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The bathypelagic postlarva of *Stereomastis panglao* collected from Suruga Bay, Japan (Crustacea, Decapoda, Polychelidae)

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Abstract. — A morphological description of the postlarval specimen of the polychelid lobster *Stereomastis panglao* Ahyong & Chan, 2008, collected from Suruga Bay, on the Pacific coast of Japan, and at depths of 1,305–1,565 m, was given for the first time. Larval characteristics of the previously known polychelid postlarvae and the distribution range of *S. panglao* were also noted.

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Key words: Decapoda, bathypelagic plankton, Stereomastis, larval morphology, DNA barcoding

■ Introduction

In the late 19th century, Spence Bate (1882) first described the polychelid larval form from the H.M.S. "Challenger" collections as a new species under the new genus name '*Eryoneicus*', which is allied to *Willemoesia*. Since his description, 140 years have passed, but details of the life history of polychelids remain unknown, largely due to difficulty in obtaining and rearing these deep-sea animals. Modern DNA barcoding technique has been applied to polychelid *Polycheles* and *Pentacheles* species to confront this difficulty in recent years (Torres *et al*., 2014; Konishi *et al*., 2021), but not to *Stereomastis*, which constitutes 45% of the total species in the family, yet.

Since Spence Bate's (1882) report, more than thirty so-called larval 'species' have been described as '*Eryoneicus*' from the world's oceans, in parallel with descriptive studies on adult polychelid taxonomy. On the other hand, irrespective usage of larval 'species' as in the adult species caused taxonomic complications. It was impossible to know which adult and larval species belonged together (Holthuis, 1962). Addressing this issue, the generic name '*Eryoneicus*' was suppressed by the International Commission on Zoological Nomenclature (Holthuis, 1962; ICZN, 1964). Notwithstanding, larval students frequently use the suppressed name '*Eryoneicus*' probably as a matter of convenience (e.g., Hernández *et al*., 2007).

During the past decades, we have conducted mesopelagic surveys in Suruga Bay, Pacific coast of Japan, and occasionally collected polychelid postlarvae. Among these, one of the specimens was a round triangle in outline with conspicuous posterolateral spines (Fig. 1). In our preliminary study on specific identification using DNA barcoding analyses revealed that this specimen was the postlarva of *Setereomastis panglao* Ahyong & Chan, 2008 (Yanagimoto *et al*., 2019). The present paper describes the detailed morphology of this specimen.

■ Materials and Methods

The polychelid postlarva was caught during a research cruise of the R/V Hokuto (Tokai University) in Suruga Bay (34°56′N–34°58′N, 138°37′E–138°38′E), on 14 May 2014, using a bottom larval net, at depths of 1,305–1,565 m.

For details on the methods and procedures

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Fig. 1. Postlarva of *Stereomastis panglao*. Photograph of the whole body in dorsal view.

for DNA barcoding identification in our preliminary study (Yanagimoto *et al*., 2019; see **Appendix**).

The morphological observations and measurements of the postlarval specimen were taken using a Nikon SMZ800 stereomicroscope, and an Olympus BX41 microscope equipped with a drawing tube. Total length (TL) was measured as the distance from the frontal margin of the carapace to the posterior end of the telson. Carapace length (CL) was measured as the distance from the frontal margin to the posterior margin along the median line, and carapace width (CW) as the greatest distance across the carapace excluding the lateral spines (see Fig. 2B). Abbreviations for the middorsal spine arrangement are as follows — ap: anterior pillar, pp: posterior pillar, |: position of cervical groove. The postlarva specimen used in the study was deposited at the Hokkaido University Museum under the accession No. ICHUM-6156.

■ Morphological description of *Stereomastis panglao* postlarva

Dimensions: CL = 16.2 mm, CW = 15.2 mm, TL = 25.6 mm.

Colour (Fig. 1): Cephalon and pleon basically translucent. Parts of posterior carapace ridge, cephalic and thoracic appendages, and inner gastric regions orange-red.

Carapace (Fig. 2A–C): Globular and triangular ovoid-shaped in dorsal view, CL slightly longer than CW (CL/CW = 1.03). Rostrum truncated, with minute two spines medially. Cervical groove approximately at middle longitudinal position of CL (Fig. 2B); two longitudinal carinae with spines on each side of branchial region. Orbital sinus oblique U-shaped. Spine arrangement on middorsal line as "1, 1, 2, ap, 1 | 2, 2, pp, 2", from rostrum to posterior margin; posterior margin slightly curved backward.

Antennule (Fig. 2D): Biramous. Peduncle three-segmented; basal segment flattened, distolaterally with 1 large and wide spine, its outer margin bearing thin setae; medially with 1 inner hook-like spine. Exopod flagellum twelve-segmented, distal segment with 6 setae. Endopod flagellum multi-segmented with numerous aesthetascs and setules, approximately 2.5 times longer than exopod flagellum.

Antenna (Fig. 2E): Biramous. Coxal region with 1 long renal process, basal region with 1 short anterolateral spine. Exopod (scaphocerite) spoon-shaped plate, with 45/48 marginal plumose setae. Endopod flagellum long, multi-segmented.

Eye (Fig. 2C): Eyestalk fixed, with 1 acute spine on upper side, cornea absent.

Mandible (Fig. 3A): No molar processes; inner edge with 12/15 triangular teeth. Palp three-segmented, with numerous setae. Paragnath small, forming digitiform plate.

Maxillule (Fig. 3B): Biramous, basial endite with 2/3 distal cuspidate and 27/31 marginal setae. Coxal endite with 25/28 setae. Endopod not found.

Maxilla (Fig. 3C): Biramous. Endopodal region trilobed, consists of two finger-like projections with long setae and 1 low subtriangular lobe with short marginal setae. Scaphognathite elongated, large, with numerous marginal plumose setae.

Maxilliped 1 (Fig. 3D): Endopod with tapered

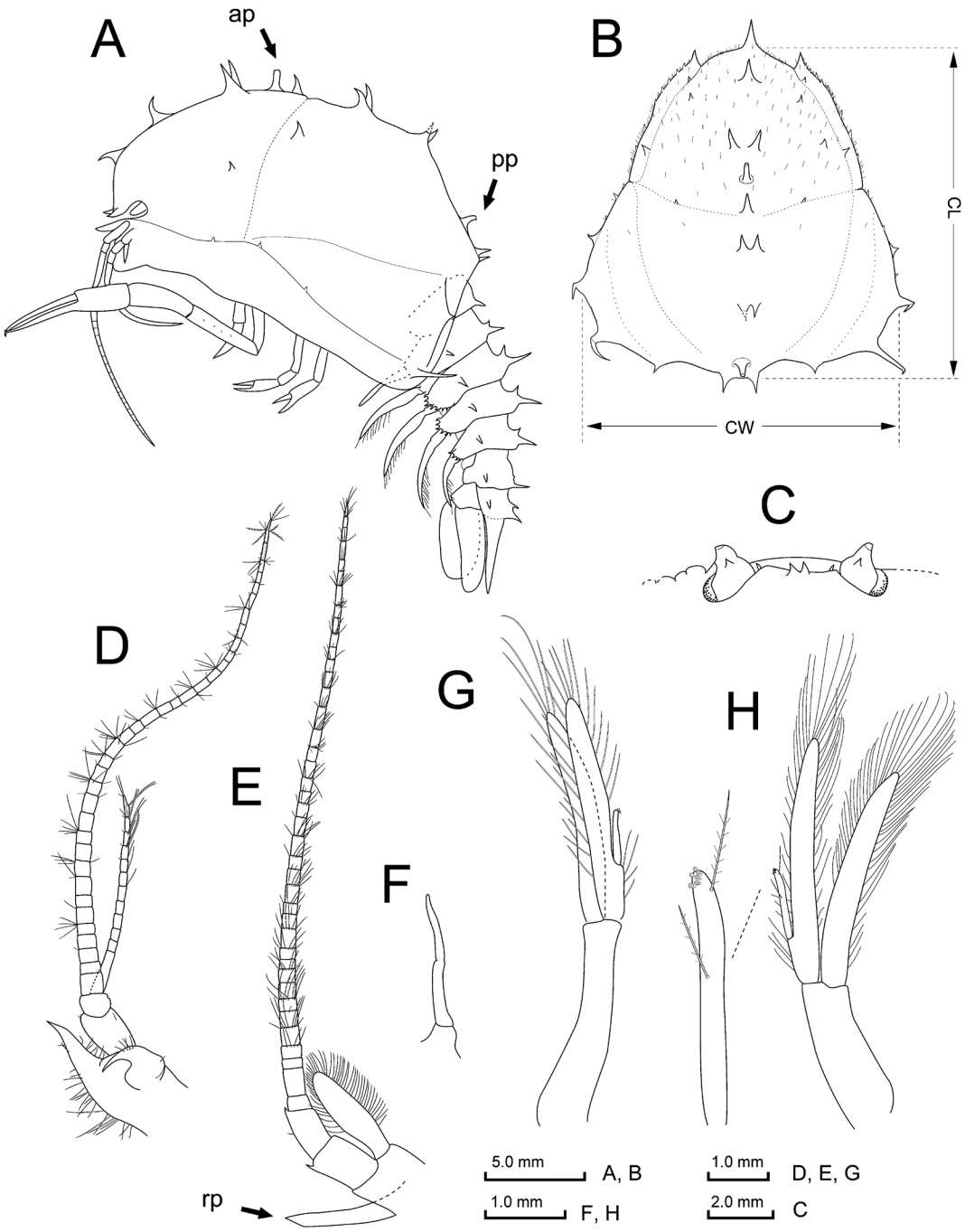

Fig. 2. Postlarva of *Stereomastis panglao*. A: whole body in lateral view, B: carapace in dorsal view, C: enlarged frontal region showing rostrum, orbit and eyes, D: antennule (right), E: antenna (right), F: pleopod 1 (right), G: pleopod 2 (right), H: pleopod 5 (right). Abbreviations: ap = anterior pillar, CL = carapace length, CW = carapace width, pp = posterior pillar, rp = renal process.

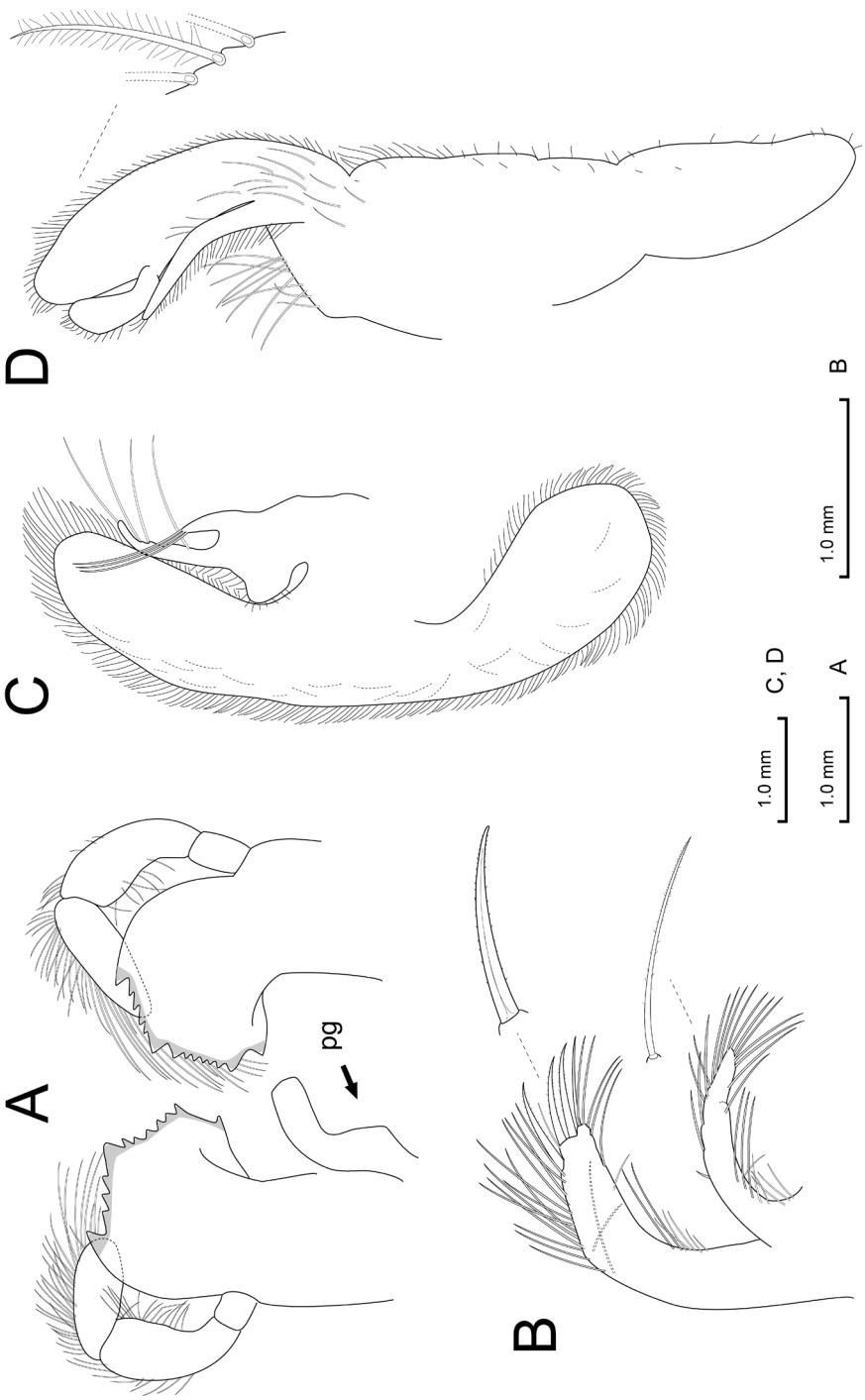

Fig. 3. Postlarva of *Stereomastis panglao*. A: mandibles in ventral view, B: maxillule (right), C: maxilla (right), D: maxilliped 1 (right). Abbreviations: pg = paragnath.

slender lobe. Exopod broad and elongate, consisting of anterior and posterior lobes with numerous marginal plumose setae; distal half of anterior lobe bilobed. Basal part with 10/12 long inner setae.

Maxilliped 2 (Fig. 4A): Endopod four-segmented; distal segment with 3 stout spines and 6 setae; other segments inner margin densely lined with long setae.

Maxilliped 3 (Fig. 4B): Endopod five-segmented, distal 3 segments with numerous long setae on both margins, proximal 2 segments on inner margin. Outer basal part with 1 reduced subtriangular epipod.

Pereiopods (Fig. 4C–E): Pereiopod 1 chelate, largest, more robust than Pereiopods 2–4; occlusal margins of both dactylus and pollex with minute cutting plates (Fig. 4C). Pereiopods 2–4 cheliform (Fig. 4D), pereiopod 5 not chelate, distolateral corner of propodus just weakly produced (Fig. 4E).

Pleon (Fig. 2A): Pleura of somite 1 with 1 dorsal spine on mid-posterior margin. Pleonites 2–5 with rounded rectangular pleura with serrate margins; longitudinally bi-spinous median carina on each somite, anterior spine smaller than posterior one, forming falcate outline as a whole in lateral view, each somite with 1 pair of lateral spines.

Pleopods (Fig. 2F–H): Pleonite 1 uniramous (Fig. 2F). Pleonite 2–6 biramous; endopod with numerous marginal plumose setae and 1 *appendix interna* bearing 6 cincinnuli on its distal end; exopod with numerous plumose setae marginally. Uropod (pleopod of pleonite 6) with wide flat endopod, exopod with numerous long plumose setae marginally.

Telson (Figs. 1, 2A): Oblanceolate with two spinous carinae dorsally, lateral margin with denticules and numerous long setae.

Discussion

Larvae of the Polychelidae have seldom been collected to date, and it is almost impossible to rear in laboratory conditions at present by their bathypelagic nature. Therefore, there have been few morphological studies on ontogenetic stages with evident specific identification, not to mention physiological and ecological studies. Identification of the wild-caught larvae has been mainly inferred from the adult species distributed in the area where the larvae were collected (Calman, 1925; Barnard, 1950; Bernard, 1953; Quintana & Retamal, 1984; Fredj & Laubier, 1985; Boyko, 2006). Currently, among the 38 species of the family (Chan, 2010; WoRMS, 2023), only two species, *Polycheles typhlops* and *Pentacheles laevis*, have a direct correspondence between larva and adult, based on laboratory hatching and/or DNA barcoding (Guerao & Abelló, 1996; Torres *et al*., 2014; Konishi *et al*., 2021). The present description is the third example of wild-caught larvae of polychelids with certain parentage by molecular techniques, and the first one in the genus *Stereomastis*.

Bernard (1953) analyzed the wild-caught specimens of polychelid larvae by allometric methods, and he categorized the I–XIII stages for some '*Eryoneicus*' species. However, we are unable to determine the accurate postlarval stage of our specimen of *S. panglao* with only one data. In addition, as noted by Harvey *et al*. (2006), polychelid larvae have an ambiguous property in the early developmental phase. The larvae appear to change its morphology gradually through successive moults, and no true metamorphosis has been observed between different stages (Bernard, 1953; Williamson, 1983; Torres *et al*., 2014). It is very difficult to discriminate the zoea, postlarva and juvenile, because of not only their presumable gradual morphological transition but fundamental difficulty in laboratory-rearing observation. Indeed, it may become more reality the ambiguous na-

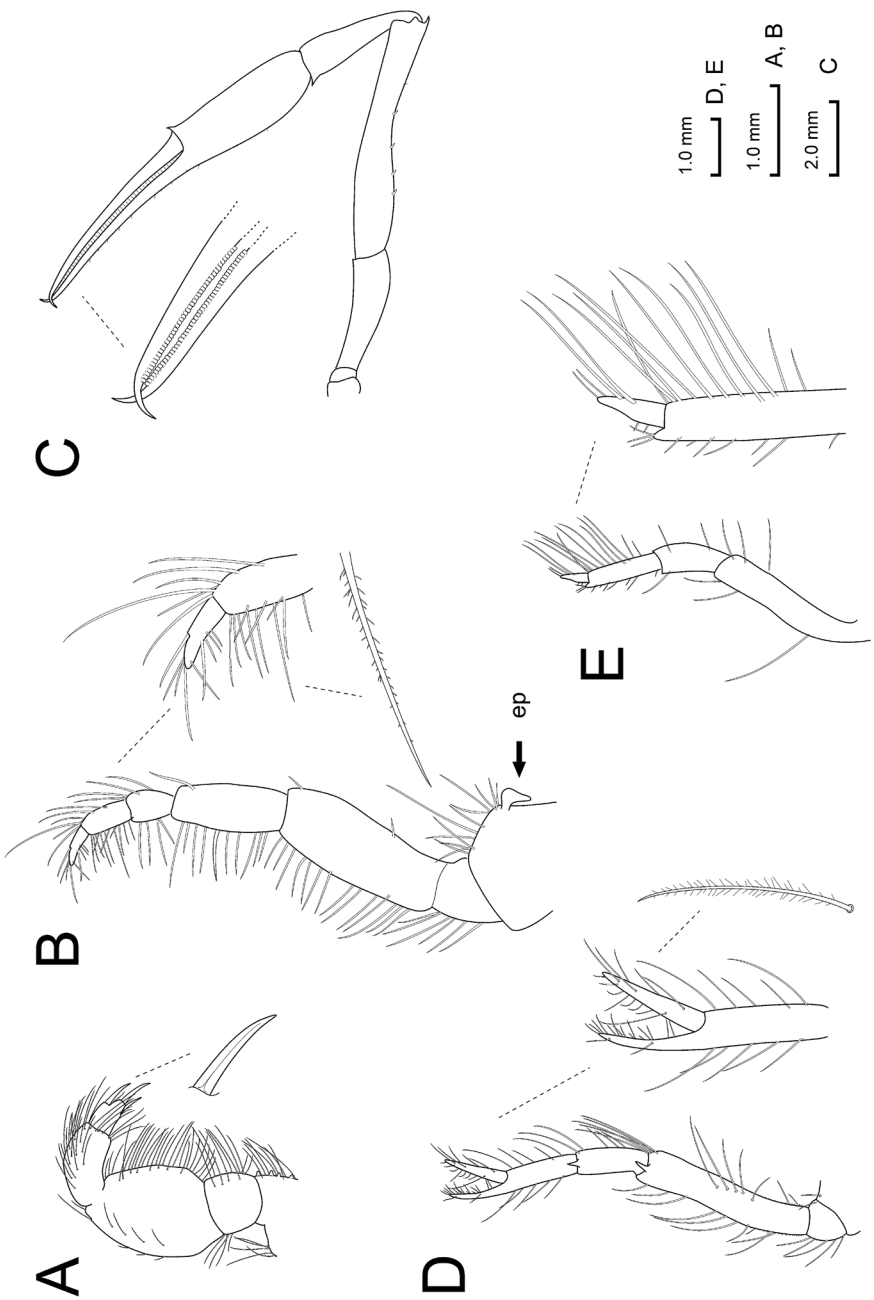

Fig. 4. Postlarva of *Stereomastis panglao*. A: maxilliped 2 (right), B: maxilliped 3 (left), C: pereiopod 1 (left), D: pereiopod 4 (left), E: pereiopod 5 (left). Abbreviations: ep = epipod.

Table 1. Comparison of selected larval characteristcs in previously described polychelid postlarvae.

Species	Carapace					Maxilliped 3	References
	outline image in dorsal view	CL/CW ratio[1)]	long PSL	rostral spine	middorsal spination[2)] (anterior | posterior)	epipod	
Cardus crucifer [as '*E. inermis*'][3)]	Pentagonal	1.03	No	Simple	p | p	Developed	[1]
Pentacheles laevis	Circular ovoid	1.02	No	Bifurcate	2,p | 2,2,p,2	Developed	[2] [3]
Polycheles typhlops	Circular ovoid	1.10	No	Simple	1,1,1,2,p | 2,2,p,2	Reduced	[4]
Stereomastis pacifica (megalopa)	Ovoid	1.09	No	—	1,2,1 | 2,2,1,2[4)]	Reduced	[5]
Stereomastis pacifica (juvenile)	Ovoid	1.06	No	—	1,2,1,1,2 | 2,1,2 [4), 5)]	Reduced	[5]
Stereomastis sculpta [as '*E. caecus*']	Ovoid	—	Yes	Bifurcate	1,2,1,p,1 | 2,2,p,2	—	[6] [7] [8]
Stereomastis sculpta [as '*E. faxoni*']	Ovoid	1.26	No	Bifurcate	2,1,2,p,1,1 | 2,2,p,2	—	[6] [9] [10]
Stereomastis nana [as '*E. hibernicus*']	Ovoid	1.29	No	Bifurcate	1,1,2,p,1 | 2,2,p,2	—	[7] [8]
Stereomastis nana [as '*E. indicus*']	Ovoid	—	No	Bifurcate	1,1,2,1,1 | 2,2,1,2[4)]	—	[11]
Stereomastis phosphorus [as '*E. denticulatus*']	Ovoid	1.17	No	Bifurcate	1,1,2,p,1 | 2,2,p,2	—	[1]
Stereomastis suhmi [as '*E. suhmi*']	Ovoid	—	No	Bifurcate	1,1,2,2,p,1 | 2,2,2,p,2	Reduced	[1]
Stereomastis suhmi	Ovoid	—	No	Bifurcate	1,1,2,2,p,1 | 2,2,2,p,2	—	[12] [13]
Stereomastis andamanensis [as '*E. spinoculatus*']	Ovoid	1.16	No	Bifurcate	1,1,2,p,1 | 2,2,p,2	—	[1]
'*E. spinoculatus*'	Ovoid	—	(Yes)	Bifurcate	1,1,2,1,1 | 2,2,1,2[4)]	Reduced	[6]
'*E. spinoculatus*'	Triangular	1.20	Yes	Bifurcate	1,1,2,p,1 | 2,2,p,2	—	[14]
Stereomastis panglao	Triangular	1.07	Yes	Bifurcate	1,1,2,p,1 | 2,2,p,2	Reduced	this study

CL: carapace length, CW: carapace width, PLS: posterolateral spine, —: no data.
1) Calculated from the original figure in some cases, 2) Vertical line "|" = position of cervical groove, p = pillar, 3) Larval species names '*Eryoneicus*' used in the original paper are shown in bracket,4) No mentions about pillars, 5) It is rather "1,2,1,1|2,2,1,2" judging from their Fig. 3.
[1] Bernard, 1953; [2] Boyko, 2006; [3] Konishi *et al*., 2021; [4] Torres *et al*., 2014; [5] Quintana & Retamal, 1984; [6] Bouvier, 1905, 1917;
[7] Sund, 1915, 1920; [8] Selbie, 1914; [9] Barnard, 1950; [10] Gordon, 1960; [11] Alcock & Anderson, 1899; [12] Calman, 1925;
[13] Tiefenbacher, 1994; [14] Kensley, 1968.

ture of the term "postlarva" as claimed by Møller *et al*. (2020).

Table 1. compares the selected characteristics in the previously described polychelid postlarvae, primarily in the genus *Stereomastis*. Additionally, several previous authors mentioned the larval specimens in *Stereomastis pacifica* (as *S. sculpta pacifica*), *S. auriculata* (as *Polycheles auriculatus*), *S. talismani* (as *P. talismani*) and *S. helleri*, respectively, although they gave no morphological descriptions in detail (Wicksten, 1980; Ahyong & Chan, 2004; Boyko, 2006; Komai & Komatsu, 2009). The present postlarva differs from those previously known genera *Cardus*, *Polycheles*, and *Pentacheles* in that the outline image of cephalothorax from the dorsal view is slightly posteriorly expanded and triangular, and a reduced epipod on the maxilliped 3. Among previously described postlarvae of the genus *Stereomastis*, *P. panglao* is also most similar to '*Eryoneicus spinoculatus*', recorded from the Atlantic and Indo-Pacific area, including Malaysia and Papua region as a larval species. In contrast, the CL/CW ratio of the postlarva of *S. panglao*, together with *S. pacifica*, is less than 1.10, while that of the other congeners ranges from 1.16–1.29. In the adult *S. panglao*, the middorsal spine arrangement is "1, 1, 2, 1 | 2, 2, 1, 2" counting to the figures of the original description by Ahyong & Chan (2008). This is almost the same as the postlarval arrangement "1, 1, 2, p, 1 | 2, 2, p, 2" except for the pillars. Bernard (1953) also identified '*E. spinoculatus*', bearing the same middorsal spination, as a larval form of *S. andamanensis* whose distribution is worldwide. We cannot discuss the validity of his identification at present, because of the paucity of available data on morphological variation during developmental stages and in individuals.

One of the important morphological characteristics of polychelid larvae is the middorsal spination on the cephalothorax. The spine arrangement is almost uniformly "2, 2, p, 2" posterior to the cervical groove, but varies in the anterior region among species, even within species as pointed out by Bernard (1953). In any case, morphological data on polychelid larvae are overwhelmingly lacking, and we should be the mind that there are still no reliable morphological characteristics to distinguish the various genera of this family.

Since Yokoya's (1933) pioneering work, the family Polychelidae in Japan and the adjacent waters includes 12 species ranging 5 genera (Okada *et al*., 1966; Okutani, 1969; Galil, 2000; Kuramochi *et al*., 2004; Ahyong, 2009, 2012; Yamamoto & Nagasawa, 2011; Komai & Komatsu, 2009; Komai & Tsuchida, 2014).

Ahyong & Chan (2008) stated that the distribution of *S. panglao* was restricted to the Bohol and the Suru Sea at depths of 784–1,773 m, while the present postlarva was collected in Suruga Bay at depths of 1,305–1,565 m. Our detection of the larvae of *S. panglao* does not necessarily confirm that the adults of the species inhabit the same area. Undeniably, the zoeas or postlarvae may have drifted, like leptocephalus larvae of the Anguilliformes (Tsukamoto, 2006), from the far southern sea area to Suruga Bay by chance due to the Kuroshio Current.

Despite the paucity of ecological data, the polychelid lobsters are known to live exclusively in deep waters 300–6,000 m. Their larvae have not been collected from shallow waters and are thought to develop adaptation in the deep waters of the aphotic zone as adults live. The degeneracy of the eyes at the time of hatching may be a result of adaptation to such a mesopelagic or bathypelagic life history. In this respect, we must be careful not to equate this species with the majority of decapods of which larvae grow at the surface as planktons. The Kuroshio Current moves northward along the Pacific coast, including Suruga Bay, passing through the waters around Taiwan. Although the larvae could have been transported from Taiwan, from the mesopelagic nature of

the polychelid larvae, they cannot be considered equivalent to common decapod zoeas and megalopas of shallow water habits. Therefore, it is unable to conclude at this time whether the floating larvae drifted from the southern coastal waters, or whether the adults originally inhabit Suruga Bay and its vicinity.

The life history of polychelids, including their ecology, is still little revealed. Further advanced research and the steady accumulation of specimen data will be strongly encouraged.

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Appendix—Summary of DNA barcoding and specific identification in our previous work (translated from Yanagimoto *et al.*, 2019)

METHODS: Muscle samples from the postlarva to be used in PCR amplification of the COI and ITS1 gene were extracted using Quick Gene[1]. The PCR amplification was done using the universal primers LCO1490 and HCO2198. The PCR reactions were carried out in a volume of 10 μL containing 20–50 ng template DNA, 1 μL of 10×PCR buffer, 0.8 μL of dNTP (2.5 mM), 1 μL of each primer (10μ M), 0.05 μL of 5 U/μL TAKARA Ex Taq Polymerase Hot Start Version[2] in a Model 9700 Thermal Cycler[3]. The amplified products were electrophoresed on a 1.5% agarose gel and subsequently stained with ethidium bromide for band characterization which was done using UV transillumination. The remnants of the primers and dNTP were removed by treatment of the amplicons with ExoSAP-IT[4] after which they were subjected to direct sequencing using the PCR primers. DNA for cycle sequencing reactions were carried out using a BigDye Terminator Ver3.1 kit[3] and sequencing was conducted on an ABI3730XL Automatic Sequencer[3] with forward and reverse primers. The primers used for sequencing were the same as those for PCR amplification. The ITS1 region was amplified with primers MD-1 and 5.8SH. PCR amplification, thermocycling conditions, cycles, and so on were the same as those used for the COI region. PCR products with ITS sequences were cloned into electrocompetent *E. coli* using a TOPO TA cloning kit[5]. Eight white colonies were randomly selected and then amplified by PCR conducted using primers of M13 and its reverse primers. The resultant sequences were edited and aligned using ATGC software[6]. Kimura's 2-parameter (K2P) genetic distance and the phylogenetic tree's construction were determined using MEGA 5.05. The postlarval nucleotide sequence data were entered into a DNA database under accession numbers LC076645–LC076650.

RESULTS: We obtained 5 base sequences in the ITS1 region of the postlarva. The average number of base substitutions in these sequences was 0.4 bases, while the average percentage of base substitutions was 0.1%. Blast analysis

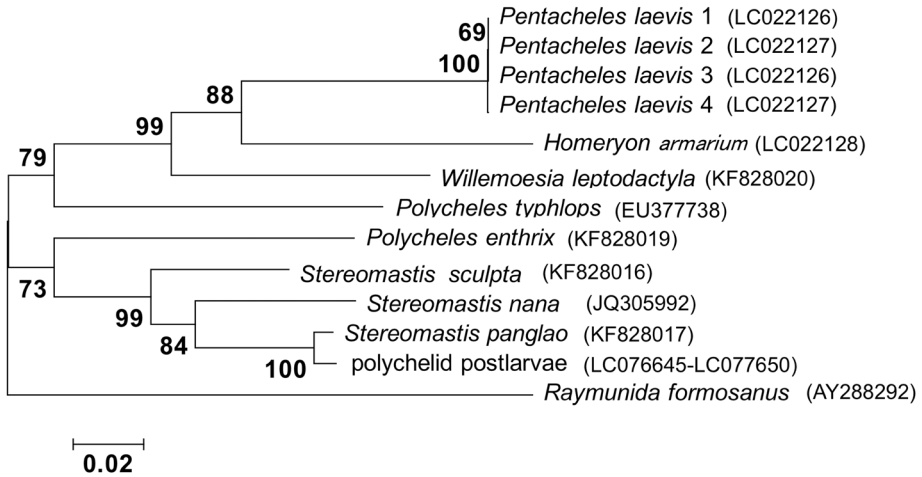

Fig. A1. Neighbor-joining tree of the nucleotide sequences of COI region constructed using Kimura two-parameter distances for polychelid species and the postlarvae. The first and second numbers after the species name indicate individual numbers. Numbers beside internal branches indicate bootstrap probabilities based on 1,000 pseudoreplicates. Bootstrap probabilities higher than 50% are shown. (Modified from Fig. 2 in Yanagimoto *et al*., 2019)

of the sequences showed high homology with polychelid species, namely *Pentacles laevi*s, *Homeryon armarium*, and *Polycheles typhlops*. Comparing the data of the three species with high homology to the ITS1 sequence obtained here, the average of base substitutions ranged from 88–104, and the average percentage of base substitutions ranged from 19.6–23%. The high rate of base substitutions and the ITS1 sequence of the parental species of this larva was not found in the existing data. Blast analysis of the sequence of the COI region of the larvae showed that the top group with high homology rates was the genus *Stereomastis*, including *S. panglao* (98%), *S. sculpta* (92%), and *S. nana* (92%). A phylogenetic tree was constructed using the nucleotide sequences of the top homologous species and the outgroup which had the highest homology among non-polychelid species (Fig. A1). The sequence of the postlarva formed a clade with a high confidence level with the sequence of *S. panglao*, followed by the sequence of *S. nana* and *S. sculpta*. The base substitution ratio was 1.2% different from that of *S. panglao*, and more than 8.3% different from that of other species. Although here we did not use adult specimens of *S. panglao*, but of nucleotide sequences registered in a database [No. JQ305991–2], these data strongly support that our specimen is the postlarva of *S. panglao*.

1) Wako, 2) TAKARA, 3) Applied Biosystems, 4) GE Healthcare, 5) Invitrogen, 6) GENETYX.