THE FRESHWATER CRABS OF SULAWESI,
WITH DESCRIPTIONS OF TWO NEW GENERA AND FOUR NEW SPECIES
(CRUSTACEA: DECAPODA: BRACHYURA: PARATHELPHUSIDAE)

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ABSTRACT. – The taxonomy of the parathelphusid freshwater crabs of the genera Parathelphusa H. Milne Edwards, 1853, and Nautilothelphusa Balss, 1933, of Sulawesi is revised. Thirteen Sulawesian species are now recognised in Parathelphusa, with the problems associated with P. celebensis (De Man, 1892) and P. pallida (Schenkel, 1902) resolved, five taxa (Telphusa celebensis var. pareparensis De Man, 1892, Potamon (Potamonautes) celebensis var. croceum Schenkel, 1902, Potamon (Potamonautes) celebensis var. tenuipes Schenkel, 1902, Potamon celebensis var. possoensis Roux, 1904, Potamon celebensis var. linduensis Roux, 1904) previously regarded as their synonyms are resurrected as valid species, and two (Parathelphusa sorella, P. ferruginea) are described as new. One taxon, Parathelphusa matannensis (Schenkel, 1902), is referred to a new genus, Syntripsa, and a new species (S. flavichela) is described from Lake Towuti and Lake Mahalona. A new genus and new species, Migmathelphusa olivacea, is described from Lake Poso. A synopsis is also provided of the three known species of Sundathelphusa from Sulawesi. A key to all genera and species treated is provided.

KEY WORDS. – Sulawesi, Crustacea, Brachyura, Parathelphusidae, new species, taxonomy.

INTRODUCTION

The Indonesian island of Sulawesi, better known in the older scientific literature as Celebes, is central to many ideas on biogeography in Southeast Asia, especially with regards to the tectonic movements of the Sunda and Sahul Plates. In the study of terrestrial and freshwater organisms, most of the ideas contained in Wallace’s (1869) original ideas on animal distribution (marked by the well known Wallace’s Line between Borneo and Sulawesi) are still valid. For freshwater crabs, the family Potamidae stops in Borneo, well west of Wallace’s Line (see Ng, 1988a). The Parathelphusidae, however, have members on both sides of the line. One genus in particular, Parathelphusa, has good numbers of species on both sides of the line, but does not occur further east of Sulawesi. Considering that true freshwater crabs are valuable as biogeographic indicators (Ng & Rodriguez, 1995), clearly, a better understanding of biogeography of the island can be derived if the rather confused taxonomic state of the freshwater crabs of Sulawesi, can be clarified.

In the last major work on the freshwater crabs of Sulawesi by Bott (1970c), three genera, viz. Sundathelphusa Bott, 1970, Parathelphusa H. Milne Edwards, 1853, and Nautilothelphusa Balss, 1933, with 10 species, were recognised from Sulawesi. Although Bott (1970c) regarded the family Sundathelphusidae as a good family, all current indications are that this family should be synonymised with Parathelphusidae Alcock, 1910 (see Ng & Sket, 1996).

In Parathelphusa, Bott (1970c) recognised five species as from Sulawesi, viz. P. pantherina (Schenkel, 1902), P. sarasinorum (Schenkel, 1902), P. lokaensis (De Man, 1892), P. pallida (Schenkel, 1902), and P. celebensis (De Man, 1892). In the genus Nautilothelphusa, Bott (1970c) recognised two species, Nautilothelphusa zimmeri (Balss, 1933) and N. matannensis (Schenkel, 1902). Subsequently, Ng (1988a) regarded Potamon (Parathelphusa) matannensis as belonging to Parathelphusa H. Milne Edwards, 1853, and to Nautilothelphusa Balss, 1933, but he did not elaborate or provide details. Ng (1993) subsequently described a new species, Parathelphusa ceophallus, from Pulau Buton off southeastern Sulawesi, and in contrast to Bott’s views, he considered the taxonomy of P. celebensis and P. pallida yet to be resolved. He referred to the two species, their presumed synonyms and undescribed species as the P. celebensis complex.

In recent years, several key collections have been made in
Sulawesi which allow their taxonomy to be re-appraised and clarified. In the present study, all the species and subspecies which have been referred to *Parathelphusa* and *Nautilothelphusa* were examined and are redescribed here. Five species, viz. *Parathelphusa crocea* (Schenkel, 1902) and *P. pareparensis* (De Man, 1892), regarded as junior synonyms of *P. celebensis* by Bott (1970c); and *P. possoensis* (Roux, 1904), *P. tenuiipes* (Roux, 1904) and *P. linduensis* (Roux, 1904), formerly regarded as junior synonyms of *P. pallida* by Bott (1970c), are now recognised as valid taxa. Two new species of *Parathelphusa* are diagnosed. *Nautilothelphusa* remains a monotypic genus. *Parathelphusa matannensis* (Schenkel, 1902) is referred to a new genus, *Syntripsa*, and a new species is diagnosed. A new genus and new species, *Migmathelphusa olivacea*, is also described. A key to *Parathelphusa*, *Nautilothelphusa*, *Syntripsa* and *Migmathelphusa*, as well as their constituent species, is provided.

Measurements given for the crabs are listed as carapace width by carapace length. The width taken is measured across the widest part of the carapace. Where the anterolateral or epibranchial teeth/spines are long and developed, the width taken is that which is the widest between the bases of these teeth. The length was measured from the median point of the frontal margin to the median point of the posterior margin of the carapace. The anterolateral armature is considered here to include the external orbital tooth, followed by the epibranchial teeth. The strength and prominence of the anterolateral teeth is a difficult character to use at times, although in most cases, the differences are distinct. A well demarcated tooth is one in which it is distinctly separated from the adjacent one by a deep or prominent cleft or incision. The tooth may also be low, blunt or sharp. In some cases, the tooth may be very low but nevertheless separated from the adjacent one by a deep incision. The postorbital crista in most species is sharp (i.e. it is clearly cristate) – and where it ends is a useful taxonomic character. The postorbital crista tends to become progressively weaker as it approaches the anterolateral margin – it may remain as a ridge or break up into a series of striae and/or granules. Where the clearly cristate part of the postorbital cristae ends is useful – it may terminate at the base of the epibranchial teeth, stop just before it, or ends well before it. The form of the ambulatory dactyl is useful in some cases. In apparently more terrestrial species (but not always), the dactylus tends to proportionately longer and more slender. In more fully aquatic species, the dactylus is usually relatively shorter and broader.

The Indonesian terms Gua and Sungai refer to cave and river respectively. The abbreviations G1 and G2 are used for the first and second gonopods respectively. The terminology used essentially follows that used by Ng (1988a). Specimens are deposited in Museum Zoologicum Bogoriense (MZB), Bogor, Java, Indonesia; Naturhistorisches Museum Basel (NMB), Basel, Switzerland; Nationaal Natuurhistorisch Museum (ex Rijksmuseum van Natuurlijke Historie, RMNH), Leiden, The Netherlands; Museum für Naturkunde der Humboldt-Universität zu Berlin (MNHB), Berlin, Germany; and the Zoological Reference Collection (ZRC), Raffles Museum of Biodiversity Research, Department of Biological Sciences, National University of Singapore.

The species in this paper are treated in groups that make comparisons easiest. For example in *Parathelphusa*, taxonomically clear cut species are dealt with first. Most of the species previously confused with *P. celebensis* and *P. pallida* are then dealt with together. New species are described after the older taxa are treated. This layout, however, can be confusing if information on specific taxa is sought, and as such, to help the reader, the pagination for the various species treated is highlighted in the genus and species key below.

### Key to the species of *Parathelphusa* and allied genera of Sulawesi

1. Anterolateral margin of carapace with two or more visible teeth, teeth occasionally very low but always discernible at least as low lobes
   - 1
2. Anterolateral margin of carapace with only one visible tooth (occasionally almost undiscernible)
   - 3
3. Carapace squarish. Frontal margin with well developed deeply recessed median triangle. Chela and fingers slender, outer surfaces not prominently convex. Propodus of last pair of ambulatory legs broad. Third pair of ambulatory meri longest
   - 3
4. Carapace narrowly to broadly transverse. Frontal margin with well developed median triangle which is relatively level with rest of frontal margin. Chela and fingers stout, outer surfaces convex. Propodus of last pair of ambulatory legs narrow. Second pair of ambulatory meri longest
   - 4
   - 5
   - 6

*Migmathelphusa olivacea*, new genus, new species (pg. 416)

4a. Carapace dorsal surface rugose. Epigastric and postorbital cristae distinct, rugose but not sharp. Posterior margin of epistome continuous, without distinct clefts or fissures. Third maxillipod merus with notch or deep depression on the anterior margin.
Cheliped fingers with pair of large opposable molariform teeth, even in small specimens. Dorsal subterminal spine on ambulatory merus strong, sharp .............................................. 5 (Syntripsa, new genus) (pg. 408)

4b. Carapace dorsal surface smooth. Epigastric and postorbital cristae strong and sharp. Posterior margin of epistome not continuous, antero-lateral margin of epistome recessed. Third maxilliped merus with anterior margin flushed. Cheliped fingers with small teeth, not molariform. Dorsal subterminal spine on ambulatory merus small and sharp or absent ............................................. 6 (Parathelphusa) (pg. 384)


6a. Anterolateral teeth well demarcated, usually prominent, triangular ................................................................. 7

6b. Anterolateral teeth not well demarcated, very low to almost confluent with each other ................................ 10

7a. External orbital angle triangular. First and second epibranchial teeth triangular to acutely triangular... 8

7b. External orbital angle triangular to broadly triangular. First epibranchial tooth blunt and low or almost confluent with external orbital angle. Second epibranchial teeth blunt and low but distinct ......... 9

8a. Carapace rusty-red in life or freshly preserved. Dorsal surface of carapace prominently rugose and finely granulose. Postorbital cristae does not reach anterolateral margin, stopping before beginning of cervical groove ...................................... Parathelphusa ferruginea, new species (pg. 406)

8b. Carapace, cheliped and ambulatory legs spotted with distinct rosette pattern when alive or freshly preserved. Dorsal surface of carapace slightly rugose, appearing mostly smooth. Postorbital cristae reaches the base of the first epibranchial tooth ................................................................. Parathelphusa pantherina (pg. 385)

9a. Anterolateral regions smooth. Postorbital cristae end well before anterolateral margin. First and second epibranchial teeth well demarcated but blunt, with distinct notch between external orbital angle and first epibranchial tooth and between first and second epibranchial teeth. Ambulatory merus smooth throughout, no trace of dorsal subterminal angle or spine. Colour in life dark yellow to yellowish-green, in preservative deep olive-green ................................................. Parathelphusa sarellae, new species (pg. 387)

9b. Anterolateral regions with strong striae. Postorbital cristae end at base of second anterolateral tooth. First epibranchial tooth low, weakly demarcated from external orbital tooth, may be almost confluent with it, second epibranchial tooth low, blunt, relatively broad. Ambulatory merus with dorsal subterminal angle, not spiniform but may be relatively sharp. Colour in preservative yellowish brown ............................................. Parathelphusa soorella, new species (pg. 389)

10a. Cleft present on postorbital cristae where cervical groove begins. Upper margin of frontal median triangle separated from lateral margins by distinct gap. G1 proximal outer margin with distinct, broad, deep V-shaped cleft...... Parathelphusa cephalus (pg. 391)

10b. Postorbital cristae more or less continuous. Upper and lateral margins of frontal median triangle fused, confluent or upper margins not discernible, absent. G1 proximal outer margin with shallow cleft or appearing almost entire ................................................................................ 11

11a. Epibranchial teeth low but discernible............... 12

11b. Epibranchial teeth almost confluent with rest of anterolateral margin ...................................................... 13

12a. Postorbital cristae ends at base of second epibranchial tooth, epibranchial teeth relatively distinct............. Parathelphusa celebensis (pg. 393)

12b. Postorbital cristae ends between base of first and second epibranchial teeth, epibranchial teeth low, knob-like. Parathelphusa tenuipes (pg. 397)

13a. Branchial regions highly inflated, swollen. Anterolateral margin diverges sharply after external orbital angle. Cornea of eye reduced. G1 relatively long, slender ................................................. Parathelphusa sorella, new species (pg. 403)

13b. Branchial regions gently convex, not prominently inflated. Anterolateral margin diverges gently after external orbital angle. Cornea of eye not reduced. G1 relatively short, stout or slender ........................................ 14

14a. Dactylus of ambulatory leg relatively long, slender. Fingers longer then palm of cheliped ................. Parathelphusa pareparensis (pg. 399)

14b. Dactylus of ambulatory leg relatively short, broad. Fingers shorter than or subequal to palm of cheliped ...................................................................................... 15

15a. Dorsal margin of frontal median triangle distinct. G1
relatively stout, stocky .................................................  Parathelphusa pallida (pg. 395) 15b. Dorsal margin of frontal median triangle weak or indistinct. G1 comparatively slender......................... 16

16a. Post orbital cristae reach base of second epibranchial tooth. Suture between thoracic sternites 3 and 4 absent ................................................. Parathelphusa crocea (pg. 402)

16b. Postorbital cristae reach base of first epibranchial tooth or stops short of anterolateral margin and ends at cervical groove. Suture between thoracic sternites 3 and 4 distinct................................................. 17

17a. Frontal median triangle broad, low. Postorbital cristae does not reach anterolateral margin, stopping on meeting cervical groove................................................. Parathelphusa linduensis (pg. 403)

17b. Frontal median triangle relatively narrow, high. Postorbital cristae does not reach anterolateral margin, stopping at base of first epibranchial tooth ................. Parathelphusa possoensis (pg. 398)

18a. Anterolateral margins of adult specimens strongly convex, carapace appearing transversely ovate. G1 tip truncate .......... Sundathelphusa cassiope (pg. 418)

18b. Anterolateral margins of adult specimens gently convex, carapace appearing more squarish. G1 tip rounded to sharp ................................................. 19

19a. External orbital angle hardly separated from rest of anterolateral margin, margin appearing almost confluent. Branchial regions distinctly swollen, surface smooth. G1 almost straight with distal part slightly curved .......... Sundathelphusa rubra (pg. 419)

19b. External orbital angle distinctly separated from rest of anterolateral margin by a notch. Branchial regions not prominently swollen, surface lined with striae. G1 curving outwards ................................................. Sundathelphusa minahassae (pg. 419)

GECARCINUCOIDEA Rathbun, 1904

PARATHELPHUSIDAE Alcock, 1910

Parathelphusinae Alcock, 1910: 70.

Parathelphusa H. Milne Edwards, 1853

Potamon (Parathelphusa) - Rathbun, 1905: 228 (part).
Parathelphusa (Parathelphusa) - Bott, 1970c: 118.

Type species. – Parathelphusa tridentata H. Milne Edwards, 1853; subsequent designation by Rathbun (1905). Gender of genus: feminine.

Diagnosis. – Carapace transverse, smooth, glabrous, regions distinct. Frontal margin with distinct and well developed median triangle. Anterolateral margin with 2 epibranchial teeth and an external orbital angle, all of which may be reduced. Posterior margin of epistome with distinctly triangular median lobe. Third maxilliped exopod with long flagellum extending beyond width of merus. Chelipeds unequal in large adult males. Male abdomen distinctly T-shaped, narrow, with proximal segments broader but narrowing sharply from segment 5 onwards, G1 stout, simple, terminal and subterminal segments indistinctly or cannot be demarcated; terminal segment conical to subtruncate; G2 shorter than G1, basal segment subequal to or longer than well developed distal segment.

Remarks. – Parathelphusa H. Milne Edwards, 1853, is a speciose genus of freshwater crabs with members mainly Sundiac in distribution with outliers in the Philippines, Sulawesi, Bali and Lombok. Excluding the species presently treated in this study, 42 species have been recognised thus far (Bott, 1970c; Chia & Ng, 1998; Ng, 1988a, 1990, 1992, 1993, 1995b, 1997; Ng & Goh, 1987, 1997; Ng & Takeda, 1992, 1993; Freitag & Yeo, 2004). The genus Parathelphusa was first established by H. Milne Edwards, 1853, for two new species: P. tridentata and P. sinensis. No type species was indicated. Subsequently, Rathbun (1905) identified P. tridentata as the type of Parathelphusa. Her designation of the type species is valid under Article 69(a) of the International Code of Zoological Nomenclature (ICZN, 1999). The genus has a very confused taxonomic history. Two synonyms are Palawanthelphusa Bott, 1969, and Mesothelphusa De Man, 1892 (see Ng, 1988a). Palawanthelphusa was established by Bott (1969a) for three species from Northern Borneo and Palawan Islands and it was eventually regarded as a junior synonym of Parathelphusa by Ng and Goh (1987). Mesothelphusa was use for P. celebensis by De Man (1892), but subsequently Ng (1988a) commented that the subgeneric characters cited by Bott (1970b, c) to distinguish it from Parathelphusa sensu stricto were vague and in many instances, overlapping, and he synonymised both taxa.

A new genus, Syntripsa, is here established for Potamon (Parathelphusa) matannensis Schenkel, 1902, as there are several diagnostic characters which distinguish it from both
Nautilothelphusa Balss, 1933, and Parathelphusa (see also Ng, 1988a). Of the five species of Parathelphusa from Sulawesi, Ng (1993) regarded the taxonomy of *P. celebensis* and *P. pallida* as difficult despite Bott’s (1970c) conclusions, and Ng (1993) contends that there are more than two species in what he referred to as the *P. celebensis* - *P. pallida* complex. This study confirms that the complex contains seven species (see below). This means that the genus *Parathelphusa* now contains 47 known species (Table 1).

*Parathelphusa pantherina* (Schenkel, 1902)  
(Figs. 1, 3A-E, 36A, 37A)

Potamon (Parathelphusa) pantherina Schenkel, 1902: 522, Pl. 10  
Fig. 11-13.

Potamon (Parathelphusa) pantherinus - Rathbun, 1905: 236.

Parathelphusa (Mesothelphusa) pantherina - Roux, 1915: 267, 249.

Parathelphusa (Mesothelphusa) pantherina - Balss, 1934: 178.

Fig. 1. *Parathelphusa pantherina* (Schenkel, 1902), paralectotype male (42.4 x 31.2 mm, NMB 21A): A, dorsal view; B, frontal view; C, ventral view.
Table 1

LIST OF KNOWN SPECIES OF PARATHELPHUSA H. MILNE EDWARDS, 1853
(SQUARE PARENTHESIS REFER TO THE ORIGINAL GENUS THE SPECIES WAS DESCRIBED IN OR THE PROVENANCE)

Parathelphusa balabac Ng & Takeda, 1993 [Balabac Island, Philippines]
Parathelphusa batamensis Ng, 1992 [Batam Island, Indonesia]
Parathelphusa baweaneis Ng, 1997 [Bawe Island, Indonesia]
Parathelphusa bogorensis Bott, 1970 [Java, Indonesia]
Parathelphusa cabayugan Freitag & Yeo, 2004 [Palawan, Philippines]
Parathelphusa celebensis (De Man, 1892) [Thelphusa] [Sulawesi, Indonesia]
= Potamon (Potamonautes) celebens var. immaculata Schenkel, 1902
Parathelphusa ceophallus Ng, 1993 [Sulawesi, Indonesia]
Parathelphusa convexa De Man, 1879 [Java and southern Sumatra, Indonesia]
= Telphusa convesus Herklots, 1861 (nomen nudum)
= ?Ozius frontalis Targioni-Tozzetti, 1872
= Parathelphusa dentipes Heller, 1862
Parathelphusa crocea (Schenkel, 1902) [Potamon (Potamonautes)] [Sulawesi, Indonesia]
Parathelphusa ferruginea Chia & Ng, 2006 [Sulawesi, Indonesia]
Parathelphusa linduensis (Roux, 1904) [Potamon] [Sulawesi, Indonesia]
Parathelphusa lombokensis Bott, 1970 [Lombok, Indonesia]
Parathelphusa lokaensis (De Man, 1892) [Thelphusa] [Sulawesi, Indonesia]
= Potamon (Parathelphusa) tridentatum var. incertum Lanchester, 1900
= Parathelphusa lokaensis var. lanchesteri Nobili, 1901
Parathelphusa maindroni (Rathbun, 1902) [Potamon (Parathelphusa)] [Sumatra, Indonesia; Peninsular Malaysia]
Parathelphusa malaysiana Ng & Takeda, 1992 [Peninsular Malaysia]
Parathelphusa manguao Freitag & Yeo, 2004 [Palawan, Philippines]
Parathelphusa mindoro Ng & Takeda, 1993 [Mindoro Island, Philippines]
Parathelphusa modiglianii Nobili, 1903 [Mentawai Islands, Indonesia]
Parathelphusa nagasakti Ng, 1988 [Tioman Island, Peninsular Malaysia]
Parathelphusa nana Ng & Takeda, 1993 [Palawan, Philippines]
Parathelphusa nitida Ng, 1986 [Kalimantan, Indonesia]
Parathelphusa obtusa (Bott, 1969) [Palawanthelphusa] [Palawan, Philippines]
Parathelphusa owum Ng, 1995 [Sabah, Malaysia]
Parathelphusa oxynosa Nobili, 1901 [Sarawak, Malaysia]
Parathelphusa palawanensis (Bott, 1969) [Palawanthelphusa] [Palawan, Philippines]
Parathelphusa pallida (Schenkel, 1902) [Potamon (Potamonautes)] [Sulawesi, Indonesia]
= Potamon (Potamonautes) celebens var. annulipes Schenkel, 1902
Parathelphusa pantherina (Schenkel, 1902) [Potamon (Parathelphusa)] [Sulawesi, Indonesia]
Parathelphusa paraparensis (De Man, 1892) [Thelphusa] [Sulawesi, Indonesia]
Parathelphusa parma Ng & Takeda, 1993 [Balabac Island, Philippines]
Parathelphusa possoensis (Roux, 1904) [Potamon (Potamonautes)] [Sulawesi, Indonesia]
Parathelphusa pulcherrima (De Man, 1902) [Potamon (Parathelphusa)] [Sarawak, Malaysia; Brunei]
Parathelphusa quadrata Ng, 1997 [Lombok, Indonesia]
Parathelphusa rasilis Ng & Takeda, 1993 [Palawan, Philippines]
Parathelphusa reticulata Ng, 1990 [Singapore]
Parathelphusa sabari Ng, 1986 [Kalimantan, Indonesia]
Parathelphusa saginata Ng & Takeda, 1993 [Palawan, Philippines]
Parathelphusa sarasinorum (Schenkel, 1902) [Potamon (Potamonautes)] [Sulawesi, Indonesia]
Parathelphusa sarawakensis Ng, 1986 [Sarawak, Malaysia]
Parathelphusa shelfordi Nobili, 1901 [Sarawak, Malaysia]
Parathelphusa sorella Chia & Ng, 2006 [Sulawesi, Indonesia]
Parathelphusa tenuipe (Schenkel, 1902) [Potamon (Potamonautes)] [Sulawesi, Indonesia]
Parathelphusa tera Chia and Ng, 1998 [Kalimantan, Indonesia]
Parathelphusa torta Chia & Ng, 1998 [Kalimantan, Indonesia]
Parathelphusa tridentata H. Milne Edwards, 1853 [Sumatra, Indonesia]
= Alpheus tridens Weber, 1795 (as 3 dens) (nomen nudum)
= Cancer (Thelphusa) tridens De Haan, 1835 (preoccupied name, nomen nudum)
= Telphusa triodon Herklots, 1861 (nomen nudum)
Parathelphusa undulata Chia & Ng, 1998 [Kalimantan, Indonesia]
Parathelphusa valida Ng & Goh, 1987 [Sabah, Malaysia]
**Parathelphusa pantherina** - Bott, 1970b: 338; 1970c: 123, Pl. 23 Fig. 75-77, Pl. 31 Fig. 94.


**Diagnosis.** – Carapace flat, spotted in life, dorsal surfaces smooth; cervical groove shallow, narrow; H-shaped central depression pronounced. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae almost reaching anterolateral margin, stopping just before base of first epibranchial tooth. Front with slight depression, entire; frontal median triangle distinct, complete, ventral sides recessed. External orbital angle broadly triangular, outer margin almost straight, about 2 times length of inner margin, first and second epibranchial teeth distinctly triangular. Posterolateral regions lined with oblique striae. Suture between thoracic sternites 2 and 3 almost complete, gently concave towards buccal cavity to almost straight. Palm of chelipeds inflated, fingers shorter then palm, pollex and dactylus pigmented black throughout half the length towards tip. Ambulatory legs relatively long, second pair longest. Dorsal margin of merus smooth, without distinct subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, gently sinuous. G1 slender, relatively straight, directed upwards, outer margin almost straight, proximal part not clefted; distal part tapering. G2 with well developed distal segment, about 0.6 times length of basal segment.

**Distribution.** – Lake Matano, South Sulawesi.

**Remarks.** – *Parathelphusa pantherina* was first described by Schenkel (1902) from seven male specimens from Lake Matano. In his paper, Schenkel (1902) did not specify a holotype. Bott (1970c) in his monograph, designated a male specimen 36.0 by 28.0 mm as the lectotype. He also noted that together with the same lot (NMB 21a) as the lectotype, there was also a paralectotype female. This second bit of data is confusing. Listed in the Basel Museum catalogues under NMB 21a are five male specimens of *Parathelphusa pantherina*, and a physical check by the first author at NMB verified this. According to the catalogue cards, of these five males, one specimen was the one selected by Bott (1970c) as the lectotype and was subsequently relabelled NMB 21b. The rest are therefore paralectotypes. However, for some inexplicable reason, this lectotype male is now dried while the rest of the specimens are still in alcohol.

Of all the species of *Parathelphusa* found in Sulawesi, *P. pantherina* is the only one which is as distinctly spotted. Dark-red rosettes extend from the carapace to the ambulatory legs, and this pattern is even discernible in long preserved specimens. This character, along with its flat carapace and distinctive slender, relatively straight G1 easily differentiates it from all its congeners in Sulawesi.

**Parathelphusa sarasinorum** (Schenkel, 1902) (Figs. 2, 3F-I)

*Potamon* (*Potamonautes*) *sarasinorum* Schenkel, 1902: 525, Pl. 10 Fig. 13b; Rathbun, 1905: 200.

*Parathelphusa* (*Mesothelphusa*) *sarasinorum* - Roux, 1915: 247, 249.

*Parathelphusa* (*Parathelphusa*) *sarasinorum* - Bott, 1970b: 338; 1970c: 124, Pl. 23 Fig. 78-80, Pl. 31 Fig. 93.

**Material examined.** – Lectotype: male (38.9 x 31.5 mm) (NMB 22b), Lake Poso, Central Sulawesi, coll. Sarasin, 1901.

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**Fig. 2. Parathelphusa sarasinorum** (Schenkel, 1902), lectotype male (38.9 x 31.5 mm, NMB 22b): A, dorsal view; B, frontal view; C, ventral view.

**Diagnosis.** – Carapace flat, dorsal surfaces smooth, light yellow to yellowish-green when live; cervical groove shallow, narrow; H-shaped central depression distinct. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae not reaching anterolateral margin, stopping just posterior to base of first epibranchial tooth. Frontal margin entire, straight; frontal median triangle distinct, complete. External orbital angle triangular, outer margin convex, about 1.8 times length of inner margin, first and second epibranchial teeth blunt, relatively broad, directed forwards, outer margins slightly truncate, distinct notch between external orbital angle and first epibranchial tooth, and between first and second epibranchial teeth. Posterolateral regions lined with few oblique striae. Suture between thoracic sternites 2 and 3 almost complete, gently concave towards buccal cavity. Palm of chelipeds inflated, longer than pollex, pollex pigmented brown throughout length, dactylus pigmented black throughout length. Ambulatory legs of normal length, second pair longest. Dorsal margin of merus with slight cristae, without distinct subterminal spine. Male

![Fig. 3. Left G1 and G2. A-E, Parathelphusa pantherina (Schenkel, 1902), paralectotype male (42.4 x 31.2 mm, NMB 21A): A, G1 ventral view; B, G1 dorsal view; C, G1 distal part, ventral view; D, G1 distal part, dorsal view; E, G2. F-I, Parathelphusa sarasinorum (Schenkel, 1902), lectotype male (38.9 x 31.5 mm, NMB 22B): F, G1 ventral view; G, G1 dorsal view; H, G1 distal part, ventral view; I, G1 distal part, dorsal view. Scale bars = 1.0 mm.](image-url)
abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, gently sinuous. G1 gently curving outwards, directed upwards, outer margin slightly sinuous, proximal part not clefted; distal part tapering. G2 with well developed distal segment, about 0.6 times length of basal segment.

**Distribution.** – Lake Poso, Central Sulawesi.

**Remarks.** – Bott (1970c) designated one male (NMB 22b) as the lectotype from the original syntype series of six males and two females originally described by Schenkel (1902) from Lake Poso. The remaining specimens are thus paralectotypes.

*Parathelphusa sarasinorum* has blunt first and second epibranchial teeth that are relatively broad and directed forwards. The outer margins of the epibranchial teeth are slightly truncate with a distinct notch between external orbital angle and the first epibranchial tooth, and between the first and second epibranchial teeth. These are characters unique only to *P. sarasinorum*, easily distinguishing it from all other Sulawesi congeners. The only species that superficially resembles *P. sarasinorum* is perhaps *Migmathelphusa olivacea*, new species. *Migmathelphusa olivacea* also resembles *P. sarasinorum* in its live coloration, both being deep olive- to yellowish green with a yellow tinge on the edge of the carapace. However, *P. sarasinorum* differs from *M. olivacea* in that the latter species has a proportionately much broader propodus on the last pair of ambulatory leg compared to *P. sarasinorum* (Fig. 35A vs. Fig. 2A), possesses a distinctive long and slender G1 with its tip directed inwards (Fig. 36A-D), a G2 that has a proportionately short distal segment (Fig. 36E). In *P. sarasinorum*, the G1 is relatively shorter (Fig. 3F-I) and the G2 has a relatively longer distal segment (0.6 times length of basal segment vs. 0.4 times for *M. olivacea*).

*Parathelphusa lokaensis* (De Man, 1892)

(Figs. 4–6)

*Telphusa celebensis* var. *lokaensis* De Man, 1892: 300.

*Telphusa celebensis* - De Man, 1892: 297 (part).

*Potamon celebensis lokaensis* - De Man, 1898: 436

*Potamon* (*Potamonautes*) *celebensis lokaensis* - Schenkel, 1902: 531; Rathbun, 1905: 200.

*Potamon celebensis lokaensis* - Roux, 1904: 561, 568.

*Parathelphusa (Mesothelphusa) lokaensis* - Bott, 1970c: 126, Pl. 24 Figs. 83-84.

**Material examined.** – Lectotype: male (24.3 x 20.0 mm) (RMNH D 1286), Loka near Bonthain, South Sulawesi, ca. 5°30’S 119°50’E; coll. M. Weber, Oct-Nov.1888. Paralectotype: 1 male (RMNH D 2586), same data as lectotype. Others: 1 male (24.5 x 20.2 mm) (NMB 23Vc); Matinangkette, South Sulawesi, coll. Sarasin, 1901; 2 females (NMB 23Vb), Marangka, South Sulawesi, coll. Sarasin, 1901; 1 male (NMB 23Va), Loka, Bonthain, South Sulawesi, coll. Sarasin, 1901; 3 females (NMB 23Vd), Bonthain, South Sulawesi, coll. Sarasin, 1904; 1 female (21.7 x 17.6 mm) (RMNH D 1285) (syntype of *Telphusa celebensis* De Man, 1892, part), Luwu district, Palopo, Central Sulawesi, coll. M. Weber, Feb-Apr.1889; 1 male, 1 female (MZB 646), Sungai Lampea, Malili, Central Sulawesi, ca. 2°38’S 121°06’E, coll. F. Sabar, 7 Nov.1976.

**Fig. 4. Parathelphusa lokaensis** (De Man, 1892), lectotype male (24.3 x 20.0 mm, RMNH D 1286): A, dorsal view; B, frontal view; C, ventral view.

**Fig. 5. Parathelphusa lokaensis** (De Man, 1892), male (24.5 x 20.2 mm, NMB 23Vc): A, dorsal view; B, frontal view; C, ventral view.
Fig. 6. Left G1 and G2. A-E, *Parathelphusa lokaensis* (De Man, 1892), lectotype male (24.3 x 20.0 mm, RMNH D 1286): A, G1 dorsal view; B, G1 ventral view; C, G1 dorsal part, ventral view; D, G1 distal part, ventral view; E, G2. F-J, *Parathelphusa lokaensis* (De Man, 1892), male (24.5 x 20.2 mm, NMB 23Vc): F, G1 ventral view; G, G1 dorsal view; H, G1 distal part, ventral view; I, G1 distal part, dorsal view; J, G2. Scale bars = 1.0 mm.
**Diagnosis.** – Carapace flat, dorsal surfaces smooth; cervical groove shallow, narrow; H-shaped central depression distinct. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae reaches anterolateral margin, stopping just anterior of base of second epibranchial tooth. Front entire, straight; frontal median triangle distinct, incomplete, dorsal margin weak. External orbital angle broadly triangular, outer margin sinusuose, serrate, about 2 times length of inner margin, first epibranchial tooth weakly demarcated from external orbital angle, appears somewhat confluent in some specimens, outer margin serrate, second epibranchial tooth low, blunt, relatively broad, directed obliquely, outer margins serrate. Anterolateral margin convex, lined with oblique striae. Posterolateral region lined with oblique striae. Suture between thoracic sternites 2 and 3 complete, almost straight. Palm of chelipeds inflated, longer than pollex. Ambulatory legs long, second pair longest. Ambulatory merus broad. Dorsal margin of merus with slight cristae, without distinct subterminal spine, although there is usually a small angle present which may be sharp. Male abdomen reaching imaginary line joining anterior edges of cheliped bases. T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 concave; lateral margins of segment 6 subparallel, gently sinuous. G1 gently curving outwards, directed upwards, outer margin almost straight, proximal part not clefted; distal part gently tapering; tip gently flared. G2 with well developed distal segment, about 0.6 times length of basal segment.

**Distribution.** – South and Central Sulawesi.

**Remarks.** – *Parathelphusa lokaensis* was first described by De Man (1892) as a variety of *P. celebensis* from specimens obtained from Loka, close to Bonthain. Examination of the toposcope material from Bonthain, and comparing with congenic materials, confirms that *P. lokaensis* is a valid species (cf. Bott, 1970c: 126). In the RMNH are two syntype males, and RMNH D 1286 is here designated as the lectotype of the species.

*Parathelphusa lokaensis* differs from its Sulawesi congeners by having an external orbital angle that is broadly triangular, with the outer margin uneven to sinuous. Its first epibranchial tooth is also almost confluent with the external orbital angle, and the second epibranchial tooth is relatively broad, low and blunt. The anterolateral margin of *P. lokaensis* is distinctively serrate, even more so when compared to *P. celebensis*. All these characters, combined with its relatively broad ambulatory merus, easily distinguishes *P. lokaensis* from the other *Parathelphusa* species known from Sulawesi.

The type of *P. lokaensis* was from Bonthain in southern Sulawesi, and the present record of it from Sungai Laempur (Malili) and near Palopo in the central part of the island is rather surprising. Yet comparisons of the specimens do not show any major differences. The only difference noteworthy is that the specimens from central Sulawesi have the first epibranchial tooth somewhat lower and less discernible. Their G1 structures, however, are very similar. Of course, since the specimens from Central Sulawesi are not adult males (Malili: one young male and one juvenile, MZB 646; Palopo: one female specimen, RMNH D 1285, part of the type series of *P. celebensis*), not that much more can be said. When adult males from this locality become available, differences may avial themselves. For the moment, despite the fact that we are dealing with an apparently more highland taxon from three disjunct localities, it seems best to regard the specimens as one species.

*Parathelphusa ceophallus* Ng, 1993

(Fig. 7)

*Parathelphusa ceophallus* Ng, 1993: 179, Figs. 1, 2.

**Material examined.** – Holotype: male (23.1 x 18.1mm) (RMNH D 42418), Jismil Camp, a few kilometres from Labuhan Tobela, along Sungai (River) Labuhan Tobela, rivulet through hardly disturbed primary evergreen rainforest, boulder covered with calcareous deposits, 150 m, northern Pulau Buton, 4°26’30”S 122°59’E, Southeast Sulawesi, coll. J. van Tol, 12-18 Nov.1989.

**Diagnosis.** – Carapace dorsal surfaces smooth; cervical groove shallow, narrow; H-shaped central depression pronounced; branchial regions slightly inflated. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin, with slight cleft at beginning of cervical groove; outer edge of cristae not reaching anterolateral margin, stopping before very shallow cleft separating first and second epibranchial teeth. Front slightly sinusuous, entire; frontal median triangle distinct, but upper ridged margin does not join lateral margins, separated by small but distinct gap. Anterolateral margin arcuate, weakly cristae, external orbital angle broadly triangular, outer margin almost straight, about 3 times length of inner margin, first and second epibranchial teeth very low, lobiform, barely discernible. Posterolateral regions lined with distinct oblique striae. Suture between thoracic sternites 2 and 3 incomplete, gently concave towards buccal cavity. Palm of chelipeds slightly inflated, fingers longer than palp, pollex not pigmented black but dactylus pigmented black throughout length. Ambulatory legs relatively short, second pair longest. Dorsal margin of merus slightly cristate, gently serrated, without distinct subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases. T-shaped; segment 6 distinctly longer than segment 7; lateral margins of segment 7 concave; lateral margins of segment 6 subparallel, gently sinuous. G1 gently curving outwards, directed upwards, outer margin slightly sinuous along distal two-thirds, proximal part with very deep V-shaped cleft; distal part tapering. G2 with well developed distal segment, about 0.6 times length of basal segment. (Adapted from Ng, 1993)

**Distribution.** – Pulau Buton, Southeast Sulawesi.

**Remarks.** – Ng (1993), commented that *P. ceophallus* is most similar to species of the *P. celebensis - P. pallida* complex. However, it can be distinguished from the *P. celebensis* complex in that it possess a cleft on the postorbital cristae where the cervical groove begins (Fig. 7A) versus the cleft being absent in other species of the complex. The dorsal
Fig. 7. *Parathelphusa ceophallus* Ng, 1993, holotype male (23.1 x 18.1mm) (RMNH D 42418): A, right dorsal view of carapace; B, frontal view of carapace; C, frontal median triangle; D, anterior thoracic sternum; E, male abdominal segment 4-6 and telson; F, left third maxilliped; G, right fourth ambulatory leg; H, left G1 ventral view; I, left G1 dorsal view; J, left G1 distal part, ventral view; K, left G1 distal part, dorsal view; L, left G2 (after Ng, 1993: Figs. 1, 2). Scale bars: A-G = 1.0 mm; H, I, L = 0.5 mm; J, K = 0.25 mm.
margin of the frontal median triangle of *P. ceophallus* is also separated from the lateral margins by a distinct gap (Fig. 7C). *Parathelphusa ceophallus* also possess a very distinct, broad and deep V-shaped cleft along the proximal outer margin of its G1, against a shallow cleft or the margin appearing entire that the other species of the complex possess (Fig. 7H, I).

The other two characters that Ng (1993) used to differentiate *P. ceophallus* from the rest of the complex, namely a low, less distinct epibranchial teeth and the outer edge of the postorbital cistae stopping well before the anterolateral margin are no longer applicable as several poorly known taxa in this group are now better understood. While they work for *P. pallida* and *P. celebensis* s. str., *P. possoensis*, *P. crocea* and *P. linduensis* all have very low epibranchial teeth that are almost continuous with the anterolateral margin like *P. ceophallus*. *Parathelphusa linduensis* and *P. sorella* also have its outer edge of the postorbital cistae stopping well before the anterolateral margin. However, *P. ceophallus*, can still be distinguished from these on the basis of the form of its cervical groove, frontal median triangle and G1 (see also Ng, 1993). It is also the only member of the species complex known from Pulau Buton thus far.

*Parathelphusa celebensis* (De Man, 1892)

(Figs. 8-11, 14A-E)

*Telphusa celebensis* De Man, 1892: 297 (part), Pl. 17, Pl. 18 Fig 7.


*Potamon (Potamonautes) celebensis* - Ortmann, 1897: 305, 309.

*Potamon (Potamonautes) celebensis* - Schenkel, 1902: 528, Pl. 10 Fig. 9, 13a; Rathbun, 1905: 198.

*Potamon (Potamonautes) celebensis* var. *immaculata* Schenkel, 1902: 531.

*Potamon celebensis* - Roux, 1904: 568.

*Potamon celebensis* var. *immaculata* - Roux, 1904: 566.

*Potamon (Potamonautes) celebensis* var. *immaculata* - Rathbun, 1905: 199.

*Parathelphusa (Mesotelphusa) celebensis* - Roux, 1915: 247, 249.


*Parathelphusa (Mesotelphusa) celebensis* - Bott, 1970b: 338; Bott, 1970c: 127, Pl. 24 Figs. 85-87, Pl. 31 Fig. 95.

*Parathelphusa celebensis* - Ng, 1988b: 23.


Fig. 8. *Parathelphusa celebensis* (De Man, 1892), lectotype male (18.8 x 15.2 mm, RMNH D 2385): A, dorsal view; B, frontal view; C, ventral view.
Diagnosis. – Carapace convex, dorsal surfaces smooth; cervical groove shallow, but distinct; H-shaped central depression pronounced. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae not reaching anterolateral margin, stopping before base of second epibranchial teeth. Front almost straight, entire; frontal median triangle distinct, but dorsal ridged margin absent. Anterolateral margin slightly serrated, external orbital angle broadly triangular, outer margin almost straight, about 2.8 times length of inner margin, first and second
2 and 3 incomplete, almost straight. Palm of chelipeds slightly inflated, fingers shorter than palm, pollex not pigmented black but dactylus pigmented black throughout length. Ambulatory legs relatively short, second pair longest. Dorsal margin of merus slightly crystalline, without distinct subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, gently sinuous. G1 slender, relatively straight, directed upwards, outer margin gently sinuous along distal two-thirds, proximal part without cleft; distal part sharply tapering. G2 with well developed distal segment, about 0.6 times length of basal segment.

**Distribution.** – South Sulawesi and the southern parts of Central Sulawesi, bordering South Sulawesi.

**Remarks.** – *Parathelphusa celebensis* was first described by De Man (1892) from 10 male and 17 female specimens from Palopo and Luwu, Sulawesi. In his paper, he provided a detailed description and detailed figures of *P. celebensis*, but he did not designate a holotype. Bott (1970c) subsequently examined toptotypic material from Luwu, and added a detailed diagnosis and photographs. These papers, together with our re-examination of type material and a large toptotypic series collected from Palopo (ZRC 2000.2564, ZRC 2000.2566), now allow us to provide a detailed diagnosis of *P. celebensis* s. str..

While *P. celebensis* and *P. pallida* are superficially very similar, they can most easily be distinguished by the form of the anterolateral margin. In *P. celebensis*, the epibranchial teeth, while relatively low, are usually discernible, and separated from each other by clear notches. In the few cases where one side of the carapace have some of the teeth lower than normal, the remaining teeth are distinct or the teeth on the other carapace side are typical for the taxon. In *P. pallida*, the teeth on the anterolateral margin are very low, with the notches between them shallow, the margin often appearing almost entire. In addition, the branchial regions of *P. celebensis* are more swollen than those of *P. pallida*, especially when observed frontally and the specimens of similar size and sex (Fig. 10B, 11B vs. Fig. 12B). Most significantly, the structures of their G1s are different, with that of *P. celebensis* (Fig. 14A-D) more slender and the distal part more tapering compared to *P. pallida* (Fig. 14F-I). The large series of specimens of both species are our disposal confirms the usefulness of these features. Occasionally, the form of the anterolateral teeth may be very low in *P. celebensis* (e.g. Fig. 11A) and cannot be used to effectively separate the two species, but in such cases, the more swollen form of the carapace and G1 structure are still diagnostic. In addition, the two species do not seem to have completely overlapping ranges, with *P. celebensis* occurring mainly in the southern parts of Sulawesi, whilst *P. pallida* is present in the central areas around the Malili lake system.

Bott (1970c: 128) apparently did not examine the type series of *P. celebensis*. We examined two lots labelled as types in the RMNH. One lot, RMNH D 2585, contains a male and a female which agree very well with the other specimens from the type locality we have seen and matches our present definition of the species. The male specimen is still a juvenile but its G1 structure, although immature, agrees well with what is described and figured here for the species. The other lot, RMNH D 1285, with only one relatively small female, is problematic. It is clearly not *P. celebensis* as defined here and with regards to its carapace and ambulatory leg features, is actually much closer to *P. lokaensis*. This specimen (RMNH D 1285) is here referred to that species.

Bott (1970c) regarded *P. crocea* (Schenkel, 1902) and *P. pareparensis* (De Man, 1892) as junior synonyms of *P. celebensis*. However, on examining the type material of *P. crocea* and additional specimens, we find that it differs from *P. celebensis* in several key aspects (see discussion for *P. crocea*) and should be regarded as a valid species. As for *P. pareparensis*, from the diagnostic description and figures of the carapace by De Man (1892), and examination of a good series of material from around Parepare (type locality) and Maros, we have no doubt it is also a good taxon (see discussion for *P. pareparensis*). *Potamon (Potamonautes) celebense var. immaculata* Schenkel, 1902, on the other hand, after examining the type specimens, is similar to *P. celebensis* in all essential features, even in the form of the G1. We thus follow Bott (1970c) in regarding it as a junior synonym of *P. celebensis*. Bott (1970c: 128) had selected a lectotype male for *Potamon (Potamonautes) celebense var. immaculata*, and although he did not give any measurements of this specimen in his text, the specimen he selected, a male 33.3 by 26.1 mm, had been separated from the rest of the type material in the Basel Museum on his instructions. It is here regarded as the lectotype of the taxon (Fig. 11).

The record of Ng (1988b) of *P. celebensis* collected from caves in Maros is maintained. The carapace features of these specimens (Ng, 1988b) agree well with the concept of the species as presently defined. The eye cornea of these specimens is well developed, easily differentiating them from the cavernicolous *P. sorella*, new species (Fig. 24A, B). There is a complete suture between thoracic sternal segments three and four in these specimens. In smaller specimens of *P. celebensis*, this suture is very faint and indistinct but becomes increasing more distinct in larger crabs. In *P. sorella*, however, the suture between sternal segments two and three is incomplete. *Parathelphusa celebensis* is thus merely a facultative cavernicol.

Diagnosis. – Carapace convex, dorsal surfaces smooth; cervical groove shallow, but distinct; H-shaped central depression pronounced. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae not reaching anterolateral margin, stopping between base of first and second epibranchial teeth. Front sinuous, entire, median point with distinct depression; frontal median triangle distinct, lateral and dorsal ridge distinct and complete. Anterolateral margin granulated, external orbital angle broadly triangular, outer margin almost straight, about 2.7 times length of inner margin, first and second epibranchial teeth very low almost continuous with anterolateral margin. Posterolateral regions lined with distinct oblique striae. Suture between thoracic sternites 2 and 3 complete, almost straight. Palm of chelipeds slightly inflated, fingers shorter than palm. Ambulatory legs relatively long, second pair longest. Dorsal margin of merus slightly cristate, without distinct subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, gently sinuous. G1 relatively stout, curved slightly outwards, directed upwards, outer margin very gently sinuous along distal two-thirds, proximal part with slight cleft; distal part tapering. G2 with well developed distal segment, about 0.5 times length of basal segment.

Distribution. – Central and South Sulawesi, especially around the Malili Lakes System (Lake Towuti, Lake Mahalona, Lake Matano) up to the Poso area.

Remarks. – Schenkel (1902) described Potamon
(Potamonautes) celebensis var. pallidum from Kalaena on the basis of two male specimens. Bott (1970c) in his monograph designated one male (NMB 23VIb) as the lectotype. Bott (1970c) also regarded Parathelphusa tenuipes, P. linduensis and P. possoensis as junior synonyms of P. pallida. However, on examining the type specimens of the respective taxa and additional specimens, we find that P. tenuipes, P. linduensis and P. possoensis should be regarded as valid species (see discussion for these species). Parathelphusa annulipes on the other hand, after examining the type specimens, is similar to P. pallida, with their external morphologies virtually identical. It is here regarded as a junior synonym of P. pallida, as had been indicated by Bott (1970c).

Parathelphusa tenuipes (Schenkel, 1902) (Fig. 15)

Potamon (Potamonautes) celebensis var. tenuipes Schenkel, 1902: 530.
Potamon celebensis var. tenuipes - Roux, 1904: 565.
Potamon (Potamonautes) celebensis tenuipes - Rathbun, 1905: 199.
Parathelphusa (Meostelphusa) pallida (part) - Bott, 1970c: 128.

Material examined. – Holotype: female (32.6 x 24.4 mm) (NMB 23 IIa), Lake Poso, Tomini Gulf, Central Sulawesi, coll. Gesch & Sarasin, 1901.

Diagnosis. – Carapace convex, inflated, dorsal surfaces

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Fig. 14. G1 and G2. A-E, Parathelphusa celebensis (De Man, 1892), male (33.3 x 26.1 mm, NMB 23IVa): A, left G1 ventral view; B, left G1 dorsal view; C, left G1 distal part, ventral view; D, left G1 distal part, dorsal view; E, left G2. F-J, Parathelphusa pallida (Schenkel, 1902), lectotype male (23.9 x 18.3 mm, NMB 23Vlb): F, right G1 dorsal view; G, right G1 ventral view; H, right G1 distal part, dorsal view; I, right G1 distal part, ventral view; J, G2. Scale bars = 1.0 mm.
smooth; cervical groove deep and distinct, almost reaching anterolateral margin; H-shaped central depression shallow. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae almost reaching anterolateral margin, stopping at base of first epibranchial tooth. Front almost straight, entire; frontal median triangle distinct, very broad, dorsal ridge distinct but weak and incomplete. Anterolateral margin smooth, external orbital angle broadly triangular, low, outer margin almost straight, about 2.2 times length of inner margin, first and second epibranchial teeth low but discernible, knob-like. Posterolateral regions lined with distinct oblique striae. Palm of chelipeds slightly inflated, fingers subequal to palm. Ambulatory legs relatively long, second pair longest. Dorsal margin of merus slightly cristate, without distinct subterminal spine.

**Distribution.** – Lake Poso, Central Sulawesi.

**Remarks.** – Schmekel (1902) only examined one female from Lake Poso, near Tomini Gulf when he described *Potamonautes (Potamonautes) celebens* var. *tenuipes*. It was regarded as a junior synonym of *P. pallida* by Bott (1970c). However, despite the species represented by only a single female type specimen, there are still sufficient characters that differentiate it from *P. pallida*, and it is here regarded as a valid species.

*Parathelphusa tenuipes* differs from *Parathelphusa tenuipes* it from specimen, there are still sufficient characters that differentiate a junior synonym of Lake Poso, near Tomini Gulf when he described (*Remarks* following characters. The cervical groove of *Distribution* spine.


**Diagnosis.** – Carapace inflated, dorsal surfaces smooth; cervical groove shallow, narrow; H-shaped central depression pronounced; branchial regions inflated. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae not reaching anterolateral margin, stopping at base of first epibranchial teeth. Front slightly sinuous, entire; frontal median triangle distinct but relatively narrow, upper ridged margin weak, lateral margins strong, distinct. Anterolateral margin smooth, external orbital angle low, broadly triangular, outer margin almost straight,

![](image)

*Parathelphusa possoensis* (Roux, 1904)

(Figs. 16, 20A-E)

*Potamon (Potamonautes) celebens* (part) - Schmekel, 1902: 528, Pl. 10 Fig. 9, 13a.

*Potamon celebens* var. *possoensis* Roux, 1904: 564, Fig. B.

*Parathelphusa (Mesotelphhusa) pallida* (part) - Bott, 1970c: 128.


**Diagnosis.** – Carapace inflated, dorsal surfaces smooth; cervical groove shallow, narrow; H-shaped central depression pronounced; branchial regions inflated. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae not reaching anterolateral margin, stopping at base of first epibranchial teeth. Front slightly sinuous, entire; frontal median triangle distinct but relatively narrow, upper ridged margin weak, lateral margins strong, distinct. Anterolateral margin smooth, external orbital angle low, broadly triangular, outer margin almost straight,
about 2 times length of inner margin, first and second epibranchial teeth very low, lobiform, barely discernible. Posterolateral regions smooth, lined with weak oblique striae. Suture between thoracic sternites 2 and 3 incomplete, almost straight with respect to buccal cavity, suture between sternites 3 and 4 distinct but incomplete. Palm of chelipeds slightly inflated, fingers shorter than palm, pollax and dactylius usually unpigmented in most specimens, dactylius of major chela of large males pigmented black throughout length. Ambulatory legs relatively short, second pair longest. Dorsal margin of merus slightly cristate, gently serrated, without distinct subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 concave; lateral margins of segment 6 subparallel, gently sinuous. G1 curved sharply outwards, directed upwards, outer margin convex along distal two-thirds, proximal part with deep V-shaped cleft; distal part tapering. G2 with well developed distal segment, about 0.4 times length of basal segment.

**Distribution.** – Lake Poso, Central Sulawesi.

**Remarks.** – *Potamon celebensis* var. *possoensis* was first described from one small male and one female specimen from Lake Poso (also spelled Posso), Central Sulawesi, by Roux (1904) from specimens which Schenkel (1902) thought were *Parathelphusa pallida*. However, Roux (1904), in describing this taxon, did not designate a holotype. Bott (1970c) did not examine the specimens and regarded *P. possoensis* as a junior synonym of *P. celebensis*. However, on examination of the syntypes and the large number of topotypic specimens, *P. possoensis* possesses several diagnostic features and is here regarded as a valid species. The male (NMB 23VIII) is hereby designated as the lectotype of *P. possoensis*. The lectotype male (NMB 23VIII) is a relatively small specimen and although it is an adult male, the G1 is still relatively juvenile in form. As such, an adult G1 (male, 27.0 by 20.9 mm) (ZRC 2000.1682) is illustrated here instead (Fig. 20A-D).

*Parathelphusa possoensis* differs from *P. pallida* in the following characters. The outer edge of the postorbital cristae of *P. possoensis* does not reach the anterolateral margin, stopping at the base of the first epibranchial teeth, while for *P. pallida*, the outer edge of the postorbital cristae similarly does not reach the anterolateral margin but stops between the base of the first and second epibranchial teeth (Fig. 16A vs. Fig. 12A); the anterolateral margin of *P. possoensis* is smooth while that of *P. pallida* is finely granulated; the suture between thoracic sternites two and three is incomplete in *P. possoensis* while the suture for *P. pallida* is complete; the ambulatory legs of *P. possoensis* is relatively shorter while that for *P. pallida* is relatively longer (Fig. 16A vs. Figs. 12A, 13A); and most significantly, the G1 of *P. possoensis* is curved sharply outwards while the curvature of the same structure on *P. pallida* is less pronounced (Fig. 20A, B vs. Fig. 14F, G).

**Parathelphusa pareparensis** (De Man, 1892)  
(Figs. 17-19, 20F-J)

*Telphusa celebensis* var. *pareparensis* De Man, 1892: 301, Pl. 18 Fig. 7e.  
*Potamon celebensis* var. *pareparensis* - Roux, 1904: 265.  
*Potamon (Potamonautes) celebensis pareparensis* - Rathbun, 1905: 198.  
*Parathelphusa (Mesotelphusa) celebensis* (part) - Bott, 1970c: 127.

**Material examined.** – Lectotype: male (22.3 x 17.6 mm) (RMNH D 2587), river near Pare-Pare, South Sulawesi, coll. M. Weber, 24 Sep.-6 Oct.1888. Others: 1 male (29.5 x 22.9 mm), 2 females (ZRC 2000.2570), Maros, Kappang Guà Tanette, along subterranean stream, South Sulawesi, coll. L. Deharveng, 8 Jul.1988; 2 males, 5 females (MZB 1257), Sungai Bantimurung, Kab. Maros, South

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Fig. 16. *Parathelphusa possoensis* (Roux, 1904), lectotype male (23.9 x 18.3 mm, NMB 23VIII): A, dorsal view; B, frontal view; C, ventral view.

Fig. 17. *Parathelphusa pareparensis*, lectotype male (22.3 x 17.6 mm) (RMNH D 2587): A, dorsal view; B, frontal view.

**Diagnosis.** – Carapace convex, branchial regions inflated, dorsal surfaces smooth; cervical groove shallow, but distinct; H-shaped central depression pronounced. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae does not reach anterolateral margin, stopping between base of second epibranchial teeth and start of cervical groove. Front sinuous, entire, median point with slight depression; frontal median triangle distinct, dorsal ridge indistinct. Anterolateral margin smooth, external orbital angle broadly triangular, low, outer margin almost straight, about 3.2 times length of inner margin, first and second epibranchial teeth low but distinct, almost continuous with anterolateral margin. Postero lateral regions lined with distinct oblique striae. Suture between thoracic sternites 2 and 3 incomplete, almost straight. Palm of chelipeds slightly inflated, fingers longer than palm. Ambulatory legs long, second pair longest. Dactylus of ambulatory legs long, slender. Dorsal margin of merus slightly cristate, without distinct subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, gently sinuous. G1 relatively slender, curved, directed upwards, outer margin gently sinuous along distal two-thirds, proximal part with small cleft; distal part tapering slightly. G2 with well developed distal segment, about 0.5 times length of basal segment.

**Distribution.** – Known for certainty only from caves as well as rivers and streams in the vicinity of Maros, South Sulawesi.

**Remarks.** – *Telphusa celebensis* var. *pareparensis* was first described by De Man (1892) on the basis of three males and seven females from around Parepare, Sulawesi. He also noted that a young female from Maros corresponds to his variety *pareparensis* as well. Subsequently Bott (1970c) regarded *P. celebensis* var. *pareparensis* as a junior synonym to *P. celebensis* but apparently, he neither looked at the specimens examined by De Man (1892) nor examined topotypic material. In this study, with the detailed diagnosis and figure of the carapace by De Man (1892) and the examination of a syntype male and topotypic material from around Parepare and Maros, we are certain *P. pareparensis* is a valid species, and the taxon is hereby resurrected. The syntype male examined in this study is here designated as the lectotype of the species.

Fig. 18. *Parathelphusa pareparensis* (De Man, 1892), male (29.5 x 22.9 mm, ZRC 2000.2570): A, dorsal view; B, frontal view; C, ventral view.

Fig. 19. *Parathelphusa pareparensis* (De Man, 1892), young female (25.8 x 19.9 mm) (ZRC 2000.2570), photographed shortly after preservation showing fresh coloration pattern: A, dorsal view; B, dorsal view of carapace; C, frontal view.
The closest congener to *Parathelphusa pareparensis* is *P. celebensis* and it belongs to the *P. pallida* - *P. celebensis* species complex. *Parathelphusa pareparensis* is similar to *P. celebensis* in that the outer edge of the postorbital crista stops at the base of the second epibranchial tooth, the dorsal ridge of the frontal median triangle is indistinct and that the external orbital angle is broadly triangular. *Parathelphusa pareparensis* shares some similarity with *P. pallida* in that both their epibranchial teeth are low, almost continuous with the anterolateral margin.

However, examination of a good series of comparative material of *P. celebensis* and *P. pallida* from the vicinity of Maros, shows that *P. pareparensis* differs in several key aspects. *Parathelphusa pareparensis* differs from *P. celebensis* and *P. pallida* in the following characters. Firstly, the fingers of the cheliped of *P. pareparensis* is longer than the palm compared to both *P. celebensis* and *P. pallida* in which the fingers are shorter than the palm. Although variation in the length of fingers relative to palm due to size differences have often been observed in some freshwater crabs, those of *P. pareparensis* are probably not due to allometric growth. Comparative sized male specimens of all three species of *Parathelphusa* were examined to ascertain the usefulness of this character. The fingers of *P. pareparensis* were consistently longer than those of *P. pallida* and *P. celebensis*, to the extent that the fingers were always longer than the palm. In this case, the character of fingers longer than palm is useful in differentiating the species. The dactylus of the ambulatory legs of *P. pareparensis* is also proportionately longer and comparatively more slender than those of both *P. celebensis* and *P. pallida*. Thirdly, the outer edge of the postorbital cristae stops between the base of the second epibranchial teeth and the start of the cervical groove.

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Fig. 20. Left G1 and G2. A-E, *Parathelphusa possoensis* (Roux, 1904), male (27.0 x 20.9 mm, ZRC 2000.1682): A, G1 ventral view; B, G1 dorsal view; C, G1 distal part, ventral view; D, G1 distal part, dorsal view; E, G2. F-J, *Parathelphusa pareparensis* (De Man, 1892), male (29.5 x 22.9 mm, ZRC 2000.2570): F, G1 ventral view; G, G1 dorsal view; H, G1 distal part, ventral view; I, G1 distal part, dorsal view; J, G2. Scale bars = 1.0 mm.
a feature diagnostic for this species. Lastly, the G1 of *P. pareparensis* is relatively more slender and longer as compared to that of *P. celebensis* and *P. pallida*.

The fresh coloration of *P. pareparensis* is rather striking when compared to the drabber and more uniform colours of typical *Parathelphusa* species. After a few months in preservative, the recent specimens had the median part of the carapace and most of the ambulatory legs (except for the proximal-most parts) purple, with the rest of the surfaces cream coloured. The pattern is still evident even in freshly preserved specimens (Fig. 19).

**Parathelphusa crocea** (Schenkel, 1902)
(Figs. 21, 23A-E)

*Potamon (Potamonautes) celebensis croceus* Schenkel, 1902: 350.

*Potamon (Potamonautes) celebensis croceus* - Rathbun, 1905: 199.

*Parathelphusa (Mesotelphusa) celebensis* (part) - Bott, 1970c: 127.


**Diagnosis.** – Carapace convex, dorsal surfaces smooth; cervical groove shallow, but distinct, almost reaching anterolateral margin; H-shaped central depression pronounced. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae reaches anterolateral margin, stopping at base of second epibranchial teeth. Front almost straight, entire; frontal median triangle distinct, height of frontal median triangle relatively higher, dorsal ridged margin indistinct. Anterolateral margin smooth, external orbital angle triangular, low, outer margin almost straight, about 2.5 times length of inner margin, first and second epibranchial teeth low almost confluent with anterolateral margin. Posterolateral regions lined with distinct oblique striae. Suture between thoracic sternites 2 and 3 complete, almost straight, suture between sternites 3 and 4 absent. Palm of chelipeds slightly inflated, fingers shorter than palm. Ambulatory legs relatively short, second pair longest, dactylus of last ambulatory leg, relatively shorter and broader. Dorsal margin of merus slightly cristate, without distinct subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, relatively straight. G1 slender, relatively sinuous, directed upwards, outer margin gently sinuous along distal two-thirds, proximal part with distinct cleft; distal part tapering, directed inwards. G2 with well developed distal segment, about 0.7 times length of basal segment.

**Distribution.** – Around the vicinity of Ussu and Maros, South Sulawesi.

**Remarks.** – *Potamon (Potamonautes) celebensis var. croceum* was described from a single male specimen from the vicinity of Ussu by Schenkel (1902). Bott (1970c) regarded it as a junior synonym of *P. celebensis*. However, there are enough key differentiating characters to regard *P. crocea* as a valid species although both taxa occur in South Sulawesi.

The frontal median triangle of *P. crocea* is relatively higher compared to the frontal median triangle of *P. celebensis* (Fig. 21B vs. Figs. 8B, 9B, 10B, 11B). *Parathelphusa crocea* has an orbital angle that is lower and more broadly triangular compared to that of *P. celebensis* (Fig. 21A vs. Figs. 8A, 9A, 10A, 11A). The first and second epibranchial teeth of *P. crocea* are almost confluent with the anterolateral margin while the first and second epibranchial teeth of *P. celebensis* are low but distinct (Fig. 21A vs. Figs. 8A, 9A, 10A, 11A). The suture between thoracic sternites two and three of *P. crocea* is complete while the suture for *P. celebensis* is incomplete. One distinguishing character is that the dactylus of the last pair of ambulatory leg of *P. crocea* (Fig. 21A) which is relatively shorter and broader than that of *P. celebensis* (Figs. 10A, 11A). Lastly, the G1 of *P. crocea* is relatively more sinuous and it possess a distinct cleft in the proximal part (Fig. 23A-D) compared to that of *P. celebensis* which is relatively straighter and does not possess a clear cleft in the proximal part (Fig. 14A-D). *Parathelphusa crocea* should thus be regarded as a valid species, distinct from the sympatric *P. celebensis*.

![Fig. 21. *Parathelphusa crocea* (Schenkel, 1902), holotype male (26.3 x 21.3 mm, NMB 23IIIa): A, dorsal view; B, frontal view; C, ventral view.](image-url)
**Parathelphusa linduensis** (Roux, 1904)  
(Figs. 22, 23F-J)

*Potamon* (*Potamonauta*) *celebense* (part) - Schenkel, 1902: 528, Pl. 10 Fig. 9, 13a  
*Potamon celebense* var. *linduensis* Roux, 1904: 562, Fig. A.  
*Parathelphusa* (*Mesotelphusa*) *pallida* (part) - Bott, 1970c: 128, Pl. 24 Fig. 83-84.

**Material examined.** – Lectotype: male (24.8 x 19.7 mm) (NMB 23 VIIa), Lake Lindu, Central Sulawesi, 1°18’S 120°05’E, coll. Gesch & Sarasin, 1904. Paralectotypes: 1 male (NMB 23 VIIa), same data as lectotype; 2 males, 2 females (NMB 23 VII), same data as lectotype.

**Diagnosis.** – Carapace convex and inflated, dorsal surfaces smooth; cervical groove shallow, but distinct; H-shaped central depression pronounced. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin; outer edge of cristae not reaching anterolateral margin, stopping when it meets cervical groove. Front sinusous, entire, median point with distinct depression; frontal median triangle distinct, broad, low, dorsal ridge absent. Anterolateral margin smooth, external orbital angle broadly triangular, outer margin almost straight, about 2.5 times length of inner margin, first and second epibranchial teeth very low, almost continuous with anterolateral margin. Posterolateral regions smooth. Suture between thoracic sternites two and three incomplete, almost straight. Suture between thoracic sternites three and four distinct, sinusous. Palm of chelipeds slightly inflated, fingers shorter than palm. Ambulatory legs relatively short, second pair longest. Dorsal margin of merus slightly cristate, without distinct subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, gently sinusous. G1 relatively stouter, relatively curved, directed upwards, outer margin sinusous along distal two-thirds, proximal part with slight cleft; distal part tapering. G2 with well developed distal segment, about 0.5 times length of basal segment.

**Distribution.** – Lake Lindu, Central Sulawesi.

**Remarks.** – Roux (1904) described *Potamon celebense* var. *linduensis* from five males and seven females from Lake Lindu which Schenkel (1902) had regarded as *Potamon celebense*. Bott (1970c) subsequently examined two syntype males and a female but did not designate a lectotype. In this study, the male measuring 24.8 by 19.7 mm (NMB 23 VIIa) is designated as the lectotype.

*Parathelphusa linduensis* in this study is regarded as a valid species and not a junior synonym of *P. pallida* as by Bott (1970c). *Parathelphusa linduensis* differs from *P. pallida* in the following characters. The carapace for *P. linduensis* is relatively more inflated than that of *P. pallida*, particularly in the gastric regions (Fig. 22A vs. Figs. 12A, 13A). The outer edge of the postorbital cristae of *P. linduensis* stops where it meets the cervical groove, while the outer edge of the postorbital cristae of *P. pallida* stops just before the anterolateral margin, between the bases of the first and second epibranchial teeth (Fig. 22A vs. Figs. 12A, 13A). The frontal median triangle for *P. linduensis* is broad and low with the dorsal ridge being absent while the frontal median triangle for *P. pallida* is distinct with all the lateral ridges and the dorsal ridge being sharp and distinct (Fig. 22B vs. Figs. 12B, 13B). For *P. linduensis*, the anterolateral margin is smooth compared to *P. pallida* which is finely granulated. The suture between thoracic sternites two and three is incomplete for *P. linduensis* while the suture between sternites two and three for *P. pallida* is complete. The suture between thoracic sternites three and four is distinct and sinusuous in *P. linduensis*, while in *P. pallida* this suture is absent. Lastly, the G1 for *P. linduensis* is relatively more curved in the distal half as compared to that for *P. pallida* which is relatively straighter (Fig. 23F, G vs. Fig. 14F, G).

**Parathelphusa sorella**, new species  
(Figs. 24, 26A-E)

**Material examined.** – Holotype: male (40.2 x 26.1 mm) (ZRC 1990.490), Gua Saripa, near Teduung village, Maros, South Sulawesi, coll. P. Leclerc, 25 Jul.1989. Paratypes: 1 male (47.4 x 30.7 mm) (ZRC, ex MZB 006), Gua Saripa, lake, Samanggi, Kabupaten Maros, South Sulawesi, 1°18’S 120°05’E, coll. C. Rahmadi & F. Brehier, 2 Aug.2001; 1 female (39.7 x 26.4 mm) (MZB 13), 1 female (23.0 x 15.4 mm) (ZRC, ex MZB 13), Gua Saripa, Samanggi, Kabupaten Maros, South Sulawesi, 5°2’35.2”S 119°42’9”E, coll. C. Rahmadi & F. Brehier, 2 Aug.2001; 1 female (39.7 x 26.4 mm) (MZB 13), 1 female (23.0 x 15.4 mm) (ZRC, ex MZB 006), Gua Saripa, gallery Cacing, Kecamatan Simbang, Kabupaten Maros, South Sulawesi, coll. C. Rahmadi, 18 Apr.2002; 1 male (43.1 x 28.0 mm) (MZB 2002.0001), Gua Saripa, lake, Kecamatan Simbang, Kabupaten Maros, coll. Y. R. Subardjono & C. Rahmadi, 18 Apr.2002; 1 male (22.9 x 15.0 mm) (ZRC, ex MZB), spring of 

![Fig. 22. Parathelphusa linduensis (Roux, 1904); lectotype male (24.8 x 19.7 mm, NMB 23VIIa): A, dorsal view; B, frontal view; C, ventral view.](image-url)

**Diagnosis.** – Carapace convex, branchial regions highly inflated, dorsal surfaces smooth; cervical groove deep and distinct; H-shaped central depression shallow. Epigastric and postorbital cristae continuous, shallow but distinct, subparallel to frontal margin; outer edge of cristae not reaching anterolateral margin, stopping at start of cervical groove. Front sinuous, entire, median point with distinct depression; frontal median triangle distinct, dorsal ridge absent. Cornea of eye reduced. Anterolateral margin smooth, diverges sharply after external orbital angle, external orbital angle broadly triangular, low, outer margin almost straight, about 3.0 times length of inner margin, first and second epibranchial teeth very low almost continuous with anterolateral margin. Posterolateral regions lined with distinct oblique striae. Suture between thoracic sternites 2 and 3 incomplete, concave towards buccal cavity. Suture between thoracic sternites 3 and 4 complete, forming 2 convex semicircles towards buccal cavity, resembling a “W” shape, reaching suture between sternites 2 and 3. Palm of chelipeds slightly inflated, fingers longer than palm. Ambulatory legs relatively short, second pair longest. Dorsal margin of merus slightly cristate, without

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**Fig. 23.** Left G1 and G2. A-E, *Parathelphusa crocea* (Schenkel, 1902), holotype male (26.3 x 21.3 mm, NMB 23IIIa): A, G1 ventral view; B, G1 dorsal view; C, G1 distal part, ventral view; D, G1 distal part, dorsal view; E, G2. F-J, *Parathelphusa linduensis* (Roux, 1904), male (24.8 x 19.7 mm, NMB 23VIIa): F, G1 ventral view; G, G1 dorsal view; H, G1 distal part, ventral view; I, G1 distal part, dorsal view; J, G2. Scale bars = 1.0 mm.
distinct subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 subequal to segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, gently sinuous. G1 relatively long, slender, distinctly curved, directed upwards, outer margin concave along distal two-thirds, proximal part without cleft; distal part sharply tapering. G2 with well developed distal segment, about 0.6 times length of basal segment.

**Distribution.** – Caves in the vicinity of Maros, South Sulawesi.

**Etymology.** – “Sorella” is Greek for an old man with a foot in the grave. This species is so named alluding to it being found in caves, which is often associated in Greek myths as the entrance to the underworld. The name is used as a noun in apposition.

**Remarks.** – The sole male holotype of *Parathelphusa sorella* was collected from within a cave. This species is likely to be a cavernicolous species as it possess reduced corneas similar to the cavernicolous freshwater crabs described by Holthuis (1979, 1980) from Borneo and New Guinea and Ng and Sket

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*Fig. 24. Parathelphusa sorella*, new species, holotype male (40.2 x 26.1 mm, ZRC 1990.490): A, dorsal view; B, frontal view; C, ventral view.
(1996) from Bohol, Philippines. This species is closely allied to *P. pallida* and *P. celebensis* and is a member of this complex. It is closer to *P. pallida* in that its first and second epibranchial teeth are very low and almost continuous with the anterolateral margin. It resembles *P. celebensis* in that its dorsal ridge of the frontal median triangle is absent. It is also similar to *P. pareparensis* in that the fingers of its cheliped are also longer than the palm and that the outer edge of the postorbital cristae ends at the start of the cervical groove.

However, it differs from *P. pallida*, *P. celebensis* and *P. pareparensis* in a number of distinctive characters. Firstly, the branchial regions of *P. sorella* are highly inflated, to the extent that the anterolateral margin diverges sharply even after the second epibranchial teeth (Fig. 24A, B). The branchial regions of its three closest congeners, *P. pallida*, *P. celebensis* and *P. pareparensis* are not as inflated and swollen (Figs. 8A, 9-13A, 17-19A). Secondly, the frontal margin of *P. sorella* is sinuous, with a distinct depression in its median point as compared to those of *P. pallida*, *P. celebensis* and *P. pareparensis*, which are straight (Fig. 24A vs. Figs. 9-13A, 17-19A). However, the value of the character of the sinuous frontal margin is difficult to ascertain. Ng and Tan (1998) in their remarks for *Isolapotamon naiaidis* Ng, 1986, from Borneo, mentioned that the form of the frontal margin varies with size and becomes more sinuous and lower in large specimens. This is especially so in specimens with inflated or swollen branchial regions (as in the case of *P. sorella*), and the frontal margin could then be more sinuous. The lack of a large series of specimens of *P. sorella* for examination of the frontal margin for size variation makes a clearer conclusion difficult.

The cornea of the eye of *P. sorella* is very much reduced in comparison to *P. pallida*, *P. celebensis* and *P. pareparensis*. The cornea of the eye can show slight variability within some species of *Sundathelphusa* (see Ng & Sket, 1996) from the Philippines, but not to the degree observed here for *P. sorella*. The suture between thoracic sternites three and four of *P. sorella* is complete, forming two convex semicircles towards the buccal cavity, resembling a “W” shape, that reaches the anterolateral margin, with slight cleft at beginning of cervical groove; outer edge of the postorbital cristae ends at the start of the cervical groove.

**Diagnosis.**—Carapace slightly inflated, rusty-red in life, dorsal surfaces rugose; cervical groove shallow, indistinct; H-shaped central depression distinct. Epigastric and postorbital cristae continuous, sharp, subparallel to frontal margin, with slight cleft at beginning of cervical groove; outer edge of the postorbital cristae ends at the start of the cervical groove.

**Parathelphusa ferruginea**, new species

(Figs. 25, 26F-J)

*Materiel examined.*—Holotype: male (36.0 x 28.5 mm) (MZB 1491), Lake Towuti, Tanjung Timbala, southeast of Timampu, sand and rocks, South Sulawesi, 2°42'37.7" S 121°26'06.9" E, coll. C. D. Schubart et al., 25 Jan.2000. Paratypes: 4 males, 5 females, 1 juvenile (ZRC 2000.1715), 2 males, 2 females (MZB), same data as holotype; 2 males, 2 females (ZRC 2000.1687), Lake Towuti, Tanjung Bahasa, large rocks (south of Timampu), South Sulawesi, 2°40'53.5" S 121°26'06.9" E, coll. C. D. Schubart et al., 25 Jan.2000; 8 males, 1 female (ZRC 2000.1690), Lake Towuti, Timbala, southeast of Timampu, sand and rocks, South Sulawesi, coll. C. D. Schubart et al., 25 Jan.2000; 3 males, 2 females (ZRC 2000.1689), Lake Towuti, Timbala, southeast of Timampu, sand and rocks, South Sulawesi, coll. C. D. Schubart et al., 25 Jan.2000; 4 females (ZRC 2000.2558), Lake Towuti, about 8 km south of Timampu, between Tandjung Subaloateh and Tandjung Petea (Station 8), South Sulawesi, coll. M. Kottelat, 2 Jul.1988; 1 female (ZRC 2000.2559), Lake Towuti, station 1, about 3 km south of Timampu, estuary of Sungai Baturu, South Sulawesi, coll. M. Kottelat, 22 Jun.1988; 1 male, 2 females (ZRC 2000.2560), Lake Towuti, about 8 km south of Timampu, between Tandjung Subaloateh and Tandjung Petea (Station 8), South Sulawesi, coll. M. Kottelat, 2 Jul.1988; 1 male (MNHB 27373), Lake Towuti, South Sulawesi, 2°50.74" S 121°26.09" E, coll. M. Glaubrecht & T. von Rintelen, 21 Aug.1999; 1 male, 1 female (MNHB 27370), Lake Towuti, South Sulawesi, 02°40.89" S 121°41.49" E, coll. Brinkmann & T. von Rintelen, 1 Apr.2000. Others: 3 males, 2 females (ZRC 2000.1692), 1 female (MZB 1492), Lake Mahalona (north and northwest coast), under rocks and sandstone terraces, South Sulawesi, 2°33'54.3" S 121°29'44.1" E and 2°34'42.2" S 121°29'06.2" E, coll. C. D. Schubart et al., 27 Jan.2000; 1 female (ZRC 2000.1693), Sungai Mahalona, ca. 2 km from Lake Mahalona, clinging to rock in strong current, South Sulawesi, 2°36'38.1" S 121°31'51.7" E, coll. C. D. Schubart et al., 27 Jan.2000.

**Material examined.**—Holotype: male (36.0 x 28.5 mm) (MZB 1491), Lake Towuti, Tanjung Timbala, southeast of Timampu, sand and rocks, South Sulawesi, 2°42'37.7" S 121°26'06.9" E, coll. C. D. Schubart et al., 25 Jan.2000. Paratypes: 4 males, 5 females, 1 juvenile (ZRC 2000.1715), 2 males, 2 females (MZB), same data as holotype; 2 males, 2 females (ZRC 2000.1687), Lake Towuti, Tanjung Bahasa,
edge of cristae not reaching anterolateral margin, stopping distinctly before beginning of cervical groove. Front slightly sinuous, entire; frontal median triangle distinct. Anterolateral region with oblique striae, external orbital angle triangular, outer margin about 2 times length of inner margin, outer margin convex, tip of orbital angle extends to line with frontal margin, first and second epibranchial teeth sharp, acutely triangular. Posterolateral regions lined with distinct oblique striae. Suture between thoracic sternites 2 and 3 complete but weak, straight with respect to the buccal cavity. Palm of chelipeds slightly inflated, fingers shorter than palm, pollex and dactylus pigmented dark brown to black. Ambulatory legs relatively long, second pair longest. Dorsal margin of merus slightly cristate, with sharp, distinct subterminal spine. Male abdomen reaching imaginary line joining median point of anterior and posterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, gently sinuous. G1 relatively straight, directed upwards, outer margin gently sinuous along distal two-thirds, proximal part without V-shaped cleft; distal part tapering with tip with flared opening. G2 with well developed distal segment, about 0.5 times length of basal segment.

**Distribution.** – Lake Towuti and Lake Mahalona, South Sulawesi.

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**Fig. 26.** Left G1 and G2. A-E, *Parathelphusa sorella*, new species, holotype male (40.2 x 26.1 mm, ZRC 1990.490): A, G1 ventral view; B, G1 dorsal view; C, G1 distal part, ventral view; D, G1 distal part, dorsal view; E, G2. F-J, *Parathelphusa ferruginea*, new species, holotype male (36.0 x 28.5 mm, MZB 1491): F, G1 ventral view; G, G1 dorsal view; H, G1 distal part, ventral view; I, G1 distal part, dorsal view; J, G2. Scale bars = 1.0 mm.
Parathelphusa ferruginea is distinct from members of the P. pallida - P. celebensis species group as well as P. lokaensis, in having a rugose, rusty-red carapace in life as well as in freshly preserved specimens, sharp, acutely triangular epibranchial teeth and a outer edge of the postorbital cristae that stops at the beginning of the cervical groove. Parathelphusa ferruginea is also distinct from the nearest geographical congener, P. pantherina, in having a rugose, rusty-red carapace, which in P. pantherina is smooth and spotted (Fig. 25A vs. Fig. 1A). The outer edge of the postorbital cristae of P. ferruginea stop just before the beginning of the cervical groove as compared to P. pantherina, whose postorbital cristae stops just before the base of the first epibranchial tooth (Fig. 25A vs. Fig. 1A).

The external orbital angle of P. ferruginea reaches to a level in line with the frontal margin while that of P. pantherina does not reach the frontal margin (Fig. 25A vs. Fig. 1A). The epibranchial teeth of P. ferruginea are acutely triangular compared to P. pantherina which are triangular (Fig. 25A vs. Fig. 1A). Finally, the G1 tip of P. ferruginea has a more distinct flared opening compared to P. pantherina (Fig. 26F-I vs. Fig. 3A-D).

**Syntripsa, new genus**

*Potamon (Parathelphusa) - Schenkel, 1902: 517; Rathbun, 1905: 233.*
*Parathelphusa (Parathelphusa) - Roux, 1915: 247, 249.*
*Parathelphusa - Balss, 1934: 178.*
*Nautiothelphusa - Bott, 1970c: 133.*
*Parathelphusa - Ng, 1988a: 96.*

**Diagnosis.** – Carapace narrowly transverse to squarish, inflated, rugose, regions distinct, frontal margin with distinct and well developed deeply recessed median triangle, anterolateral margin with 2 epibranchial teeth and external orbital angle, tip of external orbital angle usually extends just beyond frontal margin. Posterior margin of epistome fused, continuous. Third maxilliped exopod with long flagellum extending beyond width of merus. Anterior margin of third maxilliped merus with median notch. Chelipeds unequal even in small specimens. Larger chela very stout, inflated, base of finger with large, white, molariform teeth even in small specimens. Ambulatory meri with a sharp subdistal spine on anterior margin. Male abdomen distinctly T-shaped, narrow, with proximal segments broader but narrowing sharply from segment 5 onwards. G1 stout, simple, terminal and subterminal segments indistinctly or cannot be demarcated, terminal segment tapering to sharp point, G2 shorter than G1, with basal segment subequal to, or longer than well developed distal segment.

**Type species.** – *Potamon (Parathelphusa) matannensis* Schenkel, 1902, by present designation.

**Etymology.** – “Syntripsa” is Greek for the smasher, a mythological fiend who broke pots in the kitchen. This is in allusion to the large powerful chela with the white molariform teeth, which is likely to be used to destroy freshwater molluscs. The gender of the latinised name Syntripsa is feminine.

**Remarks.** – Potamon (Parathelphusa) matannensis has been placed in Parathelphusa by most workers (Roux, 1915; Balss 1934) until Bott (1970c) transferred it to Nautiothelphusa, because it has the tip of the external orbital angle extending to just beyond or beyond the frontal margin, as with N. zimmeri. Ng (1988a) regarded Potamon (Parathelphusa) matannensis as a Parathelphusa species but he did not elaborate further, only mentioning that details of the synonymy and transfer would be published elsewhere. This, however, was never done.

*Potamon (Parathelphusa) matannensis* and *S. flavichella*, new species, possess a number of characters that easily differentiate it from both Parathelphusa and Nautiothelphusa, viz. it has a fused and continuous posterior epistome margin without any pronounced clefts or notches (Fig. 37B); the base of its cheliped finger has very large, white, molariform teeth (Fig. 27C, 29A, 30B); and the anterior margin of the third maxilliped merus has a distinct median notch (Fig. 38B). In the latter genera, the posterior epistomal margin is not fused (the clefts or fissures demarcating the various parts are still distinct), with a semicircular depression in the posterior-lateral epistome margin. For Syntripsa, the remnants of the fissure separating the different parts of the posterior epistomal margin can still be visible (Figs. 27A, 37B), but the parts are completely fused and the margin is smooth. The chelae of Parathelphusa and Nautiothelphusa also do not have large molariform teeth, with the cutting margins just lined by normal small teeth. In large specimens of some Parathelphusa species, one or two of the sub-basal teeth may be much larger than the others, but never become molariform or otherwise specialised. Finally, there is no depression on the dorsal margin of the third maxilliped merus of Parathelphusa and Nautiothelphusa species, it being relatively straight and perpendicular to the lateral margins. These differences are also valid when compared to Mignathelphusa, new genus. These characters warrant the establishment of a new genus, Syntripsa, of which Potamon (Parathelphusa) matannensis Schenkel, 1902, is now designated as the type species.
Syntripsa matannensis (Schenkel, 1902)
(Figs. 27, 28, 31A-E)

Potamon (Parathelphusa) matannensis Schenkel, 1902: 517, Pl. 10
Fig. 13d, Pl. 11 Fig. 14; Rathbun, 1905: 247, 249.
Parathelphusa matannensis - Balss, 1934: 178.
Nautilothelphusa matannensis - Bott, 1970c: 133, Pl. 25 Figs. 5-7.
Parathelphusa matannensis - Ng, 1988a: 96.


Diagnosis. – Carapace narrowly transverse to squarish, inflated, rugose, branchial regions inflated, deep reddish purple when live; cervical groove shallow, indistinct; H-shaped central depression shallow. Epigastric and postorbital cristae continuous, weak, subparallel to frontal margin; outer edge of cristae reach anterolateral margin, stopping just above base of first epibranchial tooth. Front entire with shallow depression medially; frontal median triangle distinct, complete, deeply recessed. Eyestalk white. Epistome posterior margin fused, continuous. External orbital angle triangular, outer margin convex, about 2 times length of inner margin, tip of external orbital angle usually extends just beyond frontal margin, first and second epibranchial teeth triangular, equal, directed forwards, outer margins almost straight. Third maxilliped merus anterior margin with a median notch. Posterolateral regions lined with few oblique striae. Suture between thoracic sternites 2 and 3 complete, straight. Chelipeds strongly asymmetrical even in smaller specimens, larger chela very stout, inflated, base of finger with large, white, molariform teeth, palm of chelipeds inflated, longer than pollex, pollex and dactylus pigmented black throughout.

Fig. 21. Generic characters of Syntripsa. Syntripsa matannensis (Schenkel, 1902), lectotype male (31.3 x 25.6 mm, NMB 20a): A, fused continuous epistome margin; B, third maxilliped merus with median notch on anterior margin; C, base of cheliped finger with large, white, molariform tooth. Scale bars = 1.0 mm.
The key characters that differentiate...are enough distinct characters to differentiate them.

Even if future collections show both of them to be syntopic, known only from Lake Mahalona and Lake Towuti thus far.

Syntripsa matannensis designated as the lectotype of the species (Fig. 28).

31.0mm (NMB 20a) from the original series is here designate a lectotype. The male specimen measuring 25.2 by

designate a holotype. Bott (1970c) in his monograph

females from Lake Matano, Sulawesi. However, he did not

(31.3 x 25.7 mm, NMB 20a): A, dorsal view; B, frontal view; C,

Distribution. – Lake Matano, South Sulawesi.

Remarks. – Schenkel (1902) described Potamon (Parathelphusa) matannensis from a single male and three females from Lake Matano, Sulawesi. However, he did not designate a holotype. Bott (1970c) in his monograph examined only a female (NMB 20b) but he too did not designate a lectotype. The male specimen measuring 25.2 by 31.0mm (NMB 20a) from the original series is here designated as the lectotype of the species (Fig. 28).

Syntripsa matannensis is known only from its type locality, Lake Matano, while Syntripsa flavichela, new species, is known only from Lake Mahalona and Lake Towuti thus far. Even if future collections show both of them to be syntopic, there are enough distinct characters to differentiate them. The key characters that differentiate S. matannensis and S. flavichela are elaborated at length under S. flavichela.

length. Ambulatory legs of normal length, pigmented white between joints, second pair longest. Dorsal margin of merus with slight cristae, with distinct, sharp, subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 concave; lateral margins of segment 6 subparallel, gently sinuous. G1 slender, gently curving outwards, directed upwards, outer margin slightly sinuous, proximal part slightly clefted; distal part tapering, tip slightly flared. G2 with well developed distal segment, about 0.5 times length of basal segment.


Material examined.


Diagnosis. – Carapace narrowly transverse to squarish, inflated, slightly rugose, branchial regions inflated, red spots on cream carapace with golden-cream chela when live; cervical groove shallow, distinct; H-shaped central depression distinct. Epigastric and postorbital cristae continuous, distinct, subparallel to frontal margin; outer edge of cristae does not reach anterolateral margin, stopping before base of first epibranchial tooth. Front entire, with shallow depression medially; frontal median triangle distinct, complete, deeply recessed. Eyestalk cream coloured. Epistome posterior margin fused, continuous. External orbital angle triangular, outer margin convex, about 2.3 times length of inner margin, tip of external orbital angle usually extends just beyond frontal margin, first and second epibranchial teeth triangular, equal, directed forwards, outer margins almost straight. Third maxilliped merus anterior margin with a median notch. Posterolateral regions lined with few oblique striae. Suture between thoracic sternites 2 and 3 complete, straight. Chelipeds cream-coloured, strongly asymmetrical even in smaller specimens, larger chela very stout, inflated, base of finger with large, white, molariform teeth, palm of chelipeds inflated, longer than pollex, pollex and dactylus pigmented black throughout the length. Ambulatory legs relatively long, second pair longest. Dorsal margin of merus with slight cristae, with distinct, sharp, subterminal spine. Male abdomen reaching posterior half of imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 concave; lateral margins of segment 6 subparallel, gently sinuous. G1 stout, almost straight, directed upwards, outer margin straight, proximal part without a cleft; distal part tapering, tip slightly
Fig. 29. *Syntripsa flavichela*, new species, holotype male (59.1 x 46.7 mm, MZB 1483): A, dorsal view; B, dorsal view of carapace; C, frontal view.
flared. G2 with well developed distal segment, about 0.5 times length of basal segment.

**Distribution.** – Lake Towuti and Lake Mahalona, South Sulawesi.

**Etymology.** – This species is named “flavichela” which alludes to its yellowish chelae which is evident even in small specimens. The name is used as a noun in apposition.

**Remarks.** – The genus *Syntripsa* presently has two species, viz. *S. matannensis* (Schenkel, 1902) and *S. flavichela*, new species. *Syntripsa flavichela* differs from *S. matannensis* in the following key characters. In terms of live coloration, the carapace of *S. favichela* has red spots throughout on a cream to light olive-green carapace, with cream coloured chela and the fingers pigmented black throughout their length. Its eye stalk is cream coloured and the joints of the ambulatory legs are not pigmented white. *Syntripsa matannensis*, however, is deep reddish purple overall and also has deep reddish purple chela with the fingers completely pigmented black. It has white eye-stalks and the joints of the ambulatory legs are pigmented white.

*Syntripsa flavichela* has a less rugose carapace with a distinct cervical groove and a distinct H-shaped depression while *S. matannensis* has a more rugose carapace with an indistinct, shallow cervical groove and a shallow H-shaped central depression (Fig. 29A, B vs. Fig. 28A). The outer edge of the postorbital cristae of *S. flavichela* stops short of the anterolateral margin, reaching just before the base of the first epibranchial tooth, whereas that of *S. matannensis* reaches the anterolateral margin, stopping just above the base of the first epibranchial tooth (Fig. 29A, B vs. Fig. 28A). The male abdomen of *S. matannensis* reaches an imaginary line joining the anterior edges of the cheliped bases, while for *S. flavichela*, the male abdomen stops at the median point before the anterior edges of the cheliped bases (Fig. 30A vs. Fig. 28C). The G1s of both *S. matannensis* and *S. flavichela* are also different. The G1 of *S. flavichela* is stout, straight, with a straight outer margin and lacks a cleft on the proximal part (Fig. 31F, G). The G1 of *S. matannensis* on the other hand is slender, being gently curving outwards, with a slightly sinuous outer margin and a proximal part that is gently clefted (Fig. 31A, B).

**Nautilothelphusa Bals, 1933**

[Parathelphusa] (Nautilothelphusa) Bals, 1933: 94.


**Diagnosis.** – Carapace squarish, rugose. Frontal margin with distinct, well developed median triangle, deeply recessed. Anterolateral margin with 2 epibranchial teeth; external orbital angle larger, extends beyond frontal margin, all teeth acutely triangular. Posterior margin of epistome with distinctly triangular median lobe. Third maxilliped exopod with long flagellum extending beyond width of merus. Chelips equal even in large adult males, fingers very slender, with both pollex and dactylus longer than palm. Last pair of ambulatory leg with very broad (dorsoventrally flattened) propodus. Male abdomen distinctly T-shaped, narrow, with proximal segments broader but narrowing sharply from segments 5 onwards. G1 stout, simple, terminal and subterminal segments indistinctly or cannot be demarcated, terminal segment truncate; G2 shorter than G1, basal segment longer than well developed distal segment.

**Remarks.** – This genus was established by Balss (1933) (as a subgenus) for an unusual new species he described from “Java” (actually Sulawesi, see later) - [Parathelphusa] (Nautilothelphusa) zimmeri. Its squarish carapace shape, peculiar lateral carapace armature, flattened last pair of ambulatory propodi and very short stout G1 with a flared tip are diagnostic features. Bott (1970c) recognized the genus but expanded its definition to include *Parathelphusa matannensis* (here referred to its own new genus, *Syntripsa*). Ng (1988), in a brief commentary on the genus *Parathelphusa* and related genera, noted that the inclusion of *P. matannensis* in *Nautilothelphusa* was not coherent and transferred it back to *Parathelphusa*. In the process, he also did not recognize Bott’s (1970c) *Palawanthalmphusa* as a valid genus and iso synonymised it with *Parathelphusa* (see also Ng & Goh, 1987).

The features of *Nautilothelphusa* are unusual in that it suggests the species is more natatorial than *Parathelphusa* and *Syntripsa* species. The carapace shape and dorsoventrally flattened last pair of ambulatory propodi, reminiscent of those in swimming crabs of the family Portunidae suggests this. However, the species has yet to be observed actually

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Fig. 30. *Syntripsa flavichela*, new species, holotype male (59.1 x 46.7 mm, MZB 1483): A, ventral view; B, major chela.
swimming. The legs, however, have been seen to be used to help
them burrow backwards into the sand. The long slender chelae
(in both sexes) suggest that their food is different, perhaps
being more dependent on worms or small fish. Certainly, they
are not the more massive structures seen in adult
Parathelphusa and Syntripsa which can be used to crush the
many mollusks in the lakes. In its ambulatory legs, Nautilothelphusa is very similar to Migmathelphusa, although the distance between and different origins of Lake Poso and the Malili Lakes suggests the similarities may be
due to convergent evolution, and perhaps a product of living
in lakes.

**Nautilothelphusa zimmeri (Balss, 1933)**
(Figs. 32-34, 37C, 38C)

[Parathelphusa] (Nautilothelphusa) zimmeri Balss, 1933: 94, Pl. 2
Figs. 4, 5.
Para-Nautilothelphusa zimmeri - Balss, 1934: 179.
Nautilothelphusa zimmeri - Bott, 1970c: 132, Pl. 25 Figs. 2-4, Pl.
31 Fig. 99.

**Material examined.** – Holotype: male (23.2 x 20.5 mm) (MZB 48),
Bogor? (data incorrect, specimen almost certainly from Sulawesi),
coll. B. Kramei, 7 Oct.1909. Others: 1 male, 3 females (MZB 643),

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Fig. 31. Left G1 and G2. A-E, Syntripsa matannensis (Schenkel, 1902), lectotype male (31.3 x 25.6 mm, NMB 20a): A, G1 ventral view;
B, G1 dorsal view; C, G1 distal part, ventral view; D, G1 distal part, dorsal view; E, G2. F-J, Syntripsa flavichela, new species, holotype male
(59.1 x 46.7 mm, MZB 1483): F, G1 ventral view; G, G1 dorsal view; H, G1 distal part, ventral view; I, G1 distal part, dorsal view; J, G2.
Scale bars = 1.0 mm.

**Diagnosis.** – Carapace squarish, flat, dorsal surfaces rugose; cervical groove shallow, narrow; H-shaped central depression distinct. Epigastric cristae weak but present, postorbital cristae weak to absent, epigastric cristae subparallel to frontal margin. Frontal margin strongly sinuous, entire; frontal median triangle distinct, but deeply recessed. Anterolateral margin with 2 epibranchial teeth; external orbital angle acutely triangular, extends beyond frontal margin, outer margin almost straight, about 2.6 times length of inner margin, first and second epibranchial teeth acutely triangular. Posterolateral regions lined with distinct oblique striae. Suture between thoracic sternites 2 and 3 complete, gently concave towards buccal cavity. Chelipeds equal even in large adult males. Palm of chelipeds slightly inflated, finger slender, longer than palm, pigmented brown throughout length. Ambulatory legs relatively slender, long, third pair longest, last pair of ambulatory leg with very broad propodus. Dorsal margin of merus smooth, with distinct, sharp subterminal spine. Male abdomen reaching imaginary line joining median points of anterior and posterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, gently sinuous. G1 stout and simple, curving gently inwards, directed upwards, outer margin sharply concave along distal two-thirds, proximal part without cleft; distal part truncate with flared tip. G2 with well developed distal segment, about 0.3 times length of basal segment.

**Distribution.** – Lake Mahalona, Lake Towuti and Lake Matano, South Sulawesi.

**Remarks.** – The locality on the label of the holotype specimen is listed as Bogor. This is an error. *Nautilothelphusa zimmeri* is not found in Java. From collections made, this species is...
thus far found only in Sulawesi where it is certainly an endemic. The G1 and G2 of the type specimen is relatively small and in poor condition (Fig. 34A-C) but agrees with those of larger and better-preserved specimens (Fig. 34D-H).

It appears that on the basis of the collections on hand, each of the freshwater lakes in Sulawesi has its own assemblage of freshwater crabs. With the exception of Syntripsa flavichela and Parathelphusa ferruginea which has been collected from both Lake Towuti and Lake Mahalona, N. zimmeri has been collected from three of the five Malili lakes, namely Lake Matano, Lake Mahalona and Lake Towuti. There are waterways connecting the three lakes, but these are interspersed by rapids. Examination of the external morphology and gonopodal characters indicate all the specimens from the three lakes are one species for the moment. There are differences observed in the colour of the specimens from Lake Mahalona and Lake Towuti, as well as subtle differences in cheliped setation, third maxilliped proportions and male abdomen ratios, but we are reluctant to recognize the two as separate species for the moment, even though the indications are clearly there. Certainly, their G1 structures are effectively identical. A more extensive study with more material of both sexes, perhaps with molecular tools, may throw more light on the matter (Koller et al., in preparation; D. Wowor, C. D. Schubart, pers. comm.). If they should prove different, it will not come as any surprise.

Fig. 34. Left G1 and G2. Nautilothelphusa zimmeri (Balss, 1933): A, D, G1 ventral view; E, G1 dorsal view; B, F, G1 distal part, ventral view; C, G, G1 distal part, dorsal view; H, G2. A-C, holotype male (23.2 x 20.5 mm, MZB 48); D-H, male (41.8 x 35.1 mm) (ZRC 2000.1711). Scale bars = 1.0 mm.
Migmathelphusa, new genus

**Diagnosis.** – Carapace narrowly transverse to squarish, flat, regions distinct, frontal margin with distinct and well developed deeply recessed median triangle, anterolateral margin with 2 epibranchial teeth and external orbital angle; external orbital angle not reaching beyond level of frontal margin. Epigastric cristae strong, sharp, subparallel to frontal margin. Postorbital cristae weak to absent. Third maxilliped exopod with flagellum extending beyond width of merus. Chelipeds equal even in adult male specimens. Chela slender, fingers almost equal in length to palm of chela. Male abdomen distinctly T-shaped, narrow, with proximal segments broader but narrowing sharply from segments 5 onwards. Ambulatory legs long with third pair longest, propodus of last pair broad. G1 very slender, simple, terminal and subterminal segments indistinctly or cannot be demarcated, terminal segment tapered to sharp, G2 shorter than G1, with basal segment longer than well developed distal segment.

**Etymology.** – The genus name is derived from the Greek “Migma” which means “a mixture”, as this genus has an eclectic but distinct mix of characteristics; in combination with “Thelphusa”, a typical suffix to many freshwater crab genera.

**Type species.** – *Migmathelphusa olivacea*, new species, by present designation.

**Remarks.** – A new genus, *Migmathelphusa*, is established for *Migmathelphusa olivacea*, a new species described here. Superficially, *M. olivacea* resembles *Parathelphusa sarasinorum* in coloration, while its relatively broader last ambulatory propodus resembles that of *Nautilothelphusa zimmeri*. However, *M. olivacea* possesses a number of distinctive characteristics that warrant a new genus. Firstly, the postorbital cristae is weak or absent; and the G1 is slender and long, with the G2 possessing a short distal segment, about 0.40 times the length of the basal segment.

*Migmathelphusa olivacea*, new species

(Figs. 35, 36, 37D, 38D)


**Diagnosis.** – Carapace narrowly transverse to squarish, flat, branchial and gastric regions slightly inflated, dorsal surfaces smooth, deep olive-green when live; cervical groove distinct, narrow; H-shaped central depression distinct. Epigastric cristae strong, sharp, subparallel to frontal margin; postorbital cristae weak to absent. Front entire with slight depression; frontal median triangle distinct, complete, ventral sides strongly recessed. External orbital angle triangular, outer margin convex, about 2 times length of inner margin, first and second epibranchial teeth, blunt, low, acutely triangular, directed forwards, outer margins slightly truncate. Posterior lateral regions lined with few oblique striae. Suture between thoracic sternites 2 and 3 incomplete, weak. Palm of chelipeds slightly inflated, subequal to pollex, pollex and dactylus lightly pigmented brown throughout length. Finger slender, subequal to palm. Ambulatory legs long, third pair longest, propodus of last pair broad. Dorsal margin of merus with slight cristae, without distinct subterminal spine. Male abdomen reaching imaginary line joining anterior edges of cheliped bases, T-shaped, segment 6 distinctly longer than segment 7; lateral margins of segment 7 gently concave; lateral margins of segment 6 subparallel, gently sinuous. G1 slender, gently curving outwards with tip directed inwards, outer margin straight, proximal part not clefted; distal part sharply tapering, curved ventrally. G2 with well developed distal segment, about 0.4 times length of basal segment.

**Colour in preservative.** – Deep olive-green.

**Etymology.** – The name alludes to the olive-green colour of the animal.

**Distribution.** Lake Poso, Central Sulawesi.

Fig. 35. *Migmathelphusa olivacea*, new genus, new species, holotype male (33.2 x 29.1 mm, MZB 1486): A, dorsal view; B, frontal view; C, ventral view.
Fig. 36. Left G1 and G2. *Migmathelphusa olivacea*, new genus, new species, holotype male (33.2 x 29.1 mm, MZB 1486): A, G1 ventral view; B, G1 dorsal view; C, G1 distal part, ventral view; D, G1 distal part, dorsal view; E, G2. Scale bars = 1.0 mm.

Fig. 37. Frontal views showing posterior margin of epistome. A, *Parathelphusa pantherina* (Schenkel, 1902) (38.5 x 30.3 mm, ZRC 2000.1705), unfused margin; B, *Syntripsa flavichela*, new species, holotype male (59.1 x 46.7 mm, MZB 1483), fused margin; C, *Nautilothelphusa zimmeri* (Balss, 1933), male (42.7 x 37.4 mm, ZRC 2000.1711), unfused margin; D, *Migmathelphusa olivacea*, new genus, new species, holotype male (33.2 x 29.1 mm, MZB 1486), unfused margin.
Remarks. – *Migmathelphusa olivacea* shares characters of *Nautilothelphusa zimmeri* and *Parathelphusa sarasinorum*. It is similar to *N. zimmeri* in that *M. olivacea* has a rather squarish rather than transverse carapace, a broad last ambulatory propodus, a weak to absent postorbital cristae, slender fingers in which the pollex is subequal to the palm and its third pair of ambulatory merus is longer than the rest. However, *M. olivacea* differs from *N. zimmeri* in that it has a long slender G1 with the tip directed inwards (versus short) (Fig. 36A-D vs. Fig. 34A–G), a G2 with a relatively longer distal segment (0.4 times basal segment vs. 0.3 times) (Fig. 36E vs. Fig. 34H), the absence of a sharp distinct subterminal spine on the ambulatory merus (Fig. 35 vs. Fig. 32, 33), the external orbital angle does not extend beyond the frontal margin (Fig. 35A vs. Fig. 32A, 33A, B) and the frontal margin is only slightly depressed and not deeply depressed medially as in *N. zimmeri* (Fig. 35B vs. Fig. 32B).

Superficially, *M. olivacea* resembles *P. sarasinorum* which is also found in Lake Poso in that the carapace of *M. olivacea* has a deep olive-green coloration with a yellow tinge on the margin. *M. olivacea* also has an external orbital angle that does not extend beyond the frontal margin and epibranchial teeth that are blunt, low, acutely triangular, directed forwards with the outer margins slightly truncate. However, *M. olivacea* is different in that it has inflated branchial and gastric regions (Fig. 35A vs. Fig. 2A). *Migmathelphusa olivacea* is here recognised as a new genus as it has a distinctive long slender G1 with its tip directed inwards, a G2 with a short distal segment as well as the unique and distinct combination of characters as noted above.

**Sundathelphusa Bott, 1969**

*Sundathelphusa* Bott, 1969a: 363.  
*Archipelothelphusa* Bott, 1969a: 363.

Type species. – *Potamon (Geothelphusa) cassiope* De Man, 1902, by original designation.

Remarks. – The genus *Sundathelphusa* Bott, 1969, currently contains some 28 species from Philippines, Sulawesi, Moluccas and eastern Borneo (Ng & Stuebing, 1989; Ng, 1991b; Ng & Sket, 1996; Takeda & Ng, 2001). Although Bott (1969a, 1970c) regarded *Archipelothelphusa* Bott, 1969 (type species *Thelphusa grapsoides* H. Milne Edwards, 1853) as distinct from *Sundathelphusa* Bott, 1969 (type species *Potamon (Geothelphusa) cassiope* De Man, 1902), Ng & Sket (1996) argued that there are no clear differences which can be used to distinguish the two and consequently synonymised them. Most of the known species are from the Philippines, although there are still a good number of undescribed species from there (unpublished data). There are only two known species from northeastern Borneo (*S. aspera* Ng & Stuebing, 1989, *S. tenebrosa* Holthuis, 1979), with two others from the Moluccas (*S. aruana* Roux, 1911), *S. halmaherensis* (De Man, 1902)). Sulawesi has only three known species thus far, viz. *S. cassiope* (De Man, 1902), *S. minahassae* (Schenkel, 1902), and *S. rubra* (Schenkel, 1902). A fourth species is now being described from Lake Poso (Schubart & Ng, in press).

The present exercise provides just a synopsis of the three species now known from Sulawesi, which will help workers identify the species there. A more detailed study and analysis is not done now as this will be conducted at a later date when the whole genus is revised and reappraised to assess its composition and homogeneity. Since the bulk of the species are from the Philippines, this can only be done after the fauna there is better understood.

**Sundathelphusa cassiope** (De Man, 1902)  
(Figs. 39A, 40)

*Potamon (Geothelphusa) cassiope* De Man, 1902: 568, Pl. 20 Fig. 18; Rathbun, 1905: 211.

*Potamon (Geothelphusa) minahassae* – Schenkel, 1902: 540, Pl. 11 Fig. 15 (part); Rathbun, 1905: 211 (part).

*Potamon cassiope* – Roux, 1904: 570.

*Potamon minahassae* – Roux, 1904: 570.
Sundathelphusa cassiope cassiope – Bott, 1970c: 76, Pl. 11 Figs. 24-29, Pl. 28 Fig. 47; Ng & Stuebing, 1989: 13.


Remarks. – De Man (1902) described this species from a series of specimens from Minahassa in northern Sulawesi, Batjan in Moluccas and Soah Konorah in Halmahera. Bott (1970c: 76) selected a male specimen (39.0 by 31.0 mm) from northern Sulawesi in the Senckenberg Museum as the lectotype of the species. The rest of the three species known from Sulawesi, S. cassiope is easily distinguished from the other two by its proportionately much broader carapace with a strongly convex anterolateral margin which appears distinctly transversely subovate. The carapaces of S. minahassae and S. rubra on the other hand, have less convex anterolateral margins and appear more squarish.

Of the three species known from Sulawesi, S. cassiope is easily distinguished from the other two by its proportionately much broader carapace with a strongly convex anterolateral margin which appears distinctly transversely subovate. The carapaces of S. minahassae and S. rubra on the other hand, have less convex anterolateral margins and appear more squarish.

With regards to the strongly convex anterolateral margins and relatively swollen carapace, S. cassiope is perhaps most similar to S. aruana (Roux, 1911) (Figs. 42A, 43) from nearby Moluccas. We examined the lectotype male of Potamon (Geothelphusa) aruana Roux, 1911 (parallectotype male, 27.9 by 21.5 mm, NMB 695a) and the two can easily be distinguished. Compared to S. aruana, S. cassiope has a relatively less swollen carapace, an external orbital angle which is more distinctly cut from the rest of the anterolateral margin by a deep cleft (vs. shallow), and the G1 being relatively straighter with the tip truncate (vs. more curved with the tip sharp). There can be little doubt that the two are separate taxa.

Sundathelphusa minahassae (Schenkel, 1902) (Figs. 39B, 41)

Potamon (Geothelphusa) minahassae Schenkel, 1902: 540, Pl. 11 Fig. 15 (part); Rathbun, 1905: 211 (part).
Potamon minahassae – Roux, 1904: 570.
Sundathelphusa cassiope cassiope – Bott, 1970b: 337; Bott, 1970c: 77, Pl. 14 Figs. 70-72, Pl. 29 Fig. 62; Ng & Stuebing, 1989: 13.


Remarks. – Schenkel (1902) described the species on the basis of three young males and three males from Tomohon. Bott (1970c: 77) selected a 27.0 by 21.0 male specimen in the Museum of Genf as the lectotype of the species. The rest of the specimens in NMB are thus paralectotypes.

The squarish carapace and rugose dorsal surfaces easily distinguishes Sundathelphusa minahassae from all Sulawesi congeners. These differences are apparent even on the many small specimens examined here.

Sundathelphusa rubra (Schenkel, 1902) (Figs. 42B, 44)

Potamon (Geothelphusa ?) rubrum Schenkel, 1902: 537, Pl. 11 Fig. 16; Roux, 1904: 570.
? Potamon (Geothelphusa) angustipes Schenkel, 1902: 533, Pl. 11 Fig. 17; Roux, 1904: 570; Rathbun, 1905: 510.
Potamon (Geothelphusa) ruber – Rathbun, 1905: 211.
Sundathelphusa rubra – Bott, 1970c: 74, Pl. 12 Figs. 33-35, Pl. 28 Fig. 49; Ng & Stuebing, 1989: 13.

Material examined. – Lectotype: male (22.6 by 17.4 mm) (NMB 38a), Panu River southern part of Matingang mountain chain, northern Sulawesi, ca. 1000 m, coll. M. Schenkel. Aug.1894. Others: 3 males, 2 females (ZRC 2000.1695), small river, between forest

Fig. 39. Dorsal views. A, Sundathelphusa cassiope (De Man, 1902), parallectotype male (25.6 by 21.8 mm, NMB 984a); B, Sundathelphusa minahassae (Schenkel, 1902), parallectotype male (39.0 by 30.4 mm, NMB 34a).
Fig. 40. *Sundathelphusa cassiope* (De Man, 1902), paralectotype male (25.6 by 21.8 mm, NMB 984a). A, G1 ventral view; B, G1 dorsal view; C, G1 distal part, ventral view; D, G1 distal part, dorsal view; E, G2. Scale bars = 1.0 mm.
Fig. 41. *Sundathelphusa minahassae* (Schenkel, 1902), paralectotype male (39.0 by 30.4 mm, NMB 34a). A, G1 ventral view; B, G1 dorsal view; C, G1 distal part, ventral view; D, G1 distal part, dorsal view; E, G2. Scale bars = 1.0 mm.
and rice fields, water pH 6.5; Kakaskesen, 1°20'34.2"N 124°50'29.7"E, coll. C. D. Schubart et al., 30 Jan.2000.

**Remarks.** – Schenkel (1902) described *Potamon (Geothelphusa ?) rubrum* (from Matinang) on the basis of three males and ? *Potamon (Geothelphusa) angustipes* (from Masarang) on the basis of two males. No holotypes were designated for either species. Bott (1970c) examined both taxa but did not select any lectotypes. We here select the best specimen of *Potamon (Geothelphusa ?) rubrum* in NMB, a male 22.6 by 17.4 mm, as the lectotype of the species to fix its identity (Fig. 44).

The carapaces of *S. cassiope* and *S. rubra* are both prominently swollen, with the dorsal surface strongly convex and the branchial regions raised. In addition, their G1 terminal segments are proportionately much shorter than those of other Sulawesi species. The same is true of *Potamon (Geothelphusa) angustipes* Schenkel, 1902, a species that was tentatively synonymised with *S. rubra* by Bott (1970c: 74) (see also Schenkel, 1902: 533, Pl. 11 Fig. 17).

**GENERAL DISCUSSION**

The most interesting freshwater crab taxa in Sulawesi are mainly from the two ancient lake systems there. Members of three of these lake-dwelling genera: *Nautilothelphusa*, *Syntripsa* and *Migmatothelphusa* (four species in total) all have unusual adaptations. Species of *Nautilothelphusa* and *Migmatothelphusa* have very delicate pincers, suggesting they specialise on more soft bodied prey like worms and insect larvae, or are detritivores; and the last ambulatory propodi are also relatively more flattened and paddle-like, indicating that they probably burrow into soft substrate more frequently. *Syntripsa* species on the other hand, are stockier taxa, with stout carapaces and one chela (in both sexes) enlarged with a powerful molariform tooth for crushing molluscs. *Nautilothelphusa zimmeri* is known from Matano, Mahalona and Towuti, all three lakes of which are interconnected by fast-flowing shallow streams. The two species of *Syntripsa* on the other hand, are more restricted. *Syntripsa matannensis* is only known from Lake Matamano whilst *S. flavichela* is only known from Lakes Mahalona and Towuti. It thus appears that the rapids that separate the lakes have been effective in isolating the populations and causing speciation. The lake-restricted distribution patterns of *Nautilothelphusa* and *Syntripsa* may be due to their habitats. *Migmatothelphusa olivacea* on the other hand, is from Lake Poso to the northwest of these three lakes. Lake Poso also has an undescribed species of *Sundathelphusa* which has an enlarged chela for crushing molluscs (Schubart & Ng, in press). So it appears that all the major lakes have both a molluscivore and vermivore/detritivore form. Both systems of lakes have a high diversity of molluscs (Sarasin & Sarasin, 1897, 1898; Bollinger, 1914; Brooks, 1950; Whitten et al., 1987; Marwoto, 1997; Bogan & Bouchet, 1998) so the evolution of specialised molluscivorous crabs is not surprising, especially considering crabs are major predators of molluscs in the sea (Vermeij, 1993; Ng & Tan, 1985).

The major lakes of Sulawesi have been the subject of many studies, with the freshwater fish diversity especially well examined (Kottelat, 1991; Kottelat et al., 1993) (see also Whitten et al., 1987). There are 13 lakes on the island, of which Towuti and Poso are the second and third largest lakes in Indonesia respectively, with Matano (at 590 m) the deepest lake in Southeast Asia (Fernando, 1984). Three of these lakes, Matano, Mahalona and Towuti (the so-called Malili Lake System, which includes two very small lakes, Wawantoa and Masapi) are perhaps the best studied (Whitten et al., 1987). All three are tectonic lakes connected by shallow rapids, streams and rivers (Sarasin & Sarasin, 1905; Brooks, 1950; Fernando, 1984). Lake Poso is a different matter. It is geographically separate from the Malili lakes (with no hydrological linkage) and has its own peculiar fauna (see Fernando, 1984; Whitten et al., 1987). Interestingly, both lake systems have their own suite of freshwater crab species. The Malili Lake System has five species, viz. *Parathelphusa pantherina*, *P. ferruginea*, *Syntripsa matannensis*, *S. flavichela* and *Nautilothelphusa zimmeri*. The situation in Lake Poso is also interesting, with at least four species, viz. *Parathelphusa sarasinorum*, *P. possoensis*, *P. tenuipes* and *Migmatothelphusa olivacea*. Of these, *P. possoensis* and *P. tenuipes* are typical *Parathelphusa* species and presumably are restricted to the tributaries of the lake (the biology of *P. tenuipes* is poorly known) and only *P. sarasinorum* and *M. olivacea* can be considered “true” lake species. It is interesting to note that *P. sarasinorum* and *M. olivacea* are very similar morphologically in many ways, and are probably closely related. While the relatively delicate pincers and flattened ambulatory propodi of *Migmatothelphusa olivacea* are

Fig. 42. Dorsal views. A, *Sundathelphusa aruana* (Roux, 1911), paralectotype male (27.9 by 21.5 mm, NMB 695a); B, *Sundathelphusa rubra* (Schenkel, 1902), lectotype male (22.6 by 17.4 mm, NMB 38a).
Fig. 43. *Sundathelphusa aruana* (Roux, 1911), paralectotype male (27.9 by 21.5 mm, NMB 695a). A, left G1 ventral view; B, left G1 dorsal view; C, left G1 distal part, ventral view; D, left G1 distal part, dorsal view, (E) left G2. Scale bars = 1.0 mm.
Fig. 44. *Sundathelphusa rubra* (Schenkel, 1902), lectotype male (22.6 by 17.4 mm, NMB 38a). A, left G1 ventral view; B, left G1 dorsal view; C, left G1 distal part, ventral view; D, left G1 distal part, dorsal view; E, left G2. Scale bars = 1.0 mm.
reminescent of those of *Nautilothelphusa zimmeri*, these features are probably due to convergence – their carapace and G1 structures being rather different. The only other part of the world where the decapod crustaceans from ancient lakes have been studied in any detail is Lake Tanganyika in Africa, viz. the Platyplethysinae (Potamonaudidae) (see Cumberlidge et al., 1999). The ancient lakes of Sulawesi also have species-flocks of prawns of the genus *Caridina* (Atyidae) (Schenkel, 1902; Wolterek, 1937), and their taxonomy is currently now under study.

The caves of Sulawesi have been surveyed in depth only in recent years, and until the present study, no troglobitic true freshwater crab (sensu Guinot, 1988) has been found. The discovery of the cavernicolous *Parathelphusa sorella*, new species, is thus of interest. While troglobitic species of the allied genus *Sundathelphusa* have been reported from the Philippines (Ng & Sket, 1996; Takeda & Ng, 2001), it has been surprising that no troglobitic *Parathelphusa* species has been found in Sulawesi until now (see also Ng, 1988b). As to other cave brachyurans from Sulawesi, Ng (1991a) had reported on a cave hymenosomatid (*Cancrocaeca xenomorpha*), while Narese & Ng (2006) described a new species of *Sarasmoides* (*Sarasmidae*), both from the Maros area. *Parathelphusa sorella* has a reduced cornea, which is typically associated with obligate troglotobites (see Guinot, 1988, 1994). However, it lacks the long pereiopods often (but not always) observed in such organisms. The live coloration of *P. sorella* is not known, but on the basis of the freshly preserved type specimens which are much paler than preserved specimens of other epigean species collected at the same time, *P. sorella* is probably light coloured in life. Several other species, notably *P. pallida*, *P. celebensis* and *P. pareparensis*, are also represented in the caves but most are clearly primarily epigean taxa. Of these, *P. pareparensis* is noteworthy as it has relatively longer ambulatory legs.

One of the problems encountered in the present study is how we should look at the phylogenetic relationships between the various genera and species now identified from the island. Is it possible that on the basis of morphology alone, paraphyletic or even polyphyletic taxa are being recognized and/or established here? It is possible. The genus *Parathelphusa* itself is unlikely to be monophyletic as it stands, and the divisions that may eventually be identified are unlikely to split only on geographic lines. The genus has a very high diversity in Borneo, and any study on the composition and affinities of *Parathelphusa* can only be done when this fauna is considered. The continued discovery of new taxa from there (e.g. Chia & Ng, 1998) and the number of new species still to be described (P. K. L. Ng, unpublished data) is suggestive that we still do not know the fauna there well enough. While we have found distinct morphological features that justify the removal of two Sulawesi species to their own genus (*Syntripsa matannensis* and *S. flavichela*), much less can be said of the others. Certainly, the *P. sarasinorum* looks very distinct from more typical *Parathelphusa* species and may need to be transferred out. The establishment of *Migmathelphusa* was warranted as it possesses a suite of atypical features, yet its relationship with *P. sarasinorum* is also quite evident, and begs the question if the two taxa form a monophyletic lineage separate from other *Parathelphusa* species. Morphology alone may not be enough to resolve the problems. The taxonomic challenges posed by *P. celebensis* and *P. pallida* are not exactly resolved in this study. It has been clarified in that the types have been re-examined and figured, and although we have examined a good series of specimens of both species and they are now much better defined, the geographical coverage is still quite limited, at least with regards to the much wider area they are known or believed to occur. Certainly, many parts of Sulawesi, especially the central and southern parts remain poorly explored with regards to freshwater crabs. Unpublished data on hand suggests more species are likely to be recognized in the future once wider collections are made. *Nautilothelphusa zimmeri* is a very peculiar looking species, but the present discovery of *Parathelphusa ferruginea* at least places it closer to other *Parathelphusa* species, at least on the basis of external morphology. Still, despite their superficially similar carapaces and general features, it is clear that *Nautilothelphusa* has become more specialized, if the flattened last ambulatory propodus and very short and stout G1 structure, are to be regarded as indicators. The same can be said of relationships between *Syntripsa* and *Parathelphusa* sensu lato. There are many superficial similarities between the two *Syntripsa* species and *Parathelphusa ferruginea*, and their G1s at least are generally similar in form. Their phylogenetic relationship, however, is not known. Clearly, a concise study of all these genera and species, perhaps also using molecular markers, is the only way to throw more light on this complex matter. For the moment, the recognition of discrete taxa based on morphology seems to be the best taxonomic compromise available.

While the lake-fauna inevitably attracts a great deal of attention, the cave-fauna has also proven to be very interesting, especially with the present discovery of the first troglobitic *Parathelphusa* from Sulawesi (*P. sorella*). The relationships and speciation patterns of the limestone fauna, especially in the Maros karst area needs further study. It seems likely that with broader and more intensive surveys, more troglobitic parathelphusids will be found. Cai & Ng (2005) described a new genus of cave prawn, *Marosina* (Atyidae) from Maros, and it seems likely that the crabs and prawns of these limestone formations have undergone another radiation, not unlike that taking place in the ancient lakes. It is clear, however, from the present study, that there have been several speciation events involving *Parathelphusa* and its allies since they colonized Sulawesi, presumably from Borneo. There have been at least two lake-based radiations (Poso and Malili) and one cave-based one (Maros). The full picture is likely to be more complex but very interesting biogeographically.

The genus *Sundathelphusa*, although treated here in a rather more cursory manner, merits more study, especially since it has a peculiar distribution in Sulawesi. Members of the genus are only found on the northern part, not extending further south than Lake Poso (Schubart & Ng, in press). Interestingly, species are also found in the northeastern “arm”
of Sulawesi, where no species of *Parathelphusa* is known or has been found. In fact, *Parathelphusa* seems to gradually disappear as one heads northwards. This distribution is unlikely to be an artifact or poor collections as this northern area has been extensively collected. The two genera can certainly be sympatric (e.g. in Lake Poso, Schubart & Ng, in press). To explain the distribution patterns of *Sundathelphusa* and *Parathelphusa* on Sulawesi will be a challenge. The genus *Sundathelphusa* has the highest diversity in the Philippines (excluding Palawan and Mindoro), and also occurs in the Moluccas as well as northeastern Borneo. They are not know further south or in other parts of Sundania (i.e. other parts of Borneo, Palawan, Mindoro, Java, Sumatra or Peninsular Malaysia). The distribution of *Sundathelphusa* is so unusual that it certainly merits a detailed multi-disciplinary study, the results of which are likely to have a major bearing on what we know about biogeography in that part of the world.

ACKNOWLEDGEMENTS

This study started some 20 years ago when Maurice Kottelat sent the second author several batches of crabs from Sulawesi for study and got him interested in the fauna there. He has been helpful with data and material for which the second author is grateful. Louis Deharveng was also most kind in sending the second author material over the years for examination. We are also very grateful to the many curators in the Museum Zoologicum Bogoriense, Naturhistorisches Museum Basel, Nationaal Naturhistorisch Museum (Leiden), Museum für Naturkunde der Humboldt-Universität zu Berlin and the Raffles Museum of Biodiversity Research in Singapore, who have loaned us material and allowed us to check their holdings. A key part of this study was based on a collection passed to us by Daisy Wowor and Yayuk Suhardjono with their colleagues (notably C. D. Schubart, Leong Tzi Ming and Cahyo Rahmadi, for which we are most grateful. Louis Deharveng was also most kind in checking their holdings. A key part of this study was based on a collection passed to us by Daisy Wowor and Yayuk Suhardjono with their colleagues (notably C. D. Schubart, Leong Tzi Ming and Cahyo Rahmadi, for which we are most grateful.

LITERATURE CITED


