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Comparative Systematics of Subterranean Amphipod Crustaceans (Hadzioidea)

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COMPARATIVE SYSTEMATICS OF SUBTERRANEAN AMPHIPOD CRUSTACEANS (HADZIOIDEA)

by

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B.S. May 1998, Eastern Connecticut State University (Willimantic, Connecticut)

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ABSTRACT

COMPARATIVE SYSTEMATICS OF SUBTERRANEAN AMPHIPOD CRUSTACEANS (HADZIIDAE)

Thomas R. Sawicki
Old Dominion University, 2004
Director: Dr. John R. Holsinger

The research project presented in this doctoral dissertation is a compilation of six published papers. Therefore, instead of being a single comprehensive project, it is composed of a number of sub-projects. Introductory and summary sections provide structure for the compilation of papers.

The research for this dissertation investigates the systematics of genera within the amphipod families Hadziidae Karaman, 1943 and Melitidae Bousfield, 1973. In the family Hadziidae, *Bahadzia patilarga* is described from an anchialine cave on the southern coast of Cuba, *B. caymanensis* is described from a weakly brackish-water pool in a small cave on Grand Cayman Island in the Cayman Islands, *B. yagerae* is thoroughly redescribed, and a phylogenetic analysis of *Bahadzia* and a number of outgroup genera is performed.

Two new genera, *Paraholsingerius* and *Tamaweckelia* and two new species, *P. mexicanus* and *T. apalpa* are desribed from caves in eastern Coahuila and southern Tamaulipas, Mexico respectively. *Holsingerius smaragdinus* previously known from a single cave in Val Verde Co., Texas, is elevated to the new genus *Paraholsingerius* and a second population of *P. smaragdinus* is recorded from northern Coahuila, Mexico. A new record for *Paramexiweckelia* from a cave in north-central Coahuila is documented.

Four new stygobitic species of *Hadzia* are described from subterranean waters in the Philippines, Palau and Guam. *Liagoceradocus* is synonymized with *Hadzia* and an updated diagnosis for the latter is provided.

In the family Melitidae three new species of *Tegano* are described, two from Panglao Island, Bohol, Philippines and one from Peleliu Island, Palau. *Tegano* is synonymized with *Sriha*. A new species of *Melita* is described that has characters intermediate between those used to define the genera *Abludomelita*, *Melita* and *Paraniphargus*. Based on this new species and studies by previous authors, it is suggested that *Abludomelita* may need to be synonymized with *Melita*. The genus *Paraniphargus* is synonymized with *Melita*.

Flagitopisa philippensis is redescribed based on collections made from various localities throughout the Philippines. Paratypes of *Psammogammarus fluviatilis* also from the Philippines were examined and in both this species and *F. philippensis*, a new structure was described, which consists of a weakly stalked, subovate coxal-like gill attached to the ventral surface of the first pleonite, just anterior to pleopod 1. Based on this unique character, *P. fluviatilis* is reassigned *Flagitopisa*.

This thesis is dedicated to my niece Bayleigh and my nephew Jack; may they grow up in a world enlightened by inquiry, not darkened by ignorance.

ACKNOWLEDGMENTS

I would like to thank my major advisor, Dr. John R. Holsinger, for his assistance, patience and support and for being second author on the papers presented in Sections 2-7. I am also grateful to my graduate committee members, Drs. Kent E. Carpenter and Michael F. Gable, for their input, support and encouragement over the years.

I would like to acknowledge the Graphic Office at Old Dominion University for generating numerous maps, slides, posters, etc., during the entire project and Tamara Connolly for her help with many of the figures. I would also like to acknowledge numerous people who assisted with the individual sub-projects:

I thank Jeff Bozanic, Jill Yager and the Biokarst Association of Cuba for assistance with collecting specimens of *Bahadzia patilarga* and *B. yagarae*. I am grateful to Jerry H. Carpenter for providing specimens of *B. caymanensis* from Grand Cayman Island. Thanks to James Brown, Dean A. Hendrickson, Thomas M. Iliffe, Jean Krejca, James R. Reddell, Charlie Savvas and Peter Sprouse for collecting and or making available to us specimens from caves in Mexico. We also thank T. M. Iliffe and J. R. Reddell for contributing additional useful information on the collecting sites. I would like to thank Thomas M. Iliffe, Yolanda Iliffe, Jeff Bozanic, Boris Sket and the late Dennis Williams for the collection of numerous specimens throughout Palau, Guam and the Philippines. Dr. William Hammer, Dr. John Maciolek, Toshiro Paulis and Francis Tubarong for providing invaluable information about the islands of Palau and their caves

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SECTION 1

INTRODUCTION

The crustacean order Amphipoda, represented by approximately 7,000 described species, is the most abundant member of the superorder Pericarida (Bousfield 1982). Amphipod crustaceans inhabit freshwater, brackish, marine and occasionally even terrestrial environments. The worldwide distribution and taxonomic diversity of the Amphipoda may be unparalleled among all crustacean groups. Amphipods have been recorded from shallow tropical shores to the benthos of arctic seas, from cold mountain trickles up to 2,500 m elevation to desert thermal springs. The order Amphipoda is divided into three and sometimes four suborders. With more than 5700 species, Gammaridea is the largest, most taxonomically and ecologically diverse of these suborders (Barnard and Karaman 1991).

Approximately 13% of all described species in the suborder Gammaridea occur in subterranean environments. The number of gammaridean amphipod species inhabiting subterranean environments is remarkable, possibly making it the most abundant and taxonomically diverse invertebrate group that commonly occurs in subterranean aquatic habitats (Holsinger, 1993, 1994a). Approximately 20% of the subterranean species inhabit brackish and/or marine waters and 80% freshwater habitats (Holsinger 1993). Most subterranean amphipod species are stygobites (or stygobionts), which are obligatory to hypogean groundwater habitats. Stygobites are characterized by troglomorphisms, including the loss or drastic reduction of pigmentation and eyes. Other troglomorphic

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The model journal used to format this dissertation was Journal of Crustacean Biology.

characteristics include attenuation of the body and elongation of appendages.

FAMILY HADZIIDAE

Hadziid amphipods are predominately marine with a distribution that is largely circumtropical. Species within this family are largely stygobitic, often living in anchialine and sometimes-freshwater caves (Barnard and Barnard 1983). The distribution of hadziid amphipods is largely circumtropical (Holsinger 1994a).

Of the approximately 26 genera currently described assigned to family Hadziidae, 10 are monotypic. Another five genera have only two species. To date there are approximately 70-75 species within the family Hadziidae. Many hadziid amphipods are found in anchialine caves on islands and the high degree of endemism inherent to organisms living on islands is only increased by the fact that hadziids also live in caves. Combine these facts with the low dispersal rates of amphipod crustaceans that brood their young, and have no dispersal stage, and the large numbers of monotypic genera is not surprising. As a result of this study two new hadziid genera *Tamaweckelia* and *Paraholsingerius* are erected, the genus *Holsingerius* is redefined, the genera *Liagoceradocus* and *Hadzia* are synonymized, eight new species are described and *Bahdzia yagerae* is thoroughly redescribed. A phylogenetic analysis of the hadziid genus *Bahadzia* along with seven other hadziid genera was performed.

MELITA

The genus *Melita* is cosmopolitan, and very common in shallow waters of the West

Pacific. Numerous stygobitic species have been described in recent years that appear to have been derived from a *Melita*-like progenitor. This has resulted in the description of a number of new genera, which are often based on a specific degree of reduction in the mandibular palp. For example, the genus *Tegano* was described by Barnard and Karaman (1982). and was established on the basis of a single species, *Melita seticornis*, which is characterized by a reduction of the third segment of the mandibular palp. Other melitid-like genera that have been described on the basis of a varied reduction of the palp include, *Sriha*, *Fiha*, *Pasmmoniphargus* and *Phreatomelita* (Stock 1988).

For this study a careful examination of these genera was conducted. The description of three new *Tegano* species, two of which are from a single, small island in the Philippines, has resulted in the discovery of synapomorphies that link the genera *Tegano* and *Sriha*. The description of three new species of *Tegano* and the synonymy of *Tegano* and *Sriha*, brings the number of species within the genus to five. This study also demonstrates a high degree of variation in the reduction of the mandibular palp, both interspecifically and intraspecifically, within the genus *Tegano* and strongly argues against using the character as the primary factor in determining generic status for melitids. A new stygobitic species of *Melita* is described from a freshwater cave on Guam. This species possesses characters intermediate between the genera *Abludomelita*, *Melita* and *Paraniphargus*. The description of this species brings the number of stygobitic species in the genus *Melita* to approximately six. The genus *Paraniphargus* is synonymized with *Melita*, and the taxonomic status of *Abludomelita* and *Melita* is discussed.

SECTION 2

BAHADZIA PATILARGA, A NEW SPECIES OF SUBTERRANEAN AMPHIPOD CRUSTACEAN (HADZIIDAE) FROM CUBA

Since the initial description of the genus *Bahadzia* by Holsinger (in Holsinger & Yager 1985) on the basis of two stygobitic species from anchialine caves in the Bahamas and Turks and Caicos, seven more species have been described. These species are found in the Bahamas, Turks and Caicos, Cuba, Hispaniola and on the Yucatan Peninsula. To date, the only species of *Bahadzia* described from Cuba is *B. yagerae* (Ortiz and Pérez 1995). The present paper describes a second species of *Bahadzia* from the southern coast of Cuba. Although both this new species and *B. yagerae* exist in caves approximately 17 km apart, and both have eye spots, they are otherwise morphologically distinct. The following description raises the number of species in the genus to ten.

SYSTEMATICS

Family Hadziidae Karaman, 1943

Genus *Bahadzia* Holsinger, 1985 (in Holsinger & Yager, 1985)

Bahadzia patilarga n. sp.

Figs. 2.1-2.4

Material examined.—CUBA. Metanzas Province: Cueva de los Carboneros, Playa Girón, holotype ♀ (4 mm), A. Pérez, 11 June 1998; 2 paratypes (♀ and juvenile), J. Yager, 14 September, 1992, and 2 paratypes (♂ and ♀), J. Bozanic, 15 September 1992.

The holotype is deposited in the crustacean collection of the Center of Marine

Research, University of Havana, Cuba (No. 178). The paratypes are in the collection of John R. Holsinger (H-3242, H-3249).

Diagnosis.—Small to medium sized stygobitic species easily distinguished from other members of the genus except *Bahadzia yagerae* Ortiz and Pérez 1995 by having a tiny, round, pigmentless eye, but differing from *B. yagerae* by having proportionately longer pereopods 6 and 7. Further distinguished from all other species within the genus by possessing a much shorter row of setae on the extreme inner margin of the inner plate of maxilla 2 and fewer setae on anterior margin of the propod of gnathopod 2 of the female. Largest male 6.0 mm; largest female 6.5 mm.

Female.—Head with tiny round, pigmentless eye or eye spot. Antenna 1 approximately 40% longer than body and 2.25 times longer than antenna 2; primary flagellum with up to 39 segments, accessory flagellum 3-segmented, subequal in length to the first 3 primary flagellar segments; peduncular segments becoming progressively shorter distally. Antenna 2: flagellum with up to 14 segments; peduncular segment 4 approximately 15% longer than segment 5. Mandible: molar well developed; spine row with 2 modified tooth-like spines distally and about 10 weakly serrate spines; lacinia mobilis of left mandible 4 dentate, that of right 3 dentate and smaller; incisor of left mandible 5 dentate, that of right 4 dentate and narrower; palp segment 3 as long as combined lengths of 1 and 2, bearing 1 long A seta, long row of approximately 13 D setae and 3-4 apical E setae. Lower lip: inner lobes distinct; lateral processes short, rounded apically. Maxilla 1: inner plate with 15 short, lightly plumose setae; outer plate bearing 9 pectinate spines; left and right palps similar, expanded and rounded distally, broad apex with 11 bladespines and single short, naked setae. Maxilla 2: inner plate narrowing distally, with row of approximately 45 naked submarginal facial setae and row of approximately 5 thicker setae located distally on extreme inner margin. Maxilliped: apex of inner plate even, armed on inner half with 4-5 short spines and a few short setae, inner margin with row of 10 weakly plumose setae; outer plate broader than inner with row of naked setae on inner margin and distally; palp segment 3 pubescent distally, distal inner margin of segment 3 slightly lobate; palp segment 4 almost as long as segment 3, nail small and spine-like.

Gnathopod 1: propod subrectangular about twice as long as broad, posterior margin heavily setose distally, palm short, transverse but lobate at defining angle and bearing 3 spines on lobe; carpus approximately 2 times as long as propod, bearing several clusters of long setae toward distal end; merus weakly lobiform and pubescent; basis with 7 long setae on posterior margin; coxa long and deep with about 9 short setae and 3 short spines. Gnathopod 2: propod subrectangular, palm short, oblique bearing short setae and 3 long setae at defining angle, posterior margin with 4 sets of long setae, anterior margin with a few setae, not in clusters; carpus approximately 28% longer than propod, posterior margin with 9 clusters of long setae; basis with 5 long setae; coxa deeper than broad, margin with about 6 setae and 4 short spines. Pereopod 3: coxa relatively small, deeper than broad, margin with 3 short setae. Pereopod 4: coxa broadly expanded distally and excavate posteriorly, margin with 13 short setae. Pereopod 6 approximately 5% longer than body, approximately 7% longer than pereopod 7 and 90% longer than pereopod 5. Pereopods 5-7: basis relatively narrow, with rather large, bluntly rounded distoposterior lobes. Dactyl of pereopod 5 approximately 50% length of corresponding propod; dactyls of pereopods 6 and 7 respectively, approximately 30% and 13% of corresponding propods. Coxal gills on 2-6 subovate, with short peduncle, very large on pereopods 2-4.

Brood plates sublinear, small relative to gills.

Pleonal plates: posterior margins with 1 setule each, posterior corners small but distinct; ventral margin of plate 1 without spines, plates 2 and 3 with 1 spine. Pleopods normal, coupling spines rather long. Uropod 1: inner ramus shorter than peduncle, longer than outer ramus, bearing about 5 spines; peduncle with 12 spines, 1 of which is basofacial in position. Uropod 2: inner ramus approximately 15% longer than peduncle, longer and broader than outer ramus, armed with 13 spines; outer ramus with about 6 spines; peduncle with 9 spines 4 of which form a comb row on dorsodistal end. Uropod 3 approximately 23% length of body; inner ramus slightly longer and broader than outer ramus, margins with short spines and plumose setae; outer ramus with short terminal segment, inner margin with plumose setae and a few spines, outer margin with spines only; peduncle without spines. Telson rather long and narrow, in two separate lobes; lateral margins with about 5 spines each, none in sets of two; medial margins with 3-4 small spines each; apices with 1-2 short spines and 3 long, distally plumose setae.

Male.—Differing from female as follows: maxilla 1 inner plate with 7 short, weakly plumose setae; palp of maxilla 1 with 12 bladespines and without short naked setae. Gnathopod 2: dactyl and propod proportionately longer; propod palm long, oblique with double row of about 9 blunt tipped spines; defining angle with 3 long setae; posterior margin longer than palm, with 4 sets of setae. Distal margin of peduncle of uropod 3 with 2 spines.

Etymology.—The word "patilarga" is Spanish vernacular commonly used in Latin American countries to describe legs that are larger than normal. It is used here as a noun in apposition alluding to the extremely long pereopods 6 and 7 of the species.

Remarks.—Bahadzia patilarga was informally referred to as "cubensis" in an article written for a general SCUBA diving magazine and was not intended to be a formal taxonomic publication. Therefore the name "cubensis" is unavailable and invalid and should not be considered a synonym or *nomen nudum*.

Type-locality.—This species is known only from the type-locality, Cueva de los Carboneros.

DISCUSSION

Bahadzia patilarga is recorded to date from a single anchialine cave, Cueva de los Carboneros, which is located in Playa Giron on the southern coast of Cuba in Matanzas Province. Playa Giron is commonly known in America as the Bay of Pigs. Collection of *B. patilarga* was made at or near the halocline, where it occurs sympatrically with remiped and thermosbaenacean crustaceans. This association with remipeds and thermosbaenaceans and its specific microhabitat defined as being near or within the halocline of anchialine caves is very common, although not ubiquitous, for this genus. Based on research in caves of the Yucatan Peninsula, Pohlman et al. (1997) noted that these crustacean taxa might be utilizing a chemoautotrophic energy source existing near the halocline. They suggested that a similar phenomenon may occur in anchialine caves throughout the Caribbean and southern Atlantic, where organisms such as *Bahadzia* exist. Pohlman et al. (1997) noted a dramatic drop in oxygen concentration precisely at the halocline, where they surmised that chemoautotrophism was occurring. Although no field data are available for the oxygen concentration at the halocline in the type locality for *B. patilarga*, it is interesting to note that, as with many (but not all) species of *Bahadzia*, *B. patilarga* has extremely large gills. Enlarged gills may be an adaptation for living in low oxygen environments.

Based on a track synthesis, Holsinger (1989, 1992) predicted the occurrence of *Bahadzia* in Cuba. The description of *Bahadzia patilarga* above brings the number of species so far discovered on the island to two. Both species exist in single caves a mere 17 km apart. Recent explorations by one of us (TRS) resulted in the discovery of a remiped crustacean in a cave on the northern coast of Cuba, also in Matanzas Province. Based on this discovery and the fact that remipeds and *Bahadzia* are often found living sympatrically, it is predicted that additional populations of *Bahadzia*, quite possibly representing new species, will be found in caves on the northern coast of Cuba.

SECTION 3

SYSTEMATICS OF THE SUBTERRANEAN AMPHIPOD GENUS *BAHADZIA* (HADZIIDAE), WITH DESCRIPTION OF A NEW SPECIES, REDESCRIPTION OF *B. YAGERAE*, AND ANALYSIS OF PHYLOGENY AND BIOGEOGRAPHY

The genus *Bahadzia*, first described by Holsinger (in Holsinger and Yager, 1985), is of stygomorphic facies and occurs primarily in anchialine caves. Exploration of caves throughout the Bahamas, Turks and Caicos Islands, Hispaniola, Cuba and the Yucatan Peninsula in Mexico has resulted in the description of ten species of *Bahadzia*. The description below raises the number of species in the genus to 11 and extends the range of the genus to the Cayman Islands. *Bahadzia yagerae*, first described by Ortiz and Pérez (1995) on the basis of two female specimens, is thoroughly redescribed including the description of a mature male specimen.

The phylogeny and biogeography of *Bahadzia* is examined cladistically using a morphological data set. This study expands on the phylogenetic analysis performed by Holsinger (1992) and more than doubles the number of characters examined in that study. The phylogenetic relationship of *Bahadzia* to other hadziid and melitid genera is also examined in the present analysis.

SYSTEMATICS

Family Hadziidae Karaman, 1943

Genus *Bahadzia* Holsinger, 1985 (in Holsinger and Yager 1985)

Bahadzia caymanensis n. sp.

Figs. 3.1-3.5

Material examined.—CAYMAN ISLANDS. Grand Cayman Island: West Bay Cave, holotype ♀ (5.0 mm), 27 paratypes, J.H. Carpenter, 8 January 1997.

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 1006978); paratypes are in the collection of J. R. Holsinger (H-3667).

Diagnosis. Small to medium sized stygobitic species that can easily be distinguished from other members of the genus, except *Bahadzia yagerae* Ortiz and Pérez and *B. patilarga* Sawicki *et al.* (Sawicki *et al.*, 2003) by having a tiny, round, pigmentless eye. The new species differs from *B. yagerae* by having proportionately longer pereopods 6 and 7, and from *B. patilarga* by having proportionately shorter pereopods 6 and 7 and shorter antenna 1. Further distinguished from all other species in the genus by possession of two-segemented accessory flagellum on antenna 1. Largest males, 4.5 mm; largest female, 6.5 mm.

Female.—Head with tiny round, pigmentless eye or eye spot. Antenna 1 approximately 75% length of body and approximately 2 times longer than antenna 2; primary flagellum with up to 24 segments, accessory flagellum two-segmented, subequal in length to the first two primary flagellar segments; peduncular segments becoming progressively shorter distally. Antenna 2: flagellum with up to ten segments; peduncular segment 4 subequal in length to segment 5. Mandible: molar well developed; spine row with about 13 weakly serrate spines; lacinia mobilis of left mandible four-dentate, that of right two-dentate and smaller; incisors of left and right mandibles six-dentate; palp segment 3 approximately 20% shorter than combined lengths of 1 and 2, bearing one long A seta, long row of approximately nine to ten comparatively short D setae and three to four E setae; B and C setae absent. Lower lip: inner lobes poorly developed or vestigial; lateral processes short, rounded apically. Maxilla 1: inner plate with 18 short, lightly plumose setae; outer plate bearing nine pectinate spines; left and right palps similar, expanded and rounded distally, broad apex with eight bladespines and two short, naked setae. Maxilla 2: inner plate narrowing distally, with row of approximately 42 naked submarginal facial setae and row of approximately 14 thicker setae located on extreme inner margin. Maxilliped: apex of inner plate even, armed on inner half with five to six short spines, inner margin with row of 11 weakly plumose setae; outer plate rounded distally, armed with single short spine and numerous setae on distal margin; palp segment 3 pubescent distally, distal inner margin of segment 3 not lobate; palp segment 4 as long as segment 3, nail small and spine-like.

Gnathopod 1: propod subrectangular about twice as long as broad, posterior margin setose distally, palm short, transverse but lobate at defining angle and bearing four spines on lobe; carpus approximately 40% longer than propod, bearing several clusters of long setae on posterior margin and toward distal end; merus weakly lobiform distally and pubescent; basis with nine long setae on posterior margin; coxa long with about three to four short spines and 11-12 short setae. Gnathopod 2: propod subrectangular about twice longer than propod of gnathopod 1, palm short, oblique, bearing one short spine and two long setae at defining angle, posterior margin with five sets of long setae, anterior margin with five sets of one or two setae; carpus subequal in length to propod, posterior margin with seven clusters of long setae; basis with five long setae on posterior margin; coxa longer than broad, margin with about three to four short spines and seven to eight short setae. Pereopod 3: coxa relatively small, deeper than broad, margin with three short setae. Pereopod 4: coxa broadly expanded distally and excavate posteriorly, margin with 15 short setae. Pereopod 6 approximately 80% length of body, approximately 25% longer than pereopod 7 and approximately 35% longer than pereopod 5. Pereopods 5-7: basis relatively narrow, with rather large, bluntly rounded distoposterior lobes. Dactyl of pereopod 5 approximately 30% length of corresponding propod; dactyls of pereopods 6 and 7 respectively, approximately 33% and 26% length of corresponding propods. Coxal gills on pereopods 2-6 subovate, with short peduncle, very large on pereopods 2-4. Brood plates sublinear, small relative to gills.

Pleonal plates: posterior margins with one setule each, posterior corners small but distinct, ventral margin of plate 1 without spines, plate 2 with one spine, plate 3 with two spines. Pleopods normal, two rather long coupling spines on peduncle. Uropod 1: inner ramus shorter than peduncle, longer than outer ramus, bearing about six spines; peduncle with 11 spines, one of which is basofacial in position. Uropod 2: inner ramus subequal to peduncle, longer and broader than outer ramus, armed with ten spines; outer ramus with about six spines; peduncle with nine spines, six forming a comb row on dorsodistal end. Uropod 3 approximately 13% length of body; inner ramus subequal in length to outer ramus, margins with short spines and plumose setae; outer ramus with short terminal segment, inner margin with plumose setae and a few spines, outer margin with spines only; peduncle with five spines. Telson rather long and narrow, in two separate lobes; lateral margins with about two to five small spines, none in sets of two; medial margins with two to three small spines, apices each with one or two short spines and three long, distally plumose setae.

Male.—Differing from female in structure of gnathopod 2 as follows: dactyl and propod proportionately longer; propod palm long, oblique, with double row of about six blunt-tipped spines, defining angle with two long and one short setae, posterior margin longer than palm, with four sets of setae.

Etymology.—This species is named for its occurrence on Grand Cayman Island.

Distributional ecology.—This species is known only from its type-locality, West Bay Cave. According to J. H. Carpenter (pers. comm.) the type-specimens were collected from a shallow, weakly-brackish pool in a small cave. Very little is known about the ecology of the type-locality for *B. caymanensis*, and it is unclear if the specimens were restricted to the weakly-brackish shallow water pool or washed out from a lower anchialine cave habitat.

Bahadzia yagerae Ortiz and Peréz, 1995

Figs. 3.6-3.8

Bahadzia yagerae Ortiz and Peréz, 1995: 166-168, Figs. 1-4 [type-locality: Cueva Susana, Playa Girón, Metanzas Province, Cuba].

Material examined.—CUBA. Metanzas Province: Cueva Susana, Playa Girón, 5 paratypes, J. Yager 27 June 1994, and 2 paratypes D. Williams, 11 September 1992.

Holotype (not examined in the present study) deposited in the collection of the Institute of Ecology and Systematics of the Department of Science, Technology and Environment, Cuba. The Paratypes are in the collection of J. R. Holsinger (H-3250, H-3792).

Diagnosis.—Small to medium sized stygobitic species, similar to *Bahadzia caymanensis* and *B. patilarga* by having a tiny, round, pigmentless eye, but differing from all other species of *Bahadzia* by possession of at least 50 pectinate spines on distal end of outer plate of maxilla 1.

Female.—Corresponding to the description of Ortiz and Peréz (1995) with the following additions and corrections. Mandible: molar well developed; spine row with about 11 weakly serrate spines; lacinia mobilis of left mandible four-dentate, that of right two-dentate and smaller; incisor of left mandible 5-dentate, that of right five-dentate and narrower; palp segment 3 subequal to the combined lengths of 1 and 2, bearing long row of approximately 22-23 D setae and three to four E setae; A, B, and C setae absent. Lower lip: inner lobes present and distinct; lateral processes short, rounded apically. Maxilla 1: inner plate with 17 short, lightly plumose setae: outer plate bearing at least 50 pectinate spines; left and right palps similar, expanded and rounded distally, broad apex with nine bladespines and one short, naked setae. Maxilla 2: inner plate narrowing distally, with row of approximately 48 naked submarginal facial seatae and row of approximately 17 thicker setae located on extreme inner margin. Maxilliped: apices of inner plate even, armed on entire distal end with approximately nine short spines, inner margin with row of 17 weakly plumose setae; outer plate rounded distally, armed with single short spine on distal margin and few naked setae; palp segment 3 pubescent distally, distal inner margin of segment 3 not lobate; palp segment 4 as long as segment 3, nail small and spine-like.

Gnathopod 1: propod subrectangular about twice as long as broad, posterior margin heavily setose distally, palm short, transverse but lobate at defining angle and bearing three spines on lobe; carpus approximately 80% longer than propod, bearing several clusters of long setae on posterior margin and toward distal end; merus weakly lobiform and pubescent; basis with 12 long setae; coxa long and deep with about three to four short spines and eight to niine short setae. Gnathopod 2: propod subrectangular, palm short, oblique, bearing three long setae at defining angle, posterior margin with six sets of long setae, anterior margin with three sets of setae; carpus approximately 20% longer than propod, posterior margin with nine clusters of long setae; basis with six long setae on posterior margin; coxa deeper than broad, margin with 12 short setae.

Pleopods normal, peduncles each with two rather large coupling spines, and one unmodified spine on distal inner margin. Uropod 1: inner ramus shorter than peduncle, longer than outer ramus bearing about five spines; peduncle with 13 spines, one of which is basofacial in position. Uropod 2: inner ramus subequal in length to peduncle, longer and broader than outer ramus, armed with 11 spines; outer ramus with about six spines; peduncle with 12 spines, eight of which form a comb row on dorsodistal end. Uropod 3: approximately 15% length of the body; inner ramus slightly larger than outer ramus, margins with short spines and plumose setae; outer ramus with short terminal segment, inner margin with short spines and plumose setae, outer margin with spines only; peduncle with six spines. Telson rather long and narrow, in two separate lobes; lateral margins with about six spines, none in sets of two; medial margins with two to four spines, apices each with one or two small spines and three long, distally plumose setae.

Male.—Differing from female in structure of gnathopod 2 as follows: dactyl and propod proportionately longer; propod palm long, oblique with double row of about 14 blunt tipped spines, defining angle with three long setae, posterior margin longer than palm with four sets of setae.

Distributional ecology.—This species is known only from its type-locality, Cueva Suzana, an anchialine cave on the southern coast of Cuba. Specimens were collected at or below the halocline from a depth of approximately 15 m in water with 35 ppt salinity.

Remarks.—In the original description by Ortiz and Pérez (1995), the holotype was said to be 1.5 cm in length, but this was an error inasmuch as both the drawing and description indicated the holotype to be only 5 mm (0.5 cm) in length. This error was inadvertently repeated by Jaume and Wagner (1998).

PHYLOGENETIC ANALYSIS

Cladistic Methods.—A phylogenetic analysis was performed using PAUP, version 4.0b10, in which all characters were left unordered and unweighted. During all searches the ancestral condition was left 'unknown.' Character states were not assigned relative to a primitive/derived condition, i.e., a character state of 0 does not necessarily reflect the primitive state. During the Bootstrap analysis, the following options were in effect: full heuristic search with 1000 bootstrap replicates, and 50% majority rule consensus; TBR branch swapping was performed on minimal trees only (steepest descent by random stepwise addition), Multrees option in effect. The resulting tree was evaluated and edited in MacClade Version 4.0.

Taxa.—The cladistic analysis was perfomed on the genus *Bahadzia*, and eight other outgroup genera within the Hadziidae/Melitidae family complex (Table 3.1). The choice of outgroups used was based on a number of different criteria. *Protohadzia* and *Saliweckelia* are fully marine genera within the family Hadziidae, living in shallow coastal waters in the Caribbean. *Metaniphargus* is found in the fresh water layer of an anchialine cave in Venezuela and in brackish water in anchialine caves throughout the greater Caribbean and in the intertidal zone from Oahu, Hawaii. These genera are potentially related to *Bahadzia*. Holsinger (1992) conducted a cladistic analysis on the genus *Bahadzia* and 13 genera of the "weckeliid group" in the family Hadziidae. This analysis suggested that two of the "weckeliid group" genera, *Mayweckelia* and *Tuluweckelia*, are sister genera to *Bahadzia* and may even be derived from a *Bahadzia*-like ancestor. *Mayaweckelia* and *Tuluweckelia* were included in the present analysis to further explore this relationship using a different and larger data set. *Melita stocki*

Table 3.1. Outgroup genera used for the cladistic analysis.

Outgroup Genera	Species examined
Metaniphargus	*jaimaicae, curasavicus*
Mayaweckelia	*yucatanensis, cenoticola*
Saliweckelia	*holsingeri, emarginata*
Protohadzia	*schoenerae*
Weckelia	*caeca*
Tuluweckelia	*cernua*
Paramexiweckelia	*particeps, ruffoi*
Melita	*stocki*

Karaman was included as a very generalized hadziid/melitid type.

With the exception of *Melita stocki, Protohadzia schoenerae* Zimmerman and Barnard, and the two species of *Saliweckelia*, whose character states were based on descriptions and drawings from the literature, all other species used in this analysis were examined from preserved material (see Appendix B for a list of the characters).

Table 3.2. Character matrix. See Appendix B for a description of characters. Characters are numbered according to their listing in Appendix B.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Metaniphargus	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0
Mayaweckelia	0	1	0	0	0	0	0	-	-	-	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	1	0
Saliweckelia	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1	1	0
Protohadzia	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0
Weckelia	0	1	0	0	1	0	0	-	-	-	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Tuluweckelia	0	1	0	0	0	0	0	-	-	-	1	0	1	0	1	1	0	0	0	0	1	0	0	1	0	1	0
Paramexiweckelia	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0
Melita stocki	0	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0
williamsi	0	1	0	0	1	0	1	1	1	1	0	0	1	1	1	0	1	0	0	1	1	1	0	0	1	1	0
stocki	0	1	0	0	1	0	1	1	1	1	0	0	1	1	1	0	1	0	0	0	1	1	1	1	1	1	0
setimana	0	1	1	0	1	0	1	1	0	0	0	0	1	0	1	0	1	1	0	0	1	1	1	1	1	1	0
obliqua	0	1	1	0	1	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	1	1	1	1	0
latipalpus	0	1	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0	1	?	0	1	1	1	1
bozanici	0	1	0	1	1	0	1	1	1	1	1	1	1	0	1	1	0	0	0	1	0	0	1	1	1	1	0
setodactylus	1	1	0	1	0	0	1	1	1	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	1	1	0
jaraguensis	1	1	1	1	0	0	1	0	1	1	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	1
yagerae	0	1	1	0	1	1	1	0	1	1	1	1	0	0	1	0	1	0	0	1	0	1	1	0	1	1	0
patilarga	1	1	1	1	0	1	1	1	0	1	1	1	0	0	1	0	1	0	1	1	0	0	0	0	1	1	0
caymenensis	0	0	0	1	1	1	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0

RESULTS

The phylogeny shown in Fig. 3.10 suggests that the genus *Bahadzia* may not be monophyletic, inasmuch as *B. latipalpus* Stock and *B. jaraguensis* Jaume and Wagner are in the same clade as the sister genera *Mayaweckelia* and *Tuluweckelia*. All other *Bahadzia* species are found within one clade, which in turn is divided into two groups: those species found in the Bahamas and Turks and Caicos Islands, and those found in Cuba, Mexico and the Cayman Islands. The Bahamian/Turks and Caicos clade is relatively well defined. *Bahadzia williamsi* Holsinger and *B. stocki* Holsinger form one pair of sister species, and *B. setimana* Stock and *B. oblique* Stock form another pair. The two Yucatan species *B. bozanici* Holsinger and *B. setodactylus* Holsinger do not form sister species and the two Cuban species *B. yagerae* and *B. patilarga* also do not fall out as sister species in the analysis. However, these four species and *B. caymanensis* collectively form a western Caribbean clade. The two species found on the island of Hispaniola, *B. latipalpus*, and *B. jaraguensis*, are sister species in this analysis and form a clade with the outgroup genera *Mayaweckelia* and *Tuluweckelia*.

DISCUSSION

Based on the geographic distribution of *Bahadzia*, most species of which are clustered in widespread insular habitats (Fig. 3.9), it could be hypothesized that the derived phylogeny would be highly predictable and resolved. The presently known species of *Bahadzia* are restricted to the Bahamas, Cuba, Hispaniola, Yucatan Peninsula (including Cozumel Island) and the Cayman Islands. With two exceptions, there appears to be a relationship between species distribution and phylogeny. The species found in the Bahamas/Turks and Caicos group together and the Hispaniola species group together. However, the species found in Cuba and the Yucatan Peninsula of Mexico do not form nested subgroups relative to their geographic distribution. Given the close geographic proximity of these species, this lack of resolution is surprising. For instance the type-localities of the two Cuban species, *B. patilarga* and *B. yagarae*, are separated by only 17 km. Although *B. latipalpus* and *B. jaraguensis* do form a nested subgroup relative to their distribution, they also form a clade with the outgroup genera *Mayaweckelia* and *Tuluweckelia*.

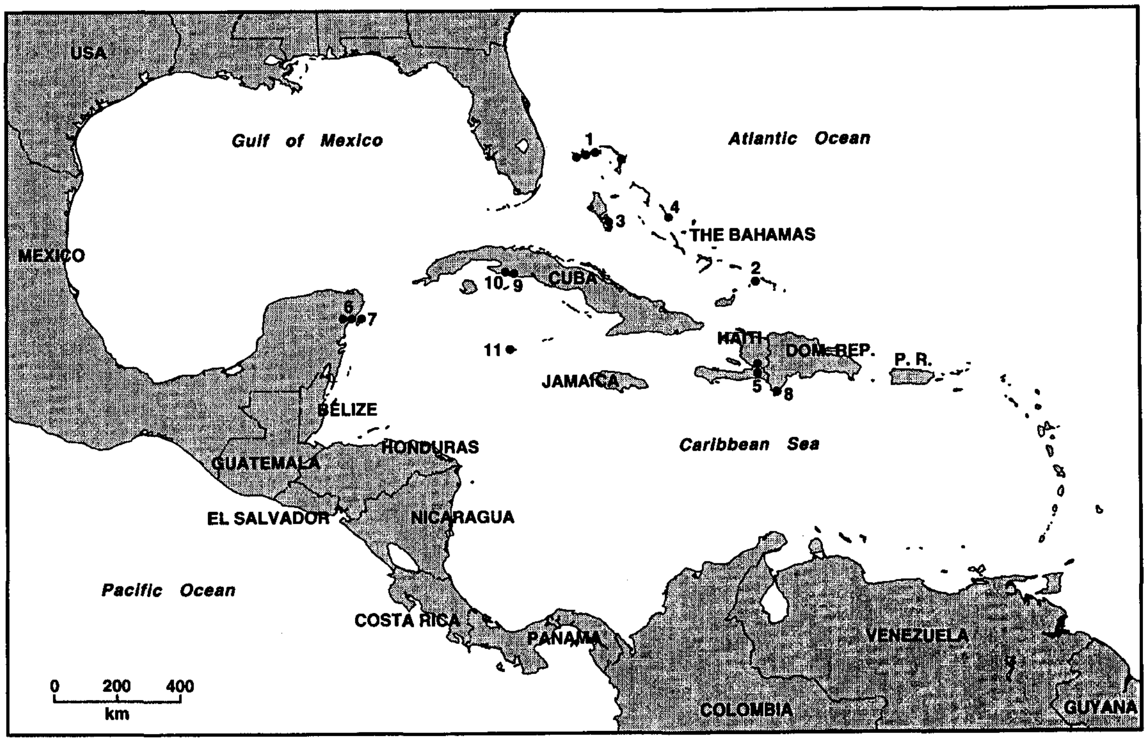

Fig. 3.9. Geographic distribution of *Bahadzia*. 1, *williamsi*; 2, *stocki*; 3, *setimana*; 4, *obliqua*; 5, *latipalpus*; 6, *bozanici*; 7, *setodactylus*; 8, *jaraguensis*; 9, *patilarga*; 10, *yagerae*; 11, *caymanensis*.

Most species of *Bahadzia* live within a very narrowly defined ecological niche at or near the halocline in anchialine caves. Physiochemical *in situ* measurements in these caves, such as Mayan Blue Cenote, a cave on the Yucatan Peninsula where *B. bozanici* is found, have shown a large drop in oxygen levels at the halocline to less than 1 mg/l

(Pohlman *et al.*, 1997). Most species of *Bahadzia* have very large coxal gills relative to other stygobitic and epigean amphipod species, and this may be an adaptation to living and feeding within this low oxygen environment. Pohlman *et al.* (1997) conducted a stable isotope study of the water in Mayan Blue Cenote and concluded that chemoautotrophic nitrifying bacteria played a key role as the base of the food chain for the stygobitic fauna in this cave. In anchialine caves of Cuba inhabited by *Bahadzia*, Yager (1994) reported measurements of dissolved oxygen, temperature and salinity similar to those in Mayan Blue Cenote. Most species of *Bahadzia* appear to be adapted to life in this unique ecosystem typical of anchialine cave waters. The base of the food chain may be a chemoautotrophic bacterium located at the halocline of these caves, where temperature, salinity and oxygen requirements appear to be very narrowly defined. *Bahadzia* is not the only crustacean that is adapted to this specific physical and chemical environment. A number of other taxa of crustaceans are almost always found living sympatrically with *Bahadzia*, including thermosbaenaceans, remipedes, cirolanid isopods and ostracods. Pohlman *et al.*, (1997) were able to define the trophic structure of these crustacean groups within Mayan Blue Cenote. Based on the data reported by these workers, we suggest that there are very specific physical, chemical and biological selective pressures acting on species of *Bahadzia* and other crustaceans living at or near the halocline in anchialine caves. Moreover, these selection pressures are apparently very different from those found in most other aquatic subterranean habitats.

With regard to habitat, *Bahadzia latipalpus* and *B. jaraguensis* are exceptional in comparison with the eight species recorded from anchialine waters; however, as previously noted the ecology of *B. caymanensis* is unclear. *Bahadzia latipalpus* was collected from fresh and oligohaline well water (Stock, 1985) and *B. jaraguensis* was taken from weakly brackish water on the cave floor in mats of filamentous green algae (Jaume and Wagner, 1998).

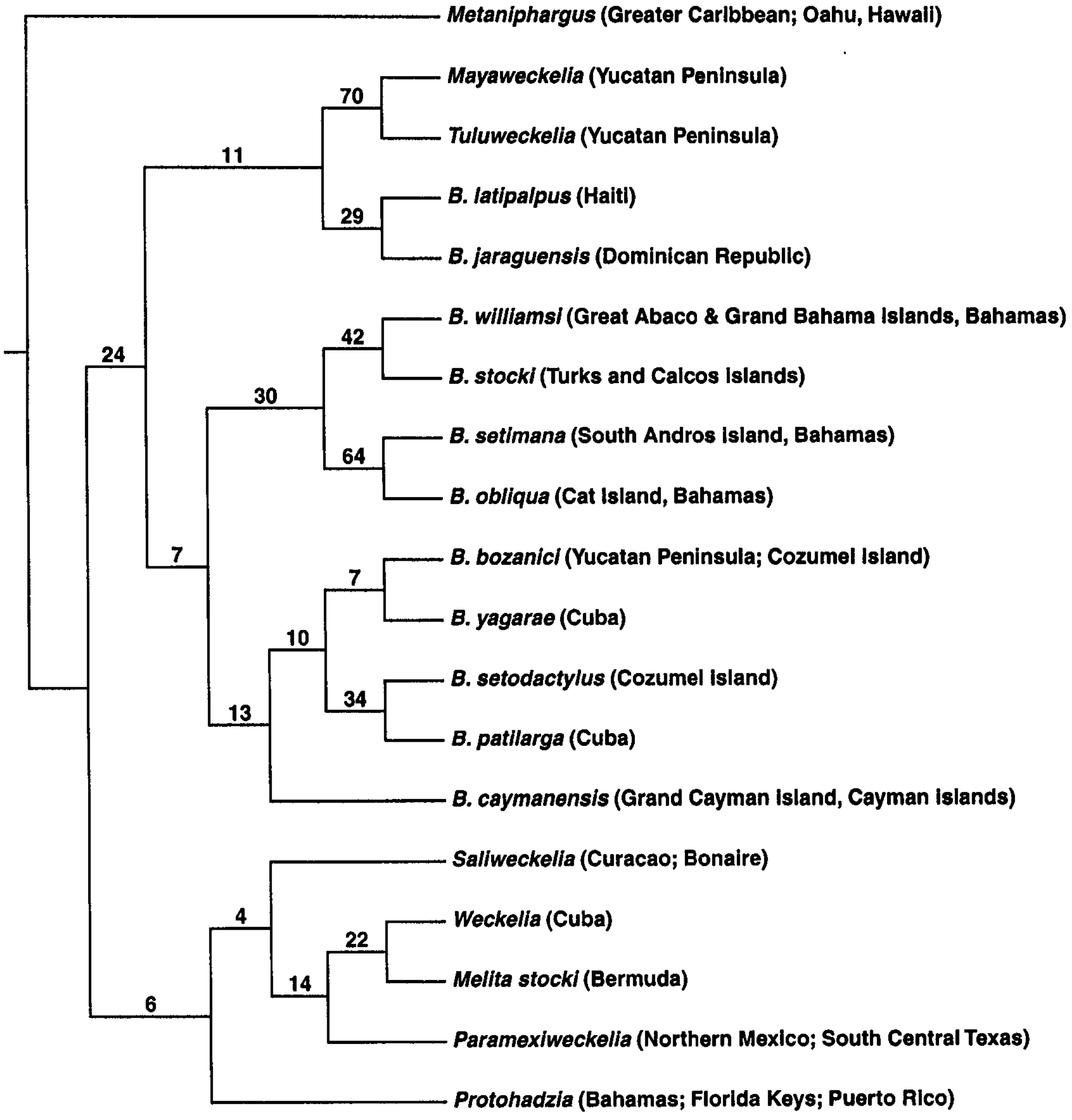

Fig. 3.10. Phylogenetic analysis of the genus *Bahadzia*, including 8 outgroup taxa; characters unordered and unweighted; bootstrap proportions are listed on the branches (CI: 0.31; RI:0.52; RC 0.16; length 86; min. possible length: 27; max. possible length: 150;).

It is perhaps significant that *Mayaweckelia* and *Tuluweckelia* also occur in either fresh or weakly-brackish water (Holsinger, 1977, 1990) and that an earlier cladistic analysis by Holsinger (1992) of "weckeliid group" genera and the genus *Bahadzia,* suggested that *Mayaweckelia* and *Tuluweckelia* are sister genera to *Bahadzia.* Our present analysis offers further support of this hypothesis. In contrast to the anchialine cave-dwelling species of *Bahadzia*, *B. latipalpus* and *B. jaraguensis* live under very different physiochemical and biological selection pressures and display morphological differences as well. Holsinger (1992) suggested that the putative common ancestor of *Bahadzia*, *Mayaweckelia* and *Tuluweckelia* might not have differed significantly from modern *Bahadzia*. With the exception of two characters, which include absence of the mandibular palp and second segment of the outer ramus of uropod 3, both apparently relatively uncomplicated structural losses, *Mayaweckelia* and *Tuluweckelia* share more apomorphic characters with *Bahadzia* than any "weckeliid group" genus. Moreover, both *Mayaweckelia* and *Tuluweckelia* were excluded from the "weckeliid group" in a recent redefinition of the group by Holsinger and Ruffo (2002).

Our observations suggest that strong selection pressures may act on marine amphipods that invade anchialine and later freshwater caves, and that these pressures may result in morphological convergence of species from different lineages. Conceivably, this has occurred in the species of *Bahadzia* on Hispaniola and the species of *Mayaweckelia* and *Tuluweckelia* on the Yucatan Peninsula. Continued research utilizing molecular data may assist in resolving the phylogeny of *Bahadzia* and determine whether or not this genus is monophyletic. Molecular data may also help us to clarify the relationship between *Bahadzia* and other species in the hadziid/melitiid family complex.

SECTION 4

NEW SPECIES AND NEW RECORDS OF WECKELIID AMPHIPOD CRUSTACEANS (HADZIIDAE) FROM SUBTERRANEAN WATERS IN NORTHERN MEXICO AND SOUTHERN TEXAS, WITH DESCRIPTIONS OF THE NEW GENERA *PARAHOLSINGERIUS* AND *TAMAWECKELIA*

The taxonomic diversity of stygobitic weckeliid amphipod crustaceans in subterranean groundwater habitats of south-central Texas and northeastern Mexico is remarkable (Holsinger and Minckley 1971, Holsinger 1973, Holsinger and Longley 1980, Holsinger 1982, Holsinger 1992). To date six genera and 10 species of weckeliid amphipods are described from this region. In addition, stygobitic bogidieliid, crangonyctid and sebid amphipods are also recorded from south-central Texas (Holsinger and Longely 1980). Although the majority of this diversity has been recorded from the Edwards Aquifer in Texas, collecting efforts in Mexico, where suitable collecting sites are more widely dispersed, continue to turn up new populations and species of weckeliid amphipods.

The descriptions of two new genera and species brings the total number of weckeliid genera from northern Mexico and south-central Texas to eight and the number of species to 12. The description of *Tamaweckelia apalpus* n. sp. from southern Tamaulipas marks the furthest southern extension of this group recorded to date. A newly discovered population of *Paraholsingerius smaragdinus* is recorded from Mexico, 30 km south of its type-locality, and another population of this species is recorded from a cave in Reeves County Texas. A second species of the new genus *Paraholsingerius* is described from southern Coahuila. In addition to the new taxa, a new locality for *Paramexiweckelia* *ruffoi* is recorded from a cave in Coahuila, marking a significant range extension for this species from southern Texas into northern Mexico.

SYSTEMATICS

Family Hadziidae S. Karaman, 1943

Paraholsingerius, new genus

Diagnosis.— Similar to *Holsingerius* except as follows: mandible incisors normal or with long spade-like extensions; lacinia mobilis normal or spade-like. Inner plate of maxilla 1 not greatly expanded, with plumose apical setae. Inner and outer plates of maxilla 2 not greatly elongate. Inner plate of maxilliped not elongate or rectangular. Uropod 1 and 2 with row of plumose setae on outer ramus or on both rami.

Type species.—Holsingerius smaragdinus Holsinger 1992 by original designation. Gender is masculine.

Etymology.—The generic name *Paraholsingerius* is derived by a combination of "*Para*" from the Greek meaning "besides, near or by" and "*Holsingerius*," the name of a closely related weckeliid genus.

Paraholsingerius smaragdinus (Holsinger), NEW COMBINATION

Fig. 4.1

Holsingerius smaragdinus Holsinger, 1992:12-16 [type-locality: Emerald Sink

(Cave), Val Verde County, Texas].

Material examined.—MEXICO. Coahuila, Municipia Ciudad Acuña: Sontano de Amezcua, 5 ♀ (1 ovigerous), Dean A. Hendrickson et al., 25 March 1997 (specimens in collection of J.R. Holsinger (H-3729). TEXAS. Reeves County: Phantom Lake Cave, ca. 52 km W of Fort Stockton, 1 juvenile ♂, Jean Krejca, 15 April 2001.

Diagnosis.—Distinguished by characters given in previous description by Holsinger (1992:12-16) with the following addition: right mandible with or without vestigial lacinia mobilis.

Distribution.—The collection of *Paraholsingerius smaragdinus* from Sontano de Amezcua marks the second known locality for this species and the first for Mexico. This discovery extends the range of the *P. smaragdinus* 30 km south of the type-locality, which is located near Langtry, just north of the Rio Grande (Fig. 13).

The single male (4.0 mm) collected from a breakdown room in Phantom Lake Cave, Texas is morphologically close to and probably conspecific with *P. smaragdinus*; however, additional specimens, preferably adults, are needed to determine the exact taxonomic status of this population. Thus, it is tentatively assigned to the species pending further study.

Variation.—Specimens from the Mexican population of *P. smaragdinus* lack a vestigial lacinia mobilis on the right mandible but are otherwise identical to those from the type-locality (Emerald Sink) in Val Verde Co., Texas.

Ecology.—Sontano de Amezcua is briefly described by Botosaneanu et al. (1998). The amphipods were collected from a freshwater stream in the cave, whereas stygobitic cirolanid isopod *Cirolanides texensis mexicensis* was collected from a sump in the cave (Botosaneanu and Iliffe 2002). According to J. R. Reddel (in litt.), Sontano de Amezcua has a highly diverse stygofauna consisting of isopods (cirolanids, stenasellids, asellids), amphipod crustaceans and catfish (*Prietella phreatophila*)

Remarks.—Holsinger (1992) mistakenly described uropod 2 as having a row of plumose setae on the inner ramus, but they are on the upper margin of the outer ramus as shown in Fig. 4.1.

Paraholsingerius mexicanus, n.sp.

Figs. 4.2-4.6

Material examined.—MEXICO. Coahuila, Candela: Gruta de Carrizal, ♀ holotype (7.3 mm), 7 ♀ paratypes, 2 ♂ paratypes, T. M. Iliffe, 20 March 1998; and 1 ♀ paratype, T. M. Iliffe 8 November 1997.

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 XXXXXXX); paratypes are in the collection of J.R. Holsinger (H-3760, H-3857).

Diagnosis.—Medium sized stygobitic species distinguished from *P. smaragdinus* by having *mandibles with spade-like extensions of the incisors and spade-like lacinia* *mobilis on the left mandible.* Further distinguished by having only moderately developed distoposterior lobes on bases of pereopods 5-7; pleonal plates bearing only one small setule on distoposterior margin; *uropods 1 and 2 bearing long plumose setae on both rami.* Largest female 7.5 mm; largest male 6.0 mm.

Female.—Antenna 1: 1.06 times longer than body 2.4 times longer than antenna 2, primary flagellum with up to 65 segments, lacking esthetascs; accessory flagellum absent. Antenna 2 with up to 12 segments. Mandible: molars prominent, right mandible with vestigial lacinia mobilis, incisor proximal margin 7 dentate with long spade-like distal extension, up to 5 serrate accessory spines, plumose molar seta; left with long spade-like lacinia mobilis bearing 4 weak dentations along proximal margin, incisor proximal margin 7 dentate with long spade-like distal extension, up to 6 serrate accessory spines, molar without seta. Lower lip without inner lobes. Maxilla 1: inner plate expanded distally with up to 28 plumose apical setae ; outer plate with 7 apical comb spines; palps 2 segmented, symmetrical, bearing 3 apical spines on the distal margin and up to 15 setae along outer margin. Maxilla 2: inner margin of inner plate narrowing distally, with oblique submarginal row of up to 25 plumose setae. Maxilliped: inner plate highly setose, bearing 3 bladespines apically and row of naked setae along inner margin; outer plate with 3 bladespines and 5-6 long setae apically; inner apical margins of inner and outer plates with weak crenulation; palp 3 segmented, segment 3 bilobed and pubescent distally, not expanded.

Gnathopod 1: propod 70% length of carpus palm short, transverse with 5-6 tiny spines and 2 setae, posterior margin longer than palm, pubescent; carpus produced posteriorly into prominent pubescent lobe, bearing several groups of long setae; posterior margin of basis setose; coxa as broad as deep, with 3 short, marginal setae. Gnathopod 2: propod relatively narrow, elongate, narrowing slightly and unevenly distally, palm slightly oblique, short, armed with few setae and short spines with 2 long setae at the defining angle, both anterior and posterior margins bearing row of long setae; dactyl longer than palm, nail short; carpus subtriangular, posterior margin lobiform and pubescent, lobe broadest proximal to distal end, bearing long setae along posterior and distoposterior margins; basis posterior margin bearing numerous long setae; coxa subequal to gnathopod 1 bearing 2 marginal setules. Pereopods 3 and 4 subequal, bases rather broad and bearing short spines on anterior margin and slightly longer (slender) spines on posterior margin; coxae about as deep as broad with 2 marginal setules; coxa 4 dorso-posterior margin not excavate. Pereopod 5 ca. 70% length of body, pereopods 6 and 7 subequal ca. 82% length of body. Bases of pereopods 5-7 not greatly expanded, distoposterior lobes moderately developed; dactyl of pereopod 5 about 65% length of corresponding propod, dactyls of pereopods 6 and 7 ca. 53% length of corresponding propods; dactyl of pereopod 5 with 5 setules on upper margin, dactyls of pereopods 6 and 7 with 7 setules on upper margins. Coxal gills relatively small, ellipsoidal, with distinct peduncles. Brood plates relatively small, narrow, and nonsetose in material examined.

Pleonal plates bearing one small setule on distoposterior margins, corners not greatly produced. Pleopod peduncles with 5-6 coupling spines each on inner margins. Uronites 1 and 2 with 2 small dorsodistal spines each, uronite 3 with 4 such spines. Uropod 1: inner ramus subequal to outer, and peduncle, with about 5 apical spines, lateral margins with long plumose setae, upper margin with 2 spines; outer ramus with about 3 apical spines, upper margin with double row of plumose setae, and 4 spines. Uropod 2: inner ramus subequal in length to outer, with about 5-6 apical spines, upper margin with long plumose setae and one long spine, lower margin with apical setae; outer ramus with about 4 apical spines and double row of plumose setae and 2 spines on upper margin; peduncle ca 78% length of rami armed with 2 spines. Uropod 3: about 20% length of body, ca.70% length of uropod 1; rami folacious, subequal, outer margin of outer ramus with 3 sets of doubly inserted spines, inner margin of outer ramus and both margins of inner ramus with plumose setae and spines. Telson rather long, about 1.5 times longer than broad; apical margin with deep, V-shaped cleft extending ca. 73% distance to base; apical lobes bearing 3 spines each; lateral margins lacking spines.

Male.—Differing from female as follows: Gnathopod 1: dactyl and propod proportionately longer and broader; propod palm long, oblique with double row of about 10 spines, defining angle with 1 seta and one spine; posterior margin slightly longer than palm, pubescent with single long seta. Gnathopod 2: dactyl and propod proportionately longer and broader; propod palm long, oblique with double row of about 13 spines; defining angle with 2 long setae; posterior margin subequal to palm with 3 sets of long setae.

Etymology.—The epithet *mexicanus* denotes the presence of this species in Mexico.

Type-locality.—This species is known only from the type-locality, Gruta de Carrizal, which is located approximately 225 km SW of Nuevo Laredo and 80 km N of Monterrey, Mexico. According to T. M. Iliffe (pers. comm.) specimens were collected from the water column with a plankton net and vials at depths of 0-13 m.

***Tamaweckelia*, new genus**

Diagnosis.—Without eyes and pigment, of subterranean facies. Interantennal (lateral) lobe of head present, rounded anteriorly. Antenna 1: elongate, length subequal to body, 3.7 times longer than antenna 2; accessory flagellum absent. Mandible: lacinia mobilis absent from right; molar setae absent from left; palp lacking. Maxilla 1: inner plate with numerous naked, apical setae; outer plate with 7 apical, serrate and/or pectinate spines; *palp possibly vestigial, or absent.* Maxilla 2: inner plate broader than outer with oblique facial row of naked setae; both plates with numerous course setae apically. Maxilliped: inner-distal margin of inner plate with one plumous spine, apical margin with bladelike spines; article 3 of palp apically expanded, pubescent and bilobed distally. Lower lip: outer lobes high, well developed; inner lobes weak but present; lateral (mandibular) processes relatively long and slender.

Gnathopod 1: propod 65% length of carpus; palm short, transverse; coxal plate enlarged, slightly expanded distally, as deep as corresponding body segment. Gnathopod 2: propod elongate, 1.12 times longer than the carpus; palm short, weakly oblique with 4 long setae on medial-posterior margin, two subequal in length to the propod; coxal plate enlarged, as deep as corresponding body segment. Gnathopods 1 and 2 propod posterior margins pubescent; posterior margins of carpus of gnathopod 1 and 2 broadly lobiform and pubescent. Male gnathopod 2 unkown. Pereopods 3 and 4 subequal in length; coxal plates similar, much smaller than gnathopods, shallower than corresponding body segments; coxa 4 dorso-posterior margin not excavate. Bases *of pereopods 5-7 greatly expanded,* lobate; dactyls without setules on anterior margin.

Posterior corners of pleonal plates rounded, bearing one large setule each; ventral margin of plate 3 with 1 spine. Uropods 1 and 2, rami bearing normal spines, *without row of long plumose setae on upper margin.* Uropod 1, 1.4 times longer than uropod 3.

Uropod 3 biramus; rami 1-segmented, subequal (magniramus) but different in width and setal pattern (dispariramus). Telson *Holsingerius*-like, 50% length of uropod 3 with 3-4 distal spines and *5-6 spines on the lateral margins*; apical margin incised ca. 78% the distance to base.

Coxal gills pedunculate, variable in shape and size, on pereopods 2-6. Brood plates sublinear, very large. Largest female 7.0 mm; male unknown.

Type-species.—*Tamaweckelia apalpa* by monotypy. Gender is feminine.

Etymology.—The generic name is derived by a combination of *Tama*, which alludes to geographic placement in the Mexican state of Tamaulipas, and *Weckelia*, the name of a related, Greater Antillean genus.

Relationships.—Differing from *Holsingerius, Paraholsingerius* and all other "weckeliid" genera from Texas and northern Mexico by the absence of a palp on maxilla 1. Further distinguished from *Holsingerius* and *Paraholsingerius* by the presence of inner lobes on the lower lip; coxa of gnathopod 2 slightly bigger than 1; greatly expanded bases of pereopods 5-7; uropod 1 longer than uropod 3; and telson with strongly spinose lateral margins.

Tamaweckelia apalpa, n. sp.

Figs. 4.7-4.11

Material examined.—MEXICO. Tamaulipas, Municipia Ciudad Mante: Manantial de

San Rafael de Los Castro, holotype ♀ (6.0 mm), D. A. Hendrickson et al., 13 March 1997, and 6 paratypes ♀, on same date; additional paratypes include 3 subadults and 1 juvenile collected by J. Brown and J. Krezca, 2 Jan. 2000.

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 XXXXXXX); paratypes are in the collection of J. R. Holsinger (H-3730 and H-XXXX).

Diagnosis.—Distinguished by the unique characters of the genus (above), especially absence of a palp on maxilla 1.

Female.—Antenna 1 subequal in length to body, 3.7 times longer than antenna 2, primary flagellum with up to 52 segments, lacking esthetascs; accessory flagellum absent. Antenna 2 with up to 11 flagellar segments. Mandible: molars prominent, right mandible without lacinia mobilis, incisor 6-dentate, up to 8 serrate accessory spines, plumose molar seta; left with small apically serrate lacinia mobilis, incisor 7-dentate, up to 6 serrate accessory spines, molar without seta. Lower lip: inner lobes weak but present. Maxilla 1: inner plate with up to 14 apical, naked setae; outer plate with 7 apical serrate spines; palp absent or vestigial. Maxilla 2: inner plate narrowing distally, with oblique, submarginal row of up to 29 naked facial setae. Maxilliped: inner plate bearing 3 long bladespines apically and row of naked setae on inner margin, inner-apical margin bearing single plumose spine; outer plate slightly broader, bearing short row of blade spines on inner-apical margin; palp segment 3 broadened distally, apically bilobed and pubescent.

Gnathopod 1: propod proportionately small, palm short, with few tiny spines and 2 setae, posterior margin without setae but pubescent; carpus longer than propod, produced posteriorly into prominent, pubescent lobe which is broadest proximal to distal end, bearing several groups of long serrated setae; posterior margin of basis setose; coxa rather deep, expanded distally with 7 short marginal setae. Gnathopod 2: propod relatively narrow, elongate, palm slightly oblique, short, armed with 2-3 short setae and 4 long setae: 2 medial, subequal in length to the propod and 2 at defining angle, 50% length of propod, both anterior and posterior margins bearing few long setae, posterior margin pubescent; dactyl short, rather stout, nail short; carpus posterior margin lobiform and pubescent, lobe broadest distally, bearing 4 clusters of long serrate setae; posterior margin of basis setose, coxa slightly larger than gnathopod 1, deeper than broad, not distally expanded with 4 short marginal setae. Pereopods 3 and 4 subequal, bases not greatly broad, each bearing one stout spine and 2 to 3 smaller spines on posterior margin and few short spines on anterior margin, coxae about as deep as broad bearing 1 to 2 setules, coxa 4 dorso-posterior margin not excavate. Bases of pereopods 5-7 greatly broad, distoposterior lobes well developed. Relative length of pereopod 5 unknown. Pereopod 6 ca. 60% length of body, 1.22 times longer than pereopod 7, dactyls of pereopods 6 and 7 ca. 46-47% length of corresponding propods; dactyls without setules on anterior margins. Coxal gills large, subovate, with distinct peduncles. Brood plates extremely prominent, long, narrow.

Pleonal plates with produced posterior corners, bearing one long spine each, ventral margin of plate 3 with 1 spine. Uronites 1 and 2 with 2 small dorsodistal spines each, uronite 3 with 4 such spines. Uropod 1: inner ramus subequal in length to outer, shorter than peduncle, with about 4 apical and 4 lateral spines; outer ramus with about 4 apical and 5 lateral spines; peduncle bearing about 8 spines, 3 of which are relatively large basofacial spines. Uropod 2: inner ramus slightly longer than outer with about 4 apical and 5 lateral spines; outer ramus with about 4 apical and 3 lateral spines. Uropod 3 rami foliaceous, subequal, ca. 18% length of body, ca. 72% length of uropod 1; inner margin of outer ramus and both margins of inner ramus with plumose setae and spines, outer margin of outer ramus with 3 sets of doubly inserted spines. Telson rather long, about 1.7 times longer than broad; apical margin with deep, V-shaped cleft extending ca. 78% distance to base; apical lobes bearing 3-4 spines each; lateral margins with 5-6 spines.

Male.—Unknown, however 2 specimens collected on 2 January 2000 may be subadult males (ca. 5.5 mm), inasmuch as brood plates where absent.

Etymology.—"*a*" from the Greek for without, combined with "palp" based on the absence of the palp on maxilla 1.

Type-locality.—This species is known only from the type-locality, Manantial de San Rafael de Los Castro. The entrance to this cave is a pit, 4 m deep. A spring ("manantial" in Spanish) at the bottom of the pit provides access to a fissure that drops to a depth exceeding 60 m (Villalobos 1999). The cave is described in some detail by Botosaueanu et al. (1998) and Hendrickson et al. (2001). Stygobitic cirolanid isopods (*Sphaerolana interstitialis*), mexistenasellid isopods, atyid shrimps (*Troglomexicanus huastecae*) and catfish (*Prietella lundbergi*) are also reported from this cave by these authors.

New genus? New species?

Fig. 4.12

Material examined.—MEXICO. Tamaulipas, Municipia Ciudad Mante: Manantial de San Rafael de Los Castro, partial specimen, sex and size unknown, D. A. Henderickson et al., 13 March 1997. This specimen is in the collection of J. R. Holsinger (H-3730).

Remarks.—A single, isolated head was with the collection described above as *Tamaweckelia apalpa* n. sp. Mouthparts differ from *T. apalpa* n. sp. as follows: mandible: right incisor spade-like, without dentation; left mandible incisor spade-like, weakly serrated; lacinia mobilis with small serrations distally. Maxilla 1: vestigial, one-segmented palp present, bearing up to 6 spines with comb-like setae on apical margin.

It is unclear whether this specimen represents a new taxon, or is an aberrant specimen of *Tamaweckelia apalpa*. Of the 11 specimens collected from Manantial de San Rafael (the type locality of *T. apalpa*) these different morphological features were observed only in this single head. The lack of the remaining body precludes further study of this potentially new taxon until additional specimens can be obtained.

Paramexiweckelia ruffoi Holsinger

Paramexiweckelia ruffoi Holsinger 1993:1-98, figs. 1-5 [type-locality: unnamed spring on east side of Devils River, ca. 32 km north of Del Rio, Val Verde County, Texas.]

Material examined.—MEXICO. Coahuila, Melchor Múzquiz: mine above El Socavón #2, 2 ♀, D. A. Hendrickson et al., 22 March 1997. TEXAS. Val Verde County:

Dandridge Spring on east bank of Devils River, ca. 4.8 km above mouth of Dry Devils, 1 ♀, D. A. Hendrickson, H. Krejca, P. Sprouse and C. Savvas, 22 February 1998.

Remarks.— Two specimens, approximately 9 mm in length, with non-setose broodplates, were collected from a flooded mine near El Melchor Múzquiz (see Hendrickson et al. 2001), marking the first Mexican record for this species. Dandridge Spring is the second Texas location for this species and is located approximately 50 km north of the type-locality.

DISCUSSION

Barnard and Karaman (1982) elevated *Texiweckelia samacos* to the genus *Holsingerius* based on: a) lacinia mobilis absent from right mandible; b) greatly expanded inner plate of maxilla 1, bearing approximately 40 apical setae; c) elongate inner plate of maxilla 2, with relatively straight inner margin and oblique row of approximately 100 facial setae; d) elongate, rectangular-shaped inner plate of maxilliped, which bears a row of setae on medial margin that extends well below base of the plate; and e) coxa 1 larger than coxa 2. Among the eight weckeliid genera of northern Mexico and south-central Texas, the possession of characters b, c and d above appear to be autapomorphies that are unique to *Holsingerius samacos*. Plumose setae on one or both rami of uropods 1 and 2 are synapomorphies for *Paraholsingerius smaragdinus* and *P. mexicanus*, which are not shared by *Holsingerius samacos* (Table 4.1).

Paraholsingerius mexicanus possesses a notable autapomorphy: mandibular incisors with spade-like extensions. *Paraholsingerius smaragdinus* and *P. mexicanus* are synapomorphic for plumose setae on the rami of uropods 1 and 2; however, whereas *P. mexicanus* has these setae on both rami, *P. smaragdinus* has them only on the outer ramus of each uropod. Coxae 1 and 2 are subequal in *P. mexicanus*, but in *P. smaragdinus*, coxa 1 is much larger than coxa 2. If additional populations are discovered that share the unusual spade-like incisors of *P. mexicanus*, a new genus may be warranted. Given that this single character is autapomorphic, it is felt that the other character differences between *P. mexicanus* and *P. smaragdinus* are specific differences predicted by the large geographic distances between populations of the two species (Fig 4.13).

Table 4.1. Generic character matrix for 8 closely related genera in Texas and northern Mexico based on characters used by Barnard and Karaman (1982) and an additional character from the present study.

	Lacinia mobilis: absent/vestigial	Maxilla 1: inner plate greatly expanded	Maxilla 2: elongate inner plate	Maxilliped: elongate/rectangular inner plate	Gnathopods: Coxa 1 larger than Coxa 2	Uropods 1 and 2: with plumose setae on rami
Texiweckelia	Yes	No	No	No	Yes	No
Texiweckeliopsis	Yes	No	No	No	Yes	No
Paraholsingerius n. gen.	Yes	No	No	No	Yes	Yes
Holsingerius	Yes	Yes	Yes	Yes	Yes	No
Tamaweckelia n. gen.	Yes	No	No	No	No	No
Mexiweckelia	No	No	No	No	No	No
Paramexiweckelia	No	No	No	No	No	No
Allotexiweckelia	Yes	No	No	No	Yes	No

Botosaneanu and Iliffe (2002) described a subspecies of the cirolanid isopod *Cirolanides texensis*, *C. texensis mexicensis*, from various caves in northern Mexico, including Sontano de Amezcua, which is the new locality for *P. smaragdinus*. *Cirolanides t. mexicensis* was erected because of two small differences between the Texas and Mexican populations on opposite sides of the Rio Grande. These included the presence of one additional strong spine on the palm of the gnathopod propodus and generally smaller body size of the Mexican relative to the Texan subspecies. The two populations of *P. smaragdinus* also have very small morphological differences on opposite sides of the Rio Grande. The Mexican population lacks a vestigial lacinia mobilis on the right mandible. Although this difference is not considered significant enough to warrant dividing the species into subspecies, it is noteworthy inasmuch as this parallel between these two crustacean species suggests that the Rio Grande may be at least a minimal dispersal barrier for subterranean populations inhabiting caves on opposite sides of the river.

To date *Tamaweckelia apalpa* is known only from Manantial de San Rafael de Los Castro, a submerged cave located just west of Ciudad Mante (Fig. 13). Both Botosaneanu et al. (1998) and Villalobos et al. (1999) provide a detailed description of the physical environment of this cave. *Tamaweckelia apalpa* was collected in company with stygobitic isopods of the genus *Mexistenasellus* (Stenasellidae) and *Sphaerolana interstitialis* (Cirolanidae) and stygobitic catfish (Ictaluridae) during the Blindcat Collecting Expedition to the Sierra de El Abra led by Dr. Dean A. Hendrickson in 1997 (see Villalobos et al. 1999 and Hendrickson et al. 2001). The type-locality of *T. apalpa* marks the extreme southern range for weckeliid amphipods of south-central Texas and northern Mexico. Three morphological characters distinguish *Tamaweckelia* from *Paraholsingerius* and *Holsingerius*: 1) maxilla 1 lacking or with vestigial palp; 2) bases of pereopods 5-7 greatly expanded; 3) telson with 5-6 lateral spines; however, similarity in the shape of the telson suggests shared ancestry between these 3 genera.

Tamaweckelia apalpa may occur sympatrically and possibly syntopically with another stygobitic amphipod in Manantial de San Rafael de Los Castro. Such an occurrence seems conceivable, inasmuch as *Mexiweckelia colei* and *Paramexiweckelia* *particeps* occur together in springs in central Coahuila (Holsinger and Minckley 1971 and Holsinger 1982), as well as the co-occurrence of as many as four other weckeliid amphipods in the artesian well at San Marcos, Texas (Holsinger and Longley 1980). Differences, especially in the mouthparts, of these species may indicate a partitioning of habitat resources. The differing mouthparts in the single head collected together with *T. apalpus* strongly suggests the presence of a second species from this cave and the potential of resource partitioning. Additional specimens from the locality are needed to determine the exact taxonomic status of this aberrant specimen.

The descriptions of *Paraholsingerius mexicanus* and *Tamaweckelia apalpus* bring the total number of weckeliid amphipods recorded to date from northern Mexico and south-central Texas to eight genera and 12 species. Along with hadziid amphipods, which encompass the weckeliids, other non-crangonyctid amphipods, including bogidiellids, sebids, and what is apparently the first record of an ingolfiellid, have been recorded from this region, as well as other groups of stygobitic crustaceans, e.g., cirolanid and stenasellid isopods and thermosbaenaceans. This remarkable taxonomic diversity is attributed to the fact that the current range of these stygobionts was covered by shallow marine embayments during the late Cretaceous and/or early Cenozoic. The present freshwater stygobionts are apparently marine relicts that evolved from ancestors by stranding when these shallow seas retreated (Holsinger and Longley 1980, Bowman 1982, Holsinger 1986, Holsinger 1992). Given the geologic time scale and the possibility for repeated marine transgressions, the diversity of stygobitic marine relicts on the southern North American continent is not surprising.

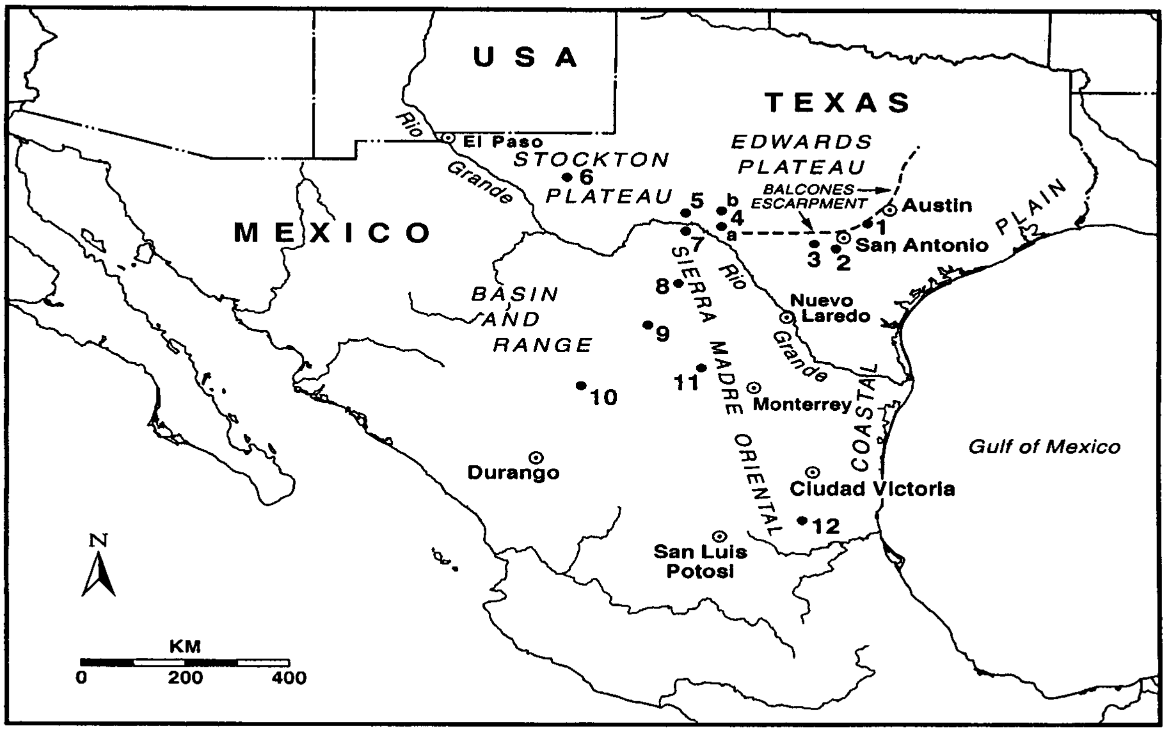

Fig. 4.13. Geographic distribution of stygobitic hadziid amphipods in northern Mexico and south-central Texas. Solid circles indicate known localities as follows: 1) artesian well and San Marcos springs, San Marcos, Hays Co., TX – *Texiweckelia texensis*, *Texiweckeliopsis insolita*, *Holsingerius samacos* (well only) and *Allotexiweckelia hirsuta* (well only); 2) deep artesian wells near Von Ormy, Bexar Co., TX – *Texiweckeliopsis insolita* (Verstraeten well no. 1) and *Allotexiweckelia hirsuta* (O. R. Mitchell well no. 2 and Verstraeten well no. 1); 3, Hondo Creek hyporheic, Medina Co., TX – *Mexiweckelia hardeni*; 4a) unnamed spring east of Devils River and 4b) Dandridge spring, Val Verde Co., TX – *Paramexiweckelia ruffoi*; 5) Emerald Sink (cave), Val Verde Co., TX – *Paraholsingerius smaragdinus*; 6) Phantom Lake Cave, Reeves Co., TX – *Paraholsingerius smaragdinus*; 7) Sóntano de Amezcua, Coahuila, MX – *Paraholsingerius smaragdinus*; 8) cave above El Socavón #2, Melchor Múzquiz, Coahuila, MX – *Paramexiweckelia ruffoi*; 9) thermal spings in Bolsón de Cuatro Ciénegas, Coahuila, MX – *Mexiweckelia colei* and *Paramexiweckelia particeps*; 10) Cueva de la Siquita, Durango, MX – *Mexiweckelia mitchelli*; 11) Gruta de Carrizal, Coahuila, MX – *Paraholsingerius mexicanus*; 12) Manantial de San Rafael de los Castro, Tamaulipas, MX – *Tamaweckelia apalpa*.

Further collection efforts should yield additional species from these areas, especially in Mexico where numerous, remote collecting sites may still exist. These additional collections should shed more insight into the evolutionary relationships of the weckeliid genera.

SECTION 5

FOUR NEW SPECIES OF THE SUBTERRANEAN AMPHIPOD GENUS *HADZIA* (HADZIIDAE) FROM CAVES IN THE WEST PACIFIC, WITH RE-EVALUATION OF THE TAXONOMIC STATUS OF THE GENUS

The genus *Hadzia* was first established by S. Karaman (1932), on the basis of two species originally described from the former Yugoslavia. *Hadzia fragilis* was described from the northwestern coastal region of Croatia, near Dubrovnik and just inland from Dubrovnik in Herzegovina, whereas *Hadzia gjorgjevici* was described from two locations near Skopje, in Macedonia. More recently G. Karaman (1984) described two subspecies—*H. fragilis drinensis* from hyporheic waters in the Drina River and *H. gjorgjevici crispata* from freshwater caves near Titograd, in Montenegro. G. Karaman (1989) also described the subspecies, *H. fragilis stochi*, from a cave in northeastern Italy near La Peschiera del Timavo.

Barnard (1965) described *Liagoceradocus* from Ifaluk Atoll, in the Caroline Islands on the basis of two tiny specimens. Subsequently, eight species of this genus were described, all from the Indo-West Pacific region except for *L. acutus*, which is described from anchialine waters in a lava cave on Lanzarote in the Canary Islands in the eastern Atlantic.

In the present study, four new species of *Hadzia* are described from what are apparently all anchialine caves in the Philippines, Palau and Guam. Careful examination of these species, combined with a re-evaluation of species previously assigned to *Hadzi*a and *Liagoceradocus*, strongly support the merger of these two genera. The closely similar morphology of *Hadzia*, *Metaniphargus* and *Metahadzia* is discussed and is believed to be indicative of a close evolutionary relationship.

SYSTEMATICS

Hadzia Karaman

Hadzia S. Karaman, 1932: 213.

Liagoceradocus Barnard, 1965: 505.

Diagnosis.—Without eyes or pigment, of subterranean facies. Antenna 1 longer than antenna 2; accessory flagellum with 1 or 2 segments (usually 2, second segment sometimes reduced). Mandible molar triturative, incisors well developed, right lacinia mobilis usually bifurcate with serrate margins, left lacinia mobilis well developed, normal; palp well developed, 3 segmented. Maxilla 1: inner plate with apical plumose, or naked setae; outer plate with 6 to 11 apical, serrate spines; palps sometimes asymmetrical, left palp bearing slender spines apically, right palp bearing robust spines apically. Maxilla 2: inner plate bearing row of oblique facial setae; apices of inner and outer plates bearing numerous course setae. Maxilliped: inner plate with several bladespines apically; outer plate usually with row of bladespines on inner margin; palp segment 3 often excavate, heavily setose distally.

Gnathopod 1: propod shorter than carpus; palm usually transverse sometimes bearing bifid spines at the defining angle. Gnathopod 2: propod elongate, longer than carpus, larger than propod 1; palm oblique, usually subequal in length to the posterior margin of the propod, bearing short double row of stout spines and setae; carpus usually expanded into distoposterior lobe. Male gnathopod 2 propod expanded, palm elongate, longer than posterior margin of propod, bearing long double row of stout spines and few setae; carpus with distoposterior lobe. Pereopods 3 and 4 often subequal in length, similar; coxal plate of pereopod 4 unlobed. Bases of pereopods 5-7 weakly lobate, not greatly expanded; pereopods 6 and 7 often subequal in length, usually longer than pereopod 5.

First pleonal plate without spines on ventral margin; pleonal plates 2 and 3 with variable numbers of spines on ventral margin. Pleopods normal, bearing 2 coupling spines; pleopod 3 sometimes sexually dimorphic. Uropod 1 usually with single basofacial spine. Uropod 2 peduncle often with distinct dorsodistal comb row of spines; upper margin of rami often with row of small tooth spines. Uropod 3 elongate, magniramous, dispariramous, outer ramus 2-segmented, inner ramus subequal in length to or longer than the first segment of the outer ramus. Telson usually longer than broad with variable numbers of lateral and apical spines.

Type species: *Hadzia fragilis* Karaman, *1932.*

Remarks.—Liagoceradocus was first established by Barnard (1965) on the basis of two specimens of a new species collected from an algal wash at a depth of approximately 1.8 m at Ifaluk Atoll in the Caroline Islands. To date nine species of *Liagoceradocus* have been described and all but one is from either the West Pacific or Indian Oceans. The exception is *L. acutus*, which was described from anchialine water in Jamos de Agua lava cave on Lanzarote in the Canary Islands by Andres (1978). However, the taxonomic status of *Liagoceradocus* has been disputed by several workers. Ruffo (1982) considered *Hadzia* to be a senior synonym of both *Liagoceradocus* and *Metahadzia* and Karaman (1984) also considered *Liagoceradocus* and *Metahadzia* to be indistinguishable from *Hadzia*. However, Stock (1983), on the basis of a cladistic analysis, considered *Hadzia* and *Liagoceradocus* separate genera. Rondé-Broekhuizen and Stock (1987) also considered *Hadzia* and *Liagoceradocus* to be distinct genera based on a number of characters they considered to be synapomorphies for species in *Liagoceradocus*. Careful examination of these characters during this study suggests a high degree of variability and overlap of these characters, with no clear distinction between the genera. We have therefore concluded that *Hadzia* and *Liagoceradocus* should be synonymized.

However, as might be expected, a difference among the species of *Hadzia* exist in different geographic regions: the presence of tooth spines on the upper margin of one or both rami of uropod 2 is found for all species of *Hadzia* described from the Indo-West Pacific region but not by any species of *Hadzia*, including *H. acuta*, from the Mediterranean or Atlantic regions. No other characters were found that separate species in different geographic regions. On the contrary, all other characters appear to show a great deal of overlap and inconsistency.

It should be noted, however, that *H. branchialis*, from the Cape Range Peninsula in Western Australia is unique in its possession of large, unstalked coxal gills (Bradbury and Williams 1996), whereas *H. lobifera* from Basakana Island in the Solomon Islands and *H. uncifera* from Vatulele Island in Fiji (Stock and Iliffe 1991) are unique for sexual dimorphism in pleopod 3 of the male. These characters, which appear to be unique to given species, are considered autapomorphic and not unusual considering the geographic isolation of the species. Pending further study, they are not considered important enough to be generic differences.

Hadzia guamensis, n.sp.

Figs. 5.1-5.5

Material Examined.—GUAM. Marbo Cave, ♀ holotype (3.0 mm), 21 paratypes, T. M. Iliffe, 20 January 1985; Marbo Cave, 10 paratypes, D. Williams and J. Bozanic, 2 May 1985; Faifai Beach Cave, 22 paratypes, T. M. Iliffe, 22 January 1985; Pagat Point Cave, 12 paratypes, T. M. Iliffe et al. 23 January 1985; Ritidian Cave, 4 paratypes, T. M. Iliffe and D. Williams, 26 January 1985; Tarague Water Well, 1 ♀ paratype, T. M. Iliffe, 26 January 1985; Tweeds Cave, 1 ♀ paratype, T. M. Iliffe, 28 January 1985.

The holotype is deposited in the National Museum of Natural History (Smithsonian Instituion) under the catalogue number of the former United States National Museum (USNM XXXXXXX); paratypes are in the collection of J. R. Holsinger (H-2497) and the National Museum of Natural History (USNM 364310).

Diagnosis.—Small stygobitic species distinguished by having relatively few D-setae on segment 3 of mandibular palp; relatively few spines on margins of pereopods 5-7; relatively few spines on both rami of uropod 3 (except *H. palauensis*). Largest males 2.5 mm; largest females 3.0 mm.

Description.—Antenna 1 ca. 83% length of body, 2.3 times longer than antenna 2, primary flagellum with up to 21 segments, aesthetascs present on flagellar segments 4-20; accessory flagellum 2-segmented, the second segment reduced. Antenna 2 with up to 8 segments. Mandible: right mandible molar prominent with seta, lacinia mobilis bifid, larger bifurcation bearing small, serrated teeth, incisor 5 dentate, up to 4 accessory spines; left molar prominent without seta, lacinia mobilis 4 dentate, normal, incisor 6 dentate; palps bearing 3-5 D-seta. Lower lip without inner lobes. Maxilla 1: inner plate bearing 7-10 apical setae, naked under light microscopy; outer plate with 7 apical comb spines; palp 2-segmented, asymmetrical, right palp bearing 6 stout spines and 1 seta along apical margin, left palp bearing 5 slender spines and 1 seta along apical margin. Maxilla 2: inner lobe narrowing distally, with oblique submarginal row of up to 10 naked setae. Maxilliped: inner plate narrow, not expanded, bearing up to 6 bladespines distally; outer plate with up to 6 bladespines on inner apical margin, weakly expanded along outer margin; palp 3 segmented, segment 3 excavate, pubescent distally.

Gnathopod 1: propod 88% length of carpus, palm transverse with up to 8 setae of variable length, posterior margin longer than palm; dactyl slightly longer than palm; carpus posterior margin moderately produced bearing up to 9 long setae; merus posterior margin pubescent, distoposterior margin slightly extended distally, bearing up to 3 long setae; basis bearing only 2 long setae; coxa only slightly less broad than deep, bearing 5 marginal spines. Gnathopod 2: propod elongate, ca. 1.5 times longer than carpus, palm oblique, shorter than posterior margin of propod, bearing up to 5 setae with 2 relatively long and 2 relatively short setae at the defining angle; dactyl subequal to palm; carpus subtriangular, posterior margin lobiform and pubescent; basis with only one long seta; coxa deeper than broad with up to 3 marginal spines. Pereopod 3 slightly smaller than 4, coxa deeper than broad; basis not expanded, bearing up to 3 setae. Pereopod 4: coxa larger than pereopod 3, only slightly deeper than broad, not excavate posteriorly, bearing up to 4 setae on the distal margin; basis slightly expanded relative to pereopod 3, bearing up to 6 setae. Pereopod 5 ca. 46% length of body, pereopod 6 ca. 56% length of body, pereopod 7 ca. 51% length of body; bases of pereopods 5-7 not greatly expanded, distoposterior lobes weakly developed; dactyl of pereopod 5 ca. 63% length of corresponding propod, dactyl of pereopod 6 ca. 45% length of corresponding propod; dactyl of pereopod 7 ca. 33% length of corresponding propod. Coxal gills on 2-6 relatively small, subovate, with distinct peduncles; brood plates subequal in length to gills, stout, setose distally.

Pleonal plates bearing 1-2 small setules on posterior magins, distoposterior margins weakly produced, pleonal plate 2 bearing 1 spine on ventral margin; plate 3 with 2 spines on ventral margin. Pleopods bearing 2 small coupling spines each. Uronites not fused, without spines. Uropod 1: outer ramus 70% length of inner, with about 3 apical and 2 lateral spines; inner ramus 70% length of peduncle, bearing about 5 apical and 1 lateral spine; peduncle with about 8 spines, 1 basofacial and 2 on upper distal margin. Uropod 2: outer ramus about 70% length of inner, 78% length of peduncle, bearing 4 apical and 2 lateral spines, upper margin bearing row of small tooth spines; inner ramus 1.1 times longer than peduncle, bearing 3-4 apical and 3 lateral spines, upper margin with row of small tooth spines; peduncle bearing 4 spines, 3 of are on the dorsodistal end. Uropod 3: about 20% length of body; inner ramus 78% length of outer, bearing 9 spines and 1 setule; outer ramus 2 segmented, first segment bearing 4 apical and 6 lateral spines; peduncle bearing 2 spines. Telson longer than broad, each lobe bearing about 5 spines.

Male.—Differing from female as follows: gnathopod 2: dactyl and propod proportionately longer and broader; palm long, oblique with double row of about 7-8 spines, defining angle with 2 long setae; posterior margin of propod with up to 4 long setae.

Etymology.—The epithet *guamensis* is based on the occurrence of this species on the island of Guam.

Type-locality.—The type-locality, Marbo Cave, is located on the east coast of Guam adjacent to Andersen South Air Force Base (Fig. 5.21).

Ecology and Distribution.—Marbo cave is located at the base of a hill, 300 m inland and consists of a collapse chamber subdivided by breakdown into four pools at varying light levels. Water temperature was 26.3°C, salinity $4.3^{o}/_{oo}$, with a maximum depth of 6 m at the time of collection. Amphipods were collected from the surface of a log in a shallow, darker section of the cave. Three species of shrimp and a crab were also collected from the pool. As presently known, *H. guamensis* is recorded from six localities on the island of Guam (Fig 5.21).

Hadzia philippinensis, n. sp.

Figs. 5.6-5.10

Material Examined.--PHILIPPINES. Bohol, Panglao Island: Well no. 1, Danao/L. Tauala, ♂ holotype (3.0 mm), 23 paratypes, B. Sket, February 1985; Cansista Cave, 1 ♀ paratype, T. M. Iliffe and D. Williams, 2 April 1985; Victoria Memorial Park Cave, Taloto, 6 paratypes, T. M. Iliffe and D. Williams, 9 April 1985; Tauala Cave, 57 paratypes, 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 XXXXXXX); paratypes are deposited in the National Museum of Natural History (USNM 364310) and Ljubljana University.

Diagnosis.—Small stygobitic species of subterranean facies distinguished by a relatively short segment 3 of the maxilliped palp and relatively few D-setae but with segment slightly longer and slightly more D-setae than *Hadzia guamensis*, and *H. palauensis*; trifurcate lacinia mobilis on right mandible; without spines on ventral margins of pleonal plates 2 and 3 (except *H. palauensis*); 2 basofacial spines on uropod 1. Largest males 3.0 mm; largest females 3.0 mm.

Description.—Antenna 1 ca. 1.1 times longer than body, 2.4 times longer than antenna 2, primary flagellum with up to 20 segments, aesthetascs present on flagellar segments 6-19; accessory flagellum 2-segmented, the second segment reduced. Antenna 2 with up to 6 segments. Mandible: right mandible molar prominent, with seta, lacinia mobilis trifurcate, larger two trifurcations with small serrated teeth, incisor 6 dentate, up to 5 accessory spines; left molar prominent, without seta, lacinia mobilis 4 dentate, normal, incisor 6 dentate; palps bearing 6 D-setae. Lower lip without inner lobes. Maxilla 1: inner plate bearing up to 11 apical setae, naked under light microscopy; outer plate with 8 apical comb spines; palps 2 segmented, asymmetrical, right palp bearing 5 stout spines and 1 seta along apical margin, left palp bearing 5 slender spines and 1 seta along apical margin. Maxilla 2: inner lobe narrowing distally, with oblique submarginal row of up to 12 naked setae. Maxilliped: inner plate narrow, not expanded, bearing 7-8 blade spines along apical margin; outer plate expanded along outer margin, bearing 3-4 large bladespines on inner apical margin; palp 3 segmented, segment 3 excavate, pubescent distally.

Gnathopod 1: propod 86% length of carpus, palm transverse, with up to 8 setae of variable length, posterior margin ca. 2 times longer than palm bearing few setae; dactyl subequal in length to palm; carpus posterior margin moderately produced bearing numerous long setae; merus slightly expanded along medial-posterior margin, pubescent; basis bearing few long setae; coxa deeper than broad, bearing 3 marginal spines. Gnathopod 2: propod elongate, ca. 1.5 times longer than carpus, palm oblique, shorter than posterior margin of propod, bearing double row of 8 spines, numerous setae of various lengths with 2 stout spines and 2 long setae at defining angle; dactyl subequal to palm; carpus subtriangular, posterior margin lobiform and pubescent; basis with few long setae; coxa deeper than broad with up to 3 marginal spines. Pereopod 3 subequal to 4, coxa deeper than broad, bearing 3-4 marginal setae; basis weakly expanded, bearing up to 6 setules. Pereopod 4: coxa larger than pereopod 3, only slightly deeper than broad, not excavate posteriorly, bearing up to 4 setules on the distal margin; basis slightly expanded relative to pereopod 3, bearing up to 7 setae. Pereopod 5 ca. 64% length of body, pereopod 6 ca. 89% length of body, pereopod 7 ca. 77% length of body. Bases of pereopods 5-7 not expanded, pereopods 5 and 6 distoposterior lobes not developed, weakly developed on pereopod 7; dactyl of pereopod 5 ca. 52% length of corresponding propod, dactyls of pereopods 6 and 7 ca. 36% length of corresponding propods. Coxal gills on 2-6, relatively small, subovate, with distinct peduncles; brood plates subequal in length to gills, stout, setose distally.

Pleonal plates bearing 1 small setule on posterior margins, distoposterior margins weakly produced, without spines on ventral margins. Pleopods bearing 2 small coupling spines each. Uronites not fused, without spines. Uropod 1: outer ramus ca 93% length of outer, ca. 68% length of peduncle, bearing 4-5 apical and 2 lateral spines; inner ramus ca. 74% length of peduncle bearing up to 5 apical and 2 lateral spines; peduncle with 9 spines, 2 of which are basofacial. Uropod 2: outer ramus ca. 67% length inner, 78%

length of peduncle bearing 5-6 apical spines, upper margin with row of small tooth spines; inner ramus ca. 1.1 times longer than peduncle bearing 6 apical and 3 lateral spines, upper margin with row of small tooth spines; peduncle with 7 spines, 4 of which form short comb row. Uropod 3: ca. 24% length of body; inner ramus 95% length of outer, bearing 8 spines; outer ramus 2 segmented, first segment bearing 4 apical and 8 lateral spines; peduncle bearing 1-2 spines. Telson longer than broad, each lobe bearing 6 spines.

Male.—Differing from female as follows: gnathopod 2: dactyl and propod proportionately longer and broader; palm long, oblique, with double row of 8 spines, defining angle with 2 spines and 2 long setae; posterior margin of propod with 4 setae.

Etymology.—The epithet *philippinensis* is based on the occurrence of this species in the Philippine archipelago.

Type-locality.—The type-locality, Well no. 1, Danao/L. Tauala, Panglao Island, is just off the coast of Bohol Island (Fig. 5.22).

Ecology and Distribution.—*Hadzia philippinensis* is recorded from four locations on Panglao Island, Bohol. Tauala Cave is a sinkhole containing a pool regularly used by local villagers for bathing and washing laundry. Water temperature and salinity were respectively $4^{o}/_{oo}$ and 29°C at the time of collection. Cyclopoid copepods, ostracods, isopods (Gnathiidea sp.), mollusks and crabs were also collected. Cansista Cave is a collapse sinkhole containing a pool in darkness about 8 to 10 m below the surface of the ground. Salinity in the pool was $6^{o}/_{oo}$ and maximum depth about 4 m. Also collected from the cave pool were shrimp, isopods (Gnathiidea sp.), mollusks, crabs and polychaetes. Victoria Memorial Park Cave occurs in a cemetery on the outskirts of Tagbilaran City. This small collapse cave contains a clear pool in total darkenss floored with gravelly breakdown. In addition to amphipods, shrimp, ostracods and cyclopoid copepods were also collected.

Hadzia spinata, n. sp.

Figs. 5.11-5.15

Material Examined.—PALAU. Ngermeuangel: Lake 2A Cave, ♀ holotype (4.5 mm), T. M. Iliffe and J. Bozanic, 2 March 1985; 1 ♀ paratype, T. M. Iliffe and D. Williams, 14 March 1985; Urukthapel (Ngeruktabel) Island , Cenote Cave, 1 ♀ paratype, T. M. Iliffe and D. Williams, 2 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 XXXXXXX); paratypes are deposited in the National Museum of Natural History (USNM 364310).

Diagnosis.—Medium sized stygobitic species distinguish by gnathopod 1 carpus relatively elongate, highly setose; gnathopod 2 carpus relatively elongate, distoposterior margin not expanded apically; female gnathopod 2 palm oblique, longer than posterior margin of propod, strongly armed with double row of spines; uropod 3 outer ramus lower margin with plumose setae; uropod 3 relatively elongate. Male unknown; largest females 6.0 mm.

Description.—Antenna 1 ca. 1.4 times longer than body, 2 times longer than antenna 2, primary flagellum with up to 33 segments, aesthetascs present on flagellar segments 16-30; accessory flagellum 2-segmented, the second segment well developed. Antenna 2 with up to 9 segments. Mandible: right mandible molar prominent with seta, lacinia mobilis bifid, both bifurcations bearing small, serrated teeth, incisor 5 dentate, up to 5 accessory spines; left molar prominent, without seta, lacinia mobilis 4 dentate, normal, incisor 5-6 dentate; palps bearing up to 13 D-setae. Lower lip without inner lobes. Maxilla 1: inner plate bearing up to 14 apical setae, naked under light microscopy; outer plate with 8 comb spines; palps 2 segmented, virtually symmetrical, up to 7 relatively stout spines and 5 long setae along apical margin. Maxilla 2: inner lobe narrowing distally, with oblique submarginal row of up to 16 naked setae. Maxilliped: inner plate narrow, inner-apical margin bearing 2-3 heavy spines; outerplate expanded slightly bearing 5-6 blade spines along inner margin; palp 3 segmented, segment 3 excavate, pubescent distally.

Gnathopod 1: propod ca. 58% length of carpus, palm weakly oblique, bearing double row of up to 10-11 small spines, 5 setae of various lengths and 4 stout, bifurcated spines at the defining angle, posterior margin slightly shorter than palm; dactyl subequal in length to palm; carpus posterior margin not produced bearing 5 sets of long setae of varying number, anterior margin bearing 6 sets of long setae of varying number; merus posterior margin expanded medially, pubescent, bearing numerous long setae along distoposterior margin; basis bearing numerous setae along both the anterior and posterior margin; coxa deeper than broad, bearing up to 7 marginal spines. Gnathopod 2: propod elongate, ca. 1.4 times longer than carpus, palm oblique, longer than posterior margin of propod, bearing a double row of up to 15 stout spines, up to 8 setae of varying lengths, and 6 setae at the defining angle; dactyl subequal to palm; carpus elongate, weakly subtriangular, distopostrior margin weakly pubescent, posterior margin bearing 8 sets of long setae of varying number; basis with 7 long setae along posterior margin and few short setae along anterior margin; coxa deeper than broad with up to 10 marginal spines. Pereopod 3: subequal in length to 4, coxa deeper than broad bearing 10 marginal setae; basis not expanded, bearing 6 setae on both the anterior and posterior margins. Pereopod 4: coxa larger than 3, only slightly deeper than broad, not excavate posteriorly, bearing up to 14 marginal setules; basis not expanded bearing 7 setae along posterior and 5 setae along anterior margin. Pereopod 5: ca. 94% length of body, pereopod 6 ca. 1.3 times length of body, pereopod 7 ca. 1.18 times length of body; bases of pereopods 5-7 weakly expanded, distoposterior lobes present; dactyl of pereopod 5 ca. 36% length of corresponding propod; dactyl of pereopod 6 ca. 21% length of corresponding propod; dactyl of pereopod 7 ca. 20% length of corresponding propod. Coxal gills on 2-6 relatively large, subovate, with distinct peduncles; brood plates relatively long, narrow, and nonsetose in material examined.

Pleonal plates bearing 2-4 small setules on posterior margins, distoposterior margins weakly produced; pleonal plate 2 bearing 2 spines on ventral margin; plate 3 with 3 spines on ventral margin. Pleopods bearing 2 small coupling spines each. Uronites not fused; uronite 2 with 2 dorsolateral spines on posterior margin. Uropod 1: rami subequal in length, 95% length of peduncle, inner ramus bearing 4 apical and 2 lateral spines; outer ramus bearing 4 apical and 4 small lateral spines; peduncle bearing 11 spines, 1 of which is basofacial. Uropod 2: outer ramus ca. 90% length of inner, 90% length of peduncle, bearing 4 apical spines and 3 sets of doubly inserted lateral spines; inner ramus subequal in length to peduncle, bearing 4 apical and 7 lateral spines, upper margin with row of small tooth spines; peduncle with 12 spines, 10 of which form strong comb row on dorsodistal end. Uropod 3: about 50% length of body, rami subequal in length ca. 2.5 times longer than peduncle, inner ramus bearing up to 25 spines; outer ramus 2 segmented, first segment with 5-6 apical spines, upper margin with 5 sets of triply inserted spines, lower margin with 6 spines and 6 plumose setae; peduncle with 3 spines. Telson longer than broad, each lobe with about 7 spines.

Etymology.—The epithet *spinata* is from the latin *spina* and is based on the relatively long, double set of spines on the palms of female gnathopods 1 and 2.

Type-locality.—The type locality, Lake 2A Cave, is located about 40 m inland from the eastern coast of Ngermeuangel Island, Palau (Fig. 5.23).

Ecology and Distribution.—Lake 2A Cave is roughly triangular in shape, 110 m long by 50 m wide and 15 m deep. The 4-5 m wide by 2.5 m high underwater entrance to Lake 2A Cave is in the northwestern corner of the lake. A spacious, completely submerged chamber extends back over 160 m from the entrance to a silt plug at 36 m depth. Massive sponge-covered stalactites and columns partition the chamber, while thick silt covers the floor. Slight water currents were observed only at the entrance and at the restriction in the deepest part of the cave. Salinity at 10-24 m depths was $31^{0}/_{00}$ and the temperature was 29°C. Taxa previously described from this cave include the mysid *Palaumysis simonae*, the tanaidacean *Apseudes bowmani* and the halocyprid ostracod *Euconchoecia bifucata pax.* Also collected from the cave were calanoid, harpacticoid and cyclopoid copepods, polychaetes and shrimp.

This species is also recorded from Cenote Cave on the island of Ngermeuangel in Palau. The cave was named for its resemblance to the cenotes or sheer-walled limestone sinkholes with water that is common to the Yucatan Peninsula karst. This cave, located about 75 m inland from the coast, is a 15 m diameter, 20 m deep pit that requires ropes to descend. A large clear pool at the bottom of the shaft extends back under an overhang into a short, dimly illuminated section of the cave. The pool is floored with a jumble of breakdown rock and several large logs, pinching out at a maximum depth of 11 m. The disarticulated remains of at least four human skeletons were found scattered in the rear section of the pool. Surface water temperature in the pool was 26.3°C, while at 11 m the temperature and salinity were 28.8°C and $26^{o}/_{oo}$, respectively. Other specimens collected from the cave-included isopods (*Limnoria* sp.), ostracods, calanoid copepods (Epacteriscidae), fish larvae, polychaetes, ophuiroids and shrimp. Also found were specimens of a primitive new genus of misophrioid copepod represented by three species inhabiting anchialine caves on opposite sides of the Pacific and in the eastern Atlantic (Boxshall and Iliffe 1987, 1990). *Expansophria apoda* was described from Cenote Cave, while *E. dimorpha* inhabits an anchialine lava tube cave in the Canary Islands and *E. galapagensis* was collected from deep tectonic fissures in coastal volcanic rocks of the Galapagos Islands. A second species of misophrioid, *Misophria kororiensis*, was found in South Point Cave on Koror Island, Palau (Boxshall and Iliffe 1987)

Hadzia palauensis, n. sp.

Figs. 5.16-5.19

Material Examined.—PALAU. Eil Malk Island: Tide Rope Cave, ♀ holotype (2.0 mm), 2 ♀ paratypes, 1 ♂ paratype,T. M. Iliffe and D. Williams, 10 March 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 XXXXXXX); paratypes are deposited in the National Museum of Natural History (USNM 364310).

Diagnosis.—Small stygobitic species distinguished from all species of *Hadzia* except *H. philippinensis* by having a relative short segment 3 of the mandibular palp and relatively few D-setae on segment 3 of the mandibular palp, except *H. guamensis*; relatively few apical setae on the inner lobe of maxilla 1; relatively few setae on the inner margin of segment 2 of the maxilliped palp; article 5 of gnathopod 1 weakly pubescent; without spines on ventral margins of pleonal plates 2 and 3, except *H. philippinensis*; both rami of uropod 3 with relatively few spines (similar to *H. guamensis*). Largest males 2.0 mm; largest females 2.0 mm.

Description.—Antenna 1 ca. 89% length of body, 1.77 times longer than antenna 2, primary flagellum with up to 12 segments, aesthetascs present on flagellar segments 4-11; accessory flagellum 2 segmented, the second segment well developed. Antenna 2 flagellum with up to 5 segments. Mandible: right mandible molar prominent, apparently with seta, lacinia mobilis bifid, both bifucations bearing small, serrated teeth, incisor 6 dentate, up to 4 accessory spines; left molar prominent, without seta, lacinia mobilis 5 dentate, normal, incisor 6 dentate; palps bearing 4-5 D-setae, palp segment 3 relatively short, stout. Lower lip unknown. Maxilla 1: inner plate with up to 7 apical setae, naked under light microscopy; outer plate with 7 comb spines; palps 2 segmented, asymmetrical, right palp bearing 5 stout spines and 1 seta along apical margin, left palp bearing 5 relatively slender spines and 1 seta along apical margin. Maxilla 2: inner lobe narrowing slightly distally, with oblique submarginal row of up to 9 naked setae.

Maxilliped: inner plate narrow, bearing few spines along apical-innerapical margin; outer plate expanded relative to inner with 4-5 stout spines along inner margin; palp 3 segmented, segment 3 excavate, pubescent distally.

Gnathopod 1: propod ca.67% length of carpus, palm transverse, bearing few setae and 3 spines at the defining angle, posterior margin slightly longer than palm; dactyl longer than palm; carpus posterior margin not produced bearing up to 3 long setae, distomedial margin with 4 long setae, 2 setae on the anterior margin; merus distoposterior margin expanded, weakly pubescent, bearing 2-3 long setae on distoposterior margin; basis bearing 2 long setae on the posterior margin; coxa slightly deeper than broad, expanded distally with up to 3 marginal spines. Gnathopod 2: propod elongate, ca. 1.9 times longer than carpus, palm oblique, slightly shorter than posterior margin of propod, bearing double row of 4 spines, 3-4 setae of varying length, and 2 large spines and 2 setae at the defining angle; dactyl subequal in length to palm; carpus subtriangular, posterior margin pubescent bearing up to 9 setae; basis bearing 2 long setae along the posterior margin; coxa deeper than broad with 2 marginal spines. Pereopod 3: subequal in length to 4, coxa deeper than broad bearing 2-3 marginal setae; basis not expanded bearing up to 5 small spines. Pereopod 4: coxa about as deep as broad, not excavate posteriorly, bearing 4 small marginal spines; basis not expanded armed with only 1 small spine along posterior margin. Pereopod 5: ca. 70% length of body, pereopod 6 ca. 90% length of body, pereopod 7 relative length unknown; bases of pereopods 5-7 not expanded, distoposterior lobes weakly developed; dactyl of pereopod 5 ca. 53% length of corresponding propod, dactyl of pereopod 6 ca. 42% length of corresponding propod, dactyl of pereopod 7 unknown. Coxal gills on 2-6 relatively large, subovate, with distinct peduncles; broodplates relatively short, narrow, and nonsetose in material examined.

Pleonal plates bearing 1 small spine on posterior margins, distoposterior margins weakly produced; no spines on ventral margins. Pleopods bearing 2 small coupling spines each. Uronites not fused, without spines. Uropod 1: outer ramus ca. 80% length of inner, 63% length of peduncle, with up to 4 apical and 1 lateral spine; inner ramus ca. 79% length of peduncle, bearing 4 apical and 1 lateral spine; peduncle with 5 spines, 1 of which is basofacial. Uropod 2: outer ramus ca. 71% length of inner, 81% length of peduncle, with 6 apical and 1 lateral spine; inner ramus ca. 1.2 times longer than peduncle, with 5 apical, 2 lateral spines and upper margin with row of small tooth spines; peduncle with 2 spines on dorsodistal end. Uropod 3: about 27% length of body, rami subequal in length; inner ramus bearing up to 7 spines; outer ramus 2 segmented, first segment with 2 apical and 5 lateral spines; peduncle with 2 spines. Telson longer than broad, each lobe with about 5 spines.

Male.—Differing from female as follows: gnathopod 1: almost identical except palm with 3-4 additional small spines. Gnathopod 2: dactyl and propod proportionately longer and broader; palm long, oblique, with double row of 10 spines, defining angle with 2-3 spines and 1 seta; posterior margin with up to 3 setae (Fig. 23).

Etymology.—The epithet *palauensis* refers to the occurrence of this species in the Palau archipelago.

Type-locality.—This species is known only from its type-locality, Tide Rope Cave on Eil Malk Island, Palau (Fig. 5.23).

Ecology and Distribution.—Tide Rope Cave is a narrow intertidal fissure extending inland from the shoreline of an enclosed marine lake. A knotted rope, hung in the lake near the cave entrance and presumably used for tidal measurements by Dr. William Hamner, gave the cave its name. The cave is about 15 m long with depths to 1.5 meters and possesses moderate tidal currents. Also collected from this cave was a new species of tanaidacean, *Nesotanais maclaughlinae*, with its only congener inhabiting an anchialine lake on Rennell Island in the Solomon Islands (Gutu and Iliffe 1989).

DISCUSSION

With the description of the four new species herein and the synonymy of *Liagoceradocus*, 14 species are now assigned to the genus *Hadzia*. Previously, *Hadzia* was restricted to two species, *H. fragilis* and *H. gjorgjevici*, both found in the western part of the former Yugoslavia. *Hadzia fragilis* is recorded from localities near the Adriatic coast and *H. gjorgjevici* from more inland localities, near Skopje, in Macedonia (Ruffo and Krapp-Schickel 1969). *Liagoceradocus* was almost entirely restricted to the Indo-Pacific region except for *L. acutus* from Lanzarote in the Canary Islands.

The description of four new species of *Hadzia* from the Philippines, Palau and Guam greatly extends the range of the genus as we have defined it in this paper (Fig. 5.20). We predict that as suitable habitats are sampled on West Pacific islands east of Guam, additional species of *Hadzia* will be discovered, further bridging the gap between the western Pacific species, and *H. lonomaka* in the Hawaiian Islands.

The new species of *Hadzia* also possess many characters that apparently bridge the morphological gaps previous authors have used to separate *Hadzia* from *Liagoceradocus*. Stock (1983) and Rondé-Broekhuizen and Stock (1987) listed numerous characters, considered synapomorphic for species of *Liagoceradocus*, to separate the genera (Table 5.1). However, every character used to define *Liagoceradocus* in the past has exceptions. It is noteworthy that most, but not all of these exceptions, are found within the four new species described in this study.

In addition, many characters unite the species now assigned to *Hadzia*: 1) presence of large aesthetascs on antenna 1 (a character not common on many closely related genera within the family Hadziidae); 2) lacinia mobilis on right mandible usually bifurcate (*H. philippinensis* is the only exception), with serrate margins; 3) asymmetrical palps on the first maxilla; 4) inner lobes of lower lip absent. In addition, there is a high degree of similarity in the gnathopods, pereopods, and uropods.

One other character may also unite these species: segment 3 of the maxilliped palp is excavate and pubescent distally. Examination of the literature suggests this character may be present many species of *Hadzia*. The presence or absence of this character is very difficult to determine under light microscopy and scanning electron micrographs of this appendage in other species of the genus is necessary to determine whether or not it is found in all species of *Hadzia*.

Hadzia, as defined in this paper, is closely similar morphologically to both *Metahadzia* and *Metaniphargus*. The former genus consists of six species, five recorded from the greater Mediterranean region and one from Somalia in eastern Africa. *Metahadzia* is differentiated from *Hadzia* on the basis of two characters that include a comparatively elongate mandibular palp with concave inner margin and absence or near absence of D-setae on this segment. Both of these characters appear to be apomorphic and may well be derived from the plesiomophic state of these characters in the genus *Hadzia*.

Metaniphargus consists of approximately 22 species, all recorded from the West Indian region except one from Oahu in the Hawaiian Islands (see Stock, 1985; Vonk, 1991). As far as we can determine only the proportionately shorter inner ramus (endopodite) of uropod 3, which according to Stock (1985) is "(much) shorter than the exopodite," morphologically separates this genus from *Hadzia.*

Table 5.1. Characters considered synapomporhic for *Liagoceradocus* species by Stock (1983) and Rondé-Broekhuizen and Stock (1987), and the species that show exception to these.

Characters considered syanapomorphic for *Liagoceradocus* species	***Hadzia* species (as currently defined) which are exceptions**
Sexual dimorphism of propod of gnathopod 1.	*H. guamensis; H. philippinensis* (no sexual dimorphism)
Sexual dimorphism of propod of gnathopod 2.	*H. fragilis; H. gjorgjevici* (sexual dimorphism present)
Widening of the outer lobe of the maxilliped.	*H. palauensis; H. guamensis* (outer lobe not widened)
Absence of plumose setae on both rami of uropod 3.	*H. spinata*; *H. lonomaka*; *H. branchialis* (plumose setae present on at least one ramus)
Presence of dorsodistal combspine row on the peduncle of uropod 2.	*H. palauensis; H.guamensis* (combspine row vestigial or absent)
Carpus of gnathopd 1 elongate, almost linear, not triangular to trapezoidal	*H.guamensis; H. philippinensis; H. palauensis* (carpus subtriangular)

In addition, with exception of the single species in the Hawaiian Islands, *Metaniphargus* is geographically restricted to the West Indies. However, in *Metaniphargus jamaicae* from Jackson Bay Cave, which was originally placed in the genus *Hadzia* (Holsinger, 1974) and possibly one or more other species (e.g., *M. plumicauda* from Haiti – see Stock, 1985), the inner ramus of uropod 3 in some specimens approaches the length of the outer ramus. The reliability of this character is thus somewhat questionable, and if nothing else is strong evidence for an extremely close relationship between these two genera. Also of interest is the presence of both

Metaniphargus and *Hadzia* in the Hawaiian Islands, where *M. laakona* is recorded from the intertidal of Kawela Bay, Oahu (Vonk, 1991), and *H. lonomaka* is described from Cape Kinau, Maui (Barnard, 1977). Morphologically primarily the relative length of the inner ramus of uropod 3 separates these species, which is proportionately much longer in *Metaniphargus laakona.* The latter species also differs by having a recurved lobe on the first segment of the endopodite of pleopod 3 and a much longer distal spine on the peduncle of uropod 1. As presently known, both species are sole representatives of their respective genera in the Hawaiian Islands, where they are apparently geographically remote from other species in either genus. However, Vonk (1991) called attention to the morphological similarity of *M. laakona* and *M. sabulonis* from Grand Cayman Island in the Caribbean and suggested that populations of *Metaniphargus* might have expanded their range from the Caribbean westward into the eastern Pacific prior to the closing of the isthmian corridor in the late Miocene. *Hadiza* on the other hand has a much broader distribution (Fig. 5.20) and probably reached the Hawaiian Islands from other parts of the Pacific. An alternative hypothesis for the occurrence of these two closely similar genera in the Hawaiian Islands is that *Metaniphargus* arose independently in the Pacific from a putative ancestor common to both this genus and *Hadzia.*

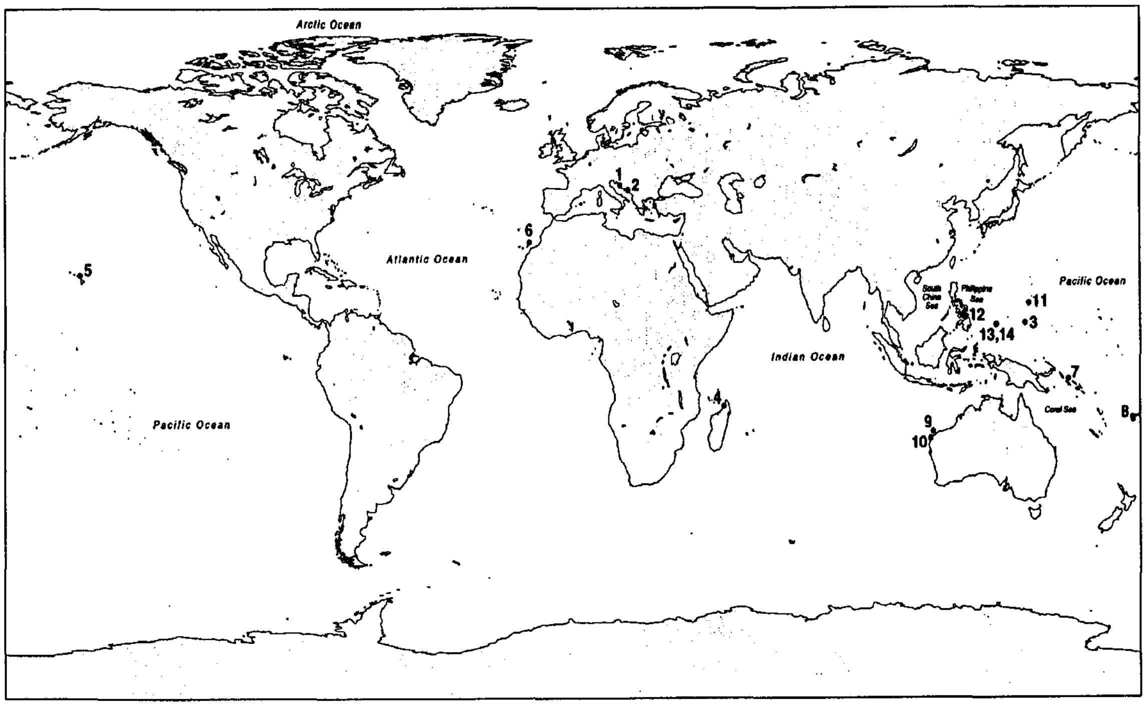

Fig. 5.20. Global distribution of species of the genus *Hadzia*. Solid circles indicate known localities as follows: 1) northwest coastal area of Croatia, near Dubrovnik and just inland from Dubrovnik in Herzegovina, hyporheic waters in the Drina River near Titograd, in Montenegro and in northeastern Italy near La Peschiera del Timavo – *H. fragilis*; 2) two locations near Skopje, in Macedonia and freshwater caves near Titograd, in Montenegro – *H. gjorgjevici*; 3) Ifaluk Atoll, Caroline Islands – *H. pusilla*; 4) Platier á microatolls de Sarodrano, Madagascar – *H. dentifera*; 5) Maui, Hawaiian Islands – *H. lonomaka*; 6) Lanzarote Island, Canary Islands – *H. acuta*; 7) Basakana Island, Solomon Islands – *H. lobifera*; 8) Vatulele Island, Fiji – *H. uncifera*; 9) Barrow Island, Western Australia – *H. subthalassica*; 10) Cape Range Peninsula, Western Australia – *H. branchialis*; 11) Guam – *H. guamensis* (see also Fig. 5.21); 12) Panglao Island, Bohol, Philippines – *H. philippinensis* (see also Fig. 5.22); 13) Ngeruktabel Island, Palau – *H. spinata* (see also Fig. 5.23); Eil Malk Island, Palau – *H. palauensis* (see also Fig. 5.23).

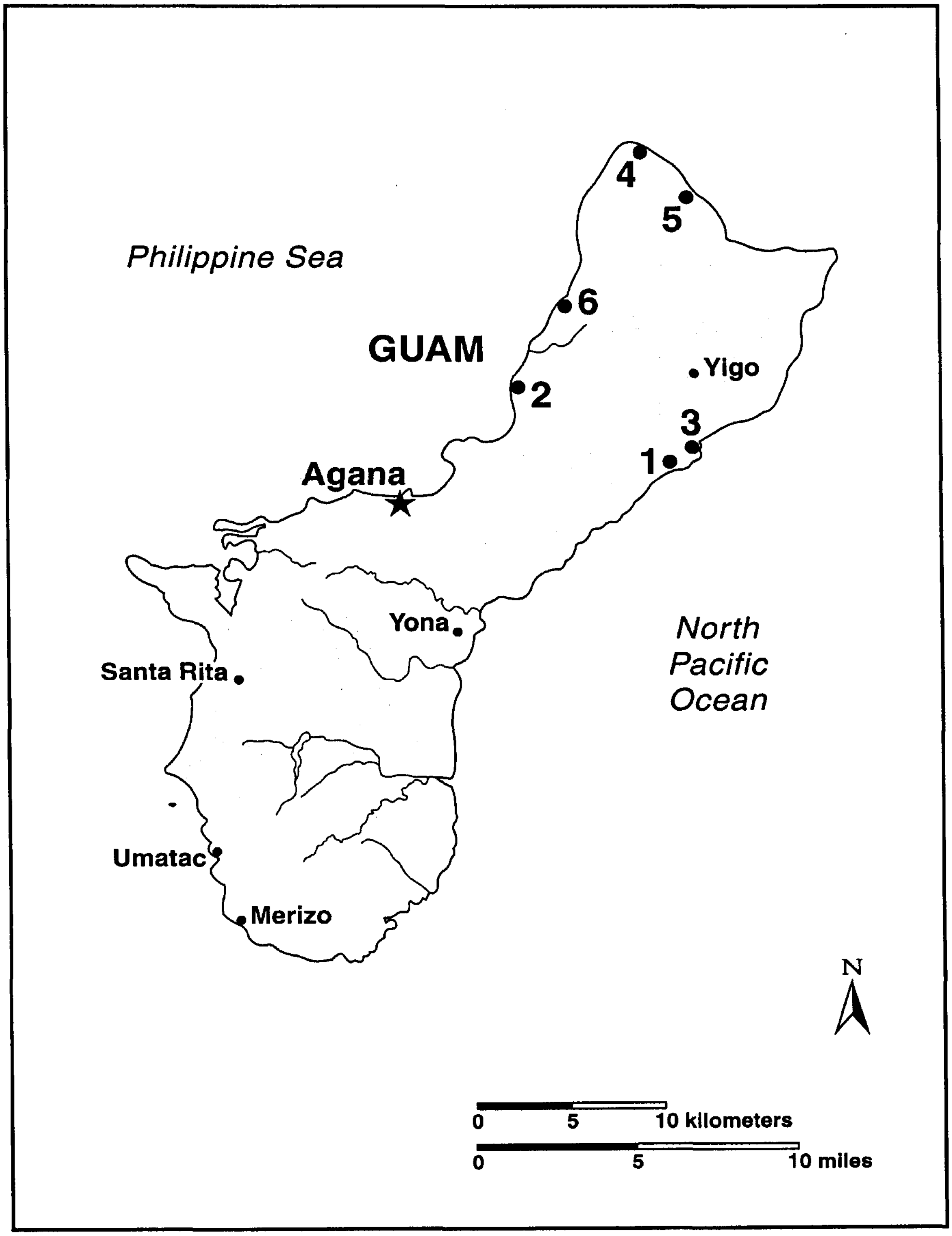

Fig. 5.21. Geographic distribution of *Hadzia guamensis* on the island of Guam. Solid circles indicate known localities as follows: 1) Marbo Cave; 2) Faifai Cave; 3) Pagat Point Cave; 4) Ritidian Cave; 5) Tarague Water Well No. 4; 6) Tweed's Cave.

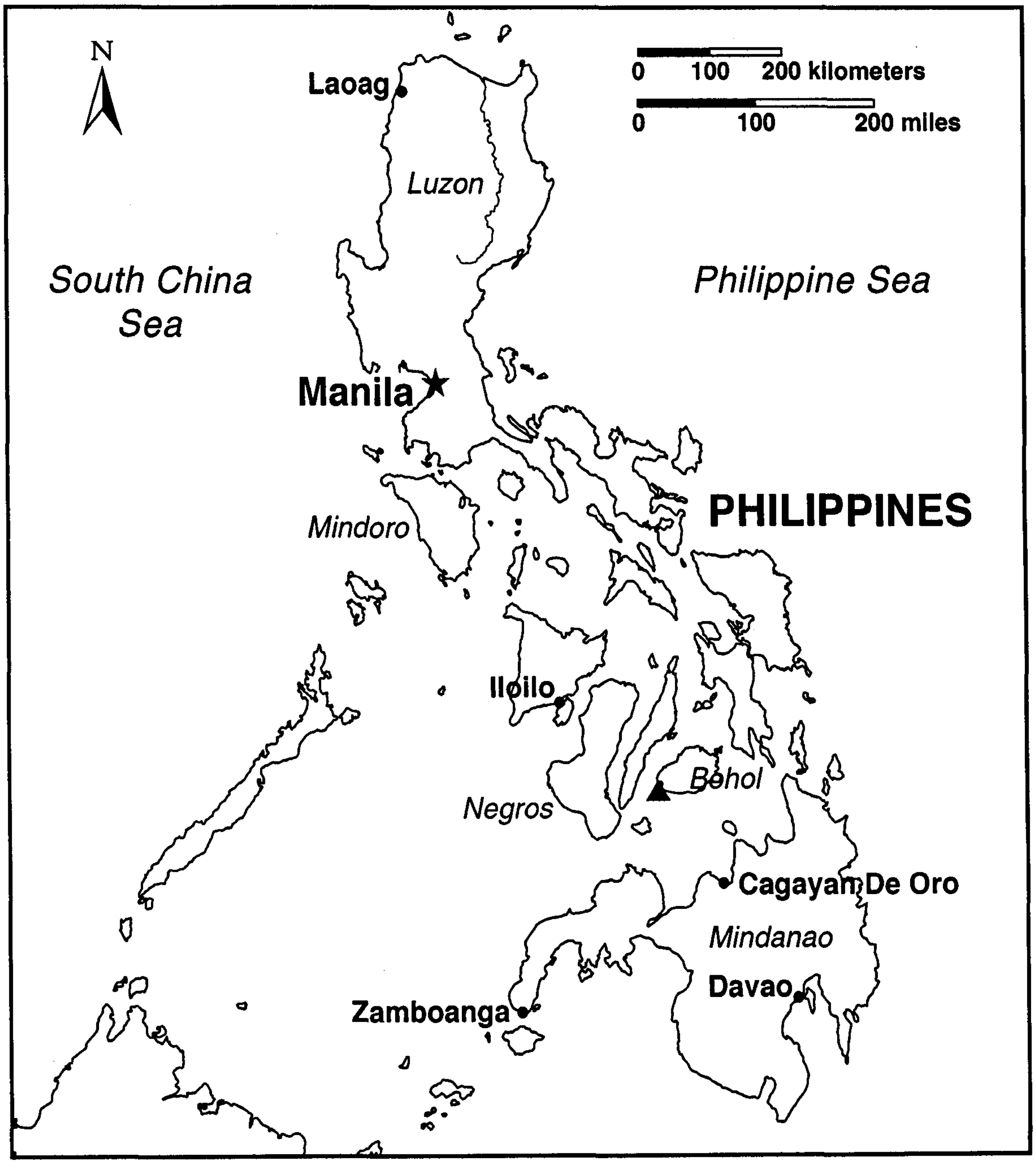

Fig. 5.22. Geographic distribution of *Hadzia philippinensis* on Panglao Island, Bohol, Philippines. Solid triangle indicates the location of the island on the southwest corner of the island of Bohol. *Hadzia philippinensis* was collected from the following locations: 1) Well no. 1, Danao/L. Tauala; 2) Cansista Cave; 3) Victoria Memorial Park Cave; 4) Tauala Cave.

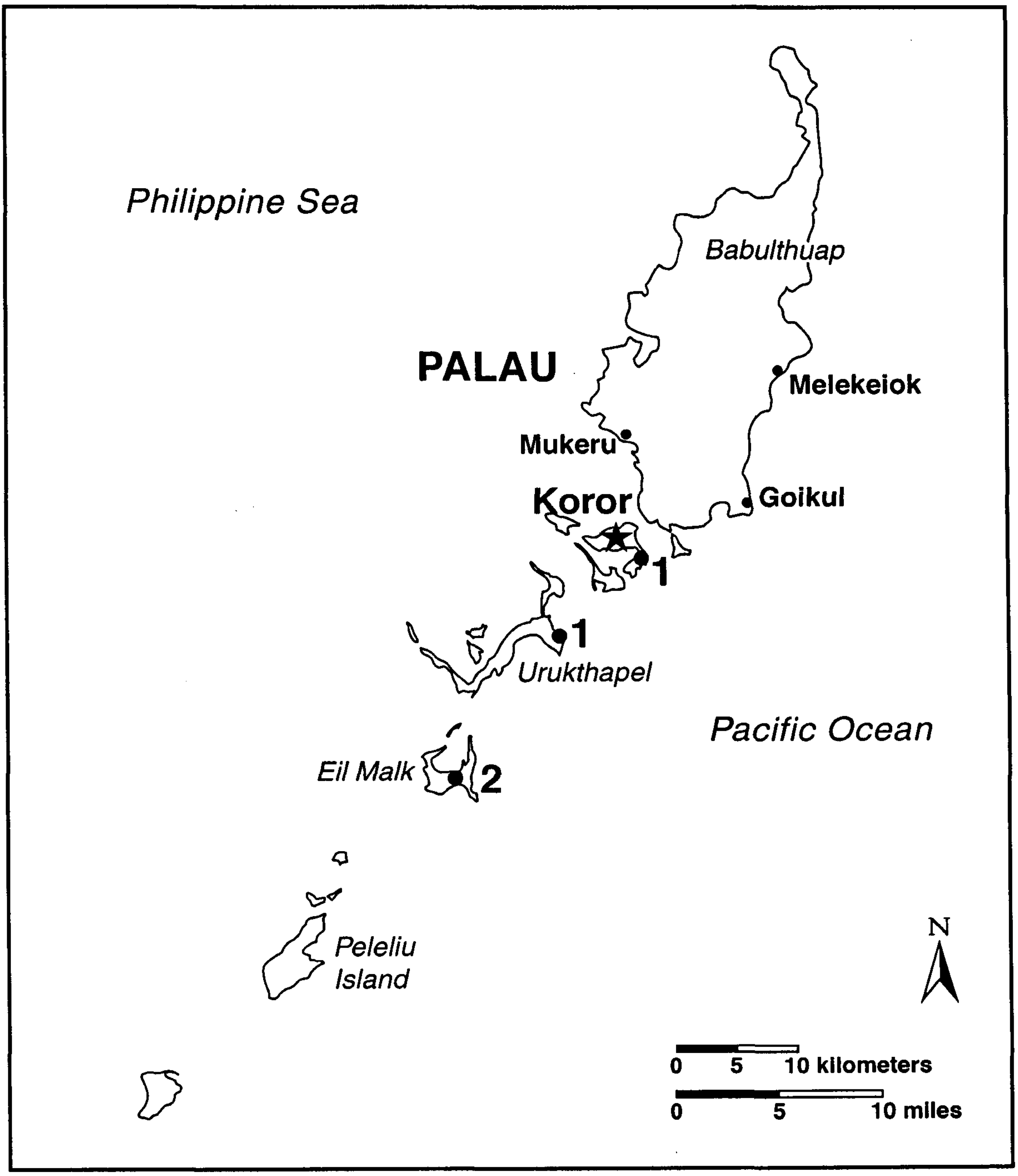

Fig. 5.23. Geographic distribution of *Hadzia* species on islands in the Palau archipelago. Solid circles indicate known localities as follows: 1) *H. spinata* – Lake 2A cave, Ngermeuangel Island, and Cenote Cave, Urukthapel (Ngeruktabel) Island; 2) *H. palauensis* – Tide Rope Cave, Eil Malk Island.

SECTION 6

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

The genus *Tegano* was described 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 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 epigean, the description of this species brings the number of species in the genus recorded from subterranean waters to seven. The genus *Paraniphargus* from the Andaman Isles and Java is synonymized with *Melita*, and the taxonomic status of *Abludomelita* and *Melita* is discussed.

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 stongly 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 *Quadras* 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* have a number of synapomorphies that link these genera: 1) usually with distinct, pigmented ommatidia; 2) usually with highly setose antenna 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 not usually 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 n. sp.

Figs. 6.1-6.5

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 XXXXXXX).

Diagnosis.—Small to medium sized species distinguished by a 3-segmented mandibular palp (except *T. excavatus*); 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, ca. 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 7-dentate, with 4 serrate accessory spines; palp's 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; palps 2 segmented, virtually symmetrical, bearing 6 apical spines and 3 subapical setae. Maxilla 2: inner plate narrowing distallybearing 9-10 setae along inner margin. Maxilliped: inner plate relatively narrow, bearing few spines along the apical magin; outer plate expanded, bearing numerous spines along inner and apical margins; palp 3-segmented, apical margin of segment 3 with setae.

Gnathopod 1: propod ca. 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, ca 2.1 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 pocket proximal to the defining angle; dactyl curves back on palm, insets slightly in propod; propod posterior margin bearing 5 sets of numerous setae, longer than palm; 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 5 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 ca. 52% length of body, pereopods 6 and 7 subequal ca. 60% length of body; bases of pereopods 5-7 not expanded, distoposterior lobes not developed; dactyls of pereopods 5 and 6 ca. 30% length of corresponding propods; dactyl of pereopod 7 ca. 21% length of corresponding propod. Coxal gills on 2-6 relatively large, subovate, with distinct peduncles.

Pleonal plates distoposterior margins with small tooth-like extensions; 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 ca. 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 ca. 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 "*clavat*" comes from the latin for club and is based on the club-like propods of gnathopod 1 and gnathopod 2.

Type-locality.—This species is known only from its type-locality, Tauala Cave, Panglao Island, Bohol, Philippines (Fig 6.21). Tauala Cave is presumably 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 $4^{0}/_{00}$ at the time of collection. Cyclopoid copepods, ostrocods, isopods, molluscs, crabs and a new species of *Hadzia* (Sawicki, Holsinger and Iliffe, in ms) were also collected.

Tegano panglaoensis n. sp.

Figs. 6.6-6.9

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 States National Museum (USNM XXXXXXX); paratypes are in the collection of Ljubljana University.

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; female 2.0 mm.

Male.—Eye present. Antenna 1 ca. 1.1 times longer than body, ca. 1.66 times longer than antenna 2, primary flagellum with 13 segments; accessory flagellum 2-segmented, second segment highly vestigial. Antenna 2 flagellum 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 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 bearing 4 large bladespines, inner margin with numerous spines; palp 3-segmented, segment 3 bearing numerous setae along inner apical margin.

Gnathopod 1: propod ca. 80% length of carpus, palm transverse, bearing double row of 5-6 spines, 2-3 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 anterior margin with up to 5 long setae; coxa deeper than broad, with 6 marginal setae. Gnathopod 2: propod elongate, ca. 2.2 times longer than carpus, palm oblique with 6 spines, 2 at the defining angle and 4 setae, 1 at the defining angle, propod posterior margin bearing subequal in length to palm with 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 gnathopod 1, with 5 marginal setae. Pereopod 3: subequal in length to 4, coxa slightly deeper than broad with 6 marginal setae, basis slightly expanded bearing 5 long setae along posterior margin. Pereopod 4: coxa slightly 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 2-6 small, subovate, with distinct peduncles.

Pleonal plates distoposterior margins with small tooth-like extensions; 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 3 apical and 2 lateral spines; peduncle bearing 7 spines, 1 of which is basofacial. Uropod 2: outer ramus 75% length of inner with 4 apical and 1 lateral spine; inner ramus 92% length of peduncle with 4 apical and 2 lateral spines; peduncle bearing 4 spines. Uropod 3: ca. 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 one seta.

Female.—Differing from male as follows: Gnathopod 2: dactyl and propod proportionately shorter and narrower; propod only 1.07 times 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, posteriorventral margin bearing row of 11 short spines.

Etymology.-- The epithet *panglaoensis* denotes the presence of this species on Panglao Island, Bohol, Philippines.

Type-locality.—Hinagdanan Cave, Panglao Island, Bohol, Philippines (Fig 6.21). This species is known only from its type locality.

Tegano barnardi n. sp.

Figs. 6.10-6.14

Material Examined.—PALAU. Peleliu Island: Airport Well Cave, ♂ holotype (4.5 mm), 35 ♀ paratypes, 22 ♂ 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 XXXXXXX); paratypes are in the collection of J. R. Holsinger (H-3730) and the National Museum of Natural History (accession number 364310).

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

Female.—Antenna 1 ca. 1.3 times longer than body, ca. 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; palps 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 3-segmented, segment 3 with numerous long setae apically.

Gnathopod 1: propod ca. 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 ca. 86% longer than carpus, palm oblique with 8-9 small spines, 3 long setae, 2 of which are at the defining angle with 1 large spine; propod posterior margin bearing 4 sets of setae, ca. 1.6 times longer than the palm; 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 ca. 81% length of body, pereopod 6 ca. 95% length of body, pereopod 7 ca. 1.04 times length of body; bases of pereopods 5-7 slightly expanded, distoposterior lobes not developed; dactyl of pereopod 5 ca. 43% corresponding propod; dactyl of pereopod 6 ca 31% length of corresponding propod; dactyl of pereopod 7 ca. 36% length of corresponding propod. Coxal gills on 2-6, relatively large, subovate, with distinct peduncles; broodplates sublinear, small relative to gills.

Pleonal plates distoposterior margins with weakly developed tooth-like extensions; plate 1 without ventral spines; plates 2 and 3 with one ventral spine each. Pleopods normal bearing 2 coupling spines. Uropod 1: outer ramus ca. 85% length of inner, bearing 4 apical and 2 lateral spines; inner ramus ca. 94% length of peduncle bearing 4 apical and 2 lateral spines; peduncle with 5 spines, 1 of which is basofacial. Uropod 2: outer ramus ca. 74% length of inner bearing 4 apical and 2 lateral spines; inner ramus ca. 1.14 times longer than peduncle with 4 apical and 2 lateral spines; peduncle bearing 4 spines. Uropod 3: ca. 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 setae; posterior margin shorter than 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 6.22). This natural limestone "well" 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 floor extends underwater along the sides 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.

Type-species.—*Cancer palmatus* Montagu, 1804

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 on the fact that the two species were from subterranean freshwater habitats. Schellenberg (1931) emphasized two characters shared by the species of *Paraniphargus*: 1) inner margins of maxilla 2 naked; 2) outer ramus of uropod 3 without second segment. Character 1 was examined for a number of species of

Melita in our present study and appears to have a great deal of variation and is highly reduced in some species, including the new species of *Melita* described below. In addition, many species of *Melita* have a greatly reduced second segment of uropod 3 (Zeidler 1989). The variation noted in these characters suggests that species in the genus *Paraniphargus* cannot be distinguished from many species of *Melita*. For this reason, *Paraniphargus* is synonymized with *Melita*.

Melita almagosa sp. n.

Figs. 6.15-6.19

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 XXXXXXX); paratypes are in the collection of J. R. Holsinger (H-3559).

Diagnosis.—Small to medium sized stygobitic species of troglomorphic facies, distinguished by 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 ca. 77% length of body, ca. 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; palps 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 to7 long spines apically; outer plate expanded, inner and apical margins with row of heavy bladespines; palp 3-segmented, stout, segment 3 bearing numberous spines and setae apically.

Gnathopod 1: propod ca. 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 pubescent on the posterior medial margin; basis bearing up to 3 long setae on posterior margin; coxa deeper than broad with 7 marginal setae. Gnathopod 2: propod elongate, ca. 1.13 times 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, ca. 1.66 times longer than palm; carpus subtriangular, posterior margin with 5 sets of long setae, merus distoposterior margin with small, tooth-like extentsion; 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 ca. 76% length of body, pereopod 6 ca. 85% length of body, pereopod 7 ca. 82% length of body; coxa of pereopod 6 anterior ventral margin with hook-spine, medial lobate extension with serrate posterior margin; pereopods 5-7 bases weakly expanded, distoposterior lobes weakly developed; dactyl of pereopods 5, 6 and 7 ca. 27%, 30% and 28% relative to corresponding propods. Coxal gills on pereopods 2-6, subovate with distinct peduncles; broodplates sublinear, slightly larger than corresponding gills.

Pleonal plates distoposterior margins with weakly developed tooth-like extensions, without ventral spines. Pleopods normal, bearing 2 coupling spines. Urosomites not fused, without dorsal spines or teeth. Uropod 1: outer ramus ca. 63% length of inner, bearing 5 apical and 1 lateral spine; inner ramus ca. 87% length of peduncle with 4 apical and 2 lateral spines; peduncle with 6 spines, 1 of which is basofacial. Uropod 2: outer ramus ca. 71% length of inner, with 4 apical and 1 lateral spine; inner ramus subequal in length to peduncle, with 4 apical and 3 lateral spines; peduncle bearing 3 spines. Uropod 3: ca. 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, cleft to base, narrowing distally, wider than long, bearing one 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, propod anterior margin weakly pubescent. Pereopod 6 coxa normal, without spines or serrations.

Etymology.—The epithet *almagosa* denotes the presence of this species in Almagosa Springs, its type-locality and only locality known to date.

Type-locality.—This species is known only from Almagosa Spring, a freshwater resurgence of a limestone aquifer, which is restricted to this part of the island (Fig 6.23). According to Adam Asquith (pers. comm.), the type series of 25 specimens 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. 6.20). Barnard and Karaman (1982) described *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 that there were four hadzioid genera—*Sriha*, *Fiha*, *Psammoniphargus* 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 on the small island of Panglao, just off the south coast of Bohol, Philippines, and these species have a number of synapomorphies 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 *Tegano 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 apomorphic characters noted for the palm of gnathopod 1, inner lobes on lower lip and similarly shaped telson. These synapomorphies 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 melitioids. It is noteworthy that in the original description, Karaman (1984) noted the morphological similarity between *T. seticornis* and *T. vababundus*, which we have stongly 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 loss 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 circumtropical and temperate waters (Barnard and Barnard

1983). The distribution of *Melita* throughout the tropical Indo-Pacific region also puts it 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) 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 and 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. Bousfield and Chevrier (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 *Meltia almagosa* and the synonymy of *Paraniphargus*, bring the total number of *Melita* species to approximately 78 and the number of species of *Melita* reported from subterranean habitats to approximately 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 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 freshwaters caves is not surprising.

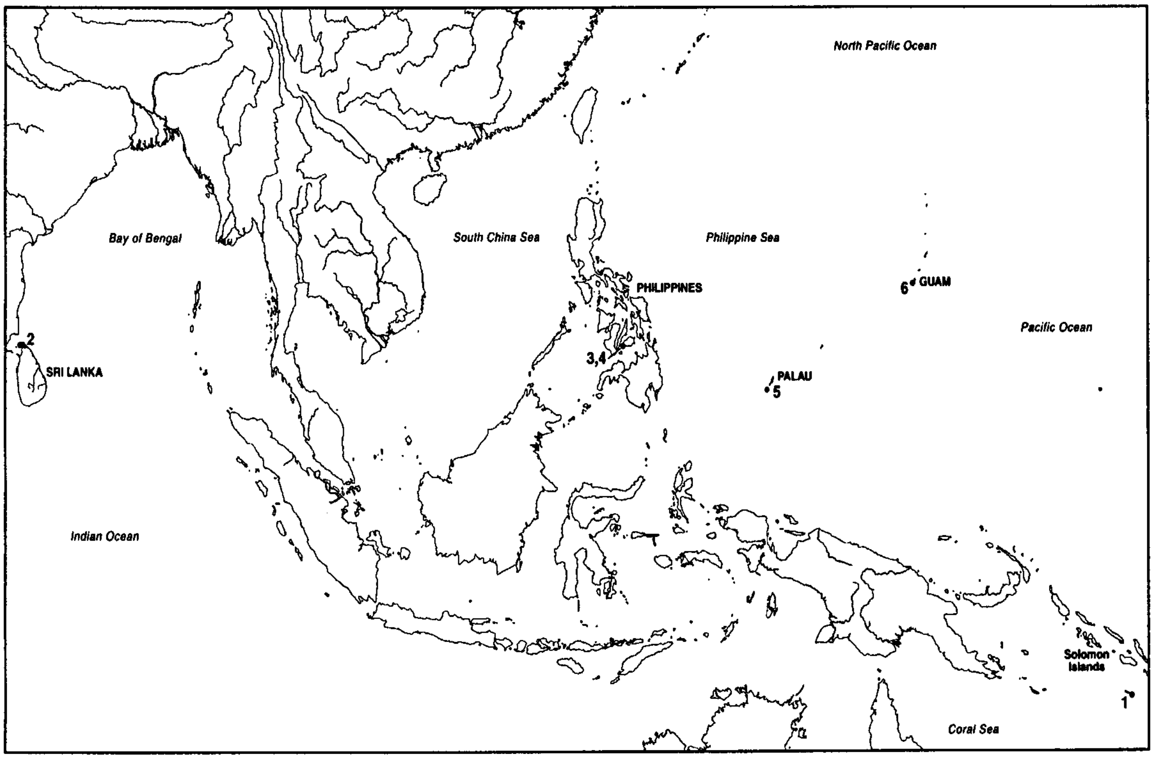

Fig. 6.20. Geographic distribution of species of *Tegano* and *Melita almagosa*. Solid circles indicate known localities as follows: 1) Rennell Island, Solomon Islands, *T. seticornis*; 2) Sri Lanka, *T. vagabunda*; 3) Panglao Island, Bohol, Philippines, *T. clavatus* (see Fig. 6.21); 4) Panglao Island, Bohol, Philippines, *T. panglaoensis* (see Fig. 6.21); 5) Peleliu Island, Palau, *T. barnardi* (see Fig. 6.22); 6) Guam, *Melita almagosa* (see Fig. 6.23).

The genus *Josephella* was described 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 synapamorphies of species of *Josephella* and *Melita*, noteably 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.

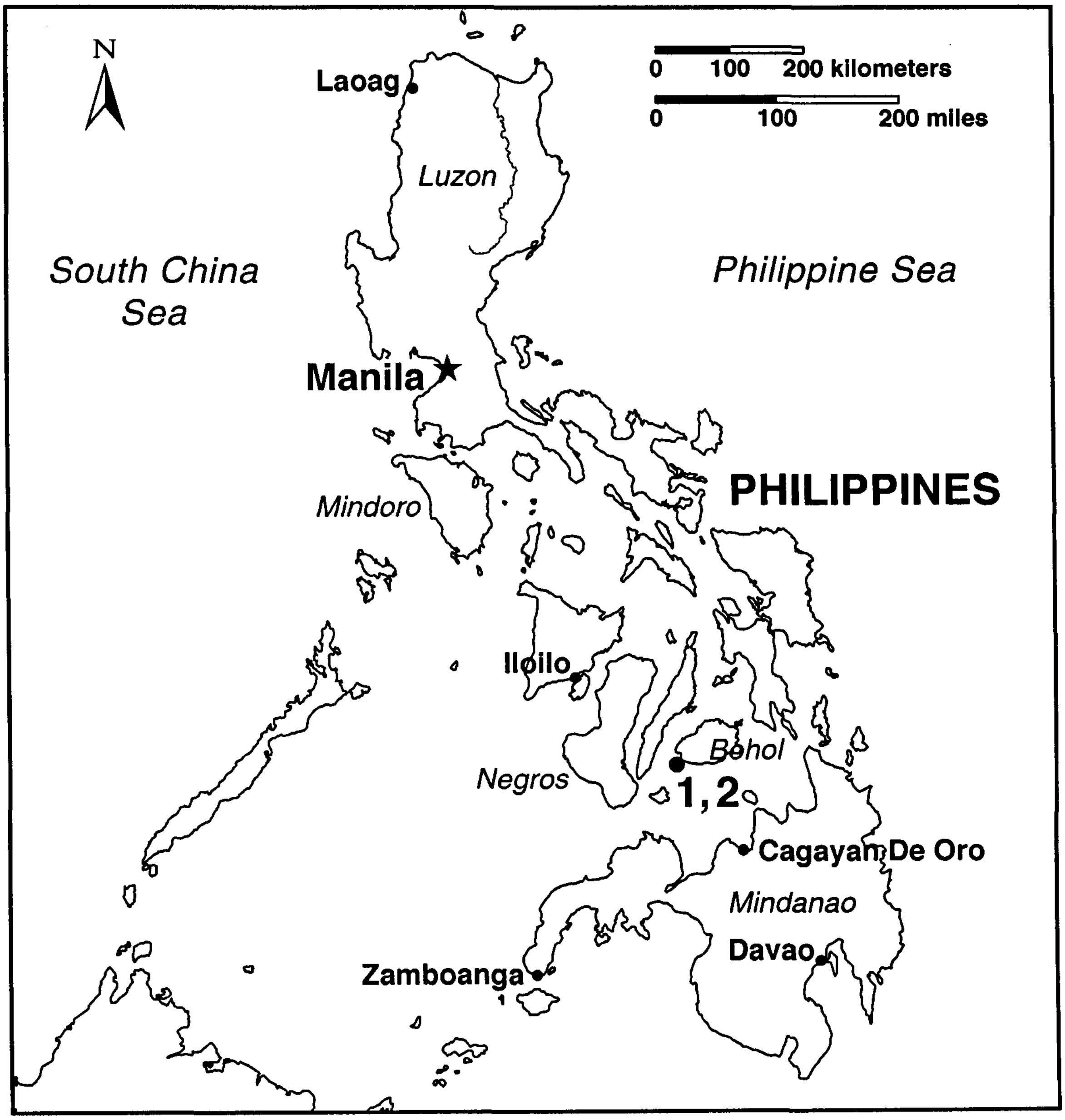

Fig. 6.21. Geographic distribution of *Tegano clavatus* (1) and *T. panglaoensis* (2) on Panglao Island, Bohol, Philippines. Solid circle denotes only known locality inhabited by both species.

Our present study suggests that a great deal of morphological similarity exists between species of *Melita* and *Josephella*, including sexual dimorphism of coxal plate 6 and reduction of the inner ramus of uropod 3. These strong similarities suggest a sistergroup relationship of these genera and perhaps after further study even the need to synonymize them.

The genus *Melita* is widespread throughout the West Pacific, with an affinity to enter insular anchialine cave habitats. As such, a great deal of morphological variation is predicted. 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*, *Josephella* and other melitid genera.

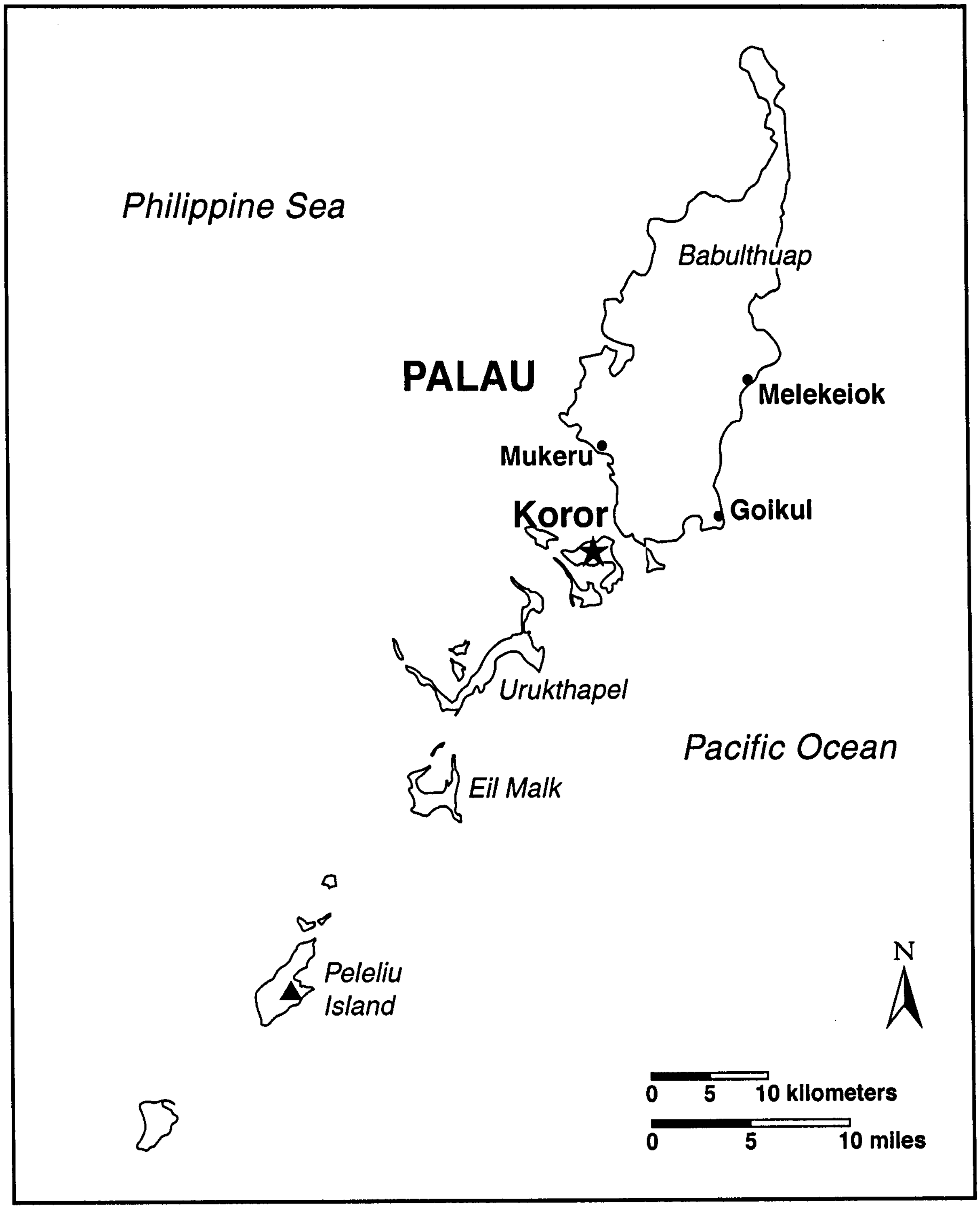

Fig. 6.22. Geograhic distribution of *Tegano barnardi* on Peleliu Island, Palau. Solid triangle denotes only known locality.

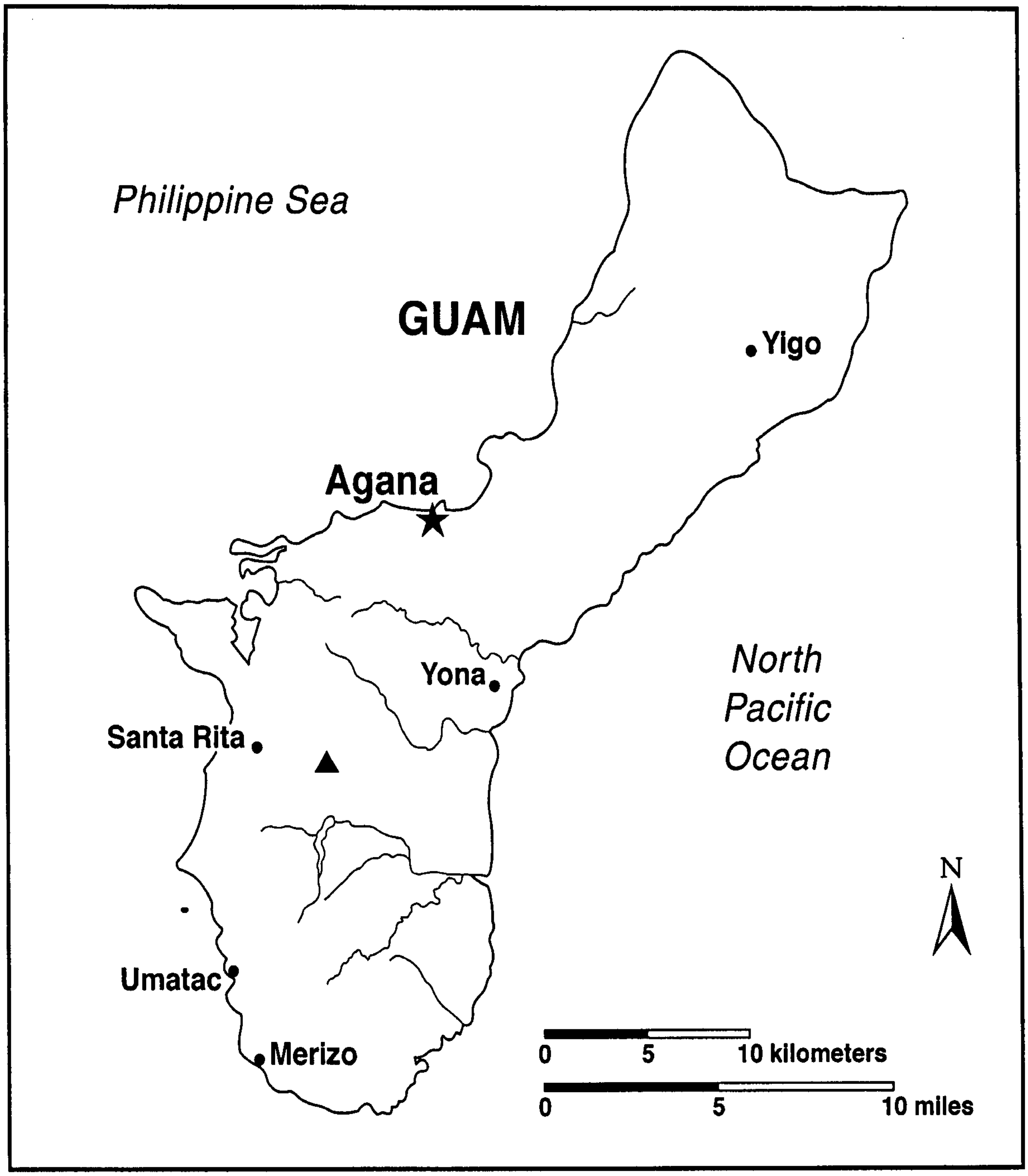

Fig. 23. Geographic distribution of *Melita almagosa* on Guam. Solid triangle denotes approximate location of only known locality.

SECTION 7

REDESCRIPTION OF THE SUBTERRANEAN AMPHIPOD CRUSTACEAN *FLAGITOPISA PHILIPPENSIS* (HADZIOIDEA: MELITIDAE), WITH NOTES ON ITS UNIQUE MORPHOLOGY AND CLARIFICATION OF THE TAXONOMIC STATUS OF *PSAMMOGAMMARUS*

Niphargus philippensis was described by Chilton (1920) on the basis of specimens collected, from a well near Los Baños, on the southern shore of Laguna de Bay, Luzon Island, Philippines. The species was later reassigned the genus *Eriopisa* (Gauthier 1936; Monod 1938; Stock and Nijssen 1965; Stock 1980). Karaman and Barnard (1979) and Barnard and Barnard (1983) placed the species in the genus *Psammogammarus*. Finally, G. Karaman (1984) placed the species into a new genus *Flagitopisa*, but gave little reason for doing so except that *F. philippensis* is the only freshwater species in the *Eriopisa* complex, which otherwise consisted of the genera, *Eriopisa*, *Victoriopisa*, *Tunisopisa* and *Psammogammarus*.

Stock (1987) questioned the genus *Flagitopisa* and he (Stock 1991) later described a new species, *Psammogammarus fluviatilis*, whose type-locality is only 25 km from the type-locality of *F. philippensis*. Stock (1991) described *P. fluviatilis* as being morphologically very similar to *F. philippensis*, differing primarily by an overall smaller body size, shorter, less spinose uropod 3, and with a coxal gill on pereopod 7. Our examination of the paratypes of *P. fluviatilis* indicate that the gill Stock described as being on pereopod 7 is in fact attached to the ventral surface of the first pleonal segment (pleonite 1), just anterior to pleopod 1 and is identical to this structure in *F. philippensis*.

New collections of *F. philippensis* in recent years have provided us with the opportunity to examine numerous specimens from different localities and it is now obvious that Chilton (1920) did not describe the large gill on the first pleonite. Our examination of specimens from populations in different geographical locations in the Philippine archipelago have resulted in the description of this highly unusual character.

SYSTEMATICS

Flagitopisa Karaman

Flagitopisa G. Karaman, 1984: 49-50

Type-species *Niphargus philippensis* by monotypy Chilton 1920

Diagnosis.—Corresponding to the diagnosis given by Karaman (1984) with the following addition: weakly stalked, subovate coxal gill, attached to the ventral surface of the first pleonal segment, just anterior to pleopod 1. Largest males 7 mm; largest females 6.5 mm.

Flagitopisa philippensis (Chilton 1921)

Figs. 7.1-7.5

Material examined.—PHILIPPINES. Camarines Sur Province, Luzon Island: well atTigaon, 20 specimens, T. M. Iliffe, 4 April 1985; well, Pinet Ocampo, 6 specimens, T. M. Iliffe, 4 April 1985; Bohol Island, Maitom Cave, B. Sket, February 1995; Quilas Cave, B. Sket, February 1995; pump wells, B. Sket, February 1995; open well, B. Sket, February 1995; pump well, B. Sket, February 1995; spring below C. Serapia, B. Sket, February 1995; C. Serapia, B. Sket, February 1995; Anislag Cave, B. Sket, February 1995; Badyang Cave, B. Sket, February 1995; Badyang Brook, B. Sket, February 1995; Spring 1 Roxas Park, B. Sket, February 1995; Spring 2 Roxas Park, B. Sket, February 1995; Inambakan, Boho, B. Sket, February 1995.

Diagnosis.—Corresponding to the characters of the genus as given above.

Description of female.—Antenna 1 ca. 1.4 times longer than body and 3.2 times longer than antenna 2; primary flagellum with up to 44 segments, accessory flagellum 1-segmented. Antenna 2: flagellum with up to 7 segments. Mandible: right mandible molar well developed, with seta, lacinia mobilis 3 dentate; incisor 6 dentate, with 8 serrate accessory spines and 4 small setae; left molar prominent, with seta, lacinia mobilis 6 dentate, incisor 7 dentate; palp segment 3 with 4-5 D setae and 4 E setae. Lower lip with inner lobes. Maxilla 1: inner plate with up to 15 apical plumose setae; outer plate with 9 pectinate spines; palps 2-segmented, second segment bearing 8 spines and 2 long setae apically. Maxilla 2: inner plate bearing dorsal oblique row of up to 20 setae, inner and apical margins bearing numerous setae. Maxilliped: inner plate narrow, bearing 2 spines along inner apical margin and 8-9 spines along apical margin; outer plate expanded with numerous long setae along inner and apical margins; palp 3-segmented, segment 2 with numerous long setae along inner margin, segment 3 longer than wide, weakly pubescent distally.

Gnathopod 1: propod ca. 72% length of carpus, palm transvers bearing 7-8 long setae and up to 6 small setae medially and 8 spines, 4 of which are bifurcate at the defining angle; dactyl subequal in length to palm; carpus elongate, posterior margin with numerous long setae; merus expanded distally, pubescent, with up to 10 setae along distoposterior margin; basis with 9 long setae along posterior margin; coxa deeper than broad with 8 marginal setae. Gnathopod 2: propod elongate and expanded, ca. 1.7 times longer than carpus, palm oblique with 5 long setae and 6 short setae and 2 stout spines medially, defining angle with 2 spines and 2 long setae; propod posterior margin bearing numerous setae; carpus weakly subtriangular, posterior margin with 5 sets of setae; basis with 4 sets of long setae on posterior margin and few shorter setae on anterior margin; coxa only slightly deeper than broad with 10 marginal setae. Pereopod 3: subequal in length to 4, coxa about as deep as broad with 10 marginal setae; basis expanded with 7 long setae on posterior margin. Pereopod 4: coxa posterior margin not excavate, slightly broader than deep with 8 marginal setae; basis expanded with 8 long setae on posterior margin. Pereopod 5: ca. 44% length of body; basis weakly expanded, distoposterior lobe not developed; dactyl ca. 16% propod. Pereopod 6 ca. 71% length of body; basis posterior margin expanded relative to pereopod 5, distoposterior lobe well developed; dactyl ca. 16% length of propod. Pereopod 7 ca. 75% length of body; basis posterior margin expanded greatly, distoposterior lobe well developed; dactyl ca. 22% length of propod. Coxal gills on 2-6, subovate, with distinct peduncles; brood plates subequal in length to gills, narrow, with small lateral and distal setae.

Pleonal plate 1 with weakly stalked, subovate "coxal-like" gill, attached to the ventral surface, just anterior to pleopod 1;distoposterior margin rounded, with 6 small spines. Pleonal plates 2 and 3 distoposterior margin rounded with numerous small spines along ventral and posterior margins. Pleopods normal, bearing 2 coupling spines. Uropod 1: outer ramus ca. 89% length of inner, bearing 5 apical and 4 lateral spines; inner ramus ca. 79% length of peduncle with 5 apical and 4 lateral spines; peduncle with

13 spines, 1 of which is basofacial. Uropod 2: outer ramus ca. 72% length of inner bearing 3 apical and 4 lateral spines; inner ramus 1.07 times longer than peduncle, with 6 apical and 3 lateral spines; peduncle with up to 4 spines. Uropod 3: ca. 48% length of body; inner ramus small, scale-like, with small apical seta; outer ramus 2-segmented, first segment armed with numerous clusters of spines, second segment ca. 48% length of segment 1, with 7 long, thin setae apically and numerous lateral spines. Telson short, cleft to base, wider than long, bearing 3 lateral and 2 apical spines.

Male.—Differing only slightly from the female as follows: palm of gnathopod 2 with additional spines and setae.

Type-locality.—The type locality of this species is a well at Los Baños, Laguna Province, on the south shore of Laguna de Bay, 25 km SW of Santa Cruz and 54 km SE of Manila (Fig. 7.6).

Distribution and Ecology.—Until recent years, *Flagitopisa philippensis* was known only from its type locality. In April of 1985, Thomas M. Iliffe collected the species from two new, separate locations, both wells on Luzon Island in Camarines Sur Province. In February of 1995, one of us (BS) made numerous collections of this species from wells and springs on the island of Bohol in the Philippines marking a significant range extension for *F. philippensis*. Specimens from all locations have so far been collected either from either wells or springs.

Flagitopisa fluviatilis (Stock), NEW COMBINATION

Psammogammarus fluviatilis Stock, 1991:227-233. [type-locality: Pagsanjan Falls, Laguna Province, Luzon Island, Philippines].

Diagnosis.—Distinguished from F. philippensis primarily by overall smaller body size and the length and spination of uropod 3. Otherwise corresponding to the diagnosis given by Stock (1991).

Remarks.— Stock (1987) questioned the diagnosis of the monotypic genus *Flagitopisa* by Karaman (1984) on the premise that *Flagitopisa* was described largely on plesiomorphic characters. Stock (1991) described the new species *Psammogammarus fluviatilis* and noted the presence of a large "coxal" gill on pereopod 7. Examination of the paratypes of *P. fluviatilis* during this study indicates that the gill is attached to the ventral surface of the first pleonal segment (pleonite 1), just anterior to pleopod 1. *Psammogammarus fluviatilis* and *F. philippnesis* are synapomorphic for this highly unusual character and are otherwise morphologically very similar. Based on their overall morphological similarity and the highly unusual pleonal gill, *P. fluviatilis* is reassigned to *Flagitopisa*. Despite the rejection of the genus *Flagitopisa* by Stock (1987), the name *Flagitopisa* is available according to the rules of zoological nomenclature and is therefore used here for this unique genus.

DISCUSSION

Recent collections of *Flagitopisa philippensis* have extended the range of this species to Bohol, approximately 550 km SSE of the type locality (Fig. 6). This significant range extension and recognition of the large, subovate "coxal-like" gills attached to the ventral surface of the first pleonite have necessitated the redescription of the species. Chilton's original description of this species, although relatively good for the standards of that day, failed to recognize the conspicuous gills on pleonite 1.

Psammogammarus fluviatilis, which we have reassigned to the genus *Flagitopisa* herein, was described by Stock (1991) from coarse sand interstices on the bank of Pagsanjan Falls in Laguna Province on Luzon Island. In his description of this species, a coxal gill was said to occur on the seventh pereopod and was considered a plesiomorphic character (Stock 1991). Although *F. fluviatilis* was found in an area only 25 km from the type locality of *F. philippensis*, Stock noted that his material differed from the latter in having an overall smaller body size, and a shorter, less spinose uropod 3. As pointed out below, these small differences may well be influenced by adaptation of this species to an interstitial environment. In contrast, *F. philippensis*, which appears to reach sexual maturity at a larger size, has been collected from wells and springs, where it apparently inhabits more "open" subterranean water, with larger living space. Stock (1991) also suggested that segment 3 of the maxilliped palp was elongate in *F. fluviatilis* and globular in *F. philippensis*, but our comparison of the paratypes of *F. fluviatilis* with recently collected specimens of *F. philippensis* revealed no difference in this character between the species. This mistake can be attributed to Chilton's original figure, which erroneously showed segment 3 of the maxilliped palp to be globular in shape.

Examination of the paratypes of *F. fluviatilis* clearly shows that the "coxal gill" described by Stock (1991) as being attached to the base of pereopod 7 is in fact attached to the ventral surface of pleonite 1, and is therefore identical to the pleonite "coxal-gill" of *F. philippensis*. Outside of these two species, we know of no other species of hadzioid amphipods with gills on the pleonites. However, pleonite gills do occur in some species of crangonyctid amphipods, but in this group they differ from the pleonite gill in *Flagitopisa* and in marked contrast are slender, "finger-like" processes lacking a stalk or peduncle. The occurrence of this unique structure in these Philippine stygobites is apparently an unsual apomorphic character that alone clearly distinguishes *Flagitopisa* from *Psammogammarus*, *Eriopisa*, *Victoriopisa*, and *Tunisopisa*, the genera traditionally placed in the *Eriopisa* complex (Van Der Ham and Vonk 2003).

Despite the closely similar morphology of *F. philippensis* and *F. fluviatilis*, the differences between the two are greater than between the geographically widely separated populations of the former species in the Philippine archipelago (Fig. 6). Although we attribute much of the difference between these species to size-related changes associated with ad hoc adaptations for living in structural different subterranean habitats, we agree with Stock (1991) that *F. fluviatilis* should remain a separate species.

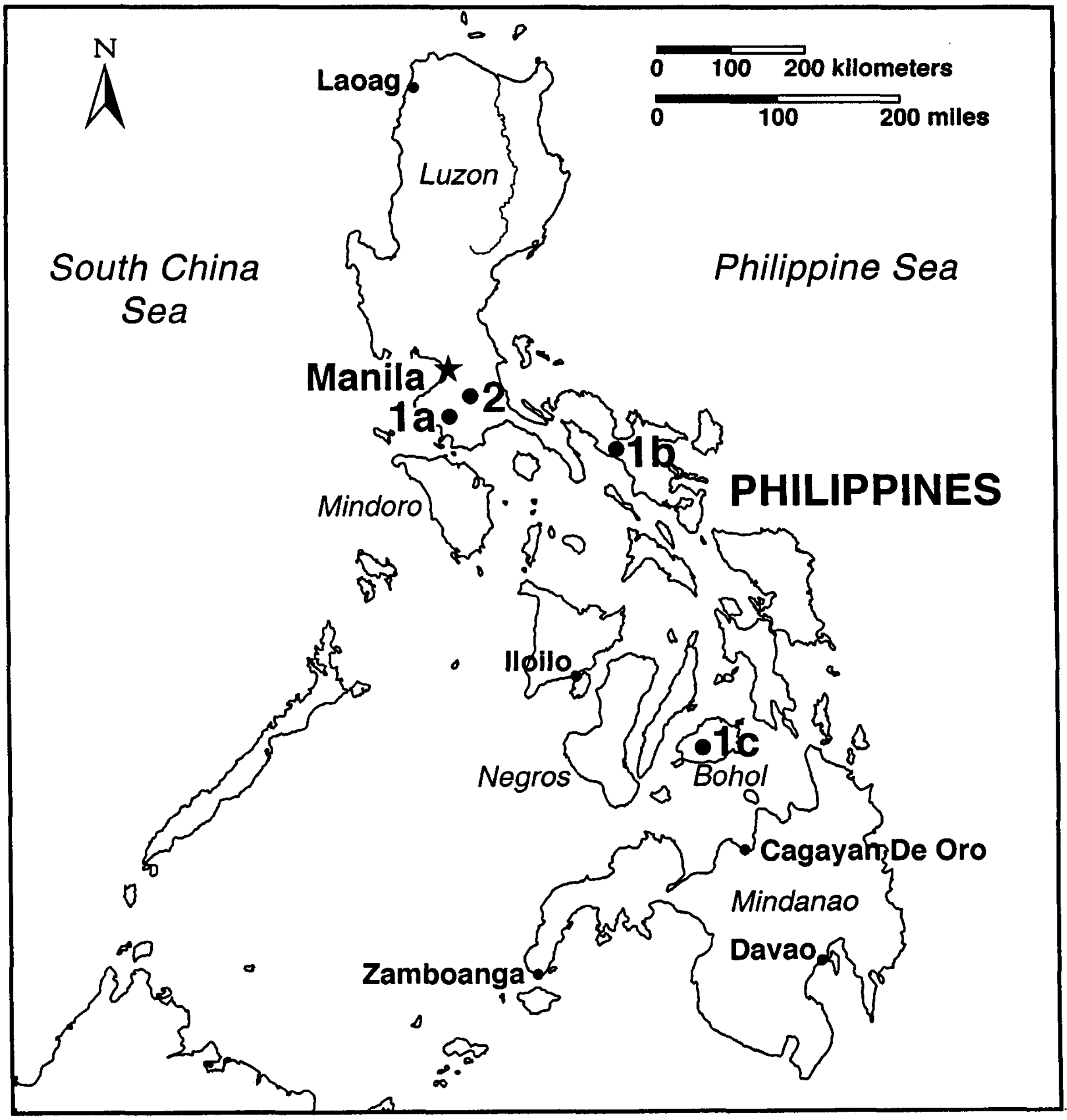

Fig. 7.6. Distribution of *Flagitopisa* in the Philippine archipelago. Solid circles indicate known localities as follows: 1a) *Flagitopisa philippensis*—Type-locality, Luzon Island, near Los Baños, on the southern shore of Laguna de Bay; 1b) Luzon Island, in the Camarines Sur Province, approximately 240 km SE of the type locality; 1c) the island of Bohol, approximately 550 km SSE of the type locality; 2) *Flagitopisa fluviatilis*—Luzon Island, Laguna Province, Pagsanjan Falls.

SECTION 8

SUMMARY

BAHADZIA

With the description of *Bahadzia patilarga* and *B. caymanensis*, there are now 11 species with the genus. Holsinger (1992a) conducted a cladistic analysis of weckeliid group genera and included the genus *Bahadzia*, which suggested that *Mayaweckelia* and *Tuluweckelia* are sister genera to *Bahadzia*. The cladistic analysis conducted during this study included all known species within *Bahadzia*, along with a number of weckeliid and other genera. In addition to including many more and different taxa, the cladistic analysis performed during this study used over two times the number of characters as Holsinger (1992a). It is noteworthy that in both studies *Bahadzia*, *Mayaweckelia* and *Tuluweckelia* are suggested to share a common ancestor. The phylogeny derived during this study was weakly supported statistically, due in great part to the large amount of convergence that seems to be common in many groups of stygobitic amphipods; however, the fact that two differing studies, using different taxa and characters both indicated a sister group relationship between *Bahadzia*, *Mayaweckelia* and *Tuluweckelia* may suggest strong support for this nested subset, even thought the overall analysis is not strongly supported.

MEXICO

The descriptions of *Paraholsingerius mexicanus* and *Tamaweckelia apalpus* bring the total number of weckeliid amphipods recorded to date from northern Mexico and south-central Texas to eight genera and 12 species. *Tamaweckelia apalpus* may occur sympatrically and possibly syntopically with another stygobitic amphipod in Manantial de San Rafael de Los Castro. Further collection efforts should yield additional species from these areas, especially in Mexico where numerous, remote collecting sites may still exist. These additional collections should shed more insight into the evolutionary relationships of the weckeliid genera.

HADZIA

With the description of four new species from the Philippines, Palau and Guam and the synonymy of *Liagoceradocus*, there are now 14 species assigned the genus *Hadzia*. It is predicted that as suitable environments are sampled on West Pacific islands east of Guam, additional species of *Hadzia* will be discovered, further bridging the gap between the western Pacific species, and the isolated Hawaiian species.

TEGANO AND *MELITA*

With the description of three new species, and the synonymy of the genus *Sriha*, there are now five species within the genus *Tegano*. These species have an Indo-pacific distribution. The presence or absence of a mandibular palp has been an important taxonomic character in determining both taxonomic and phylogenetic status of hadziid and melitid species (Holsinger 1992a, Stock 1988). Results of this study show a great deal of interspecific and intraspecific variation in this character. This may have a significant effect on the classification of stygobitic amphipods in the future.

Currently, there are approximately 76 species within the genus *Melita*. The description of *Meltia almagosa* brings the number of stygobitic species of *Melita* to approximately seven, most of which are found in interstitial habitats, and with the synonymy of the genus *Paraniphargus* the number of *Melita* species from freshwater habitats to eight, most found very near coastal areas.

The pattern of marine ancestors entering first anchialine and later freshwater cave habitats is common within hadziids e.g., weckeliid genera (Holsinger and Longley 1980, Bowman 1982, Holsinger 1986, Holsinger 1992). Based on the hadziid-weckeliid model and given the affinity for *Melita* species to enter anchialine habitats, their movement into freshwater caves may be expected.

FUTURE STUDIES

Cladistic studies based on morphological characters of stygobitic amphipods are problematic at best. This study shows a great deal of convergence in characters, e.g., loss of mandibular palp in the hadziid weckeliid genera in the Caribbean, Mexico and south-central Texas and the loss of mandibular palp in many melitid-like genera of the West Pacific. Many of these species have a tendency to live in fresh or weakly brackish water. It may be hypothesized that as marine species move first into anchialine and then freshwater cave habitats that these unique environments select against the presence of a mandibular palp. However, it is also possible that the loss of the mandibular palp is the result of a founder effect and is a completely random phenomenon based on the genetic makeup of the founding population or a combination of both hypotheses. Other important characters have been the length of the inner ramus of uropod 3 and presence or absence of the second segment of the outer ramus of uropod 3. In both cases overlap and variations are noted in these characters (Holsinger 1974, Stock 1977, Zeidler 1989).

Results of this study suggest that strong selection pressures may act on marine amphipods that invade anchialine and later freshwater caves, and that these pressures may result in morphological convergence of species from different lineages. In order to adequately test phylogenetic hypotheses, molecular studies may provide a more robust methodology. For instance, a molecular study of *Bahadzia*, *Mayaweckelia* and *Tuluweckelia* would be a strong test of the hypothesis that species within these genera share a common ancestor. In addition, molecular analyses may help resolve the relationship of species in the *Abludomelita-Melita* complex, as well as determine the phylogenetic relationship between hadziid and melitid species.

LITERATURE CITED

Andres, H. G. 1978. *Liagoceradocus acutus* sp. n., ein Gammaride aus der Jameos del Aqua auf Lanzarote (Amphipoda, Crustacea).—Mitteilungen aus dem Zoologischen Institut und Zoologischen Museum der Universität Hamburg 75: 249-253.

Barnard, J. L. 1965. Marine Amphipoda of atolls in Micronesia.—Proceedings of the United States National Museum 117: 459-552.

—. 1977. The cavernicolous fauna of Hawaiian lava tubes 9. Amphipoda (Crustacea) from brackish lava ponds on Hawaii and Maui.—Pacific Insects 17: 267-299.

—, and C. M. Barnard. 1983. Freshwater Amphipoda of the World. Hayfield Associates, Mt. Vernon, Virginia. pp. 1-830.

—, and G. S. Karaman. 1982. Classificatory revisions in gammaridean amphipods (Crustacea), part 2.—Proceedings of the Biological Society of Washington 95: 167-187.

Botosaneanu, L., and T. M. Iliffe. 2002. Notes on the intraspecific variability of *Cirolanides texensis* BENEDICT, 1896 (Isopoda: Cirolanidae) from Texas and Mexico.—Bulletin de L'Institut Royal des Sciences Naturelles de Belgique, Biologie 72: 113-117.

Botosaneanu, L., T. M. Iliffe, and D. A. Hendrickson. 1998. On a collection of stygobitic cirolanids (Isopoda: Cirolanidae) from northern Mexico, with description of a new species.—Bulletin de L'Institut Royal des Sciences Naturelles de Belgique, Biologie 68: 123-134.

Bousfield, E. L. 1970. 71. Terrestrial and Aquatic Amphipod Crustacea from Rennell Island.—The Natural History of Rennell Island British Solomon Islands 6: 155-168.

—. 1973. Shallow-Water Gammaridean Amphipoda of New England. Comstock Publishing Associates, Cornell University Press. pp. 312.

Bowman, T. E. 1982. Three new stenasellid isopods from Mexico (Crustacea: Asellota).—Association for Mexican Cave Studies Bulletin 28: 25-38.

—, and T. M. Iliffe. 1987. *Anopsilana lingua*, a new freshwater troglobitic isopod from the Palau Islands (Flabellifera: Cirolanidae).—Proceedings of the Biological Society of Washington 100: 347-352.

Boxshall, G. A. and T. M. Iliffe. 1987. *Anopsilana lingua*, a new freshwater troglobitic isopod from the Palau Islands (Flabellifera: Cirolanidae).—Proceedings of the Biological Society of Washington 100: 347-352.

—, and T. M. Iliffe. 1990. Three new species of misophrioid copepods from oceanic islands.—Journal of Natural History 24: 595-613.

Bradbury, J. H. and W. D. Williams. 1996. Two new species of anchialine amphipod (Crustacea: Hadziidae: *Liagoceradocus*) from Western Australia.—Records of the Western Australian Museum 17: 395-409.

Chilton, C. 1920. *Niphargus philippensis*, a New Species of Amphipod from the Underground Waters of the Philippine Islands.—Philippine Journal of Science 17: 515-523.

Gauthier, H. 1936. *Eriopisa seurati*, mouvel aphipode du Sud-Tunisien.—Bulletin de la Société d' Histoire Naturelle du l' Afrique du Nord 27: 133-143.

Gutu, M. and T. M. Iliffe. 1989. Description of two new species of Tanaidacea (Crustacea) from the marine water caves of the Palau Islands (Pacific Ocean).—Travaux du Muséum d'Histoire Naturelle "Grigore Antipa" 30: 169-180.

Hendrickson, D. A., J. K. Krejca and J. M. R. Martinez. 2001. Mexican blindcats genus

Prietella (Siluriformes: Ictaturidae): an overview of recent explorations.—Environmental Biology of Fishes 62: 315-337.

Holsinger, J. R. 1973. Two new species of the subterranean amphipod genus Mexiweckelia (Gammaridae) from Mexico and Texas, with notes on the origin and distribution of the genus.—Association for Mexican Cave Studies Bulletin 5: 1-12.

—. 1974. A New Cavernicolous Amphipod Crustacean of the Genus *Hadzia* (Gammaridae) from Jamaica, With Notes on the Distribution and Taxonomic Status of the Genus.—Annales de Spéléologie 29: 647-655.

—. 1977, A new genus and two new species of subterranean amphipod crustaceans (Gamaridae s. lat.) from the Yucatan Peninsula in Mexico. *In* J.R. Reddell ed., Studies on the caves and cave fauna of the Yucatan Peninsula.—Association of Mexican Cave Studies Bulletin 6: 15-25.

—. 1982. *Paramexiweckelia* a new genus of subterranean amphipod crustacean (Hadziidae) from northern Mexico.—International Journal of Speoleology 12: 37-44.

—. 1986. Zoogeographic patterns of North America subterranean crustaceans. Pp. 85-106 *in* R. D. Gore and K. L. Heck, eds., Crustacean Issues 4, Crustacean Biogeography. Rotterdam: A. A. Balkema.

—. 1989. Preliminary zoogeographic analysis of five groups of crustaceans from anchialine caves in the West Indian region.—Proceedings of 10th International Congress of Speleology 1: 25-26.

—. 1990, *Tuluweckelia cernua*, a new genus and species of stygobiont amphipod crustacean (Hadziidae) from anchialine caves on the Yucatan Peninsula in Mexico.—

Beaufortia 41: 97-107.

—. 1992a. Two new species of the subterranean amphipod genus *Bahadzia* (Hadziidae) from the Yucatan Peninsula region of southern Mexico, with an analysis of phylogeny and biogeography of the genus.—Stygologia 7: 85-105.

—. 1992b. Four new species of subterranean amphipod crustaceans (Artesiidae, Hadziidae, Sebidae) from Texas, with comments on their phylogenetic and biogeographic relationships.—Texas Memorial Museum Speleological Monographs 3: 1-22.

—. 1993. *Paramexiweckelia ruffoi*, a new species of subterranean amphipod crustacean (Hadziidae) from south-central Texas, with observations on phylogenetic and biogeographic relationships.—Bollettino Museo Civico di Staria Naturales di Verona 20: 89-103.

—. 1994. Pattern and process in the biogeography of subterranean amphipods.—Hydrobiologia 287: 131-145.

Holsinger, J. R., and G. Longley. 1980. The subterranean amphipod crustracean fauna of an artesian well in Texas.—Smithsonian Contributions to Zoology 308: 1-62.

—, and W. L. Minckley. 1971. A new genus and two new species of subterranean amphipod crustaceans (Gammaridae) from northern Mexico.—Proceedings of the Biological Society of Washington 83: 425-444.

—, and S. Ruffo., 2002, *Indoweckelia superstes* n. gen. n. sp.from the subterranean waters of Socotra Island: the first weckeliid amphipod crustacean (Hadziidae) found in the Indo-West Pacific Region.—Bollettino del Museo Civico di Storia Naturale di Verona 26: 27-36.

—, and J. Yager, 1985. A new genus and two new species of subterranean amphipod crustaceans (Hadziidae) from the Bahamas and Turks and Caicos Islands.—Bijdragen tot de Dierkunde 55: 283-294.

Jarrett, N. E. and E. L. Bousfield. 1996. The Amphipod Superfamily Hadzioidea on the Pacific Coast of North America: Family Melitidae. Part I. The *Melita* Group: Systematics and Distributional Ecology.—Amphipacifica Journal of Systematic Biology 2: 3-74.

Jaume, D. and H. P. Wagner, 1998, New cave-dwelling amphipods (Lysianassidae, Hadziidae) from the Dominican Republic (Hispaniola).—Contributions to Zoology 68: 37-66.

Karaman, G. S. 1981. Redescription of *Melita planaterga* Kunkel 1910 from Bermuda Islands with revision of genera *Melita* Leach and *Abludomelita* n. gen. (Contribution to the Knowledge of the Amphipoda 119).—Poljopriveda I Sumarstvo 27: 29-50.

—. 1984a. Contribution to the Knowledge of the Amphipoda 133. New Data on a Genus Hadzia S. Kar. In Yugoslavia.—Poljoprivreda I Šumarstvo 30: 13-31.

—. 1984b. Revision of the *Eriopisa*-Complex of Genera (Gammaridea) (Contribution to the Knowledge Contribution to the Knowledge of the Amphipoda 139).—Poljopriveda I Sumarstvo 30: 39-72.

—. 1989. *Hadzia fragilis stochi*, n. ssp., from Italy (Amphipoda, Gammaridea, Hadziidae).—Fragmenta Balcanica Musei Macedonici Scientiarum Naturalium 14: 69-80.

—, and J. L. Barnard. 1979. Classificatory revision in gammaridean Amhipoda (Crustacea), part 1.—Proceedings of the Biological Station of Washington 92: 106-165.

Karaman, S. 1932. Beitrag zur Kenntnis der Süsswasser-Amphipoden.—Prirodoslovne

Razprave 2: 179-232.

—. 1943. Die unterirdischen Amphipoden Sudserbiens. Srpska Kral'evska Akademiia Posebna Izdan'a.— CXXXV Prirodn'achki i Matematichki Spici Okhridski Zbornik 34: 163-312.

Leach, W. E. 1814. Crustaceology.—Edinburgh Encyclopaedia, 7: 402-403

Monod, T. 1938. Sur un localité nouvelle d' *Eriopisa seruati* H. Gauthier, 1936.—Bulletinde la Société Zoologique de France 63: 244-247.

Montagu, G. 1804. Description of Several Marine Animals Found on the South Coast of Devonshire.—Transactions of the Linnean Society of London 7: 61-85.

Ortiz, M. & A. Pérez. 1995. Una Nueva Especie de Anfípodo Cavernícola Hadzioideo (Amphipoda, Gammaridea) de Cuba.—Graellsia 51: 165-168.

Pohlman, J. W., T. M. Iliffe and L. A. Cifuentes. 1997. A stable isotope study of organic cycling and the ecology of an anchialine cave ecosystem.—Marine Ecology Progress Series 155: 17-27.

Ruffo, S. 1982. Studi Sui Crostacei Anfipodi. 92. Nuovi Anfipodi Di Acque Sotterranee Della Somolia.—Monitore zooligico italiano 27: 97-113.

—. 1985. Nuovi Anfipodi mesopsammici delle Isole Andamane (Crust. Amphipoda).—dal Bollettino del Museo Civico di Storia Naturale Verona 6: 419-440.

—, and G. Krapp-Schickel. 1969. Hydrobiologie der Randhöhlen Teil II. Troglobionte Amphipoden aus Karstsiphonen von Istrien.—Int. Revue ges. Hydrobiol 54: 685-696.

Rondé-Broekhuizen, L. M. and J. H. Stock. (1987). *Liagoceradocus acutus* Andres, 1978, A Blind Anchihaline Amphipod from Lanzarote: Redescription, Taxonomic Status and Occurrence.—Bulletin Zoölogisch Museum 11: 25-37.

Sawicki, T. R., J. R. Holsinger, M. Ortiz and A. Pérez. 2003. *Bahdazia Patilarga*, a new species of subterranean amphipod crustacean (Hadziidae) from Cuba.—Proceedings of the Biological Society of Washington 116: 198-205.

Schellenberg, A. 1931. Amphipoden der Sunda-Expeditionen Thienemann und Rensch. Archiv für Hydrobiologie, Supplement 8: 493-511.

Stock, J. H. 1977. The Taxonomy and Zoogeography of The Hadziid Amphipoda, with emphasis on the West Indian taxa.—Studies on the Fauna of Curacao and Other Caribbean Islands 55: 1-130.

—. 1980a. Regression model evaluation as exemplified by the genus *Pseudoniphargus* (Amphipoda).—Bijdragen Tot De Dierkunde 50: 104-144.

—. 1980b. The right generic names of some Amphipoda.—Annals and Magazine of Natural History 5: 192-194.

—. 1983. The stygobiont Amphipoda of Jamaica.—Bijdragen tot de Dierkunde 53: 267-286.

—. 1985, Stygobiont Amphipoda from Haiti.—Bijdragen tot de Dierkunde 55: 391-400.

—. 1987. *Psammogammarus initialis* n. sp., a new mediolittoral interstitial amphipod crustacean from Tenerife.—Stygologia 3: 264-277.

—. 1988. Two new stygobiont Amphipoda (Crustacea) from Polynesia.—Stygologia 4: 79-100.

—. 1991. A new species of *Psammogammarus* (Amphipoda, Melitidae) from river alluvia in Luzon, Philippines.—Stygologia 6: 227-233.

—, and T. M. Iliffe. 1991. Two new species of *Liagocerdocus* (hypogean Amphipoda) from south-western Pacific islands, with key to the world species.—Invertebrate Taxonomy 5: 807-825.

—, and H. Nijssen. 1965. *Eripoisa longiramus* n. sp. a new subterranean amphipod from a Red Sea island.—Bulletin of the Sea Fisheries Research Station Haifa 38: 28-39.

Tattersall, W. M. 1925. Freshwater Amphipoda from the Andaman Isles.—Records of the Indian Museum 27: 241-247.

Van Der Ham, J. L. and R. Vonk. 2003. A phylogenetic analysis of the *Eriopisa* comlex (Crustacea: Amphipoda: Melitidae) and a new species from beach interstitial in Venezuela.—Journal of Natural History 37: 779-796.

Villalobos, J. L., F. Alvarez and T. M. Iliffe. 1999. New species of troglobitic shrimps from Mexico, with the description of *Troglomexicanus*, new genus (Decapoda: Palaemonidae).—Journal of Crustacean Biology 19: 111-122.

Yager, J., 1994, *Speleonectes gironensis*, new species (Remipedia: Speleonectidae), from anchialine caves in Cuba, with remarks on biogeography and ecology.—Journal of Crustacean Biology 14: 752-762.

Zeidler, W. 1988. A new Species of *Melita* (Crustacea: Amphipoda: Melitidae) from northern New South Wales with a Note on the Genus *Abludomelita* Karaman, 1981.—Proceedings of the Linnean Society of New South Wales 110: 327-338.

APPENDIX A

FIGURES OF DRAWINGS FOR ALL NEW AND REDESCRIBED SPECIES FROM SECTIONS 2-7

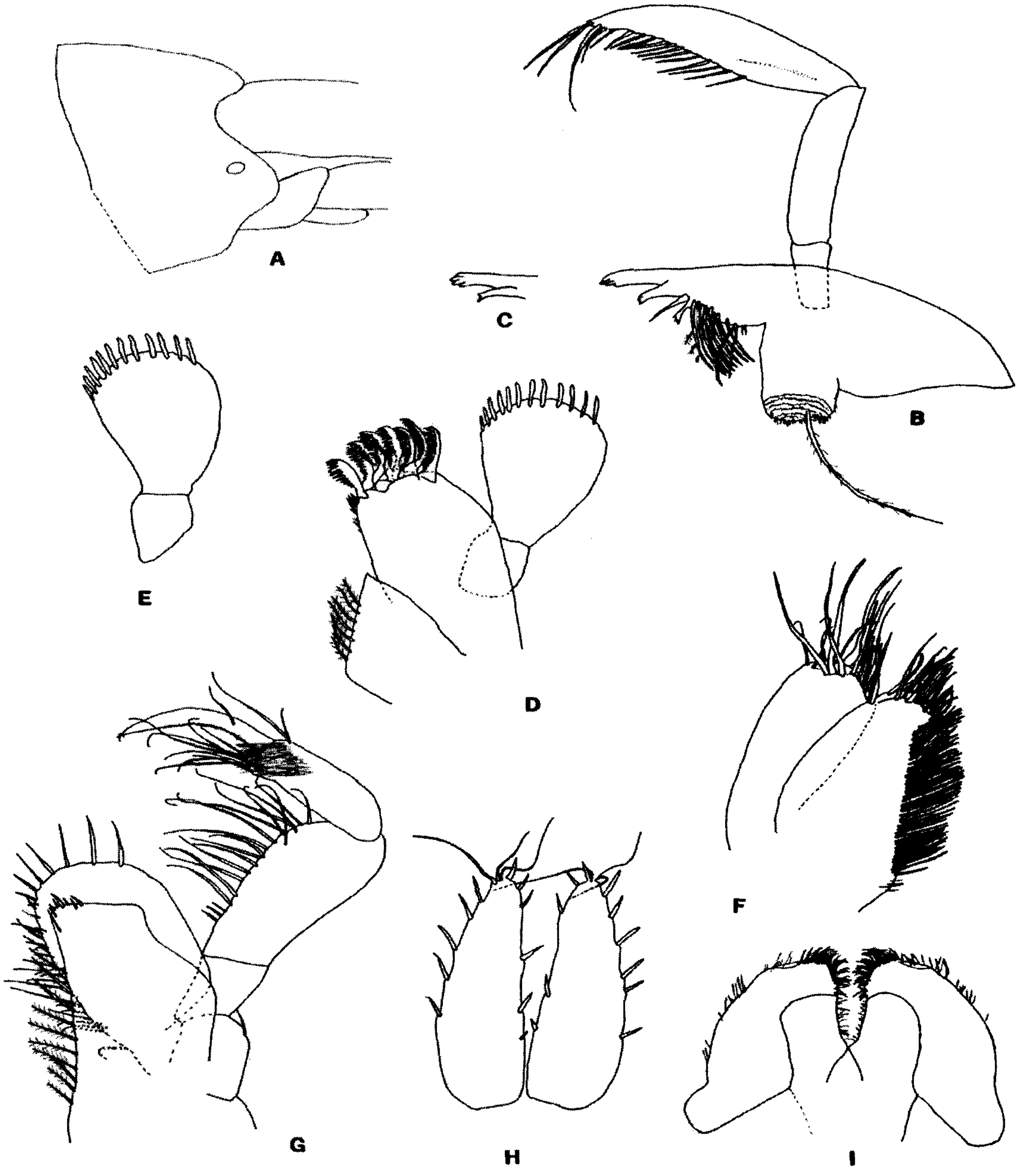

Fig. 2.1. *Bahadzia patilarga* n. sp., paratypes from Cueva de los Carboneros, Playa Giron, Cuba. Juvenile (2.5 mm): A, head region with eyespot. Female (6.5 mm): B, left mandible; C, incisor and lacinia mobilis of right mandible F, maxilla 2; G, maxilliped. Male (6.0 mm): D, maxilla 1; E, palp of other maxilla H, telson; I, lower lip.

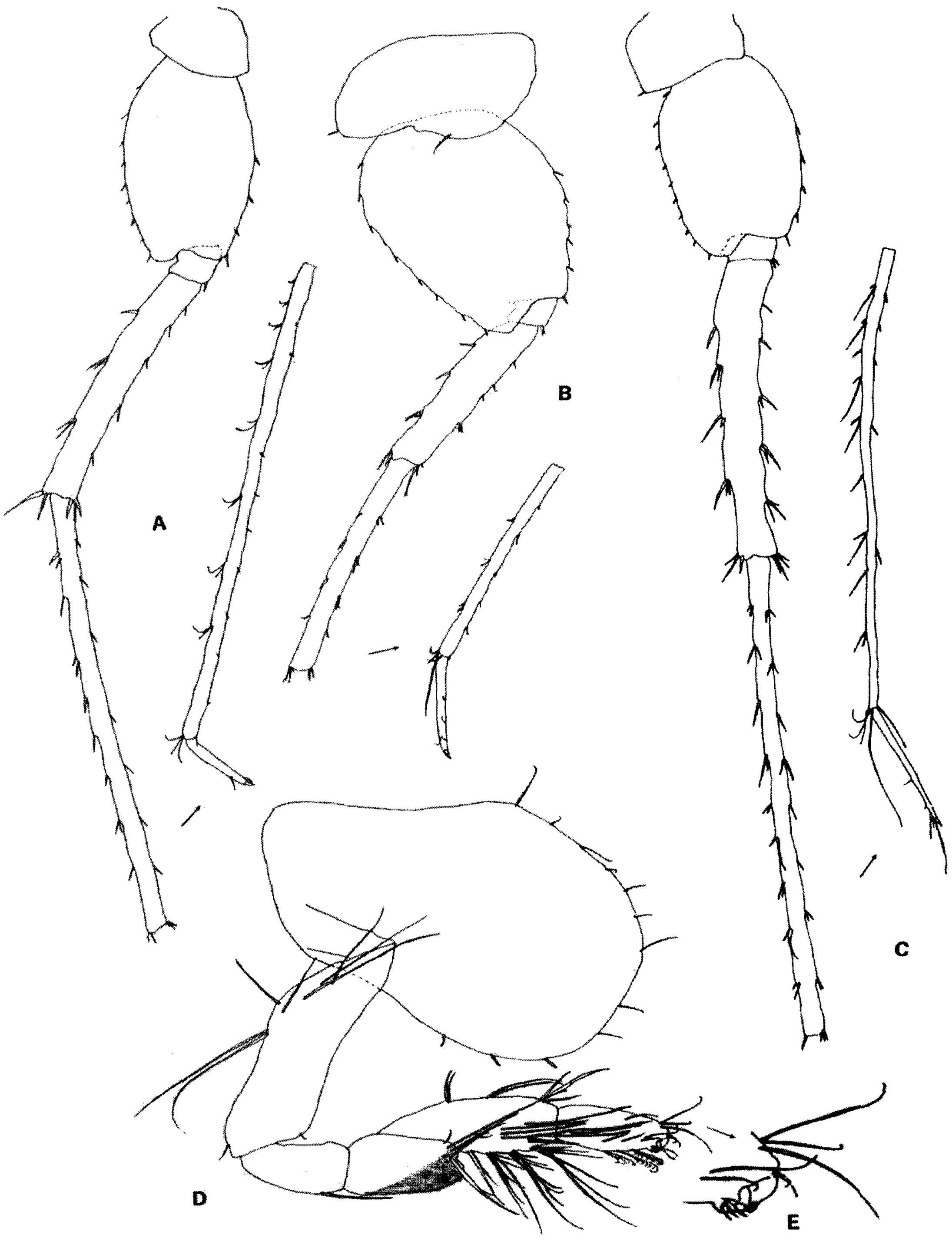

Fig. 2.2. *Bahadzia patilarga* n. sp., paratypes from Cueva de los Carboneros, Playa Giron, Cuba. Male (6.0 mm): A, B, C, pereopods 7, 5, 6. Female (6.5 mm): D, gnathopod 1; E, enlarged distal end of propod and dactyl of gnathopod 1.

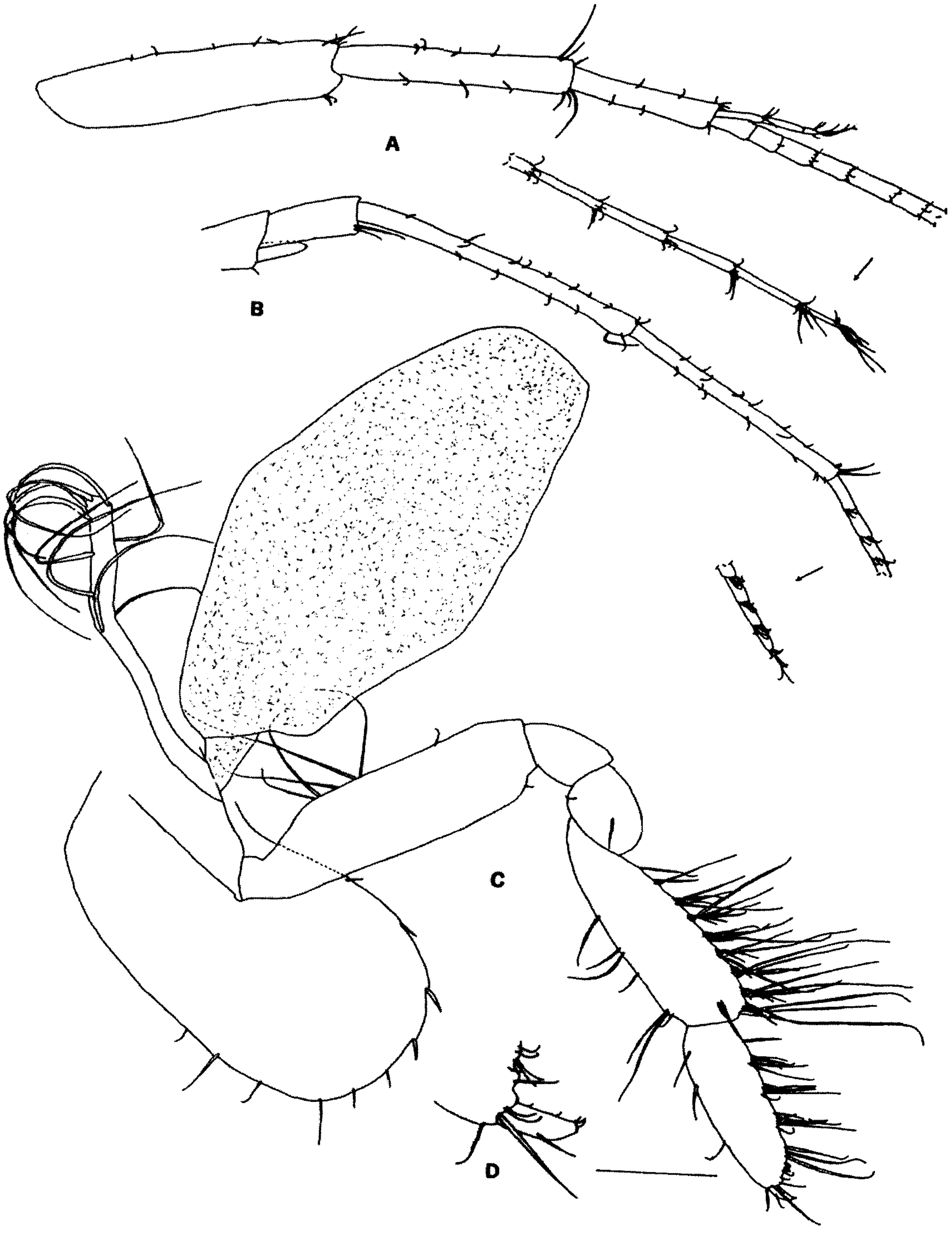

Fig. 2.3. *Bahadzia patilarga* n. sp., paratype from Cueva de los Carboneros, Playa Giron, Cuba. Female (6.5 mm): A, B antennae 1, 2; C gnathopod 2; D, enlarged distal end of propod and dactyl of gnathopod 2.

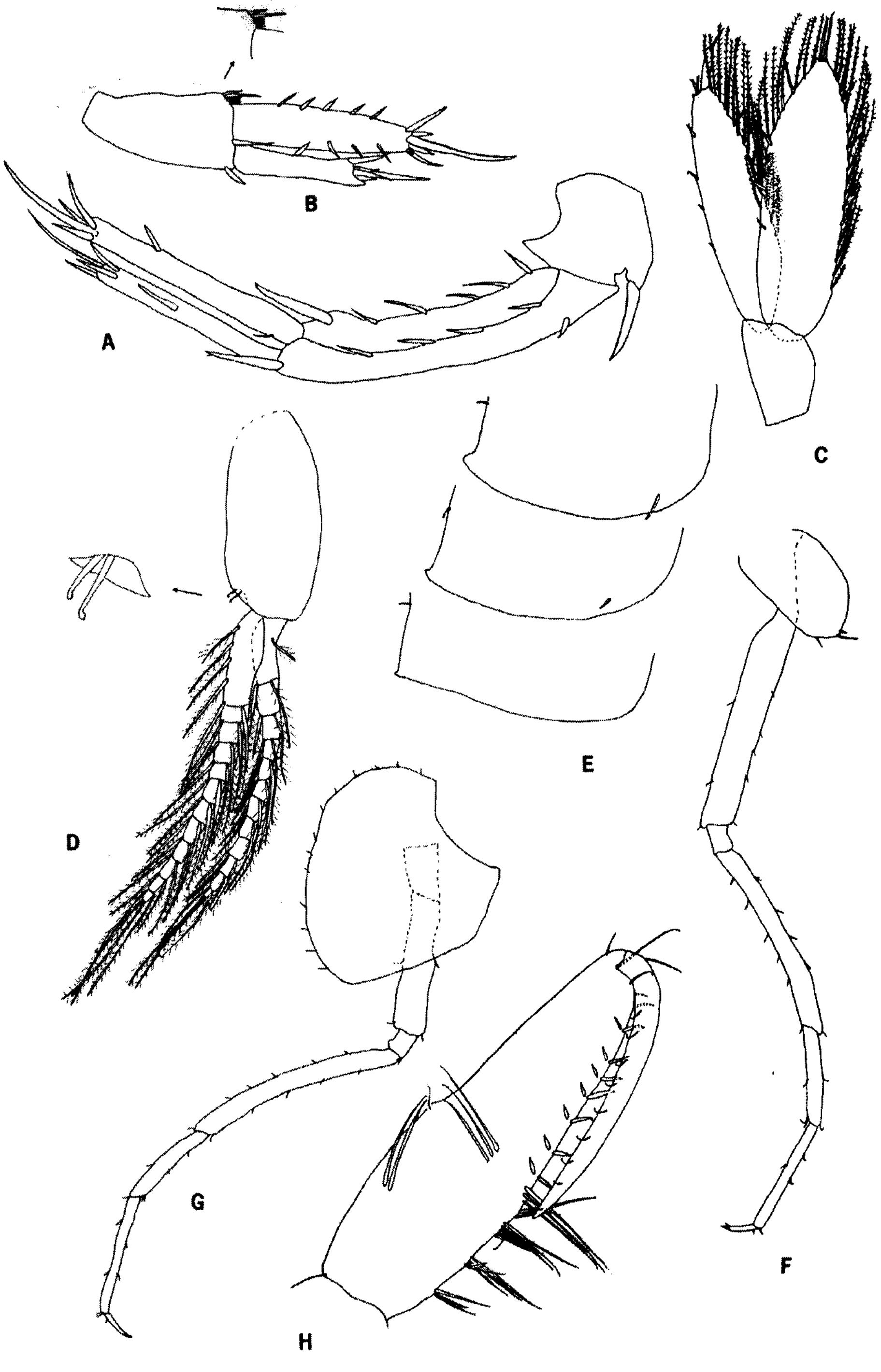

Fig. 2.4. *Bahadzia patilarga* n. sp., paratypes from Cueva de los Carboneros, Playa Giron, Cuba. Female (6.5 mm): A, uropod 1; B, uropod 2 (distomedial spine row enlarged); C, uropod 3; D, pleopod 1 (coupling spines enlarged); E, pleonal plates. Male (6.0 mm): F, G, pereopods 3, 4; H, propod and dactyl of gnathopod 2.

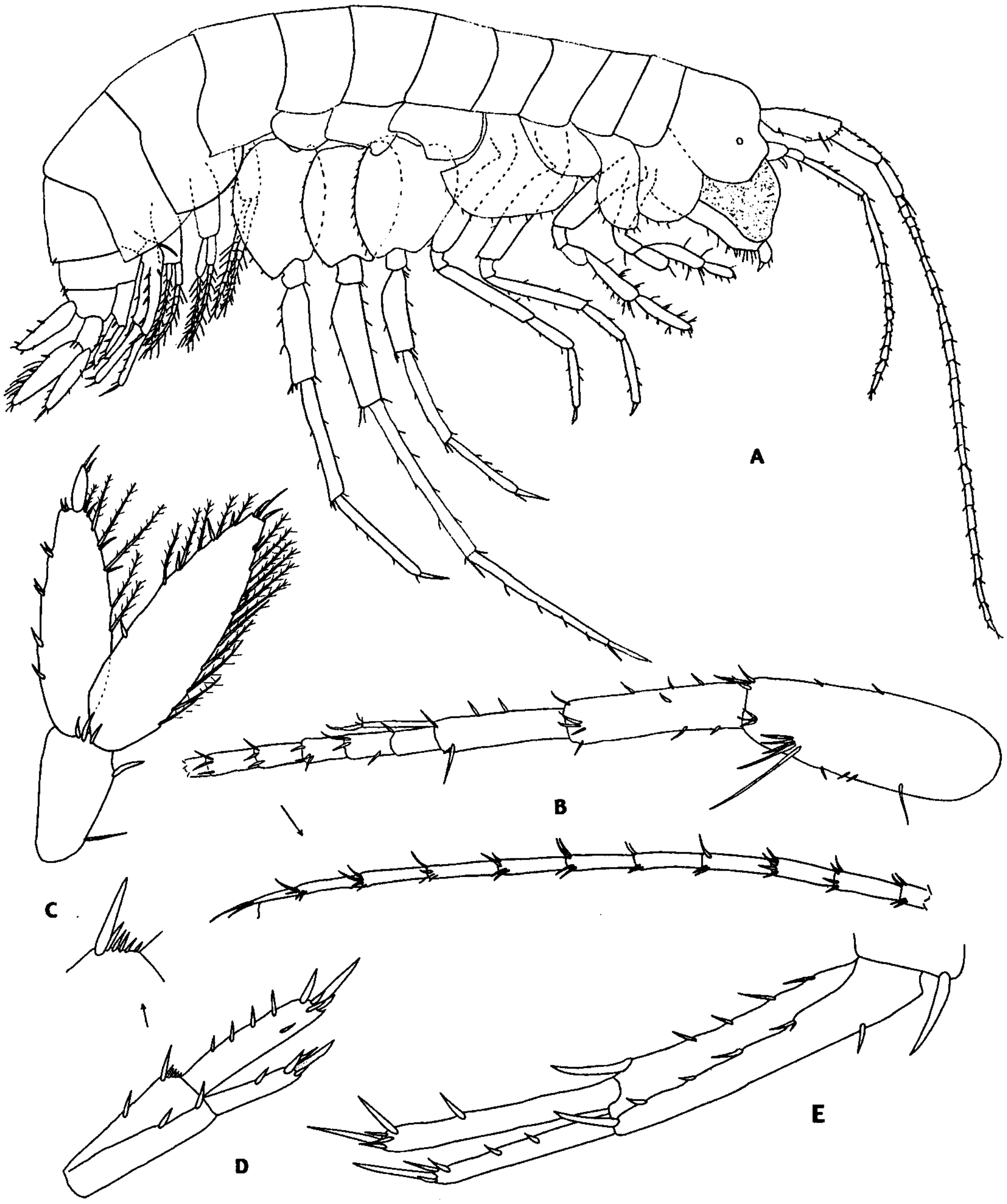

Fig. 3.1. *Bahadzia caymanensis*, n. sp., Holotype female, 5.0 mm. A, entire animal from right side. Paratype female, 6.5 mm. B, antenna 1; C, uropod 3; D, uropod 2 (distomedial combspine row enlarged); E, uropod 1.

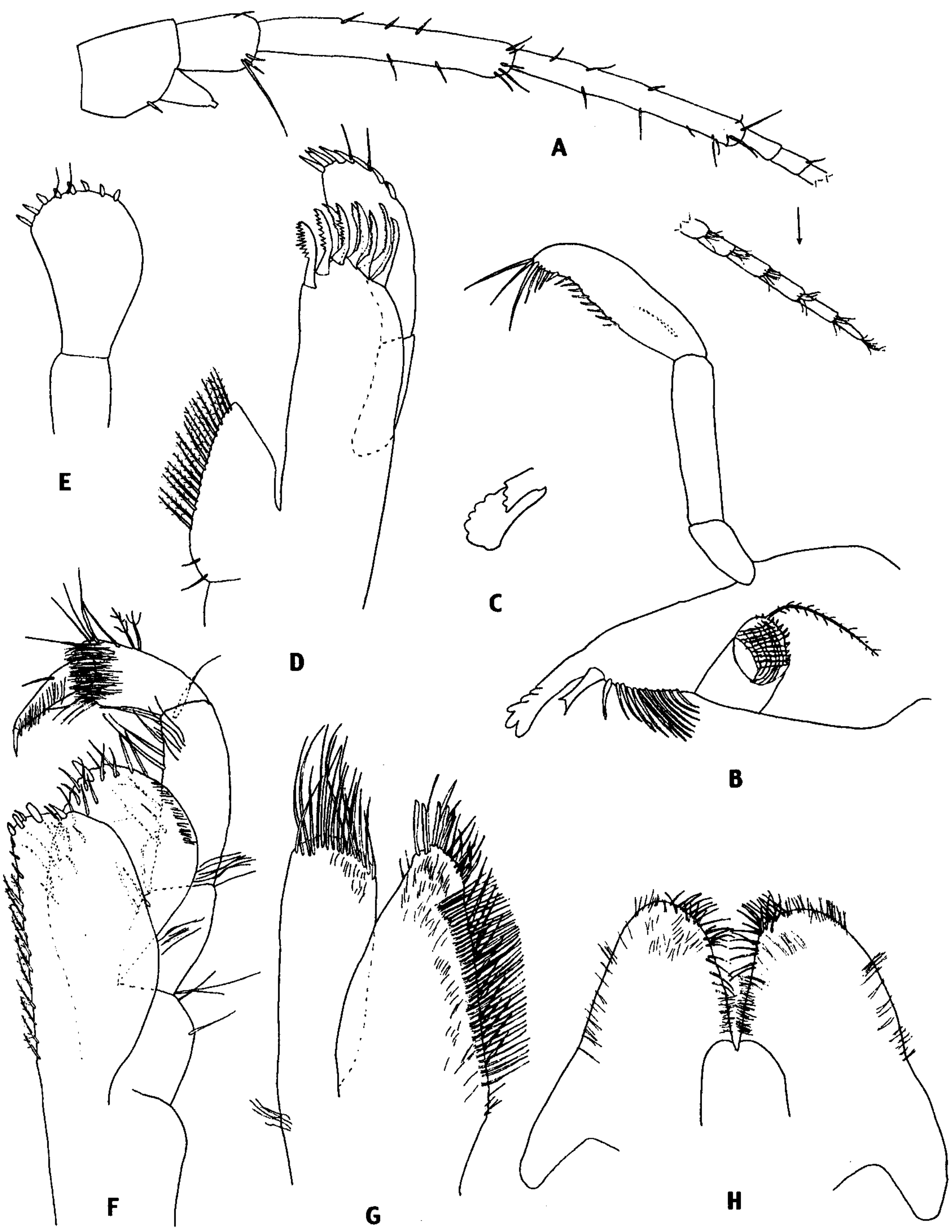

Fig. 3.2. *Bahadzia caymanensis*, n. sp., paratype female, 6.5 mm. A, antenna 2; D, maxilla 1; E, palp of other maxilla 1; F, maxilliped; G, maxilla 2; H, lower lip. Paratype female 5.7 mm. B, right mandible; C, incisor and lacinia mobilis of left mandible.

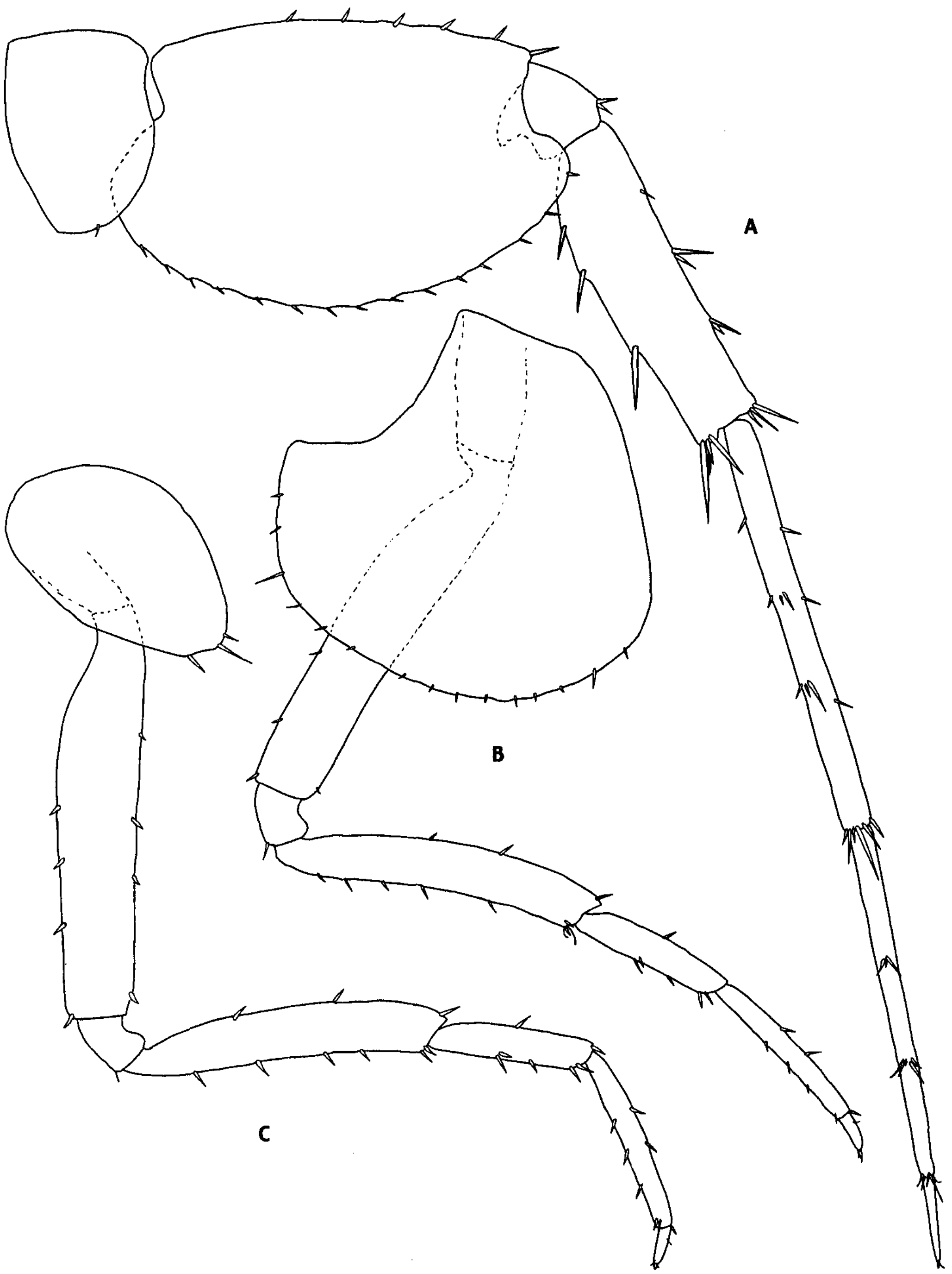

Fig. 3.3. *Bahadzia caymanensis*, n. sp., paratype female, 6.5 mm. A, pereopod 7; B, pereopod 4; C, pereopod 3.

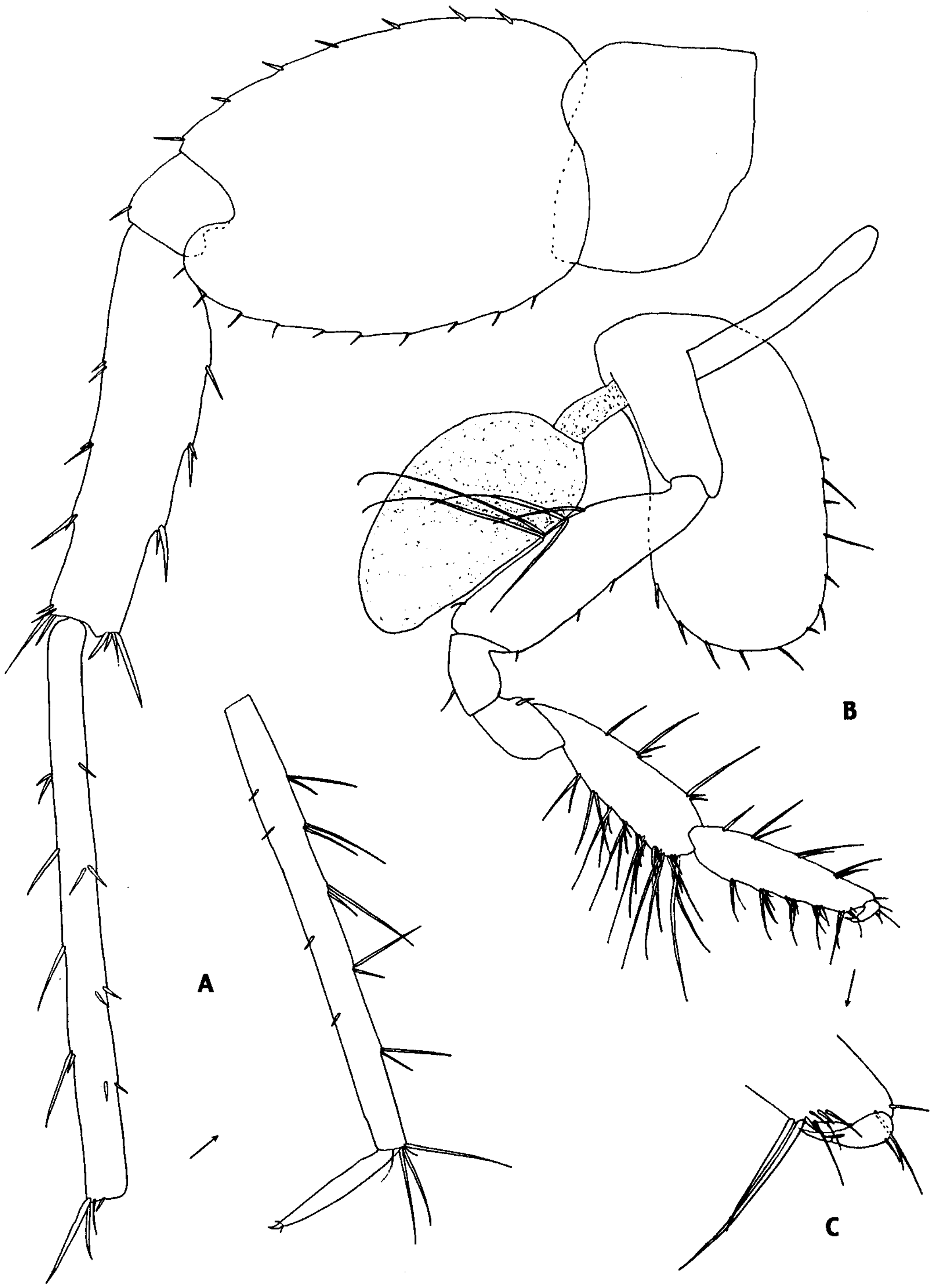

Fig. 3.4. *Bahadzia caymanensis*, n. sp., paratype female, 6.5mm. A, pereopod 6; B, gnathopod 2; C, enlarged distal end of propod and dactyl of gnathopod 2.

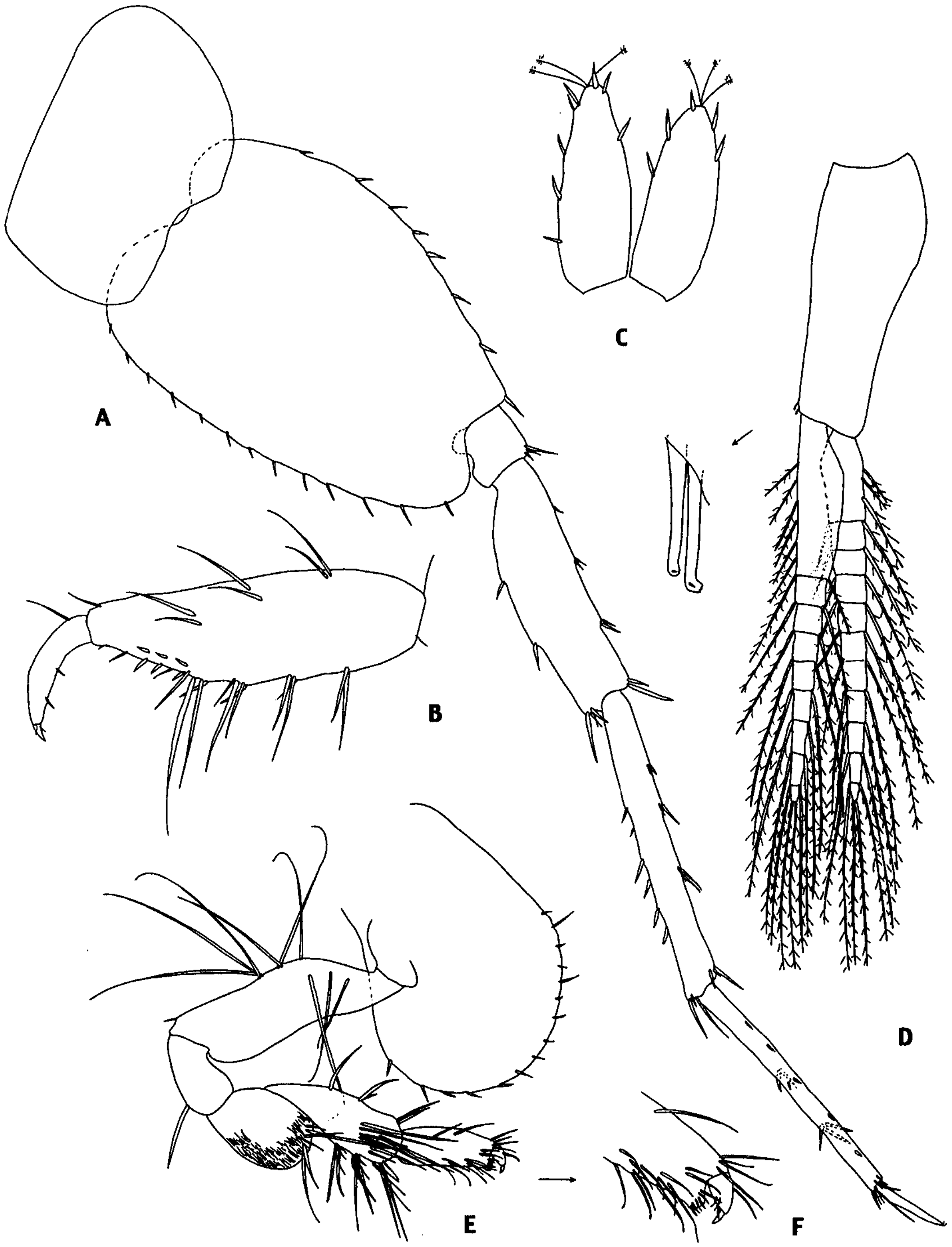

Fig. 3.5. *Bahadzia caymanensis*, n. sp., paratype female, 6.5 mm. A, pereopod 5; C, telson; D, pleopod 1 (coupling spines enlarged); E, gnathopod 1; F, enlarged distal end of propod and dactyl of gnathopod 1. Paratype male 4.5 mm. B, propod and dactyl of gnathopod 2.

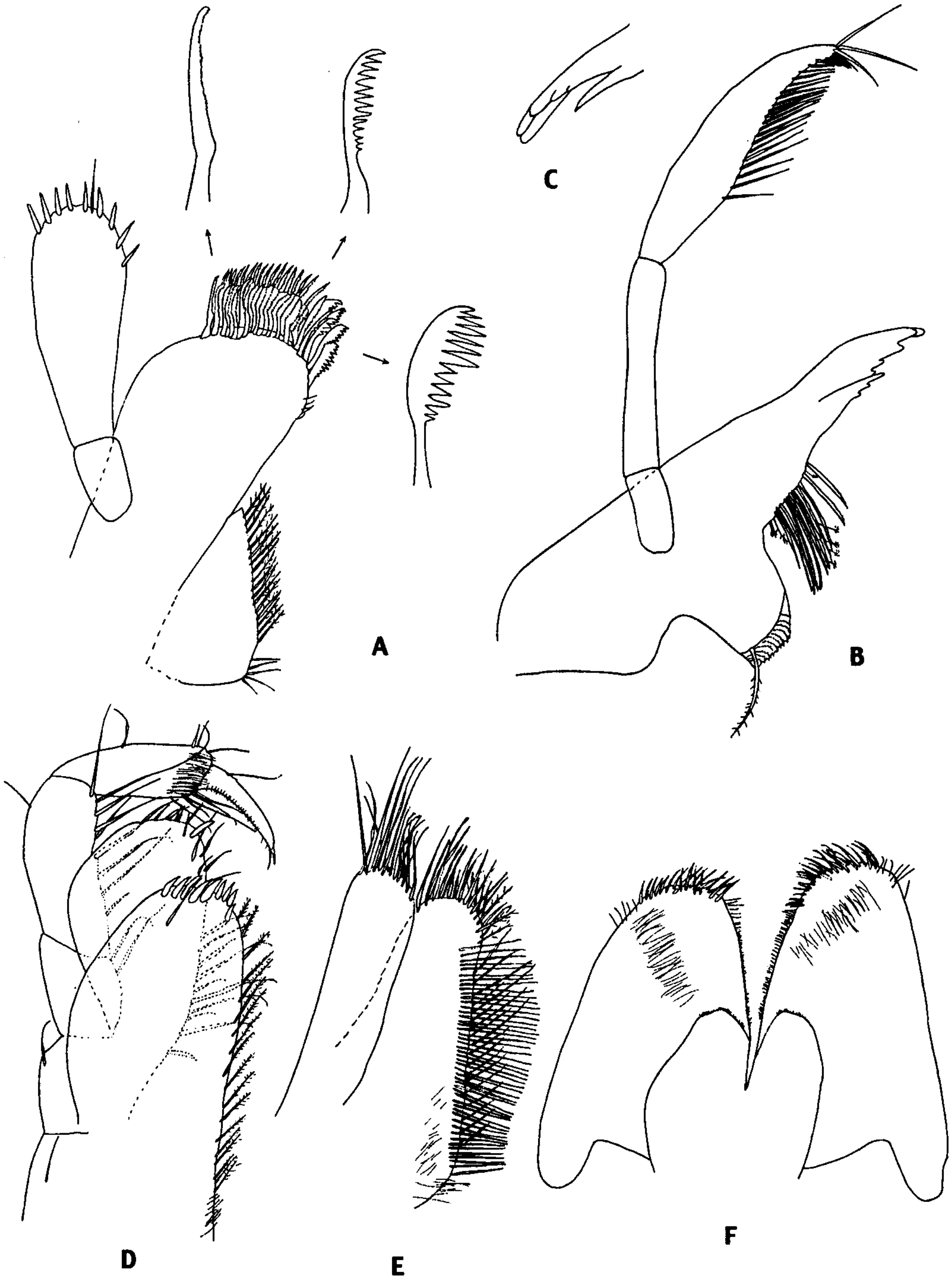

Fig. 3.6. *Bahadzia yagerae*, paratype female, 5.8 mm. A, maxilla 1 with enlargements of 3 different types of comb spines; B, left mandible; C, incisor and lacinia mobilis of right mandible; D, maxilliped; E, maxilla 2. Paratype female, 5.0 mm. F, lower lip.

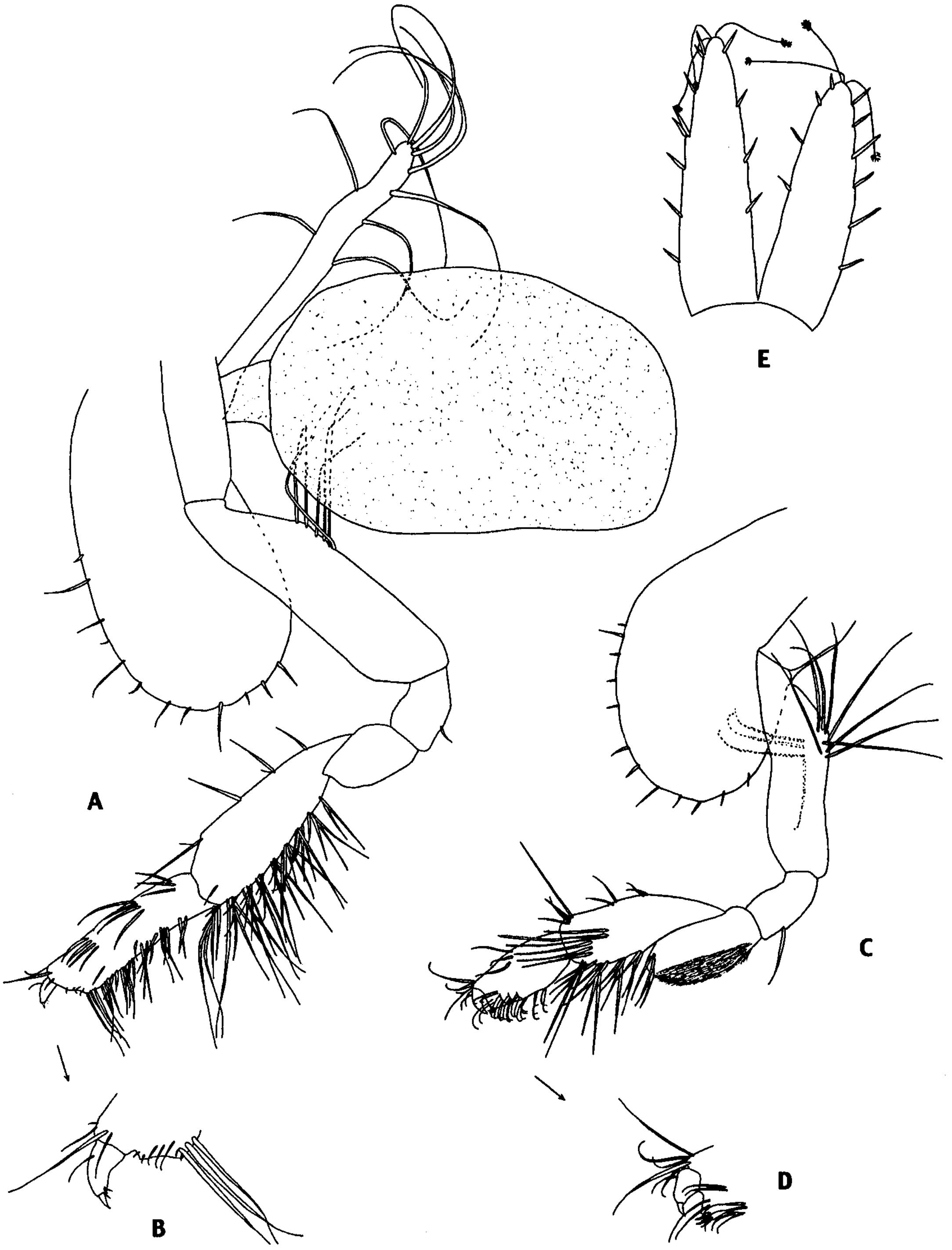

Fig. 3.7. *Bahadzia yagerae*, paratype female, 5.8 mm. A, gnathopod 2; B, enlarged distal end of propod and dactyl of gnathopod 2; C, gnathopod 1; D, enlarged distal end of propod and dactyl of gnathopod 1; E, telson.

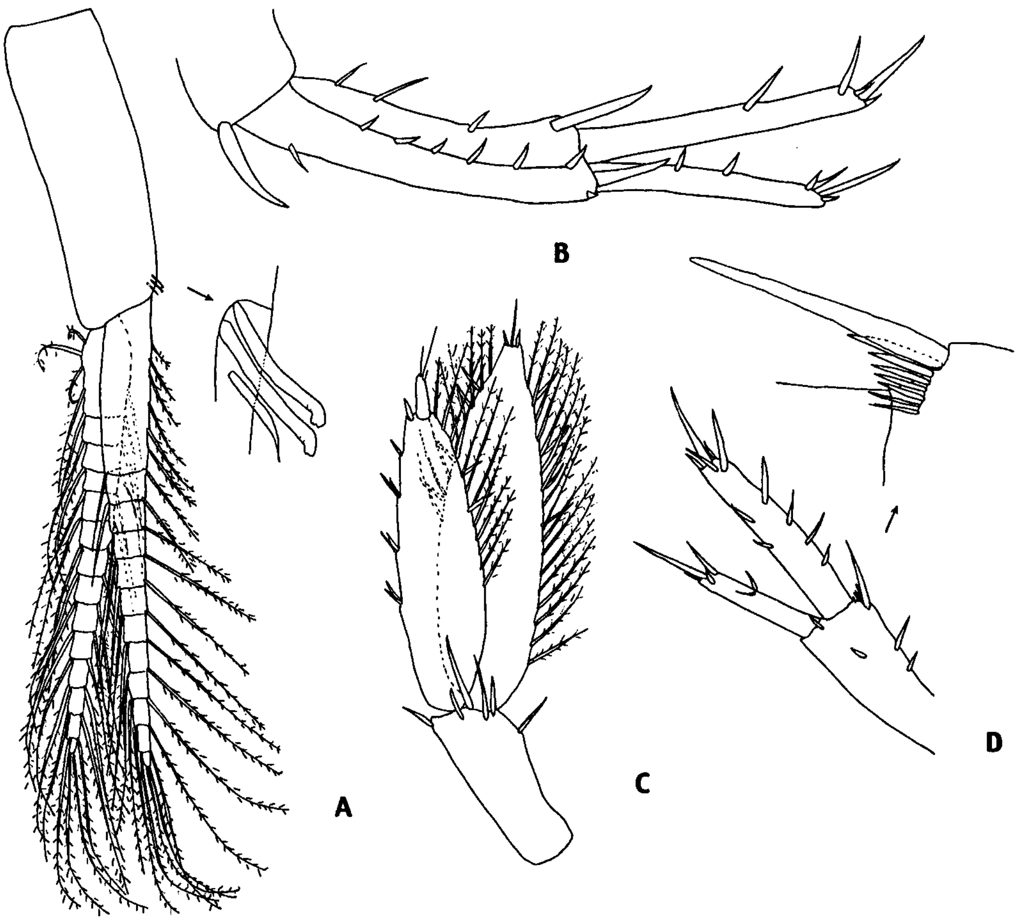

Fig. 3.8. *Bahadzia yagerae*, paratype female, 5.8 mm. A, pleopod 1 (coupling spines enlarged); B, uropod 1; C, uropod 3; D, uropod 2 (distomedial combspine row enlarged).

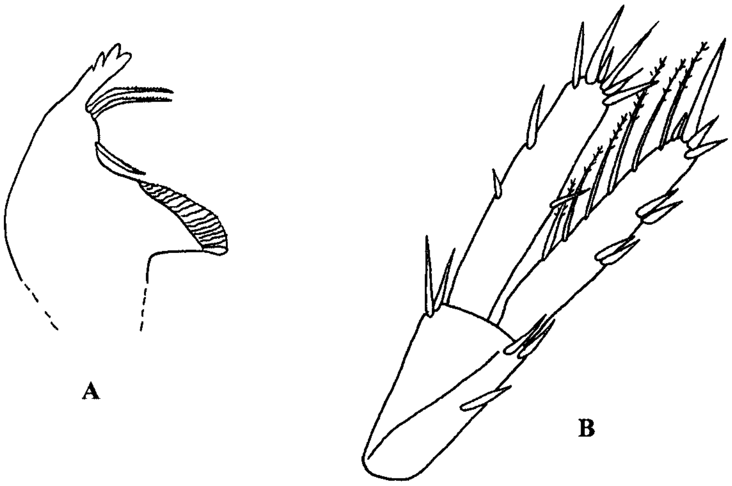

Fig. 4.1. *Paraholsingerius smaragdinus*, paratype from Sontano de Amezcua, Municipia Ciudad Acuña, Mexico. Female (6.0 mm): A, right mandible; B, uropod 2.

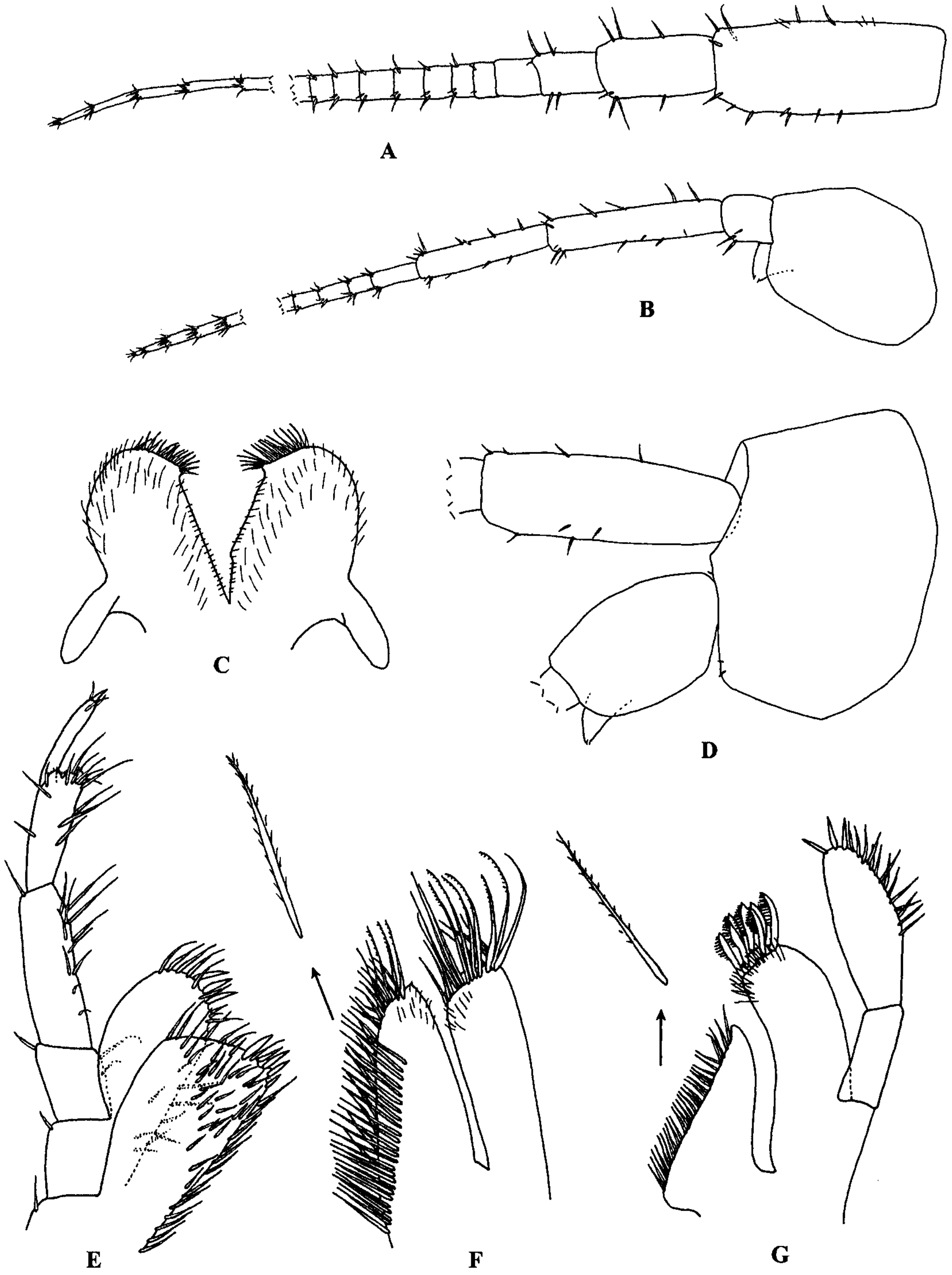

Fig. 4.2. *Paraholsingerius mexicanus* n. sp., paratypes from Gruta de Carrizal, Candela, Mexico. Female (7.5 mm): A, B, antennae 1, 2; C, lower lip; E, maxilliped; F, maxilla 2; G, maxilla 1. Female (6.5 mm): D, head.

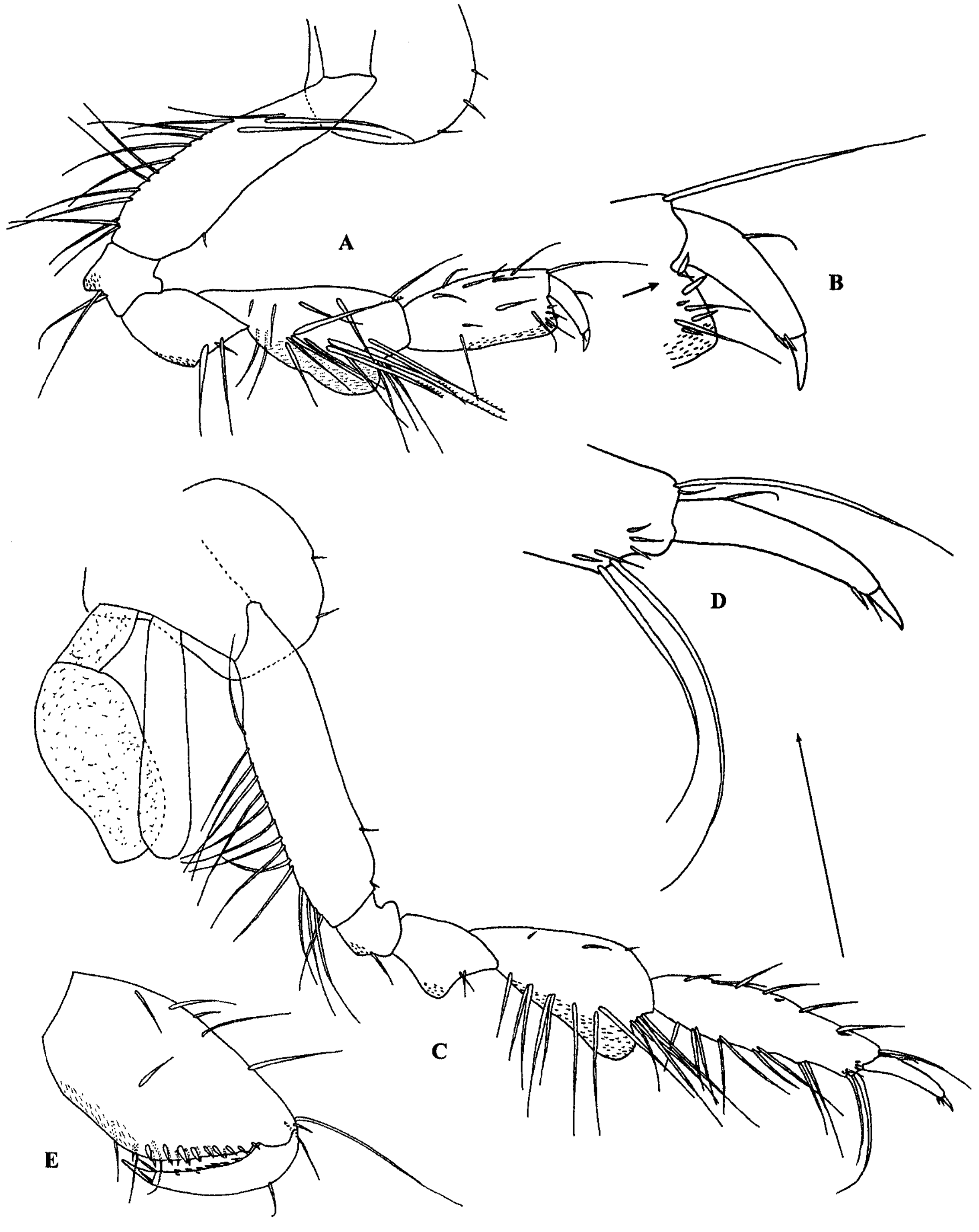

Fig. 4.3. *Paraholsingerius mexicanus* n. sp., paratypes from Gruta de Carrizal, Candela, Mexico. Female (7.5 mm): A, gnathopod 1; B, enlarged distal end of propod and dactyl of gnathopod 1; C, gnathopod 2; D, enlarged distal end of propod and dactyl of gnathopod 2. Male (6.0 mm): E, propod and dactyl of gnathopod 1.

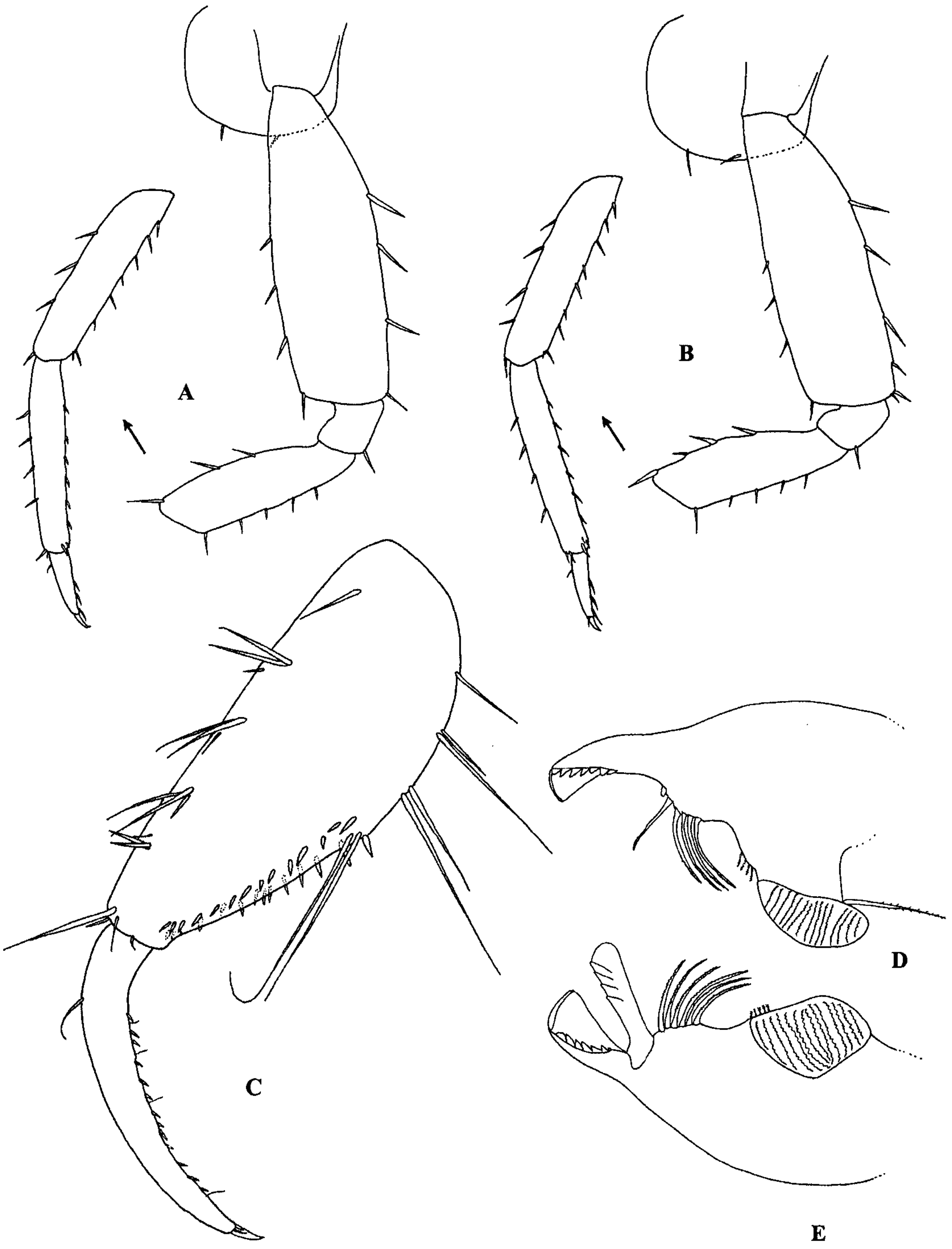

Fig. 4.4. *Paraholsingerius mexicanus* n. sp., paratypes from Gruta de Carrizal, Candela, Mexico. Female (7.5 mm): A, pereopod 3; B, pereopod 4; D, right mandible; E, left mandible. Male (6.0 mm): C, propod and dactyl of gnathopod 2.

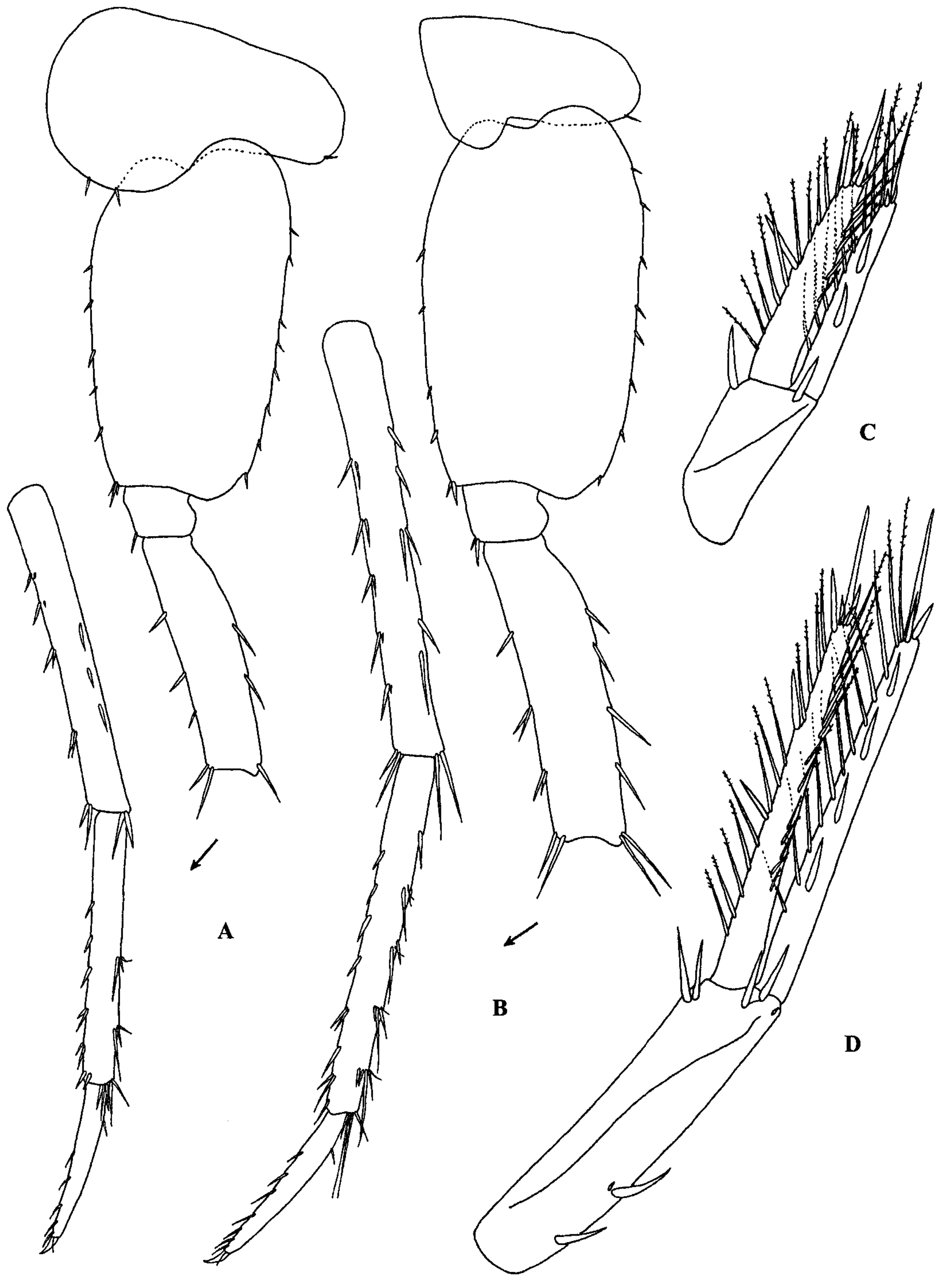

Fig. 4.5. *Paraholsingerius mexicanus* n. sp., paratype from Gruta de Carrizal, Candela, Mexico. Female (7.5 mm): A, pereopod 5; B, pereopod 6; C, uropod 2; D, uropod 1.

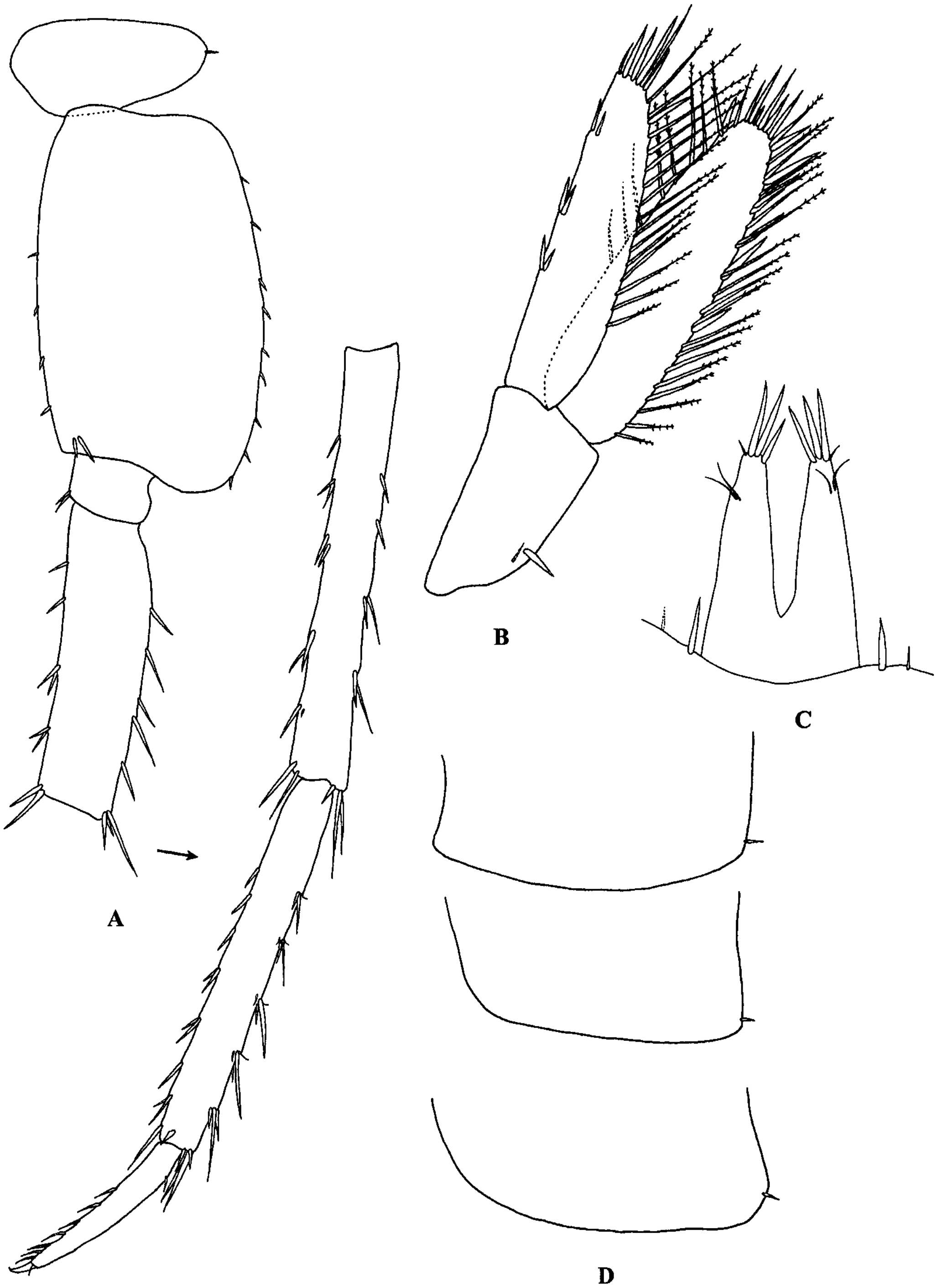

Fig. 4.6. *Paraholsingerius mexicanus* n. sp., paratype from Gruta de Carrizal, Candela, Mexico. Female (7.5 mm): A, pereopod 7; B, uropod 3; C, telson; D, pleonal plates 1-3.

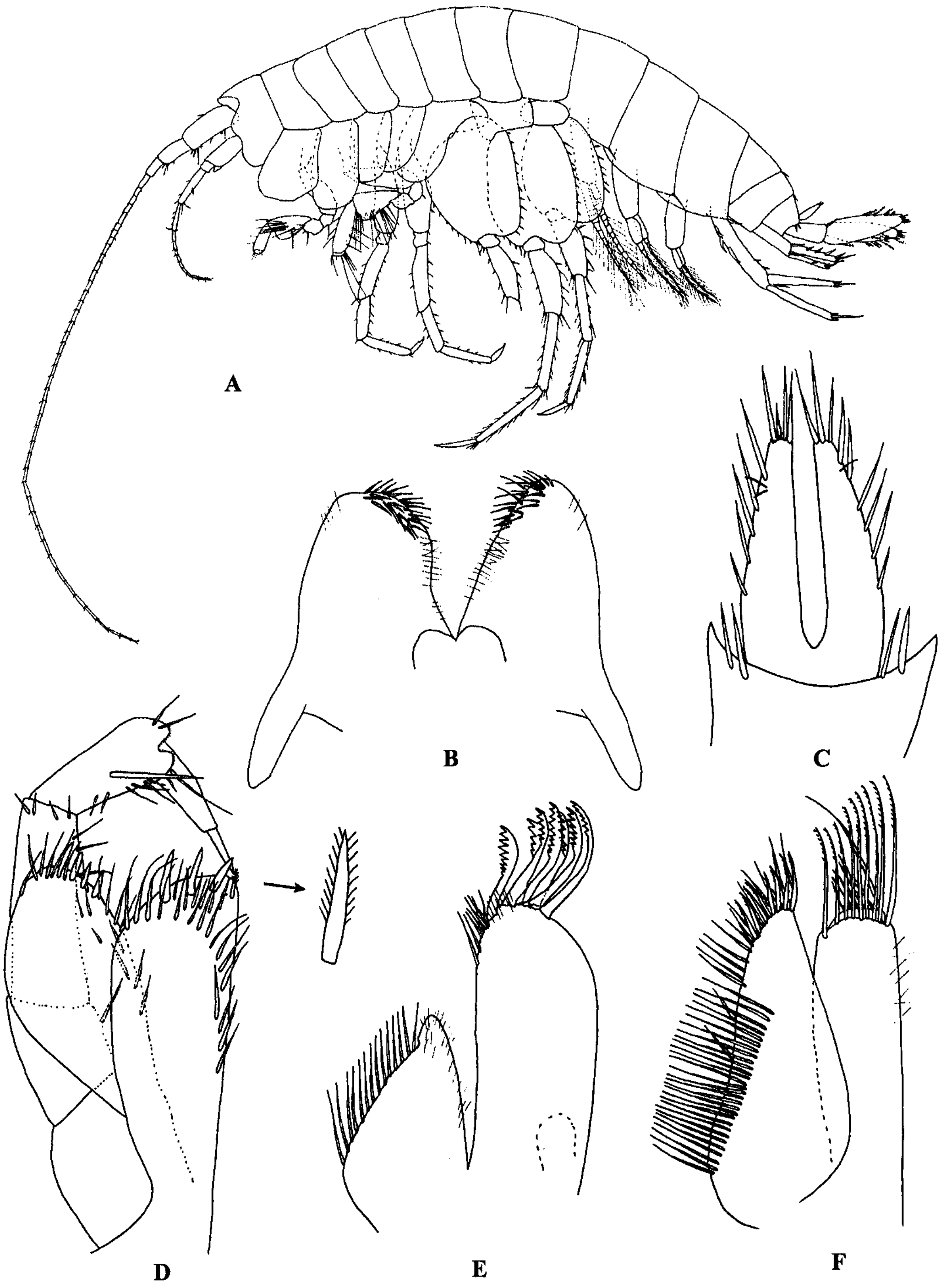

Fig. 4.7. *Tamaweckelia apalpa* n. sp., paratypes from Manantial de San Rafael de Los Castro, Municipia Ciudad Mante, Mexico. Female (7.0 mm): A, whole animal from left side. Female (5.5 mm): B, lower lip; C, telson and posterior end of uronite 3; D, maxilliped. Female (5.0 mm): E, maxilla 1; F, maxilla 2.

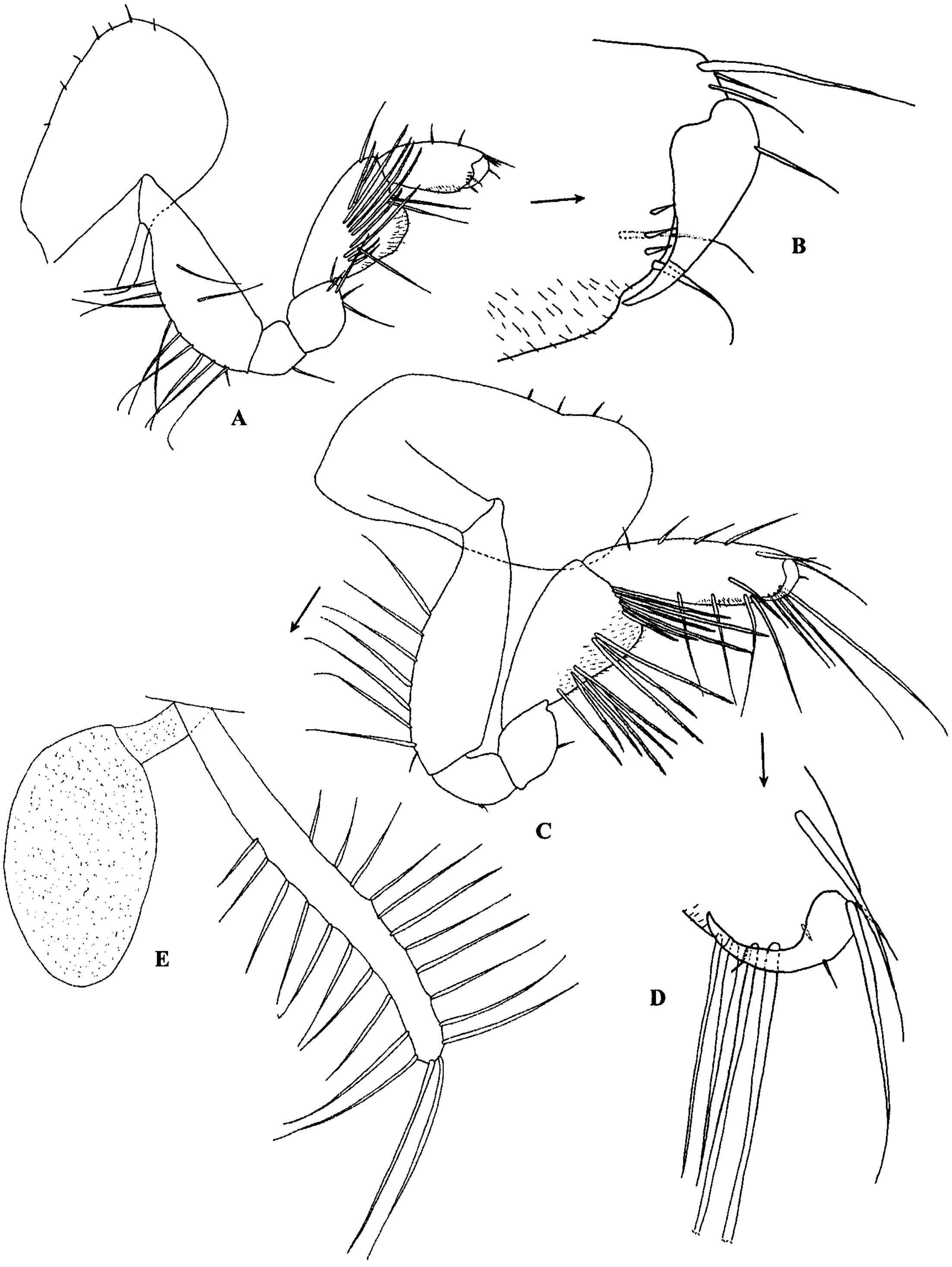

Fig. 4.8. *Tamaweckelia apalpa* n. sp., paratype from Manantial de San Rafael de Los Castro, Municipia Ciudad Mante, Mexico. Female (5.5 mm): A, gnathopod 1; B, enlarged distal end of propod and dactyl of gnathopod 1; C, gnathopod 2; D, enlarged distal end of propod and dactyl of gnathopod 2; E, brood plate and gill of gnathopod 2.

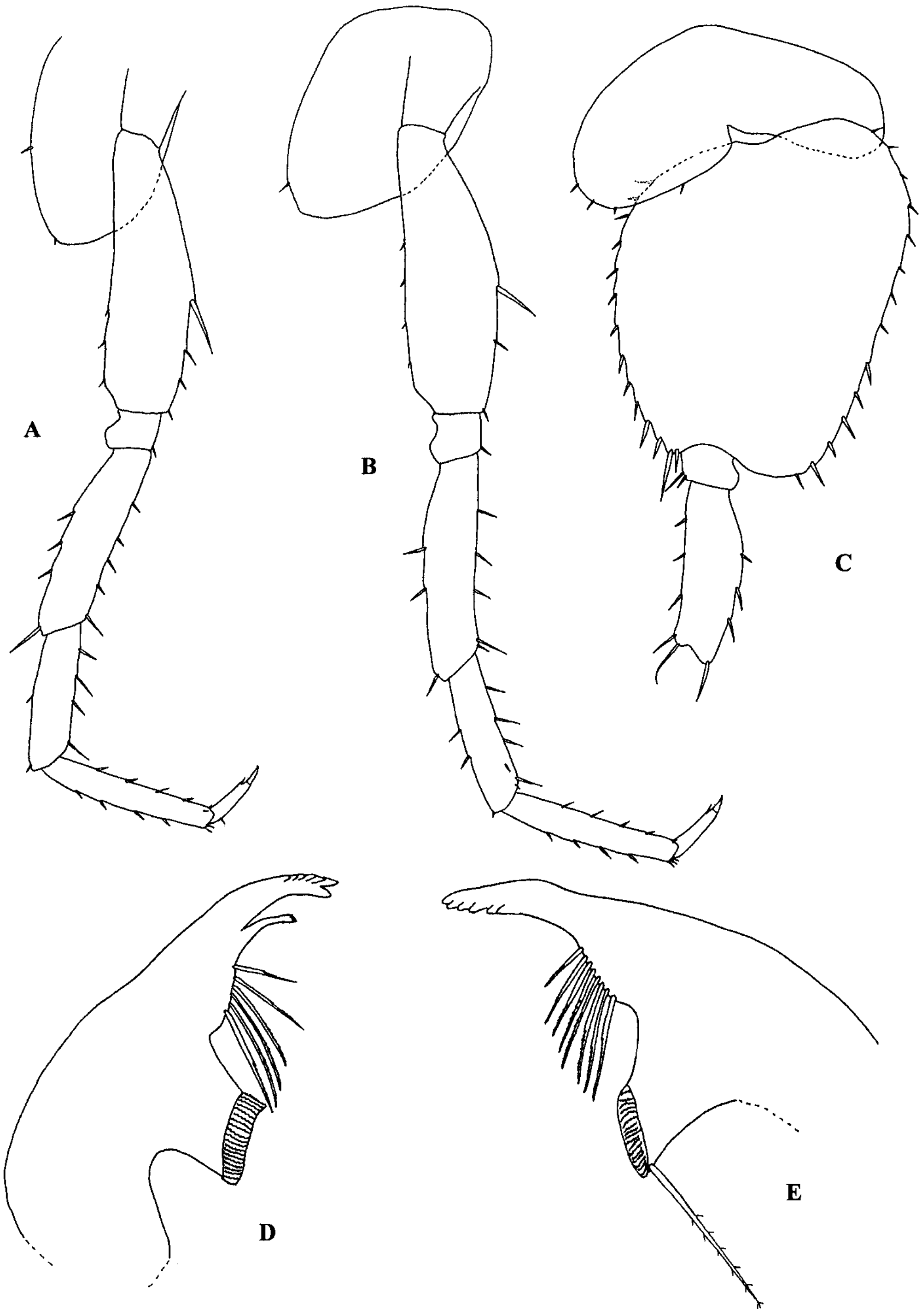

Fig. 4.9. *Tamaweckelia apalpa* n. sp., paratype from Manantial de San Rafael de Los Castro, Municipia Ciudad Mante, Mexico. Female (5.5 mm): A, pereopod 3; B, pereopod 4; C, pereopod 5; D, left mandible; E, right mandible.

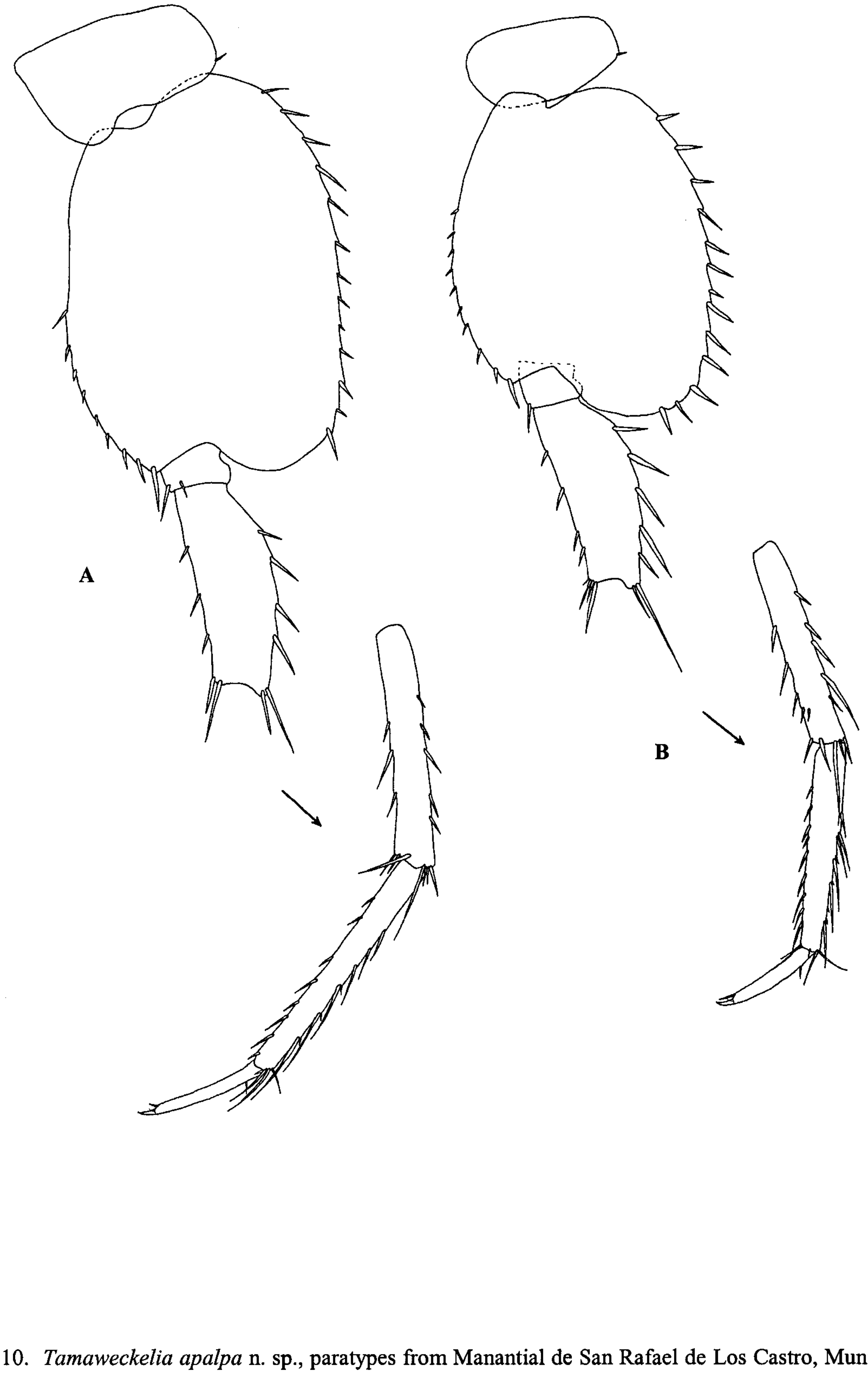

Fig. 4.10. *Tamaweckelia apalpa* n. sp., paratypes from Manantial de San Rafael de Los Castro, Municipia Ciudad Mante, Mexico. Female (5.5 mm): A, pereopod 6. Female (4.0 mm): B, pereopod 7.

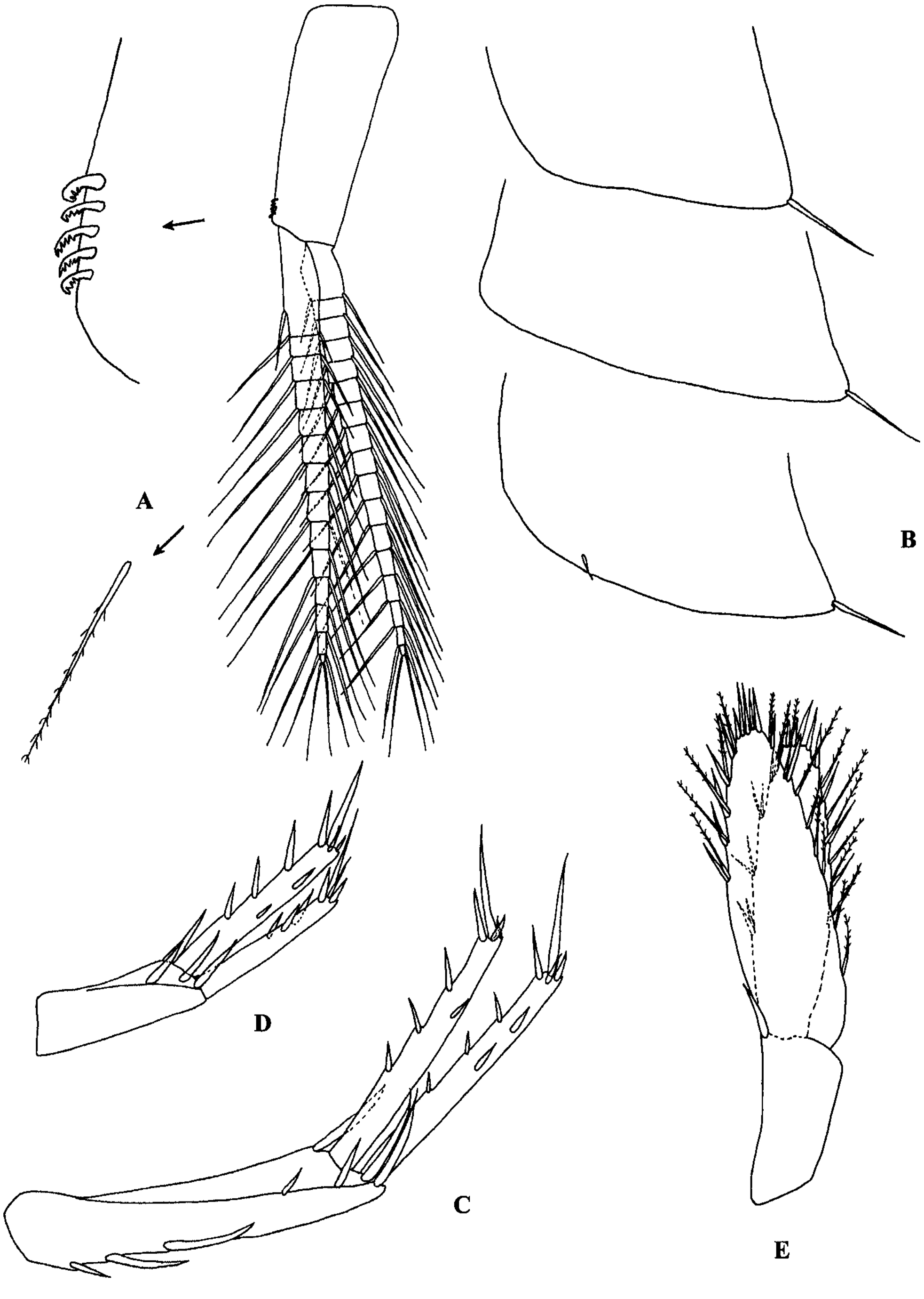

Fig. 4.11. *Tamaweckelia apalpa* n. sp., paratype from Manantial de San Rafael de Los Castro, Municipia Ciudad Mante, Mexico. Female (5.5 mm): A, pleopod 1 (coupling spines enlarged and seta showing plumosity); B, pleonal plates 1-3; C, uropod 1; D, uropod 2; E, uropod 3.

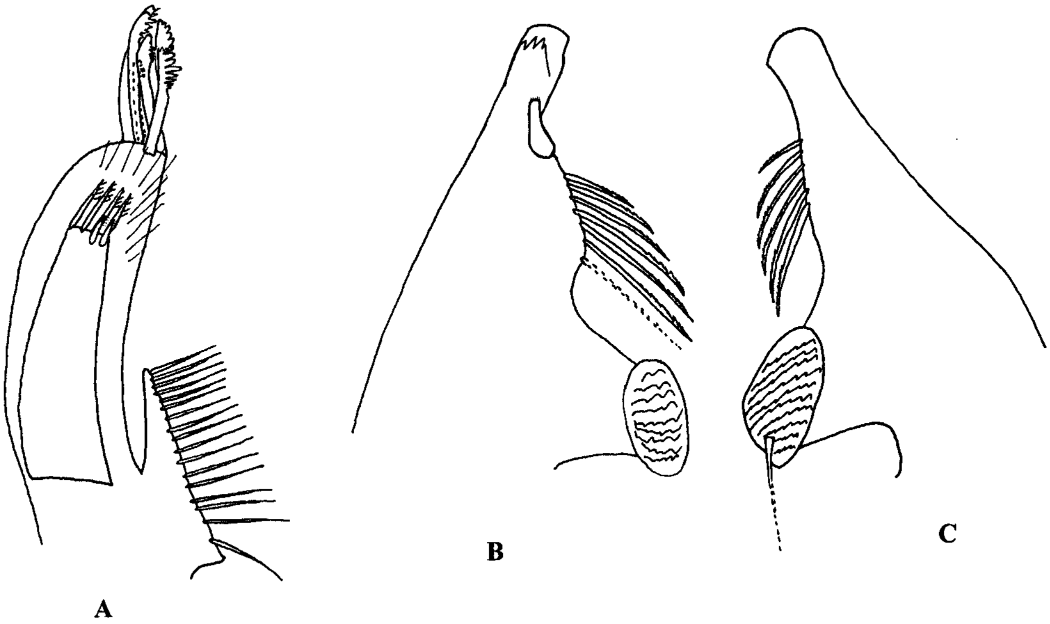

Fig. 4.12. New genus? New species? sex unknown, size unknown, from Manantial de San Rafael de Los Castro, Municipia Ciudad Mante, Mexico: A, maxilla 1; B, left mandible; C, right mandible.

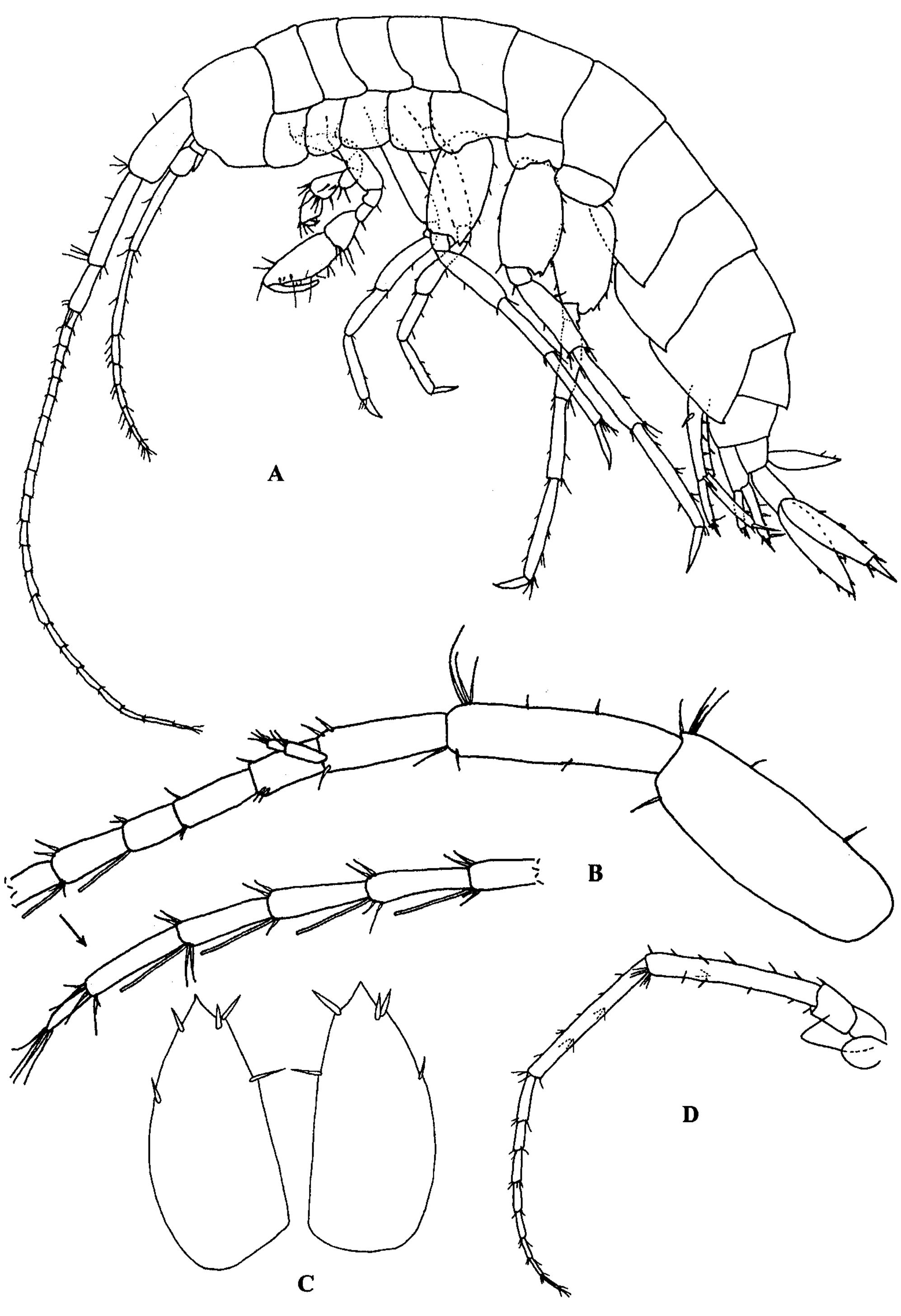

Fig. 5.1. *Hadzia guamensis*, n. sp., paratype, Faifai Beach Cave, Guam. Male (2.8 mm): A, whole animal from left side. Paratypes, Marbo Cave, Guam. Female (2.5 mm): B, antenna 1; D, antenna 2. Male (2.5 mm): C, telson.

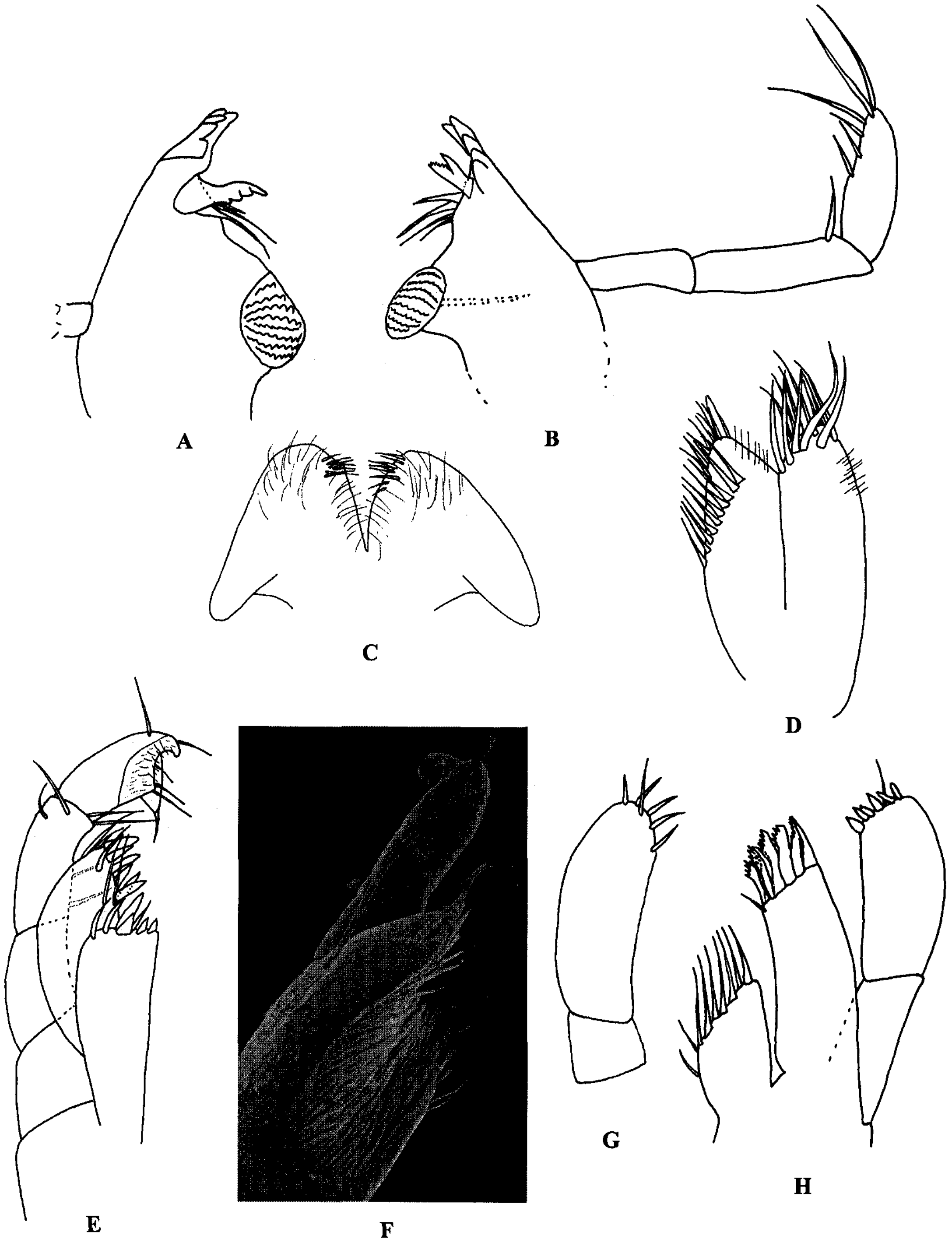

Fig. 5.2. *Hadzia guamensis*, n. sp., paratypes, Marbo Cave, Guam. Female (2.5 mm): A, left mandible; B, right mandible; H, right maxilla 1. Male (2.5 mm): C, lower lip; D, maxilla 2; E, maxilliped; G, left maxilla 1 palp. Second female (2.5 mm): F, SEM distal end of segment 3, left maxilliped palp.

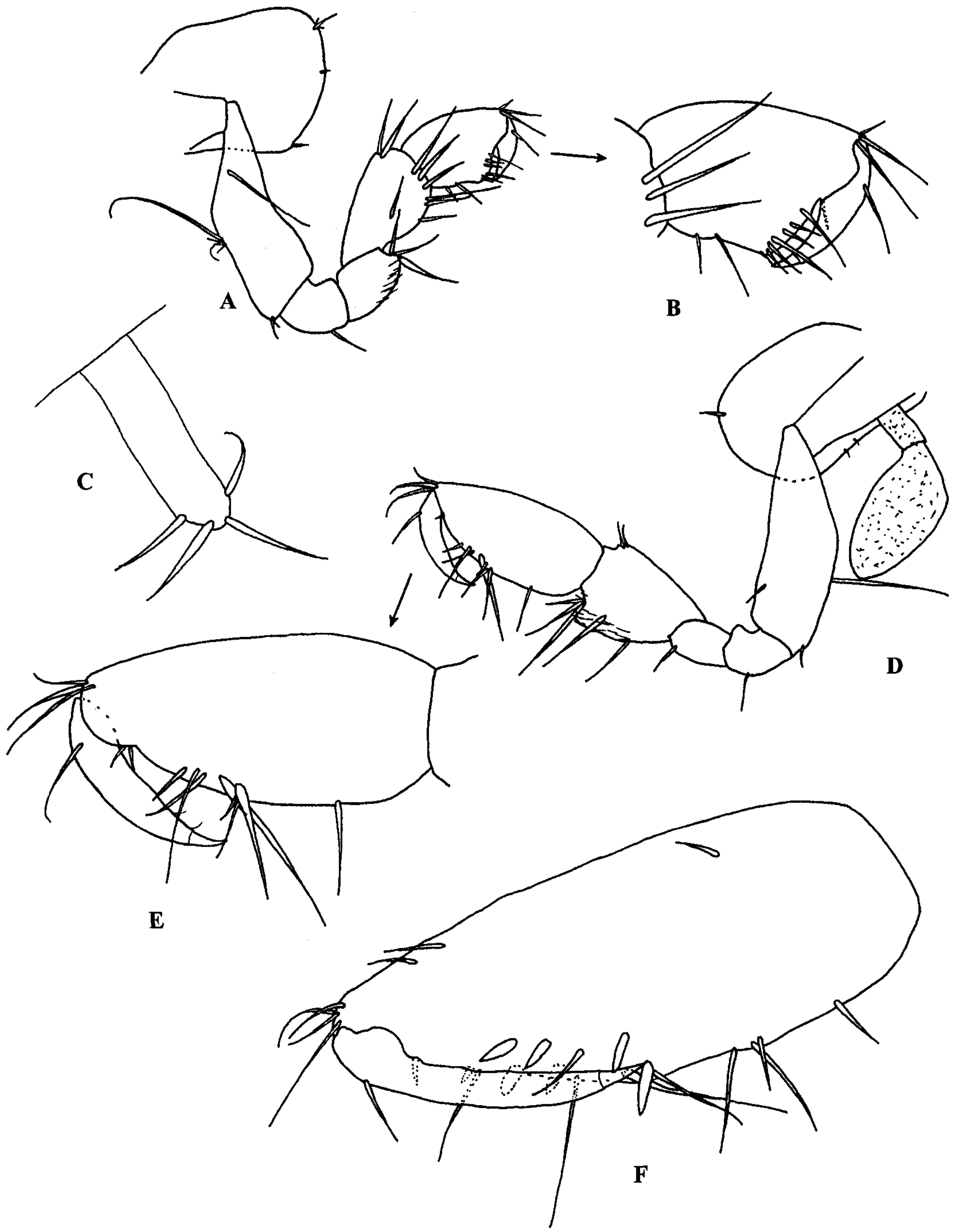

Fig. 5.3. *Hadzia guamensis*, n. sp., paratypes, Marbo Cave, Guam. Female (2.5 mm): A, gnathopod 1; B, enlarged propod and dactyl of gnathopod 1; D, gnathopod 2; E, enlarged propod and dactyl of gnathopod 2. Male (2.5 mm): F, propod, gnathopod 2. Paratype, Tarague Water Well Cave, Guam. Female (3.0 mm): C, brood plate, gnathopod 2.

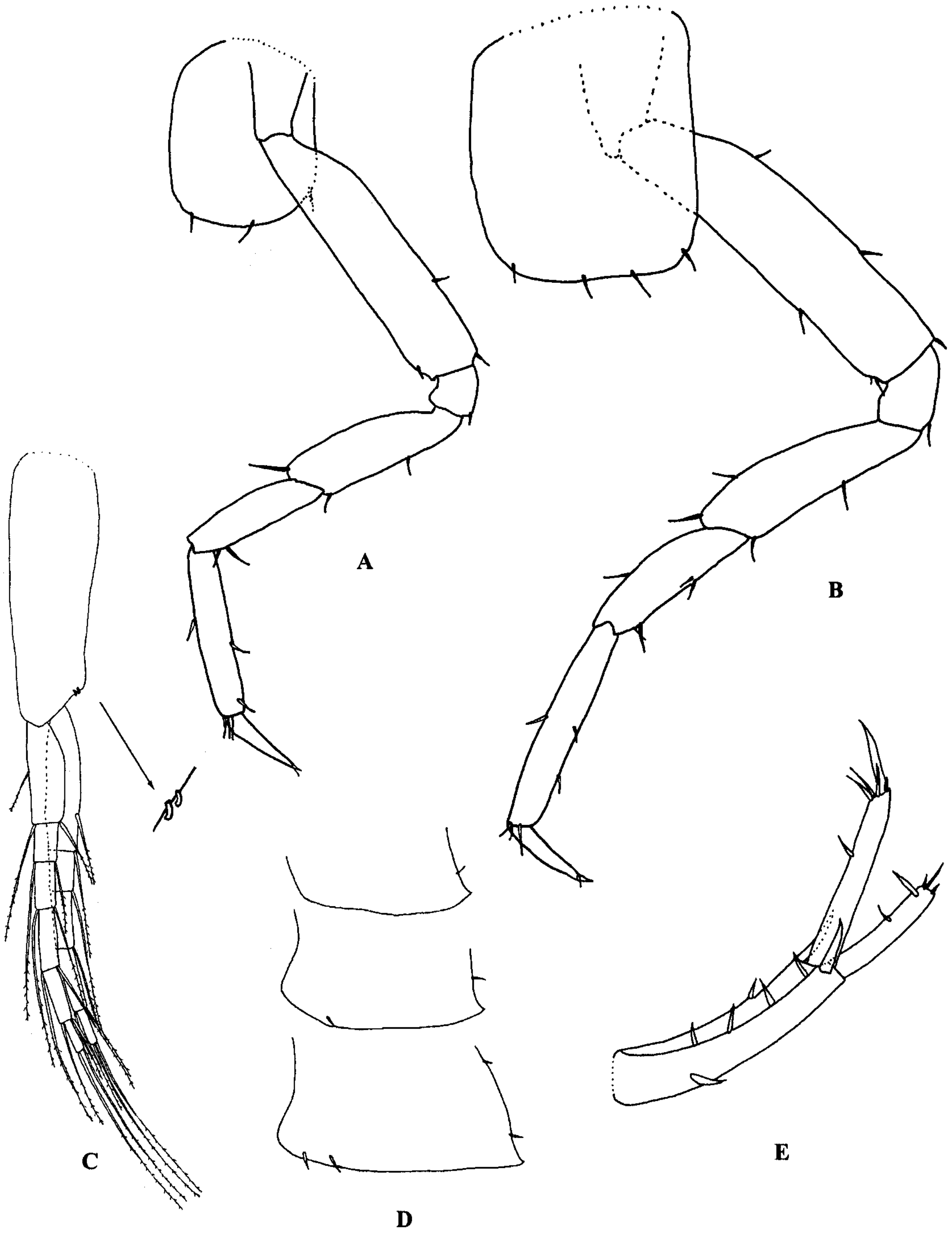

Fig. 5.4. *Hadzia guamensis*, n.sp., paratypes, Marbo Cave, Guam. Female (2.5 mm): A, pereopod 3. Male (2.5 mm): B, pereopod 4; C, pleopod 1, (coupling spines enlarged); D, pleonal plates 1-3; E, uropod 1.

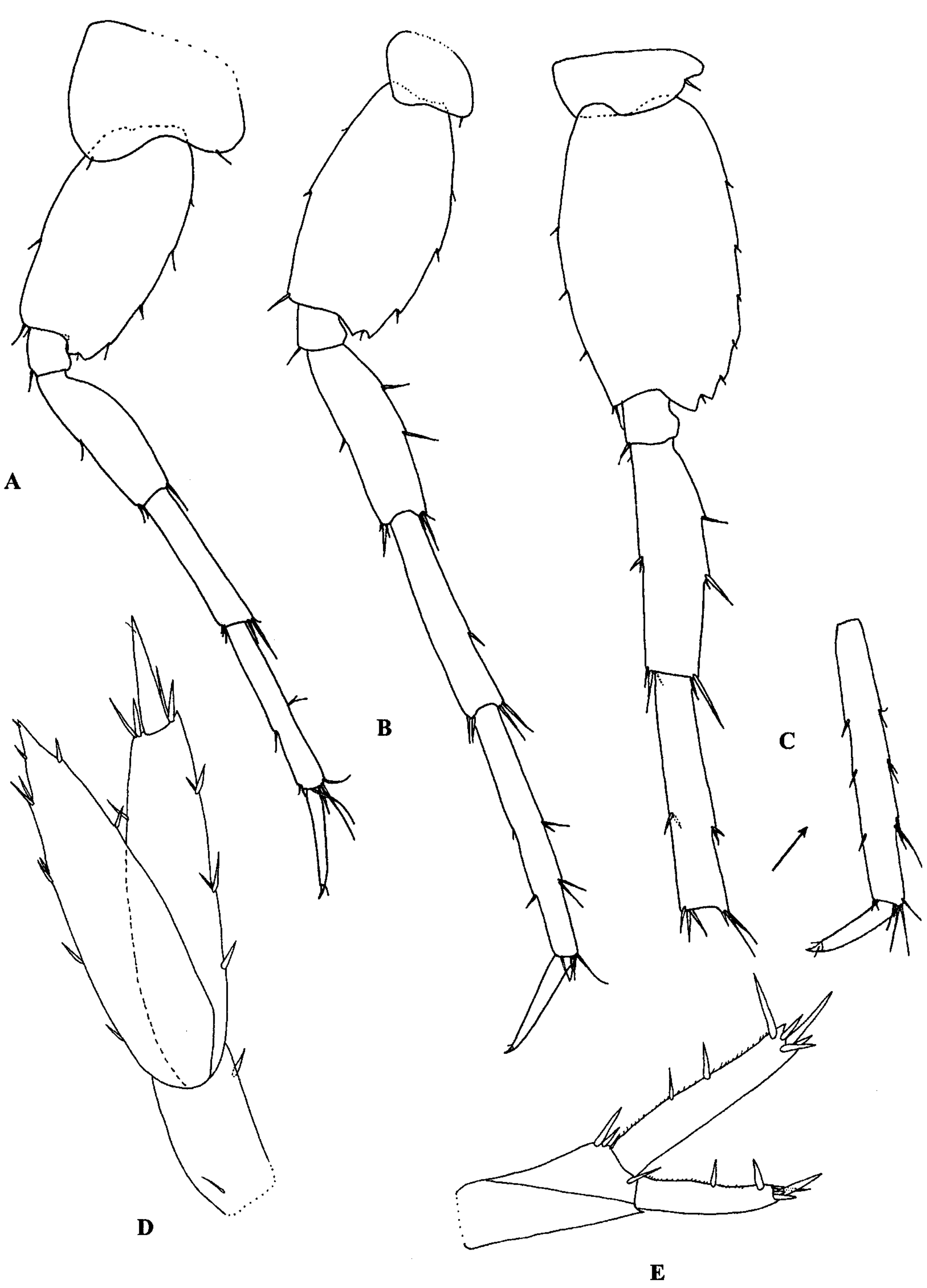

Fig. 5.5. *Hadzia guamensis*, n. sp., paratypes, Marbo Cave, Guam. Female (2.5 mm): A, pereopod 5. Female (2.0 mm): B, pereopod 6; D, uropod 3. Male (2.3 mm): C, pereopod 7. Male (2.5 mm): E, uropod 2.

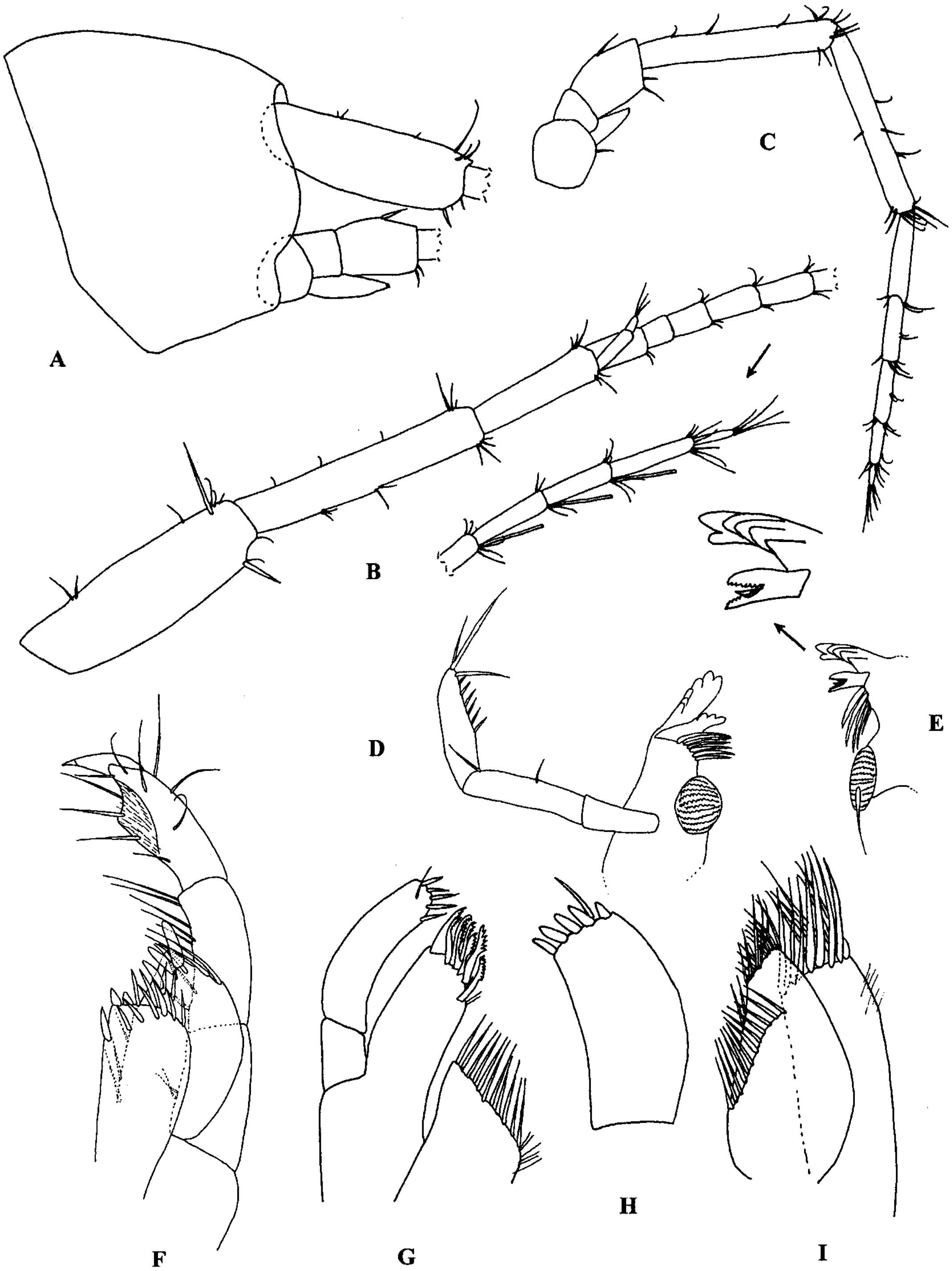

Fig. 5.6. *Hadzia philippinensis*, n. sp., paratypes, Tauala Cave, Panglao Island, Bohol, Philippines. Female (2.2 mm): A, head. Female (2.7 mm): B, antenna 1; C, antenna 2; D, left mandible; E, right mandible, lacinia mobilis and incisor enlarged; F, maxilliped; G, left maxilla 1; H, palp of right maxilla 1; I, maxilla 2.

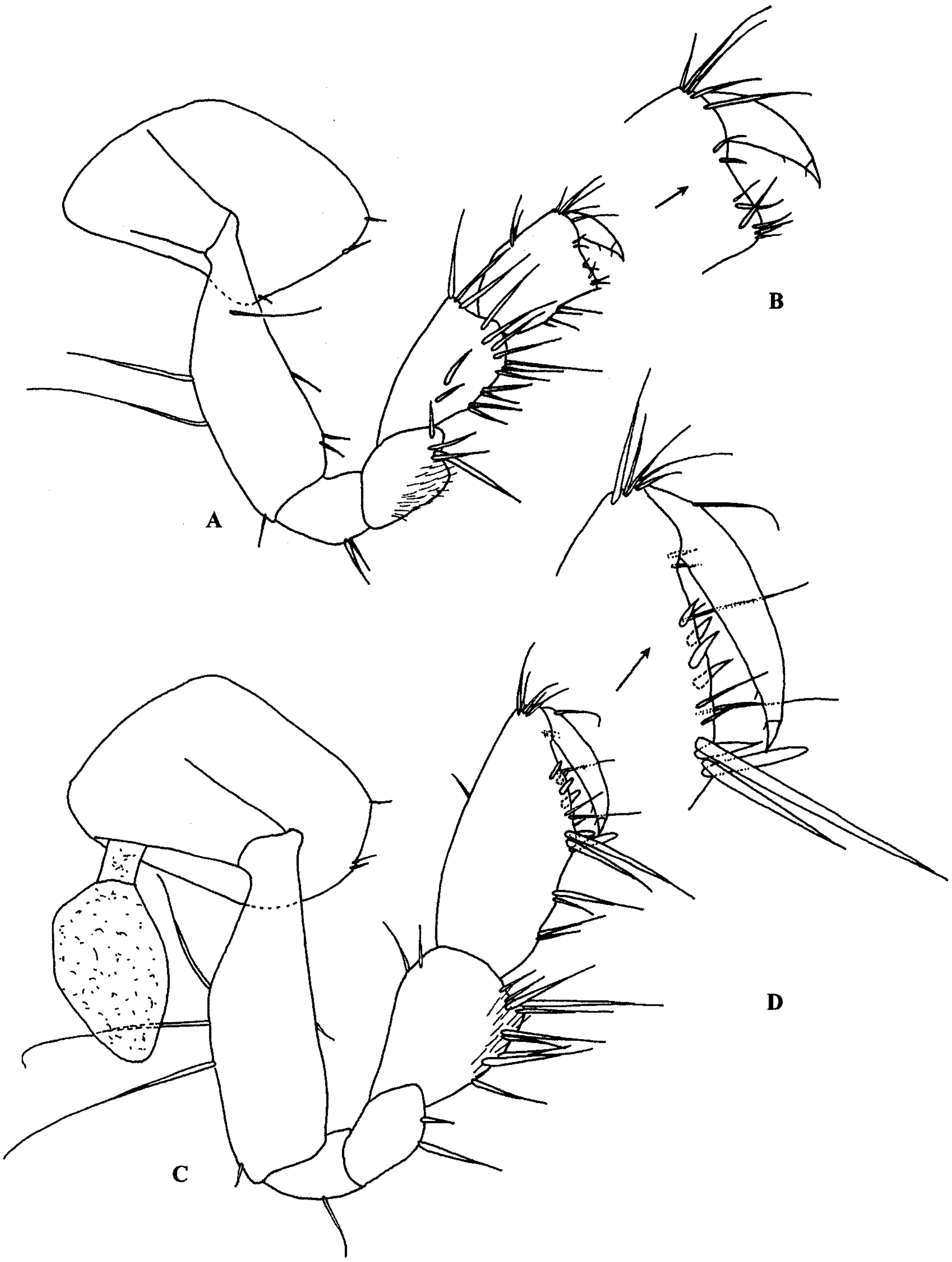

Fig. 5.7. *Hadzia philippinensis*,n. sp.,. paratype, Tauala Cave, Panglao Island, Bohol, Philippines. Female (2.7 mm): A, gnathopod 1; B, enlarged distal end of propod and dactyl of gnathopod 1; C, gnathopod 2; D, enlarged distal end of propod and dactyl of gnathopd 2.

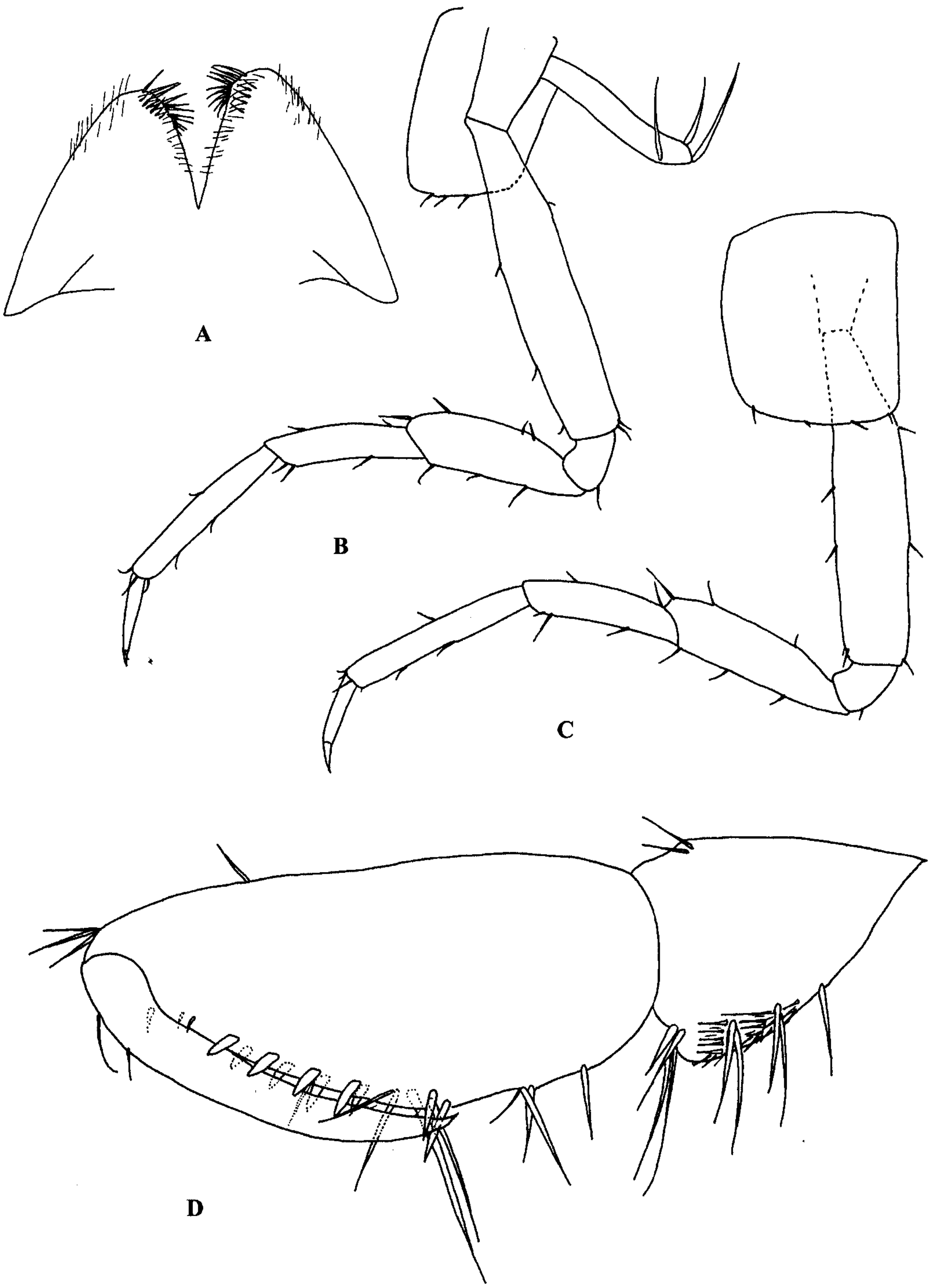

Fig. 5.8. *Hadzia philippinensis*, n. sp., paratypes, Tauala Cave, Panglao Island, Bohol, Philippines. Male (2.0 mm): A, lower lip; D, carpus, propod and dactyl of gnathopod 2. Female (2.7 mm): B, pereopod 3; C, pereopod 4.

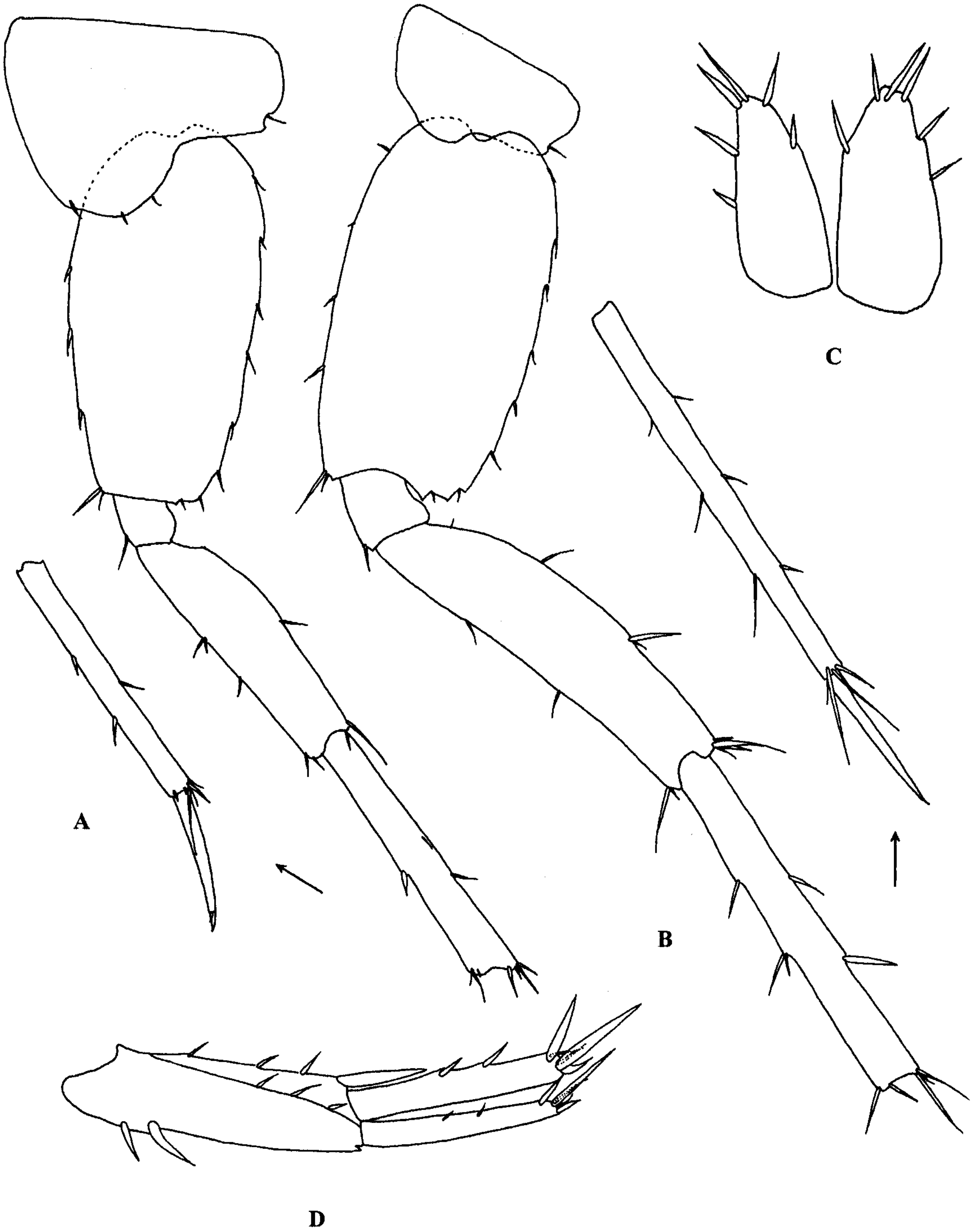

Fig. 5.9. *Hadzia philippinensis*, n. sp.,. paratypes, Tauala Cave, Panglao Island, Bohol, Philippines. Female (2.7 mm): A, pereopod 5; B, pereopod 6. Male (2.0 mm): C, telson; D, uropod 1.

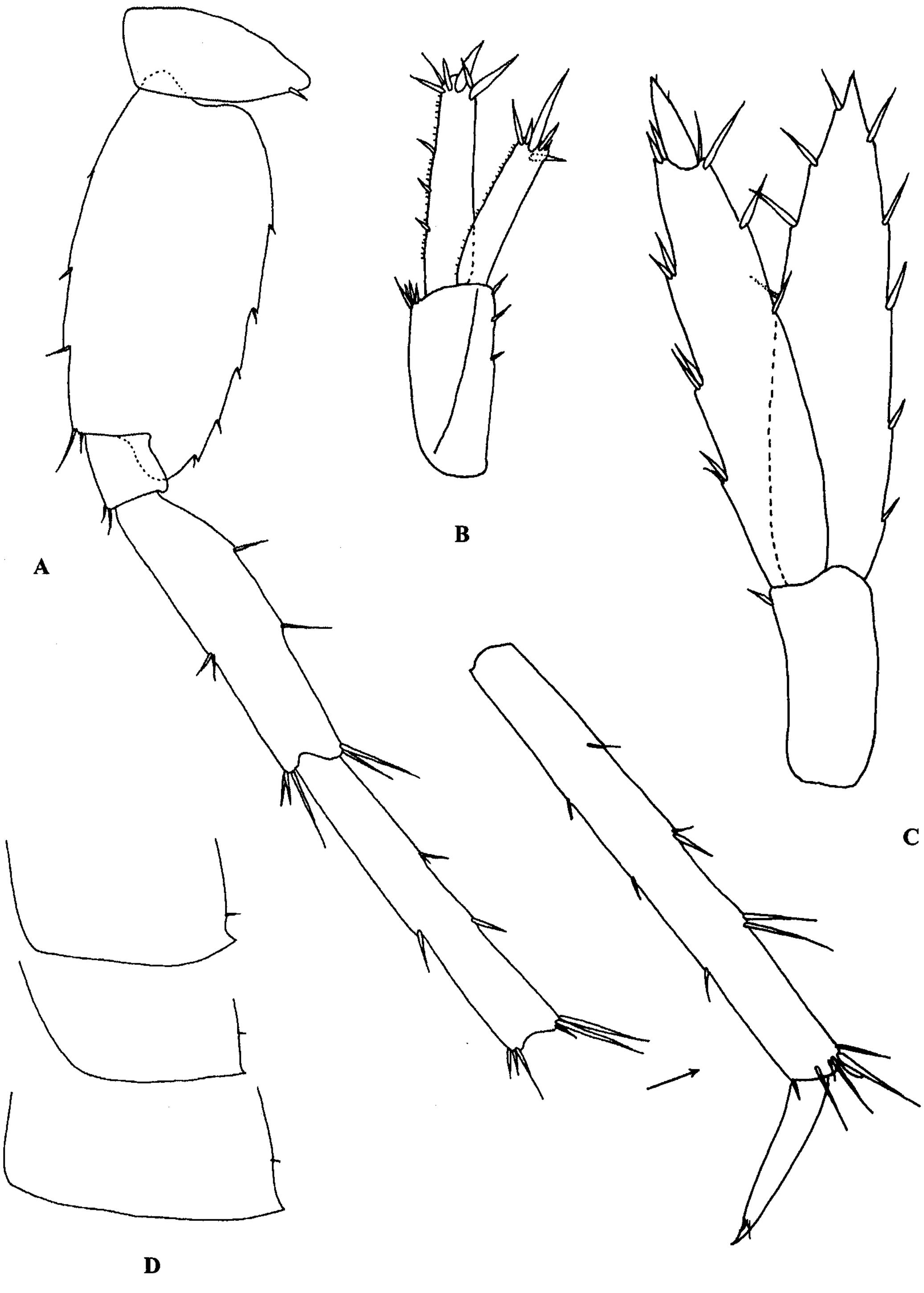

Fig. 5.10. *Hadzia philippinensis*, n. sp., paratypes, Tauala Cave, Panglao Island, Bohol, Philippines. Male (2.0 mm): A, pereopod 7; B, uropod 2; C, uropod 3. Female (2.7 mm): D, pleonal plates 1-3.

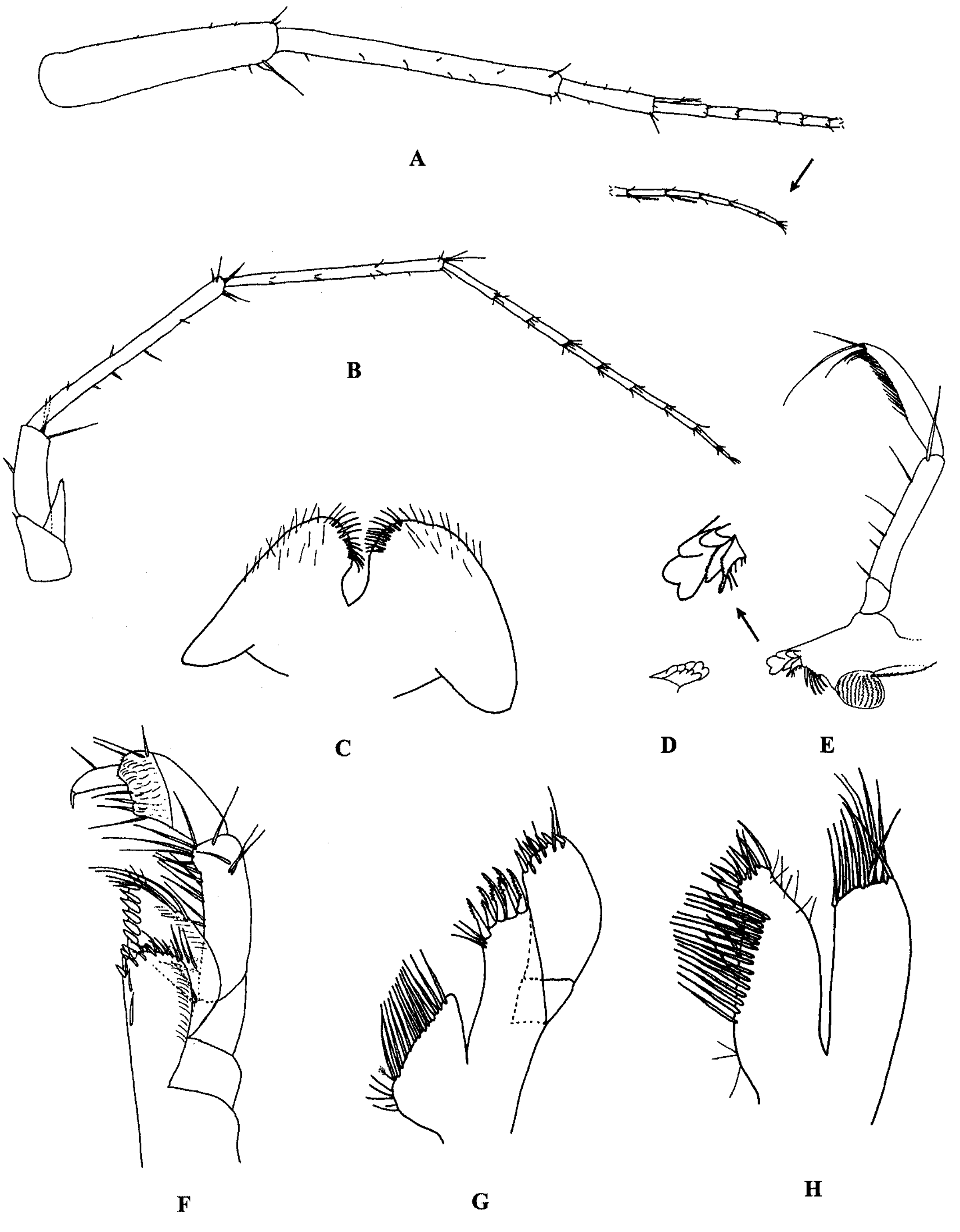

Fig. 5.11. *Hadzia spinata*, n. sp., paratype, Lake 2A Cave, Ngeruktabel Island, Palau. Female 5.0 mm): A, antenna 1; B, antenna 2; C, lower lip; G, maxilla 1; H, maxilla 2. Paratype, Cenote, Ngeruktabel Island, Palau. Female (6.0 mm): D, left lacinia mobilis and incisor; E, right mandible (lacinia mobilis and incisor enlarged); F, maxilliped.

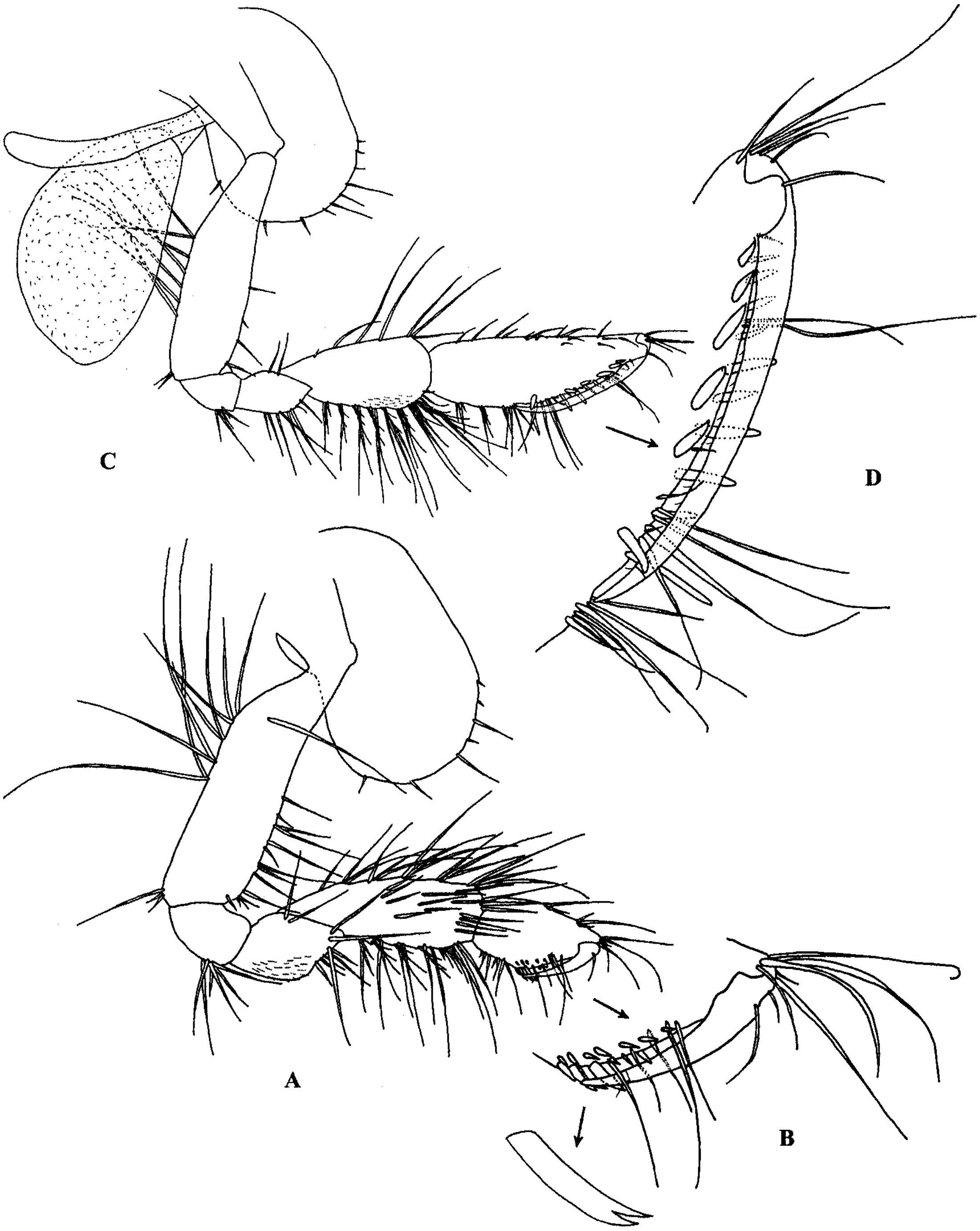

Fig. 5.12. *Hadzia spinata*, n. sp., paratype, Cenote, Ngeruktabel Island, Palau. Female (6.0 mm): A, gnathopod 1; B, enlarged distal end of propod and dactyl of gnathopod 1, with enlarged bifurcate spine from the defining angle of the palm; C, gnathopod 2; D, enlarged distal end of propod and dactyl of gnathopod 2.

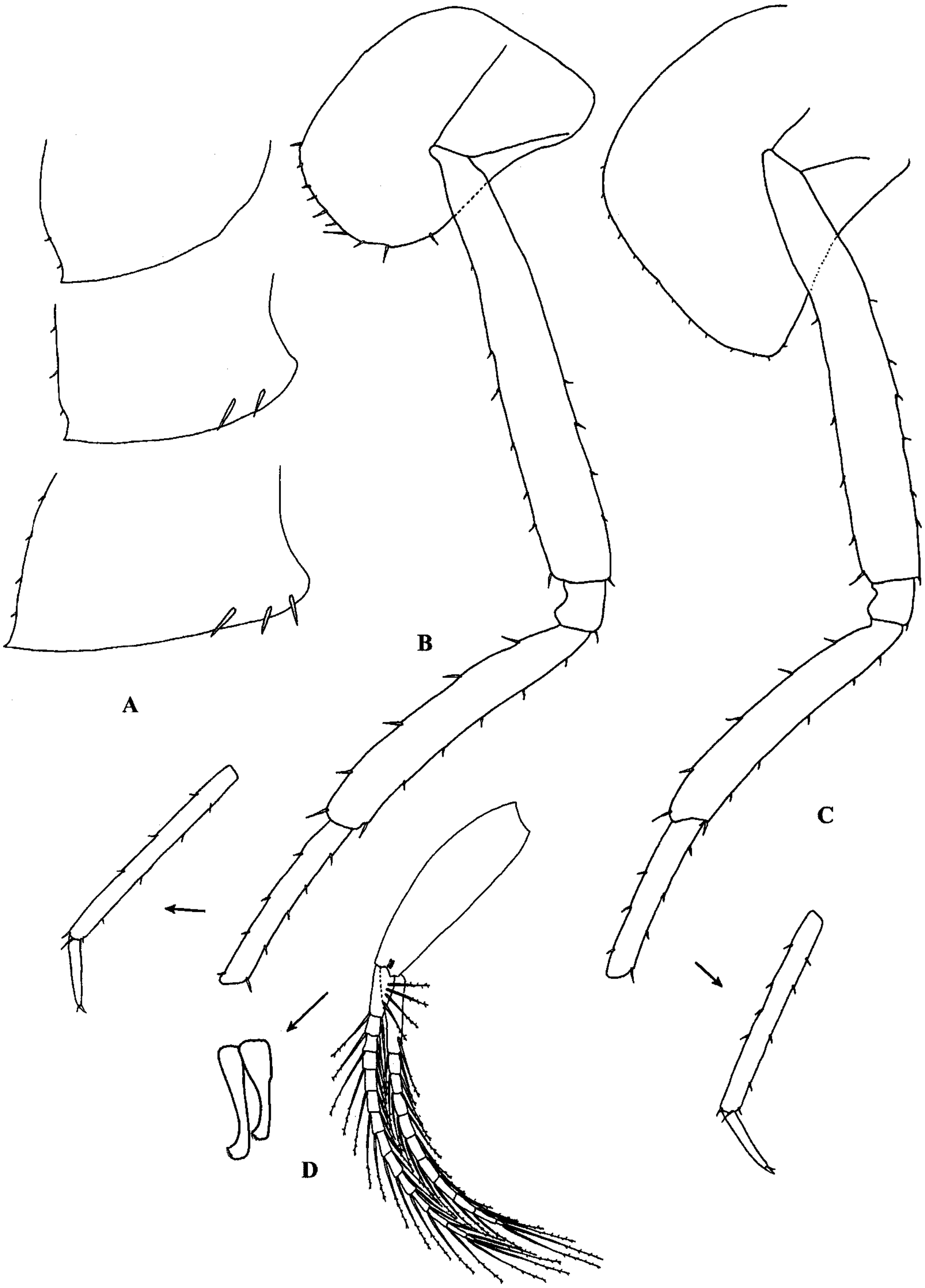

Fig. 5.13. *Hadzia spinata*, n. sp., paratype, Cenote, Ngeruktabel Island, Palau. Female (6.0 mm): A, pleonal plates 1-3; B, pereopod 3; C, pereopod 4; D, pleopod 1 with enlarged coupling spines.

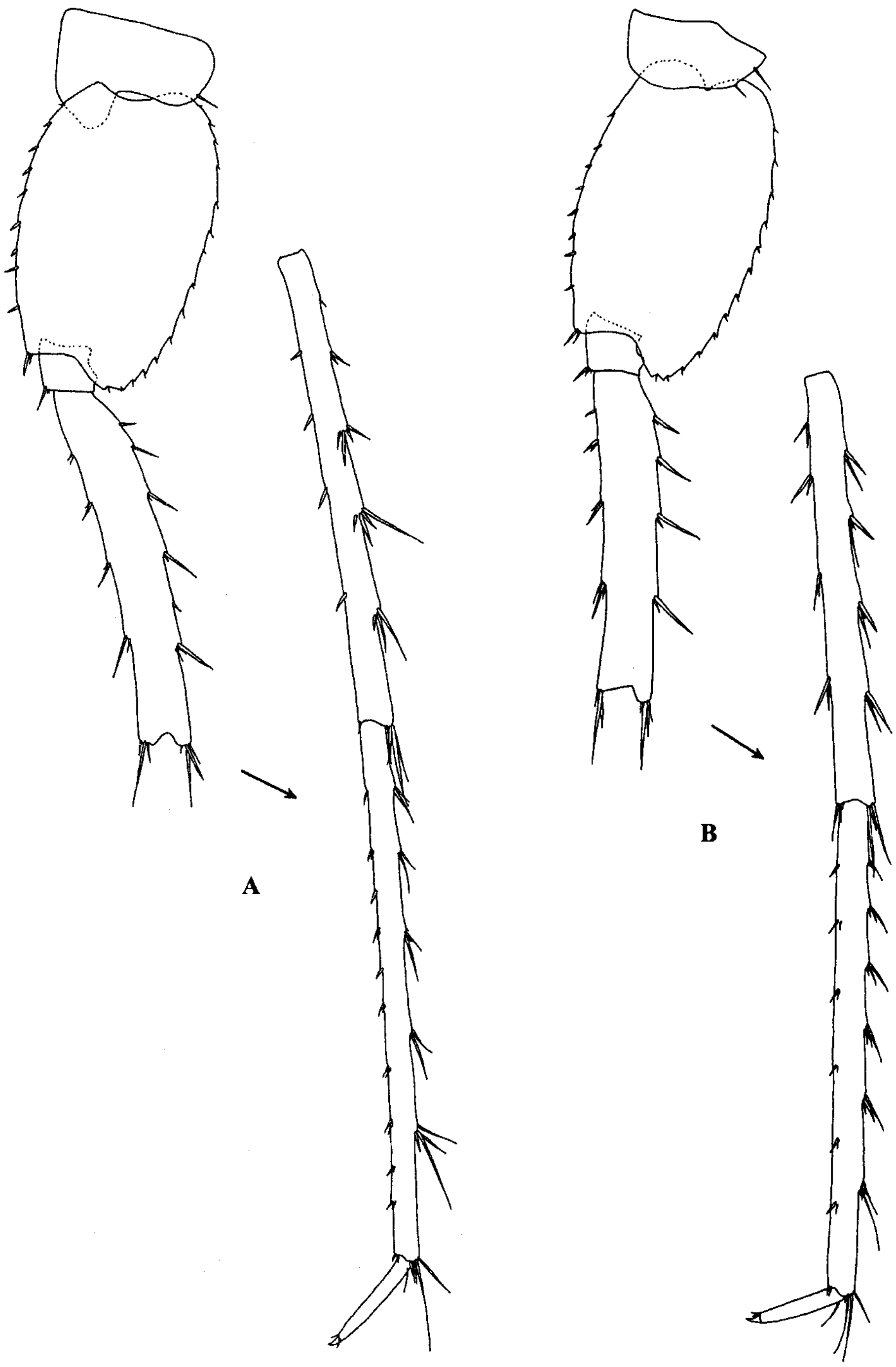

Fig. 5.14. *Hadzia spinata*, n. sp., paratype, Cenote, Ngeruktabel Island, Palau. Female (6.0 mm): A, pereopod 6; B, pereopod 7.

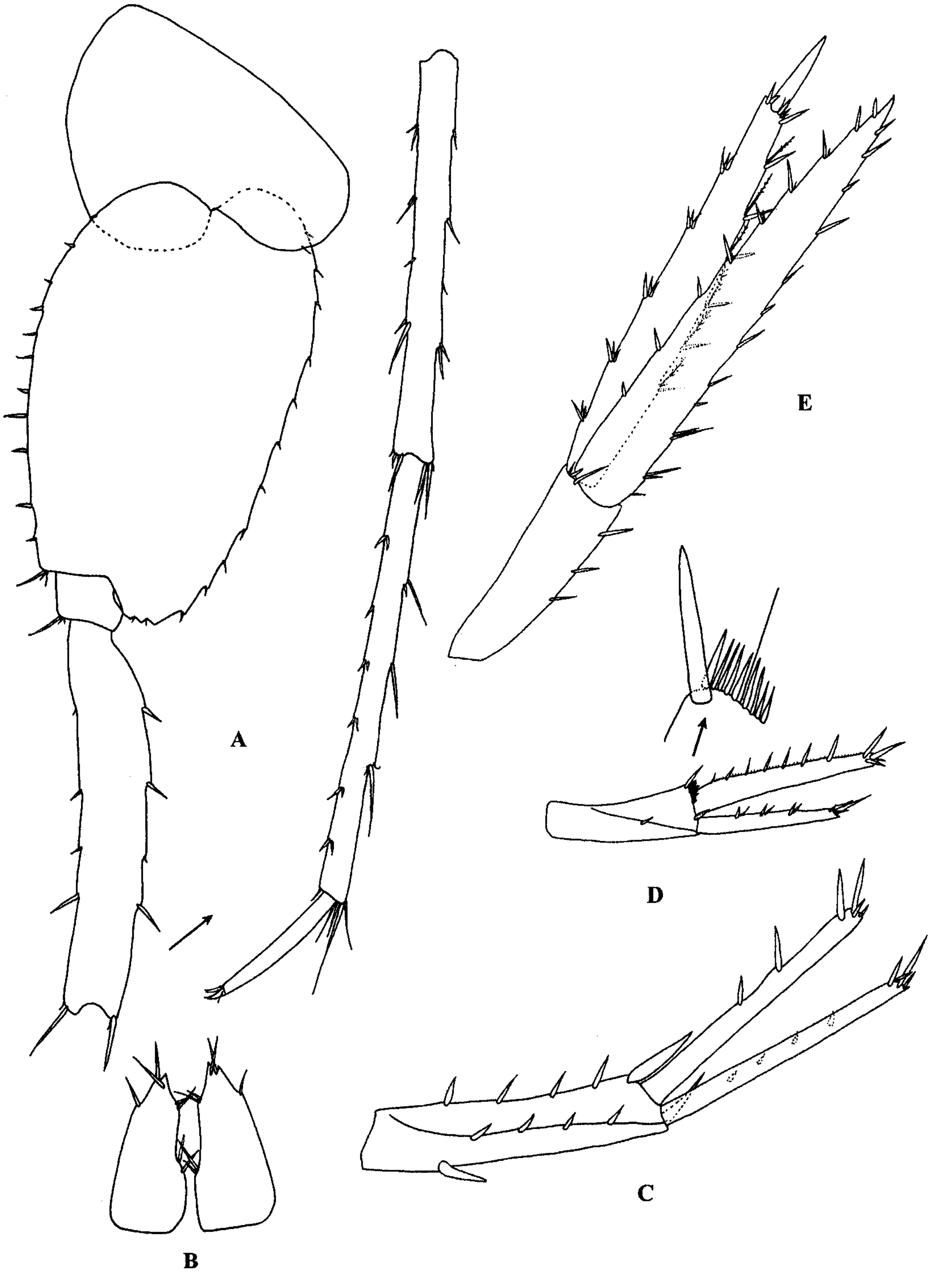

Fig. 5.15. *Hadzia spinata*, n. sp., paratype, Cenote, Ngeruktabel Island, Palau. Female (6.0 mm): A, pereopod 5; B, telson; C, uropod 1; D, uropod 2 (distodorsal combspine row enlarged); E, uropod 3.

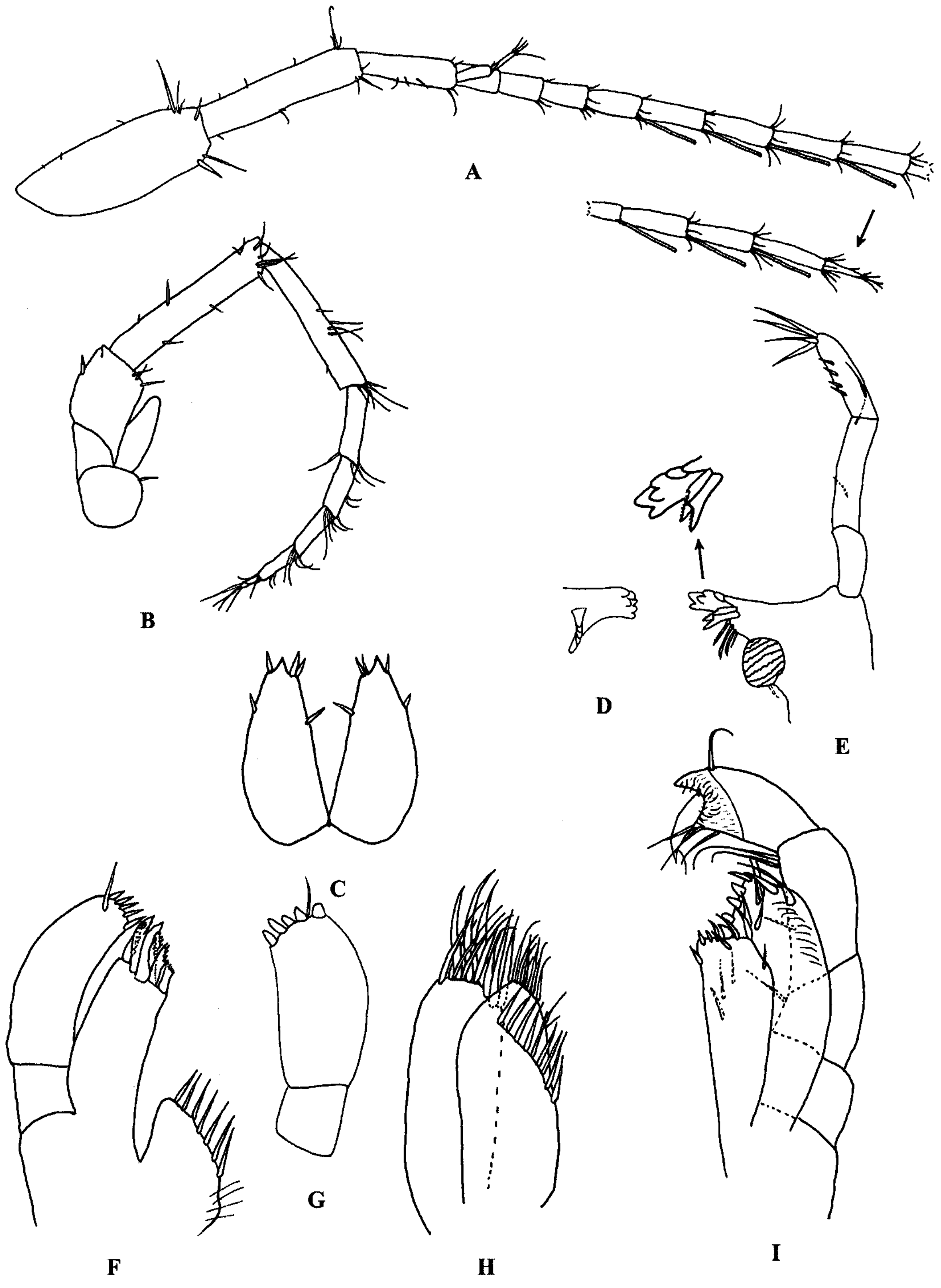

Fig. 5.16. *Hadzia palauensis*, n. sp., paratype, Tide Rope Cave, Eil Malk Island, Palau. Female (2.0 mm): A, antenna 1; B, antenna 2; C, telson; D, left lacinia mobilis and incisor; E, right mandible (lacinia mobilis and incisor enlarged); F; right maxilla 1; G, palp of left maxilla 1; H, maxilla 2; I, maxilliped.

Fig. 5.17. *Hadzia palauensis*, n. sp., paratypes, Tide Rope Cave, Eil Malk Island, Palau. Female (2.0 mm): A, pereopod 7 (in part); C, gnathopod 1; D, enlarged distal end of propod and dactyl of gnathopod 1; E, gnathopod 2; F, enlarged distal end of propod and dactyl of gnathopod 2; G, brood plate, gnathopod 2. Male (2.0 mm): B, carpus, propod and dactyl, gnathopod 2.

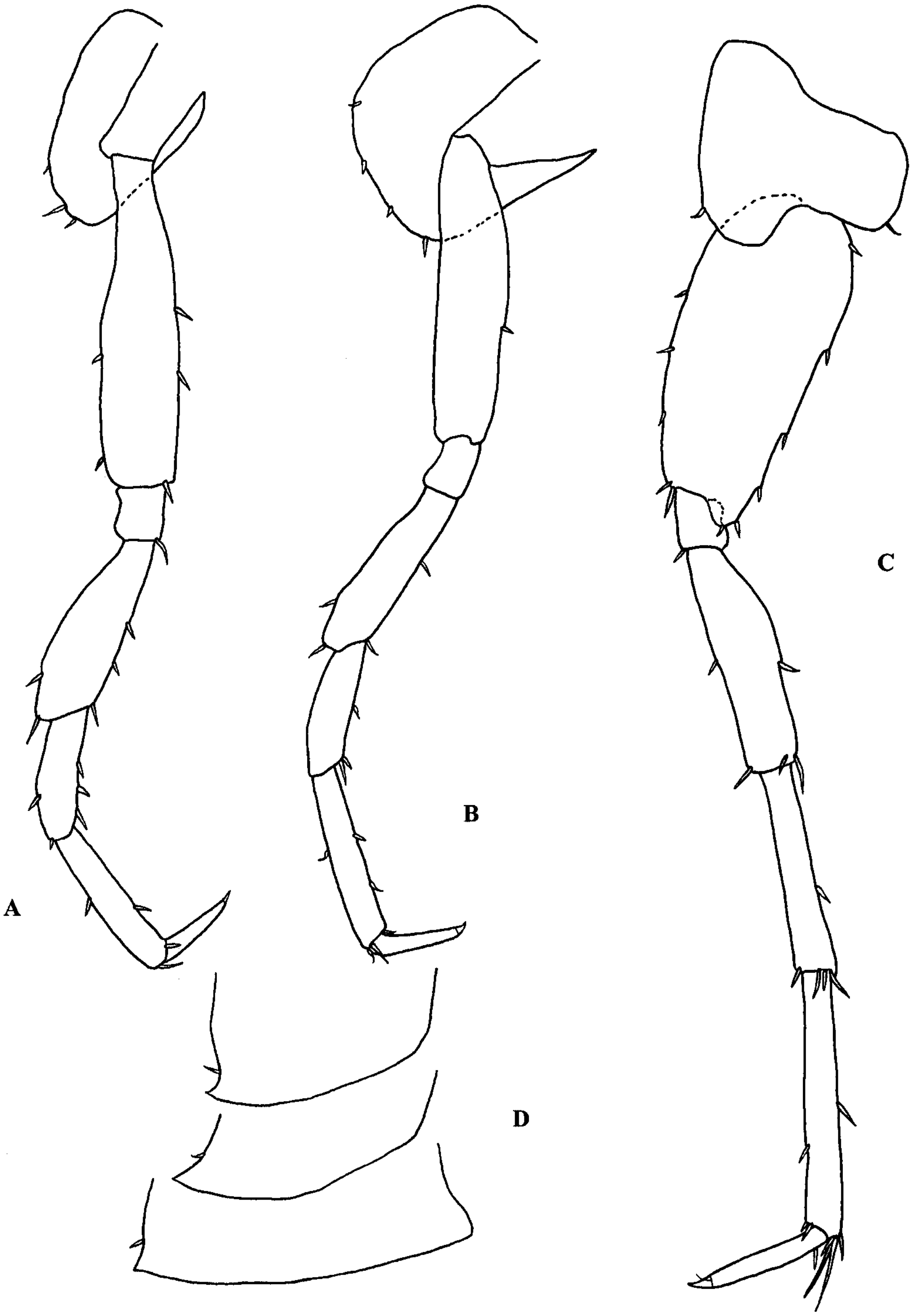

Fig. 5.18. *Hadzia palauensis*, n. sp., paratype, Tide Rope Cave, Eil Malk Island, Palau. Female (2.0 mm): A, pereopod 3; B, pereopod 4, C, pereopod 5; D, pleonal plates 1-3.

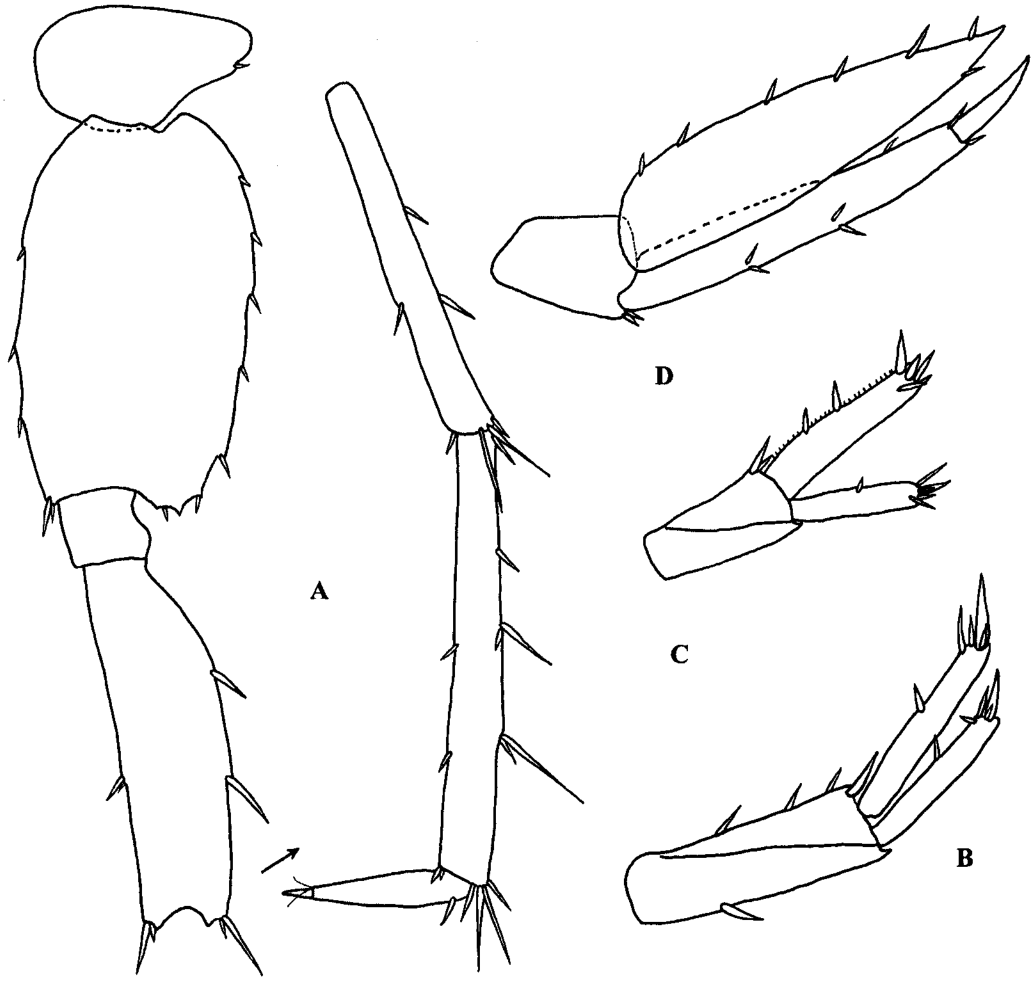

Fig. 5.19. *Hadzia palauensis*, n. sp., paratype, Tide Rope Cave, Eil Malk Island, Palau. Female (2.0 mm): A, pereopod 6; B, uropod 1; C, uropod 2; D, uropod 3.

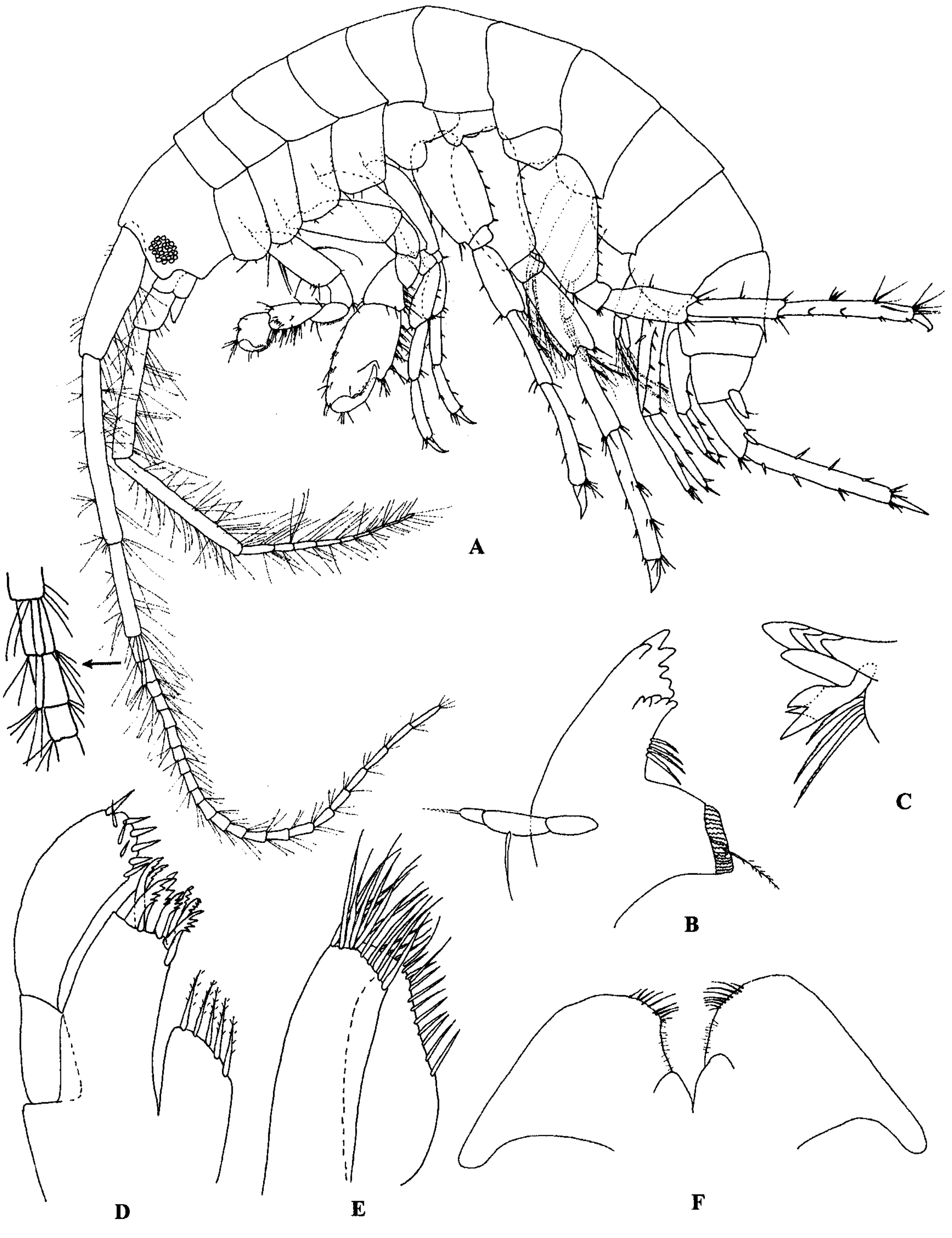

Fig. 6.1. *Tegano clavatus* n. sp., holotype, Tuala Cave, Panglao Island, Philippines. Male (4.2 mm): A, whole animal; B, left mandible; C right mandible incisor and lacinia mobilis; D maxilla 1; E, maxilla 2; F lower lip.

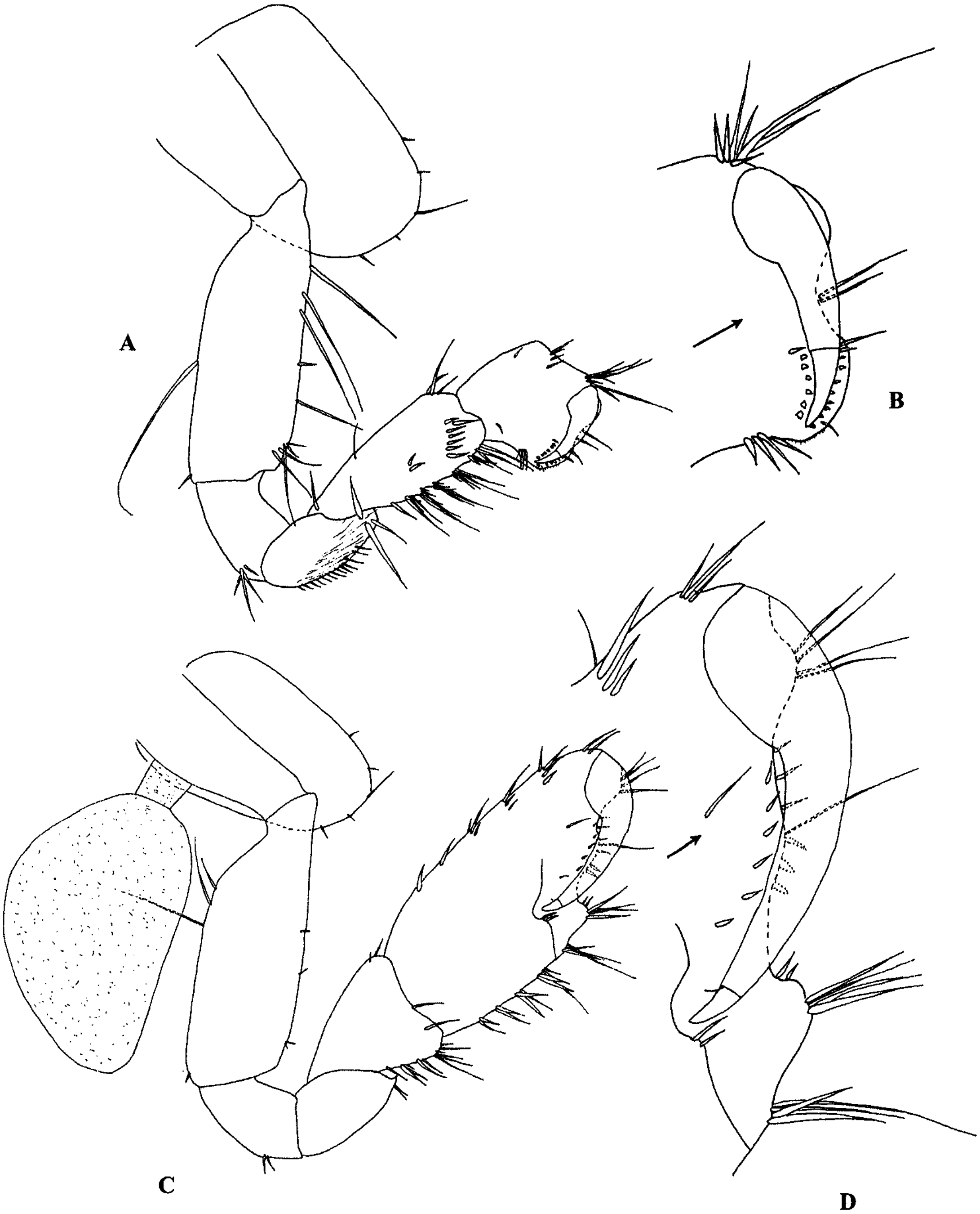

Fig. 6.2. *Tegano clavatus* n. sp., holotype, Tuala Cave, Panglao Island, Philippines. Male (4.2 mm): A, gnathopod 1; B, enlarged propod and dactyl of gnathopod 1; C, gnathopod 2; D, enlarged propod and dactyl of gnathopod 2.

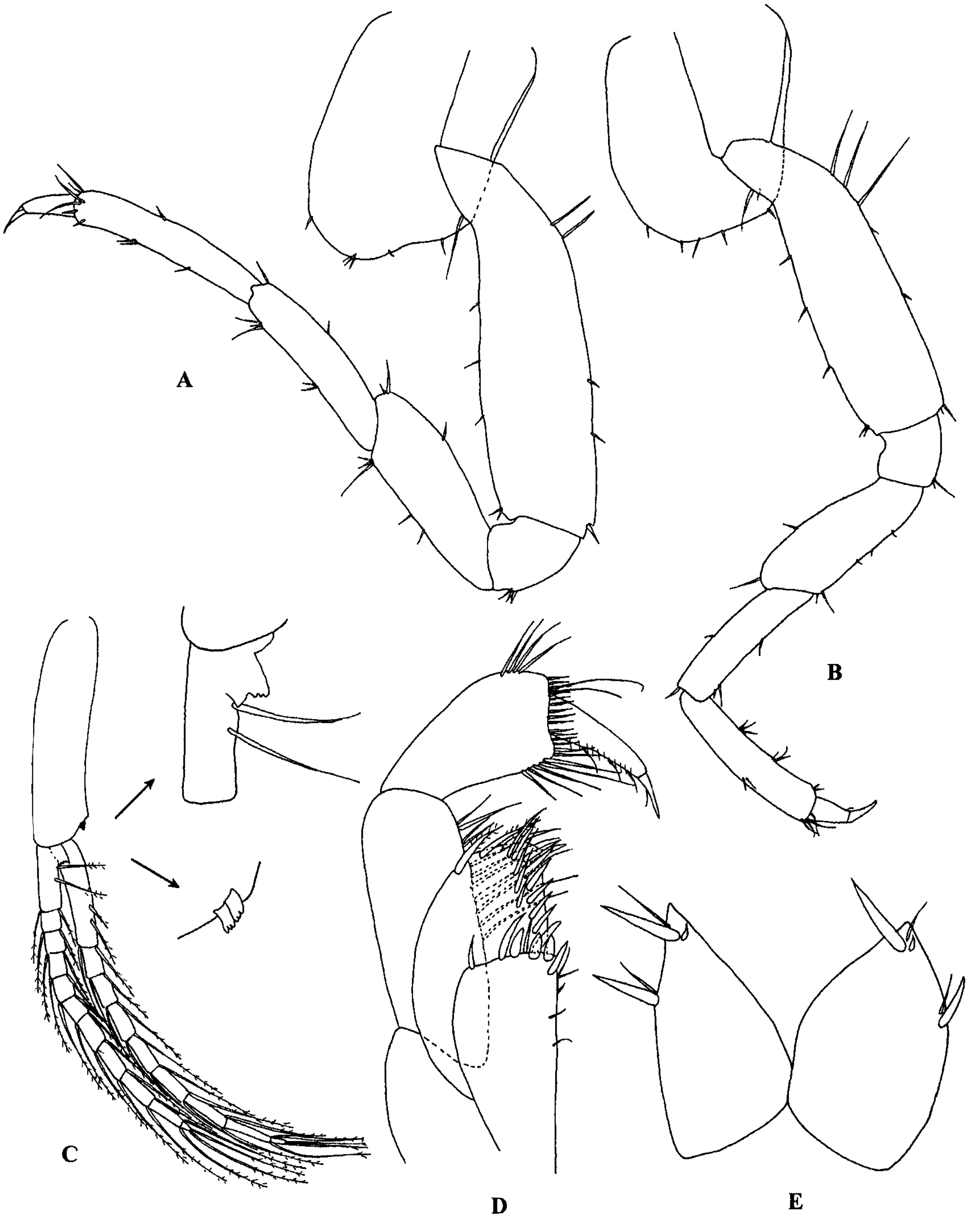

Fig. 6.3. *Tegano clavatus* n. sp., holotype, Tuala Cave, Panglao Island, Philippines. Male (4.2 mm): A, pereopod 3; B, pereopod 4; C, pleopod 1 (coupling spines and serrated extension on the first segment of the inner ramus enlarged); D, maxilliped; E, telson.

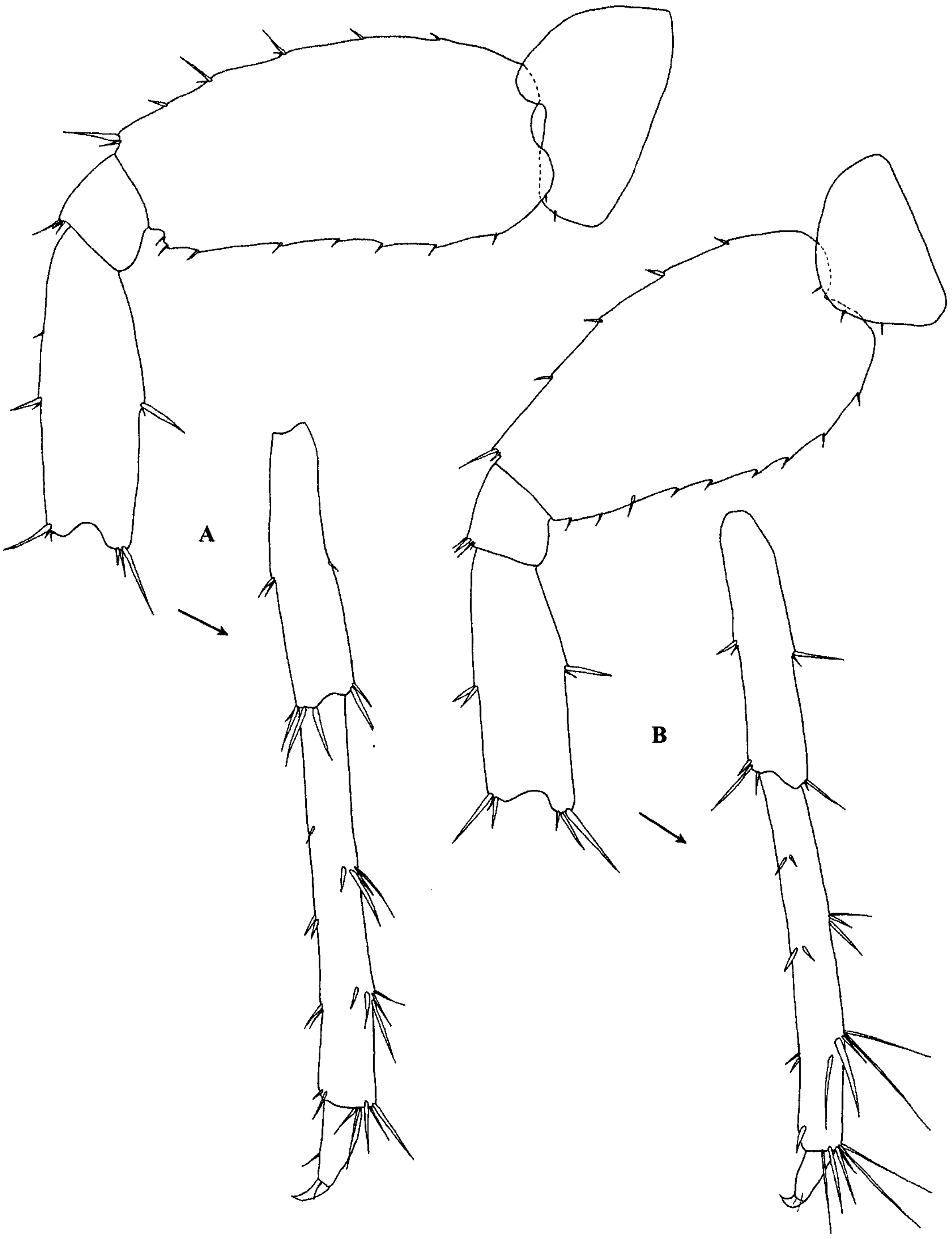

Fig. 6.4. *Tegano clavatus* n. sp., holotype, Tuala Cave, Panglao Island, Philippines. Male (4.2 mm): A, pereopod 6; B, pereopod 7.

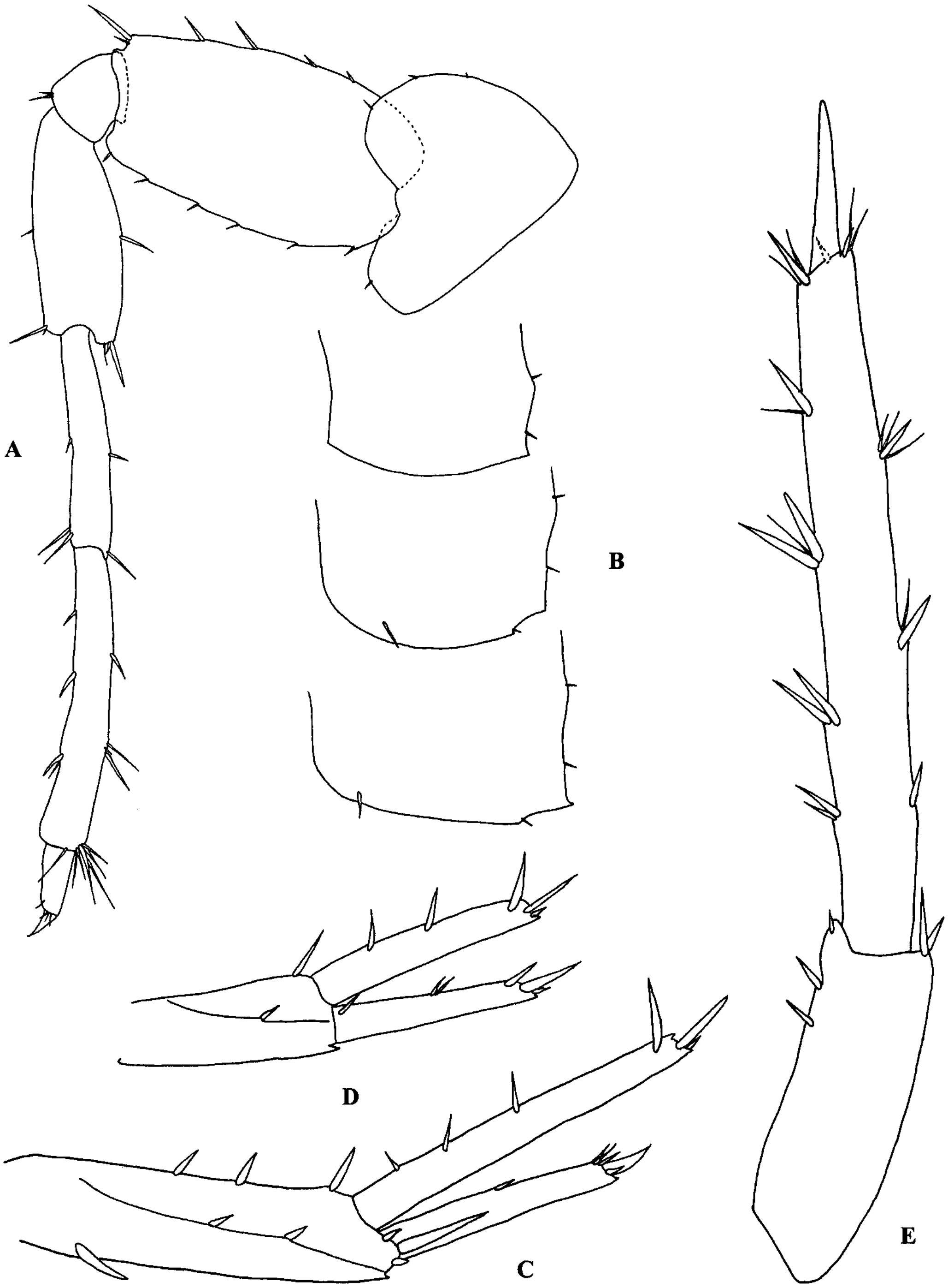

Fig. 6.5. *Tegano clavatus* n. sp., holotype, Tuala Cave, Panglao Island, Philippines. Male (4.2 mm): A, pereopod 5; B, pleonal plates; C, uropod 1; D, uropod 2; E, uropod 3.

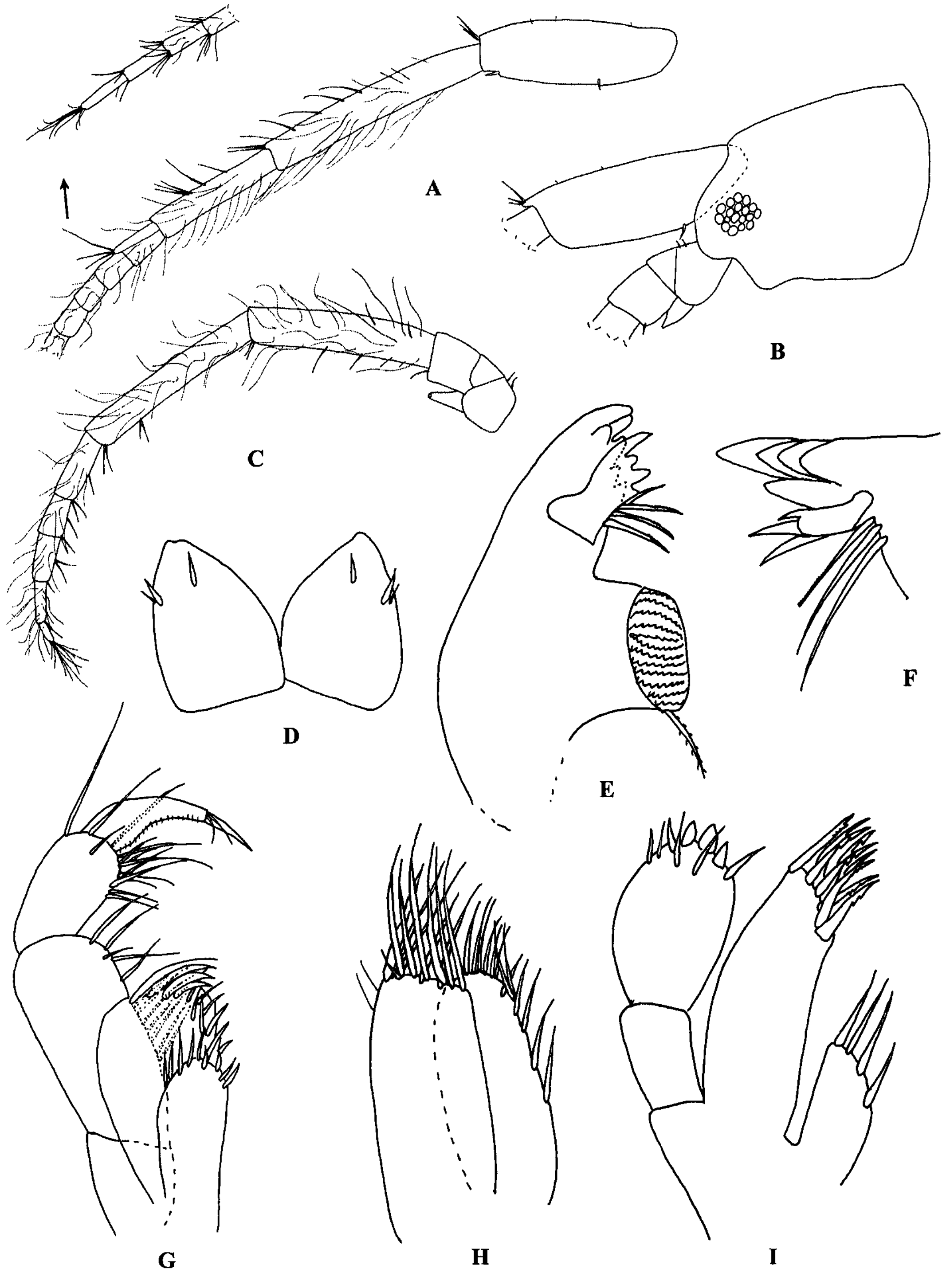

Fig. 6.6. *Tegano panglaoensis* n. sp., paratype, Hinagdanan Cave, Panglao Island, Philippines. Male (2.3 mm): A, head; B, antenna 1; C, Antenna 2; D, telson; E, left mandible; F, right mandible incisor and lacinia mobilis; G, maxilliped; H, maxilla 2; I, maxilla 1.

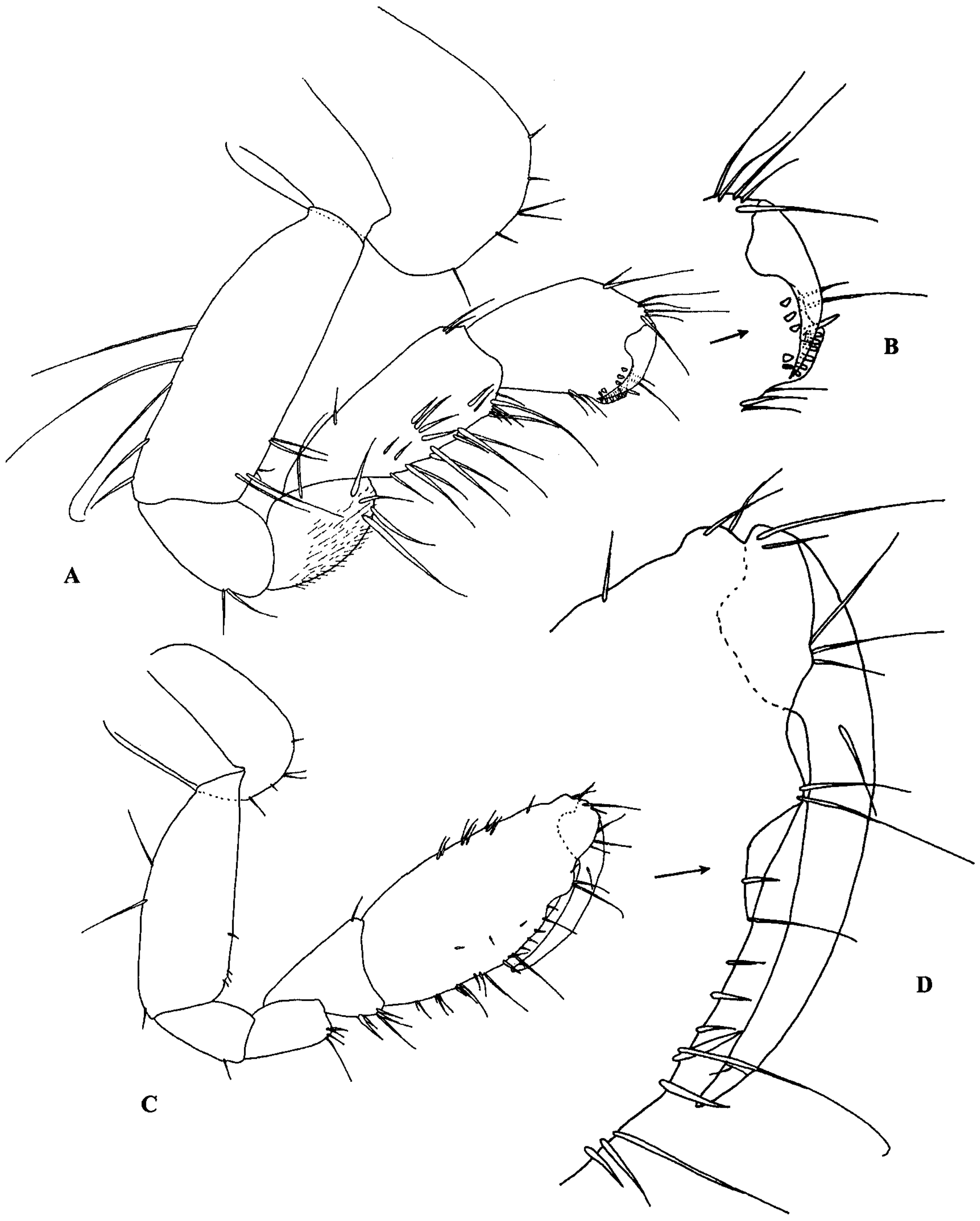

Fig. 6.7. *Tegano panglaoensis* n. sp., paratype, Hinagdanan Cave, Panglao Island, Philippines. Male (2.3 mm): A, gnathopod 1; B, enlarged propod and dactyl of gnathopod 1; C, gnathopod 2; D, enlarged propod and dactyl of gnathopod 2.

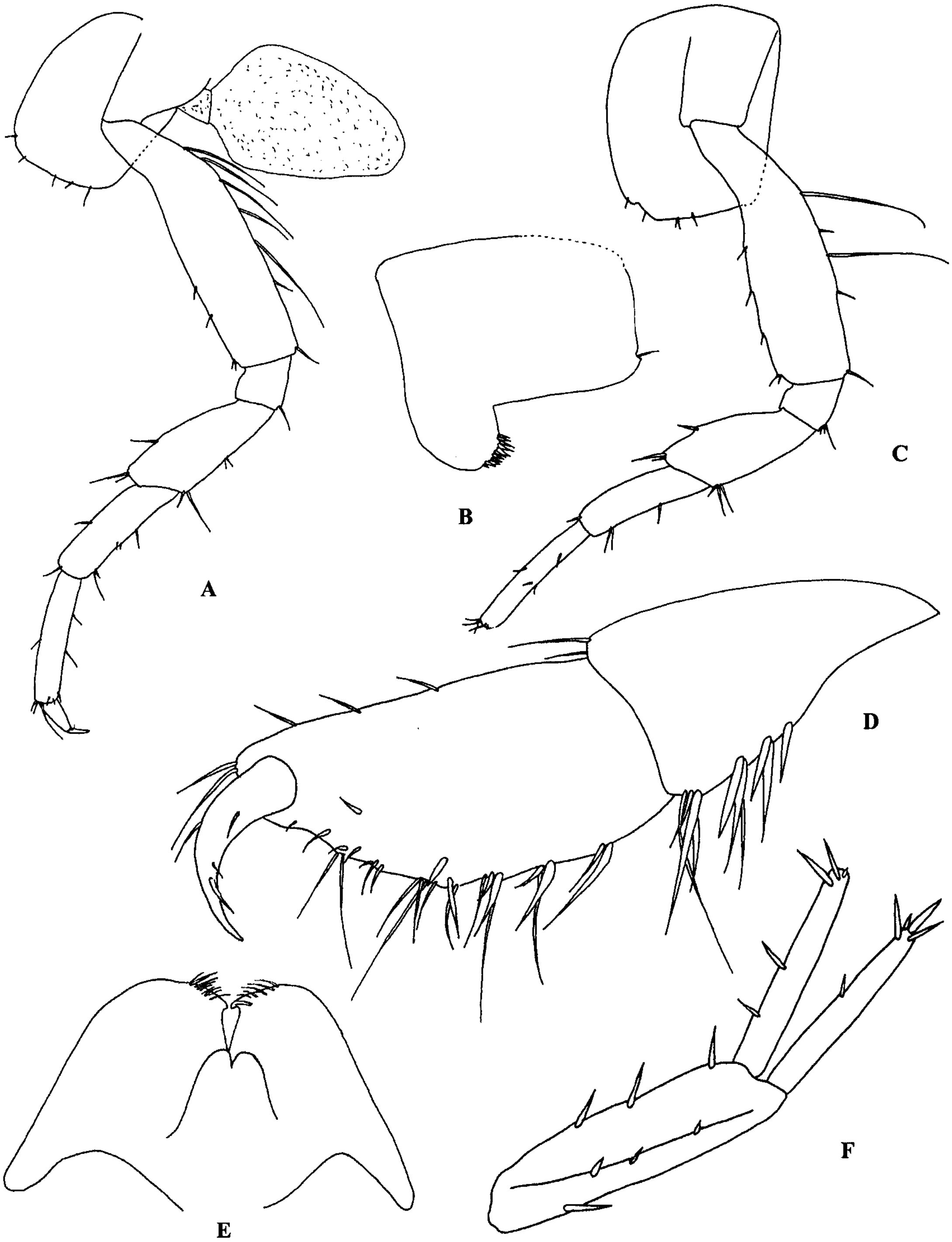

Fig. 6.8. *Tegano panglaoensis* n. sp., paratype, Hinagdanan Cave, Panglao Island, Philippines. Male (2.3 mm): A, pereopod 3; C, pereopod 4; E, lower lip; F, uropod 1. Female (2.0 mm): B, pereopod coxa 6; D, carpus, propod and dactyl of gnathopod 2.

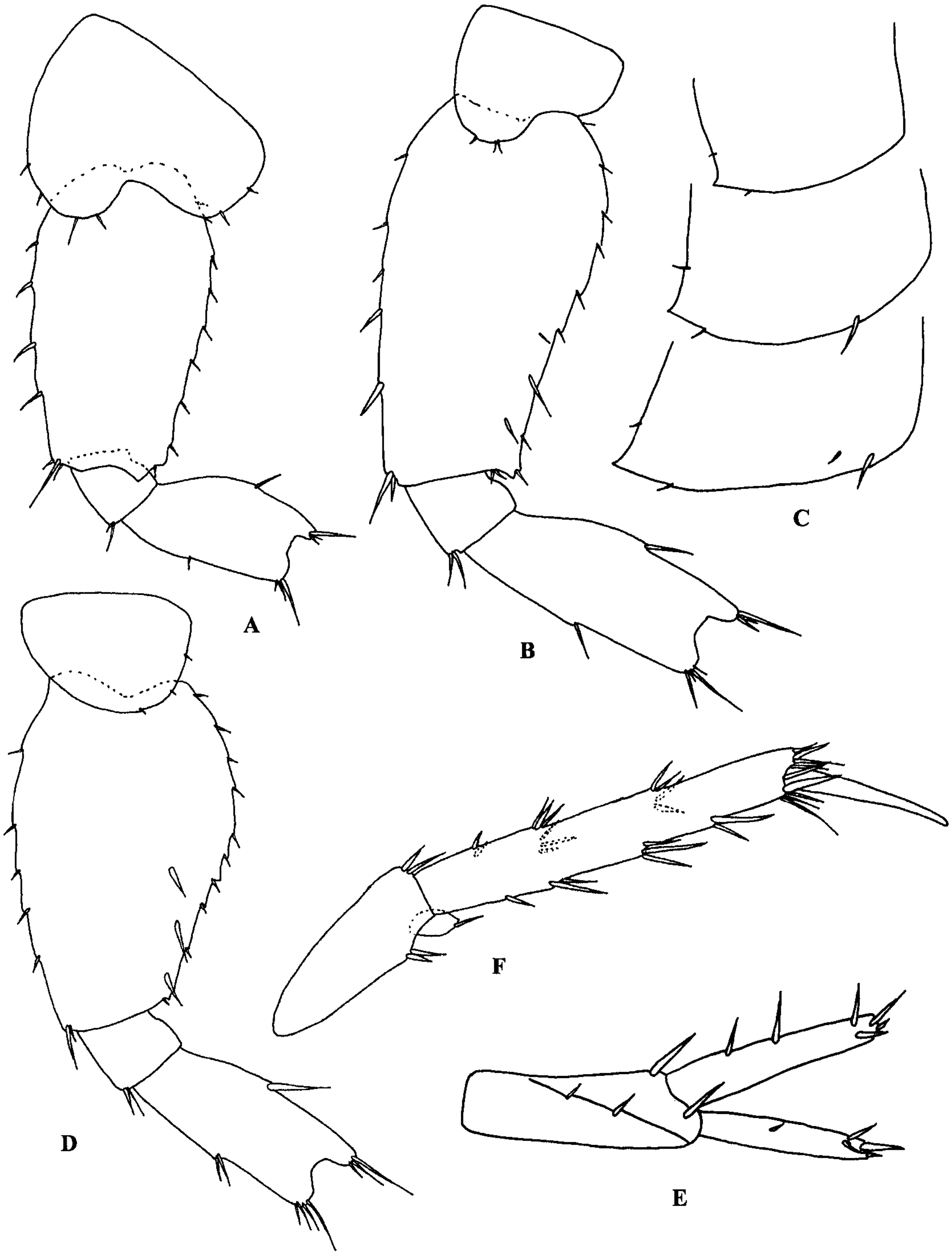

Fig. 6.9. *Tegano panglaoensis* n. sp., paratypes, Hinagdanan Cave, Panglao Island, Philippines. Male (2.3 mm): A, pereopod 5; B, pereopod 6; C, pleonal plates; D, pereopod 7; E, uropod 2; F, uropod 3.

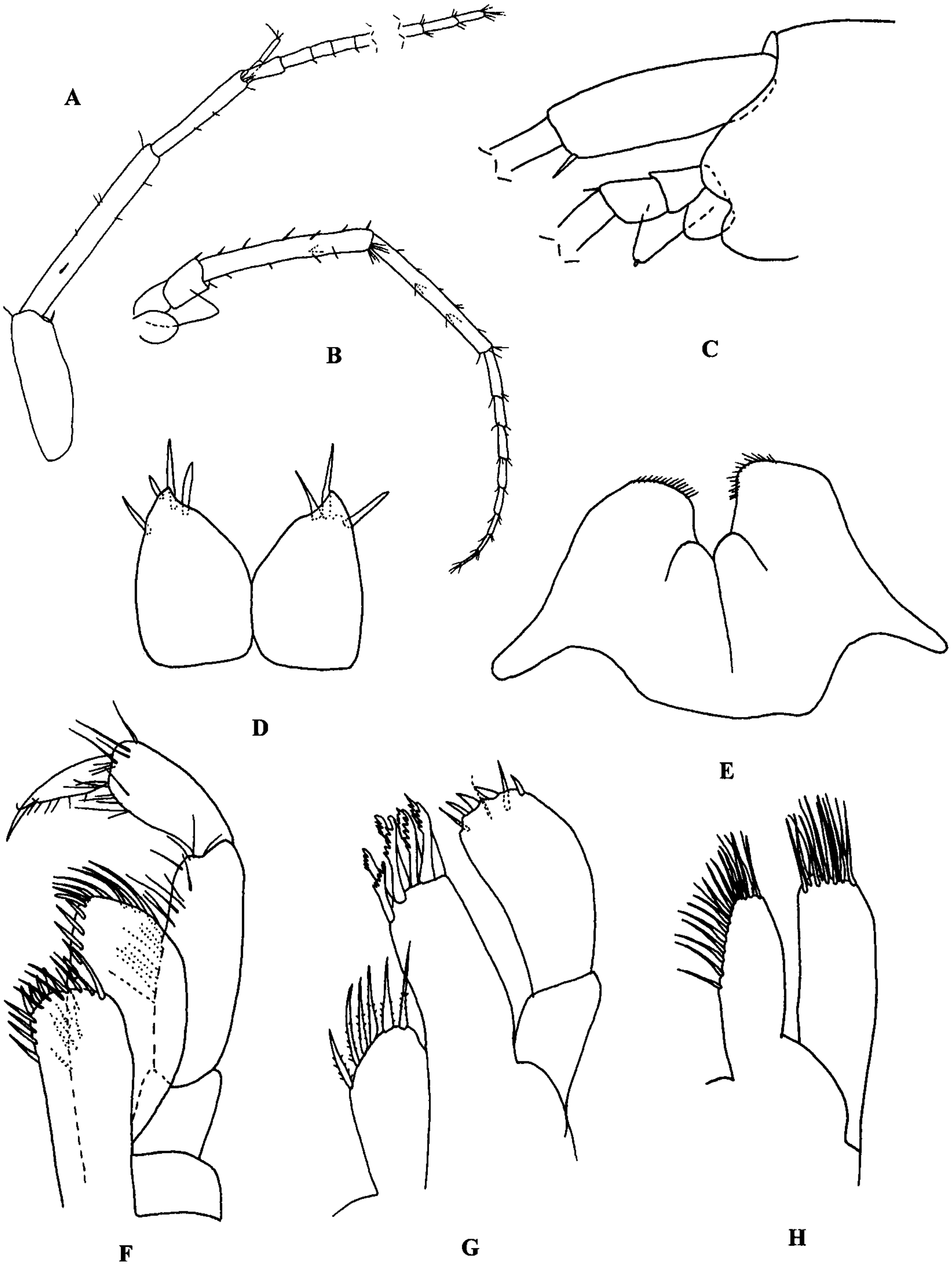

Fig. 6.10. *Tegano barnardi* n. sp., paratypes, Airport Well Cave, Peleliu Island, Palau. (Male 4.0 mm): A, antenna 1; B, antenna 2. Female (3.5 mm): C, head; D, telson; E, lower lip; F, maxilliped; G, maxilla 1; H, maxilla 2.

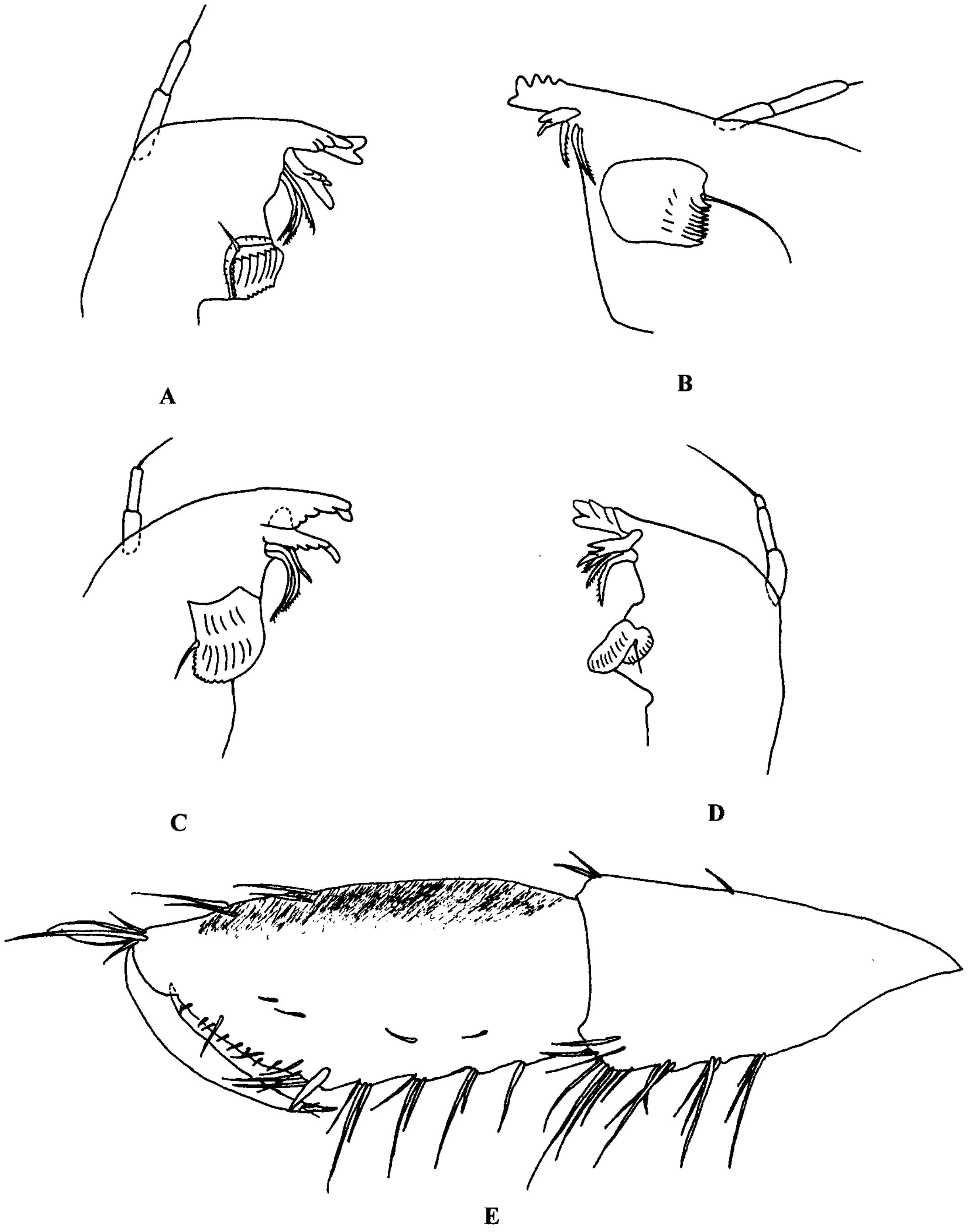

Fig. 6.11. *Tegano barnardi* n. sp., paratypes, Airport Well Cave, Peleliu Island, Palau. (Male 3.5 mm) A, left mandible; B, right mandible; Female (3.3 mm): C, left mandible; D, right mandible with 3-segmented palp; Female (3.5 mm): E, carpus, propod and dactyl of gnathopod 2.

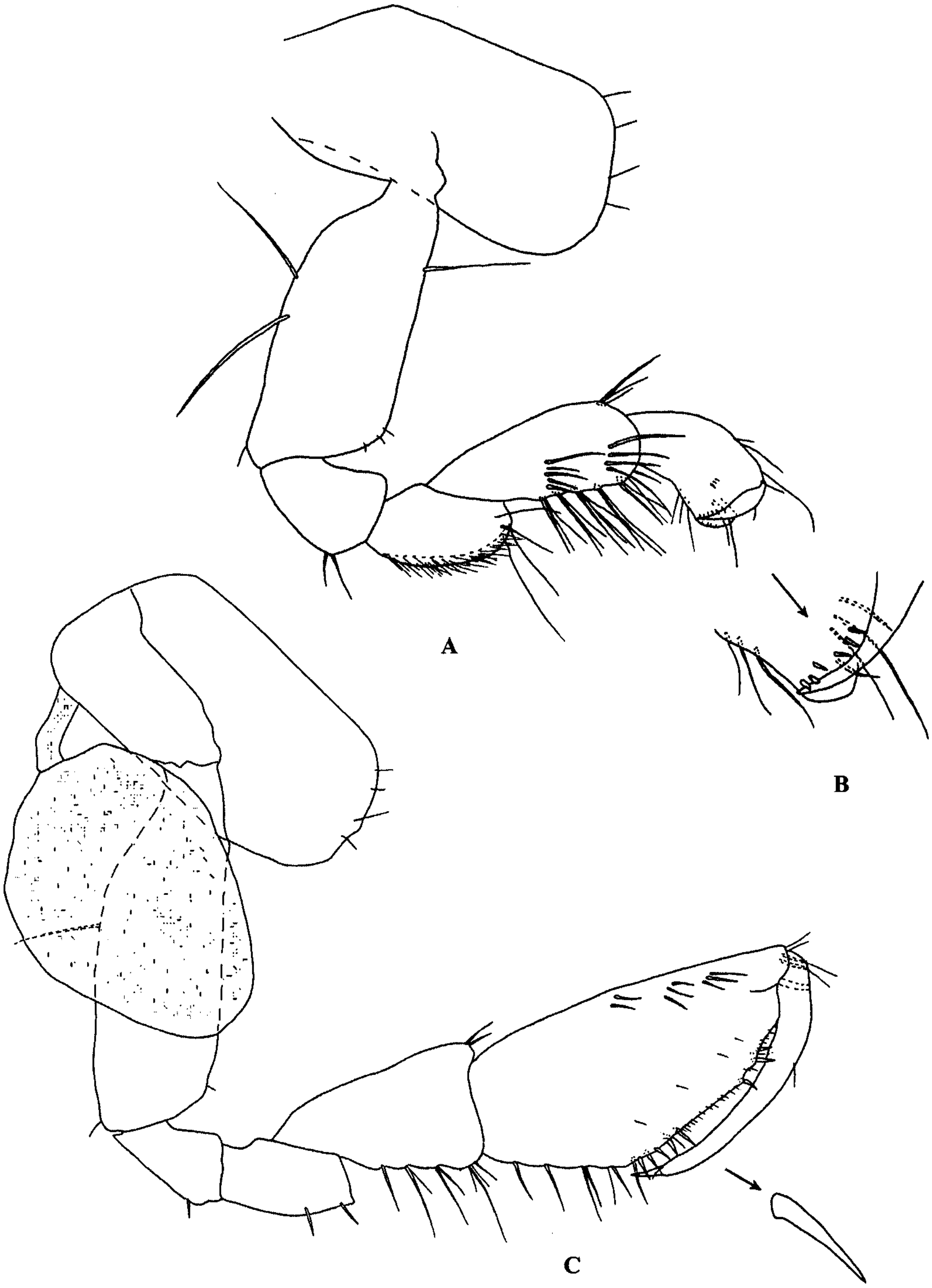

Fig. 6.12. *Tegano barnardi* n. sp., paratype, Airport Well Cave, Peleliu Island, Palau. (Male 4.0 mm): A, gnathopod 1; B, enlarged propod and dactyl of gnathopod 1; C, gnathopod 2 with enlarged palmar spine.

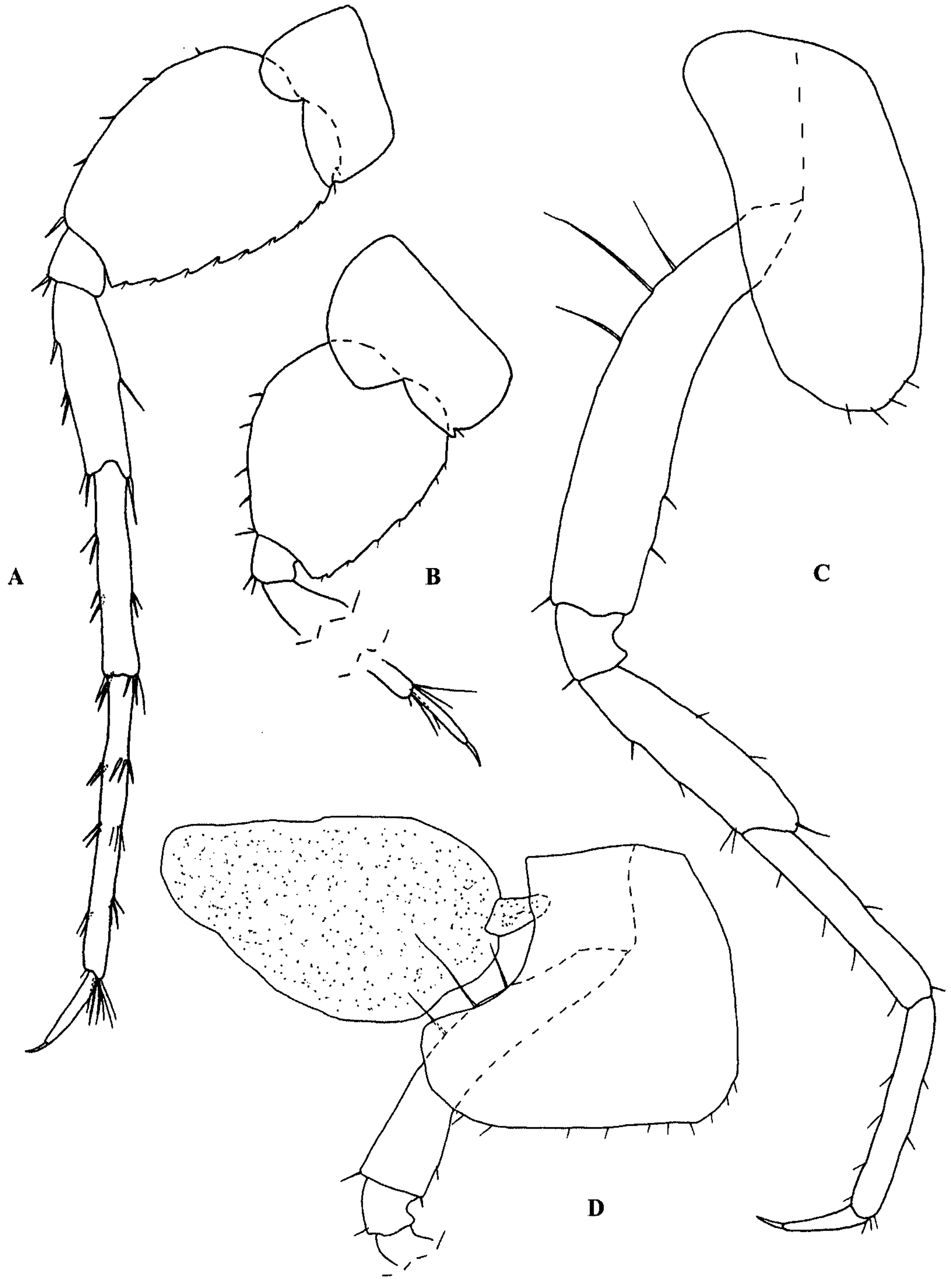

Fig. 6.13. *Tegano barnardi* n. sp., paratypes, Airport Well Cave, Peleliu Island, Palau. Female (3.3 mm): A, pereopod 6; B, pereopod 5. Male (4.0 mm): C, pereopod 3; D, pereopod 4.

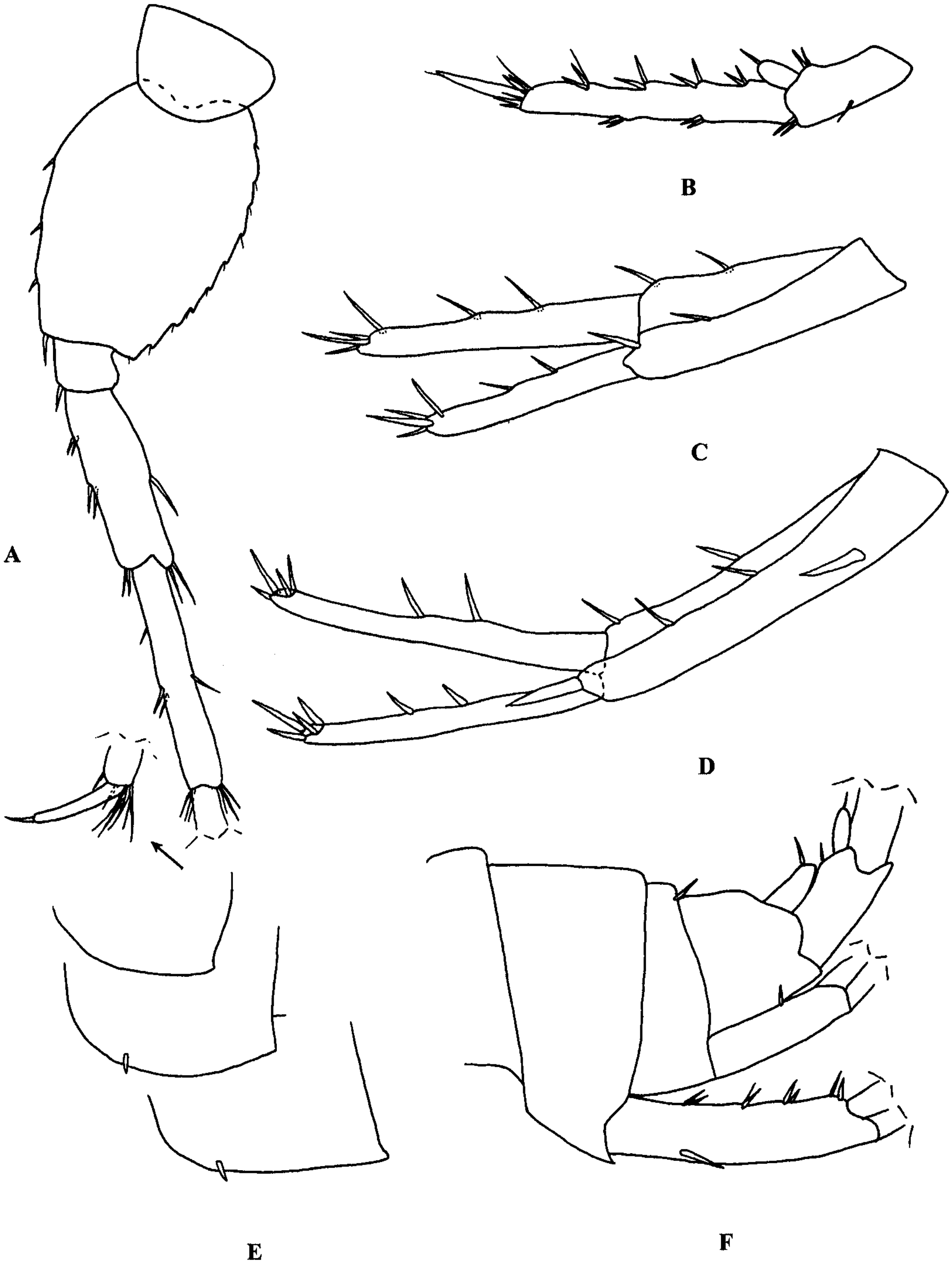

Fig. 6.14. *Tegano barnardi* n. sp., paratypes, Airport Well Cave, Peleliu Island, Palau. Female (3.5 mm): B, uropod 1; D, uropod 3; E, pleonal plates; F, urosomites. Male (4.0 mm): A, pereopod 7; C, uropod 2.

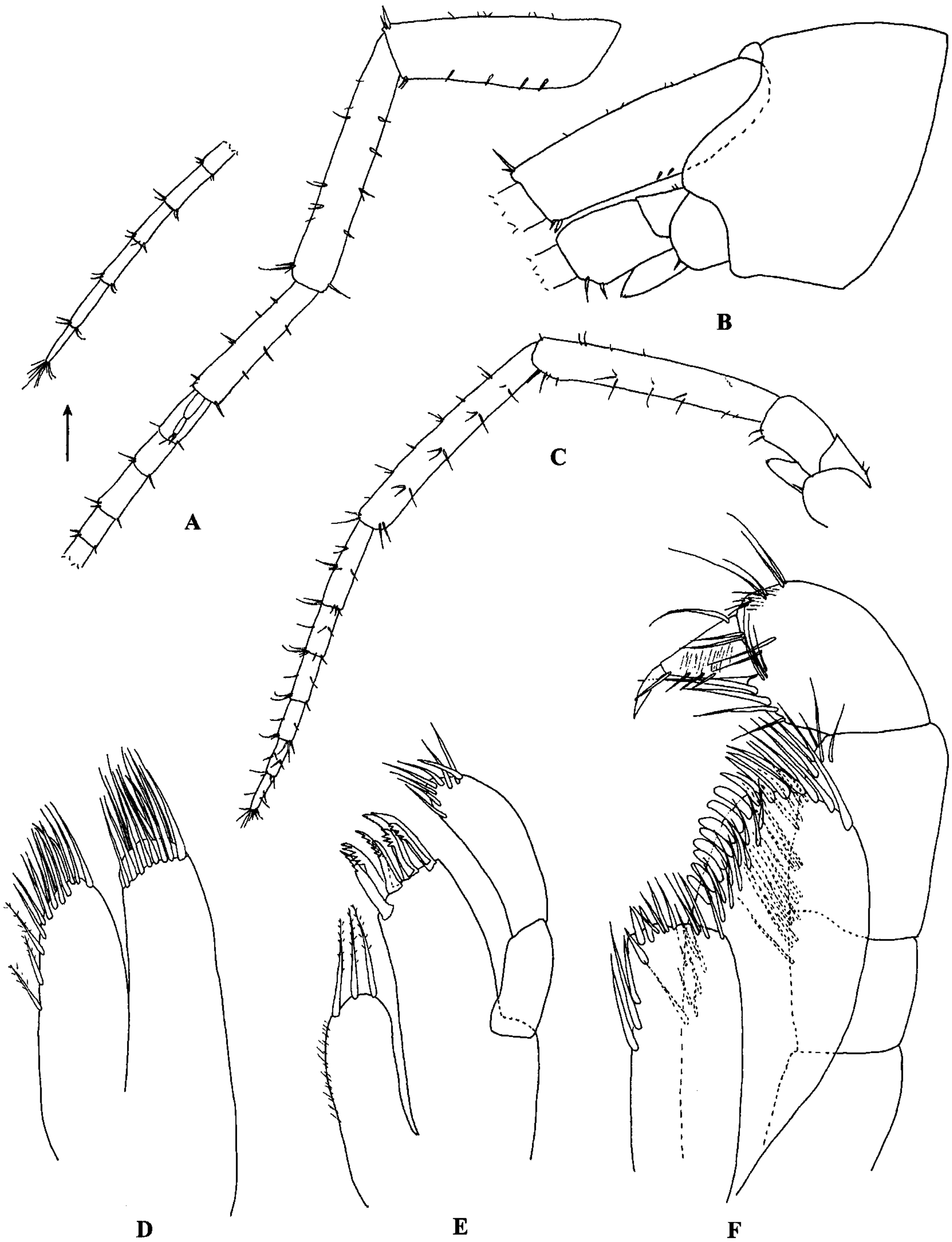

Fig. 6.15. *Melita almagosa* n. sp., paratypes, Almagosa Springs, Guam. Male (4.2 mm): A, antenna 1; C, antenna 2; D, maxilla 2; E, maxilla 1. Second Male (4.2 mm): head. Male (4.5 mm): maxilliped.

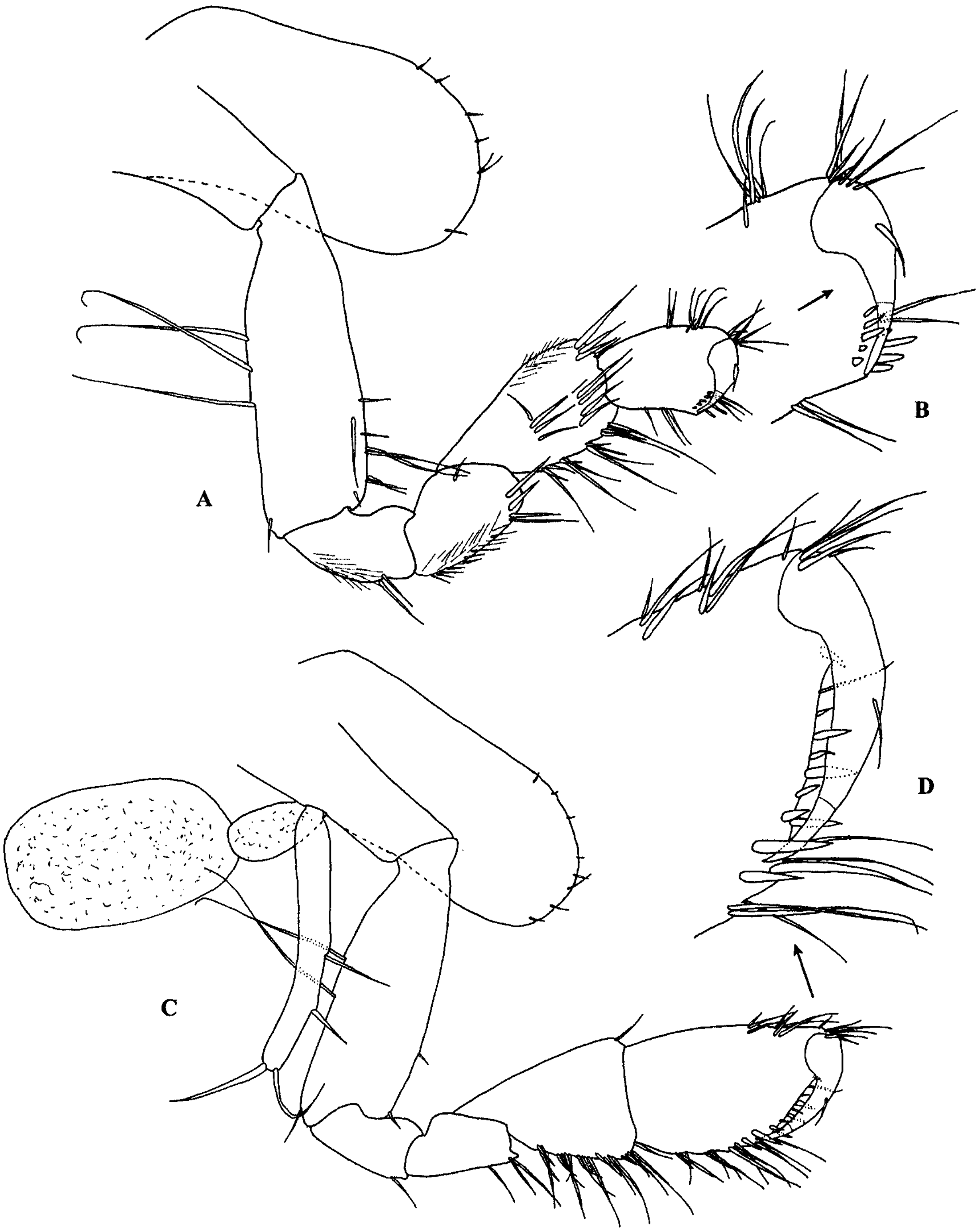

Fig. 6.16. *Melita almagosa* n. sp., paratype, Almagosa Springs, Guam. Female (3.2 mm): A, gnathopod 1; B, enlarged propod and dactyl of gnathopod 1; C, gnathopod 2; D, enlarged propod and dactyl of gnathopod 2.

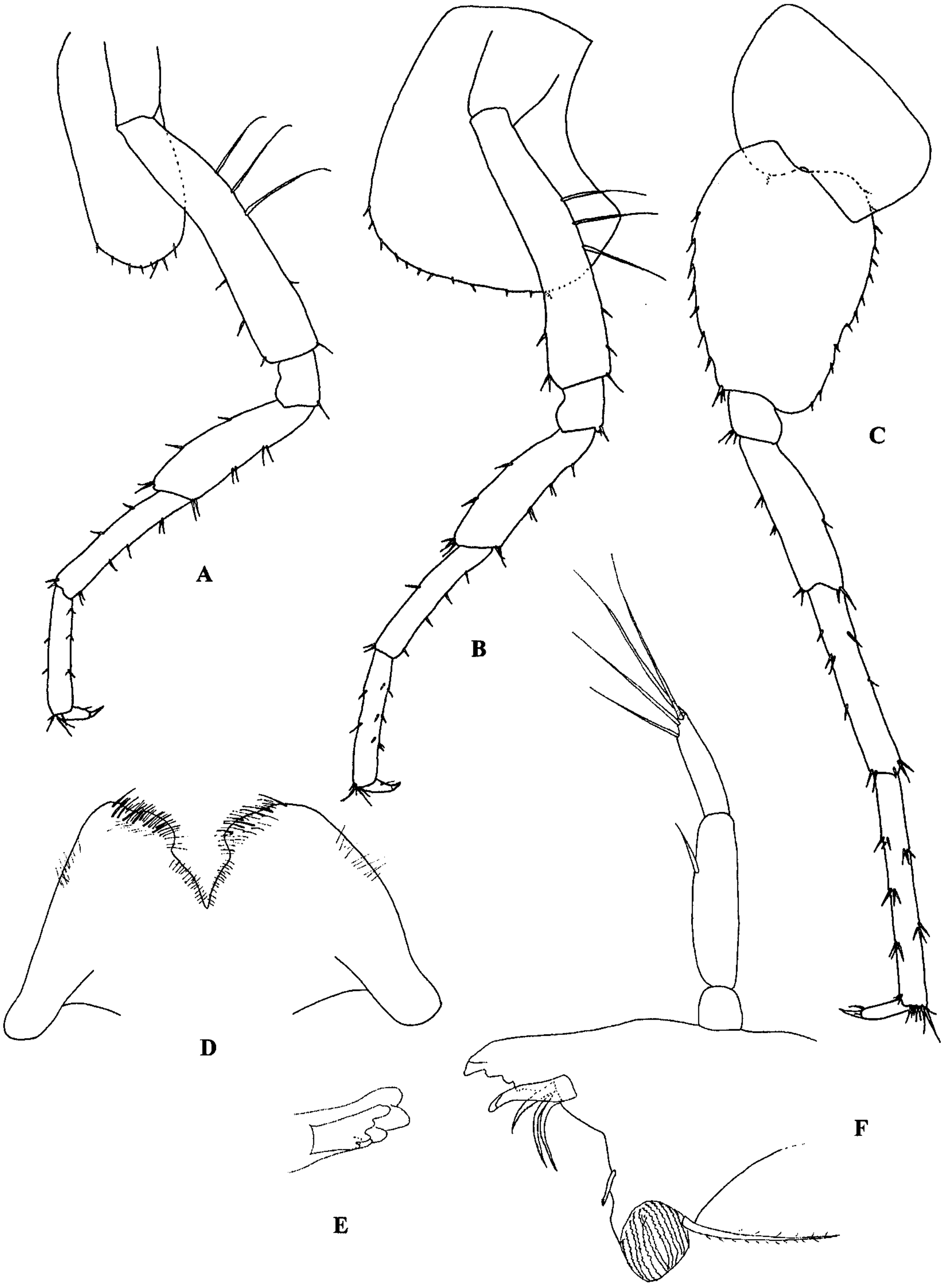

Fig. 6.17. *Melita almagosa* n. sp., paratypes, Almagosa Springs, Guam. Male (4.2 mm): A, pereopod 3; B, pereopod 4; C, pereopod 5; E, left mandible incisor and lacinia mobilis; F, right mandible. Female (3.2 mm): D, lower lip.

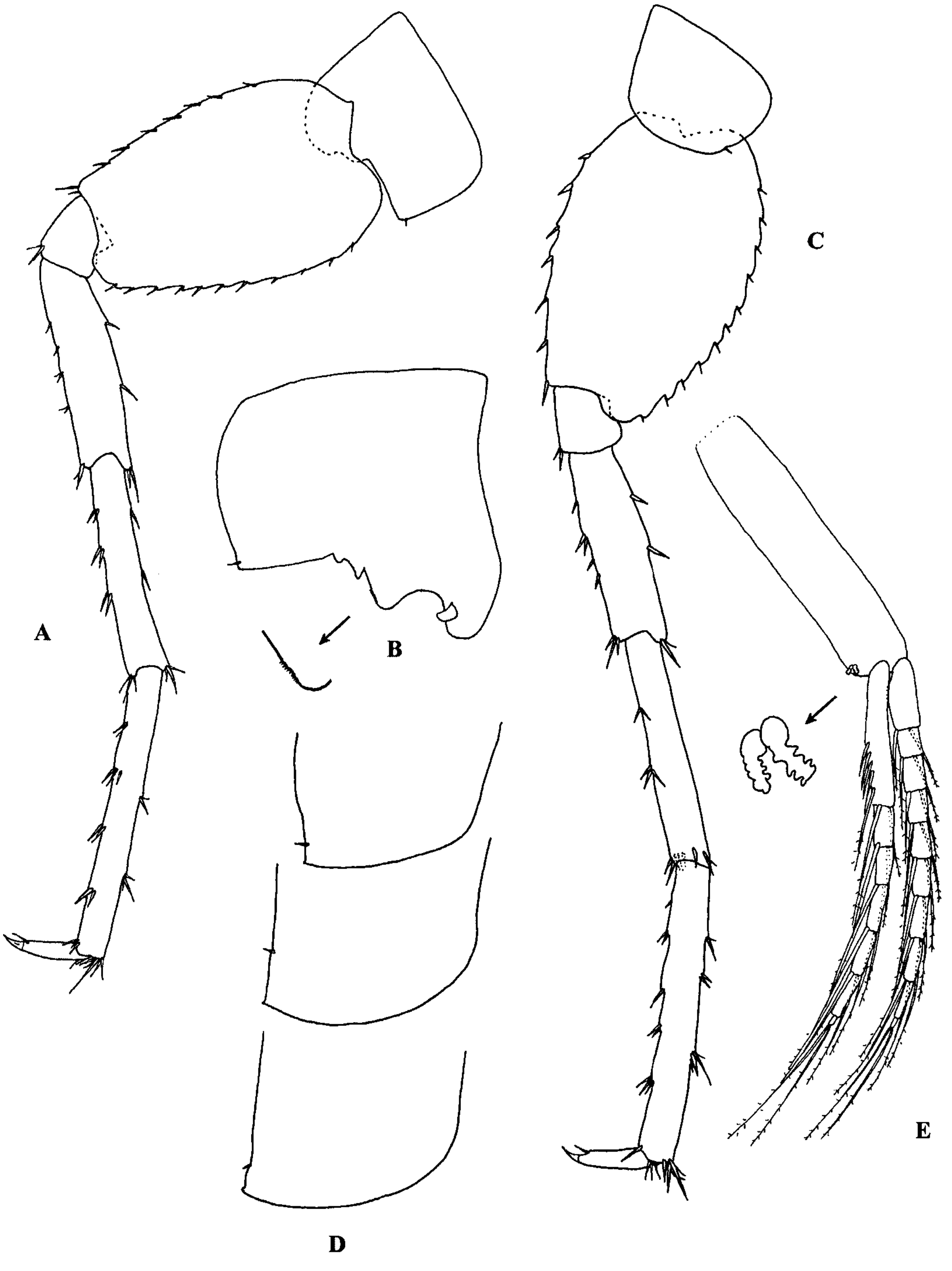

Fig. 6.18. *Melita almagosa* n. sp., paratypes, Almagosa Springs, Guam. Male (4.2 mm): A, pereopod 6; C, pereopod 7; D, pleonal plates; E, pleopod 1 (coupling spines enlarged). Female (3.2 mm): pereopod 6 coxa (serrate posterior margin on medial lobate extension enlarged).

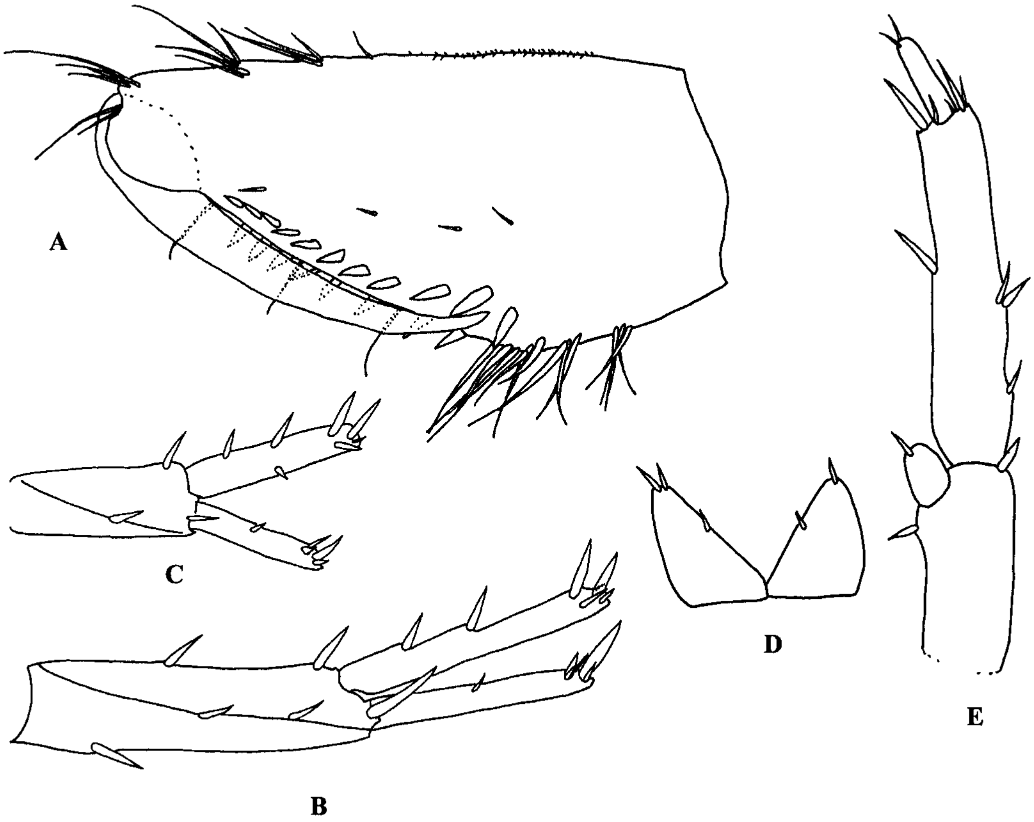

Fig. 6.19. *Melita almagosa* n. sp., paratypes, Almagosa Springs, Guam. Female (3.2 mm): B, uropod 1; C, uropod 2; D, telson; E, uropod 3. Male (4.2 mm): propod and dactyl of gnathopod 2.

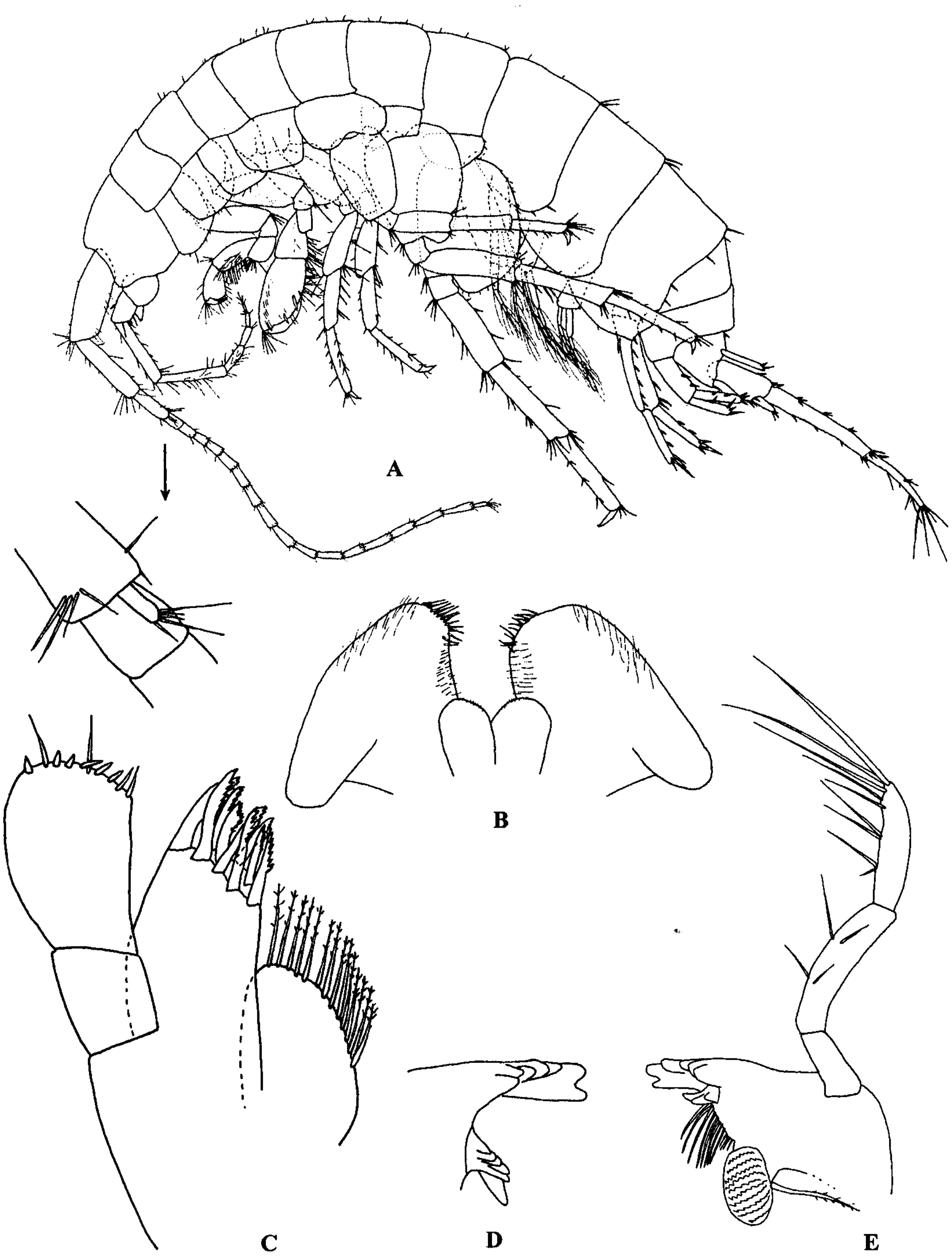

Fig. 7.1. *Flagitopisa philippensis* n. sp., paratypes, Spring 1 Roxas Park, Bohol Island, Philippines. Male (5.0 mm): A, whole animal. Male (7.0 mm): B, lower lip; D, left mandible incisor and lacinia mobilis; E, right mandible. Female (6.0 mm): maxilla 1.

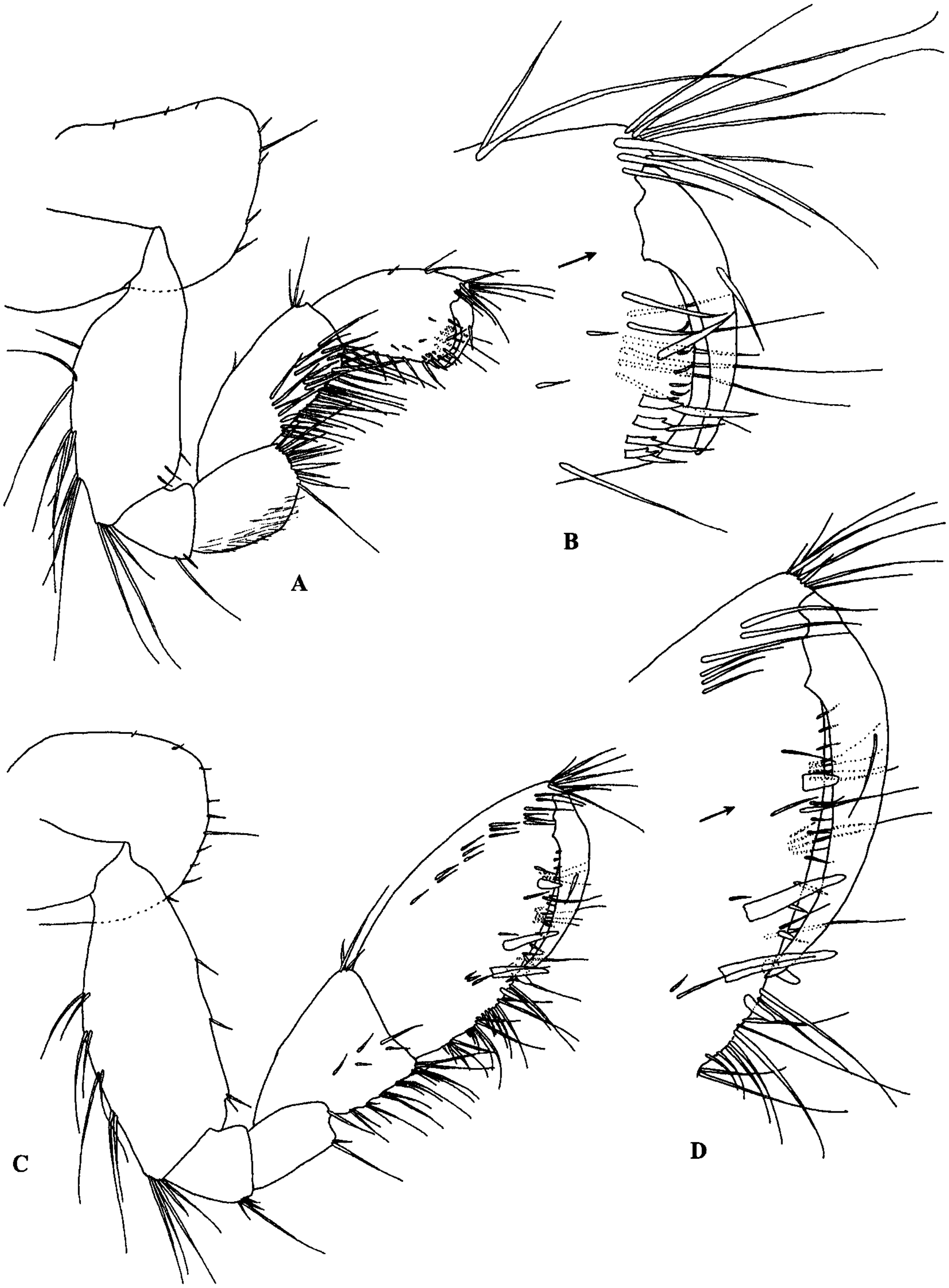

Fig. 7.2. *Flagitopisa philippensis* n. sp., paratypes, Spring 1 Roxas Park, Bohol Island, Philippines. Male (7.0 mm): A, gnathopod 1; B, enlarged distal end of propod and dactyl of gnathopod 1; C, gnathopod 2; D, enlarged distal end of propod and dactyl of gnathopod 2.

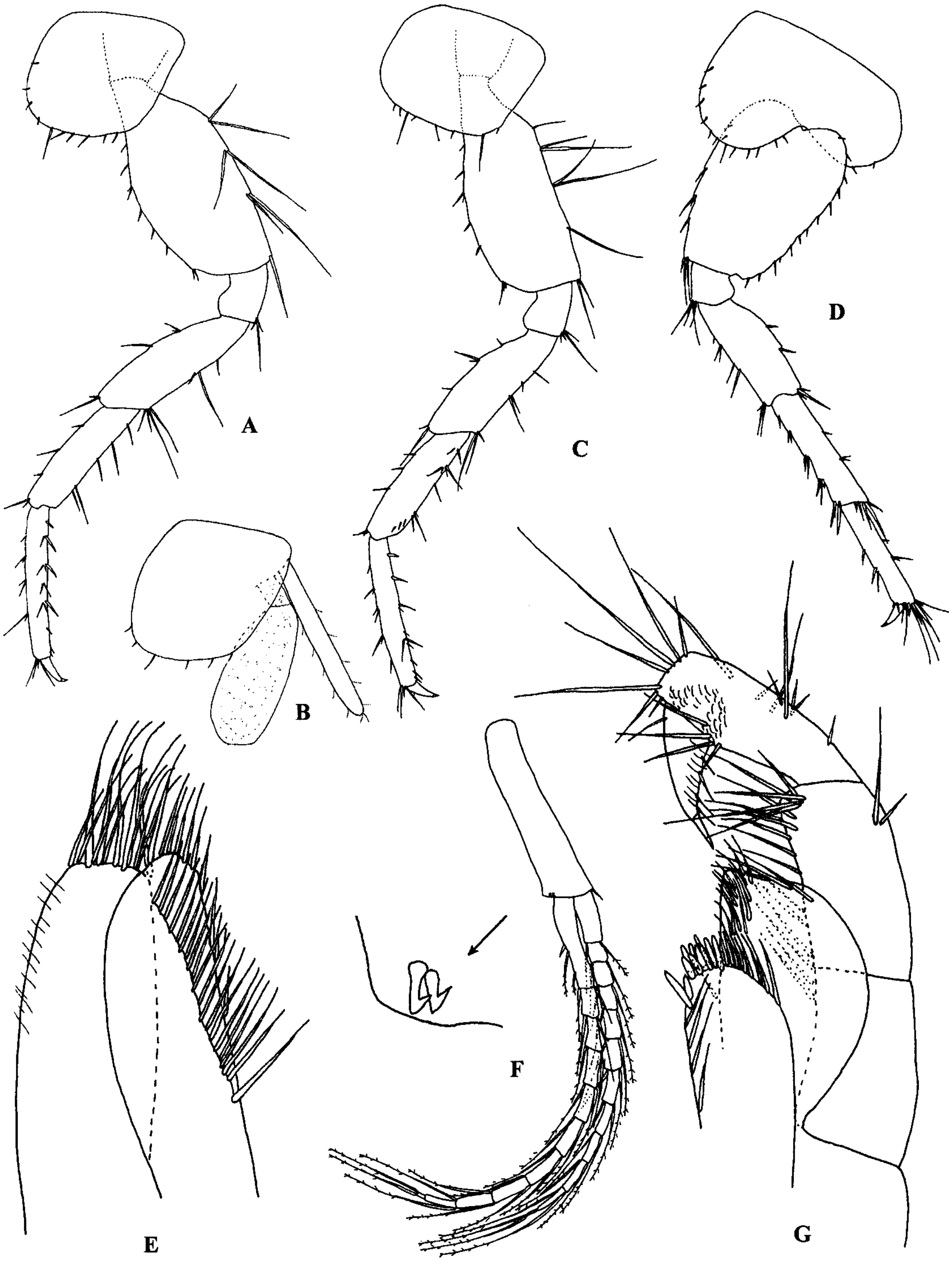

Fig. 7.3. *Flagitopisa philippensis* n. sp., paratypes, Spring 1 Roxas Park, Bohol Island, Philippines. Male (7.0 mm): A, pereopod 3; C, pereopod 4; E, maxilla 2; F, pleopod 1 (coupling spines enlarged); G, maxilliped. Female (6.0 mm): B, pereopod 3 coxal plate with brood plate and gill; D, pereopod 5.

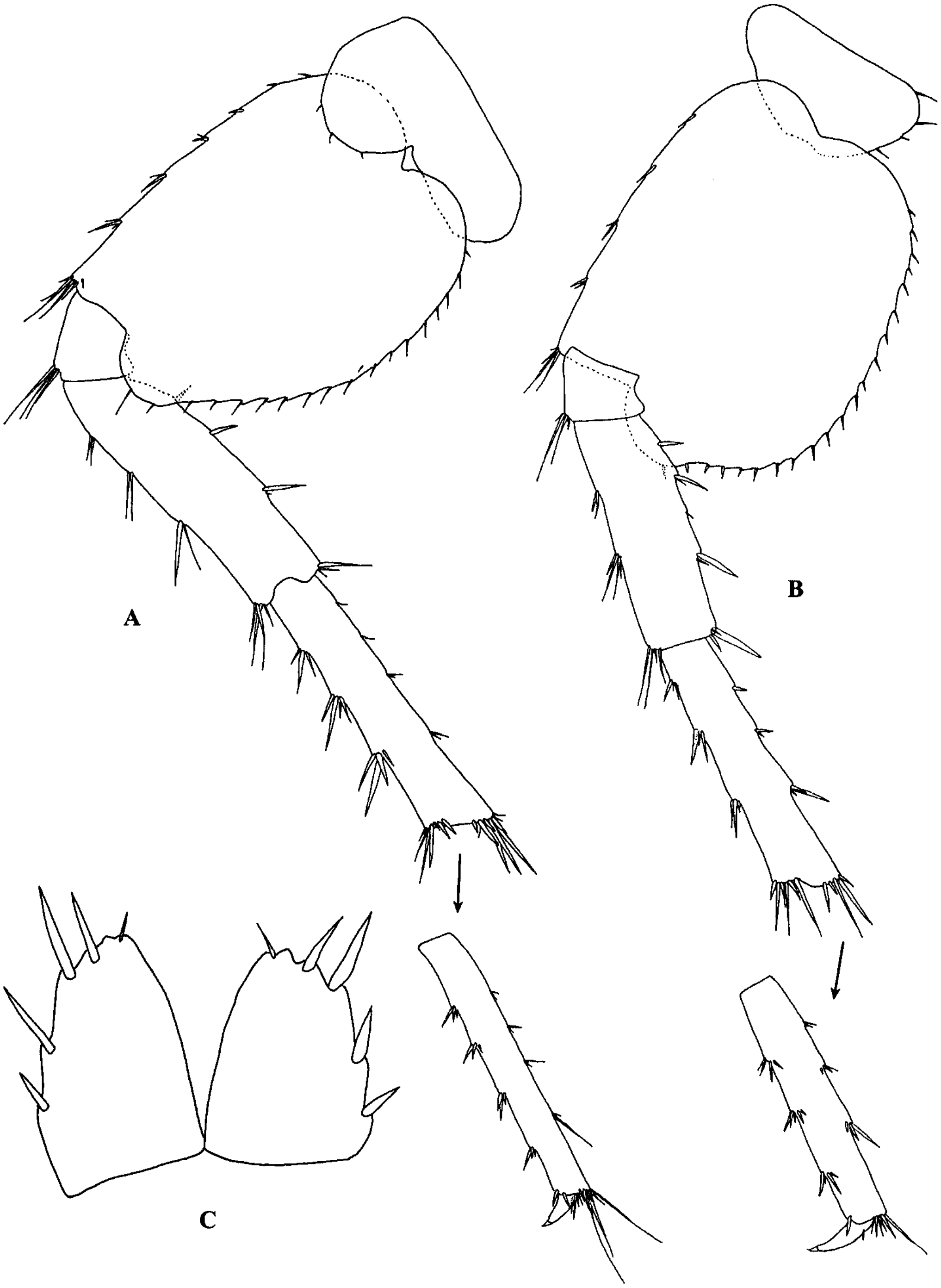

Fig. 7.4. *Flagitopisa philippensis* n. sp., paratypes, Spring 1 Roxas Park, Bohol Island, Philippines. Male (7.0 mm): A, pereopod 6; B, pereopod 7. Female (6.0 mm): C, Telson.

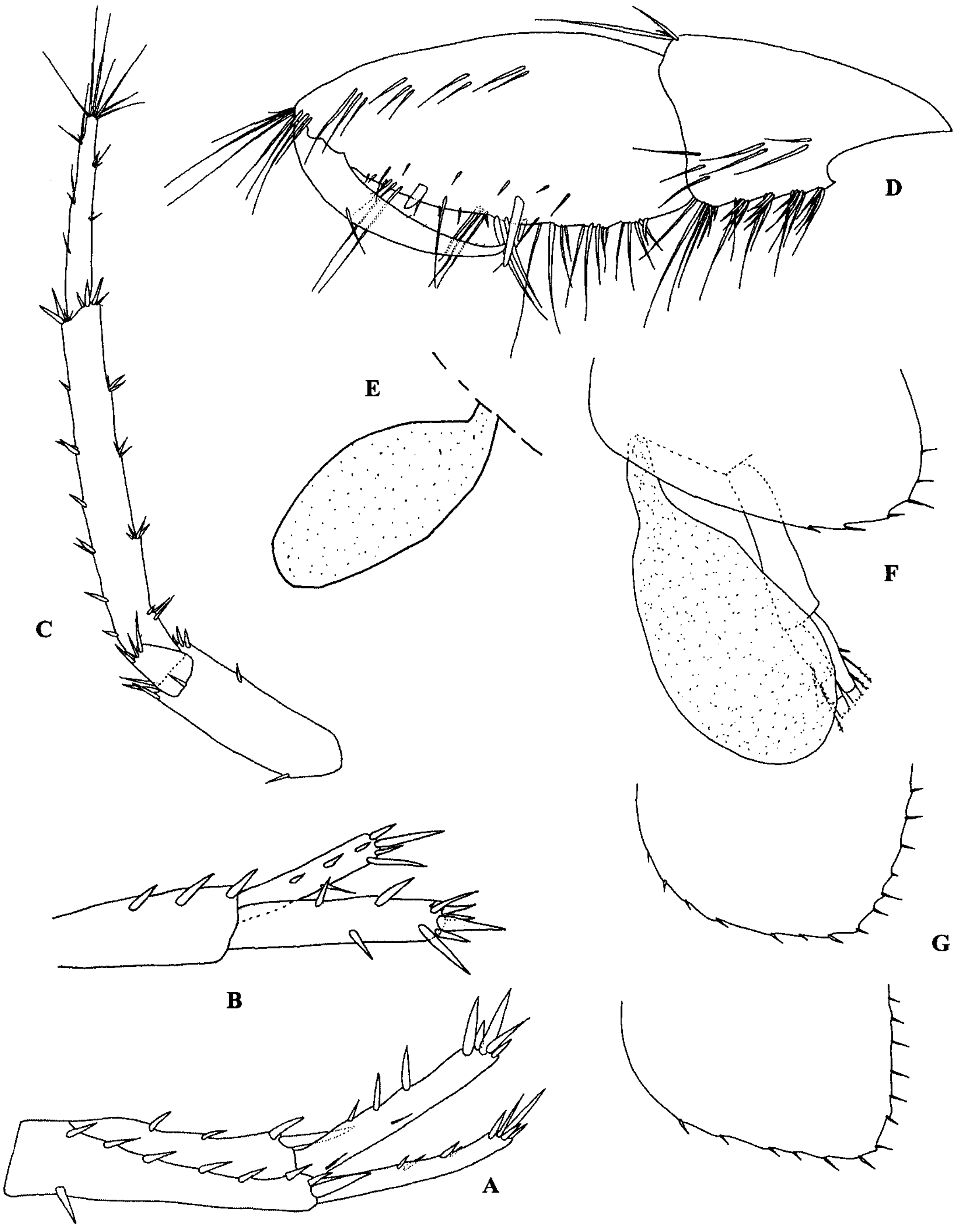

Fig. 7.5. *Flagitopisa philippensis* n. sp., paratypes, Spring 1 Roxas Park, Bohol Island, Philippines. (Male 7.0 mm): A, uropod 1; B, uropod 2; F, pleonal plate 1 with gill attached anterior to pleopod 1; G, pleonal plates 2 and 3. (Female 6.0 mm): C, uropod 3; D, carpus and propod of gnathopod 2. Paratype, Spring 2, Roxas Park, Bohol Island, Philippines. (Second Female 6.0 mm): E, pleonal gill drawn from opposite perspective.

APPENDIX B

LIST OF CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS OF *BAHADZIA* AND SELECTED TAXA (SECTION 2)

1. Antenna 1 longer than body.
2. Accessory flagellum of antenna 1 with 3 segments.
3. Accessory flagellum of antenna 1 subequal in length to first 3 primary flagellar segments.
4. Antenna 1 more than twice as long as antenna 2.
5. Antenna 2 peduncular segments 4 and 5 subequal in length.
6. With tiny round pigmentless eye.
7. Mandibular palp present.
8. A-seta present on mandibular palp.
9. 16-25 D setae on mandibular palp.
10. Mandibular palp segments 1 and 2 subequal in length to 3.
11. Inner lobes of lower lip not vestigial, present and distinct.
12. Inner plate of maxilla 1 with 15-25 apical setae.
13. Apical setae on inner plate of maxilla 1 naked.
14. Number of spines on outer plate of maxilla 1 reduced to 8 or less.
15. Maxilliped outer plate without row of spines.
16. Posterior lobe of merus (segment 4) of gnathopod 1 (both sexes) strongly produced forward and narrowing distally.
17. Carpus of gnathopod 1 at least 50% longer than corresponding propod.
18. Lateral surfaces of uropods 1 and 2 pubescent.

19. Pereopod 6 longer than body.
20. Distal end of peduncle of uropod 2 with row of comb spines.
21. Uropod 3 with more than 7 spines on outer margin of outer ramus.
22. Pleopod 1 with 2 coupling spines and one unmodified spine adjacent to coupling spines.
23. One or more sets of doubly inserted spines/spine-setules on lateral margins of telson.
24. Basofacial spine on peduncle of uropod 1.
25. With second segment on outer ramus of uropod 3.
26. Presence of setae on rami of uropod 3.
27. Presence of subdistal spiniform process on the dactylus of pereopods 5, 6 and 7.

VITA

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