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New Aegisthidae (Copepoda: Harpacticoida) from western Pacific cold seeps and hydrothermal vents

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Hyperbenthic harpacticoid samples from Japanese hydrothermal vents in the Okinawa Trough and cold seep sites in Sagami Bay were examined and resulted in the discovery of four new species belonging to three new genera of Aegisthidae (Copepoda: Harpacticoida). Females of ***Nudivorax todai* gen.** et **sp. nov.** possess a large area of flexible integument between the cephalosome and the first pedigerous somite which is suggestive of a gorging feeding strategy. Main diagnostic characters separating the new genus from other Aegisthidae are provided by the unusually short caudal rami, the complete lack of integumental surface lamellae, and the presence in the male of a linear array of pores along the rostral margin which appears to be sensory in function. ***Scabrantenna yooi* gen.** et **sp. nov.** displays several similarities with *Aegisthus aculeatus* Giesbrecht, 1891 but is highly distinctive in its male morphology which includes extremely atrophied mouthparts and a unique prehensile antenna. ***Jamstecia terazakii* gen.** et **sp. nov.** is only known from a single female caught in the Okinawa Trough. ***Jamstecia* gen. nov.** is most closely related to *Andromastax* Conroy-Dalton & Huys, 1999 but can be distinguished on the basis of the elongate antennules, the antennary morphology, the absence of lateral spinous processes on the cephalosome and swimming legs 2–4, and differences in the mandibular palp and armature of the maxilliped. ***Andromastax cephaloceratus* sp. nov.** differs from the type species *A. muricatus* Conroy-Dalton & Huys, 1998 primarily in the presence of long spinous processes on the cephalosome and the absence of the inner seta on the female P5.

ADDITIONAL KEYWORDS:—Aegisthidae – hydrothermal vents – cold seeps – hyperbenthos – taxonomy – copepod – Western Pacific.

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INTRODUCTION

The Aegisthidae is traditionally regarded as one of the three exclusively holoplanktonic families within the Harpacticoida. In contrast to the other families, Miraciidae and Clytemnestridae, which primarily occur in the epipelagic zones of the oceans, aegisthids are typically mesopelagic or even bathypelagic. The recent discovery of a new primitive genus *Andromastax* Conroy-Dalton & Huys from hydrothermal vent sites at the Galapagos Rift raised the suspicion that the family might also be distributed in the hyperbenthic environment (Conroy-Dalton & Huys, 1999). The latter, together with anchihaline caves and hydrothermal vents (and cold seeps) was recognized by Huys & Boxshall (1991) as one of the key habitats on the Earth's surface in our continuous search for copepods of high phylogenetic significance. In response to the limited accessibility of these habitats, a number of sophisticated sampling techniques and sampling gear has been developed in recent years. For example, the Japan Marine Science and Technology Center (JAMSTEC) invested much effort in the design of suitable methods for sampling the benthopelagic organisms which inhabit the water overlying hydrothermal vents and cold seeps. Initially, benthopelagic sampling was performed by newly designed nets attached to the deep-sea submersible *Shinkai 2000* (Kikuchi *et al.*, 1990) but this method showed serious limitations in the quantitative estimation of benthopelagic plankton. This led to the alternative solution of attaching sampling gear to the highly successful Deep Tow System of JAMSTEC. The design of a multiple opening and closing plankton sampler (DT-MPS) by modification of Terazaki's (1991) vertical multiple plankton sampler (ORI-VMPS) allowed benthopelagic sampling at a distance of 0.5 to 3 m above the bottom. Using this sampling gear hyperbenthic copepods were collected in the cold seep area southeast off Hatsushima Island (Toda *et al.*, 1995) and around the hydrothermal vent fields in the Okinawa Trough (Fig. 1). This paper reports on the discovery of three new genera and four new species of Aegisthidae found in these samples, doubling the number of known species within the family.

MATERIAL AND METHODS

Specimens were dissected in lactic acid and the dissected parts were mounted on slides in lactophenol mounting medium. Preparations were sealed with Glyceel or transparent nail varnish. All drawings have been prepared using a camera lucida on an Olympus BH-2 or a Zeiss Axioskop differential interference contrast microscope. Females and males of *Nudivorax todai* gen. et sp. nov. were examined with a Philips XL 30 scanning electron microscope. Specimens were prepared by dehydration

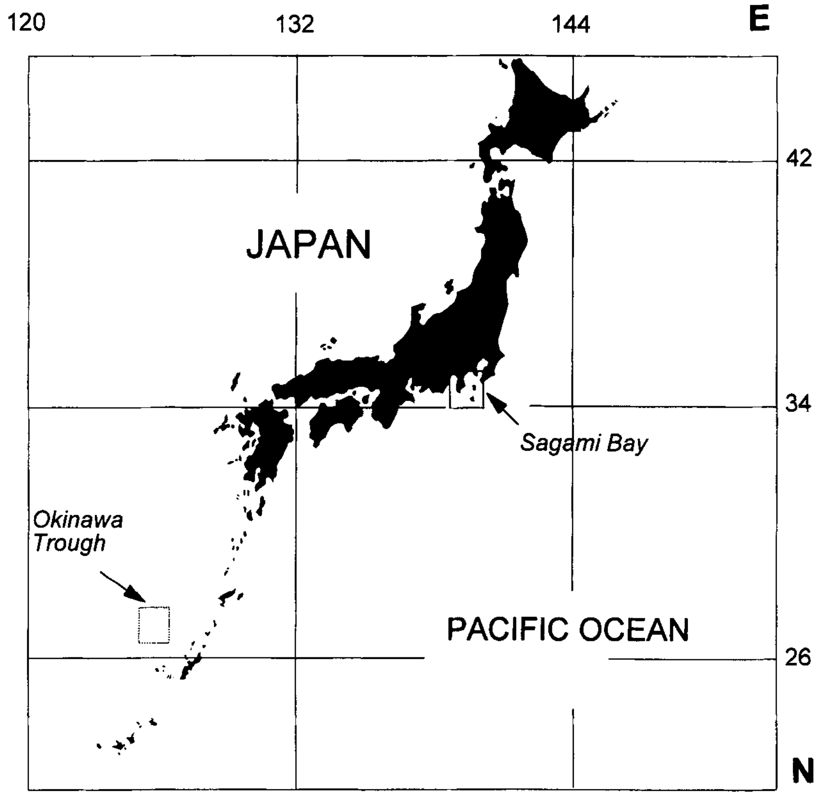

Figure 1. Map showing position of Sagami Bay and Okinawa Trough.

through graded acetone, critical point dried, mounted on stubs and sputter-coated with palladium.

The descriptive terminology is adopted from Huys & Boxshall (1991). Abbreviations used in the text are: ae, aesthetasc; P1–P6, first to sixth thoracopod; exp(enp)-1(2,3) to denote the proximal (middle, distal) segment of a ramus. Type series are deposited in the collections of The Natural History Museum (NHM).

SAMPLING SITES

Cold seep sites

Plankton samples were collected at the southeast side of Hatsushima Island in Sagami Bay during 21–23 February 1992. A multiple plankton sampler (DT-MPS) attached to the lower part of the Deep Tow system was used to collect benthopelagic samples from 0.5 to 3 m above the bottom. The DT-MPS is an opening/closing sampler with four plankton nets (for more technical details, see Terazaki (1991) and Toda *et al.* (1995). The Hatsushima area is known for its cold seep sites dominated by large colonies of the giant vesicomyid clam *Calyptogena soyoae* Okutani (Hashimoto *et al.*, 1989). Five transects in the area were sampled during the *Kaiyo Maru* DK–92–2–SGM–OGS cruise. Cold seep samples were collected along the second,

TABLE 1. Locality data of stations sampled with Deep-Tow system in Okinawa Trough

Station	Date	Latitude (N)	Longitude (E)	Time (min)	Depth (m)
DT1-1	30 Jan 1993	28°23.755′	127°37.844′	14	667
DT1-2	30 Jan 1993	28°23.755′–28°23.877′	127°37.844′–127°38.082′	18	667–629
DT1-3	30 Jan 1993	28°23.887′–28°23.962′	127°38.082′–127°38.772′	43	629–605
DT1-4	30 Jan 1993	28°23.962′–28°24.057′	127°38.772′–127°39.125′	21	605–629
DT2-1	31 Jan 1993	28°23.754′–28°23.799′	127°38.444′–127°38.402′	16	641
DT2-2	31 Jan 1993	28°23.799′–28°23.397′	127°38.402′–127°38.385′	22	641–711
DT2-3	31 Jan 1993	28°23.397′–28°23.027′	127°38.385′–127°38.412′	30	711–583
DT2-4	31 Jan 1993	28°23.027′–28°23.910′	127°38.412′–127°38.416′	8	583–610
DT4-1	31 Jan 1993	28°26.141′–28°26.144′	127°38.439′–127°38.325′	15	823
DT4-2	31 Jan 1993	28°26.144′–28°25.909′	127°38.325′–127°38.012′	19	823–780
DT4-3	31 Jan 1993	28°25.909′–28°25.824′	127°38.012′–127°37.853′	15	780–759
DT4-4	31 Jan 1993	28°25.824′–28°25.791′	127°37.853′–127°37.594′	15	759–728

third and fourth transects. Detailed sampling characteristics of the individual transects and preliminary results of the benthopelagic plankton samples are given by Toda *et al.* (1995).

Hydrothermal vent sites

Transects were sampled near and around vent fields in the Okinawa Trough at depths of 186–823 m using DT-MPS. Sampling characteristics of the various sites are compiled in Table 1.

SYSTEMATICS

Family Aegisthidae Giesbrecht, 1892

***Nudivorax* gen. nov.**

Diagnosis

Aegisthidae. Body without surface reticulation or spinous processes. Caudal rami distinctly shorter than rest of body. Rostrum completely incorporated into cephalic shield. Coxae of P2–P4 without outer spinous process. P1 endopod indistinctly 2-segmented. Distal outer element of P1 exp-3 spiniform.

Swimming leg armature formula:

	coxa	basis	exopod	endopod
P1	0-0	1-I	I−1;I−1;I,2,2	0−1;1,2,3
P2	0-0	1-0	I−1;I−1;III,I+1,2	0−1;0−2;1,2,2
P3	0-0	1-0	I−1;I−1;III,I+1,2	0−1;0−2;1,2,I+2
P4	0-0	1-0	I−1;I−1;III,I+1,3	0−1;0−1[♂:2];1,2,I+1

Sexual dimorphism in general body shape, rostrum, antennule, antenna, labrum, mandible, maxillule, maxilla, maxilliped, P1 inner basal spine, P2–P4 bases, P4 endopod, P5, P6, genital segmentation, anal somite and body size. Males non-feeding.

Female

Cephalosome separated from first pedigerous somite by dorsal area of folded integument; anterior margin without large pores. Antennule 7-segmented; without spinous processes on anterior margin of segment 2. Antenna with indistinctly 3-segmented exopod (armature formula 1–1–1); endopod with 3 lateral and 6 apical elements. Mandible with 2-segmented palp bearing 2 setae on apical segment. Maxillule with 3 elements on coxal endite and 8 elements on palp. Maxilla with 4 endites on syncoxa (formula [4,3,3,2]); allobasis with 2 anterior and 3 posterior elements; endopod with formula [2,2,4]. Maxilliped with 3 spines and 3 setae on protopod and 1 lateral plus 3 apical setae on endopod. P1 with inner basal seta shorter than endopod. P5 1-segmented; with 1 (basal) seta and 3 spines along outer margin, and 2 spines plus 1 seta apically. P6 with 3 elements.

Male

Prosome without dorsal area of folded integument between cephalosome and first pedigerous somite. Cephalosome with linear array of pores along anterior margin. Anal somite bilaterally constricted; operculum incised and lobate. Antennule 9-segmented, with geniculation between segments 7 and 8; segments distal to geniculation not prolonged. Antenna with indistinctly 3-segmented exopod (formula [1, 1,1]); allobasis without abexopodal seta; endopod with 3 lateral and 6 apical elements. Mandible strongly reduced; palp 1-segmented with 2 apical setae. Maxillule reduced; 3-segmented; coxal endite with 3 elements; some outer distal setae of palp reduced. Maxilla with reduced praecoxal endites; some setae on allobasis strongly reduced; endopod with formula [2,2,4]. Maxilliped more slender than in ♀; protopod with 6 setae; endopodal setae with stronger spinules. P1 inner basal spine distinctly longer than in ♀. Bases of P2–P4 with inner lobate extension. P4 enp-2 with additional inner seta. P5 indistinctly 2-segmented; basis and exp-1 partly fused; exp-2 with 2 outer spines, 2 apical spines and 2 inner setae. P6 with 1 vestigial and 2 well developed setae; medial margin with 2 spinular tufts.

Type and only species

Nudivorax todai gen. et sp. nov.

Etymology

The generic name is derived from the Latin *nudus*, meaning naked and referring to the complete absence of surface reticulation on the body somites, and *vorax, voracis*, meaning gluttonous, voracious, alluding to the presence of membranous integument between the cephalosome and the first pedigerous somite which indicates a gorging feeding strategy.

Nudivorax todai gen. et sp. nov.

Type locality

Sagami Bay, southeast of Hatsushima Island, transect 5, Stn 3, depth 1306.4 m.

Material examined

Holotype ♀ dissected and mounted on 23 slides (type locality; NHM reg. no. 1998.246). Paratypes are 10 ♀ ♀ and 4 ♂ ♂, all collected in Sagami Bay. Sampling details and registration numbers are given in Table 2.

TABLE 2. ***Nudivorax todai* gen.** et **sp. nov.** Sampling details and registration numbers of paratypes

Transect	Station	Depth (m)	Specimens	Preservation	NHM Reg. no.
2	2	941.6	1 ♀	alcohol	1998.250
2	3	1116.4	1 copepodid	alcohol	1998.251
3	2	1240.8	2 copepodids	alcohol	1998.252–3
5	2	1306.4	4 ♀ ♀, 2 ♂ ♂, 1 copepodid	4♀ ♀, 1 ♂, 1 cop. in alcohol 1 ♂ on SEM stub	1998.254–9
5	3	1306.4	5 ♀ ♀, 2 ♂ ♂, 4 copepodids	2 ♀ ♀, 4 copepodids in alcohol 1 ♀ on 9 slides 2 ♂ ♂ on 18 slides each 2 ♀ ♀ on SEM stub	1998.260–5 1998.247 1998.248–9

Description of female

Total body length 1800 µm (measured from anterior margin of cephalic shield to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 450 µm. Urosome distinctly narrower than prosome (Fig. 2A). Cephalic shield separated from first pedigerous somite by dorsal area of loosely folded, membranous integument; this area particularly visible in lateral aspect when cephalosome is ventrally deflected (arrowed in Fig. 2B), but completely concealed in specimens where first pedigerous somite has telescoped into the posterior part of the cephalosome (arrowed in Fig. 2C).

Prosome (Fig. 2A,B) 5-segmented, comprising cephalosome and 4 free pedigerous somites. Cephalosome and prosomites (bearing P1–P4) without surface reticulation. Ornamentation consisting of pores and few sensillae; P1-bearing somite without sensillae.

Cephalosome bell-shaped, with rounded anterior margin and slightly swollen posterolateral angles; pleural areas strongly developed, rounded. Rostrum completely incorporated into cephalic shield. Pedigerous somites without spinous processes. Hyaline frills of prosomites plain and smooth.

Urosome (Figs 2A, B, 8A–C) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with pattern of surface ornamentation consisting of small spinules or denticles dorsally and ventrally. Hyaline frills of urosomites denticulate.

Genital double-somite (Fig. 8A–C) with transverse surface ridge dorsally and laterally, indicating original segmentation; completely fused ventrally. Genital field positioned far anteriorly, near articulation with P5-bearing somite (Fig. 8A); copulatory pore minute (arrowed in Fig. 9C); gonopores fused medially forming single genital slit covered on both sides by well developed opercula derived from sixth legs; P6 elongate, with 2 long pinnate setae apically, separated by small lobate process, and minute seta on subdistal inner margin (Fig. 9C).

Anal somite (Fig. 8C) with large anal opening; anal operculum vestigial, bordered by tiny spinules anteriorly.

Caudal rami (Figs 2,8A) closely adpressed medially and fused distally (Fig. 8a); distinctly shorter than rest of body, about 2.35 times length of body somites combined; covered with dense pattern of spinules. Each ramus with 7 setae; seta 1 minute (Fig. 8c) and typically positioned asymmetrically on both rami (in proximal third; Fig. 8A); seta II spiniform, unipinnate and with subapical flagellate extension (Fig. 8F);

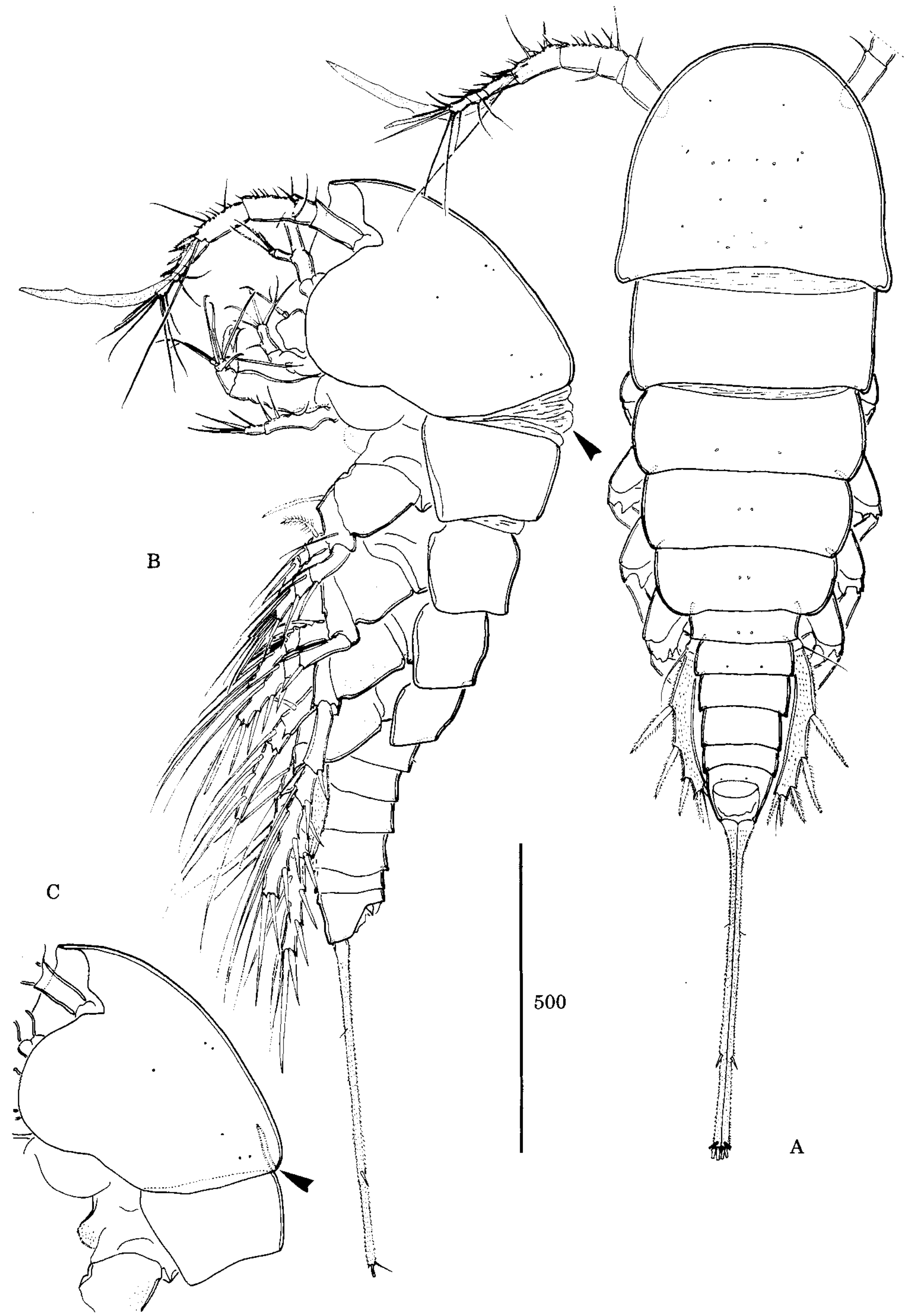

Figure 2. ***Nudivorax todai*** **gen.** et **sp. nov.** (♀). A, habitus, dorsal; B, habitus, lateral [arrow indicating folded membranous integument]; C, cephalosome and first pedigerous somite, lateral, in telescoped condition [arrowed].

other setae broken or incomplete in most specimens: seta III absent in all specimens examined but possible position indicated by scar (Fig. 8G), setae IV and V fused basally, seta VI minute and displaced ventrally, seta VII tri-articulate at base.

Antennule (Fig. 3A) 7-segmented, segment 2 longest; with small sclerite around base of segment 1; most segments with irregular pattern of fine spinules; majority of setae short and pinnate. Armature formula: 1-[1], 2-[4 bare + 8 pinnate], 3-[4 bare + 9 pinnate + (1 bare + ae)], 4-[3 bare + 1 pinnate], 5-[2 bare], 6-[1 bare + 1 pinnate], 7-[6 + acrothek]. Apical acrothek consisting of well developed aesthetasc fused basally to slender seta; aesthetasc on segment 3 large (310 μm), fused to short seta (Fig. 3D); both aesthetascs with supporting chitinous rib. Long seta on segment 3 pinnate in proximal portion. No spinous processes present on segment 2.

Antenna (Figs 4A, B, 9D) 3-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa irregular in shape, with pattern of fine spinules. Basis and proximal endopod segment completely fused forming elongate allobasis with 1 abexopodal seta in distal third. Exopod indistinctly 3-segmented with segments 2 and 3 incompletely fused (Fig. 9D); proximal segment about 2.5 times as long as wide, other segments minute; armature formula [1,1,1] with middle seta longest. Endopod elongate, longer than allobasis; lateral armature arising in proximal half, consisting of 1 short and 2 long pinnate setae; apical armature consisting of 1 short spiniform and 5 long setae (1 claw-like, 4 fused basally in pairs; Fig. 4B). Both allobasis and endopod with numerous minute spinules.

Labrum with elaborate spinular ornamentation as in Figure 4C.

Mandible (Fig. 3B) with long coxa bearing well developed gnathobase; cutting-edge with 8 major teeth alternating with smaller ones around distal margin, several patches of minute spinules and 1 unipinnate seta at dorsal corner. Palp minute, 2-segmented; basal segment unarmed; distal segment longer than wide, with 1 naked seta and 1 longer, bipinnate seta.

Paragnaths strongly developed lobes with medially directed hair-like setules (Fig. 4D); separated by medial lobe covered with dense pattern of short setules.

Maxillule (Fig. 5B). Praecoxa with numerous spinules around or near outer margin; arthrite strongly developed, with 2 swollen plumose setae on anterior surface and 11 spines/setae around distal margin. Coxa with cylindrical endite bearing 2 plumose setae and 1 curved unipinnate spine. Basis without discrete rami; slightly bilobate distally; inner lobe with curved spine and 2 plumose setae, outer lobe with 3 simple and 2 geniculate setae.

Maxilla (Fig. 4E) comprising syncoxa, allobasis and 3-segmented endopod. Syncoxa with spinular patches near and along outer margin and around base of proximalmost endites; with 4 endites: proximal praecoxal endite lobate, positioned far proximally, with 4 bipinnate setae; distal praecoxal endite almost entirely incorporated into syncoxa, represented by 3 setae; coxal endites closely set near articulation with allobasis, both cylindrical and with 3 and 2 setae, respectively. Allobasis drawn out into long slightly curved, sparsely pinnate claw; accessory armature consisting of 1 pinnate seta and 1 curved pinnate spine on posterior surface, 1 curved spine and 1 short naked seta on anterior surface, and 1 naked seta near boundary with first endopod segment; posterior surface also with short tube pore and numerous spinules. Endopod with armature formula 1-[2 geniculate], 2-[2 geniculate], 3-[1 geniculate + 3 bare].

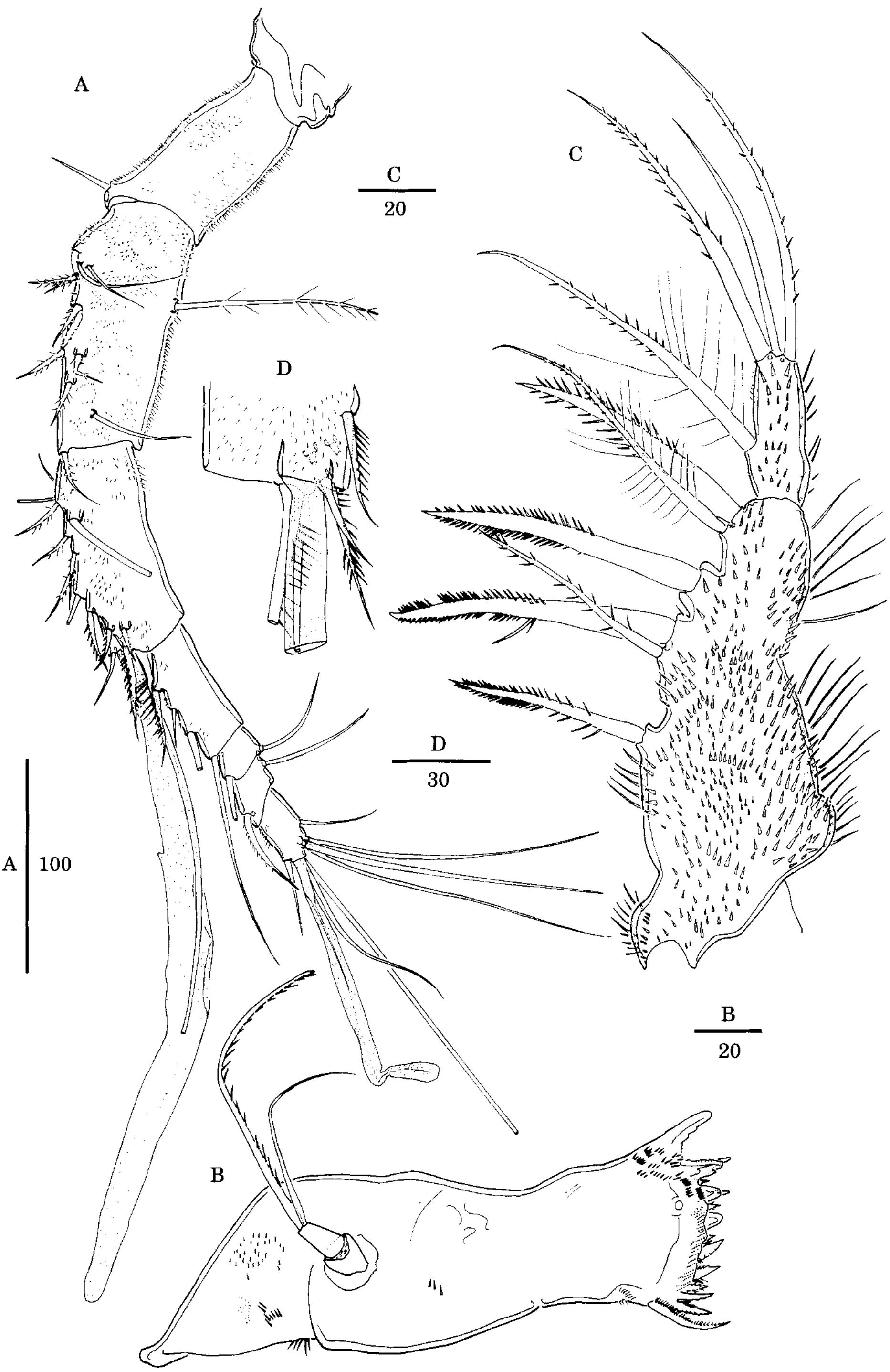

Figure 3. ***Nudivorax todai* gen.** et **sp. nov.** (♀). A, antennule, dorsal; B, mandible; C, maxilliped. D, anterior margin of antennulary segment 3, ventral.

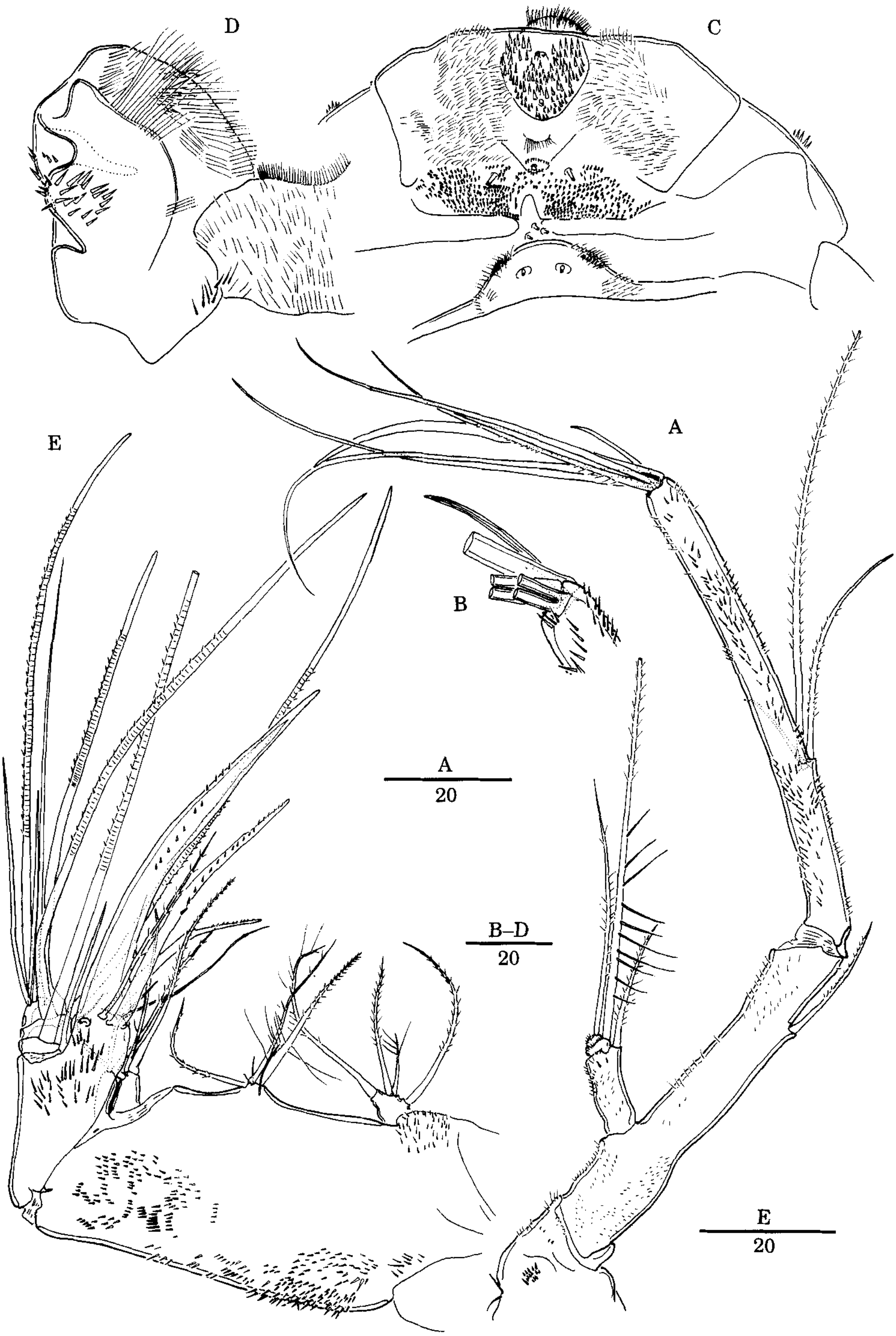

Figure 4. ***Nudivorax todai*** **gen.** et **sp. nov.** (♀). A, antenna; B, detail of distal armature of antennary endopod; C, labrum, posterior; D, left paragnath, anterior; E, maxilla.

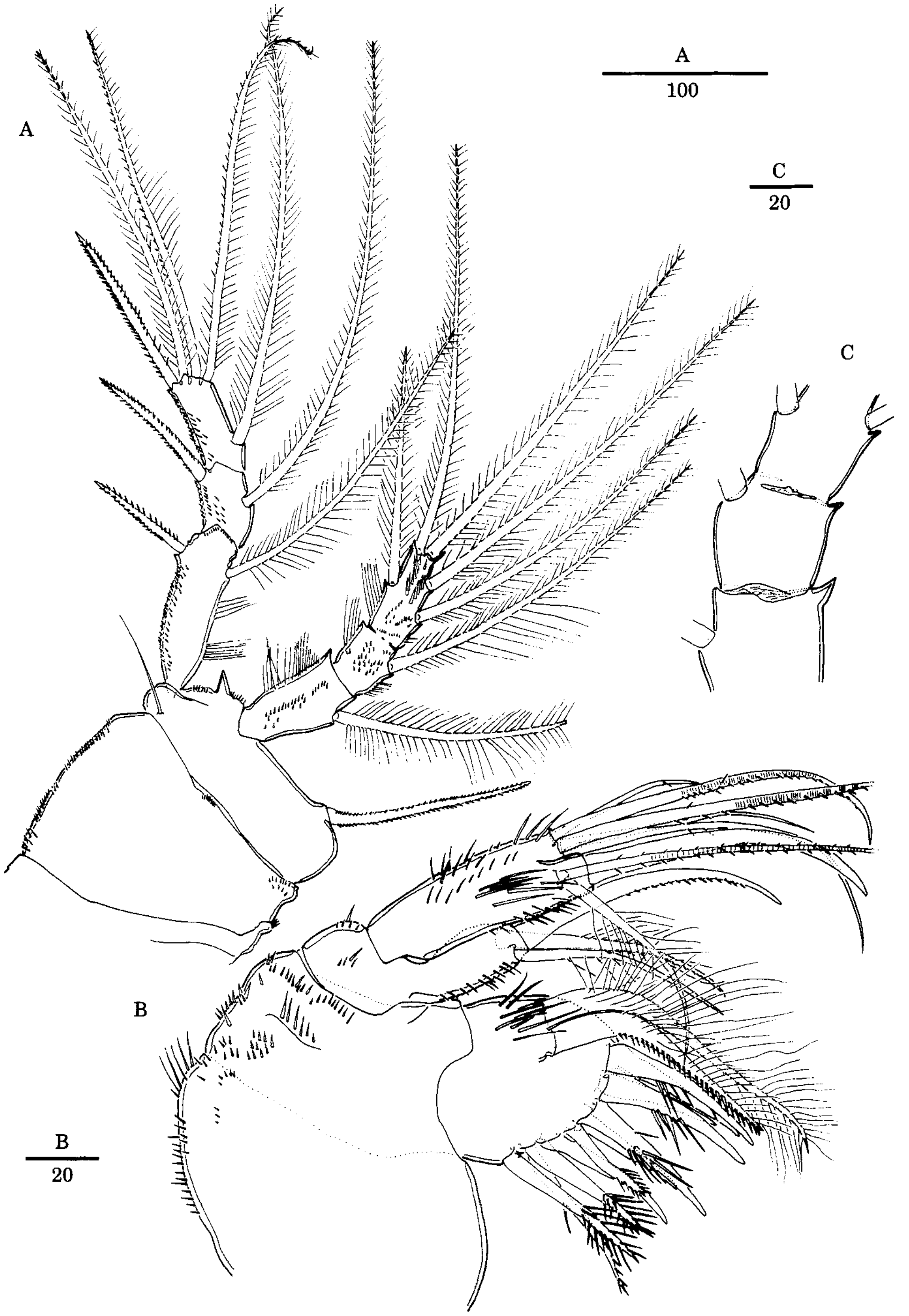

Figure 5. ***Nudivorax todai* gen.** et **sp. nov.** (♀). A, P1, anterior; B, maxillule, anterior; C, P1 endopod, posterior.

Maxilliped (Fig. 3C) 2-segmented, comprising undivided protopod and 1-segmented endopod. Both segments covered with dense pattern of small spinules; outer margin with longer spinules (endopod) or setules (arranged in two groups reflecting fused syncoxa and basis). Protopod large, with 6 elements representing 4 vestigial endites; endite 1 represented by bipinnate seta, endite 2 with 1 large bipinnate spine and 1 bipinnate seta, endite 3 represented by small cylindrical process with large bipinnate spine, endite 4 with 1 large bipinnate spine and 1 slender seta (plumose proximally, pinnate distally). Endopod without surface sutures marking original segmentation; about 3 times as long as wide; with 1 semiplumose seta laterally and 3 setae apically (middle one bare and shortest; others longer and bipinnate).

Swimming legs P1–P4 (Figs 5A, 6, 7A) with indistinctly 2-segmented (P1 endopod; derived by fusion of middle and distal segments; Fig. 5c) or distinctly 3-segmented (P1 exopod; P2–P4) rami; endopods distinctly shorter than exopods. Spine and setal formula as for genus. Intercoxal sclerites large and wide. Coxae without outer spinous processes; with pattern of surface spinules as figured. Bases with anterior patch of surface spinules as figured; inner margin with setular tuft and/or small rounded process in P2–P4; inner basal spine of P1 bipinnate, distinctly shorter than endopod; outer basal seta of P1, P3 and P4 short, of P2 vestigial (arrowed in Fig. 6B). All segments with pattern of spinules as figured. Posterior surface of P2–P4 enp-1 and enp-3 with row of coarse spinules (not figured). Outer margins of endopodal segments with long setules. Spine and setal formula as for genus. Exopodal spines bipinnate in P1, serrate or pectinate in P2–P4. Distal inner seta of enp-3 setiform in P1–P2, spiniform and rod-shaped in P3–P4.

Fifth pair of legs (Fig. 8A) very large, extending to posterior margin of anal somite; joining in ventral midline but not fused medially; distinctly curved inwards. P5 uniramous, indistinctly 2-segmented with incomplete suture line along inner margin marking boundary between protopod and exopod; outer basal seta slender, plumose; exopodal armature consisting of 3 serrate spines (pinnate proximally) along outer margin and 1 dorsal, sparsely plumose seta flanked by outer biserrate and inner uniserrate spine around apex; dorsal seta arising from small tubercle (Fig. 8H); entire leg covered with dense pattern of minute spinules.

Description of male

More slender than ♀. Body length 1500 μm (measured from anterior margin of cephalic shield to posterior margin of caudal rami). Largest width measured at about halfway the cephalic shield length: 295 μm. Urosome distinctly narrower than prosome (Fig. 10A).

Prosome (Figs 9A, 10A) 5-segmented, comprising cephalosome and 4 free pedigerous somites. Cephalosome bell-shaped, with rounded anterior margin, constricted at level of antennules; pleural areas well developed but less rounded than in ♀. Rostrum completely incorporated into cephalic shield. Anterior margin between bases of antennules with series of large valve-like pores (Figs 10A, B, 13A, B). Additional similar pores present dorsally in anterior half of cephalic shield. Prosomites without surface reticulation but integument slightly folded on cephalic shield and first pedigerous somite; ornamentation consisting of sensillae, pores and irregular pattern of tiny spinules. Hyaline frills plain and smooth. No spinous processes present.

Urosome (Figs 9A, 10A) 6-segmented, comprising P5-bearing somite, genital

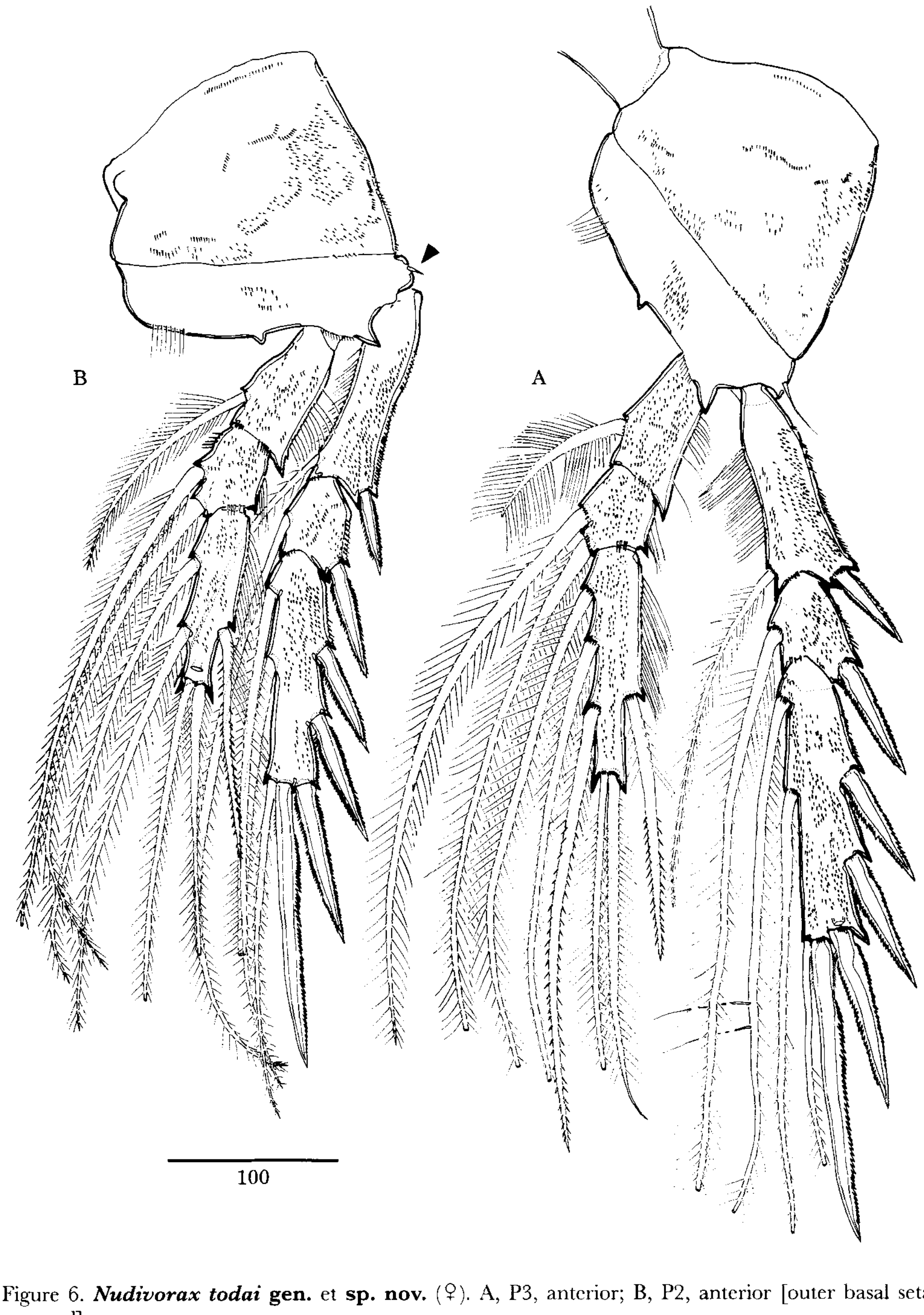

Figure 6. ***Nudivorax todai* gen.** et **sp. nov.** (♀). A, P3, anterior; B, P2, anterior [outer basal seta arrowed].

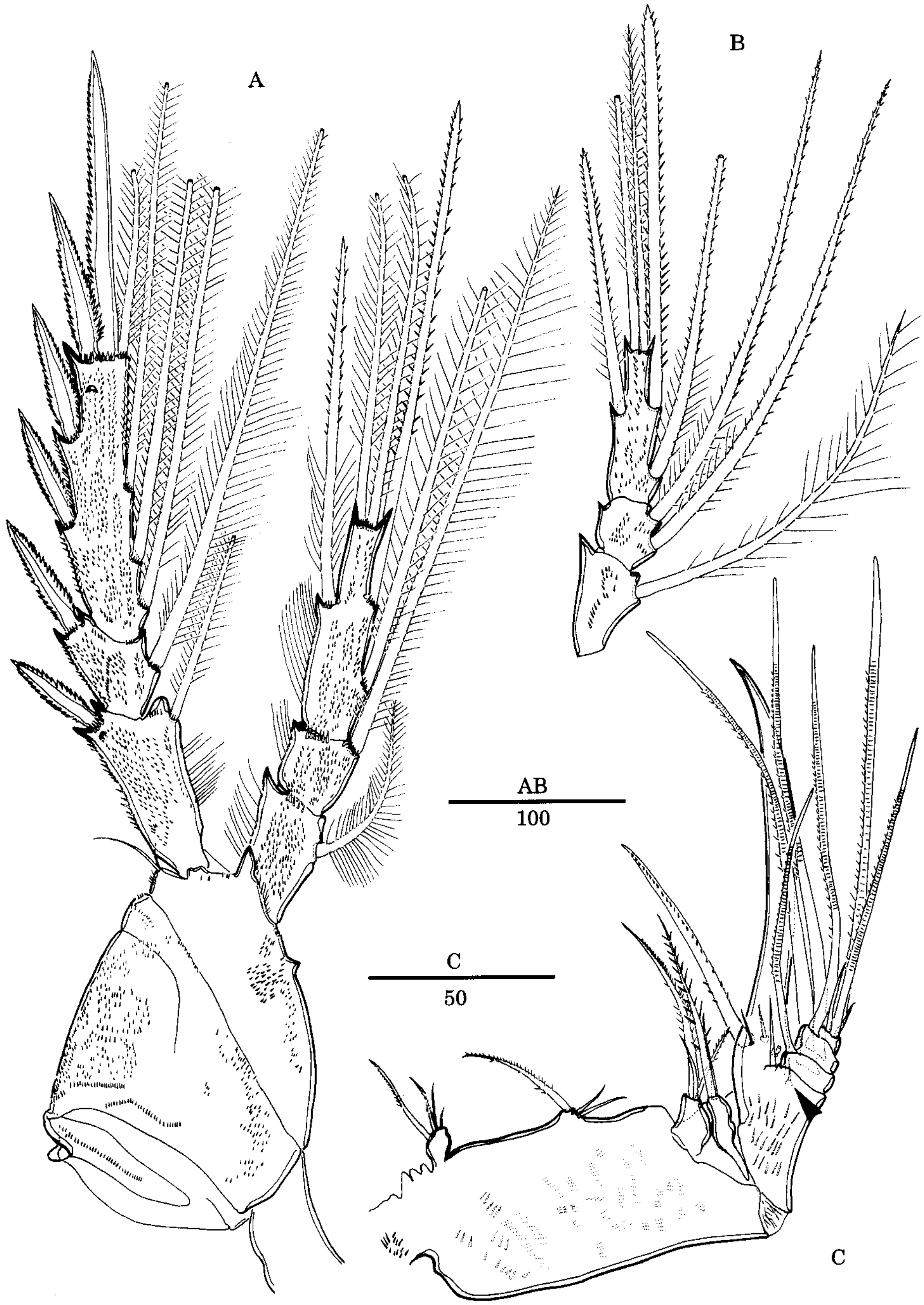

Figure 7. ***Nudivorax todai*** **gen.** et **sp. nov.** A, P4 (♀), anterior; B, P4 endopod (♂), posterior; C, Maxilla (♂) [arrow indicating rudimentary seta on posterior surface].

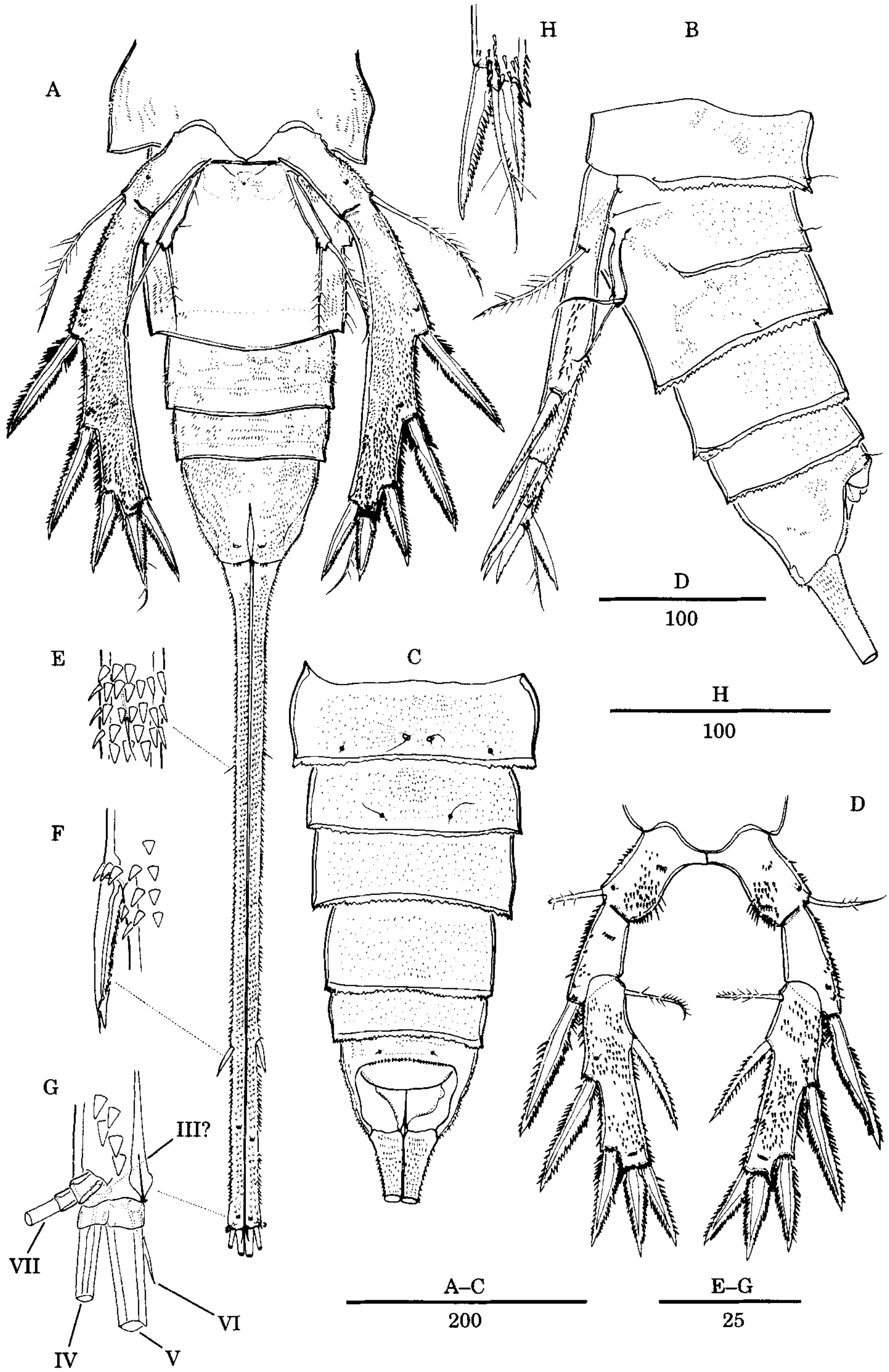

Figure 8. ***Nudivorax todai* gen.** et **sp. nov.** A, urosome (♀), ventral; B, urosome (♀), lateral; C, Same, dorsal; D, Fifth pair of legs (♂), anterior. E, region around seta I; F, seta II; G, distal margin of caudal ramus, dorsal; H, distal part of P5, posterior.

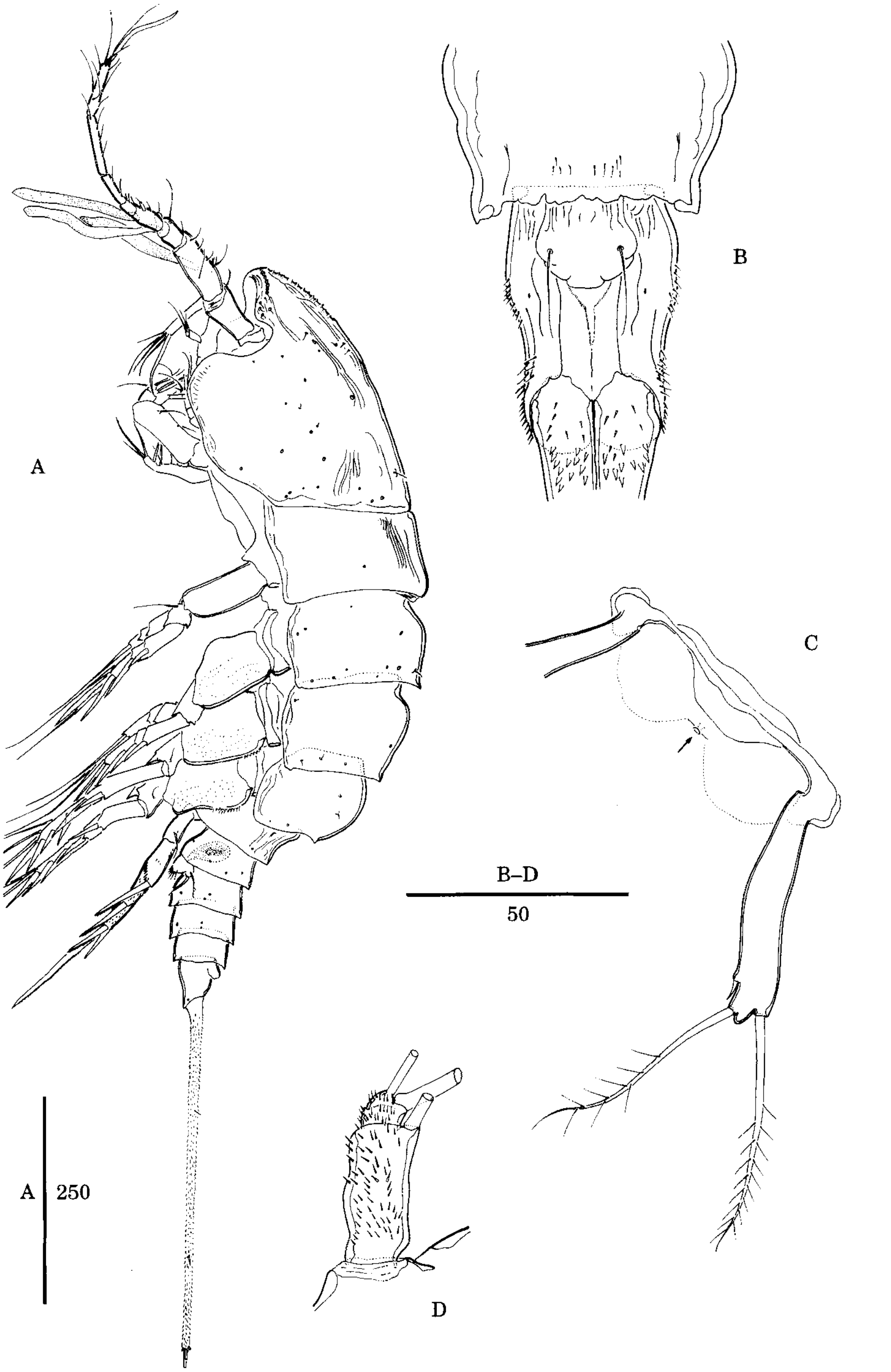

Figure 9. ***Nudivorax todai* gen.** et **sp. nov.** A, habitus (♂), lateral; B, penultimate and anal somites (♂), dorsal; C, genital field (♀), ventral [minute copulatory pore arrowed]; D, antennary exopod (♀).

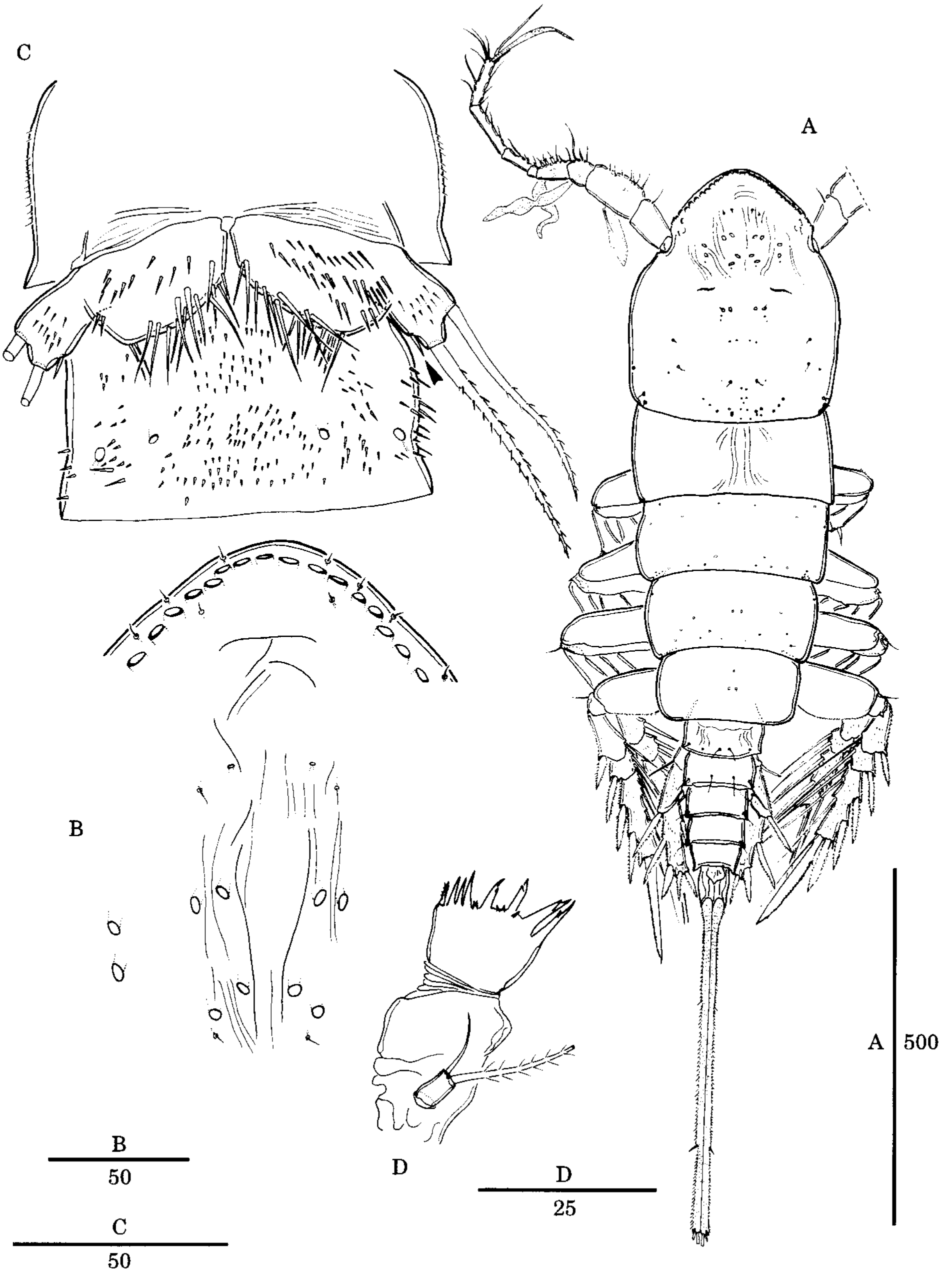

Figure 10. ***Nudivorax todai*** **gen.** et **sp. nov.** (♂). A, habitus, dorsal; B, anterior area of cephalosome, dorsal; C, genital and first abdominal somites, ventral [arrow indicating inner vestigial seta]; D, mandible.

somite and 4 abdominal somites. Surface ornamentation pattern consisting of patches of minute denticles present both dorsally and ventrally (e.g. Fig. 10C). All urosomites without paired spinous processes; posterior margin irregularly denticulate dorsally and laterally (Fig. 9B).

Anal somite (Fig. 9B) long and narrow, with lateral constrictions; anal opening narrow and probably non-functional; anal operculum forming part of lobate anterior portion of somite, margin without spinules but several incisions; paired dorsal sensillae very long.

Antennule (Fig. 11A) 9-segmented; haplocer with geniculation between segments 7 and 8, and segments distal to geniculation not extremely elongate. Segment 2 largest. Segment 4 represented by small sclerite (Figs 11A, 15B). Segmental homologies: 1-I, 2-(II–VIII), 3-(IX–XII), 4-XIII, 5-(XIV–XVII), 6-XVIII, 7-(XIX–XX), 8-(XXI–XXIII), 9-(XXIV–XXVIII). Armature formula: 1-[1], 2-[11 + ae], 3-[6 + ae], 4-[2], 5-[2 + 3 modified + (1 + ae)], 6-[1 + 1 modified], 7-[2 + 1 modified], 8-[4], 9-[10 + acrothek]. Modified setae on segments 5–7 consisting of proximal multispinulose part and distal flagellate part (Figs 11D, 15A). Other setae bare; those on proximal segments usually short. Apical acrothek consisting of aesthetasc and slender seta. Aesthetascs large, with supporting chitinous rib; that of segment 5 fused basally to short seta (Figs 11D, 15A).

Antenna (Fig. 12A) sexually dimorphic in allobasis, exopod and free endopod. Allobasis with similar ornamentation but without abexopodal seta. Exopod indistinctly 3-segmented (Fig. 15C); slightly shorter than in ♀ and with coarser spinules proximally; apical setae distinctly shorter than in ♀ and seta of exp-2 without long pinnules. Free endopod shorter than allobasis, with reduced surface ornamentation; lateral armature consisting of 1 minute and 2 long setae; distal armature consisting of 6 elements: 1 long and 1 short pinnate spine, 1 pinnate and 3 geniculate setae (the setae basally fused in pairs).

Labrum (Fig. 13C) highly folded; median distal margin with densely packed spinules (Fig. 13D). Paragnaths (Fig. 13C) rudimentary.

Mandible (Figs 10D, 14A) strongly reduced. Gnathobase separated from rest of praecoxa by annulated constriction; with 1 short pinnate seta at dorsal corner and 7 pointed teeth around apical margin. Palp minute, 1-segmented; with 1 short, naked and 1 longer, bipinnate seta apically.

Maxillule (Figs 11B, 14B) significantly reduced but with basic segmentation and armature as in ♀. Praecoxa with transverse constriction; arthrite (Fig. 14C) constricted basally, with reduced armature consisting of 2 short setae on anterior surface and 10 spines/setae around distal margin. Coxa with lobate endite bearing 1 short, naked and 2 long bipinnate setae (Fig. 14D). Basis rectangular, without distinct lobes; armature consisting of pinnate claw, and 4 long plus 3 short bipinnate setae.

Maxilla (Fig. 7C) reduced but with basic segmentation as in ♀; consisting of syncoxa, allobasis and 3-segmented endopod. Syncoxa with 4 small endites; position and armature as in ♀ but most setae distinctly shorter or reduced. Allobasis drawn out into strong, slightly curved, naked claw; accessory armature consisting of 1 minute seta and 1 pinnate spine on posterior surface, 2 minute setae on anterior surface, and 1 short seta (arrowed in Fig. 7C) near boundary with first endopod segment; posterior surface also with short tube pore and numerous spinules. Endopod with armature formula 1-[2 geniculate], 2-[2 geniculate], 3-[2 geniculate + 2 short bare].

Maxilliped (Fig. 11C) 2-segmented, comprising protopod and endopod. Protopod very large, with dense pattern of spinules on anterior surface; original separation of syncoxa and basis marked by small surface suture (arrowed in Fig. 11C); armature consisting of 4 syncoxal and 2 basal setae. Endopod rectangular, about 2.4 times as long as wide; with incomplete surface suture marking original segmentation (arrowed

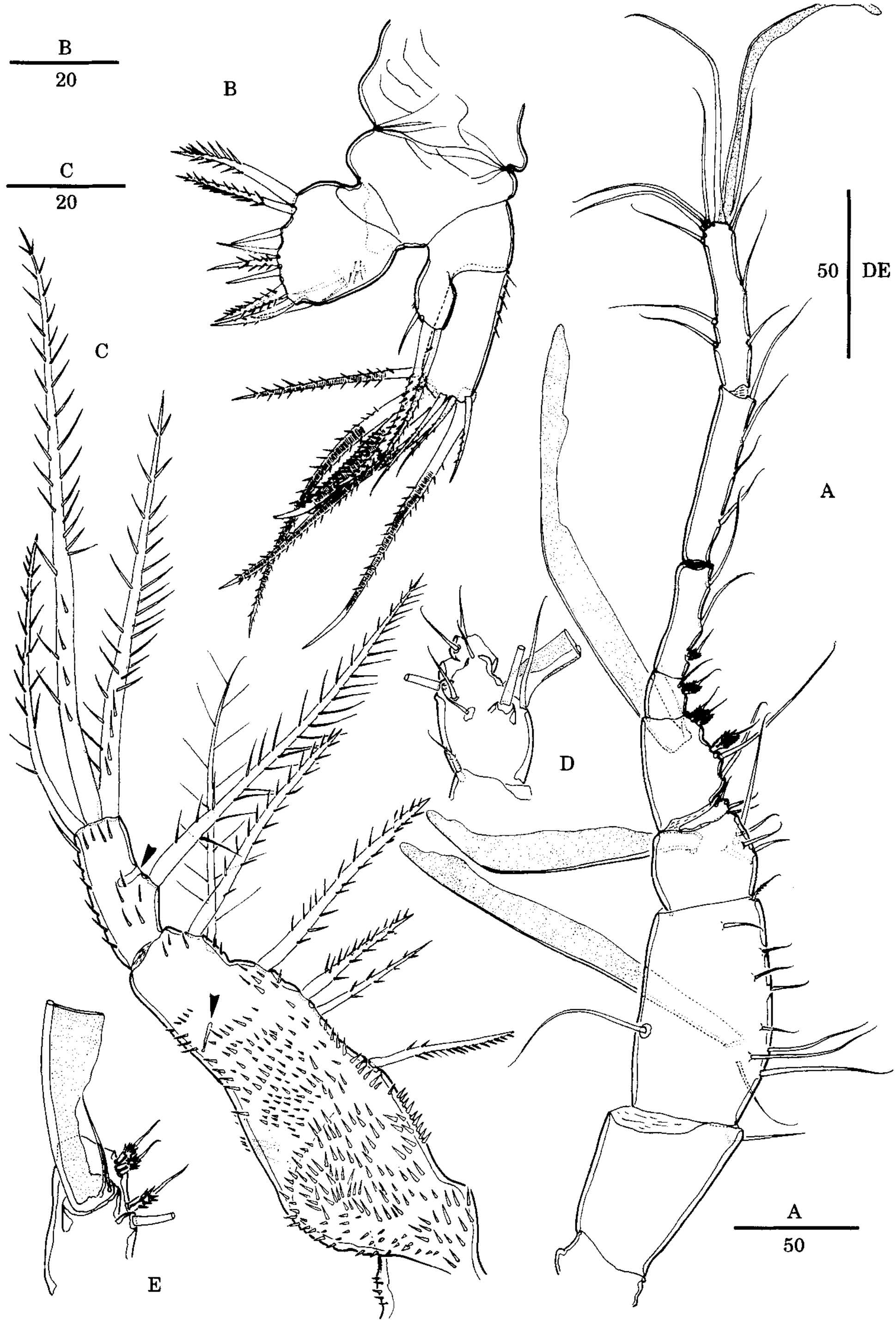

Figure 11. ***Nudivorax todai* gen. et sp. nov.** (♂). A, antennule, dorsal; B, maxillule, posterior; C, maxilliped [membranous inserts marking original segmentation arrowed]. D, antennulary segments 3–4, anterior; E, distal half of antennulary segment 5, anterior.

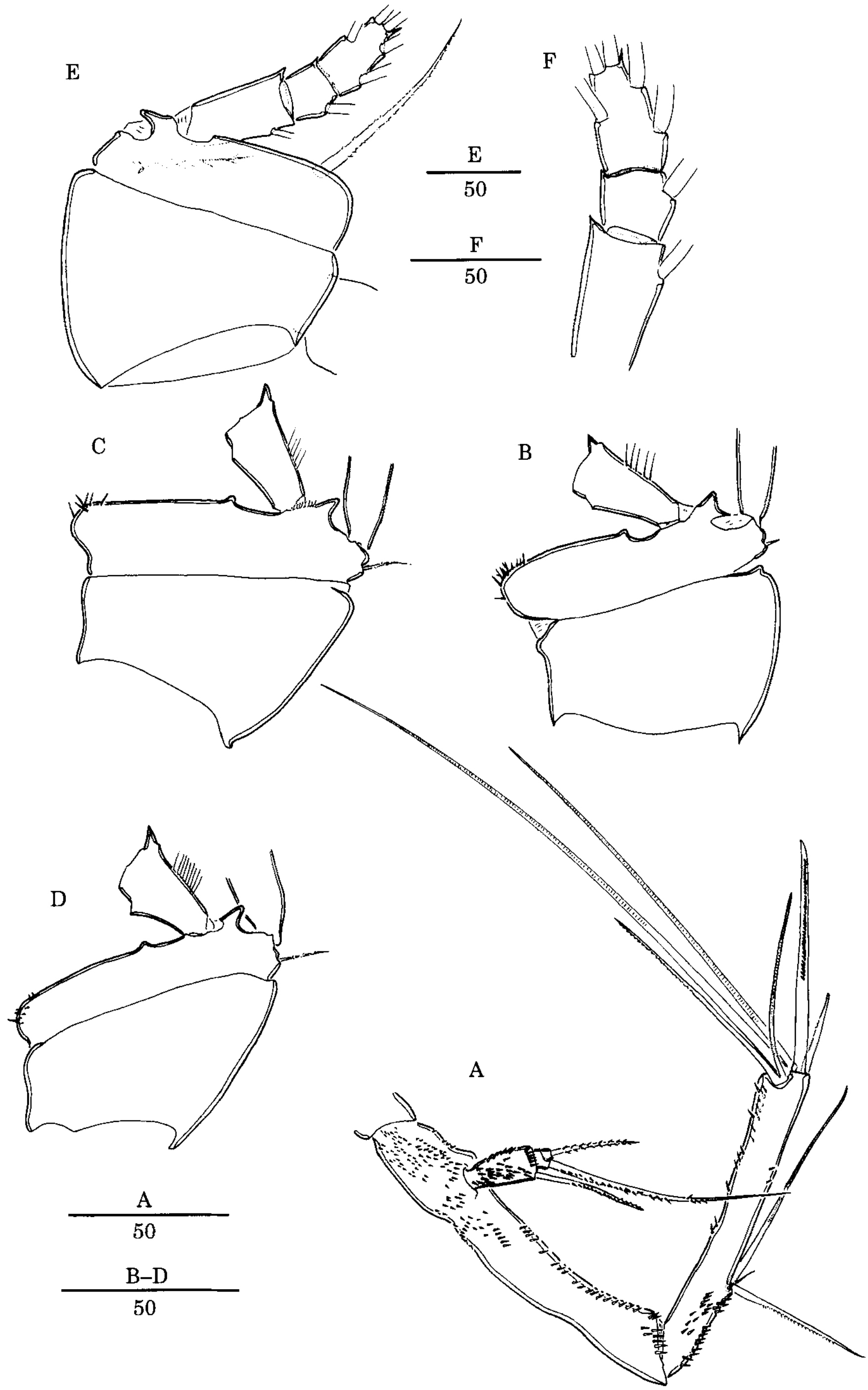

Figure 12. ***Nudivorax todai* gen.** et **sp. nov.** (♂). A, antenna; B, protopod and proximal exopod segment of P2; C, protopod and proximal exopod segment of P3; D, protopod and proximal exopod segment of P4; E, protopod and endopod of P1, posterior; F, P1 endopod, posterior.

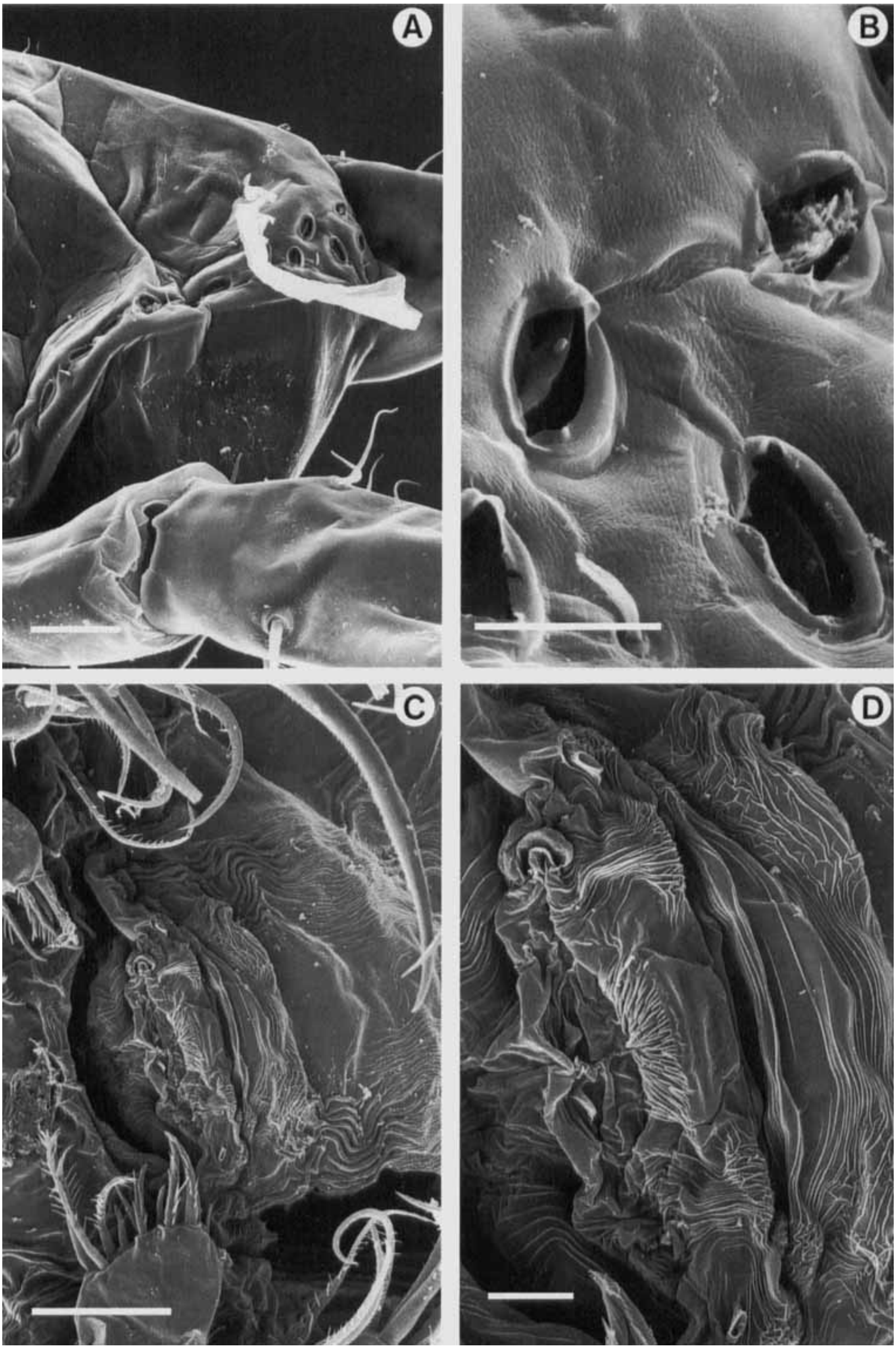

Figure 13. ***Nudivorax todai* gen.** et **sp. nov.** (♂). A, lateral view of cephalosome showing pore; B, detail of cephalosomic pores; C, oral area; D, detail of labrum. Scale bars: 20 μm (A, C), 5 μm (B), 10 μm (D).

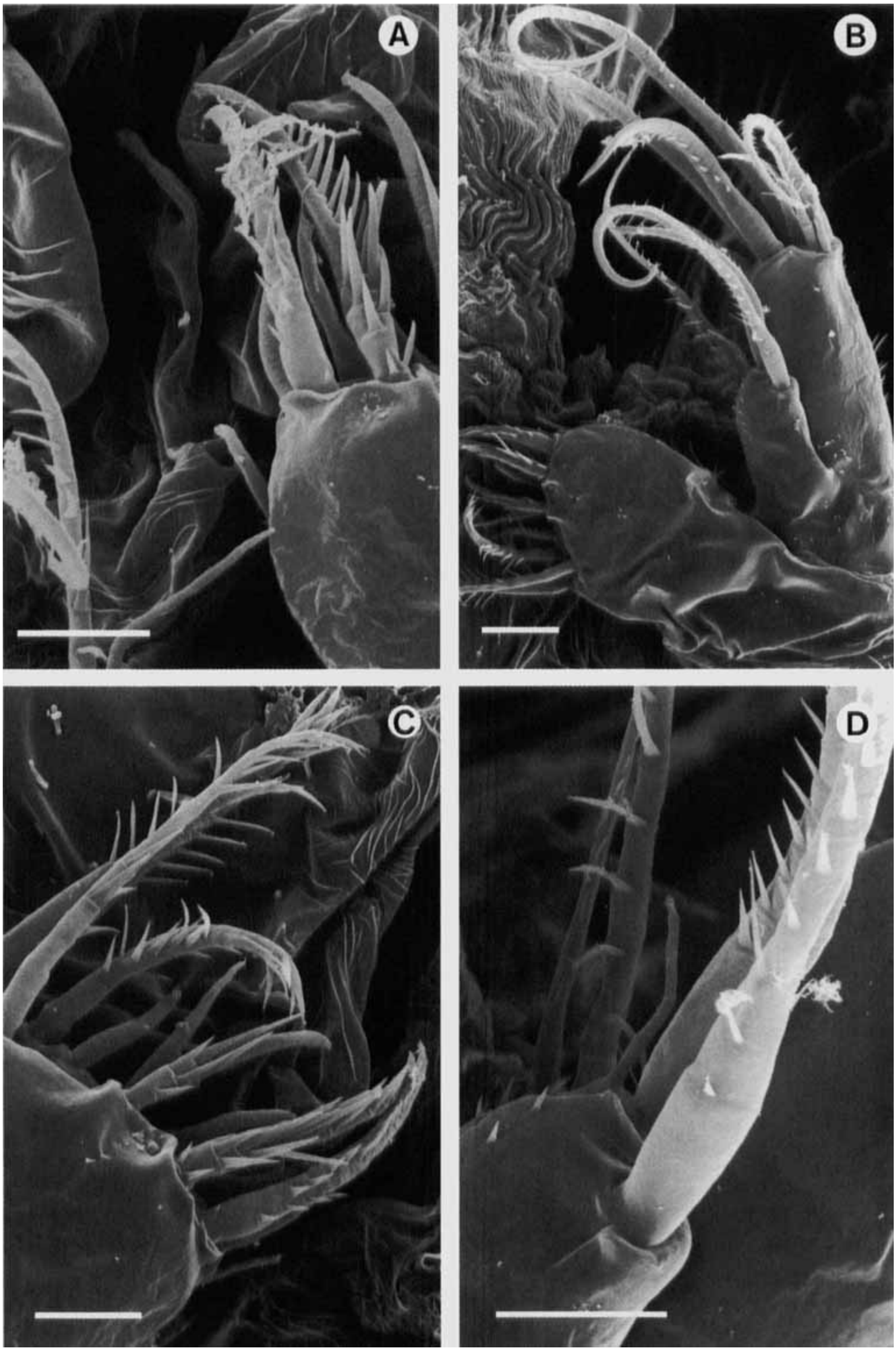

Figure 14. ***Nudivorax todai* gen.** et **sp. nov.** (♂). A, mandibular gnathobase; B, maxillule, posterior; C, detail of maxillulary arthrite; D, coxal endite of maxillule. Scale bars: 5 µm (A, C, D), 10 µm (B).

in Fig. 11C); with 1 lateral and 3 apical pinnate setae (of different lengths); spinules on setae much stronger than in ♀.

P1 (Figs 12E,F, 15D) endopod indistinctly 2-segmented as in ♀; inner basal spine much longer than in ♀, extending beyond distal margin of endopod (Fig. 12E).

P2–P4 bases (Fig. 12B–D) with inner lobate expansion; setular tuft along inner margin replaced by spinules. P4 enp-2 (Fig. 7B) with 2 inner setae.

Fifth pair of legs (Fig. 8D) joining midventrally but not fused medially. P5 elongate, directed medially and backwardly; indistinctly 3-segmented, comprising basis (or undivided protopod) and 2-segmented exopod; segmentation between basis and proximal exopod segment marked by incomplete surface suture both posteriorly and anteriorly. Basis drawn out into narrow extension medially; with outer pinnate seta. Exp-1 with outer serrate spine. Exp-2 longest; armature consisting of 2 serrate spines along outer margin, 2 serrate spines apically, and 1 pinnate seta plus 1 pinnate spine along inner margin. Entire leg with surface spinules as figured in Fig. 8D. Integumental pores present on all segments (1 on basis and exp-1; 2 on exp-2).

Sixth pair of legs (Fig. 10C) not fused medially, symmetrical. Each P6 bilobate with outer lobe bearing armature consisting of 2 pinnate setae and inner vestigial element (arrowed in Fig. 10C); anterior surface with short spinules, inner distal margin with cluster of long spinules

Etymology

The species is named in honour of Dr Tatsuki Toda (Soka University, Tokyo), in recognition of his contributions to the study of the benthopelagic fauna of Sagami Bay.

Remarks

Females of the new genus differ from those of other aegisthid genera in having an area of flexible, loosely folded integument positioned between the dorsal cephalic shield, covering the cephalosome, and the tergite of the first pedigerous somite (Fig. 2A–C). A smaller strip of similar membranous integument is also present dorsally between the first and second pedigerous somites. From a comparison of specimens fixed at different stages of contraction, it is apparent that significant dorsal and lateral distension of the prosome can take place during feeding. In other aegisthids the first pedigerous somite, although free along its lateral and dorsal margins, is functionally incorporated into the cephalosome by complete fusion ventrally and usually additional fusion of the respective pleural areas ventrolaterally (Huys, 1988; figs 6A, 7E). In the non-feeding males of *Nudivorax* these membranous integumental areas are completely absent. It is postulated here that these areas in the female evolved concurrently with the adoption of an opportunistic feeding strategy such as gorging. The presence of flexible integument in immediately distal to the cephalic region would allow for the substantial distension of the midgut caused by the consumption of large food items. This mechanism is very similar to that described for certain misophrioid genera. Many deepwater taxa of this order, such as the bathypelagic *Benthomisophria* species, are opportunistic macrophages (Boxshall, 1984). The presence of a carapace-like extension enclosing and protecting the distensible, membranous tergite of the first pedigerous somite enables them to gorge on large food items. In some genera such as *Expansophria* Boxshall & Iliffe, 1987 the carapace is secondarily lost, although expansion is still

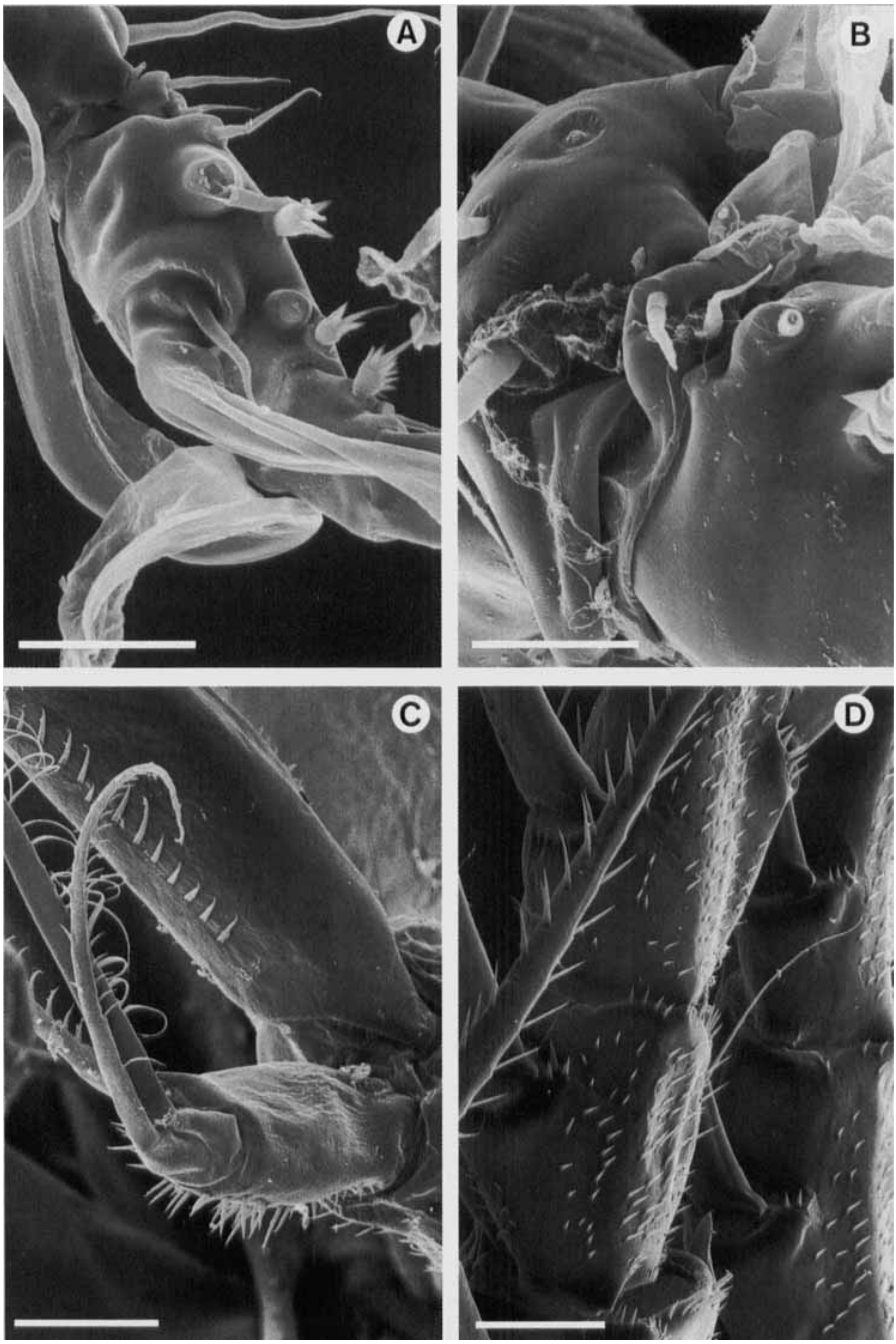

Figure 15. ***Nudivorax todai* gen.** et **sp. nov.** (♂). A, antennule, anterior view of segments 4–6; B, antennule, anterior view showing rudimentary segment 4; C, antennary exopod; D, anterior view of P1 endopod and exopod, showing incomplete fusion of middle and distal segments. Scale bars: 20 μm (A), 10 μm (B-D).

possible due to the flexible anterior part of the first tergite (Boxshall & Iliffe, 1987). In *N. todai* the tergite is not modified and distension is brought about by the proliferation of the arthrodial intersomitic membranes.

A conspicuous feature of male *N. todai* is the presence of a transverse linear array of large pores around the rostral margin of the dorsal cephalic shield (Fig. 13A). These pores appear to have valve-like structures which allow them to be closed off (Fig. 13B). Similar linear aggregations of pores have been described for the female of the deepwater cyclopinid *Cyclopicina longifurcata* T. Scott, 1901, however, in this species the pores are found in the female and are arranged along the ventrolateral margin of the cephalic shield. Huys & Boxshall (1990) compared these structures with those reported for certain males in other cyclopoid families such as the Notodelphyidae (Hipeau-Jacquotte, 1986) and Oithonidae (Nishida, 1986) and suggested that they are sensory in function. We speculate that the rostral array in the male of *N. todai* has evolved in connection with the enhancement of the chemosensory system required for mate location, and thus detection of pheromones at low concentrations, in a chemically diluted environment such as the deep sea.

The complete absence of surface reticulation and spinous processes on both the cephalosome and body somites are unique features within the Aegisthidae. *Nudivorax* is also the only genus in which the caudal rami are distinctly shorter than the rest of the body, indicating an epibenthic or hyperbenthic lifestyle. In the bathypelagic *Aegisthus* species the extremely long caudal rami significantly enhance buoyancy and can attain several times the total length of the body somites combined (see e.g. Gamô, 1983: fig. 1A).

The new genus clearly represents an isolated branch within the Aegisthidae and the morphology of its antennules and mouthparts suggests a relatively early divergence in the evolutionary history of the family. For example, the female antennules display the maximum number of setation elements expressed in the family: 12, 13 + (1 + ae) and 4 on segments 2–4, respectively as opposed to at most 9, 12 + (1 + ae) and 3 in other genera. The male antennules are relatively unmodified and the segments distal to the geniculation are not yet prolonged like in the more advanced genera *Aegisthus, Andromastax* and *Scabrantenna* gen. nov. The absence of spinous processes on the anterior margin of the second antennulary segment in both sexes of *N. todai* possibly suggests that these structures evolved secondarily in the other genera, however outgroup comparison is required to assess the polarity of this character (Huys *et al.*, in prep.). Another indication of the primitive position of the new genus is provided by the male mouthparts which are atrophied as in other aegisthid genera but have retained the full complement of armature elements as found in the female. The presence of vestigial segment boundaries in the male maxilliped (arrowed in Fig. 11C) is also noteworthy.

Other useful diagnostic characters of *N. todai* include the extreme reduction of the outer basal seta of P2, the complete reduction of the abexopodal seta on the male antenna, the absence of a distinct rostrum in both sexes and the spiniform nature of the distal outer element on P1 exp-3.

Scabrantenna gen. nov.

Diagnosis

Aegisthidae. Body with complex surface reticulation but without distinct spinous processes. Caudal rami slightly longer than rest of body. Antenna with distinctly

Swimming leg armature formula:

	coxa	basis	exopod	endopod
P1	0-0	1-1	I-1;I-1;1,2,2	0-1;1,2,3
P2	0-0	1-0	I-1;I-1;III,I+1,2	0-1;0-2;1,2,2
P3	0-0	1-0	I-1;I-1;III,I+1,2	0-1;0-2;1,2,I+2
P4	0-0	1-0	I-1;I-1;III,I+1,3	0-1;0-1[♂:2];1,2,I+1

3-segmented exopod (formula [1,1,1]). Coxa of P4 only with outer spinous process. P1 endopod distinctly 2-segmented. Distal outer element of P1 exp-3 setiform.

Sexual dimorphism in general body shape, rostrum, antennule, antenna, labrum, mandible, maxillule, maxilla, maxilliped, P1 inner basal spine, P2–P4 bases, P4 endopod, P5, P6, genital segmentation, anal somite and body size. Males non-feeding.

Female

Rostrum small, spiniform. Anal operculum obsolete. Antennule 7-segmented; with 1 spinous process on distal anterior margin of segment 2. Antennary endopod with 3 lateral and 7 apical elements. Mandible with 2-segmented palp bearing 2 setae on apical segment. Maxillule with 3 elements on coxal endite and 7 elements on palp. Maxilla with 4 endites on syncoxa (formula [4,3,2,2]); allobasis with 2 anterior and 3 posterior elements; endopod with formula [1,2,4]. Maxilliped with 3 spines and 3 setae on protopod and 1 lateral plus 3 apical setae on endopod. P1 inner basal seta longer than endopod. P5 1-segmented; with 1 (basal) seta and 3 spines along outer margin, and 2 spines plus 1 seta apically. P6 with 1 rudimentary and 2 well developed elements.

Male

Rostrum strongly developed, spiniform. Middorsal integument of cephalosome and P1-bearing somite strongly folded. Anal somite bilaterally constricted; operculum weakly developed, rounded, smooth. Antennule 9-segmented with geniculation between segments 7 and 8; segment 8 very elongate. Antennary allobasis with strong spinular cluster at distal abexopodal margin but without seta; endopod with strong spinular row along inner margin, 2 lateral and 6 apical elements (innermost a spinous claw). Mandible extremely reduced; palp 1-segmented without distinct setae. Maxillule extremely reduced; not segmented; all endites atrophied. Maxilla with reduced coxal endites, praecoxal endites absent (formula [0,0,2,2]; allobasis with 2 accessory minute setae; endopod with formula [1,2,4]. Maxilliped reduced; protopod with only 1 seta; lateral and outer distal setae of endopod reduced in size. P1 inner basal spine distinctly shorter than in ♀. Bases of P2–P4 with inner lobate extension. P4 enp-2 with additional inner seta. P5 indistinctly 2-segmented; basis and exp-1 partly fused; exp-2 with 2 outer spines, 2 apical spines and 2 inner setae. P6 with 1 rudimentary and 2 well developed setae; medial margin with long setules.

Type and only species

Scabrantenna yooi gen. et sp. nov.

Etymology

The generic name is derived from the Latin *scaber*, meaning rough, and *antenna*, meaning sail-yard, and refers to the strong spinular row on the male antennary endopod.

Gender
Feminine.

Scabrantenna yooi gen. et **sp. nov.**

Type locality
Okinawa Trough, Stn DT2-3, depth 583–711 m.

Material examined
Holotype ♀ dissected on 14 slides (Type locality; NHM reg. no. 1998.229). Paratypes are 1 ♂ dissected on 11 slides (Stn DT2–3; NHM reg. no. 1998.230) and 14 ♀♀, 1 ♂ in alcohol (Stn DT2–3: 10 ♀♀, 1 ♂; Stn DT4–3: 3 ♀♀; Stn DT4–4: 1 ♀; NHM reg. nos 1998.231–245).

Description of female
Total body length 3530 μm (measured from anterior margin of cephalic shield to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 450 μm. Urosome distinctly narrower than prosome (Fig. 16A).

Prosome (Figs 16A, B, 17A) 5-segmented, comprising cephalosome and 4 free pedigerous somites. Cephalosome and prosomites (bearing P1–P4) with complex surface reticulation consisting of anastomosing pattern of longitudinal and transversal lamellae as indicated in Fig. 17A. Additional ornamentation consisting of sensillae and pores, particularly around posterior margin of somites; P1-bearing somite without sensillae; conspicuous aggregation of paired pores present middorsally near hind margin of cephalosome.

Cephalosome bell-shaped, with pointed anterior margin and slightly swollen, crenate, posterolateral angles; pleural areas strongly developed, margin slightly denticulate; posterior margin smooth. Rostrum (Figs 16A, 17A) small, represented by short spiniform projection; slightly recurved dorsally; dorsal pore and sensillae absent.

First pedigerous somite completely separated from dorsal cephalic shield; posterior margin smooth. Posterior margin of somites bearing P2–P4 (Fig. 17A) with small spinous processes of varying size dorsally and laterally, dorsal ones being largest; posterolateral corners produced into spinous attenuation, increasing in size in successive somites; posterior margin denticulate.

Urosome (Fig. 17B–D) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. All urosomites with pattern of surface ornamentation consisting of surface anastomosing lamellae dorsally (Fig. 17C) and laterally (Fig. 17D); small spinules or denticles present dorsally, laterally and ventrally. Posterior margin of all urosomites (except anal somite) distinctly serrate dorsolaterally and dorsally; plain ventrolaterally and ventrally. P5-bearing somite (Fig. 17C) with lateral bulges.

Genital double-somite (Fig. 17C,D) with serrate transverse surface ridge dorsally and dorsolaterally, indicating original segmentation; completely fused ventrolaterally and ventrally. Genital field positioned far anteriorly, close to articulation with P5-bearing somite (Fig. 17B); copulatory pore minute; gonopores paired, covered on both sides by well developed opercula derived from sixth legs; P6 very elongate (Fig.

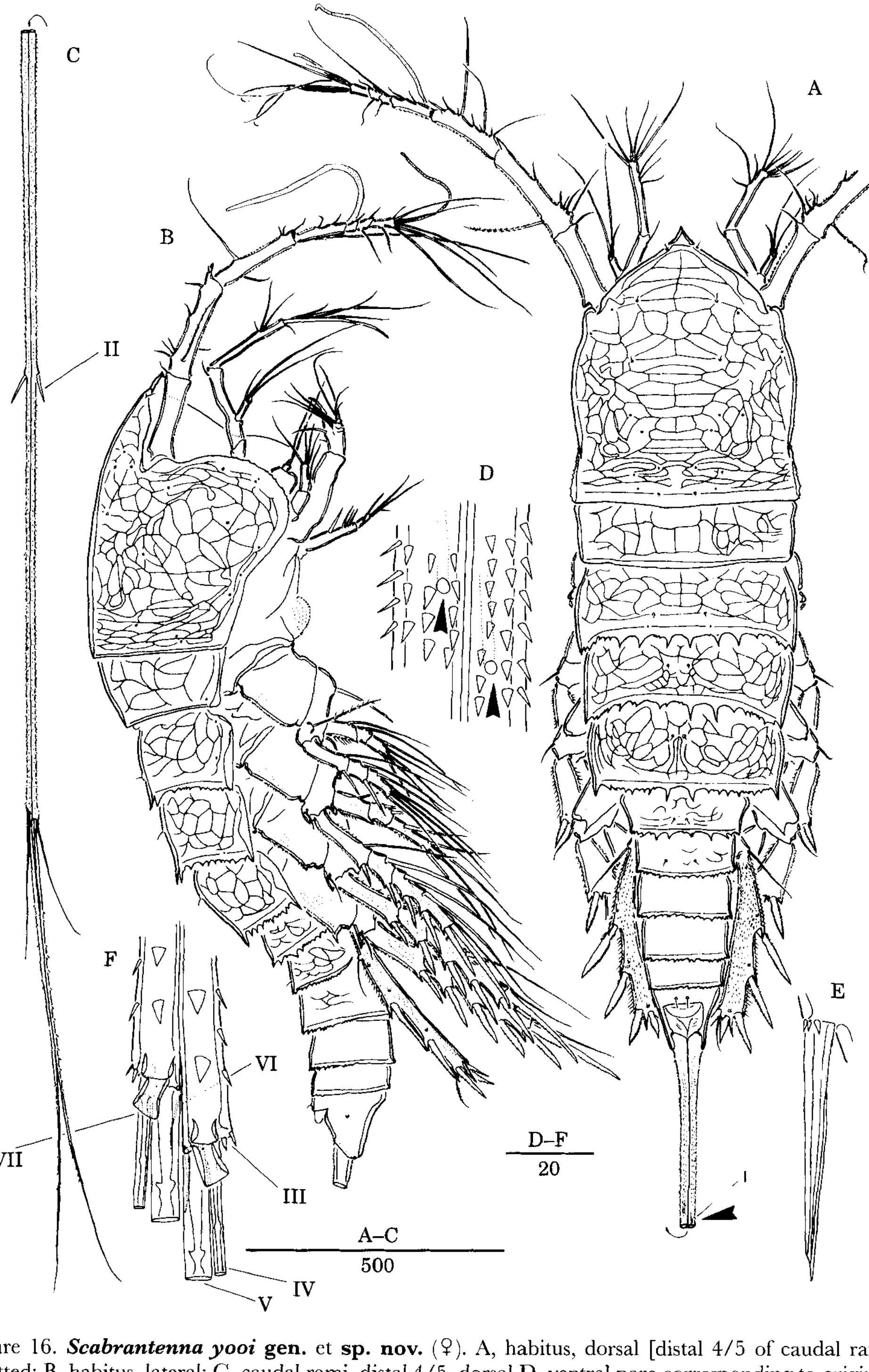

Figure 16. ***Scabrantenna yooi* gen. et sp. nov.** (♀). A, habitus, dorsal [distal 4/5 of caudal rami omitted; B, habitus, lateral; C, caudal rami, distal 4/5, dorsal D, ventral pore corresponding to original position of seta I (arrowed in A); E, seta II, dorsal; F, distal end of rami showing insertion sites of setae II-VII, dorsal.

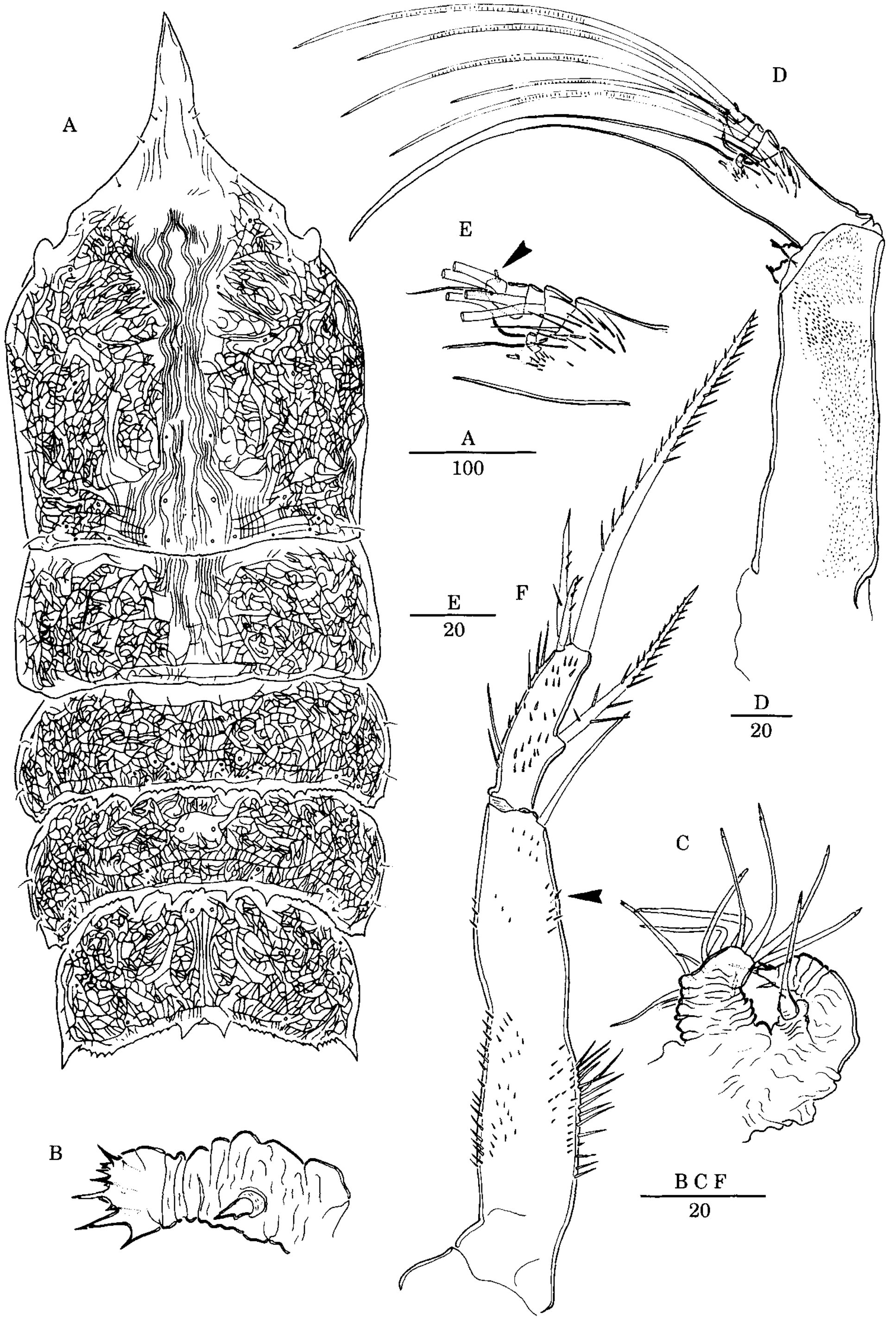

Figure 17. ***Scabrantenna yooi* gen. et sp. nov.** (♀). A, prosome, dorsal, showing fine details of surface ornamentation; B, urosome, ventral [caudal rami omitted]; C, same, dorsal; D, same, lateral; E, right P6.

17B), with 1 long and 1 short naked seta apically, and minuscule seta on subdistal inner margin (Figs. 17E).

Anal somite (Fig. 17B–D) with large anal opening, flanked by spinules laterally; anal operculum obsolete; dorsal sensillae positioned anterior to anal opening; ventral hind margin with large raised pores.

Caudal rami (Fig. 16A, C–F) slightly asymmetrical; closely adpressed medially but apparently not fused; slightly longer than rest of body, about 1.18 times length of body somites combined; covered with dense pattern of denticle-like spinules. Each ramus with 6 setae; seta I absent, replaced by minute pore (arrowed in Fig. 16D) which is typically positioned asymmetrically on both rami in proximal quarter (arrowed in Fig. 16A); seta II spiniform with peculiar tip (Fig. 16E); seta III missing in all specimens examined but position indicated by large lateral scar (Fig. 16F; see ♂ caudal ramus in Figure 23F for shape and size of seta III); setae IV and V large, V over 3 times the length of IV; seta VI minute and displaced ventrally (Fig. 16F); seta VII presumably tri-articulate at base, positioned subterminally (Fig. 16F).

Antennule (Fig. 18A–D) 7-segmented; with small sclerite around base of segment 1; all segments with irregular dense pattern of minute spinules. Armature formula: 1-[1 pinnate], 2-[2 bare + 7 pinnate], 3-[5 bare + 7 pinnate + (1 bare + ae)], 4-[1 bare + 2 pinnate], 5-[1 bare + 1 pinnate], 6-[1 bare + 1 pinnate], 7-[5 bare + 1 pinnate + acrothek]. Apical acrothek consisting of well developed aesthetasc (210 µm) fused basally to short seta (Fig. 18B). Aesthetasc on segment 3 large (340 µm), fused to short seta. Both aesthetascs without distinct supporting chitinous rib. Segment 2 longest; anterior margin with spinous process distally (Fig. 18D). Distal margin of segment 3 with series of dentate processes dorsally (Fig. 18C) and very long seta with proximal pinnate portion ventrally.

Antenna (Fig. 20A, D,E) 3-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa irregular in shape, with few spinules. Basis and proximal endopod segment completely fused forming elongate allobasis with 1 pinnate, abexopodal seta distally (derived from endopod). Exopod (Fig. 20E) arising from small pedestal; distinctly 3-segmented; proximal segment about 3 times as long as wide, with 1 short bipinnate seta; exp-2 and -3 minute, each with 1 very long, pinnate seta. Endopod elongate, slightly longer than allobasis; lateral armature arising in distal half, consisting of 1 minute and 2 long bipinnate setae; apical armature (Fig. 20D) consisting of 1 long naked, 1 short bipinnate, 5 long pinnate setae (1 claw-like and 4 long setae fused basally in pairs). Both allobasis and endopod with numerous fine surface spinules.

Labrum (Fig. 20B) well developed; with elaborate spinular ornamentation along distal margin and numerous on posterior face.

Mandible (Fig. 19A) with large coxa bearing well developed gnathobase; cutting-edge with 7 major teeth, alternating with smaller ones, around distal margin; teeth of dorsal half pinnate, those of ventral half cuspidate; with several patches of minute spinules and 1 bipinnate seta at dorsal corner. Palp (Fig. 19E) small, 2-segmented; basal segment largest, unarmed; distal segment small, with 2 long, basally fused, bipinnate setae; both segments covered with minute spinules.

Paragnaths (Fig. 19B) well developed hirsute lobes.

Maxillule (Fig. 19C). Praecoxa with transverse fold and few spinules around outer margin; arthrite strongly developed, with 2 large, swollen, plumose setae on anterior surface and 10 spines around distal margin. Coxa with cylindrical endite bearing 2 bipinnate setae and 1 curved bipinnate spine. Basis without discrete rami; apical

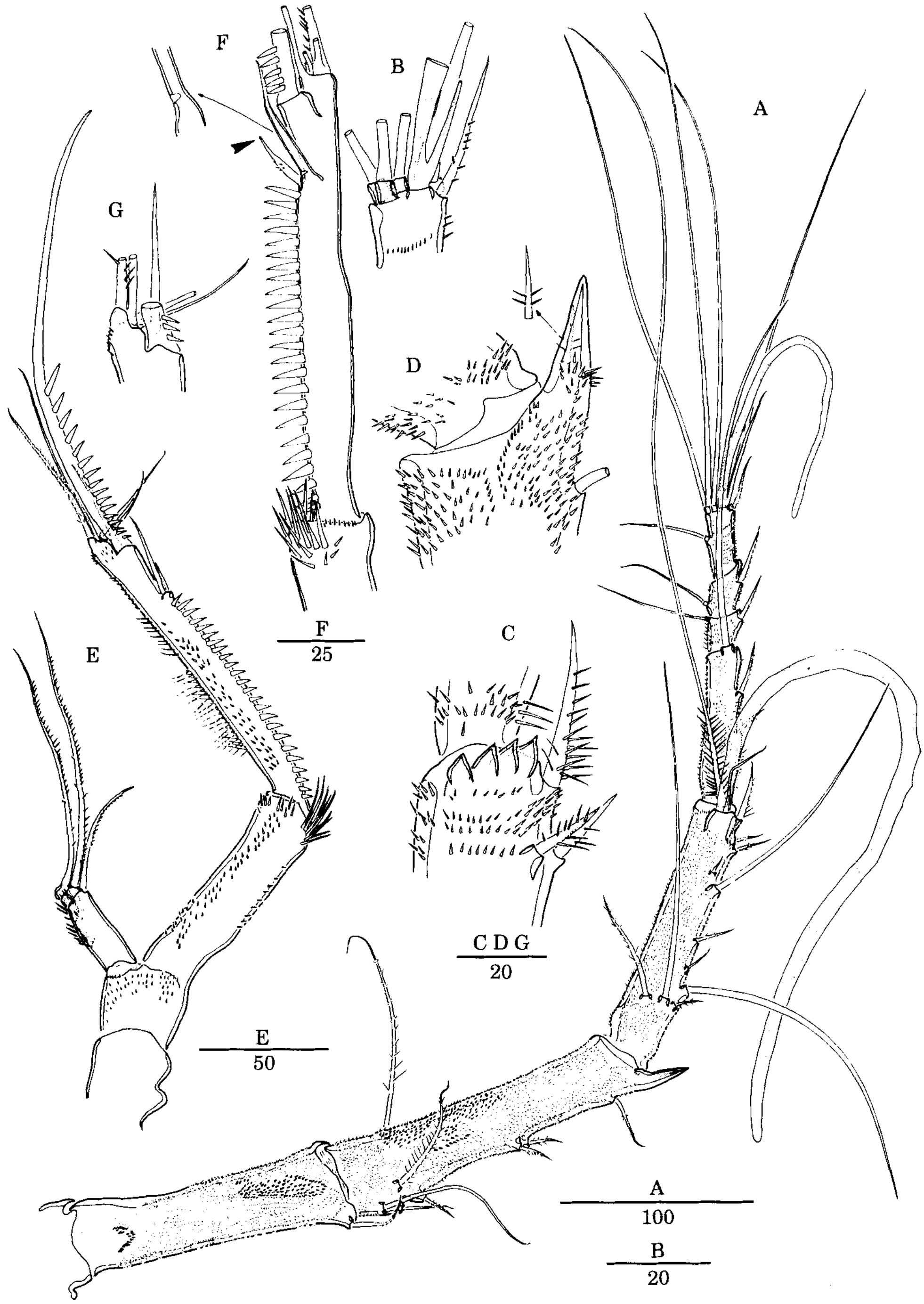

Figure 18. ***Scabrantenna yooi* gen. et sp. nov.** A, antennule (♀), ventral; B, antennulary segment 7 (♀), distal part, ventral; C, distal margin of antennulary segment 3 (♀), dorsal; D, anterior spinous process of antennulary segment 2 (♀); E, antenna (♂), anterior; F, free endopod of antenna (♂), posterior [arrow indicating apical pore on short lateral seta]; G, detail of distal armature of antenna (♂), anterior.

Figure 19. ***Scabrantenna yooi* gen. et sp. nov.** (♀). A, mandible; B, right paragnath; C, maxillule, posterior; D, maxilla, anterior. E, mandibular palp.

margin not bilobate; elements grouped in inner cluster consisting of stout, curved pinnate spine and 2 bipinnate setae, and outer cluster consisting of 4 pinnate setae, increasing in length medially.

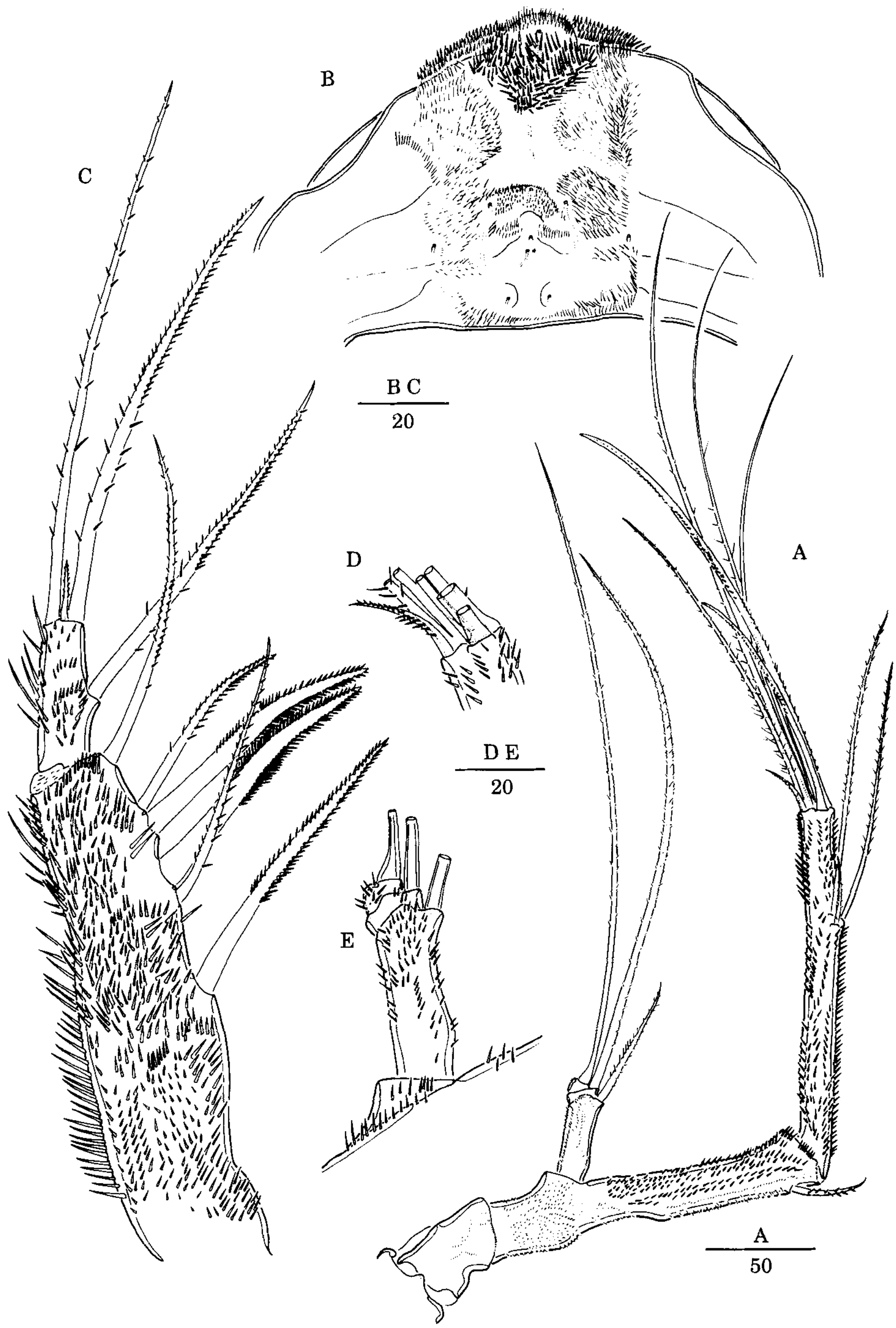

Figure 20. ***Scabrantenna yooi* gen.** et **sp. nov.** (♀). A, antenna; B, labrum, posterior; C, maxilliped. D, distal armature of antennary endopod; E, antennary exopod.

Maxilla (Fig. 19D) comprising syncoxa, allobasis and 3-segmented endopod. Syncoxa large and elongate, with numerous minute spinules; with 4 weakly developed endites: proximal praecoxal endite lobate, positioned far proximally, with 1 plumose and 3 pinnate setae; distal praecoxal endite almost entirely incorporated into syncoxa, represented by 3 setae; coxal endites closely set near articulation with allobasis, with 2 setae each. Allobasis drawn out into strong curved, sparsely pinnate claw; accessory armature consisting of 1 minute seta and 1 curved spine on anterior surface, 1 pinnate spine and 1 slender seta on posterior surface, and 1 naked seta near boundary with first endopod segment; posterior surface also with short tube pore. Endopod with armature formula 1-[1 geniculate], 2-[2 geniculate], 3-[2 geniculate + 2 bare].

Maxilliped (Fig. 20C) 2-segmented, comprising undivided protopod and 1-segmented endopod. Protopod very long, covered with dense pattern of fine spinules; outer margin with longer spinules; with 6 elements representing 4 vestigial endites; endite 1 represented by bipinnate spine, endites 2 and 3 with 1 large bipinnate spine and 1 bipinnate seta, endite 4 with long bipinnate seta. Endopod without surface sutures marking original segmentation; about 3 times as long as wide; with 1 bipinnate seta laterally and 1 short bipinnate spine flanked by 2 long bipinnate setae apically.

Swimming legs (Figs 21A–C, 22A,B) with 2-segmented (P1 endopod; derived by fusion of middle and distal segments; enp-2 with membranous insert and vestige of frill indicating original segmentation: Fig. 21A) or 3-segmented (P1 exopod, P2–P4) rami; endopods distinctly shorter than exopods. Intercoxal sclerites large and wide; with minute surface spinules, in P2–P3 with long setules along distal margin. Praecoxae with spinular row around distal margin. Coxae with characteristic pattern of surface spinules as figured; with small (P4) or without (P2–P3) spinous process arising from distal outer margin. Bases with numerous surface spinules as figured; inner margin with setules and small rounded process in P2–P4; inner basal spine of P1 bipinnate, distinctly longer than endopod; outer basal seta long in P1, short in P2–P4. All segments with dense pattern of spinules as figured. Posterior surface of P2–P4 enp-1 and enp-3 with row of coarse spinules. Outer margins of endopodal segments with long setules. Spine and setal formula as for genus. Exopodal spines bipinnate in P1, serrate or pectinate in P2–P4; distal outer element of P1 exp-3 setiform. Distal inner seta of enp-3 setiform in P1–P2, spiniform and rod-shaped in P3–P4.

Fifth pair of legs (Fig. 17B, D) very large, almost extending to posterior margin of anal somite; joining in ventral midline but not fused medially; distinctly curved inwards. P5 uniramous, 1-segmented with vestigial suture line along inner margin marking boundary between protopod and exopod; outer basal seta slender, plumose; exopodal armature consisting of 3 serrate spines (pinnate proximally) along outer margin, and 1 dorsal plumose seta flanked by outer biserrate and inner uniserrate spine around apex; entire leg covered with dense pattern of minute spinules and 4 pores anteriorly.

Description of male

Distinctly more slender than ♀. Body length 3320 µm (measured from anterior margin of cephalic shield to posterior margin of caudal rami). Largest width measured at P2-bearing somite: length: 360 µm. Urosome distinctly narrower than prosome (Fig. 23A).

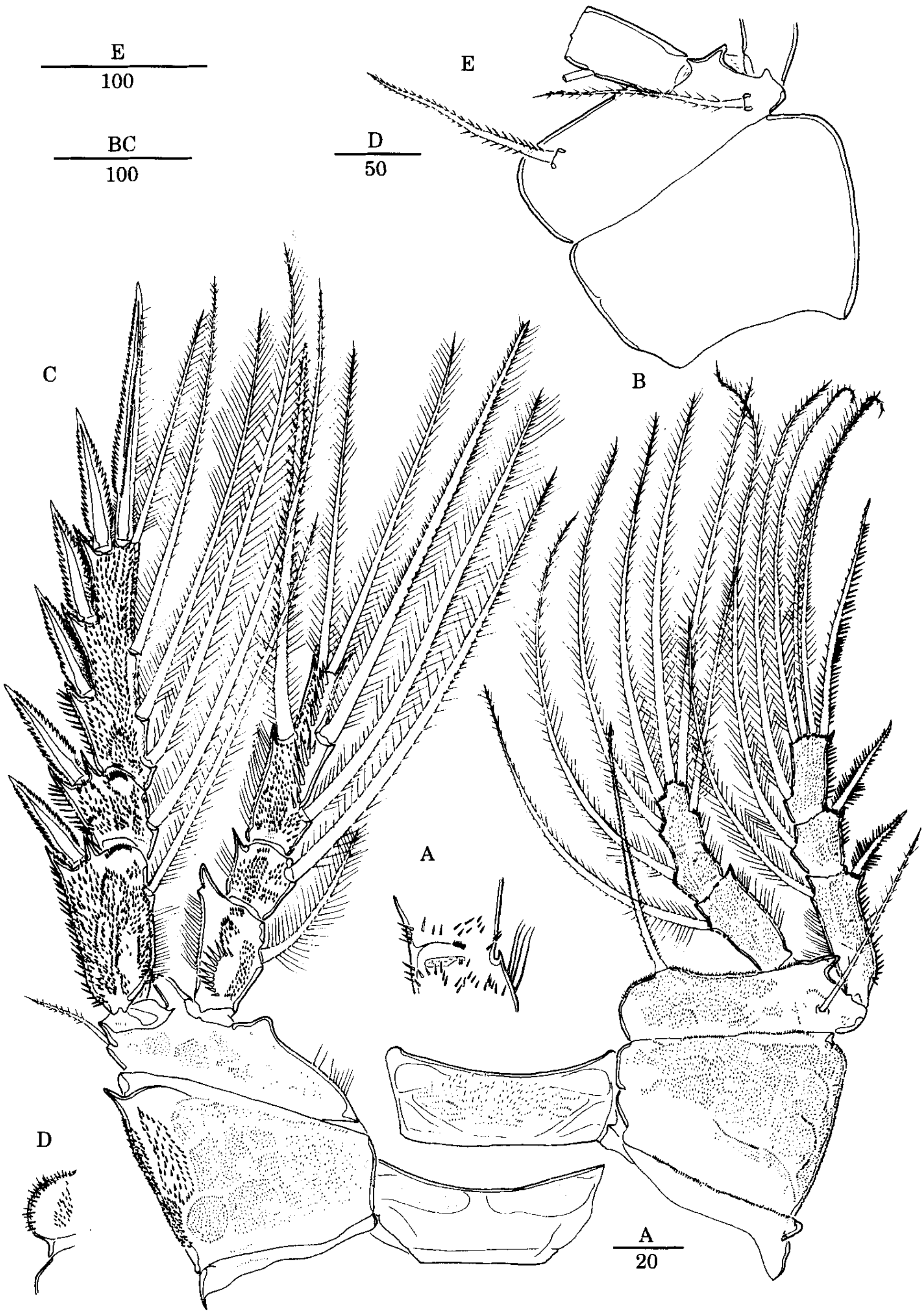

Figure 21. ***Scabrantenna yooi* gen.** et **sp. nov.** A, P1 enp-2 (♀), posterior [showing fusion of ancestral middle and distal segments]; B, P1 (♀), anterior; C, P4 (♀), posterior; D, P4 basis (♂), medial lobate extension; E, P1 basis (♂), anterior [surface ornamentation omitted].

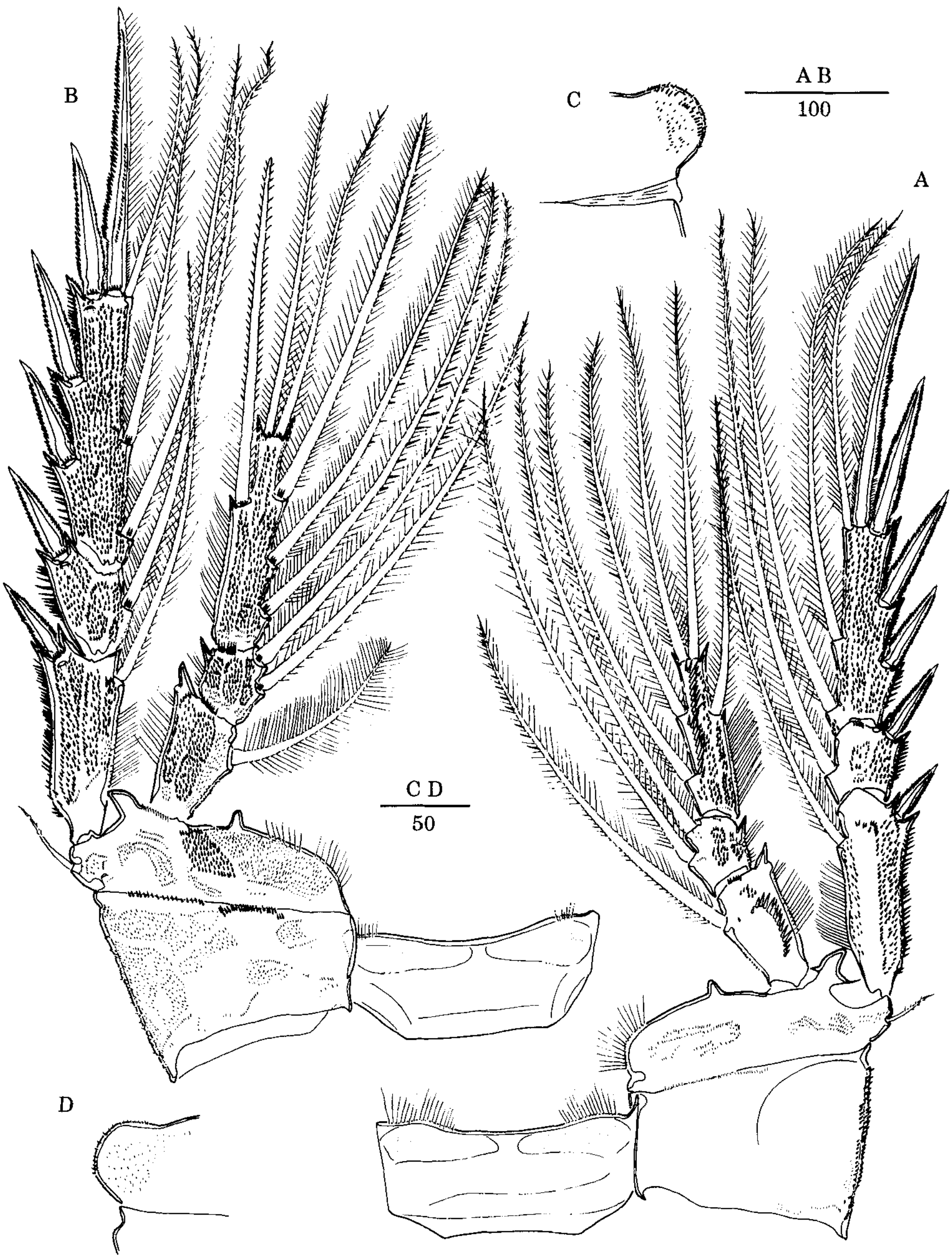

Figure 22. ***Scabrantenna yooi* gen.** et **sp. nov.** A, P2 (♀), posterior; B, P3 (♀), anterior; CAD, medial lobate extension of bases P2–P3 (♂).

Prosome (Figs 23A, 24A) 5-segmented, comprising cephalosome and 4 free pedigerous somites. Cephalosome and prosomites (bearing P1–P4) with complex surface reticulation consisting of anastomosing pattern of longitudinal and transversal lamellae as indicated in Figure 24A; middorsal surface of cephalosome and first

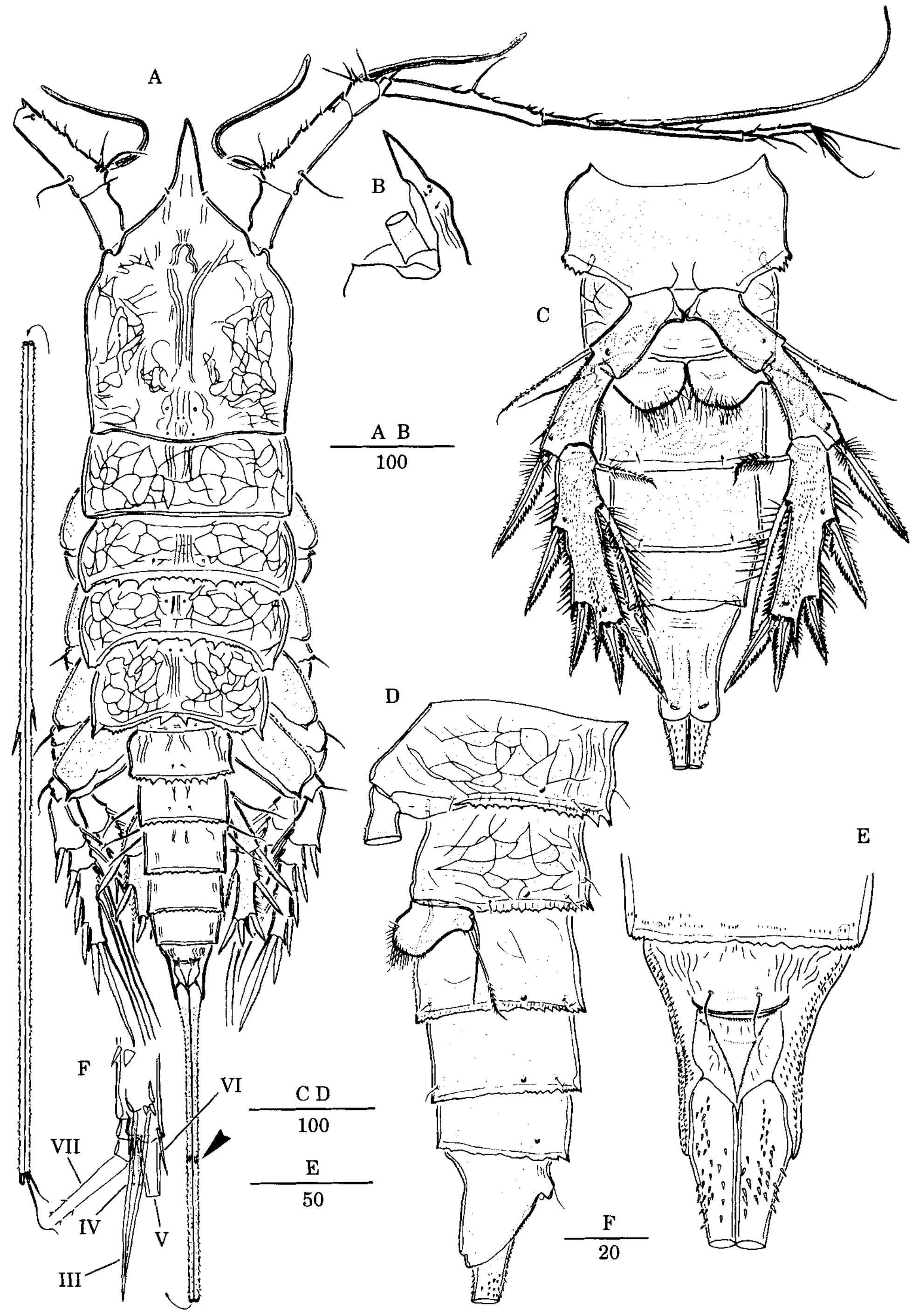

Figure 23. ***Scabrantenna yooi* gen. et sp. nov.** (♂). A, habitus, dorsal [arrow indication original position of seta I]; B, rostral area, lateral; C, urosome, ventral [caudal rami omitted]; D, same, lateral; E, anal somite, dorsal. F, distal margin of caudal ramus, ventral.

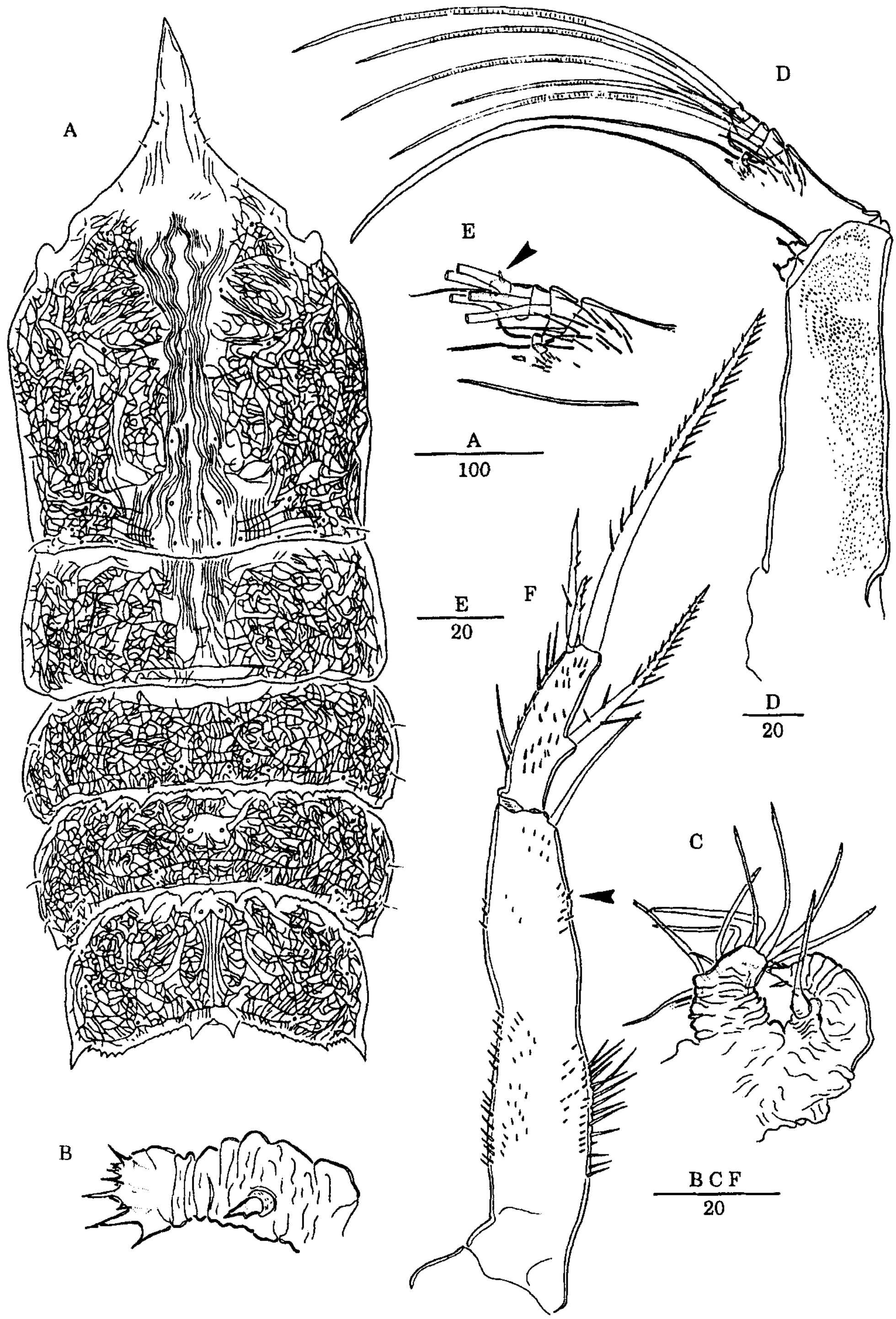

Figure 24. ***Scabrantenna yooi* gen. et sp. nov.** (♂). A, prosome, dorsal, showing fine details of surface ornamentation; B, mandible; C, maxillule; D, maxilla, posterior; E, maxillary endopod, posterior [vestigial element arrowed]; F, maxilliped [tube pore arrowed].

pedigerous somite strongly folded. Additional ornamentation consisting of sensillae and pores, particularly around posterior margin of somites; P1-bearing somite without sensillae.

Cephalosome (Fig. 24A) produced into long spinous rostral projection, bearing several sensillae at its base and slightly deflected ventrally (Fig. 23B); posterior margin smooth. Prosomites without distinct spinous processes; denticulate posterior margins similar to those of ♀.

Urosome (Fig. 23A,C,D) 6-segmented, comprising P5-bearing somite, genital somite and 4 abdominal somites. Surface ornamentation pattern consisting of minute denticles present ventrally, laterally and dorsally on all urosomites; P5-bearing and genital somites also with dorsal and lateral pattern of anastomosing surface lamellae. All urosomites without paired spinous processes; posterior margin denticulate dorsally and laterally.

Anal somite (Fig. 23E) much narrower than in ♀, medially constricted; dorsal anterior surface folded; anal opening probably not functional; anal operculum weakly developed, smooth; dorsal sensillae positioned anterior to anal opening.

Antennule (Fig. 25A) 9-segmented; haplocer with geniculation between segments 7 and 8, and segments 5 and 8 very elongate. Segment 1 with minute spinules along both anterior and posterior margins. Segment 2 with small spinous process at anterior distal corner (Fig. 25C). Segment 4 represented by small U-shaped sclerite (Fig. 25D). Segmental homologies: 1–I, 2-(II–VIII), 3-(IX–XII), 4–XIII, 5-(XIV–XVII), 6–XVIII, 7-(XIX–XX), 8-(XXI–XXIII), 9-(XXIV–XXVIII). Majority of setae in proximal half minute. Armature formula: 1-[1], 2-[9 + 1 pinnate + ae], 3-[6 + ae], 4-[2], 5-[1 + 1 pinnate + 3 modified + (1 + ae)], 6-[1 + 1 modified], 7-[2 + 1 modified], 8-[4], 9-[10 + acrothek]. Modified setae on segments 5–7 consisting of proximal multispinulose part and distal flagellate part. Anterodistal seta of segment 7 fused at base. Apical acrothek consisting of extremely long aesthetasc and slender seta. Aesthetascs large, with supporting chitinous rib.

Antenna (Fig. 18E–G) sexually dimorphic in allobasis, exopod and free endopod. Allobasis with less dense spinular pattern but with cluster of long spinules at distal abexopodal margin; abexopodal seta absent. Exopod distinctly 3-segmented; spinules on exp-1 stronger than in ♀; ornamentation of setae largely as in ♀ but setae of exp-2 and -3 distinctly shorter. Free endopod with reduced surface ornamentation but outer margin with double row of setules and inner margin with conspicuous linear comb consisting of strong spinules (Fig. 18F); lateral armature consisting of 2 minute setae (short one with apical pore; long one fused at base); distal armature consisting of 6 elements (Fig. 18G): 2 pairs of basally fused, short setae apically, and 1 long curved claw (with strong spinules in proximal half) plus 1 short naked seta subapically.

Labrum strongly folded. Paragnaths obsolete.

Mandible (Fig. 24B) completely atrophied; strongly reduced in size and gnathobasal ornamentation. Gnathobase separated from rest of praecoxa by annulated constriction; with several pointed teeth around apical margin; 3 rudimentary structure of glandular nature discernible internally. Palp minute, 1-segmented; tapering distally towards bifid apex; without setae.

Maxillule (Fig. 24C) completely atrophied, without distinct segment boundaries and strongly wrinkled. Praecoxal arthrite with total of 12 setae. Coxal endite drawn out into seta and bearing minute accessory seta. Palp bent medially, with 4 vestigial setae.

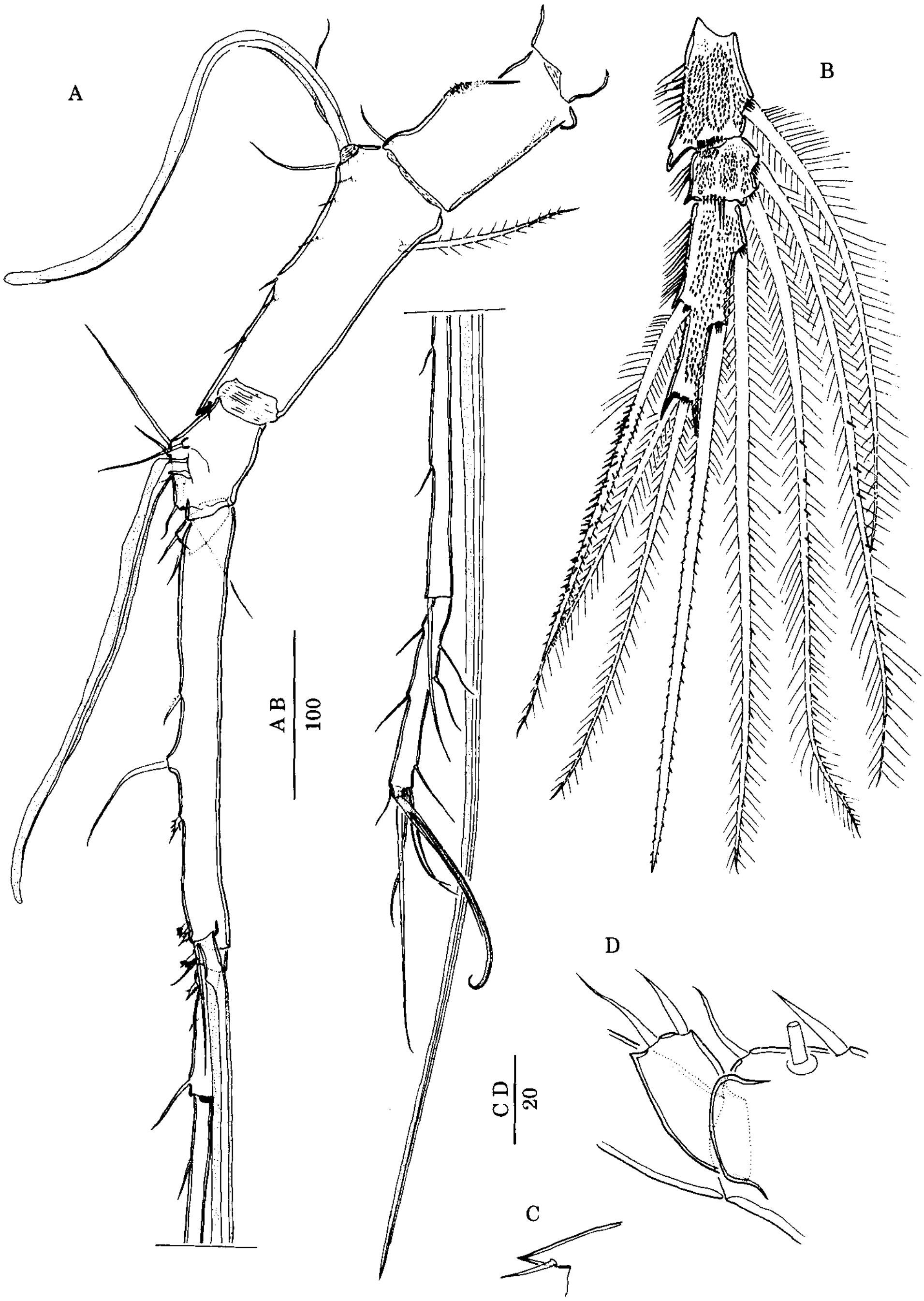

Figure 25. ***Scabrantenna yooi* gen.** et **sp. nov.** (♂). A, antennule, ventral; B, P4 endopod. C, anterior spinous process on antennulary segment 2; D, rudimentary segment 4, dorsal.

Maxilla (Fig. 24D) consisting of syncoxa, allobasis and 3-segmented endopod. Syncoxa more slender than in ♀; praecoxal endites absent; coxal endites minute lobes near boundary with allobasis, with 2 setal vestiges each. Allobasis drawn out into slender, strongly curved, naked claw; accessory armature strongly reduced (Fig. 24E), represented by 1 short seta at boundary with enp-1 and 1 setal vestige on posterior surface; posterior tube pore present. Endopod with armature formula 1-[1 geniculate], 2-[2 geniculate], 3-[1 naked + 2 geniculate + 1 setal vestige (arrowed in Fig. 24E)].

Maxilliped (Fig. 24F) 2-segmented, comprising protopod and endopod; more slender than in ♀. Protopod with strongly reduced surface ornamentation and enditic armature represented by single seta near boundary with endopod; medial margin with patch of strong spinules and small tube pore (arrowed in Fig. 24F). Endopodal armature similar to that of ♀ but lateral and outer distal setae markedly shorter.

P1 (Fig. 21E) inner basal spine much shorter than in ♀, not extending to distal margin of enp-2.

P2–P4 bases (Figs 21D, 22C,D) with inner, lobate expansion; setules along inner margin replaced by spinular patch. P4 enp-2 (Fig. 25B) with 2 inner setae.

Fifth pair of legs (Fig. 23C) joining midventrally but not fused medially. P5 elongate, directed medially and backwardly; indistinctly 3-segmented, comprising basis (or undivided protopod) and 2-segmented exopod; segmentation between basis and proximal exopod segment marked by incomplete surface suture both posteriorly and anteriorly. Basis drawn out into narrow extension medially; with outer pinnate seta. Exp-1 with outer serrate spine. Exp-2 longest; armature consisting of 2 serrate spines along outer margin, 2 serrate spines apically, and 2 pinnate setae along inner margin. Entire leg with surface spinules as figured in Fig. 23C. Anterior integumental pores present on all segments (1 on basis and exp-1; 2 on exp-2).

Sixth pair of legs (Fig. 23C,D) not fused medially, symmetrical. Each P6 with outer naked, middle pinnate and inner vestigial element; anterior surface with short spinules, inner distal margin with cluster of long setules.

Etymology

The species is dedicated to Prof. Kwang-Il Yoo (Hanyang University, Seoul) who guided and advised the senior author during his graduate courses and introduced him into the taxonomic study of copepods.

Remarks

Scabrantenna can be considered a transitionary genus between the more primitive genera, *Nudivorax* and *Andromastax*, and the truly planktonic Aegisthidae, *Aegisthus mucronatus* and *A. aculeatus*. It shares with *Aegisthus* the strongly reduced mouthparts (complete enditic/gnathobasal atrophy of mandible, maxillule, maxilla and maxilliped) and the distally elongate antennules in the male. *S. yooi* is particularly reminiscent of *A. aculeatus* in the female morphology, such as the shape of the rostrum, the 7-segmented antennule and the form of the maxilliped.

In most Aegisthidae the rostrum is better developed in the female than in the male, attaining an extreme sexual dimorphism in *A. mucronatus*. Based on observations of intermoult stages of the latter, Johnson (1937) demonstrated that the long prominent rostrum, present in the adult female and copepodid V male, is completely absorbed in the adult male at the final moult, resulting in a bluntly rounded rostral area. In other aegisthids there seems to be a similar but less pronounced degeneration process, however, in *Scabrantenna* the reverse condition is found in which the rostrum is weakly developed in the female but represented by a large frontal projection in the male.

The most distinctive feature of the new genus is the antenna which displays a remarkable sexual dimorphism. In the male the exopodal seta on the allobasis is replaced by a tuft of strong spinules. The free endopod is bordered along its inner margin by a row of prominent, outwardly directed spinules which form an almost linear array with the spinules found on the terminal claw. The antenna is clearly prehensile and capable of seizing, however, the significance of this modification is not well understood. In view of the non-feeding strategy of the male it is unlikely that the antenna, is involved in food manipulation and hence a role in mate guarding seems more likely.

There exists some confusion over the precise homology and armature of the caudal rami in Aegisthidae. Giesbrecht (1892) misinterpreted these appendages as extremely long "setiferous" setae, each borne on a very short ramus which is itself largely incorporated into the anal somite. Various authors have adopted this interpretation even though it had been suggested by Scott (1909) that the long setae might actually represent the "furcal joints". Although Boxshall (1979) re-iterated that the caudal rami themselves are extremely long and bear short setae at their apical ends, the earlier erroneous interpretation unfortunately persisted in the literature (e.g. Gamô, 1983). It has been difficult to assess the number of caudal setae in previous studies since in the majority of specimens hauled up from deeper waters the fragile caudal rami are either incomplete or some of the terminal setae have been broken off. Scott (1909) for example stated that the caudal rami terminated in 1 plumose and 2 simple setae whereas according to Boxshall (1979) each ramus is armed with a lateral seta in the middle third and at least 2 apical setae, one of which is plumose. Huys (1988) failed to find more than 2 apical setae in his northeastern Atlantic *Discovery* material of *A. mucronatus.* Conroy-Dalton & Huys' (1998) suspected that the total number of setae in *A. muricatus* is at least 6 even though the maximum number of setae observed in any specimen never exceeded 5. The consistent presence of a large ventral scar near the apical margin in all specimens examined led these authors to suggest that seta III had been dislodged. The discovery of an almost perfectly preserved male specimen of *S. yooi* revealed the precise number of setae and confirms Conroy-Dalton & Huys (1998) observation. The posterolateral seta III is well developed and spiniform (Fig. 23F) and inserts subdistally on the ventral surface. Its position coincides with the scar found in *N. todai*, *A. muricatus*, *A. cephaloceratus* and *J. terazakii.*

Jamstecia **gen. nov.**

Diagnosis

Aegisthidae. Body with complex surface reticulation. Caudal rami 1.5 longer than rest of body. Paired spinous processes present dorsally on somites bearing P2–P5, genital double-somite (♀) and second abdominal somite. Coxae of P2–P4 with series of small dentate processes. P1 endopod 2-segmented. Distal outer element of P1 exp-3 setiform.

Swimming leg armature formula:

	coxa	basis	exopod	endopod
P1	0-0	1-1	I-1;I-1;1,2,2	0-1;1,2,3
P2	0-0	1-0	I-1;I-1;III,I+1,2	0-1;0-2;1,2,2
P3	0-0	1-0	I-1;I-1;III,I+1,2	0-1;0-2;1,2,I+2
P4	0-0	1-0	I-1;I-1;III,I+1,3	0-1;0-1[♂:2];1,2,I+1

Sexual dimorphism unknown. Males presumably non-feeding.

Female

Rostrum small, spiniform. Somites bearing P2–P4 with small lateral spinous processes laterally. P5-bearing somite with 4 spinous processes; both proximal and distal halves of genital double-somite and second abdominal somite with 2 processes. Anal operculum weakly developed, clearly denticulate. Antennule 7-segmented; with 2 spinous processes on anterior margin of segment 2. Antenna with 2-segmented exopod (formula [0,2]); endopod with 2 (possibly 3) lateral and 7 apical elements. Mandible with 2-segmented palp bearing 2 setae on apical segment. Maxillule with 3 elements on coxal endite and 8 elements on palp. Maxilla with 4 endites on syncoxa (formula [4,3,2,2]); allobasis with 2 anterior and 3 posterior elements; endopod with formula [1,1,4]. Maxilliped with 2 strong spines and 4 setae on protopod; endopod with 1 seta laterally and 2 setae (plus setal vestige) apically. P1 inner basal seta slightly longer than endopod. P5 1-segmented; with 1 (basal) seta and 3 spines along outer margin and 2 spines plus 1 seta apically. P6 with 1 long seta and 2 vestigial elements.

Male

Unknown.

Type and only species

Jamstecia terazakii gen. et sp. nov.

Etymology

The generic name is derived from the acronym JAMSTEC, the Japan Marine Science and Technology Center, whose Deep Tow System was used to collect benthopelagic copepods in the Sagami Bay and Okinawa Trough.

Gender

Feminine.

***Jamstecia terazakii* gen. et sp. nov.**

Type locality

Okinawa Trough, Stn DT2–3, depth 583–711 m.

Material examined

Holotype ♀ dissected on 15 slides (NHM reg. no. 1998.228).

Description of female

Total body length 3380 µm (measured from anterior margin of cephalic shield to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 390 µm. Urosome distinctly narrower than prosome (Fig. 26A,B).

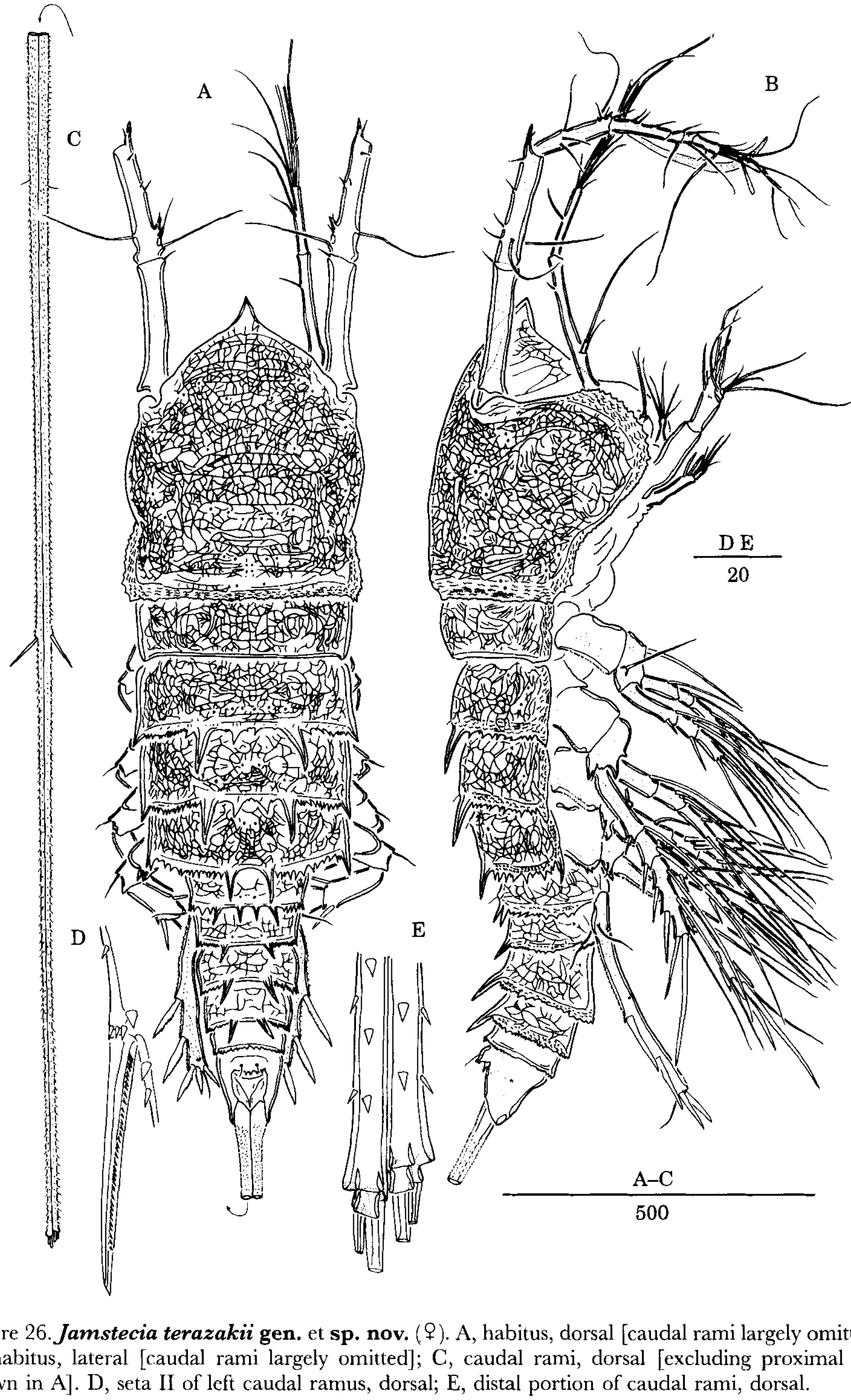

Figure 26. ***Jamstecia terazakii*** **gen.** et **sp. nov.** (♀). A, habitus, dorsal [caudal rami largely omitted]; B, habitus, lateral [caudal rami largely omitted]; C, caudal rami, dorsal [excluding proximal part shown in A]. D, seta II of left caudal ramus, dorsal; E, distal portion of caudal rami, dorsal.

Prosome (Fig. 26A,B) 5-segmented, comprising cephalosome and 4 free pedigerous somites. Cephalosome and prosomites (bearing P1–P4) with complex surface reticulation consisting of anastomosing pattern of longitudinal and transversal lamellae but not with secondary and tertiary lamellae as in *S. yooi* or *A. cephaloceratus*. Additional ornamentation consisting of sensillae and pores, particularly around posterior margin of somites; P1-bearing somite without sensillae; aggregation of paired pores present middorsally near hind margin of cephalosome.

Cephalosome bell-shaped, with spinous anterior margin and slightly swollen posterolateral angles; pleural areas strongly developed, with serrate margin; posterior margin denticulate. Rostrum (Fig. 26A,B) small, represented by short spiniform projection; sensillae apparently absent.

First pedigerous somite completely separated from dorsal cephalic shield; posterior margin smooth. Somites bearing P2–P4 (Fig. 26A,B) with paired spinous processes posterodorsally, those of P4-bearing somite more closely set to dorsal midline; posterolateral corners produced into small spinous attenuation, increasing in size in successive somites; posterior margin denticulate.

Urosome (Fig. 27A,B) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. P5-bearing somite, genital double-somite and second abdominal somite with surface ornamentation consisting of anastomosing lamellae dorsally (Fig. 26A) and laterally (Fig. 27B).

P5-bearing somite (Fig. 26A) posteriorly with 4 spinous processes dorsally; posterior margin distinctly denticulate dorsally and laterally.

Genital double-somite (Figs 26A, 27A,B) with denticulate transverse surface ridge dorsally and laterally, indicating original segmentation; completely fused ventrally; original segmentation also marked by position of paired dorsal processes. Genital field positioned far anteriorly, close to articulation with P5-bearing somite (Fig. 27A); copulatory pore minute (Fig. 27D); gonopores paired, covered on both sides by well developed opercula derived from sixth legs; P6 very elongate, dilated distally; with 1 long, sparsely plumose seta apically, and 2 rudimentary setae on subdistal inner margin (Fig. 27D).

First free abdominal somite with paired spinous processes dorsally and denticulate posterior margin; penultimate somite without spinous processes, posterior margin denticulate.

Anal somite (Fig. 27C) with pattern of minute spinules dorsally and laterally, with few surface lamellae ventrally (Fig. 27A); anal opening large, flanked by spinules laterally; and operculum weakly developed, denticulate; dorsal sensillae positioned anterior to anal opening; ventral hind margin with minute spinules and paired pores.

Caudal rami (Fig. 26A, C) slightly asymmetrical; closely adpressed medially but apparently not fused; about 1.5 times length of body somites combined; covered with dense pattern of denticle-like spinules. Each ramus with 7 setae; seta I minute, located in proximal 1/5; setae II spiniform and pinnate (Fig. 26D); seta III missing but position indicated by large lateral scar (Fig. 26C); setae IV and V large; seta VI missing, position marked by minute scar at inner ventral subdistal corner; seta VII presumably tri-articulate at base, positioned subterminally (Fig. 26e).

Antennule (Fig. 28A,C–E) 7-segmented; with small sclerite around base of segment 1; all segments with irregular pattern of minute spinules. Segment 1 longest (measured along posterior margin). Armature formula: 1-[1], 2-[8 bare + 1 pinnate], 3-[8 bare + 3 pinnate + (1 + ae)], 4-[2 bare + 1 pinnate], 5-[1 bare + 1 pinnate], 6-[1 bare

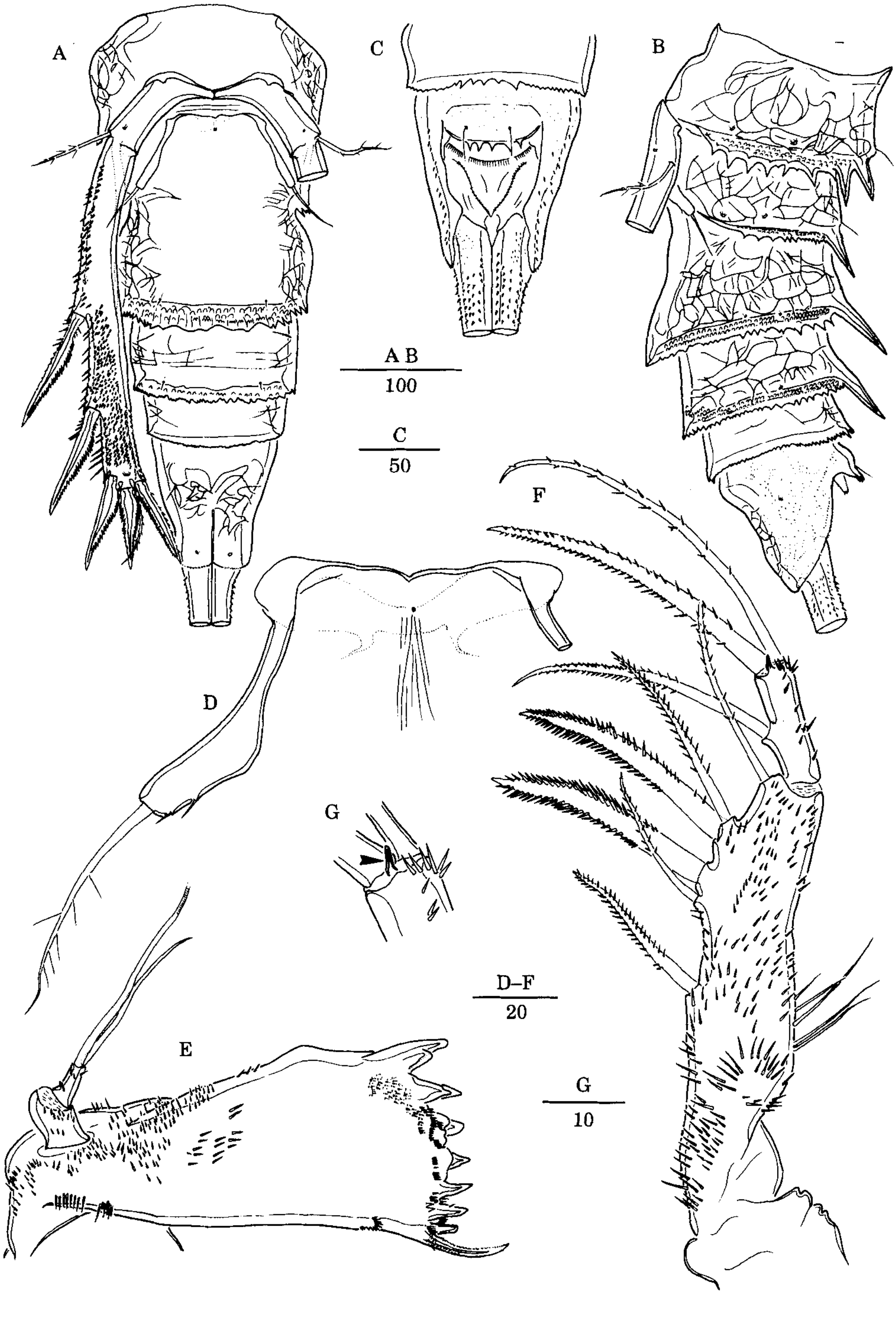

Figure 27. ***Jamstecia terazakii* gen. et sp. nov.** (♀). A, urosome, ventral [Left P5 exopod and caudal rami omitted]; B, same, lateral; C, anal somite, dorsal; D, genital field, ventral [left P6 omitted]; E, mandible; F, maxilliped; G, tip of maxillipedal endopod showing vestigial element [arrowed].

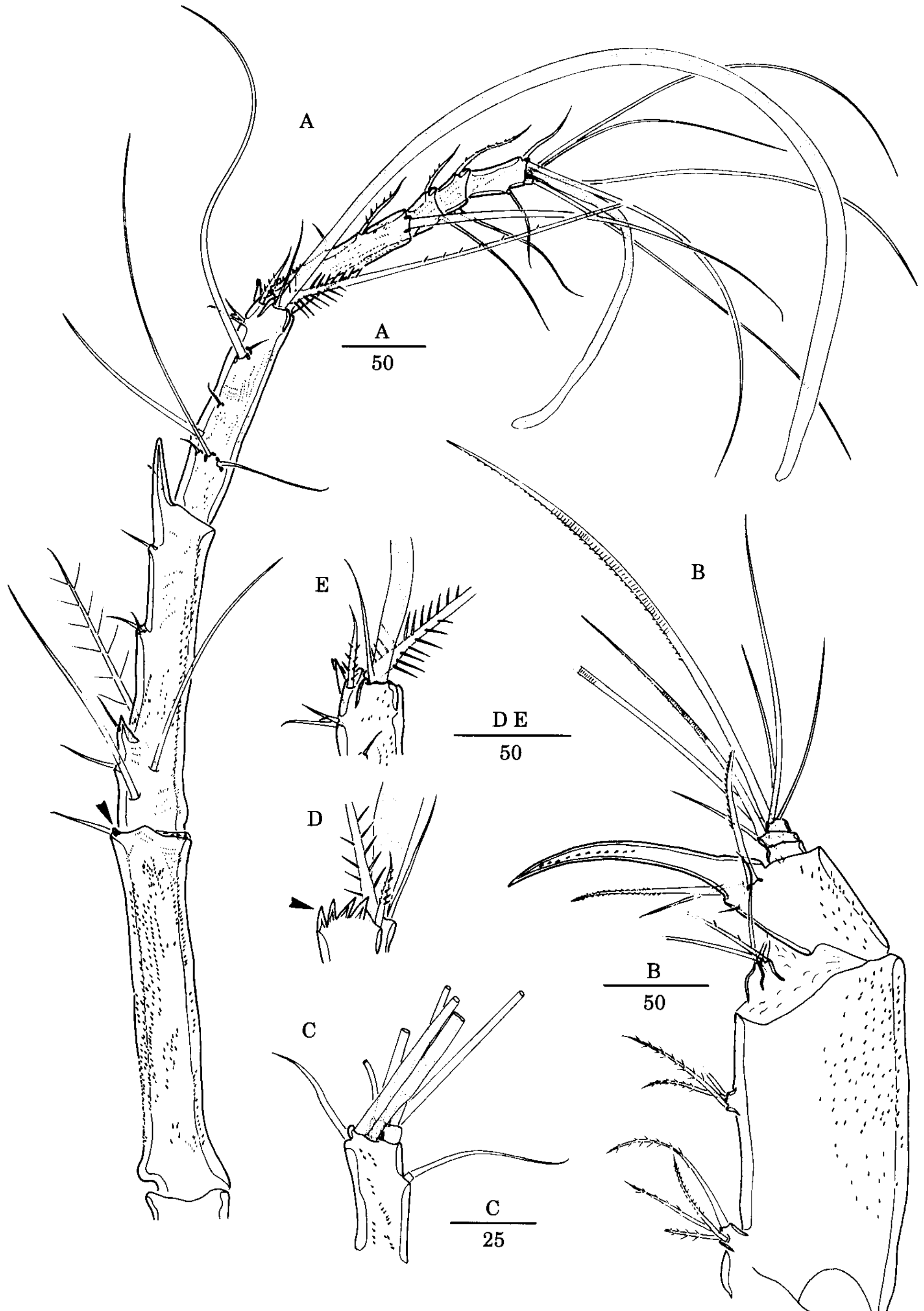

Figure 28. ***Jamstecia terazakii* gen. et sp. nov.** (♀). A, antennule, ventral [minute anterior process on segment 1 arrowed]; B, maxilla [damaged]. C, antennulary segment 7, ventral; D, distal margin of antennulary segment 3, dorsal (spinular ornamentation arrowed); E, same, ventral.

+ 1 pinnate], 7-[6 bare + acrothek]. Apical acrothek consisting of well developed aesthetasc (220 μm) fused basally to slender seta (Fig. 28C); aesthetasc on segment 3 large (630 μm), fused to short seta (Fig. 28E). Anterior margin of segment 2 with short spinous process proximally and large spinous process distally; distal margin of segment 3 strongly dentate (arrowed in Fig. 28D). Apical seta of segment 3 pinnate in proximal portion (Fig. 28E).

Antenna (Fig. 29A, E–G) 3-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa small, with few minute spinules. Basis and proximal endopod segment completely fused forming very elongate allobasis with 1 abexopodal seta distally (derived from endopod). Exopod (Fig. 29G) 2-segmented; proximal segment about 1.9 times as long as wide, with minute surface spinules, unarmed; distal segment minute, with very long, basally fused pinnate seta and short, naked seta. Endopod only half the length of allobasis; covered with numerous minute denticles; lateral armature (Fig. 29F) consisting of 1 naked and 1 pinnate seta (and possibly third element represented by tubercle: arrowed in Fig. 29F); apical armature consisting of 7 setae of varying lengths (4 of which basally fused in pairs) (Fig. 29E).

Labrum well developed; with elaborate spinular ornamentation along distal margin as in Fig. 29B.

Mandible (Fig. 27E) with large coxa bearing well developed gnathobase; cutting-edge with 7 major teeth around distal margin, several patches of minute spinules and 1 unipinnate seta at dorsal corner. Numerous spinules present around insertion site of palp. Palp small, 2-segmented; basal segment largest, unarmed; distal segment small and narrow, medially directed, with 1 short and 1 long seta.

Paragnaths (Fig. 29C) well developed hirsute lobes.

Maxillule (Fig. 29D). Praecoxa with transverse fold and few spinules around outer margin; arthrite strongly developed, with 2 large, swollen, plumose setae on anterior surface (see inset) and 10 spines/setae around distal margin. Coxa with cylindrical endite bearing 2 pinnate setae and 1 slightly curved bipinnate spine. Basis without discrete rami; apical margin not bilobate; elements grouped in inner cluster consisting of curved, sparsely pinnate spine and 2 bipinnate setae, and outer cluster consisting of 3 bare and 2 pinnate setae.

Maxilla (Fig. 28B) partly damaged during dissection; comprising syncoxa, allobasis and 3-segmented endopod. Syncoxa large, with minute spinules in outer half; with 4 weakly developed endites: proximal praecoxal endite lobate, positioned far proximally, with 1 plumose and 3 pinnate setae; distal praecoxal endite almost entirely incorporated into syncoxa, represented by 3 setae; coxal endites closely set near articulation with allobasis, both cylindrical and with 2 setae. Allobasis drawn out into strong curved, sparsely pinnate claw; accessory armature consisting of 1 minute seta and 1 curved spine on anterior surface, 1 bipinnate seta and 1 slender seta on posterior surface, and 1 naked seta near boundary with first endopod segment. Endopod with armature formula 1-[1 geniculate], 2-[1 geniculate], 3-[1 geniculate +3 bare].

Maxilliped (Fig. 27F) 2-segmented, comprising undivided protopod and 1-segmented endopod. Protopod very long, covered with dense pattern of fine spinules; outer margin with few long setules; with 6 elements representing 4 vestigial endites; endite 1 represented by bipinnate spine, endites 2 and 3 with 1 large bipinnate spine and 1 bipinnate seta, endite 4 with 1 bipinnate seta. Endopod without surface sutures marking original segmentation; about 3.5 times as long as wide; with 1

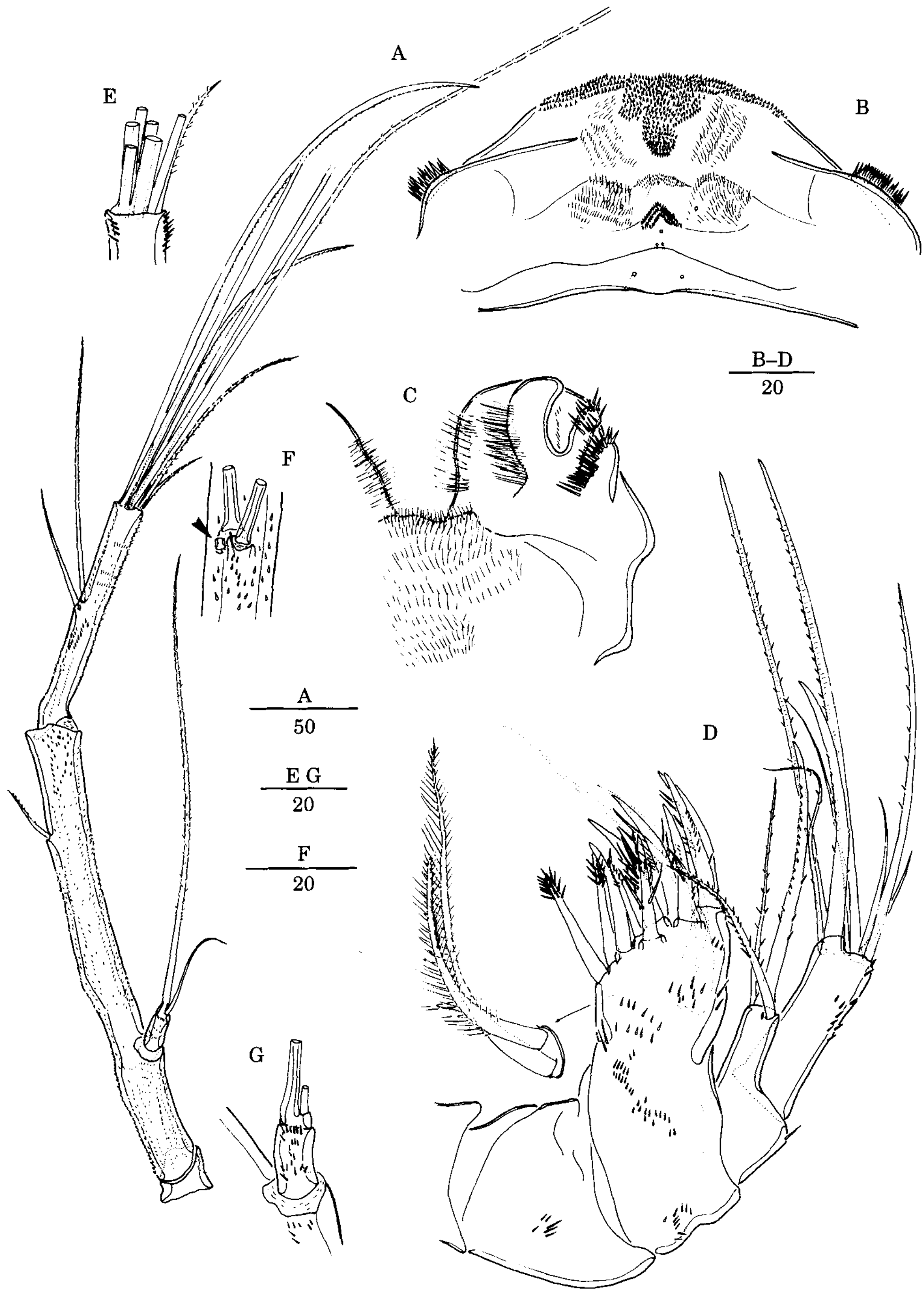

Figure 29. ***Jamstecia terazakii* gen. et sp. nov.** (♀). A, antenna; B, labrum, posterior; C, paragnaths, anterior; D, maxillule, posterior [Inset: anterior surface elements on arthrite. E, antennary endopod, distal armature; F, antennary endopod, lateral armature (arrow indicating third element, probably broken); G, antennary exopod].

bipinnate seta laterally, and 1 strong bipinnate spine and 1 bipinnate seta apically; vestige of third (middle) apical element discernible (arrowed in Fig. 27G).

Swimming legs (Figs 30A–C, 31A–C) with 2-segmented (P1 endopod; derived by fusion of middle and distal segments) or 3-segmented (P1 exopod; P2–P4) rami; endopods distinctly shorter than exopods. Intercoxal sclerites large and wide; with few spinules/setules or completely lacking in ornamentation. Coxae with characteristic pattern of surface spinules as figured; outer margin with series of dentate processes (particularly well developed in P4: Fig. 31C). Bases with numerous surface spinules as figured; inner margin with setular tuft and small rounded process in P2–P4; inner basal spine of P1 bipinnate, slightly longer than endopod; outer basal seta long in P1, short in P2–P4. All segments with dense pattern of spinules as figured. Posterior surface of P2–P4 enp-1 and enp-3 with row of coarse spinules. Outer margins of endopodal segments with long setules. Spine and setal formula as for genus. Exopodal spines bipinnate in P1, serrate or pectinate in P2–P4. Distal outer element of P1 exp-3 setiform. Distal inner seta of enp-3 setiform in P1–P2, spiniform and rod-shaped in P3–P4.

Fifth pair of legs (Fig. 27A) very large, almost extending to posterior margin of anal somite; joining in ventral midline but not fused medially; distinctly curved inwards. P5 uniramous, 1-segmented with vestigial suture line along inner margin marking boundary between protopod and exopod; outer basal seta sparsely plumose; exopodal armature consisting of 3 serrate spines (pinnate proximally) along outer margin, and 1 dorsal plumose seta flanked by outer biserrate and inner uniserrate spine around apex; entire leg covered with dense pattern of minute spinules and 4 pores anteriorly.

Variability

The left P1 exp-3 had an atypically long outer distal seta (Fig. 30B).

Male

Unknown.

Etymology

The species is named in honour of Prof. Makoto Terazaki (Tokyo University).

Remarks

Generic assignment of the new species is hampered by the lack of information on the male. *J. terazakii* is obviously closely related to *Andromastax muricatus* by virtue of the spinous process pattern on the trunk somites, the presence of 2 spinous processes on segment 2 of the female antennule and the shape of the rostrum.

The female of *J. terazakii* can be readily identified without dissection by the long and slender antennules, resulting from secondary elongation of segment 1 which unlike in other aegisthids has become the longest antennulary segment. The elongate antenna differs significantly from that of other members of the family in that the free endopod is distinctly shorter than the allobasis and the 2-segmented exopod is strongly reduced in size, bearing a characteristic armature of 1 very long seta and 1 accessory seta. *J. terazakii* also differs from *Andromastax* in the maxilliped which has a different enditic setation formula on the syncoxa and only 2 well developed apical

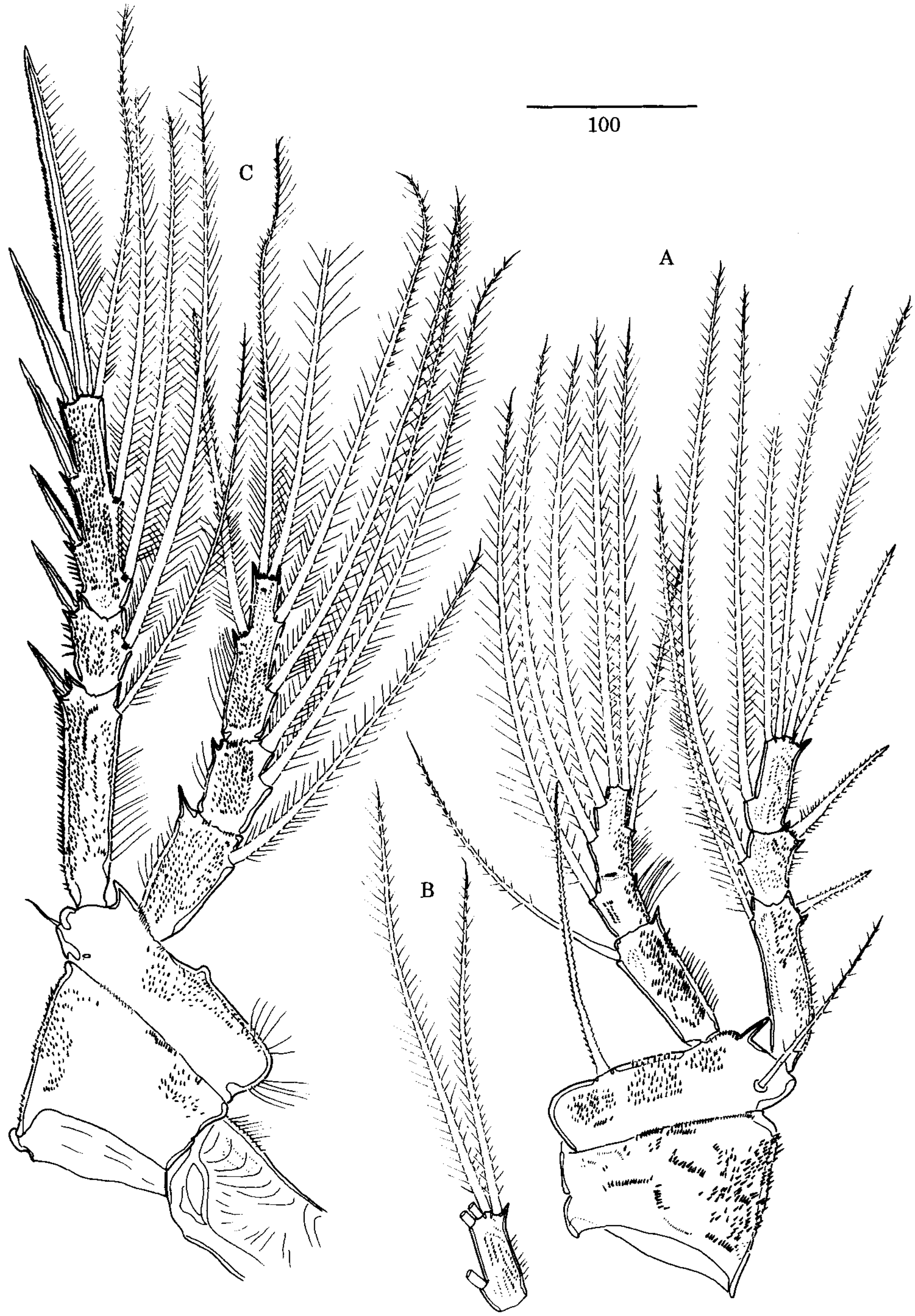

Figure 30. ***Jamstecia terazakii* gen. et sp. nov.** (♀). A, P1, anterior; B, P1, aberrant armature on left exp-3; C, P2, anterior.

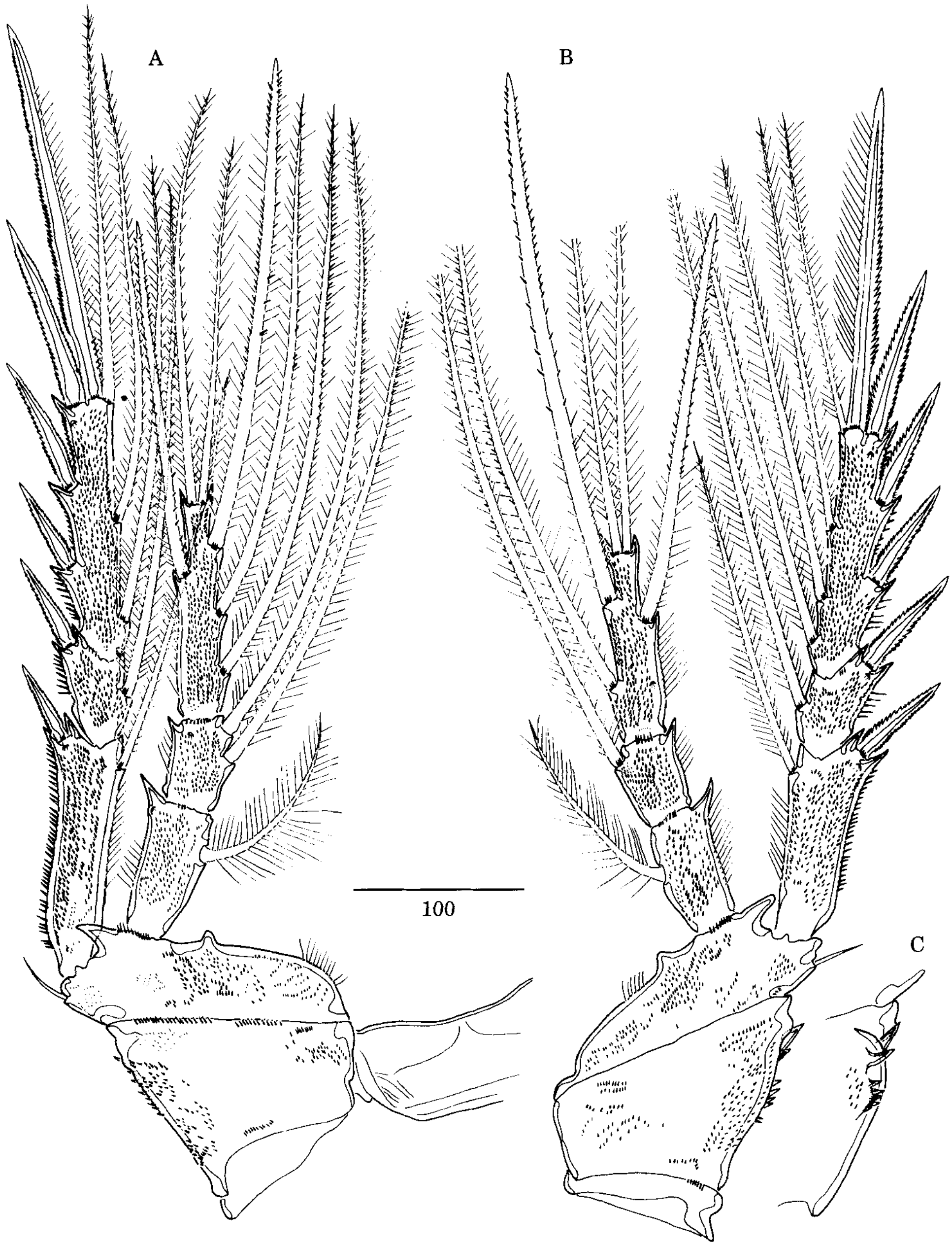

Figure 31. ***Jamstecia terazakii* gen.** et **sp. nov.** (♀). A, P3, anterior; B, P4, anterior; C, outer margin of P4 coxa, posterior.

elements on the endopod. Other differences include the absence of lateroventral spinous processes on the cephalic shield, the reduced armature on the female P6 and the peculiar shape of the mandibular palp. The outer spinous processes on the coxae of P2–P4 in *Andromastax* are not developed in *J. terazakii*. Instead, a series of dentate processes (particularly well developed in P4) is found along the outer margin which might either represent a precursor stage of the spinous process or an entirely new, non-homologous structure.

The discovery of a second, allopatric, *Andromastax* species (to be described below) however, has demonstrated that intrageneric variability is limited and embraces primarily differences encountered in body and swimming leg ornamentation, P5 setation and caudal ramus length. Species discrimination based solely on males appears to be difficult, and mouthpart armature patterns are extremely conservative within the genus. It is therefore preferred to place *J. terazakii* in a distinct genus rather than to widen significantly the boundaries of *Andromastax*.

Andromastax Conroy-Dalton & Huys, 1999

***Andromastax cephaloceratus* sp. nov.**

Type locality

Okinawa Trough, Stn DT4–2, depth 780–823 m.

Material examined

Holotype ♀ dissected on 14 slides (type locality; NHM reg. no. 1998.266); paratypes are 1 damaged ♂ dissected on 12 slides (Stn DT2–3; reg. no. NHM 1998.267), and 12 ♀♀ and 1 copepodid preserved in alcohol (Stn DT1–3: 3♀♀; Stn DT1–4: 4♀♀; Stn DT2–2: 1 ♀, 1 copepodid; Stn DT2–3: 2 ♀♀; Stn DT4–3: 1 ♀; Stn DT-4–4: 1 ♀; NHM reg. nos 1998.268–280).

Description of female

Total body length 3055 μm (measured from anterior margin of cephalic shield to posterior margin of caudal rami). Largest width measured at posterior margin of cephalic shield: 388 μm. Urosome distinctly narrower than prosome (Fig. 32A).

Prosome (Fig. 33A) 5-segmented, comprising cephalosome and 4 free pedigerous somites. Cephalosome and prosomites (bearing P1–P4) with complex surface reticulation consisting of anastomosing pattern of longitudinal and transversal lamellae as indicated in Figure 33A. Additional ornamentation consisting of sensillae and pores, particularly around posterior margin of somites; P1-bearing somite without sensillae; conspicuous aggregation of paired pores present middorsally near hind margin of cephalosome.

Cephalosome bell-shaped, with pointed anterior margin and slightly swollen posterolateral angles; pleural areas strongly developed, with spinous process at base of antennae and denticulate margin posterior to this structure; posterior margin denticulate, with large, paired, posteriorly directed spinous processes. Rostrum (Figs. 32A, 33A) small, represented by pointed, anteriorly directed projection; sensillae absent.

First pedigerous somite completely separated from dorsal cephalic shield; posterior margin straight, not denticulate. Somites bearing P2–P4 (Figs 32A,B, 33A) with paired spinous processes posterodorsally, those of P4-bearing somite more closely set to dorsal midline; posterior margin denticulate; posterolateral corners of P4-bearing somite produced into spinous attenuation.

Urosome (Figs 32A, 33B–D) 5-segmented, comprising P5-bearing somite, genital

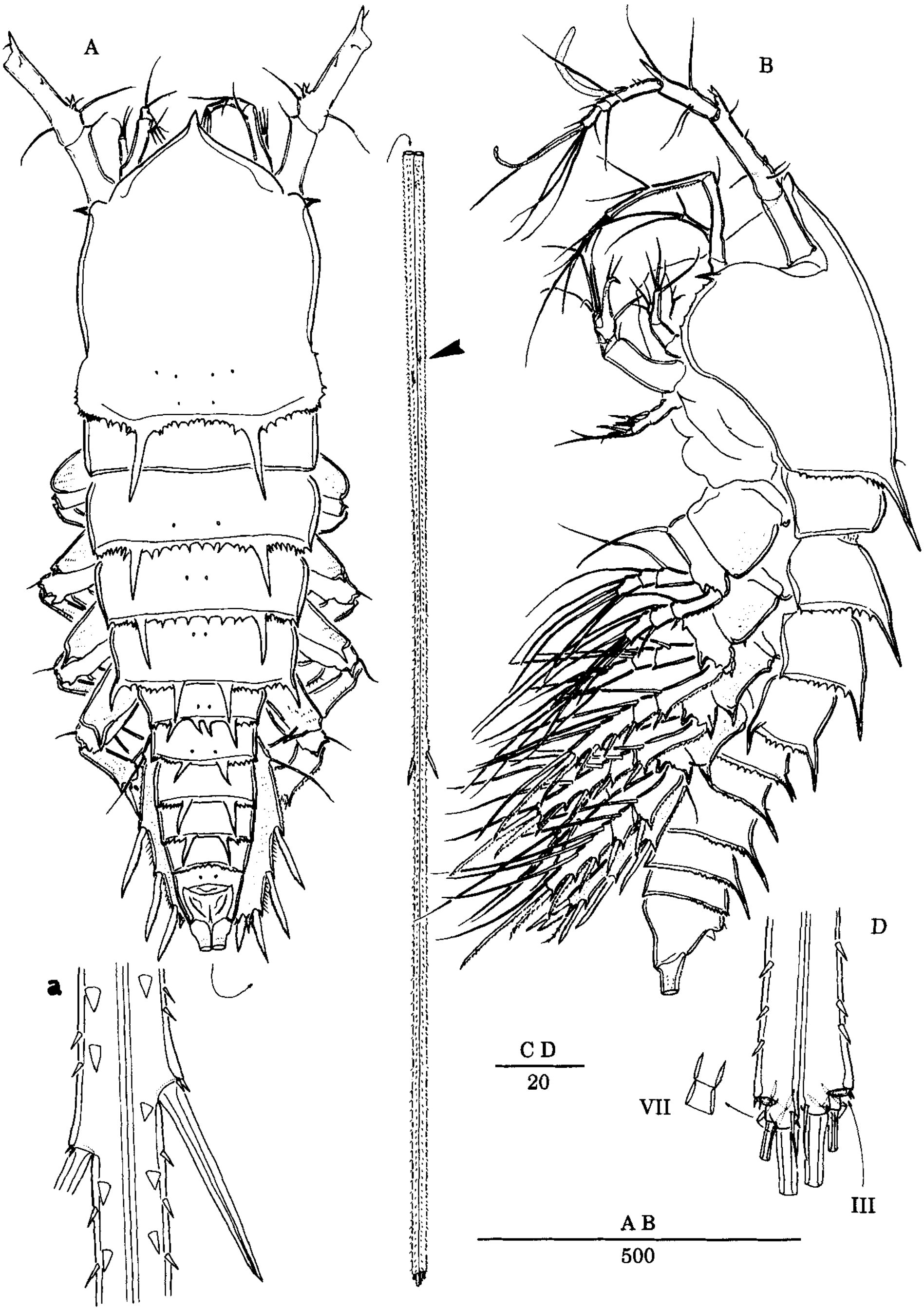

Figure 32. ***Andromastax cephaloceratus* sp. nov.** (♀). A, habitus, dorsal [distal antennulary segments omitted; arrow indicates position of pore replacing seta I]; B, habitus, lateral [caudal rami omitted]. C, area around seta II of caudal ramus, dorsal; D, distal end of caudal ramus, ventral.

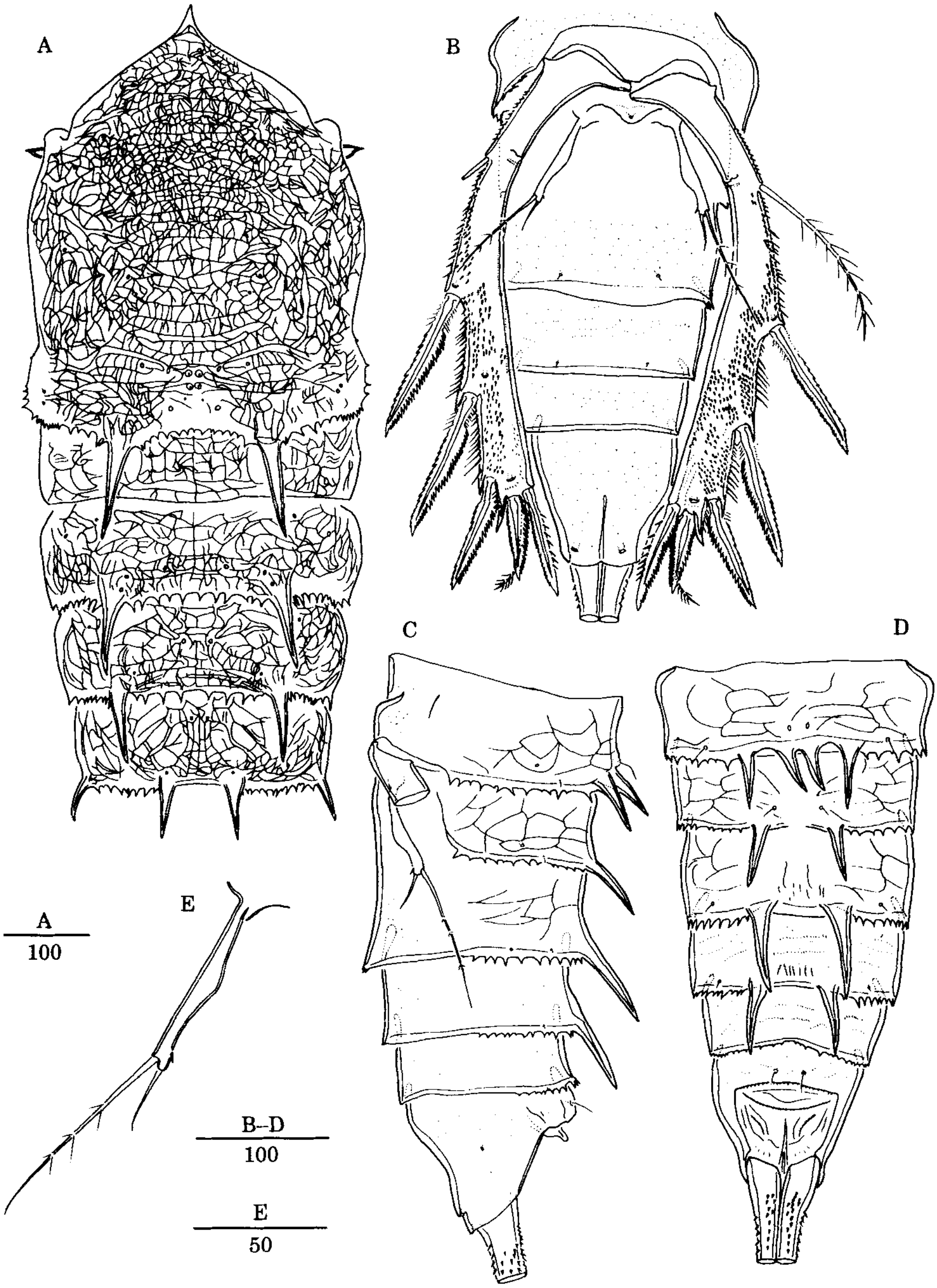

Figure 33. ***Andromastax cephaloceratus* sp. nov.** (♀). A, prosome, dorsal, showing fine details of surface ornamentation; B, urosome, ventral [caudal rami omitted]; C, same, lateral [P5 omitted]; D, same, dorsal; E, right P6.

double-somite and 3 free abdominal somites. P5-bearing somite and genital double-somite with dorsal pattern of transverse and longitudinal lamellae; other urosomites with small spinules or denticles dorsally (Fig. 33D) and ventrally (Fig. 33B).

P5-bearing somite (Fig. 33C,D) posteriorly with 4 spinous processes dorsally; posterior margin denticulate dorsolaterally.

Genital double-somite (Fig. 33B–D) with denticulate transverse surface ridge laterodorsally and laterally, indicating original segmentation; completely fused mid-dorsally and ventrally; original segmentation also marked by position of paired dorsal processes. Genital field positioned far anteriorly, close to articulation with P5-bearing somite (Fig. 33B); copulatory pore minute; gonopores paired, covered on both sides by well developed opercula derived from sixth legs (Fig. 33E); P6 very elongate, with lateral bulge medially, with 1 long sparsely plumose and 1 short naked seta apically, and minute setule on subdistal inner margin (Fig. 33E).

First free abdominal somite with paired spinous processes dorsally and denticulate posterior margin laterodorsally; penultimate somite without spinous processes, posterior margin denticulate dorsally and smooth ventrally (Fig. 33B, D).

Anal somite (Fig. 33D) with large anal opening; anal operculum vestigial, bordered by tiny spinules anteriorly; dorsal sensillae positioned anterior to anal opening.

Caudal rami (Fig. 32A, C,D) closely adpressed medially but apparently not fused; about 1.4 times length of body somites combined; covered with dense pattern of denticle-like spinules. Each ramus with 6 setae; seta I absent, replaced by minute pore (arrowed in Fig. 32A) which is typically positioned asymmetrically on both rami in proximal quarter; seta II spiniform (Fig. 32C) positioned slightly asymmetrically on opposite sides; seta III missing in all specimens examined but position indicated by large lateral scar ventrally (arrowed in Fig. 32D); setae IV and V large; seta VI minute and displaced ventrally (Fig. 32D); seta VII tri-articulate at base, positioned subterminally (Fig. 32D).

Antennule (Fig. 34A, E) 7-segmented; with small sclerite around base of segment 1; all segments with irregular pattern of minute spinules. Armature formula: 1-[1], 2-[6 bare + 2 pinnate], 3-[8 bare + 2 pinnate + (1 bare + ae) + 1 spine], 4-[2 bare + 1 pinnate], 5-[1 bare + 1 pinnate], 6-[1 bare + 1 pinnate], 7-[5 bare + 1 pinnate + acrothek]. Apical acrothek consisting of well developed aesthetasc (210 μm) fused basally to slender seta; aesthetasc on segment 3 about 220 μm, fused to short seta; both aesthetascs with supporting chitinous rib. Segment 2 longest; anterior margin with short spinous process proximally and large spinous process distally. Distal margin of segment 3 dentate dorsally (Fig. 34E).

Antenna (Fig. 35A) 3-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa irregular in shape, with few spinules. Basis and proximal endopod segment completely fused forming elongate allobasis with 1 abexopodal seta distally (derived from endopod). Exopod 3-segmented; proximal segment about 5 times as long as wide, with 1 short bipinnate seta; middle and distal segments minute, each with 1 very long pinnate seta. Endopod elongate, longer than allobasis; outer margin with 3 rows of long spinules; lateral armature arising in distal half, consisting of 1 minute and 2 long naked setae; apical armature consisting of 1 short spiniform, 1 short basally pinnate and 4 long pinnate setae (1 claw-like). Allobasis, exopod and endopod all with numerous minute surface spinules.

Labrum (Fig. 35B) well developed; with elaborate spinular ornamentation along distal margin as figured.

Mandible (Fig. 34B) with large coxa bearing well developed gnathobase; cutting-edge with 8 major teeth alternating with smaller ones around distal margin, several patches of minute spinules and 1 pinnate seta at dorsal corner. Palp minute, 2-

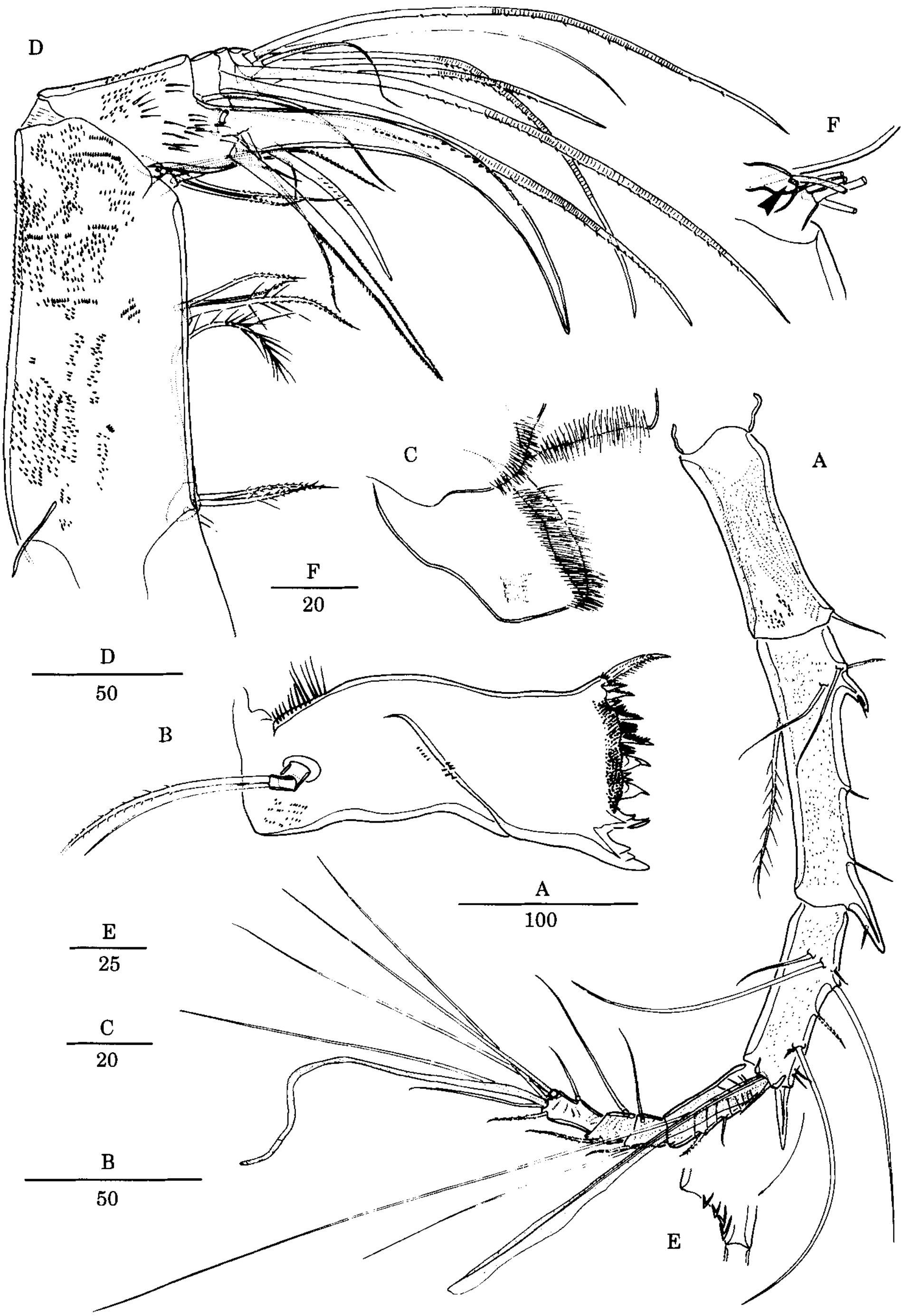

Figure 34. ***Andromastax cephaloceratus* sp. nov.** (♀). A, antennule, ventral; B, mandible; C, right paragnath, anterior; D, maxilla. E, distal margin of segment 3, dorsal; F, coxal endites of maxilla with possibly broken element arrowed.

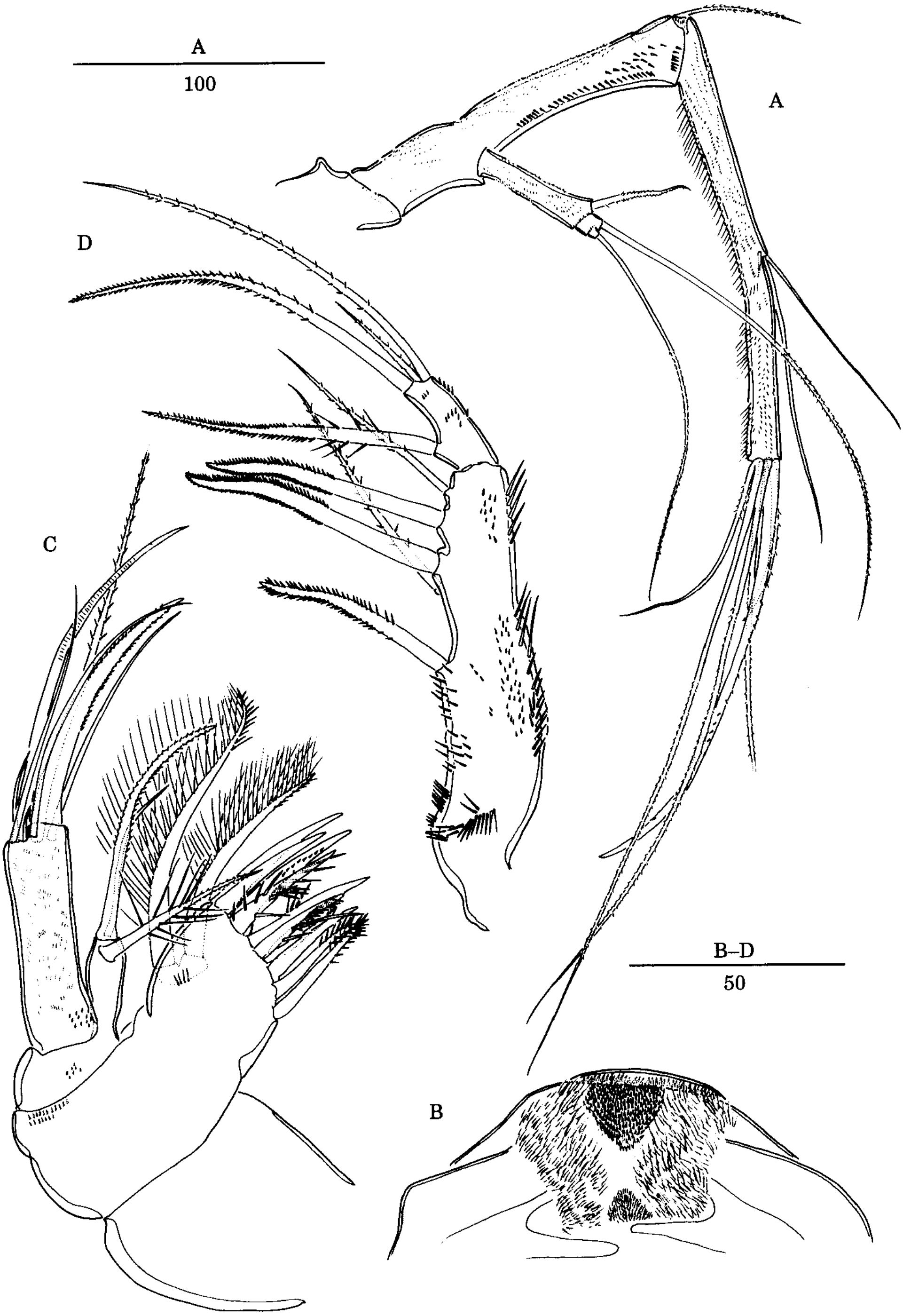

Figure 35. ***Andromastax cephaloceratus* sp. nov.** (♀). A, antenna; B, labrum, posterior; C, maxillule, posterior; D, maxilliped.

segmented; basal segment largest, unarmed; distal segment small, with 1 naked seta and 1 longer, pinnate seta.

Paragnaths (Fig. 34C) well developed hirsute lobes separated by median swelling bearing fine spinules.

Maxillule (Fig. 35C). Praecoxa with transverse fold; arthrite strongly developed, with 2 large, swollen, plumose setae on anterior surface and 10 spines/setae around distal margin. Coxa with cylindrical endite bearing 1 naked and 2 pinnate setae. Basis without discrete rami; apical margin not bilobate; elements grouped in inner cluster consisting of curved bipinnate spine and 1 naked and 1 bipinnate seta, and outer cluster consisting of 4 bare setae and 1 long bare, weakly geniculate claw.

Maxilla (Fig. 34D) comprising syncoxa, allobasis and 3-segmented endopod. Syncoxa large, with numerous minute spinules in outer half; with 4 weakly developed endites: proximal praecoxal endite lobate, positioned far proximally, with 4 pinnate setae; distal praecoxal endite almost entirely incorporated into syncoxa, represented by 3 pinnate setae; coxal endites closely set near articulation with allobasis, both cylindrical and with 3 setae (Fig. 34F). Allobasis drawn out into strong curved, sparsely pinnate claw; accessory armature consisting of 1 minute seta and 1 curved spine on anterior surface, 1 bipinnate spine and 1 slender seta on posterior surface, and 1 naked seta near boundary with first endopod segment; posterior surface also with short tube pore. Endopod with armature formula 1-[1 geniculate + 1 bare], 2-[2 geniculate], 3-[2 geniculate + 2 bare].

Maxilliped (Fig. 35D) 2-segmented, comprising undivided protopod and 1-segmented endopod. Protopod very long, with irregular spinular pattern; outer margin with longer spinules (arranged in two groups reflecting fused syncoxa and basis); with 5 elements representing 4 vestigial endites; endite 1 with 1 bipinnate spine, endite 2 with 1 large bipinnate spine and 1 bipinnate seta, endite 3 with 1 large bipinnate spine, endite 4 with 1 bipinnate seta. Endopod without surface sutures marking original segmentation; about 3 times as long as wide; with 1 bipinnate seta laterally and 3 bipinnate setae apically (middle one much shorter than others).

Swimming legs (Figs 36A,B, 37A,B) with indistinctly 2-segmented (P1; derived by fusion of middle and distal segments: Figs 36A, 41G,H) or distinctly 3-segmented (P2–P4) rami; endopods distinctly shorter than exopods. Intercoxal sclerites large and wide; completely lacking in ornamentation. Praecoxae with spinular row around distal margin. Coxae with characteristic pattern of surface spinules as figured; with small (P2) or large (P3–P4) spinous process arising from distal outer margin. Bases with numerous surface spinules; inner margin with setular tuft and small rounded process in P2–P4; inner basal spine of P1 bipinnate, about as long as endopod; outer basal seta long in P1, short in P2–P4. All segments with dense pattern of spinules as figured. Posterior surface of P2–P4 enp-1 and enp-3 with row of coarse spinules. Outer margins of endopodal segments with long setules. Spine and setal formula as for genus. Exopodal spines bipinnate in P1, serrate or pectinate in P2–P4. Distal segment of P1 exopod with setiform outer element; distal inner seta of enp-3 setiform in P1–P2, spiniform and rod-shaped in P3–P4.

Fifth pair of legs (Fig. 33B) very large, extending to posterior margin of anal somite; joining in ventral midline but not fused medially; distinctly curved inwards. P5 uniramous, 1-segmented with vestigial suture line along inner margin marking boundary between protopod and exopod; outer basal seta slender, plumose; exopodal armature consisting of 3 serrate spines (pinnate proximally) along outer margin, and 1 dorsal plumose seta flanked by outer biserrate and inner uniserrate spine around

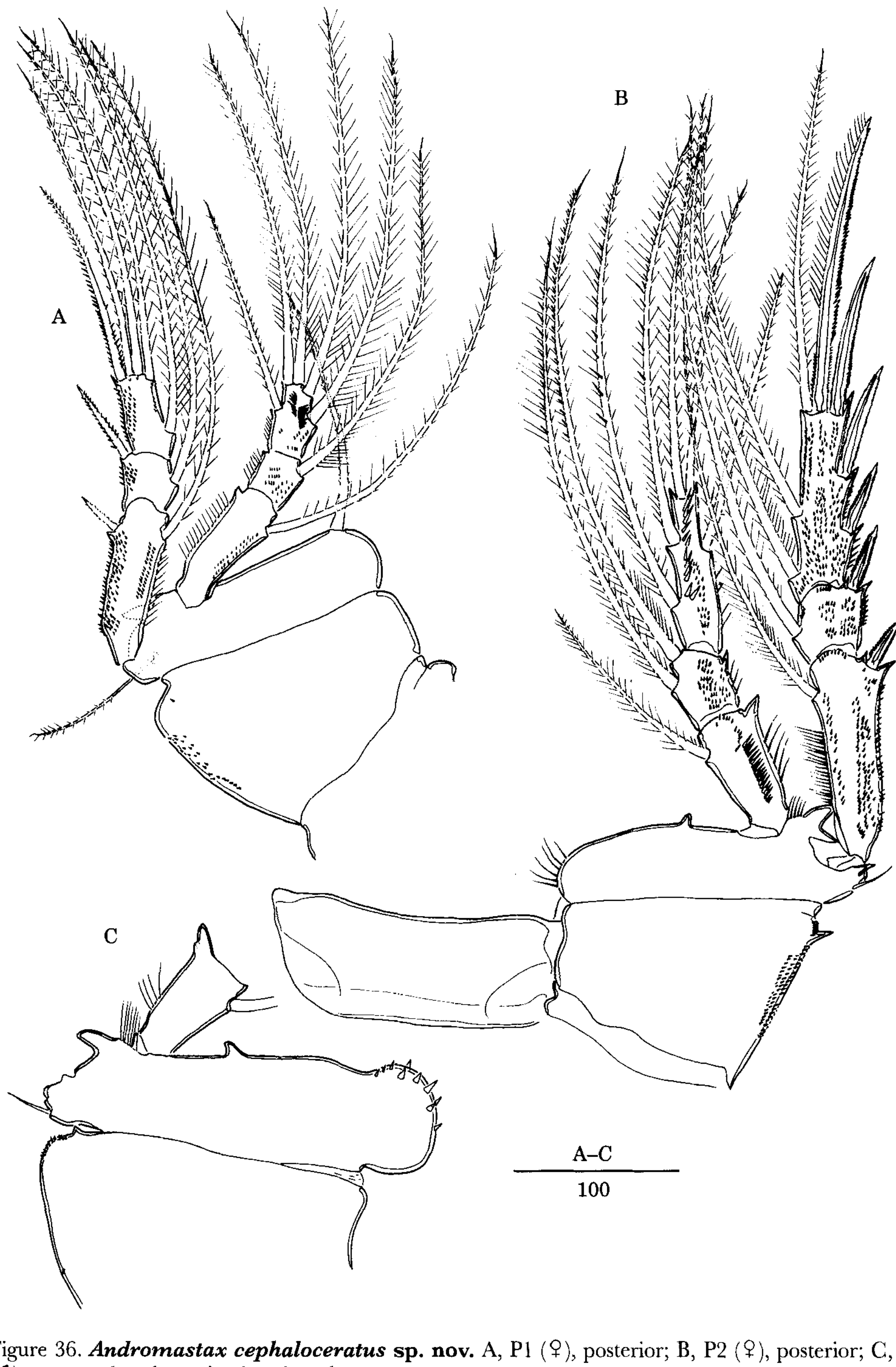

Figure 36. ***Andromastax cephaloceratus* sp. nov.** A, P1 (♀), posterior; B, P2 (♀), posterior; C, P2 (♂), protopod and proximal endopod segment.

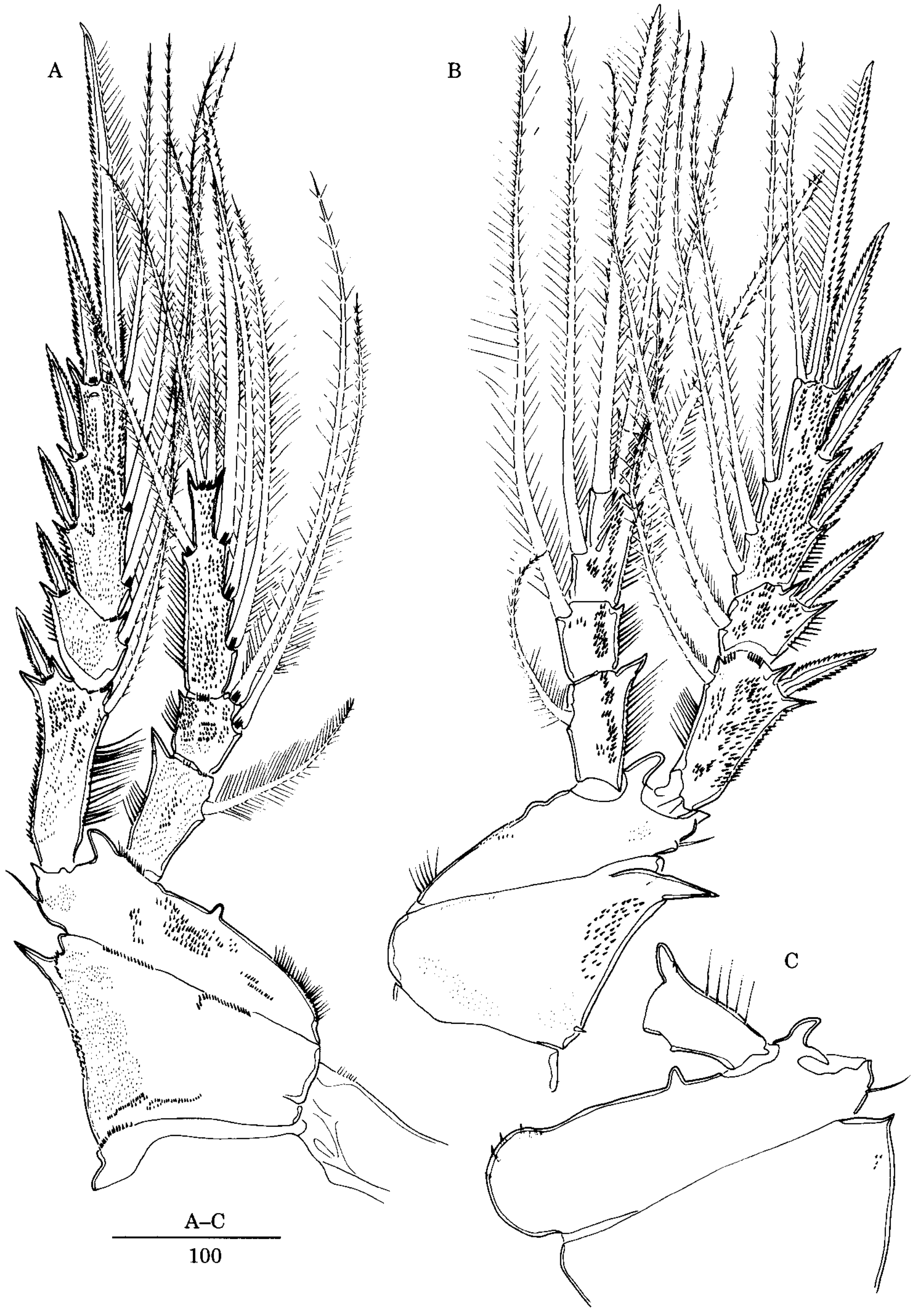

Figure 37. ***Andromastax cephaloceratus* sp. nov.** A, P3 (♀), anterior; B, P4 (♀), posterior; C, P3 (♂), protopod and proximal endopod segment.

apex; dorsal seta arising from small tubercle; entire leg covered with dense pattern of minute spinules and 3 pores anteriorly.

Description of male

Slightly more slender than ♀. Body length 2850 µm (measured from anterior margin of cephalic shield to posterior margin of caudal rami). Largest width measured at about halfway the cephalic shield length: 380 µm. Urosome distinctly narrower than prosome (Fig. 38A).

Prosome (Fig. 38A,B) 5-segmented, comprising cephalosome and 4 free pedigerous somites. Cephalosome and first pedigerous somite (P1) without conspicuous surface ornamentation; other prosomites (bearing P2–P4) with irregular surface reticulation consisting of anastomosing pattern of longitudinal and transversal lamellae as indicated in Figure 38A; middorsal surface of cephalosome and first pedigerous somite moderately folded. Additional ornamentation consisting of sensillae and pores, particularly around posterior margin of somites; P1-bearing somite without sensillae; conspicuous aggregation of paired pores present middorsally near hind margin of cephalosome (Fig. 38A).

Cephalosome bell-shaped, shorter than in ♀; with slightly concave anterior margin; without spinous process at base of antennae; posterior margin concave, smooth. Rostrum (Fig. 41A) small, triangular; slightly delimited at base by strong transverse folds but not articulating; with middorsal pore and 8 marginal sensillae.

Pattern of paired spinous processes of somites bearing P2–P4 similar as in ♀ but individual size much smaller; posterior margin of these somites denticulate. Posterolateral corners of P4-bearing somite produced but spinous process smaller than in ♀.

Urosome (Fig. 38A,C,D) 6-segmented, comprising P5-bearing somite, genital somite and 4 abdominal somites. Surface ornamentation pattern consisting of longitudinal lamellae and few minute denticles present. All urosomites without paired spinous processes; posterior margin denticulate dorsally and laterally.

Anal somite (Fig. 41B) somewhat narrower than in ♀, medially constricted; dorsal anterior surface folded; anal opening narrow and probably not functional; anal operculum semi-circular, posterior margin smooth; dorsal sensillae positioned anterior to anal opening.

Antennule (Figs 39A, E; 41D,E) 9-segmented; haplocer with geniculation between segments 7 and 8; segment 8 extremely elongate. Segment 1 with minute denticles posteriorly and spinules anteriorly. Segment 4 represented by small U-shaped sclerite (Fig. 39a). Segmental homologies: 1-I, 2-(II–VIII), 3-(IX–XII), 4-XIII, 5-(XIV–XVII), 6-XVIII, 7-(XIX–XX), 8-(XXI–XXIII), 9-(XXIV–XXVIII). Armature formula: 1-[1], 2-[11 + ae], 3-[5 + 1 pinnate spine + ae], 4-[1 + 1 pinnate spine], 5-[1 + 3 pinnate spine + (1 + ae)], 6-[1 + 1 pinnate spine], 7-[2 + 1 pinnate spine], 8-[3 + 1 pinnate], 9-[10 + acrothek]. Anterodistal seta of segment 7 fused at base and with subapical pore. Apical acrothek consisting of extremely long aesthetasc and slender seta. Aesthetascs large, with supporting chitinous rib. Anterodistal seta of segment 7 fused at base and with subapical pore (arrowed in Fig. 41b).

Antenna (Fig. 40B) sexually dimorphic in allobasis, exopod and free endopod. Allobasis with more elaborate ornamentation in basal portion (around base of exopod); abexopodal spinules of ♀ absent in ♂; abexopodal seta rudimentary. Exopod indistinctly 3-segmented; with more and coarser spinules than in ♀;

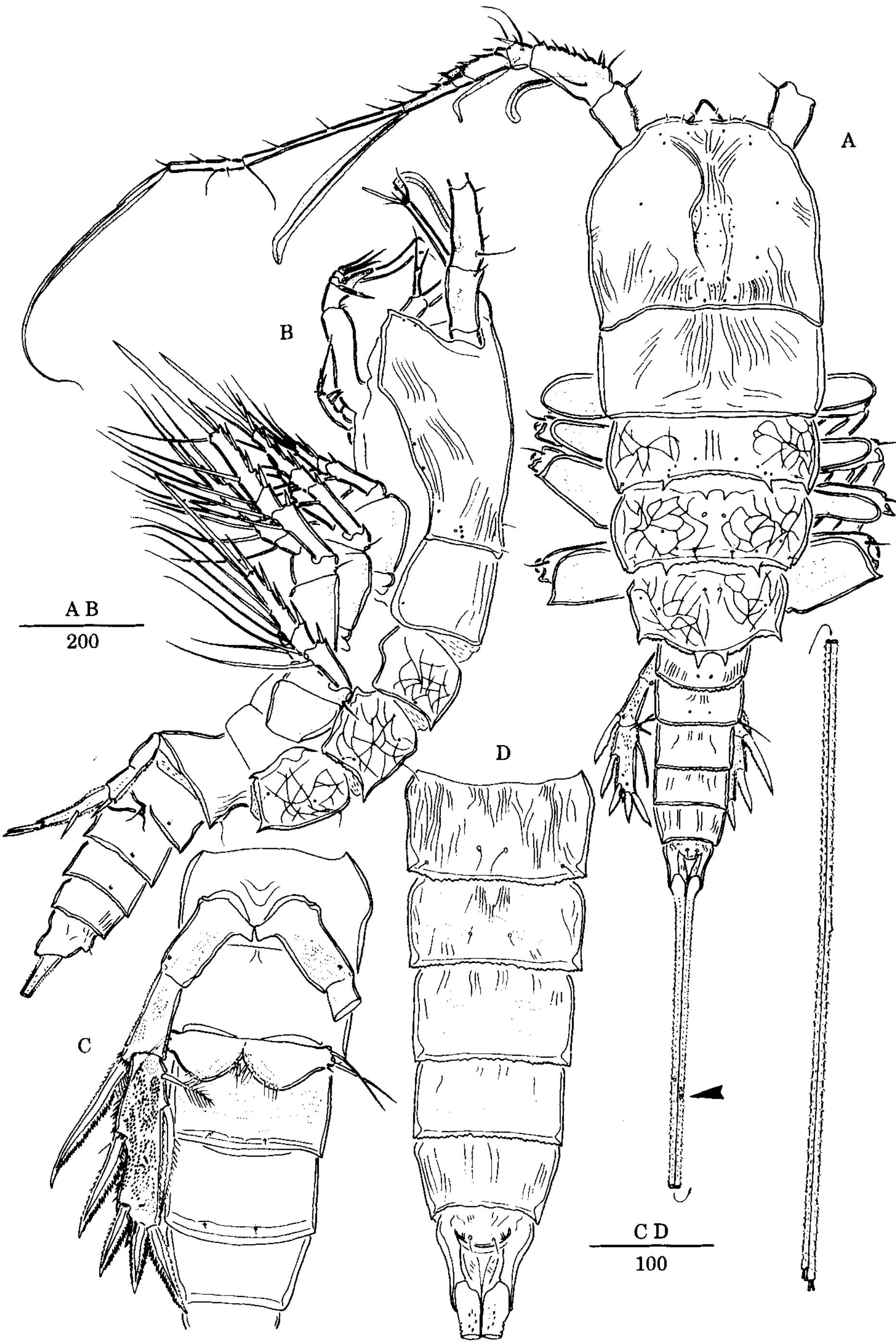

Figure 38. ***Andromastax cephaloceratus* sp. nov.** (♂). A, habitus, dorsal [arrow indicating position of pore replacing seta I]; B, habitus, lateral [distal antennulary segments and caudal rami omitted]; C, urosome, ventral [left P5 exopod and anal somite omitted]; D, same, dorsal [caudal rami omitted].

Figure 39. ***Andromastax cephaloceratus* sp. nov.** (♂). A, antennule, ventral; B, mandible; C, maxillule, posterior; D, maxilla. [Arrows in A, C and D marking missing setae] E, antennulary segment 4, dorsal; F, mandibular palp viewed from different angle.

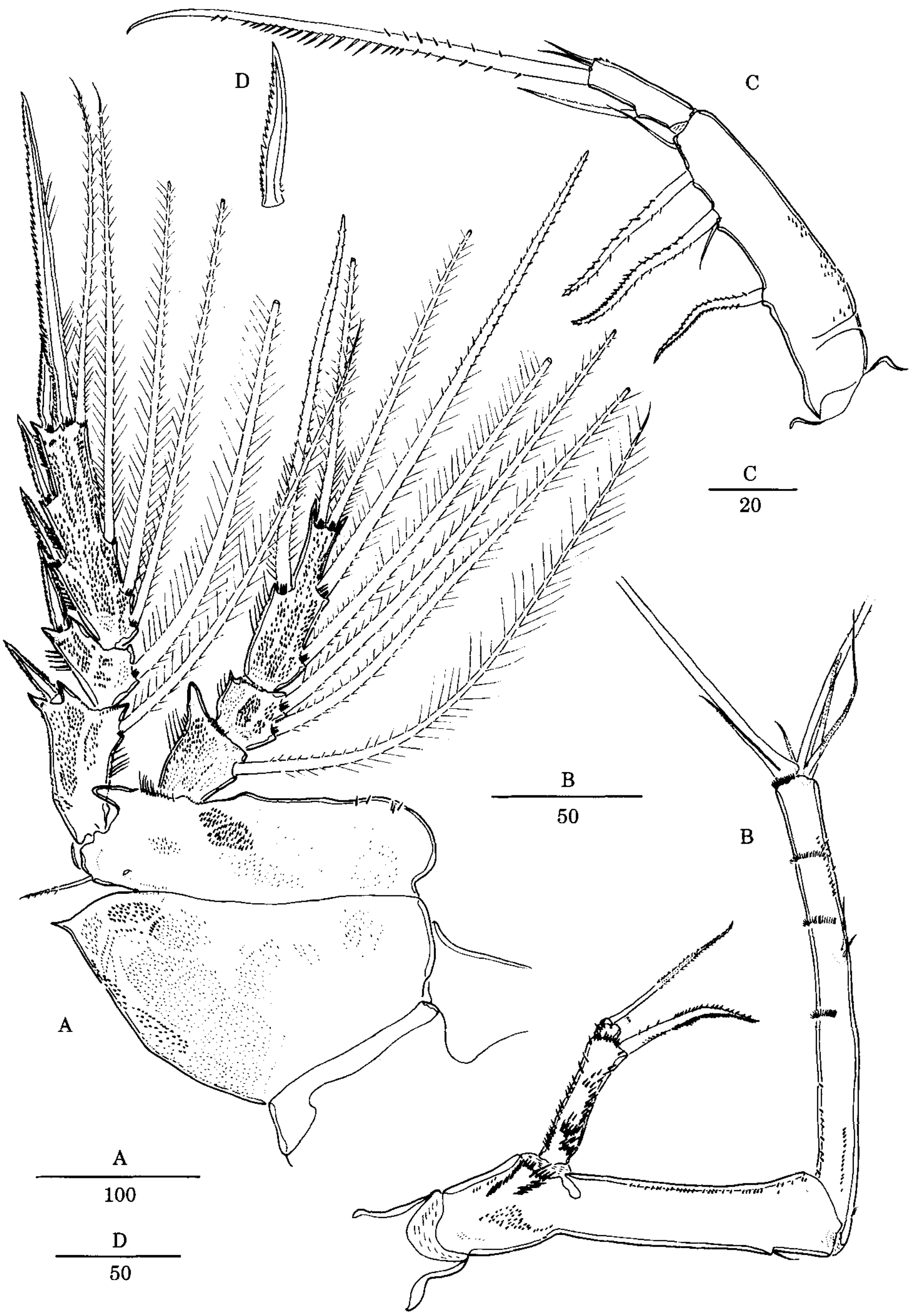

Figure 40. ***Andromastax cephaloceratus* sp. nov.** (♂). A, P4, anterior; B, antenna; C, maxilliped. D, outer distal spine of P4 exp-3.

ornamentation of setae largely as in ♀ but seta of exp-3 (and probably exp-2) distinctly shorter. Free endopod with reduced surface ornamentation; lateral armature consisting of 2 minute setae; distal armature consisting of 6 elements only: 1 long and 3 short pinnate setae, and 1 additional long naked seta fused basally to short pinnate one.

Labrum strongly wrinkled, as in type species.

Mandible (Fig. 39B,F) strongly reduced in size and gnathobasal ornamentation. Gnathobase separated from rest of praecoxa by annulated constriction; apical margin with 4 large pointed teeth and several smaller ones. Palp 2-segmented; distal segment with short, basally fused seta and longer pinnate seta apically.

Maxillule (Fig. 39C) significantly reduced. Praecoxal arthrite grossly reduced in size compared to palp; with reduced armature consisting of 2 short setae on anterior surface and 10 spines/setae around distal margin. Coxa with lobate endite bearing 1 short and 1 long bipinnate seta. Basis rectangular, elongate; armature as in ♀ but outer setae more reduced.

Maxilla (Fig. 39D) damaged (setae missing on coxal endites, allobasis and enp-1); consisting of syncoxa, allobasis and 3-segmented endopod; number of armature elements as in ♀. Syncoxa with 4 small endites; position as in ♀ but most setae distinctly shorter. Allobasis drawn out into strong, curved, pinnate claw; accessory armature as in ♀ except for anterior naked spine being replaced by robust, coarsely spinulose, blunt spine. Similar spine presumably also present on proximal endopod segment (as revealed by large scar). Endopod with armature formula 1-[1 modified spine? + 1 long geniculate], 2-[2 long geniculate], 3-[2 long geniculate + 2 short bare].

Maxilliped (Fig. 40C) 2-segmented, comprising protopod and endopod; shorter than in ♀. Protopod with strongly reduced surface ornamentation, without setules along outer margin; position and number of elements as in ♀ but seta of second endite vestigial and distalmost seta (endite 4) much shorter and naked. Endopodal armature consisting of 1 short pinnate seta laterally and 1 pinnate claw plus 2 short naked setae apically.

P1 (Fig. 41C,F) exopod 3-segmented; inner basal spine much shorter than in ♀ and minutely pinnate.

P2–P4 bases (Figs 36C, 37C, 40A) with inner lobate expansion; setular tuft along inner margin replaced by spinules or denticles. P2–P4 exp-3 outer distal spine (Fig. 40A,a) distinctly curved; outer margin serrate, inner margin smooth with few spinules. P4 enp-2 (Fig. 40A) with 2 inner setae.

Fifth pair of legs (Fig. 38C) joining midventrally but not fused medially. P5 elongate, directed medially and backwardly; indistinctly 3-segmented, comprising basis (or undivided protopod) and 2-segmented exopod; segmentation between basis and proximal exopod segment marked by incomplete surface suture both posteriorly and anteriorly. Basis drawn out into narrow extension medially; outer seta missing from both sides but position indicated by scar. Exp-1 with outer serrate spine. Exp-2 longest; armature consisting of 2 serrate spines along outer margin, 2 serrate spines apically, and 2 pinnate setae along inner margin. Entire leg with surface spinules as figured in Fig. 38C. Anterior integumental pores present on all segments (1 on basis and exp-1; 2 on exp-2).

Sixth pair of legs (Fig. 38C) slightly fused medially, symmetrical. Each P6 with 2 naked setae and inner vestigial element; anterior surface with short spinules, inner distal margin with cluster of long setules.

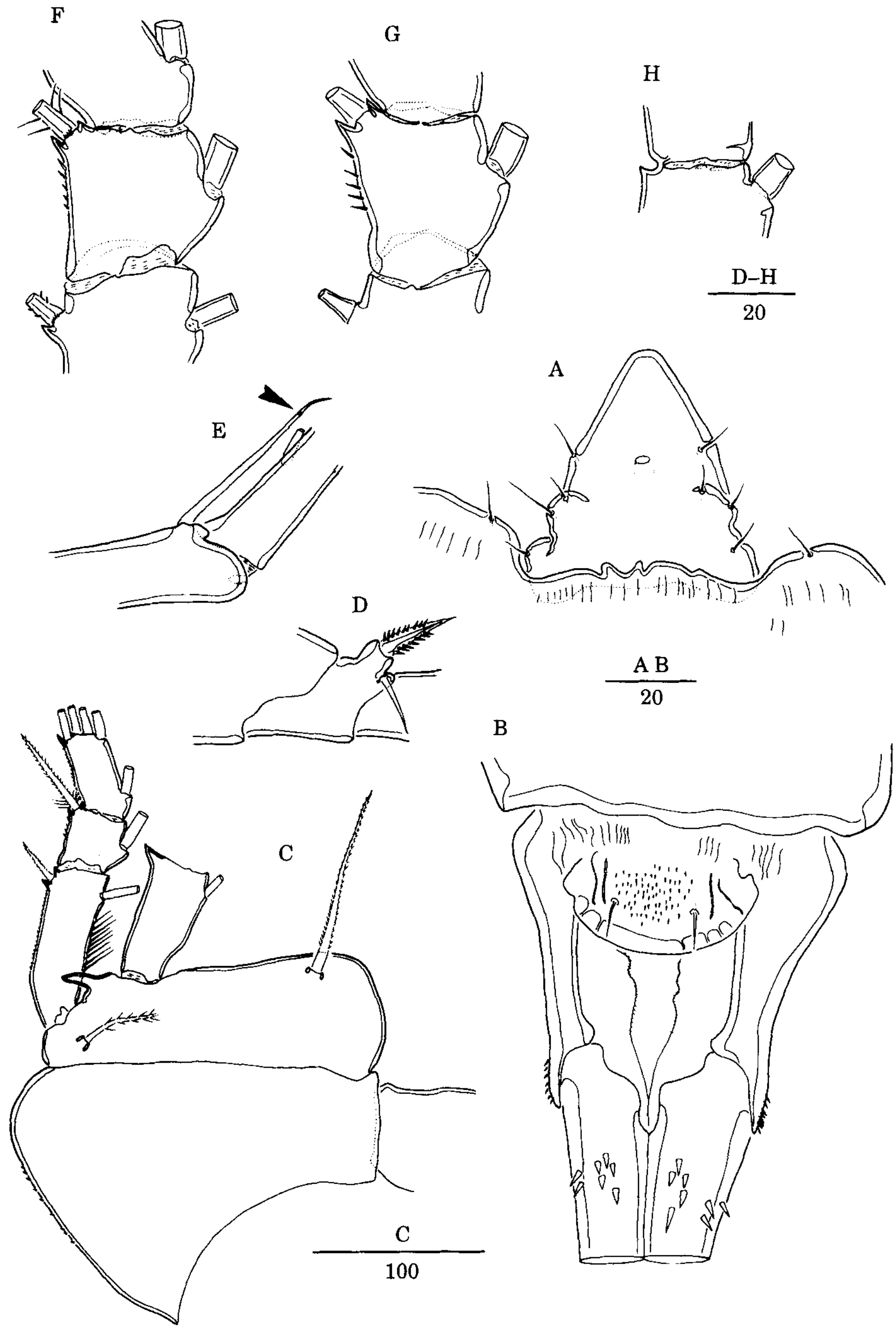

Figure 41. ***Andromastax cephaloceratus* sp. nov.** A, rostrum (♂), dorsal; B, anal somite (♂), dorsal; C, P1 (♂) [distal part of endopod omitted]. D, antennulary segment 4 (♂), dorsal; E, geniculation between antennulary segments 7 and 8 (♂); arrow indicating pore on sensory seta; F, segmental boundaries between exopodal segments of P1 (♂), anterior; G, same (♀); H; surface suture between ancestral middle and distal exopodal segments of P1 (♀), anterior.

Etymology

The species name is derived from the Greek *kephale*, meaning head, and *keras*, meaning horn, and refers to the large posteriorly directed spinous processes on the cephalic shield.

Remarks

The new species is placed in *Andromastax* on account of its spinous process pattern on the trunk somites in conjunction with the presence of lateral processes on the cephalic shield, the coxae of P2–P4 and the anterior margin of segment 2 of the female antennule. Additional justification for this placement is found in the sexual dimorphism of the swimming legs and mouthparts. The male maxilla of *A. cephaloceratus* is probably the key appendage even though it is damaged in the only specimen that could be obtained. In contrast to other aegisthid genera, males of *Andromastax* can be unambiguously identified by the presence of the two robust, coarsely spinulose, blunt spines on the maxilla. Such a modified element is present on the maxillary allobasis of *A. cephaloceratus* and the large scar on the proximal endopod segment indicates that the second spine was probably broken off during specimen handling (arrowed in Fig. 39D). Other characters unique to *Andromastax* males are the modified distal outer spine of P2–P4 exp-3 and the sexually dimorphic segmentation of the P1 exopod (2-segmented in ♀, 3-segmented in ♂).

Females of *A. cephaloceratus* can be readily distinguished from those of the type species by the presence of large, backwardly directed spinous processes arising from the dorsal posterior margin of the cephalosome and by the absence of the inner seta on the P5 exopod. Other differences in the body ornamentation of *A. cephaloceratus* include the more pointed anterior portion of the cephalosome, the longer dorsal spinous processes on the somites bearing P2–P4 and the fact that only in the P4-bearing somite the posterolateral corners are produced into a spinous attenuation. The P5-bearing somite and genital double-somite display a dorsal pattern of transverse and longitudinal lamellae in *A. cephaloceratus* whereas in the type-species only a spinular pattern is found. The caudal rami are distinctly shorter in *A. muricatus* (1.15 times length of body somites combined as opposed to 1.4 in *A. cephaloceratus*).

Males of both species are much more similar and can be differentiated only on the basis of relatively subtle characters. The male of the new species clearly shows a reduced surface ornamentation in comparison to that of *A. muricatus*. In contrast to the elaborate pattern in the latter species (Conroy-Dalton & Huys, 1999: fig. 5A) the cephalosome and first pedigerous somite are entirely lacking in cuticular lamellae and the pattern of subsequent pedigerous somites consists solely of primary lamellae. The mandibular palp of *A. cephaloceratus* is 2-segmented instead of unisegmented and appears to have a more complex ornamentation on the gnathobase. Additional differences can be discerned in the relative proportion of individual spines and setae on the antenna, maxillule and maxilla but these are of minor significance.

DISCUSSION

The present discovery of four new species of Aegisthidae appears to reinforce Conroy-Dalton & Huys' (1999) recent supposition that the family is not exclusively planktonic but might well assume a wide distribution in the hyperbenthic zone of the deep sea. The co-existence of three new species *S. yooi*, *J. terazakii* and *A. cephaloceratus* at a single locality (DT2–3) in the Okinawa Trough is remarkable, and suggests that the species diversity of the family is grossly unknown. It would be unwise, however, to claim that Aegisthidae is a faunal element typical for hydrothermal vents even though 5 out of 8 species have now exclusively been reported from these habitats. Their unexpected discovery is clearly related to the aroused interest and enhanced sampling activity in hydrothermal vent areas. The fragmentary knowledge on species diversity and distribution of Aegisthidae is solely the result of sampling bias and reflects the logistic difficulties encountered in sampling this environment. More concerted effort in the study of the hyperbenthic habitat will undoubtedly lead to the discovery of geographically widely separated, but morphologically closely related species such as *A. muricatus* in the Galapagos Rift and *A. cephaloceratus* in the Okinawa Trough. This find is intrinsically interesting as it challenges the presumed cosmopolitan distribution of the two holoplanktonic species *A. mucronatus* and *A. aculeatus*. Due to their large size and straightforward diagnostic characters, the detailed morphology of these species has deserved only relatively little attention. In reality, and in concordance with recent work on other planktonic copepod families (Oncaeidae, Oithonidae, Acartiidae, etc.), it might well be that they represent species complexes which have as yet remained unrecognized.

Huys (1988) commented on the tremendous sexual dimorphism displayed in the genus *Aegisthus* as a result of the atrophy of the male mouthparts. With the discovery of additional taxa it appears that this trend is universally adopted in the Aegisthidae, irrespective of the feeding strategy in the female or the vertical zonation of the species, although the degeneration of the respective limbs can be expressed at various levels. This can range from moderate reduction with retention of the full complement of armature elements (*Nudivorax*) to complete atrophy with total degeneration of endites and gnathobases (*Scabrantenna, Aegisthus*). Linked to the atrophy of the mouthparts is the total breakdown in functionality of the alimentary tract. This is not only discernible in the oral region by the degeneration of the labrum and paragnaths but is also expressed at the posterior end of the digestive tract. The anal somite is sexually dimorphic in shape, often bilaterally constricted, and the anal opening appears to be non-functional.

The present descriptions have also revealed the significance of sexual dimorphism on the swimming legs. A number of characters were found to be shared by all genera and conceivably remained unnoticed thus far in previously described species: (1) the modification of the inner portion of the P2–P4 bases into a lobate extension in the ♂; (2) the presence of an additional seta on P4 enp-2 in the ♂; (3) sexual dimorphism in the length of the inner basal spine of P1. It should be noted here that sexual dimorphism in the latter character can be expressed in two ways. In *Andromastax* and *Scabrantenna* the inner basal spine is longest in the female, whereas in *Nudivorax* the opposite trend is found.

We have refrained from presenting a phylogenetic analysis at the generic level since this would require a revision of the type genus *Aegisthus* which is beyond the scope of this paper. There are several indications that this genus is ill-defined and that its three species (*A. mucronatus, A. aculeatus, A. spinulosus*) need to be re-allocated. This revision, the analysis of the phylogeny within the Aegisthidae and their relationships to the other families of the Cervinioidea will be the subject of a forthcoming paper (Huys *et al.*, in prep.).

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