*). The largest and latest

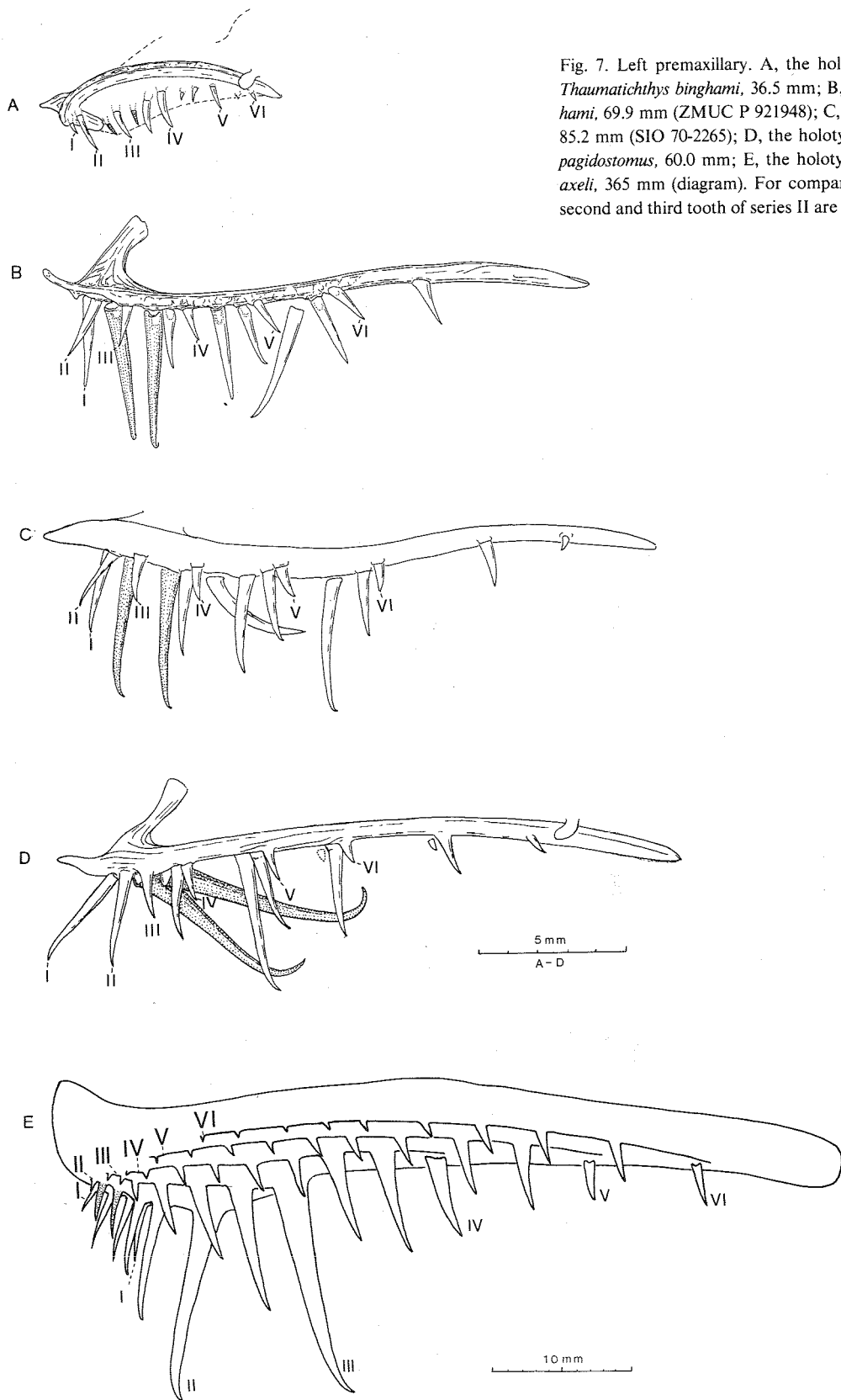


Fig. 7. Left premaxillary. A, the holotype of *Thaumatoichthys binghami*, 36.5 mm; B, *T. binghami*, 69.9 mm (ZMUC P 921948); C, *T. axeli*, 85.2 mm (SIO 70-2265); D, the holotype of *T. pagidostomus*, 60.0 mm; E, the holotype of *T. axeli*, 365 mm (diagram). For comparison the second and third tooth of series II are dotted.

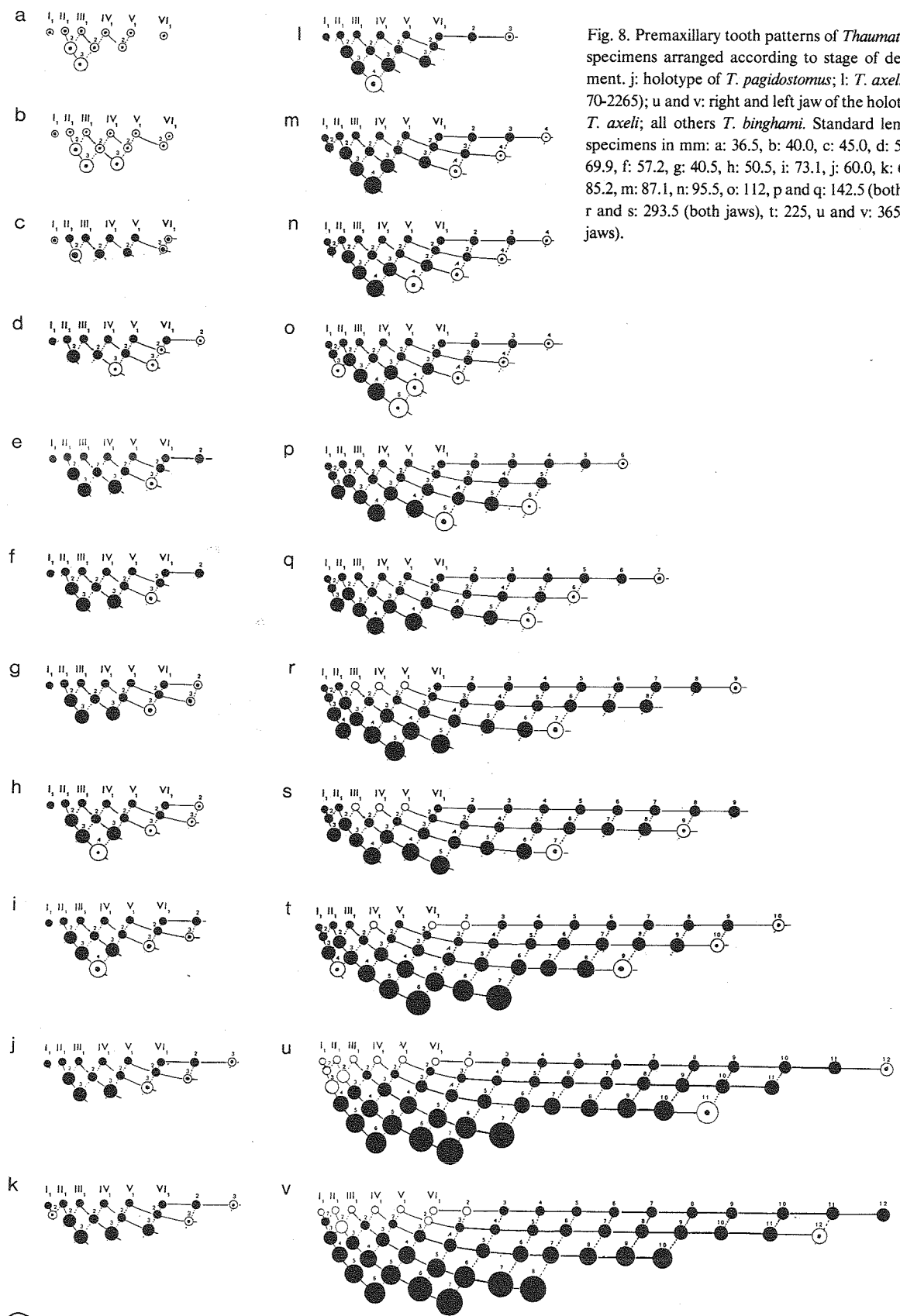


Fig. 8. Premaxillary tooth patterns of *Thaumatoichthys* specimens arranged according to stage of development. j: holotype of *T. pagidostomus*; l: *T. axeli*, (SIO 70-2265); u and v: right and left jaw of the holotype of *T. axeli*; all others *T. binghami*. Standard length of specimens in mm: a: 36.5, b: 40.0, c: 45.0, d: 51.5, e: 69.9, f: 57.2, g: 40.5, h: 50.5, i: 73.1, j: 60.0, k: 67.0, l: 85.2, m: 87.1, n: 95.5, o: 112, p and q: 142.5 (both jaws), r and s: 293.5 (both jaws), t: 225, u and v: 365 (both jaws).

○ Teeth in development.
 ○ Assumed lost teeth. ● Fully developed teeth, including broken or partly resorbed.

Table 1. No. of premaxillary teeth in oblique longitudinal series I-VI.
Incompletely developed, broken and assumed lost teeth included.

species:	<i>binghami</i>	<i>pagidost.</i>	<i>binghami</i>	<i>axeli</i>	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>axeli</i>
mm s.l.:	36.5-57.2	60.0	67.0-73.1	85.2	87.1-95.5	112-142.5	225-293.5	365
no. specimens:	7	1	3	1	2	2	2	1

series	I							l	r
I	1	1	1 - 2	1	2	3	3 - 4	6	6
II	2 - 4	3	3 - 4	4	4	4 - 5	4 - 6	7	7
III	2 - 3	3	3	3	3 - 4	4 - 5	5 - 7	8	7
IV	2 - 3	3	3	3	4	4 - 6	7 - 9	10	11
V	2 - 3	3	2 - 3	2	4	4 - 6	8 - 10	12	11
VI	1 - 2	3	2 - 3	3	4	4 - 7	9 - 10	12	12

total:	10 - 15	16	14 - 16	16	21 - 22	24 - 31	37 - 46	55	54
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developed teeth of the largest specimens show greater variation. All specimens show the very regular increase in tooth length in each series, but comparison of corresponding teeth of the different specimens shows considerable variation. Table 2 gives a summary of the lengths of these first developed teeth of each series which are most numerously represented in the material. In spite of the variation found in the *T. binghami* specimens, the holotype of *T. pagidostomus* differs very significantly from *T. binghami* in this character. Of the 13 teeth which are fully developed in this specimen, 8 are distinctly longer than the longest corresponding teeth found in *T. binghami*, and the remaining 5 are near or above the average length of the corresponding teeth of this species.

The length of each tooth of the 85.2 mm *T. axeli* (SIO 70-2265) is within the observed range of the corresponding tooth in *T. binghami*, and in most cases remarkably close to the average length of these. No conclusion can be drawn from a comparison of the tooth lengths of the holotype of *T. axeli* with those of *T. binghami*. As mentioned above, most of the first developed teeth are missing in the large specimen, and the remaining of these are more or less reduced in length by wear, resorption, and imbedding in the jaw bone. The length of the corresponding later developed large teeth present only in this specimen and the three largest *T. binghami* varies greatly without any indication of difference between the two species.

The teeth of the lower jaw (Fig. 9) are shorter and less curved than those of the upper jaw. Like the premaxillary teeth they increase in number and

length with increasing size of the specimen, varying from 9-10 and a greatest length of 1.2-1.5 mm in the smallest, to 22-30 and 5.6-10.3 mm in the three largest *T. binghami*, and 39-40 and 10.5 mm in the holotype of *T. axeli*. They are arranged in distinct anteromedial series, each of two to four teeth of increasing length with the smallest outermost as in the premaxillaries. No specific differences in the pattern, number or length of these teeth could be observed.

Table 2. Length of anterior premaxillary teeth in oblique longitudinal series I-VI. Incompletely developed or broken teeth not included.

Tooth no.	no. specimens	<i>binghami</i>		<i>axeli</i>	<i>pagidostomus</i> (SIO 70-2265) (holotype)	
		range	av.			
I	1	14	2.2-3.5	2.75	3.0	3.8
	17		1.1-2.3	1.88	1.9	3.0
II	2	16	3.0-5.6	4.25	4.5	6.5
	16		3.8-5.8	4.81	4.8	7.0
III	1	14	1.1-1.8	1.36	1.1	1.5
	2	16	0.8-2.3	1.81	1.9	3.3
	13		1.8-3.4	2.75	2.5	4.3
IV	1	15	0.6-1.5	1.06	1.0	1.4
	17		0.9-2.3	1.68	2.0	2.4
V	1	14	0.6-1.4	1.02	0.9	1.0
	14		0.8-2.6	1.78	2.4	3.4
VI	1	14	0.8-1.6	1.14	0.8	1.3
	13		0.8-1.9	1.52	1.6	1.5

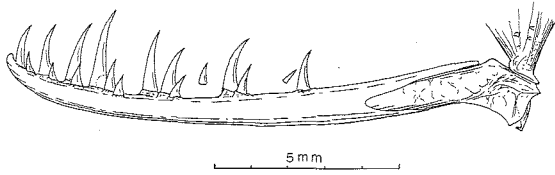


Fig. 9. Lower jaw of *Thaumalachthys binghami*, 69,9 mm (ZMUC P 921948).

3. Illicium and esca

In the female larva 6.3 mm s.l. the tiny club-shaped illicium protrudes on top of the head above the anterior margin of the eye which at this stage is large and in normal position (Bertelsen 1951). In the 22.6 mm specimen (Fig. 15) the illicium has moved forward and protrudes on the snout in front of the eye and a short distance above the symphysis of the upper jaw.

At metamorphosis the anterior ends of the premaxillaries become separated and are prolonged beyond the tip of the lower jaw. Anteriorly they are connected by a membranous fold of the skin of the snout. The articulation between illicium and its pterygiophore is imbedded in this fold and surrounded by a small bulb of connective tissue. The illicium projects from the underside of this membrane, a short distance behind its incurved anterior edge, which is supported by the crossing pair of elastic bands connecting the ascending process of each premaxillary with the anterior end of the maxillary and palatine of the opposite side (cf. Fig. 17). These ligaments are most probably derivatives of the subcutaneous connective tissue and appear to develop during metamorphosis.

In the specimens of less than about 50 mm, the esca is carried on a short free illicial stem as described and figured by Parr (1927). In the larger specimens it becomes sessile with the skin of its base confluent with that of the membrane.

The pterygiophore (or basal bone) of the illicium is short (about 15% s.l.) and lies in the shallow groove between the anterior ends of the frontals. Its retractor and exertor muscles are very thin and weakly developed.

In descriptions of the structure of ceratioid escas the terms "anterior" and "posterior" assumes an erect position of illicium. The upside-down esca of *Thaumalachthys* is best observed in an anteroventral view (Figs 10 and 12) in which the anterodorsal oriented part, which in the following will be termed

"upper", corresponds to "posterior" in other esca descriptions.

In all the *Thaumalachthys* specimens, the esca consists of the following elements:

- 1) An internal black bulb-shaped photophore with an unpigmented distal field of varying size.
- 2) A low, more or less pigmented base, confluent with the pigmented skin of the short illicium stem or, in older specimens, directly with the membranous skin fold.
- 3) A distal lobed, somewhat inflated, unpigmented disc, more or less distinctly divided into an upper pair of lateral wings and a lower median broad tongue. The lower lateral angles of this tongue are drawn out into a pair of pointed, tentacle-like lobes, and one or two similar pairs are formed by extensions of the lateral wings.
- 4) A curved denticle imbedded in the lower median tongue. (This structure is missing in some specimens).
- 5) Two simple, median appendages close to each other on the upper part of esca. The uppermost of these is short, tapered, and unpigmented in all the examined specimens. The second, more distally positioned appendage, is untapered, more or less pigmented, and of extremely variable size in the different specimens.

The ontogenetic and individual variation of the esca in the specimens here assigned to *T. binghami* is illustrated in Fig. 10A-P, in which all the escas are shown in anteroventral view and drawn to the same scale except for the two largest for which a half as large magnification was used.

There is no distinct change in the relative size of the esca with increasing length of fish. The diameter of the internal bulb varies between 2.1% and 4.0% s.l. in the specimens. The unpigmented field of this bulb varies in size from a relatively narrow split (e.g. Fig. 10D, K and N) to a wide oval, covering the main part of the distal surface (Fig. 10J). This indicates that the light from the photophore can be varied by changing the contraction of this field. No opening of the luminous gland of the inner bulb could be observed on the outer surface of esca. If present, the pore is extremely small and undistinguishable in the semitransparent, more or less folded skin on the upper part of esca at the bases of the unpaired appendages where it should be expected.

The pointed lateral lobes vary in number. However, most of the specimens with standard length

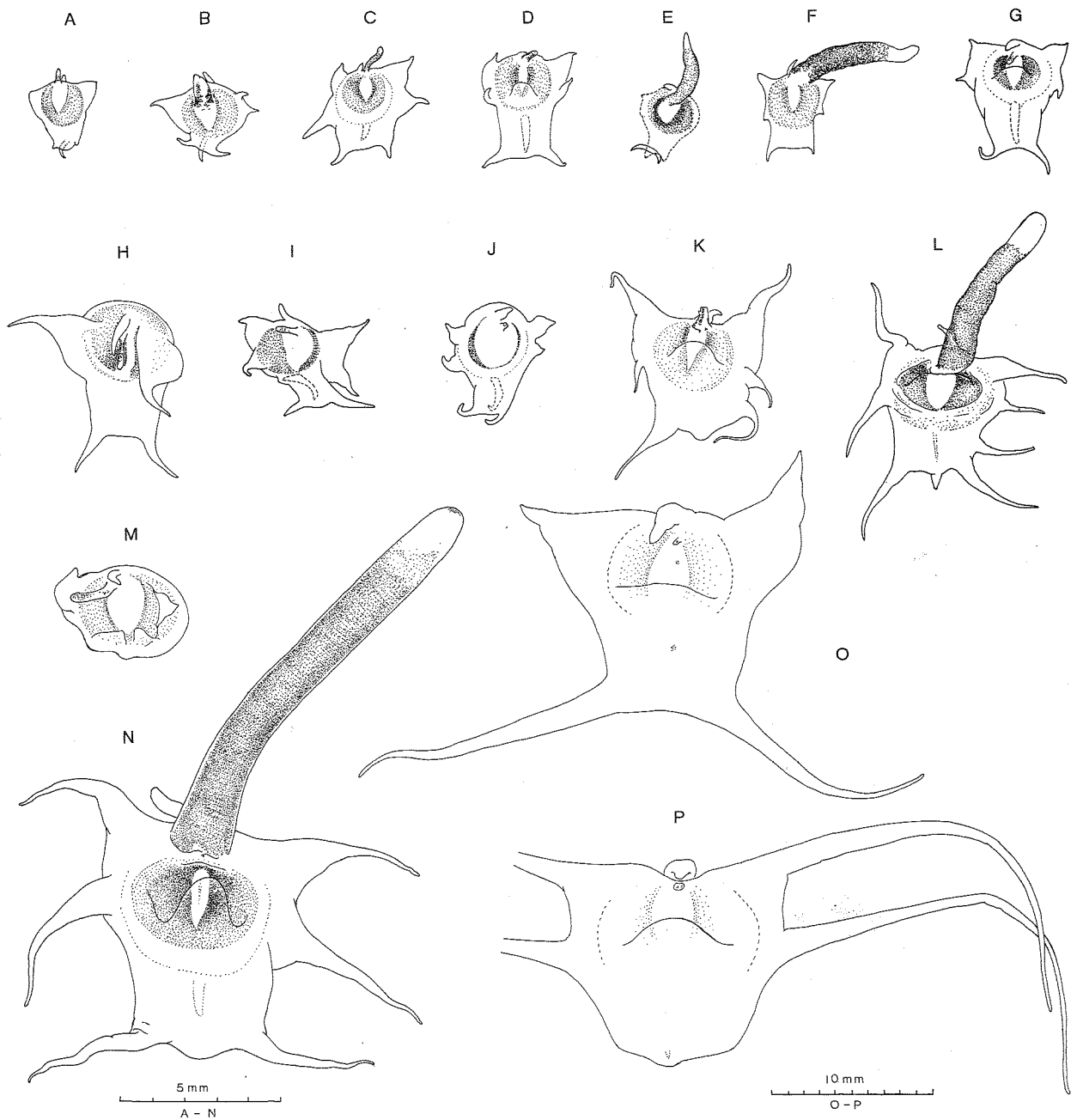


Fig. 10. Escae of *Thaumatoichthys binghami* in anteroventral views. A, 40.0 mm (BOC 3713); B, 40.5 mm (UMML 30866); C, 45.0 mm (Texas Univ. 69A-11-91); D, 50.5 mm (UMML 31363); E, 51.5 mm (USNM 214570); F, 58.0 mm (UMML 31362); G, 57.2 mm (UMML 26927); H, 67.0 mm (UMML 30926); I, 69.9 mm (ZMUC P 921948); J, 73.1 mm (ZMUC P 921947); K, 95.5 mm (UMML 30930); L, 87.1 mm (USNM 214571); M, 112 mm (UMML 27394); N, 142.5 mm (ZMUC P 921950); O, 225 mm (UMML 30958); P, 293.5 mm (USNM 214571).

between 50 and 142.5 mm (Fig. 10C-N) show a basic pattern of three pairs; two upper pairs on the lateral wings and one pair on the median tongue. The exceptions are: 1) the 51.5 mm USNM specimen (Fig. 10E), in which the outer skin of the esca is torn, 2) the 112 mm UMML specimen (Fig. 10M), in which the lobes are represented by low irregular folds and may be in a state of regeneration, 3) the 87.1 mm USNM specimen (Fig. 10L) which, in addition to the three pairs, has an additional, lateral, pointed lobe on the left side at the base of the median tongue and, furthermore, a median short pointed lobe at the tip of this between the lowermost pair, and 4) the 67.0 mm UMML specimen (Fig. 10H) which, like the youngest specimens described below, has a single pointed lobe on each lateral wing.

The esca of the juvenile 40 mm BOC specimen (Fig. 10A) is extremely similar to that of the 39 mm holotype of *T. binghami* described and figured by Parr (1927). In these specimens only the upper angles of the lateral wings are slightly pointed, and the median tongue carries a pair of very small points. In the 45 mm specimen from Texas University (Fig. 10B), all three lobes are developed on the left side, while the right lateral wing has a single point only.

In the two largest specimens, the 225 mm UMML specimen (Fig. 10O) and the 293.5 mm USNM specimen (Fig. 10P), the esca differs from the smaller specimens in having only two pairs of lateral lobes. Furthermore they differ from each other in the position and development of these. In the UMML specimen, the lobes seem to represent the uppermost and lowermost pair of the smaller specimens. Each of the broad lateral wings ends in a single short point, while the pair on the median tongue is prolonged into slender tentacles.

In the USNM specimen, both pairs of lobes are prolonged into slender tentacles and, according to their position, they seem to represent the lobes of the lateral wings of the smaller specimens, while the median tongue is short and without lobes.

The median appendage which is uppermost in the illustrations is short and unpigmented in all the specimens, and varies from a tiny wart (Fig. 10D) to a length of about half the diameter of the internal bulb (Fig. 10H).

The pigmented second median appendage shows extreme variation in development. In 8 of the 11 specimens less than 75 mm s.l. and in the 112 mm specimen with the esca in an apparent state of regeneration, this appendage is of similar thickness

and as long as or only a few times longer than the uppermost appendage and carries relatively few scattered melanophores. In five specimens, [the 40.5 mm UMML 30866 (Fig. 10B), the 51.5 mm USNM specimen (Fig. 10E), the 58 mm UMML 31362 (Fig. 10F) and the 87.1 mm and 142.5 mm ZMUC specimens (Fig. 10L and N)], this appendage is much thicker than the upper appendage and increases greatly in relative length with increasing lengths of the specimens. In the smaller of these specimens, it has a length of about half the diameter of the inner bulb, in the intermediate from 1½-2½, and nearly three times the bulb diameter in the largest specimen. These enlarged appendages are heavily pigmented except for the distal transparent tip. In the 95.5 mm UMML 30930 (Fig. 10K), this appendage is torn.

Finally, the two largest specimens of 225 and 293.5 mm (Fig. 10O and P) both differ from all the others in having only a tiny wartlike rudiment of this appendage, each with a few remaining melanophores.

In 11 of the 17 examined specimens, including the smallest as well as the largest one, a well developed 1-2 mm long, curved denticle could be observed in the median tongue of esca (Fig. 11). The denticle is pointed at both ends. The distal end protrudes as a small hook on the dorsocaudad oriented back of the median tongue.

In six specimens no spine could be found by external examination of this semi-transparent organ. However, a very thin bony remnant of the denticle was found by superficial dissection of the esca of the 225 mm specimen. In two of the others, the spine may be lost (the specimen with esca in apparent regeneration (Fig. 10M) and the 87.1 mm USNM specimen (Fig. 10L), in which the skin of the back of

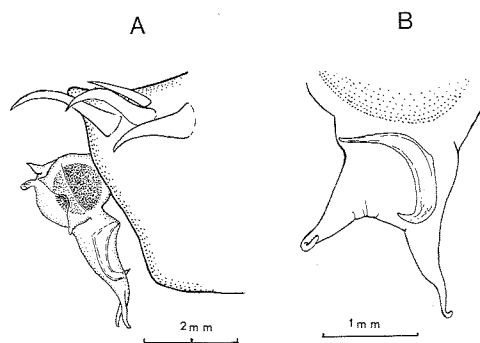
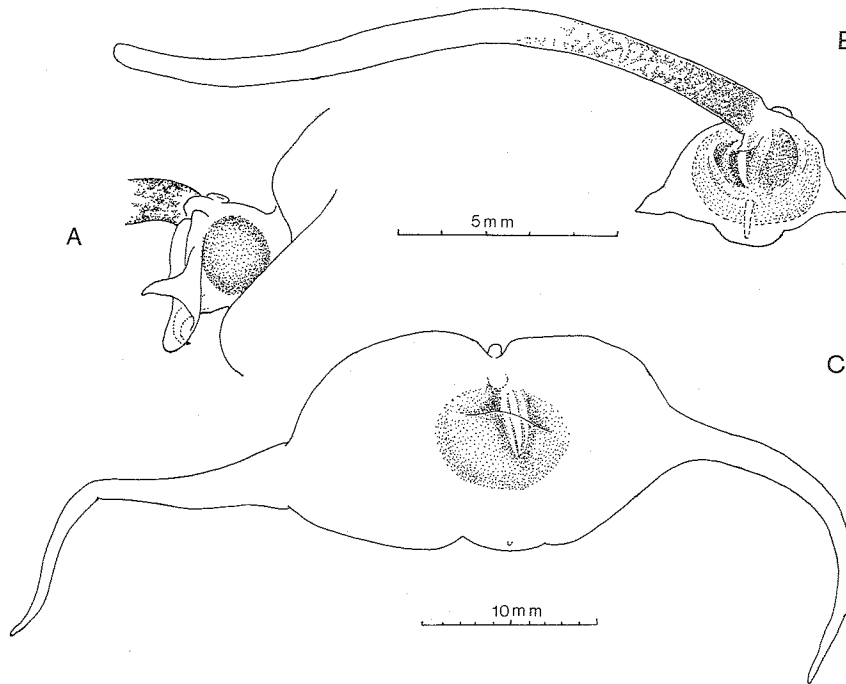


Fig. 11. Escae of *Thaumataichthys binghami*. A, lateral view of a 57.2 mm specimen (UMML 26927); B, median tongue of esca of a 69.9 mm specimen (ZMUC P 921948).



B Fig. 12. Escae of *Thaumaticthys axeli*. A and B, 85.2 mm (SIO 70-2265), in lateral and anteroventral views; C, the 365 mm holotype.

the esca tongue is slightly torn), but in the well preserved escae of the remaining three specimens (Fig. 10F, H, and K), the lack of denticle can hardly be explained as artifacts.

In both specimens of *T. axeli*, the escae differ from those of *T. binghami* in three characters: 1) only a single pair of lateral pointed lobes is present, 2) the uppermost median appendage is represented by an untapered, small wart, and 3) the median tongue is represented by a low crest without pointed lobes (Fig. 12). This tongue encloses an approximately 2 mm long, curved denticle in both specimens.

In the 85.2 mm SIO specimen (Fig. 12A and B), the lower angle of each lateral wing is drawn out into a short, pointed lobe. In the 365 mm holotype (Fig. 12C) this pair of lobes is prolonged into slender tentacles.

In the SIO specimen the second median appendage is stout, untapered, and 15 mm long or about five times as long as the diameter of the bulb. The proximal third of the appendage is pigmented. In the holotype only a low indistinct unpigmented wart represents this appendage.

In the holotype of *T. pagidostomus*, the esca is damaged; only the inner bulb with the loosely attached 2.1 mm long, curved denticle remains. Smith & Radcliffe describe (1912, p. 580) the illicium and esca as "a slender pedicel bearing at its tip a sharp toothlike process that curves backward". In their

illustration, the esca is pictured as a simple small globe with the denticle protruding at the tip. However, the fact that no lobes or appendages on esca are mentioned or pictured need not indicate that the species differs from other *Thaumaticthys* in this character. In their figure, the esca has a diameter of about 1% s.l. or somewhat less than the present diameter of the inner bulb, which is now 1.0 mm or 1.7% s.l. This might indicate that the damage to the esca occurred during capture.

4. Sense organs

As normal in female ceratioids, the relative size of the eyes of *Thaumaticthys* is largest in the young larvae and their growth is nearly stopped after metamorphosis. In the 6.3 mm larva (Bertelsen 1951), the diameter of the pigmented eyeball (the choroid) is 0.9 mm or 14% s.l. In the 18.5 mm specimen the diameter has increased to 1.5 mm (8% s.l.) which is about the same size as in the recently metamorphosed 36.5 mm holotype of *T. binghami*. In all the metamorphosed specimens of 40 to 142.5 mm, the diameter of the pigmented eyeball varies between 1.2 and 1.9 mm, with a slight increasing trend with increasing length of fish; in the three largest specimens (225-365 mm s.l.), this diameter is 2.3-2.5 mm. This stagnation of growth corresponds to a decrease in the relative size of the eye from a

diameter of 3.0% to 4.4% s.l. in the four specimens of less than 50 mm to 0.7%-0.8% s.l. in the two largest specimens (cf. Appendix Table 1). The structure of the eye of the holotype of *T. axeli* is described by Munk (1964) and the external examination of the present material shows full agreement with this description. In spite of the extremely small relative size of the eyes in the larger specimens, no indication of degeneration could be observed. In external view they seem very similar to those of female ceratiids as described by Munk (1964, 1966), with a thick transparent sclera and a relatively very large lens located behind the iris. In the best preserved specimens a narrow, anterior, aphakic aperture can be observed.

In the larvae the eyes are in the normal lateral position, filling the space between the short snout, the frontals and the normally developed upper maxillary muscles, levator maxillae superioris (Fig. 15). With metamorphosis the snout and upper jaws are greatly prolonged, and similarly the levator maxillae superioris increase greatly in size and length; the eyes are displaced backwards and downwards into a position below the levator maxillae superioris and closely above the angles of the mouth, where they protrude slightly on the sides of the broad and flat head (Pl. 2). As a result of this displacement of the eyes, the optic nerves and the very feeble eye muscles cross the lateral surface of the strong levator maxillae (cf. Fig. 17A).

In the larval females the relatively well developed olfactory organ is placed in the narrow space between the eye and the heads of maxillary and premaxillary (Fig. 15). With metamorphosis it follows the displacement of the eye, remaining in a position closely anteroventrad to this. In the metamorphosed specimens, the olfactory organ is raised on a somewhat rectangular lobe with the nostrils at the distal corners (Plate 2 and Fig. 7A and D). The lobe is about twice as long as broad, and has a relative length of about 2% s.l. or about half the eye diameter in the smallest specimen, and two to three times this diameter in the largest. In most of the specimens this nasal papilla is preserved in a downward directed position, hanging over the posterior end of the premaxillary near the angle of the mouth.

Four series of lateral line organs can be distinguished: 1) the lateral line of the body posteriorly extends to the base of the caudal fin, and continues on the head in 2) the supraorbital, 3) the suborbital, and 4) the mandibular series. No preopercular series could be observed. Each organ consists of a

small elongated untapering papilla arising from the center of a small, white spot in the skin. The papillae are unpigmented at tip and more or less pigmented at base. The organs are connected in series by thin, more or less distinct white lines (Pl. 2). In most of the series the papillae are very small, with a slight tendency to increase in size anteriorly on snout and lower jaw. However, in the suborbital series the anteriormost 10-15 papillae are greatly enlarged, forming a very distinctive series of flaps extending along the posterior third of the upper jaw, below the nasal papilla and slightly beyond the eye. The largest of these papillae are about one-fifth of the length of the nasal papilla.

Numerous white-tipped papillae of similar appearance, and presumably belonging to the same sensory system, are present in the roof of the mouth, especially in its anterior part in front of the lower jaw on both sides of esca. The largest of these papillae are arranged in three groups along the ventral side of each premaxillary (Pl. 2). The largest and anteriormost of these groups is situated below the base of the articular process of the premaxillary and close behind the anteriormost teeth. It consists of 10-15 white-tipped stout papillae closely set on a low, somewhat ridge-shaped common base. Their greatest height, including the base, is about the same as the length of the nasal papilla or about 2% s.l. The second of these groups consists of 4-5 papillae which, in the older specimens, are raised on a common stout stem. The posteriormost group consists of a more variable number of papillae, and may be absent in the younger specimens. In the older ones it contains 5-8 irregularly arranged papillae, some of which are separate and others are raised on one or two stems, each with two or more papillae. Single, much smaller papillae, are scattered over the roof of the mouth between the enlarged groups and are most numerous posterior to these.

5. Ovaries

All the examined specimens are immature. In the two largest specimens the ovaries consist of a pair of relatively thin-walled sacks, each about 50 mm long and 15 mm in greatest width in the 365 mm holotype of *T. axeli*, and about 30 x 6 mm in the 293.5 mm *T. binghami*. In both specimens the slightly folded walls of the ovaries are covered with a single layer of oocysts 0.05-0.1 mm in diameter.

Spines are present in the skin of the lower part of the body in all the metamorphosed specimens. In the youngest, they are restricted to the opercular region of the head and the ventral side of the body, except for the caudal peduncle where they reach the dorsal midline. With increasing size of specimens the spines gradually cover the ventral side of the lower jaw, a greater part of the body sides, and the anal and caudal fin rays. The skin of the dorsal side of the head, the pectoral and dorsal fins and a posteriorly tapering field of the back, remains naked. Each spine arises from the center of a more or less circular plate. The spines are conical, acute, straight or slightly curved, and usually of a length of about half the diameter of their basal plate.

The spines increase in number and size with increasing size of the specimens, but decrease in relative size. The diameter of the c. 10 largest spine plates in a field of about the same relative size on the same locality on the side of the body, was measured in series of specimens (Fig. 13). In the smallest specimen, a 40 mm *T. binghami*, this diameter varied between 0.35 and 0.5 mm or 0.9%-1.3% s.l., while in the 293.5 mm specimen of this species as well as in the 365 mm holotype of *T. axeli*, it was 0.9-1.4 mm or 0.25%-0.45% s.l.

The relative diameters of these spine plates were found to be distinctly larger in the 60 mm holotype of *T. pagidostomus* than in *T. binghami* specimens of the same length, while those of the two specimens of *T. axeli* fall within the variation observed in *T. binghami*.

In the most recently preserved specimens, the color of the skin is dark brown to velvet black. The part of the roof of the mouth which extends beyond the lower jaw is brown, while the walls of the mouth cavity enclosed by this jaw are nearly or completely unpigmented.

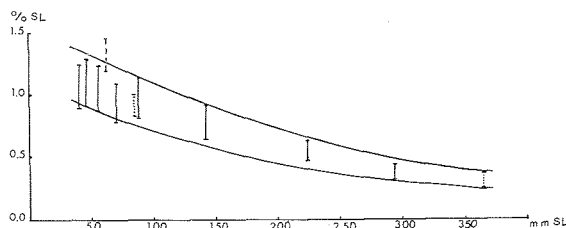


Fig. 13. Diameter of spine plates in percent of standard lengths (cf. text). (— *T. binghami*, - - - *T. pagidostomus*, and . . . *T. axeli*).

The only previously known males of *Thaumathichthys* are 3 larvae of 4.4, 6 and 24 mm in total length, described by Bertelsen (1951). The largest of these is probably at a stage approaching metamorphosis, according to its relatively advanced testes and the fact that it was caught in a pelagic net fishing at a depth of about 1500 m.

Like most of the female specimens made available to us, the single adolescent male ZMUC P 921946 (Fig. 14A) was obtained in the Tongue-of-the-Ocean Programme of the University of Miami. It was caught on 10 May 1973 at station CI 89, 24°47'N, 77°39'W in a semi-balloon trawl fishing at the bottom at a depth of 1938 m. It is 45 mm in total length, 31 mm in standard length.

In general appearance and body proportion (Table 3) it is similar to most other metamorphosed ceratioid males, differing from females in its lack of esca, slender shape, pointed snout with hooked denticles at the tip of the jaws, and enlarged olfactory organs.

In order to preserve this unique specimen for future studies (comparisons with the still unknown *Lasiognathus* male, etc.) it was not cleared, and was stained with an alizarin-alcohol solution only at the snout. Combined with superficial dissection the more important osteological features could in this way be observed (Fig. 14C-E and G). The tip of the jaws carries 4 upper and 7 lower denticles (Fig. 14E-G). Those of the upper jaw are arranged in two bilateral symmetrical pairs. The denticles of the upper pair are the largest, 1.3 mm long, and ventrolaterally curved. Those of the lower pair are more strongly hooked, with the distal end curved downwards and the sharp tips thus pointing backwards nearly parallel to their slender shafts. In each side the two denticles are closely set, and their somewhat expanded bases are indistinctly separated, while no connection between the bases of those of left and right side is present. They are carried mainly by the head of the premaxillary at the place of its undeveloped ascending process. Otherwise the premaxillary is of normal appearance, with well developed, mediocaudal directed, articular processes and without any trace of resorption, except for the complete lack of teeth.

The maxillaries are similarly well developed. The head of each carries two processes, the inner and shorter of which is turned underneath the articular process of the premaxillary, and the other lies

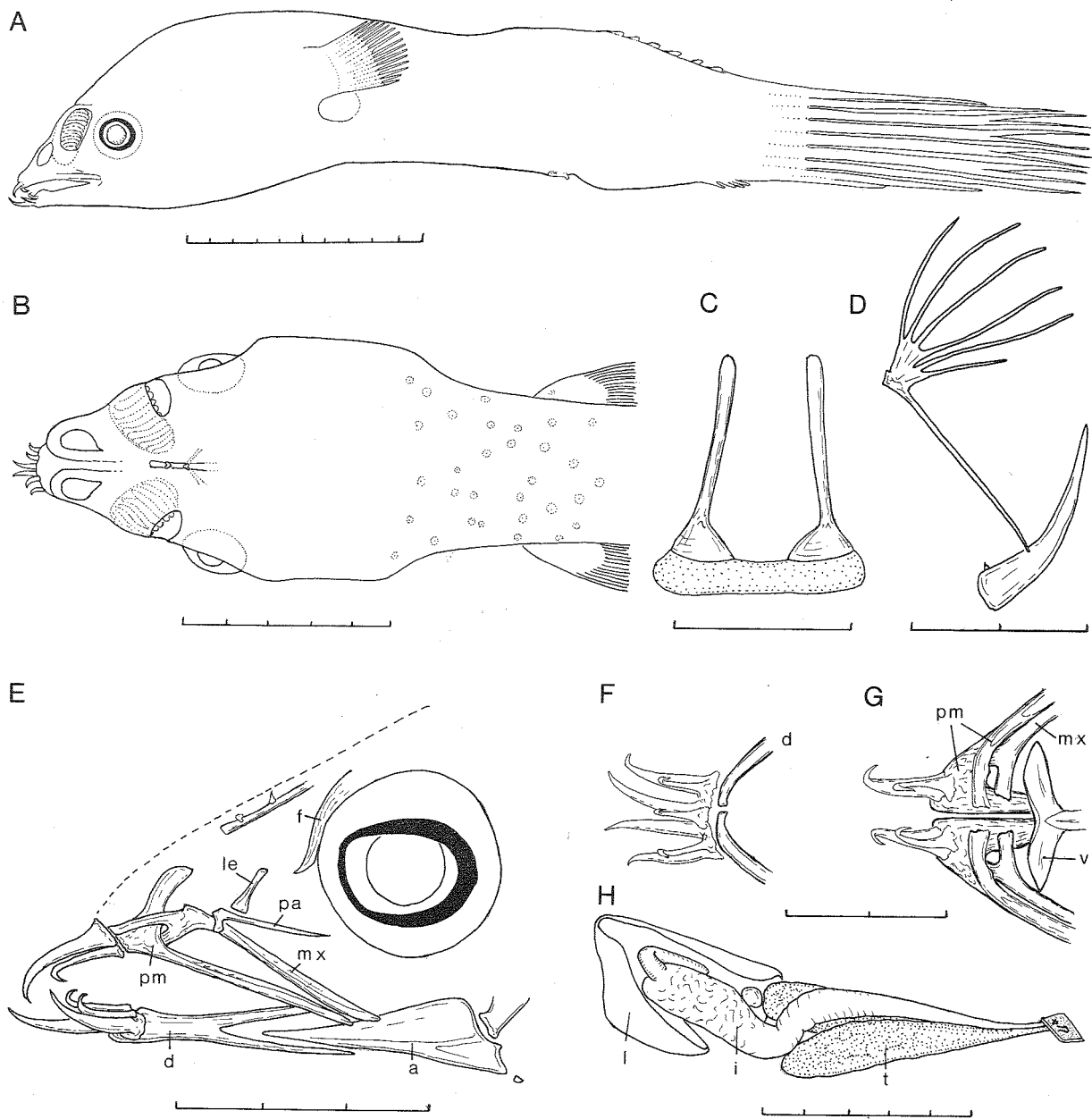


Fig. 14. Male of *Thaumaticichthys* (?) *binghami*, 31 mm. A, lateral view; B, dorsal view of head (torn skin and broken fin rays reconstructed); C, pelvic bones; D, operculum and suboperculum; E, skeleton of jaws; F, denticles of lower jaw in dorsal view; G, denticles on tip of upper jaw in ventral view (abbreviations in E-G as in Fig. 1); H, viscera (i: intestine, l: liver, t: testes).

close to the outer surface of this process, reaching the base of the uppermost denticle.

The seven denticles of the lower jaw are arranged in two bilateral, symmetrical series: a lower and outer row of four large denticles with dorsolaterally curved, pointed tips - and an inner series of three shorter denticles placed just above the spaces between the 4 larger ones. Like the lower pair of the

upper jaw, the three shorter denticles have slender shafts and similarly hooked tips. The somewhat expanded bases of these seven lower denticles are fused and by connective tissue attached to the tips of the dentaries. As in the premaxillaries, no teeth or traces of teeth sockets are present.

The frontals are broad and short, and their lateral, anterior tips are behind the posterior ends of

Table 3. Measurements of males.

	adolescent mm	larva mm
Total length	45	24
Standard length	31	18.5
% of s.l.	%	%
Tip of snout to gill opening	42	42
Length of snout	12.0	5.4
Width between sphenotics	19.4	21.6
Length of upper jaw*	9.7	12.0
Length of lower jaw*	16.1	16.8
Diameter of pigmented eyeball	5.2	8.6
Horizontal diameter of olfactory organ	ca. 10	ca. 5
Greatest depth of head	26	ca. 54
Greatest depth of body	22.5	ca. 54
Longest ray of caudal fin	45	40
Longest ray of pectoral fin	10	18.5

* Denticles not included

the lateral ethmoids (Fig. 14E). The pterygiophore of illicium is short and has no connection with the denticle and jaw mechanism. It carries rudiments of illicium and the second cephalic ray, but no trace could be found of the denticlelike, minute bone formations observed by Bertelsen (1951) on each side of the illicium in the larval male.

The operculum and suboperculum (Fig. 14D) have the shape characteristic to the genus. The upper part of operculum is divided into 6 radiating slender branches, and suboperculum is posteriorly tapering into a slender curved tip, and anteriorly truncate with an anterodorsal spine.

The posterior ends of the pelvic bones are expanded and connected by a band of cartilage (Fig. 14C), which is folded in such a way that the pelvic bones are very closely set (artificially stretched out in the illustration).

The numbers of fin rays are: D 6, A 4, C 9 and P 15-15.

Both eyes have circumlental aphakic apertures. In the right eye the pupil and retinal cup are nearly circular, but oval in the left one (Fig. 14E), probably due to shrinking (for this reason corrected in Fig. 14A). The diameter of the pigmented part of the right eye is 1.6 mm (5.2% s.l.). The diameter of the transparent outer coat of the eyeball is 2.1 mm.

The olfactory organs are very large, about 3 mm (c. 10% s.l.) in horizontal diameter, each with 13

olfactory lamellae. The covering skin, including the bridge between the nostrils, is torn, but, as reconstructed in Fig. 14A and B, the posterior nostril is much larger than the anterior.

The skin contains numerous small spines scattered over the body from the occipital region to the base of the caudal fin. In the preserved specimen it is dark brown. Subdermally the head and body are covered with a layer of dusky pigment of nearly uniform density.

The vicera is shown in Fig. 14H. The liver is relatively small. Oesophagus is narrow, and the nearly straight intestine empty. The testes are immature, each about 6.5 mm in total length and 1.2 mm in greatest width.

A comparison with the 18.5 mm s.l. male larva shows the main features of the male metamorphosis. As shown in Table 3, the most significant changes in relative body proportions are a prolongation of the snout and a reduction of the depth of head and body. The relative length of the pectoral fin is somewhat reduced, while the length and width of head and length of jaws and caudal fin are about the same. The larva has small teeth in the jaws, three in each premaxillary and five in each side of the lower jaw, and no denticles.

The eyes of the three larvae are circular and lack aphakic aperture. During the larval development they increase in actual size but decrease in relation to the standard length, from more than 15 to less than 9%. According to the comparison with the adolescent male, the growth of the pigmented eyeball stops at metamorphosis. Its actual diameter is the same (1.6 mm) in the 18.5 mm larva as in the 31 mm adolescent male.

The olfactory organs of the 18.5 mm male are slightly larger than in the smaller larvae, but in height only about 5 per cent of the standard length, and the nostrils are tiny.

The club-shaped testes of the 18.5 mm specimen are in beginning development but only about 0.5 mm in greatest diameter, and in estimated volume about 10% of those of the adolescent male. Compared with this, its liver, stomach and diameter of oesophagus are considerably larger. In linear dimensions the liver is about twice and in estimated volume about 8 times that of the 31 mm specimen.

Considering the much more slender shape of the adolescent male, these reductions might indicate that the feeding of the male is nearly or completely arrested after the metamorphosis of the jaw mechanism.

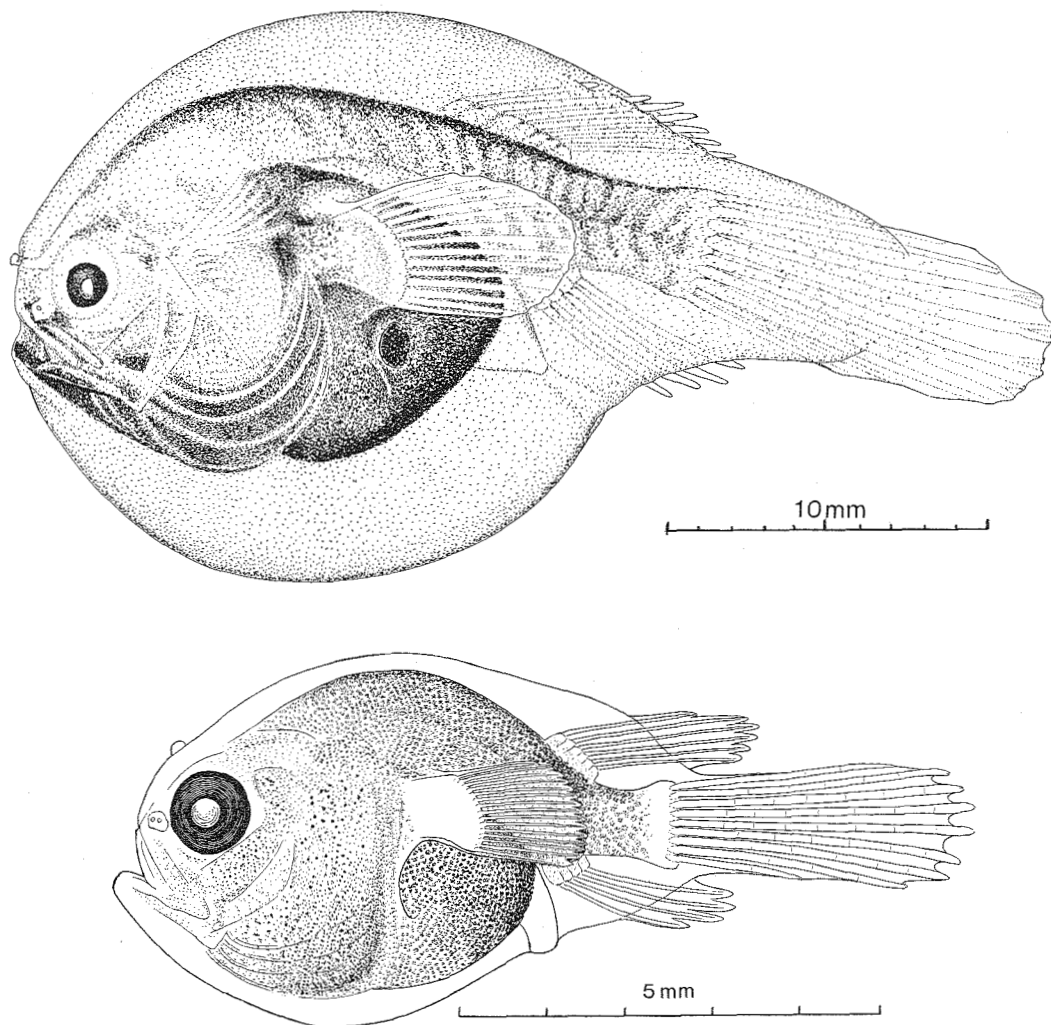


Fig. 15. Female larvae of *Thaumatchthys*. Above, 22.6 mm (LACM 31107-1). Below, 6.5 mm (*Dana St. 3999*, from Bertelsen 1951).

C. LARVAE

Bertelsen (1951) tentatively referred four larvae, 4.4, 6, 10 and 24 mm in total length, to *Thaumatchthys pagidostomus*. Comparison of his description of the osteology of the largest of the specimens with that of the adolescents and adults here presented, confirms the correctness of the reference to this genus. This appears from several characters, and, in particular, from the presence of a multiradiate operculum which, among ceratioids, is found only in *Thaumatchthys*.

Furthermore, these larvae differ from all other known ceratioid larvae in that the subdermal pigment layer covers the whole surface of head and body with concentrations along the margin of the gillcover, on peritoneum, and on the back. There is less or no pigment on the pectoral lobes and at the

base of the caudal fin. Scattered small melanophores are present in the outer transparent skin.

The female larva, LACM 31107-1 (Fig. 15), recorded by Brewer (1973), fits this description. It is somewhat larger, 34.1 mm in total length (22.6 mm s.l.), than the largest of the previously known specimens, and, in accordance with this, the pigmentation of the outer skin is more densely pigmented. Its meristic and morphometric characters are given in App. Table 1.

Bertelsen's (1951) specific identification of the larvae was based on the assumption that *T. binghami* had only four dorsal fin rays as by mistake stated by Parr (1927). As no significant differences in pigmentation or other characters between the larvae from different areas could be found it has not been possible to refer them to species.

III. DISTRIBUTION

The known 32 records of *Thaumatichthys* indicate a worldwide distribution of the genus in the tropical zones of the oceans (Fig. 16). The holotype of *T. pagidostomus* was caught in the Gulf of Tomini, off Sulawesi (Celebes). The holotype of *T. axeli*, the second specimen referred to this species, and one larva came from the eastern Pacific between lat. 09° and 32°N close to the American west coast. The type of *T. binghami*, the 22 other metamorphosed females referred to this species, the metamorphosed male, and one of the larvae are all caught between lat. 10° and 30°N in the Gulf of Mexico, the Caribbean Sea, and the adjacent Atlantic waters off the Bahamas. Finally, two larvae were collected in the eastern central Atlantic off the Gulf of Guinea, and one larva in the Indian Ocean in the southern part of the Mozambique Channel. Except for the two larvae which were caught 450-500 miles off the African coast, all the specimens came from positions less than 250 nautical miles from land.

Of the 32 specimens representing *Thaumatichthys*, 5 larvae and 3 of the youngest metamorphosed specimens were caught in open pelagic nets fishing well above the bottom, while all the remaining 24 specimens were caught in bottom trawls.

The three smallest larvae (less than 6.5 mm s.l.) were caught in open nets fishing in maximum depths of about 20 to 100 m below the surface. The two

larger larvae (18.5 and 22.6 mm) were obtained in nets which had their main fishing depths at about 1500 and 780 m, respectively. Finally, the three young metamorphosed *T. binghami* of 36.5, 40.0, and 45.0 mm were caught in pelagic hauls with estimated maximum depths of 1000 to 1750 m.

Of the 20 *T. binghami* females (40.5 - 293.5 mm) from bottom trawls, 18 were caught on the continental slope at depths between 1270 and 2193 m, one at 1100 m, and a single specimen from the central Gulf of Mexico at 3151 to 3200 m. The single, metamorphosed male was caught together with one of the females at 1938 m.

Both specimens of *T. axeli* were caught at abyssal depths of 3570 and 3595-3695 m, respectively. Finally, the holotype of *T. pagidostomus* was obtained at 1440 m.

Thus, it appears that the young larvae of *Thaumatichthys* are epipelagic as those of other ceratioids. The older larvae and youngest metamorphosed females are meso- and bathypelagic, and at a length of 40 to 50 mm they become benthic in contrast to all other known ceratioids. Most *T. binghami* and the only known *T. pagidostomus* are caught on the continental slope in bathyal depths of between 1000 and 2000 m, while both specimens of *T. axeli* were obtained in abyssal depths of about 3600 m.

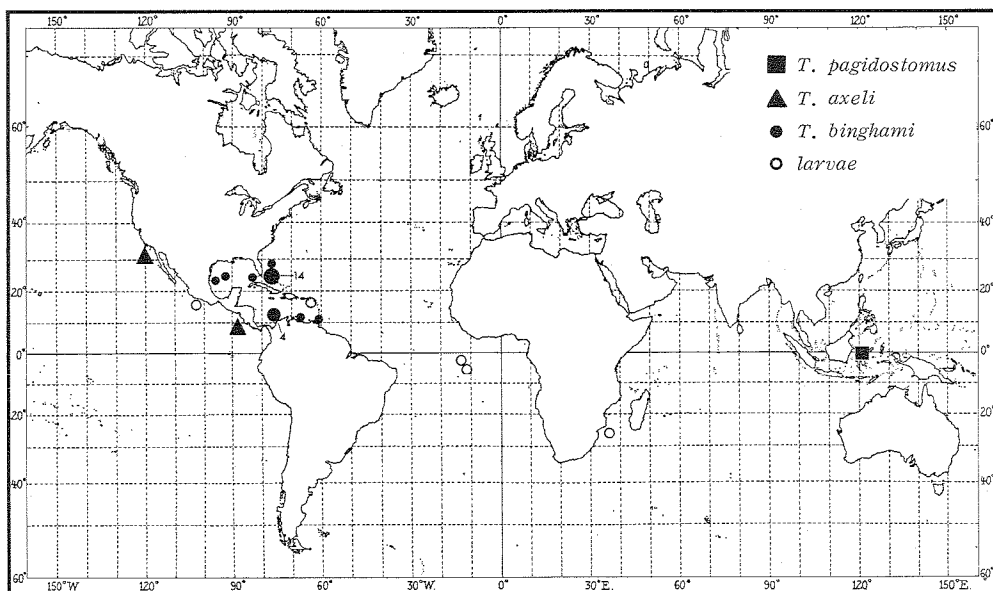


Fig. 16. Known distribution of *Thaumatichthys* species.

IV. BIOLOGY AND FUNCTION OF JAW MECHANISM

In his description of *Galatheathauma axeli*, Bruun (1953, 1956) assumed that adolescent and adult *Thaumatchthys* might be benthic. He wrote: "There is a possibility that our fish was caught as the trawl was on its way up; but if that were so, it is strange that it had never been caught before. It seems to me to be far more probable that we here have a deep-sea angler-fish which lives close to the bottom. There it need only lie with its jaw open, leaving the large light organ ... to lure the fish or prawn to it; ..." This assumption has now been supported by the numerous records of specimens caught in bottom trawls and by the continued lack of catches in pelagic nets except for larvae and juveniles. Furthermore, as discussed below, several features in the morphology of *Thaumatchthys* may be regarded as adaptations to benthic life. As a final proof of the correctness of this assumption, stomach contents of unquestionable benthic origin was found in one of the specimens here described.

Most of the specimens were examined for stomach contents, but, except for the largest specimen of *T. binghami*, they were all empty. The stomach of this individual contained three well preserved specimens (50-80 mm long) of the holothurian *Bentho-dytes typica*. According to Bent Hansen (Zool. Mus., Copenhagen), who has kindly identified the specimens, this species occurs in abyssal and bathyal depths. Its anatomy suggests that it is benthic. A piece of dead sargasso weed and some undeterminable plant remnants were found imbedded between the holothurians.

The extraordinary jaw mechanism of *Thaumatchthys* has been commented on by several authors. Smith & Radcliffe (1912) named the first known specimen *pagidostomus*, i.e. "trap-mouth", and wrote "It would appear that the cavernous, elastic mouth is a trap into which the food is lured and dispatched". Regan (1926) pictured the similar jaw mechanism of *Lasiognathus saccostoma* with opened and closed premaxillaries, and wrote "... the prey, which is evidently enclosed by the downward movement of the premaxillaries, the bristle-like teeth being used not for piercing, but to close the aperture of the pouch", and Bruun (1956) called the *Galathea* specimen "a living 'mouse-trap' with bait".

The main element of this mechanism is shown in Fig. 17. The anterior tip of each premaxillary is connected with the head of the maxillary and of the

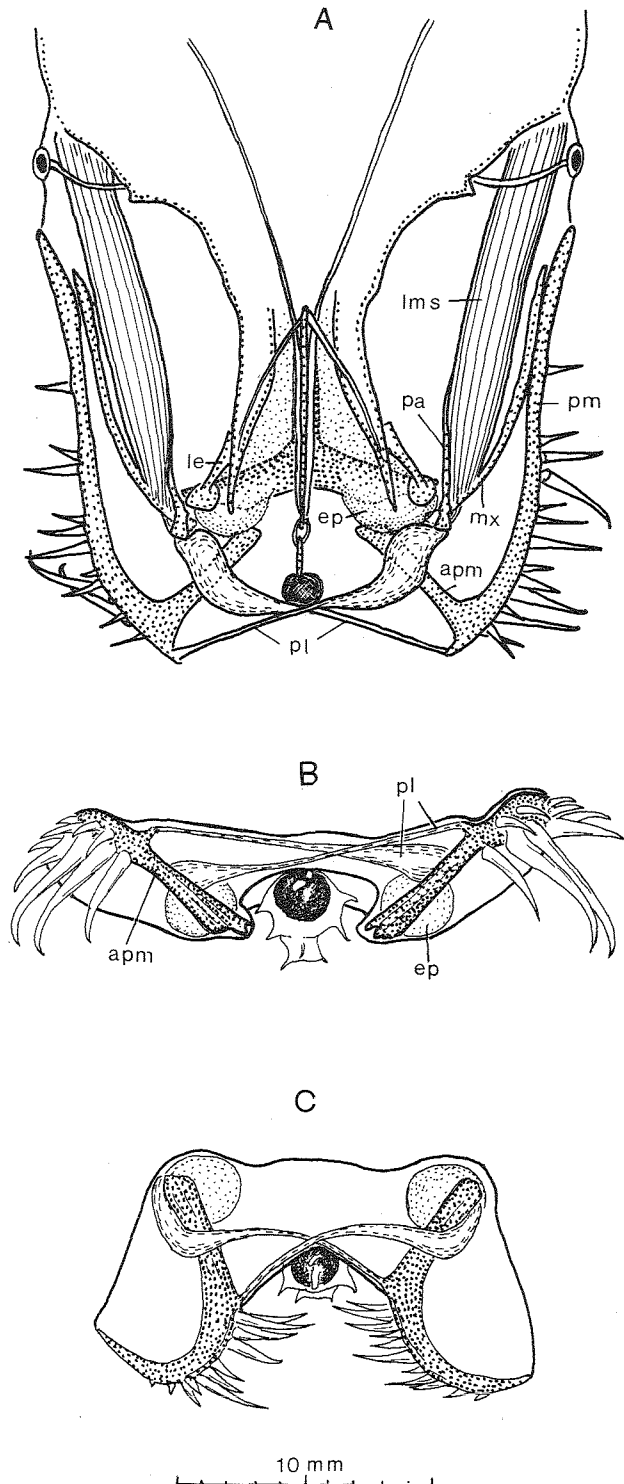


Fig. 17. Jaw mechanism of *Thaumatchthys binghami*. A, dorsal view; B and C, anterior views; A and B, open; C, closed. (apm: articular process of premaxillary, ep: projection of ethmoid cartilage, lms: levator maxillae superioris, pl: premaxillary ligaments; other abbreviations as in Fig. 1).

palatine of the opposite side by a very elastic ligament (here termed "the premaxillary ligaments"). The two ligaments cross each other in front of the esca. Their more slender distal parts in front of this crossing support the edge of the membrane connecting the premaxillaries; posteriorly they are club-shaped and inflated and pass over the long articular processes of the premaxillaries. The premaxillary processes, which are loosely attached to the maxillaries by ligaments, are able to rotate on the semispherical projections of the ethmoid cartilage. In relation to the longitudinal axis of the head, the premaxillaries are rotated nearly 180° when they are moved from the open to the closed position. The articular processes of the premaxillaries point obliquely down and inwards when the jaws are lifted, and up and outwards when they are lowered. In both positions the elastic premaxillary ligaments pull the tips of the premaxillaries towards each other, thus contributing to the opening as well as the closing of the mechanism. This can be observed directly on the preserved specimens in which the ligaments are still very elastic. When the premaxillaries are pushed from the open position in which they are usually preserved, the ligaments are stretched until a certain intermediate position is reached, and will then snap the jaws together into the closed position.

However, the long and extremely well developed upper jaw muscles (*levator maxillae superioris*) which posteriorly are inserted on the hyomandibulars and anteriorly on the anterior end of the maxillaries, form the main "spring" of the "trap". Their contraction will cause a back and slightly outwardly directed pull on the maxillaries which, directed by the cartilages and ligaments, is transferred into an up and outward pull in the articular processes of the premaxillaries in such a way that these long processes, like a pair of handles, will turn the jaws downwards into the closed position. As no muscles are present which can account for the lifting of the premaxillaries, it must be assumed that the relapse into this position is accomplished by the elastic ligaments, bones, and cartilages of the mechanism when the levator muscles are relaxed.

This highly specialized jaw mechanism permits the upper and lower jaw to function independently. With the premaxillaries in open position ready for

catch, the lower jaw will be able to open and close in connection with the respiration, and a prey trapped by the long teeth of the closed premaxillaries can be transported further into the mouth within reach of the pharyngeal teeth by movements of the lower jaw.

By means of the extensor and flexor muscles of the illicium, the esca can be raised to a more exposed position under, or in juveniles in front of, the incurved anterior edge of the membrane connecting the premaxillaries, and inclined down and backwards toward the roof of the mouth. Possibly the main function of these muscles is to produce a vibrating movement of the lure.

When the premaxillaries are closed, the esca is completely hidden and protected (Fig. 17 and Plate 2), with the possible exception of the greatly prolonged median appendage of certain specimens (Figs 10 and 12).

According to their positions, the eyes, olfactory organs, and the enlarged sensory papillae on the head are adapted to detecting prey or enemies near the sea floor. The small eyes on the edge of the depressed head will be able to scan the bottom close to the jaws. Most probably they function merely as light detectors because the lens, as in other female ceratioids, is situated close to the retina and probably cannot produce clear images (Munk 1966). This seems to exclude the possibility that the light from the esca can be used directly in search of food. The downward directed nasal papillae and enlarged sensory papillae of the subopercular series, as well as the enlarged papillae on the roof of the mouth, are in an optimal position for the detection and examination of prey on the sea floor.

The fact that the only known stomach contents of a *Thaumatichthys* consists of holothurians (which might not be expected to be attracted by light) as well as of quite large plant remnants, confirms the impression obtained through examination of the food of other ceratioids (Bertelsen 1951, Pietsch 1974, Nolan & Rosenblatt 1975) that, in spite of their highly specialized feeding mechanisms, these fishes tend to be omnivorous. By means of these mechanisms, they are enabled to catch otherwise difficultly obtained prey, but they will swallow anything that might serve as food.

V. CLASSIFICATION AND RELATIONSHIPS

with a comparative description of the osteology of *Lasiognathus*

The family Thaumatchthyidae was erected by Smith & Radcliffe (1912) in connection with their description of its first known species, *T. pagidostomus*. They distinguished the family from "the Ceratiidae" which, at that time, included all other known genera of ceratioids, "by the greatly expanded and depressed head, the slender body, the shape of the upper jaw, the dentition, the absence of free dorsal spines, the remarkable modification of the illicium, etc."

In connection with the preliminary descriptions of new genera and species of ceratioid fishes, Regan (1925) divided the suborder into six families. In one of the new families, the Oneirodidae, he placed *Oneirodes* Lütken, 1871, *Dolopichthys* Garman, 1899, *Lophodolus* Lloyd, 1909, and a new genus, *Lasiognathus*, which he defined (l.c.) as "Near *Dolopichthys*, but upper jaw projecting far in advance of lower, and premaxillaries connected with head by a wide membrane, which permits them to meet anteriorly either above the snout or below it". *Thaumatchthys* Smith & Radcliffe, 1912, is not mentioned in this paper, but in Regan's more detailed revision of the suborder Ceratioidea (Regan 1926), it is included in the Oneirodidae with the definition "Resembles *Lasiognathus* in structure of mouth, but is generically distinguished by the shorter head, the dentition, the illicium, and the spinate skin of the lower half of the fish". Regan & Trewavas (1932) kept *Lasiognathus* and *Thaumatchthys* in the Oneirodidae and erected for *T. binghami* Parr, 1927, a new genus *Amacrodon* based on its apparent great difference from *Thaumatchthys* in dentition. Bruun (1953) did not state directly his reasons for placing *Galatheathauma axeli* in a new genus separate from *Thaumatchthys*. Whitley (1970) erected a new family, Galatheathaumatidae, for this species, solely based on the statement that "it differs from other families of angler-fishes in having the luminous lure forked and hanging down from the palate inside the mouth". No reference was made by Whitley to *Thaumatchthys* or *Amacrodon*.

Pietsch (1972) resurrected the family Thaumatchthyidae Smith & Radcliffe, 1912, to include *Lasiognathus* Regan, 1925, *Thaumatchthys* Smith & Radcliffe, 1912, and *Amacrodon* Regan & Trewavas, 1932 (*Galatheathauma* Bruun, 1953, is not mentioned). He states (l.c.) that "... these genera

possess several important and unique characters that justify familial status", but no characters other than the projecting upper jaw and the presence of denticles on the esca are mentioned.

As will appear from the preceding description of the individual and ontogenetic variations observed in the now known specimens, none of the differences between *Thaumatchthys* and the type species of the two genera *Amacrodon* and *Galatheathauma* are of an order which justifies a separation on generic level, for which reason they are here synonymized.

To evaluate the justification of placing *Thaumatchthys* and *Lasiognathus* in a family separate from the Oneirodidae, it is necessary to consider the characters which are common to these two genera as well as those which link *Lasiognathus* to the oneirodids. For this reason the osteology of a specimen of *Lasiognathus* was examined*. As the main features of its osteology will appear directly from the illustrations (Fig. 18), and as a complete description would be outside the scope of this paper, only those details will be considered here which seem relevant to the discussion of its relationships.

The three characters which are common to these two genera and distinguish them from all other ceratioids will be discussed first:

1) The jaws. In contrast to all other ceratioids, the premaxillaries of *Thaumatchthys* and *Lasiognathus* are extended far beyond the lower jaw, carry long, hooked teeth, are anteriorly separated and connected only by a membrane, and can be turned upwards and downwards (in the latter position enclosing the lower jaw). In both genera the upper jaw is posteriorly connected to the dentary by means of thin ligaments instead of the solid labial cartilage which, according to Pietsch (1972, 1974), is found in all members of the Oneirodidae.

However, in a number of details this jaw mechanism is differently developed in the two genera.

In contrast to *Thaumatchthys*, the articular processes of the premaxillaries of *Lasiognathus* are relatively short and do not reach the ethmoid cartilage but are attached to anterolateral projections of a well developed, anteriorly notched symphyseal

* This 40.1 mm specimen (SIO 73-305) is recorded by Nolan & Rosenblatt (1975) and kindly presented to the ZMUC. As it lacks esca no specific identification is possible.

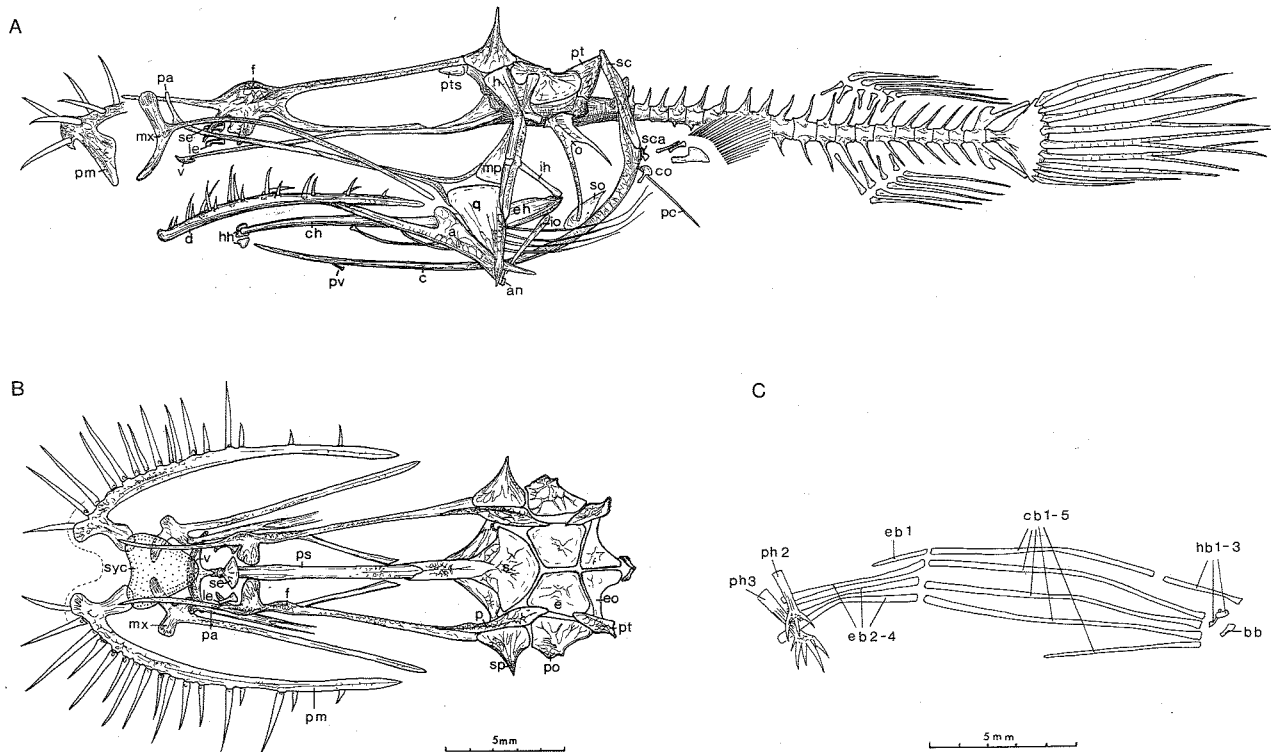


Fig. 18. Skeleton of *Lasiognathus* sp., 40.1 mm (SIO 73-305). A, lateral view; B, dorsal view of head; C, branchial arches. (syc: symphyisial cartilage; other abbreviations as in Figs 1 and 5).

cartilage (syc in Fig. 18). This cartilage is present in all oneirodids (Pietsch 1974), but absent in *Thaumatichthys* (cf. p. 9). As in the oneirodids, the posterior end of this cartilage slides on the anterior, slightly concave dorsal surface of the ethmoid cartilage. Furthermore, the dorsal as well as the ventromedial processes of the head of the maxillaries are extremely large and prolonged and clasp the lateral sides of the symphyisial cartilage. The levator maxillae superioris muscles are shorter and are attached by a slender ligament to the ventromedial process of the head of the maxillae, rather than behind this head as in *Thaumatichthys*. No premaxillary ligaments are developed (cf. p. 29-30).

The premaxillary teeth of *Lasiognathus* tend to be grouped in oblique series (of 1+1+2+3+3+2+2+1 in left side of the examined specimens), with the anteromedial teeth increasing in length as in *Thaumatichthys*, but the arrangement in regular longitudinal series found in this genus is not distinctly developed.

2) The esca denticles. In most of the genera of ceratioids which have spines in the skin (*Himantolophus*, *Ceratiias*, *Gigantactis*, etc.), similar dermal spines may be present on the stem of illicium and base of esca, but only *Thaumatichthys* and *Lasio-*

gnathus carry specially developed and arranged denticles on, or imbedded in the distal part of esca.

However, from the descriptions and personal examination of the esca denticles of the holotype of *Lasiognathus saccostruma* and the three specimens of this genus described by Maul (1961, 1962) it appears that, besides in numbers (3), they differ from that of *Thaumatichthys* in shape, colour and position. While the latter is compact and pointed at both ends, transparent and deeply imbedded in the tissues of esca, those of *Lasiognathus* are darkly coloured and have a broad and hollow conical base which is attached superficially in the skin of esca, and thus seems much more similar to skin spines than the *Thaumatichthys* denticle. Additionally, in the *Lasiognathus* species the esca denticles are either borne directly on the esca, or on a filament arising from the esca bulb (Nolan & Rosenblatt 1975).

3) The branching of operculum. In contrast to all other ceratioids, the upper branch of operculum in *Thaumatichthys* and *Lasiognathus* is divided into two or more branches. A more or less broadly expanded upper branch of the operculum with supporting ribs is found in certain oneirodid

genera (e.g. *Chaenophryne* and *Danaphryne*), but in no case with the posterior end divided into two or more points.

The operculum in *Thaumatichthys* is split up into a total of 5-13 radiating rays, including those which seem derived from the lower expanded branch. In *Lasiognathus*, the lower branch of the bifurcated operculum is slender and undivided, while the upper branch is expanded, and in all examined specimens more or less distinctly divided into two by supporting ribs and a low incurvation of its posterior margin. The upper operculum branch may carry a third point as shown in the left operculum of one of the specimens described by Maul (1961). We have examined the small holotype of *Lasiognathus beebi* (USNM 170956) and found it in poor condition. The left operculum figured by Gregory (1933:403), is shriveled and deformed. The three rays of the upper branch of the right operculum are actually ridges, and the shape of the operculum more closely resembles that of the dashed line in Gregory's drawing (see also Bertelsen 1951).

From this it will appear that, in spite of the similarities, these three characters differ significantly in a number of details in the two genera. Especially in possessing a symphyseal cartilage and in the shape of operculum, *Lasiognathus* is less distinct from other ceratioids and more similar to the Oneirodidae than *Thaumatichthys*.

Furthermore, *Lasiognathus* differs from *Thaumatichthys* and shows similarities to Oneirodidae in the following characters:

- 1) a normally developed supraethmoid is present (Fig. 18B)
- 2) the frontals are anteriorly notched, each with a straight, anteriorly directed slender branch and a ventromedial curved shorter branch; behind the anterior branches each frontal has two ventromedial extensions which contact the parasphenoid; the anterior is short and broad, the posterior long and slender; posteriorly the frontals are widely separated and extremely narrow (Fig. 18A and B)
- 3) the anterior ends of the parietals overlap the posterior part of the frontals (Fig. 18B)
- 4) the sphenotics are large (Fig. 18A and B)
- 5) a small anterior extension of the pterotic overlaps the posterolateral surface of the sphenotic (Fig. 18A and B)
- 6) the epiotics are closely adjoined behind the supraoccipital (Fig. 18B)

- 7) the first epibranchials are present (Fig. 18C)
- 8) the illicium is carried in normal position by a very long pterygiophore, which slides in a deep groove in the upper surface of the skull and between the dorsal muscles of the anterior part of the body
- 9) the third pectoral radial is much larger than the second (Fig. 18A)
- 10) the pelvic bones are close set and not posteriorly connected by cartilage
- 11) the posterior margin of the hypural plate is unnotched (Fig. 18A)
- 12) the skin lacks spines
- 13) none of the adaptations to benthic life observed in *Thaumatichthys*, i.e., the depressed shape of head and anterior part of body, the ventrad displacement of eyes and olfactory organs, and the special development of downward oriented, enlarged sensory papillae, are present.

As the male of *Lasiognathus* is unknown, no comparison with characters observed in the male of *Thaumatichthys* is possible. However, this male shows some differences from oneirodids, additional to those observed in the females:

- 1) the upper denticles are few (4), symmetrically arranged and not fused at base (in oneirodids five to more than twenty, irregularly arranged and emerging from a common bony plate)
- 2) they are carried by the head of the unresorbed premaxillary (in oneirodid males, the premaxillaries are nearly completely resorbed).

Pietsch (1974) illustrated the phenetic relationships of nine oneirodid genera in the form of a dendrogram based on an analysis of 28 osteological characters each of which were divided into primitive and derived states according to their occurrence in all ceratioids. If the same characters of *Lasiognathus* are evaluated and treated in the same manner, the genus fits into the dendrogram, and would represent a branch close to that of the genus *Dolopichthys*.

The close relationship with oneirodids which, in contrast to *Thaumatichthys*, is found in *Lasiognathus*, and the fact that the two genera show quite noticeable differences even in details of the characters they share might raise the question whether they might be of different descent, and that their similarities might be explained as convergent adap-

tations. This, however, is hardly probable as it is strongly contradicted by the fact that the three characters which they share and which distinguish them from all other ceratioids seems mutually independent; i.e., the development of denticles on esca as well as the branching of operculum can hardly be supposed to be connected with the specialization of the jaw mechanism.

Most of the characters in which *Thaumatichthys* differs from *Lasiognathus* might be explained as direct results of its unique specialization towards benthic life. The change in shape of head and the displacement of illicium and reduction of its pterygiophore might have led to the change in shape of frontals and in jaw mechanism, which again might have led to the loss of the symphyseal cartilage and supraethmoid. It seems more difficult to explain the presence in *Thaumatichthys* of a deep posterior notch in the hypural plate which, according to Pietsch (1972, 1974), is absent in all oneirodids and should be regarded as a primitive character. Possibly the reestablishment of this notch might be caused by some change in the function of the caudal fin in connection with the returning to benthic swimming.

Thus, it becomes a subjective choice whether the genera *Lasiognathus* and *Thaumatichthys* both should be included in the Oneirodidae as Regan (1926) did, or placed together in *Thaumatichthyidae* as proposed by Pietsch (1972), or whether each of them should be referred to a family of its own. The differences between the two genera seem in fact to be of a similar order as those which separate *Lasiognathus* from oneirodids, and as those which are used for the separation of several of the six ceratioid families which are based on a single genus each. However, to avoid superfluous alterations we prefer to retain *Thaumatichthyidae* Smith & Radcliffe in the enlarged sense proposed by Pietsch.

The separation to species promulgated here of the known specimens of *Thaumatichthys* is in accordance with their distribution. The specimens from the western North Atlantic area are all referred to *T. binghami*. As the esca is badly preserved in the holo-

type and only known specimen of *T. pagidostomus* from near Sulawesi (Celebes), the only observed characters which distinguish *T. binghami* from this species are small but, according to the observed intraspecific variations, significant differences in length of certain premaxillary teeth (p. 18), in relative length of the premaxillary bone (p. 11), and relative size of skin spines (p. 24). The holotype of *T. axeli* and the only other metamorphosed specimen from the eastern Pacific were found to differ from *T. binghami* only in certain esca characters (p. 22). In the characters which distinguish *T. pagidostomus* from those referred to *T. binghami* they are similar to the latter.

As shown (p. 21), considerable differences were observed in the number and development of the different appendages of the esca in species of *Thaumatichthys*. The most conspicuous is the development of the second of the two medium appendages which, in some specimens, is developed into a large wormlike organ, a small digitiform in others, and nearly completely absent in the two largest Caribbean specimens as well as in the large holotype of *T. axeli*. If the different developments of this appendage represent specific differences, the Caribbean material should, besides *T. binghami*, include one or two new species (two of which were collected within a few kilometers of each other) and, furthermore, the smaller Pacific specimen referred to *T. axeli* should represent a distinct species. Such a separation seems most unlikely, and is in no way supported by a comparative examination of measurements and counts.

On the basis of the available material, it is more reasonable to conclude 1) that the intraspecific variation in the esca appendages is somewhat larger in *Thaumatichthys* than usually assumed in the ceratioids; 2) that the enlargement of the second median appendage of the *Thaumatichthys* esca starts at a somewhat different size or age of individuals; 3) that this fragile, wormlike part of the "bait", which is left unprotected when the upper jaws are closed, is exposed to attack from predators and is normally lost in older individuals.

VI. TAXONOMY

Family THAUMATICHTHYIDAE

Smith & Radcliffe, 1912.

Thaumatichthyidae Smith & Radcliffe, 1912.

Thaumatichthyidae (to include *Thaumatichthys*, *Lasiognathus*, and *Amacrodon*): Pietsch 1972; Brewer 1973; Nolan & Rosenblatt 1975.

Oneirodidae (in part): Regan 1925, 1926; Regan & Trewavas 1932; Bertelsen 1951.

Galatheathaumatidae (separate for *Galathea-thauma*) Whitley, 1970.

Type genus: *Thaumatichthys* Smith & Radcliffe, 1912.

Females: The family Thaumatichthyidae is related to Oneirodidae but distinguished from this and all other families of the suborder Ceratioidei in each of

the following characters: premaxillaries extending far beyond the lower jaw, anteriorly separated, only connected by an elastic wide membrane; 1-3 denticles on esca; upper arm of operculum divided into two or more branches. Furthermore, it differs from all other families in the following combination of characters: parietals present; pterosphenoids present; hyomandibular with double head; quadrate spine well developed; two hypurals; six branchiostegal rays; epi- and ceratobranchial teeth absent; three pectoral radials; pelvic bones rod-shaped, slightly expanded distally; illicium and esca light organ present; second cephalic ray rudimentary, labial cartilage absent.

Males and larvae only known in *Thaumatichthys*, cf. this genus.

Key to the genera of THAUMATICHTHYIDAE (females)

- 1 a. Head narrow, illicium and its pterygiophore long, in normal position on head; esca with three denticles; skin naked; D 5, A 5 *Lasiognathus*
- 1 b. Head broad, depressed; illicium and its pterygiophore short; esca sessile in roof of mouth, with one denticle; skin of lower part of head and body spiny; D 6-7, A 4 *Thaumatichthys*

Further diagnostic characters of the genus *Lasiognathus* will appear from the following diagnosis for *Thaumatichthys*. For synonymy and key to the species of *Lasiognathus*, cf. Nolan & Rosenblatt (1975).

Genus *Thaumatichthys* Smith & Radcliffe, 1912

Thaumatichthys Smith & Radcliffe, 1912; Regan 1926; Parr 1927; Regan & Trewavas 1932; Bertelsen 1951; Pietsch 1972; Brewer 1973.

Amacrodon Regan & Trewavas, 1932; Parr 1934; Bertelsen 1951; Pietsch 1972.

Galatheathauma Bruun, 1953; Bruun 1956; Wolff 1960, 1961; Whitley 1970.

Type species: *Thaumatichthys pagidostomus* Smith & Radcliffe, 1912.

Females of the genus *Thaumatichthys* are distinguished from the only other genus of the family as well as from all other known ceratioid fishes in being benthic, having the esca sessile in the roof of the mouth and with a deeply imbedded single curved denticle, depressed head with eyes and olfactory

papillae posteroventrad displaced to the corner of the mouth, and operculum divided into 6-13 radiating rays.

Furthermore, it differs from *Lasiognathus* in the following characters: symphyseal cartilage absent; supraethmoid absent in juveniles, incompletely developed in adults; frontals anteriorly unnotched and lacking posterior ventromedial extensions; sphenotic small with short spine; head of maxillary with short processes; first epibranchials absent; second and third pectoral ray of nearly equal size, fusing with age; pelvic bones widely spaced, distally connected by a band of cartilage; hypural plate with a deep posterior notch; six to seven dorsal and four anal fin rays; pterygiophore of illicium short, completely hidden under skin of head; esca with one to three pairs of lateral, pointed lobes, in larger specimens prolonged into tapering tentaclelike filaments and two median appendages, the posterior one pigmented and, in certain stages, greatly prolonged; enlarged sensory papillae under eye and anteriorly in roof of mouth; skin with spines on lower part of head and body.

Thaumaticthys males differ from all other known ceratioid males in the development and position of the denticles on the snout. They have toothless but otherwise unresorbed premaxillaries carrying at tip 4 separate denticles arranged in two pairs above each other; the lower pair shorter and more strongly hooked than the upper; on tip of lower jaw 7 denticles, fused at base and arranged in a lower transverse series of 4 and an upper of 3 which are shorter and more hooked than in the

lower series. Furthermore, they are distinct from all other ceratioids in having operculum divided into several (7-13) radiating rays, and from *Lasiognathus* in lacking supraethmoid and in having 6-7 dorsal, 4 anal fin rays and spiny skin.

Thaumaticthys larvae differ from all other ceratioid larvae in having a layer of subdermal melanophores covering the whole surface of the head and body, and, furthermore, from *Lasiognathus* in number of dorsal and anal fin rays.

Key to the species of THAUMATICHTHYS (females)

- 1 a. Length of premaxillary 33% s.l. Anterior premaxillary teeth long: I 1:3.8, II 1:3.0, II 2:6.5, II 3:7.0, III 2:3.3, III 3:4.3, IV 2:2.4 and V 2:3.4 mm *pagidostomus* (off Sulawesi)
- 1 b. Length of premaxillary 23.5%-27.0% (average 25.4%) s.l. (in specimens of 40 mm and more). Anterior premaxillary teeth somewhat shorter: I 1:2.2-3.5, II 1:1.1-2.3, II 2:3.0-5.6, II 3:3.8-5.8, III 2:0.8-2.3, III 3:1.8-3.4, IV 1:0.9-2.3 and V 2:0.8-2.6 mm 2
- 2 a. Esca with two or three pairs of lateral pointed lobes which in larger specimens are prolonged into tapering tentaclelike filaments; the uppermost median appendage of esca digitiform and tapering *binghami* (Caribbean and adjacent waters)
- 2 b. Esca with a single pair of lateral pointed lobes which in larger specimens are prolonged into tapering tentaclelike filaments; the uppermost median appendage of esca wartlike and un-tapering *axeli* (tropical eastern Pacific)

Thaumaticthys pagidostomus

Smith & Radcliffe, 1912

(Figs 3, 7, 8, 13, 16)

Thaumaticthys pagidostomus Smith & Radcliffe, 1912, p. 580-581; Regan 1926, p. 31; Parr 1927, p. 24; Regan & Trewavas 1932, p. 91; Bertelsen 1951, p. 121 (in part).

Holotype USNM 72952, a female 60.0 mm s.l. Albatross St. 5607, off Sulawesi (Celebes) 00°04'S, 121°36'E, beam trawl at 1440 m, 18 Nov. 1909.

Diagnostic characters in the key.

No other records.

Thaumaticthys binghami

Parr, 1927

(Figs 1, 3-11, 13, 14, 16, 17; Pls 2, 3)

Thaumaticthys binghami Parr, 1927, p. 24-25.

Amacrodon binghami, Regan & Trewavas 1932, p. 91; Parr 1934, p. 7; Bertelsen 1951, p. 122.

Holotype BOC 2015, a female 36.5 mm s.l. Pawnee St. 25, 24°51'N, 76°37'W, pelagic net with 8000 feet wire, 17 March 1927.

Diagnostic characters in the key.

Examined material (including the holotype): Seventeen female specimens 36.5-293.5 mm s.l. (cf. App. Table 1), all from the Caribbean and adjacent areas. Three specimens 36.5-45.0 mm caught pelagic in intermediate depths, the other 14 specimens, 40.5-293.5 mm, in bottom trawls at 1100-3200 m (cf. p. 29).

After this study was finished we have been informed that in the Tongue-of-the-Ocean Programme of UMML additionally 6 *Thaumaticthys* females, 55.6-134.0 mm, have been obtained, all in semi-balloon trawl at depths from 1387 to 2193 m and inside the area 23°52'-24°46'N, 75°26'-77°22'W. According to information on their esca characters, kindly furnished by Dr. Jon C. Staiger, they represent *T. binghami*.

The metamorphosed male, 31.0 mm (ZMUC P921946) and the male larva, 18.5 mm (*Dana* St. 1186), both from the same area, most probably belong to this species.

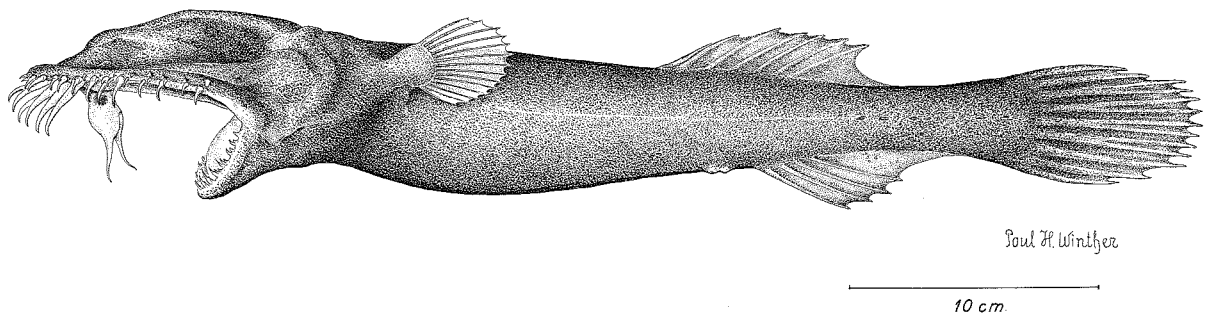


Fig. 19. The holotype of *Thaumatischthys axeli*.

Thaumatischthys axeli

(Bruun, 1953)

(Figs 2, 3, 6, 7, 8, 12, 13, 15, 16, 19; Pl. 1)

Galatheathauma axeli Bruun, 1953, p. 174-177, 1956, p. 174-177; Wolff 1960, p. 175, 1961, p. 137; Munk 1964, p. 10; Whitley 1970, p. 246.

? *Thaumatischthys pagidostomus*, Brewer 1973, p. 25.

Holotype ZMUC P92166, a female 365 mm s.l. (Fig. 19). *Galathea* St. 716, 09°23'N, 87°32'W, in herring otter trawl at 3570 m, 6 May 1952.

Diagnostic characters in the key.

A second female specimen of 85.5 mm, SIO 70-2265, Melville Expedition MV 69-VI, St. 9,

31°19.7'N, 119°39.2'W, in otter trawl at 1968-2019 fathoms (3595-3695 m) depth, 18 Dec. 1969. A female larva of 22.6 mm (LACM 31107-1) from the same eastern Pacific area may belong to this species (Fig. 15).

***Thaumatischthys* sp.**

Thaumatischthys pagidostomus (?) Bertelsen, 1951.

Three larval specimens, one male of 4.4 mm in total length from the Indian Ocean south of Madagascar (*Dana* St. 3964), one male of 6 mm (*Dana* St. 4000), and one female of 10 mm in total length (*Dana* St. 3999) from the equatorial east Atlantic cannot be referred to species.

VII. SUMMARY

This study is based on the 365 mm large holotype of *Thaumatischthys (Galatheathauma) axeli* (Bruun 1953) caught in the east Pacific by the Galathea Expedition, the eight previously known 3-60 mm specimens which are here referred to this genus, and seventeen 40.5-293.5 mm specimens not previously recorded.

A general description of the genus is presented, including the osteology, dentition, jaw mechanism and illicium and esca structures of the females and a description of the previously unknown male.

On this basis the taxonomy of the genus is revised. The genera *Amacrodon* Regan & Trewavas, 1932, and *Galatheathauma* Bruun, 1953, are synonymized with *Thaumatischthys* Smith & Radcliffe, 1912, and it is concluded that the known specimens of this genus represent three species: *T. pagidostomus* Smith & Radcliffe, 1912, *T. binghami* Parr, 1927, and *T. axeli* (Bruun, 1953).

The relationships of *Thaumatischthys* to other genera of Ceratioidea is discussed mainly on the basis of a comparative study of a representative of the genus *Lasiognathus* Regan, 1925, which together with *Thaumatischthys* forms the family Thaumatischthyidae Smith & Radcliffe, 1912, as resurrected by Pietsch (1972). It is shown that besides the characters which the two genera have in common and which separate them from all other ceratioids, *Lasiognathus* differs from *Thaumatischthys* and shows similarities to the family Oneirodidae in a great number of characters. This might warrant the erection of a separate family for the genus *Lasiognathus*, but in order to avoid superfluous alterations we prefer to retain Thaumatischthyidae in the enlarged sense proposed by Pietsch. Diagnosis of the family and keys to its genera and the species of *Thaumatischthys* are provided.

Appendix Table 1. Morphometric and mesteristic characters of the

species	<i>axeli</i> (holotype)	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>axeli</i>	<i>binghami</i>
Cat. no.	ZMUC P92166	USNM 214571	UMML 30958	ZMUC 1) P921950	UMML 27594	UMML 30930	USNM 214571	SIO 70-2265	ZMUC 2) P921947
Locality	9°23'N 87°32'W	9°58'N 76°29'W	24°23'N 77°23'W	10°10'N 76°14'W	11°25'N 67°10'W	24°15'N 76°07'W	9°58'N 76°29'W	31°20'N 119°39'W	11°30'N 60°14.5'W
Depth	3680 m	1271 m	1510 m	1100 m	1783- 1866 m	1737 m	1271 m	3700- 3800 m	1464- 1848 m
Total length mm	438.5	358.5	286	187.5	139.5	121.5	112.1	112.2	88.8
Standard length mm	365	293.5	225	142.5	112	95.5	87.1	85.2	73.1
No. of dorsal rays	6	7	7	7	7	6	7	7	7
No. of anal rays	4	4	4	4	4	4	4	4	4
No. of pectoral rays	14-14	15-15	15	15	15	14	15-15	16-16	15-15
No. of caudal rays	9	9	9	9	9	9	9	9	9
No. of vertebrae	21	21	..	21	21	22	21
No. of teeth in premaxillary:									
present	45-43	35-34	42	30-31	24	22	21	16	16
lost	10-11	3- 3	3
longest tooth, mm	21.5	24.0	15.2	11.3	9.8	8.1	5.0	4.8	5.7
No. of teeth in dentary	39-40	22	30	31-27	25	20	14	17	12
longest tooth, mm	10.5	10.3	7.9	5.6	3.8	2.4	2.6	1.5	1.5
No. of teeth in									
2. pharyngobr.	15-17	..	c16	..	12-11	10-11	..	8-8	6-6
3. pharyngobr.	25-24	..	c20	..	15-15	13-14	..	9-9	7-6
longest tooth, mm	5.5	..	c2.5	..	2.3	c2	..	2.2	1.6
Measurements in % of standard length:									
Tip of pmx - gill opening	41	c46	42.5	c45	40.5	44	45.5	c35	33.5
Tip of pmx - praeopercle	32.4	32.6	32.5	32.5	33.0	32.5	33.4	30.6	31.2
Scull length	23.3	29.0	c31	c31.5	28.2	c27	31.4	27.2	29.0
Width of head between:									
sphenotics	19.7	21.6	20.0	18.5	17.4	17.4	18.1	18.1	18.6
posttemporals	13.8	17.0	17.8	16.0	13.0	14.7	13.6	12.0	14.6
Least width of frontals	c4	6.5	7.5	c7	7.4	6.3	c7	6.3	6.7
Width between angular spines	34	31.8	33.5	31.5	28.5	24.6	28.0	24.6	28.0
Sphenot.-posttemp.	11.6	c8.5	12.5	12.6	c10.5	11.5	10.9	12.0	12.1
Sphenot.-angular spine	12.3	c10	13.8	11.8	10.7	11.5	10.1	10.8	12.1
Length of upper jaw	25.6	23.9	25.5	25.1	25.9	24.6	25.7	26.5	25.3
Length of lower jaw	22.5	20.1	21.8	20.9	22.4	20.4	20.0	c21	19.0
Diameter of eye	0.7	0.8	1.1	1.2	c1.8	1.8	1.5	2.2	1.9
Length of illicium	5.8	6.1	c6.5	6.0	c4.5		4.8	5.8	c5
Length of basal bone	13.6	c15		c14	15.8		15.0	14.1	13.1
Diam. of esca gland	2.5	2.7	3.8	3.5	3.2	3.0	3.0	2.9	2.6
Depth of body		c10	c13	c7.5	c10	c9.5	c8.5		
Least depth of caudal peduncle	c7	6.1	8.0	c7	6.6	6.8	c7		
Predorsal length	61.0	c67	62.0	c71	62.0	63.0	62.5	62.0	62.0
Preanal length	72.0	c85	77.0	81	78.0	78.0	81	73.5	76.0
Longest ray of:									
caudal fin	20.1	32.2	27.2	31.5	24.5	27.2	28.5	31.6	21.5
dorsal fin		9.5	14.1	16.5	c13.5		10.9	17.2	14.8
anal fin	c11.5	6.2	10.4	11.2	c10		9.8	12.7	14.8
pectoral fin	8.5	8.5	11.6	9.8	c9	c12.5	10.9	c9.5	10.5

1) Gift from National Fisheries Service, Pascagola, now deposited in ZMUC.

2) Gifts from UMML, now deposited in ZMUC.

Thaumatichthys species (*T. axeli* and *T. pagidostomus* in italics)

<i>binghami</i>	<i>binghami</i>	<i>pagidost.</i> (holotype)	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>binghami</i>	<i>binghami</i> (holotype)	sp. (larva)
ZMUC 2)	UMML	USNM	UMML	UMML	USNM	UMML	Texas Univ.	UMML	BOC	BOC	LACM	
P 921948	30926	72952	26927	31362	214570	31363	69-A-11-91	30866	3713	2015	31107-1	
10°03'N	24°20'N	00°04'S	23°33'N	23°48'N	25°41'N	23°39'N	22°52'N	28°38'N	25°39'N	24°51'N	17°02'N	
76°27'W	75°58'W	121°36'E	82°47'W	77°04'W	91°02'W	76°48'W	96°18'W	76°49'W	77°18'W	76°37'W	102°08'W	
1270-1820 m	1682 m	1440 m	1638-1757 m	1366 m	3151-3200 m	1307-1324 m	0-1550 m	1290 m	1050-1100 m	8000 f	780 m	
							pelagic		pelagic	pelagic	pelagic	
89.0	87.0	78.0	72.8	75.0	67.5	67.5	61.0	56.0	54.5	50.0	34.1	
69.9	67.0	60.0	57.2	58.0	51.5	50.5	45.0	40.5	40.0	36.5	22.6	
7	7	7	7	7	7	7	7	7	7	6	7	
4	4	4	4	4	4	4	4	4	4	4	4	
15-15	16	16-16	15-15	15	15	15	15	15	15	15	14-14	
9	9	9	9	9	9	9	9	9	9	9	9	
20	..	20	21	..	21	..	21	..	21	..	21	
14	16	16	14	..	13	16	11	15	12	12	..	
..	
5.8	4.3	7.0	4.8	..	4.3	5.2	3.0	4.5	1.7	1.5	..	
17	16	13	13	..	12	10	10	9	9	7	..	
1.9	2.0	2.0	1.2	..	1.5	1.5	1.2	1.2	(0.6)	
8- 8	c7	4- ?	4- 4	5- 5	4	5- 6	
9-10	c10	8- 8	6- 6	7- 7	5	7- 8	
1.5	..	2.0	1.5	c1.0	1.2	c1.0	
36-37	43		40.0	42.0	40.0	48.5	47.0	43.4	45.0	c44	c40	
30.8	33.8	35.0	33.8	30.2	31.0	34.5	32.0	c33	25.5		c26.5	
26.6	c29	29.0	29.1	27.5	27.5	31.5	31.0	c26	28.2		c26.5	
19.2	18.2	17.5	17.8	19.5	19.4	21.0	20.0	c18.5	19.0	21.8	22.1	
15.0	14.5	13.8	12.9	14.8	13.2	14.9	15.1		14.7		22.1	
7.4	6.3	7.5	6.6	6.9	7.8	8.0	6.7	c8	7.3		c17	
27.8	27.0	32.4	22.7		27.2		28.9		31.3	c23		
12.2	11.4	10.7	11.5	c11.5	12.6	13.7	14.9		16.8		c17	
12.8	13.2		13.6	14.4		13.9	15.2		15.6	16.5	27.4	
24.3	25.0	32.8	25.5	26.0	23.4	26.5	26.3	27.0	25.0	17.8	15.5	
19.6	21.7	26.2	20.4	20.0	21.8	21.8	22.2		19.7	18.2	20.4	
2.4	2.2	2.5	2.6	3.3	2.3	2.8	3.3	3.0	3.0	4.4	6.2	
c5.5			5.9		4.8		5.6		5.7	5.5	3.5	
14.3	14.6	16.5	13.6	13.8	13.6		16.2	17.8	11.7		14.2	
2.1	3.6		2.8	2.6	3.3	3.4	3.7	4.0	3.0	3.3		
	12.4			13.0	13.0	14.3	15.6	c14	18.7	13.1	80	
	8.4	c7.5		9.1	10.2	9.3	11.6	9.4	13.5	9.3		
62.5	66.0	64.0	62.9	60.5	60.0	65.0	c65	c60	60.0	c63	66.3	
72.5	77.0	78.0	76.3	c80	78.0	80.0	c80	c43	73.0	c71	73.0	
27.4	30.0	c30	27.2	29.3	31.0	33.6	38.0	38.0	36.3	c33	51.0	
14.9	14.3	c12	c13	15.6	c18.5		c19	c25	c22.5		38.0	
14.3	11.2	c13	c13		c14.9		c10		c18.5		31.0	
12.3	12.7	c12	11.8	c13	14.7	13.5	15.5	16.5	16.7	15.4	23.0	

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