Zootaxa 1852: 37–49 (2008)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Three new species of the freshwater snail genus *Tylomelania* (Caenogastropoda: Pachychilidae) from the Malili lake system, Sulawesi, Indonesia

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Abstract

The ancient Malili lake system on the Indonesian island Sulawesi hosts a large species flock of the viviparous freshwater gastropod *Tylomelania*. Molecular and morphological data have previously shown that this species flock resulted from three independent lake colonizations and subsequent adaptive radiations. In a recent taxonomic revision of these radiations 25 species have been recognized. Here we describe three new species from the system found during new sampling campaigns. Despite their highly distinct shell morphology, these species were previously overlooked because of their very restricted distribution range and, in one case, the very small size. Of these new species, two are endemic to a section of the Larona River, which drains the entire lake system, while the third species has only been found at one locality in central Lake Mahalona. The discovery of these species can contribute significantly to our understanding of evolution in the entire species flock, as two of the species form a basal branch of an entire clade and all show a high degree of habitat specialization. The local endemism of the Larona River species in particular makes them highly vulnerable to extinction caused by habitat destruction.

Key words: ancient lakes, freshwater, adaptive radiation

Introduction

The Indonesian island Sulawesi is the largest, ecologically most diverse (Whitten *et al.* 2002) and possibly also oldest (Hall 2002) island in the oceanic island area commonly known as Wallacea (Dickerson 1928). Its fauna is particularly rich in endemic taxa and has its fair share of endemic genera as well (Whitten *et al.* 2002). Among these is the viviparous pachychilid freshwater gastropod *Tylomelania* Sarasin & Sarasin, 1898 (Caenogastropoda: Cerithioidea). This group is mainly known for its speciose species flocks in the ancient lakes of Sulawesi, viz. Lake Poso and the Malili lakes (Fig. 1). These have recently been shown to constitute model cases of adaptive radiation (Rintelen *et al.* 2004; Rintelen & Glaubrecht 2005).

In the Malili lakes the detailed taxonomic study of new material collected since 1991 has led to a considerable revision of previous species diversity estimates in these lakes. Bouchet (1995) considered the number of 23 originally described species from both Lake Poso and the Malili lakes (species described by Sarasin & Sarasin 1897; 1898; Kruimel 1913) to be too high and suggested that only twelve biospecies occur in all ancient lakes of Sulawesi. Rintelen & Glaubrecht (2003) described two new lacustrine species from the Malili lakes and proposed 16 valid taxa to occur there alone, which is also the number described by the Sarasins and Kruimel for these lakes. Finally, 25 taxa have been recognized in a recent revision of the Malili lakes taxa including the description of nine new species (Rintelen *et al.* 2007).

Intensive new sampling from 2002–2005 in the Malili lake area has provided a hitherto unparalleled coverage of the system. As a first result from the analysis of this new material we here describe three new species

Accepted by B. Ruthensteiner: 29 Jul. 2008; published: 18 Aug. 2008

lacking from the recent revision of the Malili species flock and discuss their impact on the understanding of evolution in the entire radiation.

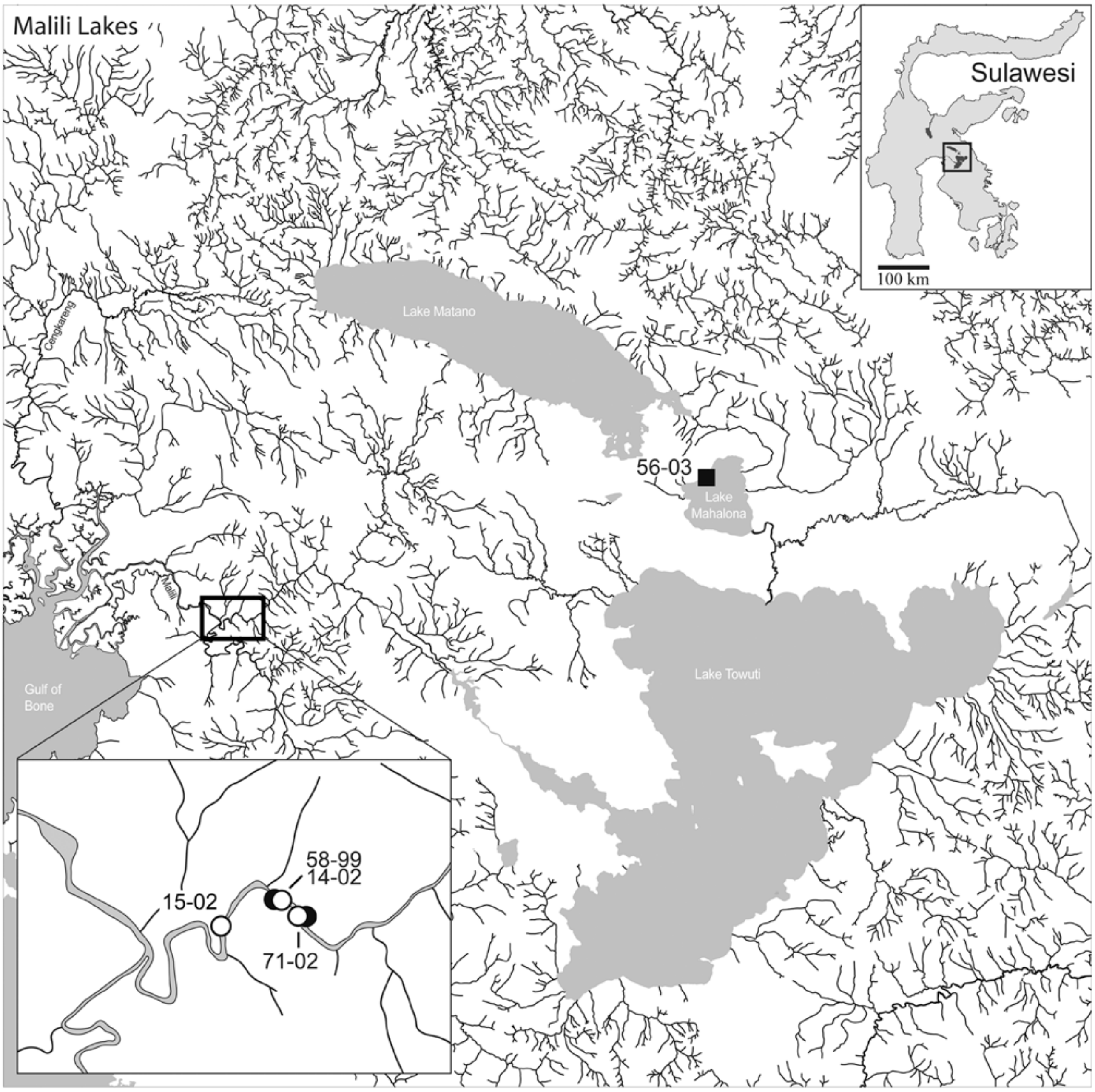

FIGURE 1. Sulawesi and the Malili lake system with sample sites. Locality numbers are the original field numbers and correspond to those in Tab. 1.

Material and methods

Material. This study is based on material collected by the authors in the Malili lake system in 1999, 2002 and 2003, respectively (Tab. 1). All samples are preserved in 70% or 95% ethanol and have been deposited in the Museum Zoologi Bogor (MZB) and the Museum für Naturkunde Berlin (ZMB).

Methods. Shells were measured to 0.1 mm using an electronic calliper. Standard shell parameters were taken following Dillon (1984). Embryonic shells were measured to 0.1 mm using an ocular micrometer; parameters were taken as in adult specimens.

TABLE 1. List of sampling stations with locality details. The locality numbers correspond to those in Fig. 1.

Locality number (Field code)	Locality	Coordinates	Collection date
58-99	Larona River, at road Malili-Soroako	2°70.29‘S, 121°9.81‘E	Aug. 27, 1999
14-02	Larona River, at road Malili-Soroako	2°40.36‘S, 121°9.79‘E	Oct. 25, 2002
15-02	Larona River, at road Malili-Soroako	2°40.55‘S, 121°9.54‘E	Oct. 25, 2002
71-02	Larona River, at road Malili-Soroako	2°40.42‘S, 121°9.91‘E	Dec. 2, 2002
56-03	Lake Mahalona, NW shore, at rocky cape	2°34.72‘S, 121°29.12‘E	Sept. 9, 2003

Anatomy was studied with a stereo microscope; the sex ratio is given as the proportion of males among sexed individuals.

Radulae and embryonic shells were studied by scanning electron microscopy (SEM). The radulae were cleaned enzymatically with proteinase K as described by Holznagel (1998), sonicated and then mounted on aluminium specimen stubs with adhesive pads. Embryonic shells were cleaned mechanically, sonicated, and mounted on adhesive carbon-coated pads. Both radulae and embryonic shells were coated with gold-palladium and studied on a LEO 1450VP scanning electron microscope (software: 32 V02.03) at 10 kV. The dimensions of the initial whorl of embryonic shells were measured to 1 µm by SEM using the attached software. In radulae, teeth were counted and total radula length measured to 0.1 mm.

Polymerase chain reaction (PCR) was used to amplify a ~890 bp region of the mitochondrial 16S ribosomal RNA gene using primers 16SF 5' TCGCACCAGCGATAGCTAGTT (this study) and H3059 5' CCGGTYTGAACTCAGATCATGT (Wilson *et al.* 2004) in four specimens of two of the new species. The molecular methods have been described in detail by Rintelen *et al.* (2004). The sequences were combined with the dataset from Rintelen *et al.* (2004) including two species of *Pseudopotamis* Martens, 1894 from the Torres Strait Islands as outgroup and were aligned with Clustal X 1.8.1 for Windows (Thompson *et al.* 1997) using default settings. The resulting alignment was corrected manually. The phylogeny was estimated by Maximum Likelihood (ML) with Treefinder (Jobb 2005). For the ML analyses an appropriate model of sequence evolution was selected using MrModeltest 2.2 (Nylander 2004) and PAUP*4.0b10a (Swofford, 2002), and consequently based on both the Hierarchical Likelihood Ratio tests and the Akaike Information Criterion the GTR + I + Γ model was chosen. The ML analysis was done with the Treefinder default settings, as was an additional bootstrap analysis with 1000 replicates.

All new sequences have been deposited in GenBank (accession numbers EU881923-EU881926).

Results

Systematic account

Caenogastropoda

Cerithioidea

Pachychilidae

***Tylomelania* Sarasin & Sarasin, 1898**

Tylomelania baskasti sp. nov.

Type material. Indonesia, Sulawesi, Larona River: Holotype (Fig. 2A; 52.3 mm x 17.7 mm, loc. 71-02), MZB Gst. 12.109; paratypes (Fig. 2B-D): loc. 14–02, MZB Gst. 12.110, n=5; ZMB Moll. 190533, n=7; loc. 15-02, MZB Gst. 12.111, n=12; ZMB Moll. 190534, n=16; loc. 71-02, MZB Gst. 12.112, n=14; ZMB Moll. 190535, n=17.

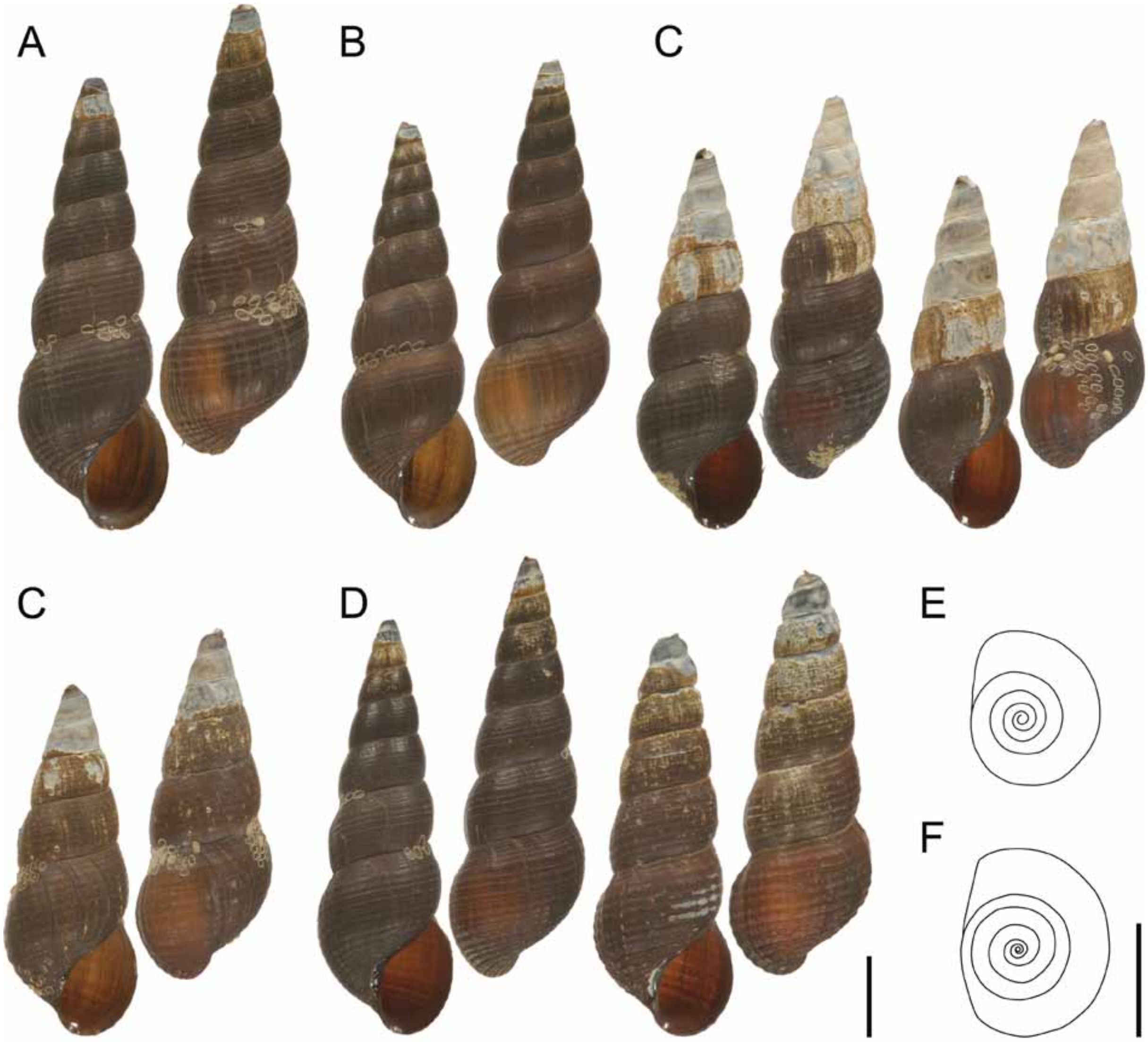

FIGURE 2. *T. baskasti* **sp. nov.**; A–D. shells, A. holotype, MZB Gst. 12.108 (loc. 71-02), B. paratypes, ZMB Moll. 190535 (loc. 71-02), C. paratypes, ZMB Moll. 190534 (loc. 15-02), D. paratypes, ZMB Moll. 190533 (loc. 14-02). Scale bar = 1 cm. E–F. opercula, E. paratype, ZMB Moll. 190534 (loc. 15-02), F. paratype, ZMB Moll. 190533 (loc. 14-02). Scale bar = 0.5 cm.

Etymology. The new species has been named *baskasti* in honour of Bas Kast, who has generously supported research on these snails at the Museum für Naturkunde.

Description. Shell (Fig. 2A–D): Medium sized to large, brown, elongate conic, spire angle 13–25°. Top whorls in adult specimens always corroded to a varying degree, 4–9 remaining whorls, can reach up to 54.7 mm (Tab. 1). With spiral ribs only. Aperture oval, pointed at top and slightly siphonated at base. Columella and interior of aperture brown, in few specimens slightly whitish coating.

External morphology: Headfoot black with fine orange dots, sometimes rather dense, foot more intensely pigmented, mantle edge serrated to a varying degree. Body coiled in 3–6 whorls.
Operculum (Fig. 2E,F): roundish-ovate, last whorl inflated, multispiral with 5–7 whorls (n=3).

Radula (Fig. 3A,B): 160–194 rows, 16.4–24.2 mm long, on average 8.8 teeth per mm (n=12). Central tooth with pointed and enlarged major denticle. Glabella with very slightly rounded base. Lateral teeth with pointed and enlarged major denticles and 2–3 minor denticles on each side. Marginal teeth shovel-like, inner and outer marginals with three almost equal-sized denticles each.

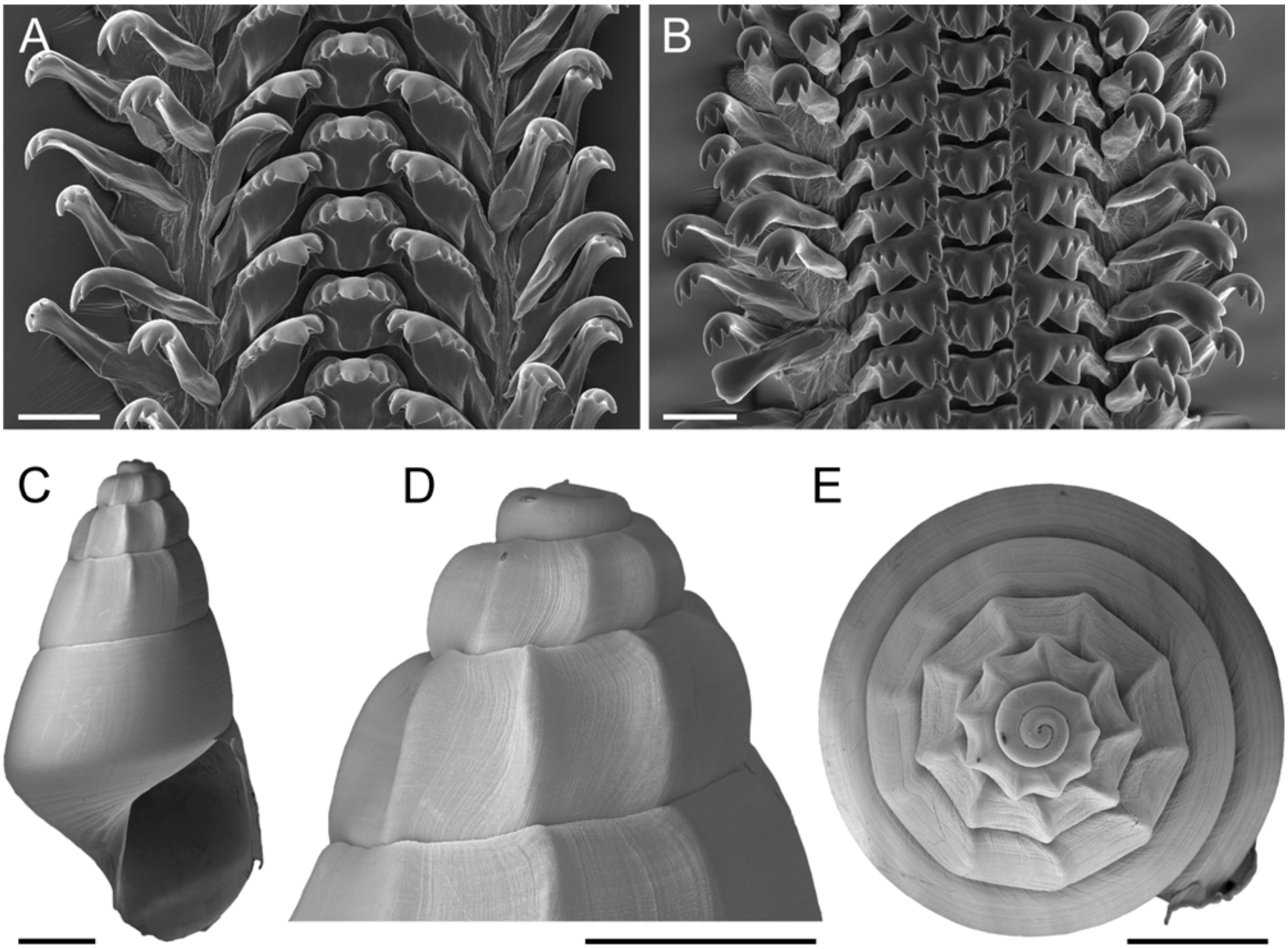

FIGURE 3. *T. baskasti* **sp. nov.**, ZMB Moll. 190534 (loc. 15-02). A–B. radula, A. segment, frontal, B. segment, apical (45°). Scale bar = 0.1 mm. C–E. embryonic shells, C. lateral view, D. apical whorls, lateral, E. apical view. Scale bar = 1 mm.

Reproductive biology: Brood pouch contains 4–12 embryos, their size can reach 8.4 mm (n=5) (Tab. 3).

Embryonic shells (Fig. 3C–E): Elongate-conic, axial ribs emerging on the 2nd to 3rd whorl and fading on the 5th whorl. Spiral striae emerge on 3rd to 4th whorl (Tab. 3).

Distribution and habitat. South Sulawesi, lower reaches of Larona River (Fig. 1B).

This species was collected in shallow water (0.1–0.5 m depth) in less turbulent zones at the river bank on soft substrate. As deeper parts of the river were not accessible for sampling because of strong currents, *T. baskasti* must not necessarily be restricted to shallow water.

Taxonomic remarks. Shell shape and radula of *T. baskasti* are similar to that of *T. lalemae* (Kruimel, 1913) from Lake Towuti. The shell of *T. baskasti* is more fragile and always lacks the conspicuous white aperture of *T. lalemae*, though. The radula of *T. baskasti* also closely resembles that of all other described riverine species of Sulawesi such as e.g. *T. perfecta* (Mousson, 1849). *T. baskasti* can be unambiguously distinguished from those taxa by its characteristic shell and the molecular data clearly confirm its relationship to the Malili lakes species flock (compare also below, *Discussion*).

***Tylomelania sinabartfeldi* sp. nov.**

Type material. Indonesia, Sulawesi, Larona River: Holotype (Fig. 4A; 24.0 mm x 18.5 mm, loc. 58-99), MZB Gst. 12.112; paratypes (Fig. 4B): loc. 58-99, MZB Gst. 12.113, n=53; ZMB Moll. 108315, n=65; loc. 71-02, ZMB Moll. 112690, n=2; loc. 58-99 (leg. Rainer Masche 2007), ZMB Moll. 192697, n=3.

Etymology. The new species has been named *sinabartfeldi* in honour of Sina Bartfeld, who contributed to supporting malacological research.

Description. Shell (Fig. 4A,B): Medium sized, brown, two shapes: conic or subglobose, transitory forms exist. Spire angle 45–85°. Top whorls in adult specimens always corroded to a varying degree, 3–6 remaining whorls, can reach up to 27.2 mm (Tab. 2). With spiral ribs only. Aperture oval, pointed at top and slightly siphonated at base. Columella and interior brown.

TABLE 2. Shell parameters of the three new species. Values represent, from top, range, mean and standard deviation, and sample size. h—shell height; w—shell width; aph—aperture length; apw—aperture width; bwl—body whorl; angle—spire angle; n.a.—not applicable.

Species	h (mm)	w (mm)	aph (mm)	apw (mm)	bwl (mm)	whorls (N)	angle (°)	axial ribs (N, on bwl)
T. baskasti	9.5–54.7 37.47 ±9.864 69	4.2–18.1 13.84 ±2.794 69	4.2–16.0 11.70 ±2.481 69	2.1–9.4 7.00 ±1.424 69	6.2–25.8 19.04 ±4.284 69	4–9 7.1 ±1.31 69	13–25 20.4 ±2.51 67	n.a.
T. sinabartfeldi	14.4–27.2 20.86 ±2.499 118	10.6–20.8 16.40 ±1.754 118	8.3–14.0 10.92 ±1.107 118	4.9–9.4 7.26 ±0.801 118	11.1–23.7 16.70 ±2.180 118	3–6 4.5 ±0.90 118	45–85 63.5 ±6.80 112	n.a.
T. hannelorae	10.6–13.9 12.31 ±1.022 9	5.5–6.8 5.91 ±0.398 9	3.9–4.6 4.3 ±0.254 9	2.3–2.7 2.57 ±0.138 9	6.9–7.9 7.34 ±0.375 9	3–5 4.3 ±0.71 9	11–17 13.3 ±2.00 9	15–21 17.7 ±2.19 8

TABLE 3. Embryonic shell parameters of Malili lake system *Tylomelania*. Values represent, from top, range, mean and standard deviation, and sample size. juv.—juveniles in broodpouch; h max—embryo shell height; ax 3rd—axial ribs on third whorl; n.a.—not applicable.

Species	juv. (N)	h max (mm)	whorls (N)	axial ribs (N)	ax 3rd (N)
T. baskasti	1–4 2.5 ±1.05 6	5.7–8.4 7.16 ±1.062 5	5.50–6.25 6.0 ±0.35 4	25–30 27.8 ±2.22 4	8–9 8.8 ±0.50 4
T. sinabartfeldi	11–67 31.0 ±31.24 3	1.2–2.9 2.67 ±0.321 3	3.0–4.0 3.3 ±0.35 10	9–15 12.6 ±2.30 7	n.a.
T. hannelorae	1–2 1.3 ±0.58 3	2.4–3.1 2.70 ±0.361 3	4.5 - 1	18 - 1	10 - 1

External morphology: Headfoot black, mantle edge serrated to a varying degree. Body coiled in 2.5 whorls.

Operculum (Fig. 4C): roundly-ovate, last whorl inflated, multispiral with 4–5 whorls.

Radula (Fig. 5A–D): 176–231 rows, 18.9–25.5 mm long, on average 9.6 teeth per mm (n=9). Central tooth with very large and almost squarish major denticle and two minor denticles on each side. Glabella with slightly rounded base. Lateral teeth with very much enlarged squarish major denticles and two minor denticles on each side. Marginal teeth shovel-like, inner and outer marginals with three denticles each, the outermost ones considerably wider than the inner ones. Inner marginals larger than outer ones.

Reproductive biology: Brood pouch contains 11–67 embryos, their size can reach 5.0 mm (Tab. 3).

Embryonic shells (Fig. 5E–K): Conic, with no or few and comparatively weak axial ribs emerging on the 2nd whorl and fading on the 3rd whorl (Tab. 3).

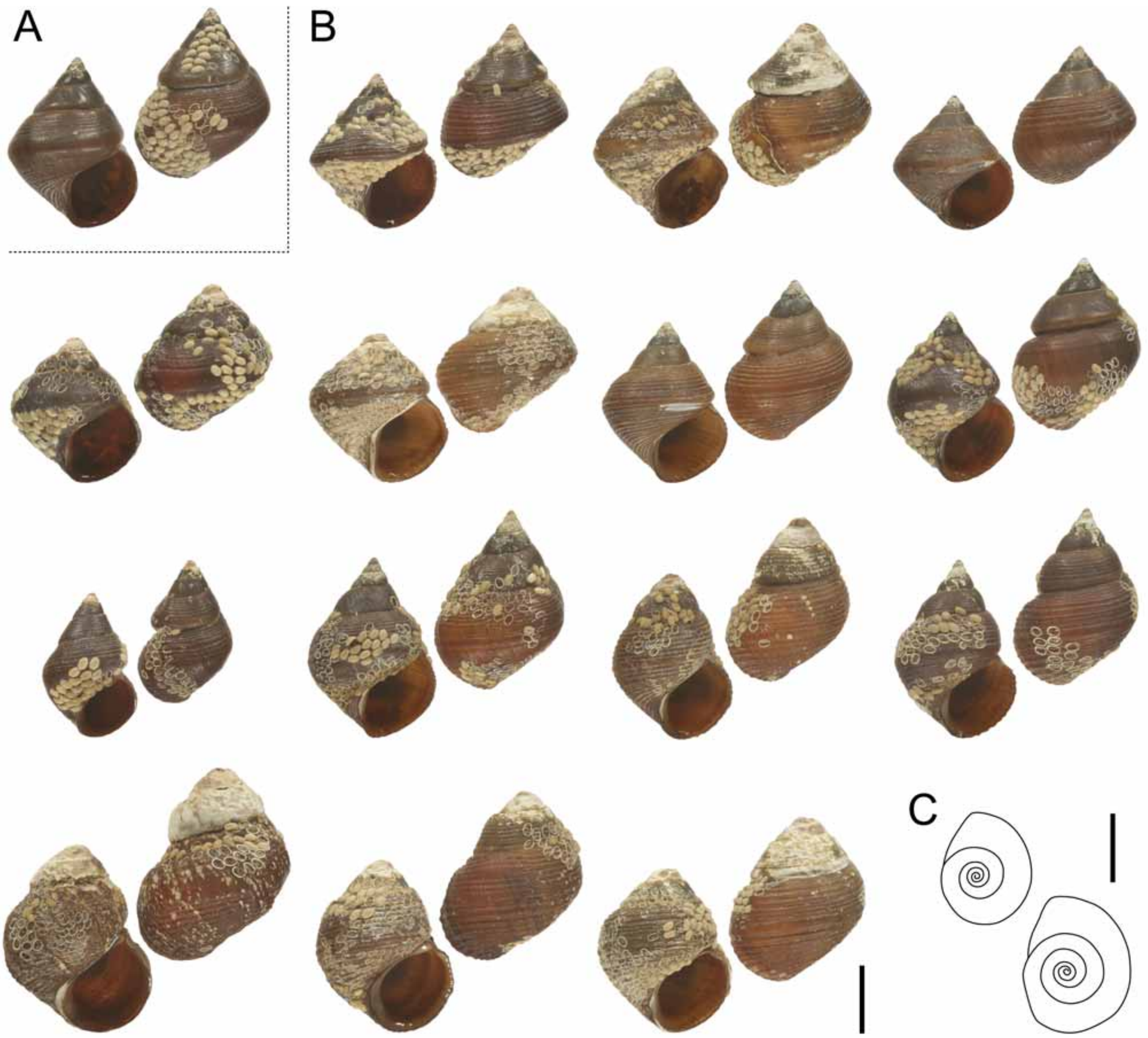

FIGURE 4. *T. sinabartfeldi* **sp. nov.** (loc. 58-99). A–D. shells, A. holotype, MZB Gst. 12.112, B. paratypes, ZMB Moll. 108315. Scale bar = 1 cm. C. opercula, ZMB Moll. 108315. Scale bar = 0.5 cm.

Distribution and habitat. South Sulawesi, lower reaches of Larona River (Fig. 1B).

On submerged logs exposed to strong current, collected in 0.1–1 m depth. As with *T. baskasti*, the inaccessibility of deeper parts of the river because of the strong currents does not allow us to estimate its depth range with any certainty.

Taxonomic remarks. The two extremely distinct shell forms encountered in this species are suggestive of two morphs or even two taxa at first glance. A comparison of the entire series revealed transitions between both forms, though, and as a consequence an attempt to unambiguously sort the sample into the two forms failed (compare Fig. 4). Radula and embryonic shell comparisons between specimens chosen from both extremes of shell form also failed to show any difference (Fig. 5) and both forms were sampled from the same

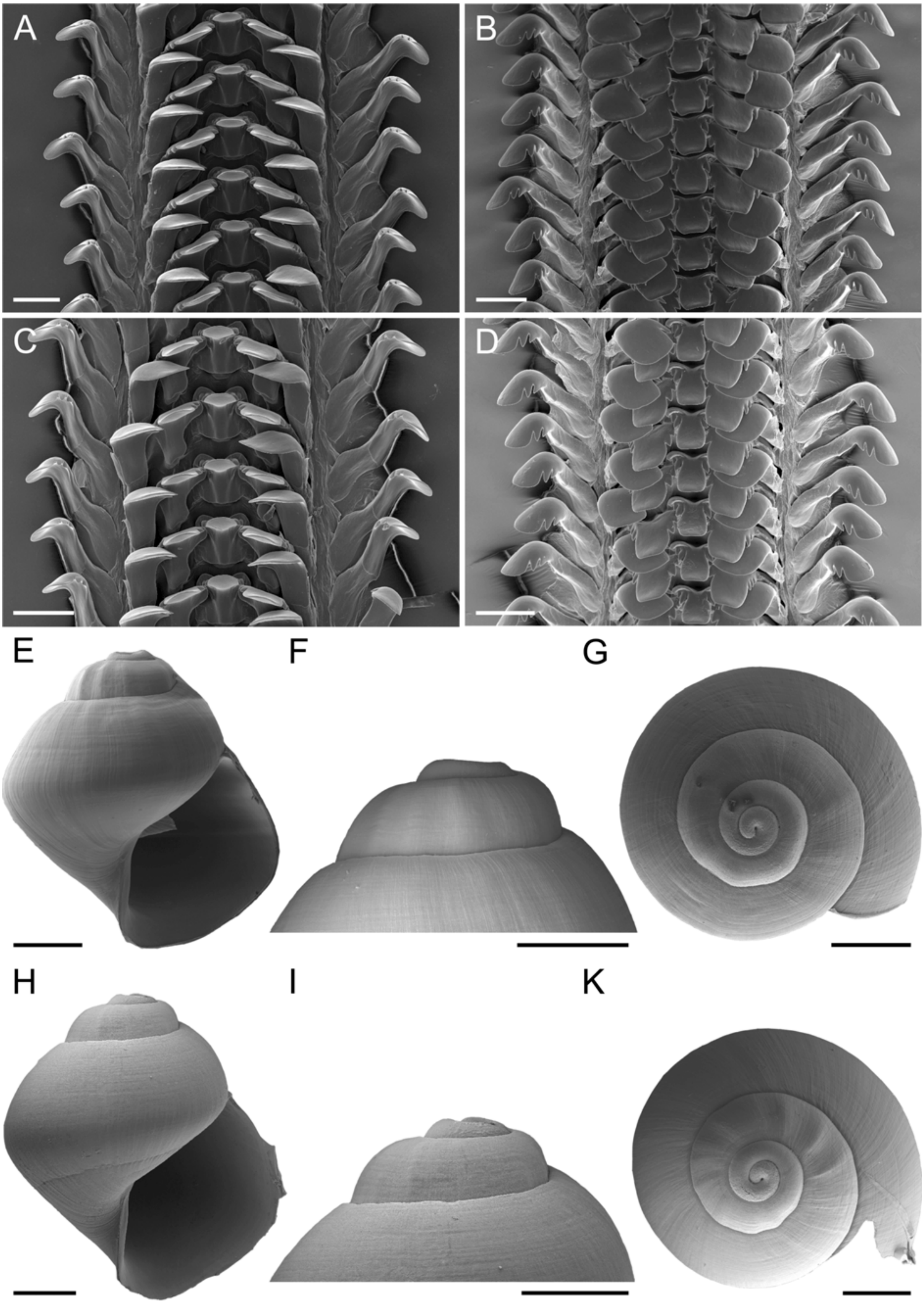

FIGURE 5. *T. sinabartfeldi* **sp. nov.**, ZMB Moll. 108315 (loc. 58-99). A–D. radula, A,B, keeled shell morph, A. segment, frontal, B. segment, apical (45°); C,D. round shell morph, C. segment, frontal, D. segment, apical (45°). Scale bar = 0.1 mm. E–K. embryonic shells, E–G, round shell morph, E. lateral view, F. apical whorls, lateral, G. apical view; H–K, keeled shell morph, H. lateral view, I. apical whorls, lateral, K. apical view. Scale bar = 0.5 mm.

log without any observable difference in distribution. We thus suggest that *T. sinabartfeldi* as described here represents one highly variable species with respect to shell form. If this variability is an expression of ecophenotypic variation remains open to speculation at this point.

Despite the high intraspecific variability in shell shape, both the subglobose and conic form of *T. sinabartfeldi* do not resemble any other species of *Tylomelania*.

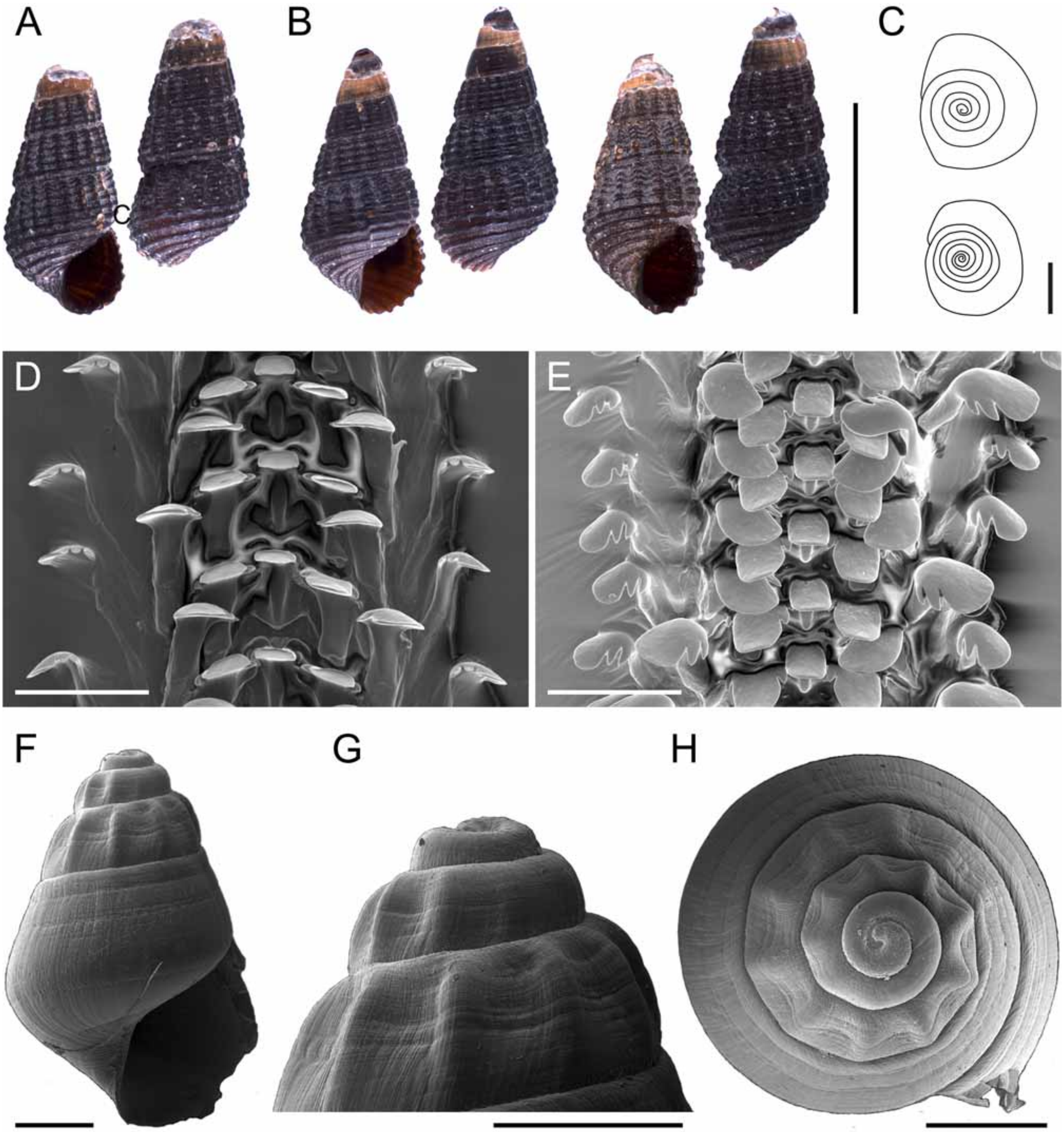

FIGURE 6. *T. hannelorae* **sp. nov.** (loc. 57-03). A–B. shells, A. holotype, MZB Gst. 12.114, B. paratypes, ZMB Moll. 190713. Scale bar = 1 cm. C. opercula, ZMB Moll. 190713. Scale bar = 1 mm. D–E. radula, ZMB Moll. 190713. D. segment, frontal, E. segment, apical (45°). Scale bar = 0.1 mm, F–H. embryonic shells, ZMB Moll. 190713. F. lateral view, G. apical whorls, lateral, H. apical view. Scale bar = 0.5 mm.

***Tylomelania hannelorae* sp. nov.**

Type material. Indonesia, Sulawesi, Lake Mahalona, loc. 56-03: Holotype (Fig. 6A; 11.8 mm x 5.5 mm), MZB Gst. 12.114; paratypes (Fig. 6B), MZB Gst. 12.115, n=3; ZMB Moll. 190713, n=5.

Etymology. The new species has been named *hannelorae* in honour of Hannelore Glaubrecht, for her emotional participation in our Sulawesi research.

Description. Shell (Fig. 6A,B): Small, dark brown, elongate conic, spire angle 11–17°. Top whorls in adult specimens always corroded to a varying degree, 3–5 remaining whorls, can reach up to 13.9 mm (Tab. 2). Axial and spiral ribs form reticulated pattern. Aperture oval, pointed at top and slightly siphonated at base. Columella and interior dark brown.

External morphology: Headfoot black, mantle edge serrated to a varying degree.

Operculum (Fig. 6C): ovate, last whorl strongly inflated, multispiral with 10 whorls.

Radula (Fig. 6D,E): 28–44 rows, 2.1–3.2 mm long, on average 13.7 teeth per mm (n=5). Central tooth with very large and elongate squarish major denticle and one minor denticle on each side. Glabella narrow, with convex base. Lateral teeth with very much enlarged squarish major denticles and one minor denticle on each side. Marginal teeth shovel-like, inner and outer marginals with three denticles each, the outermost ones considerably wider than the inner ones.

Reproductive biology: Brood pouch contains 1–2 embryos, their size can reach 3.1 mm (Tab. 3).

Embryonic shells (Fig. 6F–H): Ovate-conic, with strong axial ribs emerging on the 2^{nd} to 3^{rd} whorl and fading on the 5^{th} whorl. Shallow, widely spaced spiral ribs emerge on 3^{rd} to 4^{th} whorl (Tab. 3).

Distribution and habitat. South Sulawesi, Lake Mahalona, cape on NW shore (Fig. 1B).

This species was collected on rocks in shallow water (less than 0.5 m depth).

Taxonomic remarks. *T. hannelorae* is the smallest species within the Malili lakes species flock. Its size in combination with the reticulate shell sculpture generally can serve to distinguish it unambiguously from all other species in the system. While *T. hannelorae* might be mistaken for subadult specimens of *T. confusa* Rintelen, Bouchet & Glaubrecht, 2007, at first glance, the shell corrosion of the upper whorls characteristic for older animals will allow identifying any specimen as a fully grown adult.

Molecular phylogeny. The topology of the 16S ML phylogram based on 851 bp of mitochondrial 16S rDNA (Fig. 7) is basically identical to the tree presented in Rintelen *et al.* (2004) except for the inclusion of two of the new species described here, *T. baskasti* and *T. sinabartfeldi* (all attempts to sequence *T. hannelorae* failed). Both species belong to a clade of smooth-shelled or spirally-ribbed taxa (clade Malili 2, compare Rintelen *et al.* 2004, 2007), where they form a poorly supported subclade which is sistergroup to all remaining species of clade Malili 2 but for one individual of *T. sarasinorum* (Kruimel, 1913) from the outlet bay of Lake Towuti clustering with *T. baskasti* and *T. sinabartfeldi*. While the three haplotypes of *T. sinabartfeldi* are identical, *T. baskasti* appears paraphyletic with an intraspecific sequence divergence of 0.6% (p-distance).

Discussion

Species diversity in the Malili lakes. The gastropod species flock of *Tylomelania* stands out as the second most diverse ancient lake radiation within a single genus after the Tanganyikan *Lavigeria* (Rintelen *et al.* 2007). If endemic species diversity of molluscs per area is considered, the lakes are second only to Lake Ohrid. The addition of the three new taxa described here provides further evidence for the exceptional scope of this radiation.

While two of the new species are from the Larona River, which is draining the entire Malili lake system, these species are nevertheless subsumed with the truly lacustrine taxa here. Their shell morphology bears more resemblance to that of the other lacustrine taxa than to the widely occurring riverine species and, more importantly, the molecular phylogeny shows them to be part of the lake radiation.

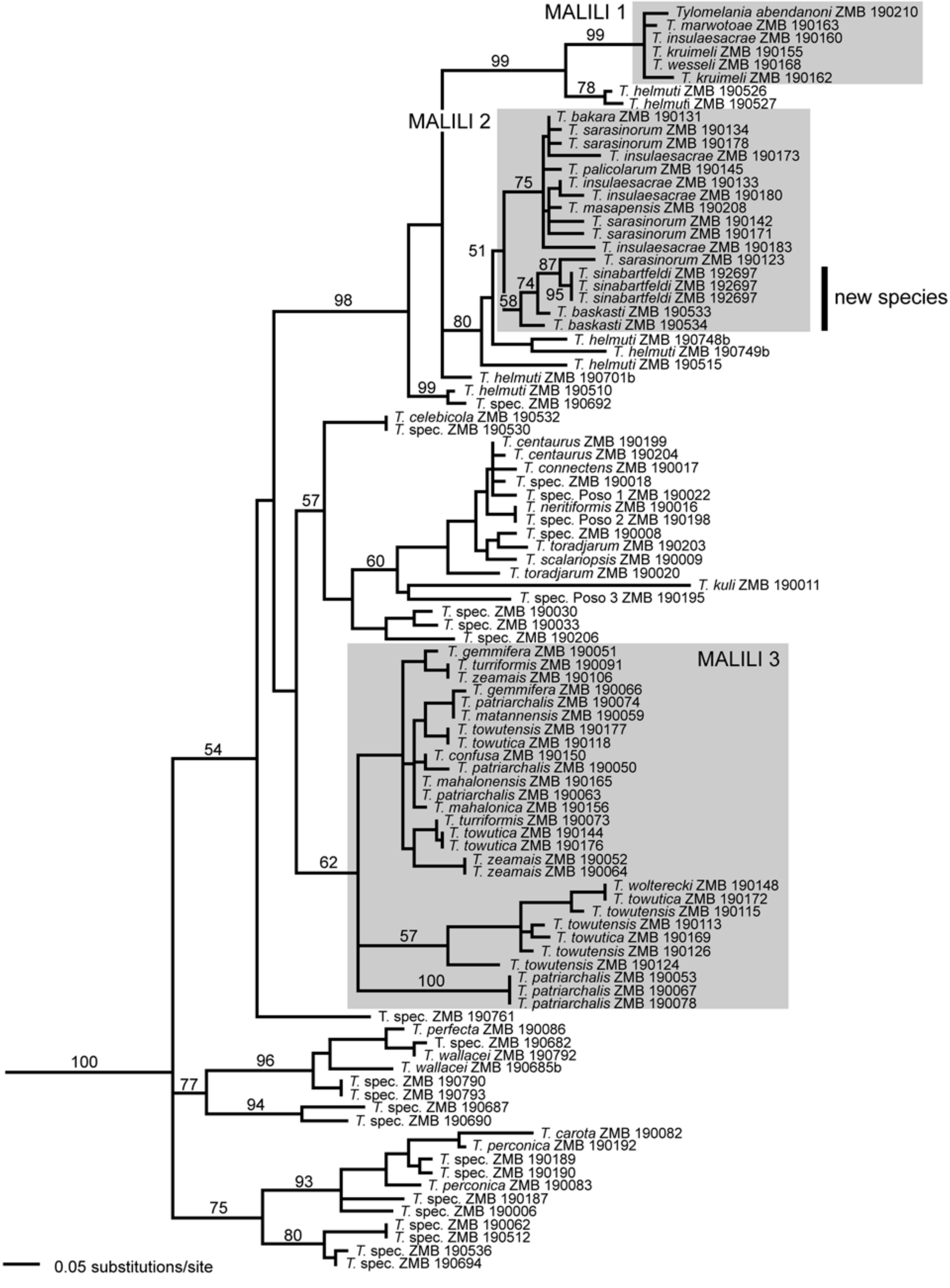

FIGURE 7. Molecular phylogeny of *Tylomelania*. Maximum Likelihood phylogram based on 851 bp of mitochondrial 16S rDNA (outgroup not shown). Malili lake species are marked by grey boxes, the position of the new species is indicated by a black bar. Numbers on branches are ML bootstrap values.

The third new species, *T. hannelorae*, occurs in Lake Mahalona and was previously overlooked because of its small size. Lake Mahalona harbours nine species of *Tylomelania*, thus, six of which are endemic to the lake. Considering that Lake Mahalona has a size of only 24 km², this seems a rather remarkable degree of endemism.

Evolution of the lacustrine species flock. The new species provide interesting new insights into several aspects of the evolution of the Malili lakes species flock. The fact that *T. baskasti* and T. *sinabartfeldi* together with a specimen of *T. sarasinorum* form the sister group to all other species in one of the three Malili lake clades in molecular phylogeny might indicate that this species group owes its origin to a lake colonization from the Larona River area, or alternatively may point towards a colonization of the Larona River from Lake Towuti. The molecular data presented here do not allow distinguish between both hypotheses, but the close link between the lacustrine species of Lake Towuti and the newly discovered Larona River taxa certainly warrants a detailed investigation based on more samples. Particularly interesting is the grouping of a haplotype of the Lake Towuti species *T. sarasinorum* with the two riverine taxa suggestive of introgression, which has been suspected to play a major role in the evolution of the Malili lakes species flock before (Rintelen *et al.*, 2007; Glaubrecht & Rintelen, in press).

Two of the new species, *T. sinabartfeldi* and *T. hannelorae*, have a highly specialized radula which is typical for hard substrate, particularly rock dwellers, in *Tylomelania* (Rintelen *et al.* 2004, 2007; Glaubrecht & Rintelen in press). While *T. hannelorae* occurs on rock, all specimens of *T. sinabartfeldi* have been collected from wood. *T. baskasti* in contrast has an unspecialized radula characteristic of riverine taxa or some lacustrine soft substrate dwellers (Rintelen *et al*. 2007; Glaubrecht & Rintelen in press). Nevertheless, even this species may be considered specialized as it occurs exclusively on soft substrates.

Radula shape, substrate specialization and the tolerance of a strong current of the Larona River species *T. sinabartfeldi* closely resemble that of *T. wesseli* Rintelen, Bouchet & Glaubrecht, 2007. *T. wesseli* is endemic to the Tominanga River, which connects two of the Malili lakes, Lake Mahalona and Lake Towuti. This finding not only suggests parallel evolution in a similar environment, but also emphasizes that the rivers within the lake system, and according to the data presented here also Larona River, rather represent fast-flowing parts of the lakes than a typical riverine environment for the snails. This could also be interpreted as evidence for a long existence of the present-day drainage system.

Conservation aspects. All three new species seem to have a rather narrow distribution range. *T. hannelorae* was found at one cape in Lake Mahalona only, while the two Larona River species were collected within a ca. 1.5 km stretch of the river. Due to the inaccessibility of the upper reaches of the river, both species may actually occur further upstream, but two hydroelectric dams build since the 1960s will certainly limit their potential range in this direction to not more than eight kilometers. In its lower reaches the Larona River becomes rather more sluggish and the two species apparently do not tolerate this pronounced change in habitats. The local endemism of the three new species renders them potentially vulnerable to extinction through habitat destruction. This danger is most eminent for the Larona River species, as a third large hydroelectric dam is currently under construction less than 3 km above the uppermost sampling station of the two taxa. So far the construction related environment degradation through e.g. an increased sediment load does not seem to have had severe effects; at least the population of *T. sinabartfeldi* was still observed to prosper (Rainer Masche, pers. comm. 2007).

Acknowledgements

We are very grateful to Ristiyanti Marwoto (MZB) for the immense support in arranging the field trips of 1999 and 2003, when the material studied here was sampled. We also thank LIPI (Indonesian Institute of Sciences) for the permit to conduct research in Indonesia. Invaluable support was experienced from INCO at

Soroako, Lake Matano. Many thanks go to Claudia Dames, Jutta Simonis and Silke Tenner (ZMB) for their assistance in the collection of morphological data. We thank Martin Haase and an anonymous referee for their comments which helped to improve this paper. This study was made possible through funding from the Deutsche Forschungsgemeinschaft (DFG) through grants GL 297/1-1 and GL 297/7-1.

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