

TWO NEW SPECIES OF THE RARE LOBSTER GENUS *THAUMASTOCHELES* WOOD-MASON, 1874 (REPTANTIA: NEPHROPIDAE) DISCOVERED FROM RECENT DEEP-SEA EXPEDITIONS IN THE INDO-WEST PACIFIC

Su-Ching Chang¹, Tin-Yam Chan^{1,2,*}, and Shane T. Ah Yong³

¹ Institute of Marine Biology, National Taiwan Ocean University, Keelung 20224, Taiwan, R.O.C.

² Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung 20224, Taiwan, R.O.C.

³ Australian Museum, 6 College Street, Sydney, NSW 2010, Australia

ABSTRACT

Specimens of species closely related to the rare deep-sea lobster *Thaumastocheles japonicus* Calman, 1913 were obtained from recent deep-sea expeditions in the West Pacific. Close examination of these specimens, as well as molecular analysis, showed that they represent two species new to science, with many morphological and significant genetic differences (barcoding gene COI sequence divergences 11.5–14.8%) between each other as well as *T. japonicus*. Re-examination of the specimens previously assigned to *T. japonicus* revealed that true *T. japonicus* has a more northern distribution, from Japan to the South China Sea and the Philippines. The two new species have more southern distributions with *T. bipristis* n. sp. restricted to the Philippines and Indonesia, and *T. massonktenos* n. sp. being widely distributed in the Indo-West Pacific, from the South China Sea to Madagascar and New Caledonia. The genetic data also suggest that *T. dochmiodon* Chan and de Saint Laurent, 1999 may represent a polymorphic male form of *T. japonicus*.

KEY WORDS: lobsters, Indo-West Pacific, Nephropidae, *Thaumastocheles*

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INTRODUCTION

Although rare and bizarre looking, the deep-sea lobsters previously assigned to a family Thaumastochelidae Bate, 1888 (the family status is no longer recognized; see Tshudy et al., 2009; Chan, 2010), are very characteristic in having the first chelipeds greatly unequal with the right side extremely elongate and pectinate. Currently, three genera and six species of extant “thaumastocheliforms” (see Ah Yong et al., 2010 for the use of this term) are known, but most genera and species were only discovered after 1988 (see Chan, 2010). The fossil record of the thaumastocheliform lobsters extends back to the Cretaceous in the genus *Oncopareia* Bosquet, 1854, and the Eocene to Recent for the genus *Dinocheilus* Ah Yong, Chan and Bouchet, 2010. From the late Cretaceous to early Tertiary, the thaumastocheliforms were common at shelf depths, but since the Miocene they appear to have moved into deeper slope habitats where they principally occur today (Tshudy, 2003). To date six fossil thaumastocheliforms are known, summarized by Tshudy and Saward (2012).

The recent and ongoing French deep-sea expeditions in the Indo-West Pacific have yielded more thaumastocheliform material. Amongst these specimens, a unique specimen from the Philippines was recently described as a new genus and species, *Dinocheilus ausubeli* Ah Yong, Chan, and Bouchet, 2010. All other thaumastocheliform specimens obtained from these recent French deep-sea expeditions are generally similar to *Thaumastocheles japonicus* Calman, 1913 but exhibit differences in the armature of the outer mar-

gin of the major chela dactylus or on the pleon. As most specimens of *T. japonicus* previously reported from the various localities in the Indo-West Pacific are either incomplete or rather small, there are uncertainties about their precise identities, especially, whether they really all belonged to the same species (see Chan and de Saint Laurent, 1999); all are re-examined and compared with the recently collected specimens. Nowadays, DNA barcoding often can provide useful genetic information for species delimitation and positively assigning incomplete or young specimens to species (Lin et al., 2004; Konishi et al., 2006; Costa et al., 2007; De Grave et al., 2010; Palero et al., 2011; Bracken-Grissom et al., 2012). Thus, every attempt has been made to sequence the barcoding gene COI and 16S rRNA for the specimens previously assigned to *T. japonicus* as well as those recently collected specimens similar to *T. japonicus*. Representatives of the two other known species in *Thaumastocheles* Wood-Mason, 1874, namely *T. zaleucus* (Thomson, 1873) and *T. dochmiodon* Chan and de Saint Laurent, 1999, are also sequenced to assess the genetic distance amongst the species in this genus. Very fortunately, the 16S rRNA and part of the COI gene of the holotype of *T. japonicus* (collected in 1898) were successfully obtained, and the genetic data show that there are actually three species in the material studied. The present work reports this finding and describes the two new species discovered. Another interesting finding from the genetic data is that *T. dochmiodon* is very likely a polymorphic male form of *T. japonicus*.

* Corresponding author; e-mail: tychan@mail.ntou.edu.tw

MATERIALS AND METHODS

Molecular Protocols

Specimens sequenced in the present work are presented in Table 1. Genomic DNA was extracted by Genomic DNA Mini Kit (Geneaid). Partial sequences of mitochondrial cytochrome *c* oxidase I (COI) and 16S ribosomal RNA (16S rRNA) genes were amplified by the universal primers LCO1490/HCO2198 (Folmer et al., 1994) and 16SF (Xu et al., 2009)/16SR (5'-CCG GTC TGA ACT CAA ATC GTG-3', newly designed by L. M. Tsang, pers. commun.), respectively. The PCR amplifications were performed in a 50 μ l volume containing 100-500 ng of the DNA extract, 5 μ l of 10 \times polymerase buffer, 2.0-2.5 mM of MgCl₂, 200 nM of each primer, 300 nM of dNTPs (TaKaRa), 1.5 U of *Taq* polymerase (5 U/ μ l, TaKaRa). The PCR cycling profiles were as follows: 5 min at 94°C for initial denaturation, followed by 35 cycles of 40 s at 94°C, 40 s at 48-49°C (depending on genes), 40 s at 72°C, and a final extension step at 72°C for 5 min. The PCR products were sent to a commercial company for further purifying (Geneaid) and sequencing (ABI 3730 XL automated sequencer). The sequence dataset was aligned by BIOEDIT v. 7.1.3 (Hall, 1999). Uncorrected nucleotide divergences (*p*-distance) between individuals were estimated by MEGA v. 5.1 (Tamura et al., 2011). MrModeltest v. 2 (Nylander, 2004) was used to evaluate the best-fit model of nucleotide substitution based on the Akaike information criterion (AIC). The phylogenetic topology was constructed by Bayesian Inference (BI) using MrBayes v. 3.2.1 (Ronquist et al., 2011). Two independent runs were performed with 1×10^6 generations each sampled every 100 generations. The initial 15% of generations were discarded as burn-in and a 50% majority-rule consensus was obtained from remaining sampled post burn-in trees to estimate posterior probabilities (Pp). Posterior probabilities > 0.5 are indicated at nodes.

Morphological Protocols

Morphological terminology generally follows Chan and de Saint Laurent (1999). Carapace length (cl) is measured dorsally from the orbital margin to the posterior margin of the carapace. The abbreviation, "CP," preceding the station numbers indicates the collecting gear, the French beam trawl. Specimens are deposited in the Muséum national d'Histoire naturelle, Paris (MNHN), National Taiwan Ocean University, Keelung (NTOU), Natural History Museum, London (BMNH), National Museum of the Philippines, Manila (NMCR), National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), Zoologische Staatssammlung München (ZSM), Natural History Museum and Institute, Chiba (CBM), and Museum and Art Gallery of the Northern Territory, Darwin (NTM). The following specimens of *T. japonicus*, reported previously in Chan and de Saint Laurent (1999) and collected later from Taiwan, were re-examined for comparison: Japan, off Odawara, Yenoshima, 200 fms (366 m), July 1898, holotype female cl 54.6 mm (NHM 1917.7.30.1); Sagami Bay, Enoshima, 800 m, May 1905, 1 male cl 36.9 mm (ZSM A20120314).—Taiwan, 24°51'60''-24°54'876''N, 122°04'250''-122°04'586''E, 500-630 m, 19 May 1998, 1 female cl 44.0 mm (NTOU M01737); Dasi fishing port, Yilan County, commercial trawler, September 1998, 1 female cephalothorax cl about 37.0 mm (NTOU M01738); TAIWAN 2001, stn CP90, 24°53'60''N, 122°01'39''E, 300-330 m, 10 May 2001, 1 female cl 26.5 mm (NTOU M00168).—Pratas (Dongsha), South China Sea, R/V "Fisheries Researcher I," 430 m, 21 April 1995, 1 female cl 42.9 mm (NTOU M01741, exTFRI).—Philippines, AL-BATROSS, stn 5127, 10°02'45''N, 121°48'15''E, 958 fms (1753 m), 4 February 1908, 1 female cl 19.0 mm (USNM 106926).

RESULTS

The phylogenetic tree of combined COI (459-657 bp) and 16S (425 bp) (Fig. 1) reveals 4 strongly corroborated clades within the genus *Thaumastocheles*. These four clades

Table 1. Thaumastocheliform material, locality, voucher and GenBank accession numbers used in this study.

Species	Locality	Voucher no.	Genbank accession no.	
			COI	16S rRNA
<i>Thaumastocheles japonicus</i> , holotype	Japan	NHM 1917.7.30.1	KF278689	KF278704
<i>Thaumastocheles japonicus</i> 1	Taiwan	NTOU M01737	KF278687	KF278696
<i>Thaumastocheles japonicus</i> 2	Taiwan	NTOU M00168	KF278681	KF278707
<i>Thaumastocheles japonicus</i> 3	Taiwan	NTOU M01738	KF278682	KF278693
<i>Thaumastocheles japonicus</i>	Philippines	USNM 106926	—	KF278702
<i>Thaumastocheles dochmiodon</i> , holotype	Taiwan	NTOU M01751	KF435135	KF435134
<i>Thaumastocheles dochmiodon</i> , paratype	Taiwan	NTOU M01736	KF278679	KF278690
<i>Thaumastocheles dochmiodon</i>	Taiwan	NTOU M01739	KF278678	KF278700
<i>Thaumastocheles dochmiodon</i> 1	Japan	CBM-ZC 6578	KF278684	KF278698
<i>Thaumastocheles dochmiodon</i> 2	Japan	CBM-ZC 7796	KF278683	KF278694
? <i>Thaumastocheles dochmiodon</i> 3	Australia	NTM Cr006896	—	KF278691
? <i>Thaumastocheles dochmiodon</i> 4	Australia	NTM Cr007532	—	KF278701
? <i>Thaumastocheles dochmiodon</i> 5	Australia	NTM Cr007353	—	KF278699
<i>Thaumastocheles bipristis</i> sp. nov., holotype	Philippines	NMCR	KF278685	KF278706
<i>Thaumastocheles bipristis</i> sp. nov.	Indonesia	USNM 107527	—	KF278695
<i>Thaumastocheles massonktenos</i> sp. nov., holotype	Solomon Island	MNHN-IU-2008-10556	KF604906	KF435129
<i>Thaumastocheles massonktenos</i> sp. nov., paratype 1	Papua New Guinea	MNHN-IU-2011-1825	KF604900	KF435131
<i>Thaumastocheles massonktenos</i> sp. nov., paratype 2	Papua New Guinea	MNHN-IU 2011-885	KF604901	KF435125
<i>Thaumastocheles massonktenos</i> sp. nov., paratype 3	Papua New Guinea	MNHN IU-2013-1041	KF604905	—
<i>Thaumastocheles massonktenos</i> sp. nov.	Philippines	MNHN-IU-2012-772	—	KF435132
<i>Thaumastocheles massonktenos</i> sp. nov., 1	New Caledonia	MNHN-IU-2012-771	KF604902	KF435128
<i>Thaumastocheles massonktenos</i> sp. nov., 2	New Caledonia	MNHN-IU-2012-780	KF604904	KF435127
<i>Thaumastocheles massonktenos</i> sp. nov., 3	New Caledonia	MNHN-IU-2012-778	—	KF435126
<i>Thaumastocheles massonktenos</i> sp. nov., 4	New Caledonia	MNHN-IU-2012-779	—	KF435133
<i>Thaumastocheles massonktenos</i> sp. nov.	Madagascar	MNHN-IU-2012-773	KF604903	KF435130
<i>Thaumastocheles massonktenos</i> sp. nov.	South China Sea	NTOUM 01740	—	KF278692
<i>Thaumastocheles zaleucus</i>	Gulf of Mexico	USNM 068658	KF278686	KF278705
<i>Dinochelus ausubeli</i> , holotype	Philippines	NMCR	KF278680	KF278697
<i>Thaumastochelopsis brucei</i> , paratype	Coral Sea	QMW25868	KF278688	KF278703

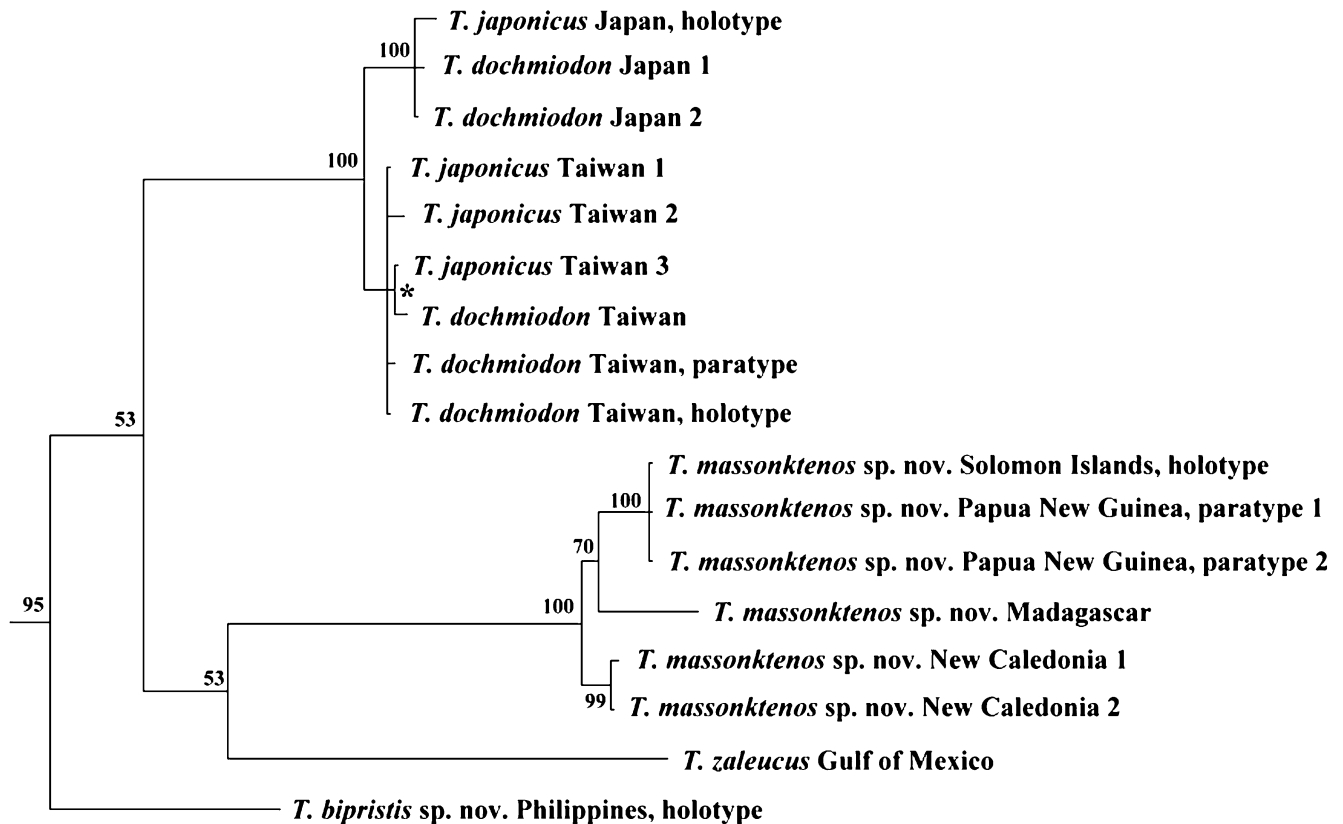


Fig. 1. Bayesian phylogenetic tree from combined segments of COI + 16S rRNA genes (~1.0 kb) amongst the species of the genus *Thaumastocheles*. Nodal support values represent Bayesian posterior probabilities, * = 100. Out-groups (not shown) were *Thaumastochelopsis brucei* Ah Yong, Chu and Chan, 2007, *Dinocheilus ausubeli* Ah Yong, Chan and Bouchet, 2010.

have 7.5–12.2% sequence divergences (10.6–15.9% in COI) amongst them but only 0.0–1.8% divergences (0.0–3.5% in COI) within each clade (Table 2). Within the clade containing *T. japonicus* and *T. dochmiodon*, surprisingly there is only 0.0–0.3% genetic divergence (COI divergence 0.0–0.7%) between *T. japonicus* and *T. dochmiodon* from Taiwan, which is even lower than the divergences between the Japanese and Taiwanese populations of *T. dochmiodon* (1.4–1.7% genetic overall, COI divergences 2.0–2.6%). Although only a partial COI (459 bp) sequence was successfully obtained for the holotype of *T. japonicus*, it is genetically 98.2–98.3% similar (partial COI similarity 97.1–97.4%) to *T. japonicus* from Taiwan and almost identical to *T. dochmiodon* from Japan (99.5–99.7% similar overall, COI similarity 99.1–99.3%). Amongst the other three clades, *T. zaleucus* differs from *T. japonicus*/*T. dochmiodon* by 11.2–12.0% (15.0–15.9% in COI). The clade consisting only of a recently collected specimen from the Philippines (NMCR) has 7.5–8.0% genetic divergence (10.6–11.5% in COI) from *T. japonicus*/*T. dochmiodon*, and 11.5% (15.0% in COI) divergence from *T. zaleucus*. The remaining clade of southern hemisphere Indo-West Pacific specimens show 0.0–1.9% genetic divergences (COI divergence 0.0–3.5%) amongst each other but differs from the other three clades by 9.5–12.3% sequence divergence (COI divergence 13.2–14.8%).

As COI divergences of more than 10% are unexceptionally considered as different species in decapod crustaceans (Jones and Macpherson, 2007; Cabezas et al., 2009; Tsoi et al., 2011; Yang et al., 2012), the genetic results clearly show that there are two undescribed species in *Thaumastocheles*. On the other hand, the maximum COI divergences within the clade containing specimens from the various southern hemisphere Indo-West Pacific localities is 3.5%, which is similar to those amongst the different populations of *T. japonicus* (2.9%) and *T. dochmiodon* (2.6%). Therefore, the southern hemisphere material can be regarded as belonging to the same species. Of the specimens assigned to *T. japonicus* by Chan and de Saint Laurent (1999), only one specimen from Taiwan [Tai-Shi (= Dasi), 4 August 1996] could not be restudied for the present work. The male from Japan (ZSM A20120314) and a female from Pratas (NTOU M01741) could not be successfully sequenced for either the COI or 16S rRNA genes. All other specimens reported by Chan and de Saint Laurent (1999) were successfully sequenced for either or both COI and 16S rRNA genes; their sequences have less than 3.5 and 2.1% divergence, respectively, from the holotypes of *T. japonicus* or either one of the two new species (Tables 1, 2), implying that they belong to one of these three species.

<i>T. japonicus</i>				<i>T. bipristis</i> n. sp.		<i>T. massonktenos</i> n. sp.				<i>T. dochmiodon</i>			<i>T. zaleucus</i>	
Japan		Taiwan		Philippines	Solomon Islands	Papua New Guinea	New Caledonia	Madagascar	Taiwan	Japan	Gulf of Mexico			
Holo-type	1	2	3	Holo-type	Holo-type	Para-type 1	Para-type 2	–	Holo-type	Para-type	1	2		
<i>T. japonicus</i>	Holotype*	0.007	0.007	0.007	0.042	0.061	0.061	0.064	0.064	0.007	0.000	0.000	0.078	
	1	0.026	–	0.000	0.040	0.061	0.061	0.064	0.064	0.000	0.000	0.007	0.071	
	2	0.029	0.002	–	0.040	0.061	0.061	0.064	0.064	0.000	0.000	0.007	0.071	
	3	0.029	0.002	0.004	–	0.040	0.061	0.061	0.064	0.000	0.000	0.007	0.071	
<i>T. bipristis</i> n. sp.	Philippines	0.115	0.108	0.110	0.110	–	0.073	0.073	0.075	0.075	0.040	0.040	0.042	0.078
<i>T. massonktenos</i> n. sp.	Solomon Islands	0.148	0.137	0.139	0.139	0.128	–	0.000	0.000	0.002	0.061	0.061	0.061	0.099
	Papua New Guinea	Paratype 1	0.148	0.137	0.139	0.139	0.128	0.000	–	0.000	0.002	0.002	0.007	0.099
		Paratype 2	0.148	0.137	0.139	0.139	0.128	0.000	0.000	–	0.002	0.002	0.007	0.099
	New Caledonia	1	0.146	0.135	0.137	0.137	0.124	0.035	0.035	–	0.000	0.009	0.064	0.101
		2	0.143	0.132	0.135	0.135	0.121	0.033	0.033	0.033	0.002	–	0.009	0.101
	Madagascar	–	0.143	0.132	0.135	0.135	0.119	0.029	0.029	0.029	0.029	0.026	–	0.101
	Taiwan	Holotype	0.026	0.000	0.002	0.002	0.108	0.137	0.137	0.135	0.132	0.132	0.007	0.071
<i>T. dochmiodon</i>		Paratype	0.026	0.000	0.002	0.002	0.108	0.137	0.137	0.135	0.132	0.132	0.007	0.071
		–	0.031	0.004	0.007	0.002	0.110	0.139	0.139	0.139	0.137	0.135	0.004	0.071
	Japan	1	0.009	0.022	0.024	0.024	0.106	0.143	0.143	0.137	0.135	0.135	0.022	0.078
		2	0.007	0.020	0.022	0.022	0.108	0.141	0.141	0.139	0.137	0.137	0.020	0.078
<i>T. zaleucus</i>	Gulf of Mexico	–	0.159	0.150	0.152	0.152	0.150	0.146	0.146	0.135	0.132	0.141	0.150	–

SYSTEMATICS

Thaumastocheles bipristis n. sp.

Figs. 2, 7A-B

Thaumastocheles japonicus. — Chan and de Saint Laurent, 1999: 899 (in part). [not Calman, 1913].

Material Examined.—Holotype: Philippines, PANGLAO 2005, stn CP2353, 09°25'60"N, 124°02'10"E, 1767 m, 25 May 2005, female cl 58.5 mm (NMCR).

Other specimen: Indonesia, ALBATROSS, stn 5593, 4°2'40"N, 118°11'20"E, 38 fms (70 m), 29 September 1909, 1 female cl 25.0 mm (USNM 107527).

Description of females (male unknown).—Rostrum triangular, overreaching basal segment of antennular peduncle and slightly curving downwards distally; lateral margin armed with 3-6 teeth, sparsely setose (Fig. 2A, B). Carapace (Fig. 2A) with branchial surface smooth or granulate; anterior part spinulose, bearing postorbital and postantennal spines; anterior margin pubescent. Pterygostomian margin convex, with 2-4 small but distinct spines. Anterolateral angle rounded, bearing 2 or 3 indistinct spines, meeting pterygostomian margin at acute angle. Cervical, hepatic, antennal, and postcervical grooves well developed, continuous with each other; postcervical groove across dorsum; branchiocardiac groove faintly indicated. Ventral and posterior margins of carapace sparsely setose.

Eye rudimentary; stalk robust, immovable, extending to one-third of basal segment of antennular peduncle, occasionally bifurcate.

Antennular peduncle (Fig. 2B, C) more or less extending to tip of scaphocerite; basal segment falling short of midlength of scaphocerite, bearing 1 subdistal ventromesial spine followed by 0-2 additional spines. Scaphocerite with outer margin concave and unarmed; inner margin with 6-8 slender spines. Antennal peduncle overreaching scaphocerite by length of entire distal segment; ventromesial surface of basicerite with 1 large distal spine followed by 1 or 2 small spines; lateral borders of scaphocerite and basicerite, as well as peduncle, with few long setae.

Epistome (Fig. 2D) fused anteriorly with carapace, bearing 1 or 2 spines near base of antennular peduncle; posterior margin raised, granular, with a few spines.

Maxilliped 3 exceeding antennular peduncle by one-third of distal segment, densely covered with long setae, bearing long exopod nearly reaching tip of merus; mesial margin of ischium serrated with row of sharp denticles, otherwise unarmed.

Chelipeds 1 (Fig. 2E, H) dissimilar and very unequal. Right (or major) cheliped extremely long and slender, with fingers about 3.4 times as long as palm and 1.4-1.6 times longer than carapace; dactylus and pollex armed with interspersed long and short perpendicular teeth on occlusal margins, curving inward at tips; outer margin of dactylus also with interspersed larger and smaller spines (Fig. 2E) but much shorter than those on occlusal margin and rather indistinct in small individuals (Fig. 2H); outer margin of pollex smooth; palm bulbous, sparsely spinose. Left (or minor) cheliped (Fig. 2F, G) distinctly shorter than right cheliped, overreaching scaphocerite by entire length of carpus; fingers 1.9-2.5 times as long as palm,

occlusal margins armed with interspersed long and short perpendicular teeth, outer margin of dactylus smooth, outer margin of pollex with 4-8 obliquely directed spines; palm rectangular and 2.6-2.7 times longer than wide, dorsal surface spinose, otherwise smooth; outer (flexor) margin of propodus nearly straight; carpus short and stout, slightly longer than wide, smooth apart from 4 or 5 large dorsal spines; merus ventral margin bearing row of spines.

Pereiopods 2 and 3 (Fig. 2I, J) chelate; chela as long as carpus; dactylus and pollex bearing dense long setae, distal half of occlusal margins serrated with corneous denticles; palm generally smooth and unarmed; carpus with dorsal margin unarmed or indistinctly spinulose; merus distinctly less than 2 times length of carpus, sometimes bearing spines on dorsal and/or ventral margins.

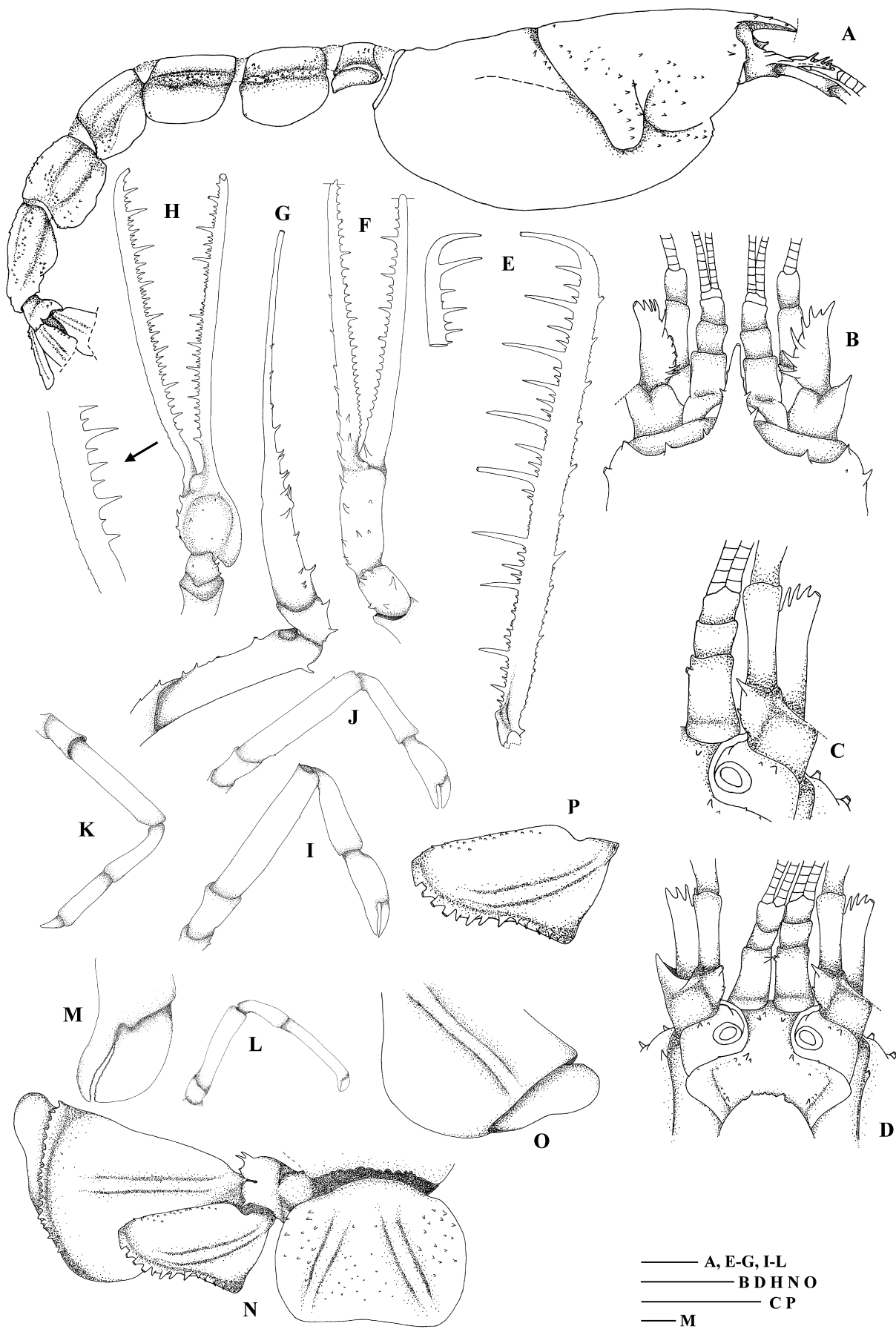
Pereiopod 4 (Fig. 2K) simple and flattened, with dactylus and anterior propodus heavily pubescent; dactylus triangular, about 2 times longer than wide; propodus, carpus and merus unarmed.

Pereiopod 5 chelate (Fig. 2L), with row of blunt denticles on occlusal margins of dactylus and pollex (Fig. 2M); dactylus, pollex and distal margin of palm pubescent; dactylus broad, more than 2 times as wide as pollex; palm to coxa unarmed.

Pleon strongly depressed (Fig. 2A). Lateral carinae of somites 1-3 as distinct tuberculate ridges; somites 4-6 with lateral carinae lobular. Tergite 1 generally smooth, greatly produced anterolaterally. Tergite 2 smooth except for some indistinct granules or spinules near lateral ridges. Tergites 3 and 4 unarmed. Tergite 5 and 6 granulated, posterior margin of tergite 6 denticulate. Pleuron 1 reduced, posterior part considerably broader than anterior part, ventral margin concave. Pleura 2 and 3 broad and smooth, about 2 times wider than long. Pleura 4 and 5 bearing few spinules or tubercles, posterior parts with distinct medial ridge. Pleuron 6 subtriangular, generally smooth except for some spines at posterior part and ventral margin. Tergites 3 and 4 setose, lateral margins of tergites 5 and 6 and ventral margins of pleura 2-6 fringed with dense long setae. Pleopod 1 reduced and thread-like. Pleopods 2-5 biramous, exopods and endopods fringed with dense long setae, endopods of pleopod 5 largest, about 1.3-1.5 times as long as tergite 6.

Telson sub-quadrate (Fig. 2N), about 1.3 times wider than long; dorsal surface tuberculate and with lateral parts sometimes distinctly spinose, bearing pair of posteriorly diverging low ridges; posterior margin slightly concave while lateral margins convex, margins unarmed but fringed with dense long setae.

Uropodal protopod short and stout, bilobed; lateral lobe bearing 2 or 3 distolateral spines; mesial lobe with distolateral angle rounded and armed with 1 strong distomesial spine, occasionally accompanied by 1 additional spine. Uropodal exopod with proximal segment large and broad, dorsal surface generally smooth but with distinct median ridge, distal margin with 16-21 teeth; distal segment (Fig. 2O) much wider than long, distal margin distinctly sinuous, concave medially, extending to distolateral angle of proximal segment. Uropodal endopod (Fig. 2P) much smaller than uropodal exopod, 1.6-1.7 times wider than long; distolateral angle truncate but followed by 10-12 teeth along



distal margin; rows of sharp granules or spinules near lateral border.

Color.—Body generally ivory white overall (Fig. 7A, B); posterior carapace, minor cheliped and pereopods 2-4 with dark brown staining probably due to reducing substrates (see Chan and de Saint Laurent, 1999).

Size.—The two females known are cl 25.0 and 58.5 mm.

Distribution.—At present only known from the Philippines and Indonesia, at depths of 70-1767 m (but see Remarks below).

IUCN Red List Conservation Assessment.—Being presently known only from two specimens from two localities, this species has been assessed as Data Deficient. Further research is therefore needed before a more accurate assessment of the conservation status of this species can be carried out.

Remarks.—Although the major chela of the holotype of *T. bipristis* is incomplete, with the distal part of merus, carpus, palm and most of the pollex missing (Fig. 7A, B), it readily differs from all other *Thaumastocheles* species in having the outer margin of the dactylus distinctly spinose rather than smooth (compare Fig. 2E with Figs. 3D-E, 4E). Moreover, *T. bipristis* exhibits 10.6-15.0% genetic divergence in COI from the other *Thaumastocheles* material (Table 2), corroborating its status as a separate species. Although *T. bipristis* is generally similar to *T. japonicus*, careful comparison reveals further morphological differences. A distinct distomesial spine at the ventral surface of the basal antennular segment is present in *T. bipristis* (Fig. 2C) but is absent in *T. japonicus* (Figs. 3C, 4C). The outer (flexor) margin of the propodus of minor chela is nearly straight in this new species (Fig. 2F) but distinctly concave in *T. japonicus* (Figs. 3F, 4F). Moreover, the tail fan of the present new species bears considerably more spines on the dorsal surfaces of the telson and uropodal endopod (Fig. 2N, P) than in *T. japonicus* (Figs. 3I, 4I).

Re-examination of the small female collected by the ALBATROSS from Indonesia (USNM 107527) showed that it corresponds morphologically to *T. bipristis* rather than to *T. japonicus*, with the spines along the outer margin of the dactylus of the major chela rather minute (Fig. 2H). The outer margin of the dactylus of the major chela is completely smooth in those specimens now identified as *T. japonicus* sensu stricto (Figs. 3D-E, 4E). Although COI sequences could not be obtained from this ALBATROSS specimen, its 16S was successfully sequenced (Table 1) and is 98.6% similar to that of the holotype of *T. bipristis*. This suggests that the Indonesian specimen is referable to *T. bipristis* and that the less developed spines on the outer margin of the dactylus of the major chela in this specimen is likely related to its small size. It should be noted that the recorded capture depth of the Indonesian ALBATROSS

specimen was only 38 fathoms (70 m), which is atypically shallow for thaumastocheliforms (see also Chan and de Saint Laurent, 1999). Until more thaumastocheliform material can be captured from upper shelf depths, such a shallow record needs to be considered as possibly erroneous.

Etymology.—The Greek “*bi*” (double) and “*pristis*” (saw) refers to the dactylus of the major chela with both the outer and occlusal margins pectinate in this species, somewhat like a double-edged saw.

Thaumastocheles massonktenos n. sp.

Figs. 5, 7C-D

Thaumastocheles japonicus. — Monod, 1973: 126, Figs. 37-39; Holthuis, 1991: 23 (in part); Chan and de Saint Laurent, 1999: 899 (in part). [not Calman, 1913].

Thaumastocheles ? *japonicus*. — Richer de Forges and Laboute, 1995: 68. [not Calman, 1913].

[?] *Thaumastocheles dochmiodon*. — Chan and de Saint Laurent, 1999: 899 (in part). [not Chan and de Saint Laurent, 1999].

Material Examined.—Holotype: Solomon Islands, SOLOMON 2, stn CP2270, 7°37.89'S, 156°58.84'E, 970-1060 m, 4 November 2004, female (carapace damaged) cl about 52.0 mm (MNHN IU-2008-10556, Barcode ID: MDECA 006-10).

Paratypes: Papua New Guinea, BIOPAPUA, stn CP 3651, 02°41'S, 150°03'E, 840-865 m, 27 August, 2010, 1 female cephalothorax cl 35.2 mm (MNHN IU-2011-885, Barcode ID: THAU002-13); stn CP 3674, 04°02'S, 150°50'E, 788-805 m, 24 September 2010, 1 female cephalothorax cl 40.8 mm (MNHN IU-2011-1825, Barcode ID: THAU001-13); MADANG, stn CP3965, 05°07'S, 145°53'E, 980 m, 1 December, 2012, 1 female cl 13.6 mm (MNHN IU-2013-1041, Barcode ID: THAU006-13).

Other specimens: Pratas (Dongsha), South China Sea, R/V “Fisheries Researcher I,” April 1995, 1 female cephalothorax cl 43.8 mm (NTOU M01740, exTFRI).—Philippines, MUSORSTOM III, stn CP55, 13°53.7'N, 199°58.5'E, 865 m, 1 right (major) cheliped 1 (MNHN IU-2012-772).—New Caledonia, 22°2'S, 165°57'E, 800 m, 1 damaged right (major) cheliped 1 (MNHN IU-2012-778); BATHUS 1, stn CP660, 21°10.5'S, 165°53.2'E, 786-800 m, 13 March 1993, 1 damaged female cephalothorax cl about 36 mm (MNHN IU-2012-779); BATHUS 2, stn CP743, 22°35.6'S, 166°26.6'E, 713-950 m, 14 May 1993, 1 male cl 14.9 mm (MNHN IU-2017-780, Barcode ID: THAU005-13); HALIPRO 1, stn CP867, 21°26.155'S, 166°18.174'E, 720-950 m, 22 March 1994, 1 damaged male cephalothorax cl about 50 mm (MNHN IU-2012-771, Barcode ID: THAU003-13).—Madagascar, stn CH135, 13°01'S, 40°01'E, 1075-1110 m, 21 January 1975, 1 damaged right (major) chela 1 (MNHN IU-2012-773, Barcode ID: THAU004-13).

Fig. 2. *Thaumastocheles bipristis* sp. nov., A-G, I-P, holotype female cl 58.5 mm, the Philippines (NMCR); H, female cl 25.0 mm, Indonesia (USNM 107527). A, body, right lateral view; B, anterior cephalothorax, dorsal view; C, left antennular and antennal peduncles, ventral view; D, anterior cephalothorax with epistome, ventral view; E, dactylus and distal part of pollex of major chela (right pereopod 1), lateral view; F, minor chela (left pereopod 1), lateral view; G, same, ventral view; H, major chela (right pereopod 1), lateral view; I-L, right pereopods 2-5, lateral view; M, chela of right pereopod 5, lateral view; N, telson and left uropods, dorsal view; O, left uropodal exopod, ventral view; P, left uropodal endopod, dorsal view. Setae omitted, scale bars: A-L, N-P = 10 mm, M = 1 mm.

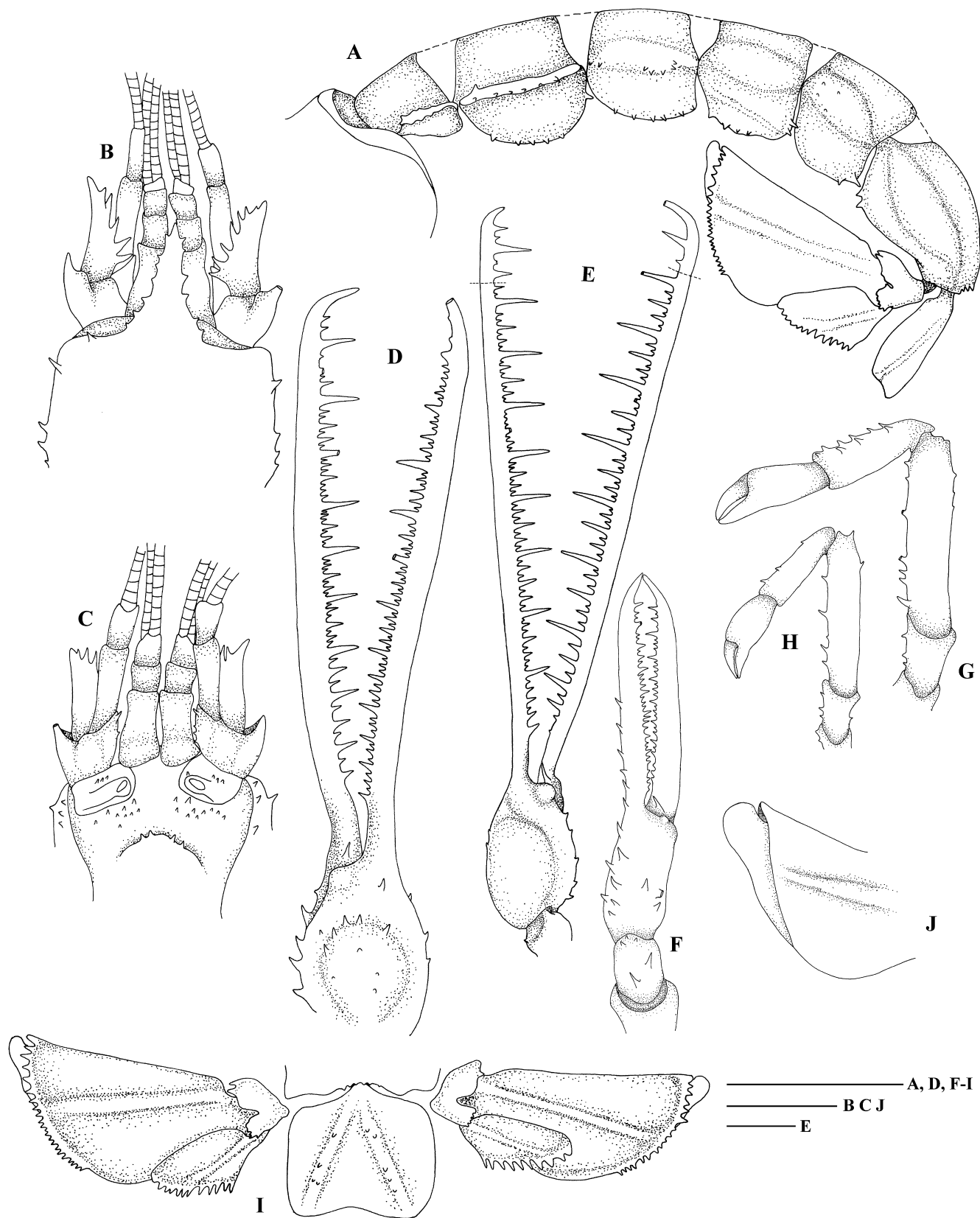


Fig. 3. *Thaumastocheles japonicus* Calman, 1913, A-D, F-J, female cl 26.5 mm, Taiwan (NTOU M00168); E, holotype female cl 54.6 mm, Japan (NHM 1917.7.30.1). A, pleon, left lateral view; B, anterior cephalothorax, dorsal view; C, anterior cephalothorax with epistome, ventral view; D, major chela (right pereopod 1), lateral view; E, same, mesial view; F, minor chela (left pereopod 1), lateral view; G, left pereopod 2, lateral view; H, left pereopod 3, lateral view; I, tail fan, dorsal view; J, right uropodal exopod, ventral view. Setae omitted, scale bars: A, D-I = 10 mm; B, C, J = 0.5 mm.

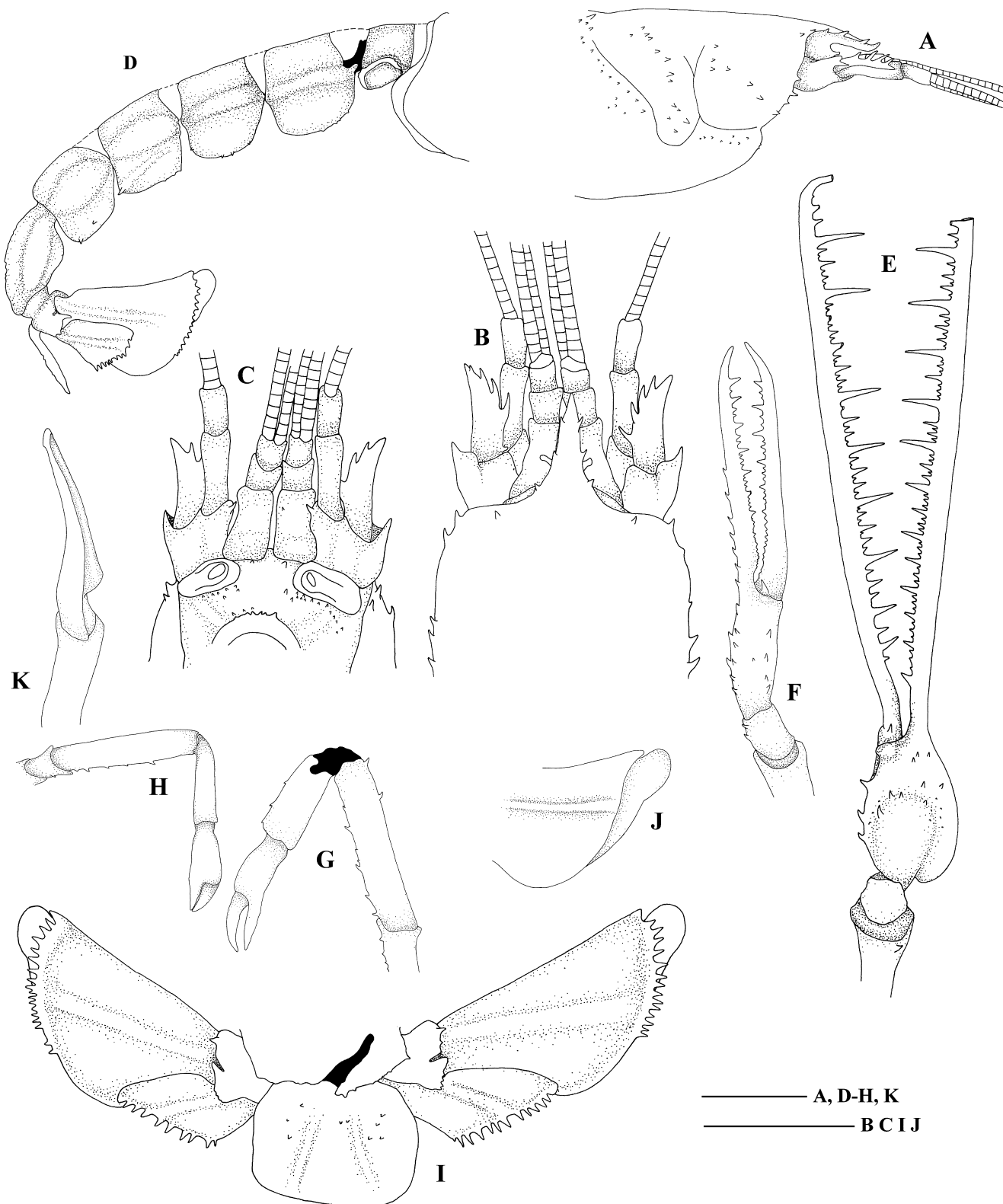
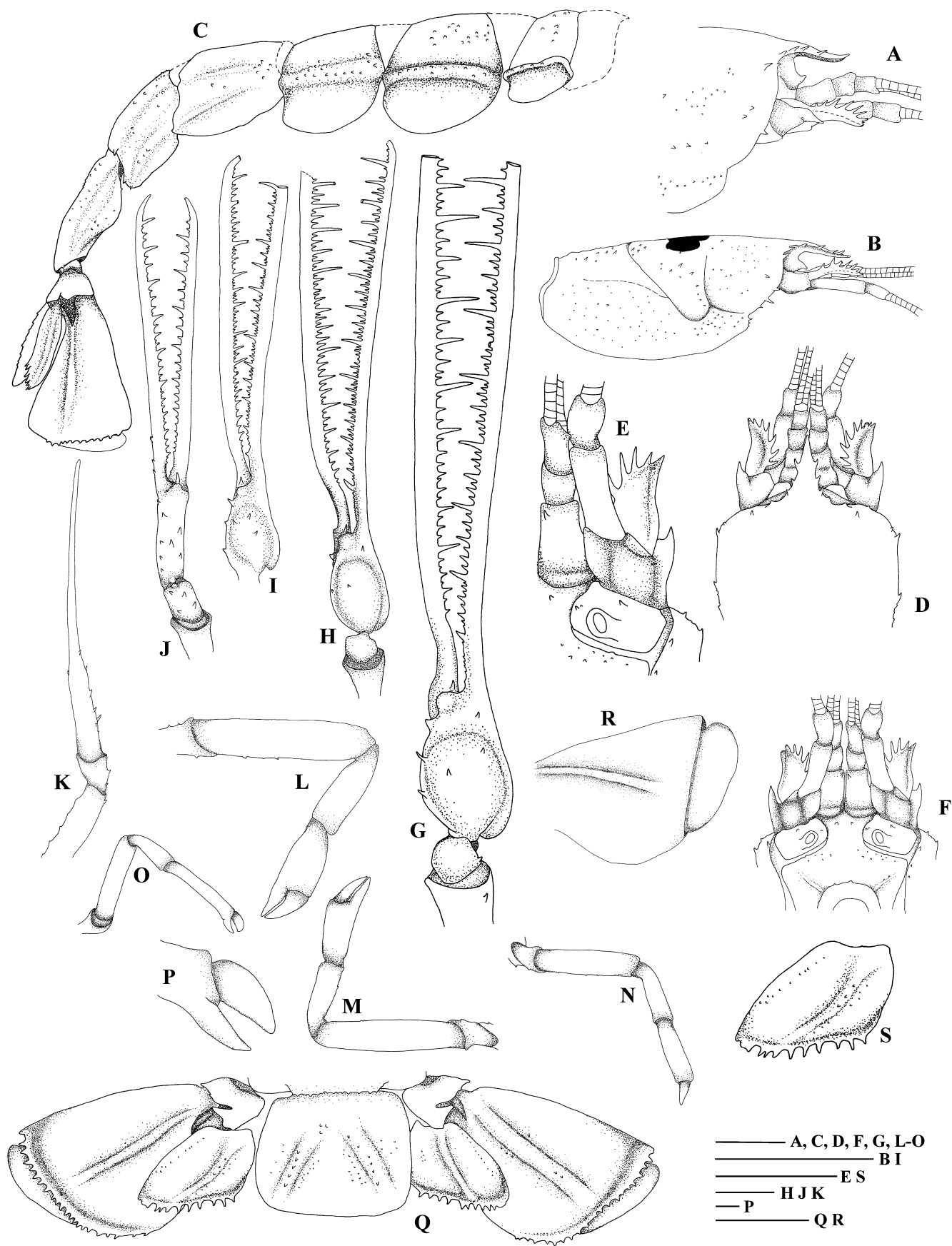


Fig. 4. *Thaumastocheles japonicus* Calman, 1913, male cl 36.9 mm, Japan (ZSM A20120314). A, anterior cephalothorax, right lateral view; B, same, dorsal view; C, same, ventral view; D, pleon, right lateral view; E, major chela (right pereopod 1), lateral view; F, minor chela (left pereopod 1), lateral view; G, left pereopod 2, lateral view; H, right pereopod 3, lateral view; I, tail fan, dorsal view; J, left uropodal exopod, ventral view; K, right pleopod 1, ventral view. Setae omitted, scale bars: A-J = 10 mm; K = 5 mm.



Description.—Rostrum triangular (Fig. 5A, B, D), generally extending to tip of second antennular segment and occasionally to tip of antennular peduncle; gently curving downwards but with tip recurved upwards; lateral margins setose, armed with 2-6 (usually 4 or 5) spines. Carapace granular and bearing some spines, including postorbital and postantennal spines, margins pubescent. Pterygostomian margin slightly convex, with 1 spine at level immediately below antennal peduncle and followed by 0-2 (usually 0) spines. Anterolateral angle rounded, margin usually smooth but occasionally bearing 3 distinct spines, meeting pterygostomian margin at blunt angle. Cervical, hepatic, antennal, and postcervical grooves well developed, continuous with each other; postcervical groove across dorsum; branchiocardiac groove faintly indicated.

Eye rudimentary; stalk immovable, triangular and not reaching one-third of basal segment of antennular peduncle.

Antennular peduncle (Fig. 5D, E) more or less extending to tip of scaphocerite; basal segment not reaching tip of rostrum, armed with 1 subdistal ventromesial spine. Scaphocerite smooth and sinuous at outer margin, armed with 6-9 slender spines along inner margin. Antennal peduncle overreaching scaphocerite by length of entire distal segment, basicerite unarmed ventrally; lateral borders of scaphocerite and basicerite fringed with long setae.

Epistome (Fig. 5F) fused anteriorly with carapace, bearing 1 tubercle or spine near base of antennular peduncle; posterior margin raised and slightly granular.

Maxilliped 3 overreaching antennular peduncle, densely covered with long setae; exopod long and more or less extending to tip of merus; mesial margin of ischium serrated with row of sharp denticles, otherwise unarmed.

Cheliped 1 dissimilar and very unequal (Fig. 5G-J). Right (or major) cheliped extremely long and slender, with fingers about 3.6-4.5 times as long as palm and 1.5-2.0 times longer than carapace; dactylus and pollex armed with interspersed long and short perpendicular teeth on occlusal margins (Fig. 5G, H; in very small individuals these teeth slightly oblique and directed anterolaterally, Fig. 5I), curving inward at tips; outer margins of dactylus and pollex smooth, completely unarmed; palm bulbous and sparsely spinose. Left (or minor) cheliped (Fig. 5J, K) distinctly shorter than right cheliped, overreaching scaphocerite by chela; fingers 2.0-2.8 times as long as palm, occlusal margins armed with interspersed long and short perpendicular teeth; outer margin of dactylus smooth; outer margin of pollex with 0-5 upwards spines; palm rectangular and about 3 times longer than wide, dorsal surface spinose, otherwise smooth; outer (flexor) margin of propodus nearly straight; carpus short and stout, slightly longer than wide, smooth apart from 4 or 5 dorsal spines; merus ventral margin bearing row of spines.

Pereiopod 2 and 3 (Fig. 5L, M) chelate; chela 1.0-1.17 (mostly 1.15-1.17) and 1.13-1.25 (mostly 1.21-1.25) times longer than carpus, respectively; dactylus and pollex bearing dense long setae, distal half of occlusal margins serrated with corneous denticles; palm generally smooth and unarmed; carpus unarmed; merus about 2 times as long as carpus, ventral margin slightly granular to spinose, dorsal margin generally unarmed.

Pereiopod 4 (Fig. 5N), simple and flattened, with dactylus and anterior propodus heavily pubescent; dactylus triangular, about 2 times longer than wide; propodus and carpus unarmed; merus with ventral margin weakly granular.

Pereiopod 5 chelate (Fig. 5O), with row of blunt denticles on occlusal margins of dactylus and pollex (Fig. 5P); dactylus, pollex and distal margin of palm pubescent; dactylus broad, more than 2 times as wide as pollex; palm to coxa unarmed.

Pleon (Fig. 5C) strongly depressed. Lateral carinae of somites 1-3 forming spinose ridges; somites 4-6 with lateral carinae lobular. Tergites 1 and 2 distinctly granulate (or spinose in small individuals). Tergites 3 and 4 unarmed. Tergites 5 and 6 sharply tuberculate, posterior margin of tergite 6 denticulate. Pleuron 1 reduced and somewhat triangular, with ventral margin slightly convex. Pleura 2 and 3 broad but less than 2 times wider than long; generally smooth, with ventral margins generally unarmed or bearing spines in small individuals. Pleura 4 and 5 bearing few spinules or tubercles, posterior parts with distinct medial ridge. Pleuron 6 subtriangular, generally smooth except for some indistinct spines. Tergites 3 and 4 setose, ventral margins of pleura 2-6 covered with dense long setae, otherwise naked or weakly pubescent. Pleopod 1 reduced and thread-like in females and small males. Pleopods 2-5 biramous, with margins of exopods and endopods heavily setose; endopods of pleopod 5 largest and as long as tergite 6.

Telson (Fig. 5Q) sub-quadrate, about 1.2 times wider than long; dorsal surface with few granules or indistinct spines, bearing pair of posteriorly diverging low ridges; posterior margin straight while lateral margins slightly convex, margins unarmed but fringed with dense long setae.

Uropodal protopod short and stout, bilobed; lateral lobe bearing 0 or 1 distolateral spine; mesial lobe with distolateral angle terminating in sharp spine but lacking distomesial spine. Uropodal exopod with proximal segment large and broad, dorsal surface generally smooth but with distinct median ridge, bearing 21-24 teeth along distal margin; distal segment (Fig. 5R) much wider than long, more or less convex and with distal margin not distinctly sinuous, distolateral angle not reaching that of proximal segment. Uropodal endopod (Fig. 5S) much smaller than uropodal exopod, 1.3-1.4 times wider than long; distolateral angle

Fig. 5. *Thaumastocheles massonkenos* sp. nov., A, C-G, L-S, holotype female cl 52.0 mm, Solomon Islands (MNHN IU-2008-10556); B, I, paratype female cl 13.6 mm, Papua New Guinea (MNHN IU-2013-1041); H, K, paratype female cl 35.2 mm, Papua New Guinea (MNHN IU-2011-885); J, paratype female cl 40.8 mm, Papua New Guinea (MNHN IU-2011-1825). A, anterior cephalothorax, right lateral view; B, carapace and anterior appendages, right lateral view; C, pleon, right lateral view; D, anterior cephalothorax, dorsal view; E, left antennular and antennal peduncles, ventral view; F, anterior cephalothorax with epistome, ventral view; G-I, major chela (right pereopod 1), lateral view; J, minor chela (left pereopod 1), lateral view; K, same, ventral view; L-O, right pereopods 2-5, lateral view; P, chela of right pereopod 5, lateral view; Q, tail fan, dorsal view; R, left uropodal exopod, ventral view; S, left uropodal endopod, dorsal view. Setae omitted, scale bars: A-O, Q-S = 10 mm; P = 1 mm.

truncated, followed by 7-10 teeth along distal margin; dorsolateral surface with few indistinct granules near lateral border.

Color.—Body generally ivory white overall (Fig. 7C, D).

Size.—Largest male about cl 50 mm and largest female cl 52 mm.

Distribution.—Indo-West Pacific. Known with certainty from the South China Sea, the Philippines, Solomon Islands, Papua New Guinea, New Caledonia and Madagascar; 713-1110 m.

IUCN Red List Conservation Assessment.—This species has been assessed as Least Concern owing to its wide distribution. There are no known major threats impacting this species. There is no commercial fishery for this species due to the depths at which it is found, and at present it is only collected by scientific cruises.

Remarks.—The large and rather intact specimen of *T. massonktenos* (median part of carapace broken, minor chela and distal part of major chela missing) from the Solomon Islands (MNHN IU-2008-10556), collected about a decade ago, is very similar to *T. japonicus*, but with the pleonal tergites considerably more granulate (Fig. 5C) and the distal segment of the uropodal exopod with a convex margin (Fig. 5Q, vs pleonal tergites generally smooth and distal segment of uropodal exopod with a distinctly concave margin in *T. japonicus*, Figs. 3A, J, 4D, J). Analysis of the barcoding gene COI revealed high sequence divergences (13.2-14.8%) between *T. massonktenos* and *T. japonicus* (Table 2, Fig. 1). Careful comparisons between *T. massonktenos* and *T. japonicus* reveal further morphological differences. There is a distinct subdistal ventromesial spine on the basal antennular segment and no distomesial spine on the ventral surface of the basicerite in *T. massonktenos* (Fig. 5E), but the reverse in *T. japonicus* (Figs. 3C, 4C). The dorsal margin of the carpus of pereopod 2 is smooth in *T. massonktenos* (Fig. 5L) but spinose in *T. japonicus* (Figs. 3G, 4G). Furthermore, the distolateral angle of the distal segment of the uropodal exopod distinctly falls short of that of the proximal uropodal exopodal segment in *T. massonktenos* (Fig. 5R), instead of extending to the latter as in *T. japonicus* (Figs. 3J, 4J).

The three specimens of *T. massonktenos* collected from Papua New Guinea have identical COI sequences to the Solomon Islands holotype (Tables 1, 2). Morphologically, the Papua New Guinean material shows that *T. massonktenos* has the minor chela with the palm more slender (about 3 times longer than wide) and the outer margin of the propodus nearly straight (Fig. 5J), and the pleonal tergites spinose even in very small individuals (Fig. 7C, D). In *T. japonicus*, the palm of the minor chela is 2.0-2.5 times longer than wide and the outer margin of the propodus is distinctly concave (Figs. 3F, 4F).

Thaumastocheles massonktenos can be readily separated from the other new species, *T. bipristis*, by the more granular pleon and convex rather than concave margin of the distal uropodal exopod segment (Fig. 5C, R vs. Fig. 2A, O). Moreover, in *T. bipristis*, the ventral surfaces of both the basal antennular segment and basicerite bear distomesial spines (Fig. 2C). In contrast to *T. bipristis*, *T. massonktenos*

lacks teeth along the outer margin of the dactylus of the major chela (Fig. 5 G-I), the palm of the minor chela is relatively slender (Fig. 5J vs. Fig. 2F), the telson has considerably fewer spines on the dorsal surface (Fig. 5Q), and the ventral margin of the pleonal pleuron 1 is convex instead of concave (Fig. 5C). Genetically, *T. massonktenos* and *T. bipristis* exhibit a COI sequence divergence of 11.9-12.8% (Table 2).

With the distinguishing morphological characteristics now more clearly understood for true *T. japonicus* and the two closely related new species, re-examination of the material reported as *T. japonicus* by Chan and de Saint Laurent (1999) revealed that most of their non-Japan/Taiwan material actually belongs to *T. massonktenos*. True *T. japonicus* ranges only from Japan to the Philippines. Analysis of COI and/or 16S sequences of specimens reported by Chan and de Saint Laurent's (1999) as *T. japonicus* confirms this conclusion. The five specimens (two represented only by a major chela or cheliped) from New Caledonia and Madagascar have only 2.9-3.5 and 0.2-0.7% sequence divergences from the Solomon Islands/Papua New Guinean material in COI and 16S rRNA genes, respectively (Tables 1, 2). Specimens from Japan and Taiwan represent *T. japonicus* sensu stricto with only 0.2-2.9 and 0.0-0.7% sequence divergence in COI and 16S, respectively (Table 2). The two specimens from the Philippines could only be successfully sequenced for 16S (Table 1). The major cheliped from the MUSORSTOM III expedition (MNHN IU-2012-772) has a 16S sequence identical to that of *T. massonktenos*, while the 16S sequence of the small ALBATROSS specimen (USNM 106926) is similar (97.9-98.1%) to that of true *T. japonicus*. Of the two specimens from Pratas, one (NTOU M01740) belongs to *T. massonktenos* (with identical 16S sequences, COI sequencing failed, Table 1). The other Pratas specimen (NTOU M01741) corresponds morphologically to true *T. japonicus* but unfortunately attempts to sequence both COI and 16S were unsuccessful. As mentioned under the account of *T. bipristis*, the Indonesian ALBATROSS specimen (USNM 107527) is not *T. japonicus* but *T. bipristis*. Thus, the present results show that *T. japonicus* actually has a more northern distribution in Japan, Taiwan, South China Sea and the Philippines. The two new species have more southern distributions, with *T. bipristis* ranging from the Philippines to Indonesia, and *T. massonktenos* ranging widely in the Indo-West Pacific, from the South China Sea to New Caledonia and Madagascar. At intermediate localities such as the Philippines and South China Sea, i.e., Pratas, more than one of these three species can occur together.

Although 11 specimens are now assigned to *T. massonktenos*, eight are represented by only a cephalothorax or major cheliped/chela. Of the three more intact specimens, two are very small (cl < 16 mm). Nevertheless, there are only 0.0-3.5 and 0.0-0.9% sequence divergences amongst them in COI and 16S, respectively (Table 1). On the other hand, surprisingly, the molecular data (Tables 1, 2) show rather low genetic divergences between *T. japonicus* and *T. dochmiodon* (COI and 16S genes divergences 0.0-3.1 and 0.0-0.7%, respectively) and with specimens from the same locality even having nearly identical sequences (COI and 16S divergence 0.0-0.9 and 0.0%, respectively), though mor-

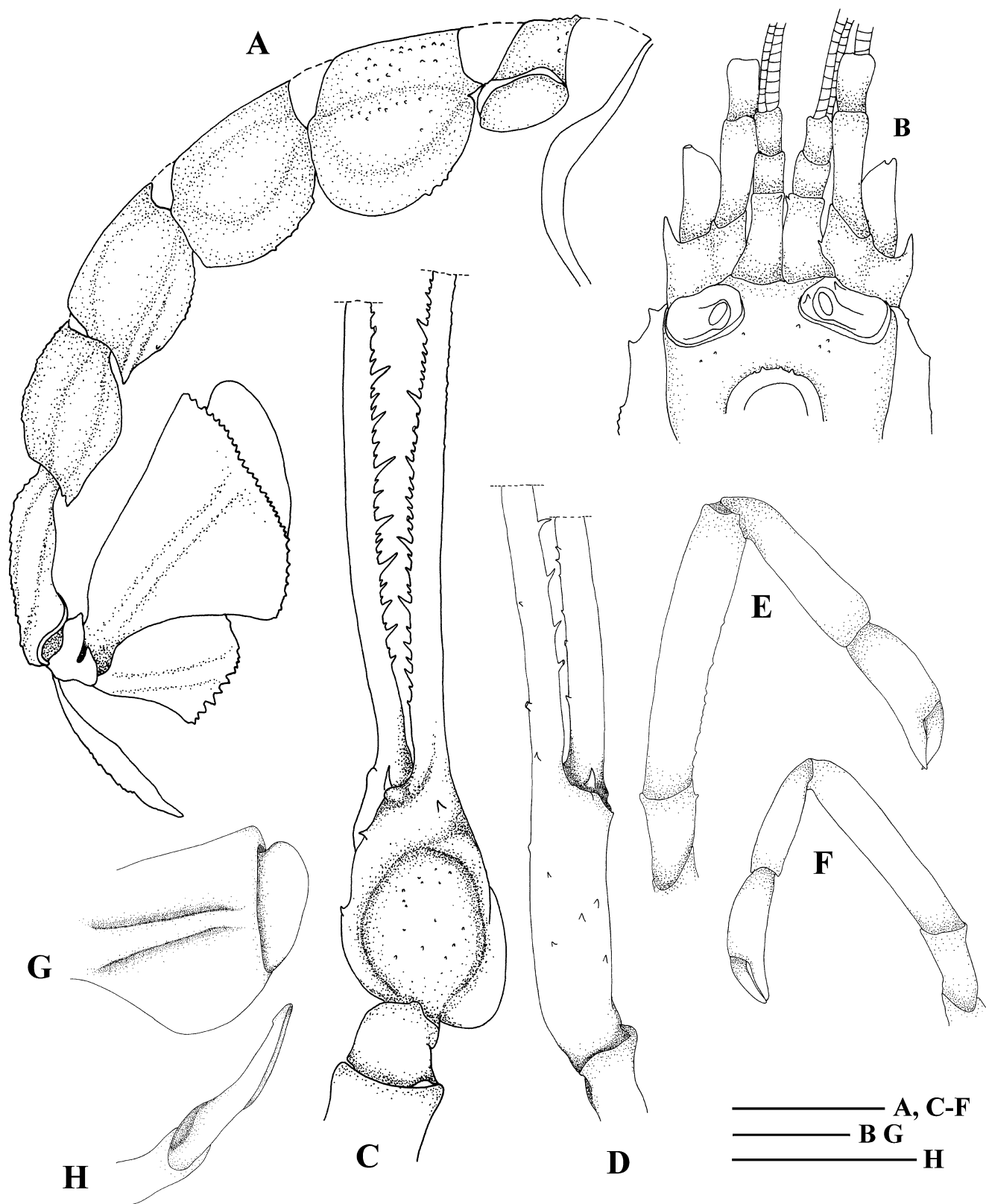


Fig. 6. ? *Thaumastocheles massonktenos* sp. nov., male cl 46.7 mm, Pratas, South China Sea (NTOU M01750, exTFRI). A, pleon, right lateral view; B, anterior carapace with epistome, ventral view; C, major chela (right pereopod 1), lateral view; D, minor chela (left pereopod 1), lateral view; E, right pereopod 2, lateral view; F, left pereopod 3, lateral view; G, left uropodal exopod, ventral view; H, right pleopod 1, ventral view. Setae omitted, scale bars: 10 mm.

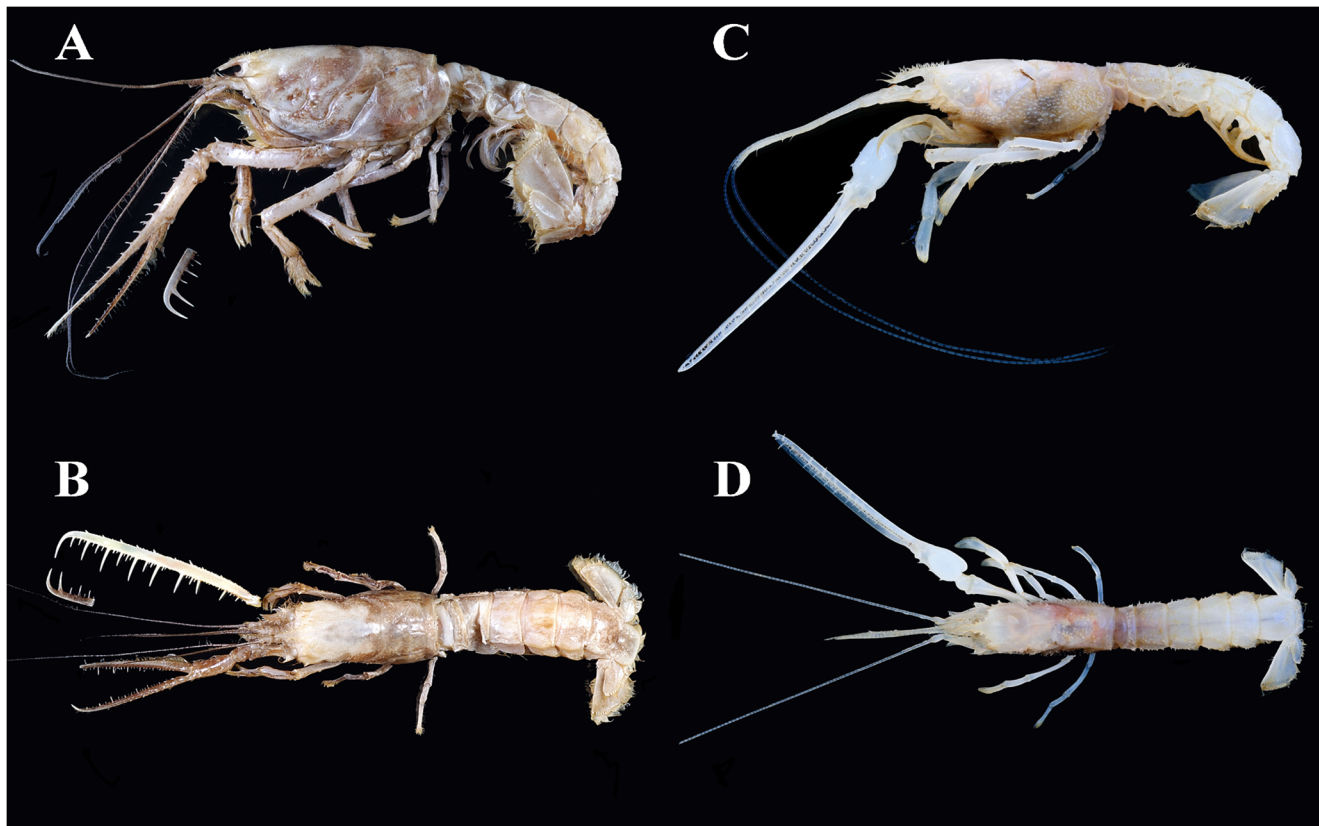


Fig. 7. A, B, *Thaumastocheles bipristis* sp. nov., holotype female cl 58.5 mm, the Philippines (NMCR); C, D, *T. massonktenos* sp. nov., paratype female cl 13.6 mm, Papua New Guinea (MNHN IU-2013-1041). A, C, lateral view (A with detached movable finger of major chela not included). B, D, dorsal view.

phologically these two nominal species have very different large chelipeds and lateral carinae of the pleon (see Chan and de Saint Laurent, 1999). *Thaumastocheles dochmiodon* is not particularly rare in Taiwan and more than 100 specimens have been collected since its description, but all are males. Moreover, all known specimens attributed to *T. dochmiodon* from Japan, Pratas, and Australia are also males (see Chan and de Saint Laurent, 1999). For *T. japonicus*, all reported specimens except one are females. The only male of *T. japonicus* known is the ZSM A20120314 specimen first reported by Doflein (1906). Because of this male *T. japonicus*, the possibility that *T. japonicus* and *T. dochmiodon* merely represented different sexes of the same species was excluded by Chan and de Saint Laurent (1999). However, our molecular evidence indicates that *T. dochmiodon* and *T. japonicus* may actually represent different sexes of the same species. Although Doflein's (1906) *T. japonicus* male failed in all genetic sequencing attempts, the present material of *T. massonktenos* includes two males. These two males, both from New Caledonia, were reported as "*T. japonicus*" by Chan and de Saint Laurent (1999). One is a very small juvenile (cl 14.9 mm, MNHN IU-2017-780) with the pleopod I still thread-like, but careful examination shows that its gonopores are located on pereopods 5. The other specimen (MNHN IU-2012-771) is a damaged cephalothorax (cl about 50 mm but with both the major and minor chelipeds present); both pereopods 5 are entirely missing, but there is no trace of gonopores on pereopods 3. Both of these males are geneti-

cally very similar to the holotype female of *T. massonktenos* (COI and 16S sequence similarities 96.5-96.7 and 99.8%, respectively, Table 2) and are thus considered conspecific. Thus, if *T. dochmiodon* and *T. japonicus* are conspecific, the differences between these two forms might represent not only sexual dimorphism but also polymorphism in males as exhibited in the mud shrimp *Austinochebia edulis* (Ngoc-Ho and Chan, 1992).

Thaumastocheles dochmiodon has been reported from Japan, Taiwan, Pratas and Australia (Chan and de Saint Laurent, 1999). As mentioned above, the Japanese and Taiwanese *T. dochmiodon* could belong to *T. japonicus*. The Pratas specimen of *T. dochmiodon* (R/V "Fisheries Researcher I," 822 m, 23 April 1995, 1 male cl 46.7 mm, NTOU M01750, exTFRI) has a 16S sequence identical to that of *T. massonktenos* (COI sequencing failed, Table 1). Re-examination of this Pratas male (Fig. 6) showed that its characteristics fit well *T. massonktenos* except for the direction of teeth along the occlusal margins of the large chelae and the lateral pleonal carinae being lobular rather than ridged (i.e. the characters used in distinguishing *T. massonktenos* and *T. japonicus* can also be applied to the various male forms). Thus, it appears that male polymorphism may also be exhibited in *T. massonktenos*. Two of the four Australian *T. dochmiodon* specimens reported by Chan and de Saint Laurent (1999) were located (F/V "Surefire," stn SB1, 14°08'S, 121°40'E, 530 m, 26 June, 1990, 1 male cl 43.2 mm, NTM CR007532 (not NTM Cr007332 as stated in

Chan and de Saint Laurent, 1999), 1 male cl 43.5 mm, NTM Cr007353). An additional Australian specimen (F/V "Territory Pearl," stn S12, 14°01'S, 122°08'E, 443 m, 26 January 1988, 1 male cl 41.4 mm, NTM Cr 006896) was also examined. These Australian specimens have identical 16S sequences to each other (COI sequencing failed, Table 1), but with sequence divergences of 4.1-4.5%, 4.1-5.0%, 3.6%, 6.9-7.2% from the Taiwan/Japan *T. dochmiodon*, *T. japonicus*, *T. bipristis* and *T. massonktenos*, respectively. As 16S sequence divergences are always less than 2.0% within the latter four forms, the genetic data imply that the Australian form may represent a further undescribed species. Morphologically, the Australian form is closest to *T. dochmiodon* from Taiwan and Japan but with a somewhat wider but less spiny body. Nevertheless, the exact identity of the Australian form may only be able to made explicit after the status of *T. dochmiodon* and possible sexual dimorphism in thaumastocheliforms are clarified, and these studies are now underway. In any case, even if sexual dimorphism and male polymorphism do occur in species of *Thaumastocheles*, the specific status of the present two new species will not be affected as their respective holotypes are females and there are very large genetic differences separating them from congeners (COI sequence divergences 10.8-15.0%, Fig. 1, Table 2).

Etymology.—The Greek "masson" (longer) and "ktenos" (comb) refers to the generally longer pectinate chelipeds 1 of this species.

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REFERENCES

- Ahyong, S. T., K. H. Chu, and T. Y. Chan. 2007. Description of a new species of *Thaumastochelopsis* from the Coral Sea (Crustacea: Decapoda: Nephropidae). *Bulletin of Marine Science* 80: 201-208.
- , T. Y. Chan, and P. Bouchet. 2010. Mighty claws: a new genus and species of lobster from the Philippine deep sea (Crustacea, Decapoda, Nephropidae). *Zoosystema* 32: 525-535.
- Bosquet, J. 1854. Les crustacés fossiles du terrain Crétacé du Duche Limbourg. *Verhandelingen van der Commission van der Geologische Beschrijving en Kaart van Nederland, Deel II*: 10-371.
- Bracken-Grissom, H. D., D. L. Felder, N. L. Vollmer, J. W. Martin, and K. A. Crandall. 2012. Phylogenetics links monster larva to deep-sea shrimp. *Ecology and Evolution* 2: 2367-2373.
- Bruce, A. J. 1988. *Thaumastochelopsis wardi*, gen. et sp. nov., a new blind deep sea lobster from the Coral Sea (Crustacea: Decapoda: Nephropidae). *Invertebrate Taxonomy* 2: 902-914.
- Cabezas, P., E. Macpherson, and A. Machordom. 2009. Morphological and molecular description of new species of squat lobster (Crustacea: Decapoda: Galatheidae) from the Solomon and Fiji Islands (South-West Pacific). *Zoological Journal of the Linnean Society* 156: 465-493.
- Calman, W. T. 1913. A new species of the Crustacean genus *Thaumastocheles*. *Annals and Magazine of Natural History* (8) 12(68): 229-233.
- Chan, T. Y. 2010. Annotated checklist of the world's marine lobsters (Crustacea: Decapoda: Astacidea, Glypheidea, Achelata, Polychelida). *Raffles Bulletin of Zoology* 23: 153-181.
- , and M. de Saint Laurent. 1999. The rare lobster genus *Thaumastocheles* (Decapoda: Thaumastochelidae) from the Indo-West Pacific, with description of a new species. *Journal of Crustacean Biology* 19: 891-901.
- Costa, F. O., J. R. de Waard, J. Boutillier, S. Ratnasingham, R. T. Dooh, M. Hajibabaei, and P. D. Hebert. 2007. Biological identifications through DNA barcodes: the case of the Crustacea. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 272-295.
- De Grave, S., K. H. Chu, and T. Y. Chan. 2010. On the systematic position of *Galatheacaris abyssalis* (Decapoda: Galatheacaridoidea). *Journal of Crustacean Biology* 30: 521-527.
- Doflein, F. 1906. Mitteilungen über japanische Crustaceen. I. Das Männchen von *Thaumastocheles zaleucus* (Will.-Suhm). *Zoologischer Anzeiger* 30: 521-525.
- 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.
- Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium* 41: 95-98.
- Holthuis, L. B. 1974. The lobsters of the superfamily Nephropoidea of the Atlantic Ocean (Crustacea: Decapoda). *Bulletin of Marine Science* 24: 723-884.
- . 1991. Marine lobsters of the world. An annotated and illustrated catalogue of species of interest to fisheries known to date. *FAO Fisheries Synopsis* 125(13): 1-292.
- Huelsenbeck, J. P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754-755.
- Jones, W. J., and E. Macpherson. 2007. Molecular phylogeny of the east Pacific squat lobsters of the genus *Munidopsis* (Decapoda: Galatheidae) with the descriptions of seven new species. *Journal of Crustacean Biology* 27: 477-501.
- Konishi, K., N. Suzuki, and S. Chow. 2006. A late-stage phyllosoma larva of the spiny lobster *Panulirussechinatus* Smith, 1869 (Crustacea: Palinuridae) identified by DNA analysis. *Journal of Plankton Research* 28: 841-845.
- Lin, C. W., T. Y. Chan, and K. H. Chou. 2004. A new squat lobster of the genus *Raymunida* (Decapoda: Galatheidae) from Taiwan. *Journal of Crustacean Biology* 24: 149-156.
- Monod, T. 1973. Sur quelques crustacés Néo-Calédoniens de profondeur. *Cahiers O.R.S.T.O.M. (Océanographie)* 11: 117-131.
- Ngoc-Ho, N., and T. Y. Chan. 1992. *Upogebia edulis*, new species, a mud-shrimp (Crustacea: Thalassinidea: Upogebiidae) from Taiwan and Vietnam, with a note on polymorphism in the male first pereopod. *Raffles Bulletin of Zoology* 40: 33-43.
- Nylander, J. A. A. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Center, Uppsala University, Uppsala.
- Palero, F., G. Guerao, P. Clark, and P. Abelló. 2011. *Scyllarus arctus* (Crustacea: Decapoda: Scyllaridae) final stage phyllosoma identified by DNA analysis, with morphological description. *Journal of the Marine Biological Association of the United Kingdom* 91: 485-492.

- Richer de Forges, B., and P. Laboute. 1995. Langoustes, langoustines etcigales de mer de Nouvelle-Calédonie. In, B. Richer de Forges (ed.), Les fonds meubles des lagons de Nouvelle-Calédonie (Sédimentologie, benthos). Etudes and Thèses 2: 45-82. O.R.S.T.O.M., Paris.
- Ronquist, F., J. Huelsenbeck, and M. Teslenko. 2011. Draft MrBayes version 3.2 manual: tutorials and model summaries.
- Shank, T. M., R. A. Lutz, and R. C. Vrijenhoek. 1998. Molecular systematics of shrimp (Decapoda: Bresiliidae) from deep-sea hydrothermal vents, I: enigmatic "small orange" shrimp from the Mid-Atlantic Ridge are juvenile *Rimicaris exoculata*. Molecular Marine Biology and Biotechnology 7: 88-96.
- Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, and S. Kumar. 2011. MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Molecular Biology and Evolution 28: 2731-2739.
- Thomson, C. W. 1873. Note from the "Challenger". Nature 8: 246-249.
- Tshudy, D. 2003. Clawed lobster (Nephropidae) diversity through time. Journal of Crustacean Biology 23: 178-186.
- , R. Robles, T. Y. Chan, K. C. Ho, K. H. Chu, S. T. Ahyong, and D. L. Felder. 2009. Phylogeny of marine clawed lobster families Nephropidae Dana, 1852, and Thaumastochelidae Bate, 1888, based on mitochondrial genespp, pp. 357-368. In, J. W. Martin, D. L. Felder, and K. A. Crandall (eds.), Decapod Crustacean Phylogenetics. Crustacean Issues 18. CRC Press, Boca Raton, FL.
- , and J. Seward. 2012. *Dinorchelus steeplensis*, a new species of clawed lobster (Nephropidae) from the London Clay (Eocene) of England. Journal of Crustacean Biology 32: 67-79.
- Tsoi, K. W., T. Y. Chan, and K. H. Chou. 2011. Phylogenetic and biogeographic analysis of the spear lobsters *Linuparus* (Decapoda: Palinuridae), with the description of a new species. Zoologischer Anzeiger 250: 302-315.
- Xu, J., T. Y. Chan, L. M. Tsang, and K. H. Chu. 2009. Phylogeography of the mitten crab *Eriocheir sensu stricto* in East Asia: Pleistocene isolation, population expansion and secondary contact. Molecular Phylogenetics and Evolution 52: 45-56.
- Yang, C. H., H. Bracken-Grissom, D. Kim, K. A. Crandall, and T. Y. Chan. 2012. Phylogenetic relationships, character evolution, and taxonomic implications within the slipper lobsters (Crustacea: Decapoda: Scyllaridae). Molecular Phylogenetics and Evolution 62: 237-250.

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