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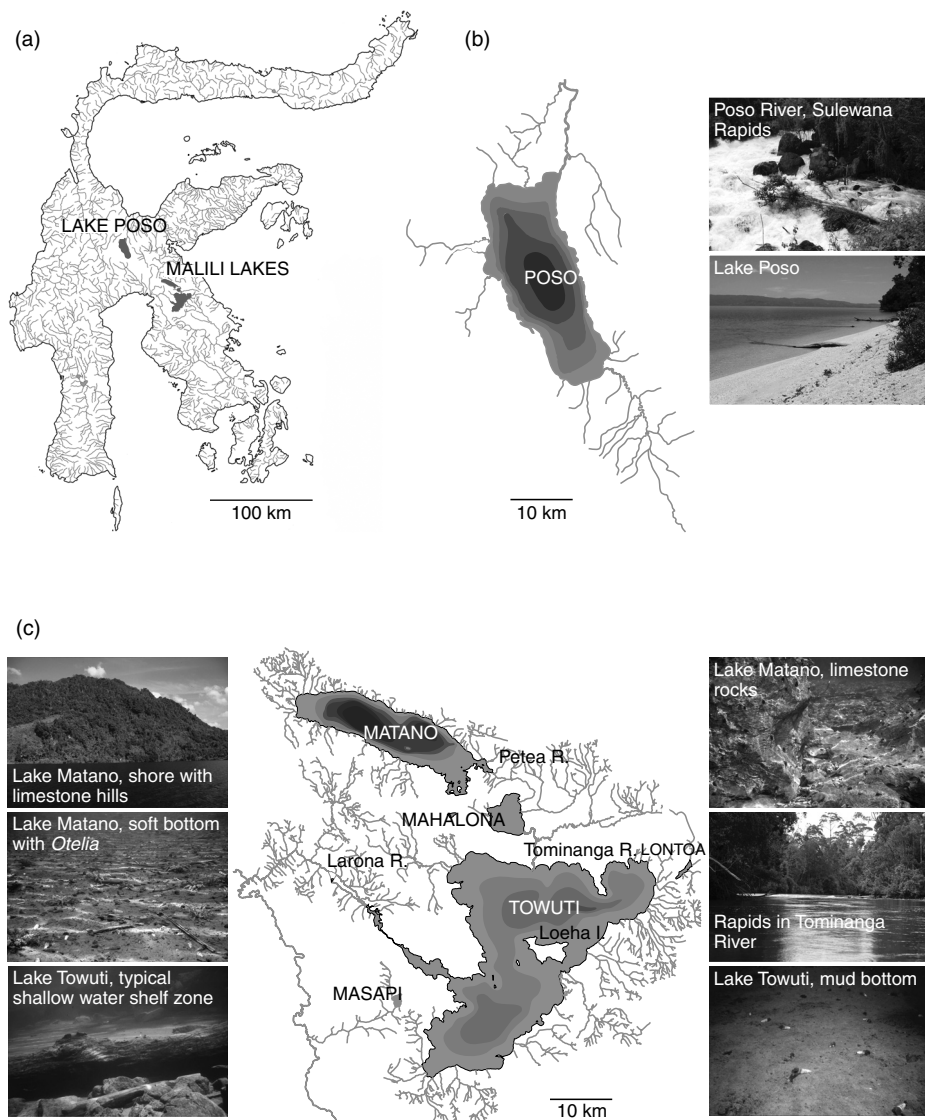
## Aquatic biodiversity hotspots in Wallacea: the species flocks in the ancient lakes of Sulawesi, Indonesia

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### 12.1 Introduction

Some of the world's most spectacular species radiations or species flocks are found in so-called 'ancient lakes'. These are long-lived lakes that have existed for 100 000 years (Gorthner et al. 1994, but see also Albrecht and Wilke 2008) or more (e.g. Lake Tanganyika and Lake Baikal). Ancient lakes are justifiably regarded as hotspots of diversification (e.g. Martens 1997, Rossiter and Kawanabe 2000), even if not all ancient lake species flocks match the diversity of the super-flock of East African cichlids (e.g. Kornfield and Smith 2000, Kocher 2004). Studies on the evolution of ancient lake organisms have continuously resulted in important insights into general patterns of speciation and radiation (e.g. Streelman and Danley 2003) ever since the seminal review of Brooks (1950).

During the last decade, smaller ancient lakes (c. <1 000 km<sup>2</sup>), which are generally less well investigated, have attracted increasing attention. In Southeast Asia, four lakes or lake systems are regarded as putative ancient lakes (Martens 1997): Lake Inlé in Burma, Lake Lanao on Mindanao, and Lake Poso and the Malili lakes on



**Figure 12.1** Indonesia, Sulawesi and the ancient lakes with characteristic habitats. (a) Sulawesi; the two ancient lake systems are highlighted in red. (b) Lake Poso. (c) Malili lake system. Lake names are printed in capital letters. Abbreviations: R., River; I., Island. See plate section for colour version.

Sulawesi (Fig 12.1). Among these lakes, only the Sulawesi lakes are clearly ancient lakes, both in terms of their estimated age and their fauna (see below for details), while the general lack of data prevents any firm conclusion about the other two systems.

**Table 12.1** The ancient lakes of Sulawesi. Based on data from Abendanon (1915a, 1915b), Giesen et al. (1991), Giesen (1994) and Haffner et al. (2001).

Lake	Area (km <sup>2</sup> )	Max. depth (m)	Transparency (Secchi disk) (m)
Poso	323.2	450	11
Matano	164.0	590	20
Mahalona	24.4	73	20
Towuti	561.1	203	22
Lontoa	1.6	3	<3
Masapi	2.2	4	<3

### 12.1.1 The ancient lakes of Sulawesi

#### Hydrology, geology and limnology

Both ancient lake systems on Sulawesi are located in the central mountains of the island (Fig 12.1a). Lake Poso (Fig 12.1b; Table 12.1) is a deep solitary lake, while the Malili system comprises five lakes sharing a common drainage (Fig 12.1c; Table 12.1). The three larger lakes of the Malili system are directly connected: Lake Matano flows into Lake Mahalona via the Petea River. In turn, Lake Mahalona spills into Lake Towuti via the Tominanga River. Lake Towuti is drained by the Larona River into the Gulf of Bone (Teluk Bone). Two smaller satellite lakes, Lake Lontoa (also known as Wawontoa or Lantoa) and Lake Masapi, are less directly connected to the system (see Fig 12.1c). The latter drains independently into the Malili River.

Lake Poso and Lake Matano are of tectonic origin, which accounts for their extraordinary depth. Lake Matano is situated in a strike-slip fault, the Matano fault, which was formed in the final juxtaposition process of South-, Southeast- and East Sulawesi since the Pliocene (*c.* 4 Ma) to the present day (Wilson and Moss 1999). The age of Lake Towuti has been estimated at 700 000 years (J. Russell pers. comm. 2011). Age estimates for the other lakes are lacking. The major ancient lakes of Sulawesi are oligotrophic, with a very low nutrient and organic content and a high transparency of up to 22 m in Lake Towuti (Giesen et al. 1991, Giesen 1994, Haffner et al. 2001, Crowe et al. 2008a, 2008b).

The lakes offer a wide range of habitats ranging from soft-bottom with sand and mud to steep rocky drop-offs (Fig 12.1). Typically, a shallow shelf zone (2–5 m) is followed by a steep slope with depth quickly increasing. Frequently, hard substrates predominate at the shoreline (0–2 m) and soft substrate in deeper water. Steep rocky areas and habitats dominated by gravel frequently interrupt these soft-bottom aggregations and dominate along some stretches of the larger

lakes. Habitat heterogeneity is high in all lakes, although there are general differences between the lakes for instance in the amount of hard substrate available in deep water (>10 m), which is largely lacking in Lake Mahalona and Lake Towuti. Extensive sand beaches are characteristic for large areas of Lake Poso, but almost entirely lacking in the Malili lakes. In the connecting and draining rivers of both lakes systems, currents of varying strength form an additional factor determining the limnic environment.

#### Exploration, fauna and species flocks

The Sulawesi lakes were first explored (Lake Poso, 1895; Malili lakes, 1896) by the Swiss naturalists Paul and Fritz Sarasin (Sarasin and Sarasin 1905). The Sarasins, focusing on the lakes' snails, did not fail to recognise the vastly different morphology of the lake species and consequently regarded them as ancient elements (Sarasin and Sarasin 1898). Roughly a decade later, the Dutch geologist E.C. Abendanon investigated the geology of both lake systems and sampled the lakes in 1909/1910 (Abendanon 1915b). In 1932, Woltereck conducted the last biological expedition with a universal approach to the lakes when he visited the Malili lakes during his 'Wallacea expedition' (Woltereck 1941). Charles Bonne sampled Lake Poso in 1941 for molluscs (Haase and Bouchet 2006). For several decades no further research on the lakes was conducted. In the late 1980s and early 1990s new collections were made in the lakes by M. Kottelat (fishes; Kottelat 1990, 1991, Larson and Kottelat 1992), and P. Bouchet in 1993 (molluscs; Bouchet et al. 1995). New species were described as an outcome of every expedition. For a summary of prior taxonomic work on the major lake taxa see Herder et al. (2006a), von Rintelen et al. (2007a), Schubart and Ng (2008) and von Rintelen and Cai (2009).

This taxonomic activity revealed that almost every taxon studied had radiated within Sulawesi lakes, and the lake fauna was discussed in the context of ancient lake radiations (Brooks 1950).

Since the late 1990s, several research groups have been working on the evolution of the major taxa in the lakes and the results of these studies are reviewed in this chapter. The speciose and morphologically diverse endemic species flocks in the ancient lakes of Sulawesi provide an excellent opportunity to study mechanisms of speciation and diversification in a comparative way across several groups of organisms with very different intrinsic properties. In addition to the groups discussed here, a number of other taxa have likely radiated in the lakes, such as hydrobiid gastropods (Haase and Bouchet 2006) and gobiid fishes (Kottelat et al. 1993). However, the general lack of data apart from species descriptions prevents a further discussion of these taxa here.

## 12.2 The species flocks in the ancient lakes of Sulawesi

### 12.2.1 Snails

Both ancient lake systems host species flocks of the viviparous freshwater gastropod *Tylomelania* (Mollusca: Caenogastropoda: Pachychilidae; Fig 12.2a). *Tylomelania* is endemic to Sulawesi (von Rintelen and Glaubrecht 2005) where it is widely distributed with approximately 75 species currently recognised (von Rintelen et al. 2010a), the majority of which are endemic to the ancient lakes. Here we summarise current knowledge on the ecological and phylogenetic patterns that have emerged so far from this model system.

#### Species diversity and distribution

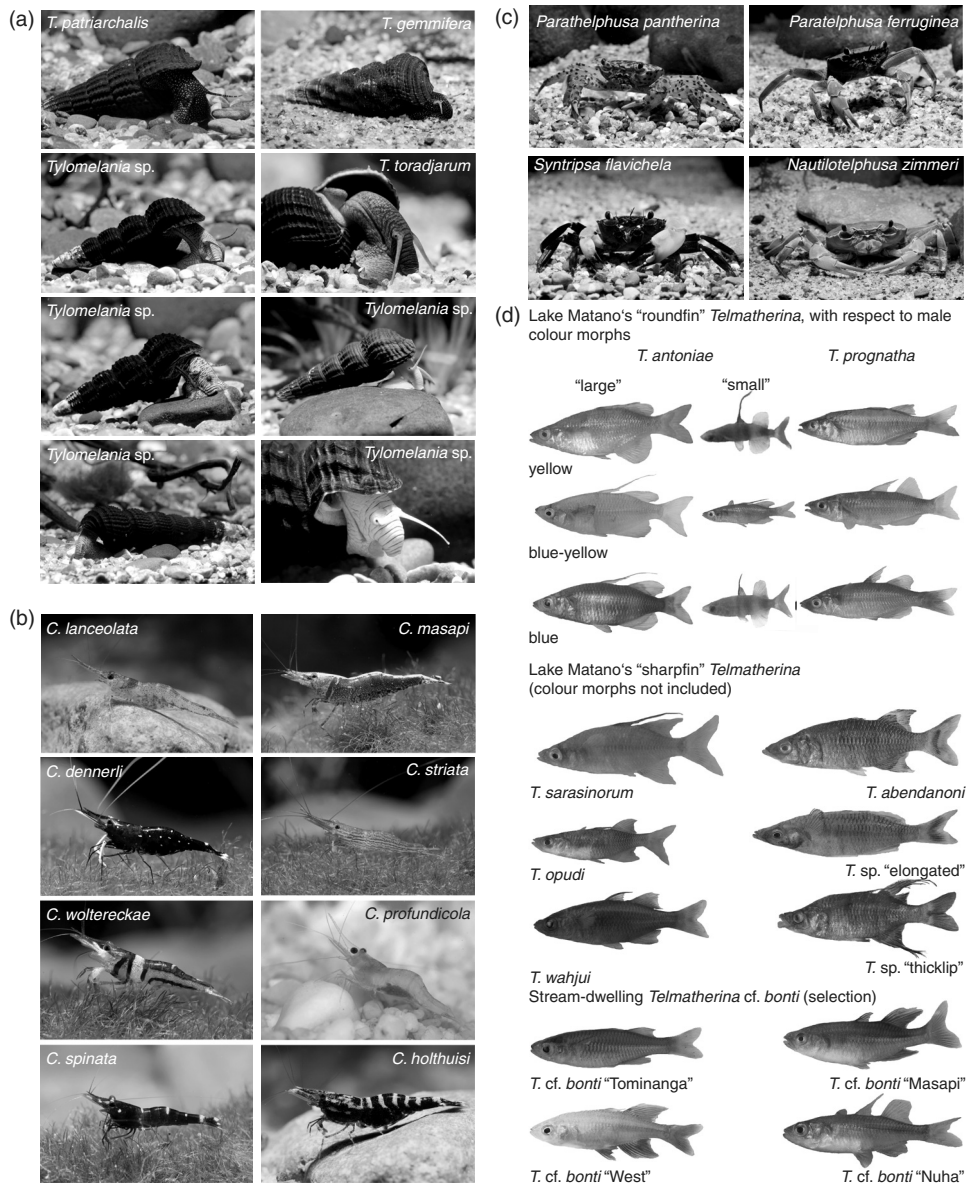
At least 53 species of *Tylomelania* occur in both ancient lake systems of Sulawesi (von Rintelen et al. 2010a), making it the most speciose of all Sulawesi lake radiations. All species are endemic to their respective lake system. A total of 28 species have been described from the Malili system (von Rintelen and Glaubrecht 2003, 2008, von Rintelen et al. 2007a) and 25 morphospecies are estimated to occur in Lake Poso and Poso River (von Rintelen et al. 2010a), albeit only seven taxa have so far been formally described from that system.

In the Malili system, 24 species (86%) are endemic to a single lake (Glaubrecht and von Rintelen 2008, von Rintelen and Glaubrecht 2008) and there are pronounced differences in species diversity in the different lakes (Table 12.2). The high level of endemism in each lake or river is a striking feature of the Malili system, which suggests, in contrast to the situation in Lake Poso, a strong influence of geographic factors in species divergence, resulting in allopatric speciation, which is perhaps not entirely unexpected given the spatial structure of the system (Fig 12.1c).

#### Lake colonisation, adaptive radiation and introgression

Molecular data (1535 bp of mitochondrial DNA from the 16S rRNA (16S) and the cytochrome oxidase subunit I (*COI*) genes) suggest four independent colonisation events in the lakes, three of these in the Malili lakes alone (Fig 12.3a; von Rintelen et al. 2004, von Rintelen et al. 2010a): four strongly supported clades are found within the lakes, one in Lake Poso and three in the Malili system, and riverine taxa are identified as sister groups to three of the four lacustrine clades.

Each colonisation event was followed by diversification into an array of morphologically distinct and ecologically specialised species (see below for details), the hallmark of an adaptive radiation (Schluter 2000). The occurrence of four independent adaptive radiations under identical (Malili system) or very similar (Poso) conditions offers the rare opportunity to study patterns of parallel evolution. These



**Figure 12.2** Characteristic species of the Sulawesi lakes. (a) Snails (*Tylomelania*) (b) Shrimps (*Caridina*). (c) Crabs (Gecarcinucidae). (d) Fishes (*Telmatherinidae*). Photographs of living animals (a–c) courtesy Chris Lukhaup. See plate section for colour version.

**Table 12.2** Species diversity (morphospecies) in the ancient lakes of Sulawesi. The total count for each lake system includes also species endemic to rivers Petea, Tominanga, Larona and Poso.

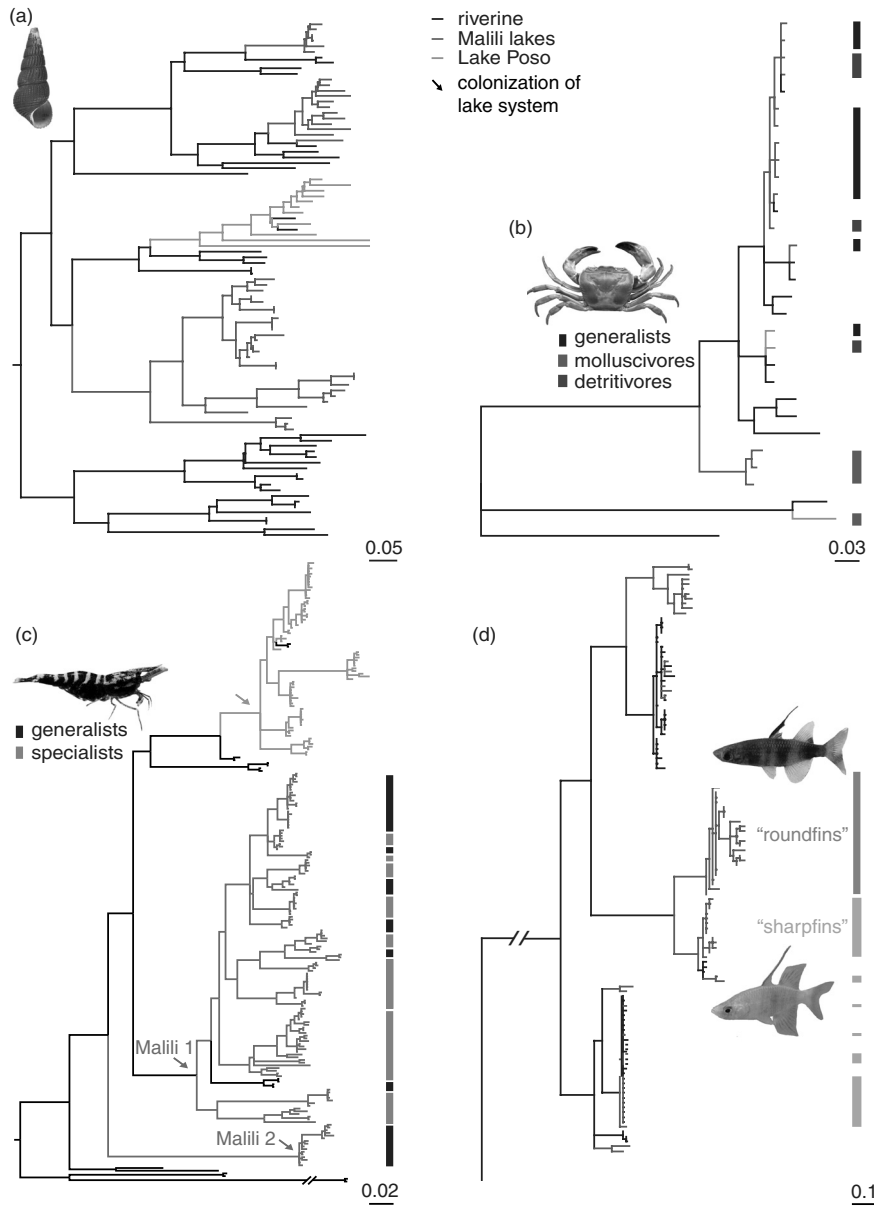
	<i>Tylomelania</i>	Gecarcinucidae	<i>Caridina</i>	Telmatherinidae
Total	53	8	18	31
Malili lakes	28	5	14	31
Lake Matano	6	3	6	10
Lake Mahalona	9	3	7	7
Lake Towuti	10	3	13	12
Lake Masapi	1	1	1	–
Lake Lontoa	2	1	1	1–2
Lake Poso	25	3	4	–

adaptive radiations differ considerably in the extent of their diversification, with species numbers and respective morphological ‘types’ ranging from 3 to 25 (Malili 1: 13 spp.; Malili 2: 12 spp.; Malili 3: 3 spp.; Poso: 25 spp.).

The high level of support for the four major lake clades contrasts with virtually no resolution at the species level for *Tylomelania*. All lacustrine morphospecies for which more than one specimen or population has been sequenced appear polyphyletic in the molecular phylogeny (von Rintelen et al. 2004, 2007a, Glaubrecht and von Rintelen 2008). This lack of resolution is even more remarkable because there is no lack of genetic structure per se in the data, as there are several well-supported subclades within three of the four major lake clades. While this pattern may be caused by several factors (see e.g. Funk and Omland 2003), a pivotal role for introgressive hybridisation is indicated by genotype–phenotype mismatches and nuclear amplified fragment length polymorphism (AFLP) data (Glaubrecht and von Rintelen 2008, von Rintelen et al. 2010a).

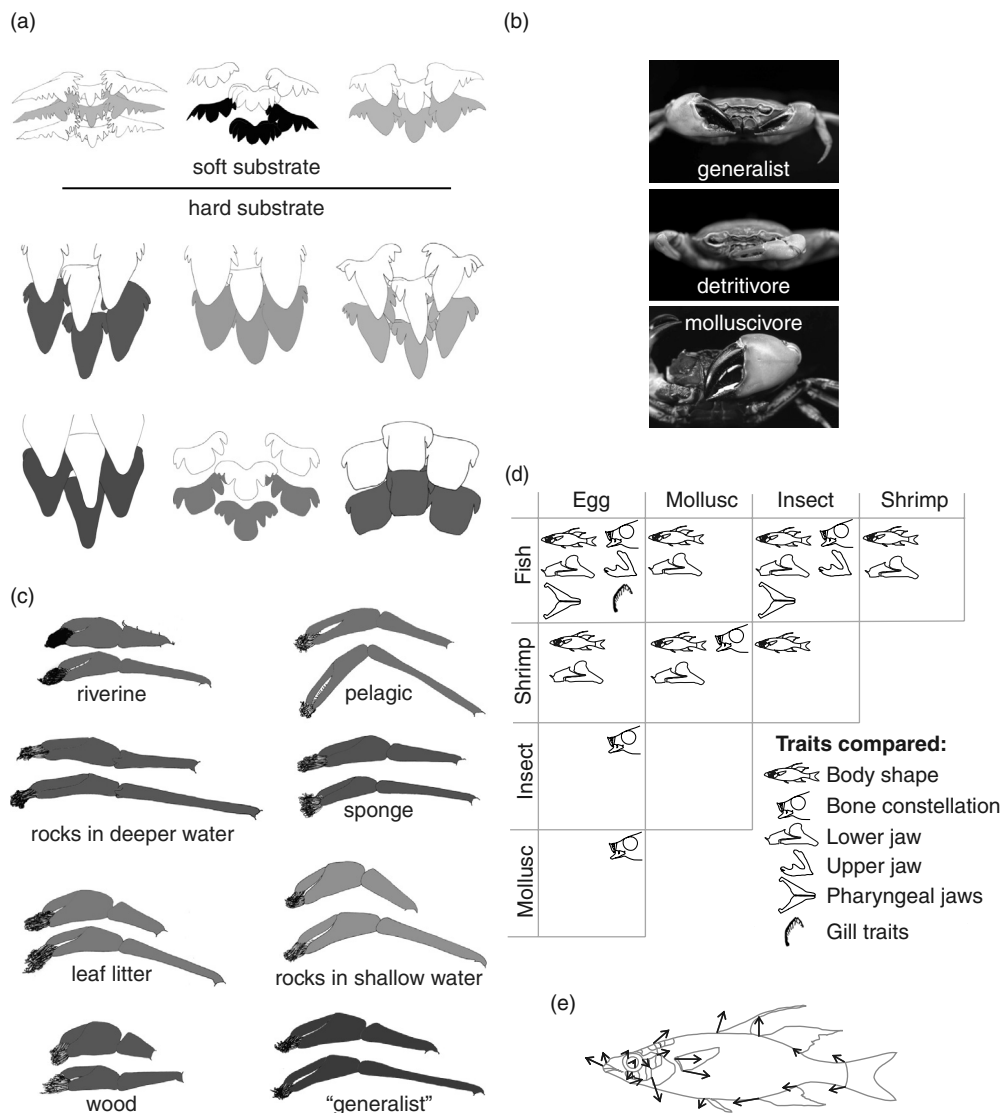
#### Adaptive radiation through trophic specialisation

The morphology of the gastropod radula (rasping tongue) is highly diverse in all lacustrine lineages (Fig 12.4c) with three to six phenotypes found in each clade (von Rintelen et al. 2010a). The radula is a pivotal part of the alimentary system in gastropods, and radular morphological differences have been demonstrated to be indicative of food and substrate preferences (Hawkins et al. 1989). Indeed, radular morphology and substrate are highly correlated in all clades (von Rintelen et al. 2004, 2010). All species in the major lakes of the Malili system and Lake Poso are specialised on either soft (mud, sand) or hard (rock, sunken wood) substrates,



**Figure 12.3** Molecular phylogenies (mtDNA) of the four major taxa in the Sulawesi lakes. (a) Snails (*Tylomelania*) (b) Crabs (Gecarcinucidae). (c) Shrimps (*Caridina*). (d) Fishes (Telmatherinidae). Bayesian inference (BI) based on mtDNA sequences. Lacustrine taxa are highlighted in red (Malili lakes) and green (Lake Poso), riverine species in black. The bars on the right highlight selected morphological or ecological groups. Modified or expanded from von Rintelen et al. 2004 (snails), von Rintelen et al. 2010b (shrimps), Schubart and Ng 2008 (crabs) and Herder et al. 2006 (fishes). Refer to these papers for methodological details. See plate section for colour version.





**Figure 12.4** Habitat and trophic specialization in the Malili lakes. (a) Snails (*Tylomelania*) – major substrate-specific radula types highlighted by colour. (b) Crabs (*Gecarcinucidae*) – chela diversification in ecogroups defined by food preference. (c) Shrimps (*Caridina*) – cheliped diversification in substrate specific ecogroups highlighted by colour; modified from von Rintelen et al. (2010). (d) Fishes (*Telmatherinidae*): significant pairwise differentiation in candidate traits among major trophic groups as defined by stomach contents. (e) Body shape variation along a multivariate axis distinguishing shrimp-feeders from fish-feeders and other trophic specialists. Vector displacements indicate the direction of variation in shape, and show substantial differences in body depth, head shape, fin position and caudal peduncle length (d and e modified from Pfaender et al. 2010). See plate section for colour version.

with about 50% of species occurring on either substrate category (von Rintelen et al. 2007a); some taxa are specialised on an even finer scale, for example occurring on wood only (Glaubrecht and von Rintelen 2008, von Rintelen et al. 2010a). Hard substrate taxa in particular show a wide range of substrate and species-specific radular forms, and there is generally a tight correlation between enlargement of radular denticles and hard substrate (von Rintelen et al. 2004). The parallel substrate-specific occurrence of most radular forms in both ancient lake systems on Sulawesi supports a tight link between radular morphology and substrate. These observations suggest a functional role for the differences found, although a detailed understanding of the underlying mechanisms requires further investigation.

Habitat specialisation (substrate and to a lesser degree depth preferences) and radular differentiation in ancient lake *Tylomelania* enable at least five, possibly up to seven species to coexist at localities with sufficiently structured habitats (Glaubrecht and von Rintelen 2008, von Rintelen et al. 2010a). These data suggest a strong role for ecological factors in the diversification and possibly even speciation of *Tylomelania* (von Rintelen et al. 2010a).

#### Coevolution with crabs

Dramatic changes in snail shell morphology are associated with lake colonisation in both ancient lake systems. The species in each lacustrine clade share characteristic shell features, such as the presence of spiral and/or axial ribs (von Rintelen et al. 2004). Species can be distinguished by their shells, although intraspecific variability is rather high (von Rintelen and Glaubrecht 2003, von Rintelen et al. 2007a). In each lacustrine clade, convergent evolution of thicker shells relative to riverine species has occurred in almost all cases (von Rintelen et al. 2004). Shell thickness can be regarded as indicative of shell strength and thus serves as an estimator of resistance to crab predation. These findings coincide with the occurrence of different species of molluscivorous crabs of the Gecarcinucidae (see 12.2.2), which possess pronounced dentition on their chelae enabling them to crack shells, in each of the lakes. These data on lacustrine gastropod shell strength, structure and also the frequent occurrence of shell repair in lacustrine *Tylomelania*, in combination with the occurrence of large molluscivorous crabs, suggests that evolution in the face of crab predation is a driving factor in initial shell divergence upon colonisation of the lakes (von Rintelen et al. 2004). The presence of massive and dentulate chelae exclusively in the molluscivorous crab species makes it very likely that this is an example of true coevolution because the development of stronger gastropod shells is likely to provoke an evolutionary response in the crabs.

#### 12.2.2 Crabs

Freshwater crabs of the family Gecarcinucidae (see Klaus et al. 2006) constitute another group of conspicuous macroinvertebrates that are abundant throughout

the benthos of all Sulawesi lakes. Most of the species currently known from freshwater streams and lakes of Sulawesi belong to the genus *Parathelphusa*. Others were recently removed from this genus and placed into separate genera, because of their morphological distinctiveness (Chia and Ng 2006). This distinctiveness is especially common in crabs from lakes, and is most likely the result of morphological differentiation as a consequence of ecological specialisation. Establishment of new genera for specialists derived from a lineage of morphologically more conserved generalists often results in paraphyletic units, which is also true in the case of Sulawesi freshwater crabs (Schubart and Ng 2008; Fig 12.3b). The genus *Sundathelphusa* represents a second lineage of freshwater crabs on Sulawesi, which is distributed throughout North Sulawesi, but also occurs in Central Sulawesi as far south as the Poso catchment.

Compared with gastropods, shrimps and fishes, lacustrine species diversity is lower among Sulawesi freshwater crabs. However, in this group there has also been an increase of species recognised within the last decade. Until the year 2000, only one crab species was known from Lake Poso (*P. sarasinorum*) and three from the Malili lakes (*Parathelphusa matannensis*, *P. pantherina*, *Nautilothelphusa zimmeri*). An expedition to both lake systems in January 2000 resulted in the discovery of two new crab species from Lake Poso and two from the Malili lakes (Chia and Ng 2006, Schubart and Ng 2008). Currently, we are investigating whether small-sized crabs from the small satellite lakes Masapi and Lontoa also deserve distinct species status.

#### Ecology and morphology

There are almost no data on the ecology of freshwater crabs from Sulawesi and most of the available information is based on occasional opportunistic observations. Each of the four larger lakes (Poso, Matano, Mahalona and Towuti) is inhabited by three crab species, with only Mahalona and Towuti sharing the same species. However, the recent findings of new species in the larger lakes revealed a pattern suggesting the existence of three ecological niches that are consistently occupied by distinct ecotypes occurring within each lake. We have termed these ecotypes (1) the 'undifferentiated or unspecialised form', (2) the 'detritivore and burrowing form', and (3) the 'molluscivore' form (Schubart and Ng 2008). Most of the lake crabs are considerably larger than their close relatives from the rivers. Nevertheless, crabs of ecotype 1 seem to retain similar proportions of their chelae and ambulatory legs. Their feeding habits and behaviour must therefore be similar to crabs from freshwater streams, which are typically opportunistic generalists. It is noteworthy that crabs occupying this niche have consequently maintained their generic classification and are *Parathelphusa sarasinorum* in Poso, *P. pantherina* in Matano and *P. ferruginea* in Mahalona and Towuti. In addition to these generalists, there are two types of specialists, easily recognisable by the shape of

the chelae. In one case, the size of the chelae is reduced to smaller tweezer-like appendages, as in the case of *Nautilothelphusa zimmeri*, which is found in the major lakes of the Malili system. This species mostly occurs on muddy or sandy substrate and is relatively difficult to find due its mimetic colouration and because it often remains buried in the soft sediment during daytime. The last pair of walking legs is modified to facilitate backward burrowing. We hypothesise that this species specialises on detritus as a food source and refer to it as the 'detritivore' eco- and morphotype (*Migmathelphusa olivacea* in Poso). There are also crabs with proportionally larger chelae that have strong molariform dentition on the cutting edges. This characteristic is otherwise only found in marine crabs that are known to feed on molluscs (and in molluscivorous crabs from Lake Tanganyika) (Vermeij 1994, Marijnissen et al. 2006). We assume and have observed that these crabs are specialised mollusc predators and thus constitute a third feeding guild, the 'molluscivores'. Two species of molluscivorous crabs of the Malili lakes have been placed in the new genus *Syntripsa* (Chia and Ng 2006). In Lake Poso the only species of *Sundathelphusa* of the ancient lakes acts as the resident molluscivore crab species, based on its chelar morphology, and was consequently named *S. molluscivora* (Schubart and Ng 2008).

#### Phylogeny and radiation

Figure 12.3b depicts the most recent mitochondrial phylogeny of Sulawesi freshwater crabs based on approximately 560 bp of 16S. River species not very closely related to one of the lake-colonising lineages are excluded. Molecular analyses reveal that there is a high likelihood of cryptic endemism in the rivers of Sulawesi: crabs from different watersheds can easily be separated genetically and many of them may represent undescribed species. *Sundathelphusa molluscivora* from Lake Poso gives the clearest evidence of independent colonisation of the lakes, because it belongs to a divergent lineage of freshwater crabs. However, the tree also reveals that the molluscivore crabs from the Malili lakes seem to have colonised the lakes independently, and probably earlier than all other taxa. This suggests that the best strategy for new lake colonisers was to specialise on the protein-rich gastropods as prey, possibly leaving vacant those niches exploiting other food sources. Currently the lakes do not harbour species that are closely related to these molluscivore forms. This argues against adaptive radiation and sympatric speciation during this first step of colonisation.

A second sweep of lake colonisation is much younger according to genetic distances among the species and compared with the closest river species. Most surprising is that the colonisation patterns continued to occur almost in parallel in the two independent lake systems. In both cases, a generalist and a detritivore lineage evolved more or less simultaneously, and probably in the presence of a molluscivore species. Moreover, in both cases, closely related river species are extant and

cluster together in monophyletic lineages and generalist and detritivore forms are genetically very similar, to the point where some cannot be distinguished with mtDNA, as in the case of *Nautilothelphusa zimmeri* and *Parathelphusa ferruginea* in Towuti-Mahalona. During these speciation processes, adaptive radiation and possibly sympatric speciation (especially in the single lake system Poso) are likely scenarios.

Overall, we can summarise that currently eight endemic species of freshwater crabs are known from the ancient lakes in Sulawesi. This number will be increased to ten, if genetically separable crab populations from Masapi and Lontoa are recognised as distinct species. This species diversity is not profuse, but the parallel ecological diversification, niche segregation and speciation patterns make these crab species an intriguing case study in evolutionary biology. Ongoing studies with nuclear DNA show that hybridisation and introgression play an important role in their evolution and diversification (P. Koller and F. Kolbinger unpublished data).

### 12.2.3 Shrimps

Among the four major groups of organisms that have radiated in the central lakes of Sulawesi are atyid freshwater shrimps (Crustacea: Decapoda: Caridea). Both lake systems harbour endemic species flocks of *Caridina*, a genus that is generally widely distributed throughout the Indo-Pacific region. With over 200 species, it is the most speciose group within the family (De Grave et al. 2008).

Species of *Caridina* from the Malili lake system were first described by Woltereck (1937a, b). Only 70 years later, new species descriptions followed (Zitzler and Cai 2006, Cai et al. 2009). Today, 21 species are known from the ancient lakes of Sulawesi (including species from the lake drainages), six from Lake Poso and 15 from the Malili lake system (Table 12.2; von Rintelen and Cai 2009). Regarding reproductive biology, all lake species produce relatively large eggs (von Rintelen and Cai 2009). This egg size is typical of direct developers that lack planktonic larval stages and live in landlocked freshwater areas for their whole life (Lai and Shy 2009).

The Malili flock represents the largest radiation within the genus and even within the family. A similar radiation is thus far known only from Lake Tanganyika. However, the Tanganyikan species flock comprises three different genera of atyid freshwater shrimps with 11 species altogether (Fryer 2006). Fryer (2006: 136) stated that ‘Tanganyikan atyids have undergone adaptive radiation in a manner analogous to that of the jaws and oral teeth of cichlid fishes’. The case for adaptive radiation in atyid shrimps has so far only been tested in the Poso (von Rintelen et al. 2007c) and Malili species flocks of *Caridina* (von Rintelen et al. 2010a). The latter will be explained in detail below. Although a direct comparison of Sulawesi and Tanganyika radiations is difficult because they belong to different genera, some of the hallmarks of adaptive radiation are apparently analogous, especially

with respect to morphological differences in feeding appendages (Fryer 2006, von Rintelen et al. 2010a). These differences mainly refer to the chelipeds or the first and second pair of claw-bearing legs (Fig 12.4c) that are used to pick up food particles from the ground (Fryer 1960).

#### Lake colonisation, hybridisation and cryptic species

A molecular phylogeny based on two mitochondrial gene fragments of 16S and *COI* revealed three ancient lake clades in Sulawesi (Fig 12.3c). One clade comprises species from Lake Poso and two clades include all Malili species (von Rintelen et al. 2010a). Thus, at least two independent colonisations of the Malili lake system can be inferred. However, because one of the two clades consists of only a single species, von Rintelen et al. (2010a) suggested an independent colonisation event without subsequent radiation, while the ancestor of the other clade gave rise to a larger radiation with 14 species.

Another result of the molecular phylogeny was the occasional mismatch between morphological and molecular data (von Rintelen and Cai 2009, von Rintelen et al. 2010a). The majority of species are monophyletic in the molecular phylogeny, but seven are not. In some cases von Rintelen et al. (2011) suggested introgressive hybridisation or incomplete lineage sorting. However, there are also likely cases of cryptic species, especially when allopatrically distributed populations of a single morphospecies appear in separate clades that are not even sister to each other (for details compare von Rintelen and Cai 2009, von Rintelen et al. 2010a).

#### Ecological diversification

For the Malili shrimp species flock it has been questioned whether this radiation was adaptive because of the lack of apparent correlation between phenotypic and environmental traits (Woltereck 1937a). However, von Rintelen et al. (2010) distinguished eight different ecogroups defined by substrate differences and morphological characters (mainly the chelipeds; Fig 12.4c). Six ecogroups corresponded to a single habitat each, such as rocks or wood, and the remaining two to several substrates each (Fig 12.4c: a lacustrine 'generalist' and 'riverine', a species whose occurrence is limited to the Malili rivers only). Species within each ecogroup had similar chelipeds, while differences in the morphology of these feeding appendages between ecogroups could be considerable (von Rintelen et al. 2010a). Based on these results, the authors divided the Malili species flock into habitat generalists and specialists (Fig 12.3c). In summary, they suggest a phenotype-environment correlation as a crucial criterion for adaptive radiation (Schluter 2000).

A special case of ecological diversification within the Malili lakes is the first known instance of a sponge-dwelling shrimp in freshwater (von Rintelen et al. 2007b). The species *Caridina spongicola* forms an exclusive and probably commensal association with an as yet undescribed freshwater sponge in the outlet bay

of Lake Towuti, the largest of the Malili lakes. Phylogenetic and ecological data suggest a comparatively recent origin of both taxa (von Rintelen et al. 2007b).

The evolution of colour patterns

Last but not least, the Sulawesi lake shrimp species show a variety of species-specific colour patterns (Fig 12.2c shows several examples from the Malili lakes) that are equally pronounced in both sexes and occasionally in juveniles (von Rintelen and Cai 2009). With such colouration, some lake species strongly resemble marine rather than typical freshwater shrimp. Although colourful species occur rarely at other localities (e.g. Yam and Cai 2003), this abundance of different body colourations within such a confined area is unique within the genus. However, it remains largely speculative whether the colour patterns of the Malili lake species have evolved under ecological (natural) selection and whether assortative mating plays a role in maintaining these patterns (von Rintelen et al. 2010a).

#### 12.2.4 Fishes

Fish species flocks restricted to freshwater lakes are one of the prime examples of adaptive radiation, and have become increasingly popular models for investigating the mechanisms driving speciation processes (Schliewen et al. 1994, Schluter 2000, Kocher et al. 2004, Seehausen 2009, Vonlanthen et al. 2009). The Malili lakes system harbours endemic species or small species flocks of several fish families, the most conspicuous being the endemic radiation of small, sexually dimorphic sailfin silverside fish (Telmatherinidae: Atheriniformes) (Kottelat 1990, 1991). Closely related to rainbow fishes (Melanotaeniidae) from Australia and New Guinea, most sailfin silverside species of the Malili lakes flock are characterised by spectacular male colour polychromatisms, with typically either yellow, blue or blue-yellow courtship colouration (Herder et al. 2006a; Fig 12.2d). Except for two species restricted to small islands off Western New Guinea or Southwestern Sulawesi, all sailfin silverside species known so far occur only in the Malili lakes drainage or surrounding river systems. Most of the species are lake dwelling (lacustrine) and restricted either to the extraordinary deep and isolated hydrological head of the lakes system, Lake Matano, or to the less isolated lakes Mahalona and Towuti (Kottelat 1990, 1991, Herder et al. 2006a). Three genera with roughly 31 morphospecies are currently recognised: *Paratherina* (4 spp.), *Tominanga* (2 spp.), and *Telmatherina* (~23 spp.) (note that the species number for stream-dwelling *Telmatherina* is still tentative; see Herder et al. 2006a for a brief review on exploration history and taxonomy). *Paratherina* and *Tominanga* inhabit in- and offshore habitats of lakes Towuti and Mahalona, *Tominanga* occur in lakes Towuti and Mahalona, and also frequently in the river connecting these lakes (River Tominanga). Only two formally described species of *Telmatherina* are present in these 'lower lakes' and the streams surrounding them: the abundant

lake-dwelling *Telmatherina celebensis*, and *Telmatherina bonti* which form a morphologically highly diverse group inhabiting nearly all permanent rivers and streams of the area, with strong indications for local differentiation (Herder et al. 2006a, b). All remaining lacustrine *Telmatherina* (morpho)species recognised so far are restricted to Lake Matano (Herder et al. 2006a).

The *Telmatherina* species flock of ancient graben-lake Lake Matano

Lake Matano is characterised by the endemism of all lacustrine sailfin silversides inhabiting it, its long-term stability as ancient and extraordinary deep graben-lake (Crowe et al. 2008a, b), and perfect settings for observational studies in its clear waters. These features make it the system of choice for several studies focusing on speciation, adaptive radiation and the maintenance of colour polymorphisms (see Herder and Schliewen 2010 for a comprehensive review). Molecular phylogenetic studies identified two sister clades of lacustrine *Telmatherina* radiating in Lake Matano, which can be recognised by the shape of their second dorsal- and anal fin. ‘Sharpfins’, characterised by conspicuously pointed, elongated fins in males of most morphospecies, are diverse in terms of morphospecies and body shapes (see Fig 12.2d). In contrast to the three morphospecies of ‘roundfins’, with rounded male fins, lake populations of sharpfins are genetically introgressed by stream populations (Herder et al. 2006b, Schwarzer et al. 2008; Fig 12.3d). Together, roundfins and sharpfins of Lake Matano were identified as an ancient monophyletic group, which is however not easily recognisable as such in analyses of nuclear and mitochondrial DNA data because of introgression from riverine invaders (Herder et al. 2006b). Morphological, ecological, behavioural and genetic analyses suggest that both radiations are adaptive with respect to habitat use and trophic ecology, but also indicate that individuals intermediate to distinct ‘morphospecies’ occur (Herder et al. 2006a, 2008, Cerwenka et al. (in press), Pfaender et al. 2010, 2011).

Sympatric speciation in Lake Matano’s roundfin *Telmatherina*

A study on the three roundfin sailfin silverside morphospecies, integrating data on morphology, ecology, mating behaviour and gene flow, provided support for the hypothesis that these lake fish evolved in full sympatry in response to ecological selection pressure within Lake Matano (Herder et al. 2008). The three roundfin morphospecies are distinguished mainly by body depth, size, and snout shape. Males are polymorphic in courtship colouration, being yellow, blue, or blue-yellow (Fig 12.2d). The smallest and most abundant species is an offshore feeder, whereas the larger two species inhabit inshore areas where they segregate according to feeding modes and microhabitat use. Population structure and mating observations support substantial but incomplete reproductive isolation of the three morphospecies, but do not indicate any restrictions in gene flow between the conspicuous colour morphs (Herder et al. 2008). Genomic signatures suggest



that the actions of selection are restricted to only small parts of the genome, a result fitting recent ideas about initial stages of ecological speciation (Nosil et al. 2009). Absence of population structure among populations within the lake and of differentiation among male colour morphs were recently confirmed also based on alternative molecular markers (Walter et al. 2009a, 2009b). Taken together, these data are consistent with incipient sympatric speciation in Lake Matano's roundfins, based on the criteria suggested by Coyne and Orr (2004). Accordingly, the small radiation of roundfins endemic to ancient Lake Matano adds one more case to the rare examples in nature where speciation is clearly not explained by separating effects of strict geographic isolation. The mechanism most likely driving roundfin speciation is adaptation to alternative modes of resource exploitation, leading to the alternative patterns of habitat use and trophic specialisation. The comparatively young age of the Matano species flock (Herder et al. 2006b, Roy et al. 2007), its compact spatial settings and the incipient character of its roundfin radiation renders this group a highly promising model group for further studies on the genomic consequences of ecological speciation.

#### Adaptive radiation in Lake Matano's sharpfins

Schluter's (2000) criteria provide a framework for evaluating the adaptive character of radiations. Common ancestry, rapid speciation and correlation of phenotypes with their environment and utility of the traits evolved are prerequisites for stating that a radiation is truly 'adaptive'. Both Lake Matano's endemic sharpfin *Telmatherina* and its sister clade of roundfins show some conspicuous trophic specialisations that suggest that traits related to feeding modes are adaptive. One sharpfin species is characterised by enlarged, puffy lips that are most likely an adaptation to shrimp feeding (Herder et al. 2006a, Pfaender et al. 2010). Another species specialised in eating the eggs of other sailfin silversides and is especially abundant at spawning sites where it uses alternative behavioural tactics for obtaining con- and heterospecific eggs (Gray et al. 2007, 2008a, Cerwenka et al. in press). To test the hypothesis that the sharpfin radiation is adaptive, a recent morphological study compared potential key traits such as shape and configuration of jaw bones, shape of the 'second set of jaws' in the fishes' throat (pharyngeal jaws), body shape, number of gill rakers and body size with stomach contents. Surprisingly it revealed fine-scale patterns of morphological differentiation among groups of sharpfins defined by stomach contents (Pfaender et al. 2010; see Fig 12.4d). The most distinct adaptations are in fish-, shrimp- and egg-feeding groups, with trait expression being widely consistent with other adaptive fish radiations. The strong correlation between morphological characters and feeding specialisation is detectable in the whole set of traits analysed, and serves as evidence for adaptation as a result of ecological selection pressure. Accordingly, this strongly supports the hypothesis that the sharpfin species flock fulfils the criterion of 'trait

utility' (Schluter 2000) – however, the biomechanical function of the specialised traits remains to be demonstrated in detail. Although introgressed by stream populations, lake populations of sharpfins clearly also fulfil the criterion of common ancestry. In line with the absence of mitochondrial lineage sorting within sharpfins (Herder et al. 2006b), molecular (Roy et al. 2007) and geological (von Rintelen et al. 2004) age estimates clearly support rapid evolution. Phenotype-specific habitat use, as evident in roundfins, remains the last of Schluter's (2000) four criteria to be critically evaluated in sharpfins.

No evidence of speciation by sexual selection:  
colour polymorphic sailfin silversides

The spectacular male colour morphs are, at least in roundfins, clearly not linked to population structure (Herder et al. 2008, Walter et al. 2009b). This contrasts with findings in African cichlid fish radiations where the evolution of alternative male colour morphs is explained by alternative female mating preferences, finally leading to speciation (Seehausen et al. 2008). Male colour morphs in Lake Matano's *Telmatherina* are probably best explained by a polymorphism maintained by heterogeneous visual environments. Gray et al. (2008b) reported differential conspicuousness of alternative male colour morphs in two contrasting courting habitats (shady root versus open beach sites), corresponding to differential reproductive fitness. Given the theoretical plausibility that environmental heterogeneity may maintain colour polymorphisms in nature (Chunco et al. 2007, Gray and McKinnon 2007), patchy distribution of opposing visual environments or other environmental factors affecting light conditions (e.g. seasonal or diurnal effects) may provide an explanation for this phenomenon. Such hypotheses await further investigation. Interestingly, colour polymorphisms occur in all major groups of the radiation, including populations inhabiting alternative habitats such as shady, fast-flowing streams or calm and open beaches of the lakes (Herder et al. 2006a), supporting the idea of common mechanisms maintaining this conspicuous phenomenon.

## 12.3 Evolution of the Sulawesi lake species flocks

Parallel radiations of gastropods (von Rintelen et al. 2004, von Rintelen and Glaubrecht 2005, Glaubrecht and von Rintelen 2008, von Rintelen et al. 2010b), parathelphusid crabs (Schubart and Ng 2008, Schubart et al. 2008), atyid shrimps (von Rintelen et al. 2007c, 2010b) and telmatherinid fishes (Herder et al. 2006b, Herder and Schlieven 2010) in the lakes, particularly the Malili system, offer an outstanding opportunity to compare diversification patterns in organisms differing in fundamental biological properties within the same environmental setting.

Detailed comparative analyses, especially on the impact of direct interactions between these animal groups for speciation, are under way. While joint in-depth analyses are not yet available, the published results (see citations above) already suggest a number of commonalities between some or all groups.

Ecological speciation in response to alternative modes of resource use has clearly been demonstrated or appears at least highly likely in all of the Malili and Poso radiations analysed so far. Specialised radular morphology in gastropods, alternative forms of chelipeds or chelae in shrimps and crabs, and an array of traits including jaw function and body shape or the number of gill rakers in sailfin silversides clearly show signatures of ecological selection with respect to trophic resource use. In line with alternative modes of habitat use and utility of the adapted traits for fine-scaled trophic adaptations, these findings clearly support the idea that speciation following disruptive ecological selection pressure is the main force explaining local diversification observed in all these morphologically and ecologically highly distinct organisms. Accordingly, all these radiations are likely to constitute cases of adaptive radiation.

Although both Poso and the Malili lakes are among the oldest freshwater lakes on earth, they are young in terms of geological timeframes. Hence, it is not surprising that their endemic radiations are apparently in the early stages of species-flock formation. This includes significant levels of hybridisation or introgression among species of lake-dwelling lineages evolving in sympatry or after multiple colonisation events (von Rintelen et al. 2004, 2007c, Herder et al. 2008). Likewise, hybridisation occurs among lake- and stream species (von Rintelen et al. 2004, Schwarzer et al. 2008), resulting in complex patterns of mitochondrial diversity in sailfin silversides and gastropods that are not consistent with nuclear DNA data and morphology (von Rintelen et al. 2004, Herder et al. 2006b, Roy et al. 2007). Theory and a few animal case studies (e.g. Schlieffen and Klee 2004, Seehausen 2004, Bell and Travis 2005, Stelkens and Seehausen 2009) suggest that reticulate evolution by hybridisation might promote adaptive divergence in species-flocks, a striking hypothesis that however remains to be tested critically in the case of radiations in the Malili lakes.

In contrast to adaptations affecting trophic morphology of all groups analysed so far, the conspicuous colour patterns occurring in sailfin silversides (body and fins), crustaceans (body and legs) and gastropods (body) most likely result from very different mechanisms. Colour most likely plays a role in species recognition and speciation in cichlid fishes, one of the prime model systems in speciation research (Streelman and Danley 2003, Seehausen et al. 2008). In Sulawesi's lacustrine atyid shrimp radiations, conspicuous colour patterns widely coincide with morphological species concepts, suggesting that colouration might indeed play a role in processes of divergence (von Rintelen et al. 2007c, 2010). Colour-driven diversification might also contribute to diversification in *Tylomelania* gastropods, because substantial numbers of morphospecies especially in Lake

Poso are characterised by bright pigmentation of the soft body, which appears difficult to explain solely in light of ecological selective pressures. However, visual systems and factors influencing patterns of mate choice are not yet explored in *Tylomelania* snails and atyid shrimps, such that further studies are required to test critically the hypothesis of colour-driven diversification in both groups. In the Malili lakes sailfin silverside radiation, conspicuous male colour polymorphisms correlate with mating success in different habitats, but are not associated to population divergence (Herder et al. 2008, Gray et al. 2008). Sailfin silversides have a pentachromatic visual system, ranging from UV to yellow including the spectra of *Telmatherina* male courtship colouration (Gray et al. 2008). Stable colour polymorphisms are the most likely explanation for this conspicuous phenomenon – there are so far no indications for a link between colour polymorphisms and speciation in sailfin silversides. Taken together, additional efforts will be required to provide a further elucidation of evolutionary responses common to all groups of organisms analysed in Sulawesi's ancient lakes so far, including potential universal patterns of radiation in the light of crucial differences explained by the organisms' particular biology.

## 12.4 Threats and conservation

The Sulawesi lakes are a 'hotspot' of Southeast Asian biodiversity and at the same time a scientific treasure trove for evolutionary biology research. Unfortunately, the lakes' environment is threatened by several factors. At both lake systems, the growth of local human communities is a general point of concern, because it seems inevitably coupled with pollution and habitat destruction. The continued activities of illegal loggers also threaten to damage lake habitats by erosion of surface soil. This effect is more severe at the Malili lakes, where the shores have been less densely populated and less accessible for a longer time than those of Lake Poso. Although all of these issues are notoriously difficult to tackle, efforts should at least be made to increase community awareness about the problems because they also have the potential to threaten the future of the local people.

More specific risks for the lake ecosystems stem from the activities of the nickel mining company P.T. Vale Indonesia at the Malili lakes, which, in addition to their role in opening up the area, directly impact the sensitive environment of the lakes. Although appreciable efforts have been made by this company to preserve the water quality in the lakes, less attention is paid to the importance of protecting the environment of the lakes and particularly the rivers connecting and draining them. The recently finished construction of a third hydroelectric dam at Larona River is just one example. A dam has also been constructed at Poso River just above the Sulewana Rapids, which are a hotspot of endemic species adapted to fast-flowing

water. New risks have emerged only during the last years, when the collecting of live snails, crabs and shrimps for export started to resemble a 'gold rush' among pet traders fuelled by the demand from aquarium enthusiasts, and an increasing number of introduced alien freshwater species appeared in the lakes (Herder et al., in prep). This enumeration of actual and potential risks to the lake biota indicates that their conservation should have a high priority. The risk from pet traders may also have beneficial side effects, though, as it has significantly increased public awareness about the lakes' unique fauna in several countries.

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