Intraspecific geographic differentiation and patterns of endemism in freshwater shrimp species flocks in ancient lakes of Sulawesi

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ABSTRACT

Freshwater shrimps of the genus *Caridina* are the most speciose group within the family Atyidae. This diversity can be witnessed in two ancient lake systems of the Indonesian island Sulawesi, where 21 currently described species, reflect the largest radiations of freshwater shrimps known worldwide. Both lake systems provide similar environmental conditions with locally heterogeneous habitats: Lake Poso is a single lake with less pronounced geographic structure than the Malili lake system with five lakes forming part of the same drainage system. The spatial subdivision in the Malili lakes and the higher number of species compared to Lake Poso (15 vs. 6) renders this system special interest for the study of geographic differentiation.

Using mitochondrial DNA data, the phylogeographic patterns of the majority of the lacustrine species in the radiations are assessed. Both lake systems have been sampled comprehensively over several years, i.e. 137 localities altogether. A molecular phylogeny based on two standard genes (16S and COI) was reconstructed. A mismatch between molecules and morphology hints towards cases of introgression or incomplete lineage sorting in some species. To analyse geographic differentiation, geographic data for each species was mapped onto the phylogeny. In addition, haplotype networks were constructed to assess intralacustrine geographic patterns. In general, the molecular phylogeny revealed that all species, with one exception, are endemic to the ancient lakes, always showing local endemism within one system or even single lakes. Species from the Malili lakes revealed more geographic differentiation than species from the solitary Lake Poso. In several species from the Malili lakes, geographically separated populations form distinct subclades, suggesting limited gene flow between these populations. In other cases, allopatrically occurring populations within species were found in separate clades that were not even sister groups to each other in the overall phylogeny. This suggests not only the existence of cryptic species but also of unrecorded endemism.

1 Introduction

Freshwater caridean shrimps occur in all biogeographic regions bar Antarctica (De Grave et al. 2008), but are in general among the less studied groups of decapod crustaceans. This might not be surprising regarding the fact that the majority of shrimp-like decapods are found in marine environments. Freshwater taxa only account for approximately a quarter of all described Caridea and are numerically dominated by the two families Atyidae and Palaemonidae (see De Grave et al. 2008). At present, the Atyidae contain 42 extant genera (De Grave et al. 2009; Cai 2010). The vast majority of species are described within the genus *Caridina* H. Milne Edwards 1837 (around 200 species were estimated by De Grave et al. 2008), which is widely distributed throughout the Indo-West Pacific. These small shrimps (2–3 cm) are often abundant in various freshwater habitats (including cave systems). Regardless of its doubtful monophyly (Page et al. 2007), *Caridina* is generally interesting for phylogeographic studies: it comprises widespread species with high dispersal abilities (catadromous marine larval development) and land-locked species with low dispersal abilities (direct larval development) only occurring in true freshwater environments (Lai & Shy 2009).

Typical land-locked freshwater habitats are, for example, highland rivers and lakes. In ancient lakes, several crustacean groups have produced extensive species flocks with a high degree of endemicity (Martens & Schön 1999). For biologists, an ancient lake is generally an extant lake that exists for at least 100,000 years (Gorthner 1994; Martens 1997). The best known example certainly is the amphipod radiation in Lake Baikal (Macdonald et al. 2005). Among the few cases of ancient lake radiations in decapod crustaceans are the endemic species flocks of freshwater crabs and shrimps in Lake Tanganyika (Fryer 2006; Marijnissen et al. 2008) and of crabs and shrimps in the two ancient lake systems of the Indonesian island Sulawesi, the former Celebes (Schubart & Ng 2008; von Rintelen & Cai 2009).

The two Sulawesi lake systems, the focus of this chapter, are located in the central mountains of the island (Figure 1A). Lake Poso (Figure 1B) is a deep, solitary and trough-like lake that is drained northwards via Poso River into the sea. The Malili lake system comprises five lakes sharing a common drainage (Figure 1C): the three larger lakes, Matano, Mahalona, and Towuti, are directly connected via Petea and Tominanga River, whereas the two smaller satellite lakes, Lontoa and Masapi, are not directly connected. The Malili system is drained westwards via Larona River into the sea (Figure 1C). The age of Lake Matano (with 590 m, the eighth deepest lake in the world) was estimated at 1–2 my (Geoffroy Hope, pers. comm.); Lake Towuti may be ca. 600,000 years old based on seismic data (James Russell, pers.comm.). Both lake systems provide similar environmental conditions (oligotrophy, very low nutrient and organic content, high transparency; Giesen 1994; Haffner et al. 2001) with locally heterogeneous habitats ranging from different types of soft (sand, mud, macrophytes) to hard substrates, such as wood or rocky drop-offs (von Rintelen et al., in press). In general, the solitary Lake Poso has a less pronounced geographic structure than the five connected Malili lakes and a less heterogeneous habitat fragmentation. The spatial subdivison makes the Malili system especially interesting for the study of geographic differentiation.

Four major groups of freshwater organisms have radiated in the central lakes of Sulawesi: fishes, snails, crabs, and shrimps (for details see von Rintelen et al., in press). Both lake systems harbour endemic species flocks of *Caridina* first described by Woltereck (1937) for the Malili lakes and by Schenkel (1902) for Lake Poso. Today, 21 endemic species are known (including the river systems), six from Lake Poso and 15 from the Malili lake system (von Rintelen & Cai 2009). The Malili flock represents the largest radiation within the genus *Caridina* and even within the Atyidae (von Rintelen & Cai 2009). A similar atyid radiation is so far only known from Lake Tanganyika. However, the Tanganyikan species flock comprises three different genera of other atyid shrimps with a total of 11 species altogether (Fryer 2006).

A recent study inferred from mitochondrial DNA sequences revealed three highly supported lake clades, one in Lake Poso and two in the Malili lake system (Figure 1D), that were interpreted as three independent lake colonizations (von Rintelen et al. 2010). In both species flocks, morphological, genetic, and ecological data were further clearly indicative of adaptive radiations, involving habitat-specific diversification of feeding appendages (von Rintelen et al. 2007, 2010). In case of the Malili lakes, von Rintelen et al. (2010) and Roy et al. (2006) already found hints for a geographic differentiation within the entire species flock and within single species, e.g. genetic differences between allopatrically occurring populations. Thus, it was suggested that inter-lacustrine allopatry plays an important role in species diversification and speciation in the Malili system (von Rintelen et al. 2010). In Lake Poso, results showed no significant intraspecific genetic structuring so far, which was accounted for by the lack of geographic subdivisions in this trough-shaped lake (von Rintelen et al. 2007).

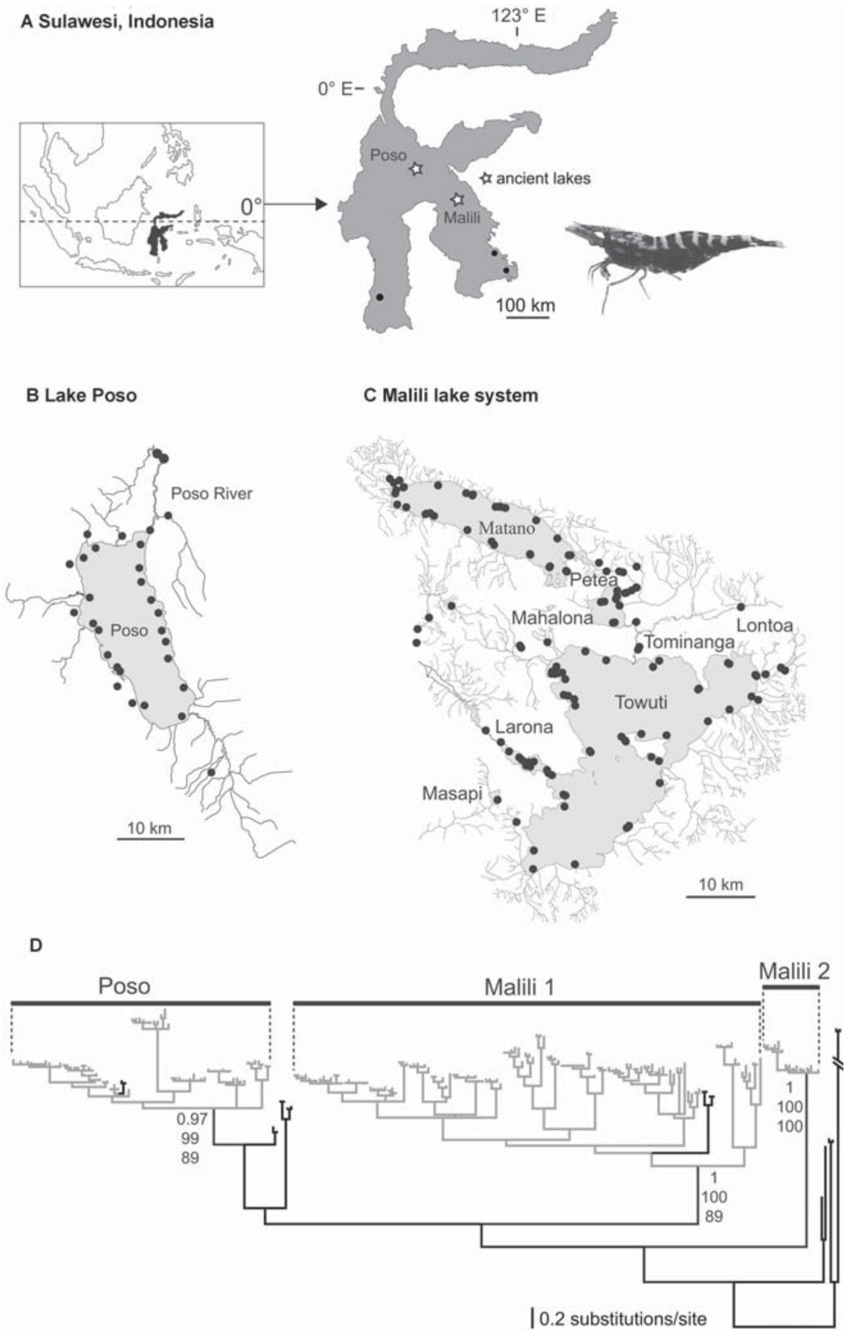

Figure 1. Sulawesi (Indonesia) and the ancient lakes. (A) Geographic location of the ancient lakes. (B) Lake Poso with collecting sites. (C) Malili lake system with collecting sites. (D) Bayesian Inference phylogram (1332 basepairs of combined 16S and COI mtDNA) showing three ancient lake clades (grey lines) in Sulawesi. The black lines indicate species from rivers outside of the lakes. Numbers next to each lake clade are, from top, Bayesian posterior probabilities, ML and MP bootstrap values (tree modified from von Rintelen et al. 2010).

Table 1. Maximum intraspecific genetic divergences (p-distance in %) within the three ancient lake clades. Source: *: von Rintelen et al. (2007); **: von Rintelen et al. (2010).

Species of *Caridina*	COI	16S
Poso (entire clade)*	**7.7**	**3.7**
*C. acutirostris**	1.2	0.7
*C. caerulea**	0.8	0.6
*C. ensifera**	2.3	0.9
*C. longidigita**	1.3	0.4
*C. sarasinorum**	0.9	0.2
*C. schenkeli**	4.9	2.1
Malili 1 (entire clade)**	**11.5**	**6.4**
*C. lingkonae***	0.8	0.4
*C. dennerli***	0.8	0.4
*C. glaubrechti***	9.7	3.1
*C. holthuisi***	5.2	2.4
*C. loehae***	2.2	0.7
*C. mahalona***	8.3	2.7
*C. masapi***	2.5	1.8
*C. parvula***	5.0	2.0
*C. profundicola***	1.8	0.4
*C. spinata***	0.5	0.0
*C. spongicola***	1.8	1.1
*C. striata***	6.8	2.0
*C. tenuirostris***	3.3	1.8
*C. woltereckae***	5.0	1.5
Malili 2**		
*C. lanceolata***	2.8	0.4

On the basis of previous studies (von Rintelen & Cai 2009; von Rintelen et al. 2007, 2010), this chapter compares results from both lake systems; it summarizes and reviews some general ideas on radiation and species diversity in both ancient lake systems, whereas in earlier molecular studies results were discussed separately and mostly at the interspecific level (Lake Poso: von Rintelen et al. 2007; Malili lake system: von Rintelen et al. 2010). As a new methodological approach in this chapter, phylogeography is studied by utilizing haplotype networks and mapping geographic distribution of haplotypes for each of the species. Hereby, new hypotheses could be tested such as populations from the Malili lakes showing higher genetic and geographic structure than populations from Lake Poso due to the higher geographic division of the Malili lake system. The so far rather superficial phylogeographic approach to the Sulawesi lake radiations of *Caridina* is therefore taken further into detail with the aim to reveal new insights into intraspecific geographic differentiation and patterns of endemism of atyid shrimps from the islands ancient lakes.

2 MATERIAL AND METHODS

Specimens were collected from both ancient lake systems and surrounding rivers between 2002 and 2007 from 137 sites (107 from the Malili lakes, 30 from Lake Poso). Sampling was either done with hand nets or with plastic containers while snorkeling and scuba diving. Sampling sites were chosen to cover all geographic subdivisions of the lakes as well as all major river systems. Basic ecological data such as substrate or depth were recorded. The dense coverage of sampling points is visualized in Figures 1A and 1C (the lack of sampling points in rivers can be attributed to the absence of shrimps, e. g. in the rivers southeast of Lake Towuti in Figure 1C). Specimens were fixed and preserved in 70–95% ethanol, vouchers are deposited in the crustacean departments of the Museum of Natural History of Berlin, Germany (ZMB), and the Museum Zoologicum Bogoriense, Indonesia (MZB); for details on voucher numbers see von Rintelen et al. (2010). Species were generally identified using a suite of morphological characters commonly employed in atyid taxonomy as described by von Rintelen & Cai (2009).

The three major lakes of the Malili lake system are drained and/or connected by the larger rivers Petea, Tominanga, and Larona (compare Figure 1C). As these can be considered extensions of the lakes themselves (albeit with currents), specimens from these rivers have been treated here as lacustrine and not as riverine samples. In consequence, these localities have been assigned to the lake of which the respective river is draining: Petea = Lake Matano; Tominanga = Lake Mahalona; Larona = Lake Towuti. The tree topology of the molecular phylogeny shown in Figures 1–3 and the maximum intraspecific genetic divergences shown in Table 1 of species from both lake systems were taken and modified from the studies by von Rintelen et al. (2007, 2010), in which two mitochondrial gene fragments, approximately 560 basepairs (bp) of the large ribosomal subunit (16S) and 861 bp of the cytochrome c oxidase subunit I (COI) were sequenced; for details on molecular methods please see von Rintelen et al. (2010). To illustrate intraspecific geographic differentiation of single species occurring in different lakes of the Malili lake system, geographic data for each species were mapped onto the phylogeny in Figure 2 (this was not done for Lake Poso species due to the single lake situation).

The dataset for haplotype networks were taken from von Rintelen et al. (2010) for both genes separately: 141 specimens of 15 species from the Malili lake system and 70 specimens of six species from Lake Poso. DAMBE v. 5.0.66 (Xia & Xie 2001) was used for reducing the dataset to unique haplotypes. Network reconstruction was done using TCS v. 1.21 (Clement et al. 2000) with a connection limit (parsimony criterion) of 95 and occasionally 90% for connection of more distant networks (as in *C. mahalona*, *C. tenuirostris*, *C. woltereckae*, *C. lanceolata*, and *C. glaubrechti*). For the analysis of intraspecific geographic differentiation between and within lakes, the geographic distribution of haplotypes was then mapped onto images of both lake systems.

3 RESULTS AND DISCUSSION

3.1 Radiation and species diversity

The three ancient lakes' clades (Figure 1D) are shown in detail for species of the Malili lake system (Figure 2) and Lake Poso (Figure 3A). The majority of species from the Malili lakes (Figure 2) form a single clade (Malili 1). The second clade (Malili 2) consists of only one species, *Caridina lanceolata*. In Lake Poso (Figure 3A), all species can be found in only one clade. These three clades were interpreted by von Rintelen et al. (2010) as three independent lake colonization events with subsequent adaptive radiations in two cases (Malili 1 and Poso).

A mainly morphology- and ecology-based revision of all ancient lake species revealed a total number of 21 species for both lake systems and, with 15 (Malili) vs. 6 (Poso) species, a higher diversity in the Malili lakes (von Rintelen & Cai 2009). This difference in taxonomic diversity is also reflected in the maximum intraspecific genetic distances found in each clade (Poso: 7.7%; Malili 1: 11.5%; Malili 2: 2.8%; COI, p-distance; Table 1). The additional molecular analyses based on mitochondrial DNA (von Rintelen et al. 2007, 2010) in part corroborated the results of

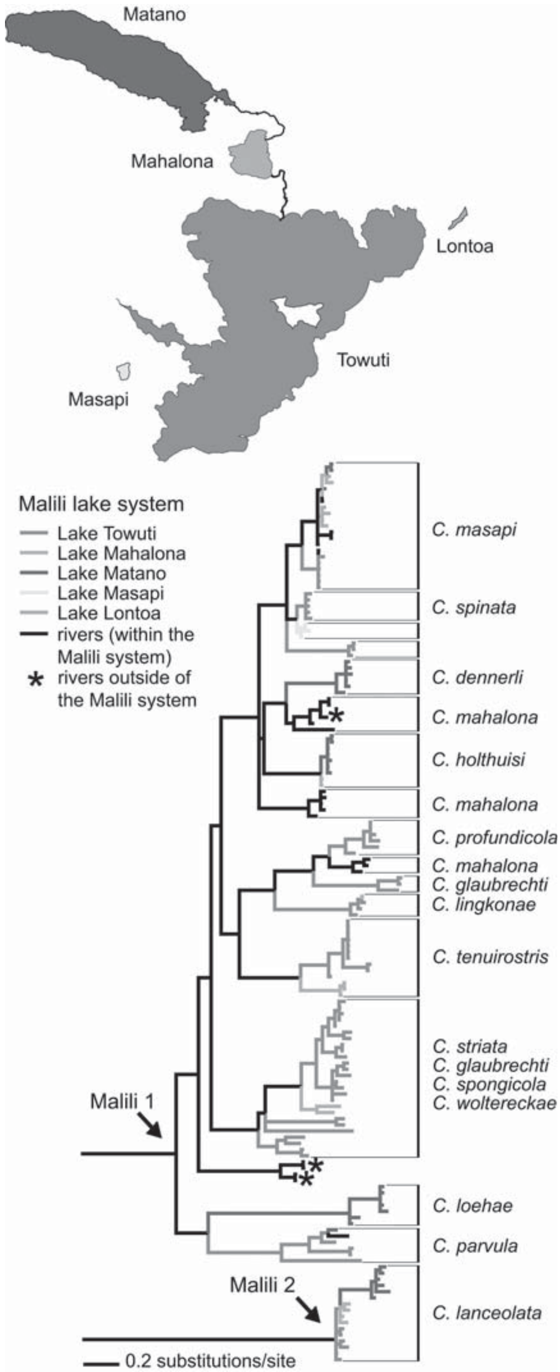

Figure 2. Bayesian Inference phylogram (1332 basepairs of combined 16S and COI mtDNA) of *Caridina* from the Malili lake system. Detail topology of the two Malili clades with its 15 species (for the entire topology, compare Figure 1D). The occurrence of sequenced specimens in single lakes and surrounding rivers are color-coded (see Figure 6 in Color insert; modified from von Rintelen et al. 2010).

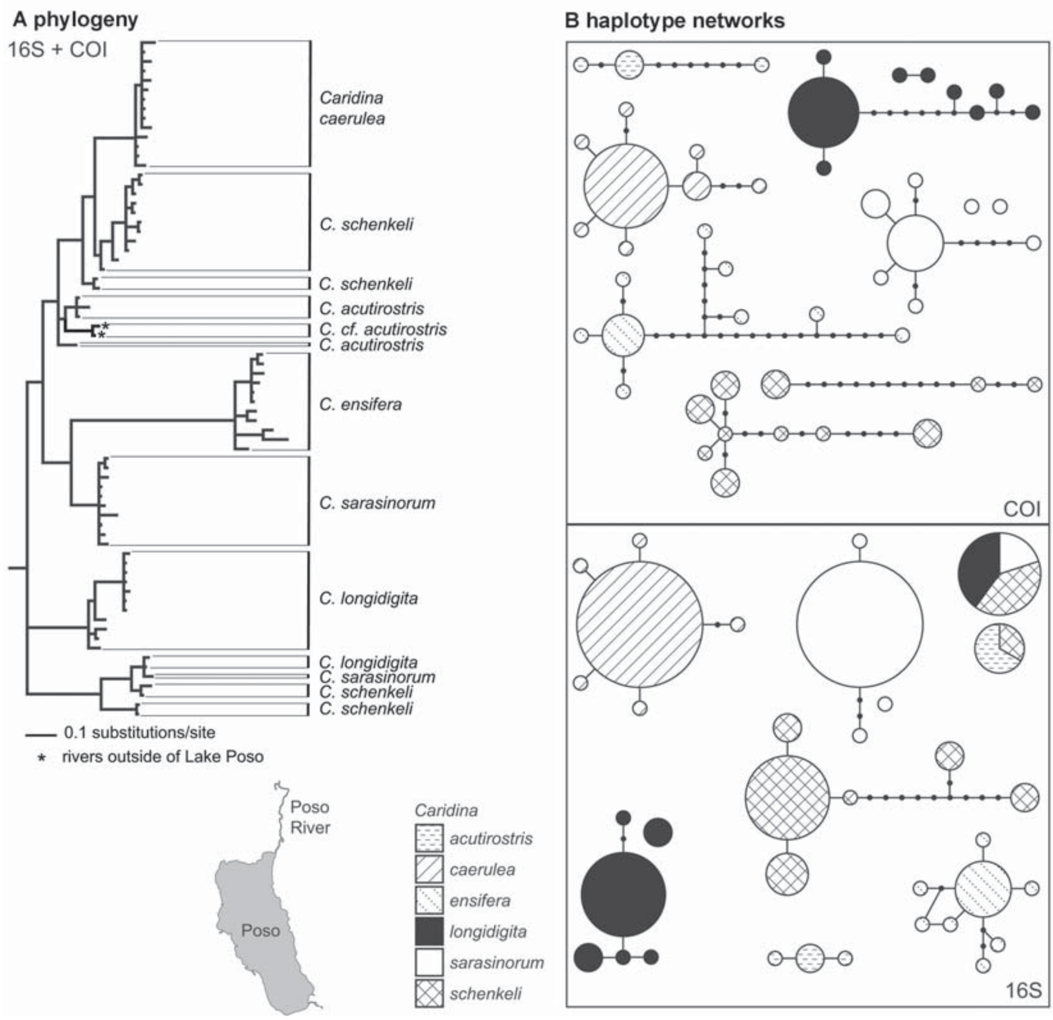

Figure 3. Lake Poso *Caridina*. (A) Bayesian Inference phylogram (mtDNA, 16S and COI) of *Caridina* from Lake Poso and surrounding rivers. Detail topology of the Poso clade with its six species (modified from von Rintelen et al. 2010). (B) Haplotype networks for the six Poso species from two mitochondrial genes, COI (upper panel) and 16S (lower panel).

the morphological species delimitation: several species from both systems appear monophyletic in the molecular phylogeny, for example *Caridina spinata*, *C. dennerli*, *C. lingkonae* from the Malili lakes (Figure 2) and *C. caerulea* , *C. ensifera* from Lake Poso (Figure 3A). However, several other species could not be recovered as monophyletic in the molecular tree, for example the *Caridina striata/glaubrechti/spongicola/woltereckae* clade (Figures 2 and 6) and *C. schenkeli*, *C. longidigita*, *C. sarasinorum* from Lake Poso (Figure 3A). Table 1 further illustrates the generally higher maximum genetic divergences (p-distance in %) in these species compared to those that appear monophyletic in the molecular tree: good examples are *Caridina striata/C. glaubrechti/C. woltereckae* (6.8%/9.7%/5.0%) vs. *C. spinata/C. dennerli/C. lingkonae* (0.5%/0.8%/0.8%) from the Malili lakes (Figure 2) and *C. caerulea* (0.8%) vs. *C. longidigita* (1.3%) from Lake Poso (Figure 3A). Haplotype networks (without geographic context) are shown for the six Poso species in Figure 3B. The COI-based networks (upper panel) show a good resolution at species level. All haplotypes appear in separated and species-specific networks, but haplotypes of three species, viz. *Caridina schenkeli*, *C. sarasinorum* and *C. longidigita*, are not always connected to their main network. In the 16S-based network (lower panel), representatives of these three species share a common haplotype which is different from their respective species-specific network (see also shared haplotype by *C. acutirostris* and *C. schenkeli*). Corrspondingly, in the phylogeny, the shared haplotypes of these species also cluster together in a single clade (Figure 3A), which is distinct from the 'main' clades comprising the vast majority of haplotypes of each species. This is an indication for additional cryptic species which appear to hybridize with these genetically heterogeneous species. Less likely is the explanation of introgressive hybridization or incomplete lineage sorting as suggested in von Rintelen et al. (2007), as these represent unrelated haplogroups.

In general, all 21 former morpho-species in both lake systems were regarded and described as valid species (von Rintelen & Cai 2009). However, previous studies using molecular methods gave evidence for mismatch between morphology and molecules, which could be explained by introgressive hybridization, incomplete lineage sorting (persistence of ancestral polymorphism after recent speciation events), or the prevalence of cryptic species (von Rintelen et al. 2007, 2010). In Lake Poso, two morphologically almost indistinguishable (except for body coloration of living specimens in the field) species, *Caridina caerulea* and *C. ensifera* (compare Figure 3A), were considered one species, before genetic data revealed the existence of a "cryptic" species (von Rintelen et al. 2007): sympatrically occurring populations appeared in two separate clades that were not sister groups to each other. All members of each clade were characterized by different color morphs ("blue" or "red") as living animals in the field (not after alcohol bleaching). Later, other morphological and behavioural differences between the two species were found. Based on these results, von Rintelen and Cai (2009) described the former unrecognized species as a new taxon. For the Malili species flock, similar cases of cryptic species were found, although with a geographic background (von Rintelen et al. 2010). In three cases (*Caridina masapi*, *C. holthuisi*, and *C. mahalona*), allopatric populations (from different lakes) of single species appeared in separate clades that are not sister groups to each other (Figure 2), e.g. a Lake Towuti clade and a Lake Matano/Mahalona clade in *Caridina holthuisi* and a separate Lake Masapi clade in *C. masapi*. Based on these results, the real species diversity might even be higher than described.

3.2 Patterns of endemism

In general, all ancient lake species are endemic to their respective lake system (von Rintelen & Cai 2009; von Rintelen et al. 2010). *Caridina mahalona* is the only species of which one specimen was also collected from a different drainage system just north of Lake Matano (asterisk within the *C. mahalona* clade in Figure 2). In both lake systems, lacustrine species mainly occurring within the lakes can be distinguished from riverine species mainly or exclusively occurring in the surrounding river systems (compare maps in Figures 4–6). In the Malili lake system, only *Caridina mahalona* is an exclusive river dweller (Figure 4). The majority (almost 80%) of the 15 Malili species are endemic to one ($n = 6$) or two lakes ($n = 5$) within the system, e.g. *Caridina profundicola* in Lake Towuti (Figures 2 and 4) or *C. dennerli* in Lake Matano (Figures 2 and 5). Only a few species are widely distributed, e.g. *Caridina lanceolata* (Figures 2 and 4). In Lake Poso, four species are exclusively lacustrine (Figure 6), i. e. they are endemic to the lake itself. The other two species only occur in the Poso river system or at the outlet of the lake but not within the lake proper (*Caridina schenkeli* and *C. acutirostris* in Figure 7).

In at least three cases from the Malili lakes, the existence of cryptic species was suggested (see above). In these species, the genetically divergent populations are restricted to different geographic

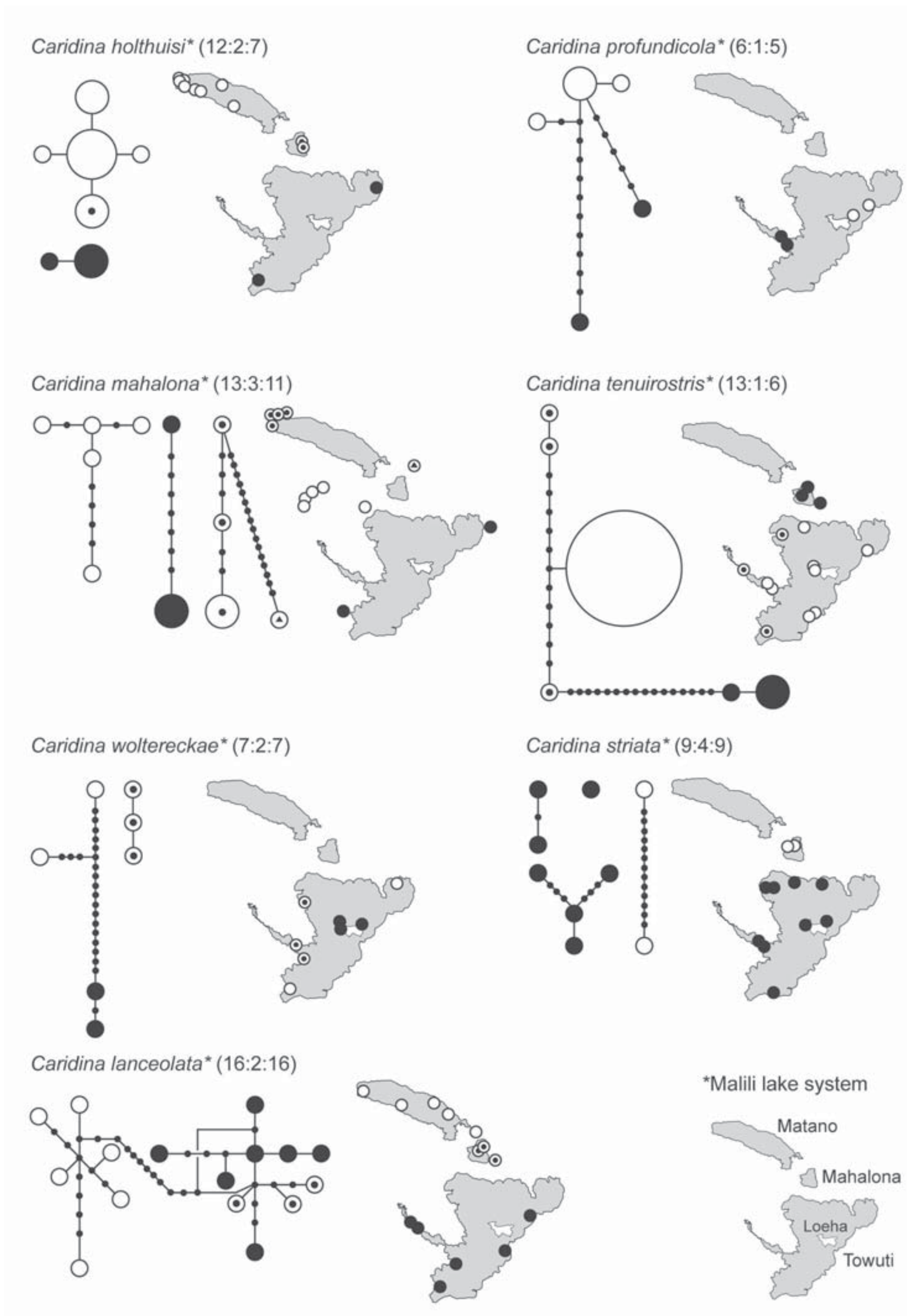

Figure 4. Phylogeography of Malili species. The COI haplotype network is shown for each species. The geographic distribution of the respective haplotypes is shown on a simplified map next to each network. The numbers in brackets indicate the species-specific haplotype information for: number of specimens examined: number of unconnected networks/haplotypes: number of haplotypes.

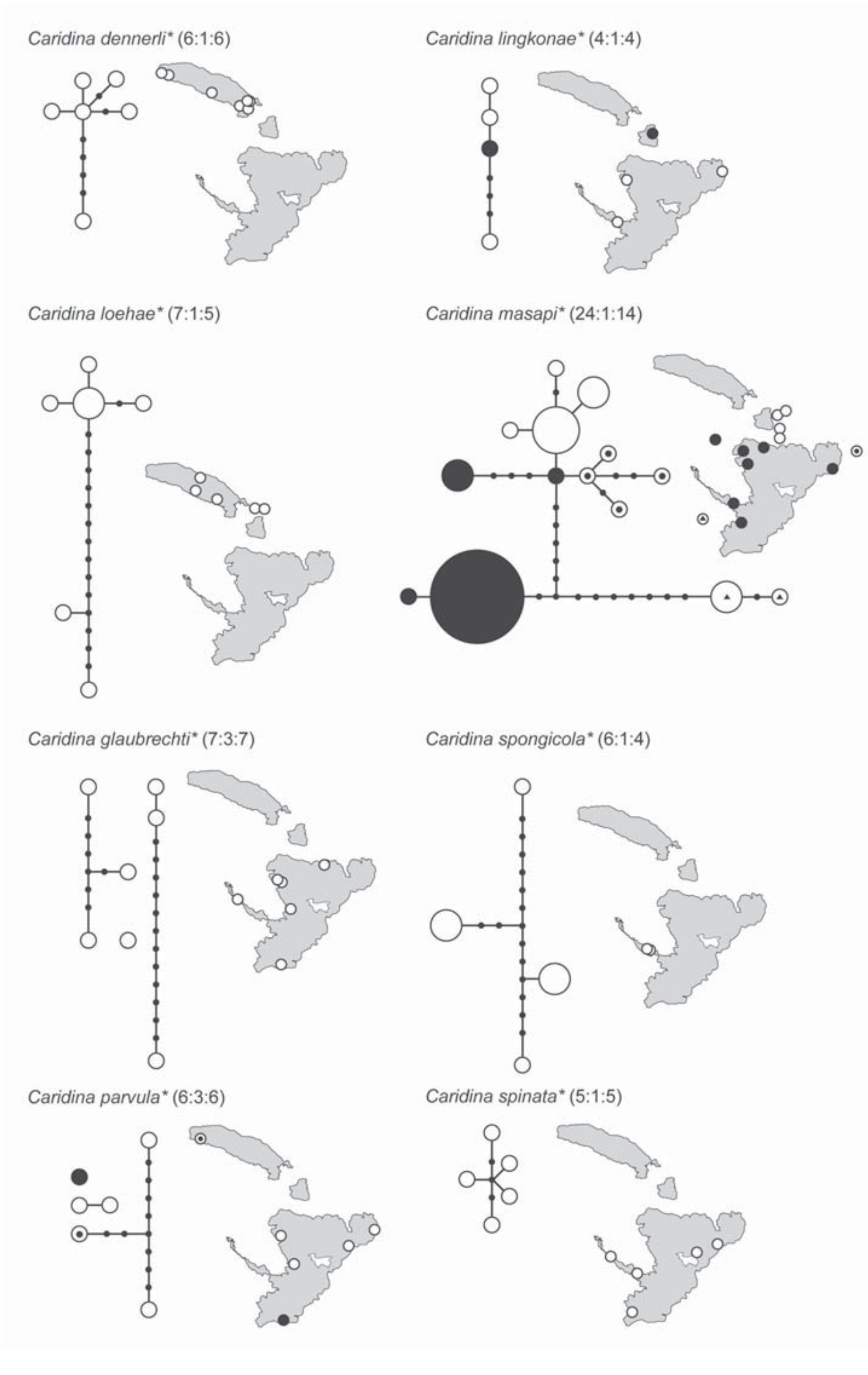

Figure 5. Phylogeography of Malili species continued. The COI haplotype network is shown for each species. The geographic distribution of the respective haplotypes is shown on a simplified map next to each network. Lake names and numbers in brackets as in Figure 4.

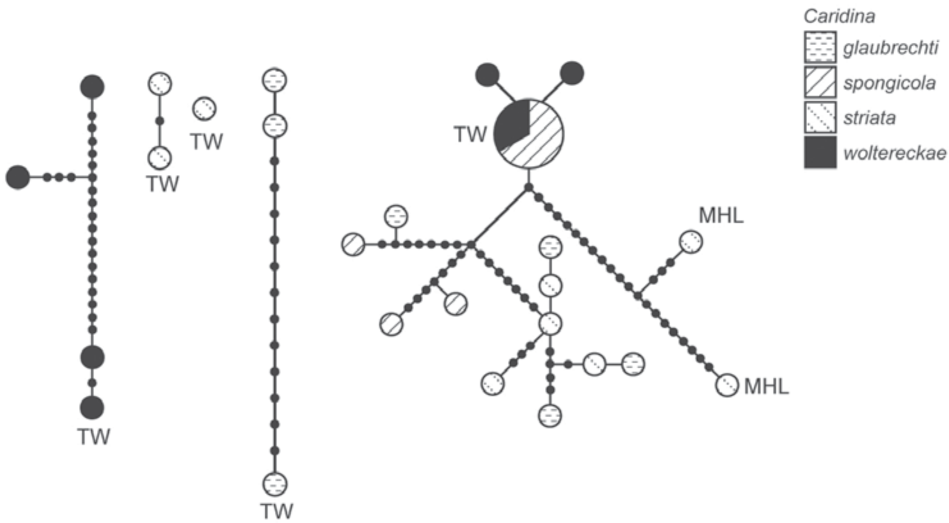

Figure 6. Phylogeography of Malili species continued. The COI haplotype network is shown for the unresolved *C. glaubrechti/spongicola/striata/woltereckae* clade. Lake names and numbers in brackets as in Figure 4.

areas of the Malili system and appear as clades in a non-sister relationship in the overall phylogeny (Figure 2). A good example is provided by the populations of *Caridina holthuisi* that are different in lakes Matano/Mahalona compared to Lake Towuti (Figures 2 and 4). In riverine *Caridina mahalona*, cryptic endemism is less obvious (Figure 4), although the distribution patterns of populations of the four clades (Figure 2) do not overlap and are restricted to different catchment areas within the Malili system (i.e. to Lake Matano catchment, Lake Mahalona catchment, to an area west of Lake Towuti and to Lake Towuti catchment; Figure 4). Another case of cryptic endemism may be present in *Caridina masapi*: the populations from the type locality, Lake Masapi, are genetically distinct and form the sister group of a *C. spinata* clade (Figure 2), making it likely that the other, geographically separated populations of this species are not conspecific (Figure 5). In Lake Poso, no cases of cryptic endemism have been recorded so far.

3.3 Geography and intraspecific differentiation

The Malili lakes and likewise the two Malili clades are strongly structured geographically. Strong intraspecific genetic differences were not only found among clades (as defined in Figure 2) and postulated above to represent cryptic species, but likewise within clades (see also von Rintelen et al. 2010). In several species, populations from different lakes form distinct subclades within clades (Figure 2) such as in *Caridina lanceolata* (Towuti/Mahalona/Matano subclades) and *C. tenuirostris* (Towuti/Mahalona subclades). These species with intraspecific allopatric distribution show higher genetic divergence as species without subclades (COI p–distance $> 2\%$, Table 1). For this type of differentiation, rivers between the respective lakes (Tominanga River and Petea River; Figure 1C) were suggested as barriers to gene flow leading to small-scale vicariance (Roy et al. 2006; von Rintelen et al. 2010). However, neither these rivers nor other potential barriers within the Malili system can be regarded as universal barriers, because in other species populations from the respective lakes are genetically only marginally distinct (von Rintelen et al. 2010), as in populations of *Caridina* *holthuisi* from lakes Matano and Mahalona (Figures 2 and 4). So far, no consistent morphological differences were found between different populations in any of the ancient lake species.

Intraspecific geographic differentiation becomes even more obvious when haplotype networks for all ancient lake species are compared (Figures 4–7). In several cases, allopatric distribution patterns were verified by unconnected networks at the 90% parsimony level (e.g. *Caridina holthuisi* in Figure 4) or if haplotypes were only connected by long branches with many missing haplotypes (e.g. the Lake Masapi populations of *C. masapi* in Figure 5). Surprisingly, and unexpected at least for Lake Poso (see von Rintelen et al. 2007), populations previously considered as uniform entities (von Rintelen & Cai 2009; von Rintelen et al. 2010) were found to be geographically subdivided. In *Caridina profundicola*, a species restricted to Lake Towuti, populations are divided into one at the eastern part of the lake and one at the outlet bay in the western part (Figure 4). These populations are separated by a comparatively high number of mutational steps (5 and 10, respectively; see Figure 4). Furthermore, the two haplotypes (single specimen for each haplotype) occurring in the western part are more distinct from each other than both from the eastern haplotypes (16 mutational steps within the western population in comparison to 5 and 10 steps between western and eastern populations). Similar examples of geographically separated populations are found in *C. woltereckae* from Lake Towuti (Figures 4 and 6) and *C. parvula* from lakes Towuti and Matano (Figure 5). In Lake Poso highest geographic differentiation is found in *Caridina ensifera* (Figure 7), which might explain its relatively high intraspecific genetic divergence (COI p–distance 2.3%; Table 1). In this species, populations from the central eastern shore of Lake Poso are genetically distinct from other populations. Other species from Lake Poso show different geographic patterns (*C. longidigita*, *C. sarasinorum*, *C. schenkeli*; Figure 7). Nevertheless, regarding the rather small number of specimens for all studied species, further sampling of the respective populations from both lake systems would be needed to test any differentiation hypothesis more thoroughly and with the corresponding F–statistics. In only few cases, no intraspecific pattern was found, e.g. in *Caridina dennerli* from Lake Matano (Figure 5), in *C. glaubrechti* and *C. spinata* from Lake Towuti (Figures 5 and 6), or in *C. caerulea* from Lake Poso (Figure 7).

4 CONCLUSIONS

The potential of geographic subdivision, past and present, to shape the evolution of species has long been known (e.g. Mayr 1963) and the resulting genetic signature in the fast-evolving mtDNA was the initially preferred tool for the comparatively new field of phylogeography (Avise et al. 1987). Ideally, the geographic placement and inferred age of a genetic subdivision will allow one to draw conclusions on the geographic causation. Here, genetic subdivisions are shown to be present in most species in the ancient lake radiations of *Caridina* of Sulawesi. While details are shown above, three more general points should be made. First of all, genetic subdivisions almost always coincide with a geographic subdivision. This may seem trivial in a strongly structured system like the Malili lakes, but is less obvious in Lake Poso due to the lack of geographic subdivision. However, the possibility of past allopatric settings cannot be ruled out as the palaeohydrology of Lake Poso is not known (von Rintelen et al. 2007). Secondly, presumed geographic barriers between the different Malili lakes (rivers Petea and Tominanga) are apparently not universal in their effect on species with a distribution across the barrier, e.g. different patterns found in *Caridina lanceolata* and *C. holthuisi*. This might indicate either a difference in the potential of individual species to cross this barrier, or a varying effectiveness of the barrier through time. Thirdly, in a few cases, such as in *C. holthuisi*, intraspecific differentiation with respect to geography is indicative of cryptic species and thus unrecorded endemism. While ecological factors have been suggested to play a major role in the Sulawesi radiations of *Caridina* (see von Rintelen et al. 2010), geographic subdivision seems to be another driving force in differentiation by limiting gene flow and dispersal between allopatric

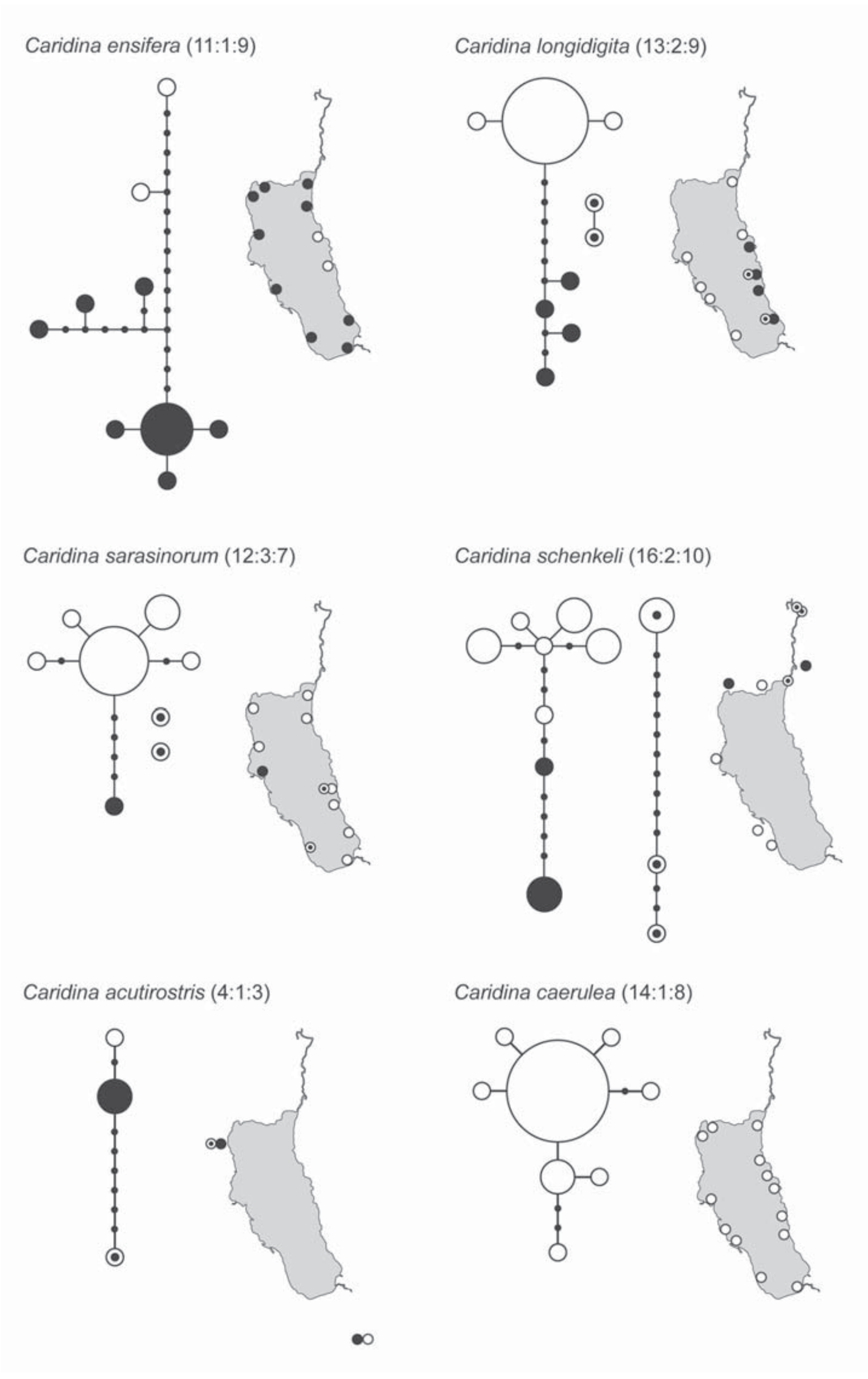

Figure 7. Phylogeography of Lake Poso species. The COI haplotype network is shown for each species. The geographic distribution of the respective haplotypes is shown on a simplified map next to each network. Numbers in brackets as in Figure 4.

populations. Corrspondingly, the higher species diversity in the Malili lake system may be explained by the pronounced geographic structure of this system.

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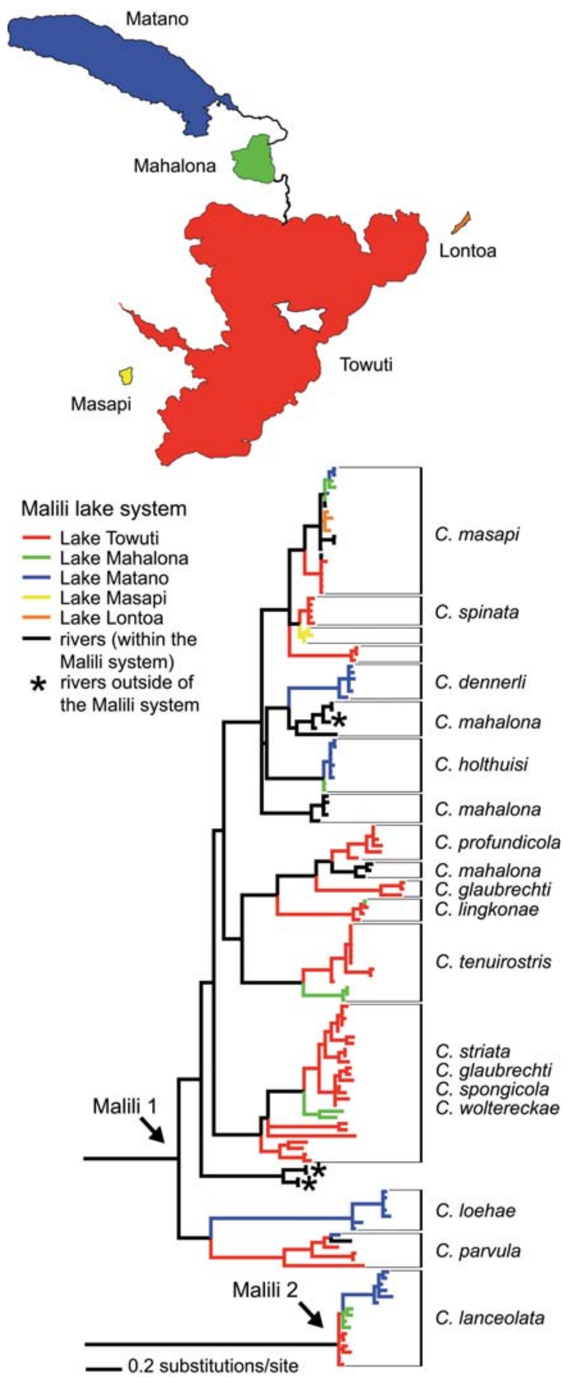

Figure 6 (Figure 2 in von Rintelen) Bayesian Inference phylogram (1332 basepairs of combined 16S and COI mtDNA) of *Caridina* from the Malili lake system. Detail topology of the two Malili clades with its 15 species (for the entire topology, compare Figure 1D in von Rintelen). The occurrence of sequenced specimens in single lakes and surrounding rivers are colour-coded (modified from von Rintelen et al. 2010).