

A new molluscivore crab from Lake Poso confirms multiple colonization of ancient lakes in Sulawesi by freshwater crabs (Decapoda: Brachyura)

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Ancient lakes are among the most stable freshwater environments on our planet, with a species richness far exceeding that of younger and less stable limnic habitats. Compared with the African rift lakes, the ancient lakes of the Indonesian island Sulawesi have received less attention, and their fauna has not been satisfactorily explored. Here, we present results on the freshwater crabs from these lakes and their phylogenetic relationships. Complementing recent descriptions of new species and genera of freshwater crabs from the *Parathelphusa* complex endemic to the Malili lake system and Lake Poso, here we report on another new species belonging to the genus *Sundathelphusa* (Potamoidea Gecarcinucidae), so far only known from one locality in Lake Poso. The morphology of the chelae of this crab is indicative of a predatory lifestyle: it probably feeds on the rich gastropod and bivalve fauna of the lake. So far, no specialized molluscivore crab has been known from Lake Poso, whereas mollusc-feeding crabs had been described from all lakes belonging to the nearby Malili system. A phylogenetic reconstruction of all known freshwater crab species from the ancient lakes, based on 562 base pairs of mitochondrial DNA (large ribosomal subunit 16S rRNA), revealed that the crabs inhabiting these lakes are not monophyletic. The large number of endemic crab species in both lake systems is thus not the consequence of a single adaptive radiation, but is the outcome of at least two independent colonizations from nearby tributaries and the subsequent specialization to the stable freshwater environment. © 2008 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2008, 154, 211–221.

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INTRODUCTION

Interest in the evolution of species flocks has directed a lot of attention to faunal studies of ancient lakes, with Lake Tanganyika, Lake Malawi, and Lake Baikal being among the best-known examples. To date, research on species flocks has mainly focused on vertebrates, with cichlid fishes from the East African lakes being probably the best known and best studied example (Meyer *et al.*, 1990; Sturmbauer & Meyer, 1992; Schliwien, Tautz & Pääbo, 1994; Goldschmidt,

1997). However, most ancient lakes also harbour one or several species flocks of invertebrates. These are often crustaceans and snails, as in Lake Tanganyika, Lake Baikal, and the Malili lakes of Sulawesi (see von Rintelen *et al.*, 2004). The available knowledge on the evolution of these invertebrate species flocks is more than rudimentary in comparison with fishes. In most cases, the basic taxonomy still needs to be established, and testing of evolutionary hypotheses can only be a long-term goal. However, hard-shelled invertebrates with a rich fossil record, like crabs and snails, promise to be extremely useful models for *in situ* studies of adaptive radiation and formation of species flocks (e.g. see Glaubrecht, 1996).

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In most of the better studied ancient lake systems, the occurrence of crustacean species flocks has already been documented (e.g. Mashiko, Kawabata & Okino, 1991; Martens, 1994; Cumberlidge *et al.*, 1999; Sherbakov, 1999; von Sternberg & Cumberlidge, 1999; Mashiko, 2000). Species flock formation is not restricted to single taxonomic groups. In the temperate Lake Baikal, freshwater gammarids (Peracarida: Amphipoda) have experienced a huge radiation with more than 250 recognized species (Sherbakov, 1999). Species flocks in tropical lakes typically consist of freshwater crabs (Brachyura: Potamoidea) and shrimps (Caridea: Atyidae), as for example in Lake Tanganyika (Mashiko *et al.*, 1991; Cumberlidge *et al.*, 1999). The ancient lakes of Sulawesi have been relatively poorly studied in terms of their crustacean fauna, and the most recent reports previous to our present study were from Schenkel (1902) and Woltereck (1937), with the latter dealing only with shrimps of the genus *Caridina* (Atyidae). Until recently, the published literature records only one endemic crab species in Lake Poso, *Parathelphusa sarasinorum* (Schenkel, 1902), and three in the Malili lake system, *Parathelphusa pantherina* (Schenkel, 1902), *Parathelphusa matannensis* (Schenkel, 1902), and *Nautilothelphusa zimmeri* (Balss, 1933) (Roux, 1915; Bott, 1970). However, a reappraisal of all extant specimens as well as recently collected material from Sulawesi has revealed a higher decapod crustacean species richness in these lakes than was previously known (Table 1; Chia & Ng, 2006; von Rintelen, 2008).

Chia & Ng (2006) recently revised the taxonomy of all of the species belonging to the genera *Parathelphusa* and *Nautilothelphusa* from Sulawesi, describing two new genera and three new species from these ancient lakes. Consequently, five genera of freshwater crabs are now known from Sulawesi, three of which are restricted to the ancient lakes: *Nautilothelphusa*, *Migmatelphusa*, and *Syntripsa*. The other two genera, *Parathelphusa* and *Sundathelphusa*, are also known from other Sundaic and Sahulian islands, the Malay Peninsula, and the Philippines. They typically inhabit streams, swamps, rice fields, and caves (see Ng, 1988, 1991; Ng & Stuebing, 1989; Ng & Takeda, 1993; Ng & Sket, 1996). In Sulawesi, nine species of *Parathelphusa* and three species of *Sundathelphusa* are currently known from outside of the lakes (streams and caves) (Bott, 1970; Chia & Ng, 2006). They represent the potential colonizers of the freshwater lake habitats.

The ancient lakes of Sulawesi consist of two hydrographically isolated freshwater systems. The Malili lake system of Sulawesi is composed of five partially connected lakes, viz. Towuti, Mahalona, Wawantoa, Masapi, and Matano, and belongs to the Larona River basin, which drains to the south. Lake Poso is a

separate lake, belonging to the Poso River and thus to a different watershed draining to the north (see Whitten, Mustafa & Henderson, 1987). The freshwater fish fauna of these lakes has been relatively well studied in recent years. Three families of freshwater fishes with high endemism rates in Sulawesi deserve mention, viz. Adrianichthyidae, Oryziidae, and Telmatherinidae. The Adrianichthyidae and Oryziidae dominate the Poso fauna, whereas the Telmatherinidae only occurs in the Malili lakes. No endemic species are shared by Matano (seven telmatherinids and one oryziid) and Towuti, Mahalona, and Wawantoa (seven telmatherinids and two oryziids) (Kottelat, 1991; Kottelat *et al.*, 1993; Herder *et al.*, 2006). Poso has its own fish fauna, with five endemic species (three adrianichthyids and two oryziids).

In this paper, we describe a new molluscivorous species of *Sundathelphusa* from Lake Poso, and discuss the evolution of feeding guilds in the freshwater crabs of the ancient lakes. The specimens examined are deposited in the Museum Zoologicum Bogoriense (MZB), Cibinong, Java, Indonesia, and the Zoological Reference Collection (ZRC) of the Raffles Museum, National University of Singapore. The abbreviations G1 and G2 are used for the male first and second pleopods, respectively. Measurements provided in millimetres are of the carapace width and length, respectively. The classification used here follows that proposed by Ng & Sket (1996), in which *Sundathelphusa* Bott, 1969, is regarded as a senior subjective synonym of *Archipelothelphusa* Bott, 1969, and *Sundathelphusidae* Bott, 1969 is a junior synonym of *Gecarcinucidae* Alcock, 1910 (see also Ng, 1988; Klaus *et al.*, 2006).

MATERIAL AND METHODS

Most specimens used for the morphological and genetic comparisons in this study were collected during a field trip to the lakes of Sulawesi in January 2000. The molecular studies were carried out at the University of Regensburg. The genomic DNA of freshwater crabs was isolated from the muscle tissue of one walking leg using the Puregene kit (Gentra Systems). Selective amplification of a 560-base-pair (560-bp) region from the mitochondrial large subunit rRNA gene (16S mtDNA) was carried out by polymerase chain reaction (PCR) (40 cycles; with 45 s at 94 °C/1 min at 48 °C/1 min at 72 °C denaturing/annealing/extension temperatures, respectively) with the primer combination 16L2 (5'-TGCCTGTTTATCAAAAACAT-3') and 1472 (5'-AGATAGAAACCAACCTGG-3') (~580 bp) or 16H37 (5'-CCGGTyTGAACCTCAAATCATGT-3') (~560 bp) (see Schubart, Cuesta & Felder, 2002; Klaus *et al.*, 2006). PCR products were purified and sequenced in an ABI Prism 310 Genetic Analyzer. Sequences were

Table 1. Gecarcinucid crabs used for DNA sequencing and subsequent phylogenetic reconstruction, including taxonomic authority, locality of collection, museum catalogue number, and genetic database (EMBL) accession number

Species	Collection site	Catalogue #	EMBL #
<i>Migmathelphusa olivacea</i> Chia & Ng, 2006	Sulawesi: Lake Poso, Tentena	ZRC 2000.1702	AM292917
<i>Nautilothelphusa zimмери</i> (Balss, 1933)	Sulawesi: Lake Matano	ZRC 2000.1711	AM234642
<i>Nautilothelphusa zimмери</i> (Balss, 1933)	Sulawesi: Lake Mahalona	ZRC 2000.1709	AM292907
<i>Nautilothelphusa zimмери</i> (Balss, 1933)	Sulawesi: Lake Towuti	ZRC 2000.1707	AM292908
<i>Parathelphusa celebensis</i> (De Man, 1892)	Sulawesi: Bissapi waterfalls, Ujungpandang	ZRC 2006.0116	AM292922
<i>Parathelphusa ferruginea</i> Chia & Ng, 2006	Sulawesi: Lake Mahalona	ZRC 2000.1692	AM292911
<i>Parathelphusa ferruginea</i> Chia & Ng, 2006	Sulawesi: Lake Towuti (purple legs)	ZRC 2000.1690	AM292909
<i>Parathelphusa ferruginea</i> Chia & Ng, 2006	Sulawesi: Lake Towuti (yellow legs)	ZRC 2000.1689	AM292910
<i>Parathelphusa pallida</i> (Schenkel, 1902)	Sulawesi: Lake Matano	ZRC 2000.1705	AM292914
<i>Parathelphusa pantherina</i> (Schenkel, 1902)	Sulawesi: tributary to Lake Matano P30	ZRC 2006.0115	AM292913
<i>Parathelphusa pantherina</i> (Schenkel, 1902)	Sulawesi: Lake Matano tributary near Soroako	ZRC 2000.1691	AM292912
<i>Parathelphusa possoensis</i> (Roux, 1904)	Sulawesi: Salopa waterfall, near Tentena	ZRC 2000.1682	AM292915
<i>Parathelphusa possoensis</i> (Roux, 1904)	Sulawesi: stream near Mayoa	ZRC 2005.0144	AM292916
<i>Parathelphusa sarasinorum</i> (Schenkel, 1902)	Sulawesi: Lake Poso, Tentena	ZRC 2000.1697	AM234644
<i>Sundathelphusa</i> sp.	Sulawesi: stream near Mayoa	ZRC 2000.1684	AM292919
<i>Sundathelphusa minahassae</i> (Schenkel, 1902)	Sulawesi: Tomohon	ZRC 2000.1681	AM234651
<i>Sundathelphusa molluscivora</i> sp. nov.	Sulawesi: Lake Poso, west coast near Taipa	ZRC 2000.1703	AM292918
<i>Syntripsa flavichela</i> Chia & Ng, 2006	Sulawesi: Lake Mahalona	ZRC 2000.1713	AM292920
<i>Syntripsa flavichela</i> Chia & Ng, 2006	Sulawesi: Lake Towuti, Larona	ZRC 2000.1688	AM292921
<i>Syntripsa matannensis</i> (Schenkel, 1902)	Sulawesi: Lake Matano	ZRC 2000.1685	AM234643
<i>Salangathelphusa brevicarinata</i> (Hilgendorf, 1882)	Thailand: Phuket: Ton Sai Falls	ZRC 2000.1918	AM234648
<i>Siamathelphusa holthuisi</i> Nayanetr & Ng, 1990	Thailand: Krathing Falls	ZRC 2000.1923	AM234650

ZRC, Zoological Reference Collection, Raffles Museum at the National University of Singapore.

aligned manually and compared with the multisequence editing program XESEE (based on Cabot & Beckenbach, 1989). There were only a few gaps, which could be aligned unambiguously. All the PCR products were purified with Microcon 100 filters or ExoSAP-IT (Amersham Biosciences), and were then sequenced with the ABI BigDye terminator mix. For verification, both strands were sequenced and the resulting nucleotide sequences data were submitted to EMBL (see Table 1 for accession numbers). DNA sequences obtained from the Gecarcinucid freshwater crabs *Salangathelphusa brevicarinata* (Hilgendorf, 1882) and *Siamthelphusa holthuisi* Nayanetr & Ng, 1990 from Thailand were included as outgroups.

Three methods of phylogenetic inference were applied to our dataset: maximum parsimony (MP) and minimum evolution (ME), using the software package PAUP* (Swofford, 2003), and Bayesian analysis (BI), as implemented in MrBayes 3.0b4 (Huelsenbeck & Ronquist, 2001). The ME and BI trees were obtained using the parameters of the best-fitting model of DNA substitution, as calculated with the software MODELTEST 3.6 (Posada & Crandall, 1998). A χ^2 test of homogeneity of base frequencies across taxa was carried out, as implemented in PAUP* (Swofford, 2003).

The MP trees were obtained by a heuristic search, with 100 replicates of random sequence addition and tree-bisection-reconnection as branch-swapping options, keeping multiple trees (MulTrees). Otherwise, the default options of PAUP* were used. Gaps were treated as 5th states. Subsequently, confidence values for the proposed groups within the inferred trees were calculated with the bootstrap method (2000 pseudoreplicates). Only minimal trees were retained, and branches of zero length were collapsed. Confidence values for the ME tree were obtained with the bootstrap method (2000 pseudoreplicates). The Bayesian analysis was run with four MCMC chains for 2 000 000 generations, saving a tree every 500 generations (with a corresponding output of 4000 trees). The $-\ln L$ converged on a stable value between 5000 and 10 000 generations ('burn-in phase'). The first 12 500 generations were not included in the analysis, so as to avoid the possibility of including random and sub-optimal trees. The posterior probabilities of the phylogeny were determined for the remaining trees. Consensus trees were constructed using the 'sumpt' option in MrBayes.

SYSTEMATIC ACCOUNT

SUNDATHELPHUSA MOLLUSCIVORA SP. NOV.

(FIG. 1–4)

Holotype – male (24.6 by 20.4 mm) (MZB 1480), under rocks, c. 2 m depth, Lake Poso, west coast, near

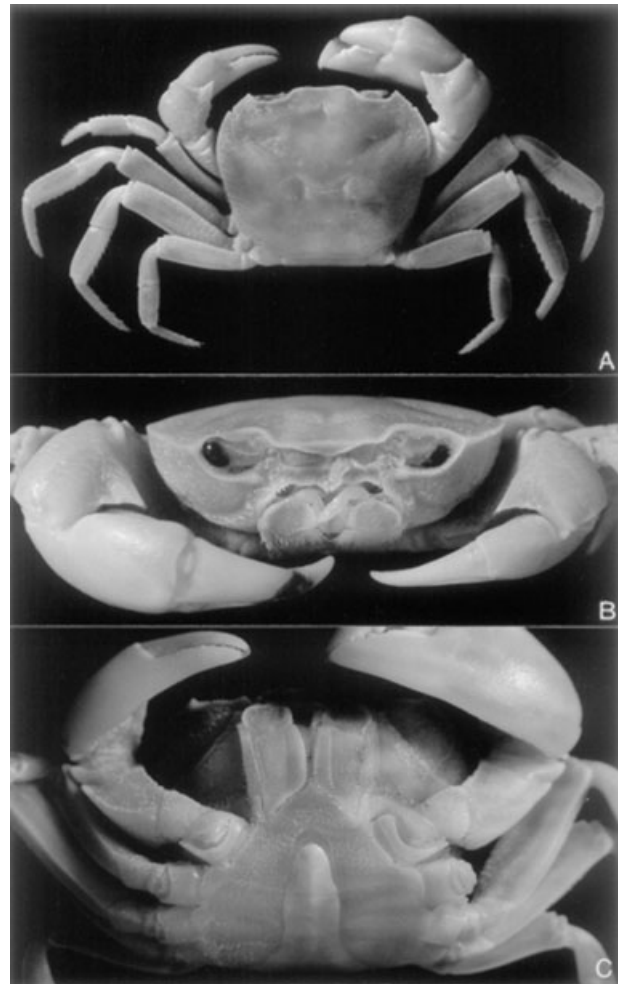


Figure 1. *Sundathelphusa molluscivora* sp. nov. Paratype male (23.5 by 19.0 mm) (ZRC 2000.1703). A, overall view; B, frontal view; C, ventral view.

Taipa, Sulawesi, Indonesia, coll. C.D. Schubart, T.M. Leong & D. Wowor, 22 January 2000.

Paratypes – eight males (smallest 11.7 by 10.2 mm, largest 23.5 by 20.4 mm), eight females (smallest 12.0 by 10.0 mm, largest 24.7 by 20.3 mm), two juveniles (ZRC 2000.1703), two males, two females (MZB 1481), same data as holotype.

Diagnosis: Dorsal surface of carapace convex, relatively smooth, not prominently inflated or swollen. Frontal medium triangle complete, margins completely fused. External orbital angle broadly triangular; anterolateral margin distinctly convex, with one distinct tooth. Adult chelipeds markedly heterochelous in both sexes; major chela with strong molariform teeth at the bases of the cutting edges of fingers. Male abdomen distinctly T-shaped: segment 6 longer

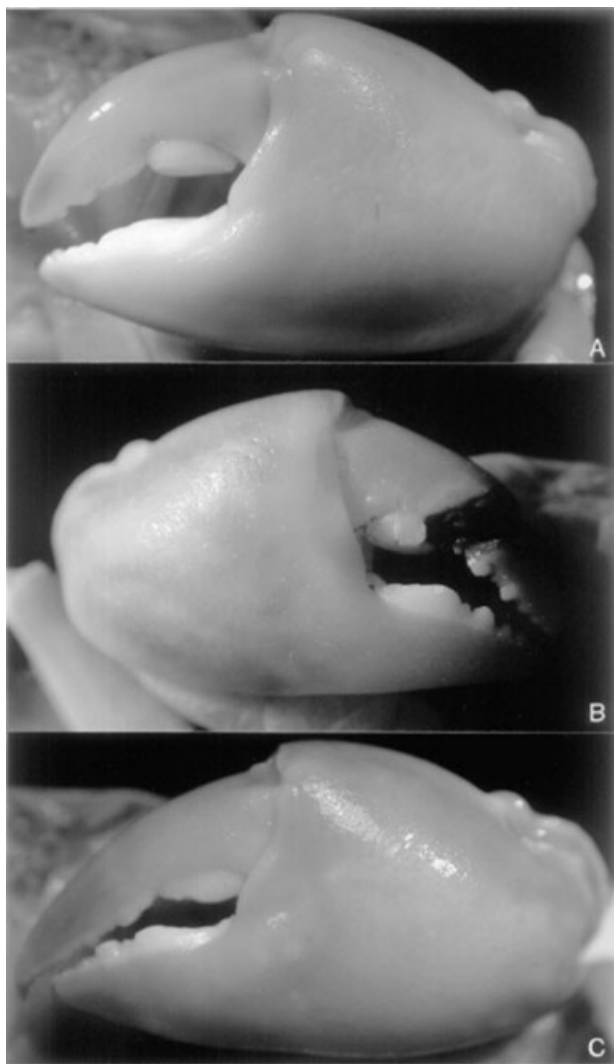


Figure 2. *Sundathelphusa molluscivora* sp. nov. Major chelae. A, male (23.5 by 19.0 mm) (ZRC 2000.1703); B, holotype male (24.6 by 20.4 mm) (MZB 1480); C, female (24.3 by 20.0 mm) (ZRC 2000.1703).

than telson. First gonopods gently curving outwards; terminal segment *c.* 0.3 times the total length.

Description of holotype: Carapace appears quadrate, widest point of carapace about one-third of the distance from front, carapace gently convex transversely; regions poorly demarcated, relatively smooth; cervical groove distinct, broad; H-shaped gastrocardiac groove distinct; shallow transverse depression between cardiac and intestinal regions. Frontal median triangle complete, lateral and dorsal margins cristate, dorsal and lateral margins fused, but suture still visible. Epigastric cristae: low, rounded, but still discernible, separated from each other by shallow cleft. Postorbital cristae: very low, rugose, almost indiscern-

ible. Frontal margin truncate, about half the maximum carapace width, appears vaguely bilobed from dorsal view; supraorbital margin entire, subparallel with frontal margin. External orbital tooth broadly triangular, clearly directed anteriorly, outer margin uneven, straight, twice as long as inner margin, separated from anterolateral margin by distinct V-shaped cleft, tip not extending beyond level of front. Anterolateral margin distinctly convex, slightly granular, and gently curving to join posterolateral margin. Posterolateral margin gently convex, converging gradually towards more concave posterior carapace margin. Suborbital, sub-branchial, and pterygostomial regions covered with scattered oblique short striae and small granules. Basal antennal segment large, subquadrate. Posterior margin of epistome with large median triangular lobe; lateral margins sinuous. Third maxilliped with ischium rectangular, submedian oblique sulcus distinct; merus subquadrate, with gentle median depression, anteroexternal angle rounded; tip of exopod reaching to midpoint of outer margin of merus, flagellum long.

Chelipeds prominently unequal. Merus with slightly serrated margins, no distinct subdistal tooth. Carpus with outer surface rugose, with well-developed inner distal spine that is somewhat laterally flattened, and proximal basal part with several small sharp tubercles. Outer surface of minor palm gently rugose to almost smooth; fingers longer than palm, cutting edges lined with numerous teeth and denticles, tip pectinated. Outer surface of major palm smooth or finely punctate; fingers subequal to length of palm, proximal two-thirds of cutting edge of pollex with large molariform tooth, rest of edge with distinct teeth; proximal one-fifth of cutting edge of dactylus with relatively smaller molariform tooth, rest of edge with numerous teeth and denticles, slender, tip pectinated.

Ambulatory legs not elongate, second leg longest. Merus with dorsal, slightly serrate margin, subdistal angle with low tooth but no spine. Carpus elongate, dorsal margin gently serrated, ventral margin smooth, and outer surface with two low ridges. Dorsal and ventral margins of propodus serrated. Dactylus slender, slightly flattened laterally, gently curved.

First to fifth thoracic sternites smooth, with scattered punctae; all sternites fused, no sutures evident. Abdominal cavity reaching to imaginary line joining anterior edge of coxae of chelipeds. Male abdomen distinctly T-shaped. Segment 1 very narrow longitudinally, proximal and distal margins gently sinuous. Segment 2 subrectangular transversely. Segments 3–5 gradually more trapezoidal; lateral margins of segment 3 convex; lateral margins of segments 4 and 5, straight to gently concave. Segment 6 longitudinally rectangular, longer than telson, and lateral

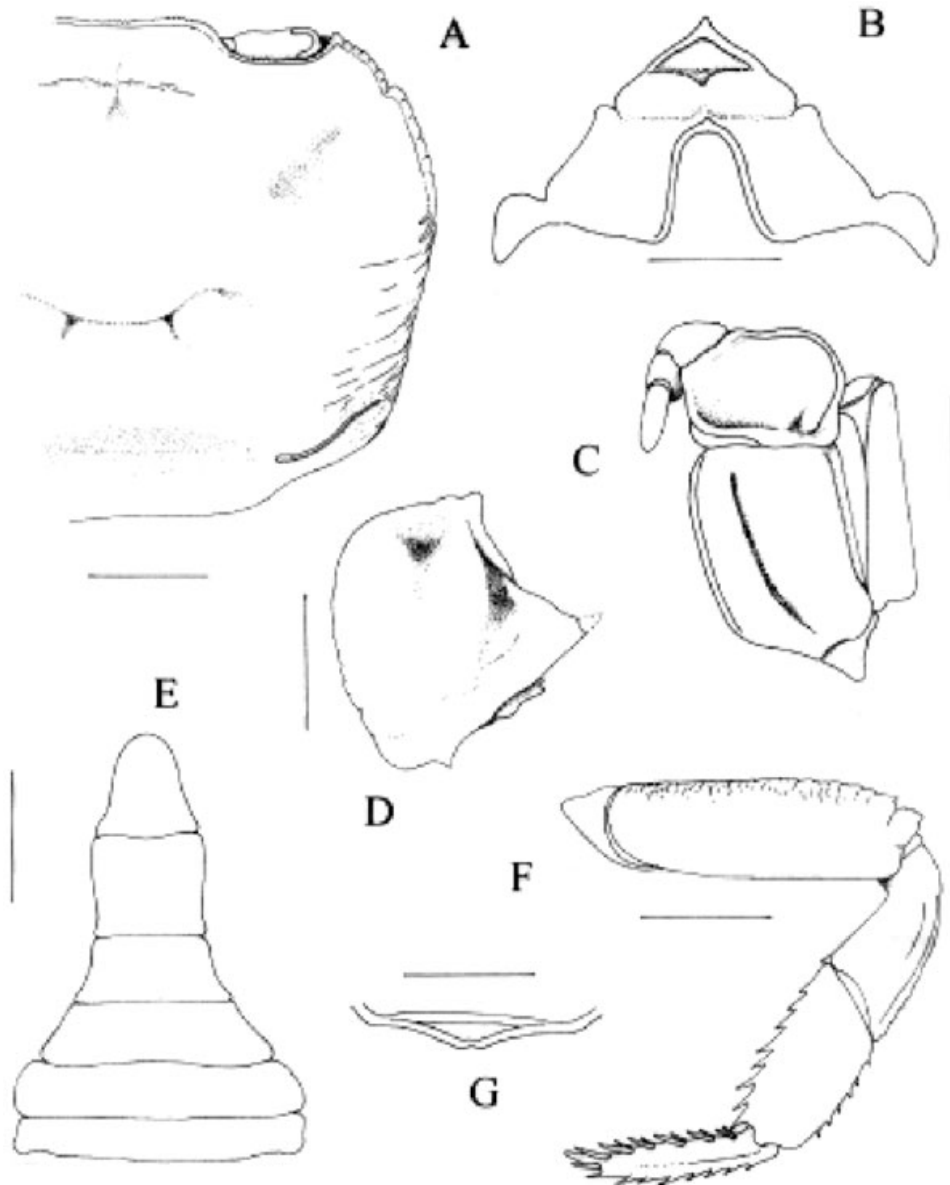


Figure 3. *Sundathelphusa molluscivora* sp. nov. Paratype male (23.5 by 19.0 mm) (ZRC 2000.1703). A, right side of carapace; B, anterior thoracic sternum; C, left third maxilliped; D, right chelipedal carpus; E, male abdomen; F, right fourth ambulatory leg; G, frontal median triangle. Scale bars: A–F, 5.0 mm; G, 1.0 mm.

margins gently sinuous. Telson longitudinally triangular, lateral margins concave, and tip rounded.

First gonopods gently curving outwards; subterminal segment with outer margin gently concave; terminal segment *c.* 0.3 times total gonopod length, slightly curved, subcylindrical, tip gently rounded. Second gonopods elongated, much longer than first; distal segment long, *c.* 0.7 times the length of the basal segment.

Paratypes: The paratype males agree with the holotype male in all major aspects, although in smaller specimens, the major chela is relatively smaller. The cara-

paces of smaller specimens also tend to be more quadrate. Females agree with the males in most non-sexual characters, although the lateral margins in larger specimens are slightly more convex, giving them a somewhat more inflated appearance. The heterochely in females is also less prominent, with the major claw being much smaller than in males of equivalent sizes, but still showing molariform dentation.

Colour in life: Pale yellow; carapace darker, somewhat olive; legs lighter; chelae homogeneously yellow, except shining white molariform teeth.

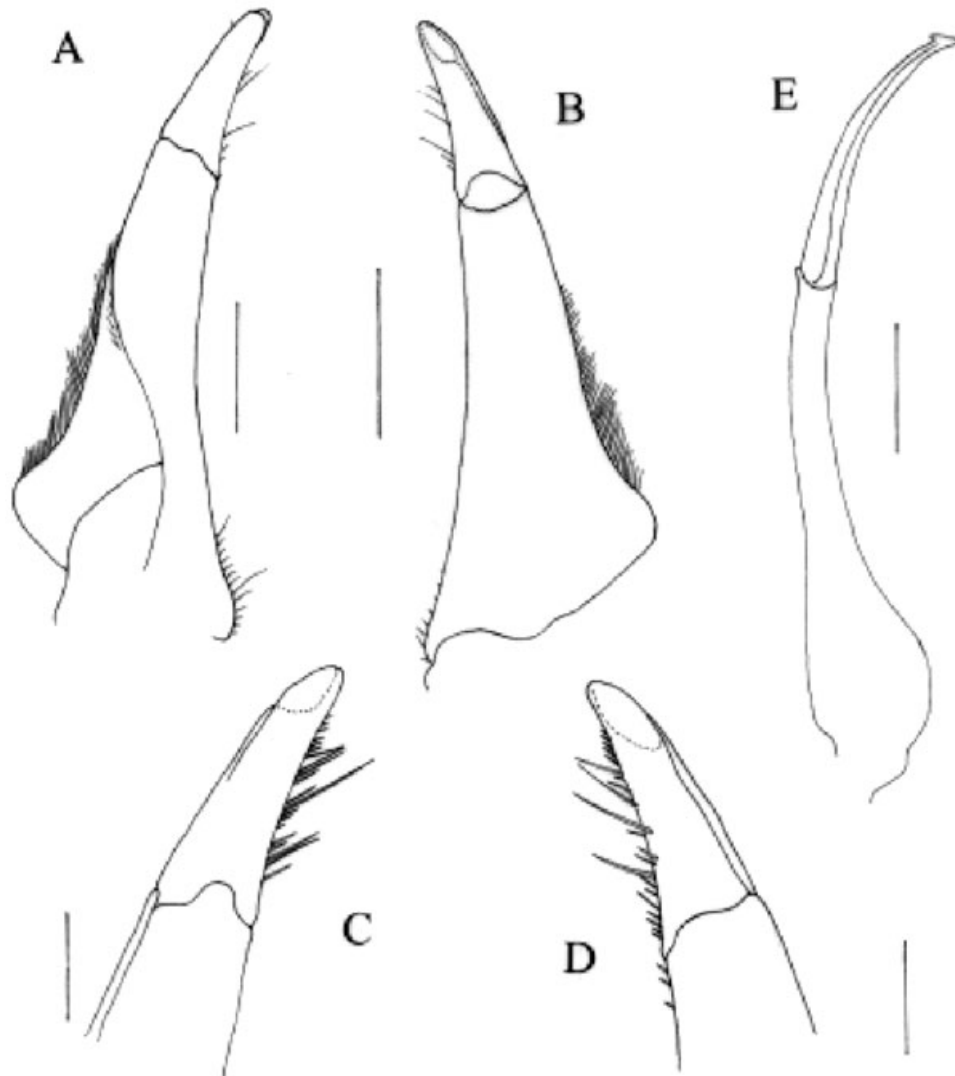


Figure 4. *Sundathelphusa molluscivora* sp. nov. Gonopods, paratype male (23.5 by 19.0 mm) (ZRC 2000.1703). A and C, left G1, ventral view; B and D, left G1, dorsal view; E, left G2. Scale bars: A, B, E, 1.0 mm; C, D, 0.5 mm.

Etymology: The name ‘molluscivora’ (mollusc-eating) is used as an adjective, and is derived from the taxon name ‘Mollusca’ and the Latin verb ‘vorare’ (to devour). It makes reference to the apparent mollusc-eating habit of these crabs, as suggested by their chelar morphology.

Distribution: This species has only been found from its type locality in Lake Poso (Sulawesi, Indonesia), to which it is probably endemic.

Remarks: The genus *Sundathelphusa* Bott, 1969 (type species *Potamon* (*Geothelphusa*) *cassiope* De Man, 1902, by original designation) currently contains 28 species from the Philippines, Sulawesi, Moluccas and eastern Borneo (Ng & Stuebing, 1989; Ng, 1991; Ng &

Sket, 1996; Takeda & Ng, 2001). The genus is dominant in the Philippines, with only three species known from Sulawesi thus far, viz. *Sundathelphusa cassiope* (De Man, 1902), *Sundathelphusa minahassae* (Schenkel, 1902), and *Sundathelphusa rubra* (Schenkel, 1902).

The authors have examined photographs of the whole type specimens, with figures of the G1s and G2s of *S. cassiope*, *S. minahassae*, and *S. rubra* that were prepared for us by Oliver Chia (National University of Singapore) at our request (see also Chia & Ng, 2006). As such, we have no doubt that our present specimens from Poso belong to a new species. The most obvious character that distinguishes adults of *S. molluscivora* sp. nov. from all congeners is the large molariform tooth on the larger chela. Such a charac-

ter is present in only two other freshwater crabs of the region, viz. *Syntripsa matannensis* (Schenkel, 1902) and *Syntripsa flavichela* Chia & Ng, 2006, both from the Malili lake system in central Sulawesi.

The carapaces of *S. cassiope* and *S. rubra* are both prominently swollen, with the dorsal surface strongly convex and the branchial regions swollen. In addition, their G1 terminal segments are proportionately much shorter. The same is true of *Potamon* (*Geothelphusa*) *angustipes* Schenkel, 1902, a species that was tentatively synonymized with *S. rubra* by Bott (1970: 74) (see also Schenkel, 1902: 533, pl. 11 fig. 17; Chia & Ng, 2006). In the form of the flat carapace and the structure of the G1, *S. molluscivora* sp. nov. is morphologically closest to *S. minahassae*. However, *S. molluscivora* sp. nov. can easily be separated, in that its anterolateral margin is more strongly convex, and the posterolateral regions are smoother, with very low transverse striae.

Two other species of *Sundathelphusa* are known from near Sulawesi in the Moluccas, viz. *Sundathelphusa aruana* (Roux, 1911) and *Sundathelphusa halmaherensis* (De Man, 1902). *Sundathelphusa molluscivora* sp. nov. differs from *S. aruana* in its prominently flatter carapace, with the latter resembling *S. cassiope* in carapace physiognomy (cf. types examined, see also Bott, 1970: 75, 76; Chia & Ng, 2006: figs 42, 43). The status of *S. halmaherensis* is not clear, as it is only known from juveniles, but it is a species with a clearly more rugose carapace (see De Man, 1902: 561, pl. 20, fig. 17; Bott, 1970: 78, pl. 14, figs 67–69; Cai & Ng, 2001: 686), and is not conspecific with the much smoother *S. molluscivora* sp. nov.

The molecular phylogeny places the new species *S. molluscivora* sp. nov. next to an unidentified species of the genus, with high confidence values. This sister species was found in a small stream draining into Lake Poso, but could not be identified to species level, because only one juvenile individual was available, and thereby lacked diagnostic morphological characters. Also, the third representative of *Sundathelphusa* in this study, *S. minahassae*, belongs to this clade. *Sundathelphusa minahassae* was collected in the northeastern part of Sulawesi, and the very long branches document pronounced genetic differences between the two species from the central highlands.

The three species of *Sundathelphusa* as a group are reciprocally monophyletic to all the other species of freshwater crabs from Sulawesi belonging to the genera *Syntripsa*, *Migmathelphusa*, *Parathelphusa*, and *Nautilothelphusa*. Within this latter group, the genus *Syntripsa* from the Malili Lakes holds the most basal position. The next split separates tributaries and the lake from the Poso system from the tributaries and lakes from the Malili system, giving the overall speciation pattern a clear hydrogeographic

component. The genera *Syntripsa*, *Migmathelphusa*, and *Nautilothelphusa* exclusively comprise lake crabs, demonstrating from their phylogenetic position that the lakes must have been colonized several times independently.

DISCUSSION

Crabs from the lakes of Sulawesi can be categorized into three different ecotypes: (1) an unspecialized, morphologically undifferentiated form; (2) a detritivore and burrowing form; and (3) a molluscivore form. In Lake Poso, as well as in all three major lakes of the Malili system, representatives of the three ecotypes are always present. Crabs of the undifferentiated form closely resemble the river crabs, and consequently remained in the genus *Parathelphusa*, despite their generally larger carapaces and chelae (see Chia & Ng, 2006). In contrast, crabs belonging to the other two ecotypes have been classified in different genera according to their conspicuous morphological differentiation (see Balss, 1933; Chia & Ng, 2006). This would seem to conflict with our current ideas of phylogenetic taxonomy, making the genus *Parathelphusa* paraphyletic. However, the taxonomy is currently maintained because the genus *Parathelphusa* as a whole, including representatives from the Malay Peninsula and other Indonesian islands, is in need of revision.

The detritivore crabs belonging to the genera *Migmathelphusa* and *Nautilothelphusa* are characterized by small chelae (especially *Nautilothelphusa*), and a last pair of walking legs with partially foliaceous carpi, probably used for burrowing backwards into the sandy sediment (CDS, pers. observ.). The two molluscivore crab species from the Malili lake system, now belonging to the genus *Syntripsa*, are the largest of all the lake crustaceans, and are characterized by their prominent molariform chelar teeth. These molariform structures are otherwise known only from the chelae of marine crabs and some species of *Platythelphusa* from Lake Tanganyika (Potamonautidae, see Klaus, Schubart & Brandis, 2006 for a revised classification), and are thus unique within the family Gecarcinucidae. Whereas many species of Gecarcinucidae have one of the male dactylar teeth enlarged (see Ng, 1990), these are never molariform.

Previous to the study by Chia & Ng (2006), only one species, *P. matannensis* (from Lake Matano), was known to have one of the chelae remarkably enlarged, with the base of the fingers possessing powerful molariform teeth (Ng, 1988). *Parathelphusa matannensis* has been referred to the new genus *Syntripsa* by Chia & Ng (2006) on the basis of the prominent chelae and other characters. The populations from Lake Matano remain in *S. matannensis*, whereas those

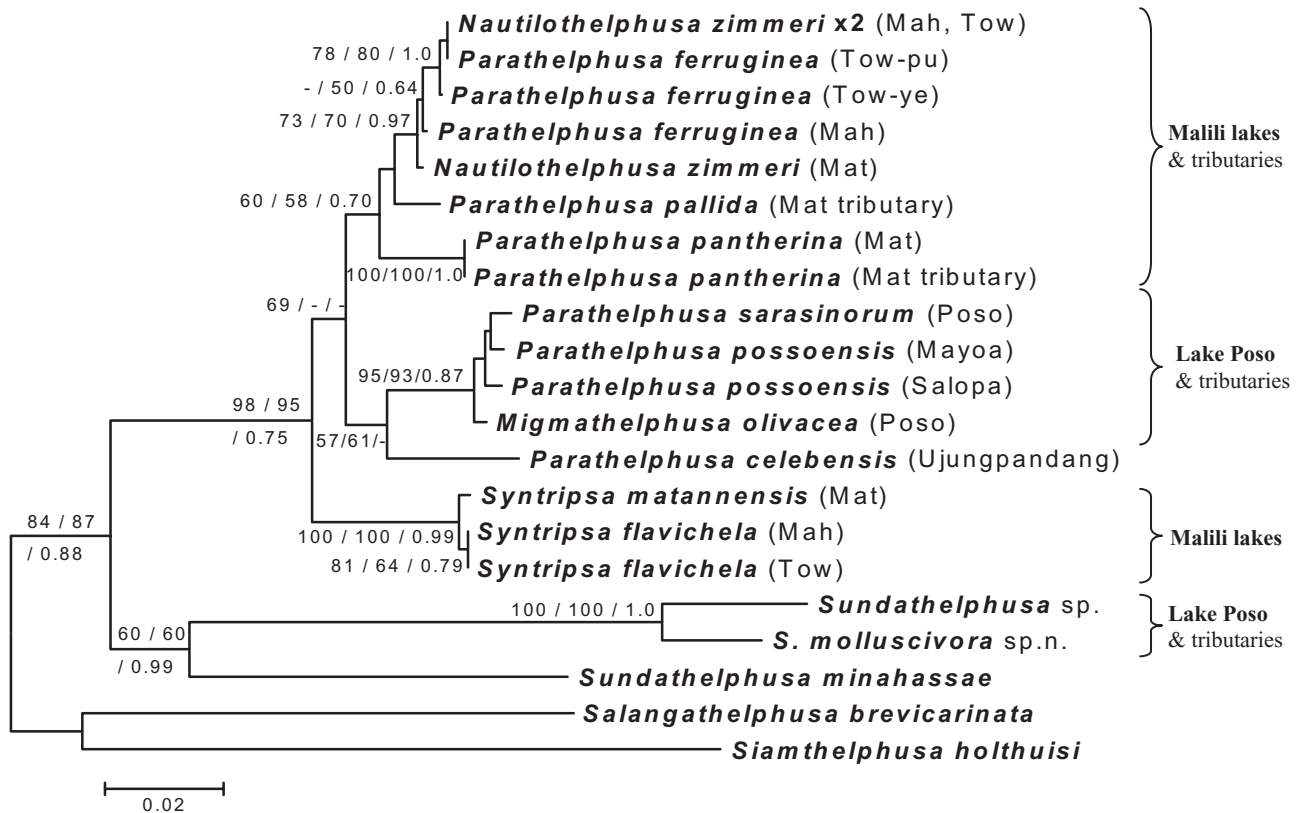


Figure 5. Bootstrap 50% majority rule consensus tree of phylogenetic relationships within freshwater crabs from Sulawesi, with two species from Thailand used as outgroups, based on maximum parsimony (MP), minimum evolution (ME) and Bayesian inference (BI) (last two with the GTR+I+G model of evolution) topologies. Confidence values from 2000 bootstrap pseudoreplicates (MP/ME) or 2 000 000 generations (BI) based on 562 base pairs of the 16S mitochondrial gene in the order MP/ME/BI; only values above 50% confidence are shown. Abbreviations: Mah, Lake Mahalona; Mat, Lake Matano; Tow, Lake Towuti.

from Lake Towuti and Lake Mahalona so far included in *P. matannensis* are now referred to a separate species, *Syntripsa flavichela* Chia & Ng, 2006. No species with massive chelae and molariform teeth have so far been reported from Poso. Bogan & Bouchet (1998) recently gave evidence for a sessile corbiculid bivalve from Lake Poso, in addition to the rich snail fauna that is present in all of the ancient lakes of Sulawesi (von Rintelen *et al.*, 2004). The discovery of a crab with a diet predominantly consisting of molluscs is therefore not surprising. Previous to the present study, only four species of crabs were known from the Poso area, viz. *Migmathephusa olivacea* Chia & Ng, 2006, *Parathelphusa sarasinorum* (Schenkel, 1902), *Parathelphusa possoensis* (Roux, 1904), and *Parathelphusa tenuipes* (Schenkel, 1902), with the first two species probably being the only ones found within the lake proper.

The question of whether the different ecotypes of crabs are based on convergent evolution or common ancestry was addressed with a molecular phylogeny

based on 16S rRNA mitochondrial DNA. Our present results demonstrate that: (1) the freshwater crab fauna of Lake Poso and the Malili lake system evolved in complete independence; (2) the molluscivore crabs of the Malili lakes (genus *Syntripsa*) colonized the lakes independently from the other two ecotypes; and (3) the undifferentiated forms and the detritivore forms of Lake Poso and the Malili lakes constitute monophyletic assemblages (Fig. 5; see also Schubart *et al.*, 2008).

The close genetic similarity between *N. zimmeri* and the recently described species *Parathelphusa ferruginea* Chia & Ng, 2006 from Lake Towuti is striking, to the extreme that a single specimen of each species shares the same 16S mtDNA haplotype. This means, that representatives cannot be unequivocally assigned to the two species based on this gene fragment, despite the fact that these crabs are morphologically very distinct and belong to different genera. We can exclude cross-contamination because we included various individuals from both species, and

sequences were obtained in two different laboratories. Newer results comparing the COI gene confirm a high degree of similarity (Schubart *et al.*, 2008). This phenomenon could be to the result of incomplete mtDNA lineage sorting or mtDNA introgression, and to our knowledge it is the first time that this has been reported for two species from different genera. It is an indication of a very recent and rapid radiation of the lake crab species *N. zimmeri*, *P. ferruginea* and *P. pantherina* from a riverine population of *Parathelphusa pallida* (Schenkel, 1902). A very rapid speciation and divergence is generally characteristic for species flocks in ancient lakes (see Albertson *et al.*, 1999; Danley & Kocher, 2001).

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