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Revision of the bathydemersal fish genus *Pycnocraspedum* (Ophidiidae; Teleostei), with description of two new species

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Abstract

A taxonomic revision of the deep-water ophidiid genus *Pycnocraspedum* Alcock, 1889 resulted in seven species being recognized, two of which are described as new: *P. africanum* **sp. nov.** from East Africa; *P. armatum* Gosline, 1954 from Hawaii, Japan and south to New Caledonia; *P. fulvum* Machida, 1984 from Okinawa Trough; *P. microlepis* (Matsubara, 1943) from off Japan to East China Sea; *P. phyllostoma* (Parr, 1933) tropical western Atlantic; *P. rowleyensis* **sp. nov.** northwestern Australia; *P. squamipinne* Alcock, 1889 previously thought to be widely distributed from East Africa to New Caledonia appears to be restricted to the Bay of Bengal. In addition, a fossil otolith-based species is recognized from the Early Pliocene of Italy: *P. cetonaense* (Schwarzhans, 1978).

Pycnocraspedum is characterized by the anterior position of the dorsal-fin origin with the first dorsal-fin pterygiophores positioned in front of the first neural spine (except above the first neural spine in one species), 4 to 6 developed gill rakers on the first gill arch, 11 to 14 precaudal vertebrae (mostly 12 to 13), and small, granular teeth resembling sandpaper with no discernable row or other pattern on jaws and palate. A revised key to the species of *Pycnocraspedum* is provided. Detailed descriptions, including otolith and morphological comparisons as well as geographical distributions are given for each species.

Key words: *Pycnocraspedum*, Ophidiidae, bathydemersal, taxonomy, biogeography, two new species

Introduction

The ophidiid genus *Pycnocraspedum* was established by Alcock in 1889 for the species *Pycnocraspedum squamipinne* Alcock, 1889 from the Bay of Bengal. Since then, four additional species have been described from Hawaii (Gosline 1954), Japan (Matsubara 1943; Machida 1984) and the Caribbean (Parr 1933), each based on unique types. Furthermore, a fossil otolith-based species of *Pycnocraspedum* has been described from the Early Pliocene of Italy (Schwarzhans 1978). The species of *Pycnocraspedum* are bathydemersal fishes living mainly at depths of 145–605 m, but as deep as 1345 m on the upper continental slopes (Nielsen *et al.* 1999, Chave & Mundy 1994). These fishes inhabit tropical to subtropical seas in the Indo-West Pacific and the tropical West Atlantic but are missing from the East Pacific and the East Atlantic (Nielsen *et al.* 1999). They are caught relatively rarely, and therefore only 38 specimens have been available for review.

Nielsen *et al.* (1999) stated that the genus *Pycnocraspedum* is in need of a full revision. The type species *P. squamipinne* has been widely reported throughout the Indo-West Pacific, while its congeners have only been recorded from the areas of their respective original description. Recently, Teena *et al.* (2021) redescribed *Pycnocraspedum squamipinne* based on two syntypes at the Zoological Survey of India (ZSI), Kolkata, India, and 15 additional newly collected specimens off southern India. Their re-description of the syntypes adds important information as well as photographs of specimens and otoliths which they supplied. However, the table of morphometrics and meristics for

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the 15 newly collected specimens shows extremely wide variability which we consider extending well beyond the limits of the species. The cause for this discrepancy is unknown and would require review of the specimens. For this reason, we have decided not to use Teena *et al.* (2021) data on *P. squamipinne* in our review.

Here, we review the extant species of the genus based on the study of available type specimens and newly collected material. The new specimens are from the Bay of Bengal off Myanmar, East Africa, Western Australia, and from the Caribbean. We recognize seven extant species, including two new species, *P. africanum* **sp. nov.** from the western Indian Ocean off East and South Africa, and *P. rowleyensis* **sp. nov.** from off northwestern Australia. The unique holotype of *Pycnocraspedum microlepis* (Matsubara, 1943) is apparently lost (Fricke *et al.* 2024) and therefore is not included in our review. We found no specimen that would match Matsubara's description, and so we maintain the species as nominally valid but requiring reassessment.

Material and Methods

Abbreviations used: SL = standard length; HL = head length; A = anal-fin ray; D = dorsal-fin ray; V = vertebra; OL = otolith length; OH = otolith height; CL = collum length in otoliths. D/V = first dorsal-fin ray above vertebra; D/A = dorsal-fin ray above first anal-fin ray; V/A = vertebra above first anal-fin ray. Counts and measurements of holotype or lectotype are mentioned first, when available; the range is given in brackets. Negative values for D/V indicate number of dorsal-fin rays in front of first vertebra. Institutional abbreviations used: BMNH = Natural History Museum, London, formerly British Museum of Natural History, London, UK; BSKU = Kochi University, Department of Biology, Faculty of Science, Kochi, Japan; IMR = Norwegian Institute of Marine Research, Bergen, Norway; IRSNB = Institut Royal de Sciences Natureles de Belgique, Brussels, Belgium; LACM = Los Angeles County Museum of Natural History, Los Angeles, California, U.S.A.; MNHN = Muséum National d'Histoire Naturelle, Paris, France; SAIAB = South African Institute for Aquatic Biodiversity, Makhanda/Grahamstown, South Africa; SMF = Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany; USNM = National Museum of Natural History, Washington D.C., U.S.A.; WAM = Western Australian Museum, Perth, Australia; ZIN = Zoological Institute, Academy of Sciences, St. Petersburg, Russia; ZMUC = Zoological Museum, University of Copenhagen, Copenhagen, Denmark; ZSI = Zoological Survey of India, Kolkata, India.

Key characters

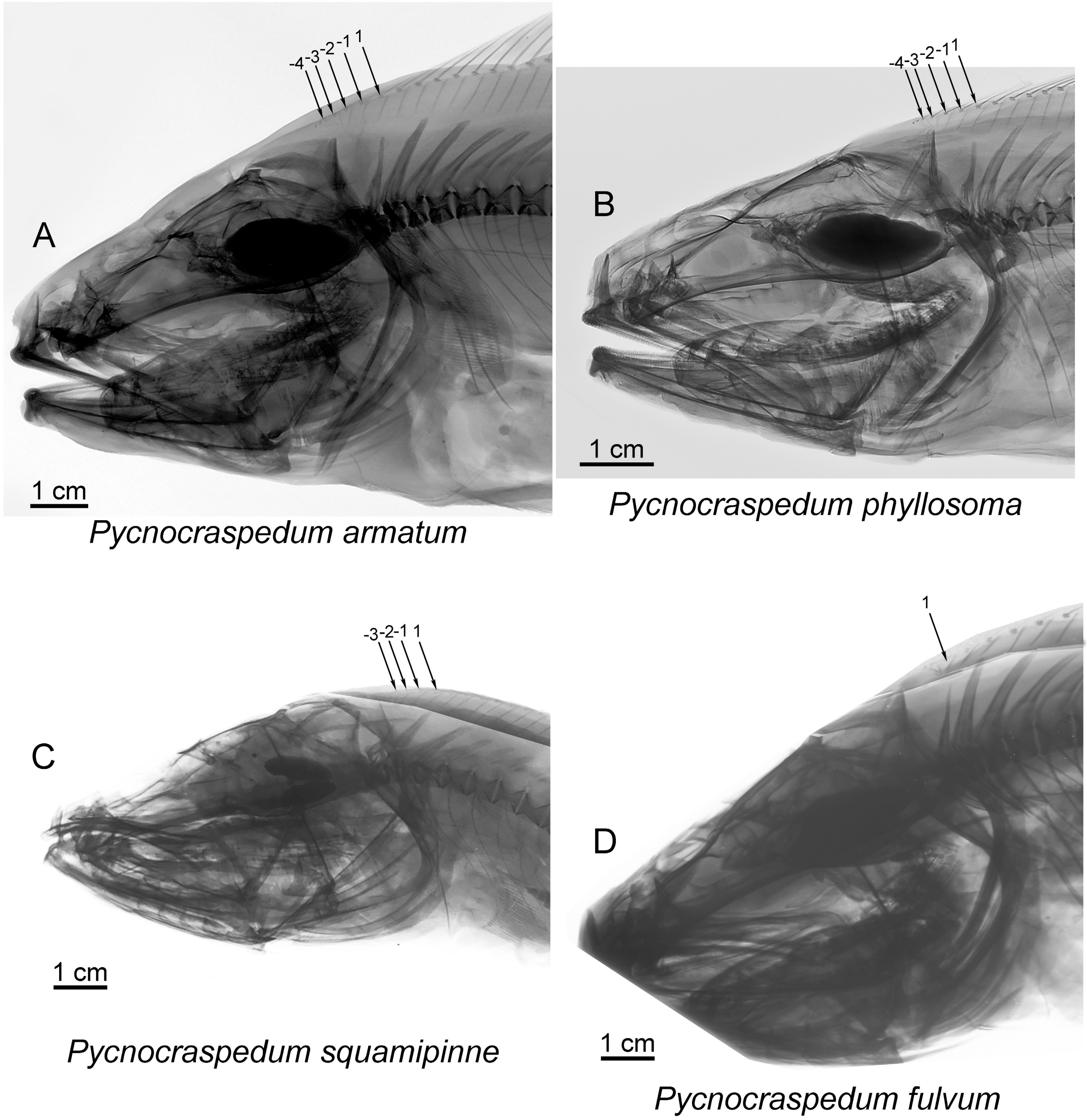
1. Origin of dorsal fin (Fig. 1). *Pycnocraspedum* is remarkable for the unusual anterior position of the dorsal-fin origin. In most ophidiiforms, the first dorsal-fin ray is positioned above the 2nd to 6th vertebra. There are a few genera where the first dorsal-fin ray can be inserted above the 1st vertebra (e.g., *Glyptophidium*, *Sirembo*, and *Spottobrotula* based on own radiographs). In *Leptobrotula*, there are 1–2 dorsal-fin rays inserted in front of the 1st vertebra. In all but two species of *Pycnocraspedum*, one to four dorsal-fin rays are inserted in front of the 1st vertebra. As many as five dorsal-fin rays are inserted in front of the 1st vertebra in *P. armatum*. The unique holotype of *P. fulvum* is the only case of the first dorsal-fin ray inserted above the 1st vertebra. Clearly, the origin of the dorsal fin in front of the vertebra is a derived, apomorphic character considering its rare occurrence in the Ophidiiformes. The forward origin of the dorsal fin, which is also observed, to a lesser extent, in a few other genera mentioned above, apparently has developed more than once, as the majority of the above genera are not considered to be interrelated.

2. Head and body proportions. Species of *Pycnocraspedum* are relatively large-headed, stout fishes. The head length is commonly less than 30% of the standard length, and the body depth at the vent is between 17 and 23% of the standard length. This makes *Pycnocraspedum* relatively robust and often retrieved in fairly good shape. The polarity of these proportional features is too variable in the order Ophidiiformes to be of phylogenetic use, but we assume that it most likely represents a plesiomorphic aspect.

3. Gill rakers on the first gill arch (Fig. 2). *Pycnocraspedum* has 4–5 (rarely 6) developed gill rakers on the first gill arch. It is an amazingly constant character, but it is also shared with a number of ophidiiform genera (Table 1). The developed gill rakers are positioned along the anterior section of the lower arm of the gill arch. The posterior section of the lower arm of the gill arch and the upper arm have about 9–12 small, rudimentary gill rakers or patches, which are often difficult to recognize and therefore are not counted here. There are instances where they appear to be completely atrophied.

TABLE 1. Selected key parameters of the currently 37 recognized ophidiid genera. Characters shared with *Pycnocraspedum* are highlighted. D/V = first dorsal-fin ray above vertebra.

Genus	gill rakers	precaudals	D/V	preop spines	pectorals	otolith
Pycnocraspedum	4 to 6	12 to 13	-5 to 1	2 to 4	24 to 28	slender + long sulcus
Abyssobrotula	8 to 11	18 to 21	>2	-	10 to 11	compressed + short sulcus
Acanthonus	11 to 22	9 to 12	>2	strong	16 to 20	compressed + short sulcus
Alcockia	7	16	>2	serrated	23	oval +short sulcus
Apagesoma	10 to 12	13 to 15	>2	-	25 to 28	compressed + short sulcus
Barathrites	5 to 7	18	>2	-	25	compressed + short sulcus
Barathrodemus	12 to 15	12 to 14	>2	-	19 to 25	oval +short sulcus
Bassogigas	7 to 9	15 to 16	>2	-	27 to 31	slender + long sulcus
Bassozetus	9 to 22	11 to 17	>2	-	21 to 29	oval +short sulcus
Bathyonus	10+	17 to 19	>2	-	16 to 19	compressed + short sulcus
Bethocometes	7 to 10	11 to 12	>2	-	27 to 33	oval + long sulcus
Dannevigia	4	17	>2	present	24 to 27	slender + long sulcus
Dicrolene	15	13 to 16	>2	3	22 to 33	oval +short sulcus
Enchelybrotula	-	22 to 23	>2	-	22 to 23	compressed + short sulcus
Epetriodus	20 to 24	12 to 13	>2	-	23 to 29	slender + long sulcus
Eretmichthys	15 to 20	14 to 15	>2	-	25 to 29	compressed + short sulcus
Glyptophidium	14 to 41	11 to 13	1 to 2	-	20 to 26	oval + long sulcus
Holcomycteronus	7 to 11	17 to 20	>2	-	15 to 21	oval +short sulcus
Homostolus	27 to 42	13	>2	1 to 3	21 to 23	oval + long sulcus
Hoplobrotula	5 to 6	13 to 15	>2	3	19 to 23	oval + long sulcus
Hypopleuron	3	22	>2	-	26	slender + short sulcus
Lamprogrammus	8 to 13	11 to 14	>2	filaments	19 to 22	slender + short sulcus
Leptobrotula	15 to 17	12	-2 to -1	present	26 to 28	oval + long sulcus
Leucicorus	8 to 12	13 to 14	>2	-	22 to 25	oval +short sulcus
Luciobrotula	3	14 to 16	>2	-	25 to 30	slender + long sulcus
Mastigopterus	10	15	>2	-	12 to 14	oval + long sulcus
Monomitopus	10 to 27	13 to 15	>2	2 to 3	26 to 34	slender + long sulcus
Neobythites	6 to 34	11 to 14	>2	0 to 3	22 to 34	slender + long sulcus
Penopus	8 to 10	18 to 19	>2	serrated	17 to 19	compressed + short sulcus
Petrotyx	3	12	>2	-	21 to 28	oval + large sulcus
Porogadus	11 to 21	14 to 19	>2	many	15 to 23	short sulcus
Selachophidium	15 to 21	17 to 18	>2	-	26 to 29	oval +short sulcus
Sirembo	3 to 5	13 to 15	1 to 5	-	21 to 28	oval + large sulcus
Spectrunculus	7 to 10	20 to 26	>2	-	23 to 33	oval + long sulcus
Spottobrotula	9 to 12	14 to 16	1 to 5	-	23 to 30	oval + large sulcus
Tenuicephalichthys	14 to 21	14 to 17	>2	-	16 to 19	compressed + short sulcus
Typhlonus	10 to 13	13 to 14	>2	-	24 to 28	compressed + short sulcus



Pycnocraspedum armatum

Pycnocraspedum phyllosoma

Pycnocraspedum squamipinne

Pycnocraspedum fulvum

FIGURE 1. Radiograph figures of selected specimens of the genus *Pycnocraspedum* to visualize position of dorsal-fin rays in relation to first vertebra; "1" denotes the first dorsal-fin ray above the first vertebra; numbers with negative denotation represent dorsal-fin rays in front of the first vertebra. **1A**) *Pycnocraspedum armatum*, USNM 227390; **1B**) *Pycnocraspedum phyllosoma* USNM 227413; **1C**) *Pycnocraspedum squamipinne*, ZMUC P771871; **1D**) *Pycnocraspedum fulvum* (holotype), BSKU 27497.

4. Dentition (Fig. 2). The dentary and premaxilla of *Pycnocraspedum* are characterized by broad, slightly convexly bent bands of minute, granular teeth, resembling sandpaper, with no discernible rows or other pattern. The vomer and palatines bear the same type of teeth but in narrower bands. The vomer is broad and boomerang-shaped or V-shaped. The diet of *Pycnocraspedum* is not known. On various radiographs, only amorphous lumps were detected in the stomach and intestines and no discernible components other than occasionally some sand grains. Based on these observations, we assume that *Pycnocraspedum* may primarily feed on soft, bottom- or near-bottom-living invertebrates.

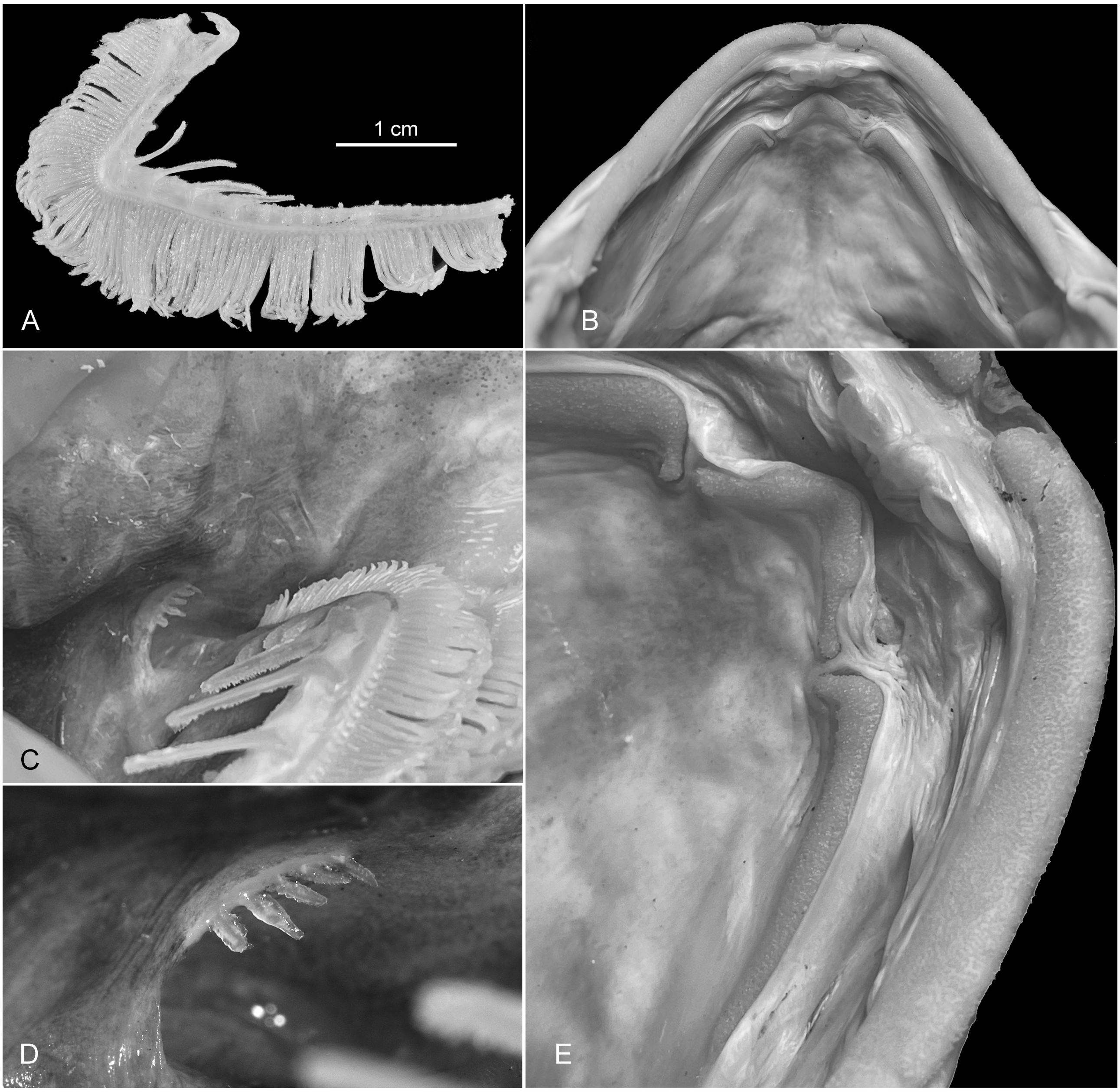


FIGURE 2. Gill rakers, pseudobranchial filaments and dentition details. **2A**) Extracted first gill arch from *Pycnocraspedum squamipinne*, ZMUC P771871; **2B, 2E**) Dentition of premaxilla, vomer and palatines of *Pycnocraspedum armatum*, USNM 227412, 2E is close-up to show sandpaper like texture of granular teeth; **2C–2D**) Pseudobranchial filaments in *Pycnocraspedum armatum*, USNM 227412.

5. Basibranchial tooth patches. The number and shape of basibranchial tooth patches are considered to be diagnostic in certain genera of the Neobythitinae (Nielsen *et al.* 1999), either for distinction of species (e.g., *Dicrolene*, see Nielsen *et al.* 1999) or genera. However, it has also been shown in certain genera, like *Porogadus* (see Schwarzhans & Møller 2021), that the number of basibranchial tooth patches can vary within species. This also appears to be the case in *Pycnocraspedum*. All specimens of *Pycnocraspedum* examined show two long median basibranchial tooth patches, but in a few instances, they may appear to be joined to a single long median patch. Small, lateral tooth patches occur as well, and these are very irregularly distributed. It is common to see a specimen with only a small left or right lateral tooth patch instead of a pair. In fact, the occurrence of a full pair of lateral tooth patches is the exception rather than the rule. *Pycnocraspedum squamipinne,* for instance, is known from specimens with two median tooth patches, the median tooth patches fused to a single long one, or two median tooth patches accompanied with one small lateral tooth patch on the left or right side. So far, no specimen has been found in *P. squamipinne* with a full set of two median and two lateral basibranchial tooth patches. A full set of basibranchial tooth patches has only been observed in the holotype of *P. fulvum*.

6. Head pore system (Fig. 3). *Pycnocraspedum* has a relatively stable head pore pattern, which consists of a large anterior supraorbital pore near the tip of the snout, and a posterior supraorbital pore in species with a fleshy flap above the opercle; 3 anterior and 3 posterior infraorbital pores, the first anterior infraorbital pore somewhat elevated and positioned just below the anterior nostril (Fig. 3); 2 lower preopercular pores, with the first one sometimes spilt into two, and no upper preopercular pore; 3 anterior and 3 posterior mandibular pores, the second anterior mandibular large and tube-like, the third posterior mandibular large and positioned in a skin fold. This shows that the head pore system is consistent with other ophidiids (own observation) except for the lack of an upper preopercular pore and sometimes the posterior supraorbital pore. The position of the first anterior infraorbital pore, the tube-like large second anterior mandibular pore and the large third posterior mandibular pore positioned in a skin fold are all considered to represent apomorphic features. Observations in other ophidioid taxa as well as data published for the Dinematichthyidae (e.g., Møller *et al.* 2004) have shown the head pore composition to be relatively stable at the species and often genus level in ophidiiform fishes. We consider the slightly reduced head pore pattern and the specialized individual pores to be derived.

7. Pseudobranchial filaments (Fig. 2). Pseudobranchial filaments are extremely small in *Pycnocraspedum*, ranging in number from 1 to 7. They are easily overlooked, damaged, or lost during handling. In past literature, presence or absence of pseudobranchial filaments has sometimes been used as a diagnostic character to distinguish between species (e.g., Machida 1984; Teena *et al.* 2021). We have not found any specimen that was completely lacking pseudobranchial filaments. We believe that reports in the literature of zero pseudobranchial filaments were probably caused by their extremely small size and ease of being damaged. We found 4 or 5 (rarely 6 or 7) pseudobranchial filaments in the specimens of most species of *Pycnocraspedum*. The exception is *P. squamipinne* with 1 or 2 pseudobranchial filaments, which in this case is also a valuable diagnostic character to distinguish this species from its congeners.

8. Preopercular spines (Fig. 4). The rear margin of the preopercle shows 1 to 4 spines at the lower edge, 2 where the vertical and the horizontal section meet forming a pair of spines bordering a bony expansion, and up to two additional, smaller spines upward along the vertical section. The spines are numbered 1 to 4 from the lower preopercle upward for convenience in the descriptions (Fig. 4). Upon describing *P. armatum*, Gosline (1954) mentioned the presence of four preopercular spines as diagnostic (and name-giving) for that species in comparison with *P. squamipinne*. Indeed, the strength, number and shape of the preopercular spines are variable and specialized in the species of *Pycnocraspedum*, and appear to be a consistent character in the various species at least above a size of about 150 mm of SL. A large, broad expansion is present at the junction of the horizontal with the vertical section of the preopercular rim bearing the lower pair of spines 1 and 2. This expansion is slightly concave in cross section, spoon-shaped with the first lower preopercular pore opening at the proximal end and often with a broad depression extending onto the adjacent section of the preopercle. The bony expansion shows two spines at its upper and lower margins, which vary in expression between the species, or rarely only a single spine (number 2; Fig. 4I) as in *P. squamipinne*. An adjacent, much smaller spine (number 3) may be located slightly upward of the broad expansion and below the second lower preopercular pores, sometimes associated with a fourth, very small spine above that pore (number 4; Fig. 4A) like in *P. armatum*. In some species, the preopercular rim below the second lower preopercular pore is marked by an obtuse to orthogonal angle instead of a spine. The bony section between the lower pair of spines and the upper spine(s) or angle is deeply concave but in some species is masked by a broad fleshy flap extending over it thus forming a more gently curved rim of the preopercle.

9. Squamation (Fig. 3). *Pycnocraspedum* shows complete squamation of the body, the head and the proximal parts of the dorsal, anal and pectoral fins. The scales on the cheeks, opercle and below the eye are usually the largest (Figs. 3A, 3C), followed in size by those on the trunk (Fig. 3B). Scales on the tip of the snout, the mandible (Fig. 3D) or on the bases of the above-mentioned fins are notably smaller. Differing from many other ophidiid genera, the scales of *Pycnocraspedum* are not so readily shed and many specimens show the scales in place thus facilitating reliable counting. We counted transversal scale rows above the origin of the anal fin (Fig. 3B) and at the same position scale rows above the lateral line. We did not include scale rows on the vertical fin bases into the count. Since we do not know how previous authors made the scale count, we use only our own counts in this respect. This is particularly critical in the case of the holotype of *P. microlepis* for which Matsubara (1943) has given a count of

25 scale rows above the lateral line, which we cannot verify due to the apparent loss of the holotype. Our counts of scale rows above the lateral line are fewer, not exceeding 23, but discounting scales on the dorsal-fin basis. The number of scale rows increases slightly with the size of the fishes, but appears to be relatively stable above a SL of about 150 mm. With that restriction in mind, we found the transversal scale count, both in total and above the lateral line, a useful character to define some of the species. The total transversal scale count, however, varies slightly on either side or depending on slightly different positioning of the count and should therefore be used with caution if used for descriptions.

10. Pyloric coeca. The pyloric coeca have been used as diagnostic character in the original descriptions of all species except *P. squamipinne*, for which, however, it was added in Teena *et al.* (2021). The count of pyloric coeca ranges from 12 to 21 in species of *Pycnocraspedum*. In most species, it ranges between 12 and 16 according to our own counts and shows a considerable degree of variability. For instance, we found 12 to 16 pyloric coeca in specimens of *P. armatum*. Matsubara (1943) noted 20 pyloric coeca in his holotype of *P. microlepis*, and Parr (1933) 21 pyloric coeca in his holotype of *P. phyllosoma*. We found that in several specimens the gut was pushed out into the mouth during depressurizing when the haul was brought to the surface and in those cases the pyloric coeca could not be counted. Thus, we could not count the pyloric coeca for *P. africanum* **sp. nov.**

11. Otoliths (Fig. 5). Sagittal otolith (otolith in the following) morphology presents a valuable character in many ophidiiform fishes (see Nolf 1980; Schwarzhans 1981; Schwarzhans *et al.* 2024). This is also the case for the otoliths of *Pycnocraspedum*. *Pycnocraspedum* otoliths are large (sometimes reaching over 20 mm in length), elongate and relatively thin. Furthermore, they are characterized by a long sulcus reaching close to the anterior and posterior rims of the otolith and which contains a single, flat, large colliculum. This combination of otolith characters is not often seen in ophidiiforms; similar patterns are seen in *Bassogigas*, *Neobythites* and few species of *Monomitopus* (see Nolf 1980 and Schwarzhans 1981). We consider this pattern as apomorphic, particularly the large, long sulcus. In *P. squamipinne* the sulcus appears somewhat reduced in length compared to the other species. We consider this to represent a reversal in polarity. A single fossil species differs from all extant ones in showing a separated long ostial and a short caudal colliculum. The fusion of the, primarily, two separated colliculi into a single undivided feature, however, is a common trend in ophidiiforms and has been observed in multiple independent lineages (Schwarzhans 1981). The cause for this development, however, has remained elusive. Another aspect observed in *Pycnocraspedum* is a pronounced ontogenetic allometry in otoliths. Otoliths of fishes smaller than about 130 mm of SL are distinctly more compressed than those from fishes larger than about 180 mm of SL. This change probably represents a change in the habit of the fishes, perhaps towards a more demersal lifestyle in the larger specimens.

Taxonomy

Order Ophidiiformes Berg, 1940

Family Ophidiidae Rafinesque, 1810

Subfamily Neobythitinae Radcliffe, 1913

Genus *Pycnocraspedum* Alcock, 1889

Pycnocraspedum Alcock, 1889: type species by monotypy *Pycnocraspedum squamipinne* Alcock, 1889.
Itatius Matsubara, 1943: type species by monotypy *Itatius microlepis* Matsubara, 1943.
Paragenypterus Schwarzhans, 1981: type species by monotypy *Brotulidarum centonaensis* Schwarzans, 1978, a fossil otolith-based taxon.

Diagnosis (adopted and altered from Nielsen *et al.* 1999). A genus of the subfamily Neobythitinae characterized by the following combination of characters: Body short with large head; upper jaw ending behind eye; hind margin of preopercle with 1 to 4, spines; 2 median basibranchial tooth patches, sometimes accompanied by additional small single or pair of lateral patches; very small, closely packed teeth resembling sandpaper surface on dentary, premaxilla, vomer and palatines; 4 to 6 developed gill rakers on first gill arch; 2–3 lower preopercular pores; no upper preopercular pore; 1 to 7 small pseudobranchial filaments; pectoral-fin rays 24 to 28; precaudal vertebrae 11 to 14 (mostly 12 to 13); 0 to 5 dorsal-fin rays in front of first vertebra; otoliths slender with long, uniform sulcus. Head and body completely covered with small cycloid scales, including bases of dorsal, anal and pectoral fins.

General description: A number of characters occur in all species of *Pycnocraspedum* in the same manner. In order to reduce redundancy, the following description summarizes those characters that are valid in all the species here studied.

Head stout, with straight, inclined dorsal profile. Opercle with sharp, slightly extruding spine. Eye moderately small. Maxilla extending far behind eye, strongly widened posteriorly upward and downward from axis and with a vertical posterior end. Narrow, poorly defined supramaxilla. Pores: 1 anterior supraorbital, no posterior supraorbital, 3 anterior infraorbital, 3 posterior infraorbital, 3 anterior mandibular, 3 posterior mandibular, 2–3 lower preopercular. Head completely covered with scales, including opercle, preopercle, cheeks, and maxilla. Scales on head larger than scales on body and peduncle.

Dentition. Minute sandpaper-like granular teeth on broad dentary and premaxillary bands, narrow palatine bands, and a narrow, boomerang-shaped vomerine patch. Basibranchial tooth patches 2 long median and 1 small lateral patch on left or right side, rarely a symmetrical pair.

Discussion: Following the synonymization of the genera *Tauredophidium* Alcock, 1890 and *Xyelacyba* Cohen, 1961 with *Acanthonus* Günther, 1878 by Girard *et al.* (2024) and the establishment of *Tenuicephalichthys* Schwarzhans & Møller 2024, the subfamily Neobythitinae now comprises 37 genera. The interrelationships of many of the neobythitine genera have remained elusive. Matsubara (1943) found *Itatius* (syn. *Pycnocraspedum*) resembling *Neobythites*, differing from *Neobythites* in: “1) bones of head soft; 2) pseudobranchiae absent; 3) developed gill-rakers on first gill-arch fewer than 5; 4) dorsal inserted above the upper angle of the gill-opening.” Gosline (1954) postulated the existence of a group of oviparous brotulid genera which he thought are intermediate between oviparous and viviparous genera and counted *Pycnocraspedum* and *Volcanus* (syn. *Luciobrotula*) to this group. Cohen (1964) added *Petrotyx* to this group and Cohen & Nielsen (1978) considered *Pycnocraspedum* belonging to a cluster with *Luciobrotula, Petrotyx* and *Spottobrotula*. Machida (1984) found *Pycnocraspedum* resembling *Neobythites*. Studies using molecular phylogenetic analysis of neobythitine taxa so far are few. Møller *et al.* (2016) did not include *Pycnocraspedum*. Girard *et al.* (2023) resolved *Pycnocraspedum* as sister taxon of *Neobythites*. Wong & Chen (2024) showed *Pycnocraspedum* in a clade with *Brotulataenia* and *Lamprogrammus*.

A comparison of the diagnostic key characters of *Pycnocraspedum*—developed gill rakers, number of precaudal vertebrae, origin of dorsal fin, presence/absence of preopercular spines, number of pectoral-fin rays, and otolith morphology—showed the highest degree of congruence with *Neobythites* (except origin of dorsal fin) and *Monomitopus* (except origin of dorsal fin and developed gill rakers) (Table 1). Particularly the origin of the dorsal fin in front of the first vertebra is an almost unique character within Ophidiiformes, shared only with *Leptobrotula*. The dorsal-fin commences above the first vertebra in some species of the genera *Glyptophidium*, *Sirembo* and *Spottobrotula* otherwise it commences above the third vertebra or posteriorly in other ophidiiforms. A low number of developed gill rakers on the first gill arch is shared with several other genera such as *Barathrites*, *Dannevigia*, *Hoplobrotula, Luciobrotula*, *Petrotyx* and *Sirembo*. Long, slender otoliths are also found in *Bassogigas*, *Epetriodus*, *Luciobrotula*, *Monomitopus* and *Neobythites*, but only in *Bassogigas*, *Neobythites* and in some species of *Monomitopus* the slender otolith shape is paired with a long sulcus. This comparison would indeed support a relationship of *Pycnocraspedum* with *Neobythites* as the most likely outcome.

Species: We consider all previously described 5 extant species as valid for *Pycnocraspedum* and describe 2 new species: *P. africanum* **sp. nov.** from the Western Indian Ocean, *P. armatum* Gosline, 1954, widely distributed in the Western and Central Pacific as far east as to Hawaii and south to New Caledonia, *P. fulvum* Machida, 1984 from Japan, *P. microlepis* (Matsubara, 1943) from Japan is considered nominally valid but could not be reassessed due to the apparent loss of the unique type, *P. phyllosoma* (Parr, 1933) from the Caribbean, *P. rowleyensis* **sp. nov.** from off northwestern Australia, and the type species *P. squamipinne* Alcock, 1889 from the Bay of Bengal. In addition, there is one fossil otolith-based species from the Early Pliocene of Italy: *P. centonaense* (Schwarzhans, 1978).

Key to the species of *Pycnocraspedum*

(see also Table 2 for the complete set of measurements and Table 3 for measurement and meristic ranges of selected traits; data for *P. microlepis* from Matsubara 1943)

1 Dorsal-fin rays 78; D/V 1 .... *P. fulvum*
\- Dorsal-fin rays 88–103; D/V-1– -5 2
2 Anal-fin rays 57–65; total vertebrae 47–51; pseudobranchials 1–2; HL 29.6–31.5% of SL; predorsal 25–29% of SL; transversal scale rows 52–58; preopercle with single, weak spine (number 2) .... *P. squamipinne*
\- Anal-fin rays 68–79; total vertebrae 51–59; pseudobranchials 4–7; HL 22.7–27.6% of SL; predorsal 17–24.5% of SL; transversal scale rows 60–90; preopercle with 2 to 4 mostly strong spines 3
3 Dorsal-fin rays 87–92; preopercle with 2 spines 4
\- Dorsal-fin rays 95–103; preopercle with 3 or 4 spines 5
4 Transversal scale rows 85–90; scale rows above lateral line 22–23; fleshy flap present between lower and upper spines on hind margin of preopercle; OL:OH (specimens larger than 15 mm OL) = 2.5–2.7 .... *P. africanum*
\- Transversal scale rows 70; scale rows above lateral line 17; fleshy flap absent on hind margin of preopercle; OL:OH (at 16.5 mm OL) = 2.1 .... *P. rowleyensis*
5 Transversal scale rows 60–68, scale rows above lateral line 15–20; pyloric coeca 12–16; preopercle with 4 spines .... *P. armatum*
\- Transversal scale rows 72–78 or not known, scale rows above lateral line 20–25; pyloric coeca 18–21; preopercle with 3 spines or not known 6
6 Transversal scale rows above lateral line 20–21 .... *P. phyllosoma*
\- Transversal scale rows above lateral line 25 .... *P. microlepis*

TABLE 2. Meristic, morphometric and otolith characters of the species of the genus *Pycnocraspedum*. For abbreviations used see "Materials and Methods."

	africanum	***armatum***	***fulvum***	***microlepis****	***phyllosoma***	***rowleyensis***	***squamipinne***
studied spec. (total)	7	14	1	1*	4	1	6
size (SL in mm)	85–420	77–334	336	~200	130–355	235	122–243
meristics	(7)	(14)	(1)		(4)	(1)	(5)
precaudal vertebrae	12–13	11–14	13		12–13	12	12–13
caudal vertebrae	39–42	39–46	42		39–42	40	35–38
total vertebrae	51–54	52–59	55		52–54	52	47–51
dorsal-fin rays	88–92	95–103	78	98	96–101	87	90–92
anal-fin rays	68–71	71–79	63	76	70–73	69	57–65
caudal-fin rays	10	10	10	10	10	10	9–10
pectoral-fin rays	25	25–26	26	26	25–27	25	25–30
D/V	-1– -3	-2– -5	1		-3– -4	-2	-1– -3
D/A	23–28	23–31	22		29–30	25	24–31
V/A	15–19	15–17	17		16–17	17	16–17
pseudobranchials	4–5	4–7	4	0?	5–6	4–5	1–2
developed gill rakers	4	4–5	4	4	4–5	4	4
transversal scale rows	85–90	60–68	60		72–78	70	52–58
scale rows above lat line	22–23	15–20	19–20	25	20–21	17	12–17
pyloric coeca		12–16	13	20	18–21	13	12–13
preopercular spines	2	4	3		3	2	1
morphometrics (% SL)	(2–4)	(4–12)	(1)		(4)	(1)	(5)
head length (HL)	25.6–27.6	23.8–26.9	27.0	23.8	22.7–26.5	25.3	29.6–31.5
body depth	19.2–22.5	19.4–23.3	19.6	<19.6	21.0–23.0	18.9	17.3–18.0
snout length	7.1–7.9	5.4–7.8	6.2	5.7	7.1–7.1	6.6	5.2–7.0
diameter of orbit	4.1–4.8	3.9–4.8	4.2	4.0	4.4–5.0	3.9	4.5–5.1
upper jaw	12.0–15.0	11.8–15.0	15.0	11.9	11.4–14.5	14.3	15.0

......*continued on the next page*

TABLE 2. (Continued)

	africanum	*armatum*	*fulvum*	*microlepis**	*phyllosoma*	*rowleyensis*	*squamipinne*
interorbital width	7.1–7.5	6.1–7.7	7.5	6.8	6.5–8.1	7.0	5.8–6.2
pelvic to anal-fin base	22.0–26.0	21.8–28.0			22.2–26.0	28.7	27.0–32.5
predorsal	20.2–24.5	17.0–22.4	25.0	18.5	18.8–23.0	23.0	25.0–29.0
preanal	43.3–52.0	40.0–48.0	47.6	40.0	41.7–51.0	50.2	46.0–52.0
prepelvic	22.9–27.5	19.3–23.3	21.8		19.1–27.0	24.8	20.0–21.5
pectoral-fin length	12.0–15.7	16.0–18.1	15.9	17.0	14.5–17.2	15.0	17.0–18.0
pelvic-fin length	12.0–12.5	17.5			11.5–13.0	13.7	11.5–14.0
otolith	(2)	(4)	(1)		(1)	(1)	(3)
OL:OH in spec. >10 mm	2.5–2.7	1.95–2.2	2.4		2.15	2.1	2.4–2.5
OH:OT	2.7–3.0	2.3–2.9	2.8		2.4	2.35	2.6–2.8
OL:CL	1.3–1.35	1.3–1.45	1.3		1.25	1.45	1.5–1.6
dorsal-rim shape	smooth	crenulated	crenulated		smooth	crenulated	low
inner face curvature	sl. bent	convex	convex		convex	convex	flat

* after Matsubara (1943)

values in brackets indicate number of studied specimens per category

TABLE 3. Ranges of selected key counts and measurements of the species of the genus *Pycnocraspedum*. D/V = first dorsal-fin ray above vertebra. Colors indicate species for ease of comparison.

total vertebrae	47	48	49	50	51	52	53	54	55	56	57	58	59
africanum					1	3	2	1					
armatum						1	1	3	2	3			1
fulvum									1				
phyllosoma						2	1	1					
rowleyensis						1							
squamipinne	2		1	2	1								

dorsal-fin rays	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103
africanum											2	1		3	1											
armatum																		2	1		1	2	1	1	1	2
fulvum	1																									
phyllosoma																			1	1	1	1		1		
rowleyensis										1																
squamipinne													2	1	2											

anal-fin rays	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79
africanum												1	2	2	1								
armatum															3	1	1	3	1	2			1
fulvum							1																
phyllosoma														1	2	1	1						
rowleyensis													1										
squamipinne	1				1	1		1	1														

pseudobranchials	0	1	2	3	4	5	6	7
africanum					4	1		
armatum					3	2		1
fulvum					1			
phyllosoma						2	3	
rowleyensis						1		
squamipinne		1	4					

D/V	-5	-4	-3	-2	-1	1
africanum			5	3	1	
armatum	3	4	4	1		
fulvum						1
phyllosoma			4			
rowleyensis				1		
squamipinne			2	2	1	

HL % of SL	22	23	24	25	26	27	28	29	30	31
africanum				1		3				
armatum		1	3	2	6					
fulvum						1				
phyllosoma	1		1	1	2					
rowleyensis					1					
squamipinne								1	2	2

Depth % of SL	17	18	19	20	21	22	23
africanum			1		1	2	
armatum			3	2	3	2	4
fulvum			1				
phyllosoma					2	1	1
rowleyensis			1				
squamipinne	4	1					

predorsal % of SL	17	18	19	20	21	22	23	24	25	26	27	28	29
africanum				1		1	1	1					
armatum	1	2	4	3		2							
fulvum									1				
phyllosoma			2	1		1	1						
rowleyensis							1						
squamipinne									2	1			1

Pycnocraspedum africanum sp. nov.

Figures 3, 5, 6, 12; Tables 1, 2

Pycnocraspedum squamipinne (non Alcock, 1889): Schwarzhans 1994 (including holotype from MNHN), Fricke *et al.* 2018 (same specimens from MNHN including holotype and paratype), Nielsen & Uiblein (2022).

Pycnocraspedum sp. cf. *squamipinne*? (non Alcock, 1889): Prokofiev (2005): 118, figs. 9–10 (same specimen from ZIN now paratype).

Material examined (7 specimens, 85–420 mm SL): Holotype: MNHN 2000–5691, 420 mm SL, 22°21'7.2"S , 43°4'4.8"E (off western Madagascar), beam trawl 450 m, Crosnier st. ch095, 27 November 1973; paratypes: MNHN 2000–5692, 330 mm SL, 12°27'7.2"S 48°12'3.6"E (Madagascar Channel), beam trawl 600–605 m, Crosnier st. ch021, 19 January 1972; 2 specimens SAIAB 98892, 100–110 mm SL, 12.6953°S 40.667°E (off northern Mozambique), haul 135, beam trawl 292 m, 23 November 2007; 1 specimen SAIAB 98894, 85 mm SL, 12.6953°S 40.667°E (off northern Mozambique), haul 136, beam trawl 391 m, 23 November 2007; 1 specimen SAIAB 98897, 95 mm SL, 11.1341°S 40.7696°E (off northern Mozambique), 24 November 2007; 1 specimen, ZIN 51521, 210 mm SL, Vityaz cruise 17, st. 2522, 21°16'S 35°41'E (off eastern South Africa), 480–500 m, 21 November 1988.

Diagnosis. Precaudal vertebrae 12–13, total vertebrae 51–54; dorsal-fin rays 88–92; anal-fin rays 68–71; pectoral-fin rays 25; long gill rakers on first gill arch 4; pseudobranchials 4–5; 1–3 dorsal-fin rays in front of first vertebra; HL 27.1–27.6% of SL; body depth at vent 21–22.5% of SL; predorsal length 23–24.5% of SL; transversal scale rows above origin of anal fin 85–90, and above lateral line 22–23; broad expansion on preopercular angle with two spines, fleshy flap on hind margin of preopercle above spine 2; otoliths >15 mm in length: OL:OH = 2.5–2.7, dorsal rim with rounded obtuse middorsal angle.

Description. Relatively robust fish with stout tapering tail and rounded snout. Maximal size of fishes investigated 420 mm SL (holotype). Preopercular rim with two blunt spines positioned at bend, fleshy flap above 2nd spine and no spine further upward.

Meristics (6 specimens): precaudal vertebrae 13 (12–13); total vertebrae 53 (51–54); dorsal-fin rays 91 (88–92); anal-fin rays 69 (68–71); pectoral-fin rays 25; caudal-fin rays 10; D/V = -2 (-1– -3); D/A = 28 (23–28); V/A = 19 (15–19); long gill rakers on first gill arch 4; pseudobranchial filaments 4 (4–5); transversal scale rows above origin of anal fin 85–90, and above lateral line 22–23; pyloric coeca unable to count.

Morphometrics (3 specimens) in % of SL: HL 27.1–27.6; body depth at vent 21 (21–22.5); diameter of eye 4.1 (4.1–4.8); upper jaw length 15 (12–15); interorbital width 7.1 (7.1–7.5); pelvic-fin base to anal-fin base 24 (24–26); predorsal length 24.5 (22.9–24.5); preanal length 52 (46.2–52); prepelvic length 27.5 (22.9–27.5); pectoral-fin length 13.5 (12–15.7); pelvic-fin length 12 (12–12.5).

Otolith morphology (4 specimens). Size up to 22 mm in length (holotype); OL:OH = 2.5–2.7 in specimens larger than 15 mm in length, 1.6 in specimens smaller than 7 mm in length, and single intermediate form with 2.3 at about 12 mm in length; OH:OT = 2.7–3.0. Thin, oval, elongated, anteriorly moderately projecting, posteriorly distinctly pointed, anterior and posterior tips inferior. Dorsal rim with broad, rounded, obtuse mediodorsal angle in large specimens and shallow ventral rim. All rims smooth in large specimens (>15 mm in length) intensely crenulated in smaller specimens (<12 mm in length). Inner face slightly bent in horizontal direction, nearly flat in vertical direction, with very long, undivided sulcus reaching close to anterior and posterior rims of otolith. Sulcus with shallow, undivided, uniform colliculum with flat to slightly concave dorsal rim and slightly convex ventral rim and rounded anterior and posterior tips. OL:CL = 1.3–1.35. Dorsal field with broad, indistinct depression; ventral field smooth, occasionally with faint central furrow. Outer face smooth in large specimens, with many radial furrows and central tubercles in small specimens.

Coloration. Live coloration unknown. Color of preserved specimens light brown.

Discussion. *Pyconocraspedum africanum* is the largest species of the genus so far known, with the holotype of 420 mm of SL. The species differs from the type species *Pycnocraspedum squamipinne* in the higher number of anal-fin rays (68–71 vs. 57–65), the higher number of pseudobranchial filaments (4–5 vs. 1–2), the more slender shape (depth at vent in % of SL 21–22 vs. 17–18) and the shorter head (27.1–27.6 vs. 29.6–31.5 % of SL). *Pycnocraspedum africanum* differs from *P. fulvum* in the higher number of dorsal-fin rays (88–92 vs. 78) and anal-fin rays (68–71 vs. 63). *Pycnocraspedum africanum* differs from *P. armatum* and *P. phyllosoma* in the lower number of dorsal-fin rays (88–92 vs. 95–103). *Pycnocraspedum africanum* resembles closest *P. rowleyensis* **sp. nov.** from off northern Western Australia in the number of dorsal-fin rays and the presence of only 2 spines on the hind margin of the

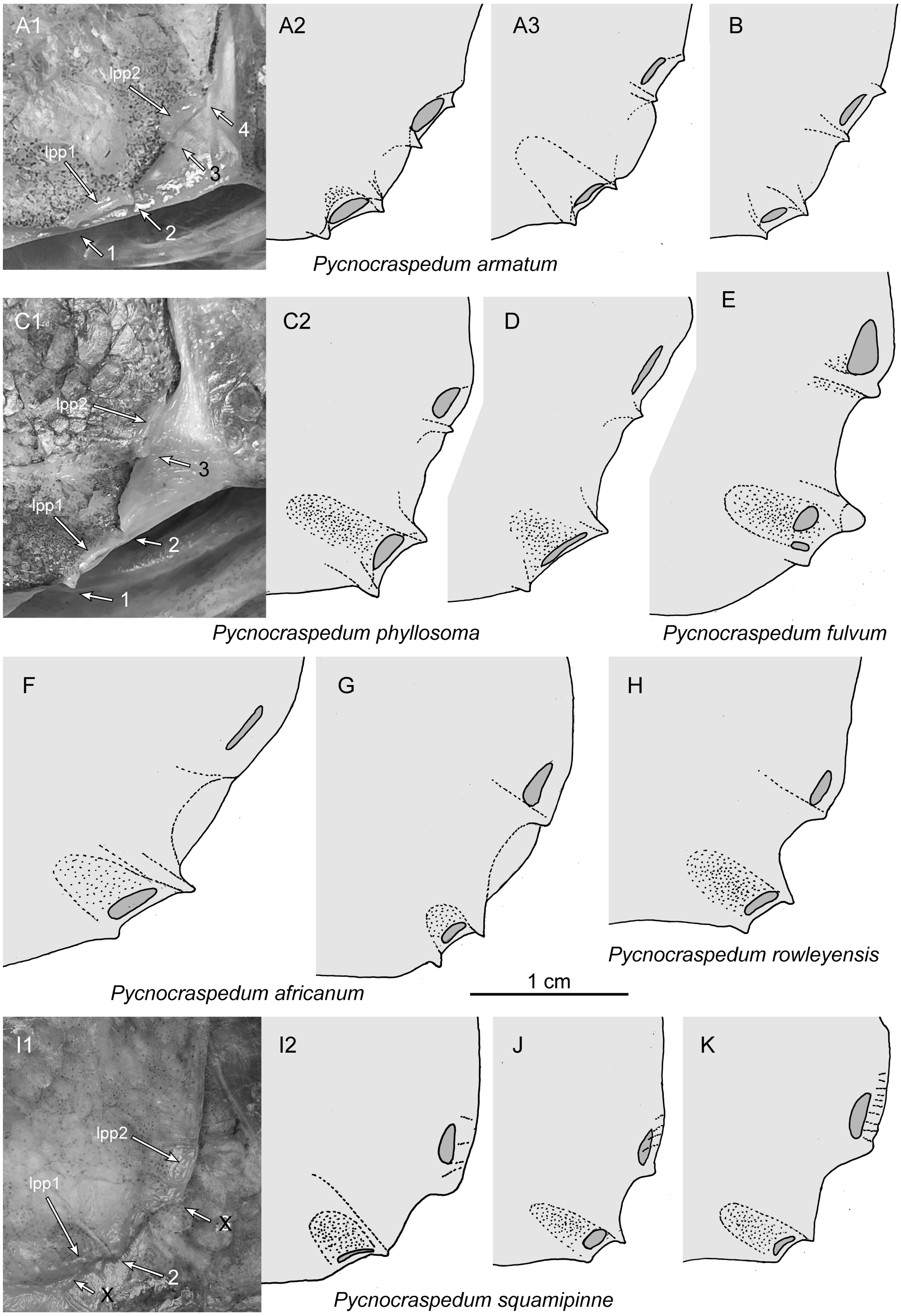


FIGURE 3. Detail figures and drawings of preopercular spines and lower preopercular pores in *Pycnocraspedum*; preopercular spines are numbered from 1 through 4 from the lower angle of the preoperculum upwards; abbreviation lpp = lower preopercular pore. **3A–3B**) *Pycnocraspedum armatum*, USNM 227412, 3A1-3A2 specimen 1 left side, 3A3 specimen 1 right side (mirror imaged), 3B specimen 2; **3C–3D**) *Pycnocraspedum phyllosoma*, 3C USNM 421587, 3D USNM 421586; **3E**) *Pycnocraspedum fulvum* (holotype), BSKU 27497; **3F–3G**) *Pycnocraspedum africanum* **sp. nov.**, 3F holotype, MNHN 2000-5691, 3G paratype, MNHN 2000-5692; **3H**) *Pycnocraspedum rowleyensis* **sp. nov.**, holotype, WAM I.28059.021; **3I–3K**) *Pycnocraspedum squamipinne*, 3I lectotype, BMNH 1890.7.31.1, 3J ZMUC P771871, 3K ZMUC P771737.

preopercle, but differs in the lower number of transversal scale rows (85–90 vs. 70), scale rows above the lateral line (22–23 vs. 17), the presence of a flashy flap above the lower preopercular spines (vs. concave section) and the more elongate otoliths (OL:OH = 2.5–2.7 vs. 2.1). *Pycnocraspedum africanum* differs from all other *Pycnocraspedum* species in the high number of transversal scale rows above the origin of the anal fin of 85–90 (vs. 52–78). The otoliths of *P. africanum* are slenderer than those of *P. armatum* and *P. phyllosoma* (OL:OH = 2.5–2.7 vs. 2.0–2.3) and are less strongly bent; and they differ from those of *P. squamipinne* in the long sulcus (OL:CL = 1.3–1.35 vs. 1.5–1.6). The otoliths of *P. africanum* are similar to those of the fossil *P. cetonanense* (Schwarzhans, 1978) differing mainly in the narrower sulcus and the single, undivided colliculum (vs. two separate colliculi).

The specimens here selected as holotype and one of the paratypes from MNHN have previously been listed by Fricke *et al.* (2018) as *P. squamipinne*. Another specimen here listed as paratype from ZIN has been tentatively attributed to *P. squamipinne* by Prokofiev (2005). He noticed certain differences from typical *P. squamipinne* specimens such as the presence of 4 pseudobranchial filaments (vs. 1–2) and a more compressed, shorter head. It is possible that a large specimen recorded by Teena *et al.* (2021) from off Chennai coast, southern India, with a suspiciously high number of transversal scale rows could potentially represent *P. africanum* as well.

Distribution. *Pycnocraspedum africanum* is a relatively deep dwelling species at 450 to 605 mm depth, while all other species mostly occur between 300 and 500 m (Nielsen *et al.* 1999). *Pycnocraspedum africanum* occurs off the East African coast from 11°S to 22°S, but could be more widely spread in the Indian Ocean subject to review of previously recorded specimens.

Etymology. Named after the continent of Africa from where the studied specimens have been obtained.

Pycnocraspedum armatum Gosline, 1954

Figures 1, 2, 3, 5, 7, 12; Tables 1, 2

Pycnocraspedum armatum Gosline, 1954: 80–81, tables 1–2, figs. 2e, 3e, off the Mauna Loa lava flow, Kona coast, Hawaii.

Pycnocraspedum armatum Gosline, 1954: Gosline & Brock (1960), Cohen & Nielsen (1978), Machida *in* Okamura & Kitajima (1984), Chave & Mundy (1994), Nielsen *et al.* (1999), Mundy (2005), Prokofiev (2005), Evseenko & Okyama (2006), ? Prokofiev (2022), Girard *et al.* (2023).

Pycnocraspedum squamipinne (non Alcock, 1889): Nielsen (1997), Fricke *et al.* (2011).

Material examined (14 specimens, 77.5–334 mm SL): specimens originally identified as *P. microlepis*: 1 specimen BSKU 5055, 234 mm SL, Mimase Fish Market, Kochi City, Kochi Prefecture, Shikoku Island, Japan, bottom trawl, 27 December 1955; 1 specimen BSKU 38643, 245 mm SL, Mimase Fish Market, Kochi City, Kochi Prefecture, Shikoku Island, Japan, bottom trawl, 14 March 1983; specimens originally identified as *P. armatum*: 2 specimens LACM 44837-1, 213–334 mm SL, RV Townsend Cromwell, st. 52–64 (off Hawaii), 16 November 1989; holotype of *P. armatum* USNM 162717, 310 mm SL, off Kona Coast of Hawaii, about 1/2 mile off shore from point of entry into sea of the 1950 lava flow, 2 June 1950; 1 specimen USNM 227389, 77.5 mm SL, 21.035°N 156.797°W (off Molokai, Hawaii), RV Townsend Cromwell, st. 40–67, 41 ft shrimp trawl, 199–233 m, 19 November 1968; 1 specimen USNM 227390, 134 mm SL, 20.98°N 156.758°W (off Maui, Hawaii), RV Townsend Cromwell, st. 35-1, 41 ft shrimp trawl, 205–209 m, 27 March 1968; 1 specimen USNM 227406, 243 mm SL, 21.0633°N 156.518°W (off Maui, Hawaii), RV Townsend Cromwell, st. 40–92, 41 ft shrimp trawl, 274–318 m, 25 November 1968; 1 specimen USNM 227408, 191 mm SL, 20.6617°N 156.684°W (off Lanai, Hawaii), RV Townsend Cromwell, st. 33–38, 70 ft shrimp trawl, 289–296 m, 9 November 1967; 2 specimens USNM 227412, 225 and 265+ mm SL, 21.53°N 158.38°W (off Hawaii), RV Townsend Cromwell, cruise 54, st. 8, 229–247 m, 24 September 1972; 1 specimen USNM 455317, 165 mm SL, 21.0108°N 156.759°W (off Maui, Hawaii), RV Townsend Cromwell, st. 40–49, 41 ft shrimp trawl, 218 m, 17 November 1968; 1 specimen USNM 455319, 276 mm SL, 20.99°N 156.751°W (off Maui, Hawaii), RV Townsend Cromwell, st. 35-2, 41 ft shrimp trawl, 201–216 m, 28 March 1968; specimens identified as *P. squamipinne*: 1 specimen MNHN 1994-0762, 99 mm SL, 22°10'58.8"S 167°15'0"E (off New Caledonia), Biocal, st. cp109, 495–515 m, 9 September 1985.

Diagnosis. Precaudal vertebrae 11–14, total vertebrae 52–59; dorsal-fin rays 95–103; anal-fin rays 71–79; pectoral-fin rays 25–26; long gill rakers on first gill arch 4–5; pseudobranchials 4–7; 2–5 dorsal-fin rays in front of first vertebra; HL 23.8–26.9% of SL; body depth at vent 19.4–23.3% of SL; predorsal length 17–22.4% of SL; rear margin of preopercle with 4 spines and fleshy flap between spines 2 and 3; transversal scale rows above origin of anal fin 60–68, and above lateral line 15–20; otoliths >15 mm in length: OL:OH = 1.95–2.2, dorsal rim crenulated or undulating.

Description. Relatively robust fish with stout tapering tail and rounded snout. Maximal size of fishes investigated 334 mm SL. Preopercular rim with 4 spines, 2 spines positioned at bend and 2 further up, with fleshy flap in between.

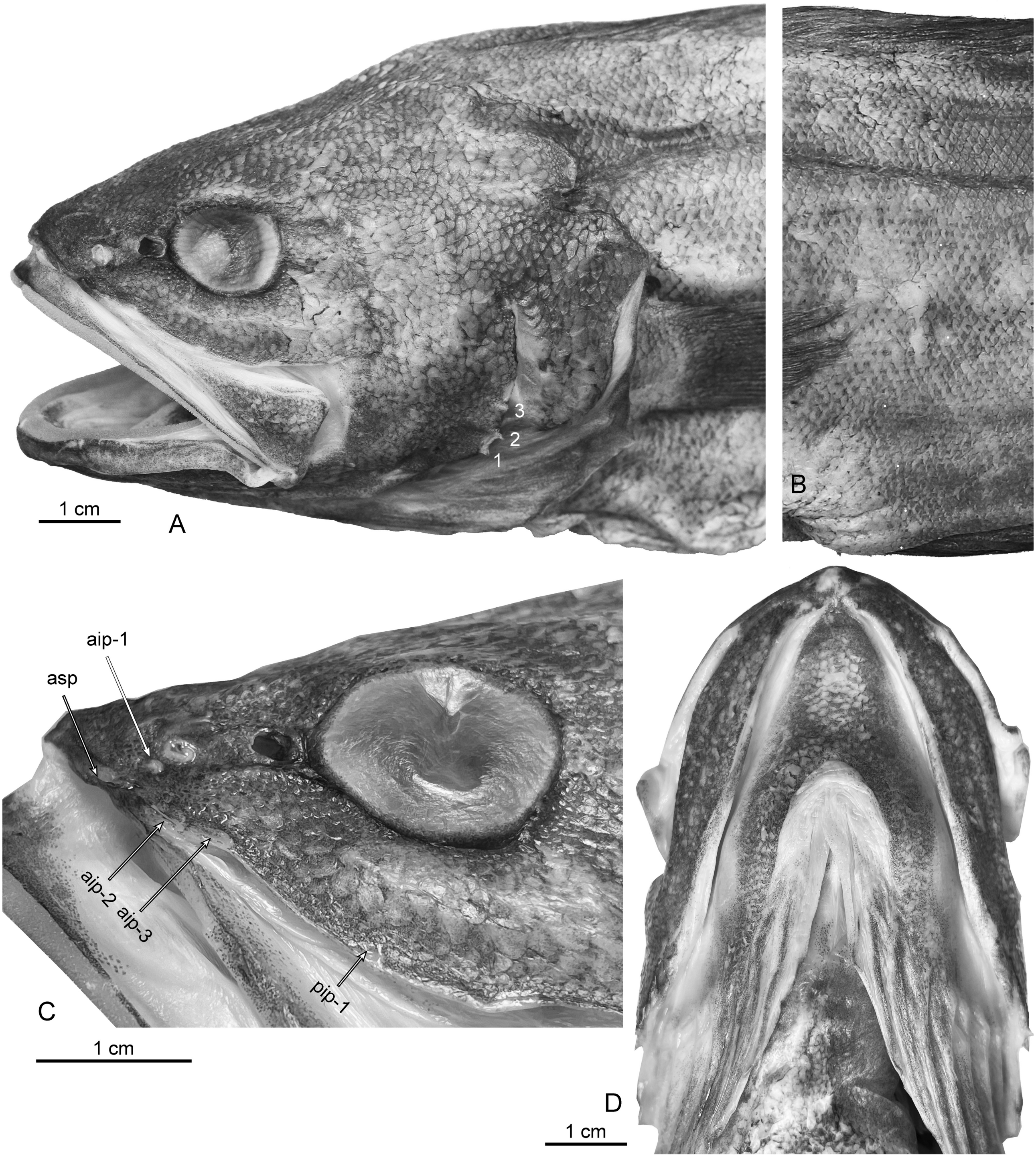


FIGURE 4. Head and body squamation details in *Pycnocraspedum phyllosoma*, USNM 421587; abbreviations used: aip-1–aip-3 = anterior infraorbital pores 1–3, asp = anterior supraorbital pore, pip-1 = posterior infraorbital pore 1; preopercular spines numbered. **4A**) head squamation in lateral view; **4B**) trunk squamation and every 10 scale row count marked by white dot; **4C**) snout squamation and pores detail; **4D**) head squamation in ventral view.

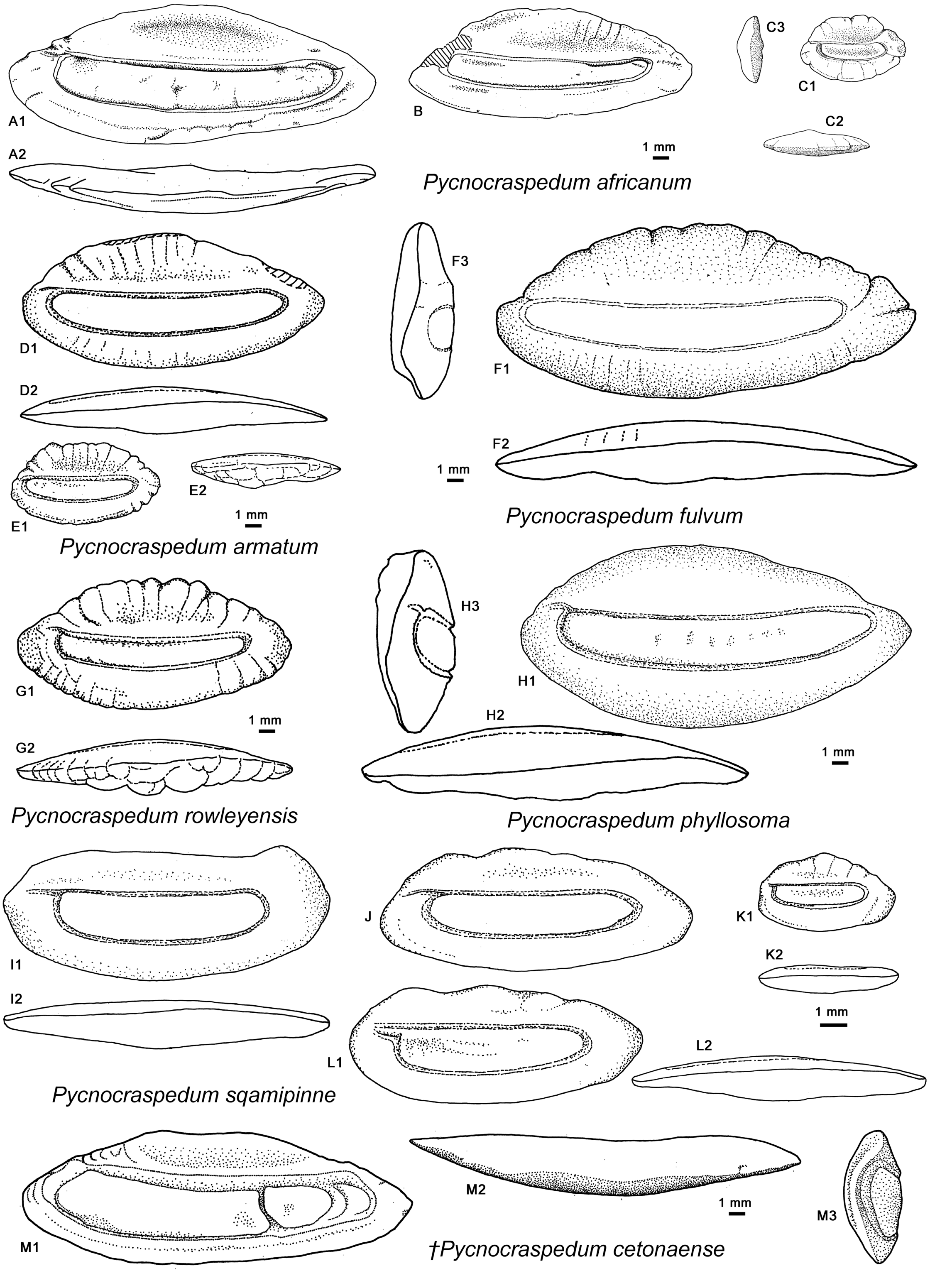


FIGURE 5. Otoliths, inner faces (if not noted otherwise) shown from right side. **5A–5C**) *Pycnocraspedum africanum* **sp. nov.**, 5A holotype, MNHN 2000-5691 (5A2 dorsal view), 5B paratype MNHN 2000-5692, 5C tentatively assigned specimen, IRSNB (5C2 dorsal view, 5C3 anterior view); **5D–5E**) *Pycnocraspedum armatum*, 5D USNM 227412 (5D2 ventral view), 5E USNM 227390 (5E2 ventral view); **5F**) *Pycnocraspedum fulvum* (holotype), BSKU 27497 (5F2 ventral view, 5F3 anterior view); **5G**) *Pycnocraspedum rowleyensis* **sp. nov.**, holotype, WAM I.28059.021 (5G2 ventral view); **5H**) *Pycnocraspedum phyllosoma*, USNM 421587 (5H2 ventral view, 5H3 anterior view); **5I–5K**) *Pycnocraspedum squamipinne*, 5I lectotype, BMNH 1890.7.31.1 (5I2 ventral view), 5J ZMUC P771871, 5L ZMUC P771739 (5L2 ventral view), 5K ZMUC P771738 (5K2 ventral view); **5M**) *†Pycnocraspedum cetonaense* (holotype) SMF P.5694 (5M2 dorsal view, 5M3 anterior view).

Meristics (14 specimens, including holotype of *P. armatum*): precaudal vertebrae 13 (11–14); total vertebrae 56 (52–59); dorsal-fin rays 98 (95–103); anal-fin rays 71 (71–79); pectoral-fin rays 26 (25–26); caudal-fin rays 10; D/V = -3 (-2– -5); D/A = 29 (23–31); V/A = 17 (15–17); long gill rakers on first gill arch 5 (4–5); pseudobranchial filaments 5 (4–7); transversal scale rows above origin of anal fin 60–68, and above lateral line 20 (15–20); pyloric coeca 12 (12–16).

Morphometrics (4–14 specimens) in % of SL: HL 24.6 (23.8–26.9); body depth at vent 22.7 (19.4–23.3); diameter of eye 4.4 (3.9–4.8); upper jaw length 13.4 (11.8–15); interorbital width 7.7 (6.1–7.7); pelvic-fin base to anal-fin base 21.2 (21.1–28); predorsal length 18.4 (17–22.4); preanal length 46.3 (40–48); prepelvic length 21.2 (19.3–23.3); pectoral-fin length 16 (16–18.1); pelvic-fin length 17.5.

Otolith morphology (4 specimens). Size up to 18 mm in length; OL:OH = 1.95–2.2 in specimens larger than 15 mm in length, 1.6 in specimens smaller than 7 mm in length; OH:OT = 2.3–2.9. Moderately thin, oval, elongated, anteriorly moderately projecting, posteriorly distinctly pointed, anterior and posterior tips inferior. Dorsal rim regularly curved, more or less strongly crenulated, undulating in largest specimen; ventral rim shallower and smoother than dorsal rim. Ornamentation of rims decreasing with size. Inner face moderately bent in horizontal direction, and slightly bent in vertical direction, with long, undivided sulcus reaching moderately close to anterior and posterior rims of otolith. Sulcus with shallow, undivided, uniform colliculum with flat to slightly concave dorsal rim and slightly convex ventral rim and rounded anterior and posterior tips. OL:CL = 1.3–1.45. Dorsal field with narrow, indistinct depression; ventral field smooth. Outer face less convex than inner face, smooth in large specimens, with many radial furrows and central tubercles in small specimens.

Coloration. Live coloration dark brown, sometimes light, speckled (HURL 2019). Color of preserved specimens light brown.

Discussion. Specimens studied from BSKU (5055 and 38643) originally identified as *P. microlepis* from the Mimase fish market in Kochi, were probably trawled in Tosa Bay, which is not far from the type locality of *P. microlepis* given as east of Kii Peninsula. The two specimens from BSKU match Matsubara's description (1943) of the unique holotype reasonably well in many aspects except for the number of pseudobranchial filaments (absent in the holotype according to Matsubara vs. 5–6 in the BSKU specimens) and pyloric coeca (20 vs. 13 in the BSKU 38643 specimen). Matsubara's description is very detailed, and therefore we consider the two specimens in question from BSKU to represent *P. armatum* rather than *P. microlepis*. The nature of *P. microlepis* thus remains elusive.

Gosline (1954) described *P. armatum* from off Hawaii based on fishes killed by the eruption of Mauna Loa in 1950. He compared *P. armatum* to the type species *P. squamipinne* but not to *P. microlepis*, which was originally described as *Itatius microlepis*. The description of the unique holotype did not contain meristics and it is difficult to assess morphometric data based on the drawing. Pseudobranchial filaments were not mentioned for *P. armatum* but were mentioned in the description of the genus as 'rudimentary'. A restudy of the holotype as well as multiple subsequently collected specimens of *Pycnocraspedum* from the Hawaiian Islands in the collections of LACM and USNM revealed a good match with the specimens from Japan (BSKU). Machida (1984) listed a difference of pyloric caeca of 12 for *P. armatum* and 20 for *P. microlepis* and 4 preopercular spines in *P. armatum* (vs. 2 in *P. microlepis*) based on the original descriptions. The specimens BSKU 5055 and 38643 from Japan have 5 to 6 pseudobranchial filaments and the specimen BSKU 38643 has 13 pyloric coeca (information provided by N. Nakayama). Therefore, we consider *P. microlepis* (Matsubara, 1943) as a nominally valid species distinct from *P. armatum* Gosline, 1954 and place the two specimens from BSKU with *P. armatum*.

Pycnocraspedum armatum is distinguished from its congeners by the higher number of dorsal-fin rays (95–103 vs. <93) except *P. phyllosoma*. Anal-fin rays also tend to be higher in number in *P. armatum* and *P. phyllosoma* (70–79 vs. 57–71). The dorsal-fin origin has a more anterior position in *P. armatum* compared to the other species with 2 to 5 fin rays before of the first vertebra (vs. 0 to 3 in other species) and a predorsal length of 17–22.4, mostly <21. Otoliths >15 mm in length of *P. armatum* and *P. phyllosoma* are more compressed than in *P. africanum* and *P. squamipinne* (OL:OH = 1.95–2.2 vs. 2.4–2.7). The distinction of *P. armatum* from *P. phyllosoma* is relatively subtle despite their wide geographic separation (see below) and confined to differences in the number of transversal scale rows (60–68 vs. 72–75), scale rows above the lateral line (15–20 vs. 20–21) and spines on the preopercle (4 vs. 3).

Distribution. *Pycnocraspedum armatum* appears to be widely distributed from Japan to Hawaii and southward to New Caledonia, and possibly Central West Pacific according to HURL (2019).

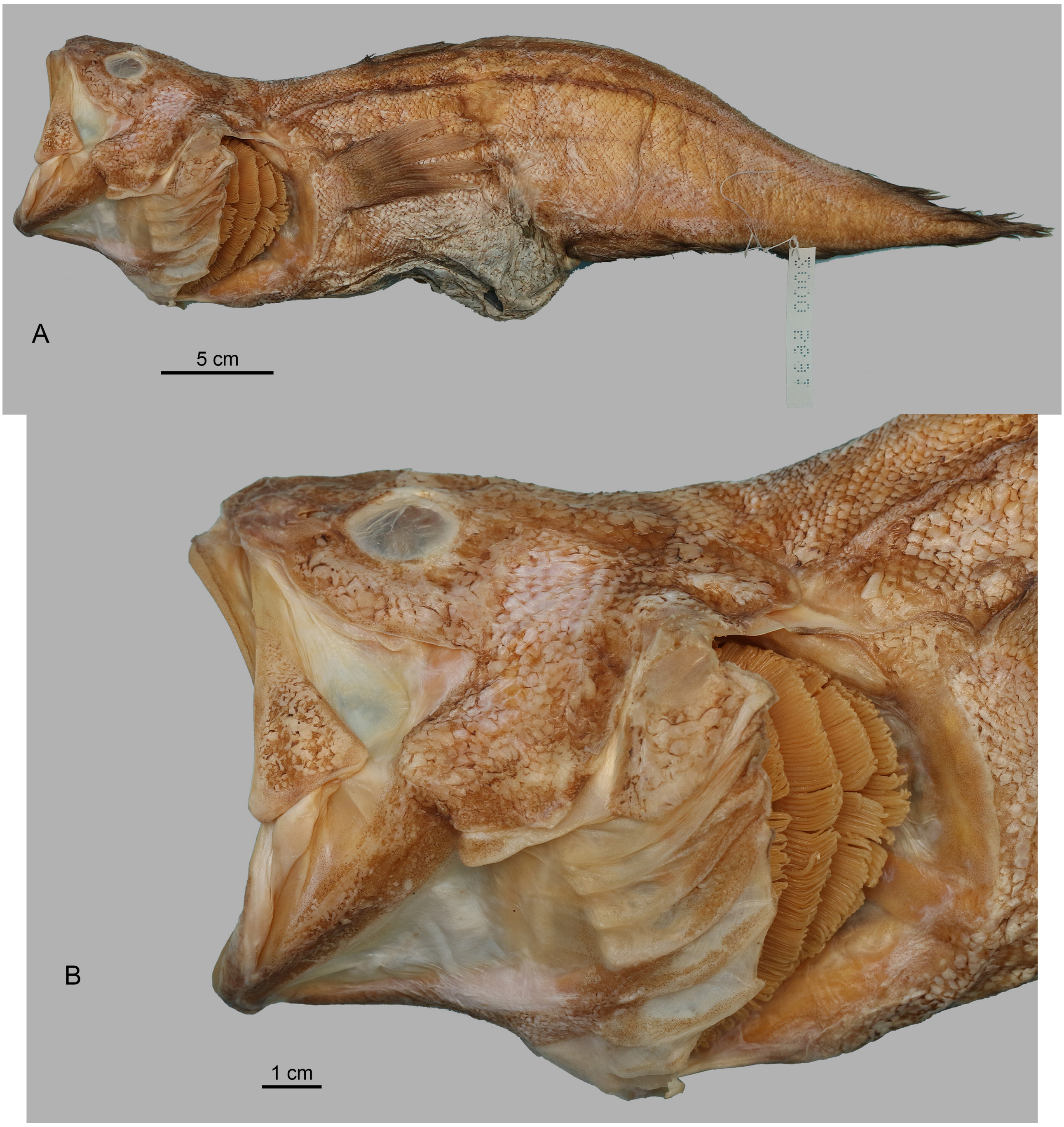


FIGURE 6. *Pycnocraspedum africanum* **sp. nov.**, holotype, MNHN 2000-5691, 420 mm SL, 22°21'7.2"S , 43°4'4.8"E, 450 m.

Pycnocraspedum fulvum Machida, 1984

Figures 1, 3, 5, 8, 12; Tables 1, 2

Pycnocraspedum fulvum Machida, 1984: 246–249, table 20, pl. 173, 28°06'N 126°23'E, Okinawa Trough.

Pycnocraspedum fulvum Machida, 1984: Nielsen *et al.* (1999), Nakabo (2000), Nakabo (2002), Shinohara *et al.* (2005), Prokofiev (2005), Evseenko & Okiyama (2006), Prokofiev (2022).

Material examined: Holotype (unique specimen): BSKU 27497, 336 mm SL, 28°06'N 126°23'E, Okinawa Trough, 143 m, 9 March 1978.

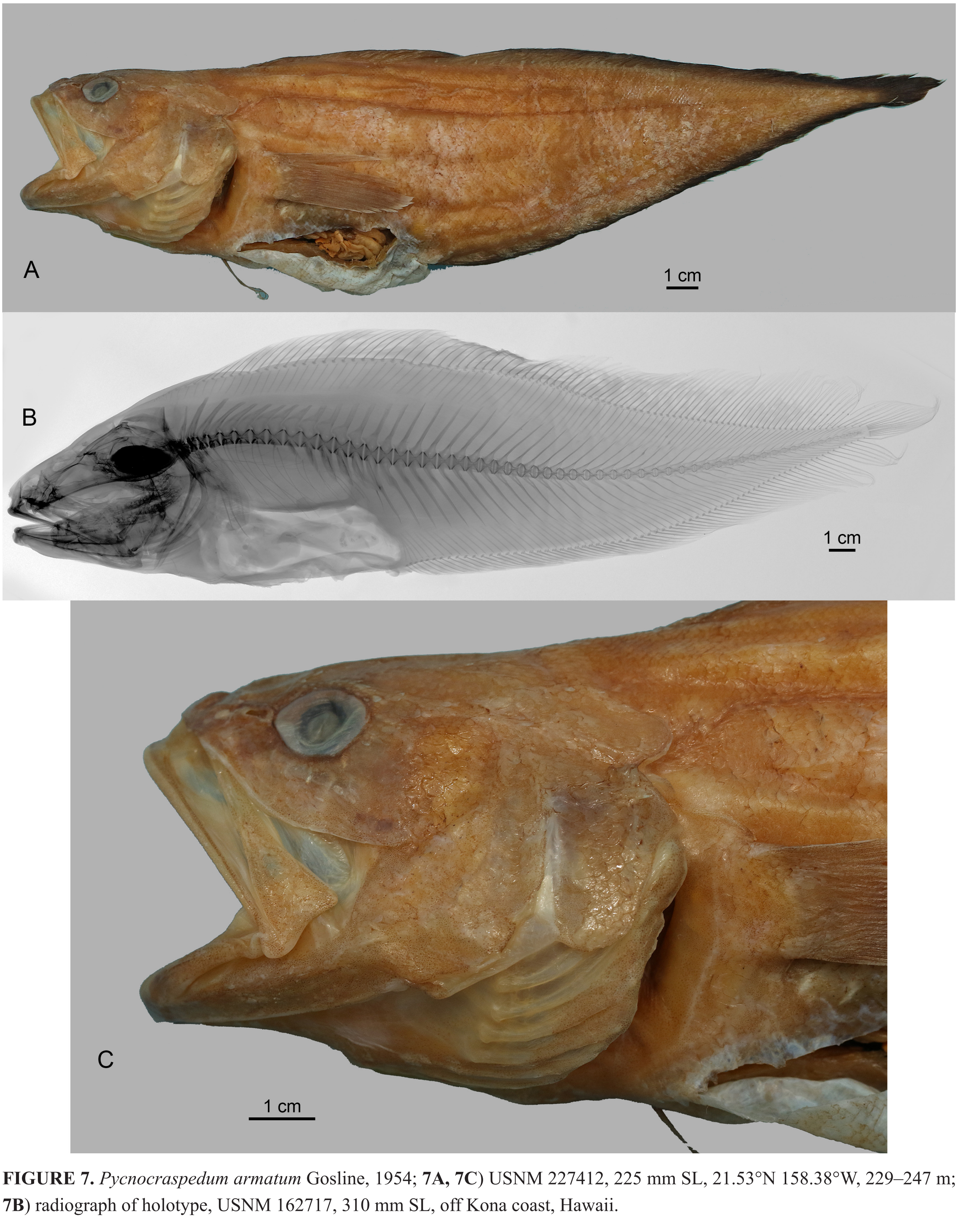


FIGURE 7. *Pycnocraspedum armatum* Gosline, 1954; **7A, 7C**) USNM 227412, 225 mm SL, 21.53°N 158.38°W, 229–247 m; **7B**) radiograph of holotype, USNM 162717, 310 mm SL, off Kona coast, Hawaii.

Diagnosis (updated from Machida, 1984)**.** Precaudal vertebrae 13, total vertebrae 55; dorsal-fin rays 78; anal-fin rays 63; pectoral-fin rays 26; long gill rakers on first gill arch 4; pseudobranchial filaments 4; first dorsal-fin ray above first vertebra (D/V = 1); HL 26.4% of SL; body depth at vent 20.8% of SL; predorsal length 24.5% of SL; rear margin of preopercle with 3 spines, 2 lower and 1 upper, with spine number 2 being exceptionally strong; concave section without fleshy flap between spines 2 and 3; transversal scale rows above origin of anal fin 60, and above lateral line 19 (17 according to Machida, 1984); pyloric coeca 13; otolith: OL:OH = 2.4.

Description (updated, only additions to diagnosis)**.** Relatively robust fish with moderately long tapering tail and rounded snout. Size of unique holotype 336 mm SL.

Meristics: caudal-fin rays 10; D/A = 22; V/A = 17.

Morphometrics in % of SL: diameter of orbit 4.4; upper jaw length 14.8; interorbital width 7.3; pelvic-fin base to anal-fin base 29.2; preanal length 44.2; prepelvic length 21.8; pectoral-fin length 15.9; pelvic-fin length not measurable (damaged).

Dentition. Basibranchial tooth patches 2 long median and 2 small lateral patches.

Otolith morphology (holotype). Size 25 mm in length; OL:OH = 2.4; OH:OT = 2.8. Thin, oval, elongated, anteriorly moderately projecting, posteriorly distinctly pointed, anterior and posterior tips slightly inferior. Dorsal rim broad, rounded, somewhat expanded and broadly crenulated. Ventral rim smooth, shallower than dorsal rim. Inner face moderately bent in horizontal and vertical directions, with very long, narrow, undivided sulcus reaching close to anterior and posterior rims of otolith. Sulcus with shallow, undivided, uniform colliculum with slightly concave dorsal rim and slightly convex ventral rim and rounded anterior and posterior tips. OL:CL = 1.3. Dorsal field with indistinct depression positioned high above sulcus; ventral field smooth, locally with faint radial furrows. Outer face with few radial furrows, slightly concave but with weak central bulge.

Coloration. Live coloration unknown. Color of preserved specimen light brown.

Discussion. *Pyconocraspedum fulvum* is readily recognized by the unusual low number of dorsal-fin rays (78) and the insertion of the first dorsal-fin ray above the first vertebra (D/V = 1). The number of anal-fin rays is also low at 63 and shared only with *P. squamipinne* (57–65). The number of transversal scale rows is low and shared only with *P. squamipinne* (60) and *P. armatum* (60) The otolith is relatively slender and large for the size of the head.

Distribution. *Pycnocraspedum fulvum* is only known from the unique holotype collected off Okinawa.

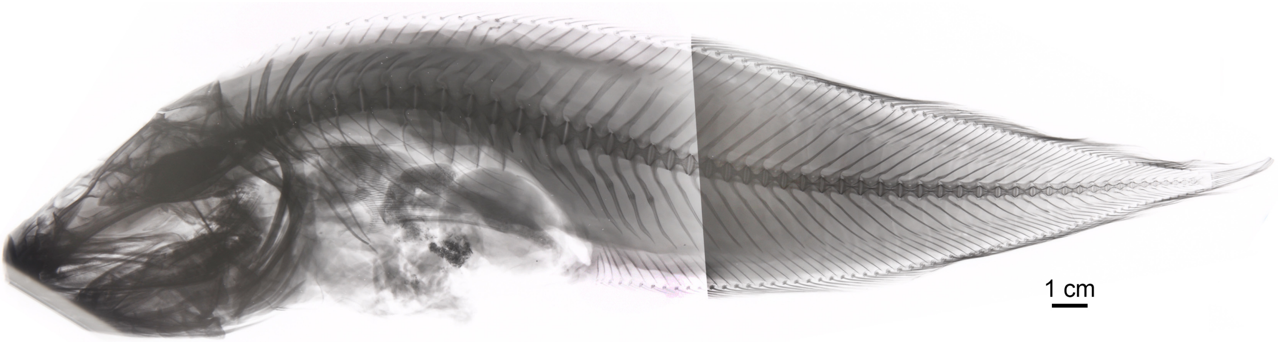


FIGURE 8. *Pycnocraspedum fulvum* Machida, 1984, radiograph of holotype, BSKU 27497, 336 mm SL, 28°06'N 126°23'E, 143 m.

Pycnocraspedum microlepis (Matsubara, 1943)

Itatius microlepis Matsubara, 1943: 40–43, figs. 2–4, Kumano-Nada, Kii Peninsula, Japan.

Pycnocraspedum microlepis (Matsubara, 1943): Machida (1984), Nielsen *et al.* (1999), Nakabo (2000), Nielsen *in* Randall & Lim (2000), Shinohara *et al.* (2001), Nakabo (2002), Evseenko & Okiyama (2006), ? Prokofiev (2022).

Remarks. Holotype apparently lost (Fricke *et al.* 2024). No specimen identified that would reasonably match Matsubara's detailed description. Matsubara (1943) gave a detailed description of *P. microlepis* and diagnostic features to distinguish the genus *Itatius* (syn. *Pycnocraspedum*) from *Neobythites*. He compared *P. microlepis* with *P. phyllosoma* (Parr, 1933), which he considered related, and found that they shared "4 developed gill-rakers on the first gill-arch, dorsal fin inserted above the upper angle of gill-opening and 20 pyloric coeca (21 in *P. phyllosoma*)." He found that *P. microlepis* differs from *P. phyllosoma* "at least in having slenderer body and lower arm of the gill-arch armed with 13 tubercular gill-rakers below the 4 developed ones" (vs. practically smooth). We can confirm the observation in respect to the gill rakers in *P. phyllosoma* but find this a rather variable and not very consistent character. From Matsubara's description we find the combination of 25 scales rows above lateral line, 20 pyloric coeca and the absence of pseudobranchial filaments to represent the most characteristic features, which is not matched in any specimen studied by us (see also discussion to *P. armatum*). In conclusion, we consider *Phyllosoma microlepis* as a nominally valid species and it is hoped that new findings matching Matsubara's description will eventually resolve its taxonomic position.

Pycnocraspedum phyllosoma **(Parr, 1933)**

Figures 1, 3, 4, 5, 9, 12; Tables 1, 2

Neobythites phyllosoma Parr, 1933: 44–46, fig. 20, off Turks Island, Bahamas, 21°30'N, 71°11'W, Pawnee St. 52.
Pycnocraspedum phyllosoma (Parr, 1933): Nielsen *et al.* (1999), Evseenko & Okiyama (2006), Prokofiev (2022).

Material examined (4 specimens, 130–355 mm SL): 1 specimen USNM 227413, 230 mm SL, 20.85°N 71.52°W (off Caicos Island), RV Oregon cr. 101, st. 5427, 40 ft shrimp trawl, 512–576 m, 27 May 1965; 1 specimen USNM 421586, 355 mm SL, 12.0832°N 68.8991°W (off Curacao), RV Curasub, Deep Reef Observation Project (DROP), May 2013; 1 specimen USNM 412587, 295 mm SL, 12.0832°N 68.8991°W (off Curacao), RV Curasub, Deep Reef Observation Project (DROP), May 2013; 1 specimen USNM 470952, 130 mm SL, 25.97°N 78.48°W, RV Gerda cr. 6720, st. 925, 10 Otter trawl, 439–457 m, 29 September 1967.

Diagnosis. Precaudal vertebrae 12–13, total vertebrae 52–54; dorsal-fin rays 96–101; anal-fin rays 70–73; pectoral-fin rays 25–27; long gill rakers on first gill arch 4–5; pseudobranchial filaments 5–6; 3–4 dorsal-fin rays in front of first vertebra; HL 22.7–26.5% of SL; body depth at vent 21–23% of SL; predorsal length 18.8–23% of SL; rear margin of preopercle with 3 spines, 2 lower and 1 upper, with flashy flap between spines 2 and 3; transversal scale rows above origin of anal fin 72–78, and above lateral line 20–21; otolith (23.3 mm in length) OL:OH = 2.15, dorsal rim smooth, ventral rim symmetrical to dorsal rim.

Description. Relatively robust fish with stout tapering tail and rounded snout. Maximal size of fishes investigated 355 mm SL. Preopercular rim with 3 spines, 2 spines positioned at bend and 1 further up, with fleshy flap in between spines 2 and 3.

Meristics (4 specimens, not including juvenile holotype of *P. phyllosoma*): precaudal vertebrae (12–13); total vertebrae 52–54; dorsal-fin rays 96–101; anal-fin rays 70–73; pectoral-fin rays 25–27; caudal-fin rays 10; D/V = -3– -4; D/A = 29–30; V/A = 16–17; long gill rakers on first gill arch 4–5; pseudobranchial filaments 5–6; transversal scale rows above origin of anal fin 72–78, and above lateral line 20–21; pyloric coeca 18–21.

Morphometrics (4 specimens) in % of SL: HL 22.7–26.5; body depth at vent 21–23; diameter of eye 4.4–5.0; upper jaw length 11.4–14.5; interorbital width 6.5–8.1; pelvic-fin base to anal-fin base 22.2–26; predorsal length 18.8–23; preanal length 41.7–51; prepelvic length 19.1–27; pectoral-fin length 14.5–17.2; pelvic-fin length 11.5–13.

Otolith morphology (1 specimen from specimen of 295 mm SL). Size 23.3 mm in length; OL:OH = 2.15; OH:OT = 2.4. Moderately thin, oval, elongated, anteriorly moderately rounded, posteriorly distinctly pointed, anterior and posterior tips positioned along median sulcus axis. Dorsal rim regularly curved, relatively high, smooth; ventral rim about as deep as dorsal rim high, smooth. Inner face distinctly bent/convex in horizontal and vertical directions, with long, undivided sulcus reaching relatively close to anterior and posterior rims of otolith. Sulcus with shallow, undivided, uniform colliculum with slightly concave dorsal rim and slightly convex ventral rim and rounded anterior and posterior tips. OL:CL = 1.25. Dorsal field smooth, without depression; ventral field smooth. Outer face nearly flat, rather smooth.

Coloration. Live coloration pale with small dark spots in small individuals (Girard *et al.* 2023). Color of preserved large specimens medium to dark brown, with dusty dark brown coloration on scales.

Discussion. *Pycnocraspedum phyllosoma* resembles *P. armatum* in many traits and differs only in relatively subtle features such as the number of spines on the preopercle (3 vs. 4), 72–78 transversal scale rows (vs. 60–68), 18–21 pyloric coeca (vs. 12–16), and a relatively dark body coloration. Its otoliths show a symmetrical shape of dorsal and ventral rim while in other species the ventral rim is shallower than the dorsal rim or vice versa in *P. squamipinne*, where the ventral rim is deeper than the dorsal rim.

Distribution. *Pycnocraspedum phyllosoma* is the only species of the genus known from the tropical West Atlantic while all other extant species of *Pycnocraspedum* occur in the Indo-West Pacific. The 136 mm SL holotype was caught pelagic in the Turks Island Passage, Pawnee St. 52.

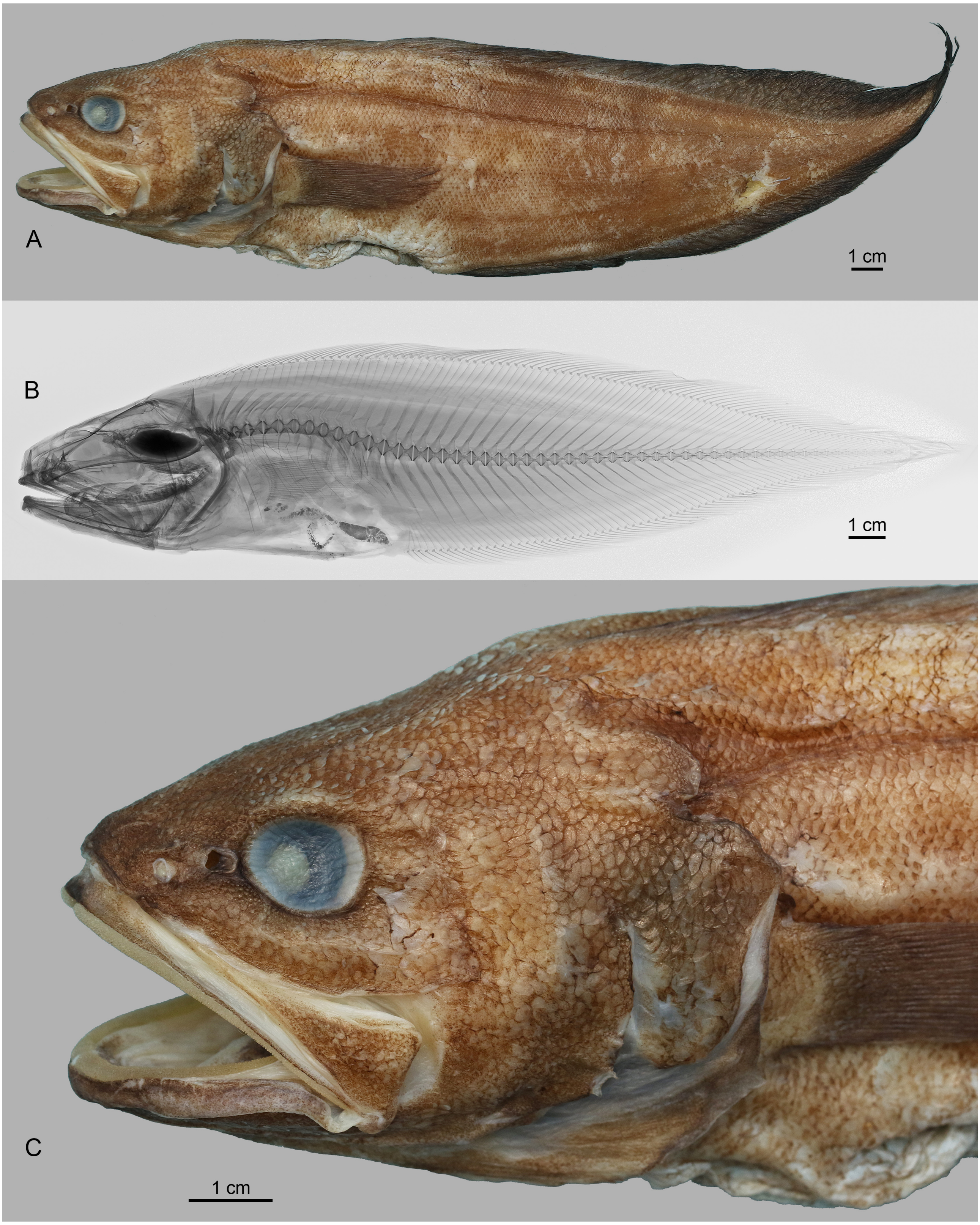


FIGURE 9. *Pycnocraspedum phyllosoma* (Parr, 1933); **9A, 9C**) USNM 412587, 295 mm SL, 12.0832°N 68.8991°W; **9B**) radiograph of USNM 227413, 230 mm SL, 20.85°N 71.52°, 512–576 m.

Pycnocraspedum rowleyensis sp. nov.

Figures 3, 5, 10, 12; Tables 1, 2

Material examined (holotype, 235 mm SL): WAM P28058.021, 18°05'S, 118°10'E, West Australia, approximately 80 km southwest of Rowley Shoals, 400 m, P. Berry and N. Sinclair, 17 August 1983.

Diagnosis. Precaudal vertebrae 12, total vertebrae 52; dorsal-fin rays 87; anal-fin rays 69; pectoral-fin rays 25; long gill rakers on first gill arch 4; pseudobranchial filaments 4–5; 2 dorsal-fin rays in front of first vertebra; HL 25.3% of SL; body depth at vent 18.9% of SL; predorsal length 23% of SL; transverse scale rows above origin of anal fin 70, and above lateral line 17; broad expansion on preopercular angle with two spines, concave section above spine 2 without fleshy flap on hind margin of preopercle; otolith (16.5 mm in length) OL:OH = 2.1, dorsal rim crenulated.

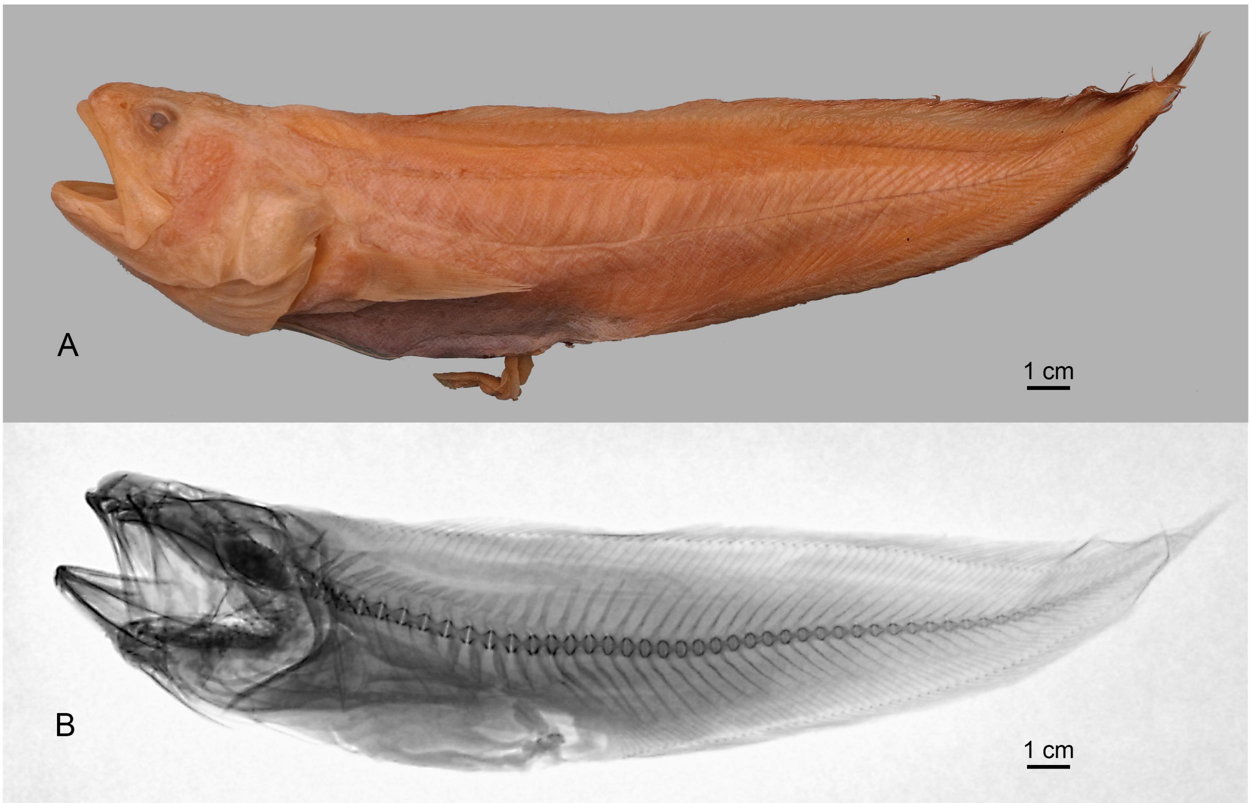


FIGURE 10. *Pycnocraspedum rowleyensis* **sp. nov.**; **10A**) holotype, WAM P28058.021, 18°05'S, 118°10'E, 400 m; **10B**) radiograph of holotype.

Description (only additions to diagnosis)**.** Relatively robust fish with moderately long tapering tail and rounded snout. Size of unique holotype 235 mm SL.

Meristics: caudal-fin rays 10; D/A = 25; V/A = 17.

Morphometrics in % of SL: diameter of orbit 3.9; upper jaw length 14.3; interorbital width 7; pelvic-fin base to anal-fin base 28.7; preanal length 50.2; prepelvic length 24.8; pectoral-fin length 15; pelvic-fin length 13.7.

Otolith morphology (holotype). Size 16.5 mm in length; OL:OH = 2.1; OH:OT = 2.35. Moderately thin, oval, elongated, anteriorly and posteriorly moderately and equally projecting. Dorsal rim rounded, intensely crenulated. Ventral rim smooth at center, anteriorly and posteriorly finely crenulated, shallower than dorsal rim. Inner face moderately bent in horizontal and vertical directions, with long, narrow, undivided sulcus reaching close to anterior and posterior rims of otolith. Sulcus with shallow, undivided, uniform colliculum with slightly concave dorsal rim and slightly convex ventral rim and rounded anterior and posterior tips. OL:CL = 1.45. Dorsal field with indistinct depression and deeply ingressing radial furrows; ventral field with faint radial furrows anteriorly and posteriorly. Outer face slightly convex with few radial furrows, and centrally with tubercles.

Coloration. Live coloration unknown. Color of preserved specimens medium brown.

Discussion. *Pycnocraspedum rowleyensis* belongs to a group of species in the genus with two preopercular spines positioned at lower corner of the margin of the preopercle. The single specimen from off northwestern Australia resembles *P. africanum* in many aspects but differs from the latter in the lower number of transverse scale rows (70 vs. 85–90) and scale rows above the lateral line (17 vs. 22-23), the concave stretch of the rear margin of the preopercle above the preopercular spines (vs. presence of a fleshy flap) and the more compressed otolith shape (OL:OH = 2.1 vs. 2.5–2.7).

Distribution. *Pycnocraspedum rowleyensis* is only known from the holotype caught off the Rowley shoals off northwestern Australia.

Etymology. Named after the Rowley Shoals, Western Australia, from where the holotype was obtained.

Pycnocraspedum squamipinne Alcock, 1889

Figures 1, 3, 5, 11, 12; Tables 1, 2

Pycnocraspedum squamipinne Alcock, 1889: 386; figured in Alcock 1898: pl. 21, fig. 1 as *Neobythites squamipinnis*, Bay of Bengal, 20°17'30"N, 88°50'E, RV Investigator, depth 193 fathoms (353 m).

Pycnocraspedum squamipinne Alcock, 1889: Menon & Yazdani (1968), Menon & Rama-Rao (1970), Menon & Rama-Rao (1975), Nielsen *et al.* (1999), Evseenko & Okiyama (2006), Psomadakis *et al.* (2020), Teena *et al.* (2021), Prokofiev (2022).

Material examined (6 specimens, 122–243 mm SL): 1 specimen lectotype, BMNH 1890.7.31.1, 20°17'30"N 88°50'E (Bay of Bengal), RV Investigator, 353 m; 1 specimen ZMUC P 771737, 226 mm SL, off Myanmar, Bay of Bengal, 18°16'N, 93°43'E, R/V *Dr. Fridtjof Nansen*, survey 2015404, st.19, bottom trawl, 127–130 m, 3 May 2015; 2 specimens ZMUC P 771736 and P 771738, 120–195 mm SL, off Myanmar, Bay of Bengal, 18°14'N, 93°38'E, R/V *Dr. Fridtjof Nansen*, survey 2015404, St. 18, bottom trawl, 466–469 m, 3 May 2015; 1 specimen ZMUC P 771739, 225 mm SL, off Myanmar, Bay of Bengal, 16°26'N, 93°57'E, R/V *Dr. Fridtjof Nansen*, survey 2015404, st. 42, bottom trawl, 274–277 m, 6 May 2015; 1 specimen ZMUC P 771871, 196 mm SL, off Myanmar, Bay of Bengal, 16°26'N, 93°57'E, R/V *Dr. Fridtjof Nansen*, survey 2018411, st. 26, bottom trawl, 241–229 m, 29 Aug. 2018.

Diagnosis. Precaudal vertebrae 12–13, total vertebrae 47–51; dorsal-fin rays 90–92; anal-fin rays 57–65; pectoral-fin rays 25–30; long gill rakers on first gill arch 4; pseudobranchials 1–2; 1–3 dorsal-fin rays in front of first vertebra; HL 29.6–31.5% of SL; body depth at vent 17.3–18% of SL; predorsal length 25–29% of SL; transversal scale rows above origin of anal fin 52–58 (58–60 in paralectotypes according to Teena *et al.* 2021), and above lateral line 13–17 (11–15 in paralectotypes according to Teena *et al.* 2021); pyloric coeca 12–13; preopercle with 1 weak spine above first lower preopercular pore and broad concave section above; otoliths relatively small, at >10 mm in length: OL:OH = 2.4–2.5, dorsal rim shallow, smooth.

Description. Relatively robust fish with stout tapering tail and rounded snout. Maximal size of fishes investigated 243 mm SL. Head stout, with straight, inclined dorsal profile. Preopercle with 1 weak spine above first lower preopercular pore, with broad concave section above and obtuse angle below second preopercular pore.

Meristics (6 specimens): precaudal vertebrae 12 (12–13); total vertebrae 49 (47–51); dorsal-fin rays 92 (90–92); anal-fin rays 65 (57–65); pectoral-fin rays 28 (25–30); caudal-fin rays 10; D/V = -2 (-1– -3); D/A = 24–31; V/A = 16–17; long gill rakers on first gill arch 4; pseudobranchial filaments 1 (1–2); transversal scale rows above origin of anal fin 52–58, and above lateral line 13–17; pyloric coeca 12–13.

Morphometrics (5 specimens) in % of SL: HL 29.6 (29.6–31.5); body depth at vent 17.3 (17–18); diameter of eye 4.9 (4.5–5.1); upper jaw length 15.4 (15.0–15.4); interorbital width 5.2 (5.2–6.2); pelvic-fin base to anal-fin base 26 (26–32.5); predorsal length 27 (25–29); preanal length 46–52; prepelvic length 20–21.5; pectoral-fin length 15.2 (15.2–18); pelvic-fin length 11.4–14.

Otolith morphology (3 specimens). Size up to 12 mm in length; OL:OH = 2.4–2.5 in specimens larger than 10 mm in length, 1.8 in specimens smaller than 6 mm in length; OH:OT = 2.6–2.8. Otolith relatively thin, elongated, anteriorly rounded, posteriorly rounded or slightly pointed; anterior and posterior tips along horizontal axis. Dorsal rim shallow, nearly flat or depressed at times, moderately lobed in small specimens; ventral rim shallow, regularly curved. All rims smooth. Inner face nearly flat, less bent than outer face. Sulcus moderately long, horizontal, with shallow, undivided, uniform colliculum with flat to straight dorsal rim and slightly convex ventral rim and rounded anterior and posterior tips. OL:CL = 1.5–1.6. Dorsal field without distinct depression; ventral field smooth. Outer face more convex than inner face, smooth.

Coloration. Live coloration unknown. Color of preserved specimens light brown.

Discussion. Teena *et al.* (2021) presented a re-description of *P. squamipinne* based on two of the three syntypes from the Bay of Bengal at ZSI (Kolkata) and 15 additional newly collected specimens off southern India. The values given for the syntypes (now paralectotypes) fall well into the range of the specimens studied by us, although they are larger at 270 and 277 mm SL than our specimens. The detailed figures of Teena *et al.* including the otolith of a 200 mm SL specimen match our descriptions reasonably well. However, the maximal range given by them for meristics and morphometrics in their table 1 exceeds all values that we recognized for *P. squamipinne*. Possibly, the maximum value refers to their largest specimen of 380 mm SL, which is also of an unusual size for this relatively small species. The cause for this discrepancy is unknown, but one possible explanation could be that the specimen(s) in question represent another species of the genus, for instance *P. africanum*. However, to resolve such speculation requires the review of the original specimens.

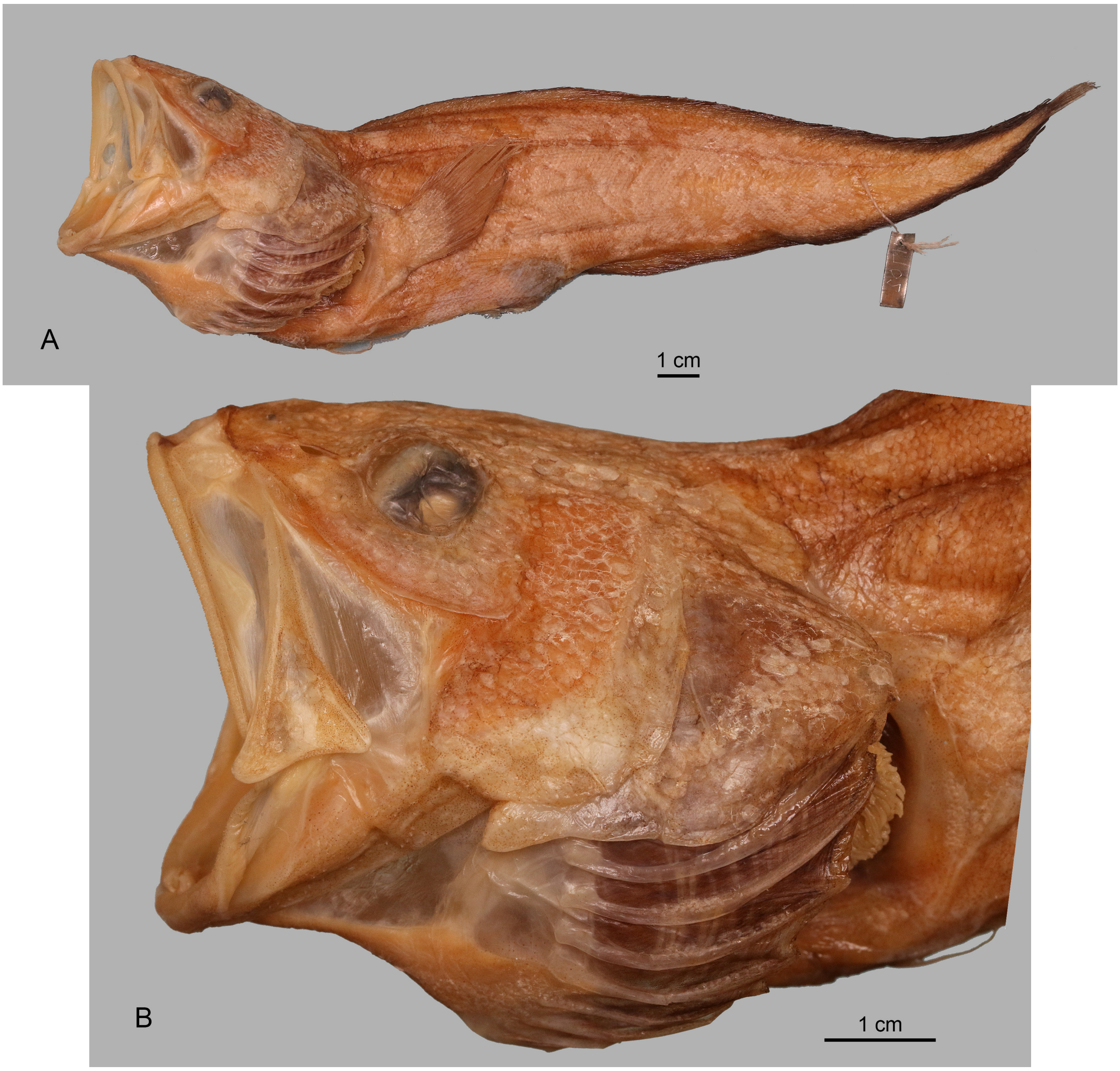


FIGURE 11. *Pycnocraspedum squamipinne* Alcock, 1889, lectotype, BMNH 1890.7.31.1, 20°17'30"N 88°50'E, 353 m.

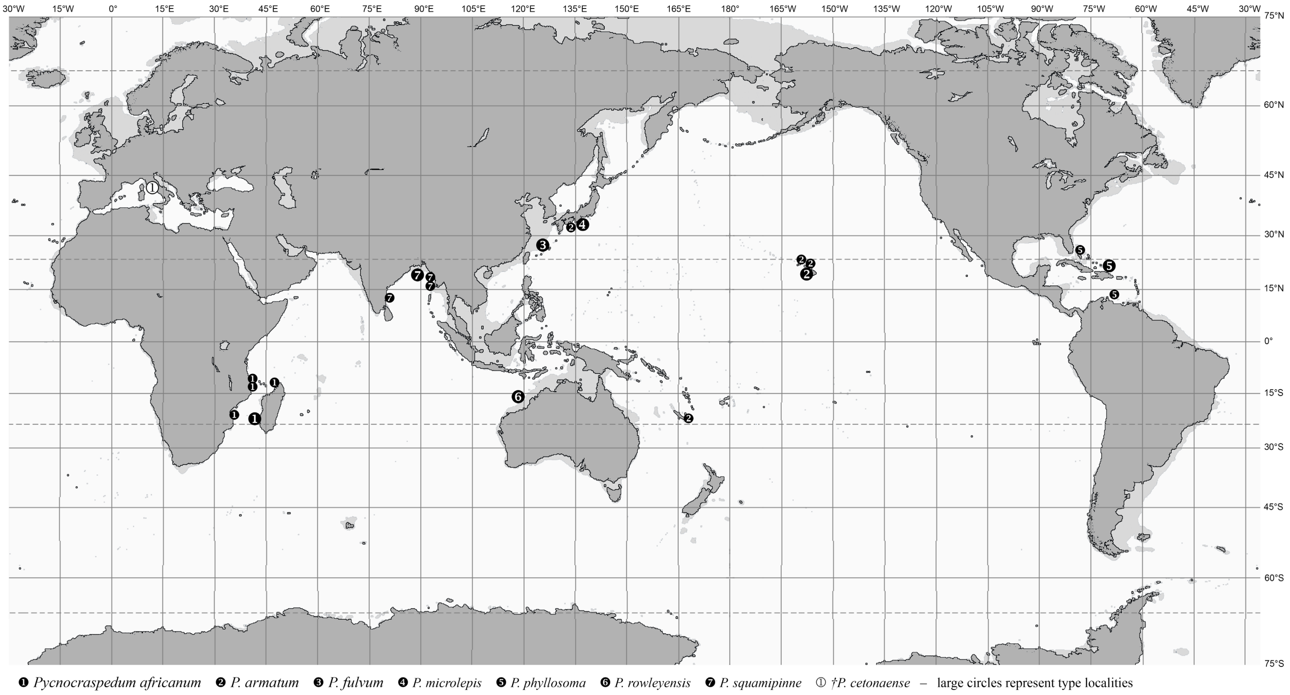


FIGURE 12. Geographic distribution of the species of *Pycnocraspedum*. One symbol can represent more than one location.

As analyzed here, *P. squamipinne* shows a number of characters that distinguish it well from its congeners. These are the low number of vertebrae (47–51 vs. 51–59), the low number of anal-fin rays (57–65 vs. 68–79, except 63 in *P. fulvum*), the low number of pseudobranchial filaments (1–2 vs. 4–7), the low number of transversal scale rows (52–58) and scale rows above the lateral line (13–17), the large head (HL in % of SL = 29.6–31.5 vs. 22.7–27.6), slender shape (body depth in % of SL = 17–18 vs. 18.9–23.3), and the predorsal length in % of SL (25–29 vs. 17–25). The rear margin of the preopercle is relatively thin and weak with only one distinct spine (the second from below as described in the chapter "Key characters"; Fig. 3). Also, the otolith morphology is distinctly different from that of its congeners being characterized by a shallow, nearly flat dorsal rim, the inner face less bent than the outer face (vs. inner face strongly or more bent than outer face) and a relatively short sulcus (OL:CL = 1.5–1.6 vs. 1.3–1.45). Furthermore, *P. squamipinne* does not seem to grow to the sizes of its congeners (maximal verified size is SL 277 mm SL vs. 345–420 mm SL).

Distribution. *Pycnocraspedum squamipinne* has been mentioned across a wide distribution range in the Indo-West Pacific from East Africa to New Caledonia. However, in our study we found that all records from outside of the Bay of Bengal represent different species*:* *P. africanum* in East Africa and mostly *P. armatum* elsewhere outside of the Bay of Bengal. It thus appears that *P. squamipinne* is endemic to the Bay of Bengal. Subject to review of certain specimens mentioned by Teena *et al.* (2021) it is possible that a second species of *Pycnocraspedum* may occur off India.

†*Pycnocraspedum cetonaense* (Schwarzhans, 1978)

Fig. 5M

Brotulidarum cetonaensis Schwarzhans, 1978: 37–38, pl. 10, fig. 115.
'*genus Neobythitinorum*' *cetonaensis* (Schwarzhans, 1978): Nolf (1980).
Paragenypterus cetonaensis (Schwarzhans, 1978): Schwarzhans (1981).
Pycnocraspedum cetonaensis (Schwarzhans, 1978): Schwarzhans (1994); Nolf (2013).

Material examined (1 specimen): The unique holotype, SMF P.5694, Cetona near Siena, Italy, Zanclean, Early Pliocene, a fossil otolith.

Discussion. *Pycnocraspedum cetonaense* was recovered from the Early Pliocene (about 5 mya) of Italy and represents the only known fossil record of the genus, based on a single large otolith. The otolith resembles in shape and proportions those of the extant *P. africanum* but differs in the relatively wide sulcus and the presence of clearly separated ostial and caudal colliculi (vs. single, fused colliculum). This record also demonstrates that the genus *Pycnocraspedum* was even more widely distributed in the past than today.

Ecology and Biogeography

The ophidiid genus *Pycnocraspedum* lives between 145 and 1345 m in the tropical and subtropical Indo-West Pacific and the tropical West Atlantic but has not been recorded from the tropical East Pacific and East Atlantic (Chave & Mundy 1994, Nielsen *et al*. 1999). The species of *Pycnocraspedum* are bathydemersal fishes, but certain species have been caught in the pelagic zone. For instance, the holotype of *P. phyllosoma,* measuring 136 mm of SL, was caught in a pelagic net off the Turks Island, Bahamas (Parr 1933), indicating that early stages have some ability for free living or pelagic life before settling to a demersal lifestyle. We also observe a relatively strong change in otolith morphology in fishes between 100 to 150 mm SL which may coincide with such a change of lifestyle. Also, Parr's holotype of *P. phyllosoma* is more high-bodied than the larger specimens of ≥ 200 mm SL, which potentially relates to the change in otolith morphology. A very high-bodied ophidiid larva of 22.5 mm SL from the "Dana" collection off New Guinea was attributed to *Pycnocraspedum* by Evseenko & Okiyama (2006), but the identification of this larva has been challenged based on molecular data (Girard *et al.* 2023).

No stomach content was analyzed in any specimens of *Pycnocraspedum* and the radiographs of the specimens did not reveal any recognizable stomach contents other than occasional small sand grains. Struhsaker (1973) reported of shrimp found in the throats of two net-caught *P. armatum*, but that was probably capture of the shrimp in the net and not indicative of natural feeding. We believe that the fishes primarily feed on soft-bodied invertebrates based on the morphology of the dentition, with all tooth-bearing elements being characterized by minute, granular teeth resembling sandpaper with no discernable rows or other pattern. We do not know whether the diet of *Pycnocraspedum* changes in any significant way during ontogeny or during the change from a more free-living to a demersal lifestyle. The life habits of *Pycnocraspedum* species are a promising field for study.

Certain species are widely distributed, particularly in the central West Pacific (*P. armatum*) while most others have more confined geographical distributions (Fig. 12). Thus, a prolonged free-living lifestyle may not necessarily have a significant effect on the geographical distribution. For instance, the type species *P. squamipinne* appears to be restricted to the Bay of Bengal, while *P. armatum* is known from Hawaii, Japan and south to New Caledonia. From the analysis of the morphological features of the recognized species in the genus, it seems that *P. squamipinne* stands out with several distinctive characters (see above) and could therefore represent the sister to all other species in the genus. However, we also recognize two pairs of species that appear to be closely related to each other. These potential geminate species are *P. africanum* and *P. rowleyensis* and the pair consisting of *P. armatum* and *P. phyllosoma*.

The species-pair *P. africanum* and *P. rowleyensis* share many meristic and morphometric characters and the presence of only 2 spines at the lower corner of the preopercle. They differ from each other in the number of transversal scale rows, scale rows above the lateral line and details of the otolith morphology. Interestingly, they occur on either side of the Indian Ocean: *P. africanum* along East Africa [possibly as far north as India, subject to review of specimens recorded by Teena *et al.* (2021)], and *P. rowleyensis* off western Australia (Fig. 12). We speculate that these two species are the result of an allopatric speciation event from a formerly more widely distributed ancestor.

Even more interesting is the apparent close relationship between *P. armatum*, the species with the widest geographic distribution range in the central West Pacific, and *P. phyllosoma*, the only species occurring outside of the Indo-West Pacific in the West Atlantic. These two species share many meristic characters, including the high dorsal-fin and anal-fin rays counts and all morphometric characters. The only subtle diagnostic differences concern the number of pyloric coeca (12–16 vs. 18–21), transversal scale rows (60–68 vs. 72–78), and the number of preopercular spines (4 vs. 3). A similar distribution pattern has been observed in a few other fish taxa. Møller & Schwarzhans (2008) noted that in the family Dinematichthyidae, the West Atlantic *Alionematichthys minyomma* (Sedor & Cohen, 1987) is closely related to the West Pacific *A. crassiceps* Møller & Schwarzhans, 2008. In the pseudoceanic family Bathyclupeidae, Prokofiev (2014) noted a close relationship between the West Atlantic

Bathyclupea schroederi Dick, 1962 and the northwestern Pacific *B. nikparini* Prokofiev, 2014. Finally, Schwarzhans & Prokofiev (2017) found in the family Acropomatidae, the West Atlantic *Parascombrops spinosus* (Schultz, 1940) to be closely related to *P. mochizuki* Schwarzhans, Prokofiev & Ho, 2017 from the northwestern Pacific. Although those examples are representative of rather different taxa of teleost fishes, they all share one particular aspect: all four examples stem from groups that are essentially Indo-West Pacific in their distribution and have only a single outlier in the West Atlantic. In all the above examples, the relationship between the West Atlantic species and its West Pacific counterpart is apparently closer than the relationship between the latter and other Indo-West Pacific species in the group. And finally, the groups in question are absent from the western coasts of the American and African continents. We believe that the West Atlantic species originated from the central West Pacific and moved across the Pacific or along the North Pacific rim at a time of a warmer climate (Dekens *et al.*, 2007) and were able to enter into the West Atlantic before the emergence of the Isthmus of Panama (see Schwarzhans & Prokofiev 2017 for further discussion). They may have subsequently become extinct in the East Pacific following cooling of the northeastern Pacific and establishment of the wide oxygen minimum zone in the deep water off the tropical East Pacific. These events and the emergence of the Isthmus of Panama put a minimum age for such an anticipated migration at about 3 to 4 million years. Preferential periods for the anticipated faunal movements could have been between the Middle Miocene and the Early Pliocene (Butzin *et al*. 2011).

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