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Revision of the species of *Caridina* (Decapoda: Atyidae) from the Western Indian Ocean islands with description of a new species

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Abstract. We provide an updated checklist and an identification key of the species of *Caridina* living in freshwater habitats of the Western Indian Ocean islands, including the Seychelles, the Comoros, Mayotte, La R union and Mauritius. We list six species including one new for science: *Caridina mauritii*, *Caridina spathulirostris*, *Caridina similis*, *Caridina natalensis*, *Caridina typus* and *Caridina henriettae* sp. nov. Molecular and morphological evidence led us to consider *Caridina richtersii* as a junior synonym of *C. spathulirostris*. Due to different life histories, some species are endemic to their island or archipelago, like *C. mauritii* and *C. spathulirostris*, endemic to Mauritius, or *C. similis* endemic to the Seychelles, whereas others have a wider distribution in the Western Indian Ocean like *C. natalensis* or *C. henriettae* sp. nov. or have an Indo-West Pacific distribution like *C. typus*.

Keywords. Integrative taxonomy, morphology, 16S, amphidromy, endemic.

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Introduction

Comoros, Seychelles and Mascarenes are three archipelagos in the Southwest of the Indian Ocean (Fig. 1). The Comoros archipelago, equidistant from the African continent and Madagascar (around 300 km), includes the islands of Grande Comore, Anjouan, Moh li and Mayotte. The Mascarene archipelago includes three main islands: La R union, Mauritius and Rodrigues. The Seychelles archipelago, comprising 115 islets, includes four main islands with small rivers or swamps: La Digue, Mah , Praslin and Silhouette.

Between 1996 and 2013, rivers of several South West Indian Ocean (SWIO) islands were surveyed for atyid freshwater shrimps (Crustacea: Decapoda: Caridea) during field trips conducted by the Muséum national d'Histoire naturelle (MNHN) in the Mascarene archipelago (La Réunion, Mauritius and Rodrigues; see Keith *et al.* 1999, 2006), in Comoros (Anjouan, Mohéli) and Mayotte (see Keith *et al.* 2006) and in Seychelles (La Digue, Mahé, Praslin and Silhouette; see Keith *et al.* 2006). Keith *et al.* 2006 reported seven species of *Caridina* in the SWIO islands, namely *Caridina longirostris* H. Milne-Edward, 1837, *C. mauritii* Bouvier, 1912, *C. richtersi* Thallwitz, 1891, *C. serratiostris* De Man 1892, *C. similis* Bouvier, 1904, *C. spathulirostris* Richters, 1880 and *C. typus* H. Milne-Edwards, 1837. More recently, in La Réunion and Mayotte, 'Ocea Consult' conducted yearly inventories to monitor the aquatic communities. In Seychelles, since 2020, the MNHN and the NGO Gaea conduct baseline surveys and annual biodiversity inventories of fish, micro- and macro-invertebrates in 15 rivers including the collection of genetic materials. These studies led to the discoveries of new occurrences of species at several sites and have improved our knowledge on the freshwater shrimps in the SWIO.

The purpose of this study is to provide an updated checklist of the species of *Caridina* from the SWIO by using an integrative taxonomic approach to assess the validity of the species listed previously and check their geographical distributions in our study area.

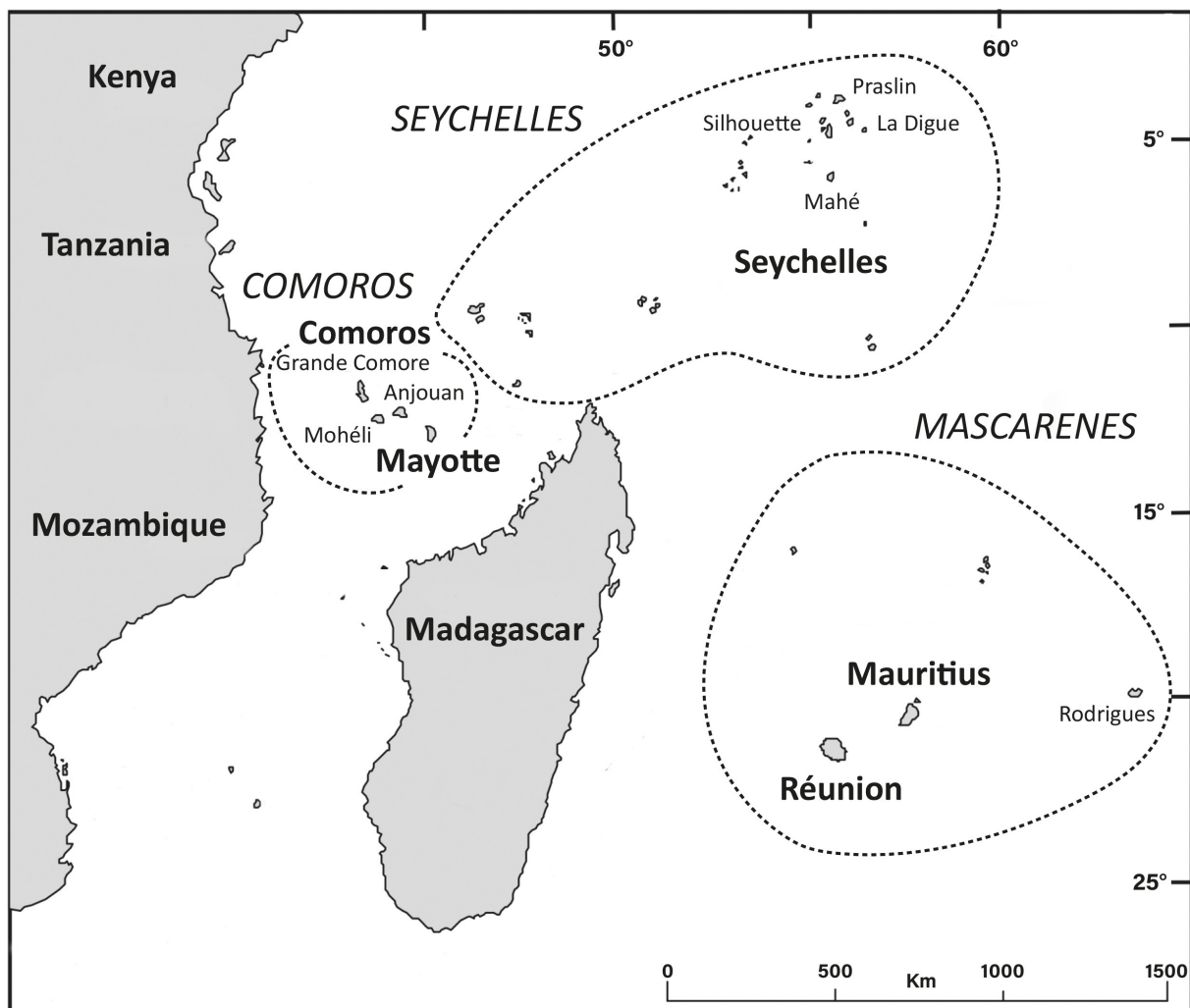


Fig. 1. Map of the South West Indian Ocean with its main archipelagos (dashed lines) and islands where *Caridina* H. Milne Edwards, 1837 were found (modified from Mulochau *et al.* 2014).

Material and methods

Sampling

Specimens from SWIO were collected by electrofishing (portable Dekka 3000 electric device, Germany or SAMUS 1000, Poland: <http://www.electro-fisher.net/>) or by hand. All material preserved in 75–95% ethanol has been deposited in the collections of the Muséum national d'Histoire naturelle in Paris (MNHN). Specimens were measured electronically under a stereo microscope using LAS X software (Leica).

DNA extraction, amplification and sequencing

DNA was isolated from abdominal tissues using the semi-automatic Eppendorf ep-Motion 5075 robot following the NucleoSpin 96 Tissue Core (Macherey-Nagel) protocol. Fragments of the mitochondrial marker 16S rRNA (~ 510 bp) were amplified using the pair of primers 16Sar-Lmod (TAC TTC TGC CTG TTT ATC AAAAA)/16Sbmod (GGT CTG AAC TCA AAT CAT GTAAA) (de Mazancourt *et al.* 2019a). 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 (MP Biomedicals). 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 (16S) 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 insure the accuracy of base calls. Chromatograms were viewed and edited using Geneious ver. 8 software (<http://www.geneious.com/>) (Kearse *et al.* 2012). All sequences are deposited in GenBank (Numbers PQ963381 to PQ963410, see Table 1).

Molecular analyses

DNA sequences were aligned using MEGA11 software (Tamura *et al.* 2021) with Muscle algorithm (Edgar 2004). Using Bayesian information criterion in jModelTest (Guindon & Gascuel 2003; Darriba *et al.* 2012) we retained the GTR + G + I model. Best-scoring ML trees were estimated using RAxML HPC2 ver. 8.2.10 (Stamatakis 2006) and best-scoring Bayesian Inference (BI) trees were estimated using MrBayes ver. 3.2.7 (Ronquist & Huelsenbeck 2003), both methods implemented in CIPRES 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 implemented in the Cyber Infrastructure for Phylogenetic Research (CIPRES) portal ver. 3.1. (<https://www.phylo.org>; Miller *et al.* 2010). One hundred independent searches, each starting from distinct random trees, were conducted. Robustness of the nodes was assessed using non-parametric bootstrapping (Felsenstein 1985) with 1000 bootstrap replicates. For the analysis, we generated 30 new 16S sequences from specimens collected during the authors' field trips, to which were added 24 sequences retrieved from GenBank for species occurring in the SWIO and/or closely related species to support the morphological comparisons (Table 1).

Morphological study

The rostrum, the cephalothorax, the pereopods 1–3 and 5 and the abdomen were observed using a stereo microscope. The proportions of the various joints of the appendages were measured using microphotographs and the LAS X software (Leica). Drawings were made using the “Digital Inking” method (Coleman 2003, 2006) by tracing vectorial paths on high-resolution photographs using a vector graphics software.

Table 1 (continued on next page). List of specimens included in the molecular analysis.

Species	Locality	Collection number	DNA voucher	Type status	16S sequence	Reference	
<i>Atyoida serrata</i> Bate, 1888	La Réunion		CA2948		PQ963394	this study	
			CA3042		PQ963401	this study	
			CA3043		PQ963402	this study	
			CA3064		PQ963409	this study	
<i>Caridina spathulirostris</i> Richters, 1880	Mauritius	MNHN-2025-125	CA2165		PQ963389	this study	
		MNHN-2025-126	CA2166		PQ963390	this study	
		MNHN-2025-127	CA2167		PQ963391	this study	
<i>Caridina similis</i> Bouvier, 1904	Seychelles	MNHN-2025-130	CA1854		PQ963384	this study	
		MNHN-2025-131	CA1855		PQ963385	this study	
		MNHN-2025-132	CA1856		PQ963386	this study	
		MNHN-2025-133	CA1857		PQ963387	this study	
<i>Caridina natalensis</i> De Man, 1908	South Africa	MNHN-IU-2018-63	CA2080		OR088398	de Mazancourt <i>et al.</i> 2023	
		MNHN-IU-2018-61	CA2079		MH644428	de Mazancourt <i>et al.</i> 2019a	
	Madagascar		CA1074		OR088348	de Mazancourt <i>et al.</i> 2023	
			CA1075		OR088349	de Mazancourt <i>et al.</i> 2023	
	Mayotte		CA1077		OR088350	de Mazancourt <i>et al.</i> 2023	
			CA1079		OR088351	de Mazancourt <i>et al.</i> 2023	
	Comoros	MNHN-IU-2018-78	CA1343		MH644416	de Mazancourt <i>et al.</i> 2019a	
		MNHN-IU-2018-77	CA1344		MH644417	de Mazancourt <i>et al.</i> 2019a	
	Seychelles		CA1116		OR088365	de Mazancourt <i>et al.</i> 2023	
			CA1117		OR088366	de Mazancourt <i>et al.</i> 2023	
	Mauritius	MNHN-IU-2017-1451	CA2157		OR088418	de Mazancourt <i>et al.</i> 2023	
		MNHN-IU-2017-1452	CA2158		OR088419	de Mazancourt <i>et al.</i> 2023	
		MNHN-IU-2017-1453	CA2159		OR088420	de Mazancourt <i>et al.</i> 2023	
		MNHN-IU-2017-1454	CA2160		OR088421	de Mazancourt <i>et al.</i> 2023	
	<i>Caridina serratirostris</i> De Man, 1892	Solomon	MNHN-IU-2018-2927	CA1351		MT303939	de Mazancourt <i>et al.</i> 2020
			MNHN-IU-2018-2931	CA1523		MT303940	de Mazancourt <i>et al.</i> 2020
<i>Caridina henriettae</i> sp. nov.	Seychelles	MNHN-2025-156	CA1491	paratype	PQ963382	this study	
		MNHN-2025-157	CA1492	paratype	PQ963383	this study	
		MNHN-IU-2015-1932	CA2026	paratype	PQ963388	this study	

Table 1 (continued).

Species	Locality	Collection number	DNA voucher	Type status	16S sequence	Reference	
<i>Caridina typus</i> H. Milne Edwards, 1837	La Réunion	MNHN-2025-154	CA2998	paratype	PQ963396	this study	
		MNHN-2025-155	CA2999	paratype	PQ963397	this study	
		MNHN-2025-151	CA3000	paratype	PQ963398	this study	
		MNHN-2025-143	CA2417	paratype	PQ963392	this study	
		MNHN-2025-144	CA2418	paratype	PQ963393	this study	
		MNHN-2025-145	CA2949	paratype	PQ963395	this study	
		MNHN-2025-148	CA3065	paratype	PQ963410	this study	
		MNHN-2025-146	CA3038	paratype	PQ963400	this study	
	Mauritius	OUMNH.ZC-2010-22-0001				KY069380	Bernardes <i>et al.</i> 2017
						KY069381	Bernardes <i>et al.</i> 2017
						KY069382	Bernardes <i>et al.</i> 2017
		La Réunion	MNHN-2025-135	CA3054		PQ963403	this study
			MNHN-2025-136	CA3058		PQ963404	this study
			MNHN-2025-137	CA3059		PQ963405	this study
			MNHN-2025-138	CA3060		PQ963406	this study
			MNHN-2025-139	CA3063		PQ963408	this study
			ZMBunid1252			KY069434	Bernardes <i>et al.</i> , 2017
		Australia	AM-P21882			DQ478562	Page <i>et al.</i> 2007
	Vanuatu	GU-721			DQ478563	Page <i>et al.</i> 2007	
	Madagascar	MNHN-IU-2018-2829	CA1038		MT303907	de Mazancourt <i>et al.</i> 2020	
		MNHN-IU-2018-2831	CA1039		PQ963381	this study	
	South Africa	MNHN-IU-2018-2844	CA2090		MT303906	de Mazancourt <i>et al.</i> 2020	
	Mayotte	MNHN-IU-2025-134	CA3027		PQ963399	this study	

Results

Molecular analyses

Phylogenetic analyses of the 16S marker (Fig. 2) allowed to recognize 7 different clades including 6 from the SWIO, all of them being strongly supported in both analyses (Bayesian PP > 0.95 and ML bootstraps > 92). Three species complexes can be identified, all with very strong statistical support values (PP = 1; B = 100).

Morphological study

Measures and observations made on the specimens allowed us to confirm the molecular results in recognizing the clades as five different species of *Caridina* in the SWIO, including one new for science (see hereafter). We couldn't get any sequence for *C. mauritii* due to the lack of fresh material, but its morphology is different enough to still be considered distinct from the other species. A key is provided at the end of the paper.

Taxonomy

Class Malacostraca Latreille, 1802
 Order Decapoda Latreille, 1802
 Family Atyidae De Haan, 1849
 Genus *Caridina* H. Milne Edwards, 1837

***Caridina nilotica* species group**

Diagnosis

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 mauritii* Bouvier, 1912**

Caridina Mauritii Bouvier, 1912a: 298.

Caridina Mauritii – Bouvier 1913a: 464 (key); 1914: 699; 1925: 210, figs 464–469.

Caridina mauritii – Costa 1980: 690. — Keith *et al.* 2006: 52.

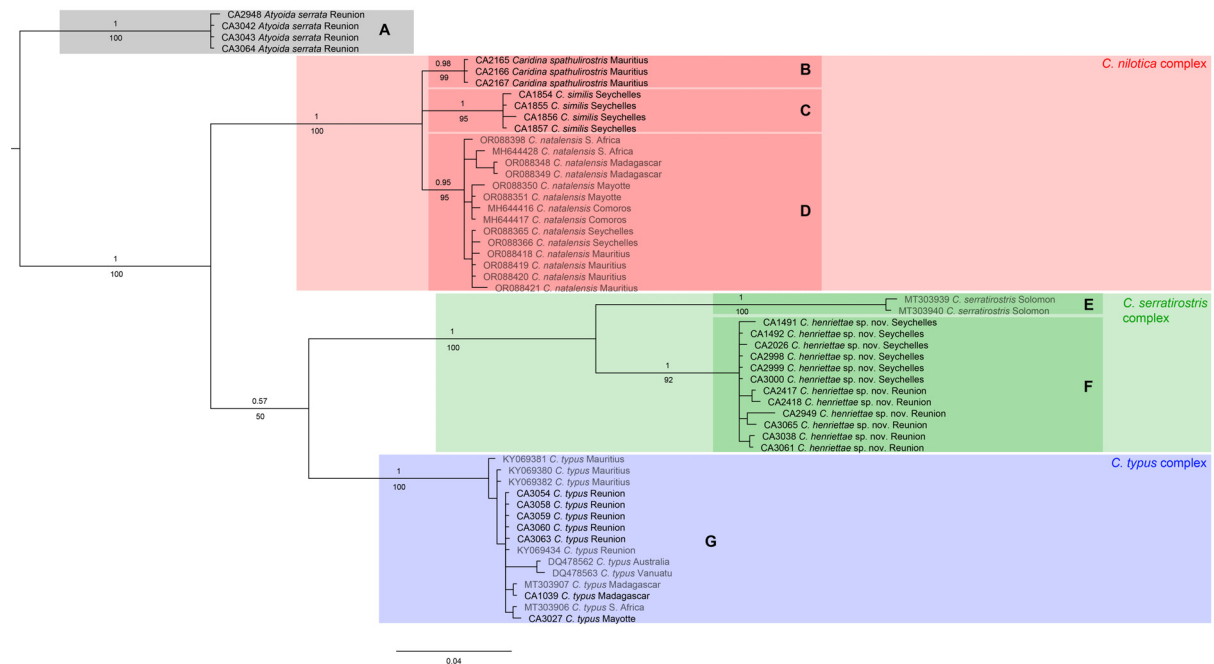


Fig. 2. Bayesian inference phylogenetic tree obtained from the 16S marker. Numbers above branches represent Bayesian posterior probabilities, numbers under branches are Maximum Likelihood bootstraps. Letters indicate clades recognized as valid species and colored boxes are species complexes.

Type locality

Near Port-Louis, Mauritius.

Material examined

No material examined.

Distribution

Endemic to Mauritius.

Habitat

Freshwater.

Remarks

This small species seems rare and a DNA barcode sequence would be needed to complete our sampling.

Caridina natalensis De Man, 1908

Figs 2D, 5B

Caridina nilotica var. *natalensis* De Man, 1908: 262, pl. 20 fig. 3.

Caridina longirostris – Richters 1880: 162–163. — Holthuis 1965: 20–23, fig. 6. — Keith *et al.* 2006: 50. — Bouchard *et al.* 2013: 9.

Caridina wycki – Ortmann 1894a: 11.1894b: 405 (part: specimens from East Africa and Dar-es-Salaam) (incorrect spelling).

Caridina wyckii – Weber 1897: 168 (part). — Richters 1880: 386 (part). — Lenz 1905: 385.

Caridina nilotica var. *brachydactyla* – Lenz 1910: 568. — Bouvier 1925: 155, figs 321–322. — Roux 1929: 303.

Caridina nilotica var. *gracilipes* – Lenz 1910: 568.

Caridina nilotica var. *natalensis* – Lenz 1912: 5. — Bouvier 1925: 154, fig. 320. — Barnard 1950: 655 (key). — Richard & Clark 2010: 317. — Klotz & De Grave 2015: 12.

Caridina brachydactyla brachydactyla – Costa 1980: 673.

Caridina brachydactyla – Bouchard *et al.* 2013: 9.

Caridina natalensis – de Mazancourt *et al.* 2019a: 379, figs 1–2, 3a–d; 2019b: 166, figs 2–5.

Caridina umtatensis – Wood *et al.* 2019: 205, fig. 3.

Not *Caridina africana* f. *natalensis* Bouvier, 1925: 214 (= *Elephantis jaggeri*).

Not *Caridina natalensis* – Richard & Clark 2009: 22, figs 7–8. — Castelin *et al.* 2013: 577 (= *Elephantis jaggeri*).

Type locality

Umgeni River, Durban, Natal, South Africa.

Material examined

See de Mazancourt *et al.* 2019a.

Distribution

Comoros (Anjouan, Mohéli), Mayotte, Seychelles (La Digue, Mahé, Praslin and Silhouette), Mauritius, La Réunion(?), Madagascar, South Africa, Tanzania and Kenya.

Habitat

Freshwater in the lower course of rivers.

Remarks

This species is easily identified by its rostrum rather constantly long, reaching well beyond scaphocerite.

***Caridina spathulirostris* Richters, 1880**
Figs 2B, 5C

Caridina serrata Richters, 1880: 163, pl. 17 figs 24–27 (junior homonym of *Caridina serrata* Stimpson, 1860).

Caridina spathulirostris Richters, 1880: 163, pl. 17 fig. 28.

Caridina spatulirostris f. *rectirostris* Bouvier, 1925: 197.

Caridina spatulirostris f. *curvirostris* Bouvier, 1925: 197.

Caridina richtersi Thallwitz, 1891: 27 (nomen novum for *Caridina serrata* Richters, 1880).

Caridina Richtersi f. *typica* Bouvier, 1912c: 165; 1925: 203.

Caridina apiocheles Bouvier, 1904: 134.

Caridina apiocheles mutation *Edwardsi* Bouvier, 1904: 134.

Caridina spathulirostris – Ortmann 1894b: 406 (key). — Bouvier 1905: 93 (key); 1912a: 291; 1913a: 464 (key); 1925: 197, figs 416–422. — Costa 1980: 691. — Keith *et al.* 2006: 60.

Caridina richtersi – Ortmann 1894b: 402 (key), 404. — Edmondson 1929: 28. — Holthuis 1954: 3. — Carpenter 1978: 350. — Costa 1980: 690. — Keith *et al.* 2006: 54 (incorrect spelling).

Caridina Richtersi – Bouvier 1904: 134; 1905: 86; 1912a: 293; 1912b: 919; 1912c: 163; 1913a: 464 (key); 1913b: 184; 1914: 699; 1925: 201, figs 432–457. — Bouvier & d’Emmerez de Charmoy 1919: 317. — Woltereck 1937a: 246 (incorrect spelling).

Caridina apiocheles – Bouvier 1905: 69, 86, fig. 3. — Bordage 1909: 108, fig. 6.

Caridina apiocheles mutation *Edwardsi* – Bouvier 1905: 69, 87, 103, fig. 3; 1912c: 166. — Bordage 1909: 108, fig. 6.

Caridina Richtersi f. *apiocheles* – Bouvier 1912a: 295; 1912c: 165; 1925: 203.

Ortmannia Edwardsi – Bouvier 1912 a: 296; 1912c: 166; 1912d: 691, fig. 3; 1913a: 459 (key); 1914: 700; 1925: 265, figs 445–447, 449, 452–453, 598–605. — Bouvier & d’Emmerez de Charmoy 1919: 317. — Woltereck 1937b: 322.

Caridina richtersi var. *apiocheles* – Bouvier 1925: 205. — Costa 1980: 690.

Ortmannia edwardsi – Edmondson 1929: 28. — Holthuis 1954: 3. — Costa 1980: 699.

Caridina richtersi var. *typica* – Costa 1980: 690.

Type locality

Pamplemousses Botanical Garden, Mauritius.

Material examined

Caridina spathulirostris Richters, 1880

MAURITIUS • 1 ♀ ovig. (cl 3.9 mm), 1 ♀ (cl 5.3 mm); quartier militaire, rivière importante; 20°17.260' S, 57°35.948' E; 390 m a.s.l.; 10 Dec. 2005; C.R. Turner leg.; MNHN-Na 772; MNHN • 1 ♀ (cl 5.8 mm); same data as for preceding; DNA voucher: CA2165; MNHN-2025-125; MNHN.

Caridina richtersii Thallwitz, 1891

MAURITIUS • 1 ♀ ovig. (cl 5.8 mm); quartier militaire, rivière importante; 20°17.260' S, 57°35.948' E; 390 m a.s.l.; 10 Dec. 2005; C.R. Turner leg.; DNA voucher: CA2166; MNHN-2025-126; MNHN • 1 ♂ (cl 6.5 mm); same data as for preceding; DNA voucher: CA2167; MNHN-2025-127; MNHN.

Distribution

Endemic to Mauritius.

Habitat

Freshwater in rivers and ponds.

Remarks

Our genetic study shows that *Caridina richtersi* Thallwitz, 1891 and *C. spathulirostris* Richters, 1880 are conspecific and we consider the former to be a junior synonym of *C. spathulirostris*. The specimens of this species are polymorphic in the shape of the rostrum and the chelipeds, which led to the description of numerous forms like *C. spathulirostris* f. *rectirostris*, *C. spathulirostris* f. *curvirostris*, *C. richtersi* f. *typica*, *C. richtersi* f. *apiocheles*. This kind of variability was also described in another endemic species of *Caridina* from the SWIO, *C. similis* (see Marquet & Keith, 2008).

Caridina similis Bouvier, 1904

Figs 2C, 5E

Caridina similis Bouvier, 1904: 135.

Caridina brevirostris f. *typica* Bouvier, 1912b: 916.

Caridina brevirostris f. *Gardinieri* Bouvier, 1912b: 916.

Caridina similis – Bouvier 1905: 88, fig. 10. – Keith *et al.* 2006: 58. – Marquet & Keith 2008: 980, figs 1–3.

Caridina brevirostris f. *similis* – Bouvier 1925: 228, figs 507–508.

Caridina brevirostris f. *typica* – Bouvier 1925: 228, figs 509–510, 514–523.

Caridina brevirostris f. *Gardinieri* – Bouvier 1925: 228, figs 505–506, 511–513.

Caridina brevirostris – Bouvier 1904: 136; 1912b: 915; 1913a: 447, pls. 27–29. — Costa 1980: 673–700.

Caridina singhalensis – Borradaile 1907: 67.

Type locality

Mahé, Seychelles.

Material examined

SEYCHELLES – **Mahé** • 8 ♀♀ ovig. (cl 4.7–6.3 mm), 1 ♀ (cl 5.9 mm), 1 ♂ (cl 4.1 mm); mare aux cochons; 4°39.029' S, 55°24.152' E; 17 Feb. 2020; P. Keith and M. Mennesson leg.; MNHN-2025-128; MNHN • 3 juv. (cl 2.4–2.9 mm); Baume Ellie; 14 Feb. 2020; P. Keith and M. Mennesson leg.; MNHN-2025-129; MNHN. – **Silhouette** • 1 ♀ ovig. (cl 4.4 mm); Anse Mandon; 4°28'1" S, 55°13'30" E; 28 Nov. 2012; P. Keith leg.; DNA voucher: CA1854; MNHN-2025-130; MNHN • 1 ♂ (cl 3.9 mm); same data as for preceding; DNA voucher: CA1855; MNHN-2025-131; MNHN • 1 ♀ ovig. (cl 5.5 mm); same data as for preceding; DNA voucher: CA1856; MNHN-2025-132; MNHN • 1 ♀ ovig. (cl 5.6 mm); same data as for preceding; DNA voucher: CA1857; MNHN-2025-133; MNHN.

See also “other material” in Marquet & Keith (2008).

Distribution

Endemic to the Seychelles (La Digue, Mahé, Praslin, Silhouette).

Habitat

Freshwater in permanent rivers.

Remarks

As for the previous species, *C. similis* shows a very variable form of the rostrum indicating numerous forms like *Caridina brevirostris* f. *similis*, *Caridina brevirostris* f. *typica*, *Caridina brevirostris* f. *Gardineri* now all junior synonyms of *C. similis* (see Marquet & Keith 2008).

Caridina typus species group

Diagnosis

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, pterygostomian 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

Figs 2G, 5F

Caridina typus H. Milne Edwards, 1837 (in H. Milne Edwards, 1834–1840): 363, pl. 25bis figs 4–5.

Caridina exilirostris Stimpson, 1860: 29.

Caridina typus f. *typica* Bouvier, 1925: 250, figs 272–295.

Caridina typus f. *caledonica* Bouvier, 1925: 253, figs 296–297.

Caridina typus – Miers 1879: 492. — Richters 1880: 162, pl. 17 fig. 23. — Pfeffer 1889: 35. — De Man 1892: 367, pl. 21 fig. 22; 1893: 300. — Sharp 1893: 111. — Ortmann 1894a: 8; 1894b: 403. — Weber 1897: 167 (part). — Hilgendorf 1898: 34. — Nobili 1899: 232. — Doflein 1900: 127. — Roux 1904: 552. — Bouvier 1904: 133. — Lenz 1905: 385; 1910: 570. — Borradaile 1907: 67. — Miyake 1938: 111, fig. 1. — Edmondson 1935: 10, fig. 3g–l. — Kubo 1938: 83, fig. 13; 1941: 307. — Kamita 1959: 21; 1961: 45, figs 15–18; 1963: 5, fig. 5; 1967: 3, fig. 4, pl. Ib. — Johnson 1960: 180; 1963: 27; 1967: 418; 1969: 110. — Holthuis 1965: 9; 1969: 93; 1978: 30; 1986: 590. — Ooishi 1970: 87. — Tiwari & Pillai 1971: 186. — Suzuki 1972: 10, figs 8–10; 2001: 138, fig. 2. — Fujino 1972: 7, fig. 8. — Kensley 1972: 36 (key), fig. 16c–d; 1981: 4. — Shokita 1975: 119; 1979: 204, pl. 1e; 1981: 15; 2002: 164; 2003: 249, figs 18g, 19c, 20l. — Shokita & Nishijima 1977: 187. — Costa 1980: 693; 1984: 205. — Hart 1983: 67. — de Silva 1983: 209. — Benzie & de Silva 1984: 623. — Gurney 1984: 568 (key). — Ng 1985: 161; 1995: 189, fig. 7. — Maciolek & Ford 1987: 628. — Coetzee 1988: 62. — Hayashi 1989: 310, fig. 168. — Bright 1989: 34. — Choy 1991: 356. — Hung *et al.* 1993: 486, figs 1c, 4a–f. — Suzuki *et al.* 1993: 56. — Suzuki & Sato 1994: 60. — Hamano & Honke 1997: 162. — Chace 1997: 21. — Shy & Yu 1998: 61. — Yeo *et al.* 1999: 225. — Ebenezer & Richard 1999: 427. — Keith *et al.* 1999: 46; 2006: 62; 2010: 46. — Ideguchi *et al.* 2000: 5. — Short 2000: 61. 2009: 36 (key), fig. 22. — Buden *et al.* 2001: 261. — Leberer & Nelson 2001: 393. — Day *et al.* 2001: 96 (key), fig. 6.3. — Keith 2002: 100. — Choy & Marquet 2002: 219. — Marquet *et al.* 2002: 222; 2003: 68. — Shokita *et al.* 2002: 76; 2003a: 101; 2003b: 117. — Davie 2002: 226.

— Leberer & Cai 2003: 354. — Cai & Anker 2004: 236. — Liang 2004: 139, fig. 65. — Wowor *et al.* 2004: 341, fig. 5f. — Bossuyt *et al.* 2004: 480, fig. 2e. — Nakahara *et al.* 2005: 305. — Cai *et al.* 2006: 412, figs 13–15; 2007: 279; 2009: 66. — Cai & Shokita 2006a: 2134. — Page *et al.* 2007: 647, figs 2–3. — Fujita 2007: 93. — Ragunathan & Valarmathi 2007: 94 (key), 96. — Karge & Klotz 2007: 92. — Nakahara *et al.* 2007: 387, figs 1c, 2a–e. — Cai & Ng 2009: 1094. — Benstead *et al.* 2009: 459. — Cai & Husana 2009: 62. — Richard & Clark 2010: 639. — Soomro *et al.* 2010: 721; 2011: 41; 2016: 569; 2020: 1333. — Saito *et al.* 2012: 27. — Cook *et al.* 2012: 289, fig. 3. — Bouchard *et al.* 2013: 9. — Emmerson 2016: 162, 173. — Fujita *et al.* 2016: 105. — Bernardes *et al.* 2017: 1 (part, ARC clade). — de Mazancourt *et al.* 2017: 226, fig. 4; 2019b: 167, figs 2–5; 2020: 34, figs 2d, 10. — Chow *et al.* 2018: fig. 1. — Choy *et al.* 2019: 115. — Short *et al.* 2019: 4, 20 (key), figs 8, 10j. — Wood *et al.* 2019: 200. — Jugovic *et al.* 2019: fig. 1. — Rahayu & Annawaty, 2019: 64. — Klotz *et al.* 2019: 164, fig. 18. — Hernawati *et al.* 2020: fig. 3. — Imai *et al.* 2020: 63, fig. 3a. — Vijayamma *et al.* 2021: 404 (key).

Caridina typa – Bouvier 1905: 88; 1913a: 465; 1914: 699; 1925: 249, figs 271–297. — Roux 1926a: 246; 1926b: 201. — Riek 1953: 117. — Choy & Horwitz 1995: 52 (key) (incorrect spelling).

Caridina typus var. *acuminata* – Bouvier 1925: 126, fig. 271 (part).

Caridina typa acuminata – Roux 1934: 222.

Caridina acuminata – Shokita 1979: 205. — Hayashi 1989: 311, fig. 169b–c, 170f.

? *Caridina* aff. *typus* – Ng 1994: 78.

Not *Caridina typus* – Spence Bate 1888: 704, pl. 119 fig. 3 (= *Caridina Spencebatei* De Man, 1892: 371 = *Atya scabra*).

Not *Caridina typus* – Weber 1897: 167 (part) (= *Caridina africana*).

Not *Caridina typus* – de Silva 1982: 135, fig. 4a–h (= *Caridina villadolidi*).

Not *Caridina typus* – von Rintelen *et al.* 2007: 1037, fig. 2; 2008: 2248, fig. 4; 2012: figs 2–5.

Not *Caridina typus* – Bernardes *et al.* 2017: 1 (part, SUL clade) (= *Caridina jeani*).

Not *Caridina typus* – Bernardes *et al.* 2017: 1 (part, TAL clade) (= *Caridina zhujiangensis*).

Type locality

Unknown, probably Mauritius according to Bouvier (1925).

Material examined

AUSTRALIA • 2 specs from GenBank: DQ478562 and DQ478563 (Page *et al.* 2007).

MADAGASCAR • 1 ♀ (cl 4.5 mm); Antsatoko River; 13°36.660' S, 50°00.341' E; 29 m a.s.l.; 6 Jul. 2008; DIAMSOI leg.; DNA voucher: CA1038; MNHN-IU-2018-2829; MNHN • 1 ♀ ovig. (cl 6.9 mm); same data as for preceding; DNA voucher: CA1040; MNHN-IU-2018-2830; MNHN • 1 ♀ ovig. (cl 7.1 mm); same data as for preceding; DNA voucher: CA1039; MNHN-IU-2018-2831; MNHN.

MAYOTTE • 1 ♀ (cl 6.1 mm); M'Tsangachei River; 12°53.066' S, 45°07.899' E; 30 Mar. 2024; P. Valade leg.; DNA voucher: CA3027; MNHN-IU-2025-134; MNHN.

MAURITIUS • 3 specs from GenBank: KY069380, KY069381 and KY069382 (Bernardes *et al.* 2017).

SEYCHELLES • 1 ♀ (cl 9.2 mm); Praslin Island, Nouvelle Découverte River; 4°19.200' S, 55°42.333' E; 16 m a.s.l.; 8 Oct. 2003; P. Bosc, H. Grondin, P. Keith and P. Valade leg.; MNHN-IU-2014-577; MNHN.

SOUTH AFRICA • 1 ♀ ovig. (cl 10.1 mm); Umtata River; 31°55.511' S, 29°08.199' E; 2 m a.s.l.; 13 Feb. 2018; L. Maliwa, M. Mlambo, G. Marquet and P. Tiberghien leg.; DNA voucher: CA2089; MNHN-

2018-2843; MNHN • 1 ♂ (cl 5.7 mm); Mpenjati River; 30°56.645' S, 30°13.660' E; 93 m a.s.l.; 15 Feb. 2018; P. Kubheka, N. McClurg, T. McClurg, L. Maliwa, M. Mlambo, G. Marquet and P. Tiberghien leg.; DNA voucher: CA2090; MNHN-IU-2018-2844; MNHN.

LA RÉUNION • 1 juv. (cl 2.4 mm); Rivière du Mât; 20°58.801' S, 55°41.989' E; 19 May 2023; P. Valade leg.; DNA voucher: CA3054; MNHN-IU-2025-135; MNHN • 1 ♂ (cl 4.6 mm); same data as for preceding; DNA voucher: CA3058; MNHN-IU-2025-136; MNHN • 1 juv. (cl 2.4 mm); same data as for preceding; DNA voucher: CA3059; MNHN-IU-2025-137; MNHN • 1 juv. (cl 1.9 mm); Rivière des Marsouins; 21°01.970' S, 55°42.943' E; 6 Aug. 2023; P. Valade leg.; DNA voucher: CA3060; MNHN-IU-2025-138; MNHN • 1 ♂ (cl 4.5 mm); same data as for preceding; DNA voucher: CA3063; MNHN-IU-2025-139; MNHN • 1 spec. from GenBank: KY069434 (Bernardes *et al.* 2017).

Distribution

Widespread from South Africa to Fiji and Australia to Japan and India.

Habitat

Freshwater in rivers.

Remarks

Caridina typus revealed to be a species complex, all characterized by the lack of teeth on the dorsal margin of the rostrum. Three clades were recognized by Bernardes *et al.* (2017), named SUL, TAL and ARC. The latter one corresponds to the true *C. typus*, while SUL is *C. jeani* and TAL is *C. zhujiangensis* (publication in prep.).

Caridina serratiostris species group

Diagnosis

Moderately robust morphology with a moderately short and straight rostrum (reaching end of antennular peduncle), armed with many dorsal teeth, at least 6 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 usually 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 henriettae sp. nov.

urn:lsid:zoobank.org:act:F229A5EF-5D4B-412D-B6F8-285C1B0B1C27

Figs 2F, 3–4, 5D, G–H

Caridina serratiostris – Holthuis 1965: 25, fig. 8. — Costa 1980: 691. — Gurney 1984: 568 (key). — Keith *et al.* 1999: 44; 2006: 56. — Keith 2002: 100. — Richard & Clark 2010: 310 (part), figs 3, 4a–n, p–q. — Bouchard *et al.* 2013: 9. — Emmerson 2016: 170. — Hoarau 2018: 1.
Caridina wyckii – Weber 1897: 168 (part).

Diagnosis

Typical morphology of the *C. serratiostris* species group: rostrum armed with many dorsal teeth, at least 6 of them on the carapace, a usually long stylocerite and a rounded endopod of the first male pleopod,

without appendix interna. Well-developed arthrobranch at the base of P1. Telson with a pair of plain long lateral spines and 1 pair of shorter, plain lateral spines. P3 propodus 11.2–12.8 as long as wide.

Etymology

The new species is dedicated to our friend Elvina Henriette, Research Scientist and Director of the NGO “Gaea Conservation Network Seychelles”, in recognition of her work and passion for the freshwater fauna of Seychelles islands.

Type material

Holotype

MAURITIUS • ♂ (cl 2.9 mm); Rivière des Anguilles; 20°28.802' S, 57°33.378' E; 13 Nov. 2002; P. Keith, G. Marquet and ARDA leg.; DNA voucher: CA2304; MNHN-IU-2015-1914; MNHN.

Paratypes

MAURITIUS • 1 ♀ (cl 4.1 mm); same data as for holotype; DNA voucher: CA2305; MNHN-2025-140; MNHN.

MADAGASCAR • 1 ♀ ovig. (cl 4.9 mm); Fanambana River (Station 37); 14°33.193' S, 50°10.393' E; 11 m a.s.l.; 7 Jul. 2008; DIAMSOI leg.; DNA voucher: CA1178; MNHN-2025-141; MNHN • 1 ♂ (cl 3.2 mm); same collection data as for preceding; DNA voucher: CA1431; MNHN-2025-142; MNHN.

MAURITIUS • 1 ♀ ovig. (cl 4.8 mm); Rivière de la Chau; 20°24.350' S, 57°42.269' E; 12 Nov. 2002; ARDA leg.; DNA voucher: CA2042; MNHN-IU-2015-1933; MNHN • 1 ♂ (cl 3.0 mm); Beau Vallon; 1913; P. Carié leg.; MNHN-IU-2015-1909; MNHN.

LA RÉUNION • 1 ♀ ovig. (cl 4.4 mm); Rivière des Embouchures; 21°2.093' S, 55°42.899' E; 13 Oct. 2015; P. Valade leg.; DNA voucher: CA2417; MNHN-2025-143; MNHN • 1 ♀ ovig. (cl 3.8 mm); same data as for preceding; DNA voucher: CA2418; MNHN-2025-144; MNHN • 1 ♀ ovig. (cl 3.6 mm); Rivière des Marsouins; 2 May 2022; Ocea Consult leg.; DNA voucher: CA2949; MNHN-2025-145; MNHN • 1 ♀ ovig. (cl 3.6 mm); Rivière des Marsouins; 21°1.970' S, 55°42.949' E; 8 Apr. 2024; P. Valade leg.; DNA voucher: CA3038; MNHN-2025-146; MNHN • 1 juv. (cl 2.4 mm); Rivière des Marsouins; 21°1.970' S, 55°42.949' E; 6 Aug. 2023; P. Valade leg.; DNA voucher: CA3061; MNHN-2025-147; MNHN • 1 juv. (cl 2.3 mm); Rivière des Roches; 21°0.398' S, 55°41.661' E; 13 Nov. 2023; P. Valade leg.; DNA voucher: CA3065; MNHN-2025-148; MNHN.

SEYCHELLES – **Mahé** • 2 ♀♀ ovig. (cl 4.1–4.7 mm), 1 ♀ (cl 4.0 mm); Bel Ombre; 4°36.966' S, 55°25.063' E; 2 Feb. 2020; P. Keith and M. Mennesson leg.; MNHN-2025-149; MNHN • 1 ♀ ovig. (cl 2.7 mm); Grand Anse; 4°40.502' S, 55°26.728' E; 20 Feb. 2020; P. Keith and M. Mennesson leg.; MNHN-2025-150; MNHN • 1 ♀ ovig. (cl 2.7 mm); same data as for preceding; DNA voucher: CA3000; MNHN-2025-151; MNHN. – **Praslin** • 1 ♀ ovig. (cl 4.1 mm); 10 Oct. 2003; no locality data; ARDA leg.; DNA voucher: CA2026; MNHN-IU-2015-1932; MNHN • 1 ♀ ovig. (cl 3.4 mm); Nouvelle Découverte; 4°20.179' S, 55°43.349' E; 19 Feb. 2024; P. Keith and M. Mennesson leg.; MNHN-2025-152; MNHN • 2 ♀♀ ovig. (cl 3.2–3.6 mm); Nouvelle Découverte; 4°20.179' S, 55°43.349' E; 21 Feb. 2020; P. Keith and M. Mennesson leg.; MNHN-2025-153; MNHN • 1 ♀ ovig. (cl 3.6 mm); same data as for preceding; DNA voucher: CA2998; MNHN-2025-154; MNHN • 1 ♀ ovig. (cl 3.4 mm); same data as for preceding; DNA voucher: CA2999; MNHN-2025-155; MNHN. – **Silhouette** • 1 ♀ (cl 3.4 mm); Anse Mandon; 4°28.014' S, 53°13.500' E; 28 Nov. 2012; P. Keith leg.; DNA voucher: CA1491; MNHN-2025-156; MNHN • 1 ♀ ovig. (cl 4.5 mm); same data as for preceding; DNA voucher: CA1492; MNHN-2025-157; MNHN • 4 ♀♀ ovig. (cl 3.3–3.7 mm), 1 ♀ (cl 3.3 mm); St Gore River; 4°30.115' S, 55°13.521' E; 18 Feb. 2020; P. Keith and M. Mennesson leg.; MNHN-2025-158; MNHN.

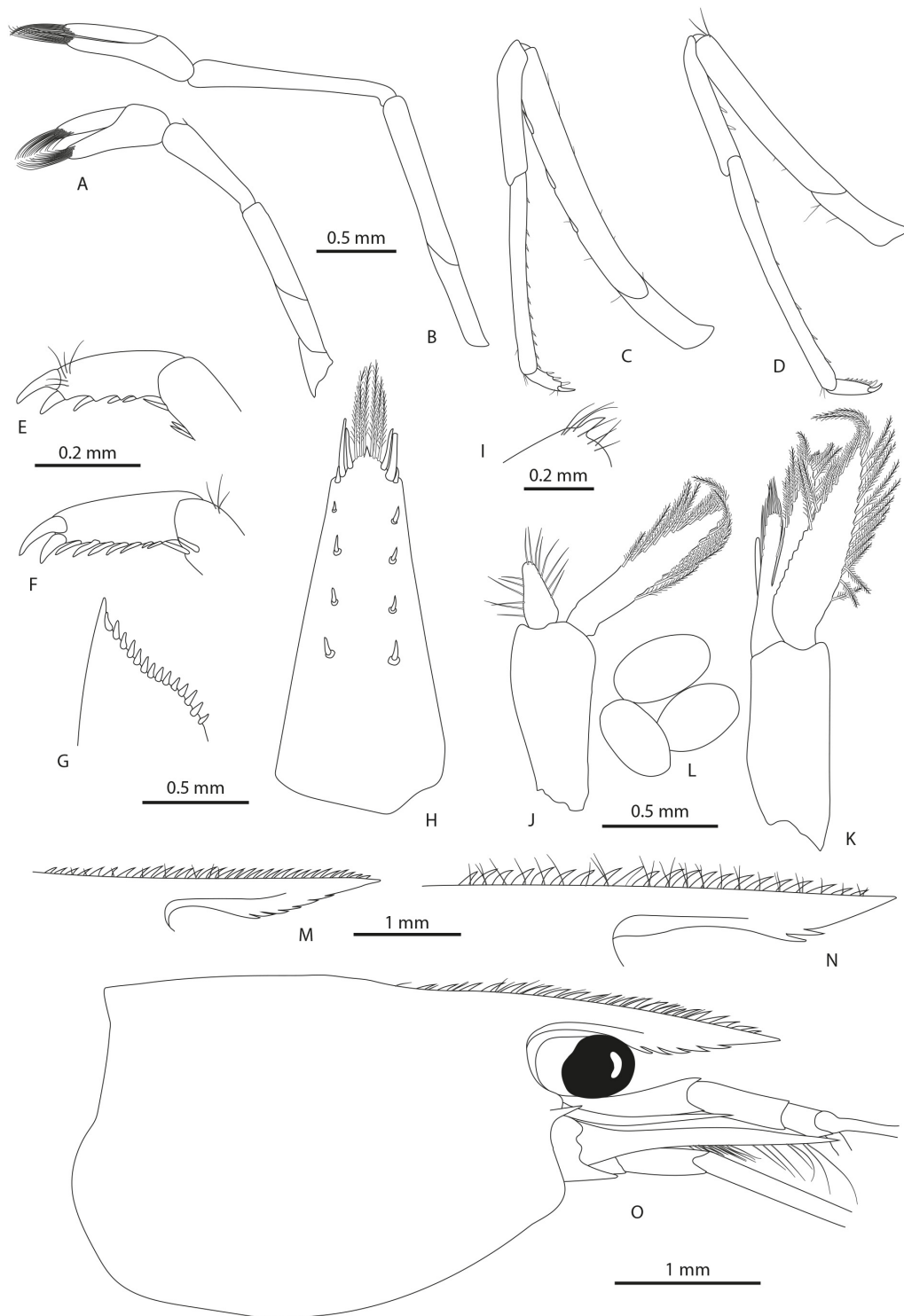


Fig. 3. *Caridina henriettae* sp. nov. **A–F, H, O.** ♂, holotype (MNHN-IU-2015-1914). **G, J–K.** ♂, paratype (MNHN-IU-2015-1909). **I, L.** Ovigerous, ♀, paratype (MNHN-IU-2015-1933). **M.** Ovigerous female, paratype (MNHN-IU-2025-143). **N.** Ovigerous female, paratype (MNHN-IU-2025-152). **A.** First pereiopod. **B.** Second pereiopod. **C.** Third pereiopod. **D.** Fifth pereiopod. **E.** Dactylus of third pereiopod. **F.** Dactylus of fifth pereiopod. **G.** Uropodal diaeresis. **H.** Telson. **I.** pre-anal carina. **J.** First male pleopod. **K.** Second male pleopod. **L.** Undeveloped eggs. **M–N.** Rostrum variation. **O.** Cephalothorax.

Description

CEPHALOTHORAX. Antennal spine ventral to inferior orbital angle. Pterygostomian margin rounded. Rostrum (Fig. 3M–O): straight, short, 0.6–0.7 of cl, reaching beyond end of antennular peduncle, armed with 19–31 teeth on dorsal margin, 6–10 of them situated on carapace behind orbital margin, ventral margin with 5–7 teeth. Eyes developed, anterior end reaching to $0.59 \times$ length of basal segment of antennular peduncle. Long antennular peduncle, 0.67 (♀) – 0.78 (♂) \times as long as carapace; second segment distinctly longer than third segment. Stylocerite reaching to middle of second segment of antennular peduncle.

PEREIOPODS. Epipods on first four pereio-pods. P1 (Fig. 3A): chela about 2.4 – $3.3 \times$ as long as wide, movable finger 3.7 – 5.8 as long as wide, 1.4 – $1.9 \times$ length of palm; carpus 3.6 – $4.6 \times$ as long as wide, well developed arthrobranch (Fig. 4). P2 (Fig. 3B) more slender and longer than first pereio-pod, with chela 3.7 – $5.2 \times$ as long as wide: movable finger 5.2 – $11.0 \times$ as long as wide, 1.4 – $2.4 \times$ as long as palm; carpus slender, 7.7 – $9.6 \times$ as long as wide. P3 (Fig. 3C): slender, dactylus (Fig. 3E) 3.2 – $4.0 \times$ as long as wide (terminal spiniform seta included), with 5–8 spiniform setae on flexor margin including terminal one; propodus 11.2 – $12.8 \times$ as long as wide, 3.2 – $4.4 \times$ as long as dactylus. P5 (Fig. 3D): dactylus (Fig. 3F) 3.9 – 4.4 as long as wide, with 7–13 spiniform setae on flexor margin; propodus 15.8 – $23.9 \times$ as long as wide, 4.4 – $50 \times$ as long as dactylus.

ABDOMEN. Third abdominal somite with moderately convex dorsal profile. Sixth abdominal somite $0.49 \times$ as long as carapace, $1.3 \times$ as long as fifth somite, shorter than telson.



Fig. 4. Dissected branchial chamber of a specimen of *Caridina henriettae* sp. nov., paratype (MNHN-2025-149) showing the developed arthrobranch at the base of the first pereopod (black arrow).



Fig. 5. Live coloration of the species of Atyidae from the South West Indian Ocean. **A.** *Atyoida serrata* Bate, 1888 from La Réunion (credit E. Vigneux). **B.** *Caridina natalensis* De Man, 1908 from the Seychelles (credit P. Keith). **C.** *Caridina spathulirostris* Richters, 1880 from Mauritius (credit Hoareau). **D.** *Caridina henriettae* sp. nov. from the Seychelles (credit P. Keith). **E.** *Caridina similis* Bouvier, 1904 from the Seychelles (credit Y. Zitte). **F.** *C. typus* H. Milne Edwards, 1837 from La Réunion (credit E. Vigneux). **G–H.** *C. henriettae* sp. nov. from La Réunion (credit E. Vigneux).

TELSON (Fig. 3H). $3.0 \times$ as long as wide, with 6 pairs dorsal spines including subterminal spines, 1 pair of plain long lateral spines, 1 pair of shorter plain lateral spines and 6–11 long, stalked, plumose processes present at rounded posterior margin.

MALE PLEOPODS. P11 (Fig. 3J): endopod rounded, $2.0 \times$ as long as wide, reaching $0.35 \times$ as long as endopod, no appendix. P12 (Fig. 3K): appendix masculina reaching $0.74 \times$ as long as endopod; appendix interna reaching $0.82 \times$ as long as appendix masculina.

PRE-ANAL CARINA (Fig. 3I). High, with a spine.

UROPODAL DIAERESIS (Fig. 3G). With 13–15 spinules.

EGGS. Ovigerous females with small eggs (Fig. 3L), size: $0.37\text{--}0.46 \times 0.24\text{--}0.27$ mm.

Distribution

South Africa, Mozambique, Madagascar, Seychelles, Comoros, La Réunion, Mauritius.

Habitat

Fresh or brackish water in the lower course and estuary of rivers.

Remarks

This new species belongs to the *Caridina serratirostris* species group based on the presence of a rostrum armed with many dorsal teeth, at least 6 of them on the carapace, with a usually long stylocerite and with a rounded endopod of the first male pleopod, without appendix interna. But it is easy to distinguish this new species from type specimens of congeners by its telson with a pair of plain long lateral spines and 1 pair of shorter, plain lateral spines (vs only a pair of plain lateral spines) and by its P3 propodus shorter $11.2\text{--}12.8 \times$ as long as wide (vs $14.2\text{--}17.1$). Among this group, our new species is closer to *C. serratirostris* than *C. celebensis* due to the presence of a well-developed arthrobranch at the base of the P1 (vs reduced or absent, see Cai & Shokita 2006b)

Richard & Clark (2010) reported this species under the name *C. serratirostris* from Mozambique and South Africa noting the presence of shorter inner lateral spines on the telson which the syntypes of *C. serratirostris* do not possess. Recent sampling trips to the localities where the species was collected in South Africa – the iLovu or the Umbilo rivers near Durban – by two of the authors (VM and GM) failed to retrieve this species, suggesting either that this area is the southern limit of its range and its presence may be occasional, or that the species does not occur there anymore due to the heavy urbanization around these rivers (pers. obs.).

Identification key for the species of *Caridina* H. Milne Edwards, 1837 from the South-Western Indian Ocean

1. Stylocerite reaching distinctly beyond the base of the second segment of the antennular peduncle *C. henriettae* sp. nov.
– Stylocerite at most attaining the end of the first segment of the antennular peduncle 2
2. Rostrum rather constantly long, reaching well beyond scaphocerite *C. natalensis* De Man, 1908
– Rostrum short or reaching at most to or slightly beyond the end of the antennular peduncle 3
3. Uropodal diaeresis with 16–23 spinules 4
– Uropodal diaeresis with 8–15 spinules 5
4. Dactylus of P5 with 26–37 spiniform setae; ovigerous female with few and large eggs
..... *C. similis* Bouvier, 1904 (Seychelles)
– Dactylus of P5 with 33–81 spiniform setae; ovigerous female with numerous and small eggs
..... *C. typus* H. Milne Edwards, 1837
5. Dorsal margin of telson unarmed; dactylus of P5 with 28–30 spiniform setae
..... *C. mauritii* Bouvier, 1912 (Mauritius)
– Dorsal margin of telson armed; dactylus of P5 with 31–60 spiniform setae
..... *C. spathulirostris* Richters, 1880 (Mauritius)

Discussion

This updated checklist of the species of *Caridina* from the SWIO gives new insights in the biogeography of the region. Some of the species listed have a wide distribution range due to their amphidromous life cycle: *C. typus* is one of the most widely distributed species of the genus being able to cross the Indo-Pacific barrier. *Caridina natalensis* and *C. henriettae* sp. nov. have a smaller range, being restricted to the SWIO, probably because of a shorter planktonic larval phase (de Mazancourt *et al.* 2023). Endemic land-locked species can be found in the Seychelles with *C. similis* and Mauritius with *C. mauritii* and *C. spathulirostris*, without mentioning the large endemic species flocks from Madagascar that were intentionally left aside from the present study due to the lack of data. The absence of such species in La Réunion Island while two co-exist in the neighboring island of Mauritius can be explained by the older age of the latter (about 10 My vs 3 My) which gave enough time for endemic species to evolve. Similarly, the granitic islands of the Seychelles were formed very early from a microcontinent separated from India in the late Cretaceous (66 My), which also explains the presence of endemic species like *C. similis* or the primary freshwater crab genus *Seychellum* (Ng *et al.* 1995).

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