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Revision of the Southeast Asian freshwater crab genus *Balssiathelphusa* Bott, 1969 (Crustacea, Decapoda, Brachyura, Gecarcinucidae)

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Lemurophusa empusa n. gen., n. sp., holotype, ♀ 24.2 × 18.5 mm (MZB Cru), Kalimantan.

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Revision of the Southeast Asian freshwater crab genus *Balssiathelphusa* Bott, 1969 (Crustacea, Decapoda, Brachyura, Gecarcinucidae)

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ABSTRACT
The systematics of the gecarcinucid genus *Balssiathelphusa* Bott, 1969 is revised. *Balssiathelphusa* has an atypical distribution pattern for a freshwater crab genus, with the four known species recorded from Sumatra, Borneo and Natuna Islands in the South China Sea. The type species, *Para-Perithelphusa sucki* Balss, 1937 [sic, see infra], is redescribed and figured, and the genus is redefined to include *B. sucki*, *B. cursor* Ng, 1986, from East Kalimantan in Indonesian Borneo, and a new species, *B. inopinata* n. sp., also from East Kalimantan. The type locality of *B. sucki* was reported as southeastern Sumatra, but the available evidence suggests the holotype was actually collected from South Kalimantan in Borneo. *Balssiathelphusa natunaensis* Bott, 1970, from Natuna Island, is transferred to a new monotypic genus, *Natunusa* n. gen., while *B. phasma* Ng & Guinot, 2014, collected from a cave in East Kalimantan, is referred to a separate genus, *Lemurophusa* n. gen. A new species, *L. empusa* n. gen., n. sp., is also described from another karst system in East Kalimantan, whereas a juvenile female from a nearby cave in East Kalimantan is treated as *Lemurophusa* sp. Particular attention was paid to the thoracic sternum and its sutures, to the median bridges between the sternites, as well to the median line, characters often overlooked but that are particularly useful in this group of small gecarcinucid crabs.

KEY WORDS
Borneo,
Sumatra,
Natuna Islands,
Kalimantan,
Gecarcinucoidea,
freshwater crab,
cave crab,
new genera,
new species.

RÉSUMÉ

Révision du genre de crabes d'eau douce d'Asie du Sud-Est Balssiathelphusa *Bott, 1969 (Crustacea, Decapoda, Brachyura, Gecarcinucidae).*

La systématique du genre gécarcinucidé *Balssiathelphusa* Bott, 1969 est révisée. *Balssiathelphusa* a une distribution atypique pour un crabe d'eau douce, ses quatre espèces étant reportées de Sumatra, Bornéo, et des îles Natuna dans la mer de Chine méridionale. L'espèce type, *Para-Peri-thelphusa sucki* Balss, 1937 [sic, voir ci-dessous], est redécrite et figurée, et le genre est redéfini pour n'inclure que *B. sucki*, *B. cursor* Ng, 1986, du Kalimantan Est dans la partie indonésienne de Bornéo, et une espèce nouvelle, *B. inopinata* n. sp., également originaire du Kalimantan Est. La localité type de *B. sucki* a été rappportée comme étant du sud est de Sumatra, mais les données disponibles montrent que l'holotype a été en fait récolté du Kalimantan Sud à Bornéo. *Balssiathelphusa natunaensis* Bott, 1970, de l'île Natuna, est transférée dans un nouveau genre monotypique, *Natunusa* n. gen., tandis que *B. phasma* Ng & Guinot, 2014, récoltée dans une grotte du Kalimantan Est, est attribuée à un genre distinct, *Lemurophusa* n. gen. Une espèce nouvelle, *L. empusa* n. gen., n. sp., est décrite d'un autre système karstique du Kalimantan Est, tandis qu'une femelle juvénile d'une cavité proche du Kalimantan Est est traitée comme *Lemurophusa* sp. Une attention particulière a été apportée au sternum thoracique, à ses sutures, aux ponts médians entre les sternites, ainsi qu'à la ligne médiane, caractères souvent négligés mais particulièrement utiles chez ces petits crabes gécarcinucidés.

MOTS CLÉS
Bornéo,
Sumatra,
îles Natuna,
Kalimantan,
Gecarcinucoidea,
crabe d'eau douce,
crabe cavernicole,
genres nouveaux,
espèces nouvelles.

INTRODUCTION

The gecarcinucid genus *Balssiathelphusa* was established by Bott (1969) for *B. sucki* (Balss, 1937) its sole and type species supposedly from southeastern Sumatra. A second species was subsequently added by Bott, *B. natunaensis* Bott, 1970, from the Natuna Islands in the southern part of the South China Sea (Bott 1970). A third species, *B. cursor* Ng, 1986, was subsequently described from eastern Kalimantan, Indonesia, in Borneo (Ng, 1986), with a fourth species, *B. phasma* Ng & Guinot, 2014, was described from a cave in East Kalimantan.

Balssiathelphusa was placed by Bott (1969, 1970) in the subfamily Spiralothelphusinae Bott, 1968, family Parathelphusidae Alcock, 1910, probably on account of its distinct frontal median triangle and twisted male first gonopod. The upper margin of the frontal median triangle in *Balssiathelphusa*, however, is not always completely confluent with the supraorbital margins, and the triangle formed is usually relatively small. This condition appears to be intermediate between the structures observed in typical gecarcinucids like *Parathelphusa* H. Milne Edwards, 1853 and *Sundathelphusa* Bott, 1969. In *Parathelphusa*, the triangle is large and prominent, with the upper margin cristate and clearly confluent with the supraorbital margin; while in *Sundathelphusa* Bott, 1969, the triangle is usually much less distinct, with the upper margin indistinct, separated from or not distinctly confluent with the supraorbital margin. Holthuis (1979) noted that the name Gecarcinucidae Rathbun, 1904, has precedence over Parathelphusidae Alcock, 1910. The value of the frontal median triangle in the higher classification of the Gecarcinucidae was also queried by Holthuis (1979: 33) who commented, "that either the presence or absence of the frontal triangle is not of the great importance Bott attached to it". Ng (1986b: 275) also questioned the usefulness of the frontal triangle in their systematics, noting that "it may not prove to be reliable". Ng & Sket (1996) treated Sundathelphusidae as a junior subjective synonym of Gecarcinucidae, arguing that the recognition of two families based on the frontal median triangle character alone was not justified. This synonymy has been followed ever since (see Ng *et al.* 2008; Cumberlidge & Ng 2009).

At the genus level, the form of the frontal median triangle can be a useful distinguishing character but is unlikely to be phylogenetically informative. The first male gonopod is at present the most reliable means of separating *Balssiathelphusa* from related gecarcinucid genera. In general form, the male first gonopod resembles most closely that of *Thelphusula* Bott, 1969 *s. str.* In *Thelphusula*, however, the frontal median triangle is neither complete nor as fully formed (except in *T. baramensis* (De Man, 1902)) (see Ng & Tan 1999). Both genera are also quite similar externally and their male second gonopods have short to very short distal articles.

The distribution of *Balssiathelphusa* is unusual, being disjunct, with the four known species recorded from widely separated localities – one in southeastern Sumatra, one in Natuna Island in the South China Sea, and two in East Kalimantan. This was one of only two genera in Southeast Asia with such a distribution, the other being *Adeleana* Bott, 1969, which has species in Sumatra and Borneo. Ng (2025) revised *Adeleana* and has shown it to belong to three separate genera. Ng *et al.* (2023: 13) discussed the possibility of *Balssiathelphusa* being polyphyletic. They noted that Klaus *et al.* (2009: 520) had showed that *B. natunaensis* and *B. cursor* belonged to a "Malesian-Australian group" but in two separate lineages; with *B. natunaensis* coming out in a subclade by itself, while *B. cursor* clustered (with poor support) with *Perithelphusa* De Man, 1899, *Stygothelphusa* Ng, 1989, and *Bakousa* Ng, 1995. Like Ng & Guinot (2014: 628) who also noted that the genus may be heterogeneous, Ng *et al.* (2023: 13) argued that any attempt to revise *Balssiathelphusa* would need a better understanding of the type species, *B. sucki*.

The present paper redescribes and refigures the type species, *Balssiathelphusa sucki*, and revises the genus. Detailed comparisons of the four *Balssiathelphusa* taxa revealed differences that warrant the recognition of three genera, two of which are here described as new. *Balssiathelphusa natunaensis* is here referred to a new monotypic genus, *Natunusa* n. gen., while *B. phasma* Ng & Guinot, 2014 is transferred to *Lemurophusa* n. gen. A second new species of *Lemurophusa* n. gen. is also described from East Kalimantan in Indonesian Borneo.

MATERIAL AND METHODS

The terminology used follows Ng (1988) and Davie *et al.* (2015). The measurements of the carapace, in millimetres, are of the maximum width and length, respectively. The carapace height is measured (as a straight line) from the base of the pterygostomial region (in frontal view) to the highest point of the gastric region. The frontal width is measured across the angles where they curve to meet the supraorbital margins.

The island of Borneo is under the jurisdiction of three different countries: Indonesia, Malaysia and Brunei. Indonesia refers to the island as Kalimantan, where five provinces are recognised (North, South, East, West and Central), each with various constituent regencies. The Natuna Islands, which belong to Indonesia and part of the Riau Province, are a relatively isolated group of 154 islands in the North Natuna Sea in the southern part of the South China Sea, with the largest being Natuna Island (see Ng *et al.* 2023).

Some of the recent specimens were obtained during two French speleological expeditions in 2007 and 2010 to the Mangkalihat Peninsula, in East Kalimantan, Indonesian Borneo. These expeditions explored various caves during which freshwater crabs were collected. 'Expédition Spéléologique à Bornéo' in 2007 (Lips *et al.* 2007) collected in Gua Kambing Cave (1°09.444'N, 117°28.479'E) and Kecabe Cave (1°38.018'N, 117°24.240'E). One species, *Balssiathelphusa phasma* Ng & Guinot, 2014 was described from Gua Kambing Cave by Ng & Guinot (2014) (here transferred to *Lemurophusa* n. gen.). Specimens from Kecabe Cave were examined in this study and are here described as a new *Lemurophusa* species. A second French speleological expedition 'Borneo 2010' (Lips *et al.* 2010) collected two species in two caves of the Merabu karst in East Kalimantan. In the Lubang Gedung Cave, a new potamid genus was described, *Ngan* Guinot & Rodríguez Moreno, 2024 (see Guinot & Rodríguez Moreno 2024). From the Lubang Tebot Cave, an unidentified juvenile female gecarcinucid specimen with slightly olive-shaped eyes and long ambulatory legs was obtained (Guinot & Rodríguez Moreno 2024). A re-examination of this juvenile female has shown that it also belongs to the new genus *Lemurophusa* n. gen. from Kecabe Cave; it is provisionally assigned to this genus, although its specific status remains uncertain.

A note, however, on the thoracic sternum is necessary. Guinot *et al.* (2013) elaborated on the different kinds of sternite arrangement in various brachyuran groups, noting the various degrees of fusion as well as pattern of lines, grooves and sutures separating them. Their nomenclature is followed here. Male and female specimens of the same species have essentially the same structure, but the condition in females is generally less pronounced. The median line (longitudinal median groove) visible externally between various sternites marks a prominent vertical longitudinal median plate present in the axial skeleton. The recognition of two subfamilies of Potamidae, Potaminae Ortmann, 1896 and Potamiscinae Bott, 1970 on the basis of the male thoracic sternal structure, was first made by Yeo & Ng (2004: 1224, figs 1, 2; 2007: 274, fig. 1). Potamines possess a distinct median bridge-like structure that interrupts the suture between thoracic sternites 7 and 8, thereby affecting the structure of the median plate; while potamiscines have the suture between thoracic sternites 7 and 8 complete and lack a bridge-like structure (see also Guinot *et al.* 2013: 266). The presence of a transverse bridge-like structure (here referred to onwards for convenience as a "bridge") also interrupts the distal and/or proximal edges of the median line between the two sides of each sternite. When absent, the median line between sternites is continuous, and this corresponds to a continuous median plate (see Guinot *et al.* 2013). The median line and associated median plates have also been used as a key character for the systematics of the American freshwater crabs of the family Trichodactylidae H. Milne Edwards, 1853 (Magalhães & Türkay 1996). Sakai *et al.* (2006) also used the arrangement of the median lines and plates in their revision of the varunid genus *Helice* De Haan, 1833, although their discussion and figures on how these characters are used is a bit confusing. In revising gecarcinucid *Adeleana* Bott, 1969, Ng (2025) also reported that there is a gap between sternites 6 and 7 (i.e., the bridge mentioned above) which interrupts the median line between sternites 6 and 7. The median line is continuous across sternites 7 and 8 (and not just sternite 8 as noted by Ng 2025). In some taxa such as *Niahusa chapmani* (Holthuis, 1979), the median line on sternite 6 is actually very wide, forming a triangular depression (Ng 2025: fig. 8C).

ABBREVIATIONS

a.s.l.	above sea level;
m	metres;
G1	first gonopod;
G2	second gonopod;
s3/4-s7/8	suture between thoracic sternites 3 and 4 - sternites 7 and 8.

Institutions

MNHN	Muséum national d'Histoire naturelle, Paris;
MRSN	Museo Regionale di Scienze Naturali (previously Museum of Zoology in the University of Turin, MRSN), Torino;
MZB	Museum Zoologicum Bogoriense, Cibinong, Bogor;
RMNH	Naturalis Biodiversity Centre, Biodiversity Institute (ex Rijksmuseum van Natuurlijke Historie), Leiden;
ZMH	Centre for Taxonomy and Morphology, Museum of Nature Hamburg, Hamburg;
ZRC	Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore.

SYSTEMATICS

Superfamily Gecarcinucoidea Rathbun, 1904
Family Gecarcinucidae Rathbun, 1904

Genus *Balssiathelphusa* Bott, 1969

Balssiathelphusa Bott, 1969: 364; 1970: 98. — Ng 1986a: 207.

Type species. — *Para-Peri-thelphusa sucki* Balss, 1937, by original designation.

Included species. — *Balssiathelphusa sucki* (Balss, 1937), *B. cursor* Ng, 1986; *B. inopinata* n. sp.

Diagnosis. — Carapace transversely ovate, wider than long, carapace high, height to width ratio 0.5; epigastric cristae low but visible; postorbital cristae low, just visible; frontal margin divided into two low lobes; frontal median triangle distinct, with dorsal crista in two parts; external orbital tooth with outer margin granulated, uneven, more than twice length of inner margin; epibranchial tooth low but distinct, separated from margin by notch; rest of anterolateral margins distinctly convex; posterolateral margin distinctly converging towards posterior carapace margin; suborbital margin without proximal tooth; epistome relatively long, width to length ratio 6.2-6.5, posterior margin with distinct subtriangular lobe, separated from lateral margin by long fissure, each lateral margin sinuous, with low lobe; third maxilliped exopod with flagellum that is as long as width of merus; ambulatory legs relatively short, length to width ratio of fourth merus 3.2; male thoracic sternum not prominently wide, length to width ratio of anterior thoracic sternites 0.4-0.5; median transverse bridges between sternites 5 and 6, and sternites 6 and 7, bridges interrupting median line on sternites 5-8; median line on sternite 5 deep, not reaching level of press-button tubercles; inner edges of s4/5 ending near median part of sternopleonal cavity, not reaching s5/6; male sternopleonal cavity deep, reaching imaginary line connecting proximal edges of cheliped coxae; male pleonal locking tubercle peg-like, positioned on median part of sternite 5; male pleon T-shaped, somite 6 elongate, length to width ratio 1.3; thoracic sternite 8 clearly exposed when pleon closed; G1 relatively slender, subterminal article with basal part wide, gradually tapering towards terminal article, terminal article demarcated by groove, terminal to subterminal article length ratio 0.26-0.32, terminal article relatively long, gently curved upwards, with sharp tip, outer lateral surfaces with numerous long and short setae; G2 shorter than G1, distal article short, 0.11-0.18 times length of basal article; vulvae not known.

Remarks

The present revision restricts *Balssiathelphusa* for just the type species, *B. sucki* (Balss, 1937), *B. cursor* Ng, 1986, and a new species from East Kalimantan. There are no major differences at the generic level that separate them even though their respective type localities are from different islands. Southeastern Sumatra (type locality for *B. sucki*) is some 1400 km southeast from Samarinda in East Kalimantan (type locality for *B. cursor*), and these locations are separated by the Java Sea. During the last glacial event, however, these areas would all have been dry land and connected by forests (Hall 1996; Voris 2000; Lohman *et al.* 2011), and the distribution of the genus would have been more continuous. The forests of Central and South Kalimantan, in any case, are poorly explored, so it seems likely that more species of *Balssiathelphusa s. str.* may be present there.

Balssiathelphusa sucki (Balss, 1937)
(Figs 1; 2; 6A-F; 16A)

Para-Peri-thelphusa sucki Balss, 1937: 147, figs 1-3.

Balssiathelphusa sucki – Bott 1969: 364; 1970: 98, pl. 17 figs 6-8, pl. 29 fig. 66. — Ng *et al.* 2008: 69 [in list]. — Cumberlidge *et al.* 2009: appendix [in list].

Material examined. — **Holotype** • ♂ 21.2 × 17.1 mm; "southeast Sumatra"; coll. F. Suck; no date (see later); ZMH-K-003545.

Diagnosis. — Epigastric cristae with rugae relatively diffuse, strongest anteriorly; epibranchial tooth distinct, external orbital tooth separated from margin by deep notch; anterolateral margin strongly convex; lateral parts of anterolateral and branchial regions covered with numerous short, oblique striae; dorsal crista of frontal median triangle with median angle; median lobe of posterior margin of epistome subtriangular; outer surface of third maxilliped weakly punctate; outer surfaces of chelae strongly punctate and granulate; male telson length to width ratio 1.4; G1 gently sinuous, ratio of terminal to subterminal article lengths 0.26, terminal article gently curved upwards; G2 distal article 0.11 times length of basal article; vulva not known.

Distribution. — Supposedly from southeast Sumatra, but probably from Tanjung in South Kalimantan, Indonesia. As noted earlier, the disjunct distributions observed in some Southeast Asian gecarcinucid genera recognised by Bott (1969, 1970) (e.g., *Adeleana*) are due to the incorrect inclusion of poorly known taxa (see Ng 2025). The situation with *Balssiathelphusa* and its type species, which is supposedly known "only from Sumatra" while congeners occur in Borneo, is different as it is probably the result of mislabelling (see earlier).

Description

Male

Carapace transversely ovate, wider than long, width to length ratio 1.2; carapace high when viewed frontally, height to width ratio 0.5; dorsal surface gently convex, branchial regions appearing swollen in frontal view (Fig. 1A-C). Dorsal surface of carapace with regions well defined; gently rugose to smooth; lateral parts of anterolateral and branchial regions covered with numerous short, oblique striae; mesogastric, urogastric, cardiac and intestinal regions with fine granules to smooth; suborbital, subhepatic, pterygostomial and sub-branchial regions with distinct striae (Fig. 1C). Epigastric cristae low, strongest anteriorly but diffused posteriorly, visibly separated by distinct Y-shaped furrow; postorbital cristae low, just discernible (Fig. 1C). Cervical groove shallow; H-shaped median gastric groove distinct (Fig. 1A, B). Frontal margin divided into two low lobes, separated by shallow concavity; margin of each lobe gently convex, confluent with supraorbital margin; frontal median triangle distinct, with dorsal crista in two parts meeting at an angle medially, fused with lateral cristae (Fig. 1A-C). External orbital tooth with outer margin granulated, uneven, outer margin about 2.5 times length of inner margin; epibranchial tooth distinct, low, separated from margin by deep notch; rest of anterolateral margins distinctly convex, cristate, lined with striae (Fig. 1A, B). Posterolateral margin almost straight, distinctly converging towards straight posterior carapace margin (Fig. 1A, B). Orbits subovate; eye filling orbital space; eye peduncle relatively short, stout; cornea large, pigmented (Figs 1A-D). Supraorbital margin

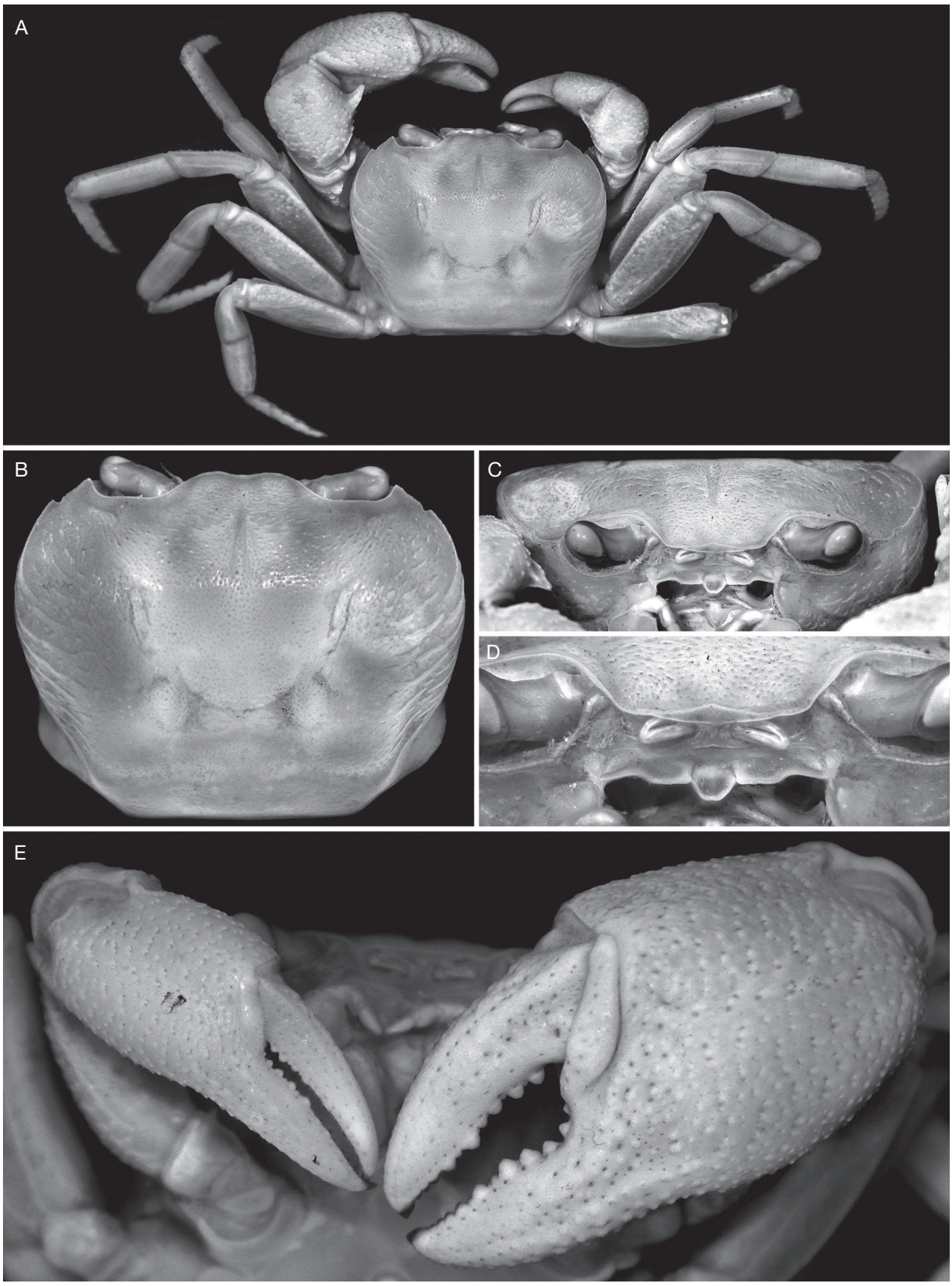

FIG. 1. — *Balssiathelphusa sucki* (Balss, 1937), holotype, ♂ 21.2 × 17.1 mm (ZMH-K-003545), "Sumatra": **A**, overall dorsal habitus; **B**, dorsal view of carapace; **C**, frontal view of cephalothorax; **D**, frontal median triangle, antennules, antennae and epistome; **E**, outer view of chelae.

smooth, almost straight medially (Fig. 1B, C). Suborbital margin concave, lined with granules, entire, without proximal tooth (Fig. 1C, D). Antennae short, not reaching cornea of eyes; antennules short, folding transversely in narrow fossae (Fig. 1C, D). Epistome relatively long, width to length ratio 6.5; posterior margin with distinct subtriangular lobe, separated from lateral margin by long fissure; each lateral margin sinuous, with low lobe (Fig. 1C, D). Mandibular palp with three articles; terminal article distinctly bilobed.

Third maxillipeds covering most of buccal cavity when closed; outer surfaces relatively smooth, with scattered punctae and small granules; ischium subrectangular, with distinct median oblique groove; merus subquadrate, just wider than long, anteroexternal angle rounded, not distinctly expanded; exopod relatively slender, reaching middle of merus, with distinct flagellum that is as long as width of merus (Fig. 2D, F).

Chelipeds asymmetrical (Figs 1A, E; 2A, B). Anterior margin of basis-ischium with strong sharp granules; margins of merus lined with prominent tubercles and granules, appearing gently serrated (Fig. 2F). Outer surface of carpus rugose, with strong tooth on inner distal margin (Figs 1A; 2A). Outer surfaces of chelae strongly granulated, punctate (Figs 1A, E; 2A, B). Fingers of major chela stout, gently curved, shorter than palm; cutting edges of both fingers with variously sized teeth; dorsal margin of dactylus and ventral margin of pollex with distinct rounded granules (Figs 1A, E; 2A). Fingers of minor chela longer, more slender, subequal in length to palm (Figs 1A, E; 2B).

Ambulatory legs relatively short; second pair longest, last pair shortest (Fig. 1A). Outer surface of merus slightly rugose, dorsal margin weakly serrated, subcristate, with subdistal angle but no obvious spine or tooth; length to width ratio of fourth merus 3.2; carpus relatively smooth, outer surfaces of first to third legs with low submedian crista, that on fourth leg smooth; outer surface of propodus smooth; dactylus relatively short, gently curved, quadrate in cross section, margins with short, sharp corneous spines (Figs 1A; 2C).

Thoracic sternum punctate, not distinctly wide, length to width ratio of anterior thoracic sternites 0.5 (Fig. 2E-H). Sternite 1 small, triangular, separated from sternite 2 by low ridge; sternites 2-4 completely fused except for lateral notches demarcating sternites 3 and 4 (Fig. 2E, F); distinct median transverse bridges present between sternites 5 and 6, and sternites 6 and 7, bridges interrupting median line on sternites 5-8; median line on sternite 5 deep, not reaching level of press-button tubercles; inner edges of s4/5 ending near median part of sternopleonal cavity, not reaching s5/6 (Figs 2E; 16A). Penis coxal, on condyle of coxa of fourth ambulatory leg. Sternopleonal cavity deep, reaching imaginary line connecting proximal edges of cheliped coxae (Fig. 2E, F). Male pleonal locking tubercle peg-like, positioned on median part of sternite 5 (Fig. 2E).

Pleon T-shaped, all somites and telson free; telson elongate, triangular, length to width ratio 1.4, lateral margins almost straight, shorter than somite 6; somite 6 elongate, length to width ratio 1.3, lateral margins distinctly concave; somites 3-5 trapezoidal, gradually decreasing in width; somite 2 subrectangular, very wide, reaching bases of coxae of fourth ambulatory legs; somite 1 longitudinally narrow, subequal in width to somite 2 (Fig. 2F-H); thoracic sternite 8 clearly exposed when pleon closed (Fig. 2G, H).

G1 relatively slender; subterminal article with basal part wide, gradually tapering towards terminal article, outer margin gently concave; terminal article clearly demarcated by groove; terminal to subterminal article length ratio 0.26, terminal article relatively long, gently curved upwards, proximal part wide, distal part narrowing to sharp tip which distinctly curves upwards, outer lateral surfaces with numerous long and short setae (Fig. 6A-E). G2 shorter than G1; distal article short, 0.11 times length of basal article (Fig. 6F).

Female

Not known.

Remarks

This species was originally described from one adult male and two juveniles from an unspecified location in southeastern Sumatra. No other data is available. The largest male was designated a "type" by Balss (1937) and is here treated as the holotype. The species has never been collected again since.

Balss (1937: 231) used an unusual way of denoting the genus and subgenus for freshwater crabs – this species was described as "*Para-Peri-thelphusa sucki* Balss, 1937" but there is no genus named "*Para-Peri-thelphusa*". It is quite clear from his introduction that his intention was to abbreviate the genus name *Parathelphusa* H. Milne Edwards, 1853 and subgenus name *Perithelphusa* De Man, 1899, for the species; and did not intend to establish a new taxon called "*Paraperithelphusa*". Balss (1934) had done something similar earlier when naming other freshwater crabs and this was discussed by Ng (2025: 17). This orthography for supraspecific taxa has not since been used by any worker.

Balss (1937) listed the species as collected by "Fritz Suck" from southeast Sumatra, and the labels in the original bottle state this clearly. The problem is that there is no record of Fritz Suck actually ever being in Sumatra. All references we have managed to find that refer to material collected by Fritz Suck are only from southeast Borneo, near the town of Tandjung (now Tanjung) that is today South Kalimantan (e.g., see Breddin 1900, 1912; Forel 1901; Schenkling 1902; Wheeler 1919; Yaakop *et al.* 2005; Seehausen & Dow 2016; Thofern *et al.* 2021). Tanjung (also known as Tanjung Tabalong) is both a town and a district and is today the administrative centre of the Tabalong Regency in the Province of Kalimantan Selatan (South Kalimantan). In addition, the Official Gazette of the city of Hamburg (1896) noted that one of the gifts to the Hamburg Museum in 1895 was by "[…] von Herrn Fritz Suck sehr werthvolle Sammelausbeute von Südost-Borneo, bestehend in Säugethieren, Vögeln, Reptilien, Amphibien, Molluske, Krebsen, ea. 2000 Insekten, Tansendfüßen [sic] und Spinnen" [from Mr. Fritz Suck, a very valuable collection from Southeast Borneo, consisting of mammals, birds, reptiles, amphibians, molluscs, crabs, approximately 2000 in-

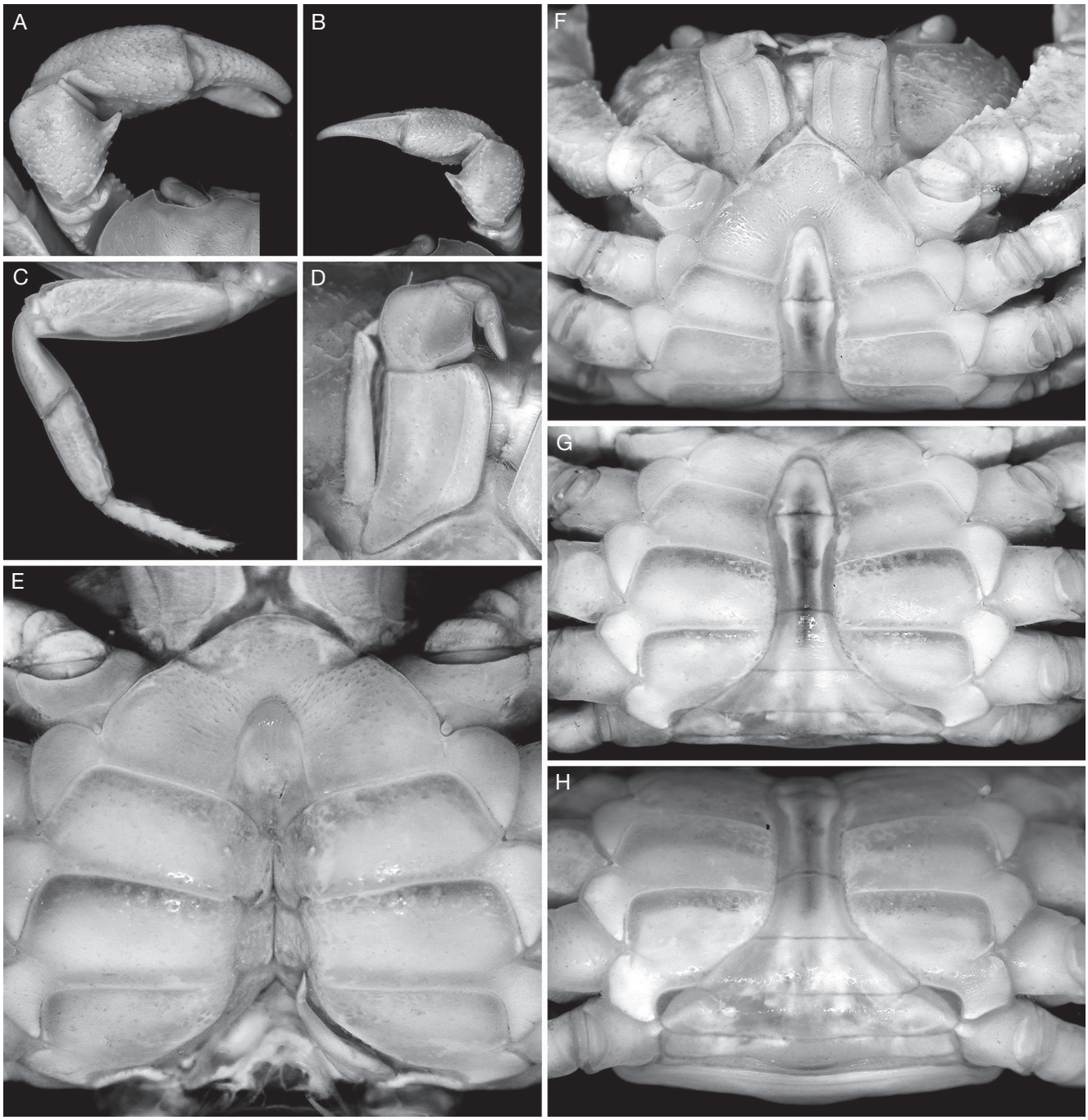

FIG. 2. — *Balssiathelphusa sucki* (Balss, 1937), holotype, ♂ 21.2 × 17.1 mm (ZMH-K-003545), "Sumatra": **A**, dorsal view of left cheliped; **B**, dorsal view of right cheliped; **C**, right fourth ambulatory leg; **D**, right third maxilliped; **E**, sternopleonal cavity; **F**, anterior thoracic sternum, telson and pleonal somites 5 and 6; **G**, thoracic sternum, telson and pleonal somites 2-6; **H**, posterior thoracic sternum and pleonal somites 1-6. A and B photographed to same scale.

sects, millipedes and spiders]. It would thus appear that the original specimen of *B. sucki* collected by Fritz Suck from southeast Borneo was accidentally labelled as being from southeast Sumatra instead. This also makes more sense as the type locality of *B. cursor*, a species morphologically similar to *B. sucki*, is in East Kalimantan.

Nothing is known about the biology of *B. sucki*, but, considering its morphology, it is probably similar to *B. cursor*, occurring in swamp forest habitats.

Balssiathelphusa cursor Ng, 1986
(Figs 3-5; 6G-M; 16B)

Balssiathelphusa cursor Ng, 1986a: 207, figs 1, 2. — Ng *et al.* 2008: 69 [in list]. — Cumberlidge *et al.* 2009: appendix [in list]. — Ng & Guinot 2014: 623. — Grinang 2022: 391 [in list].

MATERIAL EXAMINED. — **Holotype. Indonesia** • ♂ 15.4 × 13.3 mm; Wanariset Research Swamp Forest; east Kalimantan; *c.* 01°00'S, 117°00'E; leg. Rahayuningsih; 8.III.1981; MZB Cru Nr. 1279a.

FIG. 3. — *Balssiathelphusa cursor* Ng, 1986, paratype, ♂ 15.6 × 13. 4 mm (ZRC 1989.3036), Kalimantan: **A**, overall dorsal habitus; **B**, dorsal view of carapace; **C**, frontal view of cephalothorax; **D**, frontal median triangle, antennules, antennae and epistome; **E**, outer view of chelae.

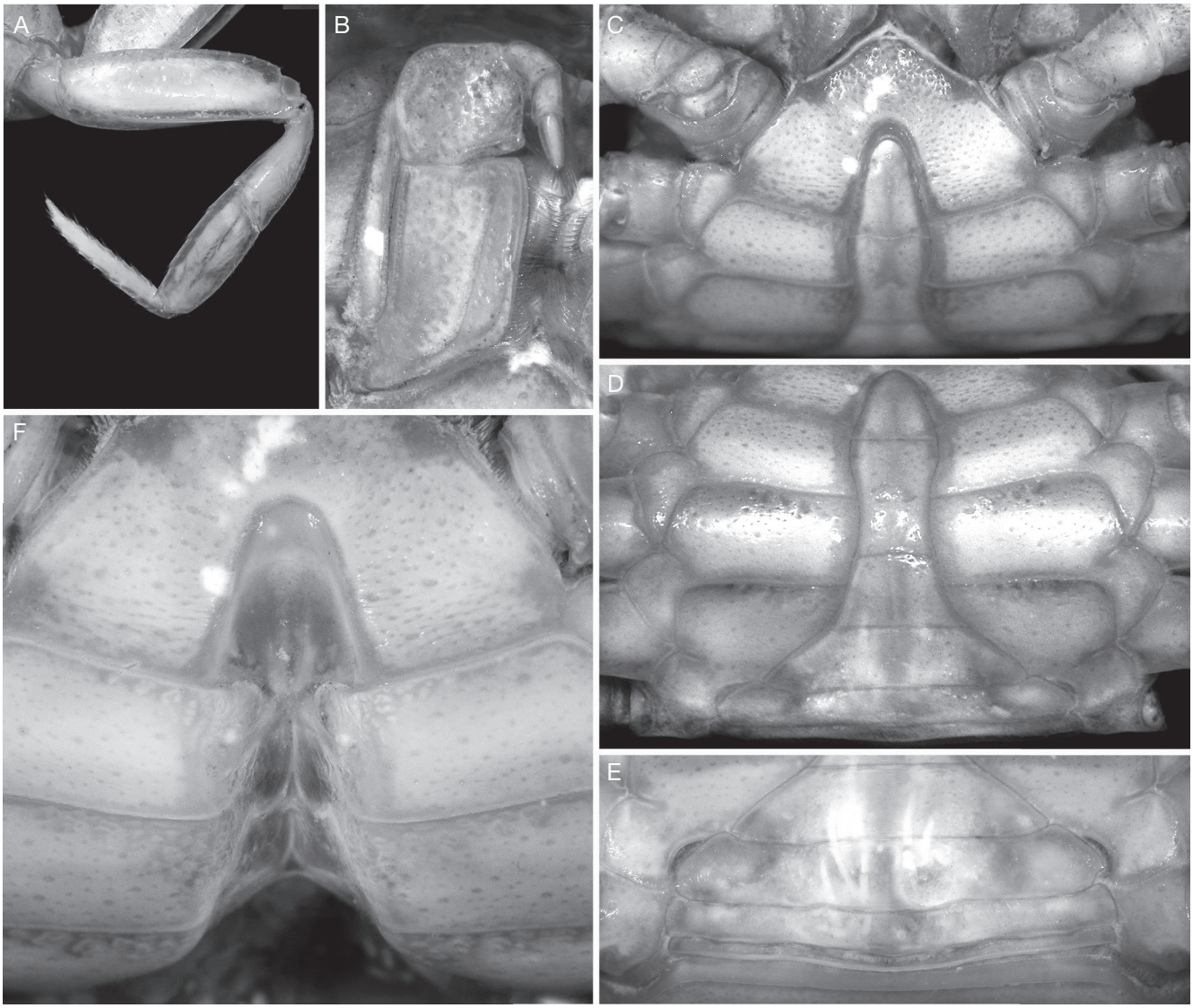

FIG. 4. — *Balssiathelphusa cursor* Ng, 1986, paratype, ♂ 15.6 × 13.4 mm (ZRC 1989.3036), Kalimantan: **A**, right fourth ambulatory leg; **B**, right third maxilliped; **C**, anterior thoracic sternum, telson and pleonal somites 5 and 6; **D**, thoracic sternum, telson and pleonal somites 2-6; **E**, posterior thoracic sternum and pleonal somites 1-4; **F**, sternopleonal cavity.

Paratypes. Indonesia • 1 ♀ 17.2 × 16.3 mm; same data as holotype; MZB Cru Nr. 1279b • 1 ♂ 15.6 × 13.4 mm, 1 ♀ 16.4 × 13.0 mm; same data as holotype; ZRC 1989.3036-3037.

ADDITIONAL MATERIAL. — **Indonesia** • 1 young ♂, 1 ♀, 1 juvenile; Wanariset swamp Forest, east Kalimantan, *c.* 1°00'S, 117°00'E; leg. Yayuk & R. Suhardjono; 28.IX.1980; MZB Cru.

DIAGNOSIS. — Epigastric cristae with rugae relatively diffuse, strongest anteriorly; epibranchial tooth small but visible, external orbital tooth separated from margin by distinct notch; anterolateral margin gently convex; lateral parts of anterolateral and branchial regions covered with numerous short, oblique striae; dorsal crista of frontal median triangle straight; median lobe of posterior margin of epistome distinctly triangular; outer surface of third maxilliped strongly punctate; outer surfaces of chelae gently punctate and granulate; male telson length to width ratio 1.5; G1 sinuous with distal part of terminal article elongate, ratio of terminal to subterminal article lengths 0.32, terminal article prominently curved upwards; G2 distal article relatively longer, 0.18 times length of basal article; vulva subovate.

DISTRIBUTION. — Known only from Samarinda in East Kalimantan, Indonesia.

DESCRIPTION

Male

Carapace transversely ovate, wider than long, width to length ratio 1.1-1.3; carapace relatively high when viewed frontally, height to width ratio 0.5; dorsal surface gently convex, branchial regions appearing swollen in frontal view (Fig. 3A-C). Dorsal surface of carapace with regions well defined; gently rugose to smooth; lateral parts of anterolateral and branchial regions covered with numerous short, oblique striae; mesogastric, urogastric, cardiac and intestinal regions with fine granules to smooth; suborbital, subhepatic, pterygostomial and sub-branchial regions with fine striae (Fig. 3C). Epigastric cristae low, strongest anteriorly but diffused posteriorly, visibly separated by distinct Y-shaped furrow; postorbital

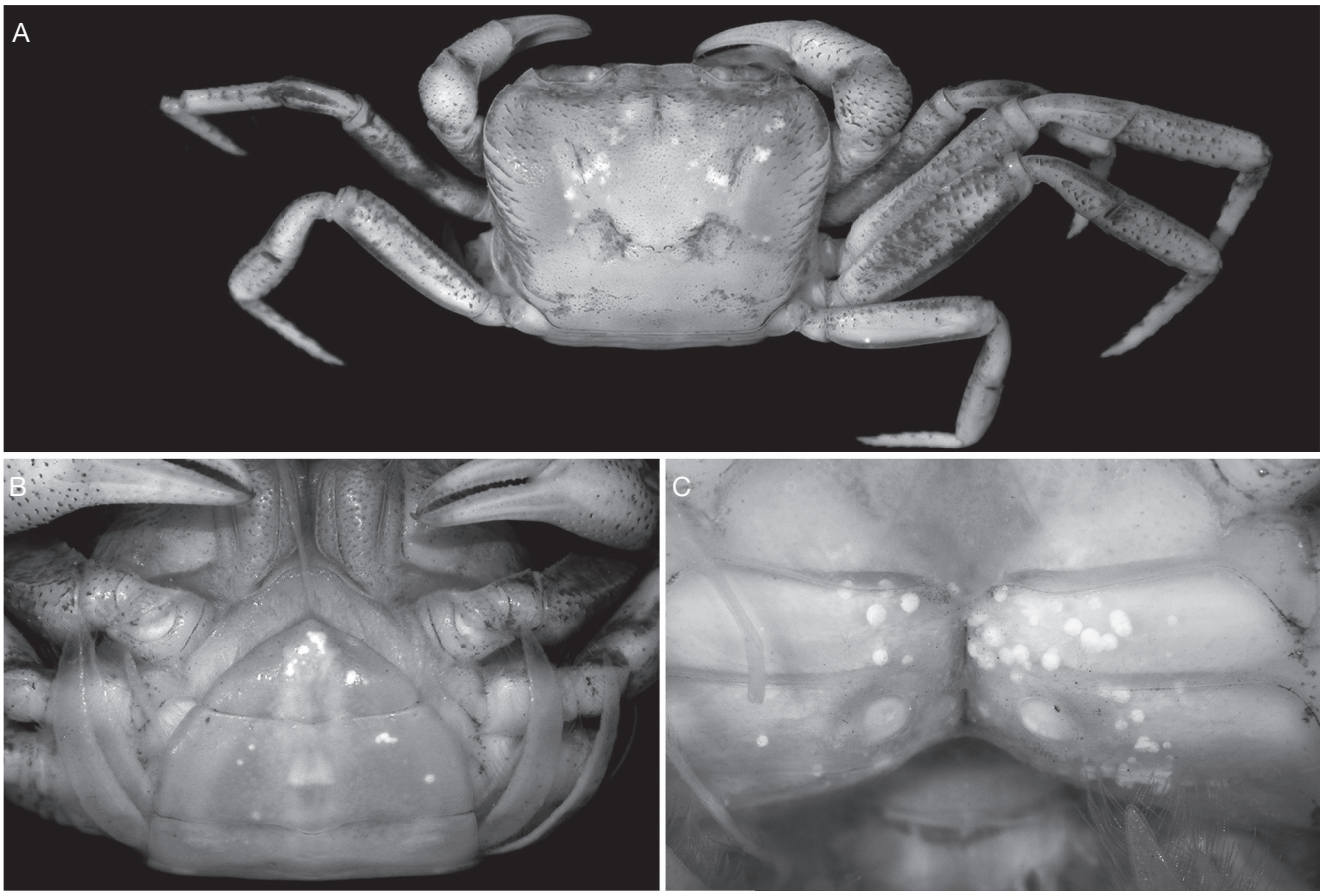

FIG. 5. — *Balssiathelphusa cursor* Ng, 1986, paratype, ♀ 16.4 × 13.0 mm (ZRC 1989.3037), Kalimantan: **A**, overall dorsal habitus; **B**, female anterior thoracic sternum and pleon; **C**, sternopleonal cavity showing vulvae.

cristae very low, just discernible (Fig. 3C). Cervical groove shallow; H-shaped median gastric groove distinct (Fig. 3A, B). Frontal margin divided into two low lobes, separated by shallow concavity; margin of each lobe gently convex, confluent with supraorbital margin; frontal median triangle distinct, with dorsal crista almost straight, fused with lateral cristae (Fig. 6H). External orbital tooth with outer margin finely granulated, almost straight, outer margin about twice length of inner margin; epibranchial tooth distinct, low, separated from margin by distinct notch; rest of anterolateral margins convex, cristate, lined with striae (Fig. 3A, B). Posterolateral margin gently convex, distinctly converging towards straight posterior carapace margin (Fig. 3A, B). Orbits subovate; eye filling orbital space; eye peduncle relatively short, stout; cornea large, pigmented (Fig. 3A-D). Supraorbital margin smooth, almost straight medially (Fig. 3B, C). Suborbital margin concave, lined with granules, entire, without proximal tooth (Fig. 3C, D). Antennae short, not reaching cornea of eyes; antennules short, folding transversely in narrow fossae (Fig. 3C, D). Epistome relatively long, width to length ratio 6.2; posterior margin with triangular lobe, separated from lateral margin by long fissure; each lateral margin sinuous, with very low lobe (Fig. 3C, D). Mandibular palp with three articles; terminal article distinctly bilobed.

Third maxillipeds covering most of buccal cavity when closed; outer surfaces distinctly punctate; ischium subrectangular, with distinct median oblique groove; merus subquadrate, just wider than long, anteroexternal angle rounded, not distinctly expanded; exopod relatively slender, reaching middle of merus, with distinct flagellum that is as long as width of merus (Figs 4B; 6G).

Chelipeds asymmetrical (Fig. 3A, E). Anterior margin of basis-ischium with strong sharp granules; margins of merus lined with prominent tubercles and granules, appearing gently serrated (Fig. 3E). Outer surface of carpus rugose, with strong tooth on inner distal margin (Fig. 3A). Outer surfaces of chelae strongly granulated, punctate (Fig. 3A, E). Fingers of major chela stout, gently curved, just shorter than palm; cutting edges of both fingers with variously sized teeth; dorsal margin of dactylus and ventral margin of pollex with low granules (Fig. 3E). Fingers of minor chela longer, more slender, subequal in length to palm (Fig. 3 E).

Ambulatory legs relatively short; second pair longest, last pair shortest (Fig. 3A). Outer surface of merus slightly rugose, dorsal margin weakly serrated, subcristate, with subdistal angle but no obvious spine or tooth; length to width ratio of fourth merus 3.2; carpus relatively smooth, outer surface of first to third legs with low submedian cris-

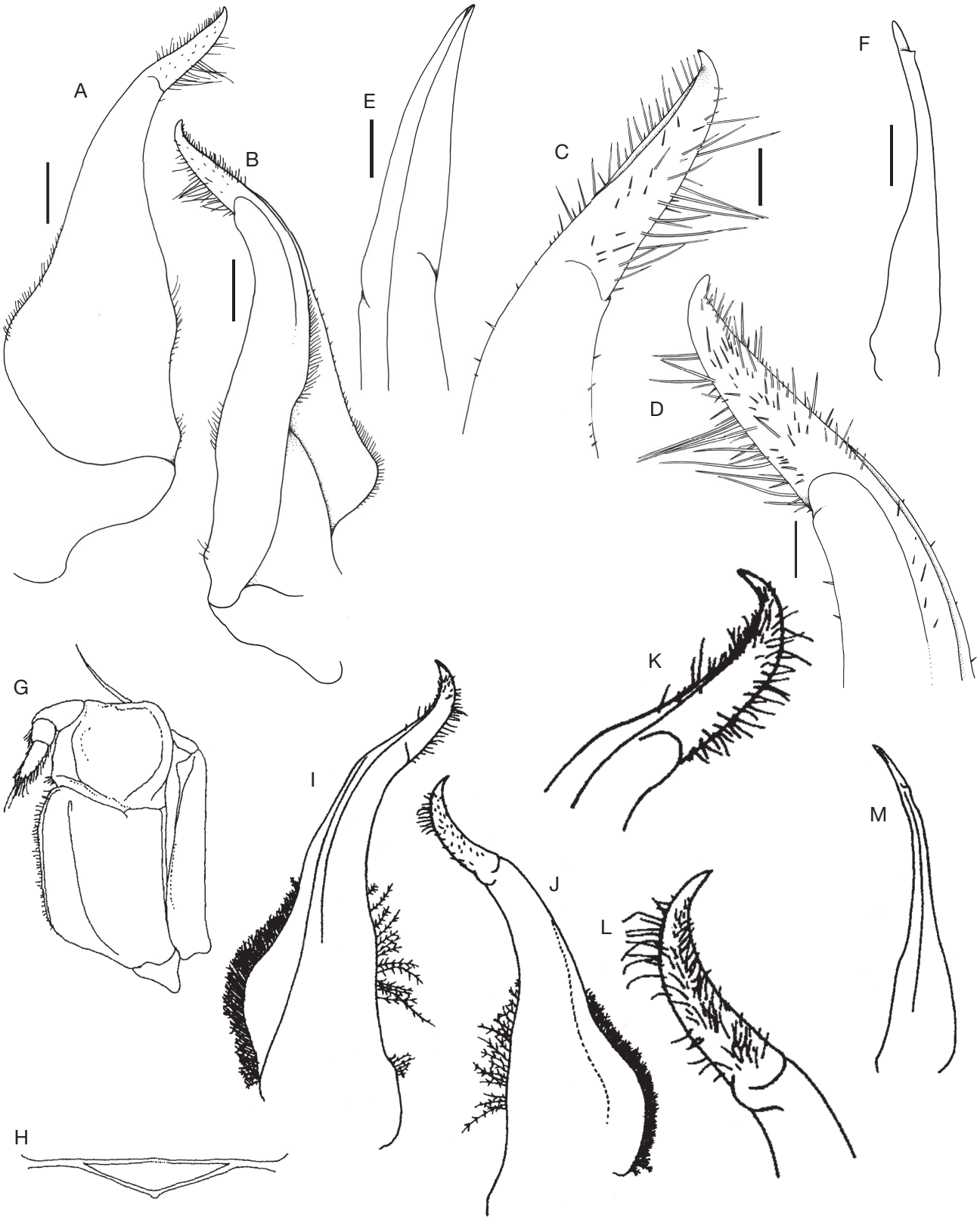

FIG. 6. — *Balssiathelphusa sucki* (Balss, 1937) (**A**-**F**), holotype, ♂ 21.2 × 17.1 mm (ZMH-K-003545), "Sumatra", and *B. cursor* Ng, 1986 (**G**-**M**), holotype, ♂ 15.4 × 13.3 mm (MZB Cru Nr. 1279a), Kalimantan. **A**, right G1 (dorsal view); **B**, right G1 (ventral view); **C**, distal part of right G1 (dorsal view); **D**, distal part of right G1 (ventral view); **E**, distal part of right G1 (dorso-mesial view, setae not drawn); **F**, right G2; **G**, left third maxilliped; **H**, frontal median triangle; **I**, left G1 (ventral view); **J**, left G1 (dorsal view); **K**, distal part of left G1 (ventral view); **L**, distal part of left G1 (dorsal view); **M**, left G2. Scale bars: A, B, F, 0.5 mm; C, D, 0.2 mm. I-M, after Ng (1986a: fig. 2A-F).

ta, that on fourth leg smooth; outer surface of propodus smooth; dactylus relatively short, gently curved, quadrate in cross section, margins with short, sharp corneous spines (Figs 3A; 4A).

Thoracic sternum punctate, not distinctly wide, length to width ratio of anterior thoracic sternites 0.4 (Fig. 2E-H). Sternite 1 small, triangular, separated from sternite 2 by low ridge; sternites 2-4 completely fused except for lateral notches demarcating sternites 3 and 4 (Fig. 4C-F); distinct median transverse bridges present between sternites 5 and 6, and sternites 6 and 7, bridges interrupting median line on sternites 5-8; median line on sternite 5 deep, not reaching level of press-button tubercles; inner edges of s4/5 ending near median part of sternopleonal cavity, not reaching s5/6 (Figs 4F; 16B). Penis coxal, on condyle of coxa of fourth ambulatory leg. Sternopleonal cavity deep, reaching imaginary line connecting proximal edges of cheliped coxae (Fig. 4C, F). Male pleonal locking tubercle peg-like, positioned on median part of sternite 5 (Fig. 4F).

Pleon T-shaped, all somites and telson free; telson elongate, triangular, length to width ratio 1.5, lateral margins almost straight, shorter than somite 6; somite 6 elongate, length to width ratio 1.3, lateral margins distinctly concave; somites 3-5 trapezoidal, gradually decreasing in width; somite 2 subrectangular, very wide, reaching bases of coxae of fourth ambulatory legs; somite 1 longitudinally narrow, subequal in width to somite 2 (Fig. 4C-E); thoracic sternite 8 clearly exposed when pleon closed (Fig. 4D, E).

G1 relatively slender; subterminal article with basal part wide, gradually tapering towards terminal article, outer margin gently concave; terminal article clearly demarcated by groove; terminal to subterminal article length ratio 0.32, terminal article long, distinctly curved upwards, proximal part wide, distal part narrowing to sharp tip that curves upwards, outer lateral surfaces with numerous long and short setae (Fig. 6I-L). G2 shorter than G1; distal article short, 0.18 times length of basal article (Fig. 6M).

Female

Anterior parts of dorsal carapace surface slightly more rugose, with more prominent granules and striae (Fig. 5A). Chelae asymmetrical but less pronounced than in male, with both chelae and fingers relatively slender (Fig. 5A, B). Pleon subovate, all somites and telson free; covering most of thoracic sternum except distal part of thoracic sternite 3 when closed; telson broadly triangular, with gently convex lateral margins, tip sharp (Fig. 5B). Vulvae large, subovate, positioned medially on sternite 5, with thin operculum, no sternal cover (Fig. 5C). Structure of the thoracic sternites agreeing with the male in all aspects; with the median line in a similar position and the bridges between sternites 5 and 6, and 6 and 7 distinct (Fig. 5C).

Colour

Freshly preserved specimens have a dirty brown coloration on the dorsal surfaces, with the ventral surfaces appearing dirty white (unpublished data).

Remarks

Balssiathelphusa cursor can easily be separated from *B. sucki*: the anterolateral margin is gently convex (Fig. 3B) (vs strongly convex in *B. sucki*; Fig. 1B); the dorsal crista of the frontal median triangle is straight (Fig. 3C, D) (vs dorsal crista of frontal median triangle straight medially bent in *B. sucki*; Fig. 1C, D); the median lobe of the posterior margin of the epistome is distinctly triangular (Fig. 3D) (vs subtriangular in *B. sucki*; Fig. 1D); the outer surface of the third maxilliped is strongly punctate (Fig. 4B) (vs weakly punctate in *B. sucki*; Fig. 2D); the outer surfaces of the chelae are gently punctate and granulate (Fig. 3E) (vs strongly punctate and granulate in *B. sucki*; Fig. 1E); the male telson is proportionately longer, the length to width ratio being 1.5 (Fig. 4C) (vs male telson shorter, the length to width ratio being 1.4 in *B. sucki*; Fig. 2F); the G1 appears more sinuous with the distal part of the terminal article elongate and prominently curved upwards (Fig. 5I-L) (vs G1 less sinuous in *B. sucki*, with the distal part shorter and less strongly curved; Fig. 5A-E); and the G2 distal article is relatively longer, being 0.18 times the length of the basal article (Fig. 5M) (vs G2 distal article 0.11 times length of basal article in *B. sucki*; Fig. 6F). The larger male cheliped in the males of *B. cursor* (Fig. 3E) is less heavily built than that of *B. sucki* (Fig. 1E) and the fingers are relatively shorter, but, as already noted for *Irmengardia* Bott, 1969, this is likely to be associated with the size of the specimen (see Ng & Yang 1985; Ng & Tan 1991; Ng 1992) and it is not a reliable taxonomic character.

All the specimens were collected from a swamp forest on muddy substrates and had semiterrestrial habits.

Balssiathelphusa inopinata n. sp.
(Figs 7; 8)

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Potamon (*Geotelphusa*) *bürgeri* – Nobili 1903: 16. (not *Potamon* (*Geotelphusa*) *bürgeri* De Man, 1899).

Parathelphusa (*Liothelphusa*) *bürgeri* – Colosi 1920: 26. (not *Potamon* (*Geotelphusa*) *bürgeri* De Man, 1899).

Material examined. — **Holotype** • ♀ 23.2 × 17.6 mm; Samarinda, Kalimantan; coll. G. Bonarelli; 1903; MRSN 1209 (ex MZUT 1571).

Diagnosis. — Epigastric cristae with rugae concentrated anteriorly; anterolateral margin gently convex, without trace of epibranchial tooth, external orbital tooth separated by shallow concavity; lateral parts of anterolateral and branchial regions covered with short, oblique striae; dorsal crista of frontal median triangle straight; median lobe of posterior margin of epistome distinctly triangular; outer surface of third maxilliped strongly punctate; outer surfaces of chelae gently punctate and granulate; male pleon and gonopods not known; vulva almost round.

Colour. — Not known.

Etymology. — The name is derived from the Latin "*inopinatus*" for "unexpected" as it had been previously believed that Nobili's (1903) record was *Balssiathelphusa cursor* and not a new species.

Fig. 7. — *Balssiathelphusa inopinata* n. sp., holotype, ♀ 23.2 × 17.6 mm (MRSN 1209), Kalimantan: **A**, overall dorsal habitus; **B**, dorsal view of carapace; **C**, frontal view of cephalothorax; **D**, **E**, frontal median triangle, antennules, antennae and epistome (viewed at slightly different angles).

Distribution. — Known only from somewhere in or around Samarinda, East Kalimantan, Indonesia (but see earlier).

Remarks

Tan & Ng (1998: 813) commented that the records of "*Potamon* (*Geotelphusa*) *bürgeri*" by Nobili (1903: 16) and "*Parathelphusa* (*Liothelphusa*) *bürgeri*" by Colosi (1920: 26) from Samarinda in southern Kalimantan are likely to belong to *Balssiathelphusa cursor* Ng, 1986. A re-examination of the only known specimen on which this record is based shows that it is actually a new species, here named *B. inopinata* n. sp.

Although known only from a female, *B. inopinata* n. sp. is clearly different from *B. sucki* and *B. cursor*. Compared to *B. sucki*, *B. inopinata* n. sp. has the epigastric cristae more discretely demarcated with the rugae concentrated anteriorly (Fig. 7A, B) (vs distinct but with the rugae more diffuse in *B. sucki*; Fig. 1A, B); there is no visible epibranchial tooth although the external orbital angle is separated from the rest of the anterolateral margin by a wide concavity (Fig. 7A, B) (vs epibranchial tooth small but visible and separated by a clear notch in *B. sucki*; Fig. 1A, B); the granules and striae on the regions adjacent to the anterolateral and posterolateral margins are relatively lower and more sparse (Fig. 7A, B) (vs granules and striae strong and dense in *B. sucki*; Fig. 1A, B); the ambulatory legs, notably the merus, are relatively longer (Figs 7A, 8B) (vs shorter in *B. sucki*; Figs 1A, 2C); and the dorsal margin of the frontal median triangle is almost straight (Fig. 7C-E) (vs crista in two parts meeting at angle medially in *B. sucki*; Fig. 1C, D).

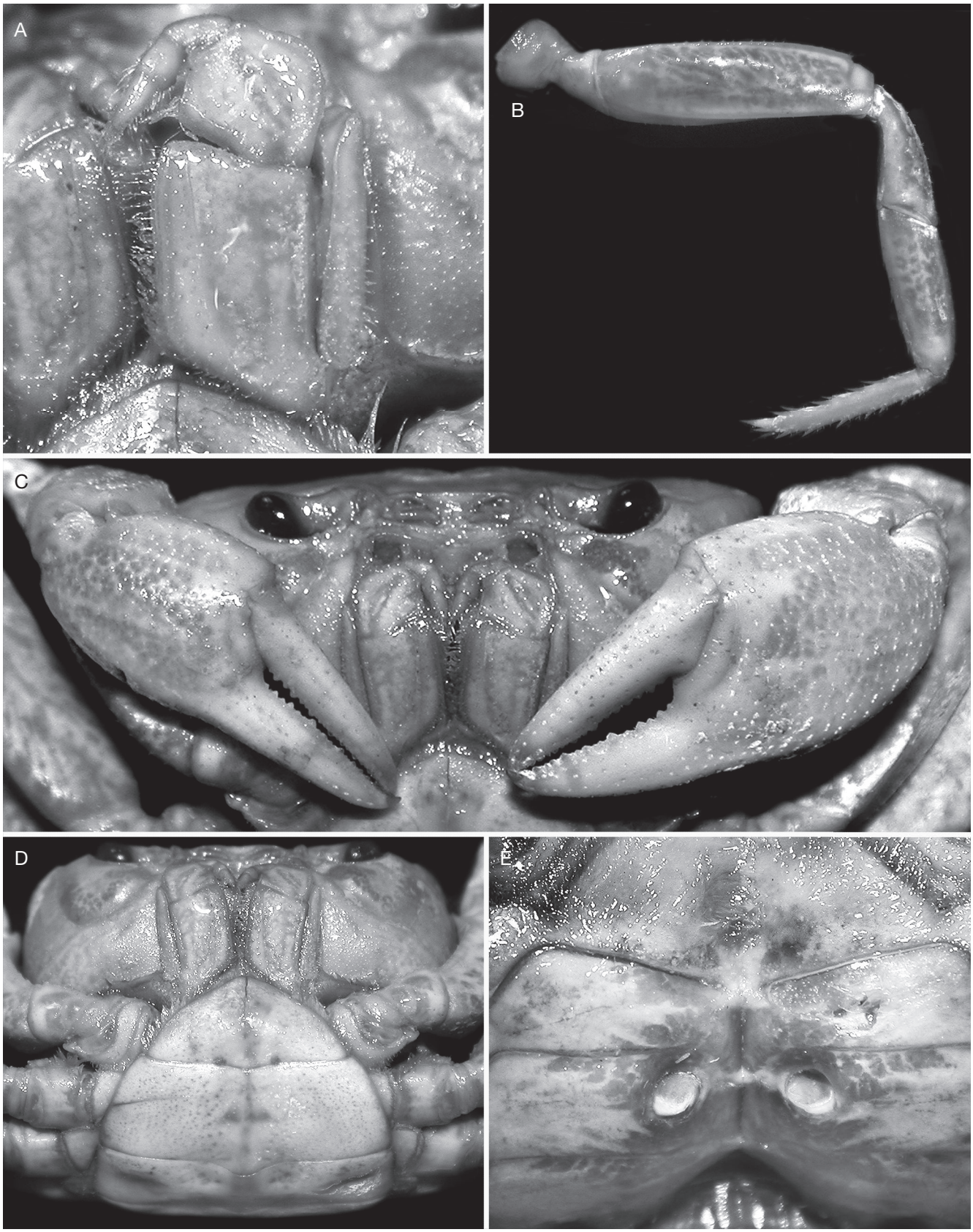

FIG. 8. — *Balssiathelphusa inopinata* n. sp., holotype, ♀ 23.2 × 17.6 mm (MRSN 1209), Kalimantan: **A**, left third maxilliped; **B**, right fourth ambulatory leg; **C**, buccal cavity and outer view of chelae; **D**, pleonal somites 4-6 and telson; **E**, sternopleonal cavity showing vulvae.

Balssiathelphusa inopinata n. sp. is similar to *B. cursor* in the form of the frontal median triangle (Figs 3C, D, 7C-E) and has the same differences with *B. sucki* with regards to the characters of the epigastric cristae, epibranchial tooth, strength of striae on the lateral regions and length of the ambulatory legs (cf. Figs 3A-D; 4A). *Balssiathelphusa inopinata* n. sp., however, has a distinctly higher carapace in the frontal view (Fig. 7C) and the vulva is more rounded in shape (Fig. 8E) (vs carapace lower in frontal view and the vulva is more ovate in *B. cursor*; Figs 3C; 5C).

The type specimen of *B. inopinata* n. sp. was collected by the well-known Italian geologist, paleontologist and anthropologist Guido Bonarelli (1871-1951). He worked in the Samarinda area of Kalimantan in Borneo for the Royal Dutch Company from 1901-1907, doing survey work for oil exploitation (Bonarelli 2001). When and exactly where Bonarelli collected the specimen of *B. inopinata* n. sp. is not known as the only data on the label was "Samarinda, Borneo, 1903". A check of the original catalogue books in the Torino Museum only showed 1903 as well. Nobili's (1903) paper was published on July 1903 so the specimen must have arrived before this date. Shortly after he arrived in Samarinda in November 1901, Bonarelli conducted a major survey of the area around Samarinda between December 1901 and April 1902, covering an area of 15 000 km^2. In February 1903, he undertook another major two month survey of the Balikpapan area in Kalimantan (some 100 km to the southwest of Samarinda), and along the coast of Koetei (present day Kutai), with more follow-up work shortly after until October 1903 (Bonarelli 2001). It is possible the specimen was from the area around Samarinda that Bonarelli surveyed between 1901-1902, and it is known his assistant returned to Italy in April 1903 so he may have brought specimens with him to Torino. This is unlikely as the specimen was recorded as collected in 1903. Nobili usually published on material reaching him relatively fast (often within months), it is more likely the specimen was collected later in 1903, possibly during his surveys around Balikpapan in February 1903, and was dispatched to Nobili a few months later. This would make sense considering Nobili's (1903) paper was released in July that year. That would, however, mean the specimen may also have come from the Balikpapan area rather than near Samarinda.

Genus *Natunusa* n. gen.

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TYPE SPECIES. — *Balssiathelphusa natunaensis* Bott, 1970, by original designation and monotypy.

DIAGNOSIS. — Carapace quadrate, just wider than long; carapace not high, height to width ratio 0.4; epigastric cristae rugose, low but visible, not cristate; postorbital cristae low, rugose, discernible, not cristate; frontal margin divided into two low lobes; frontal median triangle distinct, with dorsal crista straight; external orbital tooth with outer margin 3.0-4.0 times length of inner margin; epibranchial tooth small, low, separated from margin by small notch; rest of anterolateral margins gently convex; posterolateral margin gently convex, appearing subparallel; suborbital margin without proximal tooth; epistome relatively shorter, width to length ratio 5.3, posterior margin with broad triangular lobe, separated from lateral margin by fissure, each lateral margin sinuous, with low lobe; third maxilliped exopod with distinct flagellum that is as long as width of merus; ambulatory legs relatively short, length to width ratio of fourth merus 3.3; male thoracic sternum mostly smooth, relatively wide, length to width ratio of anterior thoracic sternites 0.4; median line across most of sternite 5, shallow, reaching level of press-button tubercles; inner edges of s4/5 continuing curving until they reach s5/6; male sternopleonal cavity reaching imaginary line connecting proximal edges of cheliped coxae; male pleonal locking tubercle on median part of sternite 5; male pleon T-shaped, somite 6 elongate, length to width ratio 1.2; thoracic sternite 8 exposed as wide plate when pleon closed; G1 slender, subterminal article with basal part wide, gradually tapering towards terminal article, outer margin distinctly concave; terminal article barely demarcated by shallow, short groove, appearing partially twisted; terminal to subterminal article length ratio 0.08, terminal article short, distinctly curved upwards, tip sharp, with numerous setae; G2 shorter than G1, distal article short, 0.08 times length of basal article; vulvae large, subovate, positioned medially on sternite 5, may be with thin operculum, no sternal cover.

ETYMOLOGY. — The name is derived from the name of the type locality, Natuna Island, in arbitrary combination with *-phusa*, a common suffix for gecarcinucid genera. The gender of the name is feminine.

REMARKS

Ng *et al.* (2023) commented that *Balssiathelphusa natunaensis* Bott, 1970, probably did not belong to the genus and should be removed. With the examination of the type species of *Balssiathelphusa*, there can now be no doubt that *B. natunaensis* should be referred to a new genus, *Natunusa* n. gen.

Natunusa n. gen. differs from *Balssiathelphusa* in the branchial regions being less inflated and lower, with the lateral carapace margins gently sinuous and almost subparallel (Fig. 9A-C) (vs branchial regions more inflated and higher, with the lateral carapace margins distinctly convex and converging towards the posterior carapace margin; Fig. 1A-C); a large subovate part of male thoracic sternite 8 is exposed when pleon closed (Fig. 9F) (vs only a narrower part of male thoracic sternite 8 exposed when pleon closed; Fig. 2H); the male anterior thoracic sternum is relatively wider transversely, the length to width ratio being 0.4 (Fig. 9E) (vs relatively narrower, with the length to width ratio 0.5; Fig. 2F); the median line on thoracic sternite 5 is shallow, and s4/5 joining s5/6 (Figs 9G; 16C; Ng *et al.* 2023: fig. 12D, E) (vs median line on thoracic sternite 5 deep, and s4/5 not joining s5/6; Figs 2E; 16A, B); and the male G1 terminal and subterminal articles are barely separated, with the terminal article very short, with the terminal article only 0.08 times the length of the subterminal article (Fig. 9A-D, F-H) (vs terminal and subterminal articles clearly separated, with the terminal article elongate; Fig. 6A-E).

Natunusa natunaensis (Bott, 1970) n. comb.
(Figs 9; 11A-H; 16C)

Balssiathelphusa natunaensis Bott, 1970: 99, pl. 36 figs 54-56, 63. — Fransen *et al.* 1997: 132. — Ng *et al.* 2008: 69 [in list]; 2023: 10, figs 2E-H; 10-13. — Klaus *et al.* 2009: 512, table 1.

MATERIAL EXAMINED. — **Holotype. Indonesia** • ♂ 23.0 × 20.0 mm; Natuna Islands; 4°N, 108°E; Natuna Regency, South China Sea; coll. A. L. van Hasselt, 1896; RMNH D29300.

OTHERS MATERIAL EXAMINED. — **Indonesia** • 4 ♂, 1 ♀; Natuna Islands, Bunguran Timur District, Ds. Ranai Darat, Air Terjun Gunung Ranai and surrounding area, Natuna Regency, South China Sea; 03°57'18.9"N, 108°21'44.3"E; coll. D. Wowor *et al.*; 31.X.2002; MZB Cru 5392, 5 (largest 12.9 × 11.3 mm) • 1 ♀ 11.5 × 10.7 mm, 1 dismembered juvenile; same data; ZRC 2021.0831 • 1 brooding ♀ 19.4 × 16.6 mm (with 27 juveniles); same data; ZRC 2021.0838.

DIAGNOSIS. — As for genus.

DESCRIPTION

Male

Carapace quadrate, just wider than long, width to length ratio 1.07-1.17; carapace not high, height to width ratio 0.4; dorsal surface gently convex, branchial regions not clearly swollen in frontal view (Fig. 9A-C). Dorsal surface of carapace with regions well defined; smooth to gently rugose; lateral parts of anterolateral and branchial regions covered with short, oblique striae; mesogastric, urogastric, cardiac and intestinal regions with fine granules to smooth; suborbital, subhepatic, pterygostomial and sub-branchial regions with fine striae (Fig. 9C). Epigastric cristae rugose, low but visible, not cristate, separated by distinct Y-shaped furrow; postorbital cristae low, rugose, discernible, not cristate (Fig. 9B, C). Cervical groove very shallow; H-shaped median gastric groove distinct (Fig. 9A, B). Frontal margin divided into two low lobes, separated by shallow concavity; margin of each lobe slightly convex, confluent with supraorbital margin; frontal median triangle distinct, with dorsal crista straight, fused or almost fused with lateral cristae (Fig. 9C, D). External orbital tooth with outer margin finely granulated, almost straight, outer margin 3.0-4.0 times length of inner margin; epibranchial tooth small, low, separated from margin by small notch; rest of anterolateral margins gently convex, cristate, lined with striae (Fig. 9A, B). Posterolateral margin gently convex, appearing subparallel, posterior carapace margin gently convex (Fig. 9A, B). Orbits subovate; eye filling orbital space; eye peduncle relatively short, stout; cornea large, pigmented (Fig. 9B-D). Supraorbital margin smooth, almost straight or gently sinuous medially (Fig. 9B, C). Suborbital margin concave, lined with small granules, entire, without proximal tooth (Fig. 9C, D). Antennae short, not reaching cornea of eyes; antennules short, folding transversely in narrow fossae (Fig. 9C, D). Epistome relatively shorter, width to length ratio 5.3; posterior margin with broad triangular lobe, separated from lateral margin by fissure; each lateral margin sinuous, with low lobe (Fig. 9C, D). Mandibular palp with three articles; terminal article distinctly bilobed.

Third maxillipeds covering most of buccal cavity when closed; outer surfaces mostly smooth; ischium subrectangular, with distinct median oblique groove; merus subquadrate, just wider than long, anteroexternal angle rounded, not distinctly expanded; exopod relatively slender, reaching middle of merus, with distinct flagellum that is as long as width of merus (Fig. 9E).

Chelipeds slightly asymmetrical (Fig. 9A). Anterior margin of basis-ischium with small granules; margins of merus lined with granules and striae. Outer surface of carpus rugose, with low tooth on inner distal margin (Fig. 9A). Outer surfaces of chelae strongly rugose. Fingers of both chelae slightly longer, much slender than palm.

Ambulatory legs relatively short; second pair longest, last pair shortest (Fig. 9A). Outer surface of merus slightly rugose, dorsal margin weakly serrated, subcristate, with subdistal angle but no obvious spine or tooth, length to width ratio of fourth merus 3.3; carpus relatively smooth, outer surface of first to third legs with low submedian crista, that on fourth leg smooth; outer surface of propodus smooth; dactylus relatively short, gently curved, quadrate in cross section, margins with short, sharp corneous spines (Fig. 9A).

Thoracic sternum mostly smooth, with scattered punctae, relatively wide, length to width ratio of anterior thoracic sternites 0.4 (Fig. 9E). Sternite 1 small, triangular, separated from sternite 2 by low ridge; sternites 2-4 completely fused except for lateral notches demarcating sternites 3 and 4 (Fig. 9E); sutures between sternites 4/5, 5/6, 6/7 medially interrupted; suture between sternites 7 and 8 complete; distinct median transverse bridges present between sternites 5 and 6, and sternites 6 and 7, bridges interrupting median line on sternites 5-8; median line on sternite 5 shallow, reaching level of press-button tubercles; inner edges of s4/5 curving until they reach s5/6 (Figs 9G, 16C). Penis coxal, on condyle of coxa of fourth ambulatory leg. Sternopleonal cavity deep, reaching imaginary line connecting proximal edges of cheliped coxae (Fig. 9E). Male pleonal locking tubercle peg-like, positioned on median part of sternite 5 (Fig. 9G).

Pleon T-shaped, all somites and telson free; telson elongate, triangular, length to width ratio 1.2, lateral margins gently convex to almost straight, shorter than somite 6; somite 6 elongate, length to width ratio 1.2, lateral margins concave; somites 3-5 trapezoidal, gradually decreasing in width; somite 2 subrectangular, wide, reaching bases of coxae of fourth ambulatory legs; somite 1 longitudinally narrow, subequal in width to somite 2 (Fig. 9E, F); thoracic sternite 8 clearly exposed as wide plate when pleon closed (Fig. 9F).

G1 slender; subterminal article with basal part wide, gradually tapering towards terminal article, outer margin distinctly concave; terminal article barely demarcated by shallow, short groove, appearing partially twisted; terminal to subterminal article length ratio 0.08, terminal article short, distinctly curved upwards, tip sharp, curving upwards, with numerous setae (Fig. 11A-D, F-H). G2 shorter than G1; distal article short, 0.08 times length of basal article (Fig. 6E).

Female

Chelae asymmetrical but less pronounced than in male, with both chelae and fingers relatively slender, longer than palm (Ng

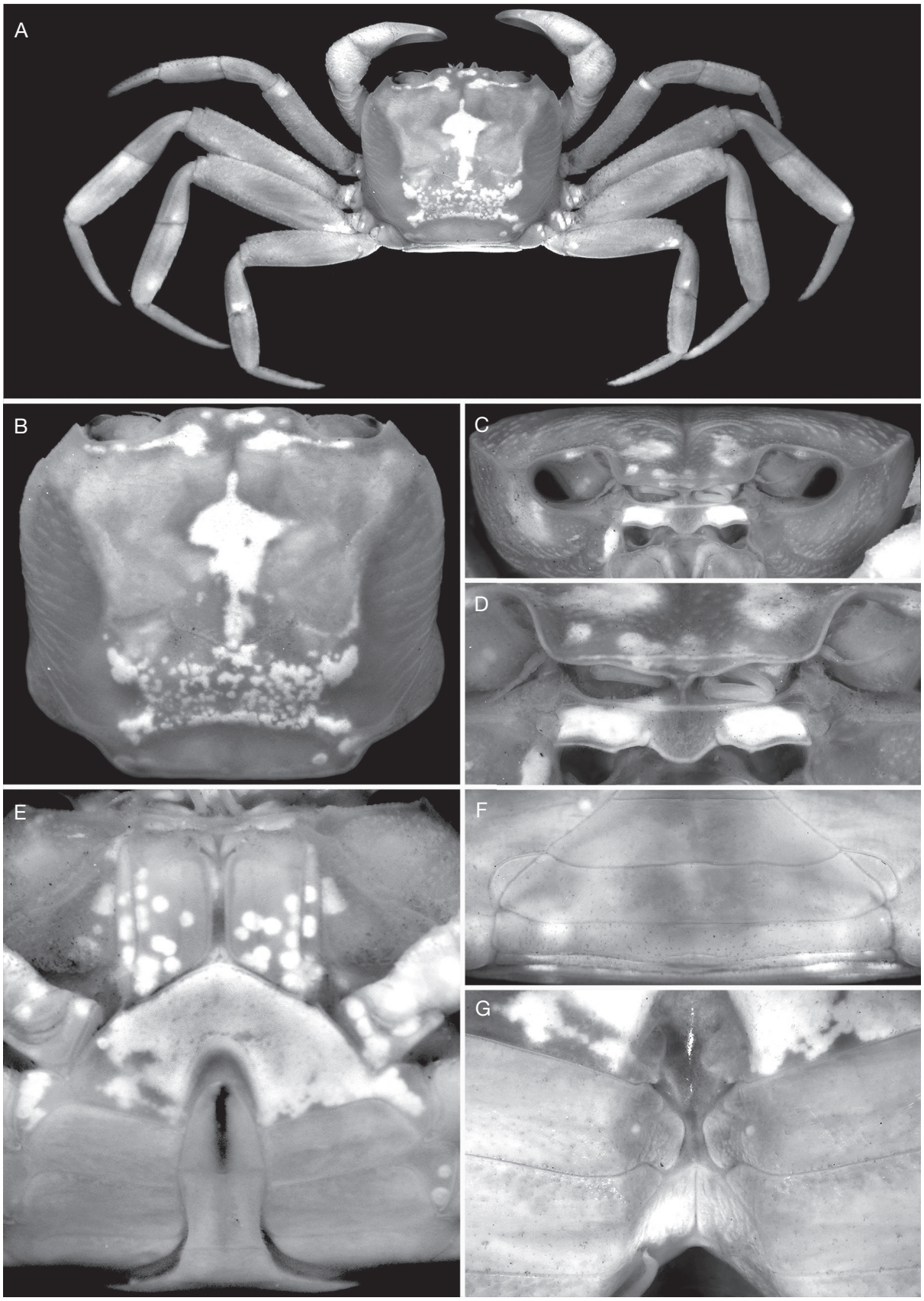

FIG. 9. — *Natunusa natunaensis* (Bott, 1970) n. comb., ♂ 12.9 × 11.3 mm (ZRC 2021.0831), Natuna Island: **A**, overall dorsal habitus; **B**, dorsal view of carapace; **C**, frontal view of cephalothorax; **D**, frontal median triangle, antennules, antennae and epistome; **E**, buccal cavity, anterior thoracic sternum, telson and pleonal somites 5 and 6; **F**, posterior thoracic sternum and pleonal somites 1-4; **G**, sternopleonal cavity.

et al. 2023: fig. 12A). Pleon subovate, all somites and telson free; covering most of thoracic sternum except distal part of thoracic sternite 3 when closed; telson broadly triangular with gently convex lateral margins, tip sharp (Ng *et al.* 2023: fig. 12C). Structure of the thoracic sternites agreeing with the male in all aspects; with s4/5 also curving to join s5/6, the median line in similar positions, and the bridges between sternites 5 and 6, and 6 and 7 distinct (Ng *et al.* 2023: fig. 12D, E). Vulvae large, subovate, positioned medially on sternite 5, may be with thin operculum, no sternal cover (Ng *et al.* 2023: fig. 12D, E).

Colour

"The species colouration is striking, with the carapace dark, purplish-brown chela and the ambulatory propodus and dactylus cream-coloured […]. There is also sexual dimorphism exhibited in the colour pattern, with the cream-colour on the ambulatory legs of females restricted to the dactylus, and not extending to the propodus." (Ng *et al.* 2023: 12).

Remarks

Bott (1970) described the species from one male 23.0 × 20.0 mm originally collected from Natuna. The species was redescribed and figured in detail by Ng *et al.* (2023) from fresh material collected.

Ng *et al.* (2023: 14) reported that the species was semiterrestrial and occurred in shallow and moderately fast-flowing highland forest streams (pH 6.9) near waterfall habitats in the pristine forest of Gunung Ranai, Natuna Island; with almost complete canopy cover and the stream substrate sandy with some rocks.

Genus *Lemurophusa* n. gen.

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Type species. — *Balssiathelphusa phasma* Ng & Guinot, 2014, by present designation.

Included species. — *Lemurophusa phasma* (Ng & Guinot, 2014) n. comb.; *Lemurophusa empusa* n. sp.

Diagnosis. — Carapace transversely ovate, wider than long, carapace not high, height to width ratio 0.4; epigastric cristae low, rugose but visible; postorbital cristae low, rugose, just discernible, not cristate; frontal margin divided into two low lobes; frontal median triangle distinct, with dorsal crista medially bent, fused with lateral cristae; external orbital tooth distinct, with outer margin about twice length of inner margin; epibranchial tooth small, low, separated from margin by notch; rest of anterolateral margins convex; posterolateral margin distinctly converging towards posterior carapace margin; suborbital margin without proximal tooth; epistome relatively narrower, width to length ratio 8.3-9.0, posterior margin with distinct low subtriangular lobe, separated from lateral margin by fissure, each lateral margin sinuous, with low lobe; third maxilliped exopod with flagellum that is as long as half width of merus; ambulatory legs long, length to width ratio of fourth merus 4.9; male thoracic sternum relatively smooth, not distinctly wide, length to width ratio of anterior thoracic sternites 0.5; median line on sternite 5 deep, reaching level of press-button tubercles; inner edges of s4/5 ending near median part of sternopleonal cavity, not reaching s5/6; male sternopleonal cavity deep, reaching imaginary line connecting proximal edges of cheliped coxae; male pleonal locking tubercle on submedian part of sternite 5; male pleon T-shaped, somite 6 elongate, length to width ratio 1.32; thoracic sternite 8 not visible when pleon closed; G1 slender; subterminal article with basal part wide, gradually tapering towards terminal article, outer margin concave, terminal article clearly demarcated by groove from subterminal article, terminal to subterminal article length ratio 0.18-0.19, terminal article relatively long, gently curved upwards, with numerous long and short setae; G2 shorter than G1, distal article short, 0.11-0.12 times length of basal article; vulvae not known.

Etymology. — The name is derived from the Latin word "*lēmurēs*" for "spirits of the dead"; in arbitrary combination with *-phusa*, a common suffix for gecarcinucid genera. This alludes to the cave habitat of the species. The gender of the name is feminine.

Remarks

Lemurophusa n. gen. differs from *Balssiathelphusa s. str.* in that the carapace is not high, appearing relatively lower in frontal view with the carapace height to width ratio 0.4 (Fig. 1C) (vs carapace distinctly higher, raised in frontal view, with the carapace height to width ratio 0.5; Fig. 10D); epistome is distinctly narrower with the width to length ratio 8.3-9.0 (Fig. 10D-F) (vs epistome wide in *Balssiathelphusa s. str.*, with the width to length ratio 6.2-6.5; Fig. 1C, D); median line on thoracic sternite 5 reaching the level of the press-button tubercles (Fig. 16D) (vs not reaching level of the press-button tubercles in *Balssiathelphusa s. str.*; Fig. 16A, B); male thoracic sternite 8 is not exposed when pleon closed (Fig. 10G) (vs part of male thoracic sternite 8 distinctly exposed when pleon closed in *Balssiathelphusa s. str.*; Fig. 2H); and ambulatory legs are very long (merus length to width ratio 4.9) with the dactylus very elongate (Fig. 10A) (vs relatively short and stout in *Balssiathelphusa s. str.*, the merus length to width ratio being 3.2 and the dactylus is distinctly less elongate; Figs 1A; 2C). Additional differences but they may not be significant at the genus level are: the posterolateral margins are more strongly converging towards the carapace margin (Fig. 10A) (vs gently converging or appearing almost subparallel in *Balssiathelphusa s. str.*; Fig. 1B); the male anterior thoracic sternum is relatively narrow transversely, the length to width ratio being 0.4 (Fig. 10H) (vs relatively wider in *Balssiathelphusa s. str.*, with the length to width ratio being 0.5; Fig. 2F); and the male G1 subterminal article is proportionately stouter (Fig. 11I) (vs distinctly more slender in *Balssiathelphusa s. str.*; Fig. 6A, B).

Compared to *Natunusa* n. gen., *Lemurophusa* n. gen. is quite different, with the lateral margins of the carapace distinctly converging towards the posterior carapace margin (Fig. 10A-C) (vs subparallel in *Natunusa* n. gen.; Fig. 9A, B); there is a distinct median line present on male sternite 6 (Fig. 10H) (vs median line absent with the two plates far apart in *Natunusa*; Fig. 9G); male thoracic sternite 8 is not exposed when the pleon is closed (Fig. 10G) (vs sternite 8 clearly exposed in *Natunusa* n. gen.; Fig. 9F); and the G1 is proportionately stouter with the terminal article long, being 0.18-0.19 times length of the subterminal article (Fig. 11I) (vs G1 slender and the terminal article is short in *Natunusa* n. gen., and with the terminal article 0.08 times length of the subterminal article; Fig. 11A, B).

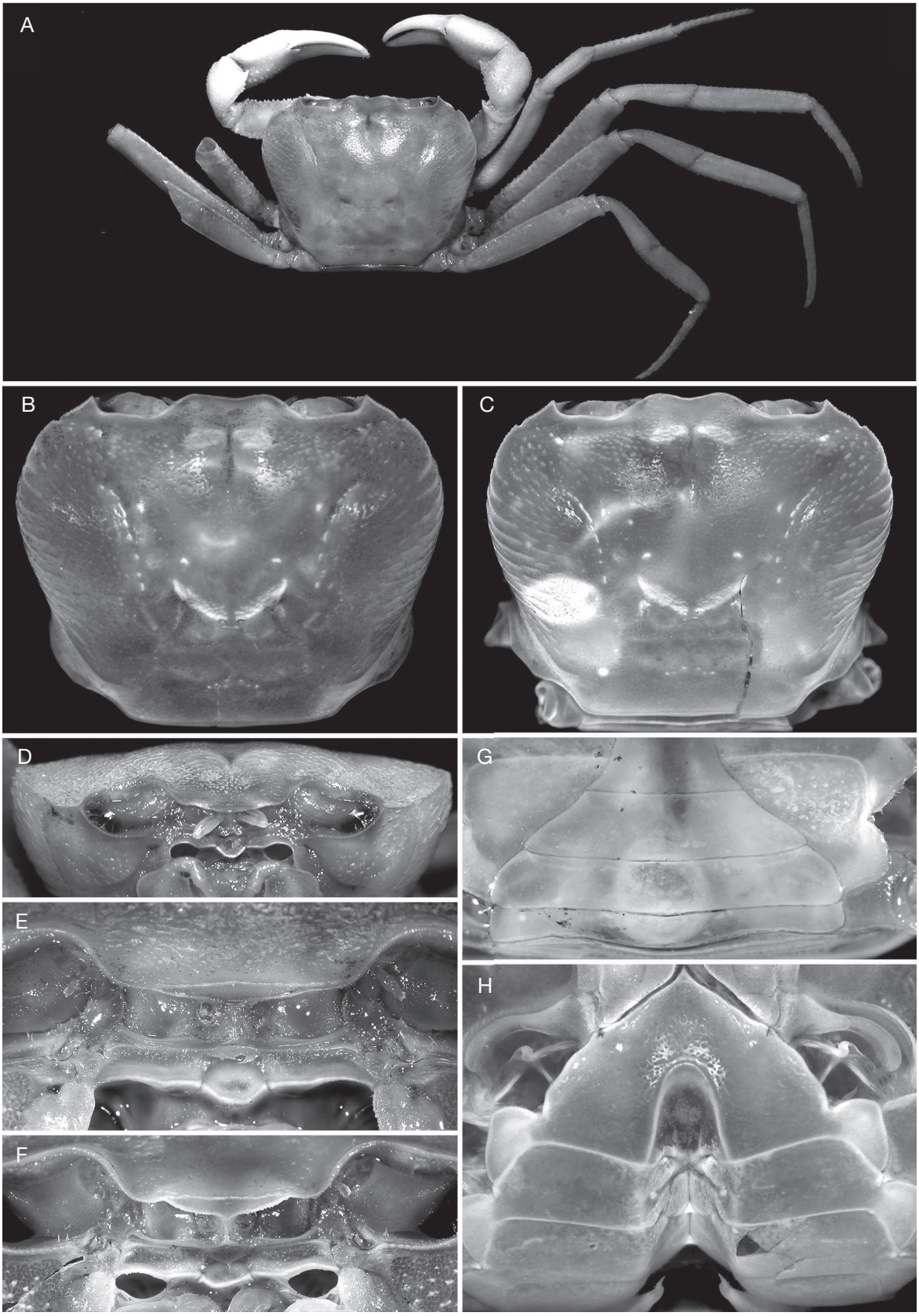

Fig. 10. — *Lemurophusa phasma* (Ng & Guinot, 2014) n. comb.: **A**, **D**, holotype, ♂ 23.1 × 18.9 mm (MNHN-IU-2013-13148), Kalimantan; **B**, **E**, paratype, ♂ 18.1 × 15.1 mm (ZRC 2014.0092), Kalimantan; **C**, **F**, **G**, **H**, paratype ♂ 23.5 × 19.0 mm (ZRC 2014.0092), Kalimantan. **A**, overall dorsal habitus; **B**, **C**, dorsal view of carapace; **D**, frontal view of cephalothorax; **E**, **F**, frontal median triangle, antennules, antennae and epistome; **G**, posterior thoracic sternum and pleonal somites 1-5; **H**, sternopleonal cavity.

Lemurophusa phasma (Ng & Guinot, 2014) n. comb.
(Figs 10; 11I-L; 16D; 17)

Balssiathelphusa phasma Ng & Guinot, 2014: 624, figs 1-3. — Grinang 2022: 391 [in list]. — Promdam *et al.* 2022: 8 [list]. — Guinot & Rodríguez Moreno 2024: 126, 127.

MATERIAL EXAMINED. — **Holotype. Indonesia** • ♂ 23.1 × 18.9 mm; main gallery of Gua Kambing, Mount Batu, Mangkalihat Peninsula, East Kalimantan; 1°09.444'N, 117°28.479'E; 454 m a.s.l.; coll. Expédition Spéléologique à Bornéo; 21.VII.2002; MNHN-IU-2013-13148.
Paratypes. Indonesia • 1 ♂ 18.1 × 15.1 mm [damaged, carapace cracked, all appendages detached], 1 ♂ 23.5 × 19.0 mm [dismembered, badly damaged, carapace detached, sternum broken, all appendages detached, damaged]; same data as holotype; ZRC 2014.0092.

DIAGNOSIS. — Carapace proportionately less wide, width to length ratio 1.20-1.23; dorsal surface of carapace with branchial regions not swollen, appearing gently convex in frontal view; frontal median triangle proportionately narrower; G1 slender, subterminal article with basal part wide, gradually tapering towards terminal article, terminal to subterminal article length ratio 0.18-0.19, terminal article relatively long, gently curved upwards, with numerous long and short setae; females not known.

DISTRIBUTION. — Known only from Gua Musang Cave in East Kalimantan, Borneo.

DESCRIPTION

Male

Carapace transversely ovate, wider than long, width to length ratio 1.20-1.23; carapace not high, height to width ratio 0.4; dorsal surface gently convex, but branchial regions not swollen in frontal view (Fig. 10A, B). Dorsal surface of carapace with regions well defined; gently rugose to smooth; lateral parts of anterolateral and branchial regions covered with short, oblique striae; mesogastric, urogastric, cardiac and intestinal regions smooth to finely granulated; suborbital, subhepatic, pterygostomial and sub-branchial regions with distinct striae (Fig. 10A-D). Epigastric cristae low, rugose but visible, separated by distinct Y-shaped furrow; postorbital cristae low, rugose, just discernible, not cristate (Fig. 10B, C). Cervical groove relatively deep; H-shaped median gastric groove distinct (Fig. 10A-C). Frontal margin divided into two low lobes, separated by shallow concavity; margin of each lobe gently convex, confluent with supraorbital margin; frontal median triangle distinct, with dorsal crista medially bent, fused with lateral cristae (Fig. 10A-C). External orbital tooth distinct, with outer margin granulated, sinuous; outer margin about twice length of inner margin; epibranchial tooth small, low, separated from margin by notch; rest of anterolateral margins convex, cristate, lined with striae (Fig. 10A-C). Posterolateral margin almost straight, distinctly converging towards gently convex to sinuous posterior carapace margin (Fig. 10A-C). Orbits subovate; eye filling orbital space; eye peduncle relatively short, stout; cornea large, pigmented (Fig. 10A-D). Supraorbital margin smooth, almost straight medially (Fig. 10B-D). Suborbital margin concave, lined with small granules, entire, without proximal tooth (Fig. 10D-F). Antennae short, not reaching cornea of eyes; antennules short, folding transversely in narrow fossae (Fig. 10D-F). Epistome relatively narrower, width to length ratio 8.3-9.0; posterior margin with distinct low subtriangular lobe, separated from lateral margin by fissure; each lateral margin sinuous, with low lobe (Fig. 10D-F). Mandibular palp with three articles; terminal article distinctly bilobed.

Third maxillipeds covering most of buccal cavity when closed; outer surfaces relatively smooth, with scattered punctae; ischium subrectangular, with distinct median oblique groove; merus subquadrate, just wider than long, anteroexternal angle rounded, not distinctly expanded; exopod relatively slender, reaching middle of merus, with distinct flagellum that is as long as half width of merus (Ng & Guinot 2014: fig. 1E).

Chelipeds elongate, approximately symmetrical (Fig. 10A). Anterior margin of basis-ischium with strong sharp granules, appearing serrated; margins of merus lined with sharp tubercles and granules, appearing gently serrated, with distinct subdistal sharp tooth on anterior margin. Outer surface of carpus gently rugose, with distinct long sharp tooth on inner distal margin, outer margin lined with small sharp granules (Fig. 10A). Outer surfaces of chelae granulated, punctate (Ng & Guinot 2014: fig. 2E, F). Fingers of chelae relatively slender, longer than palm; dorsal margin of dactylus and ventral margin of pollex with small granules; cutting edges of both fingers with variously sized teeth (Ng & Guinot 2014: fig. 2E, F).

Ambulatory legs long; second pair longest, last pair shortest (Fig. 10A). Outer surface of merus slightly rugose, dorsal margin weakly serrated, subcristate, with subdistal angle but no obvious spine or tooth, length to width ratio of fourth merus 4.9; carpus relatively smooth, outer surface of first to third legs with low submedian crista, that on fourth leg smooth; outer surface of propodus smooth; dactylus very long, gently curved, quadrate in cross section, margins with short, sharp corneous spines (Ng & Guinot 2014: fig. 2D).

Thoracic sternum relatively smooth, punctate in parts, not distinctly wide, length to width ratio of anterior thoracic sternites 0.5 (Fig. 10H). Sternite 1 small, triangular, separated from sternite 2 by low ridge; sternites 2-4 completely fused except for lateral notches demarcating sternites 3 and 4 (Fig. 10H); distinct median transverse bridges present between sternites 5 and 6, and sternites 6 and 7, bridges interrupting median lines on sternites 5-8; median line on sternite 5 deep, reaching level of press-button tubercles; inner edges of s4/5 ending near median part of sternopleonal cavity, not reaching s5/6; median plate in three separate parts corresponding to median plate for sternites 5, 6, and fused piece for sternites 7 and 8 (Figs 10H; 16D; 17). Penis coxal, on condyle of coxa of fourth ambulatory leg. Sternopleonal cavity deep, reaching imaginary line connecting proximal edges of cheliped coxae (Fig. 10H). Male pleonal locking tubercle peg-like, positioned on submedian part of sternite 5 (Fig. 10H).

Pleon T-shaped, all somites and telson free; telson elongate, triangular, length to width ratio 1.3, lateral margins gently concave, shorter than somite 6; somite 6 elongate, length to width ratio 1.32, lateral margins distinctly concave; somites 3-5 trapezoidal, gradually decreasing in width; somite 2 subrectangular, wide, reaching bases of coxae of fourth ambulatory legs; somite 1 longitudinally narrow, subequal in width to somite 2 (Fig. 10G; Ng & Guinot 2014: fig. 2A-C); thoracic sternite 8 not visible when pleon closed (Fig. 10G).

Fig. 11. — *Natunusa natunaensis* (Bott, 1970) n. comb.: **A**-**E**, holotype, ♂ 23.0 × 20.0 mm (RMNH D29300), Natuna Island; **F**-**H**, ♂ 12.9 × 11.3 mm (ZRC 2021.0831), Natuna Island; **I**-**L**, *Lemurophusa phasma* (Ng & Guinot, 2014) n. comb., holotype, ♂ 23.1 × 18.9 mm (MNHN-IU-2013-13148), Kalimantan: **A**, right G1 (dorsal view); **B**, right G1 (ventral view); **C**, distal part of right G1 (dorsal view); **D**, distal part of right G1 (ventral view); **E**, right G2; **F**, **J**, distal part of left G1 (ventral view); **G**, **H**, distal part of left G1 (dorsal views, drawn at slightly different angles); **I**, left G1 (ventral view); **K**, distal part of left G1 (dorsal view); **L**, left G2. Scale bars: A-E, J, K, 0.5 mm; C, D, F-H, I, L, 0.1 mm. A-H after Ng *et al.* (2023: fig. 13G-N); I-L after Ng & Guinot (2014: fig. 3).

G1 slender; subterminal article with basal part wide, gradually tapering towards terminal article, outer margin concave; terminal article demarcated by groove; terminal to subterminal article length ratio 0.18-0.19, terminal article relatively long, gently curved upwards, proximal part wide, distal part narrowing to sharp tip which gently curves upwards, outer lateral surfaces with numerous long and short setae (Fig. 11I-K). G2 shorter than G1; distal article short, 0.11-0.12 times length of basal article (Fig. 11L).

Female
Not known.

REMARKS
Ng & Guinot (2014: 629) noted that the cave where *Lemurophusa phasma* n. comb. was collected from a cave that "is part of the main gallery in Gua Kambing, and has numerous swiftlets living inside. Many parts of the cave floor were covered with moist guano and there are numerous cave crickets (Rhaphidophoridae), gnats, heteropteran bugs and spiders present there …" (see also Degouve *et al.* 2002: 29). While the species has not been found outside caves, it "… has a pale colouration in life and the pereopods are elongated; it does not have the reduced eyes and/or pigmentation associated with true troglobites" (Ng & Guinot 2014: 629). Guinot & Rodríguez Moreno (2024: 126-127) subsequently reported two female specimens from a nearby cave. *Lemurophusa phasma* n. comb. is probably like several other troglophiles in Borneo that are closely associated with caves but not completely adapted to a wholly cavernicolous lifestyle". This is a phenomenon that has also been observed in several other Bornean cavernicoles (see Holthuis 1986; Guinot 1988; Promdam *et al.* 2022; Guinot & Rodríguez Moreno 2024).

Lemurophusa empusa n. sp.
(Figs 12; 13)

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Balssiathelphusa phasma – Guinot & Rodríguez Moreno 2024: 126-127 (not *Balssiathelphusa phasma* Ng & Guinot, 2014).

MATERIAL EXAMINED. — **Holotype. Indonesia** • ♀ 24.2 × 18.5 mm; Kecabe Cave, Sungai Baai karst, East Kalimantan; 1°38.018'N, 117°24.240'E; 80 m; coll. Expédition Spéléologique à Bornéo; 3.VIII.2007; MZB Cru.
Paratype • 1 ♀ 22.2 × 17.2 mm; same data as holotype; MZB Cru.

ETYMOLOGY. — The species is named after Empusa, a demigoddess of Greek mythology. The name is used as a noun in apposition.

DISTRIBUTION. — Known only from the type locality, Kecabe Cave in East Kalimantan, Indonesia.

DIAGNOSIS. — Carapace proportionately wider, wider than long, width to length ratio 1.29-1.30; dorsal surface of carapace with branchial regions distinctly swollen, appearing prominently convex in frontal view; frontal median triangle relatively wider; males, not known; vulva large, round, almost completely surrounded by a rim, without a vulvar cover but entirely covered by soft membrane.

COLOUR. — The two female type specimens of *Lemurophusa empusa* n. gen., n. sp. still have the carapace and ambulatory legs brownish (in ethanol), which contrasts with the pale colour of the type specimens of *L. phasma* n. comb. This may suggest *L. empusa* n. gen., n. sp. spends more of its time outside caves.

REMARKS
Two female specimens from Kecabe Cave, preliminarily examined and identified with *Balssiathelphusa phasma* by Guinot & Rodríguez Moreno (2024: 126, 127), are here selected as the holotype and paratype of *Lemurophusa empusa* n. gen., n. sp.

Although only females of *Lemurophusa empusa* n. gen., n. sp. are available, these specimens cannot be referred to *L. phasma* n. comb. because the carapace is proportionately wider and more rectangular in shape, the width to length ratio being 1.29-1.30 (Fig. 12) (vs carapace less wide, the width to length ratio being 1.20-1.23 in *L. phasma* n. comb.; Fig. 10A-C); the dorsal surface of the carapace has the branchial regions distinctly swollen, appearing prominently convex in frontal view (Fig. 13A) (vs branchial regions only gently convex in frontal view in *L. phasma* n. comb.; Fig. 10D); and the frontal median triangle is relatively wider (Fig. 13A-C) (vs narrower in *L. phasma* n. comb.; Fig. 10D-F). It must be noted that while the gastric regions of *L. phasma* n. comb. and *L. empusa* n. gen., n. sp. are similar in form (hence their carapace height to width ratios are similar at 0.4), the branchial regions of the *L. empusa* n. gen., n. sp. are prominently more swollen giving the species a distinctly more inflated appearance (Fig. 13A). The frontal median triangle of *L. empusa* n. gen., n. sp. also appears to be wider, with the lateral parts reaching the edges of the frontal margin (Fig. 13A-C) but in *L. phasma* n. comb., it usually does not reach the lateralmost parts (Fig. 10D-F).

The type locality, Kecabe Cave, stretches 3840 m. Entrances to the north open along a cliff delimiting a huge collapse of several hundred metres in diameter. The Sungai Baai River flows over a few tens of metres in the open air at the bottom of this collapse and probably continues a good hundred metres below. The cavity has three distinct parts that are «speleologically connected» only by the overhang of the cliff. Porches open at different levels in the cliff and form three entrances about fifty metres apart. There is a large river flowing through a conduit over 15 m in diameter, with variable flow rates, with some deep pools, 600 to 800 m in size (Lips *et al.* 2007: 29-31).

The Kecabe Cave, from where the holotype and paratype of *Lemurophusa empusa* n. gen., n. sp. is described, are in separate karst formations about 50 km north-northwest of Gua Kambing, the type locality of *L. phasma* n. comb., and are separated by at least one major mountain range (Fig. 18).

Lemurophusa sp.
(Figs 14; 15)

Gecarcinucid sp. – Guinot & Rodríguez Moreno 2024: 126, fig. 8.

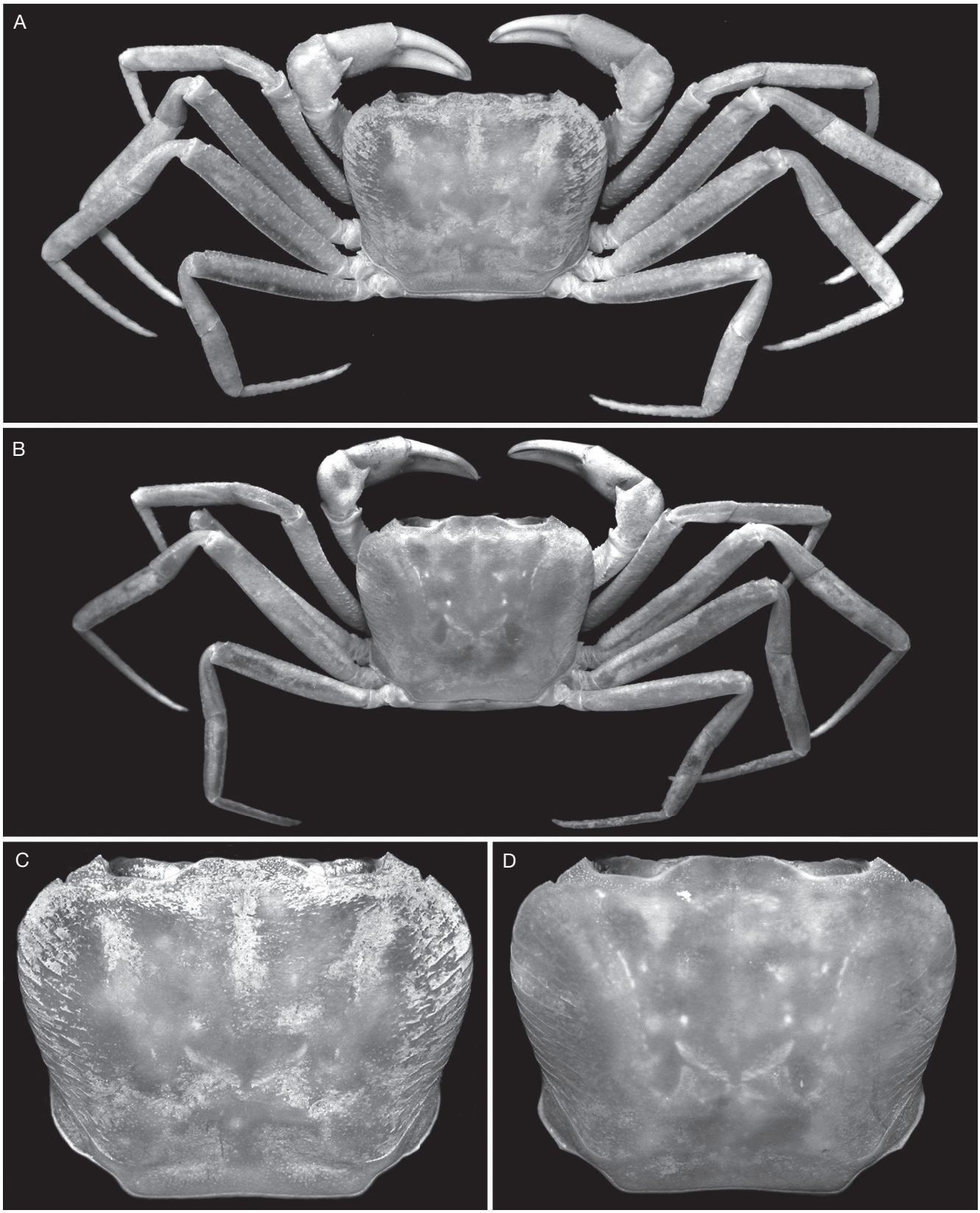

FIG. 12. — *Lemurophusa empusa* n. gen., n. sp.: **A**, **C**, holotype, ♀ 24.2 × 18.5 mm (MZB Cru), Kalimantan; **B**, **D**, paratype ♀ 22.2 × 17.2 mm (MZB Cru), Kalimantan. **A**, **B**, overall dorsal habitus; **C**, **D**, dorsal view of carapace.

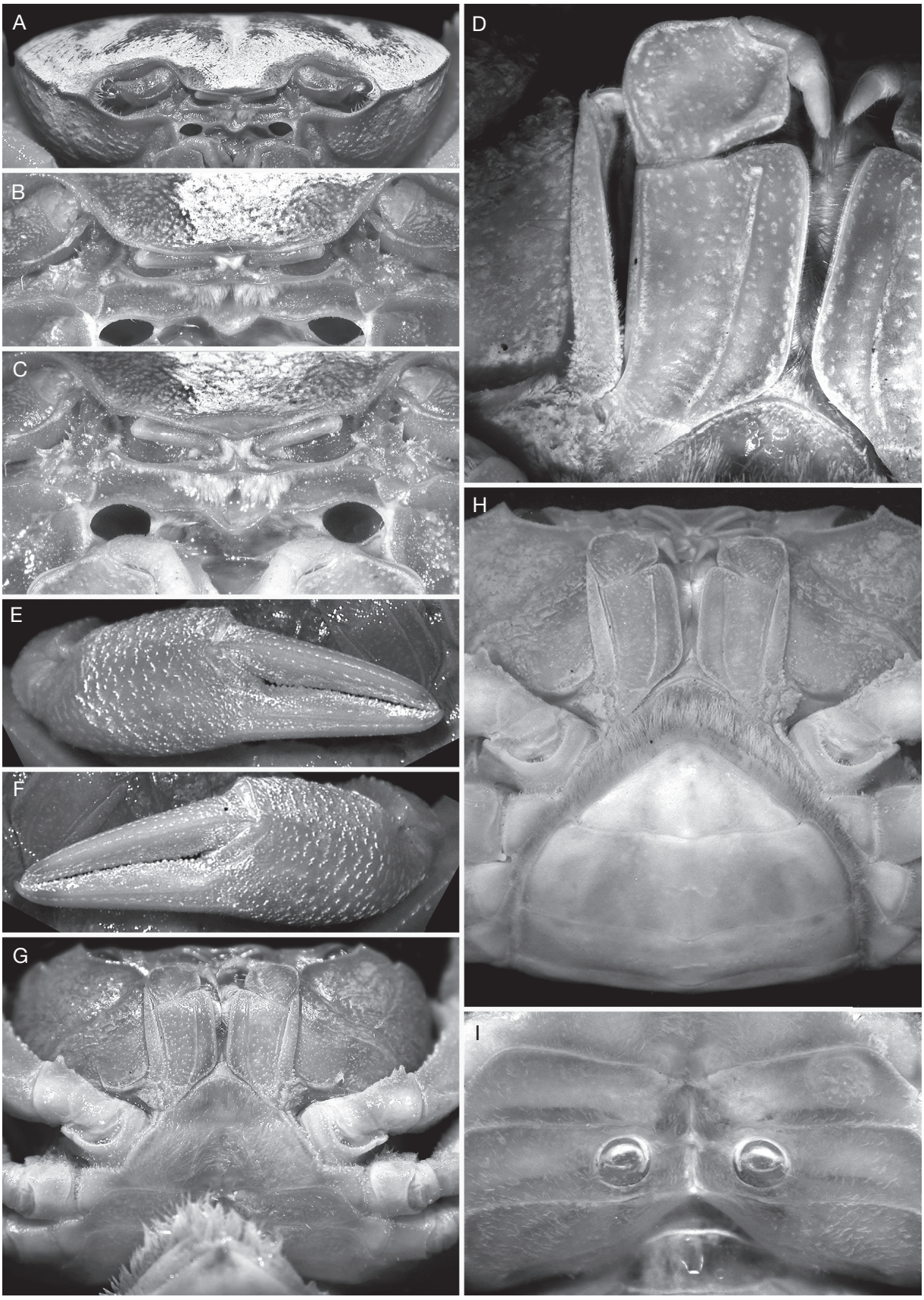

Fig. 13. — *Lemurophusa empusa* n. gen., n. sp., holotype, ♀ 24.2 × 18.5 mm (MZB Cru), Kalimantan: **A**, frontal view of cephalothorax; **B**, **C**, frontal median triangle, antennules, antennae and epistome; **D**, right third maxilliped; **E**, outer view of right chela; **F**, outer view of left chela; **G**, third maxillipeds and anterior thoracic sternum; **H**, third maxillipeds, anterior thoracic sternum and pleon; **I**, sternopleonal cavity showing vulvae.

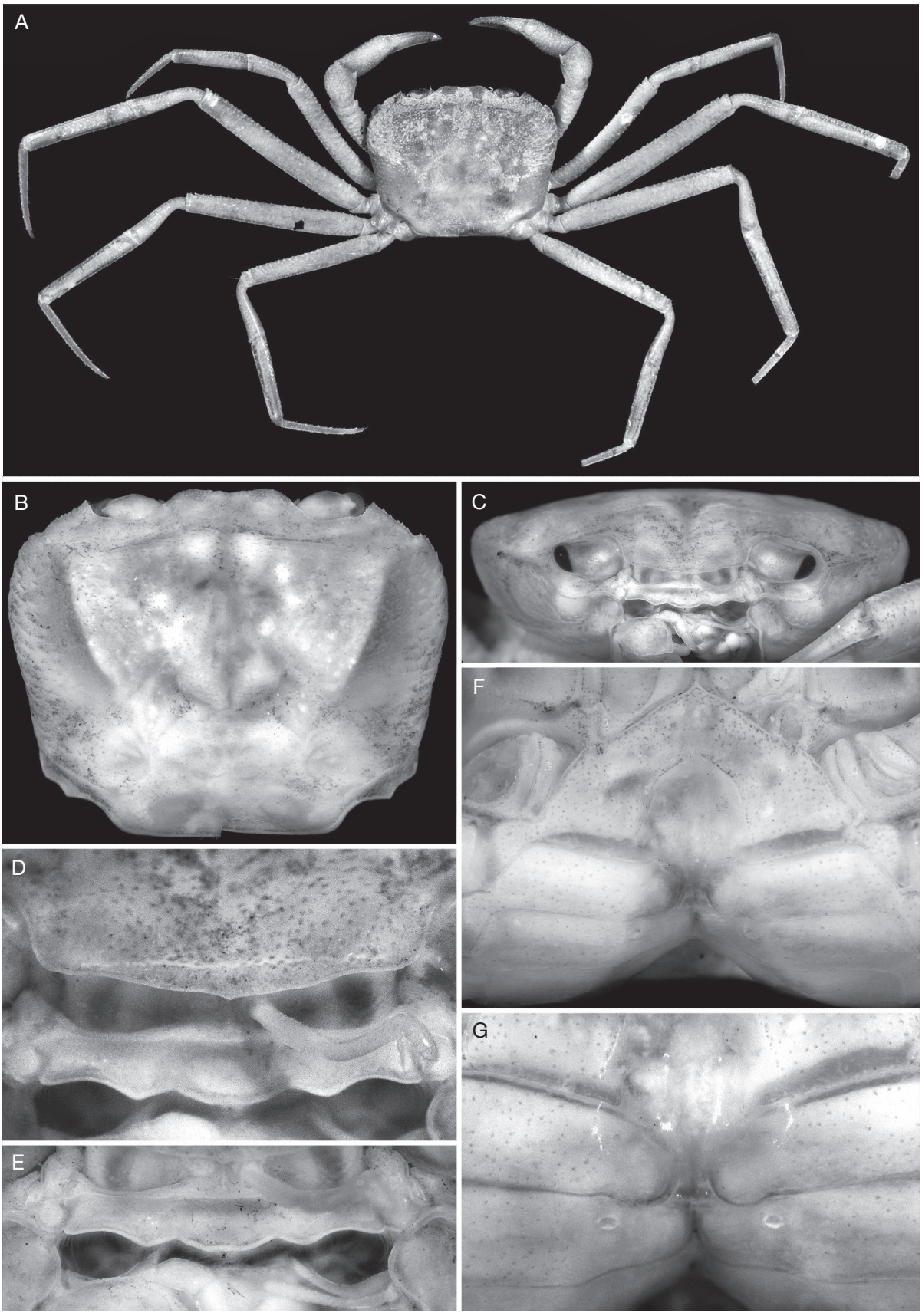

FIG. 14. — *Lemurophusa* sp., juvenile ♀ 9.9 × 7.7 mm (MZB Cru 5712), Kalimantan: **A**, overall dorsal habitus; **B**, dorsal view of carapace; **C**, frontal view of cephalothorax; **D**, frontal median triangle, antennules, antennae and epistome; **E**, antennules and epistome; **F**, anterior thoracic sternum and sternopleonal cavity; **G**, sternopleonal cavity showing vulvae. Credits: MNHN-Soubzmaigne.

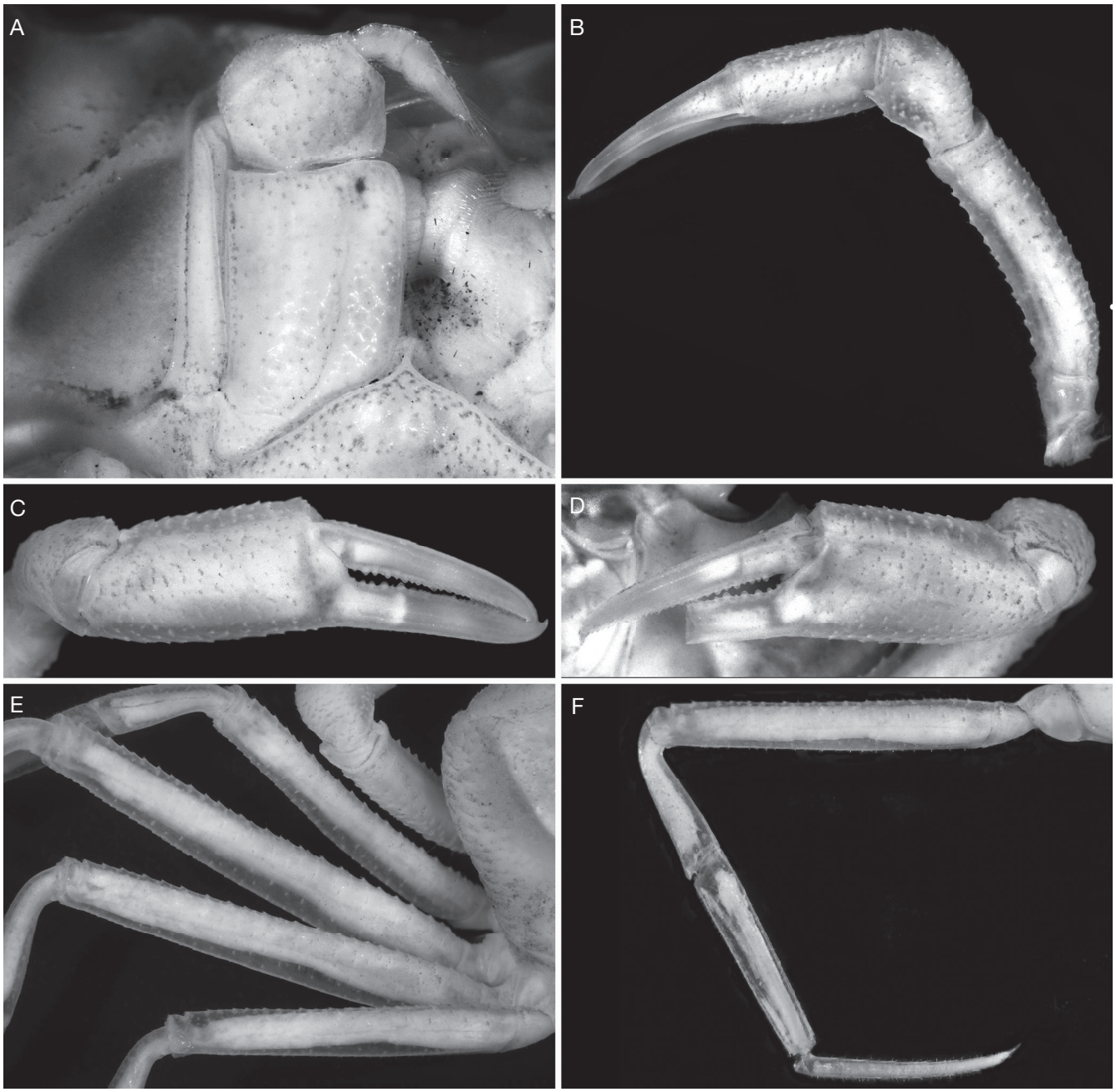

Fig. 15. — *Lemurophusa* sp., juvenile ♀ 9.9 × 7.7 mm (MZB Cru 5712), Kalimantan: **A**, right third maxilliped; **B**, dorsal view of right chela; **C**, outer view of right chela; **D**, outer view of left chela (pollex broken); **E**, left first to fourth ambulatory meri; **F**, left fourth ambulatory leg.

Material examined. — **Indonesia** • 1 juvenile ♀ 9.9 × 7.7 mm; Lubang Tebot Cave, Merabu karst, East Kalimantan; 1°34.964'N, 117°21.113'E; 360 m; coll. Borneo 2010 Expedition; 9.VIII.2010; MZB Cru 5712.

Remarks

A juvenile female (9.9 × 7.7 mm, MZB Cru 5712) was collected from Lubang Tebot Cave, a location about 10 km south-southwest of Kecabe Cave (Guinot & Rodríguez Moreno 2024: 126), who noted that this small specimen "differs from the typical *B. phasma* n. comb. in having cylindrical eyestalks tending to an ogival shape and much longer and thinner ambulatory legs". However, considering that "it could actually belong to a new genus but the fact that it is a young female does not allow recourse to the male characters", they left it under 'Gecarcinucid sp.'.

The juvenile female from Lubang Tebot Cave (MZB Cru 5712) is provisionally referred to *Lemurophusa* n. gen. but its species status is uncertain. While it shares some of the characters of *L. empusa* n. gen., n. sp. (from Kecabe Cave), notably in the more swollen carapace and the wide frontal median triangle (Fig. 14A-E), it nevertheless differs in that the carapace is relatively more rectangular in shape with the anterolateral margin less convex and the posterolateral margins

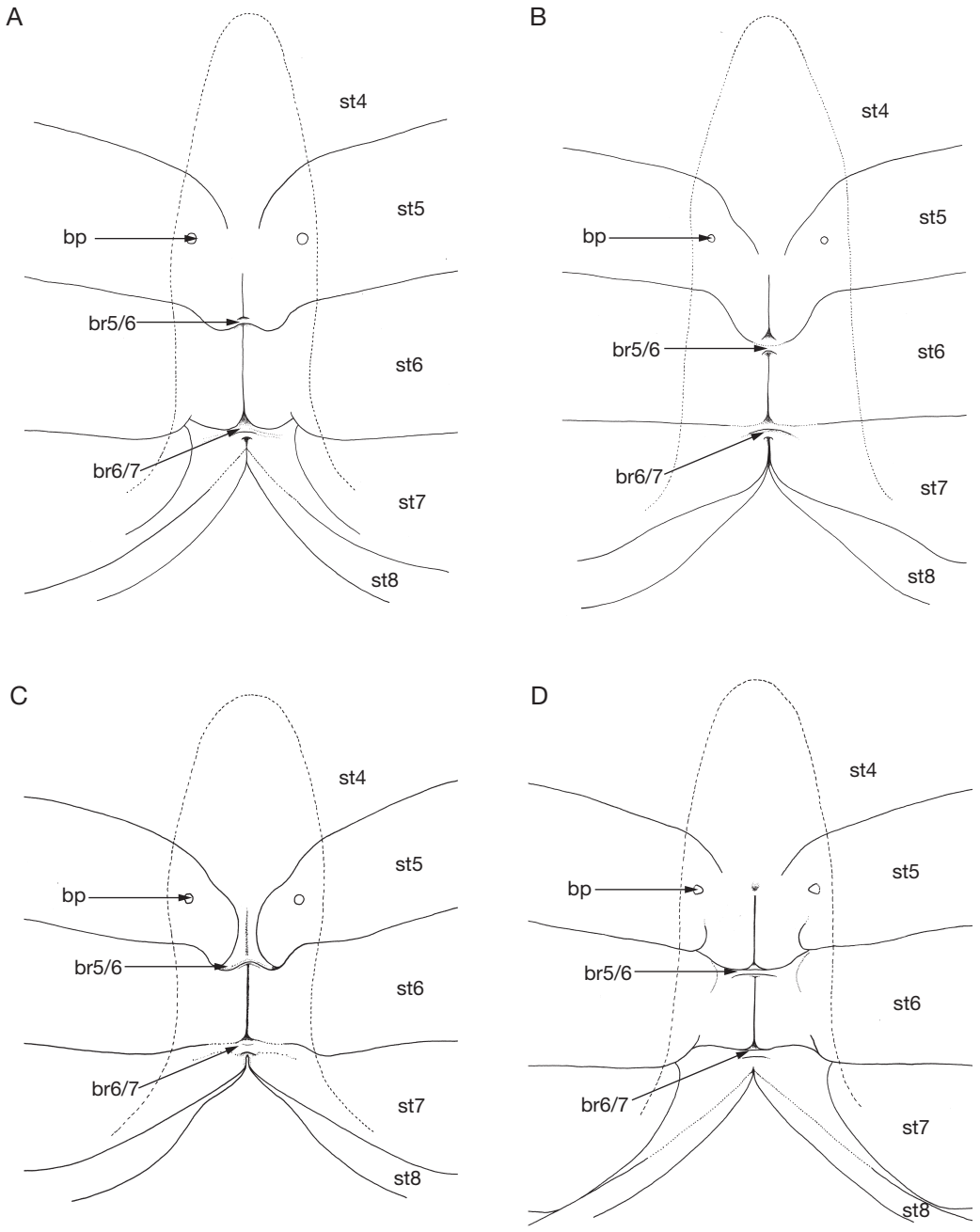

FIG. 16. — Thoracic sternums of: **A**, *Balssiathelphusa sucki* (Balss, 1937), holotype, ♂ 21.2 × 17.1 mm (ZMH-K-003545), "Sumatra"; **B**, *B. cursor* Ng, 1986, paratype, ♂ 15.6 × 13.4 mm (ZRC 1989.3036), Kalimantan; **C**, *Natunusa natunaensis* (Bott, 1970) n. comb., ♂ 12.9 × 11.3 mm (ZRC 2021.0831), Natuna Island; **D**, *Lemurophusa phasma* (Ng & Guinot, 2014) n. comb., paratype, ♂ 18.1 × 15.1 mm (ZRC 2014.0092), Kalimantan. Abbreviations: **bp**, press button tubercle of pleonal locking mechanism; **br5/6**, median bridge between thoracic sternites 5 and 6; **br6/7**, median bridge between thoracic sternites 6 and 7; **st4-8**, thoracic sternites 4-8, respectively.

almost straight (Fig. 14B) (vs anterolateral margin more convex and the posterolateral margins are more sinuous in *L. empusa* n. gen., n. sp.; Fig. 12C, D); the epigastric and postorbital cristae are relatively sharper and more prominent (Fig. 14B) (vs cristae lower and more rounded in *L. empusa* n. gen., n. sp.; Fig. 12C, D); the notch between the external orbital tooth and rest of the anterolateral margin is shallow (Fig. 14B) (vs notch deep in *L. empusa* n. gen., n. sp.; Fig. 12C, D); the ocular peduncles are relatively shorter (Fig. 14B, C) (vs longer in *L. empusa* n. gen., n. sp.; Fig. 13A); the median lobe of the posterior margin of the epistome is low (Fig. 14D, E) (vs lobe is clearly more elongate in *L. empusa* n. gen., n. sp.; Fig. 13B, C); the ischium of the third maxilliped is relatively shorter (Fig. 15A) (vs longer in *L. empusa* n. gen., n. sp.; Fig. 13D);

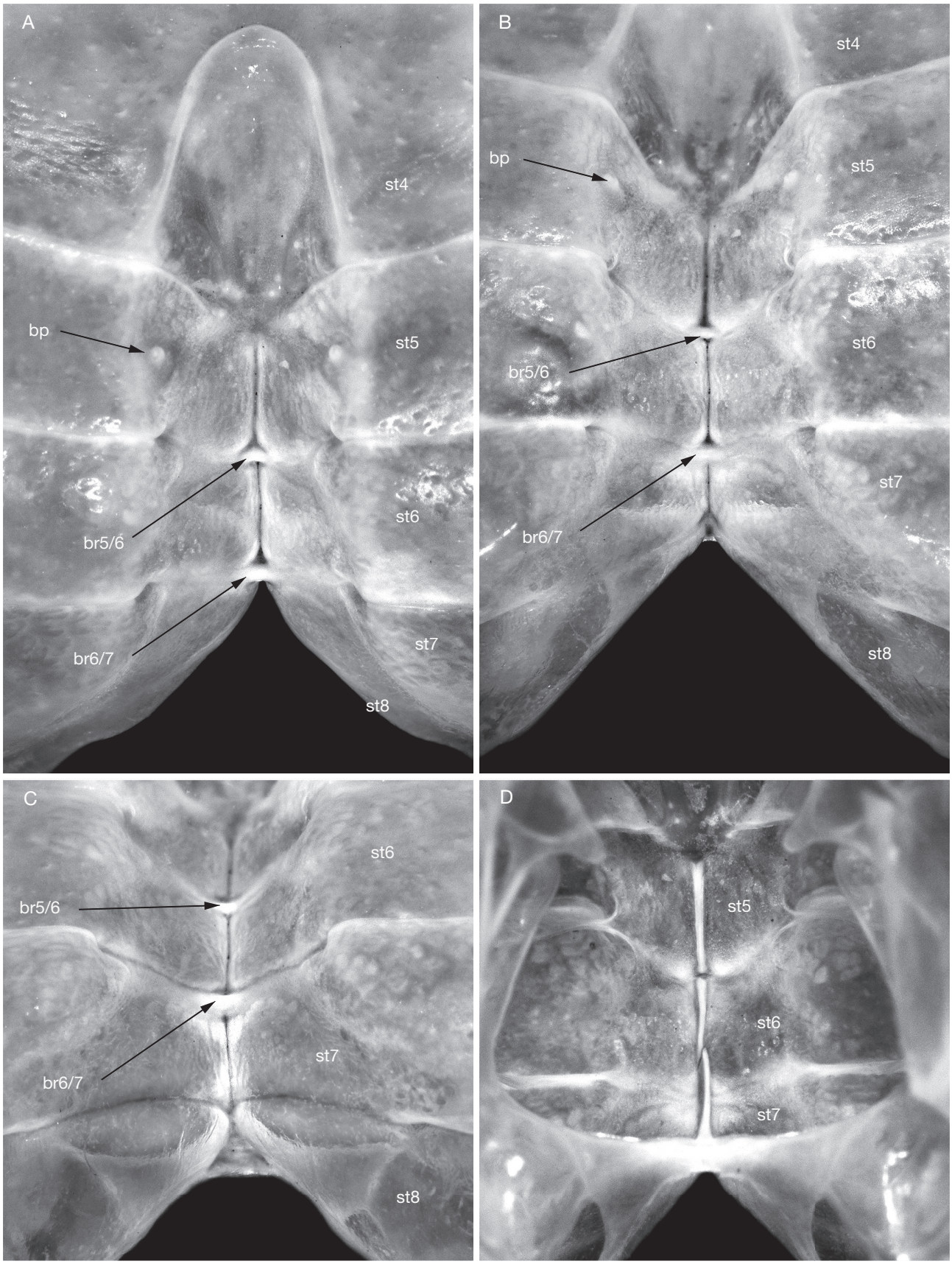

FIG. 17. — *Lemurophusa empusa* n. gen., n. sp., holotype, ♀, 24.2 × 18.5 mm (MZB Cru), Kalimantan, thoracic sternum: **A-C**, pattern of sutures in sternopleonal cavity photographed at different angles; **D**, internal skeletal view showing longitudinal median plate. Abbreviations: **bp**, press button tubercle of pleonal locking mechanism; **br5/6**, median bridge between thoracic sternites 5 and 6; **br6/7**, median bridge between thoracic sternites 6 and 7; **st4-8**, thoracic sternites 4-8, respectively.

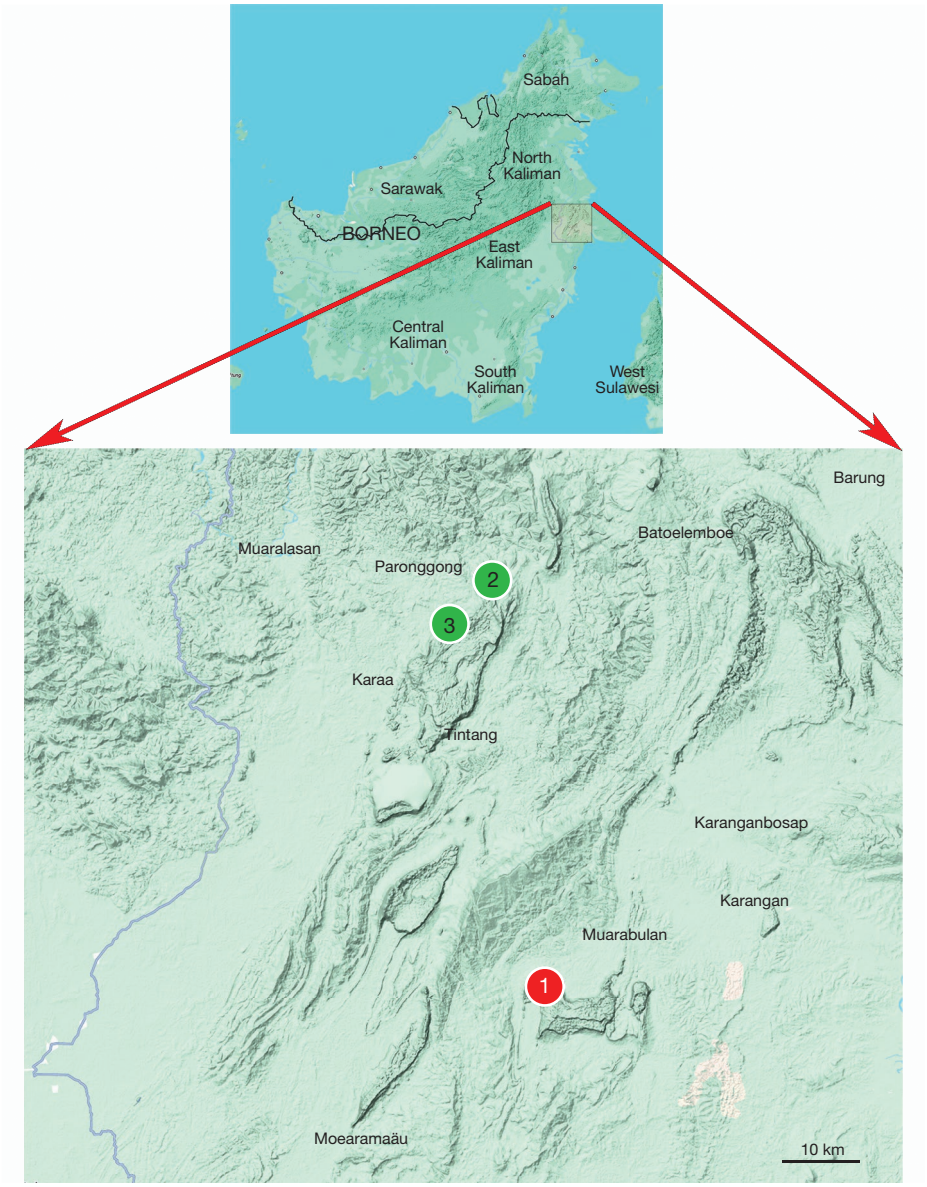

FIG. 18. —Indonesian Borneo localities of *Lemurophusa phasma* (Ng & Guinot, 2014) n. comb. (**red circle**) and *L. empusa* n. gen., n. sp. (**green circles**) in East Kalimantan, Indonesia, Borneo: **1**, Gua Kambing, Mount Batu, Mangkalihat Peninsula, 01°09.444'N, 117°28.479'E; **2**, Kecabe Cave, Sungai Baai karst, 01°38.018'N, 117°24.240'E; **3**, Lubang Tebot Cave, Merabu karst, 01°34.964'N, 117°21.113'E. From Google Maps.

and the ambulatory legs are proportionately longer and more slender (Figs 14A; 15E, F) (vs longer and relatively stouter in *L. empusa* n. gen., n. sp.; Fig. 12A, B). These differences suggest that it may represent a separate species, but the lack of adult material makes it difficult to make a more definitive decision. It is important to note that the present specimen was collected from Lubang Tebot Cave, and while this location is near Kecabe Cave (type locality of *L. empusa* n. gen., n. sp.), it is from a different cave system and it is not known if they are connected (Fig. 18). While the proportions of the ambulatory legs may be accounted for by allometric growth, juveniles of long-legged species usually have relatively longer legs (e.g., see Ng & Guinot 2001); the situation for the other differences observed is unclear.

This small specimen appears to have thoracic sternites 1-4 fused, and sternite 1 does not appear to be separated by any ridge or groove (Fig. 14F, G). In addition, while s4/5 is medially interrupted, the inner edge of each part of the suture curves to join s5/6, adjacent to bridge at s5/6 (Fig. 14F, G). This is probably because of its immaturity, as in adult specimens of *Lemurophusa* n. gen., the inner edge of s4/5 stops before the level of the press-button tubercle (Figs 10H; 16D; 17A, B). The vulva of this juvenile female is not developed (Fig. 14G), and although it resembles that of the adult (Fig. 13I), it is much smaller.

In life, the specimen of *Lemurophusa empusa* n. gen., n. sp. had a pale brown carapace colour and the pereiopods were white.

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REFERENCES

Balss H. 1934. . — Die Krabben der Reise J. W. Harms' nach der Christmas-Insel und dem Malaiischen Archipel. *Zoologische Anzeiger* 106 (10): 225–237.

Balss H. 1937. — Potamoniden (Dekapoda Brachyura) der Philippinen und des Malayischen Archipels. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 34 (3-5): 143-197, figs 1-36. https://onlinelibrary.wiley.com/doi/abs/10.1002/iroh.19370340111

Bonarelli L. 2001. — *Guido Bonarelli (1871-1951) La vita e l'opera scientifica*. Associazione Pionieri e Veterani Agip, Ancona: 1-104.

Bott R. 1968. — Potamiden aus Süd-Asien (Crustacea, Decapoda). *Senckenbergiana biologica* 49 (2): 119-130, figs 1-19.

Bott R. 1969. — Flüsskrabben aus Asien und ihre Klassifikation (Crustacea, Decapoda). *Senckenbergiana biologica* 50 (5-6): 359-366.

Bott R. 1970. — Die Süsswasserkrabben von Europa, Asien, Australien und ihre Stammesgeschichte. Eine Revision der Potamoidea und Parathelphusoidea (Crustacea, Decapoda). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, Frankfurt 526: 1-338, pls 1-58.

Breddin G. 1912. — Hemiptera Indo-Malaya nova vel minus cognita descripsit. *Archiv für Naturgeschichte* (A) 78 (6): 76-84.

Breddin G. 1900. — Hemiptera Sumatrana collecta a dom. Henrico Dohrn, enumerate et descripsit. Pars I. *Stettiner Entomologische* 61: 275-336.

Colosi G. 1920. — I Potamonidi del R. Museo Zoologico di Torino. *Bollettino dei Musei di Zoologia ed Anatomia comparata*, Università di 35 (734): 1-39.

Cumberlidge N. & Ng P. K. L. 2009. — Systematics, evolution, and biogeography of freshwater crabs, *in* Martin J. W., Crandall K. A. & Felder D. L. (eds), *Crustacean Issues 18: Decapod Crustacean Phylogenetics*: 491-508.

Cumberlidge N., Ng P. K. L., Yeo D. C. J., Magalhães C., Campos M. R., Alvarez F., Naruse T., Daniels S. R., Esser L. J., Attipoe F. Y. K., Clotilde-Ba F.-L., Darwall W., Mcivor A., Collen B. & Ram M. 2009. — Freshwater crabs and the biodiversity crisis: importance, threats, status, and conservation challenges. *Biological Conservation* 142: 1665-1673. https://doi.org/10.1016/j.biocon.2009.04.024

Davie P. J. F., Guinot D. & Ng P. K. L. 2015. — Anatomy and functional morphology of Brachyura (Chapter 71-2), *in* Castro P., Davie P. J. F., Guinot D., Schram F. R. & von Vaupel Klein J. C. (eds), *Decapoda: Brachyura, Treatise on Zoology–Anatomy, Taxonomy, Biology*. Vol. 9C-I. Brill, Leiden and Boston: 11-163. https://doi.org/10.1163/004ed

Degouve P., Lips B. & Lips J. 2002. — *Gua Kambing 2002. Expédition Spéléologique à Bornéo (Kalimantan– Indonésie). Expédition organisée par l'association « Le Kalimanthrope », avec la participation du G.S. Vulcain, du C.A.F. Albertville, de la S.D.N.O. et de l'association Centre Terre. Projet parrainé par la CREI (Fédération Française de Spéléologie)*. Activités spéléologiques – C. A. F. Albertville, 32 p.

Forel A. 1901. — Formiciden des Naturhistorischen Museums zu Hamburg. Neue *Calyptomyrmex-*, *Dacryon-*, *Podomyrna-* und *Echinopla*-Arten. *Mitteilungen aus dem Naturhistorischen Museum* 18: 45-82.

Fransen C. H. J. M., Holthuis L. B. & Adema J. P. H. M. 1997. — Type-catalogue of the Decapod Crustacea in the collections of the Nationaal Naturhistorisch Museum, with appendices of pre-1900 collectors and material. *Zoologische Verhandelingen* 311: i-xvi, 1-344.

Gazette of the City of Hamburg. 1896. — https://content.staatsbibliothek-berlin.de/dc/PPN746848072.ocr.txt

Grinang J. 2022. — A review of the freshwater crabs (Decapoda: Brachyura) of Borneo. *Malayan Nature Journal* 74 (3): 385-400.

Guinot D. 1988. — Les crabes cavernicoles du monde. *Mémoires de Biospéologie*, Paris 15: 3-40.

Guinot D. & Rodríguez Moreno P. A. 2024. — *Ngan mayla* gen. et sp. nov., a new blind potamid cave crab from Borneo, Kalimantan (Crustacea: Decapoda: Brachyura: Potamoidea, Potamidae), and three other unidentified cave crabs from the same region. *Zootaxa* 5476 (1): 115-137. https://doi.org/10.11646/zootaxa.5476.1.13

Guinot D., Tavares M. & Castro P. 2013. — Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. *Zootaxa* 3665 (1): 1-414. https://doi.org/10.11646/zootaxa.3665.1.1

Haan W. De. 1833-1849. — Crustacea, in von Siebold P. F., *Fauna Japonica, sive Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batavia imperium tenent, suscepto, annis 1823-1830 collegit, notis, observationibus a adumbrationibus illustravit. Lugduni Batavorum*, fasc. 1-8: i-xxi+vii-xvii+ix-xvi+1-243, pls 1-55, A-Q, circ., pl. 2. https://doi.org/10.5962/bhl.title.124951

Hall R. 1996. — Reconstructing Cenozoic SE Asia, *in* Hall R. & Blundell D. (eds), *Tectonic Evolution of Southeast Asia*, Geological Society of London: 153-184. https://doi.org/10.1144/GSL.SP.1996.106.01.11

Holthuis L. B. 1979. — Cavernicolous and terrestrial decapod crustacea from Northern Sarawak, Borneo. *Zoologische Verhandelingen* 171: 3-47, figs 1-9, pls 1-8.

Holthuis L. B. 1986. — Decapoda, *in* Botosaneanu L. (ed.), *Stygofauna Mundi. A faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters (including the marine interstitial)*. Leiden, The Netherlands: E.J. Brill: 589-615.

Klaus S., Brandis D., Ng P. K. L., Yeo D. C. J. & Schubart C. D. 2009. — Phylogeny and biogeography of Asian freshwater crabs of the family Gecarcinucidae (Brachyura: Potamoidea), *in* Martin J. W., Crandall K. A. & Felder D. L. (eds), *Crustacean Issues 18: Decapod Crustacean Phylogenetics*: 509-531.

Lips B., Lips J. & Robert X. 2007. — Bornéo 2007, Expédition spéléologique au Kalimantan (Indonésie), 25 juillet au 30 août 2007. *Echo des Vulcains* 65: 89-156.

Lips B., Lips J., Robert X., Sénécal P., Placido C. & Geneau A. 2010. — *Bornéo 2010 Kalimantan (Indonésie) 28 juillet au 30 août 2010*. Groupe Spéléologique Vulcain. Fédération française de Spéléologie, Lyon, 66 p.

Lohman D. J., de Bruyn M., Page T., von Rintelen K., Hall R., Ng P. K. L., Shih H.-T., Carvalho G. C. & von Rintelen T.

2011. — Beyond Wallace's Line: genetics and geology inform biogeographical insights in the Indo-Australian Archipelago. *Annual Review of Ecology, Evolution, and Systematics* 42 (1): 205-226. https://doi.org/10.1146/annurev-ecolsys-102710-145001

MAN J. G. DE. 1879. — On some new or imperfectly known Podophthalmous Crustacea of the Leyden Museum. *Notes from the Leyden Museum* 1 (2): 53-73.

MAN J. G. DE. 1892. — Decapoden des Indischen Archipels. *in* WEBER M. (ed.), *Zoologische Ergebnisse einer Reise in Niederlandisch OstIndien* 2: 265-527, pls 15-29. https://doi.org/10.1163/9789004599048_008

MAN J. G. DE. 1899. — Zoological Results of the Dutch Scientific Expedition to Central Borneo. The Crustacea. Part II, Brachyura. *Notes from the Leyden Museum* 21: 53-144, pls 5-12.

MAN J. G. DE. 1902. — Die von Herrn Professor Kükenthal im indischen Archipel gesammelten Dekapoden und Stomatopoden, *in* KÜKENTHAL W. (ed.), Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo, in Aufträge der Senckenberg. Naturforsch. Gesellschaft ausgeführt von Dr. Willy Kükenthal. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft* 25 (3): 467-929, pls 19-27. https://doi.org/10.5962/bhl.title.10409

MAGALHÃES C. & TÜRKAY M. 1996. — Taxonomy of the neotropical freshwater crabs family Trichodactylidae. I. The generic system with description of some new genera (Crustacea: Decapoda: Brachyura). *Senckenbergiana biologica* 75 (1, 2): 63-95.

MILNE EDWARDS H. 1853. — Mémoire sur la famille des Ocypodiens. *Annales de Sciences naturelles, Zoologie* (3) 20: 163-228, pls 6-11. https://www.biodiversitylibrary.org/part/167569

NG P. K. L. 1986a. — *Balssiathelphusa cursor* sp. nov., a new species of freshwater crab from East Kalimantan (Decapoda: Parathelphusidae). *Treubia* 29 (3): 207-213.

NG P. K. L. 1986b. — *Phricotelphusa hockpingi* sp. nov., a new gecarcinucid freshwater crab from Perak, West Malaysia (Decapoda, Brachyura). *Crustaceana* 51 (3): 270-276.

NG P. K. L. 1988. — *The Freshwater Crabs of Peninsular Malaysia and Singapore*. Department of Zoology, National University of Singapore, Shinglee Press: i-viii, 1-156, figs 1-63, 4 colour pls.

NG P. K. L. 1992. — The freshwater crabs and palaemonid prawns (Crustacea: Decapoda) of Batam island, Riau Archipelago, Indonesia, including descriptions of two new species. *Proceedings of the Biological Society of Washington* 105 (4): 788-794.

NG P. K. L. 1995. — The freshwater crabs and prawns (Crustacea: Decapoda) of Bako National Park, Sarawak, Malaysia, with descriptions of one new genus and three new species. *Raffles Bulletin of Zoology* 43 (1): 181-205.

NG P. K. L. 2025. — A revision of the freshwater crab genus *Adeleana* Bott, 1969 from Borneo and Sumatra (Decapoda: Brachyura: Gecarcinucidae), with descriptions of two new genera and two new species. *Journal of Crustacean Biology* 45 (3): ruaf035, 1-24. https://doi.org/10.1093/jcbiol/ruaf035

NG P. K. L. & GUINOT D. 2001. — On the land crabs of the genus *Discoplax* A. Milne Edwards, 1867 (Crustacea: Decapoda: Brachyura: Gecarcinidae), with description of a new cavernicolous species from the Philippines. *Raffles Bulletin of Zoology* 49 (2): 311-338.

NG P. K. L. & GUINOT D. 2014. — A new cavernicolous species of crab of the genus *Balssiathelphusa* Bott, 1969 (Crustacea, Brachyura, Gecarcinucidae) from eastern Borneo. *Zoosystema* 36 (3): 623-629. https://doi.org/10.5252/z2014n3a4

NG P. K. L., GUINOT D. & DAVIE P. J. F. 2008. — Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology* Supplement 17: 1-286.

NG P. K. L. & SKET B. 1996. — The freshwater crab fauna (Crustacea: Brachyura) of the Philippines. IV. On a collection of Parathelphusidae from Bohol. *Proceedings of the Biological Society of Washington* 109 (4): 695-706.

NG P. K. L. & TAN L. W. H. 1991. — *Irmengardia didacta*, a new freshwater crab (Crustacea: Decapoda: Brachyura: Parathelphusidae) from Johor, Peninsular Malaysia. *Raffles Bulletin of Zoology* 39 (1): 135-140.

NG P. K. L. & TAN S. H. 1999. — Revision of the Southeast Asian potamid crabs of the genus *Malayopotamon* Bott, 1968 (Crustacea: Decapoda: Brachyura). *Journal of Natural History* 33 (2): 207-231.

NG P. K. L., WOWOR D. & YEO D. C. J. 2023. — The freshwater Brachyura (Decapoda: Potamidae, Gecarcinucidae, Sesarmidae) of the Anambas and Natuna Islands, Kepulauan Riau Province, Indonesia. *Journal of Crustacean Biology* 43: 1-34. doi.org/10.1093/jcbiol/ruad012

NG P. K. L. & YANG C. M. 1985. — On three new species of freshwater crabs from Singapore and West Malaysia (Crustacea, Decapoda, Brachyura). *Malayan Nature Journal* 39 (1): 57-73.

NOBILI G. 1903. — Contributo alla fauna carcinologica di Borneo. *Bollettino dei Musei di Zoologia ed Anatomia comparata della Regia*, Università di Torino 18 (447): 1-32, figs 1-3. https://www.biodiversitylibrary.org/part/86178

PROMDAM R., ELLIS M. & JANTARIT S. 2022. — Brachyuran crabs (Crustacea: Decapoda) in the limestone caves of Thailand, with a checklist of freshwater cave-dwelling crabs in Southeast Asia. *Edaphologia* 110: 1-17. https://doi.org/10.20695/edaphologia.110.0_1

ORTMANN A. 1896. — Das System der Decapoden-Krebse. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere* 9: 409-453.

RATHBUN M. J. 1904. — Les crabes d'eau douce (Potamonidae). *Nouvelles Archives du Muséum d'Historie naturelle*, Series 4, 6: 225-312.

RATHBUN M. J. 1905. — Les crabes d'eau douce. *Nouvelles Archives du Muséum d'Histoire naturelle*, Series 4, 7: 159-322.

SAKAI K., TÜRKAY M. & YANG S. L. 2006. Revision of the *Helice/Chasmagnathus* complex (Crustacea: Decapoda: Brachyura). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 565: 1-76, 3 tables.

SCHENKLING S. 1902. — Neue Cleriden des Museums zu Leyden. *Notes of the Leiden Museum* 23: 123-130.

SEEHAUSEN M. & DOW R. A. 2016. — Morphological studies and taxonomic considerations on the 'reddish brown winged' group of *Neurothemis* Brauer, 1867 with the description of *N. taiwanensis* sp. nov. (Odonata: Libellulidae). *Journal of the International Dragonfly Fund* 93: 1-101.

TAN S. H. & NG P. K. L. 1998. — Revision of the genus *Thelphusula* Bott, 1969 (Decapoda: Brachyura: Gecarcinucidae) with description of a new genus and three new species. *Journal of Crustacean Biology* 18 (4): 808-822.

THOFERN D., DUPÉRRÉ N. & HARMS D. 2021. — An annotated type catalogue of the centipedes (Myriapoda: Chilopoda) held in the Zoological Museum Hamburg. *Zootaxa* 4977 (1): 1-103. https://doi.org/10.11646/zootaxa.4977.1.1

VORIS H. K. 2000. — Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* 27: 1153-1167.

WHEELER W. M. 1919. — The ants of Borneo. *Bulletin of the Museum of Comparative Zoölogy at Harvard College* 63 (3): 43-147.

YAAKOP S., DUFFELS J. P. & VISSER H. 2005. — The cicada genus *Chremistica* Stål (Hemiptera: Cicadidae) in Sundaland. *Tijdschrift voor Entomologie* 148: 247-306.

YEO D. C. J. & NG P. K. L. 2004. — Recognition of two subfamilies in the Potamidae Ortmann, 1896 (Brachyura, Potamidae) with a note on the genus *Potamon* Savigny, 1816. *Crustaceana* 76 (10): 1219-1235. https://doi.org/10.1163/156854003773123456

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