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MOLECULAR PHYLOGENY OF THE EAST PACIFIC SQUAT LOBSTERS OF THE GENUS *MUNIDOPSIS* (DECAPODA: GALATHEIDAE) WITH THE DESCRIPTIONS OF SEVEN NEW SPECIES

W. Joe Jones and Enrique Macpherson

(WJJ) Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, California, U.S.A. (jones@mbari.org);
(EM) Centro de Estudios Avanzados de Blanes (CSIC), C. acc. Cala San Francesc 14, 17300 Blanes, Spain (macpherson@ceab.csic.es)

A B S T R A C T

Numerous specimens of the genus *Munidopsis* from the East Pacific, and including the East Pacific Rise (EPR), are reviewed using morphological characters and mitochondrial cytochrome oxidase subunit I (*COI*) sequences. Six new *Munidopsis* species from the East Pacific are described (*M. bracteosa*, *M. hirsuta*, *M. kensmithi*, *M. scotti*, *M. segonzaci*, and *M. tiburon*), and the status of *M. recta* is revised. A seventh new species (*M. vrijenhoeki*) from Fiji Basin (SW Pacific) is also included. A combined morphological and molecular analysis revealed that the most common species on the EPR is *Munidopsis recta*. Most of the new species can be differentiated from closely related species by subtle morphological characters, which correspondingly match the molecular phylogeny and large molecular divergence, confirming the existence of sibling species in the genus *Munidopsis*. Most *Munidopsis* individuals formerly considered *M. subsquamosa* from the East Pacific Rise appear to be members of *M. recta*. One potential sister taxa to *M. recta* is *M. bracteosa*, which is found at the Juan de Fuca hydrothermal vents, the Mendocino Fracture Zone, and a Monterey Bay whalefall. Our findings suggest that *Munidopsis* populations are tightly interconnected between distant and discrete locations, and challenge models for the predicted dispersal of these species. Additional sampling of *Munidopsis* populations on localized habitats (wood, hydrothermal vents, and whale falls), as well as intervening abyssal areas, are required to fully understand the complex evolutionary history and diversity of this group.

INTRODUCTION

One of the most widespread, yet enigmatic, groups in the deep sea is the galatheid squat lobsters (Genus *Munidopsis* Whiteaves, 1874). In the eastern Pacific, there are about 36 recognized species, (excluding the present new species, see Baba, 2005) of which ca. 21% are from abyssal depths below 3000 m. Sampling effort in the bathyal and abyssal plains (1000 m to 5330 m), where species of *Munidopsis* are more common (Baba, 2005), has been sporadic until recently, limiting our knowledge of the distributional ranges of various species, and few data on their biology have been available (Wenner, 1982; Gore, 1983; Wilkens et al., 1990; Creasey et al., 2000; Macpherson and Segonzac, 2005).

The eastern Pacific galatheids have not received much attention since the late 19th century (Baba, 2005). Since that time, hydrothermal vent systems were discovered in the east Pacific Ocean (van Dover, 2000) resulting in increased characterization and sampling of deep-sea organisms. Two main biogeographic regions exist in the east Pacific for hydrothermal vent systems: the smaller northeast Pacific Juan de Fuca region and the expansive East Pacific Rise (EPR) (Fig. 1). The EPR is a deep-sea feature ranging over 7000 km from the Gulf of California (Guaymas Basin, 27°N) to the Pacific-Antarctic Rise (38°S) containing several well-studied hydrothermal vent areas. *Munidopsis* individuals are commonly observed at the periphery of vent fields and near active venting throughout the Juan de Fuca region and the EPR (Williams, 1988). Some of these species are found almost exclusively at hydrothermal vent environments on the EPR: *Munidopsis lentigo* Williams and Van Dover, 1983 is associated with hydrothermal vents though it has only been collected at the 21°N vents on the EPR (Williams and Van Dover, 1983). A second species, *M. alvisca* Williams, 1988, is found on hydrothermal vents in the Guaymas Basin and in the more northern Juan de Fuca Ridge (Williams, 1988; Khodkina, 1991). Both *M. lentigo* and *M. alvisca* have very restricted geographical distributions and are very distinct morphologically from other *Munidopsis* species (Williams and van Dover, 1983; Williams, 1988). These two hydrothermal vent species will be dealt with in a subsequent paper along with an analysis of habitat evolution (Jones et al., unpublished data).

A third species, *M. subsquamosa* Henderson, 1885, has been cited in the EPR hydrothermal vent systems (Ambler, 1980; Van Dover et al., 1985). However, Baba (2005) and Martin and Haney (2005) have recently proposed that these specimens belong to a complex of closely related species rather than all to *M. subsquamosa*. Addionally, Baba (2005), after the revision of the type material of *M. subsquamosa* (Boso Peninsula, Japan, at 3431 m), as well as additional specimens from different localities of the Pacific Ocean, has shown that the species is probably not distributed along the eastern Pacific. Most citations of this species in the eastern Pacific belong to *M. producta* Baba, 2005, *M. recta* Baba, 2005 or have questionable identities, e.g., Faxon (1895) Panama, at 2092-3060 m, Ambler (1980) off Oregon and Panama, at 2692-3000 m, Van Dover et al. (1985) Galapagos Rift, 2500-2600 m. These uncertainties, in conjunction with the low number of studies on this group, urge a study of the species of the genus *Munidopsis* from different localities of the EPR. A fourth species, *Galacantha diomedeae* Faxon, 1893, formerly *Munidopsis diomedeae*

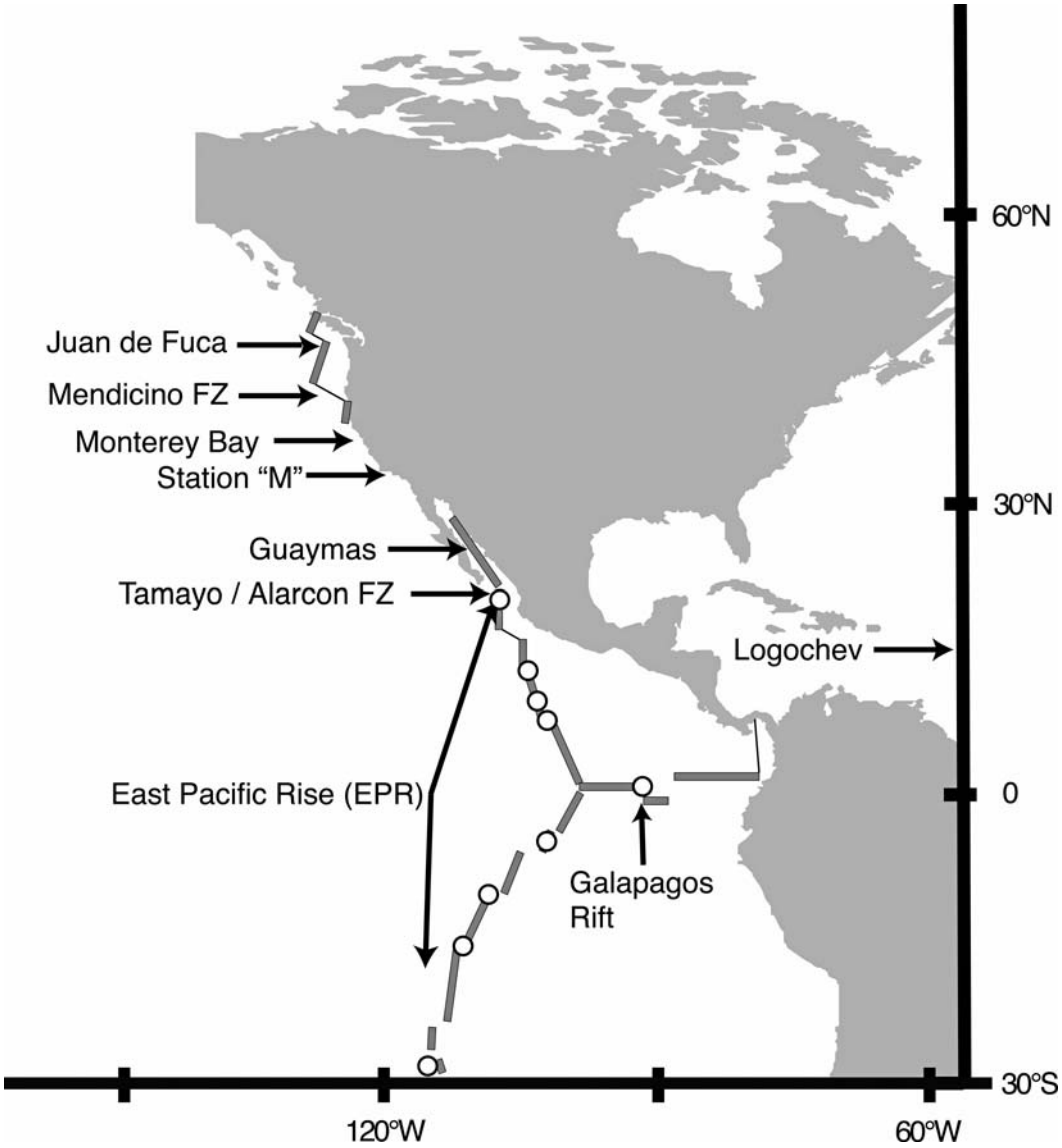

Fig. 1. Map of the east Pacific Ocean with sampling locations for *Munidopsis*.

(Macpherson, 2007) is also cited in the EPR (Khodkina, 1991), although is not considered in the present work due to lack of tissue for molecular analysis.

A key issue for the present paper is to determine the morphological and genetic identity of the *Munidopsis* species at EPR hydrothermal vents in order to properly assign individuals to species for subsequent population genetic studies. Due to the faunal similarity between the EPR and Juan de Fuca hydrothermal vents systems (Tunnicliffe and Fowler, 1996) including the purported existence of *M. subsquamosa* in the Cascadia Basin (Ambler, 1980), we included *Munidopsis* collected from the Juan de Fuca vent fields and two intermediate localities (Monterey Bay and Southern California: Station "M", Smith and Druffel, 1989) to sample *Munidopsis* from geographically intermediate, non-vent habitats (Fig. 1). In order to improve the taxonomic and phylogenetic identity of the East Pacific species, and considering the absence of molecular data in the genus *Munidopsis*, we also included one new species from the hydrothermal vents of the Fiji Basin (Southwest Pacific) and specimens of *M. exuta* from the Mid Atlantic Ridge (MAR).

Very few specimens (usually one or two) of *Munidopsis* are caught at each locality due to sampling limitations, i.e., submarine suction samplers, which prevents the evaluation of intraspecific morphological variations and specific characters. For these reasons, as in other groups with uncertain species (Chan and Chu, 1996; Sarver et al., 1998; Macpherson and Machordom, 2001), we have used, in addition to morphology, molecular characters to provide additional data to both identify species and resolve phylogenetic relationships. The use of *mtCOI* as a tool for identifying cryptic and morphologically ambigious species provides a relatively rapid means of assessing evolutionary distinctiveness of specimens (Schander and Willassen, 2005). In this paper, we have coupled DNA analysis with traditional taxonomy in

Table 1. Specimen collection sites, species identifications, and GenBank (GB) accession numbers for *Munidopsis* squat lobsters. Samples for which there is no voucher specimen is indicated by "n/a". Holotypes indicated by *, paratypes indicated by †. T- *ROV Tiburon*, A- *DSV Alvin*, J2L- *ROV JASON2*, R- *ROV ROPOS*.

Species	Locality	Dive #‡	GenBank Accession #
†*Munidopsis tiburon*	Monterey Bay Canyon	T611	DQ677673
**Munidopsis tiburon*	Monterey Bay Canyon	T611	DQ677673
**Munidopsis vrijenhoeki*	White Lady, Fiji Basin	J2L149	DQ677674 (2 individuals)
Munidopsis antonii	Station "M"	dredge	DQ677677-82
**Munidopsis segonzaci*	Station "M"	dredge	DQ677683
†*Munidopsis bracteosa*	Main Endeavour Field	R709	DQ677684
†*Munidopsis bracteosa*	Mendicino Fracture Zone	T348	DQ677685 (3 individuals)
†*Munidopsis bracteosa*	2891 m whalefall	T391	DQ677685-86 (2 individuals)
†*Munidopsis bracteosa*	2891 m whalefall	T610	DQ677685
†*Munidopsis bracteosa*	2891 m whalefall	T742	DQ677687 (2 individuals), DQ677689
**Munidopsis bracteosa*	2891 m whalefall	T742	DQ677688
Munidopsis exuta (n/a)	Logochev	A3133	DQ677690
Munidopsis exuta (n/a)	Logochev	A3133	DQ677690
**Munidopsis hirsuta*	Station "M"	dredge	DQ677693
Munidopsis recta	Galapagos Rift	A2223	DQ677697
Munidopsis recta	9°N	A2358	DQ677695
Munidopsis recta	9°N	A2362	DQ677698 (2 individuals)
Munidopsis recta	9°N	A2363	DQ677696
Munidopsis recta	9°N	A2364	DQ677699
Munidopsis recta	9°N	A3033	DQ677695
Munidopsis recta	13°N	A3036	DQ677700
Munidopsis recta	7°S	A3321	DQ677696
Munidopsis recta	11°S	A3323	DQ677695-96 (7 individuals)
Munidopsis recta	17°S	A3328	DQ677695 (3 individuals)
-5 Munidopsis recta	18°S	A3333	DQ677695
Munidopsis recta	38°S	A4088	DQ677701
Munidopsis recta	21°N	T556	DQ677702
†*Munidopsis scotti*	Seacliff GR-14	T884	DQ677703-5 (8 individuals)
**Munidopsis scotti*	Seacliff GR-14	T884	DQ677703
**Munidopsis kensmithi*	Station "M"	dredge	DQ677706
†*Munidopsis kensmithi*	Station "M"	dredge	DQ677707-9
Munidopsis verrucosus	Station "M"	dredge	DQ677710
Munidopsis albatrossae	2891 m whalefall	T769	DQ677692
Munidopsis aries	NE Atlantic, EUMELI 4	CPH15	DQ677691
Munidopsis cascadia	2891 m whalefall	T391	DQ677694

an attempt to resolve the species identity and phylogenetic relationships of *Munidopsis* from the East Pacific, including the EPR hydrothermal vents.

Materials and Methods

Samples, DNA Extraction, and Sequencing

Samples were collected from throughout the east Pacific using a variety of deep sea submersible vehicles (Table 1). Samples from the Mid Atlantic Ridge (MAR) and the western Pacific were included as comparative material. The specimens, including type material, are mostly deposited in the collections of the Scripps Institution of Oceanography, California (SIO), National Museum of Natural History, Washington, D.C. (USNM), and Muséum National d'Histoire Naturelle, Paris (MNHN). Measurements of specimens represent the postorbital carapace length. Terminology used mainly follows Baba (2005). The first spine of the lateral margin of the carapace, usually situated in the anterolateral angle, is named as first (anterolateral) spine, and the following spine as second (hepatic) spine. The abbreviations used in the text include: Mxp (maxilliped), P1 (pereiopod 1, cheliped), P2-P4 (pereiopods 2-4, first to third walking legs), M (male), F (female), ov. (ovigerous).

For several species (*M. vrijenhoeki*, *M. recta*, *M. tiburon*, and *M. exuta*), only a subset of individuals were available for morphological analysis due to sampling methodology (sample destroyed during collection or only a piece kept for DNA). In all other specimens, a small portion (50 mg) of leg tissue (usually the lower section of the 4th ambulatory leg) was excised and treated with the Qiagen DNA isolation kit, according to manufacturer's instructions (Qiagen Inc, CA). PCR conditions for amplification included 30-100 ng of template DNA, 5 µl 10X buffer (supplied by manufacturer), 5 µl $MgCl_2$ (2.5 µM), 2 µl of each primer (10 µM final conc.), 2.5 units of *Taq* polymerase (Promega Inc. WI), 5 µl of a 2 mM stock solution of dNTPs, 1 µl of 100X BSA, and sterile H_2O to a final-volume of 25 µl. Polymerase chain reaction (PCR) was performed with a Cetus 9600 DNA thermocycler (Perkin-Elmer Corporation, Connecticut). Initially, universal primers (LCO1490 and HCO2198; Folmer et al., 1994) were used to amplify approximately 700 base pairs (bp) of the mitochondrial cytochrome c oxidase subunit 1 (*COI*) fragment. However, only a few *Munidopsis* individuals provided PCR amplications suitable for sequencing. Therefore, we designed internal PCR primers in conserved regions based on *Munidopsis* sequences we were able to obtain. The primer pair gala_COIF (5′-CAT CAC TWA GWT TRA TYA TTC GAG CAG AA-3′) and gala_COIR (GAA YAG GRT CTC CTC CTC CTA C-3′) was used to amplify a fragment of 545 base pairs (bp) of the mitochondrial *CO1* gene using a thermal profile with an initial denaturation at 94°C for 4 min; 35 cycles of 94°C/1 min; 55°C/2 min; 72°C/3.5 min; and a final extension at 72°C/10 min.

PCR products were purified using Montage columns (Millipore). The purified template DNA was sequenced using Big Dye™ Terminator cycle sequencing reaction kit (PE Biosystems, Foster, CA) and ABI Prism 3100 DNA sequencers (Applied Biosystems Inc, Foster, CA). PCR products were sequenced bidirectionally from each individual sample using the same forward and reverse primers as used in PCR. DNA sequence alignments were initially constructed using Sequencher 4.1 (Gene Codes Corporation Inc. Ann Arbor, MI).

Phylogenetic trees were estimated using MrBayes version 3.1.2 (Huelsenbeck and Ronquist. 2001). Bayesian analyses for *mtCOI* were performed with parameters being estimated during the run with six Markov chains and default parameters. The Monte Carlo Markov chain (MCMC) length was 5.1×10^6 generations, and we sampled the chain every 1000

generations to minimize autocorrelation. Markov chain Monte Carlo (MCMC) convergence was assessed by visually inspecting the sample paths of model parameters (to determine an appropriate burn-in period) and by repeating the analysis at least three times with random initial parameter values (to assess the dependence of posterior distributions on initial conditions). Parameter estimates were graphically analyzed to assess stability (Tracer ver. 1.3, Rambaut and Drummond, 2003). We conservatively used the last 5000 sampled trees to estimate Bayesian posterior probabilities. If $\geq$95% of the sampled trees contained a given clade, we considered it to be significantly supported by our data (sensu Wilcox et al., 2002). Resultant trees were midpointed rooted.

RESULTS

Systematics

Munidopsis albatrossae Pequegnat and Pequegnat, 1973
Fig. 2A

Munidopsis albatrossae Pequegnat and Pequegnat, 1973: 163, figs. 1, 2.—Baba, 2005: 284.

Munidopsis aries Ambler, 1980: 17.—Wicksten, 1989: 315 (not A. Milne-Edwards, 1880).

Material Examined.—East Pacific Rise. HOPE 99. Stn PL1365, 12°45.16′N, 103°59.20′W, 24 October 1999, 2550 m: 1 F 71.9 mm (MNHN).

Monterey Bay (at a whale fall). Tiburon dive 769, 36°36.79′ N, 122°26.01′ W, 30 November 2004, 2891 m: 1 F 13.7 mm, 1 juv. 8.6 mm (USNM 1101472).

Remarks.—This species is morphologically very close to *M. aries* A. Milne-Edwards, 1880, from the Atlantic Ocean (see Macpherson and Segonzac, 2005, and references cited therein), and they have been considered as synonyms by some authors (see above). However, the genetic distance (2.8%) observed between specimens from the EPR (*M. albatrossae*) and Central Atlantic Ocean (*M. aries*, Cruise Biozaire, Stn CP15, see Macpherson and Segonzac, 2005) suggests that they are different species. The two species can be differentiated by the armature of the anterobranchial margins of the carapace: the margin after the end of the anterior branch of the cervical groove is expanded and armed with several well-developed spines in *M. aries*, whereas the margin is not expanded and only has 1-2 spines in *M. albatrossae*. *Munidopsis albatrossae* has a denticulated carina along the distolateral margin of the fixed finger.

Distribution.—*Munidopsis albatrossae* has previously been collected from Oregon to Central America, between 2850 and 3570 m (Baba, 2005). The present specimens were collected in the East Pacific Rise and Monterey Bay, between 2550 and 2891 m.

Munidopsis antonii (Filhol, 1884)

Galathodes Antonii Filhol, 1884: 230, fig. 2.

Munidopsis antonii Baba, 2005, 132, 284, figs. 52-54 (synonymy and references).—Macpherson and Segonzac, 2005: 14.

Material Examined.—Off California. Station M, centered at 34 50′N, 123 00′W, 25 February 2005, 4100 m: 3 M 11.5-42.0 mm, 1 ov. F 34.5 mm, 2 F 28.4-34.6 mm (SIO C10819, C10801, C10880, C10882).

Remarks.—*Munidopsis antonii* was described from specimens collected in the Azores Islands, at 3975-4010 m (Filhol, 1884). Baba (2005) in a revision of the type material concluded that *M. beringana*, described by Benedict (1902) from specimens from the Bering Sea, at 3241 m, was a synonym of *M. antonii*. The closest relative of *M. antonii* is the new species *M. segonzaci* (see the differences under the Remarks of *M. segonzaci*).

The intraspecific TrN sequence divergence averaged 0.2%, and the interspecific sequence divergence with other species of the present work ranged between 2.7% (with *M. exuta*) and 15.9% (*M. albatrossae*). The genetic data indicated that *M. antonii* had a considerable genetic divergence (3.7%) with its closest morphological relative (*M. segonzaci*). The molecular data also showed that the divergence was smaller with other, clearly morphologically differentiated, species, i.e., *M. exuta* (2.7%), *M. recta* (2.8%) and *M. bracteosa* (3.1%).

Distribution.—Previously known from the northwestern Atlantic (58°49′N) and Bay of Biscay to the SE Atlantic (off South Africa, 32°29′S) between 3134 and 4460 m (Macpherson and Segonzac, 2005), Pacific Ocean, off Juan Fernandez, Bering Sea, 3241 m (as *M. beringana*), southern part of Davis Strait, 2626 m, off Oregon, 2800-3990 m (Ambler, 1980, as *M. beringana*), Japan, 3420-3960 m, Tasman Sea, off Zamboanga, Costa Rica, Gulf of Panama, 366-3800 m and Indian Ocean, SW Australia, Mozambique, off Sri Lanka (Baba 2005; Macpherson and Segonzac, 2005). The present specimens were collected off California, at 4100 m.

Munidopsis bracteosa, new species
Figs. 2B, 3

Material Examined.—Monterey Bay (at a whale fall). Tiburon dive 742, 36°36.79′ N, 12°26.01′ W, 2891 m, 29 September 2004: 1 F 24.2 mm, 1 M 20.4 mm (Holotype USNM 110063), 1 M 20.0 mm (USNM 1100634, 1100635, 1100636).

Monterey Bay (at a whale fall). Tiburon dive 391, 36°36.79′ N, 122°26.01′ W, 2891 m, 6 February 2002: 1 F 30.0 mm (USNM 1100633).

Northeast Pacific (near the Juan de Fuca Ridge). Mendicino Fracture Zone. Tiburon dive 348, 40°24.02′ N, 125°46.24′ W, 2441 m, 23 August 2001: 1 M 14.0 mm, 1 F 6.8 mm (USNM 1100632).

Description.—Carapace longer than broad, dorsal surface with numerous short striae and interrupted transverse ridges on posterior half of carapace elevated and tuberculate, each stria and ridge with short setae. Cervical groove distinct; transverse depression in anterior part of cardiac region. Gastric region moderately inflated, with pair of well-developed epigastric spines, and 1-2 small unpaired spines between. Rostrum moderately short, triangular, upcurved at 45°, terminating in mid-length or end of P1 carpus, length 0.4 times remaining carapace, maximum width 0.25 carapace breadth; lateral margin ridged, dorsal surface with small short striae, bearing longitudinal carina distally sharp, proximally sweeping into gastric region. Frontal margin oblique, with antennal spine. Lateral margin having anterolateral spine (first) longer than antennal spine; second spine directly behind anterior cervical groove clearly larger than first, followed by several short spines on somewhat convex anterior branchial region and again by spine directly behind

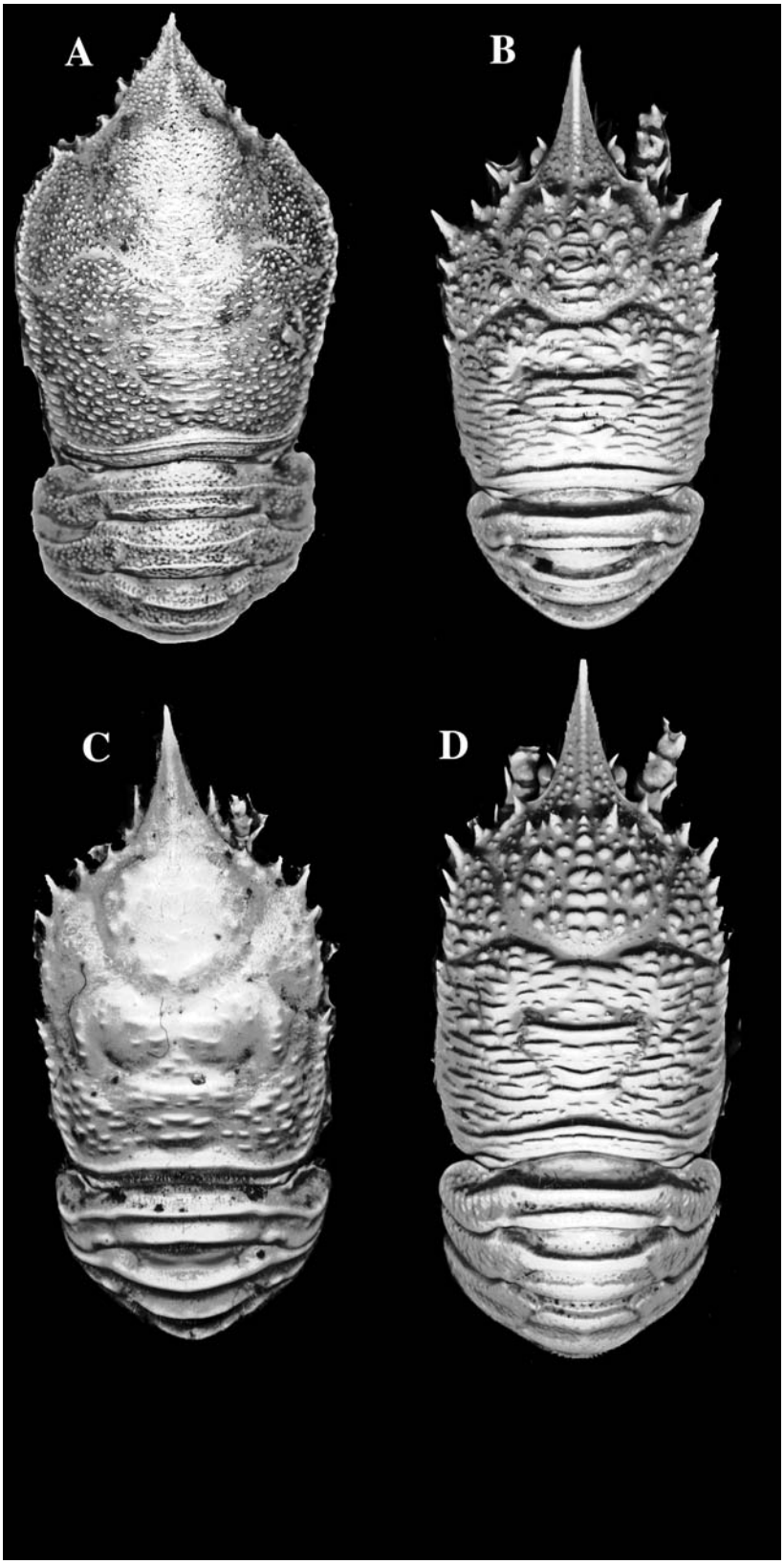

Fig. 2. A, *Munidopsis albatrossae* Pequegnat and Pequegnat, 1973, female 71.9 mm, dorsal view. B, *Munidopsis bracteosa* n. sp., holotype, male (20.4 mm), dorsal view. C, *Munidopsis hirsuta* n. sp., holotype, female (26.8 mm). D, *Munidopsis scotti* n. sp., holotype, ovigerous female (33.7 mm).

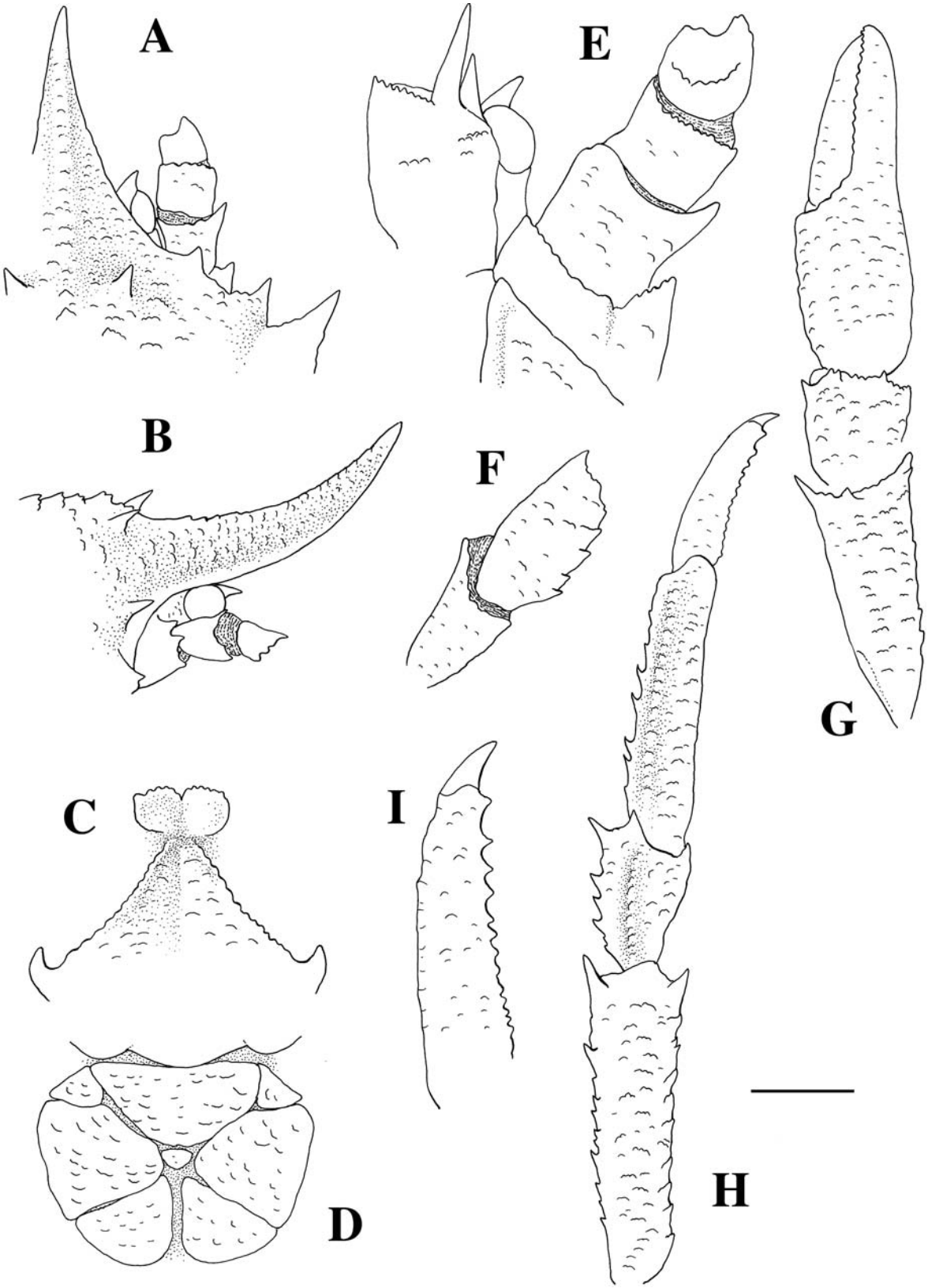

Fig. 3. *Munidopsis bracteosa* n. sp., holotype, male (20.4 mm). A, anterior portion of carapace, dorsal. B, anterior portion of carapace, lateral. C, sternal plastron, sternites 3 and 4. D, posterior part of segment 6 of pleon and telson. E, left antennule and antenna, ventral. F, merus of right mxp 3, lateral. G, right P1, lateral. H, right P2, lateral. I, dactylus of right P2. Scale: A, B, D, G, H = 5 mm; C, E, F, I = 2 mm.

posterior cervical groove. Notch at each end of anterior and posterior branches of cervical groove.

Sternum as long as wide, maximum width at sternite 7; sternites 3 and 4 with some short striae, sternite 3 moderately broad, serrate and bilobed, separated by notch, about twice wider than long; sternite 4 narrow at base of sternite 3, with margins granular, about 3 times wider than sternite 3.

Pleon squamose, with 2 elevated transverse ridges on segments 2 and 3, anterior ridge sharp; posterior ridge absent on segment 4. Segment 6 with produced posteromedian lobe slightly exceeding lateral lobes. Telson composed of 8 plates, having numerous granules; two posterior plates combined more than twice as wide as long.

Ocular peduncles fixed. Cornea ovate, greatest width clearly less than width of antennal segment 3, broad-based eyestalk mesiodorsally produced into strong eye-spine, laterally directed, shorter than cornea measured along lateral margin, mesioventrally unarmed.

Basal segment of antennule bearing distolateral spine longer than distodorsal; distomesial margin granulated.

Basal segment of antennal peduncle having small distomesial process, distolateral spine broad-based; segment 2 with well-developed distolateral spine.

Third maxilliped (Mxp 3) ischium with flexor margin sharply ridged, distally ending in small spine, extensor margin with small distal spine; 23-25 denticles on crista dentata. Merus having lateral face with short ridges, flexor margin bearing 3-4 small spines and several small denticular spines; extensor margin ending in distinct spine.

Chelipeds (P1) slightly longer than carapace, squamose, with some short setae. Merus nearly half carapace length and twice carpus length with long distomesial spine, and small distodorsal and distolateral spines; carpus as long as high, with short distomesial spine and several small distodorsal spines; palm about 1.3 times carpus length, and about 1.5 times longer than high; fingers slightly longer than palm, distally spooned, with crenulate ridges; movable finger slightly shorter.

Walking legs (P2-P4) moderately long and slender, somewhat compressed laterally, decreasing in size posteriorly, squamose from carpi to dactyli, with scattered setae; P2 longest, overreaching end of P1. P2 about 1.5 times carapace length, with merus nearly half carapace length, about 3.5 times longer than broad, twice length of carpus and 1.2-1.4 times length of propodus, dorsal margin with row of small spines, increasing in size distally, ventral margin serrate, with distal spine; carpus with row of spines along extensor margin, distal longest, lateral crest with granules; propodus 3.5-4 times as long as high, and 1.5 times longer than dactylus, with row of spines along extensor margin, flexor margin unarmed. Dactylus with terminal claw short, moderately curved; ventral margin nearly straight, with 13 teeth decreasing in size proximally, each with slender seta, ultimate tooth slightly closer to penultimate tooth than end of segment. Length of P4 merus 0.8 times that of P2.

Epipods on P1.

Remarks.—The new species is very closely related to *M. petila* Baba, 2005 from the Celebes Sea, at 5243-5163 m, in having the carapace with numerous striae, one well-developed eye-spine, small cornea, P2 exceeding P1 and segment 6 of pleon bearing produced posteromedian lobe. The new species may be differentiated from *M. petila* by the following characters:

— The gastric region has numerous small spines in addition to epigastric spines in *M. petila*, whereas these additional spines are absent in the new species.
— The first and second lateral spines are subequal in *M. petila*, while the second spine is clearly stronger than the first spine in the new species.
— The flexor margins of P2-P4 dactyli are more curved in *M. petila* than in the new species.

Molecular analyses show that *M. bracteosa* is closely related to *M. exuta* Macpherson and Segonzac, 2005, from the Atlantic Ocean (1.7% divergence), *M. recta* Baba, 2005 (1.6% divergence) and *M. scotti* n. sp. (2.6% of divergence) (see comments under Remarks of *M. recta* and *M. scotti*).

Distribution.—Eastern Pacific, near Juan de Fuca Ridge and Monterey Bay, between 2441 and 2891 m.

Etymology.—From the Latin *bractea*, scale, small leaf, in reference to the numerous interrupted ridges on the carapace.

Munidopsis cascadia Ambler, 1980

Munidopsis cascadia Ambler, 1980: 21, fig. 6.—Wicksten, 1989: 315 (list). —Baba, 2005: 286.

Material Examined.—Monterey Bay (at a whale fall). Tiburon dive 391, 36°36.79′ N, 122°26.01′ W, 2891 m, 6 February 2002, 1 M 20.4 mm (USNM 1100637).

Remarks.—The species is characterized by the body and appendages with fine plumose setae, rostrum without lateral spines, dorsal carapace surface without scaly ridges on anterior half and without spines other than pair of large epigastric spines, anterior lobe of carapace lateral margin carinate and salient, main eye-spine on mesial end of eyestalk, cornea small, distinctly less than breadth of rostrum at midlength, fixed finger of P1 with denticulate carina on distolateral margin, P2 reaching or overreaching end of P1. The closest species of the genus are *M. edwardsii* (Wood-Mason, 1891) and *M. bermudezi* Chace, 1939 (see Ambler, 1980; Baba, 2005). Molecular data show a large divergence with other species of the present work ($>$ 10.0%), being slightly smaller with *M. hirsuta* (9.0%).

Distribution.—Previously known from the type locality, Cascadia Basin off Oregon, at 2743-2926 m.

Munida hirsuta, new species
Figs. 2C, 4

Material Examined.—Off California. Station M, centered at 34°50′N, 123°00′W, 19.02.2005, 4100 m: 2 M 26.7-29.0 mm, 1 ov. F 32.7 mm, 1 F 26.8 mm, holotype, 1 F 16.3 mm (SIO C10976, C10977, C10978).

Description.—Carapace slightly longer than broad, covered with some fine setae, surface moderately smooth, bearing some small granules and some short, interrupted ridges,

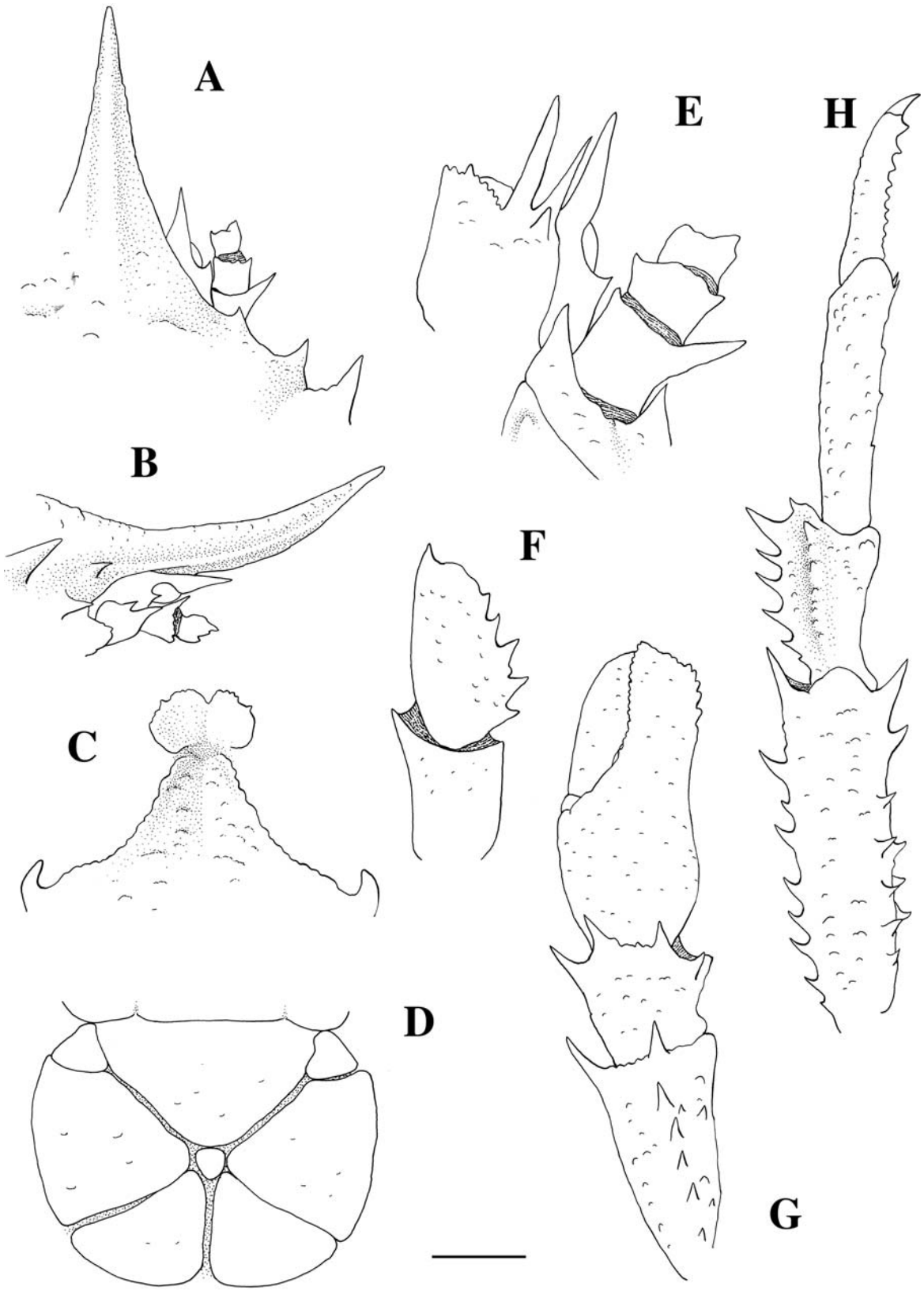

Fig. 4. *Munidopsis hirsuta* n. sp., holotype, female (26.8 mm). A, anterior portion of carapace, dorsal. B, anterior portion of carapace, lateral. C, sternal plastron, sternites 3 and 4. D, posterior part of segment 6 of pleon and telson. E, left antennule and antenna, ventral. F, merus of right mxp 3, lateral. G, right P1, lateral. H, right P2, lateral. Scale: A, B, D, G, H = 5 mm; C, E, F = 2 mm.

more numerous on posterior half; gastric region convex, without spines or blunt processes; cardiac transverse ridge preceded by shallow depression expanded laterally, anterobranchial regions slightly inflated, with some acute granules. Cardiac region faintly delineated in triangular shape, anteriorly without distinct transverse ridge but preceeded by shallow concavity anterolaterally on each side. Rostrum broadly triangular, upward directed, moderately carinate dorsally, bearing sparse granules, lateral margin carinate; length 0.3-0.4 times remaining carapace, maximum width about 0.25 carapace width. Front marginal oblique, with small antennal spine. Lateral margins convex in anterobranchial region; first lateral spine (anterolateral) slightly larger than antennal spine, forward directed, and smaller than second spine, third spine as long as first, followed by some acute granules, second spine laterally directed; deep excavation between anterior and posterior branchial regions, expanded spiny processes following excavation; notch at end of anterior branch of cervical groove.

Sternum as long as wide, maximum width at sternite 7. Sternite 3 very narrow, nearly twice wider than long, anterior margin divided into 2 lobes by deep median notch, each lobe dentate, lateral margin convex. Sternite 4 narrowly elongate anteriorly, width 3 times that of preceding sternite.

Pleon spineless, segments 2 to 4 each bearing two transverse ridges separated by shallow groove. Segment 6 without produced posteromedian lobe, not exceeding lateral lobes. Telson broader than long, divided into 8 plates.

Ocular peduncles hardly movable, relatively broad, bearing lateral and mesial eye-spines, lateral one small, mesial one strongly produced beyond cornea, usually exceeding antennal peduncle. Cornea small and lateral, narrower than mesial eye-spine.

Basal segment of antennule with long dorsolateral and distolateral spines and small distomesial granular process; small spine lateral to base of distolateral spine.

Antennal peduncle well developed; segment 1 with distomesial acute process somewhat larger than distolateral, both strong; segment 2 with one well developed distolateral and one minute distomesial spine; segment 3 unarmed.

Third maxilliped (Mxp 3) ischium with 21-22 closely placed denticles along crista dentata, extensor margin with distinct distal spine. Merus as long as ischium; flexor margin with 5 spines decreasing in size distally, extensor margin distally produced into spine.

Chelipeds (P1) setose, slightly longer than carapace, with numerous setae. Merus relatively short, not reaching tip of rostrum, bearing row of dorsal spines and some large distal spines. Carpus as long as broad, with 2 long mesial spines, and 2 distolateral spines. Palm as long as broad, somewhat depressed, unarmed, dorsally with scattered granules. Fingers as long as palm, having opposable margins straight, distally spooned, bearing denticles; fixed finger with denticulate carina on distolateral margin.

Walking legs (P2-P4) setose, moderately long. P2 about 1.5 times carapace length, overreaching end of P1. P2 merus more than 3 times longer than high, twice carpus length and nearly 1.5 times propodal length, with row of dorsal and ventral spines, increasing in size distally; carpus with some spines along extensor border, increasing in size distally, and some granules on lateral crest; propodus cylindrical in section, nearly 4 times longer than high, with 2 distal movable spinules on flexor margin; dactylus 0.8-1 times length of propodus, ending in sharp curved claw, flexor margin nearly straight, with row of 8-11 teeth diminishing in size toward base of segment, ultimate tooth equidistant between penultimate one and end of terminal claw, each tooth with seta.

Epipods present on P1.

Remarks.—*Munidopsis hirsuta* belongs to the group of species having a wide triangular rostrum, without epigastric spines or processes, main well-developed eye-spine on mesial end of eyestalk, fixed finger of P1 with denticulate carina on distolateral margin, P2 overreaching P1, and epipods on P1. The new species resembles *M. profunda* from the Celebes Sea (5163-5243 m) and Taiwan (3564-4455 m) (Baba, 2005; Osawa et al., 2006). However, they differ in the following aspects:

— The anterobranchial regions are more inflated in the new species than in *M. profunda*, and the anterobranchial margin of the carapace is clearly more convex in *M. hirsuta* than in *M. profunda*.
— The first lateral spine is clearly longer than the antennal spine in *M. hirsuta*, being smaller than the antennal spine in *M. profunda*. Furthermore, the first and second lateral spines are subequal in *M. profunda*, whereas the second spine is clearly longer than the first spine in *M. hirsuta*. Finally, the second lateral spine is forward directed in *M. profunda* whereas this spine is always laterally directed in the new species.

Molecular data show that the new species is clearly differentiated from other species of the present work (divergence >7.7%).

Distribution.—Only known from Station "M" in the East Pacific Ocean (4100 m).

Etymology.—From the Latin *hirsutus*, hairy, in reference to the short pilosity of the carapace and pleon.

Munidopsis kensmithi, new species
Figs. 5 A, B, 6

Material Examined.—Off California. Station M, centered at 34°50′N, 123°00′W, 4100 m, 30 October 2004: 1 M 25.8 mm, holotype, 1 M 17.4 mm, 1 F 34.3 mm (SIO C10973, C10974).

Description.—Carapace slightly longer than broad; dorsal surface moderately convex from side to side, covered with serrate granules, each granule with short setae; cervical groove moderately distinct, regions well defined, gastric and cardiac more convex than branchial regions. Gastric region without epigastric spines or processes. Cardiac region triangular, preceded by deep transverse groove. Rostrum triangular, broad at base, distal portion spiniform, slightly upwards directed in lateral view, 0.2-0.4 times length of remaining carapace, maximum width 0.3-0.4 times carapace

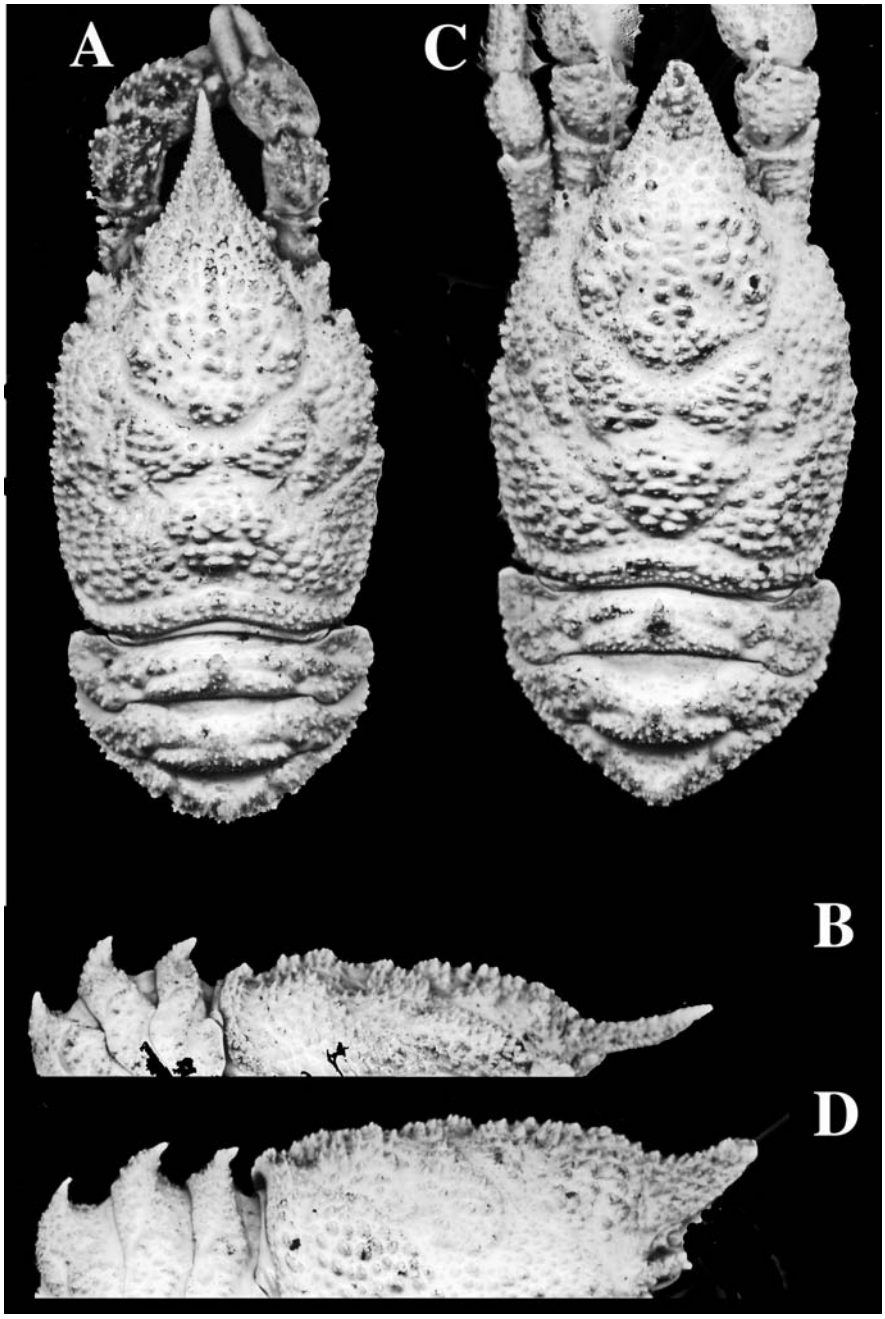

Fig. 5. *Munidopsis kensmithi* n. sp., holotype, male (25.8 mm). Carapace and pleon. A, dorsal view. B, lateral view. *Munidopsis verrucosus* Khodkina, 1973, ovigerous female (26.0 mm). Carapace and pleon. C, dorsal view. D, lateral view.

breadth; lateral margins granulate, slightly convex proximally; dorsal surface convex, with numerous granules and without dorsal carina; ventral surface with granules. Frontal margin strongly oblique, with small process behind antennal peduncle, then concavely transverse toward strong anterolateral process; lateral margins weakly convex, granular, anterolateral process followed by notch at distal end of anterior branch of cervical groove. Posterior margin preceded by elevated granulated ridge.

Pterygostomian flap with numerous granules, anterior margin angular.

Sternum as long as wide, maximum width at sternite 7; sternites 3 and 4 with granules, sternite 3 moderately broad, serrate and bilobed, separated by notch, about twice wider than long; sternite 4, with margins granular, about 3 times wider than sternite 3.

Pleon with numerous granules on transverse ridges and pleura; segments 2 to 4 each with elevated transverse ridge, followed by transverse groove, and strong median curved spine; segments 5 and 6 lacking such ridges and covered with small granules; segment 6 with weakly produced posterolateral lobes and nearly transverse posteromedian

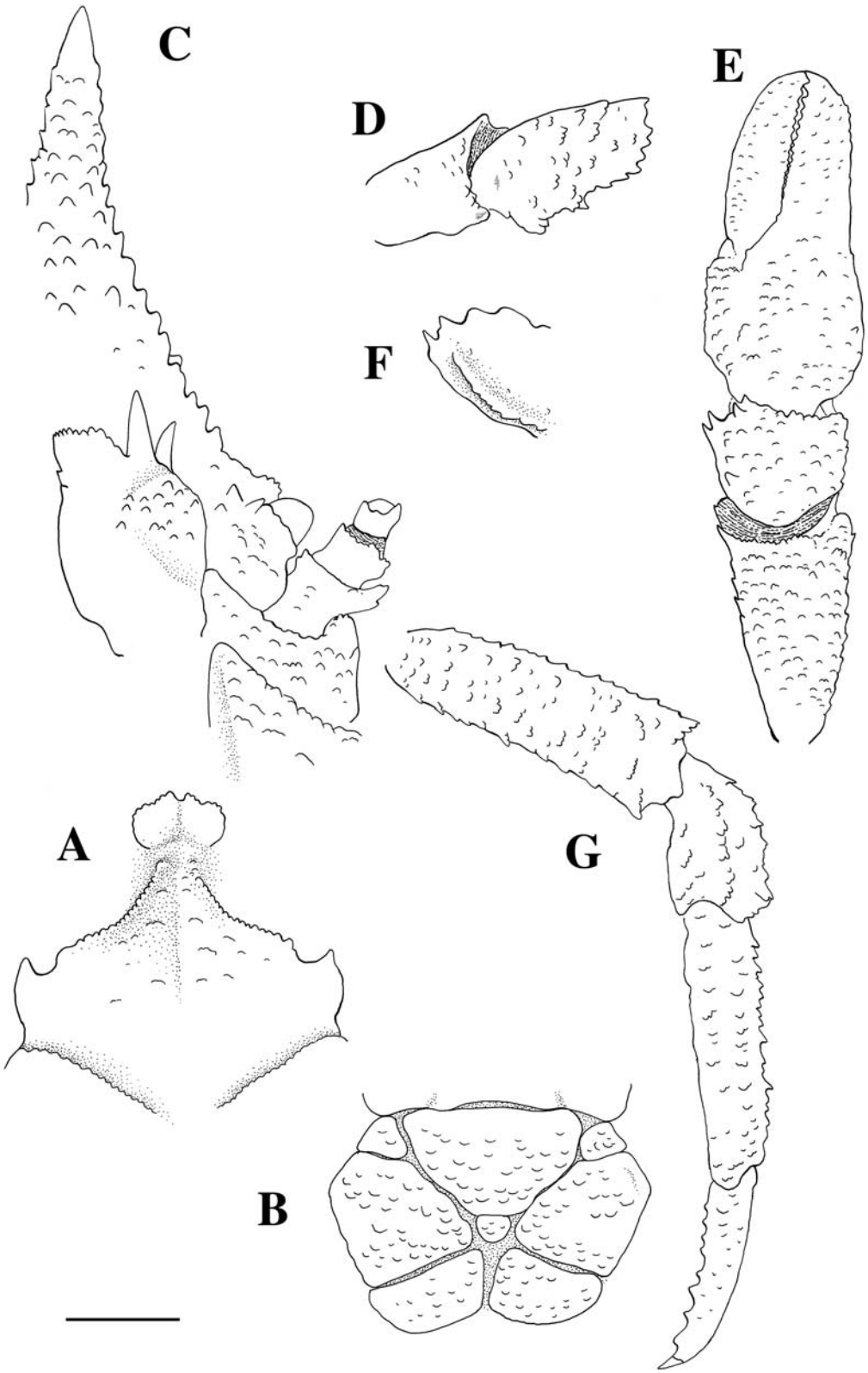

Fig. 6. *Munidopsis kensmithi* n. sp., holotype, male (25.8 mm). A, sternal plastron, sternites 3 and 4. B, posterior part of segment 6 of pleon and telson. C, anterior portion of carapace, ventral, and left antennule and antenna, ventral. D, merus of right mxp 3, lateral. E, right P1, lateral. F, distolateral carina of fixed finger of right P1, ventral. G, right P2, lateral. Scale: A, C, D, F = 2 mm; B, E, G = 5 mm.

margin. Telson composed of 8 plates, having numerous granules; two posterior plates combined more than twice as wide as long.

Ocular peduncles fixed, without eye-spine; surface with granules; semicircular cornea cupped within broad-base eyestalk, cornea slightly narrower than antennal segment 3.

Basal segment of antennular peduncle with strong dorsolateral and distolateral spines; distomesial margin produced, with small granules but no spine.

Antennal peduncle overreaching tip of cornea. Segment 1 with strong distomesial process barely reaching distal margin of segment 2, distolateral margin produced. Segment 2 with blunt distolateral spine, distomesial angle slightly produced. Segment 3 with small distomesial and distolateral processes. Segment 4 unarmed.

Third maxillipeds (Mxp 3) with ischium granular and as long as merus measured on extensor margin, flexor margin ridged, terminating in small blunt spine; 20-22 denticles along crista dentata. Merus with numerous granules on lateral surface, flexor margin with 2 blunt processes, extensor margin with small distal spine. Carpus slightly crenulated on extensor surface.

Chelipeds (P1) subequal, stout, slightly longer than carapace, covered with numerous small protuberances and granules on merus to dactylus, and with setae more dense on mesial and lateral margins of segments. Merus twice length of carpus, with a few distal spines. Carpus as long as broad, with some mesial spines and some small distodorsal spines. Palm slightly longer than carpus, and as long as broad measured at bases of fingers. Fingers 1.3-1.4 times length of palm, opposable margins nearly straight, not gaping, distally spooned; fixed finger with shallow distolateral carina.

Walking legs (P2-P4) moderately stout, somewhat compressed laterally, decreasing in size posteriorly; P2 longest, overreaching end of P1 carpus. P2 1.3-1.5 times carapace length, with merus nearly half carapace length, about 2.7-3.3 times longer than broad, nearly twice length of carpus and 1.2 times length of propodus, dorsal and ventral margins serrate, with distal blunt spines, lateral border with granules; carpus with prominent blunt spine and some smaller spines along extensor margin, lateral crest with granules, some additional granules on mesial side; propodus 3-3.5 times as long as high, and about 1.5 times longer than dactylus with numerous long setae along extensor and flexor borders, with granules along extensor margin and lateral side, flexor margin unarmed. Dactylus with terminal claw short, moderately curved; ventral margin nearly straight, with 8-9 teeth decreasing in sizes proximally, each with short seta, ultimate tooth equidistant between penultimate tooth and end of segment, penultimate tooth closer to previous one than to ultimate tooth. Length of P4 merus 0.7 times that of P2.

Epipods on P1.

Remarks.—The new species is closely related to *M. verrucosus* Khodkina, 1973 from the eastern Pacific (see below). Both species have the dorsal surface of the carapace, pleon and pereiopods armed with numerous granules and a spiniform median process on the pleon segments 2 to 4. The two species are morphologically very close, although the large molecular divergence between them (see below) indicates the existence of two sibling species. The comparison of the holotype of *M. kensmithi* with the original description of *M. verrucosus* by Khodkina (1973) and one specimen from Station M (see below), shows that they can be differentiated by the following characters:

— The distal portion of the rostrum is clearly narrower in the new species than in *M. verrucosus*. Furthermore, the rostrum is strongly upwards directed in *M. verrucosus*, instead of slightly upwards directed in the new species.
— The distal spines of the antennular basal segment are clearly longer in the new species than in *M. verrucosus*.
— Dactylus of walking legs with the penultimate tooth clearly closer to previous one than to ultimate tooth in *M. kensmithi*, whereas the penultimate tooth is equidistant to previous one and ultimate tooth in *M. verrucosus*.

The molecular data shows a nucleotide divergence of 7.6% between *M. kensmithi* and *M. verrucosus*.

Distribution.—Only known from Eastern Pacific Ocean, off California, at 4100 m.

Etymology.—The new species is dedicated to our colleague Dr. Ken Smith (MBARI), who has pioneered the long-term study of the deep-sea, particularly at Station "M".

Munidopsis recta Baba, 2005

Munidopsis recta Baba, 2005: 178, fig. 85.

Material Examined.—East Pacific Rise. Cruise AT-03, Alvin dive 3323, 11°18.215′ S, 110°32.246′ W, 2791 m, 27 December 1998: 1 M 41.7 mm, 4 ov. F 26.3-30.8 mm, 2 F 28.2-28.7 mm (USNM 1100643-1100649).

East Pacific Rise. Alvin dive 3328, 17°25′S, 113°12′W, 2582 m, 1 January 1999: 4 F 18.8-27.3 mm (MNHN).

East Pacific Rise. MBARI Cruise 2003, Tiburon dive 556, 20°50′N, 109°06′W, 2530 m (14 April 2003): 1 F 14.2 mm (SIO C10969);

East Pacific Rise. Cruise 125, Alvin dive 2363, 09°51′N, 104°18′W, 2517 m, 14 April 1991: 1 F 53.4 (SIO C10970);

East Pacific Rise. Cruise AT11-24, Alvin dive 4088, 37°48′S, 110°55′W, 2216 m, 22 March 2005: 1 F 33.5 mm (SIO C10971).

Remarks.—The specimens collected in the EPR agree quite well with the original description of the species, only known by the holotype male from the Gulf of Panama, 2950-3190 m (Baba 2005), although some slight variations have been observed. The rostrum is horizontal or slightly upcurved (upcurved at 40° in the holotype). The antennal spine is absent in the holotype, whereas this spine can be present in some specimens of the EPR (on one or both sides), being always smaller than first lateral spine of the carapace. The gastric region of the carapace is armed with group of spines and scale-like ridges in the holotype, whereas these spines are reduced or absent in several specimens of the EPR.

The intraspecific divergences averaged 0.2% (Tamura-Nei distance), and the interspecific ranged between 1.6% (with *M. bracteosa*) and 15% (with *M. albatrossae*). The minimal divergences were observed between *M. recta* and *M. bracteosa* (1.6%) and *M. exuta* (1.7%). Although the molecular divergences are small, *M. recta* is clearly dif-

ferentiated from these two species by their morphology. *M. recta* is distinguished from *M. bracteosa* by the segment 6 of pleon having the posteromedian lobe exceeded by lateral lobes in *M. recta* and exceeding beyond the lobes in *M. bracteosa*. *Munidopsis exuta*, from the Atlantic Ocean, can be distinguished from *M. recta* by the rostrum weakly carinated dorsally in *M. exuta* and with a strong dorsal carina in *M. recta*. Furthermore, the gastric region is usually armed with a group of spines in *M. recta* (but see above), being covered with numerous interrupted ridges, instead of two epigastric spines only and weak and small interrupted ridges in *M. exuta*.

Distribution.—Previously known from the Gulf of Panama, at 2950-3190 m. The new occurrences are from the East Pacific Rise, from 20°50′N to 37°47.563 S, between 2216 and 2791 m. All of these sites are at hydrothermal vent areas on the East Pacific Rise.

Munidopsis scotti, new species
Figs. 2D, 7

Material Examined.—Northeast Pacific. GR14/Seacliff site on Juan de Fuca Ridge. Cruise RIDGES 2005, Tiburon dive 884 (42°45.27′ N, 126°42.55′ W, 2715 m, 23 August 2005: 2 M 22.1-25.8 mm, 1 ov. F 40.0 mm, 1 F 28.0 mm; 4 M 19.0-25.5 mm, 1 ov. F 33.7 mm (holotype, USNM 1100638), 1 ov. F 37.1 mm (USNM 1100639 and MNHN Ga6467).

Description.—Carapace longer than broad, dorsal surface with numerous short striae and interrupted transverse ridges on posterior half of carapace elevated, each stria and ridge with short setae. Cervical groove distinct; transverse depression in anterior part of cardiac region. Gastric region moderately inflated, with pair of well-developed epigastric spines, and 2-7 additional small gastric spines. Rostrum moderately short, triangular, slightly upcurved, terminating at end of P1 merus, length 0.4 times remaining carapace, maximum width 0.25 carapace breadth; lateral margin ridged, dorsal surface with small short striae, bearing longitudinal carina distally sharp, proximally sweeping into gastric region. Frontal margin oblique, with well developed antennal spine. Lateral margin having anterolateral spine (first) as long as antennal spine; second spine directly behind anterior cervical groove, larger than first, followed by several spines and again by another spine directly behind posterior cervical groove. Notch at each end of anterior and posterior branches of cervical groove.

Sternum as long as wide, maximum width at sternite 7; sternites 3 and 4 with some short granular striae, sternite 3 moderately broad, serrate and bilobed, separated by notch, about 1.5 times wider than long; sternite 4 narrow at base of sternite 3, with margins granular, about 3 times wider than sternite 3.

Pleon with some small granules; 2 elevated transverse ridges on segments 2 and 3, anterior ridge sharp; posterior ridge absent on segment 4. Segment 6 without produced posteromedian lobe, not exceeding lateral lobes. Telson composed of 8-9 plates, having numerous granules; two posterior plates combined more than twice as wide as long.

Ocular peduncles fixed. Cornea ovate, greatest width clearly less than width of third antennal segment, broad-based eyestalk mesiodorsally produced into strong eye-spine, laterally directed, shorter than cornea measured along lateral margin, mesioventrally unarmed.

Basal segment of antennule bearing subequal distolateral and distodorsal spines; distomesial margin granular.

Basal segment of antennal peduncle having strong distomesial spine, distolateral spine short; segment 2 with strong distolateral spine.

Third maxilliped (Mxp 3) ischium with flexor margin sharply ridged, distally ending in small spine, extensor margin with small distal spine; 20-22 denticles on crista dentata. Merus with flexor margin bearing 2 spines and several small denticular spines; extensor margin ending in well-developed spine.

Cheliped (P1) longer than carapace including rostrum, squamose, each scale with short setae. Merus with distomesial, distodorsal and distolateral spines and some additional spines along dorsal side, 0.5-0.6 times carapace length and twice carpus length; carpus slightly longer than high, with well-developed mesial spine and several small distodorsal spines; palm slightly longer than carpus; fingers nearly 1.5 times longer than palm, distally spooned, with crenulate ridges; movable finger slightly shorter.

Walking legs (P2-P4) moderately long and slender, somewhat compressed laterally, decreasing in size posteriorly, squamose from carpi to dactyli, each scale with short setae; P2 longest, overreaching end of P1. P2 more than 1.5 times carapace length, with merus about 0.7 times carapace length, about 4-5 times longer than broad, 2.5-2.8 times length of carpus and 1.4-1.6 times length of propodus, dorsal margin with row of well-developed spines, increasing in size distally, ventral margin with row of short spines; carpus with row of spines along extensor margin, distal longest, lateral crest with granules; propodus 4 times as long as high, and 1.4-1.6 times longer than dactylus, with row of well-developed spines along extensor margin, flexor margin, with 2 minute distal spinules. Dactylus with terminal claw short, moderately curved; ventral margin nearly straight, with 15-16 teeth decreasing in size proximally, each with slender seta, ultimate tooth slightly closer to penultimate tooth than end of segment. Length of P4 merus 0.8 times that of P2.

Epipods on P1.

Remarks.—*Munidopsis scotti* resembles *M. geyeri* Pequegnat and Pequegnat, 1970, from the Caribbean Sea, Florida, Azores islands and off Angola, between 2650 and 4151 m (Pequegnat and Pequegnat, 1970, 1971; Macpherson and Segonzac, 2005), in having the carapace with numerous striae, one well-developed eye-spine, small cornea, P2 exceeding P1 and posteromedian lobe of segment 6 of pleon not exceeding lateral lobes. The new species may be differentiated from *M. geyeri* by the following:

— The gastric region has some small spines in addition to epigastric spines in the new species, whereas these additional spines are absent in *M. geyeri*.
— The rostrum is strongly carinated in *M. geyeri*, this carina being smoother in the new species.

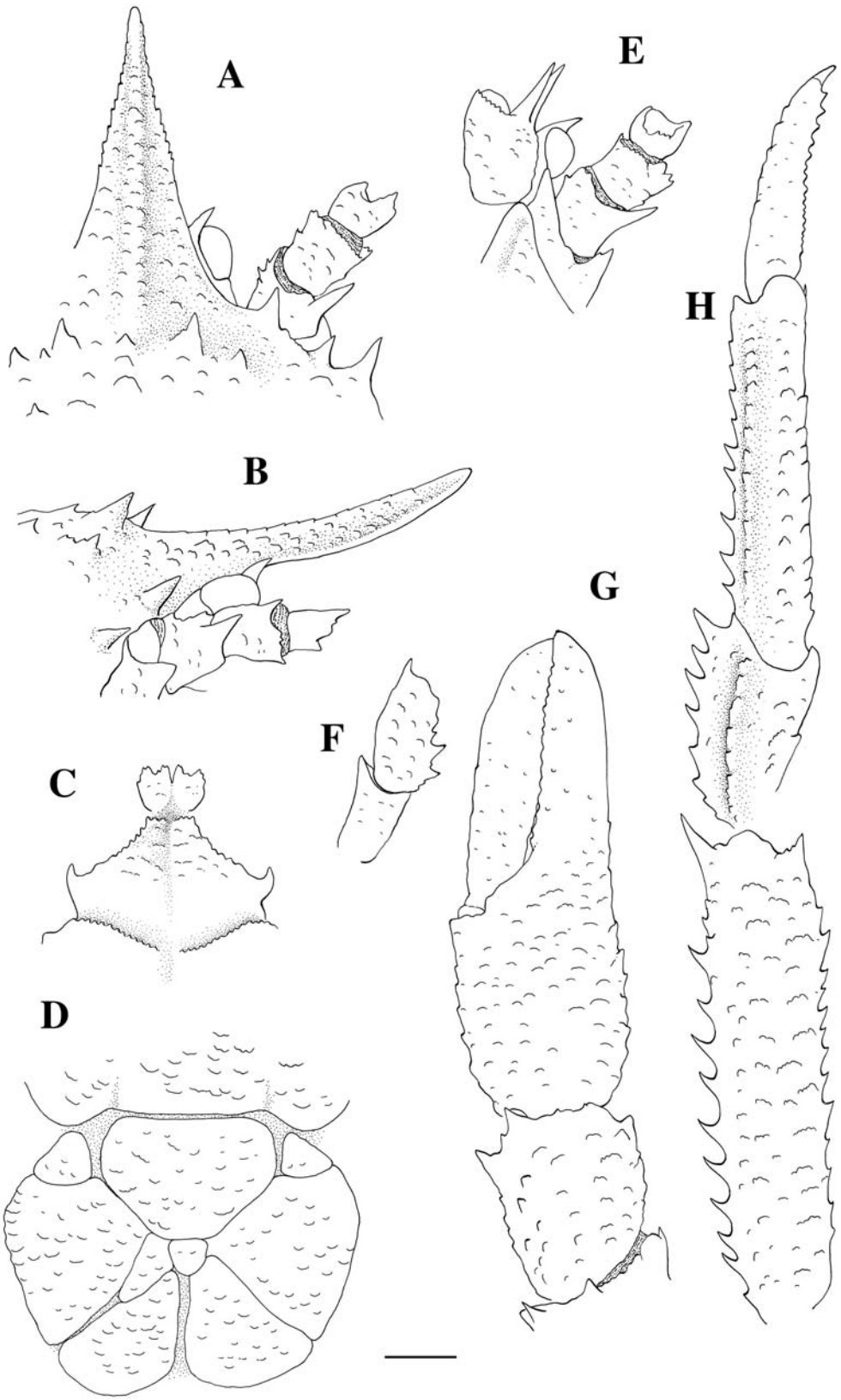

Fig. 7. *Munidopsis scotti* n. sp., holotype, ovigerous female (40.0 mm). A, anterior portion of carapace, dorsal. B, anterior portion of carapace, lateral. C, sternal plastron, sternites 3 and 4. D, posterior part of segment 6 of pleon and telson. E, left antennule and antenna, ventral. F, merus of right mxp 3, lateral. G, right P1, lateral. H, right P2, lateral. Scale = 5 mm.

— The anterior branchial margins are convex in the new species, instead of subparallel in *M. geyeri*.
— The eyespine is shorter than the cornea, measured along the lateral margin, in the new species, being as long as or longer than the cornea in *M. geyeri*.

The molecular data showed a clear nucleotide divergence with most species of the present work (Fig. 12), being smallest with *M. bracteosa* (2.6%). *Munidopsis scotti* and *M. bracteosa* can be easily distinguished by the segment 6 of the pleon having the posteromedian lobe exceeded by the lateral lobes in *M. scotti* and exceeding beyond the lateral lobes in *M. bracteosa*.

Distribution.—Northeast Pacific, on Juan de Fuca Ridge, at 2715 m.

Etymology.—This species is dedicated to Mr. Campbell "Buzz" Scott (MBARI/OceansWide), in recognition of his expertise with ROV *Tiburon* and slurp gun capture of the holotype specimen and other mobile hydrothermal vent animals.

Munidopsis segonzaci, new species
Figs. 8, 9

Material Examined.—Off California. Station M, centered at 34 50′N, 123 00′W, 4100 m, 30 October 2004, 1 M 38.4 mm, holotype, 1 M 33.0 mm (SIO C10832, C10975).

Description.—Carapace 1.2-1.3 times longer than broad, covered with granules and small tubercle-like processes, markedly on cardiac region, some short ridges on posterior half. Cervical groove moderately distinct, regions well defined, gastric and cardiac more convex than branchial regions. Gastric region with 2 epigastric spines and a few scattered small mesogastric spines. Cardiac region triangular, preceded by deep transverse groove. Rostrum spiniform, strongly upturned, dorsally not carinate, ventrally flattish, not reaching end of P1 merus. Frontal margin oblique, antennal spine absent. Lateral margins slightly convex, with 3 spines on each side: first at anterolateral angle, second and third spines smaller than first spine, situated behind end of anterior and posterior branch of cervical groove, respectively; third spine minute in the paratype. Posterior margin preceded by moderately elevated granulated ridge.

Pterygostomian flap with numerous granules, margin angular anteriorly.

Sternum as long as wide, maximum width at sternite 7; sternites 3 and 4 with granules, sternite 3 moderately broad, serrate and bilobed, separated by notch, about twice wider than long; sternite 4, with margins granulated, about 3 times wider than sternite 3.

Pleon spineless; segment 6 posteriorly bearing lateral lobes slightly exceeding nearly straight posteromedian margin. Telson composed of 10 plates.

Ocular peduncles fixed, relatively long, distally narrowed, bearing acute and curved mesial eye-spine extending beyond semicircular cornea; mesial margin strongly concave.

Basal segment of antennule with distolateral spine; distodorsal spine absent; mesiodistal margin granular.

Antennal peduncle clearly overreaching tip of eye-spine. Segment 1 with distomesial process not reaching distal margin of segment 2, distolateral margin produced. Segment 2 with blunt distolateral angle, distomesial angle granular. Segment 3 with small distomesial spine. Segment 4 unarmed.

Third maxillipeds (Mxp 3) with ischium granular and as long as merus measured on extensor margin, flexor margin ridged, terminating in small blunt spine; 20-22 denticles along crista dentata. Merus with numerous granules on lateral surface, flexor margin with 5-6 small spines, extensor margin with distal spine.

Chelipeds (P1) subequal, tuberculous on surface and thickly covered with short setae, 1.6 times longer than carapace. Merus twice carpal length, with small distomesial, distodorsal and distolateral spines, longitudinal row of small dorsal spines; carpus about 1.5 times longer than high, with small distomesial spines and some distal and dorsal spines; palm slightly longer than carpus, and about 1.5 times longer than high; fingers 1.6 times longer than palm, movable finger shorter than fixed finger, both fingers with smooth surface.

Walking legs (P2-P4) subcylindrical and slender, with scattered granules and setae, decreasing in size posteriorly; P2 longest, overreaching end of P1. P2 about twice carapace length with merus 5.5-6 times longer than broad, 2.5 times length of carpus and 1.2-1.4 times length of propodus, dorsal margin with row of small spines, increasing in size distally, ventral margin granulate; carpus with row of acute granules along extensor margin, lateral crest with small granules; propodus 5.5 times as long as high, and as long as or slightly longer than dactylus, unarmed, only minute distal movable spinule. Dactylus gently curving; mesial and lateral margins carinate, fringed with stiff setae; flexor margin with small denticles, bearing spine-like setae. Length of P4 merus 0.8 times that of P2.

Epipods on P1.

Remarks.—The new species belongs to the group of species with the carapace and pleon smooth, with few gastric spines, rostrum spiniform, P2 overreaching P1, strong eyespine on mesial end of eyestalk, cornea relatively small and fixed finger of P1 without denticulate carina on distolateral margin. The new species is closely related to *M. antonii* from the Atlantic Ocean, Indian and Pacific Oceans (see above).

Munidopsis antonii was described by Filhol (1884) using specimens collected in the Atlantic Ocean (NE of the Azores Islands in 4010 m). Subsequently, Benedict (1902), using 3 specimens from NE Pacific (Bering Sea), described a closely related species: *M. beringana*. Benedict (1902) indicated that both species could be differentiated by the curvature of the rostrum, more straight in *M. antonii* than in *M. beringana*, and the armature of the gastric region, with more spines in *M. beringana* than in *M. antonii*. However, Baba (2005) comparing syntypes of both species, demonstrated that these two characters are variable and *M. beringana* may be considered as a junior synonym of *M. antonii*.

Munidopsis segonzaci may be differentiated from *M. antonii* by the length of the rostrum, not exceeding the end

Fig. 8. *Munidopsis segonzaci* n. sp., holotype, male (38.4 mm). Dorsal view.

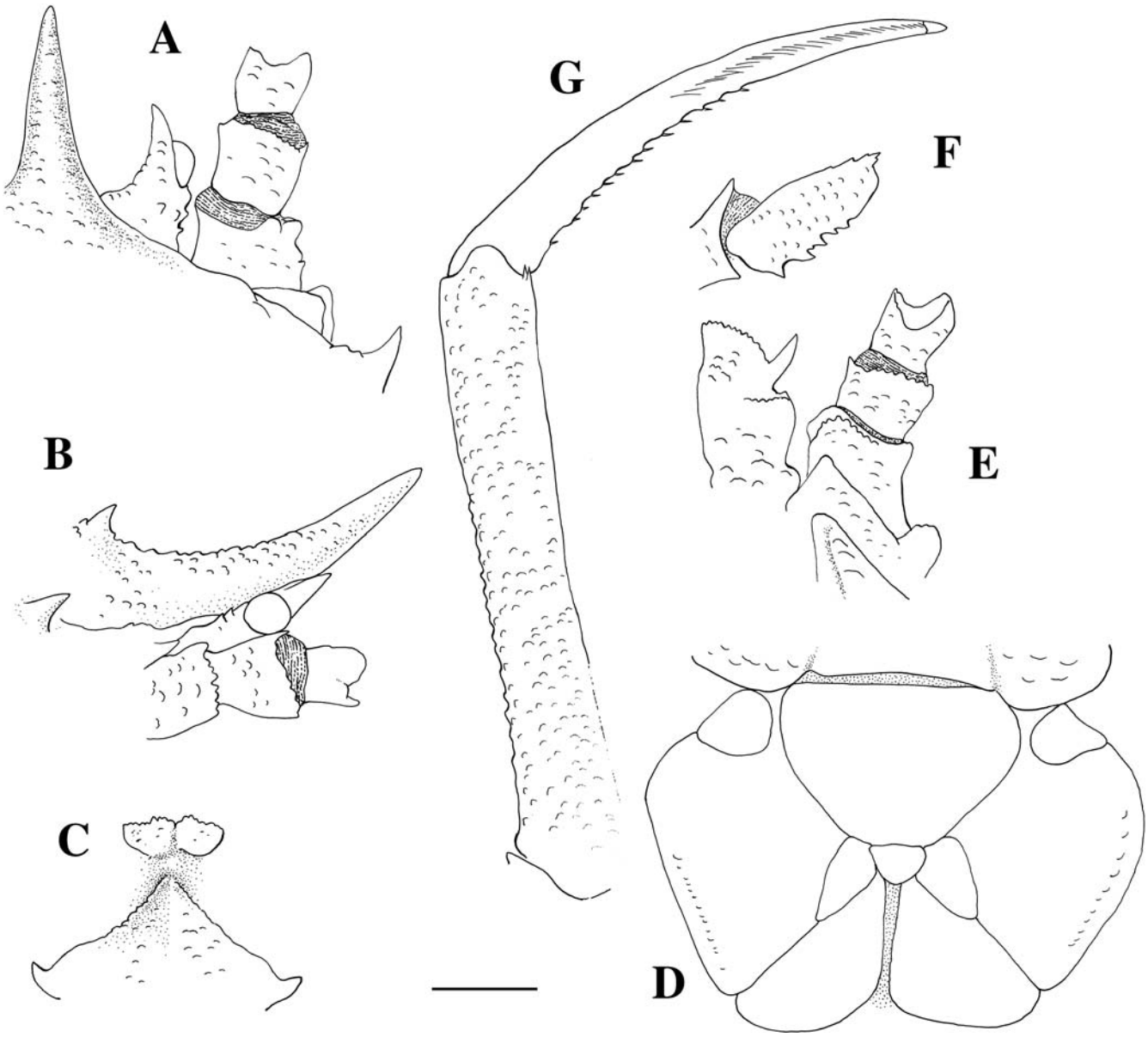

Fig. 9. *Munidopsis segonzaci* n. sp., holotype, male (38.4 mm). A, anterior portion of carapace, dorsal. B, anterior portion of carapace, lateral. C, sternal plastron, sternites 3 and 4. D, posterior part of segment 6 of pleon and telson. E, left antennule and antenna, ventral. F, merus of right mxp 3, lateral. G, propodus and dactylus of right P2, lateral. Scale = 5 mm.

of P1 merus in the new species, and always exceeding (or at least reaching end of) P1 merus in *M. antonii*. Furthermore, the mesial border of the eye-spine is strongly concave in *M. segonzaci*, but straight or slightly concave in *M. antonii* (see Baba, 2005 for the illustrations of the type specimens of *M. antonii*). The syntypes of *M. antonii* and *M. beringana* figured by Baba (2005), as well as all specimens of *M. antonii* examined in the present (see above) and previous papers (Macpherson and Segonzac, 2005) have the mesial margin of the eye-spine straight or slightly concave, therefore clearly different to that of *M. segonzaci*. The curvature and length of the rostrum, however, can be considered as a variable character (Baba, 2005). Nevertheless, comparing numerous specimens of *M. antonii* of similar sizes than *M. segonzaci* we observed that all specimens of *M. antonii* have a longer rostrum than in *M. segonzaci*, reaching the end of or exceeding P1 merus, and confirming the validity of this character to distinguish *M. segonzaci* from *M. antonii*.

The genetic data indicates that *M. segonzaci* has a considerable nucleotide divergence (3.7%) with its closest morphologically relative (*M. antonii*). Unfortunately, we have only two specimens of *M. segonzaci* to confirm the validity of the morphological differences with *M. antonii*. However, the large genetic divergence between both species supports the existence of two sibling species in the area. These results indicate that, in this group of species, small morphological distinctions can differentiate species although

further genetic studies, including specimens of *M. antonii* from different localities, are strongly recommended.

Distribution.—East Pacific, off California, at 4100 m.

Etymology.—This species is dedicated to Dr. Michel Segonzac (IFREMER, retired) for his important contributions to the knowledge of the deep-sea fauna.

Munidopsis tiburon, new species
Fig. 10

Munidopsis sp.—Ambler, 1980: 18, fig. 3.

Material Examined.—Monterey Bay Canyon. 36°38.02′N, 122°23.60′W, 2197 m, 8 August 2003: 1 M 13.7 mm, holotype (USNM 1100640).

Vance Seamount B. Tiburon dive T1012. 45°38.06′N, 130°39.88′W, 2024 m, 3 August 2006: 1 F 9.2 mm.

Vance Seamount C. Tiburon dive T1013. 45°27.02′N, 130°30.42′W, 2029 m, 4 August 2006: 1 F 17.5 mm (SIO C10972).

Monterey Bay Canyon. Tiburon dive T611. 36°38.02′N, 122°23.60′W, 2202 m, 8 August 2003; 1 M 13.1 mm.

Description.—Carapace longer than broad, dorsal surface with numerous minute granules and short setae; some short striae on posterior half of carapace. Cervical groove distinct; transverse depression in anterior part of cardiac region. Gastric region moderately inflated, with pair of well-developed epigastric spines, and 2 protogastric spines, smaller than previous ones. Cardiac region with pair of spines on anterior portion, 1-2 median spines behind this pair. Posterior margin with median spine. Rostrum moderately short, spiniform, upcurved, terminating at end of P1 merus, length 0.3 times remaining carapace, maximum width less than 0.2 carapace breadth; lateral margin unarmed, weakly ridged, dorsal surface not carinate. Frontal margin slightly oblique, without antennal spine. Lateral margin having anterolateral spine (first) long; 2 well-developed spines, smaller than first spine, behind anterior cervical groove, followed by 1-2 short spines directly behind posterior cervical groove. Small notch at each end of anterior and posterior branches of cervical groove.

Sternum as long as wide, maximum width at sternite 7; sternite 3 moderately narrow, serrate and bilobed, separated by notch, 3 times wider than long; sternite 4 narrow at base of sternite 3, about 2.5 times wider than sternite 3.

Pleon smooth, with numerous setae; 2 moderately elevated transverse ridges on segments 2 and 3; posterior ridge absent on segment 4. Segment 6 with posteromedian lobe not exceeding lateral lobes. Telson composed of 8 plates, having numerous granules; two posterior plates combined more than twice as long as wide.

Ocular peduncles slightly movable, cornea large ovate, distinctly broader than mesial eye-spine, greatest width as long as width of antennal segment 3, broad-based eyestalk mesiodorsally produced into eye-spine, laterally directed, shorter than or as long as cornea measured along lateral margin, mesioventrally unarmed.

Basal segment of antennule bearing distolateral spine clearly longer than distodorsal spine; distomesial margin granular.

Basal segment of antennal peduncle having distomesial and distolateral spines; segment 2 with well-developed distolateral spine.

Third maxilliped (Mxp 3) ischium with flexor margin sharply ridged, distally ending in small spine, extensor margin with small distal spine; 20-21 denticles on crista dentata. Merus having lateral face with minute granules, flexor margin bearing 3 small spines and a few small teeth; extensor margin ending in distinct spine.

Chelipeds (P1) 1.5 times longer than carapace, with scattered setae. Merus twice carpus length, with long distomesial, distodorsal and distolateral spines, longitudinal row of dorsal and lateral spines; carpus slightly longer than high, with well-developed distomesial spines and some distal and dorsal spines; palm slightly longer than carpus, and about 1.5 times longer than high; fingers slightly longer than palm, distally spooned, with crenulate ridges.

Walking legs (P2-P4) moderately long and slender, with scattered setae, somewhat compressed laterally, decreasing in size posteriorly; P2 longest, overreaching end of P1. P2 about twice carapace length, with merus about 0.7 times carapace length, about 4.5 times longer than broad, 2.5 times carpal length and slightly longer than propodus, dorsal margin with row of spines increasing in size distally, ventral margin with row of spines, and some small ventrolateral spines; carpus with row of spines along extensor margin, distal longest, lateral crest with small granules; propodus 7 times as long as high, and 1.5-2.0 times longer than dactylus, unarmed, only minute distal movable spinule. Dactylus with terminal claw short, slightly curved; ventral margin nearly straight, with 10-12 teeth decreasing in size proximally, each with thick seta, ultimate tooth closer to penultimate tooth than end of segment. Length of P4 merus about 0.8 times that of P2.

Epipods absent on pereiopods.

Remarks.—The present specimens are similar to the male described by Ambler (1980) as *Munidopsis* sp. from off Oregon at 1829 m. The new species is closely related to *M. bairdii* (Smith, 1884) and *Munidopsis arietina* Alcock and Anderson, 1894, from the Atlantic Ocean and the Bay of Bengal, respectively (Baba, 2005; Macpherson and Segonzac, 2005), in having the carapace with longitudinal row of submedian spines, one well-developed mesial eye-spine, cornea large, and P2 exceeding P1. The new species may be differentiated from these two species by the absence of lateral spines on the rostrum. The new species is also distinguished from *M. bairdii* by the eye-spine directed straight forward in *M. bairdii* whereas it is directed anterolaterally in *M. tiburon*. Furthermore, *M. bairdii* has 3 pairs of gastric spines (epigastric, protogastric and mesogastric pairs), whereas the mesogastric pair is always absent in *M. tiburon*.

Munidopsis arietina can also be differentiated from the new species by the following characters:

— The size of the eye-spine is clearly longer than the cornea in *M. arietina*, being shorter in the new species.

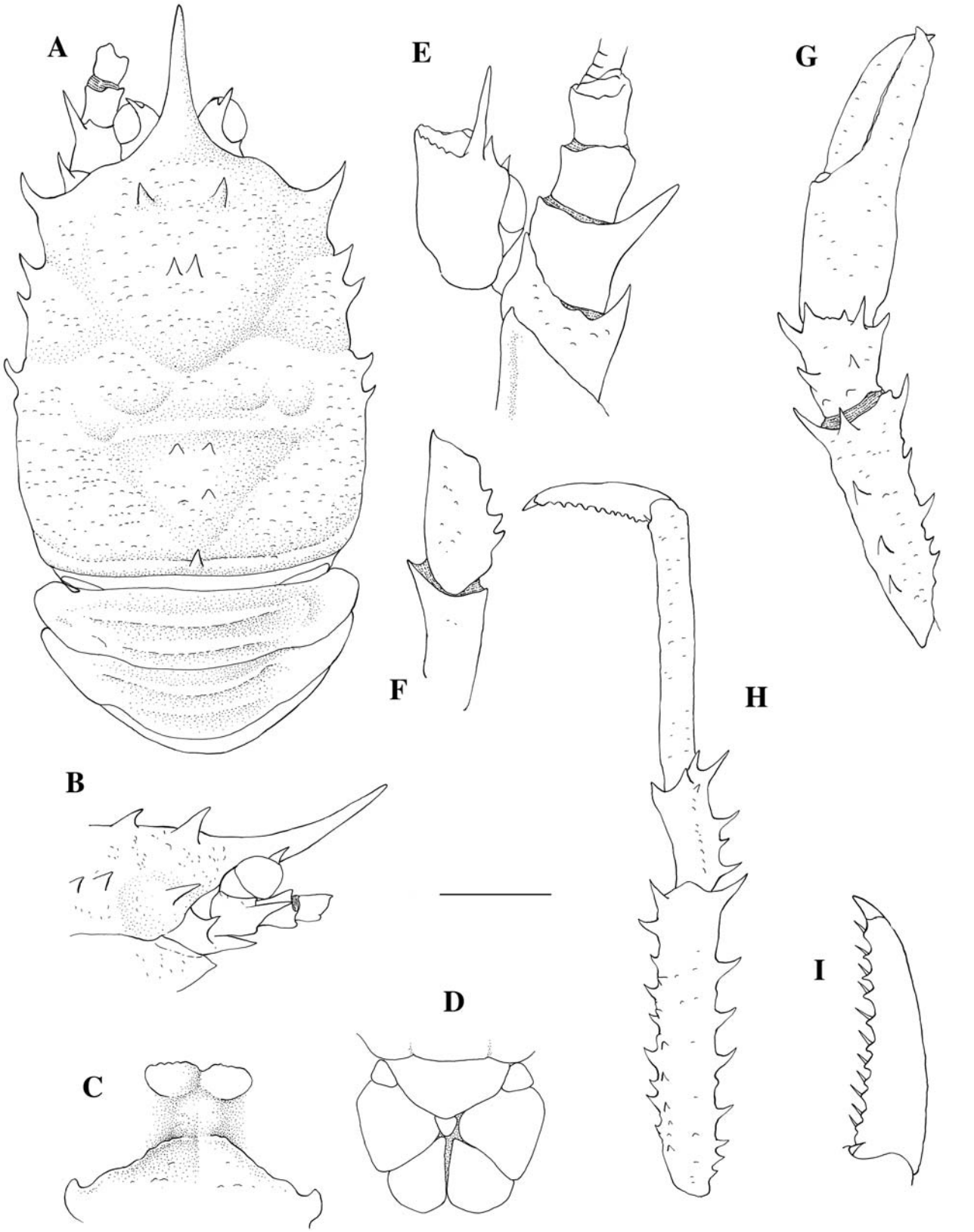

Fig. 10. *Munidopsis tiburon* n. sp., holotype, male (13.7 mm). A, carapace, dorsal view. B, anterior portion of carapace, lateral. C, sternal plastron, sternites 3 and 4. D, posterior part of segment 6 of pleon and telson. E, left antennule and antenna, ventral. F, merus of right mxp 3, lateral. G, right P1, lateral. H, left P2, lateral. I, dactylus of left P2, lateral. Scale: A, B, D, G, H = 5 mm; C, E, F, I = 2 mm.

Additionally, the cornea is clearly smaller in *M. arietina* than in *M. tiburon*.

— The first anterolateral spine is smaller than the second lateral spine in *M. arietina*, whereas it is longer in the new species.

— The flexor margins of P2-P4 dactyli are more curved in *M. arietina* than in the new species.

The molecular divergence of *M. tiburon* with other species of the present work ranged between 9.7 to 14.7%.

Distribution.—Off Oregon, at 1829 m (Ambler, 1980). The present specimens were collected in 2197 m in the Monterey Bay Canyon and 2024-2029 m from Vance B and Vance C seamounts, respectively.

Etymology.—The species is named after the ROV *Tiburon* (MBARI) that has been instrumental in collecting *Munidopsis* in Monterey Bay, the Juan de Fuca region, and the Gulf of California. The name is considered as a substantive in apposition.

Munidopsis verrucosus Khodkina, 1973
Fig. 5C, D

Munidopsis verrucosus.—Khodkina, 1973: 1156, figs. 1, 2-1; 1975: 269.—Ambler, 1980: 27.—Wicksten, 1989: 316 (list).—Baba, 2005: 298.

Material Examined.—Off California. Station M, centered at 34 50′N, 123 00′W, 4100 m, 25 February 2005: 1 ov. F 26.0 mm (SIO C10881).

Remarks.—This species is closely related to *M. kensmithi* (see above). The molecular data shows a nucleotide divergence of 7.6% between these two species. The interspecific divergence ranged between 5.5% (with *M. antonii*) and 16.2% (with *M. albatrossae*).

Distribution.—Previously known from off Chile, at 4300-4880 m (type locality), off Aleutian Islands, 2150 m and off Oregon (Tufts Plain and Gorda Ridge off California, at 3932-4194 m).

Munidopsis vrijenhoeki, new species
Fig. 11

Material Examined.—Fiji Basin "White Lady", 16°59.48′S, 173°54.89′E, 1990 m, 28 May 2005: 1 M 5.9 mm, holotype (USNM 1100641), collected from small piece of wood using suction sampler. Small leg fragments from two other individuals from this same locality were collected but not suitable for morphological analysis.

Description.—Carapace slightly longer than broad, moderately arched from side to side, slightly so from anterior to posterior end with scattered small granules and short striae, less dense on anterior half, and short setae on each stria and granule; cervical groove distinct. Pair of small epigastric spines. Rostrum triangular, wide, dorsally carinate, laterally sharply ridged, nearly horizontal; half carapace length, maximum width 0.33 carapace breadth. Frontal margin oblique, bearing well-developed antennal spine. Lateral margins subparallel, not carinate, anterolateral spine as long as antennal spine, second spine small and situated directly behind end of anterior cervical groove, as long as first, followed by serrate margin on anterior branchial region, blunt process at midlength behind notch of posterior branch of cervical groove.

Sternal plastron as long as wide, maximum width at level of sternite 7. Sternites smooth; sternite 3 medially notched, 0.5 times as wide as long, 0.3 width of sternite 4, anterior margin granular; sternite 4 subtriangular, anteriorly narrow, elongate.

Pleon unarmed, rather smooth, setose. Segments 2 and 3 each with 2 transverse ridges, anterior ridge sharply crested, posterior ridge preceded by groove. Segment 6 with posteromedian lobe nearly straight transverse, lateral lobes weakly produced. Telson composed of 8 plates, length-breadth ratio 0.5.

Ocular peduncles not movable; cornea small, greatest width clearly less than width of antennal segment 3 at midlength, cupped within broad-based eyestalk mesiodorsally produced into elongate spine, laterally with minute spine. Spine between eye and antennal peduncle absent.

Basal segment of antennule with nearly subequal distolateral and dorsolateral spines; distomesial margin crenulate.

Antennal peduncle having segment 1 with anteriorly produced strong distomesial spine nearly reaching midlength of segment 2, distolateral strong spine smaller than distomesial. Segment 2 with well-developed distolateral spine, distomesial angle acute Segment 3 with distomesial and distolateral angles acute.

Third maxillipeds (Mxp 3) relatively slender. Ischium as long as merus, 18-19 corneous denticles on crista dentata. Merus with 5 well-developed spines of irregular sizes on flexor margin, extensor distal margin with acute spine.

Chelipeds (P1) short, granular, slightly longer than postorbital carapace length, covered with numerous setae. Merus each ending at midlength of rostrum, with 3 well-developed distal spines (mesial, dorsal and lateral), dorsally with spines in longitudinal row. Carpus as long as broad, terminally bearing several spines on dorsal side, 2 spines on mesial margin, ventral surface smooth. Palm as long as broad; fingers slightly longer than palm, spooned at tips, fixed finger with denticulate carina on distolateral margin.

Walking legs (P2-4) relatively long, somewhat compressed, sparingly with long coarse setae, decreasing in length posteriorly. Meri each having dorsal crest with row of spines, ventral margin with row of spines, smaller than dorsal spines, some spines on lateral side. Each carpus with 4-5 spines on extensor margin, lateral ridge with granules. Each propodus with several small spines on proximal half of extensor margin, flexor border granular with 2 small distal spinules. Each dactylus 0.8 times length of propodus, terminal claw short, curved, flexor margin nearly straight, bearing 8-9 low, proximally diminishing teeth, each tooth with seta. P2 overreaching tip of P1 by half length of dactylus; less than 1.5 times carapace length, merus 2.3 times longer than high and 1.7 times carpus length, propodus 3.3 times longer than high.

Epipods absent from pereiopods.

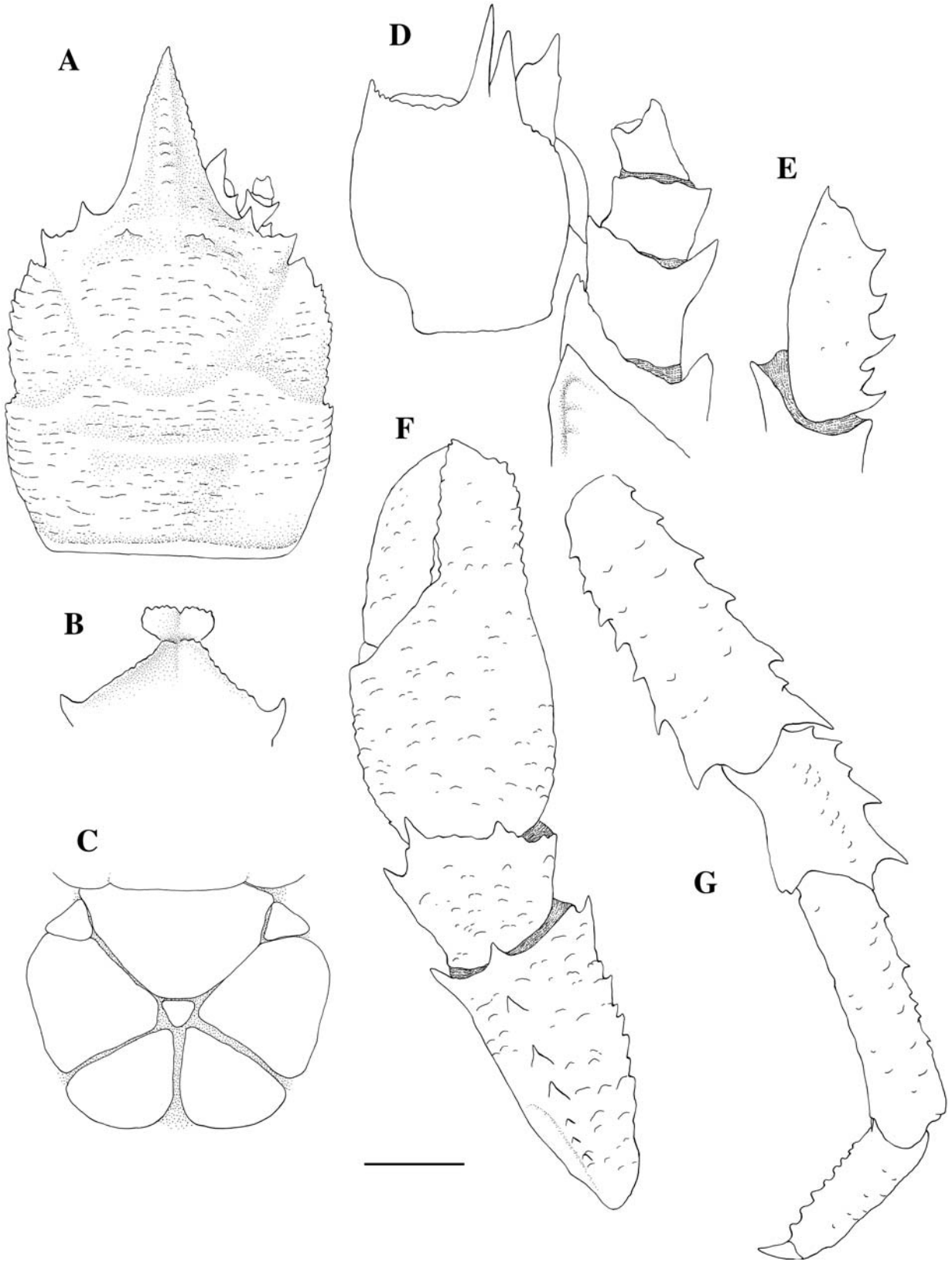

Fig. 11. *Munidopsis vrijenhoeki* n. sp., holotype, male (5.9 mm). A, carapace, dorsal view. B, sternal plastron, sternites 3 and 4. C, posterior part of segment 6 of pleon and telson. D, anterior portion of carapace, ventral, and left antennule and antenna, ventral. E, merus of right mxp 3, lateral. F, right P1, lateral. G, right P2, lateral. Scale: A = 3 mm; B, C, F, G = 1.5 mm; D, E = 0.8 mm.

Remarks.—The new species belongs to the group of species with the carapace and pleon smooth, lateral margins not carinate, rostrum triangular, P2 overreaching P1, pair of epigastric spines or processes, main eye-spine on mesial end of eyestalk, cornea relatively small and fixed finger of P1 with denticulate carina on distolateral margin. The closest species is *M. teretis* Baba, 2005 from off Durban and Tasman Sea, at 3520-3930 m (Baba, 2005) and Taiwan, at 3564-3579 m (Osawa et al., 2006). However, *M. teretis* has a blunt process mesial to the midlength of each posterior half of the carapace margin. These processes are absent in the new species.

The molecular data showed a high nucleotide divergence with other species of the present work, ranging between 9.5% (with *M. hirsuta*) and 19.6% (*M. aries*).

Distribution.—"White Lady" locality, in Fiji basin, at 1990 m.

Etymology.—The new species is dedicated to our colleague Dr. Robert Vrijenhoek (MBARI), for his support and leadership of the hydrothermal vent program.

Genetic Data

Of the 531 base pairs (bp) of mitochondrial DNA sequenced obtained using the newly designed internal primers, 180 bp were variable (59 singletons) and 121 bp were parsimony informative. The alignment of nucleotide sequences did not reveal any gaps or stop codons among the examined taxa indicating DNA sequences obtained were not a result of nuclear pseudogenes. Similarly, no heterozygous positions were observed in the sequence traces (data not shown).

The intraspecific divergences were generally very low (0-0.6%). Interspecific divergences were generally high (mean uncorrected $P = 9.22\%$, SD = 3.30%) similar to other studies on crustacean *mtCOI* (Machordom and Macpherson 2004). Within the *M. recta*/*M. bracteosa*/*M. exuta*/*M. scotti* group, sequence divergence was relatively low ($\sim$ 2%).

Phylogenetic analysis of *mtCOI* revealed several discrete clades from the East Pacific (Fig. 12). One clade includes *M. recta*, *M. bracteosa* n. sp., *M. scotti* n. sp., and *M. exuta*. A total of 22 *Munidopsis recta* individuals were analyzed from the hydrothermal vent environments of the EPR ranging from 21°N to 38°S, spanning the entire length of the EPR (7000 km). Eight haploytpes were observed in *M. recta* with very low levels of intraspecific *mtCOI* variation ($P =$ 0.62%). A total of 11 *Munidopsis bracteosa* n. sp. were analyzed from the hydrothermal vent environment of the Juan de Fuca (Main Endeavour Field), Mendocino Fracture Zone, and a 2891 m whalefall in Monterey Bay canyon. Six haplotypes were observed in *M. bracteosa* with extremely low levels of intraspecific *mtCOI* variation ($P = 0.17\%$). The most common haplotype (DQ677685) was observed in all three individuals from the Mendocino Fracture Zone and two of three *M. bracteosa* from the 2891 m Monterey Bay whalefall (Table 1). The Mendocino Fracture Zone and the 2891 m Monterey Bay whalefall are approximately 550 km away from each other. Comparison of *M. recta* and *M. bracteosa* revealed a significant genetic difference (uncorrected $P = 1.6\%$) with no sharing of *mtCOI* haplotypes between the two species. *Munidopsis recta* and *M. bracteosa* belong to an unresolved clade containing two other hydrothermal vent species of *Munidopsis* (*M. scotti* and *M. exuta*). Bayesian phylogenetic analysis failed to resolve the interrelationships among these four species. Additional DNA sequence data is required to resolve the phylogenetic relationships among the *M. recta*/*M. bracteosa*/*M. exuta*/*M. scotti* clade.

The interspecific divergences showed a wide range among the different taxa. *Munidopsis antonii* and its close relative, *M. segonzaci*, were clearly separated, with a divergence of 3.7%. A similar trend is observed between *M. verrucosus* and *M. kensmithii*. However, in the species group of *M. bracteosa*, *M. recta*, *M. scotti*, and *M. exuta*, with clear morphological differences among them, the interspecific divergences showed a wide range among the different sister taxa. (with a minimum of 1.6% between *M. bracteosa-M. exuta* and *M. bracteosa-M. recta*, and a maximum of 3.1% between *M. recta* and *M. scotti*).

Discussion

A combined morphological and molecular analyses revealed that the most common species on the EPR is *Munidopsis recta*. This species is differentiated from *M. subsquamosa* by the P2-4 dactyli that are straight on the flexor margin (strongly curved in *M. subsquamosa*), the ocular peduncles that have the cornea relatively large and distinctly broader than the eye-spine (relatively small and about as broad as the cornea in *M. subsquamosa*) (Baba, 2005). Unfortunately, we have not analyzed the specimens identified as *M. subsquamosa* and collected in the EPR by Ambler (1980) and Van Dover et al. (1985). Although these occurrences are likely *M. recta* (see Baba, 2005), confirmation of their identities requires further study.

The results obtained in the present study demonstrate the high diversity of the genus *Munidopsis* in the East Pacific and EPR and that some species can be only identified by subtle morphological characters, which are corroborated by molecular data. The sequence divergences between some species pairs (*M. verrucosus-M. kensmithii*, *M. antonii-M. segonzaci*, *M. aries-M. albatrossae*) confirmed the specific value of some morphological characters (e.g., rostrum shape, armature of the lateral margins of the carapace). These results suggested the existence of some sibling species in the genus *Munidopsis*, confirming the utility and importance of molecular data in the identification of species, in agreement with other studies carried out in decapod crustaceans (Macpherson and Machordom, 2001; Machordom and Macpherson, 2004).

The low level of genetic divergence observed among morphologically differentiated species, e.g., *M. bracteosa*, *M. recta*, *M. scotti*, *M. exuta*, could suggest a recent and/or rapid diversification. However, other species pairs, e.g., *M. antonii-M. segonzaci*, *M. verrucosus-M. kensmithi*, with few morphological differences, showed larger genetic divergences. The smallest nucleotide divergences for *mtCOI* observed in the *Munidopsis* from the EPR (1.6-1.9%) are smaller than those observed in other squat lobsters, i.e., minimum of 3.5% in species of the genus *Munida* (Machordom and Macpherson, 2004). However, they are similar or higher than those observed in anomurans of the

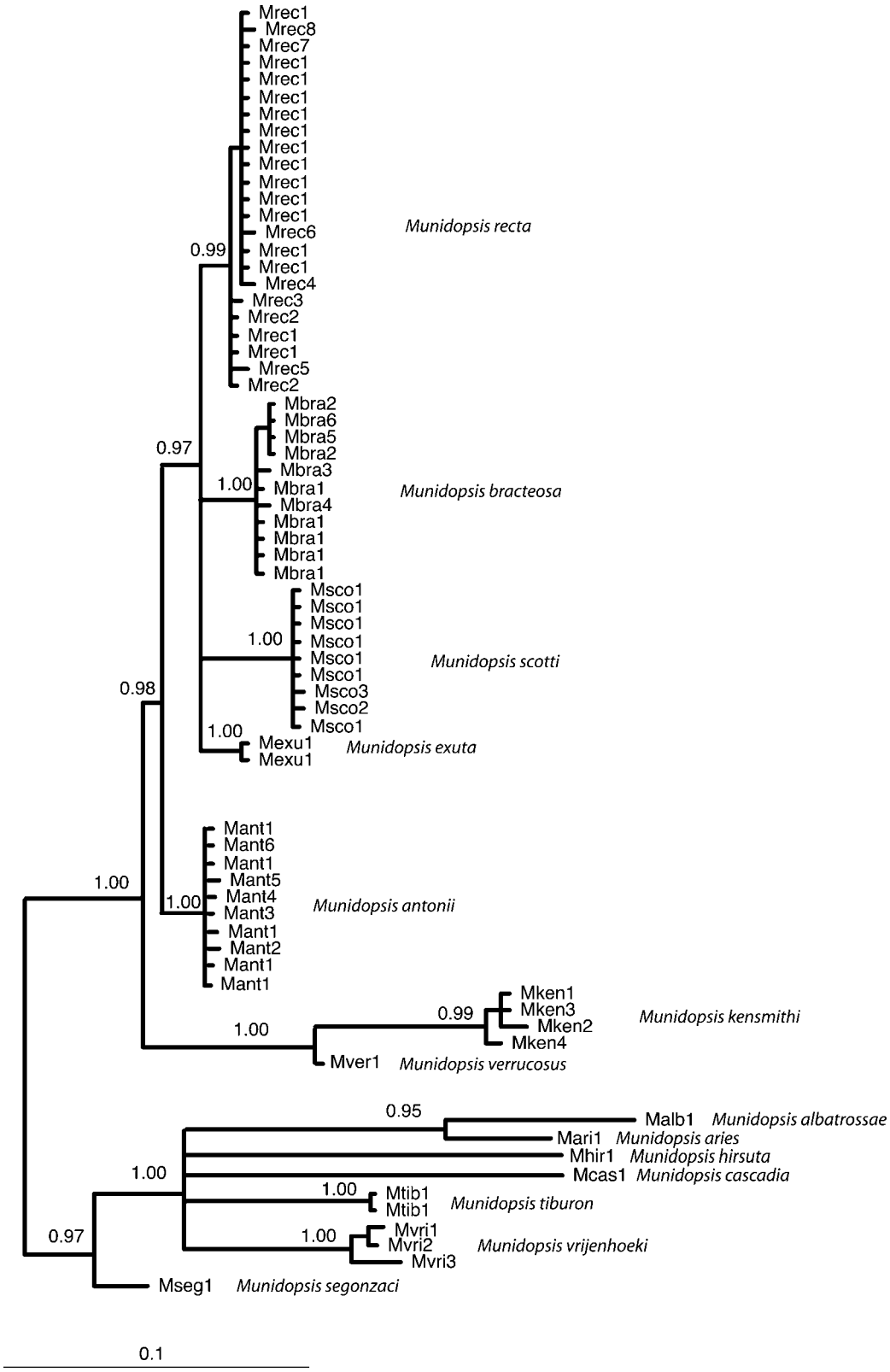

Fig. 12. Bayesian trees of the *Munidopsis mtCOI* dataset. Scale bar indicates percent sequence divergence. Only Bayesian posterior probabilities (BPP) greater than 0.95 are shown as resolved nodes. Phylogeny is midpoint rooted.

family Aeglidae (Perez-Losada et al., 2004; Lefebure et al., 2006). On the other hand, some species (e.g., *M. antonii*) showed a smaller genetic divergence with clearly morphologically differentiated species (e.g., *M. exuta*, *M. recta*) than with the morphologically closest species (*M. segonzaci*). Our results in this paper support the findings that there is no correlation between morphological and genetic divergences (Hendry et al., 2000).

Of particular interest is the placement of two *Munidopsis* individuals collected from the Logochev locality on the Mid-Atlantic Rise (MAR). Unfortunately, only small pieces of leg muscle tissue were available with no whole individuals for morphological examination. Therefore, we tentatively consider these two individuals (A3133-1 and A3133-2, Table 1) to be *M. exuta* (Macpherson and Segonzac, 2005). It is interesting to note the close phylogenetic relationship between MAR, EPR, and Juan de Fuca hydrothermal vent *Munidopsis* suggesting a relatively recent common ancestor. Additional work is required to determine the divergence time and branching pattern for *Munidopsis* species from multiple ocean basins.

It is also interesting to note the diversity of habitat type utilized by various species. For example, *M. bracteosa* were collected from natural woodfalls (Mendocino Fracture Zone), natural whalefalls (2891 m, Monterey Bay), and hydrothermal vent environments (Main Endeavour Field). As noted by Macpherson and Segonzac (2005), the abundance of certain *Munidopsis* species in vent and seep environments probably reflects the benefit derived from the organic matter produced by the chemosynthetic community inhabiting these zones (Van Dover, 1995). The ability of certain *Munidopsis* species to colonize a variety of habitats could explain the lack of genetic differentiation over a large geographic range (*M. recta* on the ~ 7,000 km EPR), in agreement with the findings of Herring and Dixon (1998) in bresiliid shrimps. These results, could be also related with the large eggs of *Munidopsis*, indicative of advanced development. In *Munidopsis polymorpha*, there are only 2 zoeal stages during which the larvae are unable to undergo locomotion (Wilkens et al., 1990). This abbreviated development is also observed in *M. serricornis* (Loven, 1852), with only three zoeal stages (Samuelsen, 1972). Deep-sea *Munidopsis* in the Eastern Pacific Ocean appear to have high population interconnectivity suggesting that these stages can float for extended periods in nutritionally poor water, as it has been suggested for Antarctic lithodid crabs (Thatje et al., 2005). Further analysis on the habitat evolution and interconnectivity of populations of *Munidopsis* will be summarized in a follow-up paper (Jones et al., unpublished data).

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