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Caridina sirindhornae sp. nov., A New Landlocked Atyid Species (Decapoda: Atyidae) from the Middle Mekong Basin, Thailand

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ABSTRACT.– A new species of landlocked and geographically restricted freshwater shrimp, *Caridina sirindhornae* sp. nov., is described from tributaries of the Mekong River in northeastern Thailand. The new species is morphologically similar to *C. sumatrensis* and *C. maeklongensis* by sharing characteristics such as a short antennular peduncle, the presence of epipods on the first four pereiopods, similar appendix interna on the male first pleopod, and a prominent subtriangular preanal carina without a spine. However, they can be distinguished by characteristics of the rostrum and egg size. Phylogenetic analyses based on partial sequences of the mitochondrial 16S rRNA and cytochrome oxidase subunit I (COI) genes (540 bp and 1,242 bp, respectively) robustly support the distinctiveness of *C. sirindhornae* sp. nov. Additionally, the findings show that the new species shares a sister relationship with *C. lanceifrons*, with a significant 16S rRNA p-distance of 6.74%, remarkably exceeding established species delimitation thresholds within the genus *Caridina*. This discovery represents the second landlocked *Caridina* species endemic to the Middle Mekong Basin in Thailand.

KEYWORDS: Crustacean, Indochina, molecular phylogeny, taxonomy, Southeast Asia mainland

INTRODUCTION

The freshwater shrimp genus *Caridina* H. Milne–Edwards, 1837 is the most species-rich genus in the family Atyidae De Haan, 1849, comprising over 350 described species worldwide and broadly distributed across the five biogeographic regions (De Grave et al., 2008; de Mazancourt et al., 2021; DecaNet, 2025; GBIF, 2025; WoRMS, 2025). The species within this genus are typically small, sometimes furnished with vibrant colors, and found in almost all types of freshwater habitat, including headwater streams, lowland rivers, lakes, estuaries, and even subterranean freshwater systems (von Rintelen and Cai, 2009; von Rintelen et al., 2012; Klotz and von Rintelen, 2014; de Mazancourt et al., 2021; Klotz et al., 2021). In terms of ecology, they play important roles as a food source for predators (Hart, 1981; Cornelissen et al., 2018) and as detritivores that consume fine-particle organic matter in freshwater environments (Hart et al., 2003; Yam and Dudgeon, 2005; Yam, 2016).

Mainland Southeast Asia is a significant hotspot for *Caridina* diversity, with at least 44 valid species documented across the region (Kemp, 1918; Do et al., 2020, 2021a, 2021b, Cai and Ng, 2000, 2007; Cai et al., 2007; Cai and Naiyanetr, 2024; Macharoenboon et al., 2024). In Thailand, taxonomy of *Caridina* has gained attention from many authors over several decades (Lanchester, 1902; Kemp, 1918; Kamita, 1966; Tiwari and Pillai, 1971; Cai and Ng, 2007; Cai et al., 2007; Naiyanetr, 2007; Do et al., 2021b; Macharoenboon et al., 2023, 2024; Cai and Naiyanetr, 2024). Recent efforts have described four newly discovered *Caridina* species endemic to Thailand and from different watersheds, including *C. panhai* Macharoenboon et al., 2023 from the Mekong Basin, *C. thai* Cai & Naiyanetr, 2024 from the Chao Phraya Basin, *C. kottelati* Cai & Naiyanetr, 2024 from southern Thailand, and *C. maeklongensis* Macharoenboon et al., 2024 from the Mae Klong Basin in western Thailand. As a result of these discoveries, the known *Caridina* fauna of Thailand has expanded to 19 species (Macharoenboon et al., 2023, 2024; Cai and Naiyanetr, 2024).

Despite considerable advancements in understanding the taxonomy and diversity of the genus *Caridina*, comprehensive surveys for these shrimps across Thailand remain incomplete, especially within the under-explored Middle Mekong Basin. This region is recognized as a significant global hotspot of freshwater biodiversity (Abell et al., 2008), exhibiting a remarkable diversity in freshwater fishes (Valbo-Jørgensen et al., 2009; Rainboth et al., 2012; Kang and Huang, 2022), mollusks (Köhler et al., 2012; Jeratthitikul et al., 2021, 2022; Pfeiffer et al., 2021), palaemonid shrimps (Cai et al., 2004; Siriwut et al., 2020) and crabs (Naiyanetr, 2007; Cumberlidge et al., 2011). While recent research has described an endemic species, *C. panhai*, from the Songkhram River, a tributary of the Mekong, we hypothesize that several other undescribed species, particularly those with limited distributions in small localized habitats, still await discovery.

The recent survey of freshwater fauna in northeastern Thailand revealed an interesting *Caridina* species inhabiting medium-sized tributaries of the Mekong River. Morphologically, it appeared similar to *C. sumatrensis* De Man, 1892, and *C. maeklongensis*, from western and southern Thailand. However, an integrative taxonomic approach, incorporating comparative morphology and molecular-based analysis, subsequently confirmed the distinctiveness of this taxon. Therefore, we propose it as a new species, *C. sirindhornae* sp. nov., and provide herein a detailed description.

MATERIALS AND METHODS

Specimen sampling

Specimens were collected using triangular dip nets from Khlong Bang Sai and Khlong Thom streams, medium-sized rivers within the Middle Mekong Basin. The living coloration of collected specimens was recorded. Selected shrimps were temporarily maintained in a small glass tank to capture photographs using a Nikon D7200 with AF-S VR with Nikkor 105 mm f/2.8G IF-ED Macro Lens. Specimens were euthanized following the protocol provided in AVMA Guidelines (2020) before fixing in 70% and 95% (v/v) ethanol, for morphological and molecular studies, respectively. All specimens, including the type series, are deposited at the Mahidol University Museum of Natural History (**MUMNH**), Department of Biology, Faculty of Science, Mahidol University, Thailand.

Morphological Study

Specimens were examined under a ZEISS Stemi 305 stereomicroscope and an Olympus CH30 light 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. All morphological measurements for species description were taken from ovigerous females, except for the first and second pleopods, which were obtained from males.

Taxonomic descriptions were made following the format of Richard and Clark (2014) and Klotz et al. (2021). The rostral formula was written in formula: (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; Pl1, first male pleopod; Pl2, second male pleopod.

DNA extraction and PCR method

Total genomic DNA was extracted from the abdominal muscle using a DNA extraction kit for animal tissue (NucleoSpin Tissue Extraction Kit, Macherey-Nagel, Germany) following the manufacturer's protocol. Fragments of two mitochondrial 16S rRNA and COI genes were amplified using the sets of primers 16Sar-Lmod (5'–AAA AAC TAT TTG TCC GTC TTC AT–3') and 16Sbmod (5'–GGT CTG AAC TCA AAT CAT GTA AA–3') (de Mazancourt et al., 2019) and COI–F–Car (5'–GCT GCT AAT TTT ATA TCT ACA G–3') and COI–R–Car (5'–TGT GTA GGC ATC TGG GTA ATC–3') (von Rintelen et al., 2007), respectively. Polymerase chain reactions (PCR) were performed using a T100™ thermal cycler (BIO-RAD) with a final reaction volume of 30 µL, containing 15 µL EmeraldAmp® GT PCR Master Mix (Takara), 1.5 µL of each primer, at least 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 46°C for COI and 50°C for 16S rRNA 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-spin^{TM} Plus Total Fragment DNA Purification Kit (iNtRON Biotechnology), and then sent for commercial sequencing using an automated sequencer (ABI prism 3730XL) in both directions (forward and reverse).

Contigs of forward and reverse strands were assembled using MUSCLE algorithm as implemented in MEGA11 v.11.0.13 (Tamura et al., 2021) before being checked and corrected manually. Sequences were aligned automatically in MAFFT v.7.49 (Katoh and Standley, 2013) by using the L-INS-i algorithm for all genes.

Phylogenetic analyses

The final concatenated dataset for phylogenetic analyses consisted of 540 bp of 16S rRNA and 1,242 bp of COI. Sequences from the genera *Atya* Leach, 1816, *Atyopsis* Chace, 1983, *Atyoida* Randall, 1840, and *Neocaridina* Kubo, 1938 were utilized as the outgroups. The GenBank accession numbers and related information for each nominal species used in phylogenetic analyses are summarized 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 models of sequence evolution for each partition were calculated using ModelFinder (Kalya-

TABLE 1. List of samples used in phylogenetic analyses, with specimen vouchers and GenBank accession numbers. n/a = data not available. References: 1 = de Mazancourt et al. (2019), 2 = Klotz et al. (2019), 3 = de Mazancourt et al. (2018), 4 = de Mazancourt et al. (2020), 5 = de Mazancourt et al. (2017), 6 = Xu et al. (2020), 7 = Do et al. (2020), 8 = Macharoenboon et al. (2024), 9 = Macharoenboon et al. (2023), 10 = Page et al. (2007a), 11 = von Rintelen et al. (2012), 12 = Bernardes et al. (2017), 13 = Levitt-Barmats et al. (2019), 14 = Shih and Cai (2007), 15 = Page et al., (2008), 16 = Page et al., (2007b), 17 = de Mazancourt et al. (2024).

Species	Voucher	Locality	Accession number		Reference
			16S	COI	
Caridina sirindhornae sp. nov.	MUMNH-CAR683-F1	Mukdahan, Thailand	PV364275	PV364386	This study
Caridina sirindhornae sp. nov.	MUMNH-CAR683-F2	Mukdahan, Thailand	PV364276	PV364387	This study
Caridina sirindhornae sp. nov.	MUMNH-CAR683-F3	Mukdahan, Thailand	PV364277	PV364388	This study
Caridina sirindhornae sp. nov.	MUMNH-CAR683-F4	Mukdahan, Thailand	PV364278	PV364389	This study
Caridina sirindhornae sp. nov.	MUMNH-CAR683-M1	Mukdahan, Thailand	PV364279	PV364390	This study
Caridina sirindhornae sp. nov.	MUMNH-CAR683-M2	Mukdahan, Thailand	PV364280	n/a	This study
Caridina sirindhornae sp. nov.	MUMNH-CAR266-F1	Amnat Charoen, Thailand	PV364281	n/a	This study
Caridina appendiculata	CA1670	Australia	MH497534	MK190059	1
Caridina brachydactyla	CA1131	Sulawesi, Indonesia	MH497502	MK190011	1
Caridina buehleri	CA1519	Solomon Islands	KY350244	MK190047	1
Caridina cf. *babaulti*	ZMB_30757-1	West Bengal, India	MN399172	n/a	2
Caridina cf. *babaulti*	ZMB_30757-2	West Bengal, India	MN399173	n/a	2
Caridina cf. *gracilirostris*	CA1238	Indonesia	MK189858	MK190015	1
Caridina gracilipes	CA1673	Flores, Indonesia	MH497535	n/a	3
Caridina gracilirostris	CA1497	Kolombangara, Solomon Is.	MT303886	n/a	4
Caridina gueryi	CA1161	Sulawesi, Indonesia	KY350241	n/a	5
Caridina lanceifrons	65	Hainan, China	MT446450	MN701605	6
Caridina lanceifrons	66	Hainan, China	MT446451	MN701606	6
Caridina longicarpus	CA1557	New Caledonia	MK189892	MK190051	1
Caridina macrodentata	CA1374	Vanuatu	MK189869	MK190030	1
Caridina macrophora	ZMB_30263	Hai Phong, Vietnam	MT526815	MT526832	7
Caridina maeklongensis	MUMNH-CAR064-9	Kanchanaburi, Thailand	PQ041485	PQ042418	8, this study
Caridina maeklongensis	MUMNH-CAR064-4	Kanchanaburi, Thailand	PQ041486	PQ042419	8, this study
Caridina neglecta	CA1703	Vella Lavella, Solomon Is.	MT303889	n/a	4
Caridina panhai	MUMNH-CAR507-F1	Sakon Nakhon, Thailand	OQ092406	OQ107450	9
Caridina panhai	MUMNH-CAR507-F2	Sakon Nakhon, Thailand	OQ092407	OQ107451	9
Caridina propinqua	isolate_2309SL	Ratgama Lake, Sri Lanka	AY708117	n/a	10
Caridina propinqua	ZMB_30260	Kien Giang, Vietnam	MT526817	MT526836	7
Caridina sumatrensis	MUMNH-CAR054-1	Ratchaburi, Thailand	PQ041492	PQ042425	8, this study
Caridina sumatrensis	ZMB_29491	Langkawi, Malaysia	FN995360	FN995572	11
Caridina typus	CT_Sar02	Sarawak, Malaysia	KY069345	KY069464	12
Caridina typus	MEFGL_CT_Sey01	Seychelles	KY069374	KY069493	12
Caridina typus	OUMNH_ZC-2010-22-0001	Mauritius	KY069380	KY069499	12
Caridina typus	ZMB_Crust_29011-1	Sulawesi, Indonesia	KY069383	KY069502	12
Caridina typus	ZMB_Crust_29416-1	Halmahera, Indonesia	KY069410	KY069529	12
Caridina typus	ZMB_Crust_29489-2	Langkawi, Malaysia	KY069416	KY069535	12
Caridina siamensis	ZMBunid1227	Mindoro, Philippines	KY436222	n/a	12
Caridina siamensis	ZMBunid1278	Taiwan	KY436224	n/a	12
Caridina weberi	MNHN-IU-2018-2867	Kolombangara, Solomon Is.	MT303920	n/a	4
Caridina weberi	MNHN-IU-2018-2876	Papua New Guinea	MT303921	n/a	4
Caridina wilsoni	GUC567	Queensland, Australia	DQ478530	n/a	10
Caridina zhujiangensis	22	Dong'ao Island, Zhuhai, China	MT446448	MN701603	6
Neocaridina denticulata	Oka6	Israel (non-native)	MN336439	MN336499	13
Neocaridina denticulata	NCd1	Taiwan	AB300173	AB300183	14
Neocaridina ketagalan	NCd4	Taiwan	AB300167	AB300180	14
Neocaridina palmata	ZMB 30256	Cao Bang, Vietnam	MT526825	MT526843	7
Neocaridina saccam	NCd8	Taiwan	AB300165	AB300178	14
Atya innocous	GUEL1	Rio Espiritu Santo, Puerto Rico	EF489987	EF489968	15
Atya scabra	ZMB_DNA510	Rio Guarumo, Panama	EF489985	EF489964	15
Atyoida bisulcata	GU755	Waiau Stream, Hawaii	DQ681278	DQ681257	16
Atyoida chacei	CA1858	Babeldaob, Palau	PP455330	n/a	17
Atyoida pilipes	GU991	Moorea, French Polynesia	DQ681279	DQ681255	16
Atyopsis moluccensis	KZ222	Petshop in Germany	DQ681281	DQ681246	16
Atyopsis spinipes	GU877	Guadalcanal, Solomon Is.	DQ681282	DQ681260	16

anamoorthy et al., 2017) based on Bayesian information criterion (BIC) as implemented in IQ-Tree v.2.1.2 (Nguyen et al., 2015) for ML analysis and PartitionFinder2 v.2.3.4 (Lanfear et al., 2017) with a heuristic search algorithm under Bayesian information criterion (BIC) for BI analysis. Only the COI gene was further partitioned into three codon positions. The best-fit substitution models are summarized in Table 2.

The ML tree was estimated in IQ-TREE v.2.2.2.7 (Minh et al., 2020) with 10,000 replicates of ultrafast bootstrap approximation (Hoang et al., 2018) to assess topology bootstrap support (BS). The BI tree was

TABLE 2. Best-fit models of nucleotide substitution for each gene partition used in phylogenetic analyses.

Gene	Codon Position	Substitution Model	
		IQ-TREE	MrBayes
16S rRNA	-	TPM3u+F+I+G4	HKY+G
COI	1	TNe+I+G4	SYM+G
COI	2	F81+F+I	F81+G
COI	3	TIM2+F+G4	HKY+G

reconstructed in MrBayes v.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 500 generations. The majority-rule consensus tree was generated after discarding the initial 25% of trees as burn-in. The convergence of the MCMC chains was visually assessed using Tracer v.1.6. The convergence of two independent runs was considered achieved when the mean standard deviation of split frequencies was below 0.01, the average effective sample size (ESS) exceeded 200, and the potential scale reduction factor (PSRF) reached 1.0. The resulting trees from both analyses were examined and edited using FigTree v.1.4.4. A clade was considered significantly supported when the ultrafast BS was ≥95% and/or the Bayesian posterior probabilities (BPP) was ≥0.95 (San Mauro and Agorreta, 2010; Hoang et al., 2018).

Genetic distances between the new species and other closely related species were examined via uncorrected p-distance method as implemented in MEGA11. Regions containing gaps resulting from sequence alignment were excluded from the calculations.

RESULTS

Systematics

Family Atyidae De Haan, 1849

Genus *Caridina* H. Milne Edwards, 1837

Remarks.– *Caridina* currently consists of at least 350 valid species distributed worldwide (DecaNet, 2025; GBIF, 2025; WoRMS, 2025). Including the new species described in this study, a total of 20 species have been recorded to date within Thailand (Cai and Naiyanetr, 2024; Macharoenboon et al., 2024; this study). They occupy a range of habitats from headwater streams to estuaries. Notably, several *Caridina* species in Thailand exhibit restricted distributions, with endemism observed in specific regions. The endemic *Caridina* species in Thailand include *C. panhai* endemic to the Mekong Basin, *C. maeklongensis* to the Mae Klong Basin, *C. gracillima* Lanchester, 1902 to southern and central Thailand, *C. thai* to central Thailand and the upper Malay Peninsula, and *C. kottelati* to the southernmost area of Thailand (Macharoenboon et al., 2023, 2024; Cai and Naiyanetr, 2024).

Caridina sirindhornae sp. nov.

https://zoobank.org/urn:lsid:zoobank.org:pub: E4F65A63-F47A-43AD-B242-846393D8794C

(Figs 1–5)

Type materials.– THAILAND • Holotype: ovigerous ♀ (CL 3.95 mm; Figs 1A, 3A), MUMNH-CAR683-H; Khlong Bang Sai Stream, a tributary of Mekong River, Mueang District, Mukdahan Province; C. Sutcharit, W. Siriwut, and K. Macharoenboon leg. • Paratypes: 8 ovigerous ♀ (CL 3.65–4.10 mm), MUMNH-CAR683-F1 to CAR683-F8; 9 ♂ (CL 2.26–2.67 mm), MUMNH -CAR683-M1 to CAR683-M9, same collection data as for the holotype • 2 ovigerous ♀ (CL 3.50–3.54 mm), MUMNH-CAR266-F1 and MUMNH-CAR266-F2; Khlong Thom Stream, a tributary of Mekong River, Chanuman District, Amnat Charoen Province; C. Sutcharit, E. Jeratthitikul, and W. Siriwut leg.

Other material examined.– THAILAND • 8 ♀ (CL 3.39–3.90), 4 ♂ (CL 2.27–2.56 mm), MUMNH-CAR 683; Khlong Bang Sai Stream, a tributary of Mekong River, Mueang District, Mukdahan Province; C. Sutcharit, W. Siriwut, and K. Macharoenboon leg. • 6 ♀ (CL 3.26–3.81 mm), 3 ♂ (CL 2.22–2.49), MUMNH-CAR266; Khlong Thom Stream, a tributary of Mekong River, Chanuman District, Amnat Charoen Province; C. Sutcharit, E. Jeratthitikul, and W. Siriwut leg.

Comparative material examined.– *C. maeklongensis* • **THAILAND** • Holotype: ovigerous ♀ (CL 3.44 mm); MUMNH-CAR064-9, Paratypes: 7 ♀ (CL 3.17–3.53 mm); MUMNH-CAR064-1, CAR064-7, CAR 064-10, CAR064-13, and CAR064-15; 4 ♂ (CL 2.87–3.25 mm); MUMNH-CAR064-2 to CAR064-5; Sai Yok Yai Waterfall, Sai Yok District, Kanchanaburi Province; E. Jeratthitikul, W. Siriwut, and K. Macharoenboon leg. • Paratypes: 2 ♀ (CL 3.55–3.97 mm); Mae Plu Stream, Si Sawat Dis-trict, Kanchanaburi Province; E. Jeratthitikul, W. Siriwut, and K. Macharoenboon leg. • 4 ♀ (CL 3.28–4.01 mm), 1 ♂ (CL 2.61 mm); MUMNH-CAR065; Khayeng Stream, Thong Pha Phum District, Kanchanaburi Province; E. Jeratthitikul, W. Siriwut, and K. Macharoenboon leg. *C. sumatrensis* • **THAILAND** • 9 ♀ (CL 3.91–4.49 mm), 3 ♂ (CL 2.51–2.94 mm); MUMNH-CAR053; Mae Klong River, Tha Maka District, Kanchanaburi

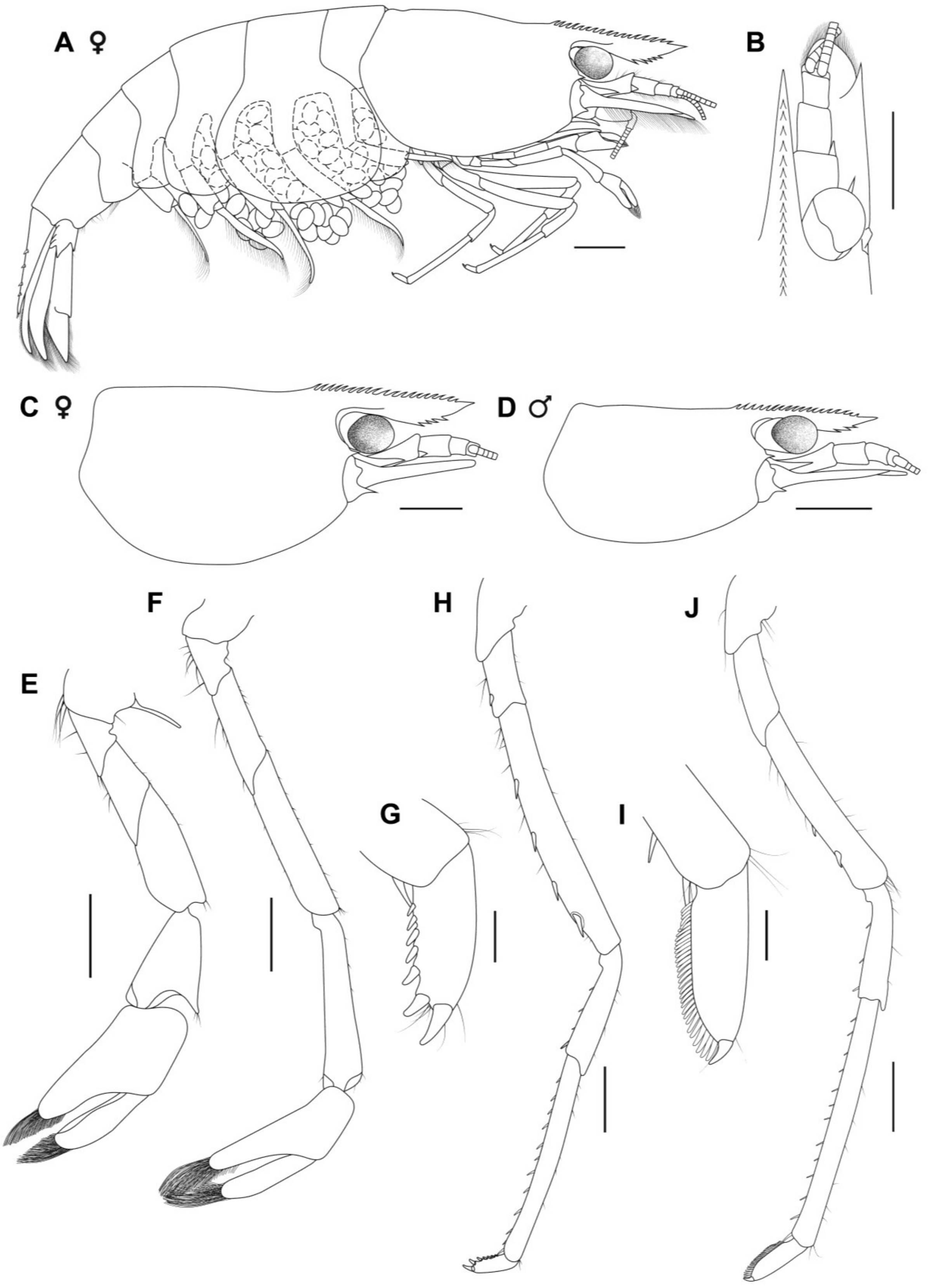

FIGURE 1. *Caridina sirindhornae* sp. nov. **A.** ovigerous female. **B.** top view of carapace. **C.** cephalothorax and cephalic appendages of female and **D.** male specimens. **E.** first pereopod. **F.** second pereopod. **G.** dactylus of third pereopod. **H.** third pereopod. **I.** dactylus of fifth pereopod. **J.** fifth pereopod. Drawings were taken from holotype MUMNH-CAR683-H (**A, B**); paratype MUMNH-CAR683-F2 (**C**); paratype MUMNH-CAR683-M2 (**D**); paratype MUMNH-CAR683-F1 (**E–J**). Scale bar: 1 mm (**A–D**); 0.5 mm (**E, F, H, J**); 0.1 mm (**G, I**).

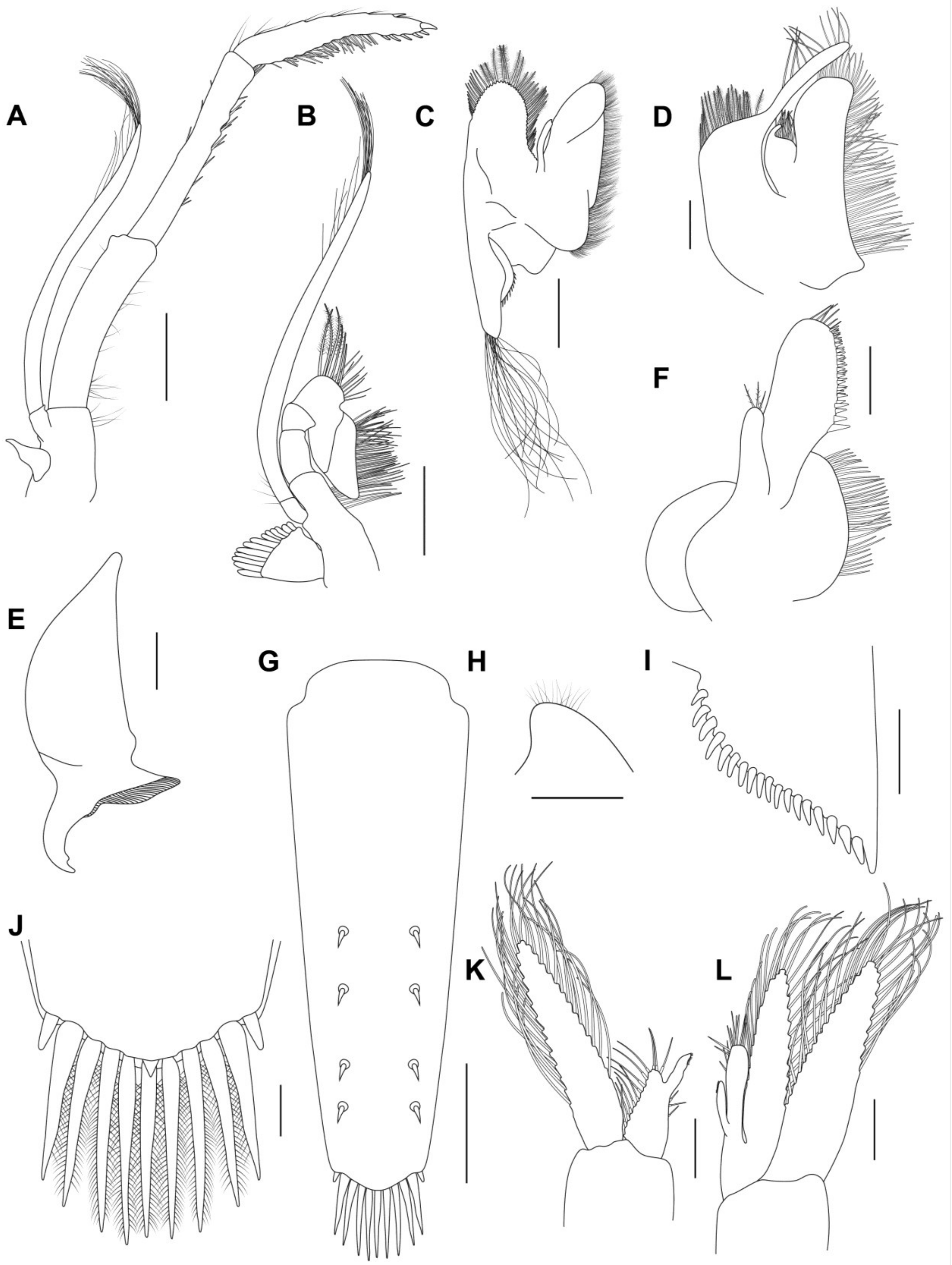

FIGURE 2. *Caridina sirindhornae* sp. nov. **A.** third maxilliped. **B.** second maxilliped. **C.** maxilla. **D.** first maxilliped. **E.** mandible. **F.** maxillula. **G** telson. **H.** preanal carina. **I.** uropodial diaeresis. **J.** distal end of telson. **K.** male first pleopod. **L.** male second pleopod. Drawings were taken from paratype MUMNH-CAR683-F3 (**A, F–J**); specimen MUMNH-CAR683-F1 (**B–E**); paratype MUMNH-CAR683-M2 (**K, L**). Scale bars: 0.5 mm (A–**C, G**); 0.25 mm (**D–F, H–I, K–L**); 0.1 mm (**J**).

Province; W. Siriwut and W. Manonai; 1 ♀ (CL 4.10 mm); MUMNH-CAR054; Mae Klong River, Photharam District, Ratchaburi Province; W. Siriwut and W. Manonai leg. • 4 ♀ (CL 3.29–4.21 mm); MUMNH-CAR055; Mae Klong River, Photharam District, Ratchaburi Province; W. Siriwut and W. Manonai leg. • 3 ♀ (CL 3.73–4.29 mm); MUMNH-CAR056; Mae Klong River, Photharam District, Ratchaburi Province; W. Siriwut and W. Manonai leg. • 4 ♀ (CL 3.57–4.08 mm), 4 ♂ (CL 2.41–2.93 mm); MUMNH-CAR706; Klong Bang Tanod River, Photharam District, Ratchaburi Province; E. Jeratthitikul and K. Macharoenboon leg.

Etymology.– The specific epithet of the new species is in honor of Her Royal Highness Maha Chakri Sirindhorn on the occasion of her 70th Birthday Anniversary and in recognition of her dedication and significant contributions to scientific and environmental pursuits.

Description.–

Cephalothorax and cephalic appendages (n = 10). CL 3.50–4.10 mm (median 3.78), width 2.67–3.00 mm (median 2.94). Rostrum straight, slightly pointed downward (Fig. 1A, C), ventrally wide at the half length then abruptly tapering toward the tip, usually reaching near or slightly beyond the end of the third segment of antennular peduncle, 0.53–0.66 (median 0.59) times as long as CL. Rostral formula: (3–4) + 14–18/ 3–4. Antennal spine placed slightly below inferior orbital angle. Pterygostomian margin round. Eye well developed, anterior end reaching to 0.58–0.80 (median 0.71) of the first segment of antennular peduncle. Antennular peduncle 0.47–0.58 (median 0.55) times as long as CL (Fig. 1A–C), first segment 1.70–2.17 (median 1.96) times as long as second segment, second segment 1.07–1.63 (median 1.15) times as long as third segment. Tooth on distolateral margin of the first segment of antennular peduncle prominent. Stylocerite reaching to 0.70–0.83 (median 0.79) of the first segment of antennular peduncle. Scaphocerite 2.56–2.84 (median 2.74) times as long as wide, distal margin with short plumose setae.

Branchial formula Podobranch on second maxilliped well-developed; one small and one large arthrobranch on the third maxilliped, pleurobranchs on all pereopods.

Mouthparts (n = 4). Mandible without palp (Fig. 2E); incisor process with 1–3 irregular teeth; two rows of setae on the inner margin; molar process truncated. Lower lacinia of maxillula sub-rectangular (Fig. 2F), with many rows of plumose setae; upper lacinia elongate, inner margin straight, with numerous conical spinules and elongate distal spinules; palp elongate, with few distal spinules. Scaphognathite of maxilla wide anteriorly (Fig. 2C), ending with a tuft of setae; short marginal setae placed along proximal triangular process; anterior margin with long plumose setae; palp slender; upper and middle endites subdivided with many rows of marginal setae; lower endite partly fused with middle endite, with relatively longer marginal setae. Palp of first maxilliped rounded and inflated (Fig. 2D), ending with finger-like projection and with plumose setae; caridean lobe broad, with marginal plumose setae; exopod well-developed with distally marginal plumose setae; ultimate and penultimate segments of endopod indistinctly divided, with marginal setae. Ultimate and penultimate segments of endopod of second maxilliped incompletely divided (Fig. 2B); inner margin of ultimate and penultimate segments with simple and pappose setae; exopod long and slender, with a tuft of long setae at tip. Third maxilliped with epipod (Fig. 2A); ultimate segment of endopod with a row of strong spinules at proximal 2/3 of posterior margin, ending with one large claw, 4–7 spiniform setae on distal 1/3 of posterior margin, 0.83–0.95 (median 0.91, n = 8) times as long as penultimate segment; exopod long and slender, with a tuft of long setae at tip.

Pereopods (n = 9). Epipod present on first four pereopods. Chelae of first and second pereopods well-developed (Fig. 1E, F).

First pereopod slender (Fig. 1E); chela 2.05–2.28 (median 2.15) times as long as wide, 1.28–1.72 (median 1.45) times as long as carpus; tips of fingers rounded, with tuft of setae near tip; dactylus 1.01–1.54 (median 1.19) times as long as palm; carpus excavated distally, 1.31–1.82 (median 1.56) times as long as wide, 0.79–0.97 (median 0.92) times as long as merus; merus 1.97–2.83 (median 2.54) times as long as wide, 1.18–1.79 (median 1.63) times as long as ischium.

Second pereopod more slender than P1 (Fig. 1F). Chela 2.56–3.11 (median 2.89) times as long as wide, 0.85–0.94 (median 0.91) times as long as carpus, tips of fingers round, with tuft of setae near tip; dactylus 1.35–1.98 (median 1.65) times as long as palm. Carpus slender, 3.79–4.33 (median 4.09) times as long as wide, 0.99–1.39 (median 1.07) times as long as merus. Merus 3.28–5.32 (median 4.36) times as long as wide, 1.15–1.78 (median 1.46) times as long as ischium.

Third pereopod not sexually dimorphic (Fig. 1H). Dactylus with 5–7 (mode 6) spinules on flexor margin (Fig. 1G), 2.56–3.51 (median 2.79) times as long as wide (including terminal claw), terminating with one large claw. Propodus with numerous spiniform setae on lateral and posterior margin, 8.76–10.20 (median 9.19) times as long as wide, 3.74–4.70 (median 4.09) times as long as dactylus. Carpus with 4–5 (mode 4)

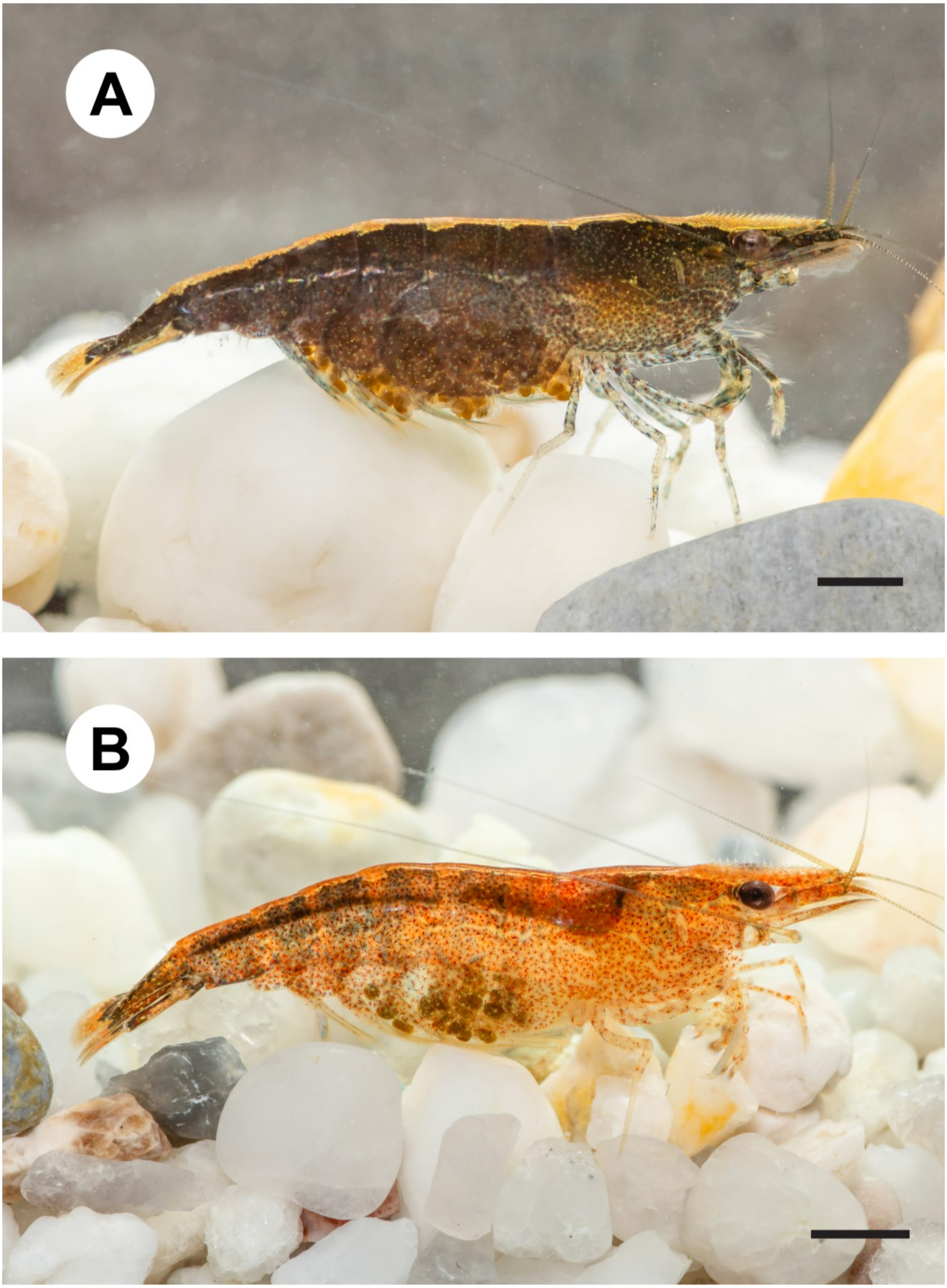

FIGURE 3. Living female of *Caridina sirindhornae* sp. nov. **A.** holotype MUMNH-CAR683-H. **B.** paratype MUMNH-CAR683-F4. Scale bar = 2 mm.

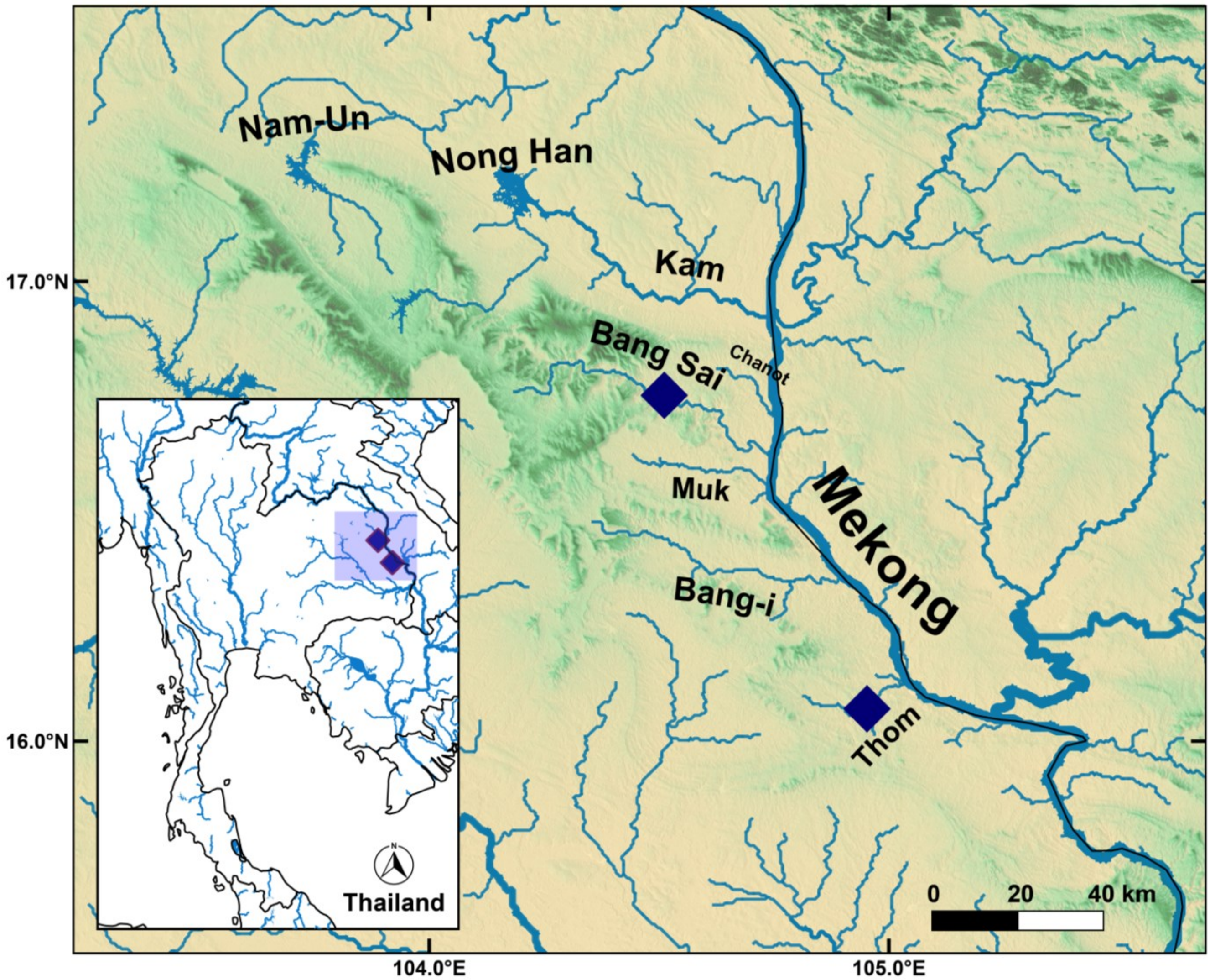

FIGURE 4. Distribution of *Caridina sirindhornae* sp. nov. Maps were created using QGIS v3.34.1. Topographic base maps of river and lake topology and map raster data were taken from HydroSHEDS database (https://www.hydrosheds.org) and NASA EARTHDATA (https://www.earthdata.nasa.gov/), respectively.

spiniform setae on posterior margin of outer surface, the distal seta largest, the other setae minute, 3.44–4.69 (median 4.43) times as long as wide, 0.52–0.69 (median 0.58) times as long as propodus. Merus with 3–4 (mode 3) large spiniform setae on posterior margin of outer surface, 5.95–7.00 (median 6.28) times as long as wide, 1.98–2.41 (median 2.09) times as long as carpus. Ischium with one spiniform seta.

Fifth pereopod slender (Fig. 1J). Dactylus with 28–35 (mode 33) spinules on flexor margin (Fig. 1I), 2.64–3.14 (median 2.85) times as long as wide (including terminal claw), terminating with one large claw; propodus with numerous spiniform setae on posterior margin, 10.00–12.36 (median 11.27) times as long as wide, 3.75–5.32 (median 4.23) times as long as dactylus. Carpus with 3–4 (mode 4) spiniform setae on posterior margin of outer surface, the distal seta largest, the other setae minute, 3.44–4.76 (median 4.16) times as long as wide, 0.44–0.53 (median 0.49) times as long as propodus. Merus with two large spiniform setae on posterior margin of outer surface, 5.07–5.86 (median 5.44) times as long as wide, 1.40–1.73 (median 1.51) times as long as carpus. Ischium without spiniform seta.

Pleopods (n = 9) Endopod of male first pleopod subtriangular (Fig. 2K), wider proximally, 1.66–2.11 (median 1.81) times as long as width, 0.29–0.37 (median 0.34) times as long as exopod length, with appendix interna emerged near the tip of endopod. Appendix masculina of male second pleopod rod-shaped (Fig. 2L), with numerous setae, 0.71–0.79 (median 0.74) times as long as endopod (including distal setae). Appendix interna very slender, reaching 0.61–0.67 (median 0.66) times the appendix masculina length.

Abdomen (n = 9). Sixth abdominal somite 0.41–0.57 (median 0.46) times carapace length, 1.35–1.60 (median 1.43) times as long as fifth somite, 0.74–0.91 (median 0.77) times as long as telson (Fig. 1A). Telson 2.28–2.91 (median 2.60) times as long as wide, with 4–5 pairs of dorsal spiniform setae and one pair of dorsolateral spiniform setae (Fig. 2G). Distal margin of telson subtriangular, with a posteromedian projection, 7–9 (mode 7) moveable plumose setae, subequal in length (Fig. 2J). Preanal carina high, subtriangular with a few setae, without a spine (Fig. 2H). Uropodal diaeresis with 16–20 short moveable spiniform setae (Fig. 2I).

Eggs Ovigerous females with 133–181 eggs (mean = 152; n = 5). Size of eye-developed eggs 0.61–0.69 × 0.37–0.44 mm (n = 40).

Coloration.– Based on female specimens, *C. sirindhornae* sp. nov. exhibits two color morphs. The typical morph has a dark brownish-gray body contrasted by a yellowish-orange rostrum and lower cephalic region (Fig. 3A). A conspicuous, bright yellow dorsal line extends longitudinally from the rostral tip to the last segment of the abdominal somite. Some abdominal somites have a transverse yellow band on dorsal surface. The bright morph displays a yellowish-orange body with an orange rostrum (Fig. 3B). The dorsal line is dull orange, extending from the rostral base to the last segment of the abdominal somite. Some abdominal somites present a transverse dull orange band on the dorsal surface. Color of eggs ranges from orange to brown.

Distribution and habitat.– The comprehensive field surveys of several tributaries in northeastern provinces indicated that the new species exhibits a significantly restricted geographical distribution. Its range is confined to two tributaries of the Mekong River, specifically Khlong Bang Sai and Khlong Thom streams (Fig. 4). This species demonstrates a preference for lotic freshwater environments. Individuals were observed inhabiting shallow areas beneath leaf litter and on vegetation near the river bank, where the substrate consisted of sand or pebbles.

Phylogenetic results.– Molecular evidence supported the new species as a monophyletic lineage with high nodal support from both analyses (BS = 100%, BPP = 1) that is distinct from other examined *Caridina* species (Fig. 5). The new species was nested with *C. lanceifrons* Yu, 1936 with high support (BS = 100%, BPP = 1). The minimum observed genetic distance of the new species was 6.7% (16S) and 12.8% (COI) to *C. lanceifrons* (Table 3). This value is considerably higher than the established species delimitation threshold of at least 3.8% for the 16S rRNA gene and 10.8% for cytochrome oxidase subunit I gene in other *Caridina* taxa, as proposed by Klotz et al. (2023). Consequently, the molecular evidence warrants the recognition of the new taxon as a distinct species.

Remarks.– Despite a close evolutionary relationship as shown in phylogenetic analyses, the new species exhibits several distinct morphological differences from *C. lanceifrons*. The rostrum of the new species is wider apically and slightly bent downward (vs lanceolate, sharply pointed, and projecting straight forward). The new species exhibits shorter antennular peduncle (0.47–0.58 vs 0.60–0.70 times as long as CL) and scaphocerite (2.56–2.84 vs 3.0–4.33 times as long as wide), while its P2 and P5 carpus are stouter (3.76–4.33 vs 4.0–5.0 as long as wide and 3.44–4.76 vs 4.33–6.25 times as long as wide, respectively). The endopod of males' first pleopod of the new species is slightly shorter than that of *C. lanceifrons* (1.66–2.11 vs 2.09–2.88 times as long as wide). The new species also possesses fewer dorsal spines on the telson (4–5 pairs vs 5–6 pairs). In addition, the new species produces smaller eggs than that of *C. lanceifrons* (0.61–0.69 × 0.37–0.44 mm vs 0.85–1.05 × 0.55–0.7 mm) (Yu, 1936, 1938; Cai 2014; Do et al., 2021b).

The new species exhibits notable morphological similarities to *C. sumatrensis* and *C. maeklongensis*, including the presence of epipods on the first four pereopods, shortened P3 and P5 dactylus, the presence of an appendix interna on the endopod of the male first pleopod, unarmed and subtriangular preanal carina, and a similar number of spiniform setae on uropodal diaeresis. Nevertheless, the new species can be distinguished from *C. sumatrensis* and *C. maeklongensis* by several key characters. The rostrum of the new species is comparatively wider apically than those of *C. sumatrensis* and *C. maeklongensis*. The endopod of the male first pleopod in the new species is also proportionally smaller (0.29–0.37 vs 0.32–0.46 in *C. sumatrensis* and vs 0.38–0.48 as long as endopod in *C. maeklongensis*). Egg size and number of eggs also differs distinctly among them (De Man, 1892; Cai et al., 2007; Cai and Naiyanetr, 2024; Macharoenboon et al., 2024; this study). Females of the new species produce a moderate number of medium-sized eggs (133–181 eggs per individual, measuring 0.61–0.69 × 0.37–0.44 mm). In contrast, *C. sumatrensis* produces a large number of small eggs (0.41–0.46 × 0.24–0.29 mm), and *C. maeklongensis* possesses fewer but very large eggs (25–35 eggs per individual, measuring 0.82–0.93 × 0.51–0.60 mm; Macharoenboon et al., 2023, 2024).

TABLE 3. Average pairwise uncorrected p-distance (%) ± SD based on mitochondrial 16S rRNA (lower diagonal) and COI (upper diagonal) genes between *Caridina sirindhornae* sp. nov. and its related taxa. n/a = data not available.

	1.	**2.**	**3.**	**4.**	**5.**	**6.**	**7.**	**8.**
1. *C. sirindhornae* sp. nov.		12.75 ± 0.33	n/a	16.39 ± 0.12	15.94 ± 0.09	17.64 ± 0.39	n/a	19.03 ± 2.78
2. *C. lanceifrons*	6.74 ± 0.47		n/a	18.91 ± 0.37	17.31 ± 0.00	20.00 ± 3.43	n/a	19.50 ± 1.98
3. *C.* cf. *babaulti*	10.10 ± 0.47	8.50 ± 0.00		n/a	n/a	n/a	n/a	n/a
4. *C. maeklongensis*	11.22 ± 0.47	9.84 ± 0.00	4.70 ± 0.26		11.27 ± 0.11	18.06 ± 0.54	n/a	17.32 ± 0.92
5. C. *sumatrensis*	10.77 ± 0.53	10.51 ± 0.00	5.70 ± 0.13	5.03 ± 0.29		18.34 ± 0.37	n/a	16.75 ± 0.57
6. *C. typus*	10.97 ± 0.41	10.11 ± 0.09	9.31 ± 0.35	11.10 ± 0.40	9.96 ± 0.28		n/a	17.97 ± 0.98
7. *C. siamensis*	12.45 ± 0.49	10.85 ± 0.13	11.41 ± 0.26	12.86 ± 0.13	12.75 ± 0.26	9.91 ± 0.18		n/a
8. *C. zhujiangensis*	9.88 ± 0.47	7.83 ± 0.00	8.50 ± 0.00	10.07 ± 0.26	9.84 ± 0.00	7.07 ± 0.12	7.83 ± 0.26	

When compared only to *C. sumatrensis*, the P5 dactylus of the new species bears fewer spinules on the flexor margin (28–35 vs 32–43), and stouter merus of P5 (5.07–5.86 vs 6.12–7.45 as long as wide). When compared only to *C. maeklongensis*, the new species differs by having a relatively longer rostrum (reaching near the distal end of the antennular peduncle vs reaching near the distal end of the second segment of the antennular peduncle), a greater number of dorsal rostral teeth (14–18 vs 9–14), a stouter P3 dactylus (2.64–3.14 vs 3.40–3.70 times as long as wide), and a well-developed posteromedian projection on the telson (vs greatly reduced) (Cai and Naiyanetr, 2024; Macharoenboon et al., 2024).

Furthermore, phylogenetic analyses in this study (Fig. 5) support the distinctiveness of the new species from *C. sumatrensis* and *C. maeklongensis*. The new species was placed sister to *C. lanceifrons*, while *C. sumatrensis* and *C. maeklongensis* formed a highly supported clade with *C.* cf. *babaulti* Bouvier, 1918 (BS = 100%, BPP = 1). These species were also separated by relatively large genetic divergence. The new species exhibited uncorrected p-distances in the 16S rRNA gene of 11.2% from *C. maeklongensis* and 10.8% from *C. sumatrensis*.

DISCUSSION

The current phylogenetic tree strongly supports a sister relationship between *C. sirindhornae* sp. nov. and *C. lanceifrons* (Fig. 5: BS = 100%, BPP = 1). In the present study, we found that both species share several diagnostic characters with *C. sumatrensis*, *C. maeklon-gensis*, *C.* cf. *babaulti*, and members of *C. typus* species group, including (1) a rostrum without subapical teeth, (2) epipod present on the first four pereopods, (3) stout P3 and P5 dactyli, (4) a short sixth abdominal somite (less than 0.6 times carapace length), (5) subtriangular preanal carina with no spine, and (6) many spinules on the uropodal diaeresis (more than 15) (De Man, 1892; Kemp, 1918; Yu, 1936, 1938; Cai, 2014; Pandya and Richard, 2019; de Mazancourt et al., 2020; Cai and Naiyanetr, 2024; Macharoenboon et al., 2024). Consistent with previous research, de Mazancourt et al. (2020) highlighted morphological evidence suggesting the placement of *C. sumatrensis* within the *C. typus* species group. However, the phylogenetic tree generated in this study yielded low nodal support at the deep node for both ML and BI analyses (Fig. 5; BS = 38%, BPP = 0.88). Therefore, the provisional placement of *C. sirindhornae* sp. nov. and *C. lanceifrons* within the *C. typus* species group remains uncertain. Further molecular analyses employing an expanded multiple gene and/or a genome sequence dataset are essential to clarify the phylogenetic relationships among these species.

In general, egg size is an important diagnostic character distinguishing between amphidromous and landlocked species in *Caridina*. Amphidromous species typically exhibit a life cycle characterized by the production of numerous small eggs, migrations between freshwater and marine environments, and extended planktotrophic larval stages (Lai and Shy, 2009; Han et al., 2011; Bauer, 2013), facilitating extensive geographic dispersal (Shanks, 2009; von Rintelen et al., 2012; Ziegler et al., 2020; de Mazancourt et al., 2023). In contrast, landlocked species produce a smaller number of large eggs, possess direct or abbreviated larval development, and complete their entire life cycle within freshwater habitats, resulting in limited geographic distribution (Fujita et al., 2011; de Mazancourt et al., 2021; Macharoenboon et al., 2023, 2024). Females of landlocked species invest significantly in yolk production, resulting in low fecundity. Their post-hatching larvae primarily rely on the yolk sac for nutrition that facilitates rapid larval development and minimizes the duration of larval stages, thereby promoting settlement in or near parental habitats. This strategy is hypothesized to be an evolutionary adaptation in landlocked species to the scarcity of food in freshwater environments (Vogt, 2013; Anger, 2016; Hamasaki et al., 2021; Kawakami et al., 2023).

Given its restricted geographic distribution in inland areas distant from the sea, *C. sirindhornae* sp. nov. should likely be classified as a landlocked species.

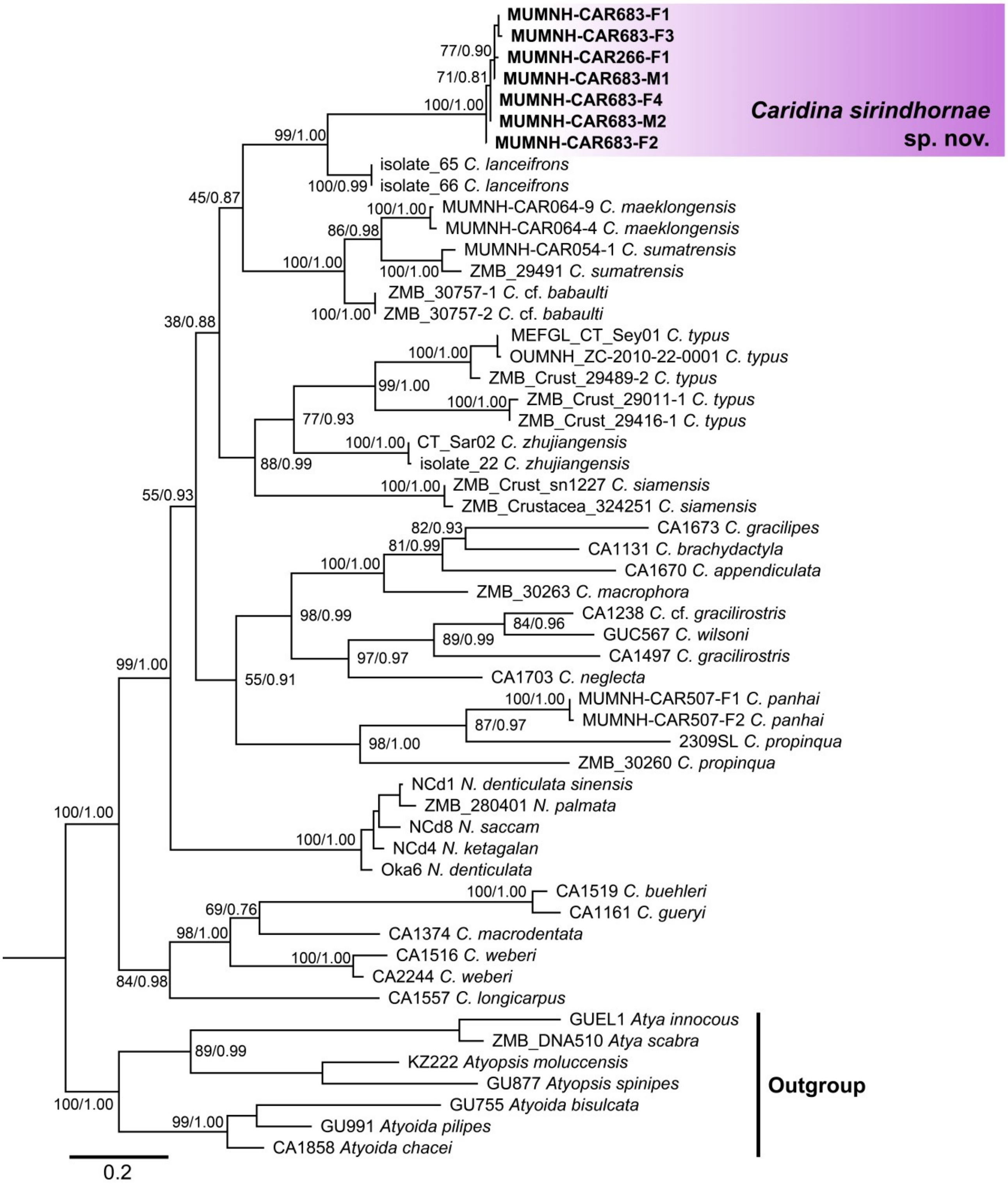

FIGURE 5. Maximum likelihood tree based on fragments of mitochondrial 16S rRNA and COI genes. Numbers on each node represent the ML bootstrap value followed by the Bayesian posterior probability.

However, its egg size (0.61–0.69 × 0.37–0.44 mm) is comparatively smaller than other reported landlocked species in Thailand, such as *C. annandalei* Kemp, 1918 (0.90–1.05 × 0.55–0.70 mm; Cai and Naiyanetr, 2024), *C. macrophora* Kemp, 1918 (0.90–0.96 × 0.52–0.58 mm; Kemp, 1918), *C. panhai* (0.94–1.06 × 0.60–0.67 mm; Macharoenboon et al., 2023), and *C. maeklongensis* (0.82–0.93 × 0.51–0.60 mm; Macharoenboon et al., 2023). Nevertheless,, its egg size remains larger than those of true amphidromous species such as *C. typus* (0.38–0.54 × 0.23–0.32 mm; de Mazancourt et al., 2020) and *C. sumatrensis* (0.41–0.46 × 0.24–0.29 mm; Macharoenboon et al., 2024). A moderate number of medium-sized eggs suggest a potential deviation from typical reproductive strategies observed in either landlocked or amphidromous shrimps, raising interesting questions about the ecological adaptations of *C. sirindhornae* sp. nov.

The observation of this moderate egg size in *C. sirindhornae* sp. nov. may align with the concept of intermediate reproductive traits found in atyid shrimps. Some freshwater atyid shrimps exhibit a moderate number of medium-sized eggs with a moderate number of larval stages such as *C. aruensis* Roux, 1911, *C. rajadhari* Bouvier, 1918, *C. moeri* Woltereck, 1984, *C. shenoyi* Jalihal, Shenoy & Sankolli, 1984, and *C. williamsoni* Jalihal, Shenoy & Sankolli, 1984 (Bouvier, 1918; Riek, 1953; Hayashi and Hamano,1984; Jalihal et al., 1984; Hancock et al., 1998; Page et al., 2005; Richard and Clark, 2010). This phenomenon may be attributed to the capability of certain freshwater species to retain a prolonged larval development in nutrient-rich aquatic environments with abundant plankton, providing enhanced larval nutrition (Vogt, 2013; Bauer, 2023). This potentially allows females to prioritize high fecundity over increased yolk content. However, given the limited information available in this study, this hypothesis remains speculative. Plankton community surveys in the region and rearing experiments to quantify larval duration are crucial to validate this hypothesis.

At present, many *Caridina* species are subjected to significant threats due to overharvesting for ornamental pets by the aquarium trade and ongoing habitat loss (De Grave et al., 2015; de Mazancourt et al., 2021; Klotz et al., 2021; de Mazancourt and Ravaux, 2024). According to the report by IUCN (2024), a total of 56 *Caridina* species have been assessed for their conservation status, which ranges from vulnerable (VU) to critically endangered (CR). Notably, over half of these species are endemic. Landlocked and endemic species whose geographic distribution is restricted to a small area thus encounter a higher risk of extinction from human activities (Régnier et al., 2009; Strayer and Dudgeon, 2010; Giam et al., 2011; Vogt, 2013).

The tributaries and mainstream of the Mekong Basin within Thailand are increasingly impacted by the presence of several dams, riprap installations, and concrete riverbank reinforcements (Li et al., 2017; Pokhrel et al., 2018; Eyler and Kwan, 2024; this study). The replacement of natural riverbanks with concrete and riprap represents a particularly severe threat, as it drastically reduces riparian vegetation (Thomson, 2002; Usuda et al., 2012; Itakura et al., 2015), a crucial habitat for *Caridina* species (Pillai, 1964; Cai and Ng, 2000; Yatsuya et al., 2013; de Mazancourt et al., 2019, 2021; Macharoenboon et al., 2024). Furthermore, the construction of dams and weirs on both main rivers and their tributaries might disrupt vital longitudinal connectivity, potentially impeding the dispersal of aquatic fauna, including *Caridina*, to adjacent streams and upstream habitats (Yatsuya et al., 2013; Fuller et al., 2015; Schmutz and Moog, 2018; Wu et al., 2019). Currently, the Mekong Basin is known to harbor two endemic *Caridina* species, *C. panhai* and *C. sirindhornae* sp. nov. (Macharoenboon et al., 2023; this study). The restricted geographic range of these endemic species makes them exceptionally vulnerable to the aforementioned habitat alterations. Consequently, future research should prioritize comprehensive assessments of the ecological consequences stemming from these modifications to establish effective conservation planning and guide potential habitat restoration efforts.

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