

NEW GENUS OF AEGISTHIDAE (COPEPODA: HARPACTICOIDA) FROM HYDROTHERMAL VENTS ON THE GALAPAGOS RIFT

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ABSTRACT

Both sexes of *Andromastax muricatus*, new genus, new species (Copepoda: Harpacticoida: Aegisthidae), are described from a hydrothermal vent on the Galapagos Rift in the eastern Pacific. This epibenthic species represents the most primitive aegisthid known to date, displaying several plesiomorphic character states in the cephalosomic appendages and in P5 and P6. The new species shares some characters with the imperfectly described *Aegisthus spinulosus*, which is removed from *Aegisthus* and placed here as a species incertae sedis in the Aegisthidae. The basic setal pattern on the caudal rami in the Aegisthidae is reconsidered and the different degrees of atrophy of the mouthparts in the nonfeeding males are discussed. It is postulated that the family evolved from an epi- or hyperbenthic ancestral stock and that the colonization of the open pelagic environment by *Aegisthus* is secondary.

In a footnote of his monumental monograph of the pelagic copepods of the Gulf of Naples, Giesbrecht (1892) introduced the family name Aegisthidae for the genus *Aegisthus* which he had proposed the previous year. Giesbrecht (1891) had established the genus for two new species, *A. mucronatus* and *A. aculeatus*, and, with the exception of Farran's (1905) description of *A. spinulosus*, these species are still the only known members of the family. Various authors (Scott, 1894; Dahl, 1895; Wolfenden, 1902; Sars, 1916) have described additional species, but all of these have been relegated to junior subjective synonyms of *A. mucronatus* (see Huys, 1988a, for review). It is now widely accepted that part of the taxonomic confusion was caused by the extreme sexual dimorphism expressed by the males as a result of the adoption of a nonfeeding strategy (Huys, 1988a).

Both *A. mucronatus* and *A. aculeatus* are highly specialized but common members of the mesopelagic and upper bathypelagic communities in all oceans. The third species, *A. spinulosus*, is known only from a single female caught in moderately deep water off the west coast of Ireland (Farran, 1905). It differs from its congeners in a number of important features, such as the presence of a segmented mandibular palp, paired dorsal spinous processes on the pedigerous somites, and a primitive setal pattern on the maxillipedal syncoxa. In view of the fragmentary original description, its status as a valid species is regarded as uncertain (Lang, 1948; Boxshall, 1979).

The Aegisthidae has generally been regarded as an extremely specialized taxon within the Cervinioidea (Huys, 1988b, 1993), representing an evolutionary "dead-end" restricted to the open pelagic. Recent investigations (Huys and Conroy-Dalton, 1997; Conroy-Dalton and Huys, in press) of the harpacticoid fauna of hydrothermal vent sites in the eastern Pacific (East Pacific Rise, Galapagos Rift, Juan de Fuca) have already revealed a number of interesting discoveries. Examination of a series of samples collected from vent fields at the Galapagos Rift resulted in the discovery of a new aegisthid which appears to be distinctly more primitive than *A. mucronatus* and *A. aculeatus*, but shows several similarities with *A. spinulosus*. The new species, the first within the family to be reported from an epibenthic habitat, is described herein and assigned to a new genus *Andromastax*.

MATERIALS 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 a Leitz Diaplan differential interference contrast microscope. Females and males were examined with a Philips XL 30 scanning electron microscope. Specimens were prepared by dehydration through graded acetone, critical-point dried, mounted on stubs, and sputter-coated with palladium.

The descriptive terminology is adopted from Huys and Boxshall (1991). Abbreviations used in the text are: ae, aesthetasc; P1-P6, first to sixth thoracopods; exp(enp)-1(2, 3) to denote the proximal (middle, distal) segment of a ramus.

The term acrothek is used to denote the trifold setal complement found apically on the distal antennular segment.

Type material was deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and in The Natural History Museum (NHM).

DESCRIPTION

Andromastax, new genus

Diagnosis.—Aegisthidae. Prosome with complex surface reticulation. Caudal rami slightly longer than rest of body. Paired spinous processes present dorsally and laterally on somites bearing P2–P4. Coxae of P2–P4 with outer spinous process. P1 endopod 2-segmented. Distal outer element of P1 exp–3 (exp–2 in ♀) setiform.

Formula for armature of swimming legs.

	coxa	basis	exopod	endopod
P1	0–0	1–1	♀: I–1; I + 1, 2, 3 ♂: 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, 1 + 2
P4	0–0	1–0	I–1; I–1; III, I + 1, 3	♀: 0–1; 0–1; 1, 2, I + 1 ♂: 0–1; 0–2; 1, 2, I + 1

Sexual dimorphism in general body shape, body ornamentation, rostrum, antennule, antenna, labrum, mandible, maxillule, maxilla, maxilliped, P1 exopod segmentation, P1 inner basal spine, P2–P4 bases, P2–P4 exp–3, P4 endopod, P5, P6, genital segmentation, anal somite, and body size. Males nonfeeding.

Female.—Rostrum small, conical. Cephalosome with spinous process near bases of antennae. Somite bearing P5 with 4 spinous processes; both proximal and distal halves of genital double-somite and second abdominal somite with 2 processes. Anal operculum weakly developed, denticulate. Antennule 7-segmented, with 2 spinous processes on anterior margin of segment 2. Antenna with 2-segmented exopod (formula [1,2]); 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 [4,3,3,3]); allobasis with 2 anterior and 3 posterior elements; endopod with formula [2,2,4]. Maxilliped with 2 serrate spines and 3 setae on protopod and 1 lateral plus 3 apical setae on endopod. P1 with 2-segmented rami; inner basal seta longer than endopod. P5 1-segmented, with 1 (basal) seta and 3 spines along outer margin, 1 inner seta, and 2 spines plus 1 seta apically. P6 with 3 elements.

Male.—Rostrum moderately developed, triangular. Cephalosome with middorsal integument strongly folded. Urosomites without dorsal processes. Anal somite bilaterally constricted; operculum semicircular, smooth. Antennule 9-segmented with geniculation between segments 7 and 8; segment 8 extremely elongate. Antenna with 2-segmented exopod (formula [1,2]); allobasis with elaborate ornamentation and rudimentary abexopodal seta; endopod with 2 lateral and 6 apical elements. Mandible extremely reduced; palp 1-segmented with 2 apical setae. Maxillule reduced, not segmented; coxal endite with 2 elements; outer distal setae of palp reduced. Maxilla with reduced proximal (praecoxal) endites; allobasis and enp–1 with modified coarsely pinnate spine; endopod with formula [2,2,4]. Maxilliped reduced; some elements of protopod and endopod reduced in size. P1 exopod 3-segmented; inner basal spine distinctly shorter than in ♀. Bases of P2–P4 with inner lobate extension. P2–P4 exp–3 distal outer spine curved. 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 setular tufts.

Type Species.—*Andromastax muricatus*, new species.

Etymology.—The generic name is derived from the Greek *anér*, *andropós*, meaning male, and *mastax*, meaning jaws, and alludes to the characteristic structure of the male maxillae.

Gender.—Masculine.

Andromastax muricatus, new species

Material Examined.—Type series collected by deep-sea submersible *Alvin* at the Galapagos Rift; 00°47.89'N, 86°09.21'W (Station 986); depth 2,494 m; 03 December 1979; washings of mussel-bed samples.

Holotype ♀ dissected on 15 slides (reg. no. USNM 243625); paratypes are 27 ♀♀ and 8 ♂♂ (1 damaged) in alcohol (reg. no. USNM 243626). Additional paratypes (1 ♂ dissected on 11 slides; 6 ♂♂ and 25 ♀♀ in alcohol) deposited in the NHM under reg. nos. 1998.281–312.

Description of Female (Figs. 1–3, 6, 8B, 9A–C, 10A–C, 11A, B, 12A, B, 14D, E).—Total body length 3,356 µm (\bar{x} = 3,490 µm; N = 10), measured from anterior margin of cephalic shield to posterior margin of caudal rami. Greatest width measured at posterior margin of cephalic shield 390 µm. Urosome

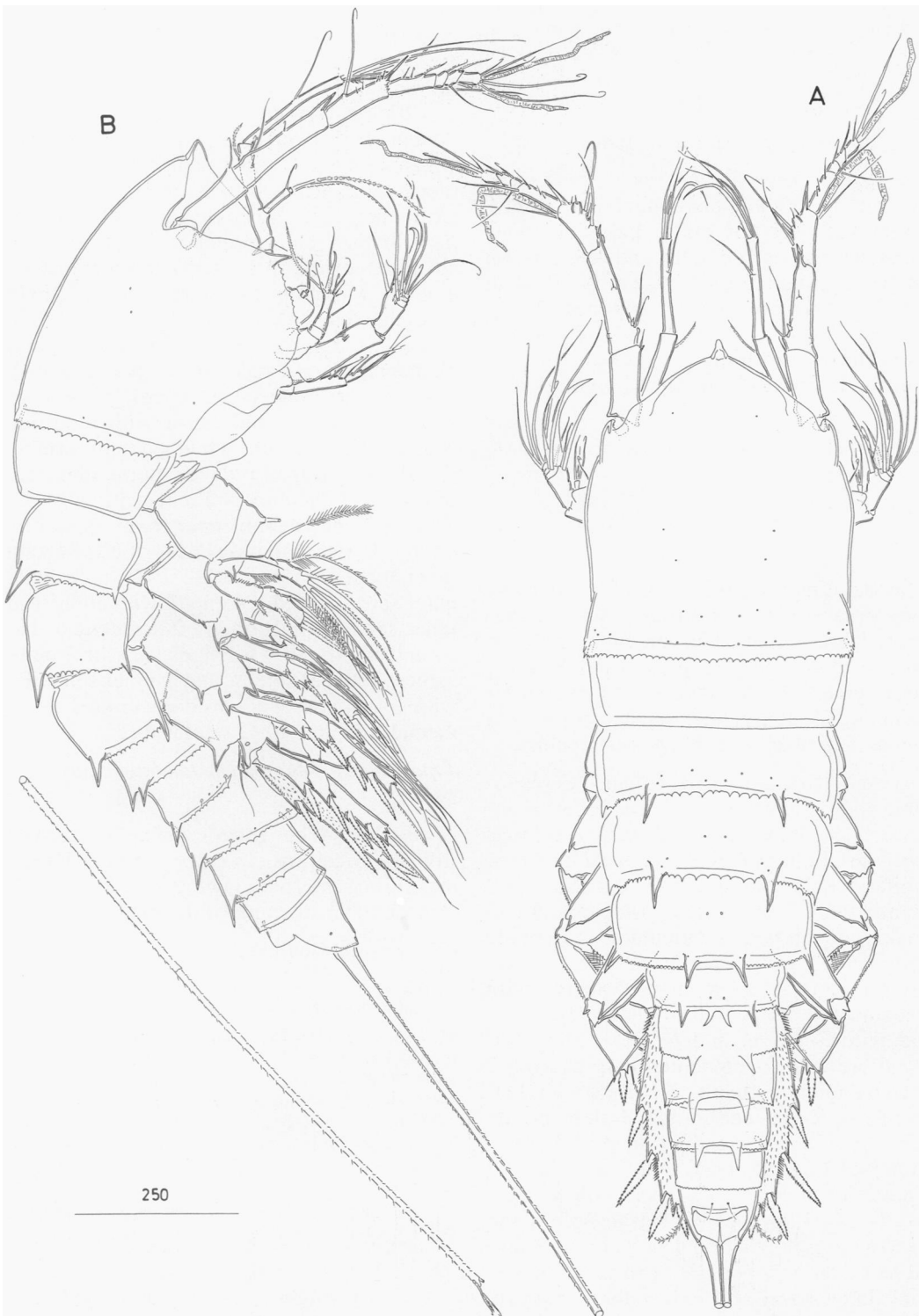


Fig. 1. *Andromastax muricatus*, new genus, new species (?). A, habitus, dorsal (caudal rami omitted); B, habitus, lateral. Surface ornamentation on body somites omitted in A, B.

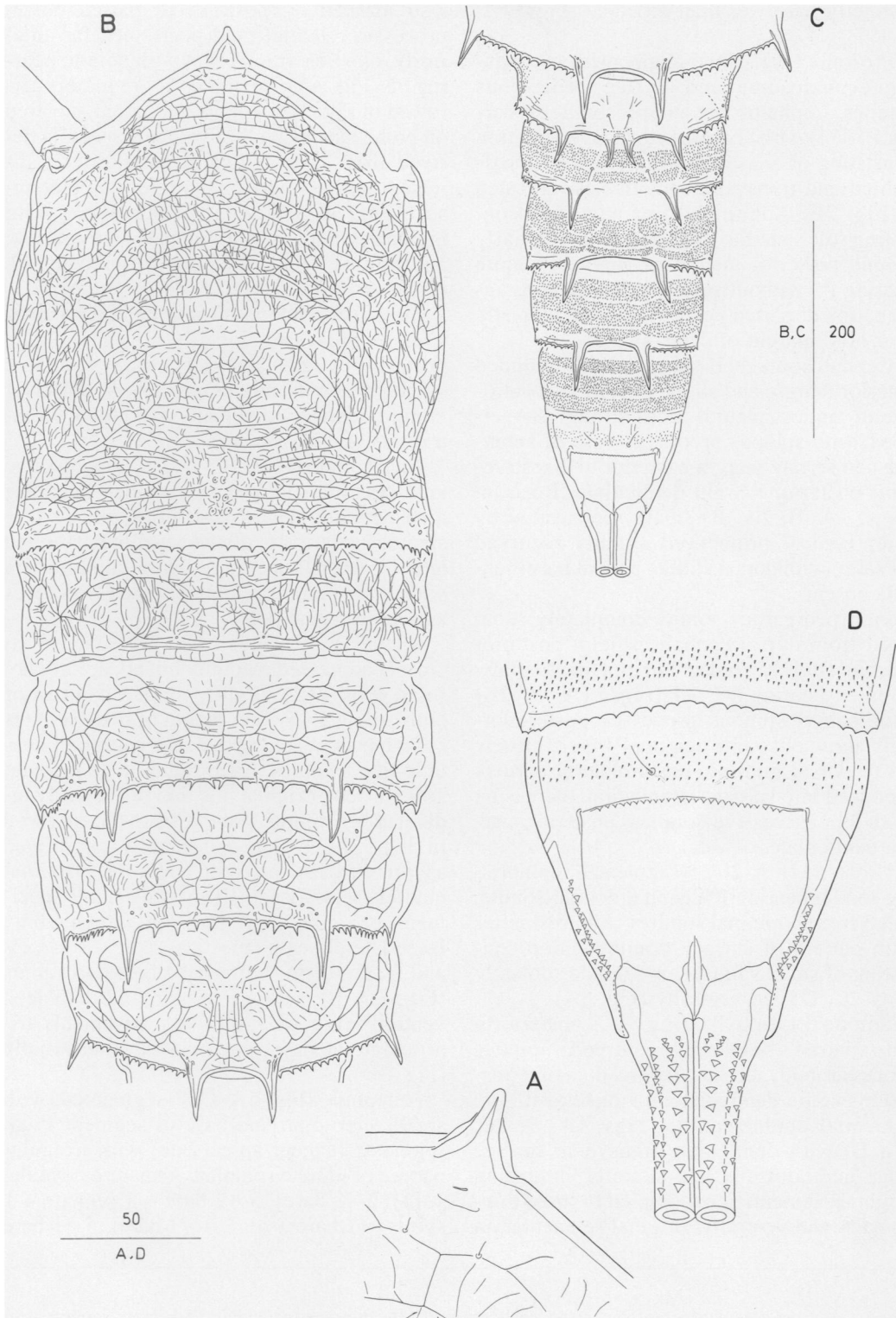


Fig. 2. *Andromastax muricatus*, new genus, new species (?). A, rostral area, dorsal; B, prosome, dorsal, showing detailed surface reticulation; C, urosome, dorsal (caudal rami omitted); D, anal somite and proximal part of caudal rami, dorsal.

distinctly narrower than prosome (Figs. 1A, 2C).

Prosome (Fig. 2B) 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 transverse lamellae as indicated in Fig. 2B. Additional ornamentation consisting of sensilla and pores, particularly around posterior margin of somites; somite bearing P1 without sensilla; conspicuous aggregation of paired pores present middorsally near hind margin of cephalosome.

Cephalosome bell-shaped, with rounded anterior margin and slightly swollen posterolateral angles; pleural areas strongly developed, with spinous process at base of antennae and serrate margin posterior to this structure; posterior margin denticulate. Rostrum (Figs. 1A, B, 2A, B) small, represented by short conical projection; slightly recurved dorsally; with dorsal slitlike pore at base; sensilla absent.

First pedigerous somite completely separated from dorsal cephalic shield; posterior margin slightly folded but not denticulate. Somites bearing P2–P4 (Figs. 1A, B, 2B) with paired spinous processes posterodorsally, those of somite bearing P4 more closely set to dorsal midline; posterolateral corners produced into spinous attenuation, increasing in size in successive somites; posterior margin denticulate.

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

Somite bearing P5 (Fig. 2C) posteriorly with paired, outwardly recurved, spinous processes both subdorsally and dorsally; posterior margin denticulate dorsolaterally.

Genital double-somite (Figs. 1A, B, 2C, 3A, B) 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 somite bearing P5 (Fig. 3A); copulatory pore minute (arrowed in Fig. 3B); gonopores paired, covered on both sides by well-developed opercula derived from sixth legs and by anteriorly directed flap arising from somite wall (see inset of Fig. 3B); P6 very elongate, with 1 long bipinnate and 1 short unipinnate seta apically, and minute seta on subdistal inner margin (Figs. 3B, 9C).

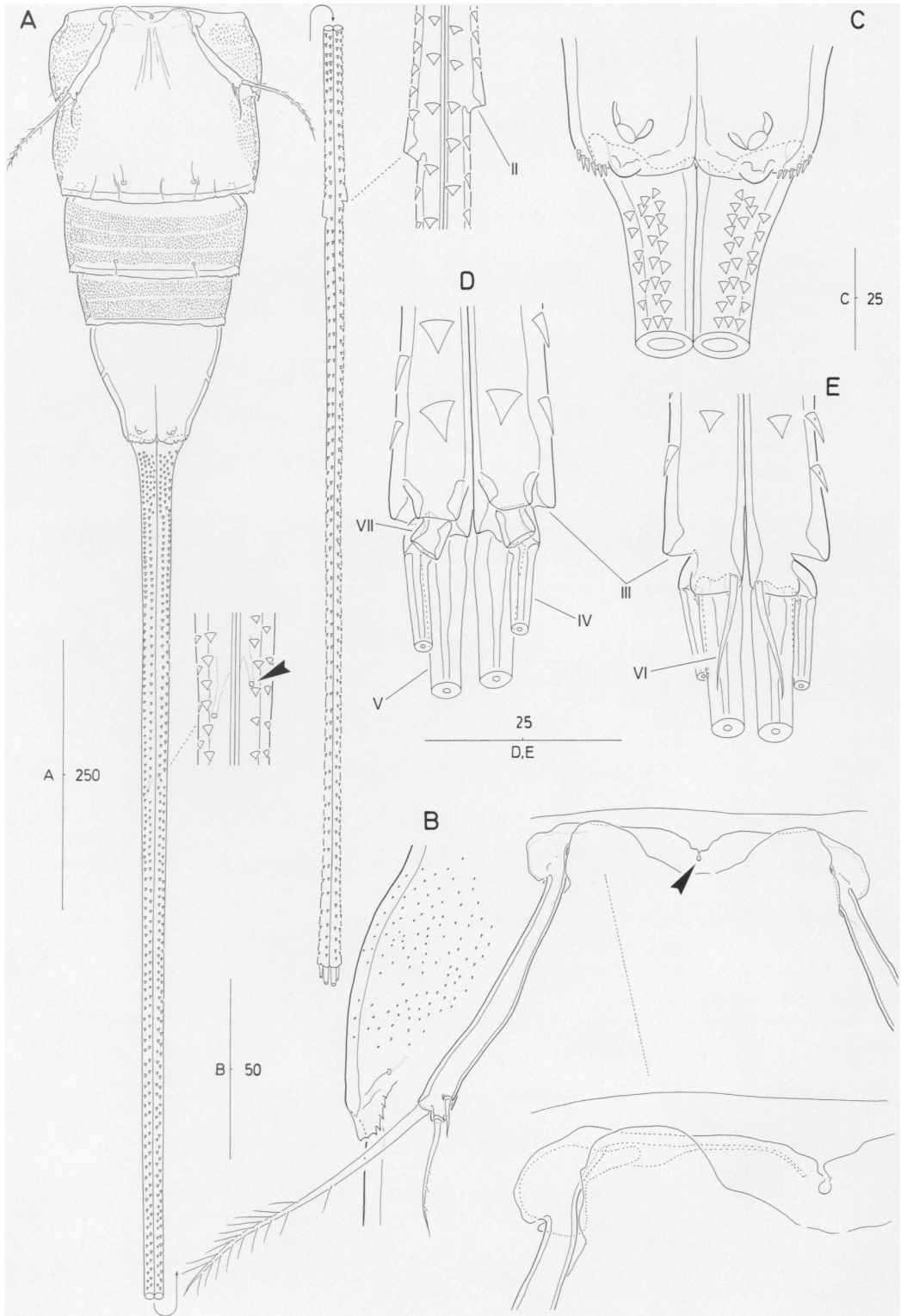
First free abdominal somite with paired spinous processes dorsally and denticulate posterior margin laterodorsally; penultimate somite without spinous processes, posterior margin denticulate dorsally and smooth ventrally (Figs. 2C, D, 3A).

Anal somite (Figs. 2C, D, 3A, C) with large anal opening, flanked by spinules laterally; anal operculum vestigial, bordered by tiny spinules anteriorly; dorsal sensilla positioned anterior to anal opening; ventral hind margin with fine spinules, small rounded processes and large raised pores.

Caudal rami (Figs. 1B, 2D, 3A, C–E) closely adpressed medially but apparently not fused (Fig. 14E); slightly longer than rest of body, about 1.15 times length of body somites combined; covered with dense pattern of denticle-like spinules. Each ramus with 6 setae; seta I absent, original position presumably indicated by minute pore (Fig. 14D; arrowed in Fig. 3A) which is typically positioned asymmetrically on both rami in proximal quarter; setae II and III missing in all specimens examined but position indicated by large lateral scars (Fig. 3A, D, E); setae IV and V large, former partly fused to ramus (Fig. 3D, E); seta VI minute and displaced ventrally (Fig. 3E); seta VII presumably triarticulate at base, positioned subterminally (Fig. 3D).

Antennule (Fig. 6A–C) 7-segmented; with small sclerite around base of segment 1; all segments (except apical one) with irregular pattern of minute spinules. Armature formula: 1–[1], 2–[8 bare], 3–[9 bare + 1 pinnate + 1 spine + (1 bare + ae)], 4–[3 bare], 5–[1 bare

Fig. 3. *Andromastax muricatus*, new genus, new species (♀). A, urosome (excluding P5-bearing somite), ventral [insets showing position of pore marking original position of seta I (arrowed), and lateral scar indicating seta II]; B, genital field (arrow indicating copulatory pore; inset showing detail of closing apparatus); C, distal part of anal somite and proximal part of caudal rami, ventral; D, distal part of caudal rami, dorsal; E, same, ventral.



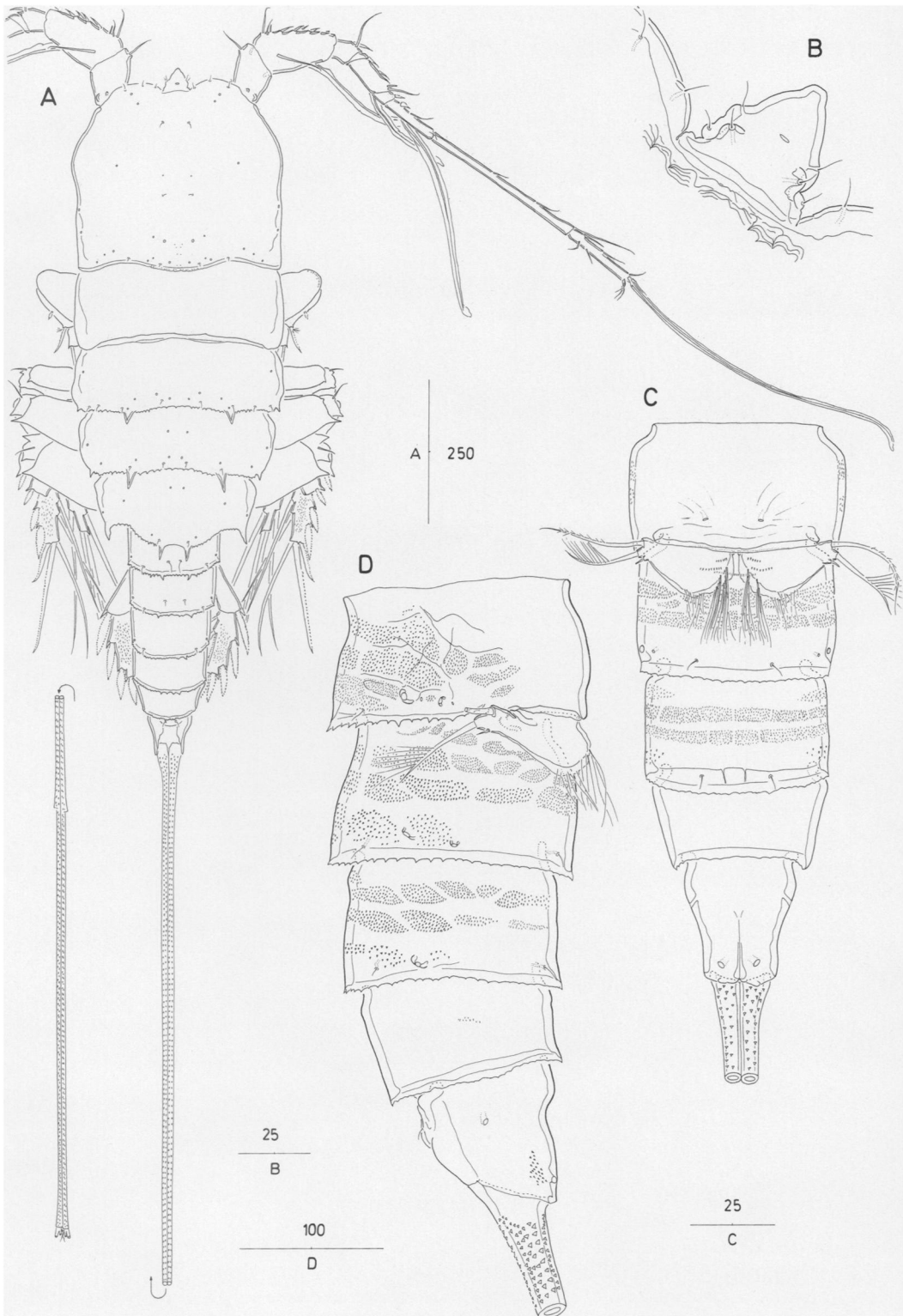


Fig. 4. *Andromastax muricatus*, new genus, new species (σ). A, habitus, dorsal (surface ornamentation on body somites omitted); B, rostral area, dorsal; C, urosome (excluding P5-bearing somite), ventral (caudal rami omitted); D, same, lateral.

+ 1 pinnate], 6-[1 bare + 1 pinnate], 7-[6 + acrothek]. Apical acrothek consisting of well-developed aesthetasc (180 μ m) fused basally to slender seta. Both aesthetascs with supporting chitinous rib. Segment 2 longest; anterior margin with short spinous process proximally (see inset, Fig. 6B) and large spinous process distally. Distal margin of segment 3 dentate dorsally (arrowed in Fig. 6B).

Antenna (Figs. 6D, 10A) 3-segmented, comprising coxa, allobasis, and free 1-segmented endopod. Coxa irregular in shape, without ornamentation. Basis and proximal endopod segment completely fused forming elongate allobasis with 1 abexopodal seta distally (derived from endopod). Exopod arising from short pedestal; 2-segmented; proximal segment about 4.5 times as long as wide, with 1 short bipinnate seta; distal segment minute, with 2 very long setae, lateral one multipinnate, apical one bipinnate. Endopod elongate, longer than allobasis; outer margin with 4 rows of long spinules; lateral armature arising in distal half, consisting of 1 minute and 2 long setae; apical armature consisting of 2 short and 4 long pinnate setae (1 clawlike). Both allobasis and endopod with numerous minute surface spinules.

Labrum well developed; with elaborate spinular ornamentation along distal margin as in Fig. 8B; anterior face with 2 pores and 2 transverse rows of setules.

Mandible (Fig. 9A) with large coxa bearing well-developed gnathobase; cutting edge with 7 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 largest, unarmed; distal segment small, with 1 naked seta and 1 longer, pinnate seta.

Paragnaths well-developed hirsute lobes.

Maxillule (Fig. 9B) with praecoxa having transverse fold and few spinules around outer margin; 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 plumose seta, 1 slender seta, and 1 curved bipinnate spine. Basis without discrete rami; apical margin not bilobate; elements grouped in inner cluster consisting of curved bipinnate spine and 2 bipinnate setae, and outer cluster consisting of 4 bare setae and 1 long bare claw.

Maxilla (Fig. 10B) comprising syncoxa, al-

lobasis, 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 2 plumose and 2 unipinnate 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 pinnate 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 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. 10C) 2-segmented, comprising undivided protopod and 1-segmented endopod. Protopod very long, covered with dense pattern of small spinules; outer margin with long setules (arranged in two groups reflecting fused syncoxa and basis); with 5 elements representing 4 vestigial endites; endite 1 represented by bipinnate spine, endite 2 with 1 large biserrate spine and 1 bipinnate seta, endite 3 with 1 large biserrate spine, endite 4 with 1 slender pinnate 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. 11A, B, 12A, B) with 2-segmented (P1; derived by fusion of middle and distal segments) or 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 and P4) spinous process arising from distal outer margin. 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 P1-P4 enp-3 with row of coarse spinules. Outer margins of endopodal segments with long setules. Spine

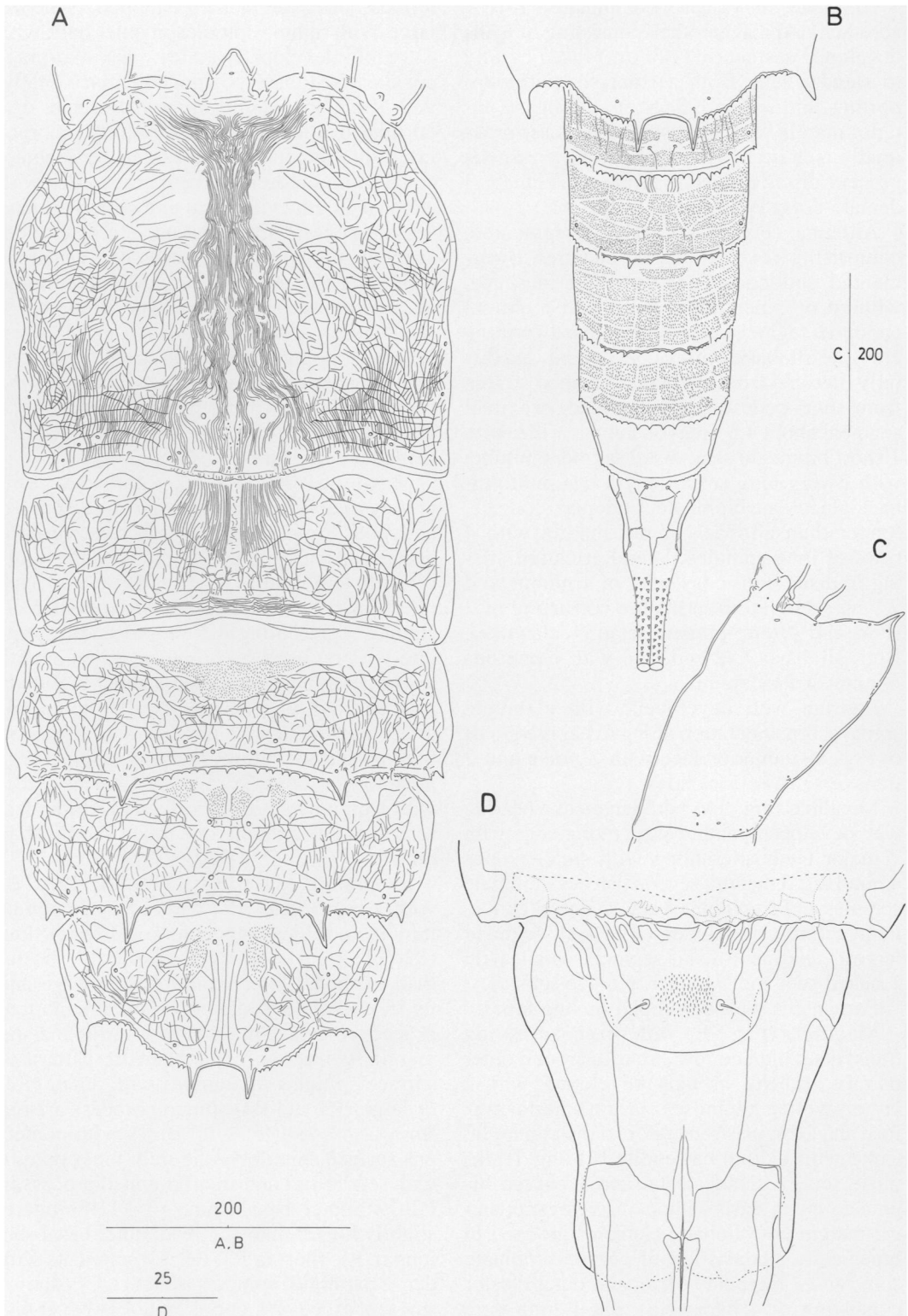


Fig. 5. *Andromastax muricatus*, new genus, new species (δ). A, prosome, dorsal, showing detailed surface reticulation; B, urosome, dorsal (caudal rami omitted); C, cephalosome, lateral; D, anal somite and proximal part of caudal rami, dorsal.

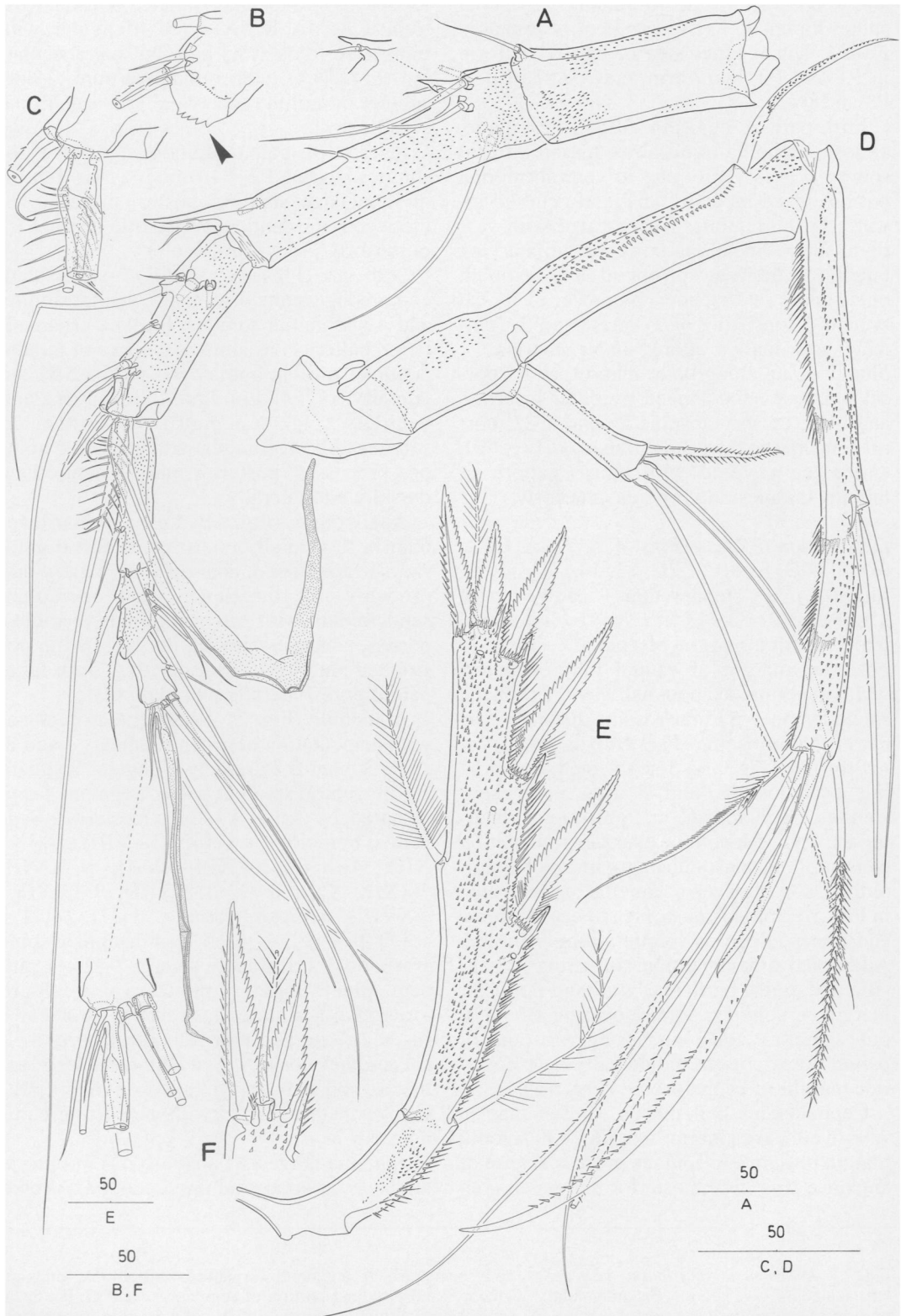


Fig. 6. *Andromastax muricatus*, new genus, new species (♀). A, antennule, ventral (insets showing dorsal view of proximal process on segment 2 and enlargement of apex of segment 7); B, distal portion of third antennular segment, dorsal (dentate distal margin arrowed); C, same, ventral; D, antenna; E, right P5, anterior; F, distal portion of left P5, posterior.

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 and P2, spiniform and rod-shaped in P3 and P4.

Fifth pair of legs (Fig. 6E, F) very large, almost extending to posterior margin of anal somite (Fig. 1A); joining in ventral midline but not fused medially; distinctly curved inward. 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, 1 plumose seta along inner margin, and 1 dorsal plumose seta flanked by outer biserrate and inner uniserrate spine around apex; dorsal seta arising from small tubercle (Fig. 6F); entire leg covered with dense pattern of minute spinules and 3 pores anteriorly.

Description of Male (Figs. 4, 5, 7, 8A, C, D, 9D–F, 10D, E, 11C, 12C, 13, 14A–C, 15).—Slightly more slender than ♀. Body length 3,180 μm (\bar{x} = 3,243 μm ; N = 6), measured from anterior margin of cephalic shield to posterior margin of caudal rami. Greatest width measured at about halfway the cephalic shield length 375 μm . Urosome distinctly narrower than prosome (Fig. 4A).

Prosome (Fig. 5A) 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 transverse lamellae as indicated in Fig. 5A; middorsal surface of cephalosome and first pedigerous somite strongly folded. Additional ornamentation consisting of sensilla and pores, particularly around posterior margin of somites; somite bearing P1 without sensilla; conspicuous aggregation of paired pores present middorsally near posterior margin of cephalosome (Fig. 5A).

Cephalosome bell-shaped, shorter than in ♀; with concave anterior margin; with smooth margin posterior to spinous process at base of antennae (Fig. 5C); posterior margin smooth

except for middorsal crenulated portion. Rostrum (Figs. 4A, B, 5A) small, triangular; with transverse folds at its base but not articulating (Fig. 14A); with middorsal pore, 2 dorsal (set on minute tubercles) and 4 marginal sensilla.

Pattern of paired spinous processes of somites bearing P2–P4 similar as in ♀ but individual size smaller; posterior margin of these somites denticulate; somite bearing P4 posteriorly produced dorsally.

Urosome (Figs. 4C, D, 5B) 6-segmented, comprising somite bearing P5, genital somite, and 4 abdominal somites. Surface ornamentation pattern consisting of patches of minute denticles present both dorsally (Fig. 5B) and laterally (Fig. 4D) on first 4 urosomites, and ventrally (Fig. 4C) on first 2 postgenital somites. All urosomites without paired spinous processes; posterior margin denticulate dorsally and laterally.

Anal somite (Fig. 5B, D) much narrower than in ♀, medially constricted; dorsal anterior surface folded; anal opening narrow and probably not functional; anal operculum semicircular, with patch of minute denticles, posterior margin smooth; dorsal sensilla positioned anterior to anal opening; with large paired pores laterally and ventrally.

Antennule (Fig. 7) 9-segmented; haplocer with geniculation between segments 7 and 8, and segment 8 extremely elongate. Segment 1 with ventral spinular patch. Segment 4 represented by small U-shaped sclerite. 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–[4 + 1 pinnate spine + ae], 6–[1 + 1 pinnate spine], 7–[2 + 1 pinnate spine], 8–[3 + 1 pinnate spine], 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 (arrowed in Fig. 7B₃, C). Aesthetascs large, with supporting chitinous rib.

Antenna (Fig. 8A) sexually dimorphic in allobasis, exopod, and free endopod. Alloba-

Fig. 7. *Andromastax muricatus*, new genus, new species (δ). A, antennule (armature omitted); B₁, antennular segments 1–7, ventral; B₂, antennular segment 8 and proximal portion of segment 9, ventral; B₃, distal portion of antennular segment 9, ventral; C, same, dorsal. Relative position of B₁₋₃ indicated in A by markers ● and ★. Arrow in B₃ and C indicating basally fused seta of acrothek on segment 9.

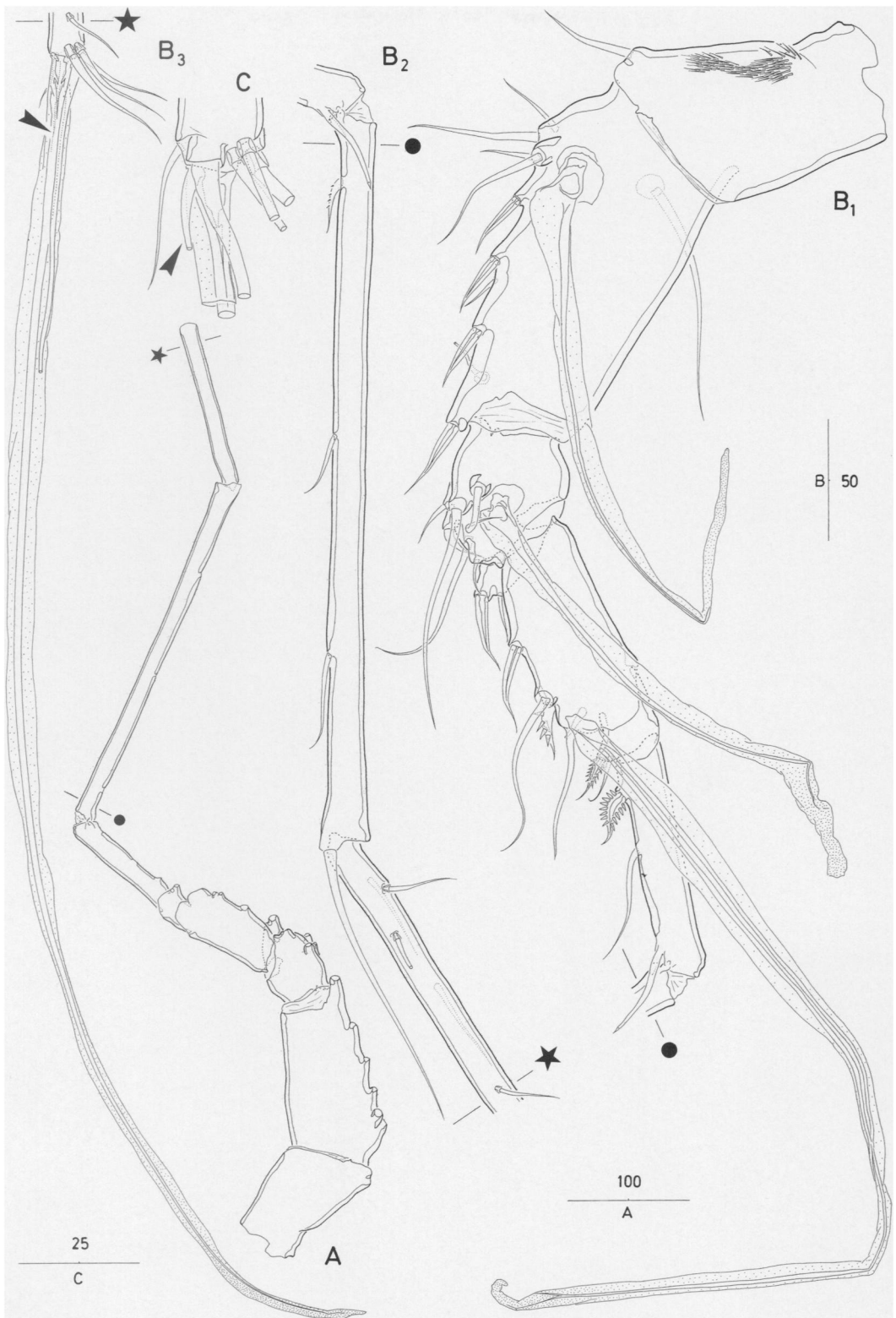




Fig. 8. *Andromastax muricatus*, new genus, new species. A, antenna (♂); B, labrum (♀), anterior; C, P5 (♂), anterior; D, genital and first abdominal somites (♂), ventral.

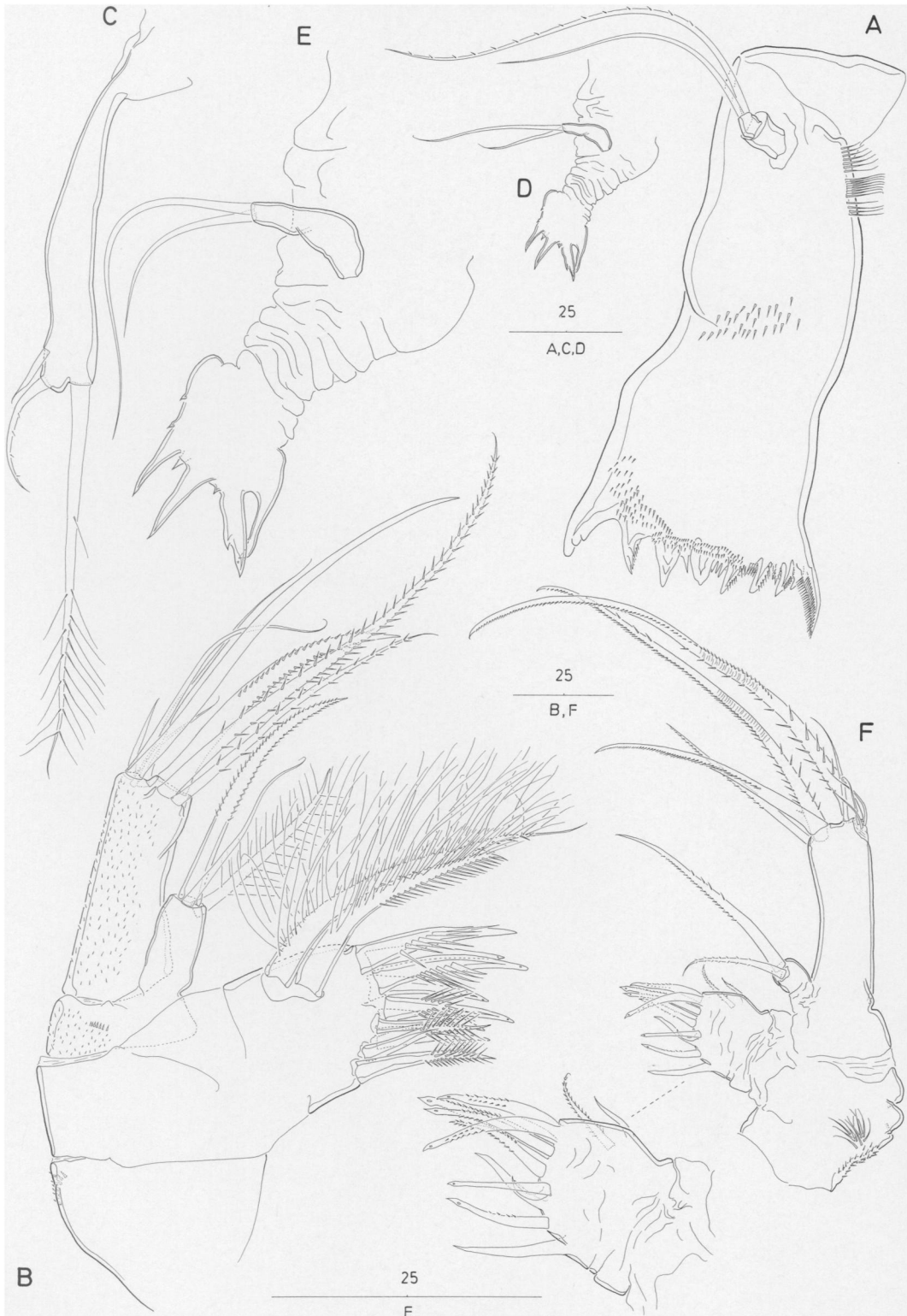


Fig. 9. *Andromastax muricatus*, new genus, new species. A, mandible (♀); B, maxillule (♀), anterior; C, armature of P6 (♀); D, mandible (♂), drawn at same scale as A; E, same (♂); F, maxillule (♂), drawn at same scale as B, anterior (inset showing detail of arthrite).

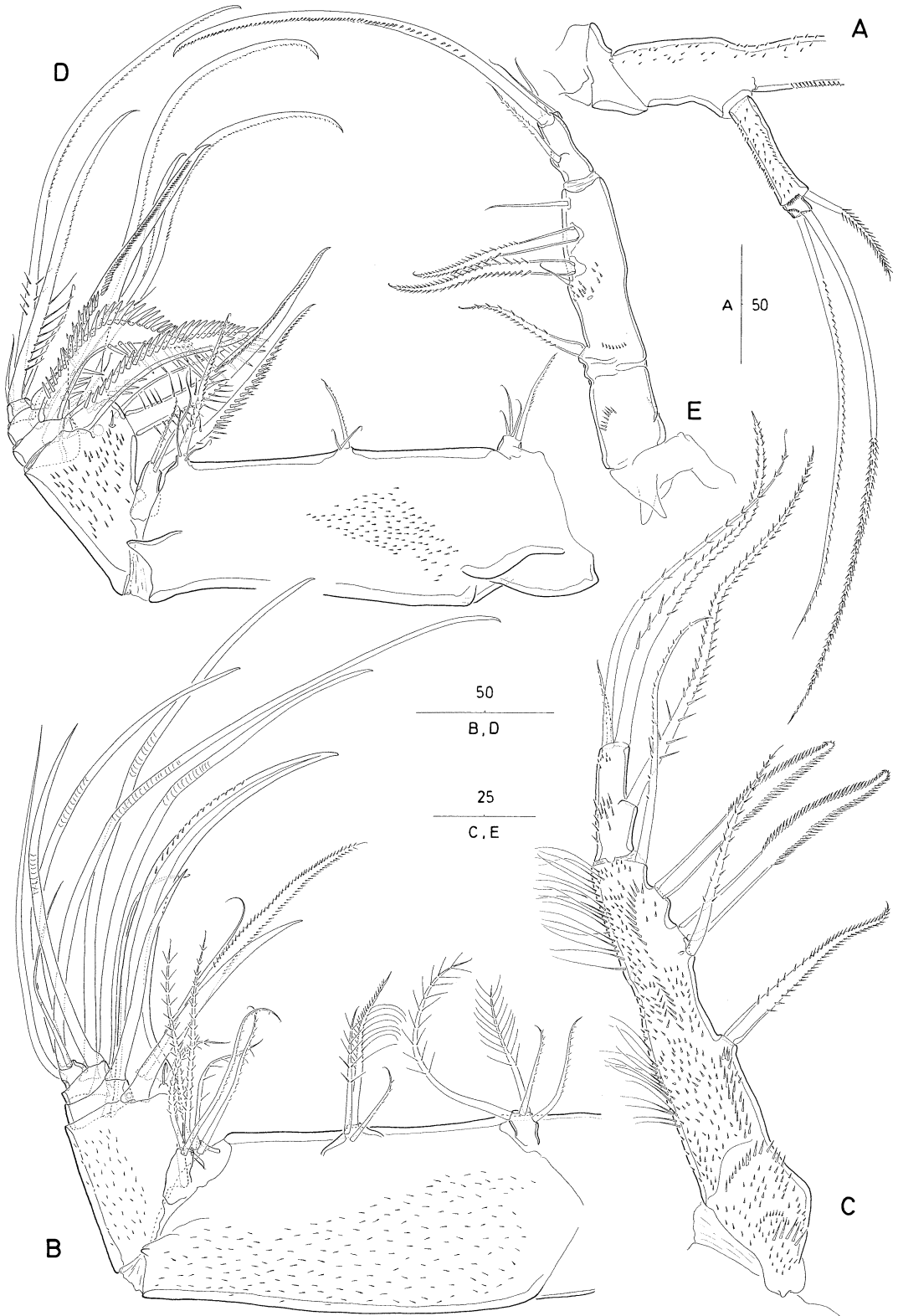


Fig. 10. *Andromastax muricatus*, new genus, new species. A, antennary exopod (♀); B, maxilla (♀); C, maxilliped (♀); D, maxilla (♂); E, maxilliped (♂).

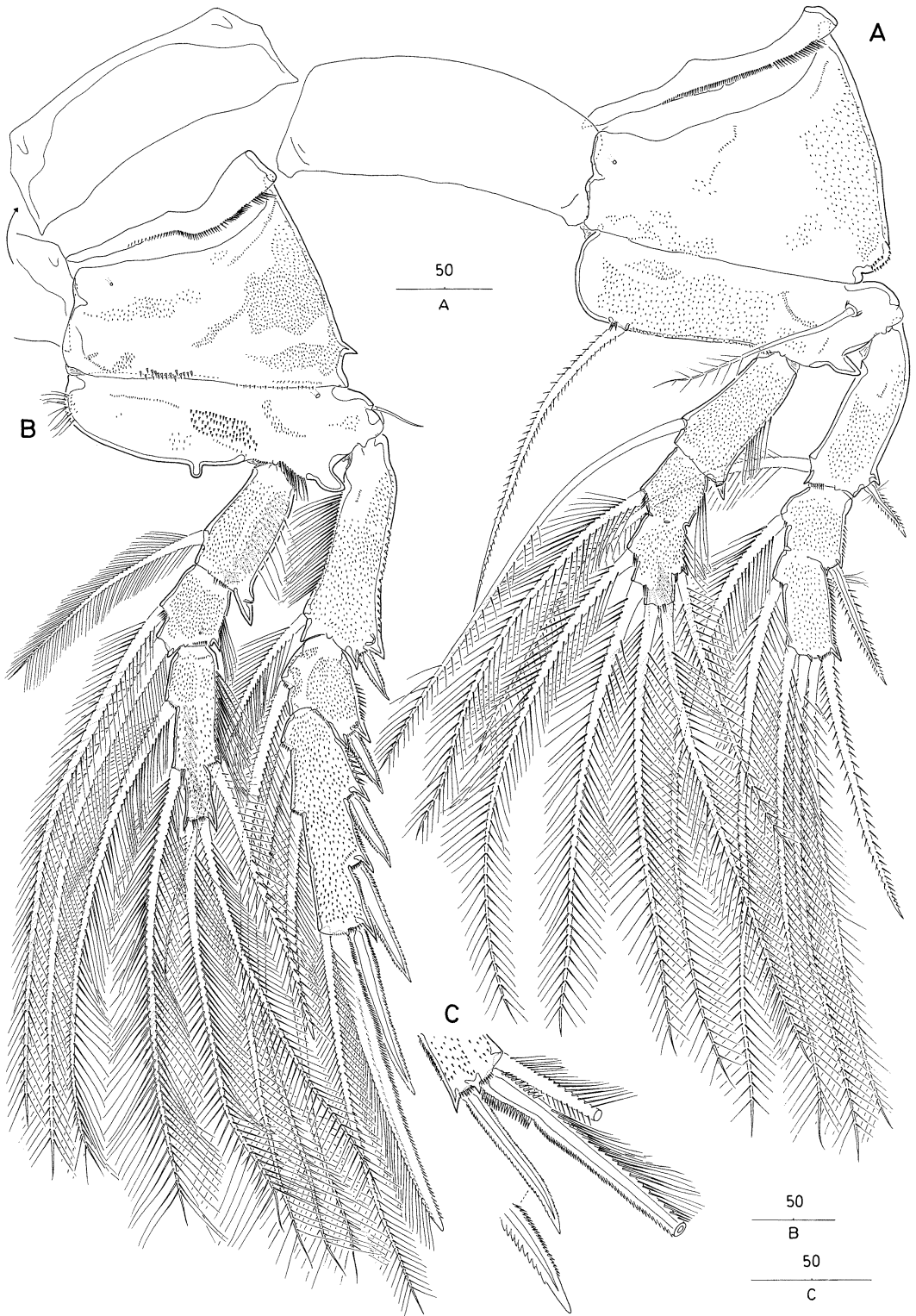


Fig. 11. *Andromastax muricatus*, new genus, new species. A, P1 (♀), anterior; B, P2 (♀), anterior; C, distal part of P2 exp-3 (♂), anterior.

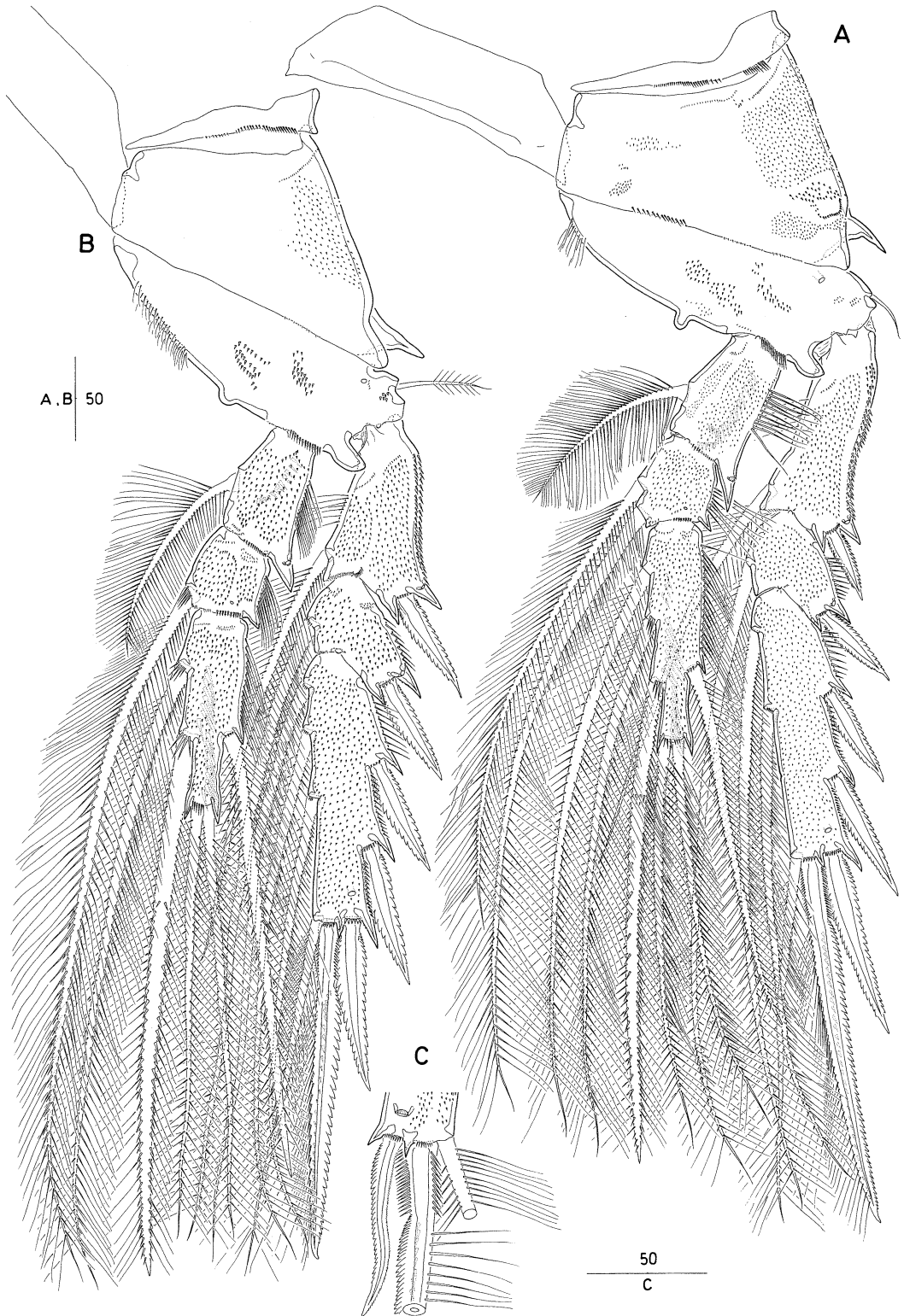


Fig. 12. *Andromastax muricatus*, new genus, new species. A, P3 (♀), anterior; B, P4 (♀), anterior; C, distal part of P3 exp-3 (♂), anterior.

sis with more elaborate ornamentation in basal portion (around base of exopod); abexopodal spinules of ♀ absent in ♂; with additional spinules along exopodal margin; abexopodal seta rudimentary. Exopod 2-segmented; slightly shorter than in ♀ and with more spinules proximally; ornamentation of setae largely as in ♀, but apical setae distinctly shorter. Free endopod with reduced surface ornamentation; lateral armature consisting of 2 minute setae; distal armature consisting of 6 elements: 2 long, composite blunt setae, 2 short naked and 2 pinnate setae.

Oral area and mouthparts greatly reduced (Fig. 15).

Labrum (Figs. 14B, 15) highly folded and strongly reduced in size; ornamentation lacking; paired pores present.

Mandible (Fig. 9D, E) strongly reduced in size and gnathobasal ornamentation. Gnathobase separated from rest of praecoxa by annulated constriction; with 4 pointed teeth around apical margin. Palp 1-segmented; with 2 naked setae apically.

Maxillule (Figs. 9F, 14C) significantly reduced, without distinct segment boundaries. Praecoxa separated from coxa by transverse membranous area along outer margin; arthrite greatly 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 reduced.

Maxilla (Fig. 10D) 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 or reduced except for single strongly developed pinnate spine on distal coxal endite. Allobasis drawn out into strong, slightly curved, pinnate claw; accessory armature as in ♀ except for anterior naked spine being replaced by robust, coarsely spinulose, blunt spine. Similar spine present on proximal endopod segment. Endopod with armature formula 1-[1 modified spine + 1 long unipinnate], 2-[2 long unipinnate], 3-[2 long pinnate + 2 short bare].

Maxilliped (Fig. 10E) 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 much shorter and naked. Endopodal armature consisting of 1 short pinnate seta laterally and 1 claw plus 2 short naked setae apically.

P1 (Fig. 13A) exopod 3-segmented; inner basal spine much shorter than in ♀ and minutely pinnate.

Outer spinous process of P2 coxa markedly smaller than in ♀ (arrowed in Fig. 13B). Bases of P2-P4 (Fig. 13B-D) with inner lobate expansion; setular tuft along inner margin replaced by spinules or denticles. Outer distal spine of exp-3 of P2-P4 (Figs. 11C, 12C, 13D) distinctly curved; outer margin serrate, inner margin minutely pinnate. Enp-2 of P4 (Fig. 13D) with 2 inner setae.

Fifth pair of legs (Fig. 8C) joining mid-ventrally but not fused medially. P5 elongate, directed medially and posteriorly; 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 not 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. 8C. Anterior integumental pores present on all segments (1 on basis and exp-1; 2 on exp-2).

Sixth pair of legs (Figs. 4C, D, 8D) not fused medially, symmetrical. Each P6 with 2 pinnate setae and inner vestigial element; anterior surface with short spinules, inner distal margin with 2 clusters of long setules.

Etymology.—The species name is derived from the Latin *muricatus*, meaning having sharp points, and refers to the paired dorsal spinous processes present on most thoracic and abdominal somites.

DISCUSSION

The new species can unequivocally be allocated to the family Aegisthidae within the superfamily Cervinioidea (as defined by Huys (1988a, 1993)) on the basis of a combination of primitive (P1-bearing somite not fused to cephalosome; P1 exp-1 with inner seta) and advanced characters (antennule ♀ 7-segmented with aesthetasc on segment 3; antenna with

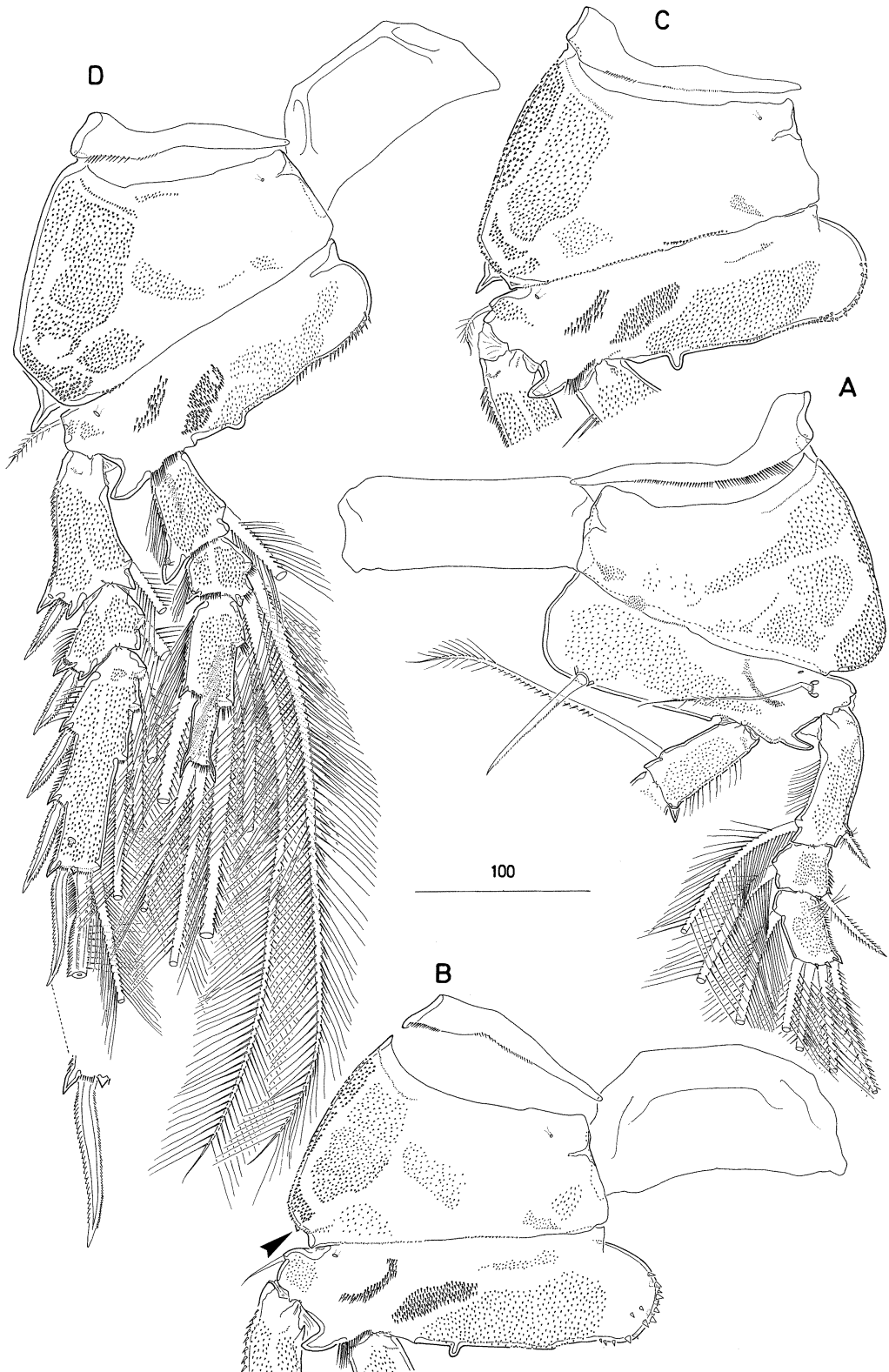


Fig. 13. *Andromastax muricatus*, new genus, new species (σ). A, protopod and exopod P1, anterior; B, protopod P2, anterior (minute spinous process arrowed); C, protopod P3, anterior; D, P4, anterior (inset showing outer distal spine of exp-3).

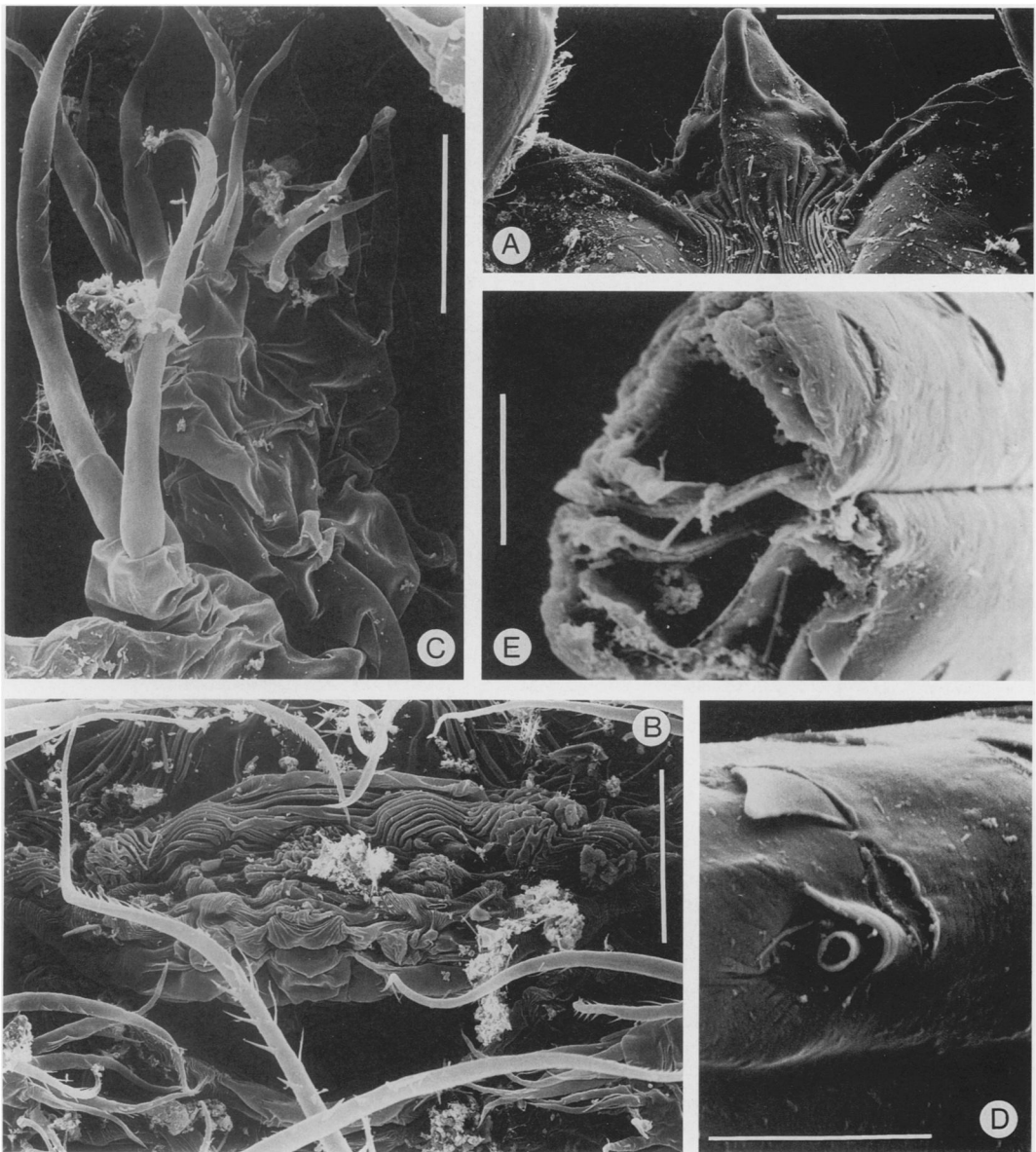


Fig. 14. Scanning electron micrographs of *Andromastax muricatus*, new genus, new species. A, rostral area (♂), ventral; B, labrum (♂); C, maxillule (♂), arthrite and coxal endite; D, caudal ramus (♀) showing tube pore replacing seta I; E, caudal rami (♀), cross section. Scale bars = 5 μ m (D, E), 10 μ m (C), 20 μ m (B), 50 μ m (A).

allobasis and 2-segmented exopod; reduced mandibular palp; maxillary endopod completely incorporated into basis and coxal epipodite absent; uniramous P5 in both sexes; P6 ♀ produced into elongate and narrow extension; extreme elongation of caudal rami). However, the inclusion of the new species in *Aegisthus*, the only genus currently recognized in the Aegisthidae, proved impossible without grossly extending its generic bound-

aries. Consequently, *Andromastax muricatus* is regarded here as the type of a new genus on account of the following apomorphies: (a) pattern of conspicuous dorsal spinous processes on trunk somites; (b) cephalosome with lateral spinous process near bases of antennae; (c) lateral process on coxae P2–P4; (d) anterior margin of female antennular segment 2 with lateral process; (e) ♂ maxillary allobasis and enp-1 with modified coarsely

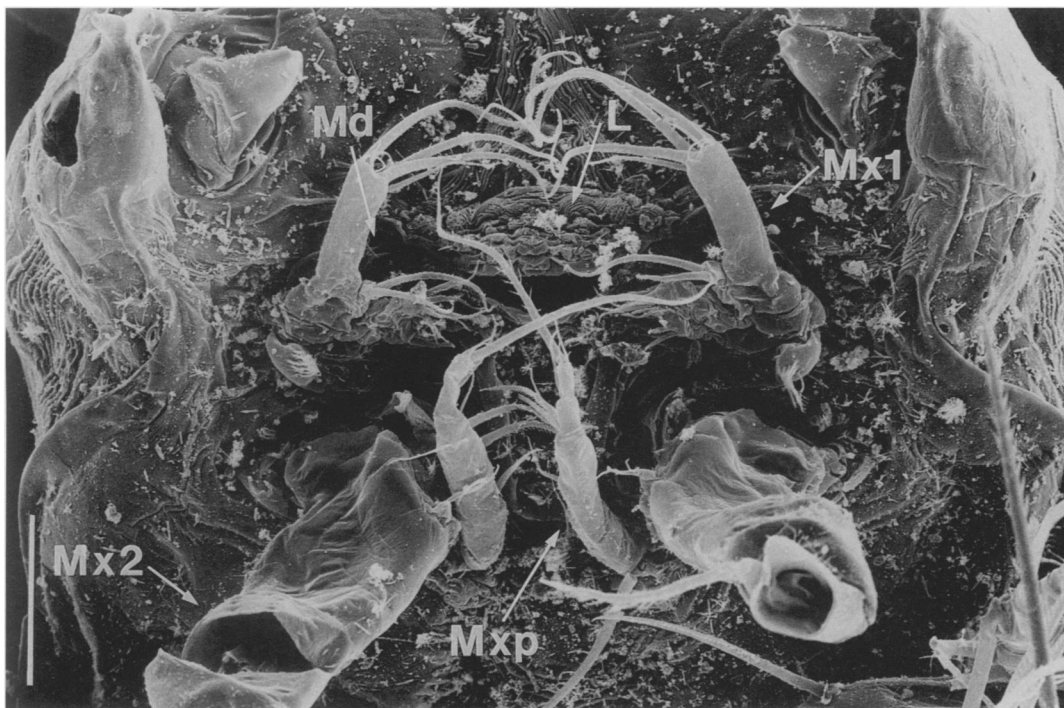


Fig. 15. Scanning electron micrograph of *Andromastax muricatus*, new genus, new species (δ). Cephalosome, ventral, showing atrophied mouthparts. Scale bar = 50 μm .

pinnate spines; (f) sexual dimorphism exhibited in distal outer spine of P2–P4 exp–3, and in segmentation of P1 exopod (2-segmented in ♀ , 3-segmented in ♂). Further differentiating characters are: (g) relatively shorter caudal rami in comparison to other aegisthid species (only about 1.15 times length of all body somites combined), and (h) sexual dimorphism of P1 inner basal spine, P2–P4 bases, P4 enp–2, and anal somite. It is noted here that detailed information on sexual dimorphism of swimming legs is as yet unavailable for *Aegisthus* and future reexamination of both *A. mucronatus* and *A. aculeatus* may reveal that at least some of the sexually dimorphic characters listed under (h) are in reality synapomorphies for the Aegisthidae as a whole.

There is compelling morphological evidence from both sexes that the epibenthic *Andromastax* is more primitive than its holoplanktonic relatives currently placed in *Aegisthus*. Plesiomorphic character states displayed by the female are: (a) mandibular palp 2-segmented and bisetose; (b) maxillary basis with 8 elements; (c) antennary exopod with 3 elements, formula [1,2]; (d) endopod

of maxilliped with 4 setae; (e) P5 exopod with inner seta; (f) P6 with 3 setae. The primitive position of *A. muricatus* is even more obvious from the male. As in other Aegisthidae, the male postantennular cephalic appendages are sexually dimorphic and show similar reductions in size and segmental expression. However they retained the full complement of armature elements as found in the female. The similarity with the female setation pattern is most striking in the endites (maxilla and maxilliped) and gnathobases (mandible and maxillule [arthrite]). The retention of the complete armature, and to a certain degree their functionality, in presumably nonfeeding males, is surprising, since these limb parts are normally involved with food manipulation in the female. The segmentation of the male mandibular palp is no longer visible, but the vestigial palp is clearly bisetose. In contrast to males of *Aegisthus*, the P6 of *A. muricatus* bears three elements instead of two.

Sexual dimorphism is widely expressed in a remarkable variety within the order Harpacticoida. Extreme sexual dimorphism, including the atrophy of mouthparts in male harpacticoids, appears to be a common phe-

nomenon in the deep sea. This has led historically to females and their respective males being frequently classified and described as separate species. This situation is well manifested in the Aegisthidae which, with three currently valid species, *Aegisthus mucronatus*, *A. aculeatus*, and *A. spinulosus*, has had a complex taxonomic history (Lang, 1948; Huys, 1988a). In *A. mucronatus* and *A. aculeatus*, the male mouthparts are greatly reduced, and the appendages are often highly membranous, showing the loss of distinct segment boundaries and reductions in segmentation and numbers of endites and armature elements. This was clearly demonstrated by Huys (1988a), who described the male cephalic appendages of *A. mucronatus* in detail for the first time. This led to the identification of the male mandible, which due to its extreme reduction and membranous nature, had frequently been overlooked or omitted from descriptions of both *A. aculeatus* and *A. mucronatus* by previous authors (Owre and Foyo, 1967; Boxshall, 1979). Boxshall (1979) stated that sexual dimorphism in male mouthparts was less pronounced in *A. aculeatus* than in *A. mucronatus*, particularly in the maxillae and maxillipeds, which more closely resemble the female condition (although unfortunately he did not provide figures for all appendages). Unpublished observations of male *A. aculeatus* revealed many differences with the type species *A. mucronatus*, indicating that the former is distinctly more primitive and possibly deserves separate generic rank (Huys *et al.*, in preparation). By comparison, male mouthparts are reduced to an even lesser extent in *A. muricatus*, with full complement of endites and setal elements found as in the female. Undoubtedly, *Andromastax* is more primitive than any other known aegisthid, in both sexes but particularly in the male.

The validity of *Aegisthus spinulosus* has been the subject of controversy. Lang (1948) regarded the similarities between *A. spinulosus* and *A. aculeatus* as remarkable, and therefore suspected that Farran's (1905) description was based on a copepodid stage of the latter. Boxshall (1979) subsequently dismissed Lang's (1948) supposition and considered *A. spinulosus* to be a valid species on the premise that Farran's description was accurate. In Farran's (1905) description of *A. spinulosus*, based on a single female, there

appears to be some anomaly in his illustrations between the lateral and dorsal habitus views. The dorsal habitus figured has one supernumerary prosomite (compared with the lateral view), and in all likelihood Farran (1905) mistakenly drew a somite (probably the P2- or P3-bearing somite) twice, when composing his illustration. These figures also appear to show that the P1-bearing somite is partly fused to the cephalosome. However, the weak notch in the lateroventral margin of the presumptive cephalothorax (his fig. 9) and the faint transverse suture discernible dorsally and laterally suggest that the P1-bearing somite is in fact free. In some aegisthids the posterior margin of the cephalosome is typically hyaline and closely adpressed to the tergite of the first pedigerous somite, making the distinction between somite boundaries difficult to discern.

Despite these anomalies, there are several similarities between *A. spinulosus* and *A. muricatus*: (a) body with spinous processes in similar position, at least for the somites bearing P2–P5; (b) 2-segmented mandibular palp bearing 2 setae; (c) maxillary armature (although Farran probably overlooked one basal seta); (d) more primitive maxillule, maxilla, and maxilliped in comparison to *A. mucronatus* and *A. aculeatus*; (e) somites bearing P2–P4 with denticulate posterior margin; (f) proportional length of caudal rami. It should be remarked here that the caudal ramus was referred to by Farran (and most earlier workers) as the "caudal seta" which according to his measurements is 1.1 times as long as the rest of the body (1.92 mm versus 1.74 mm).

In the absence of the male and the original type material, however, it is difficult to infer the relationship of *A. spinulosus* to *Andromastax*. There are a number of differences in the females which are either genuine, or a result of deficiencies in the original description: (a) lack of well-defined spinous processes on urosome; (b) lack of body reticulation; (c) proximal endite of maxilla with 5 setae; (d) most primitive setal pattern on maxillipedal protopod, formula [1,2,2,2]; (e) P6 with 2 setae. On the assumption that the additional setal elements on the maxilla and maxilliped [(c) and (d)] are real, we would regard this species as the most primitive aegisthid known. In view of the uncertainty surrounding these counts, we exclude *A. spi-*

nulosus Farran, 1905, from *Aegisthus* and consider it as a species incertae sedis in the Aegisthidae pending a forthcoming phylogenetic analysis of the family (Huys *et al.*, in preparation).

The synapomorphic character states (10–15) defined by Huys (1993) for the Aegisthidae within the Cervinioidea are supported by the discovery of *Andromastax*, subject to a few minor alterations. In a previous paper (1988a), Huys considered Farran's (1905) description of the mandible doubtful as to "... whether the bisetose process really represents the palp or is just simply part of the adjacent maxilla." From the present description of the mandible of *Andromastax*, there seems no justified reason to believe that Farran's description was erroneous for this appendage. The synapomorphic condition for the mandible of the Aegisthidae is with a vestigial, bisetose palp (as amended in Huys (1993) for character 13 from Huys (1988b) where he considers it absent in the family). The complete loss of the palp becomes a synapomorphy for the truly bathypelagic *A. mucronatus* and *A. aculeatus*. The interpretation of the caudal rami also needs reconsideration. The synapomorphy used by Huys (1993) as character 15 is that the caudal rami are at least twice as long as the total somatic body length. Since in *Andromastax* and *A. spinulosus* the caudal ramus is only slightly longer than the length of all body somites combined, the synapomorphy for the family should be reworded as "caudal rami extremely elongate."

The basic setation pattern of the caudal rami in the Aegisthidae is not well understood. Huys' (1988a) claim that there are only three setae on the caudal ramus of *A. mucronatus* is almost certainly incorrect and based on observation of damaged specimens. The discovery of *Andromastax* has revealed that the ancestral aegisthid probably exhibited the typical harpacticoid condition of 7 setae. In *A. muricatus*, seta I is absent, but its original position is indicated by a minute pore (Fig. 14D). The presence of four setae can be positively identified in the majority of specimens, and, by virtue of their position and size, they are regarded as the homologues of setae IV–VII found in other harpacticoids. Setae II and III were absent in all specimens that we examined, but their presence in complete individuals is supported by large scars indicating their respective positions along the

outer margin of the ramus. The three setae identified by Huys (1988a) correspond to setae II, III (or IV?), and VII. It is conceivable that at least the principal seta V is missing in Huys' (1988a) fig. 5 and that its position coincides with the large apical scar obscured by seta VII. The possible reduction and loss of setae in *Aegisthus* may be correlated with the exploration of the pelagic environment. However, only detailed reexamination of a large number of specimens of both *A. mucronatus* and *A. aculeatus* can either confirm or refute this hypothesis.

It is unlikely that the distribution of *A. muricatus* is dependent on hydrothermal vent conditions. In analogy with the primitive poecilostomatoid family Erebonasteridae, which was first described from hydrothermal vents (Humes, 1987), but subsequently discovered in other deep-sea habitats (e.g., Huys and Boxshall, 1990; Huys, 1991), we postulate that the Aegisthidae are widespread in the epibenthic and hyperbenthic layers of the deep sea and that their current underestimated diversity merely reflects the logistic problems involved in sampling these habitats. The habitat utilization by *A. muricatus* may be regarded as evidence that the family evolved from an epibenthic-hyperbenthic ancestral stock and that the successful colonization of the open pelagic was a secondary event.

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