Caridina maeklongensis, a new landlocked freshwater shrimp species (Crustacea: Decapoda: Atyidae) from the Mae Klong Basin, Thailand

Kongkit Macharoenboon, Varitsara Manonai & Ekgachai Jeratthitikul*

Abstract. A newly discovered landlocked shrimp, *Caridina maeklongensis*, new species, is described from the Mae Klong Basin, western Thailand. The morphology of the new species resembles *C. sumatrensis*, from which it differs in possessing a shorter rostrum with fewer dorsal teeth, a small number of very large-sized eggs, and a greatly reduced posteromedian projection on the distal end of the telson. The molecular evidence of the mitochondrial 16S rRNA gene also supports the species status of the newly described species. This is the fifth endemic species of *Caridina* known from Thailand.

Key words. crustacean, landlocked freshwater shrimp, molecular phylogeny, taxonomy, Southeast Asia

INTRODUCTION

The freshwater shrimp genus Caridina is one of the most diverse genera in the family Atyidae, containing over 300 described species worldwide (De Grave et al., 2008; De Grave & Fransen, 2011). They are detritivores that play a crucial ecological role in aquatic ecosystems by consuming and processing organic matter, thereby contributing to nutrient cycling and the health of the benthic environment (Hart, 2001; Hart et al., 2003; Yam & Dudgeon, 2006; Budeba & Cowx, 2007). Based on their life histories, Caridina can be separated into landlocked and amphidromous species. In general, the amphidromous species produce numerous small-sized eggs, tolerate high salinity, and have a prolonged, planktotrophic larval stage in brackish waters of estuaries or the open sea, allowing for extensive dispersal ability. In contrast, the landlocked species produce a small number of large-sized eggs and remain near their parental freshwater habitat throughout their life cycle (Lai & Shy, 2009; Han et al., 2011; Bauer, 2013; Yatsuya et al., 2013; Soomro et al., 2020; Hamasaki et al., 2021; de Mazancourt et al., 2021, 2023; Kawakami et al., 2023). Due to their direct or abbreviated larval development that limits dispersal ability, landlocked species are likely to settle in habitats close to or similar to those of their parents, leading to endemism (de Mazancourt et al., 2021; Hamasaki et al., 2021). Caridina panhai Macharoenboon, Sutcharit, Siriwut & Jeratthitikul, 2023 is one example of a landlocked species. It was recently

described from mainland Indochina, and is only known from the Middle Mekong Basin in Thailand (Macharoenboon et al., 2023).

The taxonomy and phylogeny of *Caridina* has been widely studied in Southeast Asian countries, including Myanmar, Vietnam, Singapore, Malaysia, Indonesia, and the Philippines (e.g., Cai & Ng, 2000; Cai & Anker, 2004; Cai & Shokita, 2006; Cai et al., 2007; von Rintelen & Cai, 2009; Do et al., 2020). However, *Caridina* species in Thailand are still poorly understood. During a recent field survey in the Mae Klong Basin of western Thailand, we collected an unknown *Caridina* species from tributaries of the Khwae Yai and Khwae Noi rivers. Morphologically, it resembled *C. sumatrensis* De Man, 1892. However, detailed morphological examination and the results of molecular analyses based on the mitochondrial 16S rRNA gene indicated that it constitutes a distinct species. Therefore, we propose it as a new species, and formally describe it herein as *Caridina maeklongensis*, new species.

MATERIAL AND METHODS

Specimen sampling. Specimens were collected using triangular dip nets from aquatic habitats within the Mae Klong Basin. The live habitus specimens were photographed in order to document body colouration using a small glass tank and a Nikon D5300 camera mounted with AF-S VR Micro-Nikkor 105 mm f/2.8G IF-ED Macro Lens, and then euthanised following the protocol described in Cooper (2011) before fixing in 95% (v/v) ethanol. All examined specimens including the type series were deposited in the Mahidol University Museum of Natural History (MUMNH), Department of Biology, Faculty of Science, Mahidol University, Thailand.

Accepted by: Yang Chien-Hui

Animal Systematics and Molecular Ecology Laboratory, Department of Biology, Faculty of Science, Mahidol University, Bangkok 10400, Thailand; Email: ekgachai. jer@mahidol.ac.th (*corresponding author)

Morphological Study. Specimen examination was made using a ZEISS Stemi 305 stereomicroscope and an Olympus CH30 microscope. Some ovigerous females and males were dissected and used in morphological character measurement. Specimen measurement was undertaken with DinoCapture software v.2.0 using photographs taken from the digital eyepiece (Dino-Lite AM423X) attached to the stereomicroscope. Measurements for species description were taken from ovigerous females, with the exception of the first and second pleopods, which were obtained from males. Carapace length was measured from the postorbital margin to the posterior margin of the carapace. Rostrum length was measured from the postorbital margin to the tip of the rostrum. The size of eggs was measured from eye-developed eggs. All of the measurements are reported in millimetres (mm). Illustrations were prepared from microphotographs using Adobe Illustrator v.28.0.

Taxonomic descriptions were made following the format of Richard & Clark (2014) and Klotz et al. (2021). The rostral formula was written as (postorbital teeth) + entire teeth on dorsal margin + subapical teeth (if any)/ventral teeth. The following abbreviations are used hereafter: CL, carapace length (mm); P1, first pereiopod; P2, second pereiopod; P3, third pereiopod; P5, fifth pereiopod; P11, first male pleopod; P12, second male pleopod.

Molecular study. Total genomic DNA was extracted from the abdominal muscle or from eggs (in case of holotype) using a DNA extraction kit for animal tissue (NucleoSpin Tissue Extraction Kit, Macherey-Nagel, Germany) following the standard procedure. Fragments of mitochondrial large ribosomal subunit rRNA gene (16S rRNA) were amplified by the set of primers 16Sar-Lmod and 16Sbmod (de Mazancourt et al., 2019), and used in phylogenetic analyses. Polymerase chain reaction (PCR) was performed using a T100[™] thermal cycler (BIO-RAD) with a final reaction volume of 30 µL (15 µL EmeraldAmp GT PCR Master Mix, 1.5 µL each primer, 10 ng template DNA, and distilled water up to 30 µL total volume). Thermal cycling was performed by initial denaturation at 94 °C for 3 min, followed by 35 cycles of 94 °C for 30 s, annealing at 52 °C for 60 s, extension at 72 °C for 90 s, and final extension at 72 °C for 5 min. Amplification of the PCR products was confirmed by 1.5% (w/v) agarose gel electrophoresis before purification using MEGAquick-spinTM Plus (Fragment DNA purification kit) and sequencing in both directions (forward and reverse) using an automated sequencer (ABI prism 3730XL). Contigs of forward and reverse strands were assembled using ClustalW as implemented in MEGA11 (Tamura et al., 2021), before being checked and corrected manually. All sequences of 16S rRNA gene obtained in this study contained 516 bp after primer trimming. They were deposited in the GenBank Nucleotide sequence database under the accession numbers PQ041485-PQ041493.

The sequences were aligned using MEGA11. The final aligned dataset for phylogenetic analyses included 524 bp of 40 16S rRNA sequences. In addition to seven sequences of

the new species, sequences of presumed close morphological relatives, such as *C. sumatrensis* (two newly obtained in this study), *C.* cf. *babaulti* Bouvier, 1918, *C. weberi* De Man, 1892, and *C. pristis* Roux, 1931 were included (De Man, 1892; Bouvier, 1918; Roux, 1931; Pandya & Richard, 2019; de Mazancourt et al., 2020). Furthermore, 15 sequences of representative *Caridina* from other species groups and five sequences of *Neocaridina* were included specifically to test the monophyly of the new species and related taxa. Seven sequences from the genera *Atya*, *Atyopsis*, and *Atyoida* were employed as an outgroup. The collection localities and GenBank accession numbers for each nominal species used in the phylogenetic analyses are listed in Table 1.

Phylogenetic trees were reconstructed using the maximum likelihood (ML) and Bayesian inference (BI) methods via the online CIPRES Science Gateway (Miller et al., 2010). The best-fit substitution model was determined using PartitionFinder2 v.2.3.4 (Lanfear et al., 2017) with a heuristic search algorithm under the Akaike Information Criterion (AICc). The program suggested the GTR+I+G model as the best-fit model, therefore it was applied in all analyses. The ML tree was estimated in IQ-TREE 2.2.2.7 (Minh et al., 2020) with 10,000 replicates of ultrafast bootstrap approximation to assess topology bootstrap support (BS). The BI tree was reconstructed in MrBayes 3.2.7 (Ronquist et al., 2012) using the Markov chain Monte Carlo technique (MCMC) by running for 10 million generations, and with a random starting tree. The resultant trees were sampled every 1,000 generations and the values were used to estimate the consensus tree topology, bipartition posterior probability (bpp), and branch lengths, after discarding the first 25% of the obtained trees as burn-in. The average effective sample size (ESS) from the MCMC analysis was >200 for all parameters. The resulting tree was examined and edited using FigTree v.1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/, accessed on February 28, 2023). A clade was considered well supported if the ultrafast BS was \geq 95% and the Bayesian bpp was ≥0.95 (San Mauro & Agorreta, 2010; Hoang et al., 2018). Moreover, genetic distances were calculated using the uncorrected p-distance method in MEGA11. Gap positions introduced during sequence alignment were excluded from the calculations.

RESULTS

Molecular phylogenies and genetic distance. Both ML and BI analyses resulted in identical tree topologies; therefore, only the ML tree is presented in Figure 1. The genus *Caridina* was not recovered as a monophyletic group. Instead, it formed a paraphyletic group containing a clade of *Neocaridina* species within it, when using *Atyopsis, Atyoida,* and *Atya* as outgroup. Specimens of the new species were recovered as a clade with strong support from both ML and BI analyses (BS = 100%, bpp = 0.99), and it was placed as a sister taxon to *C. sumatrensis*, but with partial support from only the BI analysis (BS = 86%, bpp = 0.99). The clade of the new species + *C. sumatrensis* was subsequently grouped

Macharoenboon et al.: New Caridina shrimp from Thailand

Table 1. List of samples and GenBank accession numbers used in the phylogenetic analyses of mitochondrial 16S rRNA gene.

Taxon	Locality	Voucher ID	GenBank accession	Source
Ingroups				
Caridina maeklongensis, new species	Thailand:	MUMNH-CAR064-9	PQ041485	This study
	Kanchanaburi, Sai Yok Yai Waterfall	MUMNH-CAR064-4	PQ041486	This study
		MUMNH-CAR064-7	PQ041487	This study
	Thailand:	MUMNH-CAR062-1	PQ041488	This study
	Kanchanaburi, Mae Phlu Stream	MUMNH-CAR062-2	PQ041489	This study
	Thailand:	MUMNH-CAR063-1	PQ041490	This study
	Kanchanaburi, Huai Mae Khamin	MUMNH-CAR063-2	PQ041491	This study
Caridina sumatrensis	Thailand:	MUMNH-CAR054-1	PQ041492	This study
	Ratchaburi, Mae Klong River	MUMNH-CAR055-2	PQ041493	This study
	Malaysia	ZMB:29491	FN995360	von Rintelen et al. (2012)
Caridina cf. babaulti	India: West Bengal	ZMB 30757-1	MN399172	Klotz et al. (2019)
Caridina pristis	Sri Lanka: Pussellawa	2301SL	AY708114	Bossuyt et al. (2004)
Caridina weberi	Solomon Islands: Kolombangara Island	CA1516	MT303920	de Mazancourt et al. (2020)
Caridina gueryi	Indonesia: Sulawesi	CA1161	KY350241	de Mazancourt et al. (2017)
Caridina longicarpus	New Caledonia	CA1557	MK189892	de Mazancourt et al. (2019)
Caridina turipi	Solomon Islands: Choiseul Island, Turipi River	MNHN-IU-2014-20876	MT303911	de Mazancourt et al. (2020)
Caridina panhai	Thailand: Sakon Nakhon	MUMNH-CAR507-F1	OQ092406	Macharoenboon et al. (2023)
Caridina propinqua	Sri Lanka: Rathgama Lake	2309SL	AY708117	Bossuyt et al. (2004)
Caridina brachydactyla	Indonesia	CA1131	MH497502	de Mazancourt et al. (2019)
Caridina gracilipes	Borneo	CA1673	MH497535	de Mazancourt et al. (2018)
Caridina gracilirostris	Australia	CA1678	MT303887	de Mazancourt et al. (2020)
Caridina neglecta	Solomon Island: Vella Lavella	CA1703	MT303889	de Mazancourt et al. (2020)
Caridina lanceifrons	China: Hainan	isolate_65	MT446450	Xu et al. (2020)
Caridina typus	Seychelles	MEFGL_CT_Sey01	KY069374	Bernardes et al. (2017)
	Malaysia: Langkawi	ZMB: 29489 (MY_405)	MN399191	Klotz et al. (2019)
Caridina zhujiangensis	China: Dong'ao Island	isolate_22	MT446448	Xu et al. (2020)
Caridina villadolidi	Philippines: Mindoro	ZMBunid1227	KY436222	Bernardes et al. (2017)
Caridina namdat	Vietnam: Nam Dat	ZMB 30341-4	MZ484398	Do et al. (2021a)

Taxon	Locality	Voucher ID	GenBank accession	Source
Neocaridina ketagalan	Taiwan: Taipei	NCd4	AB300167	Shih & Cai (2007)
Neocaridina denticulata	Taiwan: Kinmen	NCd1	AB300173	Shih & Cai (2007)
Neocaridina saccam	Taiwan: Taipei	NCd9	AB300169	Shih & Cai (2007)
Neocaridina palmata	Vietnam: Cao Bang,	ZMB 30256	MT526825	Do et al. (2020)
Neocaridina spinosa	China: Fujian,	NCo1	AB300174	Shih & Cai (2007)
Outgroups				
Atya innocous	Puerto Rico: Rio Espiritu Santo	GU-EL1	EF489987	Page et al. (2008)
Atya scabra	Panama: Rio Guarumo	HU-510	EF489985	Page et al. (2008)
Atyoida bisulcata	Hawaiian Island: Waiau Stream	GU755	DQ681278	Page et al. (2007)
Atyoida chacei	Palau: Babeldaob	CA1858	PP455330	de Mazancourt et al. (2024)
Atyoida pilipes	French Polynesia: Putoa Falls	GU991	DQ681279	Page et al. (2007)
Atyopsis moluccensis	Petshop in Germany	KZ222	DQ681281	Page et al. (2007)
Atyopsis spinipes	Solomon Island: Tinahula	GU877	DQ681282	Page et al. (2007)

with *Caridina* cf. *babaulti*, although with moderate support (BS = 93%, bpp = 0.92), and then with *Caridina pristis* with high support (BS = 97%, bpp = 1).

The uncorrected p-distances between 16S rRNA gene sequences among *Caridina* species varied from 4.83 to 17.37%, with an average of 12.42% (Table 2). The new species showed the closest genetic relationship to *Caridina* cf. *babaulti*, with a sequence divergence of 4.83%, while it differed from *C. sumatrensis* by 5.35%. The intraspecific divergence within the new species was 0.54%, while within *C. sumatrensis* was 1.16%.

SYSTEMATICS

Family Atyidae De Haan, 1849

Genus Caridina H. Milne Edwards, 1837

Caridina maeklongensis, new species (Figs. 2, 3, 4A–D)

Type materials. Holotype, ovigerous female (CL 3.44 mm; Fig. 2A) (MUMNH-CAR064-9), Sai Yok Yai Waterfall, Sai Yok District, Kanchanaburi Province, Thailand, 14.4363°N, 98.8516°E, coll. E. Jeratthitikul, W. Siriwut & K. Macharoenboon, 25 June 2019; Paratypes, 7 females (CL 3.17–3.53 mm)(MUMNH-CAR064-1, CAR064-7, CAR064-10, CAR064-13, and CAR064-15); 4 males (CL 2.87–3.25 mm) (MUMNH-CAR064-2 to CAR064-5), same collection data as for the holotype; 2 females (CL 3.55–3.97 mm) (MUMNH-CAR062-1 and CAR062-2), Mae Plu Stream, Si Sawat District, Kanchanaburi Province, Thailand, 14.8043°N, 98.1822°E, coll. E. Jeratthitikul, W. Siriwut & K. Macharoenboon, 25 June 2019.

Non-type materials. 13 females (CL 3.08-3.88 mm), 1 male (CL 2.76 mm)(MUMNH-CAR060), Phu Nong Pling Wetland, Thong Pha Phum District, Kanchanaburi Province, Thailand, 14.6278°N, 98.6073°E, coll. E. Jeratthitikul, W. Siriwut & K. Macharoenboon, 25 June 2019; 16 females (CL 3.20-4.16 mm)(MUMNH-CAR061), U-long Stream, Thong Pha Phum District, Kanchanaburi Province, Thailand, 14.7836°N, 98.6711°E, coll. E. Jeratthitikul, W. Siriwut & K. Macharoenboon, 25 June 2019; 8 females (CL 3.60-4.24 mm), 3 males (CL 3.13-3.25 mm)(MUMNH-CAR062), Mae Plu Stream, Si Sawat District, Kanchanaburi Province, Thailand, 14.8043°N, 98.1822°E, coll. E. Jeratthitikul, W. Siriwut & K. Macharoenboon, 25 June 2019; 6 females (CL 2.96-3.49 mm) (MUMNH-CAR063), Huai Mae Khamin Waterfall, Si Sawat District, Kanchanaburi Province, Thailand, 14.6380°N, 98.9866°E, coll. E. Jeratthitikul, W. Siriwut & K. Macharoenboon, 25 June 2019; 5 females (CL 2.96-3.49 mm)(MUMNH-CAR064), Sai Yok Yai Waterfall, Sai Yok District, Kanchanaburi Province, Thailand, 14.4363°N, 98.8516°E, coll. E. Jeratthitikul, W. Siriwut & K. Macharoenboon, 25 June 2019; 4 females (CL 3.28-4.01 mm), 1 male (CL 2.61 mm)(MUMNH-CAR065), Khayeng Stream, Thong Pha Phum District, Kanchanaburi Province,

Taxon	1.	2.	3.	4.	5.	6.	7.	%	9.	10.	11.	12.	13.	14	15.	16.	17.	18.
1. Caridina maeklongensis, new species																		
2. Caridina sumatrensis	5.35																	
3. Caridina cf. babaulti	4.83	5.48																
4. Caridina pristis	8.35	8.29	8.22															
5. Caridina weberi	12.04	11.42	10.80	11.50														
6. Caridina gueryi	13.65	14.01	13.15	14.79	12.68													
7. Caridina longicarpus	14.52	14.40	12.68	13.38	12.68	13.38												
8. Caridina turipi	96.6	9.47	7.51	9.62	9.86	11.97	12.91											
9. Caridina panhai	15.16	14.08	12.44	12.68	13.85	15.73	16.20	12.91										
10. Caridina propinqua	16.57	17.29	15.02	15.26	14.79	17.37	16.43	14.79	8.69									
11. Caridina brachydactyla	13.28	12.83	12.91	12.44	13.85	15.73	15.49	12.44	15.49	15.02								
12. Caridina gracilipes	13.82	13.22	11.50	12.91	13.85	14.79	13.85	11.74	12.21	13.85	9.39							
13. Caridina gracilirostris	16.57	15.73	15.02	15.26	15.49	16.43	15.73	15.02	15.73	15.49	13.15	12.91						
14. Caridina neglecta	13.21	12.52	11.97	12.44	12.21	12.68	15.02	10.80	13.62	13.38	9.62	9.86	10.33					
15. Caridina lanceifrons	9.83	10.33	8.22	11.27	12.44	13.38	14.32	9.15	13.62	15.96	12.44	12.68	15.02	11.27				
16. Caridina typus	11.87	10.25	9.86	11.74	11.38	13.15	12.91	8.22	13.85	15.26	14.08	12.32	16.08	12.68	11.27			
17. Caridina zhujiangensis	9.76	9.15	7.98	10.33	10.09	11.97	11.97	6.57	14.08	15.02	11.03	12.44	15.02	11.03	8.69	7.63		
18. Caridina villadolidi	11.94	11.50	10.33	13.85	12.68	12.44	14.32	8.69	14.79	17.14	13.85	13.62	15.73	13.15	10.80	9.39	7.51	
19. Caridina namdat	9.46	9.94	9.62	10.33	11.50	12.21	13.85	8.92	14.32	15.96	12.68	13.15	15.49	11.03	10.33	9.62	7.51	11.03

Table 2. Matrix of average uncorrected p-distance (%) based on 524 bp of mitochondrial 16S rRNA gene between Caridina species.

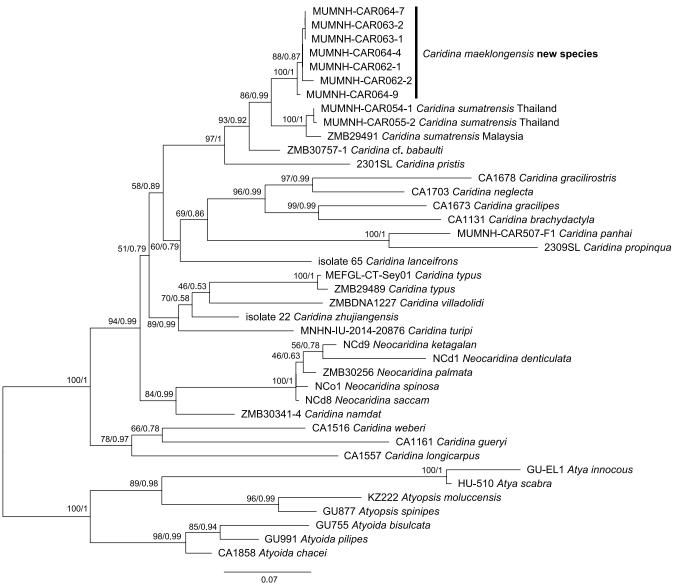


Fig. 1. Phylogenetic tree of *Caridina* and outgroups generated from maximum likelihood (ML) in IQ-TREE based on 524 bp of mitochondrial 16S rRNA gene. The numbers above the branches represent bootstrap values (BS) from ML analysis and bipartition posterior probability (bpp) from Bayesian inference analysis (BI), and are shown as ML/BI. The scale bar indicates the substitution rate.

Thailand, 14.6330°N, 98.5684°E, coll. E. Jeratthitikul, W. Siriwut & K. Macharoenboon, 25 June 2019.

Description. Cephalothorax and cephalic appendage. CL 3.17-3.97 mm (median = 3.44 mm, n = 7), width 2.12-3.06 mm (median = 2.47 mm, n = 7). Rostrum with basal ridge, slightly or moderately bent down, frequently reaching near the end of second segment of antennular peduncle, 0.38-0.54 (median = 0.46, n = 7) times as long as CL (Fig. 2A, B). Rostral formula based on seven individuals: (3-4) + 9-14 / 1–4. Antennal spine placed below inferior orbital angle. Pterygostomian margin subrectangular. Eye well-developed, anterior end reaching to 0.48-0.70 (median = 0.55, n = 7) of the first segment of antennular peduncle. Antennular peduncle 0.47-0.59 (median = 0.55, n = 7) times as long as carapace, first segment 1.63-2.47 (median = 1.80, n = 7) times as long as second segment, second segment 1.03-1.47 (median = 1.30, n = 7) times as long as third segment. Tooth on distolateral

margin of first segment of antennular peduncle prominent (Fig. 2D). Stylocerite reaching to 0.54-0.77 (median = 0.65, n = 7) of first segment of antennular peduncle. Scaphocerite 2.49–2.69 (median = 2.63, n = 7) times as long as wide, distal margin with short plumose setae.

Branchial formula. Podobranch on second maxilliped welldeveloped. Third maxilliped possesses one small and one large arthrobranch. Pleurobranchs present on all pereopods. Third maxilliped with epipod (Fig. 2E). Ultimate segment of endopod with a row of strong spinules at proximal ²/₃ of posterior margin, ending with one large claw, 5–6 spiniform setae on distal ¹/₃ of posterior margin, 0.95–1.04 (median 1.00, n=7) times as long as penultimate segment. Exopod long and slender, with a tuft of long setae at tip.

Pereopods. Epipod present on first four pereopods. Chelae of first and second pereopods well-developed (Fig. 3A, B).

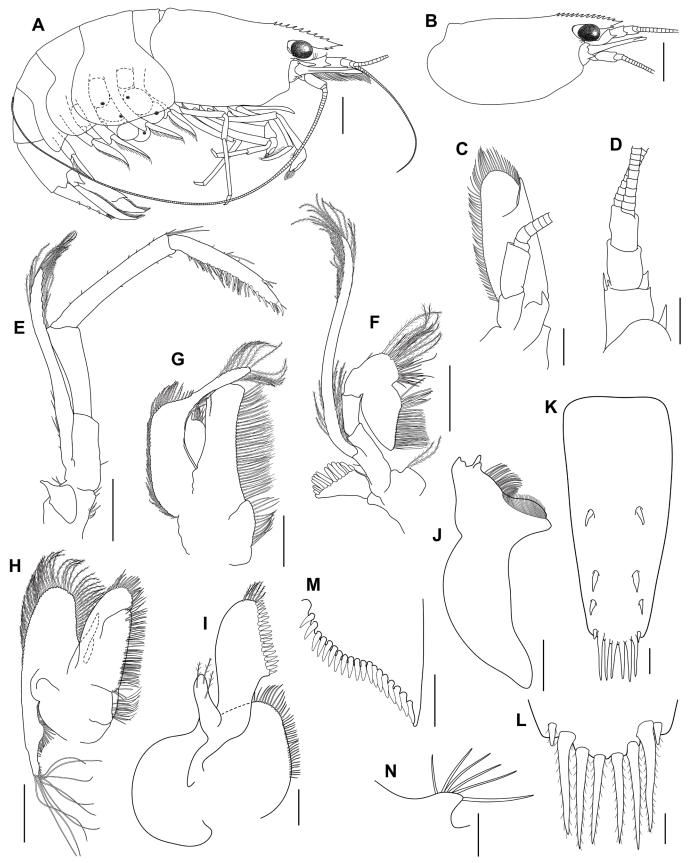


Fig. 2. *Caridina maeklongensis*, new species. A, ovigerous female; B, cephalothorax and cephalic appendages; C, scaphocerite; D, antennular peduncle; E, third maxilliped; F second maxilliped; G, first maxilliped; H, maxilla; I, maxillula; J, mandible; K, telson; L, distal end of telson; M, uropodal diaeresis; N, preanal carina. Drawings were made from holotype female, MUMNH-CAR064-9 (A) and paratype female, MUMNH-CAR064-7 (B–L). Scale bars: A, B = 1 mm; C–H, M = 0.5 mm; I–K, N = 0.2 mm; L = 0.1 mm.

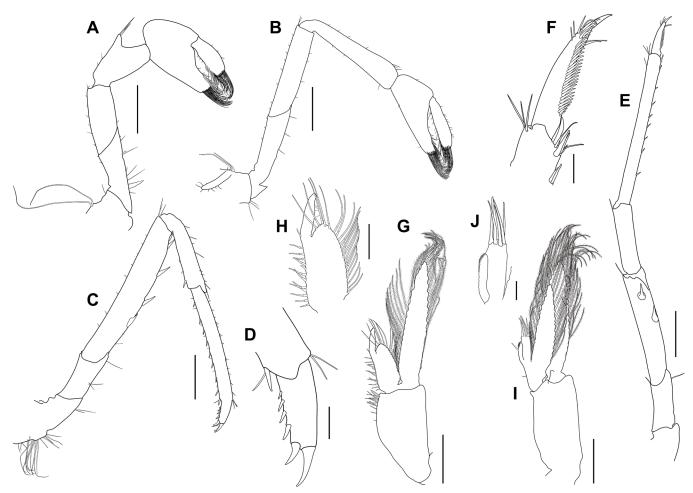


Fig. 3. *Caridina maeklongensis*, new species. A, first pereopod; B, second pereopod; C, third pereopod; D, dactylus of third pereopod; E, fifth pereopod; F, dactylus of fifth pereopod; G, male first pleopod; H, endopod of male first pleopod; I, male second pleopod; J, appendix masculina and appendix interna of male second pleopod. Drawings were made from paratype female, MUMNH-CAR064-7 (A–F) and paratype male, MUMNH-CAR064-4 (G–J). Scale bars: D, F, J = 0.1 mm; A–C, E, G–I = 0.5 mm.

First percopod short (Fig. 3A); chela 1.63-2.35 (median = 1.98, n = 6) times as long as wide, 1.09-1.53 (median = 1.26, n = 6) times as long as carpus; tips of fingers rounded, with tuft of setae near tip; dactylus 0.98-1.27 (median = 1.05, n = 6) times as long as palm; carpus excavated distally, 1.52-2.26 (median = 1.74, n = 6) times as long as wide, 0.88-1.02 (median = 0.98, n = 6) times as long as merus; merus 2.33-3.04 (median = 2.78, n = 6) times as long as wide, 1.31-2.16 (median = 1.72, n = 6) times as long as ischium.

Second percopod more slender than first percopod (Fig. 3B); chela long, 2.40–3.56 (median = 2.83, n = 6) times as long as wide, 0.72–0.78 (median = 0.74, n = 6) times as long as carpus, tips of fingers round, with tuft of setae near tip; dactylus 1.19-1.66 (median = 1.52, n = 6) times as long as palm; carpus slender, 4.57-6.09 (median = 5.10, n = 6) times as long as wide, 1.10-1.27 (median = 1.14, n = 6) times as long as merus; merus 4.06-5.93 (median = 5.31, n = 6) times as long as wide, 1.52-1.80 (median = 1.63, n = 6) times as long as ischium.

Third percopod not sexually dimorphic (Fig. 3C); dactylus with 5–7 spiniform setae on flexor margin (Fig. 3D), 2.97-3.41 (median = 3.20, n = 6) times as long as wide (including terminal claw), terminating with one large claw;

propodus with numerous spiniform setae on lateral and posterior margin, 8.36-10.82 (median = 9.35, n = 6) times as long as wide, 3.55-4.42 (median 4.05, n = 6) times as long as dactylus; carpus with 2–4 spiniform setae on posterior margin of outer surface, the distal seta largest, the other setae minute, 4.47-6.05 (median = 4.81, n = 6) times as long as wide, 0.59-0.70 (median = 0.63, n = 6) times as long as propodus; merus with three large spiniform setae on posterior margin of outer surface, 6.16-6.80 (median = 6.50, n = 6) times as long as wide, 1.89-2.27 (median = 1.99, n = 6) times as long as carpus; ischium with one spiniform seta.

Fifth pereopod slender (Fig. 3E); dactylus with 24–38 spiniform setae on flexor margin (Fig. 3F), 3.40–3.70 (median = 3.65, n = 5) times as long as wide (including terminal claw), terminating with one large claw; propodus with numerous spiniform setae on posterior margin, 10.61–14.51 (median = 13.43, n = 5) times as long as wide, 3.66–4.71 (median = 4.11, n = 5) times as long as dactylus; carpus with 2–3 (mode = 3, n = 5) spiniform setae on posterior margin of outer surface, the distal seta largest, the other setae minute, 4.19–4.89 (median = 4.37, n = 5) times as long as propodus; merus with two large setae on posterior margin of outer surface, 5.73–7.23 (median = 6.35, n = 5) times as long as

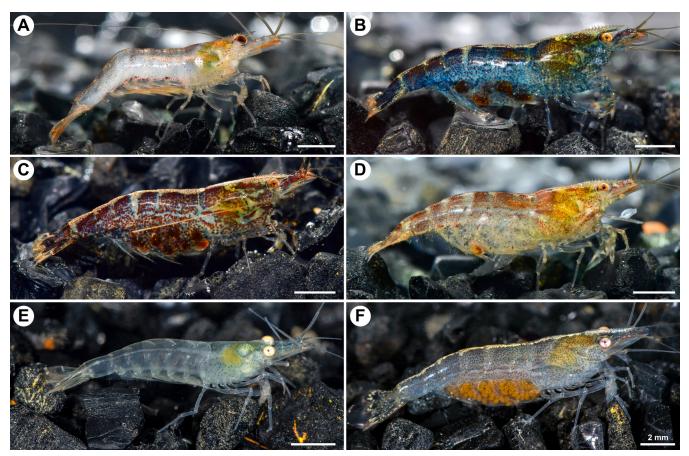


Fig. 4. Living habitus specimens of *Caridina* species from the Mae Klong Basin. A–D, *Caridina maeklongensis*, new species: A, paratype male, MUMNH-CAR064-4; B, paratype female, MUMNH-CAR064-1; C, paratype female, MUMNH-CAR064-15; and D, paratype female, MUMNH-CAR064-13. E, F, *C. sumatrensis*: E, male, MUMNH-CAR706-P2; and F, female, MUMNH-CAR706-P1.

wide, 1.54-1.64 (median = 1.59, n = 5) times as long as carpus; ischium without spiniform setae.

Pleopods (n = 4). Endopod of male first pleopod subtriangular (Fig. 3G, H), wider proximally, 2.05-2.56 (median = 2.21, n = 4) times as long as width, 0.38-0.48 (median = 0.43, n = 4) times exopod length, with elongated appendix interna, emerged near the tip. Appendix masculina of second male pleopod rod-shaped (Fig. 3I, n = 4), with numerous setae, 0.70-0.73 (median = 0.71, n = 4) times as long as endopod (including distal setae). Appendix interna slender, reaching 0.69-0.76 (median = 0.7, n = 4) times of appendix masculina length (Fig. 3J).

Abdomen. Sixth abdominal somite 0.44-0.52 (median = 0.48, n = 7) times carapace length, 1.13-1.48 (median = 1.29, n = 7) times as long as fifth somite, 0.76-0.93 (median = 0.84, n = 7) times as long as telson (Fig. 2A). Telson 2.33-2.79 (median = 2.60, n = 7) times as long as wide, with 3–4 pairs of dorsal spiniform setae and one pair of dorsolateral spiniform setae (Fig. 2K). Distal margin of telson subtriangular, posteromedian projection absent or greatly reduced, with 6–8 moveable plumose setae that are subequal in length (Fig. 2L). Uropodal diaeresis with 13–19 short moveable spiniform setae (Fig. 2M). Preanal carina subtriangular, with a few setae, without a spine (Fig. 2N).

Eggs. Ovigerous females with few eggs (25–35 eggs per individual; n = 3). Size of eye-developed eggs $0.82-0.93 \times 0.51-0.60 \text{ mm}$ (n = 30).

Colour in life. Female and male shrimps exhibit distinct colouration. Male body is translucent, decorated with scattered small dark spots (Fig. 4A). Colour of female shrimps is variable, as dark blue, copper, or brown (Fig. 4B–D). Rostrum is yellowish-orange. Cephalic region is decorated with gold, orange, and brown stripes. Each abdominal somite furnished dorsally with conspicuous yellow-orange bands. Eggs are dark brown to dark orange.

Distribution and habitat. Based on the present study, the distribution range of the new species is limited to the upper part of the Mae Klong Basin in western Thailand (Fig. 5). They are commonly found in aquatic vegetation near stream banks or ponds located near waterfalls or headwaters.

Etymology. The specific name is from its type locality, the Mae Klong Basin.

Remarks. The phylogenetic tree suggests a sister relationship between the new species and *C. sumatrensis* (Fig. 1). These two species resemble each other in having similar P1 and P2, and appendix interna on the endopod of the first pleopod in males. However, they can be distinguished by the following diagnostic features (a comparison of key characters among

Characters	C. <i>weberi</i> De Man, 1892 (from De Man, 1892; Mazancourt et al., 2020)	<i>C. sumatrensis</i> De Man, 1892 (this study)	C. <i>babaulti</i> Bouvier, 1918 (from Bouvier, 1918; Pandya & Richard, 2019)	C. maeklongensis, new species
Rostrum	Rostrum straight, short, reaching to base or near middle of second segment of antennular peduncle	Rostrum with a basal ridge, slightly bent down, reaching beyond the end of second segment of antennular peduncle	Rostrum reaching to the end of antennular peduncle or reaching to middle of 3rd antennular peduncle	Rostrum with a basal ridge, short, slightly or moderately bent down, frequently reaching near the end of second segment of antennular peduncle
Rostrum formula	(0-2) + 11-23 / 2-5	(4-6) + 17-21 / 3-6	(3-7) 14-25/3-8	(3-4) + 9-14 / 1-4
Antennular peduncle	0.64 as long as CL	0.46-0.55 as long as CL	0.6-0.8 as long as CL	0.47-0.53 as long as CL
Third maxilliped	n/a	Ultimate segment of endopod 0.74– 0.91 times as long as penultimate segment.	n/a	Ultimate segment of endopod 0.95– 1.04 times as long as penultimate segment.
P1 chela L/W	2.0 -2.3	2.11–2.66	2.2–2.6	1.63-2.35
P1 dactylus/palm	0.8–1.5	0.91 - 1.26	1.25–1.7	0.98-1.27
P1 carpus L/W	1.4-2.0	1.40–1.83	1.6–2.3	1.52-2.26
P2 chela L/W	2.5-2.9	2.71–3.40	2.5–2.9	2.40–3.56
P2 dactylus/palm	1.3-1.7	1.17-2.20	1.15-2.0	1.19–1.66
P2 carpus L/W	4.8-5.5	4.63–6.69	4.3–5.5	4.57-6.09
Setae on P3 dactylus	6–8	4–6	7–10	5-7
P3 dactylus L/W	2.8–3.7	2.23-3.13	2.5–3.5	2.97–3.41
P3 propodus/dactylus	4.0-4.6	4.34–5.67	3.5-5.2	3.55-4.42
P3 carpus L/W	n/a	4.13-5.36	n/a	4.47–6.05
Setae on P5 dactylus	47–66	32-43	30-45	24–38
P5 dactylus L/W	3.9–5.2	2.76–3.96	3.1–4.2	3.40–3.70
P5 propodus/dactylus	3.8-4.5	4.31–5.79	3.2–3.9	3.66–4.71
P5 carpus L/W	n/a	4.65–5.78	n/a	4.19–4.89
Dorsal spine on telson	5-7 pairs	3-4 pairs	4-6 pairs	3-4 pairs

Table 3. Comparison of morphological characters between C. weberi, C. sumatrensis, C. babaulti, and C. maeklongensis, new species

Characters	<i>C. weberi</i> De Man, 1892 (from De Man, 1892; Mazancourt et al., 2020)	<i>C. sumatrensis</i> De Man, 1892 (this study)	C. babaulti Bouvier, 1918 (from Bouvier, 1918; Pandya & Richard, 2019)	C. maeklongensis, new species
Plumose setae on telson	6-11 setae, intermediate setae longer than lateral ones	6-9 setae, subequal in length	4–8 setae, intermediate spines vary length, fractionally longer or shorter than the lateral spines.	6-8 setae, subequal in length
Posteromedian projection on distal end of telson	present	present	absent	greatly reduced or absent
Distal end of telson	rounded	subtriangular	rounded	subtriangular
Setae on uropodal diaeresis	17–21	15-22	12–21	13–19
Preanal carina	high, without a spine	subtriangular, high, without a spine	subtriangular, without a spine	subtriangular, high, without a spine
Appendix interna on endopod of male Pl1	present	present	present	present
Egg size	$0.35-0.42 \times 0.19-0.25 \text{ mm}$	$0.41-0.46 \times 0.24-0.29 \text{ mm}$	$0.9-1.0 \times 0.50-0.62 \text{ mm}$	$0.82-0.93 \times 0.51-0.60 \text{ mm}$

species is presented in Table 3). The rostrum of the new species is relatively shorter when compared to *C. sumatrensis* (reaching near the end of second segment of antennular peduncle vs reaching near the end of antennular peduncle). The rostral teeth of the new species are fewer than those of *C. sumatrensis*, including the dorsal teeth (9–14 vs 12–17), the ventral teeth (1–4 vs 3–6), and the postorbital teeth (3–4 vs 4–6). The new species possesses a greatly reduced or absent posteromedian projection on the distal end of the telson, whereas this character is well-developed in *C. sumatrensis*. Lastly, eggs of the new species are much larger than *C. sumatrensis* (0.82–0.93 × 0.51–0.60 mm vs 0.41–0.46)

 \times 0.24–0.29) (De Man, 1892; Cai et al., 2007; this study).

The morphology of the new species is also similar to that of C. weberi (see summary in Table 3). However, it differs from C. weberi in several characteristics. The rostrum of the new species is relatively longer than that of C. weberi (reaching to base or around the middle of second segment of antennular peduncle vs reaching to base or near middle of second segment of antennular peduncle). The dorsal teeth are fewer in the new species (9-14 vs 11-23 in C. weberi). However, the number of ventral teeth shows considerable overlap between the two species (1–4 vs 2–5 in C. weberi), and the new species possesses a larger number of postorbital teeth compared to C. weberi (3-4 vs 0-2). The new species has a shorter antennular peduncle than that of C. weberi (0.47-0.53 as long as CL vs 0.64 as long as CL). It also possesses a stouter P5 dactylus (3.40-3.70 as long as wide vs 3.9-5.2 as long as wide in C. weberi), but contains fewer spiniform setae (24-38 vs 47-66 in C. weberi). The characteristics of the distal end of the telson also differ between the new species and C. weberi. In the new species, the distal end of the telson is subtriangular in shape (vs rounded in C. weberi), it possesses a greatly reduced or absent posteromedian projection (vs well-developed in C. weberi), and has fewer spiniform setae (6-8 vs 6-11 in C. weberi). Furthermore, the size of the eggs in the new species is much larger than those in C. weberi (0.82–0.93 \times 0.51–0.60 mm vs 0.35–0.42 \times 0.19-0.25 mm) (De Man, 1892; de Mazancourt et al., 2020). Additionally, the distributions of these two species do not overlap. Caridina weberi is distributed in Indonesia (Sumba, Halmahera), Papua New Guinea, and the Solomon Islands (de Mazancourt et al., 2020), while the new species occurs only in the Mae Klong Basin in mainland Southeast Asia. Moreover, the distant phylogenetic placement (Fig. 1), and high genetic divergence (12.04%; Table 2), strongly support the conclusion that they are distinct species.

In terms of genetic divergence, the new species showed the closest divergence to the sequence identified as *C*. cf. *babaulti*. This sequence was retrieved from the GenBank database (MN399172). It has been used in a previous study and was stated to have been collected from West Bengal, India (Klotz et al., 2019). *Caridina babaulti* was originally described from Central India (Bouvier, 1918). Its distribution range covers the areas of Central, Western, and Southern India (Pandya & Richard, 2019). It was recently recorded as an introduced ornamental pet that can establish populations in open waters in Europe (Maciaszek et al., 2021). Morphologically, the

new species shared a few characteristics with C. babaulti, including the absence of a posteromedian projection and the number of spinules on the uropodial diaeresis. Both species carry large-sized eggs (0.82-0.93 × 0.51-0.60 mm in the new species vs $0.9-1.0 \times 0.50-0.62$ mm in C. babaulti), and are characterised as landlocked species (Pandya & Richard, 2019, de Mazancourt et al., 2021, 2023; Hamasaki et al., 2021). However, the new species differs from C. babaulti by having a shorter rostrum (reaching near the end of second segment of antennular peduncle vs reaching to middle of third segment antennular peduncle in C. babaulti), fewer dorsal teeth (9-14 vs 14-25 in C. babaulti), stouter P1 chelae (1.63–2.35 vs 2.2–2.6 as long as wide in C. babaulti), fewer spiniform setae on P3 dactylus (5-7 vs 7-10 in C. babaulti), fewer spiniform setae on P5 dactylus (24-38 vs 30-45 in C. babaulti), and subtriangular distal end of telson (vs rounded in C. babaulti) (Bouvier, 1918; Pandya & Richard, 2019).

Caridina sumatrensis De Man, 1892 (Figure 4E, F, 6)

- *Caridina weberi* var. *sumatrensis* De Man, 1892: 375, pl. 22, fig. 23g, Type locality: Deli, Sumatra, Indonesia, Type material: Lectotype, ZMA De 102603, ovigerous female (CL 5.3 mm) (designated by Cai & Naiyanetr, 2024). Kemp, 1918a: 99; Pillai, 1964: 43.
- Caridina weberi sumatrensis Bouvier, 1904: 132; Bouvier, 1905: 75, 83; Kemp, 1918b: 292, Bouvier, 1925: 247, fig. 567; Johnson, 1961: 46; Kazmi et al., 2002.
- *Caridina sumatrensis* Wowor et al., 2004: 343, fig. 6p, q; Cai & Shokita, 2006: 246, fig. 6C–F; Cai et al., 2007: 285, fig. 7; Cai & Naiyanetr, 2024: 774, fig. 2, 3.

Materials examined. 9 females (CL 3.91-4.49 mm), 3 males (CL 2.51-2.94 mm)(MUMNH-CAR053, used for measurement in description), Mae Klong River, Tha Maka District, Kanchanaburi Province, Thailand, 13.8679°N, 99.8167°E, coll. W. Siriwut & W. Manonai, 19 April 2019; 1 female (CL 4.10 mm)(MUMNH-CAR054), Mae Klong River, Photharam District, Ratchaburi Province, Thailand, 13.6318°N, 99.8162°E, coll. W. Siriwut & W. Manonai, 19 April 2019; 4 females (CL 3.29-4.21 mm)(MUMNH-CAR055), Mae Klong River, Photharam District, Ratchaburi Province, Thailand, 13.7152°N, 99.8492°E, coll. W. Siriwut & W. Manonai, 19 April 2019; 3 females (CL 3.73-4.29 mm)(MUMNH-CAR056), Mae Klong River, Photharam District, Ratchaburi Province, Thailand, 13.7393°N, 99.8420°E, coll. W. Siriwut & W. Manonai, 19 April 2019; 4 females (CL 3.57-4.08 mm) (used for measurement in description); 4 males (CL 2.41-2.93 mm) (MUMNH-CAR706, used for measurement in description), Klong Bang Tanod River, Photharam District, Ratchaburi Province, Thailand, 13.6537°N, 99.8116°E, coll. E. Jeratthitikul & K. Macharoenboon, 8 August 2019.

Description. Cephalothorax and cephalic appendage. CL 3.57-4.60 mm (median = 4.08 mm, n = 13), width 2.65-3.48 mm (median = 2.92 mm, n = 13). Rostrum with basal ridge, slightly bent down, frequently reaching near the end of antennular peduncle (at least reaching beyond the end of second segment of antennular peduncle), 0.50-0.60

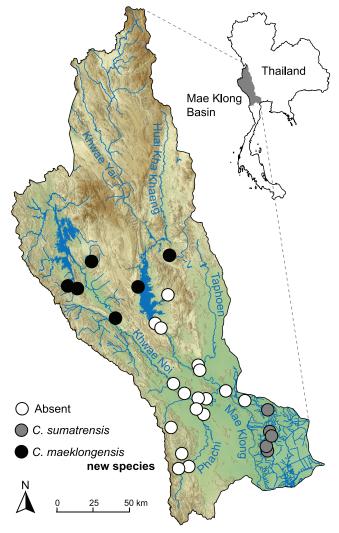


Fig. 5. Map of the Mae Klong Basin showing sampling localities of *Caridina maeklongensis*, new species (black circles) and *C. sumatrensis* (grey circle), and the localities where both species were absent (white circles).

(median = 0.55, n = 13) times as long as CL (Fig 6A, B). Rostral formula based on 13 individuals: (4-6) + 17-21 / 3-6. Antennal spine placed below inferior orbital angle. Pterygostomian margin subrectangular. Eye well-developed, anterior end reaching to 0.59–0.84 (median = 0.71, n = 13) of first segment of antennular peduncle. Antennular peduncle 0.46–0.55 (median = 0.51, n = 13) times as long as carapace, first segment 1.60–2.15 (median = 1.80, n = 13) times as long as second segment, second segment 1.03–1.33 (median = 1.16, n = 13) times as long as third segment. Tooth on distolateral margin of first segment of antennular peduncle prominent. Stylocerite reaching to 0.59–0.74 (median = 0.70, n = 13) of first segment of antennular peduncle. Scaphocerite 2.50–2.97 (median = 2.75, n = 13) times as long as wide, distal margin with short plumose setae.

Branchial formula. Podobranch on second maxilliped welldeveloped. Third maxilliped possesses one small and one large arthrobranch. Pleurobranchs present on all pereopods. Third maxilliped with epipod. Ultimate segment of endopod with a row of strong spinules at proximal $\frac{2}{3}$ of posterior margin, ending with one large claw, 5–7 spiniform setae on

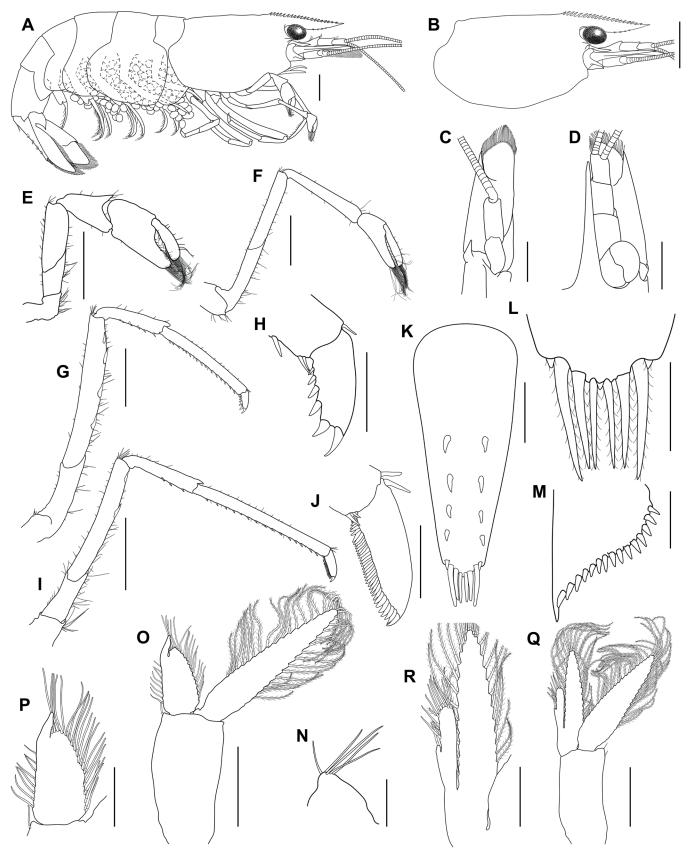


Fig. 6. *Caridina sumatrensis* De Man, 1892. A, ovigerous female; B, cephalothorax and cephalic appendage; C, scaphocerite; D, antennular peduncle; E, first pereopod; F, second pereopod; G, third pereopod; H, dactylus of third pereopod; I, fifth pereopod; J, dactylus of fifth pereopod; K, telson; L, distal end of telson; M, uropodal dieresis; N, preanal carina; O, male first pleopod; P, endopod of male first pleopod; Q, male second pleopod; R, appendix masculina of male second pleopod. Drawings were made from ovigerous female, MUMNH-CAR706-P1 (A–M) and male, MUMNH-CAR706-P2 (O–R) collected from the Mae Klong Basin, Thailand. Scale bars: A, B, E, F, G, I, K = 1 mm; C, D, M, O, Q = 0.5 mm; H, J, L, N, P, R = 0.25 mm.

distal $\frac{1}{3}$ of posterior margin, 0.74–0.91 (median = 0.83, n = 10) times as long as penultimate segment. Exopod long and slender, with a tuft of long setae at tip.

Pereopods. Epipod present on first four pereopods. Chelae of first and second pereopods well-developed (Fig. 6E, F).

First percopod short (Fig. 6E); chela 2.11-2.66 (median = 2.18, n = 11) times as long as wide, 1.31-1.62 (median = 1.48, n = 11) times as long as carpus; tips of fingers rounded, with tuft of setae near tip; dactylus 0.91-1.26 (median = 1.07, n = 11) times as long as palm; carpus excavated distally, 1.40-1.83 (median = 1.67, n = 11) times as long as wide, 0.78-1.10 (median = 0.96, n = 11) times as long as merus; merus 2.44-2.93 (median = 2.62, n = 11) times as long as long as wide, 1.15-2.14 (median = 1.84, n = 11) times as long as long as ischium.

Second percopod more slender than first percopod (Fig. 6F); chela long, 2.71-3.40 (median = 2.84, n = 11) times as long as wide, 0.65-0.87 (median = 0.74, n = 11) times as long as carpus, tips of fingers round, with tuft of setae near tip; dactylus 1.17-2.20 (median = 1.80, n = 11) times as long as palm; carpus slender, 4.63-6.69 (median = 5.72, n = 11) times as long as wide, 0.43-0.75 (median = 0.54, n = 11) times as long as merus; merus 5.00-7.41 (median = 5.83, n = 11) times as long as wide, 1.24-2.15 (median = 1.54, n = 11) times as long as ischium.

Third perception not sexually dimorphic (Fig. 6G); dactylus with 4–6 spiniform setae on flexor margin (Fig. 6H), 2.23–3.13 (median = 2.65, n = 9) times as long as wide (including terminal claw), terminating with one large claw; propodus with numerous spiniform setae on lateral and posterior margin, 8.49–11.53 (median = 9.71, n = 9) times as long as wide, 4.34–5.67 (median = 4.50, n = 9) times as long as dactylus; carpus with 3–5 spiniform setae on posterior margin of outer surface, the distal seta largest, the other setae minute, 4.13–5.36 (median = 4.69, n = 9) times as long as wide, 0.50–0.69 (median = 0.66, n = 9) times as long as propodus; merus with 4–5 large spiniform setae on posterior margin of outer surface, 6.25–6.96 (median = 6.67, n = 9) times as long as wide, 1.88–2.26 (median = 2.09, n = 9) times as long as carpus; ischium with one spiniform seta.

Fifth percopod slender (Fig. 6I); dactylus with 32–43 spiniform setae on flexor margin (Fig. 6J, n = 9), 2.76–3.96 (median = 3.41, n = 9) times as long as wide (including terminal claw), terminating with one large claw; propodus with numerous spiniform setae on posterior margin, 12.39–14.45 (median = 13.61, n = 9) times as long as wide, 4.31–5.79 (median = 4.70, n = 9) times as long as dactylus; carpus with 3–5 spiniform setae on posterior margin of outer surface, the distal seta largest, the other setae minute, 4.65–5.78 (median = 5.05, n = 9) times as long as wide, 0.45–0.56 (median = 0.52, n = 9) times as long as propodus; merus with 2–4 (mode = 2, n = 9) large setae on posterior margin of outer surface, 6.12–7.45 (median = 6.91, n = 9) times as long as wide, 1.48–1.82 (median = 1.61, n = 9) times as long as carpus; ischium without spiniform setae.

Pleopods. Endopod of male first pleopod subtriangular (Fig. 6O, P), wider proximally, 1.73-2.27 (median = 1.94, n = 7) times as long as width, 0.32-0.46 (median = 0.41, n = 7) times exopod length, with elongated appendix interna. Appendix masculina of second male pleopod rod-shaped (Fig. 6Q, R), with numerous setae, 0.74-0.81 (median = 0.77, n = 7) times as long as endopod (including distal setae). Appendix interna slender, reaching 0.55-0.64 (median = 0.61, n = 7) times appendix masculina length.

Abdomen. Sixth abdominal somite 0.32-0.50 (median = 0.43, n = 10) times carapace length, 1.10-1.54 (median = 1.29, n = 10) times as long as fifth somite, 0.60-0.99 (median = 0.82, n = 10) times as long as telson (Fig. 6A). Telson 2.33-2.96 (median = 2.71, n = 10) times as long as wide, with 3–4 pairs of dorsal spiniform setae and one pair of dorsolateral spiniform setae (Fig. 6K). Distal margin of telson subtriangular, with a posteromedian projection, and 6–9 moveable plumose setae, subequal in length (Fig. 6L). Preanal carina subtriangular, high, without a spine (Fig. 6N). Uropodal diaeresis with 15–22 short moveable spiniform setae (Fig. 6M).

Eggs. Ovigerous females with numerous eggs (Fig. 3F, 6A). Size of eye-developed eggs $0.41-0.46 \times 0.24-0.29$ mm (n = 30).

Colour in life. Female and male shrimps exhibit distinct colouration. For specimens from the Mae Klong River, male body is translucent, decorated with scattered small dark spots (Fig. 4E). Colour of female shrimps is frequently dark to light blue, decorated with scattered small dark spots (Fig. 4F). Rostrum is yellowish-orange. Each abdominal somite furnished dorsally with conspicuous yellowish-orange bands. Eggs are brown to orange.

Distribution and habitat. Indonesia (Sumatra), Philippines, Singapore, Malaysia, Thailand, Myanmar, India, Pakistan (Kemp, 1918a, b; Kazmi et al., 2002; Cai et al., 2007; Cai & Naiyanetr, 2024; this study). Based on the field survey in the Mae Klong Basin in this study, *C. sumatrensis* is restricted to the lower part of the basin (Fig. 5), and commonly found in lowland rivers and their tributaries. They are found living on aquatic vegetation near the banks.

Remarks. The morphology of *C. sumatrensis* from the Mae Klong Basin in our collection closely matches with the original description (De Man, 1892), redescription of type materials (Cai & Naiyanetr, 2024), and descriptions in previous taxonomic literature (e.g., Kemp, 1918b; Pillai, 1964; Cai et al., 2007). Particularly, the characteristic of the slightly bent downward rostrum with a ridge at the base in our samples (Fig. 6A, B) is in close agreement with illustrations by previous studies (i.e., De Man, 1892; Cai et al., 2007; Cai & Naiyanetr, 2024). Populations from Mae Klong Basin share a similar number of rostral teeth with those from the original description by De Man (1892), including the number of dorsal teeth (17–21 vs 16–20), ventral teeth (3–6 both in the Mae Klong population and the original description), and postorbital teeth (4–6 vs 5–6). The egg size of the Mae Klong

population is also congruent with previous reports ($0.41-0.46 \times 0.24-0.29 \text{ mm vs} 0.46-0.47 \times 0.28-0.29 \text{ mm by Kemp,}$ 1918b; $0.46 \times 0.28 \text{ mm by Pillai, 1964; and } 0.40-0.42 \times 0.22-0.25 \text{ mm by Cai}$ & Naiyanetr, 2024). However, the Mae Klong population possesses a slightly lower number of spiniform setae on the P5 dactylus (32-43 vs 36-57 by Kemp, 1918b; more than 40 by Cai et al., 2007; and 42-49 by Cai & Naiyanetr, 2024).

Originally, C. sumatrensis was proposed as a variant form of C. weberi, as "Caridina weberi var. sumatrensis De Man, 1892". Wowor et al. (2004) later elevated it as a valid species. This classification has been widely accepted in subsequent works (Cai & Shokita, 2006; Cai et al., 2007; Cai & Naiyanetr, 2024). Caridina sumatrensis differs from C. weberi in several points (see summary in Table 3), including having a ridge at the base of rostrum (vs absent), longer rostrum (reaching near the end of third segment of antennular peduncle vs reaching to the base or near the middle of second segment of antennular peduncle), more dorsal teeth (16-20 vs 10-19, usually 13-14), more postorbital teeth (4-6 vs 0-2), shorter antennular peduncle (0.46-0.55 as long as CL vs 0.64 as long as CL), stouter P5 dactylus (2.76-3.96 vs 3.9-5.2 as long as wide), and the distal end of telson subtriangular (vs rounded) (De Man, 1892; Cai et al., 2007, de Mazancourt et al., 2020; Cai & Naiyanetr, 2024; this study).

Caridina sumatrensis shares similarities with *C. babaulti*. However, several key morphological characteristics can be used to separate them. The P2 chela of *C. sumatrensis* is more slender than those of *C. babaulti* (2.71–3.40 vs 2.5–2.9), while the P3 dactylus of *C. sumatrensis* has fewer spiniform setae (4–6 vs 7–10). *Caridina sumatrensis* possesses a conspicuous posteromedian projection on the distal end of the telson. This feature is absent in *C. babaulti*. In addition, *C. sumatrensis* produces small-sized eggs, whereas the eggs of *C. babaulti* are much larger (0.41–0.46 × 0.24–0.29 mm vs 0.9–1.0 × 0.50–0.62 mm) (Bouvier, 1918; Pandya & Richard, 2019).

DISCUSSION

This study discovered a new freshwater shrimp, Caridina maeklongensis, new species, from the Mae Klong Basin, western Thailand. The validity of the new species is supported not only by its distinct morphological characters as described above in the remarks, but also by DNA evidence. Phylogenetic analyses consistently placed the new species as a well-supported clade distinct from other examined Caridina species (Fig. 1). The clear distinction, particularly from its sister species, C. sumatrensis, strongly indicates the potential reproductive isolation between the two species despite their distribution within the same river basin (Fig. 5), and justifies their recognition as distinct species. Furthermore, the genetic distances between the new species and closely related taxa (i.e., C. sumatrensis, C. cf. babaulti, and C. pristis), which ranged between 4.83% and 8.35% (6.17% average) in the mitochondrial 16S rRNA gene (Table 2), are comparable to established thresholds for species delimitation in other Caridina, such as at least 3.8%

in the *C. pareparensis* species group (Klotz et al., 2023), at least 6.7% among *C. tricincta* and its related species (Do et al., 2020), or at least 5.1% among *Caridina* in Australia (Short et al., 2019). Consequently, the establishment of the new taxon is warranted.

Morphological characters used in Caridina have generally relied on the shape of the rostrum, the number of rostral teeth, the characters of the telson, the number of spiniform setae on the P3 and P5 dactylus, and the characters of the uropodial diaeresis (Bouvier, 1905, 1925; Cai & Ng, 2007; Cai et al., 2007; Richard & Clark, 2014; de Mazancourt et al., 2018, 2020, 2024; Klotz et al., 2021). In our study, we consistently found these to be useful characters for species identification among the closely related species examined here (Table 3). Moreover, egg size can be used as a key character to separate similar-looking species; here it serves as a significant character for distinguishing C. maeklongensis, new species, from its relatives (Table 3). This important characteristic in the reproductive biology of *Caridina* has been used previously in several studies. For example, Kemp (1918b) and Cai & Ng (2007) noted that egg size is a useful trait to distinguish C. gracillima Lanchester, 1902 (0.55-0.66 \times 0.35–0.40 mm; Cai & Ng, 2007) from C. gracilirostris De Man, 1892 (0.46 × 0.25 mm; Cai & Ng, 2007; 0.34–0.43 × 0.19–0.26 mm; de Mazancourt et al., 2020). Cai et al. (2007) utilised egg size as one of the characters to differentiate C. propingua De Man, 1908a (0.38–0.54 × 0.25–0.30 mm) from C. johnsoni Cai, Ng & Choy, 2007 (0.60 × 0.40 mm), and C. malayensis Cai, Ng & Choy, 2007 (0.90-0.96 × 0.55-0.60 mm) from C. temasek Choy & Ng, 1991 (0.70–0.85 \times 0.44-0.54 mm). Similarly, Richard & Clark (2014) employed the size of eggs to distinguish among C. simoni Bouvier, 1904 (0.65–1.0 × 0.45–0.6 mm), C. brachydactyla De Man, 1908b (0.35–0.41 × 0.2–0.23 mm), C. gracilipes De Man, 1892 (0.35–0.39 × 0.19–0.23 mm), C. peninsularis Kemp, 1918 (0.49–0.58 \times 0.23–0.35 mm), and C. meridionalis Roux, 1926 (0.60–0.65 \times 0.35–0.39 mm).

Egg size is also particularly useful for distinguishing between landlocked and amphidromous species, along with the patterns of their distribution. Amphidromous species typically produce numerous small eggs and have a high dispersal ability, while landlocked species spawn fewer and larger eggs as well as exhibit a more restricted distribution (Lai & Shy, 2009; Han et al., 2011; Bauer, 2013; Yatsuya et al., 2013; de Mazancourt et al., 2021, 2023; Hamasaki et al., 2021). Our findings for C. sumatrensis and C. maeklongensis are consistent with this pattern. In detail, C. sumatrensis produces numerous small-sized eggs (0.41–0.46 \times 0.24–0.29 mm, this study; $0.40-0.42 \times 0.22-0.25$ mm, Cai & Naiyanetr, 2024). It occurs in lowland rivers near a coastal area (Fig. 5) where the salinity levels are higher compared to the upper section of the river (Sudta et al., 2021), and exhibits a wider distribution area covering Indonesia (Sumatra), Philippines, Singapore, Malaysia, Thailand, Myanmar, India, and Pakistan (Kemp 1918a, b; Kazmi et al., 2002; Cai et al., 2007). These characteristics suggest that C. sumatrensis is an amphidromous species. In contrast, C. maeklongensis carries a small number of very large-sized eggs (0.82-0.93

× 0.51–0.60 mm) and is restricted to a narrow area around the upper part of the Mae Klong Basin (Fig. 5), suggesting a landlocked species. Large-sized eggs also have been recorded in other previously confirmed landlocked species from Thailand as noted by Cai & Naiyanetr (2024), including *C. annandalei* Kemp, 1918 (0.95–1.05 × 0.55–0.70 mm; Cai & Ng, 2000), *C. lanceifrons* Yu, 1936 (0.80–0.90 × 0.50–0.60 mm; Do et al., 2021b), *C. macrophora* Kemp, 1918 (0.90–0.96 × 0.52–0.58 mm; Kemp, 1918b), *C. rangoona* Cai & Ng, 2000 (0.60–0.70 × 0.31–0.40 mm; Cai & Ng, 2000), *C. tonkinensis* Bouvier, 1919 (0.68–0.75 × 0.40–0.48 mm; Cai & Naiyanetr, 2024), *C. johnsoni* (0.60 × 0.40 mm; Cai et al., 2007), *C. temasek* (0.70–0.85 × 0.44–0.54 mm; Cai et al., 2007), and *C. panhai* (0.94–1.06 × 0.60–0.67 mm; Macharoenboon et al., 2023).

The discovery of a new species in this study elevates the total number of recorded Caridina species in Thailand to 19 (Cai & Naiyanetr, 2024; this study). Of these, five species are confirmed as endemic to Thailand, including C. gracillima; C. panhai; C. thai Cai & Naiyanetr, 2024; C. kottelati Cai & Naiyanetr, 2024; and the newly described C. maeklongensis (Cai & Naiyanetr, 2024; this study). The presence of endemic species, particularly within the genus Caridina, again highlights the importance of Thailand as a vital reservoir of biodiversity in freshwater ecosystems. This is especially evident in the Mae Klong Basin, where the high diversity of freshwater fauna has been well documented (Beamish et al., 2006; Naiyanetr, 2007; Kulabtong et al., 2014; Beamish & Plongsesthee, 2015; Maneechan & Prommi, 2015; Konopleva et al., 2019; Pfeiffer et al., 2021). Many of the species found there are endemic to this basin, such as freshwater mussels (Konopleva et al., 2019; Kongim et al., 2023), cyprinid fishes (Tejavej, 2012; Kangrang et al., 2016), and the freshwater shrimps described in this study. The high level of endemism of freshwater fauna in the Mae Klong Basin not only highlights the ecological significance of this region, but also emphasises the need for targeted conservation efforts to preserve these unique habitats and their fragile resident species.

ACKNOWLEDGEMENTS

We would like to express our appreciation to the field survey team, consisting of W. Siriwut and the members of the Animal Systematics and Molecular Ecology Laboratory, Mahidol University, and the Animal Systematics Research Unit, Chulalongkorn University, and S. Klomthong. We give special thanks to T. von Rintelen and W. Klotz for confirming the validation of the new species by the molecular database, P. D. Round for reading and commenting on the earlier version of this manuscript, and D. J. Anderson for comments on English grammar. Our grateful thanks also extend to the anonymous reviewers and editor for their useful comments and suggestions. This study was supported by Mahidol University under grant number RSPG02/2562. Animal use protocol in this study was approved by the Faculty of Science, Mahidol University Animal Care and Use Committee, SCMU-ACUC (MUSC61-054-456). Collection

of specimens in protected areas was conducted with permission from the Department of National Parks, Wildlife and Plant Conservation, Thailand (DNP 0907.4/14262).

LITERATURE CITED

- Bauer R (2013) Amphidromy in shrimps: A life cycle between rivers and the sea. Latin American Journal of Aquatic Research, 41: 633–650.
- Beamish FWH & Plongsesthee R (2015) Species diversity, abundance and environmental associations of loaches (Nemacheilidae and Balitoridae) in the central region of Thailand. National History Bulletin of Siam, 60: 89–111.
- Beamish FWH, Sa-ardrit P & Tongnunui S (2006) Habitat characteristics of the Cyprinidae in small rivers in central Thailand. Environmental Biology of Fishes, 76(2): 237–253.
- Bernardes SC, Pepato AR, von Rintelen T, von Rintelen K, Page TJ, Freitag H & de Bruyn M (2017) The complex evolutionary history and phylogeography of *Caridina typus* (Crustacea: Decapoda): Long-distance dispersal and cryptic allopatric species. Scientific Reports, 7: 9044.
- Bossuyt F, Meegaskumbura M, Beenaerts N, Gower DJ, Pethiyagoda R, Roelants K, Mannaert A, Wilkinson M, Bahir MM, Manamendra-Arachchi K, Ng PKL, Schneider CJ, Oommen OV & Milinkovitch MC (2004) Local endemism within the Western Ghats-Sri Lanka Biodiversity Hotspot. Science, 306(5695): 479–481.
- Bouvier EL (1904) Crevettes de la famille de Atyidés: Espèces qui font partie des collections du Muséum d'histoire Naturelle. Bulletin du Muséum d'Histoire Naturelle, 10: 129–138.
- Bouvier EL (1905) Observations nouvelles sur les crevettes de la famille des Atyides. Bulletin Scientifique de la France et de la Belgique, 39: 57–134.
- Bouvier EL (1918) Sur quelques Crustacés décapodes recueillis par M. Guy Babault dans les eaux douce de Inde anglaise. Bulletin du Muséum National d'Histoire Naturelle, Paris, 24: 386–393.
- Bouvier EL (1919) Quelques espèces nouvelles de Caridines. Bulletin du Muséum National d'Histoire Naturelle, Paris, 25: 330–336.
- Bouvier EL (1925) Recherches sur la morphologie, les variations, la distribution géographique des crevettes des la famille des Atyidés. Encyclopédie Entomologique, 4: 1–370.
- Budeba YL & Cowx IG (2007) The role of the freshwater shrimp *Caridina nilotica* (Roux) in the diet of the major commercial fish species in Lake Victoria, Tanzania. Aquatic Ecosystem Health & Management, 10(4): 368–380.
- Cai Y & Anker A (2004) On a collection of freshwater shrimps (Crustacea Decapoda Caridea) from the Philippines, with descriptions of five new species. Tropical Zoology, 17(2): 233–266.
- Cai Y & Naiyanetr P (2024) The freshwater shrimps of the family Atyidae (Decapoda, Caridea) of Thailand. Crustaceana, 97(5–9): 767–804.
- Cai Y & Ng PKL (2000) Freshwater shrimps of the genus *Caridina* H. Milne Edwards (Crustacea: Decapoda: Atyidae) from Myanmar. Proceedings of the Biological Society of Washington, 113: 931–944.
- Cai Y & Ng PKL (2007) A revision of the *Caridina gracilirostris* De Man, 1892, species group, with descriptions of two new taxa (Decapoda; Caridea; Atyidae). Journal of Natural History, 41(25–28): 1585–1602.
- Cai Y, Ng PKL & Choy S (2007) Freshwater shrimps of the family Atyidae (Crustacea: Decapoda: Caridea) from Peninsular Malaysia and Singapore. Raffles Bulletin of Zoology, 55(2): 277–309.

- Cai Y & Shokita S (2006) Report on a collection of freshwater shrimps (Crustacea: Decapoda: Caridea) from the Philippines, with descriptions of four new species. Raffles Bulletin of Zoology, 54(2): 245–270.
- Choy S & Ng P (1991) A new species of atyid shrimp, *Caridina temasek* from Singapore. Raffles Bulletin of Zoology, 39: 265–277.
- Cooper JE (2011) Anesthesia, analgesia, and euthanasia of invertebrates. ILAR Journal, 52(2): 196–204.
- De Haan W (1833–1850). Crustacea. In: Von Siebold PF (ed.) Fauna Japonica sive description animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava Imperium tenent, suscepto, annis 1823–1830 collegit, cotis, observationibus et adumbrationibus illustravit. Lugduni Batavorum, Leiden, i–xxxi, ix–xvi, pp. 1–243, pls. A–J, I–Q, 1–55, circ. tab. 2.
- De Grave S, Cai Y & Anker A (2008) Global diversity of shrimps (Crustacea: Decapoda: Caridea) in freshwater. Hydrobiologia, 595: 287–293.
- De Grave S & Fransen C (2011) Carideorum catalogus: the recent species of the Dendrobranchiate, Stenopodidean, Procarididean and Caridean Shrimps (Crustacea: Decapoda). Zoologische Mededelingen, Leiden, 85(9): 195–471.
- De Man JG (1892) Decapoden des indischen Archipels. In: Weber M (ed.) Zoologische Ergebnisse eniner Reise in Niederlandisch Ost-Indien. Volume 2. E.J. Brill, Leiden, pp. 265–527, pls. 15–29.
- De Man JG (1908a) The fauna of brackish ponds at Port Canning, Lower Bengal. Part X. — Decapod Crustacea, with an account of a small collection from brackish water near Calcutta and in the Dacca District, Eastern Bengal. Records of the Indian Museum, 2(3): 211–231.
- De Man JG (1908b) On the *Caridina nilotica* (Roux) and its varieties. Records of the Indian Museum, 2: 225–283.
- de Mazancourt V, Abdou A, Castelin M, Ellien C, Lord C, Mennesson M, Renneville C, Marquet G & Keith P (2023) Molecular ecology of the freshwater shrimp *Caridina natalensis* and comparative analysis with other amphidromous species (Decapoda, Teleostei, and Gastropoda). Hydrobiologia, 850(18): 3997–4014.
- de Mazancourt V, Boseto D, Marquet G & Keith P (2020) Solomon's Gold Mine: Description or redescription of 24 species of *Caridina* (Crustacea: Decapoda: Atyidae) freshwater shrimps from the Solomon Islands, including 11 new species. European Journal of Taxonomy, 696: 1–86.
- de Mazancourt V, Klotz W, Marquet G & Keith P (2018) Integrative taxonomy helps separate four species of freshwater shrimps commonly overlooked as *Caridina longirostris* (Crustacea: Decapoda: Atyidae) on Indo-West Pacific islands. Invertebrate Systematics, 32(6): 1422–1447.
- de Mazancourt V, Klotz W, Marquet G, Mos B, Rogers DC & Keith P (2019) The complex study of complexes: The first well-supported phylogeny of two species complexes within genus *Caridina* (Decapoda: Caridea: Atyidae) sheds light on evolution, biogeography, and habitat. Molecular Phylogenetics and Evolution, 131: 164–180.
- de Mazancourt V, Klotz W, Marquet G, Mos B, Rogers DC & Keith P (2021) New insights on biodiversity and conservation of amphidromous shrimps of the Indo-Pacific islands (Decapoda: Atyidae: *Caridina*). In: Kawai T & Rogers DC (eds.) Recent Advances in Freshwater Crustacean Biodiversity and Conservation. CRC Press, Florida, pp. 381–404.
- de Mazancourt V, Marquet G & Keith P (2024) An integrative taxonomic revision of the freshwater atyid shrimps (Crustacea: Decapoda: Caridea) of Micronesia. Diversity, 16(4): 200.

- de Mazancourt V, Marquet G, Klotz W, Keith P & Castelin M (2017) When molecules and morphology work together: lines of evidence for the validity of *Caridina buehleri* Roux (Crustacea: Decapoda: Atyidae) and for *C. gueryi* Marquet, Keith & Kalfatak as its junior synonym. Invertebrate Systematics, 31(2): 220–230.
- Do VT, Dong DV & Rintelen TV (2021a) Description of one new species of freshwater shrimp of the genus *Caridina* (Crustacea: Decapoda: Atyidae) from two karst caves of Northern Vietnam. Zootaxa, 4999(3): 228–242.
- Do VT, von Rintelen K, Klotz W, Le HA, Tran AT, Dang VD, Phan TY, Nguyen C, Hoang NK, Phan DD & von Rintelen T (2021b) Taxonomy notes and new occurrence data of four species of atyid shrimp (Crustacea: Decapoda: Atyidae) in Vietnam, all described from China. Biodiversity Data Journal, 9: e70289.
- Do VT, von Rintelen T & Dang VD (2020) Descriptions of two new freshwater shrimps of the genus *Caridina* H. Milne Edwards, 1837 (Crustacea: Decapoda: Atyidae) from northern Vietnam. Raffles Bulletin of Zoology, 68: 404–420.
- Hamasaki K, Kondo S & Dan S (2021) Larval performance of amphidromous and landlocked atyid shrimp species in the genus *Paratya* under different temperature and salinity conditions. Zoological Studies, 60: 45.
- Han CC, Chang CS, Cheng IM, Fang LS & Tew KS (2011) Population dynamics of a landlocked and amphidromous freshwater shrimp, *Caridina gracilipes* (Decapoda: Caridea) in subtropical waters. Journal of Crustacean Biology, 31(2): 278–285.
- Hart RC (2001) Rapid estimation of in situ growth rates of *Caridina nilotica* (Crustacea: Decapoda) in Lake Victoria: Description and pilot application of a simple, field-compatible technique. Limnology and Oceanography, 46: 692–698.
- Hart RC, Campbell LM & Hecky RE (2003) Stable isotope analyses and demographic responses counter prospects of planktivory by *Caridina* (Decapoda: Atyidae) in Lake Victoria. Oecologia, 136(2): 270–278.
- Hoang DT, Chernomor O, von Haeseler A, Minh BQ & Vinh LS (2018) UFBoot2: Improving the Ultrafast Bootstrap Approximation. Molecular Biology and Evolution, 35(2): 518–522.
- Johnson DS (1961) A synopsis of the decapoda Caridea and Stenopodidea of Singapore, with notes on their distribution and a key to the genera of Caridea occurring in Malayan waters. Bulletin of the National Museum of Singapore, 30: 44–79.
- Kangrang P, Thoni RJ, Mayden RL & Beamish FW (2016) Garra fluviatilis, a new hillstream fish species (Cypriniformes: Cyprinidae) from the Kwai Noi River system, Mae Khlong basin, Thailand. Zootaxa, 4175(4): 335–344.
- Kawakami Y, Hamasaki K, Kondo S & Dan S (2023) Starvation tolerance of early stage zoeae of amphidromous and landlocked shrimp species in the genus *Paratya* (Decapoda: Caridea: Atyidae) under different salinity and temperature conditions. Crustacean Research, 52: 1–13.
- Kazmi Q, Siddiqui FA & Kazmi MA (2002) Range extension of *Caridina weberi sumatrensis* De Man, 1892 (Decapoda, Caridea, Atyidae) to Sindh waters (Karachi, Pakistan). Turkish Journal of Zoology, 26: 43–46.
- Kemp S (1918a) Crustacea Decapoda of the Inle Lake Basin. Records of the Indian Museum, 14: 81–102.
- Kemp S (1918b) Zoological results of a tour in the Far East. Crustacea Decapoda and Stomatopoda. In: Annandale N (ed.) Zoological results of a tour in the Far East. Memoirs of the Asiatic Society of Bengal. Volume 6. The Asiatic Society, Calcutta, pp. 217–297.
- Klotz W, von Rintelen T & Christodoulou M (2019) Middle East Caridina (Decapoda: Atyidae): Redescription of C. fossarum

Heller, 1862, description of three new species, and remarks on the status of *C. syriaca* Bouvier, 1904 and *C. babaulti basrensis* Al-Adhub & Hamzah, 1987. Zoologischer Anzeiger, 283: 161–185.

- Klotz W, von Rintelen T, Annawaty A, Wowor D & von Rintelen K (2023) *Caridina clandestina*, new species, an unusual new freshwater shrimp (Crustacea: Decapoda: Atyidae) from the remote high elevation Napu Valley of Sulawesi, Indonesia. Raffles Bulletin of Zoology, 71: 12–25.
- Klotz W, von Rintelen T, Wowor D, Lukhaup C & von Rintelen K (2021) Lake Poso's shrimp fauna revisited: The description of five new species of the genus *Caridina* (Crustacea, Decapoda, Atyidae) more than doubles the number of endemic lacustrine species. ZooKeys, 1009: 81–122.
- Kongim B, Sutcharit C & Jeratthitikul E (2023) Discovery of a new endangered freshwater mussel species in the genus *Chamberlainia* Simpson, 1900 (Bivalvia: Unionidae) from Mekong Basin. Tropical Natural History, Supplement 7: 242–250.
- Konopleva ES, Pfeiffer JM, Vikhrev IV, Kondakov AV, Gofarov MY, Aksenova OV, Lunn Z, Chan N & Bolotov IN (2019)
 A new genus and two new species of freshwater mussels (Unionidae) from western Indochina. Scientific Reports, 9(1): 4106.
- Kulabtong S, Suksri S, Nonpayom C & Soonthornkit Y (2014) Rediscovery of the critically endangered cyprinid fish *Epalzeorhynchos bicolor* (Smith, 1931) from West Thailand (Cypriniformes Cyprinidae). Biodiversity Journal, 5(2): 371–373.
- Lai HT & Shy JY (2009) The larval development of *Caridina pseudodenticulata* (Crustacea: Decapoda: Atyidae) reared in the laboratory, with a discussion of larval metamorphosis types. Raffles Bulletin of Zoology, 20: 97–107.
- Lanchester WF (1902) On the Crustacea collected during the "Skeat" Expedition to the Malay Peninsula, together with a note on the genus *Actaeopsis*. Part I. Brachyura, Stomatopoda, and Macrura. Proceedings of the Zoological Society of London, 2: 534–574.
- Lanfear R, Frandsen PB, Wright AM, Senfeld T & Calcott B (2017) PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution, 34(3): 772–773.
- Macharoenboon K, Sutcharit C, Siriwut W & Jeratthitikul E (2023) A new species of land-locked freshwater shrimp genus *Caridina* (Decapoda: Atyidae) from Middle Mekong Basin, Thailand. Tropical Natural History, Supplement 7: 229–241.
- Maciaszek R, Jablonska A, Márton H, Prati S & Świderek W (2021) First record and DNA barcodes of non-native shrimp, *Caridina babaulti* (Bouvier, 1918) in Europe. The European Zoological Journal, 88: 816–823.
- Maneechan W & Prommi TO (2015) Diversity and distribution of aquatic insects in streams of the Mae Klong Watershed, Western Thailand. Psyche, 2015: 912451.
- Miller MA, Pfeiffer W & Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. 2010 Gateway Computing Environments Workshop (GCE) 14 November 2010, New Orleans, LA, pp. 1–8.
- Milne Edwards H (1837) Histoire Naturelle des Crustacés: Comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux. Librairie encyclopédique de Roret, Paris, 531 pp.
- Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A & Lanfear R (2020) IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution, 37(5): 1530–1534.
- Naiyanetr P (2007) Checklist of Crustaceans Fauna in Thailand (Decapoda, Stamatopoda, Anostraca, Myodacopa and Isopoda). Office of Natural Resources and Environmental Policy and

Planning - Ministry of Natural Resources and Environment, Bangkok, 196 pp.

- Page TJ, Cook BD, von Rintelen T, von Rintelen K & Hughes JM (2008) Evolutionary relationships of atyid shrimps imply both ancient Caribbean radiations and common marine dispersals. Journal of the North American Benthological Society, 27(1): 68–83.
- Page TJ, von Rintelen K & Hughes JM (2007) Phylogenetic and biogeographic relationships of subterranean and surface genera of Australian Atyidae (Crustacea: Decapoda: Caridea) inferred with mitochondrial DNA. Invertebrate Systematics, 21(2): 137–145.
- Pandya P & Richard J (2019) Report of *Caridina babaulti* Bouvier, 1918 (Crustacea: Decapoda: Caridea: Atyidae) and description of a new species *Caridina kutchi* sp. nov. from Gujarat, India. Zootaxa, 4568: 470–482.
- Pillai RS (1964) Four species of *Caridina* from Travacore, including of a new variety. Journal of the Marine Biological Association of India, 6(1): 42–47.
- Pfeiffer JM, Graf DL, Cummings KS & Page LM (2021) Taxonomic revision of a radiation of South-east Asian freshwater mussels (Unionidae: Gonideinae: Contradentini+Rectidentini). Invertebrate Systematics, 35(4): 394–470.
- Richard J & Clark PF (2014) *Caridina simoni* Bouvier, 1904 (Crustacea: Decapoda: Caridea: Atyoidea: Atyidae) and the synonymy by Johnson, 1963. Zootaxa, 3841: 301–338.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA & Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology, 61(3): 539–542.
- Roux J (1926) Crustacés Décapodes d'Eau Douce de la Nouvelle-Calédonie. In: Sarasin F & Roux J (eds.) Nova Caledonia.
 Forschungen in Neu-Caledonien und auf den Loyalty-Inseln.
 Recherches scientifiques en Nouvelle-Calédonie et aux iles Loyalty. A. Zoologie. Volume 4. C.W. Kreidel's Verlag, Wiesbaden, pp. 181–240.
- Roux J (1931). Sur une nouvelle Caridine de Ceylan. Revue Suisse de Zoologie, 38: 63–66.
- San Mauro D & Agorreta A (2010) Molecular systematics: A synthesis of the common methods and the state of knowledge. Cellular & Molecular Biology Letters, 15(2): 311–341.
- Shih HT & Cai Y (2007) Two new species of land-locked freshwater shrimp genus *Neocaridina* Kubo, 1938 (Decapoda: Caridea: Atyidae) from Taiwan, with notes on the speciation within Taiwan Island. Zoological Studies, 46(6): 680–694.
- Short JW, Page TJ & Humphrey CL (2019) Caridina biyiga sp. nov., a new freshwater shrimp (Crustacea: Decapoda: Atyidae) from Leichhardt Springs, Kakadu National Park, Australia, based on morphological and molecular data, with a preliminary illustrated key to Northern Territory Caridina. Zootaxa, 4695(1): 1–25.
- Soomro A, Suzuki H, Qureshi S & Baloch WA (2020) Migration of two atyid shrimps, *Caridina sakishimensis* (Fujino and Shokita, 1976) and *Caridina typus* (H. Millne Edwards, 1937) in Urabaru, Kikai-jima Island, Southern Japan. Pakistan Journal of Zoology, 52: 1333–1340.
- Sudta H, Veeravaitaya N, Ingthamjitr S & Boonsoong B (2021) Spatial and temporal variability in water quality, sediment, and benthic macroinvertebrates in the Mae Klong River, Thailand. Journal of Fisheries and Environment, 45(2): 55–68.
- Tamura K, Stecher G & Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis Version 11. Molecular Biology and Evolution, 38(7): 3022–3027.
- Tejavej A (2012) *Barilius signicaudus*, a new species of cyprinid fish from Maeklong Basin, western Thailand (Cypriniformes: Cyprinidae). Zootaxa, 3586: 138–147.

- von Rintelen K & Cai Y (2009) Radiation of endemic species flocks in ancient lakes: Systematic revision of the freshwater shrimp *Caridina* H. Milne Edwards, 1837 (Crustacea: Decapoda: Atyidae) from the ancient lakes of Sulawesi, Indonesia, with the description of eight new species. Raffles Bulletin of Zoology, 57(2): 343–452.
- von Rintelen K, Page TJ, Cai Y, Roe K, Stelbrink B, Kuhajda BR, Iliffe TM, Hughes J & von Rintelen T (2012) Drawn to the dark side: A molecular phylogeny of freshwater shrimps (Crustacea: Decapoda: Caridea: Atyidae) reveals frequent cave invasions and challenges current taxonomic hypotheses. Molecular Phylogenetics and Evolution, 63(1): 82–96.
- Wowor D, Cai Y & Ng PKL (2004) Crustacea: Decapoda, Caridea. In: Yule CM & Sen YH (eds.) The Freshwater Invertebrates of the Malaysian Region. Academy of Sciences Malaysia, Kuala Lumpur, pp. 337–357.

- Xu DJ, Li DX, Zheng XZ & Guo ZL (2020) Caridina sinanensis, a new species of stygobiotic atyid shrimp (Decapoda, Caridea, Atyidae) from a karst cave in the Guizhou Province, southwestern China. ZooKeys, 1008: 17–35.
- Yam RSW & Dudgeon D (2006) Production dynamics and growth of atyid shrimps (Decapoda: *Caridina* spp.) in 4 Hong Kong streams: the effects of site, season, and species. Journal of the North American Benthological Society, 25(2): 406–416.
- Yatsuya M, Ueno M & Yamashita Y (2013) Life history of the amphidromous shrimp *Caridina leucosticta* (Decapoda: Caridea: Atyidae) in the Isazu River, Japan. Journal of Crustacean Biology, 33(4): 488–502.
- Yu SC (1936). Report on the macrurous Crustacea collected during the "Hainan Biological Expedition" in 1934. Chinese Journal of Zoology, 2: 85–99.