Lake level fluctuations and speciation in rock-dwelling cichlid fish in Lake Tanganyika, East Africa

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14.1 Introduction

The East African Lakes Tanganyika, Malawi, and Victoria each harbour hundreds of endemic invertebrate and vertebrate species. The endemic cichlid fish faunas of the East African Lakes are biologically astonishingly diverse and each of the lakes contains its distinct species flock of cichlid fishes. These species flocks are viewed as the most spectacular example among living vertebrates for evolutionary phenomena termed adaptive radiation, and explosive speciation (Fryer and Iles 1972; Futuyma 1986; Coulter 1991; Martens *et al.* 1994) and provide ample opportunity of the study of the evolutionary mechanisms that might be responsible for the formation of these species flocks (Fryer and Iles 1972). Inferences about the ecological and evolutionary processes responsible for the origin of these species flocks will only be possible when they are based upon explicit phylogenetic hypotheses of the studied species linked to pathways of morphological and ecological diversification (Avise 1994). To determine the relative importance of intrinsic characteristics versus extrinsic factors for the intralacustrine evolution of these faunas may offer information about the processes that resulted in the diversification and speciation in these species flocks.

14.2 The Tanganyikan cichlid species flock

Probably due to its greater age and its probable polyphyletic origin, the Tanganyikan cichlid species flock is morphologically and behaviourally more diverse than the flocks of Lakes Malawi and Victoria (Fryer and Iles 1972) even if—in terms of numbers—it harbours the lowest number of endemic cichlid species (more than 170) (but see Snoeks *et al.* 1994). With its estimated age of 9 to 12 million years (Ma), Lake Tanganyika is considerably older than Lakes Malawi and Victoria (Cohen *et al.* 1993). Most species are therefore probably on average older and hence more genetically distinct. This makes the utilization of DNA sequences for molecular phylogenetic work more feasible than

in the younger species flocks of Lakes Malawi and Victoria (Meyer *et al.* 1990; Meyer 1993*a*). Questions about the evolution of cichlid fishes can be addressed with molecular phylogenetic techniques which avoid the potential pitfalls caused by parallel evolution of similar morphologies, in the reconstruction of the evolutionary relationships among these fishes (e.g. Meyer *et al.* 1990; Sturmbauer and Meyer 1992, 1993; Klein *et al.* 1993; Kocher *et al.* 1993; Moran and Kornfield 1993; Sturmbauer *et al.* 1994; Sültmann *et al.* 1995).

The great majority of the species of Tanganyika cichlids are confined to the patchy rocky habitats which are discontinuously distributed (Brichard 1989). Most cichlids have restricted geographic distributions within their respective lakes and only a very small number of species are found lake-wide (Fryer and Iles 1972; Brichard 1989; Snoeks *et al.* 1994; Kohda *et al.* 1996). Molecular studies indicate that rock-dwelling cichlid species in Lakes Malawi and Tanganyika are usually strongly subdivided in genetically distinguishable populations (e.g. Sturmbauer and Meyer 1992; Bowers *et al.* 1994; Moran and Kornfield 1995). Their typically high habitat specificity, site fidelity, and low capacity for dispersal are all expected to reduce gene flow between populations and be at least partially responsible for the extensive intralacustrine allopatric speciation in cichlid fishes. The high speciation rates in rock-dwelling cichlids are believed to be the result of intralacustrine speciation caused by both intrinsic (e.g. stenotopy, sexual selection) and extrinsic factors such as vicariant biogeographical processes that restrict gene flow between (micro)allopatric populations (Sturmbauer and Meyer 1992; Meyer 1993*a*; Ribbink 1994; Sturmbauer *et al.* 1997; see Chapter 7).

14.3 Lake basin subdivision and allopatric speciation

Intralacustrine allopatric speciation involving spatial isolation, either by basin sub-division or intralacustrine microallopatric segregation, has been invoked to be the most important mode of speciation in cichlid species flocks (Brooks 1950; Poll 1951; Ribbink 1986; Coulter 1991; Meyer 1993*b*). Yet the occurrence of some locally restricted sister taxa could also indicate sympatric speciation, as suggested for two small cichlid species flocks endemic to crater lakes in Cameroon (Schliewen *et al.* 1994).

Geological evidence indicates that periods of aridity that persisted for several thousands of years have caused dramatic drops in water level—of up to 600 m—that split Lake Tanganyika into three separate lakes approximately 200 000 years ago (Tiercelin and Mondeguer 1991). So far, only a few studies support the hypothesis that lake-wide phylogeographic patterns and possibly the process of speciation in lacustrine cichlids are often associated with such abiotic, historical events as lake level fluctuations (Greenwood 1964; Owen *et al.* 1990; Sturmbauer and Meyer 1992; Rossiter 1995; Sturmbauer *et al.* 1997); for geological data for the timing of speciation see Chapter 8. A recent study of the Tanganyikan rock-dwelling cichlid genus *Tropheus* showed that the amount of genetic differentiation among neighbouring *Tropheus* populations can be either considerable or quite small, depending on the sampling localities in the lake (Sturmbauer and Meyer 1992). The intralacustrine mitochondrial DNA (mtDNA) distribution of haplotypes of *Tropheus*, provides some evidence that major lake level

fluctuations may have played a dominant role in determining population genetic struc-ture and possibly speciation in rock-dwelling cichlids of Lake Tanganyika (Sturmbauer and Meyer 1992). However, biological characteristics of species, such as their capacity to disperse, to defend breeding and feeding territories, the size of their broods, and other life-history characteristics may also influence the genetic population structure, and thus be of importance for determining modes of speciation (Fryer and Iles 1972; Meyer *et al.* 1996).

14.4 Testing evolutionary hypotheses on eretmodine cichlids

In order to further test the relative importance of biotic and abiotic factors more comparative phylogeographic data are required. Here, we investigate the variation in the mtDNA control region of cichlids of the tribe Eretmodini (Poll 1986) (Fig. 14.1). This tribe comprises four species, assigned to three genera: *Eretmodus cyanostictus* Boulenger 1898, *Spathodus erythrodon* Boulenger 1900, *Spathodus marlieri* Poll 1950 and *Tanganicodus irsacae* Poll 1950. As a unique feature among lake cichlids, the eretmodines have a reduced swimbladder that allows them to live in the uppermost littoral zone in gravel and rocky shores in the surge zone of Lake Tanganyika. The limited dispersal ability of these cichlids probably caused to the formation of several allopatric colour morphs of these morphologically very similar taxa (Konings 1988; Brichard 1989). The shape of the mandibular teeth is the most important taxonomic character for the Eretmodini and reflects ecology and feeding behaviour of each species. The teeth of *Eretmodus* are spatula shaped with a slender neck region, those of *Spathodus* are cylindrically shaped, and those of *Tanganicodus* are slender and pointed. These differences in dental morphology (e.g. also the position of the mouth and the morphology of the dental arcade) are causally linked to trophic differences, for example *Tanganicodus* is an invertebrate 'picker' whereas *Eretmodus* and *Spathodus* mainly scrape algae off rocks (Yamaoka *et al.* 1986; Yamaoka 1987).

Populations studied and gene sequenced

A total of 43 specimens from 32 localities were studied (for the importance of such fine-grained sampling see Chapter 5). They were collected during two expeditions in 1991 and 1992 along the Burundian and Tanzanian coastline of Lake Tanganyika (Fig. 14.2). All voucher specimens have been deposited in the Africa Museum at Tervuren (Belgium). The specimens were identified based on Poll (1986). However, it is clear from our study that the taxonomy might need to be modified (Rüber *et al.* in preparation). Altogether 336 base pairs (bp) of the mt control region were determined (see Verheyen *et al.* 1996) (EMBL accession numbers are X90593–X90635). Based on a phylogenetic analysis of these data we examined the evolutionary history of these fishes and attempted to evaluate the importance of major lake level fluctuations on the intralacustrine speciation patterns. Only one 2 bp insertion/deletion event was found. A total of 81 positions (24%) contain variation. Even among the most diverged lineages
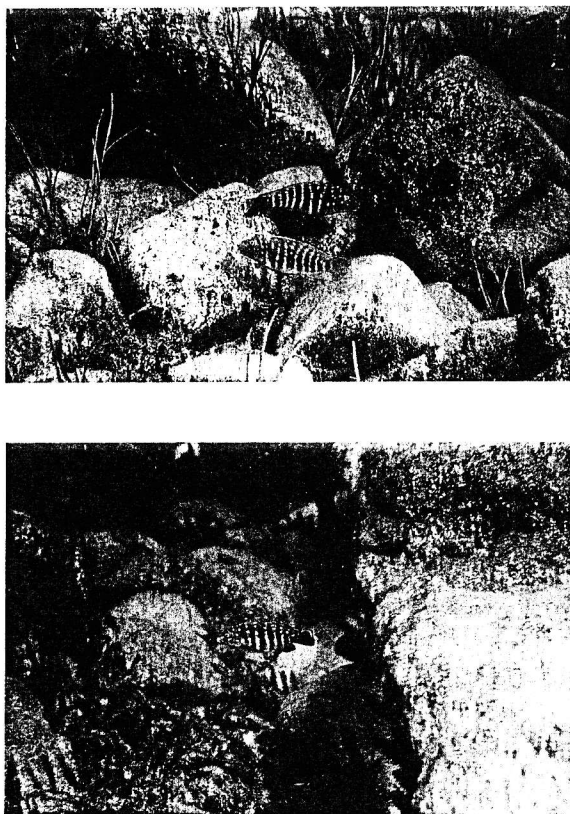
Fig. 14.1 Two cichlid fish from Lake Tanganyika: *Eretmodus cyanostictus* from Kapampa, above, and *Spathodus erythrodon* from Masanza, below. (Photos H. H. Büscher.)

within the Eretmodini transitions outnumber transversions, indicating that transitions still contain phylogenetic information (DeSalle *et al.* 1987).

Age estimates for the Eretmodini

The maximum corrected (Kimura 1980) sequence divergences within the Eretmodini were compared with those that had been found within other Lake Tanganyika cichlids (recalculated for the published sequences): the Ectodini, the Lamprologini, and the genus *Tropheus* (Sturmbauer and Meyer 1992, 1993; Sturmbauer *et al.* 1994). The calculated divergences are based on all substitutions and also on transversions only (given in parentheses): Lamprologini, 22.7% (11.0%); Ectodini, 15.7% (7.4%);
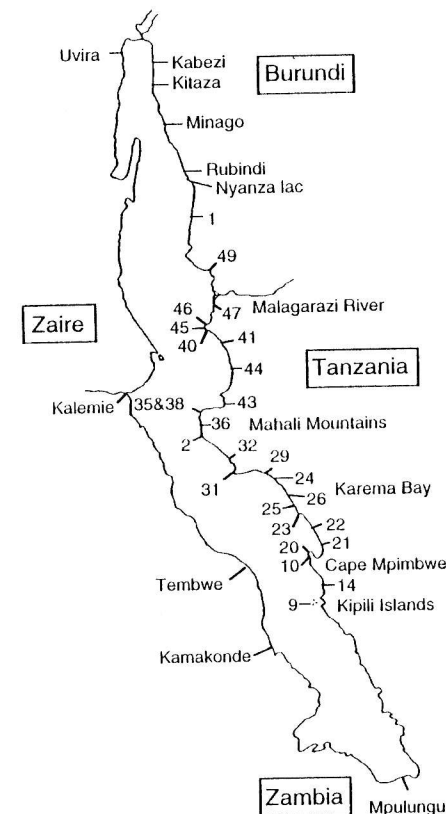
Fig. 14.2 Map of Lake Tanganyika showing all the localities and sample sites mentioned in the text. Lake Tanganyika is about 650 km in length and maximally 80 km wide.

Eretmodini, 12.5% (5.2%); *Tropheus*, 16.1% (4.7%). Assuming a comparable rate of molecular divergence among these lineages, the maximum observed corrected sequence divergence within three other Tanganyikan cichlid lineages indicates that the Eretmodini are approximately 0.5 to 0.8 times as old as the Lamprologini and the Ectodini, and approximately the same age as the genus *Tropheus* (Sturmbauer and Meyer 1992; Sturmbauer *et al.* 1997).

Phylogeny of the Eretmodini

Two major mt lineages within this tribe (A and B in Figs. 14.3 and 14.4) were identified. Lineage A contains three clades A1–A3 whereas lineage B contains four

clades B1–B4. The evolutionary relationships within the Eretmodini are corroborated by both parsimony (Swofford 1993) and neighbour-joining (Saitou and Nei 1987) phylogenetic methods, and most branches defining the major clades are supported with high bootstrap confidence (Felsenstein 1985) (Figs. 14.3 and 14.4). Differences between the parsimony and the neighbour-joining method were only observed within clade B (Figs. 14.3 and 14.4). In the parsimony trees subclade B1 is sistergroup to B2+B3+B4, whereas in the neighbour-joining tree B4 is sistergroup to B1+B2+B3. However, the relative positions of the four clades within the B-lineage are not supported by high bootstrap values (Fig. 14.3).

The current generic classification within the Eretmodini is in partial conflict with the mtDNA phylogeny obtained and may be in need of revision (Figs. 14.3 and 14.4). Clades A1 and B4 both contain mtDNA haplotypes from specimens of all three genera. The taxonomic and phylogenetic implications and the evolution of dentitional differences within the Eretmodini will be discussed elsewhere (Rüber et al. in preparation).

Sequence divergence and relative age estimates for the eretmodine radiations

Seven genetically distinct clades within two major eretmodine lineages were identified (Figs. 14.3 and 14.4). The estimated genetic divergences within the three clades from lineage A are small and similar (averages about 1.3%), suggesting that each of these radiations originated relatively recently and simultaneously in a 'secondary radiation' (Fig. 14.3). The average corrected sequence divergences between the clades within lineage A are also rather similar (about 3.1% to 3.4%) and also indicate that the A-clades are about of the same age and might have arisen in a 'primary radiation' of the A-lineage. The estimated genetic divergences within clades from lineage B are, however, higher and more variable (means range from 1.3% to 3.2%) (Fig. 14.3) hinting that those clades are of different evolutionary ages and might not have radiated within as short a time span as the clade within the A-lineage. The considerably higher average corrected sequence divergence (4.5% to 7.7%) observed between the B-clades indicate that the B-lineage is considerably older than the A-lineage.

Intralacustrine distribution of mtDNA clades

The three clades (A1–A3) show a non-overlapping phylogeographic pattern along the eastern shore of Lake Tanganyika (Fig. 14.5a; for another example of extensive within-island geographic variation see Chapter 5). Clade A1 is widely distributed and ranges from Burundi to the northern edge of the Mahali mountain area. The distribution of clade A2 is restricted to the Mahali mountain area in the central part of the lake. Clade A3 ranges from the southern edge of the Mahali mountain area to Cape Mpimbwe.

The four clades within the B-lineage also show restricted and non-overlapping geographic distributions (Fig. 14.5b). Clade B1 only contains specimens of *S. erythrodon* and ranges from Burundi to north of the Malagarazi river delta. Clade B2, which consists exclusively of *T. irsacae*, is only found south of the Malagarazi river delta. The southernmost range of the distribution of this clade is the southern edge of the Mahali
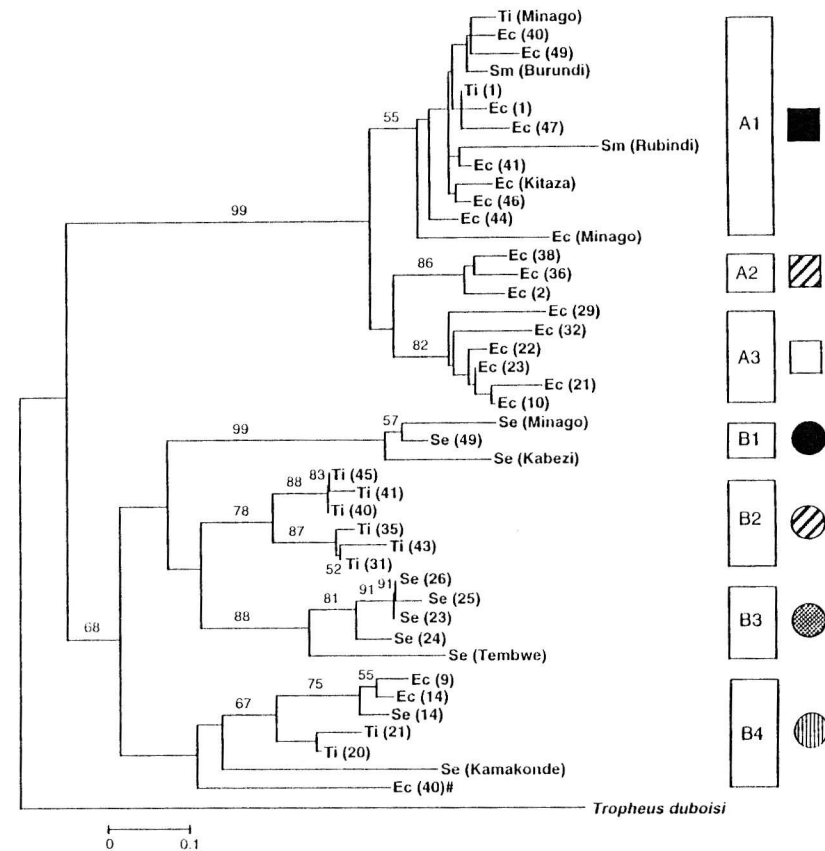
Fig. 14.3 Neighbour-joining tree (Saitou and Nei 1987) of the Eretmodini obtained using MEGA (version 1.01, Kumar et al. 1993). *Tropheus duboisi* was declared outgroup based upon a phylogenetic analysis of the major mouthbrooding lineages of Lake Tanganyika (Sturmbauer and Meyer 1993). Genetic distances were corrected for multiple substitutions (Kimura 1980). Gap sites and missing information (insertions and deletions or indels) are ignored in distance estimation; the option 'pairwise-deletion' was used to analyse sequences that contain such sites. Bootstrap values are given on those branches that were obtained in > 50% of the 1000 replications. Branches are drawn to scale, with the bar representing per cent divergence. The species names are given according to the current taxonomic assignments: Ec = *Eretmodus cyanostictus*, Ti = *Tanganicodus irsacae*, Se = *Spathodus erythrodon*, Sm = *Spathodus marlieri*. Locality names and numbers are given in parentheses. Ec (40)# indicates a morphologicaly distinct *Eretmodus* from Ec (40). Clade designations (see text) are based on neighbour-joining and parsimony analyses.
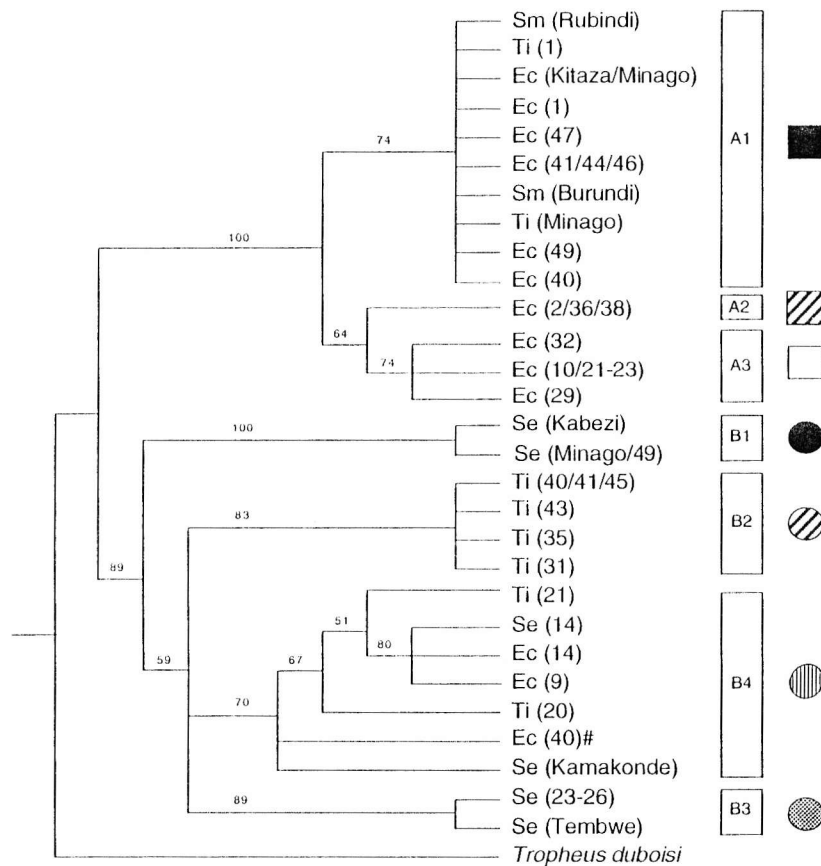
Fig. 14.4 The sequences were analysed by means of the parsimony method using PAUP (version 3.1.1; Swofford 1993). Confidence estimates were obtained using the bootstrap method (Felsenstein 1985). Strict consensus tree constructed from 275 equally parsimonious trees (tree length of 208 steps, consistency index (CI) 0.62, rescaled consistency index (RC) 0.53. Heuristic search with random addition of taxa (10 replications). Bootstrap (Felsenstein 1985) values are given on those branches that were obtained in >50% of the replications (heuristic search, simple addition of taxa, 100 bootstrap replications). The shown bootstrapped parsimony tree was not constructed using all specimens in our data set. Several of the used OTUs are represented by a consensus control region sequences of conspecific eretmodines that show identical cytochrome b sequences (authors' unpublished data). The species names are given according to the current taxonomic assignments: Ec = *Eretmodus cyanostictus*, Ti = *Tanganicodus irsacae*, Se = *Spathodus erythrodon*, Sm = *Spathodus marlier*. Locality names and numbers are given in brackets. Ec (40)# indicates a morphologicaly distinct *Eretmodus* than Ec (40). Clade designations (see text) are based on neighbour-joining and parsimony analyses.
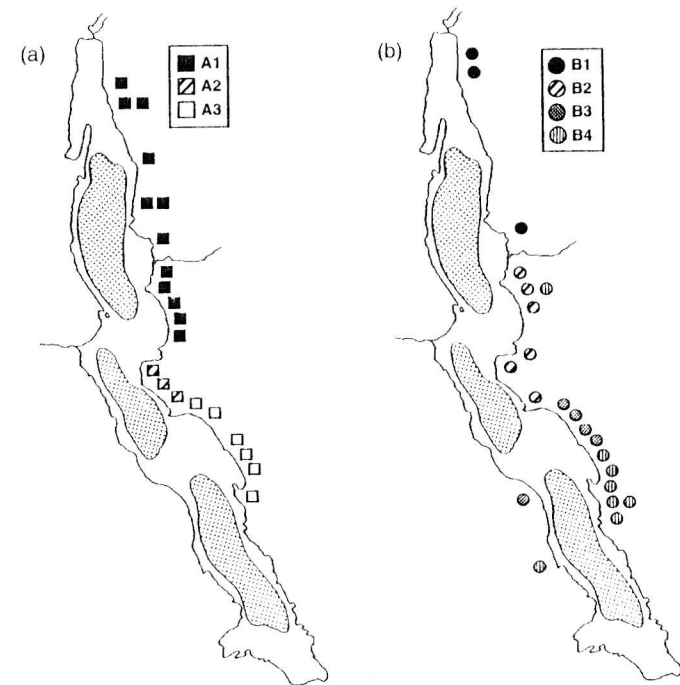

Fig. 14.5 Maps of Lake Tanganyika showing the mtDNA distribution of the studied Eretmodini. The symbols indicate genetically distinct lineages based upon the phylogenetic analyses (see Figs. 14.2 and 14.3). (a) Intralacustrine distribution of mtDNA haplotypes belonging to lineages A1, A2, and A3. (b) Intralacustrine distribution of mtDNA haplotypes that belong to lineages B1, B2, B3, and B4. Each map shows the three separate paleolakes that follow the present 600 m depth contour. The lake level dropped by almost 600 m from its current level (Tercelin and Monteguer 1991). Localities where two identical symbols (see Figs. 14.2 and 14.3) appear (e.g. locality 1) (Figs. 14.1, 14.5a) are meant to indicate that individuals with different tooth morphology and hence different generic assignment have been collected and sequenced.

mountain area. Another clade (B3) containing *S. erythrodon* is found around the Karema Bay and in Tembwe on the opposite western shore line. Clade B4 is morphologically heterogeneous and contains individuals classified as *Spathodus*, *Eretmodus*, and *Tanganicodus*. Its distribution ranges from south of Cape Mpimbwe to the Kipili Islands, the southern end of the sampling area and Kamakonde on the western shore of the lake (Fig. 14.5b).

Specimens that belong to the two most inclusive phylogenetic lineages, lineages A and B, live sympatrically along nearly the whole length of the regions collected. It seems worth pointing out that where the members of the two lineages co-occur they

generally have different tooth shapes and hence different trophic ecologies and are also identified as belonging to different genera. The geographic distributions of each clade (e.g. A1 and B1, etc.) between the two lineages are similar (Figs. 14.5a and 14.5b).

14.5 The influence of Lake Tanganyika's history on adaptive radiation

Allopatric speciation, either through geographic isolation or appropriate habitat type within the same water body, seems to be the most important mode of intralacustrine speciation for lacustrine cichlids (reviewed by Meyer 1993*b*; but see Schliewen *et al.* 1994). The age estimates for various endemic Tanganyikan lineages including the Eretmodini suggest that during the geological history of the lake, when the actual rift formation occurred, cichlids rapidly filled the available niches over the entire lake (e.g. Liem and Osse 1975; reviewed in Coulter 1991; Cohen *et al.* 1993; Meyer 1993*b*; Snoeks *et al.* 1994). When much more recent (in the Pleistocene) climatic changes resulted in lowered water levels, the single Lake Tanganyika basin became subdivided into three paleolakes for probably many thousands of years (Scholz and Rosendahl 1988; Tiercelin and Mondeguer 1991). These lake level fluctuations effectively isolated populations of cichlids, including eretmodines, into northern, central, and southern basin populations (Figs. 14.2 and 14.5). It has been suggested that not only basin subdivision but also minor fluctuations in lake level probably influenced the evolution of the littoral cichlid fauna (Fryer and Iles 1972; Coulter 1991). Sandy beaches or estuaries that separate rocky shores are supposed to act as effective barriers to gene flow, thereby influencing the distribution of genetic variation and probably speciation in these fishes (Coulter 1991). In particular, stenotopic and philopatric species like the eretmodine cichlids that seem to be adapted to living in shallow gravel and rocky shores could have been isolated by small continuous changes in lake levels. This results in physical changes of distinct habitats, such as rocky shores, that are patchily distributed along the coastline. This life-history characteristic ties these fishes strongly to their habitat and would seem to make these cichlids particularly sensitive to lake level fluctuations which will affect the availability of habitat and thereby facilitate or inhibit gene flow by creating or destroying rocky habitat. If these periods of isolation existed long enough, genetic differences between populations are likely to arise by drift and thus may or may not result in the formation of new species, depending on whether the degree of differentiation is enough to arise as a reproductive barrier (see Chapter 7). However, as shown earlier, on the basis of intralacustrine species distributions of a number of Lamprologini (Snoeks *et al.* 1994; Kohda *et al.* 1996) even the huge Malagerazi delta (Fig. 14.2) did not seem to be a strict barrier for some taxa (Figs. 14.5a, b); however, these phenotypic data for lamprologine cichlids need to be matched with future genetic data (Verheyen *et al.* in preparation).

14.6 Phylogeographic patterns in Tanganyikan rock-dwelling cichlids

The evolutionary history of the Eretmodini is strongly connected to the geological history of Lake Tanganyika. The data presented here clearly highlight the effects of lake level fluctuations on the present distribution of genetic variation in these cichlid fishes. Indeed, the distribution of recent Eretmodini mtDNA clades matches quite closely the now inundated shorelines of the three intermittant Lake Tanganyika paleolakes (Figs. 14.5a, b). The within-lake distribution of all clades, but in particular those of clades A1, A2, and A3, is restricted to the northern, central, or southern intermittent lake basins which existed about 200 000 to 75 000 years ago (Scholz and Rosendahl 1988). Also the occurrence of genetically distinct clades that show restricted distributional patterns and, furthermore, the presence of closely related populations on both sites of the lake (e.g. *Spathodus* from localities [23–26] and Tembwe, and lineage B from around the Kipili Islands and Kamakonde) suggests that major water level fluctuations in Lake Tanganyika had pronounced effects on the speciation and the distribution of the cichlid fauna from rocky littoral habitats.

Similar to what was observed for the genus *Tropheus* (Sturmbauer and Meyer 1992), but in contrast with findings in *Simochromis* (Meyer *et al.* 1996), our sequence divergence data indicate that at least two consecutive periods of rapid diversification occurred in the evolutionary history of Eretmodini clades (Fig. 14.3). This seems in particular to be the case for the A-lineage (Fig. 14. 3), whereas the ages of the B-clades seem to be varied and are in general older. Hence B-lineage eretmodine cichlids may have originated somewhat earlier and due to different causes than the members of the A mtDNA eretmodine lineage. Just as in *Tropheus* populations (Sturmbauer and Meyer 1992), the Eretmodini populations occurring over some stretches of the Tanganyika coastline appear to be effectively isolated from each other, even if they are separated by only a few kilometres (Figs. 14.3–14.5). However, one mtDNA lineage of Tropheus was found lake-wide (Sturmbauer and Meyer 1992). In contrast to this one lineage of *Tropheus*, all the genetically distinct Eretmodini lineages seem to have a restricted distribution along the rocky littoral coastline of Lake Tanganyika (Fig. 14.5). Our phylogeographic analysis reveals only two cases in which two allopatric populations share an identical haplotype (*Tanganicodus* from localities 40 and 45; *Spathodus* from localities 23 and 26). Since these localities are only about 20 km apart, the amount of gene flow of mtDNA haplotypes might be low even among geographically near populations. Since only a few individuals per locality have been analysed so far, we do not know if these two populations are fixed for these mtDNA haplotyes.

14.7 Morphology based taxonomy versus mtDNA phylogeny of the eretmodines

Morphology based taxonomy places the Eretmodini in their respective genera mainly on the basis of their dental features (Poll 1986). The major mtDNA clades contain

mostly morphologically homogeneous groups. Our mtDNA phylogeny is in partial conflict with the current generic classification of the Eretmodini. For example lineage A is mainly constituted of specimens which morphologically correspond to *E. cyanostictus* as defined by Poll (1986). However, clade A1 also contains *T. irsacae* (from localities 1 and Minago) and *S. marlieri* (Rubindi and another locality in Burundi). In addition, unpublished *S. marlieri* sequences (Sturmbauer unpublished results) were also placed within the A1 clade. Clade B4 contains the three genera, as they are currently defined. *Tanganicodus irsacae* are found in several of the mtDNA clades. These *Tanganicodus* can be differentiated on the basis of morphological features. *Tanganicodus* populations found in Minago and locality 1 resemble the fishes from the type locality (Uvira, north Zaire) and can be distinguished from the *Tanganicodus* populations found south of the Malagarazi delta by the presence of a dark spot in the soft-rayed part of the dorsal fin and by their colour pattern. Also the occurrence of two distinct *Eretmodus cyanostictus* mtDNA haplotypes that belong to clades A1–A3 and B4 at locality 40 is supported by morphological characters (Rüber *et al.* in preparation). Since the type locality of *E. cyanostictus* is Kinyamkolo (=Mpulungu) at the southern edge of the lake in Zambia, the *Eretmodus* specimens from localities 9, 14, and 40 may represent the genuine *Eretmodus cyanostictus*. The isolated occurrence of southern genuine *E. cyanostictus* at locality 40 which is separated by more than 200 km from the other members of clade B4 may represent a remnant population of a previously more widespread clade, although a translocation by the aquarium trade cannot be ruled out.

Our data suggest that the species originally assigned to three different genera represent several more genetically and morphologically distinct lineages. Since several genetically distinct lineages are found within each of the studied genera, the conclusion that *Spathodus* and *Tanganicodus* are derived monophyletic lineages with *Eretmodus* as their ancestral sister lineage (Liem 1979), needs to be re-examined. Therefore it is our intention to study other molecular markers as well as morphological characters to establish a phylogenetically based generic classification of the Eretmodini. Our results also suggest that the shape of the oral jaw teeth, which is the main morphological feature used for the present classification of the Eretmodini, may be highly variable, homoplasious, and thus not a reliable character for taxonomic purposes. These differences in the dental morphology (*e.g.* position of the mouth and the morphology of the dental arcade) of these fishes and their relative gut length are related to differences in feeding behaviour (Yamaoka 1985, 1987; Yamaoka *et al.* 1986).

In most localities where two species of the Eretmodini occurred in sympatry these were assigned to one of the two most basal branches within the Eretmodini. Sympatric taxa also seemed to differ morphologically and hence ecologically, pointing to the possibility that ecological diversification may be important for the coexistence of two eretmodine lineages. In the majority of the cases that we examined, these species pairs consisted of one species with a typical *Eretmodus*-like dentition whereas the second taxon is usually characterized by a *Tanganicodus*- or *Spathodus*-like dentition. The phylogenetic and geographic distribution of these dental characteristics might indicate that competition (niche partitioning through competition avoidance during periods of low lake stands) for food between members of the Eretmodini may have been a cause for

the multiple occurrence of similar trophic specializations (Rüber *et al.* in preparation; for other examples of parallel evolution see Chapter 10).

MtDNA phylogenies do not necessarily reflect the true species phylogeny; for example lineage sorting and the retention of ancestral polymorphisms can result in the occurrence of mitochondrial poly- and paraphyly between biological species (Moran and Kornfield 1993, 1995). Although this reasoning may be valid for the extremely young mbuna cichlids from Lake Malawi, it is not a likely explanation for the Eretmodini since they are considerably older than the Lake Malawi and Lake Victoria cichlids (Meyer *et al.* 1990; Meyer 1993b). Another explanation for the occurrence of mtDNA polymorphisms across species boundaries is introgressive hybridization after secondary contact (e.g. Dowling and DeMarais 1993). Parental-care patterns and mating systems differ between *Spathodus marlieri* and the representatives of the two other genera. However, no relevant information is available on the breeding biology of *Spathodus erythrodon* (Kuwamura *et al.* 1989) and there are no studies that allow us to refute the possibility of introgressive hybridization. To test this hypothesis it will be necessary to investigate nuclear markers and conduct breeding experiments with *Eretmodus*, *Spathodus*, and *Tanganicodus* from the different clades characterized by distinct mtDNA sequences (for examples of breeding experiments see Chapter 10).

14.8 Summary

Geographic patterns of genetic variation reveal a high degree of within-lake endemism among genetically well-separated lineages which are distributed along inferred shore lines of three historically intermittent lake basins. These facts have important implications for taxonomists, and future taxonomic work should account for them. The phylogeographic pattern of eretmodine cichlids suggests that eretmodine cichlids are poor dispersers, and that major and minor lake level fluctuations have been important in shaping the adaptive radiation and speciation in these fishes. The mitochondrially defined clades are in conflict with the current taxonomy of this group of species. Taxonomy needs to be revised in the light of apparently extensive convergent evolution in trophic morphology.

Acknowledgements

References

Avise, J. C. (1994). *Molecular markers. Natural history and evolution.* Chapman and Hall, London.

Bowers, N., Stauffer, J. R., and Kocher, T. D. (1994). Intra and interspecific mitochondrial DNA sequence variation within two species of rock dwelling cichlids (Teleostei: Cichlidae) from Lake Malawi, Africa. *Molecular Phylogenetics and Evolution*, 3, 75 82.

Brichard, P. (1989). *Cichlids of Lake Tanganyika.* TFH Publications, Neptune City.

Brooks, J. L. (1950). Speciation in ancient lakes. *Quarterly Review of Biology*, 25, 30 60, 131 76.

Cohen, A. S., Soreghan, M. J., and Scholz, C. A. (1993). Estimating the age of formation of lakes: an example from Lake Tanganyika, East African Rift system. *Geology*, 21, 511 14.

Coulter, G. W. (1991). Zoogeography, affinities and evolution with special regard to the fishes. In *Lake Tanganyika and its life*, (ed. G. W. Coulter), pp. 275 305. Oxford University Press.

DeSalle, R., Freedman, T., Prager, E. M., and Wilson, A. C. (1987). Tempo and mode of sequence evolution in mitochondrial mtDNA of Hawaiian *Drosophila*. *Journal of Molecular Evolution*, 26, 157 64.

Dowling, T. E. and DeMarais, B. D. (1993). Evolutionary significance of introgressive hybridization in cyprinid fishes. *Nature*, 362, 444 6.

Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39, 783 91.

Fryer, G. and Iles, T. D. (1972). *The cichlid fishes of the Great Lakes of Africa: their biology and evolution.* Oliver and Boyd, Edinburgh.

Futuyma, D. J. (1986). *Evolutionary biology.* Sinauer, Sunderland, MA.

Greenwood, P. H. (1964). Explosive evolution in African lakes. *Proceedings of the Royal Institution of Great Britain*, 40, 256 69.

Kimura, M. (1980). A simple method for estimating the evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16, 111 20.

Klein, D., Ono, H., O'hUigin, C., Vincek, V., Goldschmidt, T., and Klein, J. (1993). Extensive MHC variability in cichlid fishes of Lake Malawi. *Nature*, 364, 330 4.

Kocher, T. D., Conroy, J. A., McKaye, K. R., and Stauffer, J. R. (1993). Similar morphologies of cichlid fishes in Lake Tanganyika and Malawi are due to convergence. *Molecular Phylogenetics and Evolution*, 2, 158 65.

Kohda M., Yanagisawa Y., Sato, T., Nakaya, K., Niimura Y., Matsumoto, K., and Ochi, H. (1996). Geographic colour variation in cichlid fishes at the southern end of Lake Tanganyika. *Environmental Biology of Fishes*, 45, 237 48.

Konings, A. (1988). *Tanganyika cichlids.* Verduijn Cichlids and Lake Fish Movies, Zevenhuizen, Holland.

Kumar, S., Tamura, K., and Nei, M. (1993). *Molecular evolutionary genetics analysis.* (MEGA version 1.01). Pennsylvania State University, University Park, PA.

Kuwamura, T., Nagoshi, M., and Sato, T. (1989). Female to male shift of mouthbrooding in a cichlid fish, *Tanganicodus irsacae*, with notes on breeding habits of two related species in Lake Tanganyika. *Environmental Biology of Fishes*, 24, 187 98.

Liem, K. F. (1979). Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. *Journal of Zoology (London)*, 189, 93 125.

Liem, K. F. and Osse, J. W. M. (1975). Biological versatility, evolution, and food resource exploitation in African cichlid fishes. *American Zoologist*, 15, 427 54.

Martens, K., Coulter, G., and Goddeeris, B. (1994). Speciation in ancient lakes 40 years after Brooks. *Advances in Limnology*, 44, 75 96.

Meyer, A. (1993*a*). Evolution of mitochondrial DNA in fishes. In *Biochemistry and molecular biology of fishes*, Vol. 2, (ed. P. W. Hochachka and T. P. Mommsen), pp. 1 38. Elsevier, London.

Meyer, A. (1993*b*). Phylogenetic relationships and evolutionary processes in East African cichlid fishes. *Trends in Ecology and Evolution*, 8, 279 84.

Meyer, A., Kocher, T. D., Basasibwaki, P., and Wilson, A. C. (1990). Monophyletic origin of Lake Victoria cichlids suggested by mitochondrial DNA sequences. *Nature*, 347, 550 3.

Meyer, A., Morrissey, J. M., and Schartl, M. (1994). Recent origin of sexually selected trait in *Xiphophorus* fishes inferred from a molecular phylogeny. *Nature*, 368, 539 42.

Meyer, A., Knowles, L., and Verheyen, E. (1996). Widespread distribution of mitochondrial haplotypes in rock dwelling cichlid fishes from Lake Tanganyika. *Molecular Ecology*, 5, 341 50.

Moore, J. E. S. (1903). *The Tanganyika problem.* Hurst and Blackett, London.

Moran, P. and Kornfield, I. (1993). Retention of ancestral polymorphism in the mbuna species flock (Teleostei: Cichlidae) of Lake Malawi. *Molecular Biology and Evolution*, 10, 1015 29.

Moran, P. and Kornfield, I. (1995). Were population bottlenecks associated with the radiation of the mbuna species flock (Teleostei: Cichlidae) of Lake Malawi? *Molecular Biology and Evolution*, 12, 1085 93.

Owen, R. B., Crossley, R., Johnson, T. C., Tweddle, D., Kornfield, I., Davison, S., Eccles, D. H., and Engstrom, D. E. (1990). Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes. *Proceedings of the Royal Society of London B*, 240, 519 53.

Poll, M. (1951). Histoire du peuplement et origine des espèces de la faune ichthyologique du Lac Tanganika. *Annales de la Société Royal Zoologique de Belgique*, 81, 111 40.

Poll, M. (1986). Classification des Cichlidae du lac Tanganika: Tribus, Genres et Espèces. *Acad. Royale de Belgique Mém. Sci. Coll. 8° 2°série*, XLV, fascicule 2, 1 163.

Ribbink A. J. (1986). Species concept, sibling species and speciation. *Annales du Musée Royal de l'Afrique Centrale (Tervuren). Sciences Zoologiques*, 251, 109 16.

Ribbink, A. J. (1994). Alternative perspectives on some controversial aspects of cichlid fish speciation. *Advances in Limnology*, 44, 101 25.

Rossiter, A. (1995). The cichlid fish assemblages of Lake Tanganyika: Ecology, behaviour and evolution of its species flock. *Advances in Ecological Research*, 26, 187 252.

Saitou, N. and Nei, M. (1987). The neighbor joining method: a new method for constructing trees. *Molecular Biology and Evolution*, 4, 406 25.

Schliewen, U., K. Tautz, D., and Pääbo, S. (1994). Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature*, 368, 629 32.

Scholz, C. A. and Rosendahl, B. R. (1988). Low lake stands in Lake Malawi and Tanganyika, East Africa, delineated with multifold seismic data. *Science*, 240, 1645 48.

Snoeks, J., Rüber, L., and Verheyen, E. (1994). The Tanganyika problem: taxonomy and distribution patterns of its ichthyofauna. *Advances in Limnology*, 44, 357 74.

Sturmbauer, C. and Meyer, A. (1992). Genetic divergence, speciation and morphological stasis in a lineage of African cichlid fishes. *Nature*, 358, 578 81.

Sturmbauer, C. and Meyer, A. (1993). Mitochondrial phylogeny of the endemic mouthbrooding lineages of cichlid fishes from Lake Tanganyika in Eastern Africa. *Molecular Biology and Evolution*, 10, 751 68.

Sturmbauer, C., Verheyen, E., and Meyer, A. (1994). Mitochondrial phylogeny of the Lamprologini, the major substrate spawning lineage of cichlid fishes from Lake Tanganyika in Eastern Africa. *Molecular Biology and Evolution*, **11**, 691–703.

Sturmbauer, C., Verheyen, E., Rüber, L., and Meyer, A. (1997). Phylogeographic patterns in populations of cichlid fishes from rocky habitats in Lake Tanganyika. In *Molecular systematics of fishes*. (ed. T. Kocher and C. Stepien), pp. 93–107. Academic Press, San Diego, California.

Sültmann, H., Meyer, W. E., Figuero, F., Tichy, H., and Klein, J. (1995). Phylogenetic analysis of cichlid fishes using nuclear DNA markers. *Molecular Biology and Evolution*, **12**, 1033–47.

Swofford, D. L. (1993). *Phylogenetic analysis using parsimony* (PAUP version 3.1.1). Illinois Natural History Survey, Champaign, IL.

Tiercelin, J. J. and Mondeguer, A. (1991). The geology of the Tanganyika Trough. In *Lake Tanganyika and its life*, (ed. G. W. Coulter), pp. 7–48. Oxford University Press.

Verheyen, E., Rüber, L., Snoeks, J., and Meyer, A. (1996). Mitochondrial phylogeography of rock-dwelling cichlid fishes reveals evolutionary influence of historical lake level fluctuations of Lake Tanganyika, Africa. *Philosophical Transactions of the Royal Society London* B, **351**, 797–805

Yamaoka, K. (1985). Intestinal coiling pattern in the epilithic algal-feeding cichlids (Pisces, Teleostei) of Lake Tanganyika, and its phylogenetic significance. *Zoological Journal of the Linnean Society*, **84**, 235–61.

Yamaoka, K. (1987). Comparative osteology of the jaw of algal-feeding cichlids (Pisces, Teleostei) from Lake Tanganyika. *Reports of the Usa Marine Biological Institute, Kochi University*, **9**, 87–137.

Yamaoka, K., Hori, M., and Kuratani, S. (1986). Ecomorphology of feeding in goby-like cichlid fishes in Lake Tanganyika. *Physiology and Ecology Japan*, **23**, 17–29.