Three new cryptic species of the genus *Caridina* (Decapoda: Caridea: Atyidae) from Hong Kong, with notes on the *C. serrata* species group

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Abstract

Three new species of freshwater atyid shrimp, namely *Caridina chui* sp. nov., *C. bauhinia* sp. nov. and *C. argilla* sp. nov., are described from Hong Kong, southern China using an integrative taxonomic approach. All three species belong to the *C. serrata* species group and differ from the other members in characteristics of the rostrum, pereiopods, and male first and second pleopods. Phylogenetic analyses based on mitochondrial COI and 16S rRNA sequences show that the *C. serrata* species group is polyphyletic and comprised of at least four lineages. The validity of the *C. serrata* species group is discussed and more detailed diagnoses of the species group are proposed at two levels given the phylogenetic uncertainty and hence the potential systematic issue. The *C. serrata* species group *sensu stricto* is restricted to the nominal lineage containing *C. serrata* and closely related species, distinguished from other species of the *C. serrata* species group mainly by having relatively stout carpus of first pereiopod, stout appendix masculina of male second pleopod, and large number of spiniform setae on the uropodal diaeresis. To cope with potential systematic issues, the *C. serrata* species group *sensu lato* is also proposed to include most of the Chinese and Vietnamese landlocked species, which is characterised mainly by having relatively stout carpus of first pereiopod, short carpus of second pereiopod, short spiniform terminal setae on telson, and male first pleopod with relatively large endopod and an appendix interna.

Key words: Biodiversity, Crustacean, Freshwater shrimp, Systematics

BACKGROUND

The freshwater atyid shrimp genus, *Caridina* H. Milne Edwards, 1837, is a diverse genus comprising more than 340 species (DecaNet eds. 2025). Several species groups (sometimes called species complexes) were established to accommodate species that share morphological similarities, often also genetic affinity. They include the *C. brevicarpalis* group, *C. gracilirostris* group, *C. nilotica* group, *C. serrata* group, *C. serratirostris* group, *C. typus* group, C. *weberi* group and *C. yunnanensis* group (Bouvier 1925; Cai and Ng 1999 2001 2007; de Mazancourt et al. 2020). Some closely related species were also grouped into species complexes, sometimes involved the presence of cryptic species, such as the *C. indistincta*, *C. thermophila* and C. *zebra* complexes from Australia (Chenoweth and Hughes 2003; Choy et al. 2019; Short et al. 2019), or grouped into geographical clades such as the Poso and Malili clades from Sulawesi, Indonesia (von Rintelen and Cai 2009).

Among the several *Caridina* species groups or complexes, the *C. serrata* species group is especially well-represented in southern China and northern and central Vietnam. Taking Hong Kong as an exemplar, among the seven landlocked *Caridina* species recorded (see Chow et al. 2018; Chow et al. 2024), six of them belong to the *C. serrata* species group, namely *C. apodosis* Cai and Ng, 1999, *C. cantonensis* Yu, 1938, *C. logemanni* Klotz and von Rintelen, 2014, *C. ngankeeae* Chow, Chan and Tsang, 2024, *C. serrata* Stimpson, 1860 and *C. trifasciata* Yam and Cai, 2003. This species group is characterised by four features according to Cai and Ng (1999), viz. 1) presence of dorsal rostral teeth on the carapace; 2) stylocerite reaching beyond the end of the basal segment of the antennular peduncle; 3) presence of an appendix interna on the endopod of male first pleopod; and 4) large eggs with abbreviated larval development. In 2022–2023, some cryptic specimens conforming to the *C. serrata* species group, initially identified as *C. cantonensis* and *C. serrata* in the field, were collected from Hong Kong. An integrated taxonomic approach revealed that they do not belong to any known members of the species group but represent three new species which are herein described as *C. chui* sp. nov., *C. bauhinia* sp. nov. and *C. argilla* sp. nov. Stimulated by the potential non-monophyly of the *C. serrata* species group indicated in previous preliminary phylogenetic analyses (see Klotz and von Rintelen 2014; Do et al. 2020), an opportunity is herein taken to discuss the validity of this species group.

MATERIALS AND METHODS

Specimen collection

Specimens were collected using hand nets, euthanised by freezing, and preserved in > 95% ethanol. Due to conservation concern, the exact sampling localities are stored with the type materials and are not herein disclosed. Specimens examined were deposited in the Simon F.S. Li Marine Science Laboratory, The Chinese University of Hong Kong (CUHK-LMT). The abbreviations 'pocl' and 'ov.' stand for post-orbital carapace length and ovigerous, respectively.

DNA extraction, PCR and sequencing

Total genomic DNA was extracted from pleopods using the QuickExtract DNA Extraction Solution (Lucigen, Middleton, WI, USA) or the DNeasy Blood and Tissue Kit (QIAGEN, Hilden, Germany) following the manufacturer's instructions. Partial sequences of mitochondrial cytochrome c oxidase subunit I (COI) and 16S rRNA genes were amplified by PCR with primer pairs Cys F/dgH2198 (Folmer et al. 1994; Ma et al. 2021) and 16S-AR/16S-1472 (Crandall and Fitzpatrick 1996; Palumbi et al. 2002), respectively. PCR reactions were performed in a 25 μl volume containing 3–4 μL template DNA, 1X PCR reaction buffer, 200 μM dNTPs, 0.2 μM of each primer, 0.5 mM MgCl2 and 1.5U *Taq* polymerase (Takara, Kasatsu, Japan), with the following profile: initial denaturation at 95°C for 3 min, followed by 35 cycles of 95°C for 30 s, 50°C for 40 s and 72°C for 1 min, and a final extension at 72°C for 3 min. The PCR products were purified by the sequencing company (BGI, Shenzhen, China). Sequences were generated using the forward primer on an Applied Biosystems (ABI) 3700 automated sequencer using the ABI Big-dye Ready-Reaction Mix Kit (Life Technologies, Carlsbad, CA, USA), following the standard cycle sequencing protocol.

Phylogenetic analyses

Specimens and GenBank accessions included in the phylogenetic analyses are listed in Table 1. The GenBank accessions were retrieved from a number of taxonomic, phylogenetic and

population genetic literatures (Page et al. 2007a 2007b; Shih and Cai 2007; Klotz and von Rintelen 2014; Chow et al. 2018 2022; Chen et al. 2020; Do et al. 2020 2021a 2021b; Xu et al. 2020; Ma et al. 2021; Zhou et al. 2021; Guo et al. 2022; Jiang et al. 2023). As two different COI gene regions were sequenced among the previous studies, sequences of both regions were included in the analyses to increase species coverage. If the COI sequences of the two regions were generated from two different vouchered specimens, they were only concatenated and included in the analysis if the specimens were confirmed to be conspecifics on the ground of showing > 98% similarity in their 16S rRNA sequences. Sequences were aligned using MUSCLE (Edgar 2004) with alignment of COI gene confirmed by translating sequences into amino acid sequences. Poorly aligned regions of the 16S rRNA gene were trimmed using trimAl v1.3 (Capella-Gutiérrez et al. 2009) with a gap threshold of 80%. Sequences were then concatenated into a 1,727 bp-long alignment (COI: 1,239 bp; 16S: 488 bp). Kimura two-parameter (K2P) pairwise genetic distances among selected species were calculated using MEGA v7 (Kumar et al. 2016). Partitions and best-fit substitution models were determined using PartitionFinder v2.1.1 (Lanfear et al. 2017), according to the corrected Akaike information criterion (AICc). The substitution models used and partitioning for phylogenetic analyses were as follows, partition 1: COI 1st codon position (TRN + I + G), partition 2: COI 2nd codon position (TIM + I), partition 3: COI 3rd codon position (GTR + G), and partition 4: 16S rRNA (TVM + I + G). Maximum likelihood (ML) analysis was carried out using IQ-TREE v2.3.1 (Minh et al. 2020) and branch support was assessed by ultrafast bootstrapping (Minh et al. 2013) with 5,000 replicates. Bayesian inference (BI) analysis was carried out using MrBayes v3.2.7 (Ronquist et al. 2012). Two independent Markov chain Monte Carlo (MCMC) runs of four chains were performed for five million generations, sampling every 500th generation. Convergence of chains was determined by having effective sample size (ESS) > 200 for all parameters. One-fourth of the trees were discarded as burn-in. All trees were rooted by two congeners from the *C. nilotica* species group, *C. elongapoda* Liang and Yan, 1977 and *C. gracilipes* De Man, 1892, which was shown to be distantly related to the target group of landlocked atyids from East and Southeast Asia including the *C. serrata* species group, *Neocaridina, Paracaridina* and *Sinodina* (von Rintelen et al. 2012).

RESULTS

SYSTEMATICS

Family Atyidae De Haan, 1849

Genus *Caridina* H. Milne Edwards, 1837

Caridina chui sp. nov.

(Figs. 1A–L, 2)

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Material examined: Holotype: female (pocl 4.0 mm), Shing Mun, central New Territories, Hong Kong, coll. JCF Chan, 02.IV.2022, CUHK-LMT-CAR444-2. Paratypes: 2 females (pocl 4.1 and 4.6 mm), same collection data as holotype, CUHK-LMT-CAR444; 3 males (pocl 2.9–3.1 mm), 5 females (pocl 3.3–3.7 mm), 2 ov. females (pocl 3.4 and 4.2 mm), Shing Mun, central New Territories, Hong Kong, coll. JCF Chan, 07.VII.2023, CUHK-LMT-CAR502.

Comparative material examined: *Caridina cantonensis*, 4 males (pocl 2.8–4.9 mm), 2 females (pocl 4.7 and 5.0 mm), same collection data as holotype, CUHK-LMT-CAR444a; 1 male (pocl 4.0 mm), 3 females (pocl 3.3–4.7 mm), Shing Mun, central New Territories, Hong Kong, coll. JCF Chan, 07.VII.2023, CUHK-LMT-CAR502a.

Etymology: Named after Dr. Ka Hou Chu for his contribution to decapod crustacean biology, including biodiversity and conservation genetics of atyid shrimps in Hong Kong.

Description: Rostrum (Fig. 1A) straight, shallow, usually directed downwards, nearly reaching to the end of basal segment of antennular peduncle to reaching to midlength of second segment, tip sometimes directed slightly upwards, 0.25–0.35 (median 0.32) times pocl; rostral formula 2–4 + 4–7 / 0–2. Inferior orbital angle fused with antennal spine. Pterygostomial angle rounded, subrectangular, slightly produced forward. Eyes well developed with globular cornea. Antennular peduncle 0.45–0.55 (median 0.49) times pocl, basal segment 2.0–2.5 (median 2.2) times as long as second segment, second segment 1.1–1.5 (median 1.3) times as long as third segment. Stylocerite reaching to 0.00–0.55 (median 0.35) length of second segment of antennular peduncle. Scaphocerite (Fig. 1B) 2.55–2.85 (median 2.76) times as long as wide.

Sixth abdominal somite about 0.5 times pocl, about as long as telson. Telson (Fig. 1C) 2.1–2.4 (median 2.3) times as long as proximal wide, with 4 or 5 pairs of short spiniform setae dorsal

and one pair of short spiniform setae dorsolateral, posterior margin (Fig. 1D) convex with a median projection and 4 pairs of spiniform setae, sublateral pair slightly shorter than lateral pairs and inner pairs. Preanal carina (Fig. 1E) rounded, unarmed, with few setae. Uropodal diaeresis (Fig. 1F) with 15–21 movable spiniform setae, outermost one slightly longer than lateral angle.

Mandible (Fig. 1G) with incisor process ending in irregular teeth; molar process truncated. Maxillule (Fig. 1H) with lower lacinia broadly rounded, upper lacinia elongate, with numerous distinct cuspidate setae on inner margin; palp with few simple setae. Maxilla (Fig. 1I) with upper endites subdivided; palp slender; scaphognathite tapering posteriorly, fringed with long setae at posterior margin. First maxilliped (Fig. 1J) with palp ending in a projection. Second maxilliped (Fig. 1K) with well-developed podobranch. Third maxilliped (Fig. 1L) with 2 arthrobranchs, ultimate segment subequal to penultimate in length. First pereiopod with an arthrobranch. Pleurobranchs present on all pereiopods. Epipods present on third maxilliped and first four pereiopods.

First pereiopod (Fig. 2A) chela 1.85–2.05 (median 1.99) times as long as wide, 1.2–1.5 (median 1.4) times as long as carpus; tips of fingers rounded, without hooks, fingers 0.95–1.25 (median 1.06) times as long as palm; carpus strongly excavated distally, 1.35–1.60 (median 1.50) times as long as wide, 0.85–0.95 (median 0.91) times as long as merus; merus 2.4–2.9 (median 2.6) times as long as wide, longer than ischium. Second pereiopod (Fig. 2B) chela 2.40–2.90 (median 2.59) times as long as wide, 0.70–0.80 (median 0.75) times as long as carpus; tips of fingers rounded, without hooks, fingers 1.45–1.65 (median 1.56) times as long as palm; carpus 4.8–5.3 (median 5.1) times as long as wide, 1.05–1.20 (median 1.16) times as long as merus; merus 4.4–4.9 (median 4.6) times as long as wide, longer than ischium. Third pereiopod (Fig. 2C) slender, not sexually dimorphic; dactylus (Fig. 2D) with 3 or 4 accessory spiniform setae on flexor margin, 2.4–3.1 (median 2.9) times as long as wide (terminal claw and accessory spiniform setae included); propodus 7.1–8.5 (median 7.8) times as long as wide, 3.4–4.0 (median 3.5) times as long as dactylus; carpus 3.6–4.2 (median 3.9) times as long as wide, 0.70–0.75 (median 0.74) times as long as propodus, about 0.50 times as long as merus; merus 5.5–6.3 (median 5.6) times as long as wide, bearing 3 or 4 strong spiniform setae on posterior margin of outer surface; ischium with a strong spiniform seta. Fifth pereiopod (Fig. 2E) slender; dactylus (Fig. 2F) with 31–41 spinuliform setae on flexor margin, 3.1–4.0 (median 3.3) times as long as wide (terminal claw and accessory spinuliform setae included); propodus 10.2–11.7 (median 10.6) times as long as wide, 2.9–3.5

(median 3.2) times as long as dactylus; carpus 3.6–5.0 (median 4.2) times as long as wide, about 0.55 times as long as propodus, about 0.65 times as long as merus; merus 4.6–6.3 (median 5.4) times as long as wide, bearing three strong spiniform setae on posterior margin of outer surface; ischium unarmed.

Endopod of male first pleopod (Fig. 2G) subrectangular, inner and outer margins almost straight and parallel, 2.45–2.70 (median 2.66) times as long as proximal wide, anterior region only feebly bent or not bent backwards, 0.60–0.70 (median 0.66) times as long as exopod; appendix interna arising from about 0.70 of endopod, reaching beyond the distal margin of endopod by 0.20–0.35 (median 0.31) of its length. Appendix masculina of male second pleopod (Fig. 2H) stout, club-shaped, 4.4–4.8 (median 4.5) times as long as wide, with long spinuliform setae on inner and distal margin, few smaller spiniform setae on basal part, 0.75–0.85 (median 0.78) times as long as endopod; appendix interna arising from about 0.40 and reaching to about 0.75 of appendix masculina.

Eggs large, few. Size of developed eggs (with eyespots) 1.02–1.13 × 0.60–0.73 mm in diameter.

Colouration: Adult females with body tinted with yellow and scattered with red chromatophores, without apparent stripes or spots. Colouration of males unknown.

Remarks: It is unfortunate that the majority of the paratype specimens are in poor condition, where many of their pereiopods were detached and mixed with those of *C. cantonensis* collected together. This population of *C. cantonensis* is rather atypical that the rostrums of many individuals are very short viz. falling short of the end of basal segment of antennular peduncle (Fig. 1M), resembling the sympatric *C. chui* sp. nov. Nevertheless, based on the intact specimens, *C. chui* sp. nov. differs from the co-occurring *C. cantonensis* by the 1) more tapered and shallower rostrum with fewer ventral rostral teeth (0–2, mode 1 vs 0–4, mode 3 in *C. cantonensis*); 2) shorter second pereiopod fingers (1.45–1.65, median 1.56 times as long as palm vs 1.65–1.95, median 1.80 times); 3) stouter second pereiopod merus (4.4–4.9, median 4.6 times as long as wide vs 4.8–5.3, median 5.0 times); 4) slenderer third pereiopod propodus (7.1–8.5, median 7.8 times as long as wide vs 7.6–9.4, median 9.0 times) but stouter carpus (3.6–4.2, median 3.9 times as long as wide vs 4.5–5.3, median 4.6 times); 5) shorter fifth pereiopod propodus (2.9–3.5, median 3.2 times as long as dactylus vs 3.7–4.4, median 3.9 times); 6) broader telson (2.1–2.4, median 2.3 times as long as proximal wide vs 2.5–2.7, median 2.6 times); 7) longer appendix interna of male first pleopod

(reaching beyond distal margin of endopod by 0.20–0.35, median 0.31 of its length vs 0.00–0.10, median 0.06); and 8) longer appendix masculina of male second pleopod (0.75–0.85, median 0.78 times as long as endopod vs 0.60–0.65, median 0.62 times).

With a relatively more tapered rostrum, stout subrectangular endopod of male first pleopod and club-shaped appendix masculina of male second pleopod, *C. chui* sp. nov. is also similar to *C. conghuensis* Klotz & von Rintelen, 2014, *C. logemanni* Klotz & von Rintelen, 2014 and *C. mariae* Klotz & von Rintelen, 2014 within the *C. serrata* species group, but is easily distinguished by life colouration (see Klotz & von Rintelen 2014). It is phylogenetically the closest to *C. conghuensis* (Fig. 3) with a genetic distance of 3.1% (16S rRNA) and 4.9% (COI) (Table 2). It can be separated from *C. conghuensis* by the 1) shorter rostrum (0.25–0.35, median 0.32 times pocl vs 0.36–0.47, median 0.42 times in *C. conghuensis*) with fewer rostral teeth (2–4 + 4–7 / 0–2 vs 3–5 + 7–9 / 2–4); 2) broader scaphocerite (2.55–2.85, median 2.76 times as long as wide vs 2.93–3.44, median 3.13 times); 3) longer second pereiopod fingers (1.45–1.65, median 1.56 times as long as palm vs 1.31–1.37, median 1.33 times) and stouter merus (4.4–4.9, median 4.6 times as long as wide vs 4.56–5.22, median 4.96 times); 4) stouter third pereiopod dactylus and propodus (2.4–3.1, median 2.9 times and 7.1–8.5, median 7.8 times as long as wide vs 3.07–3.83, median 3.23 times and 8.63–9.67, median 8.80 times, respectively); and 5) fewer spiniform setae on the flexor margin of third pereiopod dactylus (3–4 vs 5–7).

Caridina chui sp. nov. differs from *C. logemanni* by the 1) fewer rostral teeth (2–4 + 4–7 / 0–2 vs 3–7 + 7–15 / 0–6 in *C. logemanni*); 2) slenderer first pereiopod carpus (1.35–1.60, median 1.50 times as long as wide vs 1.11–1.46, median 1.30 times); 3) stouter third pereiopod propodus and carpus (7.1–8.5, median 7.8 times and 3.6–4.2, median 3.9 times as long as wide vs 8.72–11.68, median 9.36 times and 4.18–5.78, median 4.57 times, respectively); 4) shorter fifth pereiopod propodus (2.9–3.5, median 3.2 times as long as dactylus vs 4.29–5.31, median 4.73 times); 5) broader telson (2.1–2.4, median 2.3 times as long as proximal wide vs 2.68–2.89, median 2.82 times); and 6) longer appendix interna of male first pleopod (clearly reaching beyond distal margin of endopod vs not reaching or only feebly beyond).

Caridina chui sp. nov. can be separated from *C. mariae* by the 1) fewer dorsal rostral teeth (2–4 + 4–7 vs 4–6 + 6–9 in *C. mariae*); 2) shorter stylocerite (reaching at most to 0.55 length of second segment of antennular peduncle vs reaching to at least 0.7 length); 3) stouter second pereiopod merus (4.4–4.9, median 4.6 times as long as wide vs 4.81–5.91, median 5.09 times); 4)

stouter third pereiopod (dactylus 2.4–3.1, median 2.9 times, propodus 7.1–8.5, median 7.8 times, carpus 3.6–4.2, median 3.9 times and merus 5.5–6.3, median 5.6 times as long as wide vs 2.95–3.60, median 3.2 times, 9.72–11.38, median 10.21 times, 4.54–5.21, median 5.03 times and 5.80–7.07, median 6.79 times, respectively); 5) fewer spiniform setae on the flexor margin of third pereiopod dactylus (3–4 vs 5–6); 6) broader telson (2.1–2.4, median 2.3 times as long as proximal wide vs 2.22–3.43, median 2.86 times); and 7) uniform endopod of male first pleopod (vs distally dilated) with longer appendix interna of male first pleopod (clearly reaching beyond distal margin of endopod vs not reaching or only feebly beyond).

Caridina bauhinia **sp. nov.**

(Figs. 4, 5)

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Material examined: Holotype: male (pocl 3.9 mm), Tai Lam, western New Territories, Hong Kong, coll. JCF Chan, 29.I.2022, CUHK-LMT-CAR425-6. Paratypes: 5 females (pocl 3.9–5.1 mm), same collection data as holotype, CUHK-LMT-CAR425; 4 males (pocl 2.8–3.9 mm), 4 females (pocl 3.7–4.6 mm), 2 ov. females (pocl 4.5 and 4.9 mm), Tai Lam, western New Territories, Hong Kong, coll. JCF Chan, 24.IV.2022, CUHK-LMT-CAR469.

Comparative material examined: *Caridina serrata* Stimpson, 1860, 3 males (pocl 3.6–4.6 mm), 2 females (pocl 4.5 and 4.7 mm), Fan Lau, Lantau Island, Hong Kong, coll. JCF Chan, 03.II.2022, CUHK-LMT-CAR426; 3 females (pocl 4.7–5.4 mm), Discovery Valley, Lantau Island, Hong Kong, coll. JCF Chan, 05.III.2022, CUHK-LMT-CAR432; 1 male (pocl 4.2 mm), 1 female (pocl 4.3 mm), 1 ov. female (pocl 5.3 mm), San Tau, Lantau Island, Hong Kong, coll. JCF Chan, 16.II.2022, CUHK-LMT-CAR433; 5 males (pocl 4.1–4.8 mm), 2 females (pocl 3.5 and 3.9 mm), Lung Fu Shan, Hong Kong Island, Hong Kong, coll. JCF Chan, 14.I.2022, CUHK-LMT-CAR434; 1 ov. female (pocl 4.6 mm), Sze Pak Wan, Lantau Island, Hong Kong, coll. JCF Chan, 05.III.2022, CUHK-LMT-CAR436.

Etymology: Named after the common name of the floral emblem of Hong Kong (the type locality) i.e. *Bauhinia* × *blakeana* Dunn. Used as a noun in apposition.

Description: Rostrum (Fig. 4A) straight, slightly directed downwards, nearly reaching to or slightly reaching beyond the end of basal segment of antennular peduncle, tip sometimes directed slightly upwards, 0.25–0.35 (median 0.29) times pocl; rostral formula 2–6 + 3–10 / 0–4. Inferior orbital angle fused with antennal spine. Pterygostomial angle rounded, subrectangular, slightly produced forward. Eyes well developed with globular cornea. Antennular peduncle 0.45–0.55 (median 0.48) times pocl, basal segment 2.0–2.4 (median 2.1) times as long as second segment, second segment 1.6–2.0 (median 1.8) times as long as third segment. Stylocerite reaching to 0.00–0.50 (median 0.27) length of second segment of antennular peduncle. Scaphocerite (Fig. 4B) 2.40–2.65 (median 2.56) times as long as wide.

Sixth abdominal somite about 0.5 times pocl, about 0.9 times as long as telson. Telson (Fig. 4C) 2.2–2.5 (median 2.3) times as long as proximal wide, with 4 or 5 pairs of short spiniform setae dorsal and one pair of short spiniform setae dorsolateral, posterior margin (Fig. 4D) convex with a median projection and 6–9 spiniform setae, sublateral pair slightly shorter than or subequal to lateral pairs, shorter than inner pairs. Preanal carina (Fig. 4E) rounded, unarmed, with few setae. Uropodal diaeresis (Fig. 4F) with 19–23 movable spiniform setae, outermost one slightly longer than lateral angle.

Mandible (Fig. 4G) with incisor process ending in irregular teeth; molar process truncated. Maxillule (Fig. 4H) with lower lacinia broadly rounded, upper lacinia elongate, with numerous distinct cuspidate setae on inner margin; palp with few simple setae. Maxilla (Fig. 4I) with upper endites subdivided; palp slender; scaphognathite tapering posteriorly, fringed with long setae at posterior margin. First maxilliped (Fig. 4J) with palp ending in a projection. Second maxilliped (Fig. 4K) with well-developed podobranch. Third maxilliped (Fig. 4L) with two arthrobranchs, ultimate segment subequal to penultimate in length. First pereiopod with an arthrobranch. Pleurobranchs present on all pereiopods. Epipods present on third maxilliped and first four pereiopods.

First pereiopod (Fig. 5A) chela 1.85–2.20 (median 2.07) times as long as wide, 1.3–1.5 (median 1.4) times as long as carpus; tips of fingers rounded, without hooks, fingers 0.85–1.10 (median 0.96) times as long as palm; carpus strongly excavated distally, 1.35–1.60 (median 1.54) times as long as wide, 0.85–1.00 (median 0.92) times as long as merus; merus 2.3–2.6 (median 2.4) times as long as wide, longer than ischium. Second pereiopod (Fig. 5B) chela 2.50–3.00 (median 2.76) times as long as wide, 0.70–0.80 (median 0.74) times as long as carpus; tips of

fingers rounded, without hooks, fingers 1.35–1.60 (median 1.49) times as long as palm; carpus 4.5–5.7 (median 5.2) times as long as wide, 1.05–1.15 (median 1.12) times as long as merus; merus 4.7–5.5 (median 4.9) times as long as wide, longer than ischium. Third pereiopod (Fig. 5C) slender, not sexually dimorphic; dactylus (Fig. 5D) with 4 or 5 accessory spiniform setae on flexor margin, 2.4–3.0 (median 2.7) times as long as wide (terminal claw and accessory spiniform setae included); propodus 7.1–8.2 (median 7.6) times as long as wide, 3.3–3.9 (median 3.7) times as long as dactylus; carpus 3.7–4.6 (median 4.0) times as long as wide, 0.75–0.85 (median 0.76) times as long as propodus, 0.50–0.60 (median 0.53) times as long as merus; merus 4.4–5.6 (median 5.4) times as long as wide, bearing 3 or 4 strong spiniform setae on posterior margin of outer surface; ischium with or without a strong spiniform seta. Fifth pereiopod (Fig. 5E) slender; dactylus (Fig. 5F) with 28–41 spinuliform setae on flexor margin, 2.4–3.3 (median 2.9) times as long as wide (terminal claw and accessory spinuliform setae included); propodus 10.0–12.8 (median 11.1) times as long as wide, 3.5–4.6 (median 4.1) times as long as dactylus; carpus 3.7–5.2 (median 4.3) times as long as wide, 0.50–0.60 (median 0.54) times as long as propodus, 0.65–0.75 (median 0.70) times as long as merus; merus 4.7–5.8 (median 5.0) times as long as wide, bearing 2 or 3 strong spiniform setae on posterior margin of outer surface; ischium unarmed.

Endopod of male first pleopod (Fig. 5G) subrectangular, inner margin almost straight or slightly concave, outer margin almost straight to slightly convex, 2.40–2.70 (median 2.43) times as long as proximal wide, anterior region only feebly bent backwards, 0.65–0.80 (median 0.73) times as long as exopod; appendix interna arising from 0.65–0.70 (median 0.66) of endopod, not reaching or only feebly beyond the distal margin of endopod viz. by 0.05 of its length. Appendix masculina of male second pleopod (Fig. 5H) stout, club-shaped, 4.1–5.2 (median 4.3) times as long as wide, with long spinuliform setae on inner and distal margin, few smaller spiniform setae on basal part, 0.70–0.80 (median 0.72) times as long as endopod; appendix interna arising from 0.40–0.45 (median 0.43) and reaching to 0.70–0.80 (median 0.72) of appendix masculina.

Eggs large, few. Size of developed eggs (with eyespots) 1.00–1.07 × 0.68–0.75 mm in diameter; size of undeveloped eggs 0.97–1.06 × 0.56–0.68 mm in diameter.

Colouration: Body pinkish to orangish, scattered with red chromatophores. Posterolateral margin of carapace with a red longitudinal, bent stripe. Tergum of third somite with a red transverse stripe. Distinct red spots are present on the lateral midline of pleurites. Ovigerous females are generally more deeply pigmented.

Remarks: The new species belong to a clade within the *C. serrata* species group that is characterised by a relatively short rostrum, often relatively large distal spine on the propodus of fifth pereiopod, stout subrectangular endopod of male first pleopod and club-shaped appendix masculina of male second pleopod. Members of the clade include *C. serrata*, *C. nanaoensis* Cai and Ng, 1999, *C. macauensis* Zhou, Zhang, Wong and Huang, 2021, *C. tetrazona* Chen, Chen, Zheng and Guo, 2020, *C. trifasciata* and *C. argilla* sp. nov. (Fig. 3). *Caridina bauhinia* sp. nov. is morphologically very similar to *C. serrata* (and its potential synonym *C. nanaoensis*, see Klotz and von Rintenlen 2014) in terms of morphometrics and body pattern. The new species can be distinguished from *C. serrata* by having 1) fewer dorsal rostral teeth (6–15, median 9 vs 11–17, median 13 in *C. serrata*); 2) stouter fifth pereiopod propodus and merus (10.0–12.8, median 11.1 and 4.7–5.8, median 5.0 times as long as wide vs 10.8–15.7, median 12.4 and 5.0–7.0, median 5.8 times, respectively); 3) longer endopod of male first pleopod (0.65–0.80, median 0.73 times as long as exopod vs 0.55–0.70, median 0.60 times); and 5) shorter appendix interna of male first pleopod (not reaching or only feebly beyond the distal margin of endopod vs clearly reaching beyond).

The other species of the clade, including *C. tetrazona*, *C. macauensis* and *C. trifasciata*, stand out from *Caridina bauhinia* sp. nov. with their prominently banded appearance. In terms of morphometrics, *Caridina bauhinia* sp. nov. differs from *C. tetrazona* by the 1) broader scaphocerite (2.40–2.65 times as long as wide vs 3.6 times in *C. tetrazona*); 2) third pereiopod with stouter dactylus (2.4–3.0 times as long as wide vs 2.9–3.5 times) and stouter and shorter propodus (7.1–8.2 times as long as wide vs 8.4–9.7 times; 3.3–3.9 times as long as dactylus vs 4.5–4.9 times); 3) shorter fifth pereiopod propodus (3.5–4.6 times as long as dactylus vs 4.7–5.1 times); 4) shorter appendix interna of male first pleopod (not reaching or only feebly beyond the distal margin of endopod vs clearly reaching beyond); and 5) presence of a median projection on the posterior margin of telson (vs absent).

Caridina bauhinia sp. nov. can be separated from *C. macauensis* by a number of characters, including 1) broader scaphocerite (2.40–2.65 times as long as wide vs 3.9–4.2 times in *C. macauensis*); 2) first pereiopod with stouter chela (1.85–2.20 times as long as wide vs 2.4–2.6 times), longer fingers (0.85–1.10 times as long as palm vs 0.67–0.85 times), and shorter and stouter merus (1.0–1.2 times as long as carpus vs 1.50–1.65 times; 2.3–2.6 times as long as wide vs 3 times); 3) second pereiopod with shorter fingers (1.35–1.60 times as long as palm vs 1.8–2.2 times)

and stouter carpus (4.5–5.7 times as long as wide vs 7.1–8.4 times); 4) shorter fifth pereiopod merus (1.35–1.55 times as long as carpus vs 1.71–1.78 times); 5) longer endopod of male first pleopod (0.65–0.75 times as long as exopod vs 0.45–0.50 times); and 6) shorter appendix interna of male first pleopod (not reaching or only feebly beyond the distal margin of endopod vs clearly reaching beyond).

Caridina bauhinia sp. nov. differs from *C. trifasciata* by the 1) shorter rostrum (reaching about end of basal segment of antennular peduncle vs reaching about end of second segment in *C. trifasciata*); 2) broader scaphocerite (2.40–2.65 times as long as wide vs 2.8 times); 3) slenderer first pereiopod merus (2.3–2.6 times as long as wide vs 2.0–2.2 times); 4) stouter and shorter third pereiopod propodus (7.1–8.2 times as long as wide vs 9.3–9.5 times; 3.3–3.9 times as long as dactylus vs 4.2–4.6 times); 5) shorter fifth pereiopod propodus (3.5–4.6 times as long as dactylus vs 4.5–4.8 times); and 6) shorter appendix interna of male first pleopod (not reaching or only feebly beyond the distal margin of endopod vs clearly reaching beyond).

***Caridina argilla* sp. nov.**

(Fig. 6)

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Material examined: Holotype: male (pocl 4.5 mm), Pak Nai, western New Territories, Hong Kong, coll. JCF Chan, 14.VII.2022, CUHK-LMT-CAR476-6. Paratypes: 4 males (pocl 2.7–4.0 mm), 9 females (pocl 2.9–5.1 mm), 1 ov. female (pocl 5.0 mm), same collection data as holotype, CUHK-LMT-CAR476.

Etymology: Refers to the name of the type locality, Pak Nai in Hong Kong, which literally translated as “white clay”.

Description: Rostrum (Fig. 6A) straight, slightly directed downwards, slightly falling short of or reaching to the end of basal segment of antennular peduncle, tip sometimes directed slightly upwards, 0.25–0.30 (median 0.29) times pocl; rostral formula 0–4 + 1–10 / 0–2. Inferior orbital angle fused with antennal spine. Pterygostomial angle rounded, subrectangular, slightly produced forward. Eyes well developed with globular cornea. Antennular peduncle 0.40–0.55 (median 0.46) times pocl, basal segment 2.1–2.8 (median 2.4) times as long as second segment, second segment 1.1–1.6 (median 1.2) times as long as third segment. Stylocerite reaching to 0.00–0.55 (median

405 0.22) length of second segment of antennular peduncle. Scaphocerite (Fig. 6B) 2.45–2.85 (median
406 2.62) times as long as wide.
407 Sixth abdominal somite about 0.5 times pocl, about as long as telson. Telson (Fig. 6C) 2.3–
408 2.6 (median 2.4) times as long as proximal wide, with 4 or 5 pairs of short spiniform setae dorsal
409 and one pair of short spiniform setae dorsolateral, posterior margin (Fig. 6D) convex with a median
410 projection and 3–5 pairs of spiniform setae, sublateral pair slightly shorter than lateral and inner
411 pairs. Preanal carina (Fig. 6E) rounded, unarmed, with few setae. Uropodal diaeresis (Fig. 6F) with
412 16–21 movable spiniform setae, outermost one slightly longer than lateral angle. Mouthparts not
413 dissected, morphology and gill formula as described for *C. bauhinia* sp. nov. in external view.
414 First pereiopod (Fig. 6G) chela 1.85–2.20 (median 2.00) times as long as wide, 1.4–1.5
415 (median 1.4) times as long as carpus; tips of fingers rounded, without hooks, fingers 0.70–1.00
416 (median 0.95) times as long as palm; carpus strongly excavated distally, 1.40–1.60 (median 1.47)
417 times as long as wide, 0.85–1.00 (median 0.90) times as long as merus; merus 2.0–2.6 (median
418 2.5) times as long as wide, longer than ischium. Second pereiopod (Fig. 6H) chela 2.30–2.80
419 (median 2.54) times as long as wide, 0.65–0.75 (median 0.73) times as long as carpus; tips of
420 fingers rounded, without hooks, fingers 1.40–1.65 (median 1.50) times as long as palm; carpus
421 4.6–5.6 (median 5.2) times as long as wide, 1.05–1.15 (median 1.13) times as long as merus; merus
422 4.6–5.5 (median 4.9) times as long as wide, longer than ischium. Third pereiopod (Fig. 6I) slender,
423 not sexually dimorphic; dactylus (Fig. 6J) with 4–6 accessory spiniform setae on flexor margin,
424 2.3–3.1 (median 2.8) times as long as wide (terminal claw and accessory spiniform setae included);
425 propodus 7.9–9.3 (median 8.8) times as long as wide, 3.5–4.3 (median 3.9) times as long as
426 dactylus; carpus 4.2–4.9 (median 4.6) times as long as wide, 0.70–0.80 (median 0.74) times as
427 long as propodus, 0.50–0.55 (median 0.51) times as long as merus; merus 5.2–6.3 (median 5.8)
428 times as long as wide, bearing 3 or 4 strong spiniform setae on posterior margin of outer surface;
429 ischium with a strong spiniform seta. Fifth pereiopod (Fig. 6K) slender; dactylus (Fig. 6L) with
430 23–36 spinuliform setae on flexor margin, 2.3–3.1 (median 2.8) times as long as wide (terminal
431 claw and accessory spinuliform setae included); propodus 9.8–12.7 (median 11.8) times as long as
432 wide, 3.5–5.1 (median 4.2) times as long as dactylus; carpus 4.1–5.3 (median 4.7) times as long as
433 wide, 0.55–0.60 (median 0.56) times as long as propodus, 0.65–0.70 (median 0.68) times as long
434 as merus; merus 5.1–6.5 (median 5.6) times as long as wide, bearing 2 or 3 strong spiniform setae
435 on posterior margin of outer surface; ischium unarmed.

Endopod of male first pleopod (Fig. 6M) subrectangular, inner margin slightly concave, outer margin slightly convex, 2.40–2.85 (median 2.58) times as long as proximal wide, anterior region not or only feebly bent backwards, 0.65–0.80 (median 0.68) times as long as exopod; appendix interna arising from 0.70–0.75 (median 0.72) of endopod, slightly reaching beyond distal margin of endopod by 0.05–0.25 (median 0.12) of its length. Appendix masculina of male second pleopod (Fig. 6N) stout, club-shaped, 4.6–5.1 (median 4.8) times as long as wide, with long spinuliform setae on inner and distal margin, few smaller spiniform setae on basal part, 0.70–0.75 (median 0.73) times as long as endopod; appendix interna arising from 0.40–0.50 (median 0.46) and reaching to 0.70–0.80 (median 0.75) of appendix masculina.

Eggs large, few. Size of undeveloped eggs (without eyespots) 0.97–1.05 × 0.69–0.75 mm in diameter.

Colouration: Unknown.

Remarks: *Caridina argilla* sp. nov. is very similar to its sister species *C. bauhinia* sp. nov. (Fig. 3). Most of the morphometrics overlap between the two species, but *C. argilla* sp. nov. differs by having 1) fewer dorsal rostral teeth on carapace but more on rostrum (0–4, mode 0–1 + 1–10, mode 8 vs 2–6, mode 3–4 + 3–10, mode 6 in *C. bauhinia* sp. nov.); 2) stouter second pereiopod chela (2.30–2.80, median 2.54 times as long as wide vs 2.50–3.00, median 2.76 times); 3) slenderer third pereiopod propodus, carpus and merus (7.9–9.3, median 8.8 times, 4.2–4.9, median 4.6 times and 5.2–6.3, median 5.8 times as long as wide vs 7.1–8.2, median 7.6 times, 3.7–4.6, median 4.0 times and 4.4–5.6, median 5.4 times, respectively); 4) slenderer fifth pereiopod carpus and merus (4.1–5.3, median 4.7 times and 5.1–6.5, median 5.6 times vs 3.7–5.2, median 4.3 times and 4.7–5.8, median 5.0 times, respectively); 5) fewer spiniform setae on the uropodal diaeresis (16–21, mode 18 vs 19-23, mode 21); and 5) longer appendix interna of male first pleopod (reaching beyond distal margin of endopod by 0.05–0.25, median 0.12 of its length vs not reaching or only feebly beyond by 0.05 of its length, cf. 0.15–0.55, median 0.43 in *C. serrata*). Morphological differences between *C. argilla* sp. nov. and other closely related species are similar to what have been described for *C. bauhinia* sp. nov. A genetic distance of 2.8% (16S rRNA) and 6.3% (COI) from *C. bauhinia* sp. nov. (Table 2), which is within the range recognised between sister congeners and confamiliars (see Klotz and von Rintelen, 2014; Shih et al., 2024), support the species level status of *C. argilla* sp. nov.

DISCUSSION

To date, at least 24 species from southern China and northern and central Vietnam can be assigned to the *C. serrata* species group under the current diagnosis (Table 3). Three of the four diagnostic features listed by Cai and Ng (1999), namely the presence of dorsal rostral teeth on carapace, appendix interna on male first pleopod and large eggs, are now recognised to be very common among the > 100 primary freshwater species from China and Vietnam. Although, for a number of these species, the ovigerous females and hence their egg sizes remain unknown, they are expected to be landlocked and produce large and few eggs. The most exclusive and indicative character of the *C. serrata* species group is probably the relative length of stylocerite viz. reaching beyond basal segment of the antennular peduncle, which excludes about 75% of the Chinese and Vietnamese landlocked species. Nevertheless, intraspecific variation may introduce an ambiguity when only a subset of individuals clearly qualifies for the definition. These species with such 'intermediate' stylocerite were often not considered a member of the species group (see Ng and Cai, 2000 for *C. breviata*). However, new information on the extent of infraspecific variation may well question the status of known members of the group (LH Chow, unpubl. data for *C. sphyrapoda* Liang and Zhou, 1993).

The genus *Caridina* is known to be polyphyletic and in need of revision (von Rintelen et al., 2012), and the species groups currently recognised will likely form a framework for establishing new genera in the future. The *C. serrata* species group is herein shown to be polyphyletic with at least four lineages (Fig. 3) and thus warrants a rediagnosis to facilitate the systematic revision of *Caridina*. The nominal lineage only comprises *C. serrata* and 11 closely related species, as well as *C. breviata* with 'intermediate' stylocerite. Most of the species are restricted to Hong Kong, Macau and the adjacent Guangdong Province in southern China, with a few extending their distribution to northern and central Vietnam. The second lineage consists of *C. pacbo* Do, von Rintelen and Dang, 2020, *C. pseudoserrata* Dang and Do, 2007 and *C. rubropunctata* Dang and Do, 2007, but contains an outlier, *C. namdat* Do, Dang and von Rintelen, 2021. This Vietnamese lineage, together with most of the other primarily Vietnamese species with 'short' or 'intermediate' stylocerite and some singleton species of the species group with uncertain phylogenetic position (viz. *C. ngankeeae*, *C. nguyeni* Li and Liang, 2002 and *C. stellata* Guo, Chen, Chen, Cai and Guo, 2022), are morphologically the closest to the nominal lineage. They differ

mainly in the relative length of stylocerite and the stoutness of the appendix masculina of male second pleopod. The third lineage comprises *C. caobangensis* Li and Liang, 2002 and *C. sphyrapoda* from adjacent provinces in northern Vietnam and southern China, respectively. The genetic affinity between the two species is hard to explain from morphology. While *C. caobangensis* aligns with the other Vietnamese species, *C. sphyrapoda* resembles more some species from Guizhou Province, western China, in particular the stygobitic *C. incolor* Feng, Chen and Guo, 2021 and *C. caverna* Liang, Chen and Li, 2005. Compared to the nominal lineage, *C. sphyrapoda* is different in its slenderer carpus of first pereiopod, fewer number of spiniform setae on uropodal diaeresis and shorter endopod of male first pleopod. The fourth lineage contains *C. maculata* Wang, Liang and Li, 2008, but also *C. huananensis* Liang, 2004 and *C. venusta* Wang, Liang and Li, 2008 with 'short' or 'intermediate' stylocerite. Despite occurring in the same region as the nominal lineage, they are grouped with species from Guizhou Province instead under the current dataset and bear a slight likeness to species from Hunan and Jiangxi provinces. They are distinctive from the nominal lineage in their shorter rostrum, larger number of spinuliform setae on flexor margin of fifth pereiopod dactylus, and slenderer endopod of male first pleopod and appendix masculina of male second pleopod.

Based on the concept of morphologically 'validated' molecular taxonomy (*sensu* Page et al. 2005), the nominal lineage exhibits a distinct suite of morphological characters and thus could be considered the sole members of the *C. serrata* species group in a restricted sense. Following de Mazancourt et al. (2020), a more detailed diagnosis of the *C. serrata* species group *sensu stricto* is proposed to differentiate it from the other closely related species. Information of certain characters (e.g. preanal carina) is unavailable for some species from both textual descriptions and illustrations, so it can only be generalised from other species where available. Based on morphological description alone, *C. apodosis* and *C. wumingensis* are tentatively also included in the species group *sensu stricto* (Table 2).

Caridina serrata species group *sensu stricto*

Diagnosis: Body moderately robust or robust; rostrum straight, short to medium in length, at most only slightly exceeding the distal margin of scaphocerite, armed or not on the dorsal carina, without apical teeth; antennal spine fused with inferior orbital angle; antennular peduncle about or more than half of carapace in length; stylocerite long, reaching to or beyond end of basal segment

of antennular peduncle; carpus of first pereiopod deeply excavated distally (usually < 1.6 times as long as wide); walking legs stout, not sexually dimorphic; dactyli of third and fifth pereiopod dactyli with moderate number of accessory spiniform setae on flexor margin (≤ 7 and ≤ 45 respectively); sixth abdominal somite short (around half of carapace length); preanal carina without a spine; telson with moderate number of robust spiniform terminal setae (3–5 pairs) without chitinous plug; uropodal diaeresis with large number of spiniform setae (≥ 14); endopod of male first pleopod subrectangular or subtriangular, inner margin not abruptly incised, at least about half as long as exopod but not markedly elongated (≤ 3.2 times as long as proximal wide), appendix interna subdistal; appendix masculina of male second pleopod club-shaped (usually < 5.5 times as long as wide), not reduced nor elongated (more than half as long as endopod but not reaching close to or beyond its distal margin).

Although the *C. serrata* species group *sensu stricto* would likely be valid on its own, its potential phylogenetic position at the crown might pose a systematic issue for congeners. This is especially so for the morphologically similar, primarily Vietnamese species, which form part of the stem group of the *C. serrata* species group *sensu stricto*. If the species group was to be expanded to include these morphologically similar congeners, this would introduce a large degree of morphological variation in the clade by including some deviants (e.g. *C. sphyrapoda*, *C. namdat*). A possible way to resolve the systematic issue might be the inclusion of most of the Chinese and Vietnamese species in the species group in a broad sense. A diagnosis of the *C. serrata* species group *sensu lato* is proposed to differentiate it from all congeners (except those with limited information). Future efforts to resolve the *C. serrata* species group relies on a more comprehensive phylogeny considering 1) all Chinese and Vietnamese landlocked *Caridina* species, 2) other closely related genera including *Paracaridina*, *Neocaridina* and *Sinodina*, and 3) the phylogenetic position of this assemblage with respect to the other *Caridina* species/species groups and genera of the *Caridella* group (*sensu* von Rintelen et al. 2012).

Caridina serrata species group *sensu lato*

Diagnosis: Body moderately robust or robust; rostrum straight, short to medium in length, rarely upturned and exceeding distal margin of scaphocerite, not depressed, armed or not on the dorsal carina, without apical teeth; antennal spine usually fused with, sometimes ventral to inferior

orbital angle; antennular peduncle about or more than half of carapace in length; carpus of first pereiopod stout, shallowly or deeply excavated distally (usually < 2 times as long as wide, at most about 2.5 times); carpus of second pereiopod short, subequal to merus in length (at most 0.2 times longer); walking legs stout, not sexually dimorphic; sixth abdominal somite short (around half of carapace length); pre-anal carina without a spine; telson with moderate number of robust spiniform terminal setae (3–6 pairs) without chitinous plug; uropodal diaeresis with moderate number of spiniform setae (8–24); endopod of male first pleopod at least about half as long as exopod (except in a few subterranean species), almost always with appendix interna but lacks long distal setae when it is absent. Primarily distributed in China and Vietnam.

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Figure captions

Fig. 1. A–D, *Caridina chui* sp. nov., holotype female, pocl 4.0 mm (CUHK-LMT-CAR444-2); E–L, paratype female, pocl 4.6 mm (CUHK-LMT-CAR444-8); M, *Caridina cantonensis*, female, pocl 4.7 mm (CUHK- LMT-CAR502-8). A, cephalothorax, lateral view; B, scaphocerite; C, telson; D, same, distal margin; E, pre-anal carina; F, uropodal diaeresis; G, mandible; H, maxillule; I, maxilla; J, first maxilliped; K, second maxilliped; L, third maxilliped; M, frontal region. Scale bar: M = 2.2 mm; A = 2 mm; B, C = 1.1 mm; L = 1 mm; G–K = 0.8 mm; D–F = 0.5 mm.

Fig. 2. *Caridina chui* sp. nov., holotype female, pocl 4.0 mm (CUHK-LMT-CAR444-2). A, first pereiopod; B, second pereiopod; C, third pereiopod; D, same, dactylus; E, fifth pereiopod; F, same, dactylus; G, male first pleopod; H, male second pleopod. Scale bar: A–C, E = 1 mm; G, H = 0.45 mm; D, F = 0.25 mm.

Fig. 3. Bayesian phylogenetic tree of selected landlocked *Caridina*, *Neocaridina*, *Paracaridina* and *Sinodina* species recorded from China and Vietnam, constructed using mitochondrial 16S rRNA and COI markers. Branch support values (PP/BP) are indicated as percentages. Species of the *C. serrata* species group under the diagnosis by Cai & Ng (1999) and the *C. serrata* species group *sensu stricto* rediagosed in the present study are shaded in light grey and dark grey, respectively.

Fig. 4. *Caridina bauhinia* sp. nov., A–D, holotype male, pocl 3.9 mm (CUHK-LMT-CAR425-6); E–L, paratype female, pocl 5.1 mm (CUHK-LMT-CAR425-4). A, cephalothorax, lateral view; B, scaphocerite; C, telson; D, same, distal margin; E, pre-anal carina; F, uropodal diaeresis; G, mandible; H, maxillule; I, maxilla; J, first maxilliped; K, second maxilliped; L, third maxilliped. Scale bar: A = 2 mm; L = 1.5 mm; B, C = 1.2 mm; G–K = 1 mm; D–F = 0.6 mm.

Fig. 5. *Caridina bauhinia* sp. nov., holotype male, pocl 3.9 mm (CUHK-LMT-CAR425-6). A, first pereiopod; B, second pereiopod; C, third pereiopod; D, same, dactylus; E, fifth pereiopod; F, same, dactylus; G, male first pleopod; H, male second pleopod. Scale bar: A–C, E = 1 mm; G, H = 0.6 mm; D, F = 0.3 mm.

Fig. 6. *Caridina argilla* sp. nov., A–D, G–N, holotype male, pocl 4.5 mm (CUHK-LMT-CAR476-6); E, F, paratype female, pocl 4.8 mm (CUHK-LMT-CAR476-3). A, cephalothorax, lateral view; B, scaphocerite; C, telson; D, same, distal margin; E, pre-anal carina; F, uropodal diaeresis; G, first pereiopod; H, second pereiopod; I, third pereiopod; J, same, dactylus; K, fifth pereiopod; L, same, dactylus; M, male first pleopod; N, male second pleopod. Scale bar: A = 2 mm, B, C = 1.2 mm; G–I, K = 1 mm; D–F, M, N = 0.5 mm; J, L = 0.25 mm.

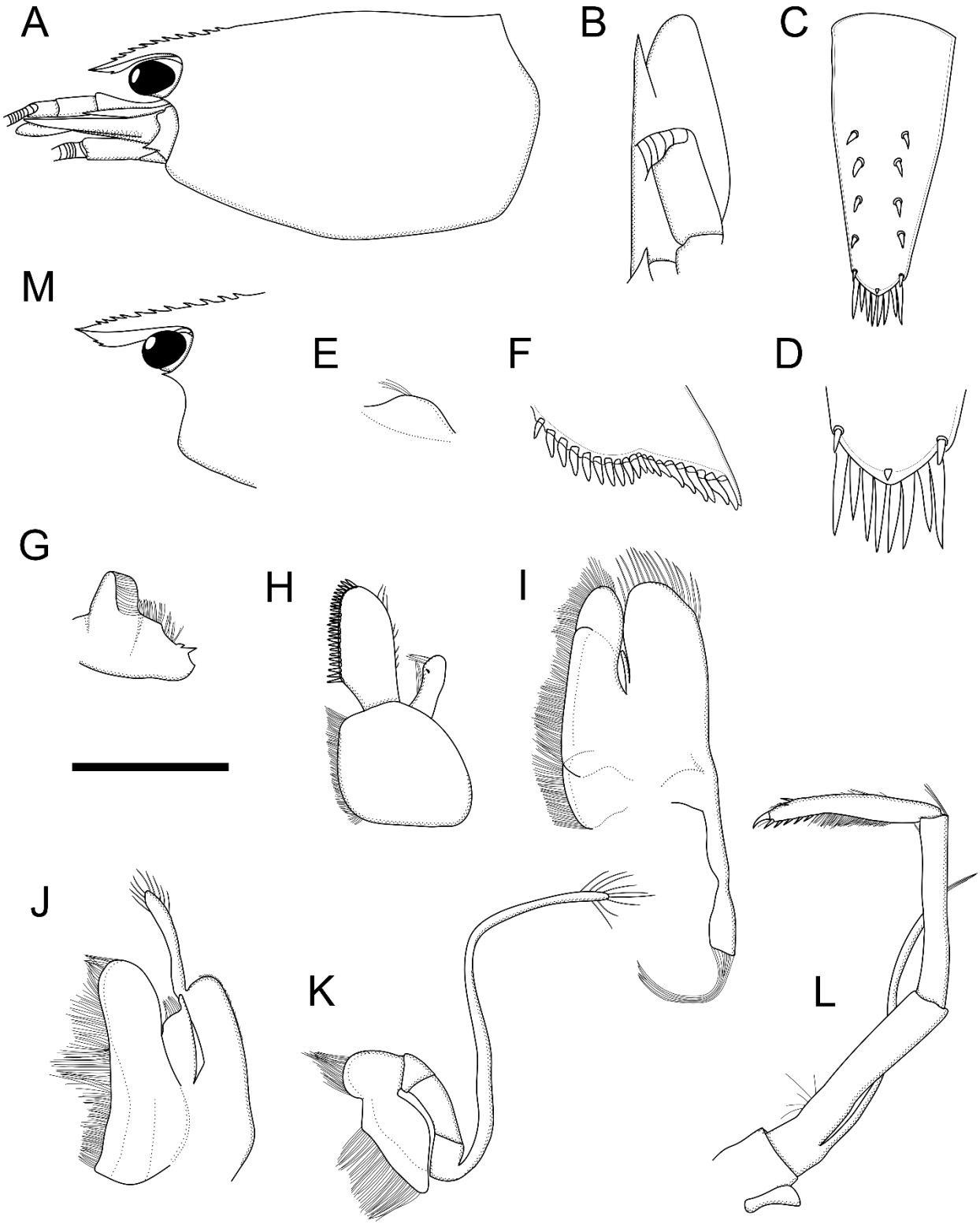

Fig. 1.

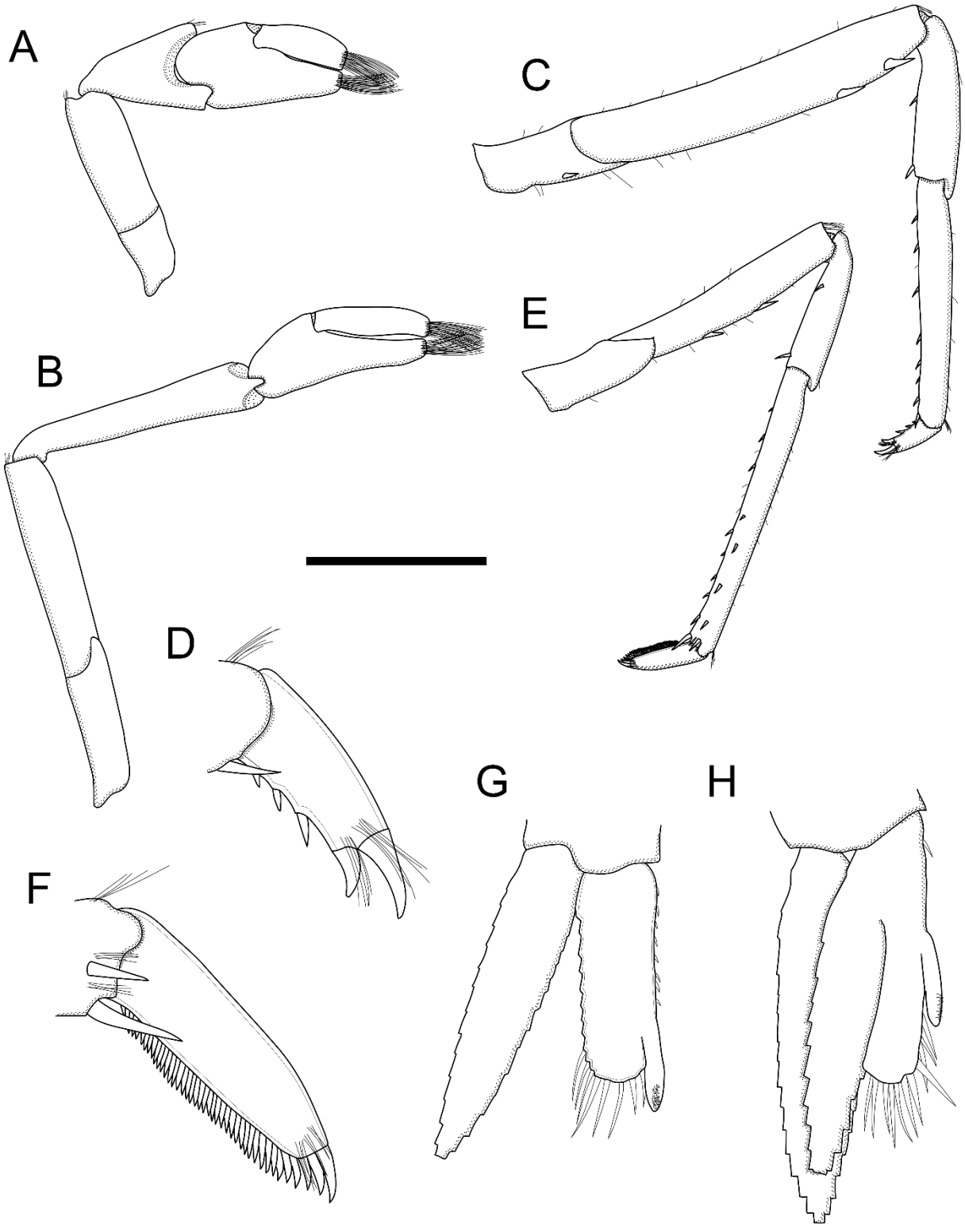

Fig. 2.

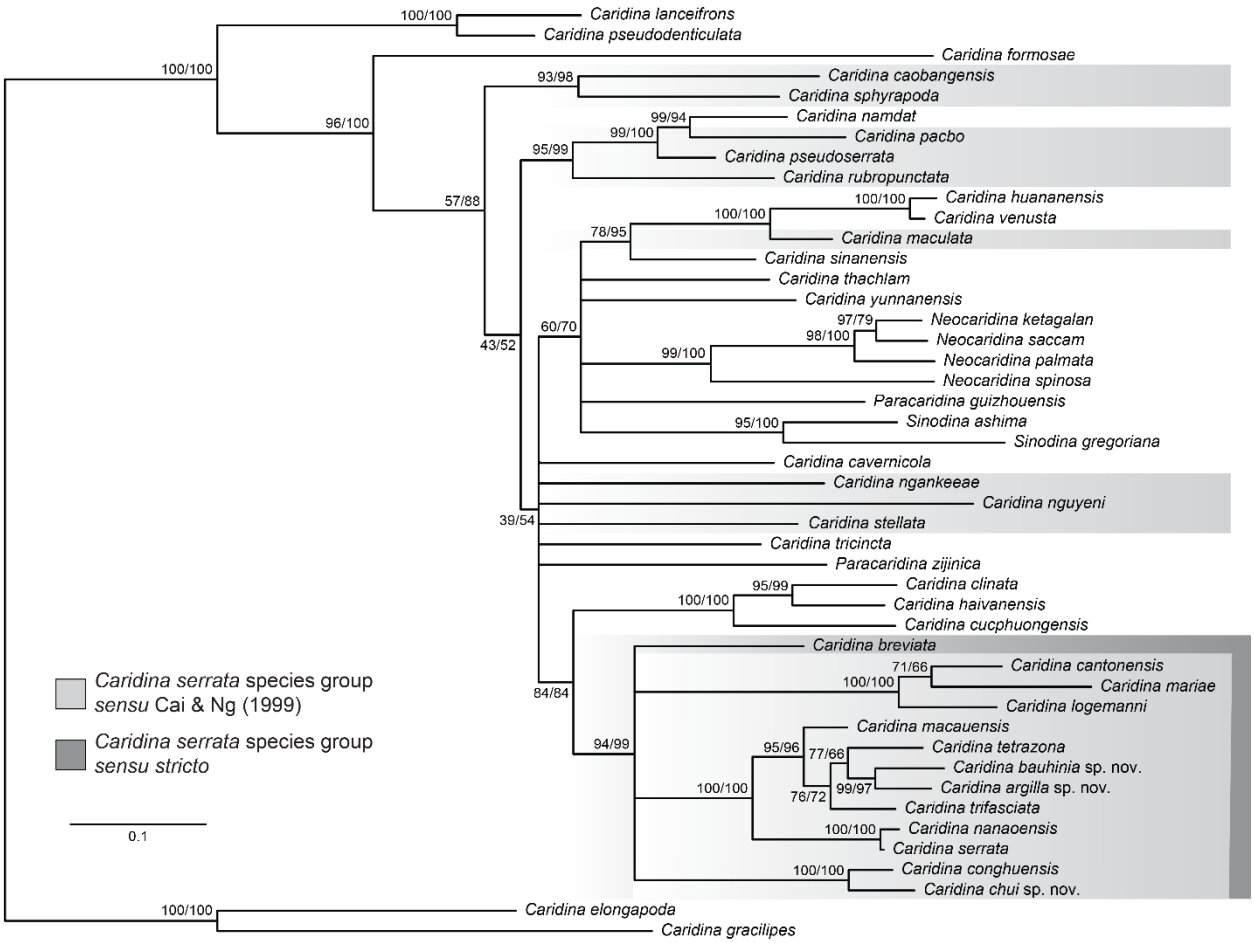
Caridina lanceifrons
Caridina pseudodenticulata
Caridina formosae
Caridina caobangensis
Caridina sphyrapoda
Caridina namdat
Caridina pacbo
Caridina pseudoserrata
Caridina rubropunctata
Caridina huananensis
Caridina venusta
Caridina maculata
Caridina sinanensis
Caridina thachlam
Caridina yunnanensis
Neocaridina ketagalan
Neocaridina saccam
Neocaridina palmata
Neocaridina spinosa
Paracaridina guizhouensis
Sinodina ashima
Sinodina gregoriana
Caridina cavernicola
Caridina ngankeeae
Caridina nguyeni
Caridina stellata
Caridina tricincta
Paracaridina zijinica
Caridina clinata
Caridina haivanensis
Caridina cucphuongensis
Caridina breviata
Caridina cantonensis
Caridina mariae
Caridina logemanni
Caridina macauensis
Caridina tetrazona
Caridina bauhinia sp. nov.
Caridina argilla sp. nov.
Caridina trifasciata
Caridina nanaoensis
Caridina serrata
Caridina conghuensis
Caridina chui sp. nov.
Caridina elongapoda
Caridina gracilipes
Caridina serrata species group sensu Cai & Ng (1999)
Caridina serrata species group sensu stricto
0.1

Fig. 3.

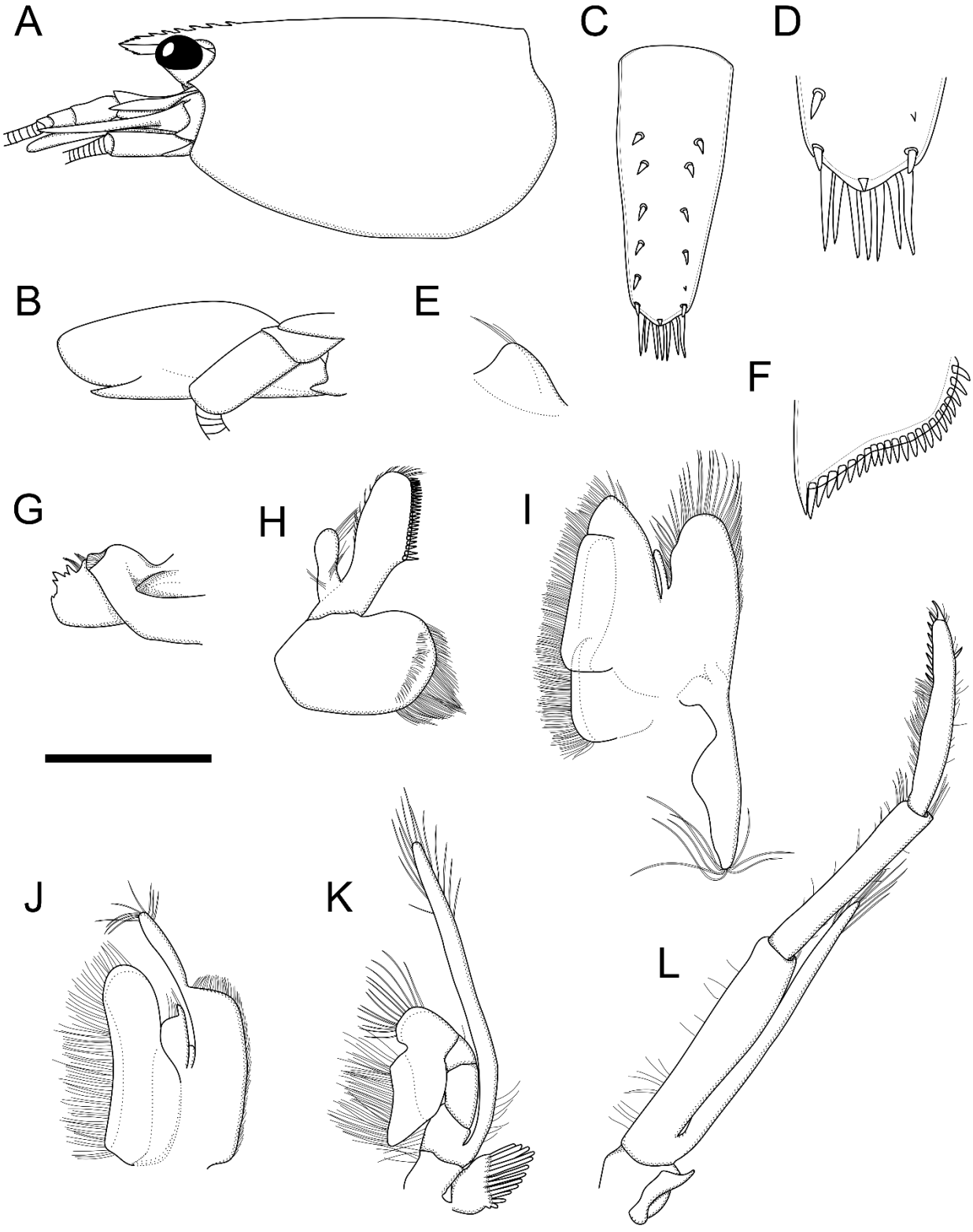

Fig. 4.

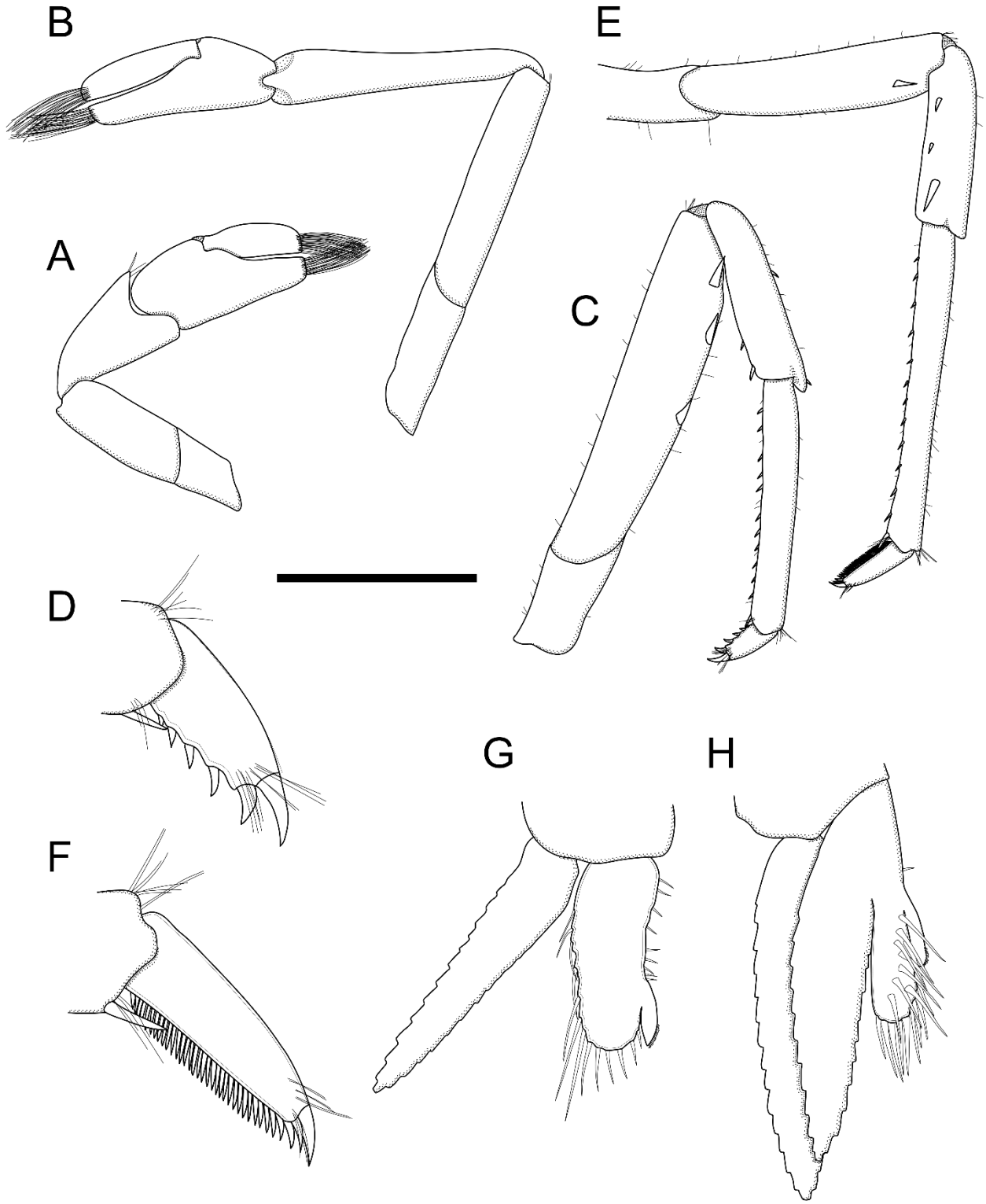

Fig. 5.

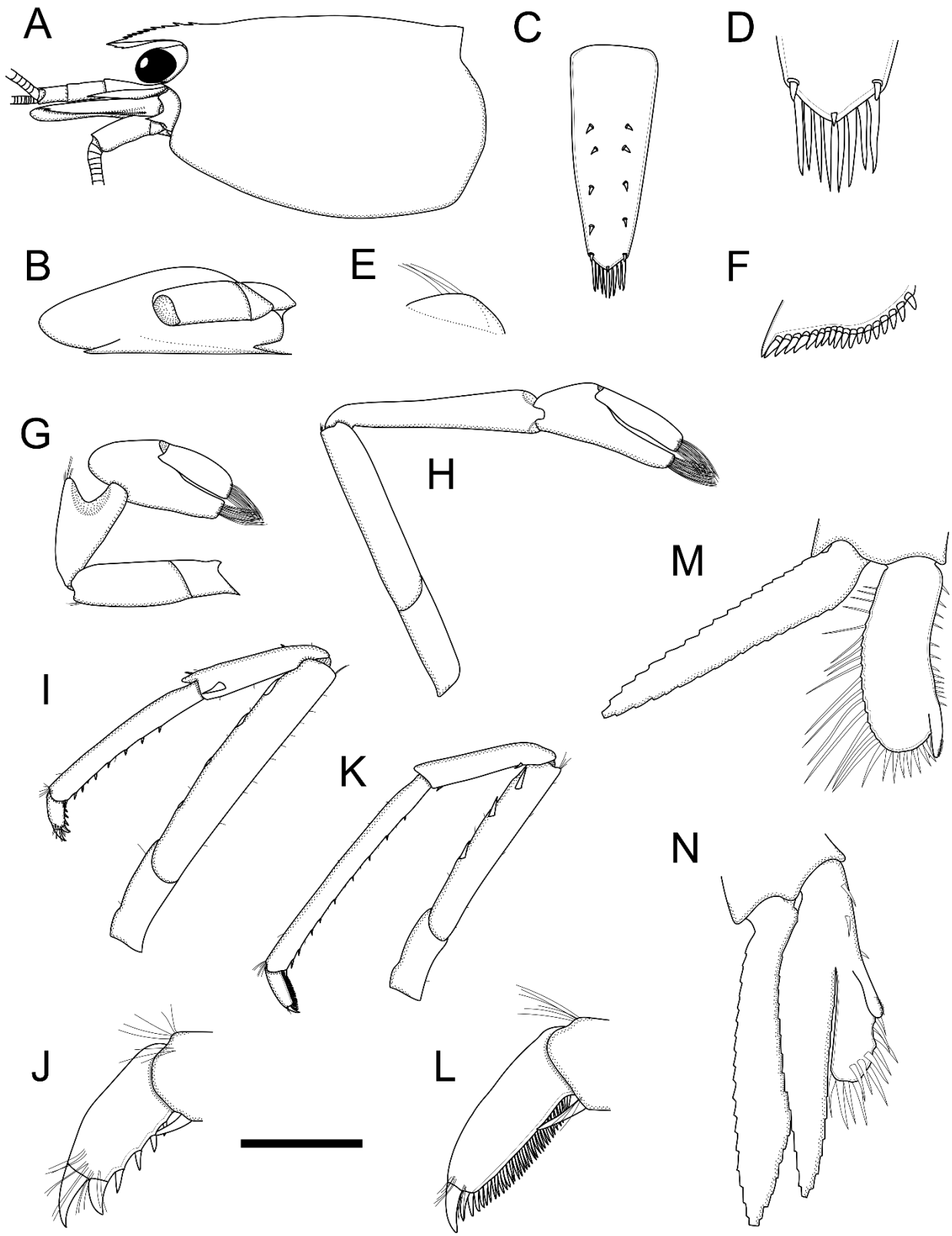

Fig. 6.

Table 1. Details of specimens and GenBank accessions included in the phylogenetic analysis. Newly generated sequences are highlighted in bold. –, missing data.

Species	Voucher ID	Sampling locality	GenBank accession no. COI	16S
Caridina argilla sp. nov.	CUHK-LMT-CAR476-4 (paratype)	Hong Kong, China	*	*
Caridina bauhinia sp. nov.	CUHK-LMT-CAR425-2 (paratype)	Hong Kong, China	*	*
Caridina breviata	OUMNH.ZC 2013-07-040	Zhapo, Guangdong, China	KP168788	KP168718
Caridina cantonensis	NCHUZOOL 13114	Zhapo, Guangdong, China	AB300190	–
	OUMNH.ZC 2013-07-015	Qingyuan, Guangdong, China	KP168802	KP168720
Caridina caobangensis	ZMB 30255	Pac Bo, Cao Bang, Vietnam	MT526826	MT526809
Caridina cavernicola	Unknown in FU	Hechi, Guangxi, China	MZ753499	MZ753802
Caridina chui sp. nov.	CUHK-LMT-CAR444-2 (holotype)	Hong Kong, China	*	*
Caridina clinata	ZMB 31777	Cuc Phuong, Ninh Binh, Vietnam	MT526827	MT526810
Caridina conghuensis	OUMNH.ZC 2013-07-025 (paratype)	Conghua, Guangdong, China	–	KP168735
	CUHK-LMT-CAR406-1	China	*	–
Caridina cucphuongensis	ZMB 31744	Cuc Phuong, Ninh Binh, Vietnam	MT526828	MT526811
Caridina formosae	NCHUZOOL 13113	Tamsui, Taipei, Taiwan	AB300189	–
	GU-987	Tamsui, Taipei, Taiwan	DQ478451	DQ478496
Caridina haivanensis	ZMB 30259	Hai Van, Thua Thien-Hue, Vietnam	MT526830	MT526813
Caridina huananensis	Unknown in FU	Qingyuan, Guangdong, China	MN701607	MT446452
Caridina lanceifrons	ZMB 29638	Da Bac, Hoa Binh, Vietnam	MT526831	MT526814
Caridina logemanni	ZMB 28221 (paratype)	Hong Kong, China	–	KP168745
	CUHK_MSL_ClogNWC01	Hong Kong, China	MZ895521	–
Caridina macauensis	SYSBM18-11-21-04 (paratype)	Macau, China	MN879768	–
Caridina maculata	OUMNH.ZC 2013-07-028	Lixi, Guangdong, China	–	KP168748
Caridina mariae	ZMB 28223 (paratype)	Conghua, Guangdong, China	–	KP168753
	Unknown in FU	Huizhou, Guangdong, China	MN701601	–
Caridina namdat	ZMB 30341-3 (paratype)	Nam Dat, Bac Kan, Vietnam	MZ484397	MZ484401
Caridina nanaoensis	ZMB 29473	China	KP168792	KP168755
Caridina ngankeeae	CUHK-LMT-CAR408-1 (paratype)	Hong Kong, China	*	*
Caridina nguyeni	ZMB 30280	Pac Bo, Cao Bang, Vietnam	MT526833	MT526816
Caridina pacbo	ZMB 30295-2 (paratype)	Pac Bo, Cao Bang, Vietnam	MT526835	MW525213
Caridina pseudodenticulata	GU-986	Dongshi, Taichung, Taiwan	DQ478459	DQ478511
Caridina pseudoserrata	ZMB 30343	Tu Do, Cao Bang, Vietnam	MT526837	MT526818
Caridina rubropunctata	ZMB 30314	Van Lang, Thai Nguyen, Vietnam	MT526838	MT526819
Caridina serrata	CUHK_MSL_CserHLF01	Hong Kong, China	MZ092943	–
	OUMNH.ZC 2013-07-020	Hong Kong, China	KP168793	KP168758
Caridina sinanensis	Unknown in FU (type series)	Sinan, Guizhou, China	MT433962	MT434873
Caridina sphyrapoda	CUHK_MSL_CapoNCP01	China	MH176649	*
Caridina stellata	Unknown in FU (type series)	Jinxiu, Guangxi, China	MZ753496	MZ753799
Caridina tetrazona	Unknown in FU (type series)	Dawanshan Island, Guangdong, China	MN701593	–
Caridina thachlam	ZMB 31781 (paratype)	Thach Lam, Thanh Hoa, Vietnam	MW506000	MW505994

Caridina tricincta	ZMB 30360-1 (paratype)	Lac Nong, Ha Giang, Vietnam	MT526839	MT526822
Caridina trifasciata	OUMNH.ZC 2013-07-033	Hong Kong, China	–	KP168767
	CUHK_MSL_CtriNBK01	Hong Kong, China	MZ092955	–
Caridina venusta	RMNH.CRUS.D.56061	Lixi, Guangdong, China	KP168812	KP168772
Caridina yunnanensis	ZMB DNA-283	China	KP168820	KP168741
Neocaridina ketagalan	NCHUZOOL 13107 (type series)	Sijhih, Taipei, Taiwan	AB300182	AB300168
Neocaridina palmata	Unknown in FU	Qingyuan, Guangdong, China	MN701612	–
	ZMB 30256	Pac Ma, Cao Bang, Vietnam	MT526843	MT526825
Neocaridina saccam	NCHUZOOL 13103 (type series)	Longci, Tainan, Taiwan	AB300177	AB300164
	GU-1000	Longci, Tainan, Taiwan	DQ681254	–
Neocaridina spinosa	NCHUZOOL 13112	Tongan, Fujian, China	AB300188	AB300174
Paracaridina guizhouensis	GBZD-562	Yuping, Guizhou, China	OR536641	OR537883
Paracaridina zijinica	OUMNH.ZC 2013-07-038	Heyuan, Guangdong, China	KP168799	KP168783
Sinodina ashima	GBZD-677 (type series)	Shilin, Yunnan, China	OR536642	OR537885
Sinodina gregoriana	GBZD-238	Weining, Guizhou, China	–	OR537881
Outgroup				
Caridina elongapoda	CUHK_MSL_ClonNTAI11	Hong Kong, China	MZ093015	–
	OUMNH.ZC 2013-07-041	Hong Kong, China	KP168821	KP168733
Caridina gracilipes	MNHN-IU-2018–207	Indonesia	MK190025	–
	ZMB 30231	Thuy Nguyen, Hai Phong, Vietnam	MT526829	MT526812

Voucher ID locations: CUHK, The Chinese University of Hong Kong; FU, Foshan University; GBZD, Guizhou Academy of Sciences; GU, Griffith University; NCHUZOOL, National Chung Hsing University; MNHN, Muséum national d'Histoire naturelle; OUMNH, Oxford University Museum of Natural History; RMNH, Naturalis Biodiversity Center Leiden; SYSBM, Sun Yat-Sen University; ZMB, Museum für Naturkunde Berlin.

Table 2. K2P pairwise genetic distances of COI (above diagonal) and 16S rRNA genes (below diagonal) among the three new species and closely related species. NA, sequence of one of the species not available.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
(1) *Caridina chui* sp. nov.	/	0.156	0.154	0.147	0.164	0.167	0.049	0.175	NA	0.153	0.151	0.133	NA
(2) *Caridina bauhinia* sp. nov.	0.077	/	0.063	0.175	0.174	0.167	0.144	0.145	NA	0.094	0.092	0.095	NA
(3) *Caridina argilla* sp. nov.	0.081	0.028	/	0.161	0.177	0.156	0.144	0.123	NA	0.094	0.086	0.086	NA
(4) *Caridina cantonensis*	0.087	0.094	0.088	/	0.105	0.084	0.147	0.168	0.152	0.155	0.152	0.152	0.148
(5) *Caridina mariae*	0.083	0.088	0.086	0.034	/	0.117	0.159	0.193	NA	0.175	0.166	0.153	NA
(6) *Caridina logemanni*	0.086	0.098	0.092	0.021	0.034	/	0.172	0.154	NA	0.137	0.121	0.136	NA
(7) *Caridina conghuensis*	0.031	0.080	0.090	0.090	0.088	0.097	/	0.166	NA	0.126	0.153	0.139	NA
(8) *Caridina serrata*	0.083	0.044	0.047	0.085	0.076	0.084	0.092	/	0.000	0.126	0.145	0.113	0.128
(9) *Caridina nanaoensis*	0.085	0.044	0.048	0.083	0.074	0.081	0.094	0.006	/	NA	NA	NA	0.128
(10) *Caridina trifasciata*	0.077	0.034	0.033	0.077	0.077	0.088	0.081	0.031	0.033	/	0.091	0.075	NA
(11) *Caridina tetrazona*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	/	0.084	NA
(12) *Caridina macauensis*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	/	NA
(13) *Caridina breviata*	0.081	0.087	0.097	0.088	0.072	0.095	0.081	0.077	0.083	0.077	NA	NA	/

Table 3. List of landlocked *Caridina* species recorded from southern China (SC), and northern (NV) and central Vietnam (CV). +, species qualified into the *C. serrata* species group under the original diagnosis by Cai & Ng (1999) and the new diagnoses, respectively; +?, species with some ambiguity.

Species	Distribution	*C. serrata* species group		
		Cai & Ng (1999)	*Sensu stricto* (Present study)	*Sensu lato* (Present study)
Caridina apodosis	Hong Kong (SC)	+	+	+
Caridina argilla sp. nov.	Hong Kong (SC)	+	+	+
Caridina bamaensis	Guangxi (SC)			+
Caridina baoting	Hainan (SC)			+
Caridina bauhinia sp. nov.	Hong Kong (SC)	+	+	+
Caridina beiliu	Guangxi (SC)			+
Caridina breviata	Macau, Guangdong (SC)	+?	+	+
Caridina cantonensis	Hong Kong, Macau, Guangdong, Guangxi (SC), Quang Nam (CV)	+	+	+
Caridina caobangensis	Cao Bang (NV)	+		+
Caridina cavernicola	Guangxi (SC)			+
Caridina chui sp. nov.	Hong Kong (SC)	+	+	+
Caridina clinata	Hainan (SC), Ninh Binh (NV)			+
Caridina conghuensis	Guangdong (SC)	+	+	+
Caridina cucphuongensis	Ninh Binh (NV)	+?		+
Caridina danxiaensis	Guangdong (SC)	+?		+
Caridina guangxiensis	Guangxi (SC)	+		+
Caridina guilin	Guangxi (SC)			+
Caridina haivanensis	Thua Thien-Hue (CV)			+
Caridina huananensis	Guangdong (SC)			+
Caridina lanceifrons	Widespread in SC, NV and CV			
Caridina laticarpalis	Guangxi (SC)			+
Caridina logemanni	Hong Kong (SC)	+	+	+
Caridina macauensis	Macau (SC)	+	+	+
Caridina maculata	Guangdong (SC)	+		+
Caridina mariae	Guangdong (SC)	+	+	+
Caridina namdat	Bac Kan (NV)			+
Caridina nanaoensis	Guangdong (SC)	+	+	+
Caridina ngankeeae	Hong Kong (SC)	+		+
Caridina nguyeni	Cao Bang (NV)	+		+
Caridina pacbo	Cao Bang (NV)	+		+
Caridina pseudoserrata	Cao Bang (NV)	+		+
Caridina qingyuanensis	Guangdong (SC)			+
Caridina rubropunctata	Thai Nguyen (NV)	+		+
Caridina serrata	Hong Kong, Guangdong (SC), Quang Nam (CV)	+	+	+
Caridina sphyrapoda	Guangxi (SC)	+		+
Caridina spinicrus	Guangxi (SC)			+
Caridina stellata	Guangxi (SC)	+		+
Caridina tetrazona	Guangdong (SC)	+	+	+
Caridina thachlam	Ninh Binh (NV)			+
Caridina tricincta	Tuyen Quang, Ha Giang (NV)	+?		+
Caridina trifasciata	Hong Kong, Guangdong (SC)	+	+	+
Caridina venusta	Guangdong (SC)			+

Caridina wumingensis	Guangxi (SC)	+	+	+
Caridina zhongshanica	Guangdong (SC)	+		+