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On two new species of the genus *Lobothelphusa* Bouvier, 1917 (Decapoda: Brachyura: Potamidae: Potaminae) from the Pegu Range, central Myanmar

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Abstract. The freshwater crab genus *Lobothelphusa* Bouvier, 1917, is known from five species (*L. crenulifera*, *L. calva*, *L. barbouri*, *L. floccosa*, and *L. woodmasoni*), which are mainly distributed in Myanmar (=Burma). In this study, we describe two new species, *L. bagoensis* and *L. thewanica*, from the Pegu Range in central Myanmar. Characters of the carapace and male first gonopod can clearly distinguish the two new species from their congeners. Molecular data derived from a partial sequence of the mitochondrial 16S rDNA support the systematic position of the new taxa.

Key words. Crustacea, Potamidae, freshwater crab, taxonomy

INTRODUCTION

The tropical hills and rivers of Myanmar have rich biodiversity and are home to many species of freshwater crabs. Despite this, the biodiversity of the freshwater crabs of Myanmar appears to be underestimated, especially in the remote regions, and there has been little scientific attention devoted to their study thus far (Cumberlidge et al., 2012). During a freshwater biodiversity survey, conducted by the Nanjing Normal University and Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences to Myanmar (April–May 2019), several potamid crabs were collected from the riparian zone along the Pegu hill streams, in Bago Division (formerly Pegu Division), Myanmar. These crabs belong to the subfamily Potaminae Ortmann, 1896, because the male thoracic sternite 8 possesses a narrow transverse ridge near the suture between thoracic sternites 7 and 8 that interrupts the median line (Yeo & Ng, 2003). Upon comparison with the morphological traits of potamines distributed in this region, we regarded the freshwater crabs as two new species of the genus *Lobothelphusa* Bouvier, 1917.

The potamid genus *Lobothelphusa* was established by Bouvier (1917) as a subgenus of *Hydrothelphusa* A. Milne-Edwards, 1872, and Bott (1970) subsequently recognised it as a valid genus. Ng et al. (2008) and Yeo & Ng (2007) recognised five species of *Lobothelphusa* based on a suite of morphological characters. Other works have included species of *Lobothelphusa* and *Acanthopotamon* Kemp, 1918 under *Paratelphusula* Alcock, 1909, instead, mainly on the basis of possessing multiple epibranchial teeth and molecular phylogenetic data (Brandis & Sharma, 2005; Klaus et al., 2019; Klaus, unpublished data). However, our unpublished molecular analysis indicated that *Lobothelphusa* and *Paratelphusula* come out in two sister clades. Although quite similar, the two genera can be clearly distinguished by morphological characters. We agree with Yeo & Ng (2007) that it seems more reasonable to recognise two genera based on morphological characters and molecular phylogeny.

The present study follows Ng et al. (2008) and Yeo & Ng (2007), in recognising *Lobothelphusa* as a distinct genus with five species, namely *L. crenulifera* (Wood-Mason, 1875) (type species), *L. calva* (Alcock, 1909), *L. barbouri* (Rathbun, 1910), *L. floccosa* (Alcock, 1910), and *L. woodmasoni* (Rathbun, 1905). The two new species described herein, *L. bagoensis* and *L. thewanica*, are most similar morphologically to *L. crenulifera* and *L. calva*, but can clearly be distinguished by the structure of the carapace and male first gonopods. In this study, we apply molecular phylogenetic analysis based on 16S rDNA (16S ribosomal RNA gene) sequences to clarify their interspecific relationship.

MATERIAL AND METHODS

Examined specimens from central Myanmar (Fig. 1) were preserved in 75% ethanol and identified under a

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Table 1. The 16S rDNA haplotypes and localities of ingroup species in the study.

Subfamily	**Species**	**Locality**	**GenBank accession number**	**Reference**
Potaminae	*Acanthopotamon panningi*	India/Nepal	FN543462	Klaus & Brandis, 2011
Potaminae	*Himalayapotamon atkinsonianum*	Nepal/India	AB290632	Yeo et al., 2007
Potaminae	*Himalayapotamon atkinsonianum*	Nepal/India	AB428510	Shih et al., 2009
Potaminae	*Himalayapotamon emphysetum*	Nepal, Lumbini	FN543464	Klaus & Brandis, 2011
Potaminae	*Himalayapotamon emphysetum*	Nepal, Lumbini	LR131126	Klaus & Brandis, 2018
Potaminae	*Himalayapotamon koolooense*	India, Bhin valley	LR131128	Klaus & Brandis, 2018
Potaminae	*Himalayapotamon* sp.	India, Uttaranchal	AB428511	Shih et al., 2009
Potaminae	*Himalayapotamon sunkoshiense*	Nepal, Bagmati	LR131131	Klaus & Brandis, 2018
Potaminae	*Himalayapotamon sunkoshiense*	Nepal, Bagmati	LR131130	Klaus & Brandis, 2018
Potaminae	*Lobothelphusa bagoensis*, new species	Myanmar, Bago	OK509066	This study
Potaminae	*Lobothelphusa thewanica*, new species	Myanmar, Bago	OK509068	This study
Potaminae	*Paratelphusula gibbosa*	Myanmar, Bago	OK509067	This study
Potaminae	*Paratelphusula gibbosa*	Myanmar	AB428512	Shih et al., 2009
Potaminae	*Potamon algeriense*	India	AB428513	Shih et al., 2009
Potaminae	*Potamon elbursi*	Iran	HG321368	Keikhosravi & Schubart, 2013
Potaminae	*Potamon gedrosianum*	Iran, Sistan, Zabul	LT158591	Keikhosravi et al., 2016
Potaminae	*Potamon ibericum*	Iran, Gorgan, Naharkhoran	HE963848	Keikhosravi & Schubart, 2013
Potaminae	*Potamon mesopotamicum*	Syria, Tall Tamr	HE963849	Keikhosravi & Schubart, 2014
Potaminae	*Potamon persicum*	Iran, Ilam Province	HG321385	Keikhosravi & Schubart, 2013
Potaminae	*Potamon persicum*	Iran, Ilam Province	HG321383	Keikhosravi & Schubart, 2013
Potaminae	*Potamon persicum*	Iran, Isfahan, Isfahan	HE963844	Keikhosravi & Schubart, 2013
Potaminae	*Potamon persicum*	Iran, Ilam Province	HG321384	Keikhosravi & Schubart, 2013
Potaminae	*Potamon ruttneri*	Iran, Khorasan Razavi, Kalat	LT158587	Keikhosravi et al., 2016
Potaminae	*Potamon transcaspicum*	Iran, Sabzevar, Zardkoohi	HE963841	Keikhosravi & Schubart, 2013
Potaminae	*Potamon transcaspicum*	Afghanistan, Zabul, Kalat	LT158598	Keikhosravi et al., 2016
Potamiscinae	*Esanpotamon namsom*	Thailand, Udon Thani	AB428463	Shih et al., 2009
Potamiscinae	*Megacephalomon kittikooni*	Laos, Xieng Khuang	AB428462	Shih et al., 2009
Potamiscinae	*Pudaengon sakonnakorn*	Thailand	AB428484	Shih et al., 2009
Potamiscinae	*Pudaengon thatphanom*	Thailand (aquarist)	FN543465	Klaus & Brandis, 2011
Potamiscinae	*Stoliczia bella*	Malaysia, Pulau Langkawi	FM180117	Klaus et al., 2009
Potamiscinae	*Stoliczia chaseni*	Malaysia, Gunung Brinchang	AB290627	Yeo et al., 2007
Potamiscinae	*Larnaudia beusekomae*	Thailand (aquarist)	FN543460	Klaus & Brandis, 2011

stereomicroscope (Nikon SMZ645). All specimens are deposited in the following collections: holotypes, the Jiangsu Key Laboratory for Biodiversity and Biotechnology, Nanjing Normal University (NNU), Nanjing, China; and paratypes, Southeast Asia Biodiversity Research Institute (SEABRI), Chinese Academy of Sciences (CAS), Naypyidaw, Myanmar. The abbreviations are as follows: cw, carapace width; cl, carapace length; ch, carapace height; fw, frontal width; p2–p5, respectively, pereiopods 2 to 5; s1–s8, respectively, thoracic sternites 1 to 8; G1, male first gonopod; G2, male second gonopod. The terminology used follows Ng (1988), Dai (1999), and Davie et al. (2015).

Total genomic DNA was extracted from gill or ambulatory leg muscle tissue using Tiangen universal DNA purification kit (Beijing, China). The fragments of 16S rDNA were amplified by the polymerase chain reaction (PCR) using the primers 1471 and 1472 (Crandall & Fitzpatrick, 1996). The cycling parameters were identical to those found in the citations for each primer pair. Both ends of sequences were obtained by automated sequencing using Applied Biosystems 3730.

To clarify the two new species' generic relationship among the *Lobothelphusa* and other Asian potamid taxa, and those of other potamine taxa, a molecular phylogenetic tree was reconstructed based on a fragment of the 16S rDNA of 23 species (16 species in 5 genera from Potaminae and 7 species in 5 genera from Potamiscinae) (Table 1), including the three new sequences for the two new species and *Paratelphusula gibbosa* (Ng & Kosuge, 1997) obtained in this study. The specimen of *P. gibbosa* (NNU16-NBDY1) was collected from Oktwin Township, Myanmar, about 150 km north of type locality (18.798°E, 96.439°N). The four sequences of gecarcinucids were selected as outgroups (*Vanni deepta* Bahir & Yeo, 2007, HG518131; *V. travancorica* (Henderson, 1913), HG518137; *Baratha peena* Bahir & Yeo, 2007, HG518136; and *B. pushta* Bahir & Yeo, 2007, HG518135, refer to Klaus et al., 2015). Sequences were aligned using MAFFT v7.467 (Katoh & Standley, 2013) based on the G-INS-I method. The best substitution model was GTR + I + G, which was evaluated by PartitionFinder v1.1.1 (Lanfear et al., 2012) using the Akaike information criterion (AIC) and Bayesian information criterion (BIC). The maximum likelihood (ML) tree was inferred using IQ-TREE v1.7, with 1,000 bootstrap replicates (Nguyen et al., 2015). The Bayesian inference (BI) analysis was performed using MrBayes v3.2.6 (Ronquist et al., 2012). Two independent runs of four Markov Chain Monte Carlo chains (one cold chain and three heated chains) with 3,000,000 replicates sampling one tree every 1,000 generations were implemented. The first 25% were discarded as burn-in. The effective sample size (ESS) values were checked by Tracer v1.6 (Rambaut et al., 2014) to ensure that all ESS values were greater than 200. Sequences of 16S rDNA obtained in the present study have been deposited in the GenBank with accession numbers: NNU16-DYX1, OK509066; NNU16-NBDY1, OK509067; NNU16-BG1, OK509068.

SYSTEMATICS

Superfamily Potamoidea Ortmann, 1896

Family Potamidae Ortmann, 1896

Subfamily Potaminae Ortmann, 1896

Lobothelphusa Bouvier, 1917

Lobothelphusa bagoensis, new species

(Figs. 2, 3, 6A–C, 7A–D)

Material examined. Holotype: adult male (cw 39.72 mm, cl 31.98 mm, ch 20.34 mm, fw 13.68 mm), NNU16-DYX1, Taungoo Township, Pegu Range, Bago Division, 18.857°N, 96.103°E, 233 m asl, Myanmar (Fig. 1 dark blue), coll. B. Shi, 13 May 2019.
Paratypes: adult male (cw 37.38 mm, cl 30.48 mm, ch 20.86 mm, fw 12.32 mm), NNU16-DYX2, and adult female (cw 36.18 mm, cl 30.72 mm, ch 19.62 mm, fw 12.68 mm), SEABRI-DYX3, same location as holotype.
Other material: adult female (cw 37.29 mm, cl 29.67 mm, ch 19.94 mm, fw 12.47 mm), NNU16-AG2; adult female (cw 38.45 mm, cl 30.54 mm, ch 20.94 mm, fw 12.88 mm), NNU16-AG3; adult female (cw 37.67 mm, cl 29.97 mm, ch 20.03 mm, fw 12.76 mm), SEABRI-AG4; adult female (cw 39.42 mm, cl 31.28 mm, ch 21.34 mm, fw 13.52 mm), SEABRI-AG5; Oktwin Township, Bago Division, 18.789°N, 96.439°E, 38 m asl, Myanmar, coll. B. Shi, 8 May 2019.

Description. Carapace subtrapezoidal, distinctly broader than long (cw/cl = 1.23; ch/cl = 0.68); dorsal surface smooth, slightly convex longitudinally and transversely; regions indistinct, cervical grooves poorly developed, shallow, H-shaped groove well-developed (Fig. 2A). Epigastric cristae low, distinct, gently rugose, separated by groove which opens up into inverted Y-shaped gap posteriorly, positioned anterior to postorbital cristae, separated from postorbital cristae by distinct narrow groove; postorbital cristae distinct but low, straight, sharp, confluent with the first epibranchial teeth; regions behind epigastric and postorbital cristae smooth (Fig. 2A). Frontal margin almost straight or gently concave (fw/cw = 0.38), with very low, rounded granules; frontal region relatively broad longitudinally (Fig. 2A). Antennular fossae rectangular when viewed from front; supraorbital margin sinuous, cristate; infraorbital margin sinuous, slightly sloping downward, cristate; orbital region relatively broad; suborbital, pterygostomial regions granulose; eyes filling up most of orbital space; eyestalk short, stout; cornea moderately large, pigmented (Fig. 2C). External orbital angle well-developed, triangular, tip acute, outer margin distinctly convex, with deep cleft separating it from anterolateral margins; anterolateral margins convex, each with four prominent epibranchial teeth; epibranchial teeth stout, teeth 1–4 progressively smaller, tips directed anterolaterally, base of each tooth broad; posterolateral margin sinuous; posterior carapace margin convex; branchial region with very weak, oblique

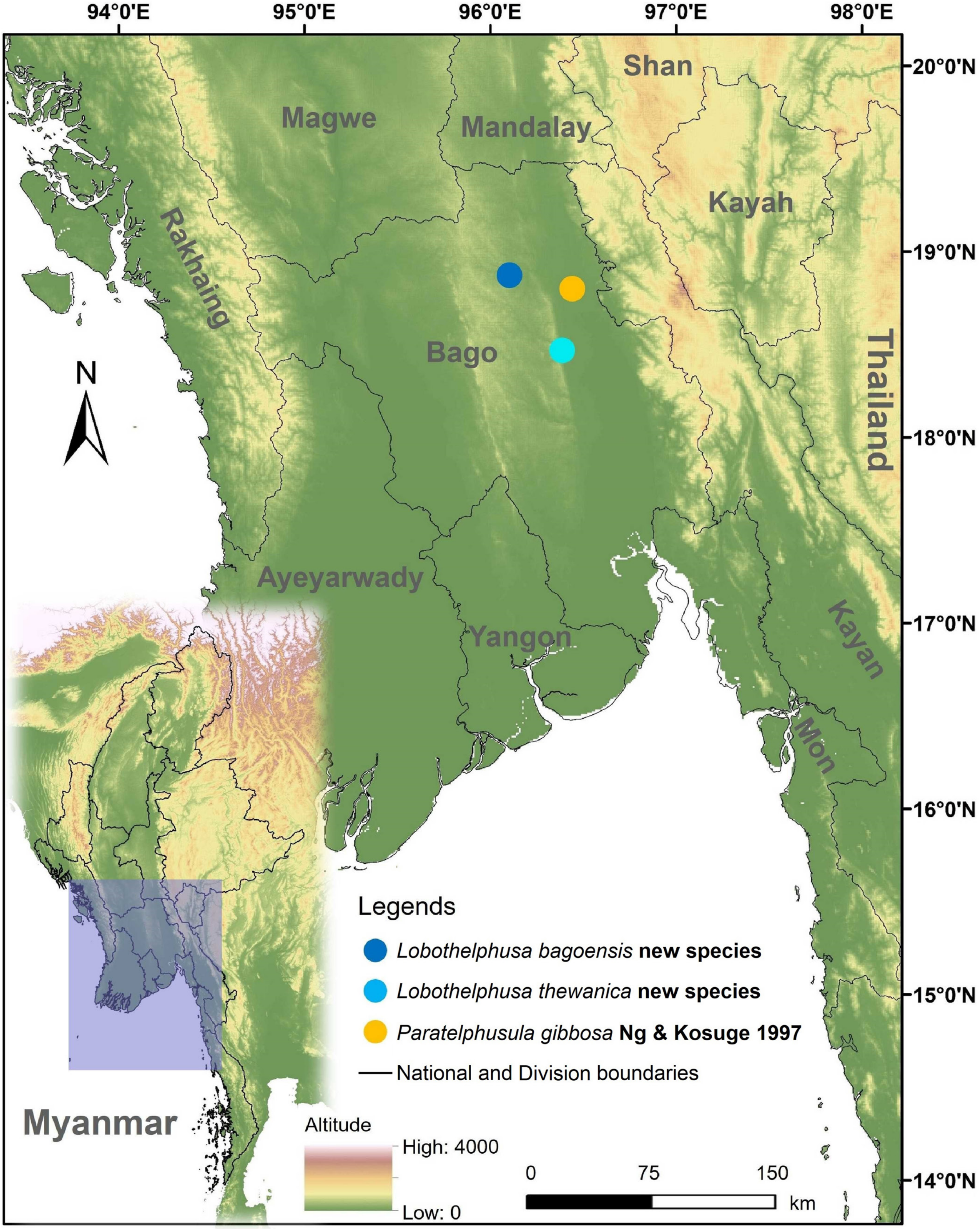

Fig. 1. Sampling sites for *Lobothelphusa bagoensis*, new species (dark blue), *Lobothelphusa thewanica*, new species (light blue), and *Paratelphusula gibbosa* Ng & Kosuge, 1997 (yellow) in Myanmar.

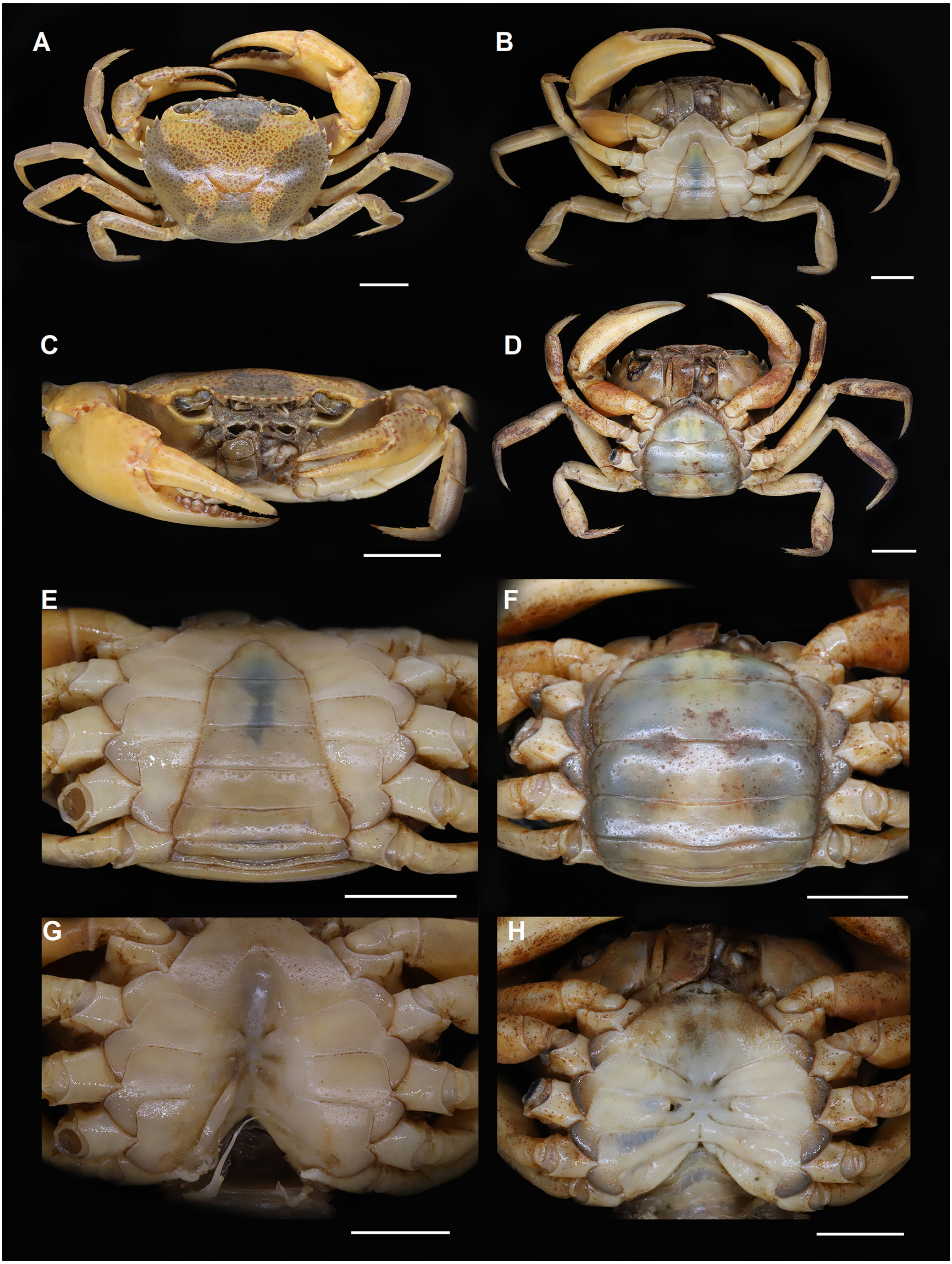

Fig. 2. *Lobothelphusa bagoensis*, new species. A–C, E, G, holotype, male, 39.72 × 31.98 mm, NNU16-DYX1; D, F, H, paratype, female, SEABRI-DYX3, 36.18 × 30.72 mm. A, dorsal view; B, D, ventral views; C, frontal view; E, F, ventral view showing anterior thoracic sternum and pleon; G, ventral view showing sterno-pleonal cavity with G1 in situ; H, thoracic sternum and vulvae. Scale bars = 1.0 cm.

striae (Fig. 2A). Posterior margin of epistome with well-developed median tooth, lateral margins sinuous (Fig. 2C). Third maxilliped glabrous; ischium subtrapezoidal, ca. 0.61 times width of length, elongate longitudinally, without median sulcus; merus subrectangular, ca. 1.76 times width; exopod reaching two-thirds length of merus, with well-developed flagellum (Figs. 2B–D, 3C).

Chelipeds asymmetric, glabrous, major chela distinctly larger; dorsal surface smooth; merus with well-developed subdistal spine on dorsal margin; carpus with strong, well-developed spine on inner distal angle, spine slightly sinuous (Fig. 2A–D). Palm of major chela longer than high, inner and outer surfaces inflated, punctate; fingers of major chela punctate, with numerous teeth of different size, large gape when finger closed, fingers slightly curved, equal in length to palm; minor cheliped similar to major cheliped (Fig. 3A).

Ambulatory legs relatively long, slender, p3 longest, p5 shortest, outer margins heavily setose; p5 propodus relatively stouter than p2–p4 propodi; dactylus slightly curved, equal in length to propodus, with short, sharp chitinous spines on margins; outer edges with thick spongy tomentum (Figs. 2A, B, D, 3B).

Male thoracic sternum smooth; thoracic sternites s1/s2 completely fused; suture thoracic sternites s2/s3 distinct; thoracic sternites s3/s4 fused, groove between sternites not discernible; sutures between thoracic sternites s4/s5, s5/s6, s6/s7 shallow, narrow; suture between thoracic sternites s7/s8 distinct (Fig. 2B, E). Pleonal locking mechanism with distinct, anteriorly directed tubercle on submedian part of sternite s5 (Fig. 2G). Narrow transverse ridge at the suture between thoracic sternites s7/s8 that interrupts the median line (Fig. 2G, H).

Male pleon narrowly triangular; telson with blunt apex and concave lateral margins, ca. 0.70 times length of width; somite 6 subrectangular, ca. 1.95 times length of width, lateral margins gently convex or straight; somites 4–6 trapezoidal, progressively less broad; lateral margins of segment 3 distinctly convex; lateral margins of somites 4 and 5 gently concave; suture between somites 5/4, 4/3 distinctly sinuous; somite 3 broader than somites 1 and 2 longitudinally; somite 2 longitudinally broader than somite 1; somite 1 longitudinally narrow (Fig. 2B, E). Female pleon ovate, covering the thoracic sternites when closed; telson broadly subtriangular, much broader than long, with convex lateral margins; somites 4–6 almost equal, broader than long, with convex lateral margins; somites 1–3 progressively longer (Fig. 2D, F).

G1 gently sinuous or straight, slender, tip of terminal segment not reaching pleonal locking mechanism in situ (Figs. 2G, 3D, E, 6A, B); groove for G2 on ventral surface; terminal segment short, conical in shape, straight, tip acute, distal part gently curved outward or straight, ca. 0.23 times length of subterminal segment; dorsal fold low, extending along proximal portion to three-quarters length of terminal segment; subterminal segment convex on upper part of inner margin (Figs. 3D, E, 6A, B). G2 length equal to length of G1; distal segment long, ca. 0.41 times length of basal segment (Figs. 3F, 6C). Vulvae on thoracic sternite 6, relatively small, subtriangular, occupying ca. 0.45 times length of thoracic sternite 6, almost reaching suture between thoracic sternites s4/s5 (Fig. 2H).

Etymology. The new species is named after the administrative region in which the type locality is situated, Bago Division, Myanmar.

Colour in life. In life, the adult animals are pale yellow with numerous reddish-brown spots dorsally, with the ventral surfaces pearly white. The ambulatory legs are pale yellow as on the carapace, but the basal parts are often pearl white. The thick spongy tomentum of the ambulatory legs is usually brownish yellow. The tips of the dactyli of the ambulatory legs are whitish-yellow. The integument at the articulations between the chela carpus and merus in the chelipeds is white (Figs. 2, 7C, D).

Ecological note. These specimens were obtained from streams in hilly terrain and were dug out from mud burrows approximately 60–80 cm deep in well-drained, silty soil along the riparian zone (Fig. 7A). The eggs from three female individuals (NNU16-AG2, NNU16-AG3, SEABRI-AG4) were observed to be a bright yellow in colour and small in size (1.5–2.0 mm diameter) (Fig. 7B), and with each female carrying 253–374 eggs.

Remarks. *Lobothelphusa bagoensis*, new species, most closely resembles congeners *L. crenulifera* (Wood-Mason, 1875) and *L. calva* (Alcock, 1909) in the general carapace features. The new species, however, differs markedly in the following: (1) the anterolateral and posterolateral margins are convex and the frontal margin is almost straight (Fig. 2A) (versus the anterolateral and posterolateral margins are slightly convex, and the frontal margin is slightly concave in *L. crenulifera* and *L. calva*, cf. Alcock, 1910: pl. 4, fig. 13; Bott, 1970: pls. 45–46, figs. 21, 22; Rathbun, 1905: pl. 12, fig. 11); (2) the frontal region is relatively broad longitudinally (Fig. 2A) (versus the frontal region relatively narrow longitudinally in *L. crenulifera* and *L. calva*, cf. Alcock, 1910: pl. 4, figs. 13, 14; Bott, 1970: pls. 45–46, figs. 21, 22; Rathbun, 1905: pl. 12, fig. 11); (3) the postorbital cristae are almost horizontal (Fig. 2A) (versus the postorbital cristae are slightly oblique in *L. crenulifera* and *L. calva*, cf. Alcock, 1910: pl. 4, figs. 13, 14; Bott, 1970: pls. 45–46, figs. 21, 22; Rathbun, 1905: pl. 12, fig. 11); (4) the G1 is gently sinuous or straight, the distal part of the terminal segment is curved outward (Figs. 3D, E, 6A, B) (versus the G1 is sinuous, the distal part is strongly curved outward in *L. crenulifera* and *L. calva*, cf. Bott, 1970: pl. 38, figs. 23, 24); (5) the dorsal flap extends along the proximal portion to three-quarters of the length of the terminal segment (Figs. 3D, E, 6A, B) (the dorsal flap extends to half or two-thirds of the terminal segment in *L. crenulifera*, cf. Bott, 1970: pl. 45, fig. 21); and (6) the subterminal segment is convex on the upper part of the inner margin (Figs. 3D, E, 6A, B) (versus the subterminal segment is slightly concave on

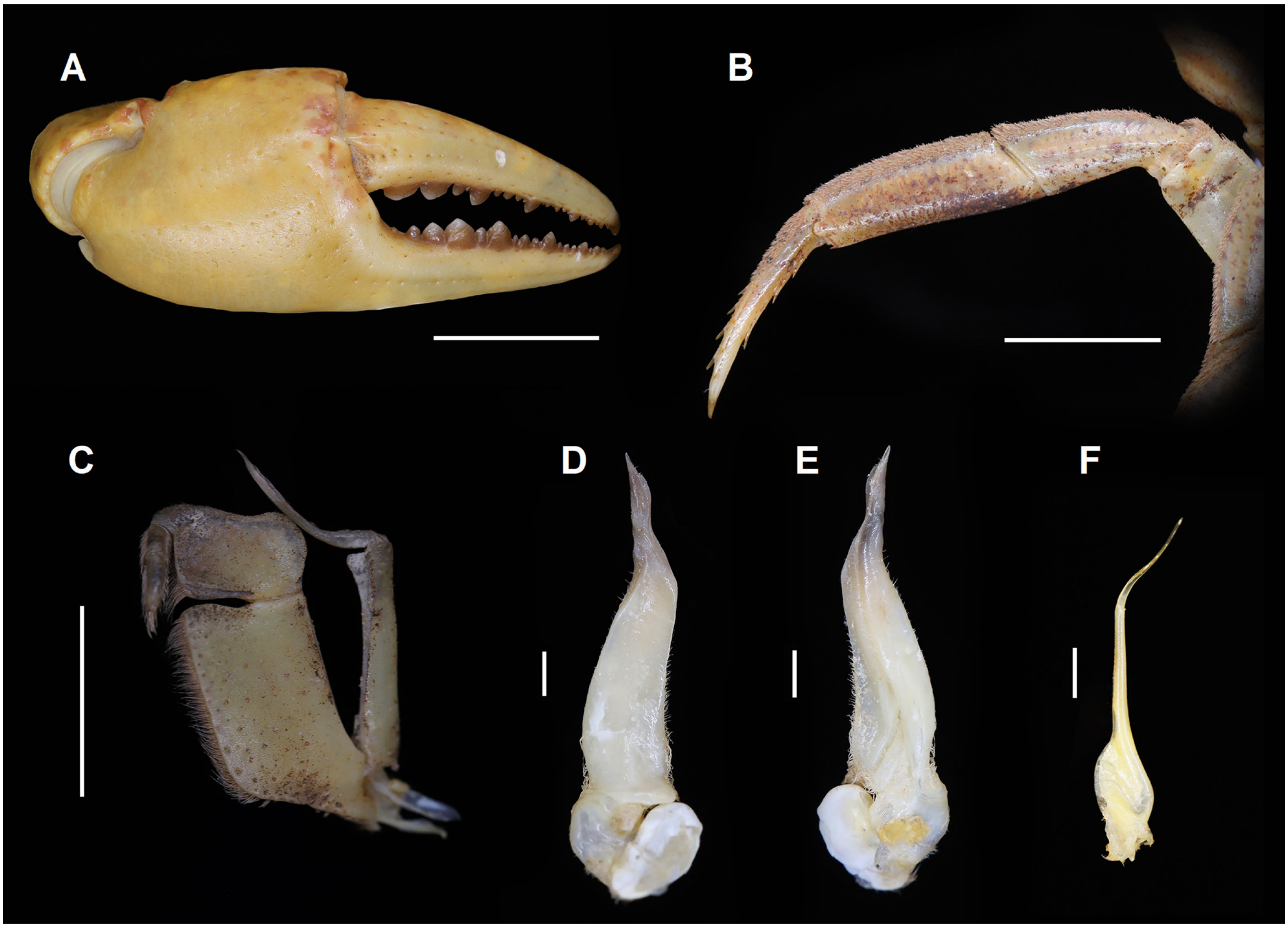

Fig. 3. *Lobothelphusa bagoensis*, new species, holotype, male, NNU16-DYX1. A, major chela (dorsal view); B, right third ambulatory leg (dorsal view); C, left third maxilliped (dorsal view); D, left G1 (dorsal view); E, left G1 (ventral view); F, left G2 (ventral view). Scale bars: A–C = 1.0 cm; D–F = 1.0 mm.

the upper part of inner margin in *L. crenulifera*, cf. Bott, 1970: pl. 45, fig. 21; the subterminal segment is distinctly concave on the upper part of inner margin in *L. calva*, cf. Bott, 1970: pl. 46, fig. 22).

Lobothelphusa bagoensis, new species, is less likely to be confused with *Lobothelphusa barbouri* (Rathbun, 1910), although these congeners do share superficial resemblance in some aspects of the carapace (Fig. 2A). The new species, however, can easily be separated from *L. barbouri* by the flat carapace with shallow cervical grooves, the outer margin of the external orbital angle being distinctly convex, and the epibranchial teeth being stouter with broader bases (versus the inflated carapace with relatively deeper cervical grooves, the outer margin of the external orbital angle being nearly straight or slightly concave, and the epibranchial teeth being relatively more slender with narrower bases in *L. barbouri*, cf. Rathbun, 1910: pl. 5, figs. 1, 2).

Lobothelphusa bagoensis, new species, is unlikely to be confused with *Lobothelphusa woodmasoni* (Rathbun, 1905). The latter is reportedly distributed in northern Myanmar and India (Rathbun, 1905; Bott, 1970). The new species can be easily distinguished from *L. woodmasoni* by its indistinct carapace regions, straight or gently concave frontal margin (Fig. 2A) (versus the carapace regions are distinct, frontal margin is concave in *L. woodmasoni*, cf. Rathbun, 1905: pl. 12, fig. 12; Bott, 1970: pl. 38, fig. 25), and the G1 terminal segment which is conical in shape, with the distal part slightly curved outward, and the pronounced dorsal fold extending to three-quarters length of the terminal segment (Figs. 2A, 3D, E, 6A, B) (versus the G1 terminal segment is narrowly conical in shape, with the distal part slightly curved inward, and without a dorsal fold in *L. woodmasoni*, cf. Bott, 1970: pl. 46, fig. 23).

***Lobothelphusa thewanica*, new species**

(Figs. 4, 5, 6D–F, 7E–G)

Material examined. Holotype: adult male (cw 31.44 mm, cl 26.14 mm, ch 15.38 mm, fw 10.96 mm), NNU16-BG1, Thewa Township, Pegu Range, Bago Division, 18.492°N, 96.387°E, 53 m asl, Myanmar (Fig. 1 light blue), coll. B. Shi, 11 May 2019.

Paratypes: adult male (cw 32.84 mm, cl 26.88 mm, ch 15.68 mm, fw 11.12 mm), NNU16-BG2; adult female (cw 29.26 mm, cl 25.69 mm, ch 14.73 mm, fw 11.24 mm), SEABRI-BG3; adult male (cw 30.26 mm, cl 24.13 mm, ch 14.44 mm, fw 9.13 mm), SEABRI-BG4; juvenile (cw 28.61 mm,

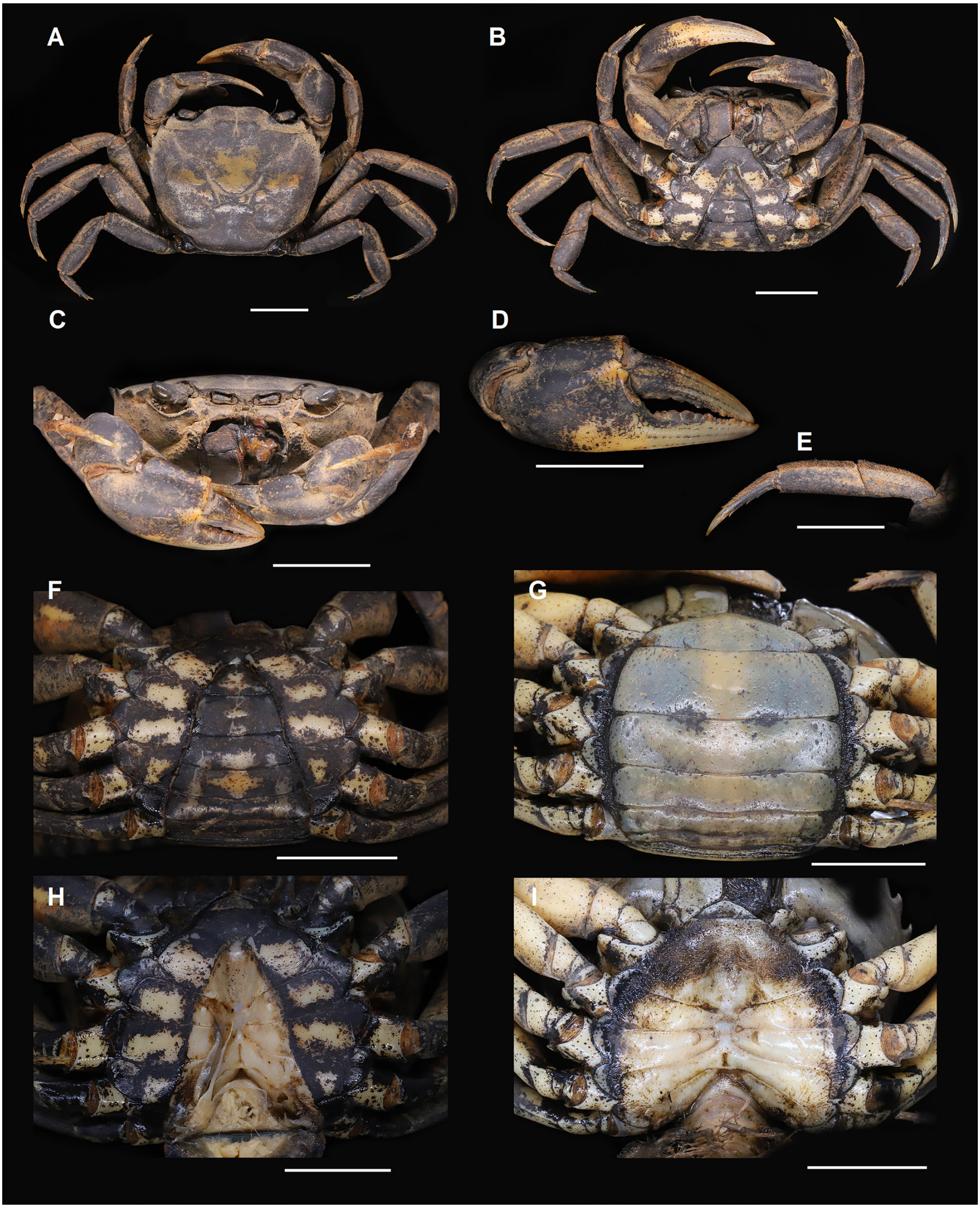

Fig. 4. *Lobothelphusa thewanica*, new species. A–F, H, holotype, male, 31.44 × 26.14 mm, NNU16-BG1; G, I, paratype, female, 32.84 × 26.88 mm, NNU16-BG2. A, dorsal view; B, ventral view; C, frontal view; D, major chela (dorsal view); E, right third ambulatory leg (dorsal view); F, G, ventral view showing anterior thoracic sternum and pleon; H, ventral view showing sterno-pleonal cavity with G1 in situ; I, thoracic sternum and vulvae. Scale bars = 1.0 cm.

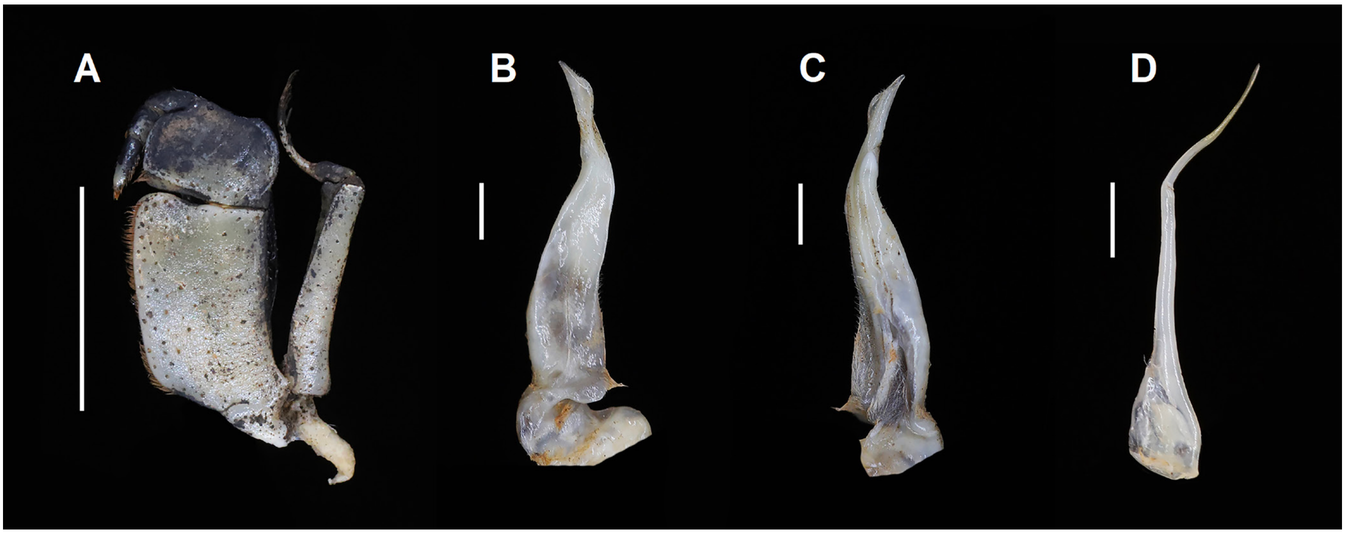

Fig. 5. *Lobothelphusa thewanica*, new species, holotype, male, NNU16-BG1. A, left third maxilliped (dorsal view); B, left G1 (dorsal view); C, left G1 (ventral view); D, left G2 (ventral view). Scale bars: A = 1.0 cm; B–D = 1.0 mm.

cl 23.57 mm, ch 13.67 mm, fw 8.78 mm), SEABRI-BG5; juvenile (cw 28.31 mm, cl 23.22 mm, ch 13.32 mm, fw 8.52 mm), SEABRI-BG6; Same location as holotype.

Description. Carapace subquadrate, slightly broader than long (cw/cl = 1.20; ch/cl = 0.58); dorsal surface smooth, gently swollen longitudinally and transversely; regions indistinct, cervical grooves developed, shallow, H-shaped groove well-developed (Fig. 4A). Epigastric cristae low, distinct, slightly rugose, separated by groove which opens up into inverted Y-shaped gap posteriorly, distinctly positioned anterior to postorbital cristae, separated from postorbital cristae by distinct narrow groove; postorbital cristae distinct, sinuous, slightly oblique, sharp, confluent with the first epibranchial teeth; regions behind epigastric and postorbital cristae smooth (Fig. 4A). Frontal margin slightly concave (fw/cw = 0.38), with very low, rounded granules; frontal region broad longitudinally (Fig. 4A). Antennular fossae rectangular when viewed from front; supraorbital margin sinuous, cristate; infraorbital margin sinuous, sloping downward, cristate; orbital region relatively broad; suborbital and pterygostomial regions granulose; eyes filling up most of orbital space; eyestalk short, stout; cornea moderately large, pigmented (Fig. 4C). External orbital angle well-developed, triangular, tip acute, outer margin convex, margins cristate, with deep cleft separating it from anterolateral margins; anterolateral margins gently convex, each with four prominent epibranchial teeth; epibranchial teeth 1–4 progressively smaller, tips directed anterolaterally, base of each tooth slightly broad; first and second epibranchial teeth distinctly broader; third and fourth epibranchial teeth slender; posterolateral margin sinuous; posterior carapace margin gently convex or straight; branchial region without oblique striae (Fig. 4A). Posterior margin of epistome with well-developed, triangular median tooth, lateral margins straight (Fig. 4C). Third maxilliped glabrous; ischium of third maxilliped rectangular, elongate longitudinally, ca. 0.65 times length of width, without median sulcus; merus squarish, ca. 1.52 times length of width; exopod reaching half-length of merus, with well-developed flagellum (Figs. 4B, C, 5A).

Chelipeds asymmetrical, glabrous, major chela distinctly larger; dorsal surface smooth; merus with well-developed subdistal spine on dorsal margin; carpus with strong, well-developed spine on inner distal angle; inner distal angle sinuous (Fig. 4A–C). Fingers of major chela with numerous teeth of different size, large gape when finger closed; fingers of minor chela similar to major chela; fingers slightly curved, equal in length to palm; palm longer than high; inner and outer surfaces inflated (Fig. 4A–D).

Ambulatory legs relatively long, slender, p3 longest, p5 shortest; p5 propodus relatively stouter than p2–p4 propodi; dactylus slightly curved, equal in length to propodus, with short, sharp chitinous spines on margins; outer edges with thick spongy tomentum (Fig. 4A, B, E).

Male thoracic sternum smooth; thoracic sternites s1/s2 completely fused; suture between thoracic sternites s2/s3 distinct; thoracic sternites s3/s4 fused, groove between sternites not discernible; sutures between thoracic sternites s4/s5, s5/s6, s6/s7, s7/s8 shallow, narrow (Fig. 4B, F, H). Pleonal locking mechanism with distinct, anteriorly directed tubercle on submedian part of sternite s5 (Fig. 4H). Narrow transverse ridge at the suture between thoracic sternites s7/s8 that interrupts the median line (Fig. 4H, I).

Male pleon narrowly triangular; telson with blunt apex and concave lateral margins, ca. 0.79 times length of width; somite 6 trapezoidal, ca. 2.12 times length of width, lateral margins straight; somites 4–6 trapezoidal, progressively less broad; lateral margins of somites 4–6 straight; lateral margins of somite 3 distinctly convex; suture between somites 5/4, 4/3 distinctly sinuous; somite 3 broader than somites 1 and 2 longitudinally; somite 2 longitudinally broader than somite 1; somite 1 longitudinally narrow (Fig. 4B, F); Female pleon ovate, covering the thoracic sternites when closed; telson

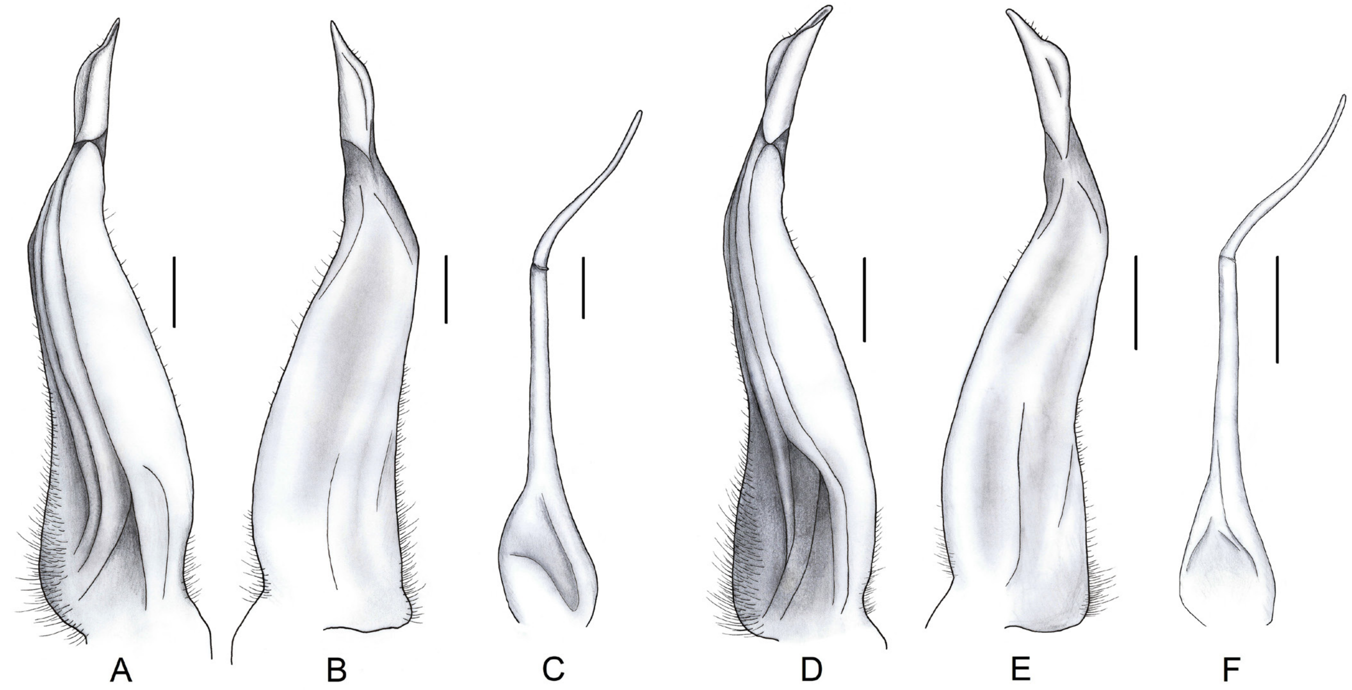

Fig. 6. Gonopods. A–C, *Lobothelphusa bagoensis*, new species, holotype, male, NNU16-DYX1; D–F, *Lobothelphusa thewanica*, new species, holotype, male, NNU16-BG1. A, D, left G1 (ventral view); B, E, left G1 (dorsal view); C, F, left G2 (ventral view). Scale bars = 1.0 mm.

broadly subtriangular, much broader than long, with slightly convex lateral margins; somites 5 longest, broader than long, with convex lateral margins; somites 4 and 6 almost equal; somites 1–3 progressively longer (Fig. 4G).

G1 slightly sinuous, slender, tip of terminal segment situated adjacent to pleonal locking structure in situ (Figs. 4H, 5B, C, 6D, E); groove for G2 on ventral surface; terminal segment relatively short, conical in shape, tip acute, distal part slightly curved outward, ca. 0.29 times length of subterminal segment; dorsal fold relatively high, extending along one-quarter to three-quarters of terminal segment, with rounded apex in medial position; subterminal segment gently convex on upper part of inner margin (Figs. 5B, C, 6D, E). G2 length equal to length of G1; distal segment long, ca. 0.48 times length of basal segment (Figs. 5D, 6F). Vulvae on sternite 6, semicircular, occupying ca. 0.50 times the length of the thoracic sternite 6, almost reaching suture between thoracic sternites s4/s5 (Fig. 4I).

Etymology. The species is named after the type locality, the township of Thewa, in the Pegu Range, Bago Division, Myanmar.

Colour in life. The adult animals are olive green dorsally with the ventral surfaces yellow. The chelipeds and ambulatory legs are pale yellow. The black colouration seen in the photographs is due to the black sediment that has strongly adhered to the exoskeleton. The thick spongy tomentum of the ambulatory legs is usually brown (Figs. 4, 7F, G).

Ecological note. Individuals were collected under stones and the layers of fallen leaves in the river or on its banks; the substrate consists mainly of stones and rocky rubble (Fig. 7E).

Remarks. The new species fits well within the morphological definition of the genus *Lobothelphusa*, particularly the flat carapace with indistinct dorsal regions, the third maxilliped ischium without a median sulcus, and the anterior margins of the ambulatory carpi, propodi, and dactyli with a thick spongy tomentum. *Lobothelphusa thewanica*, new species, is similar to *L. bagoensis*, new species, and *L. crenulifera* in the morphology of the postorbital cristae and the G1, but markedly distinct in some characters: (1) the carapace is subquadrate, the outer margin of the external orbital angle is convex, the epigastric cristae are positioned distinctly anterior to the postorbital cristae, and the third and fourth epibranchial teeth are slender (Fig. 4A) (versus the carapace is subtrapezoidal, the epigastric cristae are gently anterior or parallel to the postorbital cristae, and the third and fourth epibranchial teeth are stout in *L. bagoensis* and *L. crenulifera*, Fig. 2A, cf. Rathbun, 1905: pl. 12, fig. 11; Bott, 1970: pl. 38, fig. 23, pl. 45, fig. 21; the outer margin of the external orbital angle is more pronouncedly convex in *L. bagoensis*, Fig. 2A); (2) the G1 is slightly sinuous, with the terminal segment proportionately longer, ca. 0.29 times length of the subterminal segment, and the distal part is slightly curved outward (Figs. 5B, C, 6D, E) (versus the G1 is gently sinuous or straight, the terminal segment is relatively short, ca. 0.23 times length of the subterminal segment, and the distal part is gently curved outward in *L. bagoensis*, Figs. 3D, E, 6A, B; whereas the G1 is sinuous, the terminal segment is relatively short, ca. 0.21 times length of the subterminal segment, and the distal part is curved outward in *L. crenulifera*, cf. Bott, 1970: pl. 38, fig. 23); (3) the dorsal fold of the G1 terminal segment is relatively high, and extends along a quarter to three-quarters of the length of the terminal segment (versus the dorsal fold is low in *L. bagoensis* and *L. crenulifera*, Figs. 3D, E, 6A, B, cf. Bott, 1970: pl. 38, fig. 23; the dorsal fold extends to three-quarters of the length of the terminal

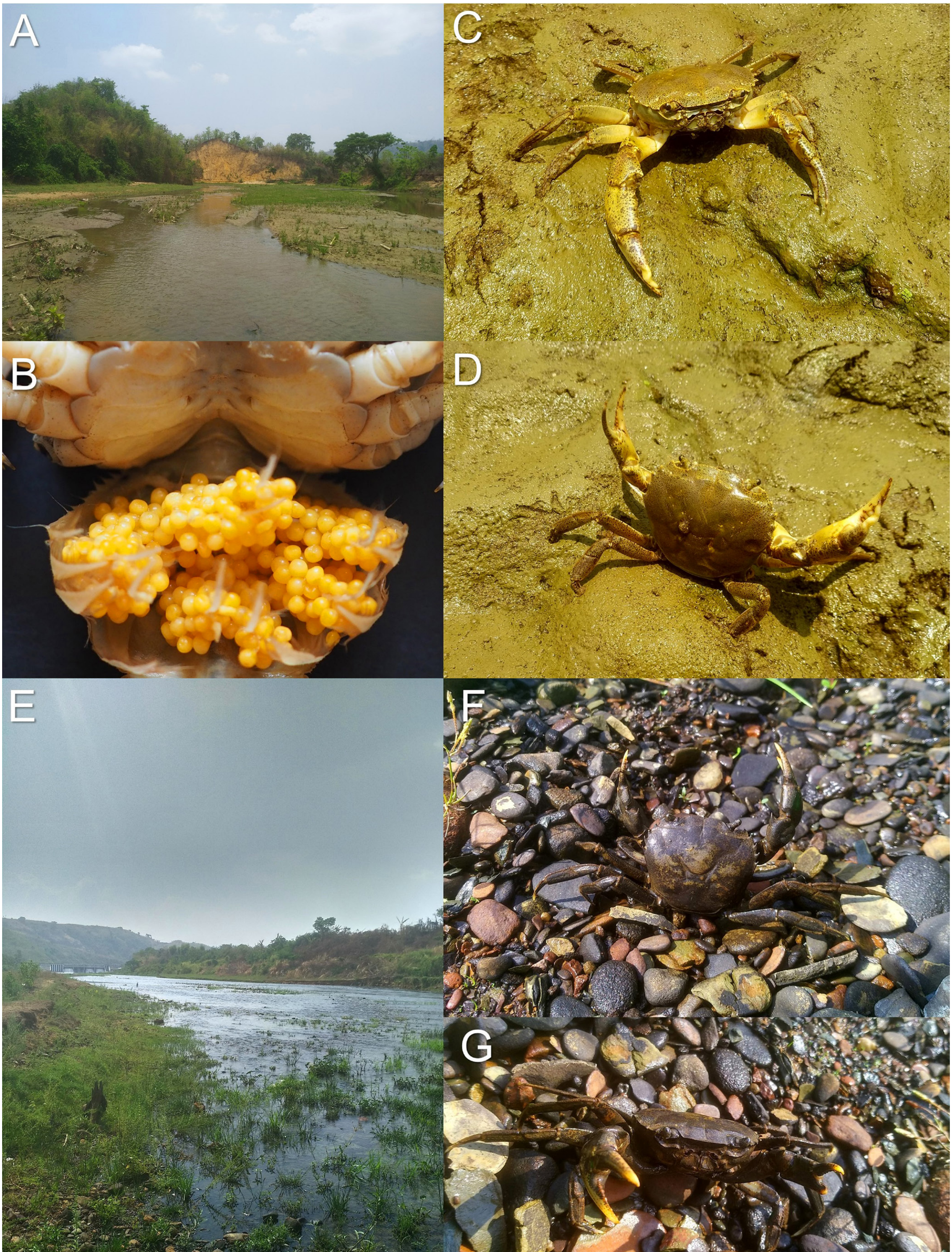

Fig. 7. Habitat and live colouration. A–D, *Lobothelphusa bagoensis*, new species: A, habitat; B, paratype, ovigerous female (SEABRI-DYX3); C, D, holotype, male (NNU16-DYX1). E–G, *Lobothelphusa thewanica*, new species: E, habitat; F, G, holotype, male (NNU16-BG1).

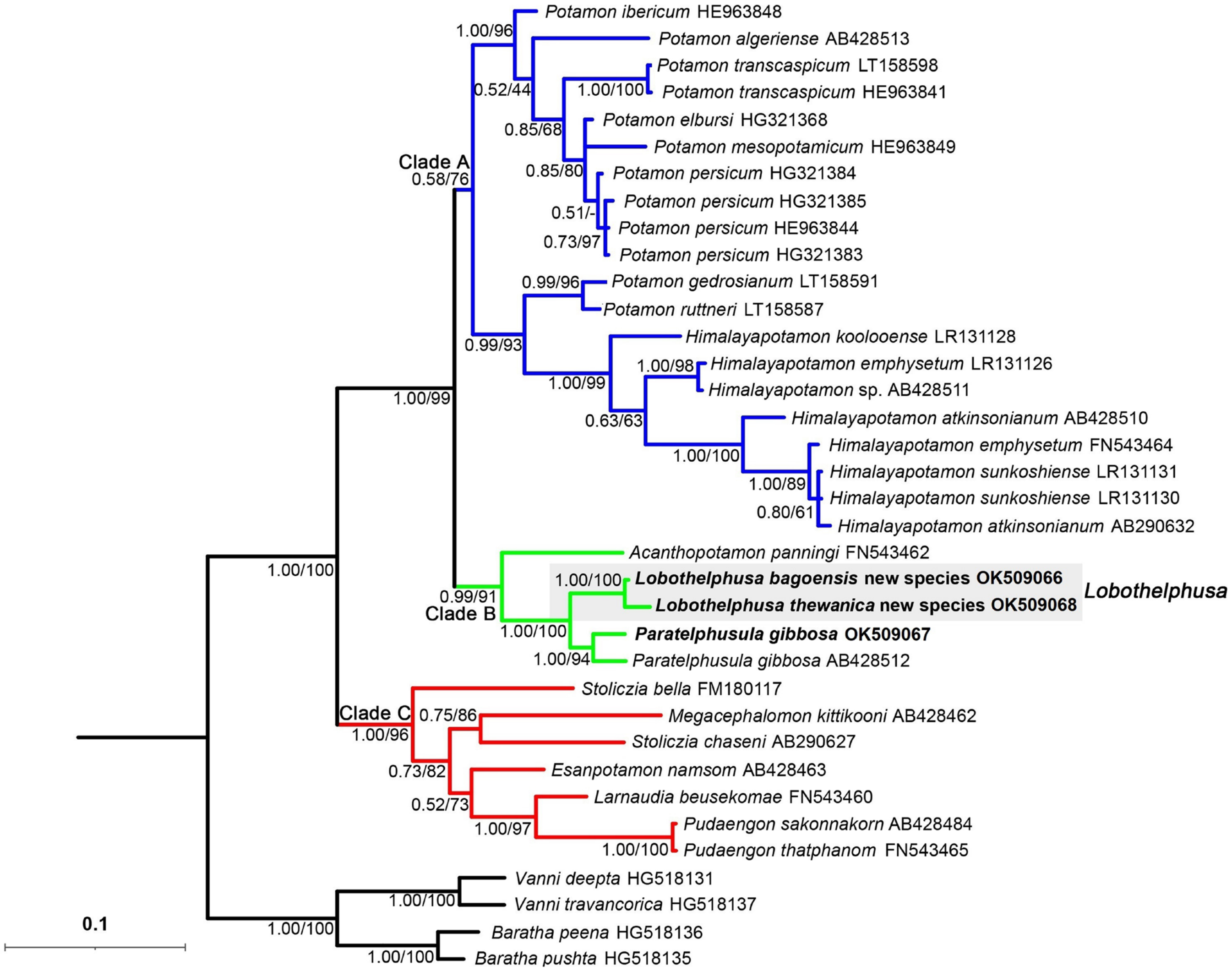

Fig. 8. The phylogenetic tree (BI and ML) for the *Lobothelphusa* species and other freshwater crabs based on 16S rDNA. Posterior probabilities and bootstrap values (PP/BV) are indicated on branches. The new species and new sequences in this study are indicated in bold.

segment in *L. bagoensis*, Figs. 3D, E, 6A, B); and (4) the G1 subterminal segment is slender, the upper part of the inner margin is gently convex (versus the upper part of the inner margin is convex in *L. bagoensis*, Figs. 3D, E, 6A, B; the upper part of the inner margin is slightly concave in *L. crenulifera*, cf. Bott, 1970: pl. 38, fig. 23).

RESULTS AND DISCUSSION

A total of three sequences of 16S rDNA were obtained from the two new species of *Lobothelphusa* and a specimen of *Paratelphusula gibbosa* in this study. The *P. gibbosa* specimen in the present study was collected from Oktwin Township (Fig. 1), about 150 km north of the type locality for this species ("Teikgyi" = Taik Kyi Township), and the morphological traits of the carapace, the epibranchial teeth, and the G1 completely agree with the holotype as described and figured by Ng & Kosuge (1997: pl. 814, figs. 1–3). Furthermore, the sequence of the 16S rDNA fragment from this specimen is also consistent with that reported by Shih et al. (2009) for *P. gibbosa*, with GenBank accession number AB428512.

A 510-bp sequence of the 16S rDNA was aligned, and the phylogenetic analysis (BI and ML) resulted in congruent tree topologies with some minor differences in the terminal lineages. The split of the Potamidae into Potaminae (Clade A and B, blue and green) and Potamiscinae (Clade C, red) is already well established and has been shown in many other studies (e.g., Shih et al., 2009, 2011; Ng et al., 2020). The species in clade A are from genera mainly distributed in Central Asia, whereas the species in clade B are mainly distributed in Myanmar. The species in Clade C are from the Indochina Peninsula region. The phylogenetic trees indicated that the two new species were nested within the Potaminae lineages in clade B with strong support (BPP/BS = 1.00/99). The two new species of *Lobothelphusa* are most closely related to *Paratelphusula* (represented by *P. gibbosa*; BPP/BS = 1.00/100). Furthermore, the present work is the first reported genetic information on *Lobothelphusa*, and has revealed that *Lobothelphusa* and *Paratelphusula* are probably sister taxa. This will need to be confirmed with the inclusion of additional species, especially the type species, from both genera.

Lobothelphusa and *Paratelphusula* are very similar in having the four prominent epibranchial teeth on the carapace anterolateral margin, the epigastric cristae positioned distinctly anterior to the postorbital cristae (Fig. 2A), and a narrow transverse ridge at the suture between thoracic sternites 7 and 8 (Fig. 2G, H) (Yeo, 2000; Yeo & Ng, 2007). Nevertheless, the two new species described here are immediately distinguishable from *Paratelphusula* by following important taxonomic characters: (1) carapace relatively lower, flatter, and gently convex transversely, with the branchial regions gently inflated or flat (Fig. 2A, C) (versus the carapace is very high, strongly swollen transversely and longitudinally, with the branchial regions strongly inflated in *Paratelphusula*; cf. Yeo, 2000; Yeo & Ng, 2007); (2) the antennular fossae are narrowly subtriangular to subrectangular (Fig. 2C) (versus the antennular fossae are clearly slit-like in *Paratelphusula*; cf. Yeo, 2000; Yeo & Ng, 2007); (3) the third maxilliped ischium is without the median sulcus (Fig. 3C) (versus the third maxilliped ischium with median sulcus in *Paratelphusula*; cf. Yeo, 2000; Yeo & Ng, 2007); and (4) the edge of ambulatory legs with thick spongy tomentum (Figs. 2A, B, D, 3B) (versus the ambulatory legs is glabrous in *Paratelphusula*; cf. Yeo, 2000; Yeo & Ng, 2007).

The genus *Paratelphusula* includes four species from Myanmar: *Paratelphusula burmensis* (Bott, 1966) distributed in Kachin Division, *Paratelphusula dayana* (Wood-Mason, 1871), the type species, distributed in Mandalay; *Paratelphusula gibbosa* distributed in Yangon Region; and *Paratelphusula peguensis* (Rathbun, 1905) distributed in Bago Division. We speculate that *Paratelphusula* species dispersed southward along the Irrawaddy River and adaptation to local habitats might have led to species divergence. The taxonomic position of *P. peguensis* may be doubtful. Yeo & Ng (2007) recognised *P. peguensis*, previously considered a synonym of *Lobothelphusa crenulifera* by Bott (1970), as a valid species on the basis of morphology. However, the morphological traits of *P. peguensis* are not fully consistent with the above-stated taxonomic characteristics of *Paratelphusula*, with the carapace morphology fitting better within the diagnostic characters of the genus *Lobothelphusa*. Therefore, we infer that *P. peguensis* may be grouped within the genus *Lobothelphusa*. However, better taxon representation in future morphological comparisons and genetic analyses are necessary in order to provide a full taxonomic revision of the affected genera.

The taxonomic positions of several *Lobothelphusa* species, e.g., *L. floccosa*, *L. woodmasoni*, and *L. barbouri*, remain uncertain in our view. The detailed description of the former is still missing. Alcock (1910) recorded that *L. floccosa* is similar to *L. crenulifera*, except the carapace is more convex. Bott (1970) regarded that *L. floccosa* is a synonym of *L. crenulifera*. Yeo & Ng (2007) resurrected *L. floccosa* as a valid species based on their examination of the syntypes, but without a more detailed explanation. In addition, the taxonomic position of *L. woodmasoni* is doubtful. It is similar to species of *Acanthopotamon* in the following features: the dorsal surface of the carapace is uneven and setose, and the dorsal flap of the G1 terminal segment is absent (cf. Rathbun, 1905: pl. 12, fig. 12; Bott, 1970: pl. 38, fig. 25, pl. 46, fig. 23) (versus the dorsal surface of the carapace is smooth, and the G1 terminal segment has a distinct dorsal flap in the *Lobothelphusa* species). With regard to biogeography, *L. woodmasoni* is distributed in India, which basically overlaps with the distribution of *Acanthopotamon* (Rathbun, 1905; Pati et al., 2019). We suspect that *L. woodmasoni* should be transferred to *Acanthopotamon* based on morphology and biogeographical insight. The historical record of *L. barbouri* from Buitenzorg (=Bogor) in Java by Rathbun (1910) is very far away from other species of *Lobothelphusa*. The morphology and distribution of *L. barbouri* needs further confirmation. *Lobothelphusa calva* is isolated in Upper Tenasserim, which could be explained by long-distance dispersal. The other four species, *L. bagoensis*, *L. thewanica*, *L. crenulifera*, and *L. floccosa* are mainly distributed in the Pegu Range. We infer that the Pegu Range might have played a critical role in allowing speciation of *Lobothelphusa* by restricting their dispersal. In addition, mountains also present a wide range of microhabitats with different ecological conditions, which can shape many unique and endemic species (Warren et al., 2014; Ye et al., 2016; Daru et al., 2017). Geographical and microecological isolation might have jointly driven the speciation of the genus *Lobothelphusa* in the Pegu Range.

Freshwater ecosystems in the tropics host diverse endemic freshwater crab faunas, and Myanmar is known for its regional biodiversity (Yeo et al., 2008; Cumberlidge et al., 2009, 2012). At least 15 genera of the family Potamidae have been recorded there (Yeo & Ng, 2007; Ng et al., 2008; Ng & Whitten, 2017). As a part of our research on the biodiversity of the freshwater crabs in Asia, we have collected more than 130 individuals of freshwater crabs from 17 localities in Myanmar, representing 11 species and 5 genera, including *Demanietta* (4 species), *Lobothelphusa* (2 species), *Paratelphusula* (1 species), *Indochinamon* (1 species), *Siamthelphusa* (2 species), and *Esanthelphusa* (1 species) (Shi et al., 2021). In recent years, many new potamid crabs have been reported from Myanmar: e.g., *Indawmon thanayei* Ng, Win Mar & Shih, 2020; *Potamiscus whitteni* Ng, Hla Htoo & Win Mar, 2020; *Indochinamon khinpyae* Ng & Win Mar, 2018; *Shanphusa ywarngan* Ng & Whitten, 2017; *Demanietta burmanica* Ng, 2018; *D. liui* Shi, Chen & Sun, 2020; and *D. lenya* Shi, Chen & Sun, 2020; as well as new material of *Inlethelphusa acanthica* Kemp, 1918 (Ng & Yeo, 2020). These suggest that knowledge on the freshwater crab fauna of Myanmar remains in a “discovery” phase. Further intensified survey efforts are urgently required for effective understanding of freshwater fauna diversity in the Indochina Peninsula region, a global hotspot of freshwater crabs.

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