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Systematics and zoogeography of the deep-sea hyperbenthic family Arietellidae (Copepoda: Calanoida) collected from the Sulu Sea

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Abstract

A faunistic survey of the deep-sea hyperbenthic copepods in the Sulu Sea, which has a deep basin and is connected via shallow straits with the Pacific and the South China Sea, was carried out in November and December 2002, using beam trawls and a mid-water trawl. Two new genera and four new species of the primitive calanoid family Arietellidae are described. A new genus *Metacalanalis* shows intermediate characteristics between those of *Metacalanus* Cleve, 1901 and *Pilarella* Alvarez, 1985. Another new genus, *Protoparamisophria*, is closely related to *Paramisophria* Scott, 1897, but exhibits more plesiomorphic states in the female genital system and appendages. Two new species of the genera *Paraugaptiloides* Ohtsuka, Boxshall and Roe, 1994 and *Sarsarietellus* Campaner, 1984 are the second and the third species, respectively, for these genera. This discovery enhances the validity of these rare genera, and sheds light on the geological history of the Sulu Sea and the evolution of the Arietellidae within it.

Keywords: *Arietellidae, Calanoida, Copepoda, deep-sea hyperbenthic, endemism, Sulu Sea*

Introduction

Deep-sea hyperbenthic copepods have been poorly understood in comparison with pelagic forms, partly due to sampling difficulties. The systematics and ecology of these copepods have been studied using specially designed gears or deep-sea research vessels (Bradford 1969; Grice and Hulsemann 1970; Grice 1972; Wishner 1980; Fleminger 1983; Alvarez 1985; Wishner and Gowing 1987; Ohtsuka et al. 1991, 1994, 1998, 2003; Nishida et al. 1999; Ferrari and Markhaseva 2000; Ohtsuka and Boxshall 2004). Considerable attention has been paid to these hyperbenthic copepods with regard to the evolution of copepods, because deep hyperbenthic waters have been suggested to have played an important role as

a refuge from anoxia in the mesopelagic zone during the Jurassic and Cretaceous (cf. Bradford-Grieve 2002).

During a research cruise of the RV *Hakuho-maru* (The Ocean Research Institute, University of Tokyo) to the Sulu Sea in November and December 2002, deep-sea hyperbenthic copepods were intensively collected with beam trawls and baited traps. Hyperbenthic copepods representing the families Aetideidae, Arietellidae, Phaennidae, Scolecitrichidae, and Tharybidae of the order Calanoida, and the family Misophriidae of the Misophrioida were successfully collected. The present paper describes two new genera, and four new species of rare genera of the primitive calanoid family Arietellidae. This discovery enhances the taxonomic validity of these genera, and sheds light on the evolution of the Arietellidae.

Materials and methods

Copepods were collected with an ORE beam trawl (3 m span) (OBT) at a station in the central Sulu Sea on 6–7 December 2002. A NORPAC net (mesh size 0.33 mm) was attached to the mouth of the OBT, set at a height of 40 cm above the bottom. Sediment was repeatedly stirred in sea-water, and the supernatant was filtered with a small plankton net (mesh size 0.1 mm). Two new hyperbenthic arietellids were captured at the same station, when an Isaac-Kidd midwater trawl (IKMT) (mesh size 1 mm) accidentally touched the bottom. Copepods were fixed in 10% neutralized formalin/sea-water immediately after capture, and then transferred to 70% ethanol. Specimens were partly dissected under a binocular microscope, and were mounted on glass slides in the medium CMC-10 (Masters Company, Inc.). Illustrations were made using a differential interference contrast microscope (Nikon Optiphoto). Type specimens are deposited in the Natural History Museum, London (NHM). Terminology follows Huys and Boxshall (1991). Setae on the terminal endopodal segment of the maxilliped are identified on the basis of Ohtsuka et al. (1994).

Phylogenetic relationships between arietellids including the two new genera described herein were analysed using PAUP 3.0s (Swofford 1993), following Ohtsuka et al. (1994). The options used in this analysis were "Branch and Bound" and "Irreversible Up".

Systematics

Family ARIETELLIDAE Sars, 1902
Genus *Metacalanalis* n. gen.

Diagnosis

Female. Body compact. Prosome plump, about 2.6 times as long as urosome; cephalosome asymmetrical anteriorly, with curved rostrum; prosomal ends almost symmetrical, without dorsolateral and ventrolateral processes. Urosome with genital double-somite wider than long; paired gonopores and copulatory pores located at mid-length of genital double-somite; each copulatory pore slit-like, located at inner corner of gonopore; seminal receptacles located ventrally, massive; anal operculum lacking; caudal rami symmetrical, nearly as long as wide.

Antennules asymmetrical, 21-segmented, left longer than right and reaching to pediger 3; posterior margin lacking long setules; first (I–IV) and last (XXIV–XXVIII) segments compound; segments II, IV, VI, VIII, and X lacking aesthetasc. Antenna with indistinctly three-segmented endopod; first endopodal segment bearing one inner seta, second and third segments bearing three and five setae, respectively; exopod indistinctly 10-segmented. Mandibular gnathobase without patch of long setules; four teeth present, dorsalmost tricuspid at tip; endopod represented by rudimentary segment with two unequal setae terminally; seta on first to fifth exopodal segments not reduced. Maxillule with one short and four long spines on praecoxal arthrite; coxal endite bearing single seta; coxal epipodite with six setae; endopod one-segmented, with two setae terminally. Maxilla with two setae and one vestigial element on first praecoxal endite; basal spine with short row of three or four minute spinules at mid-length. Maxilliped with innermost seta on fourth and fifth exopodal segments not reduced; setae *a* and *b* (see Ohtsuka et al., 1994) on sixth segment not reduced.

Leg 1 with third exopodal segment bearing only one outer spine. Some elements of legs 1–4 asymmetrical. Leg 5 symmetrical, with coxae and intercoxal sclerite separate; endopod lacking; exopod unisegmented, with two lateral and two terminal spines.

Male. Unknown.

Remarks

The new genus is similar to the genera *Metacalanus* Cleve, 1901 and *Pilarella* Alvarez, 1985, and has mixed features of these two genera. The discriminative features between these are as follows (cf. Alvarez 1985; Ohtsuka et al. 1994) (*Pilarella* versus *Metacalanus*): (1) location and configuration of female gonopores and copulatory pores (medially located and paired versus posteriorly and paired or unpaired); (2) relative length of caudal rami (about five times longer than wide versus at most twice); (3) segmentation and relative length of antennules (21-segmented in both, left antennule reaching beyond urosomal end versus 16- or 18-segmented in left and 18- or 20-segmented in right, left antennule not reaching prosomal end); (4) setal number on the second exopodal segments of antenna (three medial setae on the second segment versus only two); (5) armature of the praecoxal arthrite, coxal endite and endopod of maxillule (formula with 6, 1, 2 versus 0–2, 0–1, 0–1); (6) armature and ornamentation of elements on the maxillary endites (two distinct setae + one rudimentary element on the first praecoxal endite versus one + one). The new genus exhibits symplesiomorphies in (1), (3), (4), (5), and (6) with *Pilarella*. On the other hand, the relative shortness of the caudal rami and the antennules of the new genus are reminiscent of *Metacalanus*. The fifth leg of female *Metacalanalis* exhibits a more plesiomorphic state than those of *Metacalanus* and *Pilarella*, and is rather similar to that of another closely related genus *Paramisophria* Scott, 1897, in particular *P. reducta* Ohtsuka, Fosshagen and Iliffe, 1993 except for the absence of endopod.

Metacalanalis is distinguishable from *Metacalanus* and *Pilarella* by the combination of the following features: (1) caudal rami about 1.2 times as long as wide; (2) left antennule reaching at most to the posterior margin of pediger 3; (3) antenna showing the most primitive condition in the family Arietellidae, with an indistinctly three-segmented endopod and an indistinctly 10-segmented exopod with setal formula 0, 0, 1, 1, 1, 1, 1, 1, 0, 2; (4) praecoxal arthrite of the maxillule with one short and four long spines; (5) coxal epipodite of the maxillule with six setae; (6) basal spine of the maxilla with a short row of

minute spinules medially; (7) fifth leg of the female with a unisegmented exopod bearing two lateral and two terminal spines.

The antenna of *Metacalanalis* exhibits a primitive condition, with an indistinctly three-segmented endopod and an indistinctly 10-segmented exopod. The endopod has a suture between the second and third segments clearly visible. Only the most primitive calanoid family Pseudocyclopidae (monotypic, *Pseudocyclops* Brady, 1872) is hitherto known to bear a distinctly three-segmented antennary endopod (Huys and Boxshall 1991). A 10-segmented exopod is also the most primitive condition in copepods (Huys and Boxshall 1991).

Asymmetry of legs 1–3 is unique to the new genus, although the asymmetrical antennules are common in the hyperbenthic arietellid genera *Metacalanus* and *Paramisophria* (cf. Ohtsuka et al. 1994). These are either an adaptation to its hyperbenthic life or aberrant (see Remarks for the new species).

Type species. Metacalanalis hakuhoae n. sp. (monotypic).

Etymology

The generic name is derived from the closely related genus *Metacalanus* Cleve, 1901. Gender masculine.

Metacalanalis hakuhoae n. sp.
(Figures 1–3)

Material examined

Adult female (holotype), collected from the central Sulu Sea (08°52.66′N, 120°25.28′E~08°53.97′N, 120°25.50′E; depth 2430–2450 m) with NORPAC net set on OBT; 7 December 2002; appendages dissected on glass slides, and body proper in vial; NHM 2005.157. Copepodid V female (paratype), damaged, whole specimen; NHM 2005.158.

Description

Female (holotype). Body (Figure 1A, B) 1.55 mm, compact, plump; prosome 2.6 times as long as urosome. Cephalosome slightly asymmetrical in dorsal view; rostrum (Figure 1B, C) strongly curved, with pair of thick filaments; ventrolateral corners expanded posteriorly to cover anterior margin of pediger 1. Pedigers 1–3 with ventrolateral corners produced posteriorly; prosomal posterior ends almost symmetrical, each produced into round lobe reaching midway along genital double-somite (Figure 1D). Urosome four-segmented; genital double-somite wider than long, with ventral transverse ridge midway; genital system (Figure 1E) asymmetrical, with right seminal receptacle larger than left; paired gonopores and copulatory pores located at mid-length; each copulatory pore slit-like, located at inner corner of gonopore, connected to curved, thick copulatory pore; anal somite relatively long; caudal rami symmetrical, lacking seta I; seta VII located at base of seta VI, bent at mid-length. Two large, mature eggs visible within prosome (Figure 1B).

Antennules considerably asymmetrical, with left ca 1.5 times longer than right. Left antennule (Figure 1F, G) 21-segmented; fusion pattern and armature as follows: I–IV=9+2ae, V=2+ae, VI=2, VII=2+ae, VIII=2, IX=2+ae, X=2 (one spiniform seta),
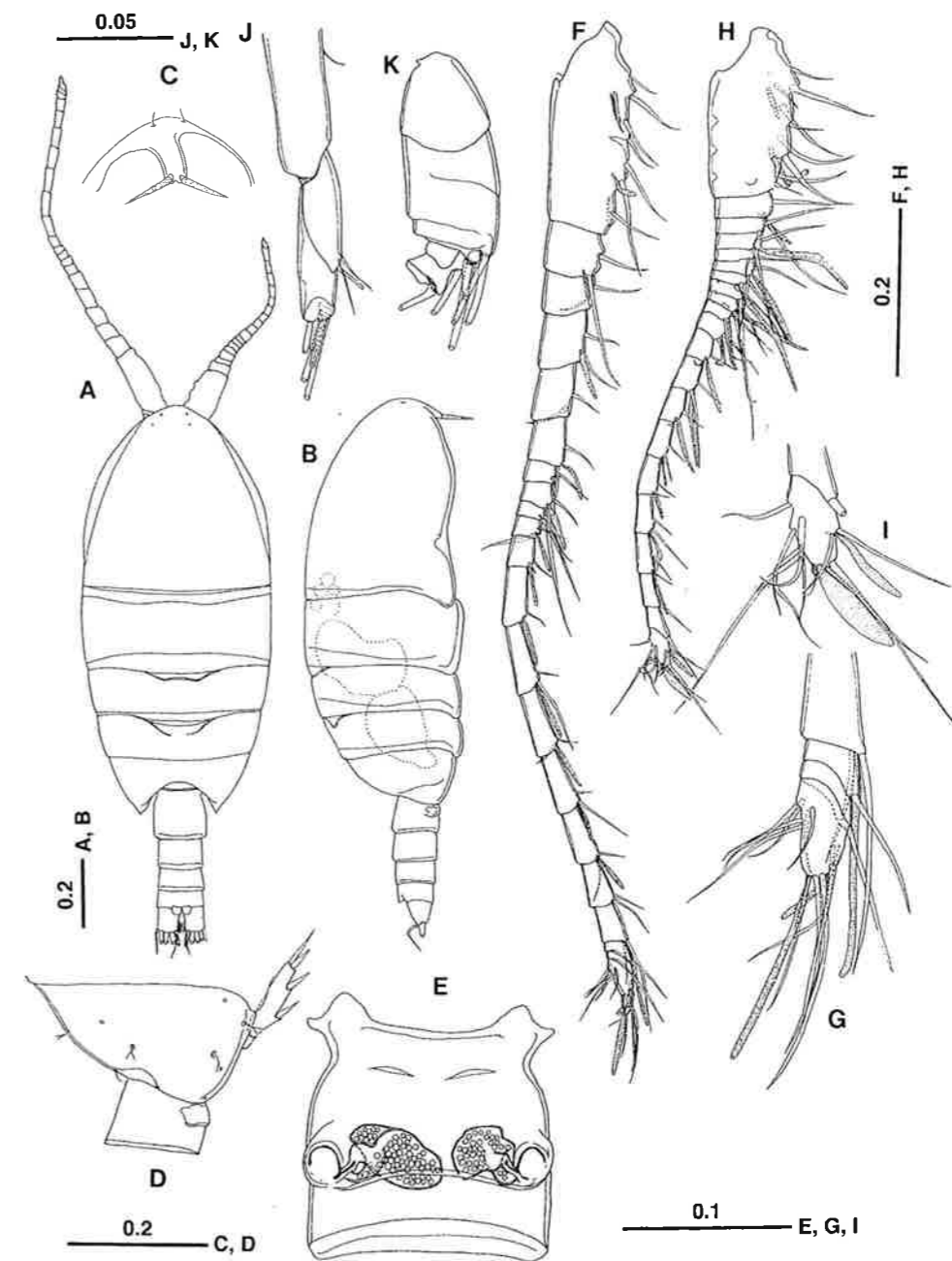

Figure 1. *Metacalanalis hakuhoae* n. gen., n. sp., female (holotype). (A) Habitus, dorsal; (B) habitus, lateral; (C) rostrum, ventral; (D) last compound pedigerous somite and genital double-somite, lateral; (E) genital double-somite, ventral; (F) left antennule; (G) terminal segments of left antennule; (H) right antennule; (I) terminal segment of right antennule; (J) terminal segments of antennary endopod; (K) antennary exopod, terminal segments missing. Scale bars in mm.
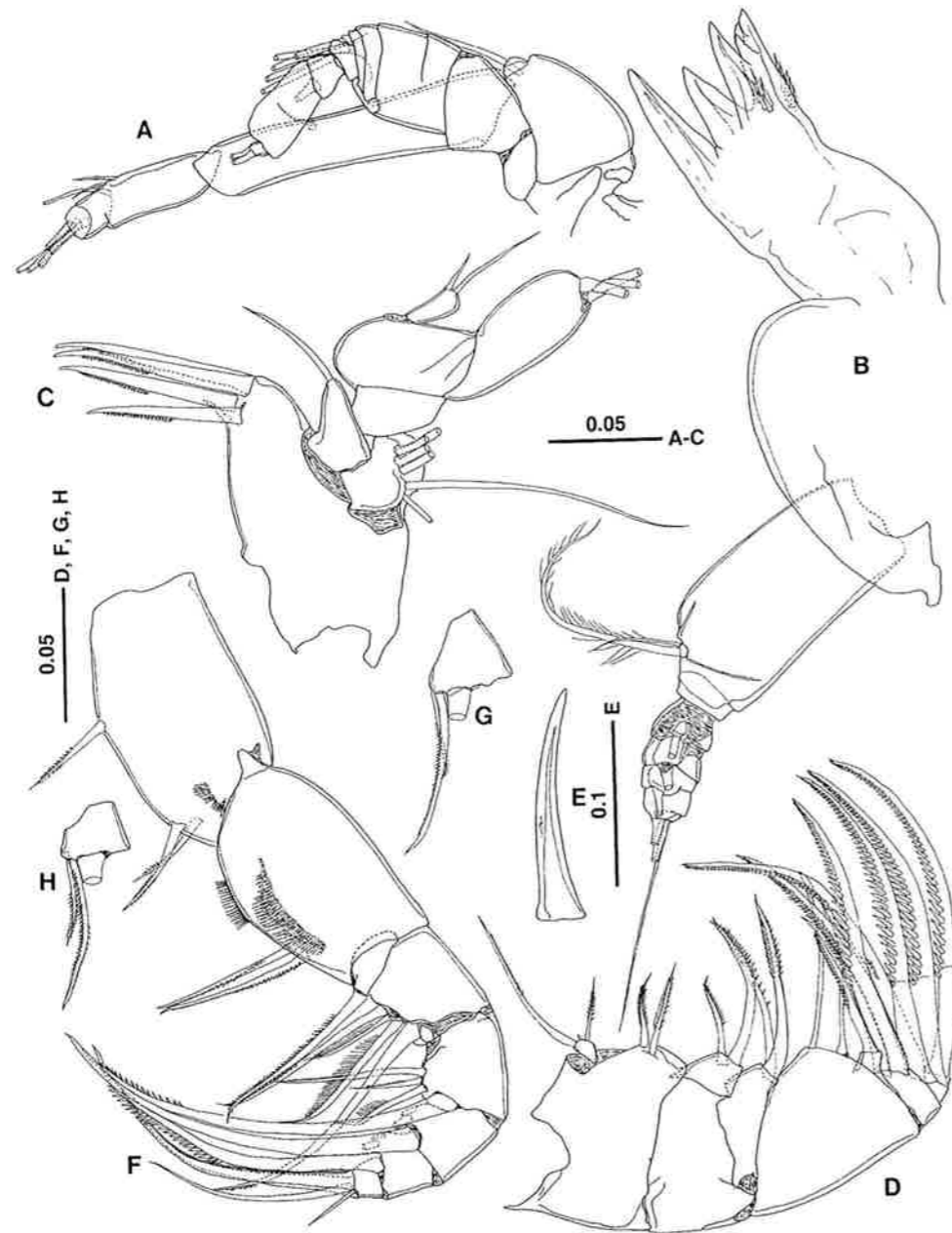
Figure 2. *Metacalanalis hakuhoae* n. gen., n. sp., female (holotype). (A) Antenna; (B) mandible; (C) maxillule; (D) maxilla; (E) basal spine of maxilla; (F) maxilliped; (G) fourth endopodal segment of maxilliped, largest seta omitted; (H) fifth endopodal segment of maxilliped, largest seta omitted. Scale bars in mm.

XI=2+ae, XII=2+ae (vestigial), XIII=2+ae, XIV=2 (one spiniform seta)+ae, XV=2 (one missing)+ae, XVI=2+ae, XVII=2+ae, XVIII=2+ae, XIX=2+ae, XX=2+ae, XXI=2+ae, XXII=1, XXIII=1, XXIV–XXVIII=12+2ae. Right antennule (Figure 1H, I) with same fusion pattern and armature as left except for distinct aesthetasc on segment XII. Antenna (Figures 1J, K, 2A) with unarmed coxa; basis with inner seta half as long as exopod;
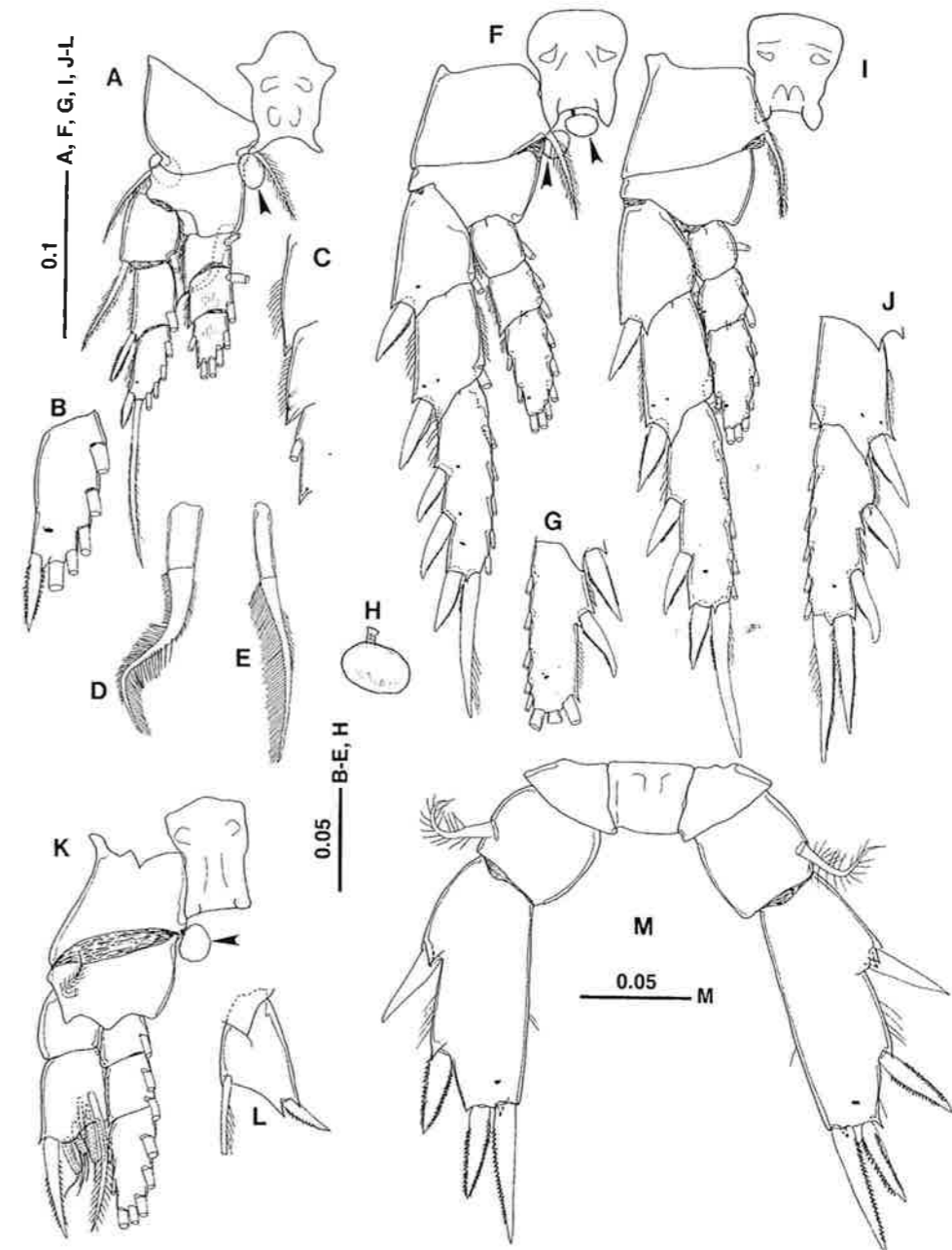

Figure 3. *Metacalanalis hakuhoae* n. gen., n. sp., female (holotype). (A) Leg 1, posterior; (B) third exopodal segment of leg 1, posterior; (C) outer lateral margin of endopod of leg 1, posterior; (D) inner basal seta of left leg 1; (E) inner basal seta of right leg 1; (F) right leg 2, anterior; (G) third exopodal segment of left leg 2; (H) phoront of apostome ciliates (?) on intercoxal sclerite of leg 2; (I) right leg 3, anterior; (J) second and third exopodal segments of left leg 3, anterior; (K) left leg 4, posterior; (L) first exopodal segment of right leg 4, posterior, second and third segments missing; (M) leg 5, posterior. Phoronts of apostome ciliates (?) indicated by arrowheads. Scale bars in mm.

endopod indistinctly three-segmented, first segment with seta at two-thirds of inner margin; second and third segments almost coalescent with suture clearly visible; second segment with three unequal setae terminally; third segment with five distal setae; exopod indistinctly 10-segmented, with setal formula of 0, 0, 1, 1, 1, 1, 1, 1, 0, 2; terminal segment lacking vestigial element as seen in *Metacalanus* (cf. Ohtsuka et al. 1994). Mandible (Figure 2B) without patch of long setules on gnathobase; cutting edge with two patches of minute spinules and four teeth, dorsalmost of which tricuspid; endopod rudimentary, one-segmented, with two plumose setae terminally; exopod five-segmented, with setal formula 1, 1, 1, 1, 2; terminal setae well developed. Maxillule (Figure 2C) with one naked short, and four serrate long spines on inner distal corner of praecoxal arthrite; coxal endite with moderately developed, serrate seta; coxal epipodite bearing six setae; basal seta absent; endopod one-segmented, bulbous, with two unequal setae; exopod one-segmented, lamellar, bearing three terminal setae. Maxilla (Figure 2D, E) stout; first praecoxal endite with two unequal spinulose setae and vestigial element; second praecoxal to second coxal endites each bearing two spinulose setae; basal spine (Figure 2E) highly sclerotized, with short row of three or four spinules at mid-length; endopod four-segmented, with setal formula 1, 3, 2, 2; setae bearing longitudinal row of large spinules. Maxilliped (Figure 2F– H) with syncoxa bearing one middle and two subterminal serrate setae and terminal patch of short spinules; basis as long as syncoxa, with two serrate medial setae, row of setules along proximal half of inner margin, and longitudinal patch of spinules; first endopodal segment almost separate from basis, with serrate seta; second to fifth endopodal segments bearing four, four, three, and three setae, respectively; sixth endopodal segment with setae *a* and *b* not reduced.

Seta and spine formula of legs 1–4 (Figure 3A–G, I–L) shown in Table I. Both rami of legs 1–3 and endopod of leg 4 three-segmented (exopods of leg 4 broken or aberrant). Asymmetry in legs 1–4. Leg 1 (Figure 3A–E) with inner basal setae asymmetrical, left (Figure 3D) thicker than right (Figure 3E); outer distal corners of three endopodal segments acutely pointed (Figure 3C). Leg 2 (Figure 3F, G) with outer spines on third exopodal segments asymmetrical in number, size and location. Leg 3 (Figure 3I, J) with outer spines on second and third exopodal segments asymmetrical in length and shape. Left leg 4 (Figure 3K) with aberrant exopod, with first segment unarmed and second bearing outer long spine and six modified setae. Terminal exopodal segments of right leg 4 missing (Figure 3L).

Leg 5 (Figure 3M) nearly symmetrical; coxae and intercoxal sclerite separate; basis bearing thick, subterminal seta on posterior surface; endopod lacking; exopod one-segmented, with two lateral and two terminal spines; acute process present at base of inner terminal spine; outer terminal process more acutely pointed in right leg than in left.

Table I. Spine and seta formula of legs 1–4 of *Metacalanalis hakohoae* n. gen., n. sp.

	Coxa	Basis	Exopod	Endopod
Leg1	0–1	1–1	I–1;I–1;I,1,4	0–1;0–2;1,2,2
Leg2	0–1	0–0	I–1;I–1;II,I,5	0–1;0–2;2,2,4
Leg3	0–1	0–0	I–1;I–1;II,I,5	0–1;0–2;2,2,4
Leg4	0–0	1–0	I–1;–; –	0–1;0–2;2,2,3

Some elements on distal exopodal segment of left leg 2 missing, but identified as spines based on their sclerotized bases. Distal two exopodal segments of leg 4 missing (–).

Male. Unknown.

Remarks

Asymmetry of legs 1–3 (maybe, leg 4 also) may be related to an as yet unknown swimming behaviour of the new genus as observed in *Paramisophria* spp. that swim with the left lateral side parallel to the bottom and the left antennule extended anteriorly (Fosshagen 1968; Ohtsuka and Mitsuzumi 1990). Bowman and González (1961) insisted that hyperbenthic calanoid copepods generally bear stouter outer spines on the exopods of legs in comparison with pelagic ones. Hence the longer spines on the second and third exopodal segments of left legs 2–4 suggest a possible peculiar swimming behaviour as found in *Paramisophria* spp. The inner basal seta of leg 1 is considered to play a role in grooming (Vaupel Klein 1972). The thicker inner basal seta of left leg 1 of the new species is likely to be adaptive for grooming the longer left antennule.

Gut content analysis revealed that the new species fed upon copepods. Stalked cysts on legs (see Figure 3A, F, H, K) are possibly assignable to phoronts of apostome ciliates (cf. Grimes and Bradbury 1992; Ohtsuka et al. 2004).

Etymology

The new specific name, *hakuhoae*, refers to the RV *Hokuho-maru*, University of Tokyo, that carried out the survey in the Sulu Sea in 2002.

Genus *Protoparamisophria* n. gen.

Diagnosis

Female. Body compact. Prosome plump, about 2.6 times as long as urosome; prosomal ends almost symmetrical, with paired dorsolateral processes and lateral round lobes. Urosome with genital double-somite longer than wide; paired gonopores located anteriorly; paired copulatory pores located midway on ventral surface; seminal receptacles asymmetrical, tube-like; anal operculum lacking; caudal rami symmetrical, longer than wide.

Antennules asymmetrical, 22-segmented, left longer than right, and reaching beyond cephalosome; first (I–III) to eighth (X) segments with row of long setules along posterior margin; segments I–III and IV separate; segments II and IV of right antennule, and I, II, and IV of left antennule lacking aesthetasc. Antenna with two-segmented endopod; first endopodal segment bearing one inner seta, and second segment with three subterminal and six terminal setae; exopod indistinctly seven-segmented; terminal segment with one vestigial and two distinct setae. Mandibular gnathobase without patch of long setules; three teeth present, dorsalmost bicuspid; endopod represented by one rudimentary segment with two unequal setae terminally; seta on first to fifth exopodal segments not reduced. Maxillule with one process and five spines on praecoxal arthrite; coxal endite bearing single seta; coxal epipodite with eight setae; rudimentary basal seta present; endopod one-segmented, with three setae terminally. Maxilla with two setae and one vestigial element on first praecoxal endite; basal spine naked. Maxilliped with innermost seta on fourth and fifth exopodal segments not reduced; setae *a* and *b* (see Ohtsuka et al. 1994) on sixth segment not reduced.

Leg 1 with third exopodal segment bearing two outer spines. Leg 5 nearly symmetrical, with coxae and intercoxal sclerite partly fused; endopod represented by acutely pointed process bearing two plumose setae; exopod indistinctly three-segmented with suture subtly

visible; first and second segments each with one outer spine; terminal segment bearing one spiniform seta and one subterminal and two terminal spines.

Male. Unknown.

Remarks

The new genus is generally similar to *Paramisophria*, but exhibits more plesiomorphic states both in the female genital system and in some appendages. In the new genus, paired copulatory pores open at mid-length on the ventral side of the genital double-somite, while in *Paramisophria* a single copulatory pore is located midway or on either the left or right side (cf. Ohtsuka and Mitsuzumi 1990; Ohtsuka et al. 1991, 1993, 1994; Heinrich 1996). The new genus displays paired, elongate seminal receptacles, each located between the corresponding copulatory pore and gonopore, with a short copulatory duct. In contrast, in some species of *Paramisophria*, the seminal receptacle is near the gonopore, with a relatively long, and in some cases, a highly curved copulatory duct (cf. Ohtsuka and Mitsuzumi 1990; Ohtsuka et al. 1993, 1994). These characteristics of the new genus seem to be relatively plesiomorphic with respect to the hypothetical calanoid ancestor as proposed by Huys and Boxshall (1991).

The exopod of the female fifth leg of the new genus displays the most primitive state in the family Arietellidae: indistinctly three-segmented; terminal segment with one outer, one subterminal and two terminal elements, all of which are separate at base from the segment. In some species of *Paramisophria* the exopod is indistinctly three-segmented, but the number of elements on the terminal segment is at most three elements and one process (in *P. japonica* Ohtsuka, Fosshagen and Go, 1991). In this case, the outer terminal spine of the new genus seems to be homologous to the terminal process of *P. japonica*. The new genus also has the following plesiomorphies, although some species of *Paramisophria* share some of them: (1) five spines and one process on the praecoxal arthrite of the maxillule; (2) the presence of a distinct seta on the coxal endite of the maxillule; (3) three setae on the maxillulary endopod; (4) two setae and one vestigial element on the first praecoxal endite of the maxilla; (5) separation of coxae and intercoxal sclerite in female leg 5; (6) two setae on the endopod of female leg 5.

Type species. *Protoparamisophria biforaminis* n. sp. (monotypic).

Etymology

The new generic name, *Protoparamisophria*, is derived from the Greek *proto*, meaning primitive, plus the closely related genus *Paramisophria*. Gender feminine.

Protoparamisophria biforaminis n. sp.
(Figures 4–6)

Material examined

Adult female (holotype), collected from the central Sulu Sea (08°57.31′N, 120°11.31′E~ 09°03.82′N, 120°12.35′E; wire out 3600 m; depth 0~1516 m) with IKMT; 6–7 December 2002; appendages mounted on glass slides, and body proper in vial; NHM 2005.159.
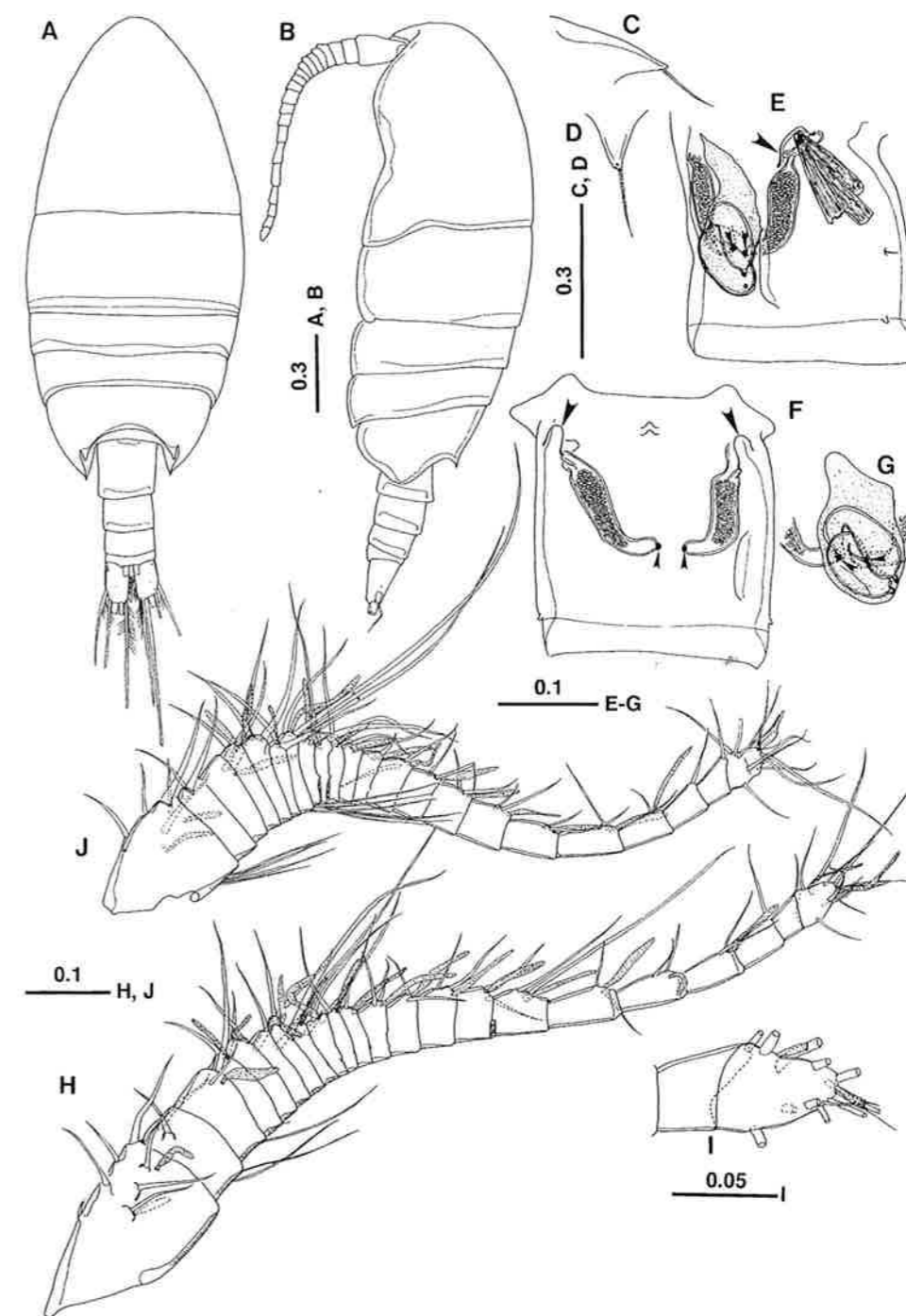
Figure 4. *Protoparamisophria biforaminis* n. gen., n. sp., female (holotype). (A) Habitus, dorsal; (B) habitus, lateral; (C) rostrum, lateral; (D) rostrum, anterior; (E) genital double-somite, left lateral, gonopore and copulatory pore indicated by large and small arrowhead, respectively; (F) genital double-somite, ventral, spermatophore remnant omitted, symbols same as in (E); (G) spermatophore remnant on genital double-somite; (H) left antennule; (I) terminal segments of left antennule; (J) right antennule. Scale bars in mm.
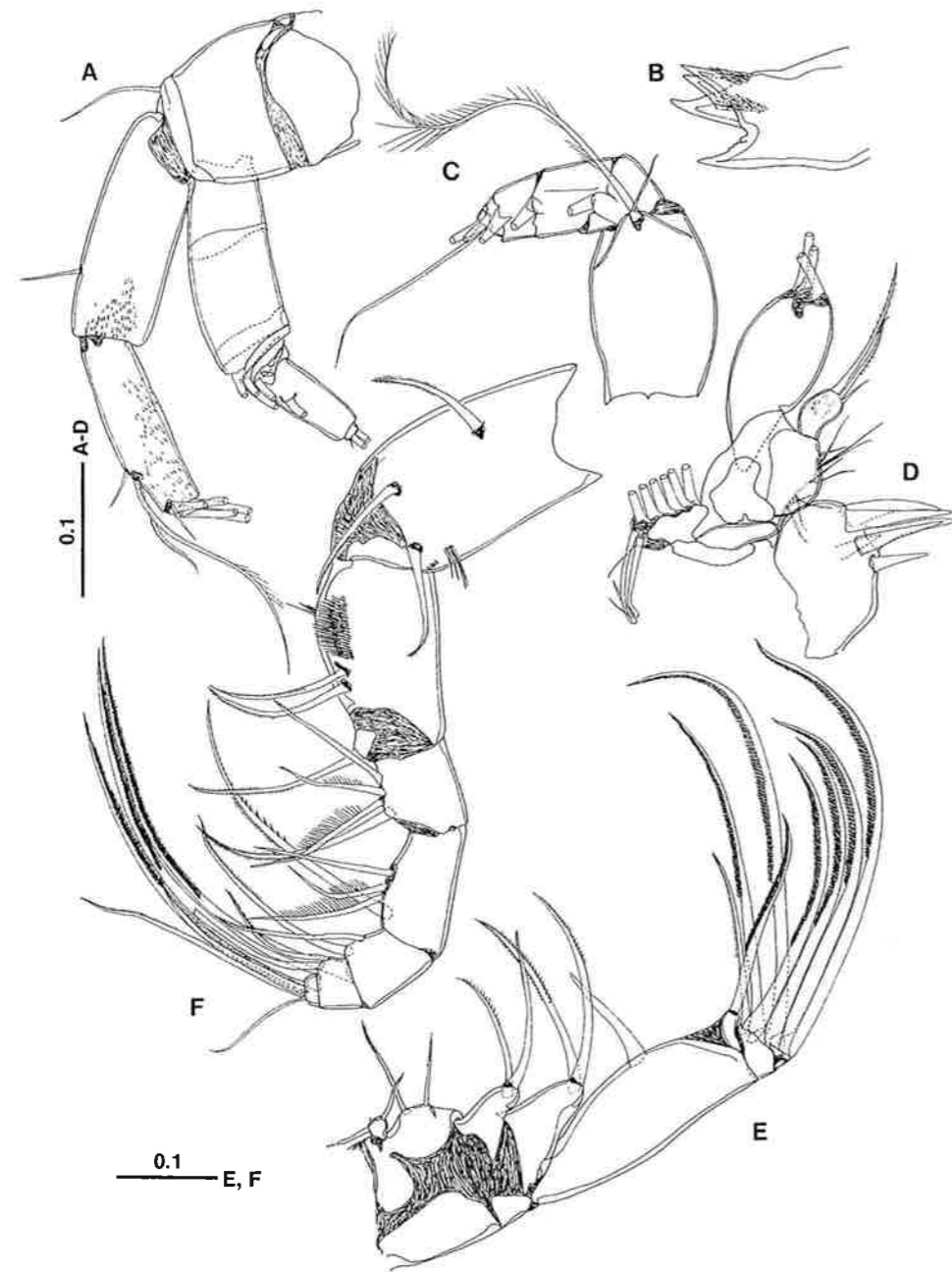
Figure 5. *Protoparamisophria biforaminis* n. gen., n. sp., female (holotype). (A) Antenna; (B) mandibular cutting edge; (C) mandibular palp; (D) maxillule, slightly stretched; (E) maxilla; (F) maxilliped. Scale bars in mm.

Description

Female (holotype). Body (Figure 4A, B) 2.28 mm, compact, plump; prosome about 2.6 times as long as urosome. Rostrum (Figure 4C, D) narrowly pointed with two fine filaments (one missing in Figure 4C, D). Pediger 1 with ventrolateral corner produced
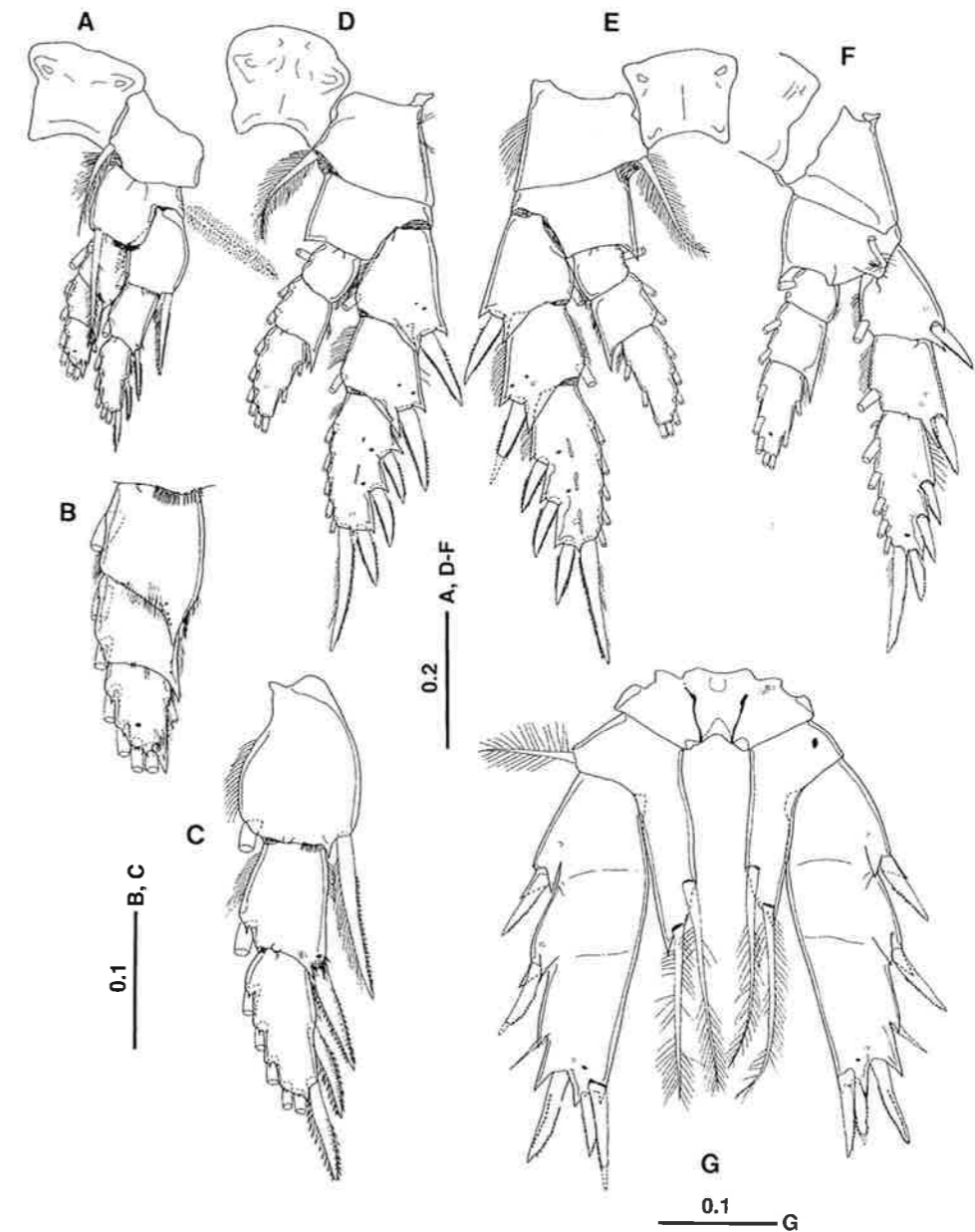

Figure 6. *Protoparamisophria biforaminis* n. gen., n. sp., female (holotype). (A) Leg 1, anterior; (B) endopod of leg 1, anterior; (C) exopod of leg 1, anterior; (D) leg 2, anterior; (E) leg 3, anterior; (F) leg 4, posterior; (G) leg 5, posterior. Scale bars in mm.

posteriorly into rounded lobe, while pedigers 2 and 3 acutely pointed; prosomal posterior ends almost symmetrical, each produced into round lateral lobe reaching beyond half of genital double-somite and dorsolateral process acutely pointed. Urosome four-segmented; genital double-somite (Figure 4E, F) asymmetrical, with longitudinal ridge on left side and paired, small papillae dorsolaterally; ventral surface with paired gonopores anteriorly

(Figure 4E, F; indicated by large arrowheads) and paired copulatory pores (indicated by small arrowheads) at mid-length; seminal receptacles asymmetrically arranged, packed with sperm; spermatophore remnant (Figure 4G) tinged brownish, covering copulatory pores, and having paired, bulbous, well-chitinized ducts, each connected to copulatory pore; caudal rami symmetrical, fringed with long setules along inner margin; caudal seta I not visible.

Antennules (Figure 4H–J) asymmetrical, with left about 1.3 times as long as right; first (I–III) to eighth (X) segments fringed with long setules along posterior margin (only scars remaining on some segments in Figure 4H, I). Left antennule (Figure 4H, I) 22-segmented; fusion pattern and armature as follows: I–III=7+2ae (ae missing), IV=2, V=2+ae, VI=2+ae, VII=2+ae, VIII=2+ae, IX=2+ae, X=2 (one spiniform seta)+ae, XI=2+ae, XII=2+ae, XIII=2+ae, XIV=2 (one spiniform seta)+ae, XV=2+ae, XVI=2+ae, XVII=2+ae, XVIII=2+ae, XIX=2+ae, XX=2+ae, XXI=2+ae, XXII=1, XXIII=1, XXIV–XXVIII=12+2ae. Right antennule (Figure 4J) with same fusion pattern and armature as left. Antenna (Figure 5A) bearing basis with inner seta at inner distal corner; endopod two-segmented, first segment with seta at distal one-third length and patch of minute spinules distally; second segment with one naked, one serrate and one plumose setae subterminally, one short and five long setae terminally, and patch of minute spinules along outer margin; exopod indistinctly seven-segmented, with setal formula 0, 0, 1, 1, 2, 1, 3 (one vestigial). Mandible (Figure 5B, C) without patch of long setules on gnathobase; cutting edge with two patches of minute spinules and three teeth, dorsalmost bicuspid; endopod rudimentary, one-segmented, with one naked, short and one plumose, long setae terminally; exopod five-segmented, with setal formula 1, 1, 1, 1, 2; terminal setae well developed. Maxillule (Figure 5D) with five naked spines and one process on praecoxal arthrite; coxal endite with short seta; coxal epipodite bearing eight setae; basal endite with minute seta; endopod one-segmented, bulbous, with three unequal setae, gradually increasing in size distally; exopod one-segmented, lamellar, bearing three terminal setae. Maxilla (Figure 5E) stout; first praecoxal endite with two unequal spinulose setae and vestigial element; second praecoxal to second coxal endites each bearing two spinulose setae; basis relatively elongate; basal spine relatively long and naked; endopod four-segmented, with setal formula 1, 3, 2, 2, all bearing longitudinal row of fine spinules. Maxilliped (Figure 5F) with syncoxa bearing one middle and two subterminal serrate setae, and terminal patch of short spinules and subterminal patch of long ones; basis shorter than syncoxa, with two subterminal serrate setae, patch of long setules midway, and longitudinal patch of spinules; first endopodal segment almost separate from basis, with serrate seta; second to fifth endopodal segments bearing four, four, three, and three setae, respectively; sixth endopodal segment with setae a and b not reduced.

Seta and spine formula of legs 1–4 (Figure 6A–F) shown in Table II. Legs 1–4 with three-segmented rami. Leg 1 (Figure 6A–C) with basis bearing row of spinules along endopodal base; all endopodal segments with outer distal corners acutely pointed, and with marginal row of setules (Figure 6A, B); first exopodal segment with row of minute spinules at distal margin; outer spines on all exopodal segments strongly serrated (Figure 6C). Inner distal corner of basis of legs 2–4 (Figure 6D–F) acutely pointed, but most sharply produced in leg 4; outer distal corner of second endopodal segments of legs 2–4 produced distally into sharply pointed process reaching beyond base of proximal outer seta on third endopodal segment.

Leg 5 (Figure 6G) slightly asymmetrical; coxae and intercoxal sclerite only partly coalescent; basis bearing thick, plumose seta at outer distal corner (left seta missing);

Table II. Spine and seta formula of legs 1–4 of *Protoparamisophria biforaminis* n. gen., n. sp.

	Coxa	Basis	Exopod	Endopod
Leg1	0–1	1–1	I–1;I–1;II,1,4	0–1;0–2;1,2,2
Leg2	0–1	0–0	I–1;I–1;III,I,5	0–1;0–2;2,2,4
Leg3	0–1	0–0	I–1;I–1;III,I,5	0–1;0–2;2,2,4
Leg4	0–0	1–0	I–1;I–1;I,III,5	0–1;0–2;2,2,3

endopod represented by acutely pointed process with one terminal and one subterminal plumose setae; exopod indistinctly three-segmented, with suture visible on both sides; first and second exopodal segments each bearing serrate spine, near base of which two processes present; third exopodal segment with proximal spiniform seta, subterminal serrate spine, and two terminal serrate spines.

Male. Unknown.

Remarks

The only specimen was collected with an IKMT originally deployed for collection of deep-water plankton and micronekton. However, the net must have accidentally touched the sea-bottom, because some sediment was found in the cod end after recovery. The asymmetrical antennules and stout outer spines on the legs of this new species strongly suggest that it is a truly hyperbenthic calanoid (cf. Bradford-Grieve 2002).

Etymology

The new specific name, *biforaminis* (Latin *bi* meaning two; Latin *foraminis* pore-bearing) alludes to the presence of paired copulatory pores on the female genital double-somite of the new taxon.

Genus *Paraugaptiloides* Ohtsuka, Boxshall and Roe, 1994

Diagnosis

Emended part only; see Ohtsuka et al. 1994. Male left geniculate antennule fringed with long setules posteriorly on compound segments I–IV only or segments I–IV to V; segment I with one or two setae. Second endopodal segment of antenna with two or three inner setae. Mandibular endopod one-segmented with two terminal setae of unequal length, or absent. Leg 4 with or without vestigial element on inner distal corner of coxa. Male fifth legs with basis and coxa of right leg separate or incompletely fused; right endopod unisegmented, rudimentary or well-developed; second exopodal segment of right leg expanded inwards or extremely elongated, third segment triangular, tapering distally, or lamellar; left endopod two-segmented, with second segment originating from inner base of first segment; second exopodal segment of left leg expanded inwards or outwards, third segment with two or three heavily chitinized, long processes.

Remarks

The monotypic genus *Paraugaptiloides* was established to accommodate *Paraugaptilus magnus* Bradford, 1974 by Ohtsuka et al. (1994). This species was first collected off New

Zealand (1697 m) (Bradford 1974), and subsequently from the south-western Indian Ocean (1060–1070 m) (Heinrich 1993). The genus is considered to be deep-sea hyperbenthic (Bradford 1974; Heinrich 1993; present study). The second congener described below was discovered in the Sulu Sea, which confirms the validity of the genus. Although known only by the male, it is readily distinguishable from other arietellid genera by a combination of the following characters: (1) presence of a large cuticular process on the left antennulary compound segment XXIV–XXV; (2) lack of a seta on the first endopodal segment of the antenna; (3) two or three inner setae on the second endopodal segment of the antenna; (4) outer seta on the fifth exopodal segment of the mandible, relatively long; (5) maxillule with one basal and two endopodal setae; (6) basal spine of the maxilla furnished with a spinular row; (7) innermost setae on the fourth and fifth endopodal segments of the maxilliped not vestigial; (8) outermost seta on the sixth endopodal segment of the maxilliped vestigial; (9) left and right endopods of the fifth leg two- and one-segmented, respectively. However, the new species described below has different armature on the antenna, mandible and leg 4 from those of *P. magnus*, and necessitates an emendation of the generic diagnosis.

Although the fifth legs of the males appear to differ greatly in these two species, some homologous structures can be clearly traced on the basis of their number and position; namely the second endopodal segment of the left leg originates from the inner proximal part of the first segment; the third exopodal segment of the left leg bears four elements; the outer terminal corner of the second exopodal segment of the right leg bears a patch of fine setules and a triangular or round process with a minute spinule terminally. These differences in the fifth legs seem to be important at the specific level.

The genus seems to be associated with the sea-bottom (Bradford 1974; Heinrich 1993; present study), although it was previously regarded as pelagic (Ohtsuka et al. 1994).

Paraugaptiloides mirandipes n. sp.
(Figures 7–10)

Material examined

Adult male (holotype), collected from the central Sulu Sea (08°52.66′N, 120°25.28′E~08°53.97′N, 120°25.50′E; depth 2430–2450 m) with NORPAC net set on OBT; 7 December 2002; appendages mounted on glass slides, and body proper in vial; NHM 2005.160.

Description

Male (holotype). Body (Figure 7A, B) 5.26 mm, relatively weakly chitinized except for leg 5; prosome approximately 2.3 times as long as urosome. Cephalosome produced posterolaterally to cover anterior part of first pediger (Figure 7B); rostrum (Figure 7C) produced posteriorly, with pair of long filaments (one accidentally lost during dissection). Second and third pedigers produced mediodorsally; fifth pediger produced posteriorly at each side into irregular processes furnished with glandular openings and hair-like sensillae; posterior margin of processes fringed with fine setules (Figure 7A, B, D–G); large spermatophore visible, extending from first pediger to genital somite (Figure 7A). Urosome five-segmented; genital somite with gonopore opening at right posterolateral corner (Figure 7A, B); second and third urosomites almost equal in length; anal somite relatively
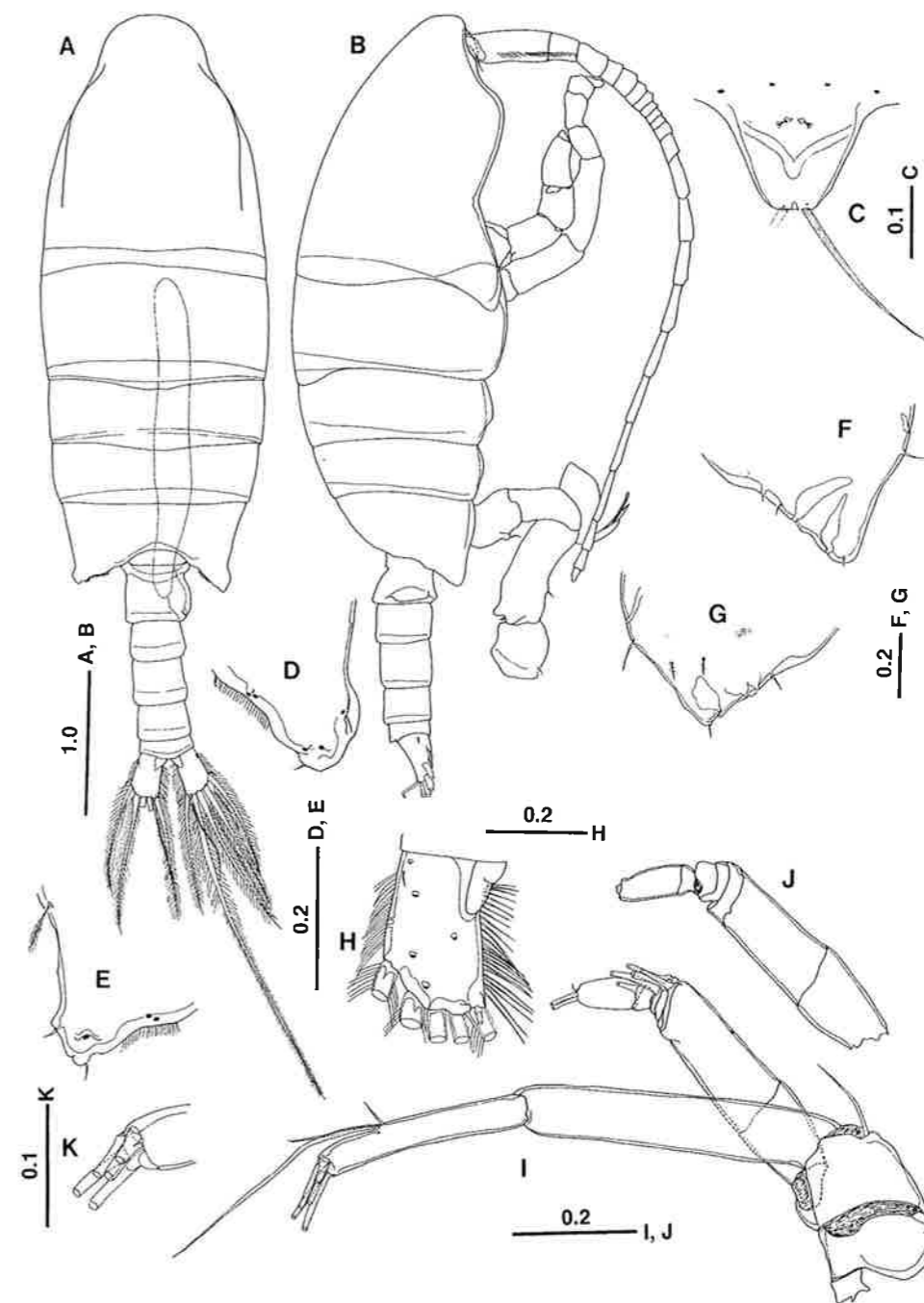
Figure 7. *Paraugaptiloides mirandipes* n. sp., male (holotype). (A) Habitus, dorsal; (B) habitus, lateral; (C) rostrum, anterior, right rostral filament missing; (D) right distal corner of prosome, dorsal; (E) left distal corner of prosome, dorsal; (F) right distal corner of prosome, lateral; (G) left distal corner of prosome, lateral; (H) left caudal ramus, dorsal; (I) antenna; (J) antennary exopod, setae omitted; (K) terminal portion of antennary endopod. Scale bars in mm.
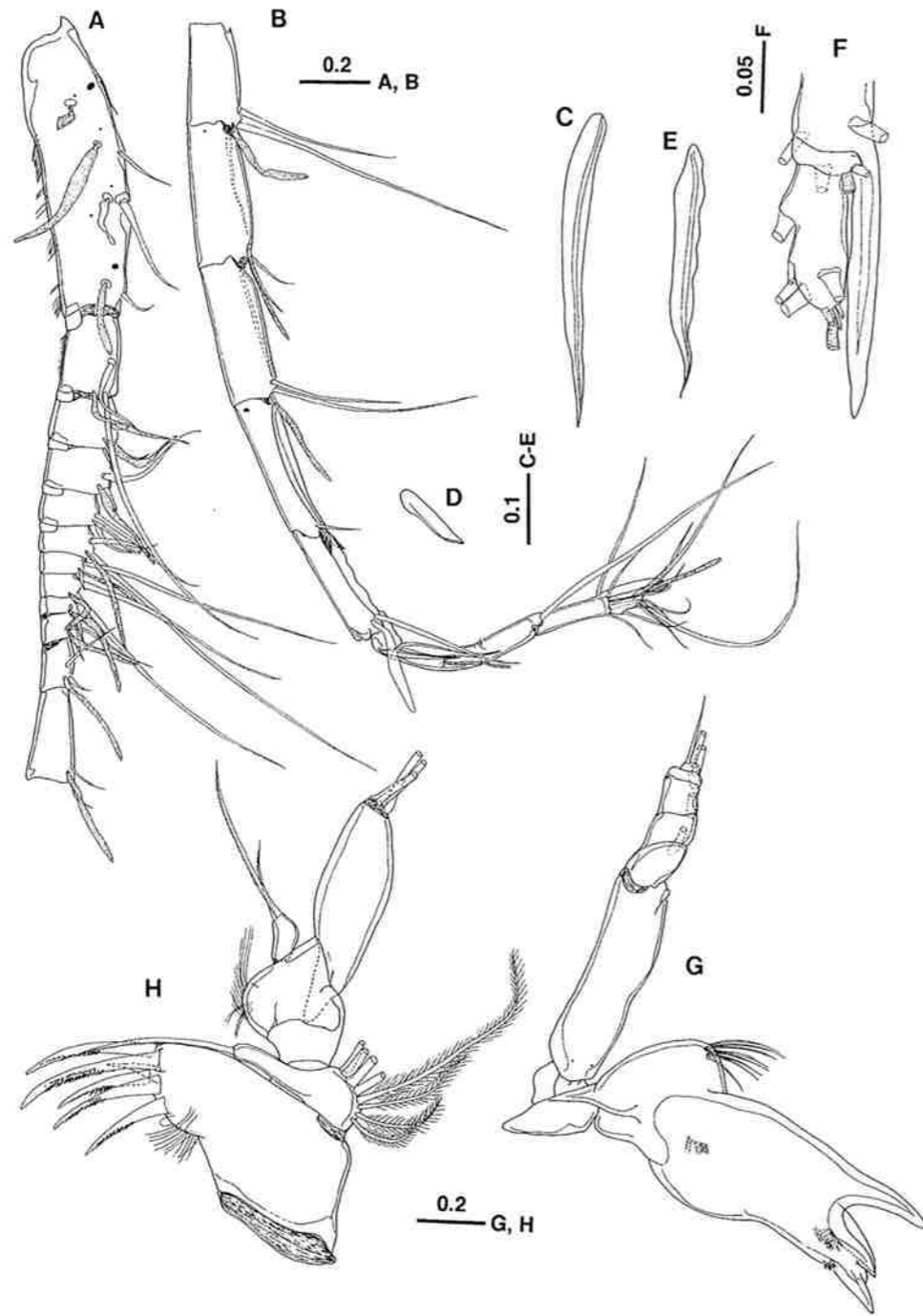
Figure 8. *Paraugaptiloides mirandipes* n. sp., male (holotype). (A) First to 12th segments of left geniculate antennule; (B) 13th to 19th segments of left antennule; (C) proximal spiniform element on antennulary segment XIX; (D) distal spiniform element on left geniculate antennulary segment XIX; (E) anterior spiniform element on left geniculate antennulary segment XX; (F) terminal segments of left geniculate antennule; (G) mandible; (H) maxillule. Scale bars in mm.
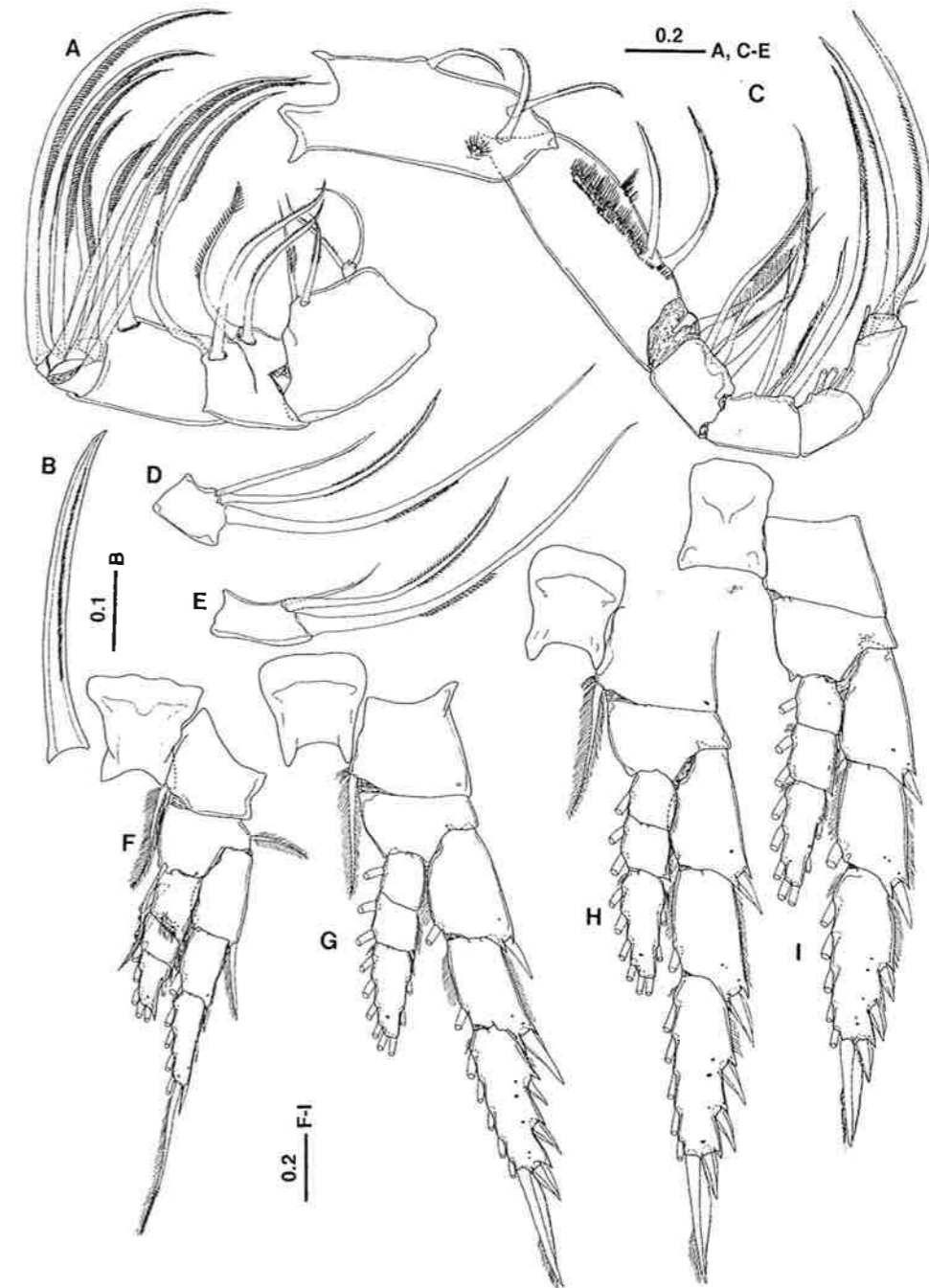
Figure 9. *Paraugaptiloides mirandipes* n. sp., male (holotype). (A) Maxilla; (B) basal spine of maxilla; (C) maxilliped, some setae on endopod omitted; (D) fourth endopodal segment of maxilliped; (E) fifth endopodal segment of maxilliped; (F) leg 1, anterior; (G) leg 2, anterior; (H) leg 3, anterior; (I) leg 4, anterior. Scale bars in mm.
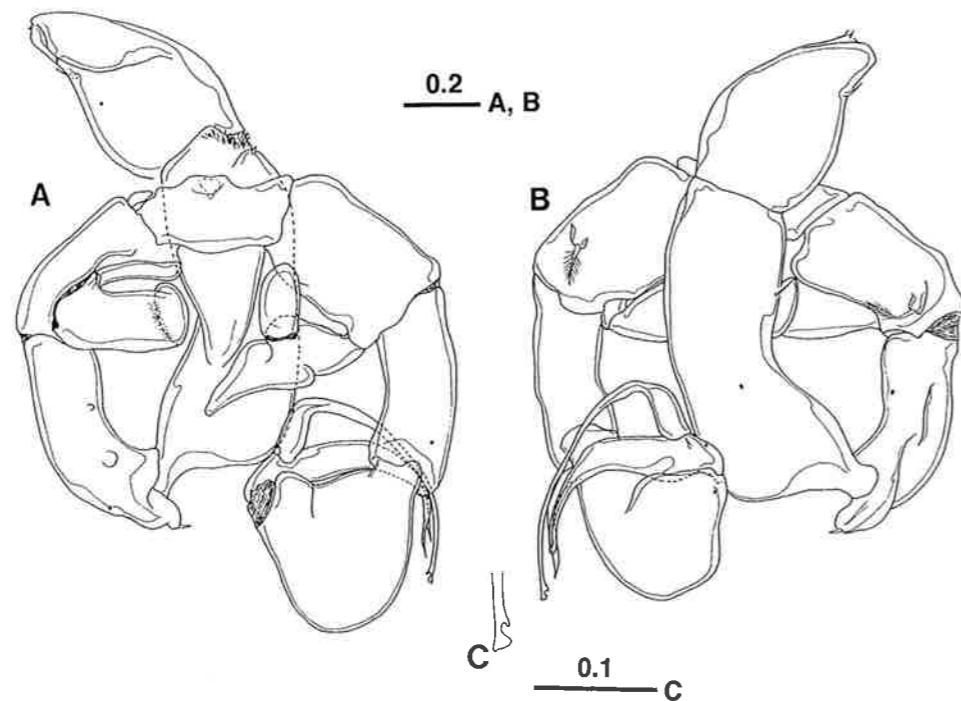
Figure 10. *Paraugaptiloides mirandipes* n. sp., male (holotype). (A) Leg 5, anterior; (B) leg 5, posterior; (C) tip of proximal element on third exopodal segment of left leg 5. Scale bars in mm.

conspicuous; caudal rami (Figure 7A, H) symmetrical, fringed with long setules on both sides; rudimentary seta I present, seta V longest.

Left geniculate antennule (Figure 8A–F) consisting of 19 segments, with first (I–IV) and second (V) posteriorly fringed with fine setules; first to fifth (VIII) segments each with square plate-like structure posterodistally; geniculation positioned between segments 17 (XX) and 18 (XXI–XXIII); large anterodistal process originating from compound segment XXIV–XXV, reaching beyond antennulary tip; terminal three segments corresponding to ancestral XXIV–XXVIII incompletely fused with fusion lines visible clearly. Fusion pattern and armature as follows: I–IV (1)=6+4ae (two elements missing in Figure 8A), V (2)=2+ae, VI (3)=2+ae, VII (4)=2+ae, VIII (5)=2+ae, IX (6)=2+ae, X (7)=1+process +ae, XI (8)=2+ae, XII (9)=1+process+ae, XIII (10)=1+process+ae, XIV (11)=2+ae, XV (12)=1+process+ae, XVI (13)=2+ae, XVII (14)=2+ae, XVIII (15)=2+ae, XIX (16)=1+process (Figure 8C)+spine (Figure 8D)+ae, XX (17)=1+process (Figure 8E)+ae, XXI–XXIII (18)=2 (one rudimentary)+2 processes+ae, XXIV–XXVIII (19)=12+process +2ae (see Figure 8F: XXIV=1+1+process; XXV=1+1+ae; XXVI–XXVIII=8+ae), Right antennule 23-segmented, reaching to anal somite (see Figure 7B). Antenna (Figure 7I–K) with unarmed coxa; basis with inner seta terminally; endopod two-segmented, first segment unarmed, second segment with three inner setae of unequal length and one reduced and five well-developed terminal setae (Figure 7K); exopod (Figure 7I, J) indistinctly seven-segmented, setal formula 0, 1, 1, 1, 1, 1, 3 (one vestigial).

Mandible (Figure 8G) with two mono- and one tricuspid teeth and two patches of setules along cutting edge; patch of long setules present near base of palp; endopod absent, but possibly represented by round prominence; exopod five-segmented, setal formula with 1, 1,

1, 1, 2. Maxillule (Figure 8H) with praecoxal arthrite bearing five serrate spines and one process; coxal endite with one serrate seta; coxal epipodite with eight setae, two of which relatively short; basis with two rows of long setules and vestigial seta; endopod one-segmented, bulbous, with two serrate unequal setae terminally; exopod one-segmented, lobate, with three long setae terminally. Maxilla (Figure 9A) with first praecoxal endite bearing two setae and one rudimentary element; second praecoxal to second coxal endites each with two serrate setae; basis bearing long spine (Figure 9B) with longitudinal row of fine spinules; endopod indistinctly four-segmented, all setae on which well developed, with setal formula 1, 3, 2, 2. Maxilliped (Figure 9C–E) with syncoxa bearing one middle and two subterminal serrate setae and subterminal patch of minute spinules; basis as long as syncoxa, with two serrate setae and longitudinal patch of fine spinules; first endopodal segment nearly incorporated into basis, with serrate seta; second to fifth endopodal segments bearing four, four, three and three setae, respectively; fifth endopodal segment slightly longer than preceding segment; terminal endopodal segment with setae *a* and *b* rudimentary.

Seta and spine formula of legs 1–4 (Figure 9F–I) as in *Protoparamisophria biforaminis*. Legs 1–4 with both rami three-segmented. Leg 1 (Figure 9F) with basis bearing anterodistal row of minute spinules near base of endopod; first endopodal segment with patch of fine setules anterodistally; outer spines on second and third exopodal segments weakly chitinized. Legs 2 (Figure 9G) and 3 (Figure 9H) similar except for shape of distal outer process on second endopodal segment. Leg 4 (Figure 9I) with round prominence at inner distal corner of basis.

Leg 5 (Figure 10) highly complex, enlarged, and heavily chitinized; coxae and intercoxal sclerite completely fused. Left leg with basis bearing plumose subterminal seta on posterior surface; endopod distinctly two-segmented, located near inner distal corner of basis, first segment diamond-shaped, second segment originating from inner midpoint of preceding segment; exopod three-segmented, first segment elongate, with minute element at outer distal corner; second segment massive, expanded outwards; third segment strongly curved, bearing proximal short seta, middle curved spine with spatulate tip (Figure 10C), and terminal bifurcate process. Right leg with basis bearing plumose seta on posterior surface; endopod one-segmented with broad base along inner margin of basis, furnished with fine setules subterminally on posterior surface; exopod indistinctly three-segmented, first segment curved inwards at mid-length, carrying two round processes on anterior surface and triangular outer distal process with fine seta; second segment extremely elongated, as long as basis and first exopodal segment combined, inserted on inner subterminal corner of preceding segment, and bearing short seta at mid-length of inner margin, distal patch of fine setules and subterminal round process with minute spinule at tip; third segment lamellar with three minute setae along distal margin.

Remarks

The new species is easily distinguishable from *P. magnus* (features in parentheses) as follows: (1) prosomal posterior corners irregularly pointed (not irregular); (2) three inner setae on the second endopodal segment of the antenna (only two); (3) absence of the mandibular endopod (one-segmented, with two terminal setae); (4) absence of a vestigial element on the inner distal corner of coxa of leg 4 (present); (5) third exopodal segment of the left fifth leg bearing three heavily chitinized processes (only two); (6) endopod of the right fifth leg well developed (relatively reduced); (7) proximal two exopodal segments of the right fifth leg extremely elongated (relatively compact).

Unidentified ciliates were attached near the distal patch of fine setules of the second exopodal segment of the right fifth leg (not illustrated in Figure 10A).

Etymology

The specific name of the new species, *mirandipes* (Latin *mirandus*, meaning surprising, plus Latin *pes* meaning leg), refers to the highly complex, enlarged fifth legs of the male.

Genus *Sarsarietellus* Campaner, 1984

Diagnosis

Emended part only: cf. Sars 1924–1925; Heinrich 1993; Ohtsuka et al. 1994. Only female known. Cephalosome with paired papillae anterolaterally. Prosomal end with or without weakly or strongly developed dorsolateral and ventrolateral processes. Genital double-somite slightly or highly asymmetrical; single copulatory pore located medially or on right side. Antennule 22- or 23-segmented. Exopod of leg 5 unisegmented, with fusion lines visible or not.

Remarks

The genus *Sarsarietellus* comprises only three species: *S. abyssalis* (Sars, 1905), *S. natalis* Heinrich, 1993, and *S. suluensis* n. sp. The new species described herein adds the foregoing features to the generic diagnosis. The anterolateral cephalic papillae are known only in *Sarsarietellus*. Since they bear a pore on tip, this organ may have a secretory function.

The presence or absence of dorsolateral and ventrolateral processes on the prosomal end in species within a single genus is also recognized within congeners in other arietellid genera such as *Arietellus* Giesbrecht, 1892 and *Paramisophria* Scott, 1897. These processes seem to have evolved convergently many times within the family Arietellidae.

Sarsarietellus suluensis n. sp.
(Figures 11–13)

Material examined

Adult female (holotype), collected from the central Sulu Sea (08°57.31′N, 120°11.31′E~09°03.82′N, 120°12.35′E; wire out 3600 m; depth 0~1516 m) with IKMT; 6–7 December 2002; appendages mounted on glass slides, and body proper in vial; NHM 2005.161.

Description

Female (holotype). Body (Figure 11A, B) 3.08 mm, robust; prosome ca 3.1 times as long as urosome. Cephalosome with round papilla anterolaterally at each side (Figure 11A, C); rostrum (Figure 11D) possibly with pair of filaments (missing). Prosomal end asymmetrical, with right side more produced outward (Figure 11B); dorsolateral and ventrolateral processes acutely pointed; ventrolateral process reaching beyond posterior margin of genital double-somite. Urosome four-segmented; genital double-somite
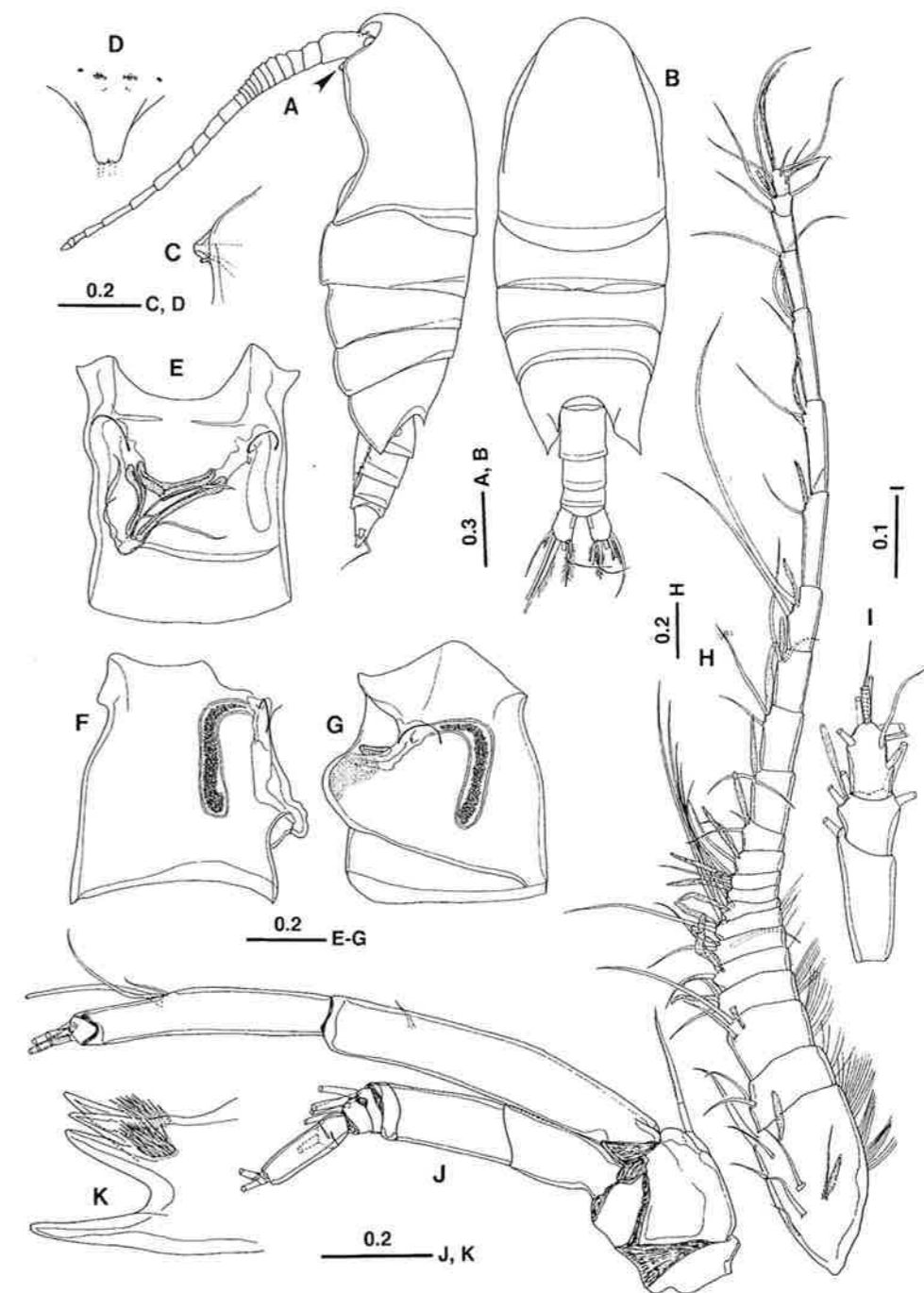
Figure 11. *Sarsarietellus suluensis* n. sp., male (holotype). (A) Habitus, lateral; (B) habitus, dorsal; (C) anterolateral papilla of cephalosome; (D) rostrum, anterior, filaments missing; (E) genital double-somite, ventral; (F) genital double-somite, right lateral; (G) genital double-somite, left lateral; (H) antennule; (I) terminal segments of antennule; (J) antenna; (K) mandibular cutting edge. Scale bars in mm.

Figure 12. *Sarsarietellus suluensis* n. sp., male (holotype). (A) Mandibular palp, phoront of apostome ciliate (?) indicated by arrowhead; (B) phoront of apostome ciliate (?) on mandibular palp; (C) maxillule; (D) maxilla; (E) basal spine of maxilla; (F) maxilliped, some setae omitted; (G) fourth endopodal segment of maxilliped, only smallest seta illustrated; (H) fifth endopodal segment of maxilliped, largest seta omitted. Scale bars in mm.
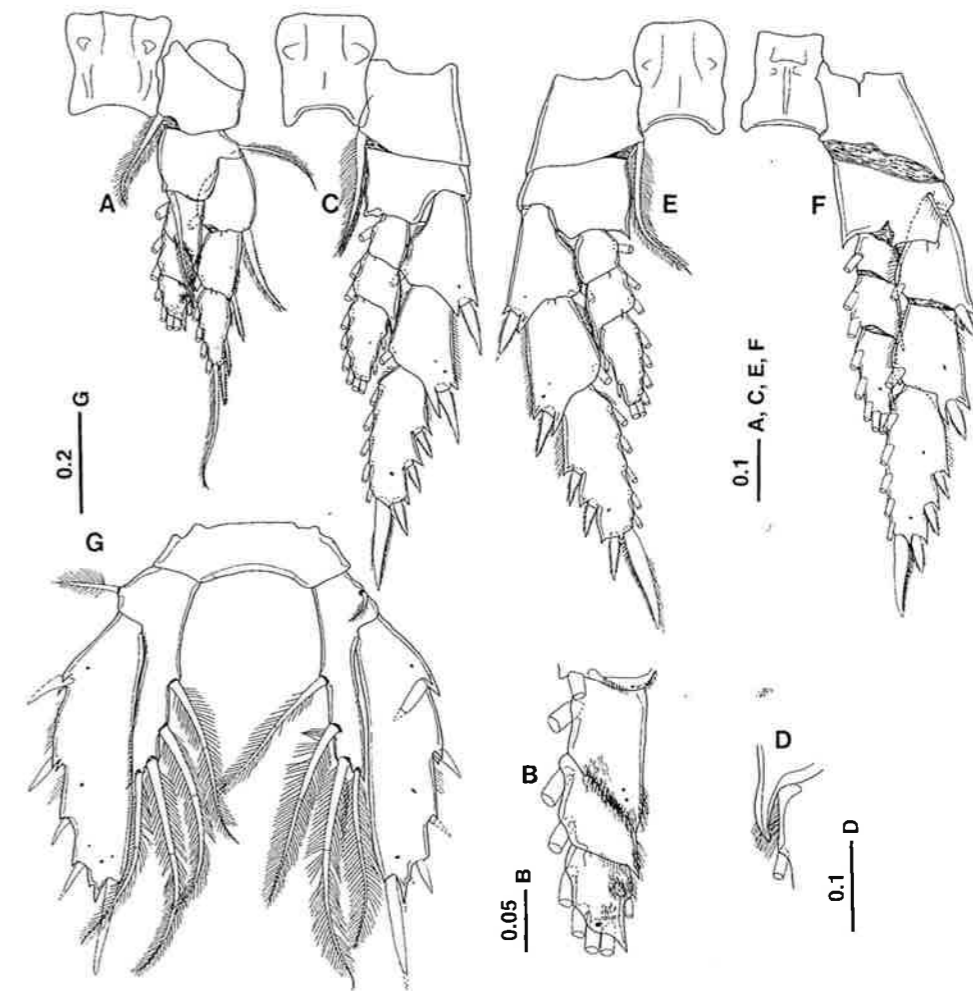

Figure 13. *Sarsarietellus suluensis* n. sp., male (holotype). (A) Leg 1, anterior; (B) endopod of leg 1, anterior; (C) leg 2, anterior; (D) outer distal corner of second endopodal segment of leg 2; (E) leg 3, anterior; (F) leg 4, posterior; (G) leg 5, posterior. Scale bars in mm.

(Figure 11E–G) slightly asymmetrical from dorsal view (Figure 11B), but highly from ventral view (Figure 11E); genital system remarkably asymmetrical, with right gonopore larger and more anteriorly located than left one; copulatory pore opening beneath irregular ventral protrusion on right side; copulatory duct heavily chitinized, Y-shaped; seminal receptacle tubular, terminating at round tip, about half as long as genital double-somite; anal somite short; caudal rami (Figure 11B) symmetrical, ornamented with fine setules along inner margin: seta I rudimentary; seta IV thickest (terminal part missing).

Antennules (Figure 11H, I) symmetrical, 23-segmented, reaching posterior margin of pediger 3; fusion pattern and armature as follows: I–III=7+2 ae, IV=2, V=2+ae, VI=2+ae, VII=2+ae, VIII=2+ae, IX=2+ae, X=2+ae, XI=2+ae, XII=2+ae, XIII=2+ae, XIV=2+ae, XV=2+ae, XVI=2+ae, XVII=2+ae, XVIII=2+ae, XIX=2+ae, XX=2+ae, XXI= 2+ae, XXII=1, XXIII=1, XXIV–XXV=2+2+ae (Figure 11I), XXVI–XXVIII=8+ae (Figure 11I). First (I–III) to eight (X) segments fringed with long setules along posterior margin. Antenna (Figure 11J) with unarmed coxa; basis with serrate seta at inner corner; endopod two-segmented, first segment with minute seta distally, second segment with three inner setae of unequal length and one reduced and five ordinary terminal setae; exopod indistinctly eight-segmented, setal formula 0, 1, 1, 1, 1, 1, 0, 3 (one vestigial).

Mandible (Figures 11K, 12A) with two mono- and one bicuspid teeth and two patches of setules along cutting edge; patch of long setules present near base of palp (not shown in Figure 11K); endopod unisegmented, with one well-developed and one rudimentary seta; exopod five-segmented, setal formula 1, 1, 1, 1, 2. Maxillule (Figure 12C) with praecoxal arthrite bearing five naked spines, one process and patch of long setules; coxal endite bearing serrate seta; coxal epipodite with eight setae; basis with two rows of long setules and one vestigial seta; endopod one-segmented, bulbous, with two serrate unequal setae terminally; exopod one-segmented, lobate, with three long setae (one missing in Figure 12C) terminally. Maxilla (Figure 12D, E) with first praecoxal endite bearing two setae and one vestigial element; second praecoxal to second coxal endites each with two serrate setae; basis elongated, bearing relatively short spine with two longitudinal rows of fine setules (Figure 12E); endopod indistinctly four-segmented, with setal formula 1, 3, 2, 2. Maxilliped (Figure 12F–H) with syncoxa bearing one middle and two subterminal serrate setae and subterminal patch of minute spinules; basis protruded midway, with two serrate setae and patch of fine spinules; first endopodal segment nearly incorporated into basis, with serrate seta; second to fifth endopodal segments bearing four, four, three, and three setae, respectively (Figure 12F–H); second endopodal segment elongate; terminal endopodal segment with reduced seta *a* and long seta *b*.

Segmentation and seta/spine formula of legs 1–4 (Figure 13A–F) as in *Protoparamisophria biforaminis*. Leg 1 (Figure 13A, B) with basis bearing anterodistal row of minute spinules near base of endopod; first and third endopodal segments with patch of fine setules on anterior surface; outer spines on second and third exopodal segments well chitinized. Legs 2 (Figure 13C, D) and 3 (Figure 13E) similar except for acuteness of process at inner distal corner of basis. Leg 4 (Figure 13F) with short basal seta on posterior surface; basal process moderately pointed at inner distal corner.

Leg 5 (Figure 13G) almost symmetrical, with coxae and intercoxal sclerite completely fused to form common base; basis bearing plumose seta near outer middle margin on posterior surface; endopod represented by process carrying four plumose setae, acutely pointed at tip; exopod unisegmented, with one long, terminal and four short, outer spines; terminal right process of exopod slightly longer than left one.

Remarks

The new species is readily distinguished from the other congeners based on: (1) well-developed dorsolateral and ventrolateral processes of pediger 5; (2) remarkably asymmetrical genital system of the genital double-somite; (3) structure of leg 5 (in particular, the non-expression of suture lines on the exopod).

Phoront of possibly apostome ciliates were found also on the mandibular palp (Figure 12A, B) of this species as well as in *Metacalanalis hakuhoae* (see Figure 3A, F, H, K).

Etymology

The specific name of the new species, *suluensis*, refers to the type locality, the Sulu Sea.

Discussion

Phylogenetic relationships among arietellids

The phylogenetic relationships among 10 arietellid genera were subject to a preliminary cladistic analysis, in which two clades were recognized: the *Metacalanus*-group

(*Crassarietellus–Paramisophria–Metacalanus–Pilarella*) and the *Arietellus*-group (*Campaneria–Sarsarietellus–Paraugaptiloides–Scutogerulus–Paraugaptilus–Arietellus*) (Ohtsuka et al. 1994). The original data matrix of Ohtsuka et al. (1994) is reconstructed and the present four new taxa are added. One additional character is evaluated as character 45: seta on exopodal segment IV of antenna (present/absent: 0/1) (see Table III). This analysis is still tentative, because both sexes are known only in five genera.

A unique tree was generated by the new analysis: tree length=196; consistency index=0.245 (Figure 14). The topology is essentially similar to that proposed by Ohtsuka et al. (1994, cf. Figures 44, 45), and suggests that the arietellid ancestor originated in deep-sea hyperbenthic layers as supposed previously (Ohtsuka et al. 1994). The two new genera fall within the *Metacalanus*-group, with *Metacalanalis* as the sister group of *Metacalanus*, and *Protoparamisophria* of *Paramisophria*. This suggests that in the *Metacalanus*-group invasion of continental hyperbenthic layer may have occurred independently at least three times, once within *Paramisophria*, once in *Pilarella*, and once in *Metacalanus*. This is strongly supported by the analysis of Jaume et al. (2000) for the genus *Paramisophria* that is broadly distributed from the continental slope water to the lower intertidal zone. According to their analysis, it may have originated from the continental shelf edge, and then colonized both shallower and deeper waters.

In this clade, miniaturization seems to have been accompanied by invasion of shallow waters. For example, the bathyal *Crassarietellus* is the largest representative (ca 4 mm in body length), while the neritic *Metacalanus* is the smallest (less than 1 mm). The same tendency is recognizable within the genus *Paramisophria*: the offshore *P. giselae* is the largest (about 3 mm), whereas the intertidal *P. platysoma* is the smallest (ca 1 mm). In contrast, such miniaturization cannot be clearly detected in the other clade, the *Arietellus*-group, since it has never invaded the shallow hyperbenthic waters.

Table III. Data matrix for analysis of relationships between 12 arietellid genera (see Ohtsuka et al. 1994 and text)

	1 2 3 4
	1234567890123456789012345678901234567890123 45
Crassarietellus	10000000000100100100001000001011000010009901
Paramisophria	11100100000111000000000000000001111000110000001
Metacalanus	10110111100111100110011110011111111211000101
Arietellus	11011111111110011011011111101110011001101111
Paraugaptilus	10011111111110110111111111100111122101111111
Scutogerulus	00000100009999991000010111111101110199999991
Sarsarietellus	11000100009999990000000100100110000099999991
Pilarella	00110110009999990010001100001011111999999991
Protoparamisophria	10100100009999990000000000000001111000999999991
Metacalanalis	00111111119999990010000100101111111999999990
Campaneria	99999999990011100010000100100199999001001101
Paraugaptiloides	99999999991111011000000100100099999000111101

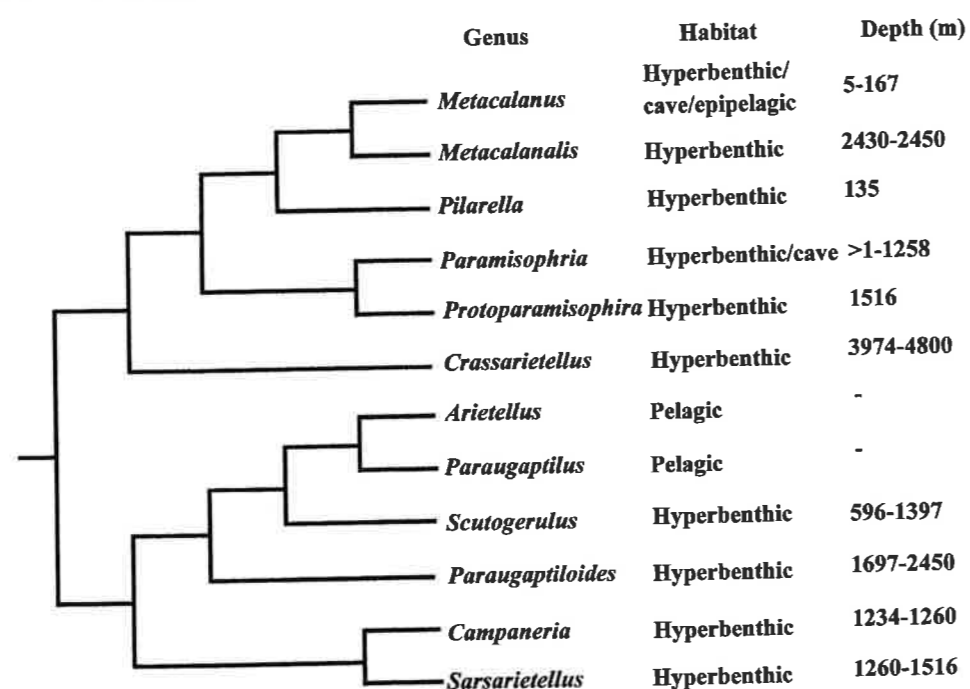| Genus	Habitat	Depth (m)
Metacalanus	Hyperbenthic/cave/epipelagic	5–167
Metacalanalis	Hyperbenthic	2430–2450
Pilarella	Hyperbenthic	135
Paramisophria	Hyperbenthic/cave	>1–1258
Protoparamisophira	Hyperbenthic	1516
Crassarietellus	Hyperbenthic	3974–4800
Arietellus	Pelagic	-
Paraugaptilus	Pelagic	-
Scutogerulus	Hyperbenthic	596–1397
Paraugaptiloides	Hyperbenthic	1697–2450
Campaneria	Hyperbenthic	1234–1260
Sarsarietellus	Hyperbenthic	1260–1516

Figure 14. Cladogram of arietellid genera including the two new genera, *Metacalanalis* and *Protoparamisophria*. Main habitat and depth range provided only for hyperbenthic genera, excluding two truly pelagic genera, *Arietellus* and *Paraugaptilus*.

Zoogeography and colonization of the Sulu Sea

Bradford-Grieve (2002) speculated upon the evolutionary history and colonizing routes of calanoid copepods through geological time. According to her, the ancestral calanoids, perhaps the Pseudocyclopoidea and Epacteriscioidea, may have appeared in the late Palaeozoic as a shallow-water hyperbenthic form. The primitive superfamily Arietelloidea, including the family Arietellidae, may have originally invaded the water column in the Devonian, and then radiated into the deep-sea in the late Carboniferous–Early Permian, when the deep water was well ventilated. Some arietelloids such as the Arietellidae are considered to have re-invaded the deep hyperbenthic zone at that time. Bradford-Grieve (2002) assumed the presence of a deep-sea dysoxic layer for the possible survival of these deep hyperbenthic species through the anoxic midwater conditions of the Cretaceous. Recently, the survival of deep-sea benthic invertebrates during these anoxic episodes has been supported also by several authors (e.g. Horne 1999; Wilson 1999). However, this hypothesis, as Bradford-Grieve (2002) pointed out, must be confirmed by molecular techniques.

Taking the geological history of the Sulu Sea into account, the evolutionary pattern and process of arietellids including those in the Sulu Sea per se are supposed. The Sulu Sea is located approximately in the centre of the Indo-West Pacific Region, and is surrounded by many islands and sills shallower than ca 400 m. It has a deep (ca 5000 m) basin and is characterized by a homogenous meso- and bathypelagic zone (500–5000 m) with fairly high water temperature (ca 10°C) and low oxygen content (1.3–1.7 ml l^{-1}) (Marumo 1975). On

the basis of biostratigraphic and sedimentary analyses, it is suggested that the Sulu Sea originated as a back-arc or intra-arc basin in the late early to early middle Miocene, and the isolation of the basin from deep waters of the Pacific occurred only 1.9 million years ago (Anonymous 1989). The occurrence of the present new taxa clearly indicates that the much higher water temperature and lower dissolved oxygen in the hyperbenthic waters of the Sulu Sea than in the other deep-sea habitats worldwide are not the limiting factors for the dispersal and survival of these copepods. While more extensive collections are needed to establish the endemism of the present taxa in the Sulu Sea, the time scale (>1 million years ago) and the extent of deep-water isolation appear to have resulted in the speciation and maintenance of a unique assemblage of hyperbenthic copepods.

If we regard depth as the most important limiting factor for colonization in the family Arietellidae, the following scenario can be proposed for the history of the family. First, the vertical distribution of the arietellid ancestors, those estimated parsimoniously from the present information, is superimposed on the branches of the foregoing cladogram (Figure 15). In the *Arietellus*-group, all genera are deep hyperbenthic except the pelagic genera *Arietellus* and *Paraugaptilus*. So the habitat transition occurred once in the ancestral clade of genera *Arietellus* and *Paraugaptilus*. Two of the new species described in this study, namely *Paraugaptiloides mirandipes* and *Sarsarietellus suluensis*, are deep-water hyperbenthic taxa, so it can be assumed that their ancestor inhabited the Sulu Sea before the isolation of the deep water. It may be that, after the semi-closure of the Sulu Sea, their ancestral species populations were isolated from the main population and undertook speciation.

In contrast, the habitat transition in the *Metacalanus*-group is more complex to elucidate. Three genera, *Metacalanalis*, *Protoparamisophria*, and *Crassarietellus*, are deep-water hyperbenthic, while the rest of the genera are shallow-water hyperbenthic. Among them, *Protoparamisophria* and *Crassarietellus* are assumed to continue in the ancestral habitat. On the other hand, uncertainty still remains as to how *Metacalanalis* invaded the deep-sea hyperbenthos of the Sulu Sea. One way is to assume that *Metacalanalis* simply remained in the ancestral habitat of the *Metacalanus*-group, i.e. the deep-sea hyperbenthos. However, the sister genera of *Metacalanalis* (*Metacalanus* and *Pilarella*) are both shallow-water hyperbenthos. The possibility of a habitat shift of the ancestral species of *Metacalanus*, *Metacalanalis*, and *Pilarella* from deep to shallow hyperbenthic layers still remains. If we could find species of *Metacalanus* and *Pilarella* in deep hyperbenthic waters of regions other than the Sulu Sea, then this would provide further evidence that they have colonized the deep hyperbenthic layers of the Sulu Sea before the closure of its sills. This would support a deep hyperbenthic ancestral state for the clade. However, if we could collect species of *Metacalanalis* from shallow water, it could be assumed that its ancestor has invaded shallow water, and next colonized the deep hyperbenthos of the Sulu Sea, thus supporting a shallow hyperbenthic ancestral state for *Metacalanalis*. The latter scenario is less likely since no member of the genus has been found in shallow water despite intensive sampling in the Atlantic and the north-western Pacific. Based on the information available, we propose that the divergence of *Metacalanus* and *Metacalanalis*, and of *Paramisophria* and *Protoparamisophri*, occurred later than 1.9 million years ago (Figure 15). Since *Metacalanalis* and *Protoparamisophria* occur only in the Sulu Sea, the closure of its sills must have occurred earlier than the divergence of *Metacalanus* and *Metacalanalis*, and of *Paramisophria* and *Protoparamisophria*. So we assume they diverged later than 1.9 million years ago (Anonymous 1989). In contrast, the ancestral species of *Paraugaptiloides* and *Sarsarietellus* must have invaded the Sulu Sea before the closure of the sills (Figure 15).
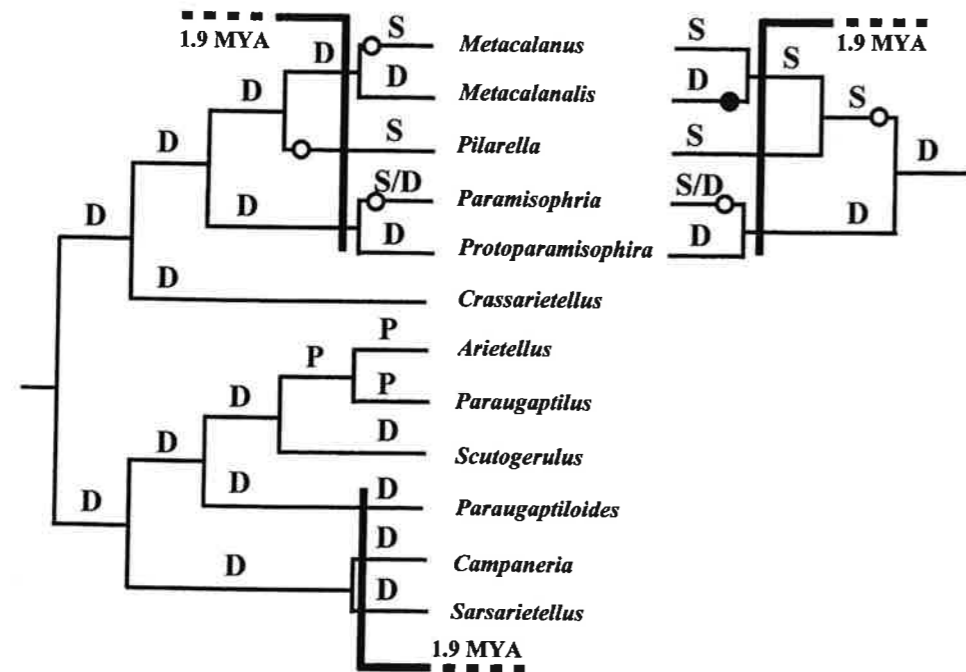
Figure 15. Cladogram depicting main habitats and colonization routes for arietellid genera and their presumed ancestors. D, deep-water hyperbenthic; S, shallow-water hyperbenthic (including cavernicolous and epipelagic); P, deep-water planktonic. In the *Metacalanus–Metacalanalis–Pilarella*-clade there are two possibilities for colonization routes (right: habitat transition from deep-sea to shallow-water hyperbenthos occurred in this clade with re-invasion of *Metacalanalis* to deep-water hyperbenthos; left: habitat shift from deep-sea to shallow-water hyperbenthos occurred independently in *Metacalanus* and *Pilarella*. (○) Habitat shift from deep-sea hyperbenthic to shallow-sea hyperbenthos; (●) habitat shift from shallow-water hyperbenthos to deep-sea hyperbenthos (see text and Figure 14).

More precise inferences regarding endemism will depend on extensive sampling and genetic analyses in future studies.

Acknowledgements

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