

Three New Species of Deep-Sea Hyperbenthic Aetideid Copepods (Crustacea) Collected from Nansei Islands, Southwestern Japan

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Abstract: Three new species of deep-sea hyperbenthic calanoid copepods belonging to the family Aetideidae are described from the Nansei Islands, southwestern Japan: *Bradyetes pacificus* n. sp., *Lutamator paradiseus* n. sp., and *Paracomantenna goi* n. sp. The genus *Bradyetes* is recorded from the Indo-Pacific region for the first time. The male of the genus *Lutamator* is described here for the first time and this record is also the first for the genus from the North Pacific. These results are further demonstration of the existence of a highly diverse copepod fauna in the deep hyperbenthic waters of Japan, similar to that already known from both the Atlantic and the southern Pacific.

Key words: Copepoda, Calanoida, Aetideidae, hyperbenthic, the Nansei Islands

Introduction

Intensive surveys of the deep-sea hyperbenthic copepods caught off the Nansei Islands, southwestern Japan, have revealed the presence of genera such as *Metacalanus* Cleve, 1901, *Paramisophiria* Scott, 1897, *Scutogerulus* Bradford, 1969 (Arietellidae), *Macandrewella* Scott, 1909, *Neoscolecithrix* Canu, 1896 and *Scolecocalanus* Farran, 1936 (Scolecitrichidae) (Ohtsuka *et al.*, 1994, 2002, 2003; Ohtsuka & Boxshall, 2004). The genera *Scutogerulus*, *Macandrewella*, *Neoscolecithrix* and *Scolecocalanus* were all recorded from Japanese waters for the first time, which suggests that the diversity of hyperbenthic calanoid copepods in these deep waters is high.

The hyperbenthic habitat has been identified as being of major significance in recent studies on the origin and evolution of calanoid copepods (Huys & Boxshall, 1991; Bradford-Grieve, 2002), and on the colonization of the pelagic realm and of anchialine caves by calanoid and other copepods (Jaume *et al.*, 2000; Bradford-Grieve, 2002). The family Aetideidae accommodates many hyperbenthic taxa (cf. Bradford & Jillett, 1980; Markhaseva, 1996), but has never been studied in detail in Japanese waters. According to Bradford-Grieve (2002), the deep-sea hyperbenthic zone has probably been colonized by calanoid copepods several times over geological time scales, and she regarded the family Aetideidae as a relatively late colonizer. Little is known of the detailed biology of hyperbenthic aetideids, except for the unique reproductive and developmental adaptations of *Bradydius* Giesbrecht, 1897 to life in hyperbenthic layers that were clarified by Matthews (1964).

The present paper deals with three new species of deep-sea hyperbenthic aetideids

collected from the Nansei Islands, southwestern Japan.

Materials and Methods

Copepods were captured using a NORPAC net (mesh size 0.3 mm) attached to the mouth of a beam trawl at two stations in the Nansei Islands, southwestern Japan: St. TY-04-X, off Amami-Oshima Island, Kagoshima, 28°22.37'N, 129°15.97'E~28°22.28'N, 129°15.43'E, 290 m depth, 21 May 2004 (local time 1110–1130); St. TY-03-11, off Kuroshima Island, Okinawa, 26°19.18'N, 127°25.56'E, 596–606 m depth, 24 May 2003 (local time 1220–1325). The gear was towed along the bottom at a speed of 2 knots for 20 minutes by the T/S *Toyoshio-Maru* of Hiroshima University. Samples were fixed with 10% neutralized formalin/sea water immediately after collection. Copepods were examined in lactophenol under a differential interference contrast microscope (Nikon Optiphot) equipped with a camera lucida. Dissected parts of copepods were mounted on glass slides using the mounting medium CMC-10 (Masters Company Inc.).

Terminology follows Huys and Boxshall (1991). Type specimens are deposited at the National Science Museum, Tokyo (NSMT-CR).

Taxonomy

Family Aetideidae Giesbrecht, 1893

Genus *Bradyetes* Farran, 1905

Remarks. The deep-sea hyperbenthic genus *Bradyetes* currently accommodates only two species, both from the Atlantic (Grice, 1972; Johannessen, 1976; Markhaseva, 1996): *B. inermis* Farran, 1905 (Ireland, off Woods Hole, Madeira, ?300–1500 m depth) and *B. matthei* Johannessen, 1976 (off Norway, 548–580 m depth). These two species differ significantly in segmentation and setation of appendages of both sexes. The only possible synapomorphies in female serving to define the genus are the presence of an aesthetasc-like element on the distal endite of the maxillipedal syncoxa, and of a heavily sclerotized seta on the maxillary basis. However, the sensory element on the maxilliped is relatively long in *B. inermis* but short in *B. matthei*. This raises some doubt over their homology. These two character states are also shared with other aetideid genera, such as *Comantenna* Wilson, 1924 and *Mesocomantenna* Alvarez, 1986, and with two species of *Paracomantenna* Campaner, 1978. In *Comantenna*, *Mesocomantenna* and *Paracomantenna magalyae* Campaner, 1978, the sensory elements are short and thick, whereas in *Bradyetes* and *Paracomantenna gracilis* Alvarez, 1986 they are long and slender. As already pointed out by Markhaseva (1996), it is evident that the genus *Paracomantenna* is not monophyletic, since important characters such as the aesthetasc-like element on the maxillipedal syncoxa may be present or absent (see Remarks on *Paracomantenna*). Alvarez (1986) pointed out that the ornamentation of the setae on the second coxal and basal endites of the maxilla in the female is an important character distinguishing between *Comantenna*, *Mesocomantenna* and *Paracomantenna*. Spinules along the inner margin of the basal spiniform seta are relatively fine and dense in *Bradyetes* and *Comantenna*, but thick and sparse in *Mesocomantenna* and *Paracomantenna* s.l. In addition, the spinules at the base of the setae on the first and second praecoxal endites of the maxilla are relatively fine in the former, but heavily sclerotized in the latter. These differences are related to feeding strategies (Alvarez, 1986). Lack of knowledge on the males of

Mesocomantenna and *Paracomantenna* s.l. also makes it more difficult to define clear boundaries between these genera.

The present new species described below is similar to the type species *B. inermis* rather than the subsequently described species *B. matthei*, and can be reasonably assigned to the genus, pending revision of this group of genera.

Bradyetes pacificus sp. nov.

(Figs. 1–3)

Material examined (types). Holotype (NSMT-Cr 16099): 1 ♀, appendages dissected and mounted on glass slides, body stored in alcohol, collected at St. TY-04-X (off Amami-Oshima Island, Kagoshima, 28°22.37'N, 129°15.97'E~28°22.28'N, 129°15.43'E, 290 m depth), 21 May 2004. Paratype (NSMT-Cr 16100): 1 ♀, partly dissected and mounted on glass slides, body proper in vial, locality and collection date same as in holotype.

Body length. Female 2.96 mm (holotype); 2.98 mm (paratype).

Description. Female. Body (Fig. 1A, B) robust; prosome approximately 3.4 times as long as urosome; cephalosome partly fused to pediger 1; rostrum (Fig. 1C, D) produced ventrally into blunt point, not bifurcate at tip; posterolateral processes of prosome (Fig. 1E, F), in dorsal view, bifurcate terminally, reaching beyond level of genital operculum. Urosomites 1–3 with striated hyaline frill along posterior margin (Fig. 1E, F); genital double-somite expanded anterolaterally; genital operculum (Fig. 1G) relatively narrow; seminal receptacles (Fig. 1B, E, G) slender, reaching beyond mid-height in lateral view (see Fig. 1E); caudal rami symmetrical, slightly longer than wide; caudal seta I minute; seta VII originating from ventral midpoint.

Antennule (Fig. 1H, I) indistinctly 24-segmented with suture between segments I and II clearly visible; fusion pattern and setal formula as follows: I–IV=7+ae (1, 2, 2+ae, 2), V=2+ae, VI=2, VII=2+ae, VIII=2, IX=2, X–XI=4+ae (2, 2+ae), XII=2, XIII=2, XIV=2+ae, XV=2, XVI=2+ae, XVII=2, XVIII=2, XIX=2, XX=2, XXI=2+ae, XXII=1, XXIII=1, XXIV=1+1, XXV=1+1, XXVI=1+1, XXVII–XXVIII=4+ae.

Antenna (Fig. 2A) with basis and endopod incompletely fused to form allobasis; coxa and basis bearing 1 and 2 setae at inner distal corners, respectively; exopod indistinctly 9-segmented, setal formula 1, 1, 1, 1, 1, 1, 1, 3; subterminal and terminal lobes of distal endopodal segment with 8 and 7 setae, respectively.

Mandibular gnathobase (Fig. 2B) with 1 simple and 5 multicusped teeth, plus spinulose seta fused to gnathobase. Mandibular palp (Fig. 2C) with endopod smaller than exopod, 2-segmented; first endopodal segment reduced, unarmed, second segment with 4 setae of unequal length terminally; exopod indistinctly 5-segmented, setal formula 1, 1, 1, 1, 2.

Maxillule (Fig. 2D, E) with praecoxal arthrite bearing 4 surface and 9 terminal elements; short, stout spinules present at base of 3 surface setae; coxal endites with 4 setae, distalmost of which with stout spinules around base; coxal epipod with 6 setae, gradually increasing in thickness distally; first basal endite with 2 heavily sclerotized setae plus fine seta; second basal endite represented by inner knob with 4 stout setae; endopod almost incorporated into basis, but trace of segmentation recognizable, with setal formula 4, 2, 6; exopod swollen distally, with 11 marginal setae.

Maxilla (Fig. 2F) with 1 short and 2 long spinulose setae on each of praecoxal and coxal endites, with dense patches of long spinules near base of setae on each endite; basis

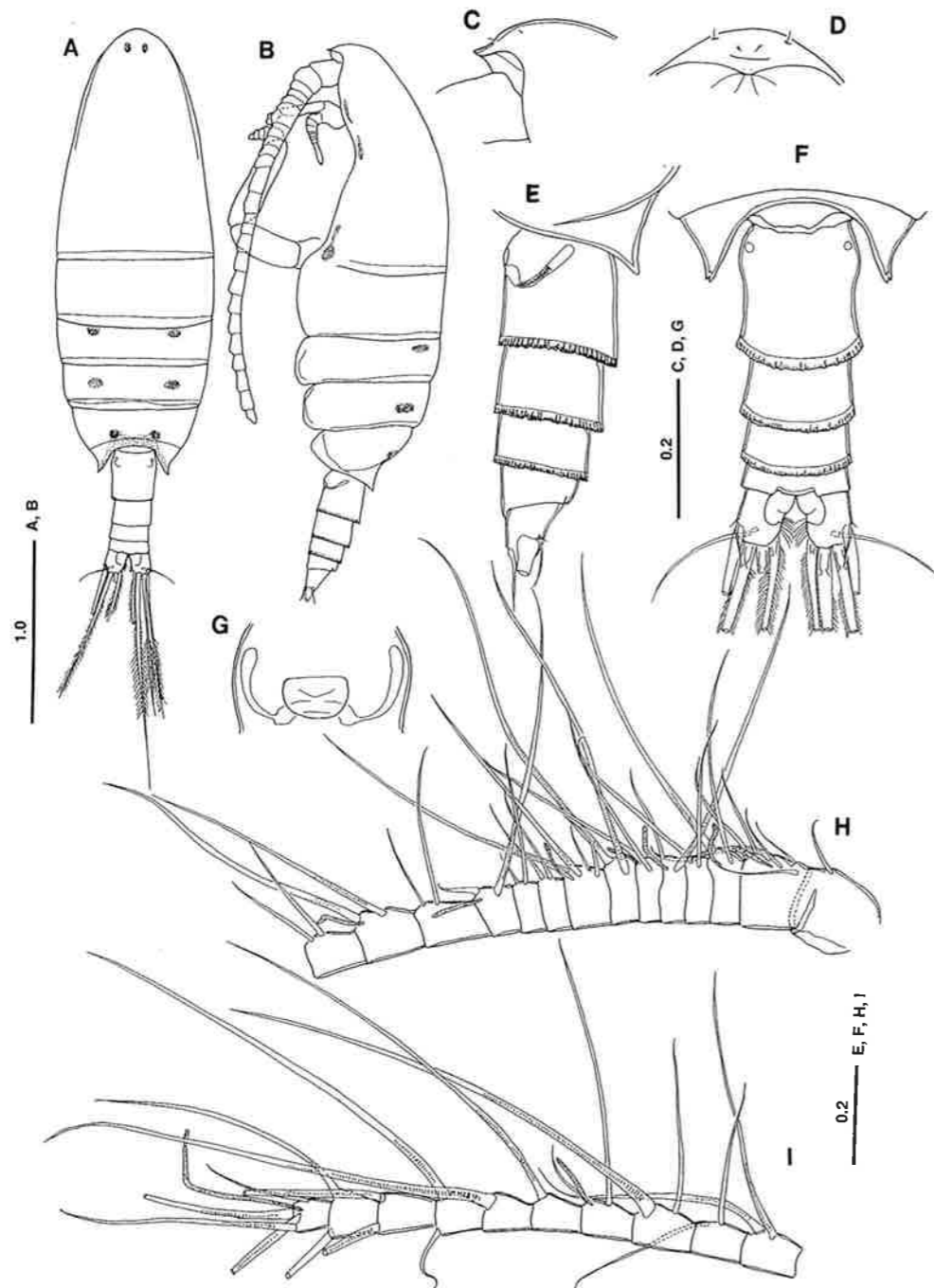


Fig. 1. *Bradyetes pacificus* n. sp., female (holotype). A, Habitus, dorsal view; B, Habitus, lateral view; C, Rostrum, lateral view; D, Rostrum, ventral view; E, Pediger 5 and urosome, lateral view; F, Pediger 5 and urosome, dorsal view; G, Genital operculum and seminal receptacles; H, Antennular segments I (first) to XVII (14th); I, Antennular segments XVIII (15th) to XXVII-XXVIII (24th). Scales in mm.

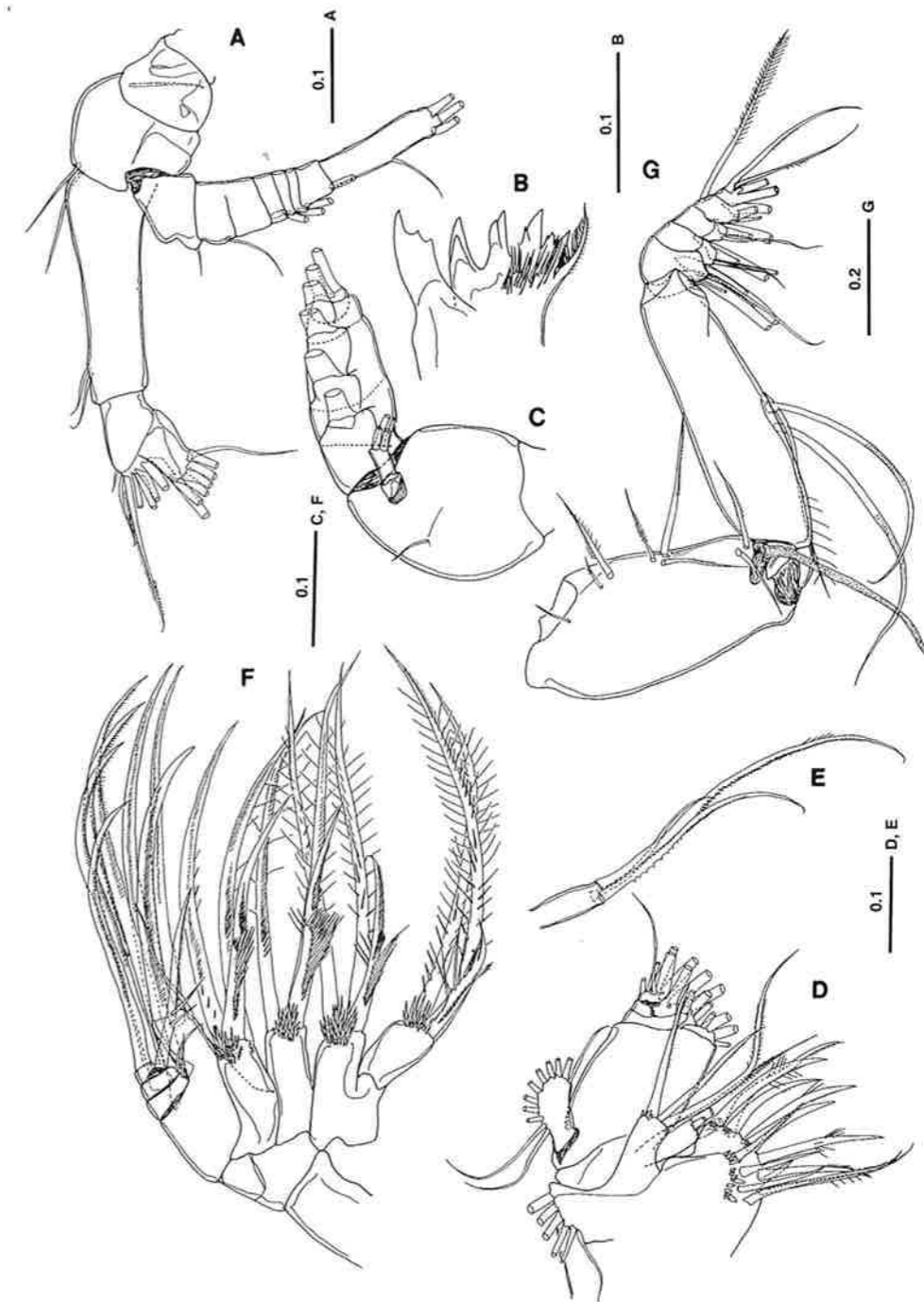


Fig. 2. *Bradyetes pacificus* n. sp., female (holotype). A, Antenna; B, Mandibular gnathobase; C, Mandibular palp; D, Maxillule; E, First basal endite of maxillule; F, Maxilla; G, Maxilliped. Scales in mm.

Table 1. Seta and spine formula of legs 1 to 4 of *Bradyetes pacificus* n. sp.

	coxa	basis	exopod			endopod		
			1	2	3	1	2	3
Leg 1	0-0	1-1	I-0;	I-1;	I, 1, 3	0, 2, 3		
Leg 2	0-1	0-0	I-1;	I-1;	III, I, 4	0-1;	1, 2, 2	
Leg 3	0-1	0-0	I-1;	I-1;	III, I, 4	0-1;	0-1;	1, 2, 2
Leg 4	0-1	0-0	I-1;	I-1;	III, I, 4	0-1;	0-1;	1, 2, 2

with 3 setae, 1 heavily sclerotized, 1 slender and 1 long; endopod indistinctly 4-segmented, second segment bearing 2 fine setae in addition to developed seta; endopodal setal formula 1, 3, 2, 2.

Maxilliped (Fig. 2G) well chitinized; syncoxa bearing 1, 2, and 3 setae on first to third endites; patch of minute prominences anteriorly at base of third endite; fourth endite with 1 naked and 2 spinulose setae and aesthetasc-like element; basis with 3 long setae midway; endopod 6-segmented, setal formula 2, 4, 4, 3, 3+1, 4; proximal setae on fifth and sixth endopodal segments fused to segment; outer spinulose seta on fifth segment well developed.

Seta and spine formula of legs 1-4 (Table 1). Leg 1 (Fig. 3A, B) with coxa unarmed; basis with minute outer seta subterminally; outer spines on first and second exopodal segments slender, ornamented with row of fine setules along inner margin; outer expansion of endopod swollen, with fine setules terminally. Leg 2 (Fig. 3C) with terminal spine on third exopodal segment coarsely serrate, serrations connected by lamella; distal outer corner of first endopodal segment not pointed. Legs 3 (Fig. 3D) and 4 (Fig. 3E) similar, but intercoxal sclerite narrower in leg 4; serrations on terminal spine of third exopodal segment connected by lamella; outer distal corner of first and second endopodal segments pointed.

Male unknown.

Coloration. In some specimens fixed with formalin/sea water, paired light brown spots are present anterodorsally and laterally on the cephalosome, and dorsally on pedigers 2 to 4 (Fig. 1A, B).

Remarks. This is the first record of the genus *Bradyetes* from the Indo-Pacific region. The new species is similar to *Bradyetes inermis* in having a long, aesthetasc-like element on the distal endite of the maxillipedal syncoxa and a reduced mandibular endopod. However it is easily distinguished from the latter by (states in parentheses for *B. inermis*): (1) the presence of a ventrally produced rostrum (rostrum absent); (2) the posterolateral angles of the prosome produced posteriorly into pointed processes (processes rounded); (3) the antennary basis with 2 setae (single seta); and (4) setal formula of mandibular endopod 0, 4 (1, 3).

Etymology. The new specific name "*pacificus* (Latin, meaning Pacific)" refers to this first report of the genus in the Pacific.

Genus *Lutamator* Bradford, 1969

Diagnosis (emended and supplemented from Markhaseva (1996)). Female. Cephalosome partly or totally fused to pediger 1. Rostrum forming bluntly rounded plate, not bifurcate at tip. Pedigers 4 and 5 completely or incompletely coalescent. Antenna with

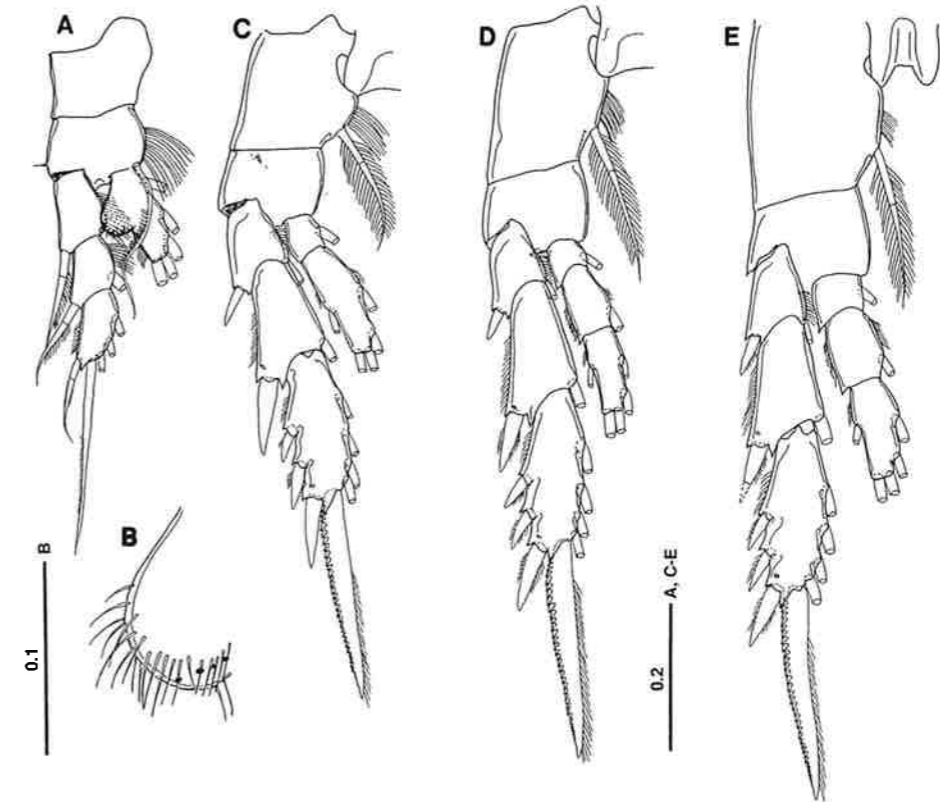


Fig. 3. *Bradyetes pacificus* n. sp., female (A-D: holotype; E: paratype). A, Leg 1, anterior surface; B, Outer expansion of endopod of leg 1; C, Leg 2, anterior surface; D, Leg 3, anterior surface; E, Leg 4, anterior surface. Scales in mm.

1 coxal and 1 or 2 basal setae; exopod as long as or longer than endopod, and as wide as or narrower than endopod; first exopodal segment with or without seta; compound distal endopodal segment with 8 or 9 setae on subterminal lobe. Mandibular basis with 0 or 1 seta; first endopodal segment with 0 or 1 seta. Coxal epipod of maxillule with 7 or 8 setae. Maxilla with patch of spinules at base of setae on each of praecoxal and coxal endites; one spiniform seta on basis heavily sclerotized; endopod 4-segmented, setal formula 1, 2, 2, 2. First syncoxal (praecoxal) endite of maxilliped with or without seta; fourth syncoxal endite with 2-4 setae, one of which longer than or as long as other setae.

Male. Cephalosome totally fused to pediger 1; rostrum forming blunt, rounded process; pedigers 4 and 5 incompletely coalescent. Antennule asymmetrical: segments XXII and XXIII separate on left but fused on right. Antenna with coxa and basis bearing 1 and 2 setae, respectively. Mandibular gnathobase reduced; palp with single basal seta; first endopodal segment bearing seta. Maxillule reduced except for exopod with 10 long setae. Maxilla wholly reduced, with vestigial elements. Maxilliped with only vestigial elements on distal lobe of syncoxa. Leg 1 as in female. Leg 5 uniramous; right leg shorter than left, 4-segmented; left 5-segmented, distal segment of which furnished with row of setules terminally.

Remarks. The genus was defined by monotypy by Bradford (1969), and redefined by Alvarez (1984). Subsequently Markhaseva (1996) emended the diagnosis in her thorough

review of the family Aetideidae. To date the deep-sea hyperbenthic genus *Lutamator* accommodates only two species, *L. hurlei* Bradford, 1969 (off New Zealand, 1357 m depth) and *L. elegans* Alvarez, 1984 (off Brazil, 460–900 m depth). The new species described below is the first from the North Pacific.

This new discovery requires the partial emendation of the generic diagnosis, although this does not disrupt its stability. Knowledge of the male allows us to define the genus more precisely, and to make inferences concerning its phylogenetic position among the other aetideids. The following combination of key characteristics serves to differentiate *Lutamator* from other genera (cf. Bradford, 1969; Alvarez, 1984; Markhaseva, 1996): (1) the female genital double-somite symmetrical; (2) the rostrum reduced to a single point, not bifurcate; (3) the penultimate exopodal segment (segment IX) of the female antenna slender, as long as proximal segments combined; (4) single seta present on each of basis and first endopodal segment of mandible; (5) the maxillipedal syncoxa lacking an aesthetasc-like element terminally; (6) an outer vestigial seta present on basis of leg 1; (7) an inner expansion of endopod of leg 1 well developed; (8) an outer spine on first exopodal segment of leg 1 strongly developed; (9) teeth on the terminal spines of the third exopodal segments of legs 2–4 with connecting membrane; (10) the coxa of leg 4 lacking processes or spinules on the posterior surface; (11) female leg 5 absent; and (12) male leg 5 uniramous on both sides.

The simple, uniramous fifth leg of male *L. paradiseus* described below is shared with *Paivella* Vervoort, 1965 and with species of *Bradydium* and *Chiridius* Giesbrecht, 1893 (cf. Vervoort, 1965; Markhaseva, 1996). However, the male can be differentiated from these three genera by a combination of the following features: (1) the absence of a bifurcate rostrum; (2) the single seta present on the mandibular basis; (3) the presence of a well-developed, outer spine on the first exopodal segment of leg 1; (4) the posterolateral angles of the prosome are not acutely pointed (acutely pointed in *Bradydium* and *Chiridius*); and (5) the absence of spinules from the endopodal surfaces of the second leg (present in *Bradydium*). It is important to note that the structure of male leg second 5 in *Lutamator* may be variable, as in *Bradydium* and *Chiridius* in which both uniramous and biramous states are found.

Lutamator paradiseus sp. nov.
(Figs. 4–8)

Material examined (types). Holotype (NSMT-Cr 16101): 1 ♀, appendages dissected and mounted on glass slides, body stored in alcohol in vial, collected at St. TY-03-11 (off Kuroshima Island, Okinawa, 26°19.18'N, 127°25.56'E, 596–606 m depth), 24 May 2003. Paratypes: 1 ♀, NSMT-Cr 16102, partly dissected and mounted on glass slides, body stored in vial; 2 ♂♂, NSMT-Cr 16103, 16104, appendages dissected and mounted on glass slides, body in vial, locality and collection date same as in holotype.

Body length. Female 3.53 mm (holotype); 3.41 mm (paratype). Male 3.37, 3.39 mm (paratypes).

Description. Female. Body (Fig. 4A, B) robust; prosome approximately 2.8 times as long as urosome; cephalosome incompletely fused to pediger 1 with suture clearly visible dorsally; rostrum (Fig. 4C, D) slightly produced, forming small triangular plate; pedigers 4 and 5 incompletely coalescent; posterolateral angles of prosome symmetrical, produced into rounded lobes extending as far as level of seminal receptacle in genital double-somite (Fig. 4E). Urosome (Fig. 4A, B, E) with first to third urosomites provided with striated

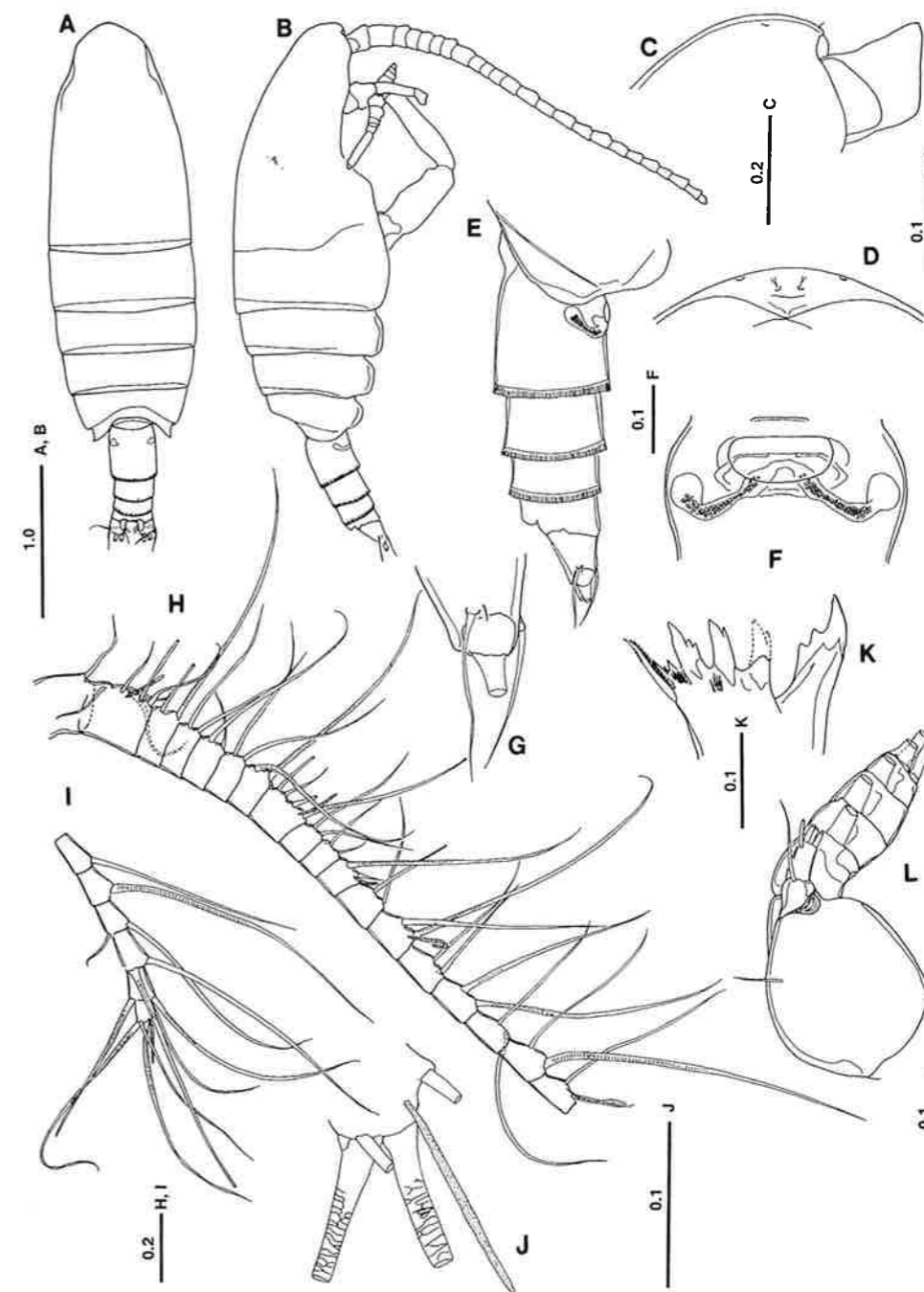


Fig. 4. *Lutamator paradiseus* n. sp., female (holotype). A, Habitus, dorsal view; B, Habitus, lateral view; C, Rostrum, lateral view; D, Rostrum, ventral view; E, Genital operculum and seminal receptacles; F, Caudal ramus, lateral view; G, Caudal ramus, lateral view; H, Antennular segments I (first) to XXII (18th); I, Antennular segments XXIII (19th) to XXVII–XXVIII (24th); J, Terminal part of antennular compound segment XXVII–XXVIII; K, Mandibular gnathobase; L, Mandibular palp. Scales in mm.

hyaline frill along posterior margin; genital double-somite (Fig. 4A, E, F) as long as next two free urosomites combined; genital operculum located at about one quarter length; paired seminal receptacles present, each terminating laterally in bulbous chamber; caudal rami bearing setules along inner margin; caudal seta I reduced, VII located ventrally.

Antennule (Fig. 4G-I) reaching to end of prosome, indistinctly 24-segmented; incomplete suture between segments I and II-IV clearly visible; segmentation pattern and setation as follows: I-IV=7+ae (1, 2, 2+ae, 2), V=2, VI=2, VII=2, VIII=2, IX=2, X-XI=4+ae (2, 2+ae), XII=2, XIII=2, XIV=2+ae, XV=2, XVI=2+ae, XVII=2, XVIII=2, XIX=2, XX=2, XXI=2+ae, XXII=1, XXIII=1, XXIV=1+1, XXV=1+1, XXVI=1+1, XXVII-XXVIII=4+ae.

Antenna (Fig. 5A, B) with exopod longer than endopod; coxa bearing single seta; basis with 2 nearly equal setae at inner distal corner; exopod indistinctly 9-segmented, setal formula 0, 1, 1, 1, 1, 1, 1, 3; seta on second segment located on rounded knob; eighth segment elongate and slender, as long as proximal segments combined; subterminal seta on eighth segment vestigial; middle seta on distal segment thick: endopod 2-segmented, proximal segment with 2 setae subterminally, compound distal segment bearing 9 setae on subterminal lobe and 6 setae plus 1 surface seta on terminal lobe.

Mandibular gnathobase (Fig. 4K) heavily chitinized, with 1 unicusped and 5 multicusped teeth, plus 1 spinulose seta. Mandibular palp (Fig. 4J) with basis bearing only single seta at midlength; endopod much shorter than exopod; exopod indistinctly 5-segmented, setal formula 1, 1, 1, 1, 2; endopod 2-segmented, proximal segment with fine seta, distal segment bearing 4 setae terminally.

Maxillule (Fig. 5C) with well developed basis and endopod; praecoxal arthrite with armature comprising 8 chitinized, 1 surface and 1 spinulose setae, plus vestigial element (arrowed in Fig. 5C); coxal epipod bearing 7 setae; coxal and first basal endites with 4 and 2 setae, respectively; basis incompletely fused to endopod; second basal endite with 4 setae; exopod bearing 11 setae along distal margin; endopod indistinctly 3-segmented, setal formula 3, 4, 4.

Maxilla (Fig. 5D) with dense patch of spinules at base of setae on each of praecoxal and coxal endites; praecoxal and coxal endites each with 1 short and 2 long spinulose setae; basis with 1 heavily sclerotized, spiniform seta and 2 spinulose setae; endopod 4-segmented, setal formula 1, 2, 2, 2; inner seta on second endopodal segment slender.

Maxilliped (Fig. 5E, F) with basis reflexed, positioned at right angle to syncoxa; first syncoxal (praecoxal) endite with vestigial seta, second and third endites bearing 2 and 3 setae, respectively, plus patch of minute spinules near base of setae on third endite; fourth endite with 4 setae, one of which as long as basis; basis bearing 3 spinulose setae midway; endopod 6-segmented, setal formula 2, 4, 4, 3, 3+1, 4; thickened seta on each endopodal segment except second, fused to segment.

Seta and spine formula of legs 1-4 as in *Bradyetes pacificus* except for missing parts (Table 1). Leg 1 (Fig. 6A, B) bearing vestigial outer seta on basis; unisegmented endopod having well developed outer expansion ornamented with fine setules terminally; exopod 3-segmented; first and second segments each with stout, hirsute spine, abruptly tapering at tip; outer spine on third segment naked. Leg 2 (Fig. 6C) with 2-segmented endopod and 3-segmented exopod; outer serrations of terminal spine on third exopodal segment connected by membrane. Leg 3 (Fig. 6D, E) as leg 2 except for 3-segmented endopod; shape of outer distal processes on first and second endopodal segments variable, even on either side of same individual. Leg 4 (Fig. 6F) missing distal exopodal segments in all specimens; endopod as in leg 4. Leg 5 absent.

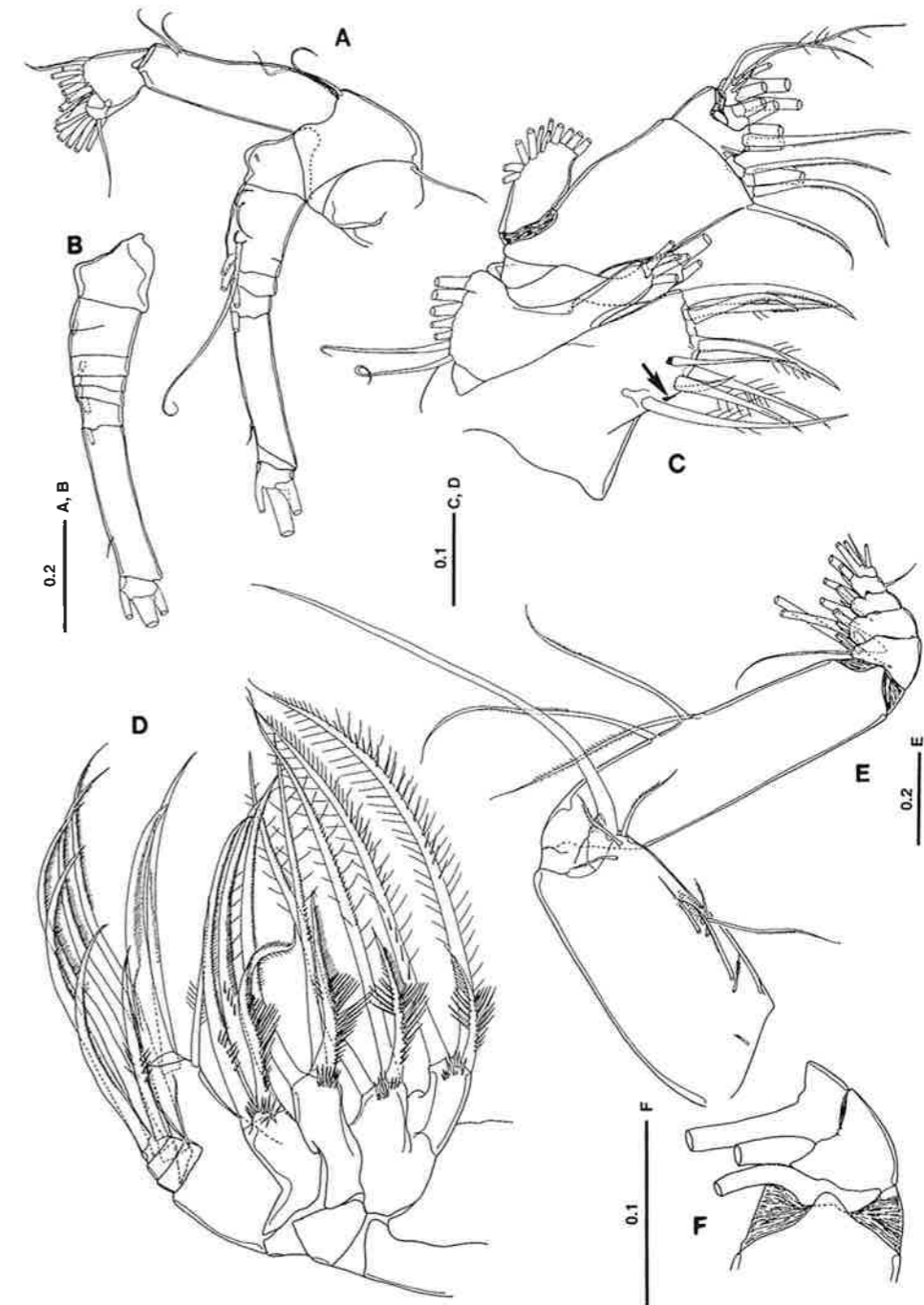


Fig. 5. *Lutamator paradiseus* n. sp., female (holotype). A, Antenna; B, Antennary exopod; C, Maxillule, vestigial element arrowed; D, Maxilla; E, Maxilliped; F, First and second endopodal segments of maxilliped. Scales in mm.

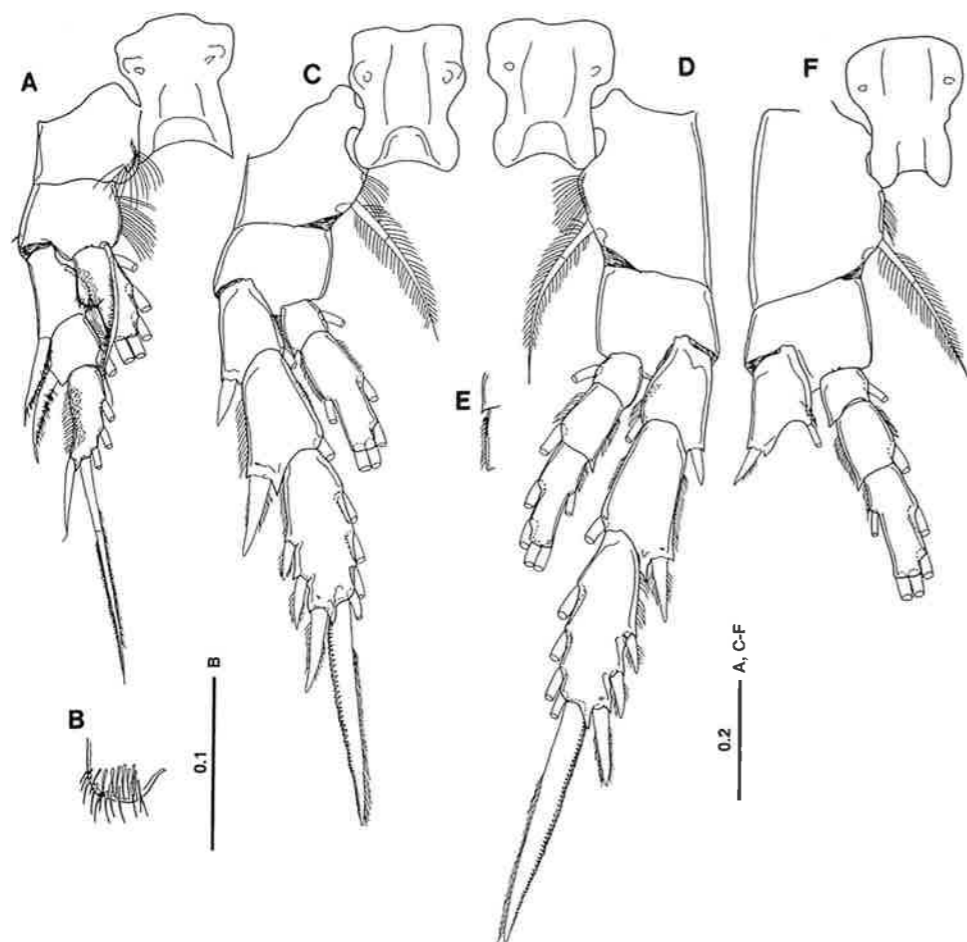


Fig. 6. *Lutamator paradiseus* n. sp., female (A-C, F: holotype; D, E: paratype). A, Leg 1, anterior surface; B, Outer expansion of endopod of leg 1; C, Leg 2, anterior surface; D, Leg 3, anterior surface; E, Outer distal corners of first and second endopodal segments of leg 3; F, Leg 4, anterior surface, distal exopodal segments missing. Scales in mm.

Male. Body (Fig. 7A) more slender than female; prosome about 2.6 times as long as urosome; cephalosome completely fused to pediger 1; rostrum as in female; pedigers 4 and 5 almost coalescent with suture visible laterally; posterolateral angles of prosome symmetrical, smoothly rounded. Urosome (Fig. 7A) with second to fourth urosomites provided with striated hyaline frill along posterior margin; second urosomite longest, as long as third and fourth urosomites combined; anal somite small; caudal rami symmetrical, as long as wide.

Antennules (Fig. 7A, C-F) with tips reaching beyond genital somite, asymmetrical with 23 segments on right and 24 on left, due to fusion between segments XXII and XXIII on right. Segmentation pattern and setation of left antennule as follows: I=1+ae, II-IV=6+4ae (2+ae, 2+2ae, 2+ae), V=2+2ae, VI=2+2ae, VII=2+2ae, VIII=2+2ae, IX=2+2ae, X-XI=4+4ae (2+2ae, 2+2ae), XII=1+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+ae, XXIV=1+1+ae, XXV=1+1+ae, XXVI=1+1, XXVII-XXVIII=4+ae; right antennule with compound segment XXII-XXIII bearing

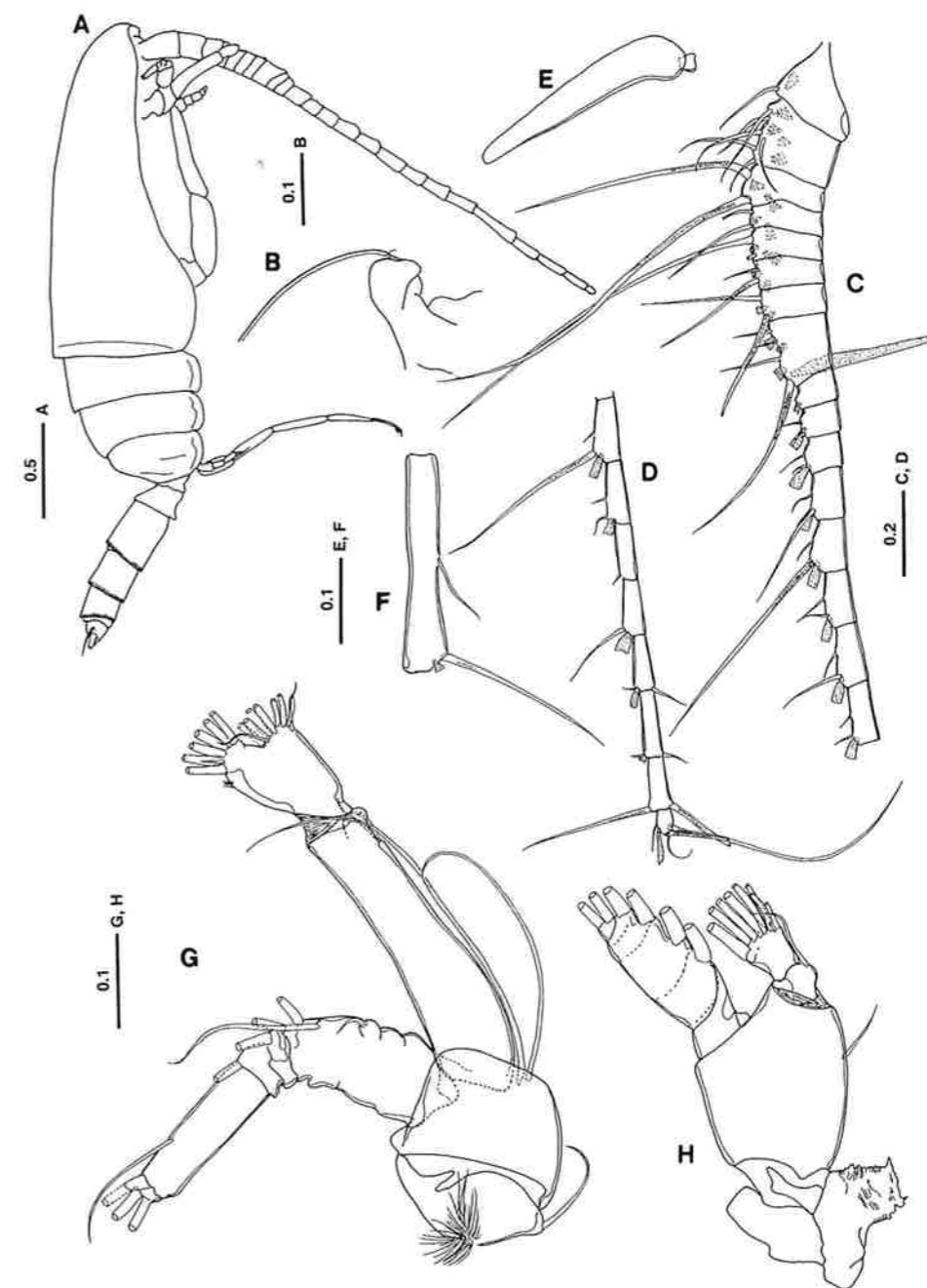


Fig. 7. *Lutamator paradiseus* n. sp., male (paratype). A, Habitus, lateral view; B, Rostrum, lateral view; C, Left antennular segments I (first) to XIX (16th); D, Left antennular segments XX (17th) to XXVII-XXVIII (24th); E, Aesthetasc on antennular segment X (proximal part of eighth compound segment); F, Right antennular compound segment XXII-XXIII; G, Antenna; H, Mandible. Scales in mm.

2+ae (1, 1+ae) (Fig. 7F).

Antenna (Fig. 7G) with patch of long setules and inner distal seta on coxa; basis with 2 unequal setae at distal corner; exopod indistinctly 8-segmented, setal formula 0, 2, 1, 1, 1, 1, 1, 3; seta on elongate seventh segment relatively longer than in female; endopod 2-segmented, proximal segment elongate, with 2 nearly equal setae; compound distal segment with 9 setae on subterminal lobe and 6 setae plus 1 surface seta on terminal lobe.

Mandible (Fig. 7H) with totally reduced gnathobase; basis with single inner seta at midlength; exopod indistinctly 5-segmented, setal formula 1, 1, 1, 1, 2; endopod 2-segmented, proximal segment with slender seta at inner distal corner, distal segment bearing 8 setae plus 1 reduced seta terminally.

Maxillule (Fig. 8A) highly reduced except for exopod; praecoxal arthrite and coxal epipod and endite unarmed; first and second basal endites bearing 3 elements; exopod well-developed, with 10 long setae with or without vestigial element at inner subterminal corner; endopod carrying 10 elements in total.

Maxilla (Fig. 8B) wholly reduced, but armed endites on praecoxa, coxa and basis, and endopod recognizable; these endites each with 3 elements except for 2 on second praecoxal endite; endopod with 6 setae and 1 vestigial element.

Maxilliped (Fig. 8C, D) with 4 vestigial elements on distal syncoxal endite (Fig. 8D); basis with 3 setae midway; endopod 6-segmented, setal formula 1, 4, 4, 3, 3+1, 4.

Leg 1 (Fig. 8E, F) as in female, except shorter setules on outer expansion of endopod and more slender outer spine on distal exopodal segment. Legs 2 to 4 (Fig. 7G, H) missing distal segments of rami; leg 2 with 2-segmented endopod.

Leg 5 (Figs. 7A, 8I) uniramous in both legs; both coxae and intercoxal sclerite fused to form common base. Right leg short, reaching one third length of left basis; coxa and basis unarmed; exopod 2-segmented, proximal with minute outer seta at midlength, distal with 2 unequal setae at tip. Left leg as long as urosome; coxa and basis unarmed; exopod 3-segmented, proximal segment as long as basis, with minute outer seta subterminally; middle segment with patch of minute setules at inner distal corner; distal segment bifurcated at tip, with middle and terminal rows of setules along inner margin.

Remarks. The female of the new species is similar to *L. elegans* in having 5 and 2 setae on the coxal and first basal endites of the maxillule, respectively. However it can be readily distinguished from the latter by: (1) the posterolateral angles of the prosome are not pointed terminally; (2) the seminal receptacle is thicker and shorter; (3) pedigers 4 and 5 are incompletely fused, with clear suture between them; (4) the maxillipedal syncoxa has an extremely elongate seta terminally, and (5) the outer spine of the first exopodal segment of leg 1 is well developed, and reaches midway along the third segment.

The pattern of mouthpart reduction in male *Lutamator paradiseus* is similar to that of other aetideids. The mouthparts of copepods are typically multifunctional and it is the food handling parts of the mouthparts that show the most profound degree of atrophy. The mandibular gnathobase, the maxillular arthrite and coxal endite, and the entire maxilla are all markedly reduced in the male of the new species. In contrast the antenna, mandibular palp and maxillular exopod all retain fans of well developed plumose setae, which are presumably involved in generating flow fields over the antennules of the male, as in *Euchaeta* males (Boxshall *et al.*, 1997). Such scanning currents passing across the sensors of the male antennules may entrain pheromonal signals and thus play a role in the mate detection behavior of the species (Ohtsuka & Huys, 2001).

Etymology. The new specific name "*paradiseus* (Latin, meaning paradisiacal)" alludes the type locality, the Nansei Islands, where we can see an extremely high,

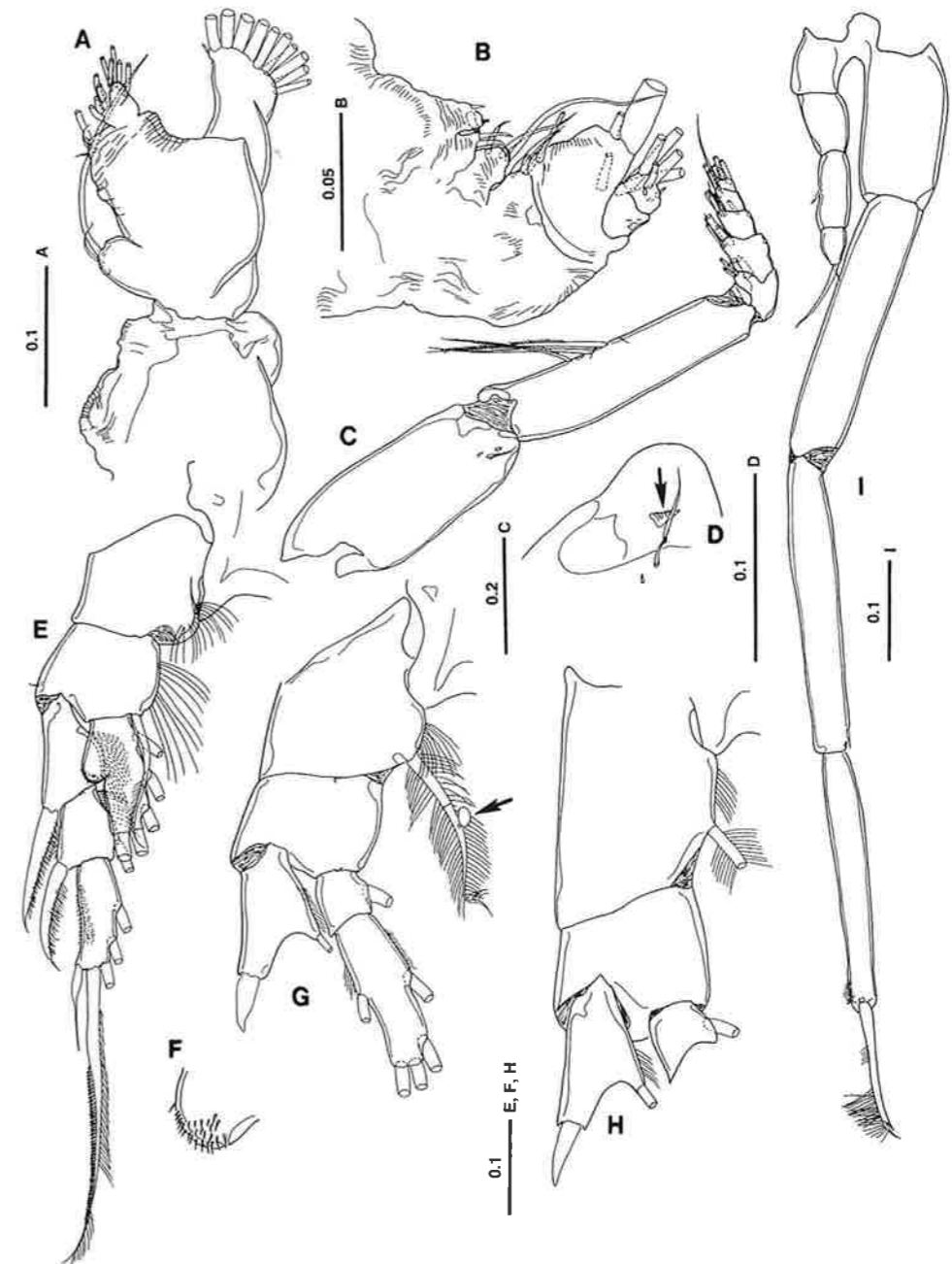


Fig. 8. *Lutamator paradiseus* n. sp., male (paratypes). A, Maxillule; B, Maxilla; C, Maxilliped; D, Distal endite of maxillipedal syncoxa with 4 elements, rudimentary element arrowed; E, Leg 1, anterior surface; F, Outer expansion of endopod of leg 1; G, Leg 2, distal exopodal segment(s) missing, anterior surface, apostome phoront (?) arrowed; H, Leg 4, anterior surface, distal segments of rami missing; I, Leg 5, anterior surface. Scales in mm.

diversified copepod fauna.

Genus *Paracomantenna* Campaner, 1978

Remarks. Since the males of some actideid genera have not yet been discovered, the diagnosis of *Paracomantenna* cannot be stabilized, despite Markhaseva's (1996) comprehensive revision of the entire Aetideidae. The following synapomorphies are shared by females of all known species: (1) rostrum absent; (2) posterolateral angles of pediger 5 strongly produced into acute, dorsally-directed processes; (3) surface of first and second endites of maxilla covered with thick spinules. The significance of these three character states at the generic level is equivocal, given that females in the closely related genus, *Mesocomantenna*, share all three synapomorphies. On this evidence the monophyletic status of *Paracomantenna* cannot be confirmed, and this uncertainty is reinforced by variability within the genus. In particular, the presence of a "digital appendage" sensu Markhaseva (1996) (an aesthetasc-like element) on the maxillipedal syncoxa is not uniform. It is present in some species but absent in others. This apomorphy has been regarded as important in previous classifications of the actideids (cf. Markhaseva, 1996; Boxshall & Halsey, 2004).

Recently Markhaseva and Schnack-Schiel (2003) have described the male of *Paracomantenna minor* (Farran, 1905) from the Great Meteor Seamount, the northeastern Atlantic. Both right and left legs 5 of the male are uniramous, which is similar to that of *Bradydium* spp. (Markhaseva & Schnack-Schiel, 2003). The male of *Mesocomantenna* is unknown at present.

Paracomantenna goi sp. nov.
(Figs. 9–11)

Material examined (types). Holotype (NSMT-Cr 16105): 1 ♀, appendages dissected on glass slides, body stored in alcohol, deposited in vial, collected at St. TY-04-X (off Amami-Oshima Island, Kagoshima, 28°22.37'N, 129°15.97'E~28°22.28'N, 129°15.43'E, 290 m depth), 21 May 2004. Paratypes: 1 ♀, NSMT-Cr 16106, partly dissected and mounted on glass slides, body in vial; 4 ♀♀, NSMT-Cr 16107–16110, whole specimens, locality and collection date same as in holotype.

Body length. Female 2.22 mm (holotype), 2.26, 2.34, 2.35, 2.32, 2.39 mm (paratypes).

Description. Female. Body (Fig. 9A, B) compact; prosome approximately 4 times longer than urosome. Cephalosome separate from first pediger; pedigers 1 to 3 each with posterolateral angles expanded to lamellar plate; rostrum (Fig. 9B, C) absent; fourth and fifth pedigers almost coalescent, but with suture visible dorsally and laterally; fifth pediger (Fig. 9A, B, D, E) strongly produced posteriorly into acutely-pointed processes reaching nearly to posterior margin of second urosomite; process directed slightly dorsally, in lateral view (Fig. 9B, D). Urosome (Fig. 9D, E) 4-segmented; urosomites 1 to 3 with striated hyaline membrane posteriorly; genital double-somite (Fig. 9D–F) symmetrical, laterally expanded at midlength; genital operculum located medioventrally; pair of seminal receptacles about one third as long as double-somite, located laterally, connected via fine seminal duct to genital operculum; anal somite small, with anal operculum weakly developed; caudal rami symmetrical, as long as wide; caudal setae I and II vestigial, seta VII located ventrally.

Antennule (Fig. 9G, H) indistinctly 24-segmented, reaching to posterior margin of

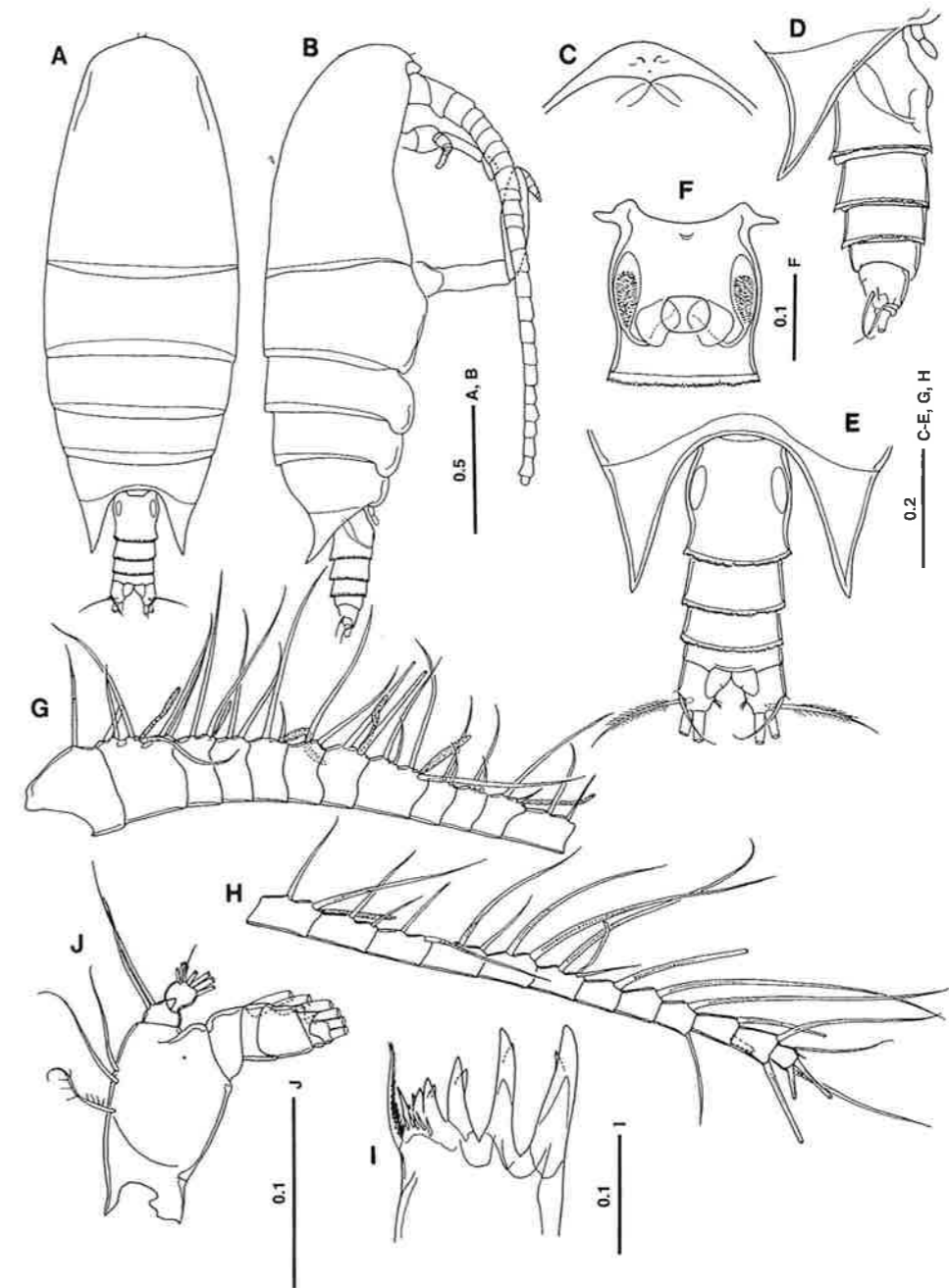


Fig. 9. *Paracomantenna goi* n. sp., female (A–H, J: holotype; I: paratype). A, Habitus, dorsal view; B, Habitus, lateral view; C, Rostrum, ventral view; D, Pediger 5 and urosome, lateral view; E, Pediger 5 and urosome, dorsal view; F, Genital double-somite, ventral view; G, Antennular segments I (first) to XV (12th); H, Antennular segments XVI (13th) to XXVII–XXVIII (24th); I, Mandibular gnathobase; J, Mandibular palp. Scales in mm.

pediger 3 (Fig. 9B); suture between 11th (XIV) and 12th (XV) segments clearly visible; fusion pattern and armature elements as follows I=1, II-IV=6+ae (2, 2+ae, 2), V=2+ae, VI=2, VII=2+ae, VIII=2, IX=2+ae, X-XI=4+ae (2, 2+ae), XII=2, XIII=2, XIV=2+ae, XV=2, XVI=2+ae, XVII=2, XVIII=2, XIX=2, XX=2, XXI=2+ae, XXII=1, XXIII=1, XXIV=1+1, XXV=1+1, XXVI=1+1, XXVII-XXVIII=4+ae.

Antenna (Fig. 10A, B) with basis incompletely fused to endopod, forming allobasis; coxa with single seta at inner distal corner; basis with 2 plumose setae of unequal length. Exopod incompletely 7-segmented; setal formula 2, 2, 1, 1, 1, 1, 1+3. Endopod longer than exopod; proximal segment with 2 subterminal setae; distal segment with 7 setae on terminal part and 8 setae plus 1 vestigial setule on subterminal part.

Mandible (Fig. 9I, J) with 5 sharply pointed, multicusped teeth in addition to simple tooth and spinulose seta on gnathobase. Palp with 3 setae along inner margin of basis. Exopod indistinctly 5-segmented; setal formula 1, 1, 1, 1, 2. Endopod 2-segmented; first segment with 2 setae, second segment bearing 8 setae plus minute seta.

Maxillule (Fig. 10C, D) with well developed praecoxal arthrite bearing 7 spiniform and 4 spinulose setae plus 2 vestigial elements with surface spinules around bases; coxal epipod with 7 well developed setae; coxal and first basal endites each with 4 setae; second basal endite with 5 setae; exopod lamellar, bearing 11 setae along outer margin and patch of fine setules terminally; endopod 2-segmented, proximal segment with 2 knobs, each bearing 4 setae, distal segment with 6 setae.

Maxilla (Fig. 10E, F) stout; first to fourth (2 praecoxal and 2 coxal) endites decorated with stout spinules at base of setae; each bearing 3 spinulose setae; one seta on fourth endite heavily chitinized; basis with 3 setae (1 heavily chitinized, 1 long and 1 simple). Endopod compact, indistinctly 4-segmented; setal formula as follows 1 long+1 vestigial, 1 long+2 vestigial, 2 long, 2 long.

Maxilliped (Fig. 10G, H) with syncoxa inserted at right angle to basis; syncoxa with 1, 2, 3 and 3 setae on first to fourth endites, respectively; rudimentary seta on hairy knob of fourth syncoxal endite (Fig. 10H); basis elongate, with patch of minute spinules proximally and 3 setae midway; endopod 6-segmented; setal formula 1, 4, 4, 3, 3+1, 4.

Seta and spine formula of legs 1-4 as in Table 1. Leg 1 (Fig. 11A) with basis bearing vestigial outer seta; outer spines on first to third exopodal segments abruptly tapering towards tip, ornamented with fine setules and minute spinules along inner and outer margin, respectively; outer expansion of endopod ornamented with minute spinules terminally. Leg 2 (Fig. 11B) with second endopodal segment distally bearing minute setules on posterior surface. Legs 3 (Fig. 11C) and 4 (Fig. 11D) similar, with outer distal corner of basis protruded into round process; second and third endopodal segments sparsely furnished with fine, short setules on posterior surface. Leg 5 (Fig. 11E) vestigial, 2-segmented with common base consisting of incompletely fused coxae and intercoxal plate; distal segment separate from common base, digitiform, unarmed.

Male unknown.

Remarks. The aetideid genus *Paracomantenna* appears to be an exclusively hyperbenthic taxon and for the first time it has been recorded from Japanese waters. *Paracomantenna* currently accommodates the following four species: *P. minor* (Farran, 1905) (off Ireland, the Great Meteor Seamount, 300-800 m), *P. magalyae* Campaner, 1978 (Brazilian coast, 100-113 m), *P. gracilis* Alvarez, 1986 (Brazilian coast, 135 m), and *P. wishnerae* Markhaseva, 1995 (tropical eastern Pacific, 768-825 m) (cf. Markhaseva, 1995, 1996; Markhaseva & Schnack-Schiel, 2003; Bradford-Grieve, 2004).

The new species is most similar to *P. wishnerae* in having sharply pointed poster-

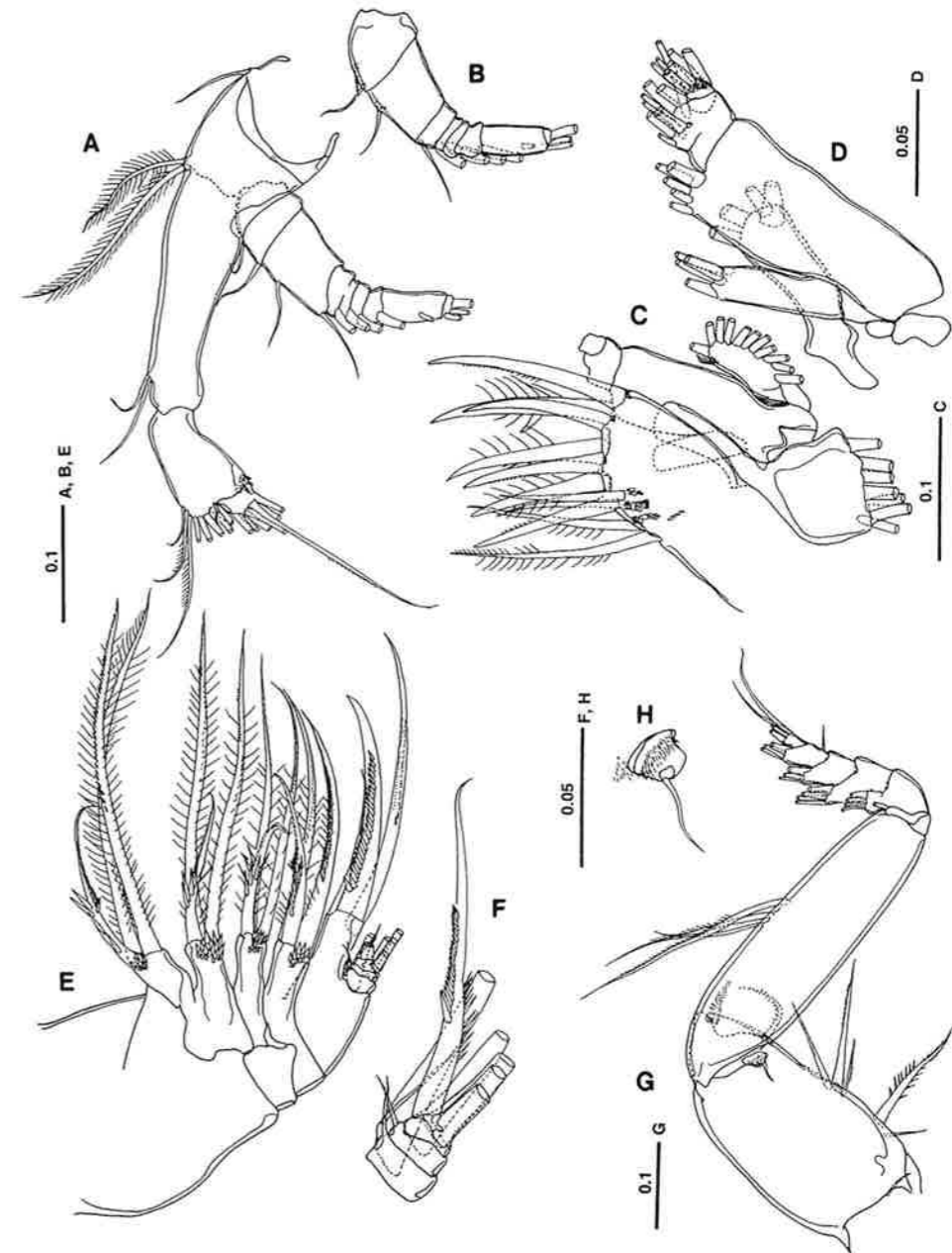


Fig. 10. *Paracomantenna goi* n. sp., female (holotype). A, Antenna; B, Antennary exopod; C, Maxillule, setae on endites and endopod omitted; D, Maxillary endites and endopod; E, Maxilla; F, Maxillary endopod; G, Maxilliped; H, Distal endite of maxillipedal syncoxa. Scales in mm.

olateral angles on the prosome and a vestigial leg 5. However it is distinguishable from the latter by the following features (states in parentheses for *P. wishnerae*): (1) posterior processes of the prosome directed slightly dorsally (directed posteriorly); (2) pedigers 1 to 3 with posterolateral angles expanded to form lamellar plates (not expanded to form such plates); (3) the caudal ramus as long as wide (longer than wide); (4) a minute seta present

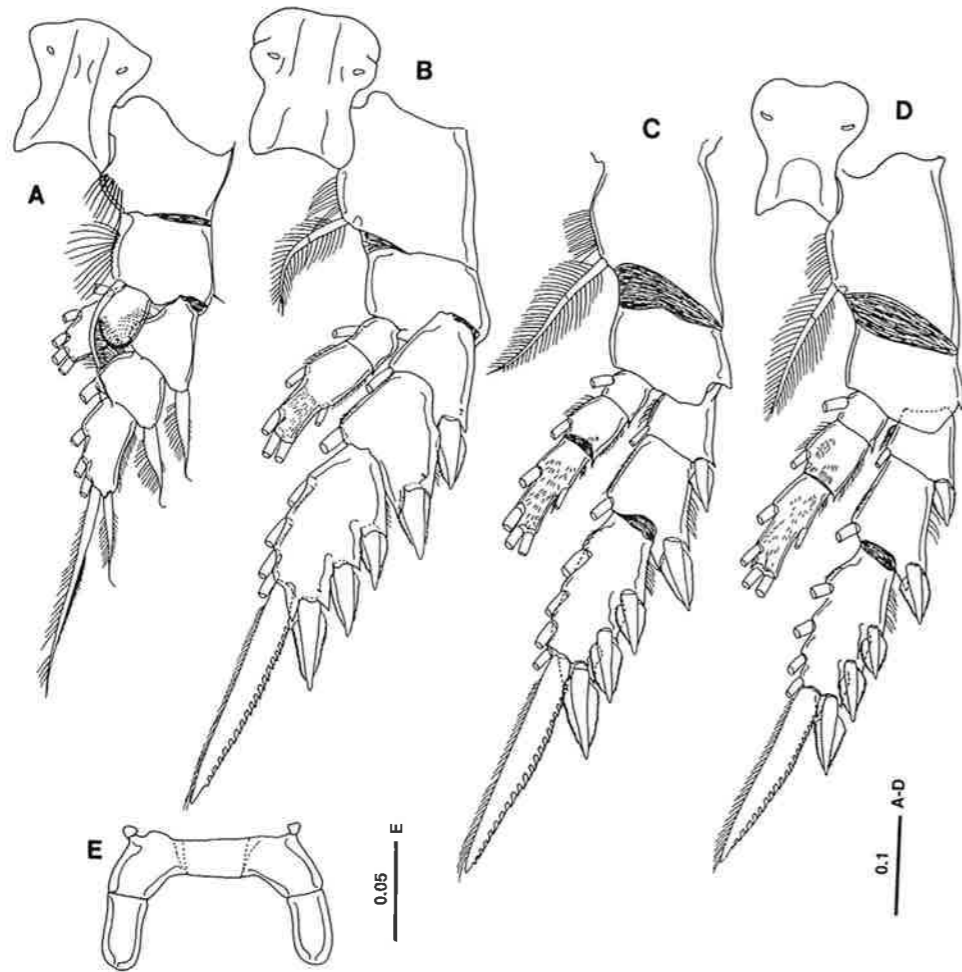


Fig. 11. *Paracomantenna goi* n. sp., female (holotype). A, Leg 1, anterior surface; B, Leg 2, anterior surface; C, Leg 3, posterior surface; D, Leg 4, posterior surface; E, Leg 5 anterior surface. Scales in mm.

on the proximal lobe of the second endopodal segment of the antenna (absent); (5) setae on the basis and the first endopodal segment of the mandible relatively long (short); (6) the second endopodal segment of the mandible with 8 setae plus a minute seta (only 8 setae); (7) greater numbers of setae (5, 8, 6) on the second basal endite and the endopod of the maxillule (4, 5, 6 based on Markhaseva, 1996: Fig. 13); (8) three setae on the fourth syncoxal endite of the maxilliped (4 setae); and (9) no serrations along the outer margin of the terminal exopodal segment of leg 2 (serrations present).

Etymology. The new species is named in honor of the captain, Mr. A. Go, of T/S *Toyoshio-Maru* in recognition of his contributions to our research.

Discussion

The present investigation in the deep-waters off the Nansei Islands, southwestern Japan, has revealed a high diversity of hyperbenthic calanoid copepods in the North

Table 2. Regional comparison of deep-sea hyperbenthic calanoid copepod genera between the North and South Pacific, the Atlantic and the Indian. ○: recorded (Atlantic: Sars, 1924, 1925; Bradford, 1969; Grice & Hulsemann, 1970; Grice 1972; Markhaseva, 1996; Jaume *et al.*, 2000; Bradford-Grieve, 2004; North Pacific: Ohtsuka *et al.*, 1994, 2002, 2003, present study; Ferrari & Markhaseva, 1996; Markhaseva & Ferrari, 1996; Ferrari & Markhaseva, 2000a; Shimode *et al.*, 2000; Bradford-Grieve, 2004; Ohtsuka & Boxshall, 2004, Ohtsuka, unpublished data; South Pacific: Bradford, 1969; Bradford & Jillett, 1980; Markhaseva, 1996; Ferrari & Markhaseva, 2000b; Bradford-Grieve, 2004; Indian: Ohtsuka *et al.*, 2002; Bradford-Grieve, 2004).

Taxon	North Pacific	South Pacific	Atlantic	Indian
Aetideidae				
<i>Aetideopsis</i>	○	○	○	
<i>Aztogekeras</i>	○			
<i>Bradyetes</i>	○		○	
<i>Bradydius</i>		○	○	
<i>Chiridius</i>	○		○	
<i>Comantenna</i>	○	○	○	
<i>Crassantenna</i>		○		
<i>Lutamator</i>	○	○	○	
<i>Mesocomantenna</i>			○	
<i>Parabradydius</i>		○		
<i>Paracomantenna</i>	○		○	
<i>Pseudeuchaeta</i>		○		
<i>Pseudotharybis</i>		○	○	
<i>Pterochirella</i>				○
<i>Sursamucro</i>		○		
Arietellidae				
<i>Campaneria</i>		○		
<i>Crassarietellus</i>			○	
<i>Griceus</i>	○			
<i>Metacalanus</i>	○			
<i>Paraugaptiloides</i>		○		○
<i>Paramisophria</i>	○		○	
<i>Sarsarietellus</i>	○		○	○
<i>Scutogerulus</i>		○		
Bathypontiidae				
<i>Alloiopodus</i>		○		
Diaixidae				
<i>Diaixis</i>			○	
Hyperbionychidae				
<i>Hyperbionyx</i>			○	
Parkiidae				
<i>Parkius</i>	○			
Phaennidae				
<i>Brachycalanus</i>	○		○	
<i>Xanthocalanus</i>	○		○	
Ryocalanidae				
<i>Ryocalanus</i>	○		○	
Scolecitrichidae				
<i>Cenognatha</i>			○	
<i>Grievella</i>		○		
<i>Macandrewella</i>	○	○		○
<i>Neoscolecithrix</i>	○	○	○	
<i>Parundinella</i>			○	
<i>Rythabis</i>			○	
<i>Scolecocalanus</i>	○	○		
Spinocalanidae				
<i>Damkaeria</i>			○	
Tharybidae				
<i>Tharybis</i>	○	○	○	
<i>Undinella</i>			○	

Pacific, similar to that already reported for the South Pacific (mainly off New Zealand) and the Atlantic (Table 2). However, taxonomic investigations on deep-sea hyperbenthic calanoids in the North Pacific are still in their relative infancy, and future work will undoubtedly reveal more genera or families from these waters. Indeed, undescribed species of *Sarsarietellus* (Arietellidae), *Comanantenna* (Aetideidae) and *Scolecocalanus* (Scolecitrichidae) collected from Japanese waters are currently awaiting description (Ohtsuka, unpublished data).

Calanoids known to inhabit the deep-sea hyperbenthos are restricted to the families Aetideidae, Arietellidae, Bathypontiidae, Diaixidae, Hyperbionychidae, Parkiidae, Phaennidae, Ryocalanidae, Scolecitrichidae, and Tharybidae (Bradford-Grieve, 2002, 2004). Within this assemblage, the hyperbenthic genera belonging to the families Bathypontiidae, Hyperbionychidae, Parkiidae, and Ryocalanidae, are either monotypic or accommodate only a few species. They are strictly confined to the deep-sea. In contrast, the other families also contain many shallow-water hyperbenthic taxa. The hypothesized evolutionary histories of these families are remarkably different, and it appears likely that they might have independently colonized deep hyperbenthic habitats several different times since the Paleozoic (Bradford-Grieve, 2002, 2004; Ohtsuka, 2004). However almost all the specialist hyperbenthic genera are widely distributed in the world oceans at present, although their distributions are relatively defined at the species level. This pattern may be explained in part by the relative homogeneity of the deep-sea environment, which permitted their ancestors to colonize ocean basins horizontally prior to speciation in response to geological events.

Acknowledgements

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