



## ***Allogalathea* (Decapoda: Galatheidae): a monospecific genus of squat lobster?**

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The genus *Allogalathea* was established by Baba in 1969 to include the well-known species *Galathea elegans*. This species is widely distributed across the Indo-West Pacific Ocean, and is characterized by living in close association with crinoids, and by its conspicuous coloration. Although the genus is considered monospecific, different colour patterns and discrete morphological variations mainly associated with the rostrum and chelipeds have been reported. These differences could point to cryptic species, thereby questioning *Allogalathea* as a monotypic taxon. To address this issue, we sequenced the mitochondrial *cytochrome oxidase I* (COI; 658 bp) and 16S rRNA (882 bp) genes and the nuclear gene *phosphoenolpyruvate carboxykinase* (PEPCK; 598 bp) in numerous specimens from eight different localities, and also examined their morphological characters. DNA sequences were analysed using maximum-parsimony, maximum-likelihood, and Bayesian approaches of phylogenetic inference. The resulting trees were combined with morphological evidence to test species boundaries. Our molecular data revealed four deeply divergent clades, which can be distinguished by subtle morphological differences in the spinulation and length: breadth ratio of the P1 carpus, spinulation of the walking legs, and shape of the rostrum. Our findings indicated that *Allogalathea elegans* is in fact a species complex comprising four different species, which, although genetically very distinct, are morphologically very similar. We provide morphological descriptions and a key to these four species of the genus.

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**ADDITIONAL KEYWORDS:** mitochondrial genes – molecular systematics – morphological characters – PEPCK gene.

### INTRODUCTION

Studies on monospecific or cosmopolitan species of a wide range of both marine and terrestrial taxa have revealed that the real diversity of many groups is currently underestimated. In effect, many such taxa have been discovered to be species complexes with high morphological similarity, but with genetically distinct species (Hebert *et al.*, 2004; Vovlas *et al.*, 2008; Demes, Graham & Suskiewicz, 2009).

Species identification among the squat lobsters of the family Galatheidae is proving particularly difficult because of their many conservative morphological

traits (Jones & Macpherson, 2007; Cabezas, Macpherson & Machordom, 2009). Traditionally, the taxonomy of this group has been based on morphological characters, but current molecular techniques have proven to be powerful tools for species delineation (Macpherson & Machordom, 2001). Within this decapod family, 12 genera are considered monospecific (e.g. *Anomoeomunida* Baba, 1993, *Enriquea* Baba, 2005, *Setanida* Macpherson, 2006, and *Tasmanida* Ahyong, 2007). However, there are few records of any of these monospecific taxa, and there is also limited collected material, with the exception of the genus *Allogalathea*, for which numerous records and specimens are available.

The genus *Allogalathea* was established in 1969 by Baba to include the well-known species *Galathea*

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*elegans* Adams & White, 1848, the original description of which was based upon specimens collected in Corregidor, the Philippines. Nevertheless, a number of taxa are now considered junior synonyms of *A. elegans*: *Galathea longirostris* Dana, 1852, from the Fiji Islands, found at 18 m; *Galathea grandirostris* Stimpson, 1858, from Kagoshima Bay, Japan, found at 9 m; *Galathea deflexifrons* Haswell, 1882, from Albany Passage, Queensland, Australia; and *Galathea longirostris* Yokoya, 1936, from Misaki, Sagami Bay, Japan. A complete list of citations and synonymies of *A. elegans* is provided in Baba *et al.* (2008, 2009). Unfortunately, the type specimens of *G. longirostris* Dana, 1852, *G. longirostris* Yokoya, 1936, and *G. grandirostris* Stimpson, 1858 are lost. The type specimen of *G. deflexifrons* Haswell, 1882 at the Australian Museum is preserved dry, and its morphological details are obscure (e.g. an epipods study), making a careful examination of the specimen without damage difficult.

*Allogalathea elegans* is considered a shallow water species, living at depths between 0 and 146 m, usually associated with crinoids, and widely distributed in the Indo-West Pacific region. The species has been cited from the eastern coast of Africa to the Fiji Islands, and from Japan to southern Australia (Baba *et al.*, 2008, 2009). This genus is easily differentiated from other genera of the family Galatheididae by a triangular rostrum, which is extremely elongate, dorsally flattened, and ventrally carinate, with between five and nine lateral teeth, and by a carapace with setiferous striae (Baba, 1969). Previous works have reported different colour patterns in this species (Miyake, 1938; Baba, 1979), and the study of numerous specimens from Indonesia revealed small differences in the setation and spinulation of the chelipeds (Baba, 1979). Furthermore, the presence and number of epipods on the pereopods and the relative length of the rostrum also vary. This variability suggests that the occurrences of *A. elegans* mentioned by different authors should be revised in order to evaluate the morphological differences previously reported, and the relative importance of the different colour patterns.

A large number of specimens of *Allogalathea* have been collected in numerous expeditions over the past decades in the Indian and western Pacific Oceans. Here, we re-examine all this material in addition to the type material of *A. elegans* from Corregidor (the Philippines), using a combined morphological and molecular approach based on two mitochondrial (*cytochrome oxidase I*, *COI*, and *16S* rRNA) and one nuclear marker (*phosphoenolpyruvate carboxykinase*, *PEPCK*). Mitochondrial genes have been typically used to elucidate phylogenetic relationships in the family Galatheididae (Lin, Chan & Chu, 2004; Cubelio

*et al.*, 2007; Schnabel, Martin & Moffitt, 2009). We also selected the *PEPCK* marker for this study because this nuclear gene has shown good potential for resolving relationships in decapods at high taxonomic levels (Tsang *et al.*, 2008; Ma, Chan & Chu, 2009), and the high divergence values reported by Tsang *et al.* (2008) for three species of *Panulirus* (approximately 6%) suggested it is also capable of resolving species-level relationships.

Our results revealed the existence of four different species that are genetically distinct yet morphologically very similar. Previous records of *Allogalathea* species are provisionally revised when a description and illustrations are available. However, the existence of additional species of *Allogalathea* is likely, and a more detailed study, including more specimens from other regions in combination with molecular data, is desirable.

## MATERIAL AND METHODS

### SAMPLING AND IDENTIFICATION

Specimens were collected by divers or using beam trawls or Waren dredges in numerous expeditions to the western Pacific Ocean, e.g. Taiwan, Mariana Islands, Philippines, Indonesia, Vanuatu, New Caledonia, and the western Indian Ocean, e.g. Madagascar, the Mozambique Channel, and the Red Sea. The measurements of specimens provided are postorbital carapace lengths. The terminology used mainly follows that of Zariquiey Álvarez (1952), Baba & de Saint Laurent (1996), and Baba (2005). Following Baba (2005), the terms flexor and extensor borders of articles are only used for the maxilipeds and dactyli of the walking legs. The following abbreviations are used in the text: F, female; M, male; Mxp, maxiliped; ovig., ovigerous; P1, pereopod 1, cheliped; and P2–P4, pereopods 2–4, first to third walking legs.

All specimens, including the types of the new species, are deposited in the Museum national d'Histoire naturelle, Paris (MNHN), Florida Museum of Natural History, Gainesville (UF), the Natural History Museum, London (BMNH), the Australian Museum, Sydney (AM), and the collection of the National Taiwan Ocean University (NTOU).

### DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

Total genomic DNA was isolated from abdominal muscle tissue or pereopods using the magnetic Charge Switch gDNA Micro Tissue Kit (Invitrogen). Three genes were amplified, two mitochondrial (*16S* rRNA and *COI*) and one from the nuclear genome (*PEPCK*). Only in some specimens representing the different mitochondrial clades was the nuclear gene amplified (see Table 1). Amplification was conducted

**Table 1.** Species of *Allogalatheia* examined genetically, and their corresponding codes in the phylogenetic tree, geographic location, depth, cruise, and GenBank accession number

Species	Code	Locality	Depth (m)	Cruise	16S rRNA	COI	PEPCK
<i>Allogalatheia babai</i> sp. nov.	Allo2	New Caledonia	15–35	LIFOU	GU392121	GU392164	X
<i>Allogalatheia inermis</i> sp. nov.	Allo3	New Caledonia	120	SMIB 5	GU392122	GU392165	X
<i>Allogalatheia babai</i> sp. nov.	Allo4	New Caledonia	15–35	LIFOU	GU392123	GU392166	GU392207
<i>Galathea</i> sp1	Allo5	New Caledonia	15–20	LIFOU	GU392124	GU392167	GU392208
<i>Allogalatheia elegans</i>	Allo6	Vanuatu	58–59	SANTO	GU392125	GU392168	GU392209
<i>Allogalatheia elegans</i>	Allo7	Vanuatu	46–55	SANTO	GU392126	GU392169	GU392210
<i>Allogalatheia babai</i> sp. nov.	Allo8	Vanuatu	18–20	SANTO	GU392127	GU392170	GU392211
<i>Allogalatheia elegans</i>	Allo9	Vanuatu	Intertidal	LIFOU	GU392128	GU392171	GU392212
<i>Galathea</i> sp2	Allo10	New Caledonia	Intertidal	LIFOU	GU392129	GU392172	GU392213
<i>Allogalatheia elegans</i>	Allo11	Vanuatu	18–20	SANTO	GU392130	GU392173	X
<i>Allogalatheia inermis</i> sp. nov.	Allo12	Vanuatu	11	SANTO	GU392131	GU392174	GU392214
<i>Allogalatheia elegans</i>	Allo13	Vanuatu	86–118	SANTO	GU392132	GU392175	GU392215
<i>Allogalatheia elegans</i>	Allo14	Vanuatu	71–104	SANTO	GU392133	GU392176	X
<i>Allogalatheia elegans</i>	Allo15	Vanuatu	0–45	SANTO	GU392134	GU392177	GU392216
<i>Allogalatheia babai</i> sp. nov.	Allo17	New Caledonia	No depth	Lagoon Samples	GU392135	GU392178	X
<i>Allogalatheia babai</i> sp. nov.	Allo18	New Caledonia	No depth	Lagoon Samples	GU392136	GU392179	GU392217
<i>Allogalatheia babai</i> sp. nov.	Allo19	New Caledonia	No depth	Lagoon Samples	GU392137	GU392180	GU392218
<i>Allogalatheia elegans</i>	Allo20	New Caledonia	No depth	Lagoon Samples	GU392138	GU392181	GU392219
<i>Allogalatheia babai</i> sp. nov.	Allo21	New Caledonia	No depth	Lagoon Samples	GU392139	GU392182	GU392220
<i>Allogalatheia babai</i> sp. nov.	Allo22	New Caledonia	No depth	Lagoon Samples	GU392140	GU392183	X
<i>Allogalatheia elegans</i>	Allo23	New Caledonia	No depth	Lagoon Samples	GU392141	GU392184	GU392221
<i>Allogalatheia elegans</i>	Allo25	New Caledonia	No depth	Lagoon Samples	GU392142	GU392185	GU392222
<i>Allogalatheia inermis</i> sp. nov.	Allo27	Thailandia	No depth	Lagoon Samples	GU392143	GU392186	X
<i>Allogalatheia inermis</i> sp. nov.	Allo28	Thailandia	No depth	Lagoon Samples	GU392144	GU392187	X
<i>Allogalatheia elegans</i>	Allo29	New Caledonia	56	Lagoon Samples	GU392145	GU392188	X
<i>Allogalatheia inermis</i> sp. nov.	Allo30	Vanuatu	11	SANTO	GU392146	GU392189	X
<i>Allogalatheia elegans</i>	Allo31	Vanuatu	102–120	SANTO	GU392147	GU392190	GU392223
<i>Allogalatheia inermis</i> sp. nov.	Allo32	New Caledonia	No depth	Lagoon Samples	GU392148	GU392191	GU392224
<i>Allogalatheia elegans</i>	Allo33	New Caledonia	No depth	Lagoon Samples	GU392149	GU392192	GU392225
<i>Allogalatheia babai</i> sp. nov.	Allo34	New Caledonia	No depth	Lagoon Samples	GU392150	GU392193	GU392226
<i>Allogalatheia elegans</i>	Allo35	New Caledonia	No depth	Lagoon Samples	GU392151	GU392194	GU392227
<i>Allogalatheia babai</i> sp. nov.	Allo36	New Caledonia	No depth	Lagoon Samples	GU392152	GU392195	GU392228
<i>Allogalatheia longimana</i> sp. nov.	Allo38	PhilippInes	111–115	MUSORSTOM 3	GU392153	GU392196	GU392229
<i>Allogalatheia elegans</i>	Allo39	PhilippInes	73–84	MUSORSTOM 3	GU392154	GU392197	X
<i>Allogalatheia elegans</i>	Allo42	Mozambique	100–110	MAINBAZA	GU392155	GU392198	GU392230
<i>Allogalatheia elegans</i>	Allo43	Madagascar	26		GU392156	GU392199	X
<i>Allogalatheia longimana</i> sp. nov.	Allo44	Philippines	189–194	MUSORSTOM 3	GU392157	GU392200	X
<i>Allogalatheia longimana</i> sp. nov.	Allo45	Philippines	120–123	MUSORSTOM 3	GU392158	GU392201	X
<i>Allogalatheia longimana</i> sp. nov.	Allo46	Philippines	111–115	MUSORSTOM 3	GU392159	GU392202	X
<i>Allogalatheia elegans</i>	Allo14196	Madagascar	0–12		GU392160	GU392203	GU392231
<i>Allogalatheia elegans</i>	Allo14641	Madagascar	24–25		GU392161	GU392204	GU392232
<i>Allogalatheia babai</i> sp. nov.	Allo7244	Okinawa	18–23		GU392162	GU392205	X
<i>Allogalatheia babai</i> sp. nov.	Allo8069	Christmas Islands	No depth		GU392163	GU392206	GU392233

**Table 2.** Primer sequences used for PCR amplification

Target gene	Primer	Direction	Primer sequence	Reference
<i>16S</i> rRNA	16S-F2	Forward	CGRGYTTTTATATCTGGTT	Present study
	16S-R	Reverse	TTATGCTACCTTRGCACAG	Present study
	16S-AR	Forward	CGCCTGTTTATCAAAAACAT	Palumbi <i>et al.</i> , 1991
	16S-BR	Reverse	CCGGTCTGAACTCAGATCACGT	Palumbi <i>et al.</i> , 1991
<i>COI</i>	LCO-1490	Forward	GGTCAACAAATCATAAAGATATTGG	Folmer <i>et al.</i> , 1994
	COI-H	Reverse	TCAGGGTGACCAAAAAATCA	Machordom & Macpherson, 2004
<i>PEPCK</i>	PEPCK-for2	Forward	GCAAGACCAACCTGGCCATGATGAC	Tsang <i>et al.</i> , 2008
	PEPCK-rev3	Reverse	CGGGYCTCCATGCTSAGCCARTG	Tsang <i>et al.</i> , 2008

using universal or newly designed primers (Table 2). Two different fragments of *16S* rRNA were amplified. For the mitochondrial genes, polymerase chain reactions (PCRs) were performed in a final volume of 50  $\mu$ L. The PCR mix contained 2  $\mu$ L of DNA template, 0.16  $\mu$ M of both primers, 0.2 mM of each deoxyribonucleotide triphosphate (dNTP), 5  $\mu$ L of buffer 10X, 3  $\mu$ L of a 50 mM solution of  $MgCl_2$ , 0.5  $\mu$ L of bovine serum albumin (BSA; 10 mg mL<sup>-1</sup>), 1.5 U of Taq DNA polymerase (Biotools) and double-distilled water (ddH<sub>2</sub>O). Nuclear PCR reactions were conducted in a 50- $\mu$ L final volume containing 2  $\mu$ L of DNA template, 0.2  $\mu$ M of both primers, 0.2 mM of each dNTP, 5  $\mu$ L of buffer 10X, 3  $\mu$ L of a 50-mM solution of  $MgCl_2$ , 1.5 U of Taq DNA polymerase (Biotools), and ddH<sub>2</sub>O. The cycling conditions for the mitochondrial genes were an initial denaturation step of 94 °C for 4 min, followed by 39 cycles at 94 °C for 30 s, an annealing temperature of 45.5 °C (*16S* rRNA) or 45–50 °C (*COI*) for 1 min, 72 °C for 1 min, and a final extension at 72 °C for 10 min. For the nuclear gene, we performed an initial step of 94 °C for 3 min followed by 35 cycles at 94 °C for 30 s, 58–60 °C for 30 s, 72 °C for 1 min, and a final extension at 72 °C for 10 min. After PCR product purification by ethanol/sodium acetate precipitation, samples were cycle-sequenced using the ABI Prism BigDye Terminator, and subsequently run on an ABI 3730 Genetic Analyzer (Applied Biosystems). All sequences were deposited in GenBank under the accession numbers provided in Table 1. Specimens used for molecular analyses can be identified by a code (Allo) in the material examined of each species (Table 1).

#### PHYLOGENETIC ANALYSIS

DNA sequences were edited using SEQUENCHER 4.6 (Gene Codes) and aligned manually in SE-AL v2.0a11 (Rambaut, 1996).

Phylogenies were constructed for each individual gene and congruence among the mitochondrial genes

was tested using the incongruence length differences (ILD) test (Mickey & Farris, 1981; Farris *et al.*, 1994), implemented in PAUP\* v4.0b10, along with the homogeneity partition test. Additionally, Bayesian tree topologies resulting from independent analyses of each of the genes were compared to find conflicting clades with support of greater than 95%, as the usefulness of the ILD test has been criticized (Barker & Lutzoni, 2002). Two different data sets were independently analyzed, one with information from both mitochondrial markers and the other with information from the nuclear gene.

The evolutionary molecular model that best fitted our data sets was selected using MODELTEST v3.07 (Posada & Crandall, 1998) under Akaike's information criterion (AIC; Akaike, 1974). This approach reduces the number of unnecessary parameters by penalizing more complex models (Nylander *et al.*, 2004). Phylogenetic reconstructions were obtained using the Bayesian-inference (BI), maximum-likelihood (ML), and maximum-parsimony (MP) methods. Bayesian analyses were performed using MRBAYES v3.1.2 (Huelsenbeck & Ronquist, 2001), with two independent runs of four Metropolis-coupled chains, with 5 000 000 generations each, to estimate the posterior probability distribution. Model parameters were estimated as part of the analysis with uniform default priors. The program TRACER v1.4 (Rambaut & Drummond, 2003) was used to assess run convergence and determine the numbers of trees needed as burn-in. Trees prior to the log-likelihood stabilization tree were discarded. To ensure that the analysis approached the optimal posterior distribution, an additional run was performed using the same conditions. Parsimony procedures were performed through a heuristic search using a tree bisection reconnection (TBR) swapping algorithm, ten random stepwise additions, and treating indels as missing data using PAUP\* v4.0b10. Maximum-likelihood analyses were conducted in PHYML v2.4.4 (Guindon & Gascuel, 2003) using the evolutionary model

selected by MODELTEST v3.7 (Posada & Crandall, 1998). The robustness of the MP and ML inferred trees was tested by nonparametric bootstrapping (Felsenstein, 1985), with 1000 pseudoreplicates in each case. Bayesian posterior probabilities (BPPs) were used as a measure of the robustness of Bayesian trees. To test the monophyly of *Allogalathea*, two species of the genus *Galathea* were included in the phylogenetic analyses. These two specimens were provisionally denoted *Galathea* sp1 and *Galathea* sp2 in the phylogenetic trees.

## RESULTS

### SYSTEMATICS

*Genus Allogalathea* Baba, 1969

*Allogalathea* Baba, 1969: 5 (gender: female); Poore, 2004: 231; Baba *et al.*, 2009: 87.

*Type species: Allogalathea elegans* (Adams & White, 1848).

*Diagnosis:* Dorsal surface of carapace unarmed, with distinct transverse striae bearing fine but coarse setae, lateral margin medially convex with row of spines. Rostrum horizontal or slightly deflected, long, dorsally flattish, carinated ventrally, with between five and nine small lateral teeth and without supraocular spines. Tergites from abdominal segments unarmed. Telson relatively short, subdivision incomplete. Ocular peduncles short, cornea well pigmented. Orbit well-delimited, lateral limit rounded or bluntly produced. Basal article of antennule with three terminal spines. Mxp3 ischium subtriangular in cross section, merus with flexor spines. P1 spinose, with setiferous squamae. P2–P4 moderately short, with row of spines on dorsal crests of meri and carpi; flexor margin of dactyli with row of teeth each bearing corneous seta. Two pairs of male gonopods. Usually associated with crinoids.

*Allogalathea babai* sp. nov. (Figs 1–6A)

*Galathea elegans* Miyake, 1938: 37, figure 1, plate 2, figure D (in part).

*Allogalathea elegans* Baba, 1969: 6, figure 1 (in part); Baba, 1977: 252 (in part); Baba, 1979: 654, figure 3 (in part); Baba, 1982: 61; Baba, 1988: 54 (in part); Steene, 1990: 158, 320; Gosliner, Behrens & Williams, 1996: 226, colour figure 820 (in part); Mine-mizu, 2000: 168, with three colour figures (in part); Jones & Morgan, 2002: 133, colour figure (no record); Kawamoto & Okuno, 2003: 93, unnumbered colour figures (in part); Poore, 2004: 231, plate 13g (in part, compilation); Kawamoto, & Okuno, 2006: 93, unnumbered colour figure (in

part); Macpherson, 2008: 289 (in part); Baba *et al.*, 2008: 53 (in part, compilation), figure 2C.

*Material examined:* Japan, Okinawa, Ie Island, 26°43.474'N, 127°49.899'E, 7 July 2004, 18–23 m: one M, 4.1 mm, one ovig. F 6.6 mm (UF 7244, Allo7244).

Mariana Islands, Guam, Luminao ref., 21 May 1999, depth 10 m, under rubble: one M 3.1 mm, one ovig. F 3.9 mm (UF 277); Pati Point, off Gorgonian, 28 July 2000, 24 m a.s.l.: one M 3.1 mm, one ovig. F 5.0 mm (UF 3856).

South China Sea. Macclesfield Bank, 24 m: one M 5.2 mm (BMNH 1892.8.28).

Indonesia. Rumphius Expedition II, East coast of Marsegu Island, 18 January 1975: one M 3.4 mm, on *Oxycomanthus bennetti* (MNHN-Ga1133); Rumphius Expedition II, Banda Sea, northern tip of Banda Sesar I., Banda Island, 30 January 1975: one F 5.6 mm, on *Oxycomanthus bennetti* (MNHN-Ga1123).

Christmas Islands. North coast: one ovig. F 3.4 mm (UF 8069, Allo8069).

Vanuatu. Santo. Stn DB33, 15°34.7'S, 167°13.8'E, 18 September 2006, 14–25 m: one M 2.4 mm (MNHN-Ga7353); Stn FR1, 15°32.3'S, 167°13.1'E, 10 September 2006, 18–20 m: one ovig. F 8.4 mm (MNHN-Ga7354, Allo8).

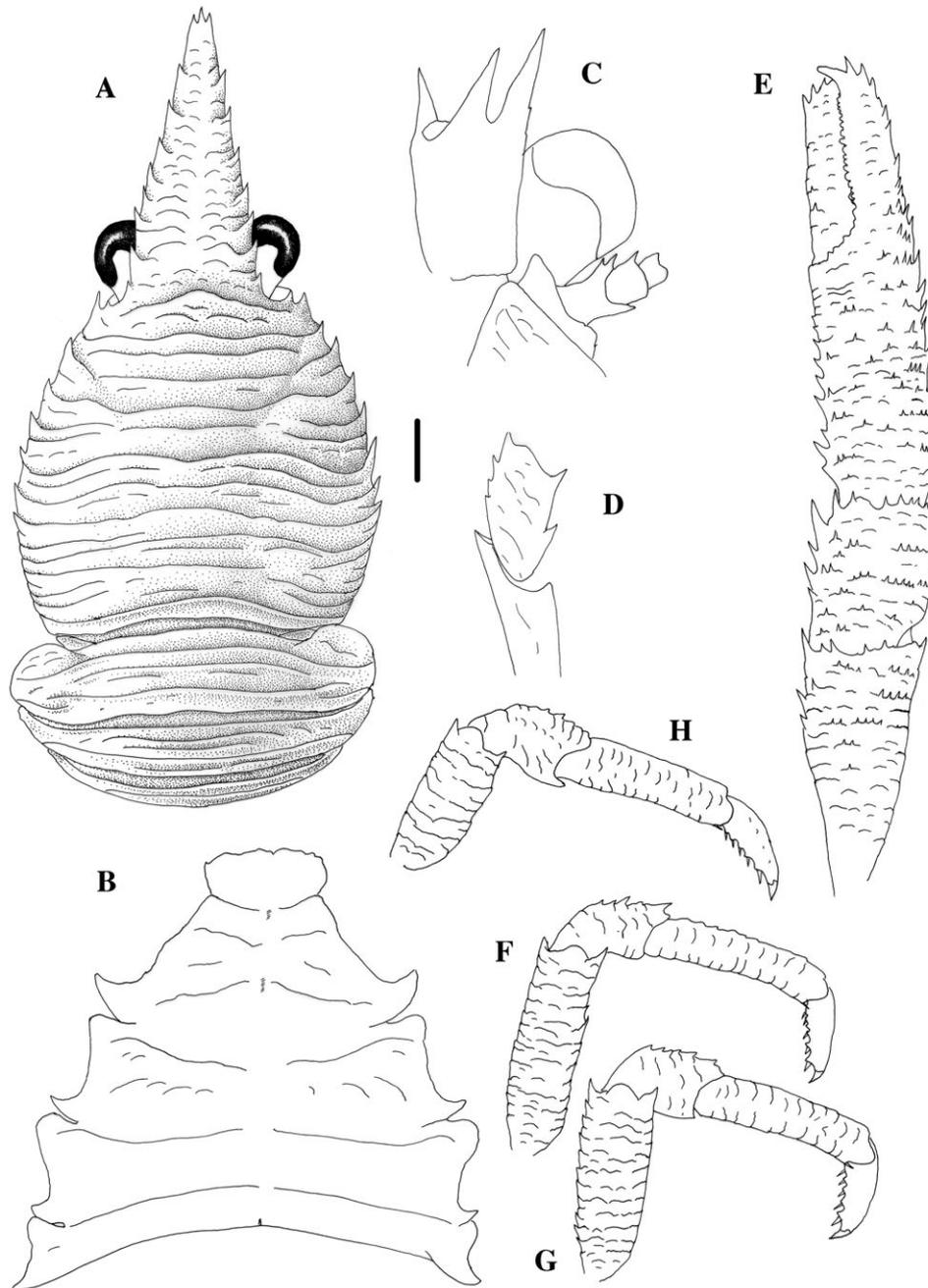
New Caledonia. Lagoon, Touho, in front of Kohé, 8 September 1993: 21 M 2.9–4.8 mm, eight ovig. F 4.7–8.5 mm (MNHN-Ga7419), one ovig. F 8.7 mm (MNHN-Ga7420, Allo17), one ovig. F 7.6 mm (MNHN-Ga7421, Allo18), one ovig. F 6.5 mm (MNHN-Ga7422, Allo19), one ovig. F 4.7 mm (MNHN-Ga7423, Allo22), one M 4.7 mm (MNHN-Ga7424, Allo34), one ovig. F 4.3 mm (MNHN-Ga7425, Allo36), one ovig. F 5.4 mm (MNHN-Ga7429, Allo21); 30 August 1993: one ovig. F 6.9 mm, one F 2.9 mm (MNHN-Ga7355).

Touho Bank, 10 m: one M 2.5 mm (MNHN-Ga7426); Touho Bank, 28 August 1993: one M 4.9 mm (MNHN-Ga7356).

Chesterfield Islands. Corail 2. Stn CP90, 19°03'S, 158°56'E, 26 July 1988, 44–48 m: one M 6.1 mm, one ovig. F 8.0 mm (MNHN-Ga7357).

Loyalty Islands. Lifou Island. Lifou 2000. Stn 1440, 20°47.2'S, 167°08.6'E, 11–16 November 2000: 15–35 m: one M 2.8 mm, one ovig. F 3.8 mm (MNHN-Ga7358); one M 3.3 mm (MNHN-7359, Allo2); one ovig. F 4.9 mm (MNHN-Ga7360); 19 November 2000, dive: one M 3.4 mm (MNHN-Ga7361, Allo4).

*Types:* The ovigerous female of postorbital carapace length 5.4 mm, from New Caledonia (lagoon 8 September 1993, MNHN-Ga7429) was selected as the holotype. All the other specimens are paratypes.

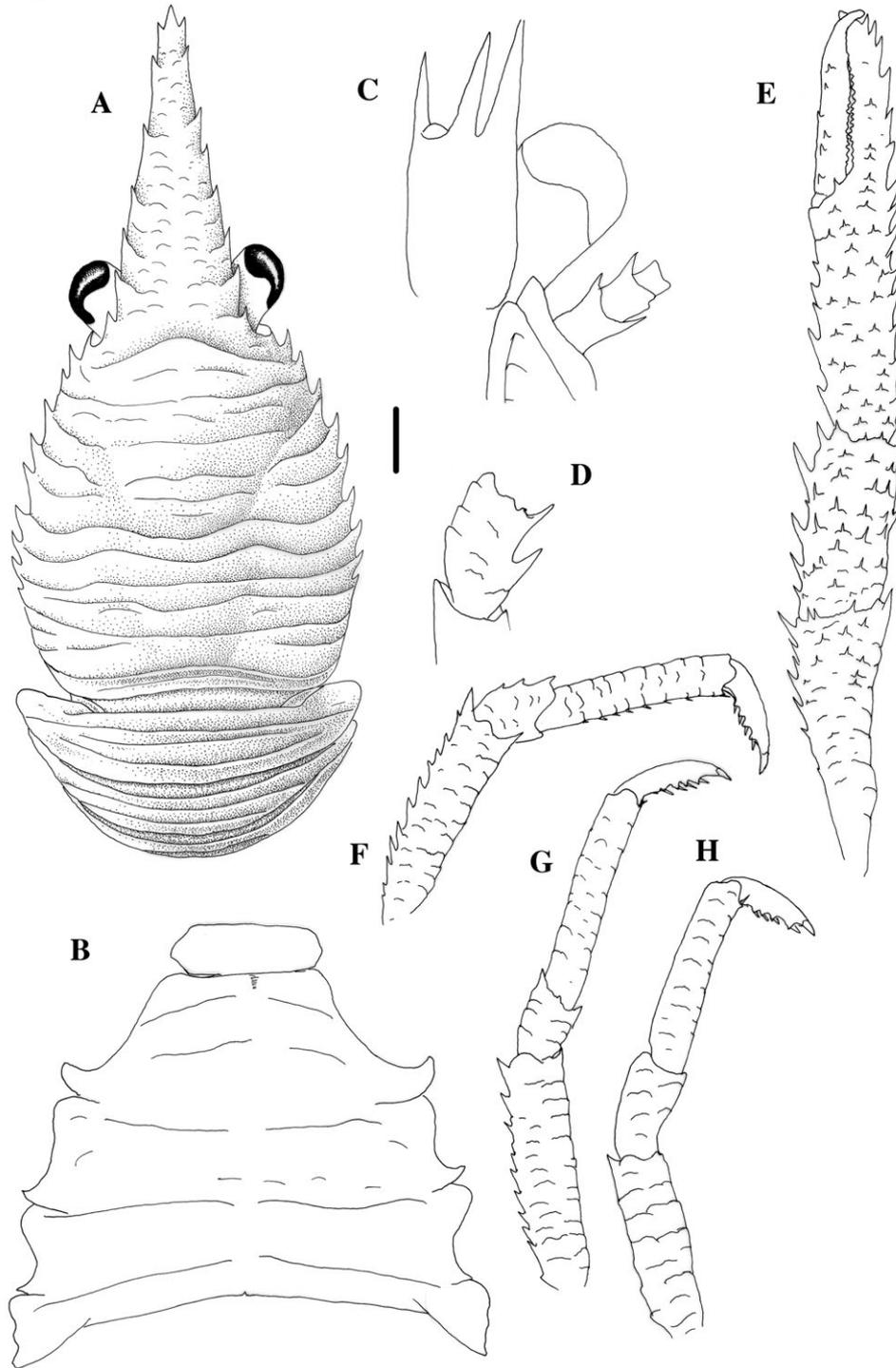


**Figure 1.** *Allogalatea babai* sp. nov., holotype (ovigerous female 5.4 mm, New Caledonia, Lagoon, 8 September 1993). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax, showing left antennule and antenna, ventral. D, right Mxp3, lateral. E, right pereopod 1, dorsal. F, right pereopod 2, lateral. G, right pereopod 3, lateral. H, right pereopod 4, lateral. Scale bar: A, E–H, 1 mm; B–D, 2 mm.

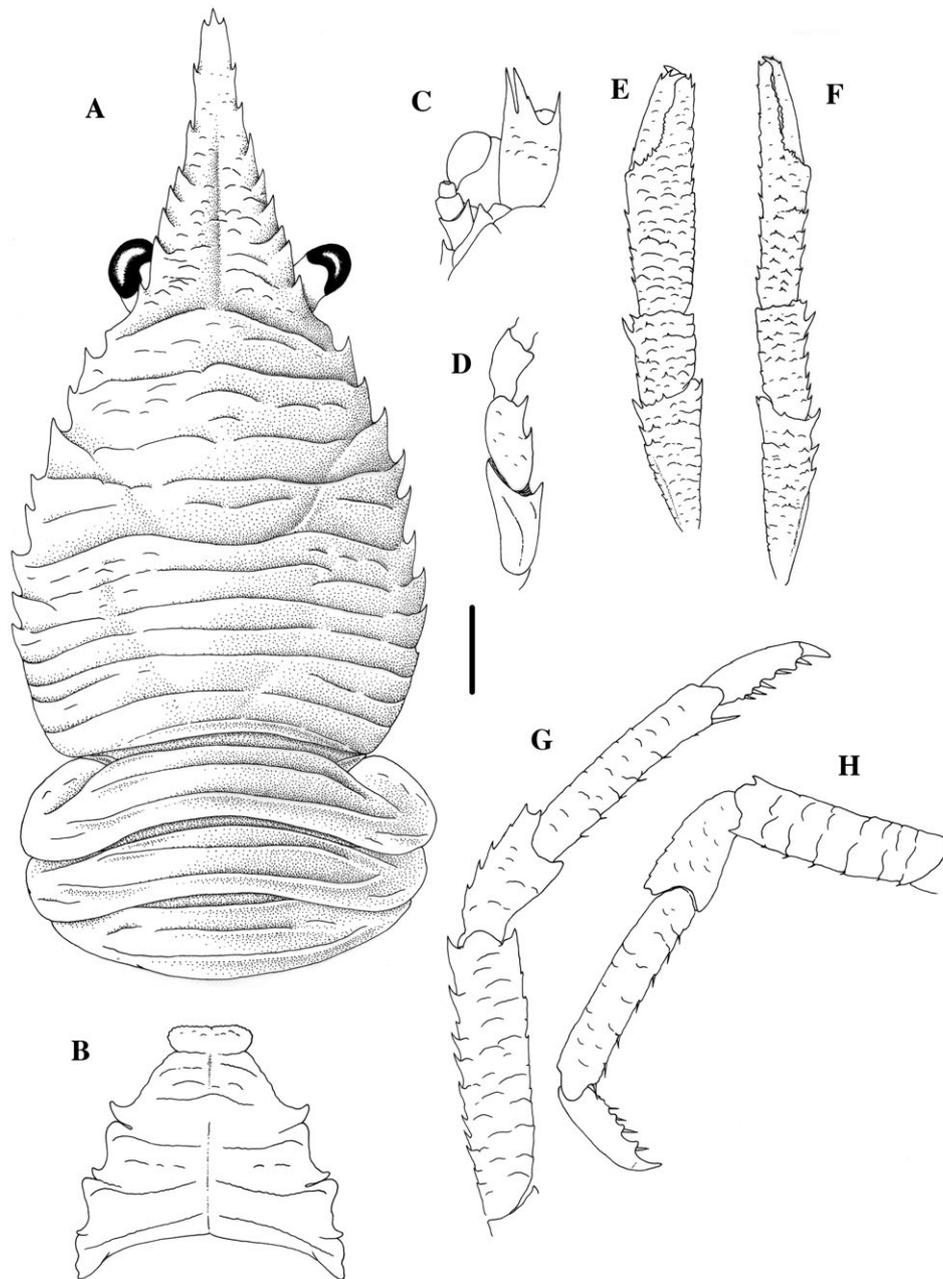
*Etymology:* This species is dedicated to Dr Keiji Baba of Kumamoto University, Japan, who described the genus *Allogalatea*, and has greatly improved our knowledge of the taxonomy of squat lobsters.

*Description:* Carapace exclusive of rostrum 0.8–1.0 times long as broad; dorsal surface nearly horizontal

from anterior to posterior, and anterior cervical groove indistinct, posterior one distinct. Gastric region with between five and seven uninterrupted ridges, with or without scales between them, anterior first and second ridges medially convex anteriorly; mid-transverse ridge uninterrupted, extending laterally to sixth marginal spines, preceded by slightly



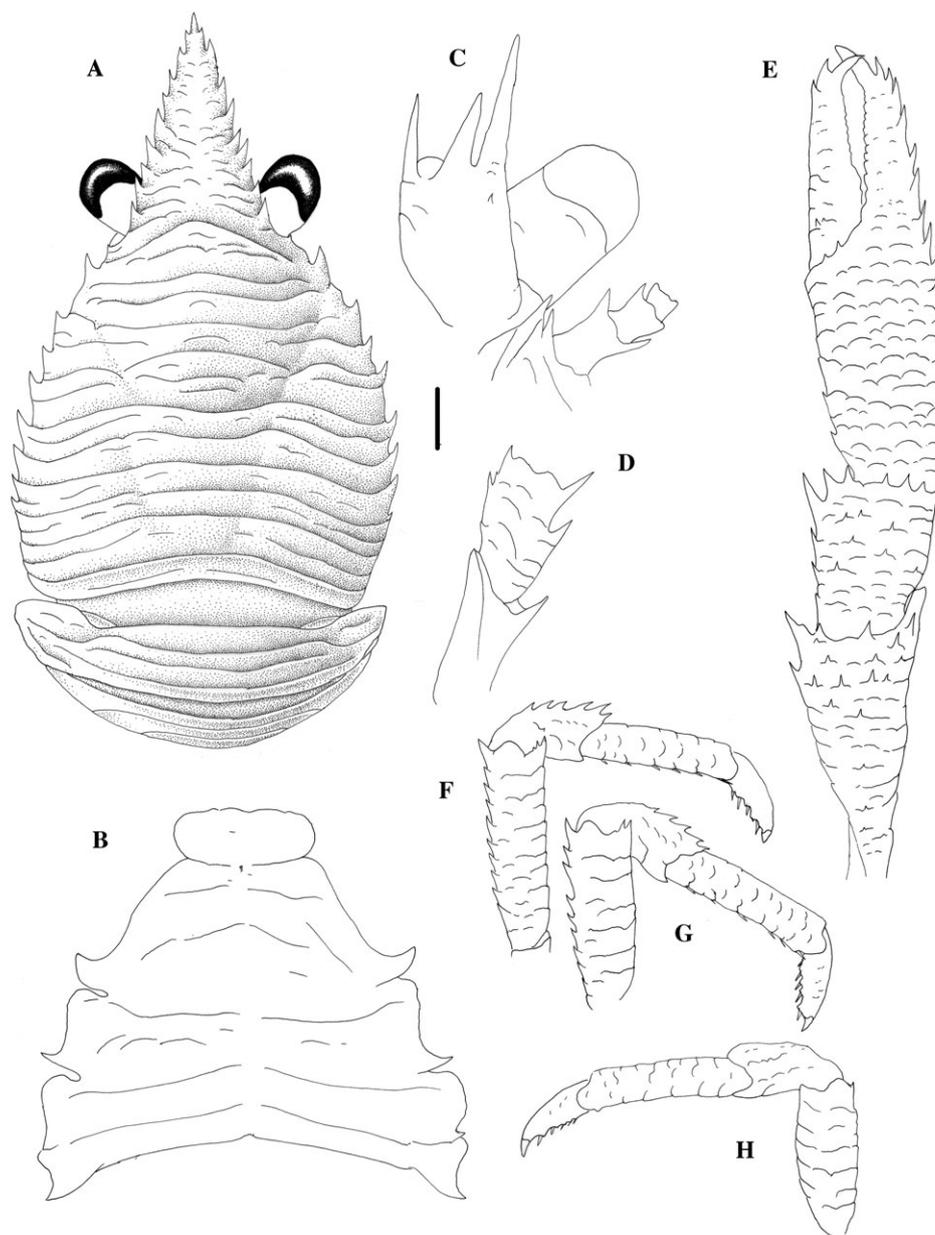
**Figure 2.** *Allogalathea elegans* (Adams & White, 1848) (ovigerous female 5.6 mm, New Caledonia, Touho Bank, 28 August 1993). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing left antennule and antenna, ventral. D, right Mxp3, lateral. E, right pereopod 1, dorsal. F, right pereopod 2, lateral. G, right pereopod 3, lateral. H, right pereopod 4, lateral. Scale bar: A, E–H, 1 mm; B–D, 2 mm.



**Figure 3.** *Allogalatheia elegans* (Adams & White, 1848), lectotype (female 5.0 mm, Philippines, Corregidor). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing right antennule and antenna, ventral. D, right Mxp3, lateral. E, right detached pereopod 1, dorsal. F, left detached pereopod 1. G, right detached pereopod 3. H, left detached pereopod 4. Scale bar: A, B–D, G, H, 1 mm; E, F, 0.5 mm. The detached pereopods could belong to the paralectotype (male 4.1 mm).

distinct cervical groove, followed by between six and nine transverse ridges, mostly interrupted. Lateral margins with eight or nine spines: two spines in front of and six or seven spines behind indistinct anterior cervical groove; first anterolateral, small, slightly posterior to level of lateral limit or orbit; second smaller than first, equidistant between anterolateral spine

and anterior cervical groove; three spines on anterior branchial region, and three or four spines on posterior branchial margin, last small. Rostrum twice as long as broad with eight or nine small lateral teeth, length 0.9 times that of carapace, and dorsal surface nearly horizontal in lateral view, with small setiferous ridges (Fig. 1A).



**Figure 4.** *Allogalatheia inermis* sp. nov., holotype (ovigerous female 7.3 mm, New Caledonia, SMIB 5, Stn DW100). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing left antennule and antenna, ventral. D, right Mxp3, lateral. E, right pereopod 1, dorsal. F, right pereopod 2, lateral. G, right pereopod 3, lateral. H, left pereopod 4, lateral. Scale bar: A, E–H, 1 mm; B–D, 2 mm.

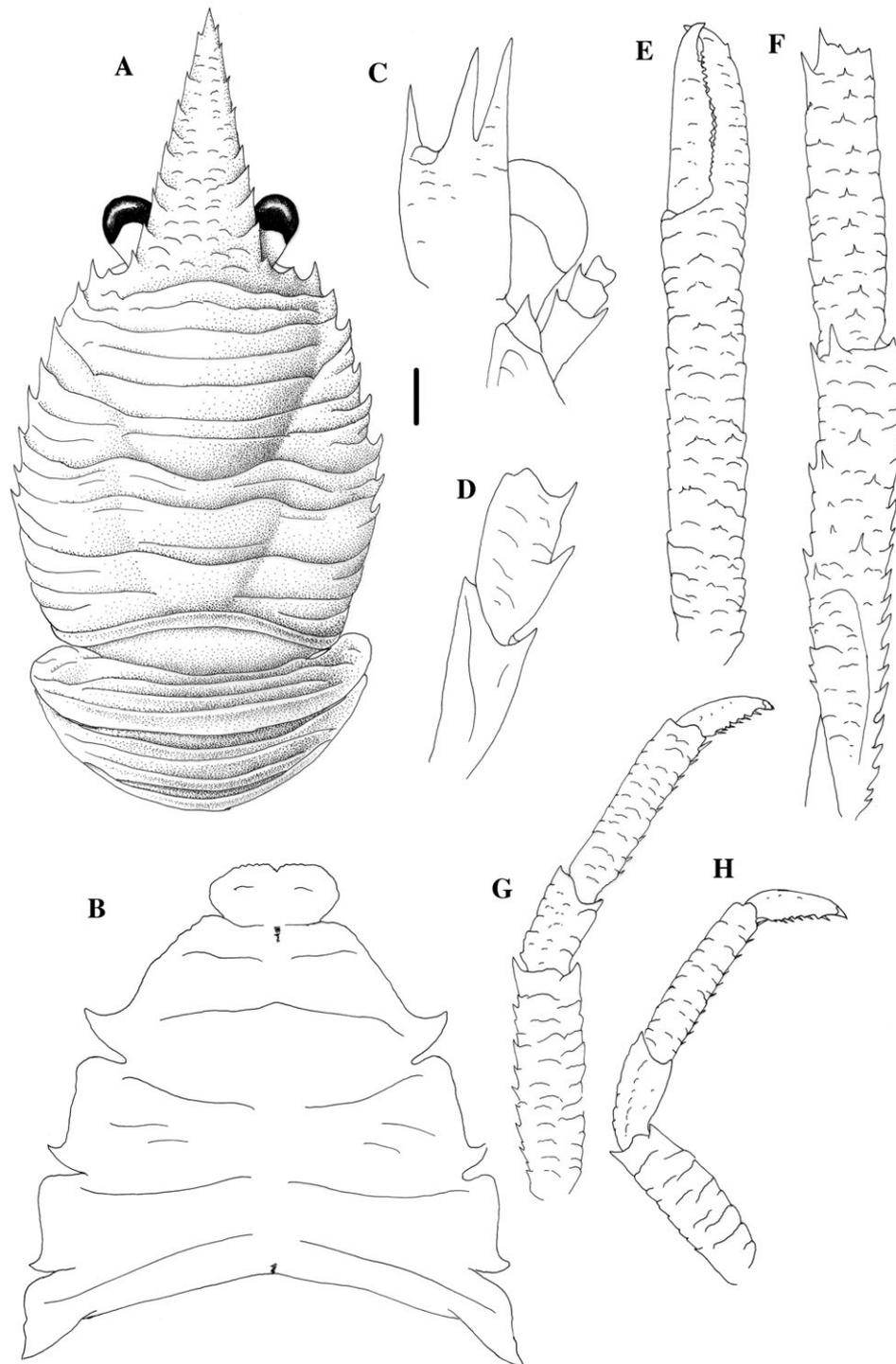
Pterygostomial flap rugose with sparse setae, anterior margin bluntly produced.

Sternal plastron 0.8 times as long as broad, lateral limits divergent posteriorly. Sternite 3 twice as broad as long, and anterior margin with minute median notch. Sternite 4 2.7 times longer and 2.7 times broader than preceding sternite, 0.5 times long as broad; sternites 4–5 with some transverse ridges bearing setae (Fig. 1B).

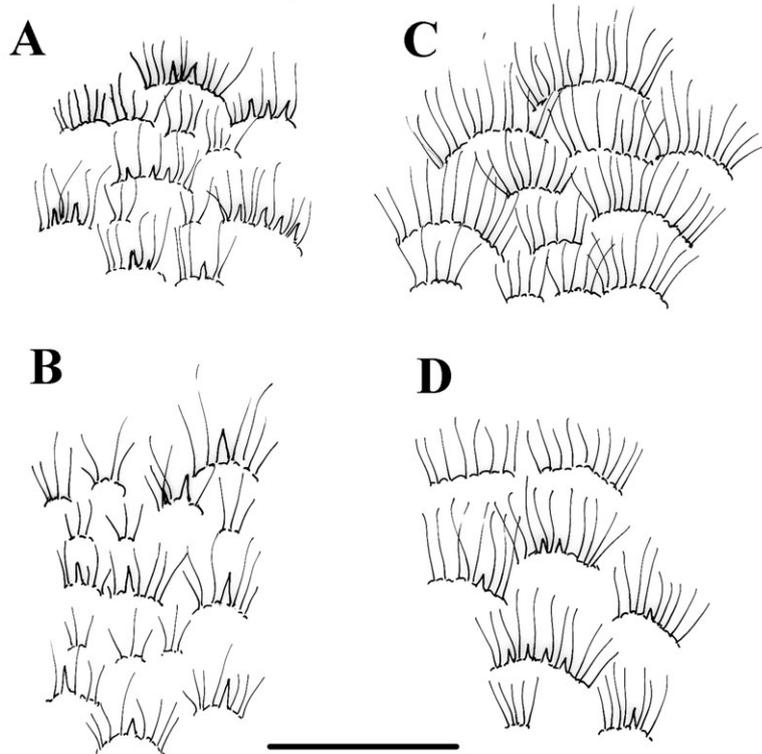
Abdominal somites 2–4 each with three or four uninterrupted transverse ridges on tergite, with or without scales in between; somite 5 with two uninterrupted ridges; somite 6 with two uninterrupted ridges and some scales.

Eyestalk (other than cornea) with short fine setae on dorsal anterior extension; cornea moderately dilated.

Article 1 of antennal peduncle with blunt distomesial process nearly reaching distal margin of article 2.



**Figure 5.** *Allogalatea longimana* sp. nov., holotype (ovigerous female, 6.5 mm, Philippines, Musorstom 3, Stn CP107). A, carapace and abdomen, dorsal. B, sternal plastron. C, anterior part of cephalothorax showing left antennule and antenna, ventral. D, right Mxp3, lateral. E, right pereiopod 1 palm and fingers, dorsal. F, right pereiopod 1 merus and carpus, dorsal. G, right pereiopod 3, lateral. H, right pereiopod 4, lateral. Scale bar: A, E–H, 1 mm; B–D, 2 mm.



**Figure 6.** Squamae on distal portion of pereopod 1 hand, showing setae and spinules, dorsal view. A, *Allogalathea babai* sp. nov., holotype (ovigerous female 5.4 mm, New Caledonia, Lagoon, 8 September 1993). B, *Allogalathea elegans* (Adams & White, 1848) (ovigerous female 5.6 mm, New Caledonia, Touho Bank, 28 August 1993). C, *Allogalathea inermis* sp. nov., holotype (ovigerous female 7.3 mm, New Caledonia, SMIB 5, Stn DW100). D, *Allogalathea longimana* sp. nov., holotype (ovigerous female 6.5 mm, Philippines, Musorstom 3, Stn CP107).

Article 2 with distolateral spine as long as distomesial, barely reaching midlength of article 3, sometimes with additional mesial spine. Article 3 with small, distinct distomesial spine. Article 4 unarmed (Fig. 1C).

Mxp3 ischium with well-developed spine on flexor distal margin; extensor margin unarmed; crista dentata with 23–27 denticles. Merus slightly longer than ischium, with two strong spines of subequal size on flexor margin, proximal one located at midlength, distal one at terminal end; extensor margin usually with three or four small spines (Fig. 1D).

P1 squamous, 2.9 (males), 2.6–2.7 (females) times carapace length, subcylindrical, most dorsal squamae with some small spinules and dense long setae. Merus 0.5–0.8 times length of carapace, 1.6–1.9 times as long as carpus, with row of mesial and distodorsal spines. Carpus 0.5–0.6 length of palm, 1.1–1.4 times longer than broad, lateral and mesial margins subparallel, with row of spines along mesial and distodorsal margins. Palm 1.8–2.4 times longer than broad, lateral and mesial margins straight or slightly convex in adult specimens; mesial row of spines, lateral

margin with row of spines continuing on to whole lateral margin of fixed finger and most scales on dorsal surface with spinules. Fingers 0.7–0.9 as long as palm, distally crossing when closed; opposable margins nearly straight; mesial margin of movable finger with two or three subterminal spines and a few dorsomesial spinules (Fig. 1E).

P2–P4 squamous, broad relative to length, weak in armature, moderately slender, somewhat compressed. Scales with dense short setae. Length of P2 1.7–1.9 times carapace length. Meri successively shorter posteriorly (P3 merus 0.9 times length of P2 merus, P4 merus 0.8–0.9 times length of P3 merus); P2 merus 0.6–0.7 carapace length, 3.2 times as long as broad, 1.3–1.4 times longer than P2 propodus. Dorsal margins of meri only have a distodorsal spine, and sometimes a row of small proximally diminishing spines on P2–P3, unarmed on P4; ventrolateral margins with strong terminal spine.

Carpi with some dorsal spines; flexor distal margins with very small distal spine. Propodi subequal in length on P2 and P3, slightly shorter on P4, 4.0–4.2 times as long as broad on P2; extensor margin unarmed; flexor margin with six or seven

slender movable spines. Dactyli subequal in length, 0.5–0.7 times length of propodi, ending in a curved, strong, sharp spine; flexor margin with prominent triangular terminal tooth preceded by five obsolescent teeth, each with seta-like movable spine (Fig. 1F–H).

Epipods present on P1 and sometimes also on P2–P3.

**Colour:** Body colour usually brown or orange, with a middle longitudinal whitish or yellowish broad stripe flanked by narrow dark-brown stripes on each side (pattern 2) (Baba, 1969, 1979) (see Appendix). P1–P4 brown, orange, or yellow; individuals with dark brown have a P1 white distal part of fingers, sometimes with whitish or yellowish dorsal stripe along merus, carpus, and hand.

**Remarks:** The colour pattern of *A. babai* sp. nov. is clearly different to the one exhibited by the other species (see below). All specimens of *A. babai* sp. nov. have a brown colour on the body and pereopods, and a median longitudinal white broad stripe flanked on either side by a narrow dark-brown stripe. Moreover, the new species has a variable number of epipods on the pereopods, suggesting that this character is not useful for species discrimination within the genus *Allogalatea* (see also *A. elegans*).

*Allogalatea babai* sp. nov. is closely related to *A. elegans*, in that both have a moderately long rostrum with spinules in most scales on the dorsal surface of the P1 palm. However, both species can be easily differentiated on the basis of other characters (see Remarks under *A. elegans*).

**Distribution and habitat:** Japan, Philippines, Mariana Islands, Guam, South China Sea, Christmas Islands, Indonesia (east coast of Marsegu Island, Banda Sea, Banda Island), Vanuatu, New Caledonia, Chesterfield, and Loyalty Islands, Dampier Archipelago, and Western Australia. Depth range: 10–48 m, usually on crinoids (*O. bennetti*).

*Allogalatea elegans* (Adams & White, 1848)

(Figs 2, 3, 6B)

*Galathea elegans* Adams & White, 1848: plate 12, figure 7; Balss, 1913: 4, figures 2 and 3; Potts, 1915: 83, figure 4, plate 1, figure 5; Miyake, 1938: 37 (in part); Melin, 1939: 77, figures 48–53 (probably in part); Barnard, 1950: 487, figures 91i–k; Miyake & Baba, 1967: 228, figure 3 (with doubt); Lewinsohn, 1969: 123, figure 24; Healy & Yaldwyn, 1970: 67, plate 31 (no record).

*Galathea longirostris* Dana, 1852: 482 (type lost; type locality: Fiji Islands, depth 18 m); Dana, 1855: plate 30, figure 11; Southwell, 1906: 220.

*Galathea longirostris* Yokoya, 1936: 138, figure 6 (holotype, female, lost; type locality: Misaki, Sagami Bay, Japan) (not *G. longirostris* Dana, 1852).

*Galathea deflexifrons* Haswell, 1882: 761; Haswell, 1882: 163.

*Galathea grandirostris* Stimpson, 1858: 90 (type lost; type locality, Kagoshima Bay, Japan, depth 9 m); Stimpson, 1907: 234; Henderson, 1888: 119, plate 12, figure 3; Borradaile, 1900: 421.

?*Galathea grandirostris* Southwell, 1906: 221.

*Allogalatea elegans* Baba, 1969: 6, figure 1 (in part); Haig, 1973: 275 (in part); Haig, 1974: 447 (in part); Baba, 1977: 252 (in part); Baba, 1979: 654, figure 3 (in part); Baba, 1988: 54 (in part); Baba, 1990: 950; Tirmizi & Javed, 1993: 27, figures 12 and 13 (with doubt); Gosliner *et al.*, 1996: 226, figure 820 (in part); Wu, Chan & Yu, 1998: 84, figures 6 and 12C; Minemizu, 2000: 168, with three figures (in part); Kawamoto & Okuno, 2003: 93, unnumbered figs (in part); Poore, 2004: 231, figure 63e, plate 13g (in part, compilation); Kawamoto & Okuno, 2006: 93, unnumbered figure (in part); Macpherson, 2008: 289 (in part); Poore, McCallum & Taylor, 2008: 18; Baba *et al.*, 2008: 53, figure 2B.

**Material examined:** Madagascar. Nosy Komba, north-western side, 13.4462°S, 48°3316'E, 26 May 2008, depth 0–12 m: one M 5.3 mm, one ovig. F 7.0 mm, one F 2.4 mm (UF14196).

Between Nosy Be and Nosy Tanikely, muddy lagoon, crinoid, 13.4572°S, 48.2484°E, 21 May 2008, depth 24–25 m: one F 4.6 mm (UF14641).

Nosy Be. Stn 10, dive, depth 26 m, P. Laboute coll. 1994: two ovig. F 5.1–5.3 mm (MNHN-Ga7372, Allo43).

South coast. Vauban. Stn CH74, 25°04.8'S, 46°55.7'E, 4 March 1973, depth 28 m: five M 2.8–5.2 mm, one ovig. F 5.0 mm, one F 3.1 mm (MNHN-Ga726).

North-western coast, 12°49.5'S, 48°30'E, 2 August 1973, depth 55 m: two M 4.6–5.3 mm, one F 2.5 mm (MNHN-Ga1503, -Ga2226, -Ga2227).

West coast, Food and Agriculture Organization of the United Nations (FAO) 26. 17°05'S, 43°50'E, 26 September 1976, depth 40–46 m: one ovig. F 5.9 mm (MNHN-Ga1486).

North-western coast, near Tanikely, 13°28'S, 48°12'E, 26 February 1971, depth 28 m: one ovig. F 5.4 mm (MNHN-Ga725).

Mitsio Islands, February 1960, depth 60 m: three M 4.1–5.7 mm, six ovig. F 4.4–6.1 mm, two F 5.2–6.6 mm (MNHN-Ga2240).

Reunion Island. MD32 Cruise. Stn CP127, 20°52.0'S, 55°37.1'E, 2 September 1982, depth 90 m: one ovig. F 5.6 mm (MNHN-Ga4583).

Mozambique. Mainbaza. Stn CP3132, 35°01'51"S, 25°11'24"E, depth 101–102 m, Richer de Forges & Corbari coll., 10 April 2009: one ovig. F 8.3 mm (MHN-Ga7373).

Gulf of Suez. A. Dolfus coll., 8 December 1928: 1 M 4.1 mm (MNHN-Ga762).

Taiwan. Longdong, Taipei County, 21 July 1999: one F 2.6 mm (NTOU). Gushan fishing port, Kaohsiung City, 14 January 1985: one M 5.2 mm (NTOU). Stn CP02, 23°38.3'N, 119°53.2'E, 27 July 2000, depth 83–95 m: one F 5.2 mm (NTOU).

Philippines. Corregidor Island: one M 4.1 mm, one F 5.0 mm (types, BMNH1843, see below).

Musorstom 3. Stn DR104, 13°56'N, 120°22'E, 1 June 1985, depth 13 m: one M 2.1 mm (MNHN-Ga7374); Stn DR117, 12°31'N, 120°39'E, 3 June 1985, depth 92–97 m: two ovig. F 3.9 mm (MNHN-Ga7396) and 5.1 mm (MNHN-Ga7397); Stn CP121, 12°08'N, 121°17'E, 3 June 1985, depth 73–84 m: one M 3.1 mm, two F 2.8–3.5 mm (MNHN-Ga7375), one M 4.5 mm (MNHN-Ga7376, Allo39), one M 3.3 mm (MNHN-Ga7377); Stn CP142, 11°47'N, 123°01'E, 6 June 1985, depth 26–27 m: two M 4.3–5.6 mm, two ovig. F 3.7–4.7 mm (MNHN-Ga7378).

Indonesia. East coast of Marsegu Island, 18 January 1975, on *Comanthina schlegeli*, one M 2.5 mm, one ovig. F 4.1 mm (MNHN-Ga 1127); one M 3.0 mm on *Oxycomanthus bennetti* (MNHN-Ga 1133).

Lilinta Bay, across from Lilinta village, Misool Island, 23 January 1975, on *Comanthina schlegeli* and *Comanthina parvicirrus*: three M 2.2–3.6 mm (MNHN-Ga 1128, 1131, 1132).

Off Museha and Wayuta estuaries, Seleman Bay, north coast of Seram (Ceram), 19 January 1975, on *Comanthina parvicirrus* and *Stephanometra spicata*: two M 2.0–2.5 mm, one ovig. F 3.3 mm (MNHN-Ga 1126, 1130).

Banda Island, 30 January 1975: one M 3.8 mm (MNHN-Ga 1120).

Southern entrance between Gunung Api Island and Bandanaira, on *Comanthina schlegeli*, 29 January 1975: one M 3.8 mm, one F 4.2 mm (MNHN-Ga 1121).

Across from Kotasirih village, Kailakat Bay, Gorong Island, 26 January 1975, on *Capillaster multiradiatus*: 1 M 5.5 mm (MNHN-Ga 1119). 25 January 1975, on *Oxycomanthus bennetti*, 1 M 2.0 mm (MNHN-Ga 1124).

Across from Kotasirih village, Kailakat Bay, Gorong Island, 27 January 1975, on *Comanthina schlegeli*: one ovig. F 5.0 mm (MNHN-Ga 1122).

Tapalol Island, off Biga Bay, Missol Island, 24 January 1975, on *Stephanometra spicata*: one M 1.6 mm (MNHN-Ga 1129).

Corindon. Stn DR258, 01°56.8'S, 119°17.3'E, 6 November 1980, depth 30 m: one M 3.7 mm (MNHN-Ga7379).

Vanuatu. Santo. Stn FR1-CF2, 15°32.3'S, 167°13.1'E, 10 September 2006, depth 18–20 m: one M 4.1 mm (MNHN-Ga7380, Allo11); Stn FR06, 15°32.6'S, 167°16.9'E, 13 September 2006, depth 3–37 m: one M 4.2 mm, one ovig. F 5.1 mm (MNHN-Ga7395); Stn ZR4, 15°33.1'S, 167°09.6'E, 17 September 2006, depth 0–45 m: one M 3.9 mm (MNHN-Ga7381, Allo15), one ovig. F 4.7 mm (MNHN-Ga7382, Allo9); Stn AT13, 15°27.8'S, 167°15.7'E, 19 September 2006, depth 146–153 m: one ovig. F 3.7 mm (MNHN-Ga7383); Stn AT14, 15°23.7/24'S, 167°12.9/13.5'E, 19 September 2006, depth 102–120 m: two ovig. F 3.3 (MNN-Ga7384) and 4.6 mm (MNHN-Ga7385, Allo31); Stn EP22, 15°37.3/37.4'S, 167°05.8/06.0'E, 21 September 2006, depth 78–91 m: one M 3.2 mm (MNHN-Ga7386); Stn FR26, 15°31.7'S, 167°09.5'E, 21 September 2006, depth 3–33 m: one M 3.5 mm, one F 1.8 mm (MNHN-Ga7387); Stn AT40, 15°23.4'S, 167°12.7'E, 27 September 2006, depth 81–94 m: one ovig. F 4.2 mm (MNHN-Ga7388); Stn AT44, 15°36.5'S, 167°02.7'E, 29 September 2006, depth 86–118 m: one ovig. F 5.8 mm (MNHN-Ga7389, Allo13); Stn DB80, 15°37.1'S, 167°07.5'E, 2 October 2006, depth 18 m: one M 2.6 mm, two F 2.2–3.0 mm (MNHN-Ga7390); Stn AT75, 15°37.0/37.3'S, 167°09.2/09.6'E, 10 October 2006, depth 52–66 m: one M 2.6 mm, two F 2.9–4.0 mm (MNHN-Ga7391); Stn AT81, 15°31.5'S, 167°11.9'E, 12 October 2006, depth 46–55 m: one ovig. F 6.0 mm (MNHN-Ga7392, Allo7); Stn AT82, 15°31.6'S, 167°12.4'E, 12 October 2006, depth 58–59 m: one ovig. F 4.9 mm (MNHN-Ga7393, Allo6); Stn AT84, 15°32.4'S, 167°14.3'E, 12 October 2006, 71–104 m: depth one ovig. F 6.0 mm (MNHN-Ga7394, Allo14).

New Caledonia. Lagoon, 30 August 1993: two M 3.0–4.1 mm, two ovig. F 3.0–4.2 mm (MNHN-Ga7398).

In front Kohe, 8 September 1993, depth 15 m: six M 3.5–4.6 mm, eight ovig. F 3.0–5.3 mm, one F 3.8 mm (MNHN-Ga7428), one ovig. F 5.4 mm (MNHN-Ga7399, Allo20) plus one ovig. F 5.2 mm (MNHN-Ga7400, Allo35) plus one M 4.5 mm (MNHN-Ga7401, Allo33).

Touho Bank, 28 August 1993: three M 2.1–4.5 mm, two ovig. F 3.1–5.6 mm, seven F 1.8–3.0 mm (MNHN-Ga7402; Ga7403, Allo25; Ga7404, Allo23; Ga7405).

Touho Channel, 4 September 1993, depth 52 m: one M 4.7 mm, two ovig. F 5.7–6.0 mm (MNHN-Ga7406); 7 September 1993, 56 m: two F 4.0–5.7 mm two F 4.0–5.7 mm plus one M 3.1 mm (MNHN-Ga7427), one F 5.7 mm (MNHN-Ga7407, Allo29).

Touho Bank. 20°44.20'S, 165°14'E, 15/16 September 1993: two M 4.2–4.6 mm, two ovig. F 4.3–5.3 mm (MNHN-Ga7408).

Touho (Kohé), Opération Montrouzier, dive, depth 15 m, 7 September 1993: one M 3.9 mm, one ovig. F 4.4 mm. (MNHN-Ga7416); same cruise, same date,

20°48.93'S, 166°16.80'E, depth 55–60 m: one F 2.3 mm (MNHN-Ga7417).

Ilot Canard, 22°09.2'S, 166°21.7'E, depth 20 m: two M 3.9–4.2 mm, two ovig. F 3.9–5.2 mm (MNHN-Ga7409).

Grand Recif Sud. Stn 302, 22°38'S, 166°49'E, depth 17 m: one M 4.1 mm, one ovig. F 7.1 mm (MNHN-Ga7410).

Plotmatre, perhaps Ilot Maitre. 22°19.35'S, 166°25.85'E, 11 November 1995, depth 20 m: one ovig. F 5.3 mm (MNHN-Ga7411).

Gail Bank, 1970, depth 30 m: one M 5.9 mm (MNHN-Ga 523).

Chesterfield Islands. Corail 1. Bank Landsdowne, August 1988: two M 3.2–4.3 mm, two ovig. F 5.1–5.7 mm (MNHN-Ga7414).

Corail 2. Stn CP25, 20°25'S, 161°05'E, 22 July 1988, depth 67–70 m: one M 2.3 mm (MNHN-Ga7415).

Eastern Australia. Albany Passage, Queensland: one specimen dry 4.5 mm (type of *G. deflexifrons* Haswell) (AM P3885).

*Types:* The female of 5.0 mm postorbital carapace length from the Philippines, Corregidor Island (BMNH1843) has been selected as the lectotype. The male specimen of 4.1 mm has been considered a paralectotype.

*Description:* Carapace, exclusive of rostrum, as long as broad; dorsal surface nearly horizontal from anterior to posterior, with distinct transverse striae bearing fine but coarse setae and cervical groove slightly distinct. Gastric region with four or five uninterrupted and one or two interrupted ridges, first anterior and second uninterrupted, ridges medially convex anteriorly; mid-transverse ridge uninterrupted, extending laterally to sixth marginal spines, preceded by distinct cervical groove, followed by between three and five transverse ridges, last one interrupted. Lateral margins with nine spines: two spines in front of and seven spines behind anterior cervical groove; first anterolateral, small, slightly posterior to level of lateral limit of orbit; second slightly smaller than first, equidistant between anterolateral spine and anterior cervical groove; three spines on anterior branchial region, and four spines on posterior branchial margin, decreasing in size posteriorly. Rostrum 2.0–2.3 times as long as broad, with seven or eight small lateral teeth, length subequal to that of carapace; dorsal surface nearly horizontal in lateral view, with small setiferous ridges (Fig. 2A).

Pterygostomian flap setiferous striae, anterior margin bluntly produced.

Sternal plastron 0.8 times as long as broad, lateral limits divergent posteriorly. Sternite 3 three times as

broad as long, anterior margin with minute median notch. Sternite 4 4.6 times longer and 2.5 times broader than preceding sternite, 0.6 times as long as broad; sternites 4 or 5 with a few short transverse ridges bearing short setae (Fig. 2B).

Abdominal somites 2–4 each with three uninterrupted transverse ridges on tergite, usually without scales in between; second ridge interrupted medially in some specimens; somite 5 with two uninterrupted ridges and few scales, somite 6 with two interrupted ridges and few scales.

Eyestalk (other than cornea) with short fine setae on dorsal anterior extension; cornea moderately dilated.

Article 1 of antennal peduncle with blunt distomesial process reaching or overreaching end of article 2. Article 2 with distolateral spine larger than distomesial, nearly reaching end of article 3. Article 3 with distinct distomesial spine reaching end of article 4. Article 4 unarmed (Fig. 2C).

Mxp3 ischium with well-developed spine on flexor distal margin; extensor margin unarmed; crista dentata with 20–23 denticles. Merus slightly longer than ischium, with two strong spines of subequal size on flexor margin, proximal one located slightly distal to mid-length, distal one at terminal end; extensor margin unarmed or with two or three small spines (Fig. 2D).

P1 squamous, 2.2–3.0 times carapace length, subcylindrical, lateral and mesial margins straight in adult specimens; each squama usually with one spinule and some long setae. Merus 0.7–0.8 times length of carapace, 1.3–1.4 times as long as carpus, with spines on mesial and distodorsal margins. Carpus 0.7–0.9 length of palm, 1.8–2.2 times longer than broad, lateral and mesial margins subparallel; mesial margin with row of spines. Palm 2.2–2.6 times longer than broad, lateral and mesial margins subparallel; mesial row of spines, lateral margin with row of spines continuing on to whole lateral margin of fixed finger, and most scales on dorsal surface with spinules. Fingers 0.8 length of palm, distally crossing when closed; opposable margins nearly straight, mesial margin of movable finger with two or three subterminal spines (Fig. 2E).

P2–P4 squamous, relatively slender, somewhat compressed, with short setae on each squama. P2 1.5–1.8 times carapace length. Meri successively shorter posteriorly (P3 merus 0.9 times length of P2 merus, P4 merus 0.8 times length of P3 merus); P2 merus 0.6–0.7 carapace length, 4.0–4.2 times as long as broad, 1.3–1.4 times longer than P2 propodus. Dorsal margins of meri with distodorsal spine and row of well-developed proximally diminishing spines on P2–P3, unarmed or with some minute spines on P4; ventrolateral margins with strong terminal spine.

Carpi with some dorsal spines on P2 and P3, unarmed on P4; flexor distal margins with small spine. Propodi slightly longer on P3 than on P2, slightly shorter on P4 than on P2. P2 propodus 4.3 times as long as broad, 1.9 times longer than P2 dactylus; extensor margin unarmed; flexor margin with between six and ten slender movable spines. P2–P3 dactyli subequal in length, slightly longer than P4 dactylus, ending in a curved, strong, sharp spine; flexor margin with prominent triangular terminal tooth preceded by four or five obsolescent teeth, each with seta-like movable spine (Fig. 2F–H).

Epipods present or absent on P1, absent on P2–P3.

*Colour:* The species has several possible body colour patterns: either uniformly dark (red, blackish purple, orange or brown) or dark, with either two narrow light stripes, or alternating longitudinal dark and light stripes (patterns 1, 3, and 4 of Baba, 1979), the number and width of which varies (see Appendix). Other colour patterns include a narrow lighter stripe in the middle of each dark stripe. Pereiopods also show variable coloration: P1 uniformly dark or with longitudinal light dorsal stripe along merus, carpus, and palm, finger tips light; some specimens with P1 uniformly dark and fingers whitish. P2–P4 uniformly dark or pale on distal portion of carpus, distal portion of propodus and entire dactylus; in some specimens, P2–P4 meri dark, and carpi, propodi, and dactyli whitish.

*Remarks:* A number of different taxa, as *G. longirostris* Dana, 1852; *G. grandirostris* Stimpson, 1858; *G. deflexifrons* Haswell, 1882; and *G. longirostris* Yokoya, 1936 have been judged to be junior synonyms of *G. elegans* Adams & White, 1848 (Ortmann, 1894; Grant & McCulloch, 1906, among others). However, Baba (1969) recommended that previous records should be revised, confirming the presence or absence of epipods on P1–P3. It should be noted that Haig (1973) pointed out that the status of three of these species could not be resolved because their types are no longer extant (see Material examined).

The description and illustration by Dana (1852) suggest that *G. longirostris* is very close to *A. elegans*, the rostrum of both having 5 to 6 small spines on each side, and the body background colour of the body of both is purplish black, with two whitish stripes. The description of *G. grandirostris* by Stimpson (1858) is very brief and not illustrated, and includes a purplish black body background colour with two light stripes. A similar short description of *G. deflexifrons* was provided by Haswell (1882), who, as a distinctive character, pointed out that the rostrum is deflected. However, examination of the type species of *G. deflexifrons* Haswell, 1882 (in photographs provided

by the Australian Museum, Sydney) indicates it is a junior synonym of *A. elegans*. The description of *G. longirostris* by Yokoya (1936), a junior homonym of *G. longirostris* Dana, 1852, is more detailed and includes illustrations (only one female was collected). The body background colour has alternating brown and white stripes, and corresponds well with the original illustration of *A. elegans*.

Considering the impossibility of knowing the exact status of *G. longirostris* Dana, 1852, *G. grandirostris* Stimpson, 1858, and *G. longirostris* Yokoya, 1936, we select the syntype female illustrated in Figure 3 as the lectotype of *G. elegans* Adams & White, 1848. This lectotype is designated as the neotype of Dana's, Stimpson's, and Yokoya's records, and therefore these names should be considered objective junior synonyms of *G. elegans* Adams & White, 1848.

*Allogalatheia elegans* is close to *A. babai* sp. nov., but the two can be distinguished by the following characters:

1. The walking legs (P2–P4) are shorter and more slender in *A. babai* sp. nov. than in *A. elegans*. The P2 merus is about three times longer than high in the new species, whereas the P2 merus is four times longer than high in *A. elegans*.
2. The dorsal margin of the P2–P3 meri is usually unarmed or has small spines in *A. babai* sp. nov., yet has well-developed spines in *A. elegans*.
3. The squamae on the dorsal side of P1 have several spinules and numerous long setae in *A. babai* sp. nov., whereas these squamae have only one spinule and a few long setae in *A. elegans*. These squamae are denser in *A. babai* sp. nov. than in *A. elegans*.
4. Epipods are always present on P1, and are sometimes present on P2–P3, in *A. babai* sp. nov., instead of being present on P1 only or absent on all pereiopods, as in *A. elegans*.

Furthermore, *A. babai* sp. nov. has a middle longitudinal light broad stripe that is never found in *A. elegans*.

*Distribution and habitat:* Mozambique, Red Sea, Madagascar, Taiwan, the Philippines, Indonesia (Banda and Celebes Seas), Vanuatu, New Caledonia and Chesterfield islands. Subtidal to depth of 120 m; usually on crinoids, e.g. *Capillaster multiradiatus*, *Comanthina schelegeli*, *Comanthina parvicirrus*, *Oxycomanthus bennetti*, and *Stephanometra spicata*.

The distribution range of *A. elegans* is probably wider, and its occurrence in the areas cited (material not examined), e.g. South Africa, Sri Lanka, Bay of Bengal, Japan, western and south-western Australia, Queensland, Great Barrier Reef, Fiji, among others, needs confirmation.

***Allogalatea inermis* sp. nov.** (Figs 4, 6C)

*Galatea elegans* Miyake, 1938: 37, figure 1, plate 2, figure E (in part); Melin, 1939: 77, figures 48–53 (in part); Utinomi, 1956: 63, plate 32, colour figure 4.

*Allogalatea elegans* Baba, 1969: 6, figure 1 (in part); Baba, 1979: 654 (in part); Baba, 1988: 54 (in part).

**Material examined:** Mozambique. Mainbaza. Stn DW3168, 26°12'S, 35°3'E, depth 87–90 m, Richer de Forges & Corbari coll., 16 April 2009: one M 6.4 mm (MNHN-Ga7362, Allo42).

Thailand. Phuket. Coral reefs: one M 3.9 mm (MNHN-Ga7363, Allo28), one F 4.9 mm (MNHN-Ga7364, Allo27).

Indonesia Rumphius Expedition II, in front of Kota-sirih village, Kailakat Bay, Gorong Island, 25 January 1975: one M 1.7 mm, one F 1.8 on *Himerometra robustipinna* (MNHN-Ga 1125).

Vanuatu. Espiritu Santo, Santo 2006. Stn NR8, 15°35.7'S, 167°07.4'E, 15 September 2006, 11 m: 1 M 3.1 mm (MNHN-Ga7365, Allo30), one ovig. F 3.6 mm (MNHN-Ga7366, Allo12).

New Caledonia. Touho Bank, 28 August 1993: one M 3.8 mm, one ovig. F 5.1 mm, one F 3.5 mm (MNHN-Ga7367); Touho, depth 10 m, one ovig. F 4.4 mm (MNHN-Ga7418).

Lagoon. Across from Kohe, 8 September 1993: one M 5.1 mm (MNHN-Ga7368, Allo32).

New Caledonia. SMIB 5. Stn DW100, 23°22.90'S, 168°05.20'E, 14 September 1989, depth 80–120 m: one ovig. F 7.3 mm (MNHN-Ga7369, Allo3).

Chesterfield Islands. Corail 2. Stn CP7, 20°52'S, 161°37'E, 20 July 1988, depth 63–64 m: one M 4.5 mm, one ovig. F 4.8 mm (MNHN-Ga7370); Stn CP90, 19°03'S, 158°56'E, 26 July 1988, depth 44–48 m: one ovig. F 4.9 mm (MNHN-Ga7371).

**Types:** The ovigerous female of 7.3 mm postorbital carapace length, from New Caledonia (SMIB 5, Stn DW100, MNHN-Ga7369) has been selected as the holotype. All the other specimens are paratypes.

**Etymology:** From the Latin *inermis* (unarmed), referring to the absence of spinules on most squamae of P1.

**Description:** Carapace, exclusive of rostrum 0.9 times as long as broad; dorsal surface nearly horizontal from anterior to posterior, and cervical groove slightly distinct. Gastric region with five or six uninterrupted and two or three interrupted ridges, usually with some scales between them, anterior first, third, and fourth uninterrupted ridges medially convex anteriorly; mid-transverse ridge uninterrupted, extending laterally to fifth marginal spines, preceded by cervical groove, followed by five or six transverse ridges.

Lateral margins with eight or nine spines: two spines in front of and six spines behind cervical groove; first anterolateral, small, slightly posterior to level of lateral limit of orbit; second smaller than first, equidistant between anterolateral spine and anterior cervical groove; three spines on anterior branchial region, and four spines on posterior branchial margin, with the last very small. Rostrum 1.3–1.6 times as long as broad, with eight or nine lateral small teeth, length 0.7 that of carapace, dorsal surface nearly horizontal in lateral view, with small setiferous ridges (Fig. 4A).

Pterygostomian flap with some ridges, anterior margin bluntly produced.

Sternal plastron 0.8 times as long as broad, lateral limits divergent posteriorly. Sternite 3 2.6 times as broad as long, anterior margin with small median notch. Sternite 4 2.6 times longer and 2.4 times broader than preceding sternite, 0.4 times as long as broad; sternites 4 and 5 with some transverse ridges bearing long setae (Fig. 4B).

Abdominal somites 2–4 each with two or three uninterrupted transverse ridges on tergite, with or without scales in between; somite 5 with two uninterrupted ridges, somite 6 with two interrupted ridges and some scales.

Eyestalk (other than cornea) with short fine setae on dorsal anterior extension; cornea moderately dilated.

Article 1 of antennal peduncle hardly visible from dorsal view, with distomesial spine reaching midlength of article 2. Article 2 with distolateral spine as long as distomesial, overreaching midlength of article 3, sometimes additional mesial spine. Article 3 with small, distinct distomesial spine. Article 4 unarmed (Fig. 4C).

Mxp3 ischium with well-developed spine on flexor distal margin; extensor margin unarmed; crista dentata with 19–24 denticles. Merus slightly longer than ischium, with two strong spines of subequal size on flexor margin, proximal one located at midlength, distal one at terminal end; extensor margin with three or four spines (Fig. 4D).

P1 squamous, 2.0–2.5 times carapace length, subcylindrical, most dorsal squamae lack spinules, and with numerous long setae. Merus 0.8 times length of carapace, 1.4–1.6 times as long as carpus, with row of mesial and distodorsal spines. Carpus 0.6–0.7 times the length of palm, 1.5–1.6 times longer than broad, lateral and mesial margins subparallel, with row of spines along mesial and distodorsal margins. Palm 1.7–1.8 times longer than broad, lateral and mesial margins convex in adult males (slightly in females); mesial margin with row of spines, lateral margin with row of spines continuing on to whole lateral margin of fixed finger, and most scales on dorsal surface without

spinules. Fingers as long as palm, distally crossing when closed; opposable margins nearly straight; mesial margin of movable finger with two or three subterminal spines (Fig. 4E).

P2–P4 squamous, weak in armature, relatively slender, somewhat compressed, with long setae. P2 1.5 times carapace length. Meri successively shorter posteriorly (P3 merus 0.9 times length of P2 merus, P4 merus 0.9 times length of P3 merus); P2 merus 0.5–0.6 times carapace length, 3.5 times as long as broad, 1.2–1.5 times longer than P2 propodus. Dorsal margins of meri with distal spine and row of small proximally diminishing spines on P2–P3, nearly unarmed on P4; ventrolateral margins with strong terminal spine. Carpi with some dorsal spines on P2 and P3, unarmed on P4; flexor distal margins with very small distal spine. Propodi subequal in length on P2 and P3, slightly shorter on P4, 3.3–3.4 times as long as broad on P2; extensor margin unarmed; flexor margin with six or seven slender movable spines. Dactyli subequal in length, 0.6 times the length of propodi, ending in a curved, strong, sharp spine; flexor margin with prominent triangular terminal tooth preceded by four or five obsolete teeth, each with seta-like movable spine (Fig. 4F–H).

Epipods present on P1, absent on P2–3.

**Colour:** Three patterns have been observed: carapace and abdomen uniformly dark, usually brown or red (pattern 1 of Baba, 1979), dark brown with two narrow light stripes (pattern 3 of Baba, 1979), and alternating dark and light longitudinal stripes (pattern 4 of Baba, 1979) (see Appendix). Pereiopods uniformly dark (red or brown) or yellowish.

**Remarks:** *Allogalatheia inermis* sp. nov. is easily differentiated from the other closely related species (*A. babai* sp. nov. and *A. elegans*) by the following features.

1. The rostrum is shorter in *A. inermis* sp. nov. (1.3–1.6 times longer than wide) than in *A. babai* sp. nov. and *A. elegans* (2.0–2.3 times longer than wide).
2. The squamae on the dorsal surface of the P1 palm are mostly unarmed in *A. inermis* sp. nov., whereas these squamae have at least one spinule in *A. babai* sp. nov. and *A. elegans*.
3. The mesial and lateral margins of P1 palm are convex in the adult males of *A. inermis* sp. nov., whereas these margins are straight in *A. babai* sp. nov. and *A. elegans*.

**Distribution and habitat:** Mozambique, Japan, Thailand, Indonesia (Gorong Island), Vanuatu, New Caledonia, and Chesterfield Islands, between a depth of

44 and 120 m. Usually living on crinoids (*O. bennetti* and *H. robustipinna*).

***Allogalatheia longimana* sp. nov.** (Figs 5, 6D)

*Galathea elegans* Haswell, 1882: 163; Grant & McCulloch, 1906: 50, plate 4, figures 6 and 6a.

*Allogalatheia elegans* Miyake, 1982: 149, plate 50, colour figure 5.

**Material examined:** Philippines. Musorstom 3. Stn CP97, 14°01'N, 120°19'E, 1 June 1985, depth 189–194 m: one M 6.7 mm (MNHN-Ga7430, Allo44); Stn CP107, 14°02'N, 120°28'E, 2 June 1985, depth 111–115 m: one M 3.8 mm (MNHN-Ga7431, Allo46), one ovig. F 6.5 mm (MNHN-Ga7432, Allo38); Stn CP124, 12°03'N, 121°35'E, 4 June 1985, depth 120–123 m: two M 6.6–7.2 mm, two ovig. F 6.3–7.5 mm (MNHN-Ga7433 and MNHN-Ga7434, Allo45).

**Types:** The ovigerous female of 6.5 mm postorbital carapace length from the Philippines (Musorstom 3, Stn CP107, MNHN-Ga7432) has been selected as the holotype. The other specimens are paratypes.

**Etymology:** From the Latin *longus* (long) and *manus* (hand), referring to the long cheliped (P1) and P1 palm, a character that separates this species from the other three species in this genus.

**Description:** Carapace, exclusive of rostrum, as long as broad; dorsal surface nearly horizontal from anterior to posterior, and cervical groove very shallow. Gastric region with five or six uninterrupted ridges and two or three interrupted ridges, usually without scales between them, anterior first and third ridges medially convex anteriorly; mid-transverse ridge uninterrupted, extending laterally to sixth marginal spines, preceded by very shallow cervical groove, followed by between six and nine transverse ridges, mostly interrupted. Lateral margins with between eight and ten spines: two spines in front of, and between six and eight spines behind, indistinct anterior cervical groove; first anterolateral, well-developed, slightly posterior to level of lateral limit of orbit; second smaller than first, equidistant between anterolateral spine and anterior cervical groove; three spines on anterior branchial region, and between three and five spines on posterior branchial margin, decreasing in size posteriorly. Rostrum moderately long, with between eight and ten small lateral teeth, 1.8 times longer than broad, length 0.7 times that of carapace, dorsal surface nearly horizontal in lateral view, with small setiferous ridges (Fig. 5A).

Pterygostomial flap with some setigerous ridges, anterior margin ending in small spine.

Sternal plastron 0.8 times as long as broad, lateral limits divergent posteriorly. Sternite 3 twice as broad as long, anterior margin with small median notch. Sternite 4 2.8 times longer and 2.8 times broader than preceding sternite, 0.5 times as long as broad; sternites 4 and 5 with a few transverse ridges bearing short setae (Fig. 5B).

Abdominal somites 2–4 each with four or five uninterrupted transverse ridges on tergite, with or without scales in between; somite 5 with 2 uninterrupted ridges, somite 6 with 2 interrupted ridges and some scales.

Eyestalk (other than cornea) with short fine setae on dorsal anterior extension; cornea moderately dilated.

Article 1 of antennal peduncle with distomesial spine reaching midlength of article 2. Article 2 with distolateral spine clearly longer than distomesial, nearly reaching end of article 3. Article 3 with small, distinct distomesial spine. Article 4 unarmed (Fig. 5C).

Mxp3 ischium with well-developed spine on flexor distal margin; extensor margin unarmed; crista dentata with 19–23 denticles. Merus slightly longer than ischium, with two or three strong spines of subequal size on flexor margin, proximal one located at midlength, distal one at terminal end; extensor margin unarmed, or with two or three small spines (Fig. 5D).

P1 squamous, 3.9–4.0 times carapace length, subcylindrical, lateral and mesial margins straight in adult specimens, most dorsal squamae unarmed or with one or two small spinules and long setae. Merus 1.1–1.3 times length of carapace, 1.3–1.6 times as long as carpus, with row of a few spines along mesial and distodorsal margins. Carpus 0.6–0.7 times length of palm, 3.8–4.0 times longer than broad, lateral and mesial margins subparallel, mesial and distodorsal margins with row of few spines. Palm 5.0–6.5 times longer than broad, dorsal surface without spinules; lateral and mesial margins subparallel, lacking spines. Fingers 0.4 times as long as palm, distally

crossing when closed; opposable margins nearly straight; mesial margin of movable finger with two or three subterminal spines (Fig. 5E).

P2–P4 squamous, slender, somewhat compressed, striae with long setae. P2 length 1.6–1.7 times carapace length. Meri successively shorter posteriorly (P3 merus 0.9 times length of P2 merus, P4 merus 0.8 times length of P3 merus); P2 merus 0.6–0.8 times carapace length, 3.5–4.0 times as long as broad, 1.3–1.5 times longer than P2 propodus. Dorsal margins of meri with distal row of small proximally diminishing spines on P2 and P3, unarmed on P4 except distal spine; ventrolateral margins with strong terminal spine. Carpi with some dorsal spines; flexor distal margins with very small spine. Propodi slightly shorter on P4 than on P2 and P3, 4.0 times as long as broad on P2 and P3; extensor margin unarmed; flexor margin with between six and eight slender movable spines. Dactyli subequal in length, half length of propodi, ending in a curved, strong, sharp spine; flexor margin with prominent triangular terminal tooth preceded by five or six obsolescent teeth, each with seta-like movable spine (Fig. 5F–H).

Epipods present on P1.

*Colour:* Body with alternating longitudinal dark-brown, white, or yellow stripes (pattern 4 of Baba, 1979). The middle stripe is always dark brown. P1–P4 brownish or yellowish.

*Remarks:* The species can be easily distinguished from the other three species of the genus according to the length of P1. The chelipeds (P1) are about four times the length of the carapace in *A. longimana* sp. nov., with the palm about twice the finger length. In the other species, the length P1 is always less than three times the carapace length, with the palm as long as or slightly longer than the fingers.

*Distribution and habitat:* Japan, the Philippines, and Queensland, Australia, between a depth of 36 and 194 m. Habitat unknown.

#### KEY TO SPECIES OF THE GENUS *ALLOGALATHEA*

1. P1 long, more than three times carapace length. Palm twice finger length... *Allogalthea longimana* sp. nov.  
P1 short, equal, or less than three times carapace length. Palm as long or slightly longer than finger length... 2
2. Rostrum short, 1.3–1.6 times longer than wide. Most scales on dorsal surface of palm without spinules. Mesial and lateral margins of P1 palm slightly convex in adult specimens..... *Allogalthea inermis* sp. nov.  
Rostrum moderately long, 2.0–2.3 times longer than wide. Most scales on dorsal surface of palm with spinules. Mesial and lateral margins of P1 palm straight or slightly convex in adult specimens..... 3
3. P2–P4 broad relative to length, P2 merus three times longer than height. Dorsal margin of P2 and P3 meri usually unarmed or with minute spines..... *Allogalthea babai* sp. nov.
4. P2–P4 moderately narrow relative to length, P2 merus four times longer than height. Dorsal margin of P2 and P3 meri have well-developed spines..... *Allogalthea elegans*

## MOLECULAR ANALYSIS

Two mitochondrial markers were amplified in 43 specimens. Phylogenetic trees were generated for the mitochondrial dataset, and on the basis of these trees we selected a subset of specimens for further sequencing of the nuclear marker (Table 1). After alignment, the two mitochondrial genes gave rise to a sequence data set comprising 1540 base pairs. The two independent *16S* rRNA fragments yielded 882 bp. Two regions between positions 245 and 280, and between positions 703 and 716, showed high variability, and both required the insertion of gaps. For this gene, 577 characters were constant, 106 were parsimony uninformative, and 199 were parsimony informative. In the *COI* sequence of 658 bp, 453 characters were constant, 35 were parsimony uninformative, and 170 characters were parsimony informative.

The data set for the nuclear gene *PEPCK* comprised 598 characters, of which 537 were constant, 30 were parsimony uninformative, and 31 were parsimony informative. No introns or indels were present in the sequences, but ambiguities such as double peaks in the chromatograms were detected, probably resulting from the heterozygosity of the specimens from which the sequence was derived. These positions were coded as ambiguities using the International Union of Biochemistry (IUB) symbols M, S, Y, R, K, or W, and were present at several sites within single sequences.

The mitochondrial genes indicated four strongly divergent clades (designated *A. elegans*, *A. babai* sp. nov., *A. inermis* sp. nov., and *A. longimana* sp. nov.) (Fig. 7). Molecular divergence among clades ranged from 8.40 to 12.06% for the *16S* rRNA gene sequences, and from 10.94 to 15.53% for the *COI* gene (Table 3). The *COI* gene was generally more variable between and within species than *16S* rRNA. Within *A. babai* sp. nov., the specimen Allo8069 from the Christmas Islands showed an intraspecific mean divergence of 4.5% for both mitochondrial genes, which is fairly high compared with divergences among other specimens. The nuclear gene showed a molecular divergence of 0.5–3.5%. The highest diver-

gence was observed between *A. babai* sp. nov. and *A. longimana* sp. nov. at 2.3–3.5%, and the lowest divergence was observed between *A. elegans* and *A. inermis* sp. nov. Lower variation in genetic divergence was detected within the groups in each species.

## PHYLOGENETIC INFERENCE

Data from the mitochondrial genes were combined in a single matrix because the incongruence length difference (ILD) test revealed no significant incongruence among gene partitions, and there were no strongly supported conflicting nodes among the tree topologies. The best-fit model selected using MODELTEST was GTR + G (the general time-reversible model; Lavane *et al.*, 1984; Rodríguez *et al.*, 1990), which rendered a  $\gamma$ -shape parameter of 0.1702 for the ML analysis. Base frequencies were A = 0.3536, C = 0.1276, G = 0.1547, and T = 0.3641, and the rate matrix was 0.8753, 11.1191, 2.2551, 0.2431, and 15.2273.

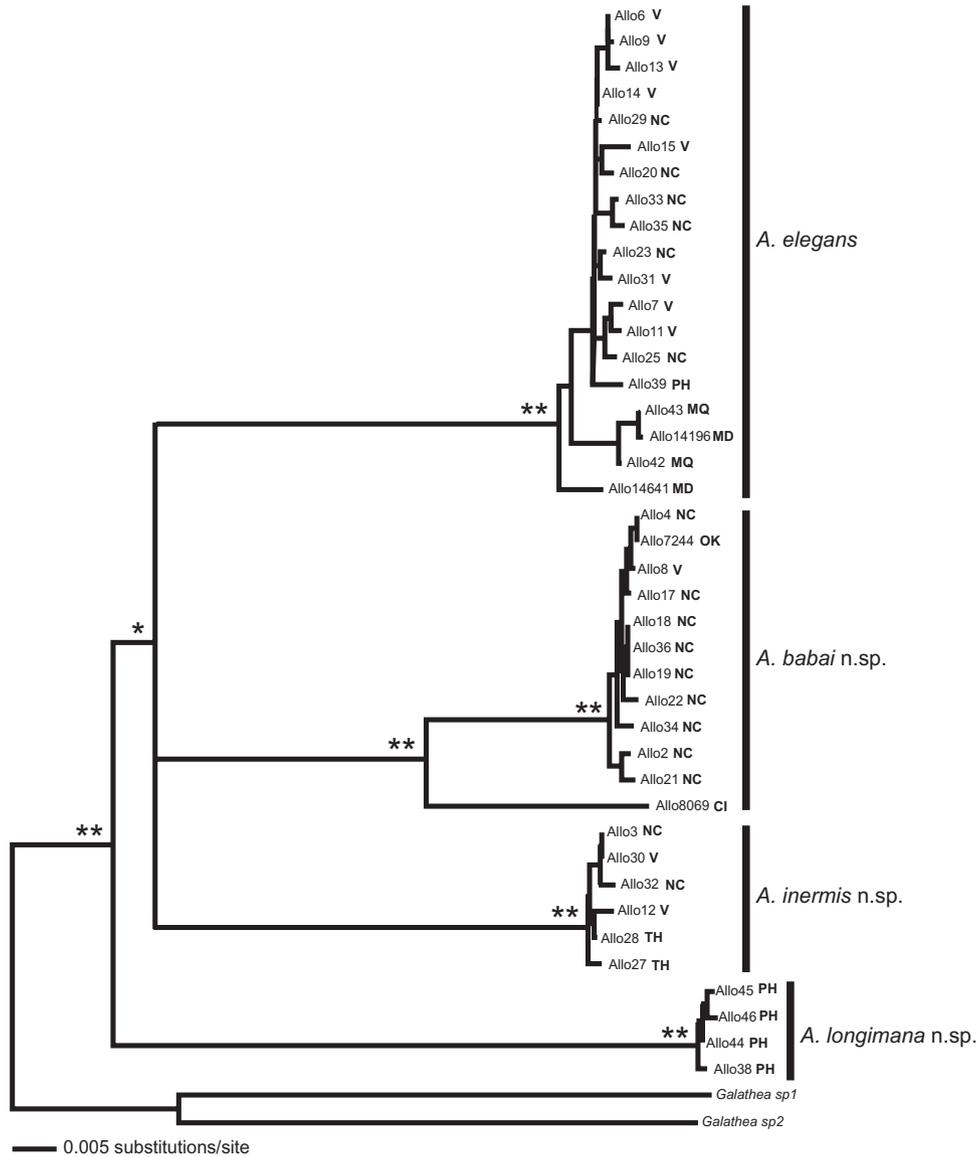
The best-fit model of evolution selected for the nuclear data set was TrN + I. Base frequencies of A = 0.2304, C = 0.2741, G = 0.2753, and T = 0.2201, and the rate matrix was 1.0000, 5.6155, 1.0000, 1.0000, and 9.7409 with an *I* value of 0.8169 for the ML analysis.

All of our MP, ML, and Bayesian phylogenetic analyses based on mitochondrial genes revealed four well-supported clades within the genus *Allogalatheia* (Fig. 7). Topologies derived from MP, ML, and BI were largely congruent although the internal nodes showed low statistical support. Our analysis suggests the existence of four deeply divergent clades, which may also be distinguished on the basis of subtle morphological differences. The monophyly of the genus was highly supported by all the tests (Fig. 7), though phylogenetic relationships were not fully resolved.

*Allogalatheia babai* n. sp., *A. elegans* and *A. inermis* n. sp. always clustered together, but bootstrap and posterior probability support was low in all the tests (MP = 77, ML = 63 and BI = 67). Phylogenetic rela-

**Table 3.** Mitochondrial pairwise distance values among *Allogalatheia* species. Distances above the diagonal refer to the *16S* rRNA gene and below the diagonal to the *COI* gene

	<i>Allogalatheia elegans</i>	<i>Allogalatheia babai</i> sp. nov.	<i>Allogalatheia inermis</i> sp. nov.	<i>Allogalatheia longimanan</i> sp. nov.
<i>Allogalatheia elegans</i>	X	8.70–9.43%	8.40–9.22%	10.33–11.02%
<i>Allogalatheia babai</i> sp. nov.	12.31–13.56%	X	8.70–9.99%	10.28–11.08%
<i>Allogalatheia inermis</i> sp. nov.	12.15–13.52%	10.94–12.31%	X	11.33–12.06%
<i>Allogalatheia longimana</i> sp. nov.	14.43–15.53%	12.86–13.67%	14.43–15.04%	X



**Figure 7.** Neighbour-joining (NJ) tree representing the phylogenetic hypothesis based on the combined data set (16S rRNA and *COI*). Bayesian posterior probabilities (BPPs) and bootstrap values (BVs): \*\*BPP = 1 and BV = 100; \*BPP = 0.67 and BV  $\geq$  65. Codes next to the specimen names correspond to the geographic location: CI, Christmas Islands; MD, Madagascar; MQ, Mozambique; NC, New Caledonia; OK, Okinawa; PH, Philippines; TH, Thailand; V, Vanuatu.

tionships among these three species were not resolved and the tree topology reflected a trichotomy. In all tests, the species *A. longimana* n. sp. occupied a basal position.

The nuclear gene *PEPCK* was unable to resolve the phylogenetic relationships among the four clades. In each analysis, the monophyly of *A. babai* n. sp. and *A. inermis* n. sp. was supported. Despite a lack of resolution for defining the other two species, our Bayesian reconstruction indicated clear differentiation of the only specimen of *A. longimana* sp. nov. examined from all other specimens of *A. elegans*.

## DISCUSSION

Throughout 250 years of Linnaean taxonomy, species descriptions have mainly relied upon the study of morphological characters. Given the criteria used to define species could sometimes be controversial (Avice, 1994), the combined use of molecular and morphological data may help clarify species boundaries (Calvo *et al.*, 2009; Santos *et al.*, 2009). The incorporation of molecular tools into systematic studies have confirmed the taxonomic status of many taxa described on the basis of morphological data

(Tautz *et al.*, 2003); however, it has also unveiled a vast diversity hidden behind a great morphological similarity (Bickford *et al.*, 2007).

Cryptic speciation has been previously reported in the family Galatheidae (Machordom & Macpherson, 2004; Macpherson & Machordom, 2005). The present study provides further evidence of the important role played by this phenomenon in squat lobsters, and confirms that the real diversity of the group is still far from being well known (Baba *et al.*, 2008). The morphological differences detected here among the four *Allogalathea* species are very subtle, but are constant in all of the specimens examined. Our results reveal the taxonomic value of characters such as those describing the spinulation and length of chelipeds (Fig. 6), spinulation of walking legs, and shape of the rostrum. These subtle traits are useful to designate species to the genus *Allogalathea*, and could probably also be used in closely related genera (e.g. *Galathea*, *Allomunida*, *Sadayoshia*, and *Lauriea*).

#### PHYLOGENETIC RECONSTRUCTION

Our phylogenetic reconstructions clearly indicate the existence of four strongly supported mitochondrial clades. Each of the clades recovered in this study are recognized as distinct species based on morphological and genomic features. The genus was identified as a monophyletic group, and although phylogenetic relationships were not fully resolved, the taxonomic status of the four species was highly supported by all the phylogenetic analyses.

The more conserved nuclear gene *PECK* was also unable to resolve phylogenetic relationships among the different groups, and only *A. babai* sp. nov. and *A. inermis* sp. nov. were recovered as monophyletic taxa. Thus, the *PEPCK* marker lacks the resolution needed to infer species-level relationships. This gene has been recently incorporated in the pool of nuclear protein coding genes used to infer relationships among high taxonomic levels of decapods (Tsang *et al.*, 2008; Ma *et al.*, 2009). Tsang *et al.* (2008) reported a mean divergence of around 6% for *PEPCK* in three species of *Panulirus*, also suggesting a good resolution power for lower taxonomic ranks (e.g. genus or species).

The maximum divergence value observed here for *PEPCK* was around 4.5%, and suggests insufficient variability for inferring phylogenetic relationships at the intrageneric level in galatheids. The use of this gene as a marker of relationships within and among different galatheid genera (e.g. *Paramunida* and *Agononida*) has also been tested, and preliminary data indicate the same lack of resolution observed here at species level, but a better capacity to resolve intergeneric relationships (unpubl. data).

Mitochondrial interspecific divergences within *Allogalathea* were clearly higher than those reported for species of other squat lobster genera, e.g. *Munida*, *Paramunida*, and *Raymunida* (Machordom & Macpherson, 2004; Cabezas *et al.*, 2009). Lower mean mitochondrial divergences than those reported in the present study would be expected to return unresolved phylogenetic trees using the nuclear gene *PECK* as the marker. Resolution could perhaps be improved by combining this nuclear marker with non-coding ribosomal genes such as *18S* rRNA or *28S* rRNA.

The position ascribed by the mitochondrial genes to the single specimen from Christmas Islands (Allo8069) within the clade *A. babai* sp. nov. is remarkable. This specimen was clearly differentiated in the phylogenetic tree from the rest of the specimens of the clade (Fig. 7), and exhibited a mean divergence according to both mitochondrial genes of around 4.5%. Although similar divergences accompanied by the corresponding morphological data have been considered sufficient evidence to describe new species of other squat lobster genera (Macpherson & Machordom, 2001; Cabezas *et al.*, 2009), we were unable to detect any morphological difference to support the idea that this specimen belongs to a different species. Furthermore, our amplification of the *PEPCK* gene failed in this specimen, and we could not confirm its genetic differentiation at the nuclear level. Hence, until more specimens can be analysed, we have designated specimen Allo8069 as *A. babai* sp. nov.

#### PHYLOGEOGRAPHIC AND EVOLUTIONARY CONSIDERATIONS

Macroecological studies have demonstrated that, in general, coastal species have smaller geographic ranges than species inhabiting the continental slope or abyssal plains (Macpherson, 2003). Until 20 years ago, species associated with deep marine strata were considered to have a wide distribution because these ecosystems were assumed to be homogenous and uniform (Wilson & Hessler, 1987).

Most species of the family Galatheidae are found in waters of the continental slope (at depths of 200–2000 m), with the exception of *Allogalathea* and closely related genera (e.g. *Galathea*; Baba *et al.*, 2008), which live in shallow waters. In general, galatheid species exhibit a moderately wide geographical range. However, numerous species of *Paramunida* and *Munida* are restricted to a single or a few sea-mounts, islands, or archipelagos (Samadi *et al.*, 2006; Cabezas *et al.*, 2009; Macpherson *et al.*, 2010; Rowden *et al.*, 2010). Although the main goal of this study was a taxonomic revision of the genus *Allogalathea*, some phylogeographic considerations can be inferred from

our molecular data because the four species show different distributions. *Allogalathea elegans* shows an exceptionally wide distribution range across the Indo-Pacific Ocean, *A. babai* sp. nov. and *A. inermis* sp. nov. are both widely distributed in the West Pacific, and *A. longimana* sp. nov. is the only species with a distribution restricted to the Philippines (Fig. 7). Although these findings suggest no pattern within the geographic ranges of each species, specimens of *A. elegans* collected in Mozambique and Madagascar clustered separately in the phylogenetic tree, indicating that populations from the Indian Ocean are genetically different to those inhabiting the Pacific. However, more extensive sampling is needed to confirm either a pattern of isolation by distance, or a vicariant event that affected these two populations. In the case of the other two species, the differences observed among specimens from New Caledonia, Okinawa, and Vanuatu (*A. babai* sp. nov.), and among those from New Caledonia, Vanuatu, and Thailand (*A. inermis* sp. nov.) were discrete, and no genetic structure was detected for the different regions.

Prior phylogeographic studies have shown effective barriers to genetic exchange between and within the Indian and Pacific Oceans (Williams & Benzie, 1997; Barber *et al.*, 2002; Crandall *et al.*, 2008). Nevertheless, our results suggest gene flow among *Allogalathea* specimens separated by thousands of kilometres, in agreement with other studies on coral reef fishes (Craig *et al.*, 2007; Horne *et al.*, 2008).

The use of molecular phylogenies to examine connectivity among marine populations can be very effective, but when the sample size is limited, as in our investigation, any weak genetic population structure must be interpreted cautiously (Hedgecock, Barber & Edmands, 2007). The apparent low genetic diversity revealed by our data could be explained by a great dispersal capability during the larval stage, yet ecological factors or historic events cannot be ruled out.

Any inferences concerning the dispersion of *Allogalathea* are highly speculative, as knowledge of larval development in Galatheidae is scarce (e.g. Guerao *et al.*, 2006). The diversification of the galatheid genus *Munida* has been dated as Middle or Late Miocene based on general mean divergence values for the 16S rRNA and *COI* genes (Machordom & Macpherson, 2004). The interspecific divergence found here for the *COI* gene ranged from 12 to 15%. Assuming a rough mean *COI* divergence of 1–2% per million years, diversification of the *Allogalathea* genus would have occurred during the Late Miocene. Although more accurate molecular calibrations are still necessary, this preliminary estimate is in agreement with dating proposed for other shallow water species distributed in the Indo-Pacific region (McCafferty *et al.*, 2002; Williams & Duda, 2008). New data

on the biology, phylogeny, and ecology of these species, as well as improved knowledge of the geological history of the Indo-Pacific region will help to clarify genetic connectivity among populations, and the true diversity and evolutionary history of the genus.

## CONCLUSIONS

The present findings illustrate the need to combine different sources of information when intraspecific variability in morphological characters is not clear. Our results highlight the importance of the subtle morphological differences mentioned by Baba for this group (1969, 1979). Characters describing the spinulation and length of chelipeds, spinulation of walking legs, and shape of the rostrum can contribute greatly to the taxonomy of *Allogalathea*. The existence of more species of *Allogalathea* is likely, and a more detailed study designed to fill in distribution range gaps, including more specimens is recommended.

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APPENDIX

Dorsal view. A, *Allogalathea babai* sp. nov., Santo, Stn FR1-CF1, ovigerous female 8.4 mm; B, *Allogalathea elegans* (Adams & White, 1848), Santo, Stn FR1-CF2, male 4.1 mm; C, *A. elegans* (Adams & White, 1848), Santo, Stn AT81, ovigerous female 6.0 mm; D, *Allogalathea inermis* sp. nov., Santo, Stn NR8, male 3.1 mm.

