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NEW SPECIES OF AMPHIPOD CRUSTACEANS IN THE GENERA *TEGANO* AND *MELITA*
(HADZIOIDEA: MELITIDAE) FROM SUBTERRANEAN GROUNDWATERS IN
GUAM, PALAU, AND THE PHILIPPINES

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A B S T R A C T

Three new species of *Tegano* are described, two from caves on Panglao Island, Bohol, Philippines, and one from a cave on Peleliu Island, Palau. *Sriha vagabunda* from Sri Lanka is reassigned to the genus *Tegano* based primarily on the high degree of similarity between *Sriha vagabunda* and species of *Tegano* and the fact that these species exhibit a great deal of variation in the reduction of the mandibular palp. A new species of *Melita* with characters intermediate between those defining the genera *Abludomelita*, *Melita*, and *Paraniphargus* is described from a spring on Guam. The characters of the new species and studies by previous authors suggest that *Abludomelita* may not be as distinct from *Melita* as previously believed. The troglomorphic genus *Paraniphargus* from the Andaman Islands and Java is re-evaluated and synonymized with *Melita*.

The genus *Tegano* was defined by Barnard and Karaman (1982) on the basis of a single species, *Melita seticornis*, in which the third segment of the mandibular palp is reduced. Other melitid-like genera have been described with variable reduction of the mandibular palp, including *Sriha*, *Fiha*, *Psammoniphargus*, and *Phreatomelita* (Stock 1988). A careful study of these genera and the description of three new species of *Tegano*, two of which are from different caves on a single small island in the Philippines, have revealed characters that unite species of *Tegano* and *Sriha*. The description of the new species of *Tegano* also demonstrates a high degree of variation in the reduction of the mandibular palp, both interspecifically and intraspecifically. The merger of the monotypic genus *Sriha* with *Tegano* and the description of three new species bring to five the number of species in the genus *Tegano*.

A new stygobitic species of *Melita* is described from a freshwater spring on Guam. This species has characters that appear to be intermediate between the genera *Abludomelita*, *Melita*, and *Paraniphargus*. Although *Melita* is predominately epigeal, the description of this species brings the number of species in the genus recorded from subterranean waters to approximately seven. The genus *Paraniphargus* from the Andaman Isles and Java is synonymized with *Melita*, and the taxonomic status of *Abludomelita* and *Melita* is discussed.

The taxonomic work in this paper is that of Sawicki and Holsinger; the remainder of the paper is the work of all three authors.

SYSTEMATICS

Tegano Barnard and Karaman

Tegano Barnard and Karaman, 1982: 176.

Sriha Stock, 1988: 89.

Type Species.—*Melita seticornis* Bousfield, 1970.

Diagnosis.—Eyes present or absent, with pigmented ommatidia when present. Antenna 1 longer than antenna 2, usually highly setose. Accessory flagellum variable, 1–2 segments, second segment sometimes vestigial. Mandibular palp reduced or absent; molar seta present on both left and right mandibles. Gnathopod 1 palm with produced lobe at defining angle; posterior margin of merus strongly pubescent. Gnathopod 2 propod much longer and broader than carpus, usually with few rows of 1–4 setae along anterior margin; carpus short, subtriangular. Pereopods 3 and 4 subequal, coxa of pereopod 4 usually not excavate posteriorly. Bases of pereopods 5–7 not usually expanded, without distoposterior lobes. Uropod 1 with single basofacial spine. Uropod 3 *Melita*-like, inner ramus 2 segmented. Telson cleft to base, usually wider than long, narrowing distally and bearing few spines distally.

Remarks.—*Sriha* was a replacement name created by Stock (1988) for the genus *Quadrus*, which was preoccupied. Stock (1988) noted two characters that separate this genus from other melitid genera, which lack or have vestigial mandibular palps: 1) mandibular palp absent or vestigial, and 2) lower lip with well-developed inner lobes. To date there are five melitid genera with either a vestigial palp or lacking it altogether—*Sriha*, *Fiha*, *Psammoniphargus*, *Phreatomelita*, and *Tegano*. The genus *Tegano* is the only one in which the mandibular palp is 3-segmented and not reduced to a 1-segmented bud. The species of *Sriha* and *Tegano* share a number of characters that link these genera: 1) typically with distinct, pigmented ommatidia; 2) usually with highly setose antennae 1 and 2; 3) lower lip with developed inner lobes; 4) palm of propod gnathopod 1 with produced lobe at defining angle; 5) bases of pereopods 5–7

usually not expanded, distoposterior lobes not developed; 6) telson completely cleft, wider than long, narrowing distally with few distal spines. Thus, the degree of reduction should not be used as the only character to define the genus. The similarities of *Sriha* and *Tegano* are striking and necessitate synonymy. Based on the description of three new species of *Tegano*, all of which share most of the characters listed above but vary greatly in the reduction of the mandibular palp (sometimes intraspecifically), it is suggested that the reduction in the mandibular palp is highly variable.

***Tegano clavatus* Sawicki and Holsinger, sp. n.**

Figs. 1–5

Material Examined.—PHILIPPINES. Bohol, Panglao Island: Tauala Cave, ♂ holotype (4.2 mm), T. M. Iliffe and D. Williams, 3 April 1985.

The holotype is deposited in the National Museum of Natural History (Smithsonian Institution) under the catalogue number of the former United States National Museum (USNM 1027094).

Diagnosis.—Small to medium sized species distinguished by a 3-segmented mandibular palp (except *T. seticornis*); a club shaped propod on gnathopod 1; small pocket proximal to the defining angle on the palm of gnathopod 2; small serrated extension on the first segment of the inner ramus of pleopod 1. Male 4.2 mm; female unknown.

Male.—Eye present. Antenna 1 subequal in length to body, 1.6 times longer than antenna 2, primary flagellum with 22 segments; accessory flagellum 2-segmented, the second segment well developed. Antenna 2 flagellum with 9 segments. Mandible: right mandible molar prominent, with seta, lacinia mobilis trifurcate, incisor 5-dentate, with 3 serrate accessory spines; left molar prominent, with seta, lacinia mobilis normal, 5-dentate, incisor 6-dentate, with 4 serrate accessory spines; palp segment 3 reduced, bearing 1 terminal seta, segment 2 bearing 1 lateral seta. Lower lip with inner lobes. Maxilla 1: inner plate with 5 apical plumose setae; outer plate with 8 pectinate spines; palp 2-segmented, virtually symmetrical, bearing 6 apical spines and 3 subapical setae. Maxilla 2: inner plate narrowing distally, bearing 9–10 setae along inner margin. Maxilliped: inner plate relatively narrow, bearing few spines along the apical margin; outer plate expanded, bearing numerous spines along inner and apical margins; palp 4-segmented, apical margin of segment 3 with setae.

Gnathopod 1: propod 75% length of carpus, palm transverse, bearing double row of 8 spines and lobate extension along the defining angle; dactyl only slightly shorter than palm; carpus elongate, posterior margin bearing 6 groups of numerous long setae; merus posterior margin pubescent; basis anterior margin with numerous long setae, posterior margin bearing only 1 long seta; coxa deeper than broad, narrowing slightly distally with 5 marginal setae. Gnathopod 2: propod elongate, about 2 times longer than carpus, palm oblique, shorter than posterior margin of propod, bearing double row of 6 small spines, defining angle with 4 setae and small pocketing proximal to defining angle; dactyl curves back on palm, inset slightly in propod; propod longer than palm, posterior margin bearing 5 sets of numerous setae; carpus subtriangular, with 4 sets of setae; merus distoposterior margin extended distally as a small tooth; coxa deeper than broad, bearing 5 marginal setae.

Pereopod 3: subequal in length to 4, coxa deeper than broad with 6 marginal setae, basis slightly expanded, with numerous small setae and 2 longer setae on posterior margin. Pereopod 4: coxa slightly deeper than broad with 5 marginal setae; basis slightly expanded, bearing numerous small setae and 3 longer setae along posterior margin. Pereopod 5, 50–55% length of body, pereopods 6 and 7 subequal, 60% length of body; bases of pereopods 5–7 not expanded, distoposterior lobes not developed; dactyls of pereopods 5 and 6, 30% length of corresponding propods; dactyl of pereopod 7, 20% length of corresponding propod. Coxal gills on pereopods 2–6 relatively large, subovate, with distinct peduncles.

Distoposterior margins of pleonal plates each with small tooth-like extension; first pleonal plate without spines along ventral margin; plates 2 and 3 with 1 spine along ventral margin. Pleopod 1 with small, serrated extension on the first segment of the inner ramus; pleopods 2 and 3, extension present but reduced; peduncle bearing 2 coupling spines. Uropod 1: outer ramus 60% length of inner, with 1 lateral and 5 apical spines; inner ramus subequal in length to peduncle, with 3 apical and 3 lateral spines; peduncle with 6 spines, 1 of which is basofacial. Uropod 2: outer ramus 85% length of inner, with 3 apical and 3 lateral spines; inner ramus subequal in length to peduncle with 3 apical and 2 lateral spines; peduncle with 2 spines. Uropod 3: about 30% length of body, *Melita*-like, inner ramus small, scale-like, with small apical seta; outer ramus 2-segmented, first segment armed with clusters of spines, second segment relatively small, unarmed. Telson short, cleft to base, narrowing distally, about as wide as long, bearing 1 spine and 1 seta along lateral margin, 1 long spine, 1 small spine and 1 seta apically.

Female.—Unknown.

Etymology.—The epithet *clavatus* comes from the Latin *clavat*, meaning club, and is based on the club-like propods of gnathopods 1 and 2.

Type-locality.—This species is known only from its type-locality, Tauala Cave, Panglao Island, Bohol, Philippines (Fig. 21). Tauala Cave is a sinkhole in karst containing a pool regularly used by local villagers for bathing and washing laundry. Water temperature and salinity were respectively 29°C and 4‰ at the time of collection. Cyclopid copepods, ostracods, isopods, molluscs, a new genus of anchialine varunine crab, *Orcovita fictilia* (Ng *et al.*, 1996), and a new species of *Hadzia* (Sawicki *et al.*, 2004) were also collected.

Panglao Island, situated only 1 km off the southwest corner of Bohol Island (Fig. 21), is a low island with numerous anchialine sinkholes and small caves formed in Pliocene/Pleistocene aged limestones. The karst features here are similar to those of the mainland of nearby Bohol (see Reeder *et al.*, 1989).

***Tegano panglaoensis* Sawicki and Holsinger, sp. n.**

Figs. 6–9

Material Examined.—PHILIPPINES. Bohol, Panglao Island: Hinagdanan Cave, ♂ holotype (2.5 mm), 1 ♀ paratype, 1 ♂ paratype, B. Sket, 2 February 1995.

The holotype is deposited in the National Museum of Natural History (Smithsonian Institution) under the catalogue number of the former United

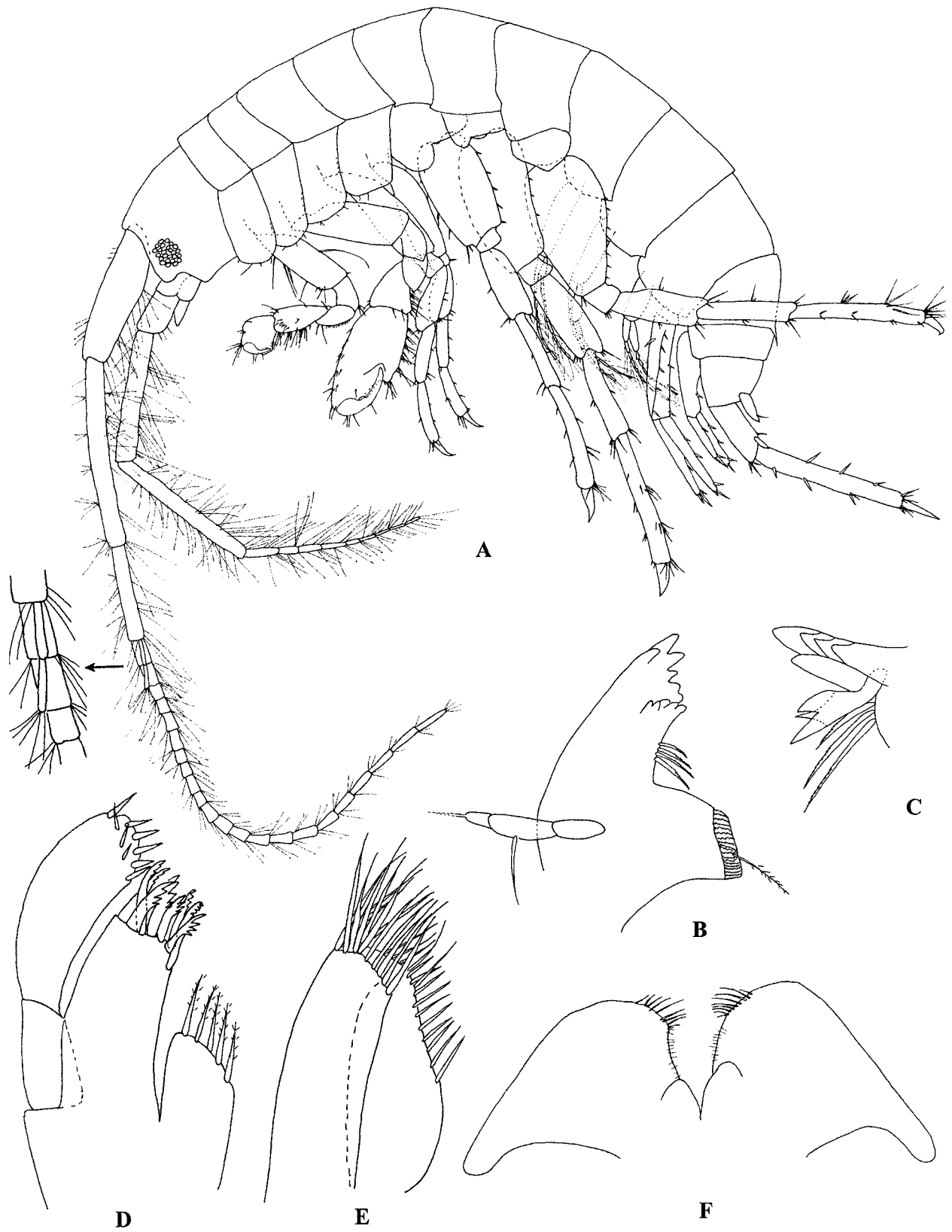


Fig. 1. *Tegano clavatus* n. sp., holotype, Taulala Cave, Panglao Island, Philippines. Male (4.2 mm): A, whole animal; B, left mandible; C, right mandible incisor and lacinia mobilis; D, maxilla 1; E, maxilla 2; F, lower lip.

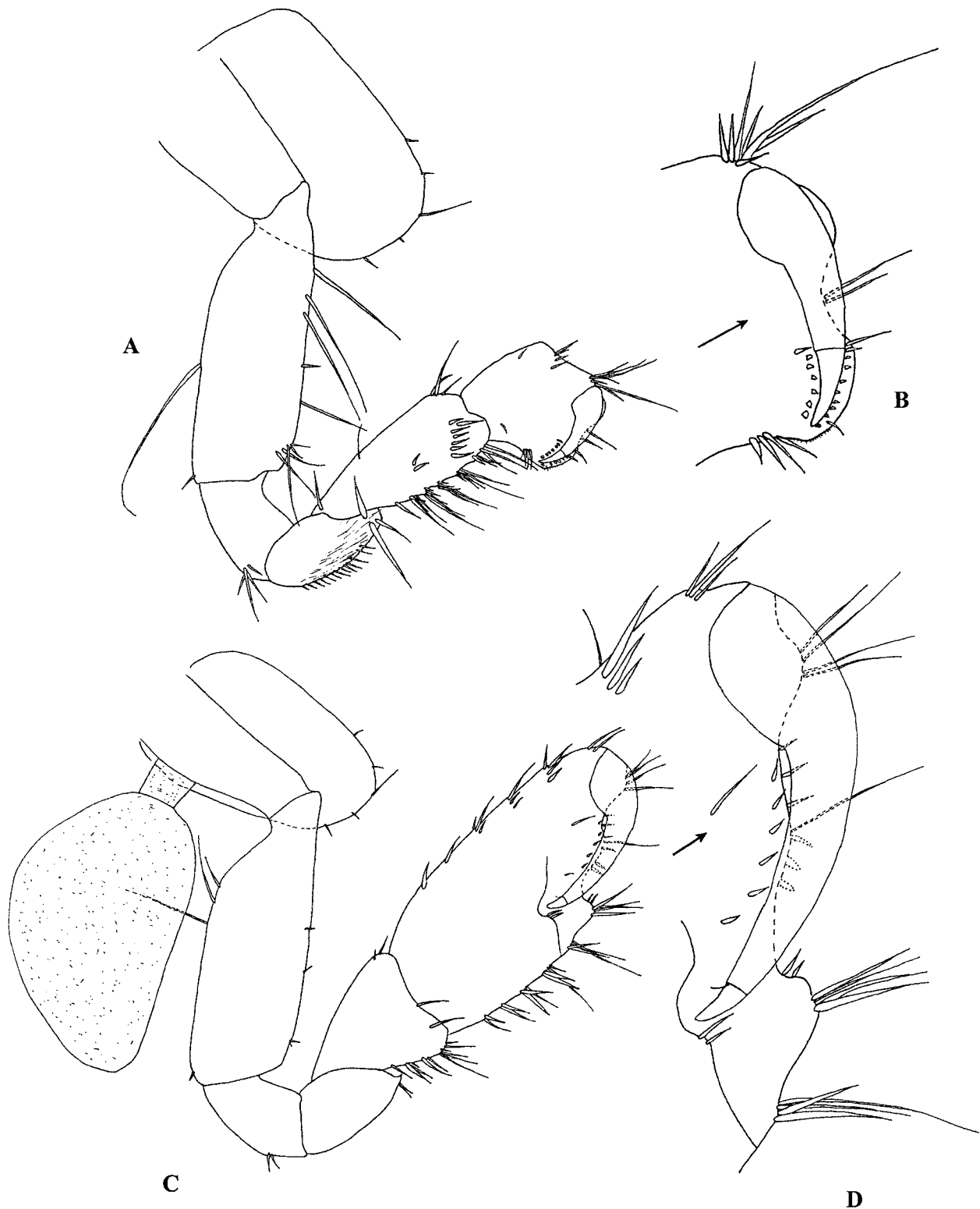


Fig. 2. *Tegno clavatus* n. sp., holotype, Taula Cave, Panglao Island, Philippines. Male (4.2 mm): A, gnathopod 1; B, enlarged propod and dactyl of gnathopod 1; C, gnathopod 2; D, enlarged propod and dactyl of gnathopod 2.

States National Museum (USNM 1027095); paratypes are in the collections of Ljubljana University and J. R. Holsinger.

Diagnosis.—Small species distinguished by segment 2 of accessory flagellum highly vestigial or absent (except

T. vagabundus); mandibular palp absent; maxilla 1 inner plate bearing apical non-plumose setae (as viewed under light microscopy). Largest male 2.5 mm; largest female 2.0 mm.

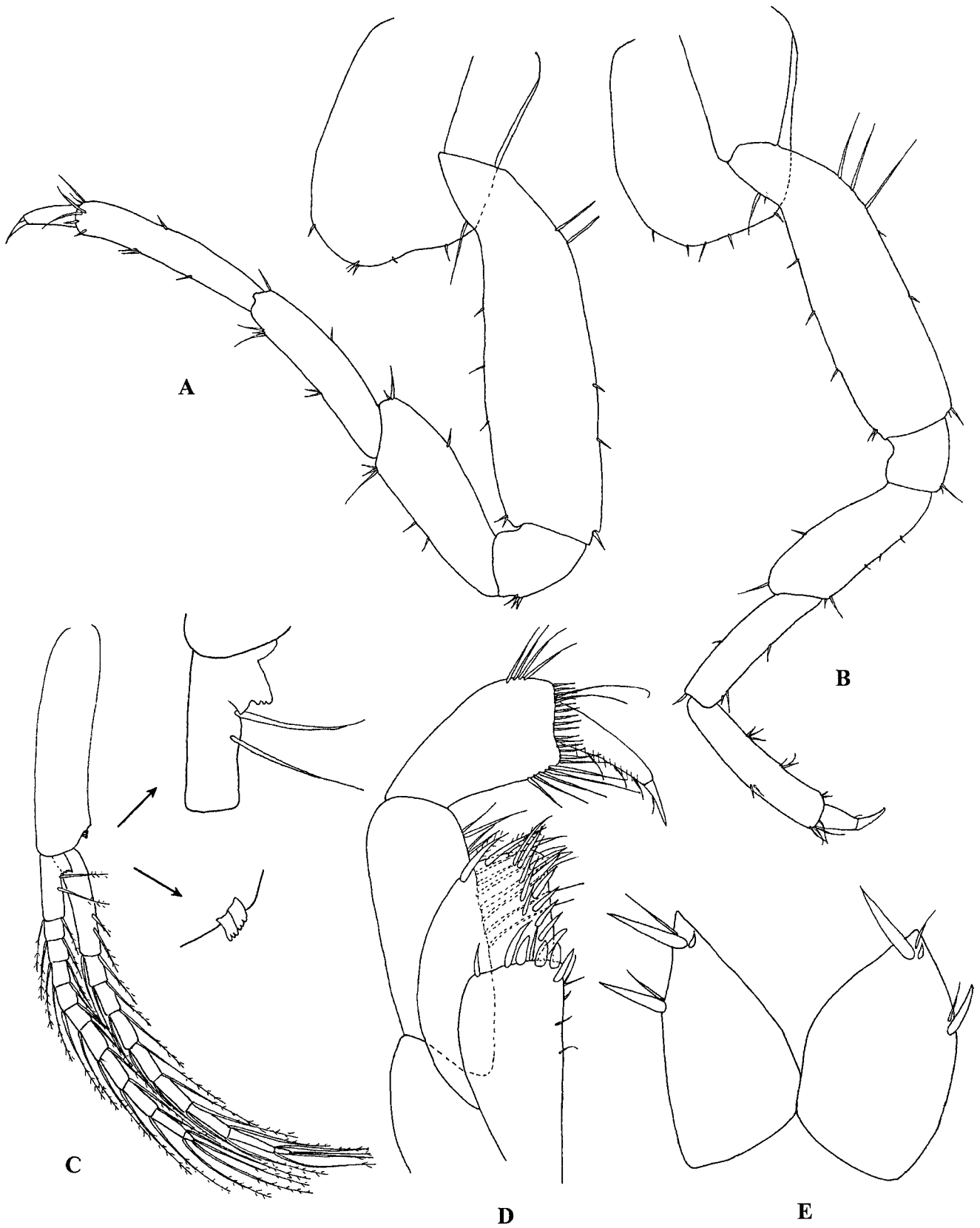


Fig. 3. *Tegano clavatus* n. sp., holotype, Taulala Cave, Panglao Island, Philippines. Male (4.2 mm): A, pereopod 3; B, pereopod 4; C, pleopod 1 (coupling spines and serrated extension on the first segment of the inner ramus enlarged); D, maxilliped; E, telson.

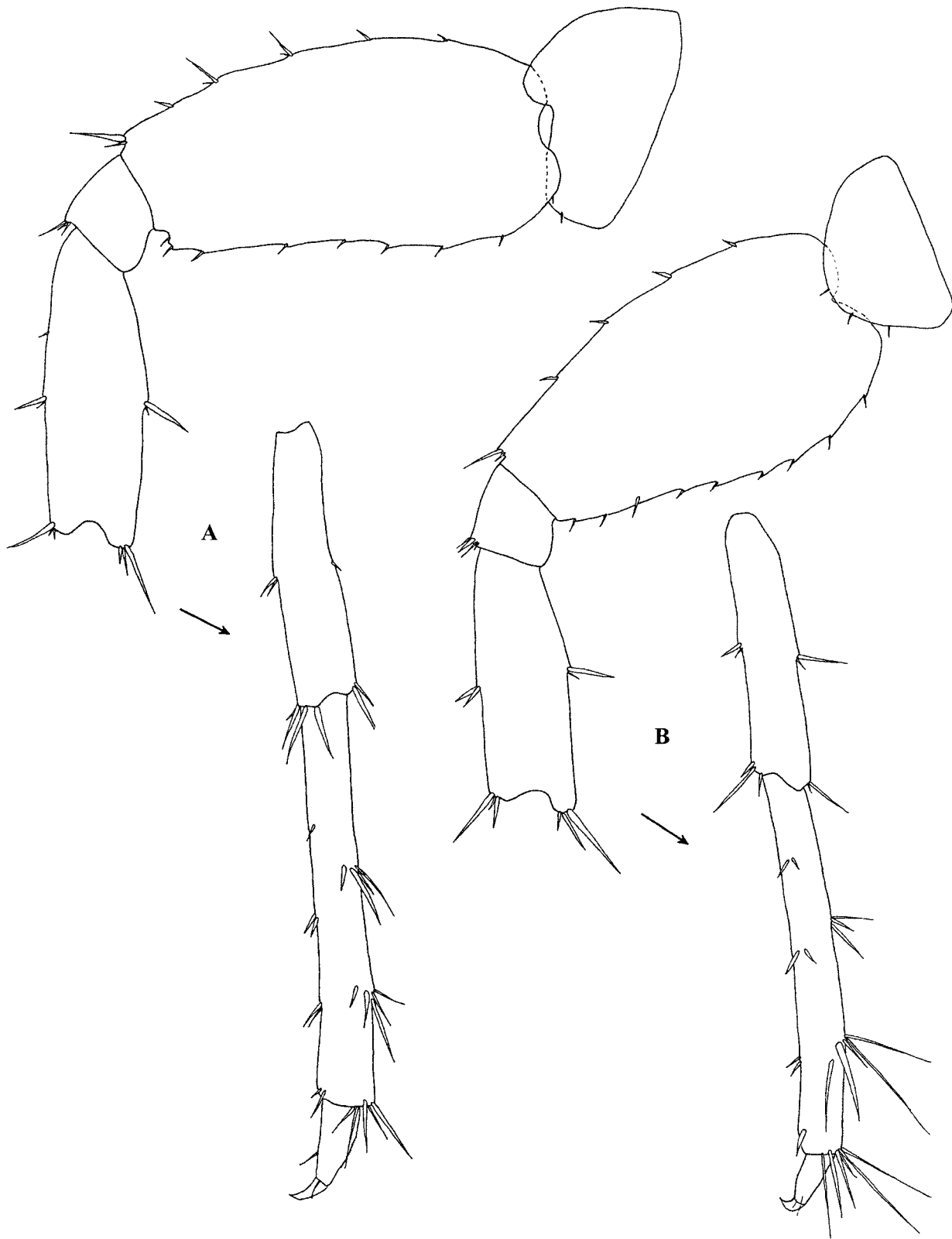


Fig. 4. *Tegano clavatus* n. sp., holotype, Tauala Cave, Panglao Island, Philippines. Male (4.2 mm): A, pereopod 6; B, pereopod 7.

Male.—Eye present. Antenna 1 slightly longer than body, 1.6 times longer than antenna 2, primary flagellum with 13 segments; accessory flagellum 2-segmented, second segment highly vestigial. Flagellum of antenna 2 with 5

segments. Mandible: right mandible molar prominent, with seta, lacinia mobilis trifurcate, incisor 5-dentate, up to 3 serrate accessory spines; left molar prominent, with seta, lacinia mobilis normal, 4-dentate, incisor 6-dentate, up to 4

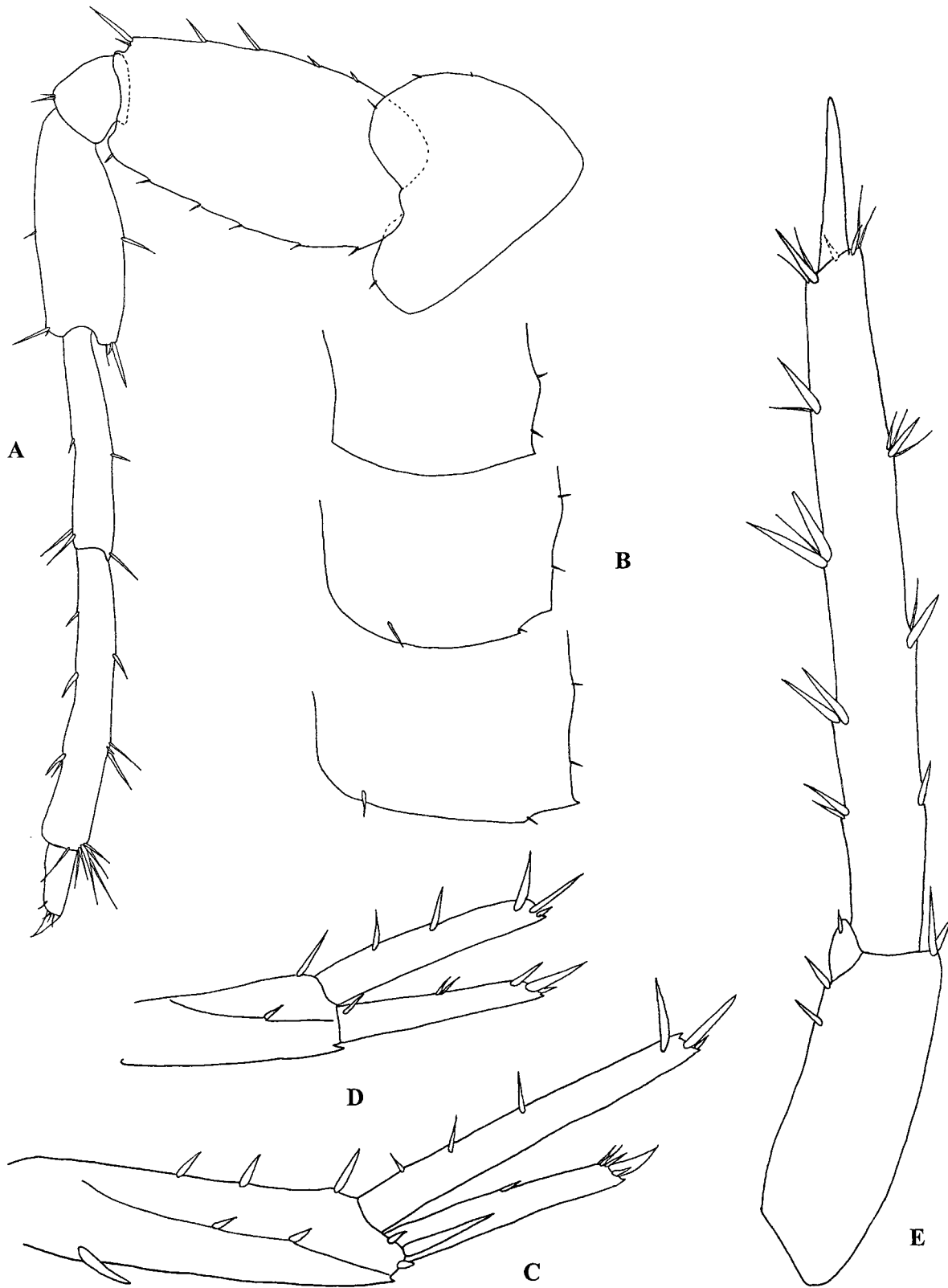


Fig. 5. *Tegano clavatus* n. sp., holotype, Tauala Cave, Panglao Island, Philippines. Male (4.2 mm): A, pereopod 5; B, pleonal plates; C, uropod 1; D, uropod 2; E, uropod 3.

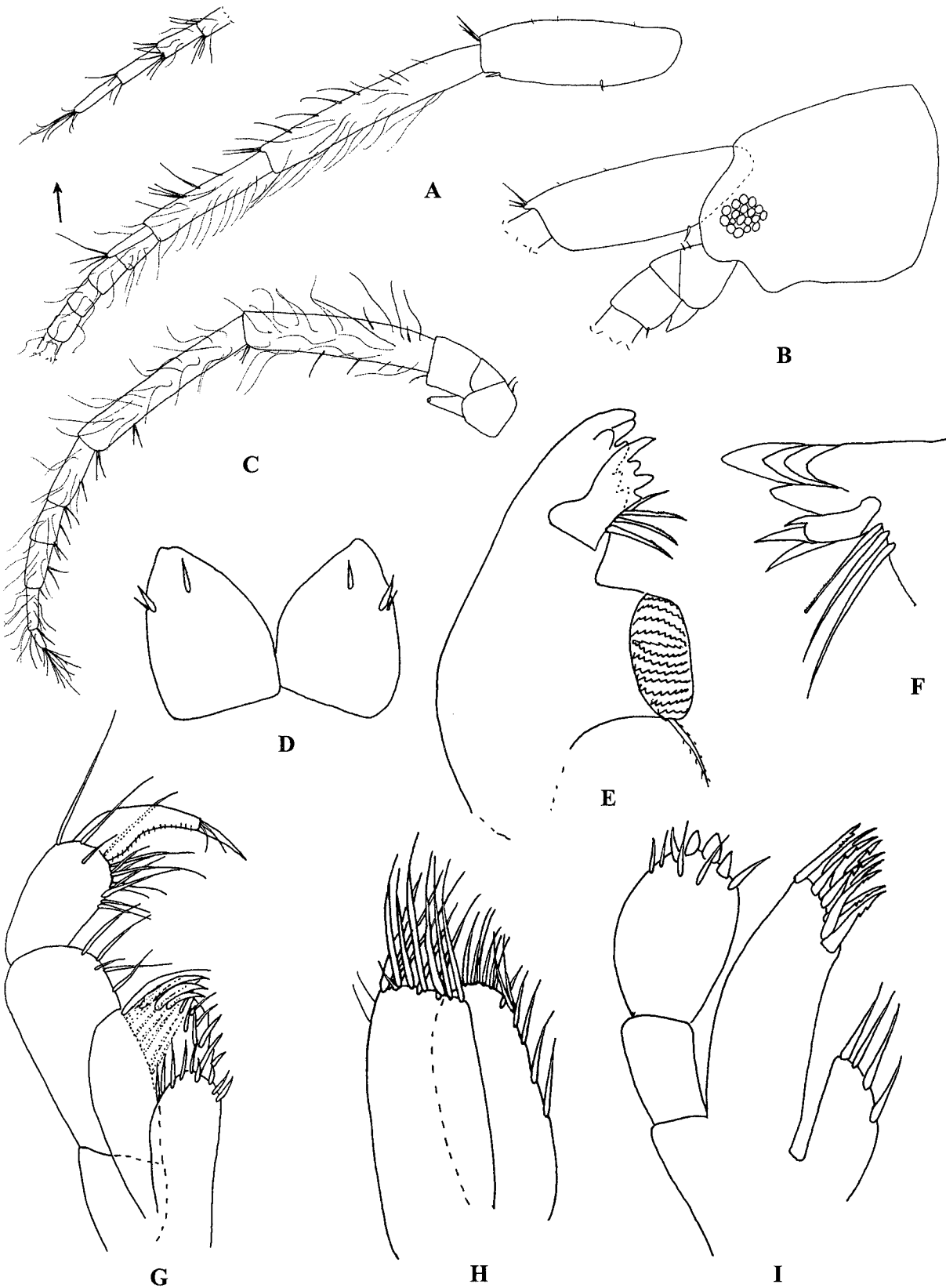


Fig. 6. *Tegano panglaoensis* n. sp., paratype, Hinagdanan Cave, Panglao Island, Philippines. Male (2.3 mm): A, antenna 1; B, head; C, Antenna 2; D, telson; E, left mandible; F, right mandible incisor and lacinia mobilis; G, maxilliped; H, maxilla 2; I, maxilla 1.

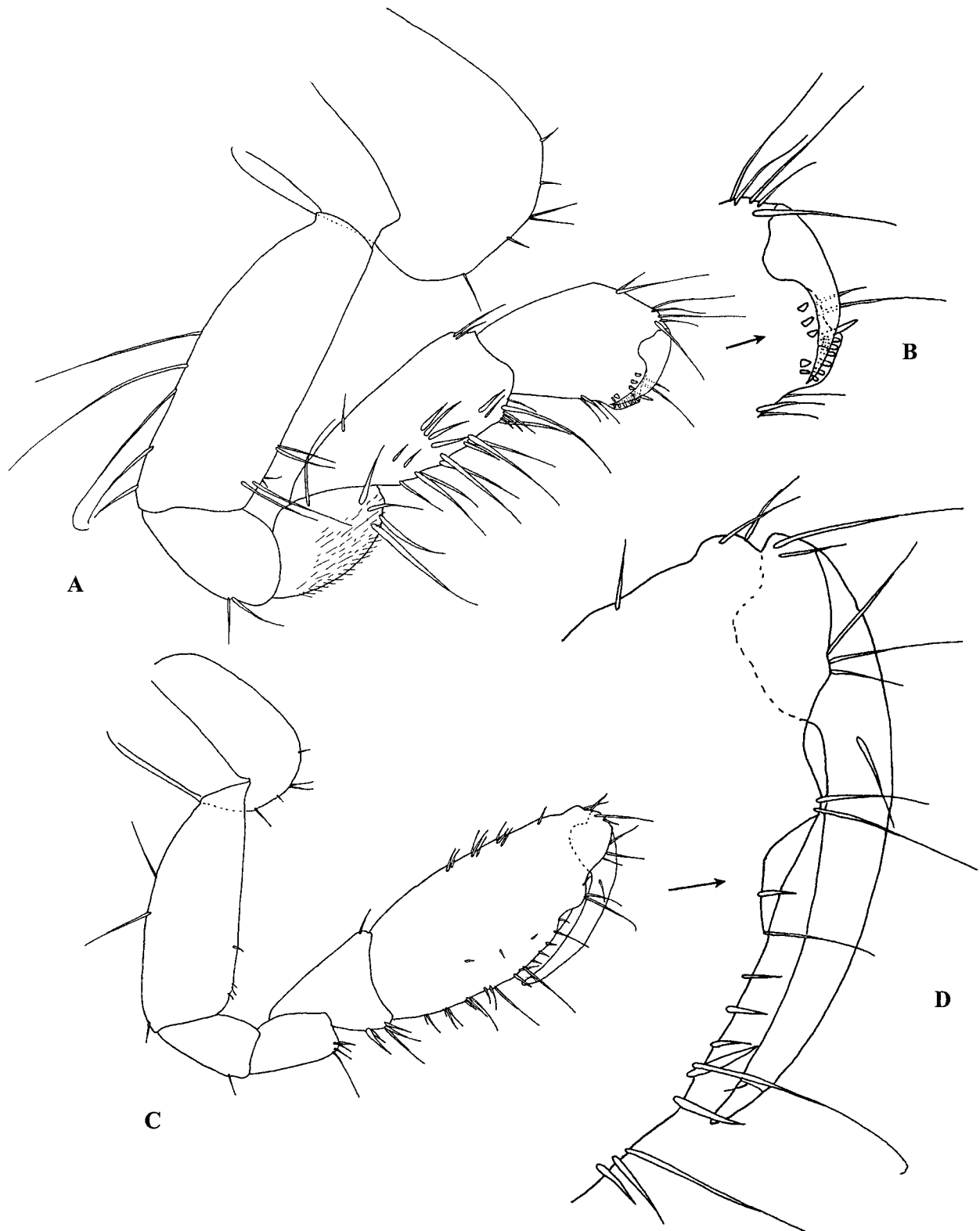


Fig. 7. *Tegano panglaoensis* n. sp., paratype, Hinagdanan Cave, Panglao Island, Philippines. Male (2.3 mm): A, gnathopod 1; B, enlarged propod and dactyl of gnathopod 1; C, gnathopod 2; D, enlarged propod and dactyl of gnathopod 2.

serrate accessory spines; palp absent. Lower lip with inner lobes. Maxilla 1: inner plate with 4 apical setae, naked under light microscopy; outer plate with 9 pectinate spines; palp 2-segmented, virtually symmetrical, bearing 5–6 stout apical

spines and 2–3 setae. Maxilla 2: inner plate bearing 4–5 setae along inner margin. Maxilliped: inner plate narrow, bearing spines along apical margin; outer plate greatly expanded, inner margin weakly crenulated, apical margin

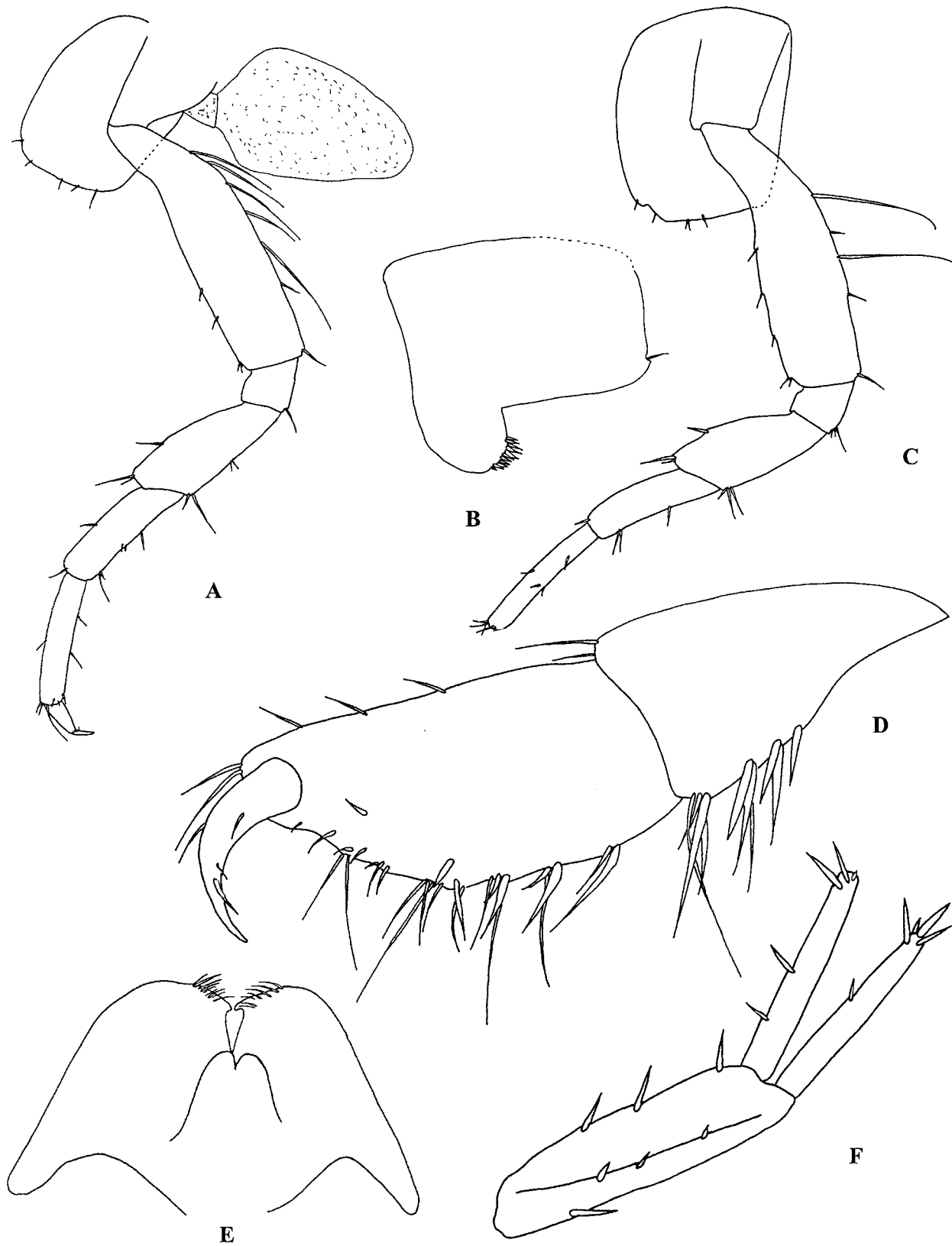


Fig. 8. *Tegano panglaoensis* n. sp., paratype, Hinagdanan Cave, Panglao Island, Philippines. Male (2.3 mm): A, pereopod 3; C, pereopod 4; E, lower lip; F, uropod 1. Female (2.0 mm): B, pereopod coxa 6; D, carpus, propod and dactyl of gnathopod 2.

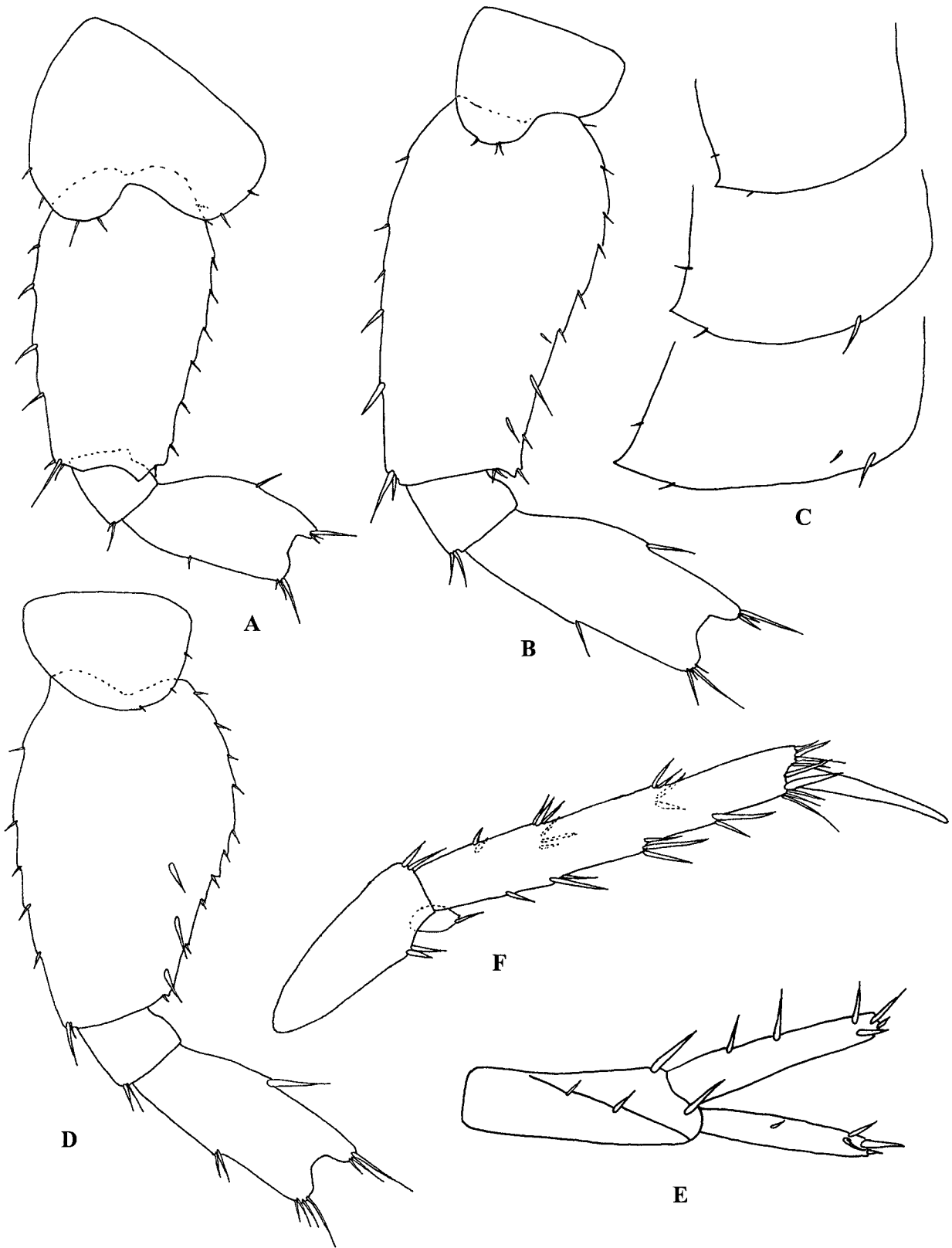


Fig. 9. *Tegano panglaoensis* n. sp., paratypes, Hinagdanan Cave, Panglao Island, Philippines. Male (2.3 mm): A, pereopod 5; B, pereopod 6; C, pleonal plates; D, pereopod 7; E, uropod 2; F, uropod 3.

bearing 4 large bladespines, inner margin with numerous spines; palp 4-segmented, segment 3 bearing numerous setae along inner apical margin.

Gnathopod 1: propod 80% length of carpus, palm transverse, bearing double row of 5–6 spines, 4 setae and lobate extension along the defining angle; dactyl subequal in length to palm; carpus elongate, posterior margin bearing 5 groups of long setae; merus posterior margin pubescent; basis posterior margin with up to 5 long setae; coxa deeper than broad, with 5 marginal setae. Gnathopod 2: propod elongate, 2 times longer than carpus, palm oblique with 6 slender spines, 2 at the defining angle and 4 setae, 1 at the defining angle; propod posterior margin subequal in length to palm, bearing 4 sets of setae; carpus subtriangular with 2 sets of setae along posterior margin; basis with only 2 setae along posterior margin; coxa deeper than broad, smaller than that of gnathopod 1, with 6 marginal setae. Pereopod 3: subequal in length to 4, coxa deeper than broad with 5 marginal setae, basis slightly expanded bearing 5 long setae along posterior margin. Pereopod 4: coxa deeper than broad with 5 marginal setae; basis slightly expanded with 2 long setae on posterior margin. Relative lengths of pereopods 5–7 unknown; bases of pereopods 5–7 not expanded, distoposterior lobes not developed. Coxal gills on pereopods 2–6 small, subovate, with distinct peduncles.

Pleonal plates: distoposterior margins each with small tooth-like extension; first pleonal plate with 1 ventral seta distally; plate 2 with 2 spines along ventral margin; plate 3 with 3 spines along ventral margin. Pleopods normal, bearing 2 coupling spines. Uropod 1: outer ramus 94% length of inner, bearing 1 lateral and 4 apical spines; inner ramus 73% length of peduncle, with 2 lateral and 3 apical spines; peduncle bearing 7 spines, 1 of which is basofacial. Uropod 2: outer ramus 75% length of inner, with 1 lateral and 4 apical spines; inner ramus 92% length of peduncle, with 4 apical and 2 lateral spines; peduncle bearing 4 spines. Uropod 3: 54% length of body, *Melita*-like; inner ramus small, scale-like, with small apical seta; outer ramus 2-segmented, first segment armed with clusters of spines, second segment relatively small, unarmed. Telson short, cleft to base, narrowing distally, wider than long, bearing 2 spines and 1 seta.

Female.—Differing from male as follows: Gnathopod 2: dactyl and propod proportionately shorter and narrower; propod only slightly longer than carpus; palm oblique with 6–7 spines and 2 longer setae; defining angle with 4 long setae and 1 spine; posterior margin longer than palm, with 4 sets of long setae. Pereopod 6: coxa anterior ventral margin lobate, posteroventral margin bearing row of 11 short spines.

Etymology.—The epithet *panglaoensis* denotes the presence of this species on Panglao Island, located only 1 km off the southwest corner of Bohol Island (Fig. 21).

Type-locality.—Hinagdanan Cave, Panglao Island, Bohol, Philippines (Fig. 21). This species is known only from its type locality, which is located near Taula Cave (see previous species) and is formed in limestone of Pliocene/Pleistocene age. It contains a large pool that is used by locals for bathing and swimming.

Tegano barnardi Sawicki and Holsinger, sp. n.
Figs. 10–14

Material Examined.—PALAU. Peleliu Island: Airport Well Cave, ♂ holotype (4.5 mm), 36 ♀ paratypes, 21 ♂ and 3 juvenile paratypes. D. Williams and J. Bozanic, 2 April 1985; 12 paratypes, T. M. Iliffe and D. Williams, 26 February 1985.

The holotype is deposited in the National Museum of Natural History (Smithsonian Institution) under the catalogue number of the former United States National Museum (USNM 1027092); paratypes are in the collection of J. R. Holsinger (H-2498) and the National Museum of Natural History (USNM 1027093).

Diagnosis.—Small stygobitic species distinguished by lacking eyes; antennae 1 and 2 without long setae; coxa 4 posteriorly excavate. Largest males 4.5 mm; largest females 4.0 mm.

Female.—Antenna 1 little longer than body, 2.2 times longer than antenna 2, primary flagellum with 23 segments; accessory flagellum 2-segmented, second segment well developed. Antenna 2 flagellum with 8 segments. Mandible: right mandible molar prominent, with seta, lacinia mobilis trifurcate, incisor 5-dentate, up to 3 serrate accessory spines; left molar prominent, with seta, lacinia mobilis normal, 5-dentate, incisor 6-dentate, with 3 serrate accessory spines; palp usually 2-segmented, sometimes 3-segmented, terminal segment with apical seta. Lower lip with inner lobes. Maxilla 1: inner plate with 6 plumose apical setae; outer plate with 8 pectinate spines; palp 2-segmented, virtually symmetrical, bearing 5 apical spines and 2 subapical setae. Maxilla 2: inner plate narrowing distally, bearing 7–8 setae along inner margin. Maxilliped: inner plate narrow, bearing spines along apical margin; outer plate expanded, apical margin bearing 6–7 bladespines, inner margin with 5–6 spines; palp 4-segmented, segment 3 with numerous long setae apically.

Gnathopod 1: propod 75% length of carpus, palm transverse bearing row of 6 small spines, 3 setae and lobate extension along the defining angle; dactyl subequal in length to palm; carpus elongate, posterior margin with 5 groups of long setae; merus posterior margin pubescent; basis posterior margin with 2 long setae; coxa deeper than broad with 4 marginal setae. Gnathopod 2: propod elongate, 86% longer than carpus, palm oblique with 8–9 small spines, 3 long setae, 2 at the defining angle with 1 large spine; propod posterior margin 1.6 times longer than the palm, bearing 4 sets of setae; carpus subtriangular, posterior margin with 4 sets of setae; basis with only 1 long seta; coxa deeper than broad with 4 marginal setae. Pereopod 3: subequal in length to 4, coxa deeper than broad, with 4 marginal setae; basis not expanded, posterior margin with 3 long setae. Pereopod 4: coxa posterior margin excavate, broader than deep, with up to 10 marginal setae, basis not expanded, bearing 3 long setae. Pereopod 5, 81% length of body, pereopod 6, 95% length of body, pereopod 7, slightly longer than body; bases of pereopods 5–7 slightly expanded, distoposterior lobes not developed; dactyl of pereopod 5, 43% length of corresponding propod; dactyl of pereopod 6, ca 30% length of corresponding propod; dactyl of pereopod 7, 36% length of corresponding propod. Coxal gills on pereopods 2–6 relatively large, subovate, with distinct peduncles; brood-plates sublinear, small relative to gills.

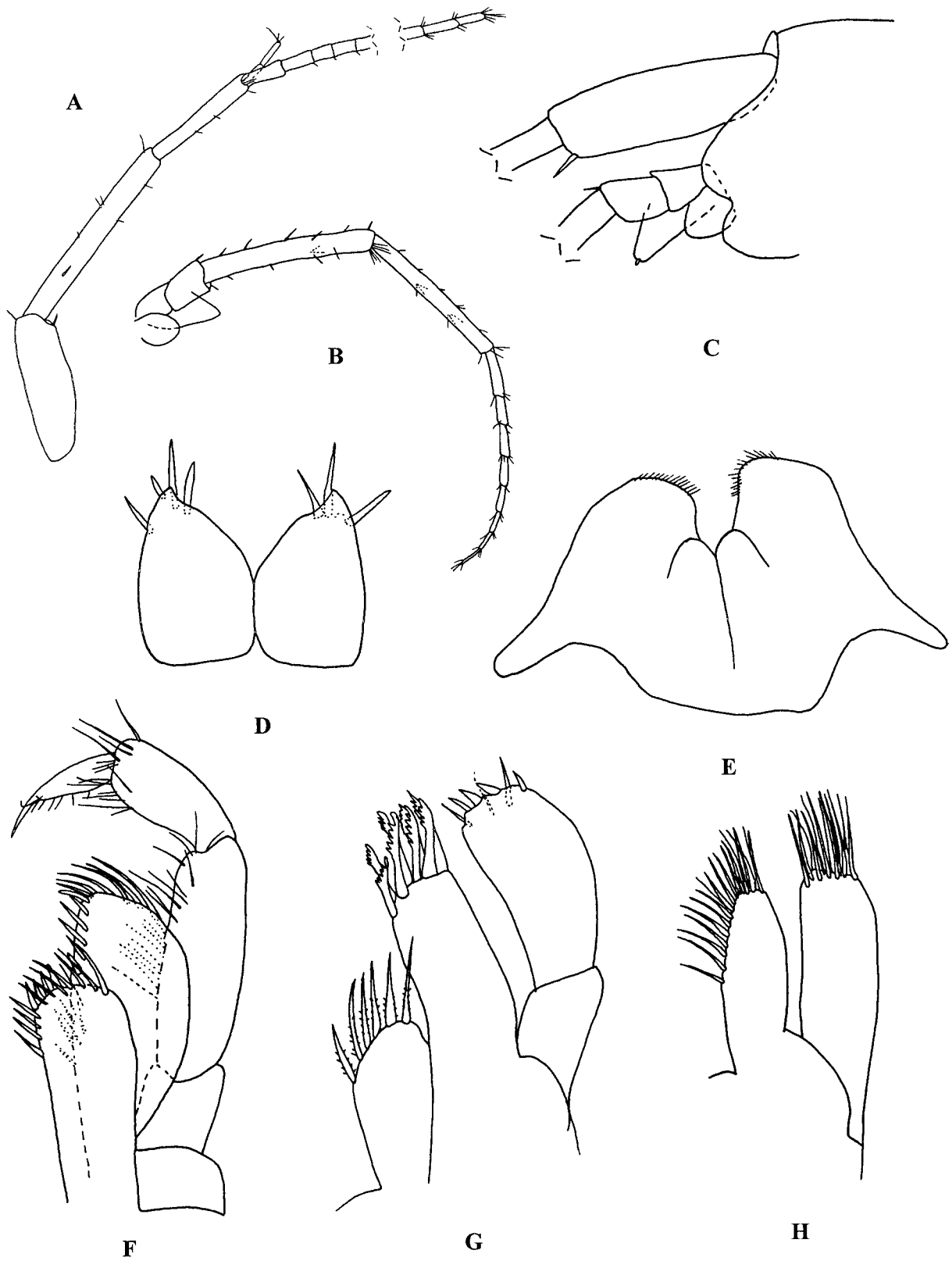


Fig. 10. *Tegano barnardi* n. sp., paratypes, Airport Well Cave, Peleliu Island, Palau. (Male 4.0 mm): A, antenna 1; B, antenna 2. Female (3.5 mm): C, head; D, telson; E, lower lip; F, maxilliped; G, maxilla 1; H, maxilla 2.

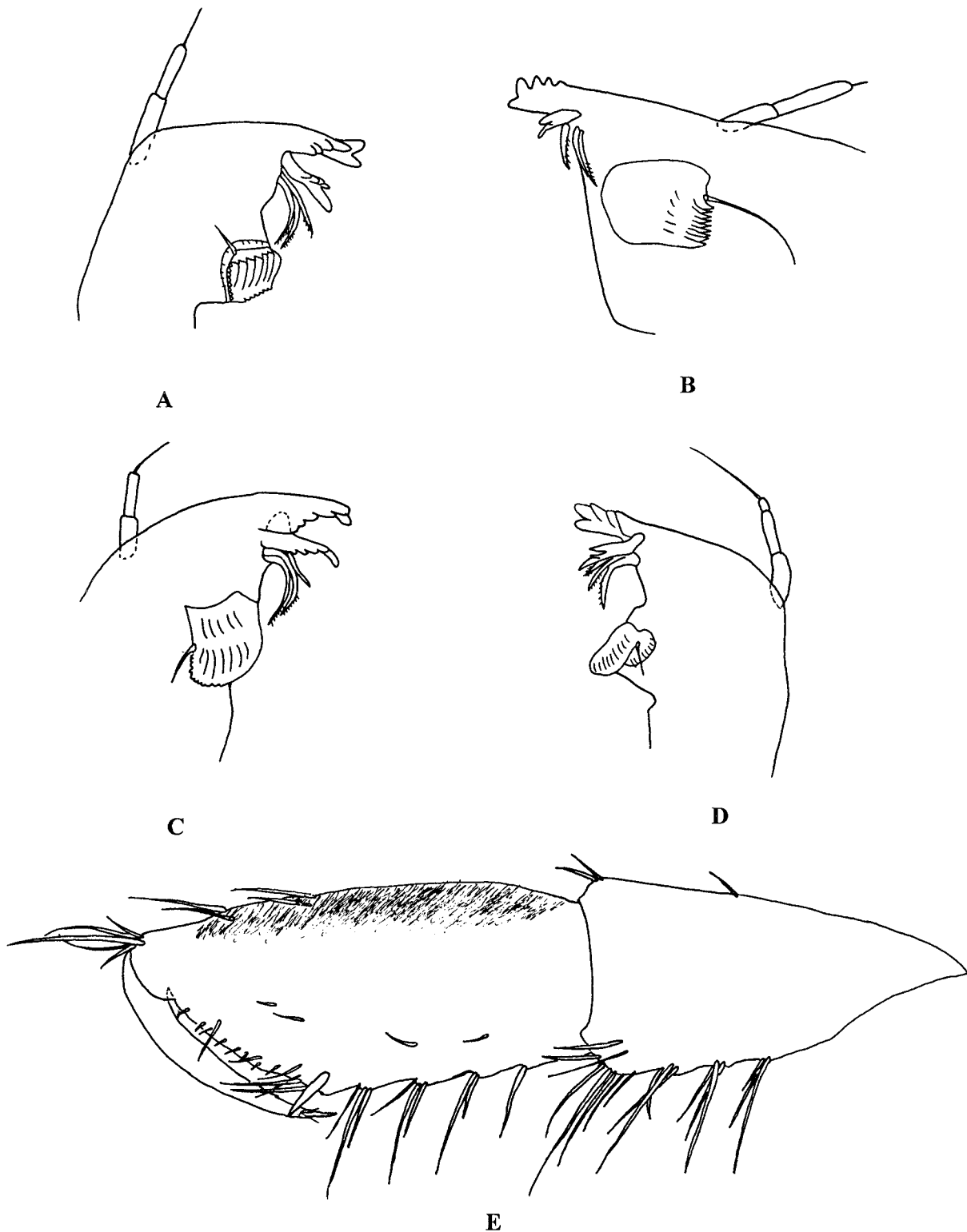


Fig. 11. *Tegano barnardi* n. sp., paratypes, Airport Well Cave, Peleliu Island, Palau. (Male 3.5 mm) A, left mandible; B, right mandible; Female (3.3 mm): C, left mandible; D, right mandible with 3-segmented palp; Female (3.5 mm): E, carpus, propod and dactyl of gnathopod 2.

Pleonal plates, distoposterior margins each with weakly developed tooth-like extension; plate 1 without ventral spines; plates 2 and 3 with one ventral spine each. Pleopods normal bearing 2 coupling spines. Uropod 1: outer ramus 85% length of inner, bearing 4 apical and 2 lateral spines;

inner ramus 94% length of peduncle bearing 4 apical and 2 lateral spines; peduncle with 5 spines, 1 basofacial. Uropod 2: outer ramus 74% length of inner bearing 4 apical and 2 lateral spines; inner ramus slightly longer than peduncle, with 4 apical and 2 lateral spines; peduncle bearing 4 spines.

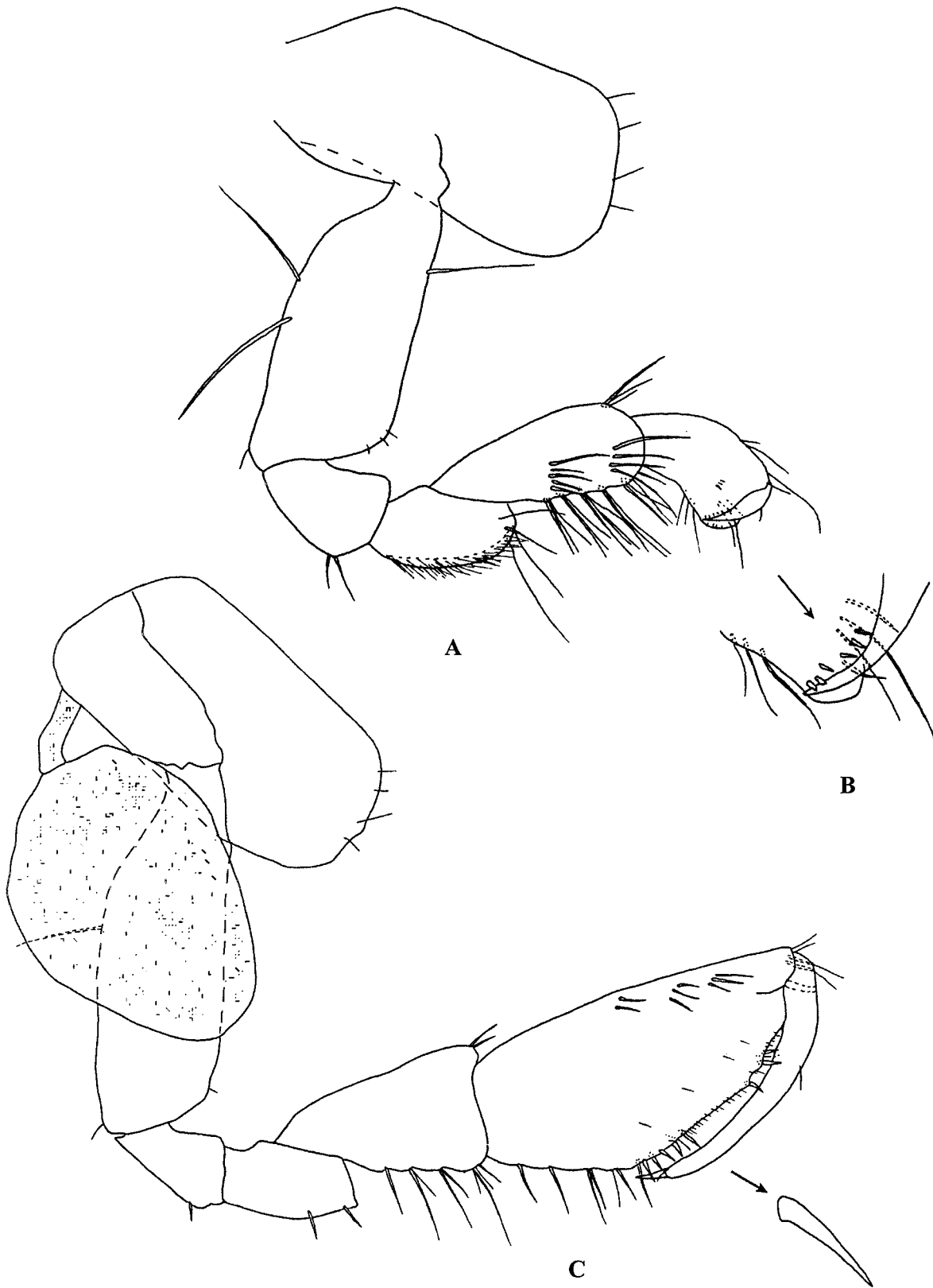


Fig. 12. *Tegano barnardi* n. sp., paratype, Airport Well Cave, Peleliu Island, Palau. (Male 4.0 mm): A, gnathopod 1; B, enlarged propod and dactyl of gnathopod 1; C, gnathopod 2 with enlarged palmar spine.

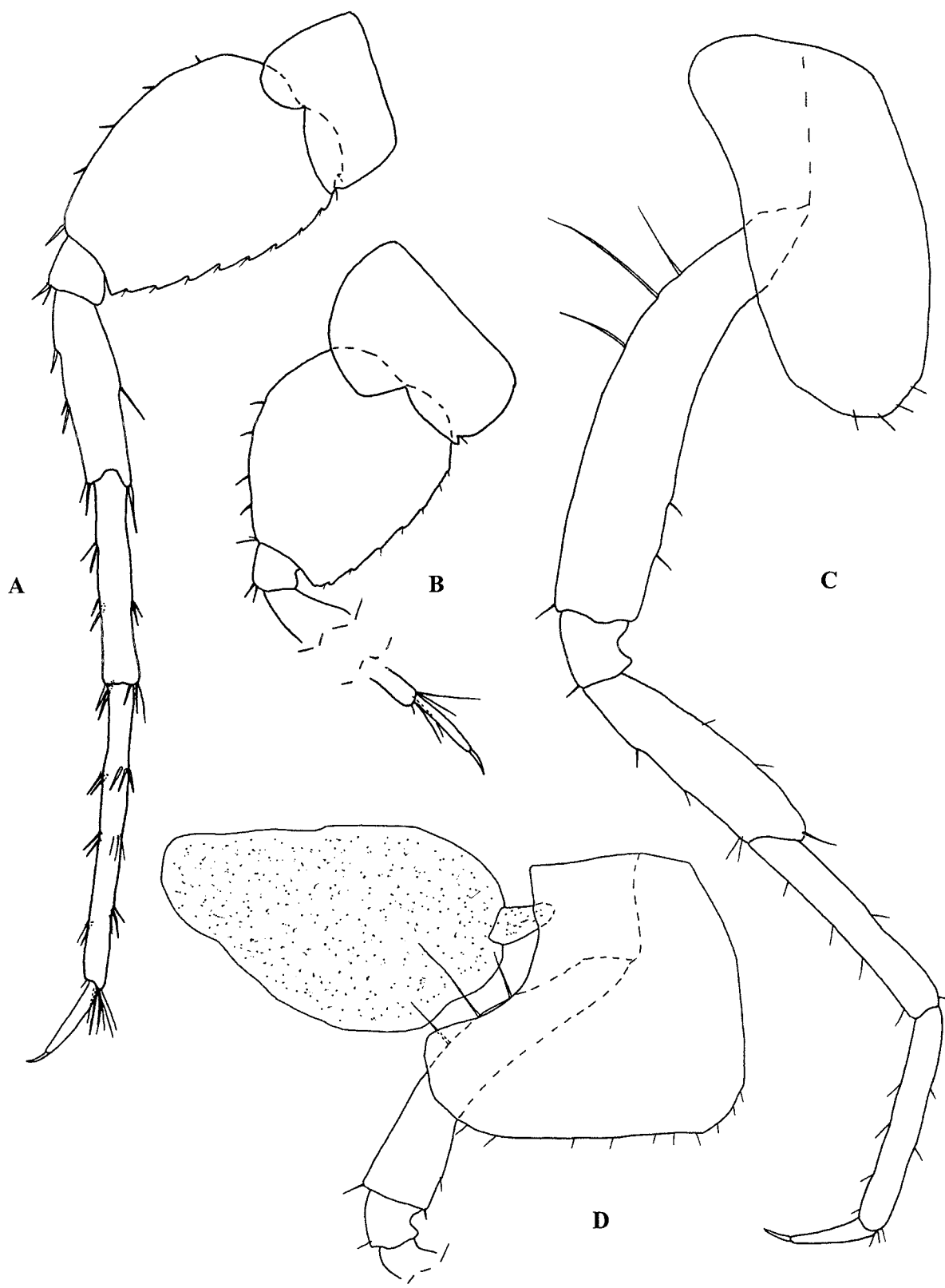


Fig. 13. *Tegano barnardi* n. sp., paratypes, Airport Well Cave, Peleliu Island, Palau. Female (3.3 mm): A, pereopod 6; B, pereopod 5. Male (4.0 mm): C, pereopod 3; D, pereopod 4.

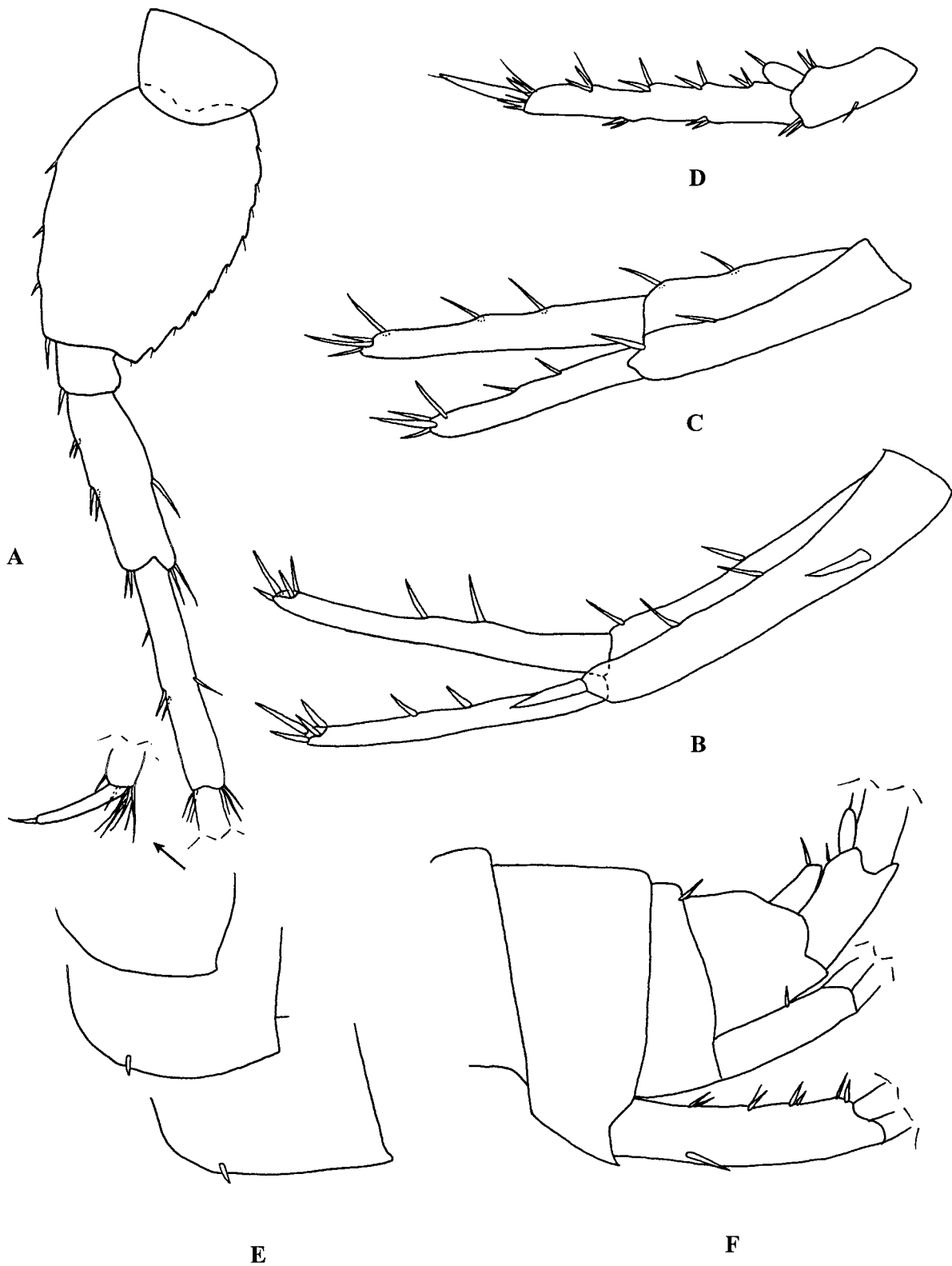


Fig. 14. *Tegano barnardi* n. sp., paratypes, Airport Well Cave, Peleliu Island, Palau. Female (3.5 mm): B, uropod 1; D, uropod 3; E, pleonal plates; F, urosomites. Male (4.0 mm): A, pereopod 7; C, uropod 2.

Uropod 3: 28% length of body, *Melita*-like, inner ramus small, scale-like, with small apical seta; outer ramus 2-segmented, first segment armed with clusters of spines, second segment relatively small, with 1 apical setule. Telson short, cleft to base, narrowing distally, wider than long, bearing 3–4 spines apically.

Male.—Differing from female as follows: Gnathopod 2: dactyl and propod proportionately longer and broader; propod palm long, oblique with numerous small to medium sized spines; defining angle with 1 long seta; posterior margin subequal to palm with 4 sets of long setae.

Etymology.—It is a great pleasure to name this species in honor of the late eminent amphipod systematist Dr. J. L. Barnard, whose contributions to amphipod taxonomy were prodigious.

Type-locality.—This species is known only from its type locality, Airport Well Cave, Peleliu Island, Palau (Fig. 22). This natural “well” is developed in highly karstified reef limestone that overlies the volcanic basement. It is covered by a tin roof and is used locally as a supply of freshwater. The 2.0 m diameter sinkhole entrance gives way to a 2.5 m undercut vertical drop directly into a clear, water table pool. This pool is floored with breakdown blocks and the bottom extends underwater to 10 m depths before ending in collapse. Although large masses of roots hang into open water near the entrance, no direct surface run-off flows into the cave. A blind, unpigmented isopod, *Anopsilana lingua*, also collected from the pool, is the first stygobitic cirolanid to be reported from the Pacific Ocean (Bowman and Iliffe 1987).

Melita Leach

Melita Leach, 1814: 403.

Paraniphargus Tattersall, 1925: 241.

Remarks.—*Paraniphargus* was established by Tattersall (1925) for a single species, *P. anandalei*, from a stream (spring flow?) in the Andaman Islands. Schellenberg (1931) added *P. ruttneri* from a spring in East Java to the genus. Both species were collected from freshwater habitats. Schellenberg (1931) noted the marine affinities of these two species and suggested a sister relationship between the genera *Melita* and *Paraniphargus*. *Paraniphargus* was maintained primarily because the two species were from subterranean freshwater habitats.

Schellenberg (1931) emphasized two characters shared by species of *Paraniphargus*: 1) inner margin of maxilla 2 naked and 2) outer ramus of uropod 3 without second segment. These characters were examined for a number of species of *Melita* in our present study. The number of setae on the inner margin of maxilla 2 is highly reduced in some species. Although some of these species have a well-developed second segment of uropod 3, including the new species of *Melita* described below, many species of *Melita* have a greatly reduced second segment of uropod 3 (Zeidler, 1989). The variation noted in these characters is a clear indication that species in the genus *Paraniphargus* cannot be distinguished from many species of *Melita*. For this reason, *Paraniphargus* is synonymized with *Melita*.

Melita almagosa Sawicki and Holsinger, sp. n.

Figs. 15–19

Material Examined.—GUAM. Almagosa Springs: ♂ holotype (5.5 mm), 24 paratypes (♀, ♂), A. Asquith and S. Miller, 15–31 March 1996.

The holotype is deposited in the National Museum of Natural History (Smithsonian Institution) under the catalogue number of the former United States National Museum (USNM 1027096); paratypes are in the collection of J. R. Holsinger (H-3559).

Diagnosis.—Small to medium sized stygobitic species of troglomorphic facies, distinguished by absence of eyes, lower lip lacking inner lobes; apical margin of inner lobe of maxilla 1 with highly reduced number of setae; inner margin of inner lobe of maxilla 2 with highly reduced number of setae; ventral margins of pleonal plates without spines; urosome lacking spines or teeth. Largest males 5.5 mm; largest females 4.5 mm.

Female.—Antenna 1, 77% length of body, 1.6 times longer than antenna 2, primary flagellum with up to 19 segments; accessory flagellum 2-segmented. Antenna 2 flagellum with up to 6 segments. Mandible: right mandible molar prominent, with plumose seta, lacinia mobilis 2 dentate, incisor 5 dentate, up to 4 serrate accessory spines; left molar prominent, with plumose seta, lacinia mobilis 4 dentate, incisor 5 dentate; palp 3-segmented, segment 3 reduced, without D-setae, with 4 E-setae. Lower lip without inner lobes. Maxilla 1: inner plate with 3 plumose setae; outer plate with 8 pectinate spines; palp 2-segmented, virtually symmetrical, bearing 8 long spines apically. Maxilla 2: inner plate narrow, with up to 3 plumose setae along inner margin, without dorsal oblique row of setae. Maxilliped: inner plate relatively narrow, bearing 2–3 stout spines and up to 7 long spines apically; outer plate expanded, inner and apical margins with row of heavy bladespines; palp 4-segmented, stout, segment 3 bearing numerous spines and setae apically.

Gnathopod 1: propod 70% length of carpus, palm transverse, bearing double row of 6 spines and 2 long setae; dactyl subequal in length to palm; carpus relatively elongate, weakly expanded, distoanterior margin weakly pubescent, posterior margin with 5 sets of long setae; merus posterior margin pubescent with up to 4 long setae on distoposterior margin; ischium posterior medial margin pubescent; basis bearing up to 3 long setae on posterior margin; coxa deeper than broad with 7 marginal setae. Gnathopod 2: propod elongate, slightly longer than carpus, palm oblique bearing double row of 6 spines, 2 large spines and 3–4 long setae at the defining angle, propod posterior margin with 3 sets of long setae, 1.6 times longer than palm; carpus subtriangular, posterior margin with 5 sets of long setae, merus distoposterior margin with small, tooth-like extension; basis posterior margin bearing 2 long setae; coxa much deeper than broad, with up to 8 marginal setae. Pereopod 3: subequal in length to 4, coxa deeper than broad with 8 marginal setae; basis not expanded bearing 3 long setae on posterior margin. Pereopod 4: coxa posterior margin excavate, slightly deeper than broad, with 12 marginal setae; basis not expanded, bearing 3 long setae on posterior margin. Pereopod 5, 76% length of body, pereopod 6, 85% length of body, pereopod 7, 82% length of body; coxa of pereopod 6 anterioventral margin with hook-spine, medial lobate extension with serrate posterior margin;

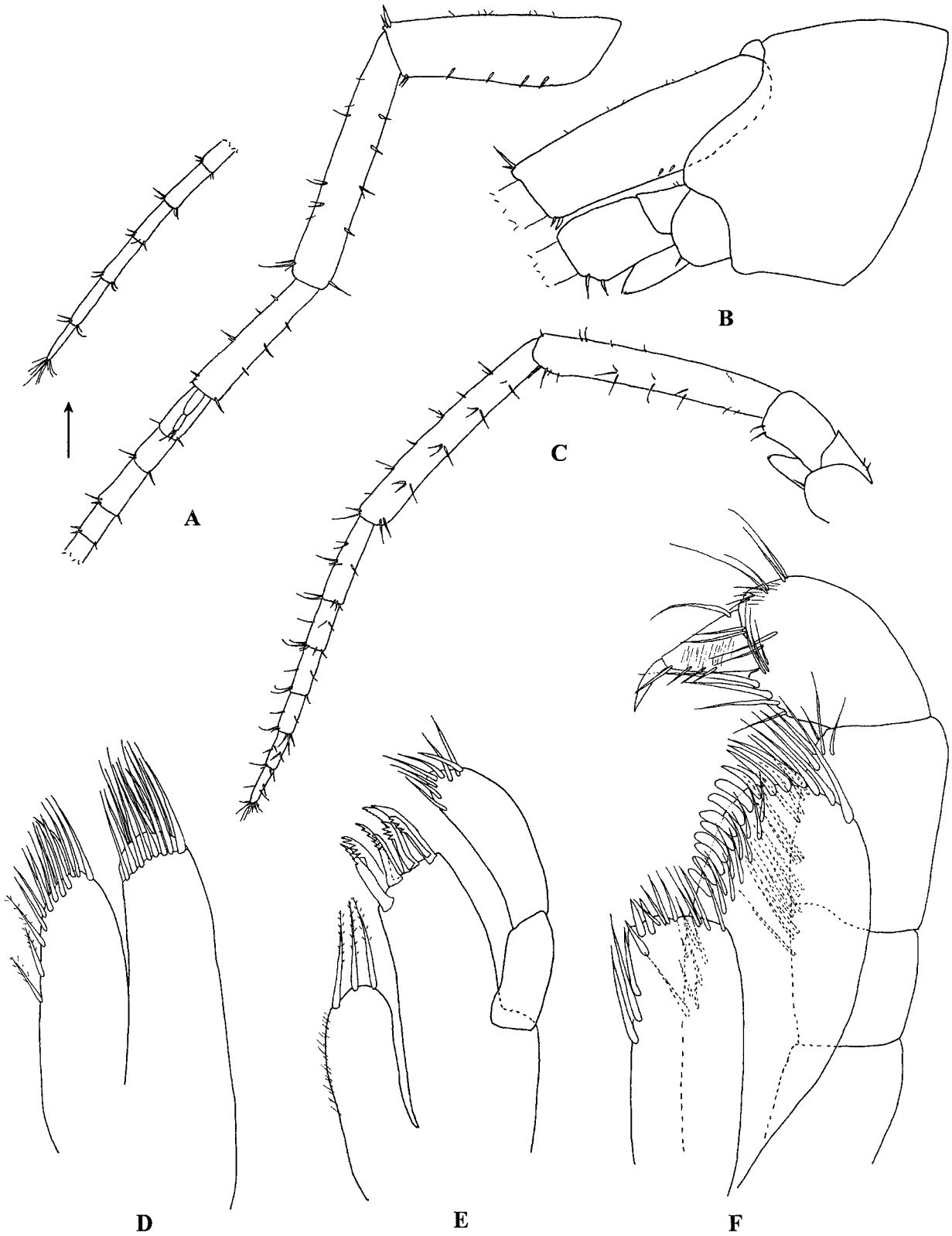


Fig. 15. *Melita almagosa* n. sp., paratypes, Almagosa Springs, Guam. Male (4.2 mm): A, antenna 1; C, antenna 2; D, maxilla 2; E, maxilla 1. Second Male (4.2 mm): B, head. Male (4.5 mm): F, maxilliped.

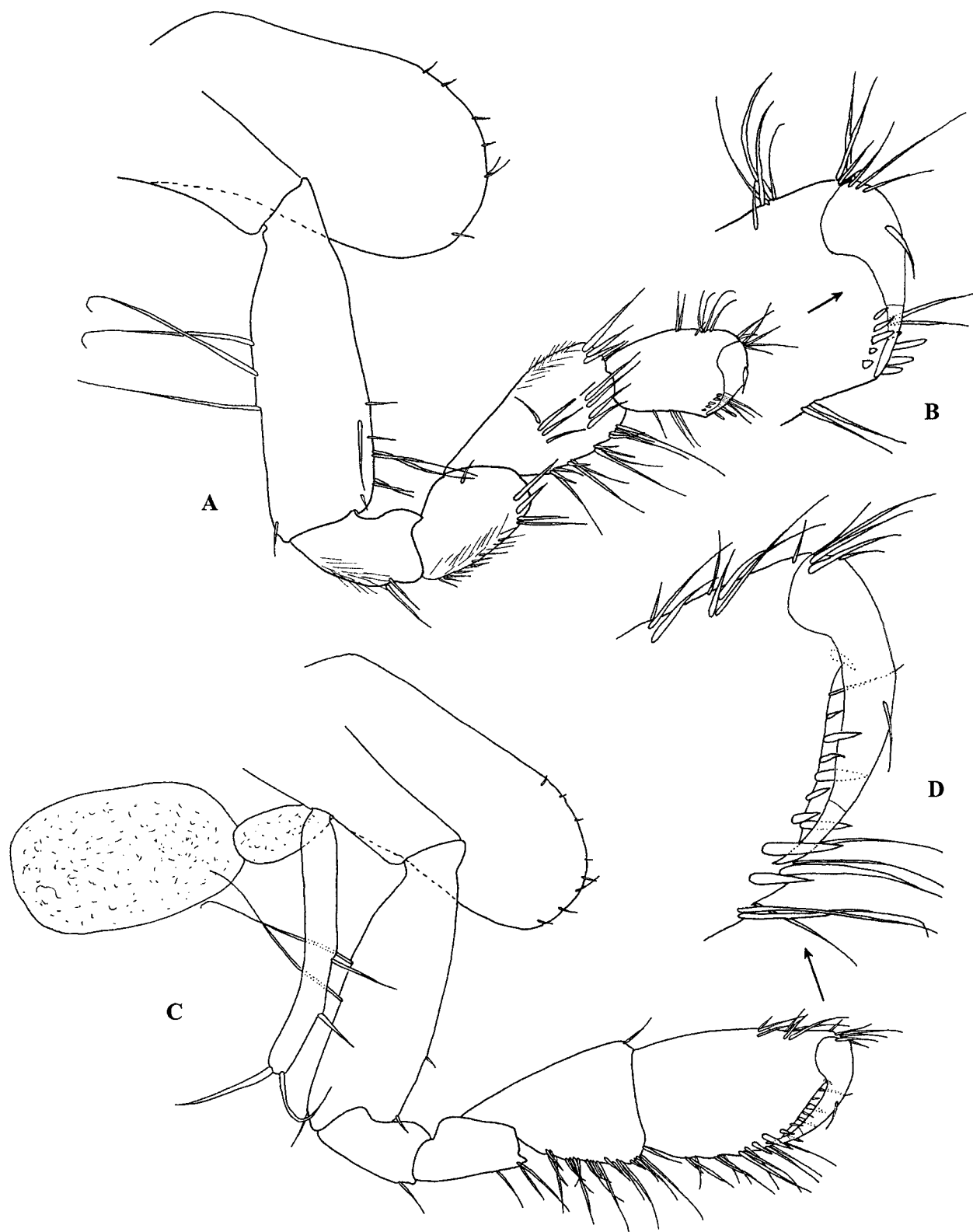


Fig. 16. *Melita almagosa* n. sp., paratype, Almagosa Springs, Guam. Female (3.2 mm): A, gnathopod 1; B, enlarged propod and dactyl of gnathopod 1; C, gnathopod 2; D, enlarged propod and dactyl of gnathopod 2.

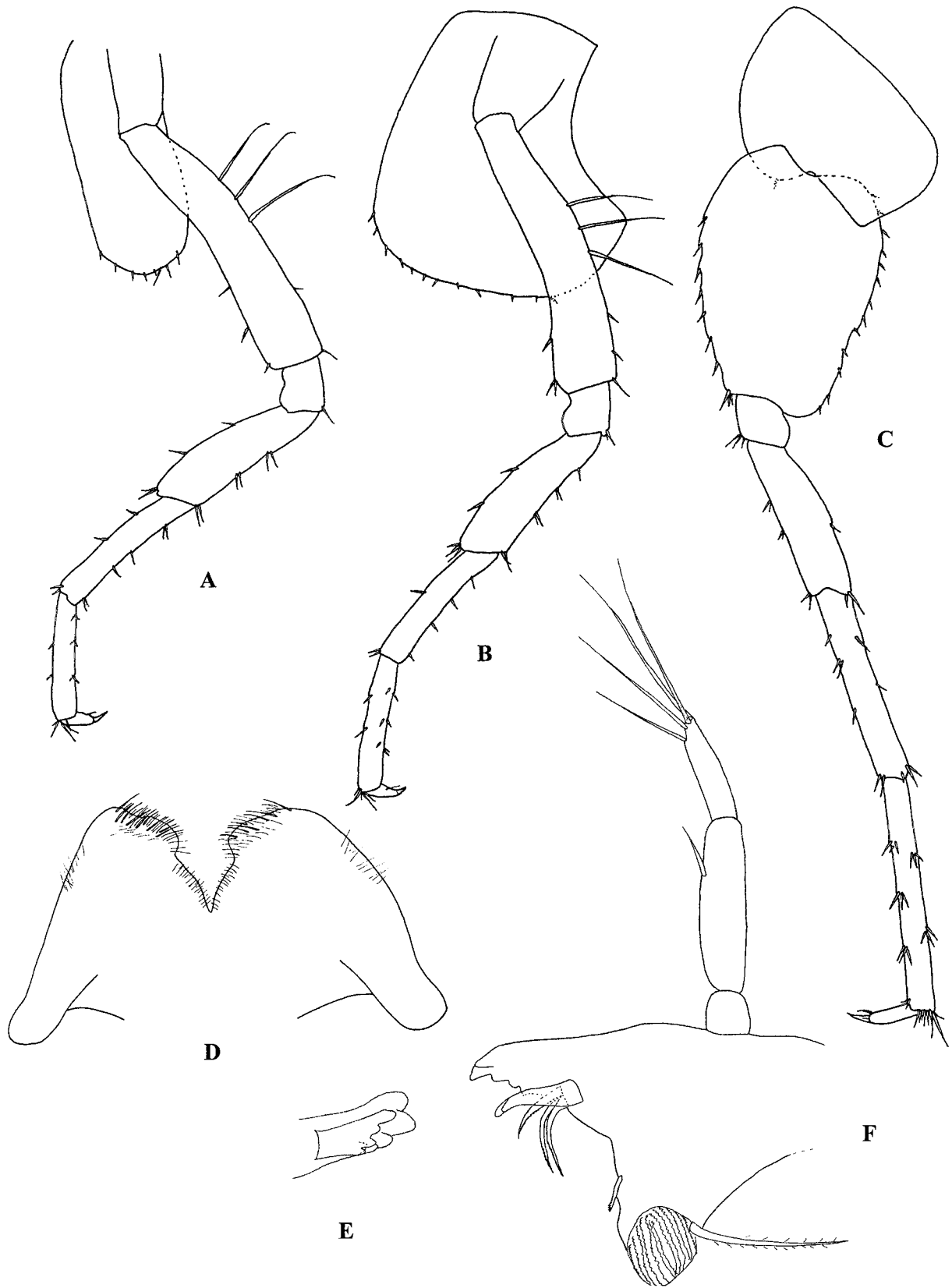


Fig. 17. *Melita algamosa* n. sp., paratypes, Almagosa Springs, Guam. Male (4.2 mm): A, pereopod 3; B, pereopod 4; C, pereopod 5; E, left mandible incisor and lacinia mobilis; F, right mandible. Female (3.2 mm): D, lower lip.

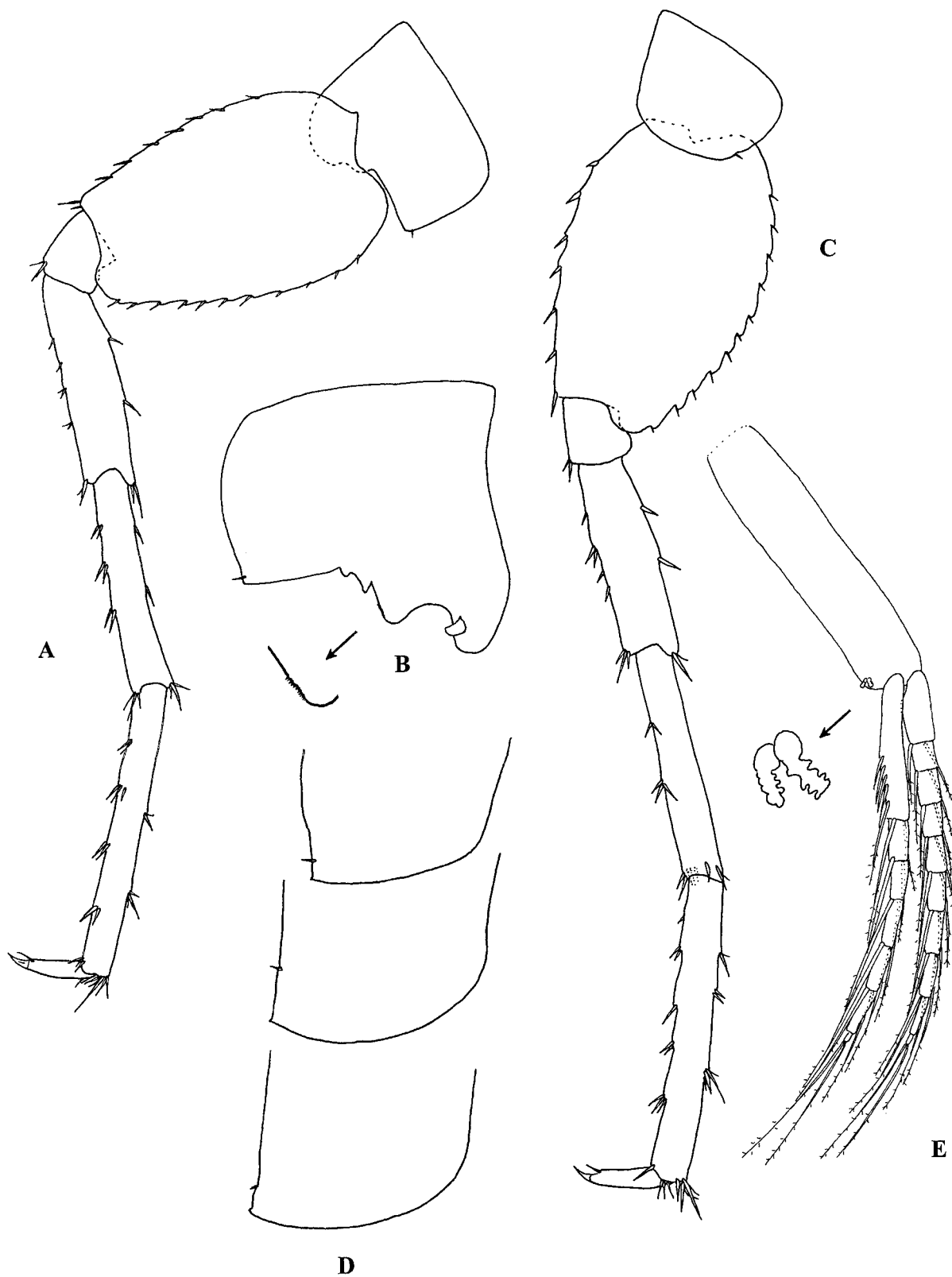


Fig. 18. *Melita almagosa* n. sp., paratypes, Almagosa Springs, Guam. Male (4.2 mm): A, pereopod 6; C, pereopod 7; D, pleonal plates; E, pleopod 1 (coupling spines enlarged). Female (3.2 mm): B, pereopod 6 coxa (serrate posterior margin on medial lobate extension enlarged).

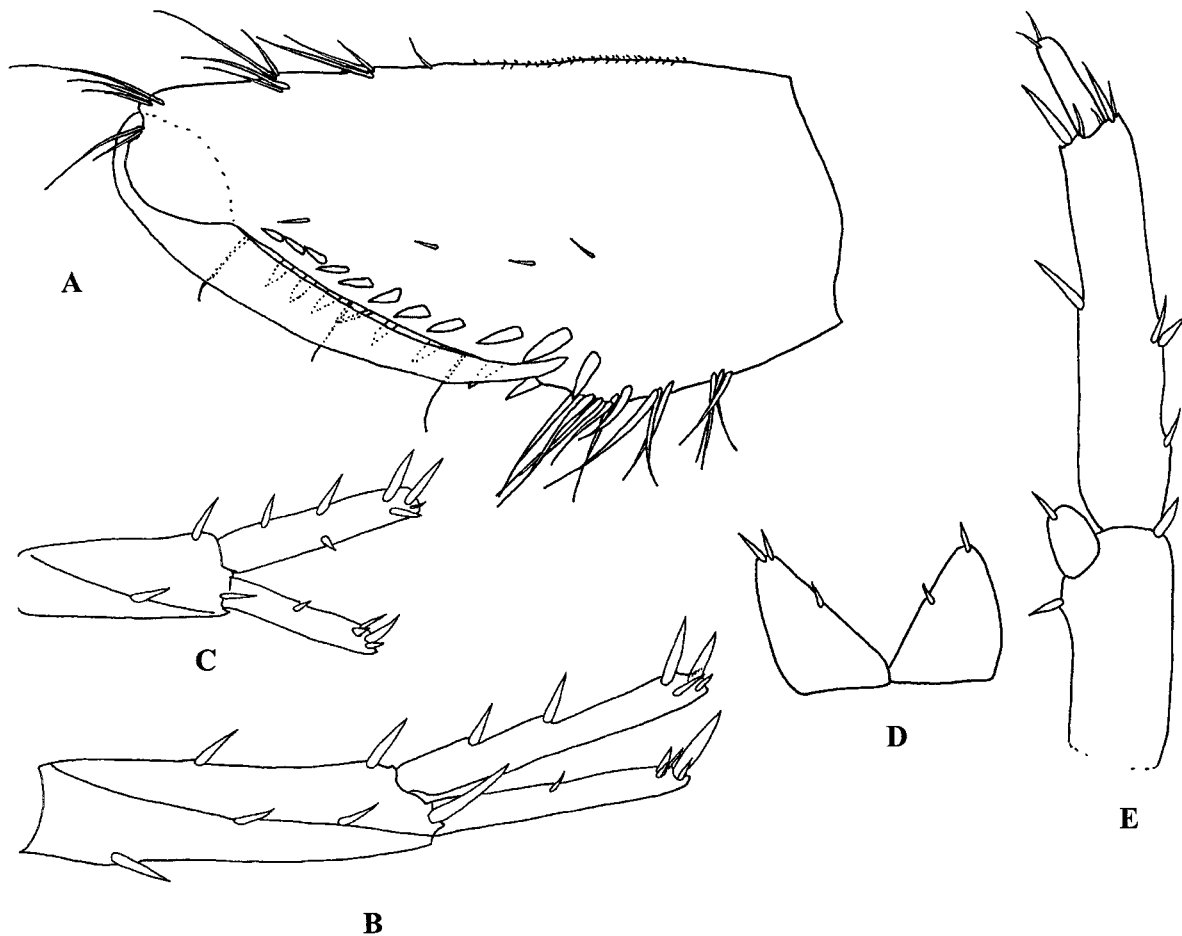


Fig. 19. *Melita almagosa* n. sp., paratypes, Almagosa Springs, Guam. Female (3.2 mm): B, uropod 1; C, uropod 2; D, telson; E, uropod 3. Male (4.2 mm): A, propod and dactyl of gnathopod 2.

pereopods 5–7 bases weakly expanded, distoposterior lobes weakly developed; dactyls of pereopods 5, 6 and 7, respectively 27%, 30% and 28% length of corresponding propods. Coxal gills on pereopods 2–6 subovate, with distinct peduncles; broodplates sublinear, slightly larger than corresponding gills.

Pleonal plates, distoposterior margins each with weakly developed tooth-like extension, without ventral spines. Pleopods normal, each bearing 2 coupling spines. Urosomites not fused, without dorsal spines or teeth. Uropod 1: outer ramus 63% length of inner ramus, bearing 1 apical and 5 apical spines; inner ramus 87% length of peduncle, with 4 apical and 2 lateral spines; peduncle with 6 spines, 1 basofacial. Uropod 2: outer ramus 71% length of inner, with 1 lateral and 4 apical spines; inner ramus subequal in length to peduncle, with 3 lateral and 4 apical spines; peduncle bearing 3 spines. Uropod 3: 20% length of body, inner ramus small, scale-like, with small apical seta; outer ramus 2-segmented, first segment weakly armed with only 4 lateral and 5 apical spines, second segment reduced, bearing 2 apical spines. Telson short, wider than long, cleft to base; lobes narrowing distally, each bearing 1 spine on inner margin and 1–2 spines apically.

Male.—Differing from female as follows: Gnathopod 2: dactyl and propod proportionately longer and broader;

propod palm long, oblique, bearing double row of 10 spines, defining angle with 3 spines and numerous long setae, anterior margin of propod weakly pubescent. Coxa of pereopod 6 normal, without spines or serrations.

Etymology.—The epithet *almagosa* denotes the presence of this species in Almagosa Springs, on the island of Guam.

Type-locality.—This species is known only from Almagosa Springs, the freshwater resurgence of an aquifer, which is developed in a restricted exposure of Miocene-aged Alifan limestone (Myroie *et al.*, 2001), in the southern part of Guam (Fig. 23). According to Adam Asquith (pers. comm.), the type series of 25 (+) specimens, some ovigerous females, was collected from tangled root mats and vegetation at the spring mouth. The amphipods were found within a few centimeters of the direct outflow from a hole or crack.

DISCUSSION

With the description of three new species and the synonymy of the genus *Sriha*, there are now five species assigned to the genus *Tegano*. These species have an Indo-Pacific distribution (Fig. 20). Barnard and Karaman (1982) defined *Tegano* on the basis of a single species, *Melita seticornis*, and the genus was said to differ from *Melita* primarily because of the reduction of the mandibular palp. Stock (1988) noted

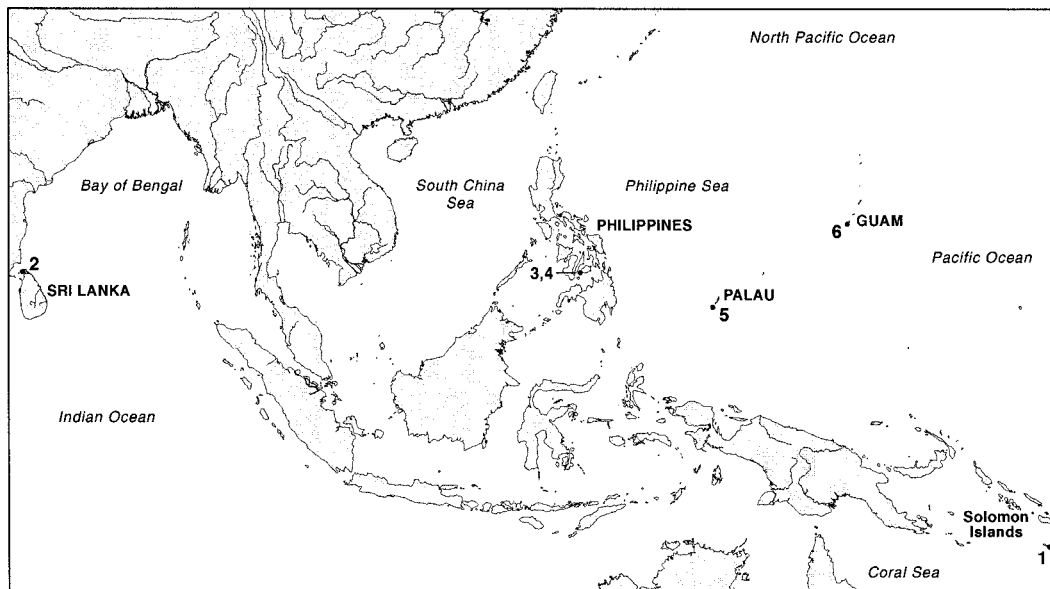


Fig. 20. Geographic distribution of species of *Tegano* and *Melita almagosa*. Solid circles indicate known localities as follows: 1) Rennell Island, Solomon Islands, *T. seticornis*; 2) Sri Lanka, *T. vagabunda*; 3) Panglao Island, Bohol, Philippines, *T. clavatus* (see Fig. 21); 4) Panglao Island, Bohol, Philippines, *T. panglaoensis* (see Fig. 21); 5) Peleliu Island, Palau, *T. barnardi* (see Fig. 22); 6) Guam, *M. almagosa* (see Fig. 23).

that there were four hadzioid genera—*Sriha*, *Fiha*, *Psamoniphargus*, and *Phreatomelita*—in which the mandibular palp was either strongly vestigial (reduced to 1-segment) or absent. *Sriha* was differentiated from these genera by the presence of inner lobes on the lower lips (Stock, 1988). *Tegano seticornis* was excluded from this list because it has a 2-segmented mandibular palp.

Tegano clavatus and *T. panglaoensis* were collected from caves on the small island of Panglao, just off the south coast of Bohol, Philippines, and these species share a number of characters with *T. seticornis* and *T. vagabundus*. Most notably these characters include a lobate extension at the defining angle of the palm on gnathopod 1, inner lobes on the lower lip, and similarly shaped telsons. The third segment of the mandibular palp of *T. clavatus* is greatly reduced and the mandibular palp is absent from *T. panglaoensis*. *Tegano barnardi* from Palau has intraspecific variation in the number of segments found in the mandibular palp and shares the characters noted for the palm of gnathopod 1, inner lobes on lower lip, and similarly shaped telson. These shared characters strongly suggest a common ancestry. The amount of variation found intragenerically and intraspecifically in the mandibular palp of *Tegano* species strongly argues against using the character as the primary factor in determining generic status for melitid amphipods. It is noteworthy in the original description that Karaman (1984) noted the morphological similarity between *T. seticornis* and *T. vagabundus*, which we have strongly affirmed in the present study.

Barnard and Barnard (1983) suggested that *Melita* is ancestral to the anchialine genus *Tegano*. A number of characters, most notably the strong reduction of the inner ramus of uropod 3 and sexually dimorphic pereopod 6 coxa (e.g., *T. panglaoensis*) strongly support this hypothesis. The genus *Melita*, which is predominantly marine, is almost cosmopolitan in distribution and inhabits both circum-

tropical and temperate waters (Barnard and Barnard, 1983). The distribution of *Melita* throughout the tropical Indo-Pacific region also puts this genus in a geographic position that supports the idea of an ancestral relationship to *Tegano*.

Karaman (1981) noted two groups of species in *Melita*: 1) those without a dorsal oblique row of setae on the inner lobe of maxilla 2, and 2) those usually lacking a second segment on the outer ramus of uropod 3. The genus *Abludomelita* was erected by Karaman (1981) for those species lacking a dorsal oblique row of setae on the inner lobe of maxilla 2 and lacking a second segment on the outer ramus of uropod 3. However, Zeidler (1989) noted a number of inconsistencies with these character states and pointed out that some species exhibit a combination of these characters. He suggested that the setation of maxilla 2 in *Melita* is not well known for all species in the genus and that the second segment of uropod 3 cannot often be easily distinguished from surrounding spines. Jarrett and Bousfield (1996) also noted inconsistencies with these characters. *Melita almagosa* exhibits characters intermediate between the two genera. It lacks a dorsal oblique row of setae on the inner lobe of maxilla 2 and has a second segment on the outer ramus of uropod 3. Zeidler (1989) concluded that a more detailed analysis of the genera *Melita* and *Abludomelita* was necessary before any final conclusions can be reached on the splitting of the genus *Melita*. The intermediate characters of *M. almagosa* strengthen the argument that the genera may be synonyms.

The description of *Melita almagosa* and the synonymy of *Paraniphargus* bring the total number of *Melita* species to at least 78 and the number of species of *Melita* reported from subterranean habitats to seven. The number of species of *Melita* from freshwater habitats is now approximately eight, but all of them are found near coastal areas. The pattern of marine ancestors invading anchialine habitats and later stranding in freshwater caves has apparently occurred many

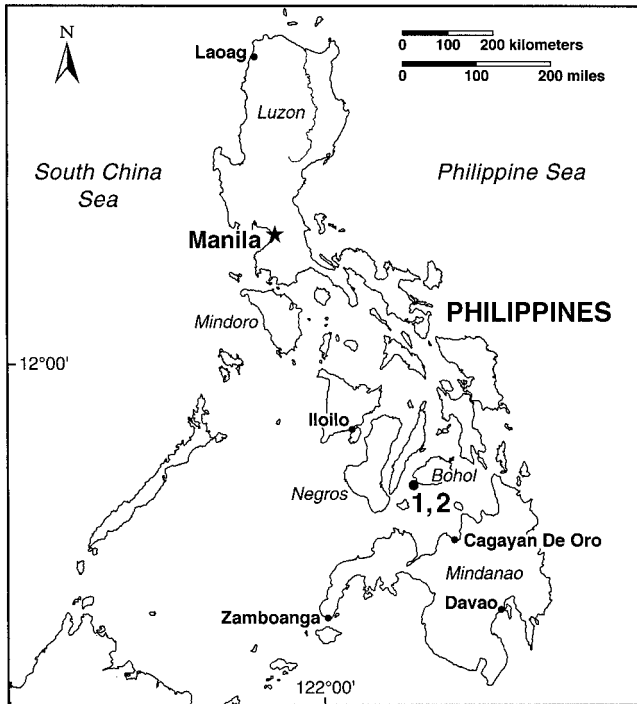


Fig. 21. Geographic distribution of *Tegno clavatus* (1) and *T. panglaoensis* (2) on Panglao Island, Bohol, Philippines. Solid circle denotes only known locality inhabited by both species.

times in closely related hadzioid amphipods (Holsinger and Longley, 1980; Stock, 1980; Holsinger, 1986; Holsinger 1994). Given the numerous examples of stranding among the hadzioids and the affinity of certain species of *Melita* for anchialine habitats, their invasion and colonization of subterranean freshwater caves is not surprising.

The genus *Josephosella* was defined by Ruffo (1985) on the basis of a single species found in beach sand interstices on South Andaman Island in the Indian Ocean. Stock (1988) described a second species of the genus, *J. hamata*, from a cave on Tongatapu, Tonga Islands, in the south Pacific. Stock noted synapomorphies of species of *Josephosella* and *Melita*, notably sexual dimorphism in coxal plate 6, but he suggested that the genera differed in too many other character states that made determination of the phylogenetic significance of this synapomorphic character difficult. More recently Stock and Iliffe (1995) described three more species of *Josephosella* and the related genus *Caledopisa* from caves in New Caledonia. Our present study suggests that a great deal of morphological similarity exists between species of *Melita* and *Josephosella*, including sexual dimorphism of coxal plate 6 and reduction of the inner ramus of uropod 3. These strong similarities suggest a sister group relationship of these genera and perhaps after further study even the need to synonymize them.

The genus *Melita* is widespread throughout the south and west Pacific, and species in the morphologically closely related genera *Tegno* and *Josephosella* are commonly found in insular caves of the region. The fact that most of these species have small eyes and are only weakly troglomorphic, combined with their presence in caves that

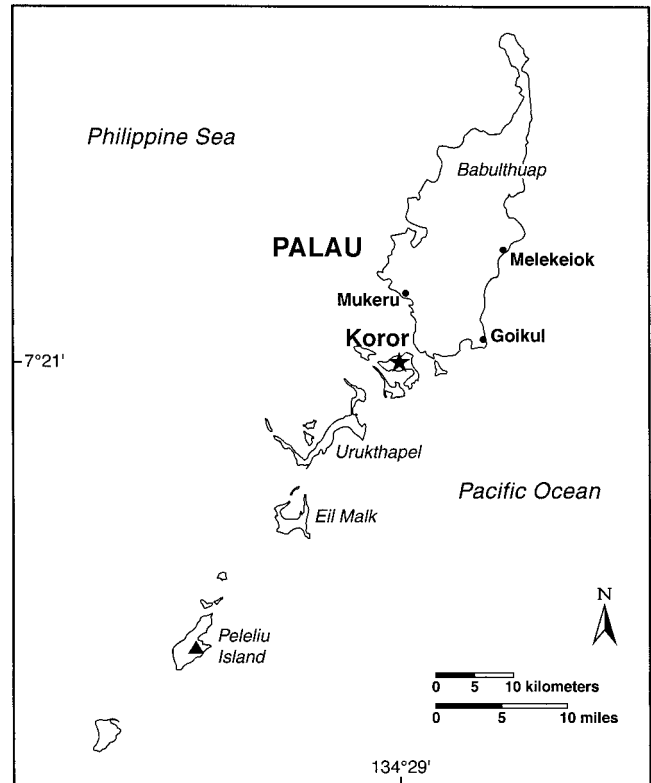


Fig. 22. Geographic distribution of *Tegno barnardi* on Peleliu Island, Palau. Solid triangle denotes only known locality.

are formed in limestones of late Tertiary and/or Quaternary age, suggest recent invasion and colonization of subterranean habitats, possibly influenced by changing sea levels in the Pleistocene.

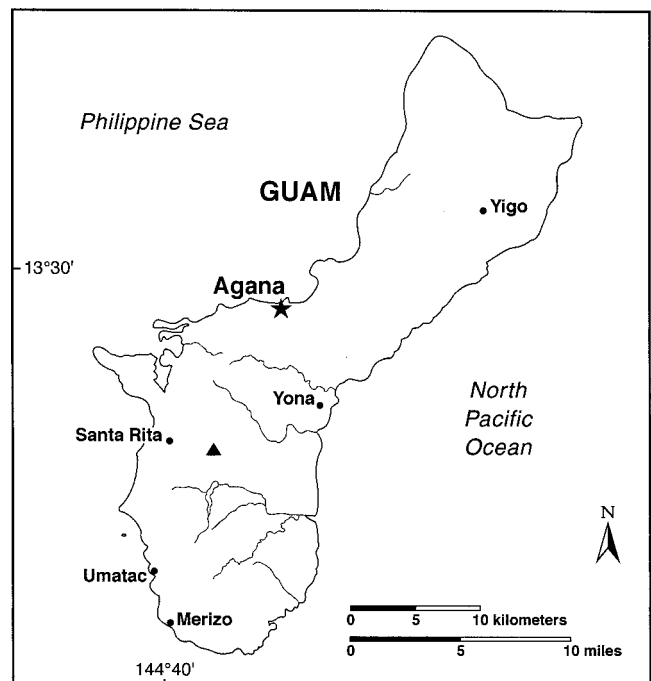


Fig. 23. Geographic distribution of *Melita almagosa* on Guam. Solid triangle denotes approximate location of only known locality.

A great deal of morphological variation is noted among the Pacific melitid amphipods, and determining the generic status of these widely dispersed, isolated species can be difficult. Phylogenetic studies based on morphological characters would be problematic at best because of the extreme amount of variation that develops in some characters from isolation. This, combined with what often appears to be convergence through similar selection pressures that characterize subterranean habitats, further complicates these studies. A molecular study, combined with knowledge of both interspecific and intraspecific variation should prove very useful in sorting out the phylogenetic relationship of *Melita*, *Abludomelita*, *Josephosella*, and other melitid genera.

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