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

THOMAS VON RINTELEN* & MATTHIAS GLAUBRECHT

*Museum für Naturkunde der Humboldt-Universität zu Berlin, Invalidenstraße 43, D-10115 Berlin, Germany
*Corresponding author: thomas.rintelen@museum.hu-berlin.de

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 this species flock to be the result of 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 also the very small size of the species. 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 show a high degree of habitat specialization while the third taxon, one of the Larona River species, is basal to an entire clade of the lake species. The local endemism of the Larona River species in particular makes them highly vulnerable to extinction caused by habitat destruction.

Keywords: 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 of 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. Bouche (1995) considered the number of 23 originally described species from both Lake Poso and the Malili lakes (Sarasin & Sarasin 1897; 1898; Kruimel 1913) to be too high and suggested that only twelve biospecies occur in all ancient lakes of Sulawesi, while 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 an hitherto unparalleled coverage of the system. As a first result from the analysis of this new material we here describe three new species lacking from the recent revision of the Malili species flock and discuss their importance for the understanding of evolution in the entire radiation.

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% ethanol and have been deposited in the Museum Zoologí 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. 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 radula was 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.

The molecular methods used in this study have been described in detail by Rintelen et al. (2004).

**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.

**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.
FIGURE 2. *T. baskasti*. 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. operculum, ZMB Moll. 190533. Scale bar = 0.5 cm.

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.
Description

Shell (Fig. 2a,b). Medium sized to large, brown, elongately 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. 2c). 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 v 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.

Reproductive biology. Brood pouch contains 4-12 embryos, their size can reach 8.4 mm (n=5) (Tab. 3). Embryonic shells (Fig. 3c-e). Elongately-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 (0.1-0.5m) in less turbulent zones at the river bank. 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.
FIGURE 4. *T. sinabartfeldi* (loc. 58-99). a-d. shells, a. holotype, MZB Gst. 12.112, b. paratypes, ZMB Moll. 108314. Scale bar = 1 cm. c. operculum, ZMB Moll. 108314. Scale bar = 0.5 cm.

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.

<table>
<thead>
<tr>
<th>Species</th>
<th>juv. (N)</th>
<th>h max (mm)</th>
<th>whorls (N)</th>
<th>axial ribs (N)</th>
<th>ax 3rd (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. baskasti</em></td>
<td>1-4</td>
<td>5.7-8.4</td>
<td>5.5-6.25</td>
<td>25-30</td>
<td>8-9</td>
</tr>
<tr>
<td></td>
<td>2.5 ±1.05</td>
<td>7.16 ±1.062</td>
<td>6.0 ±0.35</td>
<td>27.8 ±2.22</td>
<td>8.8 ±0.50</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td><em>T. sinabartfeldi</em></td>
<td>11-67</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>T. hannelorae</em></td>
<td>1-2</td>
<td>2.4-3.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.3 ±0.58</td>
<td>2.70 ±0.361</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The shell shape and radula of *T. baskasti* is similar to that of other riverine species of Sulawesi such as e.g. *T. robusta* Martens, 1897. Its shell in particular is nevertheless sufficiently distinct to distinguish it unambiguously from those taxa and the molecular data clearly confirm its relationship to the Malili lakes species flock (compare also below, Discussion).

*Tylomelania sinabartfeldi* spec. nov.

**Type material**

Indonesia, Sulawesi, Larona River: Holotype (Fig. 4a; 25.0 mm x 19.0 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.

**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 whors in adult specimens always corroded to a varying degree, 3-6 remaining whors, 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.

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

Operculum (Fig. 4c). Roundly-ovate, last whorl inflated, multispiral with 4-5 whors.

Radula (Fig. 5a,b), 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. 5c-e). Conic, with strong axial ribs emerging on the 2nd to 3rd whorl and fading on
the 5th whorl. Shallow, widely spaced spiral ribs emerge on 3rd to 4th whorl. (Tab. 3).

**Distribution and habitat**

South Sulawesi, lower reaches of Larona River (Fig. 1b).

On submerged logs exposed to strong current, collected in 0.1-1m. 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. Radula comparisons between specimens chosen from both extremes of shell form also failed to show any difference and both forms were sampled from the same 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. Whether this variability is an expression of ecophenotypic variation remains open to speculation at this point.

---

**Tylomelania hannelorae** spec. 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, elongately 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. Body coiled in # whorls.

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 elongately squarish major denticles and one minor denticles on each side. Glabella narrow, with convex base. Lateral teeth with very much enlarged squarish major denticles and one 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.

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 2nd to 3rd whorl and fading on the 5th whorl. Shallow, widely spaced spiral ribs emerge on 3rd to 4th whorl. (Tab. 3).

**Distribution and habitat**

South Sulawesi, Lake Mahalona, NW shore, cape (Fig. 1b).

This species was collected on rocks in shallow water (~0.5m).
Taxonomic remarks

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

**FIGURE 6.** *T. hannelorae* (loc. 57-03). a-c. shells, a. holotype, MZB Gst. 12.114, b. paratypes, ZMB Moll. 190713. Scale bar = 1 cm. 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.
Discussion

Species diversity in the Malili lakes

The gastropod species flock of *Tylomelania* stands out as the second 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.

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 24km², this seems a rather remarkable degree of endemicity.

Evolution of the lacustrine species flock

The new species provide interesting new insights into several aspects of the evolution of the Malili lakes radiation. Most importantly, the basal position of *T. baskasti* in one Malili lake clade in the molecular phylogeny might indicate that this species group owns its origin to a lake colonization from the Larona River area.

Two of the new species, *T. sinabartfeldi* and *T. hannelorae*, have a highly specialized radula which is typical for hard substrate, particularly rock dwellers. While *T. hannelorae* occurs on rock, all specimens of *T. sinabartfeldi* have been collected from wood.

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 c. 1.5km 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.

This study was made possible through funding from the Deutsche Forschungsgemeinschaft (DFG) through grants GL 297/1-1 and GL 297/7-1.
References


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

THOMAS VON RINTELEN & MATTHIAS GLAUBRECHT