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A NEW GENUS OF SQUAT LOBSTER (DECAPODA: ANOMURA: GALATHEIDAE) FROM THE SOUTH WEST PACIFIC AND INDIAN OCEAN INFERRED FROM MORPHOLOGICAL AND MOLECULAR EVIDENCE

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A B S T R A C T

In a previous phylogenetic analysis of numerous species of the genus *Munida* and related genera from the West Pacific based on molecular and morphological data, the monophyly of this group with the exception of *M. callista* was established. Morphologically, *M. callista* is closely related to *M. brucei*, *M. javieri*, *M. hystrix* and *M. plexaura* showing morphological differences in the shape of the rostrum, the supraocular spines, and the ridges on the epistome with respect to the genus *Munida*. Moreover, the analysis of the mitochondrial genes 16S rRNA and COI showed an independent and monophyletic lineage from the genus *Munida*. Therefore a new genus, *Babamunida*, is proposed to accommodate these five species, based on morphological characters and molecular data.

KEY WORDS: Anomura, DNA, molecular systematics, morphology, taxonomy

INTRODUCTION

Galatheidae Samouelle, 1819 is among the most diverse families of anomuran decapods and now comprises about 30 genera (Baba, 2005). Of these genera, *Munida* Leach, 1820 is perhaps the most varied and is currently represented by more than 200 species (Baba, 1988, 2005; Macpherson, 1994, 2006). In recent years and after the description of more than 100 new species of *Munida* and related taxa from the Pacific and Indian Oceans (Baba, 1988, 2005; Macpherson, 1994, 2006 and references cited therein), the genus was split into different genera, e.g., *Agononida* Baba and de Saint Laurent, 1996, *Crosnierita* Macpherson, 1998, *Enriquea* Baba, 2005, *Munida* Leach, 1820, *Paramunida* Baba, 1988, and *Raymunida* Macpherson and Machordom, 2000.

The phylogenetic analysis of these taxa using molecular and morphological data supported the taxonomic separation into several genera (Machordom and Macpherson, 2004) and pointed to the monophyly of the species of the genus *Munida* from the western Pacific, with the exception of *M. callista* Macpherson, 1994. This species showed the greatest divergence in the two genes sequenced (COI and 16S rRNA) with respect to the other species of the genus *Munida* from this area.

Munida callista is characterized by the presence of three branchial spines along the lateral margin of the carapace; the anterolateral spines are well developed, the pleomeres are unarmed and the lateral parts of the fifth to seventh thoracic sternites lack granules or carinae. Morphologically, *M. callista* is closely related to *M. hystrix* Macpherson and de Saint Laurent, 1991 from French Polynesia, *M. javieri* Macpherson, 1994 from New Caledonia and the Chesterfield, Matthew and Hunter Islands, *M. plexaura* Macpherson and de Saint Laurent, 1991 from New Caledonia and the Chesterfield Islands and *M. brucei* Baba, 1974 from Kenya and Mauritius.

In the present study, we propose a new genus to group together *M. callista*, *M. hystrix*, *M. plexaura*, *M. javieri* and *M. brucei* based on: 1) molecular data from the 16S rRNA and COI for the closely related species (*M. javieri*, *M. hystrix* and *M. plexaura*), and 2) morphological characters that separate the species of the genus *Munida* (type species *M. rugosa* (Fabricius, 1775) from NE Atlantic Ocean) from *M. callista* and related species. The molecular phylogenetic position of *M. hystrix*, *M. javieri*, and *M. plexaura* confirmed their close relationship with *M. callista* and revealed their vast divergence with respect to the other species of the genus *Munida*. In the case of *M. brucei* only the morphological characters were analyzed, due to the lack of material for the molecular analysis. To accommodate these five species, we herein describe a new genus, *Babamunida*.

MATERIALS AND METHODS

Material Analysed

Specimens of species deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN) were used for morphological and molecular analyses. Descriptive data for the first larval stage of *M. javieri* were obtained from Guerao et al. (2006), and compared with those observed here for the first zoea stage of *M. striola* Macpherson and Baba, 1993, *M. gregaria* (Fabricius, 1793) and *M. tenuimana* G.O. Sars, 1872. We sequenced part of the 16S rRNA gene for *M. hystrix*, *M. javieri* and *M. plexaura*, and obtained COI sequence data only for *M. hystrix*. For *M. callista*, we used previous molecular data obtained for this species and others by Machordom and Macpherson (2004).

DNA Extraction and Amplification

Tissue samples were preserved in ethanol and total DNA was isolated by standard proteinase K and phenol/chloroform extraction procedures (Sambrook et al., 1989). The partial 16S rRNA was amplified by polymerase chain reaction (PCR) using the primers 1471 (5′-CCTGTTTANCAAAAACAT-3′) and 1472 (5′-AGATAGAAACCAACCTGG-3′) (Crandall and Fitzpatrick, 1996). The partial COI only was amplified for two specimens of *M. hystrix*, with the following pairs of primers:

LCO1490 (Folmer et al., 1994) and the newly designed COIR1 (5′-ACNTTATATTTTATYTTYGG-3′) and COI-f (5′-GAGCTCCAGATA TAGCATTCC-3′) and COI-r (5′-AGTATAAGCGTCTGGGTAGTC-3′) (van Syoc, 1995).

In a final volume of 50 µl, the PCR mix contained 2 µl of DNA template, 0.16 µM of both primers, 0.2 mM of each dNTP, 5 µl of buffer (containing 2 mM $MgCl_2$), 1.5 U of Taq DNA polymerase (Biotools) and ddH_2O. The amplification process for the partial 16S rRNA sequence was conducted as follows: 94°C (4 min), 40 cycles at 94°C (45 s), 45.5°C (1 min), 72°C (1 min), and a final extension at 72°C (10 min). Amplification of the COI gene was performed under the same conditions except for a higher annealing temperature (50°C).

The amplified fragments, 549 bp for the 16S rRNA (after within-matrix realignment with other galatheids, Machordom and Macpherson, 2004) and 657 bp for the COI were purified by ethanol precipitation prior to sequencing both strands using "Big Dye Terminator" (Applied Biosystems, ABI) sequencing reactions. Sequences were run on an ABI 3730 Genetic Analyzer (Applied Biosystems). Forward and reverse DNA sequence strands were compared using the Sequencher program (Gene Code) after removing the primer regions. New sequences were deposited in GenBank under accession numbers EF136566-EF136571.

Only the 16S rRNA gene portion was sequenced for all the species of the proposed new genus, thus phylogenetics analyses were performed for this gene only. Parsimony tests were performed using WinClada (Nixon, 2002). Characters were coded as nonadditive, and "island hopping" conducted through 100,000 iterations, with one tree held from each, amb-poly was 10% of the characters sampled, and the random constraint was 10. The evolutionary molecular model that best fitted our data was selected using MODELTEST 3.06 (Posada and Crandall, 1998) under the Akaike information criterion (Akaike, 1974). Sequence analyses were based on the principles of maximum likelihood (ML) and neighbour-joining (NJ) with the model and parameters selected by MODELTEST using the PHYML (Guindon and Gascuel, 2003) and PAUP 4.0b10 package (Swofford, 2002) respectively.

We estimated support in the NJ (2000 pseudoreplications) and ML analyses by bootstrapping (500 pseudoreplications) (Felsenstein, 1985). We also used Bayesian analyses to calculate the posterior probabilities of the nodes in the phylogenetic trees. Four chains were run for 5,000,000 generations and trees prior to log likelihood stabilization were discarded as burn- in.

SYSTEMATICS

Galatheidae Samouelle, 1819
Babamunida n. gen.

Type Species.—*Munida callista* Macpherson, 1994, by present designation.

Included Species.—*B. callista* (Macpherson, 1994), *B. hystrix* (Macpherson and de Saint Laurent, 1991), *B. javieri* (Macpherson, 1994), *B. plexaura* (Macpherson and de Saint Laurent, 1991) and *B. brucei* (Baba, 1974).

Description.—Carapace with transverse ridges, usually granulated. Rostral spine spiniform, carinate dorsally, clearly overreaching supraocular spines; supraocular spines spiniform, carinate dorsally, well developed and not overreaching end of corneae; deep longitudinal grooves between rostrum and supraocular spines; rostral and supraocular anterior carinae, reaching the epigastric region (Figs. 1A, C). Dorsal carapace surface with at least a row of epigastric spines, largest pair usually situated directly behind supraocular spines. Frontal margins oblique, slightly concave. Anterolateral spines present. Branchial margins with 3-4 spines. Second to fourth pleomeres unarmed. Telsonal subdivision incomplete. Fourth thoracic sternite with anterior margin wide, moderately concave; median part or whole posterior margin of third sternite contiguous with fourth sternite; sixth and seventh sternites without granules or keels. Orbit visible in dorsal view, ventral margin of orbit with well developed mesial spine accompanied by additional spine at base. Eyes large, corneae strongly dilated, maximum corneal width equal to or more than 1/3 distance between anterolateral spines. Antennular basal segment with 2 distal spines; 2 additional spines on lateral margin, subdistal spine longer than proximal spine. Antennal basal segment with short distomesial spine short, never exceeding second segment; second segment with well-developed distal spines. Antennal flagellum longer than chelipeds. Epistome with ridge between marginal ridge (mouth) and ventral margin of orbit clearly separated from base of antennal peduncle, without protuberance near marginal ridge; ridge situated at base of antennule scarcely discernible (Figs. 1B, D). Merus of third maxilliped shorter than ischium, rectangular in lateral view, with 2-3 marginal spines along flexor border. Chelipeds moderately slender, elongated, usually longer and stouter in males than in females; palm compressed, as long or shorter than fingers, with row of spines along mesial, lateral and dorsal sides: movable and fixed fingers with row of spines along mesial and lateral margins, respectively. Walking legs long and slender; dactyli slender, slightly curving; flexor margin with spine-like setae. Flexor face of fifth pereiopods lacking brush of plumose setae. Male gonopods present on first and second abdominal segments. Epipods absent from pereiopods.

Etymology.—Besides making reference to *Munida*, the generic name *Babamunida* acknowledges the significant contributions of Keiji Baba to the study of the Galatheoidea. Gender: feminine.

Molecular Phylogeny

The partial COI sequence dataset obtained for *B. callista* and *B. hystrix* consisted of 657 characters, of which 337 were constant, 47 were parsimony uninformative and 273 were parsimony informative. For the 16S rRNA gene sequence analysis, the four species belonging to the new genus were evaluated together with related genera of Galatheidae (*Onconida*, *Plesionida*, *Agononida*, *Heteronida*, *Pleuroncodes*, *Cervimunida*, *Bathymunida*, *Crosnierita*, *Enriquea*, *Leiogalathea*, *Paramunida*, *Munida*, *Raymunida*, and *Alainius*). *Eumunida sternomaculata* de Saint Laurent and Macpherson, 1990 (Chirostylidae) was used as out-group. This gene showed two high variability regions between positions 232 and 292, and 364 and 376. After alignment, the resulting dataset comprised 549 characters, of which 257 were constant, 36 were variable and parsimony uninformative and 256 were parsimony informative.

Divergences among the species of *Babamunida* were in the range 5.2-11.09% for the 16S rRNA and 15.37-15.52% for the COI sequences, lower than almost all intergeneric values (Table 1). Divergence between these four species and other *Munida* species ranged from 11.02 to 16.94% for the16S rRNA gene sequence and 17.04 to 22.52% for COI. The 16S rRNA divergence between species of *Babamunida* and the type species *Munida rugosa* was 11.04 to 14.16%.

The model that best fitted our 16S rRNA gene dataset was the Tamura- Nei + I + Γ model (Tamura and Nei, 1993), which rendered a parameter α of 0.633 and I-value of 0.4106. Molecular phylogenetic analyses based on 16S rRNA indicated that *B. callista*, *B. hystrix*, *B. javieri* and *B. plexaura* constitute a monophyletic assemblage, with high support (Fig. 2). Relationships within the new genus

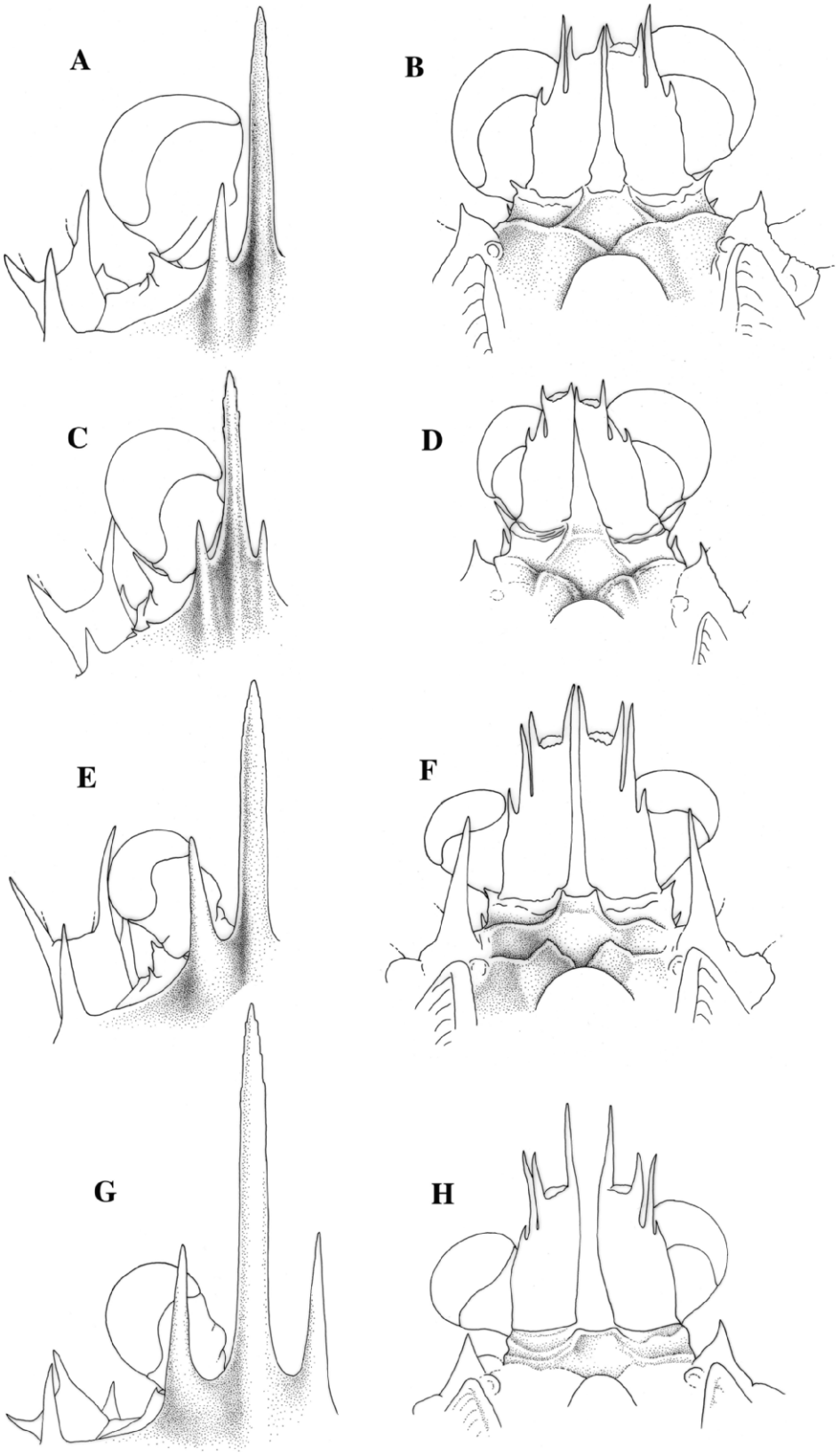


Fig. 1. A, C, E, G, Rostrum, supraocular spines and left orbital region. B, D, F, H, Ventral view of antennules and epistome. A-B, *Babamunida callista*, M, 15.8 mm CL, New Caledonia, cruise Norfolk 2, stn 2048. C-D, *B. hystrix*, M, 12.9 mm CL, French Polynesia, cruise Benthaus, stn 2008. E-F, *Munida rubridigitalis*, ov. F, 14.8 mm, New Caledonia, cruise Biocal, stn 52. G-H, *M. rugosa*. Scale: A, B, D, G, H = 5 mm; C, E, F, I = 2 mm.

Table 1. Molecular divergence ranges (in percentage) for 16S rRNA and COI sequences between *Babamunida* and closed related genera within Galatheidae.

	Range	
	16S rRNA	COI
Agononida	11.33-15.08	16.13-20.39
Alainius	14.99-17.44	16.43-19.78
Bathymunida	13.11-16.41	19.01-20.16
Crosnierita	11.28-15.66	18.41-19.02
Enriquea	15.01-17.01	19.33-21.91
Munida	11.02-16.94	17.04-22.52
Onconida	12.21-15.53	17.65-20.09
Paramunida	13.37-16.76	17.50-20.85
Raymunida	14.70-16.21	18.11-20.71
Plesionida	12.59-15.12	18.29-18.70
Leiogalathea	17.64-19.07	21.30-24.35
Heteronida	13.28-17.46	—
Pleuroncodes	16.71-17.53	19.17-19.93
Cervimunida	13.19-15.55	19.17-20.70

revealed *B. callista* and *B. plexaura* as a sister group, although only indicated by one analysis and with low support, and a second cluster formed by *B. hystrix* and *B. javieri* that was highly supported. The sister group of the new genus was found to be *Crosnierita* (*C. urizae* and *C. yante*, excluding *C. dicata*), always with strong support. Nevertheless, relationships between this group (*Babamunida* + *Crosnierita*) and the remaining groups were unresolved. The Bayesian analysis indicated that the type species, *Munida rugosa*, appears in a basal position with respect to the rest of the species of *Munida*, but also included *Pleuroncodes*, *Cervimunida*, *Raymunida*, *Alainius* and *Enriquea*. *Babamunida* was not a member of this cluster, despite the fact that its members had previously been assigned to the genus *Munida*.

Discussion

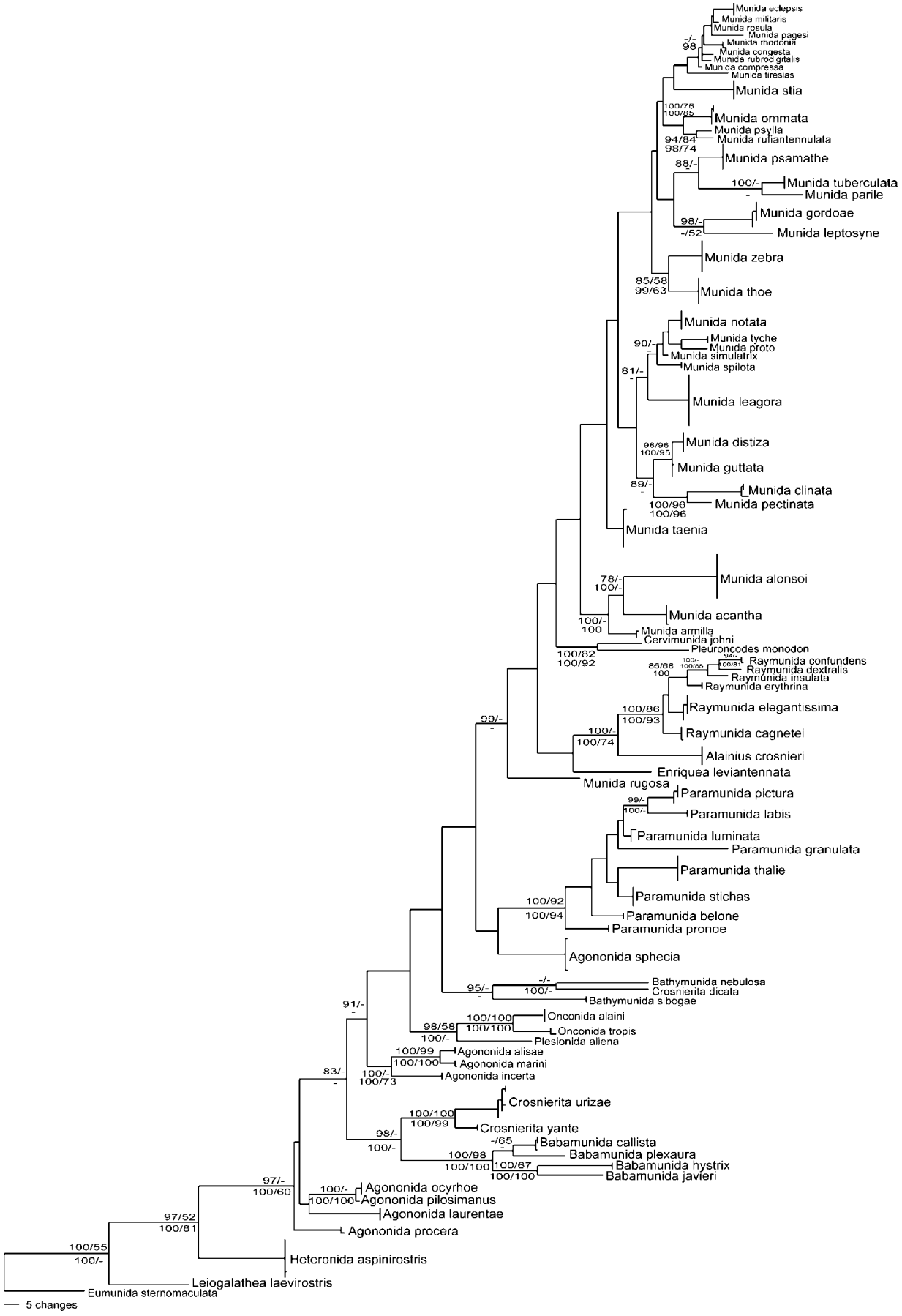
The new genus described here includes *B. callista*, *B. hystrix*, *B. javieri*, *B. plexaura*, and *B. brucei*. The latter species from Kenya and Mauritius is morphologically similar to *B. hystrix* from French Polynesia (Baba, 1974, 2005). However, we have not analysed the different genes of this species and further study will be needed to confirm its taxonomic status. The new genus is morphologically linked to *Munida*. The type species of *Munida* is *M. rugosa*, from the northeastern Atlantic. When we compared specimens of this species (NE Atlantic, MNHN) with most of the SW Pacific specimens included in Macpherson (1994), Machordom and Macpherson (2004) and other papers (see Baba, 2005; Macpherson, 2006), the most conspicuous morphological differences were: 1) the shape of the rostrum and supraocular spines, and 2) the ridges on the epistome. All other characters showed some degree of variability among species and are ineffective for distinguishing between the two genera.

In *M. rugosa* and other species of the genus *Munida*, the rostrum and supraocular spines are dorsally smooth and not carinate (Figs. 1E, G), yet they are carinate in *Babamunida*. Moreover, these carinae reach the anterior portion of the epigastric region (Figs. 1A, C). Also, the grooves between the rostrum and supraocular spines are always deeper in *Babamunida* than in *Munida*.

The ridges on the epistome differ between the two genera. The epistome is the broad median plate extending from the orbit to the mouth, and laterally to the carapace margins at the level of the mouth (see Martin and Abele, 1988 for the terminology). In Galatheidae, this structure has not been used for taxonomic purposes, although some of its characters have been used to distinguish other decapod taxa, e.g., Varunidae (Ng et al., 1999), Cambaridae (Cooper, 2006), Glypheoidea (Schram and Ahyong, 2002). On this plate, a marginal ridge is observed around the mouth. From the anterolateral portion of this marginal ridge, a lateral ridge extends anterolaterally to the carapace. The direction of this lateral ridge clearly differs in the species of *Munida* and *Babamunida*. In *Munida rugosa* and all the other species of *Munida* examined, the lateral ridge ends at the base of the basal antennal segment, at the level of the antennal gland aperture (Figs. 1F, H). In other galatheid genera (*Raymunida*, *Agononida* and *Paramunida*), this ridge runs in a similar direction (Fig. 3). However, in *Babamunida*, the lateral ridge ends at the ventral margin of the orbit, between the antennular and antennal peduncles (Figs. 1B, D, see also Macpherson and de Saint Laurent, 1991). Furthermore, in most species of *Munida* from the SW Pacific (also observed in *Cervimunida princeps* Benedict, 1902), the lateral ridge has a protuberance near the mouth (Fig. 1F). This protuberance is absent in *M. rugosa* (Fig. 1H) and in all species of *Babamunida* (Fig. 1B, D).

The morphology of the zoea I stages has been used as a source of characters to differentiate decapod crustacean genera (Schubart et al., 2002). The zoea I stage of *B. javieri* (Guerao et al., 2006) displays characters not previously described for larvae of *Munida*: namely the presence of a robust posterolateral process on the third pleomere and the $1 + 1 + 4$ pattern of setae on the endopod of the maxillule. The descriptions of the zoea I stages in other *Munida*, such as *M. subrugosa*, *M. tenuimana*, and *M. striola* do not show the process on the third abdominal somite, and the number of setae is $1 + 4$ instead of $1 + 1 + 4$ (see Guerao et al., 2006 for a complete description). This number of setae on the endopod of the maxillule has only been observed in *Cervimunida johni* (Porter, 1903) and *Sadayoshia edwarsii* (Miers, 1884) (see Fagetti, 1960; Fujita and Shokita, 2005). These larval differences would support the separation between *Munida* and *Babamunida*. However, additional data would be necessary to obtain a more complete knowledge of the relationships between larval stages and adult squat lobster genera.

The morphological characters of *Munida brucei* suggest its inclusion in the new genus, although we could not confirm this at the molecular level because of a lack of appropriate material. Our molecular results clearly suggest that *Babamunida* constitutes a well supported monophyletic genus, clearly differentiated from *Munida*. The range of inter-genus distances found between *Babamunida* and *Munida* was higher than the range between *Babamunida* and other related genera (Table 1). The closest related genus of *Babamunida* is *Crosnierita* (*C. urizae* and *C. yante*, but not *C. dicata*). Machordom and Macpherson (2004) suggested this relationship previously, although without statistical support.


Munida eclepsis
Munida militaris
Munida rosula
Munida pagesi
Munida rhodonia
Munida congesta
Munida rubrodigitalis
Munida compressa
Munida tiresias
Munida stia
Munida ommata
Munida psylla
Munida rufiantennulata
Munida psamathe
Munida tuberculata
Munida parile
Munida gordoae
Munida leptosyne
Munida zebra
Munida thoe
Munida notata
Munida tyche
Munida proto
Munida simulatrix
Munida spilota
Munida leagora
Munida distiza
Munida guttata
Munida clinata
Munida pectinata
Munida taenia
Munida alonsoi
Munida acantha
Munida armilla
Cervimunida johni
Pleuroncodes monodon
Raymunida confundens
Raymunida dextralis
Raymunida insulata
Raymunida erythrina
Raymunida elegantissima
Raymunida cagnetei
Alainius crosnieri
Enriquea leviantennata
Munida rugosa
Paramunida pictura
Paramunida labis
Paramunida luminata
Paramunida granulata
Paramunida thalie
Paramunida stichas
Paramunida belone
Paramunida pronoe
Agononida sphecia
Bathymunida nebulosa
Crosnierita dicata
Bathymunida sibogae
Onconida alaini
Onconida tropis
Plesionida aliena
Agononida alisae
Agononida marini
Agononida incerta
Crosnierita urizae
Crosnierita yante
Babamunida callista
Babamunida plexaura
Babamunida hystrix
Babamunida javieri
Agononida ocyrhoe
Agononida pilosimanus
Agononida laurentae
Agononida procera
Heteronida aspinirostris
Leiogalathea laevirostris
Eumunida sternomaculata
5 changes

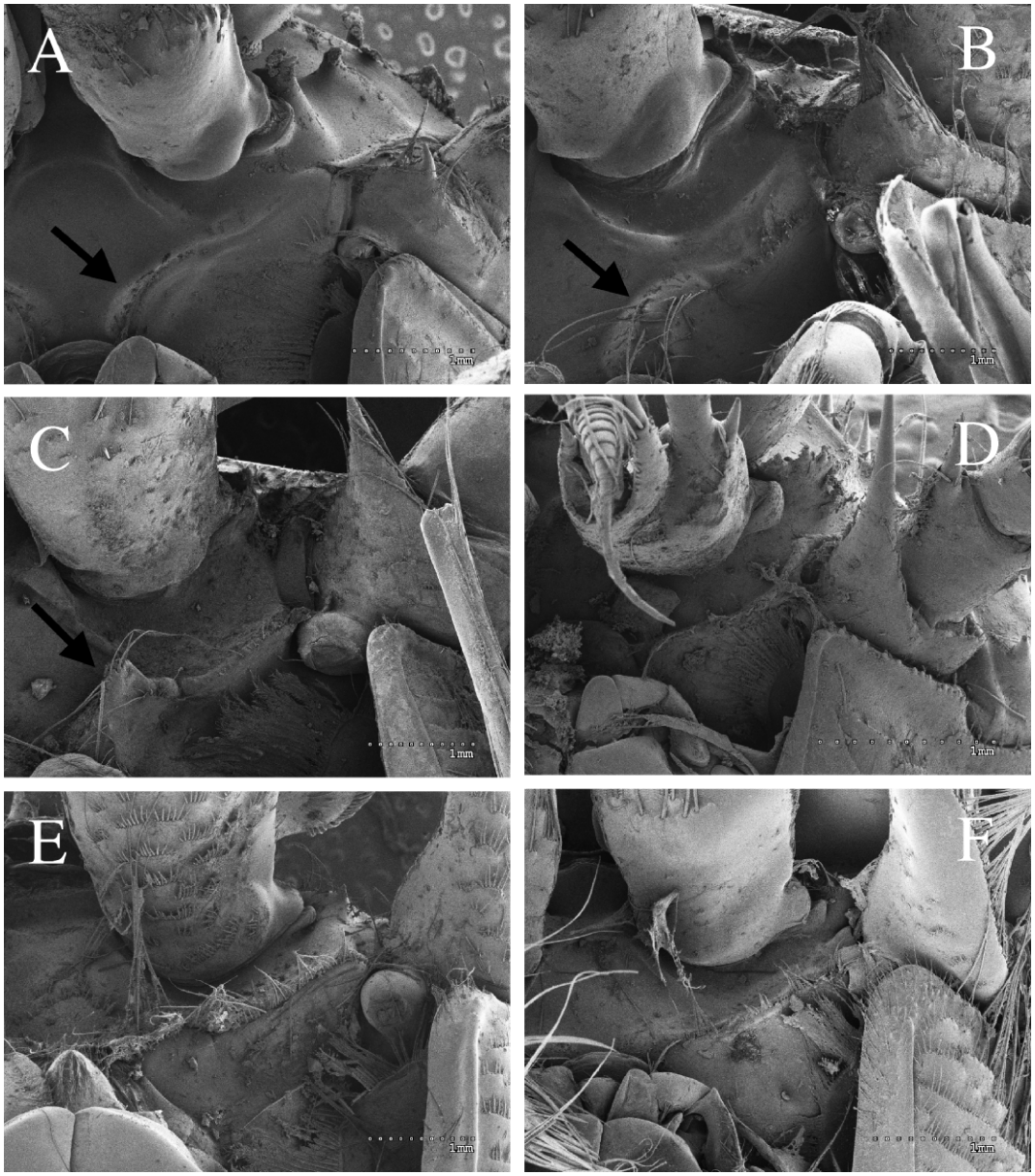


Fig. 3. Left antennule and antenna, including epistome. A, *Babamunida callista* F, 11.2 mm CL, Solomon Islands, cruise Salomon 2, stn 2200. B, *Munida rugosa* M, 18.0 mm CL, NE Atlantic, Jean Charcot, stn 9. C, *M. rubridigitalis* ov. F, 15.4 mm CL, New Caledonia, cruise Biocal, stn 52. D, *Raymunida cagnetei* M, 6.6 mm CL, French Polynesia, Marquesas Islands cruise Musorstom 9, stn 1177. E, *Agononida incerta* M, 15.2 mm CL, Indonesia, Kei Islands, cruise Karubar, stn 33. F, *Paramunida scabra* M, 12.3 mm CL, Indonesia, Kei Islands, cruise Karubar, stn 86. The arrows point out the direction of the lateral ridge. In *Babamunida* the lateral ridge ends between the antennular and antennal peduncles, and in *M. rugosa* and *M. rubridigitalis* it ends at the base of antennal segment.

Relationships between *Munida rugosa* and the other members of the genus *Munida* were not supported as a monophyletic cluster. Our 16S rRNA analysis indicated clear genetic differentiation between the specimens of *Munida* from the South Western Pacific previously analysed in Machordom and Macpherson (2004), and the type species, *Munida rugosa* from the North Eastern Atlantic Ocean. Thus, a molecular study including more species of the genus *Munida* from the Atlantic, should clarify the taxonomic and phylogenetic position of the genus between

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Fig. 2. Bayesian tree based on 16S rRNA gene sequences, showing phylogenetic relationships among *Babamunida* and related genera. Numbers above branches indicate posterior probabilities (Pp $\geq$ 80) and bootstrap values (Bv $\geq$ 50) for NJ. Numbers below branches indicate consensus values (Cv $\geq$ 95) for the MP and bootstrap values (Bv $\geq$ 50) for ML.

the two regions (D. Bailie, University of Belfast, in preparation).

The poor resolution of the relationships among the main genera could be a consequence of the rapid radiation of species of *Munida* and related genera suggested by Machordom and Macpherson (2004). Nevertheless, the use of nuclear and more conserved genes, such as the 18S rRNA gene, could help resolve relationships at the deepest nodes. Because of its slow evolution rate, this gene seems to be particularly useful for resolving phylogenetic relationships among crustaceans at the higher taxonomic levels (Spears et al., 1992; Harris et al., 2000; Macpherson et al., 2005).

The genetic relationships observed within the new genus indicated two differentiated groups, *B. callista-B. plexaura*, and *B. hystrix-B. javieri*. Intrageneric distances among them are fairly high, but within the range cited for other decapod taxa (Harrison and Crespi, 1999; Ptacek et al., 2001; Harrison, 2004). This high level of genetic divergence contrasts with the scarce number of morphological characters that differentiate the species (see Macpherson and de Saint Laurent, 1991; Macpherson, 1994). This feature, however, is not rare in crabs or squat lobsters, in which convergence in the adult form and cryptic speciation appears common (Baldwin et al., 1998; Harrison and Crespi, 1999; Macpherson and Machordom, 2005; Mathews, 2006). This intense stasis or convergence in morphological characters could be due to ecological characters or to certain morphological constraints that might be especially strong in these organisms.

The species of *Babamunida* also share several ecological characteristics. All species have conspicuous colour bands (yellow, purple or red) on the body and appendages and live in waters with hard bottoms, with numerous corals and sponges. The depth ranges of the species are: 37-119 m (*B. brucei*), 327-590 m (*B. callista*), 100-300 m (*B. hystrix*), 280-460 m (*B. javieri*), and 110-540 m (*B. plexaura*).

The combination of molecular and morphological information has proven to be very useful for resolving the phylogenetic relationships in this group, and emphasizes the importance of subtle characters of the adult and larval forms for the systematics of this genus.

Key to Species of the Genus *Babamunida*

1. Dorsal surface of carapace with numerous small spines on anterior half 2
— Dorsal surface of carapace with row of epigastric spines and 1 parahepatic spine on each side of the anterior half 3
2. Cheliped fingers more than 2.5 times as long as palm. Antennular basal article with distomesial spine as long as distolateral spine . . . . . *B. brucei*
— Cheliped fingers barely 2 times as long as palm. Antennular basal article with distomesial spine shorter than distolateral spine . . . . . *B. hystrix*
3. Whole posterior margin of third sternite contiguous to fourth sternite . . . . . *B. javieri*
— Median part of third sternite contiguous to fourth sternite 4
4. Carapace with numerous striae (ca. 14 on posterior half, including interrupted striae). Anterolateral spine of carapace reaching the level of the sinus between rostral and supraocular spines. Carpus of first walking leg with 1 spine on dorsal crest. . . . . *B. callista*
— Carapace with moderately dense striae (ca. 10 on posterior half, including interrupted striae). Anterolateral spine of carapace falling short of level of the sinus between rostral and supraocular spines. Carpus of first walking leg with 3 spines on dorsal crest. . . . . *B. plexaura*

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References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions. Automatic Control 19: 716-723.

Baba, K. 1974. *Munida brucei* sp. nov., a new galatheid (Decapoda, Anomura) from the East Coast of Africa. Annotationes Zoologicae Japonenses 47: 55-60.

———. 1988. Chirostylid and Galatheid Crustaceans (Decapoda: Anomura) of the "Albatross" Philippine Expedition, 1907-1910. Researches on Crustacea, Special Number 2: 1-203.

———. 2005. Deep-sea chirostylid and galatheid crustaceans (Decapoda: Anomura) from the Indo-Pacific, with a list of species. Galathea Report 20: 1-317.

———, 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.

Benedict, J. E. 1902. Descriptions of a new genus and forty-six new species of crustaceans of the family Galatheidae, with a list of the known marine species. Proceedings of the United States national Museum 26: 243-334.

Cooper, J. E. 2006. A new species of crayfish of the genus *Cambarus* Erichson, 1846 (Decapoda: Cambaridae) from the eastern Blue Ridge foothills and western Piedmont Plateau of North Carolina. Proceedings of the Biological Society of Washington 119: 67-80.

Crandall, K. A., and J. E. Fitzpatrick, Jr. 1996. Crayfish molecular systematics: using a combination of procedures to estimate phylogeny. Systematic Biology 45: 1-26.

Fabricius, J. C. 1775. Systema Entomologiae sistens Insectorum classes, ordines, genera, species, adjectis synonymis, locis, descriptionibus, observationibus. Flensburgi and Lipsiae, 32 + 832 pp.

———. 1793. Entomologia systematica emendata et aucta secundum classes, ordines, genera, species ajectis synonymis, locis, observationibus, descriptionibus. Halfniae 2: viii + 519 pp.

Fagetti, E. 1960. Huevos y el primer estadio larval del langostino (*Cervimunida johni*, Porter 1903). Revista Chilena de Historia Natural 55: 33-42.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783-791.

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.

Fujita, Y., and S. Shokita. 2005. The complete larval development of *Sadayoshia edwardsii* (Miers, 1884) (Decapoda: Anomura: Galatheidae) described from laboratory-reared material. Journal of Natural History 39: 865-886.

Guerao, G., E. Macpherson, S. Samadi, B. Richer de Forges, and M. C. Boisselier. 2006. Description of the first larval stage of five Galatheoidea species from Western Pacific (Crustacea: Decapoda: Anomura). Zootaxa 1227: 1-29.

Guindon, S., and O. Gascuel. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52: 696-704.

Harris, J., L. S. Maxson, L. F. Braithwaite, and K. Crandall. 2000. Phylogeny of the thoracian barnacles based on 18SrDNA sequences. Journal of Crustacean Biology 20: 393-398.

Harrison, J. S. 2004. Evolution, biogeography, and the utility of mitochondrial 16S and COI genes in phylogenetic analysis of the crab genus *Austinixa* (Decapoda: Pinnotheridae). Molecular Phylogenetics and Evolution 30: 743-754.

Harrison, M. K., and B. J. Crespi. 1999. Phylogenetics of *Cancer* crabs (Crustacea: Decapoda: Brachyura). Molecular Phylogenetics and Evolution 12: 186-199.

Leach, W. E. 1820. Galatéadées. Dictionaire des Sciences Naturelles 18: 49-56.

Machordom, A., and E. Macpherson. 2004. Rapid radiation and cryptic speciation in galatheid crabs of the genus *Munida* and related genera in the South West Pacific: molecular and morphological evidence. Molecular Phylogenetics and Evolution 33: 259-279.

Macpherson, E. 1994. Crustacea Decapoda : Studies on the genus *Munida* Leach, 1820 (Galatheidae) in New Caledonian and adjacents waters with descriptions of 56 new species. In, A. Crosnier (ed.), Résultats des Campagnes MUSORSTOM. Vol. 12, Mémoires du Muséum national d'Histoire naturelle 161: 421-569.

———. 1998. A new genus of Galatheidae (Crustacea, Anomura) from the Western Pacific Ocean. Zoosystema 20: 351-355.

———. 2006. Galatheidae (Crustacea, Decapoda) from the Austral Islands, Central Pacific. In, B. Richer de Forges and J. L. Justine (eds.), Tropical Deep-Sea Benthos. Vol. 24, Memoires du Muséum national d'Histoire naturelle 193: 285-333.

———, and M. De Saint Laurent. 1991. Galatheid crustaceans of the genus *Munida* Leach, 1818, from French Polynesia. Bulletin du Muséum national d'Histoire naturelle (4), 13, sect. A, (3-4): 373-422.

———, 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.

———, and A. Machordom. 2005. Use of morphological and molecular data to identify three new sibling species of the genus *Munida* Leach, 1820 (Crustacea, Decapoda, Galatheidae) from New Caledonia. Journal of Natural History 39: 819-834.

———, W. Jones, and M. Segonzac. 2005. A new squat lobster family of Galatheoidea (Crustacea, Decapoda, Anomura) from the hydrothermal vents of the Pacific–Antartic Ridge. Zoosystema 27: 709-723.

Martin, J. W., and L. G. Abele. 1988. External morphology of the genus *Aegla* (Crustacea: Anomura: Aeglidae). Smithsonian Contributions to Zoology 453: 1-46.

Mathews, L. 2006. Cryptic biodiversity and phylogeograhpical patterns in a snapping shrimp species complex. Molecular Ecology 15: 4049-4063.

Miers, E. J. 1884. Crustacea. In: Report on the Zoological Collections made in the Indo-Pacific Ocean during the voyage of H.M.S. Alert 1881-2: 178-322, 513-575, plates 18-34, 46-52. London: British Museum.

Ng, N. K., J. Y. Guo, and P. K. L. Ng. 1999. Generic affinities of *Eriocheir leptognathus* and *E. formosa* with description of a new genus (Brachyura : Grapsidae : Varuninae). Journal of Crustacean Biology 19: 154-170.

Nixon, K. C. 2002. WinClada ver. 1.00.08. Published by the author, Ithaca, New York.

Porter, C. E. 1903. Carcinologia Chilena. Descripción de un nuevo Galateido. Revista Chilena de Historia Natural 7: 274-277, pl. 17.

Posada, D., and K. A. Crandall. 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14: 817-818.

Ptacek, M. B., S. K. Sarver, M. J. Childress, and W. F. Herrnkind. 2001. Molecular phylogeny of the spiny lobster genus *Panulirus* (Decapoda: Palinuridae). Marine and Freshwater Research 52: 1037-1047.

Saint Laurent, M., and E. Macpherson. 1990. Crustacea Decapoda: le genre Eumunida Smith, 1883 (Chirostylidae) dans les eaux neo-caledoniennes. Memoires du Museum National d'Histoire Naturelle Serie A Zoologie 145: 227-288.

Sambrook, J., E. F. Fritsch, and T. Maniatis. 1989. Molecular Cloning: A Laboratory Manual. Second edition. Cold Spring Harbor Laboratory Press, New York.

Samouelle, G. 1819. The entomologist's useful compendium, or an introduction to the knowledge of British insects. Thomas Boys, London. 496 pp.

Sars, G. O. 1872. Undersogelser over Hardangerfjordens Fauna I Crustacea. Forhandlinger I Videnskabs-Selskabet I Kristiania 1871: 246-286.

Schram, F. R., and S. T. Ahyong. 2002. The higher affinities of *Neoglyphea inopinata* in particular and the Glypheoidea (Decapoda, Reptantia) in general. Crustaceana 75: 629-635.

Schubart, C. D., J. A. Cuesta, and D. L. Felder. 2002. Glyptograpsidae, a new brachyuran family from Central America: larval and adult morphology, and a molecular phylogeny of the Grapsidae. Journal of Crustacean Biology 22: 28-44.

Spears, T., L. G. Abele, and W. Kim. 1992. The monophyly of brachyuran Crabs: a phylogenetic study based on 18S RNA. Systematic Biology 41: 446-461.

Swofford, D. L. 2002. PAUP*: Pylogenetic Analysis Using Parsimony (* and other methods), Version 4. Sinauer Associates, Sunderland, MA.

Syoc, R. J. V. 1995. Barnacle mitochondrial DNA: determining genetic relationships among species of *Pollicipes*, pp. 269-296. In, F. R. Schram and J. T. Hoeg (eds.), New Frontiers in Barnacle Evolution. Crustacean Issues 10. A. A. Balkema, Rotterdam.

Tamura, K., and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10: 512-526.

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