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Preliminary checklist of sailfin silversides (Teleostei: Telmatherinidae) in the Malili Lakes of Sulawesi (Indonesia), with a synopsis of systematics and threats

Vorläufige Checkliste der Sonnenstrahlfische (Teleostei: Telmatherinidae) der Maliliseen Sulawesis (Indonesien), mit einer Übersicht zu Systematik und Bedrohung

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Summary: The ancient Malili Lakes in Sulawesi harbor an adaptive radiation of sailfin silversides (Teleostei: Atheriniformes: Telmatherinidae). This radiation is characterized by local endemism either to basins of Lakes Towuti, Mahalona and Lontoa (Wawontoa) or to that of Lake Matano, and by spectacular male color polymorphisms. Based on recent surveys, we report a previously undetected diversity of steam-dwelling Telmatherinidae, inhabiting a wide range of the lake system's rivers and streams and additional adjacent catchments. We provide a preliminary checklist of Telmatherinidae in the Malili Lakes system, including surrounding catchments, and add records of three yet undescribed lacustrine *Telmatherina* from Lake Matano. Distribution patterns of Lake Matano's *Telmatherina* are provided in detail, based on eight sampling locations around the lake's shoreline. Moreover, we record an increased number of color morphs in five known *Telmatherina* and summarize color polymorphisms of the species-flock. As this radiation is used as model system to address questions concerning speciation and maintenance of color polymorphisms, we provide a summary of taxonomic, systematic, ethological and evolutionary biological knowledge regarding telmatherinids, give a brief overview about the environmental settings, and discuss the serious threats endangering this endemic ichthyofauna.

Key words: Telmatherinidae, adaptive radiation, Malili Lakes system, Sulawesi, diversity, threats

Zusammenfassung: Die Maliliseen Sulawesis beherbergen eine adaptive Radiation von Sonnenstrahlfischen (Teleostei: Atheriniformes: Telmatherinidae). Diese Radiation zeichnet sich durch lokalendemische Verbreitungsmuster einerseits in den Seen Towuti, Mahalona und Lontoa (Wawontoa) oder andererseits im Matanosee, sowie durch spektakuläre Farbpolymorphismen aus. Basierend auf kürzlich erfolgten Felderfassungen stellen wir eine bislang unbekannte Diversität bachbewohnender Telmatheriniden vor, die in weiten Bereichen der Flüssen und Bächen des Seensystems sowie angrenzenden Einzugsgebieten verbreitet ist. Wir stellen eine vorläufige Checkliste der Telmatheriniden des Maliliseen-Systems einschließlich umgebender Einzugsgebiete auf und fügen Nachweise von drei bislang unbeschriebenen lakustrinen *Telmatherina* aus dem Matanosee hinzu. Verbreitungsmuster der Manatosee-*Telmatherina* werden detailliert aufgezeigt, basierend auf acht Sammelstellen rings um die Uferzone des Sees. Außerdem weisen wir eine höhere Anzahl Farbmorphen für fünf bekannte *Telmatherina* nach und fassen die Farbpolymorphismen des Artenschwarmes zusammen. Da diese Radiation als Modellsystem dient um Fragen zu Artbildung und Aufrechterhaltung von Farbpolymorphismen nachzugehen, geben wir eine Zusammenfassung über den taxonomischen, systematischen, verhaltensbiologischen und evolutionsbiologischen Forschungsstand über Telmatheriniden sowie einen kurzen Überblick über die naturräumlichen Bedingungen und diskutieren die ernsthaften Bedrohungen, die diese endemische Fischfauna gefährden.

Schlüsselwörter: Telmatherinidae, Adaptive Radiation, Maliliseen, Sulawesi, Diversität, Bedrohung

1. Introduction

Over the last 109 years a diversity of small, atheriniform freshwater fishes has been described from the island of Sulawesi (Indonesia), accounted to the family of sailfin silversides (Atheriniformes: Telmatherinidae). Only one out of the island's 16 species is found in streams of its south-western branch, the remaining 15 are endemic to the Malili Lakes system in Central Sulawesi (Kottelat 1990a, 1991). The chance to study evolution of organismic diversity within an outstanding, compact but diverse model system characterized by different degrees of isolation, has attracted recently several research groups to this system. Apart from sailfin silversides, the endemic invertebrate radiations of crustaceans (atyid shrimps and parathelphusid crabs) and pachychilid snails (von Rintelen and Glaubrecht 2003; von Rintelen and Glaubrecht 2005; von Rintelen et al. 2004) as well as the predominantly endemic diversity of diatoms (Bramburger et al. 2004, 2006) are under investigation.

Aim of the present paper is to (1) summarize present knowledge about telmatherinid taxonomy, systematics and the Malili Lakes system and (2) to provide an overview about major patterns of diversity in the Malili Lakes sailfin-silversides radiation. It is intended as a guide to upcoming work dealing with evolutionary processes of this adaptive radiation, and to drawing attention to serious threats endangering this unique diversity. It is not aimed to serve taxonomic purposes, for which more detailed examinations and a sophisticated concept of recognizing "species" within this obviously still radiating flock are required.

1.1. The Malili Lakes system

The Malili Lakes system is located in Central Sulawesi (the former Celebes) (fig. 1), consisting of five interconnected lakes. The three major lakes Matano, Mahalona and Towuti are large, deep ancient lakes of tectonic origin (Abendanon 1915a, b, Brooks 1950, Haffner et al. 2001). Lake Matano is with 590 m the deepest lake in Southeast Asia and the eighth deepest lake in the world (Hutchinson 1957). Geologically, it is a tectonic graben lake of the still active Matano fault zone (Ahmad 1977).

Lakes Matano, Mahalona and Towuti are arranged along a cascading chain with connecting rivers. Lake Matano is a steep-sided graben lake (Ahmad 1977), located 396 m above sea level (fig. 1). It is drained at its eastern corner by the extremely steep River Petea to L. Mahalona, descending 72 m of altitude along the river's total length of about 9.5 km (Abendanon 1915a, Kottelat 1991, own observations). According to our own ground checks and all accessible topographic maps (1: 50.000, Lembar 2213-13, 34) there is no major waterfall in River Petea. The river is located within a very steep valley and descends along a sequence of rapids, riffles, small falls, pools and backwaters until about 1 km ahead of L. Mahalona, where it becomes comparatively deep and calm. After Lake Mahalona, the flow continues as the overall wide and slow-flowing River Tominanga which has only one series of rapids and covers a 17 m drop in elevation before reaching L. Towuti after about 8.1 km. With approximately 560 km^2 of surface area, L. Towuti is the largest lake in Sulawesi (Haffner et al. 2001), but is with 203 m less deep than L. Matano. It is drained at its south-western corner to the Gulf of Bone by River Larona (= R. Malili).

The two small satellite lakes Lontoa (or Wawontoa; local spelling Lantoa) and Masapi are probably not of tectonic origin (Abendanon 1915a). According to Abendanon (1915b), the outflow of L. Lontoa is located at its northern corner, draining the lake to River Tominanga. In contrast, modern topographic maps based on aerial photographs show a direct connection from its southern end to L. Towuti by a small stream (1: 50.000, Lembar 2213-13, 34). Lake Masapi has a crater lake appearance, although there is no evidence for volcanism in the area (Giesen et al. 1991). It drains to River Larona, without a direct connection to the large lakes.

1.2. Discovery of the Lakes

Fritz and Paul Sarasin, two Swiss geologists and naturalists, were the first "western" visitors who explored the greater area of Lake Matano (as "Matana") and Towuti in early 1896 (Sarasin 1886). They provided a preliminary map and were the first to collect telmatherinids, which later were reported by Boulenger (1897). The Dutch geographer and geologist E. C. Abendanon explored these two lakes in 1909 and discovered Lakes Mahalona, Lontoa and Masapi (Abendanon 1915a, b). In addition, he provided the first hydrological data of the lakes as well as detailed maps of the complete lake system. Noteworthy, Abendanon precisely draw the course of River Petea (as "Patea"), which delimits for most of its stretch the north-western extreme of the area mapped in Abendanon (1915b). In the middle of its flow, Abendanon (1915b) indicated a waterfall. However, there is no indication in the map pointing to anything like a major waterfall with a drop of dozens of meters as recently claimed (Roy et al. 2004).

Brooks (1950) reviewed knowledge about the Malili Lakes and their species flocks and speculated about reasons for the patterns of their organism's distribution. Based on Abendanon's map, he focussed on the separating effect of waterfalls along River Petea, stating "…the relatively short Patea River which drains into Lake Mahalona descends 72 m., part of this drop occurring as waterfall." (Brooks 1950, p. 167).

Recent investigations of the lake's water chemistry (Giesen et al. 1991) and L. Matano's limnology (Haffner et al. 2001) underpinned that all five lakes are ultraoligotrophic, with different levels of deficiency in various trace elements.

1.3. Telmatherinid discovery, systematics and evolution

Boulenger (1897) described the first sailfin silverside as *Telmatherina celebensis*, and placed it in Atherinidae. Both syntypes originate from the collection by P. and F. Sarasin in 1896 at Lake Towuti (see Kottelat and Suttner 1988). Based on material gathered in 1909 by Abendanon at Soroako, Lake Matano, Weber (1913) described *Telmatherina abendanoni* and mentioned two additional specimens of *Telmatherina* from Lake Towuti that differed from *T. celebensis* in their number of anal fin rays; these two specimens were referred to as "Bonti" by local inhabitants. In 1922, Weber and de Beaufort described *Telmatherina bonti* based on these two specimens.

Aurich (1935) revised telmatherinids based on material collected by Woltereck's "Wallacea Expedition", redescribed *Telmatherina bonti, T. celebensis* and *T. abendanoni* based on detailed morphometric and meristic analyses, and described four new species which he placed in the new genus *Paratherina* (*P. woltereckí*, *P. labiosa*, *P. striata*, *P. cyanea*). He also provided a key to all telmatherinid species known at that time, but did not designate a type species for *Paratherina*. Aurich (1935) noticed that fin coloration is variable in *Telmatherina* from Lake Towuti (not separated to *T. bonti* / *T. celebensis*), with yellow, bluish or red margins of first and second dorsal as well as anal fins. In addition, he provided a drawing of a single male specimen of a yet undescribed *Telmatherina* from L. Matano, characterized by fleshy lips (*Telmatherina* sp. "thicklip"; see below). Unfortunately, most of Aurich's material, including all *Paratherina* type material, was destroyed in the Bavarian State Collection of Zoology, Munich, Germany (ZSM) during Second World War (Kottelat 1990a, b). Ahl (1936) described with *Telmatherina ladigesi* the first telmatherinid from outside the Malili Lakes system. The three specimens available to him were collected by Ladiges and Arnold (without collection date) from a rivulet of Makassar's hinterland. Ahl provided a short key for other *Telmatherina* species, but did not discuss to family assignment of the genus.

Brooks (1950) included the Malili Lakes into his review of "Speciation in Ancient Lakes", referred to the lacustrine Telmatherinidae as a "species flock" and discussed their potential origin and history as a consequence of isolation by tectonic processes and limited dispersal capabilities due to strongly isolating watersheds and waterfalls. He also discussed to possibility of intralacustrine speciation within Lakes Towuti and Matano.

In 1958, Munro established the family Telmatherinidae without diagnosis (Munro 1958), including the Australian *Quirichthys stramineus* Whitley (currently placed in *Craterocephalus*; Crowley and Ivantsoff 1992) and diagnosed it later using as characters "position of first dorsal fin relative to ventral-fin" and "elongated fin rays in second dorsal and anal fin" to distinguish Telmatherinidae from Pseudomugilidae and Melanotaeniidae (Munro 1967). Kottelat (1990a, 1991) recognized and revised the family based on new material, and provided a "tentative diagnosis" (1990a, p. 228-229) of the family, distinguishing it from Melanotaeniidae, Atherinidae, Dentatherinidae, Pseudomugilidae, Bedotiidae, Isonidae and Phallostethidae, which is partly in discordance with Munro's diagnosis and refers substantially to osteological characters provided by personal communication from W. Ivantsoff. According to external morphology, Kottelat (1990a) diagnosed Telmatherinidae as medium to large atherinoids (=suborder Atherinoidei within Atheriniformes) exhibiting strong sexual dimorphism with dull brown, short-finned females and yellow, blue or red male body and fin coloration and very long first and second dorsal and anal fins of males.

Kottelat (1990a, 1991) described eight new telmatherinid species, including two of the newly erected genus *Tominanga* (*T. aurea, T. sanguicauda*) and six species of *Telmatherina* endemic to Lake Matano (*T. antoniae*, *T. obscura*, *T. opudi*, *T. prognatha*, *T. sarasinorum*, *T. wahjui*). *Tominanga* is defined by its slender body and shape of pelvic fins which form a funnel-shaped ovipositor in females. He (Kottelat 1990a) validated the genus *Paratherina* from Lakes Towuti, Mahalona and Lontoa ("Wawontoa") by designation of a neotype for *P. woltereckí* and designation of *P. woltereckí* as type species. The genus is defined by scale counts and in having two rows of scales below eye (*vs.* one in *Telmatherina* and *Tominanga*). However, Kottelat's redescription of *Paratherina* species was restricted severely by limited material, i. e. a total of five juvenile specimens (2 specimens of *P. cyanea*, 2 of *P. labiosa*, and the neotype of *P. woltereckí*; sizes of only 9.6-43.2 mm SL).

Kottelat's descriptions (1990a, 1991) include male color polymorphisms in several Telmatherinids. He reported blue/yellow male morphs in *Telmatherina antoniae*, *T. celebensis*, *T. sarasinorum* and *T. wahjui*, and red/yellow male morphs in *Tominanga aurea*. However, he pointed out (Kottelat 1990a, 1991) that his review does not pretend to be complete with respect to total coverage of Telmatherinidae. His purpose was to make names available (Kottelat 1991) based on the material available to him. Consequently, he forecasted that parts of his work would have to be revised in the light of upcoming further work, especially with respect to L. Matano's telmatherinids (Kottelat 1991) and *Paratherina* (Kottelat 1990a).

In a series of popular articles, Kottelat (1989a, b, c, 1990c, 1992) provided additional information about the Lake's geographic settings and their freshwater fauna. Kottelat (1989b) illustrated yellow and blue morphs of *T. celebensis*. Later he (Kottelat et al. 1993) included all known telmatherinids in a guidebook, provided drawings and illustrated the most important characters. There, the first color pictures of *T. obscura* were made available and color pictures of some preserved material displayed only in black and white before (Kottelat 1990a, 1991) were included.

Saeed and Ivantsoff (1991) investigated osteological characters of *Pseudomugil helodes* with respect to Pseudomugilidae, Phallostethidae, Atherinidae, Notocheiridae, Isonidae, Dentatherinidae, Melanotaeniidae, Bedotiidae and *Telmatherina celebensis*, *T. bonti* and *T. ladigesi* as representatives of Telmatherinidae. They concluded that *P. helodes* from islands Batanta and Misool off New Guinea is most closely related to Telmatherinidae, but sufficiently distinct to be placed into a new genus, *Kalyptatherina*.

Saeed et al. (1994) as well as Dyer and Chernoff (1996) investigated morphological relationships among atheriniform families, supporting either family (Saeed et al. 1994) or tribe (Dyer and Chernoff 1996) rank for Telmatherinidae. Telmatherinid material in Dyer and Chernoff (1996) was restricted to *T. ladigesi*, diminishing their argumentation to place Telmatherinini + Pseudomugilini together with Melanotaeniinae and Bedotiinae into one single family Melanotaeniidae (for which, following Aarn et al. 1998, Pseudomugilidae would be the correct name).

Aarn and Ivantsoff (1997) presented a phylogenetic analysis of Melanotaeniidae based on 46 morphological characters, including the telmatherinids *Kalyptatherina helodes* and *Telmatherina ladigesi* as well as *Paratherina woltereckı*, *Telmatherina abendanoni*, *T. antoniae*, *T. bonti*, *T. celebensis*, *T. opudi*, *T. sarasinorum*, *T. wahjui*, *Tominanga aurea* and *T. sanguicauda*. They presumed monophyletic Telmatherinidae and found the family together in a polytomy with Atherinoidae, Phallostethidae, Atherinidae, Pseudomugilidae and Melanotaeniidae to be the sistergroup of Atherinopsidae and Notocheiridae.

Aarn et al. (1998) analyzed intra-telmatherinid relationships on generic level compared to Atherinidae, Melanotaeniidae and Pseudomugilidae. Based on 26 morphological characters and essentially the same telmatherinid material as Aarn and Ivantsoff (1997), they found support for monophyletic Telmatherinidae with sister group relationship between *Kalyptatherina* + *Telmatherina ladigesi* and all Malili Lakes telmatherinids; the clade *Telmatherina* + *Tominanga* + *Paratherina* was not resolved. Subsequently, they rediagnosed Telmatherinidae and erected the genus *Marosatherina* for *T. ladigesi*, which they found to differ substantially in several anatomical characters from the known telmatherinid genera. However, the authors state in the discussion, that monophyly of *Telmatherina* (also without *Marosatherina*) is doubtful, which might be the reason for low resolution in their generic tree. In addition to their phylogenetic work, Aarn et al (1998, p. 320) mentioned the occurrence of *Telmatherina bonti* in "creeks of the Matano basin and outside of the Malili lake basin, in Sungei Masiluk, a basin adjacent to Lake Towuti and draining eastern to the Banda sea", without providing reference. They speculated that *T. bonti* could turn out as sister species of all other *Telmatherina* or even all Malili Lakes telmatherinids.

Hadiaty and Wirjoatmodjo (2002) reported preliminary results from their field studies at Lake Matano, listing all seven described *Telmatherina* of the lake as well as one undescribed species of the genus. Moreover, they reported *T. bonti* to occur at the mouth of streams entering the lake at its northwestern corner.

Sparks and Smith (2004) combined in a phylogenetic analysis of Malagasy and Australasian rainbowfishes (Melanotaenioidei) DNA sequence data from nuclear and mitochondrial genes with morphological data. In this analysis, their single telmatherinid, *Marosatherina ladigesi*, was nested within Pseudomugilidae, comprising together the sister group to Melanotaeniidae. They conclude that Telmatherinidae should be included into Pseudomugilidae. However, missing representation of more than 94% of the described telmatherinid species as well as missing DNA sequence data for critical non-telmatherinid taxa (e.g. *Craterocephalus* (*Quirichtys*) *stramineus*), suggests that additional data should be analyzed before following this suggestion.

Roy et al. (2004) investigated mtDNA haplotype relationships of four fish families from L. Matano. They included the Matano-endemics *Oryzias matanensis* for Oryziidae, *Dermogenys weberi* for Hemiramphidae, undetermined *Glossogobius* for Gobiidae and undetermined *Telmatherina* for Telmatherinidae. Together with findings from cursory morphometric analyses they conclude that the endemic diversity of L. Matano's *Telmatherina* fulfills the criteria of an adaptive radiation. However, several parts in their argumentation cast serious doubts on their conclusions. First, discussion and conclusions of this work focus on and rest upon the assumption that L. Matano is "…separated from downstream lakes by a 72-m waterfall…" (Roy et al. 2004, p. 2), which is not supported by recent evidence (see above). Second, they state that L. Matano "...has been identified as the principal seeding source of endemic species within the Malili Lakes watershed…", citing Brooks (1950) and Haffner et al. (2001). This implicates knowledge about the flock's evolutionary history. However, none of both references provides any data on phylogenetic relationships. Third, Roy and coauthors claim that their "…16S rDNA sequences demonstrate common ancestry for each of the endemic genera in Lake Matano…" (Roy et al. 2004, p. 7). This conclusion appears premature because they did not include any species from outside L. Matano in their analysis, although all four genera are also present outside L. Matano. As a consequence, we cannot accept the principal line of evidence presented by Roy et al. (2004) although we do not disagree with their principal conclusion, i.e. that sailfin silversides of L. Matano represent a case of adaptive radiation.

Gray and McKinnon (2006) described in detail mating behavior of seven telmatherinid species from Lakes Matano (*Telmatherina antoniae*, *T. sarasinorum*, *T. wahjui*, *T.* "whitelips" (= *T.* "thicklip") and Towuti (*Telmatherina celebensis*, *Tominanga* sp., *Paratherina* sp.). They noted presence of two distinct size classes in *T. antoniae* but did not find differences in mating behavior among these. Phenotypes referred here to *Telmatherina opudi*/*T. obscura* were treated together with *T. sarasinorum* by Gray and McKinnon (2006). They also did not follow Kottelat's concept of separating two species of *Tominanga* as they found discrepancies between the descriptions and own observations. However, according to Kottelat, *T. aurea* is restricted to L. Mahalona which was not covered in that study. Gray and McKinnon (2006) concluded that mating behavior can be generalized in Malili Lakes telmatherinids, and they described common intra- and intersexual behavioral interactions.

Herder et al. (2006) investigated phylogenetic relationships of Malili Lakes telmatherinids, provided evidence for introgressive hybridization of stream phenotypes into the most diverse clade of L. Matano's telmatherinids and concluded that hybridization could have acted as a key factor in the generation of the flock's spectacular diversity. They provided genetic (mitochondrial and multilocus nuclear DNA) and morphometric evidence supporting the assumption of an adaptive radiation within L. Matano, with the original signal of monophyly masked secondarily by introgression. Herder et al. (2006) included a previously unknown diversity of riverine telmatherinids in their analyses and found strong support to divide them into three groups: (1) *Telmatherina* sp. "Petea", closely related to L. Matano's "sharpfins"; (2) *T.* cf. *bonti* "West", a separate, ancient clade; (3) all remaining *T.* cf. *bonti*, including those from Rivers Nuha, Tominanga, Malili and streams entering Lakes Matano and Towuti. They also included undescribed lake-dwelling phenotypes from L. Matano, *Telmatherina* sp. "thicklip" (= *T.* *"whitelips"* of Gray and McKinnon 2006); *T.* sp. "elongated", and *T. sarasinorum* "bigmouth" and "largehead", phenotypes differing in the eponymous characters from *T. sarasinorum* Kottelat. Moreover, they included *T.* cf. *celebensis* "Lontoa", a phenotype from L. Lontoa, closely related to *T. celebensis* from L. Towuti and Mahalona.

2. Material and methods

In surveys on telmatherinid diversity in dry season 2002 and wet season 2004, all major water bodies of the Malili Lake system were investigated by SCUBA and snorkeling observations down to 20 m (lakes), and by fishing, with focus on L. Matano. Fishing techniques applied were SCUBA- and snorkeling-aided gillnetting, electro-fishing, dip- and beach-netting. At Lake Matano, sampling was focused on six major sampling locations distributed almost equally around the lake (locations 1-6, fig. 2) and two additional sampling locations at the mouth of River Lawa (location 7) and the outlet to River Petea (location 8). Each of the six major sampling locations was sampled by two or three investigators for five to seven days both in dry season 2002 and wet season 2004. Voucher specimens are deposited in fish collections of ZSM (Zoologische Staatssammlung München), ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn), and MZB (Museum Zoologicum Bogoriense, Cibinong). SL refers to "standard length", measured from tip of snout to caudal flexure (Kottelat 1990a) (= end of hypural plate). The terms "morphotypes" and "color morphs" are used to classify telmatherinid diversity in a pragmatic way as long as no detailed descriptions are available, without referring to species concepts or claiming any kind of species status. Consequently, "morphotype" refers to a group of phenotypically similar individuals sharing consistent characters present in males and females. "Color morphs" are analogously understood as different color patterns expressed within "morphotypes"; these are defined to males only, as no female polychromatism was recorded.

Color descriptions are based on field observations directly after collection, with focus to overall coloration of body and fins. They describe patterns of general appearance but do not provide detailed characters for taxonomic purposes. The term "color morph" therefore represents a pragmatic simplification and does not reflect the complete variance present in color characters.

In Lake Matano, telmatherinids are separable in two groups of morphotypes, char-

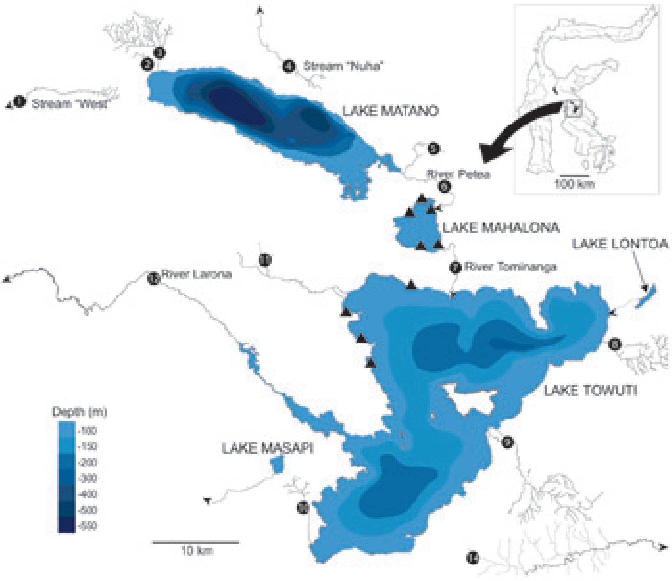


Fig. 1: The Malili Lakes system is located in Sulawesi, Indonesia. Symbols represent sampling locations of the surveys 2002 and 2004, with triangles for sampling locations at Lakes Towuti and Mahalona and black circles for locations at rivers and streams; numbers refer to table 1. © map by von Rintelen and Zitzler, modified (with permission).
Abb. 1: Das Maliliseen- System befindet sich in Sulawesi, Indonesien. Symbole markieren Sammelpunkte aus den Untersuchungsjahren 2002 und 2004. Dreiecke stehen für Sammelstellen an den Seen Towuti und Mahalona, schwarze Kreise für Probestellen an Flüssen und Bächen; die Nummerierung bezieht sich auf Tabelle 1. © der Karte liegt bei von Rintelen und Zitzler, modifiziert (mit freundlicher Erlaubnis).

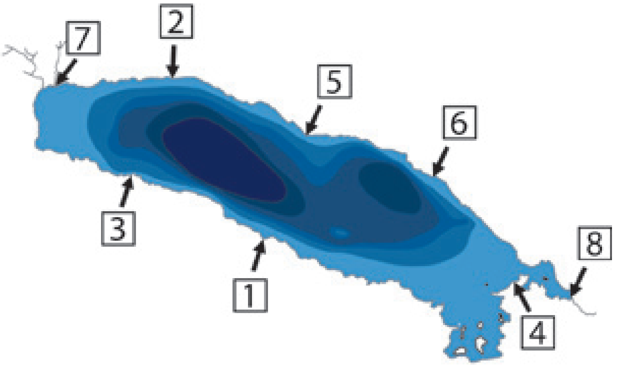
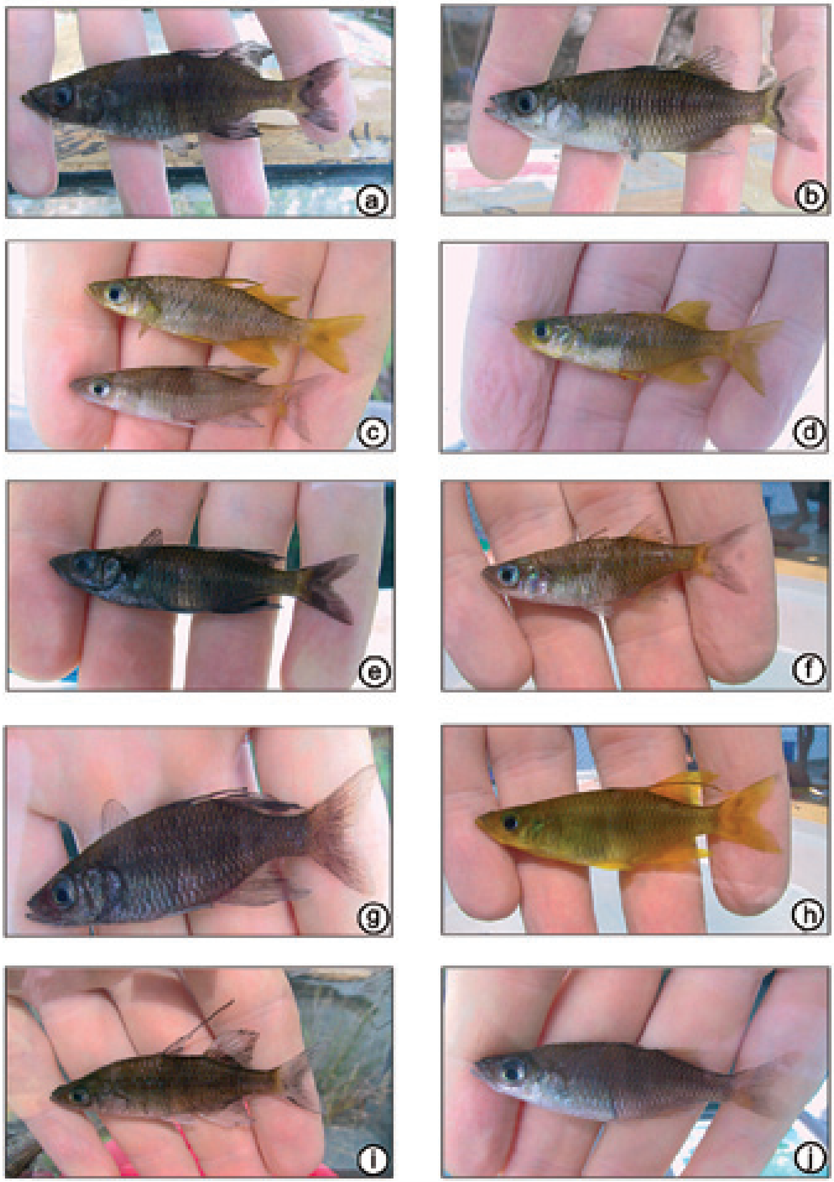


Fig. 2: The telmatherinid fauna of Lake Matano was investigated in detail at six major sampling locations (1-6) as well as at the mouth of River Lawa entering the lake at its north-western corner (7) and at the outlet area draining the lake to River Petea (8). Record of telmatherinid phenotypes is provided in table 2. © map by von Rintelen and Zitzler, modified (with permission).
Abb. 2: Die Telmatheriniden-Fauna des Matanosees wurde an sechs Hauptprobestellen (1-6) detailliert untersucht. Weitere Probestellen sind die Einmündung des Flusses Lawa am Nordwestende des Sees (7) sowie das „Outlet"-Gebiet, in dem der See in den Fluss Petea übergeht. Nachweis von Telmatheriniden- Phaenotypen findet sich in Tabelle 2. © der Karte liegt bei von Rintelen und Zitzler, modifiziert (mit freundlicher Erlaubnis).



Figs. 3a-j: "Morphotypic" and "color morph" diversity of "sharpfin" telmatherinids of Lake Matano. **a** *Telmatherina abendanoni* male, **b** *Telmatherina abendanoni* female, **c** *Telmatherina opudi* males, yellow and blue morph, **d** *Telmatherina opudi* male, yellow morph, **e** *Telmatherina obscura* male, blackish morph, **f** *Telmatherina opudi* female, **g** *Telmatherina sarasinorum* male, blue morph, **h** *Telmatherina sarasinorum* male, yellow morph, **i** *Telmatherina sarasinorum* male, grey morph, **j** *Telmatherina sarasinorum* female.

Abb. 3a-j: Morphotypische und Farbformendiversität der „sharpfin" Telmatheriniden des Matanosees. **a** *Telmatherina abendanoni* Männchen, **b** *Telmatherina abendanoni* Weibchen, **c** *Telmatherina opudi* Männchen, gelbe und blaue Morphe, **d** *Telmatherina opudi* Männchen, gelbe Morphe, **e** *Telmatherina obscura* Männchen, schwärzliche Morphe, **f** *Telmatherina opudi* Weibchen, **g** *Telmatherina sarasinorum* Männchen, blaue Morphe, **h** *Telmatherina sarasinorum* Männchen, gelbe Morphe, **i** *Telmatherina sarasinorum* Männchen, graue Morphe, **j** *Telmatherina sarasinorum* Weibchen.

acterized by shape of their second dorsal and anal fins, either pointed ("sharpfins") or rounded ("roundfins") (Herder et al. 2006, Kottelat 1991). To account for the striking size dimorphism in *Telmatherina antoniae*, "small" and "large" phenotypes are differentiated according to a gap in size frequency distribution of adult specimens between 55 and 60 mm SL.

3. Results

All telmatherinid populations observed are sexually dimorphic. "Morphotypes" and male "color morphs" are summarized in table 1 and illustrated in figures 3 to 9; sample sites are marked in figures 1 and 2. Lake Masapi was sampled intensively at two sites, without recording any telmatherinid specimen.

3.1. *Telmatherina* of Lake Matano

Seven "morphotypes" of "sharpfins" (figs. 3a-j, 4a-h) and three of "roundfins" (figs. 5a-j, 6a) are distinguished within L. Matano (tabs. 1 and 2). Five "sharpfin" morphotypes are di- or polychromatic in male coloration (tab. 1; figs. 3c-e, g-i and 4a-b, d-e). Three previously unknown "sharpfin" phenotypes are recognized and can be identified preliminarily: *Telmatherina* sp. "thicklip" (= *T.* "whitelips" in Gray and McKinnon 2006), characterized by pronounced fleshy lips and extremely prolonged tips of second dorsal and anal fins (fig. 4g-h); *T.* sp. "elongated", with short fins and an extremely slender body (figs. 4d-f); and *T. sarasinorum* "largehead / bigmouth", with a conspicuously large head / big mouth (figs. 4a-b). *Telmatherina abendanoni* is recognized in accordance

Tab. 1: List of telmatherinid species/"morphotypes" inhabiting the Malili Lakes system and surrounding catchments, their color morphs and distribution within the Malili Lakes system. ●̲ = new record, ● = previous record confirmed, * = only juveniles obtained, ** = not confirmed

Tab. 1: Auflistung der nachgewiesenen Telmatheriniden-Arten/„Morphotypen" des Maliliseen-Systems und umgebender Einzugsgebiete, ihrer Farbmorphen und Verbreitung innerhalb des Maliliseen-Systems. ●̲ = neuer Nachweis, ● = vorheriger Nachweis bestätigt; * = nur Jungfische gefangen, ** = nicht bestätigt

Telmatherinid species / "morphotypes"	Lake / Stream	Location	Drainage	blue	yellow	blue/yellow	white	oragne-red	grey/blackish
Telmatherina antoniae "large"	Matano			●	●	●̲			
Telmatherina antoniae "small"	Matano			●	●	●̲			
Telmatherina prognatha	Matano			●	●̲	●̲			
Telmatherina abendanoni	Matano								●
Telmatherina opudi / obscura	Matano			●	●̲				●
Telmatherina sarasinorum	Matano			●	●				●̲
Telmatherina sarasinorum "largehead" / "bigmouth"	Matano			●̲	●̲				●̲
Telmatherina wahjui	Matano			●	●				
Telmatherina sp. "elongated"	Matano			●̲	●̲				
Telmatherina sp. "thicklip"	Matano								●̲
Telmatherina sp. "Petea"	Petea	6	Mahalona	●̲	●̲				
Telmatherina cf. *bonti*	Lawa	3	Matano					●	
Telmatherina cf. *bonti*	Lemulengku	2	Matano					●	
Telmatherina cf. *bonti*	Saluro	5	Petea					●̲	
Telmatherina cf. *bonti*	Wawondula	11	Towuti				●̲		
Telmatherina cf. *bonti*	Tominanga	7	Towuti		●̲				
Telmatherina cf. *bonti*	Beau	9	Towuti	●̲	●̲				
Telmatherina cf. *bonti*	South Towuti	10	Towuti					●̲	
Telmatherina cf. *bonti*	Lemolemo	8	Towuti		●̲				
Telmatherina cf. *bonti*	Lakes Mahalona/Towuti							●̲	
Telmatherina cf. *bonti*	Larona (=Malili)	12	sea W (Gulf of Bone)		●				
Telmatherina cf. *bonti*	West	1	sea W (Gulf of Bone)		●̲		●̲		
Telmatherina cf. *bonti*	Nuha	4	sea E				●̲	●̲	
Telmatherina cf. *bonti**	"East-Towuti"	14	sea E						
Telmatherina celebensis	Towuti/Tominanga/Mahalona			●	●				
Telmatherina cf. *celebensis* "Lontoa"	Lontoa			●̲	●̲				
Tominanga cf. *aurea*	Mahalona/Tominanga					highly diverse			
Tominanga cf. *sanguicauda*	Towuti					highly diverse			
*Paratherina cyanea**	Towuti								
*Paratherina labiosa***	(Towuti/Mahalona)								
Paratherina striata	Towuti/Mahalona			●	●				
Paratherina wolterecki	Mahalona								●

Tab. 2: Record of telmatherinid "morphotypes" within Lake Matano. "Clade" refers to "sharpfins" and "roundfins" which have been identified as two major clades in Lake Matano according to nuclear DNA markers (Herder et al. 2006).
Tab. 2: Nachweis von Telmatheriniden- „Morphotypen" innerhalb des Matanosees. "Clade" bezieht sich auf "sharpfins" und "roundfins", die mit DNA-Kernmarkern als zwei Hauptclades innerhalb des Matanosees identifiziert wurden (Herder et al. 2006).

		Sampling locations around Lake Matano							
Telmatherinid species / "morphotypes"	**Clade**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Telmatherina antoniae "large"	"roundfins"	●	●	●	●	●	●	●	
Telmatherina antoniae "small"	"roundfins"	●	●	●	●	●	●	●	
Telmatherina prognatha	"roundfins"	●	●	●	●	●	●	●	
Telmatherina abendanoni	"sharpfins"	●	●	●	●	●	●	●	
Telmatherina opudi / obscura	"sharpfins"	●	●	●	●	●	●	●	●
Telmatherina sarasinorum	"sharpfins"	●	●	●	●	●	●	●	
Telmatherina sarasinorum "largehead" / "bigmouth"	"sharpfins"		●			●	●	●	
Telmatherina wahjui	"sharpfins"				●	●			●
Telmatherina "elongated"	"sharpfins"		●		●	●	●	●	
Telmatherina "thicklip"	"sharpfins"	●	●	●	●	●	●	●	

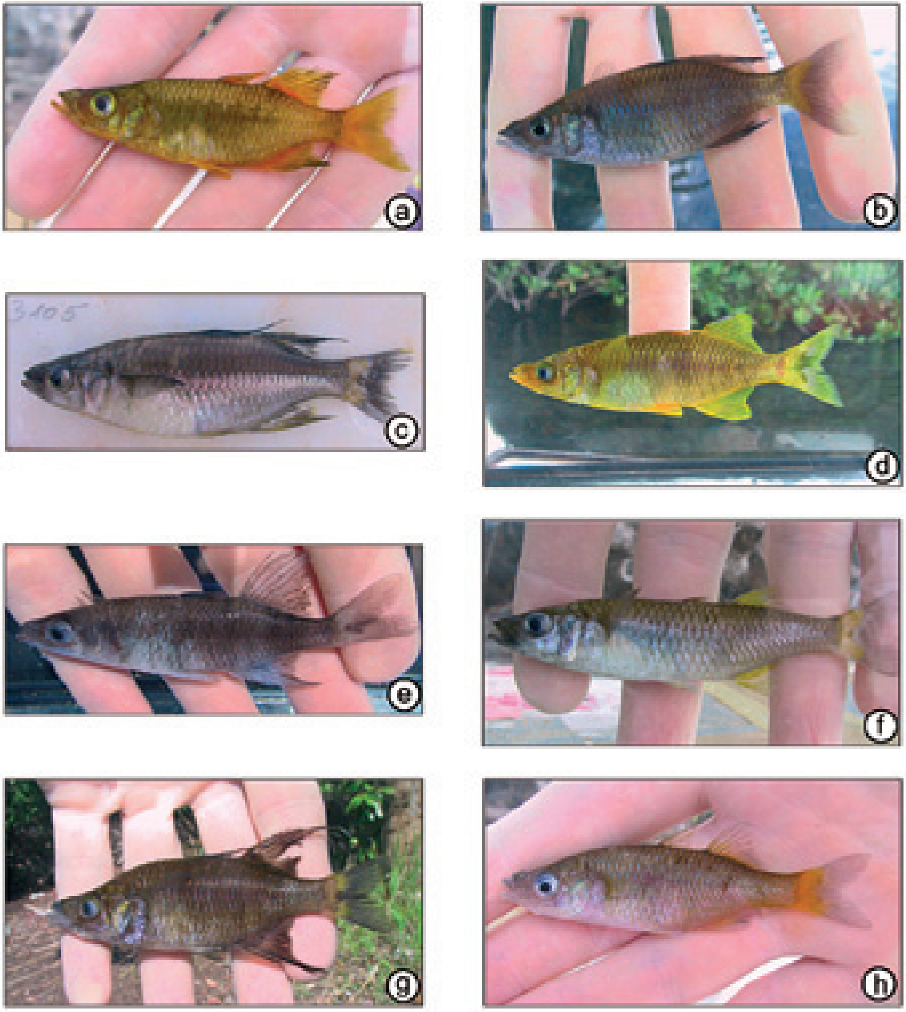
to Kottelat's (1991) concept of the species as large and slender, predatory "sharpfin" (figs. 3a-b). It appears together with *Telmatherina* sp. "thicklip" the only of L. Matano's telmatherinids without color polymorphism. *Telmatherina opudi* and *T. obscura* are characterized by only moderately elongated fins and in having a comparatively steeply angled mouth. Following the concept of Kottelat (1991), the blackish color morph is called *T. obscura* (figs. 3e), the yellow and bluish-grey *T. opudi* (figs. 3c-d, f). *Telmatherina sarasinorum* is recognized according to Kottelat (1991) by its small to medium-sized mouth and conspicuous elongated second dorsal and anal fins in males. Bright yellowish, blackish-blue and blackish-grey color morphs are present (Kottelat 1991; figs. 3g-i). *Telmatherina wahjui* was described by Kottelat (1991) as wide-headed "sharpfin" endemic to the outlet region, the small transition area between L. Matano and R. Petea (fig. 4c). Its diagnostic character is relation of snout width to snout length, resulting in a blunt, wide snout in contrast to the more elongated snout in *T. opudi* and *T. sarasinorum*. There are two male color morphs in *T. wahjui*, either blue or yellow.

Lake Matano's "roundfins" are distinguishable according to two distinct size classes of adults in *Telmatherina antoniae*: *T. antoniae* "small" is characterized by small size (<55 mm SL) and a slender body (figs. 5e-g), in contrast to larger size (>60 mm SL) and deeper body in *T. antoniae* "large" (figs. 5a-d) (Kottelat 1991, Herder et al., unpubl.). *Telmatherina prognatha*, a large predatory phenotype, is as large as *T. antoniae* "large", but as slender as *T. antoniae* "small", and is characterized by having conspicuous "beak-like" jaws (figs. 5h-j and 6a) (Kottelat 1991). In all three "roundfins", males occur in three color variants: yellow, blue or blue-yellow (bluish body and yellow fins).

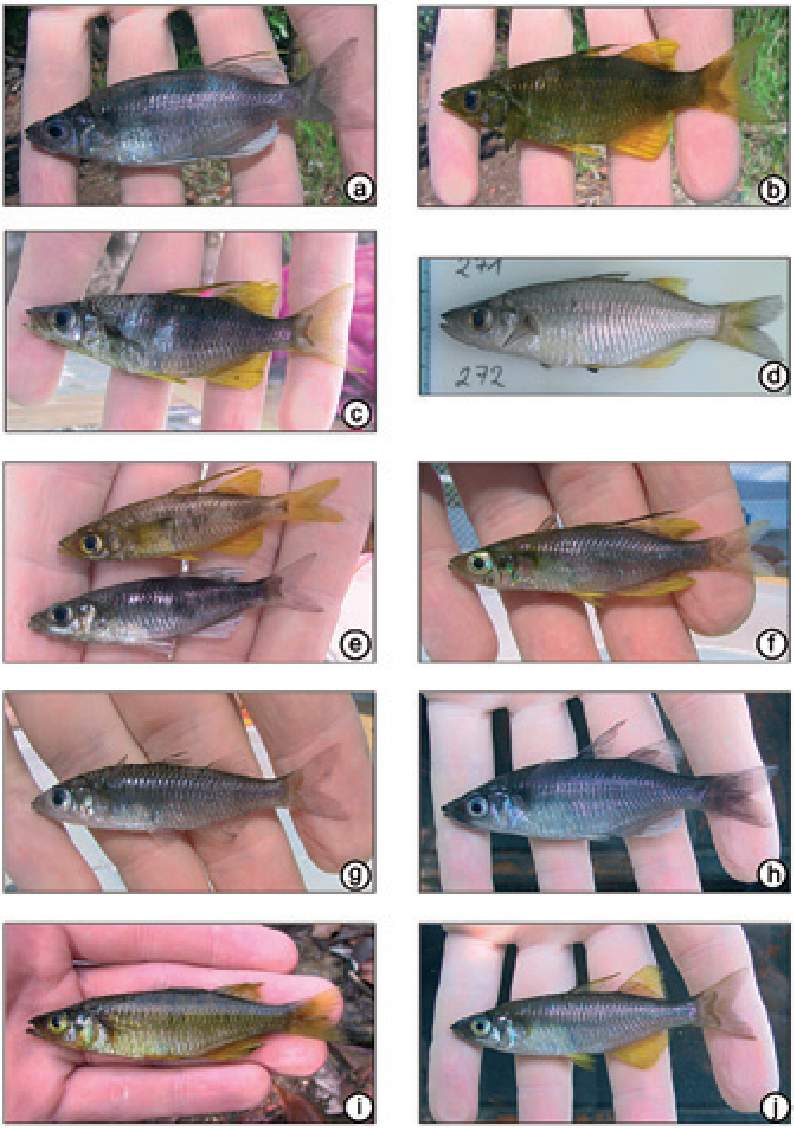
Whereas male roundfins" and "sharpfins" can be distinguished according to the shape of their second dorsal and anal fins (Kottelat 1991), females of both groups are separable according to body coloration which is silver-grey in "roundfins" (figs. 5d, g and 6a) *vs.* yellowish dusky-brown in "sharpfins" (figs. 3f, j and 4f, h); both can exhibit bluish reflections. Females can like males be assorted to the "morphotypes" listed above.

3.2. *Telmatherina* of Lakes Towuti, Mahalona and Lontoa

Telmatherina celebensis was by far the most abundant telmatherinid observed in Lakes Towuti and Mahalona. Male color morphs with either blue or yellow second dorsal and anal fins were observed frequently,



Figs. 4a-h: "Morphotypic" and "color morph" diversity of "sharpfin" telmatherinids of Lake Matano. **a** *Telmatherina sarasinorum* "bigmouth" male, yellow morph, **b** *Telmatherina sarasinorum* "largehead" male, blackish morph, **c** *Telmatherina wahjui* male, blue morph, **d** *Telmatherina* sp. "elongated" male, yellow morph, **e** *Telmatherina* sp. "elongated" male, blue morph, **f** *Telmatherina* sp. "elongated" female, **g** *Telmatherina* sp. "thicklip" male, **h** *Telmatherina* sp. "thicklip" female.
Abb. 4a-h: Morphotypische und Farbformendiversität der „sharpfin" Telmatheriniden des Matanosees. **a** *Telmatherina sarasinorum* "Großmaul" Männchen, gelbe Morphe, **b** *Telmatherina sarasinorum* "Großkopf" Männchen, schwärzliche Morphe, **c** *Telmatherina wahjui* Männchen, blaue Morphe, **d** *Telmatherina* sp. "verlängert" Männchen, gelbe Morphe, **e** *Telmatherina* sp. "verlängert" Männchen, blaue Morphe, **f** *Telmatherina* sp. "verlängert" Weibchen, **g** *Telmatherina* sp. "Dicklippe" Männchen, **h** *Telmatherina* sp. "Dicklippe" Weibchen.



Figs. 5a-j: "Morphotypic" and "color morph" diversity of "sharpfin" telmatherinids of Lake Matano (continued). **a** *Telmatherina antoniae* "large" male, blue morph, **b** *Telmatherina antoniae* "large" male, yellow morph, **c** *Telmatherina antoniae* "large" male, blue-yellow morph, **d** *Telmatherina antoniae* "large" female, **e** *Telmatherina antoniae* "small" males, blue and yellow morph, **f** *Telmatherina antoniae* "small" male, blue-yellow morph, **g** *Telmatherina antoniae* "small", female, **h** *Telmatherina prognatha* male, blue morph, **i** *Telmatherina prognatha* male, yellow morph, **j** *Telmatherina prognatha* male, blue-yellow morph.

Abb. 5a-j: Morphotypische und Farbformendiversität der „sharpfin" Telmatheriniden des Matanosees (Fortsetzung). **a** *Telmatherina antoniae* „groß" Männchen, blaue Morphe, **b** *Telmatherina antoniae* „groß" Männchen, gelbe Morphe, **c** *Telmatherina antoniae* „groß" Männchen, blaugelbe Morphe, **d** *Telmatherina antoniae* „groß" Weibchen, **e** *Telmatherina antoniae* „klein" Männchen, blaue und gelbe Morphe, **f** *Telmatherina antoniae* „klein" Männchen, blaugelbe Morphe, **g** *Telmatherina antoniae* „klein", Weibchen, **h** *Telmatherina prognatha* Männchen, blaue Morphe, **i** *Telmatherina prognatha* Männchen, gelbe Morphe, **j** *Telmatherina prognatha* Männchen, blaugelbe Morphe.

however both being characterized by a predominantly yellow to yellowish-brown body (figs. 6b-c). *Telmatherina celebensis* was also recorded within R. Tominanga. In Lake Lontoa, *Telmatherina* cf. *celebensis*, a phenotype resembling *T. celebensis*, but distinguished by its conspicuous deep body, is present (figs. 6d-f). Like *T. celebensis*, it is also characterized by yellow-blue male dichromatism (figs. 6d-e). Female specimens of both phenotypes are dusky yellowish brown with hyaline fins. *Telmatherina* cf. *celebensis* "Lontoa" was the single telmatherinid species obtained from L. Lontoa in our surveys.

3.3. *Tominanga*

The genus *Tominanga* exhibits the most complex pattern of male colorations in telmatherinids, with varying degrees of red, yellow, silver and blackish patterns (e.g. figs. 6g-j and 7a, c-d). In contrast, females are uniformly colored, with silvery body and hyaline fins (fig. 7b). Patterns of male coloration are not restricted to those described by Kottelat (1990a), who distinguished color patterns of *T. sanguicauda* inhabiting L. Towuti with blue or red body, red caudal fin, blue or red dorsals, anal and pelvic from *T. aurea* restricted to L. Mahalona, diagnosed by silvery body with yellow or red spots, caudal, dorsals and pelvic in plain red or yellow or hyaline with yellow or red dots. Illustrations presented here display only a fraction of color variation observed in male *Tominanga* in the field, including plain yellow to golden specimens in L. Mahalona (fig. 6h), individuals with silvery to yellowish body and various degrees of yellow sparkles (figs. 6g, i), bluish body with red fins (fig. 6j) or bluish body with red spots in second dorsal and anal fin combined with orange caudal (fig. 7a). Besides from Lakes Towuti and Mahalona, *Tominanga* are here also reported to occur within River Tominanga and the lower stretches of R. Petea.

3.4. *Paratherina*

Paratherina sp. comprise the largest phenotypes of Telmatherinidae. The largest is *Paratherina striata* (largest specimen obtained: 142.6 cm SL), characterized by its slightly superior or isognathous mouth, bluish body and conspicuous faint lateral stripes over a "fishbone-like" transversal pattern (figs. 7e-f, j). Two male colorations were observed, having either bluish white (fig. 7f) or yellow (fig. 7e) margins of second dorsal, anal and caudal fins. *Paratherina* cf. *cyanea* is a very slender, bluish *Paratherina* with conspicuously large eyes (fig. 8a). However, our material of this species is restricted to few obviously immature specimens. *Paratherina* cf. *woltereckі* (figs. 7h, i) is characterized in having a strongly upwards directed, superior mouth. Males possess blackish yellow, slightly elongated fins, in contrast to females characterized by short, pale yellowish to hyaline fins.

3.5. Riverine phenotypes – *Telmatherina* cf. *bonti*

Telmatherinids were found to be present in several rivers and streams, including Rivers Petea (figs. 8b-c, 9f) and Tominanga (figs. 8g, 9g), and in some rivers outside of the Malili Lakes watershed (fig. 1, tab. 1). Riverine telmatherinids exhibit a diversity of body- and fin-shapes, ranging from slender (e.g. figs. 8f and 9a) to rather high-bodied (e.g. figs. 8b-c, g, j), and rounded (e.g. fig. 8e) to pointed (e.g. figs. 8b-d, f-h, j) fins. Corresponding to the original description of *Telmatherina bonti* and consistent to Kottelat's descriptions (Kottelat 1990a), phenotypes from Lakes Mahalona and Towuti, as well as from streams draining into L. Towuti and to some extent also those from River Lawa exhibit a conspicuous "hump" at the nape (e.g. figs. 8h-j). In contrast, those from River Lemulengku (fig. 8e), R. Saluro (fig. 8f), isolated Rivers Nuha (figs.

9b-d) and "West" (fig. 9a), are more slender and lack the "hump". Phenotypes obtained from R. Tominanga show a conspicuous sub-terminal mouth (fig. 8g); like those from R. Petea, they are characterized by a rather high body. Females of all riverine populations are characterizes by brownish-grey body and hyaline, short fins (e.g. figs. 8i and 9d). Color polymorphisms in males are present in several populations, ranging from white/orange-red in River Nuha (figs. 9b-c) and yellow/bluish in R. Petea (figs. 8b, c) and R. "Beau" to yellow/white in R. "West" (fig. 9a). The dominating fin colorations of non-polymorphoc riverine populations are orange-red, yellow or white (figs. 8d-h, j; tab.1).

In accordance to previous records (Kottelat 1990a, Weber and Beaufort 1922), *Telmatherina bonti* was in the present surveys obtained directly from L. Towuti. We include here also a record from Lake Mahalona close to the mouth of R. Petea.

4. Discussion

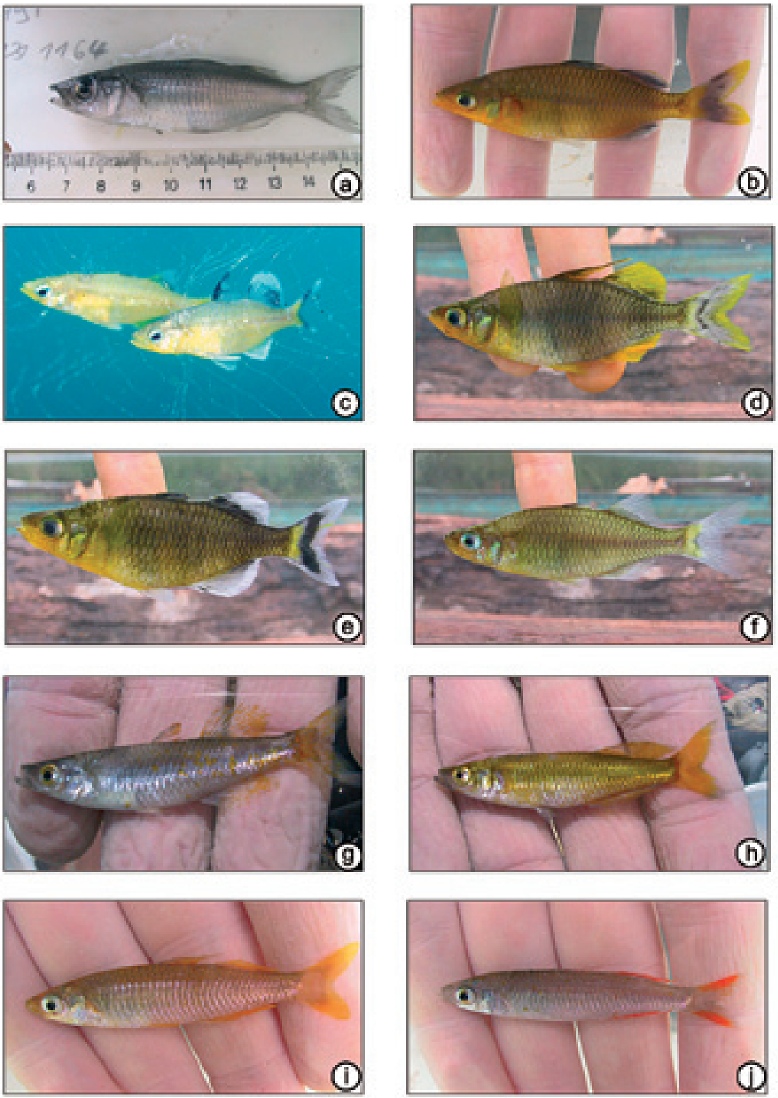
Exceeding Kottelat's revision (Kottelat 1990a, 1991) listing 15 described telmatherinid species within the Malili Lakes system, five of which are polymorphic in male coloration, we presently distinguish 19 "morphotypes" from lake (incl. *T.* cf. *bonti* from Lakes Towuti/Mahalona) and additional 13 from riverine habitats. In total, 17 of these exhibit di- or polychromatic male ornamentation (tab. 1).

4.1. The diversity of stream phenotypes

Most of the additional "morphotypes" (13) originate from riverine habitats like rivers and streams. Previous studies did not differentiate riverine telmatherinids further and referred to all phenotypes as *Telmatherina bonti*. A first step to analyzing this diversity was conducted by Herder at al. (2006), who included nine stream-dwelling telmatherinid populations in a landmark-based morphometric analysis of body shape. They demonstrated that there is low overlap in morphospace among "stream clade" telmatherinids and the adaptive radiation of L. Matano's "roundfins" and "sharpfins", though "sharpfins" are heavily introgressed by stream telmatherinids. The same analysis also provided first empirical hints suggesting inter-population variation in morphometric traits. Forthcoming analyses (Herder and Schliewen, in prep.) will evaluate interrelationship of this strongly underestimated group using population genetic and morphometric tools. However, independent of species status for different riverine populations it appears necessary to point out the high levels of phenotypic and genotypic diversity of telmatherinids inhabiting different flowing waters of the Malili Lakes system, because this fact highlights the importance of fine-scaled watershed management within the larger Malili area including damming and mining plans in selected sub-watersheds.

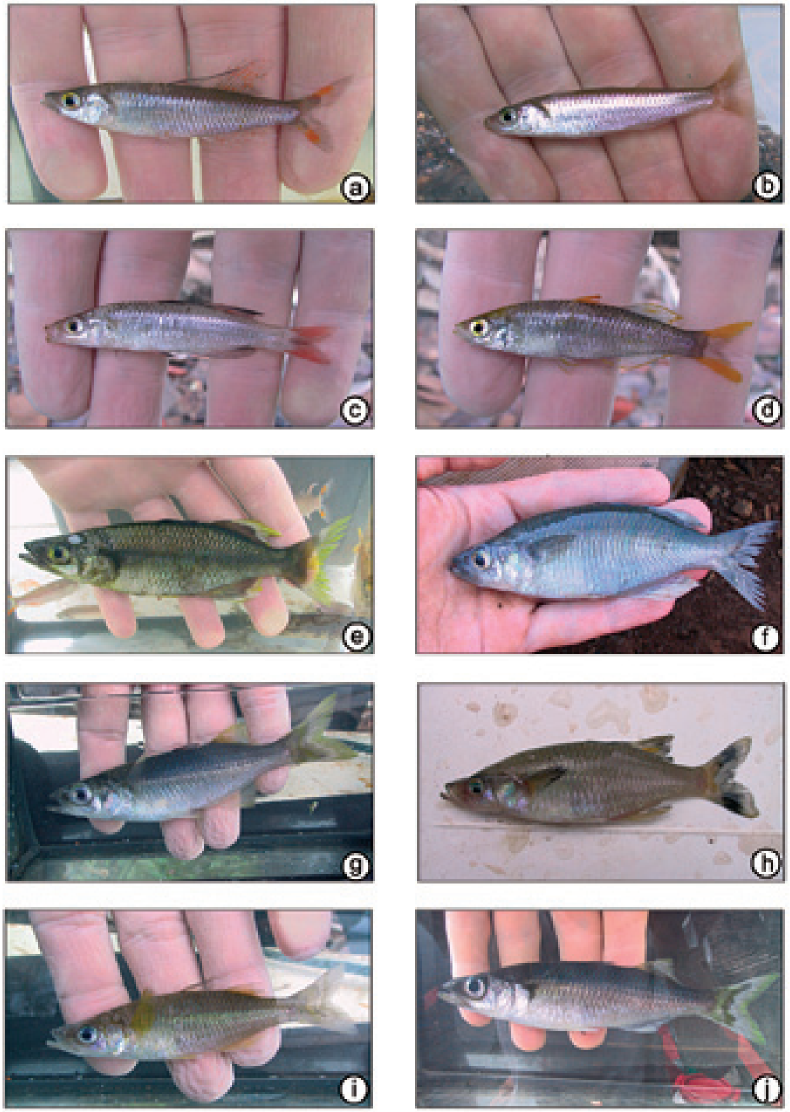
4.2. *Telmatherina* of Lake Matano

All telmatherinid phenotypes of Lake Matano are endemic to this lake. Complexity of Lake Matano's adaptive sailfin-silverside radiation is higher than initially expected, but appears still manageable for approaching questions regarding the analysis of the flock's genesis. There are no hints for clear allopatric restrictions of telmatherinids within the lake, apart from *T. wahjui* that is described from the outlet area (tab. 2; Kottelat 1991). Lake Matano's outlet area at the mouth of River Petea is here understood as an approx. 100 meters long transition zone between the lake and the stream. This area is characterized by medium to strong current, coarse substrate consisting mainly of empty bivalve shells and low depth of up to 1.5 m. These characteristics might explain the absence of most lake in-



Figa. 6a-j: "Morphotypic" and "color morph" diversity of "roundfin" telmatherinids of Lake Matano. **a** *Telmatherina prognatha* female, **b** *Telmatherina celebensis* male, yellow-blue morph (Mahalona), **c** *Telmatherina celebensis* male and female (Towuti), **d** *Telmatherina* cf. *celebensis* "Lontoa" male, yellow morph, **e** *Telmatherina* cf. *celebensis* "Lontoa" male, blue morph, **f** *Telmatherina* cf. *celebensis* "Lontoa" female, **g** *Tominanga* cf. *aurea* male, silver-yellow morph (Mahalona), **h** *Tominanga* cf. *aurea* male, yellow morph (Mahalona), **i** *Tominanga* cf. *aurea* male, silver-sparkle-yellow morph (Mahalona), **j** *Tominanga* cf. *aurea* male, silver-red morph (Mahalona).

Abb. 6a-j: Morphotypische und Farbformendiversität der „roundfin" Telmatheriniden des Matanosees. **a** *Telmatherina prognatha* Weibchen, **b** *Telmatherina celebensis* Männchen, gelbblaue Morphe (Mahalona), **c** *Telmatherina celebensis* Männchen und Weibchen (Towuti), **d** *Telmatherina* cf. *celebensis* „Lontoa" Männchen, gelbe Morphe, **e** *Telmatherina* cf. *celebensis* „Lontoa" Männchen, blaue Morphe, **f** *Telmatherina* cf. *celebensis* „Lontoa" Weibchen, **g** *Tominanga* cf. *aurea* Männchen, silbergelbe Morphe (Mahalona), **h** *Tominanga* cf. *aurea* Männchen, gelbe Morphe (Mahalona), **i** *Tominanga* cf. *aurea* Männchen, silbern gesprenkelte gelbe Morphe (Mahalona), **j** *Tominanga* cf. *aurea* Männchen, silberrote Morphe (Mahalona).



Figs. 7a-j: "Morphotypic" and "color morph" diversity of *Tominanga* (a-d) and *Paratherina* (e-j). **a** *Tominanga* cf. *aurea* male, blue-red morph (Mahalona), **b** *Tominanga* sp. female (Mahalona), **c** *Tominanga* cf. *sanguicauda* male, silver-red-black morph (Towuti), **d** *Tominanga* cf. *sanguicauda* male, silver-orange morph (Towuti), **e** *Paratherina striata* male, yellow morph (Mahalona), **f** *Paratherina striata* male, blue morph (Mahalona), **g** *Paratherina striata* female (Mahalona), **h** *Paratherina* cf. *woltereckі* male (Mahalona), **i** *Paratherina* cf. *woltereckі* female (Mahalona), **j** *Paratherina striata* female (Towuti).
Abb. 7a-j: Morphotypische und Farbformendiversität von *Tominanga* (a-d) and *Paratherina* (e-j). **a** *Tominanga* cf. *aurea* Männchen, blaurote Morphe (Mahalona), **b** *Tominanga* sp. Weibchen (Mahalona), **c** *Tominanga* cf. *sanguicauda* Männchen, silberrotschwarze Morphe (Towuti), **d** *Tominanga* cf. *sanguicauda* Männchen, silberorange Morphe (Towuti), **e** *Paratherina striata* Männchen, gelbe Morphe (Mahalona), **f** *Paratherina striata* Männchen, blaue Morphe (Mahalona), **g** *Paratherina striata* Weibchen (Mahalona), **h** *Paratherina* cf. *woltereckі* Männchen (Mahalona), **i** *Paratherina* cf. *woltereckі* Weibchen (Mahalona), **j** *Paratherina striata* Weibchen (Towuti).

habiting telmatherinids except for *T. wahjui* and *T. opudi*. However, a few specimens identifiable to Kottelat's description of *T. wahjui* (Kottelat 1991) were also obtained at other locations within the lake, all of them in the extreme shallow waters of the surge area (tab. 2).

Lake Matano's "sharpfins" are conspicuously more diverse than the "roundfins", with regard to (1) the number of "morphotypes" and to (2) character diversity within "morphotypes" (for an analysis of morphospace, see Herder et al. 2006). Diversity of "sharpfins" trophic morphology with respect to trophic ecology suggests that the process of divergence and speciation is ongoing, a hypothesis which is presently tested (Pfaender et al., in prep.). In this context, further analyses are required for understanding patterns of morphological diversity in *T. sarasinorum*/*T. sarasinorum* "largehead/bigmouth" and in *T. opudi*.

Kottelat (1991) described male color dimorphisms in two of five "sharpfin" species. Here, we add records of *Telmatherina opudi* "yellow", *T. sarasinorum* "blackish", *T.* sp. "elongated yellow", *T.* sp. "elongated blue" and T. sp. "thicklip".

We were not able to distinguish *Telmatherina opudi* and *T. obscura* following Kottelat's (1991) diagnoses using other characters than coloration. However, due to our observations, intermediate phenotypes among *T. sarasinorum*, *T. opudi* and *T. obscura* exist, and phenotypic diversity present in "sharpfins" is striking. Detailed morphological and molecular analyses of large series are required to understand the evolutionary processes shaping diversity of this group and to deduce taxonomic conclusions.

For "roundfins", we report apart from yellow and blue male morphs in *Telmatherina antoniae* "large" and *T. antoniae* "small" the occurrence of blue-yellow phenotypes having a bluish body and yellow fins. For *T. prognatha*, we add "yellow" and "blue-yellow" male morphs to the known blue one.

4.3. *Telmatherina* of Lakes Towuti and Mahalona

The presence of *Telmatherina celebensis* in River Tominanga is the first record of the species in a riverine habitat, which might point to ongoing gene flow between populations of lakes Towuti and Mahalona. Distinctiveness of *Telmatherina* cf. *celebensis* from Lake Lontoa with respect to *T. celebensis* from the large lakes is currently being investigated (Hadiaty and Herder, in prep).

4.4. *Paratherina*

A number of presently unidentifiable specimens as well as field observations of unknown phenotypes strongly suggest that species number of *Paratherina* is currently underestimated and that *Paratherina* is only insufficiently covered by our survey. However, additional material is available in the fish collection of MZB and is presently used to revise the genus (Hadiaty and Herder, in prep). Therefore, the present determinations are given with *provisio*.

Paratherina striata was previously only recorded from Lakes Towuti and Lontoa, though Kottelat (1990a) assumed it to be present in L. Mahalona, too. Here, we provide the first record for L. Mahalona. The species is dimorphic in male coloration, with either yellow or blue margins of second dorsal and anal fins. For *Paratherina* cf. *cyanea*, present sampling is limited to few specimens from L. Towuti; according to Kottelat (1990a), it is also present in L. Mahalona. Upcoming analysis of morphological characters incorporating Kottelat's material is aimed to clarify characters and infer the species' distribution. *Paratherina* cf. *wolterecki* has been reported by Kottelat (1990a) from Lakes Mahalona and Towuti. Here, we only confirm the species for its type locality, L. Mahalona. No male color dimorphism was recorded in this species. *Paratherina labiosa* has so far not been identified from the present material according to the available keys (Aurich 1935, Kottelat 1990a).

Neither the presence of *P. striata* nor *P. labiosa*, both recorded by Aurich (1935) for Lake Lontoa, were confirmed. However, the present sampling is restricted to the results of intensive fishing and snorkeling at a single site at the south-western corner of the lake. A denser sampling scheme is required for judging about *Paratherina* presence in L. Lontoa. Around this lake, the environment has undergone substantial degradation by deforestation, with almost complete absence of forest over large areas. As descriptions of the original situation are lacking, the presently observable low transparency of the lake's waters can only speculated to be a result of deforestation. Absence of *Paratherina* may be a result of those substantial environmental changes, too.

4.5. *Tominanga*

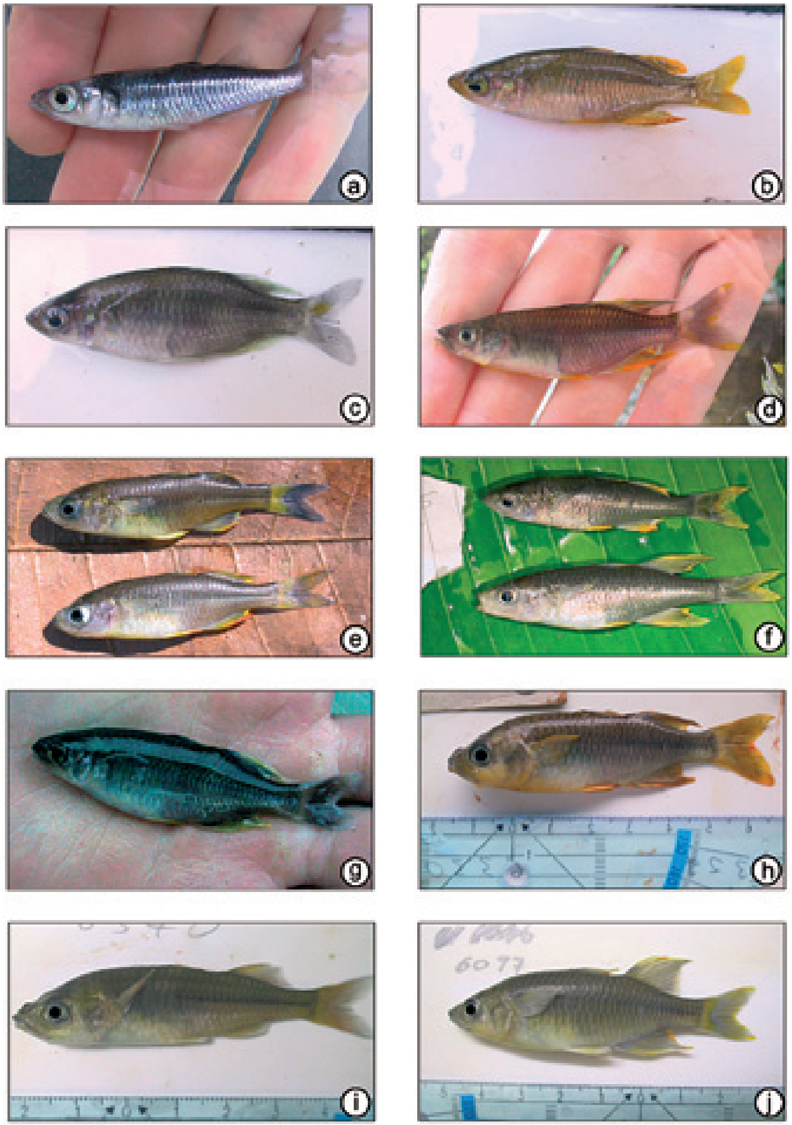
In *Tominanga*, red, orange, yellow and blackish patterns dominate male color polymorphism. Male *Tominanga* apparently represent the chromatically most diverse group of telmatherinids: Different phenotypes exhibit a mosaic of color components with plain or speckled patterns of yellow, red, orange, blackish and/or silvery colors. In contrast, no external morphological differentiation is visible, neither among specimens within each of both lakes nor among color morphs within these. However, detailed morphological examinations based on representative series of all *Tominanga* color morphs are lacking and might reveal indications supporting species status of Kottelat's (1990a) *T. aurea* and *T. sanguicauda*. Until this question is solved, we suggest using "*Tominanga* cf. *aurea*" for specimens from L. Mahalona, and "*Tominanga* cf. *sanguicauda*" for those from L. Towuti.

The present work provides the first record of the genus *Tominanga* in Rivers Petea and Tominanga, despite its etymology suggesting an original origin from River Tominanga. The only published previous record of the genus in flowing water is that of *T. sanguicauda* in its original description (Kottelat 1990a), reported to occur in a cold tributary of L. Towuti.

4.6. Threats to the lake's aquatic diversity

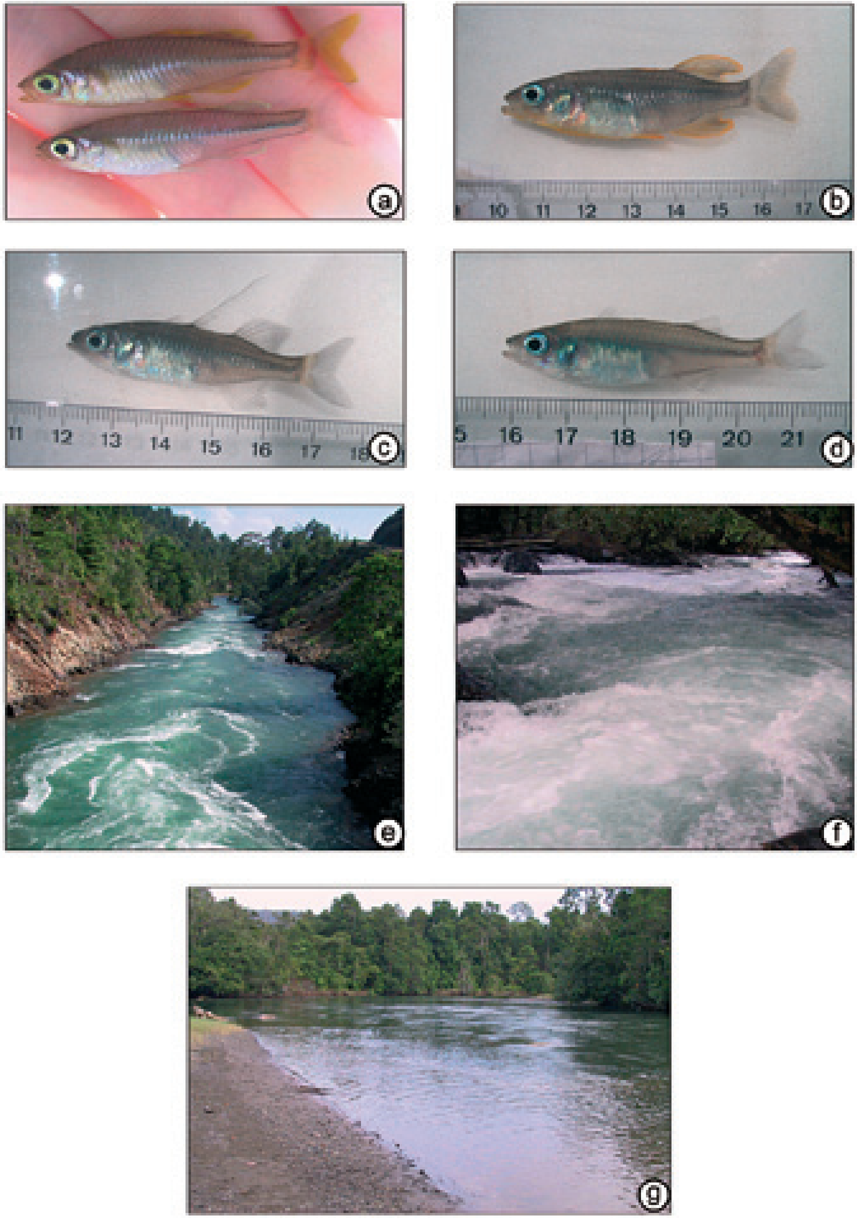
Over the last decades, nickel mining by PT INCO became a major industry at Soroako near L. Matano. Substantial parts of the area south of L. Matano have already been cleared and opened to surface mining, areas east and south-east of the lake and northwards of R. Petea are presently under digging. Exploited nickel-ore is smelted on site in several furnaces, causing environmental pollution and requiring gigantic amounts of electric energy. Hydroelectric power plants driven by a series of dams along R. Larona are used to produce the necessary electricity. However, substantial efforts are undertaken by INCO to restrict environmental impact on the lakes, especially on L. Matano. According to Giesen et al. (1991), pollution via atmospheric deposition (SO_2 dissolved in rainwater) is unlikely to lower the lake's pH due to high buffering capacity of its water. In contrast, contaminated effluents from the plant do represent a serious threat, measurable as increased levels of sulphur in lake and stream waters (Giesen et al. 1991).

The major threats to the endemic aquatic fauna are represented undoubtedly by INCO's activities for water regulation besides erosion by increased land-use and logging. River Larona has already been transformed from a natural river to an artificial channel, L. Towuti and R. Larona are dammed, and mining with massive earthmoving goes on along R. Petea (Herder, pers. obs.). Giesen et al. (1991) list additional plans of INCO to manage water resources of the Malili Lakes system, including ca-



Figs. 8a-j: “Morphotypic” and “color morph” diversity of *Paratherina* (a) and riverine phenotypes *Telmatherina* cf. *bonti* (b-j). **a** *Paratherina* cf. *cyanea* (Towuti), **b** *Telmatherina* cf. *bonti* “Petea” male, yellow morph, **c** *Telmatherina* cf. *bonti* “Petea” male, blue morph, **d** *Telmatherina* cf. *bonti* “Lawa” male, yellow-red morph, **e** *Telmatherina* cf. *bonti* “Lemulengku” males, **f** *Telmatherina* cf. *bonti* “Saluro” males, **g** *Telmatherina* cf. *bonti* “Tominanga” male, **h** *Telmatherina* cf. *bonti* “South Towuti” male, **i** *Telmatherina* cf. *bonti* “South Towuti” female, **j** *Telmatherina* cf. *bonti* “Lemolemo” male.

Abb. 8a-j: Morphotypische und Farbformendiversität von *Paratherina* (a) und flussbewohnenden Phaenotypen *Telmatherina* cf. *bonti* (b-j). **a** *Paratherina* cf. *cyanea* (Towuti), **b** *Telmatherina* cf. *bonti* „Petea” Männchen, gelbe Morphe, **c** *Telmatherina* cf. *bonti* „Petea” Männchen, blaue Morphe, **d** *Telmatherina* cf. *bonti* „Lawa” Männchen, gelbrote Morphe, **e** *Telmatherina* cf. *bonti* „Lemulengku” Männchen, **f** *Telmatherina* cf. *bonti* „Saluro” Männchen, **g** *Telmatherina* cf. *bonti* „Tominanga” Männchen, **h** *Telmatherina* cf. *bonti* „South Towuti” Männchen, **i** *Telmatherina* cf. *bonti* „South Towuti” Weibchen, **j** *Telmatherina* cf. *bonti* „Lemolemo” Männchen.



Figs. 9a-g: “Morphotypic” and “color morph” diversity of riverine phenotypes *Telmatherina* cf. *bonti* (a-d) and habitat illustrations of the rivers interconnecting or draining the three major lakes (e-g). **a** *Telmatherina* cf. *bonti* “West” males, blue and yellow morph, **b** *Telmatherina* cf. *bonti* “Nuha” male, orange morph, **c** *Telmatherina* cf. *bonti* “Nuha” male, white morph, **d** *Telmatherina* cf. *bonti* “Nuha” female, **e** River Larona, **f** River Petea, **g** River Tominanga.

Abb. 9a-g: Morphotypische und Farbformendiversität flussbewohnender Phänotypen *Telmatherina* cf. *bonti* (a-d) und Abbildung der Flüsse, die die drei Hauptseen verbinden bzw. entwässern (e-g). **a** *Telmatherina* cf. *bonti* „West” Männchen, blaue und gelbe Morphe, **b** *Telmatherina* cf. *bonti* „Nuha” Männchen, orange Morphe, **c** *Telmatherina* cf. *bonti* „Nuha” Männchen, weiße Morphe, **d** *Telmatherina* cf. *bonti* „Nuha” Männchen, **e** Laronafluss, **f** Peteafluss, **g** Tominangafluss.

nalization of Rivers Petea and Tominanga, construction of a channel leading waters from L. Masapi to L. Towuti, redirection of the northwards-draining River Nuha into L. Matano, erection of an additional dam at R. Larona (already reality), construction of a sluice on R. Petea to store water in L. Matano and permanent increase of water level in L. Towuti by damming. These activities may have extreme impacts on the endemic aquatic diversity of the Malili-Lake System and should be adjusted to sustainable preserve this unique lake system.

Additional threats come from habitat loss due to mining activities and population increase. For example, streams in the former mining area south-east of L. Matano have been found either not to exist anymore or to have changed to biologically dead remains, filled with mud, oil and waste; only one of these contained fish, which, however, were stocked African "Tilapia" (Herder, pers. obs.). Likewise, streams north-east of L. Matano have been found to be extremely degraded by oil contamination, massive gathering of water and input of waste. However, this area is an upcoming mining area and will also be lost within near future.

A recent meeting on "The Ecology and Limnology of the Malili Lakes" (Bogor, Indonesia 20-22 March 2006) organized by PT INCO initiated discussion and intellectual exchange among scientists from various fields, all conducting research at the Malili Lakes. It became obvious that there exists a deficiency among scientific knowledge, mostly scattered to specialists, and information received and finally taken into consideration by PT INCO and the local authorities. The leading representative of PT INCO expressed that his company has deep interest to minimize environmental impacts to the lakes and assured that scientific results available on the lake system's ecology will be considered in upcoming planning. In this context, he recognized the previously undetected diversity of stream telmatherinids and announced to preserve Rivers Petea and Tominanga by establishing buffer areas between mining areas and the rivers, accompanied by abandonment of canalization.

Finally, introduction of foreign fish species is another potential threat for the lakes endemic fauna, a topic under investigation in context of our recent surveys (Herder et al. in prep.). Introduction of not native fish species can cause serious threats to the native fauna (Kottelat et al. 1993, Whitten et al. 2002) and has already been reported to affect endemic radiations in Sulawesi (Kottelat 1990d). Therefore, we strongly demand to avoid any introduction of animals not native to one of the lakes ecosystems.

5. Conclusions

Telmatherinidae of the Malili Lakes are much more diverse than previously known, with regard to both, "morphotypic" diversity and color morphs. Male color di- or polymorphism is the striking characteristic of this species-flock and is found in the majority of species/"morphotypes", including all three presently recognized genera. Among lacustrine telmatherinids, diversity is highest in L. Matano's "sharpfins". With regard to lacustrine species of Lakes Towuti and Mahalona, a close faunistic relationship between both water bodies is evident. An initially unknown diversity of stream-dwelling telmatherinids was discovered and remains to be studied in detail.

The adaptive radiation of sailfin-silversides has great potential to become a reference system allowing evolutionary biologists to test ideas regarding radiation processes and maintenance of color polymorphisms, using a compact model system of manageable diversity. Comparative approaches for invertebrate radiations bear the chance to test the influence of various parameters to different groups of organisms. Probably the most interesting point for speciation research is represented by the various degrees of isolation between the lakes, allowing to approach the impact of introgressive hybridization to adaptive radiations under sympatric, parapatric and allopatric scenarios.

However, present and planned constructions aimed to intensify usage of the lakes water resources for energy supply as well as massive loss of stream habitats due to mining activities are a major threat to the aquatic diversity. To avoid that the endemic radiations of the Malili Lakes system become natural history in near future, policy of water management has to take into account the biodiversity of streams and rivers and natural distribution patterns of the organisms within the lakes system. Drainages which are separated naturally should not inconsiderately be connected by man, and the rivers between the lakes should be treated as vulnerable pathways. Also, complete destruction of stream drainages within current and upcoming mining areas should be avoided to allow, at least partial, for recolonization of ecosystems after exploitation of nickel ore. The authors are convinced that long-term sustainability of mining around the Malili Lakes can be increased significantly by incorporating the available and upcoming scientific results into management decisions.

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Literature

Aarn, Ivantsoff, W. 1997. Descriptive anatomy of *Cairnsichthys rhombosomoides* and *Iriatherina werneri* (Teleostei: Atheriniformes), and a phylogenetic analysis of Melanotaeniidae. Ichthyol. Explor. Freshwaters 8, 107-150.

Aarn, Ivantsoff, W., Kottelat, M. 1998. Phylogenetic analysis of Telmatherinidae (Teleostei: Atherinomorpha), with description of *Marosatherina*, a new genus from Sulawesi. Ichthyol. Explor. Freshwaters 9, 311-323.

Abendanon, E.C. 1915a. Midden-Celebes-Expeditie. Geologische en geographische Doorkruising van Midden-Celebes (1909-1910), Atlas. E. J. Brill, Leiden.

Abendanon, E.C. 1915b. Midden-Celebes-Expeditie. Geologische en geographische Doorkruising van Midden-Celebes (1909-1910), vol. 2. E. J. Brill, Leiden.

Ahl, E. 1936. Beschreibung eines neuen Fisches der Familie Atherinidae aus Celebes. Zool. Anz. 114, 175-177.

Ahmad, W. 1977. Geology along the Matano Fault Zone East Sulawesi, Indonesia. Regional Conference on the Geology and Mineral resources of South East Asia, Jakarta.

Aurich, H.J. 1935. Mitteilungen der Wallacea-Expedition Woltereck. Mitteilung XIV. Fische II. Fam. Atherinidae. Zool. Anz. 112, 161-177.

Boulenger, G.A. 1897. An account of the freshwater fishes collected in Celebes by Drs P and F. Sarasin. Proc. Zool. Soc. Lond., Spec. Proc. Sarasin Expedition: 426-429.

Bramburger, A.J., Haffner, G.D., Hamilton, P.B. 2004. Examining the distributional patterns of the diatom flora of the Malili Lakes, Sulawesi, Indonesia. Proc. 17th Int. Diatom Symp. Ottawa, Canada, 11-25.

Bramburger, A.J., Haffner, G.D., Hamilton, P.B., Hinz, F., Hehanussa, P.E. 2006. An examination of species within the genus *Surirella* from the Malili Lakes, Sulawesi Island, Indonesia, with descriptions of 11 new taxa. Diatom Res. 21, 1-56.

Brooks, J.L. 1950. Speciation in ancient lakes (concluded). Quart. Rev. Biol. 25, 131-176.

Crowley, L.E.L.M., Ivantsoff, W. 1992. Redefinition of the freshwater fish genus *Craterocephalus* (Teleostei: Atherinidae) of Australia and New Guinea with an analysis of three species. Ichthyol. Explor. Freshwaters 3, 273-287.

Dyer, B.S., Chernoff, B. 1996. Phylogenetic relationships among atheriniform fishes (Teleostei: Atherinomorpha). Zool. J. Linn. Soc. 117, 1-69.

Giesen, W., Baltzer, M., Baruadi, R. 1991. Integrating conservation with land-use development in wetlands of South Sulawesi. Directorate General of Forest Protection and Nature Conservation, Bogor.

Gray, S., McKinnon, J.S.. 2006. A comparative description of mating behavior in the endemic telmatherinid fishes of Sulawesi's Malili Lakes. Env.. Biol. Fishes 75, 471-482.

Hadiaty, R.K., Wirjoatmodjo, S. 2002. Studi pendahuluan Biodiversitas dan distribusi Ikan di Danau Matano, Sulawesi Selatan (Preliminary study: Biodiversity and distribution of fishes in Lake Matano, South Sulawesi). J. Iktiol. Indonesia 2, 23-29.

Haffner, G.D., Hehanussa, P.E., Hartoto, D. 2001. The biology and physical processes of large lakes of Indonesia: Lakes Matano and Towuti, pp. 182-192. In: The Great Lakes of the world (GLOW) – Food web, health and integrity (Munawar, M., Hecky, R.E. eds). Backhuis Publishers, Leiden.

Herder, F., Nolte, A.W., Pfaender, J., Schwarzer, J., Hadiaty, R.K., Schliewen, U.K. 2006. Adaptive radiation and hybridization in Wallace's dreamponds: evidence from sailfin silversides in the Malili Lakes of Sulawesi. Proc. Roy. Soc. Lond. B. 273, 2209-2217.

Hutchinson, G.E. 1957. A treatise on limnology. John Wiley & Sons, New York.

Kottelat, M. 1989a. Der Matano-See. DATZ 42, 616-618.

Kottelat, M. 1989b. Der Towuti-See. DATZ 42, 681-684.

Kottelat, M. 1989c. Die Süsswasser-Fauna von Sulawesi. DATZ 42, 555-558.

Kottelat, M. 1990a. Sailfin silversides (Pisces: Telmatherinidae) of Lakes Towuti, Mahalona and Wawontoa (Sulawesi, Indonesia) with descriptions of two new genera and two new species. Ichthyol. Explor. Freshwaters 1, 35-54.

Kottelat, M. 1990b. The ricefishes (Oryziidae) of the Malili Lakes, Sulawesi, Indonesia, with description of a new species. Ichthyol. Explor. Freshwaters 1, 151-166.

Kottelat, M. 1990c. Der Mahalona-See. DATZ 43, 485-488.

Kottelat, M. 1990d. Synopsis of the endangered Buntingi (Osteichthyes: Adrianichthyidae and Oryziidae) of Lake Poso, Central Sulawesi, Indonesia, with a new reproductive guild and descriptions of three new species. Ichthyol. Explor. Freshwaters 1, 49-67.

Kottelat, M. 1991. Sailfin silversides (Pisces: Telmatherinidae) of Lake Matano, Sulawesi, Indonesia, with descriptions of six new species. Ichthyol. Explor. Freshwaters 1, 321-344.

Kottelat, M. 1992. Neu beschriebene Fische von Sulawesi. DATZ 45, 653-659.

Kottelat, M., Suttner, E. 1988. Catalogue des types de poissons du Musée d'histoire naturelle de Bâle (Naturhistorisches Museum Basel). Verh. Naturforsch. Ges. Basel 98, 51-57.

Kottelat, M., Whitten, T., Kartikasari, S.N., Wirjoatmodjo, S. 1993. Freshwater fishes of Western Indonesia and Sulawesi. Periplus Editions, Hong Kong.

Munro, I.S.R. 1958. Handbook of Australian fishes, number 24. Australian Fisheries Newsletter 17, 97-100.

Munro, I.S.R. 1967. The fishes of New Guinea. Department of Agriculture, Stock and Fisheries, Port Moresby.

Roy, D., Docker, M.F., Hehanussa, P.E., Heath, D.D., Haffner, G.D. 2004. Genetic and morphological data supporting the hypothesis of adaptive radiation in the endemic fish of Lake Matano. J. Evol. Biol. 17, 1268-1276.

Saeed, B., Ivantsoff, W. 1991. *Kalyptatherina*, the first telmatherinid genus known outside of Sulawesi. Ichthyol. Explor. Freshwaters 2, 227-238.

Saeed, B., Ivantsoff, W., Crowley, L.E.L.M. 1994. Systematic relationships of atheriniform fisheswithin division 1 of the series Atherinomorpha (Actinopterygii) with relevant historical perspectives. Vopr. Ikhtiol. 34, 1-32.

Sarasin, F. 1886. Durchquerung von Südost-Celebes. Verh. Ges. Erdkunde zu Berlin 23, 339-356.

Sparks, J.S., Smith, W.L. 2004. Phylogeny and biogeography of the Malagasy and Australasian rainbowfishes (Teleostei: Malanotaenioidei): Gondwanan vicariance and evolution in freshwater. Mol. Phyl. Evol. 33, 719-734.

von Rintelen, T., Glaubrecht, M. 2003. New discoveries in old lakes: three new species of Tylomelania Sarasin & Sarasin, 1897 (Gastropoda: Cerithioidea: Pachychilidae) from the Malili Lake system on Sulawesi, Indonesia. J. Moll. Stud. 69, 3-17.

von Rintelen, T., Glaubrecht, M. 2005. Anatomy of an adaptive radiation: a unique reproductive strategy in the endemic freshwater gastropod *Tylomelania* (Gastropoda: Cerithioidea: Pachychilidae) on Sulawesi, Indonesia and its biogeographical implications. Biol. J. Linn. Soc. 85, 513-542.

von Rintelen, T., Wilson, A.B., Meyer A., Glaubrecht, M. 2004. Escalation and trophic specialization drive adaptive radiation of freshwater gastropods in acient lakes on Sulawesi, Indonesia. Proc. Roy. Soc. Lond. B 271, 2541-2549.

Weber, M. 1913. Neue Beiträge zur Kenntnis der Süsswasserfische von Celebes. Ergebnisse einer Reise von E. C. Abendanon in Celebes. Bijdr. Dierk. 19, 197-213.

Weber, M., de Beaufort, L.F. 1922. The Fishes of the Indo-Australian Archipelago. IV: Heteromi, Soleichthyes, Synentognathi, Percesoces, Labyrinthi, Microcyprini. Brill, E.J., Leiden.

Whitten, T., Henderson, G.S., Mustafa, M. 2002. The Ecology of Sulawesi. The Ecology of Indonesia Series IV. Periplus Editions, Singapore.