



Osteology of the telescopefishes of the genus *Gigantura* (Brauer, 1901), Teleostei: Aulopiformes

PETER KONSTANTINIDIS^{1*} and G. DAVID JOHNSON²

¹Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis OR 97331, USA

²Division of Fishes MRC 159, Department of Vertebrate Zoology, National Museum of Natural History, P.O. Box 37012, Washington, DC, USA

Received 26 February 2016; revised 26 May 2016; accepted for publication 8 June 2016

The two species of the family Giganturidae are highly derived aulopiform fishes that inhabit the mesopelagic realm of the oceans. Giganturids are exceptionally modified morphologically and, in particular, are characterized by numerous skeletal reductions that render the identification of the remaining elements problematic. The most debated of these are the toothed elements of the upper jaw, which have played a significant role in hypotheses about the phylogenetic affinities of the family. The largest toothed element of the upper jaw has been considered to be the premaxilla (the general consensus for the last four decades), a fused premaxilla and maxilla, or the palatine. The goal of this paper is to provide a detailed description of the osteology of adult giganturids to resolve the identification and homology of skeletal elements, particularly those of the upper jaw. Based on topological evidence, we conclude that the premaxilla is absent and that the major tooth-bearing bone in the ‘upper jaw’ is the palatine.

© 2016 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2016
doi: 10.1111/zoj.12469

ADDITIONAL KEYWORDS: *Bathysaurus* – *Gigantura chuni* – *Gigantura indica* – Giganturidae – morphology – ontogeny.

The giganturids are uniquely characterized by an array of derived and often reductive character states making them among the most specialized and distinctive of teleosts. . . Johnson & Bertelsen in Dana Report No. 91.

INTRODUCTION

The first German deep-sea expedition, Valdivia, organized by the invertebrate biologist Carl Chun, took place from 1 August 1898 to 30 April 1899. Among the ~5000 new species discovered during the expedition were three remarkable deep-sea fishes that caught Chun’s attention. Shortly after the expedition, he published an excellent drawing of the largest of the three specimens in an expedition report *Aus den Tiefen des Weltmeeres* (Fig. 1A: Chun, 1900), but left the initial description of the specimens

to August Brauer (1901), who was in charge of the Valdivia fish specimens. Brauer described the largest of the three specimens, which was caught in the Gulf of Guinea as *Gigantura chuni*, to honour the organizer of the expedition, and described the two smaller specimens, which were caught off the Chagos Islands, as a subspecies of the former (*Gigantura chuni* cf. *indica*). He concluded that the few morphological differences between the two smaller specimens and the specimen from the Gulf of Guinea were not sufficient to warrant the recognition of a second species, and furthermore that the slight differences might be ontogenetic. In the 15th volume of the series *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer Valdivia 1898–1899* (Brauer, 1906), however, Brauer elevated the two smaller individuals to a distinct species (*Gigantura indica*) and placed the genus in its own family, the Giganturidae. It was this volume that encouraged Chun to support Brauer’s application for the position as director of the natural history

*Corresponding author. E-mail: peter.konstantinidis@oregonstate.edu

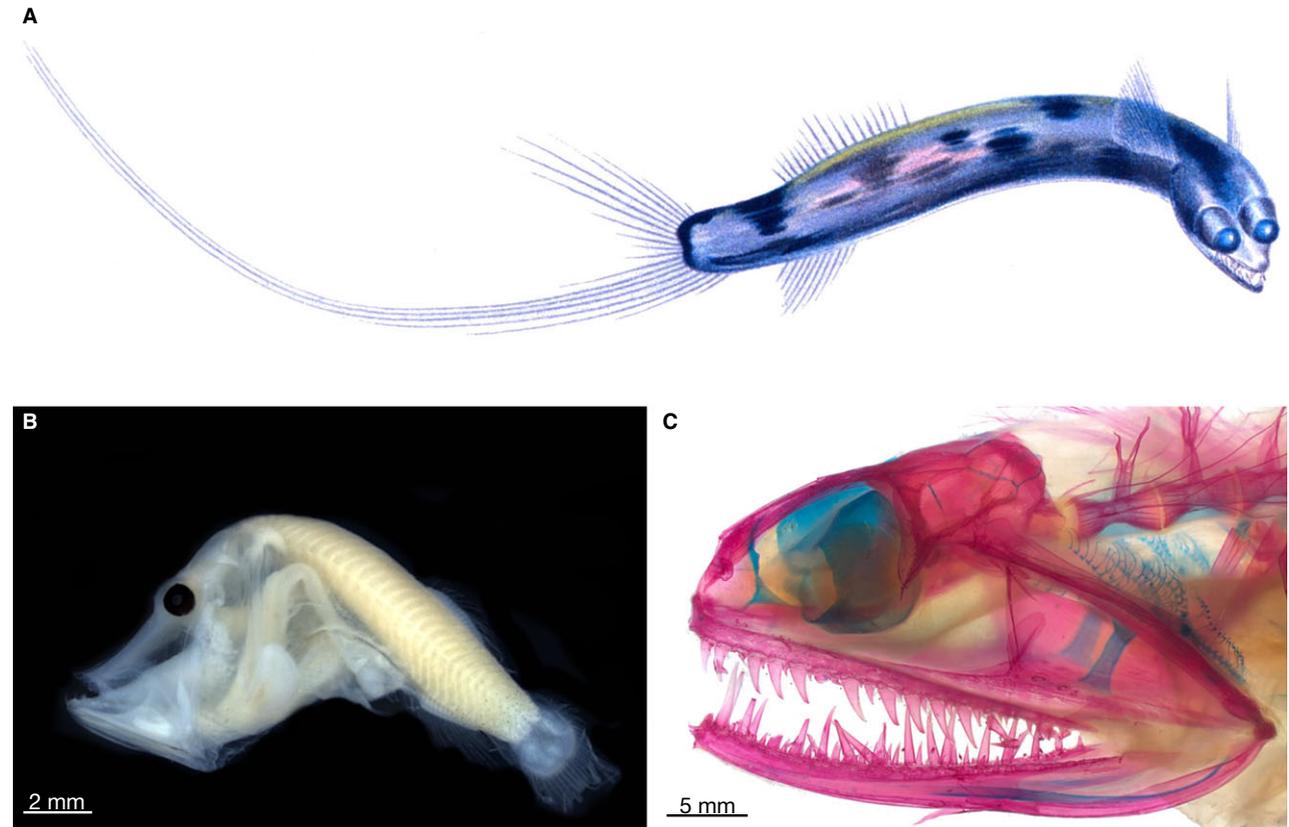


Figure 1. A, illustration of the holotype of *Gigantura chuni* from Chun's *Aus den Tiefen des Weltmeeres* (1900). B, *Gigantura indica* ('Rosaura' stage), 12 mm. C, head of USNM 221034, 163 mm, cleared and stained specimen of *G. chuni*.

museum in Berlin, a position Brauer occupied from 1906 until his sudden death on 10 September 1917 (Vanhoeffen, 1918).

Regan (1925) described two additional species of *Gigantura*, *Gigantura vorax* and *Gigantura gracilis*, based on material from the Dana expedition (1928–1930), and Walters (1961) described a fifth species in a new genus, *Bathyleptus lisae*. However, Johnson & Bertelsen accepted as valid only the two species that Brauer designated initially and synonymized *G. gracilis* and *B. lisae* with *G. indica*, and *G. vorax* with *G. chuni*.

The systematic position of *Gigantura* has been problematic, in large part because of its bizarre morphological specializations and extreme reduction of many skeletal elements, especially in the skull region (see the Results and the Discussion). Brauer (1901) was uncertain about its systematic placement but compared it with *Stylephorus* because of their superficial resemblance (e.g. both species have anteriorly directed tubular eyes, silvery coloration, and elongated caudal fin rays). Regan (1925) suggested a close relationship with iniomous synodontids. Walters (1961) acknowledged similarities to some iniomes,

but based on his interpretation of the upper-jaw bones proposed a 'subiniomous' placement. This apparently influenced Rosen & Patterson's (1969) allocation of giganturoids to subordinal status within the Salmoniformes. It is unclear what led Greenwood *et al.* (1966) to associate them with the cetomimoids. Rosen (1973) rejected Walters' (1961, 1964) proposal, and placed *Gigantura* as a 'highly modified synodontoid' in his newly diagnosed and named order Aulopiformes [essentially the 'iniomous' fishes of Gosline, Marshall & Mead (1966), minus the Myctophidae and Neoscopelidae; further corroborated by Johnson (1992)]. Ironically, a major part of Rosen's argument was based on his erroneous rejection of Walters' identification of the upper jawbones and palatine (see Discussion). Patterson & Johnson (1995) provided additional evidence from the intermusculars that *Gigantura* belongs within aulopiforms, specifically with alepisauroids (not synodontoids), and indicated that it may be linked with *Bathysaurus*. Johnson *et al.* (1996) reiterated this latter hypothesis and noted that it is corroborated by similarities in the jaws and suspensorium of the two genera. Baldwin & Johnson (1996) recovered the clade Giganturoidei,

with *Bathysauroides* as the sister group to *Gigantura* and *Bathysaurus*. Most notably, they examined the larval 'Rosaura' stage and were able to identify the distinctive elongate uncinat process on the second epibranchial that Rosen described as an unequivocal synapomorphy of Aulopiformes (Baldwin & Johnson, 1996: fig. 19). The findings of Sato & Nakabo (2003) are similar, but the authors excluded *Bathysauroides* from the Giganturoidei and placed it instead within their Chlorophthalmoidei.

Giganturids undergo one of the most drastic developmental transformations among fishes, the osteological details of which have not been demonstrated with an ontogenetic series. Fifty-four years after the description of *Gigantura*, Tucker (1954) described an 8.4-mm pre-transformation larva in great detail. The morphological details and gestalt of this larva are so distinctive that Tucker described it as a new genus and species, *Rosaura rotunda*, and placed it in its own family (Rosauridae) in the Isospondyli *incertae sedis* (Fig. 1B). The relationship between *Rosaura* and *Gigantura* remained an enigma until the mid 1960s, when Berry & Perkins (1965) first reported that *G. indica* (their *B. lisae*) and *R. rotunda* share 'certain similarities'; however, they did not specify the nature of these similarities. This statement was based on a collaborative work between E.H. ('Ahlie') Ahlstrom and Fred Berry (as stated in the introduction of Johnson & Bertelsen, 1991) that remained unpublished because of their desire to attain larval specimens and because of Ahlie's untimely death. Bill Watson (SWFC, NMFS, La Jolla) provided us with copies of Ahlie's handwritten notes in which he wrote, 'This report deals with the most striking ontogenetic changes yet demonstrated for marine fishes. It will be shown that *Rosaura* is the early developmental stage of Giganturidae...' Another 17 years passed before Johnson (1984) reported Fred and Ahlie's observation of the uniquely shared caudal fin-ray configuration of ten principal rays in the upper lobe and six or seven principal rays in the lower lobe (see Johnson & Bertelsen, 1991: fig. 6A).

The two valid species, *G. chuni* and *G. indica*, occur circumglobally in tropical and subtropical waters (*G. chuni* from 20°N to 10°S; *G. indica* from 30°N to 30°S; Johnson & Bertelsen, 1991) in depths between 500 and ~1000 m (rarely as deep as 2000 m), and are highly specialized for a deep-sea existence. Externally, the most obvious modification of giganturids is the conspicuous tubular eyes (Fig. 1C; Brauer, 1901, 1908), which have been acquired independently by members of 11 families of fishes inhabiting the 'twilight zone' of the mesopelagic (Marshall, 1971). These tubular eyes may be directed dorsally or anteriorly, and those of *Gigantura* represent one of the most striking examples of

the latter. In the mesopelagic twilight zone, these eyes would seem to be most advantageous if directed towards the surface, such that prey items would be silhouetted against the minimal light that penetrates to these depths, and we postulate that giganturids regularly orient themselves vertically in the water column, as suggested by Marshall (1971), Bruun (1957) and Johnson and Bertelsen (1991) and recently documented in a video of a closely juxtaposed pair of *G. indica* off Hawaii by the Monterey Bay Aquarium Research Institute (<https://youtu.be/rDJD-VaZ4A8>). Giganturids are synchronous hermaphrodites (Johnson & Bertelsen, 1991), an uncommon reproduction mode that separates the deep-sea aulopiforms (Davis & Fielitz, 2010) from the remaining members of the order. The most remarkable structural specializations, however, are the reductive ones of the mandibular, hyoid, and branchial arches, including the loss of the premaxilla, all ventral hyoid elements, and all but one of the ventral gill arch elements, and the dermal components of the pectoral girdle, all of which occur during a brief transformational period in early ontogeny. Most of these reductions undoubtedly facilitate the ability to engulf prey that greatly exceeds the size of the predator, e.g. Regan (1925) found a 140-mm *Chauliodus* 'neatly folded' in the stomach of an 80-mm *G. chuni* (Regan's *G. vorax*), and Walters (1961) found an 86-mm *Gonostoma* in a 77-mm specimen. Nonetheless, ingestion of relatively large prey can be facilitated by less extreme morphological modifications, e.g. those of gulper and swallower eels, black dragonfishes, and ceratioid anglers (Helfman, Collette & Facey, 1997), and chiasmodontids are capable of similar 'swallowing feats', without such extreme skeletal reductions (Marshall, 1958; Melo, 2009).

Regan (1925), Walters (1961), and Rosen (1973) provided morphological descriptions of various aspects of giganturids, but the skeletal descriptions in both publications are incomplete and inconsistent in their interpretation of some anatomical features. The purpose of this study is to give a detailed anatomical description of the skeleton of *Gigantura* to resolve the identification and homology of skeletal elements, particularly in the jaw region, and to correct other misinterpretations.

MATERIAL AND METHODS

Specimens were cleared and stained following the protocols of Taylor & Van Dyke (1985), examined using a Zeiss Discovery V20 stereomicroscope, and photographed with an attached AxioCam high-resolution digital camera. These photographs are composite images prepared with Zeiss AxioVision software to increase depth of field. Images were

adjusted for contrast and colour balance, and backgrounds were cleaned using Adobe Photoshop CC 2014. Line drawings were rendered using Adobe Illustrator CC 2014, based on images. The figure plates were assembled in Adobe InDesign CC 2014. Specimen sizes are all standard length (SL).

SPECIMENS EXAMINED FOR THIS STUDY

Bathysaurus ferox VIMS 12997, 188 mm, cleared & stained; *G. chuni* USNM 221034, 156 mm & 163 mm, cleared & stained; *G. indica* AMNH 55345, 168 mm; *G. indica* USNM 215402, 102.3 mm, cleared & stained. Institutional abbreviations follow Sabaj-Pérez (22 September 2014).

RESULTS

BRAINCASE (FIG. 2)

The anteriormost tip of the neurocranium is formed by the ethmoid, a narrow element that bears a small anterolaterally oriented process on each side (Fig. 2A–F). Lateral ethmoids are absent, and there is no trace of a lamina orbitonasalis. The ethmoid is covered posterodorsolaterally by the narrow anterior tips of the paired frontals and ventrally by a small edentulous vomer, which lacks a distinct plate-like portion at its anterior end (Fig. 2A–D). The paired nasals lie dorsolateral to the anterior tips of the frontals (Fig. 2A–D) and form the anterior extent of the supraorbital sensory canal (not illustrated). The large frontals are club-shaped, expanding laterally posterior to the orbit, where they diverge and become separated by the anterior portion of the supraoccipital (Fig. 2C, D). The suture between the frontals is smooth and without interdigitation, and their surfaces are ornamented and rough. The supraorbital canal is somewhat elevated and has four pores, one anterior just behind the nasal, two medial, and one posterior. The neurocranium of *G. indica* is similar to that of *G. chuni*.

At the anteriormost margin of the otic capsule are the large autosphenotics, with a large crest of membrane bone that forms the autosphenotic process (Fig. 2A–D). The autosphenotics provide the articulation surface for the anterior head of the hyomandibular. Posterior to the autosphenotics are the pterotics with their facet for the posterior heads of the hyomandibular (Fig. 2A–D). Ventral to the autosphenotics and pterotics are the prootics, which cover most of the ventral surface of the otic capsule and, together with the flanges of the parasphenoid, provide the foramen for the internal carotid artery (Fig. 2A, B, E–H). Walters (1961) described a basisphenoid that is absent in all our specimens.

The occipital region comprises six ossifications, the paired epioccipitals and exoccipitals, and the median supraoccipital and basioccipital. The supraoccipital is surrounded by the epioccipitals, exoccipitals, and frontals (Fig. 2C, D). The supraoccipital lacks a crest and does not border the foramen magnum dorsally (Fig. 2G, H). The epioccipitals are at the posterodorsal border of the otic capsule. The exoccipitals surround the foramen magnum entirely and, as is typical, contribute to the occipital condyle, on either side of which are small foramina for the vagal nerve (Fig. 2G, H). The basioccipital is relatively flat and partly covered by the posterior end of the parasphenoid; its exposed posterior surface is rugose (Fig. 2A, B, E, F).

The parasphenoid is the largest of the ventral series of bones. It extends from about the middle of the basioccipital anteriorly to the ethmoid and vomer, and has a dorsolateral flange on each side that, together with the prootics, form foramina for the internal carotid arteries (Fig. 2A, B, E, F).

INFRAORBITALS (FIG. 3A, B)

Six weakly ossified infraorbitals are evident only in the 163-mm *G. chuni*, wherein they are arranged in a straight line along the upper jaw. Only the dorsal edge of the infraorbital canal was stained with alizarin. There is no evidence of infraorbitals in the 156-mm *G. chuni* (USNM 221034) and the 102.3-mm *G. indica* (USNM 215402), which we presume are either lost as a result of damage or not stained with alizarin.

JAWS, SUSPENSORIUM, OPERCULAR SERIES (FIG. 3C–H)

The dentary and anguloarticular are the only two lower jaw ossifications, i.e. there is no retroarticular. The dentary is forked posteriorly and houses Meckel's cartilage and the anterior end of the anguloarticular medially (Fig. 3E, F). It bears two rows of fang-like teeth, with those of the medial row much larger than those of the lateral rows. The posterior bases of the teeth are collagenous and unossified, and thus appear to represent Fink's (1981) type-4 tooth attachment. There is no premaxilla, and the maxilla is leaf-shaped and lies at the posterior end of the palatine, lateral to the quadrate (see Discussion).

The suspensorium comprises the palatoquadrate and hyosymplectic cartilages, with their perichondral and dermal ossifications (Fig. 3C–F). The major tooth-bearing bone of the 'upper jaw' is elongated and has the same pattern of tooth arrangement and attachment as the dentary (Fig. 3C–F). We interpret this element as an amalgamation of the autopalatine and dermopalatine (palatine; see Discussion).

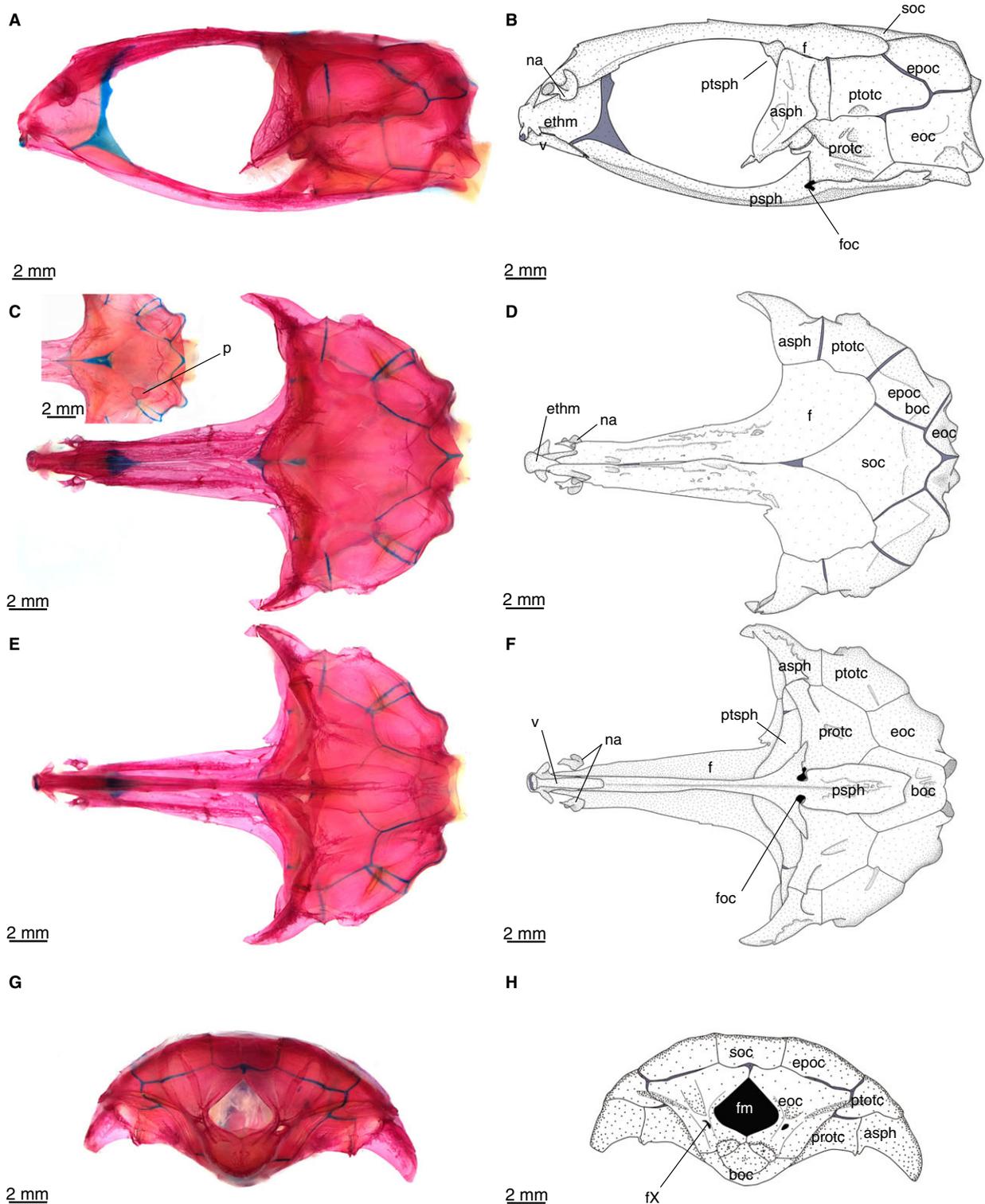


Figure 2. Photographs of cleared and stained and line drawings (mirrored) of the left side of the braincase of *Gigantura chuni*, USNM 221034, 163 mm. A, B, left lateral; C, D, dorsal. Close-up in (C) shows an element that we interpret as a parietal in USNM 221034 (156-mm specimen). E, F, ventral; G, H, posterior views. asph, autosphenotic; boc, basioccipital; eoc, exoccipital; epoc, epioccipital; ethm, ethmoid; f, frontal; fm, foramen magnum; foc, foramen for the internal carotid; fX, foramen for vagal nerve; na, nasal; p, parietal; protc, prootic; psph, parasphenoid; ptotc, pterotic; ptsph, pterosphenoid; soc, supraoccipital, v, vomer.

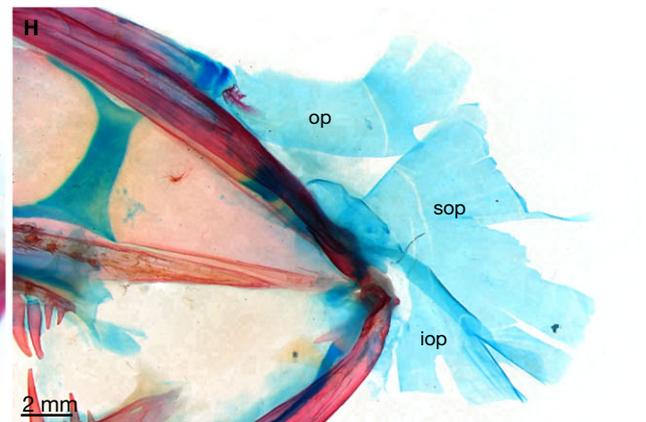
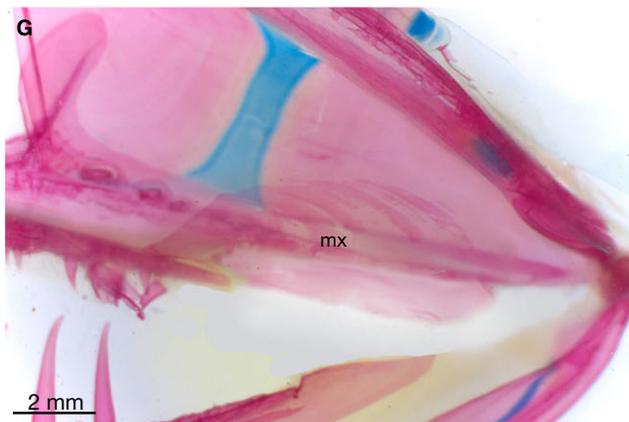
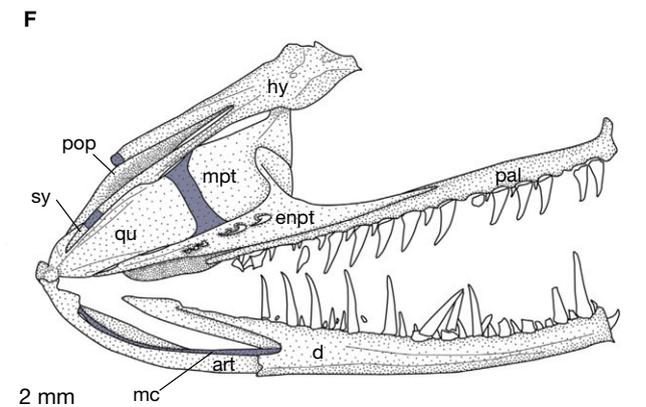
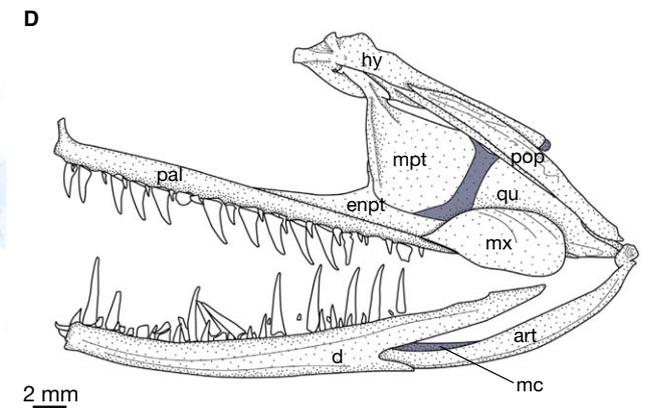
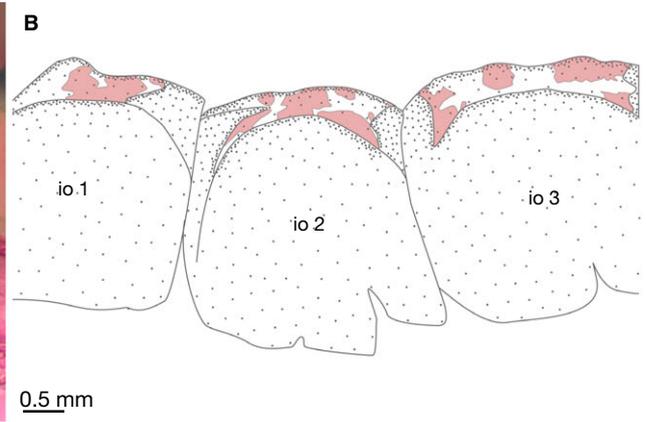
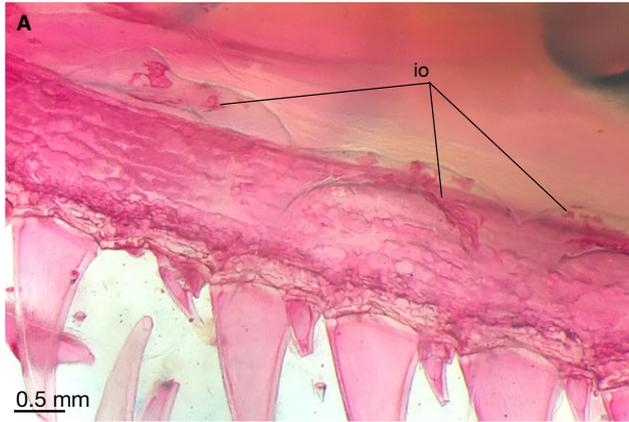


Figure 3. A–G, photographs of cleared and stained and line drawings (mirrored) of (B, D, F) left lateral views of *Gigantura chuni* USNM 221034, 163 mm. H, cleared and stained *G. chuni*, USNM 221034, 156 mm. A, B, close-up of infraorbitals 2–4; C, D, lateral views of suspensorium and jaws; E, F, medial views of suspensorium and jaws; G, close-up maxilla; H, close-up of the opercular series. art, anguloarticular; d, dentary; enpt, entopterygoid; hy, hyomandibular; io, infraorbitals; iop, interopercle; mc, Meckel's cartilage; mpt, metapterygoid, mx, maxilla; op, opercle; pal, palatine; pop, preopercle; qu, quadrate; sop, subopercle; sy, symplectic.

Anteriorly, a small 'ascending process' connects the palatine to the ethmoid (Fig. 3C–F). Posteriorly, the palatine is attached to an element that we interpret as the entopterygoid (see Discussion). The entopterygoid bears six depressible teeth that decrease in size posteriorly. The entopterygoid is attached to the palatine and to the ventral margin of the metapterygoid and quadrate (Fig. 3C–F). At about mid-length, the entopterygoid has a very large ovoid, spatulate flange that extends dorsally about three-quarters of the way up the medial surface of the metapterygoid (Fig. 3E, F). The metapterygoid lies anterior to the quadrate and is attached to the hyomandibular antero- and posterodorsally (Fig. 3C–F). The triangular-shaped quadrate is the posteroventralmost element of the palatoquadrate, and bears the condyle articulating with the anguloarticular (Fig. 3C–F). Because of the orientation of the quadrate (it is rotated anterodorsally so the body of the quadrate and the metapterygoid are anterior to the articulation with the lower jaw), its short posteroventral process is oriented anterodorsally of the articulation with the lower jaw, and embraces the small symplectic (Fig. 3E, F).

The hyomandibular is inclined anteriorly so that the shaft lies at an approximately 45° angle to the horizontal. Anteriorly, the main head articulates with the braincase through two condyles, the anteriormost of these with the autosphenotic and another just posterodorsal to that one with the pterotic. The condyle of the hyomandibular that articulates with the opercle lies at the end of an elongate shaft that runs parallel with the main shaft of the hyomandibular, which articulates with the posterodorsal tip of the small symplectic. This configuration gives the hyomandibular a striking bifurcate appearance (Fig. 3C–F). The small rod-like symplectic is fully embraced by the quadrate laterally (Fig. 3E, F). The slender, splint-like preopercle attaches closely to the main arm of the hyomandibular (Fig. 3C–F), and its pointed ventral tip is tightly attached to the short process of the quadrate that embraces the symplectic.

The opercular elements are very small and weakly ossified in all specimens examined, and only a smidgen of the anterior portion of the opercle is stained with alizarin (Fig. 3H). The opercle is narrow, and the frayed distal end curves upwards. A triangular subopercle lies below the opercle and is overlain ventrally by the irregularly shaped interopercle

(Fig. 3H). The small, fragile nature of the opercular elements suggests that they play little part in moving water across the extremely reduced gill filaments.

The ventral components of the hyoid arch, the ceratohyals, branchiostegals, hypohyals, interhyals, and the basihyal are absent.

GILL ARCHES (FIG. 4)

The gill arches are highly reduced and comprise only epibranchials 1–4, ceratobranchial 4, pharyngobranchial 3, with fused upper pharyngeal toothplate 3, and upper pharyngeal tooth plate 5. Of the first three epibranchials, epibranchial 1 is the largest and is perichondrally ossified (Fig. 4A, B). Epibranchials 2 and 3 are successively smaller and remain cartilaginous (Fig. 4A, B). *In situ*, epibranchials 1–3 are oriented anterodorsally (Fig. 4A). They bear respiratory gill filaments along their entire lengths. These and one unsupported string of filaments (presumably displaced from the very large fourth epibranchial) apparently provide the only respiratory surfaces. The only remaining ventral gill-arch element, ceratobranchial 4, is a short, rod-like element with its proximal tip inclined medially and its distal tip articulated with the large epibranchial 4 (Fig. 4C, D). Epibranchial 4 is widest dorsally, where its cartilaginous head articulates with the cartilaginous posterior end of pharyngobranchial 3, which bears three large, recurved, fang-like teeth (Fig. 4A, C, D). Posteriorly, pharyngobranchial 3 articulates with upper pharyngeal tooth plate 5, which bears four similar teeth (Fig. 4C, D). Pharyngobranchial 4 and its corresponding toothplate are absent. The dorsal gill-arch elements are reminiscent of, though not identical to those of muraenid eels.

VERTEBRAL COLUMN AND INTERMUSCULAR BONES (FIG. 5)

The vertebral column comprises 17 abdominal and 14 caudal vertebrae (31 total), including the urostylar vertebra that supports the caudal fin elements. The vertebrae are hourglass-shaped and there are no apophyses or ribs. All neural arches are fused to their respective centra. The first three abdominal vertebrae have sturdy, broad-based neural arches that are closed dorsally (Fig. 5A, B), but most of the

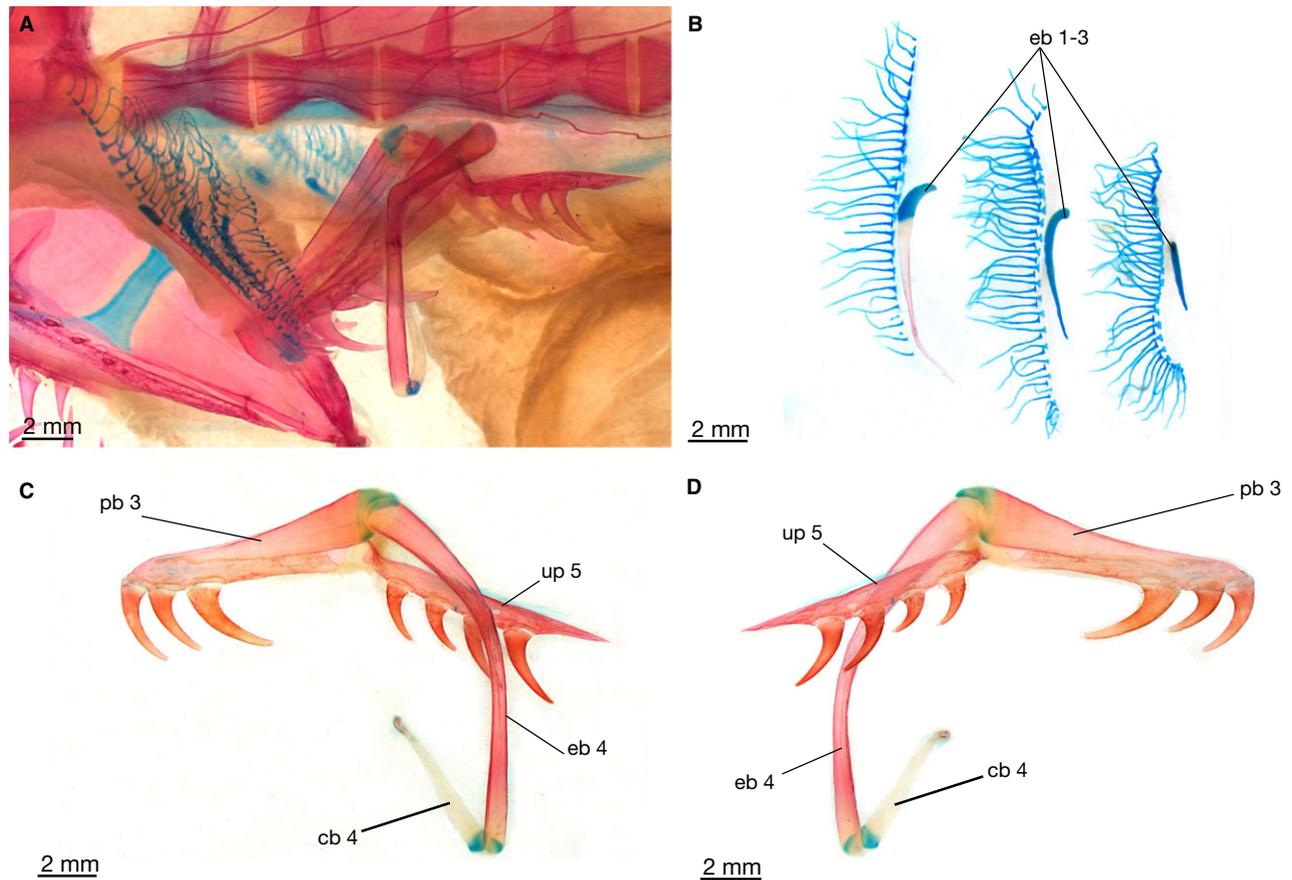


Figure 4. Photographs of cleared and stained gill arches of *Gigantura chuni* USNM 221034, 163 mm (A–C, lateral views; D, medial view). A, epibranchials 1–3 and fourth arch *in situ*. B, epibranchials 1–3 (eb 1–3) with gill filaments. C, D, dorsal gill arch elements with ceratobranchial 4 (cb 4); epibranchial 4 (eb 4); pharyngobranchial 3 (pb 3); and upper pharyngeal tooth plate 5 (up 5).

succeeding arches are long, almost filament like, and open dorsally (Fig. 5A–C). According to Baldwin & Johnson (1996), the presence of many open neural arches is a reversal within aulopiforms uniquely shared by *Gigantura* and *Bathysaurus*. Vertebra 30 bears two neural arches, the posterior of which does not contact the centrum (not shown). There is only one neural spine associated with vertebra 30 in the larger specimen (USNM 221034, 163 mm; not pictured). Rosen's (1973) specimen also had a duplicated haemal spine.

Vertebra 19 is the first with a haemal arch (Fig. 5C; vertebra 20 in the 156-mm specimen), and all but the last (that of PU2) are fused to their respective centra. The first two haemal arches are shorter than the subsequent haemal arches, and together with the haemal arches of vertebrae 20 and 21 open proximally (the haemal arches of vertebrae 19–24 are open in the 156-mm specimen).

The intermuscular bones are represented by a series of epineurals and epipleurals. The first epineural

(two in the 156-mm specimen) is located between the occiput and the first vertebra (Fig. 5A, B), and the last epineural is associated with vertebra 28 (Fig. 5D). The subsequent epineurals are longer and attached to the vertebrae anteriorly, and some, but not all, are bifurcate (Fig. 5A–C). The first epipleural is attached to the first vertebra and is displaced into the horizontal septum (Fig. 5A; Patterson & Johnson, 1995), and the last epipleural is associated with vertebra 28. Some of the epipleurals also have a bifid base, and the last two are shorter and are not attached to their corresponding centrum (Fig. 5D).

CAUDAL SKELETON AND FIN (FIG. 6)

The caudal fin skeleton supports 16 principal caudal fin rays, ten in the upper lobe and six in the lower lobe, an arrangement that is unique to *Gigantura* (Johnson & Bertelsen, 1991). The fin rays of the lower lobe are extremely elongated and twice the standard length (Fig. 1; broken distally in all our

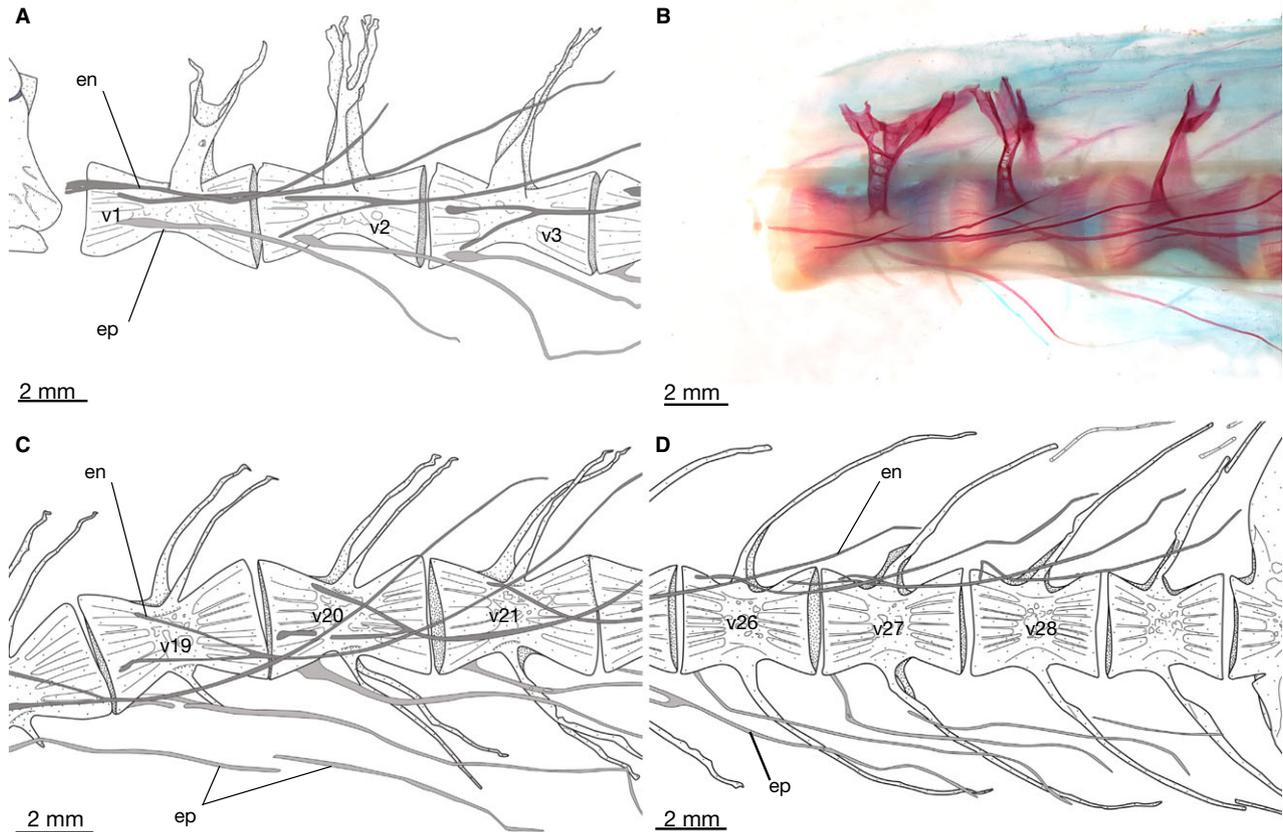


Figure 5. Vertebrae of *Gigantura chuni*, left lateral view. A, vertebrae 1–3 of USNM 221034 (163-mm specimen). B, photograph of vertebrae 1–3 of USNM 221034 (156-mm specimen). C, line drawings of vertebrae 19–21 of USNM 221034 (163-mm specimen). D, line drawings of vertebrae 26–29 of USNM 221034 (163-mm specimen). en, epineurals; ep, epineurals; v, vertebra.

specimens). There are three procurrent rays supported by the single epural, and two supported by the cartilaginous tip of the haemal spine of preural centrum 2 (Fig. 6A).

The haemal arch of preural centrum 2 is very broad because of an anterior outgrowth of membrane bone, and is autogenous from its corresponding centrum. The tip of the haemal spine of preural centrum 2 is cartilaginous and supports two procurrent fin rays. The enlarged neural arch is fused to preural centrum 2. The urostylar centrum, the two enlarged hypurals, and the parhypural are fused into a single element. The distal ends of the hypurals are cartilaginous. Dorsally, the compound centrum bears a large crest that is pierced at its base and embraces the single epural and parts of the enlarged neural arch of preural centrum 2. The epural is very wide dorsally and narrows ventrally, where it is covered by the large crest of the compound centrum. Anteriorly, the epural bears a large crest of membrane bone that embraces the neural spine of preural centrum 2 laterally. Median caudal cartilage is present

within the small gap between the upper and lower hypural plates (covered by the caudal fin rays), and two large distal radials support the uppermost caudal fin rays and the two procurrent and two principal caudal fin rays, respectively. The composition of elements of the caudal skeleton in *G. indica* is as described for *G. chuni*; however, the proportions of the elements differ conspicuously (Fig. 6B).

DORSAL AND ANAL FINS (FIG. 7A–D)

The pterygiophores of the dorsal and anal fin rays are similar in shape and form. They support 17 rays (Fig. 7A) in the dorsal fin and 10 in the anal fin (Fig. 7C). The first dorsal-fin pterygiophore inserts between the neural spines of vertebrae 15 and 16, and comprises a proximal–middle and a distal radial, whereas the succeeding pterygiophores have separate proximal and middle radials (Fig. 7B). The first ray is serially associated with the first pterygiophore (Fig. 7A). The first two anal-fin pterygiophores insert between vertebrae 22 and 23. The first ray is in

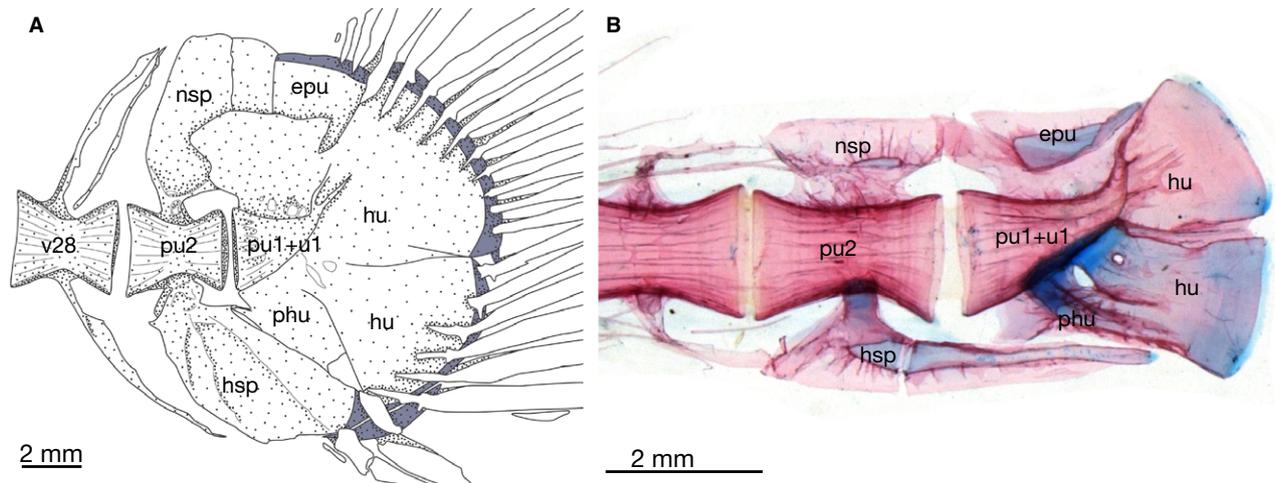


Figure 6. Caudal skeleton of *Gigantura chuni*, left lateral view: A, USNM 221034, 156 mm; B, caudal skeleton of *Gigantura indica*, USNM 215402, 102-mm. epu, epural; hsp, haemal spine; hu, hypural; nsp, neural spine; pu, preural centra; u, ural centrum, v, vertebra.

supernumerary association with the first pterygiophore (Fig. 7C), but embraces a separate distal radial. All but the first two anal-fin pterygiophores have separate proximal and middle radials (Fig. 7D), and the last has a stay (*sensu* Weitzman, 1962).

PECTORAL GIRDLE AND FIN (FIG. 7E, F)

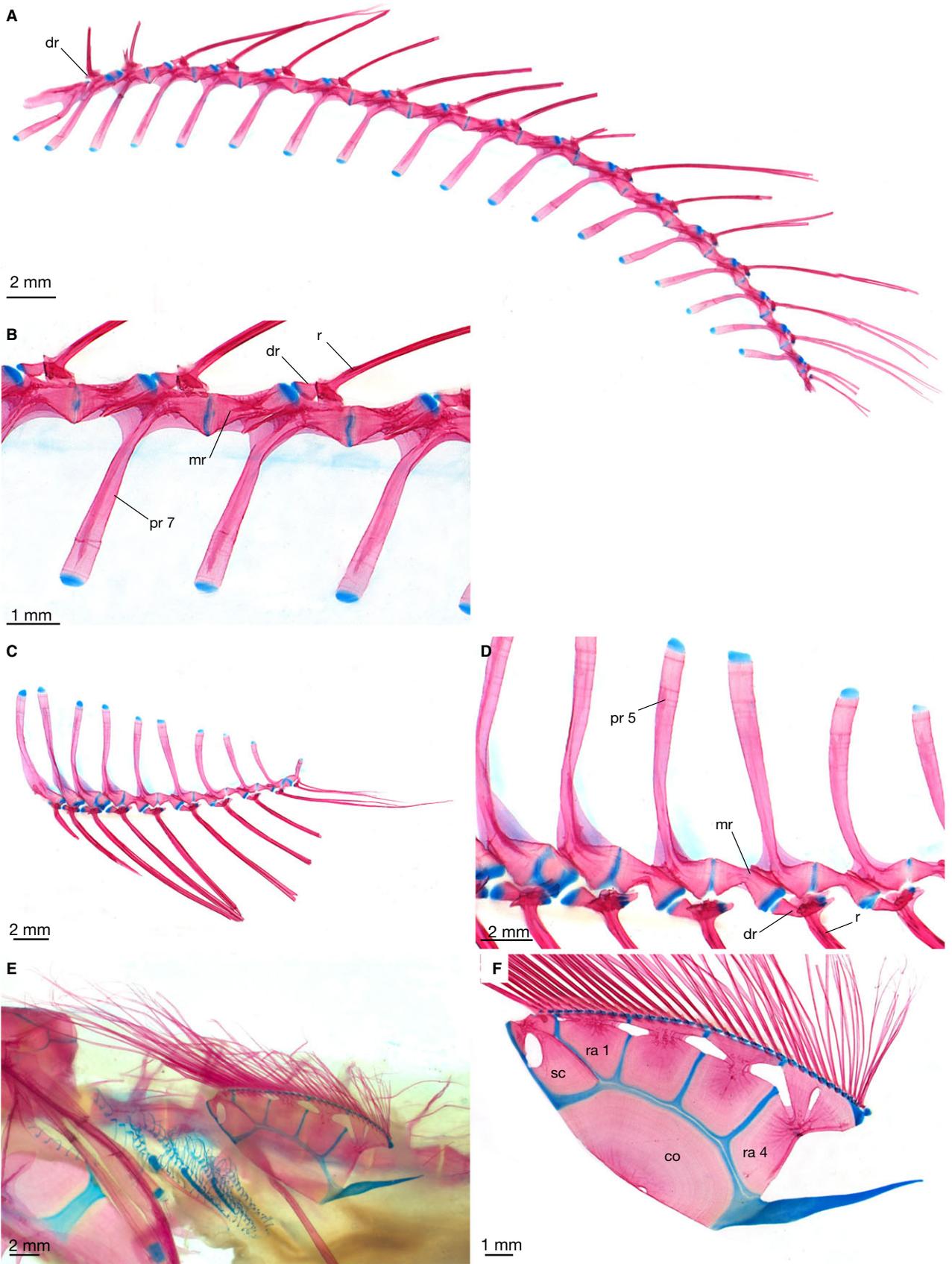
The pectoral girdle lacks all the typical dermal components, and the endoskeletal elements form a plate that is positioned high in the body wall and oriented horizontally, with the four pectoral radials oriented posterodorsally. The coracoid is the largest element and supports radials 2–4 (the fourth pierced by a foramen). Anterodorsally, the much smaller scapula supports radial 1. The scapula is pierced by a large foramen, and an extension of the scapula supports the anteriormost fin ray. At its posteroventral edge, the scapulocoracoid cartilage bears a large, unossified, posterodorsally oriented process. All radials are roughly asymmetrically hourglass-shaped. Each of the 32 fin rays articulates with a small cartilaginous distal radial. The horizontal placement of the pectoral girdle and fin adjacent to the small dorsal gill slit suggests that they may play a role in circulating water over the gill filaments, supported by the reduced first three epibranchials, as suggested by Regan (1925).

DISCUSSION

Adult giganturids are highly modified morphologically and are characterized by numerous skeletal reductions that make the identification of the remaining elements problematic. Regan (1925), Walters (1961), and Rosen (1973) interpreted the element that connects the autopalatine to the metapterygoid and quadrate as the ectopterygoid; however, we interpret this element as the entopterygoid, and the ectopterygoid is absent in *Gigantura*. The entopterygoid in *Bathysaurus* and *Gigantura* is an elongated element that bears a projection, oriented dorsally in *Gigantura* and posteriorly in *Bathysaurus*. The ectopterygoid in *Bathysaurus* is relatively small compared with the entopterygoid, and is located between the entopterygoid and the palatine (Fig. 8C; see also Johnson *et al.*, 1996: fig. 29).

The most controversial bones are the tooth-bearing elements of the upper jaw, which have played a significant role in hypotheses about the phylogenetic affinities of the family, the major issue being whether or not the maxilla is excluded from the gape by the premaxilla (Fig. 3C–F). Regan (1925; fig. 2) interpreted the large element that attaches to the suspensorium posteriorly and articulates with the ethmoid region anteriorly as either the premaxilla or

Figure 7. Cleared and stained *Gigantura chuni*, USNM 221034, 163 mm, left lateral view: A, dorsal-fin pterygiophores; B, close-up of dorsal-fin pterygiophores 7–9; C, anal-fin pterygiophores; D, close-up of anal-fin pterygiophores 5–7; E, pectoral girdle *in situ*; F, pectoral girdle *ex situ*. co, coracoid; dr, distal radial; mr, medial radial; pr, proximal radial; r, fin ray; ra, radial; sc, scapula.



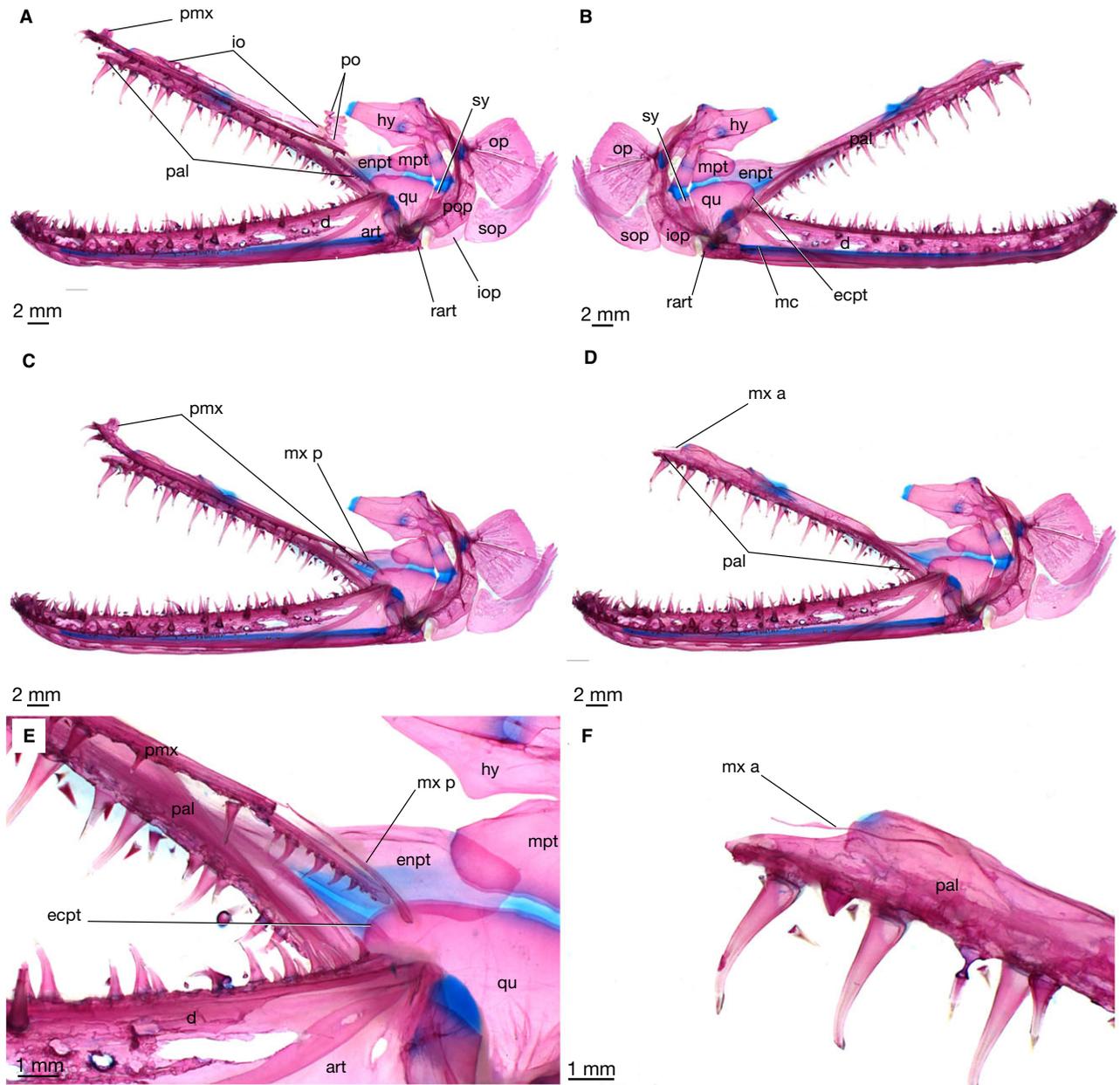


Figure 8. Cleared and stained left suspensorium and jaws of *Bathysaurus ferox*, VIMS 12997, 188 mm: A, lateral view with infraorbitals; B, lateral view with infraorbitals and premaxilla removed; C, close-up of posterior remnant of maxilla; D, close-up of anterior remnant of maxilla. art, articular; d, dentary; ecpt, ectopterygoid; enpt, entopterygoid; hy, hyomandibular; io, infraorbitals; iop, interopercle; mc, Meckel's cartilage; mpt, metapterygoid; mx a, anterior part of maxilla; mx p, posterior part of maxilla; op, opercle; pal, palatine; pmx, premaxilla; po, postorbitals; pop, preopercle; qu, quadrate; rart, retroarticular; sop, subopercle; sy, symplectic.

the fusion of the premaxilla and the maxilla (see above, Fig. 3C–F). Walters (1961; Fig. 3) disagreed with Regan and noted first that it was unlikely to have a maxillary component because the maxilla is represented by a “weakly ossified lamina which lies buried in the cheek above and behind the ‘premaxilla’”, which was “apparently...lost during the

preparation of Regan's material”. Based on our observations, it is unlikely that Regan's maxillary element was actually ‘lost’, because as Walters noted, it is deeply embedded in connective tissue. It is a very thin bony lamina and is very difficult to see. In our cleared and stained specimens, it often does not pick up alizarin. Walters argued plausibly that

Regan's premaxilla/maxilla must instead be the autopalatine, because: (1) it does not meet its counterpart in the midline; (2) its anterior end is attached to the vomer and ethmoid; (3) its posterior end is attached to what he and Regan referred to as the ectopterygoid; and (4) it does not border the posterior quarter of the upper jaw. We concur with Walters' conclusion that the large, toothed 'upper jaw' bone represents the palatine rather than the premaxilla/maxilla, but modify his conclusion only in noting that because it bears teeth, it must include a dermal component that has been ontogenetically incorporated, which is most likely a dermopalatine.

Although Walters was clearly correct that giganturids lack a premaxilla, we reject his premise that they are 'subiniomous' fishes because the maxillae are not excluded from the gape by the premaxillae. Walters noted that 'The feature which distinguishes the iniomous fishes from less advanced teleosts is that the maxillae are excluded from the gape by the premaxillae, which alone border the upper jaw. This line of reasoning leads to the conclusion that the Giganturidae are subiniomes'. As the premaxillae are absent, however, they cannot exclude the maxilla from the gape, and consequently this does not provide a test of the subiniome hypothesis. In any case, the placement of giganturids within the Aulopiiformes (and thus not subiniome), as proposed by Rosen (1973), has been supported by all subsequent analyses, both morphological and molecular (Baldwin & Johnson, 1996; Davis, 2010). As discussed below, Rosen's reasons for this placement were flawed, and the subject was not revisited until Patterson & Johnson (1995) and Baldwin & Johnson (1996) presented evidence for their aulopiiform affinities. In his groundbreaking paper on the interrelationships of higher euteleosts, Rosen (1973) rejected Walters' homology arguments and agreed with Regan (1925) that the large tooth-bearing element in the upper jaw in giganturids represents a fusion of the premaxilla and maxilla. According to Rosen, Walters' disagreement with Regan was based, in part, on his belief that Regan's '...identifications of the bones of the skull (were) inaccurate. It appears to the writer, however, that Regan was correct and that is was Walters' osteological misidentifications that led to confusion about giganturid placement...' We find it remarkable that Walters' homology of the 'upper jaw' element was summarily dismissed by Rosen (1973), and that his rejection was accepted uncritically by most subsequent authors without further discussion, including the definitive monograph of Johnson & Bertelsen (1991). Presumably they simply accepted his arguments based on his authority. Accordingly, we believe it is important to present a detailed rebuttal of Rosen's arguments.

Rosen's argument was based on a comparison of the skull of *Gigantura* with that of a 'juvenile' *Trachinocephalus myops* (Rosen, 1973: fig. 65), which he noted 'reveals several similarities'. His justification of these 'similarities' and our reasons for rejecting them are as follows.

1. 'The tooth-bearing bone identified by Walters as the autopalatine is most nearly comparable with the maxilla + premaxilla of *Trachinocephalus*, two bones which in synodontids are always long, narrow and closely appressed and fused together into a single element in the adults.' While it is true that the maxilla is long and narrow, and closely appressed to the dorsal margin of the premaxilla in most synodontoids, the premaxilla is a long but robust bone, and the two bones are never fused. In fact we know of no instance of clear evidence of any such fusion among teleost fishes.
2. 'An ossified palatine does not develop in giganturids, which appear to have retained the unossified condition of the palate as in juvenile *Trachinocephalus*.' Although it is true that juvenile synodontids have a fully cartilaginous autopalatine, adult giganturids have no cartilaginous component, so surmising that they have retained the juvenile synodontid condition is illogical.
3. 'The bone identified by Walters as the maxilla is directly comparable in position, size, and shape with the second infraorbital bone (IO₂) of *Trachinocephalus*.' There are two problems with this. First, if Walters' maxilla is instead an infraorbital, it should have a sensory canal. It does not, and Rosen never considered, or at least didn't mention, this critical detail. The second problem is more complex and relates to the fact that unbeknownst to Rosen, his 'juvenile' *Trachinocephalus* was in fact still in the larval stage. The placement and arrangement of the infraorbitals undergo major changes ontogenetically in synodontids, and those of Rosen's specimen had not yet transformed. In the larval stage, the second infraorbital lies directly above the posterior end of the upper jaws, a position similar to that of the maxilla of *Gigantura*. This positional similarity contributed to Rosen surmising that the latter is actually a second infraorbital; however, after transition from larva to juvenile *Trachinocephalus*, the infraorbital series lies relatively much farther forwards, so that the second infraorbital is above the anterior one-third of the upper jaws, and thus bears no resemblance to the position of the maxilla in *Gigantura*. Accordingly, if Rosen's comparative specimen had represented the juvenile/adult (terminal) condition, he would have no

reason to suggest that the maxilla of *Gigantura* resembles the second infraorbital of synodontids. There is irony in this, because Rosen never worked on larval stages and it is thus not surprising that he did not recognize that his only cleared and stained *Trachinocephalus* was an untransformed larva.

Additional support that the largest tooth-bearing bone in the upper jaw in *Gigantura* is the palatine and not the premaxilla, or the product of the premaxilla and the maxilla, comes from a comparison of the upper jaws in *Bathysaurus* (Fig. 8), which appears to be the sister group of *Gigantura* (Baldwin & Johnson, 1996; Davis, 2010). The first larval bathysaurid was mistakenly described as *Macristium chavesi* by Regan (1903), but in subsequent years Rosen (1971) and later Johnson (1974) discovered that *Macristium* is the larval form of bathysaurids. In larval bathysaurids the maxilla resembles the maxilla in *Rosaura* larvae in shape, relative size, and anterior connection to the ethmoid region (Fig. 8). Baldwin & Johnson (1996: character 51) considered the reduced anterior maxilla in *Bathysaurus* and the posterior maxilla in *Gigantura* as a shared character; these comparisons were based only on published drawings, and they did not examine specimens. We have examined and illustrated a 188-mm transformed juvenile *Bathysaurus* (Fig. 8). Although we agree with Baldwin & Johnson (1996) that a reduced maxilla is a synapomorphy for giganturids and bathysaurids, we disagree about the homology of the anterior remnant of the maxilla in *Bathysaurus* and a posterior remnant in *Gigantura*. In addition to the anterior remnant of a maxilla in *Bathysaurus*, we also found a posterior remnant (Fig. 8C) that was previously overlooked by Sulak (1977) and by Johnson *et al.* (1996). We believe that the posterior remnant of the maxilla in *Bathysaurus* is homologous to the maxilla in *Gigantura*. The palatine in *Bathysaurus* is the largest upper jawbone, and bears the largest dentition. It articulates with the ethmoid and vomer laterally, and with the entopterygoid, ectopterygoid, and quadrate posteriorly. The premaxilla is much thinner than the robust palatine, runs along the palatine laterally, and is only attached to the dorsal surface of the anterior tip of the ethmoid region. We conclude, therefore, that the topographic similarity (relative size and shape) and the similar attachment to the ethmoid region, and the suspensorium between the bathysaurid palatine and the upper jawbone in *Gigantura* (the ectopterygoid is reduced in *Gigantura*), is further evidence that the upper jawbone in *Gigantura* is in fact the palatine. We conclude that Rosen's rejection of Walters' well-reasoned homology

assessment was erroneous on all counts, and agree with Walters that the largest tooth-bearing element in the upper jaw of *Gigantura* is the palatine, and that the premaxilla is absent.

CONCLUSION

As Johnson & Bertelsen (1991) noted in their seminal monograph, *Gigantura* is one of the most extraordinarily specialized teleost fishes. A major aspect of this specialization is reductive, and involves the complete absence of numerous skeletal elements. In our osteological description we have documented these absences, and they are as follows.

Braincase – parietals, intercalars, lateral ethmoids, basisphenoid; pectoral girdle – post-temporals, supra-cleithra, cleithra, postcleithra; hyoid arch – basihyal, hypohyals, ceratohyals, branchiostegals, interhyals; gill arches – basibranchials 1–4, hypobranchials 1–3, ceratobranchials 1–3, 5; pharyngobranchials 1, 2, 4; suspensorium and jaws – premaxilla, ectopterygoid, retroarticular. The majority of these elements is present in the larvae and are lost ontogenetically. We plan to describe the extraordinary skeletal transformation of *Gigantura* from the larval 'Rosaura' stage to the juvenile/adult in a subsequent paper.

As we noted, a major goal of this paper was to resolve the identification of the toothed upper jaw elements, which have remained controversial since their first description by Regan (1925), although their identification as premaxillae has been the consensus opinion since Rosen (1973) argued for that hypothesis. We have shown, based on topological evidence and the refutation of Rosen's (1973) hypothesis, that there is no premaxilla and that the major tooth-bearing bone in the 'upper jaw' is in fact the palatine. This extraordinary functional replacement of the premaxilla by the palatine is unique among fishes. The extreme reduction of the hyoid arch and ventral gill arch elements, and presumably the replacement of the premaxilla by the palatine, are clearly related to the remarkable raptorial feeding mechanism of *Gigantura*, which is reminiscent of, but more extreme than, that of muraenid eels (Mehta & Wainwright, 2007, 2008). We plan to describe this mechanism in a future paper.

ACKNOWLEDGEMENTS

We would like to thank T. Sutton, K. Hartel, A. Williston, R. Feeney, M. McGrouther, and J. Leis for their curatorial support and K. Schlining and B. Robison for assistance in accessing the video. We are grateful to A. Nonaka for her assistance in accumulating literature and other technical assistance, and E. Hilton and T. Moritz for many discussions. We

also would like to thank N. Schnell, V. Springer, and W. Smith-Vaniz for comments on an earlier draft of this article, and two anonymous reviewers for their comments and suggestions. This project was supported by the Volkswagen Foundation, Germany (P. Konstantinidis) and the Herbert R. and Evelyn Axelrod Chair of Systematic Ichthyology at USNM.

REFERENCES

- Baldwin C, Johnson GD. 1996.** Interrelationships of aulopiformes. In: Stiassny MLJ, Parenti LR, Johnson GD, eds. *Interrelationships of fishes*. San Diego: Academic Press, 355–404.
- Berry FH, Perkins HC. 1965.** Survey of pelagic fishes of the California current area. *Fishery Bulletin* **65**: 675–682.
- Brauer A. 1901.** Über einige von der Valdivia-Expedition gesammelte Tiefseefische und ihre Augen. *Sitzungsberichte der Gesellschaft zur Beförderung der Gesamten Naturwissenschaften zu Marburg* **8**: 115–130.
- Brauer A. 1906.** *Die Tiefseefische. 1. Systematischer Teil. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*. Jena: G. Fischer.
- Brauer A. 1908.** *Die Tiefseefische 2. Anatomischer Teil. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899*. Jena: G. Fischer.
- Bruun A Fr. 1957.** Deep sea and abyssal depths. *Geological Society of America Memoir* **67. Volume I**: 641–672.
- Chun C. 1900.** *Aus den Tiefen des Weltmeeres*. Jena, Germany: Gustav Fischer.
- Davis MP. 2010.** Evolutionary relationships of the aulopiformes (Euteleostei: Cyclosquamata): a molecular and total evidence approach. In: Nelson JS, Schultze HP, Wilson MVH, eds. *Mesozoic fishes 4 – homology and phylogeny*. München: Dr. Friedrich Pfeil, 431–470.
- Davis MP, Fielitz C. 2010.** Estimating divergence times of lizardfishes and their allies (Euteleostei: Aulopiformes) and the timing of deep-sea adaptations. *Molecular Phylogenetics and Evolution* **57**: 1194–1208.
- Fink WL. 1981.** Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes. *Journal of Morphology* **167**: 167–184.
- Gosline WA, Marshall NB, Mead GW. 1966.** Order Iniomi: characters and synopsis of families. In: Bigelow HB, ed. *Fishes of the Western North Atlantic. Sears foundation for marine research*. New Haven, CT: Yale University, 1–18.
- Greenwood PH, Rosen DE, Weitzman SH, Myers GS. 1966.** Phyletic studies of teleostean fishes with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* **131**: 339–455.
- Helfman GS, Collette BB, Facey DE. 1997.** *The diversity of fishes*. Oxford: Blackwell Science, i-xii, 1–528.
- Johnson RK. 1974.** *Macristium* Larva from Gulf of Mexico with additional evidence for synonymy of *Macristium* with *Bathysaurus* (Myctophiformes-Bathysauridae). *Copeia* **4**: 973–977.
- Johnson RK. 1984.** Scopelarchidae: development and relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AWJ and Richardson SL, eds. *Ontogeny and Systematics of Fishes*. Lawrence, KS (American Society of Ichthyologists and Herpetologists): Allen Press, Special Publication. No. **1**: 245–250.
- Johnson GD. 1992.** Monophyly of the euteleostean clades – Neoteleostei, Eurypterygii, and Ctenosquamata. *Copeia* **1**: 8–25.
- Johnson RK, Bertelsen E. 1991.** *The fishes of the family Giganturidae: systematics, development, distribution and aspects of biology*. Copenhagen: Dana-Report Carlsberg Foundation, 1–45.
- Johnson GD, Baldwin CC, Okiyama M, Tominaga Y. 1996.** Osteology and relationships of *Pseudotrichonotus altivelis* (Teleostei: Aulopiformes: Pseudotrichonotidae). *Ichthyological Research* **43**: 17–45.
- Marshall NB. 1958.** *Aspects of deep sea biology*. London: Hutchinson & Co.
- Marshall NB. 1971.** *Exploration in the life of fishes*. Cambridge, MA: Harvard University Press.
- Mehta RS, Wainwright PC. 2007.** Raptorial jaws in the throat help moray eels swallow large prey. *Nature* **449**: 79–82.
- Mehta RS, Wainwright PC. 2008.** Functional morphology of the pharyngeal jaw apparatus in moray eels. *Journal of Morphology* **269**: 604–619.
- Melo MRS. 2009.** Revision of the genus *Chiasmodon* (Acanthomorpha: Chiasmodontidae), with the description of two new species. *Copeia* **3**: 583–608.
- Patterson C, Johnson GD. 1995.** The intermuscular bones and ligaments of teleostean fishes. *Smithsonian Contributions to Zoology* **559**: i–iv, 1–83.
- Regan CT. 1903.** On a collection of the fishes from the Azores. *Annals and Magazine of Natural History* **7**: 344–348.
- Regan CT. 1925.** The fishes of the genus *Gigantura*, A. Brauer, based on the specimens collected in the Atlantic by the 'Dana' Expeditions, 1920–22. *Annals and Magazine of Natural History* **15**: 53–59.
- Rosen D. 1971.** The Macristiidae, a ctenothrissiform family based on juvenile and larval scopelomorph fishes. *American Museum Novitates* **2452**: 1–22.
- Rosen DE. 1973.** Interrelationships of higher euteleostean fishes. *Zoological Journal of the Linnean Society* **53** (Suppl. 1): 397–513.
- Rosen DE, Patterson C. 1969.** The structure and relationship of the paracanthopterygian fishes. *Bulletin of the American Museum of Natural History* **141**: 361–469.
- Sabaj-Perez Me. 22 September 2014. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. An Online Reference. Version 5.0. Electronically accessible at <http://www.asih.org/>, American Society of Ichthyologists and Herpetologists, Washington, DC.
- Sato T, Nakabo T. 2003.** A revision of the *Paraulopus oblongus* group (Aulopiformes: Paraulopidae) with description of a new species. *Ichthyological Research* **50**: 164–177.

- Sulak KJ. 1977.** The systematics and biology of *Bathypterois* (Pisces, Chlorophthalmidae) with a revised classification of benthic myctophiform fishes. *Galathea Report* **14**: 49–108.
- Taylor WR, Van Dyke CC. 1985.** Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybiurn* **9**: 107–120.
- Tucker DW. 1954.** Report on the fishes collected by S.Y. “Rosaura” in the North and Central Atlantic, 1937–38. Part I. Families Carcharhinidae, Torpedinidae, Rosauridae (Nov.), Salmonidae, Alepocephalidae, Searsidae, Clupeidae. *Bulletin of the British Museum (Natural History) Zoology* **2**: 163–214.
- Vanhoeffen E. 1918.** Zur Erinnerung an August Brauer. *Mitteilungen aus dem Museum fuer Naturkunde in Berlin Zoologische Reihe* **9**: 1–12.
- Walters V. 1961.** A contribution to the biology of the Giganturidae, with description of a new genus and species. *Bulletin of the Museum of Comparative Zoology* **125**: 297–319.
- Walters V. 1964.** Order Giganturoidei. *Memoirs Sears Foundation for Marine Research* **1**: 566–577.
- Weitzman SH. 1962.** The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. *Stanford Ichthyological Bulletin* **8**: 1–77.