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A New Species of Land-locked Freshwater Shrimp Genus *Caridina* (Decapoda: Atyidae) from Middle Mekong Basin, Thailand

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ABSTRACT.– A newly discovered freshwater shrimp in the genus *Caridina* H. Milne-Edwards, 1837 from Thailand is described here as *C. panhai* **sp. nov.** The distinctiveness of the new species was supported by both morphological investigation and molecular analysis based on a concatenated dataset of two mitochondrial genes (16S rRNA and COI). Diagnostic characters of the new species include the strongly convex rostrum, very slender carpus of second pereopod (8.11–10.04 times as long as wide), and the reduced epipod on second and third pereopods. Intriguingly, females of *C. panhai* **sp. nov.** possess a small number of very large eggs (22–36 eggs per individual), which is characteristic of land-locked species. The new species is the first land-locked *Caridina* species discovered in Thailand, and its range is restricted to the Middle Mekong Basin in the northeast part of the country. By including historical records, there are 15 species of *Caridina* found in Thailand.

KEYWORDS: crustacean, freshwater fauna, molecular phylogeny, taxonomy, Southeast Asia

INTRODUCTION

The freshwater shrimp genus *Caridina* H. Milne Edwards, 1837, which comprises over 300 valid species worldwide, is one of the most diverse groups in the family Atyidae De Haan, 1849 (De Grave et al., 2015; de Mazancourt et al., 2021; GBIF, 2023). In general, *Caridina* can be found in a variety of freshwater habitats such as headwater streams, lakes, ponds, and lowland rivers, as well as in brackish water and brine of coastal areas (Page et al., 2007; Cai et al., 2007; De Grave et al., 2008; Bernardes et al., 2017; de Mazancourt et al., 2021). In terms of ecology, they can be categorized into two groups based on their life history, namely amphidromous species and land-locked species (Lai and Shy, 2009; Han et al., 2011; Yatsuya et al., 2013). An amphidromous species spawns numerous small-sized eggs, and their larvae require saline water to develop and migrate to coastal areas after hatching. Such behavior gives them relatively high dispersal ability and allows them to widely expand their range. In contrast, a land-locked species produces a small number of large-sized eggs and lives in freshwater for its entire life, without migrating to the sea. Their larvae require less time to develop to the juvenile stage. In addition, they tend to colonize the same habitats as the parents or places nearby (Hamasaki et al., 2021). These factors result in relatively low dispersal ability for land-locked species, which are typically endemic to a particular area (Page et al., 2008; Bauer 2013; Yatsuya et al., 2013; de Mazancourt et al., 2021).

The systematics of *Caridina* in mainland Southeast Asia has received attention from several authors in recent decades (i.e., Ng and Choy, 1990; Johnson, 1961a, b; Yeo et al., 1999; Cai and Ng, 1999, 2000; Li and Liang, 2002; Cai et al., 2007; Do et al., 2020, 2021). However, Thailand still lacks a robust taxonomic revision of this genus, as well as some basic knowledge in other aspects including their biology, geographic distribution, and evolution. Based on literature records, 14 *Caridina* species have been reported from Thailand, namely *C. typus* H. Milne Edwards, 1837; *C. laevis* Heller, 1862; *C. gracilirostris* De Man, 1892; *C. sumatrensis* De Man, 1892; *C. weberi* De Man, 1892; *C. gracillima* Lanchester, 1901; *C. brachydactyla* De Man, 1908; *C. propinqua* De Man, 1908; *C. macrophora* Kemp, 1918; *C. peninsularis* Kemp, 1918; *C. tonkinensis* Bouvier, 1919; *C. lanceifrons* Yu, 1936; *C. temasek* Choy and Ng, 1991; and *C. johnsoni* Cai et al., 2007. The majority of these were described from the southern and central regions of Thailand (Lanchester, 1901; Kemp, 1918; Kamita, 1966; Tiwari and Pillai, 1971; Junk, 1977; Cai et al., 2007; Cai and Ng, 2007; Naiyanetr, 2007; Do et al., 2021), while other parts of the country have mostly been neglected from checklists and surveys.

Recent field surveys in the Middle Mekong Basin of northeastern Thailand have yielded an unknown *Caridina* species that possesses a unique strongly convex rostrum, very slender second pereopod chela

TABLE 1. List of samples used in phylogenetic analyses, with specimen vouchers and GenBank accession numbers. n/a = data not available. References: 1 = Page et al. 2007, 2 = Shih and Cai, 2007, 3 = Bernardes et al., 2017, 4 = de Mazancourt et al. 2017, 5 = de Mazancourt et al., 2018, 6 = de Mazancourt et al., 2019, 7 = de Mazancourt et al., 2020, 8 = Do et al., 2020, 9 = Xu et al., 2020, 10 = Klotz et al., 2021.

Taxon	Locality	Voucher ID	16S	COI	Reference
Caridina panhai sp. nov.	Akat Amnuai, Sakon Nakhon, Thailand	MUMNH-CAR507-F1 (paratype)	OQ092406	OQ107450	This study
Caridina panhai sp. nov.	Akat Amnuai, Sakon Nakhon, Thailand	MUMNH-CAR507-F2 (paratype)	OQ092407	OQ107451	This study
Caridina panhai sp. nov.	Akat Amnuai, Sakon Nakhon, Thailand	MUMNH-CAR507-M1 (paratype)	OQ092405	OQ107452	This study
Caridina panhai sp. nov.	Bueng Khong Long Lake, Bueng Kan, Thailand	MUMNH-CAR115-F1	OQ092408	n/a	This study
Caridina acutirostris	Sulawesi, Indonesia	ZMB_30212–1	MT769137	MT769192	10
Caridina acutirostris	Sulawesi, Indonesia	ZMB_30212–2	MT769138	MT769193	10
Caridina africana	South Africa	CA1628	MK189899	MK190058	6
Caridina appendiculata	Australia	CA1670	MH497534	MK190059	6
Caridina appendiculata	Australia	CA1708	MK189903	MK190063	6
Caridina brachydactyla	Indonesia	CA1131	MH497502	MK190011	6
Caridina brevicarpalis	Matepono River, Guadalcanal, Solomon Island	GUC881	DQ478485	n/a	1
Caridina brevicarpalis	Solomon Islands	CA1521	MK189887	MK190049	6
Caridina buehleri	Solomon Islands	CA1519	KY350244	MK190047	6
Caridina caerulea	Sulawesi, Indonesia	ZMB_28062–1	MT769139	MT769194	10
Caridina elongapoda	Malaysia	CA1899	MK189924	MK190085	6
Caridina ensifera	Sulawesi, Indonesia	ZMB_28055–1	MT769141	MT769196	10
Caridina gracilipes	Borneo	CA1673	MH497535	n/a	5
Caridina gracilipes	Australia	CA1694	MH497540	n/a	5
Caridina gracilirostris	Kolombangara Island	CA1497	MT303886	n/a	7
Caridina gracilirostris	Australia	CA1678	MT303887	n/a	7
Caridina gueryi	Sulawesi, Indonesia	CA1161	KY350241	n/a	4
Caridina jeani	Vanuatu	CA1370	MK189867	MK190028	6
Caridina lanceifrons	Dongfang, Hainan, China	65	MT446450	MN701605	9
Caridina lanceifrons	Dongfang, Hainan, China	66	MT446451	MN701606	9
Caridina leucosticta	Japan	CA1913	MH497557	n/a	5
Caridina lilianae	Sulawesi, Indonesia	ZMB_29807–1	MT769154	MT769208	10
Caridina longicarpus	New Caledonia	CA1557	MK189892	MK190051	6
Caridina longidigita	Sulawesi, Indonesia	ZMB_28061–1	MT769159	MT769213	10
Caridina macrodentata	Vanuatu	CA1374	MK189869	MK190030	6
Caridina marlenae	Sulawesi, Indonesia	ZMB_29519–10	MT769165	MT769219	10
Caridina neglecta	Vella Lavella, Solomon Island	CA1703	MT303889	n/a	7
Caridina neglecta	Kolombangara Island	CA1938	MT303890	n/a	7
Caridina opaensis	Sulawesi, Indonesia	ZMB_29008–1	MT769179	MT769233	10
Caridina poso	Sulawesi, Indonesia	ZMB_29621–1	MT769181	MT769236	10
Caridina propinqua	Rathgama Lake, Southern Province, Sri Lanka	2309SL	AY708117	n/a	1
Caridina propinqua	Giang Thanh, Kien Giang, Vietnam	ZMB_30260	MT526817	MT526836	8
Caridina sarasinorum	Sulawesi, Indonesia	ZMB_28056–1	MT769184	MT769239	10
Caridina schenkeli	Sulawesi, Indonesia	ZMB_29159	AM747699	AM747774	10
Caridina typus	Sarawak, Malaysia	CT_Sar02	KY069345	KY069464	3
Caridina typus	Seychelles	MEFGL_CT_Sey01	KY069374	KY069493	3
Caridina villadolidi	Mindoro, Philippines	ZMBunid1227	KY436222	n/a	3
Caridina weberi	Kolombangara Island	CA1516	MT303920	n/a	7
Caridina weberi	Papua New Guinea	CA2244	MT303921	n/a	7
Caridina zhujiangensis	Dong'ao Island, Zhuhai, China	isolate_22	MT446448	MN701603	9
Neocaridina ketagalan	Taipei, Taiwan	NCd4	AB300167	AB300180	2
Neocaridina palmata	Ha Quang, Cao Bang, Vietnam	ZMB 30256	MT526825	MT526843	8
Neocaridina saccam	Taipei, Taiwan	NCd9	AB300169	AB300181	2
Neocaridina denticulata	Kinmen, Taiwan	NCd1	AB300173	AB300187	2
Neocaridina spinosa	Tongan, Fujian, China	NCo1	AB300174	AB300188	2

and carpus, and very large-sized eggs. An integrative approach involving detailed morphological examination and molecular analyses confirms the taxonomic validity of this taxon. In this study, we thus propose it as an additional new species, and provide a description herein. This is the first *Caridina* species discovered in Thailand since Kemp (1918) originally described *C. macrophora* and *C. peninsularis* from southern Thailand.

MATERIALS AND METHODS

Specimen sampling

Freshwater shrimps were collected by triangular dip net from aquatic habitats (i.e., streams, rivers, and ponds) from the Middle Mekong Basin in northeastern Thailand during field surveys between 2018 and 2020 The live habitus specimens were photographed to document their body coloration. The methods used for euthanasia followed Cooper (2011) under the protocol approved by Mahidol University-Institute Animal Care and Use Committee (approval number MU-IACUC 2018/004). Specimens were preserved in 75% and 95% (v/v) ethanol for long-term storage and molecular work, respectively. Voucher specimens were deposited into the Mahidol University Museum of Natural History (MUMNH), Department of Biology, Faculty of Science, Mahidol University, Thailand. Specimens were observed under ZEISS Stemi 305 stereo microscope and Olympus CH30 microscope. Specimens were photographed by digital eyepiece (Dino-Lite AM423X). Morphological characters were measured via DinoCapture software v.2.0 and reported in millimeters. All measurements were taken from ovigerous females except first and second pleopods, which were observed using male shrimps.

DNA extraction and PCR method

For molecular work, genomic DNA was extracted from the abdominal muscle using NucleoSpin tissue kit (MACHEREY-NAGEL, Germany). Two mitochondrial genes were used as genetic markers, including a fragment of approximately 520 bp of the large ribosomal subunit rRNA gene (16s rRNA) and a fragment of 820 bp of the protein-coding Cytochrome c oxidase subunit I (COI). Two sets of primers, 16Samod (5'–AAA AAC TAT TTG TCC GTC TTC AT–3') and 16Sbmod (5'–GGT CTG AAC TCA AAT CAT GTA AA–3') for 16s rRNA gene, 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') for COI gene, were used in PCR (von Rintelen et al., 2007). DNA amplification was performed using T100 thermal cycle (Bio-Rad Laboratories, USA), with the following conditions: 5 min at 94 °C; 30 cycles of denaturation for 60 s at 94 °C, annealing for 45 s at 46–50 °C, and elongation for 90 s at 72 °C; pre-denaturation for 3 min at 94 °C; and post-elongation for 4 min at 72 °C. The final total PCR volume was 30 μl, consisting of 15 μl of EmeraldAmp PCR Master Mix (TAKARA BIO INC.), 1.5 μl of both forward and reverse primers, 9 μl of distilled water, and 3 μl of the template DNA. The newly obtained nucleotide sequences in this study were deposited in the GenBank database under accession numbers OQ092405–OQ092408 for 16s rRNA, and OQ107450–OQ107452 for COI.

Phylogenetic analyses

The data matrix used in phylogenetic analyses included sequences from four individuals of the unknown species and other *Caridina* species retrieved from the GenBank database consisting of 44 sequences from 29 species in order to confirm the taxonomic validity of the unknown species. Five species of atyid freshwater shrimp genus *Neocaridina* Kubo, 1938 were utilized as the outgroup. Details of specimens used in molecular analyses are shown in Table 1. Sequences were aligned automatically in MAFFT v.7.49 (Katoh and Standley, 2013) by using L-INS-i algorithm for both 16S rRNA and COI genes.

Phylogenetic trees were estimated using the maximum likelihood (ML) and Bayesian inference (BI) methods through the online CIPRES Science Gateway server (Miller et al., 2010). The best-fit models of nucleotide substitution for each gene were determined by ModelFinder (Kalyaanamoorthy et al., 2017) as implemented in IQ-Tree 2.1.2 (Nguyen et al., 2015) for ML analysis and jModeltest v.2.1.10 (Darriba et al., 2012) based on Bayesian Information Criterion for BI analysis. The selected best-fit models are presented in Table 2. The ML trees were executed in IQ-Tree 2.1.2 (Nguyen et al., 2015), with 1,000 bootstrap replications; the BI analyses were conducted in MrBayes v3.2.6 (Ronquist et al., 2012), using 10,000,000 generations of Metropolis-coupled Markov chain Monte Carlo (MCMC), with tree sampled every 2,000 generations, and the first 25% of obtained trees were discarded as burn-in. Tracer v.1.6 was used to check the stationary conditions of all parameters (Rambaut et al., 2018).

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

Molecular marker	Codon position	Substitution model	
		IQ–TREE	MrBayes
16S	-	TVM+G4	HKY + I + G
COI	1	TIM3e+FQ+I+G4	SYM + G
COI	2	HKY+I	HKY + G
COI	3	TIM2+F+G4	GTR + G

RESULTS

SYSTEMATICS

Family Atyidae De Haan, 1849

Genus *Caridina* H. Milne Edwards, 1837

Caridina panhai sp. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:9F378666-8565-4A15-ACD6-5DF9C44F5B33
(Figs 1–5)

Type materials.– THAILAND • Holotype: ovigerous ♀, carapace length 3.70 mm, MUMNH-CAR507-H1; Nam Chan Reservoir, Akat Amnuai District, Sakon Nakhon Province; collected on 18 Jan 2020; 17.5983 °N, 104.0126°E. • Paratypes: 9 ovigerous ♀, MUMNH-CAR507-F1–F9; 6 ♂, MUMNH-CAR507-M1–M6; same collection data as for holotype.

Other materials examined.– THAILAND • 5♀, 3♂, MUMNH-CAR115; Bueng Khong Long Lake, Bueng Khong Long District, Bueng Kan Province; collected on 9 Apr 2018; 17.9603°N, 104.0376°E. • 3♀, 3♂, MUMNH-CAR153; small canal near road no. 2094, Seka District, Bueng Kan Province; collected on 6 Jan 2018; 17.83552°N, 103.9400°E. • 3♀, 2♂, MUMNH-CAR173; Nong Loeng Reservoir, Phon Charoen District, Bueng Kan Province; collected on 6 Jan 2018; 18.0341°N, 103.6301°E. • 3♀, 1♂, MUMNH-CAR 369; collected on 05 Jan 2018; small canal near road no. 5027, Phon Phisai District, Nong Khai Province; 17.9764°N, 103.0845°E.

Etymology.– The specific name of the new species, *C. panhai* sp. nov. is named in honor of Prof. Dr. Somsak Panha (Chulalongkorn University, Thailand), a famous Thai taxonomist, for his dedication and substantial contributions to the systematics of invertebrates in Thailand and Southeast Asia.

Description

Cephalothorax and cephalic appendage (n = 7). Carapace length 2.54–3.51 mm (median 3.09), width 1.75–3.30 mm (median 2.36). Rostrum (Fig. 1A, C) slender, strongly convex between base to near proximal 2/3, then curved upward to the tip, reaching near or slightly beyond the end of the third segment of antennular peduncle, 0.74–1.00 (median 0.84) times as long as carapace, rostral formula (2–3) + 9–15 / 1–4. Antennal spine placed below inferior orbital angle. Pterygostomian margin subrectangular. Eye well developed, anterior end reaching to 0.42–0.70 (median 0.55) of first segment of antennular peduncle. Antennular peduncle (Fig. 1A, C) 0.72–0.84 (median 0.79) times as long as carapace, first segment 1.19–1.68 (median 1.38) times as long as second segment, second segment 1.47–1.83 (median 1.69) times as long as third segment. Tooth on distolateral margin of first segment of antennular peduncle prominent and acute. Stylocerite reaching to 0.76–0.86 (median 0.80) of first segment of antennular peduncle. Scaphocerite 3.09–3.53 (median 3.19) times as long as wide, distal margin with short plumose setae.

Branchial formula. Podobranch on second maxilliped reduced to a thin plate. Third maxilliped possesses one small and one large arthrobranch. Pleurobranchs present on all pereopods.

Mouthparts (n = 3). Mandible without palp (Fig. 2E), incisor process with 5–6 irregular teeth, two rows of setae placed along 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), tapering posteriorly, 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 (Fig. 2D), ending with finger-like projection and with few 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, 7–10 spiniform setae on distal 1/3 of posterior margin, 0.80–0.86 (median 0.83, n=7) times as long as penultimate segment. Exopod long and slender, with a tuft of long setae at tip.

Pereopods (n = 7). Epipod present on first two pereopods but reduced in second pereopod. Epipod on third pereopod absent or sometimes reduced. Epipod on last two pereopods always absent. Chelae of first and second pereopods well-developed (Fig. 1E, F).

First pereopod slender (Fig. 1E); chela 3.20–3.69 (median 3.39) times as long as wide, 0.98–1.19 (median 1.07) times as long as carpus; tips of fingers

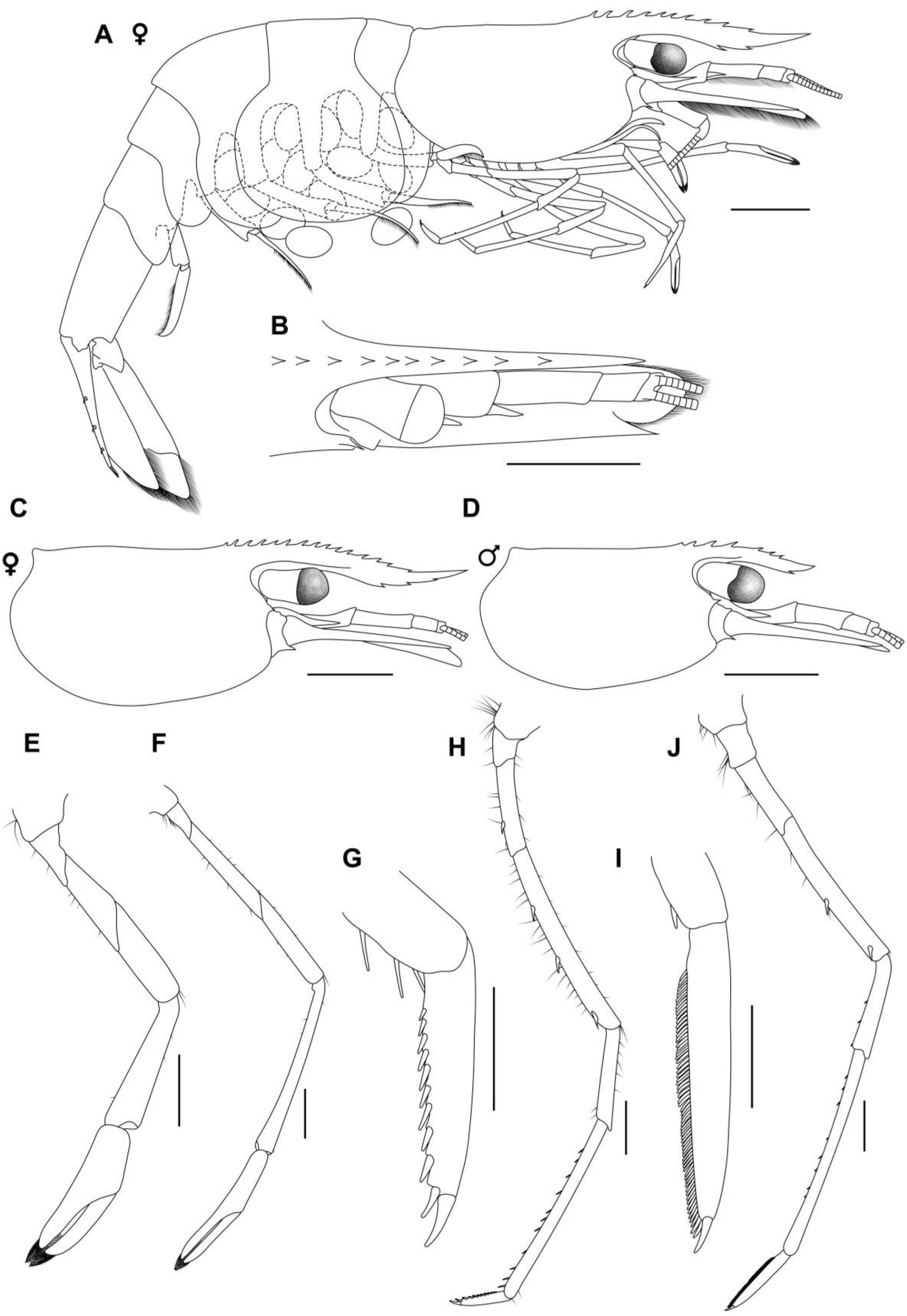

FIGURE 1. *Caridina panhai* sp. nov. **A.** ovigerous female. **B.** top view of carapace. **C.** cephalothorax and cephalic appendages of female and **D.** male specimens. **E.** first pereopod. **F.** second pereopod. **G**. dactylus of third pereopod. **H.** third pereopod. **I.** dactylus of fifth pereopod. **J.** fifth pereopod. Drawings were taken from paratype MUMNH-CAR507-F9 (**A, B, E–J**); paratype MUMNH-CAR507-F8 (**C**), and paratype MUMNH-CAR507-M6 (**D**). Scale bar: A–D, H, J = 1 mm; E, F = 0.5 mm; G, I = 0.1 mm.

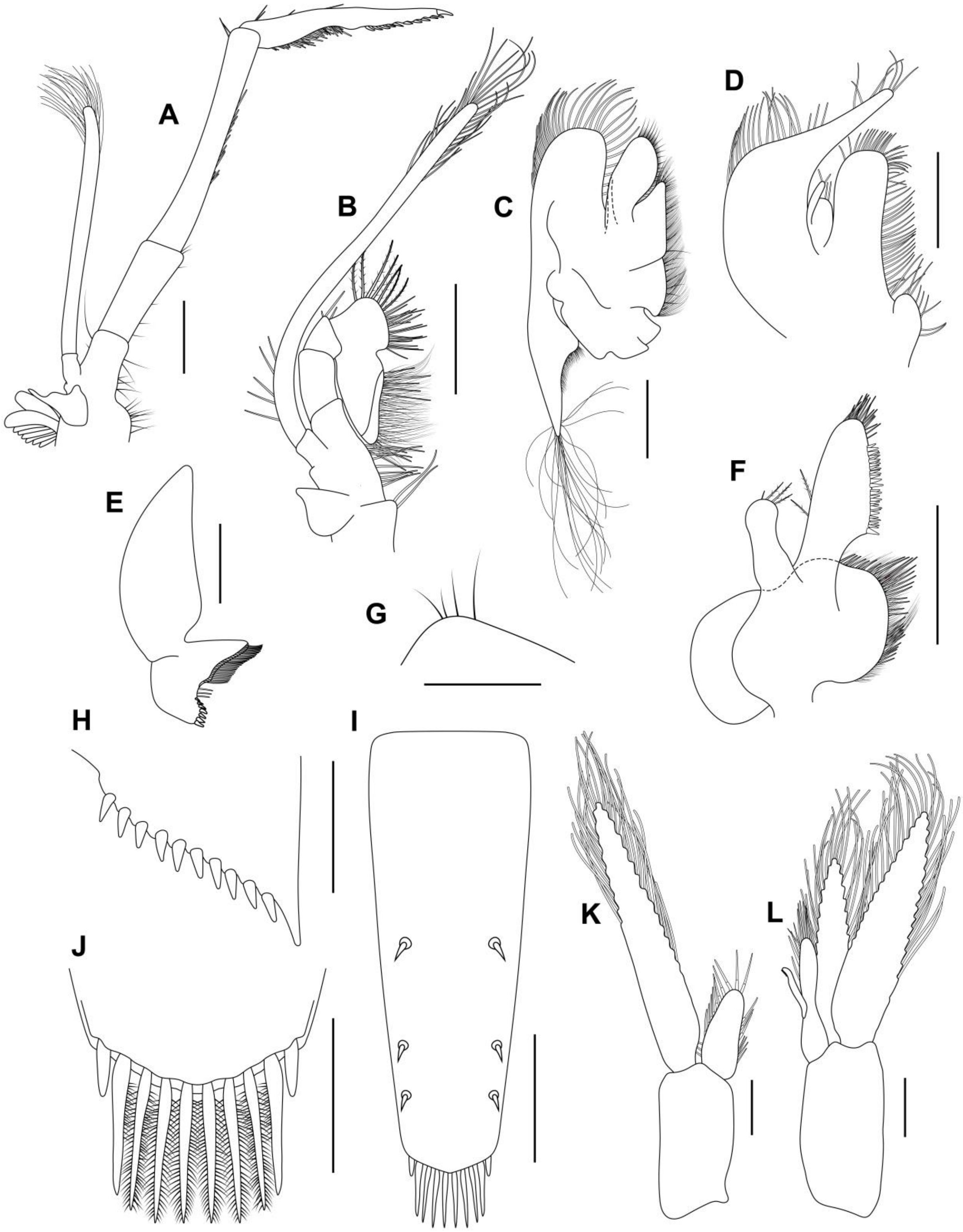

FIGURE 2. *Caridina panhai* sp. nov. **A.** third maxilliped. **B.** second maxilliped. **C.** maxilla. **D.** first maxilliped. **E.** mandible. **F.** maxillula. **G.** preanal carina. **H.** uropodal diaeresis. **I.** telson. **J.** distal end of telson. **K.** first pleopod. **L.** second pleopod. Drawings were taken from paratype MUMNH-CAR507-F9 (**A–J**); paratype MUMNH-CAR507-M6 (**K, L**). Scale bar: I, J = 0.5 mm; A–H, K, L = 0.25 mm.

rounded, with tuft of setae near tip; dactylus 1.19–1.55 (median 1.31) times as long as palm; carpus excavated distally, 3.47–4.24 (median 3.72) times as long as wide, 1.24–1.42 (median 1.34) times as long as merus; merus 3.10–4.05 (median 3.45) times as long as wide, 1.06–1.33 (median 1.21) times as long as ischium.

Second pereopod extremely slender (Fig. 1F); chela very long, 6.03–7.05 (median 6.37) times as long as wide, 0.69–0.77 (median 0.75) times as long as carpus, tips of fingers round, with tuft of setae near tip; dactylus 0.90–1.40 (median 1.08) times as long as palm; carpus very slender, 8.11–10.04 (median 8.82) times as long as wide, 1.62–1.89 (median 1.76) times as long as merus; merus 4.52–6.33 (median 5.68) times as long as wide, 0.93–1.26 (median 1.06) times as long as ischium.

Third pereopod not sexually dimorphic (Fig. 1H); dactylus with 8–10 spinules on flexor margin (Fig. 1G), 4.50–6.04 (median 5.28) times as long as wide (including terminal claw), terminating with one large claw; propodus with numerous spiniform setae on lateral and posterior margin, 10.03–15.82 (median 13.04) times as long as wide, 2.66–3.34 (median 3.09) times as long as dactylus; carpus with 3–4 spiniform setae on posterior margin of outer surface, the distal seta largest, the other setae minute, 5.72–7.01 (median 6.31) times as long as wide, 0.52–0.60 (median 0.57) times as long as propodus; merus with three large spiniform setae on posterior margin of outer surface, 8.08–10.21 (median 9.31) times as long as wide, 1.76–2.19 (median 1.91) times as long as carpus; ischium with one spiniform seta.

Fifth pereopod slender (Fig. 1J); dactylus with 57–68 spinules on flexor margin (Fig. 1I), 5.25–7.21 (median 5.83) times as long as wide (including terminal claw), terminating with one large claw; propodus with numerous spiniform setae on posterior margin, 11.81–14.37 (median 13.41) times as long as wide, 2.29–2.76 (median 2.55) times as long as dactylus; carpus with 3–4 (mode 3) spiniform setae on posterior margin of outer surface, the distal seta largest, the other setae minute, 4.48–5.61 (median 4.97) times as long as wide, 0.42–0.51 (median 0.48) times as long as propodus; merus with two large spiniform setae on posterior margin of outer surface, 6.75–8.70 (median 7.60) times as long as wide, 1.49–1.92 (median 1.66) times as long as carpus; ischium without spiniform seta.

Pleopods (n = 6). Endopod of male first pleopod subtriangular (Fig. 2K), wider proximally, 2.06–2.50 (median 2.21) times as long as width, 0.28–0.30 (median 0.29) times exopod length, without appendix interna. Appendix masculina of second male pleopod rod-shaped (Fig. 2L), with numerous setae, 0.66–0.81 (median 0.70) times as long as endopod (including distal setae). Appendix interna very slender, reaching 0.59–0.69 (median 0.64) times appendix musculina length.

Abdomen (n = 7). Sixth abdominal somite 0.63–0.79 (median 0.75) times carapace length, 1.84–2.15 (median 2.02) times as long as fifth somite, 0.94–1.27 (median 1.03) times as long as telson (Fig. 1A). Telson 2.58–3.03 (median 2.74) times as long as wide, with 3–4 pairs of dorsal spiniform setae and one pair of dorsolateral spiniform setae (Fig. 2I). Distal margin of telson subtriangular, without posteromedian projection, frequently with one median moveable plumose seta and 4–5 pairs of moveable plumose setae, subequal in length (Fig. 2J). Preanal carina stout, with a few setae, without a spine (Fig. 2G). Uropodal diaeresis with 7–12 short moveable spiniform setae (Fig. 2H).

Eggs. Ovigerous females with few eggs (22–36 eggs, n = 5). Size of eye-developed eggs 0.94–1.06 × 0.60–0.67 mm (n = 20).

Coloration.– In living specimens (Fig. 3), body brown to thistle green, furnished with numerous scattered black spots. Cephalic region and first to second dorsal somites darker than other parts. Each somite with a dorsal dark stripe. Eggs greenish brown.

Distribution and habitat.– Based on the materials in this study, the distribution of *C. panhai* sp. nov. is limited to the Songkhram River and tributaries that drain into the Middle Mekong River, in northeast Thailand (Fig. 4). This species can be found in lentic freshwater habitats, such as marsh, pond, lake, and paddy field. They were found living on aquatic vegetation in shallow areas, where the bottom substrate was mud and clay.

Phylogenetic results.– The molecular analyses indicated *C. panhai* sp. nov. as distant phylogenetically from other members of *Caridina*, with high support (100 ML bootstrap value and 1.00 BI Bayesian posterior probability; Fig. 5), and nested it as a sister clade to *C. propinqua* s.s. Page et al. (2007).

Remarks.– The new species shares the characteristics of a short-rostrum and slender second pereopod carpus with *C. excavatoides* Johnson, 1961; and *C. temasek*. However, it can be distinguished from these three species by having a longer rostrum that reaches beyond the end of antennular peduncle (vs rostrum that reaches between the base and the end of the third segment of antennular peduncle), much more slender second pereopod chela (6.03–7.50 times as long as wide vs 3.0–5.3 times as long as wide), and larger eggs (0.94–

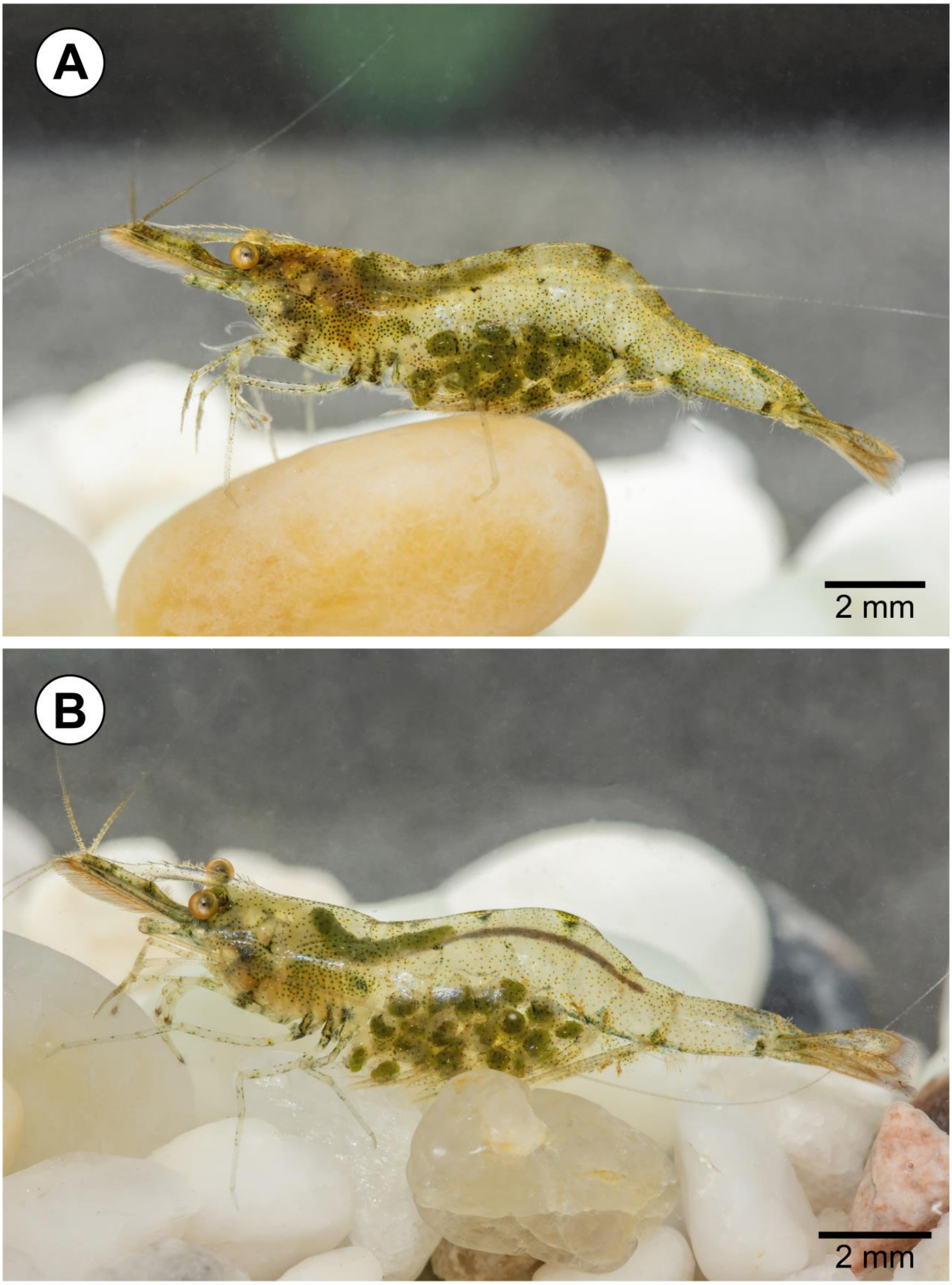

FIGURE 3. Living female of *Caridina panhai* sp. nov. Photos was taken from **A.** MUMNH-CAR507_P1 and **B.** MUMNH-CAR507_P2.

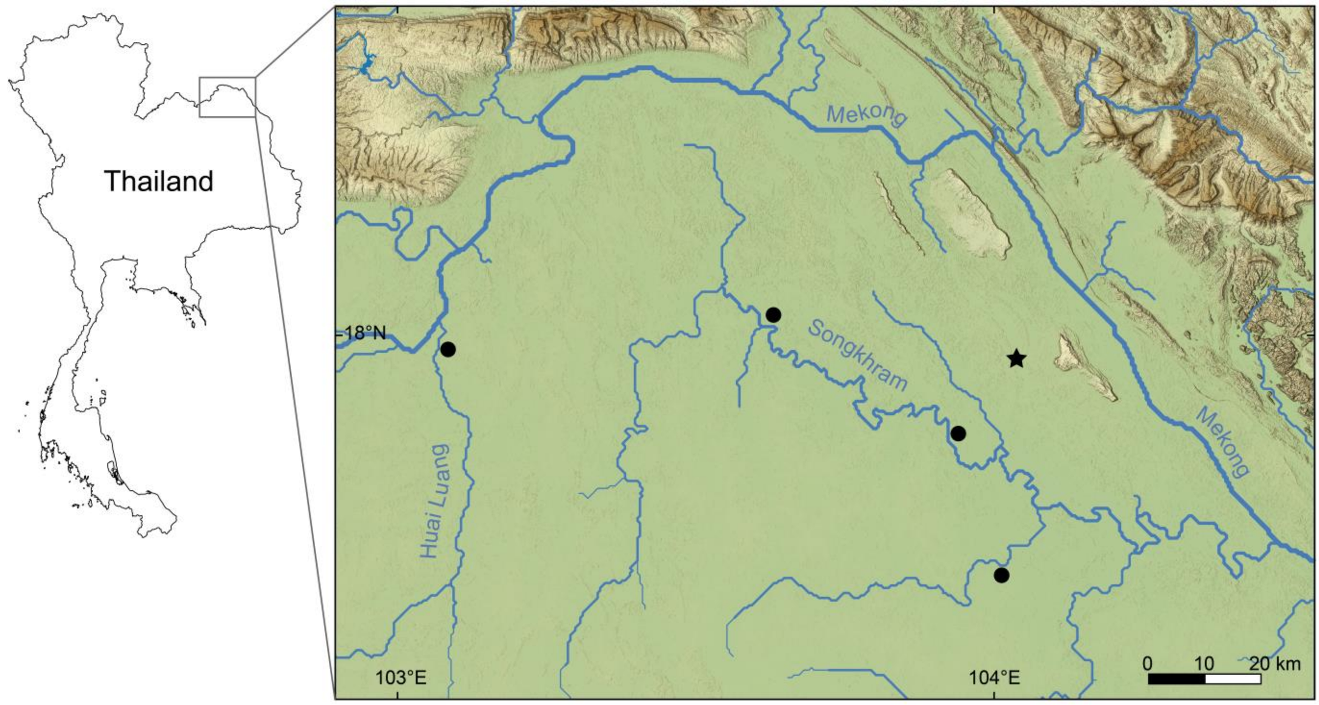

FIGURE 4. Map of Thailand showing the distribution of *Caridina panhai* sp. nov. (Black star for the type locality and black circles for other materials). Maps were generated using QGIS v3.24.3 by compiling, river and lake topology from the HydroSHEDS database (https://www.hydro sheds.org), and map raster data from the NASA EARTHDATA (https://www.earthdata.nasa.gov/).

1.06 × 0.60–0.67 mm vs 0.40–0.85 × 0.25–0.54 mm). In addition, the first pleopod of the new species also lacks appendix interna (vs present in *C. temasek*), and the third pereopod is not sexually dimorphic (vs sexually dimorphic in *C. thambipilaii*) (Johnson, 1961a; Choy and Ng, 1991; Cai et al., 2007).

Caridina panhai sp. nov. closely resembles *C. laevis*, but can be distinguished by having a longer rostrum that reaches slightly beyond the end of the third segment of the antennular peduncle (vs reaching between the middle of second segment to the middle of third segment of antennular peduncle); fewer dorsal teeth (9–15 vs 15–22), fewer postorbital teeth (2–3 vs 4–5); more slender first pereopod carpus (3.47–4.24 times as long as wide vs 2.6–2.7 times), and much more slender second pereopod carpus (8.11–10.04 times as long as wide vs 6.5–7.4 times) (Heller, 1862; De Man, 1892; Pillai 1964).

Caridina panhai sp. nov. is also similar to *C. tonkinensis* Bouvier, 1919. However, the new species differs from *C. tonkinensis* by the absence of a spine on preanal carina (vs presence), more slender P2 carpus (8.11–10.04 times as long as wide vs 4.4 times as long as wide), fewer spiniform setae on fifth pereopod dactylus (57–68 vs approximately 80), the feature of plumose setae at distal end of telson (subequal in length vs two median pairs shorter than the others), and larger eggs (0.94–1.06 × 0.60–0.67 mm vs 0.68–0.75 × 0.47–0.48 mm) (Bouvier, 1919; Cai et al., 2007).

The new species is very similar to *C. excavata* Kemp, 1913 from India by sharing a very slender second pereopod chela, the shape of rostrum, and large-sized eggs. However, the new species differs from *C. excavata* by having more convex rostrum; fewer number of ventral teeth (1–4 vs 2–8); more slender first pereopod carpus (3.47–4.24 times as long as wide vs 3 times), much longer second pereopod carpus (8.11–10.04 times as long as wide vs 5.5 times), greater number of spiniform setae on fifth pereopod dactylus (57–68 vs 40–50), and greater number of dorsal spiniform setae on telson (3–4 pairs vs 2 pairs) (Kemp, 1913). In addition, the distribution range of the new species is limited to the Middle Mekong Basin in northeast Thailand, whereas *C. excavata* is dispersed along the Brahmaputra River in Assam State, India (Kemp, 1913). Both species carry large-sized eggs, and are characterized as land-locked species (Yatsuya *et al.* 2013; de Mazancourt et al., 2021). Thus, they are each distributed in their own limited area, since land-locked species spend their whole life in freshwater without migration, and tend to colonize in or near parental habitats (Bauer 2013; Hamasaki et al., 2021). Unfortunately, the molecular data of *C. excavata* was not available in the current study. However, considering the significant differences in morphology and their geographic distributions, there is no doubt that they are distinct species.

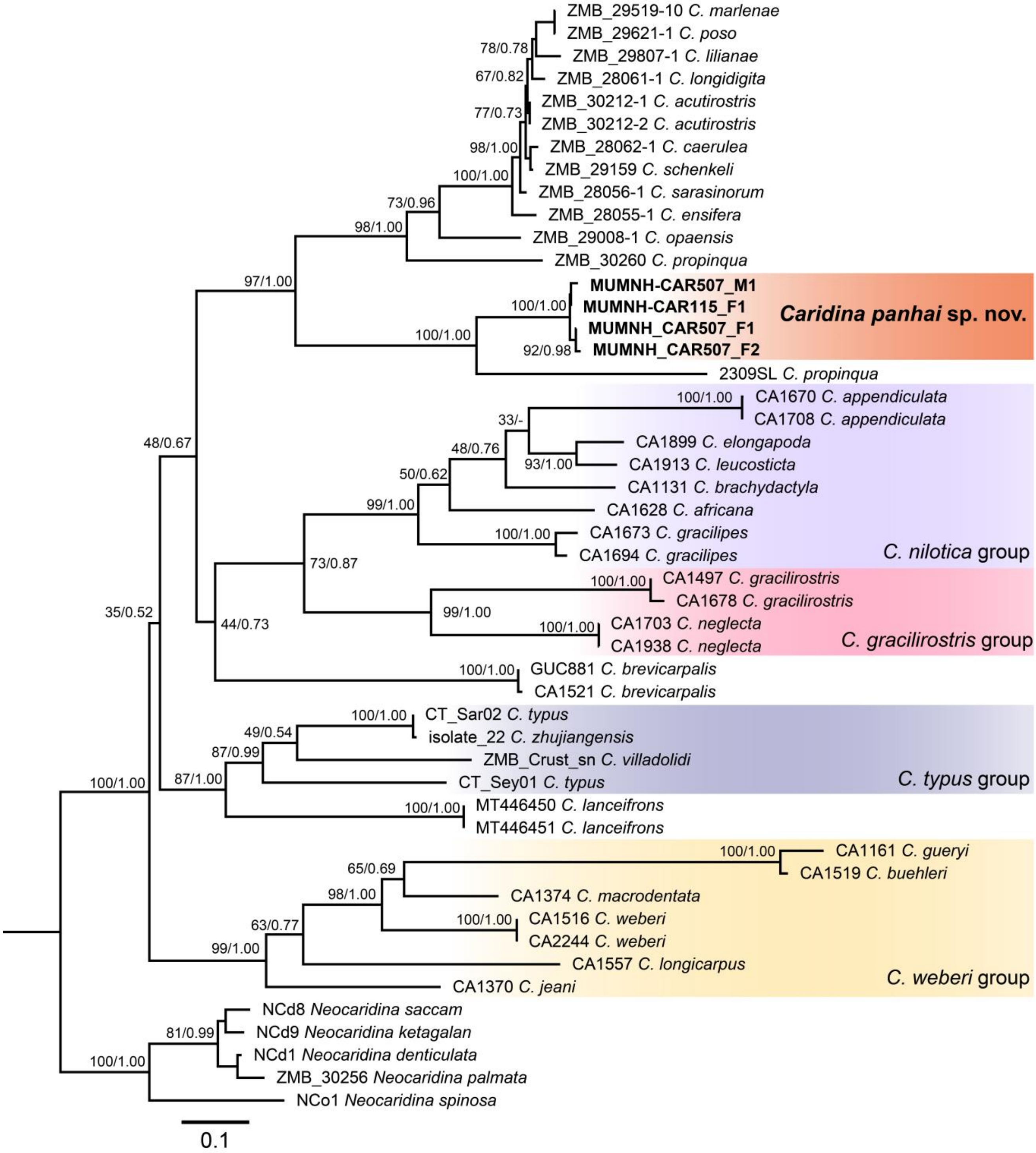

FIGURE 5. Maximum Likelihood tree of *Caridina* and outgroups based on 16S rRNA and COI genes. Numbers at each node show ML bootstrap value followed by Bayesian posterior probability.

DISCUSSION

Caridina panhai sp. nov. would be included in the *C. nilotica* group based on morphology alone, because they possess several similar characters, such as a rostrum that extends beyond the end of third antennular peduncle, a dorsal hump on the third abdominal somite, and few moveable setae on the uropodal diaeresis (usually less than 15) (Richard and Clark, 2005, 2014; de Mazancourt et al., 2018, 2020; Cai, 2020). However, the molecular analyses indicated that this new species split apart from the *C. nilotica* group (Fig. 5).

In fact, it differs from members of the *C. nilotica* group in having reduced epipods on the second and third pereopods (vs usually present on first four pereopods) (Cai et al., 2007; de Mazancourt et al., 2018, 2020).

According to the current phylogenetic tree, *C. panhai* sp. nov. is nested with *C. propinqua* sensu Page et al. (2007), but with a great distance between the two, and their morphology is very different (De Man, 1908a; Cai et al., 2007). This could be a consequence of taxon sampling bias. The overall sampling of the genus *Caridina* is far from complete, especially for the mainland Southeast Asia taxa. Further work requires more comprehensive sampling, including genetic data from species such as *C. laevis* and *C. excavata*, in order to accurately examine phylogenetic relationships with this new species.

This species is the first endemic land-locked *Caridina* species to be discovered in northeast Thailand. Thus, there are now 15 species of *Caridina* known to exist in Thailand. At present, several species of *Caridina* such as *C. apodosis* Cai and Ng, 1999 and *C. striata* von Rintelen and Cai, 2009 are severely threatened due to habitat destruction and overharvesting for aquarium trades (De Grave et al., 2015; de Mazancourt et al., 2021; IUCN, 2022). Extensive information regarding systematics, biology, and geographical range of each species will be essential for conservation management in the future. Moreover, Thailand is a part of several significant freshwater ecoregions, which are the Lower and Middle Salween Basins, Middle Mekong Basin, Mae Khlong Basin, Chao Phraya Basin, and Malay Peninsula Basin (Abell et al., 2008). Future field surveys and phylogenetic studies in all of these regions will allow us to better understand the evolution and biogeography of *Caridina* in mainland Southeast Asia.

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