First Occurrence of the Genus *Australatya* (Crustacea: Decapoda: Atyidae) in Melanesia and Polynesia with Description of a New Species[1]

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Abstract: During specific inventories led by the Muséum national d'Histoire naturelle (MNHN, Paris), numerous specimens of Atyidae, particulary of *Atya*-like shrimps were collected in Melanesia (Vanuatu, Solomon Islands) and in Polynesia (Futuna, Samoa). These specimens were morphologically and genetically examined. Our study revealed that some specimens belonged to a new species in the genus *Australatya* Chace, 1983. The aim of this paper is to describe this new species, *Australatya keithi* sp. nov., and discuss the distribution of its genus in the studied area.

Keywords: freshwater shrimp, taxonomy, amphidromy, morphology, DNA, 16S

Until recently, the taxonomy of Atyidae was mainly based on morphological characters. But in the *Caridina* genus, some characters have been proven highly variable within a species (e.g., rostrum shape and indentation or coloration) and therefore taxonomically uninformative, making it difficult to establish boundaries between them (von Rintelen and Cai 2009, de Mazancourt et al. 2017). Thus, there is a need for an integrative and standardized approach to improve the group's systematics, focusing on informative morphological features and using molecular characters (Page et al. 2005, Page and Hughes 2011). To illustrate this problem, we focus here on the genus *Australatya* Chace, 1983. It has a wide but disjoint distribution in the Indo-Pacific region and includes until now only three species: *Australatya striolata* (McCulloch and McNeill 1923) and *Australatya hawkei* Choy, Page, and Mos, 2019 from Australia and *Australatya obscura* Han and Klotz 2015 from the Philippines, Taiwan (Han and Klotz 2015), and Ryukyu islands (Inui et al. 2019). This genus occurs in the higher course of tropical rivers like other *Atya*-like shrimps (*Atyoida pilipes* (Newport, 1847) or *Atyopsis spinipes* (Newport, 1847)). Only a few studies provided DNA data for species of *Australatya* (see Cook et al. 2012, Han and Klotz 2015, Choy et al. 2019).

One of the aims of the Muséum national d'Histoire naturelle (MNHN, Paris) is to carry out faunistic inventories of rivers in tropical islands in order to establish better protection of these fragile ecosystems and, in this context, to clarify the taxonomy of poorly known organisms. For our study, several Pacific islands were surveyed: Futuna (Territory of Wallis and Futuna) in October 2004 (Mary et al. 2006), Upolu (Samoa) in July 2008 (Keith et al. 2013), and again in August 2014. Kolombangara and Vella Lavella islands (Solomon Islands), respectively, in November 2015 and October 2016, and Santo and Aneityum (Vanuatu), respectively, in July 2005 and June 2015. As we collected specimens from these different islands from the

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Pacific Science (2020), vol. 74, no. 3:297–308
doi:10.2984/74.3.7

Pacific Ocean, we started to question the identity of some specimens previously identified as *Atyoida pilipes* or *Atyopsis spinipes* collected from these islands. The aim of this study is thus to combine morphological data with a 16S rDNA analysis to investigate the "*Atya*-like" shrimps present in the sampled area.

MATERIAL AND METHODS

Collection of Specimens

Specimens from Pacific islands were collected by electrofishing (portable Dekka 3,000 electric device, or SAMUS 1,000: http://www.electrofisher.net/). All material was preserved in 75%–95% alcohol and has been deposited in the collections of the MNHN in Paris.

Morphological Comparison

The rostrum, the general cephalon, the pereopods 1, 2, 3, and 5 and the abdomen were observed using a stereoscopic microscope. The proportions of the various joints of the appendages were measured using microphotographs and AnalySIS Works software (Olympus). Drawings were made using the "Digital Inking" method (Coleman 2003, 2006) by tracing vectorial paths on stacks of high-resolution photographs using Adobe Illustrator (CS6).

Abbreviations for Morphological Analyses

The following abbreviations are used in the present text: cl, carapace length (mm): measured from the post-orbital margin to the posterior margin of the carapace. P1: first pereopod. P2: second pereopod. P3: third pereopod. P5: fifth pereopod. Pl1: first male pleopod. Pl2: second male pleopod.

DNA Extraction, Amplification, and Sequencing

Molecular analyses were conducted on mitochondrial DNA, on the 16S ribosomal RNA fragment, in order to differentiate each specimen by species and location. A total of 10 specimens of *Australatya* were genetically studied.

Total DNA was extracted from abdominal muscle samples using the NucleoSpin 96 Tissue Core (Macherey-Nagel) protocol. For each sample, PCR reactions contained: 15.44 µl of H_2O, 2 µl of Taq buffer (15 mM + $MgCl_2$), 1 µl of DMSO (1 ng/ml), 1 µl of BSA, 0.8 µl of dNTP (6.6 mM), 0.32 µl of Forward primer (16Sar-Lmod: TACTTCTGCCTGTTTATCAAAAA), and 0.32 µl of Reverse primer (16Sbmod: GGTCTGAACTCAAATCATGTAAA), both at 10 pM, 0.12 µl of Taq polymerase (Qiagen), and 3 µl of purified DNA from extraction. PCR program was: 4 min at 94 °C, then 35 cycles in three steps with 30 s at 94 °C, 40 s at 42 °C, and 1 min at 72 °C. The program finished with 7 min at 72 °C. PCR products were sequenced using Sanger method in both directions to minimize mistakes.

Molecular Analysis

Analyses were performed using Geneious 7.1.8. A multiple alignment was realized between all sequences with the MUSCLE algorithm (Edgar 2004). Using Bayesian information criterion in jModelTest (Guindon and Gascuel 2003, Darriba et al. 2012) we retained the GTR + G + I model. From this alignment, a phylogenetic tree was produced by MrBayes 3.2.6, available on CIPRES Science Gateway V3.3 server (Miller et al. 2010, https://www.phylo.org), running for 10,000,000 generations, a sampling frequency of 1,000 and a burn in of 10%. Support for nodes was determined using posterior probabilities calculated by MrBayes. With MEGA X (Kumar et al. 2018), another phylogenetic tree was made by maximum likelihood using the same substitution model. Robustness of the nodes was assessed using non-parametric bootstrapping (Felsenstein 1985) with 1,000 bootstrap replicates.

Species delimitation analyses were realized with the ABGD v. 07/12/18 method (Puillandre et al. 2011) to estimate intra and interspecific divergence in our data using JC69 distances. Priors were left as default (Pmin: 0.001; Pmax 0.1; 10 steps; relative gap width: 1.5; 20 bins).

RESULTS AND DISCUSSION

Morphological Analyses

Measures and observations made on the specimens caught allowed us to separate them into three genera, that is, *Atyoida*, *Atyopsis*, and *Australatya*. The general criteria to identify species of the genus *Atyoida* are P1 and P2 with chelae heteromorphic (with or without palm), P3 without meral spur in large males, 3rd maxilliped with uncinate terminal spine, Pl1 of male with endopod tapering sinuously but rather regularly to slender apex, for genus *Atyopsis* are P1 and P2 with chelae monomorphic (without palm), P3 with prominent spur on merus in large males, 3rd maxilliped not terminating in single apical spine, Pl1 of male with endopod rigid, rhomboidally oval, submarginally spinose, for *Australatya* are P1 and P2 with chelae monomorphic (without palm), P3 without meral spur in large males, interno-inferior margin of merus forming a carina with 4–9 strong teeth-like spiniform setae, third maxilliped dimorphic between sexes, with uncinate terminal spiniform seta (nail) partially concealed by dense serrate setae in males, tip rounded, without a nail in females, Pl1 of male with endopod tapering to slender apex. The species found in this last genus is new. The description of this species follows thereafter. 11 specimens of *Australatya* have been identified in our samples: 3 from the Solomon Islands, 2 from Futuna, 4 from Samoa, and 2 from Vanuatu.

Phylogenetic Analysis

A total of 34 sequences of 16S were used in the analysis, including 10 sequences of *Australatya* newly produced and 3 retrieved from GenBank. As outgroups, 8 sequences of *Atyopsis*, 12 of *Atyoida* and one of *Atya gabonensis* were retrieved from GenBank (Table 1).

As the two phylogenetic trees obtained by Maximum Likelihood (ML) and Bayesian Inference (BI) were congruent, only the Bayesian tree is shown here. Support values above branches are BI posterior probabilities and below branches are ML bootstrap numbers (Figure 1). These trees confirm the presence of the *Australatya* genus in our samples. Most of the nodes are highly supported (PP > 0.98 and B > 95) in both ML and BI methods. The ABGD method found 8 species in our sampling: *Atya gabonensis*, *Atyoida bisulcata*, *Atyoida pilipes*, *Atyopsis spinipes*, *Atyopsis moluccensis*, *Australatya obscura*, *Australatya striolata*, and the new species we caught, *Australatya keithi* sp. nov. This indicates that the latter is genetically distinct from the other species. The names of the taxa in the tree (Figure 1) appear in accordance with the ABGD results, except for *Australatya striolata* and *Australatya hawkei* which are clustered together in a single species in the analysis. All the specimens identified as the new species described in the present study cluster in a same highly supported clade (PP = 1; B = 100). There seems to be some population structure within that species, with two clusters being distinctly separated from the specimens from Futuna and Samoa, one with specimens collected from Vanuatu and the other with specimens from the Solomon Islands.

Taxonomy

Family Atyidae De Haan, 1849
Genus *Australatya* Chace, 1983
Australatya keithi sp. nov.
(Figure 2)

Material examined — *Holotype*. Vanuatu (Aneityum): Inwe Lengei River, 1♂, cl 5.5 mm (MNHN-IU-2018-3302; DNA: CA1957), 20° 12.409′ S, 169° 48.131′ E, June 24, 2015, 200 m a.s.l., coll. D. Kalfatak, C. Lord, G. Segura. *Paratypes*. Vanuatu (Aneityum): 1♀ ovig., cl 6.8 mm (MNHN-IU-2018-3303; DNA: CA1958), same data as holotype; Vage River, Solomon Islands (Kolombangara): 1♀ ovig., cl 4.0 mm (MNHN-IU-2018-3300; DNA: CA1934), 08° 05.112′ S, 156° 59.867′ E, November 10, 2015, coll. P. Keith, G. Marquet, C. Lord; Maravari River, Vella Lavella: 1♀ ovig., cl 4.0 mm (MNHN-IU-2018-3301; DNA: CA2359), 1 specimen (MNHN-IU-2018-3308; DNA: CA1944), 07° 51.703′ S,

TABLE 1

Sequences Data

Species	Collection Number	Status	DNA Number	GenBank Number	Locality	Reference
Australatya keithi sp. nov.	MNHN-IU-2018-3304	Paratype	CA1947	MT790339	Samoa (Upolu)	This study
	MNHN-IU-2018-3305	Paratype	CA1948	MT790340	Samoa (Upolu)	This study
	MNHN-IU-2018-3306	Paratype	CA2422	MT790343	Samoa (Upolu)	This study
	MNHN-IU-Na-15761	Paratype	CA2133	MT790341	Wallis & Futuna (Futuna)	This study
	MNHN-IU-Na-15761	Paratype	CA2433	MT790344	Wallis & Futuna (Futuna)	This study
	MNHN-IU-2018-3302	Holotype	CA1957	MT790337	Vanuatu (Aneityum)	This study
	MNHN-IU-2018-3303	Paratype	CA1958	MT790338	Vanuatu (Aneityum)	This study
	MNHN-IU-2018-3300	Paratype	CA1934	MT790335	Solomon Islands (Kolombangara)	This study
	MNHN-IU-2018-3308	Paratype	CA1944	MT790336	Solomon Islands (Vella Lavella)	This study
	MNHN-IU-2018-3301	Paratype	CA2359	MT790342	Solomon Islands (Vella Lavella)	This study
Australatya striolata			GU 9998	AY795035	Australia	Page et al. 2005
Australatya hawkei			N2	MN244315	Australia	Choy et al. 2019
Australatya obscura			TVR-2015	KP168717	Taiwan	Klotz and von Rintelen 2014
Atyoida pilipes	MNHN-IU-2013-11820			KP725498	Fiji	Aznar-Cormano et al. 2015
	MNHN-IU-2013-11819			KP725499	Fiji	Aznar-Cormano et al. 2015
	MNHN-IU-2019-242		CA1949	MT117771	Samoa	Lorang et al. 2020
Atyoida tahitensis	MNHN-IU-2012-1051			KP725497	French Polynesia (Tahiti)	Aznar-Cormano et al. 2015
			GU991	DQ681279	French Polynesia (Moorea)	Page et al. 2007
	MNHN-IU-2018-3290	Neotype	CA2376	MT117805	French Polynesia (Tahiti)	Lorang et al. 2020
	MNHN-IU-2018-3299		CA1977	MT117779	Cook Islands (Rarotonga)	Lorang et al. 2020
Atyoida cf. *pilipes*			GUAP1	DQ681276	Micronesia (Kosrae)	Page et al. 2007
			GU786	DQ681277	Vanuatu (Efate)	Page et al. 2007
Atyoida bisulcata			KC2138	DQ079704	Hawaii	Porter et al. 2005
			GUKZ287	EF489995	Hawaii	Page et al. 2008
			GU755	DQ681278	Hawaii	Page et al. 2007
Atyopsis moluccensis			GU899	DQ681280	Pet shop in USA	Page et al. 2008
			KZ222	DQ681281	Pet shop in Germany	Page et al. 2007
	ULLZ 9174			EU868634	Aquarium trade	Bracken et al. 2009
	NTOU M00728			KF023110	Hong Kong	De Grave et al. 2014
Atyopsis spinipes			GU877	DQ681282	Solomon Islands (Guadalcanal)	Page et al. 2007
			GU1132	EF489996	East Timor	Page et al. 2008
	MNHN-IU-2012-1067			KP725500	Samoa	Aznar-Cormano et al. 2015
	MNHN-IU-2012-1066			KP725501	Samoa	Aznar-Cormano et al. 2015
Atya gabonensis			GUKZ437	EF489989	Pet shop in Germany	Page et al. 2007

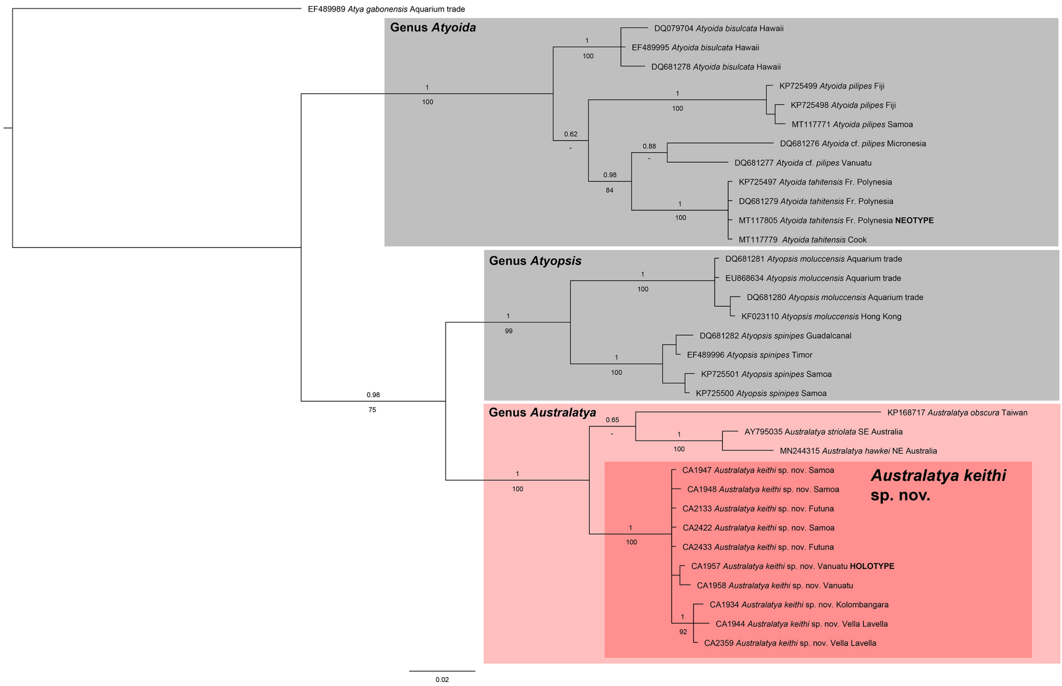

FIGURE 1. Phylogenetic tree of *Australatya keithi* sp. nov. and other Indo-Pacific *Atya*-like species built using Bayesian Inference. Values above branches indicate posterior probabilities, those below are bootstrap values. Scale represents genetic distance.

156° 41.748′ E, October 10, 2016, coll. P. Keith and C. Lord; Ma'epu stream, Savai (Samoa): 1♂ juvenile, cl 3.2 mm (MNHN-IU-2018-3307), 13° 51.919′ S, 171° 41.174′ W, July 07, 2014, 20–50 m a.s.l., coll. P. Gerbeaux; Tuafaleloa River (Upolu): 1♀ ovig., cl 5.3 mm (MNHN-IU-2018-3304; DNA: CA1947) and 1♀ ovig., cl 5.7 mm (MNHN-IU-2018-3305; DNA: CA1948), 13° 53.644′ S, 171° 30.922′ W, July 08, 2014, 100 m a.s.l., coll. P. Gerbeaux; Faleata River, 1♀ ovig., cl 5.0 mm (MNHN-IU-2018-3306; DNA: CA2422), 13° 43.741′ S, 172° 18.832′ W, July 12, 2014, 195 m a.s.l., coll. P. Gerbeaux; Vainifao River, Futuna (Wallis and Futuna): 1♀, cl 6.1 mm (MNHN-Na-15761; DNA: CA2133) and 1♂ (MNHN-Na-15761; DNA: CA2433), 14° 17.802′ S, 178° 8.423′ W, October 12, 2004, 151 m a.s.l., coll. P. Keith, G. Marquet, N. Mary.

Comparative material — *Australatya hawkei* Choy, Page & Mos, 2019

Australia. MNHN-Na-14383. Freshwater creek in Big Table Land, 1♀ ovig., cl 10.0 mm, North-East Queensland, November 18, 1993, coll. K. McDonald.

Description — *Cephalothorax* (Figure 2*M*): Carapace length 4.0–6.1 mm ($N = 7$). Carapace smooth, inferior orbital angle fused with a distinct antennal tooth; pterygostomian margin rectangular rounded. Rostrum short, 0.2–0.3 of cl, reaching near to end of basal segment of antennular peduncle, with feebly marked lateral carina, dorsal ridge unarmed. The number of ventral teeth on the rostrum varies from 0 to 4. Rostrum formula 0/0–4. Eyes well developed. Antennular peduncle stout, 0.56 (♀)–0.46 (♂) times as long as carapace; basal segment shorter than half length of antennular peduncle, second segment longer than third segment. Stylocerite reaching 0.86 length of the basal segment of antennular peduncle.

Pereiopods: P1 and P2 similar in size and shape. P1 chela (Figure 2*A*) atyoid in shape, without palm, 4.5–5.3 times as long as wide,

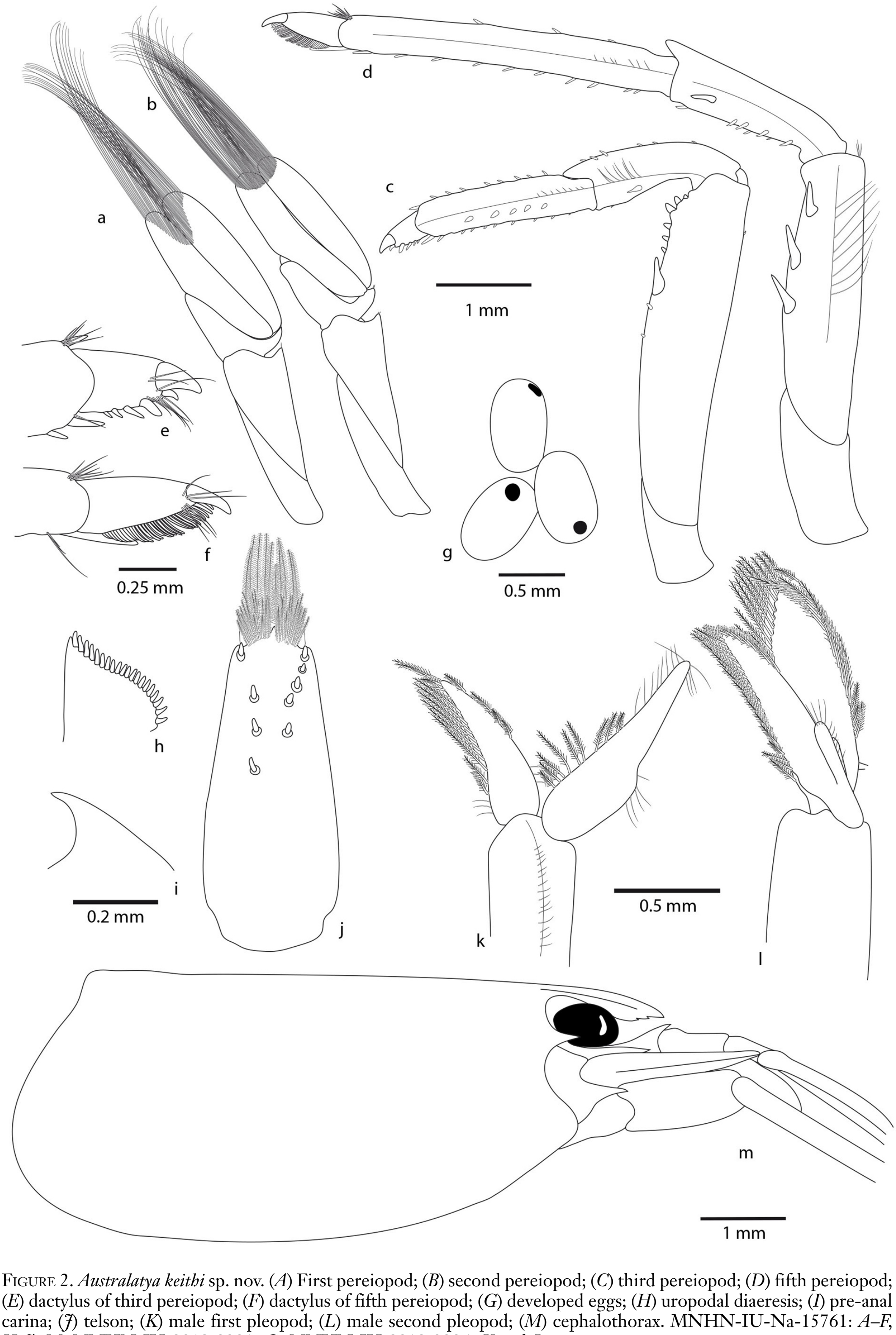

FIGURE 2. *Australatya keithi* sp. nov. (*A*) First pereiopod; (*B*) second pereiopod; (*C*) third pereiopod; (*D*) fifth pereiopod; (*E*) dactylus of third pereiopod; (*F*) dactylus of fifth pereiopod; (*G*) developed eggs; (*H*) uropodal diaeresis; (*I*) pre-anal carina; (*J*) telson; (*K*) male first pleopod; (*L*) male second pleopod; (*M*) cephalothorax. MNHN-IU-Na-15761: *A–F*, *H–J*, *M*; MNHN-IU-2018-3301: *G*; MNHN-IU-2018-3306: *K* and *L*.

without hooks; dactylus 4.9–5.8 times as long as wide, with tufts of long setae distally; carpus short, cup-like 1.3–1.8 times as long as wide. P2 chela (Figure 2*B*) atyoid in shape without palm, 4.4–5.3 times as long as wide, tips of fingers rounded, without hooks, dactylus 5.1–6.0 times as long as wide, with tufts of long setae distally; carpus short, cup-like 1.2–1.7 times as long as wide. P3 (Figure 2*C*) moderately strong, with a row of small plumose setae on lateral margin from ischium to propodus; dactylus (Figure 2*E*) 1.4–2.71 times as long as wide (terminal spiniform seta included), terminating in one large claw with 5–6 accessory spiniform setae on flexor margin, first spiniform setae distinctly smaller than second; propodus with numerous small spiniform setae on ventral margin, distal pair of spiniform setae not much prolonged, propodus 3.3–4.4 times as long as wide, 2.4–6.1 times as long as dactylus; merus with an interno-inferior margin forming a very distinctive carina with 5–7 strong, teeth-like spiniform setae. P5 (Figure 2*D*) slender, dactylus (Figure 2*F*), 1.6–3.5 times as long as wide (terminal spiniform seta included), terminating in one large claw, with 23–32 spiniform setae on flexor margin extending lateral to distal claw; propodus 6.3–8.6 times as long as wide, 3.6–6.8 times as long as dactylus.

Abdomen: Sixth abdominal somite 0.43 length of carapace, 1.25 times as long as fifth somite, 0.87 times as long as telson.

Telson (Figure 2*J*): slightly tapering distally, 2.4–3.5 times as long as proximally wide, distal margin broadly rounded with a median projection, lateral angles not overreaching distal margin, dorsal with 4–5 pairs of short spiniform setae and one pair of short spiniform setae dorsolateral; distal margin with 2 strong spiniform setae lateral, in between 6–10 long, plumose setae overreaching lateral spiniform setae.

Pl1 (Figure 2*K*): Endopod of male subtriangular, 2.3 times as long as wide, reaching 0.29–0.41 times of exopod, with an appendix on the subdistal outer margin which reaches beyond distal end of endopod with most of its length.

Pl2 (Figure 2*L*): Appendix masculina on second pleopod reaching 0.54–0.56 times length of endopod; appendix interna reaching 0.77 of appendix masculina.

Triangular preanal carina (Figure 2*I*) with a spine.

Uropodal diaeresis (Figure 2*H*) with 15–21 spinules.

Eggs (Figure 2*G*): developed (visible eyes) 0.32–0.45 × 0.52–0.71 mm, undeveloped 0.33–0.34 × 0.51–0.57 mm.

Etymology — This new species is named *keithi* in honor of Philippe Keith, professor at the MNHN, who made extensive collections of both freshwater fish and crustaceans for more than 20 years in the Pacific islands in particular in Kolombangara, Vella Lavella (Solomon Islands), in Santo (Vanuatu archipelago), and Futuna island, where he collected, with one of us, the new species here described, and photographed it (Figure 3); we appreciate his flawless friendship, his constant enthusiasm in the field and his dedication to his team.

Habitat — This species, largely rheophile, was collected in the uppermost sections of streams (Figure 3*B*). It shared this habitat with other "*Atya*-like" shrimp (*Atyoida pilipes*, *Atyopsis spinipes*) and with medium sized palaemonids like *Macrobrachium latimanus* (von Martens, 1868).

Color pattern — Body overall dark with white dorsal stripes on the abdomen (Figure 3*A*).

Distribution — This species occurs in Melanesia (Solomon Islands, Vanuatu) and in West Polynesia (Futuna and Samoa) (Figure 4).

Comparison

Genus *Australatya* Chace, 1983 now includes four species: *Australatya keithi* sp. nov., *A. striolata* (MacCulloch and McNeill, 1923), and *A. hawkei* Choy, Page and Mos, 2019, both from Australia, and *A. obscura* Han and Klotz 2015 from Taiwan, the Philippines, and Ryukyu islands. Morphologically, specimens of the new species differ from *A. striolata* by their rostrum armed with fewer ventral teeth 0–4 (vs 4–8 in *A. striolata*) and their shorter P3 propodus, 3.3–4.4

FIGURE 3. (*A*) Live coloration of an ovigerous female of *Australatya keithi* sp. nov. caught on Santo Island (Vanuatu) (Credit: P. Keith). (*B*) Vainifao River on Futuna Island (Wallis and Futuna Territory, France), habitat of *Australatya keithi* sp. nov. (Credit: A. Dutartre).

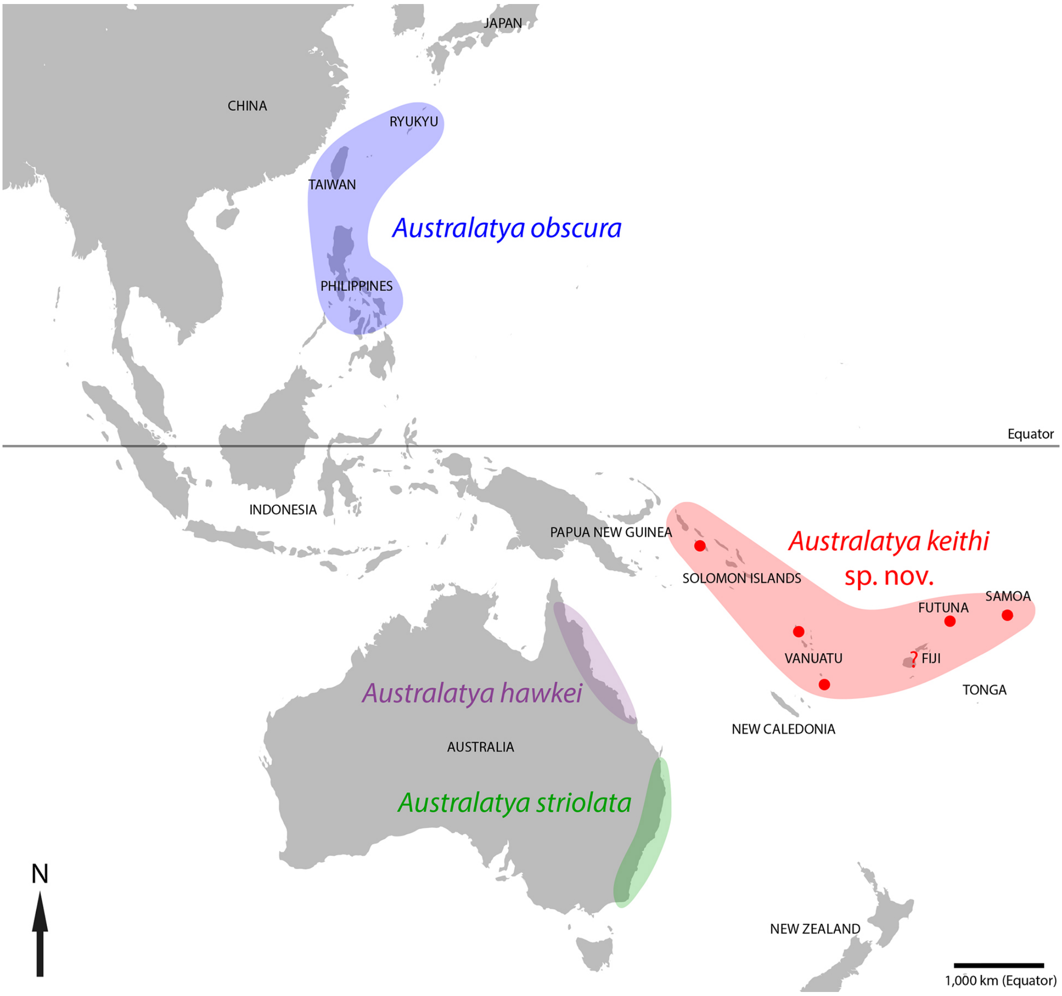

FIGURE 4. Current known geographical distribution of the four species of *Australatya*. Red dots indicate sampling sites from the present study.

times as long as wide (vs 5.1–6.3). They differ from *A. hawkei* by their rostrum armed with fewer ventral teeth 0–4 (vs 5–8 in *A. hawkei*) and their shorter P3 propodus, 3.3–4.4 times as long as wide (vs 5.0–6.7). They differ from *A. obscura* by their longer P1 carpus and P2 carpus 1.3–1.8 (vs 0.8–1.0 in *A. obscura*) and 1.2–1.7 (vs 0.9–1.0), their P3 shorter propodus 3.3–4.4 times as long as wide (vs 5.3–6.9), and simple dactyli of the fifth pereiopod (vs. biunguiculate).

Remarks

According to Han and Klotz (2015), the row of prominent, teeth-like spiniform setae on the interno-inferior margin of the merus of the third pereiopod, always present in adult specimens of *Australatya*, with the sexual dimorphism of the distal segment of the third maxilliped seems to be the best character to distinguish this genus from all other *Atya*-like genera of the Indo-Pacific region. Our new species here described presents these same characteristics, thus confirming its placement within *Australatya*.

Furthermore, *Australatya keithi* is differentiated from *Atyopsis spinipes* by its much smaller body size; its merus of male specimens lacking a massive spur vs. having a massive spur in large males; its endopod of males first pleopod tapering from proximal to distal vs. not tapering from proximal to distal, rhomboidally oval, submarginally spinose; appendix masculina on second pleopod of males with spinose area distal to tip of appendix interna vs. spinose over more than half length; lateral angles of telson not overreaching distal margin vs. overreaching.

The new species is distinguished from *Atyoida pilipes* by its chelae not sexually dimorphic vs. dimorphic, with palm in male specimens, and its appendix masculina on second pleopod of males with spinose area distal to tip of appendix interna vs. spinose area overlapping a part of the appendix interna.

Identification Key

1.1 Short P3 propodus 3.3–4.4 times as long as wide, ... ***A. keithi* sp. nov.**
(Solomon Islands, Vanuatu, Samoa, Futuna)
1.2 Long P3 propodus 5.0–6.9 times as long as wide 2
2.1 Short P1 carpus and P2 carpus 0.9–1.0 (Han and Klotz 2015)...................................... .... ***A. obscura***
(Taiwan, Ryukyu, Philippines)
2.2 Long P1 carpus and P2 carpus 1.0–1.8 and 1.0–1.7 (Smith and Williams 1982) 3
3.1 Rostrum length/carapace length 0.32– 0.45 (Smith and Williams 1982)............................ .... ***A. striolata***
(Australia: New South Wales, South Queensland)
3.2 Rostrum length/carapace length 0.21– 0.31 (Choy et al. 2019)........................... ***A. hawkei***

(Australia: North Queensland)

ACKNOWLEDGEMENTS

For Futuna: We thank A. Malau, head of the Environment office of Wallis and Futuna, P. Vanal and D. Labrousse. We also thank the King of the Sigave Kingdom, the King of the Alo Kingdom and the head of the rural economy office from Futuna. We acknowledge for their help on the field: Besamino, A. Dutartre, C. Flouhr, M. Juncker, N. Leleiva, N. Mary, P. Sasal, and Soseto. For Solomon Islands: We thank Philippe Gerbeaux, Clara Lord, and Robson Hevalo for their help collecting specimens in the field. Part of the study was made possible by a grant given to the French Ichthyological Society as part of the 'Critical Ecosystem Partnership Fund (CEPF)' (Melanesia hotspot). The Critical Ecosystem Partnership Fund is a joint initiative of l'Agence Française de Développement, Conservation International, the Global Environment Facility, the Government of Japan, the MacArthur Foundation and the World Bank. Part of the sampling was made possible by a grant of the Fondation de France for a freshwater fish biodiversity study. We acknowledge customary landowners and tribes for allowing the expedition team to enter their customary lands. We also thank the Solomon Islands Government for the support and facilitation of the legal process that have allowed the expedition team to conduct the scientific research in Solomon Islands and ESSI which organized the trip very efficiently. For Samoa: We acknowledge the Samoan Ministry of Natural Resources Environment and Meteorology, Conservation International, the Japan International Cooperation Agency, the University of The South Pacific and the International Union for Conservation of Nature. J. Atherton (CI) and N. Doherty (MNRE) played a major role in the mapping, coordination and logistic arrangements. With his presence in the field we are very happy to thank P. Gerbeaux. For Vanuatu: The study was made possible by a grant given to the French Ichthyological

Society in the framework of the 'Critical Ecosystem Partnership Fund (CEPF)' (Melanesia hotspot). We acknowledge the Department of Environmental Protection and Conservation for providing us the research permit. We thank the TAFEA Province Secretary General, the Aneityum provincial area secretary, Mr Ruben Niriam and the Tanna provincial area secretaries. We are particularly grateful to Chief Simon Nijina (Analcahat Chief), Chief Jack Nipveae (Secretary for the Nelvou Aneityum Council of Chiefs), Chief Samson on Green Hill, and Bob Kev (Green Hill school headmaster) and his sister Marie Kev and to the local communities who allowed us to survey the rivers. This work was made possible thanks to the Service de Systématique Moléculaire of the MNHN and its staff for allowing us to produce the molecular data presented in this study.

Finally, we thank Tim Page and an anonymous reviewer for their helpful comments that helped us improve the manuscript.

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