


Article

An Integrative Taxonomic Revision of the Freshwater Atyid Shrimps (Crustacea: Decapoda: Caridea) of Micronesia

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Abstract: Twelve species of atyid shrimps are reported from three Micronesian islands (Babeldaob, Pohnpei, and Guam) and studied using a combined morphological and molecular approach. Among them, three are new records for the area (*Caridina appendiculata*, *Caridina lobocensis*, and *Caridina rubella*), while three new species are here described: *Atyoida chacei* sp. nov., *Caridina ponapensis* sp. nov., and *Caridina rintelenorum* sp. nov. Descriptions for these new species, diagnoses for poorly known species, and taxonomic notes are provided herein and their biogeography is discussed.

Keywords: Atyidae; island; amphidromy; morphology; DNA; 16S

1. Introduction

Micronesia is a vast expanse of more than 2000 islands and atolls in the North Pacific Ocean, stretching from the Caroline and Mariana islands in the West to the Marshall, Nauru, and Kiribati islands in the East (Figure 1). Among these, only a few high islands possess surface running water, all situated in the western part of the region, in Palau, the Mariana Islands, and the Federated States of Micronesia.

At the western edge of the Caroline Islands, the Republic of Palau comprises a curved archipelago of approximately 350 islands lying between 4 and 8 degrees north latitude and 131 and 135 degrees east longitude. The high island of Babeldaob covers 334 km², accounting for over 80% of the country's total landmass, with its highest elevation point being only 230 m. Aged as being from 30 My, it is the crest of the Palau-Kyushu ridge [1]. In the Federated States of Micronesia, there are rivers on Yap, Pohnpei, Kosrae, and Weno (Chuuk). The high island of Pohnpei (formerly known as Ponape) is situated at 6°54' N latitude and 158°14' E longitude (Figure 1). It covers 345 km² of surface and the highest elevation point is 791 m. Aged as being from 8.7 My, this volcanic island was not only the remnant of a hotspot trace but was also produced in a fracture-induced subduction-related tectonic environment [2]. The Mariana Islands are a crescent-shaped archipelago comprising the summits of 15 mostly dormant volcanic mountains. At the southern end of the chain, Guam (formally the Territory of Guam) is an unincorporated and organized territory of the United States of America. It is located at 13°28' N and 144°45' E, and is 50 km long and 6 to 19 km wide, with an area of 549 km². The highest point is Mount Lamlam, at 407 m above sea level. It belongs to the Mariana ridge, which was created by the colliding Pacific and Philippine Sea tectonic plates [3].

In tropical oceanic islands, freshwater fauna is dominated by amphidromous organisms, i.e., the adults live and reproduce in the rivers but the larvae need saltwater to develop into juveniles [4]. Among these, shrimps of the family Atyidae De Haan, 1849 are the most prominent and diverse group. Characterized by the presence of tufts of setae at the tip of their chelae, they have an important ecological role in breaking down organic matter on the riverbed and filtering particles from the water. Many species, however, are



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threatened by human activities, whether directly or through global changes impacting their environment [5].

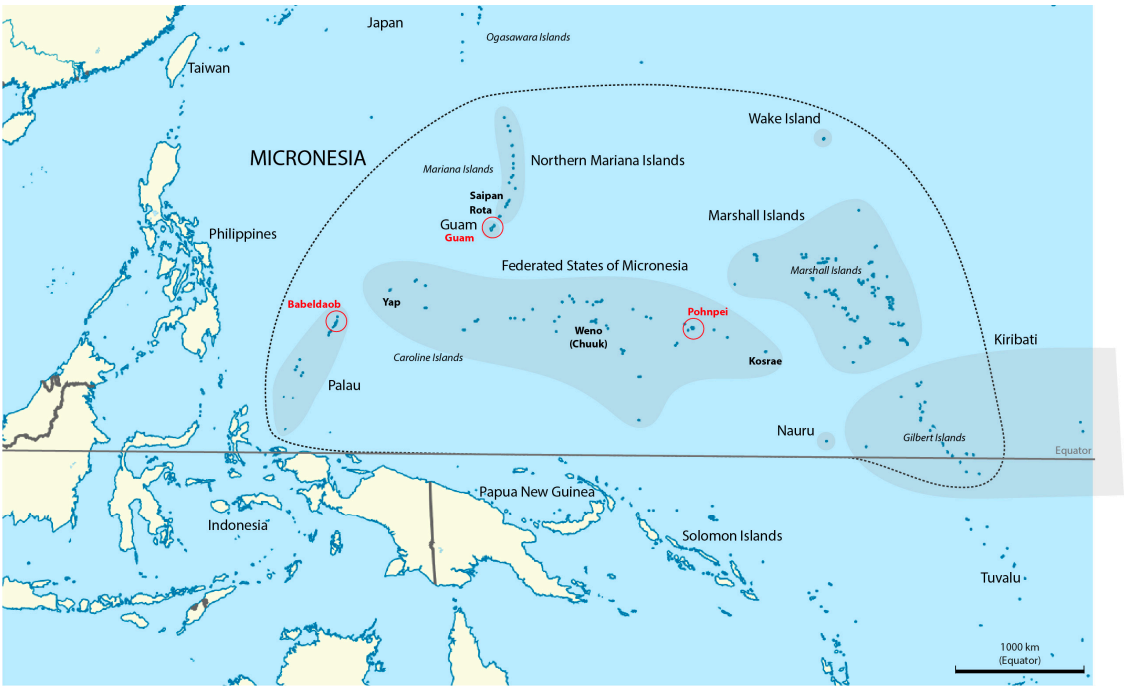


Figure 1. Map of Micronesia with the three surveyed islands circled in red.

The atyid shrimp fauna of Micronesia has been studied in the past, with most records focusing on single islands (see Table 1) as early as Schenkel [6], who reported *Atyoida pilipes* from Pohnpei, or Bouvier [7], who reported three species from the Mariana Islands. The latest publications are those by de Mazancourt et al. [8,9], describing a new species from Pohnpei Island and another from Palau and Guam. The current consensus states that nine species in five genera of atyid shrimps are present in the area, namely: *Antecaridina lauensis*, *Atyoida pilipes*, *Atyopsis spinipes*, *Caridina gracilirostris*, *C. cf. serratirostris*, *C. typus*, *C. variabilirostris*, *C. variabilis*, and *Halocaridinides* sp.

Table 1. List of species of Atyidae reported from Micronesia. Remarks: (1) Reported as *Ortmannia alluaudi* [7] (no island specified) and as *Atya serrata* [10] (from Rota Island) [11]. (2) No island specified [7], reported from Rota Island [10]. (3) Reported as *C. nilotica* var. *wycki* [12], *C. brachydactyla*, *C. longirostris*, *C. vitiensis*, and *C. weberi* [13], *C. weberi* [14], *C. weberi* and *C. sp.* [15], and *C. weberi* [16].

Country	Palau	USA	Federated States of Micronesia			Remarks	
Island Species	Babeldaob	Guam	Marianas	Yap	Pohnpei		Kosrae
<i>Atyoida pilipes</i>	[17]	[11,18,19]	[7,10]		[13–15]	[16,20,21]	1
<i>Atyopsis spinipes</i>	[17]	[11,18,19]	[22]		[13]	[16]	
<i>C. gracilirostris</i>	[17]			[23]			
<i>C. serratirostris</i>	[17]			[23]		[20]	
<i>C. typus</i>	[17]	[11,18,19,24]	[7,10]	[23]	[13,15]	[16]	2
<i>C. variabilirostris</i>					[8,13–15]	[16]	3
<i>C. variabilis</i>	[9,17]	[9,11,18,19,24]	[7]	[23]			4
<i>Antecaridina lauensis</i>		[18]					
<i>Halocaridinides</i> sp.		[18,25]					5

In order to update our knowledge of the decapod crustacean fauna of Micronesia, two freshwater surveys were conducted by a team from the Muséum national d’Histoire

naturelle of Paris, the first one on Babeldaob Island (Palau) between 27 February and 3 March 2011 [26] and the second one on Pohnpei Island (Federated States of Micronesia) between 9 and 15 March 2012 [27].

The aim of the present work is to report the results from these field trips to Micronesia and to update the checklist of atyid shrimps from the area based on specimens from various museum collections.

2. Materials and Methods

Collection of specimens. Specimens from Pohnpei and Babeldaob were collected by electrofishing (portable Dekka 3000 electric device, Germany), an efficient sampling method that allows temporarily stunning aquatic macrofauna while limiting disturbance of the substrate and vegetation [28]. All material preserved in 75–95% alcohol has been deposited in the collections of the Muséum national d’Histoire naturelle in Paris (MNHN). Specimens collected by dip net in Guam and preserved in ethanol were sent to us by D. C. Rogers and are now deposited in the Museum für Naturkunde in Berlin (ZMB). Rivers and sites surveyed in Pohnpei, Guam, and Babeldaob are indicated in Figure 2 and detailed in Table 2. The sampling was complimented by specimens collected in Palau by H.A. Fehlmann in 1955–1956 (see [29]) and G.R. Bright (see [17]) and loaned from the National Museum of Natural History of the Smithsonian Institution (USNM, Washington, DC, USA). Comparative material was loaned from Naturalis Biodiversity Center, Leiden (RMNH) and the Naturhistorisches Museum, Basel (NMB).

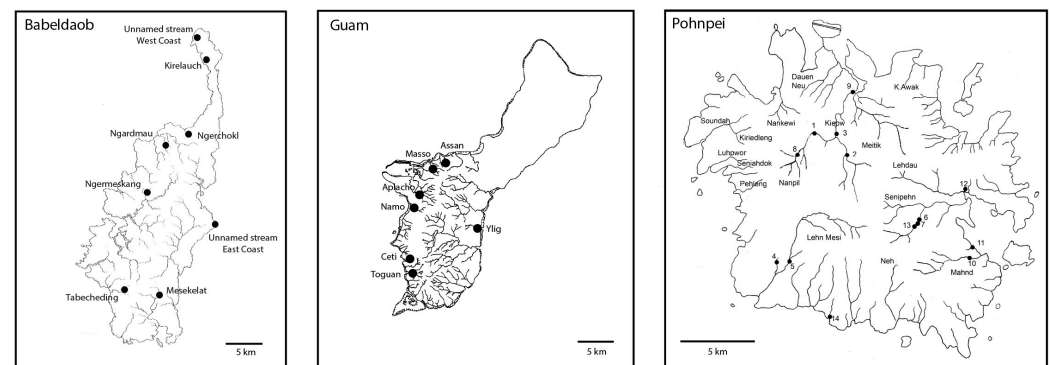


Figure 2. Rivers and sites surveyed in Babeldaob, Guam, and Pohnpei (dots: prospected sites).

Table 2. Sampling localities data.

Island	Rivers	Localities	Dates	Coordinates	Altitude (m)
Babeldaob	Tabecheding	Station 1	27 February 2011	07°27.169' N 134°31.748' E	28
	Ngerchokl	Station 2	27 February 2011	07°36.527' N 134°36.958' E	36
	Kirelauch	Station 3	28 February 2011	07°41.417' N 134°37.754' E	29
	Unnamed stream (west coast)	Station 4	28 February 2011	07°43.056' N 134°36.924' E	10
	Unnamed stream (east coast)	Station 5	28 February 2011	07°29.909' N 134°38.099' E	7
	Ngermeskang	Station 6	1 March 2011	07°32.484' N 134°34.670' E	75
	Ngardmau (waterfall)	Station 7	2 March 2011	07°35.482' N 134°35.573' E	41
	Mesekelat	Station 8	3 March 2011	07°26.305' N 134°34.328' E	20

Table 2. Cont.

Island	Rivers	Localities	Dates	Coordinates	Altitude (m)
Pohnpei	Nanpil	Station 1	9 March 2012	06°55.242' N 158°12.265' E	127
		Station 2	9 March 2012	06°54.498' N 158°13.270' E	93
		Station 3	9 March 2012	06°55.111' N 158°12.878' E	52
		Station 8	13 March 2012	06°54.252' N 158°11.491' E	180
		Station 9	13 March 2012	06°56.609' N 158°13.550' E	5
	Lehn mesi	Station 4	10 March 2012	06°51.055' N 158°10.890' E	197
		Station 5	10 March 2012	06°51.107' N 158°11.896' E	139
		Station 6	12 March 2012	06°51.895' N 158°15.810' E	81
	Senipehn	Station 7	12 March 2012	06°51.906' N 158°16.010' E	95
		Station 13	15 March 2012	06°51.795' N 158°15.622' E	119
	Mahnd	Station 10	14 March 2012	06°50.221' N 158°17.212' E	107
	“River 1”	Station 11	14 March 2012	06°51.120' N 158°17.854' E	5
	“Petroglyphe River”	Station 12	14 March 2012	06°53.221' N 158°17.44' E	5
	“River 2”	Station 14	10 March 2012	06°48.579' N 158°12.639' E	5
Guam	Assan		30 January–3 February 2011	13°28.168' N 144°42.762' E	11–16
	Masso		30 January–3 February 2011	13°27.200' N 144°41.871' E	34
	Aplacho		30 January–3 February 2011	13°24.345' N 144°41.187' E	58–75
	Namo		30 January–3 February 2011	13°23.904' N 144°39.959' E	4
	Ceti		30 January–3 February 2011	13°19.514' N 144°40.183' E	197
	Toguan		30 January–3 February 2011	13°17.117' N 144°39.955' E	15–41
	Ylig		30 January–3 February 2011	13°23.589' N 144°45.636' E	2

DNA extraction, amplification, and sequencing. DNA was extracted from abdominal muscle samples using the semi-automatic Eppendorf ep-Motion 5075 robot. Fragments of the mitochondrial 16S rRNA (~520 bp) were amplified using primers adapted from Palumbi [30] to our taxa: 16Sar-Lmod (TACTTCTGCCTGTTTATCAAAAA) and 16Sbmod (GGTCTGAACTCAAATCATGTAAA). DNA amplification was performed in 20 µL PCR reactions, containing approximately 3 ng of template DNA, 2.5 mM MgCl₂, 0.26 mM of each nucleotide, 0.3 µM of each primer, 5% DMSO, 1 ng of BSA, and 1.5 units of QBIOTAQ polymerase (MPBiomedicals). Amplification products were generated by an initial denaturation step of 4 min at 94 °C followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 40 s, extension at 72 °C for 60 s, and a final extension step at 72 °C for 7 min. PCR products were sequenced using the same primers and in both directions to ensure the accuracy of base calls. Chromatograms were edited using

Geneious v.8 software (<http://www.geneious.com> [31]). All newly produced sequences were deposited in GenBank (Numbers from PP455322 to PP455351, see Supplementary Table S1).

Molecular analyses. DNA sequences were aligned using MEGA v. 11 software [32] with Muscle algorithm [33]. Using Bayesian information criterion in jModelTest v.2.1 [34,35], we retained the GTR + G + I model. Best-scoring ML trees were estimated using RAxML HPC2 v.8.2.10 [36] and best-scoring Bayesian Inference (BI) trees were estimated using MrBayes v.3.2.7 [37]; both methods were implemented in the Cyber Infrastructure for Phylogenetic Research (CIPRES) portal v.3.1. (<https://www.phylo.org> [38]) with the previously determined model, running for 10,000,000 generations, a sampling frequency of 2000, and a burn-in of 10%. Support for nodes was determined using posterior probabilities calculated by MrBayes that were implemented in CIPRES. One hundred independent searches, each starting from distinct random trees, were conducted. Robustness of the nodes was assessed using non-parametric bootstrapping [39] with 1000 bootstrap replicates. We considered a group to be moderately supported if it had a bootstrap value (B) comprised between 75% and 89% and Bayesian posterior probabilities (PP) between 0.8 and 0.95 and highly supported if $B \geq 90\%$ and $PP \geq 0.95$. For the analysis, we generated 29 new 16S sequences from specimens collected during the authors' field trips, to which were added 34 sequences retrieved from GenBank for species occurring in Micronesia and/or closely related species to support the morphological comparisons (Supplementary Table S1).

Morphological analyses. The rostrum, the cephalothorax, the pereopods 1, 2, 3, and 5, and the abdomen were observed using a stereomicroscope. The proportions of the various joints of the appendages (see [40] for detailed measurement method) were measured using microphotographs and the AnalySIS Works software (Olympus, Hamburg, Germany) or LAS (Leica, Heerbrugg, Switzerland). Drawings were made using the "Digital Inking" method [41,42] by tracing vectorial paths on high-resolution photographs using Adobe Illustrator (Mountain View, CA, USA). Diagnoses and/or descriptions are only appended for poorly known or new species.

3. Results

3.1. Molecular Analyses

The phylogenetic tree that was obtained (Figure 3) showed 17 distinct terminal clades, 11 of them including specimens from Micronesia (noted A–K in Figure 3). The specimens are distributed in two strongly supported main clades, the first one considered as the *Atya* group, containing sequences of *Atyopsis* and *Atyoida*, and the other one as the *Caridina* group, which contains all the sequences of *Caridina*. Within the latter, species complexes as defined by [43] are recognized: the *C. weberi* complex, *C. typus* complex, *C. serratiostris* complex, and *C. nilotica* complex. Even though all of these appear as strongly supported clades (with the exception of the *C. weberi* complex, appearing as polyphyletic but with low support values), the relationships among the complexes are poorly supported in this analysis.

3.2. Morphological Analyses

Our morphological study of the specimens confirmed the results of the molecular study in recognizing the 11 clades of the 16S tree as separate species. In addition, one species was morphologically identified from collection specimens but could not be included in the molecular study. Nevertheless, its morphological characteristics are sufficient to distinguish it from all of the other species, allowing us to place it within the *C. graciliostris* complex.

See further below for a detailed taxonomic account of the species.

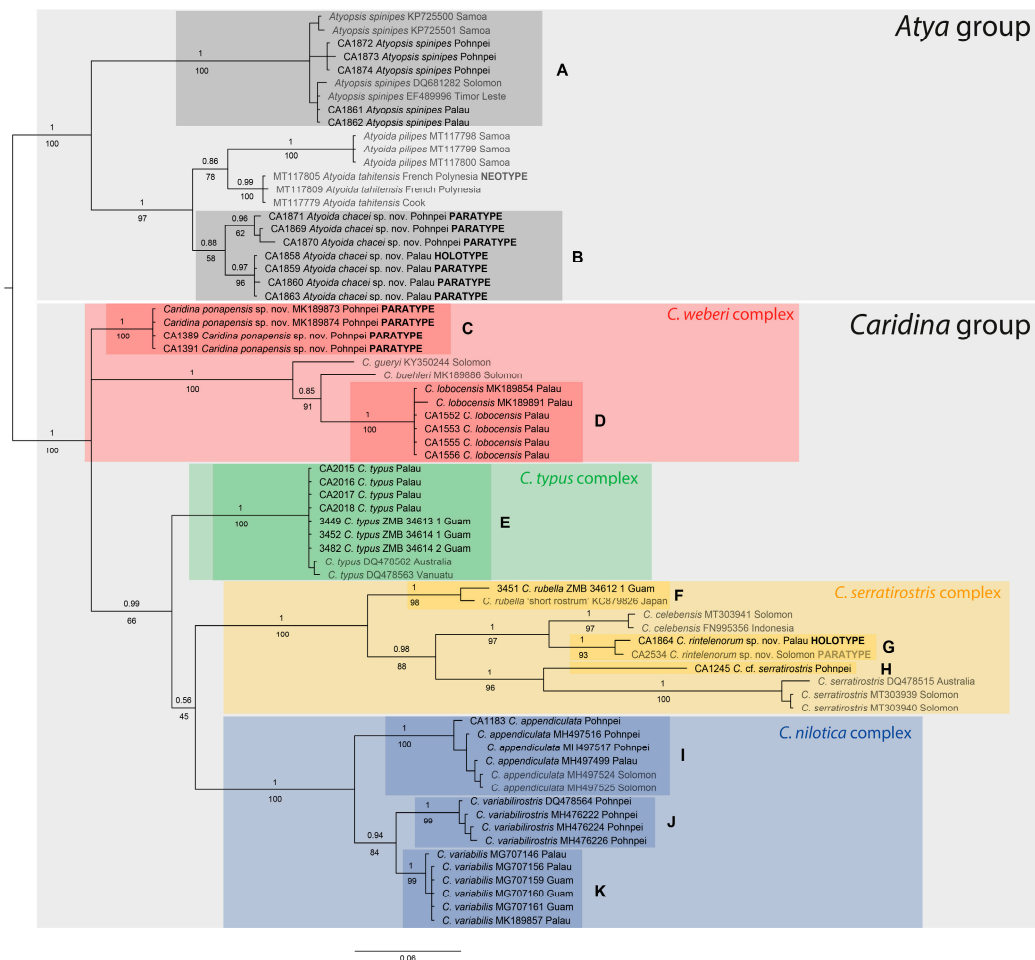


Figure 3. Phylogenetic tree of the atyid species from Micronesia obtained by Bayesian inference from the 16S rRNA. Numbers above branches indicate Bayesian posterior probabilities, numbers under branches indicate maximum likelihood bootstraps. Letters A–K for the clades refer to the species listed in the taxonomic account.

3.3. Taxonomic Account

Family Atyidae De Haan, 1849

Diagnosis (from [7]): freshwater shrimps from small to large size (4–120 mm). Body usually pigmented, except for some subterranean species. Ocular peduncle without projection on the dorsal margin near the cornea. Last two articles of antennular peduncle longer or as long as wide; stylocerite without dorsal process, or vestigial one. Mandibles without palp but with a well-developed molar process. Exopodite of maxillae with a posterior tuft of long setae. Exopodite of third maxillipeds prolonged by a transverse or oblique projection on its antero-internal angle; epipodites of third maxilliped very reduced or vestigial, without posterior lobe. Dactylus of second maxilliped longer or as long as propodus. Dactylus of third maxilliped armed with a rather strong spine, arched and never styliform. Chelipeds with simple carpus and ending in a chela. Dactylus of walking legs moderately long, flattened or conical, armed with a terminal spine and a series of spinules, and numerous and contiguous on the fifth pereopods. Epipods always lack a projection. Telson without median stylus on its posterior margin.

Genus *Atyopsis* Chace, 1983

Diagnosis (from [44]): body pigmented, eyes well developed; rostrum not strongly compressed laterally, median dorsal carina typically unarmed, ventral keel with 2–16 teeth; anterior margin of carapace armed with antennal spine, pteygostomial margin sharply acute; supraorbital spines absent; telson with posterolateral angles overreaching setigerous

posterior margin; third maxilliped not terminating in single apical spine; pereopods without exopods; first and second pereopods with chelae monomorphic (without palm), fingers tipped with brushes of long setae adapted for filter feeding, carpus of both appendages excavate distally, little if at all longer than broad; third pereopod of large males with prominent spur on merus; branchial complement consisting of five pleurobranchs, three arthrobranchs, one podobranch, five epipods (reduced posteriorly), no mastigobranchs; first pleopod of male with endopod rigid, rhomboidally oval, submarginally spinose; second pleopod of male with appendix masculina subcylindrical, spinose over entire length distal to base of appendix interna.

Atyopsis spinipes (Newport, 1847)

Figures 3A and 9A

- *Atya spinipes* Newport 1847: 159 [type locality: Philippine Islands];
- *Atyopsis spinipes*—Chace 1983 [44]: 35, Figures 20–22.

Material examined

PALAU: Babeldaob Island. Tabecheding river, station 1, 27 February 2011, 07°27.169' N, 134°31.748' E, observed only; Ngerchokl river, station 2, 27 February 2011, 07°36.527' N, 134°36.958' E, observed only; Tireloich river, station 3, 07°41.417' N, 134°37.754' E, 28 February 2011, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois, observed only; Ngardmau waterfall, station 7, 2 March 2011, 07°35.482' N, 134°35.573' E, observed only; USNM 105280: 4 ♀, cl 7.3 mm–11.0 mm, south fork of Arakitaoch stream, station 170A, 26 November 1956, coll. H.A. Fehlmann; USNM 190993: 1 ♀, cl 12.0 mm, Metengakakumer river, station 2-MR-4-05, 13 February 1973, coll. G. Bright. Tissue only: CA1861 and CA1862, no locality data.

Koror Island. USNM 104899: 1 ♀, cl 8.3 mm, station 216, 7°20.424' N, 134°29.642' E, 11 October 1955, coll. H.A. Fehlmann.

FEDERATED STATES OF MICRONESIA: Pohnpei Island. Nanpil river station 1, 9 March 2012, 127 m a.s.l., 06°55.242' N, 158°12.265' E; Nanpil river station 2, 9 March 2012, 93 m a.s.l., 06°54.498' N, 158°13.270E, observed only; Nanpil river station 3, 9 March 2012, 52 m a.s.l., 06°55.111' N, 158°12.878' E, observed only; Lehn Mesi river station 1, 10 March 2012, 197 m a.s.l., 06°51.055' N, 158°10.890' E, observed only; Lehn Mesi river station 2, 10 March 2012, 139 m a.s.l., 06°51.107' N, 158°11.396' E, observed only; Senipehn river station 2, 12 March 2012, 95 m a.s.l., 06°51.906' N, 158°16.010' E, observed only; Nanpil river station 5, 5 m a.s.l., 06°56.683' N, 158°13.550' E, observed only; Mahnd river, 14 March 2012, 107 m a.s.l., 06°50.609' N, 158°17.212' E, observed only; unnamed river 1 estuary, 5 m a.s.l., 06°51.120' N, 158°17.854' E, observed only; Senipehn river station 3, 119 m a.s.l., 06°51.795' N, 158°15.622' E, observed only, M. Castelin, P. Keith, P. Gerbeaux, G. Marquet and L. Taillebois. Tissue only: CA1873 CA1872 and CA1874, no locality data, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois.

Short diagnosis

Body pigmented, eyes well-developed. Rostrum not strongly compressed laterally, dorsal carina typically unarmed, ventral margin with two–six discrete teeth, and anterior margin of carapace armed with antennal spine. Pterygostomian margin sharply acute. first and second pereopods with chelae monomorphic (without palm); fingers tipped with brushes of long setae adapted for filter feeding. Third pereopods of large males with prominent spur on merus.

Distribution

Pacific, extending from the Philippines and Indonesia to Samoa.

Habitat

This species prefers fresh and fast-flowing waters. Its biotope is characterized by rocky walls under waterfalls, where individuals aggregate in great numbers.

Genus *Atyoida* Randall, 1840

Diagnosis (from [44]): body pigmented, eyes well developed; rostrum not strongly compressed laterally, median dorsal carina typically unarmed, ventral keel with zero–four teeth; anterior margin of carapace armed with antennal spine, pterygostomian margin sharply or bluntly acute; supraorbital spines absent; telson with setigerous posterior margin overreaching posterolateral angles; third maxilliped with uncinat terminal spine; pereopods without exopods; first and second pereopods with chelae heteromorphic (with or without palm), fingers tipped with brushes of setae, carpus of both appendages excavate distally, little if at all longer than broad; third pereopod without meral spur in large males; branchial complement consisting of five pleurobranchs, three arthrobranchs, one podobranch, five epipods, and five mastigobranchs; first pleopod of male with endopod tapering sinuously but rather regularly to slender apex; second pleopod of male with appendix masculina sub-cylindrical, spinose over more than distal half.

Atyoida chacei sp. nov.

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Figures 3B, 4 and 9B

- *Atyoida* cf. *pilipes*—Lorang et al., 2020 [45]: 300, Figure 1;
- *Atya serrata*—Miyake, 1938 [10]: 111;
- *Atyoida pilipes*—Chace, 1983 [44]: 13, Figures 5–8 (part).—Maciolek and Ford, 1987 [13]: 628.—Nelson et al., 1996 [14]: 11.—Buden et al., 2001 [15]: 260.—Leberer and Cai, 2003 [18]: 354.—March et al., 2003 [20]: 126.—Page et al., 2007 [21]: 139, Figure 1 (part); 2008 [46]: 73, Figure 4 (part).—Benstead et al., 2009 [16]: 459.

Material examined

Type material:

PALAU: Babeldaob Island. Holotype: MNHN-IU-2024-439 (DNA: CA1858), 1 ♂, cl 4.7 mm, Tireloich river (Station 3), 07°41.417' N, 134°37.754' E, 28 February 2011, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet and L. Taillebois. Paratypes: MNHN-IU-2024-440 (DNA: CA1859), 1 ♂, cl 4.7 mm, MNHN-IU-2024-441 (DNA: CA1863), 1 ♂, cl 4.5 mm, and MNHN-IU-2024-442 (DNA: CA1860), 1 ♀, cl 7.5 mm, same data as holotype. CA1863, no locality data. USNM 104901: 6 ♀ ovig., cl 5.9–7.3 mm and 1 ♀, cl 4.9 mm, Arakitaach river (station 241), 7°32.836' N, 134°35.782' E, 18 October 1955, coll. H.A. Fehlmann. USNM 104926: 1 ♂, cl 4.2 mm, 1 ♀ ovig., cl 6.0 mm and 4 ♀, cl 4.0 mm–6.8 mm, Station 170-A, 27 November 1956, coll. H.A. Fehlmann. USNM 105280: 1 ♀, cl 5.8 mm, South Fork of Arakitaach river (station 170-A), 7°31.556' N, 134°34.206' E, 15 November 1956, coll. H.A. Fehlmann. **Arakabesan Island:** USNM 172586: 1 ♀ ovig., cl 7.0 mm, below reservoir, station 2 A14-01, 9 August 1976, coll. G. Bright.

FEDERATED STATES OF MICRONESIA: Pohnpei Island. MNHN-IU-2024-443 (DNA: CA1869): 1 ♂, cl 4.6 mm, MNHN-IU-2024-444: 1 ♀, cl 5.1 mm, MNHN-IU-2024-445 (DNA: CA1870): 1 ♀ ovig., cl 6.7 mm and MNHN-IU-2024-446 (DNA: CA1871), Senipehn river (Station 7), 06°51.906' N, 158°16.010' E, March 12 2012, 95 m a.s.l., coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. ZMB 8926: 4 ♀, cl 4.7–6.1 mm, February 1880, coll. O. Finsch.

Comparative material:

Atyoida pilipes (Newport, 1947): See [45].

Atyoida tahitensis Stimpson, 1860: See [45].

Description

Cephalothorax. Rostrum short (Figure 4o–q), 0.2–0.4 of cl, reaching near to or slightly beyond end of basal segment of antennular peduncle, with dorsal margin convex, ventral margin usually unarmed, sometimes with 1–2 teeth; antennal spine fused with inferior orbit angle, acute; pterygostomian margin acute.

Eyes well-developed. Antennular peduncle stout (Figure 4o), 0.46 (♀)–0.65 (♂) times as long as carapace; basal segment shorter than half length of antennular peduncle, second segment longer than third segment. Stylocerite reaching near to or slightly beyond end of basal segment of antennular peduncle.

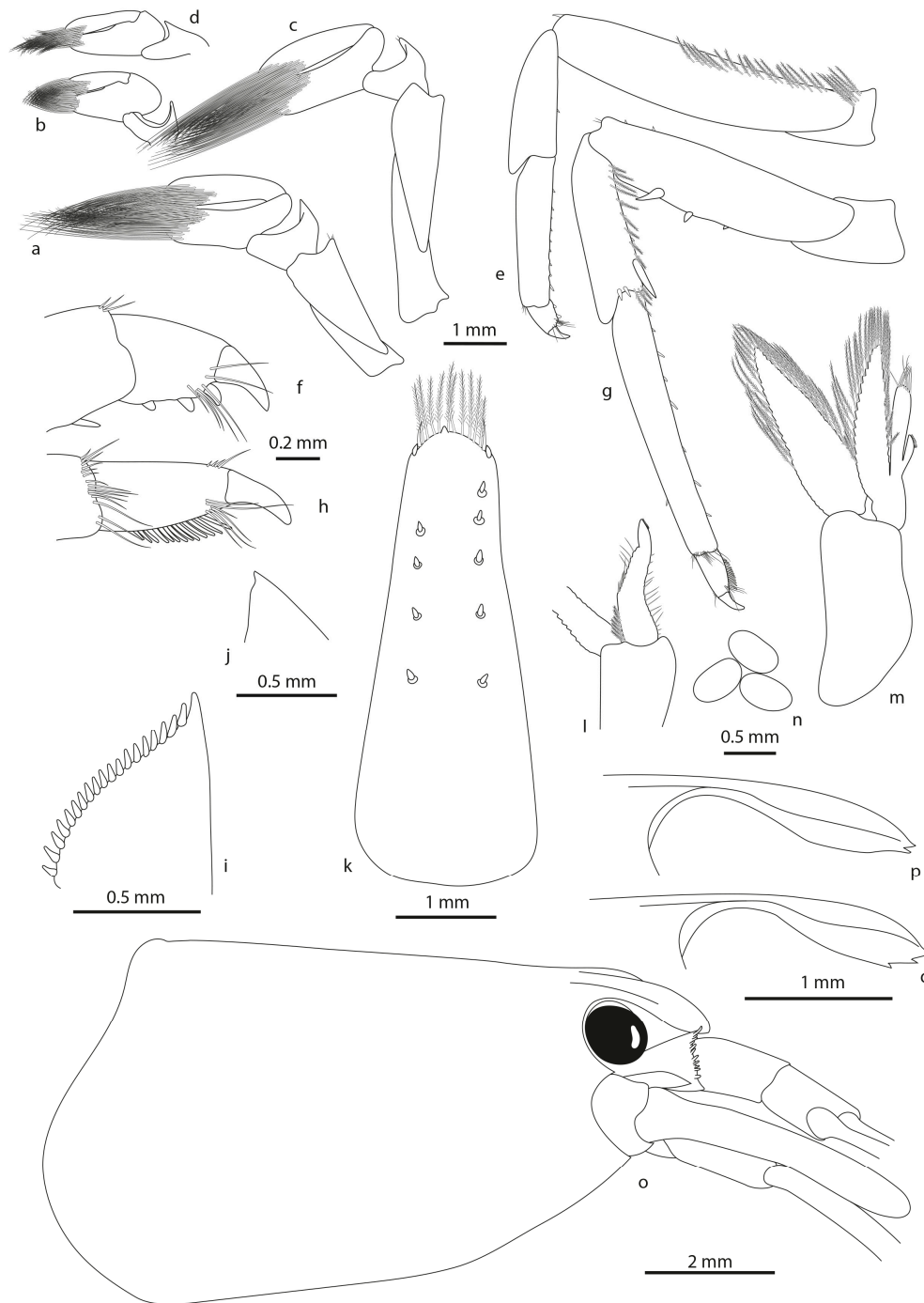


Figure 4. *Atyoida chacei* sp. nov. (a) first pereiopod of female; (b) first pereiopod of male; (c) second pereiopod of female; (d) second pereiopod of male; (e) third pereiopod; (f) dactylus of third pereiopod; (g) fifth pereiopod; (h) dactylus of fifth pereiopod; (i) uropodal diaeresis; (j) pre-anal carina; (k) telson; (l) male first pleopod, endopod; (m) male second pleopod; (n) undeveloped eggs; (o) cephalothorax; (p,q) rostrum variations. Holotype MNHN-IU-2024-439 (DNA: 1858): i, l, m, and p. Paratypes: MNHN-IU-2024-440 (DNA: CA1859): b, d, and q; MNHN-IU-2024-442 (DNA: CA1860): e, f, j, k, and o; MNHN-IU-2024-446 (DNA: CA1871): a, c, g, h, and n.

Pereiopods. Epipods on first four pereiopods. P1 and P2 similar in size and shape. Chelae dimorphic, ortmannioid in shape (palm present, Figure 4b,d) mostly in males and atyoid (palm virtually absent, Figure 4a,c) mostly in females. P1 (Figure 4a,b) chela about 1.9–4.2 times as long as wide, movable finger 3.9–5.9 times as long as wide, 1.7–2.0 times length of palm with tufts of long setae distally, carpus excavated strongly anteriorly, 1.0–1.3 times as long as wide. P2 (Figure 4c,d) chela 2.2–3.9 times as long as wide; dactylus 3.7–6.3 times as long as wide, 2.4 times length of palm with tufts of long setae distally, P2 carpus excavated strongly anteriorly, 1.0–1.8 times as long as wide. P3 (Figure 4e) with row of setae on outer surface of merus, very short dactylus (Figure 4f) ending in a strong claw, 1.7–3.2 times as long as wide (terminal spine included) with 2–6 spines on flexor margin in addition to the terminal spine; propodus 3.0–6.6 times as long as wide, 2.5–3.7 times as long as dactylus. P5 (Figure 4g) with setae only present on carpus; dactylus (Figure 4h) short, 2.1–3.5 times as long as wide with 8–18 spines on flexor margin; propodus 5.9–13.4 times as long as wide, 3.3–5.6 times as long as dactylus.

Abdomen. Sixth abdominal somite 0.45 times length of carapace, 1.2 times as long as fifth somite, 0.79 times as long as telson.

Telson (Figure 4k) 2.4–2.8 times as long as wide, with from two to eight pairs of dorsal spinules, often not in pairs, one pair of dorsolateral spinules near dorsal end; posterior margin rounded with 8–11 plumose intermediate setae distinctly longer than lateral ones.

Male P11 (Figure 4l): Endopod subtriangular, 3.4 times as long as wide, reaching 0.59 times length of endopod, with a distinct appendix interna near distal end of endopod.

Male P12 (Figure 4m): Appendix masculina reaching 0.58 times length of endopod, inner and distal surface densely lined with long spines; appendix interna at basal 0.27 times length of appendix masculina, extending to distal 0.33 times length of appendix interna.

Prenal carina triangular (Figure 4j) without spine.

Uropodal diaeresis (Figure 4i) with 15–20 spinules.

Eggs (Figure 4n): undeveloped: 0.31–0.29 mm × 0.52–0.51 mm.

Etymology

A. chacei sp. nov. is named in honor of Fenner A. Chace, Jr (1908–2004) as an acknowledgement to his posthumous cooperation with us on the study of *Atya*-like shrimps of the Indo-Pacific region and for being the first to suggest that the *Atyoida* from Palau may belong to a distinct species.

Colour pattern

Body transparent, flanks whitish ornamented with numerous dark blue-black spots and stripes all over the body.

Distribution

Reported only from Babeldaob Island and Pohnpei Island in Micronesia.

Habitat

This species is largely rheophile and prefers fresh and fast-flowing waters.

Remarks

Atyoida chacei sp. nov. resembles *A. pilipes* and *A. tahitensis* (Table 3) by its short, unarmed, bent rostrum, as well as by the proportions between the joints of pereiopods and the presence of ortmannioid and atyid chelae. The absence of caridinoid chelae in males or in females in these three species distinguishes them from *A. serrata* (Bate, 1888) and *A. bisulcata* Randall, 1840. Indeed, in these two species, the chelae are trimorphic: atyoid, caridinoid, and ortmannioid (see [44]).

Due to their high morphological variability, finding diagnostic characters to separate *A. chacei* sp. nov. from *A. pilipes* or *A. tahitensis* turned out to be a difficult task (see Table 3), so much so that they could be considered to be cryptic species, as they can only be distinguished by the following characters:

- Frequently, presence of one or more teeth on the ventral margin of the rostrum, vs. always 0 in *A. pilipes* and *A. tahitensis*. This character was already highlighted by

Chace (1983): “Of 613 specimens with complete rostra from the Palau Islands, 270 have no ventral rostral teeth, 240 have 1, 97 have 2, 5 have 3, and 1 has 4”;

- Two–eight pairs of dorsal spinules, often not in pairs for *A. chacei* sp. nov. (vs. one–five pairs of dorsal spinules, often not in pairs for *A. pilipes*, vs. from two to four pairs of dorsal spinules, often in pairs for *A. tahitensis*);
- Posterior margin rounded with from 8 to 11 plumose intermediate setae distinctly longer than lateral ones (vs. 4 to 9 plumose intermediate setae distinctly longer than lateral ones for *A. pilipes*, vs. with 6 to 10 plumose intermediate setae distinctly longer than lateral ones for *A. tahitensis*);
- By the size of undeveloped eggs ($0.51\text{--}0.52\text{ mm} \times 0.29\text{--}0.31\text{ mm}$ (vs. $0.47\text{--}0.60\text{ mm} \times 0.31\text{--}0.39\text{ mm}$ for *A. pilipes*, vs. $0.55\text{--}0.70\text{ mm} \times 0.29\text{--}0.54\text{ mm}$ for *A. tahitensis*)).

Nevertheless, following an integrative taxonomy framework, their genetic distinctiveness (16S p-distances: 9–15%) coupled with their discrete geographical distribution provides enough evidence to distinguish the two species as distinct taxa, as it was the case for other species of freshwater shrimps (e.g., [47–49]).

Table 3. Morphological comparison between the three known species of *Atyoida*. Measurements in bold are discriminant.

		<i>Atyoida chacei</i> sp. nov. (n = 11)	<i>Atyoida pilipes</i> (n = 39)	<i>Atyoida tahitensis</i> (n = 22)
P1	Dactylus length/width	3.9–5.9	3.5–6.1	3.9–6.0
	Chela length/width	1.9–4.2	1.7–4.7	1.8–3.9
	Carpus length/width	1.0–1.3	0.9–1.4	0.8–1.2
P2	Dactylus length/width	3.7–6.3	3.6–5.3	3.9–5.7
	Chela length/width	2.2–3.9	2.1–4.3	1.9–4.0
	Carpus length/width	1.0–1.8	1.0–1.6	1.0–1.5
P3	Dactylus spines number	2–6	3–5	3–6
	Propodus length/dactylus length	2.5–3.7	2.2–3.7	1.8–3.1
	Dactylus length/width	1.7–3.2	1.7–3.7	2.2–3.3
	Propodus length/width	3.0–6.6	3.9–7.5	3.9–5.4
P5	Dactylus spines number	8–18	4–14	5–13
	Propodus length/dactylus length	3.3–5.6	2.9–4.8	2.7–5.8
	Dactylus length/width	2.1–3.5	2.1–5.1	1.7–4.4
	Propodus length/width	5.9–13.4	6.0–10.4	6.0–10.4
Rostrum	Dorsal teeth number	0	0	0
	Ventral teeth number	0–2	0	0
	Length/carapace length	0.2–0.4	0.2–0.3	0.2–0.3
Uropod	Diaeresis spines number	15–20	15–22	14–18
Telson	Distal setae number	8–11	4–9	6–10
	Length/width	2.4–2.8	2.3–3.1	2.5–3.2
	Dorsal spines number (left + right)	2–5 + 4–8	1–5 + 1–4	2–4 + 2–3
Eggs	Size (mm)	0.51–0.52 ×	0.47–0.60 ×	0.55–0.70 ×
		0.29–0.31	0.31–0.39	0.29–0.54

Genus *Caridina* H. Milne Edwards, 1837

Diagnosis: From small- to medium-sized shrimps (cl: 10–40 mm); ocular peduncle with variable corneal dilatation; rostrum strongly compressed laterally, with or without serration on both margins; carapace with antennal spine on the infraorbital angle, protruding or fused with it; pterygostomian margin unarmed, supraorbital spines absent; third maxilliped with a series of unequal spines on the dactylus; pereopods without exopods; first pereopods

shorter than second, both with palm, fingers tipped with brushes of setae, carpus of P1 sometimes excavated, P2 never, both clearly longer than broad; branchial complement consisting of five pleurobranchs, three arthrobranchs, and one podobranch, with variable number of epipods and five mastigobranchs; first pleopod of male with a flat endopod of diverse shapes, with or without appendix; second pleopod of male with appendix masculina sub-cylindrical, spinose over more than distal half.

Caridina weberi species group

Diagnosis (from [43]): robust morphology with a straight or bent rostrum, armed or not on the dorsal margin, without apical teeth, the antennal spine fused with the inferior orbital angle, antennular peduncle equal to or more than half of carapace in length, pterygostomian margin rounded, stout walking leg segments, the carpus of the first pereopod often deeply excavated, a short sixth abdominal somite (around half of carapace length), a high pre-anal carina with no spine or a small one, a great number of spinules on the uropodal diaeresis (>15), long and plumose terminal setae on the telson clearly longer than lateral ones, and a long subrectangular endopod of the first male pleopod with a short appendix on the subdistal outer margin.

Caridina ponapensis sp. nov.

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Figures 3C, 5 and 9C

- *Caridina* cf. *weberi* Pohnpei—de Mazancourt et al., 2019 [47]: 166, Figures 2–5;
- Non *Caridina weberi parvirostris*—Maciolek & Ford, 1987 [13]: 628;
- Non *Caridina weberi*—Maciolek & Ford, 1987 [13]: 628 (part?).—Nelson et al., 1996 [14]: 11 (part?).—Buden et al., 2001 [15]: 257 (part?).

Material examined

Type material

FEDERATED STATES OF MICRONESIA: Pohnpei Island. Holotype: MNHN-IU-2024-447: 1 ♂ cl 2.4 mm, Nanpil river (station 2), 9 March 2012, 93 m a.s.l., 06°54.498' N, 158°13.270' E, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois.

Paratypes: MNHN-IU-2024-448: 1 ♀ ovig. cl 3.0 mm Nanpil river (station 1), 9 March 2012, 127 m a.s.l., 06°55.242' N, 158°12.265' E, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. MNHN-IU-2024-449: 1 ♂ cl 2.4 mm, Nanpil river (station 2), 9 March 2012, 93 m a.s.l., 06°54.498' N, 158°13.270' E, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. MNHN-IU-2024-450 (DNA: CA1390): 1 ♀ cl 3.8 mm and MNHN-IU-2024-451 (DNA: CA1391): 1 ♀ ovig. cl 3.7 mm, Lehn Mesi river (station 2), 06°51.107' N, 158°11.396' E, 10 March 2012, 139 m a.s.l., coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. MNHN-IU-2024-452 (DNA: CA1388): 1 ♀ ovig. cl 3.5 mm and MNHN-IU-2024-453 (DNA: CA1389): 1 ♀ ovig. cl 2.9 mm, Senipehn river (station 2), 95 m a.s.l., 06°51.906' N, 158°16.010' E, 12 March 2012, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. MNHN-IU-2024-454: 1 ♀ ovig. cl 3.1 mm; Mahnd river, 06°50.609' N, 158°17.212' E, 14 March 2012, 107 m a.s.l., coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois.

Comparative material

Caridina weberi De Man, 1892: Syntypes MNHN-IU-2015-1755 2 ♂ cl 4.4–4.5 mm, 1 ♀ ovig. cl 6.1 mm.

Caridina parvirostris De Man, 1892: Syntypes MNHN-IU-2015-1748 cl. 3.1–3.2 mm, 1 ♀ cl. 4.2 mm.

Caridina keiensis Roux, 1911: Lectotype NMB 6.IV.b 1 ♀ ovig. cl 5.7 mm; Paralectotypes NMB 6.IV.a 2 ♂ cl 2.6 mm; NMB 6.IV.b 1 ♀ cl 5.5 mm; one male cl 3.4 mm.

Description

Cephalothorax. Suborbital angle indistinguishably fused with antennal spine. Pterygostomian margin rounded. Rostrum (Figure 5m,n): curved down, short, 0.2–0.3 of cl, not

overreaching first segment of antennular peduncle, armed with four–six teeth on dorsal margin, zero of them situated on carapace behind orbital margin, ventral margin with zero–one teeth.

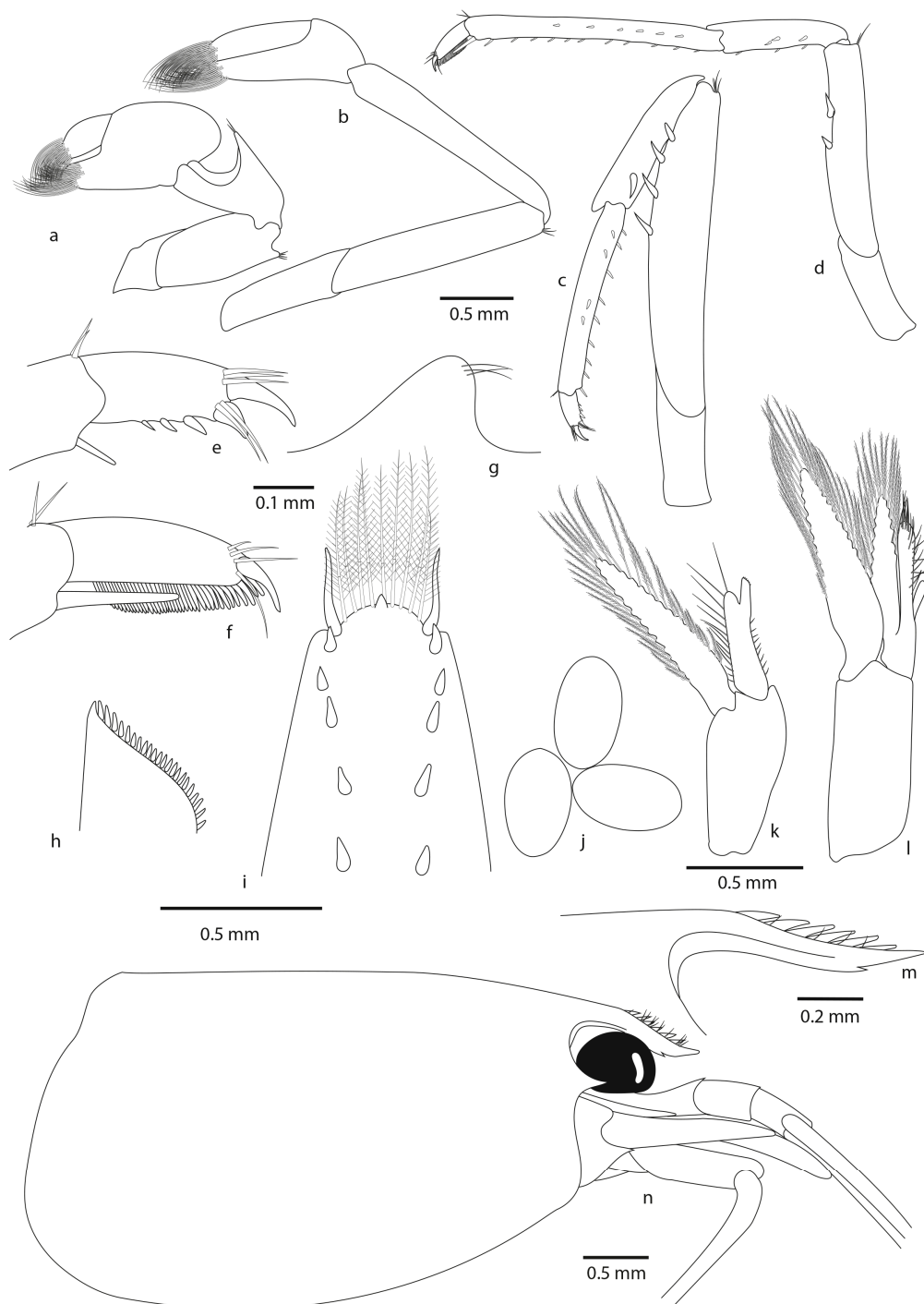


Figure 5. *Caridina ponapensis* sp. nov. (a) first pereopod; (b) second pereopod; (c) third pereopod; (d) fifth pereopod; (e) dactylus of third pereopod; (f) dactylus of fifth pereopod; (g) pre-anal carina; (h) uropodal diaeresis; (i) telson; (j) undeveloped eggs; (k) male first pleopod; (l) male second pleopod; (m) rostrum; (n) cephalothorax. Holotype: MNHN-IU-2024-447: **h**, **k**, **l**, and **m**. Paratypes: MNHN-IU-2024-451 (DNA: CA1391): **a–f**, **i**, **j**, and **n**; MNHN-IU-2024-452 (DNA: CA1388): **g**.

Eyes well-developed, anterior end reaching to 0.7 times length of basal segment of antennular peduncle. Antennular peduncle 0.57 times as long as carapace. Anterolat-

eral angle reaching 0.28 times length of the second segment, second segment distinctly shorter than third segment. Stylocerite reaching to 0.9 times length of basal segment of antennular peduncle.

Pereiopods. Epipods on first four pereiopods. P1 (Figure 5a): chela about 1.8–2.0 times as long as wide, movable finger 2.0–3.3 times as long as wide, 0.5–1.2 times length of palm; carpus 1.3–1.9 times as long as wide. P2 (Figure 5b) more slender and longer than first pereiopod with chela 2.4–2.6 times as long as wide; movable finger 4.0–4.5 times as long as wide, 1.3–1.8 times length of palm; carpus slender 5.6–6.5 times as long as wide. P3 (Figure 5c): stout, dactylus (Figure 5e) 2.4–3.7 times as long as wide terminal spiniform (seta included) with five–six spines on flexor margin in addition to the terminal spine; propodus 7.9–8.9 times as long as wide, 3.5–4.8 times as long as dactylus. P5 (Figure 5d): dactylus (Figure 5f) 3.0–4.3 times as long as wide with 29–39 spiniform setae on flexor margin; propodus 10.6–15.7 times as long as wide, 4.1–5.2 times as long as dactylus.

Abdomen. Third abdominal somite with moderately convex dorsal profile. Sixth abdominal somite 0.48 times as long as carapace, 1.5 times as long as fifth somite, 0.86 times as long as telson.

Telson (Figure 5i) two times as long as wide, with four pairs of dorsal spinules and one pair of dorsolateral spinules; posterior margin with a median process, rounded with five–nine very long intermediate plumose setae longer than lateral ones.

Male Pl1 (Figure 5k): Endopod subtriangular, 0.53 times length of exopod, appendix interna stout, exceeding end of endopod.

Male Pl2 (Figure 5l): Long appendix masculina on second pleopod reaching 0.85 times length of endopod; appendix interna reaching about 0.64 times length of appendix masculina.

Preanal carina high (Figure 5g) and unarmed.

Uropodal diaeresis (Figure 5h) with 19–24 spinules.

Eggs sized: 0.43–0.50 mm × 0.25–0.29 mm (Figure 5j).

Habitat

This new species is largely rheophile and prefers waters that are fresh and fast-flowing from the lower to the higher courses.

Etymology

C. ponapensis sp. nov. is named after the former name of Pohnpei, Ponape, from where this new species is endemic.

Colour pattern (Figure 9C)

Body transparent with spots of chromatophores scattered over the body.

Distribution

This new species seems endemic to Pohnpei Island.

Remarks

Based on the form of the rostrum, the high pre-anal carina, the large number of uropodal teeth, and the shape of the telson, this new species belongs to the *C. weberi* species group. In this group, it is most similar to *C. parvirostris* by its short curved-down rostrum and slender P2 carpus: 5.6–6.5 (vs. 6.0–7.4). However, it could be easily separated from *C. parvirostris* by lower numbers of dorsal and ventral teeth on the rostrum, respectively, 4–6 (vs. 8–10) and 0–1 (vs. 2). This new species is also similar to *C. keiensis* by its rostrum (lower numbers of dorsal and ventral teeth on the rostrum, respectively, 4–6 (vs. 2–13) and 0–1 (vs. 1–2)) and its relatively long stylocerite reaching to 0.90 times the length of the basal segment of antennular peduncle (vs. 0.92), but it could be easily distinguished by its longer P2 carpus 5.6–6.5 (vs. 3.5–4.5), and the size of the eggs 0.43–0.50 mm × 0.25–0.29 mm (vs. 0.39–0.42 mm × 0.24–0.25 mm).

Caridina lobocensis Cai, Choy & Ng, 2009

Figures 3D and 6.

- *Caridina lobocensis* Cai, Choy, and Ng, 2009: 68, Figures 2–4 [type locality: Tributary of Loboc River, Loboc (approx. 9°38.206' N, 124°1.807' E), Bohol Island, Philippines];
- ? *Caridina lobocensis*—de Mazancourt et al., 2019 [47]: 166, Figures 2–5.

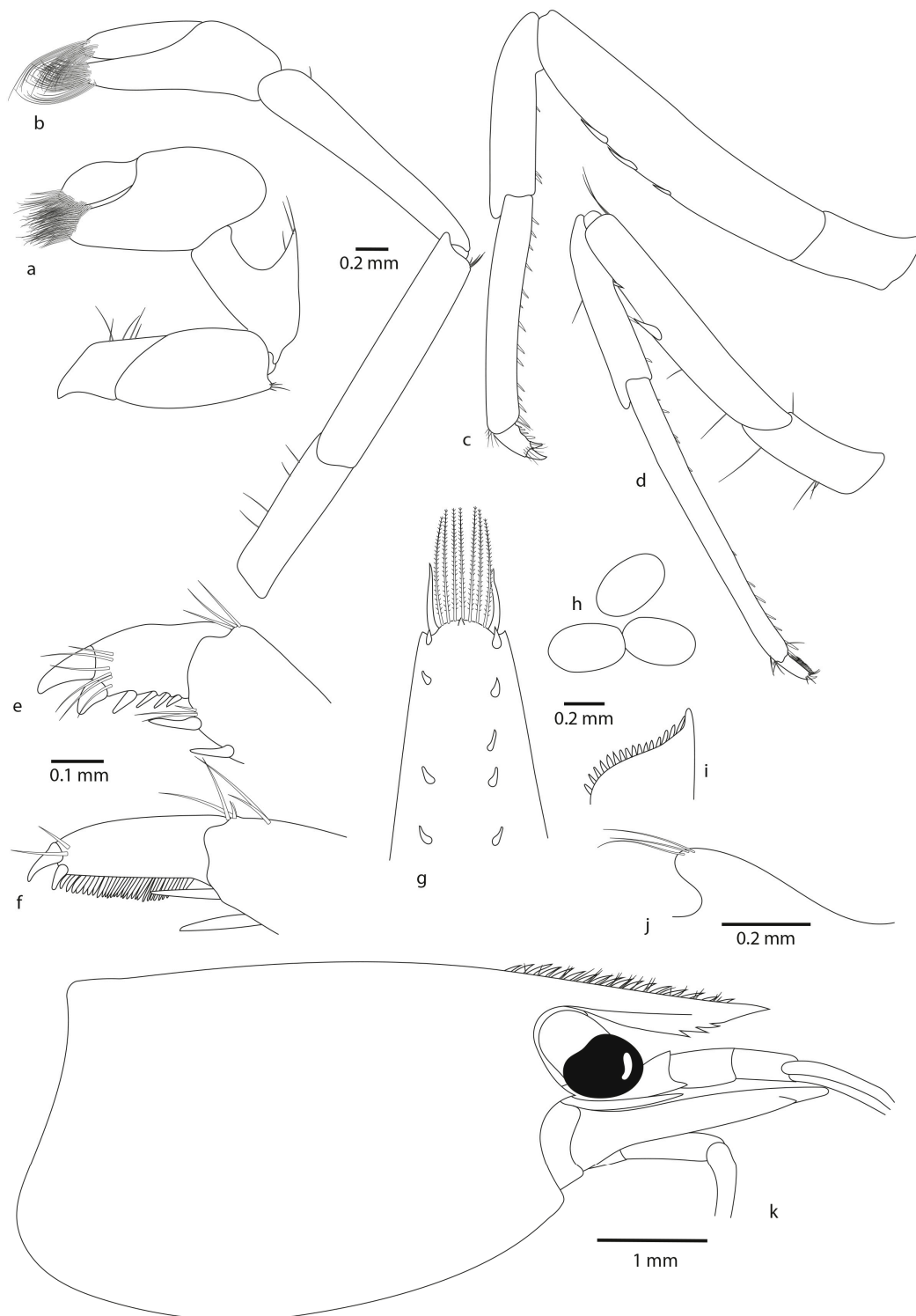


Figure 6. *Caridina lobocensis*. (a) first pereiopod; (b) second pereiopod; (c) third pereiopod; (d) fifth pereiopod; (e) dactylus of third pereiopod; (f) dactylus of fifth pereiopod; (g) telson; (h) undeveloped eggs; (i) uropodal diaeresis; (j) pre-anal carina; (k) cephalothorax. MNHN-IU-2024-459 (DNA: CA1555): a, b, j, and k; MNHN-IU-2024-455 (DNA: CA1552): d and f; MNHN-IU-2024-456 (DNA: CA1553): g, h, and i; MNHN-IU-2024-460 (DNA: CA1556): c and e.

Material examined

PALAU: Babeldaob Island. MNHN-IU-2024-455 (DNA: CA1552): 1 ♀ ovig. cl 4.6 mm and MNHN-IU-2024-456 (DNA: CA1553): 1 ♀ ovig. cl 4.2 mm, Ngerchokl river (Station 2), 07°36.527' N, 134°36.958' E, 27 February 2011, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. MNHN-IU-2024-457 (DNA: CA1056): 1 ♀ ovig. cl 4.2 mm and MNHN-IU-2024-458 (DNA: CA1554): 1 ♀ ovig. cl 4.3 mm, Tireloich river (Station 3), 07°41.417' N, 134°37.754' E, 28 February 2011, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. MNHN-IU-2024-459 (DNA: CA1555): 1 ♀ ovig. cl 4.3 mm, West Coast stream Northern Tip (Station 4), 07°43.056' N, 134°36.924' E, 28 February 2011, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. MNHN-IU-2024-460 (DNA: CA1556): 1 ♀ ovig. cl 4.4 mm, Ngermesakang river (Station 6), 75 m a.s.l., 07°32.484' N, 134°34.670' E, 1 March 2011, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. USNM 105446: 2 ♀, cl 4.3–4.8 mm and 1 juv. cl 2.3 mm, Station 122, 7°42.885' N, 134°37.386' E, 23 August 1955, Coll. F.M. Bayer. USNM 105447: 2 ♀ ovig., cl 4.4–5.0 mm and a juv. cl 3.0 mm, Station 241, 7°32.833' N, 134°35.766' E, 18 October 1955, coll. H.A. Fehlmann. USNM 105448: 1 ♀ ovig., cl 3.0 mm and 2 ♀, cl 3.0–3.9 mm, Arakitaoch river, cascade zone, 7°31.557' N, 134°34.202' E, 4 November 1956, coll. H.A. Fehlmann. **Koror Island:** USNM 105445: 2 ♀, 4.5–4.9 mm, Station 194, 7°20.421' N, 134°29.642' E, 30 September 1955, coll. H.A. Fehlmann.

THE PHILIPPINES. RMNH.CRUS.D.54659: 1 ♀ ovig., cl 7.1 mm, Barrio Mainit, Tayabas, Quezon Province, Luzon, 2 November 1986, coll. D.S. Bale.

Description

Cephalothorax. Suborbital angle indistinguishably fused with antennal spine. Pterygostomian margin rounded. Rostrum (Figure 6k): straight, short, 0.4–0.5 times length of cl, reaching middle of the third segment of antennular peduncle, armed with 12–17 teeth on dorsal margin, 1–3 of them situated on carapace behind orbital margin, ventral margin with 2–3 teeth.

Eyes well-developed, anterior end reaching to 0.7 times length of basal segment of antennular peduncle. Antennular peduncle 0.54 times as long as carapace. Anterolateral angle reaching 0.28 times length of the second segment, second segment slightly shorter than third segment. Stylocerite reaching to the basal segment of antennular peduncle.

Pereiopods. Epipods on first four pereiopods. P1 (Figure 6a): chela about 1.3–1.6 times as long as wide, movable finger 1.9–2.4 times as long as wide, 0.5–0.7 times length of palm; carpus 1.3–1.6 times as long as wide. P2 (Figure 6b) more slender and longer than first pereiopod with chela 2.2–2.8 times as long as wide: movable finger 3.5–5.0 times as long as wide, 1.3–1.7 times length of palm; carpus slender 4.3–5.5 times as long as wide. P3 (Figure 6c): stout, dactylus (Figure 6e) 3.7–4.4 times as long as wide (terminal spiniform seta included) terminating in two very strong claws with four-five spiniform setae on flexor margin; propodus 7.3–9.9 times as long as wide, 3.7–4.4 times as long as dactylus. P5 (Figure 6d): dactylus (Figure 6f) with two strong claws, 2.5–3.7 as long as wide with 31–33 spiniform setae on flexor margin; propodus 11.7–14.3 times as long as wide, 4.3–7.4 times as long as dactylus.

Abdomen. Third abdominal somite with moderately convex dorsal profile. Sixth abdominal somite 0.45 times as long as carapace, 1.3 times as long as fifth somite, and 0.77 times as long as telson.

Telson (Figure 6g) two times as long as wide, with four pairs of dorsal spinules and one pair of dorsolateral spinules; posterior margin without a median process, rounded with from seven to nine very long intermediate plumose setae longer than lateral ones.

Pl1 and Pl2: no males in our collected specimens. According to Cai et al. [50], “Endopod of male first pleopod subtriangular, half-length of exopod, appendix interna stout, exceeding end of endopod. Appendix masculina of male second pleopod 2/3 length of endopod, with appendix interna reaching base of distal one-third of appendix masculina”.

Uropodal diaeresis (Figure 6i) with 16–21 spinules.

Pre-anal carina (Figure 6j) elevated, without spine but with a few stiff setae.

Ovigerous females with eggs sized 0.37–0.43 mm × 0.22–0.27 mm (Figure 6h).

Habitat

This species is largely rheophile and prefers waters that are fresh and fast-flowing waters the lower to the higher courses.

Colour pattern

Unknown.

Distribution

This species has been found in Palau and the Philippines.

Remarks

Our specimens agree well with those described from Bohol Island (Philippines) by Cai et al. [50] in relation to their long stylocerite, their stout first pereopod, their short fingers, their third to fifth pereopods ending in two claws, and their egg size. The rostrum in our specimens seems shorter: reaching the middle of the third segment of antennular peduncle (vs. reaching slightly beyond end of antennular peduncle) and its pterygostomial margin is rounded (vs. pterygostomial margin subrectangular), but we consider these differences to be within intra-specific variability. This species is closely related to *C. buehleri* and *C. gueryi*, both recently re-described by de Mazancourt et al. [43], but they are clearly separated in our molecular analyses and they can be distinguished by its P1 chela 1.3–1.6 times as long as wide (vs. 2.2–2.3 for *C. buehleri* and 1.9–2.4 for *C. gueryi*), and by its P5 dactylus with two strong claws (vs. one strong claw for *C. buehleri* and *C. gueryi*). Its P2 carpus is 4.3–5.5 times as long as wide and its P5 propodus is 4.3–7.4 times as long as its dactylus (vs., respectively, 5.5–6.2 and 3.8–4.1 for *C. buehleri*). Its rostrum is armed with dorsal teeth, one–three of them situated on carapace behind orbital margin (vs. three–five for *C. gueryi*) and its P5 dactylus has 31–33 spiniform setae on its flexor margin (vs. 26–31 for *C. gueryi*).

Caridina typus species group

Diagnosis (from [43]): robust morphology with a straight rostrum, armed or not on the dorsal margin, without apical teeth, antennal spine fused with inferior orbital angle, antennular peduncle equal or more than half of carapace in length, pterygostomial margin blunt to rather narrowly rounded, stout walking legs, carpus of first pereopod excavated, short sixth abdominal somite (less than half of carapace length), high pre-anal carina with no spine or a small one, a great number of spinules on the uropodal diaeresis (>15), plumose terminal setae on the telson subequal to lateral ones or slightly longer, and a long subrectangular endopod of the first male pleopod with a short appendix on the subdistal outer margin.

Caridina typus H. Milne Edwards, 1837

Figure 3E

- *Caridina typus* H. Milne Edwards, 1837: 363 [type locality unknown].

Material examined

PALAU: Babeldaob Island. MNHN-IU-2018-3355 (DNA voucher: CA2015): 1 ♀ ovig. cl 5.2 mm; MNHN-IU-2018-3356 (DNA voucher: CA2016): 1 ♀ ovig. cl 4.5 mm; MNHN-IU-2018-3357 (DNA voucher: CA2017): 1 ♀ cl 5.0 mm and MNHN-IU-2018-3358 (DNA voucher: CA2018): 1 ♀ ovig. cl 5.5 mm, no locality data, February–March 2011, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. Ngerchokl river, 07°36.527' N, 134°36.958' E, 27 February 2011, M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois, observed only. Tireloich river, 07°41.417' N, 134°37.754' E, 28 February 2011, M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois, observed only. West coast unnamed stream, 07°43.056' N, 134°36.924' E, 28 February 2011, M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois, observed only.

FEDERATED STATES OF MICRONESIA: Pohnpei Island. Nanpil river (station 5), 06°56.683' N, 158°13.550' E, 5 m a.s.l.; Mahnd river, 14 March 2012, 107m a.s.l., 06°50.609' N, 158°17.212' E, observed only.

GUAM. ZMB 34613 (DNA: CA2791 and CA2792): two specimens, Ylig river, 13°23.589' N 144°45.636' E, 2 m a.s.l., January 2011, coll. D.C. Rogers, A. Farahi, and T. Jones. ZMB 34614 (DNA: CA2794 and CA2795): two specimens, Taguan river, January 2011, coll. D.C. Rogers, A. Farahi, and T. Jones.

Distribution

This species has a wide distribution in rivers of the Indo-West Pacific area ranging from South and East Africa to Japan, Fiji, and Australia.

Remarks

This species here reported from Palau and Guam is found in most of the Indo-Pacific region (from Madagascar to Fiji).

Caridina serratirostris species group

Diagnosis (from [43]): moderately robust morphology with a moderately short and straight rostrum (reaching end of antennular peduncle), armed with many dorsal teeth, at least six of them on the carapace, without apical teeth, the antennal spine ventral to the inferior orbital angle, a long antennular peduncle (about half the carapace length) with an unusually long stylocerite (reaching end of first segment of antennular peduncle), pterygostomian margin rounded, segments of walking legs very slender, sixth abdominal somite about half of carapace length, a small pre-anal carina sometimes bearing an acute spine, a great number of spinules on the uropodal diaeresis (>15), numerous, long, and plumose terminal setae on the telson, and a rounded endopod of the first male pleopod, without appendix interna.

Caridina cf. *serratirostris*

Figures 3H and 7.

Material examined

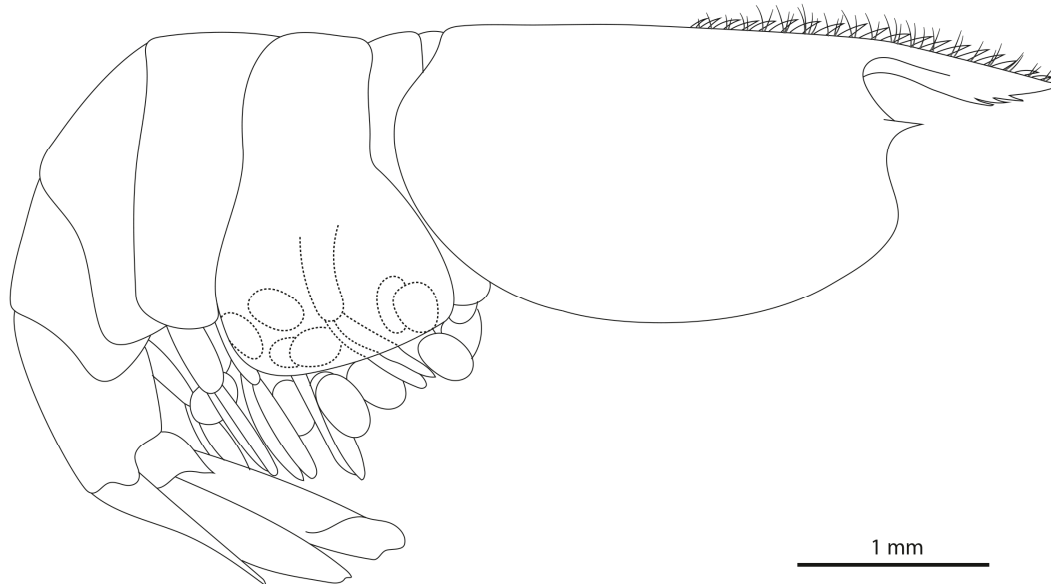


Figure 7. *Caridina* cf. *serratirostris*. Lateral view of the single ovigerous female, MNHN-IU-2024-461 (DNA: CA1245).

FEDERATED STATES OF MICRONESIA: Pohnpei Island. MNHN-IU-2024-461 (DNA: CA1245): 1 ♀ ovig. cl 2.5 mm, Nanpil river (station 3), 9 March 2012, 52 m a.s.l., 06°55.111' N, 158°12.878' E, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois.

Distribution

Reported only from Pohnpei Island.

Remarks

This species is distinct from all the others known in this group based on molecular data (minimum 16S p-distance: 14%), but the only specimen available is too damaged to provide a sufficient morphological description. Rostral formula: 19 (10)/3, rostrum 0.38 times as long as carapace length, egg size 0.40–0.43 mm × 0.23–0.26 mm (Figure 7).

Caridina rintelenorum sp. nov.

urn:lsid:zoobank.org:act:FF389D46-B517-4D59-9102-34638B8B62C2

Figures 3G, 8 and 9D.

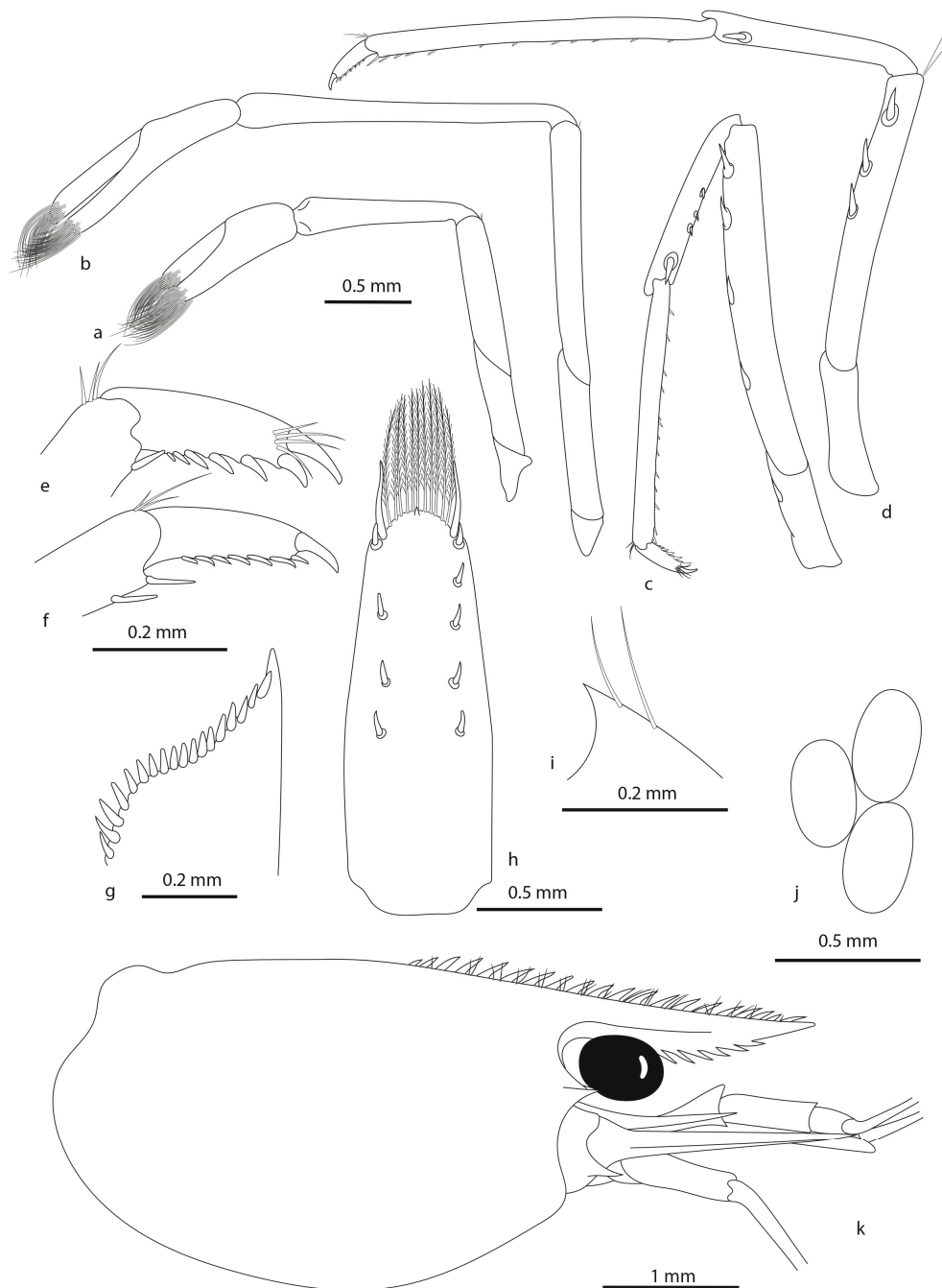


Figure 8. *Caridina rintelenorum* sp. nov. (a) first pereopod; (b) second pereopod; (c) third pereopod; (d) fifth pereopod; (e) dactylus of third pereopod; (f) dactylus of fifth pereopod; (g) uropodal diaeresis; (h) telson; (i) pre-anal carina; (j) undeveloped eggs; (k) cephalothorax. Holotype: MNHN-IU-2024-462 (DNA: CA1864): a–g and i–k. Paratype: MNHN-IU-2024-463 (DNA: CA2534): h.

Material examined

Type material

PALAU: Babeldaob Island. Holotype: MNHN-IU-2024-462 (DNA: CA1864): 1 ♀ ovig. cl 3.3 mm, Ngardmau river, waterfall, 07°35.482' N, 134°35.573' E, 2 March 2011, coll. M. Castelin, P. Gerbeaux, P. Keith, G. Marquet, and L. Taillebois.

Paratypes: RMNH.CRUS.D.16641: 1 ♀ ovig. cl 2.9 mm, stn. 122, Luhet river, Ollei village, Ngarchelong peninsula, 23 August 1955, coll. A. Fehlmann, George Vanderbilt Foundation; USNM 105450: 1 ♀ ovig., cl 3.0 mm and 1 juv. cl 2.0 mm, Station 122, 7°42.888' N, 134°37.383' E, 23 August 1955, coll. F.M. Bayer. USNM 172595: 1 ♂ cl 2.2 mm, 1 ♀ ovig. cl 2.6 mm and 1 juv. cl 1.9 mm, Ngerbekuu river, station 1NBK4-12, 1 June 1978, coll. G. Bright. USNM 172596: 1 ♀ ovig. cl 2.7 mm, Ngerbekuu river, station 1NBK4-11, 1 June 1978, coll. G. Bright.

SOLOMON ISLANDS. Isabel Island. MNHN-IU-2024-463 (DNA voucher: CA2534): 1 ♀ ovig. cl 2.9 mm, Hobolito river, 7°37.510' S, 158°32.434' E, 24 October 2019, coll. R. Causse, P. Keith, and C. Lord.

Comparative material

Caridina celebensis. **INDONESIA.** Paralectotype (lectotype designated in [51]), MNHN-IU-2015-1926: 1 ♀ ovig. cl 3.5 mm, Sulawesi, Luwu, river near Palopo, February 1889, coll. M. Weber. **SOLOMON ISLANDS: Kolombangara Island.** MNHN-IU-2018-2941: 1 ♀ ovig. cl 3.1 mm, Lodumoe river, 07°50.961' S, 157°04.320' E, 16 November 2015, coll. P. Keith, C. Lord, and G. Marquet. MNHN-IU-2018-2942: 1 ♀ ovig. cl 3.2 mm, same collection data as for preceding. MNHN-IU-2018-2943 (DNA: CA1518): 1 ♀ cl 3.5 mm, Munga river, 07°54.420' S, 156°57.932' E, 5 m a.s.l., 19 November 2015, coll. P. Keith, C. Lord, and G. Marquet. MNHN-IU-2018-2944: 1 ♀ ovig. cl 3.4 mm, Liva river, 08°03.863' S, 157°10.633' E, 14 m a.s.l., 11 November 2015, coll. P. Keith, C. Lord and G. Marquet. **Vella Lavella Island.** MNHN-IU-2018-2945: 1 ♀ ovig. cl 3.5 mm, Wariassi river, 29 October 2016, coll. P. Keith, and C. Lord. **VANUATU: Efate Island.** MNHN-IU-2018-2946 (DNA: CA1381): 1 ♀ cl 3.0 mm, Marona river, 17°33'51.860" S, 168°17'08.140" E, 5 m a.s.l., 9 November 2014, coll. A. Acou, G. Marquet, and M. Mennesson. MNHN-IU-2018-2947: 1 ♀ ovig. cl 3.4 mm, Mele river, 17°40.578' S, 168°15.462' E, 9 November 2014, 32 m a.s.l., coll. A. Acou, G. Marquet and M. Mennesson.

Description

Cephalothorax. Antennal spine ventral to inferior orbital angle. Pterygostomian margin rounded. Rostrum (Figure 8k): straight, 0.5–0.6 times length of cl, reaching to base of third segment of antennular peduncle, armed with 19–21 teeth on dorsal margin, 7–10 of them situated on carapace behind orbital margin, ventral margin with 5–8 teeth. Eyes developed, anterior end reaching to 0.65 times length of basal segment of antennular peduncle. Long antennular peduncle, 0.69 (♀) times as long as carapace. Second segment distinctly longer than third segment. Long stylocerite reaching beyond end of first segment of antennular peduncle.

Pereiopods. Epipods on first four pereopods. P1 (Figure 8a): chela about 2.1–3.1 times as long as wide, movable finger 2.5–5.2 times as long as wide, 0.9–1.6 times length of palm; carpus 3.4–4.9 times as long as wide. P2 (Figure 8b) more slender and longer than first pereopod, with chela 5.0–6.1 times as long as wide: movable finger 6.2–7.0 times as long as wide, 1.3–1.4 times length of palm; carpus slender, 8.0–12.3 times as long as wide. P3 (Figure 8c): slender, dactylus (Figure 8e) 3.7–4.0 times as long as wide (terminal spiniform seta included), with 6–9 spiniform setae on flexor margin including terminal one; propodus 12.1–14.1 times as long as wide, 3.8–4.5 times as long as dactylus. P5 (Figure 8d): dactylus (Figure 8f) 3.7–4.5 as long as wide, with 7–13 spiniform setae on flexor margin; propodus 15.5–17.4 times as long as wide, 4.1 times as long as dactylus.

Abdomen. Third abdominal somite with moderately convex dorsal profile. Sixth abdominal somite 0.45 times as long as carapace, 1.6 times as long as fifth somite, shorter than telson.

Telson (Figure 8h). 2.4 times as long as wide, with four pairs of dorsal spinules and one pair of dorsolateral spinules; posterior margin with a median process, rounded, with 7–12 very long intermediate plumose setae longer than lateral ones.

Male pleopods. No males.

Pre-anal carina (Figure 8i). High, with a spine.

Uropodal diaeresis (Figure 8g). With 14–19 spinules.

Eggs (Figure 8j). Size: 0.34–0.41 mm × 0.19–0.24 mm.

Habitat

This new species occurs in the lower to middle course of the rivers, sometimes in slightly brackish conditions.

Etymology

C. rintelenorum sp. nov. is named in honor of Kristina and Thomas von Rintelen (Museum für Naturkunde, Berlin, Germany) as an acknowledgement to their continuous support for the research of the first author and their years of study of atyid shrimps from South-East Asia.

Colour pattern

Body (Figure 8d) with more or less wide transverse bands of whitish, brownish, or dark color. Pereiopods with alternating bands of light and dark color.

Distribution

This species occurs in Palau and Solomon Islands (Isabel Island) and is expected to have a wider distribution in the region.

Remarks

This species is more similar to *C. celebensis* than to *C. serratirostris* by its shorter rostrum reaching to the base of the third segment of the antennular peduncle (vs. reaching beyond the end of the antennular peduncle), with fewer dorsal teeth, 19–21 (vs. 22–26); its longer P2 carpus, 8.0–12.3 as long as wide (vs. 8.3–10.9), and P2 chela 5.0–6.1 times as long as wide (vs. 3.7–5.1), but its shorter movable finger 1.3–1.4 times the length of the palm (vs. 1.7–1.9) and P5 propodus 15.5–17.4 times as long as wide (vs. 18.7–24.0) and 4.1 times as long as the dactylus (vs. 4.5–5.5).

This new species differs from *C. celebensis* by its shorter rostrum, being 0.5–0.6 times length of cl (vs. 0.6–0.9), and by its P5 propodus 4.1 times as long as the dactylus (vs. 3.4–3.9).

Caridina rubella Fujino & Shokita, 1975

Figure 3F.

- *Caridina rubella* Fujino and Shokita, 1975: 102, Figure 6 [type locality: Izaga Cave, Miyako Island, Ryukyu, Japan].—Shokita and Nishijima, 1976 [52]: 71.—Shokita, 1979 [53]: 203; 2003 [54]: 250, Figures 18F and 19I; 2006 [55]: 61.—Maciolek, 1983 [25]: 607.—Cai and Anker, 2004 [56]: 243, Figures 6 and 7.—Fujita and Shokita, 2005 [57]: 203.—Cai and Shokita, 2006 [51]: 2145, Figures 6F–J, 7 and 8.—Fujita, 2007 [58]: 92; 2018: 16.—Cai and Ng, 2009 [59]: 1094.—Weese et al., 2012 [60]: 109.—De Grave et al., 2022 [61]: 711, Figures 1 and 2.
- *Caridina* sp. 1—Marquet et al., 2003 [62]: 74.

Material examined

GUAM. ZMB 34612: 1 ♀, Fai Fai Cave, 13°31.700' N, 144°48.233' E, coll. D.C. Rogers.

Distribution

This species has a wide distribution in anchialine habitats in the Pacific: Japan (Ryukyu), Philippines (Bohol, Palawan, Panglao), Indonesia (Sulawesi), New Caledonia (Loyalty), Cook Islands, French Polynesia (Tahiti), Niue, Tonga (Tongatapu), Western Samoa (Upolu), Solomon Islands (Nggela Pile), and Guam.

Remarks

The single female specimen collected from Fai Fai Cave in Guam agrees well with the published descriptions of the species [51,61,63], having a rostral formula of 10 + 28/12 and a rostrum 1.19 times as long as the carapace. Interestingly, our sequence clusters with a 16S sequence of the short-rostrum morph of the species from Miyako Island which is thought to represent the “real” *C. rubella*, whereas the long-rostrum morph from the same area potentially represents an undescribed species [60]. Consequently, it appears that this species is morphologically variable, as recently illustrated by De Grave et al. [61], but probably hides cryptic species. A molecular study of this species from its whole range would be needed to clarify its status.

Caridina nilotica species group

Diagnosis (from [43]): slender morphology, with a mostly long rostrum (longer than the antennular peduncle) but variable, the antennal spine ventral to the inferior orbital angle, a long antennular peduncle (subequal to carapace length), segments of walking legs slender, a typical dorsal hump over the third abdominal somite, a long sixth abdominal somite (always more than half of carapace length), a small pre-anal carina sometimes bearing an acute spine, a moderate number of spinules on the uropodal diaeresis (<15), fewer, medium to short and terminal setae on the telson and a subtriangular endopod of the first male pleopod with or without an appendix on the subdistal outer margin or even placed at the distal end. An oblique red band on the cephalothorax is very characteristic.

Caridina appendiculata Jaliha & Shenoy, 1998

Figures 3I and 10A.

Caridina appendiculata Jaliha and Shenoy, 1998: 128 [type locality: River Bari (approx. 8°21.070' S, 120°10.928' E), Flores, Indonesia].—Cai and Ng, 2007 [64]: 1590.—Klotz et al., 2007 [65]: 7, Figure 3 (part), 4.—de Mazancourt et al., 2018 [66]: 1433, Figure 1, 4.; 2019 [47]: 166; 2020 [43]: 3, 78 (key), Figures 2H and 25C.—Short et al., 2019 [67]: 4, 15, Figure 7.—Hernawati et al., 2020 [68]: Figure 3.

- *Caridina gracilirostris*—De Man, 1892 [69]: 399 (part).—Holthuis, 1978 [70]: 35 (part);
- *Caridina* sp. *E*—Page et al., 2007 [21]: 648, Figures 2 and 3.—Cook et al., 2011 [71]: 278, Figure 3.

Material examined

PALAU: Babeldaob Island. MNHN-IU-2018-127 (DNA: CA1021): 1 ♀ ovig., cl 3.9 mm, small stream East Coast, near the estuary (Station 5), 07°29.909' N, 134°38.099' E, 2 March 2011, 0 m a.s.l., coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois.

FEDERATED STATES OF MICRONESIA: Pohnpei Island. MNHN-IU-2018-128, 1 ♀ ovig., cl 3.2 mm and MNHN-IU-2018-129, 1 ♀ ovig., cl 3.6 mm (DNA: CA1333); Nanpil river estuary, 5 m a.s.l., 06°56.609' N, 158°13.550' E, coll. P. Keith, P. Gerbeaux, G. Marquet, L. Taillebois, and M. Castelin, 13 March 2012; MNHN-IU-2018-130, 1 ♀ ovig., cl 3.0 mm (DNA: CA1330), MNHN-IU-2018-131, 1 ♀ ovig., cl 3.4 mm and MNHN-IU-2018-132, 1 ♀ cl 3.1 mm; unnamed river, estuary, 5 m a.s.l., 06°48.579' N, 158°12.639' E, coll. P. Keith, P. Gerbeaux, G. Marquet, L. Taillebois, and M. Castelin, 15 March 2012. MNHN-IU-2024-464 (DNA: CA1183), 2 ♀ ovig., cl 3.2–3.6 mm, Nanpil river estuary (Station 9), 06°56.609' N, 158°13.550' E; 13 March 2012; 5 m a.s.l., coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. MNHN-IU-2018-130, 1 ♀ ovig., cl 3.0 mm, 1 ♀, cl 3.1 mm, River 2, 15 March 2012, 5 m a.s.l., 06°48.579' N, 158°12.639' E, coll. M. Castelin, P. Keith, P. Gerbeaux, G. Marquet, and L. Taillebois. USNM 104882: 1 juv. cl 2.8 mm, south fork of Arakitaach river, station 170-A, 7°31.556' N, 134°34.199' E, 15 November 1956, coll. H.A. Fehlmann. USNM 172592: 4 ♀, cl 2.9–3.6 mm, Metengalakumer river, station 1MR4-08, 17 November 1977, coll. G. Bright. MNHN-IU-2018-127, 1 ♀ ovig., cl 3.9 mm (DNA: CA1021), small stream East Coast, near the estuary, 0 m a.s.l., 07°29.909' N, 134°38.099' E, 2 March 2011, coll. P. Keith, P. Gerbeaux, G. Marquet, L. Taillebois, and M. Castelin.

Distribution

C. appendiculata Jaliha and Shenoy, 1998 is known from Australia, Indonesia (Flores, Obira, and Sulawesi), Solomon Islands (Kolombangara, Isabel), Micronesia (Pohnpei), Palau, and Vanuatu (Aneityum, Efate, Epi and Santo) [66].

Habitat

All specimens were found in a typical brackish water environment (brackish water pool or colonizing the lower part of rivers, near the estuary).

Remarks

de Mazancourt et al. [66] redescribed this species in detail.

Caridina variabilis de Mazancourt, Marquet, Rogers & Keith, 2018

Figures 3K and 10C,D.

- *Caridina variabilis* de Mazancourt, Marquet, Rogers, and Keith, 2018b: 43, Figure 4 [type locality: Palau, Babeldaob Island, Tabecheding River, 07°27.169' N, 134°31.748' E].—de Mazancourt et al., 2018 [9]: 6, Figure 2; 2019 [47]: 167, Figures 2–5; 2020 [43]: 20, 31;
- *Caridina brachydactyla uncata* de Mazancourt, Marquet, Rogers, and Keith, 2018: 40 (nomen nudum);
- *Caridina nilotica* var. *brachydactyla*—Bouvier, 1925 [7]: 155 (part, specimens from Marianas);
- *Caridina weberi*—Leberer and Nelson, 2001 [19]: 389;
- *Caridina brachydactyla*—Bright, 1989 [23]: 35.—Leberer and Cai, 2003 [18]: 354;
- *Caridina mertonii*—Leberer and Cai, 2003 [18]: 354;
- *Caridina longirostris*—Leberer and Nelson, 2001 [19]: 389;

Material examined

See [9].

Distribution

This species occurs only in Guam and Palau [9].

Remarks

Holthuis (year unknown) named specimens from Palau, based on material collected by H. A. Fehlmann on the 30 October 1956 from Arakitaoh stream and deposited in USNM as *C. brachydactyla uncata* (“holotype” USNM 105430, “paratypes” USNM 105434) but never described or published this taxon. This species was previously confused with *C. brachydactyla* De Man, 1908 or *C. mertonii* Roux, 1911, depending on its variable morphology (see [9]).

Caridina variabilirostris de Mazancourt, Marquet & Keith, 2018

Figures 3J and 10B.

- *Caridina variabilirostris* de Mazancourt, Marquet, and Keith, 2018: 7, Figures 3 and 4 [type locality: Federated States of Micronesia, Pohnpei Island, Nanpil river, 06°54.252' N, 158°11.491' E, 180 m a.s.l.].—de Mazancourt et al., 2019 [47]: 167, Figures 2–5; 2020 [43]: 20, 30;
- *Caridina brachydactyla*—Maciolek and Ford, 1987 [13]: 628;
- *Caridina vitiensis*—Maciolek and Ford, 1987 [13]: 628;
- *Caridina longirostris*—Maciolek and Ford, 1987 [13]: 628;
- *Caridina* sp.—de Mazancourt et al., 2017 [40]: 249, Figures 2 and 5;
- *Caridina weberi*—Maciolek and Ford, 1987 [13]: 628.—Nelson et al., 1996 [14]: 11.—Buden et al., 2001 [15]: 257.—Page et al., 2007 [21]: 649, 650, Figures 2 and 3.—von Rintelen et al., 2008 [72]: 2248, Figure 4.—Benstead et al., 2009 [16]: 459.—de Mazancourt et al., 2017 [40]: 226, Figure 4;
- *Caridina nilotica* var.? *wycki*—Roux, 1925 [12]: 149.

Material examined

See [8].

Distribution

This species is known from Pohnpei only thus far [8].

Remarks

This species used to be confused with *C. brachydactyla* De Man, 1908 or *C. mertoni* Roux, 1911 (see [8]).

Caridina gracilirostris species group

Diagnosis (from [44]): slender morphology with a very long and upcurved rostrum (twice the carapace length), armed with few dorsal teeth (fewer than 10), apical teeth present, the antennal spine ventral to the inferior orbital angle, a long antennular peduncle (more than 0.70 times as long as carapace), pterygostomian margin rounded, segments of walking legs slender, a typical dorsal hump over the third abdominal somite, a long sixth abdominal somite (always more than half of carapace length), a small pre-anal carina bearing or not an acute spine, few spinules on the uropodal diaeresis (>10), very few short terminal setae on the telson, and endopod of the first male pleopod subtriangular mostly without an appendix but, when it is present, on the subdistal outer margin, it reaches beyond distal end of endopod by a short length.



Figure 9. Coloration in life. (A) *Atyopsis spinipes* from Pohnpei (P. Keith); (B) *Atyoida chacei* sp. nov. from Palau (H. Ketebengang, inaturalist.org); (C) *Caridina ponapensis* sp. nov. from Pohnpei (P. Gerbeaux); (D) *Caridina rintelenorum* sp. nov., paratype MNHN-IU-2024-463 from Isabel, Solomon Islands (P. Keith).

***Caridina gracilirostris* De Man, 1892**

- *Caridina gracilirostris* De Man, 1892: 399, pl. 25, Figure 31a–d [type locality: River near Maros (approx. 5°0.594' S, 119°35.381' E), Sulawesi (Celebes), Indonesia];
- *Caridina gracilirostris*—Bright, 1979 [17]; 1989 [23]: 34, Table 1.

Material examined

PALAU: Babeldaob Island. USNM 104882: 1 ♂, cl 4.2 mm, 3 ♀ ovig., cl 4.6–5.7 mm and 1 juv. cl 2.8 mm, south fork of Arakitaach river, station 170-A, 7°31.556' N, 134°34.206' E, 15 November 1956, coll. H.A. Fehlmann. USNM 172593: 1 ♂, cl 3.1 mm, Metengalakumer river, Station 1MR4-03, 17 November 1977, coll. G. Bright. USNM 172594: 1 ♂, cl 3.5 mm, Ngerhekuu river, station 1NBK4-10, 1 June 1978, coll. G. Bright.

Distribution

C. gracilirostris is widely distributed in the tropical and subtropical Indo-Pacific region: Indonesia, the Philippines, India, Australia, the Solomon Islands, and Palau [43].

Habitat

In the lower course of streams under marine influence, very often in brackish water.

Remarks

de Mazancourt et al. [43] redescribed this species in detail.



Figure 10. (A) *Caridina appendiculata* from Pohnpei (P. Keith); (B) *Caridina variabilirostris* from Pohnpei (P. Gerbeaux); (C) *Caridina variabilis* from Guam (M. Sasazuka, One's habitat); (D) *Caridina variabilis* from Babeldaob (P. Keith).

4. Discussion

In the *Caridina nilotica* species group, *C. variabilis* from Palau and Guam is distinct from *C. variabilirostris* endemic to Pohnpei. The same biogeographic pattern appears in the

C. weberi species group: *C. lobocensis* from Palau and Bohol is distinct from *C. ponapensis* sp. nov., which is endemic to Pohnpei. For the other species of Atyidae with wide distribution in the Indo-Pacific or Pacific Ocean (*Atyopsis spinipes*, *Caridina typus*), the species occur in all Micronesian islands.

Atyopsis spinipes was reported from Guam [18] and Kosrae [16] but not from Yap [23]. According to Bright [23], “*Atyopsis* and *Atyoida* which were very abundant in both Palau and Pohnpei, were conspicuously absent from Yap. The smaller, mostly intermittent streams of Yap may not have adequate habitat to support these two genera, which are found only in permanently flowing, swift streams, especially in cascade areas”.

Caridina typus was reported from Guam [18], from Yap [23], and from Kosrae [16].

Caridina serratiostris was reported by Leberer and Nelson, 2001 from Guam and Yap [23]. Surprisingly, this species was assigned to *C. mertoni* in Guam [18]. Based on the present study, *C. serratiostris* does not occur in Micronesia, but two related species, *C. rintelenorum* sp. nov. in Palau and the undescribed *C. cf. serratiostris* in Pohnpei, do.

In the present work, we make the assumption that *C. brachydactyla* reported from Yap [23] is *C. variabiliostris*, that *C. weberi* from Kosrae [16] is *C. ponapensis* sp. nov., and that *C. weberi* from Guam [18] is *C. lobocensis*.

The different geological histories between Pohnpei, Palau, Guam, and Yap (Figure 11) would explain our hypotheses. Pohnpei and Kosrae islands lie on the Pacific plate and were not only the remnants of a hotspot trace but were also produced in a fracture-induced subduction-related tectonic environment and aged as being from 14.8 to 0.1 My and 2 to 1 My, respectively [2]. On the contrary, Yap Islands, aged as being from 7.6 to 10.9 My [1] do not have the same geological history: they form an island arc system on the eastern convergent margin of the Philippine Sea Plate (PSP) and are connected to the Palau island arc (including the high island Babeldaob aged as being from 30 My) in the South and the Izu-Mariana arc system (including the high island Guam aged from 43.8 to 13.5 My [73]) in the North. Tectonically, Palau and Guam lie on the PSP and Pohnpei and Kosrae on the Pacific Plate, east of the Mariana–Yap–Palau trench system along the Caroline ridge (Figure 11).

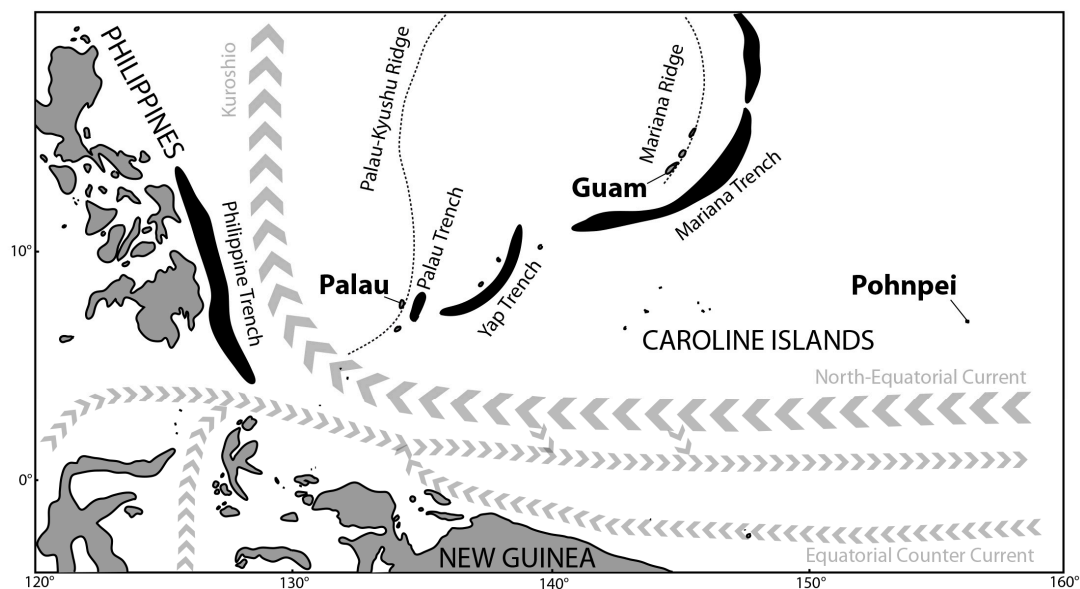


Figure 11. Main surface currents (arrows), trenches (in black), and ridges (dotted lines) in the Micronesian area (from [2]).

Furthermore, several authors have suggested that deep-sea trenches in conjunction with oceanic currents may constitute biogeographic genetic breaks for species with a marine planctonic phase. For example, Mennesson [74] explains the biogeographic genetic break between South Pacific islands (Futuna and Samoa) and French Polynesian islands by a

combination of parameters, such as oceanic currents and/or deep-sea trenches of Tonga and Kermadec. Indeed, Palau, Yap, and Guam are isolated, respectively, by the Palau trench, Yap trench, and Mariana trench from Pohnpei and Kosrae. The isolation of these islands is reinforced by two strong currents: the westward North Equatorial Current and the eastward Equatorial Counter Current (Figure 11). This isolation can explain a higher rate of endemism for Sicydiinae (four species [75]) from the relatively young island of Pohnpei compared to Palau (zero species) and Guam (zero species), which are significantly older.

On the other hand, despite the long distance (1296 km) between Babeldaob and Guam, de Mazancourt et al. [40] showed that some haplotypes are shared, and thus, genetic exchanges occur between populations from these two islands. These genetic exchanges are contrasting with results from the reef fish fauna. Indeed, according to Kulbicki et al. [76], “the reef fish fauna of Palau (1284 taxa) belongs to the Melanesian province (PNG, New Caledonia, Fiji, Vanuatu, Solomon Islands) and not to Micronesia (Caroline Islands, Marshall Islands, Marianas) or West Pacific (the biogeographical province which includes the nearby Philippines despite the geographical vicinity)”. We can suppose that the larval migration of amphidromous species may be different (e.g., active or passive swimming, differences in depth during the migration, etc.) from that of the marine reef species. This might explain the presence of *C. lobocensis* in both the Philippines and Palau, and its presence would be expected in Guam. It is the same case in freshwater gobies, for example with *Smilosicyopus fehlmanni* (Parenti and Maciolek, 1993) described from Palau, not occurring in Guam but reaching Papua, Australia, the Solomon Islands, and from Vanuatu to New Caledonia [77]. In contrast, *Smilosicyopus leprurus* (Sakai and Nakamura, 1979) described from Ishigaki Island (Japan) occurs from Palau [26] and Guam [78] to Papua and Australia [77]. *Sicyopus zosterophorus* (Bleeker, 1857) described from Bali occurs in Palau [79] and Guam.

Key for studied species:

- 1.1 Pereiopods P1 and P2 carpus identically shaped.2
- 1.2 Pereiopods P1 and P2 carpus differently shaped; P2 carpus is more elongated than that of P1.3
- 2.1 Cephalothorax anterior border bearing a strong spine; straight rostrum rounded at its extremity with 2 to 6 small ventral teeth. *Atyopsis spinipes*
- 2.2 Cephalothorax anterior border acute bearing no spine; curved rostrum with 0 to 4 small ventral teeth. *Atyoida chacei* sp. nov.
- 3.1 Eyes with cornea reduced to a small dark spot. *Caridina rubella*
- 3.2 Eyes with cornea normally developed.4
- 4.1 Teeth absent on dorsal margin of rostrum. *Caridina typus*
- 4.2 More or less abundant teeth present on dorsal margin of rostrum.5
- 5.1 Long stylocerite reaching or exceeding the first article of the antennal peduncle.6
- 5.2 Short stylocerite, failing to reach the first article of the antennal peduncle.8
- 6.1 Dorsal border of rostrum with 1–3 teeth located on the cephalothorax, posterior to the eye; P1 carpus 1.3–1.6 as long as wide. *C. lobocensis*
- 6.2 Dorsal border of rostrum with 7–10 teeth located on the cephalothorax, posterior to the eye; P1 carpus 3.4–4.9 as long as wide.7
- 7.1 Rostrum reaching to the base of the third segment of the antennular peduncle with 19–21 dorsal teeth *C. rintelenorum* sp. nov.
- 7.2 Rostrum reaching beyond the end of the antennular peduncle with 21–26 dorsal teeth. *C. cf. serratirostris*
- 8.1 Short rostrum, curved downwards, 0.2–0.3 of cl, armed with 4–6 teeth on dorsal margin, 0 of them situated on carapace behind orbital margin. *C. ponapensis* sp. nov.
- 8.2 Relatively long rostrum, 0.6–2.1 of cl, armed with 5–26 teeth on dorsal margin, 0–4 of them situated on carapace behind orbital margin.9
- 9.1 Uropodal diaeresis with 6–10 spiniform setae and a very long and upcurved rostrum with 5–9 dorsal teeth, widely spaced. *C. gracilirostris*

- 9.2 Number of spiniform setae on uropodal diaeresis 8–15 and a long or short rostrum with 8–26 dorsal teeth, closely set10
- 10.1 Pre-anal carina with a prominent finger-like backward striking tooth.*C. appendiculata*
- 10.2 Pre-anal carina unarmed.11
- 11.1 P5 dactylus with a single terminal spine and a short distal propodus seta; posterior margin of the telson with intermediate setae longer or equal than lateral ones.*C. variabilirostris*
- 11.2 P5 dactylus with two strong distal spines and a very long distal propodus seta; posterior margin of the telson with intermediate setae shorter or equal than lateral ones.*C. variabilis*

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d16040200/s1>, Table S1: List of sequences included in the phylogenetic analysis.

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