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A new species of *Bemlos* Shoemaker, 1925 (Amphipoda: Aoridae) from deep water off Tanabe Bay, Japan, with a review of the deep-sea aorids and their adaptations to the deep sea

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ABSTRACT

A new species of aorid amphipod, *Bemlos seisuiae* **sp. nov.**, is described from deep muddy bottom off Tanabe Bay, Japan. The new species is characterized by its conspicuously slender and elongated pereopods 3–6. The aorids reported from deep water are reviewed, and their morphological adaptations to deep water are discussed.

Keywords: northwestern Pacific Ocean, taxonomy

INTRODUCTION

Aoridae Stebbing, 1899 is a diversified amphipod family of which members are often reported as tube dwellers or burrowers (Enequist, 1949; Barnard *et al.*, 1991; Dixon & Moore, 1997; Myers, 2009). The family currently contains 252 species belonging to 25 genera (Horton *et al.*, 2018), reported worldwide, mainly from shallow marine or blackish water and rarely from deep water (Myers, 1988a, 2009). Twenty aorid species belonging to six genera have been documented in Japan (Ariyama, 2007, 2013; Ariyama & Taru, 2017), though all the species were recorded from intertidal or subtidal water.

During a survey of the deep-sea benthic fauna in the Sea of Kumano and off Tanabe Bay by TRV *Seisui-maru* (Mie University; research cruise 1803), an amphipod specimen attributed to the family Aoridae was collected. It revealed to represent a new species. We herein describe the species and also provide a review of all the deep-sea aorid species.

MATERIALS AND METHODS

A fresh specimen of the new species was collected from muddy bottom off Tanabe Bay, Japan. Measurements for the dorsal length are given as the length from the tip of rostrum to the posterior margin of the telson. The specimen was dissected under a binocular stereomicroscope, and the appendages were mounted in Hoyer's medium on glass slides. Observations and line drawings were made by using a light microscope with the aid of drawing tube (Y-IDT, Nikon, Tokyo, Japan). The specimen was deposited in the National Museum of Nature and Science, Tokyo (NSMT).

SYSTEMATICS

Family Aoridae Stebbing, 1899

Genus *Bemlos* Shoemaker, 1925

Bemlos seisuiae sp. nov.

[New Japanese name: *Yurei-maeashi-yokoebi*]

(Figs. 1–6)

Material examined. Holotype: NSMT-Cr 25890, male, 8.3 mm, off Tanabe Bay, 686–740 m deep, muddy bottom, 26 April 2018, TRV *Seisui-maru*, beam trawl (towed from 33°32.689'N, 135°07.529'E to 33°33.179'N, 135°06.877'E).

Diagnosis. Eyes very small. Accessory flagellum multi-articulated. Mandibular palp article 3 subequal to article 2 in length, weakly incurved, not falcate, with dense short setae, long serrulate setae (setae of 2 distinct lengths). Left mandibular molar with oblique lamellae. Maxilliped without wing-like flanges on anterior margin. Coxae discontiguous. Male gnathopod 1 subchelate, carpus shortened; propodus much larger, longer than carpus. Male gnathopod 2 subchelate, carpus not shortened; carpus, propodus with dense long setae. Pereopods 3–6 slender, elongated, basis rectilinear. Pereopod 5 propodus with several robust setae on flexor margin. Pereopod 6 dactylus longer than half of propodus. Pereopod 7

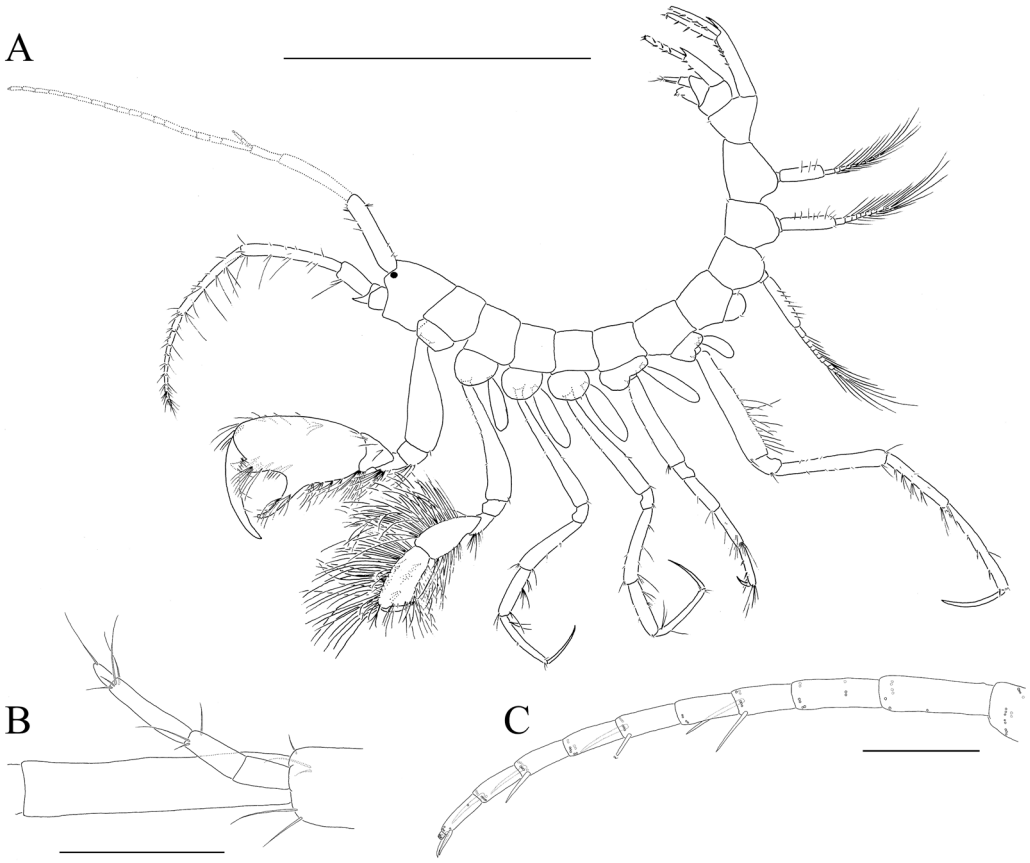

Figure 1. *Bemlos seisuiae* **sp. nov.**, holotype male, 8.3 mm (NSMT-Cr 25890). Habitus (setae partly omitted; antenna 1 drawn based on right antenna 1, except for peduncular article 1), lateral view (**A**). Right antenna 1, flagellar article 1 and accessory flagellum, medial view (**B**). Left antenna 2 flagellum (setae omitted), lateral view (**C**). Scale bars: **A** = 5.0 mm; **B**, **C** = 0.3 mm.

unknown. Uropods 1, 2 biramous, inner ramus with ventral robust seta(e) in addition to normal dorsal, apical robust setae. Uropod 3 biramous, peduncle short, medial margin expanded with row of short setae, outer ramus with long distal setae, lacking article 2. Sexual dimorphisms unknown.

Description. Based on holotype male, 8.3 mm. Body (Fig. 1A) slightly compressed dorsoventrally, surface smooth. Pereonites without sternal spines. Coxae discontiguous.

Head. About 1.7 times length of pereonite 1 in dorsal margin; rostrum indistinct; lateral cephalic robes weakly convex; eyes very small, less than 15% length of head. Antenna 1 peduncular articles 1:2:3 length 17:16:4, article 1 with robust seta distoventrally; flagellum approximately 1.3 times length of peduncle with 18 articles, article 1 twice length of article 2, distalmost article minute; accessory flagellum (Fig. 1B) with 4 articles. Antenna 2 shorter than antenna 1; peduncle, length ratio of articles 3–5 about 5:14:12; flagellum (Fig. 1C) subequal to peduncular article 5 in length, with 10 articles, article 1 longer than article 2, articles 3–9 subequal in length, distalmost article minute, articles 3, 5, 7, 9 each with 2 robust setae distoventrally, article 8 with single robust seta distoventrally.

Mouthparts. Upper lip (Fig. 2A) normal, rounded ventrally. Lower lip (Fig. 2B) normal, setulose; outer plate, mandibular process developed, apical lobule with 4 or 5 robust setae. Mandible (Fig. 2C1–3, D): palp article 1 longer than wide, unarmed, article 2 about 3.5 times longer than article 1, article 3 subequal to article 2 in length, weakly incurved, not falcate distally, with dense marginal short setae, groups of long serrulate setae (setae with 2 distinct lengths); left, right incisors 4-dentate; left, right laciniae mobiles 4-, 3-dentate, respectively; left, right accessory setal rows including 7, 6 setae, respectively; molar plate with oblique lamellae, with single molar blade. Maxilla 1 (Fig. 2E): palp article 1 short, with distolateral seta, article 2 incurved, beyond outer plate, bearing 7 (left) or 8 (right) robust setae apically, short slender seta laterally, ventral surface with row of setae subdistally; outer plate truncate, incurved, apical margin with 6 (left) or 10 (right) dentate robust setae; inner plate small, with long serrulate seta distomedially. Maxilla 2 (Fig. 2F) normal; outer plate longer than inner plate, with long serrulate, simple setae distally; inner plate with serrulate setae on apical to medial margin, dorsal surface with oblique facial row of plumose setae. Maxilliped (Fig. 2G) with palp article 2 long beyond apex of outer plate, article 3 with 3 long robust setae distally, article 4 with long, robust seta apically; outer plate broad, with row of robust setae medially to distally, lateral margin convex, unarmed; inner plate truncate, with 3 distal small robust setae, followed by inward small robust seta.

Pereon. Gnathopod 1 (Fig. 3A1) enlarged; coxa shallow, longer than deep; basis broadened distally; carpus short, triangular; propodus (Fig. 3A2) enlarged, posterior margin with large produced teeth, posterodistal corner with small teeth overlapping dactylus; dactylus long, falcate, without teeth on posterior margin. Gnathopod 2 (Fig. 3B1) subchelate, length ratio of basis to dactylus about 12:2:3:7:7:3; coxa rounded trapezoidal; basis broadened distally, with row of short setae on anterior margin; carpus, propodus densely covered with long setae anteromedially, posteromedially; propodus (Fig. 3B2) with oblique palm, finely dentate, without

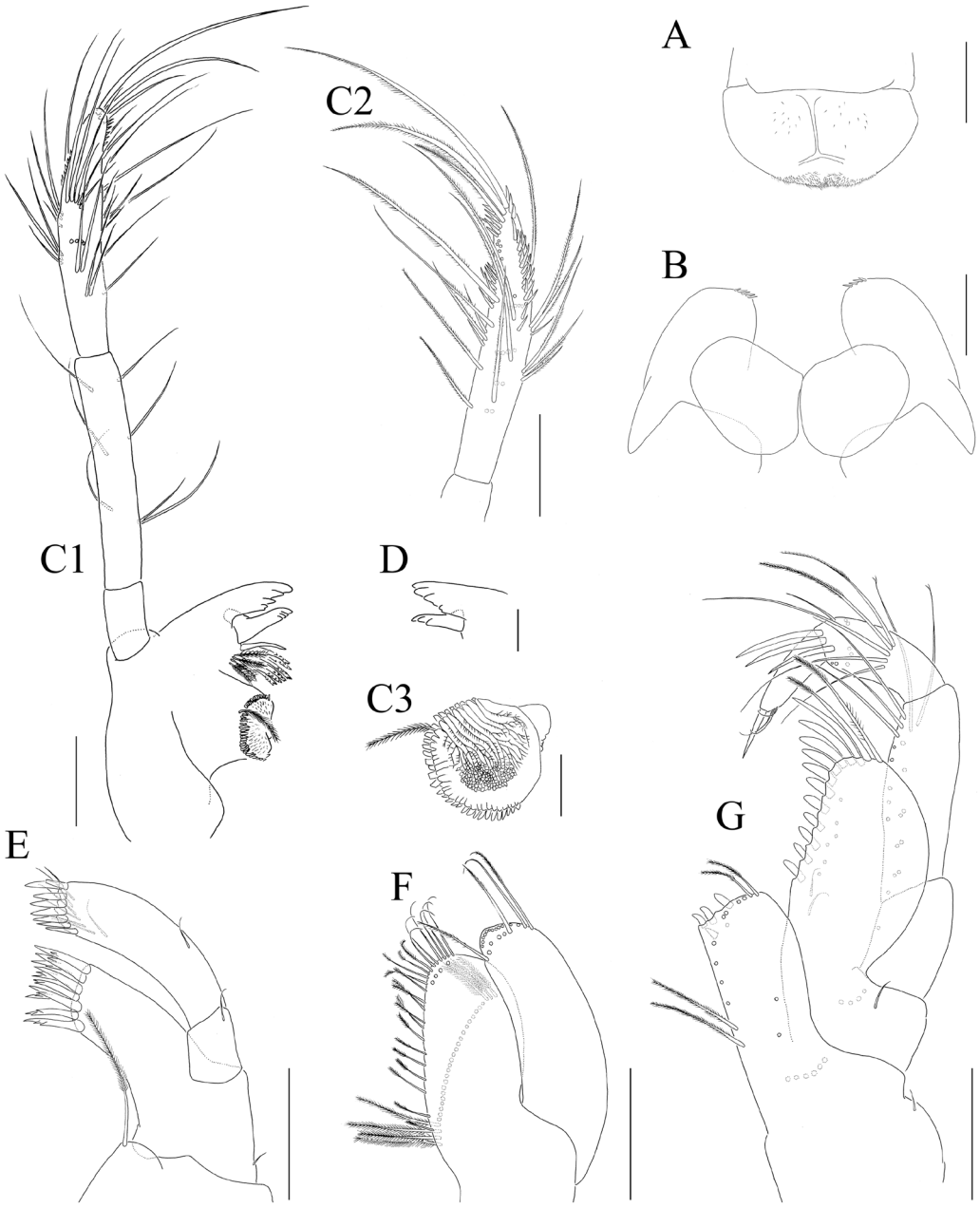

Figure 2. *Bemlos seisuiae* **sp. nov.**, holotype male, 8.3 mm (NSMT-Cr 25890). Upper lip, anterior view (**A**). Lower lip (setules omitted), ventral view (**B**). Left mandible, medial view (**C1**). Palp article 3 of left mandible, lateral view (**C2**). Molar of left mandible, medial view (**C3**). Incisor and laciniae mobilis of right mandible (**D**). Right maxilla 1, dorsal view (**E**). Left maxilla 2 (setae partly omitted), ventral view (**F**). Right maxilliped (setae partly omitted), dorsal view. Scale bars: **A**–**C2**, **E**–**G** = 0.2 mm; **C3**, **D** = 0.1 mm.

robust setae; dactylus long, slightly beyond propodus palm, falcate, toothed on posterior margin.

Pereopods 3, 4 (Fig. 4A, B) similar to each other, slender, elongated, length ratio of basis to dactylus about 14:2:8:6:7:5; coxa semi-circular; basis slightly broadened distally; merus weakly curved posteriorly; propodus slightly tapering; dactylus tapering, distally acute. Pereopod 5 (Fig. 4C) slender, length ratio of basis to dactylus about 14:3:6:6:6:2; coxa bilobate; propodus with 3 robust setae on flexor margin; dactylus short. Pereopod 6 (Fig. 4D) slender, strongly elongated, about 1.8 times longer than pereopod 5, length ratio of basis to dactylus about 15:3:13:9:22:8; coxa bilobate; basis, posterior margin with row of plumose setae on distal half; propodus with robust setae on distoflexor corner; dactylus long, acute. Pereopod 7 coxa semicircular; basis–dactylus unknown.

Coxal gills slender, on gnathopod 2, pereopods 3–6 coxae. Gill on pereopod 6 smaller than others.

Pleon. Epimeral plates normal, without teeth or notch on margin; epimeral plate 1 with short simple seta ventrally. Pleopods 1–3 (Fig. 5B) similar to each other; peduncle rectangular, with several plumose setae laterally, coupling spines on distomedial margin; rami articulated, with many plumose setae, inner ramus longer than outer ramus.

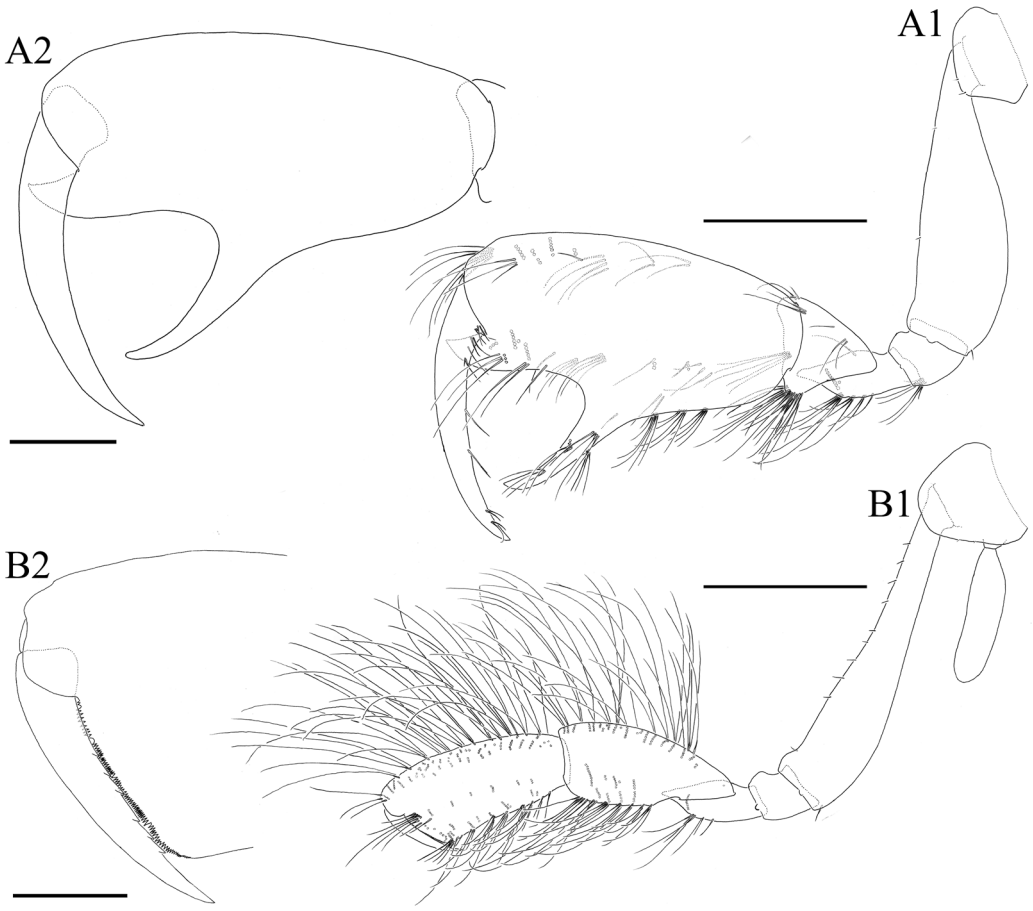

Figure 3. *Bemlos seisuiae* **sp. nov.**, holotype male, 8.3 mm (NSMT-Cr 25890). Left gnathopod 1 (setae partly omitted), lateral view (**A1**). Propodus and dactylus of left gnathopod 1 (setae omitted), lateral view (**A2**). Left gnathopod 2 (setae partly omitted), lateral view (**A1**). Propodus palm and dactylus of left gnathopod 2 (setae omitted), lateral view (**A2**). Scale bars: **A1**, **B1** = 1.0 mm; **A2**= 0.5 mm; **B2** = 0.2 mm.

Urosome (Fig. 5A). Uropod 1 (Fig. 5C) biramous; peduncle with 2 robust setae dorsolaterally, 3 robust setae dorsomedially, distolateral corner with simple seta, ventrodistal end with inter-ramal process; outer ramus slightly longer than peduncle (inter-ramal process excluded), with 3 robust setae dorsolaterally, 3 robust setae dorsomedially, 3 robust setae distally; inner ramus subequal to outer ramus in length, with 5 robust setae dorsally, 2 robust setae proxoventrally, 5 robust setae distally. Uropod 2 (Fig. 5D) biramous; peduncle dorsolateral margin with robust seta subdistally, simple seta distally, dorsomesial margin with robust seta distally, ventrodistal end with inter-ramal process; outer ramus 1.2 times length of peduncle (inter-ramal process excluded), with 3 robust setae dorsolaterally, 3 robust setae dorsomedially, 5 robust setae distally; inner ramus slightly longer than outer ramus, with 4 robust setae dorsolaterally, 4 robust setae dorsomedially, robust seta proxoventrally, 5 robust setae distally. Uropod 3 (Fig. 5E1) biramous; peduncle expanded medially, with 4 short setae dorsomedially, short seta distolaterally; outer ramus slightly tapering distally, with short, long seate distally, lacking article 2 (Fig. 5E2); inner ramus slightly shorter than outer ramus, tapering distally, with robust seta dorso-subdistally, 1 or 2 robust seta(e), simple seta distally. Telson (Fig. 5F) wider than long, with pair of telsonic cusps, 2 setae distolaterally.

Coloration immediately after fixation. Body, appendages generally cream without mottling; eyes white (Fig. 6) but faded in preservation over time.

Distribution. Known only from type locality, deep muddy bottom (686–740 m) off Tanabe Bay, Japan.

Etymology. The new species is named after TRV *Seisui-maru*. The specific name is a noun in the genitive case.

Remarks. The new species is characterized by the conspicuously slender and elongated pereopods 3–6. This is a potentially new genus because of the 1) very small eyes, 2) mandibular molar plate with oblique lamellae, 3) very slender and elongated pereopods 3–6 with rectilinear basis, and 4) uropod 3 outer ramus lacking article 2. We have provisionally placed the new species in *Bemlos* Shoemaker, 1925 pending the collection of additional material and/or molecular sequencing.

Bemlos seisuiae **sp. nov.** resembles species of *Globosolembos* Myers, 1985 and *Plesiolembos* Myers, 1988 in sharing a uropod 3 outer ramus that lacks a second article. The new species, however, can be distinguished from these species by the conspicuously slender and elongated pereopods 3–6 with a rectilinear basis and the presence of several robust setae on the flexor margin of pereopod 5 propodus.

Nomenclatural statement: A life science identifier (LSID) number was obtained for the new species: urn:lsid:zoobank.org:pub:C5516A60-A6F6-478E-B5C8-0FC0E93638D6.

REVIEW OF THE DEEP-WATER AORIDS

Species belonging to Aoridae have been mainly reported from shallow water. Only sixteen species belonging to the following

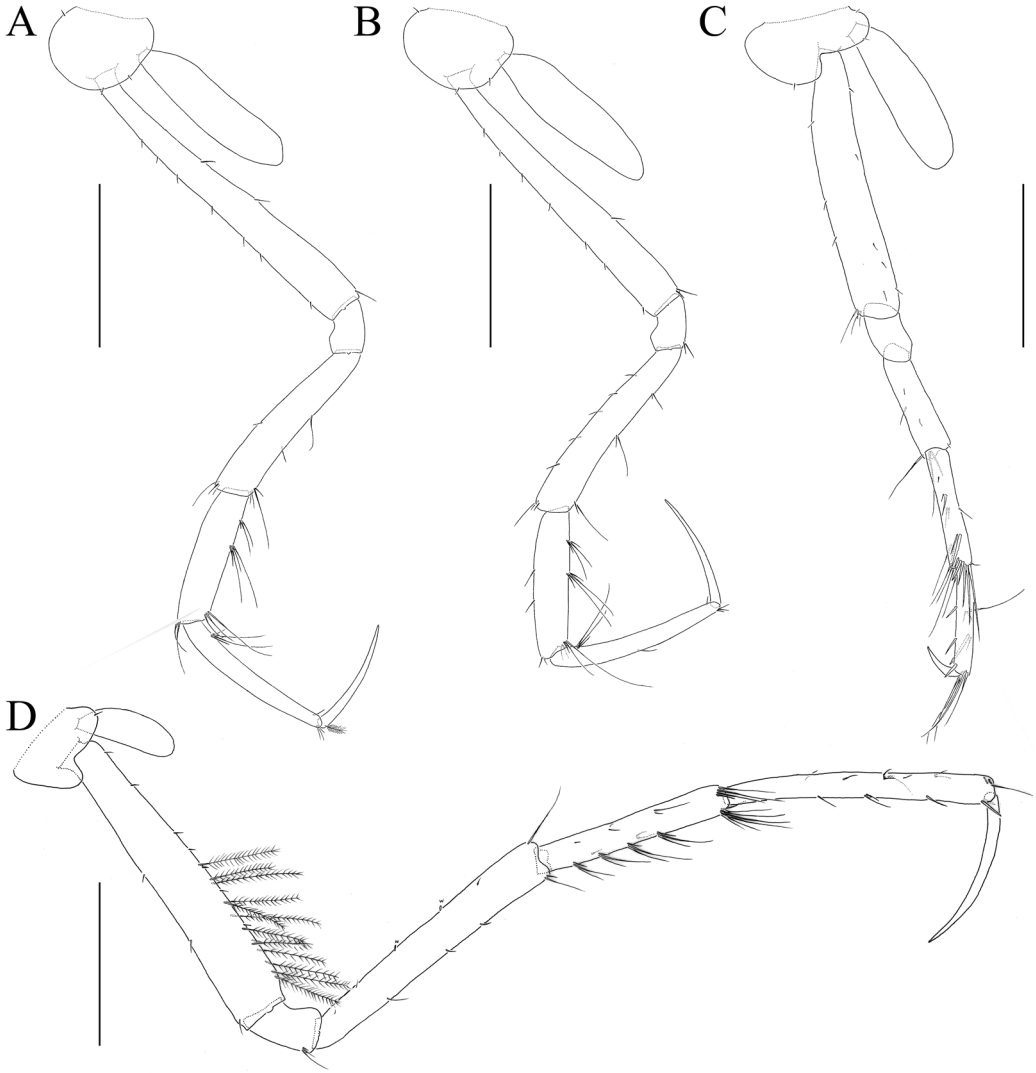

Figure 4. *Bemlos seisuiae* **sp. nov.**, holotype male, 8.3 mm (NSMT-Cr 25890). Left pereopods 3–6, lateral views (**A–D**). Scale bars = 1.0 mm.

eight genera, out of a total of 252 species belonging to 25 genera (Horton *et al.*, 2018), are nevertheless reported from water deeper than 200 m deep (Table 1): *Autonoe* Bruzelius,1859 (seven species) known mainly from the North Atlantic; *Camacho* Stebbing, 1888 (three species) southwestern Indian southwestern Pacific oceans and the North Sea; *Bemlos* (two species) North Pacific; *Archaeobemlos* Myers, 1988 (monotypic) southwestern Pacific; *Chevreuxius* Bonnier, 1896 (monotypic) northeastern Atlantic; *Lembos* Bate, 1857 (eight species, including one from deep water) southeastern Atlantic; and *Microdeutopus* Costa, 1853 (12 species, including one from deep water) Mediterranean and North Atlantic. Some species such as *Microdeutopus anomalus* (Rathke, 1843) or *Autonoe longipes* (Liljeborg, 1852) are reported mainly from shallow water but occasionally from deep water. The deepest species is *Lembos lobata* Barnard, 1962 collected from Cape Basin off South Africa at the depth of 4893 m. *Bemlos seisuiae* **sp. nov.**, is the first deep-sea aorid from the northwestern Pacific.

The reduction of eyes appears to have occurred independently in several linages of the deep-sea aorids, thus representing a convergent adaptation to the darkness of deep waters. There is no eye-less species in shallow-water aorids, whereas all species collected from depths of more than 1000 m have no or vestigial eyes.

Compared with shallow water species, the coxal plates of deep-sea aorids tend to be reduced. Those of *Chevreuxius gradimanus* Bonnier, 1896 and *Camacho* species are particularly small. Dahi (1977) explained that the coxal plates form a ventral groove to maintain efficient aeration for the gills by concentrating pleopod currents, and as a result, help respiration. He also indicated that coxal plates can be reduced in taxa such as tube-building species (their tube can function as coxal plates and ventral groove), species with very small and slender bodies (respiration should not offer great problem for them), and species living under considerable degree of water movements, which suggest that the reductions of the coxal plates is linked to respiration.

The reduction of coxal plates observed in deep-sea aorids suggests that they either build more efficient tubes for respiration than in shallow-water species or that they do not need pleopod current for respiration. It is difficult to discuss the validity of the first possibility because of the very limited information on the ecology of deep-water aorids. Deep-sea crustaceans generally have a low respiration rate and their oxygen requirements are small (Wilson & Ahyong, 2015) so it is possible that some deep-sea aorids have evolved a reduction in their respiration rate and thus obtain adequate oxygen without pleopod currents, with a reduction of the coxal plates.

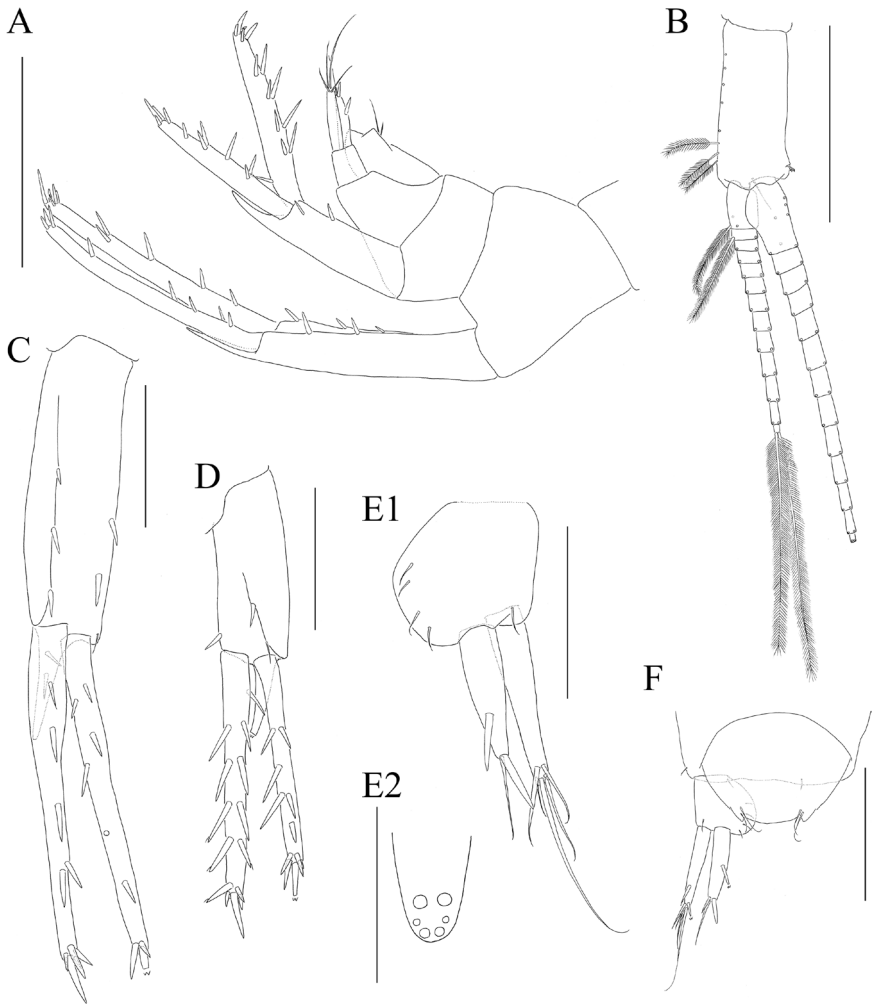

Figure 5. *Bemlos seisuiae* **sp. nov.**, holotype male, 8.3 mm (NSMT-Cr 25890). Urosome, right side, lateral view (**A**). Left pleopod 1 (setae partly omitted), posterior view (**B**). Right uropod 1, dorsal view (**C**). Right uropod 2, dorsal view (**D**). Right uropod 3, dorsal view (**E1**). Apical part of right uropod 3 outer plate (setae omitted), dorsal view (**E2**). Left uropod 3 and telson, dorsal view (**F**). Scale bars: **A**, **B** = 1.0 mm; **C**, **D**, **F** = 0.5 mm; **E1** = 0.3 mm; **E2** = 0.1 mm.

Figure 6. *Bemlos seisuiae* **sp. nov.**, holotype male, 8.3 mm (NSMT-Cr 25890). Coloration immediately after fixation with 99% ethanol. Scale bar = 5.0 mm.

Slender and elongated pereopods are observed in the new species, as well as in the species of *Camacho* and some species of *Autonoe*. The elongation of appendages is found in many deep-sea crustaceans (Watling & Thiel, 2015; Wilson & Ahyong, 2015) as well as in many cave-dwelling arthropods (Howarth, 1983; Culver *et al.*, 2010). This is thought to be an adaption to muddy environment to help support their bodies on the soft muds of the sea floor (Watling & Thiel, 2015), as well as adaptation to darkness by having increased tactile sensitivity (Howarth, 1983). The elongation of pereopods is, however, not a general trend in deep-sea aorids. Some species such as *C. gradimanus* have short pereopods.

Aorid males usually have an enlarged gnathopod 1 of varying shape (e.g., subchelate in *Autonoe*, *Bemlos* or *Lembos*; carpochelate in *Chevreuxius*, *Grandidierella* Coutière, 1904 and *Microdeutopus*; merochelate in *Aora* Krøyer, 1845 and *Aoroides* Walker, 1898). Nevertheless, almost all the deep-sea aorids have a subchelate gnathopod 1. Only two species, *C. grandimanus* and *M. anomalus*, have a carpochelate gnathopod 1, and none of the deep-sea aorids have a merochelate gnathopod 1. The enlargement of the male gnathopod 1 is moreover weakened in some linages of deep-sea aorids. *Bemlos edentulous* (Barnard, 1967), *L. lobata*, and all the *Camacho* species have a small gnathopod 1 (subequal to gnathopod 2 in size and

Table 1. Aorid species previously reported from depths of more than 200 m.

Taxon	Depth (m)	Distribution	References
***Archaeobemlos* Myers, 1988**			
A. philacanthus (Stebbing, 1888)	50–411	SW Pacific	Pirlot, 1934; Myers, 1988b
***Autonoe* Bruzelius, 1859**			
A. angularis (Ledoyer, 1970)	100–400	Mediterranean	Ledoyer, 1970, 1977; Myers, 1974
A. catalaunica Ruffo, Cartes & Sorbe, 1999	389–601	Mediterranean	Ruffo *et al.*, 1999
A. borealis (Myers, 1976)	70–430	N Atlantic	Myers, 1976, 1998; Just, 1980
A. longicornis (Chevreux, 1909)	1360–1865	NE Atlantic	Chevreux, 1909; Myers & Cunha, 2004
A. longidigitans (Bonnier, 1896)	950–1096	N Atlantic	Bonnier, 1896; Stebbing, 1906; Stephensen, 1944; Myers, 1979
A. longipes (Liljeborg, 1852)	10–375	N Atlantic, Arctic Ocean	Liljeborg, 1852; Stephensen, 1942; Myers, 1979
A. megacheir Sars, 1879	100–575	NE Atlantic	Stephensen, 1942; Myers, 1976
***Bemlos* Shoemaker, 1925**			
B. edentulus (Barnard, 1967)	791–842	NE Pacific	Barnard, 1967
B. seisuiae **sp. nov.**	686–740	NW Pacific	This study
***Camacho* Stebbing, 1888**			
C. bathyplous Stebbing, 1888	77–2640	SW Pacific, SW Indian Ocean	Stebbing, 1888, 1908; Hurley, 1954; Barnard, 1961
C. faroensis Myers, 1998	600–1005	North Sea, NE Atlantic	Myers, 1998; Tato *et al.*, 2018
C. nodderi Coleman & Lörz, 2010	414–657	SW Pacific	Coleman & Lörz, 2010
***Chevreuxius* Bonnier, 1896**			
C. grandimanus Bonnier, 1896	351–950	NE Atlantic	Bonnier, 1896; Myers, 1998
***Lembos* Bate, 1857**			
L. lobata Barnard, 1962	4893	SE Atlantic	Barnard, 1962
***Microdeutopus* Costa, 1853**			
M. anomalus (Rathke, 1843)	0–200	N Atlantic, Mediterranean	Myers, 1969

shape). Myers (1988a) indicated that such unmodified male gnathopod 1 could be neotenous.

Myers (1988a) discussed the phylogenetic positions of three deep-sea aorids, *Autonoe longidigitans* (Bonnier, 1896), *B. edentulous*, and *L. lobata*, and concluded these species are polyphyletic. The sixteen deep-sea aorids we review are belong to many genera, and thus, from multiple ancestral sources. These species, therefore, have independently evolved these features.

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