

PHYLOGENETIC RELATIONSHIPS OF SPECIES OF *RAYMUNIDA*
(DECAPODA: GALATHEIDAE) BASED ON MORPHOLOGY AND
MITOCHONDRIAL CYTOCHROME OXIDASE SEQUENCES, WITH THE
RECOGNITION OF FOUR NEW SPECIES

E. Macpherson and A. Machordom

(EM) Centro de Estudios Avanzados de Blanes (CSIC), Camí de Santa Bàrbara s/n, 17300 Blanes, Girona, Spain (e-mail: macpherson@ceab.csic.es); (AM) Museo Nacional de Ciencias Naturales (CSIC), José Gutiérrez Abascal 2, 28006 Madrid, Spain (e-mail: mcna133@mncn.csic.es)

A B S T R A C T

The species of the genus *Raymunida* from the Pacific and Indian oceans are revised using morphological characters and the mitochondrial cytochrome oxidase subunit I sequences. Four new species are described (*R. confundens*, *R. dextralis*, *R. erythrina*, and *R. insulata*), and the status of *R. bellior* and *R. elegantissima* are revised. The species of *Raymunida* can be identified by subtle morphological characters, which match differences in mitochondrial nucleotide sequences. Therefore, the sequence divergences confirm the specific and phylogenetic value of some morphological characters (e.g., length of the mesial spine on the basal antennal segment, length of the walking legs). Furthermore, they confirm the importance of the color pattern as a diagnostic character. The widespread species (*R. elegantissima*), known from the Philippines to Fiji, shows minimal divergence between specimens from different localities (maximum of 3 nucleotide differences or 0.2% mean divergence). The phylogenetic reconstruction agreed with the monophyletic condition of *Raymunida* and its differentiation with respect to the genus *Munida* (in which *Raymunida* species had previously been included) and *Agononida*.

The genus *Raymunida* has recently been created to include those species of the genus *Munida* Leach, 1820, characterised by the presence of four spines on each branchial margin of the carapace; abdominal tergites unarmed; epipods on the first, second, and third pereopods; one spine on the frontal margin between supraocular and anterolateral spines; one distal spine on the flexor margin of the carpus of the third maxilliped; the merus of the second pereopod clearly more slender than those of the third and fourth pereopods; and the presence of several long marginal spines on the endopod of the uropods (Macpherson and Machordom, 2000). The genus currently contains three species recorded from numerous localities of the Pacific and Indian oceans: (1) *R. elegantissima* (De Man, 1902) from the eastern Indian Ocean, Malay Archipelago, Indonesia, Philippines, Japan, western and eastern Australia, New Caledonia, Bellona Island, Vanuatu and Futuna Island, between 20 and 440 m; (2) *R. bellior* (Miyake and Baba, 1967) from Japan, Philippines, Loyalty, Chesterfield, and Futuna Islands, between 80 and 330 m; and (3) *R. cagnetei* from the Marquesas

Islands, between 53 and 112 m (Baba, 1988; Macpherson, 1994, 1996, 1999; Macpherson and Machordom, 2000). Although several morphological differences among the three species exist, very few specimens (usually 1 or 2) of *R. elegantissima* and *R. bellior* are caught in each locality, which prevents the evaluation of intraspecific morphological variations and specific characters. Furthermore, the color pattern, which differentiates many species of galatheid decapods (Macpherson, 1994), is lost in preserved material. Therefore, the identification and occurrence of *R. elegantissima* and *R. bellior* in some localities are doubtful, and a revision of these specimens has been recommended (Macpherson, 1994, 1996, 1999). For these reasons, as in other groups with dubious species (Chan and Chu, 1996; Sarver *et al.*, 1998), we have used, in addition to morphology, molecular characters in order to provide supplementary support to the species identifications.

Molecular data are a complementary approach to morphology, especially in discriminating cryptic or sibling species (Knowlton, 1993; Sarver *et al.*, 1998) and constructing phylogenetic relationships (Avise, 1994). Mi-

Table 1. Species studied for mitochondrial DNA sequences, including sampling localities, expedition, station, and codes used in Figure 7 and Table 2.

Code	Species	Locality	Expedition	Station	GenBank A. No.
RCA1	<i>Raymunida cagnetei</i>	Marquesas Is.	Musorstom 9	1177	AF 283869
RCA2	<i>Raymunida cagnetei</i>	Marquesas Is.	Musorstom 9	1177	AF 283870
RCA3	<i>Raymunida cagnetei</i>	Marquesas Is.	Musorstom 9	1177	AF 283871
RCO1	<i>Raymunida confundens</i>	Chesterfield Is.	Musorstom 5	315	AF 283872
RCO2	<i>Raymunida confundens</i>	New Caledonia	Smib 8	178	AF 283873
RDE1	<i>Raymunida dextralis</i>	Loyalty Is.	Musorstom 6	419	AF 283874
REL1	<i>Raymunida elegantissima</i>	Bellona Is.	Corail 1	unnumbered	AF 283875
REL2	<i>Raymunida elegantissima</i>	Wallis Is.	Musorstom 7	498	AF 283876
REL3	<i>Raymunida elegantissima</i>	Philippines	Musorstom 1	57	AF 283877
REL4	<i>Raymunida elegantissima</i>	Vanuatu	Musorstom 8	966	AF 283878
REL5	<i>Raymunida elegantissima</i>	Vanuatu	Musorstom 8	966	AF 283879
REL6	<i>Raymunida elegantissima</i>	New Caledonia	Lagon Est	640	AF 283880
REL7	<i>Raymunida elegantissima</i>	Fiji	Musorstom 10	1363	AF 283881
RER1	<i>Raymunida erythrina</i>	Futuna Is.	Musorstom 7	515	AF 283882
RER2	<i>Raymunida erythrina</i>	Vanuatu	Musorstom 8	1077	AF 283883
RIN1	<i>Raymunida insulata</i>	Seychelles Is.	Cepros	unnumbered	AF 283884
MRH1	<i>Munida rhodonia</i>	New Caledonia	Halipro 1	854	AF 283885
MRH2	<i>Munida rhodonia</i>	New Caledonia	Halipro 1	854	AF 283886
MRU1	<i>Munida rubrodigitalis</i>	New Caledonia	Biocal	52	AF 283887
AIN1	<i>Agononida incerta</i>	New Caledonia	Bathus 3	824	AF 283888
AIN2	<i>Agononida incerta</i>	New Caledonia	Bathus 3	824	AF 283889

tochondrial DNA sequences have been used in many groups of decapods: Penaeidae (Palumbi and Benzie, 1991; Baldwin *et al.*, 1998), Nephropidae (Tam and Kornfield, 1998), Palinuridae (Sarver *et al.*, 1998), Hippidae (Tam *et al.*, 1996), Cancridae (Harrison and Crespi, 1999), Portunidae (Chu *et al.*, 1999), and they have provided information for taxonomic studies and phylogenetic reconstructions. The present study examines species of *Raymunida* from many localities of the Pacific and Indian oceans by comparing morphological characters and a partial sequence of the cytochrome oxidase gene in the mitochondrial genome. Our objectives are (1) to study the material classified as *R. bellior* and *R. elegantissima* in order to verify the possible existence of new species, corroborating the morphological distinctions with molecular data; (2) to assess which morphological characters have a specific phylogenetic value; and (3) to validate the status of the genus *Raymunida*, erected on the basis of morphological characters, by comparing molecular data of its species with those of *Munida* Leach, 1820, and *Agononida* Baba and de Saint Laurent, 1996.

MATERIALS AND METHODS

The collections of *Raymunida* specimens in the Muséum national d'Histoire naturelle de Paris (MNHN) and National Museum of Natural History, Washington, D.C., were examined. For morphological descriptions,

measurements given are of carapace length, excluding rostrum, and the terminology used mainly follows Macpherson (1994). Color notes are based on slides taken of living material. To avoid repetitious descriptions, a brief diagnosis is provided for each species, without mentioning the characters included in the generic description. *Raymunida cagnetei* is not included (see Macpherson and Machordom, 2000). Additional data on the geographic location of the stations are to be found in the following papers: "Albatross" Expedition (Baba, 1988), Musorstom Expeditions (Macpherson, 1994, 1996, 1999). The synonymies provided here are based on the original descriptions and on recent papers.

For molecular analysis, we used samples from several localities and species from the western Pacific (e.g., Musorstom Expeditions) and western Indian oceans (Cepros Expedition), preserved in 70% alcohol and deposited in the Muséum national d'Histoire naturelle, Paris. Specimens from the "Albatross" Expedition were not used as nucleotide sequences could not be obtained (probably they were originally preserved in Formalin); therefore, the unique specimen identified as *Raymunida bellior* was used only for the morphological study (see below). We also compared molecular data of the species of *Raymunida* with those of two species of *Munida* (*M. rhodonia* Macpherson, 1994, and *M. rubrodigitalis* Baba, 1994) and one species of *Agononida* (*A. incerta* (Henderson, 1888)). From each specimen, the fifth pereopod was taken. Collection locations and number of specimens of *Raymunida* analysed are shown in Table 1. The sequences have been deposited in GenBank (Table 1). *Platyriocheir formosa* (Chan *et al.*, 1995) (Family Grapsidae) (GenBank Accession Numbers AF105249 and AF105250) was used as outgroup.

Total DNA was extracted from tissues preserved in ethanol. We ground the samples to a powder in liquid nitrogen before adding 600 μ l of CTAB lysis buffer (2% CTAB, 1.4 M NaCl, 0.2% β mercaptoethanol, 20 mM EDTA, 0.1 M TRIS pH = 8) and digesting them with proteinase K (100 μ g/ml) at 60°C for 2–5 h. The rest of

the extraction followed the phenol/chloroform method (Sambrook *et al.*, 1989). The partial COI was amplified by polymerase chain reaction (PCR). The primers used were LCO1490 (Folmer *et al.*, 1994), and COI-H 5'TCAGGGTGACCAAAAAATCA3' (6 bases shorter than HCO2198 of Folmer *et al.*, 1994). The following cycles were used in the amplification: 92°C (5 min), 40 cycles of 94°C (30 s), 50°C (1 min), 72°C (1 min), and a final extension of 72°C (10 min). The PCR mix, for a final volume of 50 µl, was 1–3 µl DNA, 0.5 µM each primer, 0.2 mM of each dNTP, 2 mM MgCl₂, 1 U *Tth* DNA polymerase (Biotools), the corresponding buffer and ddH₂O. The products were visualised under UV light in 1.5% agarose gels stained with ethidium bromide, with a co-migrating 100 bp ladder molecular-weight marker to confirm the correct amplification. The amplified fragments (around 700 bp) were purified in "Biotools" columns for the sequencing of both strands (using the same primers as for the amplification). Sequence gels were run on an ABI 377 DNA sequencer (Applied Biosystems).

The sequences obtained were aligned and verified with the forward and reverse overlap sequences with the Sequencer program (Gene Code Corporation). The translation to proteins was also verified with this program and with MacClade (Maddison and Maddison, 1992), where we designated each position in the codons.

Nucleotide saturation was analysed by plotting transition/transversion rate against uncorrected p divergence values. The sequences analysed followed the principles of MP (maximum parsimony), NJ (neighbour joining), and ML (maximum likelihood). The best model of evolution that fit our data was obtained using the program Model Test 2.1 (Posada and Crandall, 1998). Thus, the GTR (General Time Reversible model, Lavane *et al.*, 1984, Rodríguez *et al.*, 1990) distance was used. The parsimony analyses were performed by heuristic search with TBR branch swapping and 10 replicates of random addition of taxa. The maximum likelihood approach was performed using Quartet Puzzling analysis (with 1,000 replications). The PAUP* (Swofford, 2000) package was used for these treatments. Transitions/transversions ratio was estimated using maximum likelihood approach. To determine whether a particular tree topology is a significantly worse explanation of the data than an alternative tree, we used both Wilcoxon signed-ranks (Templeton, 1983) and Kishino-Hasegawa (Kishino and Hasegawa, 1989) tests, as implemented in PAUP.

RESULTS

Systematics

Raymunida bellior

(Miyake and Baba, 1967)

Fig. 1A–D

Munida bellior Miyake and Baba, 1967, p. 216, figs. 3, 4.—Baba, 1988, p. 90.

not *Munida bellior*.—Macpherson, 1994, p. 450, fig. 66 (color) [in part = *Raymunida confundens*, new species; *R. dextralis*, new species; *R. elegantissima* (de Man, 1902)]; 1996, p. 390, fig. 12 (color) [in part = *R. elegantissima* (de Man, 1902); *R. erythrina*, new species].

Material Examined.—**Philippines**. Between Masbate and Leyte. "Albatross," stn. 5398, 209 m: 1 female, 9.5 mm.

Diagnosis.—Carapace with transverse ridges with some very short, not iridescent, setae,

without long iridescent simple setae. Gastric region with row of 4 pairs of epigastric spines. One parahepatic, 3 branchial anterior, and 1 postcervical spine on each side. Second and third abdominal tergites without long iridescent simple setae, with 1 main continuous transverse stria. First segment of antennal peduncle with 1 long distal spine on mesial margin, overreaching antennal peduncle and reaching end of basal segment of antennular peduncle (excluding distal spines); second segment with 2 long distal spines, mesial distal spine slightly longer than lateral spine, overreaching antennal peduncle; third segment unarmed. Merus of third maxilliped unarmed on extensor margin. Chelipeds with numerous long plumose setae. Palm 0.75 fingers length. Palm with several spines scattered on mesial and dorsal sides and 1 row of dorsolateral spines, continuing along proximal half of fixed finger; movable finger with 1 spine on proximal part of mesial margin. Second pereopod 2.4 times carapace length; merus as long as carapace, about 7 times as long as high, 3 times carpus length and about 1.3 times propodus length; propodus about 9 times as long as high and 2.7 times dactylus length. Merus with spines along dorsal border, increasing in size distally, ventral margin with few distal spines. Carpus with some dorsal spines and 1 distoventral spine. Propodus with 5 movable ventral spines. Dactylus short, with dorsal margin slightly convex, curving distally, ventral border indented, with 8 movable spinules along entire ventral margin. Merocarpal articulation of third walking leg slightly overreaching frontal margin of carapace and not exceeding sinus between rostral and supraocular spines.

Color.—(from Miyake and Baba, 1967) Ground color of carapace and abdomen reddish brown. Carapace with broad V-shaped band of reddish brown placed on posterior half. Proximal and distal portions of each joint of cheliped more emphasized with reddish brown color than other portions, fingers light seashell pink. Merus of each ambulatory leg with three bands of reddish brown, carpus with a single band of reddish brown at proximal portion, propodus with two bands, dactylus reddish brown.

Distribution.—Sagami Bay, Japan (type locality), Philippines, between 80 and 209 m.

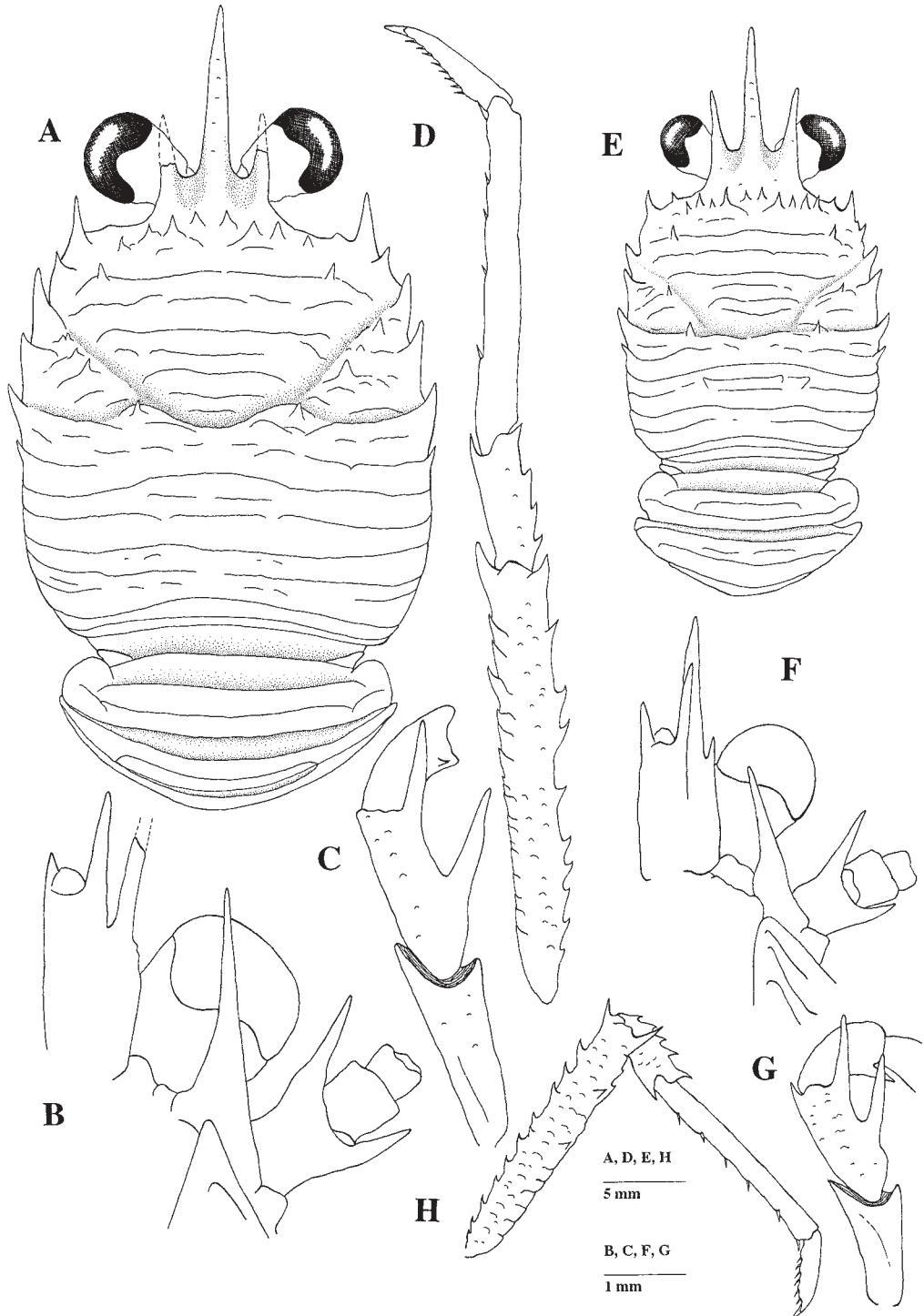


Fig. 1. A–D *Raymunida bellior* (Miyake and Baba). Philippines. “Albatross,” stn. 5398, female (CL = 9.5 mm). A, carapace and abdomen, dorsal view; B, ventral view of cephalic region, showing antennular and antennal peduncles; C, right third maxilliped showing ischium, merus, and carpus, lateral view; D, left first walking leg. E–H *Raymunida elegantissima* (de Man). Malaysia. “Albatross,” stn. 5593, female (CL = 6.2 mm). E, carapace and abdomen, dorsal view; F, ventral view of cephalic region, showing antennular and antennal peduncles; G, right third maxilliped showing ischium, merus and carpus, lateral view; H, right first walking leg. (Setae not illustrated.)

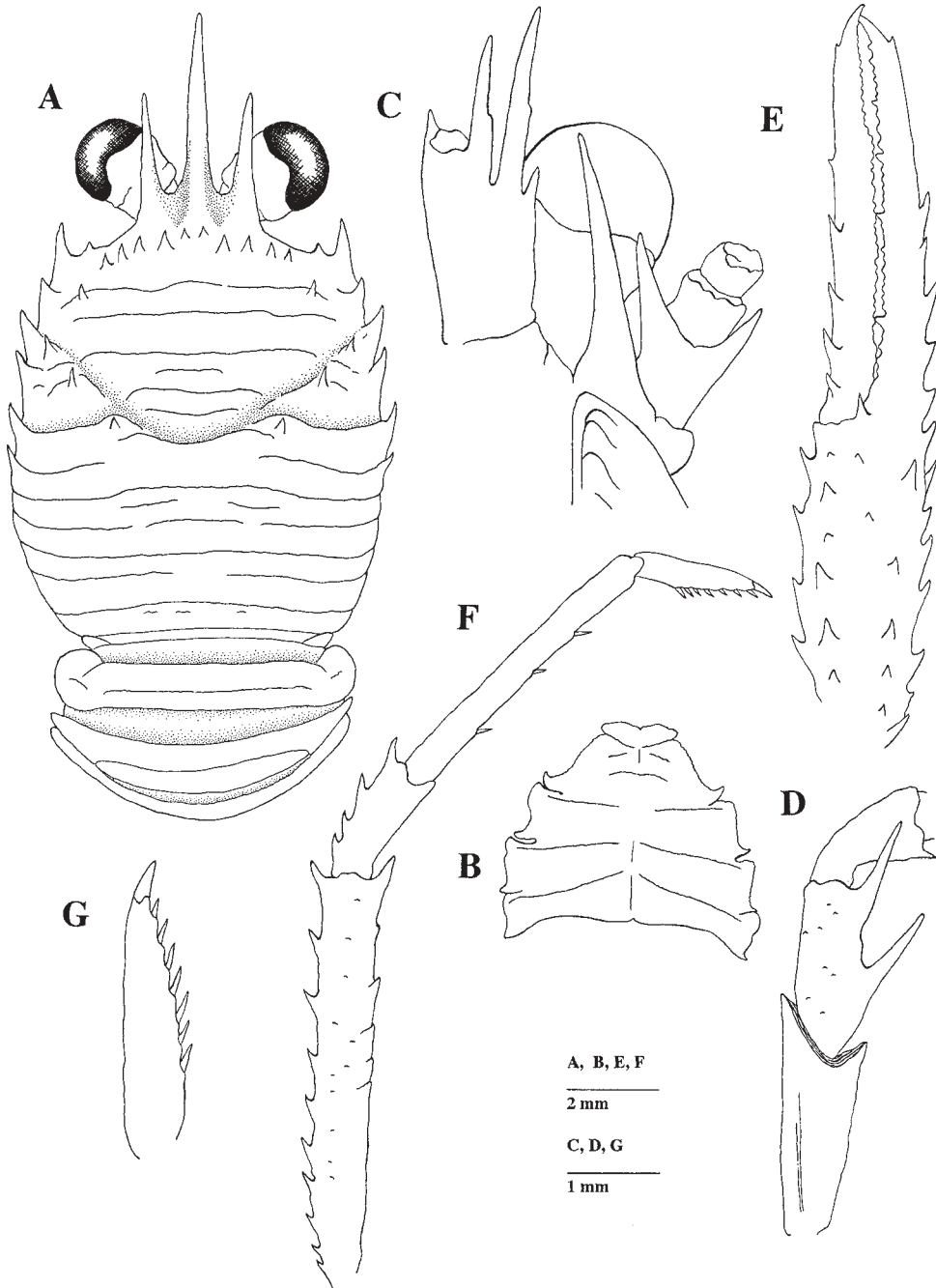


Fig. 2. *Raymunida confundens*, new species. Holotype, New Caledonia. Smib 8, stn 178, female (CL = 7.6 mm). A, carapace and abdomen, dorsal view; B, sternal plastron; C, ventral view of cephalic region, showing antennular and antennal peduncles; D, right third maxilliped showing ischium, merus, and carpus, lateral view; E, right cheliped showing propodus and chela, dorsal view; F, right first walking leg, lateral view; G, dactylus of first right walking leg, lateral view (Setae not illustrated).

***Raymunida confundens*, new species**

Fig. 2

Munida bellior.—Macpherson, 1994, p. 450 (in part) [not *Raymunida bellior* (Miyake and Baba, 1967)].

Material Examined.—**Chesterfield Islands.** Musorstom 5, stn 315, 330 m: 1 male (broken). **New Caledonia.** Smib 8, stn 178, 400 m: 1 female, 7.6 mm (holotype) (MNHN-Ga 4376).

Diagnosis.—Carapace with transverse ridges with dense very short, not iridescent, setae and few long iridescent, simple setae. Gastric region with a row of 9 or 10 epigastric spines. One parahepatic, 2 branchial anterior, and 1 postcervical spine on each side. Abdominal tergites with some long iridescent, simple setae. Second and third tergites with 1 main continuous transverse stria. First segment of antennal peduncle with 1 long distal spine on mesial margin, clearly overreaching antennal peduncle and reaching end of basal segment of antennular peduncle (excluding distal spines); second segment with 2 strong distal spines, mesial distal spine longer than lateral spine, overreaching third antennal segment; penultimate segment unarmed. Merus of third maxilliped unarmed on extensor margin or with small distal tooth. Chelipeds with numerous long iridescent, simple setae. Palm slightly shorter than fingers. Palm with several spines scattered on mesial and dorsal sides and 1 row of dorsolateral spines, continuing along proximal half of fixed finger; movable finger with several spines on first 0.66 of mesial margin. Second pereopod 2.5 times carapace length; merus as long as carapace, about 7.5 times as long as high, 3 times carpus length and about 1.2 propodus length; propodus about 9 times as long as high and 2.3 times dactylus length. Merus with spines along dorsal border, increasing in size distally, ventral margin with few distal spines. Carpus with some dorsal spines and 1 distoventral spine. Propodus with 4 movable ventral spines. Dactylus short, with dorsal margin convex, curving distally, ventral border indented, with 7 movable spinules along entire ventral margin. Merocarpal articulation of third walking leg overreaching frontal margin of carapace and not reaching level of sinus between rostrum and supraocular spines.

Color.—Ground color of carapace and abdomen red, with transverse white bands on striae, base of rostrum and supraocular spines

white; median and lateral parts of second abdominal segment with white spots. Chelipeds and walking legs red; distal parts of cheliped fingers whitish. Walking legs with red and white bands.

Distribution.—New Caledonia and Chesterfield Islands, between 330 and 400 m.

Etymology.—From the Latin *confundo*, confusion.

***Raymunida dextralis*, new species**

Fig. 3

Munida bellior.—Macpherson, 1994, p. 450 (in part), fig. 66 (color) [not *Raymunida bellior* (Miyake and Baba, 1967)].

Material Examined.—**Loyalty Islands.** Musorstom 6, stn 419, 285 m: 1 ovig. female, 12.3 mm (holotype) (MNHN-Ga 2578).

Diagnosis.—Carapace with transverse ridges with dense very short, not iridescent, setae and some long iridescent, simple setae. Gastric region with a row of 4–6 pairs of epigastric spines. One parahepatic, 3 branchial anterior, and 1 postcervical spine on each side. Abdominal tergites with some long iridescent, simple setae. Second and third tergites with 1 main continuous transverse stria. First segment of antennal peduncle with 1 long distal spine on mesial margin, clearly overreaching antennal peduncle and reaching end of basal segment of antennular peduncle (excluding distal spines); second segment with 2 long distal spines, mesial distal spine slightly longer than lateral spine, overreaching third antennal segment; penultimate segment unarmed. Merus of third maxilliped unarmed on extensor margin. Chelipeds with numerous long iridescent, simple setae. Palm slightly shorter than fingers. Palm with several spines scattered on mesial and dorsal sides and 1 row of dorsolateral spines, continuing along proximal half of fixed finger; movable finger with several spines on proximal half of mesial margin. Second pereopod 2.5 times carapace length; merus as long as carapace, about 7 times as long as high, 3 times carpus length and about 1.2 propodus length; propodus about 10 times as long as high and 3 times dactylus length. Merus with spines along dorsal border, increasing in size distally, ventral margin with few distal spines. Carpus with some dorsal spines and one distoventral spine. Propodus with 5 movable

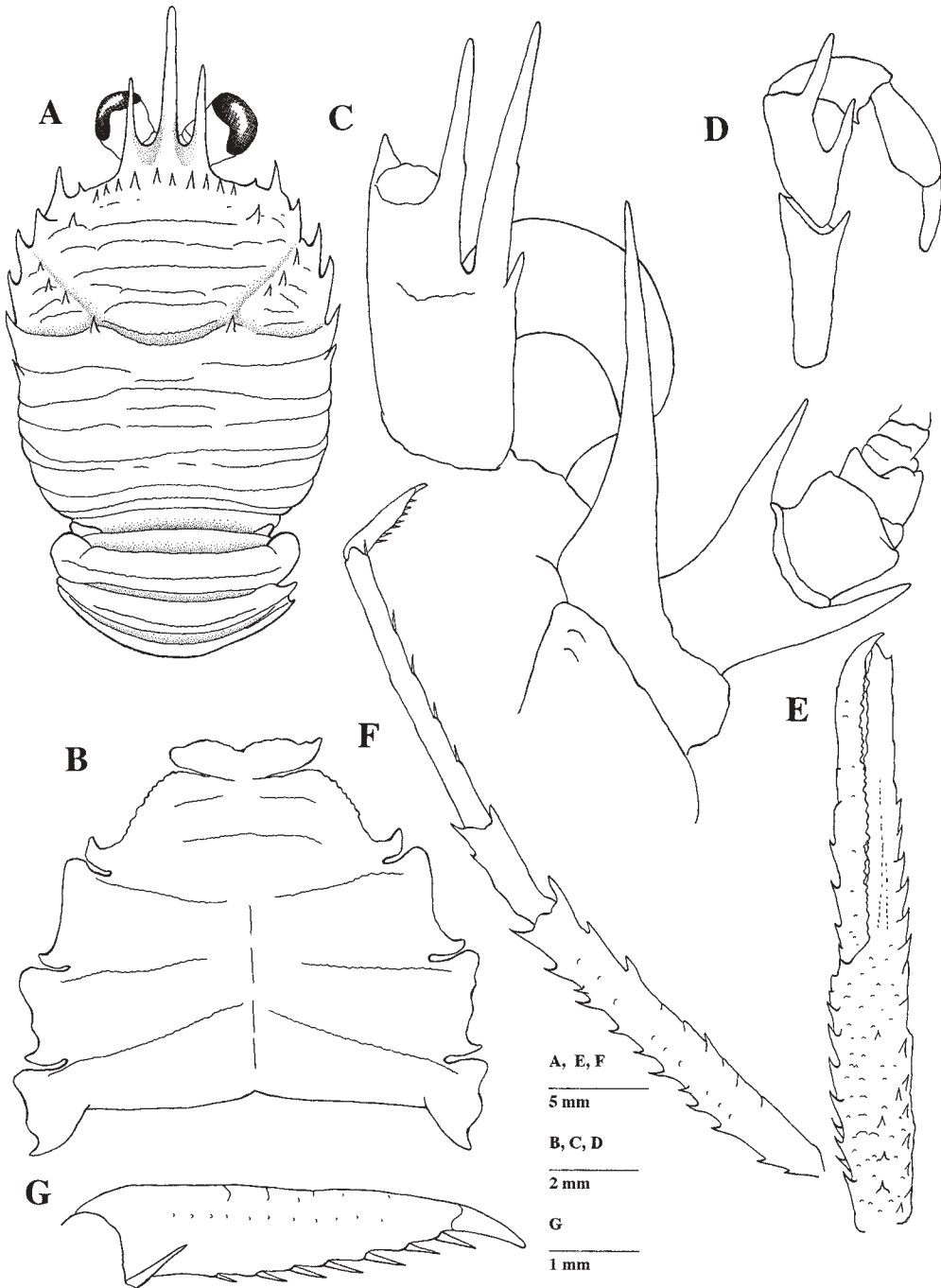


Fig. 3. *Raymunida dextralis*, new species. Holotype, Loyalty Islands. Musorstom 6, stn 419, ovigerous female (CL = 12.3 mm). A, carapace and abdomen, dorsal view; B, sternal plastron; C, ventral view of cephalic region, showing antennular and antennal peduncles; D, right third maxilliped showing ischium, merus and carpus, lateral view; E, right cheliped showing propodus and chela, dorsal view; F, right first walking leg, lateral view; G, dactylus of first right walking leg, lateral view (Setae not illustrated).

ventral spines. Dactylus short, with dorsal margin convex, curving distally, ventral border indented, with 6 or 7 movable spinules along entire ventral margin. Merocarpal articulation of third walking leg clearly overreaching frontal margin of carapace and reaching level of sinus between rostrum and supraocular spines.

Color.—Ground color of carapace and abdomen red, with transverse white bands on striae, base of rostrum and supraocular spines white; median and lateral parts of second abdominal segment with white spots. Chelipeds red, fingers with red and white bands. Walking legs with red and white bands.

Distribution.—Loyalty Islands, 285 m.

Etymology.—From the Latin *dextrale*, bracelet, in reference to the red and white bands on the walking legs.

Raymunida elegantissima (de Man, 1902)

Fig. 1 E–H

Munida elegantissima de Man, 1902, p. 726, pl. 24, figs. 42, 42a, b.—Baba, 1988, p. 94.—Macpherson, 1994, p. 465; 1999, p. 418 (in part).

Munida bellior.—Macpherson, 1994, p. 450 (in part); 1996, p. 390 (in part) [not *Raymunida bellior* (Miyake and Baba, 1967)].

Material Examined.—**Malaysia.** “Albatross.” Off north-eastern Borneo, Sibuko Bay, stn. 5593, 70 m: 1 female, 6.2 mm. **Philippines.** “Albatross.” Verde Island Passage, stn. 5179, 68 m: 1 male, 7.2 mm.—Musorstom 1, stn 57, 96–107 m: 1 male, 4.9 mm; 2 ovig. females, 7.2 and 7.3 mm; 1 female, 2.6 mm.—Musorstom 1, stn. 62, 179–194 m: 1 female, 3.7 mm.—Musorstom 2, stn. 8, 85–90 m: 1 male, 8.4 mm; 1 ovig. female, 9.3 mm.—Musorstom 2, stn. 47, 81–84 m: 1 male, 5.3 mm; 2 ovig. females, 9.0 and 9.8 mm.—Musorstom 3, stn. 117, 92–97 m: 1 male, 4.5 mm; 1 female, 2.9 mm. **New Caledonia.** Lagon, stn. 640, 50–80 m: 1 ovig. female, 9.3 mm. **Chesterfield Islands.** Chalcal 1, stn. 2, 80–120 m: 1 male, 5.2 mm. **Belona Island.** Corail 1, without position: 1 ovig. female, 12.2 mm. **Futuna Island.** Musorstom 7, stn. 498, 105–160 m: 1 female, 4.8 mm. **Vanuatu.** Musorstom 8, stn 966, 128–150 m: 2 males, 7.6 and 8.5 mm; 1 ovig. female, 10.3 mm; 1 female, 8.9 mm; 1 juvenile, 3.2 mm. **Fiji.** Musorstom 10, stn. 1363, 18°12.4'S, 178°33.0'E, 144–150 m: 1 ovig. female, 7.3 mm.

Diagnosis.—Carapace with transverse ridges with dense, very short, not iridescent, setae and some long, iridescent, simple setae. Gastric region with row of 5 or 6 pairs of epigastric spines. One parahepatic, 1–3 branchial anterior, and 1 postcervical spine on each side. Abdominal tergites with some long, iridescent, simple setae. Second and third ter-

gites with 1 main continuous transverse stria preceded by 1 secondary continuous or interrupted striae. First segment of antennal peduncle with 1 long distal spine on mesial margin, slightly overreaching antennal peduncle and not reaching end of basal segment of antennular peduncle (excluding distal spines); second segment with 2 long distal spines, mesial distal spine slightly longer than lateral spine, overreaching third antennal segment; penultimate segment unarmed. Merus of third maxilliped with distal spine on extensor margin. Chelipeds with numerous long iridescent, simple setae. Palm half as long as fingers. Palm with several spines scattered on mesial and dorsal sides and 1 row of dorsolateral spines, continuing along fixed finger; movable finger with several spines on proximal half of mesial margin. Second pereopod 2.5 times carapace length; merus as long as carapace, about 6.5 times as long as high, 4 times carpus length and about 1.4 times propodus length; propodus about 10 times as long as high and 2.4 times dactylus length. Merus with spines along dorsal border, increasing in size distally, ventral margin with few distal spines. Carpus with some dorsal spines and 1 distoventral spine. Propodus with 5–7 movable ventral spines. Dactylus short, with dorsal margin convex, curving distally, ventral border indented, with 6 or 7 movable spinules along entire ventral margin. Merocarpal articulation of third walking leg nearly reaching level of frontal margin of carapace.

Color.—Ground color of carapace and abdomen red, with transverse white bands on main striae, base of rostrum and supraocular spines red. Chelipeds and walking legs red, without colored bands and with some small whitish spots; distal part of cheliped fingers whitish.

Distribution.—Philippines, Malaysia (type locality), New Caledonia, Chesterfield Islands, Belona Island, Futuna Island, Vanuatu, and Fiji, between 50 and 160 m.

Raymunida erythrina, new species

Fig. 4

Munida bellior.—Macpherson, 1996, p. 390 (in part), fig. 12 (color) [not *Munida bellior* (Miyake and Baba, 1967)].

Munida elegantissima.—Macpherson, 1999, p. 418 (in part) [not *Munida elegantissima* de Man, 1902].

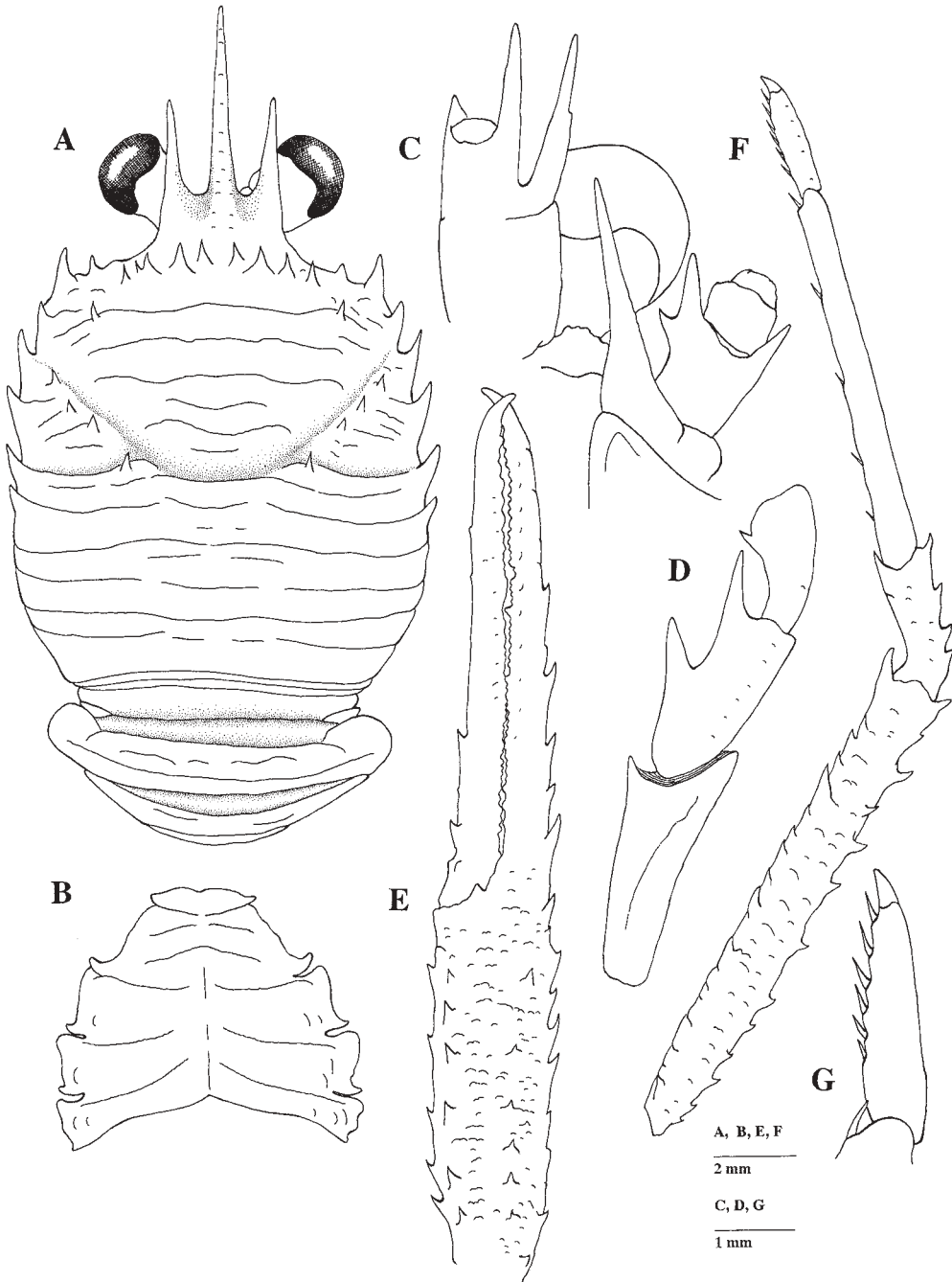


Fig. 4. *Raymunida erythrina*, new species. Holotype, Futuna Island. Musorstom 7, stn. 515, female (CL = 9.0 mm). A, carapace and abdomen, dorsal view; B, sternal plastron; C, ventral view of cephalic region, showing antennular and antennal peduncles; D, left third maxilliped showing ischium, merus, and carpus, lateral view; E, right cheliped showing propodus and chela, dorsal view; F, left first walking leg, lateral view; G, dactylus of first left walking leg, lateral view (Setae not illustrated).

Material Examined.—**Futuna Island.** Musorstom 7, stn. 515, 224–252 m: 1 female, 9.0 mm (holotype) (MNHN-Ga 3657). **Vanuatu.** Musorstom 8, stn. 1077: 180–210 m: 1 ovig. female, 9.3 mm.

Diagnosis.—Carapace with transverse ridges with very short, not iridescent setae, and few long iridescent, simple setae. Gastric region with row of 4 or 5 pairs of epigastric spines. One parahepatic, 3 branchial anterior, and 1 postcervical spine on each side. Abdominal tergites with some long iridescent, simple setae. Second and third tergites with 1 main continuous transverse stria, preceded by 1 secondary interrupted or continuous stria. First segment of antennal peduncle with 1 long distal spine on mesial margin, exceeding antennal peduncle and not reaching end of basal segment of antennular peduncle (excluding distal spines); second segment with 2 distal spines, mesial distal spine slightly longer than lateral spine, not overreaching antennal peduncle; penultimate segment unarmed. Merus of third maxilliped unarmed on extensor margin. Chelipeds with long simple setae, more abundant on mesial and lateral borders. Palm 0.75 fingers length. Palm with several spines scattered on mesial and dorsal sides and 1 row of dorsolateral spines, continuing along proximal 0.66 of fixed finger; movable finger with 2 spines on proximal part of mesial margin. Second pereopod 2.6 times carapace length; merus longer than carapace, about 7.5 times as long as high, 4 times carpus length and about 1.4 times propodus length; propodus about 10 times as long as high and 3 times dactylus length. Merus with spines along dorsal border, increasing in size distally, ventral margin with few distal spines. Carpus with some dorsal spines and 1 distoventral spine. Propodus with 4 or 5 movable ventral spines. Dactylus short, with dorsal margin slightly convex, curving distally, ventral border with 5 or 6 movable spinules along entire margin. Merocarpal articulation of third walking leg clearly overreaching frontal margin of carapace and sinus between rostrum and supraocular spines.

Color.—Ground color of carapace and abdomen reddish. Some small white spots scattered on dorsal surface of carapace and abdominal segments. Rostrum and supraocular spines reddish. Chelipeds and walking legs reddish, with small scattered white spots. Mesial and lateral border of palm and fingers

whitish, white spots more numerous on distal portion of fingers.

Distribution.—Vanuatu, Futuna Island, between 180 and 252 m.

Etymology.—From the Greek *erythros*, red, in reference to the ground color of the carapace and abdomen.

Raymunida insulata, new species

Fig. 5

Material Examined.—**Seychelles Islands.** Cepros cruise, 23.10.1987, 04°46.5'S, 56°38.4'E, 200 m: 1 female, 16.5 mm (holotype) (MNHN-Ga 4377).

Diagnosis.—Carapace with transverse ridges with some very short, not iridescent, setae, without long, iridescent, simple setae. Rostrum and supraocular spines probably regenerating. Gastric region with row of 4 pairs of epigastric spines. One parahepatic, 3 branchial anterior, and 1 postcervical spine on each side. Abdominal tergites with some long, iridescent, simple setae. Second and third tergites with 1 main continuous transverse stria. First segment of antennal peduncle with 1 long distal spine on mesial margin, exceeding antennal peduncle and reaching end of basal segment of antennular peduncle (excluding distal spines); second segment with 2 distal spines, mesial distal spine slightly longer than lateral spine, reaching end of antennal peduncle; penultimate segment unarmed. Merus of third maxilliped unarmed on extensor margin. Chelipeds with long simple setae, more numerous on mesial and lateral borders of articles. Palm 0.66 fingers length. Palm with several spines scattered on mesial and dorsal sides and 1 row of strong dorsolateral spines, continuing along fixed finger; movable finger with spines on proximal 0.66 of mesial margin. Second pereopod 2.2 times carapace length; merus shorter than carapace, about 7 times as long as high, 2 times carpus length and about 1.4 times propodus length; propodus about 8 times as long as high and 2 times dactylus length. Merus with spines along dorsal border, increasing in size distally, ventral margin with 2 distal spines. Carpus with 3 dorsal spines and 1 distoventral spine. Propodus with 5 movable ventral spines. Dactylus short, with dorsal margin slightly convex, curving distally, ventral border with 9 movable spinules along entire margin. Merocarpal articulation of third walking

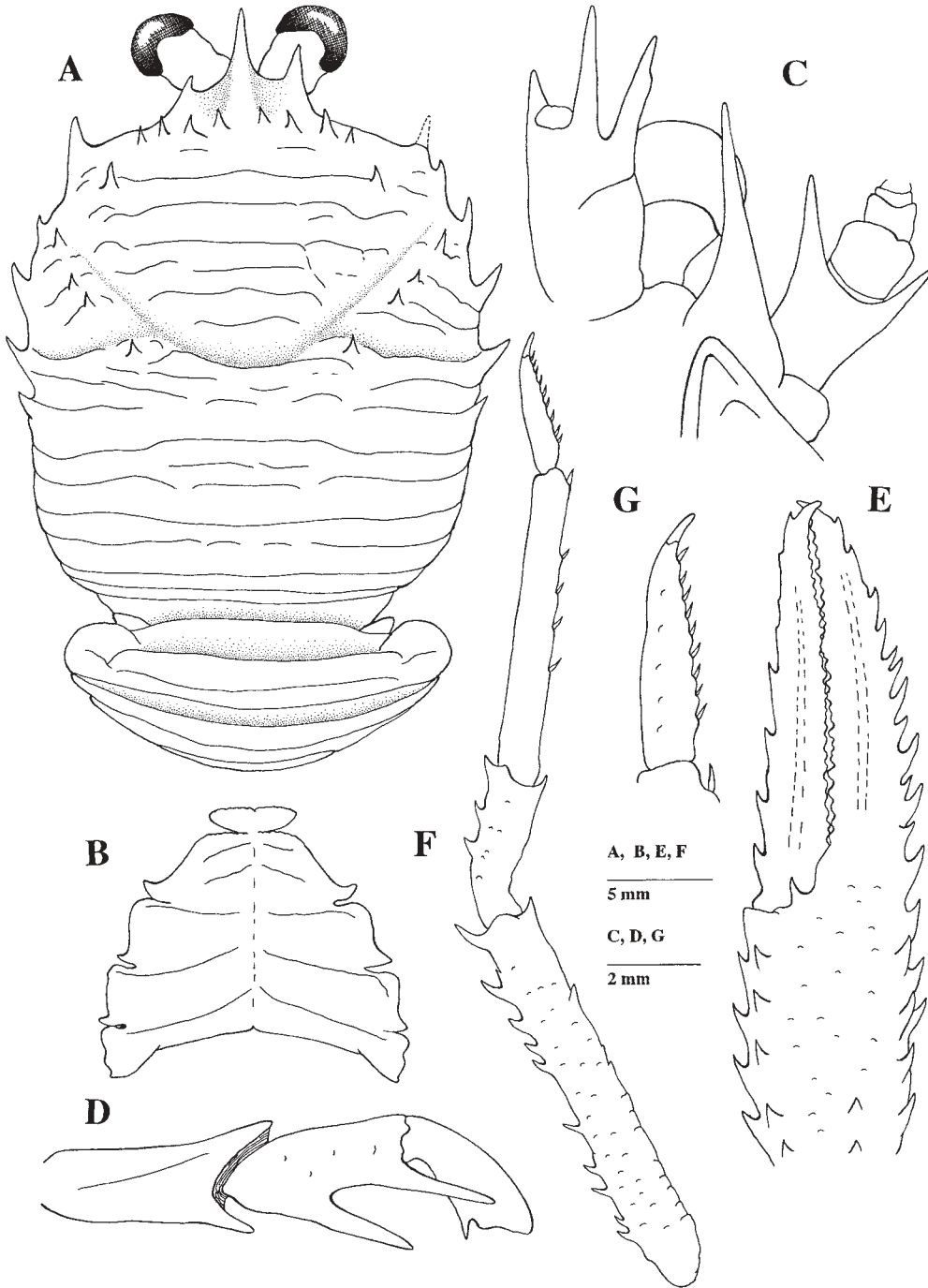


Fig. 5. *Raymunida insulata*, new species. Holotype, Seychelles Islands. Cepros cruise, female (CL = 16.5 mm). A, carapace and abdomen, dorsal view; B, sternal plastron; C, ventral view of cephalic region, showing antennular and antennal peduncles; D, left third maxilliped showing ischium, merus, and carpus, lateral view; E, right cheliped showing propodus and chela, dorsal view; F, right first walking leg, lateral view; G, dactylus of first right walking leg, lateral view (Setae not illustrated).

leg slightly overreaching frontal margin of carapace and not reaching sinus between rostrum and supraocular spines.

Color.—Unknown.

Distribution.—Seychelles Islands, 200 m.

Etymology.—From the Latin *insula*, island, in reference to the type locality.

General Remarks

Including the descriptions given above, the genus *Raymunida* contains seven species: *R. bellior*, *R. cagnetei*, *R. confundens*, *R. dextralis*, *R. elegantissima*, *R. erythrina*, and *R. insulata*. These species can be distinguished by several constant morphological characters. The most useful characters are: the length of the mesial spine of the first segment of the antennal peduncle, the presence/absence of one distal spine on the extensor border of the merus of the third maxilliped, the spinulation and setal type of the chelipeds, the length of the walking legs, and the number of striae on the second and third abdominal segments. Furthermore, the color pattern can be very useful as a specific character.

The length of the mesial spine of the first segment of the antennal peduncle divided the species in two groups: Four species (*R. bellior*, *R. confundens*, *R. dextralis*, and *R. insulata*) are distinguishable by the long mesial spine of the first antennal segment, reaching or overreaching the end of the basal segment of the antennular peduncle (excluding the distal spines), whereas this spine never reaches the end of the basal segment of the antennular peduncle in the second group (*R. cagnetei*, *R. elegantissima*, and *R. erythrina*).

Among the species of the first group, *R. bellior* is distinguished from *R. confundens*, *R. dextralis*, and *R. insulata* by the presence of numerous plumose setae on the chelipeds, and the carapace lacks long setae dorsally, whereas in the other three species the cheliped setae are simple and the carapace has long setae dorsally. *Raymunida insulata* can be distinguished from *R. confundens* and *R. dextralis* by the following characters: the palms of the chelipeds each have a row of strong dorsolateral spines, continuing along the whole length of the fixed finger in *R. insulata*, whereas the spines on the fixed finger are not strong and never overreach the

proximal half of the lateral margin of the fixed finger in the other two species. *Raymunida confundens* and *R. dextralis* are distinguishable by the length of the walking legs: the merocarpal articulation of the third walking leg does not reach the sinus between the rostrum and the supraocular spines in *R. confundens*, whereas this articulation overreaches the sinus in *R. dextralis*. The color patterns are also different as follows: In *R. bellior* the ground color of the carapace and abdomen is reddish brown, the carapace has a broad V-shaped band of reddish brown on the posterior half, and the walking legs have reddish brown bands. In *R. dextralis* the ground color of the carapace and abdomen is red, with transverse white bands on the striae; the base of the rostrum and supraocular spines are white, and the cheliped fingers and walking legs have red and white bands. The color pattern in *R. confundens* is quite similar to that of *R. dextralis*; however, the cheliped fingers and walking legs have no white bands. The color pattern in *R. insulata* is unknown.

The second group of species (*R. cagnetei*, *R. elegantissima*, and *R. erythrina*) also differ in several constant characters. *Raymunida erythrina* has the merus of the third maxilliped unarmed on the extensor margin, and the merocarpal articulation of the third walking leg clearly overreaches the frontal margin of the carapace. In the other two species the merus of the third maxilliped has a distal spine on the extensor margin, and the merocarpal articulation of the third walking leg does not reach the frontal margin of the carapace. *Raymunida elegantissima* and *R. cagnetei* can be distinguished by the following characters: The merocarpal articulation of the third walking leg overreaches the level of the first branchial spine of the carapace, and the second abdominal segment has a secondary stria in *R. elegantissima*; whereas in *R. cagnetei* the merocarpal articulation of the third walking leg only reaches the level of the first branchial spine of the carapace, and the second abdominal segment is occasionally preceded by 2 small median scales. Furthermore, the color pattern of *R. cagnetei* is different to that of *R. elegantissima* and *R. erythrina*, having wide white vertical bands along each branchial margin of the carapace and white bands on each lateral margin of the first to third abdominal somites. These vertical

white bands are absent in the other two species. *Raymunida elegantissima* and *R. erythrina* have similar color patterns, although the transverse white bands on the striae of the carapace and abdominal somites are more conspicuous in *R. elegantissima* than in *R. erythrina*.

Raymunida elegantissima has also been cited in other localities of the Indian Ocean: Zanzibar and the Gulf of Mannar (as *Munida alcocki* Southwell, 1906) (see Baba, 1988). The specimen from Zanzibar belongs to the second group of species mentioned above (the mesial spine of the basal antennal segment does not reach the end of the basal segment of the antennular peduncle, and the merus of the third maxilliped has a distal spine on the extensor margin), and it is different from *R. insulata* from the Seychelles. Nevertheless, the specimen is damaged, and clear identification is impossible. The specimens from the Gulf of Mannar were not studied. It would be interesting to collect additional material from the Indian Ocean, in order to improve our knowledge on the taxonomic status of the genus *Raymunida* in this area.

Key to Species of the Genus *Raymunida*

1. Mesial spine of first antennal segment reaching or overreaching end of basal segment of antennular peduncle (excluding distal spines) 2
 - Mesial spine of first antennal segment not reaching end of basal segment of antennular peduncle (excluding distal spines) 5
2. Chelipeds with numerous plumose setae. Carapace lacking long setae dorsally *R. bellior*
 - Chelipeds with numerous simple setae. Carapace with some long setae dorsally 3
3. Palm of chelipeds with row of strong dorsolateral spines, continuing along whole length of fixed finger *R. insulata*
 - Palm of chelipeds with row of small dorsolateral spines, continuing along proximal half of fixed finger 4
4. Merocarpal articulation of third walking leg not reaching sinus between rostrum and supraocular spines *R. confundens*
 - Merocarpal articulation of third walking leg overreaching sinus between rostrum and supraocular spines *R. dextralis*
5. Merus of third maxilliped unarmed on extensor margin. Merocarpal articulation of third walking leg clearly overreaching frontal margin of carapace *R. erythrina*
 - Merus of third maxilliped with distal spine on extensor margin. Merocarpal articulation of third walking leg not reaching frontal margin of carapace 6
6. Merocarpal articulation of third walking leg overreaching level of first branchial spine of carapace.

- Second abdominal segment has one secondary stria *R. elegantissima*
- Merocarpal articulation of third walking leg reaching level of first branchial spine of carapace. Second abdominal segment without secondary stria *R. cagnetei*

Genetic Data

Among the 21 specimens sequenced, 16 haplotypes were distinguished. The globally empirical nucleotide composition was A = 27.75%, C = 18.03%, G = 17.55% and T = 36.67%. There was a significant bias ($P < 0.001$) in the nucleotide composition in the third codon positions (A = 42.47%, C = 9.28%, G = 3.20%, T = 45.05%) as usual for crustacean species (Hillis *et al.*, 1996; Baldwin *et al.*, 1998; Sarver *et al.*, 1998 and references therein). The alignment of 657 nucleotides sequenced did not provide any gap among the ingroup, nor with respect to the outgroup. Among the 212 informative sites, the third position was the most informative (78.3%), followed by the first (19.34%). The transition/transversion ratio, evaluated by ML on the parsimony analysis, $ts/tv = 2.16$, $\gamma = 1.71$, and the proportion of invariable sites was 0.59. All these characteristics indicate that these were mitochondrial sequences rather than nuclear pseudogenes (Zhang and Hewitt, 1996).

The intraspecific divergences averaged $\bar{p} = 0.24\%$, and the interspecific (including only *Raymunida*) $\bar{p} = 10.95\%$ (with a minimum of 7.6% between *R. elegantissima* and *R. cagnetei*, and a maximum of 13.2% between *R. confundens* and *R. elegantissima*). Interspecific distance between the two *Munida* species analysed was $\bar{p} = 6.1\%$. The divergences among *Raymunida* and the outgroup (*Platyeriocheir formosa*) or *Agononida* were $\bar{p} = 17.88\%$ and 17.73%, respectively. The mean divergence among *Raymunida* and *Munida* species was slightly smaller ($\bar{p} = 16.89\%$) (Table 2). No saturation was found in our markers in any position (Fig. 6).

The three methods of phylogenetic reconstruction recovered the same topology. The monophyly of the genus *Raymunida* was fully supported, with high bootstraps (99 or 100) (Fig. 7). Within *Raymunida*, both ML and NJ methods showed a basal cluster constituted by three species: *R. insulata*, *R. dextralis*, and *R. confundens*, the last two forming a sister group. Nevertheless, the MP tree did not clar-

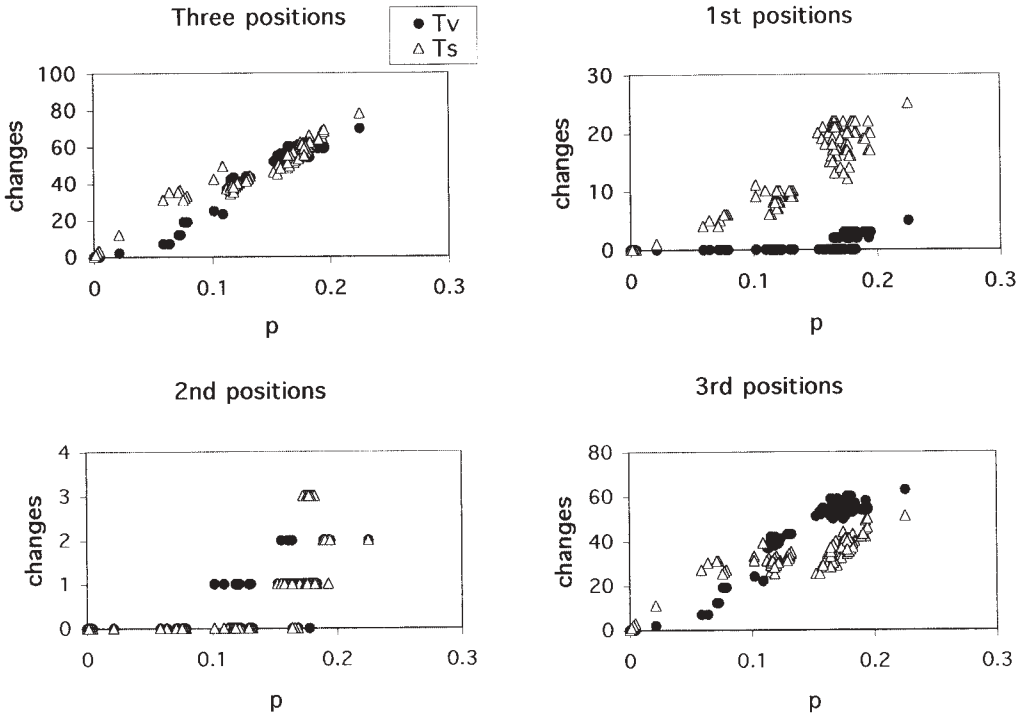


Fig. 6. Relationship between uncorrected mean divergence (p) between pairs of taxa and the number of transitional (ts) and transversal (tv) changes at different codon positions.

ify the relationships between these three species (although *R. confundens* and *R. dextralis* always constituted a sister group) and the other branch, which grouped the remaining three species (*R. elegantissima*, *R. cagnetei*, and *R. erythrina*). The phylogenetic relationships of these last three species were supported by the three methods: *R. erythrina* showed a basal position, and *R. elegantissima* and *R. cagnetei* were clustered as a sister group. The specimens of the two *Munida* species analysed were always clustered as a sister group of *Agononida*. Nevertheless, neither Kishino-Hasegawa nor Wilcoxon signed-rank tests revealed significant differences (P between 0.20 and 0.38) between the parsimony trees obtained by comparing the two hypotheses: that *Munida* is the sister group of *Agononida* (as in the tree presented) or that *Munida* could be the sister group of *Raymunida*. The trees obtained for this last hypothesis were longer than those presented here (523 steps instead of 517), but not significantly worse.

DISCUSSION

The species of *Raymunida* can be identified by subtle morphological characters and

are corroborated by mitochondrial sequences data. Thus, the sequence divergences confirm the specific value of some morphological characters (e.g., length of the mesial spine on the basal antennal segment, length of the walking legs). Furthermore, they confirm the importance of color patterns as diagnostic characters, as pointed out for other species of decapods differing little in morphology (Knowlton, 1993; Chan and Chu, 1996; Sarver *et al.*, 1998).

The use of molecular information in species that are difficult to distinguish morphologically may aid taxonomic studies (Avice, 1994) and the analysis of population subdivisions (Tam *et al.*, 1996; Chu *et al.*, 1999). Furthermore, nucleotide sequence divergences can identify characters that can reflect the phylogenetic history (Avice, 1994; Patterson *et al.*, 1993). The two main groups of species based on COI sequences (*Raymunida elegantissima*–*R. cagnetei*–*R. erythrina* and *R. confundens*–*R. dextralis*–*R. insulata*) are differentiated by the length of the mesial spine on the basal antennal segment. Other morphological characters (e.g., merus of the third maxilliped unarmed vs. armed on the

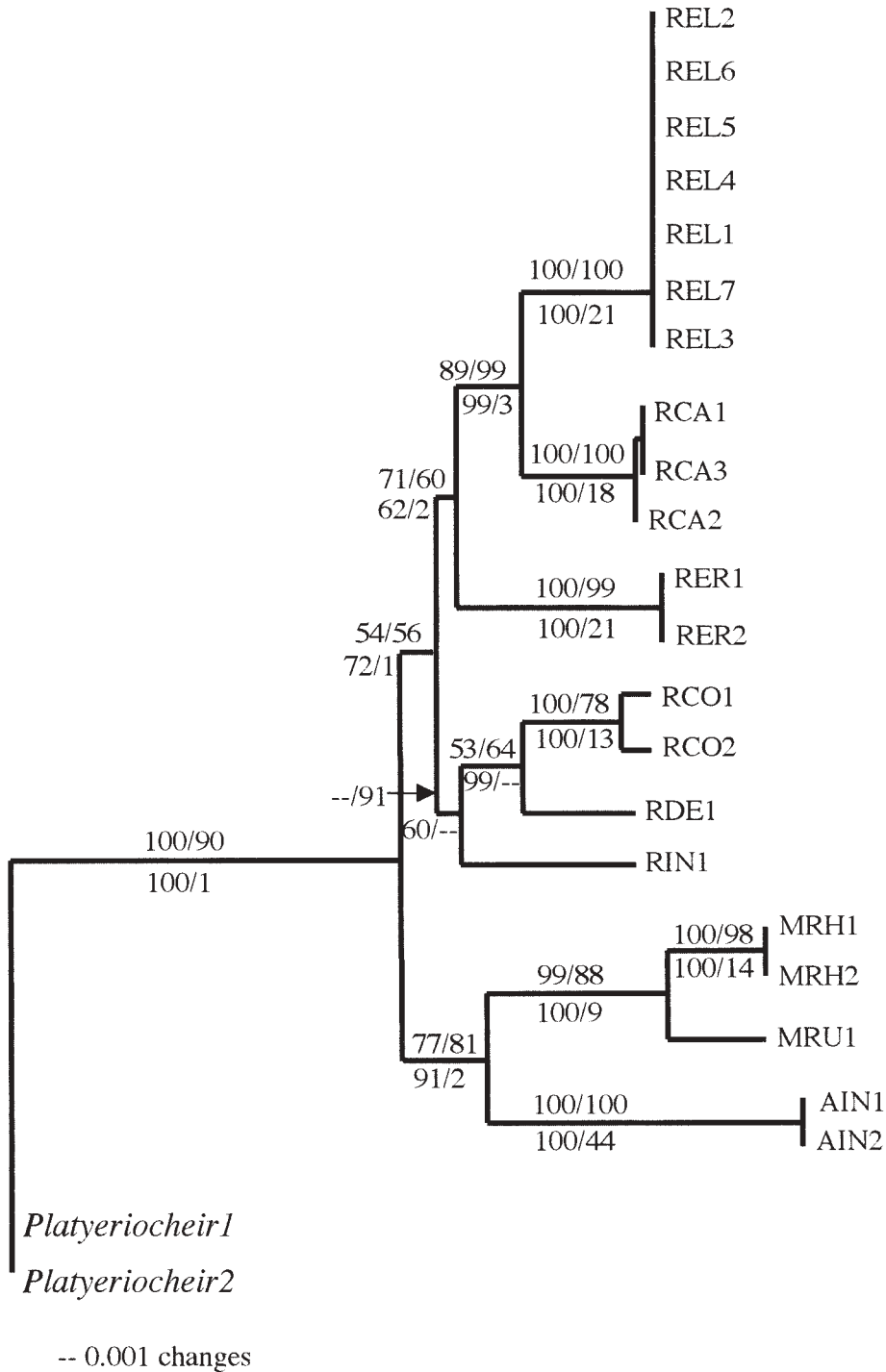


Fig. 7. Neighbour-joining tree based on GTR distances. Numbers above branches represent the bootstrap values obtained for 1,000 replications for MP (maximum parsimony) and ML (maximum likelihood); numbers below branches indicate those for NJ (neighbour joining), and Decay indices. When a particular branch was not recovered by a certain method, two hyphens replace the corresponding bootstrap or Decay value. The codes are those of Table 1. *Platyeriocheir formosa* was used as outgroup.

extensor margin, length of the walking legs) can also have an additional phylogenetic value. Following the sequence analysis, three different divergence ranges could stand out. A divergence of 0.2% was found among the *R. elegantissima* specimens analysed, inhabiting localities separated geographically by thousands of kilometers. This divergence was 10 times greater (2.1%) between two specimens of *R. confundens* from New Caledonia and Chesterfield, and finally, about 12% mean divergence differentiated *R. elegantissima* from *R. confundens* and *R. erythrina*, species clearly distinguishable by morphological characters. These divergence ranges are similar to those found for other studies on decapods at the same taxonomic levels (e.g., Palumbi and Benzie, 1991; Sarver *et al.*, 1998; Harrison and Crespi, 1999; Chu *et al.*, 1999). However, they are difficult to explain considering that these three species can be found in sympatry, although the first prefers shallower waters, if they shared a common biogeographical history. Although the biology of these species is practically unknown, it would be interesting to examine whether the mechanisms of larval dispersion or their physiology can explain such distributional patterns and degree of differentiation, as observed in other decapods (Knowlton and Weigt, 1998).

Previous data showed an important conservation in morphological or allozymic characters for Decapoda. In some cases, the morphological description could be posterior to the genetic characterization (Sarver and Foltz, 1993). For *Penaeus* species, in which genetic diversity based on electrophoretic analysis of allozymes is low, the divergence is between 8% and 24% for the partial sequences of COI (Baldwin *et al.*, 1998) or 11% for 16S (García Machado *et al.*, 1993). We found high divergences between the species of *Raymunida* analysed, which were consistent with the morphological diagnostic characters. Nevertheless, in the translation of our sequences, only one amino acid changed in one population, within the ingroup. The COI is considered one of the most conservative genes in the mitochondrial genome with respect to the amino acid substitutions (Black *et al.*, 1997). Palumbi and Benzie (1991), working on penaeid shrimp, suggested two possible explanations for the incongruence found between morphology and molecular markers: either

the mitochondrial DNA has a faster evolution rate in shrimp, or the rate of morphological divergence might be slow, possibly due to stabilizing selection on morphological or ecological characters. According to our results, this stabilizing selection may also act on proteins. The close relationships between the species studied here and some biogeographic conditions, as could happen in other Decapoda (Knowlton, 1993), could explain this morphological and allozymic stabilizing selection, while the phylogenetic relationships can be followed by the silent substitutions occurring in the DNA.

With the present data, the three methods employed for phylogenetic reconstruction agreed on the proposed monophyly of *Raymunida* and its differentiation with respect to *Munida* (in which *Raymunida* species were previously included) and *Agononida*. Only the clustering of *R. insulata* (the only species analysed from the Indian Ocean) differed in the trees obtained, because the MP could not resolve its position with high confidence. This "less robust" condition of the MP analysis was found also by Baldwin *et al.* (1998) in their *Penaeus* study, and it was attributed to the sensitivity of this method to the rate variation (Nei, 1987). Nevertheless, the Decay Index also indicated that the possible dichotomy grouping *R. insulata* with *R. dextralis*/*R. confundens* was not strongly supported by our data.

The importance of morphology *versus* molecular data to resolve the phylogeny of a group is still a source of controversy (e.g., Avise, 1994). Although additional works, including more specimens and species of related genera, are necessary, the results found in the present study illustrate a case where the taxonomic key based on morphological characters and the molecular tree are congruent and emphasize the importance of subtle characters (e.g., length of the mesial spine on the basal antennal segment, length of the walking legs, merus of the third maxilliped unarmed/armed) in the knowledge of the evolution of these species.

ACKNOWLEDGEMENTS

We are greatly indebted to A. Crosnier and B. Richer de Forges of ORSTOM for placing at our disposal the main part of the material examined. We thank R. Lemaitre (National Museum of Natural History, Washington) and Paul Clark (The Natural History Museum, London) for providing specimens of different species and localities. We also thank I. Uriz for her valuable suggestions and

A. Montilla for skillful technical assistance. The species have been illustrated by J. Macpherson.

LITERATURE CITED

- Avisé, J. C. 1994. *Molecular Markers, Natural History and Evolution*. Chapman & Hall, New York. 511 pp.
- Baba, K. 1988. Chirostyliid and Galatheid Crustaceans (Decapoda: Anomura) of the "Albatross" Philippine Expedition, 1907–1910.—*Researches on Crustacea*, Special Number 2: 1–203.
- . 1994. Deep-sea Galatheid crustaceans (Anomura: Galatheidae) collected by the 'Cidaris I' expedition off central Queensland, Australia.—*Memoirs of the Queensland Museum* 35: 1–21.
- , and M. de Saint Laurent. 1996. Crustacea Decapoda: revision of the genus *Bathymunida* Balss, 1914, and description of six new related genera (Galatheidae). Pp. 433–502 in A. Crosnier, ed. *Résultats des Campagnes MUSORSTOM*. Vol. 15. *Mémoires du Muséum national d'Histoire naturelle* 168.
- Baldwin, J. D., A. L. Bass, B. W. Bowen, and W. H. Clark, Jr. 1998. Molecular phylogeny and biogeography of the marine shrimp *Penaeus*.—*Molecular Phylogenetics and Evolution* 10: 399–407.
- Black, M. B., K. M. Halanych, P. A. Y. Maas, W. R. Hoeh, J. Hashimoto, D. Desbruyères, R. A. Lutz, and R. C. Vrijenhoek. 1997. Molecular systematics of vestimentiferan tubeworms from the hydrothermal vents and cold-water seeps.—*Marine Biology* 130: 141–149.
- Chan, T. Y., and K. H. Chu. 1996. On the different forms of *Panulirus longipes femoristriga* (von Martens, 1872) (Crustacea: Decapoda: Palinuridae), with description of a new species.—*Journal of Natural History* 30: 367–387.
- , M. S. Hung, and H. P. Yu. 1995. Identity of *Eriochelone recta* (Stimpson, 1858) (Decapoda: Brachyura), with description of a new crab from Taiwan.—*Journal of Crustacean Biology* 15: 301–308.
- Chu, K. H., J. Tong, and T. Y. Chan. 1999. Mitochondrial cytochrome oxidase I sequence divergence in some Chinese species of *Charybdis* (Crustacea: Decapoda: Portunidae).—*Biochemical Systematics and Ecology* 27: 461–468.
- de Man, J. G. 1902. Die von Herrn Professor Kükenthal im indischen Archipel gesammelten Dekapoden und Stomatopoden. Pp. 467–929 in Kükenthal, *ergebnisse einer zoologischen. Forschungsreise in den Molukken und Borneo*. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 25.
- Folmer, O., M. Black, W. Hoeh, R. Lutz, and R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates.—*Molecular Marine Biology and Biotechnology* 3: 294–299.
- García Machado, E., N. Denneboug, M. Oliva Suárez, J. C. Mounolou, and M. Monnerot. 1993. Mitochondrial 16S-rRNA gene of two species of shrimps: sequence variability and secondary structure.—*Crustaceana* 65: 279–286.
- Harrison, M. K., and B. J. Crespi. 1999. Phylogenetics of *Cancer* crabs (Crustacea: Decapoda: Brachyura).—*Molecular Phylogenetics and Evolution* 12: 186–199.
- Henderson, J. R. 1888. Report on the Anomura Collected by H.M.S. Challenger During the Years 1873–76.—*Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–1876*, *Zoology*, 27: vi + 221 pp., 21 pls.
- Hillis, D. M., C. Moritz, and B. K. Mable. 1996. *Molecular Systematics*. Second edition. Sinauer Associates, Sunderland, Massachusetts. 655 pp.
- Kishino, H., and M. Hasegawa. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea.—*Journal of Molecular Evolution* 29: 350–353.
- Knowlton, N. 1993. Sibling species in the sea.—*Annual Review of Ecology and Systematics* 24: 189–216.
- , and L. A. Weigt. 1998. New dates and new rates for divergence across the Isthmus of Panama.—*Proceedings of the Royal Society of London B* 265: 2257–2263.
- Lavane C., G. Preparata, C. Sacone, and G. Serio. 1984. A new method for calculating evolutionary substitution rates.—*Journal of Molecular Evolution* 20: 86–93.
- Leach, W. E. 1820. *Galatéadées*.—*Dictionnaire des Sciences Naturelles*, Paris 18: 49–56.
- Macpherson, E. 1994. Crustacea Decapoda: studies on the genus *Munida* Leach, 1820 (Galatheidae) in New Caledonia and adjacent waters with descriptions of 56 new species. Pp. 421–569 in A. Crosnier, ed. *Résultats des Campagnes MUSORSTOM*. Vol. 12. *Mémoires du Muséum national d'Histoire naturelle* 161.
- . 1996. Crustacea Decapoda: species of the genera *Munida* Leach, 1820 and *Paramunida* Baba, 1988 (Galatheidae) from the seas around the Wallis and Futuna Islands. Pp. 387–421 in A. Crosnier, ed. *Résultats des Campagnes MUSORSTOM*. Vol. 15. *Mémoires du Muséum national d'Histoire naturelle* 168.
- . 1999. Crustacea Decapoda: species of the genera *Agononida* Baba & de Saint Laurent, 1996 and *Munida* Leach, 1820 (Galatheidae) collected during the MUSORSTOM 8 cruise in Vanuatu. Pp. 407–426 in A. Crosnier, ed. *Résultats des Campagnes MUSORSTOM*. Vol. 20. *Mémoires du Muséum national d'Histoire naturelle* 180.
- , and A. Machordom. 2000. *Raymunida*, new genus (Decapoda: Anomura: Galatheidae) from the Indian and Pacific Oceans.—*Journal of Crustacean Biology* 20, Special Number 2: 253–258.
- Maddison, W. P., and D. R. Maddison. 1992. "MacClade: Analysis of Phylogeny and Character Evolution", version 3.05. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Miyake, S., and K. Baba. 1967. New and rare species of the family Galatheidae (Crustacea, Anomura) from the Sagami Bay in the collection of the Biological Laboratory, Imperial Household, Japan.—*Journal of the Faculty of Agriculture, Kyushu University* 14: 213–224.
- Nei, M. 1987. *Molecular Evolutionary Genetics*. Columbia University Press, New York. 512 pp.
- Palumbi, S. R., and J. Benzie. 1991. Large mitochondrial DNA differences between morphologically similar Penaeid shrimp.—*Molecular Marine Biology and Biotechnology* 1: 27–34.
- Patterson, C., D. M. Williams, and C. J. Humphries. 1993. Congruence between molecular and morphological phylogenies.—*Annual Review of Ecology and Systematics* 24: 153–188.
- Posada, D., and K. A. Crandall. 1998. Model test: testing the model of DNA substitution.—*Bioinformatics* 14: 817, 818.
- Rodríguez, R., J. L. Oliver, A. Marín, and J. R. Medina. 1990. The general stochastic model of nucleotide substitution.—*Journal of Theoretical Biology* 142: 485–501.

- Sambrook, J., E. F. Fritsch, and T. Maniatis. 1989. *Molecular Cloning: A Laboratory Manual*, Second edition. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York.
- Sarver, S. K., and D. W. Foltz. 1993. Genetic population structure in species complex of blue mussels (*Mytilus* spp.).—*Marine Biology* 117: 105–112.
- , J. D. Silberman, and P. J. Walsh. 1998. Mitochondrial DNA sequence evidence supporting the recognition of two subspecies or species of the Florida spiny lobster *Panilurus argus*.—*Journal of Crustacean Biology* 18: 177–186.
- Southwell, T. 1906. Report on the Brachyura and Anomura collected by Professor Herdman, at Ceylon, in 1902. Pp. 211–224 in W. A. Herdman, ed. Report to Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Mannar 5.
- Swofford, D. L. 2000. “PAUP*: Phylogeny Analysis Using Parsimony (*and other methods)”, version 4.0b3. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Tam, Y. K., and I. Kornfield. 1998. Phylogenetic relationships of clawed lobster genera (Decapoda: Nephropidae) based on mitochondrial 16S rRNA gene sequences.—*Journal of Crustacean Biology* 18: 138–146.
- , ———, and F. P. Ojeda. 1996. Divergence and zoogeography of mole crabs, *Emerita* spp. (Decapoda: Hippidae), in the Americas.—*Marine Biology* 125: 489–497.
- Templeton, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes.—*Evolution* 37: 221–244.
- Zhang, D. X., and G. M. Hewitt. 1996. Nuclear integrations: challenges for mitochondrial DNA markers.—*Trends in Ecology and Evolution* 11: 247–251.

RECEIVED: 10 April 2000.

ACCEPTED: 8 November 2000.