

REVISION OF THE GENUS *THELPHUSULA* (DECAPODA: BRACHYURA: GECARCINUCIDAE) WITH DESCRIPTION OF A NEW GENUS AND THREE NEW SPECIES

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ABSTRACT

The taxonomy of *Thelphusula*, a Bornean genus of gecarcinucid fresh-water crabs is revised. Two new species, *T. sabana* and *T. tawauensis*, both from Sabah, are described. A new genus and new species, *Coccusa isophallus*, which closely resembles *Thelphusula*, is described from Kalimantan. The affinities of *Terrathelphusa adipis* are reassessed and the species is transferred to *Coccusa*.

The genus *Thelphusula* was established by Bott (1969) for relatively small gecarcinucid species which have rectangular carapaces, no frontal median triangle, an almost indiscernible epibranchial tooth, straight and parallel posterolateral margins, and a male first pleopod in which the terminal segment is cylindrical to subcylindrical. Bott (1970) recognized six species and subspecies, namely, *T. buergeri* (de Man, 1899) (type species by original designation), *T. hendersoniana* (de Man, 1899), *T. melanippe melanippe* (de Man, 1899), *T. melanippe kadamiana* (Borradaille, 1900), *T. baramensis* (de Man, 1902), and *T. luidana* (Chace, 1938). Holthuis (1979) subsequently described *T. granosa* from Sarawak. Ng and Goh (1987) reviewed the species then placed in *Thelphusula* and recognized nine species in the genus, namely *T. buergeri* (de Man, 1899), *T. hendersoniana* (de Man, 1899), *T. melanippe* (de Man, 1899), *T. bidiensis* (Lanchester, 1900), *T. kadamiana* (Borradaille, 1900), *T. baramensis* (de Man, 1902), *T. luidana* (Chace, 1938), *T. granosa* Holthuis, 1979, and *T. rhadamanthysi* Ng and Goh, 1987. Ng (1989a) and Ng and Stuebing (1990) added *T. styx* and *T. dicerophilus* from Sarawak and Sabah, respectively. More recently, Tan and Ng (1997) described *T. hulu* from central Sabah.

Ng and Goh (1987) commented that *Thelphusula* was heterogeneous and three species groups could be identified, which they tentatively called the *T. buergeri*, *T. bidiensis*, and *T. melanippe* groups. The monotypic genus *Strygothelphusa* was subsequently erected for *T. bidiensis* (see Ng, 1989b) and was distinguished from *Thelphusula* sensu stricto by possessing very long ambulatory legs with a serrated dorsal meral margin, the terminal

segment of the male first pleopod being less than a quarter of the total length of the pleopod, and a male second pleopod with a long distal segment which is subequal in length or slightly shorter than the basal segment. Ng (1991) later established another new genus, *Arachnothelphusa*, for *T. melanippe* (type species by original designation), *T. kadamiana*, *T. rhadamanthysi*, and a new species, *A. terrapes* Ng, 1991. *Arachnothelphusa* differs from *Thelphusula* sensu stricto in having a distinctly rectangular carapace, long ambulatory legs (especially the meri), and the terminal segment of the male first pleopod about one-third of the total length of the pleopod. *Parathelphusa* (*Liothelphusa*) *nobilis* Colosi, 1920, synonymized with *T. hendersoniana* by Bott (1970), was also tentatively resurrected as a valid species and provisionally transferred to *Arachnothelphusa*.

Recently, Ng (1995) described a new genus and new species, *Bakousa sarawakensis*, from Sarawak, and transferred *Thelphusula hendersoniana* and *Adeleana kenepai* (de Man, 1899) to it. *Bakousa* can be separated from *Thelphusula* sensu stricto mainly by possessing a proportionately stouter male first pleopod with a shorter terminal segment, and a male second pleopod which has a long distal segment longer than half the length of the basal segment.

In this paper, the genus *Thelphusula* sensu stricto is revised. Two new species are described, *T. sabana* and *T. tawauensis*, both from Sabah. Specimens from West Kalimantan, initially identified as a new species of *Thelphusula*, differ from *Thelphusula* sensu stricto in several significant characters and are here described as belonging to a new genus, *Coccusa*. *Terrathelphusa adipis* Ng

and Wowor, 1990, is transferred to this new genus.

The terminology used in this paper essentially follows that in Ng (1988). The male first pleopod is abbreviated to G1 and the second male pleopod to G2. All measurements, in mm, were taken with vernier calipers and were of the carapace width and carapace length, respectively. For the purposes of discussion, the term "pseudofrontal median triangle" here refers to an almost incomplete frontal median triangle sensu Bott (1970) (see also Ng, 1988). Specimens examined are deposited in the following museums: Museum Zoologicum Bogoriense (MZB), Bogor; Sabah Museum (SSM), Kota Kinabalu; University Malaysia, Sabah (UMS), Kota Kinabalu; National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; Nationaal Natuurhistorisch Museum (RMNH), Leiden; and the Zoological Reference Collection (ZRC), National University of Singapore.

TAXONOMY

Family Gecarcinidae

Thelphusula Bott, 1969

Thelphusula Bott, 1969: 362; Bott, 1970: 58.

Type Species.—*Potamon* (*Geothelphusa*) *buengeri* de Man, 1899, by original designation.

Diagnosis.—Carapace squarish to rectangular; anterolateral margin convex, not clearly demarcated from posterolateral margin; epibranchial tooth low, indistinct or absent; frontal median triangle complete or incomplete; postorbital cristae distinct (sometimes weak or low); epigastric lobes distinct. Exopod of third maxilliped reaching half height of merus, with well-developed flagellum longer than width of merus. Ambulatory legs not elongate. Male abdomen distinctly T-shaped. G1 slender; terminal segment cylindrical or rod-shaped, subequal to longer than half length of subterminal segment. G2 with short distal terminal segment, less than 0.15 times length of basal segment.

Remarks.—The genus *Thelphusula* as recognized here is a fairly distinct group of species, all of which are Bornean in distribution. Nine species are here recognized in *Thelphusula* sensu stricto, namely, *T. baramensis* (de Man, 1902), *T. buengeri* (de Man, 1899), *T. dicerophilus* Ng and Stuebing, 1990, *T.*

granosa Holthuis, 1979, *T. hulu* Tan and Ng, 1997, *T. luidana* (Chace, 1938), *T. sabana*, new species, *T. styx* Ng, 1989, and *T. tawauensis*, new species.

As noted by several authors (e.g., Holthuis, 1979; Ng, 1988; Ng and Stuebing, 1990), the form of the frontal median triangle can be highly variable within a genus and cannot be used as a generic or familial character, as was used by Bott (1969, 1970). In *Thelphusula*, this is clearly illustrated by species such as *T. hulu* and *T. tawauensis*, which have complete frontal median triangles, the dorsal margins being strongly cristate and completely fused with the equally strongly cristate lateral margins. *Thelphusula granosa* has both the dorsal and lateral margins of the frontal median triangle cristate, but the dorsal margin is not fused to the lateral margins. Species such as *T. buengeri*, *T. dicerophilus*, *T. luidana*, and *T. sabana* have a weak dorsal carina which is not connected to the strongly cristate lateral margins. *Thelphusula baramensis* is unique in the genus by having a complete frontal median triangle with the dorsal margin strongly cristate, but the lateral margins are not cristate. The frontal median triangle in *T. styx* is poorly defined, with the dorsal margin not cristate, and the lateral margins are not fused at the base.

KEY TO THE SPECIES OF *THELPHUSULA*

1. Dorsal surface of carapace relatively flat, pubescent, velvety to touch; lateral margins of frontal median triangle not cristate; epigastric and postorbital cristae raised, sharp; weak but distinct transverse ridge on intestinal region, reaching posterolateral margins *T. baramensis*
- Dorsal surface of carapace inflated at certain regions, usually rugose; lateral margins of frontal median triangle cristate; epigastric and postorbital cristae raised but not sharp; transverse ridge on intestinal region weak, never reaching posterolateral margins 2
2. Frontal median triangle complete 3
- Frontal median triangle incomplete 4
3. Epigastric cristae rugose, raised; cervical groove deep; G1 terminal segment tapering to a point, tip sharp *T. tawauensis*
- Epigastric cristae relatively smooth; cervical groove shallow; G1 terminal segment not tapering to a point, tip blunt *T. hulu*
4. Cervical grooves deep, extending posteriorly throughout most of posterolateral region; G1 straight, not bent outward *T. styx*
- Cervical groove relatively shallow or absent, never extending substantially posteriorly; G1 sinuous, distinctly bent outward 5
5. Carapace surface rugose; frontal median triangle wide, extending to almost entire width of frontal mar-

- gin, dorsal carina of frontal median triangle distinct
- Carapace surface smooth; frontal median triangle not extending throughout most of width of frontal margin, dorsal carina of frontal median triangle weak, with only low granular ridge present
6. Carapace very high, branchial regions inflated; lateral margins with strong rugose striae; G1 terminal segment about half as long as subterminal segment *T. dicerophilus*
- Carapace raised, branchial regions not inflated; lateral margins lined with distinct granules (single or arranged in short transverse rows); G1 terminal segment less than half length of subterminal segment *T. granosa*
7. Cervical groove relatively deep; epigastric cristae raised, rugose; postorbital cristae raised, prominent, rugose; dorsal carina of frontal median triangle represented by distinct granular ridge, pseudofrontal median triangle wide, almost as wide as frontal margin; G1 terminal segment about half length of subterminal segment *T. sabana*
- Cervical groove very shallow; epigastric cristae rather low, not rugose; postorbital cristae low, not prominent; dorsal carina of frontal median triangle represented by granular ridge, pseudofrontal median triangle about one-third width of frontal margin; G1 terminal segment about one-third length of subterminal segment
8. Outer surfaces of chelae smooth; base of G1 broad, tapering strongly toward terminal segment *T. luidana*
- Outer surfaces of chelae rugose; base of G1 not broad, not tapering strongly toward terminal segment *T. buergeri*

Thelphusula baramensis (de Man, 1902)

Figs. 1, 6A

Potamon (*Potamonautes*) *baramense* de Man, 1902: 553, pl. 20, fig. 16.

Potamon (*Potamon*) *baramense*—Rathbun, 1904: 286.

Thelphusula baramensis—Bott, 1970: 60, pl. 9, figs. 94–96, pl. 27, fig. 38; Holthuis, 1979: 33, fig. 7; Collins, 1979: 271; 1980: 81.

Material Examined.—Holotype ♂ (SMF 1792) (15.5 by 13.3 mm), Borneo: Baram River, collected by Küenthal expedition. Paratypes: 1 ♂, 2 ♀♀ (SMF 1793), same data as holotype. Other specimens: 1 ♂, 1 ♀, 1 juvenile (ZRC 1997.804), Brunei: Baram River, collected by Bukit Teraja, collected by S. C. Choy, 8 May 1989; 2 ♂♂ (ZRC 1997.806), Brunei: Kuala Belait district, Seria, peat swamp forest among pitcher plants, collected by S. C. Choy, 13 November 1988; 1 ♀ (ZRC), Brunei: tributary of Sungai Temburong, near plot 2, east ridge, night, collected by L. Das, 23 April 1992.

Diagnosis.—Carapace relatively flat, dorsal surface with very short setae, velvety, finely punctated especially on antero- and postero-lateral regions; anterolateral margin crested, not serrated; transverse carina present on cardiac region, edges nearly reaching postero-lateral margins; epibranchial tooth low but distinct, separated by narrow cleft from ex-

ternal orbital angle; external orbital angle crested; frontal margin nearly straight; frontal median triangle complete, dorsal margin strongly cristate, lateral margins not cristate; epigastric cristae confluent with postorbital cristae, both sharp and prominent; postorbital cristae not continuous with epibranchial teeth. G1 gently sinuous, terminal segment stout, cylindrical, subequal to half length of subterminal segment, tip directed slightly upward.

Remarks.—*Thelphusula baramensis* may be easily separated from congeners by its flat velvety carapace, sharp prominent epigastric and postorbital cristae, dorsal surface of the carapace possessing a distinct transverse ridge on the cardiac region. The form of the frontal median triangle is unique to the genus, being complete, with the lateral margin non-cristate.

This species seems to be amphibious in its habits. Collection data of the present lot of specimens examined seem to indicate that it is found in streams and in peat swamp forest. This species was found in heath forest of Gunung Mulu National Park (Collins, 1979). Collins (1980) subsequently reported the capture of five specimens from another ecological plot also in Gunung Mulu National Park. Otherwise, very little is known about the ecology of these crabs.

Thelphusula buergeri (de Man, 1899)

Figs. 2, 6B

Potamon (*Geothelphusa*) *Bürgeri* de Man, 1899: 121, pl. 11, fig. 14, pl. 12, fig. 14.

Potamon (*Geothelphusa*) *Bürgeri*—Lanchester, 1900: 256; Hanitsch, 1900: 10; Rathbun, 1905: 217.

Potamon (*Geothelphusa*) *Bürgeri*—Nobili, 1903: 16.

Potamon *Bürgeri*—Nobili, 1901: 5.

Potamon (*Geothelphusa*) *kuchingense*—Nobili, 1901: 5 (not *Potamon* (*Geothelphusa*) *kuchingense* Nobili, 1901).

?*Potamon* (*Geothelphusa*) *kuchingensis*—Nobili, 1905: 217 (not *Potamon* (*Geothelphusa*) *kuchingense* Nobili, 1901).

Parathelphusa (*Liothelphusa*) *Bürgeri*—Colosi, 1920: 26. *Gecarcinicus* (*Cylindrothelphusa*) *bürgeri*—Bals, 1937: 161.

Gecarcinicus (*Cylindrothelphusa*) *bürgeri* *lebangensis* Bals, 1937: 161.

Thelphusula melanippe buergeri—Bott, 1970: 61, pl. 9, figs. 4–8, pl. 27, fig. 39.

Material Examined.—Holotype, ♂ (13.2 by 10.5 mm) (RMNH 1551), Borneo: Liang Koeboeng, collected by Borneo Expedition, 1894. Paratype: 1 ♀ (RMNH 31960), same data as holotype.

Diagnosis.—Dorsal surface of carapace relatively smooth; posterolateral margins with

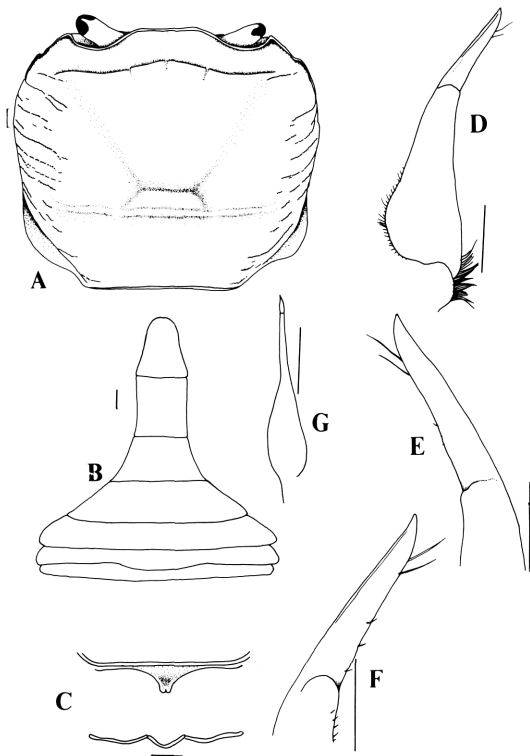


Fig. 1. *Thelphusula baramensis*. A, carapace; B, abdomen; C, epistome; D–F, left G1; G, left G2. D, ventral view; E, tip, dorsal view; F, tip, ventral view. A, B, ZRC 1997.804 (19.2 × 16.8 mm); C–F, holotype, male (SMF 1792). Scale bar = 1 mm.

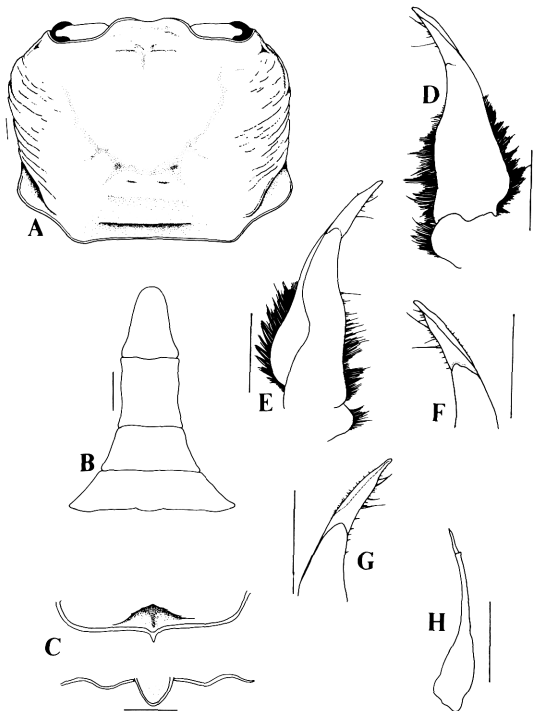


Fig. 2. *Thelphusula buergeri*, holotype, RMNH 1551. A, carapace; B, abdomen; C, epistome; D-G, left G1; H, left G2. D, dorsal view; E, ventral view; F, tip, dorsal view; G, tip, ventral view. Scale bar = 1 mm.

numerous oblique striae; anterolateral margin indistinctly separated from posterolateral margin; epibranchial tooth not visible; external orbital angle triangular, outer margin slightly longer than inner; frontal margin deflexed; frontal median triangle incomplete. G1 sinuous, slender, terminal segment cylindrical, about half length of subterminal segment.

Remarks.—Holthuis (1979) commented on this species in his comparison of *T. buergeri* with *T. granosa* and argued against Bott's (1970) action of designating *T. buergeri* as a subspecies of *T. melanippe*. This was accepted by Ng and Goh (1987) in their discussions of the genus.

Bott (1970) examined Balss' (1937) specimen of *Gecarcinus (Cylindrothelphusa) buergeri lebangensis* from Sungei Lebang in Borneo and regarded it as synonymous with *T. buergeri*. The headwaters of Sungei Lebang originate at Mt. Liang Koeboeng (present day Bukit Liyangcabung) and the two localities are about 170 km apart. The waters from Mt. Liang Koeboeng and Sungei Lebang ultimately lead to the lower Kapaus basin. It is probable that the same species are found in the same drainage. Bott's (1970) decision is followed here.

Specimens from Samarinda (eastern Borneo) recorded by Nobili (1903) and Colosi (1920) as this species are here referred to as *Balssia-thelphusa cursor* instead (see Ng, 1986).

Thelphusula dicerophilus Ng and Stuebing, 1990
Fig. 6C

Thelphusula dicerophilus Ng and Stuebing, 1990: 46, pl. 1, fig. 1.

Material Examined.—Holotype ♂ (ZRC 1989.3588) (14.0 × 12.0 mm), Malaysia, Sabah: Danum Valley, in pit-fall trap, adjacent to pool of rhinoceros mud-wallow, approximately 4°55'N, 117°46'E, collected by R. Stuebing, 4 March 1988. Paratypes: 1 ♂ (ZRC 1989.3591) (18.5 × 15.4 mm), Malaysia, Sabah: Danum Valley, in mist net in rhinoceros mud-wallow pool, collected by R. Stuebing, 2 March 1988. 1 ♀ (ZRC 1989.3593) (18.3 × 15.0 mm), Malaysia, Sabah: Danum Valley, in pit-fall trap, adjacent to pool of rhinoceros mud-wallow, collected by R. Stuebing, 1 March 1988. Other specimens: 1 ♀ (ZRC 1997.138), Malaysia, Sabah: Danum Valley Field Centre, secondary forest, pit-fall trap number 4, collected by C. Colón, 14 October 1996. 1 ♀ (ZRC 1997.139), Malaysia, Sabah: Lahad Datu, Kunak, Buturong, Binuang river, collected by R. Goh, 20 March 1989. 1 ♂ (ZRC 1997.140), Malaysia, Sabah: Danum Valley Field Centre, primary forest, pit-fall trap number 4, collected by C. Colón, 10 October 1996. 1 ♂ (ZRC 1997.141), Malaysia, Sabah: Danum Valley Field Centre, secondary

forest, pit-fall trap number 3, collected by C. Colón, 17 October 1996. 1 ♂ (ZRC 1997.142), Malaysia, Sabah: Danum Valley Field Centre, secondary forest, pit-fall trap 3, collected by C. Colón, 19 October 1996.

Diagnosis.—Carapace very high, dorsal surfaces rough, antero- and posterolateral margins with lateral striae; anterolateral margins not distinct from posterolateral margin; epibranchial tooth indistinct; external orbital angle triangular, outer margin slightly longer than inner margin; frontal margin deflexed; frontal median triangle incomplete. G1 slender, rodlike, tip tapering, slightly curved upward, terminal segment longer than half length of subterminal segment; G2 with short distal segment.

Remarks.—Examination of large specimens of this species from Danum Valley in Sabah reveals that the branchial region becomes more prominent as the crab matures. This is characteristic of this species and can be used to separate it from the other species. The greatly inflated branchial region of the crab is probably related to its habitat. The types were found in pit-fall traps and mist nets in and around rhinoceros mud-wallows (Ng and Stuebing, 1990). The more recent large specimens were obtained in pit-fall traps in secondary forest. This evidence suggests that the crab is predominantly terrestrial in habit.

Thelphusula granosa Holthuis, 1979
Fig. 6D

Thelphusula granosa Holthuis, 1979: 29, pl. 5, fig. 6.
Thelphusula granosa—Collins, 1979: 271; 1980: 81.

Material Examined.—Holotype ♂ (NFM 31970), Malaysia: Sarawak, Gunung Mulu National Park, alluvial lowland rain forest, 4°03'N, 114°56'E, collected by N. M. Collins, 13 March 1978.

Diagnosis.—Carapace high, dorsal surfaces covered with numerous distinct granules; anterolateral margins cristate; posterolateral margins with strong oblique striae, antero- and posterolateral margins gently merging with each other; epibranchial tooth indistinct; external orbital angle with outer margin longer than inner margin; frontal margin deflexed; frontal median triangle incomplete. G1 sinuous, slender, terminal segment cylindrical, tip tapered, about half length of subterminal segment.

Remarks.—This species can be easily distinguished from congeners by the distinctive granulation on its carapace. This species is

fairly common in Gunung Mulu National Park, where Collins (1980) did an ecological study to determine the habits and populations of terrestrial crabs. Collins (1980) reported that 15 out of 20 specimens of crabs caught in his pit-fall traps, about 1 km inland of the Melinau river, were *Thelphusula granosa*. The same paper also recorded another similar ecological plot conducted near the banks of the Melinau river. The crabs caught were, however, all *Terrathelphusa loxophthalma* (de Man, 1892) (identified as *Perbrinkia loxophthalma*).

Thelphusula dicerophilus and *T. tawauensis* are reported from pit-fall traps (K. Martin-Smith and R. Inger, personal communication). This suggests that these members of this genus are mainly terrestrial in habit. An excellent figure of the G1 for this species can be found in Holthuis (1979).

Thelphusula hulu Tan and Ng, 1997

Fig. 6E

Thelphusula hulu Tan and Ng, 1997: 55.

Material Examined.—Holotype ♂ (20.3 × 16.7 mm) (SSM), Malaysia: Sabah, Maliau Basin, tea-colored water stream with peat substrate in heath forest near base camp (site D), draining heath forest-submontane coniferous forest transition, collected by A. Hamid, 20 May 1996. Paratypes: 1 ♂ (21.6 × 17.6 mm) (ZRC 1997.101), Malaysia: Sabah, Maliau Basin, tea-colored water stream with peat substrate in heath forest near base camp (site D), draining heath forest-submontane coniferous forest transition, collected by S. H. Tan and T. H. T. Tan, 21 May 1996; 1 ♀ (27.9 × 22.7 mm) (ZRC 1997.102), same data as holotype; 1 ♂ (15.0 × 13.3 mm), 1 ♀ (17.9 × 15.4 mm) (UMS), Malaysia: Sabah, Maliau Basin, dark-water stream adjacent to base camp (site C), draining submontane coniferous forest, collected by K. Martin-Smith and others, 13 May 1996; 1 ♂ (13.7 × 11.8 mm), 1 ♀ (17.7 × 14.8 mm) (SSM), Malaysia: Sabah, Maliau Basin, dark-water stream adjacent to base camp (site C), draining submontane coniferous forest, collected by K. Martin-Smith and others, 13 May 1996.

Diagnosis.—Carapace gently inflated, dorsal surface granular; antero- and posterolateral margins with lateral striae, not clearly demarcated from each other; epibranchial tooth absent or very low; frontal margin triangle complete, dorsal and lateral margin strongly cristate; external orbital angle acutely triangular. G1 slender, rod-shaped, tip tapered, terminal segment, curving outward, about two-thirds length of subterminal segment.

Remarks.—This interesting species is found only in the Maliau Basin, Sabah, and is probably one of the highest recorded localities

where species of this genus occur (1,200 m above sea level). *Thelphusula luidana* was reported to be found at around 900 m asl elevation. Mount Liang Koeboeng, type locality of *T. buergeri*, was reported to be 1,322 m asl elevation (see Büttikofer, 1897: 19).

Specimens were generally caught in plastic drink bottles in which the tops were cut off and inverted onto the main body of the bottle. This formed a little channel leading into the main bottle itself. These traps were baited with chicken offal and left in streams about 1 m in depth. The crabs were usually attracted to the bait and once they entered the bottle, they seldom found their way out again. The holotype was, however, caught by hand at night, near the surface of a stream by the banks. The water in which this crab lives is stained dark brown due to leaching from a karangas forest nearby. This species differs from *T. dicerophilus*, *T. granosa*, and *T. tawauensis* in that it is mainly aquatic.

Thelphusula luidana (Chace, 1938)

Fig. 6F

Parathelphusa (*Liotelphusa*) *luidana* Chace, 1938: 19, pl. 4. *Thelphusula luidana*—Bott, 1970: 59, pl. 8, figs. 85–87, pl. 27, fig. 37.

Material Examined.—Paratypes, 1 ♂ (8.7 × 7.5 mm), 1 ♀ (8.3 × 6.2 mm), (ZRC 1990.459–460) (formerly MCZ 10079), British North Borneo: Mt. Kinabalu, Bunutan (Luidan River), 3,000 feet (900 m asl), collected by A. Griswold, Asiatic Primate Expedition, 5 July 1937. Other specimens: 1 ♀ (ZRC 1989.3640), Malaysia, Sabah: Gunung Lumaku, Mendolung, Sipitang district, seepage area under rock, 1,350 m asl, collected by Stuebing, 11 August 1989.

Diagnosis.—Carapace rectangular, dorsal surface smooth; cervical groove shallow; epigastric cristae gently merging with carapace at postorbital region; postorbital region without cristae; epibranchial tooth very low but visible, separated from external orbital angle by sharp notch; outer margin of external orbital angle more than twice length of inner margin; anterolateral margin convex; posterolateral margin converging toward posterior margin; frontal margin not distinctly deflexed; frontal median triangle incomplete. Chela outer surface smooth, no distinct gape present when closed. G1 slender, sinuous, terminal segment cylindrical, subequal to half length of subterminal segment.

Remarks.—This species is unique in the genus as the only species that has smooth outer surfaces on both chelae. It occurs sym-

patrically with *Adeleana forcarti* Bott, 1969, and *Arachnothelphusa kadamaiana* (Borradaile, 1900), although it is not known whether they occupy the same niche. *Thelphusula luidana* is a rather small-sized species. The female paratype examined measures only 8.3×6.3 mm and is almost mature. Small specimens of *Adeleana forcarti* are very similar morphologically to *T. luidana*, but can be distinguished by their lack of a frontal median triangle, a slightly more convex anterolateral margin, and by their very different G1 (see Bott, 1970).

Chace (1938) in his description of *T. luidana* mentioned that the cervical groove is absent. The cervical groove is extremely poorly developed in the paratypes examined, practically reduced to a circular, shallow depression next to the H-shaped groove.

Thelphusula sabana, new species

Figs. 3, 6G

Material Examined.—Holotype ♂ (ZRC 1997.807) (14.7 × 12.0 mm), Malaysia: Sabah, Lahad Datu, Juraco, secondary forest near oil palm plantation, collected by R. Goh, 27 March 1988.

Paratypes: 1 ♂, 1 ♀, 1 juvenile (ZRC 1997.808), Malaysia: Sabah, Lahad Datu, Juraco, same locality and date.

Diagnosis.—Carapace rectangular, dorsal surfaces rugose, especially on branchial and postorbital regions; epigastric cristae rugose, confluent with postorbital cristae; postorbital cristae rugose, not confluent with epibranchial teeth; epibranchial tooth low; anterolateral margin convex, granulated; anterolateral margin not clearly separated from posterolateral margin; posterolateral margin with lateral striae, gently convergent toward almost straight posterior carapace margin; outer margin of external orbital angles slightly granulated, about twice length of inner margin; frontal margin gently deflexed; frontal median triangle incomplete, dorsal and lateral margins cristate, but not fused to each other. Ambulatory legs normal length. G1 sinuous, bent outward, terminal segment straight, length longer than half length of subterminal segment.

Remarks.—This species can be differentiated from other species of *Thelphusula* in that the epigastric lobes and the postorbital cristae are very rugose. The carapace is also more distinctly rectangular in shape than all other species of *Thelphusula*. Juveniles of *T. hulu* are more squarish than adults which are more rec-

tangular in shape, but juveniles of *T. sabana* already possess the rectangular shape. *Thelphusula granosa* does not possess such rugose lobes and cristae, although its granules and striae on the dorsal surface of the carapace are much larger and more prominent. The G1 of *T. sabana* allies this species with *T. dicerophilus*. The G1 tip of *T. sabana* is, however, more curved up than that of *T. dicerophilus*. The neck of the subterminal segment is also proportionately longer in *T. sabana*, easily differentiating it from *T. dicerophilus*.

Thelphusula styx Ng, 1989a

Fig. 6H

Thelphusula ?*kadamaiana*—Holthuis, 1986: 594 (not *Potamon* (*Geothelphusa*) *kadamaianum* Borradaile, 1900).
Thelphusula styx Ng, 1989a: 54, figs. 1, 2.

Material Examined.—Holotype ♂ (RMNH 33953) (13.4 × 9.2 mm), Borneo, Sarawak: Gunung Mulu National Park, Gua Kelawan (Lubang Kelia) ("Bat Cave"), in pit-fall trap, just south of forest station at Long Pala (river junction), 4°01'36"N, 114°47'58"E, collected by P. Chapman, 10 February 1980.

Diagnosis.—Dorsal surface of carapace convex; cervical grooves deep, reaching posterolateral regions; frontal margin deflexed; frontal median triangle incomplete, poorly defined; outer margin of external orbital angle straight, confluent with anterolateral margins; postorbital cristae very low, rounded, confluent with low, rounded epigastric cristae. G1 slender, terminal segment one-third of total length, tip tapering; G2 without flagellum.

Remarks.—This species is known from only one specimen. It may be easily distinguished from all other species of *Thelphusula* by the deep prominent cervical groove. The cervical groove of *T. styx* is also unique in that it extends to the posterolateral region. In all other species of *Thelphusula*, the cervical groove never extends to the posterolateral region.

The shape of the G1 is also very unlike that in other species of *Thelphusula*. Whereas all other species of *Thelphusula* have a slender cylindrical terminal segment, the G1 terminal segment of *T. styx* is rather short and conical. This condition is most likely due to the size of the holotype, which is probably a juvenile.

The holotype of this species does not possess a terminal segment on the G2. It is highly unlikely that the terminal segment is absent, considering its close affiliation with *Thelphusula*. All known species of this genus pos-

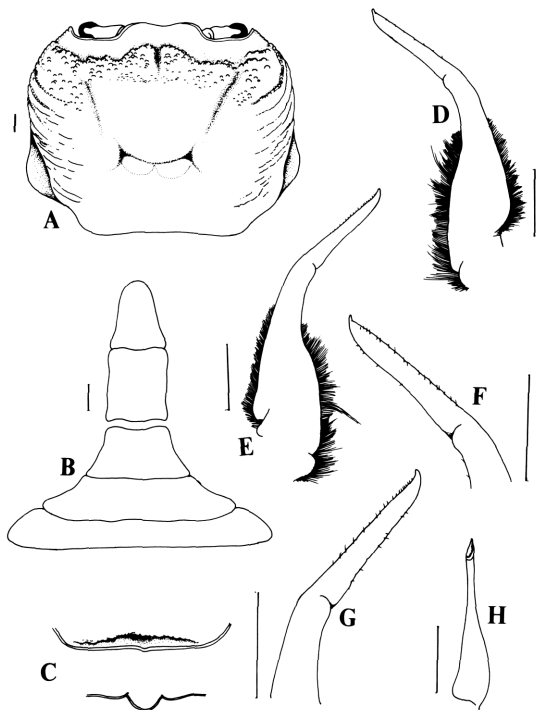


Fig. 3. *Thelphusula sabana*, holotype, ZRC 1997.807. A, carapace; B, abdomen; C, epistome; D-G, left G1; H, left G2. D, dorsal view; E, ventral view; F, tip, dorsal view; G, tip, ventral view. Scale bar = 1 mm.

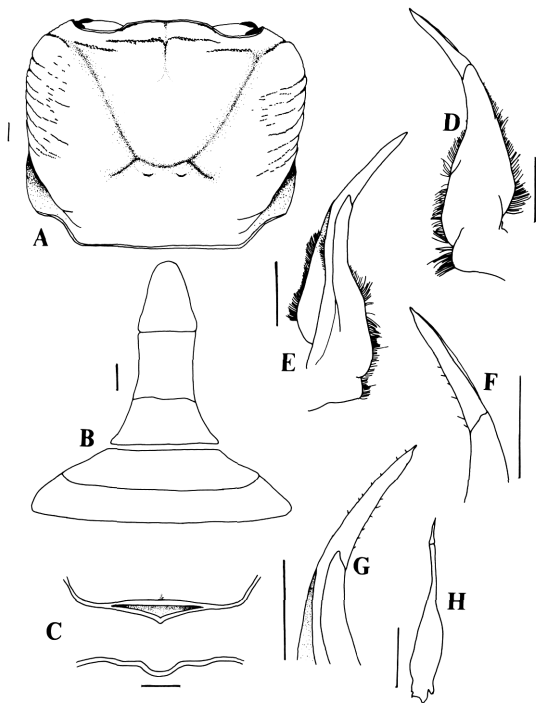


Fig. 4. *Thelphusula tawauensis*, holotype, ZRC 1997.809. A, carapace; B, abdomen; C, epistome; D–G, left G1; H, left G2. D, dorsal view; E, ventral view; F, tip, dorsal view; G, tip, ventral view. Scale bar = 1 mm.

sess a distinct terminal segment on the G2. The holotype may probably be a specimen with an aberrant G2 or one that is still undeveloped. All other taxonomic characters are in agreement of the description of the genus.

Thelphusula tawauensis, new species

Figs. 4, 6l

Material Examined.—Holotype ♂ (ZRC 1997.809) (15.7 × 12.5 mm), Malaysia: Sabah, Tawau Hills Park, Basin 1B2, collected by R. F. Inger, 1 February 1993. Paratypes: 1 ♂ (ZRC 1997.810) (17.5 × 14.1 mm), Malaysia: Sabah, Tawau Hills Park, Basin 1B1, collected by R. F. Inger, 20 August 1992; 1 ♀ (ZRC 1997.812) (15.1 × 12.4 mm), Malaysia: Sabah, Tawau Hills Park, Basin 2C4, collected by R. F. Inger, 20 August 1992; 1 ♂ (ZRC 1997.811) (16.0 × 12.9 mm), Malaysia: Sabah, Tawau Hills Park, Basin 1C5, collected by R. F. Inger, 6 October 1992.

Diagnosis.—Dorsal surface of carapace punctate, branchial regions not inflated; epibranchial teeth low but distinct; epigastric cristae rugose, not confluent with postorbital cristae; postorbital cristae high, rugose, origin distinctly posterior to epigastric lobes, not confluent with epibranchial teeth; cervical grooves very deep, reaching almost to anterolateral margins, converging at epibranchial teeth; H-shape depression deep, distinct transverse carina present on cardiac region, nearly reaching posterolateral margins; frontal median triangle complete, dorsal and lateral margins strongly cristate; ambulatory legs normal length. G1 sinuous, terminal segment bent outward, longer than half length of subterminal segment, straight.

Remarks.—This species may be easily identified by its complete and distinct frontal median triangle. The entire frontal median triangle is strongly cristate. This allies *T. tawauensis* with *T. hulu* which also possesses a complete frontal median triangle. Considerable variation in the postorbital cristae exists within this species. The postorbital cristae may be indistinct in some specimens but a faint outline can still be seen. This makes the origin of the postorbital cristae difficult to determine precisely. However, the rugose epigastric lobes are rather characteristic of this species, as are the deep cervical grooves. Another prominent feature of this species is the raised carina immediately posterior to the H-shape depression. *Thelphusula baramensis* also has a raised carina posterior to the H-shape depression. It can, however, be distinguished from *T. tawauensis* by having a

flatter carapace and more prominent and sharper postorbital cristae.

Coccusa, new genus

Type Species.—*Coccusa isophallus*, new species, by present designation.

Diagnosis.—Carapace ovate, broader than long, dorsal surface smooth, strongly inflated on all regions; cervical groove shallow, epigastric cristae low but distinct, postorbital cristae indistinct to indiscernible; epibranchial teeth low but distinct; anterolateral margin convex; posterolateral margins converging toward posterior carapace margin; frontal margin not distinctly deflexed, frontal median triangle complete or incomplete. Chela outer surface rugose to granulated; ambulatory legs normal length, meri gently serrated on dorsal margin, dactyli slender; male abdomen distinctly T-shaped. G1 slender, sinuous, terminal segment cylindrical, subequal in length to very slender subterminal segment. G2 slender, distal segment short.

Remarks.—The type species of *Coccusa*, new genus, is closely related to the genus *Thelphusula* with respect to the low epibranchial teeth, granulated chela, and the general shape of its G1 and G2. The G1 of *Coccusa isophallus*, however, is quite different from those of species of *Thelphusula* in that the terminal segment is about as long as the subterminal segment (versus about half as long). The dorsal surface of the carapace is very smooth (versus granulated and/or striated) and all regions behind the postorbital cristae are strongly inflated. The swollen carapace of *Coccusa isophallus* makes the frontal margin appear very depressed compared to those of species of *Thelphusula*. The width of the carapace versus the frontal margin is also distinctly greater than that of *Thelphusula*. Overall, the carapace shapes of species of *Coccusa* and *Thelphusula* differ markedly.

Coccusa also resembles the genus *Terrathelphusa* Ng, 1989c, due to its ovate carapace, smooth dorsal surface of the carapace, low epigastric and postorbital cristae, and the relatively low epibranchial teeth. *Coccusa* may be distinguished from *Terrathelphusa* by its much shallower cervical groove (distinct and deeper in *Terrathelphusa*). As a result of this, the dorsal surface of the carapace of species of *Terrathelphusa* appears more sculptured than that in *Coccusa*. The ratio of the

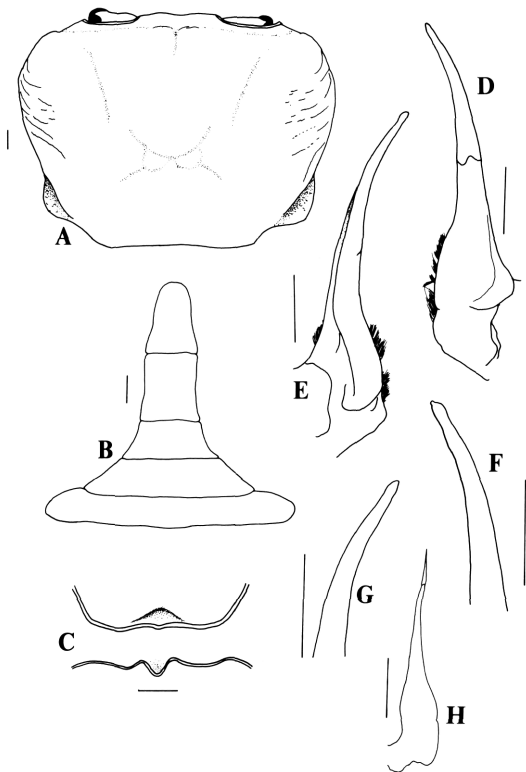


Fig. 5. *Coccusa isophallus*, holotype, MZB 1431. A, carapace; B, abdomen; C, epistome; D–G, left G1; H, left G2. D, dorsal view; E, ventral view; F, tip, dorsal view; G, tip, ventral view. Scale bar = 1 mm.

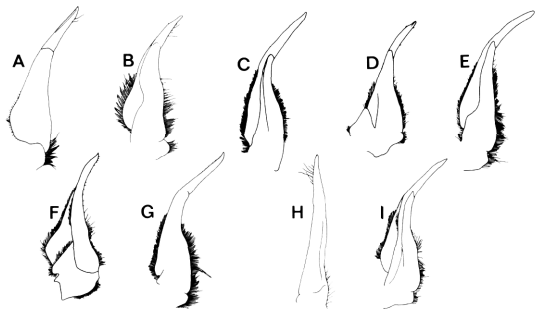


Fig. 6. Left G1 (ventral view) of nominal species of *Thelphusula*: A, *T. baramensis*; B, *T. buergeri*; C, *T. dicerophilus* (after Ng and Stuebing, 1990); D, *T. granosa* (after Holthuis, 1979); E, *T. hula* (after Tan and Ng, 1997); F, *T. ludiana* (after Chace, 1938); G, *T. sabana*; H, *T. styx* (after Ng, 1989); I, *T. tawauensis*. All drawings not to scale.

frontal margin against carapace width is also proportionately smaller in *Terrathelphusa* than in *Coccusa*. The outer surface of the chela of *Terrathelphusa* is smooth, whereas that of *Coccusa* is granulated. Most significantly, the G1 of *Coccusa* is very different from *Terrathelphusa*. The G1 of *Coccusa isophallus* is long and slender, but that of *Terrathelphusa* is stout. The G1 terminal segment of *Coccusa* is about as long as the subterminal segment, which in species of *Terrathelphusa* is proportionately much stouter (see Ng, 1989c, 1997). One species previously doubtfully referred to *Terrathelphusa*, *T. adipis* Ng and Wowor, 1990, is now transferred to *Coccusa* (see below).

Etymology.—The genus name is derived from an arbitrary combination of the Latin for berry, *coccum*, and the last three letters of the genus *Thelphusa*. Gender feminine.

Coccusa isophallus, new species

Fig. 5

Material Examined.—Holotype ♂ (MZB 1413) (17.3 × 12.4 mm), Indonesia: Kalimantan, West Borneo, Ketapang, Sei Pelang, collected by E. Cholik, 10 June 1993. Paratypes: 2 ♂, 1 ♀ (MZB 1413), 1 ♂, 1 ♀ (ZRC), same data as holotype.

Diagnosis.—Carapace ovate; cervical groove shallow, epigastric cristae low but distinct; postorbital cristae not discernible; epibranchial teeth low but prominent; H-shaped depression shallow; frontal margin not distinctly deflexed; frontal median triangle incomplete. Male holotype major chela about 3 times larger than minor; outer surface of male major chela rugose. G1 slender, sinuous, terminal segment cylindrical, about as long as subterminal segment; G2 with relatively long distal segment, about 0.9 times length of basal segment.

Remarks.—*Coccusa isophallus* is a small-sized species, with the holotype and the paratypes being fully mature at carapace widths of about 14 mm. Compared to its only congener, *C. isophallus* has an incomplete frontal margin triangle, whereas it is complete in *C. adipis*. In addition, *C. isophallus* lacks a subterminal spine on the meri of the ambulatory legs, but the spine is present in *C. adipis*. The cervical groove of *C. isophallus* is relatively shallower compared to that of *C. adipis*. Although *C. adipis* is much larger than *C. isophallus*, we do not believe that the above differences can be attributed merely to their size differences. The type locality of *C. adipis*

(Longlanuk) is geographically separated from that of *C. isophallus* by some 900 km.

Etymology.—The species name *isophallus* is Latin for equal penis, alluding to the similar length of the terminal segment and the sub-terminal segments of G1. It is used as a noun in apposition.

Coccosa adipis (Ng and Wowor, 1990)

Terrathelphusa adipis Ng and Wowor, 1990: 264.

Material Examined.—Holotype (MZB 1286), Indonesia: Kalimantan, East Borneo, Longlanuk, 1°58'S 117°50'E, collected by S. S. Liem, 14 October 1963.

Remarks.—In describing *Terrathelphusa adipis*, Ng and Wowor (1990) noted that the generic classification of this species was difficult and its general morphology allies it to several Southeast Asian genera. *Terrathelphusa adipis* was eventually tentatively referred to *Terrathelphusa* mainly because of the carapace form and well-developed triangular tooth on the inner distal margin of the third maxilliped exopod. Another notable character of *T. adipis* is its armed ambulatory merus, absent in all other species of *Terrathelphusa*. The external morphology of *T. adipis*, however, closely resembles that of *Coccosa*. The relatively shallow cervical groove and slightly rugose cheliped argues against its inclusion in *Terrathelphusa*. Therefore, *Terrathelphusa adipis* is here transferred to *Coccosa*.

ACKNOWLEDGEMENTS

We thank Robert Inger, Satish Choy, Indraneil Das, Keith Martin-Smith, and Christina Colón for referring their specimens to us for this study. Daisy Wowor (MZB), C. M. Yang (ZRC), Charles Franses (RMNH), Michael Turkey (SMF), and Rafael Lemaitre (USNM) kindly allowed us to examine specimens under their care.

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RECEIVED: 4 December 1997.

ACCEPTED: 17 February 1998.

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